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Preface

The International Crustacean Conference held in Brisbane from 2-6 July 1990 was attended by more than 200 delegates representing 32 countries. The calibre of the papers presented was extremely high and it is a matter of regret that we were unable to publish all of them in their entirety. We publish here, however, almost all of the papers presented by invited speakers at the 'plenary' sessions, and a large number of summaries from those papers presented in the other sessions. They have been grouped thematically in order of their presentation at the Conference, with an alphabetical arrangement for the summary papers.
As always, the editing of such a volume as this has been major undertaking and could not have been achieved without the willing and enthusiastic co-operation of many people. Special thanks to the other members of the organising committee: Don Fielder, Jack Greenwood, Peter Rothlisberg, Ken McKenzie, Nigel Preston and John Glaister, who all contributed to reviewing and correcting manuscripts. We are also pleased to thank the many outside referees who also gave of their time to ensure that the final published papers were of the highest quality. At the Queensland Museum thanks must go to: Neale Hall for his expert skills in desktop type-setting; John Short, John Stanisic and Glen Ingram for helping see it through the final stages, and general support; and Lynnette Dickfos, Danielle McDonald and Lisa Bamforth for administrative assistance. Kath Davie and Gillian Quinn are especially thanked for all manner of voluntary assistance with typing, photocopying, checking citations and proof-reading.
The Organising Committee is also very grateful to the Queensland Museum, and in particular Dr P.A. Jell, for support throughout the conference and its generous financial assistance to make the publication of these Proceedings possible.

P.J.F. DAVIE and R.H. QUINN
EDITORS

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ARTHROPOD PATTERN THEORY: A NEW APPROACH TO ARTHROPOD PHYLOGENY

FREDERICK R. SCHRAM AND MICHAEL J. EMERSON

Schram, F. R. and Emerson, M. J. 1991 09 01: Arthropod Pattern Theory: a new approach to arthropod phylogeny. *Memoirs of the Queensland Museum* 31: 1–18. Brisbane. ISSN 0079-8835.

A review of fossil, morphologic, developmental, and genetic evidence suggests a series of new and novel hypotheses to explain the evolution of arthropods. Termed Arthropod Pattern Theory (APT), these hypotheses are: 1. That the biramous limb was formed by the basal fusion of uniramous limbs; 2. That a uniramian diplosegment (or paired monosegments) is homologous to a single body segment, or duplomere, of arthropods bearing biramous limbs; 3. That suites of segments evolve as units with tagmata transitions, location of gonopores and anus, and body terminations occurring at specific points along the body that are shared among disparate groups. APT requires a complete reassessment of old assumptions about segment homologies within articulates. □ *Arthropoda, Crustacea, Remipedia, Euthycarcinoidea, Drosophila genetics, segment pairing, uniramy, biramy, phylogeny.*

Frederick. R. Schram , Scripps Institution of Oceanography, La Jolla, CA 92093-0202, USA; Michael J. Emerson 6 July, 1990.

Seldom does the study of fossils cause a complete reassessment of previous assumptions about evolution within an entire phylum. However, the problematic arthropod, *Tesnusocaris goldichi* (Brooks, 1955), from the Late Mississippian of west Texas (Schram and Emerson, 1986; Emerson and Schram, in press) and other fossils reveal some previously unsuspected features of arthropod anatomy that necessitate such a re-evaluation.

Brooks was uncertain in his original description of *T. goldichi* as to the exact affinities of this species, and he compared this fossil with crustaceans such as branchiopods and cephalocarids. Hessler (1969) rejected the latter assignment, and Schram (1983, 1986) suggested possible affinities with the Class Remipedia. The new material reveals the cephalic anatomy of a remipede, but thoracic appendages with most peculiar features (Fig. 1). Each trunk segment of *Tesnusocaris* possesses two pairs of ventrally placed uniramous limbs: a medial pair directed posteriorly and possibly used in sculling, and a ventral pair directed laterally and apparently used in rowing (Emerson and Schram, in press). The significance of these limbs, became apparent when they were compared to other peculiar late Palaeozoic arthropods (Emerson and Schram, 1990). This comparison suggested a novel hypothesis for the evolution of the biramous crustacean limb, *viz.*, that biramy evolved by means of the fusion of basal podomeres of adjacent uniramous limbs.

We found the above anatomical observations and the concepts they suggested interesting, although the stratigraphic position of *Tesnusocaris* in the Carboniferous might seem to contradict interpretation of this fossil as an ancestral crustacean. However, we are not proposing that *Tesnusocaris* is an ancestor, merely that its trunk limb anatomy represents a more primitive condition than that seen in biramous arthropods. Furthermore, its stratigraphic position is unimportant because there appear to be even earlier remipedes in the fossil record (Mikulic *et al.*, 1985, fig. 16). Certainly, one caveat of paleontology is that 'things are always older than you think they are', e.g. discoveries of the earliest uniramians (Mikulic *et al.*, 1985; Robison, 1990).

Other kinds of arthropods seem to share this distinctive arrangement of trunk limbs, but previously they were not recognised as such because no one had realised the possibility of such an anatomical condition. One of the best candidates is the Cambrian Burgess Shale arthropod *Branchiocaris pretiosa*. Briggs (1976) reconstructed flap-like limbs attached to a ventrolateral ridge on the trunk (Fig. 2B). He noted proximal elements that appeared to extend along the medial

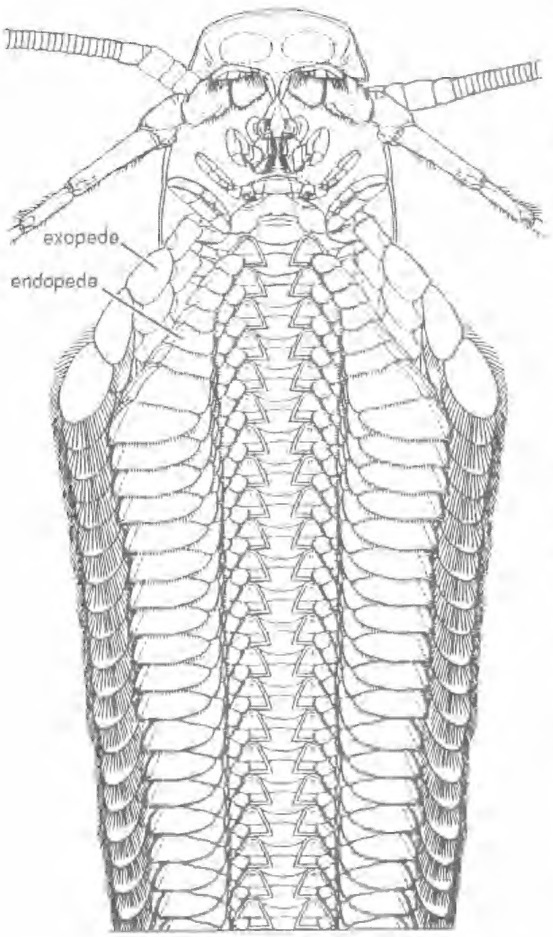

FIG. 1. Ventral reconstruction of *Tesnusocaris goldichi* from the Upper Mississippian of Texas (from Emerson and Schram, in press).

edge of the flap toward the body midline. Briggs designated the proximal elements as reinforcing structures or endites along the flaps, but in the text admitted difficulties in interpreting the fossils and pointed out the tentative nature of his reconstruction of the limbs. However, published camera lucida drawings (Fig. 2A) reveal that these medial elements have a more sagittal position than the lateral flaps. This arrangement, with rami of at least seven podomeres, simple transverse articulations between podomeres, and a flipper-like outline, suggests to us that the sagittal elements bear a clear resemblance to those of *Tesnusocaris*. The flap-like lateral elements on *Branchiocaris*, therefore, are comparable to the ventrolateral pair of limbs of *Tesnusocaris*. Careful examination of other fossil arthropods may reveal additional examples of this arrangement of trunk limbs.

The peculiar form and position of the limbs in relation to the trunk segments of animals like *Tesnusocaris* require a new set of terms to describe appendages and segments in arthropods (Emerson and Schram, 1990). The segments of insects and some myriapods are *monomeres* (or *monosegments*) with each segment bearing one pair of uniramous limbs. The monomeres of many myriapods and the fossil euthycarcinoideans are paired with the dorsal tergites fused and the ventral sternites free, thus forming *diplomeres* (or *diplosegments*). Each diplomere bears two sets of uniramous limbs, one set on each sternite. We contend that crustaceans, and by extension other arthropods that bear biramous limbs, have completely fused the ventral sternites of adjacent segment pairs, as well as the dorsal tergites, to form *duplomeres*. Arthropods like *Tesnusocaris* and possibly *Branchiocaris* are therefore *duplopodous*, displaying two sets of uniramous limbs on each *duplosegment*. The medial pair of trunk limbs on *Tesnusocaris* are known as the *endopedes*, the lateral set are the *exopedes*. Except for the above, most other fossil and living arthropods are biramous, with a single set of branched limbs on each duplosegment, although secondarily uniramous limbs have reoccurred several times.

The Euthycarcinoidea were apparently aquatic creatures that lived from Carboniferous to Triassic time. The most recent review of the group (Schram and Rolfe, 1982) agreed with the suggestion of Bergström (1980) that placed the problematic euthycarcinoideans within the Uniramia. The trunk of these fossils is divided into an anterior limb-bearing region and a posterior limbless area; differences in this regard are the basis for two subgroups (Schram and Rolfe, 1982; Starobogatov, 1988): the Sottyxerxidae (= Sottyxerxiformes) have a long anterior trunk (Fig. 3A), and the Euthycarcinidae (= Euthycarciniformes) possess a short anterior region (Fig. 3B). In both groups, the trunk is characterised by a series of diplo- and triplosegments bearing uniramous limbs that are evocative of similar conditions in extant myriapods. The euthycarcinoidean head is not well known, but appears to resemble the hypothetical primitive arthropod head of Snodgrass (1952), with an anterior procephalon bearing a single pair of antennae and a distinct posterior gnathocephalon bear-

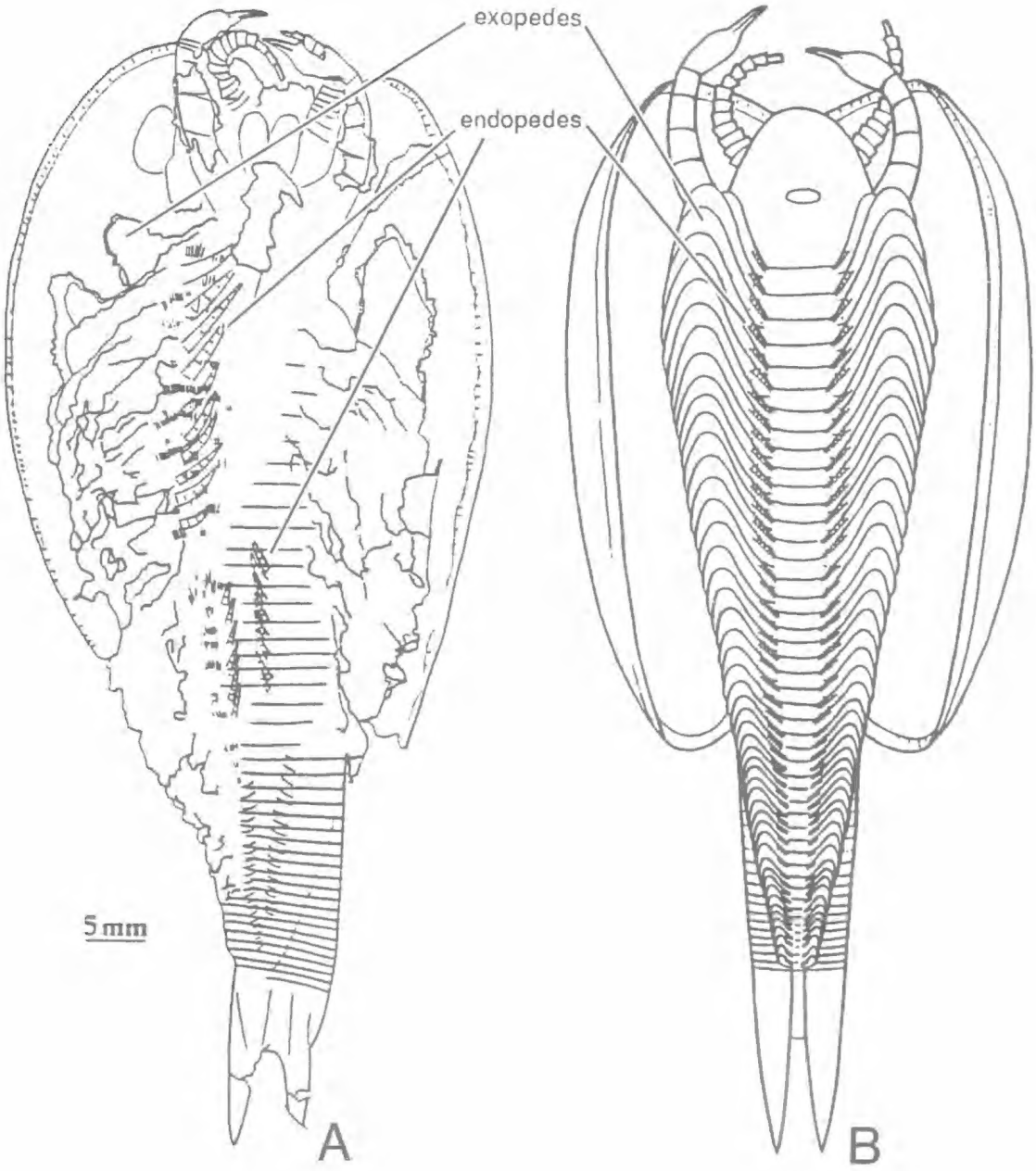

FIG. 2. Our interpretation of *Branchiocaris pretiosa*, from the Cambrian of British Columbia. A, Camera lucida drawing of USNMP 189028. B, Ventral reconstruction of the adult (modified from Briggs, 1976).

ing the mouth and a set of rarely preserved mandibles.

Comparison of *Tesnusocaris*, possibly *Branchiocaris*, and the euthycarcinoideans with the uniramians and crustaceans suggested to Emerson and Schram (1990) a new interpretation of arthropod limb evolution. However, so unusual is this interpretation that the fossils are insufficient to justify it; confirmation comes from the fields of comparative anatomy, ontogeny, and developmental genetics. The elements of Arthropod Pattern Theory (APT) are considered below.

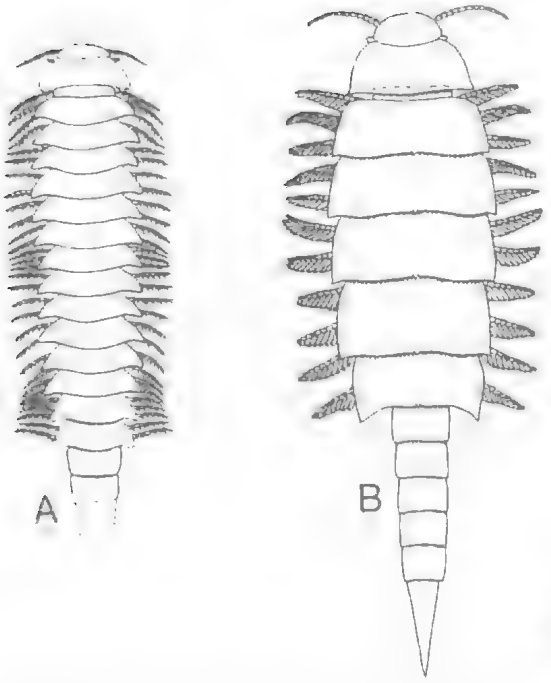

FIG. 3. Dorsal reconstruction of Euthycarcinoidea from the Middle Pennsylvanian of Illinois. A, *Pieckoxerxes pickoae*. B, *Kottixerxes gloriosus*. (modified from Schram and Rolfe, 1982).

HYPOTHESIS ONE

The biramous limb of Crustacea (and probably all arthropods bearing such) evolved by means of the basal fusion of duplopodous, uniramous limbs.

In analysing *Tesnusocaris*, Emerson and Schram (in press) considered the possibility that the two sets of separate uniramous limbs on single trunk segments were only apparently so, i.e. that the arrangement of structures seen in the fossils might represent biramous limbs in which the protopods were incorporated, or fused, into the body wall. This would be analogous to a situation in isopods. This alternative was rejected on both structural and functional grounds. The exopedes and endopedes appear to have functioned in distinctly different ways from each other and thus likely possessed different musculatures; their physical separation on the *Tesnusocaris* trunk somites seems too great to have been derived from a single limb pair; the basal segments of both limbs resemble true coxae; and the number of podomeres is more (not less) than would be expected if a biramous limb fused proximal articles into a body wall.

We concluded (Emerson and Schram, in press) that the trunk limb anatomy of *Tesnusocaris* represents two separate sets of appendages on each trunk segment. Furthermore, distinct limb and segment morphologies are recognized among living and fossil groups (Fig. 4). One condition occurs when the tergites of adjacent somites fuse to form diplosegments, while the still separate sternites each bear a pair of uniramous limbs. Examples of this condition are noted in diplopodous myriapods and euthycarcinoideans (Fig. 4A). A second condition occurs in which each monosegment bears a single pair of uniramous limbs. Examples of this condition are seen in geophilomorph centipedes (Fig. 4B) and insect thoraxes. A third condition exists

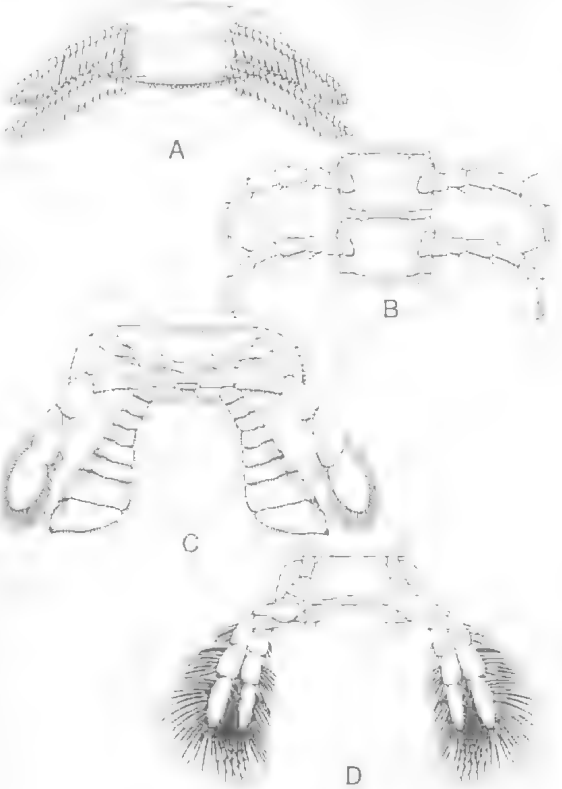

FIG. 4. Ventral views of trunk somites of various arthropods. A, Diplosegment of a generalized euthycarcinoidean with each sternite bearing a pair of uniramous limbs. B, Two monosegments of a geophilomorph centipede with uniramous limbs. C, Duplosegment of *Tesnusocaris goldichi* with two sets of uniramous limbs. D, Duplosegment of a generalized nectiopodan remipede with biramous limbs (from Emerson and Schram, 1990).

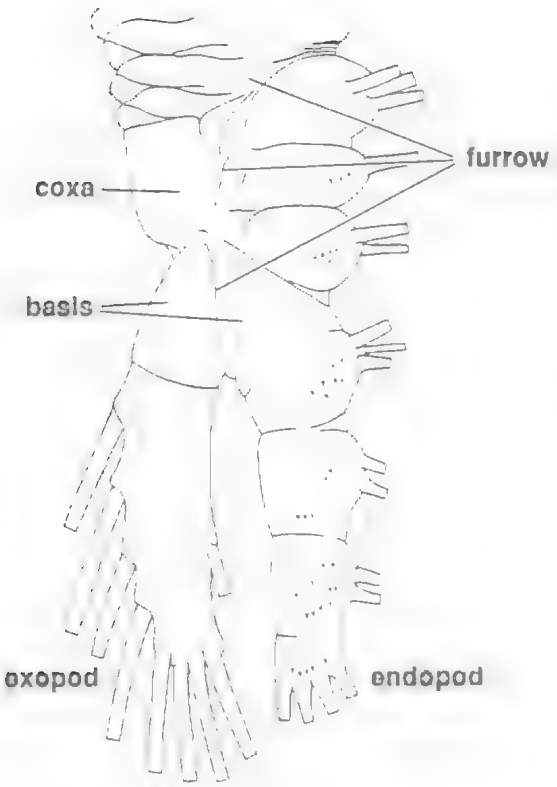

FIG. 5. Maxillule of *Skara anulata* displaying the median furrow on the protopod (from Müller and Walossek, 1985).

when both tergal and sternal fusion occur to form, what we call, duplosegments. Separate pairs of uniramous appendages give the appearance of two sets of limbs on each duplosegment. The prime example of this is *Tesnusocaris* (Fig. 4C). We hypothesise that in the final condition the basal podomeres of the separate limb pairs of a duplosegment fuse to form the common protopod of a biramous limb with exopod and endopod branches (Fig. 4D). This is exemplified by crustaceans that bear biramous limbs, trilobites, and many of the Burgess Shale arthropods.

The above may seem startling. Nevertheless, the hypothesis that there was a tendency in the early evolution of crustaceans to fuse basal podomeres gains some support from the study of several fossil and living arthropods.

For example, an interesting, but problematic, condition occurs on certain fossils. Distinct furrows exist (Fig. 5) on the anterior and posterior faces of the coxae and bases in many of the Cambrian Örsten crustaceans from Sweden (Müller and Walossek, 1985, 1988). [Lauterbach (1988) questions whether these fossils are really crustaceans.] Although the interpretation of these furrows is open to speculation, and issues of fossil preservation should not be overlooked, in light of our hypothesis, these furrows could be indications of the remnant of fused medial and lateral elements in the formation of the protopod in animals such as *Skara* and *Bredocaris*.

A more compelling line of support comes from observations of Ito (1989) who, in comparing the morphology of the copepodan trunk limb to that of nectiopodan remipedes, concluded that the basal podomeres of the nectiopodan exopod and endopod fused to each other to form the basis of the copepodan protopod (Fig. 6). Ito felt that this fusion was supported by the arrangement of the intrinsic muscles of the appendages of the two groups in question, and by the positional homology of the setose accessory fold found at the base of the exopod in many nectiopodans with the setose lateral arm of the basis in copepods. If a process of segment fusion could have evolved the crustacean basis, then it is possible that an identical process could have produced the coxa.

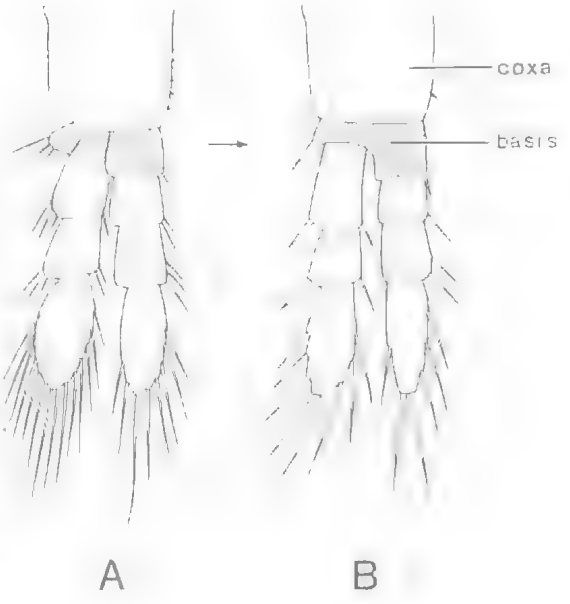

FIG. 6. Trunk limbs. A, nectiopodan; B, copepod. Shaded portion designates postulated homologous regions of the proximal podomeres of nectiopodan rami and the copepod basis (from Ito, 1989)

Although the data above suggest only that the crustacean biramous limb could have been formed by the fusion of duplopodous limbs, this process may also be extended to an explanation of the biramous limbs of other schizoramians such as trilobites, various Cambrian Burgess Shale arthropods, and extant and extinct cheliceriforms. Briggs and Fortey (1989) presented a cladistic analysis of the Burgess Shale and other arthropods that suggests that cheliceriforms, trilobites, and their Cambrian allies are more derived schizoramians than are crustaceans. We believe that in general their conclusion is valid, but just how the specific interrelationships may sort themselves according to APT features awaits more detailed development of our own character matrix.

HYPOTHESIS TWO

A uniramian diplosegment, or two monomeres, is homologous to a single crustacean (and, by extension, other biramian arthropods) body segment, or duplosegment.

The fundamental axiom of comparative anatomy of articulate invertebrates (arthropods and their allies) has been that all body segments among phyla within this group are homologous. Without any evidence to the contrary, it has never been thought necessary to question this assumption. However, if the origin of the biramous limb is hypothesised to derive from the fusion of duplopodous, uniramous elements, then that basic assumption must now be questioned. We sought support from comparative anatomy.

The nervous system of crustaceans provides several excellent examples in this regard. In the central nervous system of the cephalocarids (Elofsson and Hessler, 1990) as well as branchiopods, such as notostracans, anostracans, and conchostracans (Fig. 7C), the paired ventral cords are linked by two commissures in each segment of the head and trunk. Nerve cords in other adult crustaceans and arthropods typically exhibit various degrees of fusion, thus perhaps obscuring a similar pattern. However, in the annelids and uniramians such as centipedes, a single commissure or ganglion exists for each monosegment (Fig. 7A), and in diplopods there is only one fused ganglion per monosegment sternite, i.e. two per diplosegment (Fig. 7B). Where onychophorans fit in this regard is unclear, since they have multiple commissures along the entire length of the nerve cords but no well-organized ganglia that would mark the segments (Meglitsch and Schram, 1991: 354).

In the ontogeny of peracarid and stomatopod crustaceans, there are several instances of the occurrence of double ganglia in segments (Fig. 7D). Transitory anlagen of a second pair of ganglia occur in the sixth abdominal segments of mysids (Manton ,1928), some stomatopods (Shiino, 1942), tanaids (Scholl, 1963), and isopods (Strömberg, 1967). In addition, a transitory furrow occurs in the course of development on the sixth abdominal ganglia of amphipods (Weygoldt, 1958). The traditional interpretation of these phenomena has been that they represent the fleeting appearance of the ganglia of the supposedly ancestral seventh abdominal segment. Although this interpretation could be true, we feel that it is equally likely that these extra ganglia and the furrow may represent the delayed fusion of the second set of ganglia associated with the sixth abdominal duplomere.

A similar explanation could be applied to the strange, double arterial supply from the heart to the musculature of the first abdominal segment in certain stomatopods (Komai and Tung, 1931; Siewing, 1956; Schram, 1969). These arteries may not be a remnant of an extra segment in the anterior part of the stomatopod abdomen, as has been suggested, but rather may represent remnants within the circulatory system of a first abdominal duplosegment.

Reaka (1975, 1979) noted an unusual pattern of moult sutures in stomatopods. The median suture on the sixth, seventh, and anterior half of the eighth thoracomeres connects to a lateral suture on the posterior half of the eighth thoracic and the abdominal segments. Rather than indicating, as has been suggested, evidence for an extra monosegment in the anterior abdomen/posterior thorax, the divergent sutures within the last thoracomere may mark the separate components of an eighth thoracic duplosegment.

Dohle and Scholtz (1988) studied the early differentiation of limbs in peracarids. Two distinct cell lines give rise to the anterior and posterior regions of the limbs of the post-oral segments. It is possible that this pattern represents a remnant of the duplosegmental ancestry of those limbs, although an alternative hypothesis has been put forth based on the concept of parasegment compartmentalisation derived from work on *Drosophila* ontogeny (Martinez-Arias and Lawrence, 1985).

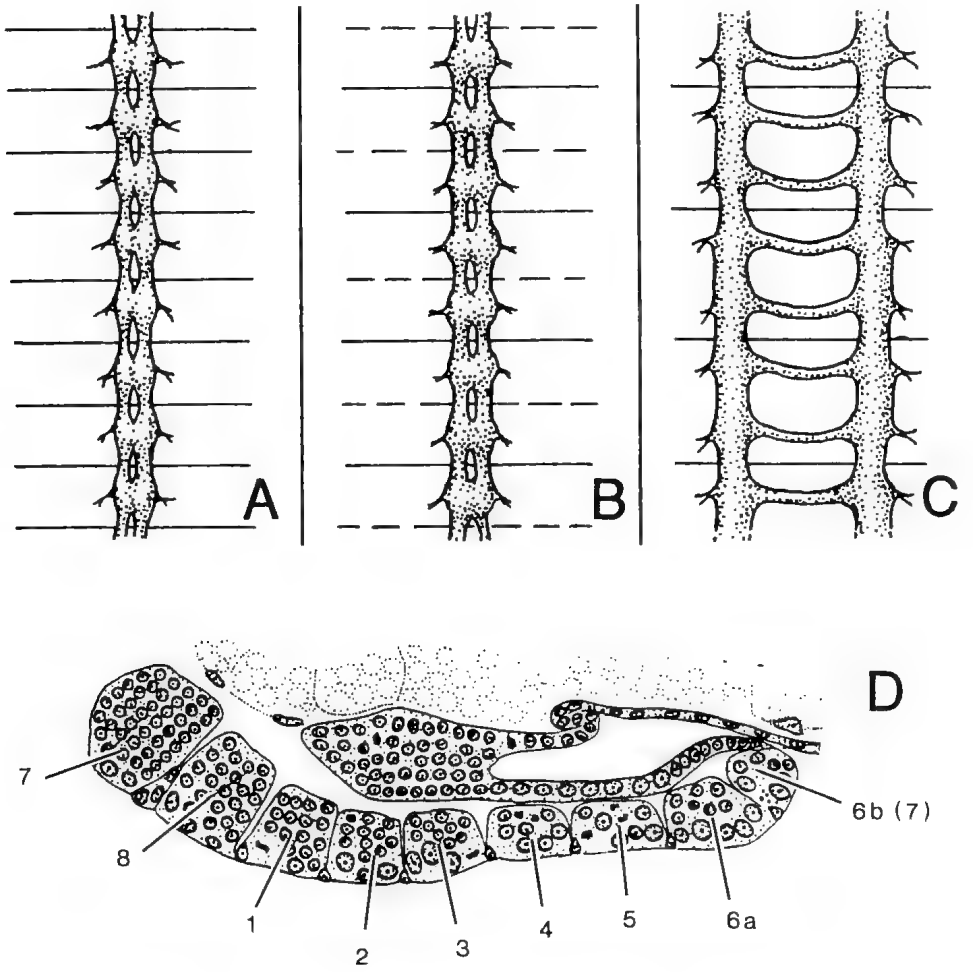

FIG. 7. Arthropod central nervous systems. A–C, Semi-diagrammatic representations of the paired ventral nerve cord of arthropods. A, Centipede, with one set of fused ganglia per monosegment; B, Diplopod, with one set of fused ganglia within each segmental component (dashed lines) of a diplosomite (solid lines); C, Conchostracan, widely spaced cords with two commissures within each duplosegment (from Emerson and Schram, 1990); D, Nerve ganglia development in *Heterotanais oerstedi* with last two thoracic and all abdominal anlagen numbered, the last two ganglia interpretable as either the last two of 7 abdominal monosegments (traditional view) or two portions of a 6th abdominal duplosegment (APT view) (from Scholl, 1963).

The above examples support our hypothesis that the crustacean segment is a composite, or duplosegment, formed from the fusion of two monosegments. Furthermore, ontogenetic and developmental patterns in uniramians seem to second the view that the segments of insects and myriapods are organized in a fundamentally different way than those of crustaceans.

In the ontogeny of *Drosophila*, the phenotypic expression of repeating monomeres (Fig. 8A) is governed by two types of pair-rule genes (Nüsslein-Volhard and Weischaus, 1980; Scott and O'Farrell, 1986), an odd pair-rule type that governs the expression of odd numbered segments, and an even pair-rule gene that controls the even numbered segments. The expression of individual monomeres depends on the interaction of both these loci. The discovery of this peculiar mode of segmental patterning was unexpected and startled those working on the genetics of fruit fly development (Nüsslein-Volhard and Weischaus, 1980: 287). This peculiar

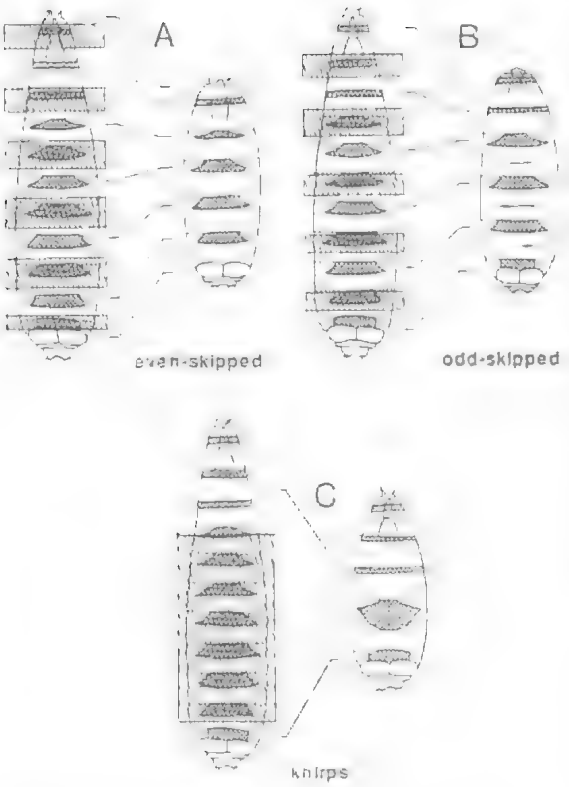

FIG. 8. Diagrammatic representations of gene mutants in *Drosophila* larvae. Pair-rule genes control expression of every other segment, be it odd or even. Gap genes control the expression of a series of segments (modified from Nüsslein-Volhard and Wieschaus, 1980).

control of segment development in *Drosophila* is still difficult to explain under the strictures of traditional views of articulate segmental homology. However, this genetic control is readily accountable in APT by the assumption of an arthropod synapomorphy of segmental patterning organized in units of two as seen in the comparative anatomy of fossil and living forms.

The manifestation of pair rules is evident in other extant uniramians as well. Scheffel (1965) noted that in the anamorphic centipedes two segments at a time are added with each moult stage, and Minelli and Bortolleto (1987) presented strong evidence for segmental pairing based on multiples of two in diplopods that typically add legs during anamorphic growth in units of two or powers thereof. Other epimorphic myriapods also exhibit some segment pairing in the trunk, *viz.* lithobiomorph and scutigeromorph centipedes, pauropods, and symphylans. In short, the segmental pairing seen throughout the uniramians, either in the genetics controlling development or the patterns of anamorphic growth and adult morphology, suggests that this feature was shared with their immediate ancestor.

In contrast to the segment pairing in uniramian ontogeny, biramian arthropods exhibit no such pattern. Segment budding in the germinal discs of crustacean embryos occurs only one at a time; and, while the appearance of segments in larvae displays no consistent pattern, leg buds in larvae typically appear one at a time (Schram, 1986). Itow (1985, 1986) found that segments appear one at a time during the early ontogeny of limulines. Although data are limited and circumstantial, budding of single segments in biramian arthropods instead of segment pairs is exactly what would be expected if a single biramian duplosegment is in fact homologous to two uniramian monosegments.

HYPOTHESIS THREE

Suites of segments in arthropods evolve as units, with the transition of tagmata, the location of gonopores and anus, and the body termination occurring at specific points along the body that are shared between disparate groups.

As we initially began our work, comparing nectiopodan remipedes, *Tesnusocaris*, and the two main groups of euthycarcinoideans, we noticed that certain zones along the length of the body seemed to be the focus of distinct anatomical events (Fig. 9). For example, duplomere 6 (d_6) not only marked the terminus of the head in the crustaceans, but also was the location of an anomalous monosegment in *Sottyxerxes multiplex* (not illustrated here) and was involved in some way in the appearance of triplosegments in the anterior trunks of all Euthycarcinidae. Furthermore, duplomeres 11–13 marked another region in these animals in which the female gonopore in nectiopodans, segmental anomalies in Sottyxerxidae, and postabdominal termination in Euthycarcinidae occurred. Finally, duplomeres 18–20 marked the location of the male nectiopodan gonopore as well as a transition of pre- and postabdominal tagmata in the sottyxerxids.

Initially, we viewed these co-occurrences as interesting but coincidental. If the patterning of

arthropod segmentation were under no particular control, we would have expected that the location of gonopores, tagmata transitions, and body terminations would have occurred randomly along the arthropod body. However, when we examined other arthropods, we noted that these same areas consistently marked either the location of prominent anatomical structures, or transitions of tagmata, or body terminations. We then realized that these patterns were not random at all.

We eventually came to refer to suites of segments as either 'fields' or 'nodes'. Fields are adjacent duplomeres that are for the most part regions of tagmatic stability, while nodes are suites of somites where anatomical events seem to focus (Figs 9–11). Duplomeres 1–4 (monomeres 1–8) mark the first field, duplomeres 5 and 6 (monomeres 9–12) are node one, duplomeres 7–10 are the second field, duplomeres 11–13 are node two, duplomeres 14–17 are the third field, duplomeres 18–20 are node three, and duplomeres 21 to the end of the body mark the fourth field. Thus the arthropod body can be divided into an alternating series of 4-2-4-3-4-3-n numbers of duplosegments (or 8-4-8-6-8-6-2n monosegments). In addition, secondary nodes appear to focus on duplomere 9 within the second field, in the euthycarcinid genera *Kottixerxes* and *Schramixerxes*, some maxillopodan crustaceans, and almost all chelicériforms, and on duplomere 16 in many crustaceans.

As noted above, the nodes are the principle places where gonopores are located, tagma boundaries occur, and bodies terminate. When shifts in the location of these structures occur during the evolution of a group they appear to take place in quantum jumps from one node to the next. As with pair-rule genes in patterning of arthropod segment differentiations discussed above, another class of genes that has been studied in insect development, gap genes, seems relevant to understanding the control exerted over the patterning of arthropod body regions. Gap genes (Fig. 8B) govern the differentiation of suites of segments; and mutations in these genes result in the deletion of entire segment series. Consequently, it is now possible to visualize the apparent movement of anatomical structures forward in the arthropod body, such as gonopores and tagma boundaries, as gap mutations interact with regulatory genes to shorten the body and shift structures in quantum jumps within the framework of the underlying 4-2-4-3-4-3-n architectural plan of fields and nodes.

The Uniramia provide a clear example of pattern evolution (Table 1; Fig. 10). Among the centipedes, the longest bodied forms are the geophilomorphs with terminal gonopores. Other centipedes show anterior shifts of the gonopores and body terminus. Scolopendromorphs (Fig. 10) delete node three and the fourth field to shift their anus and terminal gonopores to the end of the third field, and scutigeromorphs and lithobiomorphs delete the third field with the result that the anus and terminal gonopore occur in the last segments of node two. In all centipedes, the beginning of the trunk occurs within node one. In the other myriapods, the gonopores open only on monomeres of node one while the anuses and body termini occur in the last monomeres of a more posterior field or node (Fig. 10). Colloboglnathan diplopods bear gonopods and these are found on segments of node two. In the hexapod groups (insects and apterygotes) the thorax/abdomen transition is a node one event and gonopores are located at the end of the second field (Fig. 10). Thus, in uniramians, the location of gonopores and reproductive structures are located either in nodes or on the terminal segments of the fields just anterior to nodes. This pattern is so consistent that it allows us to predict, for example, that the gonopore of the strange fossil myriapod *Arthropleura* will be found probably in node one.

A similar, although more complex pattern can be found among the crustaceans (Table 2; Figs 9, 11). The longest bodied crustaceans with the most posterior location for gonopores are the nectiopodan remipedes (Fig. 9); the female pore is in node two, but the male pore is in node three. We predict that gonopores for the extinct *Tesnusocaris*, should they be found, will occur in either one or both of those same nodes. With some exceptions, gonopores of other crustaceans occur either in node two or node one. The exceptions are interesting in their own right in that their occurrence is not random. The Branchiura and Mystacocarida have gonopores on duplomere 9 (d_9) of the second field, while duplomere 16 (d_{16}) of the third field is the location of either gonopores or terminal anuses in several maxillopodan and phyllopodan groups. Both d_9 and d_{16} are two duplomeres forward of nodes two and three respectively. It is tempting to suggest, in light of what we know about gap mutations, that the shift forward in these animals might be due to a mutation that involved the expression in whole or in part of node one (a two duplomere node). The fact that these exceptions in the Crustacea are not

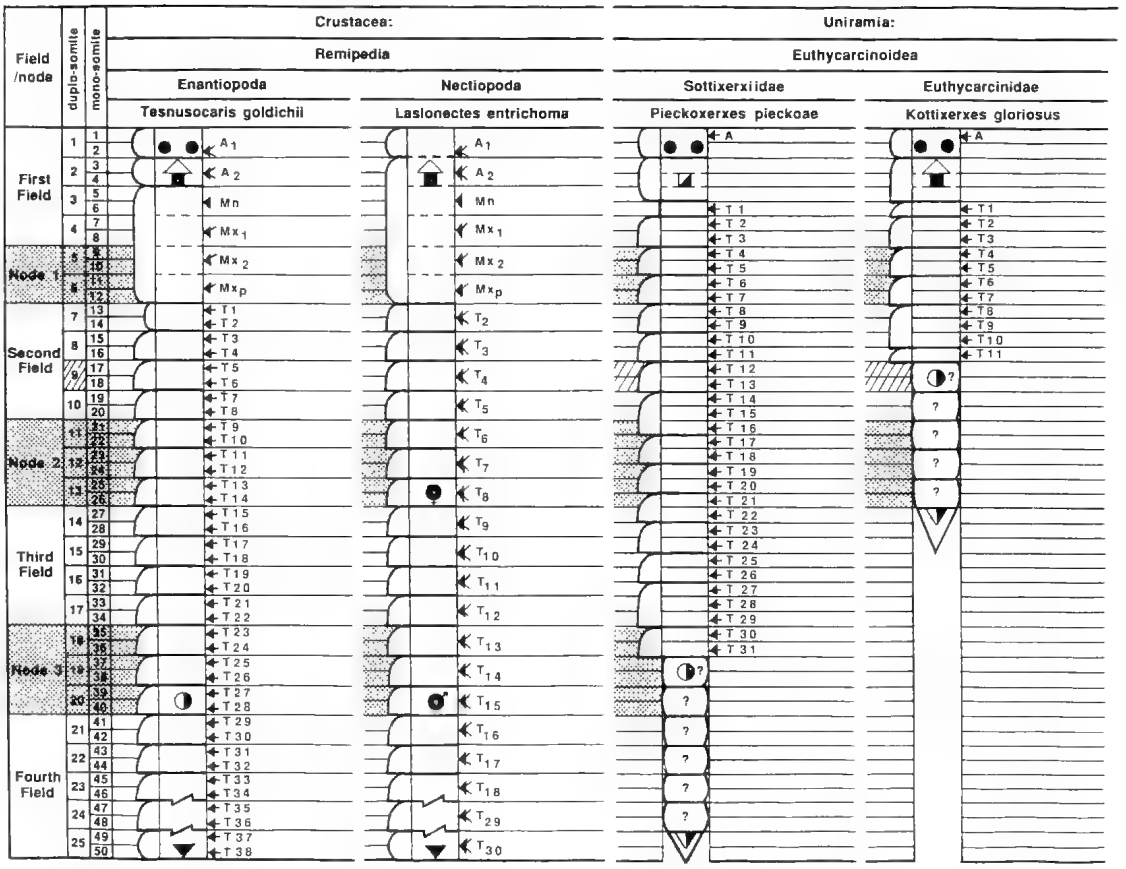

FIG. 9. Diagrammatic representations to illustrate some APT features of remipede crustacean and euthycarcinoidean uniramian body plans, with APT numeration to the left. The ? indicate uncertainty as to whether monomerous or diplomerous. Small circles = eyes, triangle = labrum, square = mouth, circle = gonopore, inverted triangle = anus, half shaded = predicted location.

random, but also conform to a pattern, indicates that some underlying genetic control of pattern formation is operational in the crustaceans.

Further confirmation of such field/node architecture is found in the patterns of early differentiation of the germinal disc of peracarids (Dohle and Scholtz, 1988). After the egg nauplius stage is passed through, the postnaupliar germ band is re-organised as the teloblasts differentiate. At that point, before the teloblasts begin to proliferate body segments, segmental compartments for the maxillules, maxillae, and first thoracomeres appear all at once on the germ band. Thus, the initiation of all of the duplosegments of the first field and node one in these peracarids are under a different, non-teloblastic control from that of the characteristic teloblastic control of the more posterior fields and nodes. Furthermore, this control is independent of whether the teloblasts are in front of or behind the blastopore, or even if there are teloblasts at all (as in amphipods.)

A similar control to that seen in Crustacea is evident in Cheliceriformes (Table 3; Fig. 11), only in this case the possible gap mutation and forward shift is a synapomorphy for the entire subphylum. Cheliceriforms are characterised by an apparent lack of events in node one. The prosoma extends from the first field into the middle of the second field. It is duplomere 9 that is either the site where the gonopores are located, as in chelicerates *sensu stricto*, or where the abdomen begins, as in fossil and extant pycnogonids and the fossils *Chasmataspis* and *Sanctacaris*. It is possible that node one was completely deleted by a gap mutation in the ancestry of cheliceriforms, consequently producing an apparent shift forward of events out of node two into d_9. Circumstantial support for such a gap mutation in the trunk region of

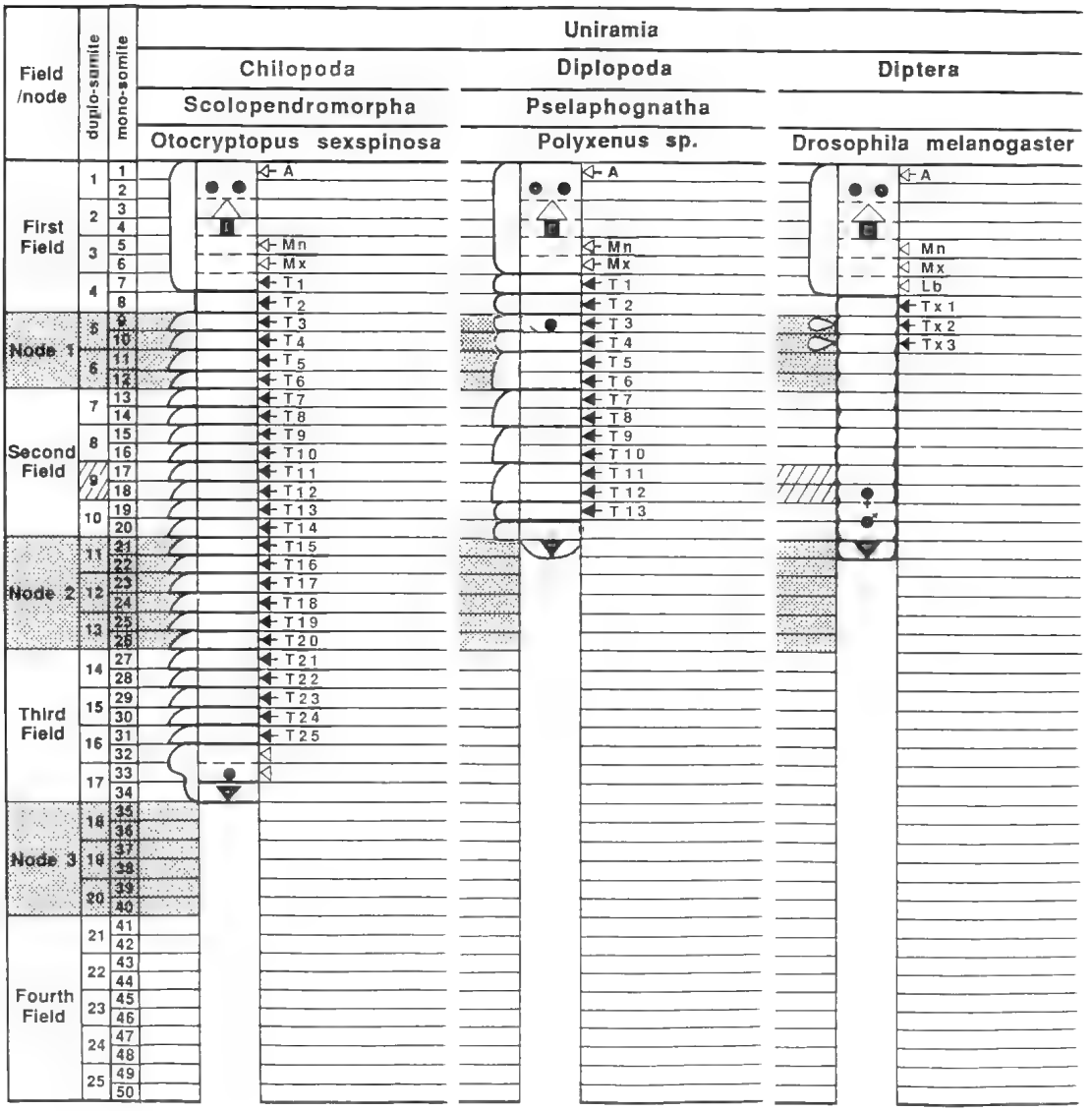

FIG. 10. Diagrammatic representations to illustrate some APT features of living uniramian body plans, with APT numeration to the left. Symbols as in Fig. 9.

cheliceriforms might be sought in the cephalic region of these animals. Cheliceriforms are characterised by loss of the deutocerebral region of the brain, and we are tempted to suggest that the apomorphies of brain structure and tagmatisation of this group of arthropods are related to some mutation(s) in the regulatory control of development that altered the patterns of 'normal' pattern expression by means of gaps in segment development. More typical pattern formation in cheliceriforms seems to prevail in the region posterior to d_9.

In addition to the above animals, various problematic fossil arthropods from the Burgess Shale and other localities appear to conform to APT (Table 4). The patterns among these fossils, compared to those in Tables 1, 2, and 3, lack information on the location of gonopores. In addition some confusion in interpretation arises related to shortcomings in the preservation of these fossils. An example of this is seen with the Cambrian arthropod *Sidneyia*. This animal has traditionally been interpreted as having a single segment head (Bruton, 1981; Gould,1989). *Sid-*

TABLE 1. Segmental patterning in Uniramia with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Geophilomorpha	hd	hd	+	+	+	+	t a,gp
Scolopendromorpha	"	"	+	+	t a,gp	–	–
Scutigeromorpha	"	begin tr	+	gp,a	–	–	–
Lithobiomorpha	"	"	+	" "	–	–	–
Polydesmoidea	"	gp	+	+	+	+	t a
Ascospermomorpha	"	"	+	+	+	+	"
Juliformia	"	"	+	+	+	+	"
Limacomorpha	"	"	+	+	+	+	"
Colobognatha	"	"	+	gpods	+	+	t a
Oniscomorpha	"	"	+	t a	–	–	–
Pselaphognatha	"	"	t a		–	–	–
Symphyla	"	"	+	t a	–	–	–
Pauropoda	"	"	t a	–	–	–	–
Arthropleura *	"	?gp	+	+	+	t a	–
Insecta	"	tx/abd	t gp	a –	–	–	–
Apterygota	"	"	"	"	–	–	–

a = anus, gp = gonopores, f = female, m = male, ? = unknown but predicted location, t = structure at terminus of region, d_n = duplomere, X/Y = transition, + = segments present but otherwise undistinguished, – = portion of or whole region deleted, hd = head, tr = trunk, tx = thorax, abd = abdomen, * = extinct.

TABLE 2. Segmental patterning in Crustacea with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Nectiopoda	hd	hd/tr	+	fgp	+	mgp	t a
Tesnusocaris *	"	"	+	?gp	+	?gp	t a
Malacostraca	"	hd/tx	+	gp	+	t a	
Copepoda	"	"	+	gp	d_{16}a		–
Mystacocarida	"	"	$d_9$gp	+	d_{16}a		-
Skara *	"	"	?$d_9$gp	+	t a	-	–
Ostracoda	"	"	+	fgp	d_{16}mgp,a	–	-
Branchiura	"	"	$d_9$gp,a	–	–	–	–
Ascothoracida	"	fgp, "	+	mgp	d_{16}a	–	-
Thoracica	"	" "	+	",a	–	–	–
Lepidocaris *	"	"	+	+	?d_{16}gp	+	t a
Anostraca$_1$	"	"	+	+	"	+	t a
Anostraca$_2$	"	"	+	+	",a		
Notostraca	"	"	+	+	"	+	t a
Conchostraca	"	"	+	+	"	+	t a
Cladocera	"	"	+	gp,a	–	–	
Leptostraca	"	"	+	gp	+	t,abd	a
Canadaspis *	"	"	+	?gp	+	"	"
Cephalocarida	"	"	+	gp	+	+	t a

Abbreviations as in Table 1.

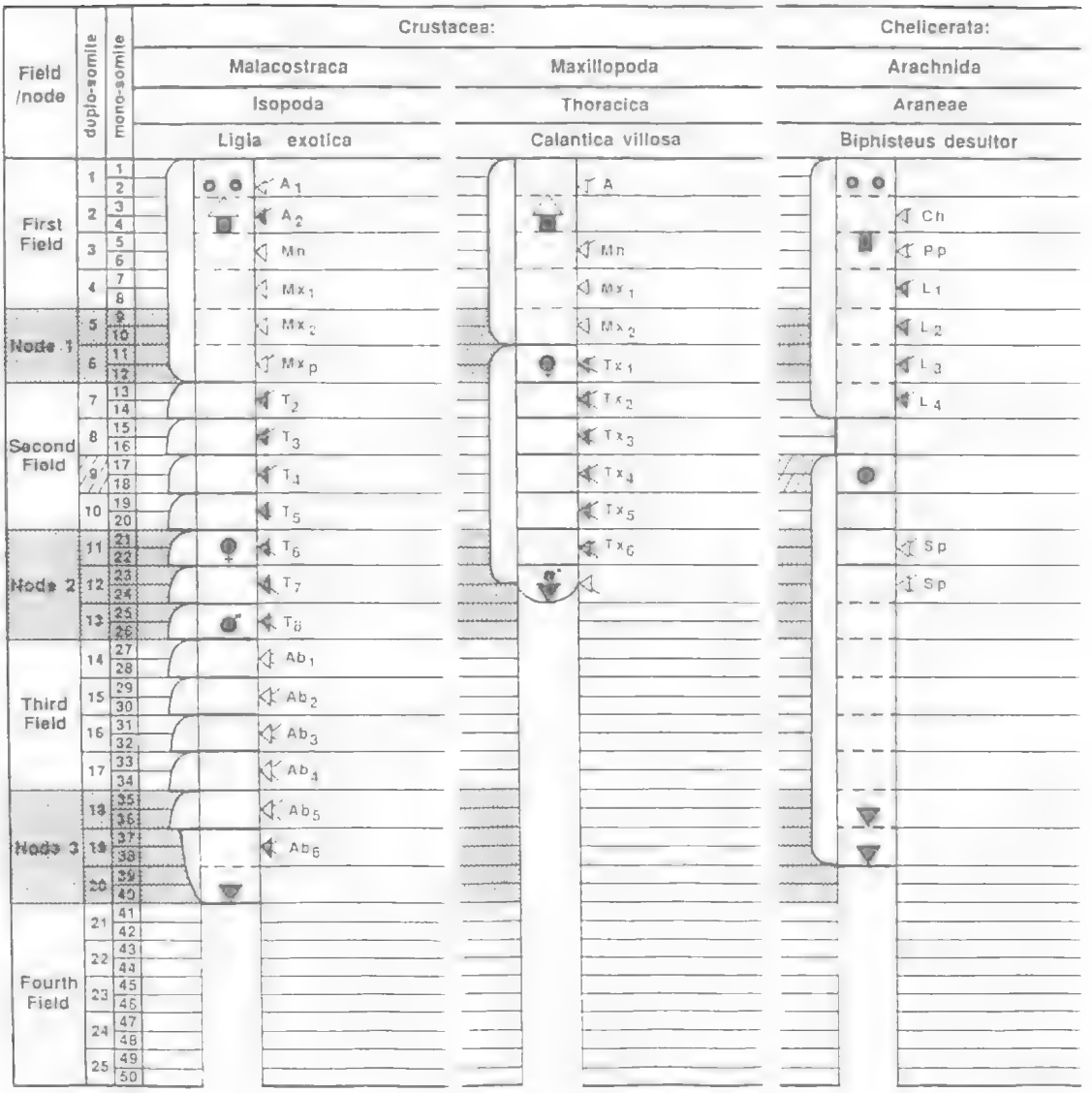

FIG. 11. Diagrammatic representations to illustrate some APT features of some advanced crustaceans and chelicerate body plans, with APT numeration to the left. Symbols as in Fig. 9.

neyia, however, has a rather subtle distinction of limbs that sets off a prosoma of four pairs of uniramous limbs posterior to the mouth from an opisthosoma with five sets of biramous limbs. This transition occurs in node one; the opisthosoma extends through the second field; and a short abdomen (or postabdomen) occupies node two. Under the traditional interpretation, *Sidneyia* is not an APT animal; under our interpretation it clearly is.

While most of the known problematic arthropod genera do display APT motifs in some way, several fossils remain enigmatic. Given the current state of our knowledge about them, the following taxa do not appear to have any APT features: *Burgessia*, *Marrella*, *Mimetaster*, and *Vachonisia*. Whether this lack is real or merely due to an inadequacy in our knowledge about incompletely preserved fossils is not known.

DISCUSSION

In the last 150 years, numerous schemes to explain arthropod phylogeny have been put for-

TABLE 3. Segmental patterning in Cheliceriformes with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Sanctacaris *	pr	pr	pr/op	+	+	a	–
Palaeoisopus *	"	"	$d_9$abd	t a	–	–	–
*Palaeopantopus**	"	"	"	a –	–	–	–
Pycnogonida	"	"	",gp,a	–	–	–	–
Synxiphosura *	"	"	?$d_9$gp	+	t a	–	–
Chasmataspis *	"	"	?$d_9$gp	+	t a	–	–
Limulus	"	"	$d_9$gp	+	a –	–	–
Erypterida *	"	"	?$d_9$gp	+	+	t a	–
Scorpionida	"	"	$d_9$gp	+	+	t a	–
Araneae	"	"	"	+	+	"	–
Solifugae	"	"	"	+	+	a –	–
Opiliones	"	"	"	+	a –	–	–
Palpigradi	"	"	"	+	+	a	
Sternarthron *	"	"	?$d_9$gp	t a	–	–	–
Uropygi	"	"	$d_9$gp	+	+	a	–
Ricinulei	"	"	"	+	a –	–	–
Acarina	"	"	"	t a	–	–	–

pr = prosoma, op = opisthosoma, abbreviations otherwise as in Table 1.

TABLE 4. Segmental patterning in various problematic fossil arthropods with reference to fields and nodes.

Taxa	F^1	N^1	F^2	N^2	F^3	N^3	F^4
Triarthrus	hd	hd/tr	+	+	+	tr/py	t a
Rhenops	"	"	+	+	+	"	t a
Naroia	"	"	+	+	+	a –	–
Olenoides	"	"		tr/py	d_{17}a–	–	–
Agnostus	"	"	t a	–	–	–	–
Yohoia	"	"	+	+	+	a –	–
Waptia	"	"	+	tx/ab	+	a –	–
Oxyuropoda	"	begin legs	+	seg. change	+	a –	–
Actaeus	"	begin tr	+	+	d_{15}a	–	–
Alalcomenaeus	"	"	+	+	"	–	–
Habelia	"	"	+	+	"	–	–
Plenocaris	"	hd/tr	+	+	a –	–	–
Leanchoilea	"	"	+	leg change	a –	–	–
Emeraldella	"	"	+	+	+	a –	–
Molaria	"	"	+	t a	–	–	–
Sartrocercus	"	"	+	t a	–	–	–
Sidneyia	"	hd/tr	+	abd.	a –	–	–
Aglaspis	"	"	+	legs end	a –	–	–
Cheloniellon	"	"	+	seg. change	–	–	–

Abbreviations as in Table 1.

ward, but no consensus has been achieved. For example, workers have either focused on development (Anderson, 1973), or morphology (Snodgrass, 1952; Manton, 1977; Gupta, 1979), or fossils (Bergström, 1979, 1980) and have developed explanations for arthropod evolution narrowly derived from those disciplines. The strength of APT is that it combines information from all these fields of study into one coherent canon.

A measure of the effectiveness of a theory is its ability to make predictions. Unlike other theories about arthropod relationships, APT offers a predictive framework that attempts to prognosticate information yet to be derived from future studies. For example, the discovery of a second set of gonopores in nectiopodan remipedes (Ito and Schram, 1988) corroborated APT because the location of the female gonopores in node two was on the segments that APT predicts. Similarly, APT can be tested by seeking gonopores and/or other structural markers on specific nodal segments on the bodies of the fossil taxa, as indicated in the tables.

Another mark of a theory's strength is how well it incorporates and reconciles apparently disparate elements of previous theories. For example, Snodgrass (1938) united the insect/myriapod and crustacean lines as the Mandibulata. Manton (1964, 1977) disagreed with that position, arguing that mandibles were convergently developed in different arthropod groups. Manton's work was seconded by Anderson (1973) who recognised what he felt were fundamentally different patterns of blastomere fates among the three major groups of living arthropods. Various authors (Gupta, 1979) have disagreed with Manton and Anderson.

A preliminary and very tentative phenogram for arthropods based on APT assumptions (Fig. 12) reveals that these old theories can cease their warring — all incorporate elements of 'truth'. The mandibulates, in the sense of Snodgrass, can be recognized as a paraphyletic group near the base of the arthropod lineage. This arrangement accommodates the continuity of blastomere fates of uniramians extending to onychophorans and clitellate annelids. The unique early ontogenetic patterns so effectively outlined by Anderson for crustaceans and cheliceriforms, can now be seen as autapomorphies for those groups. Mandibles appear to be convergently developed, in the sense of Manton (1964), but this can be accommodated within the concept of arthropod monophyly, in the sense of many authors in Gupta (1979). The concepts of Arachnomorpha (Stormer, 1944) and Schizoramia (Hessler and Newman, 1975) also have validity, and the positioning of many Burgess Shale arthropods relatively high in the arthropod genealogy (Briggs and Fortey, 1989) deserves careful consideration.

Figure 12 is not a cladogram but merely represents at best a crude first guess of possible relationships within the arthropods. A character matrix for APT features is being prepared. How this will translate into a specific cladogram for arthropods must await the completion of that work. However, certain broad patterns can be discerned from the above analysis that prompt us to offer (Fig. 12) a phylogram of arthropod types displaying the distribution of major APT characters and other non-APT features. Essentially, the evolution of arthropods can be seen as a progressive series of events from a diplomerous, uniramous animal through to a fully duplomerous, biramous condition. Some uniramians, such as insects and geophilomorph centipedes manifest a secondary monomery, and cheliceriforms (as well as a few crustaceans) manifest a secondary uniramy. Nevertheless, the main thrust of arthropod evolution appears to have been focused on progressive control over duplication cycles (Minelli and Bortoletto, 1987; Jacobs, 1990) such that diplomeres were fused to form duplomeres, and diplo- and duplomeres were genetically controlled as unit fields and nodes. The end point of this evolution was a developmental and functional system that allowed for more effective limb and tagmata specialisations than were possible in less derived articulates such as annelids.

A confirmation of sorts for the above scheme comes from the study of molecular sequence data. Among the most controversial analyses of molecular phylogeny is that of the 18S ribosomal RNA sequencing of Field *et al.* (1988), wherein metazoans were viewed as polyphyletic. A reanalysis of that data, however, by Lake (1990) reveals a broad pattern of metazoan evolution that is more in accord with traditional interpretations of animal history and a branching sequence for arthropods similar with what we suggest here (Fig. 12). In Lake's analysis, the myriapods and insects are sister groups to the biramian arthropods in a transition series leading to a clade that includes annelids and molluscs. Lake feels the paraphyly of the arthropods evident in his scheme is not strongly supported by the nature of the molecular data available, and that much

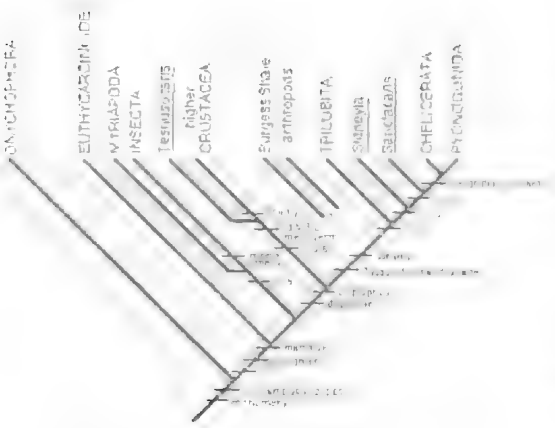

FIG. 12. Phenogram of possible arthropod relationships according to APT portraying the distribution of various APT and traditional characters discussed in the text.

more data are needed from a variety of arthropods before a more definitive answer can be obtained concerning the relationships of protostomes. However, his analysis does seem to support both the idea of the uniramians as an early offshoot of the arthropod lineage, as we advocate here, and the close relationship of crustaceans and cheliceriforms, as suggested by Briggs and Fortey (1989) and by us.

A species is neither completely derived nor completely primitive; each is a mosaic of features suited to the individual functional needs of that species. The challenge of phylogenetic studies is to sort those features and arrive at some judgment of the relative significance of each. We have approached all arthropod characters with an open mind, and willingly entertained the unthinkable by treating even old and long established assumptions as if they were just newly formed hypotheses. Furthermore, we believe much is to be gained by bridging disparate fields of research in an attempt to find common patterns. A certain smugness has formed around the idea that fossils can never really make any substantial contributions toward understanding phylogeny, other than filling in the details of a particular group's history. For example, Wilmer (1990: 76) bluntly stated, 'It actually seems unlikely...that any one author's view of metazoan phylogeny has ever been substantially formed, or substantially altered after formation, by reference to the paleontological record.' In contrast, we feel that fossils can make a great contribution towards understanding animal evolution, as they have in the present case. Furthermore, we caution against too much reliance on the use of exclusive paths to 'truth', e.g. such as those represented by molecular data. All lines of research are productive, but theories are not to be viewed as either entirely true or completely false. They are merely useful for a time in organizing facts and indicating potentially informative lines of research (Wenner and Wells, 1990).

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CRUSTACEAN EVOLUTIONARY EVENTS: SEQUENCES AND CONSEQUENCES

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Crustacean evolution is visualised as proceeding through a space-time continuum in which the Red Queen and stasis have operated. Under these conditions, evolutionary bursts were fuelled by major environmental changes following which the new diversities of taxa, having expanded into any newly available niches, returned to the Red Queen or stasis mode.

After some polyphyly in the Cambrian, which remains poorly understood, the major radiations in Crustacea seem to conform to such a scenario, particularly from the Hercynian tectonic epoch onwards. Important events following this include the initiation of Tethys, Carboniferous–Permian glaciations, peats and coals, Pangaea, Triassic desertic conditions, Mesozoic Tethys, the Purbeckian–Wealden, break-up of Gondwana, the Danian crisis, origin of the psychrosphere and Palaeogene Tethys, Paratethys, the Mediterranean Messinian event, the Central American filter, impingement of India against the Himalayas and of the Australian Block against the Indonesian arc, Pleistocene glaciations. Illustrations of the evolutionary effects for crustaceans are given mainly from the Ostracoda, although examples from other taxa are also cited.

Consequently, after preliminary discussion of such factors as limitations in the fossil record and convergence, new event-triggered phylogenies are derived for the main crustacean classes, maxillopodans and Ostracoda.

The role of humans in passive crustacean dispersal is analysed briefly, stressing the importance of history for a proper understanding of this phenomenon. □ *Biogeography, palaeontology, evolution, Crustacea, Ostracoda, man.*

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The thesis that evolution is event-triggered is well on the way to becoming a new orthodoxy in evolutionary science. Citing Benson (1985: 35), 'We are today in the middle of such a change: from the acceptance of continuity as a necessary and sufficient procedural assumption to a concurrence that interrupted stasis is an obvious condition of development.' Later in the same book Fischer (1985, fig. 7-1) correlated biotic crises with cycles of climatic change, sea level variation and vulcanism for the entire Phanerozoic (Cambrian–Recent).

There is a further modal constraint upon this paper. Van Valen (1973) propounded an evolutionary theory that all groups, 'go extinct at a rate that is constant for a given group' even in a constant physical environment. This rationale goes under the attractive name of the Red Queen hypothesis. At the court of the Red Queen extinction is inevitable, an entropic effect. Stenseth and Maynard Smith (1984) proposed an alternative hypothesis, that evolutionary stasis would be maintained until the physical environment was disturbed; then they demonstrated mathematically that both the Red Queen and stasis were feasible. This combined model is more generalised than the Macarthur-Wilson equilibrium hypothesis, in which species number is a dynamic equilibrium between immigrant taxa and those which become extinct (Webb, 1985), because it allows for the development of new taxa *in situ* following environmental change and extinction without necessitating stimulation of such evolution by immigrant competitors, although this is not excluded.

Summarising, crustacean evolution is visualised as proceeding through an Earth space-time continuum in which the Red Queen and stasis have operated. Under these conditions, evolutionary bursts were fuelled by major environmental changes after which the new diversities of taxa, having expanded into any newly available niches, returned to the Red Queen or stasis mode. The paper first briefly outlines the stratigraphy of crustacean evolution and the contemporary major environmental changes; then develops phylogenies based in the geological record; and finally cautions that passive dispersal of some crustaceans by humans can distort biogeographic (and any linked phylogenetic) patterns.

CRUSTACEAN EVOLUTION AND MAJOR ENVIRONMENTAL CHANGES

CAMBRIAN

The Cambrian Period is highly significant for the evolution of life on Earth. Although several major groups had appeared in the Ediacaran (latest Precambrian), their distribution is patchy; first appearance of widespread, richly diverse and abundant fossils is generally a diagnostic feature of Cambrian sequences. Briggs and Fortey (1989), summarising the early radiation and relationships of the major arthropodan taxa, provide a cladogram which indicates that crustaceans and crustacean-like animals occupy a primitive position among early biramian arthropodans. Their data come from the Middle Cambrian Burgess Shale fauna of British Columbia, Canada, which contains several possible crustaceans of uncertain affinities, including *Waptia*, *Odaraia*, *Branchiocaris*, *Perspicaris*, *Plenocaris* and *Canadaspis*. All were extinct by the close of the Cambrian. Boxshall (1983) also refers to the crustacean-like taxa of the Burgess Shale and includes the barnacle-like *Priscansermarinus* in his list. Confirmation that the latter is a barnacle requires the discovery and description of, 'identifiable cirriped structures, such as cirri, within the capitulum.' (Collins and Rudkin, 1981: 1011).

Canadaspis was once regarded as the earliest phyllocarid (Briggs, 1978) but this view no longer prevails and Dahl (1987) even thinks that it may not be a crustacean. Similarly, *Branchiocaris* (Briggs, 1976) seems a plausible early branchiopodan but is separated in time from more generally-accepted fossil branchiopods by about 200 million years. Briggs (1983) is unconvinced of a crustacean affinity and is similarly critical of *Waptia*, *Odaraia*, *Plenocaris* and *Perspicaris*. Note that the mandible is unknown for most of these taxa except *Canadaspis* and *Branchiocaris*, and that the *Branchiocaris* mandible is certainly non-crustacean (Briggs, 1976: 11–12).

The other Cambrian fauna with major relevance for crustacean phylogeneticists is that of the bituminous limestone Örsten of Sweden. The Phosphatocopida (Müller, 1979a), Skaracarida (Müller and Walossek, 1985) and Orstenocarida (Müller and Walossek, 1988) are all preserved in such complete detail that their assignment to Maxillopoda can be sustained. Of these taxa, Skaracarida and Orstenocarida were apparently extinct by the end of the Cambrian but Phosphatocopida lingered into the Early Ordovician and seem closely related to Bradoriida, both orders being referrable to the Subclass Ostracoda (Maddocks, 1982; McKenzie, Müller and Gramm, 1983). Bradoriids are the commonest, most diverse and most abundant Cambrian crustaceans. They occur in Cambrian rocks almost everywhere but their geological succession and geographical distribution has been worked out most completely in China (Huo and Shu, 1985; Huo *et al.*, 1989). Huo and Shu (1983, 1985) regard naupliine bradoriids as the earliest crustacean ancestors.

The favourable environmental setting for this first evolutionary burst among crustaceans was due to the widespread marine transgression that followed a latest Precambrian glacial epoch of continental emergence. Workers on all fossil groups concur that seas were epicontinental and relatively shallow. There was also a major global climatic change from cold in the earliest Cambrian to warm in the remainder of the Period (Boucot and Gray, 1987: 33–36).

ORDOVICIAN AND SILURIAN

During the next two geological periods, the major crustacean diversifications took place among ostracodes. Maddocks (1982: 227) notes, 'This Ordovician burst of adaptive radiation of calcareous shelled types, near-simultaneous origin of the major post-Cambrian orders and rapid disappearance of Cambrian stocks is a common evolutionary pattern in many invertebrate phyla.' Thus, as Bradoriida and Phosphatocopida died out, Leperditicopida, Beyrichicopida, Podocopida, Platycopida and entomozoacean Cladocopida all evolved. The Silurian saw the initiation of the Halocyprida via Entomoconchacea (Kornicker and Sohn, 1976a). No definite Ordovician Myodocopida are known although, if the phylogeny in Kornicker and Sohn (1976b) is correct, they would have split from Cladocopida and Halocyprida before these evolved. The most characteristic Lower Palaeozoic groups, however, were Leperditicopida and Beyrichicopida. The former were an offshoot from the main lineages of ostracode evolution — their intralamellar radial carapace structures are unique within the subclass (Sohn, 1974) — and they include the largest known ostracodes (Abushik, 1979); the latter very often are spectacularly-ornamented (Kesling, 1969). Indeed, Beyrichicopida were the most abundant Ordovician (Sarv, 1972) and Silurian (Siveter, 1978) crustaceans. Their radiation during these periods was extremely complex, as the rapid evolution of numerous genera went hand in hand with almost equally numerous extinctions (Scott,

1961, figs 47, 65). Beyrichicopid systematics were long bedevilled by unrecognised homeomorphies until Scandinavian workers established the crucial importance for their classification of sex dimorphic features (Schallreuter, 1988). The role of homeomorphy in crustacean evolution is referred to again in the Discussion section of this paper.

Equally important was evolution of the first phyllocarids, beginning in the Early Ordovician with the archaeostracan *Ceratiocaris* (Rolfe, 1969). The lower Palaeozoic Archaeostraca are regarded as part of the ancestral stock of all malacostracans by some workers (Dahl, 1987).

The initiation of another maxillopodan subclass occurred during the Late Silurian. *Cyprilepas holmi*, of Estonia, was identified as a pedunculate cirriped by Wills (1963). Newman and Hessler (1989, fig. 5) derive the evolution of all Pedunculata and Sessilia from this ancestral type. Finally, F. R. Schram illustrated a Silurian remipede during his talk at the conference. This is the earliest known representative of the Remipedia.

Environmental triggers to the evolution and radiations of as many as seven ostracode orders and *Ceratiocaris* surely included the widespread tectonism of the mid-Ordovician. Seas remained epicontinental and relatively shallow and initially they were warm. There is evidence for glaciation in Arabia, northern and southern Africa, and South America, dated at near the Ordovician–Silurian boundary (Boucot and Gray, 1987, fig. 3). A good discussion is provided by Fischer (1985). This geologically short-lived global cooling indicates more varied climates at the inter period boundary and was followed by mid-Silurian tectonism.

Devonian and Early Carboniferous

It could be convincingly argued that this was the most important geological interval for development of the main crustacean stocks. The first shrimp-like decapods — *Palaeopalaemon* — evolved then (Sturgeon *et al.*, 1964). Other Devonian malacostracans were no less remarkable, including *Eocaris* and *Devonocaris* of uncertain affinities and the first palaeostomatopod hoplocarids (Brooks, 1969, fig. 157); also 21 genera of archaeostracan phyllocarids (Rolfe, 1969, fig. 122), such as *Echinocaris* (Sturgeon *et al.*, 1964) and *Nahecaris* (Bergstrom *et al.*, 1987).

The record for other crustacean classes was even more noteworthy. The first Branchiopoda appeared, via the Spinicaudata and Lipostraca (note however that Schram has recently illustrated a possible Silurian anostracan). Spinicaudata are conchostracans; and they entered the geological record represented by 4 families (Tasch, 1969). Lipostraca were primitive anostracans (Scourfield, 1926). Additionally, acrothoracic barnacles evolved (*Trypetesa*).

The most abundant and diverse Devonian crustaceans, however, remained the Ostracoda, and numerous very rich faunas have been described (Pokorny, 1950; Becker and Bless, 1974; Tschigova, 1967; Jones, 1968; Polenova, 1968, 1974; Adamczak, 1968, 1976; Kesling and Chilman, 1978; Becker, 1988). While beyrichicopids still dominated, there were also many podocopids, platycopids and myodocopids; and 15 genera of leperditicopids (Abushik, 1979; Jean Berdan, per. comm. 1981) although the Order became extinct by the Carboniferous. This was also the time for diversification in entomoconchacean halocyprids (Kesling, 1954) and for the major radiation in entomozoacean cladocopids (Gruendel, 1962; Gooday, 1978).

Devonian climates are summarised in Boucot and Gray (1987: 38–43, figs 6–8) and a plausible palaeogeography is given by Rickard and Belbin (1980). Peats, red beds and marginal marine evaporites were typical on land and near the shoreline. Seas were epicontinental and mainly shallow, but reached basinal depths in regions characterised by the Thuringia-facies the most complete discussion of which is given by McKenzie (1987) who cites important prior references. The general tectonics of the Hercynian epoch are outlined by Carey (1987). Some idea of the complexity of the movements is given in the team project on the Omolon region, Siberia (Simakov *et al.*, 1983). It seems that provincialism characterised the Early Devonian whereas Late Devonian faunas were more widespread. Steiner (1967) linked the mid-Devonian biotic crisis to the dynamics of the Milky Way galaxy; for Fischer (1985) astronomical factors have neither the amplitude nor the frequency to account satisfactorily for the faunal changes which he believes were a response to a major reversal in climatic cycle, from 'greenhouse' to 'icehouse' state (Fischer, 1985, fig. 7-1). Note, however, that the tectonic setting overlapped into the Carboniferous, terminating with the definitive establishment of Tethys.

Reappraising the crustacean faunas of the Devonian, it is evident that the radiations and initiations in malacostracans (Phyllocarida, Ho-

plocarida, Decapoda), branchiopods (Spinicaudata, Lipostraca) and Ostracoda can all be explained as triggered by the mid-Devonian crisis. By its close, the Lipostraca apparently had vanished from the geological record.

On the other hand, the Early Carboniferous heralded further initiations of major crustacean groups, among them the important remipede *Tesnusocaris* (Schram and Emerson, 1986). Malacostracan initiations were primitive hoplocaridan animals (*Crangopsis*), pygocephalomorphs (*Tealliocaris*, *Pseudotealliocaris*), anthracocaridomorph tanaidaceans (*Anthracocaris*), primitive spelaeogriphaceans (*Acadiocaris*), as well as palaeocaridacean ancestors of the Syncarida (Brooks, 1969, fig. 157; Briggs and Clarkson, 1985; Schram *et al.*, 1986; Schram, 1984, 1988). Branchiopoda were represented by the earliest Notostraca as well as by spinicaudate conchostracans; pedunculate barnacles by *Praelepas*; ostracode initiations included cyprellid and rhombinid myodocopids, and the Darwinulacopina (Sohn, 1988).

Environments and facies of the Early Carboniferous have been exhaustively studied. The malacostracan fossils were preserved in shoreline, tidal flat, brackish-marine, deltaic and nearshore freshwater lake habitats, including coaley and apatite-rich facies (Briggs and Clarkson, 1983, 1988). Many Ostracoda also have been described from similar facies (Bless, 1973, 1983; Bless and Massa 1988; Jones 1989). Further offshore, Thuringia-type faunas persisted (Devolvé and Lethiers, 1986).

During the hot and humid climates of the time, limnic basins of thalassogenic type were widespread especially in northern continental areas. Ostracoda, in particular, were quick to exploit such niches via a number of families; typical genera included *Geisina*, *Carbonita*, *Whiplella*, *Darwinula* and *Tomiella* (Carbonel *et al.*, 1988, fig. 25). Their assemblages, and those of the contemporary conchostracans, were the earliest widespread continental crustacean faunas.

Later Carboniferous, Permian and Triassic

The profound changes in crustacean faunas during the later Carboniferous, Permian and Triassic were well typified by ostracodes. At the end of the Carboniferous, the following marine groups were extinct: beyrichiacean beyrichicopids; Entomozoacea and Entomoconchacea; the myodocopid families Cyprellidae, Cypridinellidae and Rhombinidae; Eridostraca; and Leperditicopida. The Permo-Triassic marine extinctions included Beyrichicopida which had dominated for most of the Palaeozoic, and also the kloedenellocopine platycopids. On land, the crisis was even more severe with only *Darwinula* and one cytheracean genus surviving into the mid-Triassic.

Other apparent victims of this series of major biotic crises were palaeocaridacean syncarids, trypetesid barnacles, *Acadiocaris*, the remipedes *Tesnusocaris* and *Cryptocaris*, and anthracocaridomorph tanaidaceans such as *Eucryptocaris*. But the lineal descendants of these taxa continued to evolve. Thus, although the earliest isopod is a Carboniferous phreatoicoid the next fossils in this group do not appear until the Jurassic.

The initiations and radiations were just as important. For Ostracoda, there were marine radiations in Bairdiacea (Kristan-Tollmann, 1970, 1971; Bolz, 1971) and Healdiacea, and evolution of the family Glorianellidae in brackish environments (Gruendel, 1978); also polycopacean cladocopids, thaumatocypridacean halocyprids and cytherellocopine platycopids (Gramm, 1968; Kornicker and Sohn, 1976a). On land, Darwinulocopina were still widespread but the faunas also included representatives of 10 non-darwinulacopine families and by, 'the end of the Late Permian, freshwater ostracode associations reached maximum species diversity and geographic differentiation for the Palaeozoic' (Carbonel *et al.*, 1988: 452).

Other crustacean initiations during the Permian included penaeid and astacid Decapoda, cumaceans, stygocaridacean syncarids (*Clarkecaris*), and perhaps the first leptostracan phyllocarids (Brooks, 1969; Rolfe, 1969; Glaessner, 1969). The Triassic was marked by the first appearances of mysids, syncaridacean syncarids, zaptellid acrothoracican barnacles, and glypheoid and eryonoid Decapoda.

Several major palaeogeographic and climatic changes were associated with these faunal developments. The continents coalesced forming Pangaea, its two main landmasses, Laurasia and Gondwana, being separated by a dominantly shallow Tethys. There was some mid-Carboniferous tectonism. Climates were glacial at higher latitudes during the Carboniferous–Permian nadir of the 'icehouse state' cycle (Fischer, 1985, fig. 7-1), but warm and humid in the tropics. During the Permian, the continents emerged and there was a salinity crisis in the mainly epicontinental seas. Towards the close of the Triassic, on the other hand, although the world

had warmed up again, climates were desertic not humid.

In marine habitats generally, ostracodes remained the dominant crustacean group in the later Carboniferous and Permian, and were excellent environmental indices in the generally shallow continental shelf seas (Melynk and Maddocks, 1988; Costanzo and Kaesler, 1987; Bless, 1987); however, Kozur (pers. comm., 1989) insists on the occurrence of some true deepwater facies (deeper than mesobathyal) in the Middle–Late Permian of Tethys.

During the Triassic, many Tethyan facies and faunas were cosmopolitan from Europe through to Asia and even the Americas (Kristan-Tollmann *et al.*, 1987; Sohn, 1987; Kristan-Tollmann, 1988).

Niche-diversification was particularly marked on land, where brackish, freshwater and mineralised lakes were all common, each with characteristic faunas. This provided opportunities for many entrepreneurial groups, notably including syncarids and Notocostraca, although the commonest assemblages by far consisted of spinicaudate conchostracans or ostracodes. By the mid-Triassic many of these ostracodes (Carbonel *et al.*, 1988, fig. 27) and also the vertexiid Spinicaudata (Tasch, 1969) had died out, presumably victims of the change to desertic climates. But Kazacharthra (Chen and Zhou, 1985) first appeared in the Late Triassic.

Jurassic and Cretaceous

Crustacean diversity in the Jurassic and Cretaceous was considerable in all major taxa and in all aquatic environments, continental as well as marine. Thus, in the Jurassic six more decapod superfamilies became established (Glaessner, 1969), along with numerous pedunculate barnacles (Newman, Zullo and Withers, 1969, table 2), rodgerellid Thoracica; and apseudomorph tanaidaceans. Verrucomorph, brachylepadomorph and balanomorph sessile barnacles radiated in the Late Jurassic–Early Cretaceous, but many lepadomorph genera also became extinct in the Jurassic and by the end of the Cretaceous. The Early Cretaceous saw the evolution of tanaidomorph tanaidaceans (Schram *et al.*, 1986); and the oldest fossil copepod has been identified from the Early Cretaceous of Brazil. Ascothoracida (*Endosaccus*) evolved in the Late Cretaceous.

Evolutionary peaks, in what has been called the Mesozoic explosion of the ostracode Cytheracea, characterised the mid-Jurassic, mid-Cretaceous and Late Cretaceous (Whatley and Stephens, 1975). Their initiations and extinctions clearly express a Red Queen evolutionary pattern (Oertli, 1985, tables 5,6,8). Other initiations include the first Macrocyprididae (Maddocks, 1990), Sigilliacea (Szczechura and Blaszyk, 1968); and Punciacea (Herrig, 1988). The Mesozoic–Tertiary distribution via Tethys and Gondwana of entocytherid parasites is linked to the fossil history of their host taxa — phreatoicoids, cirolanids, sphaeromids, gammarideans, astacids, parastacids and potamids (McKenzie, 1973).

Continental interiors were characterised by large lake systems (including saline lakes) in tectonic depressions and intermontane basins, as in China (Chen, 1987). *Darwinula* and limnocytherid cytheraceans were widespread earlier, but by the Purbeckian–Wealdean epoch of alternating transgression/regression cypridaceans had taken over (Anderson, 1971; Colin and Danielopol, 1979, 1980; Ye, 1984; Su, 1987). However, most of the characteristic genera of this first continental cypridacean radiation were short-lived. With respect to conchostracans, the spinicaudate families Estheriellidae, Ipsilonliidae and Asmussiidae all died out in the Cretaceous but this was balanced by evolution of the order Laevicaudata.

World climates were in their 'greenhouse' phase according to Fischer (1985, fig. 7-1). Thus, it was generally warm to hot and humid everywhere until the close of the Cretaceous. Volcanic activity peaked in the mid-Cretaceous. High sea-levels characterised the mid-Jurassic, mid-Cretaceous and Late Cretaceous. The mid-Jurassic black marls indicate relatively deep epicontinental marine basins, with *Liasina* and metacope ostracodes (Oertli, 1963). Summarising the Cretaceous history of Africa, Reyment and Dingle (1987) recorded that rifting to open the South Atlantic began in the Late Jurassic but there were still connections in the Brazil–west Africa region until the mid-Cretaceous as shown by many common ostracodes (Malz, 1980). Then the break-up of Gondwana, and provincialism in the Southern Hemisphere, initiated.

Marine environments were dominated by the classic Tethys of Suess (1893) which is a mid-Mesozoic phenomenon. The analysis in McKenzie (1987) demonstrates that Tethys was not broad and uniform, as supposed by some palaeocartographers, but comprised wide continental shelves and sinuous intervening usually epibathyal deepwater facies, plus some small confined basins. It was

affected by tectono-eustatic variations in sea level which were more or less marked according as they were in or out of phase with crustal movements (Reyment and Bengtson, 1985). Thus, along the southern flank of Tethys in northern Africa and the Middle East, Jurassic–Cretaceous facies were transitional from freshwater to mineralised sabkha to brackish to shallow marine (including bituminous basinal marls) in phase with tectonism and eustasy. Ostracoda are reliable palaeoenvironmental indices (Damotte *et al.*, 1987; Majoran, 1989; Basha, 1985; Rosenfeld and Raab, 1974, 1984; Honigstein *et al.*, 1989; Al-Abdul-Razzaq and Grosdidier, 1981; Al-Furaih, 1980). The contemporary deeper-water basinal facies which covered, for example, much of France by the mid-Cretaceous (Oertli, 1985) indicate commencement of a change in Tethys, from epicontinental to truly oceanic.

The tectono-eustatic transgressions of the Cretaceous were well-marked elsewhere in the world, notably in Africa, Australia and the Americas. The characteristic crustaceans of their fossil faunas were usually ostracodes (Dingle, 1984; Kroemmelbein, 1975; Hazel and Brouwers, 1982; Bertels, 1975) or barnacles (Newman and Hessler, 1989) although many Late Cretaceous decapod-rich zones occur in the United States (Bishop, 1987).

Wholesale extinctions that devastated many groups of animals marked the Mesozoic–Cenozoic boundary. The classic study of this event has noted a major species level change in Ostracoda and the extinction of numerous marine barnacles (Kaufmann, 1985: 191); many decapod genera also died out (Glaessner, 1969, fig. 251). The environmental model proposed to account for this envisages a major eustatic sea level rise associated with active tectonism accompanied by climatic warming during the earlier Late Cretaceous, followed by sudden and widespread oxygen-depletion in the oceans and marine temperature decline during the Danian; several other possible causes are also discussed, including an extraterrestrial iridium-rich event (Kaufmann, 1985).

Cenozoic

The Cretaceous decimations paved the way for development of the modern Crustacea. This is well brought out by the suprageneric taxa of Decapoda; Glaessner (1969, Fig. 251) shows that 32 of 51 surviving families evolved in the Tertiary–Recent. Barnacle genera with fossil records tell the same story; Newman, Zullo and Withers (1969, table 2) show that 38 of 62 genera evolved in the Tertiary–Recent, and that 27 of these were balanomorphs. For Ostracoda, the Aquitaine Basin, France (McKenzie *et al.*, 1979) has over 1100 Tertiary–Recent species; and of the more than 200 genera less than 10% have Cretaceous or earlier records.

The initiations of new major groups include 4 of the extant branchiopod orders (Fryer, 1987). There were important adaptive radiations in Copepoda, Isopoda, brachyuran Decapoda and, probably, Amphipoda. But many groups have no appreciable fossil record: including Ctenopoda, Onychopoda and Haplopoda (cladocerans); Mystacocarida; Cephalocarida; several orders of Copepoda; Branchiura; Rhizocephala; Bathynellacea; Thermosbaenacea; Euphausiacea; and Tantulocarida. This will be discussed below.

The Cenozoic also saw important extinctions, among them the rodgerellid and zapfellid Ascothoracica. Further, 26 ostracode genera had disappeared from the Aquitaine Basin by the end of the Tertiary (McKenzie *et al.*, 1979: 140).

The environmental triggers to such developments had various tectonic, eustatic and climatic components. Very important among these was the origin of the psychrosphere. The establishment of regions of abyssal and greater depths, that is the realm of true oceans, had probably begun in the mid-Cretaceous but the earliest psychrospheric ostracode assemblages have been dated as Eocene, based on Deep Sea Drilling Project cores (Benson, 1975). McKenzie (1987) considered that the ubiquity of new and specialised deep sea ostracode taxa was an indication of the comparative recency of this niche. The figures for crustaceans of the hadal zone are interesting from this point of view. Table 1 has been abstracted from Belyaev (1989). It shows that by far the largest number of crustaceans living in this deepest zone belong to comparatively young groups such as the Isopoda and Amphipoda. Even in the older groups most hadal species represent geologically young taxa, e.g. 6 ostracode Conchoeciidae (Late Cretaceous–Recent); 10 cirripede Scalpellidae, of which genera with fossil records date from the Late Cretaceous or Eocene; and 20 species of the Recent tanaidacean suborder Neotanaidomorpha (Belyaev, 1989).

During much of the Palaeogene and until the mid-Miocene, Tethys was a world-encompassing ocean in low latitudes that was psychrospheric at depth; across its entire extent

TABLE 1. Hadal Crustacea (cf. Belyaev, 1989).

Taxa	Number of Species
Calanoid Copepoda	32
Cirripedia	10 (all Scalpellidae)
Ostracoda	14 (6 Conchoecetidae)
Mysidacea	12
Cumacea	11
Tanaidacea	57 (20 Neotanaidomorpha)
Isopoda	140
Amphipoda	64

ostracode assemblages contained numerous common genera (McKenzie, 1967). Tectonic pulses in the Middle East closed off western Tethys from the Indo-Pacific in the mid-Miocene. Two related events then had considerable impact upon Mediterranean faunas (Roegl and Steininger, 1984). First came the establishment of Paratethys and its sometimes linked sometimes separate component basins with their highly characteristic ostracode faunas (Pokorny, 1952; Stancheva, 1965; Sheidayeva-Kulieva, 1966; Krstic, 1971; Sokac, 1971; Yassini, 1987) which exhibited an almost 100% turnover as basinal salinities alternated between marine, brackish and fresh in phase with tectonism and eustasy (Table 2). Destructive in a faunal sense was the Messinian (Late Miocene) crisis during which the Mediterranean dried out and thick beds of gypsum were deposited — an index for this epoch is the Paratethyan euryhaline ostracode *Cyprideis pannonica*. As a result, when the ocean refilled in the Pliocene, faunas were replaced from the Atlantic. For crustaceans, the consequences were twofold. Firstly, modern Mediterranean species have almost no links with Indopacific faunas except for a few relicts, and some Lessepsian migrants (Por, 1971) via the Suez Canal filter. Secondly, because of the Gibraltar Sill only shallow-adapted Pliocene species entered from the Atlantic, thus the Mediterranean deepwater ostracode fauna differs from that of other older oceans (Bonaduce *et al.*, 1983).

TABLE 2. Ostracode assemblages of the Paratethys in northwest Bulgaria (Stancheva, 1965), showing a near-complete faunal turnover in the same basin at each Stage boundary.

Stage	Total species (subspecies)	Common species with next older Stage
Pontian	47(5)	None
Maeotian	7(3)	1
Sarmatian	109(9)	2
Badenian	52(1)	-

In the Indo-West Pacific, an important tectonic event was the impingement of the Australian Block against the Indonesian Arc. Unlike the earlier suturing of India with the Himalayas (which closed off a former marine corridor), this event led to faunal mixing and a new burst of marine speciation. McKenzie (1981, 1986) believes that evolution of the ostracode Subfamily Renaudcyprinae and many island assemblages in the southwest Pacific have resulted as responses to the complex Neogene regional tectonics. On the other hand, Newman (1986) ascribes the development of the barnacle fauna of the isolated Hawaiian Archipelago to long range chance dispersal during and since the Neogene.

At the western end of Tethys, a critical Neogene event was the emergence of the Isthmus of Panama which closed off the Caribbean and Gulf of Mexico from the Pacific seaboard of the Americas. Cronin (1985) and Cronin and Schmidt (1988) have discussed evolution in the ostracode genera *Puriana* and *Orionina* as an effect of this event.

On land, apart from Paratethys, large Cenozoic basins characterised by variable salinities are known from the Amazon region (Purper, 1979; Purper and Pinto, 1985) and China (Yang *et al.*, 1988). But the most important events were the glaciations of the Pleistocene Epoch. Glaciers covered much of North America, Europe and Asia wiping out all but a few relictual faunas. The reoccupation of these niches, following the last retreat of the ice sheets about 11,000 years ago, has been effected especially by parthenogenetic taxa. On other continents, endemism characterises the continental aquatic and also the terrestrial crustacean faunas. This is scarcely surprising given the long isolation of South America, south Africa, India and Australia from the northern Palaearctic and Nearctic provinces. Thus, Australia has mainly endemic faunas of anostracans, anaspidaceans, phreatoicoids, and calanoid copepods as well as ostracodes.

DISCUSSION

The detail provided in the foregoing section is clearly sufficient to sustain the thesis that evolution is event-triggered. Evidently, the first evolutionary burst of Crustacea occurred in

pre-Tethyan early Palaeozoic seas; the second main episode was associated with shallow Tethys, Pangaea, and then the Laurasia and Gondwana landmasses (late Middle Devonian to Middle Cretaceous); while the third main episode relates to the evolution of deep, psychrospheric modern oceans and present continental assemblies, beginning around the middle Cretaceous (McKenzie, 1987, 1989).The data are biassed towards Ostracoda because they are the most abundant crustacean fossils. Two recent bibliographies (Kempf, 1980, 1988), both incomplete at their dates of publication by about 10% according to the author, list nearly 5100 taxonomic papers. The preponderance of these papers refer to fossil species. Numbers of described fossil Ostracoda are not known with certainty but are in any case over 30,000 and increase by several hundred species a year.

For many reasons, some of which are discussed briefly below, it is difficult to specify a typical crustacean facies. Nevertheless, the distinctiveness of the phylum is generally acknowledged. This consensus is due primarily to the work of Manton (1973) who characterised crustaceans as distinct from Chelicerata, Trilobita and Uniramia. Her assessment was vindicated on embryological grounds by Anderson (1973).

The observation has already been made that some Recent crustacean orders are not represented in the fossil record. There are a variety of reasons for this, most commonly that many groups have a wholly soft anatomy which would not be likely to fossilise except under specially favourable conditions. Other reasons include small size; unsuitable niches such as ephemeral ponds, leaf litters and caves; and inapposite habits of life such as the parasitism of rhizocephalans, branchiurans and some copepods.

Nevertheless, it is not difficult to make reasonable statements on the evolution of such taxa based on their morphology, habits and palaeobiogeography. Thus, none of the branchiopod orders once classed together as cladocerans are likely to predate the Early Cretaceous. Haplopoda (only one genus — *Leptodora*) are highly specialised marine planktic predators with a restricted Holarctic distribution (Fryer, 1987). Given that the present world ocean with its characteristic psychrosphere only initiated in the mid-Cretaceous and that there was a virtually complete turnover in oceanic plankton during the Cretaceous mass extinctions and, further, the extent of the Pleistocene ice sheets, it is unlikely that *Leptodora* initiated much before the later Neogene. Similarly, Onychopoda are represented by few genera and although marine species are distributed worldwide the freshwater species are Holarctic. Onychopoda are also characterised by a Ponto-Caspian radiation of endemic species (Fryer, 1987). Thus, their evolution possibly correlated with that of Paratethys in the mid-Miocene. Ctenopoda and Anomopoda are certainly older and, for the latter group, fossils are known from the Oligocene and Early Cretaceous (Fryer, 1987; Jell and Duncan, 1986) — Fryer (1987) does not accept the Permian fossils described by Smirnov (1970) as anomopodans. Both groups are freshwater in origin. The numerous records of fossil freshwater ostracodes and conchostracans from every type of continental habitat make it unreasonable to claim that Ctenopoda and Anomopoda could have evolved much before the earliest accepted anomopodan fossils. Most evolutionists would agree with these conclusions since cladocerans are generally regarded as neotenic.

As further examples, the austral biogeography of the branchiuran *Dolops* and some continental calanoid copepods suggests that they probably evolved on Gondwana before it fragmented, i.e. before the mid-Cretaceous; but no phylogeny that I am aware of regards these groups as ancestral maxillopodans. Finally, but importantly, Cephalocarida (Sanders, 1963; Hessler, 1964) also have no appreciable fossil record. Their biogeography indicates wide distribution from the Americas to Asia and New Zealand, always in nearshore marine environments. This suggests that cephalocarids were dispersed via Tethys. They probably initiated prior to the mid-Cretaceous evolution of the intervening Atlantic but after the Late Devonian–Early Carboniferous, because cephalocarid fossils have not been reported from the many suitable Tethyan and other nearshore facies of this interval that would have favoured their preservation if present.

The fossil record has much more use for crustacean evolution than the simple provision of initiation times. It also demonstrates clearly that in many groups initiation is soon followed by an adaptive radiation; and as often as not a Red Queen pattern of extinctions follows this phase of diversification. Fig. 1 provides examples from barnacles, decapods and ostracodes. Further, it commonly happens in the fossil record that only one or a few taxa belonging to some particular group survive through a major biotic crisis and this survivor or survivor group

may then embark upon a new adaptive radiation or else stagnate in an evolutionary sense. The continental ostracode *Darwinula* is an excellent example. It evolved in the Carboniferous, radiated and diversified into several genera and even families by the end of the Permian, was the sole survivor of this darwinulocopine diversity after the Permo–Triassic extinctions, stagnated through the Mesozoic and most of the Cenozoic, but may now be at the threshhold of a new adaptive radiation as it is relatively species-rich and virtually euryoecious in modern continental environments and has given off the genus *Microdarwinula* (Danielopol, 1968). The fossil record also has examples of groups which became established early and have maintained a relatively limited diversity ever since. The longest surviving examples of this pattern are the Remipedia; further, the notostracans *Triops* and *Lepidurus* had split off from each other by the Triassic and have remained species-poor but persistent since then. A third pattern in the record is that in which a group initiates and then rapidly becomes extinct. A good example is provided by Kazacharthra (Late Triassic–Early Jurassic).

Very useful in the study of evolution is the principle of reductionism, termed oligomerisation by crustacean workers.

When we look, for example, at the multi-segmented and highly spinose limbs of the Cambrian maxillopodan orders Phosphatocopida, Skaracarida and Orstenocarida and compare them with the same limbs in podocopid ostracodes, cephalocarids, and copepods, the modern groups are obviously oligomerised respective to the Cambrian taxa. Exploitation of this principle, however, forms the basis of much crustacean arboriculture (to borrow D.T. Anderson's felicitous term).

On the other hand, the multiple instances of convergence (or homeomorphy) in all crustacean groups are often very difficult to deal with phylogenetically, as all workers appreciate. Less appreciated are instances of anhomeomorphy, i.e. of dissimilarities which separate taxa that in reality are monophyletic. Thus, the common characters which formerly united cladocerans now have been exposed as instances of convergence between four distinct orders (Fryer, 1987). But the anhomeomorphies between Spinicaudata and Laevicaudata (conchostracans) as elucidated by Fryer (1987) should not obscure the stem monophyletic relationship between these two branchiopod orders; the fossil record indicates that Laevicaudata split off from some Spinicaudata in the Early Cretaceous.

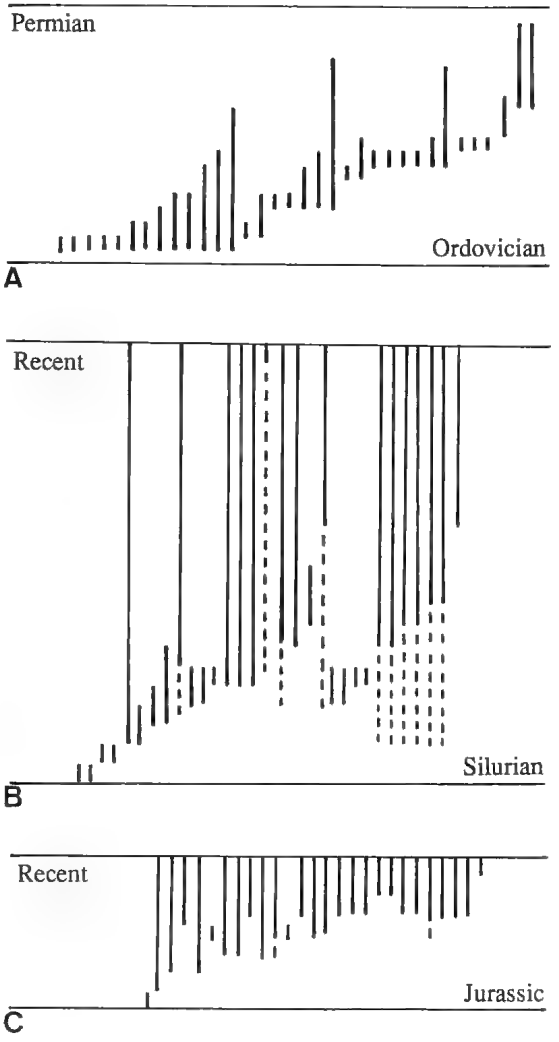

FIG. 1. A, normal radiation and Red Queen evolution/extinction in genera of Ordovician to Permian ostracodes, superfamily Drepanellacea (Scott, 1961). B, radiation, Red Queen evolution/extinction and stasis in families and genera of Silurian to Recent barnacles, Lepadomorpha (Newman *et al.*, 1969). C, radiation and stasis in families of Jurassic to Recent decapods, Brachyura (Glaessner, 1969).

Also difficult to cope with is the common occurrence of neoteny, mentioned earlier with respect to cladocerans. The recent description of a punciacean ostracode, *Manawa staceyi*, suggests that it too has several neotenic features to go with its highly-oligomerised chaetotaxy, including a shallow dome-like univalve in early ontogeny (Swanson, 1989).

A further factor which contributes to the complexity of elucidating crustacean evolution is the

frequency of mosaic evolution. This is rarely emphasised nowadays in crustacean studies although it is a characteristic phase in the evolution of numerous groups (Colin and Danielopol, 1980).

Every crustacean is a melange of primitive and derived characters. While this truth is not restricted to living taxa it leads to considerable difficulties in arriving at a plausible phylogeny on the basis solely of the Recent fauna. The problem was well aired by Dahl (1963: 13–15, figs 1,2) who warned that the main lines of phylogenies were conjectural,'for at present we possess no actual evidence demonstrating any case of a group at subclass or higher level being derived from another group.' (Dahl, 1963 : 13). The value of the punctuational equilibria hypothesis in this context lies in the fact that we would anticipate that aspect of phylogeny. On the other hand, constant reference to the fossil record enables the building of a tentative basic phylogeny that is anchored in geological time rather than in a cladistics which ignores this crucial restraint. The reasoning followed in developing a time-oriented phylogeny for Crustacea can be illustrated by reference to two fundamental crustacean characters, the carapace (or headshield) and the antennule.

There are only two arguments against the primitive nature of the crustacean cephalic shield. Firstly, some Cambrian fossils which seem to have crustacean affinities lack one, e.g. *Yohoia*. Considerable new evidence would have to be uncovered before this argument could be sustained. Thus, in Briggs and Fortey (1989, fig. 1), *Yohoia* lies between the chelicerate-like animals and the trilobites; and all the crustacean-like Cambrian fossils in their cladogram have a well-defined cephalic shield. Parenthetically, these mid-Cambrian crustacean-like taxa seem a polyphyletic cluster; their precise relationships to each other and to Crustacea remaining poorly understood. The second argument contends that Cambrian crustaceans lacking a cephalic shield have not been preserved. This argument fails because the two best known apposite Cambrian faunas, those of the Burgess Shale and the Orsten, are found in deposits that are highly-favourable to the preservation of soft anatomies: if such forms were present they surely would have been found by now. Further detailed discussion on the carapace is provided in Jones and McKenzie (1980).

My position with regard to the crustacean antennule is more controversial. Crustaceans have three types of antennule: uniramous, biramous and triramous. Uniramous antennules are typical of Maxillopoda and Branchiopoda; biramous antennules occur in the phyllocarids, eumalacostracans and Remipedia; triramous antennules feature in Hoplocarida. Kunze (1983) proposed recently that, ' Hoplocarida and Eumalacostraca evolved independently from separate "phyllocarid-like" ancestors.' The triramous hoplocarid antennule is a key apomorphy in her analysis.

Recapping, the earliest fossils assigned to Hoplocarida are Devonian palaeostomatopods. The earliest maxillopodans are Cambrian Bradoriida, Phosphatocopida, Skaracarida and Orstenocarida. The oldest-known definite phyllocarids are Ordovician, but a Cambrian origin for the group is probable. The oldest remipede has a Silurian age; the earliest Eumalacostraca are Devonian. Adaptive radiations shortly after their evolution certainly characterise the Bradoriida, Phosphatocopida, Phyllocarida and Eumalacostraca. The Skaracarida and Orstenocarida seem short-lived Cambrian groups. The Remipedia represent the pattern of a long-surviving group with limited numbers.

The simplest phylogenetic pathway that is consistent with this record suggests that the ancestral forms were Early Cambrian bradoriid maxillopodans with an uniramous antennule. Phyllocarids (biramous antennule) branched off in the mid-Cambrian, possibly from bradoriids of the suborder Abdomina (Huo and Shu, 1983). In the Devonian, Branchiopoda (uniramous antennule) split off from the Maxillopoda; but Eumalacostraca (biramous antennule) and Hoplocarida (triramous antennule) diverged separately from phyllocaridan stock (Kunze, 1983). Remipedia (biramous antennule) evolved in the Silurian or earlier, possibly from phyllocarid-like taxa. Cephalocarida (uniramous antennule) may have initiated in post-Permian Tethys as discussed previously, splitting off from as yet unknown branchiopod-like forms (Fig. 2). As a systematic exercise, it elevates Hoplocarida to the same subclass status as Eumalacostraca and Phyllocarida; but Maxillopoda, Remipedia and Branchiopoda retain their rank as classes. Note that subclass and class divergences are attuned to major Palaeozoic events.

Given this groundplan, the subdivision of classes and subclasses can proceed under similar chorological and event-triggered constraints. Remipedia are a small group whose biogeography and subsequent evolution was crucially influenced by the mid-Cretaceous separation of Africa from the Americas (Schram and Emerson,

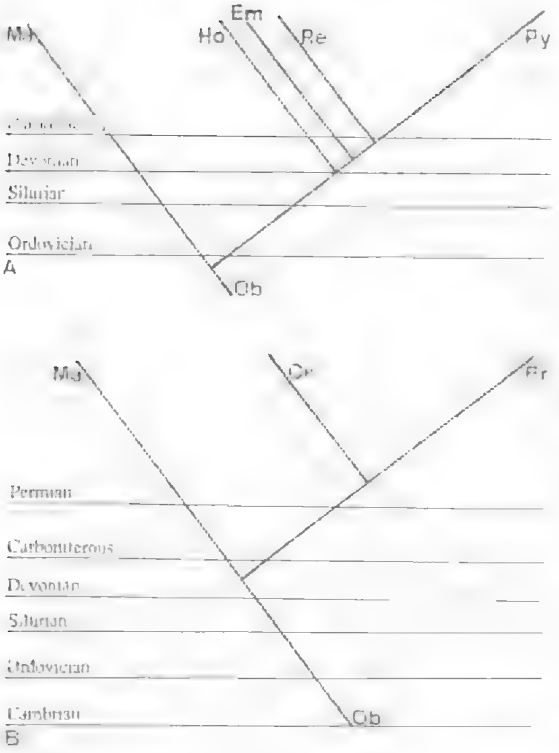

FIG. 2. A, phylogeny of Maxillopoda (Ma), Hoplocarida (Ho), Eumalacostraca (Em), Remipedia (Re) and Phyllocarida (Py) from an origin in bradoriid Ostracoda (Ob). B, phylogeny of Maxillopoda (Ma), Cephalocarida (Ce) and Branchiopoda (Br) from an origin in bradoriid Ostracoda (Ob).

1986, lower figure, p. 17). Interrelationships of the orders of Branchiopoda will be published by Fryer; but neither the evolution of Anostraca from Lipostraca, Kazacharthra from Notostraca and Laevicaudata from Spinicaudata nor the timings of these events seem much in dispute. The evolution and relationships of the families of Hoplocarida seem well understood, those of Phyllocarida and Eumalacostraca less so, but all three are beyond my expertise. This leaves Maxillopoda.

Maxillopoda were originally defined by Dahl (1956) to include Mystacocarida, Copepoda, Branchiura and Cirripedia. Later, the class was redefined to include also Ostracoda, Tantulocarida and the Cambrian orders Skaracarida and Orstenocarida (Grygier, 1987; Boxshall and Huys, 1989; Müller and Walossek, 1988). The two latter orders, with Bradoriida and Phosphatocopida (Ostracoda), serve to emphasise the early adaptive radiation of maxillopodans and the equally important subsequent early extinctions.

Thanks to painstaking work by Müller (1979a, 1982) and Müller and Walossek (1985, 1988), the anatomies of Phosphatocopida, Skaracarida and Orstenocarida are known in considerable detail. A comparison indicates clearly that the most generalised limbs are those of the phosphatocopid suborder Vestrogothiina in which the antennule is reduced (*Falites*), the antenna through to the maxilla are biramous and closely similar in morphology, the 6th and 7th limbs are modified from the antenna-maxilla pattern and the 8th 'limb' is lamellar (possibly a furca). In Hesslandonina, the antennule is small and uniramous, antenna and mandible are biramous and similar, and the maxillule, maxilla, 6th and 7th limbs while differing somewhat from the antenna-mandible pattern are also similar (Müller, 1979a, 1982).

The organisation of Skaracarida limbs resembles that of Hesslandonina, i.e. uniramous antenule, look-alike antenna and mandible, similar maxillule, maxilla and maxilliped; but the rest of the body is strikingly distinctive comprising 10 circular limbless segments, followed by a telson and 3-segmented furcae (Müller and Walossek, 1985).

Bredocaris, the representative of Orstenocarida, has differentiated anterior limbs, comprising uniramous antennule, biramous antenna, mandible with well defined coxal gnathobase, maxillule; but the maxilla and 7 thoracopods are similar to each other. The body ends in a short abdomen and furcae (Müller and Walossek, 1988).

The earliest fossils of these maxillopodan orders are Early Cambrian naupliine Bradoriida, the most primitive of which (*Shensiella*) seems to have possessed four body segments not including the telson, indicated by lobe-like expansions of the soft and very thin outer surface of the carapace shield (Huo and Shu, 1983: 87). The progressive decrease in lobes through stratigraphically higher beds indicates fusion of the body segments terminating in an unsegmented body (*Hanchungella*). This ancestral stock then divides into the Lipabdomina (lacking an abdomen) and Abdomina (with an abdomen). Jones and McKenzie (1980) also suggested such a division in Bradoriida but regarded it as evidence for polyphyly. However, the discovery of Naupliinae substantiates a monophyletic origin for the order.

Fig. 3 presents phylogenies of the early Max-

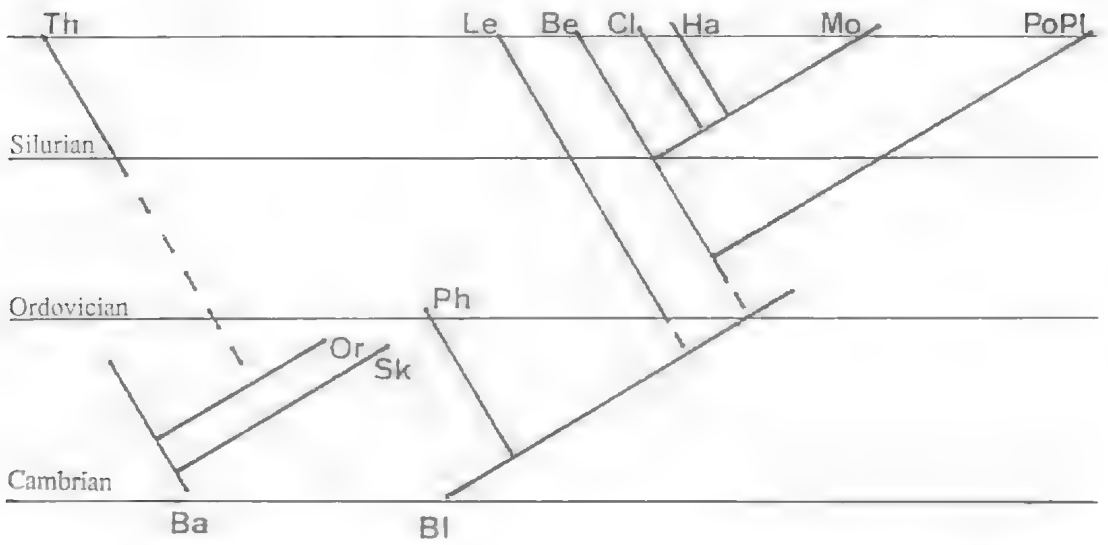

FIG. 3. Phylogenies of the maxillopodan orders and the superorder Thecostraca. Left hand side shows the phylogeny of Skaracarida (Sk), Oerstenocarida (Or) and Thecostraca (Th) from an origin in bradoriid Abdomina. Right hand side shows the phylogeny of the ostracode orders Phosphatocopida (Ph), Leperditicopida (Le), Beyrichicopida (Be), Cladocopida (Cl), Halocyprida (Ha), Myodocopida (Mo) and Podocopida/Platycopida (PoPl) from an origin in bradoriid Lipabdomina..

illopoda based on an origin in naupliine Bradoriida. On the left, the orders Skaracarida and Orstenocarida split successively from Abdomina; and Thecostraca are interpreted as diverging from Orstenocarida (Müller and Walossek, 1988). On this main branch, Tantulocarida evolved subsequently from thecostracans (Boxshall and Lincoln, 1987); Branchiura also from Thecostraca; Copepoda from Skaracarida-like forms; and Mystacocarida from Copepoda (Boxshall and Huys, 1989, fig. 6).

Copepod specialists will decide whether or not the Early Cretaceous parasitic species from Brazil is close to the ancestral Copepoda. Based on geological history, copepods probably diversified nearshore and on land after the Triassic; profited from the mid-Cretaceous opening of the Atlantic; were exposed to Cretaceous decimation; and underwent an adaptive radiation especially in the oceans during the Cenozoic. Mystacocarida, with their interstitial and cavernicole life habits and longitudinal distribution from Europe to southern Africa, probably evolved from copepod ancestors during the opening of the Atlantic. A possible geological history for some Branchiura was given earlier.

The right hand side of Fig. 3 provides a phylogeny based on Lipabdomina and shows evolution of the ostracode orders. Phosphatocopida diverged via Oepikalutidae (Jones and McKenzie, 1980) in the Midddle Cambrian; Beyrichicopida in the Late Cambrian possibly via Beyrichonidae (McKenzie, Müller and Gramm, 1983); Leperditicopida perhaps in the Late Cambrian (Scott, 1961). Podocopida branched off from Beyrichicopida in the Early Ordovician, and Platycopida possibly from Podocopida in the Late Ordovician; while Myodocopida evolved from Beyrichicopida in the Ordovician, giving rise to Cladocopida and Halocyprida in the Ordovician and Silurian respectively, as discussed earlier. The cladistics of the three latter groups is based mostly on Kornicker and Sohn (1976b). Kornicker (pers. comm., 1981) accepts the ordinal status of Cladocopida. Lastly, the photograph of an *Amphissites* soft anatomy in Müller (1979b) shows that a beyrichicopid origin for podocopids and platycopids is plausible.

EPILOGUE

History is the biostratigraphy of *Homo sapiens*, now self-recognised as a rather insensitive dominant in the organic world. A main feature of this dominance has been the passive dispersal of thousands of species, usually deliberate but also, on numerous occasions, accidental. Thus, ever since the first human settlements people have transformed their sur-

rounding environments by the cultivation of exotic but useful plants. The earliest such introductions can be dated archaeoethnobotanically, but most information on the spread of useful plants is accessed by studying socio-economic history.

Many crustaceans have minute dessication-resistant eggs that could be transported easily with seeds of exotic cereals and other plants, in soil packed around cuttings; also as dust carried with trade goods, and by travellers and migrating peoples. Both archaeoethnobotanical and historical records were cited by McKenzie and Moroni (1986) in documenting the role of humans as an agent of crustacean passive dispersal via useful plants with respect to the many ostracode *ospiti esteri* (foreign guests) of northern Italian ricefields. These species originated variously, in Africa, Australia, Asia and South America. None of them have been identified in European Tertiary and Quaternary fossil assemblages. The authors also stressed that numerous other exotic plants could have been the first vectors for such introductions (McKenzie and Moroni, 1986). Margaritora, Ferrari and Crosetti (1987) found a Far East *Moina* (cladoceran) in an Italian ricefield which they thought came in with seed exchanges; and Ferrari (pers. comm., 1989) has identified an Oriental calanoid copepod in northern Italy.

Marine Crustacea are also susceptible to passive dispersal by humans, the principal vector in this instance being shipping ballast. The earliest ballasts were large stones — clumps of ballast stones can still be seen on atolls, such as Aldabra in the Indian Ocean — and the mud and water associated with these could harbour small crustaceans. Thus the homogeneity of shallow water ostracode assemblages in island groups of Micronesia (Weissleader *et al.*, 1989) may well be due in part to passive dispersal via frequent inter-island voyages.

Sea trade was well established even before Roman times and by the 12th century Islam controlled the Asian sea routes. With the Chinese invention of bulkheads (Needham, 1971), large ships capable of long oceanic voyages could be built. The Ming admiral Zhung He established a Chinese hegemony in the Indian Ocean early in the 15th century, but this lapsed when later Ming emperors adopted an isolationist policy. In 1492, Columbus discovered America and in 1493 Vasco da Gama sailed round southern Africa to India. Soon Portugal, Spain, Holland, France and Britain were colonising and trading directly in Asia and the Americas. When needed, ballast was dredged up by shipboard pumps from harbour bottoms. This practice continues and now poses a serious quarantine problem worldwide. For example, around 60 million tonnes of ballast water are discharged in Australian waters each year; and crustaceans are known to be among the numerous organisms dispersed internationally in this way (Australian Quarantine and Inspection Service pamphlet, 1990). My own research has concentrated upon trade in the Mediterranean for which the historical records are excellent, particularly those in the Venetian archives (Borelli, 1985). Maddocks (pers. comm., 1988) has suggested that some unexpected ostracode distributions off Florida may be due to passive dispersal in the ballast of pirate ships during the 16th to 18th centuries.

Many discontinuous distributions of Recent crustacean species and genera are simply explained by passive dispersal in ballast sludge during the past 500 years. Apart from taxa cited in McKenzie (1989), the ostracodes *Mungava* and *Dolerocypria* (Wouters, 1987a, 1987b) and the harpacticoid *Darcythompsonia* (Fiers, 1986) could have been distributed passively in such a manner.

Obviously, any taxa spread by humans on land or by sea are allochthonous to the geological evolution of Crustacea; and phylogenetic interpretations based upon such distributions are faulty. Because crustacean taxonomy itself is only about 250 years old many of these dispersals predate it; but others, particularly of small species, are still occurring.

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ZOOGEOGRAPHY OF THE PENAEIDAE

W. DALL

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The Penaeidae are tropical stenotherms, mostly inhabiting shallow, silty inshore environments. Their present distribution appears to be largely determined by a combination of geological history, temperature, ocean currents, ocean deeps and coastal geography. Penaeids are almost six times more diverse in the Indo-West Pacific Region than in the Western Atlantic, which may be related to continental shelf area or the length of shoreline. Most extant genera probably originated in the Tertiary, and there is evidence that some species have separated within the last 2 million years. Except for a few pelagic and deep-water species, the penaeid populations of the Indo-West Pacific, Eastern Pacific and Western Atlantic Regions are discrete. Within each region, two or more subregions have been defined, supported by cluster analysis of the Indo-West Pacific Region. Reasons for these divisions are discussed, particularly the barriers to penaeid movements from the Indo-Malaysian to the Tropical Australia Subregion. These barriers appear to be primarily deep water and unfavourable currents along the steep northern and southwestern coasts of New Guinea. Possible causes of Southern Hemisphere endemism in the Penaeidae are discussed. Because of the absence of fossil records extinction hypotheses cannot be tested, but the apparent absence of amphitropicality in the family and the limited geographic range of many species suggest that evolution within the Southern Hemisphere can account for the endemism of penaeid species there. The unique genera *Macropetasma* and *Artemesia* could be relicts of Miocene, relatively cool-water populations, but there is no firm evidence to support this. ☐ *Penaeidae , zoogeography, tropics, endemism, temperature, ocean currents, ocean deeps, Indo-West Pacific, Eastern Pacific, Western Atlantic*

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The Penaeidae is the best-known family within the Penaeoidea in the decapod Suborder Dendrobranchiata. The 171 known species within 17 genera (Table 1) are predominantly tropical and subtropical. About 80% of these species usually live in depths of <100 m; the remainder normally either inhabit deeper water (10 *Metapenaeopsis* spp.; most *Parapenaeus* spp.; all *Penaeopsis* spp.) or are pelagic (all *Funchalia* spp. and *Pelagopenaeus*). Many of the deep-water and pelagic species appear to be widely distributed, *Funchalia villosa* and *F. woodwardi*, for example, having been recorded in the Pacific, Atlantic and Indian Oceans. Records of the distribution of these pelagic species are, however, too sparse to discuss their zoogeography, so most of this review is devoted to the better-known shallow-water Penaeidae.

All shallow-water Penaeidae so far investigated have a planktonic larval phase of about 2–3 weeks, followed by inshore or estuarine early juvenile stages (Dall *et al.*, 1990). Most species prefer soft substrates, ranging from mud to sand, but a number — probably around 25% — (mainly *Metapenaeopsis* spp., *Heteropenaeus*, *Trachypenaeopsis*), prefer harder substrates such as coral rubble. There is one commensal with corals (*Metapenaeopsis commensalis*).

Both biotic and physical factors are likely to influence the distribution of marine crustaceans such as the Penaeidae. They are subject to considerable predation pressure (Dall *et al.*, 1990); in some areas the population density is high and interactions between species may be important. However, while no studies on the effects of such biotic factors have been made, the physical environment appears to be more important in determining the distribution of penaeids. Their life histories suggest there are four principal factors that may affect their distribution :

1. Temperature. As tropical stenotherms they are restricted to the warmer waters of the world. In lower latitudes, cold winds from continental land masses may cool inshore waters or cause upwelling and thus be barriers to distribution; cold currents from higher latitudes may have a similar effect. Conversely, warm currents may extend the latitudinal range of penaeids along a coast.

2. Oceanic larval advection. The pelagic larval

TABLE 1. Genera of the Penaeidae, the world-wide number of species within each genus and the number of species within each region. IWP, Indo-West Pacific; EP, Eastern Pacific; WA, Western Atlantic; EA, Eastern Atlantic; (P), pelagic, probably present in all oceans; number in parentheses, additional species also present in Western Atlantic.

Genus	Total species	Species per region			
		IWP	EP	WA	EA
Artemesia	1	–	–	1	–
Atypopenaeus	4	4	–	–	–
Funchalia	4	(P)	(P)	(P)	(P)
Heteropenaeus	1	1	–	–	–
Macropetasma	1	1	–	–	–
Metapenaeopsis	49	40	3	5	1
Metapenaeus	25	25	–	–	–
Parapenaeopsis	16	14	1	–	1
Parapenaeus	12	10	–	1	1
Pelagopenaeus	1	–	1	–	–
Penaeopsis	6	5	–	1	(1)
Penaeus	28	14	5	8	1(1)
Protrachypene	1	–	1	–	–
Tanypenaeus	1	–	–	1	–
Trachypenaeopsis	2	1	–	1	–
Trachypenaeus	17	10	5	2	–
Xiphopenaeus	2	–	1	1	–
Total	171	125*	16*	21*	4*

* not including *Funchalia* and *Pelagopenaeus*.

life makes most species susceptible to the influences of currents flowing in unfavourable directions, such as towards higher latitudes or from inshore to offshore.

3. Oceanic deeps. These constitute a barrier for shallow-water species, especially when they are very close inshore or in conjunction with unfavourable currents.

4. Coastal geography. Since most species live in shallow waters, particularly in the early juvenile stages, lack of suitable inshore habitats may constitute a barrier. Thus a desert coastline with high inshore salinities, or a very rocky coast with deep water inshore, may restrict the distribution of some species.

DISTRIBUTION IN TIME

The Penaeidae are an ancient group. Penaeoidea have been recorded in the Mesozoic, back to the Upper Triassic, mostly in various shales of central Europe, the eastern Mediterranean and Great Britain (Glaessner, 1969), with a few in North America (Herrick and Schram, 1978). Crustacea are, however, poor candidates for fossilisation, particularly the thinner-shelled groups such as penaeids (Bishop, 1986). Further, the normal environmental conditions of penaeids are not conducive to fossilisation because of the presence of numerous scavengers and bioturbation of the sediment by a large burrowing infauna (Plotnick, 1986). Hence the penaeid fossil record is very sparse. The Penaeidae first appear in Jurassic deposits and become more common in the Cretaceous. Most of these earlier Penaeidae became extinct at the end of Mesozoic, *Penaeus* being the only surviving genus. Apart from one *Penaeus* record from India in the early Tertiary, no fossils of more recent origin have been found, so geological evidence of the origins of the remaining 16 extant genera is completely lacking.

The times at which existing genera diverged have therefore to be estimated by other means. Limited data are available from biochemical genetics, supported by palaeogeography (Dall *et al.*, 1990). These authors calculate from genetical data that *Metapenaeus* could have separated from *Penaeus* between the early Tertiary and the Pliocene. The genetic distances within these genera indicate that some present species evolved between the Miocene and the Pleistocene. While estimates of divergence times from biochemical genetics are imprecise, they can be improved by palaeographical evidence. Separation of the Atlantic Ocean from the rest of the Tethys Sea by closure of the Mediterranean during the Miocene isolated its warm shallow-water fauna (Por, 1986). Although North and South America were not joined during the Oligocene–Miocene and the present Isthmus of Panama was not established until the Pliocene (White, 1986), physical conditions in the proto-Caribbean and Pacific had begun to differ by the late Miocene (Keigwin, 1978). Fossil evidence also suggests that the two faunas were distinct at this time (Ekman, 1953). Penaeid genera common to the Atlantic, Pacific and Indian Oceans today were presumably in existence before the separation of the Atlantic. These are the shallow-water genera *Penaeus*, *Metapenaeopsis*, *Parapenaeopsis*, *Trachypenaeus* and *Trachypenaeopsis*. On this basis, excluding the deep-water or pelagic genera (*Funchalia*, *Parapenaeus*, *Pelagopenaeus* and *Penaeopsis*), seven may have originated since the Miocene. Thus the combined evidence suggests that the

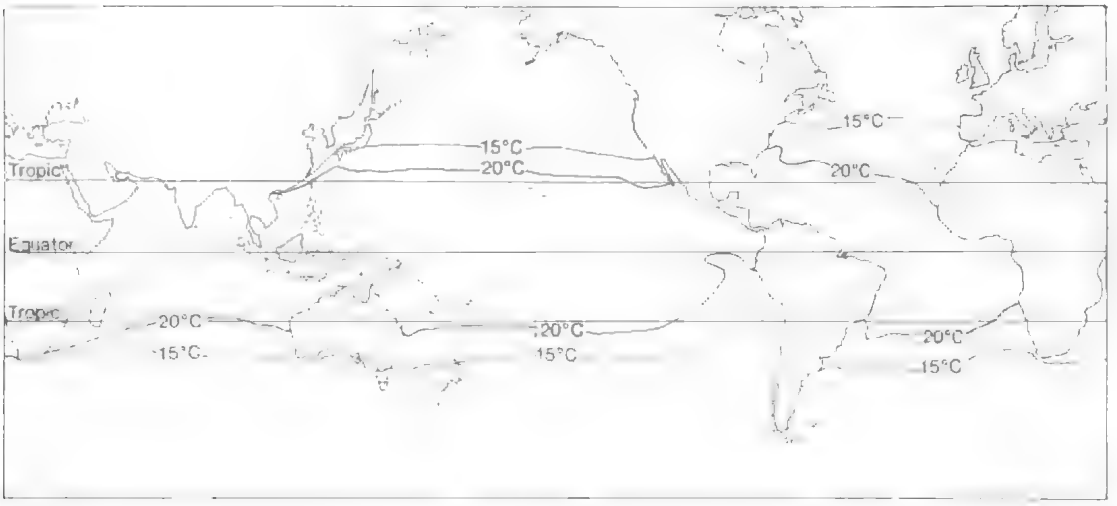

FIG. 1. Location of 20°C and 15°C minimum winter sea surface temperature isotherms. They correspond with the isocrymal lines (coldest 30 consecutive days of the year) of the Northern and Southern hemispheres.

majority of present penaeid genera may have originated in the last 10–15 million years.

WORLD DISTRIBUTION

The Penaeidae are distributed throughout the world, but their latitudinal distribution is limited by temperature. Most species occur within the isotherms of 20°C minimum winter temperatures (Fig. 1). Between the 20°C and 15°C isotherms the number of species falls to about 30% of those within the 20°C isotherms. In these cooler zones, the growth and activity of most species are minimal in winter, but temperatures in summer are usually high enough for them to achieve growth rates comparable with those of fully tropical species. Only two species are abundant outside the 15°C isotherms: *Penaeus chinensis* in the Pohai and Yellow Seas and *Artemesia longinaris* in southeastern South America. Both have adapted to survive temperatures down to about 6°C, but, in addition, the adaptive behaviour of *P. chinensis* enables it to cope with the hostile winter environment. It migrates into the deeper waters of the Yellow Sea at the onset of winter and returns to exploit the rapid warming of the shallow waters in spring and subsequent summer temperatures of 25°C (Chang Cheng, 1984). A similar strategy is not available to *Artemesia*, as water temperatures in the southern half of its range do not rise above 20°C, but winter temperatures are not as severe as in the Pohai Sea (Angelescu and Boschi, 1959).

REGIONAL DISTRIBUTION

Ekman (1953) divided the shallow, warm-water marine faunas of the world into Indo-West Pacific, Eastern Pacific, Western and Eastern Atlantic Regions. This classification has been followed by Briggs (1974) for various taxonomic groups and by Abele (1982) for Crustacea. The Atlantic is clearly separated from other oceans by the Americas and the Afro-European landmasses, and the deep ocean separates the Atlantic into eastern and western faunas. The Eastern Pacific fauna is separated from the rest of the Pacific by a wide expanse of deep ocean, containing very few islands. Eastward movement of warm-water planktonic larvae is discouraged by the westward Equatorial Current, which is fed in this region by cold currents flowing towards the equator along the west coasts of North and South America. Only species with an exceptionally long larval life can be transported eastward from the Central Pacific (Scheltema, 1988). The fauna of the Eastern Pacific Region does, however, have some affinities with that of the central Western Atlantic, as the final separation of the two oceans did not occur until the early Pliocene and twin species are common (Ekman, 1953). Examples in the Penaeidae are *Trachypenaeus pacificus* : *T. similis* and *Xiphopenaeus riveti* : *X. kroyeri*

(western and eastern coasts of the Isthmus, respectively).

The remainder of the Pacific is not separated zoogeographically from the Indian Ocean and the two are usually grouped together as the Indo-West Pacific Region. Springer (1982), from a study of shallow-water fishes, proposed that the Pacific Plate should be designated as a separate region, but this is not supported by the distribution of corals and echinoderms (Ekman, 1953), nor by that of the Penaeidae (Dall *et al.*, 1990).

Although the number of penaeid genera in the Indo-West Pacific and Western Atlantic Regions is similar, there is great disparity in the number of species (Table 1). Excluding *Funchalia* and *Pelagopenaeus*, the Indo-West Pacific contains 73% of known species, compared with 12% in the Western Atlantic. Abele (1982) found similar ratios for other decapod Crustacea (Portunidae, Parthenopidae, *Sesarma* spp. and *Alpheus* spp.). He also notes that the ratios are due to the large number of congeneric species in the Indo-West Pacific, rather than an increase in the number of genera. Abele (1982) discusses several hypotheses to account for this. On a small scale there is a positive correlation between habitat complexity (e.g. sandy beaches, sand-mud beaches, mangroves, corals and rocky intertidal) and crustacean species diversity, but this does not appear to be valid for zoogeographical regions. It would also be unlikely to apply to the Penaeidae, which occupy similar habitats both latitudinally and longitudinally. Briggs (1974) suggests that the number of species of tropical shallow-water marine animals is directly correlated with continental shelf area. Abele (1982) obtained a positive linear correlation between continental shelf area and numbers of warm shallow-water marine crustacean species in the four major regions. He also obtained a positive log-log relationship between Caribbean island perimeter and number of marine shrimp species (penaeids and carids). Shoreline length may be the reason for the higher penaeid species diversity in the Indo-West Pacific, as the factors that tend to isolate penaeid populations are related to the shoreline.

Subregions

There are considerable differences in geographical ranges in the Penaeidae, both between and within genera (Dall *et al.*, 1990). Thus the most ancient genus *Penaeus* is, with few exceptions, the most widely ranging. *Penaeus japonicus, P. latisulcatus, P. marginatus, P. monodon* and *P. semisulcatus* have been recorded in most of the warmer waters of the Indo-West Pacific. In the Eastern Pacific, all *Penaeus* species are found in both subregions, while in the Western Atlantic they extend through at least two subregions, with *P. notialis* occurring on both sides of the Atlantic. The deeper water genera *Parapenaeus* and *Penaeopsis* are also wide ranging, but generally less so than *Penaeus*. The remaining genera are mostly more restricted in range, about 50% of all penaeid species being endemic to one or two subregions. (Some species within these genera with an apparent wide range, such as *Metapenaeopsis mogiensis* and *M. hilarula,* may be complexes of species, A. Crosnier, pers. comm.).

Dall *et al.* (1990) define and discuss penaeid subregions within each of the regions. They used the distribution of species with a restricted range, particularly those endemic to a particular area, to define subregions. Geography and temperature data were also taken into account. These were confirmed for the present study for the Indo-West Pacific Region by cluster analysis of the presence-absence data of all species on the basis of euclidean distance with group average hierarchical clustering (Fig. 2). Bray-Curtis group average hierarchical clustering gave similar groupings, but with Southeast and Southwest Australia separated from the other subregions and closest to the West Pacific. (Reliable cluster analyses for the subregions defined by Dall *et al.* (1990) for the Eastern Pacific and Atlantic were

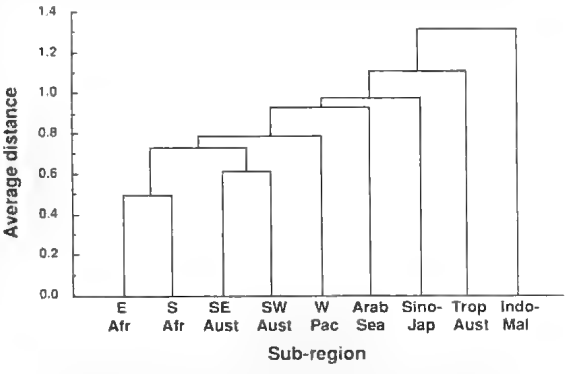

FIG. 2. Group average hierarchical cluster analysis of Indo-West Pacific Subregions, using presence-absence data of all species, based on euclidean distance. Abbreviations: E Afr, East African; S Afr, South African; SE Aust, Southeast Australian; SW Aust, Southwest Australian; W Pac, West Pacific Oceania; Arab Sea, Arabian Sea; Sino-Jap, Sino-Japanese; Trop Aust, Tropical Australian; Indo-Mal., Indo-Malaysian.

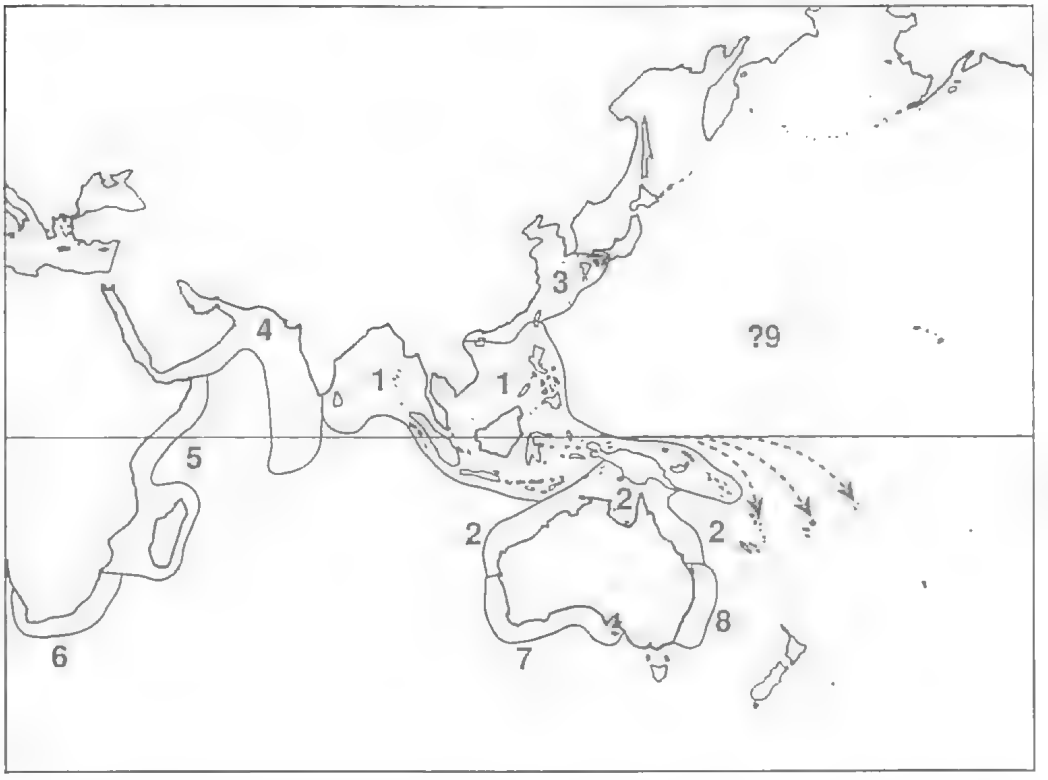

FIG. 3. Subregions of the Indo-West Pacific Region. 1, Indo-Malaysian; 2, Tropical Australian; 3, Sino-Japanese; 4, Arabian Sea; 5, East African; 6, South African; 7, Southwest Australian; 8, Southeast Australian; ?9, Pacific Oceania; arrows, extension of Malay-Indonesian Subregion (see text for definitions).

not feasible because of the paucity of species in these areas).

INDO–WEST PACIFIC SUBREGIONS
(Fig. 3; Table 2).

1. *Indo-Malaysian.* This is defined in the south by the oceanic deeps off southern Indonesia, which extend into the Timor Sea, to the west of the Aru Islands, coming close inshore at the neck of West Irian. To the east, oceanic deeps and westward equatorial currents form a major barrier, while to the north falling temperatures close off the subregion. There is no obvious barrier in the west, the shallow coastal waters of the Straits of Malacca running without apparent interruption through the Bay of Bengal. However, there is a steady decrease in the diversity of penaeid species diversity from Malaysia to the Bay of Bengal (Dall *et al.*, 1990), as in other faunas (Ekman, 1953). Dall *et al.* (1990) suggest that unfavourable currents, plus the strongly monsoonal climate of India may restrict the westward movement of penaeids. The southern tip of India has been arbitrarily selected as the western boundary of this subregion.

2. *Tropical Australia.* This subregion extends from the southern coast of New Guinea to the 20°C winter isotherm on the east and west coasts of Australia. The significance of the barriers to the northeast and northwest are discussed in detail below.

3. *Sino-Japanese.* The southern boundary is defined by the 20°C isotherm. The diverse fauna of the Gulf of Tonkin and southern China decreases sharply to the north due to cold continental influences, but the Equatorial Current runs offshore to the northeast, raising the minimum winter temperature in the Sea of Japan and giving this area a large and distinctive penaeid fauna.

4. *Arabian Sea.* This subregion, from the southern tip of India to Cape Guardafui at the entrance

TABLE 2. Total number of species and endemic species in the subregions of the Indo-West Pacific Region. Indo-Mal, Indo-Malaysian; Trop Aust, Tropical Australia; Sino-Jap, Sino-Japanese; Arab Sea, Arabian Sea; E Afr, East Africa; S Afr, South Africa; SW Aust, Southwest Australia; SE Aust, Southeast Australia; O, Pacific Oceania.

	Indo-Mal.	Trop Aust	Sino-Jap	Arab Sea	E Afr	S Afr	SW Aust	SE Aust	O
Total species	84	52	36	38	20	15	8	8	20
Endemic species	22	13	10	3	2	1	2	3	2

to the Red Sea, has extensive arid coastlines; the hypersaline inshore waters and cold continental winter winds probably act as barriers to less adaptable species. The Red Sea is usually treated as a separate subregion because of its distinctive fauna (Ekman, 1953; Briggs, 1974), but the penaeid fauna differs only in having fewer species and has therefore been included in this subregion.

5. *East African Coast.* This extends from Cape Guardafui to Durban. Briggs (1974) regards the coast from the Gulf of Iran to the southern tip of Africa as one subregion, but the East African Coast appears to support a more diverse and possibly larger penaeid population than the Arabian Sea (Crosnier, 1965). Neither the northern nor the southern boundaries are well defined, but there is a drop in species diversity around the latitude of southern Madagascar.

6. *South Africa.* This subregion could be included in East Africa, except for the appearance of *Macropetasma africanus* at Durban. This species becomes common on the south coast, west of Algoa Bay, where other penaeid species are rare, and is unique in that it extends northward along the west coast of southern Africa from Cape Town to Swakopmund, in the cool waters derived from the Benguela Current.

7. *Southwestern Australia.* The 20°C isotherm defines the northern boundary of this subregion, which extends across southern Australia because of the influence of the warm southerly Leeuwin Current. There are two endemic species: *Metapenaeopsis fusca* and *M. lindae.*

8. *Southeastern Australia.* The 20° C and 15° C isotherms define the northern and southern limits of this subregion. It has three endemic species, *Penaeus plebejus, Metapenaeus bennettae* and *M. macleayi*; the first two appear to be siblings of widely distributed species.

9. *Pacific Oceania.* The penaeid population of this subregion appears to be mostly an extension of the Indo-Malaysian fauna; it is therefore doubtful that it is a valid penaeid subregion (indicated by the query in Fig. 3). Two endemic species have been identified: *Metapenaeopsis tarawensis* and *M. commensalis*, both inhabitants of coral reefs and the latter a commensal with corals. *M. commensalis* may be more widespread than the published record indicates.

Western Atlantic Subregions

(Fig. 4; Table 3.)

The Western Atlantic Region extends from Martha's Vineyard, 43°N to Puerto de Rawson, 43°S. The subregions are:

1. *Caribbean.* This extends from southeast Florida through the Caribbean to Sao Luis, Brazil, but stops at the entrance of the Gulf of Mexico. Geographically this area is analogous to the Indo-Malaysian Subregion of the Pacific. It has the greatest penaeid species diversity (16) within the Atlantic Ocean, with three endemic species (*Tanypenaeus caribeus, Trachypenaeopsis mobilispinis, Trachypenaeus similis*). The eastern boundary is defined by a marked drop in species diversity, which appears to be due to a strong westward current, plus a monsoonal climate in eastern Brazil.

2. *Eastern Brazil* (Sao Luis to Cabo Frio). The southern boundary at Cabo Frio is caused by a cooler-water coastal northerly current meeting the warm southerly Brazilian Current and diverting it offshore. There are no endemic species, but the species composition is appreciably different from that of the Caribbean.

3. *Gulf of Mexico.* This is defined by *Penaeus aztecus, P. duorarum* and *P. setiferus*, which are plentiful in the Gulf of Mexico, but do not extend eastwards into the adjacent Caribbean Sub-

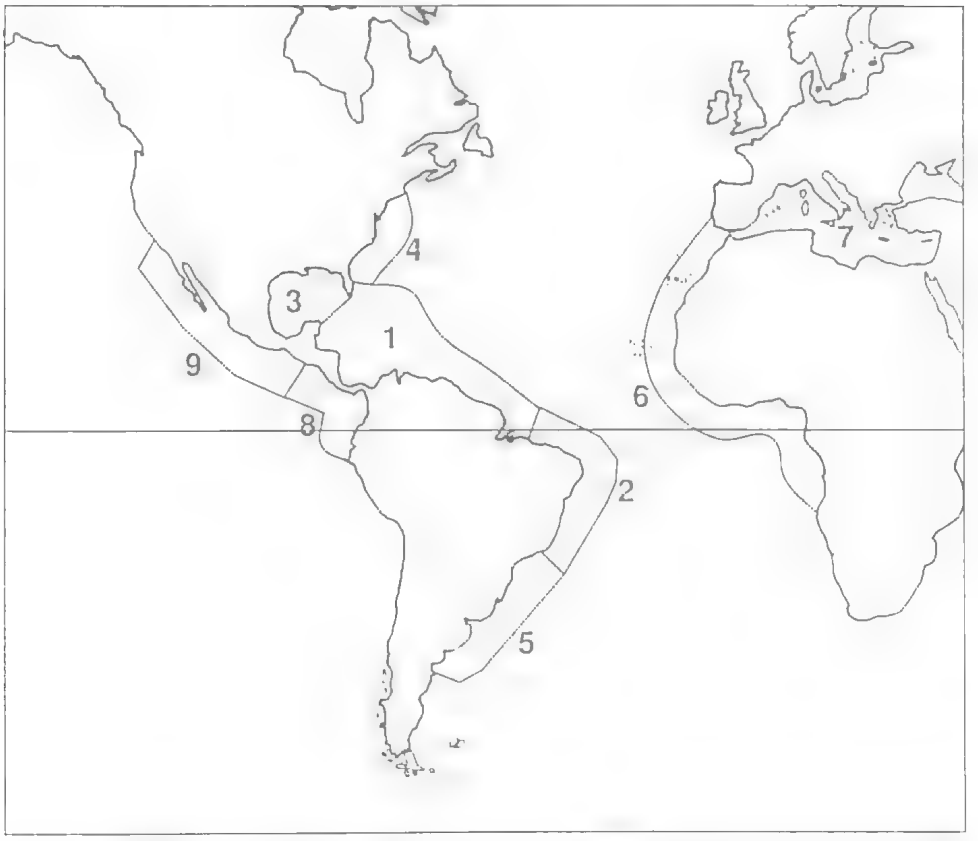

FIG. 4. Subregions of the Western Atlantic, Eastern Atlantic and Eastern Pacific Regions. Western Atlantic: 1, Caribbean; 2, Eastern Brazil; 3, Gulf of Mexico; 4, Eastern USA (Carolinean); 5, Southeast South America. Eastern Atlantic: 6, Eastern Atlantic; 7, Mediterranean Sea. Eastern Pacific: 8, Panamanian; 9, Mexican (see text for definitions).

region. Also, low winter temperatures in the north of the Gulf reduce the species diversity (7 compared with 16 in the Caribbean).

4. *Eastern USA* (Carolinean) (Martha's Vineyard to southeast Florida). Cape Hatteras is the northern limit of abundant penaeid distribution, but there have been records of *Penaeus aztecus* as far north as Martha's Vineyard.

5. *Southeast South America* (Cabo Frio, Brazil to Puerto de Rawson, Argentina). *Penaeus paulensis* and *Artemesia longinaris* are endemic species in this well-defined cooler-water subregion.

Eastern Atlantic Subregion

These are shown in Fig.4 and detailed in Table 3.The Eastern Atlantic Region includes the Mediterranean Sea, usually considered to be a separate zoogeographical area. Also, at least five Indo-West Pacific species (*Penaeus japonicus*, *P. semisulcatus*, *Metapenaeus monoceros, M. stebbingi, Trachypenaeus curvirostris*) have migrated through the Suez Canal from the Red Sea (Lessepsian migration)(Gab-Alla *et al.*, 1990). In the Atlantic, penaeids normally extend as far north as about 40°N in Portugal, but in the south the cold Benguela Current limits the distribution to about 16°S in Angola. Thus the subregions are:

6. *Eastern Atlantic* (Lisbon, Portugal, 40°N, to Porto Alexandre, Angola, 16° S).

7. *Mediterranean Sea.* This subregion has only two of the six species found in the Eastern Atlantic, apart from the Lessepsian migrants.

Eastern Pacific Subregions

(Fig. 4; Table 3)

Eastern Pacific Region is reduced latitudinally

TABLE 3. Total number of species and endemic species in the Subregions of the Western Atlantic, Eastern Atlantic and Eastern Pacific Regions. Car, Caribbean; E Br, Eastern Brazil; GoM, Gulf of Mexico; E US, Eastern USA (Carolinean); S SA, Southeastern South America; E A, Eastern Atlantic; Med, Mediterranean Sea; Mex, Mexican; Pan, Panamanian.

	Car	E Br	GoM	E US	S SA	E A	Med	Pan	Mex
Total species	16	11	7	7	4	6	2	12	11
Endemic species	3	0	0	0	2	2	0	5	3

in both the north and south by cold currents flowing towards the Equator; the continental shelf is mostly narrow and there are relatively few islands to support populations of penaeids. Penaeid species composition changes markedly in the El Salvador region, which has been selected as a boundary between the northern and southern subregions. These are:

8. *Panamanian.* El Salvador to Punta Aguja, Peru. The unique *Protrachypene*, *Parapenaeopsis balli* (the only *Parapenaeopsis* in the Western Hemisphere) and three species of *Trachypenaeus* define this subregion.

9. *Mexican.* San Francisco Bay (northern limit of penaeid records) to El Salvador. Here the penaeid diversity is lower than in the Panamanian, with three endemic species *Metapenaeopsis beebei*, *M. kishinouyei* and *Trachypenaeus brevisuturae*.

BARRIERS TO DISTRIBUTION

Low temperature, and thus latitude, has been mentioned as one of the principal boundaries to penaeid distribution. These boundaries may be modified by warm currents flowing away from the equator, or cold currents flowing towards it. Thus the northern boundaries of the South African, Southwest and Southeast Australian Subregions, and the southern boundary of the Sino-Japanese Subregion, defined by the 20°C winter isotherm, extend outside the tropics (Fig. 1). In all cases there is a marked drop in species diversity outside the 20°C isotherm, with the appearance of one or more endemic species (Table 2). There are comparable subregions in the Western Atlantic. In the Eastern Atlantic and Eastern Pacific, where cold currents flow towards the equator, the north–south extent of the subregions is considerably less than in the Western Atlantic (Fig. 4) and Indo-West Pacific (Fig. 3). In addition, the paucity of species in the Eastern Atlantic does not permit the definition of a possible subregion between Portugal and Cape Verde on the western tip of Africa.

Within the tropics, the less obvious limits — ocean currents, oceanic deeps, coastal geography — appear to be responsible for most of the discontinuities in penaeid distribution. Examples of how these barriers may operate in the Tropical Australian Subregion, which is apparently contiguous with the Indo-Malaysian Subregion, are described below and shown in Fig. 5. (The well-known water barriers of Wallacia that separate the terrestrial floras and faunas of Australia–New Guinea from southeast Asia are due to long-term movements of the tectonic plate [see review by Whitmore, 1981]; these barriers are not relevant to marine faunas with dispersive planktonic larvae.)

The Indo-Malaysian penaeid fauna attenuates along the north coast of New Guinea from west to east. In eastern New Guinea and the Solomon Islands, only 17 species, four of which are deep-sea, are common to the Indo-Malaysian Subregion, which contains 84 species. All of the 13 shallow-water species are wide-ranging: *Penaeus* spp. (7); *Metapenaeus* spp.(4); *Heteropenaeus longimanus* ; *Trachypenaeopsis richtersii*. The New Guinea Trench runs close to the steep mid-northern coast of New Guinea, resulting in a very narrow continental shelf (Fig. 5). Further to the east the end of the New Britain Trench comes close inshore. Except for the Sepik River, there are no major rivers along this coast and no extensive marine estuaries. The westward Equatorial Current flows close inshore for most of the year (Lindström *et al.*, 1987). The southeast coast of New Guinea is similar geographically to the north coast, but has an alongshore eastward current (CSIRO, unpubl.), which thus discourages westward migration of Penaeidae (such as *Metapenaeus affinis* and *M. anchistus*) from the eastern end of New Guinea towards Tropical Australia.

To the northwest of Australia the Java Trench extends along southern Indonesia, reaching in the east, past the island of Sumba; deep water

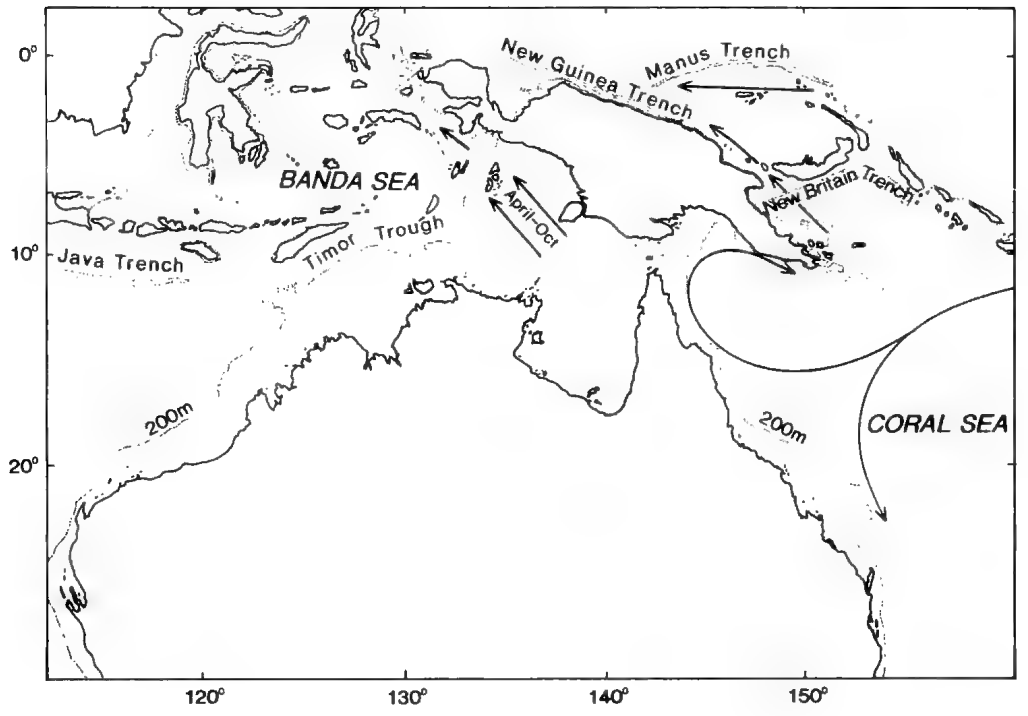

FIG. 5. Geographical features that tend to isolate the Tropical Australian Subregion from the Indo-Malaysian Subregion. Arrows indicate surface currents.

continues to the northeast as the Timor Trough, followed by the Aru Basin, coming close inshore at the neck of New Guinea (Fig. 5). Here the continental shelf is very narrow, which probably inhibits coast-wise migration of penaeids. The Banda and Aru Basins are fed by southerly inflows from the Pacific Ocean and this water then flows southwesterly through the Timor Trench (Van Aken *et al.*, 1988; Postma and Mook, 1988). Thus the net flow of intermediate and deep water is towards the Indian Ocean. In addition, from April to October the southeasterly trade winds produce a northwesterly shallow-water flow, which appears to cause upwelling and lower water temperatures (Fleminger, 1986). This cold water then joins the surface currents flowing to the northwest, carrying any penaeid larvae away from the extensive shallow coastal regions of southern New Guinea and Australia.

The effects of the November–March monsoon season on shallow-water movements do not appear to have been documented for this area. In open waters the winds tend to be northwesterly during this period, which would enhance migration of penaeid larvae towards Australia. But the discontinuity between Indo-Malaysian and Tropical Australia faunas indicates that some kind of year-round barrier exists. (This barrier is, of course, only partial; there are many species common to both subregions.) The western end of New Guinea is geographically complex, with mountain ranges from 1000 m to over 4000 m high. Winds originating in the north-northwest and flowing across the neck of New Guinea (about 1000 m high), could be deflected by the much higher mountains in the east, resulting in local southerly, or even south-westerly winds crossing the south coast. Such winds would probably be cool and could produce further inshore upwelling. Also, Fleminger (1986) reviewed evidence that, during the Pleistocene glaciation, water temperatures in this region may have been unusually cool for the tropics, due to cool prevailing winds and upwelling; this cooling may have acted as a barrier to tropical stenotherms. Dall *et al.* (1990) point out that during the maximum of the Quaternary Glacial Period the lowered sea levels would have resulted in most of the sea between New Guinea and Australia becoming dry land. There would have been a steep coast, with virtually no shallow

TABLE 4. Apparent sibling species in the temperate subregions of southern continents and their more widely-ranging, usually tropical 'parent' species.

Subregion	Sibling species	Parent species
Southeast South America	*Penaeus paulensis*	?*P. aztecus*
South Africa	*Metapenaeopsis scotti*	?*M. philippii*
Southwest Australia	*M. insona*	*M. quinquedentata*
	M. fusca	*M. barbata*
	M. lindae	?*M. acclivis*
Southeast Australia	*M. insona*	*M. quinquedentata*
	Metapenaeus bennettae	*M. moyebi*
	Penaeus plebejus	*P. latisulcatus*

water, connecting the two subregions, probably eliminating the migration of shallow-water penaeids during the last glacial period. The migration of penaeids towards the northern Australian area from Indonesia, appears, therefore, to have been restricted since the Pleistocene.

The northwest coast of Australia, which is arid, with hypersaline inshore waters also appears to be unfavourable to penaeid colonisation. Of 36 shallow-water species in northern and northeastern Australia, only 18 also occur in the far northwest of the continent.

SOUTHERN HEMISPHERE ENDEMISM IN THE PENAEIDAE

The Northern Hemisphere has only one subregion (the Sino-Japanese) outside the tropics that includes endemic species, whereas in the Southern Hemisphere the South African, Southwest Australian, Southeast Australian and the Southeast South American Subregions all contain endemic species (Tables 2, 3). Some of these are closely similar to more widely distributed tropical species and may be sibling species (Table 4), but there are also three Southern Hemisphere species which do not have any close affinities. *Metapenaeus macleayi* in Southeast Australia is distinctive within its genus, but *Macropetasma africanus* in South Africa and *Artemesia longinaris* in Southeast South America are more exceptional. Both are monospecific genera, they are quite different from one another and from other genera, both fossil and present, of the Penaeidae. *Artemesia* and, to a lesser extent *Macropetasma* inhabit waters cooler than is usual for the Penaeidae.

Newman and Foster (1987) conclude that endemism of barnacles in the Southern Hemisphere is due to:

1. Extinction processes (either at low latitudes or of Northern Hemisphere counterparts).
2. Evolution of long indigenous taxa.

Unlike barnacles, the Penaeidae have a very poor fossil record and extinction hypotheses cannot be tested, but as a predominantly tropical group, extinction within the tropics is probably less likely than in more widely ranging groups. There do not appear to be any clear examples of amphitropicality in the Penaeidae. There are Northern or Southern Hemisphere endemic species, but no matching pairs of species, nor are there any species with a clear break in distribution in the tropics. *P. aztecus* and *P. paulensis* in the Western Atlantic may be amphitropical species, but the affinities of the Western Atlantic complex of grooved *Penaeus* species needs further research. *Metapenaeopsis acclivis* and *M. lindae* in the Indo-West Pacific may also be amphitropical, but there are significant morphological differences between them and this genus also needs further research. The most usual situation is for a northern or southern endemic to have a closely related species, which could be a parent, in the adjacent tropics (Table 4).

The uniqueness of *Macropetasma* and *Artemesia* suggests that they could be relict species from much more widely ranging populations. Dall *et al.* (1990) examine the possibility that they could be Gondwana relicts, but find this hypothesis to be untenable. *Macropetasma* is unique among the Penaeidae in possessing photophores; *Artemesia* superficially resembles some deep-water Penaeoidea. Thus they could be relicts of a deep-water, possibly amphitropical group, but there are no similar extant deep-sea genera to support this hypothesis and wholesale extinction would need to be invoked. Alternatively, they could have been once widely distributed in the cooler conditions of the Miocene and subsequently became extinct in the tropics (Valen-

tine, 1984). Although plausible, in the absence of any supporting data, this hypothesis must also remain pure conjecture.

However, the rate of evolution of penaeid genera, discussed earlier, suggests that *Macro-petasma* and *Artemesia* could well have evolved since the middle Tertiary. (*Protrachypene* is another unique monospecific genus in the Eastern Pacific Region that has presumably evolved since the Caribbean fauna became separated from that of the Eastern Pacific in the Miocene). *Metapenaeus macleayi* and the sibling species listed in Table 4 could have evolved more recently. Dall *et al.* (1990) estimate from genetical evidence that the sibling species *Metapenaeus bennettae* and *Penaeus plebejus* in Southeast Australia probably evolved in the last two million years. This area was separated geographically from the rest of the Indo-West Pacific during the last glacial epoch. The cold-adapted *Penaeus chinensis* must also have evolved from the closely similar and geologically ancient *P. merguiensis - indicus* group since the last glacial epoch; the shallow Pohai and Yellow Seas would have been isolated lakes or dry land at the height of this period. Dall *et al.* (1990) point out that the lowering of sea-levels in the late Tertiary and Quaternary would have produced extensive land bridges in former shallow seas; these would have acted as effective barriers and thus enhanced penaeid speciation during this period. The limited range of many species of Penaeidae also point to such processes in the evolution of the family.

In summary, in the absence of fossil evidence to the contrary, evolution of pre-existing taxa can account for the endemism of the Southern Hemisphere Penaeidae.

Macropetasma and *Artemesia* may be exceptions and are relicts of widely-ranging Miocene populations, but further evidence is needed to support this hypothesis.

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ORIGINS OF SOUTHERN HEMISPHERE ENDEMISM, ESPECIALLY AMONG MARINE CRUSTACEA

WILLIAM A. NEWMAN

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There are a number of hypotheses to explain the high endemism above the species level in the Southern Hemisphere. The separation of Gondwana from Laurasia by the Tethys Sea during the Mesozoic and the subsequent breakup of Gondwanaland evidently explains some of the terrestrial and freshwater endemism. Marine endemism is not generally explained by these events however, but rather by late Mesozoic and Tertiary reliction of tropical forms, or by extinction of Northern Hemisphere portions of amphitropical forms. Amphitropicality apparently can result from dispersal across the tropics. But it can also result from exclusion of an earlier biota from the tropics. Exclusion often involves replacement by more advanced forms concomitant, at least since the Miocene, with warming and compression of the tropics.

Areas of endemism in both hemispheres can be relatively localised and this provides insights into why a number of older taxa have survived there while going extinct elsewhere. Areas of marine endemism in the Southern Hemisphere are presently more evident in southeast Australia, Tasmania, and New Zealand than in other Southern Hemisphere outposts apparently because much of it has developed in the western Pacific since the breakup of Tethys. □ *Crustacea, Southern Hemisphere, endemism, Gondwana, Tethys, reliction, amphitropical, dispersal, vicariance.*

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There is a high degree of endemism in the Southern Hemisphere, compared to the Northern Hemisphere, on land and fresh water and, perhaps surprisingly, in the sea. While it is generally most pronounced in Australia, New Zealand, and islands of the southwest Pacific, some extends around the Southern Hemisphere, to oceanic islands as well as the southern parts of South America, Africa, and India.

No one hypothesis explains the situation, although the breakup of Gondwanaland, after its long separation from Laurasia by the Tethys Sea, is apparently the best explanation for many of the freshwater and terrestrial forms that are sufficiently old and lack propagules capable of long range, trans-oceanic dispersal. The marine situation is less clear since most forms have, or had, significant dispersal capabilities, and many of the Southern Hemisphere endemics are too young to have been part of Gondwanaland (McDowall, 1978; Newman, 1979). There is a growing consensus that much of the apparent endemism in the Southern Hemisphere is due to the extinction of Northern Hemisphere counterparts rather than its having evolved there (Eskov and Golovatch, 1986; Newman and Foster, 1987).

In the present paper some crustacean distributions will be examined for endemism, especially in the Southern Hemisphere. But before getting to them, a brief discussion of climatic change, the development of tropical provincialism following the breakup of Gondwanaland and Tethys, and examples and hypotheses relevant to the matter of Southern Hemisphere endemism, are in order. Some marine molluscs will be used as examples because, by and large, they have a good fossil record.

BREAKUP OF GONDWANA AND TETHYS, AND CONCOMITANT CLIMATIC CHANGE

It has long been recognised that the marine climate was equably warm up to relatively high latitudes in the late Mesozoic (Murray, 1896), but it is only in recent years that we have come to accept that in the Late Cretaceous, approximately 100 million years before present (MYBP), the super continent Pangea was being split into Laurasia and Gondwana with the tropical sea known as Tethys in between (Kennett, 1982; Windley, 1984). A Tethyan marine biota was not only distributed throughout this sea, it included a

large pantropical element that circled the globe via oceanic currents and islands of Panthalassa, the present day Pacific (Hamilton, 1956).

With continued continental drift, the Atlantic began to open up and Gondwana to fragment. Both processes led to the breakup of Tethys and, hence, to the tropical provincialism we see today (Ekman, 1953). Significant events in the breakup of Tethys included the northward movement of Africa and its contact with Eurasia in the lower Miocene, about 18 MYBP, followed by the closure at Suez, virtually cutting off the tropical Indian Ocean from the Atlantic in the Middle Miocene, 12–14 MYBP (Kennett, 1982; Windley, 1984). Likewise, New Guinea-Australia moved north to contact southeast Asia, thereby diverting the North Equatorial Current from the Indian Ocean to the North Pacific in the Upper Miocene, approximately 7 MYBP (Kennett *et al.*, 1985). The Panamic closure separated the widening Atlantic from the tropical East Pacific in the Pliocene, (3.1- 3.6 MYBP [Rosenblatt and Waples, 1986]).

With the onset of the Tertiary, the shallow equable seas of the Mesozoic began to cool and retreat, at low as well as high latitudes (Shackleton, 1984). This trend persisted throughout the Paleogene, about 25–30 MYBP. Then a new trend, correlating with the establishment of circum-Antarctic deep-water circulation near the end of the Oligocene, set in (Van Andel, 1979). It is noteworthy that, while the poles continued to cool, the tropical regime reversed and began to warm to the extent that for the most part, the tropics are warmer today than they were at the close of the Cretaceous (Shackleton, 1984). As will be discussed below, this warming phenomenon was used by Valentine (1984), in lieu of the biological factors of Théel (1911), in explaining amphitropical reliction via exclusion from the deep tropics. These two hypotheses stand in marked contrast to migration across the tropics, especially during the Pleistocene, utilised by Darwin (1859) in explaining amphitropicality.

HYPOTHESES RELEVANT TO SOUTHERN HEMISPHERE ENDEMISM

Five hypotheses relevant to the origin of Southern Hemisphere endemism are identified here, and they can be divided between three categories. The categorization is not intended to be precise; rather, it is simply to give us areas on which to focus. The hypotheses, listed here, are elaborated upon below:

I) Centres of origin.

II) Dispersal to the Southern Hemisphere followed by extinction in Northern Hemisphere (includes one form of amphitropicality, cf. III B, 2 below).

III) Vicariance: Relict and relic biotas[1]; involves two processes (A and B), the second and sometimes the first being followed by extinction in the Northern Hemisphere:

A. The breakup of Pangea and/or Gondwana.

B. The breakup of Tethys. Relicts and relics of Tethys fall into two principal types:

1. Those resulting from division of the tropics.
2. Those resulting from exclusion from the tropics (second form of amphitropicality).

I. Centre of Origin

The taxon in question evolved in the region where it is found (Fig. 1). Species can certainly be found at or near their place of origin, but the probability decreases with the age of the species, and that higher taxa evolved where they are presently found decreases dramatically with taxonomic rank. Therefore, a centre of origin hypothesis is risky unless one has an excellent stratigraphic record. The hypothesis can often be falsified by the discovery of a single fossil or living population in the 'wrong place' and therefore it should be proffered with caution. In order to emphasise this point, we can now look at some examples of molluscs that would have fallen under a centre of origin hypothesis had it not been for the fossil record.

Scattered populations of a gastropod, *Neritopsis radula*, range across the Indo-West Pacific, from islands off East Africa to the Hawaiian Archipelago. One might conclude that the present distribution includes the centre of origin. However, approximately 100 fossil species of *Neritopsis* are recognised and *N. radula*, the sole surviving member of the Neritopsidae, is itself known from the Eocene of the Paris Basin (Batten, 1984). Hence, it is a Tethyan relic at the familial as well as generic and specific levels; a relic par excellence.

Another Tethyan relic is the bivalve mollusc *Neotrigonia* represented by six extant species found around Australia. They are the last surviv-

[1] A 'relict' population is one separated from a parent population by some vicariant event while a 'relic' population consists of the last survivors of an ancient radiation

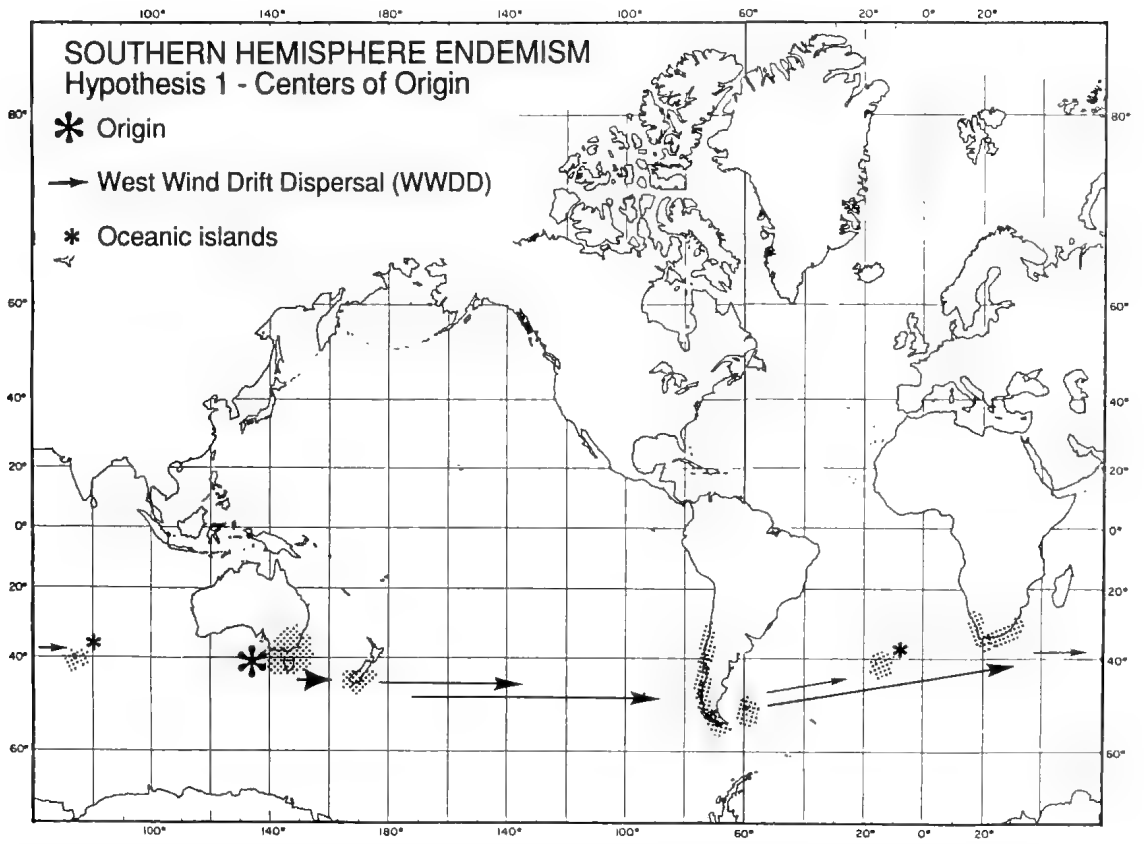


FIG. 1. Hypothesis 1 — Centre of Origin. The origin of a hypothetical Southern Hemisphere endemic has been arbitrarily placed in southeastern Australia (large asterisk). The taxon may subsequently disperse, in this example, via the West Wind Drift (Fell, 1962) to South America, South Africa etc. (arrows) and involving oceanic island stepping stones (small asterisks; stippling indicates presence of established populations). Presence on oceanic islands is evidence for post-Gondwanan long-range dispersal (Newman, 1979a). The hypothesis can be falsified by fossil evidence from other continental sediments of Gondwanan age, or by appropriate evidence from the Northern Hemisphere.

ing members of the Trigoniidae which became largely extinct at the end of the Cretaceous in the North Pacific and Europe (Stanley, 1984). Unlike the Indo-West Pacific Tethyan relic *Neritopsis*, *Neotrigonia* is a Southern Hemisphere endemic as well, by virtue of having gone extinct in the Northern Hemisphere. The commonness of this latter pattern is illustrated by the following three relic gastropod molluscs of the Southern Hemisphere: 1) *Campanile symbolicum* of southwestern Australia, the sole surviving species of the Campanilidae which flourished in Tethys of the early Tertiary (Houbrick, 1984a); 2) *Diastoma melanoides* of southern Australia, the sole surviving species of the Diastomatidae which flourished in the Eocene of Tethys (Houbrick, 1984b); and 3) *Gourmya gourmyi* of New Caledonia, New Hebrides, the Chesterfield Islands and Marion Reef of the Coral Sea, the sole surviving species of the genus which traces back to the Eocene of the Paris Basin, Tethys to the end of the Miocene, and the Pliocene of Japan (Houbrick, 1984c).

As well as emphasising the value of the fossil record, the foregoing gives some perspective. While the course of extinction that led to these Southern Hemisphere endemics apparently had its roots in the Paleogene, it apparently did not become highly restrictive until the Neogene. These examples demonstrate how readily a centre of origin hypothesis can be falsified (Eskov and Golovatch, 1986; Newman and Foster, 1987) and the issue will be taken up shortly concerning some crustaceans.

II. Dispersal to Southern Hemisphere

Immigration from the Northern to the Southern Hemisphere, with subsequent extinction in

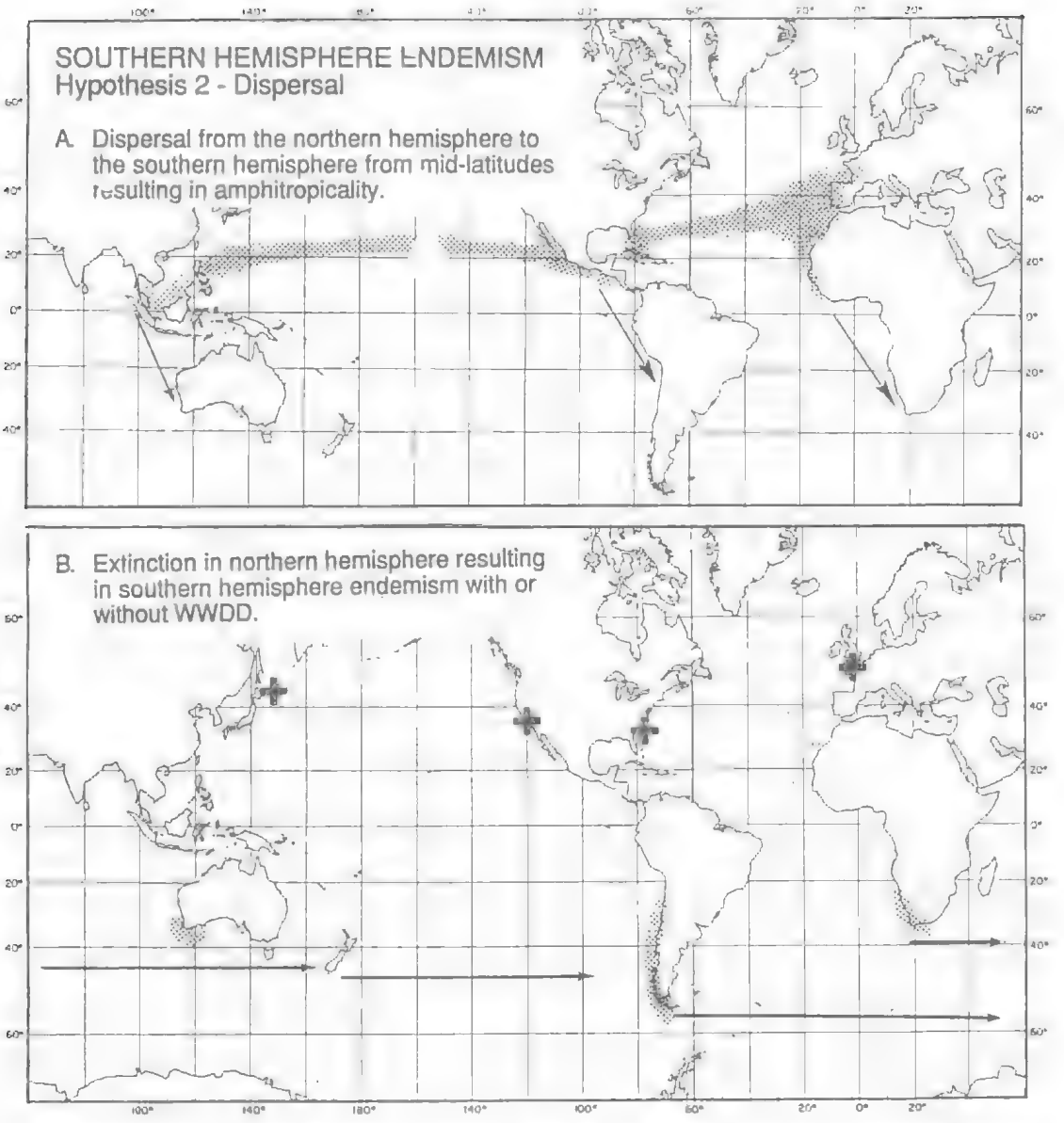


FIG. 2. Hypothesis 2 — Dispersal and Extinction. A, Dispersal of Northern Hemisphere propagules (stippled, planktonic or benthic) to the Southern Hemisphere, whereby the taxa involved become amphitropical (Darwin, 1859). Immigration is most easily accomplished where eastern boundary conditions exist (arrows), beneath a shallow thermocline and or during cool periods such as the Pleistocene. B, If Northern Hemisphere amphitropical counterparts of Southern Hemisphere immigrants go extinct (crosses), the immigrants become Southern Hemisphere endemics. Southern Hemisphere immigrants may disperse via the West Wind Drift (arrows). Evidence needed to falsify hypothesis 1 generally supports this and subsequent hypotheses to one extent or another.

the Northern Hemisphere, is a simple and straight forward way of explaining both amphitropicality and Southern Hemisphere endemics (Fig. 2). Migration during the Pleistocene, across the tropics, could have been by way of high mountains for terrestrial forms, or across equatorial waters for marine forms (Darwin, 1859). It is of course also possible to go beneath tropical waters, especially under eastern boundary conditions where the thermocline is

shallow and upwelling prevails (Ekman, 1953; Hubbs, 1952).

The foregoing molluscan examples are not envisaged as falling into this category because they were apparently originally wide-ranging Tethyan populations. Thus it may be difficult to decide between this hypothesis and that covered under III B, 2 below, since both are two-step processes involving extinction in the Northern Hemisphere. But because the present hypothesis involves migration across the tropics rather than exclusion from the tropics in establishing amphitropicality, the distinction is important to our understanding.

III. Vicariance

Such hypotheses for the origin of Southern Hemisphere endemism involve two processes: A) the breakup of Pangea and Gondwanaland (Fig. 3); and, B) events included in and following the breakup of Tethys (Figs 4 and 5).

A., Relicts and relics of Gondwanaland seem to be limited primarily to terrestrial and freshwater biotas and examples among the freshwater crustaceans will be taken up shortly.

B., Tethyan relicts and relics (III B), on the other hand, include many marine forms. Two patterns can be identified and they need to be distinguished here. The first (Fig. 4) involves retreat of warm seas of the world, since the Cretaceous, towards centres of distribution. The second (Fig. 5) involves splitting of primarily Paleogene tropical populations into amphitropical populations beginning in the Oligocene (Kennett, 1982; Newman and Foster, 1987). Both processes may ultimately lead to hemispheric endemism, commonly in the Southern Hemisphere and especially in the southwestern Pacific.

AMPHITROPICAL DISTRIBUTIONS

Examples of molluscs given above (the bivalve, *Neotrigonia*, and the gastropods *Campanile*, *Diastoma*, and *Gourmya*) are all Southern Hemisphere endemics with Tethyan histories. They appear to be a subset of the Indo-West Pacific relict pattern, a pattern also observed at bathyal depths by Ameziane-Cominardi *et al.* (1987) and Richer de Forges (1990). However, these authors do not explore the possibility of their once having been amphitropical. Therefore we can move on to amphitropical distributions and their role in the origin of Southern Hemisphere endemism.

There are numerous examples of amphitropical distributions (cf. Good, 1964; Van Balgooy, 1971; Randall, 1981; Springer, 1982; Briggs, 1987a, b), and hypotheses regarding their origins were recently reviewed (Newman and Foster, 1987). There were two noted above deemed relevant to marine forms – that of Darwin (1859) involving migrations across the tropics especially during the Pleistocene (Fig. 4) and that of Théel (1911) and Valentine (1984) involving the splitting of a previously tropical biota into northern and southern populations (Fig. 5).

Darwin's (1859) hypothesis involved cooling during the glacial epochs whereby some terrestrial and marine plants and animals could have ranged across the tropics to become amphitropical when the cool period abated. This hypothesis has been popular with marine biogeographers studying fish and plankton, especially those working with plankton or under eastern boundary conditions such as along the shores of the tropical East Pacific, or elsewhere where upwelling occurs (Hubbs, 1952; Brinton, 1962; Van der Spoel and Heyman, 1983; Fleminger, 1986). Although the tropical East Pacific can become relatively warm during El Niño period (Ramage, 1986) it is generally cool compared to the same latitudes in the West Pacific due to prevailing currents from the north and especially the south, and the upwelling associated with them. From deep-sea drilling results, it is known that the belt was much narrower during the last glacial period, 18 000 YBP, than it is today (Moore *et al.*, 1980). Amphitropicality, established by migration across the tropics at such times, would then be followed by extinction, generally in the Northern Hemisphere whereby the Southern Hemisphere populations become endemic at some level.

On the other hand, Théel's (1911) hypothesis for the origin of amphitropicality concerns splitting of tropical populations; that is, peripheral reliction through replacement in the deep tropics by more advanced forms via competition. Valentine (1984) looks as well to the physiological impact of warming of the deep tropics noted above under climatic change[2]. These two hypotheses seem to go hand in hand since many modern forms (structurally more advanced and often known to be geologically younger) commonly dominate the deep tropics while some

[2] Briggs (1987a) dismisses Shackleton's earlier temperature curves for high and low latitudes over the past 100 MY because of a difficulty with the method due to water tied up in glacial ice. However, he does not cite Shackleton (1984) where the difficulty is apparently taken into account.

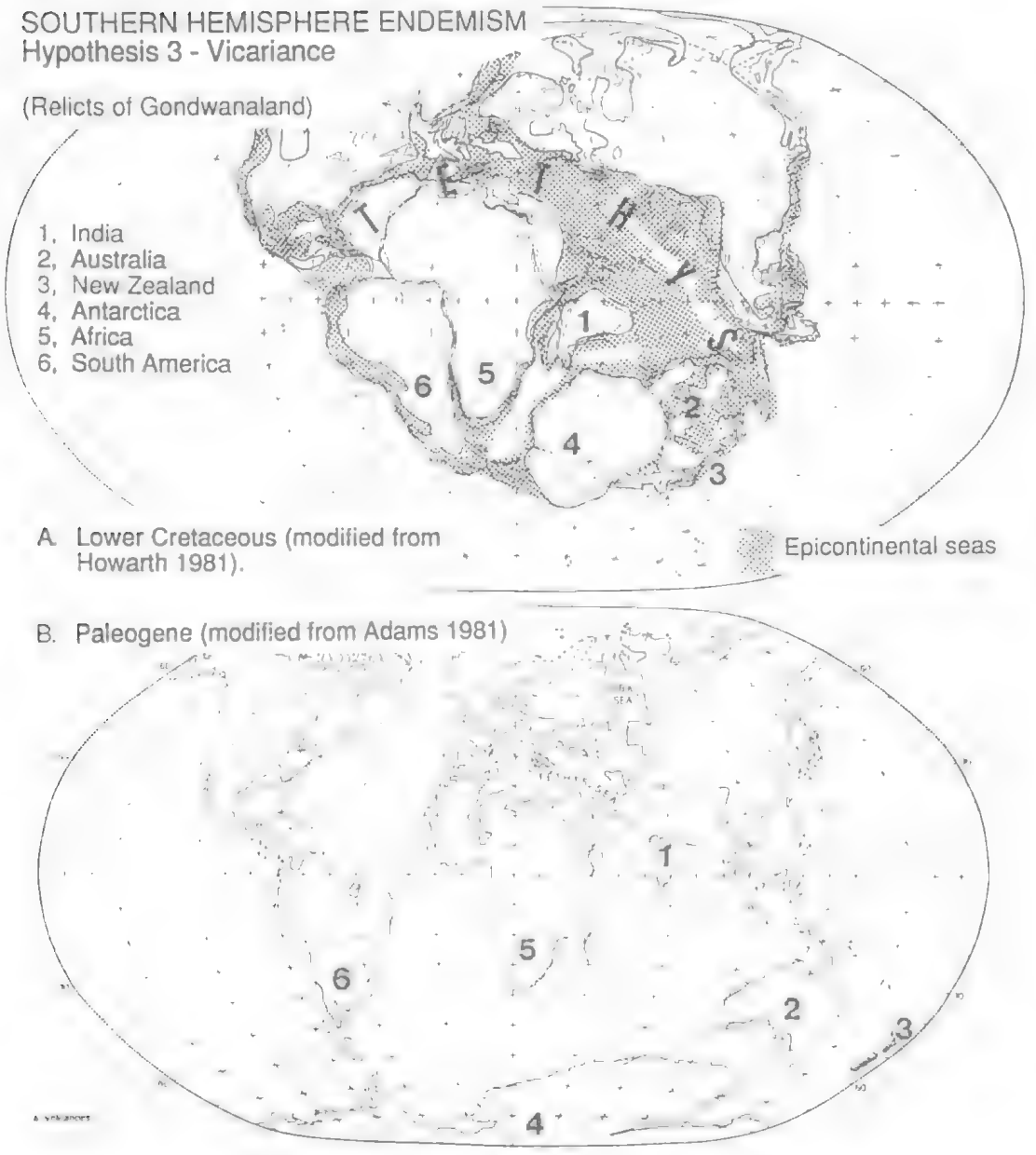


FIG. 3. Hypothesis 3 — Vicariance. Relicts and relics of Gondwanaland. A, Contiguity of the six Gondwanan continents and the extent of Tethyan and adjacent epicontinental seas (stippled, modified from Howarth, 1981). Tethys virtually separated Gondwana from Laurasia during the Mesozoic, up through the Cretaceous. During this time, tropical Tethys formed a significant barrier to dispersal between Laurasia and Gondwana for terrestrial and freshwater forms. On the other hand, cosmopolitan elements of the Tethyan marine biota girdled the earth during this period via currents and oceanic islands of Panthalassa (Hamilton, 1956). B, Positions of the six Gondwanan continents by the Palaeogene (modified from Adams, 1981). The breakup of Gondwanaland apparently explains the distribution of many terrestrial and freshwater forms endemic to the Southern Hemisphere.

older forms tend to be peripheral (Théel, 1911; Newman and Foster, 1987). Since temperature is presently apparently the primary factor in maintaining the separation between some amphitropical populations, the current hypothesis is classified as vicariant. It is instructive in this regard that in situations such as the East Pacific some populations have not been split completely (Ekman, 1953) and these have been termed 'paramphitropical'[3].

THE METHOD USED FOR ANALYSIS

The material covered in the foregoing introduction includes areas of historical geology and climatology as well as considerations of present day distributions of some marine molluscs having a significant fossil record. These data were integrated to varying degrees into hypotheses involving the origins of Southern Hemisphere endemism. This background can now be applied to the distribution patterns seen in a number of freshwater as well as marine crustaceans. The question is often whether the present distribution of a given taxon is more or less as far as the radiation reached, or is the result of reliction of a once much wider pattern. Obviously to have been wide ranging, a taxon would have to have radiated at one time or another, but the place of origin and the direction of the radiation are usually lost in antiquity. Likewise, the course of a subsequent reliction is also often difficult if not impossible to document.

Distributions are plotted where appropriate, and inspected for the patterns noted above, plus other patterns such as amphi-Atlantic distributions in forms having no obvious means of dispersal. Patchiness, disjunctions, and latitudinal and longitudinal ranges are also very important, but above all there are the areas of endemism. Indications from the fossil record are also plotted if appropriate. The patterns observed can then be checked against available hypotheses for Southern Hemisphere endemism; namely, origin, migration, Gondwanan and Tethyan relictions, and amphitropicality.

[3] The term 'paramphitropical' identifies transtropical species, genera or even higher taxa that show preferences (relative abundance, condition, habitat, emergence etc.) for the higher portions of their latitudinal range (Newman and Foster, 1987; see *Lyreidus tridentatus* in the West Pacific, and *Cancer* in the East Pacific and elsewhere at bathyal depths in the tropics, in the following discussion).

What little evidence there is, such as one important fossil locality for the brachyuran *Cancer* (Miocene of Java) or two extant localities for the cephalocarid, *Hutchinsoniella*, is often taken at face value. This is certainly open to criticism but the conclusions drawn are generally falsifiable. Therefore, as long as the pitfalls are known, there is no harm in this approach since it appears to be capable of generating testable hypotheses having predictive value (Ball, 1975).

CRUSTACEAN DISTRIBUTIONS

Abele's (1982) discussion of the biogeography of Crustacea includes some aspects of paleogeography, patterns of species richness, migrations and morphology. It also provides distributional information on the Cephalocarida, Branchiopoda, Remipedia, Ostracoda, Mystacocarida, Branchiura, Copepoda, Cirripedia, Leptostraca, Hoplocarida, Syncarida, Pancarida (Thermosbaenacea), Mysidacea, Cumacea, Spelaeogriphacea, Amphipoda, Isopoda, Tanaidacea, Euphausiacea, Amphionidacea and some Decapoda. This informative material includes biological aspects such as habitat requirements, life history and dispersal capabilities. However, the single distributional chart given includes the Cephalocarida, Anaspidacea, Spelaeogriphacea, Mystacocarida, and Pancarida (Thermosbaenacea); a montage that is not particularly informative. Schram (1986) adds to this background, in good part by plotting the distributions of a number of crustaceans on separate charts, some of which illustrate amphitropicality and/or Southern Hemisphere endemism. While both authors note the classical freshwater relicts of Gondwanaland such as Anaspidacea, Parastacidae and Phreatoicidea, neither notes Southern Hemisphere endemism among marine forms.

Relicts and Relics of Gondwanaland

Since Gondwanan distributions should be relatively easy to identify, and since this paper is primarily involved with the origin of Southern Hemisphere endemism among the crustaceans, some apparent Gondwanan examples will be given first. Abele (1982) reviews the situation for the branchiopods and argues that while passive dispersal may occur, the distribution of genera may be more the result of continental movements. Likewise, Tasch (1987) concludes that the distribution of conchostracans between the five Gondwanan continents was by nonmarine dispersal in the Palaeozoic or Mesozoic.

These findings do not preclude long-range dispersal, but if it is taking place now it is not particularly evident. Much the same has been said for other fresh water groups; the branchiuran genus *Dolops*, the phreatoicid isopods, parastacoid astacurans, and anaspidaceans. According to Abele (1982), *Dolops* only occurs in Tasmania, South America and Africa, but it is parasitic on freshwater fishes whose distribution is beyond the scope of the present paper. Perhaps the strongest cases can be made for the phreatoicids (Fig. 6A; India, Australia, Tasmania, New Zealand, and Africa but, curiously, not South America), and parastacids (Australia and New Guinea, Tasmania, New Zealand, South America, and Madagascar but not Africa or India) (Williams, 1974; Holthuis, 1986).

The anaspidaceans apparently descended from the Palaeocaridacea, marine forms present in both the Northern and Southern Hemispheres from the Carboniferous into the Permian (Europe, North and South America; Schram, 1986). Since fossil anaspidaceans are known from only the Triassic and Cretaceous of Australia, we are left with the conclusion that they evolved there from marine forms. Gondwana was essentially intact at the time and therefore the occurrence of stygocaridids in New Zealand and South America as well as mainland Australia is consistent with the hypothesis.

It should be noted however that a rather well developed nauplius is passed through in the egg of *Anaspides tasmaniae*. This suggests that anaspidaceans are not too far removed from having had larval stages and, judging from other malacostracans, this indicates that they are not too far removed from the marine environment. Therefore it is possible that the occurrence of stygocaridids in New Zealand and South America in addition to Australia is a West Wind Drift distribution (WWDD; Fell, 1962) rather than a Gondwanaland pattern per se. This is much the explanation given by Feldmann (1986) for the eaglid decapods of fresh waters in southwestern South America, except that their apparent ancestor went extinct in New Zealand.

Relicts and Relics of Tethys

Molluscs were used above in exploring Indo-West Pacific and southwestern Pacific endemism because their past distributions were well documented in the fossil record. All were Tethyan, yet some remained tropical while others, probably having had an amphitropical component, became Southern Hemisphere endemics.

There are numerous crustaceans that appear to be Tethyan relicts, but the degree to which these are documented by the fossil record varies considerably. There are some caridean shrimp, including *Procaris*, that are relicts without a fossil record. They are particularly interesting because they are largely restricted to refugial hypogeal and anchialine habitats and then frequently on oceanic islands of the Atlantic and Indo-West Pacific Oceans (Abele, 1982; Maciolek, 1983; Hart *et al.*, 1985; Schram, 1986).

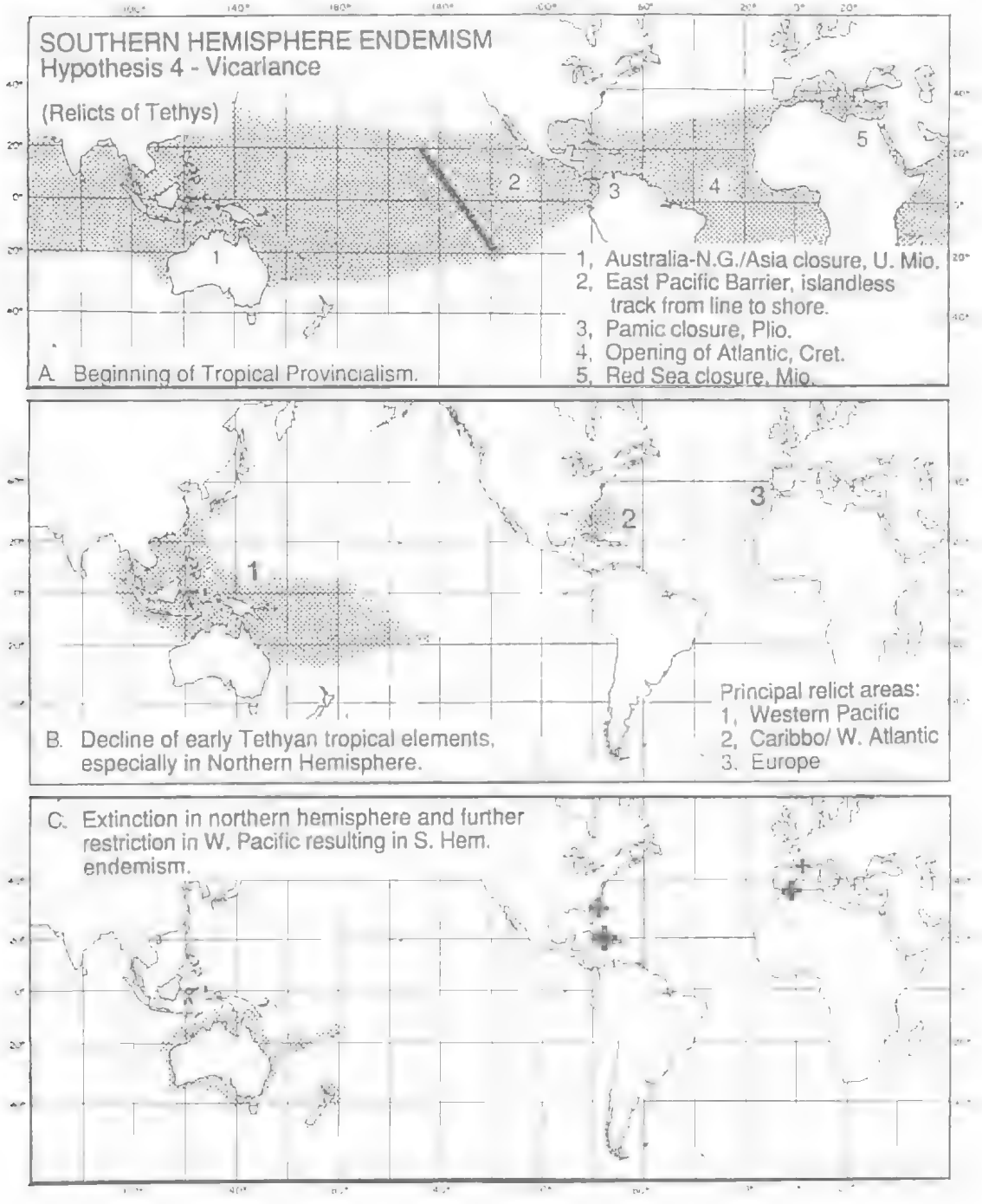
The refugial aspect of oceanic island cannot be over emphasized, as illustrated by the distribution of some other shallow water crustaceans of the Indo-Pacific and Atlantic; namely, the acorn barnacle *Tesseropora* (Oligocene–Recent) and a species each of the burrowing barnacles (Devonian–Recent) *Lithoglyptes* and *Kochlorine* (Newman and Ross, 1977; Schram, 1986, respectively). Both of these groups are more restricted in the Atlantic than in the Indo-Pacific, so that if reliction continues one might expect the Atlantic populations would go extinct first.

While there is evidently a greater diversity of Tethyan relicts in the Indo-Pacific than in the

FIG. 4. Hypothesis 3 – Vicariance. Deep tropical relicts and relics of Tethys. A, Contemporary configuration of the world with the approximate limits of the tropical belt (stippled). Barriers to transtropical dispersal that led to the tropical provincialism we see today include: 1, the Australian-New Guinea/southeast Asia closure (Upper Miocene) blocking equatorial currents between the Pacific and Indian Oceans; 2, the East Pacific Barrier or islandless track between the black bar and the Americas; 3, the Panamic closure (Pliocene) separating the East Pacific from the western Atlantic; 4, the opening up of the Atlantic (cf. Fig. 3); and 5, the closure at Suez (Miocene). B, Decline of Tethyan tropical elements concomitant with cooling at the poles and warming of the tropics, the latter beginning in the Miocene (Shackleton 1984) and the former culminating in the Pleistocene. Principal relict areas initially in: 1, the West Pacific; and 2, the western Atlantic, but also 3, in Europe/North Africa apparently due to the Gulf Stream. Deep tropical elements belonging to this class had pretty much gone extinct in the East Pacific and most of the eastern Atlantic, concomitant with the loss of coral reefs there (Newell, 1971). C, Further decline of this class of relicts included extinction in the Northern Hemisphere and much of the Southern Hemisphere, except for the Indo-West Pacific. Of particular interest here are West Pacific endemics, some of which became restricted to the southwest Pacific as Southern Hemisphere endemics.

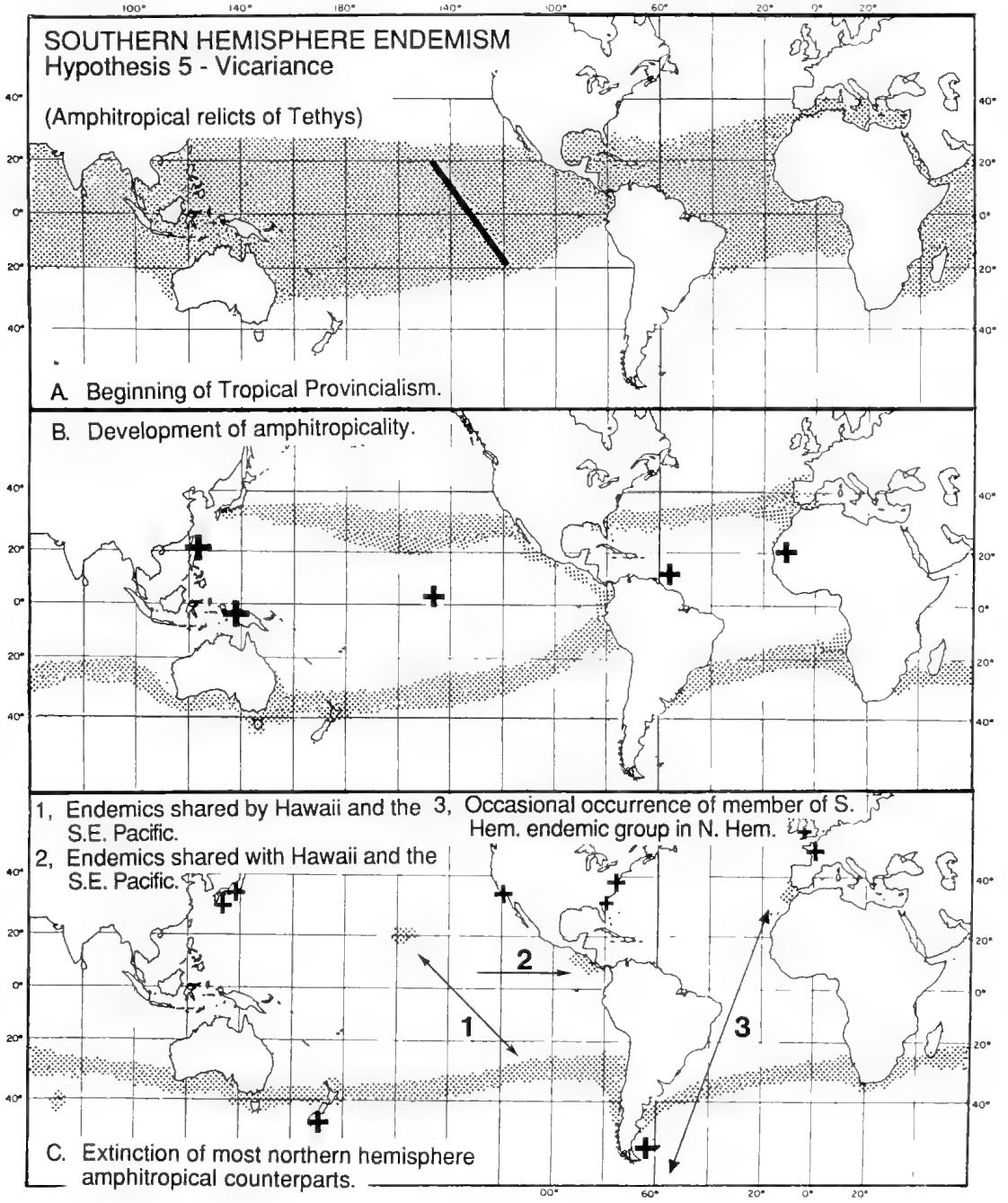
Atlantic, there are some crustaceans at high taxonomic levels that appear to be endemic to the Atlantic; namely, the Remipedia, Pancarida, Spelaeogriphacea, and the Mystacocarida (Pancarida and Mystacocarida have recently been discovered elsewhere). These groups are restricted to anchialine, brackish, fresh water hypogeal and marine interstitial refugial habitats. Unlike the shrimp just noted, they are blind and otherwise have life histories that are apparently not conducive to long range dispersal.

The Remipedia, known from the Caribbean and allied to *Tesnusocaris* from the middle Car-



boniferous of Texas at the time of Abele (1982), have since turned up on the opposite side of the Atlantic, in the Canary Is. (Schram, 1986, fig. 3-3; Schram *et al.*, 1986, fig. 39). Likewise, the Spelaeogriphacea, known to Abele (1982) from freshwater caves in South Africa and from the Carboniferous of Canada, is now known from freshwater in Brazil (Pires, 1987).

Pancarids were originally known from various ground waters around the Mediterranean, from anchialine situations in the Caribbean, and freshwater caves in Texas (Stock, 1976; Bowman and Iliffe, 1988; Schram, 1986, fig. 17-3). Abele (1982) summarises the explanation of Stock (1976) and previous authors for their amphi-Atlantic distribution; namely, Tethyan relicts 'stranded' in-



land by changes in sea level during the Miocene. But it needs to be recalled that the Miocene Atlantic was nearly as wide as it is today, and Schram (1986), citing Macquire (1965), favors plate tectonics as the vicariant event. Pancarids co-occur with remipeds in the Caribbean (Bowman and Iliffe, 1988) which also occur on both sides of the Atlantic, as does one species of cephalocarid to be taken up below and the spelaeogriphaceans in fresh water noted above. Thus, the situation for pancarids is evidently better explained by a tendency to enter ground water and other refugia prior to the opening up of the Atlantic. This is especially attractive when it is noted the Texas locality appears to be on the edge of the Mississippian embayment. That there are in some respects more primitive representatives in marine situations in the Caribbean (Bowman and Iliffe, 1988) is not at all incompatible with an explanation involving reliction via opening up of the Atlantic unless one is willing to speculate that *Monodella* evolved independently on both sides.

Schram (1986) noted that the distribution of pancarids was congruent with that of certain copepods, mysids, isopods and amphipods on both sides of the Atlantic, and that representatives of the last were also known from the Indo-Pacific. Thus, these groups are Tethyan relicts. That the Pancarida was also in fact once a wide-ranging Tethyan group was recently revealed by the discovery of a species in Cambodia (Cals and Boutin, 1985).

Until recently, the mystacocarids presented an enigma to me because they could be envisaged either as having extended their range from the Atlantic around the southern ends of South America and South Africa into the southern extremes of the Indo-Pacific since the Cretaceous (Schram, 1986, fig. 34-4, a centre of origin hypothesis), or as having been excluded from oceans of the world except the Atlantic. The latter, a reliction hypothesis, received some support in the fact that their present distribution is apparently amphitropical and that the South American species belong to a distinct genus, *Ctenocheilocaris* (Hessler, 1988), whereby diversity is greater in the Southern than in the Northern Hemisphere. Since this symposium, R.R. Hessler has shown me a photomicrograph of a mystacocarid B. Knott sent from Western Australia. Therefore, as far as the present pattern is concerned, the centre of origin hypothesis has been falsified. But, as with virtually all groups, we still do not know when or where the mystacocarids originated.

Amphitropical Distributions

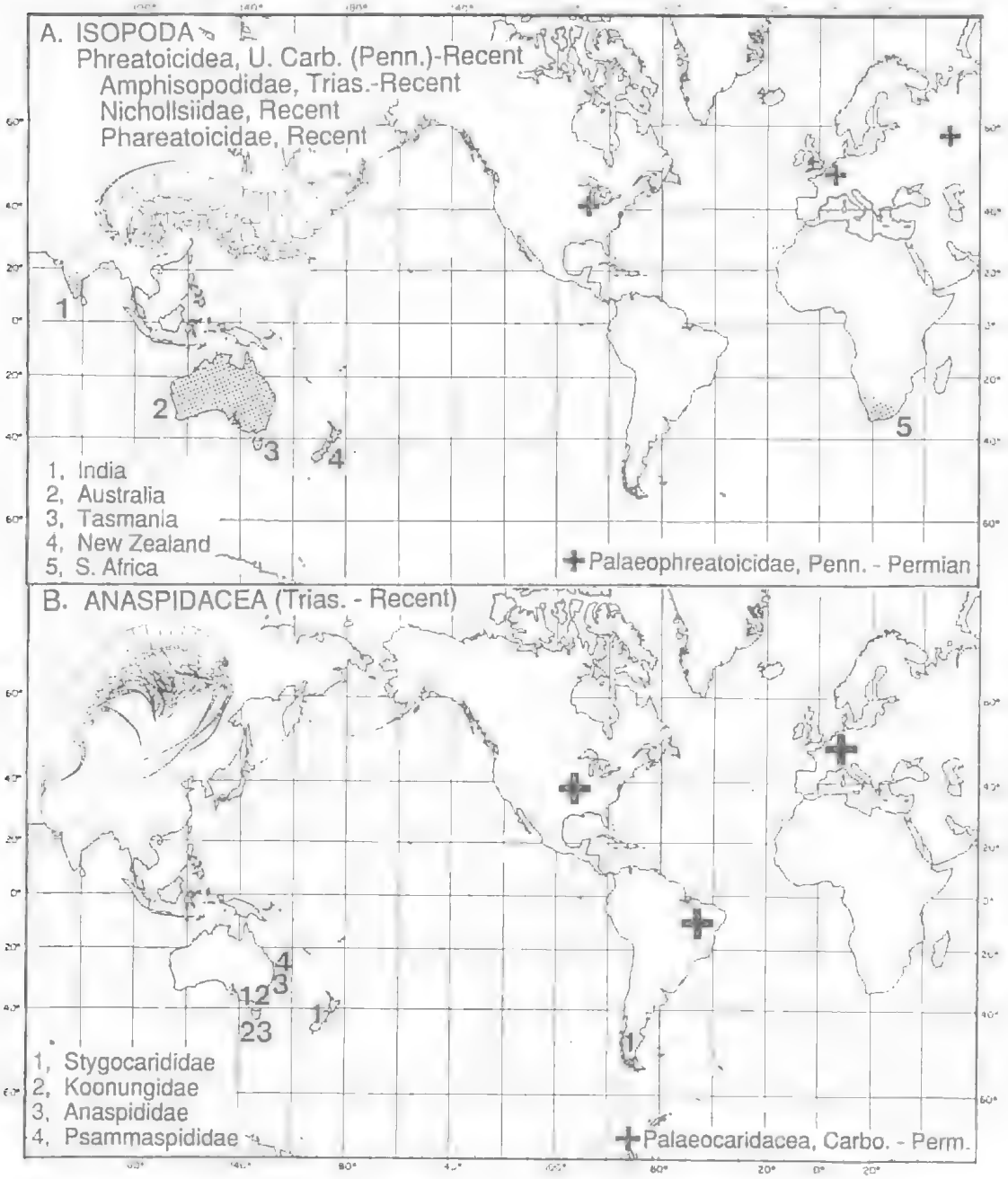
Schram (1986) plots a number of distributional patterns, several of which, including that for the mystacocarids just noted, can be observed to have an amphitropical component. One involves the bathysquillid hoplocarids which apparently have Jurassic affinities. They are known from the Caribbean, and also from the Indo-West Pacific where they are amphitropical (Schram, 1986, fig. 5-7). Then there is the asellote isopod, *Nannoniscus*, dubbed by Schram (1986, fig. 12-6) as 'ubiquitous' but actually as far as it is known strongly amphitropical, especially in the Atlantic. Another of this group might include a wood-boring amphipod, *Chelura terebrans*, of the North Atlantic, South Africa, S.E. Australia and New Zealand had it not been inferred that the

FIG. 5. Hypothesis 5 — Vicariance. Amphitropical and paramphitropical relicts and relics of Tethys: A, Contemporary configuration of the world with the approximate limits of the tropical belt (stippled, cf. Fig. 4A for fuller explanation). Tropical forms are not equally steno- or eurytopic, nor do they have identical temperature optima. Consequently there are patterns within such a uniformly stippled area reflecting these and other characteristics, such as substrate or water mass preferences. B, Evolution of advanced, presumably more competitive tropical forms (Théel, 1911), and/or warming of the tropics beginning in the Miocene (Valentine, 1984), excluded many older elements from the central and deep tropics. Thus a distinct class of Tethyan relicts known as paramphi- and amphitropicals was produced (stippling). Paramphitropicals tend to occur under eastern boundary conditions, as indicated by the stippling in the East Pacific. The eastern Atlantic could also be stippled, but examples of paramphitropicality are apparently uncommon there. These patterns can be detected to varying degrees in both oceanic and coastal forms. C, With further reliction, many Northern Hemisphere populations become extinct, whereby their Southern Hemisphere counterparts become endemic. The fact of extinction in the Northern Hemisphere is based on the fossil record, although some quasi Southern Hemisphere endemics (widely distributed populations in the south but with some Northern Hemisphere representation) can be interpreted as belong to this class. Remnants of previous connections with the Northern Hemisphere include 1, endemics shared between Hawaii and the South Pacific, 2, endemics shared with the East Pacific as well as Hawaii and the South Pacific, and 3, endemics having representation elsewhere in the Northern Hemisphere such as in the northeast Atlantic as indicated here (Newman ,1986; Newman and Foster, 1987).

species had been introduced to the Southern Hemisphere (and to California) by ships.

Abele (1982) and Hessler (1984) review and Schram (1986) plots the distribution of cephalocarids (Fig. 7A), but none attempts to analyse the overall pattern. It can be argued the distribution is poorly known and likely too incomplete to allow an analysis. After all, there are but four genera, nine species and about eleven localities in the world to work from. At first glance the pattern may appear little more than random, but on close inspection and the application of biogeographical principles, patterns become evident.

The first cephalocarid genus, *Hutchinsoniella*, was described some 40 years ago. It is still monotypic and known only from the Atlantic where, instructively,



it is amphitropical (Fig. 6A). The second genus, *Lightiella*, discovered in California at about the same time, is now known by two species from the Caribbean and one from New Caledonia (a relatively isolated southern outpost). It is therefore at least Tethyan as well as amphitropical in distribution. Likewise, species of *Sandersiella*, a genus first described from Japan, have turned up on both sides of South America, with that from the east coast (southern Brazil) also occurring on the southwest coast of Africa (Namibia). Thus, not only are all three of these genera apparently amphitropical, two are Tethyan, and the last is amphi-Atlantic (Hessler and Sanders, 1973) at much the same latitudes as the Spelaeogriphacea noted above. And finally, there is the monotypic New Zealand genus *Chiltonella*, whose discovery makes the diversity of cephalocarids greater in the Southern than in the Northern Hemisphere. Along with the species of *Lightiella* from New Caledonia, these taxa have a geographical refugial aspect to their distribution in addition to their minuscule size and habitat.

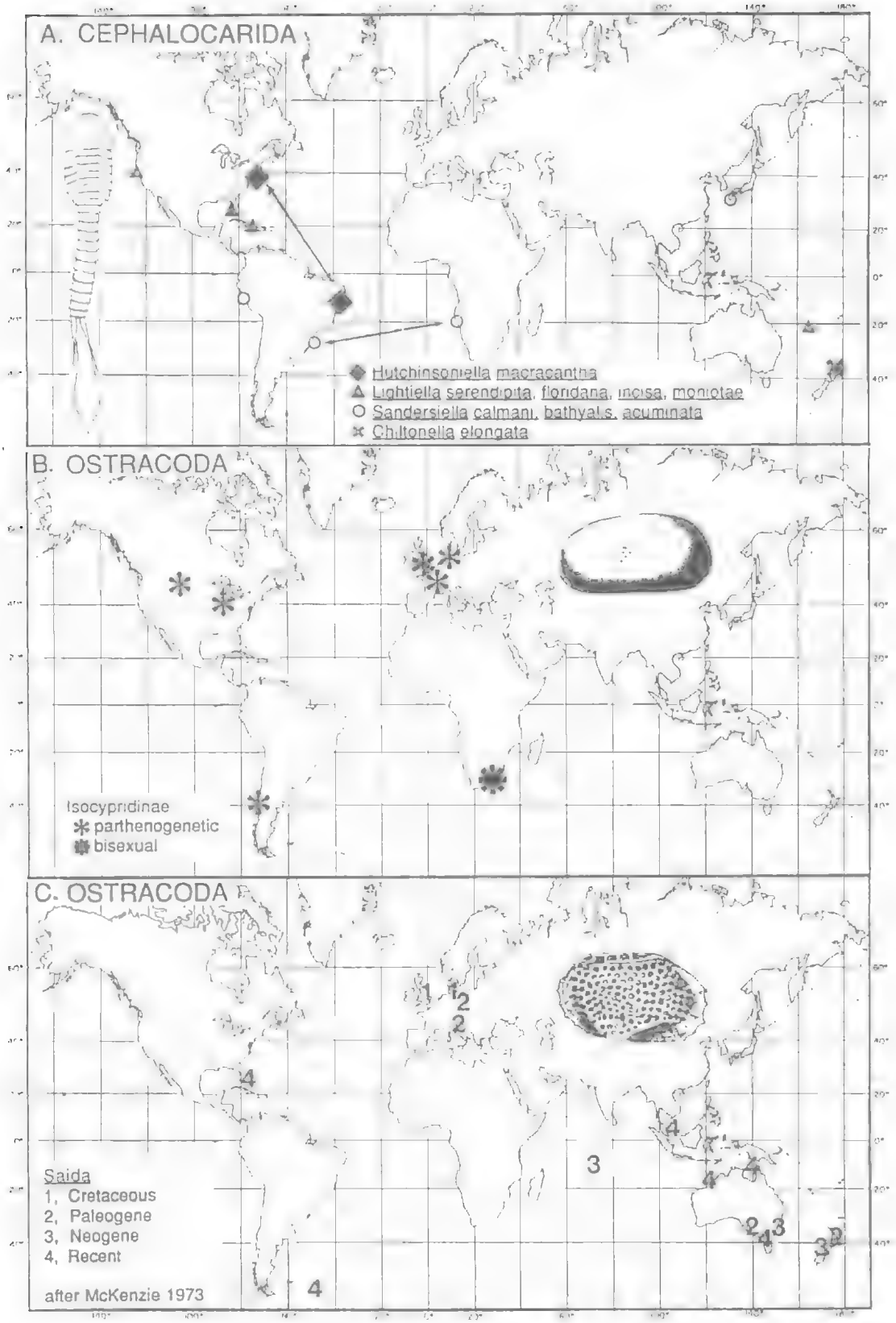
Abele (1982) notes that there has been little local differentiation among cephalocarids and therefore concludes that they are specialists rather than generalists as suggested by Hessler and Sanders (1973). There is no question that they are specialised in size and structure for the refugium afforded by flocculent sediments, and it is probably characteristic of forms so limited, like the mystacocarids in interstitial waters, to show little subsequent diversification. But there is also no question that while specialised, cephalocarids have retained primitive traits known in no other living crustaceans, such as utilising the antennular gnathobases for feeding, multiple ontogeny stages, and second maxillae which are almost indistinguishable from thoracic limbs (cf. Müller and Walossek, 1988). Furthermore, the cephalocarids had to evolve from something not too dissimilar, and there is nothing living from which they can be derived (Hessler and Newman, 1975). In consideration of this and their highly relict geographical distribution, it is clear that the more generalised ancestor of cephalocarids entered this refugium a long time ago (Hessler and Sanders, 1973), likely before the breakup of Pangea and certainly before the breakup of Gondwanaland.

Ostracod biogeography is reviewed by Abele (1882) who cites previous authors who have noted, for example, some freshwater forms with Brazil/West African affinities datable to continental connections during the Early Cretaceous. He goes on to note that arguments for passive dispersal via birds etc. cannot be excluded, as they so readily can for other trans-Atlantic endemics including the species of *Sandersiella* and the spelaeogriphaceans noted above whose amphi-Atlantic aspects could well date back to the same epoch.

Schram (1986) plots two distributions (Fig. 7B, C) displaying amphitropicality, one from the freshwater isocypridine ostracods, the other for the marine genus *Saida*, the latter being the most relevant here. The fossil record for *Saida* begins in the Cretaceous and ends in the Paleogene in northern Europe (Fig. 7C). It also begins in the Cretaceous of Australia where it survives today. Until recently the genus was thought to have gone extinct in the Northern Hemisphere whereby it was considered a Southern Hemisphere endemic. However, there are now (Whatley, pers. comm.) several additional Recent localities known in the world (on the Florida Slope and in the South China and the South Scotia Sea; Fig. 7C). Thus, the genus may presently be paramphitropical. Whatever the case, the example of *Saida* appears to be close to, if not a subset of, Fleming's (1979) observation that much of the marine fauna of New Zealand (and hence at least southeastern Australia) had its roots in northern Europe where it died out in the Miocene.

If it were not for the fossil record, we would

FIG. 6. A, Isopoda, Phreatoicidea, known from four of the six Gondwanan continents including India. While the Phreatoicidae and Nichollsiidae (stippled) are Recent, the Amphisopodidae are known as far back as the Triassic. This is strongly indicative of a Gondwanan distribution, especially since they are freshwater forms. However, their northern hemisphere counterpart, the Palaeophreatoicidae (crosses), are sufficiently old (Pennsylvanian-Permian, Schram, 1986) to make them relicts of Pangean as well. B, Syncarida, Anaspidacea: The distribution of anaspidaceans centers on southeastern Australia, with one of the four families ranging east to New Zealand and southern South America. Known from fresh water as far back as the Triassic, their closest relatives, the Palaeocaridacea (Carboniferous–Permian), are known from marine deposits in North and South America as well as Europe (crosses, Schram, 1986). Like the phreatoicids, conventional wisdom is that anaspidaceans are Gondwanan relicts of Pangea. However, their closest ancestors, the palaeocaridaceans, were marine, and a well developed nauplius is passed through in the egg of at least *Anaspides*. Therefore, the occurrence of one family in New Zealand and South America could have been by West Wind Drift dispersal rather than via the breakup of Gondwanaland.


A. CEPHALOCARIDA
Hutchinsoniella macracantha
Lightiella serendipita, floridana, incisa, monotae
Sandersiella calmani, bathyalis, acuminata
Chiltonella elongata
B. OSTRACODA
Isocypridinae
parthenogenetic
bisexual
C. OSTRACODA
Saida
1, Cretaceous
2, Paleogene
3, Neogene
4, Recent
after McKenzie 1973

have no way of knowing the long history of *Saida* nor that it may have long had a paramphitropical component. It is examples like this that cause pause in accepting a Southern Hemisphere origin for the anaspidaceans. Further along these lines are two groups of barnacles, acrothoracicans and balanomorphs, once potential candidates for a Southern Hemisphere origin but now also known to be or once to have been amphitropical. Both groups of barnacles have Tethyan representatives in the tropics.

Acrothoracican barnacles are mostly found burrowing in limestone substrates and they range from Devonian to Recent. Schram (1986, fig. 41-3) plotted the distribution of a species each of the generalized lithoglyptid genera *Lithoglyptes* and *Kochlorine*. These were dubbed 'circumtropical', but it can be observed that the two species are not only quite patchily distributed but are almost mutually exclusive; that is, *Lithoglyptes spinatus* occurs in the Caribbean and Indo-West Pacific while *Kochlorine hamata* occurs in the East Pacific, eastern Atlantic and the Indo-Pacific. The patchiness is interesting because it also can be seen from the data on *Cryptophialus*, the more advanced of the two acrothoracican genera in the Cryptophialidae (Tomlinson, 1969; Fig. 8A). Like *Kochlorine*, populations are known from the East Pacific and eastern Atlantic, but in the East Pacific *Cryptophialus* is amphitropical. Then, instructively, there are no records for *Cryptophialus* from the Indian Ocean, except from southern Madagascar; and records from the West Pacific tend to be insular, on or near the Pacific Plate (Fig. 8A).

The second and more primitive genus of the Cryptophialidae, *Australophialus* (Fig. 8B), was until recently known by four species in the Southern Hemisphere, one each from New Zealand and Antarctica, and two in South Africa (Tomlinson, 1969; Newman and Ross, 1971). Like the species of *Cryptophialus*, these are found in shallow water except for a bathyal species in the Antarctica. When *Australophialus* was thought to be austral, it would have been a likely candidate for a Gondwanan origin and distribution. However, a species was recently discovered living at bathyal depths off Gibraltar (Turquier, 1985) whereby *Australophialus* became amphitropical (Newman and Foster, 1987). It could be argued that the Gibraltar species had migrated under equatorial waters from South Africa, but the otherwise relict pattern of the genus suggests that, like *Cryptophialus*, it was once more widely distributed in the world, especially the Northern Hemisphere.

A similar switch in our understanding involves the distribution of the acrothoracican, *Trypetesa*, once the sole representative of the Trypetesidae. However, unlike *Australophialus*, its several species have a relict distribution primarily in the Northern Hemisphere on both sides of the North Pacific and North Atlantic. The species are refugial on two counts; 1, they are only found burrowing in the interior of gastropod shells inhabited by hermit crabs; and 2, primarily in latitudinal transitions zones or ecotones (Newman, 1979b, fig. 10). *Trypetesa* would have been a candidate for Northern Hemisphere endemism until it was discovered that there were representatives (two species and a new genus) in southern Madagascar (Turquier, 1977), a refugial region for other marine as well as terrestrial and freshwater species. Thus, this presumed Northern Hemisphere endemic family became amphitropical.

It is instructive to note that the Acrothoracica is known since the Devonian and is therefore the oldest crustacean group having a fossil record covered herein. Interestingly, the distribution

FIG. 7. A, Cephalocarida (locality data from Hessler,1984). Monotypic *Hutchinsoniella* is amphitropical in the western Atlantic, *Lightiella* and *Sandersiella* are Tethyan and amphitropical in distribution, with *S. bathyalis* being amphi-Atlantic, and monotypic *Chiltonella* a Southern Hemisphere endemic. Hence, the Cephalocarida has a relict Tethyan distribution with pronounced amphitropical character and a greater diversity surviving in the southern than in the northern hemisphere. B, Ostracoda, Isocyprídae (modified from Schram, 1986 after McKenzie, 1973, with deletions from McKenzie, pers. comm.). Isocyprids are freshwater amphitropicals previously thought to have a wider distribution in the southern than in the northern hemisphere. However, the southern Australian representatives have since been removed from the group (McKenzie, pers. comm.). C, Ostracoda, *Saida* (modified from Schram, 1986 after McKenzie,1973, with additions from McKenzie and from Whatley, pers. comm.); a marine, perhaps paramphitropical genus with a fossil record stemming back to the Cretaceous of Europe and Australia and, until recently, thought to be a Southern Hemisphere endemic. Since McKenzie (1973), the genus has turned up in the Paleogene of the southern United States and the Cretaceous of Western Australia (McKenzie, pers. comm.), and from the Recent of the Florida Slope, the South China Sea and the South Scotia Sea from moderately deep to deep water (Whatley, pers. comm.).

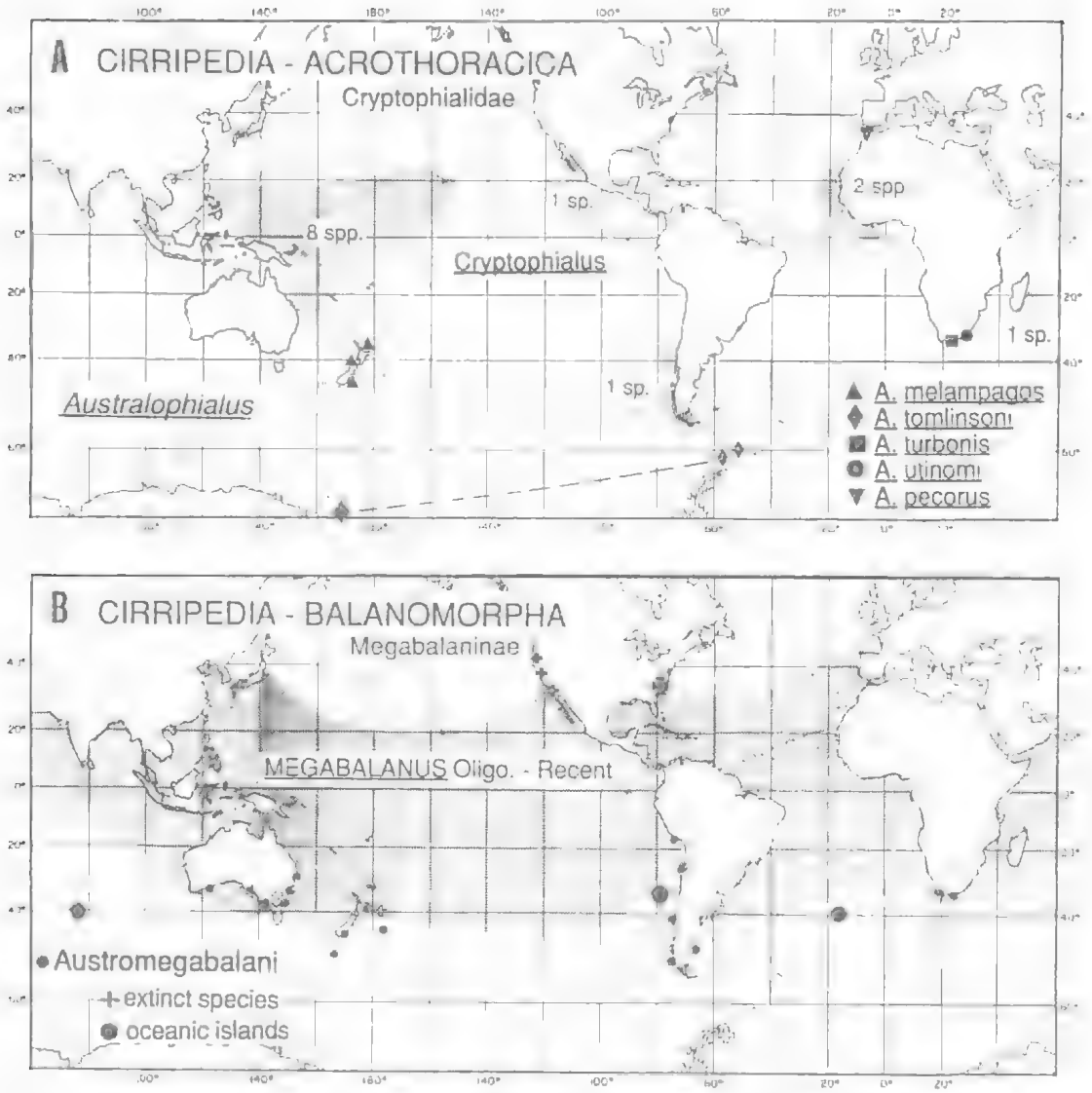


FIG. 8. Cirripedia. A, Acrothoracica, Cryptophialidae. The primarily tropical genus, *Cryptophialus* (stippled), has a distinctly relict Tethyan distribution that is curiously amphitropical in the East Pacific and East Atlantic/Madagascar. The genus *Australophialus* could have been a candidate for a Gondwanan distribution, but recently a species was discovered off Gibraltar, whereby it became an amphitropical rather than a Southern Hemisphere endemic (Newman and Foster, 1987). B, Balanomorpha, Megabalaninae. The advanced tropical genus, *Megabalanus* (stippling), appeared in the Oligocene while the somewhat more primitive Austromegabalani (dots) did not appear until the Miocene in the Southern Hemisphere. The age of the megabalanines as a whole and the occurrence of Austromegabalani on oceanic islands indicated that the latter were not Gondwanan (Newman, 1979a), and the discovery of fossil Austromegabalani on both coasts of North America (crosses) indicated that the Austromegabalani had once been amphitropical (Zullo, 1986; Newman and Foster, 1987).

patterns of shallow-water representatives of all three families have distinct relict characteristics, i.e. patchiness, much regional endemism, and amphitropicality favoring the Southern or the Northern Hemisphere depending on the group.

The balanomorph barnacles first appear in the Upper Cretaceous and the megabalanines appeared in the Oligocene. Several genus-group taxa were recognised as Southern Hemisphere endemics (Newman, 1979a) and one is referred to as the

Austromegabalani here (Fig. 7B). Considering the relatively young age of the subfamily and the occurrence of species of Austromegabalani on oceanic islands of the austral region, it was concluded that they owed their circum-austral distribution to the West Wind Drift rather than to Gondwanaland. Yet, they could have been Southern Hemisphere in origin. It was therefore instructive when it was discovered that the Austromegabalani had once occurred on both coasts of North America (Zullo, 1986; Zullo and Guruswami-Naidu, 1982). Thus it is evident that they were not only Tethyan but were apparently amphitropical.

It is important to note that, as *Austrophialus* is to *Cryptophialus*, the Austromegabalani are more primitive than their tropical counterpart, *Megabalanus*. This fits the Théelian (1911) hypothesis involving replacement in the tropics by advanced forms and the origin of amphitropicality. Competition, predation and other biological factors may have been involved, but warming of the tropics, the amendment to the Théelian hypothesis for the origin of amphitropicality advanced by Valentine (1984), is likely also part of the explanation, especially when one considers the basis for paramphitropical distributions (cf. Newman and Foster, 1987). Now we can look at some other groups, keeping these patterns and apparent trends in mind.

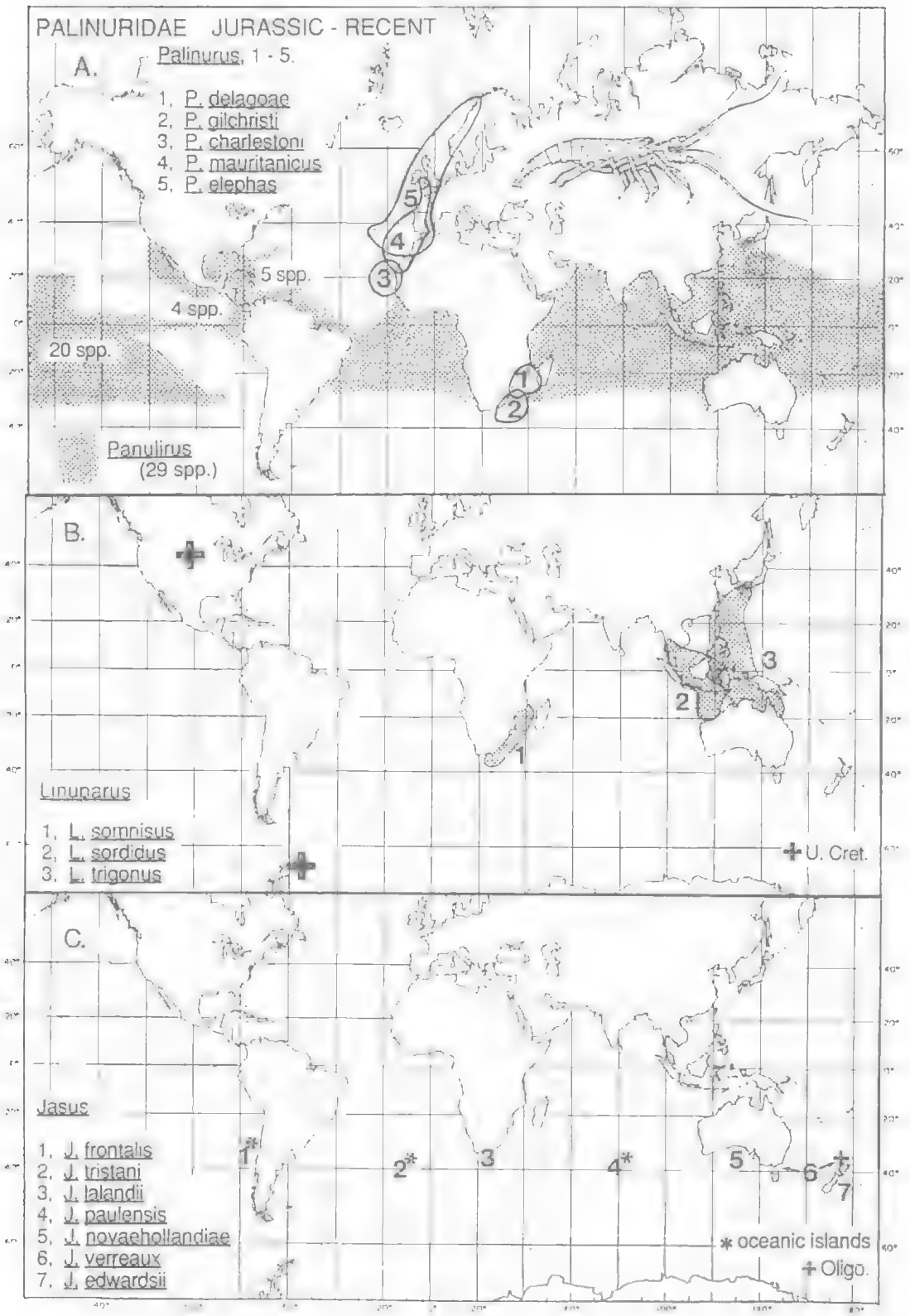
The Palinura, which includes the spiny lobsters and their allies, first appear in the Triassic (Glaessner, 1969). The valuable monograph on the identification of lobster tails (Williams, 1986) also includes a substantial amount of data on current distributions. It was disappointing to find that nothing noteworthy appeared in a preliminary plot of the distribution of genera and species of slipper lobsters (Scyllaridae, Lower Cretaceous–Recent). While diverse in shallow water, the slipper lobsters have a highly derived morphology which likely reduces their interactions on reefs with spiny lobsters to an appreciable extent. Therefore, perhaps unjustly, the details of their distribution will be ignored here.

The spiny lobsters, (Palinuridae, Jurassic) are another matter. The stridulator *Panulirus* (Upper Cretaceous) is well represented in shallow-water tropical waters, there being 24 Indo-Pacific and five tropical Atlantic species (Fig. 9A). On the other hand, another stridulator, *Palinurus*, is represented by five species having a curious distribution in the northeastern Atlantic and southeast Africa (Fig. 9A). It seems prudent to suggest that this amphitropical distribution is the result of reliction rather than migration across the tropics, since a somewhat comparable pattern is known among gastropod molluscs (Gosliner, 1989) as well as the burrowing barnacle *Australophialus* noted above. It is interesting to speculate that if the conditions that have brought about such reliction were to continue, and if species richness and wide ranges are hedges against a taxon's extinction, as with the trypetesid acrothoracicans, one would expect *Palinurus* to become a Northern Hemisphere endemic.

There is another class of reliction among the Palinura, a long recognized example being the Polychelidae; relatively common in shallow water in the Jurassic but now found only at bathy-abyssal depths (Glaessner, 1969). Similarly, the Glypheidae (Triassic– early Tertiary; Greenland, Europe, North America, Australia, New Zealand), were thought extinct since the early Tertiary (Glaessner, 1969) until *Neoglyphus* was discovered at moderate depths in the Philippines (Forest and Saint Laurent, 1981; Forest, Saint Laurent and Chace, 1978). And finally in this category is *Linuparus* which occurred fairly commonly at mid to high latitudes in both hemispheres in the Upper Cretaceous (Bishop and Williams, 1986; Feldmann, 1984, 1988; Feldmann and Tshudy, 1989; Tshudy and Feldmann, 1988), but is presently represented by but three species found at moderate depths; two on the shelf forming the boundary between the Indian and Pacific Oceans and one off southeastern Africa (Fig. 9B).

Centres of Origin

The southern spiny lobster, *Jasus*, a nonstridulator first appearing in the Oligocene of New Zealand, is represented by seven extant species distributed around the Southern Hemisphere (Fig. 9C). They occur on a number of oceanic islands including Tristan da Cunha and Amsterdam/Saint Paul, as well as on the shores of Australia, New Zealand and South Africa (Holthuis and Sivertsen, 1967; Williams, 1986; Pollock, 1990). Taking their Oligocene record at face value and the fact that a good part of their distribution has been via the West Wind Drift (Newman, 1979a), it does seem unlikely that their distribution can be traced back to the breakup of Gondwanaland. Thus we are left with the suggestion that the genus was southern in origin (Pollock, 1990). However, from the foregoing, especially the history of the Austromegabalani which includes two austral groups having much the same distributions as the groups


PALINURIDAE JURASSIC - RECENT
A.
Palinurus, 1 - 5.
1, P. delagoae
2, P. gilchristi
3, P. charlestoni
4, P. mauritanicus
5, P. elephas
5 spp.
4 spp.
20 spp.
Panulirus
(29 spp.)
B.
Linuparus
1, L. somnisus
2, L. sordidus
3, L. trigonus
U. Cret.
C.
Jasus
1, J. frontalis
2, J. tristani
3, J. lalandii
4, J. paulensis
5, J. novaehollandiae
6, J. verreaux
7, J. edwardsii
* oceanic islands
Oligo.

of *Jasus* (Newman, 1979a), and the apparent origin of a brachyuran *Lyreidus* to follow, it would seem equally if not more likely that *Jasus* or its immediate ancestor once had at least a Tethyan if not an amphitropical distribution in the past. While this hypothesis cannot be readily falsified, the alternative (a Southern Hemisphere origin) can be, by virtue of the fossil record.

The ranninid brachyuran, *Lyreidus*, hitherto considered Southern Hemisphere in origin (Feldmann, 1986), appropriately follows here because the alternative hypothesis just noted can be applied. Taking the present distribution at face value, *Lyreidus* appears to be Tethyan (Indo-West Pacific/West Atlantic) and *L. tridentatus* (Hawaii/Japan, one locality off the Philippines and Australia/New Zealand; cf. Feldmann, 1986) may be paramphitropical rather than simply West Pacific. Thus it does not seem that *Lyreidus* was austral in origin. Further suspicion is cast by new fossil evidence indicating that a Tethyan origin with an amphitropical component is likely. Feldmann (1990) has reported on the existence of an ancestral stock, for at least *L. channeri* and *L. nitidus*, from Eocene rocks in both New Zealand *and* the northeast Pacific. Thus the pattern and history appears to be similar to that of *Linuparus* and glypheids, although less severely restricted.

As a final application of the biogeographical principles being used here I would like to analyse the distribution of the brachyuran crab *Cancer* (Fig. 10). The process is instructive because, contrary to previous views, it provides insights into the development of endemism at moderate to high latitudes through reliction rather than radiation. The distribution of *Cancer*, known to Ekman (1935, in 1953), was elaborated upon by MacKay (1943) and Nations (1975, 1979). Nations, who much improved the quality of the taxonomic data base, followed Ekman concerning an inferred North Pacific origin for the genus, and he postulated coastal migration routes about the world to account for the present distribution.

More recently Carvacho (1989) endorsed the biogeography scenario of previous authors, i.e. *Cancer* originated in the Miocene of the North Pacific where most species are found today. Radiation followed: 1, up and over the pole into the Atlantic; 2, down the East Pacific to South America; and hence, 3, to Australia and New Zealand via Antarctica (against the West Wind Drift). However, Nations (1979) was apparently unaware and Carvacho ignored the potential significance of Crosnier's (1976) report of a new species from Madagascar and Reunion I. and Takeda's (1977) records from the Hawaii Islands. The latter relict populations could conceivably be worked into the hypothesis but the former does not fit into a North Pacific origin and radiation hypothesis very well at all. Likewise, records of a cancrid in the Mio-Pliocene of Kerguelen (Richers de Forges, 1977; Noel and Lemaire, 1990) cause further pause. Clearly, as with *Lyreidus* and *Jasus* noted above, a more plausible alternative needs to be explored.

Could the distributional pattern of *Cancer* available to Carvacho have been better explained as the result of reliction than of radiation? In addition to appearing distinctly Tethyan, the pattern reveals other relict elements including: 1, an east–west disjunction in the North Pacific in which one species (*C. amphioetus*) is shared by both regions; 2, an amphitropical pair (*C. porteri* - *C. johngarthi*) displaying low latitude submergence in bridging the gap between hemispheres in the East Pacific (thus making the distribution paramphi- rather than pure amphitropical); 3, a species in South America (*C. polydon*) in the Pliocene of North America and therefore once amphitropical; and, 4, the genus being amphitropical in the Indo-West Pacific, the Southern Hemisphere representatives being in relict areas (southeastern Australia, intro-

FIG. 9. Palinura, Palinuridae (Jurassic; distributional data for extant forms from Williams, 1986). A, The spiny lobster, *Palinurus* (Upper Cretaceous) includes five species, two in southeast Africa and three ranging from North Africa to Norway, an amphitropical distribution with representatives of the widely distributed tropical genus, *Panulirus*, in between. It would appear that *Panulirus* replaced *Palinurus* in the tropics of at least the Atlantic if not the Indian Ocean, the Indo-West Pacific and elsewhere. B, *Linuparus*, widely distributed in shallow water to relatively high latitudes in both hemispheres in the Upper Cretaceous (Bishop and Williams, 1986; Feldmann and Tshudy, 1989), is presently represented in two relict areas by three species in moderately deep water. C, *Jasus* (Oligocene of New Zealand), occurs on oceanic islands as well as continents reached by the West Wind Drift. It therefore occupies a time frame and pattern comparable to that of the Austromegabalani (Fig. 9B) and thus does not likely represent a Gondwanan distribution. *Jasus* has been inferred to have originated in the Australia/New Zealand region (cf. Pollock, 1990) but, considering the relictions of Palinura noted above, and some others noted in the text, an amphitropical Tethyan reliction rather than a southern hemisphere origin and radiation is a distinct possibility.

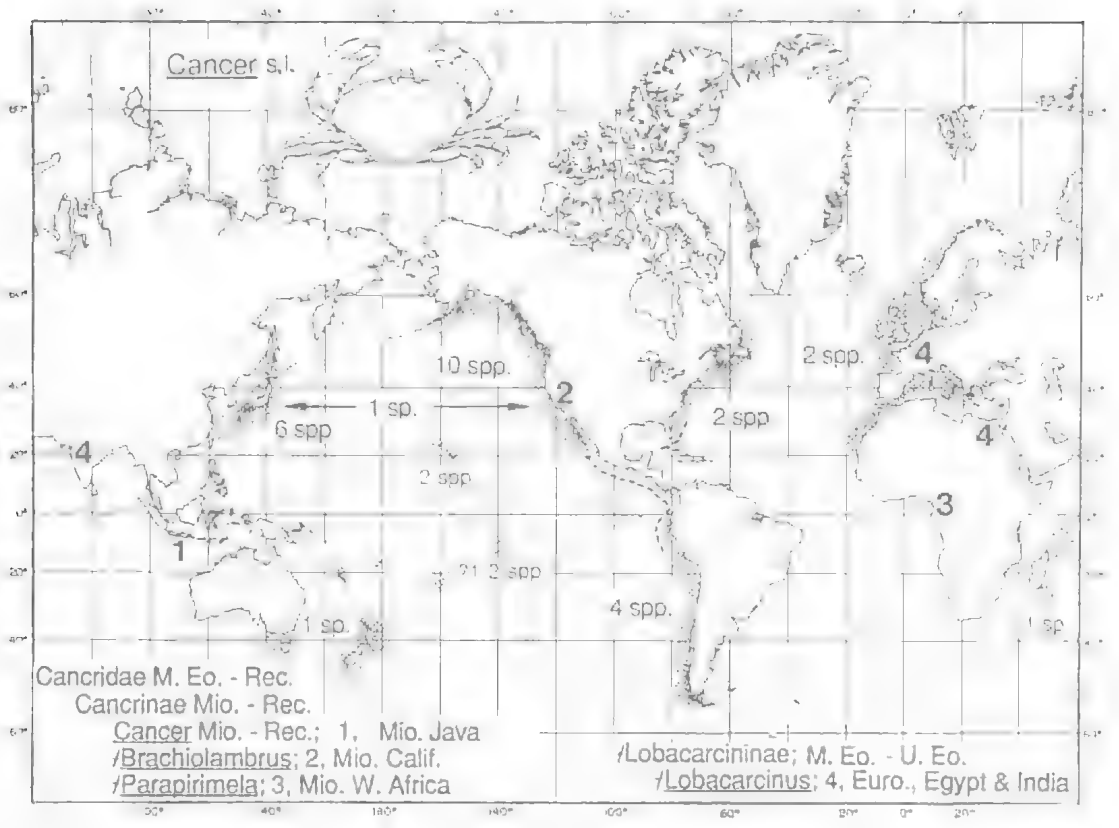


FIG. 10. Cancridae, *Cancer*. There has been a consensus that *Cancer* originated in the North Pacific where most species are found today (Ekman, 1953; Nations, 1979; Carvacho, 1989). But a plot of the present distribution actually appears to be Tethyan, with a strong paramphi- amphitropical component. The present plot includes a deep-water species from Madagascar, Reunion and Seychelles (Crosnier, 1976), Hawaii (Takeda, 1977), Marquesas and Austral Is. (Poupin and Richer de Forges, this volume), and elsewhere in the Pacific including New Caledonia (Davie, pers. comm.).

duced, or perhaps reintroduction from New Zealand [cf. McLay, 1988], and Madagascar).

These facts suggest Tethyan reliction. So does the unique offshore dispersal of outer coast *C. magister* larvae, compared to those of the inland-sea population in British Columbia described by Jamieson and Armstrong (this volume); possibly a relic behavioural pattern related to their once having had more western populations as far west as northern Japan. This is a testable hypothesis because one species, *C. amphioetus*, presently has relict populations in North America and Asia. Do the larvae of the western populations behave like those of offshore *C. magister*? Yet it can always be argued that the apparently relict distributional aspects are perhaps still compatible with the North Pacific Miocene origin and subsequent radiation hypothesis. Therefore we need to probe the matter a little further.

A look at the fossil record of the Cancridae, of which *Cancer* is the sole surviving genus, reveals some facts that are unreconcilable with the North Pacific origin and radiation hypothesis: 1, *Cancer* itself went extinct in the deep tropics (Java) in the Miocene; 2, *Brachiolambrus* went extinct in the Miocene of California; 3, *Parapirimela* went extinct in the Miocene of West Africa; 4, *Lobacarcinus* (monotypic subfamily Lobacarcininae) went extinct in the upper Eocene of Egypt and India (Glaessner, 1969). Thus the Cancridae had a tropical/subtropical history in the Palaeogene, before the tropics began to narrow in the Oligocene and to warm in the Miocene. These observations, the present paramphitropical distribution, and the relict patterns pointed out above, are not characteristics of a relatively

recent radiation but rather reliction of a previously wide ranging Tethyan complex.

There are some unpublished data that also need to be mentioned. A *Cancer* (identified by Crosnier) has recently been taken from deep water in French Polynesia (Marquesas and Austral Is.; Poupin and Richer de Forges, 1990, this volume). Crosnier (pers. comm.) has indicated that the form is very similar to *Cancer guezei* Crosnier from Madagascar, Reunion, and the Seychelles, to a smaller but similar form from Kiribati (= Gilbert Is.), and to *C. sakaii* from Japan. He further notes that this group has a relatively narrow depth range: one record as shallow as 400 m and another as deep as 700 m, but generally between 450 m and 550 m. Knowledge of these relict populations beneath tropical waters on the Pacific Plate in the South Pacific, along with previous knowledge of *Cancer* from Hawaii and off Madagascar, on the Mascarene Plateau, and in the Miocene of Java, is compatible with a Tethyan rather than a North Pacific origin hypothesis.

While the time frame is such that the amphiparamphitropical distribution of *Cancer* developed in response to much the same conditions responsible for the amphitropical distributions noted above in connection with Southern Hemisphere endemism, *Cancer* appears to be doing better in the northern than in the Southern Hemisphere. Other exceptions to the more general trend noted earlier include the Trypetesidae among the barnacles and *Palinurus* among the lobsters. Therefore, while Tethyan reliction, often with an amphitropical component, apparently has generally led to Southern Hemisphere endemism, occasionally it may lead in the opposite direction.

CONCLUSIONS

A number of hypotheses have been explored to explain Southern Hemisphere endemism among the Crustacea. Of the *bona fide* endemics taken into consideration, the phreatocids, parastacids, *Dolops*, and perhaps the anaspidaceans were Gondwanan, while the aeglids and perhaps *Jasus* appear to have had a non-Gondwanan but perhaps southern origin. On the other hand, the ostracod, *Saida*, originally thought endemic to southeast Australia and having a well documented fossil record in northern Europe, is now known to be living in the South Scotia and China Seas, and on the Florida Slope, so that it is perhaps still a Tethyan paramphi- if not amphitropical taxon. Other forms, such as *Lyreidus*, *Australophialus* and the Austromegabalani, were previously candidates for a Southern Hemisphere origin, but they are now known to be or to have been amphitropical.

An amphitropical history in the origin of Southern Hemisphere endemism in some forms leads to the consideration of a variety of other crustaceans (cephalocarids; *Cryptophialus*, the Trypetesidae and other acrothoracicans among the barnacles; and the palinurans and some brachyurans among the decapods) that presently display an amphitropical pattern. Some of these appear on the verge of becoming Southern Hemisphere endemics (*Saida* and *Australophialus*), or vice versa (*Palinurus*, Trypetesidae and the Cancrinae).

What the refugial characteristics are that have led to the preservation of Southern Hemisphere endemics among the marine invertebrates have not to my knowledge been identified. But, as for terrestrial and freshwater forms, they probably involve the relative isolation of Southern Hemisphere outposts from each other as well as from the Northern Hemisphere. However, while some Southern Hemisphere endemics enjoy fairly wide distributions, many marine as well as freshwater and terrestrial endemics are found in relatively discrete areas such as southeastern Australia, southern South America, and the southernmost parts of Africa and India. It seems inescapable, whether Gondwanan or Tethyan in origin, that they have been relegated to these areas by reliction. But this does not explain why they have been spared where they are while going extinct elsewhere. For areas like New Zealand, Madagascar, New Caledonia etc., the additional water barriers are an obvious isolating mechanism, especially for terrestrial and freshwater forms, but what about on the continents? A working hypothesis would seem to be that, in addition to isolation, there are currently ecological parameters that have been operating over comparable periods of time, Southern outposts as defined by a high degree of endemism are generally rather restricted and therefore may represent transition zones between biotic provinces. If so, the endemics would be ecotone species enjoying relief from biological interactions afforded by such refuges (Newman, 1979b; Laguna, 1990).

Relatively few examples from the Crustacea have been given here and I apologize for whatever well documented ones may have been missed. Undoubtedly new discoveries of living and fossil forms will shed light on current prob-

lems as well as uncover those yet unrecognised. The process will undoubtedly lead to much refined if not better hypotheses enhancing our understanding of the origin of Southern Hemisphere endemism.

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DISTRIBUTION, AFFINITIES AND ORIGIN OF THE PUNCIIDAE (CRUSTACEA: OSTRACODA)

K.M. SWANSON

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The punciid ostracod has, since its discovery been recognised as a probable living representative of the Palaeozoic Kirkbyacea. Similarities in larval development of the carapace are discussed including a comparison of the manawan nauplius with an unusual Ordovician 'larva' *Melopetasus*. Internal structure, reticulation, muscle scars, ornamentation and the frill of the punciid carapace more closely resemble the kirkbyid pattern than that considered typical for modern, extant, podocopid ostracods. The anatomy of the punciid trunk displays remarkable similarity posteriorly to that found on the extant platycopid *Cytherella*. This condition is considered plesiomorphic for ostracods. □ *Crustacea, Ostracoda, Kirkbyacea, Punciidae, Palaeozoic/Recent, carapace morphology, soft anatomy, homologies.*

K.M. Swanson, Geology Department, University of Canterbury, New Zealand; 6 July, 1990.

The recent recovery of rare, live specimens of the punciid ostracod *Manawa staceyi* has led to a dramatically improved, though incomplete, understanding of the anatomical and ontogenetic peculiarities of the Punciidae (Swanson, 1989a, b). Specimens of the remaining punciid genera *Promanawa* and especially *Puncia* also occur rarely, in both cases however, only disarticulated valves have been found. From the time of its initial discovery (Hornibrook, 1949) *Puncia* has been recognised as an animal whose biology, once documented, could have profound effects in areas much broader than the discipline of ostracodology from whence such data was generated.

Although '..reluctant to assert that a representative of a group of ostracods, which apparently died out elsewhere in the Devonian (400 MYBP), is still living in the South Pacific', Hornibrook (1949) established (a) that both *Puncia* and *Manawa* were unlike any other known living ostracod, and (b) *Puncia* most closely resembled members of the Palaeozoic (Lower Ordovician – Upper Devonian) ostracod family Eurychilinidae. Later, after a more detailed re-examination of the 1949 specimens and additional fossil material of *Puncia* from the Miocene (20 MYBP) of New Zealand, he concluded 'The only feasible conclusion is to regard the Punciidae as a relict group of Paleocopida, which were the dominant order of ostracodes in the Palaeozoic' (Hornibrook, 1963).

It is not the purpose of this paper to document historically the development of punciid classification since that time, such interests are adequately accommodated elsewhere (Swanson, 1989a). It should be noted however, that the dolonic dimorphism displayed by a number of eurychilinids is not found in the frill of *Puncia* (Swanson, 1985). Additionally the 'lunettes' of *Manawa* which Hornibrook felt may indicate a brooding capability, are now considered a simple, economic form of buttressing between the carapace proper and its sole (Swanson, 1989a). In most sexually dimorphic podocopid ostracods, males and females may be distinguished by variations in carapace shape and size; Nohara and Nakasone (1982), after examining a number of valves of *Manawa konishii*, considered equivalent differences also occur in the punciids.

In many respects, the release of some anatomical and ontogenetic details for *Manawa staceyi* (Swanson, 1989b) created more difficulties than were solved. At least three instars carry a single, horizontal, shield-like carapace; a feature hitherto unrecorded for ostracods. Although the adults are bivalved, each valve is extended laterally during ambulatory excursions presenting an exaggerated gape. This contrasts sharply with a vertical stance and 15 – 20° gape (Benson, 1981) for 'normal' ostracods. Anatomically, *Manawa staceyi* possesses a segmented abdomen and paired furcaxlamellae; metanaupliar development witnesses the addition of four pairs of homonomous, thoracic legs, the anterior – most progressively assuming a locomotory/trophic role. Cephalisation, however, remains incomplete at maturity. Since the appearance of

Late Cretaceous – Recent distribution of the ostracod genera *Manawa, Promanawa* and *Puncia*

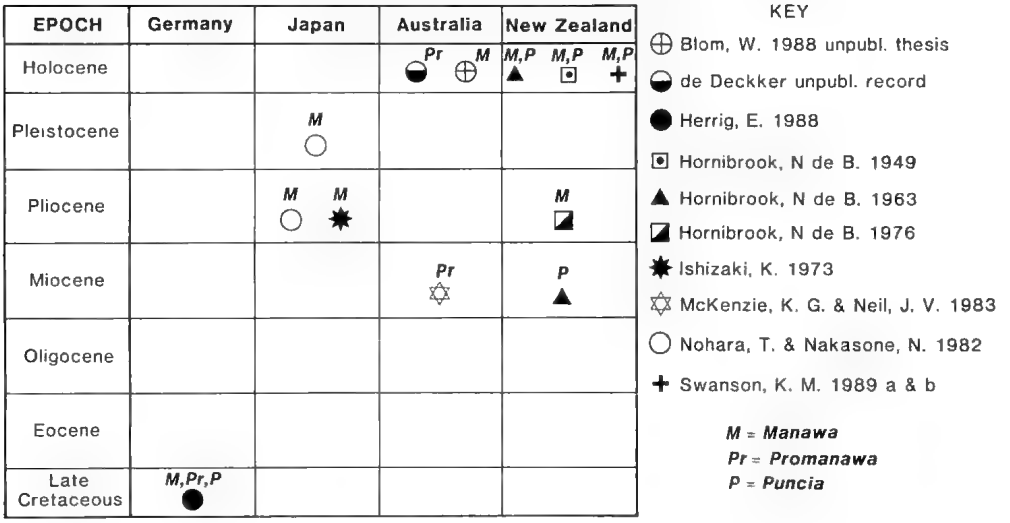


FIG. 1. Upper Cretaceous – Recent distribution of the ostracod genera *Manawa*, *Promanawa* and *Puncia*.

the 1989 papers I have become aware of other work (Fig. 1) which in retrospect adds considerably to the discussion of some 'manawan novelties'. Conversations with a number of Palaeozoic ostracod researchers at the 1989 'European Ostracodologists' Meeting' in Frankfurt and progress in my own investigation of platycopid and polycopid ontogeny now mean that sufficient new data are available to warrant a reassessment of the punciid ostracod and its relationship to other crustaceans.

THE PUNCIID CARAPACE

Larvae

As previously stated, the single, dome-shaped carapace carried by the nauplius of *Manawa staceyi* (Figs 3D, E) is unique for ostracods and possibly for Crustacea. Phaselus larvae, first described from the Ordovician (500–400 MYBP) of Spitsbergen by Fortey and Morris (1978), were considered by those authors to be the remains of 'nauplius-like' trilobite larvae. Schram (1982) disputed this claim, including in his reasoning the fact that a doublure is not unique to trilobites (the presence of a doublure on phaselus larva was seen by Fortey and Morris as a key indicator that such remains were trilobitan). By definition (Harrington, *et al.*, 1959) the earlier described carapace sole (Swanson, 1989b) of *Manawa* also qualifies as a doublure. Schallreuter (1979) considered similar remains from Upper Ordovician erratics on the Isle of Sylt as representing 'an ontogenetical stage of a bilateral-symmetrical animal (? trilobite).' Significantly, a smaller larval form (*Melopetasus*), which displays quite remarkable similarities to the carapace of the manawan nauplius, was also isolated (compare Fig 3D, E, G, H). The weight of evidence, I believe, favours acceptance of the Ordovician dome-shaped larvae as punciid-like (or at least ostracodal) rather than trilobitan. One must acknowledge that the position of the phaselus (a bilaterally symmetrical body created by the folding of a dome along a 'dorsal' axis) in this scenario is problematic. In *Manawa staceyi*, during the transition from nauplius to metanauplius, the naupliar dome occasionally shows evidence of slight infolding (Fig. 3D); examples of the exaggerated phaselus-type fold, however, have never been recovered from modern sediments. Either the phaselus is unrelated to the manawan-type naupliar dome (favoured by this author) or it may represent an additional larval stage which has subsequently been eliminated from the 'punciid' ontogeny.

In the Cambrian (520 MYBP), phosphatocopine bivalvedness (exhibited by *Hesslandona unisulcata*) is achieved by the folding of the carapace along a dorsal mid-line (Müller,1982). This contrasts with modern podocopid ostracods in which an array of complex hinge structures develop around a dorsal, mid-line suture (see Swanson, 1990). It is most likely that the plesio-

morphic crustacean naupliar condition occurs within a variety of forms described from the Upper Cambrian of Sweden (Müller and Walossek, 1986, 1988; Walossek and Müller, 1989). In fact, as indicated by those authors, the Cambrian larval types A and B are remarkably similar to the free-living naupliar groundplan exhibited by a number of extant crustaceans. To date no equivalent of the manawan naupliar dome has been recorded from the Cambrian, acknowledging the possibility that such remains are overlooked simply because they are so unfamiliar.

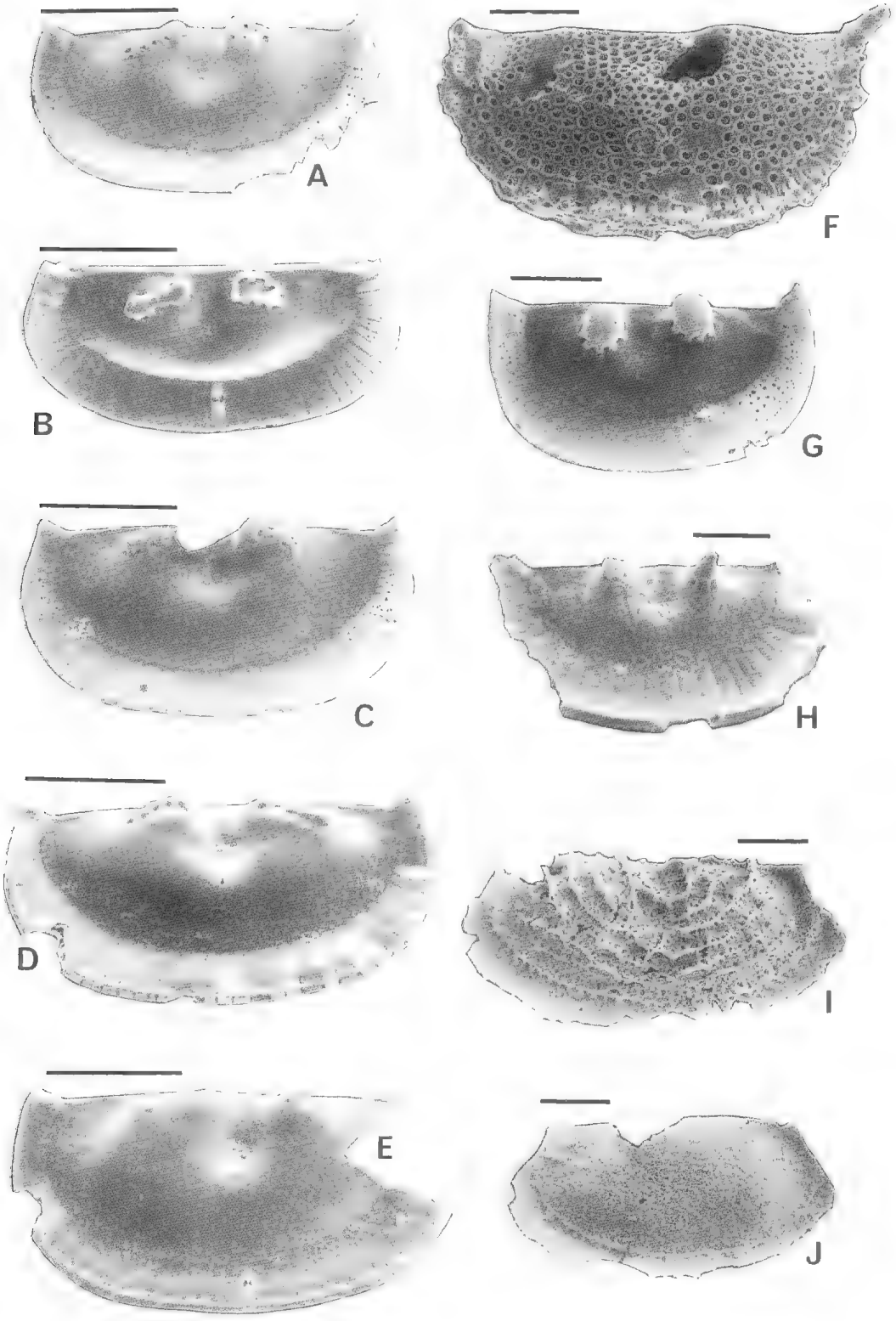
Extant species of *Manawa* occur in shallow, high-energy, marine environments; as a consequence one is led to speculate that the development of a relatively heavy naupliar carapace, although offering protection, also locked such larvae into a non or poorly dispersive, benthic mode. The fact that nauplius larvae are recovered in reasonable numbers with the adults suggests the eggs also remain quite localised during development (there is to date no evidence of brooding); no podocopid ostracods, as far as I am aware, utilise a saturation method of egg production/fertilisation to promote dispersal into the plankton. Perhaps therefore we should, as Hornibrook suggested, consider the puncliids as relict, a shadow of their former selves, the Kirkbyacea – the assumed ancestral stock of the Punciacea (Swanson, 1989a) – whose more recent (15 MY – present day) distribution (Fig. 1) in a series of isolated, widely-distributed pockets is the remains of a diversive/dispersive event which climaxed some three to four hundred million years ago.

Muscle Scars

In ostracod taxonomy, muscle scars are an extremely useful tool. Most specimens (fossil and living) of puncliid ostracods display a full complement of well-preserved scars; in contrast, representatives of the Palaeozoic Kirkbyacea, although nearly always presenting the characteristic 'kirkbyan pit' externally, more often than not have the internal muscle scar detail obliterated as a result of imperfect preservation (G. Becker, pers. comm.). In his description of the central muscle scar field of one group of kirkbyaceans, Sohn (1954) concluded '...even the best preserved specimens show only one knob on the inside of the valve without any trace of areas of attachment of accessory muscles'. Results of a recent re-examination of a number of Sohn's types indicate a variety of muscle scar types as diverse as that expected for 'modern' podocopid ostracods. The complete muscle scar pattern for puncliids was first described by McKenzie and Neil (1983) from the carapace of a new genus *Promanawa*. It consists of a central adductor group of six scars arranged biserially, two dorsal scars (the larger occurring on an elevated node) and a single mandibular scar. Frontal scars were considered absent. Such a pattern, they concluded, indicated the puncliids were benthic crawlers with a mandibular coxale capable of a transverse biting action (Swanson, 1989b). The kirkbyid pattern, assuming *Aurikirkbya wordensis* (Hamilton, 1942) is representative, also possesses two dorsal scars and a weakly developed mandibular scar (Becker, 1989). In contrast however, the central adductor area consists of an undifferentiated node and a frontal scar is also present. Becker (1989) concluded that this species was probably a nectobenthic filter-feeder. Ostracods generally exhibit a variety of often quite complex central muscle scar patterns. Thus, it seems probable that an apparent lack of differentiation in the kirkbyid node reflects imperfect preservation rather than some anatomical peculiarity. Contrasts in the central muscle scar fields, as they are presently understood, cannot therefore be used reliably as evidence against a kirkbyacean-punciacean continuum. Additionally, as noted by McKenzie and Neil (1983), *Promanawa australiensis* does have a well developed 'kirkbyid pit' externally; other members of the Puncliidae do not, presumably because they have a much weaker reticulum

Frill

'The puncliid selvage is at least an analogue of the velar ridge in Beyrichicopida and might well be homologous with it' (McKenzie and Neil, 1983). This is not supported by my work on *Manawa* which indicates that the ventral lunettes are structurally and functionally (?) quite distinct. From the outset, discussion on the relationship between the extant Puncliidae and a possible Palaeozoic predecessor has invariably been dominated by the presence/absence of homologous structures in the frill. 'In summary, then, I see no objective basis to separate *Puncia* and *Manawa* from the Palaeozoic Beyrichiidae, which as I understand them include Palaeozoic straight-backed ostracods, with both cardinal angles well defined; a marginal frill typically extends adjacent to the free margins from cardinal angle to cardinal angle; the frill is doubly walled and has inner partitions corresponding to exter-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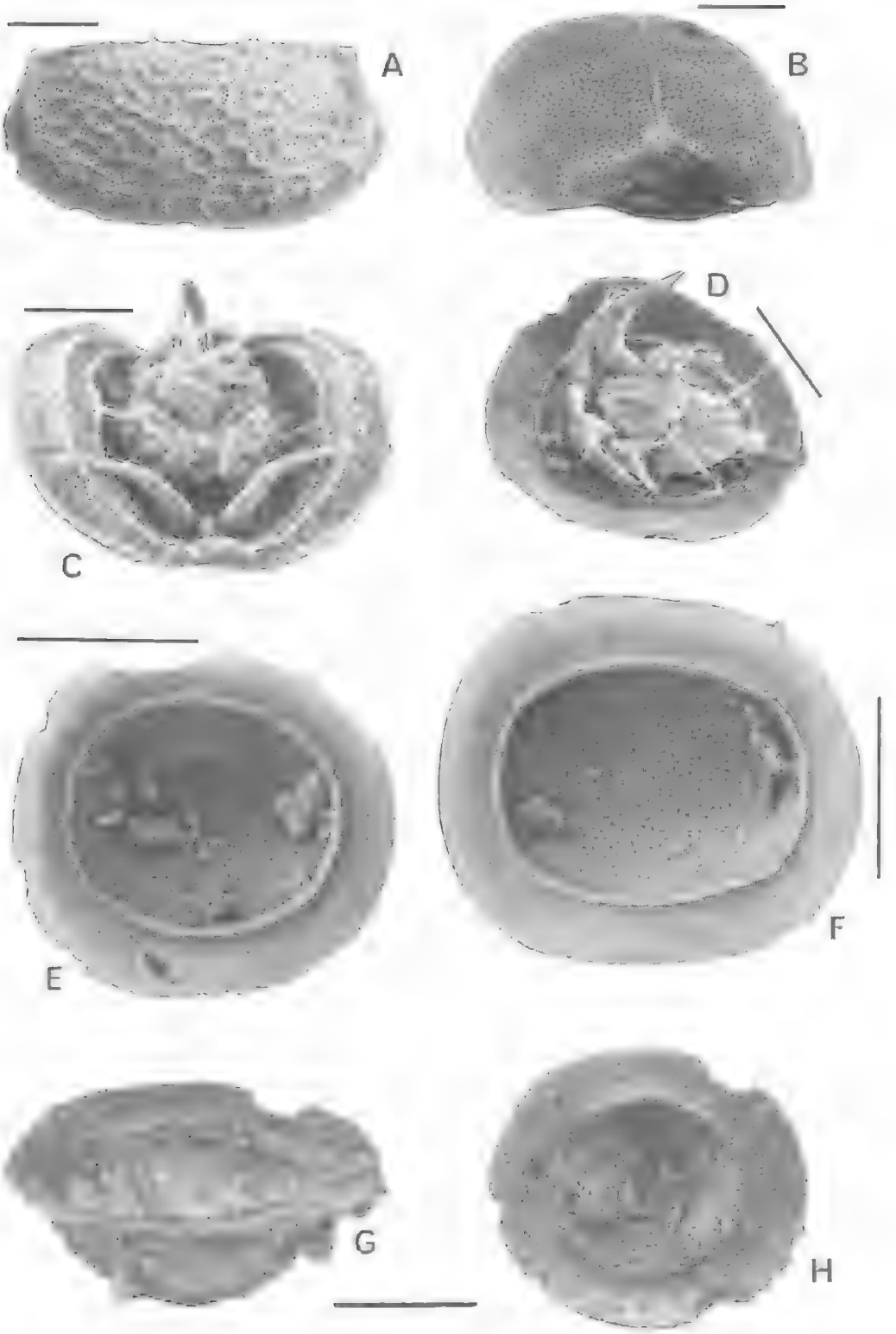
nal radial striae; in general, dimorphic pouches are formed by swelling of the frill, but such pouches are unknown in several early, primitive genera' (pers. comm. from F.M. Swartz to N. de B. Hornibrook). In most respects our assessment of the Palaeozoic ostracod frill remains unchanged, acknowledging that 'the ability of forming adventral extensions has been acquired independently in different, remotely related groups of Palaeocopa' (Jaanusson, 1957). With the availability of modern analogues/homologues (*Puncia and Promanawa*), it is now possible to compare and contrast this unique structure in detail. The total number of chambers in each frill is quite variable: 35 in *Coronakirkbya hamori*, (Kozur, 1985), noting the specimen is fragmented; 37–38? in *Coronakirkbya krejcigrafi*, fragmented; 31 in *Aurikirkbya* sp. A also fragmented (Becker, 1978); 55 in *Coronakirkbya fimbriata* (pers. comm. G. Becker). This pattern is repeated in the Punciacea: 28 in *Puncia goodwoodensis*, (Hornibrook, 1963); 40 in *Promanawa australiensis*, (McKenzie and Neil, 1983); 42 in *Puncia novaezealandica*, (Hornibrook, 1963); 43 in *Puncia* sp. A (Fig. 2E). In *Puncia* and *Promanawa* the septa which divide the frill into approximately 40 chambers are not radial pore canals (Swanson, 1985); additionally, access to the domicilium via these chambers is prevented by a thin, calcareous (?) wall or membrane (Fig. 4B). At the ventral edge of the frill, each chamber may be completely or only partially sealed, the latter resulting from incomplete calcification (Fig. 4B). A similar situation occurs in most Kirkbyacea, in the hollinacean *Oepikium* and in eurychilinids (Jaanusson, 1957), noting however that in these Palaeozoic taxa most chambers are circular/ovoid in section rather than rectangular. Although some specimens give an indication that the kirkbyid frill is composed of a row of distinct tubules, I suspect that this is an artefact of preservation/extraction and that in life the gaps between individual chambers were closed by a thin calcareous bridge. Ventral chamber exits, where present, were also extremely small since in many instances the ventral extremity of the calcareous bridge is tapered to a fine edge (Becker, 1978, pl.3, figs 17a–c, 18b). Determination of the function of the frill must await the discovery of living specimens of *Puncia* or *Promanawa*, however the possibility that these structures performed a dual role as both benthic support and gas-filled floatation-aid cannot be excluded. Adamczak (pers. comm.) has also found some form of membraneous (?) closure in the crumen of the Ordovician genus *Craspedobolbina*; this he felt could indicate a ballast/brooding function for that structure. Although McKenzie and Neil (1983) suggested the punciid frill did not appear till quite late in ontogeny ('until after the development of the anlages of reproductive characters in the soft anatomy'), evidence from imperfect ontogenetic sequences for *Puncia* (Fig 2A – E), *Aurikirkbya* and *Coronakirkbya* (Becker, 1978, pls. 3, 4) indicate that it is carried by 'early' juvenile stages as well.

Pores and Setae

Marginal pore canals with their associated setae, as found in most podocopid ostracods, do not occur within the Punciidae. Okada (1982) observed that in some taxa (*Bicornucythere bisanensis*) 'no pore runs along the marginal zone, though many pores appear to run radially in the marginal area of the carapace when observed from the lateral side with a light microscope'. One may conclude that in some podocopids the so called marginal pores are in fact wrongly identified. The stratigraphic record of ostracods gives clear evidence that the contact margin between the two valves has been a zone of considerable evolutionary innovation. Increasingly, workers on Palaeozoic assemblages are recognising a wealth of structural detail in the calcified inner lamella and it is now established that the lack of a duplicature is not a determinant of the 'palaeocopid' condition (Gramm, 1988; Schallreuter, 1988). In *Manawa* and *Puncia* the upper surfaces of the carapace are pierced by evenly-spaced, small, simple sensillia or 'normal' pores. The sole[1] of the manawan valve

FIG. 2. Scale bar = 200 μm unless otherwise stated. A–E, incomplete ontogenetic sequence for *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Note progressive reduction in sub-dorsal protuberance towards adulthood. F, *Coronakirkbya fimbriata* juvenile paratype, Lower Permian, West Texas. USNM 118486. Scale bar = 300 μm. G, *Puncia* sp.B. Cavalli Islands, New Zealand, 17 metres. Juvenile? Compare and contrast sub-dorsal nodes with Figs B and H. Scale bar = 100 μm. H, *Puncia novaezealandica* Cavalli Islands, New Zealand, 17 metres. Note sub-dorsal spines. Scale bar = 100 μm. I, *Promanawa exposita* Upper Cretaceous erratic, Insel Rügen, Jasmund, Germany. Scale bar = 100 μm. J, *Puncia levis* Upper Cretaceous erratic, Insel Rügen, Jasmund, Germany. Scale bar = 100 μm.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displays an inner (close to the contact margin) and outer row of pores from which moderately long sensory setae exit (Figs 3C, 4F). A single row of between 12–15 equivalent pores and setae may be found on the proximal edge of the upper surface of the sole (Fig. 3A). Examination of the carapace of *Puncia* between the frill and the contact zone clearly indicates that the manawan pore pattern is repeated in this genus (Fig. 4A, C).

Significantly, the outermost row of setae on the ventral (when the carapace is gaping) surface of the frill are extremely long (equal to the total width of the frill in most cases). The flexibility of these setae (Fig. 4A) suggests a sensory role within the cavity created by the frill and the substrate, rather than one associated with the lateral extremities of the frill. Clearly, as the carapace gape is increased the distance between the contact margin (and therefore the animal) and the substrate is reduced to a point where such setae would no longer drape; in fact during ambulatory excursions it is likely that they are drawn across the substrate. If the puncids are capable of dispersal by floatation, it seems likely that the animal would then assume a passive/defensive role, i.e. the carapace would be closed; during such times extreme setal length in an area surrounding the carapace opening would obviously be advantageous.

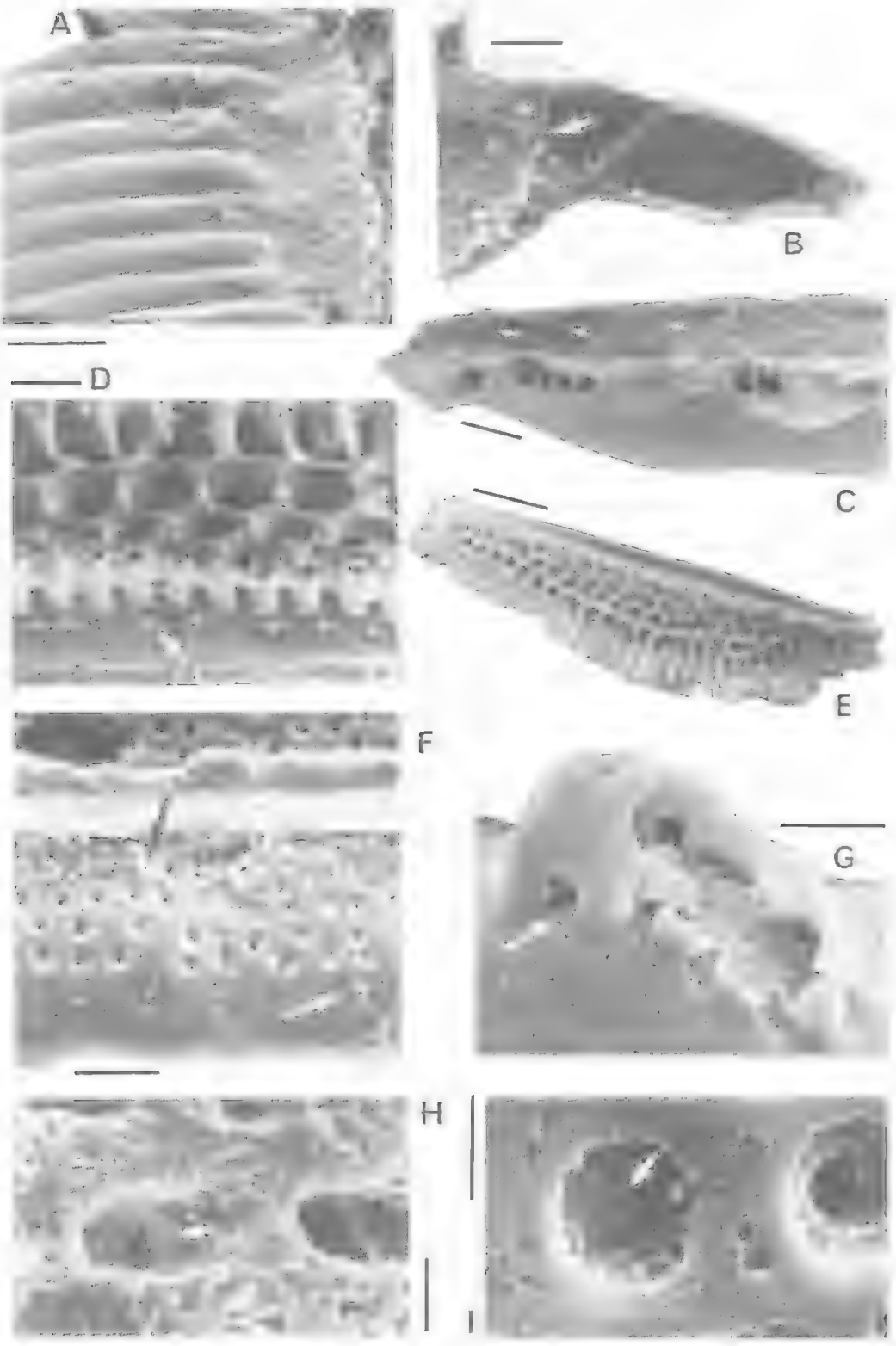
Details of pore types and their distribution for Palaeozoic ostracods remain scanty, although pores have been used as stable 'landmarks' in a recent study of evolutionary change in species of *Amphissites* from the Lower Carboniferous of Australia and Upper Caroniferous of Texas (Jones, 1988). From my examination of micrographs of *Coronakirkbya fimbriata* I see no evidence of pore exits similar to those found on the underside of the puncild frill (Fig. 4A). In all instances, however, specimen/detector angles were not optimal for such a search. One row of assumed pore exits (Fig. 4D) does clearly duplicate that found on *Puncia* close to the contact margin (Fig. 4C). Because of their position close to the contact margin/sole, these may be considered analogues of 'modern' podocopid marginal pores which penetrate the carapace between the outer lamella and the duplicature. There is some evidence to suggest that the oldest 'ostracods' (see discussion Swanson, 1989a) were also open-gaped with pore exits concentrated on the carapace sole in a fashion similar to that exhibited by *Manawa*. The setal arrangement in *Puncia* therefore could represent an evolutionary intermediate step appropriate to a wide-gaped ostracod, in which a domiciliar 'early warning' system is afforded by the frill and extremely long setae. In extant benthic podocopid ostraceds, because of their vertical orientation, carapace shape and narrow gape, the greatest concentration of the longest and most diverse sensory receptors (marginal pores and their setae) occur around the valve periphery near the contact margin.

Lobes

In both the Kirkbyacea and the Puncilidae some representatives carry externally near their dorsal margins structures ranging from 'lobes' (used advisedly since Jaanusson, 1957 considered lobes as external expressions of internal relief) as in *Aurikirkbya* and *Coronakirkbya* to bulbs, ridges and spines, as in *Puncia* (Figs 2 E, G, H). An incomplete developmental sequence for *Puncia* sp. A (Figs 2A – E) clearly illustrates the progressive reduction in relief of two perforated, mid-dorsal, admarginal ridges. Although equivalent hollows are found on the interior of the valves, they are poor reflections of the external condition, especially in juvenile valves. Structural duplicates (for which subsurface and internal carapace detail is not available) in the Kirbyacea show a similar developmental pattern through ontogeny. In species of *Puncia*, the shape of these admarginal lobes is extremely variable; elongate, bulbous and spinose forms all occurring in the New Zealand assemblage (Figs

[1] Examination of the contact margin to determine the existence of a duplicature and its relation to the outer lamella have not been undertaken. Note however the structural blue-print for the sole is established with the carapace of the nauplius.

FIG. 3. Scale bar = 100 μm unless otherwise stated. A, *Manawa tryphena* Cavalli Islands, New Zealand, 8 metres. B, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Entire carapace in life position. C, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Entire carapace in life position inverted to expose soft anatomy. D, *Manawa staceyi* Cavalli Islands, 17 metres. Nauplius. Note slight bending of carapace. E, *Manawa staceyi* Cavalli Islands, 17 metres. Naupliar carapace. Arrow indicates double-walled nature of sole. F, *Manawa staceyi* Cavalli Islands, 17 metres. Metanaupliar carapace. G, *Melopetasus syltensis* Ordovician, Isle of Sylt, North Sea, Geologisch - Palaeontologisches Institut der Universität Hamburg (GPIH 5223). Oblique view of "larval" carapace. H, Vertical view, specimen as for 3G.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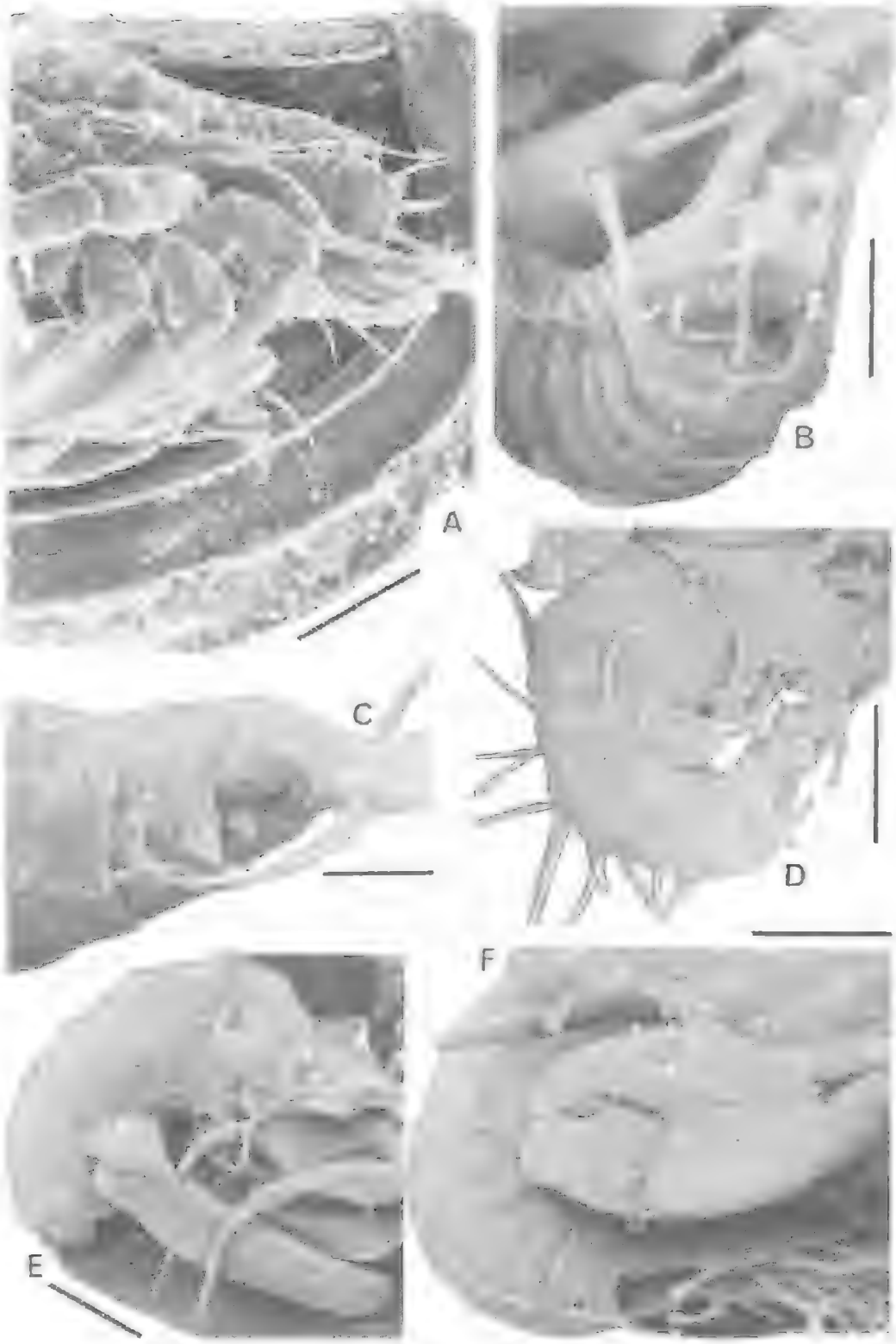
2A; 3G, H). Alternatively, in *Manawa* (Fig. 3A, B), *Promanawa* (Fig. 2I) and *Puncia* (Fig. 2J) lobate surface-swellings may occur in zones equivalent to L1 and L3 on paleocopids. Functionally, the more compact and defined ridges, knobs and spines remain a mystery. The fact that their surface expression is more pronounced earlier in ontogeny suggests some form of larval aid, noting that the subsurface detail in adults has not been investigated. Shape does not appear to influence the basic pattern of the components making up the larval admarginal 'lobe'. The dome or roof is always smooth and, unlike the rest of the carapace, unperforated; the lobal floor has a rough texture which suggests the epicuticle envelopes the entire structure. Lastly, the basal periphery of the lobe is interrupted by a number of portals in which the carapace perforations are organised in a roughly semi-circular pattern (Fig. 4G).

Internal Structure

Earlier (Swanson, 1989a), I gave an indication that the internal structure of the puncliid carapace also warranted further investigation. In both *Manawa* and *Puncia*, numerous, small (2–5μm) 'ducts' perforate the carapace wall perpendicular to the external surface, excluding lobes and frills or their equivalents (Fig. 4B,I; Swanson, 1989a, pl.2, fig.10). In benthic podocopid ostracods, the calcified portion of the carapace consists of a reticulate chitin fabric the interstices of which are filled with fine crystals of calcium carbonate; in those ostracods (e.g. pelagic myodocopids) for which flexibility and/or low weight seem a priority a lamellar chitin structure similar to that found in decapod Crustacea occurs (Bate and East, 1972, 1975). The carapace of most podocopid ostracods is also pierced by small 'normal' pores which display an enormous variety of form. Generally, such structures provide (a) exits for sensory setae and (b) accommodation for basal accessories of such setae. Both *Manawa* and *Puncia* do have normal pore exits but these are easily distinguished from the perforations presently under discussion (Swanson, 1989a, figs 2, 3, 9, 10; Fig. 4F, I) by the fact that the latter do not have setae. They may be densely-packed, simple, vertical tubules (*Puncia*, Fig. 4A, B, G) or larger countersunk forms in which the external rim is either papillate (*Manawa staceyi*, Swanson, 1989a, figs 3, 5) or spinose (*Manawa tryphena*, Swanson, 1989a, fig. 2). Both manawan types of duct are extremely complex internally with 'epicuticular' lining forming 2–3 continuous, membraneous bridges across each duct.

Studies of the calcified portions of the ostracod carapace clearly indicate that such structures are an economic solution to an architectural problem. 'The carapace is impregnated with massive layers of calcite during the molting and consequent growth process (unlike phyllopods and cladocerans). The result is a heavily armoured animal. There have existed through geologic time as many as twenty to thirty thousand species, all representing experiments in carapace design. As unlikely as the basic body plan may seem, it has obviously been successful' (Benson, 1981). As could be anticipated, therefore, the carapace of benthic ostracods is internally coherent with few breaks (normal pores) interrupting that continuity and often with external beams and ridges providing additional strength at a

FIG. 4. A, *Puncia* sp.A. Cavalli Islands, New Zealand 17 metres. Internal surface of frill (left = ventral) showing pore exit and seta (arrowed). Scale bar = 20 μm. B, *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Longitudinal section of frill showing exposed chamber and septa (upper surface = ventral). Note break is slightly oblique therefore top of next chamber also exposed. Arrow indicates 'calcareous' membrane which closes the domicilium to the frill. Note also imperfect calcification of frill at distal (right hand) extremity. Scale bar = 20 μm. C, *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Frill and external ventral periphery of domicilium. Note pore exists and setae (arrowed) below carapace sole. D, *Coronakirkbya fimbriata* Lower permian, West Texas. USNM 118488. Ventral periphery of domicilium showing assumed pore exists (arrowed). Scale bar = 30 μm. E, *Coronakirkbya fimbriata* Lower Permian, West Texas. USNM 118488. Ventral view of entire carapace, contact margin at top of picture. Scale bar = 300 μm. F, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Contact zone or sole of left valve showing two rows of pores and associated setae. Scale bar = 20 μm. G, *Puncia* sp.A. Cavalli Islands, New Zealand, 17 metres. Subdorsal protuberance. Note carapace perforations continue under portal (arrow) and contrasting texture of external carapace surface and protuberance floor. Scale bar = 50 μm. H, *Yurikirkbya wordenvi*. Middle Permian, West Texas, USNM 110232a. Partial view of surface reticulation. "Membranous" closure (partial) at base of each reticulation arrowed. Scale bar = 60 μm. I, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Note "equivalent" partial closure of one reticulation (arrowed). Scale bar = 4 μm.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minimum cost physiologically (Sylvester-Bradley and Benson, 1971, figs 1–3; Bate and East, 1972, fig. 2; Okada, 1982, text-figs 1, 16).

Why have the punciids taken the development of carapace perforations to such extremes? One possible answer lies in the unique gait of the animal. Whilst walking, both valves are carried aloft and extended, supported by relatively thin and poorly chitinised cephalic and thoracic appendages. I have already indicated that a pivotal, side to side rocking motion for *Manawa staceyi* as it walks (Swanson, 1989a) would suggest that the weight loss, resulting from a densely perforated valve, provides a partial solution to some locomotory problems. The relatively high density of perforations in *Manawa* may be used also as additional evidence to indicate the value of the frill of *Puncia* as a buoyant balancing aid. Almost all Kirkbyacea present a punctate pattern externally which duplicates that described for the punciids. Whether these negative carapace features penetrate the entire thickness of the carapace wall in the Palaeozoic forms is unknown.

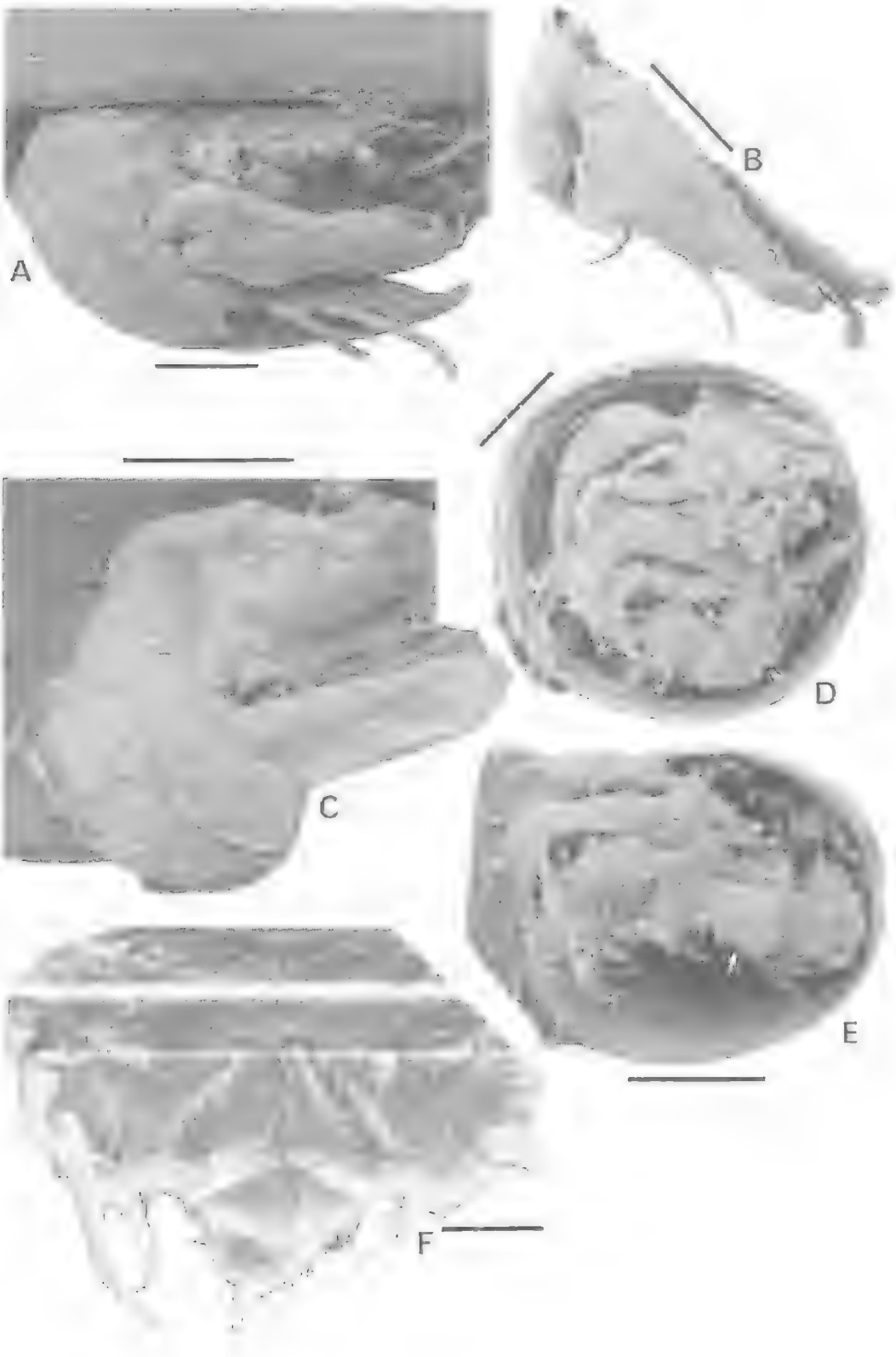
In some kirkbyids, however, the internal expression of the reticulum (if it exists) could be masked by a very thin 'calcified' membrane which may represent an extension of the inner lamella (H. Kozur, pers. comm.). Such a membraneous layer is commonly encountered in specimens of punciid ostracod and although extremely thin and transparent is sufficiently electron dense to obscure structural detail below (Swanson, 1989a, fig. 14, top right hand third of micrograph). Becker (1989) has also described subsurface closures of puncta in the kirkbyid *Aurikirkbya wordensis* which parallel those found in *Manawa* (Fig. 4H, I). I am unaware of the existence of equivalent structures in other extant ostracods.

Soft Anatomy

It is not my intention in this paper to discuss homologisation of manawan appendage segments, but detailed histological and scanning electron microscope examinations of their development through ontogeny are proceeding. One must acknowledge that whatever the resulting interpretation it will inevitably not meet with universal acceptance. 'Although the terms exopodite, endopodite, epipodite and the like are applied to ostracode limbs by various authors (not always harmoniously) in fact it is very difficult to homologise the individual parts of ostracode limbs with those of other Crustacea' (Maddocks, 1982). Previously, I suggested that the punciids have only three cephalic appendages (antennule, antenna and mandible) and four pediform thoracic legs. This condition (the possession of four thoracic segments) had also been proposed for Cambrian bradoriid ostracods (McKenzie and Jones, 1979). This is clearly at odds with the generally accepted limb/tagma formula for ostracods. 'It seems clear that the first four limbs belong to the cephalon and the last two to the thorax, but the fifth limb has been claimed for both' (Maddocks, 1982).

Anderson (1965, 1967) acknowledged that embryological studies of post-mandibular segment formation is of little value in assessing phylogenetic affinities amongst non-branchiopods because the possibility of paraphyletic derivation can never be excluded. Equivalent studies may prove useful in some areas of punciid biology (segmental origin of limbs) and phylogeny. The fundamental difficulty associated with the concept of a specific group of limbs allocated to specific tagma is how does one prove it and to what end? In most Crustacea, the mesoderm of the post-naupliar region even in its earliest stages gives evidence of differentiation into somite rudiments of post-maxillulary segments; i.e., differentiation of some mesodermal tissue into cellular clumps from which thoracic elements are derived is initiated during the naupliar stage. Consequently, it would be difficult to divide such a developmental sequence when it is effectively a continuum.

FIG. 5. Scale bar = 100 μm unless otherwise stated. A, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Posterior of body (male) including thoracic/abdominal elements and right valve. Scale bar = 40 μm. B, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Ventral oblique view of abdominal segments and furca. Anal flap arrowed. Scale bar = 20 μm. C, *Cytherella* sp.A. West Coast South Island, New Zealand 500 metres. Posterior-most abdominal segments and furca (male). Note anal flap and faecal pellet (arrowed). Scale bar = 40 μm. D, *Cytherella* sp.B. Off Kaikoura, South Island, New Zealand, 380 metres. Trunk showing segmentation and genital lobe, gravid female. E, *Cytherella* sp.B. Off Kaikoura, South Island, New Zealand, 380 metres. Trunk showing abdominal and thoracic (incomplete) segmentation and hemipenes, male. F, *Cytherella* sp.C. West Coast South Island, New Zealand, 910 metres. Ventral oblique view of furca, trunk and hemipene.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In terms of 'phylogenetic' studies, Anderson (1965, 1967) gave indication of a embryological developmental progression from that of the cephalocarids in which 'mesodermal segmentation precedes ectodermal segmentation in the primitive manner'; to the derived malacostracan condition in which 8 mesoteloblasts '....bud off successive rows of 8 cells which form the somite rudiments of individual segments, and a corresponding row of ectoteloblasts bud off ectoderm which lies outside the somite rows and becomes segmentally associated with them'. Embryological studies of 'primitive' and 'modern' ostracods may give some indication of polarity within Anderson's sequence and as a result confirm or refine present concepts of ostracod phylogeny and relationships with other Crustacea.

Abdomen

Ostracoda are generally regarded as non-segmented and cephalised (McKenzie, 1983), and their trunk and abdominal reduction, as a result of segmental loss, is the most extreme of any crustacean. Nevertheless, after a study of the chitino-skeleton of several living taxa, Schultz (1976) concluded that ostracods had abdominal segmentation earlier in their phylogeny. On the basis of this evidence and the possession of other 'primitive' limb and carapace characters, at least five groups of ostracods are repeatedly utilised as providing examples of bauplans (acknowledging such constructions only as indications of what is possible) from which 'modern' ostracods may have evolved. I have excluded the Polycopidae from this discussion because they have fewer segments in the trunk (Fig. 6D, E). Saipanettid ostracods will be discussed only in a general sense because detailed electron micrographs were not available for study. As noted by Maddocks (1982), Schulz considered *Saipanetta* to represent a phylogenetic intermediate between the ancestral Platycopina and descendant Podocopina. On the basis of the carapace detail Schallreuter and Jones (1984) included the Puncciocopa (Kirkbyacea and Puncciacea) in the extant Platycopa. Discussion of morphological aspects of the abdomen of the platycopid *Cytherella* is warranted because superficially, at least, it appears to resemble that described for *Manawa staceyi* (Swanson, 1989a).

The trunk of male cytherellids is dominated by paired hemipenes which are attached to the body on or near segments 5 to 7 (Figs 5E, F, 6A – C). Chitinous skeletal elements of the abdomen are produced anteriorly to provide what may be structural support for each hemipenis and genital lobe (in females). From the present study the precise origin of each hemipenis could not be determined; what is encouraging however is (a) its structural variation between taxa and (b) the existence of 'segmentation' (Fig. 5E, F) indicating a potential source of important taxonomic and phylogenetic information. The anlage of the hemipenis appears quite early in ontogeny (A-3 or A-4), as does abdominal segmentation (Fig. 6C).

Kornicker (1975) argued that the position of the furca relative to the anus should be given more emphasis in ostracod classification. Schulz (1976) figured the cytherellid trunk as being composed of ten segments, a telson and furca; according to him the anus was located between the tenth segment and the telson, dorsal to the furca. Kornicker (1975) also placed the cytherellid anus dorsal to the furca but behind the telson. Scanning electron microscope examination of a number of critical-point dried specimens of *Cytherella* confirms Kornicker's view. The anus occurs after the last full segment and an anal flap is present (Fig. 5C). Also of interest is the presence of a 'faecal' pellet composed of coccolith remains which may indicate that cytherellids operate as 'collectors' (Kornicker, 1975: 41) rather than as efficient benthic filterers (Cannon, 1933). Note also that the posterior-most (in life position) ventral elements of the furca may also function as 'housekeeping' accessories (Fig. 5F).

Members of the Puncciidae also have ten trunk segments with a poorly understood 'reproductive' element between segments 5 and 7. Both *Cytherella* and *Manawa* carry paired lamel-

FIG. 6. Scale bar = 100 µm unless otherwise stated. A, *Cytherella* sp.D. West Coast South Island, New Zealand, 320 metres. Ventral oblique view of male abdominal segments, furca and hemipenes. B, *Cytherella* sp.E. West Coast South Island, New Zealand 320 metres. Hemipenes and abdomen (male). C, *Cytherella* sp.B. Off Kaikoura, South Island, New Zealand 380 metres. Trunk and hemipene of juvenile male. D, *Polycope* sp. Inside Crayfish Reef, Kaikoura, South Island, New Zealand, 14 metres. Entire adult enclosed in right valve, abdominal segments arrowed. E, *Polycope* sp. Inside Crayfish Reef, Kaikoura, South Island, New Zealand, 14 metres. Entire juvenile enclosed in right valve, abdominal segments arrowed. F, *Manawa staceyi* Cavalli Islands, New Zealand, 17 metres. Metanauplius 3, anal segment and furcal anlage. Scale bar = 10 µm.

liform furcae, the setae of which differ numerically (more in *Cytherella*) and structurally (derived ?). The anal position in *Manawa* duplicates that found in *Cytherella* although in the former the anal flap occurs after the 'telson' (Fig. 5B). Both Kornicker (1975) and Schulz (1976) indicated that in *Saipanetta* the anus exits dorsal to the furca. This was seen by Kornicker (1975) as confirmation of the podocopid status of the saipanettids, since members of the Myodocopida (with which *Saipanetta* has some furcal similarity) have the anus ventral to the furca. The fact that *Saipanetta* has six trunk segments and a telson shows that its abdominal condition is more derived than that of platycopid or punciid ostracods but less than that of most extant ostracods.

Abdominal evidence for a direct punciid-platycopid link (Schallreuter and Jones, 1984) is not convincing; when combined with substantial contrasts in anatomy and carapace structure it seems unlikely. I suggest that segmentation of the trunk and abdominal configuration as found in *Cytherella* and *Manawa* is the plesiomorphic condition for ostracods. This does not exclude the possibility that both lineages developed independently.

CONCLUSIONS

1. As indicated by Hornibrook (1949) and confirmed by the present study, the carapace of the Punciidae is unlike that found on any other extant ostracods.

2. On the basis of detailed comparison of a number of key carapace characters it is concluded that punciid ostracods are the only living representatives of the predominantly Palaeozoic Kirkbyacea.

3. Similarities in abdominal soft anatomy of platycopid and punciid ostracods probably reflect the plesiomorphic ostracodal condition; contrasts in other aspects of soft anatomy and the carapace suggest that the inclusion of Punciocopa in the extant order Platycopa is unwarranted.

4. The position of some Cambrian bradoriid 'ostracodes' in which the abdomen is reduced or absent should now be reassessed.

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DISTRIBUTION OF MANGROVE SESARMID CRABS (CRUSTACEA: BRACHYURA) IN NORTHEASTERN AUSTRALIA

Sesarmid crabs have been shown to be an important component of mangrove ecosystems in tropical Australia (Robertson, 1986; Smith, 1987). Despite their dominance in mangrove forests (Jones, 1984) there is little information on the distribution of sesarmid crabs both between and within estuaries of tropical Australia. P. Davie (Queensland Museum) is working on the taxonomy of the group and is describing the new species discussed in this paper.

Materials and Sampling Sites

Pitfall traps were used to determine crab abundances. Within estuary sampling was undertaken at Hinchinbrook Island, Murray River and Cape Ferguson (Fig. 1). Between estuary sampling was undertaken in the Endeavour, Morgan, Claudie, Escape and Wenlock Rivers (Fig. 1). Opportunistic hand collections of crabs were also available from the Fly River.

Results

Five species accounted for over 90% of crabs captured at Hinchinbrook Island, Murray River and Cape Ferguson. At the mouth of these estuaries, in high salinity regions, *Sesarma semperi longicristatum* dominated in the low intertidal adjacent to the mudflat. This species was replaced by *S. messa* which dominated catches in the intertidal region up to the terrestrial mangrove interface where *S. fourmanoiri* dominated. In the medium and lower salinity regions of estuaries the mangrove region is reduced to normally less than 50m. As such, the dominant crab distributions showed no difference with intertidal position. *S. messa* dominated the medium salinity regions of the mangrove forests, giving way to *S. brevipes* in the low salinity regions. *S. brevicristatum* was sub-dominant in the medium and low salinity regions. The Endeavour, Morgan and Claudie Rivers had within estuary crab distributions similiar to those described above. The Wenlock River had a completely different sesarmid fauna to the northeast coast rivers. *S. darwinensis* dominated high salinity low intertidal regions and was co-dominant with *Sesarma* sp. nov. 2 in the mid- to high intertidal regions. In the low salinity regions *Sesarma* sp. nov. 1 dominated. The Escape River could only be sampled in the medium and high salinity regions. Within estuary crab distributions reflected both east coast and Wenlock River distributions. *S. semperi longicristatum* and *S. messa* distributions were similiar to the other east coast rivers and *S.* sp. nov. 2 replaced *S. fourmanoiri* as well as being co-dominant with *S. messa* in the medium salinity regions. In the Claudie River *S.* sp. nov. 2 was noticed adjacent to a large population of *S. fourmanoiri*. *S. messa* and *S.* sp. nov. 2 were both collected from the lower reaches of the Fly River. Fig. 1 shows the distributions of *S. messa*, *S. fourmanoiri* and *S* sp. nov. 2 found in these surveys.

Discussion

Davie (1985), in trying to explain the apparent segregation of northern coast endemic species to westwards of the Torres Strait region, suggested that current flow westwards through Torres Strait could effectively prevent northern derived species from colonizing eastern Australia, but that tropical east coast fauna could be swept via larvae or adults onto northern coasts. The present study shows that Torres Strait is not a barrier for at least one typical northern species, *S.* sp. nov. 2, which is able to penetrate some distance south along eastern Cape York Peninsula and onto the coast of Papua New Guinea. The existing distribution patterns of the dominant sesarmid crab fauna associated with mangroves in NE Australia and SW PNG can only partially be explained by simple physical coastal oceanographic features. As Davie (1985) suggested, further studies are needed to elucidate larval/adult distribution patterns for these species. If the dominant sesarmid species are 'keystone species', then knowledge of the colonization factors which determine distribution is important. As the tropical littoral zones come under increasing pressure through urbanization, development and subsequent pollution, together with the predicted effects of the 'greenhouse phenomena', a correct understanding will be imperative when the biological components of these littoral ecosystems are forced to adapt and alter distribution patterns.

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LATITUDINAL VARIATIONS IN SETTLEMENT AND SURVIVAL OF THE PEDUNCULATE BARNACLE, *POLLICIPES POLYMERUS* SOWERBY

The pedunculate barnacle, *Pollicipes polymerus*, has a broad distribution range along the West Coast of North America, from British Columbia, Canada, to Punta Abreojos, Baja California, Mexico. Brooding activity indicates two geographically disparate races corresponding to the cold and warm water temperature zones north and south of Point Conception, California (34° 16' 12" N) (Cimberg, 1981). Settlement and recruitment were monitored on two California populations that corresponded to these two races: a southern race from La Jolla (32° 52' 12" N) and a northern race from Bodega Head (38° 18' 30" N).

The cyprid larvae of *Pollicipes* settle preferentially on the peduncles of adult conspecifics facilitating settlement and recruitment measurements. The index of settlement is defined as the mean number of spat/adult; spat being individuals <1 mm rostro–carinal (R–C) length. Recruitment is defined as the mean number of juvenile barnacles in the 1–9 mm R–C length. Generally barnacles this size remain attached to the adult peduncles. From observations off La Jolla, growth of barnacles in newly established aggregates is quite rapid reaching mean R–C lengths in less than one month. By five months a mean R–C length of almost 15 mm is attained (Hoffman, 1989).

We define survival as the mean number of juvenile/adult divided by the mean number of spat/adult from the preceding month's sample. The rationale being that the spat grow quickly reaching the juvenile size range during their first month of existence. Although settlement occurs year round off La Jolla with peaks (133–290 spat/adult) occurring during the early spring, the percent survival from spat to juvenile peaks (19%) during the late autumn–early winter months. At Bodega Head, settlement occurs from April through January peaking during the early summer (22.6 spat/adult) and early winter (26–37 spat/adult). Survivorship in the northern population peaks (37–64%) during the summer months. It is proposed that the lower survivorship in the La Jolla race may be due to desiccation and/or temperature stresses exerted on the recently settled spat along the warmer and drier southern California coastline.

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PHYLOGENETIC AND BIOGEOGRAPHIC RELATIONSHIPS OF THE SUBTERRANEAN AMPHIPOD GENUS *BAHADZIA* (HADZIIDAE) IN THE WEST INDIAN REGION

As presently known, the subterranean amphipod genus *Bahadzia* is composed of 7 species: 4 from anchialine caves in the Bahamas and Turks and Caicos Islands, 1 from shallow (mostly freshwater) wells in southeastern Haiti, and 2 (descriptions in prep.) from anchialine caves on the Yucatan Peninsula and the nearby island of Cozumel. A cladistic analysis of the genus, using PAUP, suggests that nested subsets of species correspond closely to geographically separate areas. The geographic distribution of *Bahadzia* is nearly congruent with the distributions of 4 other small, monotypic subterranean crustacean genera, including the remipede *Speleonectes*, the thermosbaenacean *Tulumella*, the cirolanid isopod *Bahalana*, and the decapod shrimp *Agostocaris*. Preliminary track analysis and observations on natural history suggest that *Bahadzia* and these other stygobiont taxa, have shared a similar distributional history.

A second cladistic analysis, which compares *Bahadzia* with most other hadziid genera in the greater West Indian region, strongly supports the possibility suggested previously that *Bahadzia* is more closely allied phylogenetically with the freshwater genus *Mayaweckelia* and its sister genus (description in press) from caves on the Yucatan Peninsula, than with any other genus or group of genera in the family Hadziidae.

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THE CONSERVATION STATUS OF AUSTRALIAN FRESHWATER CRAYFISH

In a recent review of the conservation status of Australian freshwater crustaceans (Horwitz 1990), relevant issues dealing with the freshwater crayfish fauna of Australia were included; this paper summarises that information.

Twenty five species have been included in a provisional list of threatened crayfish species and these include: i) three species of smooth freshwater crayfish belonging to the genus *Cherax*; indications are that the impact of aquaculture and commercial and recreational fishing has resulted, or may result, in declines in the population numbers, genetic variability or distributional ranges for these species. ii) thirteen species of spiny crayfish: ten of these belong to the genus *Euastacus* and are confined to highland rainforested regions along the eastern seaboard of Australia where their habitat is continually threatened by agricultural and forestry activity and where only a few of the species are adequately reserved. Three very large species belonging to the genera *Euastacus* and *Astacopsis* are subjected to pressure resulting from effectively unrestrained recreational fishing and habitat alteration; and iii) nine species of burrowing crayfish belonging to the genus *Engaeus*; this genus can be characterised by a few species with broad distributions and many species with very restricted distributions. The listed species are potentially threatened by agricultural activity and again not all are adequately reserved.

Taxonomic problems have prevented proper assessments being made for species in at least four genera (*Tenuibranchiurus*, *Geocherax*, *Parastacoides* and *Engaewa*), even though populations for each of these are known to be threatened or have become extinct already.

Three major habitat types are important because they harbor distinctive freshwater crustaceans and because they are threatened in Australia. These habitats which either include crayfish in their faunal assemblages or require crayfish to create the microhabitat conditions necessary for other crustaceans, include: i) caves and mound springs, which are subjected to pressures resulting from habitat alteration (eutrophication, trampling by cattle, off-road vehicles etc.) and the effects of water drawdown; ii) highland rainforested areas in eastern Australia; and iii) other subterranean habitats, created by crayfish, including their burrows in permanent water, in seasonally inundated areas, or even on hill-slopes. Crayfish burrows harbour a distinctive faunal assemblage (termed 'pholeteros'); pollution and the alteration of water table levels are the most likely areas which might affect both the crayfish which create the habitat, and the assemblage itself.

The above issues would be at least partially resolved by improving the reservation status of identified species and habitats. Furthermore, as we increase our knowledge base we will need to modify the status given to species and habitats. The most urgent information required to update these findings must be the precise effects on species of a wide range of potentially threatening processes (effects of pesticides, heavy metals, sedimentation, swamp drainage, changes in nutrient concentrations, introduction of exotic diseases etc.). With this data, status could be reviewed on a regular basis to remove any impeding effect that outdated listings might have on appropriate developments.

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REPRODUCTION IN SAND DWELLING TALITRID AMPHIPODS: EVOLUTIONARY ADAPTATION FOR TERRESTRIAL LIFE

Within the Amphipoda reproductive potential can be evaluated by measuring a number of factors including longevity, egg size and brood production. Some previous workers have suggested that mean brood size (number of eggs) is related to habitat, decreasing from marine through supralittoral to terrestrial amphipods. Supralittoral talitrids include two ecomorphological groups (Bousfield, 1982) - the beach fleas with well described patterns of reproduction and the beach hoppers investigated here.

Brood characteristics were measured for three species of sandhoppers from Maine, USA (*Platorchestia platensis*, *Talorchestia megalophthalma* and *Talorchestia longicornis*) and two species from New Zealand (*Talorchestia quoyana* and *Talorchestia cookii*). The results were combined with literature values to provide a comparison of 10 sandhoppers, ranging in body length from 2 to 21 mm (Williams, 1978; Morino, 1978; Venables, 1981; Van Senus, 1988). Some species, for example *P. capensis*, show a good correlation between brood size and female body length whilst others, including *P. platensis* and *T. quoyana*, are more variable. The combined results suggest no obvious relationship between average female length and brood size, which varied between 2 and 24 eggs.

For *T. quoyana* from New Zealand, females of 17 mm body length (minimum rostrum to telson distance when animal was straightened) had the highest brood numbers (mean = 24.0; SE = 2.0) and the egg size was large (mean = 1.33 mm maximum diameter, SE = 0.12). Brood mortality was low over the four developmental stages. Similar patterns were seen in other genera and species of supralittoral sandhopper. The overall reproductive potential of sandhoppers is less than subtidal amphipods (Fenwick, 1984) and aquatic gammarids (Steele and Steele, 1975). They are, however, within the range recorded for beach fleas and euterrestrial amphipods (Duncan, 1969; Wildish, 1979; Friend, 1980).

Recent studies on the physiological ecology of sandhoppers show they are well adapted for aerial existence and are able to withstand greater water loss during desiccation than many marine and terrestrial species (Marsden, 1989). The sand beach habitat is physically demanding and amphipods may be exposed to vigorous wave and tidal action. In addition, storm events cause massive and rapid substratum movements and overturn. Most sandhoppers have evolved a thick and tough cuticle to resist these crushing and abrasive events and as a result their cutaneous respiration is low. Mating strategies and behaviour patterns of sandhoppers most likely provide increased brood protection. The consistency of brood size between sandhoppers of a wide size range may indicate phylogenetic constraints on reproduction. The evolution of larger eggs allows the release of larger hatchlings which are more tolerant of desiccation in the strand line habitat.

The life history strategies of sandhoppers are well adapted for the biotic and physical factors operating within the sand beach ecosystems. Compared with other talitrids, sandhoppers have achieved a larger body size, have high resistance to desiccation and have complex behaviour patterns to avoid being displaced by the tide. It is concluded that sandhoppers have evolved reproductive strategies for exploiting sand beach habitats. These are not seen necessarily as an integral part of the colonisation of truly terrestrial habitats.

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DIVERSIFIED REPRODUCTIVE TRAITS AMONG LOCAL POPULATIONS OF A FRESHWATER PRAWN, *MACROBRACHIUM NIPPONENSE* (PALAEMONIDAE: CARIDEA: DECAPODA) — EVIDENCE FOR A GENETIC BASIS

Varied egg and clutch sizes among local populations of the freshwater prawn *Macrobrachium nipponense* (de Haan) in Japan have been previously reported i.e. laying many small eggs (0.05 mm^3 in single egg volume) each spawning by estuarine populations, a few large eggs (0.1 mm^3) by inland freshwater populations, and a moderate number of medium-sized eggs by coastal lagoon populations (Mashiko, 1990). Such populations with different reproductive traits were occasionally found even within a single water system for instance, the Sagami River, central Japan (Mashiko, 1983a, b). The present study examines the genetic grounds for the different reproductive traits in this species.

Materials and Methods

Two groups of individuals, one spawning large eggs (0.100 mm^3 in mean egg volume: large-egg population), and a second producing small eggs (0.051 mm^3: small-egg population) were collected from the upper basin, and the estuary respectively of the Sagami River in 1988. The two sexes were reciprocally crossed between them, and viable F1 individuals were obtained as noted previously (Mashiko, 1984). A definite number of the F1 individuals were raised under the same defined conditions and the size and number of their eggs were examined when they bred the next year. As a morphological characteristic, the number of upper marginal teeth on the rostrum was also investigated for both of the laboratory raised and field-collected individuals.

Results and Discussion

F1 individuals produced by crossing the female of the small-egg population and the male of the large-egg population (S♀ x L♂) and by crossing the two sexes in inverse combination (L♀ x S♂), laid eggs of 0.071 and 0.075 mm^3 respectively. These egg sizes were intermediate between the large and small eggs of their parental populations. On the other hand offspring produced by crossing within the large-egg population (L♀ x L♂) and the small-egg population (S♀ x S♂) laid eggs of 0.102 and 0.051 mm^3, respectively - practically unchanged from the eggs of each parental population. Thus, the different egg sizes in this species is considered to be genetically controlled as a quantitative character. Similarly the results of crossing experiments suggested a genetic basis for different clutch sizes between the two populations.

The mean number of the upper marginal teeth on the rostrum differed significantly between the two populations in the field — 11.8 ± 0.8 (SD) and 12.5 ± 0.9 for individuals with large and small eggs, respectively ($P<0.001$, t-test). Hybridized F1 individuals exhibited an intermediate tooth number between them (12.4 ± 0.4 for both of L♀ x S♂ and S♀ x L♂), while F1 individuals obtained by crossing within populations showed virtually unchanged tooth numbers from each parental population (11.7 ± 0.9 for L♀ x L♂ and 12.7 ± 1.0 for S♀ x S♂; significant difference $P<0.001$, t-test). Therefore not only the reproductive traits, but the number of upper marginal teeth on the rostrum is considered to be genetically regulated. The mean number of the teeth varied from 11.7 to 12.9 among the 22 local populations examined in Japan. These results further confirm that this species is splitting into genetically distinct local populations with modified reproductive traits.

In all F1 individuals obtained by the crosses between and within populations, the mean survivorship was over 70% throughout the zoeal stages, and over 60% during the first six months of developmental, and there was no significant differences in survivorship noted. Almost all surviving females spawned eggs. Larvae hatching ability (defined as the ratio of the females successful in larval hatching to all berried females examined) was over 90% in all groups of F1 individuals. Thus no notable reduction in viability and fertility was recognised among the hybridized individuals. This suggests that, with reduced mobility of individuals (Mashiko, 1990) spatial separation of individuals in patchy habitats in inland waters is the major cause of reproductive isolation in this species.

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KARYOTYPE ANALYSIS OF THE RED SWAMP CRAYFISH, *PROCAMBARUS CLARKII*, BY CELL CULTURE

Karyological analysis of the red swamp crayfish, *Procambarus clarkii*, was examined using a cell culturing technique.

The specimens used for the present study were collected from a rice field near Mishima City, Shizuoka Prefecture, Japan.

The procedures of the cell culture and chromosome preparations were as follows. The bodies of the specimens were sterilized with 70% ethanol before the tissues were taken out. The antennal and genital glands were dissected out aseptically and cut into 1–2 mm pieces. The pieces of tissue were immersed in calcium- and magnesium- free Hank's solution for 20 minutes, and then in collagenase solution for 1–3 hours. The dissociated cells and small clumps of cells were collected by centrifuge (1,000 rpm for 5 minutes) and then washed in PC culture medium (Table 1). The collected cells and small clumps of cells were put into plastic tissue culturing petri dishes with new PC medium at 26°C. After the epithelial and fibroblastic cells increased sufficiently (3–7 days), colchicine (0.5 µg/ml) was added to the medium for 6–15 hours.

TABLE 1. Composition of the culture medium (PC).

Amino Acids	(mg/)	Salts	(g/l)
L-Arginine.HCl	70.0	NaCl	14.85
L-Aspartic acid	30.0	KCl	0.6834
L-Asparigine,H_2O	34.0	$MgSO_47H_2O$	0.9033
L-Aranin	25.0	$MgC1_26H_2O$	0.7451
β-Aranin	25.0	$CaC1_22H_2O$	2.2455
L-Cystin	20.0		
L-Glutamic acid	67.0		
L-Glutamin	100.0	Sugars	(g/l)
Clycine	50.0	Clucose	0.360
L-Histidine	22.0	Fructose	0.900
L-Isoleucine	20.0	Saccharose	0.684
L-Leucine	60.0		
L-Lysin.HCl	70.0		
L-Metionin	15.0	Buffer	(g/l)
L-Proline	40.0	HEPES	3.5745
L-Phenilalanin	25.0		
DL-Serin	25.0		
L-Tyrosin	40.0	Antibiotics	
L-Tryptophane	10.0	Gentamycin	100ug/ml
L-Threonine	30.0		
L-Valine	25.0	Serum	
L-Cystein.HCl	0.1	10% Fetal Bovin Serum	
L-Hydroxyproline	10.0		

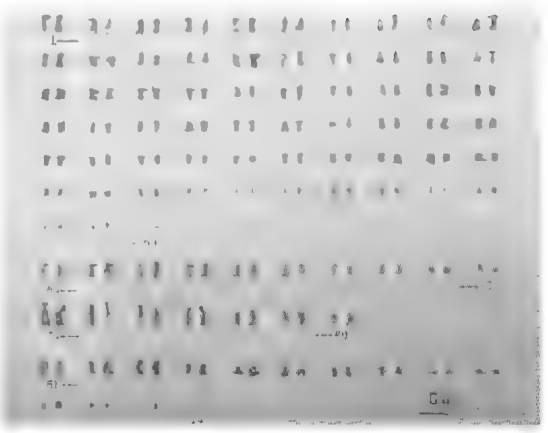

FIG.1. Karyotype of the red swamp crayfish, *Procambarus clarkii*.

The increased cells were removed by trypsin treatment and treated with hypotonic solution (0.01 M KCl) for 6–12 minutes. The cells were fixed in fresh ethanol and acetic acid solution (3:1). The chromosome preparation was modified from our routine air-drying method for Crustacean chromosome preparations (Murofushi and Deguchi, 1983).

The diploid chromosome number of *P. clarkii* was 188 (2n) with considerable variation in size as was found by Murofushi *et al.* (1984). The chromosomes were classed as 63 pairs of meta-, 10 pairs of submeta-, 7 pairs of subtelo- and 14 pairs of acrocentrics (Fig. 1). The metacentric chromosome numbers formed 67%, and others were 15% in acro-, 10% in submeta- and 8% in subtelocentrics. The culture method provided more cells in mitotic metaphase than direct treatment with colchicine. The chromosomes were also more distinct.

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MOLECULAR DIVERGENCE AND HOST RELATIONSHIPS IN NEW ZEALAND REPRESENTATIVES OF THE PEA CRAB GENUS *PINNOTHERES*

The Pinnotheridae is a family of decapod crustaceans comprising more than 120 mostly microphagous and commensal species. As symbionts of a variety of aquatic invertebrates, pinnotherids typically live in an intimate association with their host depending on it for an almost lifelong source of nourishment and shelter, together with a site for mating. The New Zealand pinnotherid fauna was thought to comprise only one species, *Pinnotheres novaezelandiae* Filhol, associated with a multitude of hosts. Recently, however, a separate species, *P. atrinicola* Page, has been described which is regarded as being host specific to the horse mussel *Atrina zelandica* Gray (Page, 1983, 1984). The biological status of the groups of crabs ascribed to the taxon *P. novaezelandiae*, but found within different host species in New Zealand waters is the focus of this paper.

Results

The biological status of the taxon *P. novaezelandiae* was investigated by a survey of electrophoretically detectable genetic variation of populations from throughout the North Island of New Zealand. Pea crabs from 11 host populations from six geographically disparate localities were subjected to cellulose acetate and poly-acrylamide electrophoresis. Forty-one enzyme systems were screened for polymorphism. Clearly resolved enzyme phenotypes were obtained at 23 presumptive loci, of which 15 exhibited polymorphism.

An analysis of electromorph frequency data revealed *P. novaezelandiae* is highly genetically structured and typified by high levels of polymorphism, results atypical of brachyuran crabs (mean proportion of loci polymorphic 99% criterion, P = 41.51; mean expected heterozygosity H_E = 0.142). Of particular significance, is the pattern of genetic differentiation observed among populations of *P. novaezelandiae*. Hierarchical F-statistics (Wright, 1978) indicated that the preponderance of inter-population differentiation can be attributed to differences in electromorph frequency among host-associated populations of *P. novaezelandiae* within a sampling locality (F_{PL} = 0.261, F_{LR} = -0.015, F_{RT} = -0.003; where P = Population, L = Locality, R = Region) (Stevens, 1990a). In addition, heterogeneity χ^2 analyses indicated significant deviations from homogeneity among host-associated populations within a locality. For example, populations from the Manukau Harbour and the Bay of Islands exhibited significant heterogeneity at 80% and 46.6% of non-monomorphic loci respectively. Geographic differentiation was thus a comparatively insignificant factor in the structuring of the sampled *P. novaezelandiae* populations. Individuals belonging to two genetically very distinct units were found within a newly recorded host species, *Mactra ovata ovata* Gray at Green and Wood Bays, Manukau Harbour (minimum genetic distance separation from other *P. novaezelandiae* D = 0.214 and 0.046 respectively) (Stevens, in press B). A Hardy-Weinberg and F-statistic analysis of populations nominally *P. novaezelandiae* found in three different species of hosts (*Perna canaliculus, Mytilus edulis aoteanus, Chione stutchburyi*) at Opua, Bay of Islands 1986–1990 indicated the host-associated populations of *P. novaezelandiae* exhibited such a pronounced pattern of homozygote excess, differentiation and disturbance from genetic equilibrium in sympatry that it is unreasonable to consider them as a single panmictic population (Stevens, in press A).

Discussion

It is concluded that significant genetical (and hence biological) discontinuities based on host origin exist within the currently recognised taxon. Such a conclusion is supported by qualitative differences in host recognition observed between different host-associated populations of *P. novaezelandiae* (Stevens, 1990b). Conservatively these discontinuities indicate host race development, although a viable alternate hypothesis would be the presence of cryptic, host-specific biological species within *P. novaezelandiae*.

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GILL AREAS AND EVOLUTIONARY RELATIONSHIPS IN TALITRID AMPHIPODS

Bousfield (1984) has identified 4 eco-morphological groupings of talitrids: palustral talitrids (1); beachfleas (2); sandhoppers (3); and landhoppers (4). Within the landhoppers, two sub-groups are recognised, one of which (4a) is believed to share ancestry with palustral amphipods, the other (4b) is considered a more recent group related to beachfleas. The groupings, although polyphyletic, provide a reasonable overview of the probable pathways of talitrid evolution. Tasmania's diverse range of temperate habitats provides representatives of all the major talitrid groups, including about 20 species of landhopper.

Published work (Moore and Taylor, 1984; Spicer and Taylor, 1986) provides data for gill surface areas in beachfleas, sandhoppers and one landhopper from Group 4a. We have added data for a palustral talitrid, Group 4a landhoppers (6 spp.) and a Group 4b landhopper, allowing us to review all of Bousfield's talitrid groupings in the context of gill surface area relationships.

Results and Discussion

Relationships between gill area and dry body weight are described by the typical allometric relationship ($y = ax^b$), enabling statistical comparisons of regression slopes and elevations to be carried out on double log transformed data for all 8 species investigated. Only 2 species (within one genus) differed in slope, indicating that allometric relationships were similar in all species and groups; visual comparison indicates that this holds for published data also. However, most comparisons of elevation were statistically significant, indicating that differences between species are maintained throughout the size range.

To relate these data to Bousfield's hypotheses, gill areas were calculated from our and published data for a standardised, 2mg dry weight, animal — a realistic size for our species although a small beachflea or sandhopper. Calculated areas are consistent with the proposed phylogenies. Thus the semi-aquatic palustral species exhibited the largest area; although no data for Hyalidae exist the close correspondence with aquatic gammarids (calculated from Moore and Taylor, 1984) suggests that the palustral species resemble the aquatic ancestral condition. In comparison sandhoppers (Spicer and Taylor, 1986) have by far the smallest areas, in keeping with the intense desiccatory stress imposed by their long evolutionary history on sandy beaches. The beachfleas (Spicer and Taylor, 1986), commonly found under wrack and presumably subjected to reduced stress, show a lesser, but still considerable, reduction. The area calculated for the Group 4b species was within the beachflea range and was the smallest of any landhopper investigated, consistent with the proposed supralittoral phase in the group's history. Most Group 4a landhoppers approximated the palustral species, supporting the argument that they entered moist, non-desiccatory terrestrial habitats without an intervening supralittoral phase. Those Group 4a species that did exhibit a clear reduction in gill area are apomorphic species (Friend, 1987).

However, consideration of the partitioning of area between the five pairs of gills raises questions. Landhoppers show very marked reduction in the area of gills 3, 4 and 5 compared with the palustral species, presumably because they carry fewer and larger eggs than aquatic amphipods. The similarity in total area between Group 4a and palustral talitrids is achieved by a pronounced increase in the area of gills 2 and 6, this is inconsistent with the view that gill areas in these animals represent a 'carry over' from aquatic origins and suggests that terrestrial selection pressures have been involved.

It is not immediately apparent how the large area of gills 2 and 6 might be adaptive since it is counterproductive for control of water loss and is unlikely to be necessary for improved oxygen uptake or ammonia excretion in these permeable animals. Preliminary work suggests that, like aquatic amphipods, landhoppers use their gills for ion uptake, and ion availability may be a major determinant of terrestrial survival (Spicer *et al.*, 1987). Since permeability restricts landhoppers to moist microhabitats, it may also be that it has proved easier to retain the low blood PCO_2 characteristic of aquatic organisms, and increase the areas of gills 2 and 6 to facilitate CO_2 removal, than to evolve efficient blood buffering capacity with high internal CO_2 concentrations as in other terrestrial taxa.

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COMPARISON OF MORPHOLOGICAL AND MOLECULAR PHYLOGENY OF THE DECAPODA

LAWRENCE G. ABELE

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Decapod phylogenies based on morphological and molecular data are similar in topology for the taxa in common; both trees recognise a dendrobranchiate lineage, a caridean lineage (including procaridids), a stenopodidean lineage, and a reptant lineage. The two trees are compared with respect to homoplasy levels using consistency indices, homoplasy excess values, and bootstrap values for the various nodes. In all cases the molecular data exhibit considerably less homoplasy. It is suggested that molecular and morphological data be viewed as complementary because in many cases comparative morphology has suggested the research question. Significant questions on decapod phylogeny remain with the reptant infraorders. □ *Decapoda, phylogeny, morphology, molecular data, nucleotide sequences, 18S ribosomal RNA.*

Lawrence G. Abele, Department of Biological Science, B-142, Florida State University, Tallahassee, FL 32306, USA; 20 March, 1991.

Decapods are among the best known of the crustaceans, although their phylogenetic relationships are poorly understood. Recent reviews of decapod phylogeny (Burkenroad, 1963, 1981; Glaessner, 1969; De Saint Laurent, 1979a; Felgenhauer and Abele, 1983; Abele and Felgenhauer, 1986) have resulted in recognition of a fundamental division of the decapods into two groups, the Dendrobranchiata (penacid shrimp and their relatives) and the Pleocyemata (all other decapods). This division is based on the fact that all pleocyemates incubate their embryos on the pleopods, with eclosion occurring at a zoeal or later larval stage, in contrast to dendrobranchiates and euphausiaceans, which release embryos free into the sea with eclosion occurring at a naupliar stage. Furthermore, dendrobranchiates have a unique gill morphology consisting of a central branchial axis and paired lateral branches each with subdivided secondary rami (= the dendrobranchiate condition). The male petasma might also be a unique dendrobranchiate feature as Burkenroad (1963) suggested that this structure is not homologous to that found in euphausiaceans and some reptants. All other morphological characters generally cited for dendrobranchiates are either found in other taxa or are pleisiomorphic and uninformative relative to the Decapoda.

The above analyses and diagnoses were based on morphology, while the analysis of Kim and Abele (1990) used nucleotide sequences of 18S ribosomal RNA in a phylogenetic study of selected decapods. Here I briefly review the classification and phylogeny of the Decapoda and, using new sequence data for a dendrobranchiate, several carideans and a brachyuran crab, compare molecular results to those obtained from morphological data.

MATERIALS AND METHODS

A summary classification of the Decapoda is given in Table 1 along with a list of the decapod taxa used in this study. Kim and Abele (1990) provided details on sequencing methods and alignment of the sequences, and all molecular data have been deposited in GenBank. The list of morphological characters is given in Appendix I (derived from Abele and Felgenhauer, 1986, figs 2–5). Phylogenetic analyses were performed using PAUP 3.0 (Swofford, 1990). A dendrobranchiate shrimp, *Penaeus aztecus*, was used as the outgroup for the molecular data while *Euphausia* sp. was used as the outgroup for the morphological data.

RESULTS

Molecular Analysis

Maximum parsimony analysis yielded a single minimum-length tree (Fig. 1a) of 432 steps with a consistency index of 0.692 based on 195 phylogenetically informative characters. The two dendrobranchiates are joined by a node (A) that is 35 steps from the node (B) joining the pleocyemates (*Penaeus aztecus* is 17 steps from the node (A) while *Sicyonia brevirostris* is 40 steps from

TABLE 1. Summary classification of the Decapoda (modified from Bowman and Abele, 1982) with respect to the taxa used in this study.

	Number of Nucleotides
Decapoda	
Suborder Dendrobranchiata	
Family Penaeidae	
Penaeus aztecus Ives	1,301
Family Sicyoniidae	
Sicyonia brevirostris Stimpson	1,884
Suborder Pleocyemata	
Infraorder Caridea	
Family Alpheidae	
Alpheus heterochaelis Say	1948
Family Atyidae	
Typhlatya rogersi Chace and Manning	1995
Family Procaridae	
Procaris ascensionis Chace and Manning	1869
Family Palaemonidae	
Palaemonetes kadiakensis Rathbun	1,153
Infraorder Stenopodidea	
Family Stenopodidae	
Stenopus hispidus (Olivier)	1,415
Infraorder Astacidea	
Family Astacidae	
(several taxa, morphological data)	
Family Cambaridae	
Procambarus leonensis Hobbs	1,721
Infraorder Thalassinidea	
Family Axiidae	
Coralaxius abelei Kensley and Gore (morphological data)	
Infraorder Brachyura	
Family Raninidae	
Ranilia muricata H. Milne Edwards	1,127
Family Portunidae	

the node). The next branch off the tree (B-C) is 33 steps and leads to a node (C) that joins all caridean shrimp, including *Procaris ascenscionis* which comes off this node (C) with a branch length of 19; a relatively long branch (C-D) of 52 steps leads to a node (D) joining the three remaining caridean shrimps [an atyid, *Typhlatya rogersi*, comes off first with a branch length of 27 steps followed by a branch (D-E) of 24 steps leading to a node (E) joining an alpheid, *Alpheus heterochaelis*, with a branch length of 19 steps and a palaemonid, *Palaemonetes kadiakensis*, with a branch length of 14 steps]. Returning to the main branch, there is a segment (B-F) of 28 steps with a side branch of 35 steps leading to a stenopidid shrimp, *Stenopus hispidus*. The next branch (F-G) is 38 steps and leads to a node (G) with one branch of 11 steps leading to the crayfish *Procambarus leonensis*; the next branch (G-H) is 14 steps and leads to a node (H) that joins two brachyuran crabs, *Ranilia muricata* with a branch length of 8 steps and the blue crab *Callinectes sapidus* with a branch length of 18 steps.

The data were also evaluated by the bootstrap method (Felsenstein, 1985) which involves random sampling of the original data set with replacement until a new data set equal in size to the original is obtained. Each of the new data sets (in this case 100) is analyzed using maximum parsimony and the number of times each node occurs is recorded. This method provides an indication of the level of support for each node in the tree with 95% considered to be statistically significant. The bootstrap value joining the two dendrobranchiates is 95% while that of (B) joining all pleocyemates is 94%. The values for the caridean shrimps (C, D, E) are 99–100%. The value for the node (F) joining the so-called reptant taxa is 86%, if *S. hispidus* is considered a member of this group. The value is 96% (node G) for taxa traditionally considered to be reptants and the value for the node joining the two brachyuran crabs is 100%. These results suggest considerable support for the relationships diagramed in Fig. 1a.

Morphological Analysis

Maximum parsimony analysis of the morphological data using *Euphausia* sp. as the outgroup yielded a single minimum length tree (Fig. 1b) of 74 steps with a consistency index of 0.568 based on a total of 40 phylogenetically informative characters. The first branch to come off the tree with a length of 3 steps leads to *Penaeus*; this is followed by a branch that leads to a node (C) joining *Procaris* (5 steps) and a caridean (8 steps); the next branch leads to *Stenopus* (2 steps) while the terminal node joins an axiid (9 steps) and an astacid crayfish (2 steps).

A bootstrap analysis reveals limited support (55%) for the pleocyemate lineage (node B) and somewhat larger values for the Caridea (67%, node C), the Stenopididea (65%, node D) and the Reptantia (82%, node E).

DISCUSSION

Comparison of Trees

Comparison of Fig 1a and 1b reveals that the two trees have similar topologies for the taxa in common. Both trees recognize a dendrobranchiate lineage separate from all other decapods,

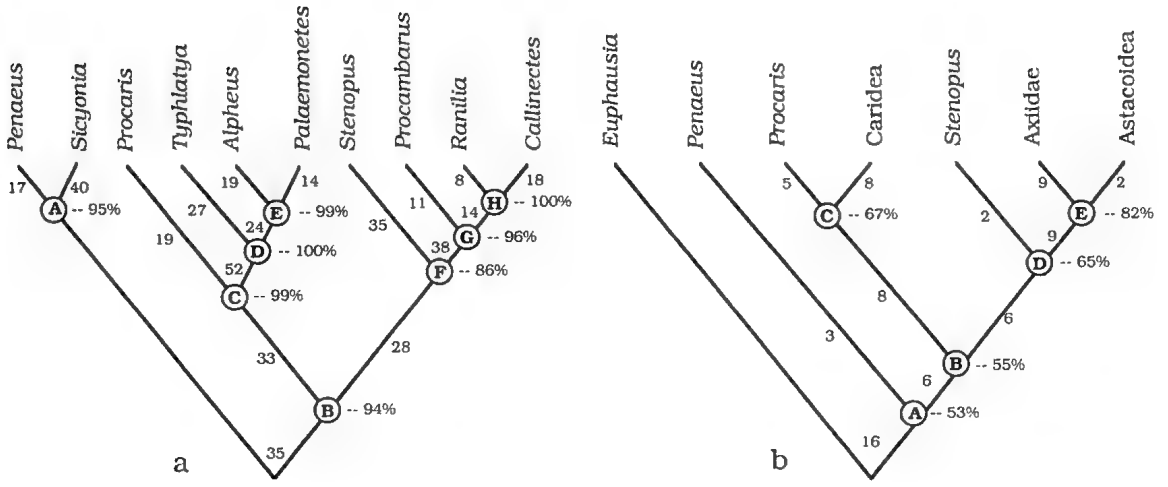

FIG. 1. Relationships among the taxa shown as inferred by maximum parsimony analysis. a, based on nucleotide sequences of 18S ribosomal RNA, tree length = 432 steps based on 195 characters, CI = 0.692. b, based on morphological data, tree length = 74 steps based on 40 characters, CI = 0.568. % numbers adjacent to nodes are bootstrap values based on 100 replicates.

a caridean lineage, a stenopodidean lineage and a reptant lineage.

There are several approaches to comparing and evaluating the reliability of phylogenetic hypotheses based on maximum parsimony (Archie, 1989b). A common approach has been to compare consistency indices (CI) among the trees. CI is the minimum number of steps on the tree when no homoplasy is present divided by the observed number of steps. While this seems a reasonable approach to use, Archie (1989a) showed that the CI is highly and negatively correlated with the number of taxa and proposed another statistic for comparative purposes. In the present case the number of taxa does not differ much (7 *vs* 10) and the CI for the molecular data set of 10 taxa is higher than that for the morphological data (0.692 *vs* 0.568). Another approach (Archie, 1989b) is to compare the maximum number of steps possible on a tree to both the minimum possible and the observed number of steps.

For the morphological data the maximum tree length is 104, the minimum length is 42 while the observed is 74. Archie (1989b) suggested using these values to calculate a ratio, HERM (= homoplasy excess ratio maximum), which is the maximum number of steps minus the observed divided by the maximum number minus the minimum possible number of steps. Thus the value is 1 when no homoplasy is present and 0 when there is no phylogenetic information in the data. For the morphological data, HERM = 0.484. This somewhat low value is not unexpected given the relatively low bootstrap values obtained for each of the tree nodes (Fig. 1b). An examination of the characters mapped out on the tree reveals that 25 of the 40 reverse at least once and only 15 (indicated by an asterisk in Appendix I) map without homoplasy. It is interesting to note that of the latter 15 characters, 10 are concerned with the presence/absence of exopods and gills on the pereiopods.

The molecular data demonstrate considerably less homoplasy. The maximum tree length (without *Sicyonia,* which was dropped to facilitate comparisons) is 508, the minimum possible is 275 and the observed is 340 resulting in a homoplasy excess ratio maximum (HERM) of 0.721. This relatively high value is consistent with the high bootstrap values obtained (Fig. 1a).

Does this mean that molecular data are more reliable than morphological data with reference to decapod phylogeny? Probably not as it may be possible to select a different suite of morphological features with less homoplasy. It should also be emphasized that a single morphological character may be of such fundamental biological importance that it alone can provide strong evidence for evolutionary relationships. No single nucleotide site could ever provide such evidence. The morphological and molecular data sets should be viewed as complementary. Centuries of comparative morphology have provided the background and in many cases posed the interesting questions that may be further investi-

TABLE 2. Comparison of data derived from parsimony analyses of morphological and molecular data.

	Molecular	Morphological
Number of Taxa	10	7
Number of Variable Characters	582	57
Number of Phylogenetically Informative Characters	195	40
Tree Length	432	74
Consistency Index	0.692	0.568
HERM	0.721	0.459
Bootstrap values		
Pleocyemata	94%	55%
Caridea	100%	67%
Stenopodidea	86%	65%
'Reptantia'	96%	82%
Brachyura	100%	NA

gated with molecular data. For example, the comparative morphological investigation of Wingstrand (1972) on pentastome spermatozoan morphology posed the question of their relationship to crustaceans that caused Abele *et al.* (1989) to further test (and support) this relationship using molecular data. What that study and the present one do indicate is that nucleotide sequences of 18S ribosomal RNA are reliable data for reconstructing crustacean phylogenies.

Status of Decapod Phylogeny

Analyses of morphological data (Burkenroad, 1963, 1981; Schram, 1984; Abele and Felgenhauer, 1986) suggested abundant support for the recognition of the Dendrobranchiata. Kim and Abele (1990) provided molecular evidence in support of this group and inclusion here of a second dendrobranchiate (*S. brevirostris*) supports these previous results. Although Abele and Felgenhauer (1986) discussed reasons for rejecting the concept of a taxon Natantia (originally defined to include penaeids, stenopodids and carideans), the term is occasionally used in defining spermatozoan types because penaeids, procaridids and carideans all have 'unistellate' or thumbtack spermatozoa (Jamieson, 1991; Felgenhauer and Abele, 1991). In contrast, stenopodids, the other so-called natant, have a very different spermatozoan structure (Felgenhauer and Abele, 1991) and I would only repeat an earlier conclusion (Burkenroad, 1963; Abele and Felgenhauer, 1986) that there is little evidence to support the concept of a Natantia and many reasons for rejecting it.

Additional questions on classification and relationships centre on taxa in the suborder Pleocyemata. One area of discussion concerns the limits of the Caridea and whether or not it includes procaridid shrimp. Schram (1986) recognized two infraorders, the Procaridídea and Caridea, placing them in the Suborder Eukyphida, a term coined by Boas for carideans and resurrected by Burkenroad (1981) and Schram (1984, 1986). The disagreement is really one of terminology because there is ample morphological evidence that procaridids and carideans share a common origin (Abele and Felgenhauer, 1986; Kensley and Williams, 1986; Schram, 1986), a conclusion that is strongly supported by the molecular data presented here. It is also clear that procaridids are separated from other carideans by a relatively long molecular distance (52 steps, Fig. 1a) as well as by differences in gill formulae (Burkenroad, 1984; Abele and Felgenhauer; 1986, fig. 7). The term Caridea is well known and in common usage and, therefore, I would propose to continue its use recognising within it a taxon Procaridídea Chace and Manning, to include the two genera *Procaris* and *Vetericaris*, and a second taxon Eucaridea to include the remaining caridean taxa.

The taxon Stenopodidea continues to be problematic. De Saint Laurent (1979a) and others (Felgenhauer and Abele, 1983; Schram, 1984; Abele and Felgenhauer, 1986) considered the Stenopodidea to be an independent taxon more closely related to reptants than to any other group. The molecular analysis of Kim and Abele (1990) and that reported here supports these earlier results. In addition, as mentioned above, the spermatozoan morphology of *S. hispidus* (Felgenhauer and Abele, 1991; Jamieson, 1991) is unlike that of any other decapod known, emphasising its rather isolated position.

There has been considerable discussion over the classification and phylogeny of the Brachyura (see Rice, 1980, 1983). Recent data on spermatozoan ultrastructure (Jamieson, 1989, 1990, 1991) and nucleotide sequences of 18S ribosomal RNA (Spears *et al.*, in prep.) support the exclusion of the Dromiacea from the Brachyura as well as the inclusion of the Raninidae in the Brachyura. The notion of the Podotremata, Heterotremata and Thoracotremata as taxonomic or phylogenetic units based on the location of the male and female genital openings appears to be unwarranted, for these groups appear to be morphological grades, as stated by Guinot (1977), rather than phylogenetic groupings.

The challenge now facing those interested in

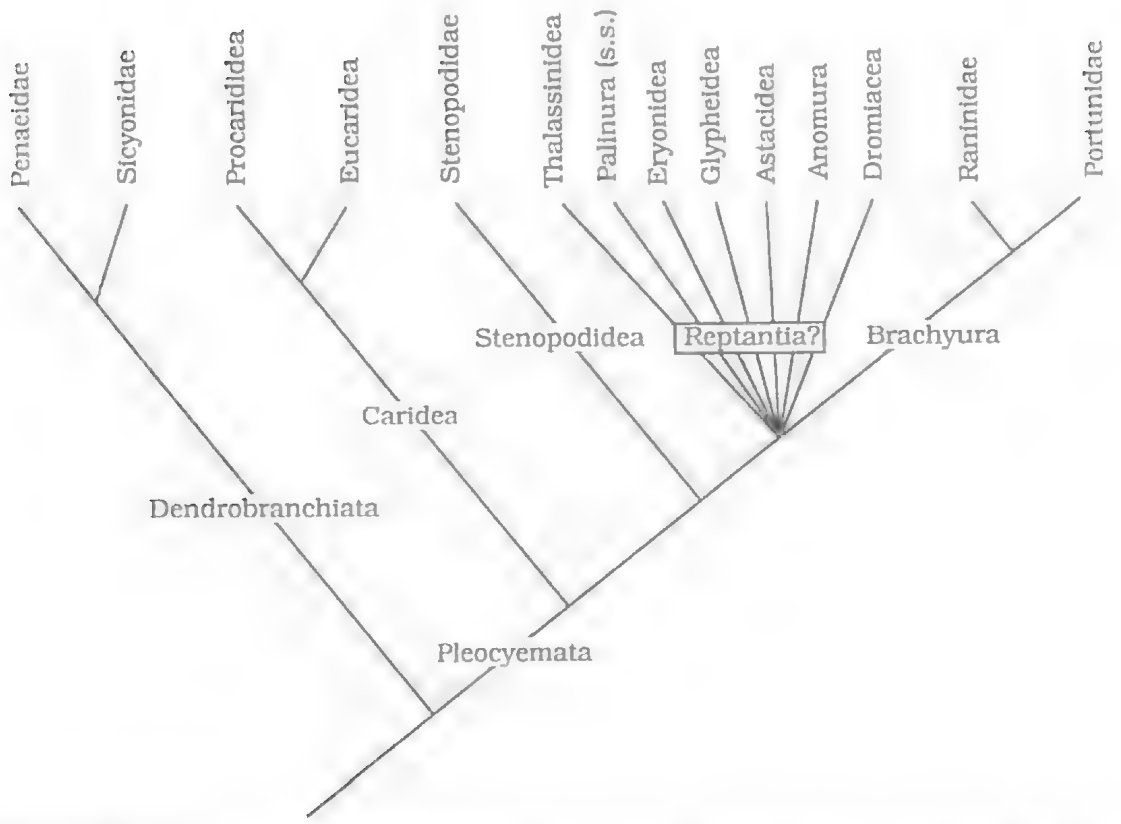

FIG. 2. Summary of phylogenetic relationships of the Decapoda based on both molecular and morphological data.

decapod evolution centres on taxa placed in the Reptantia. There seem to be as many groupings of these taxa as there are authors who have studied them. De Saint Laurent (1979a) and Burkenroad (1981) did not evaluate phylogenetic relationships but simply listed the groups that each recognized as belonging to the Reptantia if indeed such a group is even valid. For example, De Saint Laurent (1979a) listed the following reptant taxa: Scyllaridea, Eryonidea, Glypheidea, Astacidea, Thalassinacea, Anomala, Dromiacea, and Brachyura. Burkenroad (1981) listed only the Palinura, Astacina, Thalassinidea, Anomala, and Brachyura. Bowman and Abele (1982) and Schram (1986) listed the Astacidea, Thalassinidea, Palinura, Anomura, and Brachyura as infraorders in the Suborder Reptantia. The major differences among the authors are that De Saint Laurent (1979a) splits the Palinura into the Scyllaridea (although by priority of the constituent taxa one might select Palinuridea as the appropriate name), Glypheidea and Eryonidea and separates the Dromiacea from the Brachyura. The recognition of the Glypheidea as a distinct lineage by De Saint Laurent is based on study of the only extant member of this group, *Neoglyphea inopinata* (Forest and De Saint Laurent, 1981). She further suggested that the form of eryonid referred to as *Eryoineicus* is an adult secondarily adapted to a bathypelagic existence rather than a larval form as suggested by others. In addition, Burkenroad (1981) pointed out that eryonoids differ in a number of features from scyllarids and questioned the unity of the Palinura. Hence, there appear to be sufficient differences among the members of Palinura (*sensu lato*) to warrant separating the groups, especially to call attention to the need for further study. Although some preliminary molecular data are available (unpublished) they are insufficient to comment further at this time. There are also sufficient differences, noted by De Saint Laurent (1979b), among members of the Thalassinidea to raise

questions about the phylogenetic status of this taxon.

In conclusion, a proposed phylogeny summarising our current knowledge based on morphological and molecular data is given in Fig. 2. The major questions that remain concerning decapod phylogeny and classification at the 'Infraorder' level are with the so-called reptant groups.

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APPENDIX I. LIST OF CHARACTERS AND CODES USED. ASTERISKS INDICATE CHARACTERS THAT MAP WITHOUT HOMOPLASY

ANTENNA II
- *1. Scaphocerite present (0), reduced or absent (1)

MAXILLA I
- 2. Palp: present and segmented (0), fused 11), absent (2)

THORACOPOD I (MAXILLIPED 1)
- 3. Modified as a maxilliped; no (0), yes (1)
- 4. Endopod; 7 segments (0), <7 segments (fused and/or rudimentary) (1), absent (2)
- 5. Exopod; pediform with flagellum (0), lamellar with flagellum (1), lamellar without flagellum (2)
- 6. Exopodal lobe (= caridean lobe); present (1), absent (0)

THORACOPOD II (MAXILLIPED II)
- 7. Modified as a maxilliped: no (0), yes (1)
- 8. Endopod; 7 segments (0), <7 segments (fused and/or rudimentary) (1), pediform (0), lamelliform (1)

THORACOPOD III (MAXILLIPED III)
- 9. Modified as a maxilliped; no (0), yes (1)
- 10. Endopod; 7 segments (0), <7 segments (fused and/or rudimentary) (1), completely fused (2)

PEREIOPOD I
- 11. Distal segments of endopod; achelate (0), subchelate (1), chelate (2)
- *12. Exopod; present (0), reduced (1), absent (2)

PEREIOPOD II
- 13. Distal segments of endopod; achelate (0), subchelate (1), chelate (2)
- *14. Exopod; present (0), absent (1)

PEREIOPOD III
- 15. Distal segments of endopod; achelate (0), subchelate (1), chelate (2)
- *16. Exopod; present (0), absent (1)

PEREIOPOD IV
- *17. Exopod; present (0), absent (1)

PEREIOPOD V
- *18. Exopod; present (0), absent (1)

THELYCUM
- 19. Thelycum on female; present (0), absent (1)

PLEOPOD I
- *20. Petasma; present (0), absent (1)
- 21. Appendix interna; present (0), absent (1)
- 22. Appendix masculina; present (0), absent (1)
- *23. Configuration of pleopod; biramous (0), uniramous (1)

PLEOPOD II
- 24. Appendix interna: present (0), absent (1)
- 25. Appendix masculina; present (0), absent (1)

PLEOPOD III
- 26. Appendix interna; present (0), absent (1)

PLEOPOD IV
- 27. Appendix interna; present (0), absent (1)

PLEOPOD V
- 28. Appendix interna; present (0), absent (1)

UROPOD
- 29. Diaeresis; absent (0), present (1), present with accessory spines (2)

FOREGUT
- 30. Cardiac pads; absent (1), present (0)
- 31. Ossicles; all present (0), loss of some (1), loss of all (2), modified (3)

DEVELOPMENT
- *32. Larva: nauplius (0), zoea (1)
- *33. Eggs; free (not incubated) (0), attached to pleopods (incubated) (1)

GILLS
- 34. Gill structure; dendrobranchiate (0), trichobranchiate (1), phyllobranchiate (2)

SECOND ABDOMINAL PLEURON
- 35. Arrangement of second pleuron; nonoverlapping (0), overlapping (1)

BRANCHIAL FORMULA

Maxilliped III
- 36. Podobranch; present (0), absent (1)
- 37. Arthrobranch; two present (0), one present (1), absent (2)
- 38. Pleurobranch; present (0), absent (1)

Pereiopod I
- 39. Podobranch; present (0), absent (1)
- *40. Arthrobranch; two present (0), one present (1), absent (2)
- *41. Pleurobranch; present (0), absent (1)

Pereiopod II
- 42. Epipod; present (0), absent (1)
- 43. Podobranch; present (0), absent (1)
- *44. Arthrobranch; two present (0), one present (1), absent (2)
- 45. Pleurobranch; present (0), absent (1)

Pereiopod III
46. Epipod; present (0), absent (1)
47. Podobranch; present (0), absent (1)
*48. Arthrobranch: two present (0), one present (1), absent (2)
49. Pleurobranch; present (0), absent (1)
Pereiopod IV
50. Epipod; present (0), absent (1)
51. Podobranch; present (0), absent (1)
*52. Arthrobranch; two present (0), one present (l), absent (2)
53. Pleurobranch; present (0), absent (1)
Pereiopod V
54. Epipod; present (0), absent (1)
55. Podobranch; present (0), absent (1)
56. Arthrobranch; two present (0), one present (1), absent (2)
57. Pleurobranch; present (0), absent (1)

APPENDIX II. INPUT DATA MATRIX

Taxon	1111111111222222222233333333334444444444555555551234567890123456789012345678901234567890123456789012345678901234567
Euphausia	0100000000000000000000000000000010000000000000000000000000
Penaeus	0010201010202020000011011111110000010010001000100110011110
Procaris	0111101010000000001110011111111011211111100110011001101111
Caridea	0111111111202000001100000000101112110011011101110111011110
Stenopus	0110O01010212121111110111111100O1110100100O100O100O1001110
Axiid	1211201010212101111100100000100112100100100000000001001111
Astacoid	1110001010212121110110111100100111102100100010001000011110

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ULTRASTRUCTURE AND PHYLOGENY OF CRUSTACEAN SPERMATOZOA

B.G.M. JAMIESON

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The flagellate spermatozoon of the Remepidia (*Speleonectes*), differs from the invertebrate 'primitive sperm' (aquasperm) only in lacking a mitochondrial midpiece and in containment in a spermatophore. A flagellum occurs elsewhere in Crustacea only in the Maxillopoda (Ascothoracica, Cirripedia, Branchiura, Mystacocarida) and in the related Pentastomida, only the Ascothoracica, of these, retaining the plesiomorphic basal flagellar insertion. Cephalocarid (*Hutchinsoniella*) sperm resembling those of remipedes but lacking the flagellum may represent the ground plan for the Phyllopoda, hitherto thought to be the simple, amoeba-like sperm seen in euphyllopods and conchostracans. The *Nebalia* sperm, lacking an acrosome and with microtubular arms, supports the phyllopod status of phyllocarids. Copepod sperm show no clear affinities with other groups, though the stellate acrosome-less sperm of the cyclopoid *Chondracanthus* resembles that of some branchiopods. Ostracod sperm include a filiform type performing undulatory waves by means of wing-like structures originating from the endoplasmic reticulum. In the Malacostraca, stomatopod (*Squilla, Oratosquilla*) sperm are ovoidal, lacking appendages, with acrosome (re-acquired?) and a perforatorium; absence of a nuclear membrane, and diffuse chromatin are decapod tendencies: unusual, doublet centrioles are a peracarid-decapod feature. The syncarid (*Anaspides tasmaniae*) sperm has a subacrosomal filament [perforatorium], exeptional for Crustacea in being coiled. A syncarid apomorphy is the cytoplasmic 'skirt', a plesiomorphy the condensed chromatin and persistent nuclear membrane. Peracarid monophyly is confirmed by presence, with the questionable exception of tanaids, of a cross striated pseudoflagellum (possibly a centriolar rootlet homologue) joining the main body at junction of acrosome and nucleus. Tanaid sperm, rounded, lacking appendages, with large acrosome and scattered mitochondria, seen also in syncarids and stomatopods, possibly indicate a basal rather than terminal or intercalated position of the tanaids in the Peracarida. Euphausid and stenopodid sperm, ovoidal and lacking appendages, apparently lack an acrosome. Dendrobranchiate (penaeid), procaridean, caridean shrimps and prawns have sperm with a single acrosomal spike but rarely have arms analogous with those characteristic of decapods. Several spikes containing microtubules which traverse the nucleus and often contain chromatin are characteristic of Palinura (*Panulirus, Jasus*): Astacidea (Astacidae, Nephropidae); Thalassinidea; Anomura (Paguridae, Diogenidae, Coenobitidae); and Brachyura, though microtubules are reduced or absent above the 'oxyrhynchs'. The acrosome of Eubrachyura resembles that of paguroids, and especially in its subspheroidal shape *Pagurus* and *Clibanarius*, suggesting a paguroid-brachyuran (sister-group?) relationship while the thalassinid (*Callianassa*) acrosome differs greatly from that of the Astacidea-Anomura-Brachyura assemblage, contraindicating a thalassinid origin of the Brachyura. The discoidal acrosome and reduced arms of dromiid (*Dromidia, Petalomera*) sperm may be plesiomorphic conditions of a group with no close relationship to other brachyurans. Phylogenetic heterogeneity of the Podotremata is supported by differences between dromiid and raninoid sperm and similarities (postnuclear tail) between *Ranina* and majids. The conventional oxystomate-oxyrhynch-cancrid-brachyrhynch subdivision of the Brachyura is not supported by sperm ultrastructure. Dorippids and portunids, with similar sperm, are placeable in the Heterotremata, whereas the former classification separates the two families in the Oxystomata and Brachyrhyncha, respectively. Familial characteristics of sperm are exemplified by the distinctive 'xanthid ring' basal around the perforatorium of xanthids. Thoracotremata (Mictyroidea, Grapsoidea and Ocypodoidea) appear to be typified by presence of an apical opercular button, concentric lamination of the outer acrosome zone and modification of the xanthid ring. □ *Crustacea, phylogeny, spermatozoa, ultrastructure*

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Spermiocladistics, the use of spermatozoal ultrastructure for reconstruction of phylogeny (Jamieson, 1987), has recently been vindicated (Abele *et al.*, 1989) from a parsimony analysis of RNA sequences which verified attribution of the Pentastomida to the Crustacea on the basis of sperm ultrastructure (Wingstrand, 1972). The present paper presents a preliminary survey of sperm ultrastructure in crabs (Brachyura) as a contribution, pending further descriptive work and a computer analysis, towards elucidation of the phylogeny of this group. A phylogenetic review of the sperm of the Crustacea, which includes new ultrastructural observations, will first be presented. A phylogenetic parsimony analysis derived solely from sperm ultrastructure of the type attempted by Jamieson *et al.* (1987) for Oligochaeta will be deferred pending accumulation of additional data.

CRUSTACEAN SPERMATOZOA

A phylogenetic tree of the Crustacea based on the somatic cladistic analyses of Schram (1986) is given in Fig. 1. Other phylogenies significantly differing from this might have been used in this essentially heuristic survey (e.g. Bowman and Abele, 1982). The ultrastructure of spermatozoa of the included groups is indicated diagrammatically according to accounts published by authors cited in the text, below, for these taxa.

CLASS REMIPEDIA

The Remipedia are primitive, cavernicolous crustaceans only recently described (Yager, 1981) and placed at the base of the crustacean phylogenetic tree by Schram (1986). The body lacks tagmosis into thorax and abdomen. The head is small and the trunk is divided into many segments, each bearing biramous, paddle-like appendages. The single known species, *Speleonectes benjamini*, is hermaphrodite.

Spermatophores are produced each of which is about 38 µm long with three to possibly six sperm (nuclei) individually located at the proximal end. Each sperm cell (Fig. 1) has three distinct regions: a large nucleus, an acrosomal complex and a flagellum. A flagellum is elsewhere seen in the Crustacea only in the Maxillopoda. The ovoid nuclei are approximately 8–9 µm long and 5 µm wide.

The inverted cup-shaped, electron dense acrosome is apical on the nucleus. An acrosomal rod penetrates much if not all of the length of the nucleus (as in cephalocarids). Several mitochondria scattered in the cytoplasm are possibly eliminated by maturity. A flagellum, of the 9+2 pattern (origin unknown but presumably postnuclear), extends several times the length of the nucleus. Centrioles were not observed (Yager, 1989).

Jamieson (1987) drew parallels between the albeit aflagellate spermatozoon of the Cephalocarida and the flagellated aquasperm of the Xiphosura (with no implication of relationship) and suggested that this similarity, together with the flagellate condition of maxillopod sperm, seemed to suggest that ancestral crustaceans had a primitive sperm *sensu* Franzén (1956, 1970), the aquasperm, in the author's terminology, which in its least modified manifestation has been termed the plesiosperm (Jamieson, 1986). The remipedian sperm constitutes a remarkable validation of this view as it has the characters we might ascribe to a cephalocarid sperm if a flagellum were added; though mitochondria have not been seen in the cephalocarid. Yager (1989) appears correct in deducing that the rounded form of the nucleus in the remipedian sperm indicates that it is more plesiomorphic than that of the Ascothoracica (see below), hitherto thought to be the most plesiomorphic for the Crustacea, in which the nucleus is cylindrical.

Although the occurrence of a 'primitive' sperm in early evolution of the Crustacea can now confidently be asserted, presence of this (though somewhat more modified than the plesiosperm) in Remipedia does not obligatorily demand, nor does it contest, the status of most primitive crustacean taxon envisaged for the Remipedia by Schram (1986). Abele *et al* (pers. comm.) have suggested from analysis of rRNA sequences that remipedes are phylogenetically allied to the copepod-cirripede section of the Maxillopoda and are nearer to the Copepoda.

CLASS MAXILLOPODA

Until discovery of remipedes, the most basic crustacean sperm, and still the least modified maxillopod sperm, (Grygier, 1980, 1981, 1982) was that of the starfish parasite *Dendrogaster* (Ascothoracica) (Fig. 1).

The anterolateral position of the acrosome in *Dendrogaster* is a notable modification, however; it consists of an empty vesicle overlain by an electron dense layer. The head is bullet-shaped, the midpiece, approximately as long but half as wide, has six or more swellings, possibly representing mitochondria; the post-

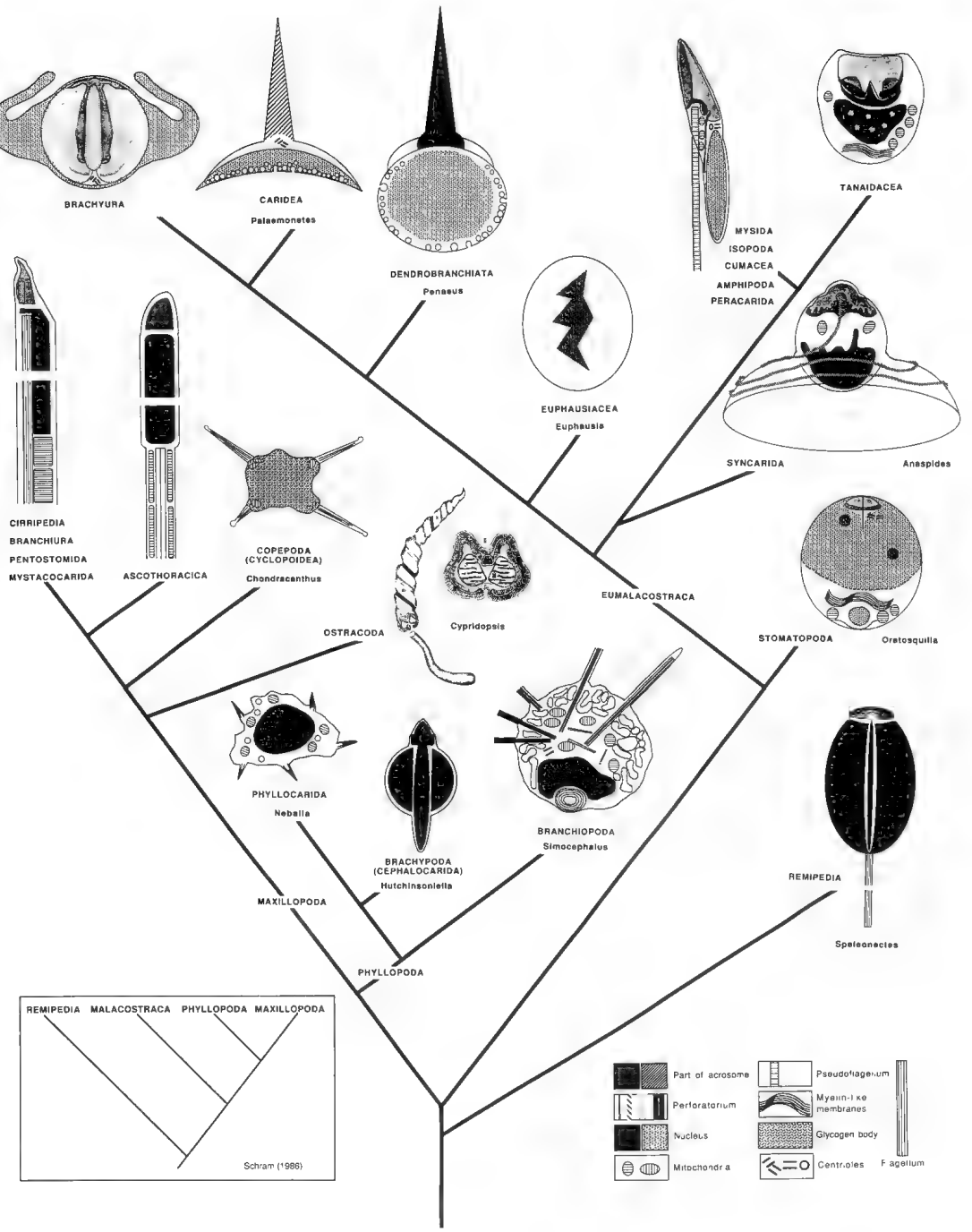


FIG. 1. Phylogeny of the chief groups of the Crustacea, based on Schram (1986; see inset) with diagram of spermatozoal ultrastructure after authors cited in the text. Original.

erior nuclear fossa houses the basal body of the 9+2 axoneme.

The flagellate condition of the ascothoracican sperm is elsewhere restricted (apart from the Remipedia) to the related maxillopod groups Mystacocarida (Brown and Metz, 1967) (Fig. 2G, H), Branchiura, and the related pentastomids, (Wingstrand, 1972; Abele *et al.*, 1989) and Cirripedia (Turquier and Pochon-Masson, 1969, 1971; Munn and Barnes, 1970a, b; Pochon-Masson *et al.*, 1970; Kubo *et al.*, 1979; Healy and Anderson, 1990) (Fig. I, 2K). These maxillopods, with the exception of the Ascothoracica, are unified by the synapomorphic origin of the flagellum at the anterior end of the nucleus. The Ascothoracica, with their postnuclear axoneme, appear to be an isolated relict, preserved through the adoption of parasitism, that arose near the base of the Maxillopoda.

Copepoda

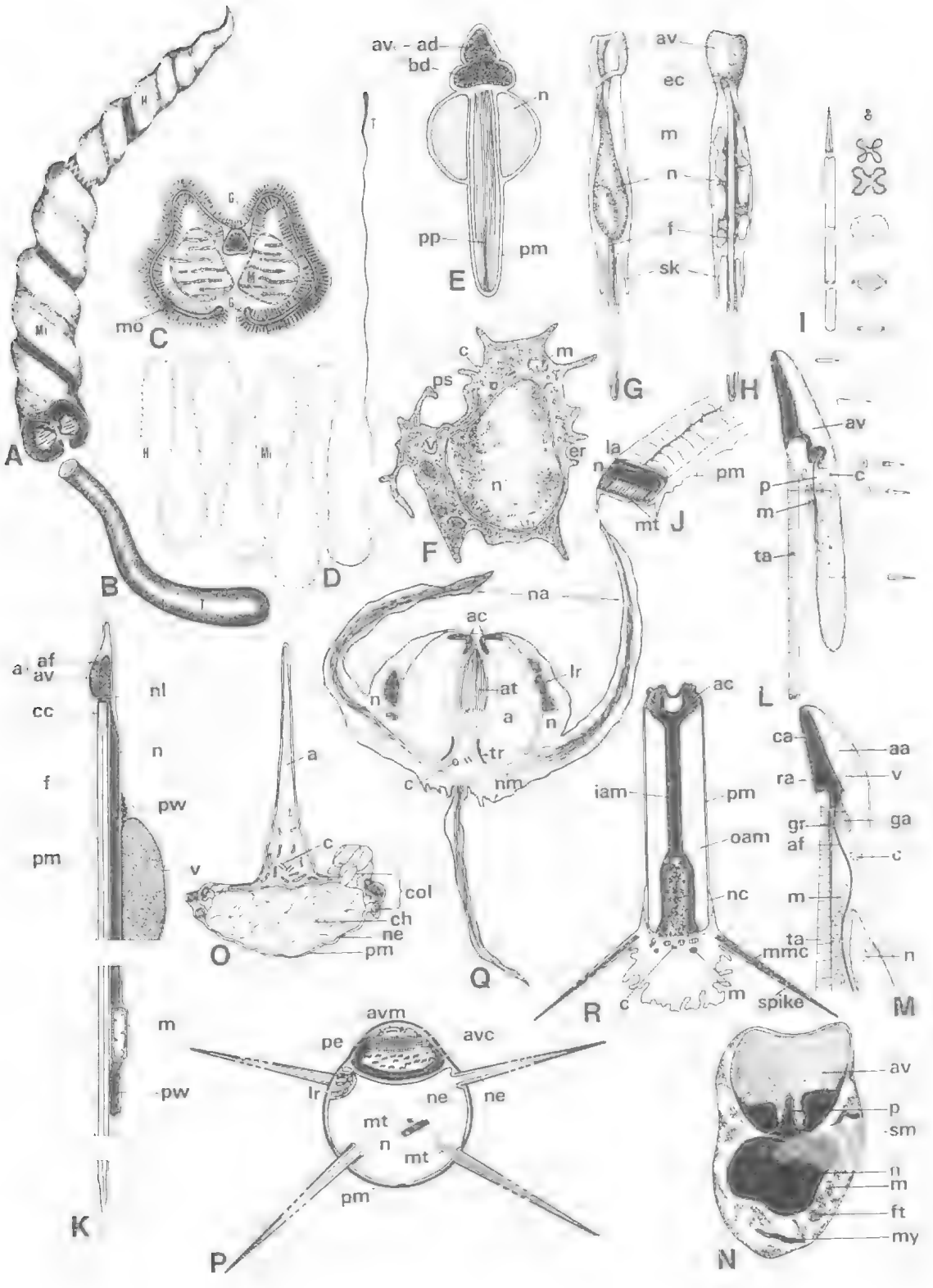
Copepods, usually placed in the Maxillopoda, have a wide variety of aflagellate sperm (Coste *et al.*, 1979; Pochon-Masson and Gharagozolou-van Ginneken, 1979; Rousset *et al.*, 1978; Brown, 1970; Raymont *et al.*, 1974; Manier *et al.*, 1978).

Their form is very variable. In *Tisbe holothuriae* (Harpacticoida) (Fig. 2I) the spermatozoon is elongate with definite head and neck (Pochon-Masson *et al.*, 1970; Pochon-Masson and Gharagozolou-van Ginneken, 1977, 1978, 1979); in *Chondracanthus angustatus* (Cyclopoida) the form is star-shaped (Rousset *et al.*, 1978). In the Calanoida, *Calanus hyperboreus* has a discoidal spermatozoon (Brown, 1970) while in *Calanus finmarchicus* it is oblong (Raymont *et al.*, 1974). Caligoida have a globular spermatozoon in *Neobranchia cygniformis* (Manier *et al.*, 1978) whereas in *Lernanthropus kroyeri* (Fig. 2J) it has the form of an elongate spindle with sinuous contours (Coste *et al.*, 1979). Mitochondria are represented in all groups except the Caligoida. Only in *Neobranchia cygniformis* do centrioles persist into the mature spermatozoon. Microtubules are present only in elongate sperm (*Lernanthropus kroyeri*) or in those with spine-like protuberances (*Chondracanthus angustatus*). The acrosome varies from a twisted point on the tip of the nucleus in *Tisbe holothuriae* to merely a dense plate on the nucleus in *L. kroyeri* or, possibly, a group of vesicles in *Neobranchia cygniformis*.

The sperm of the cyclopoid *Chondracanthus angustatus* (Fig. 1) deserve special mention as they show remarkable similarities to those of the Branchiopoda and Phyllocarida. The mature (spermatophoral) spermatozoon of *C. angustatus* consists of a globular region with irregular contours from which arise three or four ribbon-like arms, with axial microtubules, which give the gamete a stellate appearance. Mitochondria

FIG. 2. Ultrastructure of the spermatozoa of some major groups of the Crustacea. From Jamieson (1987) after various authors. A–D, Ostracod, *Cypridopsis*. A, head and middle part. B, Tail. C, Enlarged cross section from middle region. D, Complete sperm (from Reger, 1970a). E, Cephalocarid, *Hutchinsoniella macracantha* (from micrographs by Brown and Metz, 1967). F, Branchiopod, *Polyartemia forcipata* (from Wingstrand, 1978). G, H, Mystacocarid, *Derocheilocaris typicus* (after Brown and Metz, 1967). I, Copepod, Harpacticoid, *Tisbe holothuriae* (after Pochon-Masson and Gharagozolou van-Ginneken, 1977). J, Copepod, Siphonostomid, *Lernanthropus kroyeri*, mid-region of sperm (from Coste *et al.*, 1979). K, Cirripede, Generalized diagram (from Pochon-Masson *et al.*, 1970). L, Isopod, *Armadillium vulgare* (from Reger *et al.*, 1979). M, Isopod (from Cotelli *et al.*, 1976). N, Tanaid, *Tanais cavolinii* (from Cotelli and Lora Lamia Donin, 1980). O, Crangonid shrimp, *Crangon vulgaris* (from Pochon-Masson 1968b). P, Decapod, Palinura, *Panulirus argus* (from Talbot and Summers ,1978). Q, Decapod, Brachyura, Generalized oxythynch sperm (from Hinsch, 1973). R, Decapod, Astacidea, *Homarus americanus* (Talbot and Chanmanon ,1980a).

Abbreviations. a= acrosome; aa= amorphous part of acrosome; ac= apical cap; ad= anterior disc; af= acrosomal filament (perforatorium); at= acrosomal tubule; av= acrosomal vesicle; avc= contents of acrosomal vesicle; avm= acrosome vesicle membrane; bd= basal disc; c= centriole; col= collar; ec= electron dense core; f= flagellum; ft= foamy texture; G1, G2= grooves on surface of sperm; ga= granular part of acrosome; gr= groove; H= head; la= laminar acrosome; iam= inner acrosomal material; lr= lamellar region; m= mitochondrion; Mi= middle part of sperm; mmc= microtubule membrane complex; mo= membranous organelle; mt= microtubules; my= myelin figure; n= nucleus; na= nuclear arms; nc= nuclear cuff; ne= nuclear envelope; nl= nuclear lamella; nm= nuclear membrane; oam= outer acrosomal membrane; p= perforatorium; pe= periacrosomal material; pm= plasma membrane; pp= posterior projection; ps= pseudopodium; pw= periflagellar wall; ra= reniform part of acrosome; sk= skirtlike structure; sm= subacrosomal material; T= tail part of sperm; ta= cross striated tail-like appendage; tr= thickened ring; v= vesicle.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are grouped at the bases of the arms. The swollen portion of the sperm is entirely occupied by nucleoplasm. A nuclear envelope is absent. The chromatin is finely granular and homogeneous. Centrioles and acrosome are absent. As in phyllocarids and branchiopods, an acrosome is absent; numerous vesicles produced in the late spermatid from the nuclear membrane are not considered to be acrosomal (Rousset *et al.*, 1978).

Ostracoda

Ostracods, regarded from somatic morphology as derived from the base of the Maxillopoda (Fig. 1), have aflagellate filiform sperm performing undulatory waves generated by peculiar membranous organelles (Tétart, 1967; Reger, 1970a; Reger and Florendo, 1969a, b) (Fig. 2 A–D), the contractile bands of Gupta (1968) or wing-like structures of Zissler (1966, 1969). Recently Wingstrand (1988) has described non-filiform sperm in ostracods.

CLASS PHYLLOPODA

The classification of Schram (1986) which places the Branchiopoda, Brachypoda (Cephalocarida) and Phyllocarida in an enlarged Phyllopoda is observed here.

Cephalocarida

The cephalocaridan sperm was described by Brown and Metz (1967) for *Hutchinsoniella macrantha* (Figs. 1, 2E). Before discovery of remipedes, cephalocarids were generally regarded as the most plesiomorph crustaceans on general anatomy, including (Paulus, 1979) that of the ommatidia.

Although the sperm is acentriolar and aflagellate, and mitochondria have not been observed, it has an anterior pointed acrosome and a rounded nucleus perforated by a rod which is interpreted as equivalent to the perforatorium of *Limulus* by Baccetti (1979). This, with flagellation of maxillopod sperm, suggested (Jamieson, 1987) that ancestral crustaceans had a primitive sperm *sensu* Franzén (1956, 1970), a fact since demonstrated by Yager for remipedes. Because of the absence of a flagellum, cephalocarid sperm are more derived than those of remipedes.

Branchiopoda

The branchiopods, widely regarded (Siewing, 1963) as a basal group for the Crustacea have profoundly modified sperm, supporting the advanced position given to the group by Schram (1986). Wingstrand (1978) concludes from an exemplary study of the astounding variety and bizarre forms of branchiopod sperm (Berard, 1974; Brown, 1969; Delavault and Berard, 1974; Garreau de Loubresse, 1967) that the ancestral branchiopods must have had simple, amoeba-like sperm of the type seen in euphyllopods and conchostracans. There is, however, no suggestion that this amoeboid form seen, for instance, in *Polyartemia forcipatus* (Fig. 2F), represents a primitive sperm type for the Crustacea as a whole and a flagellated form of the cephalocarid sperm may reasonably be envisaged as ancestral in the Phyllopoda.

Phyllocarida

Phyllocarid (*Nebalia*) sperm have no polarity; no acrosome; and possess pseudopodia-like lobes; and 20–30 spines, each supported by nine small tubules. The large number of spines is considered by Jespersen (1979) to indicate that they are not modified flagella. Although this may well be correct, it may be noted that larger numbers of modified axonemes occur in each sperm of catenulid turbellarians. Phyllocarid sperm were considered nearest to those of branchiopods by Jamieson (1989c) who noted that Lauterbach (1975), on other grounds, had suggested a branchiopod origin for phyllocarids and hence the Malacostraca. I concur here with Schram (1986) in excluding the Phyllocarida from the Malacostraca and allying them with the former Branchiopoda and Cephalocarida in the Phyllopoda. However, spermatological evidence appears to support a sister-group relationship between phyllocarids and branchiopods, with cephalocarids as the sister-group of the phyllocarid-branchiopod assemblage (Fig. 1) contrary to the sister-group relationship of cephalocarids and branchiopods recognized by Schram for extant forms.

CLASS MALACOSTRACA

Stomatopoda

The sperm of *Squilla mantis* has been described by Cotelli and Lora Lamia Donin (1983), that of *Oratosquilla stephensoni* by Jamieson (1989c) and that of *Gonodactylus bredinii* by Felgenhauer and Abele (1990). Each stomatopod sperm (Fig. 1), aflagellate and obovoid, is surrounded by an electron dense coat. A spermatophore is absent. In contrast, spermatophores are present in eucarids, peracarids (isopods, amphipods and mysidaceans) and copepods. The

discus-shaped acrosome vesicle, is penetrated and underlain by a straight, slender acrosome rod (perforatorium) ensheathed, below the vesicle, in subacrosomal material. Feulgen-positive granular material, indicating chromatin, fills most of the length of the cell but there is no certain nuclear membrane. Two centrioles, consisting of doublets each with a radial 'foot' as in decapods and peracarids, occur near the acrosome and like it are embedded in the chromatin. Myelin-like membranes are associated with degenerating mitochondria in the posterior region of the cell. Thiéry-positive granules are aggregated as a glycogen body posteriorly in the cell. Stomatopods resemble decapods in their diffuse sperm chromatin but are placed below the syncarid-peracarid-decapod assemblage.

If, as is generally agreed, syncarids originated from the malacostracan stem above the departure of the Hoplocarida but at the base of the Eumalacostraca (Brooks, 1969; Jespersen, 1983), the development in stomatopods of a diffuse nucleus and disappeance of a discrete nuclear membrane must be considered parallelisms (not synapomorphies) with these conditions in decapods. The nuclear membrane tends to be disrupted in dendrobranchiate shrimps and prawns (Talbot and Summers, 1978), is usually intact in procarideans and carideans, and is usually disrupted in Anomura and Brachyura.

Syncarida

Each spermatozoon of the syncarid *Anaspides tasmaniae* (Fig. 1), described by Jespersen (1983), is surrounded by a capsule (coat) as in stomatopods, and, as in the latter, a spermatophore is absent. A very elongate subacrosomal filament (perforatorium) bypasses the nucleus as in isopods, amphipods and cumaceans, rather than penetrating it as in stomatopods. In *Anaspides* the perforatorium makes a posteriorly widening spiral of 3–4 turns, a remarkable convergence to the condition in the xiphosuran *Limulus*. As in stomatopods, subacrosomal material forms a sheath around the filament. Posteriorly the filament forms, with the peripheral cytoplasm, a membranous skirt, not seen in other crustacean sperm, which gives the sperm the form of a bell. An axoneme is absent at all stages. The nucleus is condensed with a persistent envelope.

In the phylogram (Fig. 1) somatic evidence for the position of the syncarids at the base of the eumalacostracans has been accepted. Similarities of syncarids with most peracarids are the presence of a perforatorium (itself a plesiomorphy) which, as questionable synapomorphies, (1) is filiform and (2) bypasses the nucleus. The caridoid escape reaction (Dahl, 1983) unites syncarids, eucarids and peracarids.

Peracarida

Monophyly of peracarids has been denied by Wattling (1981) who considers that they consist of three independent lineages from a syncarid-like ancestor, the mysidaceans; the amphipods; and an isopod-tanaid-cumacean assemblage. From sperm ultrastructure this is clearly incorrect. Thus, in mysidaceans, amphipods, isopods (Fig. 2L, M) and Cumacea each sperm consists of two convergent linear components: the main body of the sperm, containing the nucleus and capped by the acrosome, and joining this anteriorly, a transversely striated tail-like but non-flagellar structure (possibly a centriolar rootlet homologue) (references in Cotelli *et al.*, 1976; Reger *et al.*, 1970; Reger *et al.*, 1979; Fain-Maurel *et al.*, 1975a,b). This highly peculiar morphology is unlikely to have originated more than once.

Tanaid sperm, rounded, lacking appendages, with large acrosome and scattered mitochondria (Cotelli and Lora Lamia Donin, 1980) (Fig. 2N), seen also in syncarids and stomatopods, possibly indicate a basal rather than terminal or intercalated position of the tanaids in the Peracarida but these may represent apomorphies related to the specialized fertilization biology of tanaeids, with fertilization in a tube. Presence of the perforatorium in non-tanaid peracarids may be a plesiomorphy or a reacquisition. It has been suggested, however, that the gamete described by Cotelli and Lora Lamia Donin (1980) is in fact a spermatid and that mature tanaid sperm conform, by light microscopy, to the typical peracarid structure (Siegs, pers. comm.). This observation, if verified, would unite all peracarids as a monophyletic entity.

Eucarida

Order Euphausiacea

Euphausid sperm, ovoidal and lacking appendages, and with irregular central material which may be chromatin (Jamieson, unpublished) (Fig. 1), but otherwise virtually unknown, give little indication of the eucarid ground plan. If lack of arms were plesiomorphic for eucarids, the arms of most decapods would have to be regarded as having developed independently of those of phyllopods. This is further suggested by their absence from non-eucarid malacostracans.

ORDER DECAPODA

Since completion of the draft of this review, a review of decapod sperm by Felgenhauer and Abele (in press) has been made available to me through the kindness of the authors. Brief references to species which they investigated is made in the following account of decapod sperm.

SUBORDER DENDROBRANCHIATA

SUPERFAMILY PENAEOIDEA

The Penaeoidea, which, with the Sergestoidea, form the Dendrobranchiata, were at one time grouped with the crangonid and palaemonid shrimps within the Natantia as opposed to the Reptantia which contained, *inter alia*, hermit crabs, crayfish, lobsters and crabs. Penaeoids are now regarded as distinct from the Suborder Eukyphida, containing the Procarididea and the Caridea, and the Euzygida, containing the Stenopodidea (Schram, 1986). Paraphyly of penaid and eukyphid shrimps, as opposed to monophyly of the Natantia, appears to be indicated from rRNA studies by Abele *et al.* (pers. comm.). These authors, with considerable justification, retain the names Caridea for Eukyphida, and Stenopodidea for Euzygida and are followed here.

Although it does not establish (nor does it contraindicate) its monophyly, the old group Natantia is characterized by uniformity of gross spermatozoal ultrastructure. Similarities include division of the spermatozoon into three regions: acrosomal spike, cytoplasmic collar and nucleus. However, some claims made by Talbot and Summers (1978) and Kleve *et al.* (1980) for characteristics uniting natantian sperm (absence of centrioles, dissolution of the nuclear envelope with confluence of nucleoplasm and cytoplasm to form spermioplasm) and supposedly distinguishing them from 'reptant sperm' are unreliable, being typical of the penaeids but not of carids, though some disruption of the nuclear envelope occurs in the carid *Palaemonetes*. The single spike, giving what is paradoxically but conveniently called the 'unistellate' condition, distinguishes 'natantian' sperm from the 'multistellate' sperm (with more than one spike or arm) of the Astacidean-Palinuran-Decapod assemblage. The distinction goes deeper as the natantian spike is acrosomal in function, contains actin and undergoes a Ca^{++} dependent reaction (*Penaeus aztecus*, *P. setiferus*, Brown *et al.*, 1976; *Sicyonia ingentis*, Clark *et al.*, 1981, Clark and Griffin, 1988; *S. brevirostris*, Kleve and Clark, 1976, Brown *et al.*, 1977). Fluorescein labelled anti-actin indicates that it is the spike which contains actin, and therefore functions like an acrosome filament (perforatorium). Acridine orange and PAS positive response of the amorphous cap from which the spike arises suggest that the cap is at least analogous to an acrosome vesicle (Brown *et al.*, 1976). In *Macrobrachium rosenbergii*, although the sperm first attaches to the egg by its wide base, the spike bends within 15 seconds and penetrates the egg investment from which the sperm base is released (Lynn and Clark, 1983a). The multiple spikes of nonnatant decapods are not acrosomal and contain either cords of microtubules or extensions of the nucleus or both.

Sperm ultrastructure has been described for the penaeids *Penaeus aztecus*, Clark *et al.*, 1973 (Fig. 1); *P. japonicus*, Ogawa and Kakuda, 1987; *P. setiferus*, Lu *et al.*, 1973; Felgenhauer, Abele and Kim, 1988; Felgenhauer and Abele, 1990; *Sicyonia brevirostris*, Brown *et al.*, 1977; and *S. ingentis*, Kleve *et al.*, 1980, Shigekawa *et al.*, 1980, Shigekawa and Clark, 1986, Clark *et al.*, 1981, Clark and Griffin, 1988.

The spermatozoon of *Sicyonia ingentis* well exemplifies penaeid sperm though the acrosome (spike) region is more elaborate than in *Penaeus*. The sperm is composed of a spherical mainbody which is partially encompassed by a morphologically complex cap region (acrosomal complex) from which extends the single spike. The mainbody houses an uncondensed Feulgen-positive nuclear region which is surrounded posteriorly and laterally by a cytoplasmic layer. A single layer of 0.06 μm vesicles lines the periphery of this layer; the bounding membranes of the vesicles are apposed to and appear to fuse with the plasma membrane. Large, 0.7 μm vesicles containing whorled membranous and granular material extend from the inner surface of the cytoplasmic layer into the central fibrillar region. A nuclear membrane is also absent in the sperm of *Penaeus setiferus* (Lu *et al.*, 1973). In *Sicyonia* the nucleus is separated from the cap-like acrosomal complex by a dense plate and a highly organized crystalline lattice which is composed of geometric 350 Å squares. The cap region consists, in posterior–anterior sequence, of the dense plate; the crystalline lattice; convoluted membrane pouches surrounding these; a central granular core immediately anterior to the lattice and medial to the pouches; spherical bodies (voids in the core substance); an electron

dense saucer-shaped plate embedded in the centre of the cap and with 12–15 petaloid radiating extensions; and a large anterior granule. The anterior granule gives RNA-ase stable red fluorescence with acridine orange staining. It is conical, with its concave posterior surface applied to the saucer-shaped plate. The spike, which is helicoidal and approximately 6 μm long, extends from the anterior end of the granule. Cap and spike are bound by a double membrane formed by fusion of the plasma membrane and the convoluted pouch membrane. The pouches and anterior granule, which are PAS-positive, and the spike are considered to comprise the acrosome (Kleve *et al.*, 1980).

Although the nucleus is typically subspheroidal in penaeids, it is shown to be considerably depressed antero-posteriorly in *Penaeus japonica* by Ogawa and Kakuda (1987).

Suborder Pleocyemata

I here follow the taxonomic synopsis of Bowman and Abele (1982) in placing all remaining decapods in the Pleocyemata.

Infraorder Caridea *s.lat.*

The Infraorder Caridea *s.lat.*, as recognized by Bowman and Abele (1982) contains the infraorders Procarididea and Caridea *sensu* Schram 1986. These two groups will be termed the procarideans and carideans here. Their sperm resemble those of dendrobranchiates but there are tendencies for the nucleus to become basally concave so that the sperm, with its anterior spike, takes on a tack-shape, and for development of cross striated longitudinal fibres in the spike. Cross striation is, however, described for the spike of *Penaeus setiferus* by Felgenhauer *et al.* (1988) in the absence of fibres. Felgenhauer and Abele (1990) distinguish those carideans in which the spike is solid and contains cross striated fibrils (e.g. *Palaemonetes*) from those in which the spike is tubelike with distinct electron dense walls containing anastomozing radial fibrils (e.g. *Rhynchocinetes*, Dupré and Barros, 1983; *Procaris ascensionis*, Felgenhauer *et al.*, 1988).

The sperm of *Procaris ascensionis* has a typical tack or 'inverted umbrella' shape. It is said to differ from sperm of carideans *sensu stricto* in having fibrous ridges on the free margins of the cell body and in lacking periodic cross striations of the fibres which form the spike (Felgenhauer *et al.*, 1988). However, these striations are absent from some caridean sperm.

The spermatozoa of caridean shrimps have been described or at least illustrated ultrastructurally for the oplophoroid *Paratya australiensis*, Jamieson and Robertson, in prep.; *Atya margaritacea* and *Typhlatya rogersi*, Felgenhauer and Abele, 1990; the bresilioid *Rhynchocinetes typus*, Barros *et al.*, 1986; the palaemonoids *Palaemon elegans*, Pochon-Masson, 1969; *P. serratus*, Sellos and Le Gal, 1981; *Palaemonetes paludosus*, Koehler, 1979 (Fig. 1); *Palaemonetes kadiakensis*, Felgenhauer *et al.*, 1988, Felgenhauer and Abele, 1990; and *Macrobrachium rosenbergii*, Lynn and Clark, 1983a, b, Dougherty, 1987, Dougherty *et al.*, 1986, Harris and Sandifer, 1986; and the crangonoids *Crangon septemspinosa*, Arsenault *et al.*, 1979, 1980, Arsenault, 1984; *C. vulgaris*, Pochon-Masson, 1968b (Fig. 2O); and the hippolytid *Hippolyte zostericola*, Felgenhauer and Abele, 1990.

Cross striations typical of, but not constant for, the spike of the caridean sperm are seen in that of *Macrobrachium rosenbergii*, Lynn and Clark, 1983a, b; *Palaemonetes paludosus* and *Palaemon elegans*, Pochon-Masson, 1969. These elements of the spike continue into the cap-like expansion at its base lying on the nucleus. The caridean spike has been said not to be membrane bound and to be little more than a naked perforatorium of a secondarily simplified acrosome (Pochon-Masson, 1969). However, the same author also states that it is delimited by a simple membrane covered by the plasma membrane in *Palaemon*. A bounding membrane is said to be absent in *Crangon septemspinosa* by Arsenault (1979). Cross striations were not seen in the spike of *Crangon vulgaris* examined by Pochon-Masson (1968b) nor in *Paratya australiensis*, (Jamieson and Robertson, in prep).

In *Paratya* the nucleus is subspheroidal as in penaeids, but it is depressed in other carideans. It is ellipsoidal in *Palaemon elegans* (Pochon-Masson, 1969); oblong or oblate spheroidal (Arsenault *et al.*, 1979), having the form roughly of an ellipsoid with somewhat flattened free surface, in *Crangon septemspinosa*; while in *Palaemonetes paludosus* the nucleus has become inverted cup-shaped, giving the sperm, with its terminal spike, the approximate form of a tack (Koehler, 1979). Transition from an ovoid (plesiomorphic) to the concave (apomorphic) form occurs in spermiogenesis in *P. paludosus*. Persistence of the nuclear envelope appears usually to set carideans apart from penaeids, though some disruption of the envelope occurs in *Palae-*

monetes paludosus, (Koehler, 1979). In this species the envelope is said to be multilayered on the free, concave side but to be lost on the convex side nearest the spike, allowing the uncondensed chromatin to merge with the cytoplasm to form so-called spermioplasm as in *Sicyonia*; there are numerous PAS-positive vesicles, each with at least two membranes, embedded in the nucleus near its free, concave surface and originating by pinocytosis of the cell surface in the spermatid. Vesicles are normally present peripheral and mostly basal to the nucleus in caridean, as in penaeid sperm. They form a wide reticular zone around the base and sides of the nucleus in *Paratya australensis*.

The sperm of *Rhynchocinetes typus*, described by Barros *et al.* (1986) from a scanning electron microscope examination, is of particular interest as it forms a link morphologically with the higher, non-natant decapods in having 11 coplanar radial arms in addition to the typical natantian terminal spike. Contact with the egg continues to be made by the terminal spike which exerts a lytic action. It remains to be determined whether the arms are homologous with those of higher decapods.

Mitochondria occur in the cytoplasmic collar of carid sperm but mostly lateral to the nucleus (*Crangon vulgaris*, Pochon-Masson, 1968b; *Palaemon elegans*, Pochon-Masson, 1969; *C. septemspinosa*, Arsenault *et al.*, 1979). Centrioles have been observed (generally absent from dendrobranchiate sperm) between the spike and the nucleus, in the cytoplasmic 'collar' region, in several carids (*Crangon vulgaris*, Pochon-Masson, 1968b; *C. septemspinosa*, Arsenault *et al.*, 1979; *Palaemon elegans*, Pochon-Masson, 1969).

Origin of the acrosome during spermiogenesis from the Golgi apparatus is argued for *Crangon septemspinosa* by Arsenault *et al.* (1979), but generally in decapods a Golgi apparatus has not been reported and origin of the acrosome appears to be from vesicles derived from the endoplasmic reticulum.

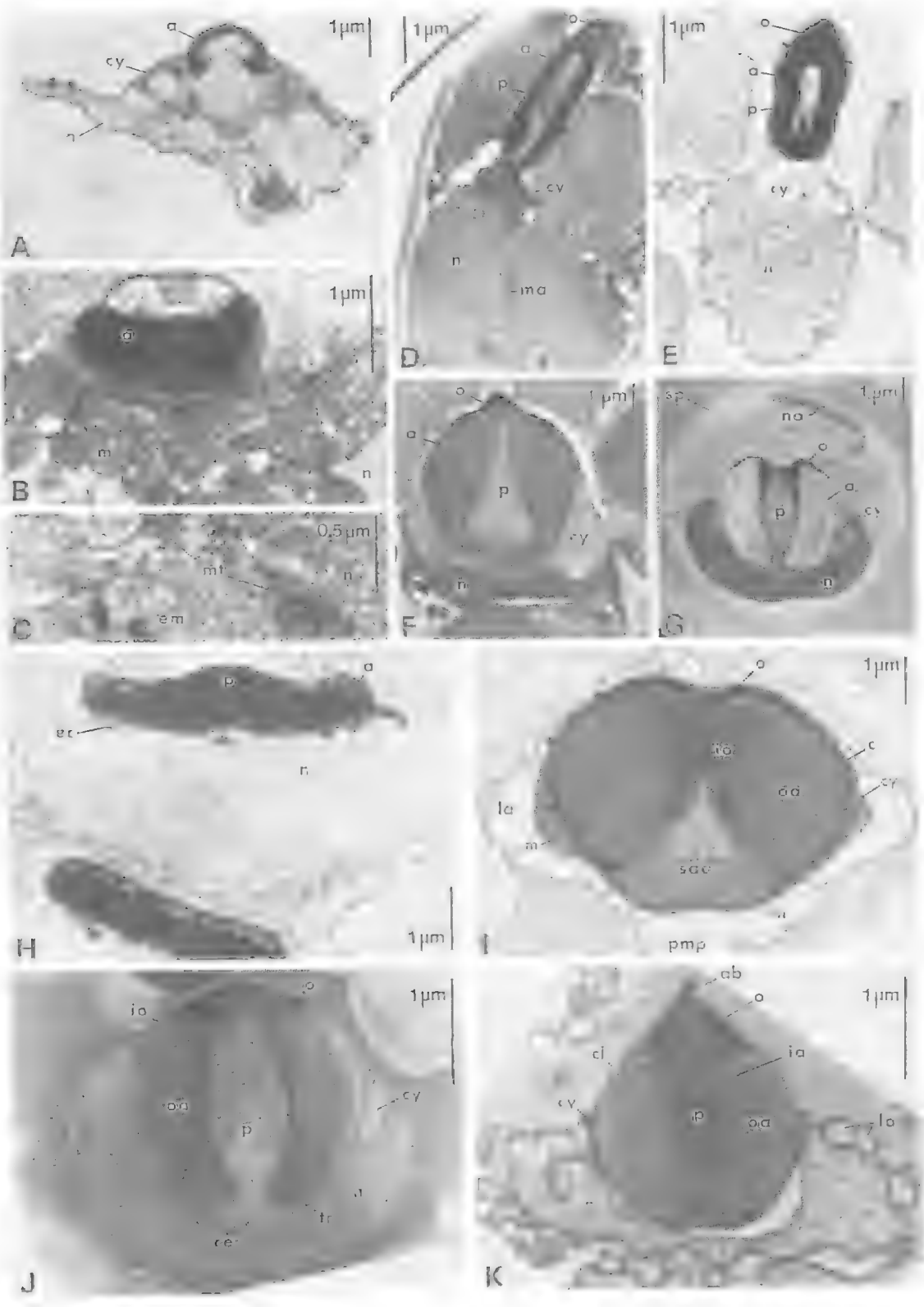
INFRAORDER STENOPODOIDEA

Sperm structure in this taxonomically problematic group has been examined, for *Stenopus hispidus*, by Felgenhauer and Abele (1990). The sperm of *S. hispidus*, were considered by Felgenhauer and Abele (1990) to resemble those of stomatopods as Burkenroad (1981) had suggested from a light microscope study of the sperm of *S.* cf. *scutellus*. The spermatozoon of *S. hispidus* is a simple elliptical cell, *ca.* 7–10 µm in diameter, with a prominent lamellar body located on one side against the plasma membrane, and resembling that flanking the acrosome in brachyurans. No distinct acrosomal region or stellate appendages were present. Felgenhauer and Abele (1990) doubted, however, that the sperm were mature on the grounds that arms, typical of other reptants, were absent. The absence of an acrosome is a notable difference from stomatopod sperm and, with the ellipsoidal armless form, is here seen as a notable resemblance to euphausid sperm of possible phylogenetic significance.

INFRAORDER ASTACIDEA

Ultrastructural studies of the Astacidea include the families Astacidae (*Astacus astacus* = *A. fluviatilis*), Pochon-Masson, 1968b, López-Camps *et al.*, 1981; *A. leptodactylus* — spermatocytes only — Eliakova and Goriachkina, 1966; *Cambaroides japonicus*, Kaye *et al.*, 1961; Yasuzumi *et al.*, 1961; Yasuzumi and Lee, 1966; *Cambarus* sp., Anderson and Ellis, 1967; *Pacifastacus leniusculus*, Dudenhausen and Talbot, 1979a, 1982; *Procambarus clarkii*, Moses, 1961a, b); *P. leonensis*, Felgenhauer and Abele, 1990); Nephropidae, subfamily Nephropinae (*Nephrops norvegicus*, Chevaillier, 1965, Chevaillier and Maillet, 1965; Chevaillier, 1966b, 1967a, 1967b, 1968); subfamily Homarinae (*Homarus americanus*, Talbot and Chanmanon, 1980a (Fig. 2R), 1980b; *H. vulgaris*, Pochon-Masson, 1965b, 1965c, 1968a; Enoplometopidae (*Enoplometopus occidentalis*, Haley, 1986) and Parastacidae (*Cherax tenuimanus*, Beach and Talbot, 1987, Jamieson, un-

FIG. 3. Micrographs of the ultrastructure of the sperm of some decapods. A, a parastacid, *Cherax tenuimanus*. B and C, a palinurid, *Jasus novaehollandiae*. C, microtubular arm of *J. novaehollandiae*. D, a galatheid, *Allogalathea* sp. E, a porcellanid, *Petrolisthes lamarckii*. F, diogenid, *Clibanarius* corallinus. G, a majid, *Menaethius monoceros*. H, a dromiid, *Petalomera lateralis*. I, a raninid, *Ranina ranina*. J, a portunid, *Caphyra rotundifrons*. K, a mictyrid, *Mictyris longicarpus*. All original. Abbrevations: a= acrosome; ab= apical button; c= capsule; ce= centriole; cl= concentric lamellae; cy= cytoplasm; ec= extensions of capsule; em= extra-cellular matrix; ia= inner acrosome zone; la= lateral arms; m= mitochondria; ma= microtubular arm; mt= microtubules; n= nucleus; na= nuclear arm; o= operculum; oa= outer acrosome zone; p= perforatorium; pmp= posterior median process; sac = subacrosomal chamber; sp= spermatophore; tr= thickened ring.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published) and *C. albidus*, Beach and Talbot, 1987).

The acrosomal-nuclear complex is elongate in the Nephropidae (Figs 2R, 4) but compact and dome-shaped in the Astacidae and Parastacidae (Figs 3A, 4). *Enoplometopus* is exceptional for the investigated Nephropidae in its dome-shaped acrosome, wider than long (Fig. 4), resembling that of the Astacidae. This supports exclusion of *Enoplometopus* from the Nephropidae by De Saint Laurent (1988), who placed it in a separate family, the Enoplometopidae, and superfamily, the Enoplometopoidea.

Astacidae and Parastacidae

Sperm ultrastructure of astacids and parastacids indicates combined monophyly of the two families. The nucleus of the spermatozoon of *Astacus astacus* is a biconcave disc with major axis perpendicular to that of the gamete and with a sinuous outline. As in other decapods, the chromatin forms a fine, weakly osmiophile network of fibrils varying from 20 Å to 200 Å (Pochon-Masson, 1968b; Yasuzumi and Lee, 1966; Moses, 1961a). Occasional clear spaces contain microtubules. In the equatorial plane the nucleus is elongated to form the characteristic spikes (spines, arms or pseudopodia). These number four in *Cambaroides* and *Procambarus clarkii* but exceed 20 in *P. leonensis* and five, six, or seven in *Cambarus viridis* (references in Moses, 1961a, b; Felgenhauer and Abele, 1990). Elsewhere folds of the nuclear envelope surround mucoid digitations arising from the convoluted membranes in outer parts of the cell (Pochon-Masson, 1968b).

There is evidence for formation of lamellar material peripheral to the nucleus from the nuclear membrane, from smooth ER, and from mitochondria and for formation of the wall of the spines from the nuclear membrane and also from the convoluted membranes (Kaye *et al.*, 1961; Eliakova and Goriachkina, 1966; Yasuzumi and Lee, 1966; Anderson and Ellis, 1967; Pochon-Masson, 1968b; Moses, 1969a, b; Dudenhausen and Talbot, 1979). Yasuzumi and Lee (1966) have demonstrated that the convoluted membranes, especially surrounding the nuclear membranes, are the site of TTPase.

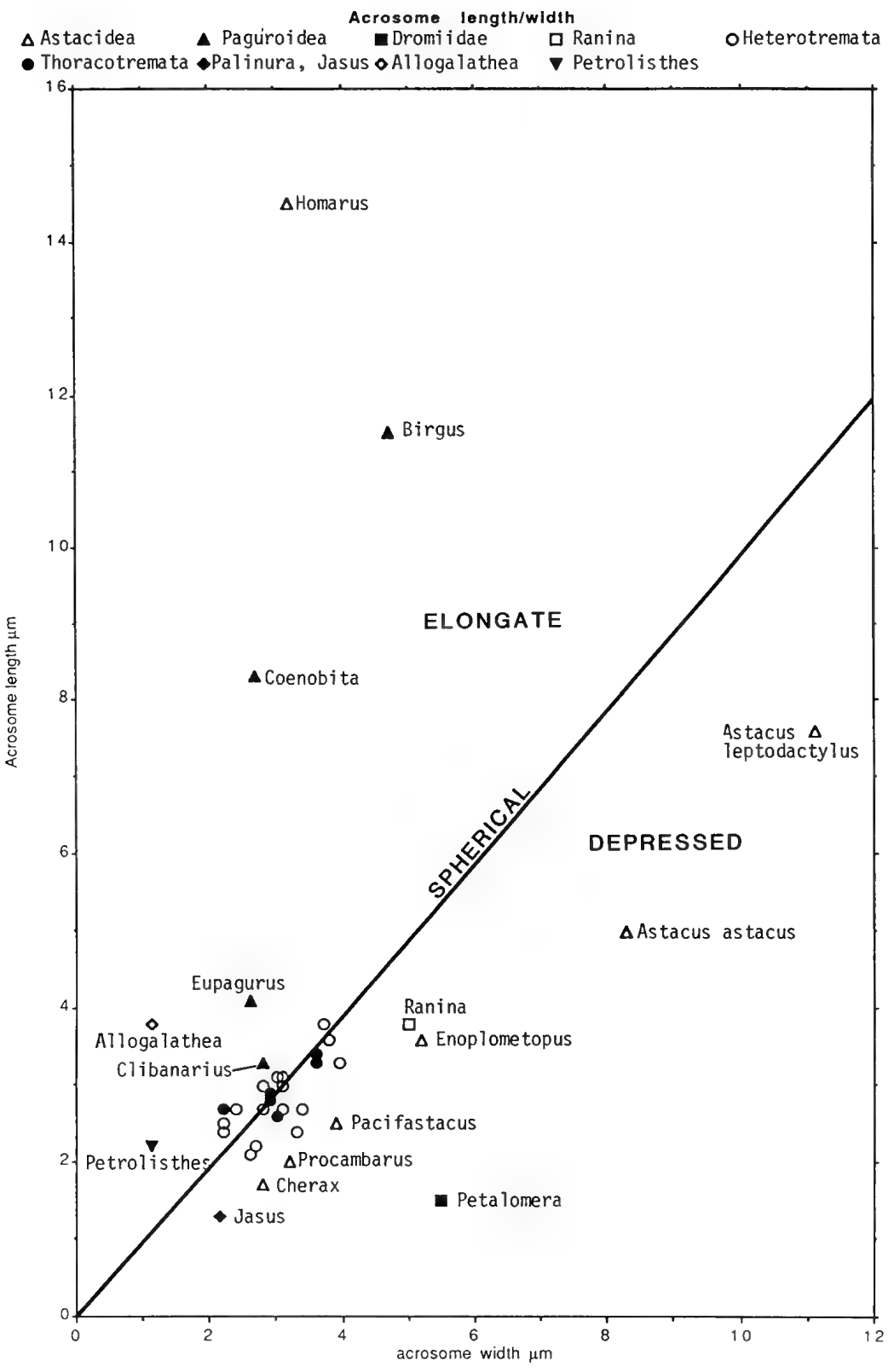
It is considered by Moses (1961b) and Anderson and Ellis (1967), for Astacidea, and by Talbot and Chanmanon (1980a), for *Homarus*, that the nuclear membrane becomes fused with the plasma membrane as a 'tegument' containing 'spermioplasm', admixed nucleoplasm and cytoplasm.

Microtubules, *c.* 200 Å (Pochon-Masson, 1968b), 220–310 Å (Yasuzumi and Lee, 1966) or *c.* 300 Å wide (Anderson and Ellis, 1967), with associated DNA, form several parallel bundles some of which extend into the spines (Moses, 1961a, b; Anderson and Ellis, 1967; Pochon-Masson, 1968b), each of which contains, for instance, 30 evenly spaced microtubules in *Cambaroides* (Yasuzumi and Lee, 1966). The microtubules probably are responsible for movement of the spines which has been observed in crustacean sperm (Pochon-Masson, 1968b).

Centrioles are said to be absent from the mature sperm of *A. astacus* by Pochon-Masson (1968b) and were observed to disintegrate by maturity in *Procambarus* (Moses, 1961a,b) and *Cambaroides* (Yasuzumi *et al.*, 1961) but persist in the mature sperm in *Cambarus* (Anderson and Ellis, 1967). No Golgi apparatus is known in spermatids or spermatozoa of crayfish but lamellar ER in the spermatid resembles this structure (Kaye *et al.*, 1961).

The acrosome in all investigated astacids and parastacids is a dense inverted cup-shaped structure, crescentic in longitudinal section, with the opening towards the nucleus. It is wider than long, in contrast with nephropids (*Homarus*, *Nephrops*) in which, with the exception of *Enoplometopus*, it is greatly elongated (Fig. 4). In *Astacus astacus*, the acrosome is differentiated into an apical operculum (Pochon-Masson, 1968b) or apical formation (López-Camps *et al.*, 1981) and a more basal, thick doughnut-like ring. No such apical differentiation is recognized in *Procambarus clarkii*, *P. leonensis*, *Cambarus* sp. and *Cambaroides japonicus* (Moses, 1961a; Felgenhauer and Abele, 1990; Anderson and Ellis, 1967; Yasuzumi and Lee, 1966, respectively). In *Cherax albidus* (Parastacidae) some apical whorled material is present within the vesicle but is absent in *C. tenuimanus* (present study; Beach and Talbot, 1987) (Fig. 3A). The mature acrosome of *Pacifastacus* is again differentiated as an apical cap consisting of whorled stacks of lamellae in addition to crystalline inner acrosomal material; and outer acrosomal material which is homogeneous except for a periph-

FIG. 4. Plot of acrosome length against width for various reptants. Standard deviations for each species are not shown but are small.


Acrosome length/width
Astacidea
Paguroidea
Dromiidae
Ranina
Heterotremata
Thoracotremata
Palinura, Jasus
Allogalathea
Petrolisthes
Homarus
Birgus
Coenobita
ELONGATE
SPHERICAL
DEPRESSED
Astacus leptodactylus
Astacus astacus
Eupagurus
Ranina
Enoplometopus
Allogalathea
Clibanarius
Pacifastacus
Petrolisthes
Procambarus
Cherax
Petalomera
Jasus
Acrosome length µm
acrosome width µm
0
2
4
6
8
10
12
14
16

eral electron dense band (Dudenhausen and Talbot, 1982). At maturity in *Cambarus* the crescent is embedded in dense material within the filamentous spermioplasm (Anderson and Ellis, 1967). It seems possible that the reported absence of an operculum in some species may be due to slight immaturity of the spermatozoon and that the internalized whorls of *Cherax albidus* represent an intermediate ontogenetic stage of the acrosome.

In all examined Astacidae and Parastacidae there is a large subacrosomal chamber. In *Cambaroides*, *Cambarus* and *Procambarus*, a plug-like mass of granular material with filamentous extensions fills the posterior opening of the acrosome. Thin beaded filaments, also shown for both *Cherax* species by Beach and Talbot (1987), extend into the central concavity from this basal material.

At full development an apical process (horn-like process of Yasuzumi and Lee, 1966 or anterior acrosomal process of Anderson and Ellis, 1967), which is possibly a derivative of the sustentacular cells (Moses, 1961a), emerges from the anterior region of the acrosome. This is clearly the structure questionably considered an acrosomal tubule in *Procambarus leonensis* by Felgenhauer and Abele (1990). As in most other Malacostraca, the acrosome does not appear to be a Golgi derivative, the hall-mark of the acrosome in other animal groups. Dudenhausen and Talbot (1979) state that the proacrosomal vesicles, which fuse to form the acrosome, originate from the ER in *Pacifastacus*. Yasuzumi *et al.* (1961) state that the acrosome forms from granules in the spermatid similar to those found in the interzonal spindle region in the meiotic divisions.

In *A. astacus* the sperm is not freed from a mucoid sphere until it reaches the external medium when, as in *Pacifastacus*, the spines unfold. The PAS-positive mucoid sheath is provided by the intercalary cells (Moses, 1961a).

Nephropidae

The spermatozoa of *Homarus americanus* (Talbot and Chanmanon, 1980a) (Fig. 2R) and *H. vulgaris* (Pochon-Masson, 1965c, 1968b) conform with the gross ultrastructural pattern described for the Astacidae but differ, chiefly, in the pronounced elongation of the acrosome (Fig. 4) which projects as a cylinder. Each sperm is 17 or 19 μm long and consists of acrosome, subacrosomal region, collar containing various organelles, nucleus, and spikes (here three) each 20 μm long in *H. vulgaris* and 38 μm long in *H. americanus*) which are extensions of the nucleus. The acrosome is traversed throughout its length by a weakly PAS-positive electron dense column, the inner acrosomal material, which widens at the ends to form a deep fossa enclosing the finely granular plug-like subacrosomal material, posteriorly, and a flange supporting an apical cap anteriorly. This column is surrounded by a wider zone, strongly PAS-positive and of moderate to low electron density, the outer acrosomal material (Talbot and Chanmanon, 1980a). The apical cap, which is weakly PAS-positive, has four concentric zones which, centripetally, are (1) an external wide crystalline zone, (2) a narrow electron dense crystalline zone, (3) a crystalline moderately electron dense zone which is a cup-shaped extension of the central, inner acrosomal material (all three identical with the opercular sphincter in *H. vulgaris*, *sensu* Pochon-Masson, 1968b), and (4) the moderately dense contents of this cup (apical portion of central canal, Pochon-Masson, 1968b) which are continuous with the central column. The tip of the cap is deeply indented (Talbot and Chanmanon, 1980a). The acrosome is bounded by a single, tripartite membrane. The acrosome of *H. vulgaris* is almost identical but the central column is penetrated throughout its length by a narrow central canal (Pochon-Masson, 1968b).

The collar and region subjacent to the subacrosomal material, contains small mitochondria with poorly developed cristae and, centrally, a pair of centrioles. The subacrosomal material, which is more dense basally than elsewhere, and the collar are in direct continuity with the chromatin of the nucleus. The nucleus extends for a short distance as a 'cuff' around the base of the acrosome and is not delimited from the acrosome by a membrane. Elsewhere, though, it is bounded by a membrane which appears to be a product of the fusion of the nuclear envelope and the plasma membrane. This composite membrane projects outwards as the spikes or nuclear processes but the nuclear chromatin, which is granular or fibrillar and uncondensed, is said not to extend into them. The processes are traversed by microtubules ensheathed in and interwoven by sheet membranes. The microtubule-membrane complexes of the spikes converge in the region of the collar and interconnect to form (as in the axiid, below) a three-sided vault the apex of which immediately underlies the base of the acrosome (Talbot and Chanmanon, 1980a).

The acrosome reaction of the *H. americanus* sperm has been elegantly described by Talbot

and Chanmanon (1980b) and corresponds closely to the report of Pochon-Masson (1965c, 1968b) for *H. vulgaris* (see also Brachyura, Pochon-Masson, 1968a) but cannot be described here.

The ultrastructure of the sperm of the Subfamily Nephropinae, exemplified by *Nephrops norvegicus* (Chevaillier and Maillet, 1965) is essentially similar to that in the Homarinae described above. There are again three nuclear processes containing a complex system of lamellae but remarkably, unlike homarine sperm, the processes lack microtubules. Only the basal part of the spine contains lamellae and is Feulgen (DNA) positive. The acrosome ("capsule") is elongate and consists of a peripheral region and an axial baton. The baton is here interpreted as the homologue of the subacrosomal material or perforatorium in homarines, differing in being (like the entire acrosome) much more elongate. This is bounded by a space (here considered the equivalent of the central canal of *H. vulgaris*) surrounded by an inner fibrillar and, external to this, a homogeneous layer together probably equivalent to the inner acrosomal material (central column) in *Homarus*. It is proteinaceous and PAS negative. The peripheral region is clearly the homologue of the outer acrosomal region and, like it, is PAS-positive. A proteinaceous "apical granule" is possibly the equivalent of the homarine apical cap (operculum).

ENOPLOMETOPIDAE

As indicated above, the sperm of *Enoplometopus occidentalis*, described by Haley (1986), who termed it an axiid, appears to the writer to be remarkably similar to that of the Astacidae and Parastacidae and to differ from that of the Nephropidae, in which it has also been placed, and from the paguroid-brachyuran assemblage in the structure of the acrosome vesicle. This has the form of a thick walled inverted cup, wider than long, enclosing a very spacious subacrosomal space in which there is finely granular material but no perforatorium. Centrioles at the base of the acrosome produce microtubules which extend between membranes of the lamellar region distally through the uncondensed nucleus as the cores of three radial arms. Decondensed nuclear material surrounds these microtubular cores at least in the bases of the arms. The nuclear and plasma membranes are fused except where the acrosome lies between them. Two types of mitochondrion-like structures are present. The first do not survive into early spermatids while the second form (apparently from membranes of the lamellar region according to Haley but possibly in fact generating these) during spermiogenesis.

INFRAORDER THALASSINIDEA

The Thalassinidea contains seven families of which only two families have representatives which have been investigated for sperm ultrastructure: *Callianassa australiensis* (Callianassidae) and *Thalassina anomala* (Thalassinidae) (Tudge, pers. comm.). *C. australiensis* has a spherical sperm with four radiating microtubular arms; a small, flat acrosome; the remainder of the sperm body being composed of nuclear and cytoplasmic material. *T. anomala* has a morphologically different sperm being more oblong in shape and possessing a larger acrosome vesicle capped by an operculum with three horizontal layers. The acrosome vesicle is anterior to the cytoplasmic region, from which several microtubular arms originate, and a small nuclear region is present posteriorly.

INFRAORDER PALINURA

The ultrastructure of the spermatozoon of the spiny lobsters, *Panulirus argus* and *P. guttatus*, has been investigated by Talbot and Summers (1978), that of *Jasus novaehollandiae* by Jamieson (in prep.) (Fig. 3B,C) (Palinuridae) and that of *Scyllarus chacei* (Scyllaridae) by McKnight and Hinsch (1986).

Each *Panulirus* sperm (Fig. 2P) is spherical and consists of a nucleus, lamellar region and, at one pole, the acrosome. The nucleus contains uncondensed, Feulgen-positive chromatin and is limited by an intact nuclear envelope which is very closely applied to the plasma membrane except where the nucleus abuts the acrosome and lamellar regions. A variable number (3–12) of spikes radiates from the nucleus. They are extensions of the nucleus and are bounded by its envelope. Microtubules span the nucleus and extend into the spikes. The chromatin is continuous with the lumen of the spike but does not extend into it. The spikes are stationary and the sperm is non-motile. The lamellar body, which lies at one side of the base of the acrosome and external to the nuclear envelope, contains numerous stacks of membranes and small mitochondria-like bodies.

The acrosome vesicle (PAS-positive region) is lens shaped and is limited entirely by a membrane. It is structurally complex and is divisible

into four discrete zones which are respectively, in posterior-anterior sequence, homogeneous; scrolled; crystalline; and flocculent. The homogeneous region forms an electron dense cap situated in a depression in the nucleus and surrounding the scroll and part of the crystalline regions. The scroll region is electron dense with numerous lucid channels which produce the distinctive scroll pattern. The crystalline region is dome-shaped and in section has a very regular grid arrangement of dense squares which in longitudinal section are seen to be vertical rods. The fourth, anteriormost, region contains a dispersed flocculent moderately dense material with coalesced beads or granules. The vesicle is surrounded by periacrosomal material which is flocculent near the base of the acrosome and filamentous at the apex. It includes electron dense bundles of filaments which in longitudinal sections appear as dense cores in pockets formed between the acrosomal and plasma membranes. Microtubules and centrioles were sometimes seen in the basal part of the periacrosomal region (Talbot and Summers, 1978).

The acrosome of *Scyllarus chacei* is unique in investigated Crustacea in having electron dense rays (40 in number) radiating from a dense disc which lies at the apex of the bell shaped vesicle, under the plasma membrane, like the struts of an umbrella. Beneath these the acrosome contains homogeneous, scrolled and crystalline areas. The nuclear membrane is folded and irregular and the chromatin diffuse. The cytoplasmic area contains the lamellar complex, a few mitochondria and a large number of microtubules. The number of microtubular arms arising from the body of the sperm as extensions of the cytoplasm is not specified (McKnight and Hinsch, 1986).

Panulirid sperm conform to the general 'reptant' plan and are nearest to those of the astacids such as *Homarus* and *Nephrops*. The latter differ, however, in having a constant number (three) of spikes and in having a very elongate acrosomal vesicle with the periacrosomal material (percutor organ or perforatorium) extending up into the base of the vesicle. Possession of crystalline material (Talbot and Summers, 1978; McKnight and Hinsch, 1986) is an unusual condition for decapods, shared with nephropids, though with doubtful homology. In the absence of a basal invagination of the acrosome, the palinurid sperm differs conspicuously from sperm of astacids and the anomuran-brachyuroid assemblage and it would not appear that palinurids are near the ancestry of the latter assemblage.

INFRAORDER ANOMURA (*s. strict.* Anomala *s.* Schram, 1986)

The Anomura contain 13 families. Sperm morphology at the light and electron microscope level has been carried out on representatives from six of these: within the Paguroidea, the Diogenidae (*Clibanarius longitarsis*, Dhillon, 1964, 1968; *Clibanarius taeniatus*, *Clibanarius virescens*, Tudge, unpubl.; *Clibanarius corallinus*, Jamieson, in prep. (Fig. 3F); *Dardanus* sp., and *Diogenes* sp., Tudge, unpubl.); the Coenobitidae (*Coenobita clypeatus*, Hinsch, 1980 a, b; *Coenobita spinosus*, Tudge, unpubl., and *Birgus latro*, Tudge and Jamieson, 1991); and the Paguridae (*Pagurus* (=*Eupagurus*) *bernhardus*, Pochon-Masson, 1963; Chevaillier, 1966, 1967, 1968, 1970); in the Galatheidae, *Allogalathea* sp. (Jamieson, in prep.) (Fig. 3D); in the Porcellanidae, *Petrolisthes lamarckii* (Jamieson, in prep.) (Fig. 3E) and in the Hippidae, *Emerita talpoida*, Pearse *et al.*, 1942; Barker and Austin, 1963; *E. analoga*, Vaughn,1968a, b; Vaughn *et al.*, 1969; Vaughn and Locy, 1969; Vaughn and Thomson, 1972; and *E. asiatica*, Subramoniam, 1977).

Most of the anomurans have sperm morphology characterised by an elongate to oblate, complex acrosome projecting anteriorly to the nuclear material and capped by an electron-dense, domed or conical operculum; and three long microtubular arms (possibly more in the Hippidae), radiating from the cytoplasmic region anterior to the nucleus; and diffuse chromatin. *Clibanarius* spp. and *Pagurus bernhardus*, are exceptional only in having a shorter, more ovoid acrosome.

A scatter diagram showing the proportions of the acrosomes (length: width) in various reptants, including anomurans, is given in Fig. 4.

BRACHYURA

In the present study of brachyuran spermatozoal ultrastructure it is proposed to investigate the validity of two conflicting classifications of the Brachyura. The first, which has been summarized by Warner (1977) and is the more familiar to most workers, divides the Brachyura into five sections, the Dromiacea, Oxystomata, Oxyrhyncha, Cancridea and Brachyrhyncha. This classification, with included families for which sperm ultrastructure is known, is shown in Table 1.

Footnotes in the Table allude to the alternative

TABLE 1. Ultrastructural investigations of spermatozoa of the Brachyura.

Higher taxon & Family	Species	Sperm ultrastructure
Dromiacea[1]		
Dromiidae	*Dromidia antillensis* Stimpson	Brown (1966a, 1970); Felgenhauer and Abele (1990)
	Petalomera lateralis (Gray)	Jamieson (1990)
Oxystomata		
Raninidae[2]	*Ranina ranina* (Linneaus)	Jamieson (1989b)
Oxyrhyncha		
Majidae[3]	*Chionoecetes opilio* (Fabricius)	Beninger *et al.* (1988)
	Libinia dubia Milne Edwards	Hinsch (1973)
	Libinia emarginata Linnaeus	Hinsch (1969, 1971, 1973, 1986); Vaughn and Hinsch (1972); Hernandez *et al.* (1989)
	Macrocoeloma trispinosum (Latreille)	Hinsch (1973)
	Menaethius monoceros (Latreille)	Present study
	Mithrax sp. Latreille	Hinsch (1973)
	Pitho lherminieri Rathbun	Hinsch (1973)
	Podochela gracilipes Stimpson	Hinsch (1973)
	Podochela risei Stimpson	Hinsch (1973)
	Stenorhynchus seticornis Lamarack	Hinsch (1973)
Parthenopidae[3]	*Heterocrypta granulata* (Gibbes)	Hinsch (1973)
	Parthenope serratus (H. Milne Edwards)	Hinsch (1973)
Cancridea		
Cancridae[3]	*Cancer borealis* Stimpson	Langreth (1965, 1969)
	Cancer irroratus Say	Langreth (1965, 1969)
	Cancer magister Dana	Langreth (1965, 1969)
	Cancer pagurus Linnaeus	Pochon-Masson (1968a)
	Cancer productus Randall	Langreth (1965, 1969)
Brachyrhyncha		
Portunidae[3]	*Callinectes sapidus* Rathbun	Brown (1966a,b); Felgenhauer and Abele (1990)
	Portunus pelagicus (Linnaeus)	Jamieson (1989b, 1990); Jamieson and Tudge (1990)
	Carcinus maenas (Linnaeus)	Chevaillier (1966b, 1967, 1969); Goudea (1982); Pearson and Walker (1975); Pochon-Masson (1962 [spermiogenesis only], 1965, 1968b); Reger *et al.* (1984)
	Ovalipes ocellatus	Hinsch (1986)
	Caphyra laevis (A. Milne Edwards)	Present study
	Caphyra rotundifrons (A. Milne Edwards)	Present study
Dorippidae[3]	*Neodorippe astuta* (Fabricius)	Jamieson and Tudge (1990)
Calappidae[3]	*Calappa hepatica* Alcock	Present study
Xanthidae[3]	*Menippe mercenaria* (Say)	Brown (1966a)
	Atergatis floridus (Linnaeus)	Jamieson (1989a, 1989c)
	Liagore rubromaculata De Haan	Jamieson (1989a)
	Etisus laevimanus Randall	Jamieson (1989a)
	Pilodius areolatus (Milne-Edwards)	Jamieson (1989a)
	Eurypanopeus depressus (Smith, 1869)	Felgenhauer and Abele (1990)
	Eurytium limosum (Say, 1818)	Felgenhauer and Abele (1990)
Leucosiidae[3]	*Iliacantha subglobosa* (Stimpson, 1871)	Felgenhauer and Abele (1990)
Pinnotheridae[4]	*Pinnixia* sp. White	Reger (1970c)
Grapsidae[4]	*Eriocheir japonicus* De Haan	Du *et al.* (1987); Yasuzumi (1960)
	Grapsus albolineatus Lamarck	Present study
	Sesarma erythrodactyla Hess	Present study
	Sesarma reticulatum (Say)	Felgenhauer and Abele (1990)
Geryonidae[4]	*Geryon fenneri* Manning & Holthuis	Hinsch (1988)
	Geryon quinquedens Smith	Hinsch (1988)
Mictyridae[4]	*Mictyris longicarpus* Latreille	Present study
Ocypodidae[4]	*Ocypoda ceratophthalma* Ortmann	Present study
	Uca dussumieri H. Milne Edwards	Present study
Macrophthalminae[4]	*Macrophthalmus crassipes* H. Milne Edwards	Present study

1, 2, 3, 4 Attributions in the alternative system of Guinot (1978) are: [1]Podotremata, Dromiacea [2]Podotremata, Archaeobrachyura [3]Heterotremata [4]Thoracotremata.

TABLE 2. Brachyuran classification of Guinot (1978).

Section	Sub-section	Superfamily	Sperm ultrastructure known
Podotremata	Dromiacea	Homolodromoidea	
		Dromioidea	Dromiidae*
	Archaeobrachyura	Homoloidea	
		Raninoidea	Raninidae*
		Tymoloidea	
Eubrachyura[4]	Heterotremata	Dorippoidea	Dorippidae*
		Calappoidea	Cancridae, Calappidae*
		Portunoidea	Portunidae*
		Xanthoidea	Xanthidae*, Geryonidae
		Majoidea	Majidae*
		Parthenopoidea	Parthenopidae
		Bellioidea	
		Leucosioidea	Leucosiidae
Thoracotremata	Gecarcinoidea	Grapsoidea	Grapsidae*
		Mictyroidea	Mictyridae*
		Pinnotheroidea	Pinnotheridae
		Hexapodoidea	
		Ocypodoidea	Ocypodidae*
		Hymenostomatoidea	

*Jamieson, Jamieson and Tudge.
[4]De Saint-Laurent (1980b).

classification, developed by Guinot (1977, 1978) in which the Brachyura are divided into three groups: the Podotremata (in turn divided into the Dromiacea and Archaeobrachyura), the Heterotremata and the Thoracotremata (Table 2).

It will be shown that Guinot's classification, though requiring modification, is more congruent with sperm ultrastructure than is that presented by Warner. Guinot's system is based on two, and only two, apomorphies: location of female pores on the sternum of segment 6; and location of the male pores on the sternum of segment 8; these contrast with a plesiomorphic location on the coxa of the corresponding ambulatory limb. The Thoracotremata possess both apomorphies; the Heterotremata have only the first, the male pores remaining plesiomorphically coxal, though in some families they have migrated to a coxosternal position (Palicidae, some xanthoids) or even a lateral sternal position (some portunids, e.g. *Callinectes*); the Podotremata, as the name suggests, have female and male pores on the coxae. Although this classification is better supported by sperm ultrastructure, recognition of the Heterotremata on a single apomorphy, the sternal female pores, might not be expected to give a robust group though more confidence might be attached to the Thoracotremata based on the apomorphic, sternal location of female and male pores. Even if acquisition of sternal female pores were a unique, monophyletic event, the Heterotremata must be paraphyletic if its descendants (Thoracotremata) are not included in it as a subset. In Fig.5 paraphyly of the Heterotremata and monophyly of the included Thoracotremata is indicated.

This caveat does not, however, undermine the terminal group, the Thoracotremata and this group is supported by spermatozoal apomorphies. The six species of the Thoracotremata examined here (Fig. 8) show three synapomorphies (Fig. 5): (1) concentric lamellation of the outer acrosome zone is present in five species, though varying in development in these and apparently absent in *Uca dussumieri*; (2) the operculum has an apical button (not seen in *Macrophthalmus*); and (3) a differentiation of the acrosome contents which appears to be an extension of the basal ring ('xanthid ring' of Jamieson, 1989a) is present in at least the grapsids, the mictyrid and *Ocypoda*, its homology being uncertain in *Uca* and *Macrophthalmus*.

In contrast to spermatozoal support for at least the thoracotreme assemblage, the Dromiacea–Oxystomata–Oxyrhyncha–Cancridea–Brachyrhyncha classification (henceforth D–B classification) is

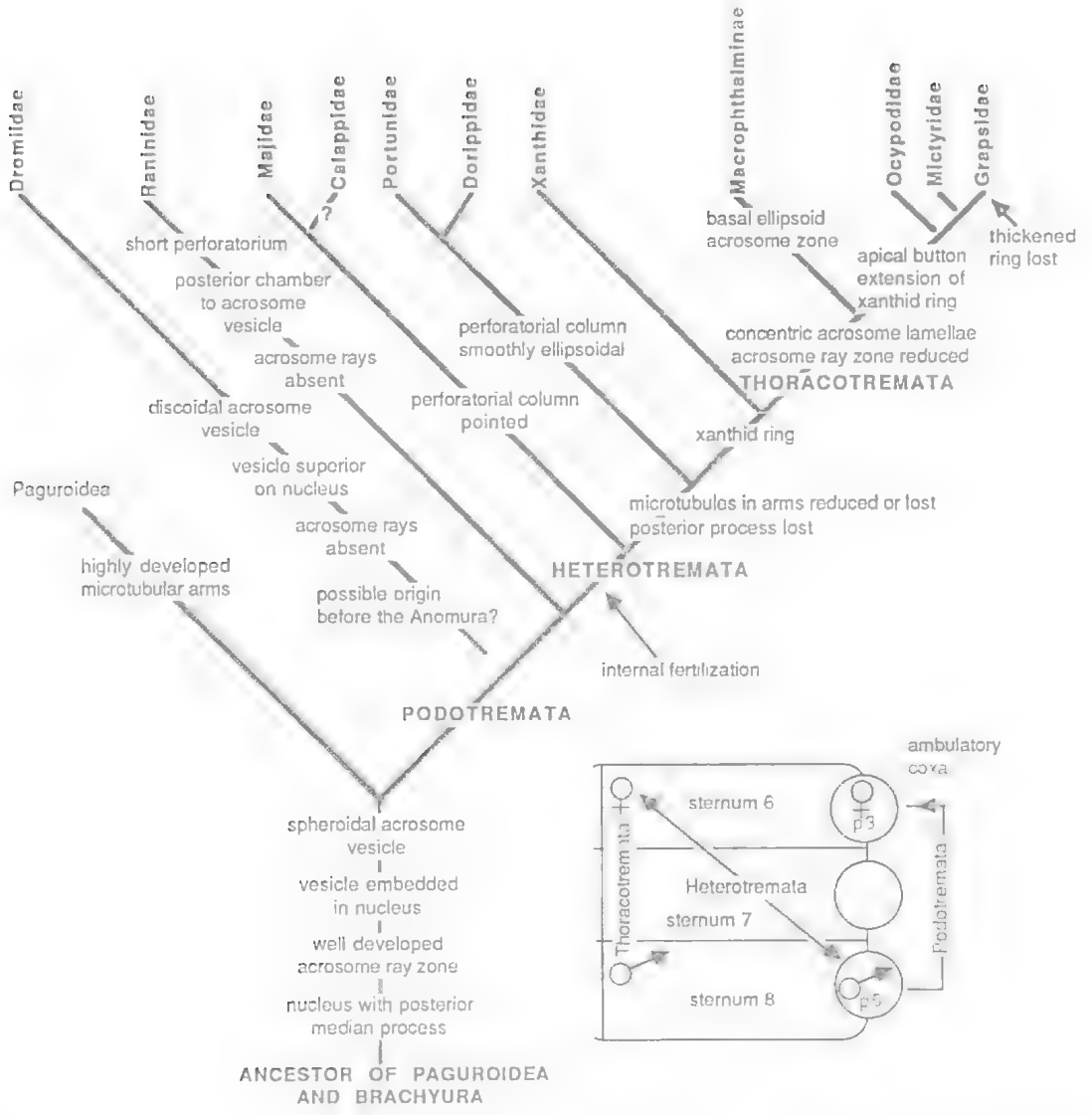


FIG. 5. Tentative, heuristic phylogeny of the Brachyura derived from consideration of the ultrastructure of spermatozoa superimposed on a phylogeny deduced from the classification of Guinot (1977, 1978) which is indicated at bottom right. The phylogeny is limited to the families investigated in the present study and, while it shows perceived trends in spermatozoal anatomy, may be expected to be modified when further taxa are examined.

refuted by the very close, and distinctive, similarity of the sperm of portunids (*Portunus*, *Callinectes*, *Carcinus*, *Caphyra*) with those of the Dorippidae, exemplified by *Neodorippe*, (Fig. 7A). In the D-B system dorippids are placed with raninoids in the Oxystomata while portunids are far removed, in the Brachyrhyncha. The sperm of *Ranina*, described by Jamieson (1989b) (Figs 3I, 6B) is radically different from that of *Neodorippe*. The heterogeneity of the Oxystomata and Brachyrhyncha appears to be endorsed from studies of larval stages (Rice, 1980; Wear and Fielder, 1985).

It might alternatively be argued that the Thoracotremata do not have their origin in the Heterotremata and that the two are independent, monophyletic groups originating from a common ancestor. This view has been espoused by De Saint-Laurent (1980) but the overlap in zoeal morphology demonstrated by Rice (1981), with that

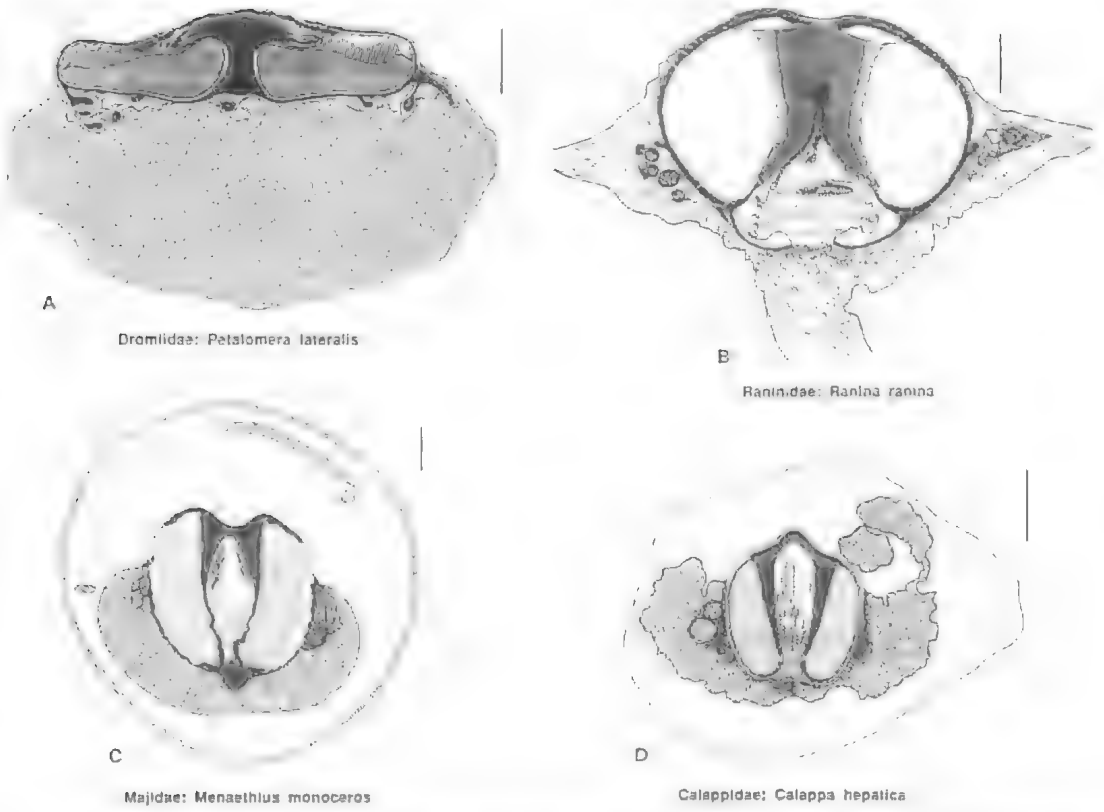


FIG. 6. A–D, Semi-diagrammatic longitudinal sections of spermatozoa from selected brachyuran families. A and B, Podotremata; C and D, Heterotremata. Traced from micrographs. Scale bars = 1μm.

in spermatozoal ultrastructure suggests that thoroacotremes arose from paraphyletic heterotremes as proposed above.

A systematic account of brachyuran sperm now follows.

Dromiacea

Dromiidae. The dromiid sperm, as exemplified by *Petalomera lateralis* (Figs 3H, 6A) and *Dromidia antillensis*, differs markedly from spermatozoa of other crabs (the Oxystomata–Oxyrhyncha–Cancridea–Brachygnatha {O–C–B} assemblage or the raninoid–heterotreme– thoracotreme assemblage) in the discoid, relatively undifferentiated acrosome capping, but not embedded in the nucleus (plesiomorphies); the capitate form of the perforatorium and the composition of this (autapomorphies); the greater, apomorphic, reduction of cytoplasm and organelles, including mitochondria and centrioles; and the absence (*Petalomera*) or brevity (*Dromidia*) of nuclear arms. In view of some similarities of the acrosome to those of Eubrachyura (non-dromiaceans) suggestive of relationship, brevity of arms may be secondary by reduction. Presence of well developed nuclear arms is a synapomorphy of all investigated non-dromiid brachyurans and of the Palinura, Astacidea and Anomura while absence is a symplesiomorphy of other Malacostraca. Absence from dromiid sperm of a posterior median process of the nucleus, which is present in *Pagurus* (Pochon-Masson, 1968a), *Ranina* (Jamieson, 1989b) and majids (Hinsch, 1973; there attributed to a generalized oxyrhynch, Fig. 2Q), is presumably an apomorphic loss, if dromiids are indeed brachyurans. If brevity of lateral arms in dromiids were plesiomorphic, the Dromiacea might be derived from early decapods before evolution of the Palinura-Astacidea-Anomura-Brachyura assemblage as suggested (Rice, 1983; Wear and Fielder, 1985) by their non-brachyuran, anomuran type larvae. If dromiids are monophyletic with true crabs, zoeal morphology would demand a basal position in the Brachyura.

Raninoidea

Raninoids, with dorippoids and calappoids, constitute the spermatologically heterogeneous and clearly polyphyletic Oxystomata (Warner, 1977) or the Archaeobrachyura, containing only raninoids, homoloids and tymoloids, of Guinot (1978). Homoloids and tymoloid sperm are unknown ultrastructurally and therefore the archaeobrachyuran grouping cannot be fully tested spermatologically. Nevertheless, the sperm of *Ranina ranina* (Figs 3I, 6B) is sufficiently similar to those of eubrachyurans and different from those of dromiids to suggest that the Podotremata (Dromiacea and Archaeobrachyura) is a paraphyletic assemblage. Several features are shared between the sperm of *R. ranina* and those of the Eubrachyura. These were previously considered to be synapomorphies (Jamieson, 1989b) but may be plesiomorphies carried over from similar morphology known for anomurans and particularly paguroids: the large spherical, multi-layered, capsule-bound acrosome vesicle (contrast the disc-shaped acrosome of dromiids); the electron dense operculum capping the vesicle; an invaginated core, or perforatorium; concentric zonation of the contents of the vesicle; a layer of cytoplasm, between the acrosome vesicle and the nucleus, which contains mitochondria (mostly degenerating) and lattice-like lamellar complexes or membrane remnants; a diffuse nucleus which is bounded externally by a combined nuclear and plasma membrane and cups the scanty cytoplasm and the large acrosome vesicle; and lateral arms into which the chromatin extends. These arms contain microtubules in 'oxyrhynchs' (Hinsch, 1973) and anomurans (Tudge, unpublished) but microtubules are reduced or absent at maturity in the arms of higher crabs though also shown for the portunid *Carcinus maenas* by Pochon-Masson (1968b). Significant differences of the *Ranina* sperm from those of the O–C–B, including *Portunus*, are: anterior termination of the subacrosomal space at the equator of the acrosome and its conical form (plesiomorphy or raninoid apomorphy?), in the latter assemblage reaching the operculum; differentiation within the subacrosomal material of a coiled, filiform putative perforatorium (plesiomorphy, or apomorphic homoplasy with Anaspidacea?) whereas the entire subacrosomal contents in the O–C–B form a stout perforatorial column; subdivision from the acrosome vesicle in *Ranina* of a posterior acrosomal chamber; and differentiation of the walls of this, lining the subacrosomal chamber, as longitudinal corrugations (raninoid autapomorphies) (Jamieson, 1989b). A further supposed difference, plesiomorphic persistence in *Ranina* of numerous well developed, simple mitochondria in contrast to a stated degeneration, with greater development of a myelin-like lamellar complex, in the O–C–B can now be less certainly maintained as apparently intact mitochondria are demonstrated in the present work for *Macrophthalmus crassipes*. The posterior median process seen in the nucleus of *R. ranina* is also seen in *Pagurus* (Pochon-Masson, 1968a), suggesting that raninoids are plesiomorphic in this respect, and in majids (Hinsch, 1973). This possibly supports origin of majids from the base of the Eubrachyura advocated by Rice (1983). Sperm ultrastructure is consistent with the view that the Raninoidea are the plesiomorphic sister-group of the Oxyrhyncha–Cancridea–Brachyrhyncha assemblage or of the Heterotremata–Thoracotremata assemblage.

Majidae and Parthenopidae

Majids and parthenopids constitute the Oxyrhyncha in the classification summarized by Warner (1977). Both are heterotremes in the classification of Guinot (1977, 1978). Some 10 species, in 6 genera of majids have been examined for sperm ultrastructure (Table 1), of which *Menaethius monoceros* is illustrated here (Figs 3G, 6C). The sperm of this species and those described, notably by Hinsch (1973), are characterized by a broad operculum which is highly unusual in being depressed centrally or (*Podochela*, Hinsch, 1973) at least flattened. In *M. monoceros* the operculum is not only depressed centrally but is also perforate (Figs 3G, 6C). A further feature of majid sperm is the squat, pointed approximately rhombohedroidal shape of the perforatorial column. As a third feature, there is a posterior median extension of the nucleus, in addition to the nuclear arms, which is also present in *Ranina ranina*, in which, as in the majid *Pitho* (Hinsch, 1973) it is particularly well developed. The constancy of this process in majids is questionable but apparent absence may be due to fixation and/or facultative withdrawal in life as it is variably in evidence in *Menaethius monoceros*. Strong development of microtubules in the arms, demonstrated by Hinsch (1973) is here regarded as a plesiomorphic condition further supporting a basal position for majids as microtubules are reduced or absent from 'higher' crabs. The state of maturity and fixation of sperm may well effect the visibility of microtubules.

Hinsch (1973) attributes a very similar form, relative to majid sperm, to the parthenopids *Parthenope serratus* and *Heterocrypta granulata* (though with different layering of the acrosome contents) and sees the posterior process as a basic 'oxyrhynch' character. However, from a study of the megalopa, Rice (1988) regards majids as a monophyletic group quite distinct from the remaining Brachyura and states that there is no justification for retaining them with parthenopids in the Oxyrhyncha. In contrast to the basal position of majids, studies of the zoea led Rice (1981) to regard parthenopids as highly evolved products of a lineage including portunids and geryonids. Guinot (1978) notes that the unity of majids is demonstrated by interruption of the sternal sutures (4/5–7/8). With condensation of the nervous system, she considers this to indicate that majids are advanced heterotremes The posterior process, occurring also in the 'outgroup' Paguroidea, is here seen as a plesiomorphy retained paraphyletically in raninoids and majids to be apomorphically lost in higher crabs (Fig.5). Therefore parsimony favours a more basal position of majids in the phylogeny (Fig. 5) from a purely spermatological viewpoint, as advocated by Rice (1981) from zoeal morphology.

As a symplesiomorphy, centrioles are present in majids, as *inter alia* in parthenopids, portunids, dorippids, and *Macrophthalmus* but not in, for instance, xanthids (Hinsch, 1973; present study).

As parthenopid sperm have not been examined in the present study it is not possible to adjudicate the position of this family spermatologically. *Heterocrypta* is distinguished from other crabs, including *Parthenope*, in the unusually large amount of cytoplasm between the nucleus and the acrosome. From the micrographs by Hinsch (1973) both genera have a wide, thin, very slightly convex operculum perhaps more like opercula of majids than other families and the perforatorial column, in *Parthenope*, at least, is approximately rhombohedroidal, but these are insufficient grounds for recognizing a particular relationship with majids.

Calappidae

Spermatozoal evidence is insufficient for placement of the calappids of which only *Calappa hepatica* has been examined (Fig. 6D). The general morphology of the acrosome is reminiscent in some respects of the majid *Menaethius*, including the relatively straight, anteriorly divergent inner margins to the outer acrosome zone, the approximately rhombohedroidal perforatorial column and the well developed thickened ring, but the operculum differs notably from majids in being pointed apically. Placement near the majids in the phylogram (Fig. 5) merely indicates, therefore, a 'nearest neighbour' in terms of general gestalt. Investigation of the sperm of additional calappids, with other families, may yet contribute to resolution of the phylogenetic position of this family. It is regarded from zoeal morphology as a fairly advanced family which may be near the ancestry of the Cancridae, Corystidae and Atelecyclidae (Rice, 1981).

Cancridae

Cancrid sperm have not been investigated in the present work but that of *Cancer pagurus* has been briefly mentioned by Pochon-Masson (1968a) and four additional *Cancer* species have been used in a combined account of spermiogenesis (chiefly of *C. borealis*) by Langreth (1965, 1969) (Table 1). Some discussion of these is warranted as the Cancridea constiute one of the five major subdivisions of the Brachyura in the system summarized by Warner (1977). The Cancridae are placed with the Corystidae in a restricted superfamily Corystoidea by Guinot (1978) (Table 2).

In the mature sperm of *C. borealis* illustrated by Langreth (1965), the large, dense operculum is craterlike and centrally perforate but as the pointed tip of the perforatorium protrudes through it, perforation of the operculum may indicate that the acrosome reaction has commenced. This is supported by mention by Langreth of penetration of the 'cap' only at maturity. Otherwise the sperm is portunid-like, with, in the terminology of the present work, an inner dense zone differentiated externally as an acrosome ray zone and surrounded by the large, electron pale, outer zone. A conspicuous thickened ring is present in continuity with the thinner but distinctly developed, similarly electron dense capsule. DNA is present throughout the length of the rather short arms. No posterior median process is present. The shape of the perforatorial column, widest at its posterior forth and tapering almost straight to a pointed tip differs from the more bulbous form in portunids.

Although little can be stated with certainty as to similarity and relationships with other families, this sperm is at a similar morphological level to those of portunids and does not in itself

support recognition of a separate higher category for cancrids.

PORTUNIDAE AND DORIPPIDAE

The sperm of *Caphyra laevis C. rotundifrons* (Fig. 3J) and *Portunus pelagicus* (Fig. 7B) show the typical portunid ellipsoidal perforatorium. The sperm of *Carcinus maenas* has been described by Pochon-Masson (1968a). Remarkable intrageneric uniformity is seen in *Caphyra*. A sister-group relationship of *C. laevis* living in colonies of the soft coral *Xenia*, and *C. rotundifrons*, living in tufts of the turtle weed, *Chlorodesmis*, on coral reefs (here Heron Island) is to be suspected. Each species mimics the colour of its host species.

Ultrastructural comparison between the sperm of the dorippid crab *Neodorippe astuta* (Fig. 7A) and the portunid *Portunus pelagicus* (Fig. 7B) has been shown by Jamieson and Tudge (1990) to support placement of dorippids with portunids and their relatives in the heterotreme section of the Eubrachyura and not, as in Table 1, with *Ranina ranina* (in the Archaeobrachyura or the Oxystomata). Characteristic eubrachyuran features of the *N. astuta* sperm (absent from *R. ranina*) are the long perforatorium (short and conical with a unique subacrosomal chamber in *R. ranina*) extending almost to the operculum; presence in the perforatorium of longitudinally arranged convoluted tubules; a zone of acrosomal rays forming the outer part of an inner dense zone; the presence of a thickened ring surrounding the basal part of the perforatorium; and, basally, two centrioles (absent from *R. ranina* but also from some eubrachyurans). The sperm of *N. astuta* is more similar to those of portunids (*P. pelagicus*, *Caphyra laevis* and *C. rotundifrons*, present account; *Carcinus maenas*, Pochon-Masson, 1968a; and *Ovalipes ocellatus*, Hinsch, 1986) than to that of other investigated Brachyura. A smoothly rounded (bulbous) ellipsoidal perforatorial column (more slender in *C. maenas* and *Neodorippe*), well developed acrosome ray zone, and persistence of centrioles characterizes portunids and dorippids; general similarity of gestalt is apparent although difficult to quantify (Fig. 7A, B). Spermatologically dorippids and portunids thus appear to form a monophyletic group within the Heterotremata, though this does not in itself validate the Heterotremata. It has been shown above (see also Fig. 5) that the Heterotremata form a paraphyletic group unless their descendants (the Thoracotremata) are included as a subset.

GERYONIDAE

The sperm of *Geryon fenneri* and *G. quinquedens*, described by Hinsch (1988), are unspecialized heterotreme sperm. They have lost the posterior nuclear process of the raninoids but lack the xanthid ring (see below), though placed in the Xanthoidea by Guinot (1978).

LEUCOSIIDAE

Little can be said of the sperm of the leucosid *Iliacantha subglobosa* illustrated by Felgenhauer and Abele (1990) beyond the fact that it is a strongly triradiate sperm, with 3 well developed arms, a feature which appears plesiomorphic for heterotremes.

XANTHIDAE

Features of xanthid sperm, illustrated in Fig. 7C for *Pilodius areolatus*, which are seen in other higher Eubrachyura and in raninoids (albeit some of them symplesiomorphies include: the large subspheroidal acrosome (a similarity of the raninoid+eubrachyuran assemblage contrasting with the disc-shaped dromioid acrosome); enclosure of the acrosome by a thin layer of cytoplasm which is in turn cupped by the nucleus; extension of the nucleus as lateral arms; presence of cytoplasm (here vestigial) in the basal region of each nuclear arm; absence of the posterior median process (presence being a paguroid-raninoid-majid feature, loss of which is here seen as an apomorphy), and topographical equivalence and presumed homology of components of the acrosome, *viz.* the electron dense capsule; inner and outer dense zones, surrounding the longitudinal axis; peripheral vesicular contents; an apical operculum; subopercular- or subcap-zone; and basally open subacrosomal chamber enclosing perforatorial material. Eubrachyuran features of xanthids, not seen in raninoids, include: anterior termination of the subacrosomal space and enclosed perforatorium at the base of the operculum (contrasting with termination at the equator of the acrosome in raninoids); modification of the capsule around the base of the perforatorium as a thickened ring; absence of longitudinal corrugations lining the subacrosomal chamber (presence is a raninoid autapomorphy); and degeneration of all mitochondria (some apparently persisting in raninoids) (Jamieson, 1989b).

A notable xanthid autapomorphy is differentiation of the posterior region of the inner dense zone surrounding the perforatorium as a prominent strongly electron dense ring, the 'xanthid

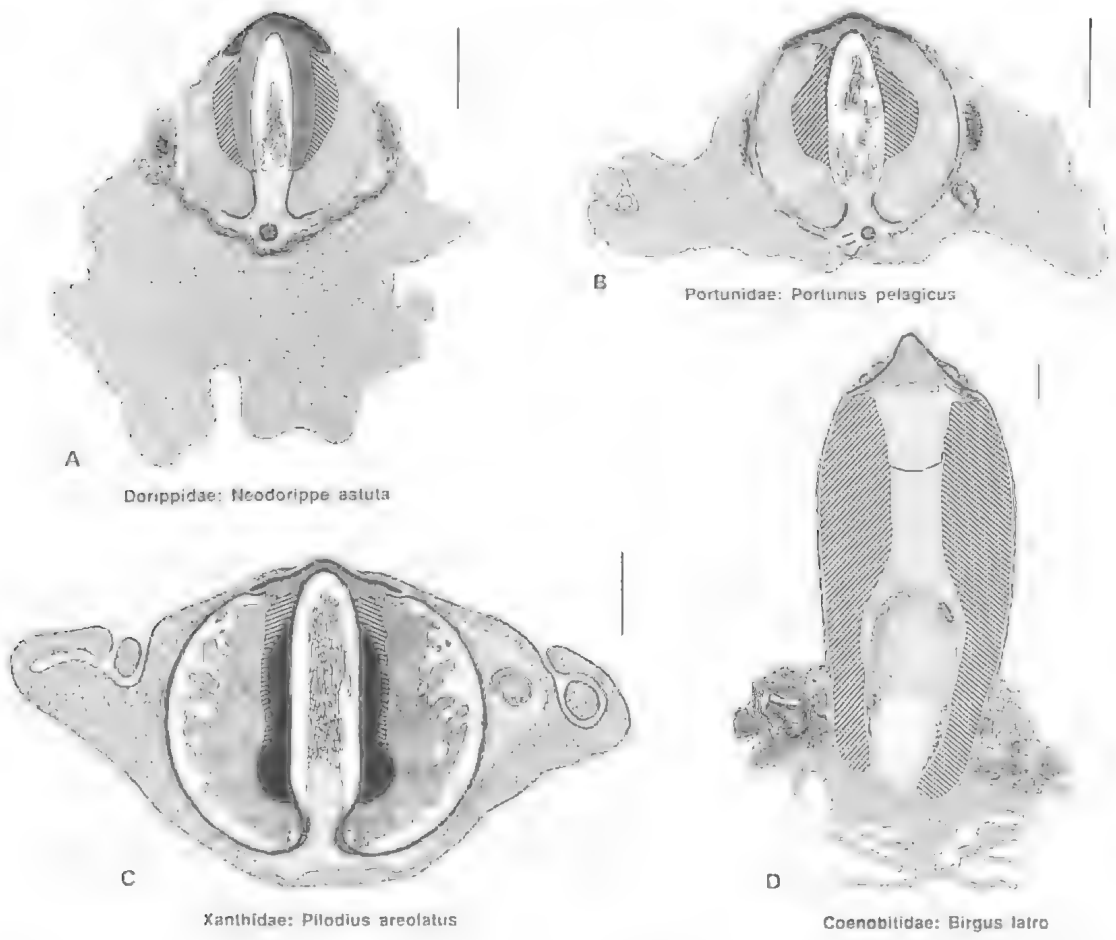


FIG. 7. A–C, Semi-diagrammatic longitudinal sections of spermatozoa from selected brachyuran families. Heterotremata. D, Semi-diagrammatic longitudinal section of coconut crab spermatozoon. Anomura. Traced from micrographs. Scale bars = 1µm.

ring', shown for all four species, in separate xanthid genera, examined by Jamieson (1989a). What is here considered to be an elaboration of this ring, to form a funnel-like structure, is seen in the Thoracotremata and suggests origin of the latter from the Xanthoidea or their immediate ancestors. Rice (1981, 1983) saw primitive xanthids as ancestors of what are here termed heterotreme and thoracotreme brachyurans (excepting the majids, which, it is here concurred, seem more basal). Christensen (1988) considered that the Xanthidae 'may lie at or near the stem of the higher eubrachyurans', thereby giving xanthids a higher position though, like Rice, recognizing their pivotal position in generation of further families. I have inclined to the higher position for the xanthids (Fig. 5) rather than postulate that the xanthid ring has been lost in the portunid-dorippid branch.

THORACOTREMATA

Rice (1981) observes that migration of the female and male pores from the coxae to the sterna of segments 6 and 8 respectively, typifying the Thoracotremata, frees the ambulatory limbs from a reproductive function. The sperm of the Thoracotremata are here examined for two grapsids, *Grapsus albolineatus* (Fig. 8A) and *Sesarma erythrodactyla* (Fig. 8B); the mictyrid *Mictyris longicarpus* (Figs 3K, 8C); the ocypodids *Ocypoda ceratophthalma* (Fig. 8D) and *Uca dussumieri* (Fig. 8E); and the macrophthalmid *Macrophthalmus crassipes* (Fig. 8F). All of these sperm show general eubrachyuran ultra-

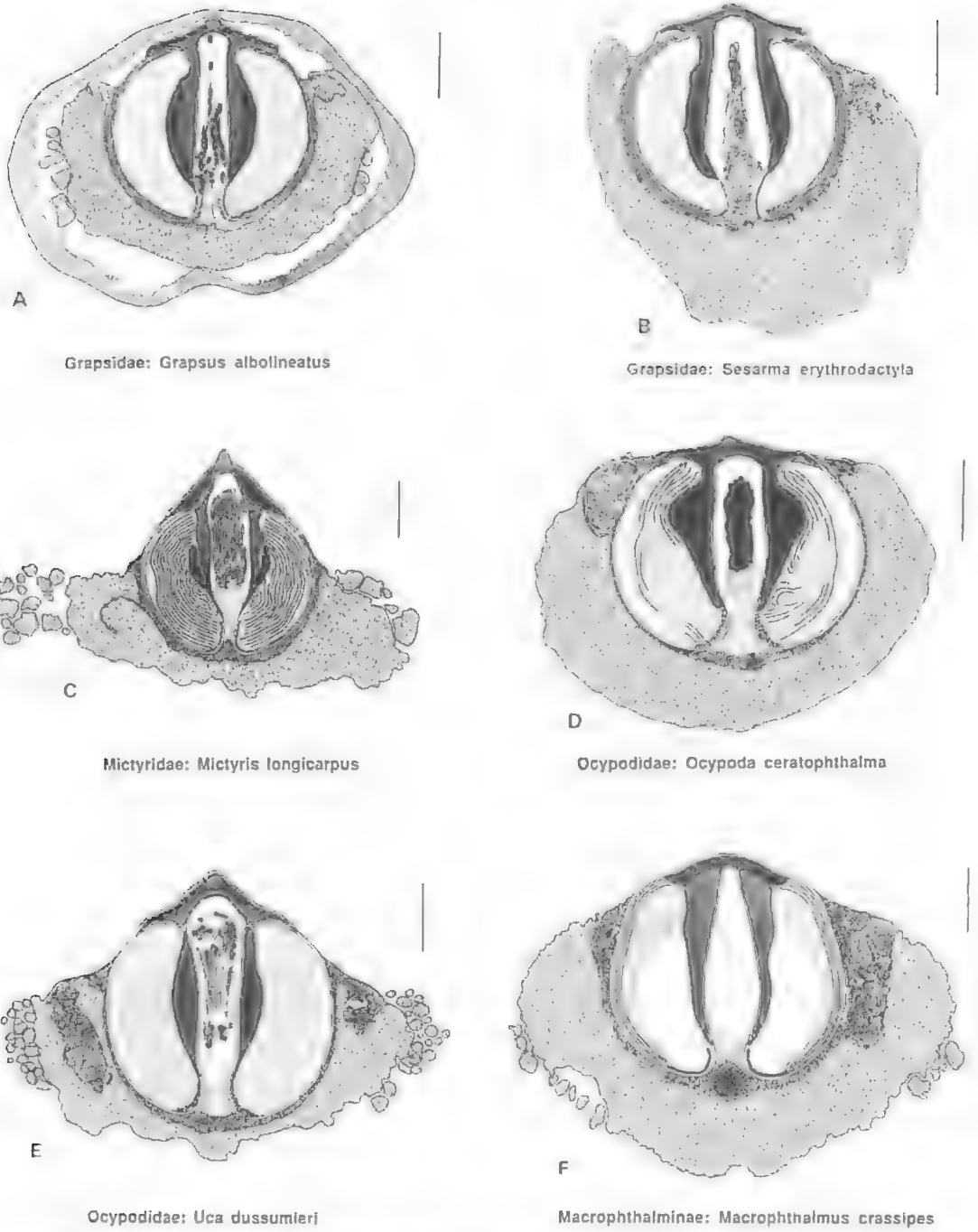


FIG. 8. A–F, Semi-diagrammatic longitudinal sections of spermatozoa from selected brachyuran families. Thoracotremata. Traced from micrographs. Scale bars = 1μm.

structure but, as noted above, thoracotremate synapomorphies are apparent.

The first of these synapomorphies, concentric lamellation of the outer acrosome zone is present in five of these six species, though varying in development but apparently is absent in *Uca dussumieri*. It reaches its greatest development in Mictyris longicarpus. This lamellation is fore-

shadowed in some heterotremes, being indicated by Brown (1966b) for the portunid *Callinectes sapidus*.

The electron dense operculum is interrupted apically by a well defined vesicle which may be ellipsoidal or (*M. longicarpus*) pointed, which I have termed the apical button. This is not seen in *Macrophthalmus* which appears distinctive in other respects.

The differentiation of the acrosome contents which appears to be an extension of the basal ring ('xanthid ring' of Jamieson, 1989a) is present in at least the grapsids, the mictyrid and *Ocypoda*, its occurrence and homology being uncertain in *Uca* and *Macrophthalmus*.

Both grapsids, *Grapsus albolineatus* and *Sesarma erythrodactyla*, are clearly apomorphic in absence of the so-called thickened ring which surrounds the base of the perforatorial column in all examined families, from majids to mictyrids in the phylogeny (Fig. 5). In grapsids the capsule of the acrosome, of which the thickened ring is a specialization in other taxa, is nevertheless intact.

The acrosome ray zone, so well developed in paguroids, such as *Birgus* (Tudge and Jamieson, 1991), as in crabs (portunids, dorippids and xanthids), is so reduced in the Thoracotremata as to be unrecognizable with certainty

Distinctive features of the sperm of *Macrophthalmus* relative to other thoracotremes are the absence of the apical button and presence of a large posterior ellipsoidal, almost spheroidal, acrosome zone peripheral to the inner dense zone and abutting on the thickened ring though extending pre-equatorially. No certain equivalent of the xanthid ring is seen though it is not inconceivable that this zone is a great enlargement of this ring. A further peculiarity of *Macrophthalmus* is that the perforatorial column tapers uniformly from approximately its posterior fourth to a rounded apical point whereas in the other five species the apex of the column is broad (though as always much narrower than the length of the column) and is flattened or gently convex. In the phylogram (Fig. 5) *Macrophthalmus* has been placed below the ocypodids, mictyrid and grapsids as this is more parsimonious than assuming that it is derived above this assemblage by loss of the apical button. From zoeae, Rice (1981) recognizes the Macrophthalminae as a subfamily, less advanced than the Ocypodinae, in the family Ocypodidae, the latter possibly derived from grapsids. The higher status for the grapsids in the spermatozoal phylogeny (Fig. 5) takes into account loss of the thickened ring which is present from majids to ocypodids.

The sperm of the Pinnotheridae (*Pinnixia* sp.) and Geryonidae (*Geryon fenneri* and *G. quinquedens*, considered heterotremes, above) are known only from the literature (Reger, 1970b; Hinsch, 1988) and differences in fixation and staining protocols and mode of illustration relative to those employed in the present study make it difficult to draw comparisons with thoracotreme sperm described here. Generally their structure is not inconsistent with that presented here for thoracotremes but concentric lamellation of the acrosome, if present, is not preserved by the techniques employed. An apical button appears definitely to be absent in spermathecal sperm of *Geryon* while an apical interruption of the opercular density in that of *Pinnixia*, also from the spermatheca, possibly corresponds with a button. In *Pinnixia* a poorly defined zone external to the innermost dense zone may be equivalent to the extended xanthid ring typical of thoracotremes.

Thus although the Heterotremata *sensu stricto* appear to be a paraphyletic assemblage, and as such to be a grade rather than a clade, three albeit inconstant synapomorphies within the Thoracotremata suggest that the species examined here, at least, form a monophyletic group.

CONCLUSIONS

Occurrence in *Speleonectes* of a flagellate spermatozoon approaching in structure the invertebrate 'primitive sperm' (aquasperm) is consistent with the supposedly primitive status of the Remepedia but does not rule out an alternative placement with the ascothoracican through cirripedian section, also with flagellated sperm, of the Maxillopoda.

Cephalocarid (*Hutchinsoniella*) sperm resembling those of remipedes but lacking the flagellum may represent the ground plan for the Phyllopoda, hitherto thought to be the simple, amoeba-like sperm seen in euphyllopods and conchostracans. The *Nebalia* sperm, lacking an acrosome and with microtubular arms, supports the phyllopod status of phyllocarids. Nevertheless, the possibility exists that the malacostracan acrosome is a new development, in view of evidence that their acrosome originates from the endoplasmic reticulum and not, as is usual, from the Golgi. If so, one of the objections to relating phyllocarids to Malacostraca would be lost.

Copepod sperm show no clear affinities with

other groups, though the stellate acrosome-less sperm of the cyclopoid *Chondracanthus* resembles that of some branchiopods. Ostracod sperm include a filiform type performing undulatory waves by means of wing-like structures originating from the endoplasmic reticulum.

In the Malacostraca, stomatopod (*Squilla, Oratosquilla, Gonodactylus*) sperm are ovoidal, lacking appendages, with acrosome and a perforatorium; absence of a nuclear membrane, and diffuse chromatin are decapod tendencies; unusual, doublet centrioles are a peracarid-decapod feature. The syncarid (*Anaspides tasmaniae*) sperm has a subacrosomal filament [perforatorium], exceptional for Crustacea in being coiled. A syncarid apomorphy is the cytoplasmic 'skirt', a plesiomorphy the condensed chromatin and persistent nuclear membrane. Peracarid monophyly is confirmed by presence, with the questionable exception of tanaids, of a cross striated pseudoflagellum (possibly a centriolar rootlet homologue) joining the mainbody at junction of acrosome and nucleus. Tanaid sperm, rounded, lacking appendages, with large acrosome and scattered mitochondria, seen also in syncarids and stomatopods, possibly indicate a basal rather than terminal or intercalated position of the tanaids in the Peracarida.

Euphausid sperm, ovoidal and lacking appendages, are insufficiently known to contribute to determination of the eucarid ground plan. Pending confirmation, they and the stenopodideans appear unique in the Malacostraca (phyllocarids excluded) in lacking the acrosome. Dendrobranchiate (penaeid) and procaridean and caridean shrimps and prawns have sperm with a single acrosomal spike but rarely have arms analogous with those characteristic of decapods. Spermatologically, the unistellate condition affords some support for the concept of the Natantia. It is difficult to envisage the spike as a symplesiomorphy of a paraphyletic Natantia which was replaced by the reptantian acrosome. However, paraphyly of the Natantia is indicated in parsimony analysis of 18S rRNA sequences by Kim and Abele (1990).

Several spikes containing microtubules which traverse and often contain chromatin are characteristic of Palinura (*Panulirus, Jasus*); Astacidea (Astacidae, Nephropidae); Thalassinidea; Anomura (Paguridae, Diogenidae, Coenobitidae); and Brachyura, though microtubules are reduced or absent above the 'oxyrhynchs'. The acrosome of Eubrachyura resembles that of paguroids, and especially in its subspheroidal shape *Pagurus* and *Clibanarius*, suggesting a paguroid–brachyuran (sister-group?) relationship while the thalassinid (*Callianassa*) acrosome differs greatly from that of the Astacidea–Anomura–Brachyura assemblage, contraindicating a thalassinid origin of the Brachyura.

The discoidal acrosome and reduced arms of dromiid (*Dromidia, Petalomera*) sperm may be plesiomorphic conditions of a group with no close relationship to other brachyurans. Phylogenetic heterogeneity of the Podotremata is supported by differences between dromiid and raninoid sperm and similarities (postnuclear tail) between *Ranina* and majids. The conventional oxystomate-oxyrhynch-cancrid-brachyrhynch subdivision of the Brachyura is not supported by sperm ultrastructure. Dorippids and portunids, with similar sperm, are placeable in the Heterotremata, whereas the former classification separates the two families in the Oxystomata and Brachyrhyncha, respectively, but the Heterotremata *sensu* Guinot is a paraphyletic assemblage, representing a grade typified by migration of the female pores onto the sternum, unless it is enlarged to include the thoracotremes. In contrast examined Thoracotremata (Mictyroidea, Grapsoidea and Ocypodoidea) appear to form a monophyletic group typified by presence of an apical opercular button, concentric lamination of the outer acrosome zone and modification of the xanthid ring, though none of these three characters is sufficiently constant to allow a monothetic definition of the group.

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A PHYLOGENETIC ANALYSIS OF THE ISOPODA WITH SOME CLASSIFICATORY RECOMMENDATIONS

RICHARD C. BRUSCA AND GEORGE D.F. WILSON

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The phylogenetic relationships of the isopod crustacean suborders are assessed using cladistic methodology. The monophyly of the Flabellifera was tested by including all 15 component families separately in the analysis. Four other peracarid orders (Mysidacea, Amphipoda, Mictacea, and Tanaidacea) were used as multiple out-groups to root our phylogenetic estimates within the Isopoda. A broad range of possible characters for use in assessing isopod relationships is discussed and a final data (character) matrix was selected. This data matrix, comprising 29 taxa and 92 characters, was subjected to computer-assisted analysis using four different phylogenetic programs: HENNIG86, PAUP, PHYLIP, and MacClade. Phylogenetic hypotheses from the literature (particularly Wägele, 1989a) are discussed and compared with our own conclusions.

The following hypotheses are suggested by our analysis. The Isopoda constitutes a monophyletic group. The Phreatoicidea is the earliest derived group of living isopods, followed by an Asellota–Microcerberidea line, and next the Oniscidea. Above the Oniscidea is a large clade of 'long-tailed' isopod taxa (Valvifera, Anthuridea, Flabellifera, Epicaridea, Gnathiidea). The Microcerberidea is the sister group of the Asellota, but probably should not be included in the Asellota. The Oniscidea constitutes a monophyletic group. The monotypic taxon Calabozoidea is either a primitive oniscidean, or is a sister group of the Oniscidea (*Calabozoa* is not an asellotan). Our cladistic analysis suggests that the primitive isopod body plan was one in which well-developed lateral coxal plates were lacking, the pleopods were multiarticulate, the uropods arose on the posterior margin of the pleotelson, the telsonic region was not elongate, and the mandibular molar process was a broad flat grinding structure. Extant taxa with this body plan (Phreatoicidea, Asellota, Microcerberidea) occur primarily in relictual habitats. Oniscidea conform to this body plan except in possessing lateral coxal plates.

The long-tailed isopod morphology (broad flat uropods, an elongate telsonic region, and well-developed lateral coxal plates) appears to be a derived condition within the Isopoda. Suborders and families with this body plan appear to be most speciose, or to have had their origin, in the Southern Hemisphere. The 'caridoid'-like pleonal morphology of many long-tailed isopods (Flabellifera, Gnathiidea, Anthuridea) is thus secondarily derived and convergent to the condition seen in the mysidaceans and other true caridoid crustaceans. The broad, elongate tailfan of the long-tailed isopod taxa is not used for a caridoid-like tail locomotory behaviour (e.g. the 'caridoid escape reaction'), but rather as a steering/stabilising plane. The emergence of the long-tailed body plan seems to have coincided with a shift in isopod habits from infaunal to more active, swimming, epifaunal lifestyles. Accompanying this transition was enlargement of the lateral coxal plates (perhaps to increase hydrodynamic streamlining of the body) and a shift to active carnivory and predation, and eventually parasitism in several groups.

The Suborder Flabellifera (as it is currently recognised) is not a monophyletic taxon. Three taxa usually ranked at the subordinal level (Anthuridea, Gnathiidea and Epicaridea) have their phylogenetic origins within the lineage of families that currently constitutes the Flabellifera. The Protognathiidae is not closely related to the Gnathiidea. Protognathiidae is probably closely related to Anuropidae and is part of a clade culminating in the parasitic family Cymothoidae. Wägele's (1989a) recently proposed new classification of the Isopoda, including his new suborders Sphaeromatidea and Cymothoida (*sic*), is not corroborated by our phylogenetic analysis. Unambiguous sister group relationships cannot be hypothesised for the long-tailed isopod taxa with the current data base. A new formal classification of the order Isopoda must await better resolution of the phylogeny based upon an expanded data set. □ *Isopoda, phylogeny, classification, morphology, biogeography.*

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'Amidst this prudent love of obscurity, the one feature of moral character which they possess in common is strong evidence that all of them must have sprang from a common origin.'

The Reverend T.R.R. Stebbing (1893), Speaking of isopods.

Most of the isopod suborders were described and delineated in the early part of the nineteenth century, but for the past 150 years classification of these suborders and their families has been unsettled. Until fairly recently many workers included the Tanaidacea within the Isopoda and included either (or both) the Gnathiidea and Anthuridea within the Flabellifera (or 'Cymothoidea') (Bate and Westwood, 1863–68; Stebbing, 1893; Sars, 1897; Richardson, 1905; Smith and Weldon, 1923; Hale, 1929; Nierstrasz and Schuurmans-Stekhovan, 1930; Menzies, 1962; Naylor, 1972). Hansen (1916) and Monod (1922) recognised the necessity of separating the tanaidaceans from the isopods, and also removed the gnathiids and anthurideans from the Flabellifera. Some authorities sought to establish a fundamental split between the gnathiids and the remaining Isopoda. Monod (1922) called the gnathiids Decempedes ('10-footed'), and all other isopods the Quatuordecempedes ('14-footed'). Following Latreille (1804), Menzies (1962) used the name Tetracera for the non-gnathiid isopods. Menzies (1962) chose to retain the anthurideans within the Flabellifera, but later removed them (Menzies and Glynn, 1968).

Karaman (1933) allied *Microcerberus* with the Anthuridea, and many subsequent workers accepted this placement (Remane and Siewing, 1953; Chappuis and Delamare, 1954; Lang, 1960; Schultz, 1979; Kussakin, 1973). However, Lang (1961) created a new suborder for this genus, the Microcerberidea, and Wägele (1982b, 1983b) argued against any relationship between the microcerberids and anthurideans, instead suggesting that the former were highly specialized asellotans.

The name 'Cirolanoidea" has been used in different ways by different workers. Richardson (1905) considered it a synonym of her 'Flabellifera' (following Sars to include the Aegidae, Anthuridae, Cirolanidae, Corallanidae, Cymothoidae, Excorallanidae, Gnathiidae, Limnoriidae, Serolidae, and Sphaeromidae). Menzies (1962) considered the Cirolanoidea to be a subtribe of his tribe Flabellifera, synonymous to the Cymothoidea of some previous authors (including the Anuropidae, Cirolanidae, Limnoriidae, Sphaeromidae). Wägele (1989a) used Leach's (1814) spelling of 'Cymothoida', for his newly proposed suborder (for the Aegidae, Anuropidae, Bopyridae [=Epicaridea], Cirolanidae, Corallanidae, Cymothoidae, Gnathiidae, Phoratopodidae, Protognathiidae, and Tridentellidae).

In 1983 Van Lieshout erected a new monotypic suborder (Calabozoidea) for *Calabozoa pellucida*, a ground-water isopod from Venezuelan wells, and discussed its possible affinities to both the Oniscidea and the Asellota. Wägele (1989a) argued for placing the Calabozoidea near the Asellota, depicting these two suborders as sister groups on his phylogenetic tree.

Recent summaries by Bowman and Abele (1982), Brusca and Iverson (1985), Schram (1986), and Brusca and Brusca (1990) took the conservative approach in recognizing 9 suborders (Table 1, Figs 1–3), maintaining separate subordinal status for the Microcerberidea, Anthuridea, Gnathiidea, and Epicaridea.

An examination of previously published studies concerning isopod phylogeny reveals a fairly broad range of ideas (Fig. 4). Beginning with Hansen (1905), however, two taxa have dominated the literature as contenders for the title of 'most primitive living isopods", the Flabellifera and the Asellota. Schultz (1969, 1979) deviated markedly from this pattern, and his phylogeny depicted the Gnathiidea as the most primitive living isopod group. Schram (1974) appears to have been the only person to have previously specifically espoused the Phreatoicidea to be the earliest derived isopod suborder.

Supporters of the 'Asellota-are-primitive' hypotheses have included Hansen (1925), Monod (1922), Birstein (1951), Zenkevich and Birstein

FIG. 1. Examples of 'short-tailed' isopod suborders. A, Phreatoicidea (*Mesamphisopus depressus* after Nicholls, 1943). B, Asellota (*Janiropsis montereyensis*, after Menzies, 1952). C, Microcerberidea (*Microcerberus* sp., after Argano, 1988). D, Calabozoidea (*Calabozoa pellucida*, after Van Lieshout, 1983). E, Oniscidea (*Armadillidium vulgare*, after Sutton, 1972).

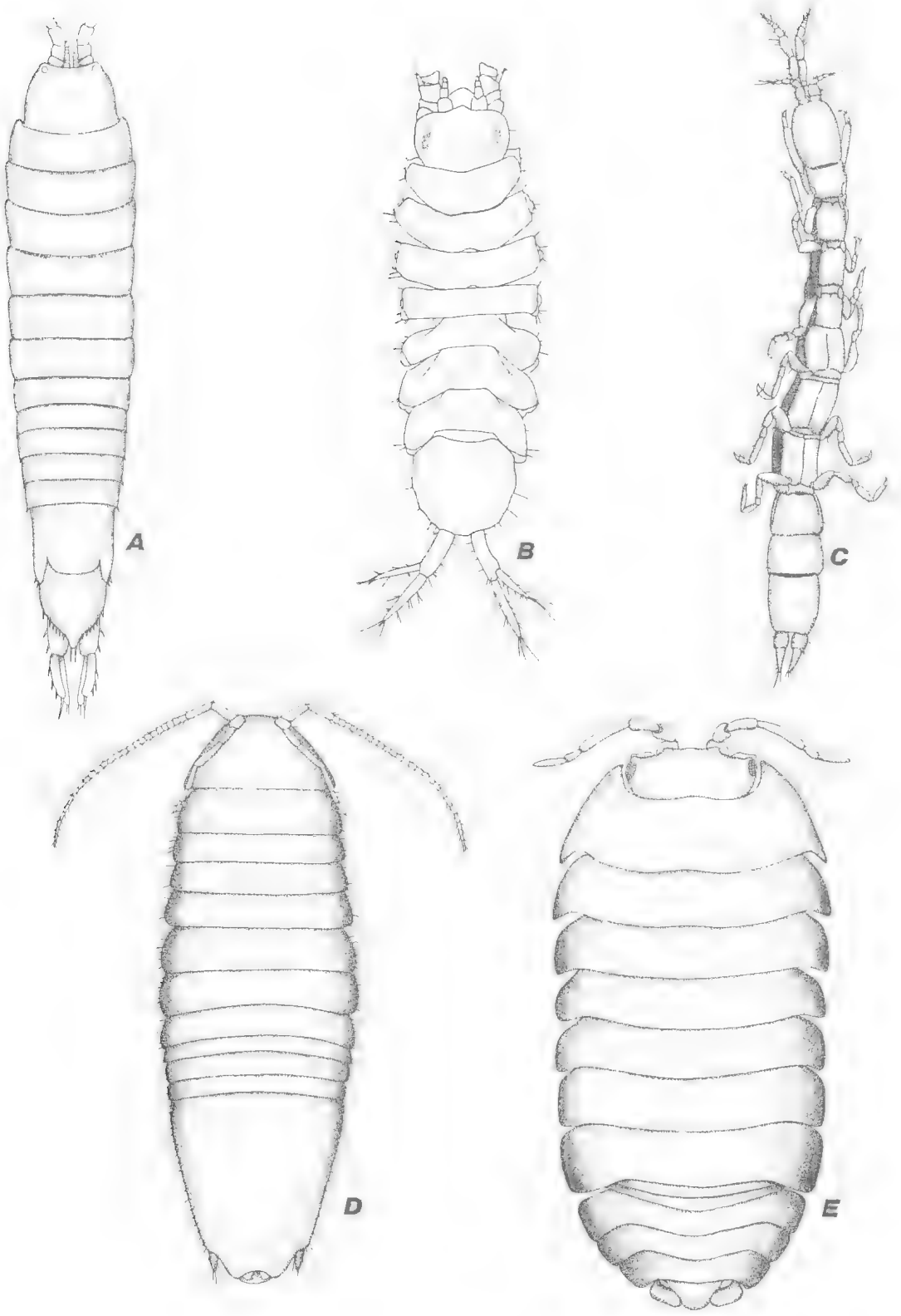

A
B
C
D
E

TABLE 1. Taxa analysed in the present study.

OUT-GROUPS
Order MYSIDACEA
Order MICTACEA
Order TANAIDACEA
Order AMPHIPODA
IN-GROUPS
Order ISOPODA
Suborder Phreatoicidea
Suborder Asellota
Suborder Microcerberidea
Suborder Oniscidea
Infraorder Tylomorpha
Infraorder Ligiamorpha
Suborder Calabozoidea
Suborder Valvifera
Suborder Epicaridea
Suborder Gnathiidea
Suborder Anthuridea
Suborder Flabellifera
Family Aegidae
Family Anuropidae
Family Bathynataliidae
Family Cirolanidae
Family Corallanidae
Family Cymothoidae
Family Keuphyliidae
Family Limnoriidae
Family Lynseiidae
Family Phoratopodidae
Family Plakarthriidae
Family Protognathiidae
Family Serolidae
Family Sphaeromatidae
Family Tridentellidae

(1961), Belyaev (1966), and most recently Schmalfuss (1989). Although Schmalfuss' tree has the appearance of a cladogram, it appears to be an intuitive tree based on *ad hoc* assumptions of ancestry. It used 4 specific synapomorphies to define 8 isopod suborders. Schmalfuss did not describe his method of tree construction, tree selection, character analysis, or character polarity assessment; did not calculate tree lengths or homoplasy values; did not describethe characters he utilised; and, rooted his tree based on ambiguous statements regarding *ad hoc* hypothetical morphotypes rather than on methods such as out-group or ontological analysis. It should be noted that for 8 taxa there exist 660,032 possible tree topologies (Felsenstein, 1978).

Supporters of 'Flabellifera-are-primitive' hypotheses have included Racovitza (1912), Strömberg (1972), Kussakin (1973, 1979), Bruce (1981), and Wägele (1989a). Among the Flabellifera, the Cirolanidae (especially *Bathynomus*) is usually chosen as the model for the archtypical ancestral isopod. Kussakin (1979) refined his earlier views to present a phylogeny in which a 'cirolanid-like ancestor' (but that was not yet a 'true' flabelliferan) gave rise to an Anthuridea/Microcerberidea line as the most primitive living isopod group, followed by the Oniscidea and Valvifera, with the extant Flabellifera, Phreatoicidea, and Asellota being the most highly derived taxa. Kussakin (1979) came to this conclusion despite his contention that the most primitive arrangement of pereopodal coxae occurs in the Asellota, a group in which he noted, 'the coxopodite still looks like a normal segment'. Within the flabelliferan line, Kussakin hypothesized three lineages. One lineage lead to predacious/parasitic lifestyles (Cirolanidae, Aegidae, Cymothoidae, and ultimately the Epicaridea); the other two lines were said to have given rise to benthic herbivores and detritivores, such as the Serolidae and Sphaeromatidae. He allied the Anuropidae with the Valvifera and Oniscidea, rather than with the Flabellifera. Kussakin described (but did not depict on his phylogenetic tree) the Asellota arising from a hypothetical ancestral cirolanid stem group, via the Phreatoicidea. Bruce (1981) supported Kussakin's (1979) views, and further hypothesised the Phoratopodidae to be the sister group of the Valvifera. Nicholls (1943, 1944), Dahl (1954), and Strömberg (1972) also argued that the Phreatoicidea originated from an ancient Flabelliferan stock close to the modern Cirolanidae.

Wägele (1981) claimed that 'general agreement exists among isopod workers that the ancestral isopod body shape and external features were certain to have been similar to those of living Cirolanidae (though perhaps lacking coxal plates),' but later stated that the Cirolanidae could not possibly be considered as primitive isopods and that they were the probable sister group of the Anthuridea. Still later Wägele (1989a) claimed that the (hypothetical) ancestor of the Isopoda was cirolanid-like, even though his 'Hennigian' phylogenetic analysis confirmed that the Cirolanidae was a highly derived group (Fig. 4D).

Strömberg (1972) counted the number of hypothesised plesiomorphic features occurring in each of the isopod suborders, concluding on this basis that the Flabellifera (notably the Cirolani-

dae) were the most primitive living group and the stem group from which all other isopod suborders were derived. He presented an argument for close alliance between the Flabellifera, the Epicaridea, and the Gnathiidea.

All of the above hypotheses, except Wägele (1989a), consisted of *ad hoc* tree construction and evolutionary narratives in the traditional, or orthodox, sense. Each was based on a small set of selected characters that held sway over all others. Most relied on a mix of both primitive and derived features to infer relationships. None was based on a large data set of empirically evaluated characters, and none used any strict analytical methodology. Most, if not all, relied upon the (stated or unstated) *ad hoc* selection of an extant group of isopods to represent a primitive ancestral morpholype. From these *a priori*-selected hypothetical ancestors, evolutionary scenarios were inferred, and trees were constructed based upon these scenarios. Because the phylogenetic scenarios cited above were not derived from empirical analyses of the data, nor utilized any repeatable methodology, it would be unfair (and difficult) to compare them directly to the present study. It is interesting to note that, despite the fact that the Phreatoicidea have the oldest known fossil record (Pennsylvanian; Schram, 1970, 1974), none of the above proposals hypothesised this group (or a phreatoicid-like morphology) to represent the ancestral isopod type.

The only previous attempt to undertake a phylogenetic analysis of the Isopoda based on a large data set and a specific methodology was Wägele's (1989a) recent study (Fig. 4D). Wägele proposed a sweeping reorganisation of isopod classification. Some of the many changes he proposed included the complete elimination of the Suborder Flabellifera, and the reduction to family status of the suborders Gnathiidea and Epicaridea (reducing the families of the latter to subfamilies and eliminating the name Epicaridea altogether). However, even though Wägele's study was based on a larger set of characters than any previous analysis, it was still based on an *ad hoc* hypothetical ancestral morphotype, the phylogenetic tree was computed by hand, and no attempt was made to achieve either global or in-group parsimony or utilise any strict criteria of tree construction or tree selection. Wägele's classification scheme was not strictly cladistic in that it did not recognise the sister group arrangements of his cladogram.

In data sets with more than a few taxa, the number of possible trees quickly becomes astronomical. An analysis of the 10 nominate isopod suborders alone requires assessment of 282 million possible trees, 34.5 million of which are bifurcating trees (Felsenstein, 1978). The present study analyses 29 taxa, for which there are 8.7×10^{36} possible bifurcating trees. Hence, to select a single shortest tree with the highest degree of parsimony and the lowest level of homoplasy by 'eyeballing the data' is difficult, if not impossible. Nevertheless, Wägele's (1989a) analysis was a very important step forward in isopod phylogenetics, and was the first published study at the subordinal level to use a relatively large data set and provide lists of general synapomorphies that define putative monophyletic lines. For these reasons, we compare our analysis closely to that of Wägele in the discussion section at the end of this paper.

METHODS

Out-Groups

The questions of peracarid monophyly and the phylogenetic sequence of appearance of the peracarid orders have long been favorite subjects of debate among carcinologists. Nearly every imaginable topology of phylogenetic relationships among the In 1981 peracarida has been proposed at one time or another. There is no need to review this debate here (Dahl, 1977; Watling, 1981, 1983; Schram, 1981, 1986; Dahl and Hessler, 1982; Hessler, 1983; Brusca, 1984). However, most published ideas over the years have suggested that the sister group of the Isopoda is either the Amphipoda or the Tanaidacea. The recently described Mictacea may also be closely related to the isopods (Schram, 1986). Because of this uncertainty, we use four out-groups in our analysis: Mysidacea, Amphipoda, Mictacea, and Tanaidacea. The increased accuracy of character polarity assessment and tree resolution that can be achieved by use of the multiple out-group method has been explained by Maddison *et al.* (1984) and others, the basic premise being that cladograms should be globally parsimonious.

In-Group

Our in-group includes all 10 nominate isopod suborders (Table 1), plus the 15 nominate flabelliferan families. The relationships of the families included within the Flabellifera have been controversial, and it has been frequently suggested that the Flabellifera is a non-monophyletic taxon. Kussakin (1979), Bruce (1981), and

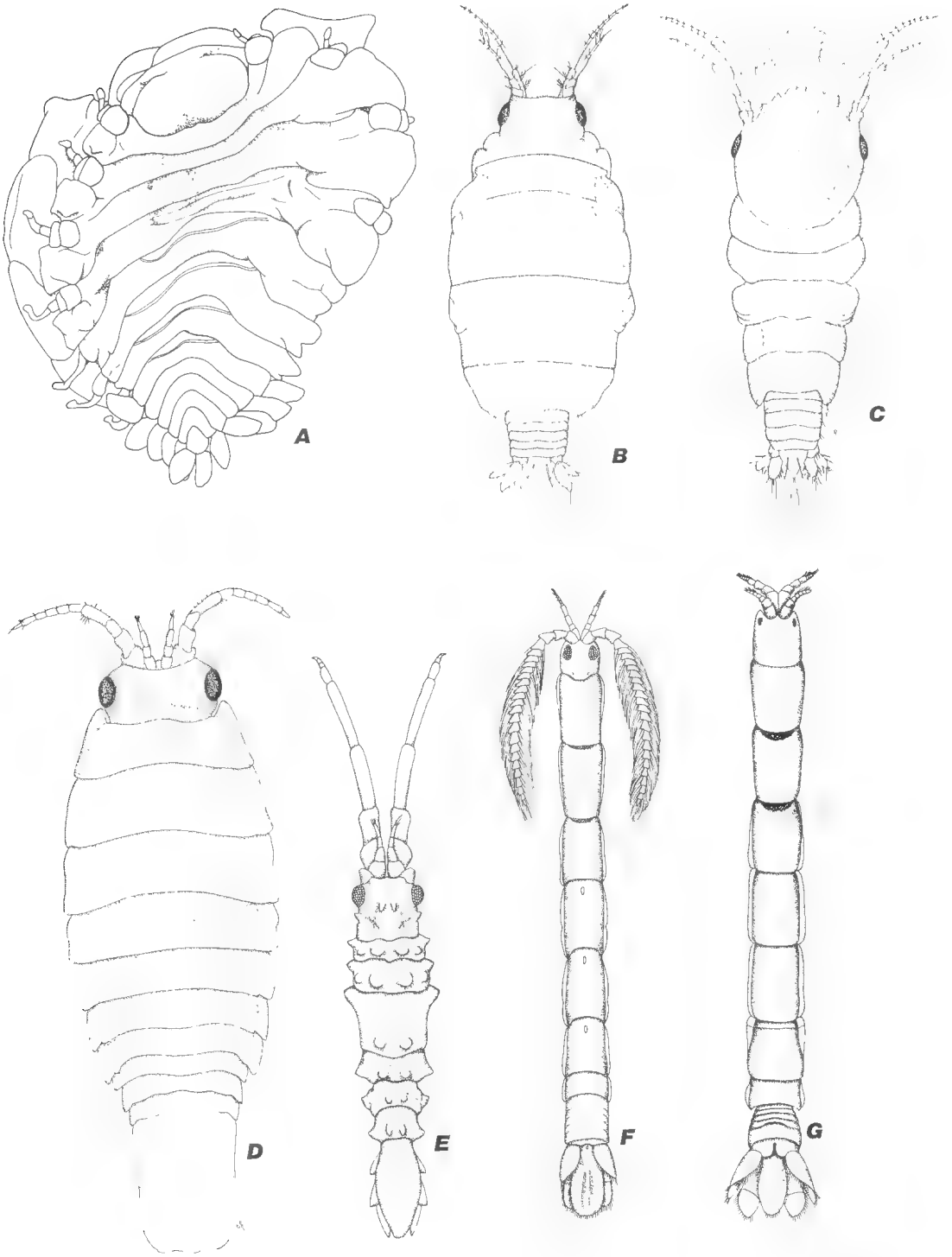


FIG. 2. Examples of various 'long-tailed' isopod suborders. A, Epicaridea (*Argeia pugettensis*). B–C, Gnathiidea (B, *Gnathia tridens* female; C, *Gnathia tridens* male). D, Valvifera, Idoteidae (*Idotea metallica*). E, Valvifera, Arcturidae (*Idarcturus hedgpethi*). F, Anthuridea, Anthuridae (*Haliophasma geminata* male). G, Anthuridea, Paranthuridae (*Paranthura elegans*).

Wägele (1989a) depicted this group paraphyletically on their trees of the Isopoda. Wägele (1989a) recommended a reorganisation of the Isopoda that would eliminate three currently recognized suborders, the Flabellifera, Epicaridea, and Gnathiidea. Although Wägele's tree and classification are not corroborated by the present study, the Flabellifera as it is currently recognized is almost certainly not a monophyletic taxon. Wägele reorganized the above suborders into two new groups, which he called the Cymothoida (*sic*) and the Sphaeromatoidea, subsuming the Gnathiidea, Epicaridea, and several flabelliferan families into the former. (Note that Wägele's Cymothoida is not the equivalent of Cymothoidea of Richardson, 1905, and others).

In the present study, we test the monophyly of the Flabellifera by including all of its component families in the analysis with the other suborders of the Isopoda. We recognize the following nominate families of Flabellifera: Aegidae Dana, 1853; Anuropidae Stebbing, 1893; Bathynataliidae Kensley, 1978; Cirolanidae Dana, 1853; Corallanidae Hansen, 1890; Cymothoidae Leach, 1818; Keuphyliidae Bruce, 1980; Limnoriidae White 1850; Lynseiidae Poore, 1987; Phoratopodidae Hale, 1925; Plakarthriidae Richardson, 1904; Protognathiidae Wägele and Brandt, 1988; Serolidae Dana, 1853; Sphaeromatidae Burmeister, 1834; and, Tridentellidae Bruce, 1984.

The two infraorders of Oniscidea Latreille, 1803 (Tylomorpha Vandel, 1943 and Ligiamorpha Vandel, 1943; see Holdich *et al.*, 1984) are also analysed separately because opinion has been divided on whether or not the Tylidae are true oniscideans (Kussakin, 1979; Holdich *et al.*, 1984; Wägele, 1989a; Schmalfuss, 1989).

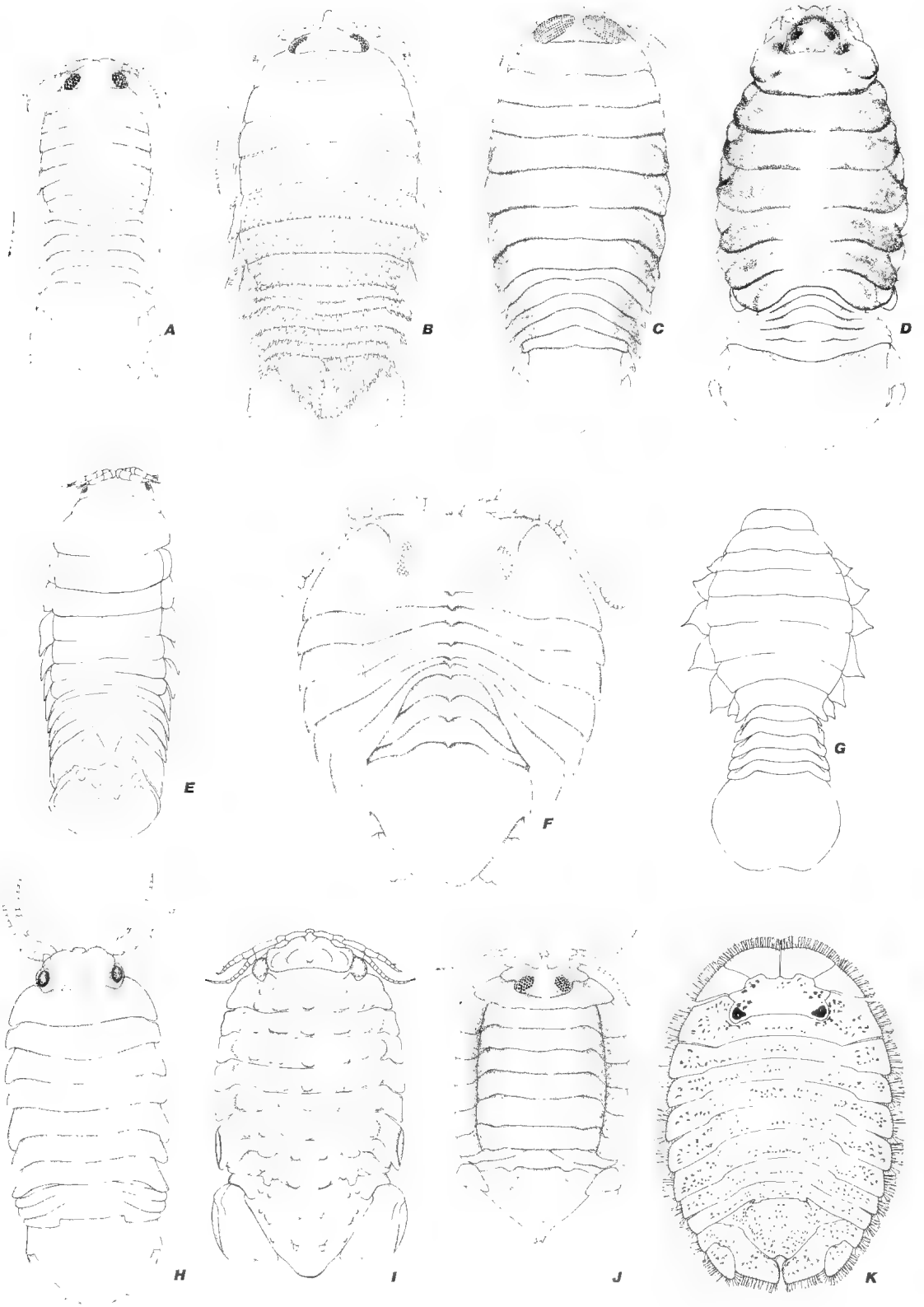
Three taxa that are included in our analysis require brief comment. The Calabozoidea is a monotypic ground-water (freshwater) taxon so far known only from Venezuela. In her original description, Van Lieshout (1983) suggested possible affinities of *Calabozoa* to both the Asellota and the Oniscidea. We have examined specimens of *Calabozoa* and found Van Lieshout's illustrations and description misleading; new illustrations of the male pleopods 1 and 2 are provided in Fig. 10. *Calabozoa* appears to possess no asellotan synapomorphies. Wägele and Brandt (1988) created the Protognathiidae based upon their examination of a single, apparently manca-stage, individual. Wägele (1989a) concluded that this new family was the sister group of the Gnathiidea. In the present study we argue that protognathiids share no unique synapomorphies with gnathiids, although some superficial similarities are present. Wägele (1983b, 1989a) has argued that the Microcerberidea are members of the asellote superfamily Aselloidea. Although the microcerberids have several features typically viewed as asellotan (6-articulate antennular peduncle; pleonites 3–5 fused with the pleotelson; females lacking first pair of pleopods; male second pleopod with endopod transformed into a complex gonopod), they lack other features generally also regarded as definitive synapomorphies of the Asellota (e.g. antennal peduncle with a scale; female pleopod 2 uniramous; exopods of male second pleopods modified to work with the elongate geniculate endopods in sperm transfer; and, possibly, the unique asellotan spermathecal duct). For these reasons we treat the Asellota and Microcerberidea as separate groups (OTU's) in our analysis.

Data Sources

Specimens were examined for all taxa treated except Protognathiidae. Material was examined on loan from a variety of institutions, and during visits to the U.S. National Museum of Natural History, Smithsonian Institution (USNM), Los Angeles County Museum of Natural History (LACM), Zoologisch Museum, Amsterdam (ZMA), Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM), Victoria Museum, Melbourne (VM), San Diego Natural History Museum (SDNHM), and Scripps Institution of Oceanography (SIO). In addition to examining specimens, the original literature was extensively perused.

Scoring of Characters

One of the advantages of the available computer-assisted numerical techniques (see below) is that they treat each character independently. Thus, if the state of a particular character is unknown, inapplicable, or we have simply been unable to resolve it to our satisfaction, we have scored it as 'missing data' (indicated by a '?' in the data matrix). In preliminary analyses, characters for which no clear polarity could be established were not coded in any primitive-derived sequence, but were left to change in any direction such that simple parsimony (fewest changes) was the arbiter. These unpolarised (nonadditive or unordered) characters are indicated in the character discussions below. These analyses proved useful in assessing character homoplasy.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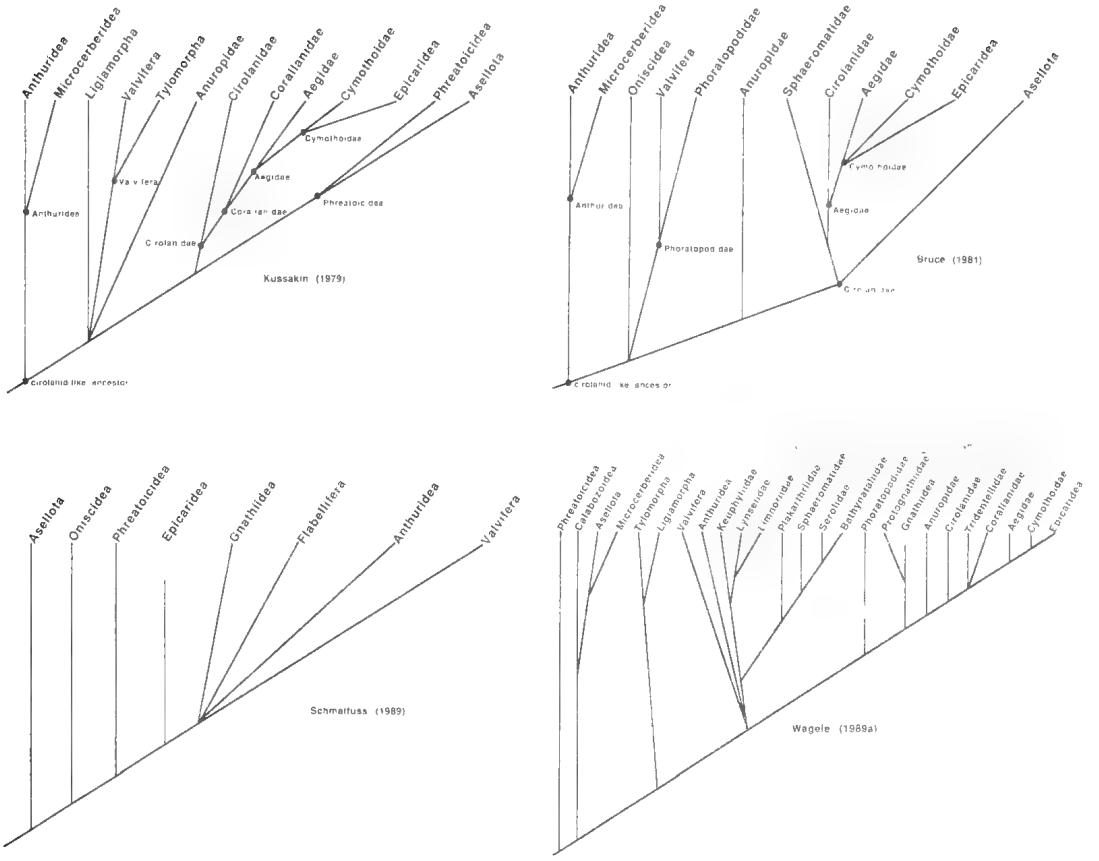

FIG. 4. Some evolutionary trees from previous studies, by Kussakin (1979), Bruce (1981), Schmalfuss (1989), and Wagele (1989a).

For the final analyses, however, we decided to analyse the data with all characters left unordered (nonadditive).

If a character state judged to be plesiomorphic is present for only some members of the taxon in question, e.g. 'accessory flagellum on antennule in most gammaridean amphipods', it is scored present in the data matrix for the entire taxon unless otherwise stated, i.e. the derived condition is presumed to define a subset within the taxon. Conversely, of course, if an apomorphic state is present in only some members of the taxon in question, the entire taxon is not scored apomorphic for that character, but is scored plesiomorphic. Initially polarized characters were scored as indicated in the ordering of the character state numbers: 0 = plesiomorphic, 1 = apomorphic, 2 = more apomorphic than 1, etc. Homology decisions were made on the basis of ontogenetic data and comparative morphology (positional data and anatomical similarity).

Phylogenetic Analysis

The character state data were analysed with four numerical cladistic analysis packages: HENNIG86 (version 1.5), PHYLIP (version

FIG. 3. Examples of various isopod families and genera of the suborder Flabellifera. A, Cirolanidae (*Metacirolana joanneae*, SDNHM). B, Tridentellidae (*Tridentella glutacantha*, from Delaney and Brusca, 1985). C, Aegidae (*Aega plebeia*, from Brusca, 1983). D, Cymothoidae (*Ceratothoa gilberti*, from Brusca, 1981). E, Limnoriidae (*Limnoria quadripunctata*). F, Serolidae (*Serolis carinata*, SDNHM A.0114). G, Anuropidae (*Anuropus bathypelagicus*). H, Sphaeromatidae (*Gnorimosphaeroma insulare*). I, Sphaeromatidae (*Exosphaeroma amplicauda*). J, Sphaeromatidae (*Bathycopea daltonae*). K, Sphaeromatidae (*Paraleptosphaeroma glynni*).

3.2), PAUP (version 3.0), and MacClade (version 2.1). HENNIG86 is advantageous because of its speed, successive weighting algorithm, ability to depict polytomous tree branches, and ability to store many equal-length trees in memory. The successive weighting program (Farris, 1969, 1989) is useful in reducing the impact of homoplasous characters on tree topology. Despite Platnick's (1989) recommendation of HENNIG86 as the program of choice, PAUP, MacClade, and the PHYLIP program package remain useful for comparative and analytical purposes (Sanderson, 1990). PAUP is by far the most user-friendly, is useful to check different character optimisations (a feature currently absent from HENNIG86) on the final trees, and to obtain detailed computations of C.I. (consistency index), character changes, and OTU apomorphy lists. The program MacClade 3.0 was used (on a Macintosh Computer) to branch swap on the final set of trees, in order to evaluate changes in tree length, homoplasy levels, and character placement on selected alternative trees, including those of Schmalfuss (1989), Wägele (1989a), and others. MacClade and PAUP are extremely useful in their user-friendly ability to generate graphic representations of character traces on trees, although MacClade is seriously hindered by its inability to depict multifurcations.

The principal statistics used in tree evaluation were overall tree length (step length) and consistency index (C.I.). Consistency and retention indices for each individual character were also computed and used to evaluate their overall homoplasy levels.

Carpenter (1988) recently argued that consensus trees should not be used to construct cladograms. However, we agree with Anderberg and Tehler (1990) that strict consensus trees are both useful and informative because they reduce the conclusions to only those components which all equal-length shortest trees have in common. In fact, they are probably a necessity when high levels of homoplasy invest a data set. Even if successive weighting (i.e. the successive approximations character weighting method of Farris, 1969) is used, multiple equally parsimonious trees may derive from a data set high in homoplasy. Thus, we believe that when numerous equally parsimonious trees exist, a strict consensus tree should be presented.

In order to distinguish between some closely related taxa, we included some characters that are currently known to be unique to a given suborder or family (Appendix III). However, because we were concerned in this study with identifying sister group relationships within the Isopoda, we did not make an effort to identify all of the unique synapomorphies that define only individual taxa (suborders or families). Some characters that proved to define only terminal taxa in our final trees were early-on suspected to be useful in distinguishing larger sister groups. These may be viewed as 'uninformative' characters in the final trees by some workers. However, they were important in comparative analyses and tree testing, and as additional taxa and data are described some of these characters may no longer remain unique to a single terminal taxon. For these reasons, we felt it was important to leave them in the data matrix, thus allowing others to use our data set as a starting point for further tree testing. The data set is available on diskette on request.

DISCUSSION OF CHARACTERS

Stalked Eyes

Mysidaceans and mictaceans have compound eyes set on short, movable eyestalks (although eyestalks are absent in the mictacean *Hirsutia*). In amphipods, a 'rudimentary eyestalk' has been reported from ingolfiellids. Dahl (1977) and Lowry and Poore (1989) have argued that this small process in ingolfiellids is not a true eyestalk, but rather is a cuticular process or scale. Lowry and Poore's argument hinged on the observation that unequivocal eye stalks in other peracarids have 'an attitude and position very different' than seen in the ingolfiellids. Dahl's argument was based on the absence of 'dioptric and nervous elements' in this structure. The first argument is not particularly strong because the position and attitude of peracarid eye stalks vary greatly. A positional change in the ingolfiellids could have been caused by a lateral rotation of the entire eye-antennular-antennal complex. Dahl's argument is stronger, although it relies on reductions rather than homologies. Among tanaidaceans, articulated eye-lobes occur in some Apseudomorpha and Tanaidomorpha, including those with eyes in a variety of positions ranging from that seen in the Mictacea to that seen in the ingolfiellids. In amphipods and isopods the eyes are entirely sessile, although they may be elevated on lobes of varying sizes in some species of Phreatoicidea, Gnathiidea, Valvifera, and Asellota. At the level of the Peracarida most workers might regard motile stalked eyes as the

ancestral condition, and sessile eyes (and loss of eyes) as derived conditions. However, as Bowman (1984) has noted, the primitive condition in Crustacea is still unknown. Thus we left this character unordered in all analyses. Character No.1 is: eyes stalked and basally articulated (0), *vs* eye stalks reduced, lobe-like, but sometimes with basal articulation (1), *vs* eyes sessile (2).

Carapace

Character 2 describes the development of the carapace. In mysidaceans the carapace generally covers all 8 thoracomeres and laterally covers the bases of the maxillae and maxillipeds (state 0). In all other peracarids, the carapace is either reduced or absent. In tanaidaceans and mictaceans, lateral carapace folds still cover the bases of the maxillae and maxillipeds (state 1). In amphipods and isopods a carapace is absent (or exists only as a head shield) and there are no lateral carapace folds (state 2). Because of controversy regarding the origin (and convergent reductions) of the crustacean carapace, character 2 was left unordered in initial analyses.

Moulting

Isopods are apparently unique among crustaceans in that the moulting is biphasic, the posterior exoskeleton being shed earlier than the anterior exoskeleton (George and Sheard, 1954; Price and Holdich, 1980a, b). The break between the two halves occurs at the junction of pereonites 4 and 5, and the two halves are out of synchrony throughout the moult cycle. Character 3 is: monophasic moulting (0) *vs* biphasic moulting (1).

Heart and Branchial Structures

Mysidaceans, tanaidaceans, and mictaceans utilise thin-walled vascularised regions on the carapace for respiratory exchange (pereopodal gills are absent). However, loss of free carapace folds in the Amphipoda and Isopoda necessitated the transfer of respiratory functions to other areas of the body (Grindley and Hessler, 1971). Amphipods have unique medial pereopodal epipodites ('coxal gills') presumed to function in respiratory exchange. Whether the medial epipods of amphipods are homologous to the lateral epipods of other crustaceans is not known. In non-isopod peracarids, the heart is positioned in the thorax. The isopod heart is located in thoracomeres 7/8 and the pleon, and they utilize the pleopods for respiration. Character 4 is: heart entirely thoracic (0) *vs* heart thoraco-abdominal (1). Character 5 is: branchial structures cephalothoracic (0) *vs* branchial structures abdominal (1). Only isopods are scored apomorphic for these two characters.

Body Shape

Living mysidaceans are laterally compressed. Most isopods have dorsoventrally flattened bodies. Although the bodies of amphipods (gammarideans) and phreatoicideans superficially appear laterally compressed, their bodies are actually more cylindrical or tubular (semicircular in cross-section). The apparent lateral compression in these two groups is an illusion created by the large, ventrally expanded, pereonal coxal plates and pleonal epimeres in amphipods, and the large pleonal epimeres of most phreatoicideans. Some phreatoicideans also have lateral expansions of the pereonal tergites (i.e. true epimeres, or 'pleura') that hang down to give the body an amphipod-like appearance. The cylindrical nature of the phreatoicidean body was recognised long ago (Nicholls, 1943, 1944) although not all authors have acknowledged it (Wägele, 1989a). In mictaceans, and in anthuridean and microcerberid isopods (as well as many arcturid Valvifera and some Asellota) the body is also cylindrical, or semicircular in cross-section. Subcylindrical bodies also may occur in the Lynseiidae. Given the variety of body shapes that occur in the isopods and other peracarid orders, we can make no judgment on which shape is primitive and which is derived. Body form is probably strongly selective and based largely on a group's behaviour and preferred habitat, and therefore any real phylogenetic signal we may seek has a high probability of being obscured. For example, we could identify 'narrow and elongate' as a potentially homologous feature, but in fact this would introduce obvious homoplasy because the groups that would be so classified, the Anthuridea and the Microcerberidea, are probably narrow for entirely different reasons; the former are tubiculous and the latter are interstitial. Consequently, we have been cautious regarding use of body form in our analysis.

Some isopods carry the flattened (depressed) body form to an extreme. Several flabelliferan families (Bathynataliidae, Keuphyliidae, Plakarthriidae, and Serolidae) have extremely broad and flattened bodies, with broad coxal plates and the cephalon encompassed by the first pereonite or at least surrounded by the first pereonite coxal region (character 7) (*Serolis*, Fig. 3F). The Sphaero-

matidae also includes a number of genera with extremely flattened bodies (*Amphoroidella*, *Chitonopsis*, *Naesicopea*, *Paracasidina*, *Playtnympha*, *Platysphaera*, *Paraleptosphaeroma*, *Platycerceis*), as does the Idoteidae (*Moplisa*) and Cirolanidae (*Hansenolana*). However, these cases are uncommon and are assumed to represent derived conditions in these three families. They also differ from the above taxa in that the cephalon is not entirely encompassed by pereonite I and the lateral coxal plates are not free. Illustrations of the dorsal aspect of phoratopodids tend to depict these animals as markedly flat and broad. However, the body of phoratopodids is actually dorsally arched and straight-sided, reminiscent of the cirolanid genus *Politolana* and many sphaeromatids (Bruce, 1981, pers. obs.).

In the Anuropidae the body is greatly inflated and globular (character 89), reminiscent of certain hyperiid amphipods. Anuropids are apparently all parasites on gelatinous zooplankton, a feature also shared with most, if not all, hyperiid amphipods (character 90).

In two flabelliferan families, Limnoriidae and Lynseiidae, the orientation of the head on the pereon differs from that seen in all other isopods. In these two groups, the head is set off from the first pereonite (second thoracomere) and is capable of left-right rotation (character 40); in all other isopods the head fits snugly against the first pereonite and is usually somewhat immersed in it, restricting head movement to a flexion in the dorso-ventral plane.

In the family Serolidae, the tergite of the seventh pereomere (and sometimes also the sixth) is reduced and fused with the adjacent anterior tergite, rendering it indistinguishable dorsally (character 69).

Gut Tube

The gut tube of mysidaceans and amphipods has an endodermally derived midgut region (a 'true midgut'). It has long been known, however, that isopods lack an endodermally derived midgut (see recent reviews by Bettica *et al.*, 1984, Forgarty and Witkus, 1989, and Hames and Hopkin, 1989). The entire gut tube of an isopod is ectodermally derived; the only endodermally-derived structure is the 'hepatopancreas' (the digestive caeca). According to Scholl (1963) the gut of tanaidaceans may also be entirely ectodermal. The condition in mictaceans is not known. Character 8 is: gut tube with endodermally derived midgut (0) *vs* gut tube entirely ectodermally derived, without a true midgut region (1).

Striated Muscles

Nylund (1986), Nylund *et al.* (1987), and Tjønneland *et al.* (1987) have described a pattern of membrane systems in the heart myofibers of isopods that they claim is unique within the Malacostraca. We do not find the reasoning given by Nylund *et al.* (1987) for placement of the isopods as a sister group to all other eumalacostracans to be logical, because it relies on differences between groups rather than on similarities among them, to define relationships. Nevertheless, ultrastructure of the heart myofibres appears to be a unique synapomorphy for isopods. Character 9 is: striated muscles of typical malacostracan type (0) *vs* striated muscles with unique myofibril ultrastructure (1).

Second Thoracomere

Mysidaceans, mictaceans, amphipods, and most isopods have a free second thoracomere (thus one pair of maxillipeds), although the fossil pygocephalomorphans have two sets of maxillipeds. In gnathiid isopods, the second thoracomere is partly or wholly fused to the cephalon, and the second thoracopods form a second pair of maxillipeds (called pylopods). In the praniza stage these appendages are prehensile and used for attachment to the host; in adults they are more typically maxilliped-like. Gnathiids are the only isopods in which the second thoracomere and its appendages are entirely integrated into the head. Dorsal, medial-only fusion of the second thoracomere with the cephalon occurs in several genera in various other isopod suborders and families (Bathynataliidae, Serolidae, several sphaeromatid genera [*Ancinus*, *Bathycopea*], some Valvifera [*Lyidotea*, Arcturidae], some Asellota [*Stenasellus*], some Microcerberidea [*Microcerberus mexicanus*], and some Phreatoicidea), but these cases are not full fusion and do not incorporate the first percopods into the mouth field, as in gnathiids. Complete fusion of the second thoracomere to the cephalon may occur in several deep-sea Asellota genera (*Haplomesus*) but, again, the first percopods are not modified as maxillipeds or appendages of the buccal field. These represent derived conditions found within the Asellota and occur only in certain deep-sea forms. Character 10 is: second thoracomere free, not fused to cephalon (0) *vs* second thoracomere entirely fused to cephalon, with its appendages (the pylopods) functioning

with the cephalic appendages and serving as a second pair of maxillipeds. Gnathiidea is the only taxon scored apomorphic for character 10.

Thoracic Exopods

In mysidaceans and mictaceans, all the thoracopods (primitively) bear exopods. In tanaidaceans, only the anterior thoracopods have exopods. In amphipods and isopods, no thoracopods have exopods. Character 11 is: at least some thoracopods with exopods (0); exopods absent from all thoracopods (1).

Embryogeny and Hatching Stages

All Peracarida have direct development, and in all orders except Mysidacea and Amphipoda the young leave the marsupium as mancas, resembling small adults but with the last (seventh) pair of pereopods not yet developed. However, in some hyperiid amphipods the young do emerge as virtual mancas, with the seventh legs undeveloped or as little more than a limb bud (Bate, 1861; Laval, 1980). Bruscа (1984) suggested that the mancoid stage in peracarids may be the product of variations in timing in embryogeny and hatching. Its absence in mysidaceans and amphipods may be tied to a more rapid embryological development (or to delayed postembryonic hatching) in these taxa (Steele and Steele, 1975). Manca-like hatching stages also occur in bathynellaceans (which may hatch with several posterior thoracopods undeveloped). Moreover, some thermosbaenaceans and bathynellaceans never develop posterior legs even as adults. In gnathiids, the young leave the marsupium as a morphologically very distinct mancoid stage called the praniza 'larva' (Wägele, 1988).

Mysidaceans and amphipods also differ from other peracarids by possession of ventral flexure of the embryo within the embryonic membrane, all other peracarids having a dorsal embryonic flexure. The embryos of mysidaceans and amphipods develop a ventral (=caudal) furrow that separates the caudal papilla from the ventral part of the rest of the embryo. This is presumably linked to the presence of ventrally curved embryos, completion of cleavage in the early stages, and early appearance of the egg-nauplius stage in these groups rapid early holoblastic cleavage. In all other peracarids that have been studied (except perhaps thermosbaenaceans), development is slower, the naupliar and metanaupliar somites appear nearly simultaneously, body somites begin proliferating before the the dorsal (=caudal) furrow forms, and the embryos curve dorsally, (Weygoldt, 1958; Strömberg, 1972). Eucarids in general tend to have ventral flexure of the embryos. Character 51 is: embryos curve ventrally (mysidaceans and amphipods) (0), *vs* embryos curve dorsally (all other peracarids) (1). Character 12 is: hatching stage not a manca (0) *vs* hatching stage a manca (1). Character 13 is: without a praniza stage (0) *vs* with a praniza stage (1). Characters 12 and 51 were left unordered in the initial analyses.

Body Symmetry

Only in the isopod Suborder Epicaridea does loss of body symmetry typically occur in adult females. Some species of Cymothoidae may become twisted to one side or the other, but this is not regarded as true asymmetry in the sense of loss of, or gross modification of, appendages on one side of the body, as in the epicarideans. Some epicarideans (most Cryptoniscidae and Entoniscidae) may be so modified as to resemble little more than large egg sacs. Character 14 is: adult females bilaterally symmetrical (0) *vs* adult females with loss of symmetry (1).

Parasitism

Adult female epicarideans are obligate parasites on other crustaceans; the miniature males live in close association with the female, usually buried among the female's pleopods. Character 15 is: adults not parasitic on other crustaceans (0) *vs* adults obligate parasites on other crustaceans (1); only Epicaridea is scored apomorphic for this character. Adult Cymothoidae are obligate and permanent hematophagic parasites on freshwater and marine fishes. Character 66 is: adults obligate and permanent parasites of fishes. Only the Cymothoidae are scored apomorphic for this character. Members of the Aegidae, Corallanidae, and Tridentellidae — which are often referred to as 'parasites' — do not attach permanently to their prey, nor do corallanids restrict their diet to fishes. Species in these families can be considered as micropredators or temporary parasites.

Cuticular Sensilla

Holdich (1984) has described two types of cuticular sensilla that he regards as unique to the Oniscidea. The first (character 16) is the cuticular tricorn sensillum, which he adequately documents for the Oniscidae (*Oniscus*) and Porcellionidae (*Porcellio*, *Porcellionides*), somewhat less convincingly for the Armadillidiidae (*Armadillidium*) and Armadillidae (*Venez-*

illa), and even less convincingly for the Ligiidae (*Ligia, Ligidium*), Philosciidae (*Philoscia*), Tylidae (*Tylos*), Platyarthridae (*Platyarthrus*), Trichoniscidae (*Androniscus, Trichoniscus*), and Scyphacidae (*Alloniscus, Deto*). Powell and Halcrow (1982) document tricorns on *Oniscus asellus*, but not on *Ligia baudiniana* or any non-oniscidean species they studied. Modified tricorns similar to those of the aquatic genus *Haloniscus* can been seen on SEM photographs of the uropods of *Calabozoa* (Van Lieshout, 1983, fig. 5d–e). We have scored both oniscidean infraorders (Tylomorpha and Ligiamorpha) and the Calabozoidea apomorphic (1) for this character. The second kind of sensillum is the 'antennal and uropodal spikes' (character 17), which are complex compound sensillar structures at the tips of the antennae and uropodal rami. We have scored both oniscidean infraorders apomorphic (1) for this character.

Pereon and Pereopods

In Isopoda and other peracarid taxa, the pereopods tend to form two functional groups: an anterior set of legs that are directed forwards (antero-ventrally), and a posterior set of legs that are directed backwards (postero-ventrally). Often this grouping allows the anterior legs to have a somewhat (or extremely) different role in locomotion or feeding than the posterior legs.

In Phreatoicidea, Asellota, and Microcerberidea, the legs are grouped 4:3 (four pairs of anterior pereopods directed forwards and three pairs of posterior pereopods directed backwards). This seems to be the case with the terrestrial isopods and the Calabozoidea as well, although the strong isopody in these taxa tends to decrease the difference between the anterior and posterior groups. The 4:3 grouping may be a natural tagmosis for the isopods owing to the biphasic molt boundary between pereonites 4 and 5.

Nevertheless, most other isopods show a clear 3:4 tagmosis. The 3:4 condition prevails in all families of flabelliferans, as well as the Anthuridea, Gnathiidea, Epicaridea, and the genus *Hadromastax* (currently placed in the family Limnoriidae, but being elevated to separate family status by Bruce and Müller). The predatory and parasitic isopods (Anthuridea, Anuropidae, Cirolanidae, Corallanidae, Cymothoidae, Protognathiidae, Tridentellidae, Epicaridea) have 3 pairs of raptorial or grasping anterior limbs, while the 4 pairs of posterior limbs are dedicated more for locomotion. In the strictly parasitic Cymothoidae and Epicaridea, all 7 pairs of legs are strongly prehensile. However, the limbs of cymothoids and epicarideans appear fundamentally different. In epicarideans, the dactyl is a short acute hook that folds against a greatly enlarged or swollen propodus, which in turn usually articulates on a small triangular carpus. In cymothoids, the dactyl is greatly elongated and articulates on an elongate propodus; the carpus is not reduced or triangular shaped, and it usually has an indentation to receive the tip of the dactyl. We believe that Wägele's (1989a) homologisation of these two kinds of legs is probably in error.

The Plakarthriidae seems unique in its possession of a 1:6 arrangement of the legs; the basis of pereopod 1 is directed posteriorly, whereas in the rest of the legs the bases are directed anteriorly. However, this may be a secondary effect of the overall body form and orientation of the pereonites, so we have scored this character with a '?' for this family. Although the Gnathiidea have a more highly derived body tagmosis, their anterior 3 pereopods are still directed anteriorwards, and the remaining limbs are directed post-

FIG. 5. Examples of isopod antennules. A, Flabellifera, Aegidae (*Aega longicornis*, type). B, Flabellifera, Cymothoidae (*Nerocila acuminata*, from Bruscа, 1978). C, Flabellifera, Cirolanidae (*Parabathynomus natalensis*, USNM 170251), note sensilla (insert figure to right). D, Flabellifera, Cirolanidae (*Bathynomus giganteus*, SDNHM). E–F, Flabellifera, Cirolanidae (*Bathynomus doderleini*, USNM 39321): E, ventral view, F, dorsal view; note 'scale' (insert figure to right of E). G, Oniscidea (*Ligia exotica*, USNM 43352). H, Oniscidea (*Ligidium ungicaudatum*, USNM 83070). I, Anthuridea (*Cyathura guaroensis*, from Bruscа and Iverson, 1985). J, Anthuridea (*Calathura* sp., USNM 99253). K, Anthuridea (*Malacanthura caribbica*, USNM 173521). L, Phreatoicidea (*Phreatomerus latipes*, USNM 60659). M, Gnathiidea (*Bathygnathia cavirostris*, USNM 10580). N, Flabellifera, Bathynataliidae (*Bathynataliа gilchristi*, USNM 170545). O, Serolidae (*Serolis albida*, USNM 123900). P, Serolidae (*Serolis bromleyana*, USNM 123911). Q, Flabellifera, Anuropidae (*Anuropus antarcticus*, USNM 112260). R, Valvifera, Idoteidae (*Synidotea francesae*, from Bruscа, 1983). S, Flabellifera, Plakarthriidae (*Plakarthrium punctatissimum*, USNM 32500). T, Epicaridea (*Scalpellomiscus penicillatus*, after Grygier, 1981). U, Epicaridea (*Pseudasymmetrione mexicana*, after Adkinson and Heard, 1980). V, Flabellifera, Limnoriidae (*Limnoria kautensis*, after Cookson and Cragg, 1988).


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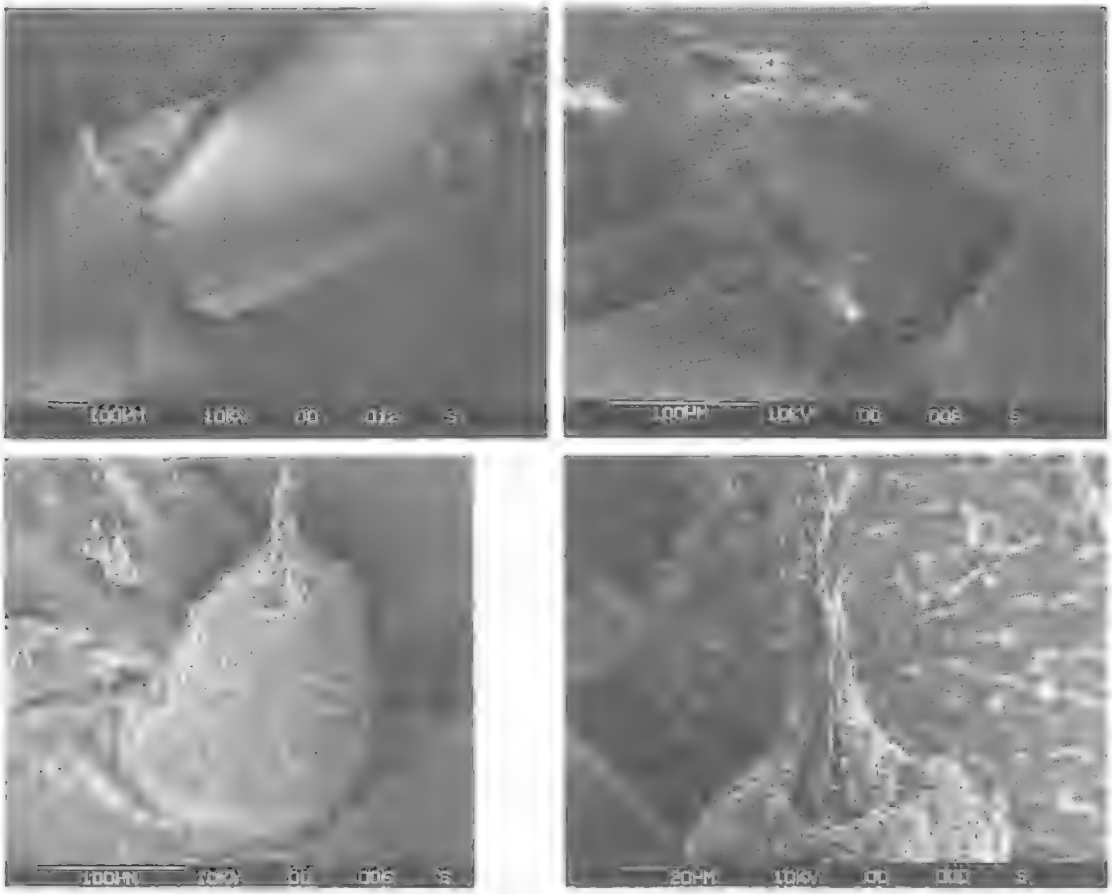


FIG. 6. Scanning electron micrographs of the antennular scale of *Bathynomus giganteus* (Flabellifera, Cirolanidae). Images show 4 different magnifications.

eriorwards; this is most easily seen in the active praniza stage.

In the Valvifera, both the 3:4 and 4:3 condition occurs; Arcturidae and Amesopodidae have the 4:3 condition, whereas Chaetiliidae, Holognathidae, Idoteidae and Xenarcturidae have the 3:4 condition. In the Pseudidotheidae the fourth leg is directed straight out to the side, and species in this family may appear to be 3:4 or 4:3, or even one condition on the left side and the other condition on the right. Because the 3:4 condition is considered primitive in this suborder (Brusca, 1984: 104) Valvifera are scored for that state.

The out-group taxa show a variety of functional groupings, which may or may not be homologous with the situation seen in the Isopoda. The tanaidaceans and gammaridean amphipods have a 4:3 grouping, similar to the Phreatoicidea. In mictaceans, the grouping appears to be 2:5. At least this is the case in *Mictocaris*: the condition in *Hirsutia* is less clear, but it appears to be the same. Mysidaceans have no distinct functional grouping of the pereopods, i.e. all legs arise more or less straight out, ventrolaterally from the body.

Hence, four pereopodal conditions, or 'states' exist for character 18: 2:5, 3:4, 4:3, and no functional grouping. The relative polarity or direction of evolutionary change(s) associated with this character is unknown, and this character was initially left unordered in the data set. The states of character 18 are assigned the following codes in the data matrix: 0 = no functional grouping (mysidaceans); 1 = 3:4; 2 = 4:3; 3 = 2:5.

In adult Gnathiidea, the seventh pereonite is reduced and without pereopods (character 19). Although the seventh pereonite may be lacking in some anthuridean genera (*Colanthura*, *Cruregens*, etc.; Poore, 1984) and in a few deep-sea Asellota (Wilson, 1976; 1989), this condition

is not regarded as primitive in these suborders. It is probable that genera of isopods in which sexually mature adults lack the seventh pereonites evolved by way of neotenic events.

In the Phoratopodidae, the posterior pereopods form sculling 'oars', and the dactyls are reduced or lost (character 88). Flattened posterior swimming pereopods also occur in some Munnopsidae (Asellota) and, to a limited extent, some Cirolanidae (*Natatolana*), but it is not the primitive condition for these two families.

True chelipeds do not occur in isopods, except for a few rare cases such as the unusual genera *Carpias* (Asellota) and *Chelanthura* (Anthuridea) although various subchelate and prehensile conditions do occur. In three groups, Aegidae, Cymothoidae, and Epicaridea, the pereopods are prehensile. In aegids, pereopods 1–3 only are prehensile; in cymothoids and epicarids all 7 pairs of pereopods are prehensile. We define a prehensile pereopod as one in which the dactyl is as long or longer than the propodus, acute, and recurved. Although the pereopods of most epicarideans are prehensile and used for clinging to their host (crustaceans), they differ fundamentally from the legs of aegids and cymothoids, as noted above, with which they may not be homologous. At least some of the anterior pereopods of serolids, phoratopodids, certain Sphaeromatidae (*Bathycopea*, *Tecticeps*), and astacillid valviferans are subchelate, but we do not regard these conditions as homologous to the prehensile pereopods of cymothoids, aegids or epicarideans. Character 65 is: pereopods not prehensile (except at most pereopod 1) (0); pereopods 1–3 prehensile (Aegidae, Cymothoidae, Epicaridea) (1).

Antennules

The antennules of mysidaceans, mictaceans, and amphipods are biramous. In these groups the flagella arise from the third peduncular article, as in other Peracarida and Eumalacostraca. The antennules of tanaidaceans may be either biramous, with the flagella arising from the fourth article (Apseudomorpha) or uniramous (Neotanaidomorpha, Tanaidomorpha). The antennules of nearly all isopods are uniramous (see Figs. 5 and 6 for examples of isopod antennules). However, the literature contains many allusions to taxa that allegedly possess antennular scales, or other structures said to represent vestigial flagella or remnants of the missing antennular ramus (presumably the exopod). These various taxa belong to three suborders: Flabellifera, Anthuridea, and Epicaridea. These matters are briefly reviewed below. In the following discussion, the 'peduncle' of the antennule is defined as the enlarged, basal region of the antennule that bears intrinsic musculature. The flagella of isopod antennules lack intrinsic musculature (i.e. no muscles have their origin in the flagellum); flagella arise from the distal-most peduncular article.

As in so many other instances, Calman (1909) appears to have been the first to comment on the possible generality and significance of scales on the antennules of isopods, noting their presence in two groups, the genus *Bathynomus* (Cirolanidae) and 'cryptoniscan larvae of certain epicarideans.' Calman did not indicate which epicarideans he was referring to, nor did he provide figures of these structures. However, he referred to them as 'minute vestiges of the inner flagellum', and was presumably referring to species of Bopyridae *sensu lato*. Hansen (1925) repeated Calman's remarks, as have many subsequent workers. Wägele (1983a) used Calman's comment as a basis for 'homologisation of this (scale-bearing) article with the last peduncular segment of other Malacostraca,' on the apparent assumption that the antennular peduncle of isopods is homologous to the protopod of the other segmental body appendages. Menzies (1957) added an overtone of generality with a passing comment in his widely cited limnoriid monograph, which reads: 'The conspicuous scale attached to the first antenna of *Paralimnoria* is also characteristic of the genus *Limnoria* and, as Calman remarks, of the genus *Bathynomus* (Cirolanidae) and cryptoniscids (suborder Bopyroidea). It has since been found on *Mesanthura* (Suborder Anthuridea, Miller and Menzies, 1952, p. 8) and the young of *Cirolana* (unpubl. data) and it is possibly characteristic of isopods in general' (*sic*). Menzies (1957) provided an illustration of this structure for *Paralimnoria andrewsi*.

In *Bathynomus* (*B. giganteus*, *B. doederleni*, *B. kapala*) the 'antennular scale' takes the form of a large, cuticularized, volcano-like process with a deep pit at the terminus from which arise numerous long setae (Fig. 6). Under light microscopy this scale resembles a large complex sensillum. However, SEM examination reveals the scale to be covered with a cuticle bearing the same type of cuticular surface structure seen on the rest of the body, and to be encircled basally by what may be an articular membrane. Thus, we tentatively interpret this structure as a true scale,

i.e. vestigial second ramus. However, in the similar appearing *Parabathynomus* a scale does not exist, although a sensory pit is present in the same position on the peduncle, and arising from it is the same kind of setal cluster seen in *Bathynomus*. The two kinds of sensory structures are precisely in the same place, and look very similar in all respects, except that in *Parabathynomus* the sensory pit sits on the cuticular surface, rather than at the end of a scale. In another very similar genus, *Booralana*, a cluster of sensory setae arises from a very shallow depression at this same location on the third peduncular article, but there is neither a 'scale' or a distinct pit.

As for the antennular 'scale' of the cryptoniscus stage, Calman appears to have been relying on Bonnier (1900) and Giard and Bonnier (1887), who stated that the antennules of epicarideans 'are often biramous, with numerous sensory filaments.' The cryptoniscus stage of the family Bopyridae *sensu lato* possesses complex antennules of uncertain homologisation. The first article, and often the second, typically bear toothed 'gnathobasic margins' that are of importance in species-level taxonomy. One to three lobes may arise from the third article, each highly invested with bundles of long setae. It is these sensory lobes that Bonnier and Calman presumably interpreted as scales, or vestigial rami or flagella. When several of these sensory lobes are present, only one (usually the largest) bears aesthetascs, the others are much smaller and bear only 'simple' sensory setae. Thus, the large lobe could reasonably be homologised to a reduced antennular flagellum, but the other one or two lobes appear to be large, complex sensilla, or possibly one of these represents a true antennular scale. Nielson and Strömberg (1973) described these lobes in an unidentified bopyrid as being 'heavily equipped with sensory hairs, densely crowded together...', and noted that the antennule is 'apparently an effective sensory organ as well as an accessory adhesive one.' The lobes have been clearly figured by Nielson and Strömberg (1965), Bourdon (1968), Grygier (1981), and others. Grygier (1981) described the antennular peduncles of *Scalpelloniscus penicillatus* and *S. binoculis* as 3-articulate, noting that the third article bears a 'pair of 1-merous rami and a large, ventrolateral bulb completely covered with brush-like bundle of capillary aesthetases...'. Kensley (1979) has described the antennules of the cryptoniscus stage of *Zonophryxus trilobus* (Dajidae) also as bearing a trilobed second article.

In limnoriids, most species do possess an antennular scale on the distal margin of the third peduncular article. In some species, this 'scale' resembles little more than a large, simple seta (*Paralimnoria andrewsi* Calman). In most, however, it is a small, one-piece, articulating, setae-bearing structure not unlike that of young bopyrids. The antennular scales of limnoriids are very small and difficult to observe without the use of a scanning electron microscope (for good illustrations and SEM photographs see: Kussakin and Malytina, 1989, fig. 3; Cookson and Cragg, 1988, figs. 3d, 4d; Cookson, 1989, PhD Diss.). L.J. Cookson (pers. comm.) feels that the Keuphyliidae (*Keuphylia nodosa*) possesses a scale similar to that of limnoriids but we have not observed this scale ourselves nor was it illustrated by Bruce (1980).

In the case of the Anthuridea, 'scales' or vestigial flagellar processes almost certainly do not exist. We have examined dozens of anthuridean species and failed to find anything resembling a scale or vestigial ramus. We are aware of two reports of such structures in anthurideans. The first was by K.H. Barnard (1925) who claimed an antennular scale was present on *Xenanthura brevitelson*. Kensley (1980), using SEM techniques, showed this structure to merely be a large sensillum. The other claim was that of Miller and Menzies (1952), who noted an antennular scale in a single female specimen of *Mesanthura hieroglyphica* (from Hawaii). Miller and Menzies stated, "An antennal scale here observed on the first antenna of a female specimen has not, to our knowledge, been reported previously in the Anthuridae. Because of its minute size and its position, it is not readily seen, hence may have been overlooked in other species in the family. It was not found, however, in the other Hawaiian anthurids described in this paper' (*sic*). Their 'scale' appears identical to the sensory seta shown by Kensley for *X. brevitelson*.

The final group said to possess antennular scales, 'the young of *Cirolana*', was cited by Menzies (1957) as, '...(unpubl. data)...'. To our knowledge, Menzies never published these 'data', nor has anyone else shown antennular scales in this genus. One of us (RCB) has examined hundreds of young Cirolanidae, in *Cirolana* and many other genera, and has never seen antennular scales in any genus of this family other than *Bathynomus*.

In summary, we conclude that only *Bathynomus*, limnoriids, the cryptoniscus stages of bopyrids, and perhaps keuphyliids may possess

structures on the antennules that might be reasonably interpreted as scales. Although we are not entirely convinced that these minute, uniarticulate structures are anything more than complex sensilla, we have entered this character into the data matrix anyway. For character 20, all four out-groups are scored as possessing a biramous antennule (or a scale), and among the isopods the epicarideans and limnoriids are scored the same (0); Cirolanidae is scored '?' because apparently only the genus *Bathynomus* (of a total of approx. 45 genera) has a scale; Keuphyliidae is also scored '?' because we are uncertain whether a scale is actually present in this group. All other isopods are scored 1 — lacking antennular scales.

Mysidaceans, mictaceans, amphipods, and other Eumalacostraca (except tanaidaceans) appear to primitively possess a 3-articulate antennular peduncle. It seems reasonable to homologise these articles to the 3-articulate protopod of other crustacean appendages. Nevertheless, this is not a certain homologisation because in all crustacean nauplii this appendage is uniramous. Moreover, the Apseudomorpha tanaidaceans have the accessory flagellum on the fourth article of the antennule, arguing for a four-articulate protopod in this group.

Most isopod workers have regarded the antennular peduncle of the Isopoda to be 3-articulate. However, Bruce (1981, 1986) felt that isopods 'primitively' have 4-articulate antennular peduncles because he interpreted the small fourth article that occurs in many groups (that most other workers view as the first flagellar article) as the last, or fourth, peduncular article. Due to this different interpretation of the fourth article of Cirolanidae (and other non-asellote/non-phreatoicidean groups), Bruce (1981, 1986) and Wägele (1983a) were at odds over whether the 'primitive' isopod antennular peduncle was 3-articulate (Wägele) or 4-articulate (Bruce). Wägele's opinion is based on the third article of *Bathynomus* bearing the scale, which he homologises with a vestigial second flagellum, and at this time we are inclined to accept this homology argument, especially given that the primitive eumalacostracan condition is almost certainly a 3-articulate antennular peduncle. We see no reason not to accept that the small fourth article of *Bathynomus* is homologous with the short fourth article of most other Cirolanidae, Anthuridea, Bathynataliidae, Gnathiidea, and other taxa (Fig. 5), but do not consider this article to be part of the peduncle. Our examination of the antennule of *Bathynomus giganteus* (cuticle cleared with xylene) indicates that the 4th article lacks intrinsic musculature, thus conforming to our definition of the flagellar article. Several other authors that have alluded to a 4-jointed antennular peduncle in *Bathynomus* may have been misinterpreting the first (proximal) article for two articles, due to the presence of a strong ridge on the medial surface of that joint, such that it could be easily mistaken for two pieces (Fig. 5 C–F). The fourth peduncular article of Bathynataliidae noted by Kensley (1978) and Bruce (1986) corresponds to the small first flagellar article of other flabelliferan families.

A 4-articulate antennular peduncle unquestionably does occur in two flabelliferan groups, Phoratopodidae and Serolidae. But, in both of these cases the 'extra' fourth article is neither basal nor does it appear to be homologous to the short fourth article noted above in other isopods, but rather appears to be the result of a subdivision of the third article into two large equi-width joints with continuous marginal contours. In the Serolidae we have examined, the fourth and fifth articles contain no intrinsic musculature. Van Lieshout's (1983) description of Calabozoidea states *Calabozoa pellucida* has a 3-articulate peduncle, but her figure 2C gives the appearance of a 4-articulate peduncle, possibly with a sensillum on the fourth article. Our observations of *Calabozoa* indicate that the antennule comprises only 4 articles, presumably a 3-articulate peduncle and uniarticulate flagellum (the terminal article bears one aesthetasc and one large seta). The antennules of oniscids are so reduced that we score them as undecided ('?') for this character. Character 21 is: antennular peduncle 3-articulate with an undivided third article (0) *vs* 4-articulate, presumably by way of subdivision of the third article (1). Only phoratopodids and serolids are scored apomorphic for this character.

Reduction of the antennules probably occurs in at least some species in every isopod suborder, and may occur in various conditions within a single suborder or family. When the antennules are reduced, a corresponding reduction of the deutocerebrum and its olfactory lobes also usually occurs (where it has been studied). The mode of reduction in the various suborders clearly differs. Reduction typically accompanies exploitation of parasitic or interstitial habitats. Valviferans have a 3-articulate peduncle, with the flagellum often reduced to one or a few

vestigial articles. Although antennular reduction is rare in gnathiids, some species also have a 2-articulate peduncle and the flagellum reduced to a few articles. In the interstitial Microcerberidea, reduction is such that the peduncle cannot be distinguished from the flagellum. A similar reduction takes place in the parasitic Cymothoidae and Epicaridea. Epicarideans have highly reduced antennules, usually of 2–3 articles; a 3-articulate peduncle is generally apparent during larval stages, but reduced in adults. In oniscideans reduction results in very small, 1-, 2-, or 3-articulate antennules, which in some cases are not even mobile (although Holdich, 1984: figs 24, 53, shows 4-articulate antennules in *Porcellio* and *Deto*). Setation on the second and/or third article suggests that loss of both peduncular and flagellar articles has probably occurred in the Oniscidea. Oniscidean antennules also differ in arising directly between the antennae, instead of antero-medially to them, as in most other isopods (character 22). Some anthuridean species also have small, 3-articulate antennules, with setation again suggesting loss of one of the peduncular articles as well as most of the flagellar articles.

Among the Flabellifera, all manner of antennule reduction occurs. In many cases, it appears that the two basal-most articles have fused, as in many Cirolanidae (*C. tuberculata*, Delaney, 1986; *C. triloba*, *C. furcata*, *C. similis*, and *C. vetoriae*, Bruce, 1981; *Neocirolana bicrista*, Holdich *et al.*, 1981); many *Corallana* and *Excorallana* (Delaney, 1982, 1984), and perhaps *Plakarthrium*. In *Anuropus*, only two antennular articles remain, and their homology is uncertain. However, the second (distal) article in *Anuropus* is unique in being enormously expanded and scalloped (character 23). In most limnoriids, the peduncle appears to have lost one article, and the flagellum is also reduced to only a few articles, although mancas tend to have all 3 peduncular articles. In Lynceidae and Keuphyliidae, all 3 peduncular articles are present and the flagellum is reduced to 3 very short articles. The antennules are very short in the Cymothoidae and the distinction between the peduncle and flagellum is indiscernible, the entire structure usually being reduced to 7 or 8 short articles (Fig. 5). Reduced antennular flagella are common in various species in many genera of Cirolanidae, wherein a 3-articulate peduncle bears a flagellum reduced either by loss or fusion (or both) of the flagellar articles (some *Eurydice*, *Metacirolana*, *Cirolana*, etc.).

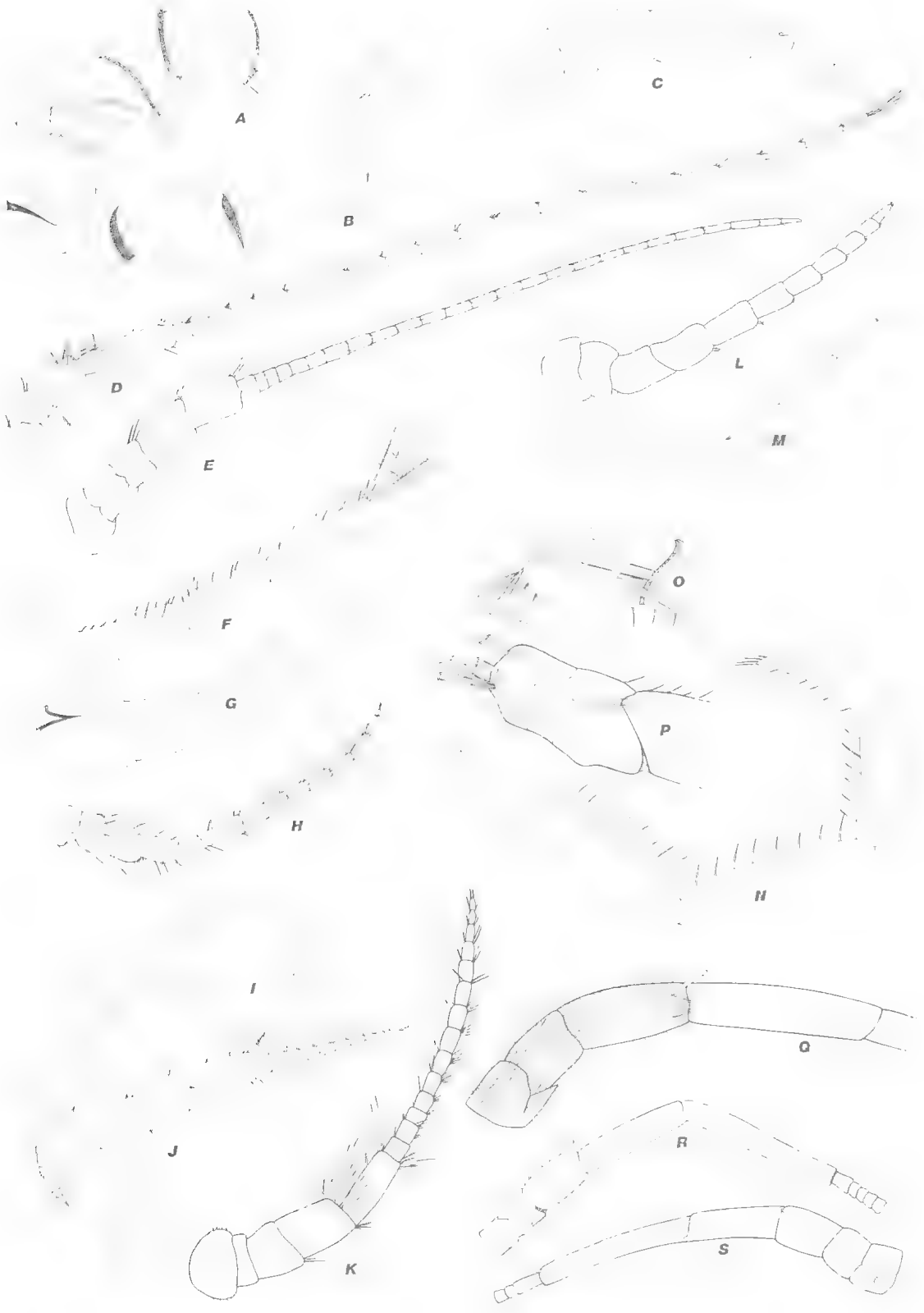
In examining these various antennular reductions, it is obvious that they are not all homologous. In fact, reduction in most, or even each, group could have been by entirely separate evolutionary events. Some may be homologous reductions, but until detailed ultrastructural and anatomical studies have been accomplished a judgment in this regard cannot be made. For this reason, we have not used antennular reduction as a character in the data set.

Antennae

A review of the literature suggests that confusion exists regarding the number of articles in the antennal peduncle of peracarids (Fig. 7). Much of this confusion seems to have derived from viewing the number of peduncular articles as a single feature, when in fact it should probably be examined as at least two separate features (the number of articles in the protopod; and, the number of proximal articles of the ramus that combines with the protopod to form a functional unit recognized as the peduncle). We define peduncle as the enlarged basal articles of the antenna that bear intrinsic musculature. The flagella of isopod antennae lack intrinsic musculature, i.e. no muscles have their origin in the flagellum.

The antenna of mysidaceans has a 3-articulate protopod (at least primitively, e.g. *Mysis*), which

FIG. 7. Examples of isopod antennae. A, Flabellifera, Cirolanidae (*Bathynomus giganteus*, SDNHM), dorsal aspect showing articulation with head, base of antennule, and floating cuticular piece on articulating membrane. B, Flabellifera, Cirolanidae (*Bathynomus doderleini*, USNM 39321, dorsal aspect). C, Phreatoicidea (*Phreatomerus latipes*, USNM 60659). D, Flabellifera, Cirolanidae (*Eurydice caudata*). E, Flabellifera, Aegidae (*Aega longicornis*, holotype). F, Gnathiidea (*Bathygnathia curvirostris*, USNM 10580), note fusion of distal articles (3 and 4, or 4 and 5). G, Valvifera, Idoteidae (*Synisoma* sp.). H, Valvifera, Idoteidae (*Synidotea francesae*, holotype). I, Anthuridea (*Malacanthura caribbica*, USNM 173521). J, Anthuridea (*Calathura* sp., USNM 99253). K, Flabellifera, Cirolanidae (*Poljnlana wirksteini*, holotype). L, Flabellifera, Cymothoidae (*Nerocila acuminata*). M, Flabellifera, Anuropidae (*Anuropus antarcticus*, USNM 112260). N–P, Valvifera, Pseudidotheidae (*Pseudidotheca micrsa*, USNM 139139). N, entire antenna, with 4-articulate peduncle and 2-articulate flagellum; O–P, first two peduncular articles, seen from both sides. Q, Oniscidea, Ligiamorpha (*Ligia baudiniana*, SDNHM). R, Oniscidea, Ligiamorpha (*Ligia exotica*, USNM 43252). S, Oniscidea, Ligiamorpha (*Ligia occidentalis*, SDNHM).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combines with the first two or three flagellar articles to form a 5- or 6-articulate peduncle, although the protopod articles are fused into 1 or 2 pieces in most living species. A large lamellar scale (the scaphocerite) arises from the third protopodal article in mysidaceans. Mictaceans and amphipods have 2-articulate protopods, that combine with the first 3 flagellar articles to form 5-articulate peduncles (although this is reduced in some amphipods). Mictaceans, and perhaps some apseudomorph tanaidaceans, have a scale on the second article, suggesting that it could be homologous with the third protopodal article of mysidaceans. Amphipods lack an antennal scale. The antennal peduncle of most isopods also comprises 5 articles, although in some taxa it is reduced to 4 or fewer articles, and in the Asellota and Microcerberidea (and possibly some Cirolanidae) a 6-articulate peduncle occurs. A review of these conditions in isopods is given below.

Milne Edwards and Bouvier (1902) described the antennal peduncle of *Bathynomus* (Cirolanidae) as 6-articulate. However, they apparently mistook the large articulating membrane between articles 1 and 2 for an extra article (as noted by Bruce, 1986). Hansen (1903) also described the antennal peduncle of *Bathynomus* as 6-articulate, but Hansen was focusing on a minute strip of sclerotised cuticle at the base of the antennal peduncle, at the edge of the articulating membrane, that he considered to be the vestige of a proximal antennal article, or precoxa. Hansen's conclusion that this cuticular fragment is homologous to a precoxal article was based on the observation that it moved ('articulated') within the antennal socket when the antenna was moved. Hansen (1903) also claimed to have found 6-articulate antennal peduncles in several species of *Cirolana*, and in the asellote genera *Eurycope* and *Asellus*. Hansen (1905a, 1916) later added *Conilera* (Cirolanidae) and *Ligia* (Oniscidea) to the list of taxa with 6-articulate antennal peduncles, and in his 1925 review added *Janira maculosa* (another asellote), concluding that the 6-articulate condition was primitive in isopods, and loss of the precoxa was a derived condition.

In Hansen's view, then, the primitive isopod antenna was similar to that of mysidaceans, with a 6-articulate peduncle composed of a 3-articulate protopod (comprising the precoxa, coxa, and basis) plus the first three articles of the endopodite; the rest of the endopodite forming the flagellum. Hansen also noted that in most Asellota and in *Ligia* with a 6-articulate peduncle, the third article bears a movable scale, or 'squama', representing the vestigial exopod.

Calman (1909) agreed with Hansen's conclusions, noting that the antennal peduncle of isopods normally comprises 5 articles, but that in the Asellota, *Bathynomus*, and *Cirolana* it is 6-articulate, and in some Asellota with 6-articulate peduncles a scale occurs on the third article. Wägele (1983a; referring to the protopod as the 'basipodite') agreed with Hansen's conclusions that a 6-articulate peduncle is the primitive isopod condition. Wägele used figures taken from Hurley (1957) and Vandel (1960) to illustrate 6-articulate peduncles in an asellote (*Iathrippa longicauda*) and a ligiid (*Ligia italica*), following Hansen in his claim that in the Asellota and Ligiidae a small exopodite (scale) occurs on the third peduncular article. Wägele (1983b) also argued that a 6-articulate antennal peduncle is characteristic of the Microcerberidea. Other authors have agreed or disagreed with Hansen's opinion regarding the occurrence of a 6-articulate peduncle in isopods.

The literature thus contains references to 6-articulate antennal peduncles occurring in at least some genera in four groups: Asellota, Microcerberidea, Oniscidea (Ligiidae), and Cirolanidae. The contention of a 6-articulate peduncle in the Isopoda is tied to Hansen's and Calman's homologisation of isopod antennae with a 'primitive' crustacean somite appendage with a 3-articulate protopod comprising a precoxa, coxa and basis, with the paired rami arising from the latter. However, it is of considerable interest to note that, among the Malacostraca, an antennal precoxa (and hence a 3-articulate protopod) unquestionably occurs only in the groups described above — the mysidaceans and certain isopods. In all other malacostracans the protopod comprises only 2 articles, and the rami (or scale) arises from the second article. This suggests the possibility that the primitive state in Crustacea is a 2-articulate antennal protopod.

We have examined the cuticular piece noted by Hansen on the articulation membrane of the antenna of *B. giganteus* and also found it to move when the antenna is moved. However, this piece does not articulate with any other article, or with the head, but simply floats free upon the membrane. A similar free-floating cuticular piece occurs in many genera of Cirolanidae (as noted above), although it has rarely been noticed due to its small size and failure to be removed with the antenna upon dissection. Bruce (1986) commented on these structures, noting their presence

in at least 12 Australian genera of Cirolanidae and illustrating them for three species (*Bathynomus immanis*, *Cirolana cranchii*, and *Natatoluna rossi*). Homologisation of this piece with a true basal, or 'precoxal' article seems a reasonable hypothesis, although in our opinion still very much open to testing. Moreover, we know of no flabelliferan isopod that has an antennal scale.

In Ligiidae, the antennal peduncle is usually 5-articulate, or occasionally 4-articulate. In this family, both the first and second article may be split by 'fracture lines' (often subcuticular) on one side, so that an observation from only one side of the appendage might give the illusion of there being more than one article present — a situation somewhat analogous to that noted above for the antennule of *Bathynomus*. We have examined *Ligidium ungicaudatum*, *Ligia occidentalis*, *L. baudiniana*, and *L. exotica* and can find no trace of a precoxal article. Richardson (1905), Van Name (1936), Sutton (1972), Kensley and Schotte (1989), and others have also noted that the antennal peduncle of Ligiidae is no more than 5-articulate. Fragmentation, splitting, ridges, etc. occur on the proximal articles of the antennal peduncles in many groups, including Ligiidae, Anthuridea, Phreatoicidea, and others. This splitting may have led some authors to mistakenly interpret one of the pieces as a small precoxal article (and thus describe a '6-articulate' peduncle). The first mention of an 'extra' article at the base of the antenna in ligiids was apparently Hansen (1916) who stated, '...In *Ligia oceanica* we found not only six joints in the peduncle, but even an exopod or squama on the third joint...'. Hansen's illustration shows what appears to us to be a 5-articulate peduncle, with the first and second articles fragmented; his 'precoxal remnant' appears to be a fragmented plate of the first article, and his 'scale' appears to be the protruding edge of a fragment on the second article. The inner margin of the second article is often slightly elevated, to form a low lobe-like ridge, that has perhaps been mistaken for a 'scale' in *Ligia*. Wägele's (1983a) illustration of *Ligia italica* (after Vandel, 1960), showing a 6-articulate peduncle and a scale, is probably such a misinterpretation.

In the Asellota, 6-articulate antennal peduncles do occur in numerous genera of many families (Fresi, 1972; Gruner, 1965; Hessler, 1970; Siebenaller and Hessler, 1977; Wilson, 1976; 1980a, 1986a; Wilson and Hessler, 1981); e.g. Haplomunnidae (*Haplomunna*, *Munella*, *Thylakogaster*, *Abyssaranea*); Desmosomatidae (*Balbidocolon*, *Eugerda*, *Chelator*, *Mirabilicoxa*, *Momedossa*, *Prochelator*, *Torwotia*, *Whoia*, *Thaumastosoma*); Nannoniscidae (*Hebefustis*, *Exiliniscus*, *Panetela*, *Rapaniscus*, *Regabellator*); Munnopsidae (*Eurycope*); Janiridae (Jaera, Janiropsis); Pleurocopidae (*Pleurocope*); and Munnidae (*Munna*). Antennal scales occur on the third peduncular article in many of these same asellote taxa, and also on the third article of some species with fewer than 6 articles in the peduncle, such that one would interpret the antenna as retaining the 3-articulate sympod, but with only 1 or 2 articles of the endopod contributing to the peduncles.

Wägele (1982b, 1983b) illustrated a 5-articulate antennal peduncle for *Microcerberus mirabilis*, although he stated that a 6-articulate antennal peduncle is diagnostic for the Microcerberidea. Wägele (1983b) clearly shows a 'precoxal article' on the antenna of *Microcerberus tabai*. Baldari and Argano (1984) figured a 5-articulate peduncle in *Microcerberus redangensis*, but stated that it was 4-articulate. Pennak (1958) claimed *M. mexicanus* had a 5-articulate peduncle. Messana *et al.* (1978) clearly showed and stated that *Microcerberus anfindicus* has a 6-articled peduncle. Perhaps both the 5-articulate and 6-articulate conditions occur within the Microcerberidea but, since the 6-articulate condition definitely does occur we regard it as the primitive state.

Nicholls (1943, 1944) noted that the antennal peduncle of phreatoicids was 5-articulate, but that a ridge (or groove) lines the lower boundary of the antennal socket that might suggest the existence of a former proximal (precoxal) article that had been incorporated into the head. However, such a ridge occurs in many isopods, including *Bathynomus*, and Milne Edwards and Bouvier (1902) and Hansen (1903) regarded it as simply part of the head skeleton.

An antennal scale probably does not exist in the Anthuridea. In some species, such as *Mulacanthura caribbica*, a minute, simple, unjointed, non-articulating structure exists on the 5th peduncular article; it appears to be a superficial cuticular structure, perhaps a sensillum of some kind. We have seen no such structure, or anything resembling a scale, in species of *Calathura* or *Mesanthura* that we have examined. Kensley (pers. comm.) has taken SEM photographs of many anthuridean species, including species that Menzies and K.H. Barnard claimed had antennal scales, and failed to find anything

other than various, small, superficial, cuticular structures (spines and setae).

In valviferans, the first two articles of the antennal peduncle are more-or-less fused and operate as a single unit, although the cuticle of these two articles often appears to be 'fragmented' into several pieces. Bruce (1980) described *Keuphylia nodosa* (Keuphyliidae) as having a 5-articulate antennal peduncle with a scale on the second article. We have examined this species and consider this structure is not a true 'scale'; it appears to be a cuticular fold or a one-piece sensory lobe, and it is on the second (not the third) peduncular article.

Character 24 is: antennal peduncle 6-articulate (0) *vs* antennal peduncle 5-articulate (1). Mysidaceans, tanaidaceans, microcerberids and asellotes are scored (0); all other taxa in the data matrix are scored (1). In Cirolanidae both conditions might exist (given the hypothesis that the small cuticular pieces on the articulating membrane in some species represents a vestigial basal article), and the condition in limnoriids and protognathiids is uncertain; hence these three taxa are scored (?). Character 24 was left unordered in initial analyses.

Character 25 is: antenna biramous, or with a vestigial second flagellum or scale (0) *vs* antenna uniramous, and without a vestigial second flagellum or scale (1). Mysidaceans, tanaidaceans, mictaceans, and asellotes are scored primitive for this character (0); all other taxa are scored (1). The 'scale' drawn by Bruce (1980) on *Keuphylia* appears to us to be a non-articulating sensory lobe on the second peduncular article.

Character 26 is: Antennae present (0) *vs* antennae vestigial in adults (1). Only Epicaridea is scored derived (1) for this character.

Mandibles

Of the many different 'characters' recognisable on isopod mandibles, many show so much homoplasy that they are of little use at the subordinal level of analysis. In some groups, such as many phreatoicids and asellotes, all of the typical peracaridan mandibular structures persist, at least on the left mandible. However, reduction, loss, or extreme specialisation of the mandibular palp, molar process, spine row, and lacinia mobilis appears to have occurred at least several times in most isopod suborders. Although clear trends can often be seen, especially within certain family clusters, the high level of overall homoplasy in modifications of most of these structures reduces their usefulness in phylogenetic analysis at the subordinal level.

The isopod mandibular palp, like that of other peracarids, is primitively 3-articulate. Kussakin (1979:26) illustrated a 4-articulate mandibular palp for *Caecocassidias patagonica* (Sphaeromatidae) and for *Cyathura polita* (Anthuridea), even though he described the Isopoda as having mandibular palps of 3 or fewer articles. Kussakin's figures of 4-articulate mandibular palps are almost certainly in error. Like Hansen (1890) and Bruce (1983, 1988) for several species of Aegidae, Kussakin probably mistook a fold at the base of the proximal palp article for an articulation.

Reduction of the mandibular palp (to one or two articles) has occurred in several taxa, and complete loss of the palp has occurred in many groups (Oniscidea, Calabozoidea, Keuphyliidae, Lynseiidae, Gnathiidea, Epicaridea, some Anthuridea, some Cirolanidae, many genera of Asellota, and all non-Holognathidae Valvifera). In gnathiids (praniza) and epicarideans, the mandibles are modified as small scythe-like pointed stylets with serrate cutting edges.

There are two fundamentally different kinds of mandibular molar processes in isopods. A broad, flat or truncated, grinding molar process is characteristic of Phreatoicidea, Asellota, Microcerberidea, Oniscidea, Valvifera, and most genera in the flabelliferan family Sphaeromatidae. A thin, elongate, blade-like, slicing molar process, with a row of teeth or denticles along the anterodistal margin, is characteristic of the primitive Anthuridea (Hyssuridae), and the flabelliferan families Anuropidae, Cirolanidae, Phoratopodidae, and Protognathiidae; a reduced blade-like molar process, or its apparent vestige, occurs in most species in the flabelliferan families Aegidae, Corallanidae, Cymothoidae, and Tridentellidae. Bruce (1981) suggested that the molar process of Phoratopodidae is 'vestigial'. However, our observations of *Phoratopus remex* Hale indicate that, while the molar is slightly reduced in size, it is nonetheless a well-developed, serrate, blade-like structure similar to that of Cirolanidae. The serrate condition also exists in the Anuropidae and Protognathiidae, in which it is (as in Cirolanidae) 'articulated' on the body of the mandible. In Corallanidae and Tridentellidae (and the cirolanid genus *Calyptolana* Bruce) the molar process is also 'articulated' and blade-like, but shows a loss of the serrate toothed margin and a reduction in size (and even complete disappearance in some genera and species).

In the primitive anthurideans (Hyssuridae) the blade-like molar process also occasionally 'articulates' on the body of the mandible and may bear a serrate or toothed margin (Poore and Lew Ton, 1988a; Wägele, 1981b).

In the sphaeromatid subfamilies Ancininae and Tecticeptinae (*Ancinus*, *Bathycopea*, and *Tecticeps*), the molar process is either absent or vestigial (Tecticeptinae) or modified as a thin blade-like structure (Ancininae). However, we do not regard the molar of Ancininae to be homologous to the blade-like molar described above for the Anthuridea and other flabelliferan families. In ancinines, the molar is apically acute (not rounded), lacks teeth or denticles at the antero-distal margin, and bears large knife-like serrations along the postero-distal margin. Ancininae and Tecticeptinae possess all the other features typical of Sphaeromatidae.

A molar process is absent in the Epicaridea and Gnathiidea, and in the flabelliferan families Limnoriidae, Lynseiidae, Bathynataliidae, Keuphyliidae, Plakarthriidae, and Serolidae. The molar process is also secondarily vestigial or absent in some genera of Sphaeromatidae and Idoteidae, and in a few anthuridean and oniscidean families.

In most isopods, the incisor is a multilobed grasping structure, but in groups specialised for predation or parasitism the incisor is typically blade-like and/or acute, for piercing tissues (Protognathiidae, Corallanidae, Tridentellidae, Aegidae, Cymothoidae, praniza stage of Gnathiidea). In most Limnoriidae the incisor process bears a unique 'rasp and file' structure, and a similar condition appears to be approximated in the Lynseiidae (Menzies, 1957; Poore, 1987; Cookson and Cragg, 1988).

The presence and size of the lacinia mobilis and spine row components vary greatly among the Peracarida. In the Isopoda, the nature of these structures appears to be closely tied to lifestyle (especially feeding behaviour) and hence strongly selected for and perhaps of limited phylogenetic value above the generic level. The presence of both a lacinia and spine row (on both the right and left mandible) is presumably the primitive peracaridan condition (Dahl and Hessler, 1982), and in many mysidaceans, mictaceans, and amphipods a gnathal lacinia and associated spine row persist. However, in many isopod groups these structures have been modified, reduced, or lost, especially on the right mandible. No doubt a wealth of phylogenetic information will become available once a more thorough understanding of pattern and homology among these structures has been achieved.

In most Phreatoicidea, Asellota, Oniscidea, Calabozoidea, and Valvifera, a lacinia and spine row, often closely associated with one another, are usually present (at least on the left mandible). The lacinia and spine row are often modified, reduced, or lost in the various flabelliferan families and genera. A distinct lacinia and spine row are usually absent in the Anthuridea, although remnants may persist in the primitive family Hyssuridae (Poore and Lew Ton, 1988a); the unique 'lamina dentata' of anthurideans is presumably the homologue of one or both of these mandibular structures. In the Microcerberidea, the lacinia is absent and only a row of small spines is present. In the Phreatoicidea, a spinose lobe may be present in lieu of a distinct lacinia and spine row, at least on the left mandible; the homology of this spinose lobe is uncertain, but it may represent either a fusion of the lacinia and spine row, or a loss of the lacinia and specialization of the spine row. A somewhat similar appearing modification occurs in certain Asellota (*Asellus*), Cirolanidae, and Keuphyliidae. The Limnoriidae have a somewhat similar structure (called the 'laciniod spine'), and in the unusual genus *Hadromastax* only a single simple spine remains. In the Serolidae, two spine-like structures of uncertain homology are usually present, both articulating; one may represent the lacinia and the other a single, enlarged spine of the spine row, or both may be enlarged spines. In the Phoratopodidae and Sphaeromatidae a large gnathal lacinia, with an associated spine row, is generally present. In the Bathynataliidae a large gnathal lacinia is also present, but with no trace of the spine row. In the Anuropidae, Protognathiidae, Corallanidae, Tridentellidae, Aegidae and Cymothoidae the lacinia and spine row is absent or reduced to a few, vestigial, spinelike structures. Mandibular characters used in the analysis follow.

Character 27 is: mandible with a lamina dentata — a synapomorphy unique to the Anthuridea. Character 28 is: mandibles of adult males grossly enlarged, projecting anteriorly, forceps-like — a synapomorphy unique to the Gnathiidea (although convergently approximated in the unique cirolanid species *Gnatholana mandibularis* Barnard). Character 29 is: mandibles lost in adult females — also a synapomorphy unique to the Gnathiidea. Character 30 is: molar process a broad flat grinding structure (0) *vs* molar process a thin blade-like slicing structure (1). Taxa in


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which the molar process is absent are scored '2' for this character. Character 50 describes four states of the mandibular incisor: broad and multitoothed (0); teeth reduced to form a serrate or crenulate margin (1); teeth lost (or fused?) to form a conical projection with basal 'rasp and file' (2); and, incisor modified as a recurved, hooklike, acute or subacute piercing-slicing structure (3). Character 91 is: mandibles modified as elongate scythe-like structures with a serrate cutting edge (Epicaridea and Gnathiidea).

The following taxa are scored as lacking a mandibular palp (character 35): Ligiamorpha, Tylomorpha, Calabozoidea, Epicaridea, Gnathiidea, Keuphyliidae, and Lynceiidae. Loss of the mandibular palp in certain genera of Anthuridea and Asellota is assumed to have taken place independently after the evolution of these suborders, i.e. it is a secondarily derived feature in these taxa. The situation in Valviferans is debatable; Brusca (1984) suggested that presence of a mandibular palp was the primitive valviferan condition and loss of the palp occurred after the origin of the unique species *Holognathus stewarti*, whereas Poore (1990) suggested that the ancestral valviferan had already lost the mandibular palp and it reappeared later in *H. stewarti*. We choose the more parsimonious alternative and assume that the mandibular palp did not reappear within the Valvifera (*sensu* Brusca, 1984). Valviferans are thus scored '0' for character 35.

Maxillules

The typical isopod maxillule comprises 1 or 2 proximal articles, and two distal lobes — an inner (medial) and outer (lateral) lobe. Most workers regard these lobes as endites although the precise homologies of the maxillulary articles is uncertain, and the two distal lobes are referred to in the literature by a variety of terms, e.g. inner and outer lobes, plates, endites, or rami; or, exopod and endopod. Furthermore, the proximal articles and region of articulation between the articles and lobes are rarely figured in the literature. Calman (1909) and Hansen (1925) viewed this appendage as comprising only the articles of the protopod, the two proximal articles being the precoxa and coxa, the outer lobe the basis, and the inner lobe an endite of the precoxa.

In mysidaceans, amphipods and tanaidaceans, at least primitively, there are also two lobes that are clearly endites arising from the second and third articles, as well as a short palp. In mictaceans two lobes also exist, but the nature of their articulation and the proximal lobes of this appendage are uncertain. Bowman and Iliffe (1984) refer to these lobes as both endites and as endopod (the distal 'endite') and exopod (the proximal 'endite'). Bowman *et al.* (1985) referred to these structures simply as the 'inner' and 'outer' lobes. Mictaceans, like isopods, lack a maxillulary palp.

In a number of isopod taxa the maxillules are highly modified. In the anthurideans, the outer lobe is a slender stylet and the inner lobe is minute (presumably vestigial) or absent. The maxillules of anthurideans have rarely been illustrated (Poore, 1978, fig. 17b; Poore and Lew Ton, 1988, fig. 7; and, Poore and Lew Ton, 1990, fig. 3). In the primitive anthuridean family Hyssuridae the maxillule bears apical denticles or spines; in the more advanced families (Anthuridae, Antheluridae, Paranthuridae) the apical spines are largely reduced, or fused, often resulting in a simple serrate distal margin. Somewhat similar conditions (outer lobe a long slender stylet with apical teeth, inner lobe reduced or absent) exist in the Gnathiidea (praniza stage), Aegidae, Bathynatallidae, Cymotholdae, Lynceiidae, Plakarthriidae, and Tridentellidae. In the Corallanidae the maxillule is highly modified as a single elongate stylet with the apex forming an acute recurved piercing hook. It seems unlikely that these are all homologously

FIG. 8. Examples of isopod maxillipeds. A, Oniscidea, Ligiamorpha (*Ligia exotica*, male, USNM 43352). B, Oniscidea, Tylomorpha (*Tylos niveus*, male, USNM 67703). C, Phreatoicidea (*Phreatoicus australis*, male, USNM 59116). D, Asellota (*Paramunna quadratifrons*, coxa and epipod not shown; SDNHM specimen). E, Asellota (*Janiropsis* sp., male; SDNHM specimen). F, Asellota (*Lirceus hoppinae*, male, USNM 230328). G, Flabellifera, Cirolanidae (*Anopsilana* sp., male, SDNHM specimen). H, Flabellifera, Serolidae (*Serolis albida*, gravid female, USNM 123900). I, Flabellifera, Anuropidae (*Anuropus antarcticus*, non-gravid female, USNM 173141). J, Gnathiidea (*Bathygnathia curvirostris*, male, USNM 10580). K, Flabellifera, Cirolanidae (*Acirolana chamensis*, paratype, LACM type No. 3014). L, Flabellifera, Aegidae (*Aega longicarnis*; type). M, Flabellifera, Cymotholdae (*Hironeca convexa*, female, attached oostegite not shown, from Brusca 1981). N, Gnathiidea (*Gnathia stygia*, USNM 112376). O, pylopod of *Bathygnathia curvirostris*, male, USNM 10580). P, pylopod of *Gnathia stygia*, USNM 112376). Q, Anthuridea (*Cyathura guaroensis*, from Brusca and Iverson 1985).

derived morphologies. The maxillules are vestigial or lost in adult gnathiids and epicarids. Uncertainty regarding the homologies of the maxillulary articles limits the number of potential characters available on this appendage for phylogenetic analysis.

Character 31 is: maxillule present (0), *vs* reduced or vestigial in adults (1), *vs* lost in adults (2). Character 31 was left unordered in initial analyses. Character 32 is: maxillule with palp (0) *vs* without palp (1). Character 92, the single acute hook-like lobe, is unique to the Corallanidae.

Maxillae

The homologies of the maxillary articles of isopods are also unsettled. As with the maxillules, there are 1 or 2 proximal articles and 2 distal lobes — an inner (medial) lobe, and an outer (lateral) lobe; the outer lobe is generally divided into two. The proximal articles and articulation of the two distal lobes are rarely illustrated in the literature. Calman (1909) and Hansen (1925) viewed the maxilla as lacking rami and comprising only the protopodal articles with their endites; that is, precoxa, coxa, and basis, with the coxa being expanded as an endite forming the inner lobe, and the basis bearing an endite that forms the split (bilobed) outer lobe. As with the maxillules, the inner and outer lobes of the maxillae have usually been regarded as endites, but they have been referred to in the isopod literature as rami, lobes, plates, endites, and exopod/endopod.

The maxillae of mysidaceans retain both the endopod and exopod, as simple one- or two-articulate platelike structures, and both rami bear endites. Amphipod maxillae primitively resemble those of isopods but without the divided outer lobe, although in most modern groups they are reduced to one or two simple lobes (as in many oniscideans). The maxillae of mictaceans are very similar to those of most isopods, with a divided outer lobe. The maxillae of tanaidaceans also resemble those of isopods, at least in their primitive form (*Halmyrapseudes*, Sieg *et al.*, 1982), although in most tanaidaceans the maxillae are highly reduced. No isopods retain the primitive crustacean condition of a maxillary palp (the 'palp' of Cirolanidae referred to by Bruce, 1986 is actually the inner lobe).

Character 34 is: maxillary outer lobe undivided (0) *vs* divided into two lobes (1). Mictaceans, tanaidaceans, and isopods are apomorphic for this character, although in many groups (most scored '?' in the data matrix) the maxillae are highly modified or reduced to a single lobe or a stylet (see below). In some groups, the maxillae are extremely reduced, vestigial, or absent altogether (Gnathiidea, Epicaridea, Anthuridea). In the Anthuridea the maxillae are minute and more-or-less fused with the paragnath (hypopharynx), or absent altogether. In Protognathiidae the outer lobe is apparently absent (Wägele and Brandt, 1988). In the oniscids the maxillae are short and plate-like with 2 non-articulating lobes, but the homology of these 2 lobes is not clear. Because the variety of maxillary reductions in isopods are likely to be the result of different evolutionary processes (nonhomologous features), most of these characteristics have not been included in the data set. Character 36 is: maxilla modified into a stylet-like lobe with recurved apical (hooklike) setae, a condition seen in certain flabelliferan families (Corallanidae, Tridentellidae, Aegidae, Cymothoidae). Character 33 is: maxillae highly reduced and 'fused' to the paragnath, or absent altogether (Anthuridea only). Among the Isopoda, only the Phreatoicidea retain the primitive peracaridan filter setae row on the medial margin of the maxilla (character 74).

Maxillipeds

As in most other peracarids, the maxilliped of isopods consists of four distinct regions: a proximal article (the coxa); the basis, with an enlarged, distal, anteriorly directed, blade-like lobe (the endite); an epipod of varying size and shape, lateral to the coxa; and, a palp (primitively comprising the remaining 5 articles of the appendage — the ischium through dactylus) (Fig. 8). Amphipods differ from isopods in possessing (primitively) a 4-articulate maxillipedal palp, and two endites (an inner and an outer) arising from the basis and ischium respectively.

The maxillipedal palp is reduced in some taxa in almost all suborders (most Oniscidea [Trichoniscidae, Tylidae, Oniscidae, Armadillidiidae], Calabozoidea, many Anthuridea, Gnathiidea, Anuropidae, Aegidae, and Cymothoidae). Wägele's (1989a) claim that a 2-articulate maxillipedal palp with spines on only the terminal article is a synapomorphy uniting the genus *Rocinela* (Aegidae) as the sister group of the Cymothoidae is incorrect. Most (if not all) *Rocinela* have 3-articulate maxillipedal palps with spines on the two distalmost articles (the apical article is minute and easily overlooked). In most isopod taxa, the maxillipedal endites can

be hooked together by coupling setae (coupling hooks), e.g. Phreatoicidea, Asellota, some Valvifera, Epicaridea, Gnathiidea, most Flabellifera. Coupling setae also occur on the maxillipeds of some Mictacea and most Tanaidacea. Maxillipedal coupling setae are absent in Microcerberidea, Ligiamorpha, Tylomorpha, Calabozoidea, Anthuridea, and Amphipoda. They have presumably been lost in amphipods as a result of the maxillipeds being fused together; this is also the case in certain tanaid families in which the maxillipeds are fused, such as Leptognathiidae, Pseudotanaidae, and Nototanaidae. Coupling setae may be missing in the anthurideans owing to the immovable fusion of the maxillipedal coxae and epipods to the head. Coupling setae are also usually absent in isopod taxa that have reduced endites e.g. Corallanidae, Aegidae, Cymothoidae, Lynseiidae, some Cirolanidae; or highly modified maxillipeds (Anuropidae, Plakarthriidae, Protognathiidae, Serolidae).

In isopods (as in most peracarids) a lamellar epipod usually arises from the coxa of the maxilliped. In several groups, the epipod may have its proximal part marked off from its distal part by a transverse suture (many Valvifera, Phreatoicidea, and Flabellifera). In males and nonovigerous females, the epipods often seem to function as 'cheeks', forming an operculum for the oral field. In gravid females of some taxa (Anthuridea, many Flabellifera), the epipods tend to be oriented in such a way to function as accessory marsupial plates to prevent loss of the embryos from the anterior region of the marsupium. The isopod epipod is never branchial, as it is in tanaidaceans. In mysidaceans, the epipod is posteriorly directed and carried under the carapace. Epipods are known from all isopod suborders except Epicaridea, Gnathiidea, Microcerberidea and Calabozoidea. Maxillipedal epipods are also apparently absent in the families Anuropidae, Corallanidae, and Plakarthriidae, and the unique genus *Hadromastax*. In Cirolanidae, Aegidae, and Cymothoidae the epipod is apparently reduced or absent in all life stages except brooding females. Wägele and Brandt's (1988) claim that *Protognathia* lacks maxillipedal epipods was based on their study of the single manca-stage individual. Because this genus (and family) was erected on the basis of manca specimens, the status of the adult maxilliped cannot be determined. Incomplete data on the precise distribution of occurrence of maxillipedal epipods prevent us from using this potentially important feature in the data analysis.

In at least some isopod groups (e.g. some Phreatoicidea, Asellota, Valvifera, Flabellifera, Epicaridea, and Gnathiidea), the maxillipeds of gravid females also bear posteriorly-directed, oostegite-like, often setose lappets. The function of these lappets is not known, but they may function as an oostegite (to close the anterior region of the marsupium), or they may drive a water current through the marsupium.

Several authors have suggested that the posterior cervical groove (*fossa occipitalis*) on the head of some isopods represents the incomplete line of fusion between the cephalon and first thoracomere. However, these lateral or complete grooves occur sporadically in many distantly related genera (*Mesamphisopus*, *Idotea*, *Ligia*, some Sphaeromatidae, etc.) in many suborders, thus rendering this character unsuitable for phylogenetic analysis at higher taxonomic levels.

Character 37 is: left and right maxillipeds fused together; this condition occurs only in amphipods and some tanaidaceans (not primitively, however). Character 38 is: coxae of maxillipeds fused to head; this derived condition occurs only in the Anthuridea. Character 39 is: maxillipedal endite without coupling setae (0) *vs.* with coupling setae (1). Mysidaceans lack coupling setae, but they occur in at least some mictaceans, tanaidaceans, and isopods. Because the character states of the mysidaceans and the amphipods may not be homologous, this character was left unordered in initial analyses. Character 41 is: maxilliped with 2–3 endites (0) *vs* 1 endite only (1). Amphipods have 2 maxillipedal endites (one on the basis and one on the ischium), mysidaceans have 0–3 endites, and all other taxa in the analysis have one endite (on the basis). Character 42 is: maxilliped biramous; in this analysis, only the mysidaceans have a biramous maxilliped (0), all other taxa have a uniramous maxilliped (1). Character 44 is: maxillipedal basis elongated and waisted (medially narrowed); this feature occurs only in the Lynseiidae and Limnoriidae.

Pereopodal Coxae

In many isopods and amphipods, the coxae of the pereopods are expanded laterally into flattened lamellar structures called coxal plates. We define lateral coxal plates as ventrolateral expansions of the pereopodal coxae that extend freely (as 'plates') to overhang the coxa-basis hinge of the leg. Within the Crustacea, such lateral coxal plates occur only among the isopods and amphipods.

In gammaridean amphipods, the presence of well-developed lateral coxal plates is generally viewed as the primitive condition, although this has not been demonstrated by any rigorous phylogenetic analysis of the Amphipoda as a whole. Coxal plates are lacking only in relatively specialized amphipod groups, such as the tube-building Corophioidea, the vermiform and interstitial Ingolfiellidae, the pelagic Hyperiidae, and the aberrant Caprellidae. In these groups, the coxae form simple rings around the bases of the pereopods. The lateral coxal plates of gammaridean amphipods are generally large and not fused to their respective pereonal tergites; they can usually be dissected free from the body with the leg.

The lateral coxal plates of isopods are generally fused dorsally and ventrally to their respective tergites, although on pereonites 2–7 (and occasionally pereonite 1) the line of dorsal fusion is usually demarcated. They are often quite large (flabelliferans, most valviferans, Tylomorpha), although in some they may be small (some Valvifera). In some isopod groups — Valvifera, Anthuridea, Calabozoidea, Serolidae, and some Epicaridea and Oniscidea (in *Porcellio*, but probably not in *Ligia*) — the coxae also expand inward over the sternum. These sternal coxal plates have rarely been figured or discussed (Sheppard, 1957), and they may be absent in females bearing oostegites. Sternal coxal plates are clearly absent in many taxa, in both males and females (Phreatoicidea, Asellota, Plakarthriidae, Phoratopodidae). Due to uncertainty regarding the accurate taxonomic distribution and nature of the sternal coxal expansions, we were unable to incorporate this feature into the data set. However, this anatomical feature clearly holds great potential as a source of important data on isopod relationships, and bears further investigation. It may eventually be shown that sternal coxal plates co-evolved with lateral coxal plates, but were subsequently lost in some families. The various conditions of isopod coxae are summarized below.

In the Anthuridea, the coxae are extremely elongated and fused almost indistinguishably with their respective somites; this is perhaps an adaptation to the elongate body form and tube-dwelling lifestyle of anthurideans. They may be well-defined ventrally, but at most are demarcated dorsally only by a faint line. Strictly speaking, because anthurideans do not have large coxal plates that hang free to cover their coxa-basis articulations, by the above definition they do not have true lateral coxal plates. However, the reduction and fusion of the coxae with the body wall is taken to be a derived state of 'coxal plates present' and thus this group is scored as possessing lateral coxal plates. In many anthuridean species, the coxae are expanded as sternal coxal plates and appear to be fused along the ventral midline such that there is no clear distinction between the sternite and the coxa.

In the Asellota, Microcerberidea, and Phreatoicidea the coxae may be small or expanded (see Figs. 1, 2, and 9), but they usually have well-defined, though largely immovable, articulations with their respective pereonites (at least on some somites). Although they may be expanded anteriorly or posteriorly along the edges of their respective somites, they never extend ventrolaterally as free lamellar plates overhanging the coxa-basis articulation (not even the enlarged first pair of coxae in the asellote *Stenetrium* hang ventrally to cover the coxa-basis articulation) (Schultz, 1978; Wilson, 1980a). Thus we do not regard these three groups as having lateral coxal plates. In species of Asellota and Phreatoicidea with small coxae, distinct tergal epimeres, lappets, or spines may be present.

In the Calabozoidea, the lateral coxal plates are large, though indistinguishably fused dorsally to their respective pereonites (Van Lieshout, 1983; pers. obs.). The lateral coxal plates of oniscideans are also large, and sometimes dorsal sutures are visible, as in the Tylidae.

In the Epicaridea, lateral coxal plates are present in females, but are highly variable in size, ranging from very small and often unrecognisable posteriorly (in Bopyrinae) to large and prominent (in Orbioninae and Ioninae). Sternal coxal plates appear to be present at least in the Bopyridae.

In the flabelliferan families, large lateral coxal plates are typically present on all pereonites (Fig. 3). Usually they are indistinguishably fused to the first pereonite (or largely so), but more clearly defined by so-called 'suture lines' on pereonites 2–7. In 4 families (Serolidae, Plakarthriidae, Keuphyliidae, and Bathynataliidae) all of the lateral coxal plates are enormously expanded, and coxae 2–6 or 2–7 freely articulate with their respective pereonites, including those of the first pereonite (Wilson *et al.*, 1976, Kensley, 1978; Bruce, 1980, pers. obs.). In Serolidae the degree of free articulation is minimal, but a clear articulatory suture is present and movement of the coxal plate results in movement of the ventral coxal region on the sternum. In the

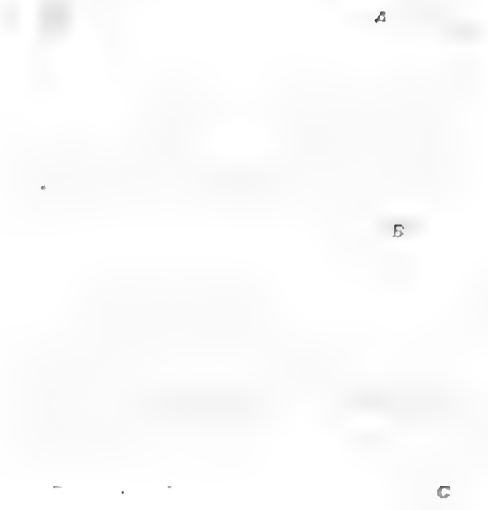

FIG. 9. Lateral views of a flabelliferan and two phreatoicideans, illustrating development of the pereopodal coxae. A, *Rocinela propodialis* (type, USNM 29248). B, *Phreatoicopsis terricola* (USNM 78431). C, *Phreatoicus australis* (USNM 59116; anterior is to the right).

Phoratopodidae (which is monospecific and known from only two female specimens) the coxal plates are enormously expanded ventrolaterally, clearly marked off from their respective pereonite, but yet they are not freely articulating (Hale, 1925; Bruce, 1981, pers. obs.).

Character 43 is: without lateral coxal plates (0), *vs* with lateral coxal plates (1). Character 85 is: lateral coxal plates, if present, not fused with their respective pereonites (Plakarthriidae, Keuphyliidae, and Bathynataliidae are score 1; Serolidae is scored '?').

Pereopodal Epipods

Character 45 is: with lateral epipods on pereopods (mysidaceans) (0) *vs* without lateral epipods on pereopods (mictaceans, tanaidaceans, amphipods, isopods) (1). Character 46 is; pereopods without medial epipods on pereopods (0) *vs*. with medial epipods on pereopods (1). Only the Amphipoda have medial epipodal gills arising from the coxae. In the gammarideans, these are usually paired, thin-walled, leaf-shaped, respiratory structures that are present on pereopods 2–7 (although they may be absent from 2 or 7). They may be stalked, foliate, or dendritic, and they are particularly large and convoluted in terrestrial species, presumably to compensate for loss of respiratory body surface area where the general body cuticle is hardened and waxy to prevent water loss. In some brackish and fresh-water amphipods, finger-like accessory gills and sternal gills may also occur (fresh-water Gammaridae, Crangonycidae, Hyalellidae and Pontoporeiinae). Whether the medial epipodal gills of amphipods are homologous to the lateral epipodal gills of mysidaceans and other Malacostraca, or are uniquely derived in amphipods, is not known.

Oostegites

Although many isopods have oostegites on the first five pairs of pereopods, the number and placement actually varies considerably within any given suborder, and even within a family (and occasionally within a single genus, e.g. *Sphaeroma*). In some groups (Tylomorpha, Aegidae, Cymothoidae, many Epicaridea) oostegites may form on all 7 pairs of pereopods, whereas in some genera of Arcturidae (Valvifera) only a single pair of oostegites ever develops (on pereopods 4). The Asellota and the Phreatoicidea almost always have oostegites on pereopods 1–4, and sometimes on the maxillipeds as well. The anthurideans usually have 3 or 4 pairs of oostegites. Other isopods are much more variable. In gammaridean amphipods, marginally setose oostegites usually occur on the coxae of pereopods 2–5. In Mictacea, the marsupium is formed by oostegites that may be marginally setose and occur on the coxae of pereopods 2–6 (*Hirsutia*), or not setose and occur on pereopods 1–5 (*Mictocaris*). Among isopods, some groups have marginal setae on the oostegites and others lack setae.

Oostegites are reduced or lost in many unrelated isopod groups that have evolved alternative or accessory means of incubating the embryos. For example, the evolution of sternal pockets or folds for incubating embryos is often correlated with the habit of conglobation, or folding the body ventrally so that the cephalon and pleotelson are appressed. Harrison (1984a, b, c) provides an excellent overview of brood pouch morphology in the family Sphaeromatidae, illustrating the usefulness of these features at the generic level. Some sphaeromatids have the brood pouch composed only of oostegites. Other genera have a brood pouch composed of large, opposing, sternal pockets formed of cuticular folds; these may extend from the posterior mar-

gin of the sternum and open anteriorly (posterior pockets), or they may extend from the anterior sternal region to open posteriorly (anterior pockets). In still other sphaeromatid genera, paired invaginations of the sternal cuticle occur that extend into the body cavity but open via narrow slits (referred to as 'internal pouches'). Internal pockets and pouches occur in sphaeromatid genera that conglobate (or fold) and have reduced or lost the oostegites. In some cases, the oostegites are entirely lost (*Dynamenella*), and in other cases they are rudimentary (many species of *Sphaeroma*). All plant- and wood-boring species of *Sphaeroma* seem to show reduction of the oostegites; non-boring species have all the oostegites fully formed, presumably working in concert with the internal pockets to form the marsupium.

In the cirolanid genus *Excirolana*, there are 3 pairs of greatly reduced oostegites, but these do not form a marsupium. Instead, the eggs drop from the oviducts into a pair of sacs ('uteri') formed by a single layer of cells and located in the thorax lateral to the gut. These sacs have been viewed as enlarged oviducts (Klapow, 1970, 1972; Jones, 1983). The embryos are brooded here, and since the sacs do not open to the outside during development this may be viewed as a form of ovoviviparity. In the cirolanid genus *Eurydice* there are 5 pairs of oostegites, but in addition the sternum is displaced dorsally either side of the nerve cord, with the marsupium and developing embryos filling the entire pereon, surrounding the gut. Klapow (1970) suggested that the brooding modifications in *Excirolana* and *Eurydice* are related to the habitats in which most species occur — wave washed sand beaches. Harrison (1984a, b,c) suggested similar correlations in certain sand beach sphaeromatids that have large sternal brood pockets (*Tholozodium*, *Sphaeromopsis*, *Dynamenella*, *Ancinus*, *Leptosphaeroma*, *Paradella*).

Ligiamorphans belonging to the conglobating genera *Armadillo* and *Armadillidium* have a brood pouch composed of oostegites, but in addition the sternum bears 5 pairs of invaginations which surround the gut within the body cavity for brooding the embryos. The brood pouch in the conglobating genus *Helleria* is also composed of oostegites, but the posterior wall of the marsupium extends into the pleon as a large pouch (Mead, 1963; Mead and Gabouriaut, 1988). In the conglobating genus *Tylos*, portions of the sternites of ovigerous females are displaced dorsally and pressed against the dorsal cuticle, and the developing embryos fill the body.

Oostegites appear to be absent altogether in the Microcerberidea, and sternal invaginations or folds are also apparently absent, although the female has been described for only a single species (Wägele, 1982a, b). Wägele speculated that the embryos of microcerberids might be laid free among sand grains — a behaviour currently unknown in any isopod species. However, since all peracarids undergo direct development, and many isopods rely on internal brooding, it would seem more likely that the embryos of microcerberids would also be brooded internally, in uteri or the general body cavity.

In the parasitic epicaridean family Cryptoniscidae, the embryos are brooded in sternal invaginations formed by ventrolateral folds of the body wall, whereas in the family Dajidae the brood pouch is formed from ventral extensions of the sternites. Gnathiids lack oostegites altogether and brood the embryos within the body cavity. Klapow (1970) claimed that the fertilised ova develop within the ovaries themselves in *Paragnathia*. At least some amphipods are also known to utilise internal brood chambers (*Cystosoma*).

As seen from the above review, aspects of oostegite morphology may be useful within families and genera, but no clear pattern of oostegite morphology is discernible at the level of isopod suborders (except perhaps for the Phreatoicidea, the Asellota, and the Microcerberidea), and therefore oostegite characters were not included in the data analysis.

Spermathecal Duct

Wilson (1986b) summarised and elaborated upon our knowledge of a unique vagina-like anterodorsal copulatory structure, the 'spermathecal duct' (or less descriptively, the 'cuticular organ') that occurs in female Asellota. Although all other isopod suborders have not yet been systematically surveyed for this structure, preliminary studies have so-far failed to reveal its presence in any other groups. Character 47 is presence of the asellote 'cuticular organ' or spermathecal duct (Wilson, 1986b; Wilson, 1991). Only the Asellota is scored derived for this character.

Genital Pores

Information on isopod genitalia has been recently summarised (Wilson, 1991). Important patterns are apparent in the position of the genital pores. In the Malacostraca, genital pores typi-

cally occur on the coxae of thoracopod 6 in females, and thoracopod 8 in males. These are relatively conservative features, although the peracarids show some variation.

The Phreatoicidea are the only isopods with both female and male pores located on the coxae. In male phreatoicids, the genital papillae (penes) occur on the medial side of coxae 7 and can be quite large; they are likely to be the primary intromittent organs in this group. In all other isopod suborders, the penes are located on the sternum, usually near the posterior margin of the sternite of thoracomere 8, rather than on the coxae. A single, notable, and important exception to this occurs in the asellote genus *Vermectias* Sivertsen and Holthuis, 1980 in which the coxae of the seventh pereopods appear to be divided into 2 pieces, one of which is slightly expanded medially onto the sternum and bears the penes upon it (Just and Poore, pers. comm.). Within the Asellota, and the Isopoda in general, the penes show a trend toward migration medially, often with fusion at the midline. Fusion of the penes occurs throughout the Isopoda and this feature has probably evolved independently in several suborders (Wilson, in press) making it of little use for the present study. The coxae/penes condition noted above in *Vermectias* may represent an early evolutionary stage in the migration of the penes from the coxae to the sternum, and perhaps also an early stage in the evolution of sternal coxal plates upon which the penes may be borne. In two suborders (Valvifera and Oniscidea) the penes arise from the sternum of pleomere 1, or from the articulating membrane between pleomere 1 and pereonite 7. Among the non-isopod Peracarida, a variable pattern also exists. The Mysidacea and the Mictacea have coxal openings for the vas deferens, whereas the Amphipoda and Tanaidacea have penes on the eighth thoracosternite.

In most female isopods and tanaidaceans, the oopore is situated ventrally on the sternite of pereonite 5. In the phreatoicids, however, the pore is clearly present on the medial side of the coxa. Coxal oopores also are found in the Mysidacea, Amphipoda, and perhaps the Mictacea (although our inspection of non-ovigerous female *Mictocaris* failed to reveal any oopores, either sternal or coxal). The situation of the oopore is more complicated in those isopod groups where the coxae are expanded as sternal coxal plates covering the ventral surface. Available data do not allow us to assess whether the oopores simply moved medially with the coxae, or whether they first migrated onto the sternite and then subsequently penetrated the coxae when the pores were covered by the expanding coxal plates. Further, the precise position of the oopore is unknown for many groups. Character 48 is: male penes on coxae (0) *vs* penes on sternite (1). Character 49 is: penes on thoracomere 8 (0) *vs* penes on pleomere 1, or on the articulating membrane between pleomere 1 and thoracomere 8 (1). Only Valvifera, Ligiamorpha, Tylomorpha, and Calabozoidea are scored apomorphic for character 49.

Excretory Organs

The primary excretory organs among the Malacostraca are antennal glands and maxillary glands. All crustaceans have antennal glands during their ontogeny, but many lose them in adulthood and instead rely on maxillary glands as the primary excretory organs. Adult isopods, tanaidaceans, and cumaceans lack antennal glands, or possess only a rudimentary antennal gland, and the maxillary gland is well developed (Strömberg, 1972). Conversely, adult mysidaceans and amphipods (and the Eucarida) have well-developed antennal glands. Siewing (1952, 1953, 1956) noted that in at least some lophogastrid mysids (*Eucopia*) small functional maxillary glands may also be present, thus possibly reflecting an ancestral condition in which both pairs of segmental nephridia were functional in adults. The condition in Mictacea is not known. Schram and Lewis (1989) have suggested that a series of segmental glands may have primitively been present, one pair in each crustacean head somite. Character 52 is: primary adult excretory organ antennal gland (0) *vs* maxillary gland (1); no polarity is assumed.

Pleopods

The pleopods of isopods have multiple functions, including respiration, swimming, and copulation. Two key synapomorphies uniquely defining the Isopoda are: Character 4, thoracoabdominal heart, and Character 5, respiratory pleopods. These features are obviously functionally/anatomically linked. The only other malacostracans known to utilise the pleopods as the principal respiratory organs are the stomatopods (Burnett and Hessler, 1973; Kunze, 1981), in which the heart also extends into the pleon.

The primitive malacostracan pleopod is a narrow biramous limb with multiarticulate rami. This type of pleopod is found in the Mysidacea and the Amphipoda. Broad, flat pleopods with

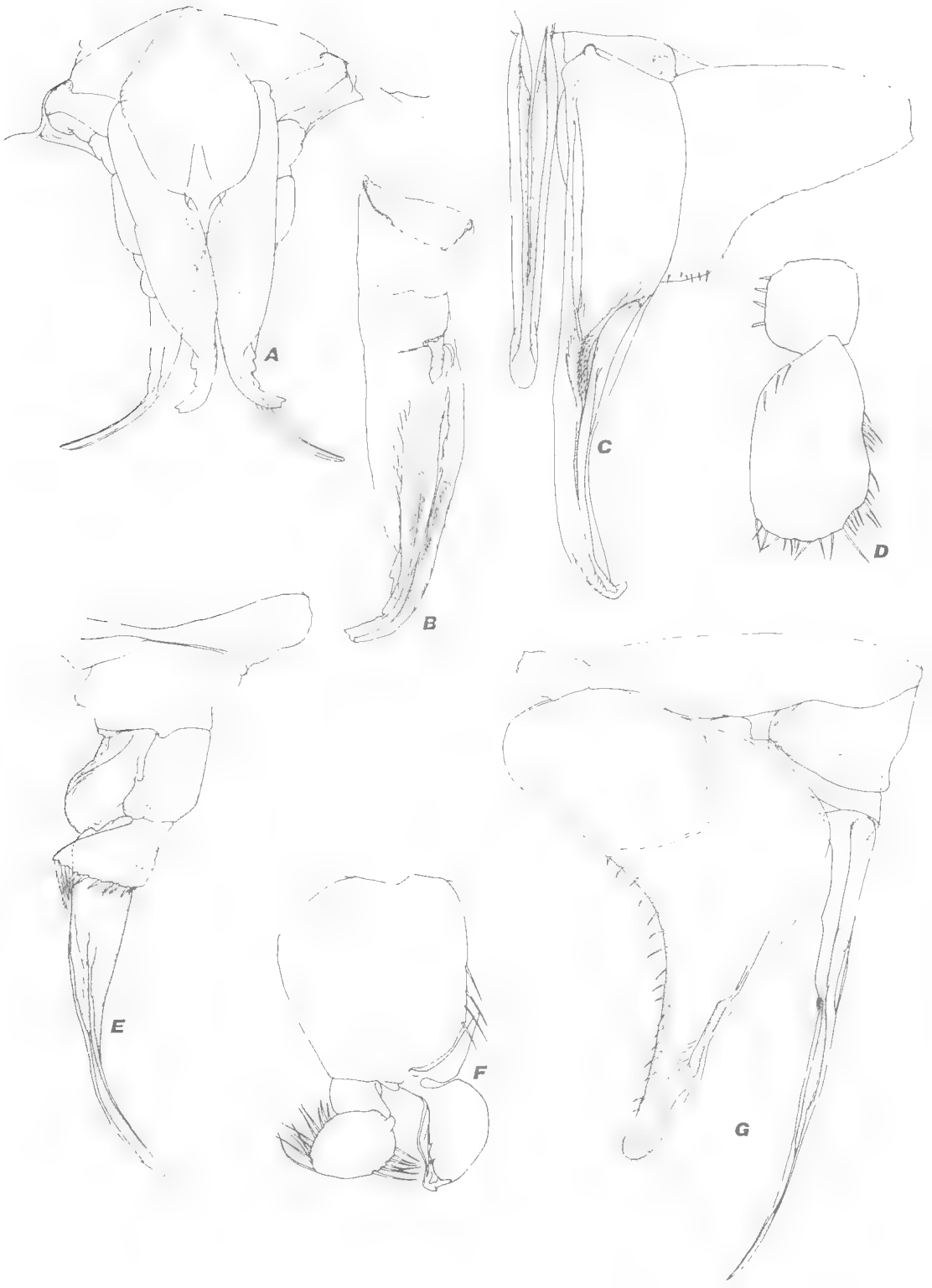
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TABLE 2. Comparison of basally derived Isopoda ('short-tailed' taxa). Legend: M = male; F = female.

	Reduction of pleomeres 1–2	Fusion of pleomeres 3–5	Condition of pleopod 1	Condition of pleopod 2	Condition of pleopod 3	Pereopodal coxae
Phreatoicidea	not reduced	free	M, biramous F, biramous	M, biramous F, biramous	biramous	free
Asellota	free, short & narrow (to variously fused)	fused	M, uniramous F, absent	M, biramous (endopod geniculate) F, uniramous	biramous	free
Microcerberidea	free, not short (ring-like)	fused	M, uniramous F, absent	M, biramous F, absent	uniramous	free
Atlantasellidae	free, broad	fused	M, uniramous F, absent	M, biramous F, absent	uniramous	free
Calabozoidea	strongly reduced	free	M, biramous (in juveniles) F, biramous	M, biramous F, biramous	biramous	fused dorsally; with sternal plates
Oniscidea	somewhat reduced	free	M, biramous F, biramous	M, biramous F, biramous	biramous	fused dorsally; with sternal plates

no more than two segments in the rami are found in the Mictacea, Tanaidacea, and the Isopoda. Character 53 is: narrow, multisegmented pleopodal rami (0) *vs* broad, flat, 1- or 2-articulate pleopodal rami (1). In phreatoicideans and many asellotes, especially primitive Asellota (Aselloidea, Stenetrioidea), the posterior pleopods bear 2-segmented exopods. In all other isopods the pleopodal exopods are always uniarticulate, although they may occasionally bear transverse 'suture lines'. Character 77 is: exopods of at least posterior pleopods biarticulate (0), *vs* no pleopods with biarticulate exopods (1).

In all non-isopod peracarids (except Mictacea), pleopods are primitively used for swimming. The pleopods of isopods are also well-developed for this function in most groups, with broad rami and swimming setae on at least some pairs. Several groups (Asellota, Microcerberidea, adult Epicaridea, Ligiamorpha, Tylomorpha, adult Cymothoidae) no longer swim with their pleopods, and use them only for respiration. Calabozoidea are said to swim (Van Lieshout, 1983:175), although behavioural observations may have not been made. In the groups that do swim, a trend occurs in most suborders wherein the posterior pleopods may be naked (with reduced or no marginal setae) and serve primarily for respiration. Loss of marginal setae typically occurs on pleopods 3–5, or 4–5, or just 5, and it may occur on both rami or only on the endopods. In the family Cymothoidae, the mancas and juveniles have swimming setae on the pleopods, but the obligate parasitic adults do not.

The Asellota and Microcerberidea share a number of pleopodal features. In both of these suborders females lack the first pair of pleopods (character 78), and in males the first pleopods (if present) are uniramous (character 81). The first pleopods of males are fused together to assist the second pleopods in sperm transfer in the higher Asellota. In addition, the male second pleopodal exopod is a small, non-lamellar structure, whereas the endopod is modified as a copulatory gonopod (character 79). Female microcerberids also lack pleopods on the second pleonite (character 82), and the third pleopods are uniramous and fused into a single piece to form an operculum over pleopods 4 and 5 (character 83). In male microcerberids, the second pleopodal exopod is reduced to a simple 1- or 2-articulate ramus, probably not involved in sperm transfer; the endopod is complex and highly variable in shape, but never geniculate (character 84). In the Asellota, females have uniramous second pleo-

FIG. 10. Comparison of male pleopods 1 and 2 in calabozoans, asellotans, and oniscideans. A, *Calabozoa* (Calabozoidea), penes and pleopods 1–2 in situ (ventral view). B, *Calabozoa* (Calabozoidea), left pleopod 1 (dorsal view). C, *Armadillidium* (Oniscidea), penes and right pleopod 1 in situ (dorsal view). D, *Asellus* (Asellota), right pleopod 1 (ventral view). E, *Calabozoa*, left pleopod 2 (ventral view). F, *Asellus*, right pleopod 2 (ventral view). G, *Armadillidium*, right pleopod 2 (ventral view).

pods (character 75), and males have the exopod of the second pleopod highly modified to function in concert with a large geniculate endopod in sperm transfer (character 76).

Terrestrial pleopodal respiration by use of pseudotracheae is found only in the Tylomorpha and Ligiamorpha, though not in all families (not Ligiidae or Trichoniscidae). In addition, the Oniscidea and the Calabozoidea share several unique pleopodal similarities (Table 2, Fig. 10). The endopods of male pleopods 1 and 2 are styliform and greatly elongated (only pleopod 2 in Ligiidae), presumably participating in copulation and/or sperm transfer (character 54). And, on pleopods 3–5 (in both sexes) the exopods are broad, heavily chitinised, and opercular, while the endopods are thick and tumescent (character 56). In most isopods, the endopods are thin walled and nearly the same size as the exopods.

In the recently described family Lynceiidae (Poore, 1987) the fifth pleopods are reduced to a single plate (character 70). Poore suggested that this attribute was the only unique apomorphy of this family, and we agree.

Other Pleonal Features

Most malacostracans have 5 free more-or-less equal pleonites, and primitively the 6th pleonite is free from the telson and pleomere 5. In the Microcerberidea and the Asellota, pleonites 1 and 2 are completely free and the remaining pleonites and telson are fused into a single unit with no lateral incisions indicating the fused somites. (The single exception to this appears to be the odd asellote *Vermectias*, which has 3 free pleomeres; Just and Poore, pers. comm.). A somewhat similar condition appears to be the primitive state for the Sphaeromatidae, but this is presumably a convergence. In sphaeromatids, the primitive condition exhibits lateral incisions demarcating the vestiges of the fused pleomeres, hence we do not regard this to be a condition homologous to that of asellotans. Some authors have suggested a close affinity between the Serolidae and certain Sphaeromatidae (*Ancinus, Tecticeps, Bathycopea*) on the basis of a similar pleonite reduction (Hansen, 1905a; Sheppard, 1933). However, in serolids pleonites 4–6 are fused to the telson and pleonite 1 is reduced, whereas in sphaeromatids pleonites 3–6 (at least) are fused with the telson, lateral incision lines primitively demarcate the positions of the fused pleomeres, and the first pleonite is never markedly reduced. Other isopods have variously modified pleonites, but no other suborders or families show a pleonite reduction like that seen in the Asellota and Microcerberidea as the primitive condition.

Character 80 is pleonites 1–5 either free or variously fused, but never (in the primitive condition) with pleonites 1–2 free and 3–5 fused to the pleotelson (0), *vs* pleonites 1–2 free and the remaining pleonites and telson fused into single integrated unit (1). The variety of pleonite reductions seen throughout the isopods make it difficult to find further useful homologies. In two taxa, Phreatoicidea and Limnoriidae, pleonite 5 is always manifestly longer than all other pleonites (character 73). In the Calabozoidea, pleomeres 1 and 2 are reduced to only the sternal plates (character 86).

Within the Malacostraca, broad fan-like uropods arising from the sixth pleomere and functionally associated with the telson is the plesiomorphic state. This 'tailfan' arrangement is an integral aspect of Calman's caridoid facies (Hessler, 1983). Unlike other Eumalacostraca, the Isopoda (and some other Peracarida) show a good deal of variation in uropod morphology and position (Figs 1–3) and the uropods function in a variety of ways. The caridoid-like tailfan of the Cirolanidae and related families has been taken by many workers as evidence that these taxa are primitive isopods, or at least that they represent an archtypical 'caridoid' isopod body plan. However, isopods (like amphipods, tanaids, and perhaps mictaceans) lack the 'caridoid escape behavior', and those groups with fan-like uropods do not use their flattened uropods for propulsion, as in true caridoids (e.g. mysidaceans, euphausiids, or natantians). Instead, they appear to use their uropods as lift planes and steering devices (unpubl. obs. of living *Bathynomus, Cirolana*, and other flabelliferans).

A review of the peracarid orders reveals a clear trend toward reduction of the caridoid tailfan morphology. Although it is well-developed among the Mysidacea, the telson and uropods of spelaeogriphaceans, mictaceans and thermosbaenaceans is less well developed as a true tailfan. This is presumably tied to loss of the 'caridoid escape behaviour' in these groups. However, in these three groups the flattened, paddle-like shape of the uropods is retained and these appendages probably assist in swimming in some way. In cumaceans, tanaids, amphipods, and many isopod taxa there is nothing resembling a caridoid tailfan.

In amphipods pleopods 4, 5 and 6 are modified as 3 pairs of uropods (Character 6). The amphi-

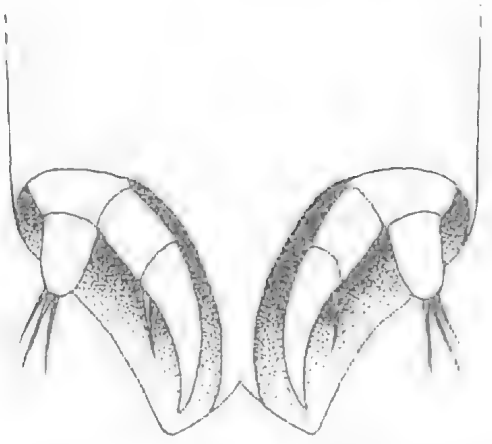

FIG. 11. *Keuphylia* (Keuphyliidae). Ventral view of pleotelson showing arrangement of uropods in ventral pocket.

pod urosome and uropods appear to be used primarily for strengthening the caudal portion of the body, and to permit jumping by rapid posterior flexion of the pleon (Barnard, 1969; Bousfield, 1973). In many Gammaridea, however, the third uropods still bear 'swimming' setae and may be used (along with the first two pairs) for paddling; males especially tend to have natatory third uropods (Barnard, 1969; Bousfield, 1973). However, the amphipod third uropod is usually substyliform and not fan-like. The majority of Gammaridea probably do not use the third uropods for active swimming and these structures are often reduced or occasionally absent in sedentary groups. The uropodal exopod in amphipods is biarticulate, and the endopod is typically uniarticulate.

In tanaidaceans, amphipods, cumaceans, and many isopods, the uropodal rami are styliform. The uropodal rami of tanaidaceans also are long, multiarticulate appendages, whereas in isopods, the rami are always short and uniarticulate. The mictacean uropodal rami can be either biarticulate (*Mictocaris*) or multiarticulate (*Hirsutia*).

In mictaceans, amphipods, and mysidaceans, the uropods arise from pleomere 6 and the telson is a distinct somite. In isopods and living tanaids, the sixth pleomere is fused with the telson, forming a 'pleotelson', although primitive fossil tanaids (see below) possessed free sixth pleomeres. Many isopods have a well developed, elongate telsonic region of the pleotelson upon which the anus and uropods are basally positioned. Other isopods have a reduced, shortened telsonic region of the pleotelson, and the anus and uropods are positioned in the posterior region of the pleotelson (terminal or subterminal). The uropods always arise on either side of the anus.

Dahl (1954) suggested that the primitive phreatoicidean condition was flabelliferan-like ('cirolanoid'-like), unlike the adult morphology of living Phreatoicidea. This argument was based on observations made on developmental stages taken from the brood pouch of the South African phreatoicid *Mesamphisopus capensis*. We do not find Dahl's argument (or his illustrations) convincing. The kinds of morphological changes he described can be easily explained by natural developmental allometry commonly seen in most crustaceans. Brenton Knott (pers. comm.) has seen no evidence of lamellar uropods or other 'cirolanoid' morphology in the developmental stages of any Australian phreatoicids.

Character 57 is: uropods broad and flattened (0); uropods flattened but only somewhat broadened (1); uropods styliform (2). This character was analysed unordered in initial analyses. Character 58 describes the shape of the pleotelson. State '0' is: telsonic region of the pleotelson well-developed and elongate, with the anus and uropods at the base of the pleotelson (at the position of pleomere 6) — this is the condition seen in mysidaceans, amphipods, mictaceans, and many isopods. State '1' is: telsonic region very short, with the anus and uropods positioned terminally on the pleotelson; this condition occurs in the Tanaidacea, Phreatoicidea, Asellota, Calabozoidea, Microcerberidea, Tylomorpha, and Ligiamorpha. Because the polarity and precise homology of these conditions is uncertain, character 58 was left unordered in initial analyses. A unique up-turned pleotelson apex occurs in the Phreatoicidea (character 72).

In mysidaceans, mictaceans, tanaidaceans, and amphipods, the uropodal rami are composed of 2 or more articles; in all isopods they are uniarticulate. Character 59 is: uropodal rami may be multiarticulate (0), *vs* uropodal rami always uniarticulate (1). In three families (Keuphyliidae, Bathynataliidae, Plakarthriidae) the uropods arise not on the anteorlateral margin of the pleotelson, but rather posterolaterally, where they lie in shallow ventral channels or furrows (character 55) (Fig. 11). In serolids there is also a tendency toward this feature, but it is not present in all species, hence they are scored '?' for this character.

Character 60 is: uropodal exopod folded dorsally over pleotelson (a unique synapomorphy of

FIG. 12. *Haliophasma geminata* (Anthuridea). SEM of pleon (lateral view). Note deep fluting between pleomeres 5 and 6, and between and between pleomere 6 and telson. Despite fluting, a continuous cuticular covering connects these somites and no articular membranes are present. Also note large opercular first pleopods (compliments of B. Kensley).

Anthuridea). Character 61 is: uropods modified as a pair of ventral opercula covering the entire pleopodal chamber (a unique synapomorphy for the Valvifera). Character 62 is: uropods form a ventral, operculate, anal chamber beneath pleotelson, covering the anus and distal-most pleotelson region but not covering the pleopods (a unique synapomorphy of the Tylomorpha). Character 63 is: uropods directed ventrally and identical to other pleopods (a unique synapomorphy of the Anuropidae, and presumably an adaptation to a swimming pelagic lifestyle). Character 67 is: uropodal endopod claw-like. We regard this as a unique synapomorphy of the Keuphyliidae. Although the uropodal endopod in *Paralimnoria* is acute, it is not recurved and claw-like as in Keuphyliidae (and, the endopod of *Limnoria* is neither acute nor claw-like). Character 68 is: uropodal exopod claw-like (a unique synapomorphy of the Limnoriidae). Character 71 is: uropods highly modified and represented by a single, elongate, clavate piece, or by an elongate, clavate peduncle with reduced rami — a unique apomorphy of the Bathynataliidae. Character 87 is: uropods of a single piece, rami fused to peduncle — a unique apomorphy of the Calabozoidea.

In all living tanaidaceans and isopods, the sixth pleomere is fused to the telson, forming a pleotelson. However, fossil tanaids of the infraorder Anthracocaridomorpha have 6 free pleomeres (and thus lack a pleotelson), and this is presumably the primitive condition for this group (Schram, 1974; Sieg, 1984; Schram *et al.*, 1986). Some cumaceans and thermosbaenaceans also have a pleotelson. A pleotelson is present in all isopods.

Many authors have alluded to a free telson in some genera of anthuridean isopods. The presence of a free (unfused) sixth pleomere in some Anthuridea has been debated at least since Calman (1909). Wägele (1981, 1989a) claimed that the sixth pleomere is always fused to the telson in anthurideans (thus a true pleotelson is always present). Bowman (1971) stated that the sixth pleomere was free in anthurideans. Kensley and Schotte (1989) stated, 'Pleonites 1–5 free or fused, pleonite 6 partly or completely fused with telson'. In his diagnosis of *Paranthura* Poore (1984) stated, 'Pleonites usually distinct from each other and from telson.' Poore and Lew Ton's (1985a) diagnosis of *Apanthura* stated, 'pleonite 6 free from others and from telson', and their diagnosis of *Cyathura* (1985b) stated, 'pleonite 6 free or fused to telson.' However, Poore (pers. comm.) has most recently stated that he no longer believes the sixth pleonite to ever be freely articulating with the telson in anthurideans.

The sixth pleomere is clearly fused to the telson (forming a pleotelson) in many anthurideans (*Pseudanthura*). However, in many genera pleomere 6 appears to be free (*Amakusanthura*, *Calathura*, *Exallanthura*, *Haliophasma*, *Heteranthura*, *Leptanthura*). In most species in these genera, under both light and scanning microscopy, pleomere 6 and the telson are clearly separated from one another dorsally by a deep groove (Poore and Lew Ton, 1988b, fig. 11a) and, using forceps, the telson can often be flexed against the sixth pleonite. This groove is often shown in drawings and electron micrographs of anthurideans (Fig. 12). Even in some species in which pleonites 1–5 are fused (medially or entirely), the sixth pleonite may appear free (*Haliophasma geminata*).

To resolve this issue, we sectioned specimens

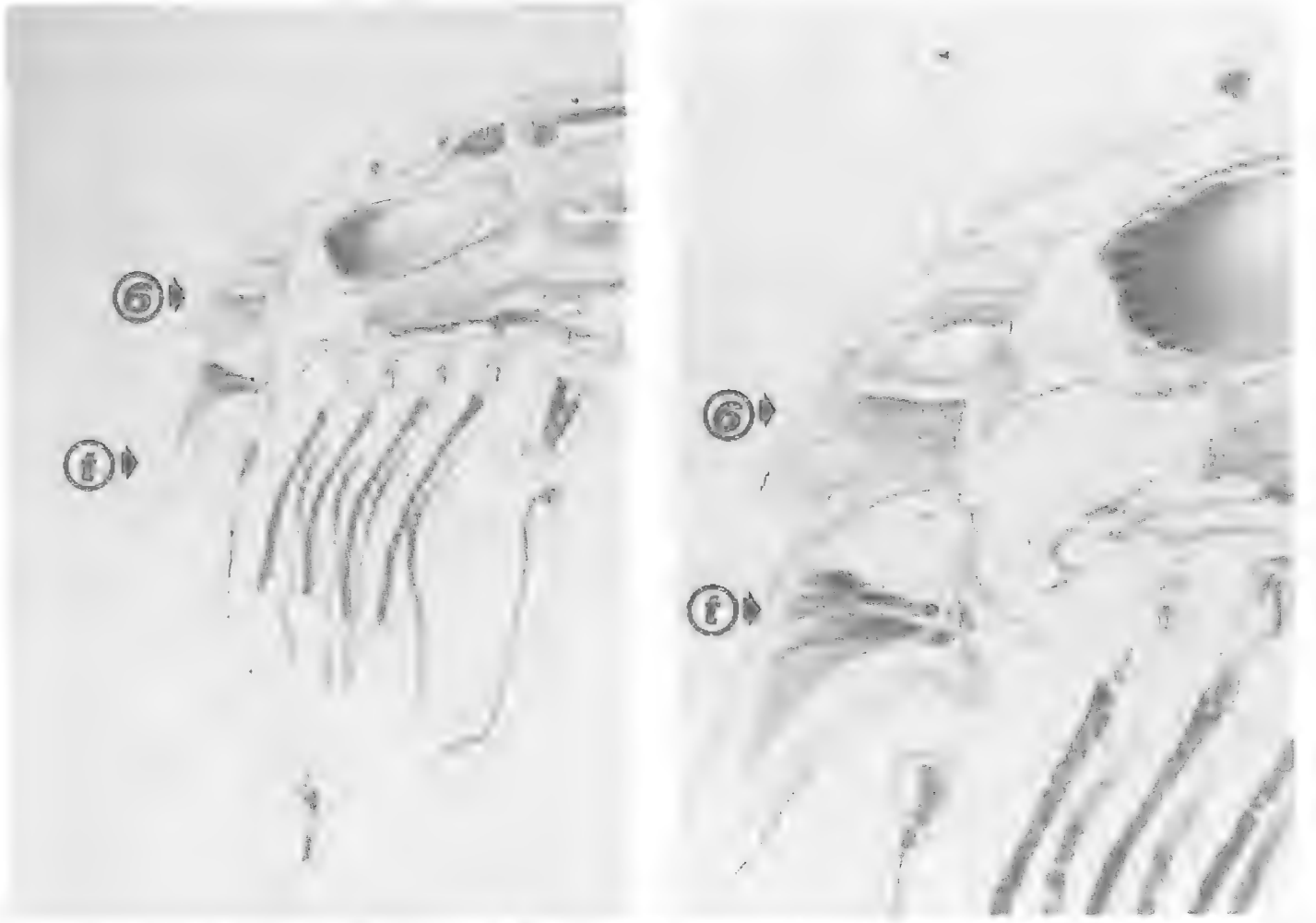

FIG. 13. *Paranthura elegans* (Anthuridea). Median saggital section through pleon showing fusion of pleomeres 5 and 6, and fusion of pleomere 6 with telson. Despite fluting, a continuous cuticular covering connects these somites and no articular membranes are present. Also note large opercular first pleopods. Arrows indicate pleomere and telson.

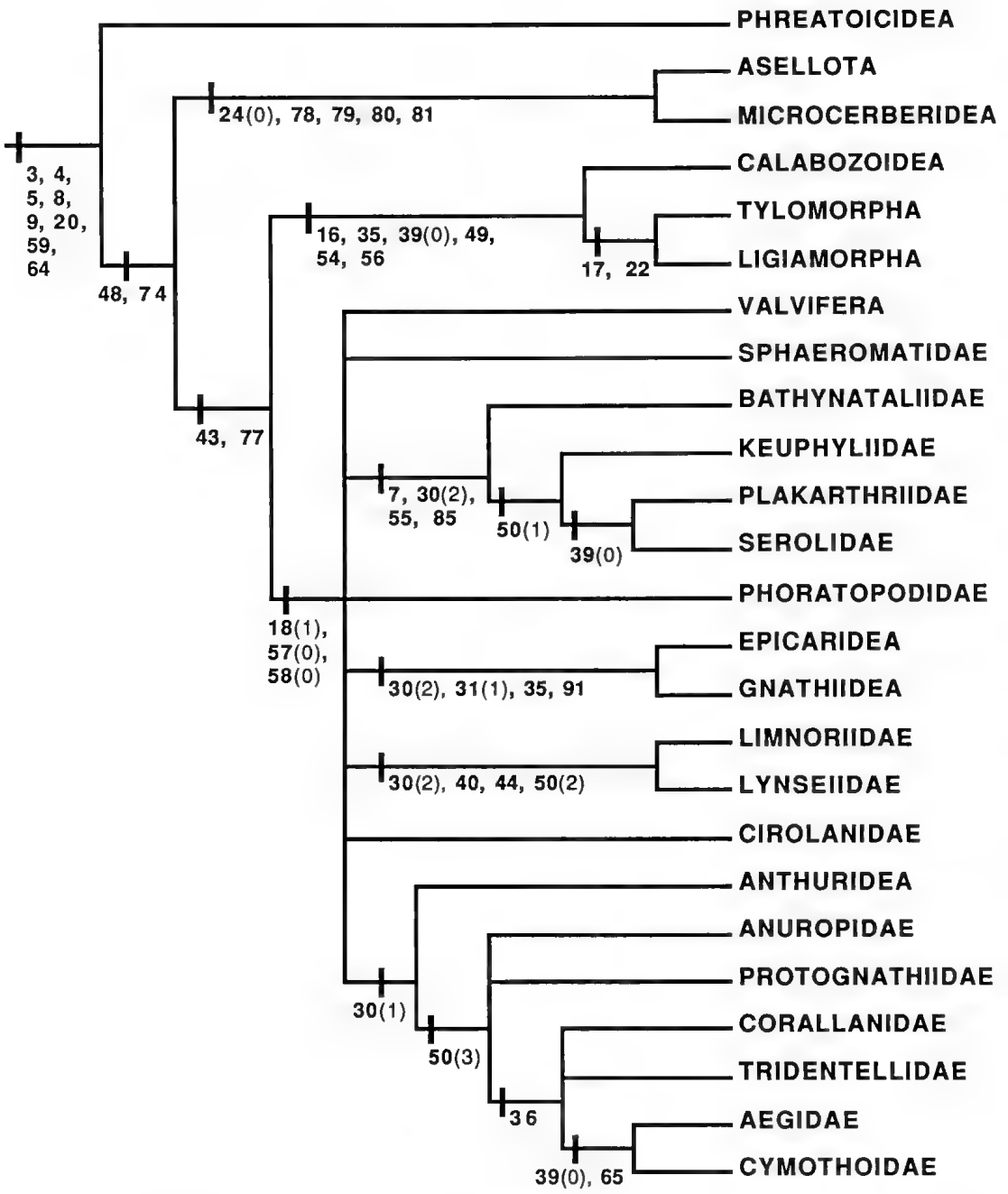

FIG. 14. Cladogram of the Isopoda (Nelson strict consensus tree, built from 16 equal-length trees). Length = 133; C.I.=0.75. Character numbers on tree correspond to character list in Appendix I. Synapomorphies of terminal taxa are not shown on tree (see Appendix III).

of *Paranthura elegans* a species common in San Diego Bay. Under SEM and light microscopy, this species appears to possess a free sixth pleomere. However, our longitudinal sections show unequivocally that no articular membrane is present between the telson and the sixth pleonite (Fig. 12). In fact, the cuticle is even thicker in the region of fusion than it is elsewhere

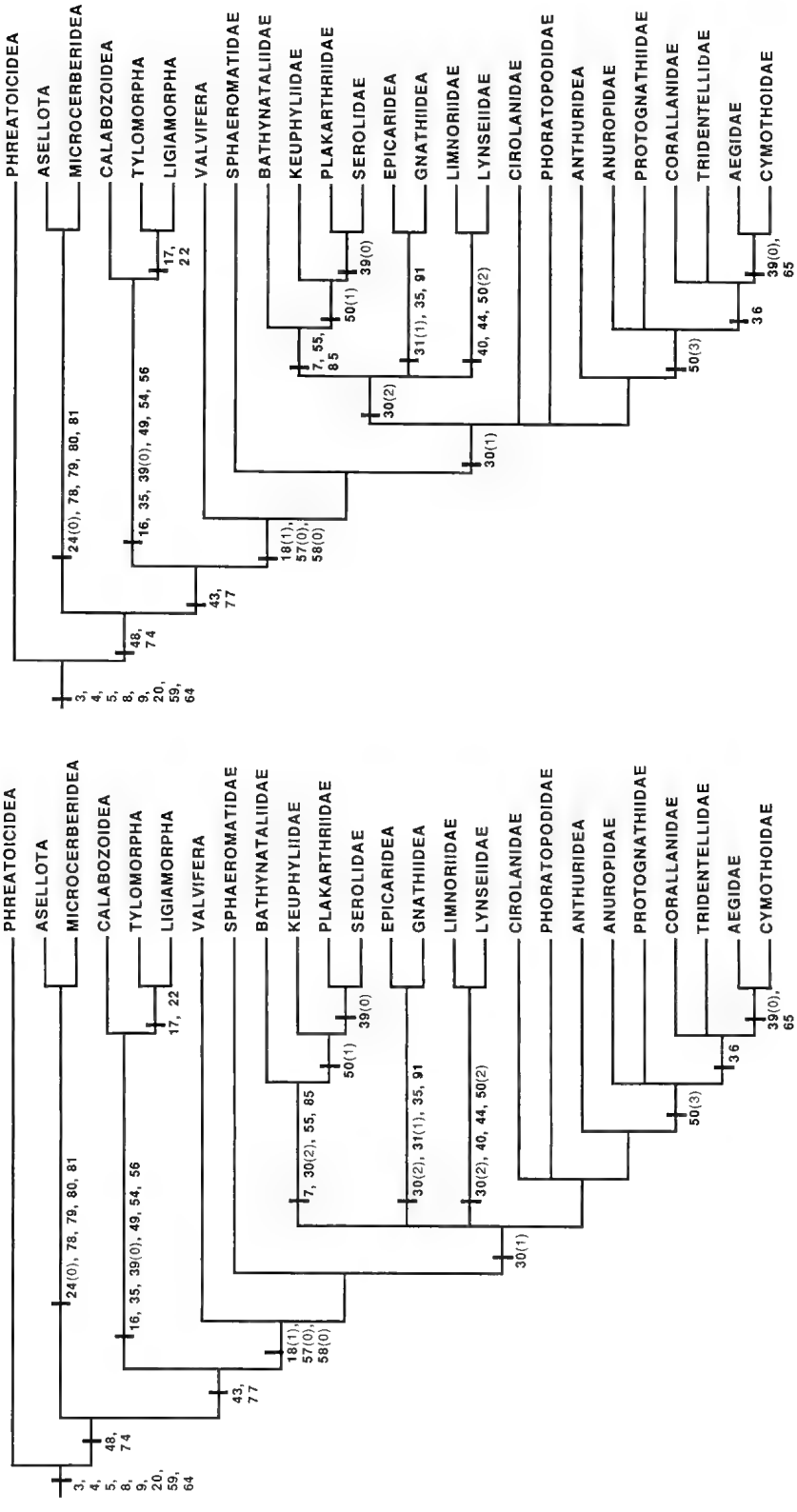

FIG. 15. Two of the 16 equal-length trees from which the consensus tree (Fig. 14) was constructed. These trees emphasize mandibular features (characters 27–30, 35, 50, 91) over character 39 (maxillipedal endite with *vs.* without coupling spines). Both trees are 129 steps long, with a C.I. of 0.78 (0.67 excluding uninformative characters).

on the pleon. Although specimens of *Paranthura* have some flexibility between these two segments, this is apparently due to the deep fluting of the cuticle at the area of fusion, and not due to a true articular membrane. This fluting is what creates the deep dorsal groove that is so visible in this, and presumably other, species. Hence, unless additional observations of other species indicate otherwise, we take the conservative approach and assume that anthurideans also possess a pleotelson.

Although fusion of pleomere 6 to the telson occurs in some species in at least four peracarid suborders (tanaids, cumaceans, thermosbaenaceans, isopods), it appears to have been derived independently in three, if not all four, of these groups. Only in the Isopoda do all species possess a pleotelson. Character 64 is: pleomere 6 freely articulating with telson (0); pleomere 6 always fused with telson, forming a pleotelson (1). Only isopods are scored (1).

RESULTS AND DISCUSSION

Analysis Procedure

Our analytical strategy was as follows. We assembled a data set based on the character analyses described above, and input data files were generated for HENNIG86, PAUP, and MacClade. The data were first analysed with PAUP and HENNIG86. A pool of multiple, equal-length trees was studied and all homoplasous characters were reassessed. Several characters were eliminated from the analysis at this stage because they were simply too high in homoplasy and/or their precise homologies seemed questionable, e.g, sternal coxal plates. The final character list (the numbered characters noted in the previous section) and OTU-character data matrix are provided in Appendices I and II.

Trees were first constructed with the characters polarised as indicated in the descriptive character analysis above. However, it quickly became evident that, due to high homoplasy levels (especially reversals) unambiguous judgments could not be made regarding character state transformations. Hence, the final analyses were done with all characters unpolarised, i.e. programs set to nonadditive, and allowed to change in any direction. This procedure makes no assumptions as to what the primitive or derived states are for any characters in the data set. In respect for the high levels of homoplasy inherent in such a large data set (especially for arthropods), comparisons of trees generated from ordered and unordered characters is an informative and cautious approach. In fact, binary characters are treated no differently in additive (ordered) *vs* nonadditive (unordered) analyses (unless such a program option is specifically selected); the only way in which the nonadditive analysis differs from the additive one is in its effect on multistate characters. The nonadditive analysis counts any character state change equally, as a single step, e.g. for a multistate character, a change from state 0 to state 2, or state 2 to state 0, is still counted as one step.

The non-additive analysis using the branch swapping algorithm of HENNIG86 (mhennig + bb) found 16 equally short trees (length = 129 steps; C.I. = 0.78). The Nelson strict consensus tree of these 16 trees is 133 steps long (C.I. = 0.75) and is shown in Fig. 14. This tree could not be improved by application of the successive character weighting method to the suite of 16 trees from which it was derived. These results were verified by analysing the data with PAUP 3.0. The PAUP analysis, using the MULPARS option, found the same 16 trees and produced an identical strict consensus tree. All statistics were identical for the PAUP and HENNIG86 trees.

Our final data set and consensus tree were coded into MacClade format, along with the trees of Wägele (1989a), Schmalfuss (1989), and others. MacClade was used to examine the effects on tree parsimony and character placement of different tree topologies generated by manual branch swapping, and to determine precisely how other trees differed from our own by graphically tracing character state changes for each character.

The Cladogram of Isopods

In the following discussion, character numbers (see appendix I) are indicated parenthetically in boldface. Synapomorphies defining terminal taxa are not shown on the tree (Fig. 14), but are listed in Appendix III and were noted in the previous section (character discussions). In our consensus tree (Fig. 14), the Phreatoicidea unambiguously arises as the basal most node, retaining two key symplesiomorphies that are lost in virtually all other isopod suborders: coxal penes (48) and the large row of filter setae on the medial margins of the maxillae (74). The notion that phreatoicids might represent an ancient isopod group was first advanced by Chilton (1883) and repeated by several other workers in the early part of this century. However, the specific hypothesis that Phreatoicidea are the most primitive living isopods has apparently

been previously suggested only by Schram (1974). Synapomorphies defining the Phreatoicidea include the upturned pleotelson (72) and elongate fifth pleomere (73). The most parsimonious tree depicts the loss of the antennal scale (25) at the origin of the isopod line, with its reappearance in the Asellota. An alternative, but less parsimonious scenario posits the loss of the antennal scale three times — in the Phreatoicidea, the Microcerberidea, and above the asellote-line in the cladogram.

The Asellota-Microcerberidea and Oniscidea-Calabozoidea lines arise next. The asellotans and microcerberids are sister groups. Among other things, they share the interesting attribute of a 6-articulate antennal peduncle (24), a feature that also occurs in mysidaceans, but is not seen in amphipods, mictaceans, tanaids, or any other isopod group. They also share the following additional synapomorphies: females lack first pair of pleopods (78); male second pleopods with a small non-lamellar exopod and a large endopod modified into a complex gonopod (79); pleomeres 1 and 2 free, 3–5 fused to pleotelson (80); and, male pleopod 1, if present, uniramous (fused and working with the second pleopods in sperm transfer in the higher Asellota) (81).

All isopod taxa beyond the Asellota-Microcerberidea line are distinguished by the presence of lateral coxal plates (43) and the absence of 2-articulate exopods on all pleopods (77). The Ligiamorpha and Tylomorpha are sister groups, supporting the contention that the Oniscidea is a monophyletic clade. The Calabozoidea is the sister group of the Oniscidea. (These three taxa are united by at least six synapomorphies: characters 16, 35, 49, 54, 56, and 39-reversal).

All isopod taxa above the oniscidean line are distinguished by three unique features: pereopods 1–3 are directed anteriorly, and pereopods 4–7 are directed posteriorly (18); the telsonic region of the pleon is greatly elongated, positioning the anus and uropod articulation anteriorly on the pleotelson (58); and, the uropods are broad and flat (not styliform) (57). We refer to these taxa as the 'long-tailed' isopods.

The relationships of the long-tailed isopod taxa cannot be unambiguously resolved with our data set. They comprise an unresolved 8-way polytomy on the consensus tree. Each of these 8 lines represents a distinct clade that appeared in all 16 primary trees. These 8 clades are: (1) Valvifera; (2) Sphaeromatidae; (3) Phoratopodidae; (4) Cirolanidae; (5) Epicaridea-Gnathiidea; (6) Limnoriidae-Lynseiidae; (7) a clade of 4 flat-bodied families (Bathnataliidae, Keuphyliidae, Plakarthriidae, and Serolidae); and, (8) a clade of 7 predacious-parasitic taxa, including the Anthuridea and 6 families currently recognised as flabelliferans. The latter clade culminates in the Cymothoidae, hence we refer to this group as the 'Cymothoid-line'.

Greater resolution of the long-tailed clade exists, of course, in each of the 16 primary trees. These 16 trees differed little from one another, and only in regard to subtle rearrangements of the 8 long-tailed lines noted above. If preference is given to mandibular characters (characters 27–30, 35, 50) over those of the maxillipedal coupling spines (character 39), much more resolution is achieved. Figure 15 shows two such trees. In these two trees the Valvifera and Sphaeromatidae are at the base of the long-tailed line. Of the long-tailed taxa, only these two groups retain the primitive grinding mandibular molar process (character 30); all taxa above Valvifera and Sphaeromatidae have a blade-like slicing molar process (or the molar process is lost).

According to our analysis, the ancestral isopod morphology included a very short telsonic region on the pleotelson, positioning the anus and styliform uropods terminally or subterminally on the pleotelson. We refer to the groups that possess this shortened pleotelsonic morphology as the 'short-tailed' isopods (Phreatoicidea, Asellota, Microcerberidea, Oniscidea, and Calabozoidea). This condition also occurs in extant tanaidaceans, although this could represent a parallelism because some fossil tanaidaceans are known to possess elongate telsons (Schram *et al.*, 1986). These short-tailed forms are largely infaunal and are not strong swimmers. Most are herbivores or scavengers.

The shift away from the short-tailed morphology to the long-tailed morphology (elongate telsonic region, positioning the anus and uropods basally on the pleotelson) occurred subsequent to the appearance of the oniscidean line. This reversion to a broad mysid-like tailfan within the Isopoda (characters 57 and 58 on the trees) appears to have corresponded to the emergence of isopods as active swimmers in the water column. However, as we noted earlier, isopods (and other non-mysidacean peracarids) lack the caridoid 'escape behaviour' and do not possess the massive pleonal musculature seen in the true caridoid taxa. Thus, the main effect of 're-invention' of a tailfan in swimming isopods was not

for direct propulsion, but more likely to provide a planar surface or rudder during swimming. We have observed this apparent function in swimming *Bathynomus*, *Cirolana*, juvenile Cymothoidae, and others. Within the long-tailed line, a trend can also be seen for enlargement of the lateral coxal plates. This may serve to increase the hydrodynamic streamlining of the body, perhaps in the same fashion as the enlarged pleura on many swimming caridoid malacostracans. Furthermore, as Hessler (1982) has noted, enlarged lateral coxal plates were impractical in the Asellota (and Phreatoicidea) because the coxae are still mobile in these groups. Also within the long-tailed line is a trend away from primary herbivory (Valvifera) and scavenging (Sphaeromatidae), to active predation and eventually parasitism. Within this lineage, only the Valvifera and Sphaeromatidae retain the primitive grinding mandibular molar process — all other taxa have a mandible modified more for carnivory, with the molar process (when present) modified as a slicing bladelike structure. Hence, emergence from the benthos appears to have been correlated with the evolution of a more active swimming lifestyle and carnivorous habits.

Corroborating evidence for this cladogram comes in the form of embryological and anatomical data from other studies. According to Wägele (1989a) the stomachs of phreatoicids and asellotans are the most primitive of the Isopoda, i.e. with straight, rather than curved, anterior filter channels. In addition, Strömberg (1972) has shown that the embryological median dorsal organs of isopods are of two types, one of which occurs in the Oniscidea, the other being restricted to the long-tailed taxa. Strömberg (1972) also demonstrated that the paired embryological lateral (= dorsolateral) organs of isopods are also of two types, one type in Valvifera, Flabellifera, and Anthuridea, the second type occurring only in Phreatoicidea and Asellota. Furthermore, Hessler (1982) observed that, of the isopods he studied, only the phreatoicids and the Asellota retain a coxa with the primitive capability of promotion/remotion, including an arthrodial membrane and some musculature.

Comparison With Wägele's Hypothesis

Wägele's (1989a) tree (Fig. 4D) is considerably longer than our tree (length = 153, CI = 0.65). However, the two trees share some important similarities. Both trees place the Phreatoicidea at the base of the isopod line. However, Wägele accepted Dahl's (1954) conclusion that phreatoicideans were derived from a cirolanoid ancestor, thus forcing Wägele to derive the short-tailed condition (terminal anus and uropods) in the Isopoda three separate times — in the phreatoicidean line, in the oniscid line, and in his asellote/calabozoidean line. Both our tree and Wägele's derive the Asellota after the Phreatoicidea. However, Wägele concluded that the Calabozoidea is the sister group of the Asellota, whereas we regard the calabozoids to be either primitive oniscideans, or the sister group of the Oniscidea. Both trees also derive the oniscideans above the phreatoicid/asellote lines, and then recognize several large groupings of the remaining taxa (the long-tailed isopods, as we have defined them). Both trees were unable to satisfactorily resolve the relationships of the long-tailed line. Beyond these generalities, our tree differs markedly from that of Wägele.

Wägele's tree (1989a, fig. 107) depicts 9 taxa: Phreatoicidea, Calabozoidea, Asellota, Microcerberidea, Oniscidea, Valvifera, Anthuridea, 'Sphaeromatidea' (*sic*), and 'Cymothoida' (*sic*). Wägele's Sphaeromatidea included 7 flabelliferan families: Keuphyliidae, Lynseiidae, Limnoriidae, Plakarthriidae, Sphaeromatidae, Serolidae, and Bathynataliidae. His Cymothoida included 8 flabelliferan families (Phoratopodidae, Protognathiidae, Anuropidae, Cirolanidae, Tridentellidae, Corallanidae, Aegidae, and Cymothoidae), plus the Gnathiidea and Epicaridea (Wägele reduces the latter suborder to family as the 'Bopyridae'). Wägele's suggested new Suborder Sphaeromatidea was not defined by any unique synapomorphies, but was based on a general suite of body shape criteria that we regard as (1) incorrect, (2) not applicable to all the groups included in this taxon, or (3) also present in other isopod taxa.

We have analysed most of the characters that Wägele used in his tree in our character discussions above, but we have coded/assigned many of them differently (and are thus not in agreement with Wägele's assignments of characters to taxa), or we have opted not to use some of them because we feel they are too poorly understood or are inappropriate due to their high levels of homoplasy at this level of analysis. Many character assignments in Wägele's analysis appear to be incorrect, e.g. the synapomorphic suite used to define his Sphaeromatidea; scoring the phreatoicideans as having laterally compressed bodies; assigning 2-articulate pleopodal exopods to Phreatoicidea but not Asellota; scoring the Asel-

lota as possessing an endopod on pleopod 1 of males; regarding *Rocinela* as having 2-articulate maxillipedal palps and protandric hermaphroditism, or they represent convergences/parallelisms hidden within other character complexes (styliform uropods, shortened pleotelson, vermiform body, etc.).

Wägele (1989a, b) has argued that a hypothetical, primitive, long-tailed morphology in isopods gave way to the short-tailed morphology on numerous occasions, independently, as a convergent adaptation to avoid predation by fishes. Our analysis suggests just the opposite, that the primitive condition in isopods was the short-tailed morphology, inherited from peracarid ancestors that already possessed a trend toward telson reduction and loss of the caridoid tailfan. Furthermore, it is the long-tailed isopods, not the short-tailed species, that are epibenthic and active swimmers and more often confront predatory fishes. The evolution of predator-avoidance strategies in isopods has not been extensively studied, but Brusca and Wallerstein (1979) and Wallerstein and Brusca (1982) provide comparative and experimental data suggesting that, at least for idoteids, they include features such as smaller reproductive size, cryptic colouration and body ornamentation, and certain behavioural traits.

Status of the Calabozoidea

It is evident from our observations of specimens of *Calabozoa pellucida* that it is not an asellotan isopod, but is either a primitive, aquatically-adapted oniscidean, or it is a unique creature closely related to the Oniscidea. Van Lieshout's (1983) and Wägele's (1989a) attempts to unite the Calabozoidea and Asellota were based largely on incorrect homology arguments regarding the pleopods. Although the copulatory part of the calabozoan first pleopod could be the exopod, no one has shown the uniramous pleopods of the Asellota to be either the exopod or the endopod. Furthermore, the detailed structures of the male first pleopod in both taxa are completely different (Fig. 10B *vs.* 10D). The synapomorphies proposed by Wägele for a Calabozoidea-Asellota sister group are incorrect or are symplesiomorphies. For example: a similar telsonic reduction and uropod arrangement occurs in the Phreatoicidea and the Oniscidea (hence these features should actually be symplesiomorphies on Wägele's tree); female asellotans (and microcerberideans) lack the first pair of pleopods (they are present and biramous in *Calabozoa*); and, in asellotan males the second pleopodal endopod is always geniculate (it is styliform in *Calabozoa*). The male first and second pleopods of *Calabozoa* most closely resemble those of oniscideans (Fig. 10). The presence of all 5 pairs of pleopods in female *Calabozoa*, and the absence of a 6-articulate antennal peduncle and the typical asellotan pleonite condition (pleonites 1 and 2 well-developed and usually modified as a narrow ring, pleonites 3–6 fused indistinguishably with telson) further argue against any relationship to the Asellota. In addition, calabozoans possess both dorsally-fused lateral coxal plates and sternal coxal plates, conditions typical of oniscideans but never seen in the Asellota (Table 2).

The pleopod morphology of *Calabozoa* shows many points of similarity to the highly modified copulatory structures found in the oniscideans (Fig. 10, Table 2). Male pleopods 1 and 2 possess elongate styliform gonopods, and the fused median penes arise from the articulation between pereonite 7 and pleonite 1. Furthermore, the pleopodal endopods of *Calabozoa* are somewhat thickened and tumescent as in terrestrial isopods. The adaptations of a primitive oniscidean to an aquatic lifestyle could predictably result in the differences seen between a typical oniscidean and *Calabozoa*. The maxillipeds of *Calabozoa* are very similar to those of the Ligiamorpha. The one feature of *Calabozoa* that distinguishes it from typical oniscideans is its possession of primitive, unmodified, trilobed maxillae. In oniscideans the maxillae are reduced to simple bilobed plates. The totality of these data and the positioning of the Calabozoidea on the cladogram suggest that this group represents either a very primitive, relict, aquatic oniscidean taxon, or a distinct taxon that has persisted from a line that led to the modern oniscideans.

Status of the Microcerberidea

Our analysis suggests a close relationship between the Asellota and the Microcerberidea. The synapomorphies shared between these two taxa include the following: (1) antennal peduncle 6-articulate; (2) female pleopod 1 absent; (3) male pleopod 2 with endopod modified into a complex gonopod; (4) pleomeres 1–2 free, 3–5 fused to pleotelson; and, (5) male pleopod 1 uniramous, if present (fused and working with second pleopods in sperm transfer in higher Asellota).

The Microcerberidea were regarded as anthurideans by Karaman (1933), Pennak (1958), Kussakin (1973), and others. Wägele (1983b,

1989a) reduced the Microcerberidea to a family of the asellote superfamily Aselloidea, along with Asellidae, Stenasellidae, and Atlantasellidae. Wägele's arguments for including the microcerberids in the Aselloidea relied strongly on similarities in the setae of the first pereopod, as well as the characters already mentioned. Similar setae, however, can be seen on the first pereopods of the Phreatoicidea, so setation may not be a synapomorphy at this taxonomic level. As Wägele (1983b) noted, the Atlantasellidae (originally included in the Aselloidea by Sket, 1979) have pleopods similar to the Microcerberidea, in which the second pair is absent in females and the third pair is uniramous and fused into a single piece that is operculate to pleopods 4 and 5 (in both sexes). Atlantasellids and microcerberids also share the unique 'tubular' molar process on the mandible.

We agree with Wägele (1983b) regarding the probable close relationship between *Atlantasellus* and the microcerberids. These two groups differ from each other primarily on the basis of features perhaps associated with body-size reduction and the interstitial habitus in the microcerberids (reduction of the mouth appendages, cylindrical body form), and *Atlantasellus* also bears several unique synapomorphies (inarticulate uropods, reduction of antennae). However, we consider these two groups to be distinct enough from the Asellota that we do not recommend placing them in that suborder, nor do we regard Wägele's (1989a) putative synapomorphies of the superfamily Aselloidea to be justified. All Asellota have a highly evolved male copulatory system, usually with a strongly geniculate endopod on the male second pleopod coupled with a short powerful exopod used for thrusting the endopod. Asellotans also have a distinct scale on the antenna, uniramous second pleopods in females, and a unique spermathecal duct; these features appear to be lacking in Microcerberidea and Atlantasellidae. In the latter taxa, the male second pleopodal endopod is an elongate, convoluted, straight or curved structure, and the exopod is degenerate. In addition, the third pleopod is fused into a single piece in microcerberids and atlantasellids, whereas in most Asellota both rami and the protopod are separate and unfused articles. Many of the attributes seen in microcerberids and atlantasellids constitute reductions, although the male copulatory pleopods of these groups are unlike anything seen in the Asellota.

In conclusion, the most conservative approach would be to simply transfer the Atlantasellidae to the Microcerberidea, allowing this suborder to stand as a sister group to the Asellota *sensu stricto*. We would recommend this working hypothesis until more data are available, particularly regarding the possible presence of the asellotan spermathecal duct in microcerberids and atlantasellids. In addition, we see no justification for the view espoused by Wägele (1983b) that the Microcerberidea evolved from aselloid ancestors in freshwater.

Status of the Protognathiidae

The only two described specimens of *Protognathia* (Schultz, 1977; Wägele and Brandt, 1988) appear to be mancas, although Wägele and Brandt's (1988) definition of the family assumes that the specimens are subadults or adults. The drawing of this animal by Wägele and Brandt (1988, fig. 1) even illustrates what appears to remnants of the embryonic yolk, typical of many isopod mancas. Wägele and Brandt claim that *Protognathia bathypelagica* Schultz, 1977, is a 'missing link', or 'intermediate between' the Cirolanidae and the Gnathiidea. Based on the published illustrations, we do not believe that Wägele and Brandt (1988) were actually dealing with the same species as Schultz (1977). In any case, in our opinion *Protognathia* only superficially resembles the Gnathiidea and more closely approximates the manca of a large, predatory, cirolanid-like or anuropid-like creature. The 'articulating', serrate, bladelike molar process on the mandible of *Protognathia* is characteristic of the Cirolanidae and the cymothoid-line, and this was no doubt the principal reason for Schultz's (1977) original assignment of *P. bathypelagica* to the genus *Cirolana*. The general body aspect is also similar to juveniles of the genus *Syscenus* (Aegidae), another flabelliferan family in the cymothoid-line.

The proposed Gnathiidea-*Protognathia* synapomorphies of Wägele and Brandt (1988) do not hold. First, the absence of the seventh pereopod and the expandable ventral cuticle is typical of isopod mancas. Second, the tailfan is identical to that of some cirolanids and aegids. Third, the mandible of *Protognathia* is not at all like that of the Gnathiidea, despite the possible similarity in function (predatory feeding). Homology arguments based on function alone should be viewed with caution. In fact, the mandible of *Protognathia* has features typical of Cirolanidae/Anuropidae (the articulated, serrate, bladelike molar process) and the cymothoid-line

in general (the acute bladelike incisor process of tridentellids, corallanids, aegids, and cymothoids). Fourth, the maxillae of *Protognathia* are quite different from those of gnathiids, in which they are highly reduced (males) or absent (females). The only derived feature that might be uniquely shared between *Protognathia* and the gnathiids is the plumose setation on the maxillipeds. *Protognathia*, however, has a similar setation on all of the other thoracopods as well, which is quite unlike the situation in gnathiids, suggesting that the maxillipedal setation of *Protognathia* is merely a reflection of segmental parallelism (or serial homology) in this animal and not a homologous synapomorphy shared with the gnathiids. Finally, gnathiids have but 5 pairs of walking legs, 6 free pereonites, 2 pairs of maxillipeds, and numerous other fundamental differences that suggest no close alliance whatsoever to *Protognathia*.

The above evidence forces us to conclude that *Protognathia* shares no synapomorphies with the Gnathiidea. Our phylogenetic analysis corroborates these arguments and further suggests that *Protognathia* is part of the cymothoid-line. The mandibles of *Protognathia* and *Anuropus* are enlarged and have similar 'articulations', being oriented more transversely and ventrally than in most isopods, suggesting a possible close affinity between these two groups. The large size of the pelagic *Protognathia* manca is also suggestive of *Anuropus*, which may attain an adult size in excess of 70mm (a 6.6–13.0mm manca could fit within an anuropid developmental sequence). Better resolution of protognathiid affinities must await the capture of adults of this group. Certainly Wägele and Brandt's (1988) claim that *Protognathia* is a 'surviving primitive isopod' is not correct; in both Wägele's (1989a) and our own tree, this taxon derives high up in the flabelliferan line.

Status of the Flabellifera

Our analysis corroborates the hypothesis of Wägele (1989a) and others that the Flabellifera, as it is currently recognised by most workers, is not a monophyletic taxon. The Anthuridea, Gnathiidea, and Epicaridea appear to derive from within the flabelliferan complex. However, the two suborders proposed by Wägele, Cymothoida and Sphaeromatidea, are not supported by our analysis.

Poore's (1987) proposed sister group relationship between the Lynseiidae and the Limnoriidae is corroborated by our analysis. The unusual South Pacific genus *Hadromastax* is currently placed in the family Limnoriidae. However, as Bruce (1988) noted, it appears to lack two key limnoriid attributes — a waisted maxillipedal basis and hook-like uropodal rami. Bruce and Müller (pers. comm.) plan to remove this genus to its own family. However, judging by the mandibular anatomy and other features, *Hadromastax* appears to be very closely related to the Limnoriidae/Lynseiidae clade.

The close relationship shown in our cladogram between Gnathiidea and Epicaridea is interesting and suggests that the possible common ancestor of these two groups might have been a hematophagous parasite. In addition to the synapomorphies noted on the cladogram, only in these two groups of isopods are the digestive caeca reduced to a single pair (Strömberg, 1972). Strömberg (1967, 1971, 1972) also recognised close ties between epicarideans, gnathiids, and flabelliferans, based on embryological data. Wägele's (1989a) alliance of the Epicaridea with the Cymothoidae appears unjustified. He united these taxa on the basis of five characters. Two of these characters are incorrect — epicarideans are not protandric hermaphrodites (they are facultative hermaphrodites) and cymothoids do not have quadrate uropodal peduncles. The third character, 'adults parasitic', is unlikely to be a homologous feature because cymothoids are parasites only on fishes and epicarideans only on crustaceans. The remaining two characters are apparent convergences (discussed in the previous section) resulting from the parasitic lifestyle of these taxa — hooklike pereopodal dactyls and reduced antennae. Retaining the Epicaridea as a separate suborder (or infraorder) has the further distinct advantage of not compressing the broad diversity of this group into a single highly heterogeneous family, as proposed by Wägele (1989a).

Recognition of the close relationships within a cymothoid-line (Fig. 14) is not a new idea. Brusca (1981) analysed this relationship for four of these families, and Bruce *et al.* (1982) and Delaney (1989) elaborated on this. The cymothoid-line (Fig. 14) is primarily carnivorous, emphasising predation and scavenging early on (Cirolanidae and Anthuridea), then largely predation (Anuropidae, Corallanidae, and probably Protognathiidae), then obligate predation or temporary parasitism (Aegidae and Tridentellidae), and finally obligate hematophagous parasitism (Cymothoidae).

We did not postulate any synapomorphies for

the family Sphaeromatidae, although four possible ones exist: pleonites 1–2 free (primitively), pleonites 3–6 fused to telson (with 0–3 pairs of lateral incisions demarcating fused somites); uropodal endopod more-or-less fused to peduncle and immovable; at least some maxillipedal palp articles expanded into lobes; and, pleotelson vaulted, with pleopods held in chamber. In addition, in most sphaeromatid genera at least some pleopods bear pleats and unique squamiferous tubercles. However, because this family is so large and poorly understood, it is unclear whether these features represent true synapomorphies, i.e. are primitive for the family. A cladistic analysis and taxonomic revision of the Sphaeromatidae is greatly needed.

Some flabelliferan groupings are not fully resolved in our tree, suggesting that some families may be paraphyletic or, more likely, that we have simply been unable to find satisfactory character suites to eliminate all polytomies. This does not, however, affect the basic structure of the tree, or the sister group relationships of the clades that depict the phylogeny of the group as a whole.

If the relationships in our tree (Fig. 14) are correct, the Flabellifera should be expanded to once again include the Anthuridea, Gnathiidea, and Epicaridea, or it should be split into several separate new groupings. However, because of the unresolved nodes we do not recommend a classificatory change in the Flabellifera at this time. There seems little doubt, however, that the anthurideans, gnathiids, and epicarideans are derived from deep within the currently recognised Flabellifera. Classifying these three groups within the Flabellifera is not, of course, a new idea. Indeed, Sars (1882) created the group 'Flabellifera' specifically for those isopods with tail-fans composed of lateral uropods and an elongate pleotelson (hence the name). Stebbing (1893), Sars (1897), Richardson (1905), Smith and Weldon (1923), Menzies (1962), Naylor (1972), and many others generally followed Sars' concept of Flabellifera, and included the anthurideans (and usually the gnathiids) in this group. Sars (1897) was quite correct in his summary of the situation nearly 100 years ago, when he stated, 'It is not easy to give any exhaustive diagnosis of this tribe (Flabellifera), as it comprises isopods of extremely different structure. The only essential character common to all the forms, is the relation of the uropods, which are . . lateral and arranged in such a manner as to form, with the last segment of the metasome, a caudal fan, similar to that found in some of the higher Crustacea, the shrimps and lobsters.' The only synapomorphy we can add to Sars' statement is the fact that a 3:4 functional percopod grouping seems to have evolved in concert with the long-tailed condition, and shortly thereafter the blade-like mandibular molar process.

Unresolved Phylogenetic Problems

Although we recommend some taxonomic changes (see conclusions), we do not propose a new classification of the entire order at this time. We feel that our phylogenetic hypotheses are still not robust enough to do so — the precise phylogenetic placement of several groups cannot yet be resolved to our satisfaction. Specifically, the relationships of the 8 long-tailed clades depicted in the consensus tree (Fig. 14) remain somewhat enigmatic. We believe Wägele (1989a) was premature in proposing his radical new classification of the Flabellifera. Because the long-tailed clade represents what appears to be a clearly monophyletic and easily-recognised group, with correlated anatomical and ecological attributes, we suggest that classificatory recognition of this clade is warranted and desirable.

Other Possible Tree Topologies

Because many workers have emphasised a hypothetical cirolanid-like (or flabellifera-like) ancestor for the Isopoda, we built several alternative trees to compare to ours. Each of these alternative trees was analysed with the program MacClade, with the same data set used to construct our tree (Appendices I and II). Trees identical to our cladogram (Fig. 14), but with the Cirolanidae placed at the base, are 135 steps long. Trees with the entire long-tailed grouping placed at the base, rooted in the Cirolanidae are 135 steps long. Trees with the long-tailed line at the bottom, but otherwise with the taxa in that group arranged exactly in our tree are 131 steps long. All of these trees are longer and less parsimonious than the 16 shortest trees (129 steps) summarised in our consensus tree (Fig. 14). It should be noted that if trees just one step longer are included for consideration, it can require that several hundred to several thousand new and different tree arrangements be considered. Thus selection of the shortest tree, even if it is shorter by only one step, allows one to reject entire suites of alternative hypotheses. The ability to rule out these large suites of alternative trees is, of course, the strength of the method of logical parsimony.

Biogeographic Considerations

Our analysis suggests that the Phreatoicidea and Asellota derived early in the evolution of the Isopoda, and are the most primitive living isopod taxa. According to Wägele (1981, 1983b), the occurrence of some members of these two groups in fresh water suggests that their common ancestor was a freshwater form, and that perhaps the Isopoda as a whole arose in fresh water, the marine environment having been invaded later. A more reasonable view, however, considers multiple invasions of fresh water from ancient marine stocks. There are several good reasons to accept this second alternative. First, the invasion of freshwater habitats has obviously occurred many times in the past, as evinced by the many unrelated isopod taxa that live in these habitats today, representing at least some genera in every suborder except perhaps the Gnathiidea (in addition to phreatoicideans, asellotans, and microcerberids, freshwater species occur in at least the following genera: Calabozoidea (*Calabozoa*), among the Oniscidea, *Brackenridgia*, *Cantabroniscus*, *Mexioniscus*, *Typhlotricholigioides*, *Xilolaniscus*; among Anthuridea, *Cruregens*, *Curassantiura*, *Cyathura*, *Paranthura*; among Cirolanidae, *Anopsilana*, *Antrolana*, *Bahalana*, *Bermudalana*, *Cirolanides*, *Faucheria*, *Haptolana*, *Mexilana*, *Specicirolana*, *Sphaeromides*, *Turcolana*, *Typhlocirolana*; among Cymothoidae, *Artystone*, *Asotana*, *Braga*, *Lironeca*, *Nerocila*, *Paracymothoa*, *Philostomella*, *Riggia*, *Telotha*; among Sphaeromatidae, *Sphaeroma*, *Thermosphaeroma*; among Valvifera, *Austridotea*, *Idotea*, *Mesidotea*, *Notidotea*; among Epicaridea, *Probopyrus*; and many others).

Second, fossil evidence (Schram, 1970, 1974) indicates that the Palaeozoic phreatoicideans, which are nearly indistinguishable from modern taxa, lived in marine environments, not freshwater habitats. Modern Phreatoicidea and Asellota that live in freshwater are likely to be relics of a past time when these groups were diversifying and invading many different environments. Outgroup data also suggest that the Isopoda probably evolved in a marine environment, because amphipods, mictaceans, and tanaidaceans are all primary marine groups. The fossil record is very sparse for isopods. There are no known asellotan fossils. The oldest isopod fossils are phreatoicideans: *Hesslerella shermani* Schram, 1970, from middle Pennsylvanian marine deposits of North America; Permian fossils from several marine or brackish-water localities of Laurasia; and Triassic material from Australia (fresh water). Thus, although phreatoicideans are restricted today to freshwater habitats in South Africa, Australia, New Zealand, and India, they must have had a broad global marine distribution during the Paleozoic. A few flabelliferans and presumed epicarideans are known from Mesozoic strata, while oniscideans and valviferans have been found only in Tertiary (Oligocene) deposits.

Very few specific biogeographic relationships reveal themselves in an analysis at this level. However, there are two striking patterns that are evident. First is the strong Gondwanan ties of the long-tailed clade. Many of the long-tailed lines are strictly or primarily Southern Hemisphere in distribution: Keuphyliidae is known only from the Australian region; Bathynataliidae from the southern Indian Ocean and Australia; Plakarthriidae from the Southern Hemisphere; Phoratopodidae from southern Australia; the Valvifera is probably Southern Hemisphere in origin (Brusca, 1984); and species of Serolidae occur primarily in the Southern Hemisphere. In addition, the majority of species of Cirolanidae and Sphaeromatidae also are probably known from the Southern Hemisphere. Interestingly, the earliest derived Asellota not restricted to fresh water are also largely Southern Hemisphere in distribution (Pseudojaniroidea, Stenetrioidea, and the shallow-water Janiroidean families Paramunnidae and Santiidae).

Secondly, all of short-tailed lines on the cladogram show strong relictual patterns of distribution. The Phreatoicidea, which were once widespread globally in marine environments, are now restricted to a few Gondwanan freshwater habitats. The higher Asellota (Janiroidea) are found primarily in the deep sea, where they have undergone a massive radiation to exploit an environment only recently invaded by other isopod groups. The Microcerberidea are interstitial forms. The Calabozoidea so-far are known only from freshwater wells (phreatic systems) in Venezuela. And the Ligiamorpha and Tylomorpha are, of course, the only crustaceans to have successfully radiated into all terrestrial environments.

Beyond these generalisations, the data are not yet available to discern clear historical patterns or test specific biogeographical hypotheses at the subordinal/family levels. Testable phylogenetic and biogeographic analyses are needed for each suborder, and each of the long-tailed clades, in order to determine putative ancestral geographic ranges for each of these groups (viz. Brusca, 1984) before more general statements can be

made regarding the biogeographic history of the Isopoda.

Future Research

Despite an extensive examination of available morphological characters, it is clear that the available data base needs to be expanded by the addition of new characters and by resolution of homology complexes in others. Useful new characters almost certainly exist in patterns of frontal lamina and clypeus design, details of mandibular anatomy (especially of the lacinia and spine row region), oostegite morphology, nature of the sternal coxal plates, and internal anatomy, but the existing literature is insufficient to assemble a data base on such features and additional direct observations are necessary. These data will be needed to further resolve the relationships within the long-tailed isopod clade. A phylogenetic analysis of the Sphaeromatidae is also needed and would provide valuable information for continued refinement of the flabelliferan taxa.

CONCLUSIONS

1. The Isopoda is a monophyletic group defined by the following synapomorphies: (a) sessile eyes; (b) complete loss of free carapace folds (carapace reduced to a cephalic shield); (c) thoracopods entirely uniramous; (d) antennae uniramous, without a scale (a 'scale' has either reappeared in the Asellota, or it was lost twice, once in the Phreatoicidea and again in all other non-Asellota); (e) pleomere 6 fused to telson, forming a pleotelson; (f) biphasic moulting; (g) heart thoraco-abdominal; (h) branchial structures abdominal; (i) gut tube entirely ectodermally derived, without a true midgut region; (j) striated muscles with unique myofibril ultrastructure; (k) loss of the maxillulary palp; (l) antennules uniramous, without a scale (scales reappear in the cirolanid genus *Bathynomus*, in the Limnoriidae, and perhaps in the Epicaridea); and, (m) uropodal rami always uniarticulate. Synapomorphies 'a–d' appear to be convergent in isopods and amphipods, although a strong corroboration of this must await further analyses of all peracarid suborders. Synapomorphy 'e' may (or may not) be convergent to the condition in many tanaidaceans. Synapomorphies 'f–m' are unique to the Isopoda.

2. The Phreatoicidea is the earliest derived taxon of living isopods.

3. The Microcerberidea is the sister group of the Asellota, but cannot be considered part of the Asellota unless the definition of the latter is expanded, which we do not recommend at this time.

4. The Oniscidea constitutes a monophyletic group.

5. The monotypic taxon Calabozoidea (*Calabozoa*) should be classified as primitive Oniscidea, or as the sister group of the Oniscidea (*Calabozoa* is neither an asellotan nor a sister group of the Asellota).

6. Isopods with broad, flat uropods and elongate telsonic regions (well-developed tailfans) arose subsequent to the appearance of the phreatoicid/asellote/microcerberid/oniscidean lines. The apparent 'caridoid'-like tailfan of these long-tailed isopods is thus not a primitive isopod feature, but is secondarily derived within the Isopoda and not homologous with the condition seen in the mysidaceans and other true caridoid crustaceans

7. The evolution of the long-tailed morphology may have corresponded with the emergence of isopods from infaunal environments and a subsequent radiation as active epifaunal swimmers. Paralleling this trend was a shift from a primary scavenging/herbivorous lifestyle to active predatory habits, and eventually parasitism. Also paralleling this trend was an enlargement of the lateral coxal plates, perhaps functioning to increase hydrodynamic streamlining of the body.

8. Three taxa usually ranked at the subordinal level (Anthuridea, Gnathiidea and Epicaridea) had their phylogenetic origins within the lineage of families currently regarded as Flabellifera. Thus, the definition of Flabellifera must either be expanded to accommodate these taxa, and/or the suborder Flabellifera should be reorganised into several separate groups.

9. The Protognathiidae is part of the 'cymothoid-group' of families and may be closely related to the families Cirolanidae and Anuropidae. The Protognathiidae is not the sister group of the Gnathiidea.

10. The recently proposed new suborders of Wägele (1989a), Sphaeromatidea and Cymothoida (*sic*), are not corroborated by our phylogenetic analysis. Wägele's proposition that the ancestral isopod was a long-tailed form (flabelliferan, or cirolanid-like) is not supported by our analysis. Our analysis indicates that the ancestral isopod was a short-tailed form, with a shortened telson and styliform, terminal uropods. The Gnathiidea and Epicaridea should be retained at the subordinal ranking until further analyses bet-

ter resolve the relationships of the flabelliferan families.

11. All of the primitive, short-tailed isopod taxa (Phreatoicidea, Asellota, Microcerberidea, Oniscidea, Calabozoidea) exhibit what may be viewed as relictual distributions, in isolated freshwater habitats, in ground waters, in the deep sea, or in terrestrial habitats. The most primitive living isopods, the Phreatoicidea, also have the oldest known fossil record (middle Pennsylvanian) and a modern Gondwanan distribution (Australia, Tasmania, New Zealand, southern Africa, and India). However, fossil phreatoicids are known from North American and European marine deposits, suggesting that the present-day freshwater Gondwanan pattern is a relict distribution.

12. Unambiguous sister group relationships cannot be hypothesized for all isopod taxa with the current data base, and additional data are being sought in the form of new characters. A new formal classification of the Order Isopoda must await better resolution of the phylogeny based upon an expanded data set.

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APPENDIX 1. CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

1. Eyes stalked and basally articulated (0) — Eye stalks reduced, lobe-like, but sometimes with basal articulation (1) — Eyes sessile (2).
2. Carapace covers all 8 thoracomeres and laterally covers the bases of the maxillae and maxillipeds (0) — Carapace reduced, lateral carapace folds still cover the bases of the maxillae and maxillipeds (1) — Carapace reduced to only a head shield, without lateral carapace folds (2).
3. Monophasic moulting (0) — Biphasic moulting (1).
4. Heart entirely thoracic (0) — Heart thoraco-abdominal (1).
5. Branchial structures cephalo-thoracic (0) — Branchial structures abdominal (1).
6. Pleomeres 4–6 not divided into two separate functional units (0) — Pleomeres 4–6 forming a functional unit (the urosome), and pleopods 4, 5, and 6 modified as uropods (1).
7. Body not unusually broadened and flat (0) — Body extremely broadened and flat, with large, expanded coxal plates, and with the cephalon deeply immersed in or surrounded by the first pereonite (1).
8. Gut tube with endodermally derived midgut (0) — Gut tube entirely ectodermally derived, without a true midgut region (1).
9. Striated muscles of typical malacostracan type (0) — Striated muscles with unique myofibril ultrastructure (1).
10. Second thoracomere (pereonite 1) free, not fused to cephalon (0) — Second thoracomere entirely fused to cephalon, with its appendages (the pylopods) functioning with the cephalic appendages and acting as a second pair of 'maxillipeds' (1).
11. At least some thoracopods with exopods (0) — Exopods absent from all thoracopods (1).
12. Hatching stage not a manca (0) — Hatching stage a manca (1).
13. Without a praniza stage (0) — With a praniza stage (1).
14. Adult females bilaterally symmetrical (0) — Adult females with loss of symmetry (1).
15. Adults not parasitic on other crustaceans (0) — Adults obligate parasites on other crustaceans (1).
16. Without cuticular tricorn sensilla (0) — With cuticular tricorn sensilla (1).

17. Without complex compound sensillar structures of the oniscidean type at the tips of the antennae and uropodal rami (0) — Complex compound sensillar structures at the tips of the antennae and uropodal rami (1).
18. No functional pereopodal grouping (0) — Functional pereopodal grouping 3:4 (1) — Functional pereopodal grouping 4:3 (2) — Functional pereopodal grouping 2:5 (3).
19. Seventh pereonite present and with pereopods (0) — Seventh pereonite reduced and without pereopods (1).
20. Antennule biramous, or with scale (0) — Antennule uniramous, without scale (1).
21. Antennular peduncle 3-articulate with an undivided third article (0) — Antennular peduncle 4-articulate, presumably by way of subdivision of third article (1).
22. Antennules arise above (anterodorsal to) antennae (0) — Antennules arise on same plane as antennae, directly between them (1).
23. Antennules not as described in the following (0) — Antennules greatly modified, 2-articulate, with second (distal) article greatly expanded and scalloped (1).
24. Antennal peduncle 6-articulate (0) — Antennal peduncle 5-articulate (1).
25. Antennae biramous, or with a vestigial second ramus or scale (0) — Antennae uniramous, without vestigial second ramus or 'scale' (1).
26. Antennae well developed (0) — Antennae vestigial (1).
27. Mandible without lamina dentata (0) — Mandible with lamina dentata (1).
28. Mandibles 'normal' (0) — Mandibles of adult males grossly enlarged, projecting anteriorly, forceps-like (1).
29. Mandibles present in adult females (0) — Mandibles lost in adult females (1).
30. Molar process of mandible a broad, flat, grinding structure (0) — Molar process of mandible an elongate, thin, blade-like, slicing structure (often attached to body of mandible by a flexible 'articulation', and often bearing marginal denticles or teeth) (1) — Molar process of mandible absent (2).
31. Maxillule present (0) — Maxillule reduced or vestigial in adults (1) — Maxillule lost in adults (2).
32. Maxillule with a palp (0) — Maxillule without a palp (1).
33. Maxillae not fused to paragnath (0) — Maxillae reduced, minute, fused to paragnath (or lost entirely) (1).
34. Maxillae outer lobe undivided (0) — Maxillae outer lobe divided into two lobes (1).
35. Mandible with a palp (0) — Mandible without a palp (1).
36. Maxillae not modified as follows (0) — Maxillae modified into stylet-like lobes with recurved apical (hooklike) setae (1).
37. Maxillipeds separate (0) — Left and right maxillipeds fused together (1).
38. Coxae of maxillipeds not fused to head (0) — Coxae of maxillipeds fused to head (1).
39. Maxillipedal endite without coupling spines (0) — Maxillipedal endite with coupling spines (1).
40. Head sunk into first pereonite, flexing dorsoventrally but not freely rotating (left to right) (0) — Head set off from pereon and freely rotating (1).
41. Maxillipeds with 2–3 endites (0) — Maxillipeds with only 1 endite (1).
42. Maxilliped biramous (0) — Maxilliped uniramous (1).
43. Without lateral coxal plates (0) — With lateral coxal plates (1).
44. Basis of maxilliped not elongate and waisted (0) — Basis of maxilliped elongate and waisted (1).
45. With lateral epipods on pereopods (0) — Without lateral epipods on pereopods (1).
46. Without medial epipods on pereopods (0) — With medial epipods on pereopods (1).
47. No special cuticular spermathecal ducts known to occur (0) — Unique spermathecal cuticular organs present (1).
48. Male penes on coxae (0) — Male penes on sternite (1).
49. Penes on thoracomere 8 (0) — Penes on pleomere 1, or on the articulation between thoracomere 8 and pleomere 1 (1).
50. Mandibular incisor process broad and multidentate (0) — Mandibular incisor process with teeth reduced to form serrate or crenulate margin (1) — Mandibular incisor process with teeth lost (or fused ?) to form conical projection with basal 'rasp and file' (2) — Mandibular incisor process modified into recurved or hooklike, acute or subacute, piercing-slicing structure (3).
51. Embryos curve ventrally (0) — Embryos curve dorsally (1).
52. Primary adult excretory organs are antennal glands (0) — Primary adult excretory organs are maxillary glands (1).
53. With narrow, multisegmented pleopodal rami (0) — With broad, flat, 1- or 2-articulate pleopodal rami (1).
54. Male pleopods 1 and 2 not as follows (0) — Male pleopod endopods 1 and 2 (only 2 in Ligiidae) elongate, styliform, and participating together in the copulatory process (1).
55. Uropods arise from anteroventral margin of

pleotelson (0) — Uropods arise on posteroventral surface of pleotelson, in shallow grooves or channels (1).

56. Both pleopodal rami thin and lamellar (0) — Pleopodal exopods broad and opercular; endopods thick and tumescent (1).
57. Uropods broad and flattened (0) — Uropods styliform (1).
58. Telsonic region of pleotelson well-developed, with anus and uropods at the position of pleomere 6 (at the base of pleotelson) (0) — Telsonic region greatly reduced and shortened, anus and uropods positioned terminally on pleotelson (1).
59. Uropodal rami multiarticulate (0) — Uropodal rami always uniarticulate (1).
60. Uropodal exopod not folded dorsally over pleotelson (0) — Uropodal exopod folded dorsally over pleotelson (1).
61. Uropods not modified as follows (0) — Uropods modified as a pair of opercula covering entire pleopodal chamber (1).
62. Uropods not modified as follows (0) — Uropods form ventral operculate chamber covering anal region (1).
63. Uropods unlike pleopods; associated with pleotelson (0) — Uropods directed ventrally; identical to, and functioning with, pleopods (1).
64. Pleomere 6 freely articulating with telson (0) — Pleomere 6 fused with telson, forming a pleotelson (1).
65. Pereopods 2–7 not prehensile (0) — Pereopods 1–3 (or 1–7) prehensile (1).
66. Adults not obligate and permanent parasites on fishes (0) — Adults obligate and permanent parasites on fishes (1).
67. Uropodal endopods not claw-like (0) — Uropodal endopods claw-like (1).
68. Uropodal exopods not claw-like (0) — Uropodal exopods claw-like (1).
69. Pereonite VII not as follows (0) — Pereonite VII tergite indistinct dorsally, shortened and largely or entirely fused to pereonite VI (1).
70. Pleopod 5 not reduced to a single plate (0) — Pleopod 5 reduced to a single plate (1).
71. Uropods not modified as follows (0) — Uropods modified as elongate, clavate structures with reduced rami (1).
72. Apex of pleotelson not curved dorsally (0) — Apex of pleotelson curved dorsally (1).
73. Pleomere 5 not markedly elongate and much longer than all others (0) — Pleomere 5 markedly elongate, manifestly longer than all other pleomeres (1).
74. Medial margin of maxilla with row of large filter setae (0) — Medial margin of maxilla without row of large filter setae (1).
75. Female pleopod 2 biramous (0) — Female pleopod 2 uniramous (1).
76. Male pleopod 2 not as follows (0) — Male pleopod 2 exopod modified to function in concert with large geniculate endopod in sperm transfer (1).
77. Exopods of at least posterior pleopods biarticulate (0) — No pleopods with biarticulate exopods (1).
78. Female pleopod 1 present (0) — Female pleopod 1 absent (1).
79. Male pleopod 2 with lamellar exopod (if present) and endopod either lamellar or modified (0) — Male pleopod 2 with small non-lamellar exopod and a large endopod modified into a complex gonopod (1).
80. Pleomeres not as follows (0) — Pleomeres 1 and 2 free, 3–5 always entirely fused to pleotelson (1).
81. Male pleopod 1 biramous, lamellar (0) — Male pleopod 1, if present, uniramous (fused and working with pleopod 2 in sperm transfer in higher Asellota) (1).
82. Female pleopod 2 present (0) — Female pleopod 2 absent (1).
83. Female pleopod 3 biramous, not fused into a single piece (0) — Female pleopod 3 uniramous and fused into a single piece forming an operculum over pleopods 4 & 5 (1).
84. Male pleopod 2 not as follows (0) — Male pleopod 2 exopod reduced to a simple, 1- or 2-articulate ramus, apparently not involved in copulation or sperm transfer; endopod complex and highly variable in shape, straight, curved, or slightly bent (but not fully geniculate) (1).
85. Lateral coxal plates 2–7 (if present) fused to their respective pereonites and not articulating (0) — Lateral coxal plates 2–7 (if present) not entirely fused to their respective pereonites (1).
86. Pleomeres 1 & 2 not reduced to sternal plates (0) — Pleomeres 1 & 2 reduced to sternal plates only (1).
87. Uropodal rami free (0) — Uropodal rami fused to peduncles (1).
88. Posterior pereopods 'normal' (0) — Posterior pereopods oar-like, with dactyls greatly reduced or absent (1).
89. Body not as follows (0) — Body deeply inflated (1).
90. Not parasites on gelatinous zooplankton (0) — Parasites on gelatinous zooplankton (1).
91. Mandibles not modified as follows (0) — Mandibles modified as elongate scythe-like structures with serrate cutting edge (l).
92. Maxillule not as follows (0) — Maxillule of a single elongate stylet-like lobe, with the apex forming an acute recurved piercing stylet (1).

APPENDIX II. THE DATA MATRIX

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Mysidacea      0000000000 0000000000 0000000000 0000000000 0000000000 0000000000
  0000000000 0000000000 0000?00000 00
Mictacea       11?0000??0 0100000300 0001000000 0101000010 1100100000 1?1000?000
  0000000000 000000?000 0000?00000 00
Tanaidacea     1100000100 0100000200 0000000000 0001000010 1100100100 1110001100
  0000000000 0000000000 0000?00000 00
Amphipoda      2200010000 1000000200 0001100000 0000001000 0110110100 0000001000
  0000000000 0000000000 0000100000 00
Phreatoic.     2211100110 1100000201 0001100000 0101000010 1100100000 1110001110
  0001000000 0110000000 0000?00000 00
Valvifera      2211100110 1100000101 0001100000 0101000010 1110100110 1110000010
  1001000000 0001001000 0000000000 00
Epicaridea     2211100110 1101100100 0001110002 210?100010 1110100102 1110000010
  0001100000 0001001000 0000000000 10
Gnathiidea     2211100111 1110000111 0001100112 110?100010 1110100102 1110000010
  0001000000 0001001000 0000000000 10
Anthuridea     2211100110 1100000101 0001101001 011?000100 1110100100 1110000011
  0001000000 0001001000 0000000000 00
Tylomorpha     2211100110 1100011?01 ?101100000 0101100000 1110100110 1111010110
  0101000000 0001001000 0000000000 00
Ligiamor.      2211100110 1100011?01 ?101100000 0101100000 1110100110 1111011110
  0001000000 0001001000 0000000000 00
Asellota       2211100110 1100000201 0000000000 0101000010 1100101100 1110001110
  0001000000 0001110111 1000?00000 00
Calabozo.      2211100110 1100010201 0?01100000 0101100000 1110100110 1111011110
  0001000000 0001001000 0000011000 00
Microcerb.     2211100110 1100000201 0000100000 010?000000 1100100100 1110001110
  0001000000 0001001111 1111?00000 00
Aegidae        2211100110 1100000101 0001100001 010?010000 1110100103 1110000010
  0001100000 0001001000 0000000000 00
Anuropidae     2211100110 1100000101 0011100001 010?0000?0 1110100103 1110000010
  0011000000 0001001000 0000000011 00
Bathynat.      2211101110 1100000101 ?001100002 0101000010 1110100100 111010?010
  0001000000 1001001000 0000100000 00
Cirolanid.     2211100110 110000010? 000?100001 0101000010 1110100100 1110000010
  0001000000 0001001000 0000000000 00
Coralland.     2211100110 1100000101 0001100001 010?010000 1110100103 1110000010
  0001000000 0001001000 0000000000 01
Cymothoid.     2211100110 1100000101 ?001100001 010?010000 1110100103 1110000010
  0001110000 0001001000 0000000000 00
Keuphylid.     2211101110 110000010? 0001100002 0101100010 1110100101 1110100010
  0001001000 0001001000 0000100000 00
Limnoriid.     2211100110 1100000100 000?100002 010?000011 1111100102 111000?010
  0001000100 0011001000 0000000000 00
Lynseiidae     2211100110 1100000101 0001100002 0101100001 1111100102 1110000010
  0001000001 0001001000 0000000000 00
Phoratopd.     2211100110 1100000101 1001100001 0101000010 1110100170 1110000010
  0001000000 0001001000 0000000100 00
Plakarth.      2211101110 1100000?01 0001100002 010?000000 1110100101 1110100010
  0001000000 0001001000 0000100000 00
Protognat.     2211100110 1100000101 000?100001 010?000000 1110100??3 1110000010
  0001000000 0001001000 0000000000 00
Serolidae      2211101110 1100000101 1001100002 0101000000 1110100101 1110?00010
  0001000010 0001001000 0000?00000 00
Sphaeromt.     2211100110 1100000101 0001100000 0101000010 1110100100 1110000010
  0001000000 0001001000 0000000000 00
Tridentll.     2211100110 1100000101 0001100001 010?010010 1110100103 1110000010
  0001000000 0001001000 0000000000 00
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APPENDIX III

Synapomorphies of terminal taxa. Note: this is not an exhaustive list of synapomorphies unique to each terminal taxon; it is a list of only those present in the data set used for the current analysis (see Methods section and Appendix I). Reversals and multi-state character changes are indicated by parentheses.

Anthuridea: 27, 33, 38, 39(0), 60.
Anuropidae: 23, 63, 89, 90.
Asellota: 24(0)[?], 47, 75, 76.
Bathynataliidae: 71.

Calabozoidea: 86, 87.
Corallanidae: 39(0), 92.
Cymothoidae: 66.
Epicaridea: 14, 15, 20(0), 26, 31(2), 65.
Gnathiidea: 10, 13, 19, 28, 29.
Keuphyliidae: 35, 67.
Limnoriidae: 20(0), 68, 73.
Lynseiidae: 35, 39(0), 70.
Microcerberidea: 39(0), 77, 82, 83, 84.
Phoratopodidae: 21, 88.
Phreatoicidea: 72, 73.
Protognathiidae: 39(0).
Serolidae: 21, 69.
Tylomorpha: 57(0), 62.
Valvifera: 49, 61

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THE IMPORTANCE OF TAXONOMY AND MUSEUMS IN THE 1990S

RAYMOND B. MANNING

Manning, R.B. 1991 09 01: The importance of taxonomy and museums in the 1990s. *Memoirs of the Queensland Museum* 31: 205–207. Brisbane. ISSN 0079-8835.

Much of the basic research on taxonomy is carried out in museums, traditional primary sources of information on species. Museums are characterized by their collections — archival holdings of organisms, field and historical data associated with those organisms — and library facilities, usually in volumes far beyond those available to individuals in other kinds of research laboratories. These characteristics of museums can only increase their value and the importance of the roles they play in the future, given our critical need to understand our environment and its components, especially species. Some problems facing museums are discussed, and illustrations of some of the kinds of research carried out at museums are given from ongoing research on geryonid crabs. □ *Museums, taxonomy, systematics, biodiversity, funding.*

Raymond B. Manning, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA; 6 July, 1990.

Systematics or taxonomy is the study of natural diversity, better known today by the catchword biodiversity, thanks to the efforts of E.O. Wilson and others (Wilson, 1985, 1988; Black *et al.*, 1989), and it is the kind of research characteristic of museums. Systematic research is basic to any other kind of biological study involving species, whether it be fisheries or molecular biology, ecology, behaviour, or zoogeography.

In the 1990s we seem to have reached the point where both individuals and organisations outside the systematic community, including environmentalists, legislators and sources of research funding, recognise the fundamental importance of knowledge of species diversity, museum collections which represent baseline data over time, and traditional systematic work, and appear to be beginning to appreciate the need for museum collections and systematics more than at any time in the history of systematic research, a time period spanning almost 300 years. Museums and the systematic profession in general, instead of being prepared for such a momentous change, are facing a crisis: we appear to be losing systematists and systematic organisations, including museums.

Part of the problem is that the science of systematics has never been accorded the stature it deserves among all sciences. 'Strange as it may seem, there is less attention and regard paid to systematic work at the present time than ever before.' This is not a quote from an editorial published in 1990 in 'Science' or 'Nature'. It was published by Waldo Schmitt in 1930, and it is just as valid today, 60 years later.

Further, even though museums are primary sources of information on species and even though we are in the 'information age,' automation of museums's major sources of information on species, their collections and their libraries, lags a generation or more behind current technology. Any major department store chain has in its data inventory specific information on individual items of clothing, such as a pair of slacks, including size, fabric, colour, manufacturer, and location. This volume of information on species of shrimps, even commercial shrimps, is generally unavailable from any museum collection, large or small, in machine retrievable form. Even grocery stores routinely use bar-code technology to check-out groceries and prepare bills (invoices). Museums prepare invoices the old fashioned way, as our ancestors did, by hand. The technology needed by museums has existed for years. The funding and the expertise needed to implement the technology is not yet available to most museums, which in consequence are unable to manage the vast amounts of information on species available to them.

In the past 30 years we have seen a dramatic increase in numbers of recognised species of crustaceans, especially in decapods, results of the work of a generation of specialists. In geryonid crabs, for example, specimens identified with *Geryon affinis* Milne Edwards and Bouvier and *Geryon quinquedens* Smith now have been assigned to at least 18 different species. Although this may not be true for other crustacean groups, we are about to lose a generation of giants in decapod crustacean systematics. The

list of decapod specialists now retired or near retirement includes Fenner A. Chace, Jr., Michèle de Saint Laurent, Jacques Forest, John Garth, Janet Haig, Horton H. Hobbs, Jr., L.B. Holthuis, R.W. Ingle, S. Miyake, Isabel Pérez-Farfante, Austin B. Williams, and John Yaldwyn. When Ingle retires next year, the British Museum will have one crustacean specialist on its staff, Geoffrey Boxshall; it will be without a decapod specialist for the first time this century. The Japanese crab specialist, Tune Sakai, passed away several years ago, as did Richard Bott, Ch. Lewinsohn, and Raoul Serène.

There appear to be few replacements available for these specialists, all of whom worked at the regional or international level. There are many decapod specialists today who work at the national or local level, and perhaps we are seeing a trend away from a few specialists working world-wide to numerous specialists working nationally. This trend could result in more pressure on museums to provide information on the literature as well as on species.

Not only are we losing people, including many great systematists, we are losing institutions. The Allan Hancock Foundation, one of the large, active museums in the United States with a long tradition of research, is in the process of transferring its crustacean collections to the Los Angeles County Museum. The British Museum is de-emphasising monographic work and work on local faunas, even though one of its new areas of emphasis is biodiversity. The government of New Zealand has disestablished the biosystematics programme of the New Zealand Oceanographic Institute, leaving Des Hurley and Elliot Dawson without jobs.

One bright spot is here in Australia, where the Australian Biological Resources Study, now in its 10th year, anticipates a 12.5% budget increase for 1990 (ABRS, 1990).

A wide variety of reports on the needs in and importance of systematics, prepared for a variety of organisations over the past four decades (Anonymous, 1953, 1968; Mayr and Goodwin, 1956; Michener *et al.*, 1956; Steere, 1971a, 1971b; Stuessy and Thompson, 1981; see also Brusca, 1990), all have common themes. Systematics is important, there aren't enough trained systematists, systematics as a discipline ranks somewhere under flatworms in importance, and museum collections need more support. Yet the situation may be worse today than in 1953.

I don't pretend to have the solution to this dilemma, but I do know it will take an effort to raise the level of understanding of the fundamental importance of systematics, a much higher level of funding than is now available for systematics and collections, the development of national and international forms of recognition for systematic work, a cooperative effort by those in academia and museums to interest people in systematic fields and to train them, and some long-range planning by museums, planning that includes training and jobs for future generations of systematists. Unless the effort includes creating permanent jobs in systematics, including many more support positions, the situation will not improve. Karl Schmidt (in Anonymous, 1953) made many of the same points in an article published in 1952, and noted that E. Ray Lankester had made them in the 1880s.

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NEW TECHNIQUES TO INVESTIGATE THE ONTOGENY OF SCALPELLID BARNACLES, AND THEIR PHYLOGENETIC IMPLICATIONS

Scalpellid barnacles (Thoracica: Lepadomorpha: Scalpellidae) are stalked, with a capitulum bearing more than five calcified or partly calcified plates. They are poorly known and have been rare in museum collections. Species descriptions are often based on one or few specimens. It is often difficult to assign species to many of the proposed scalpellid genera. This paper describes techniques being developed to provide comprehensive descriptions of recent rich Australian collections. As some species are known by only a few individuals, emphasis has been placed on techniques which minimise trauma to the specimen. Conchological techniques, described as destructive, semi-destructive and non-destructive, are used to examine the calcareous capitular plates, since the arrangement of these is of systematic, ontogenetic and phylogenetic significance. Consideration is also given to staining techniques, since descriptions of morphological details of trophi, cirri and complemental or dwarf males (if present) are lacking for many species.

Conchological Techniques

Destructive techniques. These are the conventional dissection techniques. In some scalpellid species the capitular plates are covered by or embedded in a thick, often opaque membrane, and removal of the membrane and/or dissection of the plates is necessary. These destructive techniques may be acceptable if several specimens are available. They are not suitable if only a few specimens exist, or for ontogenetic studies. The inherent possibility exists that plates may be lost inadvertently during dissection and the possibility of damage to fragile plates is also very real.

Semi-destructive techniques. A. Bisection of the specimen, followed by back-lighting, provides an accurate representation of the relative positions of the capitular plates. The success of this technique depends on the relative thickness of the capitular plates, their proximity to one another, and the thickness of the investing membrane.

B. Cleared (transparent) and stained specimens are widely used for vertebrate osteological studies. Preparation of such specimens involves tissue maceration in alkaline solutions (KOH or NaOH), or tissue digestion by proteolytic enzymes (e.g. trypsin). Bones are then stained for maximum definition and visibility.

Thoracicans exhibit shells composed of $CaCO_3$, mainly in the form of calcite, with little phosphate or organic matter. The calcareous portion of the thoracican shell appears during metamorphosis of the cyprid larva into the young barnacle. Vertebrate clearing and staining techniques were applied, with modifications, to scalpellid specimens. Fresh and newly preserved material was successfully cleared used KOH, but the technique can be unpredictable and difficulties arose with specimens stored in various preservatives for any length of time. The proteolytic enzyme digestion method was more successful. It was easier to prepare small, delicate specimens, and capitular plates were not so easily damaged, distorted or lost. It was also easier to clear old material, although results were not always predictable. However, material properly preserved prior to enzyme digestion generally yielded good transparent study specimens. Enzyme digestion is less harmful to the specimens than alkaline maceration. Maximum satisfactory enzyme activity occurs at pH 7.5 or above.

For all except very small specimens we removed the prosoma before processing because this enables the most rapid enzyme digestion to occur and minimises injury to the capitulum. Difficulties encountered using the enzyme technique are: (i) determination of the length of time for tissue digestion, as specimens will fall apart and/or disintegrate if over-exposed; and (ii) the length of the total process (up to 2 months in enzyme solution). The major advantage of the technique is a permanent, three-dimensional record of the capitular plate architecture.

Non-destructive techniques. Scalpellid specimens were X-rayed (another vertebrate osteological technique) with the assumption that the calcareous capitular plates would be radio-opaque. The technique is quick, economic and easy to adapt to a variety of sizes of specimens. A permanent record is obtained of the relative positions of the plates. The technique is excellent for both ontological and comparative studies. An advantage of the process is that the whole animal may be kept intact, which is important when only one or a few specimens are known. However, we have found it preferable to use bisected specimens to prevent 'shadowing' of paired plates on the X-ray image, which can sometimes hinder conchological interpretation.

Soft-part Morphology

We have adapted methods previously employed by cirripede workers. A variety of biological stains were used to examine external and internal morphological details (fast green, methyl blue, lignin pink, chlorazol black, solophenyl blue). We obtained excellent results with lignin pink and solophenyl blue. Suitably stained material was mounted in corn syrup diluted 50:50 with distilled water.

Conclusion

In the specimens studied consistent morphological and conchological differences are recognizable between the major subfamilies of the Scalpellidae (*sensu* Zevina, 1981). At the supra-specific level there appear to be few gross differences in appendages between species but differences in the form of the capitular plates are demonstrable. Criteria for the presently proposed genera need to be more critically defined, especially in the Arcoscalpellinae, with due regard to ontogenetic variations in morphology and body anatomy, complemental and dwarf males anatomy, as well as geographic and bathymetric distributions. Much more sustained, deep-water collecting needs to be done, not only in Australia but elsewhere, before a proper understanding of taxonomic variation in the Scalpellidae can be reached. Only then will their phylogenetic evolution be elucidated.

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SYMPATRIC OCCURRENCE OF TWO SUBSPECIES OF *PANULIRUS LONGIPES* MILNE EDWARDS, 1868 (DECAPODA: PALINURIDAE) AND BIOCHEMICAL EVIDENCE OF INTERBREEDING

Panulirus longipes, a common tropical lobster in the Indo-West Pacific region belonging to the Japonicus group, was distinguished by George and Holthius (1965) into two forms based on the colour pattern of the legs, the 'spotted' and the 'striped'. Furthermore, they suggested that these forms be designated as subspecies, the 'spotted' form, *P. longipes longipes*, inhabiting the western part of the species range and the 'striped' form, *P. longipes femoristriga*, found in the eastern part. These workers, however, noted that the two forms could not be sharply separated because intermediate forms with striped and spotted legs occur. This paper reports the sympatric occurrence of the 'spotted' and 'striped' forms and the observation of intermediate forms bearing stripes with spots. Using the electrophoretic methodology, it was investigated whether or not the Philippines represents a transition area where both subspecies intergrade and interbreed.

While undertaking research on some aspects of the biology of Philippine spiny lobsters, both 'striped' and 'spotted' forms of *P. longipes* were caught in the reef areas around San Vicente, Cagayan (18°30.6'N and 122°08'E) in the north-eastern-most part of Luzon Island, Philippines, comprising 12% and 3% of the landed catch, respectively. Surveys in Guiuan, Eastern Samar (10°44'N and 125°43'E) also revealed that both subspecies are sympatric in these areas. The 'striped' form, *P. longipes femoristriga* has not been reported previously in Philippine waters while *P. longipes longipes* had been previously reported from Zamboanga and Palawan (George and Holthius, 1965). In this study, *P. longipes longipes* was found to be commonly caught from waters off Eastern Samar, Pangasinan, Zambales, Cavite, Batangas, Mindoro, and Cebu.

The 'spotted' and 'striped' forms are morphologically similar in all body characters except for the markings on the legs and on the abdomen. The 'spotted' form collected from Bolinao, Pangasinan and Calatagan, Batangas typified that described by George and Holthius (1965). Five white spots are obvious on the dorsal surface of the legs which are situated at the distal regions of the propodus, carpus and merus with the two remaining spots in the central region of the merus; these spots interrupt an orange longitudinal line. The abdomen is spotted with large white dots. The 'striped' form collected from San Vicente, Cagayan has a thin, almost continuous longitudinal line on the dorsal surface of the merus, carpus and propodus; the abdomen is spotted with smaller dots. Intermediate forms collected from San Vicente, Cagayan and Guiuan, Samar exhibited variable pattern combinations: clear white spots on the fifth leg and blotches on the other legs; two longitudinal lines on the dorsal surface of the merus and carpus interrupted by white spots; all variable specimens had large white spots on the abdomen.

Electrophoretic analysis of 'spotted' samples from Bolinao (n=16) and Calatagan (n=4) and 'striped' samples from San Vicente (n=30) showed that at 14 enzyme loci examined, both forms shared alleles in 13 but diverged in a single locus, glyceraldehyde-3-phosphate dehydrogenase (Gapdh, E.C. No. 1.2.1.12). The 'spotted' form displayed a faster fixed allele with a relative mobility of 150 compared to the 'striped' form (rm 125). On the other hand, intermediate forms examined from San Vicente, Cagayan (n=7) were polymorphic for both alleles. This divergence even at a single locus is sufficient evidence of the existence of independent gene pools (Shaklee *et al.*, 1982) and therefore they can be rightfully considered subspecies at least. The polymorphism observed in intermediate forms is a strong indication of interbreeding between the two *P. longipes* subspecies. Intraspecific variations in *P. echinatus* (Vianna, 1986) consisting of "large-spotted", "small-spotted" and intermediate forms, might be a similar phenomenon.

As mentioned earlier, *P. longipes femoristriga* is reported to inhabit the eastern portion of the species' range from Japan, the Mollucas, Papua New Guinea, northeastern Australia to Polynesia (George and Holthius, 1965) and throughout the American Samoa, Guam and North Mariana Islands (MacDonald, 1979). It is conceivable that larvae from islands in the Central Pacific (e.g. Palau) may be transported by the North Pacific Equatorial Current which branches to the north as the Kuroshio and to the south as the Mindanao current off Luzon at latitude 13–14°N (Nitani, 1970). Considering this, sympatric occurrences and interbreeding of these subspecies may also be the case in other localities particularly along the Philippine Pacific coast.

Acknowledgements

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GENETIC POPULATION SUBDIVISION IN THE COCONUT CRAB, *BIRGUS LATRO* (ANOMURA: COENOBITIDAE)

The coconut crab (*Birgus latro*), the largest and most terrestrial land crab, is found only on relatively isolated tropical islands in the Indian and Pacific Oceans. In recent years, *Birgus* populations have declined rapidly or disappeared in most parts of their range, due largely to overharvesting for food. It is clear that a management program is required to protect the future survival of individual populations of this species. Information about population structuring within the species is crucial to the development of a suitable management program. This project is using genetic techniques to study the population structure of *Birgus* throughout its distribution to determine if distinct sub-populations exist and, if so, the location of their boundaries (Lavery *et al.*, in press).

Allozyme electrophoresis was used to examine over 300 specimens of *Birgus* from eight locations: Christmas Island (Indian Ocean), the Solomon Islands, Niue, the Cook Islands and four islands in Vanuatu (Tegua, Hiu, Loh and Espiritu Santo). Initially 76 enzyme systems were screened for genetic variation, resulting in the detection of 54 monomorphic loci and 7 polymorphic loci. These polymorphic loci were analysed for allele frequency differences between locations using contingency chi-square analyses. Analyses were performed at different levels of the sampling hierarchy. At the lowest level of the hierarchy, between adjacent islands (the Torres Islands in Vanuatu: Tegua, Hiu and Loh), no significant difference in allele frequencies was found. Similarly, no significant differences were found at the next two levels of the sampling hierarchy, i.e. between islands in a group (the Torres Islands and Espiritu Santo in Vanuatu) and between adjacent island groups (Vanuatu and the Solomon Islands). However, when all the Pacific Ocean samples were compared, there was significant variation in allele frequencies ($P<0.01$), with individuals from Niue being most variant. Finally, a comparison of samples from the Pacific with those from Christmas Island showed highly significant genetic differences ($P<0.001$).

A good summary of the genetic differences between locations is shown in a dendrogram of genetic distances (Fig. 1). This clearly shows that all the islands in the Vanuatu and Solomon Islands groups are quite similar. The Cook Islands and, in particular, Niue, are somewhat different from the Vanuatu/Solomon Islands group, but this level of differentiation is much smaller than that with Christmas Island.

The population genetic structure of *Birgus* is also being analysed using mitochondrial DNA (mtDNA) variation. So far, the mtDNA of approximately 50 individuals from four locations (Christmas Island, the Philippines, the Solomon Islands and Niue) has been analysed using 9 different restriction enzymes. Preliminary analysis shows that over 20 different haplotypes exist among these individuals and, significantly, no haplotype has been found to occur in more than one location. The phylogeny of these haplotypes also suggests that there exists significant geographic structure in the mtDNA variation. Such information about genetic differences between sub-populations may be interpreted in terms of the level of genetic drift or the rates of larval migration between sub-populations. Using the allozyme data alone, and interpreting these data by Slatkin's private alleles method, a migration rate between Christmas Island and the Solomon Islands of 0.3 individuals per generation was calculated. As the *Birgus* generation time may be 12 years, this would represent a migration of one individual every 40 years. In comparison, the rate of migration between the Pacific Islands was calculated to be approximately an order of magnitude less, at 3 individuals per generation, or about one individual every four years.

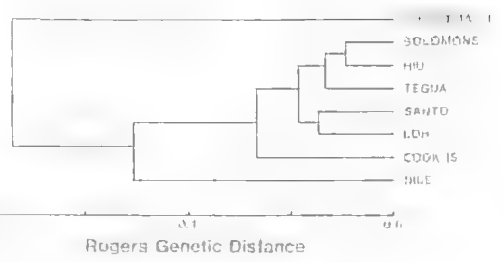

FIG. 1. Dendrogram of genetic relatedness of *Birgus* collections.

Although this study is not yet complete, the findings so far suggest that significant genetic population subdivision exists in *Birgus*. This may have important consequences for both the future management of the species and also any future artificial rearing of the coconut crab. In addition, the pattern of larval dispersal found in *Birgus* may be closely related to that of other species in this region with planktonic larvae.

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NEW OR RARE CRUSTACEANS FROM FRENCH POLYNESIA (CRUSTACEA: DECAPODA)

Since 1974, the F.R.V. 'Marara' has been used by the French Service Mixte de Contrôle Biologique (SMCB) to carry out a biological survey, throughout the Fishery Conservation Zone of French Polynesia. Among the fishing activities, traps are set on the outer slopes of the islands in depths ranging from 100 to 1000m. This has led to the discovery and description of several new species of decapod crustaceans. Some rare or recently described species have also been caught. This paper gives a list of the species concerned and the depth distributions of some of them. A list of genera of new species, now under study, is also given to emphasize the richness and high degree of endemicity of this poorly known area. The details of the gear operations and the yields of Pandalidae shrimps are given in Poupin *et al.* (1990).

Results

Species Described from the Catches of the 'Marara'

Pandalidae: *Plesionika fenneri* Crosnier, 1986; *Plesionika carstni* Crosnier, 1986.

Enoplometopidae: *Hoplometopus gracilipes* De St. Laurent, 1988.

Xanthidae: *Progeryon mararae* Guinot et Richer de Forges, 1981.

Goneplacidae: *Beuroisia manquenei* Guinot et Richer de Forges, 1981; *Mathildella maxima* Guinot et Richer de Forges, 1981.

Rare or Recently Described Species

Pandalidae: *Heterocarpus amacula* Crosnier, 1988; *Heterocarpus parvispina* de Man, 1917; *Heterocarpus ensifer* A. Milne Edwards, 1881.

Homolidae: *Hypsophrys personata* Guinot et Richer de Forges, 1981; *Hypsophrys inflata* Guinot et Richer de Forges, 1981.

Leucosiidae: *Randallia serenei* Richer de Forges, 1983.

The depth distributions of the three recently named *Heterocarpus*, formerly regarded as *H. ensifer* and *H. ensifer parvispina* (Crosnier 1988), are clearly defined and are presented together in Fig. 1.

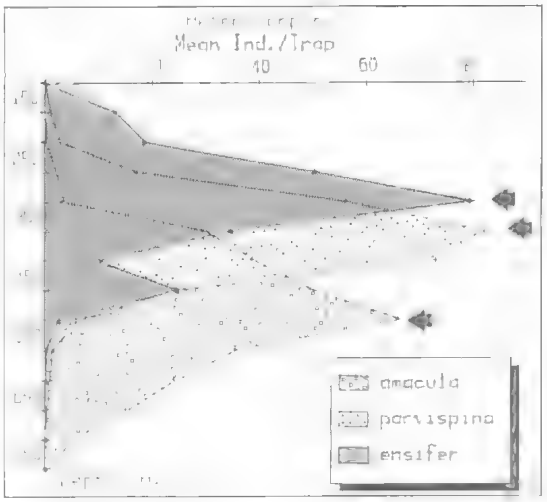

FIG. 1. Depth distributions of three close *Heterocarpus* spp. belonging to the group '*ensifer*' (*H. parvispina*: abundance x 5; *H. amacula*: abundance x 13).

Genera of the New Species, now under Study

Pandalidae: *Plesionika* sp. (three species, Crosnier).

Palaemonidae: *Periclimenes* sp.(Bruce, in press).

Enoplometopidae: *Enoplometopus* sp. (De St Laurent).

Parapaguridae: *Trizopagurus* sp. (two species, Forest).

Paguridae: *Solitariopagurus* sp. (Forest).

Galatheidae: *Eumunida* sp. (De St Laurent); *Munida* sp. (two species, De St Laurent).

Majidae: *Cyrtomaia* sp. (two species, Guinot et Richer de Forges).

Parthenopidae: *Parthenope/Platylambrus* sp. (Garth).

Grapsidae: *Euchirograpsus* sp. (Türkay); *Intesius* sp. (Guinot and Richer de Forges).

Cancridae: *Cancer* spp. (four species, Davie).

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PHRONIMIDAE (CRUSTACEA: AMPHIPODA: HYPERIIDEA) OF THE EASTERN PACIFIC

A total of 466 samples of phronimids collected from the upper 200m layer of the eastern equatorial Pacific (20°N–20°S and E of 126°W) and coastal waters of California (33–35°N and E of 122°W) were examined. All species of the Phronimidae were found in the eastern equatorial Pacific where *Phronima dunbari* Shih (1991) and *P. bowmani* Shih (1991)(formerly E. Pacific Form of *P. stebbingi* and *P. colletti* respectively [Shih, 1969]) dominated. Only *P. sedentaria* (Forskål, 1775), *P. atlantica* Guérin, 1836, and *P. stebbingi* Vosseler, 1900, occurred in the coastal waters of California.

The sympatric distribution of morphologically similar species pairs (analogous species, Shih, 1986a) is common in the eastern equatorial Pacific, e.g. *Phronima stebbingi-P. dunbari* and *P. colletti-P. bowmani* of the present study, and there are examples of chaetognaths, euphausiids and copepods in the literature. This plankton distribution pattern is probably related to the complex oceanic circulation of the area where six currents converge or diverge (Wyrtki, 1967).

Eddies from main oceanic currents bring enclosed water from one water mass to a new environment surrounded by another water mass. The best known examples are cold core rings of the Gulf Stream (The Ring Group, 1981). The entrained plankton population is subjected to continuous decay of the core water due to increasing dilution by water of the surrounding environment and is under tremendous physiological stress (Boyd *et al.*, 1978; Wiebe and Boyd, 1978). Populations of planktonic species are known to be different in genetic structure (Bucklin and Marcus, 1985) and to be distributed patchily (Wiebe, 1970). Unusual environmental stress may affect the genetic structure of a population: some copepod species in the eastern equatorial Pacific exhibit higher genetic heterogeneity than those in the equatorial and tropical central Pacific (Afnas'yev *et al.*, 1989).

The oceanic condition in the eastern equatorial Pacific, the general knowledge of oceanic eddies, the biology of a population entrained in an eddy, and diversification of genetic structure in plankton, strongly support the hypothesis of planktopatric speciation in marine zooplankton (Shih, 1986): 1. entrained population is subject to a different set of biotic and abiotic stresses; 2. modification of genetic structure occurs in a segment of the entrained population as a result of adaptation to new environmental stress; 3. successful propagation of the genetically modified segment of population leads to formation of a new taxon following succeeding reproductive isolation.

Thus planktopatric speciation probably is the answer to why there are so many analogous plankton species in the eastern equatorial Pacific.

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CLADISTIC ANALYSIS AND CLASSIFICATION OF THE GECARCINIDAE (CRUSTACEA: BRACHYURA)

The land crabs of the family Gecarcinidae constitute a circumtropical group of eighteen species belonging to the genera *Cardisoma* Latreille, 1828, *Epigrapsus* Heller, 1862, *Gecarcoidea* H. Milne Edwards, 1837, and *Gecarcinus* Leach, 1814.

The main goals of this work were: (1) to provide a phylogenetic reconstruction for the genera of the Gecarcinidae and the species of *Gecarcinus*; (2) to use phylogenetic information to improve the classification of the group, and attempt to clarify the relationships between the families Gecarcinidae, Grapsidae and the genus *Ucides* Rathbun, 1897.

Sixty-eight morphological characters were selected and analysed. These are available from the author upon request. Six species belonging to different subfamilies of Grapsidae were selected as the out-group. The cladistic analysis was undertaken using the 'Hennig 86 vers. 1.5' program.

Relationships within Gecarcinidae

The species of Gecarcinidae probably evolved from an ancestor that had the dactyli of the pereiopods armed with rows of spines; branchial and hepatic regions strongly inflated, and carapace transversely oval.

The cladogram in Fig. 1 shows that the first cladogenetic event split the genus *Cardisoma* from the group *Epigrapsus* + *Gecarcoidea* + *Gecarcinus*. The majority of the characters analysed are plesiomorphic to *Cardisoma*, and do not show great morphological modification from the typical Grapsidae facies. Its sister group *Epigrapsus* + *Gecarcoidea* + *Gecarcinus* exhibit, on the other hand, several synapomorphies concerned with the buccal region.

One character however (pterygostomian region densely setose) suggests a conflicting hypothesis for the position of the genus *Epigrapsus* in the phylogeny, as this character is shared by *Cardisoma* and *Epigrapsus* and could be interpreted as synapomorphic for them. There are however seven other homoplasic characters (shared by the group *Epigrapsus* + *Gecarcoidea* + *Gecarcinus*). Thus, the more parsimonious hypothesis is that which admits the homoplasy of the densely setose pterygostomian region character.

The next cladogenetic event split *Epigrapsus* from the group *Gecarcoidea* + *Gecarcinus*, which have deep modifications in the frontal, orbital, suborbital, pterygostomian, antennal, antennular and abdominal regions.

The third cladogenesis split *Gecarcoidea* and *Gecarcinus*.

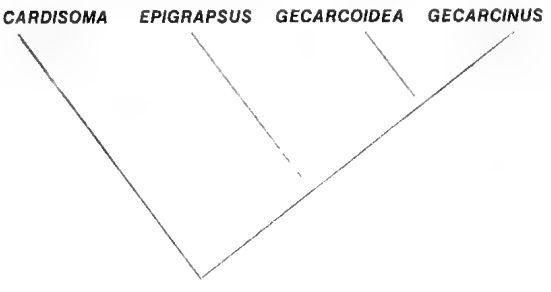

FIG. 1. Phylogenetic relationships within Gecarcinidae.

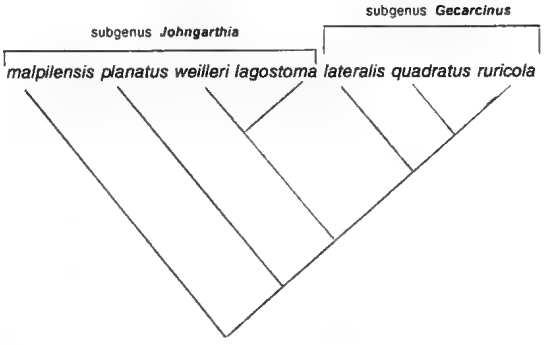

FIG. 2. Cladogram illustrating the artificial assemblage (*Johngarthia*) within the genus *Gecarcinus*.

These two genera remain rather conservative in relation to the changes in the morphology observed during the previous cladogenetic event. The strongest morphological changes occur in the orbital and buccal regions (Fig. 1).

Phylogeny of the Genus *Gecarcinus* and its Implications for the Classification of the Group

The species of *Gecarcinus* probably evolved from an ancestor which had the orbit closed by the intra-orbital spine and the palp of the third maxilliped concealed beneath the maxilliped.

Gecarcinus malpilensis proved to be the more external branch of a symmetric cladogram, and was followed in a sequence by *G. planatus* and the group formed by *G weileri* + *G. lagostoma*. The maxillipeds were the principal morphological structures affected during the evolution of these species/groups. The three last branches of the cladogram in Fig. 2 correspond to *G. lateralis*; *G. quadratus* and *G. ruricola*, which show, beside the modifications to the maxillipeds, strong modifications of the pleopods.

Türkay (1970) created the subgenus *Gecarcinus s.s.* (for *G. lateralis*, *G. quadratus* and *G. ruricola*) and *Johngarthia* (for *G. malpilensis*, *G. palanatus*, *G. lagostoma* and *G. weileri*). The subgenus *Johngarthia* from my results, however, appears to be a paraphyletic assemblage which embraces the four initial branches of an asymmetric cladogram with seven terminal taxa (Fig. 2).

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INDIVIDUAL RECOGNITION AND SUPPRESSION OF AGGRESSION AGAINST FORMER MATES IN *GONODACTYLUS BREDINI* (CRUSTACEA: STOMATOPODA)

In laboratory tests, gonodactylid stomatopods use individual recognition to mediate intra- and interspecific aggression (Caldwell, 1985). Intruders identify the odour of previous opponents and decide whether to fight based on experience with them. However little is known of stomatopod use of recognition systems in the field.

Gonodactylus bredini is a common stomatopod on the Atlantic coast of Panama where this study was conducted. Reproduction is synchronised. Breeding pairs form a few days prior to the full moon, sharing a crevice for several days. Within hours of the female spawning, the male leaves. She remains in the crevice, brooding the eggs and larvae for four weeks until they enter the plankton. Empty cavities are rare and males, after leaving their mates, may have to evict a crevice resident to secure a home (Caldwell, 1986). While searching for a crevice, a male might encounter his former mate and attempt to usurp the breeding crevice. This would jeopardise her offspring, which, in all probability, are also his. Here, I report that formerly mated *G. bredini* recognise one another and avoid fighting for several days after males leave the breeding crevice and while females are still brooding.

Procedures

Fifteen *G. bredini* male-female pairs were collected in the field, placed in artificial cavities of appropriate volume, and housed in individual aquaria. They were checked daily to determine when the female spawned and the male left the crevice, after which time he was placed in a separate container. Thirteen days later, the female, with her eggs, was placed in a similar crevice in another aquarium. At the same time, a second brooding female, matched for size and egg development, was established in a separate tank in an identical crevice. The next morning, either the paired female's original mate, or another male matched to his size, was introduced into her aquarium and all agonistic behaviors recorded (Caldwell, 1985). Contests were terminated when one animal avoided the crevice. The next day, the other male was introduced into the paired female's container and their interaction scored. The paired male was tested against the unfamiliar brooding female on the same day that the paired female was being tested against the unknown male. This comparison was completed for 12 of the 15 pairs. In the other three, the paired males died prior to testing, but their females were compared against unpaired males.

Results

One or more aggressive acts occurred in only one of the 12 interactions between members of former pairs while aggression took place in 17 of 27 interactions between non-pairs ($G = 10.9$, $P<0.001$). Contests between non-paired animals escalated rapidly. In 14 of the 17 contests between non-pair members involving aggression, the first act (either by male or female) after the male approached was a threat, lunge or strike. Eight of these contests ultimately escalated with one or both participants delivering potentially damaging strikes. The one aggressive interaction between members of a former pair involved a single lunge-threat by the female and did not escalate to physical contact ($G = 7.0$, $P<0.01$). Only one of the previously paired females responded aggressively toward her former mate. When meeting unknown males, this female, plus 2 others, were aggressive (McNemar Test, $P>0.1$). None of the paired males acted aggressively toward their former mates, but 6 were aggressive to unknown females (McNemar Test, $P<0.05$).

Discussion

Reduced aggression between former pair-members demonstrates that individuals recognise and remember one another for at least two weeks without intervening contact. Competition for cavities and the possibility that males encounter their former mates while searching for a home have probably shaped this ability. Should a male injure and/or evict his former mate while she is still brooding, the offspring probably would be lost, reducing his fitness as well as hers. Since females occasionally move their eggs to another crevice, males must recognise a specific individual and not just the brood chamber.

Brooding females appear hesitant to initiate attacks against any intruding male, making it difficult to determine if females recognise their former mates. On the other hand, males did not attack former mates, but attempted to evict other brooding females, demonstrating that it is not simply the presence of eggs that causes a reduction in aggression. When eggs were removed from females and their former mates introduced, there was no aggression. This makes it unlikely that males fail to attack because they recognize the eggs as their own (Caldwell, in prep.). Whether recognition is chemically or visually mediated is unknown, but intense initial bouts of antennulation by males suggest that they are using chemical cues.

Acknowledgements

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NITROGENOUS EXCRETION IN AQUATIC AND TERRESTRIAL CRUSTACEANS

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For water-breathing animals the most economical nitrogenous excretory product in energetic terms is ammonia (ium) and this is generally excreted across the gills. In terrestrial situations most animals produce less toxic materials, notably urea and purines, which are eliminated by the excretory organs. Crustaceans are predominantly an aquatic group and marine and freshwater species conform to the above pattern in excreting ammonia (ium). Most amphibious species generally have frequent recourse to water and show little change in the basic aquatic pattern of excretion. The small terrestrial forms, notably Amphipoda and Isopoda and the crab *Geograpsus grayi*, retain ammonia excretion but eliminate it as a gas. The gecarcinid land crabs excrete NH_4^+ in the urine whilst *Birgus latro* excretes uric acid in the faeces. Many terrestrial and some aquatic species store purines and may have purine synthetic ability. The role of stored purine is unclear but it may act as a N reserve, an ion store or as a non-toxic buffer when normal ammonia excretion is inhibited. Urea is not an important excretory product and crustaceans appear to lack a complete urea cycle. Excretory patterns are discussed in relation to the evolutionary history of the group. □

Nitrogenous excretion, Crustacea, ammonia, terrestrial Crustacea, uric acid

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The form in which animals excrete waste nitrogen and the route, or mechanisms, by which it is eliminated are quite labile, but there are several underlying factors which strongly affect the mechanism employed. Firstly, metabolism of protein yields ammonia[1], typically from transamination and deamination reactions, and the metabolically cheapest form of excretion is ammonia. Secondly, ammonia is toxic to animals, especially higher vertebrates (Campbell, 1973), although less so to crustaceans which may maintain ammonia concentrations appreciably higher than in vertebrates (Table 1). Thirdly, NH_3 is highly diffusible and cannot be contained or concentrated by cells, but in the ionic form it can be concentrated and transported by the usual ion transport mechanisms. In body fluids most ammonia is protonated (NH_3^+) and within the usual range of pH only around 1% will be present as NH_3. Elevated $[NH_4^+]$ however, leads to elevation of $[NH_3]$ with resultant toxic effects, so that ammonia concentrations must be kept within a tolerable range. Rapid excretion into large volumes of water avoids any build up in concentration. For these reasons, ammonia excretion is considered to be the preserve of water-breathers which can economically excrete their waste in the form in which it is produced.

Other forms of waste nitrogen are also eliminated by animals, chiefly purines and urea, but these have several selective disadvantages. They are more complex molecules and their synthesis requires energy and also elaborate enzyme systems (Hartenstein, 1968). This extra metabolic cost is only outweighed under conditions considered inadequate for safe excretion of ammonia, i.e. on land, especially in mesic and xeric habitats where water availability is limited.

The generalised pattern seen in animals then is as follows: water-breathers are ammonotelic excreting NH_3/NH_4^+ across suitable surfaces, usually the gills; terrestrial forms (particularly arthropods) excrete purines or, less commonly, urea, and any NH_3/NH_4^+ excretion is small and is often primarily a function of acid-base regulation.

The Crustacea are predominantly an aquatic group with the major radiation in the sea but with a substantial number of species in freshwater and only a few on land. Most species have spent their whole evolutionary history in water and ammonotelism is expected to be the standard pattern of excretion. The terrestrial forms would be expected to excrete one of the more complex, less toxic, compounds. The extent to which these predictions hold is examined below. Whilst water availability in the habitat is normally an

[1] In this review NH_3 refers to molecular ammonia, NH_4^+ to ammonium ions, and ammonia to the sum of both (=total ammonia).

TABLE 1. The concentration of ammonia in the haemolymph of a range of crustaceans.

Species	Ammonia $mmol.L^{-1}$	pH	Source
Callinectes sapidus	0.39	7.98	Cameron and Batterton (1978)
Callinectes sapidus	0.011 NH_3 0.82 NH_4^+		Kormanik and Cameron (1981b)
Carcinus maenas	0.9		Binns (1969)
Uca pugilator	20.0		Green *et al.* (1959)
Cardisoma carnifex	1.6	7.49	Wood *et al.* (1986)
Geograpsus grayi	2–3	7.59	Greenaway and Nakamura (in press)
Gecarcoidea natalis	2–4	7.55	Greenaway and Nakamura (in press)
Cherax destructor	0.1		Fellows and Hird (1979)
Notostomus gibbosus	217	7.52	Sanders and Childress (1988)
Porcellio scaber	1.5		Wieser and Schweizer (1972)

over-riding determinant of the excretory mechanism employed, there are certain other factors which may be important in determining excretory rates and patterns in Crustacea. These include the moult (at which time there is considerable catabolic and anabolic activity involving proteins), the nitrogen content of the diet and metabolic rate (including effects of temperature and season). Additionally, where ammonium is excreted in exchange for cations in the water the salinity of the latter may be important as osmoregulatory requirements may conflict with those for nitrogenous excretion. This may affect migratory species such as *Eriocheir sinensis* and prawns as well as species subject to fluctuating salinities (Regnault, 1987). The taxonomic inheritance in terms of available metabolic pathways and the length of time a species has spent in a particular habitat can also exert a major influence. This review is directed towards the effects of adaptation to terrestrial habitats on excretory mechanisms.

EXCRETION IN AQUATIC HABITATS

The formation, detoxification and elimination of ammonia by aquatic crustaceans has been the subject of several recent reviews (Kormanik and Cameron, 1981a; Evans and Cameron, 1986; Regnault, 1987) and whilst the subject is far from being totally understood available data are well documented. In consequence, nitrogenous excretion in aquatic crustaceans will be reviewed to provide a basis for the logical treatment of terrestrial groups.

AMMONIA FORMATION

Ammonia for excretion originates overwhelmingly from the catabolism of amino acids but minor amounts will result from the degradation of purines, pyrimidines, and urea of which the latter may originate from a high intake of arginine (Fig. 1).

Before the carbon skeleton of an amino acid can be utilised in the citric acid cycle its amino group must first be removed. Most commonly this is achieved by transamination, the transfer of the nitrogen containing α-amino group to an α-keto acid. The general reaction is as follows

$$\text{L-}\alpha\text{-amino} + \alpha\text{-ketogluterate} \underset{\text{transaminase}}{\overset{\text{amino acid}}{\rightleftharpoons}} \alpha\text{-keto acid} + \text{L-glutamate}$$

These reactions do not release ammonia but pass it on to an α-keto acid to form L-glutamate. Certain amino acids possess other N groups and these may be removed by deamination followed by transamination of the amino nitrogen e.g. the amide groups of asparagine and glutamine.

$$\text{Asparagine} + H_2O \xrightarrow{\text{asparaginase}} \text{Aspartate} + NH_4^+$$

$$\text{Glutamine} + H_2O \xrightarrow{\text{glutaminase}} \text{L-glutamate} + NH_4^+$$

These pathways are believed to be utilised in some crustaceans (Krishnamoorthy and Srihari, 1973; King *et al.*, 1985). Despite some controversy it is clear that glutamate itself can undergo oxidative deamination in crustaceans (Chaplin *et*

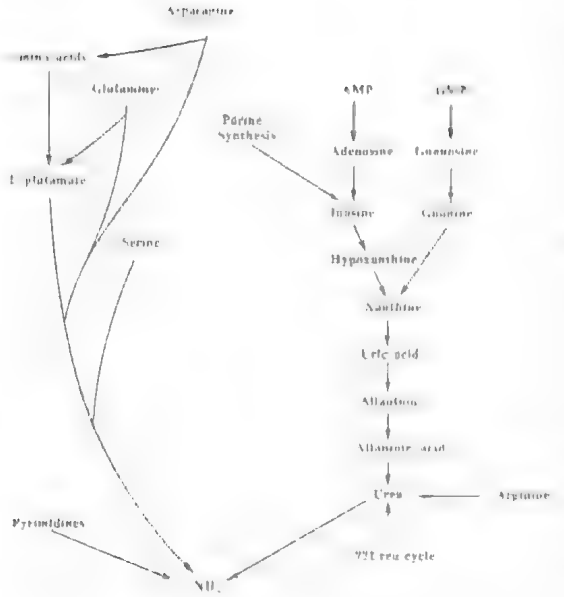

FIG. 1. Metabolic pathways producing ammonia in crustaceans.

al., 1965; Bidigare and King, 1981; Batrel and Regnault, 1965; Regnault and Batrel, 1987).

$$\text{L-glutamate} + H_2O \xrightleftharpoons{\text{GDH}} \alpha\text{-ketoglutarate} + NH_4^+$$

Indeed as glutamate is the only amino acid from which the α-amino group can rapidly be removed to release ammonia and the enzyme, glutamate dehydrogenase is very important in ammoniogenesis. In many animals, the direction of the reaction is determined by the co-factor so that oxidative deamination (NH_3 release) is stimulated by NAD^+ whilst the reducing reaction (NH_3 uptake) requires NADPH (Lehninger, 1982).

$$H_2O + \text{L-glutamate} + NAD^+ \xrightleftharpoons{\text{GDH}} NH_4^+ + NADH + H + \alpha\text{-ketoglutarate}$$

$$\alpha\text{-ketoglutarate} + NADPH + H^+ + NH_4^+ \xrightarrow{\text{GDH}} NADP^+ + H_2O + \text{L-glutamate}$$

In crustaceans the relative concentration of NAD^+ and NADH, and substrate concentrations may determine whether formation or deamination of glutamate occurs (Batrel and Regnault, 1985; Regnault and Batrel, 1987). In most cases N is transferred to glutamate and its oxidative deamination will release ammonia into the cell.

Ammonia may also be generated by catabolism of other nitrogenous compounds. Thus purine and pyrimidine nucleotides may be broken down to yield ammonia (Fig. 1), although the amounts involved are likely to be very small given the presence of scavenging pathways. Dietary intake of these components may necessitate some nitrogenous excretion, depending on the animal's requirements. In actively working skeletal muscle, the deamination of AMP results in ammonia production. Whilst AMP-deaminase has been identified in certain crustaceans its function is yet to be established (Regnault, 1987) and the importance of the pathway in overall ammonia production in crustaceans is unknown. All these pathways lead to uric acid which may then be excreted as urate, stored or degraded to urea or ammonia.

Ammonia may also be produced from urea via urease, but as a complete synthetic pathway for urea is lacking in the crustaceans examined (Hartenstein, 1970; Claybrook, 1983; Regnault, 1987) available urea is likely to be restricted to that produced from dietary arginine via arginase which is present in the midgut gland and gills of many crustaceans.

$$\text{Arginine} + H_2O \xrightarrow{\text{arginase}} \text{urea} + \text{ornithine}$$

Arginine is an essential amino acid in crustaceans that have been investigated (Zandee, 1966; Claybrook, 1983) so that urea from this source represents a dietary excess rather than a controllable form of N excretion. Urea will also be formed as an intermediary compound in uricolysis. Thus the possible generation of ammonia from urea is small.

AMMONIA DETOXIFICATION

In aquatic Crustacea, the major site of excretion is the gills (Kormanik and Cameron, 1981a; Evans and Cameron, 1986) so the ammonia generated in metabolising cells must be transported there for elimination. As the concentration of ammonia in haemolymph is high (Table 1), considerable amounts may be carried in this form. However, if production was high or excretion was discontinuous, a non-toxic molecule would be necessary for transport or temporary storage of nitrogenous waste. The obvious candidates are glutamate, the end product of transamination reactions, and glutamine which offers the advantages both of readily crossing cell membranes and of doubling the amount of NH_3 carried. In vertebrates, glutamine synthetase forms glu-

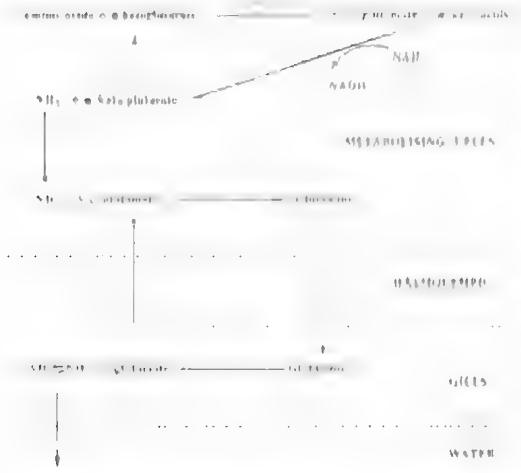

FIG. 2. A pathway for ammonia detoxification and transport in aquatic crustaceans (after King *et al.*, 1985).

tamine in the peripheral tissues and in this form waste is transported to the site of elimination (liver). There is evidence for a similar glutamine detoxification pathway in the crabs *Cancer* and *Carcinus* (Fig. 2) (King *et al.*, 1985). High levels of glutaminase in the gills of these crabs are presumed to release NH_4^+ from glutamine for elimination whilst at the site of ammonia generation (muscle), the levels of glutamine synthetase and glutamate dehydrogenase are high. Glutamine also appears to be an important vehicle for ammonia transport in *Paratelphusa hydrodromous* in freshwater (Krishnamoorthy and Srihari, 1973). This pattern does not hold for all crustaceans, however, as King *et al.* (1985) found little evidence to indicate glutamine detoxification in either *Homarus* or *Pandalus*. Evidence favours GDH as the controlling step in ammonia excretion (summarised in King *et al.*, 1985).

The formation of alanine as a detoxification and transport molecule is also possible as crustaceans possess the necessary enzyme (alanine transaminase) and indeed show high levels of alanine synthesis *in vivo* (Claybrook, 1983). There is at present no specific evidence indicating its general use for detoxification/transport purposes in crustaceans although it is important in vertebrates (Lehninger, 1982). Serine has been implicated as the main route of detoxification in the crayfish *Cherax destructor* (Fellows and Hird, 1979) and a serine cycle has been suggested in other animals (Bishop, 1976).

Other major routes of detoxification commonly seen in animals are *de novo* synthesis of purines and urea production. As the crustaceans do not appear to possess a functional urea cycle (Claybrook, 1983), synthesis of this compound from ammonia is unlikely. Although many crustaceans show periodically high levels of urea in the haemolymph (up to 28 mmol/L in *Holthuisana transversa*, P. Greenaway, unpublished) and excrete some urea, it is generally a minor component of total output. The ability to synthesise purines *de novo* is also thought to be lacking in aquatic crustaceans. The midgut gland is reported to form and excrete spherules of uric acid in several species of aquatic decapods (Fischer, 1926). The small amounts of uric acid excreted or stored are generally thought to be derived from purine catabolism rather than synthesis but this may need to be examined more closely.

ELIMINATION OF WASTE NITROGEN

AQUATIC CRUSTACEANS

There is conclusive evidence from whole animal studies that ammonia is the chief excretory product of aquatic crustaceans and that the site of excretion is the gills. Gills provide a large and well ventilated surface and the respired water carries away excreted ammonia, preventing development of gradients adverse to excretion. Waste nitrogen may arrive at the gills as ammonia (usually 99% NH_4^+ and 1% NH_3) or in detoxified forms such as glutamine and perhaps other amino acids (see above).

The processes by which ammonia is excreted have attracted considerable attention, although much of it has been concerned with osmoregulatory mechanisms rather than excretion (Evans and Cameron, 1986; Schoffeniels, 1976). Whilst the possible mechanisms of elimination of ammonia are now fairly clear, the actual mechanisms used by particular species are seldom so. It is often extremely difficult technically to distinguish between potential excretory mechanisms, and it is frequently unclear whether apparent mechanisms are primarily osmoregulatory or excretory in function as the two systems may be closely linked. Available data for crustaceans are often fragmentary and patterns generally have to be constructed from inadequate data by comparison with better understood mechanisms in fish. Potential mechanisms of excretion are presented in Fig. 3 and discussed below.

The high diffusibility of NH_3 allows loss to the water by diffusion down its partial pressure gradient either through or between the epithelial

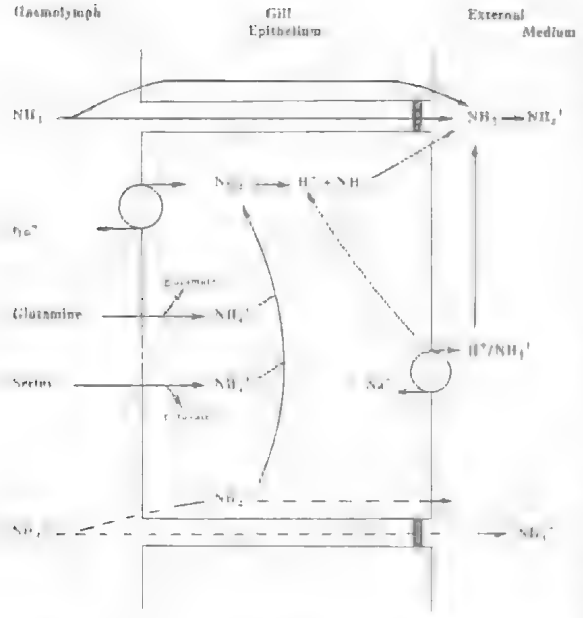

FIG. 3. Diagram summarising possible mechanisms of ammonia elimination in aquatic crustaceans.

cells. The driving gradient will be small as NH_3 forms only a small portion of total ammonia in the haemolymph (Kormanik and Cameron, 1981a). Only a small proportion of waste is likely to be lost in this way unless the gradient can be increased locally by active means (see below). Nevertheless, diffusive loss appears to be the major mechanism in the crab *Callinectes sapidus* in seawater (Kormanik and Cameron, 1981b).

Ammonium ions may also be lost directly from the haemolymph by diffusion down their electrochemical gradient. Passive, transmembrane diffusion may be impeded by the electrical charge of the ion and the pathway taken is probably paracellular, i.e. through intercellular channels and the apical junctions (Kormanik and Cameron, 1981a). There is no information on the importance of this route in crustaceans but it is likely to be minor.

As passive loss of ammonia seems to explain only a small portion of the total excretion of ammonia, the bulk must involve an active component of transport either into or out of the epidermal cell. Entry into the epithelial cells of the gill could be as NH_3, NH_4^+, or detoxified ammonia (amino acids). The neutral amino acids (glutamine particularly, serine and alanine if used) would cross the cell membrane readily but the negatively charged glutamate may require a transport mechanism. Ammonia could then be generated by removal of the amide N of glutamine, deamination of serine and transamination of other amino acids. NH_4^+ could be transported directly into the cell by Na/K activated ATPase with NH_4^+ substituting for K^+ (Towle and Holleland, 1987). NH_3 could enter by diffusion if the gradient were suitable but with active generation of ammonia in the gill epithelium the gradient may well be adverse.

The next step is the elimination of ammonia from the gill epithelial cells. The mechanisms proposed to account for this rely on amiloride sensitive entry into the cell of Na^+ from the water via sodium channels in the apical membrane (Kirschner, 1983). This is thought to create a potential gradient which favours efflux of either NH_4^+ or H^+, again through apical ion-selective channels or antiport mechanisms (Fig. 3) and results in a coupled 1:1 exchange of Na^+ with NH_4^+ or H^+. The ultimate driving force is the operation of basolaterally located Na/K ATPase (Towle and Kays, 1986) which maintains a low intracellular [Na] which allows continued apical influx of Na. Where Na^+/NH_4^+ exchange occurs, the ammonia would be eliminated directly. In the case of Na^+/H^+ exchange the loss of protons would encourage the dissociation of NH_4^+ yielding H^+ and NH_3 and the latter would be lost to the water down its partial pressure gradient (Fig. 3). If osmoregulatory requirements for uptake of Na^+ exceeded the supply of H^+ excretory ammonia, additional protons could be provided from bicarbonate via the activity of carbonic anhydrase.

There is evidence for Na^+/NH_4^+ exchange (but not for Na^+/H^+) in the marine crabs *Cancer* and *Petrolisthes* although it does not account for all the ammonia excreted (Hunter and Kirschner, 1986). In *Uca tangeri*, there is evidence for an apical H^+ pump (Krippeit-Drews *et al.*, 1989) whilst Bigalke (1986) has demonstrated a Na^+/H^+ exchanger in *Eriocheir sinensis*. A Na^+/NH_4^+ exchange has also been suggested in freshwater crayfish (Shaw, 1960). In *Eriocheir sinensis*, a small component of sodium influx apparently exchanges for NH_4^+ (Gilles and Pequeux, 1986) but in the absence of whole body flux data for Na^+ and NH_4^+ it is not clear what proportion of total N excretion this could represent. If nitrogenous excretion is normally much lower than Na influx perhaps all N could exit by this mechanism. In seawater-adapted *E. sinensis*, however, sodium influx was absent, so that ammonia in seawater animals must have been elim-

inated by other means (Gilles and Pequeux, 1986), presumably diffusion. In *Callinectes sapidus*, there is no evidence of Na^+/H^+ coupling (Pressley *et al.*, 1981) and ammonia efflux is also insensitive to amiloride indicating a lack of Na^+/NH_4^+ coupling (Kormanik and Cameron, 1981b). It is suggested that ammonia output in this species is by diffusion of NH_3.

There are then, numerous possible routes by which waste ammonia can be removed, and considerable variability in the way these routes are actually used by particular crustaceans or even within a single species under different conditions. The osmoregulatory requirements for Na^+ transport may well determine which pathways are used and, in euryhaline species, salinity may determine which is used at a particular time. A probable pattern for freshwater crustaceans is described above utilising electrical coupling of Na^+ and H^+, but in marine crustaceans where there is no osmoregulatory requirement for Na^+ a different pattern might be expected.

Other Forms of Excretion

Although ammonia is the dominant excretory product there are some data indicating low levels of excretion of other materials by aquatic Crustacea. Thus uric acid spherules are formed in cells of the midgut gland and excreted into the gut lumen in several species of crabs, the anomuran *Porcellana* and in *Panulirus* (Fischer, 1926). In *Callinectes sapidus* exposed to low temperature and salinity, crystals of uric acid appear in the cells and lumina of the labyrinth and bladder of the excretory organs (Johnson, 1980). Whether this uric acid is derived from an excess of other purines or synthesised by the animals is unknown.

Urea appears to be produced in response to elevated salinity in some crustaceans (Sharma, 1966, 1968, 1969; Krishnamoorthy and Srihari, 1973) and Horne (1968) has suggested that *Cardisoma guanhumi* may excrete urea. Further studies are required on the metabolic capabilities of these animals.

TERRESTRIAL CRUSTACEA

In terrestrial arthropods the major excretory products are purines and clearly there has been strong selective pressure for purinotelism in the terrestrial habitats. It might be expected that the terrestrial crustaceans would conform to this pattern but the limited information available indicates that this is not generally the case.

Isopoda

The isopods are the most successful of the terrestrial crustaceans with approximately 1000 species ranging from supralittoral to desert habitats. Like their aquatic relatives, they are primarily ammonotelic but with the important difference that much of the ammonia excreted is in gaseous form (Dresel and Moyle, 1950; Hartenstein, 1968; Wieser *et al.*, 1969; Wieser and Schweizer, 1970; Wieser, 1972b). Surprisingly, there have been no comprehensive investigations either on the partitioning of excretion between the possible routes or the proportions of various compounds eliminated by each route. Dresel and Moyle (1950) partitioned faecal nonprotein nitrogen in several species. Ammonia was the main nitrogenous product, uric acid made up 5–10%, amino acids 1–6% with only traces of urea. Faecal ammonia in *Porcellio scaber*, however, comprises only 10% of total ammonia excretion, the other 90% being released as a gas (Wieser and Schweizer, 1970). No data are available either for the urinary flow rate nor the concentration of nitrogenous excretory products of urine. Nevertheless, the overall dominance of gaseous NH_3 excretion is clear.

Interestingly, excretion of NH_3 is not continuous but varies diurnally with peak excretion coinciding with periods of minimal activity. It is argued that this allows excretion whilst the animal is resting in a moist microclimate thus minimising water loss during volatilization of NH_3 (Wieser *et al.*, 1969; Wieser, 1972b). This diurnal pattern of excretion may be endogenous in isopods as it is also seen in aquatic species (Kirby and Harbaugh, 1974). Excretion in terrestrial isopods also shows seasonal patterns and is affected by temperature, presumably via the effect on general metabolism (Wieser *et al.*, 1969; Wieser, 1972a, b).

Although it has been known for 40 years that volatilisation of NH_3 is the principal method of nitrogenous excretion in terrestrial isopods, the exact nature of the mechanism involved remains obscure. Given that excretion of NH_3 is not continuous, storage of ammonia between periods of elimination must occur and some method of detoxification of ammonia is indicated. However, data for routine levels of ammonia (*c.* 1.5 $mmol.L^{-1}$) and amino acids (*c.* 2 $mmol.L^{-1}$) in the haemolymph are available only for *P. scaber*, while ammonia concentrations of 1–17 $mmol.L^{-1}$ and glutamate and glutamine of 6–7 $mmol.L^{-1}$ are reported in homogenates of the body wall of *P. scaber* (Wieser and Schweizer, 1972). Infor-

mation on detoxification mechanisms is lacking for terrestrial isopods but the presence of glutamine and glutaminase in the body wall of *P. scaber* indicates a capacity for generation of ammonia from glutamine at this site (Wieser, 1972c; Wieser and Schweizer, 1972). Thus glutamine may be involved in ammonia detoxification and transport as indeed may other mechanisms suggested above for aquatic crustaceans. Further investigations are needed on this matter. Hartenstein (1968, 1970) provided some evidence for oxidative deamination in *Oniscus asellus* but amino-oxidase activity was concentrated in the hepatopancreas which is not suitably located for volatilisation of resultant NH_3.

As ammonia generated will be largely ionised at normal pH levels, the next matter for consideration is its conversion to NH_3. One possibility is that NH_3 is generated in the tissues, at the point of elimination, by local alkalinisation and the NH_3 diffuses out into the air down its partial pressure gradient. Alternatively, NH_4^+ may be eliminated into urine in the excretory organs or across the body wall into fluid (urine or pleopod fluid) which is then made alkaline (Wieser, 1972b) forming NH_3 which is lost to the air. This could be achieved by reabsorption of protons. This would presumably require ion transport across the epidermis lining the channels although it could also occur across the pleopods which have an appropriate ion-transporting epithelium (Kuemmel, 1981).

A potential mechanism for production of gaseous NH_3 which utilises the latter form of elimination was suggested by Hoese (1981). The terrestrial isopods possess a network of water-conducting channels which carry urine. Urine released into this system, from the maxilliary glands, flows along the channels on the dorsal and ventral surfaces and over the pleopods before being re-ingested at the anus (Hoese, 1981, 1982) and it was suggested that volatilisation of NH_3 would be effected during this circulation. If release of urine occurred during periods of inactivity in retreats, water loss from the system by spillage and evaporation would be minimised. This hypothesis is based on observations of micro-anatomy and fluid flow and requires physiological evidence to substantiate it. Thus it must be shown that the urine released contains adequate amounts of NH_4^+ to explain measured rates of NH_3 release. Secondly, it must be demonstrated that the fluid in the channels actually becomes alkaline as gaseous NH_3 cannot be released otherwise.

The terrestrial isopods examined all have deposits of uric acid in the body (Dresel and Moyle, 1950). There are no specific tissues in which this is located, as in the freshwater *Asellus* (Lockwood, 1959), and in *Oniscus asellus* deposits are reported as being located in the 'body wall' (Hartenstein, 1968). The highest level reported is in *Armadillidium* (*c.* 5μmol.g^{-1} wet weight) whilst levels in *O. asellus* and *P. scaber* are almost an order of magnitude lower (Dresel and Moyle, 1950; Hartenstein, 1968). It is not clear whether these deposits represent excess dietary intake of purines or if they have been synthesised *de novo* but there are no data suggesting the presence of synthetic pathways and Hartenstein (1968) considered synthesis unlikely. As uricolytic enzymes are present in *O. asellus* (Hartenstein, 1968) storage of uric acid cannot be considered obligatory and must perform some useful metabolic role.

Amphipoda

There are numerous species of terrestrial amphipods, in the Family Talitridae, ranging from supra-littoral to fully terrestrial. The latter are best represented in the Southern Hemisphere, particularly Australia and New Zealand (Hurley, 1968) where they are extremely abundant in forest and grassland habitats well inland. Knowledge of their nitrogenous excretion is poor. In the supra-littoral *Orchestia*, ammonia makes up the major portion of faecal non-protein nitrogen (Dresel and Moyle, 1950) but it is not known what portion of total nitrogen excretion this represents. Neither is it clear from this work if *Orchestia* excretes gaseous NH_3. Further work is needed on this group, particularly on the terrestrial species.

In the freshwater cave dweller *Niphargus*, spherules of uric acid are stored in special cells on the pericardial septum where the urates bind a variety of anions and cations (Graf and Michaut, 1975). These are considered to be reserves of purine and ions for metabolic usage rather than deposits of waste nitrogen derived from protein catabolism (Graf and Michaut, 1975). Data are lacking for terrestrial species.

Anomura

The Anomura are represented on land by the Coenobitidae, and include the Robber Crab, *Birgus latro*, and twelve species of shell-carrying hermit crabs, *Coenobita*, some of which occupy supra-littoral niches whilst others range inland (Hartnoll, 1988). Nitrogenous excretion has

TABLE 2. The chief excretory products and their routes of excretion in *Gecarcoidea natalis*, *Geograpsus grayi* and *Birgus latro*.

Route	% Total N output	% N Output as Ammonia	% N Output as Uric acid
Gecarcoidea natalis			
Faeces	19.0	67.03	
P	69.9	73.7	
Gas	11.1	100.0	
Total	-	91.8	2.95
Geograpsus grayi			
Faeces	12.3	27.6	
P	5.5	63.3	
Gas	63.3	100.0	
Total		90.9	0.75
Birgus latro			
Faeces	96.2	11.9	82.6
P	0.0012		
Gas	3.8	100.0	
Total		15.2	79.5

been studied only in *B. latro* (Greenaway and Morris, 1989).

B. latro is uricotelic and solid uric acid, excreted in the faeces, comprises about 80% of total non-protein nitrogenous excretory waste. The remaining faecal excretory nitrogen is largely ammonium (11.9%) with some free amino acids and urea (Greenaway and Morris, 1989). Loss of nitrogen in the excretory fluid or as gaseous NH_3 is insignificant (Table 1).

Uric acid appears as separate white portions of the faecal string, quite separate from the brown faeces comprised of food residues. Excretion is episodic with uric acid released into the gut in distinct bouts of excretion. Homogenates of the midgut gland contain xanthine oxidase, the enzyme responsible for the final step in the conversion of purine bases to uric acid and the midgut is presumed to be the active site in the final stage of uric acid production. *B. latro* can synthesise purines *de novo* but nothing is known of the metabolic pathways concerned.

Starved *B. latro* excrete uric acid at an undiminished rate and may metabolise protein during inanition. The observed output could also result from excretion of uric acid stored within the body (see below).

Large amounts of uric acid are stored by *B. latro* particularly in laboratory-maintained animals (Greenaway and Morris, 1989). Extensive white deposits occur in all tissues but it is not clear whether the urate is free in the haemocoel, or is contained in special 'urate' cells as described for the amphipod *Niphargus* (Graf and Michaut, 1975). White deposits have also been observed in *Coenobita brevimanus* (P. Greenaway, unpubl. obs.). The functional significance of urate reserves is unknown but, given that *B. latro* can excrete uric acid, their maintenance must perform some useful metabolic role. This may be to act as a mobilisable nitrogen reserve for synthesis of amino acids or perhaps as an ion store prior to ecdysis or modulation of haemolymph ions during dehydration.

Brachyura

The land crabs are drawn from some 16 different families and range from amphibious to highly terrestrial in habit (Bowman and Abele, 1982; Hartnoll, 1988).

Gecarcinidae. Early work on *Cardisoma guanhumi* discounted the urine as a significant vehicle for excretion (Horne, 1968; Gifford, 1968). Subsequent work has confirmed low urinary nitrogen concentrations (Wolcott and Wolcott, 1987a; Wolcott D.L., pers. comm.; Greenaway and Nakamura, in press) but this has little relevance to excretion as urine in land crabs is not the final excretory fluid and is passed into the branchial chambers. Here it may be extensively modified before being released as a final excretory fluid (P) (Wolcott and Wolcott, 1984, 1985; Greenaway *et al.*, 1990) in which $[NH_4^+]$ is considerably elevated (Wolcott and Wolcott,

1987b; Greenaway and Nakamura, in press). This NH_4^+ must be added to the urine during its residence in the branchial chambers, presumably via the gills but the mechanism is unknown. Any of the mechanisms described above for aquatic crustaceans could be utilised with the urine providing ions for exchange (Fig. 4). The maximum $[NH_4^+]$ recorded in P of *G. natalis* was 73 mmol.L^{-1}, but the average was much lower at c. 11 mmol.L^{-1} (Greenaway and Nakamura, in press) and similar values are reported for other gecarcinids (Wolcott, D.L., pers. comm.).

In *Gecarcoidea natalis*, the chief excretory product is ammonia which makes up 92% of the non-protein nitrogen excreted. This is eliminated largely in the excretory fluid (70%) and the remainder exits as gaseous NH_3 and faecal nitrogen (Greenaway and Nakamura, in press; Table 2). The small amount of excretion of gaseous NH_3 (Table 2) may well have originated from faeces and/or P by direct volatilisation. No significant excretion of gaseous NH_3 was reported from *C. carnifex* (Wood and Boutilier, 1985) and while Horne (1968) reported considerable gaseous excretion by *C. guanhumi* no supporting data were offered.

Routine excretion in gecarcinids is as NH_4^+ in the final excretory fluid. Total nitrogen excretion is relatively low (Horne, 1968; Gifford, 1968; Wolcott and Wolcott, 1987b; Greenaway and Nakamura, in press) and the $[NH_4^+]$ of P is normally low enough to avoid toxicity problems although blood levels are quite high (Table 1).

All species of gecarcinids studied contain deposits of uric acid (Gifford, 1968; Wood and Randall, 1981; Greenaway and Nakamura, in press). Amounts are very variable but appear to be related to diet and accumulation is greatest in laboratory specimens (Wolcott and Wolcott, 1987b). Gifford (1968) considered that uric acid deposits exist free in the haemocoel but histological evidence for this is lacking. The origin of the deposits is unclear but it is unlikely that they are derived solely from excess dietary purine compounds and *de novo* synthesis must be a possibility. As with *Birgus latro* some useful metabolic function of the reserves must be assumed as most crustaceans possess uricolytic enzymes and could degrade the deposits and excrete ammonia.

GRAPSIDAE. The only other land crab in which nitrogenous excretion has been studied is *Geograpsus grayi*, a small carnivorous species with a relatively high rate of nitrogenous excretion (c. 100 umol.kg^{-1}. h^{-1}) (Greenaway and Nakamura, in press). *G. grayi* is also ammonotelic but differs from the gecarcinids in excreting most of its waste nitrogen as gaseous NH_3 (Table 2). Release of gas is not continuous and the crab alternates between bouts of excretion lasting several days and similar periods of minimal excretion. It is probable that protein catabolism is ongoing so ammonia must be detoxified and temporarily stored between bouts of excretory activity. Possible metabolic pathways were outlined above. Excretion of gaseous NH_3 by starved animals is similar to that of fed crabs indicating continued catabolism of protein during starvation (Greenaway and Nakamura, in press). Elimination of NH_3 probably occurs in the branchial chambers where the gills provide a large surface area of epithelium with an ultrastructure suited for ion transport (Greenaway and Farrelly, 1990) and the urine again could provide a source of ions to fuel any exchange processes which may be involved. Ammonia could be lost directly in gaseous form or passed into the P as NH_4^+ and lost as NH_3 following alkalinisation.

The possibility of conflicts between ion regulatory requirements and nitrogen excretion should be considered in brachyurans. The mechanisms of elimination of ammonia described above (Fig. 4), depend on activity of basolateral Na/K–ATPase and the entry of sodium ions from the fluid bathing the gills (in this case urine). In salt replete animals, sodium is not reabsorbed from the urine (Wolcott and Wolcott, 1985; Taylor, Greenaway and Morris, unpubl. data) and this could block ammonia excretion. Greatest difficulty would be experienced by animals on a diet rich in both salt and nitrogen. Dehydration, too, could cause excretory problems as reduction and cessation of flow of excretory fluid would first elevate $[NH_4^+]$, perhaps to toxic levels, and finally eliminate excretion. Such reduction in urine flow occurs during desiccation in the gecarcinids (Kormanik and Harris, 1981). In *Cardisoma carnifex*, ammonia excretion ceases during desiccation but is elevated on rehydration suggesting interim storage in non-toxic form (Wood *et al.*, 1986). Uric acid, amino acids or protein could be utilised for this purpose. These problems could also occur in isopods if excretion relies on ammonium being excreted into the urine or across the gills into a urine or water film.

ASTACIDEA

There are numerous species of semi-terrestrial freshwater crayfish in Australia and N. America

which may spend long periods without free water, e.g. *Engaeus, Cherax*. Nothing is known of their excretory patterns during aerial exposure.

CONCLUSIONS

In aquatic crustaceans, the main excretory product is ammonia which is excreted across the gills into the respiratory water stream and carried away. This ensures that the external ammonia concentration is always low and there is a favourable gradient for excretion and no problems of toxicity. By contrast terrestrial arthropods, other than crustaceans, are mostly purinotelic and the overriding selective factor favouring this, is believed to have been the conservation of body water. Purines may be excreted in crystalline form in the faeces with minimum accompanying water loss, an important factor in the maintenance of water balance of small animals in a desiccating environment. Of the terrestrial crustaceans examined only one species is clearly purinotelic (*Birgus latro*) and, although many more species seem to have an active purine metabolism, their dominant excretory product is ammonia. Comparatively few terrestrial species have been examined and while further work may reveal a few additional purinotelic species, the group appears to be predominantly ammonotelic.

It is of interest to consider how far the various groups of terrestrial crustaceans have diverged from the typical aquatic pattern and moved towards the terrestrial system. In this we are hampered by the relative lack of information on excretion in terrestrial groups.

The gecarcinid crabs appear to have diverged least from the aquatic pattern. They continue to excrete ammonium across their gills and as respiratory water is not available they utilise the excretory fluid from the antennal organs. The volume of urine produced is limited, however, and this necessitates quite high concentrations of ammonia in the branchial chambers and may result in an adverse electrochemical gradient across the gill epithelium. Urine flow is tied to overall water balance rather than excretory requirements and this may cause excretory difficulties necessitating temporary storage of waste nitrogen in negative water balance.

Geograpsus grayi and terrestrial isopods have departed further from the aquatic pattern and have solved the loss of the respiratory water as an excretory vehicle in a different manner. They retain the respiratory medium as a vehicle for excretion by releasing gaseous NH_3. Air flow over the body or through the branchial chambers effectively prevents the buildup of ammonia next to the excretory surface maintaining a favourable gradient for excretion. Until this mechanism of excretion is better understood it will not be possible to say how much independence from water it allows. Actual elimination of NH_3 may first require transport of NH_4^+ into the excretory fluid for conversion to NH_3 or may be direct from the excretory epithelium. Excretion of gaseous NH_3 may be seen as an advance in terrestrial adaptation over that shown by gecarcinids.

Excretion in *Birgus latro* shows a complete break from the aquatic pattern of ammonotelism. The elimination of nitrogenous waste as uric acid and the associated ability to synthesise purine is a major evolutionary advance and places this species at a similar level of adaptation to the other major groups of terrestrial arthropods.

Why have terrestrial crustaceans retained ammonotelism whilst other terrestrial arthropods have not? The main considerations may be the restricted metabolic pathways present at the onset of terrestrial life and the period of evolution spent on land. As aquatic species are ammonotelic and probably lack synthetic pathways for both purines and urea, colonists would thus begin terrestrial life excreting ammonium across the gills and this would be expected to influence both behaviour and habitat selection. Moist microclimates such as leaf litter and rainforest would be favoured and activity restricted to moist conditions so that adequate excretory fluid would be available for elimination of ammonia. Such habitats are characteristic of terrestrial amphipods, isopods and crabs, and although several species live in xeric habitats, their activity is restricted and the animals have a humid retreat or burrow. It would be naive, however, to assume that limitations of the excretory system are responsible for the restricted habitats occupied e.g. *Birgus latro* has a system well tailored for terrestrial life but occupies similar habitats to other terrestrial crabs. Limitations of the reproductive and osmoregulatory systems under terrestrial conditions could equally well affect distribution. Given the habitat in which the animals are found, excretion of various forms of ammonia is feasible and may be advantageous as it carries a minimal energetic cost and requires only small changes to existing systems whilst efficiently excreting waste nitrogen

The apparent lack of synthetic pathways for excretory materials may mean that a long period of evolution on land and strong selective pressure to penetrate drier habitats is necessary before typical terrestrial patterns of excretion can be developed. Fossil evidence, although fragmentary, suggests that most groups of terrestrial crustaceans are relatively recent (and in some cases ongoing) colonists of land (Warner, 1977; Little, 1983).

The mechanisms of detoxification, transport and elimination of nitrogenous waste all require further study, particularly in the terrestrial species. In particular the significance of uric acid deposits is far from clear and we need to clarify both this aspect and the origins of the uric acid (dietary or synthesised?). The occurrence of purinotelism should also be investigated and investigations of the xeric-adapted forms such as the desert isopods *Hemilepistus* and *Venezillio*, the hermit crabs *Coenobita clypeatus* and *C. rugosus*, and the brachyurans *Holthuisana transversa* and *Potamon potamios* may be rewarding. Additionally, some terrestrial groups have not been studied at all (Amphipoda and crayfishes) and should reward future investigation.

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THE ROLE OF CRUSTACEANS IN NITROGEN RECYCLING IN A HIGH ENERGY SURF ZONE ECOSYSTEM

The Sundays River surf zone (33°58'S,29°19'E) in the Eastern Cape South Africa is considered to function as a semi-closed ecosystem (McLachlan, 1984) with the outer boundary at the edge of the surf cell circulation pattern and the landward boundary at the drift line. Surf zones exist in three major energy states: a high energy dissipative state, a low energy reflective state, and a range of intermediate states (Short and Wright, 1983). The Sundays River surf zone exists in the intermediate longshore bar trough energy state for 90% of the year, moving to a high energy dissipative state during storms and to a lower energy intermediate transverse bar rip state during calm periods. The major mechanism for the return flow of water to the nearshore is via rip currents. Three types of rips operate in the surf zone: non exchange rips which do not break through the breaker line and serve to circulate water within the inner surf zone, exchange rips which carry water from the inner to the outer surf zone and mega rips which operate during storm conditions and discharge water kilometres out to sea. Half turnover time for water in the inner and whole surf zone is in the order of hours and days, respectively (Talbot, 1986). The unit of environment used in surf zone studies is a metre strip of surf zone from the drift line to the 10m depth contour 500m offshore which encloses a volume of 2500m^3 (McLachlan and Bate, 1984). Phytoplankton (mainly the diatom *Anaulus australis*) are the major primary producers in the surf zone forming dense accumulations usually in association with rip currents. Phytoplankton accumulations are a function of diel vertical migration patterns, offshore–onshore migration and the storm calm cycle. These phytoplankton accumulations fuel three distinct food chains; the macroscopic; interstitial; and microbial loop. The macroscopic food chain consists of benthos, zooplankton, fish and birds. Benthos form 46% of total macrofaunal biomass with filter feeding bivalves the most important component. Crustaceans (mainly the three spot swimming crab, *Ovalipes punctatus*) contribute only 1% of benthic biomass. Zooplankton are a major component of the macroscopic food chain forming 40% of macrofaunal biomass with numbers and biomass dominated by crustaceans. Small penaeid prawns (*Macropetasma africanus*) and mysids (*Mesopodopsis slabberi* and *Gastrosaccus psammodytes*) contribute >90% of zooplankton biomass (Romer, 1986). The role of crustaceans in the recycling of nitrogen in the Sundays River surf zone was determined from detailed laboratory and field studies on the nitrogen requirements of surf zone phytoplankton and the nitrogen dynamics of the major macrofaunal species. The nitrogen requirements of the surf zone were calculated directly from the estimates of phytoplankton primary production. Primary production was measured using C^{14} uptake and O^2 evolution. A mathematical model incorporating temperature, light, beach state, and photo-inhibition was used to estimate annual primary production. The portion of assimilated carbon involved in cell doubling was calculated and divided by the C:N ratio of *A. australis* (C:N ratio = 6.8). Using this method the nitrogen requirements of the surf zone (inner and outer) are calculated at 13,200 gN.m^{-1}.y^{-1}. (Campbell, 1987). The forms of nitrogen excreted and the effects of mass, temperature, starvation, diet and presence/absence of sediment on excretion rates were determined for *M. africanus* (Cockcroft and McLachlan, 1987) and the mysids *M. slabberi* and *G. psammodytes* (Cockcroft *et al.*, 1988). Information on population structure, abundance, diet and feeding behaviour collected over a decade of research in this area was combined with nitrogen excretion data to construct population nitrogen budgets for these species. The amounts of nitrogen recycled by the less abundant crustacean components (crabs and small zooplankton forms) were obtained from population nitrogen budgets using literature values for nitrogen excretion rates (Cockcroft, 1988). Crustaceans recycle 2626 gN.m^{-1}.y^{-1}, in dissolved inorganic form (mainly ammonia) which constitutes 79% of the dissolved inorganic nitrogen excreted by the macrofaunal food chain. Large zooplankton forms (prawns and mysids) supply the bulk of this recycled nitrogen. This represents 20% of total surf zone phytoplankton nitrogen requirements assuming that phytoplankton utilise dissolved inorganic nitrogen only. Crustaceans also contribute 1539 gN.m^{-1}.y^{-1}, or 64% of the dissolved and particulate organic nitrogen (mainly faeces) excreted by the macrofauna. This represents 17% of total nitrogen requirements estimated for the microbial loop (Romer and McGwynne, pers. comm.). Crustaceans therefore play an important role in surf zone nitrogen recycling both in terms of phytoplankton requirements and as a link between the macroscopic and microbial loop food chains.

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INTEGRATION OF CELLULAR, ORGANISMAL, AND ECOLOGICAL ASPECTS OF SALT AND WATER BALANCE

DONNA L. WOLCOTT

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Crustaceans occupy habitats ranging from hypersaline through freshwater and terrestrial, and differing in variability of temperature, salinity, and moisture over periods of hours to months. Even in stable, isosmotic environments, they must expend energy in maintaining their internal osmotic and ionic milieu. The impetus for maintaining a constant internal environment can be traced to the deleterious effects of volume changes in individual cells, with the resulting structural and functional changes in proteins. Organisms employ a combination of inorganic ion transport and organic osmolyte deployment to match intracellular and extracellular osmolalities, thus reducing the energy required to maintain cell volume. In multicellular animals, such as crustaceans, changes in external salinity are countered by two strategies. In the first, the osmolality of the internal fluid tracks that of the external medium, transferring osmotic work to the individual cells. The second strategy involves regulation of the osmolality of the internal fluid. The work of osmo- and iono-regulation is concentrated in surfaces in contact with the external medium, such as the integument and gut. Water regulation is relegated to specialised excretory organs, such as the antennal gland, and ion transport to spatially restricted and specialised tissues, such as the gills of crabs and salt glands of *Artemia*. A number of ion transport systems important in iono- and osmoregulation have been identified in crustaceans. Many of these systems are integral to acid-base balance and nitrogen excretion as well. In addition to sharing common enzymatic pathways, ion regulation frequently occurs on morphological structures with multiple functions. Thus, the gills of decapod crabs serve gas exchange, nitrogen excretion, and ion exchange. Constraints caused by the limited number of physiological mechanisms and morphological options result in integrated responses of salt and water balance, acid-base balance, gas exchange and intermediary metabolism. Examples are given from aquatic decapods. Some terrestrial crabs employ a single behavioural modification, urine recycling at the gill, that addresses several concurrent physiological problems, such as ion depletion, water limitation and nitrogen excretion. In crustaceans in general, behavioural adaptations permit occupation of habitats that would be untenable based on physiological and morphological capabilities alone. To describe the water and salt balance of a particular organism, it is therefore necessary to integrate information from cellular mechanisms, organismal responses, and field observations. □ *Osmoregulation, ionoregulation, ion transport, volume regulation, crustaceans, terrestrial crabs, osmolytes.*

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Cell function is supported only within a narrow range of ionic and osmotic conditions. If uncompensated, chemical changes resulting from metabolic processes would inexorably move the cell from the dynamic equilibria optimal for enzyme function. Such constancy of the internal environment that exists must be maintained through dynamic, energy-requiring transport of ions, aided, and also thwarted, by passive water and ion fluxes. The energetic cost of osmo- and iono-regulation differs in degree, but is incurred by marine, brackish, freshwater, and terrestrial organisms alike.

The physical laws of thermodynamics ultimately dictate the movements of solvent and solutes across the cell membrane between the external and internal media. The forces involved, and the equations that describe them, are well reviewed in Mantel and Farmer (1983), with additional information on water fluxes in a terrestrial environment found in Greenaway (1988).

Enhanced fitness of organisms that maintain proper solute and water relations in the interior of individual cells drives evolution of osmo- and iono-regulatory systems. When cells are exposed to fluids that are anisosmotic (not isosmotic) to the cell's interior; they tend to shrink

or swell, depending on whether the fluids are hyper- or hypo-osmotic to the cytoplasm. Cell volume can be restored by the active extrusion or uptake of inorganic solutes, such as Na^+, and by manipulating the concentration of organic osmolytes, such as free amino acids (Hoffman and Simonsen, 1989; Chamberlin and Strange, 1989; Pierce, 1982). Cells of organisms that show volume regulation are able to return to their normal volume by matching the internal osmotic pressure to the new extracellular regime.

Volume regulation under anisosmotic conditions involves a number of processes. In the short term, inorganic ions are pumped into or out of the cell to bring the fluid compartments on either side of the cell membrane into osmotic balance, restoring cell volume. However, the conformation of proteins, and hence their function, is intimately dependent on the presence and concentration of particular ions. Therefore, for long-term osmotic adjustments, organisms employ a variety of organic osmolytes. Organic osmolytes, although metabolically expensive to deploy, have a distinct advantage over inorganic ions in that they do not compromise protein function even when present in high concentrations (Yancy *et al.*, 1982).

Organic osmolytes are selected for their compatibility with enzyme and other physiological functions, and on the basis of their metabolic or environmental availability (Hochachka and Somero, 1984; Gilles and Pequeux, 1983; Goolish and Burton, 1989). Across the entire spectrum of living creatures, organic osmolytes include sugars, polyols, amino acids, methylamines, and urea. Crustaceans employ all but the last two, with non-essential free amino acids being most common (Gilles and Pequeux, 1983; Chamberlin and Strange, 1989).

For both rapid volume adjustments and general cell function, movement of inorganic ions occurs through ion-specific channels and pumps, and via a variety of exchangers and cotransporters. Paramount among the transport systems is Na^+/K^+-ATPase, responsible for pumping Na^+ from the cell. The inwardly-directed electrochemical gradient for Na^+ thus created provides the motive force for the movement of other ions against their concentration gradients. The coupled movement of Cl^- and Na^+ is an example of cotransport. Most cotransport systems described so far involve coupled transport of cations and anions whose charge balance is zero. Such systems are electroneutral, or electrically 'silent'. Their operation neither affects the membrane potential nor is affected by it (Hoffman, 1986). Like cotransport systems, exchange systems (e.g. HCO_3- for Cl^-) can also be electroneutral.

Because ion transport and water balance are problems around which life evolved, the mechanisms are fairly universal. Ion transport mechanisms identified in other organisms are found to operate in crustacean tissue as well (Table 1)(Chamberlin and Strange, 1989). Some of the conflicting data surrounding the Na^+/H^+ exchanger in crustaceans may be resolved, now that the presence of an electrogenic, $2Na^+:1H^+$ exchanger has been identified, both in crab gill (*Callinectes sapidus*, Towle and Baksinski, 1989) and in lobster antennal gland (*Homarus americanus*, Franco and Ahearn, 1989).

Some progress is being made in the search for the signals and sensors whereby individual cells detect volume changes (Chamberlin and Strange, 1989). Ion channels have been identified that respond directly to the changes in hydrostatic pressure resulting from the efflux or influx of water during anisosmotic conditions by altering the transport of specific ions. Such stretch-activated ion channels respond to changes as small as 5 mmHg. The amount of membrane stretch resulting from a volume increase of even 1% would be sufficient to activate the K^+ channel in *Necturus* proximal tubule cells (Sackin, 1987). The cytoskeleton may play a role in stimulating stretch activated channels by amplifying volume-induced stretch. Stretch inactivated channels have been identified coexisting in the same neurons as stretch activated channels (Morris and Sigurdson (1989). Chamberlin and Strange (1989) speculate that coordinated activation of transporters active in volume regulation and deactivation of resting conductances would permit more rapid and energetically efficient volume regulation.

Once cells receive input signalling a change in osmotic conditions, either physically, through hydrostatically-transmitted information, e.g. stretch activated receptors, or chemically, e.g. by a variety of intracellular second messengers which integrate the cells osmoregulatory response.

Several intracellular signals have been implicated in cell volume regulation, including cyclic AMP, leukotrienes, protein kinases, and Ca^{2+}, with the possible involvment of calmodulin (Chamberlin and Strange, 1989). Current evidence confirms that cyclic AMP is an intracellular modulator of ion transport in crustaceans as well (Bianchini and Gilles, 1990).

The permeability of cells to water and ions is affected by the kinds and quantity of lipids present in the cell membrane. Changes in the quality and quantity of membrane and blood lipids, including cholesterol, correlate with changes in permeability (Chappelle and Benson, 1986; Spaargaren and Mors, 1985; Subramanyam and Krishnamoorthy, 1983) and link osmoregulation with lipid metabolism.

Since the metabolic processes discussed so far require energy, iono and osmo-regulation are interdependent with respiration and those physical and biotic factors which effect it.

In the context of multicellularity, the interaction of an organism with its environment is changed in fundamental ways. For a given amount of cytoplasm, the proportion of membrane exposed to the environment is reduced, e.g. every organism small enough to depend solely on diffusion for transport of oxygen and nutrients, and for release of metabolic wastes (approximately 1 mm maximum effective thickness, Graham, 1988) only needs to control permeability and to transport ions over a small proportion of its total plasma membrane.

Concurrent with evolution of larger body form is the development of interior fluid reservoirs and circulatory systems to enhance transport of gases and solutes. The major and initial response to variations in the environment is still confined to the integument, but the organism has the option of controlling the composition of the interior fluid spaces. Again, the driving force is the maintenance of an intracellular ionic and osmotic environment optimal for cell function. Crustaceans employ two options in dealing with salinity fluctuations. One is to allow the fluid bathing the cells, the haemolymph, to track external salinity, thus transferring the work required during anisosmotic regulation to the cell. Alternatively, they may manipulate haemolymph composition during salinity changes to minimise the osmotic work that the cells must do. The former option, osmoconformity, restricts organisms to habitats where the osmotic concentration is fairly high and stable, or commits them to volume regulation by cells during adverse osmotic conditions. The second pattern, osmoregulation, permits occupation of ionically or osmotically extreme or variable habitats. Osmoregulation and osmoconformity can exist in the same organism over different parts of the salinity scale. For instance, in marine organisms occasionally exposed to fresh water input, conforming at high salinities and hyper-osmoregulating at low salinities would be adaptive. However, the impetus for maintaining a constant ionic concentration in coelomic fluids is still to reduce the need for volume regulation by individual cells. The regulatory options adopted by different organisms are reflected in the familiar categories of osmoregulation: osmoconformity, hyperregulation, and hyporegulation, and the combinations thereof (Mantle and Farmer, 1983). As external salinity varies, the effects on cell volume will depend on the type of osmoregulation available, both at the organism's surface and at the cell (Gilles and Pequeux, 1983).

In larger organisms, and those adapted to variable habitats, tissue that regulates transport of ions and water is highly localised, with the rest of the surface fairly impermeable, thus passively restricting exchange with the environment. Rather than being uniformly deployed in the cell membrane, certain ion-transporting enzymes are restricted to or concentrated on a particular surface. For instance, Na^+/K^+-ATP-ase is highly concentrated in the basal-lateral membrane of the gill epithelial cell, where it apparently functions to transport cations, including NH_4+, between the cell interior and the haemolymph (Table 1) (Towle and Kays, 1986; Towle and Holleland, 1987). Both the activity and quantity of this enzyme increase dramatically with changes in salinity (Kirschner, 1979; Towle, 1984). On the apical surface, Na^+ is exchanged for H^+ (Table 1).

Commonly, respiratory, feeding, and locomotory functions are combined at the same surface, as is ion and solute transfer. Water flow created by feeding and locomotory currents enhances exchange of solutes across the integument by reducing the boundary layer. Most aquatic phyla are dependent on integumental gas exchange at some point in their life history (Graham, 1988). Among crustaceans, individuals depend on integumental exchange during development as eggs and larvae.

Salt and water balance are intertwined with acid-base balance, gas exchange, and through changes in free amino acid concentrations, intermediary metabolism and fluxes of ammonia. The links are forged by the commonality of biochemical mechanisms and morphological structures involved in these processes. Synthesis and catabolism of free amino acids during fluctuations in salinity links osmoregulation, nitrogen metabolism, and excretion. Use of common pathways also interconnects ion regulation and acid-base balance.

TABLE 1. Examples of ion transport pathways identified in crustaceans.

TRANSPORT MECHANISMS	SPECIES	LOCALISATION	REFERENCES
Na^+/K^+-ATPase	*Artemia salina*	metepipodites + head, maxillary gland, gut	Holliday, 1985a
		larval salt glands	Ewing *et al.*, 1974
		larval salt glands	Lowy and Conte, 1985
	Callianassa jamaicanse	larval stages	Felder *et al.*, 1986
	Callinectes sapidus	gills	Mantel and Olson, 1976
		NH_4^+activation	Towle *et el.*, 1976
		NH_4^+substitutes for K^+	Towle and Holleland, 1987
			Neufled *et el.*, 1980
		basolateral membrane	Towle and Kays, 1986
	Carcinus maenas	gills	Siebers *et al.*, 1982
		basolateral membrane	Towle and Kays , 1986
	Eriocheir sinensis		Pequeux andGilles, 1977
	Gecarcinus lateralis	gills	Mantel and Olson, 1976
	Homarus gammarus	larval stages	Thuet *et al.*, 1988
	Procambarus clarkii	antennal gland	Sarver and Holliday,unpubl.
	Uca minax		Wanson *et al.*, 1984
	U. pugilator		Graszynski and Bigalke, 1987
		gills 5 and 6	D'Orazio and Holliday, 1985
	U. pugnax	gills 5 and 6	Holliday, 1985b
	U. tangeri	basolateral gills 5,6	Graszynski and Bigalke, 1987
Na^+/H^+	*C. sapidus*		Pressley *et al.*, 1981
		gills, apical	Burnett and Towle, 1990
	Corophium curvispinum	amilioride sensitivity	Taylor and Harris, 1986
	Eriocheir sinensis	gill membrane vesicles	Grayzynski and Bigalke, 1987
			Pequeux and Gilles, 1988
	Uca tangeri		Grayzynski and Bigalke, 1987
2 Na^+/H^+	*C. sapidus*	posterior gill vesicles	Towle and Baksinsk,i 1989
	Homarus americanus	antennal gland vesicles	Franco and Ahearn, 1989
Na^+/Na^+	*C. sapidus*		Pressley *et al.*, 1981
Na^+ channel	*Uca tangeri*		Grayzynski and Bigalke, 1987
Carbonic anhydrase ($CO_2+H_2O \Leftrightarrow H^++HCO_3^-$)	*C. sapidus*		Neufeld *et al.*, 1980
		gills	Burnett *et al.*, 1981
		gills 6-8	Henry and Cameron, 1982
		cytoplasmic+membrane	Henry, 1988
	Cardisoma carnifex	gills	Randall and Wood, 1981
	Cardisoma guanhumi	gills 6-8	Henry and Cameron, 1982
	Gecarcinus lateralis	gills 8 and 9	Henry and Cameron, 1982
	Homarus gammarus		Thuet *et al.*, 1988
Cl^- channel	*Carcinus maenas*		Lucu and Siebers, 1987
	Uca tangeri	basal	in Grayzynsk and Bigalke, 1987
Cl^-/HCO_3^-	*Callinectes sapidus*	gill	Burnett and Carroll, 1989

AMMONIA

If the transport mechanisms of the gill are overwhelmed by the speed or amount of salinity change, the haemolymph concentration will change. To minimise the work that must be done to maintain volume in the face of water influx, intracellular osmotic concentration is lowered both by increasing inorganic ion excretion, and by exporting or metabolizing some of the free amino acids (FAA). Metabolism of the FAA releases ammonia, which is transported by the haemolymph, dissolved or incorporated into glutamate (Regnault, 1987), to the gill. There, ammonia is exchanged for Na^+ (Towle and Holleland, 1987; Lucu *et al.*, 1989), coupling ion uptake and nitrogen excretion. Enhanced rates of ammonia excretion during hypoionic stress have been reported in the shore crab, *Carcinus maenas* (Spaargaren, 1982; Harris and Andrews, 1985), the intertidal prawn, *Palaemon elegans* (Rathke) (Taylor *et al.*, 1987), the shrimp *Crangon crangon* L. (Regnault, 1984), *Panaeus japonicus* Bate (Spaargaren *et al.*, 1982) and several other species (Mantel and Farmer, 1983).

Ammonia excretion can respond rapidly to changes in salinity, e.g. in the intertidal prawn, *Palaemon elegans* (Rathke), which may be subjected to frequent, rapid fluxes in salinity. Declines in FAA in the tail muscle, increases in ammonia excretion and adjustments in Na^+ concentration all occur within the first two hours following a major salinity drop (Taylor *et al.*, 1987). Similar rapid shifts in ammonia excretion follow transfer to low salinity in the blue crab *Callinectes sapidus* (Rathbun) (Mangum *et al.*, 1976), whose habitat is marked by longer-term seasonal fluctuations in salinity, in addition to storm events. Organisms inhabiting estuaries with large tidal fluxes experience repetitive cycling of salinity. *Crangon crangon* in the Penze estuary, France, has enhanced rates of ammonia excretion during ebb tides, as riverine water lowers the salinity, and lowered rates of excretion during flood tide, as high salinity waters return. The ammonia excretion rate is influenced by the velocity and direction of the salinity change, and by the range of salinities involved, and is greater in the winter. In the laboratory, shrimp exposed to simulated tidal cycles of salinity under winter conditions lose 1.75 times more ammonia than those in constant salinity (Regnault, 1984). In nature, burrowing (Birchard *et al.*, 1982, Zanders and Martelo, 1984) and circatidal activity rhythms (Al-Adhub and Naylor, 1975) may reduce exposure to salinity changes and minimise the energetic cost of inhabiting a variable environment.

GAS EXCHANGE

In *Callinectes sapidus*, inorganic ions and H^+ ions compete for the same site on the haemocyanin molecule, and raise or lower the oxygen affinity, respectively (Mangum, 1986). During hypoionic exposure, enhanced production of ammonia counteracts the lowering of oxygen affinity of haemocyanin caused by reduced Ca^{2+} concentration (Weiland and Mangum, 1975). A permanent solution to reduced Ca^{2+} concentration in the haemolymph of blue crabs acclimated to low salinity is the synthesis of an alternate haemocyanin subunit, and changes in the proportions of another, such that oxygen affinity is re-established at a new, lower level (Mason *et al.*, 1983; Mangum and Rainer, 1988).

ACID-BASE BALANCE

The pH of the cell depends on the strong ion difference (SID), as well as on the partial pressure of CO_2 (P_{CO_2}) and the concentration of weak acids (Stewart, 1978). The major control of pH in water-breathing animals is through adjustments of the SID (the difference between the quantity of fully-dissociated strong base cations and strong acid anions) (Cameron, 1978; Stewart, 1978). As Cl^- and Na^+ are moved across transporting epithelia, possibly in exchange for HCO_3^- and H^+, pH can change. Protein, amino acid, and ammonia concentrations change as cell volume regulation occurs. Thus, the same systems that are involved in ion regulation affect acid-base balance as well (Cameron, 1978; Hoffman and Simonsen, 1989). Hypersaline exposure can cause acidosis, as metabolic acid production outstrips increases in bicarbonate concentration (Wheatly and McMahon, 1982), and hyposaline conditions may result in alkalosis due to excess base cations (*Carcinus maenas* L., Truchot 1973, 1981; *Callinectes sapidus*, Weiland and Mangum, 1975).

In marine aquatic crabs, the gill plays a major role in ion transport, gas exchange and ammonia excretion, with the role of the antennal gland largely that of water balance, since the urine produced is isosmotic to the blood. Several freshwater crustaceans have evolved the capacity to produce a dilute urine, and the antennal gland in these forms functions remarkably like a vertebrate kidney, playing an enhanced role in ion and acid-base balance and ammonia excretion (Wheatly and McMahon, 1982; Wheatly

and Toop, 1989). Even in these forms, the majority of ion regulation occurs at the gill (Wheatly and Toop, 1989). The gut plays a role in ion regulation and water balance, too, (review, Mantel and Farmer, 1983), but the contribution of the gills is paramount.

How is ion regulation achieved in terrestrial crustaceans, given that the major ion-permeable surfaces, the gills, are no longer immersed in large volumes of water? Are the ion-pumping, nitrogen excreting, acid-base balancing capabilities of the gills lost to the organism? Not necessarily. Precisely because the organisms are in air, voided urine is not lost to the environment, and can be passed to the gill surfaces for ion reclamation (Wolcott and Wolcott, 1985, 1991, and unpubl.). So far, several species have been shown to reclaim ions from the urine during reprocessing at the gill (Table 2). The excretory product ('P') that is eventually released by the animal can be very dilute, comparable in ion concentration to hypoosmotic urine produced by several freshwater crustaceans (Table 2). Reprocessing essentially permits the production of a dilute urine, thus circumventing behaviourally the limited abilities of the antennal gland.

Urine represents the most saline water available to hyperosmoregulating terrestrial crustaceans, and as such, is a vital resource. The red land crab, *Gecarcinus lateralis*, inhabits dry upland burrows, and its water sources are dilute. When ion concentrations in the haemolymph are experimentally depleted, they can be replenished with ions from the diet (Wolcott and Wolcott, 1988). However, even feeding crabs show declines in haemolymph osmolality when the urine is prevented from reaching the gills (Wolcott, 1991). Avoidance of standing water, as in *Gecarcoidea lalandii* (Cameron, 1981) may be an adaptation to prevent accidental dilution of urine in the branchial chamber.

Ion reclamation is not the only function of the gill that is preserved by urine reprocessing. In both *G. lateralis* and the amphibious crab, *Cardisoma guanhumi*, ammonia concentrations increase 14 and 10 fold, respectively, as urine is reprocessed into 'P' (Table 2) (Wolcott, 1991). Not all species that recycle urine use 'P' for nitrogen waste disposal, and nitrogen excretion in species that recycle urine is turning out to be highly variable (Greenaway, pers. comm., and this volume).

In air-exposed crabs, fluid in the branchial chamber, whether water from the environment or urine from the antennal glands, may provide a reservoir for acid-base adjustments in those crabs that can regulate ions (Burnett and McMahon, 1987; Burnett, 1988). *Eurytium albidigitum*, an intertidal osmoconformer, experiences emersion-induced respiratory acidosis, and is inactive when in air. In *Pachygrapsus crassipes*, an ion regulator, such respiratory acidosis is fully compensated, and crabs remain active in air. Unlike *E. albidigitum*, fluid in the branchial chamber of *P. crassipes* rapidly increases in both carbon dioxide and in titratable alkalinity upon air exposure. Burnett (1988) suggests that alkalinisation of the branchial chamber fluid maintains a steeper gradient of P_{CO2} across the gill, favouring transport of bicarbonate from the haemolymph, and counteracting respiratory acidosis. Haemolymph ion regulation may have evolved in organisms whose variable habitat or vigorous exercise resulted in acid-base imbalance, with concomitant disruption of metabolism and activity (Ballantyne *et al.*, 1987). Ion regulation in turn supported utilisation of brackish, freshwater and terrestrial habitats (Potts and Durning, 1980).

Urine passed to the branchial chamber in the amphibious crab, *Cardisoma guanhumi*, has a high pH, and very high titratable alkalinity, about 20 times greater than sea water (D. Wolcott, unpubl. data, Table 2). This may also assist movement of CO_2 across the gill, a process much slower in air than in water, reducing respiratory acidosis on emersion, and compensating for the hyper-capnic conditions inside the crabs' burrows (Pinder and Smits, 1986).

Adjustment of pH by altering the ratio of cations and anions is more rapid than relying on metabolic removal of lactate after exercise or air exposure. Osmoconformers such as *Eurytium albidigitum* and *Libinia emarginata* apparently do not use ion exchange for pH regulation, and haemolymph acidosis is uncompensated (Burnett and McMahon, 1987; Booth, 1986).

From the complex interplay of ion and osmotic regulation in extracellular fluid and cells, involving ion transport, water fluxes, acid-base balance, oxygen transport, free amino acid pools, and nitrogen excretion, it is plain that the iono- and osmoregulatory abilities of the whole organism cannot be inferred from the abilities exhibited in isolated tissues, or measured under unnatural conditions. Often, abilities of organ-

TABLE 2. Ion reclamation in hypoosmotic urine of Crustacea from fresh water habitats and reprocessed urine of crabs from terrestrial habitats.

		Haemolymph (mmol/L)	Urine (mmol/L)	P (mmol/L)	References
FRESHWATER SPECIES					
Austropotamobius pallipes	Na^+	208	11		Reigel, 1968
Corophium curvispinum	Na^+	164	15	—	Taylor and Harris, 1986
Gammarus pulex	Na^+	152	27	—	Lockwood, 1961
Gammarus duebeni	Na^+	255	83	—	Lockwood, 1961
Goniopsis cruentata	Na^+	390	190	—	Zanders, 1978
	Cl^-	370	190	—	
Macrobrachium australiense	Cl^-	150	60	—	Denne, 1968
Procambarus clarkii	Na^+	185	6	—	Kamemoto *et al.*, 1966
Pacifastacus leniusculus	Na^+	195	14	—	Pritchard and Kerley, 1970
	Cl^-	180	3	—	
TERRESTRIAL SPECIES					
Birgus latro	Na^+	—	—	59	Greenaway and Morris, 1989
	Cl^-	—	—	74	
Cardisoma guanhumi	Na^+	336	—	86	Wolcott and Wolcott, unpubl.
	Cl^-	318	—	33	
	NH_4^+	—	0.5	13	
	CO_2	—	34	6	
	TA	—	48	8	
	pH	—	8.17	7.67	
Gecarcinus lateralis	Na^+	369	—	58	Wolcott and Wolcott, 1991
	Cl^-	375	—	60	
	NH_4^+	—	0.5	10	
Ocypode quadrata	Na^+	402	—	60	Wolcott and Wolcott, 1985
	Cl^-	341	—	52	

isms in the laboratory to maintain a constant ionic milieu in the face of salinity changes fall short of values determined in the field or under more natural conditions (Flemister, 1958; Rabalais and Cameron, 1985; D'Orazio and Holliday, 1985; Zanders and Martelo, 1984; Gross, 1964; Morritt, 1988; Spicer *et al.*, 1987; Blasco and Forward, 1988). On the other hand, understanding the integrated response is not possible until the contributions of cellular and subcellular processes are appreciated. Integrated responses of many biochemical, neural, endocrinological and behavioural systems contribute to enantiostatic control of internal functions. Both the detailed, isolated mechanisms and the integrated systems must be studied before a clear picture of iono- and osmoregulation is achieved.

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THE BEHAVIOURAL BASIS OF CRUSTACEAN DISTRIBUTION IN A TIDALLY MIXED ESTUARY

Net flow in estuaries is seawards, exposing swimming animals to the risk of export to the sea. This has led to numerous investigations of mechanisms facilitating estuarine retention (Naylor, 1988). Generalisations are difficult however, partly because of differences in estuarine circulation patterns. Also, different species may be more abundant in different parts of an estuary, implying that various behavioural mechanisms may be instrumental in maintaining observed distributions. The area studied was the Conwy Estuary, the largest in North Wales, which is almost completely mixed. Here, retention strategies based on laminar flow (Cronin and Forward, 1982) cannot operate. This work investigates behavioural retention strategies of species from various habitats within the estuary, and explores the relationship between behaviour, retention and distribution.

Probably the most significant behavioural strategy is that of the planktonic copepod *Eurytemora affinis*, a euryhaline species, most numerous in the low salinity zone. Drift-net sampling on rising spring tides showed copepod abundances in the water column to be concentrated on flood tides at downstream sites and on the ebb tide at the most upstream site. This suggests a preferred region in which the majority of animals are found. Sampling over each tidal cycle for two weeks at a mid-estuary site showed distinct semi-lunar variation of the tidal abundances of *E. affinis*. Greatest abundance over neap tides was on the ebb, but was on flood tides over springs, suggesting that the population maximum moved upstream on springs and downstream on neaps. To test this, plankton samples were taken on three separate spring and neap tides. Each time a distinct population maximum was found, the position of which was further seaward on neap than on spring tides.

Independent oceanographic studies on the Conwy estuary (Shiono and West, 1987) suggest no physical mechanism which could explain these observations on the basis that *E. affinis* behaves as a passive particle. Extensive horizontal swimming by animals of this size seemed equally unlikely, but vertical migrations into the water column at different times was an attractive working hypothesis.

Endogenous locomotor activity was therefore tested for as a possible behavioural basis to these observations. Swimming activity was measured under constant conditions in the laboratory using an infra-red light beam actograph and a free-running activity rhythm in phase with the time of expected high tide was found, apparently the first in a copepod. This suggests that *E. affinis* moves into its preferred salinity zone by swimming, under endogenous control, on the state of tide providing transport in the appropriate direction. The position of this zone varies with the semi-lunar cycle, and the swimming activity of the animals appears to change accordingly.

Different retention strategies are adopted by two species of amphipod, *Gammarus zaddachi* and *Corophium volutator*. Both swim periodically in the water column and so risk export from the estuary. *C. volutator* was found fairly consistently at the mid-estuary locations, but *G. zaddachi* varied its position throughout the year with respect to salinity as also reported elsewhere by Girish *et al*, (1975). Overwintering adults and developing juveniles occurred high up the estuary whereas reproducing adults were most common in mid-estuary. Thus the adult population, particularly ovigerous females, move downstream while juveniles migrate upstream. Significantly no *G. zaddachi* were recorded at the most seaward site.

Experimental studies demonstrated the presence of endogenous swimming rhythms in both amphipod species, but that each exhibited different kinetic swimming responses in a flume tank. *G.zaddachi* showed increased swimming in higher current velocities, whereas *C. volutator* showed the opposite response. Thus *G. zaddachi* appears to use a combination of endogenously timed swimming behaviour and responsiveness to water flow to vary its position along the estuary, while *C. volutator* appears to avoid moving water and so limits displacement from its preferred habitat.

In conclusion several strategies appear to have evolved by which estuarine crustacean species maintain their distributions in an environment of net flow seawards. Moreover, the precise nature of the zonations found in each species suggest that in the Conwy Estuary, behaviour is finely tuned to ensure retention in specific environments within the estuary and not simply within the estuary itself.

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RESPIRATORY GAS EXCHANGE AND TRANSPORT IN CRUSTACEANS. ECOLOGICAL DETERMINANTS

STEPHEN MORRIS

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Crustaceans have radiated into many different environments ranging from deep sea hydrothermal vents, through the intertidal zone and freshwater to terrestrial habitats. Adaptation to these varied conditions has included marked and significant changes in both the gas exchange organs and blood pigment function. The functioning of haemocyanin, the respiratory pigment of most crustaceans, is in many species under the complex control of biochemical feed back mechanisms. Modulation of haemocyanin function can occur due to the accumulation of specific metabolites or as a result of specific compounds entering the animal from the environment. For example hydrothermal vent fauna exhibit specific adaptations to high sulphide levels and mesopelagic species containing high levels of ammonia show different but again specific adaptations. Metabolic modulation of blood pigment function occurs most extensively in the sub-littoral and intertidal species. Terrestrial species show the most marked morphological/biochemical changes in the structure and function of the gas exchange organs and appear to have abandoned complex molecular modulation of blood gas transport. The ecological physiology of these adaptive trends is considered using examples, and directions for future investigation are discussed.□
Crustacean, oxygen, carbon dioxide, haemocyanin, respiratory, gas exchange.

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The study of respiratory gas exchange and transport in crustaceans has proceeded largely on a comparative basis and for practical reasons has dealt primarily with decapod species. As a consequence, our knowledge is disproportionately based on a number of 'large' species from 'interesting or challenging' environments which are then compared to 'normal' species. However, it is by examining adaptations to extremes that the plasticity and adaptability of the Crustacea becomes apparent.

There have been a number of recent reviews that have considered adaptation to specific environments (Powers and Bliss, 1983; Vernberg and Vernberg, 1983; McMahon and Burggren, 1988; Burggren and McMahon, 1988), specific morphological adaptations (Greenaway and Farrelly, 1990) or have given general treatments (Mangum, 1983; Vernberg, 1983; Cameron and Mangum, 1983). The more general papers have not been restricted to respiratory gas exchange and transport.

The present paper, while continuing the basic principle of examining adaptation to extremes and by necessity with a bias towards the decapods, will relate specific adaptations in the gas exchange organs and haemolymph function to the special demands of various habitats. These habitats range from abyssal hydrothermal vents, through the intertidal to fully terrestrial. Often adaptations not directly related to gas exchange and transport have forced compromise on the respiratory physiology. It is not within the scope of this paper to provide a complete description of all species from each habitat. Rather, examples have been selected to demonstrate our current knowledge and to indicate those areas that warrant further study.

DISCUSSION

The two main respiratory gases, oxygen and carbon dioxide, move across the body wall of crustaceans by diffusion. This is often facilitated by a respiratory pigment, most usually haemocyanin, and there is good evidence that CO_2 excretion is aided by carbonic anhydrase (Henry, 1987). Diffusion limited gas exchange can be described by the Fick equation: $M = \frac{K \cdot A}{E} \cdot \delta P$ where M is the amount of diffused gas in mmol.min^{-1}, E is the thickness of the barrier and A the area. K is Krogh's diffusion constant (mmol.min^{-1}.atm^{-1}) and P is the partial pressure

gradient across the barrier. The diffusion constant takes into account not only diffusion through the membrane but also the solubility coefficient of the extracorporeal medium. Since CO_2 is *c.* 25 times more soluble than O_2 in water, diffusion of O_2 rather than CO_2 is the limiting factor in aquatic species. Therefore, it is the maintenance of O_2 supply that is the major modifying factor in the evolution and control of respiratory systems (McMahon and Wilkens, 1983). In air the capacity for O_2 and CO_2 are essentially the same and the outward diffusion of CO_2 therefore relatively slower; which has a major influence on the respiratory gas exchange and transport of air breathing species.

It is generally accepted that in non-malacostracan crustaceans no specialised respiratory structures are present but instead appendages, specialised parts of the integument or the body wall as a whole are employed (McLaughlin, 1983). The simplest form of malacostracan gill is a vascularised lamellar outgrowth of the thoracopod and occurs in multiple pairs in mysids and amphipods. In the isopods these structures are often elaborated (Edney, 1960). The gills of Eucarida are more complex and with few exceptions enclosed within the carapace in the paired branchial chambers through which water (or air) is moved. The most usual arrangement is for water to flow in through openings at the base of pereiopods (Milne Edwards openings) into the hypobranchial space, through the gills into the hyperbranchial space and then pumped out through exhalant openings on either side of the epistome (McMahon and Wilkens, 1983). Primitively, the gills existed as sets of four attached to each appendage but all modern decapods show a reduced number. The gills themselves fall into three categories depending on the complexity of branching: a) phylobranchiate the normal gill type for caridean shrimp and brachyuran crabs; b) trichobranchiate as found in most lobsters and crayfish; and c) dendrobranchiate as found only in penaeoids and sergistoids (McLaughlin, 1983). McMahon and Wilkens (1983) considered that this increased branching of the gills might indicate the evolution of increased surface area for gas exchange.

Perfusion of the gas exchange organs and the respiring tissues is equally important in determining rates of gas exchange. The circulatory system of crustaceans has been termed 'simple' because of the open nature of large parts of the venous system. In the smaller crustaceans this may be true but in the larger decapod species the open circulatory system is complex, highly efficient and tightly regulated (McMahon and Burnett, 1990). Haemolymph-flow through gills has been demonstrated to be organised and the direction controlled (Burggren and McMahon, 1988; Taylor, 1990). Terrestrial species exhibit highly modified gas exchange structures and have made major alterations in perfusion, with respect to breathing air instead of water, or in the case of amphibious species breathing both (see below).

Aquatic *vs* Terrestrial — A Continuum

The evolutionary and adaptive processes involved in moving from breathing water to breathing air have received some considerable study but it is only recently that we have begun to understand how the Crustacea have accomplished this. The movement of crustaceans into terrestrial environments has occurred either via the freshwater or intertidal zone habitats (Hartnoll, 1988), although in some cases it is unclear which route was followed. Those of direct marine origin tend to have a marine pelagic larval stage whereas those from freshwater benefit from an abbreviated nonplanktonic larval development providing greater independence from water (Hartnoll, 1988). Within this continuum there exist several discrete habitats, marine, estuarine, freshwater, intertidal, tidepool, amphibious, and semi- and fully terrestrial, although any species may not be limited to one.

Estuarine/Freshwater — Salinity Effects

The major challenge for species moving into estuarine habitats and from there progressively to freshwater is the maintenance of salt balance. Increased osmoregulatory work could theoretically lead to increased gas exchange but this has been difficult to demonstrate (Taylor, 1988). Moving into freshwater and more especially environments of varying salinity does, however, have some demonstrable effects (Vernberg, 1983; Cameron and Mangum, 1983; Taylor, 1988). The green shore crab *Carcinus maenas* is a typical estuarine/intertidal species. The normal estuarine, intertidal and rock pool environments are subject to frequent and often abrupt changes in salinity. After exposure to low salinity the respiration rate of *C. maenas* is significantly elevated, peaking after 3–4 h but remains elevated for several days (Taylor, 1977). This response appears to be standard for those species so far investigated (Taylor, 1988). Quite clearly there is no rapid acclimation to reduced salinity.

The increased oxygen uptake is associated with a hyperventilatory response; with the increased oxygen demand possibly being met by a tachycardia and increased cardiac output (Taylor, 1977, 1988).

The oxygen transporting properties of the haemocyanin from a number of estuarine and intertidal animals respond to salinity changes (*Carcinus maenas*, Truchot, 1973; *Callinectes sapidus*, Weiland and Mangum, 1975). These changes can occur as a result of the failure to completely regulate blood ions with respect to changing environmental salinity. In most aquatic crustaceans, such as *Carcinus*, increases in the concentrations of Ca and Mg especially, induce increased affinity for O_2 by the haemocyanin and also increase the Bohr shift (Fig. 1). The rock pool species *Palaemon elegans* shows good ion regulation and consequently no effect on oxygen affinity when exposed to low salinity (Ramirez de Isla Hernandez and Taylor, 1985; Taylor *et al.*, 1985). *Callinectes sapidus* although an osmoregulator also shows a decrease in the oxygen affinity of Hc when acclimated to low salinity and this led Mason *et al.* (1983) to suggest that some small dialysable factor may be responsible. Recently it has be shown, however, that *C. sapidus* exhibits changes in haemocyanin phenotype, the expression of which is dependent on salinity (Mangum and Rainer, 1988), and the phenotypes have different functional characteristics.

These changes with respect to acclimation salinity do not, however, always elicit the same effect *in vivo* due to concomitant changes in blood pH. Low salinity results in an increased blood pH and therefore an increase in oxygen affinity which compensates for the decreased affinity due to lowered blood ions (Fig. 1) (Truchot, 1973). There is also good evidence that some species show increased Hc levels in response to acclimation to low salinity (Sabourin, 1984; Taylor *et al.*, 1985) but this occurs slowly over a number of days and is primarily an osmoregulatory response and not respiratory.

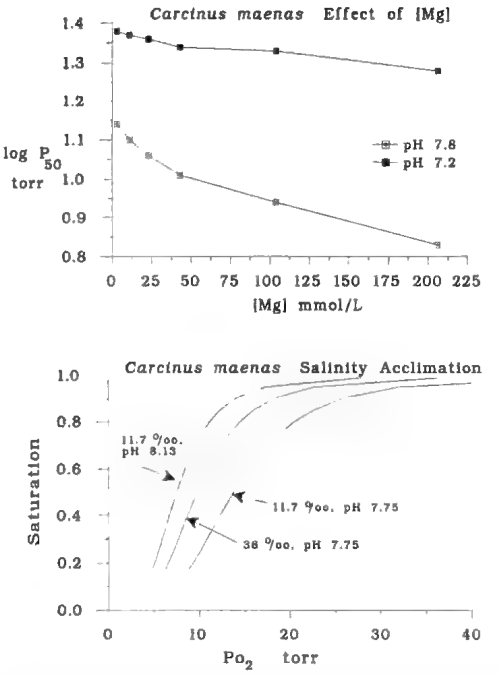

FIG. 1. Upper, The effect of Mg on the oxygen affinity (log P_{50}) of haemocyanin from *Carcinus maenas*. The increase in affinity due to higher Mg concentration is more marked at high pH. The increased divergence of the plots at pH 7.2 and pH 7.8 is due to the increased pH sensitivity, i.e. greater Bohr shift, induced by high Mg levels (after Truchot 1975);Lower, Salinity acclimation of O_2 transport in *C. maenas*. The centre curve indicates the oxygen equilibrium of blood from *Carcinus* in full strength seawater and at the *in vivo* pH. Maintaining blood pH at 7.75 but reducing salinity would reduce affinity as shown by the right curve. Salinity acclimation is normally accompanied by an increase in blood pH which compensates for the reduced affinity to actually produce a slight increase in affinity under *in vivo* conditions (left curve). Curves constructed from the data of Truchot (1973).

Sublittoral

The most common demand on the respiratory system of sub-littoral species is to maintain aerobiosis during exercise. Exercise has been used as experimental treatment by a number of workers and extensive data exist for various *Cancer* species. In *C. magister* 20 min exercise causes an increase in ventilation and perfusion (McMahon *et al.*, 1979). The increase in scaphognathite and heart beat rates is accompanied by a marked increase in oxygen uptake which is reflected in a decrease of the blood oxygen content (Fig. 2). In a parallel study (McDonald *et al.*, 1979) it was noted that 20 min exercise resulted in significant L-lactate (end product of anaerobiosis) efflux into the blood, with a significant acidosis and a rise in the partial pressure of CO_2, the latter despite the hyperventilation (Fig. 2). The anaerobic component of this response, i.e. the elevated lactate levels and the acidosis, continued to increase for some 30 min post exercise and before

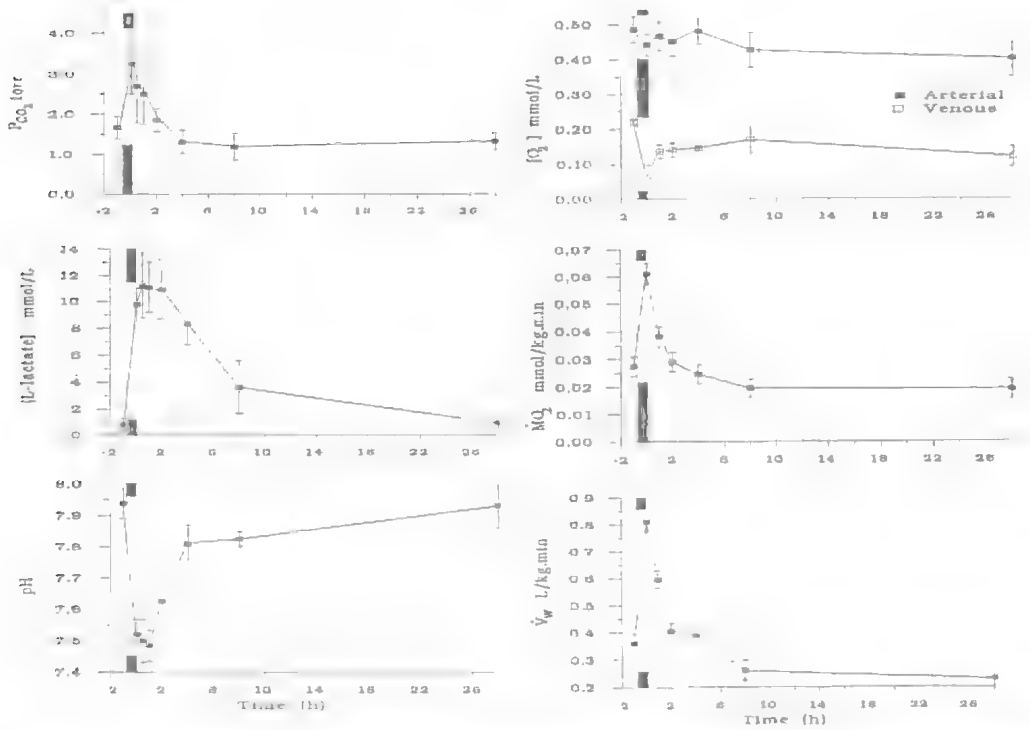

FIG. 2. Changes in respiratory blood-gas parameters, lactate and pH, oxygen uptake and ventilation volume during 20 min exercise (filled vertical bars) and 24 h recovery in *Cancer magister*. Arterial and venous blood values are supplied for O_2 content (data abstracted from McDonald *et al.*, 1979; McMahon *et al.*, 1979).

returning to normal resting values. Complete recovery of all parameters required 24 h (Fig. 2). Obviously the exchange of respiratory gas and/or transport is insufficient to maintain aerobiosis in the working muscles and supplementary anaerobic energy production is used to meet the increased demand.

Some species, normally sublittoral, contain individuals that become air exposed and the success of these individuals in breathing air may determine their survival. Small *Cancer productus* (<100g) are often found emersed in the low intertidal zone (DeFur and McMahon, 1984a). Air exposure of *Cancer* elicits a different response from exercise in that there is a decrease in oxygen uptake due to the failure of the gills as gas exchange organs but there is a similar increase in ventilation, in PCO_2 and also CO_2 content (Fig. 3) (DeFur and McMahon, 1984a,b). The response to this shortfall in oxygen supply is again the initiation of anaerobiosis and the efflux of L-lactate into the haemolymph which exacerbates the haemolymph acidosis (Fig. 3). It is important to note that attempts to compensate for this acidosis appear to involve the mobilisation of $CaCO_3$ from the carapace to produce HCO_3- (Henry *et al.*, 1981; DeFur and McMahon, 1984a; Innes *et al.*, 1986). The concomitant increase in circulating Ca will tend to have a potentiating effect on the affinity of the Hc for oxygen (see above) partially compensating for the decreased affinity due to the Bohr shift and thereby assisting oxygen loading at the gills. Again complete recovery of all parameters, especially L-lactate, required at least 24 h. Air exposure of aquatic species appears, therefore, not to be met with any special adaptive response. L-lactate may mitigate some of the effects of air exposure. Truchot (1980) reported that L-lactate increased the oxygen affinity of some crustacean haemocyanins, including *Cancer*. This effect has now been substantiated for a number of species (Bridges and Morris, 1985; Morris, 1990; discussed below). The immediate benefit would seem to be a partial compensation for the effect of a metabolic acidosis, which reduces the affinity of haemocyanin for O_2. Depending on circumstances the effect can either improve loading of oxygen at the gills or increase the size of the venous reserve, that is the amount of oxygen

remaining bound to Hc after passing through the tissues (Morris, 1990). The latter would seem to be an adaptation to exercise and the former to breathing hypoxic water.

Littoral and Pool Environment

Within the littoral zone exist a number of microhabitats of which the rock pool environment is perhaps the best studied. While conditions in the pools may be similar to those of inshore seawater they can frequently and regularly become extreme, with wide fluctuations in oxygen availability (PO_2 10 – 500 torr), temperature (-1.5 – 30°C), salinity, pH and carbon dioxide levels (Truchot and Duhamel-Jouve, 1980; Morris and Taylor, 1983). Similar environmental changes have been described for habitats on boulder and sedimentary shores (Agnew and Taylor, 1986 and citations therein). With the exception of salinity similar environmental stresses occur in freshwater bodies.

The rate of gas exchange and transport is determined by the metabolic demands of the animal, which in crustaceans with no temperature homeostasis will tend to vary with environmental temperature. The fluctuating temperatures experienced in smaller bodies of water might be expected to have significant effects on metabolic requirements. Long term (seasonal) temperature changes may be met by temperature acclimation (Newell, 1979). The pool dwelling prawn *Palaemon elegans*, which shows temperature acclimation over a period of weeks, exhibits greater thermal tolerance (survives < 0°C) than the open water species *P. serratus* and *P. adspersus* which avoid temperature extremes (Taylor, 1988). In addition to greater tolerance such species often show some metabolic independence of temperature (Q_{10} < 2.0). Fluctuating temperatures are a feature of the littoral zone generally and are reflected in intertidal hermit crabs by low Q_{10}'s of 1.4 and 1.6 (Burggren and McMahon, 1981). Similarly low Q_{10}'s were recorded for *P. elegans* but these were size dependent (Morris and Taylor, 1985a). The increased O_2 demand and CO_2 production is met by increased ventilation and perfusion together with changes in the transport properties of the blood. Oxygen transport is affected by reduction in dissolved O_2 at high temperature and by changes in the haemocyanin O_2 affinity, which arise from allosteric modulation and temperature dependent changes in pH (~ -0.016 pH.°C^{-1}). Generally, the effect of increased temperature, at constant pH, is to decrease O_2 affinity (Mangum, 1983). Acclimation of Hc oxygen affinity also seems possible. *In Carcinus* moved to a higher temperature oxygen affinity first decreased but then slowly increased, which Truchot (1975) suggested was due to an increase of a dialysable factor. Moving *Hemigrapsus nudus*, an amphibious intertidal crab, from 15 to 30°C caused urate concentrations to increase from 0.015 to 0.052 mmol.L^{-1} (Morris, Greenaway and McMahon, unpubl.). Urate has been identified as a modulator of Hc O_2 affinity (below) and may explain the above temperature effects on *Carcinus*, the haemocyanin of which is sensitive to urate (Lallier and Truchot, 1989a). This decreased O_2 affinity at higher temperature may compromise oxygen uptake, although unloading at the tissues might be enhanced. In rock pool species this is mitigated by the fact that the highest temperatures occur during periods of hyperoxia (Morris and Taylor, 1983). Conversely, hypoxia is associated with the lowest diel temperatures and reduction in oxygen demand. Apart from allosteric modulation the haemocyanin of many intertidal species shows reduced temperature sensitivity at temperatures near the environmental mean. Crustacean Hc normally exhibits a δH of -35 kJ.mol^{-1} or larger, δH being the change in the heat of oxygenation of Hc with an increase in temperature. For example in *P. elegans* δH = -1.7 kJ.mol^{-1} (Morris *et al.*, 1985) and the hermit crab *Pagurus bernhardus* δH = 0 to -18 kJ.mol^{-1} (Jokumsen and Weber, 1982). Both of these species have Hc that is especially sensitive to pH (ϕ << -1.0) which supports the suggestion that there is an inverse correlation between pH sensitivity and temperature sensitivity (Burnett *et al.*, 1988), although this seems not to be true for all species, e.g. terrestrial and hydrothermal vent species (see below). It could also be argued that those species living under a relatively constant temperature regimen exhibit no special adaptation to temperatures never encountered, and that reduced sensitivity is a response to a eurythermal environment.

During hypoxia many crustaceans can maintain a near constant oxygen consumption down to very low levels of environmental oxygen and are termed regulators (Fig. 4). Below this 'critical' PO_2 anaerobiosis becomes increasingly important. The critical PO_2 (Pc) is highly variable between species but it now appears that the Pc is correlated with the extent and duration of hypoxia experienced (Table 1). The maintenance of MO_2 is due to a response common to nearly all species investigated, a pronounced increase

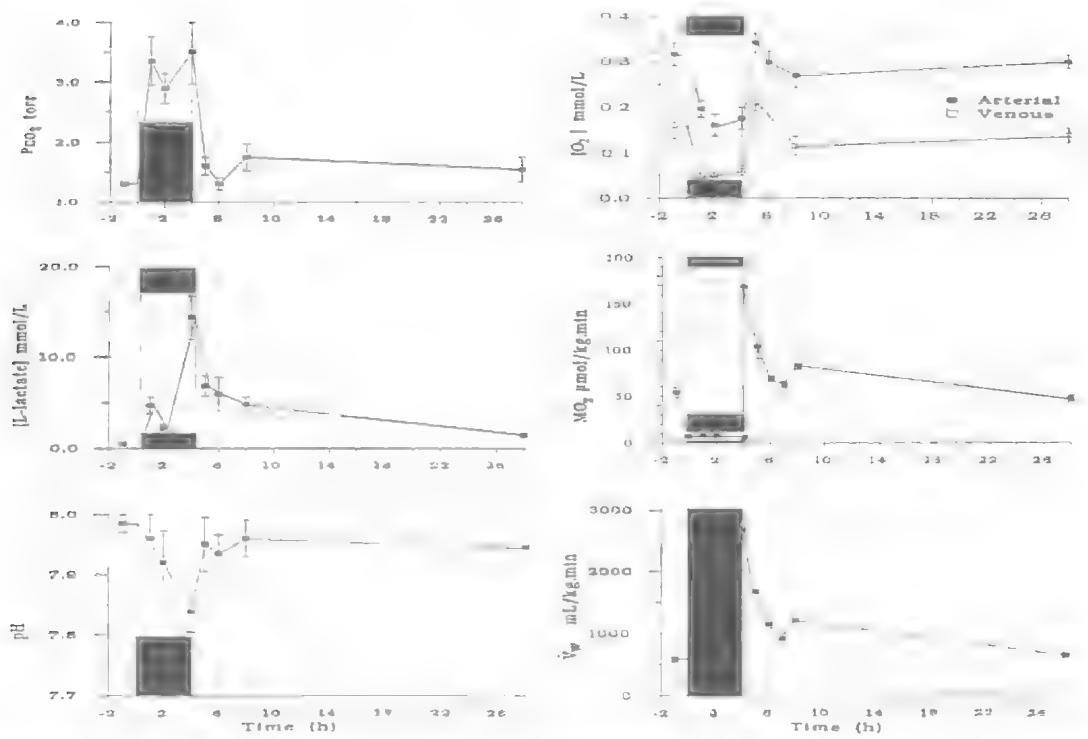

FIG. 3. Changes in respiratory blood-gas parameters, lactate and pH, oxygen uptake and ventilation volume during 4 h air exposure (filled vertical bars) and 24 recovery in *Cancer productus*. Arterial and venous blood values are supplied for O_2 content (data abstracted from DeFur and McMahon, 1984a,b).

in the rate of scaphognathite beating (Taylor, 1988). The rate of beating increases steadily until the Pc is reached, e.g. *P. elegans* (Fig. 4). Although this increased ventilation helps maintain oxygen uptake the increased work itself represents a metabolic demand and at the Pc it is considered that O_2 uptake is sufficient only to supply the pumping activity.

Taylor (1988) compares rock pool and open water species and concludes that rock pool species often show higher Hc concentrations, which increases the amount of O_2 transported, and additionally that these Hcs show high affinity and pH sensitivity. The high affinity would encourage oxygen uptake at the gills and the latter could assist in unloading at the tissues. While Hc concentration certainly is a factor it is now apparent that intertidal species, including rock pool animals have a series of mechanisms for 'fine tuning' Hc oxygen affinity (Morris, 1990). As a consequence the affinity will vary in dependence of physiological condition. The Hc of *Palaemon elegans* for example is extremely sensitive to L-lactate and affinity is markedly increased with only small changes in concentration (Table 2). The most apparent advantage of this effect is to aid the loading of oxygen at very low ambient oxygen and prevent the rapid onset of extensive anaerobiosis.

In addition to L-lactate it has been found that urate (Morris *et al.*, 1985a,b) and more recently the catecholamine, dopamine (Morris and McMahon, 1989) have marked potentiating effects on some crustacean Hcs. In *Carcinus* and the prawn *Penaeus japonicus*, which encounters hypoxic conditions in lagoons, urate accumulates in the blood with hypoxia (Lallier and Truchot, 1989a,b). In addition, blood urate levels decrease progressively as the ambient PO_2 is increased into the hyperoxic range (Lallier *et al.*, 1987). Clearly urate concentration responds to environmental oxygen levels above the Pc whereas L-lactate formation is significant below the Pc, leading Lallier and Truchot (1989a) to conclude that under normal circumstances urate is most important in regulating blood oxygen affinity. Neurohormonal modulation of pigment oxygen affinity is most likely in situations of sudden stress. Intertidal, rock pool and near shore species appear to be provided with a suite

of complementary biochemical feedback systems for regulating oxygen transport (Morris, 1990).

The blue crab *Callinectes sapidus* is also occasionally found in the intertidal zone, although it copes poorly with breathing air, and contains Hc sensitive to L-lactate and urate. Prolonged hypoxia (50–55 torr) results in enhanced blood oxygenation but not as a result of significant increases in either lactate or urate but rather due to increase in circulating Ca and by a change in the Hc phenotype (DeFur *et al.*, 1990).

The transport of CO_2 will also be affected by the above modulators since the transport of CO_2 and O_2 are linked under most circumstances (Bridges and Morris, 1989). Hypoxia in rock pools is invariably accompanied by hypercapnia, with the inverse relationship during hyperoxia, a feature which has not been rigorously duplicated in laboratory simulation studies. Simultaneous variation in CO_2 and O_2 levels in rock pools has markedly different consequences than varying O_2 alone (Bridges and Morris, 1989). Using artificial tide pools Truchot (1986) demonstrated that the blood alkalosis observed during laboratory hypoxia, as result of the hyperventilatory response, is much less obvious when the CO_2 level in the water concomitantly increases. Similarly the acidosis often observed as a result of hypoventilation during hyperoxia is considerably ameliorated. Thus rock pool animals face significantly different demands on the oxygen transport system than do species inhabiting hypoxic oceanic waters such as the oxygen minimum layer (see below).

When water PO_2 falls below the Pc many species show an important behavioral response, partial emersion. Although *P. elegans* exhibits exceptional oxyregulation, below 20 torr the prawns will partially emerse themselves at the air–water interface and by a combination of hyperventilation and pleopod beating aerate the surface film (Taylor and Spicer, 1988). Similar behaviour has been observed for freshwater crayfish, *Orconectes rusticus* (McMahon and Wilkes, 1983). This behaviour under conditions of hypoxia close to the Pc increases haemolymph oxygenation but also allows CO_2 exchange with the water, which maintains blood pH (Taylor and Spicer, 1988). Similarly, small *Cancer productus* when air exposed *in situ* where they are often partially buried take advantage of the interstitial water to reduce the degree of internal hypercapnia and acidosis (Fig. 3). Under conditions of severe hypoxia (< Pc) many of these normally obligate water breathers emerge completely from the water, e.g. *P. elegans* (Taylor and Spicer, 1988) and *Echinogammarus pirloti* (Agnew, 1985). This response, whereby under extreme conditions it is more beneficial to breathe air than water, may represent selective pressure directing some species towards an amphibious existence.

Amphibious – Air and Water Breathing

The amphibious Crustacea, both those from the supratidal and those from freshwater bodies, show varying degrees of independence from water. This may be viewed as an evolutionary trend with species such as *Carcinus maenas* (Taylor and Butler, 1978) and the crayfish *Austropotamobius pallipes* (Taylor and Wheatly, 1981) at the more aquatic end. *A. pallipes* is exemplary in that when the freshwater that it inhabits becomes very hypoxic it moves into air (Taylor and Wheatly, 1981). This initially promotes a response similar to that exhibited by *C. productus* (Fig. 3) but during a 24 h emersion period the initial increase in blood lactate and subsequently Ca appear to maintain oxygen up-

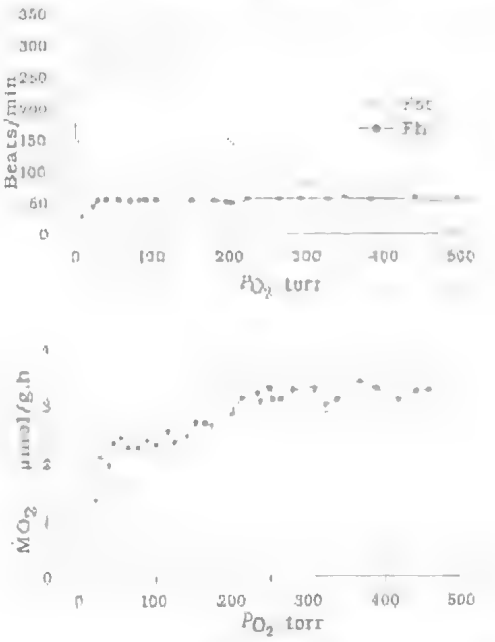

FIG. 4. Showing the regulation of $\dot{M}O_2$ (lower panel) by *Palaemon elegans* over a wide range of oxygen availability. Oxyregulation ceases at *ca.* 20 torr the critical PO_2 for this species. The upper panel shows regulation of heart rate (Fh) by *P. elegans* and the scaphognathite rate (Fsc) during hypoxia. The hyperventilatory response ceases near the critical PO_2.

TABLE 1. Critical oxygen partial pressures (*Pc*) for the regulation of oxygen consumption in selection of crustaceans from various habitats.

Species	Pc (torr)	Source
Cancer pagurus	20–40	Bradford and Taylor, 1981
Carcinus maenas[1]	60–80	Taylor (1976), Jouve and Truchot (1978)
Pachygrapsus crassipes	50	Burke (1979)
Austropotamobius pallipes	40	Wheatly and Taylor (1981)
Upogebia pugettensis[2]	45–50	Thompson and Pritchard (1969)
Callianassa californiensis[2]	10–20	Thompson and Pritchard (1969)
Palaemon adspersus	70	Hagerman and Weber (1981)
Palaemon elegans[3]	10–15	Morris and Taylor (1985b)
Palaemon serratus	50–60	Taylor (1988)
Palaemonetes varians	10–15	Hagerman and Uglow (1984)
Echinogammarus pirloti[1]	15–25	Agnew and Taylor (1985)
Echinogammarus obtusatus[1]	15–25	Agnew and Taylor (1985)
Hemigrapsus nudus[1]	<10	Morris *et al.* (In Preparation)
Gnathophausia ingens[4]	6	Childress (1975)
Acanthephyra curtirostris[4]	8	Childress (1975)
Euphausia pacifica[4]	18	Childress (1975)
Bythograea thermydron[5]	14[a], 9[b]	Mickel and Childress (1982b)

[1]Intertidal/interstitial species. [2]Intertidal burrowing species. [3]Primarily rockpool species. [4]Midwater species from the oxygen minimum layer. [5]Hydrothermal vent crab [a]Measured at 8–25°C, [b]Measured at 2°C; Species not numbered are normally aquatic/open water forms.

take and transport, and stabilise blood pH and PCO_2 (Taylor and Wheatly, 1981; Morris *et al.*, 1986b). The L-lactate produced in the initial period of hypoxia is slowly removed from the blood (Taylor and Wheatly, 1981). *A. pallipes* employs the same basic responses as fully aquatic species and this seems adequate for several days of air breathing. Compared to obligate aquatic species (*Liocarcinus*, Johnson and Uglow, 1985) *Carcinus* shows morphological adaptations in that the gills are more strongly chitinised and thus have a lesser tendency to collapse in air, allowing some gas exchange to occur across the gills.

Hemigrapsus nudus, a more truly amphibious species, spends the greater part of the day breathing air but shows no specific modification to the gills, which collapse and adhere when the crab enters air. Instead this species shows increased vascularisation of the membrane lining the branchial chamber which takes on a lung function. For example in *H. nudus* breathing air for 4 hours the venous blood oxygen content was 0.20 mmol.L^{-1} and that of the arterial blood 0.26 mmol.L^{-1}, while blood exiting the lung contained 0.30 mmol.L^{-1} oxygen (~75% saturated; Morris, Greenaway and McMahon, unpubl.). Quite clearly oxygen rich blood from the pulmonary circuit was being diluted by oxygen poor blood from the branchial circuit. Interestingly, *Hemigrapsus* Hc shows little sensitivity to lactate (Table 2) indicating a reduced dependence on modulation of respiratory pigment function, indeed air breathing by *Hemigrapsus* causes no significant lactate production (Morris, Greenaway and McMahon, in prep). In the absence of biochemical modulation of haemocyanin function *Hemigrapsus* maintains a constant arterial-venous oxygen content difference, a stable pH and a stable, if elevated blood CO_2 near 3.5 torr (Fig. 5). Amphibious species differ from aquatic species in that the blood gas and acid-base parameters during air breathing are stabilised and respiration is not significantly supplemented by anaerobiosis.

A number of amphibious species have developed unusual accessories to breathing air. These include the evolution of gas exchange windows in the merus of each walking leg of *Scopimera* (Maitland, 1986) and the visceral 'lung pump' of *Holthuisana* (Greenaway and Taylor, 1976). *Holthuisana*, in reality a semi-terrestrial crab, while breathing air ceases scaphognathite activity and instead moves the internal viscera from side to side alternately occluding and opening the branchial spaces and thereby causing a ventilatory current over the gas exchange surfaces. It is of note that while species such as *Hemigrap-*

TABLE 2. The oxygen affinity as P_{50}, its sensitivity to L-lactate and urate for some crustaceans selected with respect to habitat and mode of existence. Values assessed at the species' normal environmental temperature.

Species	P_{50}(pH7.8) (1mmol/L lactate)	$\frac{\delta \log P_{50}}{\delta \log[Lac]}$	$\frac{\delta \log P_{50}}{\delta \log[urate]}$	ϕ	Source
Palaemon elegans[1]	12.5	-0.56		-1.4	Bridges and Morris (1985)
Apohyale pugettensis[1]	16.1	-0.46		-1.67	Spicer and McMahon (1990)
Traskorchestia traskiana[3]	24.8	-0.30		-0.70	Spicer and McMahon (1990)
Bythograea thermydron[6]		-0.27		-0.3 -1.5	Sanders and Childress (Pers Com.)
Cancer pagurus[2]	14.3	-0.21		-0.86	Truchot (1980)
Callinectes sapidus[2]	6.1	-0.21	-0.11	-1.14	Booth *et al.* (1982), Bridges and Morris (1985), deFur *et al.* (1990)
Uca pugilator[3]	8.9	-0.20	0	-1.67	Byrne, Morris, Spicer and McMahon (Unpub.)
Cancer magister[2]	8.9	-0.19	-0.07	-1.03	Morris and McMahon (1989)
Acanthephyra smithi[4]	3.9	-0.17		-0.7	Sanders and Childress (1990a)
Gnathophausia ingens[4]	1.6	-0.13		-0.8	Sanders and Childress (1990b)
Carcinus maenas[1,3]	10.9	-0.10	-0.22	-0.55	Truchot (1980), Lallier and Truchot (1989a)
Austropotamobius pallipes[5]	3.9	-0.19	-0.39	-0.46	Morris *et al.* (1986a), Morris *et al.* (1985a)
Hyas coarctatus[2]	24	-0.17		-0.3 -0.7	Morris and Bridges (1989)
Ocypode saratan[7]	15.1	-0.16		-0.67	Bridges and Morris (1985)
Megalorchestia californiana[3,7]	14.7	-0.10		-0.78	Spicer and McMahon (1990)
Penaeus japonicus[a]	2.8 (1.41)[b]	-0.08	-0.03	-1.5	Lallier and Truchot (1989b)
Hemigrapsus nudus[7]	7.1	-0.06	-0.09	-0.7	Morris, Greenaway and McMahon (Unpub.)
Acanthephyra acutifrons[4]	5.2	-0.06		-0.88	Sanders and Childress (1990a)
Glyphocrangon vicaria[4]	2.5	-0.04		-0.37	Arp and Childress (1985)
Oplophorus gracilirostris[4]	5.6	-0.03		-0.66	Sanders and Childress (1990a)
Talitrus saltator[7]	17.6	-0.03	0	-0.75	Spicer, Taylor, McMahon (1990)
Holthuisana transversa[7]	4.9	0		-0.13	Morris *et al.* (1988a)
Geograpsus crinipes[8]	16.6	0	0	-0.53	Morris, Greenaway, McMahon and Sanders (In Prep)
Gecarcoidea natalis[8]	15.1	0	0	-0.38	Morris, Greenaway, McMahon and Sanders (In Prep)
Gecarcoidea lalandii[8]	12.0	0	0	-0.55	Morris, Greenaway, McMahon and Sanders (In Prep)
Birgus latro[8]	7.9	0	0	-0.68	Morris *et al.* (1988b)
Coenobita clypeatus[8]	7.2	0		-0.43	Morris and Bridges (1986)

#Values calculated using author's coefficients, [a]Lagoon species values for pH 7.6, [b]Extrapolated to pH 7.8
[1]Rockpool, [2]Sublittoral, [3]Intertidal, [4]Pelagic, [5]Freshwater, [6]Hydrothermal vent, [7]Amphibious/Semi-terrestrial, [8]Terrestrial

sus are good oxyregulators with a low Pc (Table 1). *Holthuisana* shows no obvious Pc and is an oxyconformer (Greenaway *et al.*, 1983b) and presumably elects to breathe air whenever the water becomes hypoxic. A further interesting adaptation to bimodal breathing by *Holthuisana* is the facultative switching of blood flow from the gills (water breathing) to the lungs (air breathing); the ratio being 1:6.6 in favour of lungs while in air and 1:4.1 in favour of gills in water (Taylor and Greenaway, 1984). This phenomenon almost certainly occurs in other species but it remains to be demonstrated. Other bimodally breathing species such as *Cardisoma* show well developed lungs and are equally facile at breathing air as water (McMahon and Burggren, 1988) but appear to be dependent on water for ion and osmoregulatory reasons (Greenaway, 1989).

Terrestrial — Air Breathing

A number of adaptive features exhibited by the more accomplished air-breathing amphibious species are characteristic of and considerably more developed in terrestrial species. Further modification of the gills to aid in air-breathing occurs in a number of species, e.g. *Ocypode (Greenaway and Farrelly, 1984).* Most air-

breathing species however, show reduction in gill area and extensive elaboration of the branchiostegal lining for gas exchange (Fig. 6). In *Birgus latro* the gills take no part in oxygen uptake (Greenaway *et al.*, 1988). Although crustacean lungs have assumed varying forms data from several species indicate that the lungs are very efficient in O_2 uptake, in part due to the attenuation of the epithelial cells and chitin layer (McMahon and Burggren, 1988; Greenaway and Farrelly, 1990). For example in 4 of 5 disparate species of air breathing crab Greenaway and Farrelly (1990) found that the pulmonary blood contained significantly more oxygen than the pericardial blood and the difference could be as much as 35% more, indicating that lungs are more important than gills. Indeed the most terrestrial species have become obligate air breathers and when immersed in water become increasingly anaerobic due to the reduction in oxygen diffusion at the exchange surface, e.g. *Gecarcinus lateralis* (Taylor and Spencer-Davies, 1982). Similar observations have been made for terrestrial amphipods (Spicer and Taylor, 1987). The evolution of lungs has also led to increased arterial PO_2 in some cases significantly greater than 100 torr (*Pseudothelphusa*, Innes *et al.*, 1986; *Birgus*, Greenaway *et al.*, 1988), indicating that in resting animals the physically dissolved O_2 supplies a significant part of the oxygen demand of the animal.

One considerable advantage in breathing air is the relatively greater oxygen content (57mmol.L^{-1}.$torr^{-1}$) compared with water (1.8 — 2.2 mmol.L^{-1}.$torr^{-1}$) which together with a much reduced kinematic viscosity (~8%) can make extracting oxygen from air considerably less expensive. As a consequence there is a tendency to make energetic savings by reducing the rate of ventilatory pumping, without reducing oxygen uptake (Table 3). Many amphibious species show markedly different rates in air and water (Table 3).

Relatively elevated PCO_2 in the blood is the normal condition for air breathers and is a consequence of the parameters of the Fick equation (see above). For air breathing species the reduced ventilation with respect to environmental oxygen availability will exacerbate problems of CO_2 excretion. Movement of CO_2 out of the animal into air requires a greater diffusion gradient and therefore higher internal PCO_2 values. There is some evidence that ventilatory drive may become increasingly CO_2 sensitive in terrestrial species (McMahon and Burggren,

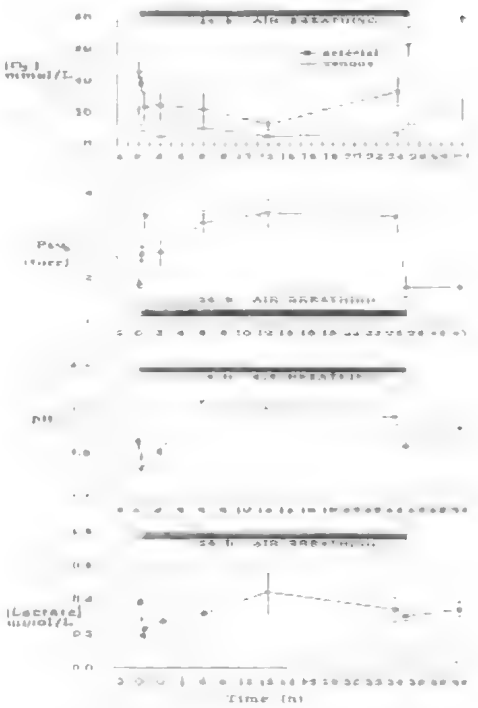

FIG. 5. Respiratory gas parameters, pH and [L-lactate] measured in the blood of *Hemigrapsus nudus* before, during and for 6 hours after 24 h air breathing (indicated by horizontal bars). Arterial and venous O_2 content is given (Morris, McMahon and Greenaway, unpubl.).

1979). The excretion of CO_2 may occur across the lungs as well as the gills and appears to be facilitated by carbonic anhydrase (CA) which catalyses the CO_2 <-> HCO_3- reaction, thereby accelerating the diffusion of CO_2 from the blood and into the epithelial cells of gas exchange organs. While the amphibious *H. nudus* has significant but low levels of CA in its lungs the terrestrial *Birgus* has CA at >25% the specific activity of the gills which may explain the measurable CO_2 loss from the blood passing through the lungs (Morris and Greenaway, 1990). The high CO_2 levels in terrestrial species does not result in a noticeably lower blood pH *cf.* aquatic species. This may be in part because of the usually higher Hc concentrations (for values see McMahon and Burggren, 1988) which may exceed 100 mg.mL^{-1} in some land crabs.

The high concentrations of Hc in the blood of most terrestrial species has been interpreted as increasing oxygen supply to the tissues (McMahon and Burggren, 1988) and while this is important during any sustained exercise the efficacy of the lungs together with Hc O_2 affinity

(Table 2) ensures that dissolved O_2 makes an important contribution. During exercise the Hc oxygen saturation in *Birgus* falls from 100% arterial and ~60% venous to only 80% and 25% by which time L-lactate concentrations have risen to over 22 mmol.L^{-1} (Greenaway *et al.*, 1988), indicating that the O_2 limiting step is diffusion from the blood into the mitochondria.

In more than 20 species of terrestrial decapod studied the haemocyanin shows no significant sensitivity to L-lactate or urate (Table 2). Indeed there appears to be a trend for increased air-breathing to be correlated with lower sensitivity. The result is that the allosteric modulation of Hc oxygen affinity used by aquatic organisms to optimise O_2 delivery during exercise or environmental hypoxia, or by proto-amphibious species to temporarily stabilise blood gas transport during forays into air, is not utilised by well adapted air-breathing species. Instead the low kinematic viscosity and high O_2 content of air appears to make compensation *via* changes in ventilatory and heart rates more economical. A further consideration is that urate is the prime nitrogenous waste in at least one species (*Birgus latro*) and accumulates as solid in the body of this and other terrestrial species (Greenaway and Morris, 1989; and citations therein). Urate solutions are saturated at low concentration and presumably there is no advantage in selecting for an effector substance which is always at maximum concentration.

The Hc of terrestrial species appears to be characterised by low pH sensitivity, the small Bohr shifts being approximately 50% the magnitude found for rock pool species (Table 2). The immediate consequence of this is that the effect of very large mixed acidosis (PCO_2 and L-lactate increase) often < pH 7.0 e.g. *Birgus latro* (Greenaway *et al.*, 1988) on Hc oxygen affinity is minimised. There have been several suggestions of a correlation between terrestriality and Hc O_2 affinity but a consideration of data collected at the species normal environmental temperature (and constant [lactate]) indicates no trend (Table 2). The problem is complicated by the modulator sensitivity of Hc in many aquatic species. The only modulating substance of note in terrestrial species would appear to be Ca which may vary in response to drinking water quality, moult stage or during exercise induced acidosis. Values for log $\delta P_{50}/\delta$log [Ca] for water breathers range from -0.28 for *Carcinus* (Truchot, 1975) to -0.82 *Callinectes* (Mason *et al.*, 1983). This coefficient varies from near 0

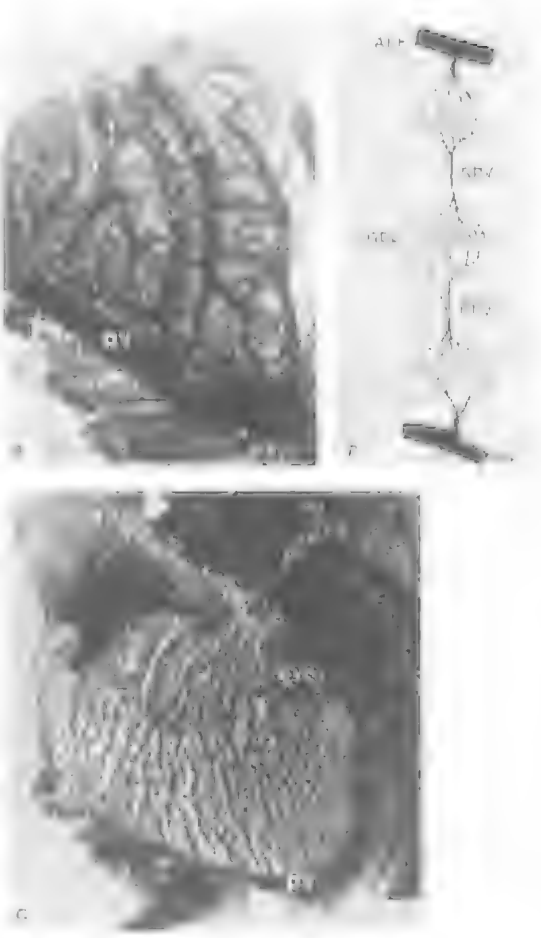

FIG. 6. Crustacean lungs. A, Corrosion cast of part of the vasculature of the lung of *Ocypode cordimanus*. Note the single set of vessels (A), which interdigitates with the efferent vessels (E). Haemolymph returning from the lung is collected by a pulmonary vein (pv), which opens into the pericardial cavity. B, Diagrammatic illustration of the pattern of haemolymph flow through the lungs in terrestrial crabs of the families Gecarcinidae, Grapsidae and Sundathelphusidae. Afferent haemolymph passes to the respiratory membrane three times before reaching the pulmonary veins. AFF, Afferent vessel; GEL, gas exchange lacunae; RPV, respiratory portal vein; PV, pulmonary vein. C, Corrosion cast of the vasculature of one lung of the terrestrial crab *Geograpsus grayi*. Note the very large pulmonary vein (pv), which collects efferent haemolymph and conveys it to the pericardial cavity. A large vessel on the inner dorsal margin of the lung distributes afferent haemolymph (arrows) (figures and legends reprinted with permission from Greenaway and Farrelly, 1990).

TABLE 3. Ventilatory frequency of some selected decapods from aquatic, amphibious and terrestrial habitats. Showing the tendency to decreased rate when breathing air.

Species	Resting Rate (beat.min^{-1})		Source
AQUATIC			
Cancer magister	75		McMahon *et al.*, 1979
Cancer productus	70		deFur and McMahon, 1984a
Cancer pagurus	82		Bradford and Taylor, 1982
Callinectes sapidus	94		Booth *et al.*, 1982
AMPHIBIOUS			
Cardisoma guanhumi	75	(AIR)	Burggren *et al.*, 1985
Gecarcoidea lateralis	161	(AIR)	Taylor and Spencer-Davis, 1981
	264	(WATER)	
Sudanonautes aubryi monodi	2	(AIR)	Cumberlidge, 1986
	46	(WATER)	
TERRESTRIAL			
Birgus latro	30		Smatresk and Cameron, 1981
Coenobita clypeatus	2		McMahon and Burggren, 1979
Holthuisana transversa	9*		Greenaway *et al.*, 1983a
Pseudothelphusa garmani	1#		Innes *et al.*, 1987

*Employs a 'lung pump' #Some evidence for 'lung pumping'

(*Coenobita*, Morris and Bridges, 1986; *Holthuisana*, Morris *et al.*, 1988a) to between -0.3 and -0.5 for several terrestrial species of *Geograpsus* and *Gecarcoidea* (Morris, Greenaway, McMahon and Sanders, unpubl.). Amongst the Amphipoda, the semi-terrestrial *Talitrus saltator* (Spicer *et al.*, 1990) and *Orchestia gammarellus* (Taylor and Spicer, 1986) produced coefficients of 0 and -0.33 respectively. Calcium sensitivity calculated from data for semi- and fully terrestrial isopods (Sevilla and Lagarrigue, 1979) indicate values ranging from -0.28 to +0.53. The significance of this Ca effect, while appreciated for amphibious/semi-terrestrial species (above), remains to be determined in terrestrial species.

The temperature sensitivity of O_2 transport warrants some consideration. In a number of semi-terrestrial/supratidal species the temperature sensitivity is reduced near to the environmental mean (*O. saratan* δH = -3 kJ.mol^{-1}, *C. clypeatus* -14.8 kJ.mol^{-1}; Morris and Bridges, 1985, 1986) and may reflect the varying temperatures that occur in beach areas. In contrast the arid-zone crab *H. transversa* also potentially experiences fluctuating temperature but shows no special adaptation of the Hc (δH = -54 kJ.mol^{-1}) but instead may avoid temperature extremes during the aquatic and fossorial phases of its life cycle. The semi-terrestrial amphipod *Talitrus saltator* shows a marked temperature sensitivity and Spicer *et al.* (1990) also suggest that cryptic and fossorial phases enable this species to escape temperature extremes which have promoted low temperature sensitivity (-11 to -21 kJ.mol^{-1}) in a range of supratidal amphipod Hcs (Taylor and Spicer, 1986). The majority of truly terrestrial species inhabit tropical/sub-tropical rainforests which are characterised by remarkably constant temperature and high humidity. *Geograpsus crinipes*, *G. grayi*, *Gecarcoidea lalandii*, *G. natalis* and *Birgus latro* all taken from the rainforest of Christmas Island all show high temperature sensitivity, at least up to 30°C (Morris *et al.*, 1988b; Morris, Greenaway, McMahon and Sanders, unpub.), whereas *Grapsus tenuicrustatus* and *Geograpsus stormi* taken from shore rocks, beach rubble and cliff faces show much lower sensitivities (-21 and -1.5 kJ.mol^{-1}). The tentative conclusion is that minimising the effect of temperature on blood O_2 transport is as important to terrestrial species from eurythermal habitats as to inter- and supratidal species. In general the blood of air breathers has become increasingly independent of biochemical modulators and instead the animals appear to rely on morphological and mechanical compensation mechanisms.

Dehydration could present a problem for air breathing species. Data from the high-shore *Cy-*

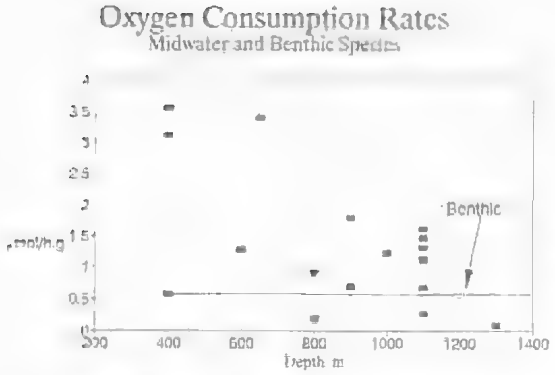

FIG. 7. Oxygen consumption rates from a variety of non-migrating pelagic species indicating reduced O_2 uptake in the deeper dwelling species. The O_2 uptake rate of benthic species appears to remain relatively constant and independent of depth (horizontal line). The rates for pelagic and benthic forms coincide near 1200 m (data from Childress, 1975; Mickel and Childress, 1982b; Childress and Mickel, 1985).

clograpsus lavauxi suggest that under normal circumstances loss of body water does not affect O_2 uptake (Innes *et al.*, 1986). Severe dehydration of *Coenobita clypeatus* appears to reduce O_2 consumption, without significant effects on CO_2 excretion, although the reasons for this are unclear (McMahon and Burggren, 1988). Dehydration is likely to be important only under exceptional circumstances but requires further investigation.

Oceanic Species

Oceanic crustaceans can be divided on the basis of habitat, sublittoral, pelagic and benthic. Vertically migrating species experience very different temperatures, oxygen availability and pressures at different depths. Benthic species and non-migratory pelagic species live at near constant temperatures and high pressure. The benthic species include the rather special case of the hydrothermal vent fauna which, in addition to high sulphide and metal levels in the water, tolerate high and widely varying temperature as well as high pressure.

There have been relatively few studies of the effect of temperature on oxygen uptake rates of oceanic species. Pelagic crustaceans living in midwater environments tend to show increased rates with temperature, with Q_{10} values of 1.5 to 3.0 (Teal, 1971; Childress, 1977). It is now well established that deep-living pelagic crustaceans have considerably lower O_2 uptake rates than do shallower-living pelagic species (Childress and Mickel, 1985), often by a factor of 20 but that this effect declines below 1500 m (Fig. 7). This decline is more than can be accounted for by temperature effects and cannot be explained by pressure (Mickel and Childress, 1982a). Childress and Mickel (1985) suggest that it is the relaxation of selection for strong swimming abilities at greater depth that allows for a reduced O_2 demand.

In migratory species the response to temperature is influenced by oxygen availability and hydrostatic pressure. The ecological significance of temperature-pressure interactions was shown by Childress (1977) working on the migrating copepod, *Gaussia princeps*. This species was most sensitive to pressure at shallow depths (100 – 300 m) during the night but that during the day, below 400 m within the oxygen minimum layer temperature determined rates. A lowered rate of oxygen uptake while in a hypoxic environment would be of direct benefit. On the basis of such studies Vernberg (1983) supports the model of George (1979; Fig. 8). This suggests that vertical migrators maintain a constant oxygen uptake as a result of the opposing effects of temperature and pressure changes. Deeper in the oxygen minimum layer environmental PO_2 may become very low (<20 torr) and oxygen potentially limiting. Midwater species appear to be adapted to this situation, however, and most exhibit critical oxygen tension (P_c) below that normally encountered in the oxygen minimum layer (Childress, 1975; Table 1). This seems to be achieved by maintaining a high flow of water over the gills, which have unusually high surface area and a high diffusion capacity (~10 fold greater normal) leading to a low δPO_2 across the gills (Belman and Childress, 1976).

There are few deep-living brachyuran species and very few studies of benthic Crustacea. Existing data indicate that there is no decrease in the O_2 consumption of benthic species in dependence of habitat depth (Childress and Mickel, 1985). Interestingly, the O_2 consumption rates of midwater and benthic species converge at about 1200 m (Fig. 7).

Respiratory gas transport in oceanic crustaceans has been infrequently examined but Arp and Childress (1985) examined the blood of a benthic (1800 m) shrimp, *Glyphocrangon vicaria*. The oxygen binding properties of this species do not appear too exceptional, with a modest Bohr shift (ϕ = -0.37, 2°C), a relatively low affinity (P_{50} = 9.0 torr, pH 8.01, 2°C) and

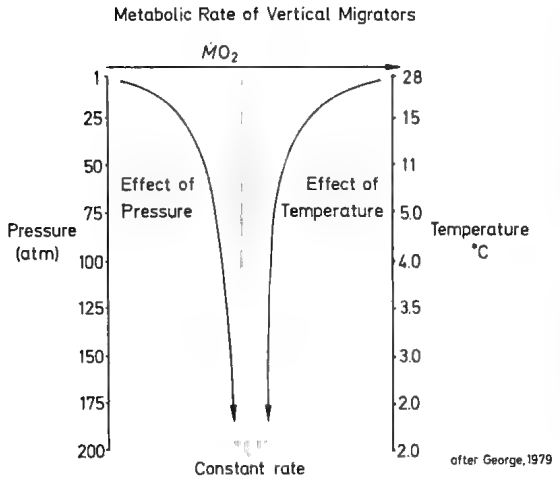

FIG. 8. Demonstrating, using the model of George (1979), how the opposing effects of increasing pressure and decreasing temperature on the metabolic rate of vertically migrating crustaceans can operate to produce a constant rate throughout the water column.

relatively low co-operativity (n_{50} = 2.6 – 3.2). An unusual aspect of the haemolymph from benthic species is the marked increase in the Bohr factor (pH sensitivity) at higher temperatures, which has also been observed in the brachyuran *Hyas coarctatus* (Morris and Bridges, 1989). The oxygen affinity of haemocyanin from these species is remarkably insensitive to temperature, for *G. vicaria* δH = -10.3 kJ. mol^{-1} (calculated from Arp and Childress, 1985) and -6.4 $kJ.mol^{-1}$ for H. coarctatus (Morris and Bridges, 1989). The normal sensitivity would be nearer to -35 $kJ.mol^{-1}$ (Bridges, 1986, table 3). It is possible that considering these animals usually occur in cold, stenothermal environments that these changes with increased temperature do not have any physiological significance.

In terms of modulator sensitivity there seems to be no special adaptation to life in the deep ocean, for example *G. vicaria* has little sensitivity to L-lactate ($\delta \log P_{50}/ \delta \log [lac]$ = -0.04) while *H. coarctatus*, which does extend in shallower water shows a greater sensitivity (-0.17). In recent investigations Sanders and Childress (1990a) have examined the oxygen transport function of Hc from a group of pelagic species, some vertical migrators. The migratory species had lower oxygen affinities but higher *in vivo* lactate levels than the non-migratory species. These shrimp Hcs exhibited, however, very little sensitivity to L-lactate and temperature seems much more important. The non-migratory species had low temperature sensitivity (δH = 0 to -5.6 $kJ.mol^{-1}$, cf. *G. vicaria* above) whereas there were very large temperature sensitivities in the migrators (δH = -135 to -140 $kJ.mol^{-1}$). Sanders and Childress (1990a) suggest that low temperature sensitivity is not a feature of benthic crustaceans alone but rather of deep living forms, in stenothermal environments. They also conclude that increased O_2 affinity at lower temperatures is adaptive, by maintaining O_2 uptake, for migrating species as they move down into the relatively cold and hypoxic oxygen minimum layer. In the warmer surface waters, where

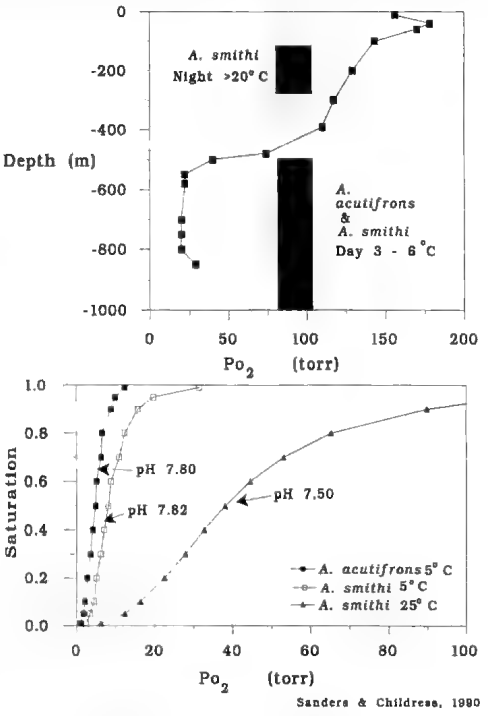

FIG. 9. Adaptation to the oxygen minimum layer. The upper panel shows the decrease in water oxygenation that occurs with increased depth (solid symbols) and the depth ranges for *Acanthephyra smithi* and *A. acutifrons* (shaded blocks). *A. acutifrons* is a non-migrating species that remains in the relatively cold oxygen minimum layer. *A. smithi* can be found within the same range during the day but at night moves into shallower water which has a higher temperature and PO_2 . The lower panel shows the oxygen equilibria of the two bloods at *in vivo* pH. Note that although *A. smithi* has a relatively low affinity pigment suited for the warmer oxygenated surface waters at depth the pigment functions much like that of the permanent inhabitants of the O_2 minimum layer (after Sanders and Childress, 1990a).

the animals are active at night, the reduced affinity will aid unloading at the tissues while loading is maintained by the relatively high PO_2 of the water (Fig. 9).

There are some deep-sea pelagic species such as *Notostomus gibbosus* that maintain their station in the water column not by swimming but by being buoyant (Sanders and Childress, 1988). This shrimp has replaced large amounts of Na^+ with trimethylamine (113 mmol.L^{-1}) and ammonium (217 mmol.L^{-1}) to achieve neutral buoyancy but these normally toxic ions have significant effects on blood pigment functioning (Sanders, Morris, Childress and McMahon, in prep.). The presence of these ions greatly reduces the affinity of the Hc for oxygen, markedly depresses co-operativity and completely suppresses the Bohr shift so that affinity remains constant with changing pH (Fig. 10). Considering that other mesopelagic species also contain these ions further investigation of Hc function under these conditions is required. However, it may be that in an animal where blood pH is determined by factors other than the respiratory CO_2 and anaerobic lactic acid production, that a pH insensitive pigment is advantageous.

Hydrothermal vent crustaceans while difficult and costly to study are of special interest due to the unique nature of their island habitats. The vent brachyuran, *Bythograea thermydron*, shows oxygen consumption rates in the normal range for shallow water brachyurans and does not show unusual temperature sensitivity of O_2 uptake (Mickel and Childress, 1982b). Oxygen binding by the haemocyanin of *B. thermydron* is, however, distinctly unusual (Sanders *et al.*, 1988). In *Bythograea* an increase from 2 to 10°C causes an affinity increase ($\delta H = +23$ kJ.mol^{-1}) but from 10 to 20°C behaves normally ($\delta H = -60$ kJ.mol^{-1}). This was in contrast to the blood of the vent caridean *Alvinocaris lusca* which exhibited a reverse temperature effect over the entire temperature range, so that affinity was lower at low temperature ($\delta H = +13$ kJ.mol^{-1}; Sanders *et al.*, 1988). The Bohr shift in *A. lusca* is twice that of *B. thermydron* (the Bohr shift is dependent on the hydrothermal vent site; Sanders, pers. com.) suggesting that in *A. lusca* significantly decreased affinity *via* a low pH will enhance O_2 delivery to the tissues. *B. thermydron*, with a low pH sensitivity, experiences decreased O_2 affinity at low and high temperature. At low temperatures the Q_{10} effect will reduce oxygen demand. As temperatures increase nearer to the vent water PO_2 decreases and *Bythograea* responds with

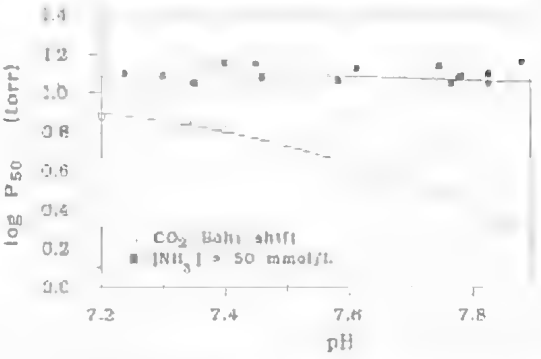

FIG. 10. The oxygen affinity (log P_{50}) of haemocyanin from the mesopelagic shrimp *Notostomus gibbosus* is shown to behave normally with respect to pH but the affinity and pH sensitivity are significantly modified by the presence of high concentrations of NH_4+ and NH_3. Under *in vivo* conditions of high ammonia and trimethylamine the oxygen affinity is both much lower and insensitive to pH (Sanders, Morris, Childress and McMahon, unpubl.)

pronounced hyperventilation (Sanders *et al.*, 1988) which is the normal response of shallow water brachyurans to hypoxic stress and results in an exceptionally low Pc (Mickel and Childress, 1982b); which should be compared with rock pool species (Table 1). This species also has pronounced anaerobic metabolic capacity for short hypoxic forays (cf. intertidal species) and interestingly L-lactate has a potentiating effect on the haemocyanin of this species, which is again reminiscent of shallow water forms. What is unusual is that thiosulphate, the detoxified product of vent sulphide, in *Bythograea* also increased Hc oxygen affinity (Sanders and Childress, in prep.). *B. thermydron* shows some specific adaptations to the variable temperature of its habitat but shows no unusual adaptations to pressure and retains the aquatic brachyuran response to hypoxia.

To conclude, the Crustacea show a range of sophistication of respiratory gas exchange and transport. Adaptations occur at the cellular and enzyme level with respect to temperature sensitivity in order to regulate O_2 demand and CO_2 production, and are exhibited by species from various habitats. Environmental hypoxia is met either by a lowering of the Pc, by improving oxygen uptake efficiency and regulating demand; or by a behavioural response, air breathing. The emergence response may represent the first steps towards terrestrialism. Aquatic and proto-amphibious species take advantage of a

range of metabolites to regulate haemocyanin oxygen affinity and this appears to have evolved from an exercise response. Some freshwater, intertidal, vertically migrating pelagic and vent species which experience varying temperature show adaptation of haemocyanin function. Species from more stable temperature regimen, both aquatic and terrestrial, show fewer adaptations in respect of temperature. Fully terrestrial species show marked changes in the morphology of the gills and especially the branchiostegal membrane.

The evolution of a lung has allowed the Crustacea to take advantage of the relatively greater concentration of O_2 in air but in the most adapted species has made them obligate air breathers. Terrestrialism is correlated with a decreased utilisation of biochemical modulation of blood gas transport and an increased importance of morphological and mechanical compensation mechanisms. While there exist clear trends within habitats and obvious transitional adaptations between habitats there are also unusual cases, e.g. thiosulphate in vent crabs and high NH_3 in some mesopelagic shrimp, that are met by unique adaptations. While it has not been possible to devote space to the special case of parasitic species it would be interesting to determine if increased dependence on a host for respiratory gas exchange released parasitic forms from the selective pressures and adaptations described in the paper.

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OSMOREGULATION IN THE FRESHWATER SHRIMP, *MACROBRACHIUM CARCINUS* (LINNAEUS)

River shrimps of the genus *Macrobrachium* are decapods of great economic importance and are widely distributed throughout Mexico, principally *M. carcinus*, *M. acanthurus*, *M. heterochirus* and *M. olfersii* in the Gulf of Mexico, and *M. americanum* and *M. tenellum* on the Pacific coast. Some of these shrimp require brackish water to complete their larval development and have different physiological responses to salinity. However, before cultivation of these species many investigations of their physiological requirements are necessary. Osmoregulation in decapods has been the subject of many investigations but data for the genus *Macrobrachium* are relatively few and most information available in this respect concerns *M. rosenbergii*. Moreira *et al.* (1983, 1987) have verified the effect of salinity in the metabolic rate of the first zoeal stages of *M. acanthurus*, *M. amazonicum*, *M. carcinus*, *M. heterochirus*, *M. holthuisi* and *M. olfersii* from Brazil, and McNamara (1987) studied osmoregulation in *M. olfersii*. The present paper reports the results of an investigation on the osmotic regulation in *M. carcinus* in relation to fast and slow salinity changes.

Materials and Methods

The osmoregulatory capacity in *Macrobrachium carcinus* was estimated by comparing haemolymph osmotic concentration with that of the external medium. Juveniles and adults (10.67–13 cm and 70–125 g, length and weight respectively) were collected in the River 'La Antigua', Ver., Mexico. The animals were acclimated in 70 L tanks in the laboratory at 20°C and 0 ppt salinity for 48 hours. After that, groups of 10 to 20 animals were placed in individual tanks to carry out the experimental protocol; this included two slow osmolarity treatments (0–7 ppt and 0–14 ppt) and two fast treatments (0–28 ppt and 0–35 ppt). One group was kept at 0 ppt throughout the experiment and served as a control. Osmolarity of the media was adjusted using a hand refractometer, reading the equivalent salinity in ppt. The osmotic pressure of 30 µL samples of haemolymph and external medium was determined in triplicate with a micro-osmometer 'µ-Osmette' (Precision Systems Inc.) every 6 hours to complete 168 hours of total observation. Haemolymph was obtained by puncture of the pericardic cavity with a capillary pipette, after the organisms had been dried with an absorbent tissue; samples were then centrifuged at 3000 rpm for 10 seconds. Concurrently pleopod setae were examined to determine moult stage.

Results and Discussion

Osmotic pressure measurements indicate that the organisms were hyperosmotic in freshwater and low salinities, maintaining their HOC (haemolymph osmotic concentrations) between 400 and 500 mOsm/kg at 0 to 15 ppt, similar to *M. olfersii* and *M. potiuna* (Moreira *et al*, 1983). On the other hand, the isosmotic point was achieved near 490 mOsm/kg (17 ppt) compared to the value of 492 mOsm/kg given for postlarvae of *M. carcinus* (Moreira *et al.*, 1987). The species remain isosmotic at high salinities (above 500 mOsm/kg) increasing their HOC with the external concentration, especially at salinities between 17 and 25 ppt. Finally, the specimens in premoult stage had a greater HOC than organisms in postmoult stages, with values of 527 and 421 mOsm/kg respectively; the smallest values occurred in individuals just moulted (408 mOsm/kg). On the other hand, the species was isosmotic in the intermoult stage, similar to *M. rosenbergii* (Stern *et al.*, 1986).

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BEHAVIOUR OF CRUSTACEA: ECOLOGICAL AND SOCIAL PERSPECTIVES

SANDRA L. GILCHRIST

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Visual, chemical, acoustical, and tactile information can vary crustacean responses to social and ecological conditions. The relative importance of the types of cues received can vary in marine, semi-terrestrial, and terrestrial environments. Some species experience only one of these types of habitats throughout their lifetimes while other species encounter all three habitats during particular life stages. Variations of ecological parameters within habitat lend specific context to actions and reactions exhibited by decapods. Population dynamics and social behaviour of decapod crustaceans are reveiwed with reference to how age structure and ecological conditions influence perception of environmental and social signals. Of particular interest are cues which relate to development of space use, home range, territoriality and food gathering relative to potentially limiting abiotic and biotic resources. As model systems, specific case analyses will be made for hermit crabs and tree crabs. □ *Crustacea, behaviour, age, structure.*

Sandra L. Gilchrist, Division of Natural Sciences, New College of USF, Sarasota, FL USA; *6 July, 1990.*

Successful invasion of terrestrial habitats by crustaceans is limited to relatively few species scattered among a small number of taxa. Only one semiterrestrial shrimp *Merguia* has been described (Abele, 1970; Bliss, 1968; Gilchrist *et al.*, 1983); however, little is known of its behaviour or physiology. Many land crabs spend a large amount of time in terrestrial habitats, although most still require an aquatic medium for reproduction (see Burggren and McMahon, 1988 for a discussion of terrestrialisation). Terrestrial species have some obvious external variations which differ from aquatic counterparts in respiratory apparatuses and in appendages (especially appendages used in arboreal movement). Behavioural modifications are much more common in crabs existing in terrestrial environments than in aquatic environments, especially relative to locomotion, communication, feeding, mating, gas exchange and osmoregulation. Development of offspring also tends to be more abbreviated as crustaceans become more terrestrialised (*Merguia*; Abele, 1970; Burggren and McMahon, 1988).

Age structure of the various populations also differs. For example, in terrestrial species juveniles rarely are encountered among adults; while in aquatic species, there may be a wide size range of individuals occupying a single habitat. Cannibalism has been noted commonly among some land crabs and may maximise distribution of food materials acquired during larval stages while reducing reproductive cost of consuming one's own offspring broadcast into an aquatic environment through supplying materials to sibling survivors (Wolcott, 1988; Helfman, 1979). While potential cannibalism may explain some age class distribution patterns, ecological factors such as environmental stress and predation by non-conspecifics are also important. There are differences in behaviour between aquatic and terrestrial juveniles as well as striking variations between juvenile and adult conspecifics associated with physiological constraints and predation. However, differences between behaviours of the aquatic and terrestrial species seem to appear after emergence onto land.

An exhaustive review of behavioural variations inter- and intraspecifically for aquatic and terrestrial crabs is beyond the scope of this analysis. Rebach and Dunham (1983) edited an excellent series of papers dealing with various aspects of behaviour. In this study, I will expand on some of the topics discussed in their series relative to age structure and ecological context.

To illustrate behavioural alterations relative to age structure and ecological conditions, I will limit this discussion to selected representatives of the Anomura (*Birgus*, *Calcinus*, *Clibanarius*, *Coenobita*, and *Pagurus*) and Grapsidae (*Aratus*). These genera show varying degrees of sociality as well as a range of terrestrialisation.

AGE STRUCTURE

The literature is replete with examples of com-

mon occurrences of adult and juvenile crabs in aquatic habitats.

Groups may gather for many reasons, for example exploitation of a common resource such as observed at areas where gastropod shells are released by predators (Gilchrist, 1982; McLean, 1974; Rittschof, 1980) and feeding sites (Scully, 1983) or aggregation to relieve environmental stress (such as shading or trickle cooling).

Aquatic hermit crabs gathering in areas where gastropods are consumed (termed predation sites) are of a wide size range even at a single site (Gilchrist, 1982; Rittschof, 1980). Typically, crabs form in a semicircular pattern downstream of the predation site with larger, interactive crabs near the front of the group and smaller crabs near the rear. Shell exchanges are common and rapid at natural sites (Gilchrist, 1982; Rittschof, 1980), some mating occurs, and in less than 1% of observations cannibalism on a smaller crab takes place. Active physical interactions are common as the crabs establish a dominance hierarchy at such sites. In shell exchange experiments conducted in the field and the laboratory, rarely is mortality among opponents recorded (major works record no mortality: Abrams, 1981; Hazlett, 1989; Imafuku, 1989). For the terrestrial hermit crab *Coenobita compressus*, newly metamorphosed juveniles seeking shells do respond to simulated predation sites (crushed gastropods; Table 1) in association with more aquatic species. Preliminary light microscope observations suggest that as the land hermits animals molt and emerge onto land, setation patterns on the appendages alter, becoming less dense and appearing shorter. Ghiradella *et al.* (1968) indicated that aesthetascs of *Coenobita* resemble chemoreceptors of terrestrial insects. Adult *Coenobita compressus* do not appear differentially attracted to crushed gastropods in greater numbers than to other carrion. Rittschof and Sutherland (1986) noted that chemical cues stimulated feeding behaviour of *Coenobita rugosus*, but did not seem important in eliciting shell seeking behaviour. Electron micrographic analyses of the setae and receptors may reveal differences in morphology and function of these structures ontogenetically with the transition from aquatic to terrestrial habitats. It is interesting to note, however, that some intertidal hermit crabs observed in the tropics do not appear to respond to predation sites (Table 2) as frequently as more temperate counterparts. Clearly, they can respond to certain gastropod fleshes, however, it is not obvious whether nonresponse to other fleshes is controlled behaviourally or at the receptor level. The mean size (hard carapace length) of crabs attending flesh sites was 7.02 mm± 1.65, indicating that for these experiments only medium to large crabs were attracted to gastropod fleshes. After a period of time (6–8 hours) hermit crabs in the experiment came to the flesh sites and consumed the gastropods. These crabs, like aquatic counterparts (Lepore and Gilchrist, 1988) may be attracted by degradation products such as putrecine and cadaverine.

TABLE 1. Responses of newly metamporphosed *Coenobita compressus* to simulated predation sites using G statistic with 1 df after correction for continuity.

	Respondents		
Flesh type	control*	treatment	significant
Acanthina brevidentata	2	101	++
Thais melones	3	14	
Nerita scabricosta	1	61	+
Cerithium stercusmuscarum	4	36	+
Anachis varia	7	58	+
Anachis fluctuata	3	30	+
Anachis rugosa	4	8	
Nassarius exilis	1	73	++
Mitra tristis	1	11	
Cantharus elegans	0	142	++
Turbonilla panamensis	1	18	
Siphonaria gigas	3	9	
Siphonaria maura	1	15	
Conus brunneus	5	11	
Littorina aspera	0	137	++

* Cage w/shell alone

As terrestrialisation increases, physiological and physical constraints tend to separate activities of different age groups both temporally and spatially. Herreid and Full (1986) observed that large *Coenobita compressus* travel faster than smaller crabs, doubling speed as leg length doubles. They also observed that smaller crabs expend more energy walking and climbing relative to balancing the shell. Thus, it would be expected that smaller crabs which may be more subject to predation and dessication would move smaller distances from refugia. Adult crabs tagged in Panama moved several hundred metres a day while smaller crabs tended to make short forays from the jungle edge to the wrack line for feeding. When climbing, large crabs fell less frequently than small ones.

Adult *Birgus* are large and somewhat solitary. Aggregations may be observed around a food source (Grubb, 1971) although burrows and rock

TABLE 2. Relative attraction to gastropod flesh by *Calcinus obscurus* in intertidal and subtidal areas of Panama. Gastropods were crushed and placed beneath cages while controls were cages alone and a cage plus a shell (controls were not significantly different, thus were pooled in the analysis). Null hypothesis that responses were independent of flesh was tested using G Statistic with 1 df after correction for continuity.

	Intertidal				Subtidal		
Gastropod flesh	Culebra	Flamenco	Naos	Taboga	Taboga	Uva	Perlas
Cantharus ringens	NS	NS	NS	NS	+	NS	NS
Cerithium stercusmuscarum	NS	+	+	+	+	+	+
Planaxis planicostata	NS	NS	NS	+	+	+	+
Anachis fluctuata	NS	NS	NS	NS	NS	NS	NS
Nerita funiculata	NS	NS	NS	NS	NS	NS	NS
Thais melones	NS	NS	NS	NS	NS	NS	NS

shelters (resting sites) are typically occupied singly. Very small individuals are not recorded co-occurring with adults (Gilbson-Hill, 1947). Much of the work with physiological parameters of *Birgus* has been done with smaller specimens (<500g; McMahon and Burggren, 1981; Morris, Greenaway and McMahon, 1988). Thus a full comparison of segregation by environmental stress is not yet practical.

Aratus, like *Birgus*, are rarely observed in groups of mixed size ranges. Within the canopy and on mangrove trunks at study sites in Sarasota and Manatee Counties in Florida, crabs with carapace widths less than 10mm were observed infrequently (Fig. 1). When a larger crab encounters a smaller one on the trunk, typically the smaller crab moves to the opposite side of the trunk. In over 50 hours of field observations, only 2 instances of conspecific predation were observed. Such predation occurred in the laboratory primarily after one crab molted, even when conditions were crowded. Beever *et al.* (1979) and Burton (1990) did not record conspecific predation. However, one of the most voracious predators of adult *Aratus* is another crustacean, *Goniopsis cruentata*. Warner (1967) describes a specific response of this predator to *Aratus*. Other invertebrate predators for adults include *Callinectes* and *Eurytium*. Birds, skunks, raccoons, and fish have been observed consuming adults. Juveniles appear to be eaten primarily by *Callinectes* and by birds (pers. obs.). *Callinectes* propel themselves up out of the water at high tide and either grab *Aratus* or knock them from the mangrove roots into the water. *Aratus* adults jump either somersaulting backwards or forwards from one horizontal surface to another when threatened by a predator. This action has been described to some extent by Ferris (1988). The crab can also leap from a lower surface to a higher one (pers. obs.). In a series of experiments where crabs were startled in the field (Table 3), larger crabs were more successful at landing or at reaching a greater height. When hanging upside down, the fourth pereiopods are used primarily in stabilizing the animal. In 2 cases where chelae were missing, animals had difficulties in making successful lands but did not fall when hanging upside down. Ferris (1988) described how these crabs right themselves when they land too far forward or upon their backs. Smaller

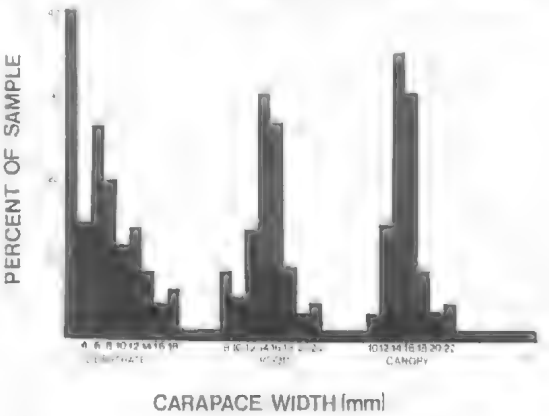

FIG. 1. Size distribution of *Aratus pisonii* on *Rhizophora mangle* at Tidy Island (Bradenton), Florida.

TABLE 3. Startle reaction of *Aratus pisonii* on roots and trunks of the red mangrove *Rhizophora mangle* at South Lido Beach in Sarasota Florida. Crabs were startled on roots by thrusting a dead *Callinectes sapidus* suspended by a thick metal rod at the crabs. On the trunk, a stuffed toy was used in a similar fashion.

	# of crabs	type of movement			relative size (carapace width in mm)	comments
		jump	horizontal	around		
roots	35	11	7	17	< 5	3 crabs which jumped made a successful landing; none jumped to a higher level — all jumped to lower level (water or lower root); most simply moved to the opposite side of the root.
	18	14	3	1	> 7	11 crabs jumped with 8 making successful landings — 6 jumped from higher to lower position and 2 jumped upward.
trunk	9	0	-	9	< 5	All crabs moved to the opposite side of the trunk and moved vertically downward.
	27	19	3	5	> 7	Most of the crabs jumped to a lower surface. When observing racoons, a predator in the area, those animals which simply move around the trunk or horizontally are captured and eaten with a high frequency. Bird predators were observed amputaing a leg as the crabs flung their bodies from the attackers.

crabs have a more difficult time in righting possibly because of the lack of experience or physical ability to do so effectively.

Wilson (1985) demonstrated that smaller *Aratus* are less tolerant of desiccation stress. Larger crabs which occupy canopy areas (temperature higher and relative humidity lower) are more tolerant physiologically and have developed behaviours (periodic dunking at high tide) which replenish water supply to the body. Thus, contact between various size classes is diminished.

Tidal clustering of crabs of mixed sizes (Fig. 2) as well as of mixed species has been observed for several intertidal species of hermit crabs (Gherardi and Vannini, 1989; Hazlett, 1966; Snyder-Conn, 1980, 1981). Such collections may aid in information exchange, shell distribution, mating, and resistance to desiccation, although exact mechanisms of the resistance are not yet fully understood. Although there is some disagreement (Gherardi and Vannini, 1989), such clustering seems to be effective in reducing desiccation. In experiments with *Clibanarus albidigitus* there were high losses of shell water in clustering crabs, however, the salinity of the shell water did not increase more than two parts per thousand (Table 4). This indicates that the shell water was probably not simply evaporating within the shell with time. The central bottom region of the cluster was cooler (2–4°C) than the surface of the cluster and the surrounding area. Perhaps by trickling water from the shells, the hermit crabs cooled the cluster by evaporation.

Land hermit crabs (*Coenobita clypeatus* and *C. compressus*, *C. perlatus* and *C. rugosus*) of different sizes will aggregate under fallen logs, in shallow leaf burrows, and beneath manmade structures, i.e, beneath houses and water troughs. There is some movement in such aggregates, with one instance of copulatory behaviour observed (pers. obs.). No shell exchanges have been noted in more than 75 hours of monitoring such aggregates of *Coenobita compressus* in Panama. As the aggregate forms, it is interesting to note that chirping sounds are heard often.

FIG. 2. Size distribution of crabs (*Clibanarius albidigitus*) found clustering on rock marl benches in Pacific Panama. Site 1 is closest to the water's edge and site 5 is 20 meters shoreward and elevated 1 meter from site 1. Five clusters were examined at each site.

TABLE 4. Clustering of *Clibanarius albidigitus* on rock marl benches in Pacific Panama. Shell water extracted using tuberculin syringe from 50 shells chosen at random in 15 separate clusters. (Salinity measured using a refractometer, did not vary more than 2ppt during observation).

Site#*	#clusters	$\bar{x}$ number crabs cluster ± sd	$\bar{x}$ cluster height ± sd	$\bar{x}$ shell water/crab at cluster beginning ± sd	$\bar{x}$ shell water crab after 3 hours ± sd
1	37	214 ± 39	4.2cm ± 1.6	.31cc ± .11	13cc ± .12
2	52	157 ± 50	4.0cm ± 1.3	.35cc ± .16	17cc ± .11
3	46	174 ± 31	3.3cm ± 1.2	.29cc ± .13	.06cc ± .13
4	29	116 ± 40	2.3cm ± 1.1	.34cc ± .16	.04cc ± .16
5	16	72 ± 16	1.8cm ± 0.7	.26cc ± .11	.11cc ± .08

*Increase in site number indicates movement shoreward of 5 metres. Sites 5 and 6 were 1 metre higher than other sites.

Accompanying the chirping sounds are rapid asynchronous flicking motions of the antennae. The intensity of these sounds appears to decrease as movement within the aggregate decreases. Grubb (1971) noted that *Birgus*, a relatively solitary hermit crab, continuously produces a clicking sound. The chordotonal organ in the antennal flagellum of *Petrochirus californiensis* (Taylor, 1967a, b) is thought to be sensitive to acoustic stimuli. However, such sensitivity has not been explored in the Coenobitidae. Although it is not clear what information is conveyed by the chirping, other accounts of sound production by land hermit crabs suggest that touch may also stimulate the behaviour (Imafuku and Ikeda, 1990). Some shell rapping and flicking with chelae occurred within *C. compressus* aggregations. In observations of the same aggregation site on 4 consecutive days, approximately 63% of the crabs were found returning all 4 days, suggesting some recognition or homing ability.

Page and Willison (1982) report broad overlaps of crab size ranges with variations in activity and distribution associated with the need for smaller crabs to replenish shell water more often and with rigid osmoregulatory requirements of small individuals. Land hermit crabs (*Coenobita clypeatus*) also may be found feeding and drinking in groups of mixed sizes, however, the time of greatest abundance varies somewhat (pers. obs.). These differences may be related to predation and physiological stress (Gilchrist, unpubl.), however, variability in 'safe sites' may cause wide fluctuations in observation (Geritz *et al.*, 1988).

SOCIAL BEHAVIOUR

Spatio-temporal variability in the environment requires that crustaceans adjust behaviourally to function efficiently. If social behaviour is an adjustment to the environment, then selection on these behaviours should occur (Seiple and Salmon, 1982). Social behaviours of crustaceans rarely exist as a single action pattern performed within a narrow intensity range; thus, plasticity of such behaviours is apparent.

Much of the work dealing with hermit crabs relates to the gastropod shell or other covering (Taylor *et al.*, 1989). More than 90% of non-taxonomic articles dealing with hermit crabs address shell or shell related phenomena. Reese (1963), Hazlett (1966), and Hazlett and Estabrook (1974) provided the basis for establishing a catalogue of behaviours observed during social interactions for several pagurids and diogenids. Acoustical displays are not included in the listing.

A brief review of shell use is important to understanding social interactions relating to this resource. Shell selection and use by hermit crabs are determined by a number of physical parameters of the shell as well as the motivation of the crab (Abrams, 1978; Dowds and Elwood, 1983, 1985; Hazlett, 1978, 1983; Kinosita and Okajima, 1968; Taylor, 1981). For adults, the shell may afford some protection but may also influence reproduction. As pointed out by Scully (1983) the relation between resource use and reproductive success is often assumed *a priori* to be correlated with fitness. Many authors have explored the influence of shell size on clutch size (Bertness, 1981; Childress, 1972; DeWilde, 1973; Fotheringham, 1980; Hazlett, 1989; Hazlett and Baron, 1989), although most major studies do not persist in observing hatch rate of eggs, recruitment into populations, and the influence of shell use on recruitment. For hermit crabs of several species observed in the laboratory the hatch rate was between 68 and 89% (Table 5) and survivorship through the glaucathoe molt was variable between species. In shell addition

TABLE 5. Laboratory observations of hatch rate for *Pagurus impressus*, *P. longicarpus*, and *P. maclaughlinae* using two methods of counting. For one data set, gravid females were weighed when captured and then again after larvae were liberated. Any eggs left on the pleopods and in the shell after 2 hours from hatching of last larvae were weighed and observed for development. The second method involved removing females from their shells, counting an aliquot of eggs, estimating egg number from the count, allowing females to re-enter a shell and then proceeding to count unhatched eggs two hours after liberation of larvae. Larvae were drawn to the surface by a strong light source and removed from the hatching tank.

Crab species	hatch rate				% surviving through glaucathoe	
	n	weighing	n	counting	weighing	counting
Pagurus impressus	20	68%	17	73%	0.1%	0.1%
Pagurus longicarpus	18	81%	17	83%	0.003%	0.002%
Pagurus maclaughlinae	23	83%	20	89%	1.1%	1.7%

experiments (Reese, 1963; Spight, 1977) some increase in population size is noted, however, I suggest that this apparent increase occurs from increased visibility of previously cryptic crabs. In a long term study of shell addition (>350,000 added to site in three years), populations of three species seemed to decrease while one species (*P. pollicaris*) increased only after two full years of shell addition (Fig. 3), added shells were assimilated into the populations. From these data alone, conclusions relating to shell use and recruitment over a long period of time seem uncertain. However, factors independent of shell use or shell availability may be used to explain the observed patterns. In 1985 and 1986 a series of strong storms occurred in the sampling area during the primary breeding season for the crabs. Few gravid females were collected, suggesting that recruitment might be low during the next 6 months. In 1987, *P. pollicaris* was collected in relatively high numbers during April and May but then decreased to near normal levels in June and July. During June and July stingrays moved into the area. Rays were observed harvesting the small hermit crabs in sandflat areas.

Aggressive behaviour of female hermit crabs

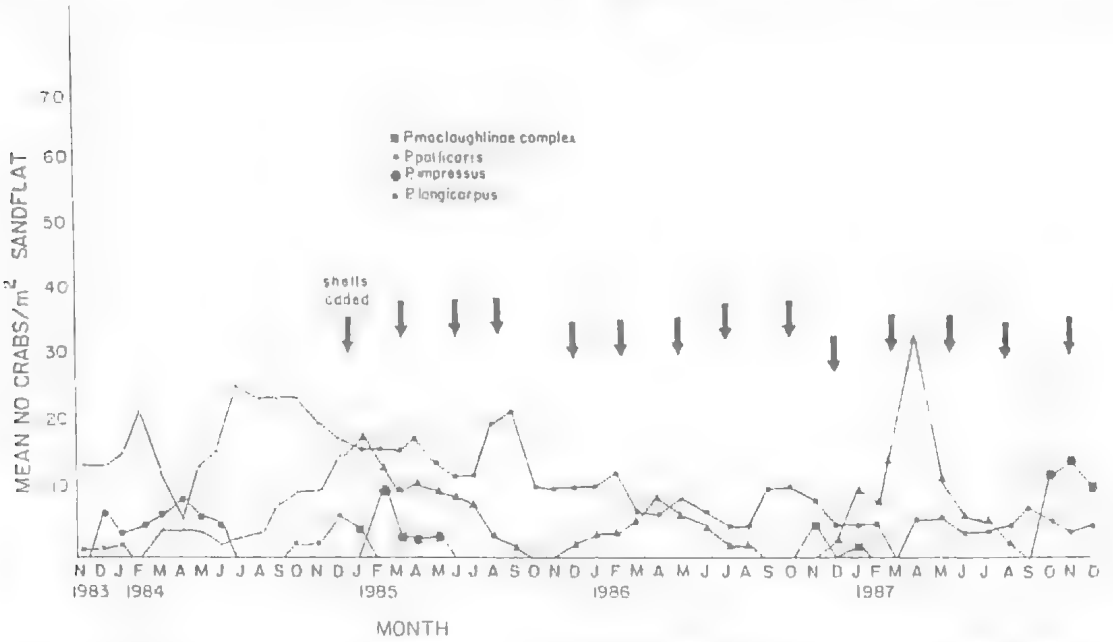

FIG. 3. Long term shell addition experiment to observe effects of available shells on recruitment. Shell additions did not significantly alter long term population patterns.

TABLE 6. Water retention of shells and hermit crab desiccation relative to shell condition for *Coenobita compressus* in Pacific Panama.

Shell type	shell condition	crab size	n	$\bar{x}$ ± sd amount of water retained (cc) after 1 hour full exposure	$\bar{x}$ ± sd time* to crab extension from shell (min)
Nerita scabricosta	with algae	< 5mm	20	–	21 ± 6
	without algae	< 5mm	20	–	15 ± 7
	hole in apex	< 5mm	20	–	13 ± 5
	with algae	> 5mm	20	–	37 ± 4
	without algae	> 5mm	20	-	24 ± 4
	hole in apex	> 5mm	20	-	19 ± 6
Turbo saxosus	with algae**	< 5mm	20	–	31 ± 5
	without algae	< 5mm	20	–	20 ± 6
	hole in apex	< 5mm	20	–	15 ± 4
	with algae	> 5mm	20	.31 ± .11	50 ± 9
	without algae	> 5mm	20	.19 ± .08	41 ± 6
	hole in apex	> 5mm	20	.06 ± .04	39 ± 14
Thais melones	with algae	< 5mm	20	.38 ± .14	64 ± 15
	without algae	< 5mm	20	.31 ± .08	51 ± 11
	hole in apex	< 5mm	20	–	30 ± 19
	with algae	> 5mm	20	.52 ± .17	81 ± 8
	without algae	> 5mm	20	.48 ± .14	74 ± 11
	hole in apex	> 5mm	20	.21 ± .11	39 ± 14

* it was observed that prior to death crabs extended from shells and did not retract upon stimulation of abdomen; crabs reaching this point were quickly rehydrated.

** shell had only sparse amounts of algae observable from aperture.

does appear to alter during brooding. Neil and Elwood (1985) observed that gravid crabs (*P. bernhardus*) have decreased levels of attack and increased levels of defensive behaviour. They also note that shell exchange is infrequent. Gilchrist (1982) found that for *Clibanarius vittatus*, *P. pollicaris*, and *P. maclaughlinae* gravid females were more likely to have greater numbers of shell co-inhabitants than males. Hazlett (1970) suggest a chemotactile discriminatory cue while Imafuku (1986) postulated that receptive females may emit a water-borne chemical which facilitates discrimination between the sexes. It is not unreasonable to speculate that other organisms might use such chemicals to orient to a female as well. Further, these shell occupants were observed eating eggs as well as abdomenal appendages of the crabs. Gilchrist (1982) and Bertness (1981) observed that gravid crabs changed shells more often than nongravid ones, contradicting the observations made by Neil and Elwood. Perhaps this difference may be explained by variations in shell co-inhabitants in the various study areas. Current observations of *P. longicarpus*, *P. maclaughlinae* and *P. pollicaris* in Sarasota Bay (unpubl. data) indicate that gravid females of these species change shells often, move into less saline waters for extended periods, and tend to be somewhat restricted in overall movement patterns.

Despite some evidence to the contrary (Gilchrist, 1982; Gilchrist and Abele, 1984; Wilber and Herrnkind, 1982), it is commonly assumed that hermit crab populations are limited by supplies of empty shells (Hazlett, 1981; Kellogg, 1976; Vance, 1972). Thus, many studies of interactions have focused on competition for this limiting resource. Consumption rate and combined effects of different sorts of variability (Chesson, 1985) are important in determining coexistence in specific natural systems. Superimposed on variation in consumption rate is the age structure pattern of the populations in that differences in shell use occur with crab age (Abrams, 1980).

Correlations have been noted between shell selection and level of environmental stress (Bertness, 1981c; Taylor, 1981, 1982; Young, 1980) as well as predation (Bertness, 1981c; Borjesson and Szelistowski, 1989).

Mortality of all life stages can result from predation (including parasitism). The type and condition of shells may afford some advantages to crabs with certain predators, however, crab

behaviour may be of equal or greater importance in circumventing predation. Crypsis, burrowing behaviour, or use of refugia such as seagrass beds may decrease predation by vertebrates. Birds, including especially gulls (Oldham, 1930) and fish, are effective predators on these crabs (*Pagurus*; Fig. 5). Use of weathered or fouled shells may provide camouflage for crabs in particular habitats (Blackstone, 1984; Conover, 1976; Jensen, 1970; Partridge, 1980). Fouling of shells by algae (Smyth, 1989) and hydroids (Jensen, 1970; Stachowitsch, 1980) may prevent boring organisms from weakening shells through bioerosion or may deter predators from handling shells. Abrams (1978) found strong selection against unused shells by *Coenobita compressus*, noting that crabs of this species modified the aperture as well as internal shell structures. *Coenobita compressus* in used shells chirped more often and for a longer period of time than crabs in newly liberated shells (Gilchrist, unpubl. data). Abrams also observed that a green alga coated the interior of the shell. In shell experiments with this crab species, aquatic juveniles with algae in the shell had greater numbers of shell cohabitants while adults with algae in the shells tended to have greater water retention and longer times to desiccation (Table 6).

Agonistic encounters relating to the shell resource are recorded commonly for aquatic hermit crabs. Hazlett (1966) gives a detailed description of many components to shell fighting (or shell exchange). Abrams (1982) studied shell exchange between many different species pairs in tropical and temperate zones and noted that crabs in adequate or high quality shells typically retained their shells. Further, he suggested that exploitative competition for new shells might be more important in understanding shell distribution among species than shell fighting.

Imafuku (1989) summarised 2 important features of shell fights: exchange of resource and variation in value of resource for individuals. Shell fights may include a variety of agonistic interactions. These typically include both visual and tactile components (Hazlett, 1966 *inter alia*). Field *et al.* (1987) explored the use of sound production by *Trizopagurus* as a defensive behaviour. It also aids in species recognition. In addition, they noted that the shell has only a small role in modifying the sound. *Coenobita clypeatus* and *C. compressus* sound production (chirping) may occur along with visual displays and tactile behaviour. Chirping frequency may increase significantly when new crabs are introduced into an area (pers. obs.). *Birgus* may also use sound in such contexts (Grubb, 1971).

Male *Aratus* observed on Tidy Island in Florida may rap chelae and the fourth pereiopods on horizontal trunks when threatened by a conspecific. In tagging experiments with large male *Aratus* (carapace width >14mm), these animals exhibited a patrolling behaviour. This consisted of moving vertically on the trunk for about a half metre (either up or down), raising the chelae while tilting the front of the body outward and then zigzagging over the trunk. The same males were found on specific trees a greater amount of time than would be expected by chance alone, suggesting further studies are necessary on the potential territorial behaviour of this crab. Several similarly sized crabs occupy a tree at one time. Rarely were overt agonistic encounters observed although numerous crabs were observed with missing chelae or ambulatory appendages. These missing appendages may be explained in part by successful avoidance of predation (Table 3). In 7 cases of aggressive encounters noted in 50 hours of observation, all were on the root area of the mangrove. In each case, one crab approached the other from above. Each crab extended and raised the chelae while moving back and forth in a semicircle. The abdomen was close to the surface while the anterior of the crab was elevated. The eyestalks were lowered to about a 45° angle with the carapace. In two cases, the crabs were 'bubbling' from the oral opening. Typically, after about 90 seconds of such posturing one crab would sidestep and move away from the encounter. In 3 instances a brief shoving match followed the semicircular movements. The match ended when one crab was pushed off the surface entirely or when the first three pereiopods of one crab were lifted off the surface. The lifted crab backed away and moved around the root away from the opponent. The crab that was knocked from the surface was missing part of the left 4th pereiopod. Only male crabs were involved in 3 encounters, only females in 2 encounters, and male-female pairs were found in 2 encounters. The only other social encounters observed for these crabs were 3 probable copulatory events. The male approached a female from above and from an angle. In each case, the male then moved over the top of the female while completely surrounding her body with the pereiopods. The male then lifted his body above the female while holding the chelae

down and clasping the female with the second pereiopods. The female then gathered her appendages close to her body, and rose from the surface. After that point, copulation proceeded much the same as observed by Warner (1967). Females were hard shelled in each case.

Other forms of social encounters for *Aratus* were observed during feeding bouts around root areas of black and red mangroves. Feeding behaviour and social interactions were noted for crabs during low tide only when roots were exposed. Activity was especially noted during crepuscular low tides.

Small animals (carapace width <5mm) move to the substrate while some water is still present. Larger crabs descend when the water has receded. However, larger crabs move further and forage longer then their smaller counterparts. Crabs consumed both plant and animal material, primarily concentrating on vegetation. If red mangrove seed pods or seedlings are available, *Aratus* will be attracted to them. On seedlings, the crabs strip the leaves entirely using the chelae to remove pieces and transfer them to the mouthparts. Seeds are scraped repeatedly, dislodging them from the substrate. Larger crabs pierce the pod and tear pieces from outside. Typically only a small amount of immediate damage is done to each pod. When more then one crab converged on a seedling, the larger crab would flick the smaller crab with a chela. If crabs were nearly equal in size, the crab arriving first would elevate from the substratum and raise one or both fourth pereiopod(s). This crab would then do a series of up and down motions with the body. The approaching crab also elevated from the substrate, advancing with the chelae extended in front of the body. The first crab continued the up and down movement increasing the frequency as the second crab moved closer. Out of 17 such encounters observed, crab 1 remained at the seedling while crab 2 moved away in 11 cases; in 4 encounters crab 2 moved away; in the remaining 2 observations, a predator (*Goniopsis cruentata*) removed one of the crabs

On trees, rarely were crabs seen foraging together. Only three instances in 75 hours of observation yielded *Aratus* individuals even feeding on leaves of the same branch. Burton (1990) and Beever *et al.* (1976) have discussed herbivory by these crabs on mangroves in some detail.

For land hermit crabs, foraging may be subject to social facilitation. Kurta (1982) found that by orienting to aggregations of crabs, individuals increased their probability of finding food. Hazlett (1968, 1972) and Scully (1983) demonstrated that hermit crabs, observing conspecifics increasing their locomotion rate toward a food source, will likewise increase their rate of locomotion. Scully goes on to observe that large aggregations of hermit crabs may repel other organisms from a food source. During my observations on *Coenobita compressus*, rarely were large aggregations noted. The only time such groups formed were when large food items (dead bird or dead fish) were available. Typically, when feeding on the beach at the wrack line, larger crabs were solitary. Smaller crabs foraged in groups of 3–8 individuals, never straying long distances along the shoreline (one crab moved about 10 metres along the shoreline but most moved within a five metre area). Within these small groups, some flicking with pereiopods occurred occasionally.

Large groups of small crabs (>25) formed around freshwater. Crabs were observed dipping the chelae into the water and moving them to the mouthparts. As larger crabs approached, smaller crabs scattered and moved back into the jungle. Large crabs either drank in the same manner as described for the smaller crabs or immersed the entire shell into the water. Feeding and drinking behaviours of these crabs are noted elsewhere (Newton and Gilchrist, 1989). Larger crabs typically maintained a relatively large distance between each other at freshwater sources. However, clicking and chirping frequency increased as new crabs approached the water source.

Most crabs appeared to scavenge or browse for food. However, predation on both plants and animals occurred. Immature insects (grubs, caterpillars, and maggots) were readily eaten as were young leaves near the jungle floor. A wide variety of items were detected by crabs including chocolate, honey, dog food, raw eggs, and cat food.

Much like their terrestrial counterparts, marine hermit crabs may feed in aggregations of mixed sizes. It is not clear, however, whether social facilitation or chemical attraction leads to increases in aggregation size. Schembri (1982) described the feeding behaviour of fifteen species of hermit crabs from southeastern New Zealand. He found a wide range of feeding mechanisms among the group including deposit feeding, browsing, suspension feeding, predation, and scavenging. He indicated that a variety of secondary mechanisms.

During aggregate feeding, observed for marine species in Sarasota Bay, not only are conspecifics found at such sites but also other species may be attracted. *Pagurus longicarpus* was found in every mixed group. As a group forms, several types of interactions may occur. If the food item is small enough, a crab may attempt to flee with it. Typically, a tugging match ensues with each contender holding on with the major chela and plucking from the food item with the minor chela. As more crabs join, larger crabs typically displace small ones. Smaller crabs climb onto the shells of these larger crabs, collecting food from the water column above the feeding crabs. Larger crabs flick other crabs with the major chelae while holding onto the food item. If the item is too large to guard in this manner, a number of larger crabs will begin feeding on the item. Smaller crabs which try to move beneath larger crabs are typically flicked away. I have observed neither shell exchanges nor mating behaviour during such feeding bouts. Hermit crab predators are also attracted to food sources, thus shell exchanges and copulation may not be productive at feeding sites. Aggregates in marine habitats may also allow crabs to avoid predators. *Callinectes* typically approaches the aggregations from downstream, rushing the group as it nears. Fishes and birds tend to move over the groups slowly, making several quick darts before the group disband. Such predator attacks on terrestrial species have not been recorded.

SUMMARY

Clearly, terrestrialisation has led to behavioural modifications in crustaceans. Physiological differences in smaller crabs on land may serve to separate them ecologically from their adult counterparts. Physiological differences in size do not seem as important in aquatic species.

Chemical, visual, and tactile inputs are important components of modulating motivation and action of terrestrial and aquatic species. However, the relative importance of the types of cues may differ in the two media. The full extent of how chemical and acoustical information may modify behaviours is still under investigation. Further study of both the receptors and responses are necessary. In addition, careful ontogenetic studies of the morphology of receptors and development of behaviours should be completed.

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INDUCED OVARIAN MATURATION OF *PENAEUS VANNAMEI* BY IMPLANTATION OF LOBSTER BRAIN

In many decapod crustaceans, control of ovarian maturation is a major problem in developing commercial aquaculture programs. Induction of ovarian maturation in *Penaeus vannamei*, by implantation of brain prepared from female lobster, *Homarus americanus*, with developing ovaries was investigated under tank culture conditions. Three of five females with brain implants were maturing while none of 10 females of the control groups with abdominal ganglion or no implant matured (Table 1). Two ripe stage V were found 17 days after implantation of lobster brain. This indicates that ovarian maturation of *P. vannamei* in tanks can be induced and accelerated by implantation of brain prepared from maturing females of another species. Ovarian maturation may be induced by a brain hormone (BH), secreted by the brain of maturing females. This brain hormone is not species specific in activity in the shrimp and lobster. I have demonstrated that ovarian maturation is induced by a gonad-stimulating hormone (GSH), secreted by the thoracic ganglion of maturing females in penaeid shrimp. This GSH may be triggered by BH, which probably is working as a gonad-stimulating hormone-releasing hormone (GSH-RH) in regulating ovarian maturation in shrimp and lobster.

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TABLE 1. Effects of implantation of brain prepared from maturing female lobster, *Homarus americanus*, on induction of ovarian maturation of *Penaeus vannamei* 17 days after treatment. * Size: 30–35g in body weight.

	No. of Shrimp	No. of females showing various stages of ovarian development					% of maturing shrimp
		I	II	III	IV	V	
Brain implantation	5	1	0	1	0	2	75.0
Abdominal ganglion implantation	5	4	0	0	0	0	0.0
No implantation	5	5	0	0	0	0	0.0

THE EFFECT OF ARTIFICIALLY LIGHTED TRAWLS ON CATCHES OF CRUSTACEANS

A series of 32 micronektonic samples were taken with a rectangular midwater trawl (8) in open oceanic water off N.W. Africa (20°30'N, 19°40'W), at a depth of 800±25m, below the effective penetration of surface daylight. The net, fitted with a sea-light and battery pack, was fished for a series of two hour tows, half with lights on and half with lights off, throughout the day and night.

Catches of crustaceans, comprising mainly of mysids and decapods, were relatively consistent in biomass (wet displacement volume), species composition, and size irrespective of the artificial lighting. Mysids were represented mainly by one species of *Eucopia*, total numbers and biomass of which were similar in most samples.

Decapoda were identified to species and the carapace length measured. The size varied from 4.5mm CL to a maximum of 35mm CL but most specimens were in the range 4.5mm–15mm CL. A total of thirty species were identified, of which four were numerically dominant and a further ten occurred in moderate numbers. There was no indication that artificial lighting had an affect on species composition. Numerically dominant decapod taxa included two species of *Gennadas*, one of *Acanthephyra* and one of *Sergia* many specimens of which were juveniles or young adults.

Preliminary statistical analyses including an analyses of variance based on the ten most abundant decapod species indicated that there was no significant difference between catches irrespective of the artificial lighting. This confirms previous work (Hargreaves, unpubl.) that catches of many decapod and mysid species found at depths of 800m off Madeira were hardly affected by lighted trawls. Initial results on crustacean biomass from paired hauls (Clarke and Pascoe, 1985) indicated that at 800m depth in the Bay of Biscay and off Madeira catches of Decapoda may be diminished with the use of lighted trawls. These indications are not supported by the present data. However differences in species sampled or in their maturity stages may be responsible for the apparent variations.

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THE RED CUTICLE ON THE CLAW OF MALE *CHERAX QUADRICARINATUS* (DECAPODA: PARASTACIDAE)

The freshwater crayfish *Cherax quadricarinatus* (von Martens) is a member of the Australian family Parastacidae. It occurs in northern Australia from Cape York through the Northern Territory (Riek, 1951).

In recent years, *C. quadricarinatus* has become the major freshwater crustacean cultured in Queensland. Features which make this species ideal for aquaculture include (i) little aggression when held at high densities (ii) good survival at high temperatures (iii) serial spawning.

A striking feature of this crayfish is the soft red cuticle that develops on the outer edge of the propodus in mature males. Growth of the red patch in relation to orbital carapace length is positively allometric. The red patch does not develop in juveniles, and typically occurs in those individuals whose orbital carapace length exceeds 23mm. Intersexes (those crayfish with both male and female genital openings and which comprised 19 in a sample of 456 individuals) develop the red patch. Occasionally, the red patch is developed by females (3 individuals in a sample of 279 females). The possible function of this sexually dimorphic feature is intriguing. A role in defence or attack is unlikely — soft cuticle makes an unsuitable weapon. A role as a visual, sexual signal is also unlikely — the crayfish are mainly active at night, and most crustaceans examined so far are red blind (Shaw and Stowe, 1982). Anecdotal reports indicate that the red patch of the male claws makes contact with the female when the male makes a series of short, sharp jabs at her during courtship.

Major differences between red patch cuticle and ordinary cuticle are: (i) it is soft, flexible and yields easily to touch. The flexibility of red patch cuticle is not achieved in the same way as occurs at hinges between body or leg segments. Hinge cuticle has no continuous lamellae running parallel to the epicuticle. (ii) It is uncalcified (sections through red patch cuticle showed no black colouration when stained using von Kossa's technique for calcium (Culling, 1974) while control sections through chick embryo were positive). (iii) exo- and endocuticle are not differentiated. In ordinary cuticle, epi-, exo- and endocuticle layers are clearly defined. At the transition zone between cuticle types the epicuticle continues without change but the width of the endocuticle decreases. In red patch cuticle no obvious distinction can be made between exocuticle and endocuticle, giving it a two-layered appearance rather than a three-layered one. (iv) the lamellae are narrow. The width of lamellae in red patch cuticle is just over one third the width of lamellae in the endocuticle of ordinary cuticle (12.5µm vs 32.5µm).

Sensilla density on red patch cuticle is similar to that on hard cuticle of the claw. It is also similar to the density on the claws of females in the region where the red patch would occur, if they had one.

Two types of sensilla, simple and plumose, occur on the ordinary cuticle adjacent to the red patch, whereas only simple sensillae appear to occur on the red patch cuticle. Whether the red patch gives the male different sensitivity to tactile or other stimulation from that of the female awaits further investigation.

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ULTRASTRUCTURE AND FUNCTION OF THE STOMACH OF PERACARIDA AND EUPHAUSIACEA

Ultrastructurally the stomach is by far the most complicated part of the alimentary canal in Peracarida and Eucarida (for references see Felgenhauer and Abele, 1985; Storch and Strus, 1989). All parts are demonstrated in scanning and transmission electron micrographs. They consist mainly of masticatory parts and filters.

The most complicated region of the stomach is the ventral surface with primary filters, secondary filters, and interolateralia (Storch, 1989; Storch and Strus, 1989; Storch, in prep.; Ullrich *et al.*, in prep.). The mesh sizes of primary and secondary filters vary considerably. Secondary filters of terrestrial Isopoda seem to be the most efficient filters in the animal kingdom. They are good for microfiltration and come very close to ultrafiltration. They are compared to the respective structures in Mysidacea, Tanaidacea, Amphipoda, and Euphausiacea.

Filters of these delicate dimensions have to be constantly cleaned to be kept functional. Spines of the medial face of the interolateralia are probably suitable for this purpose. Additionally, washing occurs when the secretion of the midgut glands move through the same opening as the filtrate but in the opposite direction.

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BIOCHEMISTRY AND FUNCTION OF CRUSTACEAN NEUROHORMONES

Triggered by various environmental stimuli, the nervous system produces and releases several peptides which enable an organism to handle specific situations. The regulatory potencies of the peptides so far postulated include cardiac control, locomotion, feeding behaviour, migration of chromatophores and retinal pigment, moult suppression/acceleration, the development of testis, oocytes and vitellogenin, limb regeneration, blood glucose adjustment, endogenous rhythmicity, lipid, carbohydrate and protein metabolism, osmo- and hydromineral and respiratory regulation, RNA/DNA synthesis, mitochondrial respiration and carotinoid metabolism: almost every aspect of crustacean life. The number of postulated factors is large (Kleinholz, 1985; Webster and Keller, 1988), the number of isolated neurohormonal peptides, however, is small and our knowledge of their physiological functions is still limited. Several factors are based on inadequate evidence or are still under discussion e.g. the neurodepressing hormone (Cooke and Sullivan, 1982). In terms of the amino acid composition, the moult-inhibiting hormone (MIH) from *Carcinus maenas*, the crustacean hyperglycemic hormones (CHH) from *Orconectes limosus*, *Porcellio dilatatus* and *Procambarus bouvieri* and the neurodepressing hormone from various species have been characterized. The primary sequence is reported for two FMRF-like peptides (FLI), a member of the pigment concentrating hormone family, from two pigment dispersing hormones, from cardioactive peptides and from the CHH of *Carcinus maenas* (Kegel *et al.*, 1989). For this 8524 Da neuropeptide the complete coding sequence for the pre-pro CHH has been obtained recently from a DNA-library (Weidemann *et al.*, 1989). MIH and the gonad (vitellogenin) inhibiting hormone (GIH/VIH) apparently belong to the CHH neuropeptide family, judging by the comparison of amino acid sequences, which have been analysed to approximately 80%. Recent observations are consistent with the hypothesis that the spectrum of functions of these identified neurohormones might be broader than their names suggest. The red pigment concentrating hormone (RPCH), for example, affects not only the erythrophores but also the pyloric rhythms by alternating the membrane potential in the lateral pyloric and pyloric dilator motor neurons. Therefore, RPCH (or a very similar molecule) is thought to release a modulator from the somatogastric ganglion. A similar modulation of proctolin on the pyloric network has been reported. In addition to glucose CHH affects trehalose and maltose blood concentrations and releases amylase from the midgut gland in crayfish. The distribution of the crustacean-cardioactive peptide (CCAP) in the central nervous system suggests that CCAP might be a novel neurotransmitter with multiple functions, e.g. modulation of the motility of isolated hindguts. In addition to these neuropeptides, which are derived from neurohemal sources such as the sinus gland or pericardial organ, numerous, mainly vertebrate-type peptides, have been described in crustacean neuronal tissue using immunocytochemical methods. The stained epitope does not necessarily prove the identity of the original antigen, either functionally or biochemically. Some of these X-like peptides with limited or no relation to vertebrate hormones, such as cholecystokinin/gastrin-like or calcitonin-like peptides have been isolated or sequenced. The physiological functions of these peptides are mostly unknown or the subject of speculation.

Opioid- and FMRFamide-like peptides have been demonstrated by HPLC, RIA and immunocytochemistry in decapod crustaceans (Jaros, 1990). The FMRFamide-like peptides (FLI3,4), isolated from *Homarus*, seem to be involved in the modulation of cardiac neuromuscular junctions (Trimmer *et al.*, 1987). The CHH release-inhibiting effect of leu-enkephalin, blocked by naloxone, was shown by Jaros *et al.* (1985). Met-enkephalin has been shown to stimulate the release of chromatophorotropic hormones and other evidence exists for the involvement of an opioid regulation of locomotor activity in *Gecarcinus lateralis*. These different results demonstrate the broad spectrum of opioid effects on crustacean physiology. An exciting future field of study for the endocrinologist is the growing body of information regarding a possible neurohormonal-immunological axis even in invertebrates. Pilot studies reveal an implication of opioids on hemocyte aggregation.

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PHOTORECEPTOR MEMBRANES AND VISUAL PIGMENTS IN THE APPOSITION EYES OF THE TERRESTRIAL CRAB, *OCYPODE RYDERI* (OCYPODIDAE), DURING THE DAILY LIGHT CYCLE

The ghost crab, *Ocypode ryderi*, is very common on the equatorial sandy beaches of the east African coast. The activity periods of these animals are ruled by the tides, and therefore they feed at the water-line of low, rising tides during both day and night. Their very large compound eyes are of the apposition type, which adapt to strongly different light intensities by changing the size of the rhabdoms in each ommatidium. These changes are controlled internally (without the need for an external zeitgeber) according to the diurnal cycle.

Morphometric studies on the form of the rhabdom and the size of its microvilli gave the following results. The rhabdom volume changes — while its length remains constant by a factor of 8. The total surface of the microvillar membranes, however, changes only by a factor of 6, because the diameter of each microvillus is slightly larger during night than day. The visual pigment molecules are closely packed in the membranes, as can be seen in electron micrographs of freeze fracture preparations, where each particle represents a group of four molecules.

The rhabdom, which consists of the rhabdomeres of eight visual cells, has a characteristic variation of its form during the daily cycle. The most distal part, which is built exclusively by the distal receptor cell, named no. 8, exhibits the greatest volume change. Its variation in diameter is paralleled by the proximal surface of the crystalline cone. The rhabdomeres of the other seven receptor cells together all arrange to form a long, thin conus. The change in its diameter is much more pronounced in the distal than in the proximal part.

The visual pigment content — as measured spectrometrically in extracts — parallels the change in microvillar surface: during the night there is 6.5 times the amount as during the day. In contrast, the protein moiety, opsin, changes significantly less — only by a factor of 4 — which means that a considerable part of it is stored in the cell during the day. It is unknown where this lipophilic material is situated.

The visual pigment, rhodopsin, consists of the protein moiety opsin and its chromophoric group, which was determined by HPLC as retinal$_1$. The characterization of the spectral properties of the pigment system in the eyes of *Ocypode* was carried out by successive irradiation of digitonin-extracts from isolated rhabdom-membranes with monochromatic lights. Short-time illumination (< 1 min) with long wavelengths (590 nm) transforms the blue sensitive visual pigment (P_{470}) into its metarhodopsin (M_{520}). Longer lasting illuminations lead to the decay of metarhodopsin into opsin and free retinal$_1$ (λmax 380 nm) or, in the presence of hydroxylamine, retinal-oxime (λmax 368 nm).

Further illuminations with light of a shorter wavelength (471 nm) lead to a decrease in absorbance around 430 nm and to an increase around 510 nm. Illuminations were carried out until no changes in the difference-spectra after illumination could be observed. Computations from the difference-spectra obtained, using nomograms from EBREY & HONIG (1977, Vision Res 17, 147), resulted in a visual pigment with a λmax of 424 nm and a metarhodopsin with a λmax of 518 nm. Light of 530 nm reconverts the metarhodopsin into rhodopsin.

Additional illumination with UV-light (348 nm) leads to a decrease of the absorbance around 350 nm and to an increase around 510 nm. The photoproduct of this conversion is thermostable at 8°C and can be reconverted into rhodopsin by illumination with 517 nm. Computations of these spectra gave a UV-visual pigment with a λmax of 355 nm and a metarhodopsin with a λmax of 510 nm.

These pigments, which are expected to occur in different receptor cells, together build a three-component-colour vision system, which is demonstrated here for the first time in a decapod crustacean.

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VENTILATION ACTIVITY AND GUT FULLNESS OF THE BURROWING GHOST SHRIMP, *CALLIANASSA AUSTRALIENSIS* DANA (DECAPODA: CALLIANASSIDAE), DURING LOW TIDE

Invertebrates that live in deep burrows in the intertidal zone are thought to gain an advantage by being insulated from environmental changes at low tide. Stress causes many intertidal invertebrates to cease feeding at some time of the tidal cycle (Newell, 1979). The shrimp, *Callianassa australiensis* feeds in burrows but may possibly change its feeding activity at low tide. This study aimed to detect and quantify changes in behaviour that may help explain the role of the tide in the feeding energetics of this species.

Methods and Materials

The study site was located on One Mile Beach on North Stradbroke Island, (27°29'S, 153°24'E). The oxygen tension of burrow water samples was determined using a portable oxygen meter and magnetic stirrer. Animals were collected by using a 'yabby pump' at different times after the tide had uncovered their burrow apertures. General physiological and morphological data collected included, sex, wet weight, carapace length, moult state, and 'empty' or 'not-empty' state of the gut of each shrimp was recorded. In one group of animals (T = 0h n = 43, T = 2h n = 38) the fresh and dry weight of the foregut and 'intestine' was obtained after dissection. The temperature of mud (30cm depth) and surface puddles were recorded in conjunction with each sample of shrimps.

Results and Discussion

The shrimps ceased ventilating and purging sediment from their burrows 2–3h after low tide. The oxygen tension of water samples taken from the burrows fell significantly at low tide, from 19.98± 1.25 kPa at 0h (N = 8) to 12.04±3.01 kPa, (N = 10, P<0.05) after 1h, but there was no further change after 3h (13.58±4.72 kPa, N = 10, P>0.20). Large amounts of oxygen were therefore available for respiration by these shrimps at low tide. Warming of the sediment during daylight low tides was less marked (at about 30cm depth, in the order of 1–2°C) than the rapid warming found in puddles on the surface of the mudflat (7–8°C). At least some shrimps pump this warm surface water through their burrows at low tide.

No significant change in wet or dry foregut weight could be detected, however, the mass of the intestines of shrimps collected after 2h of low tide was lower than that of shrimps collected at the beginning of low tide, (Mann Whitney test applied to wet weights, Z = -3.937, N1 = 43, N2 = 38). The mean percentage (prior to arcsine transformation) of the population with 'empty' intestines increased at low tide (data from 7 tides), from 5.36±6.19% to 47.51±20.44% within the first hour (using arcsine transformed data, t = -4.9058, DF = 12, P<0.0005), before levelling off (t = 2h 61.87±20.04%, t = 3h 64.00±16.83%). This change was reflected also in shrimps captured in the act of burrow ventilation/sediment purging during several low tides (pooled data, T = 0, N = 78 empty 0%; T = 1–2h, N = 65, empty 50.8%), indicating that sediment purging (with associated thermal stress) was not confined to shrimps containing faecal pellets. The decline in sediment purging behaviour at low tide occurred in parallel with, and cannot therefore be explained by, changes in gut fullness, i.e. 'feeding' activity.

Knowing the relationship of 'empty' intestine weight (log (W) = 3.736 log (L) - 3.145, N = 28, r^2 = 0.55, F = 329.8 P<<0.001) and 'not-empty' intestine weight (log (W) = 2.424 log (L) - 1.084, N = 53, r^2 = 0.67, F = 105.0, P<<0.001) to carapace length (L) allows mean faecal pellet egestion rates to be calculated. Roughly half of the population empties their intestines in the first hour of low tide, requiring those shrimps to egest faeces at 11.08 and 26.51mg wet faeces h^{-1} for shrimps with a carapace length of 8 and 12mm respectively. This result compares well with the data obtained by Frankenberg *et al.* (1967) from faecal pellets discarded by *Callichurus major* at low tide, (50.6mg wet faeces burrow $^{-1}$ h^{-1}).

A large portion of the shrimp population clears faeces from their intestines during low tide and may very well cease feeding at this time. Further work is required to establish why some shrimps fail to empty their gut and to explain the variation in response between tides.

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THE INFLUENCE OF SIZE DIFFERENTIAL ON AGONISTIC ENCOUNTERS BETWEEN INTERMOULT FRESHWATER CRAYFISH IN *CHERAX CUSPIDATUS* RIEK, 1969 (DECAPODA: PARASTACIDAE)

The resource holding potential (RHP, Parker 1974) of an animal is a measure of that individual's absolute fighting ability, and consists of a combination of its morphological and physiological traits such as body size, age, size of weapons, armour and energy reserves (Caldwell, 1987). RHP is one of several concepts generated from the application of game theory to animal contests (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981). Such concepts have enabled the formulation of testable predictions relating to the agonistic behaviour of animals under various contest conditions.

The research outlined in this paper tested two predictions of simple game theoretic models. These were:

1. an asymmetry in RHP between opponents will decide contest outcome; and

2. RHP differences between opponents will determine strategies used in contests, with escalated interactions likely to occur between opponents with similar RHP.

Methods

Sexually immature, intermoult, young of freshwater crayfish *Cherax cuspidatus* were used in experiments. Total carapace length (T.C.L.) was the RHP index employed. Crayfish were paired at five size ratios : 1:1, 1:0.9, 1:0.8, 1:0.7 and 1:0.6 and allowed to interact for 180 minutes in containers (9 x 9.5 x 9.5cm high) with no shelter present. Crayfish were released into the containers simultaneously to eliminate any possible ownership effect. Replication level was 16.

The initiator, winner, duration and type (whether fight, attack, strike or threat) of each agonistic interaction was recorded. The dominant individual for each pair was defined as the one which won at least 60% of all interactions. The size of each dominant (whether the larger or smaller member of the pair) was also recorded.

Results and Discussion

The larger animal was always dominant once the size difference was 20% or more. The larger individual was dominant significantly more often than expected by chance at the 1:0.9 ($p<0.01$) and 1:1 ($p<0.05$) size ratios. Two pairs at the 1:1 ratio had equal T.C.L. values. The remainder was separated by differences between 0.85 and 4.05%, indicating that size discrepancies of less than 5% can influence outcome of agonistic interactions.

The measurements taken for the four pairings at 1:1 and three at 1:0.9 in which the individual with smaller T.C.L. was dominant, revealed that in each case the 'smaller' animal was superior in at least one of the other potential RHP values (weight, chelae length, age). This result suggests that a single RHP index has limited utility for pairs when both members are superior in one or more morphological measurements. Such a situation is especially relevant to organisms with indeterminate growth, e.g. Crustacea.

Size discrepancy between opponents had a significant inverse relationship with total agonistic time, fight time, maximum and average bout length ($p<0.001$), fight frequency and frequency of all interactions ($p<0.01$), and strike frequency and time of threat, strike and attack combined ($p<0.05$). Attack frequency, threat frequency and attack response latency did not vary significantly between size ratios.

Size discrepancy had an inverse relationship with the proportion of interactions initiated by the smaller animal in each replicate ($p<0.05$), but formed no significant relationship with proportion of interactions won by the smaller individual ($p>0.05$). The larger animal in each pair initiated ($p<0.01$) and won ($p<0.0001$) the first agonistic interaction significantly more often than expected by chance. The smaller animal initiated a proportion of the first interactions, irrespective of size ratio.

Assessment of RHP among pairs of *C.cuspidatus* always involved agonistic interaction, possibly as a means to probe for recently moulted crayfish. Differences in RHP between opponents determined the outcome of interactions. Contests in which opponents could accurately assess the asymmetry in RHP, i.e. 1:0.6 and 1:0.7 size ratios, were settled without escalation. Those in which role assessment could not be accurately made by conventional behaviour, i.e. 1:1, 1:0.9, 1:0.8, resulted in escalation. The results of this work are in agreement with the predictions generated by simple game theoretic models.

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IONIC PERMEABILITY OF THE CUTICLE AND IONOREGULATION IN DECAPOD CRUSTACEANS

The ionic permeabilities of the isolated gill cuticle have been deduced from diffusional transcuticular potential and conductance measurements in several species of decapod crustaceans. It is established that the cuticle permeability depends upon the species considered and its ionoregulation capability, upon the localisation of the gill in the gill chamber or even upon the topographic region in a single gill and upon the nature of the ionic species.

In each case the cuticle must always be considered as a diffusion barrier for the main osmotic effectors, Na^+ and Cl^-. However, the efficiency of this barrier is low in the case of the stenohaline osmoconformers, *Homarus*, *Nephrops*, *Maia*. In hyperregulators such as *Astacus*, *Eriocheir* and *Carcinus*, the efficiency of the cuticular barrier is much higher. The cuticle permeability of the crayfish gill lamina is low for all ionic species but Cl^-. In the crayfish gill filaments and in crab gills, permeability to cations is high, but permeability to Cl^- is low.

In hyperregulators, the cuticle exhibits important differences in its electrical characteristics between the various pairs of gills or even between different topographic regions of the same gill. It shows in addition a functional asymmetry which favours ionic influxes. This asymmetry is almost nonexistent in osmoconforming species.

The physiological significance of the cuticle is discussed in relation to the ionoregulation capability of the species and more particularly to the subcuticular spaces described in all gill epithelia of hyperregulatory Crustacea facing reduced salinity. It is propounded that the gill cuticle contributes to reduce ionic leaks in regulators and yet allows for the entry

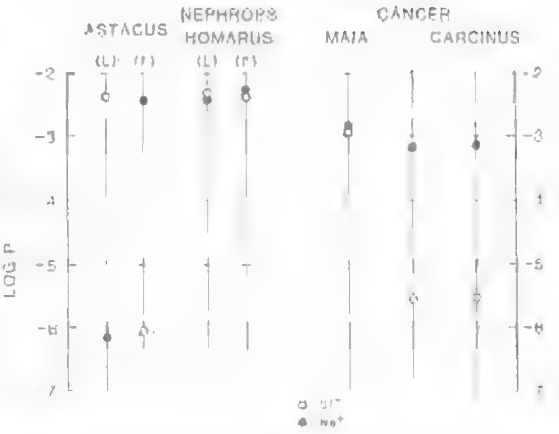

FIG. 1. Comparison of the permeability of the gill cuticle from six crustaceans to the main osmotic effectors Na^+ and Cl^-. The permeability (P) is plotted on a logarithmic scale. Notice the difference between regulators and osmoconformers either within the macrura or within the brachyura (L = gill lamina; F = gill filaments). Taking into account the electroneutrality condition, the following salt permeability sequence as related to the species would be : *Homarus, Nephrops > Maia > Cancer > Carcinus > Astacus*.

of ions across specific channels at the sites where active uptake takes place.

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NEUROENDOCRINE CONTROL OF THE OVARY AND HEPATOPANCREAS IN SIBERIAN PRAWN, *EXOPALAEMON MODESTUS*

In many decapod crustaceans, the eyestalks have an X-organ-sinus gland complex (XSC) as a neuroendocrine organ controlling various physiological phenomena such as colour change, moult, reproduction etc. Among the hormones synthesised in the XSC, gonad inhibiting hormone (GIH) is involved in the regulation of gonad maturation. Despite studies of eyestalk ablation in many species, the source of nutrients required for precocious gonad maturation, and the primary action site of GIH are not yet clear. The present study examined the effects of eyestalk factors, especially GIH, on ovarian maturation and hepatopancreatic metabolism when the eyestalks were ablated to block the GIH source.

Animals were collected from freshwater reservoirs, around the Seosan area on the west side of Korea, during the hibernating season. The prawns were transported to the laboratory and placed in a crustacean rearing chamber. The prawns were maintained in glass tanks equipped with sub-sand filters. The temperature was maintained at 25±1°C and photo-period was adjusted to 12hr light : 12hr dark. Animals were fed with chopped mussel and fish *ad libitum*. Eyestalks were ablated bilaterally by using small scissors and then cauterised. The ovaries and hepatopancreases were dissected out after two weeks for histological observation and biochemical determination (UV spectrophotometry).

Gonad index was increased more than 2% in ablated prawns compared with 0% for the controls. Mean oocyte diameter was also increased from 128 μm to 850 μm in eyestalk ablated prawns. The number of yolk granules in oocytes was markedly greater in eyestalkless than in intact prawns. The pyknotic index of hepatopancreas cells of ablated prawns was about 3 times greater than that of the controls. At the same time, a looser arrangement of hepatopancreas cells was observed after the operations than that seen in the tissue of the controls. The contents of total proteins, lipids and carbohydrates in the ovary of the destalked animals were significantly increased ($P<0.05$) although those in hepatopancreas were decreased coincidentally. However, the content of ribonucleic acid was not significantly different between two organs.

Based upon these results, the differences in biochemical constituents and the histological changes, demonstrate that organic reserves from the hepatopancreas might be mobilised into the ovary during ovarian maturation induced precociously by eyestalk ablation. The present results show that metabolic changes within the ovary and the hepatopancreas might be closely related and controlled by neuroendocrine factors.

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PATTERN AND PERSISTENCE IN THE BURROWS OF TWO SPECIES OF THE FRESHWATER CRAYFISH, *PARASTACOIDES* (DECAPODA: PARASTACIDAE), IN SOUTHWEST TASMANIA

Parastacoides spp. burrow extensively in the acid, peaty soil of western Tasmania and two or more species can commonly be found in close sympatry. The habitat is often partitioned zonally on the basis of soil conditions, especially drainage, on slopes (Richardson and Swain, 1980). This paper describes a mosaic of habitat partition between two undescribed species.

Methods

The field site, in southwest Tasmania, consists of an area of gently-sloping heathland (annual rainfall *c.* 2000 mm; mean maximum daily temperatures: 22.8°C; Watson, 1978). On a grid of 108 contiguous 4m^2 quadrats, the positions of all burrow entrances of each species were recorded four times from 1980 to 1990. *Parastacoides* sp.1 constructs burrows with several entrances grouped in and around a water-filled depression, while *P.* sp.2 burrows have only one or two entrances which are often roofed over with excavated soil.

Seven environmental parameters were measured in each quadrat: buttongrass area, soil depth, soil compressibility, water content, root depth (proportion of the soil profile occupied by roots; this horizon was clearly demarcated from inorganic soil below), mean water table depth, and water table variability.

Results and Discussion

About 160 *P.* sp.1 and 150 *P.* sp.2 entrances were present, the species sometimes within 2m of each other. The general pattern of burrow distribution varied very little over 10 years with no major burrow systems (these mostly belong to *P.* sp.1) appearing or disappearing. There has been some turnover in the overall number of entrances in both species, highest in *P.* sp.2, and an overall decline in the number of *P.* sp.2 entrances.

In these peaty, sedgeland habitats at least, *Parastacoides* burrows persist much longer than their inhabitants because the soils are very coherent and because the occupants do not have to burrow extensively to obtain food (Growns and Richardson, 1988).

Since the burrow systems are occupied by only a single adult, and burrow occupancy is greater than 90%, the stability of the burrows over the 10 year period argues that the crayfish populations are stable, or in the case of *P.* sp.2, declining. Since uncolonised habitat appears to be available to both species, what factors control population numbers?

Dry conditions in southern Tasmania over the last 10 years may be responsible for the decline in *P.* sp.2. This species occupies a drier part of the habitat and, although it can tolerate a few weeks without free water in its burrow (Fradd, 1979), it is probably more vulnerable to drought than *P.* sp.1.

For *P.* sp.1, food seems unlikely to be limiting (Growns and Richardson, 1988), physical space is available and predation of adults by birds and marsupials only occurs rarely. But there is heavy juvenile mortality during the year, or more, which they spend in the parental burrow, and there must also be heavy mortality when the sub-adults establish new burrows. Only one new system was observed in the course of this study, so sub-adults apparently take over vacant burrows.

The quadrats were ordinated on the basis of the 7 environmental variables, appropriately transformed, using principal components analysis. The first two axes accounted for 77.5% of the overall variation. The quadrats grouped on the basis of the identity of burrows which were within 0.5 m of the centre of the quadrat (where the environmental variables were measured): the groups were clearly separated. *P.* sp.1 burrows were associated with deeper, wetter, spongier soils. Unburrowed quadrats were not separated from burrowed ones, suggesting that the habitat is not saturated.

Other *Parastacoides* spp. (Richardson and Swain, 1980; Richardson and Horwitz, 1988) occur parapatrically where better drained soils on slopes rise out of deeper muck peats on valley floors; this pattern has been observed between the two species studied here at a neighbouring site. But where slopes are shallow, the change in soils is indistinct and the resulting mosaic of conditions allows fine scale coexistence as described here.

Acknowledgements

Thanks to those who helped in the field, Stephanie Kalish for laboratory assistance and the Tasmanian Department of Parks Wildlife and Heritage for permission to work in the Southwest National Park.

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GREGARIOUS BEHAVIOUR IN CRUSTACEAN MICRONEKTON: AN ECOLOGICAL PERSPECTIVE

Aggregations of aquatic crustaceans are customarily regarded as transient phenomena; groupings that have arisen through the agency of hydrological or meteorological factors, or through intermittent intrinsic factors, e.g. need to feed, mate or avoid predators. Small size or low taxonomic level is usually associated with planktonic rather than micronektonic existence. However there is abundant evidence that euphausiids, mysids, decapods and even copepods can exert some considerable influence over their position in the water column and have underrated powers of swimming.

We present evidence to show that many of these organisms are naturally gregarious and that a range of selective forces have favoured gregarious behaviour because of the advantages such associations offer over solitary existence. The principal selective forces are believed to be the same as those invoked to explain fish schooling.

1. Protection from predators. By analogy with fish schools, advantages could accrue from a) early detection; b) attack abatement; c) predator evasion; d) predator confusion (Pitcher, 1986). In addition, if predators are actually deterred from attacking schools or if early detection results in avoidance of the predator before the need for strenuous escape reactions, then there may be a considerable energy saving. There is strong evidence in support of a–d in escape responses of euphausiids and mysids. Aggregations have been shown to modify their antipredator response according to the degree of threat and aggregative state. The fact that school structure is only disrupted when the threat to individuals becomes extreme, is strong evidence for the survival value of grouping.

2. Improved feeding. Again by analogy with fish schools, the advantages should accrue from: a) finding food faster; b) more time for feeding; c) sampling food more effectively; d) information transfer; e) opportunity for copying (Pitcher, 1986). Little direct evidence exists in support of these advantages for gregarious crustaceans. In fact there is some conflicting evidence to suggest that higher foraging and feeding rates in lower density aggregations have to be traded off against safety in large groups. However, these hypotheses are difficult to test because of the problem of creating schools and presenting patchy food distributions in the water column in laboratory experiments.

3. Reproductive facilitation. There are many documented cases of crustaceans apparently aggregated for the purposes of more efficient fertilisation. However, the effect of group size on fecundity and reproductive success has not been tested.

4. Energy conservation. No data are available to test the possibility of hydrodynamic advantage by swimming in schools as has been suggested for fish. The swimming actions of crustaceans are fundamentally different from those of fish. This might be expected to result in differences in nearest neighbour distributions in schools of the two groups if animals were exploiting vortices shed from swimming appendages. No such differences have yet been described

Crustacean schools are strikingly similar to fish schools in internal structure and escape responses. A reluctance to accept that many crustacean species are naturally gregarious, and technical difficulties concerned with maintenance and recording of school behaviour in the laboratory, has delayed rigorous testing of the benefits of schooling as proposed above.

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EFFECTS OF HYDROSTATIC PRESSURE ON THE TIDAL VERTICAL MOVEMENT OF *ACETES SIBOGAE* HANSEN (CRUSTACEA: DECAPODA)

Acetes sibogae, collected at the mouth of Brisbane River (27°30'S, 153°12'E) and held in the laboratory for a minimum of 10 days, was subjected to three levels (10, 16 and 26kPa) of constant pressure and three (triangular, quadratic and sinusoidal) circatidal pressure regimes with different properties in the rate, relative rate, and acceleration of change, to test two hypotheses: (1) hydrostatic pressure of circatidal frequency and amplitude affects the tidal vertical movement of *A. sibogae* directly and/or through entraining endogenous tidal rhythms, and (2) this shrimp responds to amplitude, rate, relative rate and acceleration of hydrostatic pressure change.

At constant pressures, test animals moved up and down through the water column in the test tank with short, non-circatidal period. In contrast, *A. sibogae* responded to all the three circatidal pressure regimes (triangular, quadratic and sinusoidal) both directly, by vertical adjustment in the water column, and indirectly, by phasing endogenous rhythms in aphasic animals. Both mechanisms allow *A. sibogae* to react both predictively and immediately to pressure changes. The amplitude of circatidal hydrostatic pressure waves was shown to be implicated in initiating the tidal vertical movement of this shrimp, in contrast with the insignificant role of the rate, relative rate, or certain accelerations. This is not surprising since response to the amplitude of pressure change alone is an adequate action as there is great regularity of changes in hydrostatic pressure associated with tides. Such actions allow a predictable response, without the need to monitor changes in the rate, relative rate and acceleration.

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SENESCENCE, FLUORESCENCE AND CRUSTACEAN AGE DETERMINATION

Assessment of the age of individuals is currently a significant problem in studies of crustacean population dynamics, specifically the management of commercially important crustacean stocks, which are coming under increasing threat of over exploitation.

Several methods have been tried for assessing age in crustaceans, but all are severely restricted. The most widely used method, that involving prediction of age from body size, based on growth rates determined from modal analysis, tag recapture programs or laboratory rearing, suffers a fundamental problem — variability of growth rate between individuals. Individuals of the same chronological age, growing in the same environmental regime, may sometimes differ in their size by an order of magnitude. This phenomenon clearly limits the usefulness of body size as an indicator of age. The wide application of this method of age prediction reflects the need for, but lack of, a suitable alternative. Thus, new approaches to crustacean age determination are essential. Ettershank (1983) attempted to use the intensity of extracted chloroform-soluble fluorescence to age field-captured Antarctic krill, *Euphausia superba*. Similar extractable fluorescence had been shown to accumulate linearly with age in insects and was thought to be derived from the universally occurring lipofuscin age-pigment.

Subsequently however, work by the present author and others (Nicol, 1987; Sheehy and Ettershank, 1989; Sheehy and Roberts, in press), some of which was on crustaceans of known age, revealed some serious flaws in the methods used by Ettershank and previous workers. Most importantly, 'lipofuscin-like' extractable fluorescence did not appear to be derived from lipofuscin and its intensity bore little relationship to age. Recently, prominent workers in the broader field of gerontology have been voicing serious doubts about the biochemical extraction method for lipofuscin determination (Sohal, 1987).

Clearly, the potential of lipofuscin as an index of age in crustaceans required reassessment.

Methods and Results

Fluorescent morphological lipofuscin was identified in histological sections from a wide range of crustaceans, including several of economic importance (Sheehy, 1989, 1990a). Alternative quantification techniques were developed. Using fluorescence microscopy and new image analysis methods (Sheehy, 1989, 1990b), conclusive evidence of the physiological age dependence of lipofuscin accumulation in the Crustacea was obtained for the first time. In laboratory reared freshwater crayfish, *Cherax quadricarinatus*, of precisely known chronological age, lipofuscin quantities in the base of the olfactory lobe cell mass of the brain were superior predictors of chronological age ($r = 0.96$) to morphometric parameters, such as carapace length, normally used for this purpose. While carapace length was able to place only 51% of the experimental individuals into their correct age class, lipofuscin volume fraction correctly placed 93% of the same individuals. Lipofuscin volume fractions were similar in the olfactory lobes of crayfish of similar chronological age despite a wide disparity in body size and weight.

Discussion

The present results suggest that lipofuscin has significant potential as an index of crustacean age. Although lipofuscin accumulates with physiological age, rather than strict chronological age, and its accumulation is affected by environmental parameters such as temperature (Sheehy, 1990b), growth is also influenced by environmental factors. At this stage, there is no reason to believe that lipofuscin would not be a superior predictor of age to body size under variable field conditions. Early results suggest that it may be possible to predict absolute chronological age of field animals using relatively simple laboratory established models incorporating ambient temperature (Sheehy, 1990b).

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BRANCHIAL MODIFICATION OF URINE AND OSMOREGULATION IN THE LAND CRAB, *BIRGUS LATRO* (ANOMURA: COENOBITIDAE)

The regulatory capacity of the excretory system of *Birgus latro* was examined in relation to osmoregulation in the terrestrial environment. On land the availability of salts and water in the diet and drinking water, and evaporative water loss, may vary widely. Successful land animals, e.g. insects, mammals, generally exhibit versatile control of urinary fluid output and salt concentration.

Previous measurements on *Birgus* (Gross, 1955) indicated that the urine, like that of other anomuran and brachyuran crabs, was isosmotic to the haemolymph. Harris and Kormanick (1981) inferred that urine filtration continued even during desiccation. These observations suggested that *Birgus* may have a poor capacity for excretory regulation, the urine representing a potentially large drain on body water and ions. Gross (1955) postulated that *Birgus* osmoregulates behaviourally by choosing between drinking water sources of different salinities. However, on Christmas Island, Indian Ocean, *B. latro* range up to several kilometres from the coast, and sea water is clearly unavailable to most individuals as a source of ions and water. In rain forest, crabs drink from temporary rainwater puddles.

Crabs were maintained on fresh water and on saline (300, 600,1000 mosmol/kg sea water) drinking regimens. The final urine, released from the antennal organs, was confirmed to be isosmotic with haemolymph. However, *Birgus* exhibits branchial reprocessing of the urine, as postulated for some brachyuran terrestrial crabs (Wolcott and Wolcott, 1985, 1988). The final excretory product ('P', Wolcott and Wolcott, 1988) differs greatly in composition and flow rate from the filtered primary urine and the final urine.

The urinary apertures are directed posteriorly and open underneath the branchiostegites. Hydrophilic hairs on the scaphognathites, branchiostegites and mouthparts convey urine to the gills and to the mouth. The volume of the urine is reduced by reingestion and its composition is modified by branchial ion transport processes. Switching between fresh water and saline regimens caused rapid compensatory adjustments to drinking rate, primary urine formation (51Cr-EDTA clearance), branchial ion reabsorption and P production. The volume and concentration of the released P could be varied widely, e.g. [Na] and [Cl] <10 to >600 mmol/L. The combination of reingestion and branchial ion transport provides *Birgus* with a versatile, ion and water conserving, excretory system, well-suited to its terrestrial habitat. Animals drinking freshwater effectively reabsorbed more than 90% of the filtered water, and more than 99% of the filtered sodium and chloride. In animals drinking sea water, reabsorption of each of these components decreased to about 70%. This regulatory role for the gills is supported by strong uptake of Na and Cl from experimentally recirculated salines and by the demonstration of high activities of Na + K activated ATPases in gill extracts.

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A STUDY ON FEASIBILITY OF CHROMOSOME SET MANIPULATIONS IN THE MARINE SHRIMP, *SICYONIA INGENTIS*

The feasibility of manipulation of chromosome sets was studied in the ridgeback prawn, *Sicyonia ingentis*, to develop new techniques for chromosome karyotype study in shrimps, to elucidate the effects of hot and cold shock or chemical induction on chromosome set manipulation, and to present a cytological analysis of haploidy, diploidy, triploidy and other polyploidy. Artificially induced spawned eggs of this shrimp were fertilized by UV-irradiated sperm from the seminal receptacles of the females to induce haploidy. Normally fertilized eggs were subjected to hot, cold or chemical (colchicine or cytochlasin D) shock to induce polyploidy.

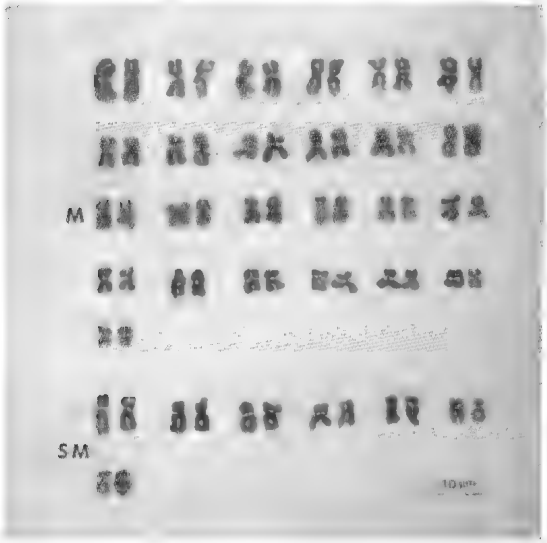

FIG. 1. Karyotype of the marine shrimp *Sicyonia ingentis* (2n = 50M + 14SM).

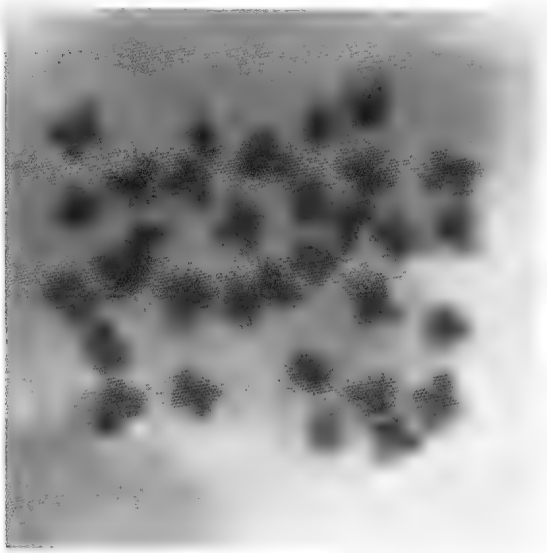

FIG. 2. Haploid chromosome of *Sicyonia ingentis*, from nauplius.

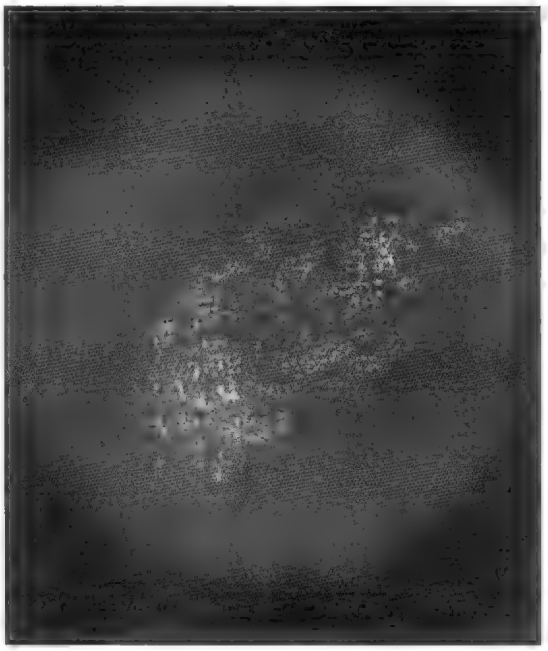

FIG. 3. Polyploid chromosome of *Sicyonia ingentis*, from egg under fluorescence microscopy.

This study showed that *S. ingentis* has 64 chromosomes (50M + 14SM) using newly developed techniques with embryos and nauplii. Chromosomes were detected successfully by fluorescence microscopy and/or air-dried method. Haploidy was induced by UV-irradiating sperms and higher haploid rate was observed in eggs than in nauplii. Triploidy and/or tetraploidy were obtained in the polyploid inducing experiments. The efficiency of induction depended heavily on the time between spawning and treatment, temperature, and duration of treatment. Because the eggs were too fragile to be handled before the formation of hatching envelopes, the second polar body could be retained more easily than the first one. However, an optimal procedure for treatment needs to be developed.

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GENETIC IDENTIFICATION OF TEN SPECIES OF PENAEID PRAWN POSTLARVAE

A study of the ecology, recruitment and dynamics of the early life-history stages of penaeid prawns is being undertaken in the Gulf of Carpentaria, northern Australia. It is essential in this study to identify to species level the individual penaeid postlarvae. Identification of specimens to species group is possible using morphological characters, however it has proved very difficult to identify all species in this way. Some of the complicating factors in this have been: the small size of individuals (down to 1 mm carapace length), developmental changes, benthic collection often resulting in broken or damaged bodies, and the large numbers requiring identification. Allozyme electrophoresis was thus employed as a tool which could solve these problems.

Two primary criteria were set for the choice of appropriate genetic enzyme markers. Firstly, the enzyme loci must exhibit a reliable and consistent difference between species which must have a true genetic basis. Secondly, the enzymes must be sufficiently strong, hardy and easy to detect, to allow the simple and rapid identification of large numbers of individuals. After examining the developmental expression of 39 enzyme loci, 2 loci, Gpi (Glucose-6-phosphate isomerase) and Pep (Peptidase, leucyl-glycine as substrate) were found which together could unambiguously identify ten species of prawn postlarvae within the genera *Penaeus* and *Metapenaeus*. These species were: the tiger prawns *Penaeus monodon*, *P. esculentus* and *P. semisulcatus*, the banana prawn *P. merguiensis*, the king prawns *P. latisulcatus* and *P. longistylus*, the endeavour prawns *Metapenaeus endeavouri* and *M. ensis*, the york prawn *M. eboracensis* and the greasyback prawn *M. moyebi*.

The techniques used (Lavery and Staples, 1990) were designed to maximise the efficiency of the identification procedure and are summarised as follows: 1) Frozen individual postlarvae plus 5 microlitres of buffer were placed in the wells of a perspex grinding chamber which had 24 wells in one line. 2) All 24 specimens were homogenised thoroughly at the same time using a 24-pin plate. 3) A slotted applicator was used to pick up a small quantity of liquid extract from all 24 specimens at one time and apply them to a cellulose acetate plate. 4) Electrophoresis was carried out for 90 to 150 minutes, followed by staining for a specific enzyme, either Gpi or Pep.

Using the two loci together, and referencing the observed banding patterns with known controls, all ten species could be identified (Fig. 1). Fewer than 5% of individuals could not be accurately identified because of low activity or smearing of bands. The technique has proved to be very efficient, with the whole procedure being carried out in less than three hours, thus making it possible for one technician with minimal equipment to identify 300 individual prawn postlarvae per day. Over 20,000 penaeid postlarvae have already been identified using this technique in the continuing programme of research on penaeid prawns in the Gulf of Carpentaria.

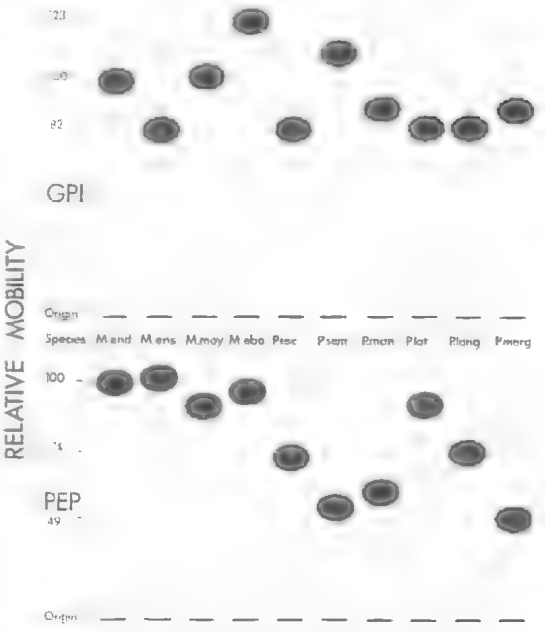

FIG. 1. Diagrammatic representation of banding patterns of ten penaeid species for the loci Gpi and Pep.

Acknowledgements

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DEVELOPMENTAL CHANGES IN THE BIOENERGETICS OF DECAPOD LARVAE

K. ANGER

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Developmental changes in bioenergetic traits of larval Decapoda are reviewed, comparing subsequent stages of a moult cycle, larval instars, or different taxa that are considered to represent a phylogenetic sequence. Recent data suggest that some developmental trends in energy partitioning might be similar on all these levels of comparison. These tendencies imply: decreasing instantaneous growth rates, increasing metabolic loss, decreasing net growth efficiency, and an increasing dependence on energy reserves accumulated in earlier stages of development. They are interpreted as signs of an increasing degree of lecithotrophy in late stages of a moult cycle, late instars of larval development, or in evolutionary advanced taxa within a phylogenetic sequence, respectively. Biochemical changes suggest a developmental shift in predominant growth mechanisms, from hypertrophy (enlargement of average cell size during development, accumulation of lipid reserves) toward hyperplasy (increase in cell number, protein accumulation). Within a moult cycle, the latter phase becomes in principle independent of external energy supply, when a critical point (the 'point of reserve saturation', or 'D_0 threshold'), has been passed. Such a bioenergetic transition, from a phase of energy accumulation to one of epidermal reconstruction, can occur also between successive instars of development: in hermit crab development, the megalopa reaches metamorphosis exclusively with energy accumulated by preceding instars. This mode of development, termed secondary lecithotrophy, is interpreted as an adaptation to extremely specialised habitat requirements (here: a mollusc shell). In the sequence Caridea–Astacidea–Anomura–Brachyura, there is an increasing trend in the average carbon/nitrogen ratio of larvae. This suggests an evolutionary tendency in the larval development of the Decapoda toward an increasing lipid content and possibly, increasing degrees of secondary lecithotrophy and habitat specialisation. It corresponds with decreasing trends in the number and variability (the latter both in relation to number and morphology) of larval instars, and an increasing degree of morphological change during development. □ *Crustacea, Decapoda, larval development, moult cycle, bioenergetics, growth mechanisms.*

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The bioenergetics of an organism can be defined through the construction of an energy budget that quantifies the fate of nutritional energy (Ivlev, 1945; Warren and Davis, 1967; Welch, 1968). The partitioning among the major energy flows (tissue and exuvia production, respiratory and excretory losses) in crustaceans is illustrated in a schematic diagram that treats these flows as black boxes (Fig. 1). While bioenergetic aspects have been studied in great detail in adult Crustacea, those of their larval stages are much less known. In the present review, I summarise recent advances in our efforts to open in larval decapod crustaceans those black boxes, and so understand in more detail how they function internally, how they are connected among each other, and how such bioenergetic traits may change during development.

Only two decades ago, virtually nothing was known about uptake and partitioning of nutritional energy in decapod larvae reared under controlled conditions in the laboratory. First quantitative data on feeding and growth were published by Reeve (1969) and Regnault (1969), who studied caridean shrimp larvae. Respiration rates had already been measured by Zeuthen (1947) in an unidentified zoea larva, and later by an increasing number of authors in various larval decapod species (Schatzlein and Costlow, 1978).

Mootz and Epifanio (1974) presented the first fairly complete energy budget for a larval decapod, the crab *Menippe mercenaria*. This study was followed by an increasing number of others that provided more or less complete information on energy partitioning in larval prawns, lobsters, anomurans, and brachyurans (Table 1). Most of these budgets have in common that they account for only gross changes during larval development, presenting 'average' flow values for subsequent instars. However, each larval instar undergoes during its

moult cycle a number of anatomical, physiological and biochemical changes that are controlled by hormonal processes (Christiansen, 1988). Hence, a much higher temporal resolution in sampling and measuring protocols, and consequently, considerably increased experimental and analytical efforts are necessary to study changes in energy partitioning of decapod and other crustacean larvae in relation to developmental processes. The first study that explicitly related bioenergetic changes in a larval decapod to the moult cycle was published only one decade ago (McNamara *et al.*, 1980).

The moult cycle can be devided into stages and substages, for which a classification system was introduced already half a century ago by Drach (1939). However, the first detailed description of anatomical changes occurring during individual moult cycles in a larval decapod appeared only recently (Anger, 1983). This description allows the identification of the major stages of Drach's classification system, and their use as a meaningful reference basis for the analysis of physiological and biochemical changes that may be observed during the course of larval development.

The following synopsis will deal exclusively with changes in bioenergetic traits as results of developmental events, and it will be based mainly on information from a few intensively studied 'model species' such as the brachyuran crabs *Hyas araneus* and *Carcinus maenas*, and the hermit crab *Pagurus bernhardus*. In these instances, sufficient experimental data obtained under constant conditions have become available to allow some generalisations and modelling. Effects caused by external factors such as temperature, salinity, and food availability must be excluded here from this review.

THE MAJOR ENERGY FLOWS

The parameters of the energy budget (Fig. 1) are linked by the following equations, from which conversion or growth efficiencies can be derived (Ivlev, 1945; Warren and Davis, 1967; Welch, 1968):

$$G = G_T + G_E = F - L - R - U \quad [eq. 1]$$

$$A = G + R + U = F - L \quad [eq. 2]$$

$$K_1 = G/F \quad [eq. 3]$$

$$K_2 = G/A \quad [eq. 4]$$

where:
A = assimilation of energy from food

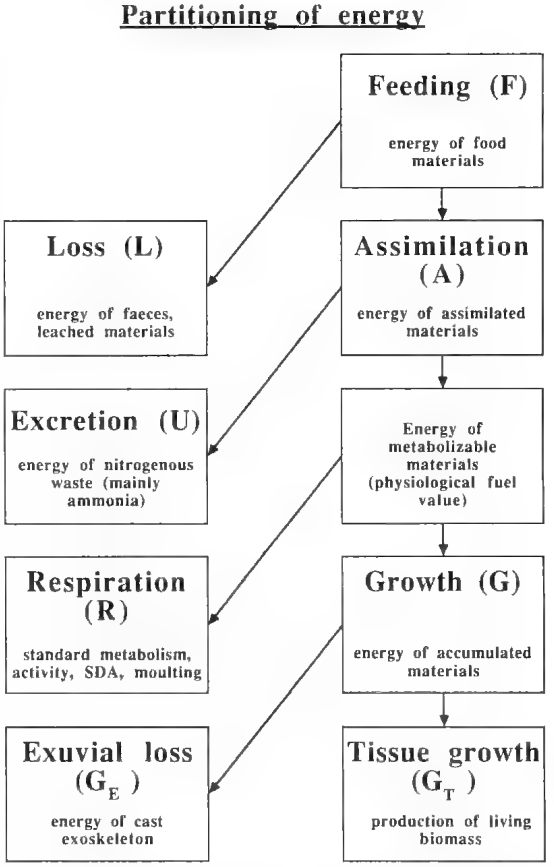

FIG. 1. Schematic diagram of energy partitioning in decapod larvae (after Ivlev, 1945; Warren and Davis, 1967; Welch, 1968).

F = food uptake
G = total body growth (briefly referred to as 'growth')
G_T = tissue growth (production of living biomass)
G_E = exuvia growth (production of cuticle materials)
K_1 = gross growth efficiency
K_2 = net growth efficiency
L = sum of losses by defaecation and leaching (loss of small particles and liquid from food, due to inefficient feeding mechanisms)
R = respiration (measured as oxygen consumption)
U = excretion of nitrogenous waste products (measured as ammonia production)

In the above form, all parameters of the budget refer to gains or losses of energy that were integrated over some period of developmental time, for instance the duration of a given moult cycle (= instar) or of complete larval development in a given species; they are expressed in energy units (Joules) per individual. Instantaneous rates of

TABLE 1. Studies on energy partitioning in larval decapod crustaceans. Taxonomical position according to Bowman and Abele (1982).

Infraorder	Family	Species	References	Remarks
Penaeioidea	Penaeidae	*Penaeus monodon*	A	1, 2, 3, 4, 5
Astacidea	Nephropidae	*Homarus americanus*	B	1
		Homarus americanus	C, D	3, 5, 6
Anomura	Paguridae	*Pagurus bernhardus*	E, F	3, 7, 8, 9
Brachyura	Xanthidae	*Menippe mercenaria*	G	1, 2, 3
		Rhithropanopeus harrisii	H	1, 2, 3, 5
	Cancridae	*Cancer irroratus*	I	1, 3
	Portunidae	*Carcinus maenas*	J	1, 2, 3, 9
	Majidae	*Hyas coarctatus*	K	2, 3, 6, 7
		Hyas araneus	L	3, 9
		Libinia ferreirae	M	3, 4, 7, 8

Remarks: 1, only cumulative budgets (average flow rates) of successive instars; 2, excretion ignored, or added to faecal losses; 3, faecal losses calculated from difference between ingestion and assimilation, or ignored; 4, energy content of larvae estimated from dry weight or ash-free dry weight (assuming a constant energy content); 5, exuvia production not considered, or data taken from literature (from other species); 6, no energy budget given, but measurements from which a partial budget may be calculated; 7, ingestion rate not measured, i.e., partitioning only of assimilated matter considered; 8, excretion data taken from literature (from other species); 9, energy content of larvae and exuviae calculated from carbon values (Salonen *et al.*, 1976). References: A, Kurmaly *et al.* (1989); B, Logan and Epifanio (1978); C, Capuzzo and Lancaster (1979); D, Sasaki *et al.* (1986); E, Anger, 1989; F, Anger *et al.* (1990); G, Mootz and Epifanio (1974); H, Levine and Sulkin (1979); I, Johns (1982); J, Dawirs (1983); K, Jacobi and Anger (1985); L, Anger and Harms (1989); M, Anger *et al.* (1989a).

energy flow, e.g. growth rate; G, will be indicated by a point above the symbol; their dimension is: Joules per individual per unit of time (h^{-1}, or d^{-1}).

Food Uptake (*F*) and Loss (*L*)

The nutrition of decapod larvae under natural conditions has been studied by few investigators (Lebour, 1922; Stickney and Perkins, 1981; Youngbluth, 1982; Harding *et al.*, 1983; Paul *et al.*, 1990), so that we know very little about their actual food sources in the planktonic environment. These few field data as well as the overwhelming amount of laboratory observations (Harms *et al.*, 1991) suggest that most decapod larvae are omnivorous, with a general preference for zooplankton as a food source.

In larval decapods, in particular in anomuran and caridean shrimp larvae, we observed frequently a very inefficient feeding behaviour: much prey is killed but then eaten only partially. This phenomenon ('sloppy feeding') was found also in some insect larvae (Johnson *et al.*, 1975) and in carnivorous copepods (Ikeda, 1977), where it was termed 'wasteful killing' or 'over-hunting', respectively. Incomplete ingestion of prey, together with leaching of liquid and small particulate materials from food during the feeding process (Dagg, 1974; Pechenik, 1979) leads to practically uncontrollable losses and thus hampers the precise measurement of actual ingestion rates in decapod larvae. The significance of this effect will probably vary with species and stage of larval development, and with the amount, size, and quality of food.

The stage of the moult cycle has a significant influence on ingestion rates. Anger and Dietrich (1984) and Dawirs and Dietrich (1986) showed in crab larvae great daily variability of feeding activity, mostly with high values in early stages (postmoult, intermoult), and strongly decreasing figures during the premoult phase of the same instar. Repeated ex-

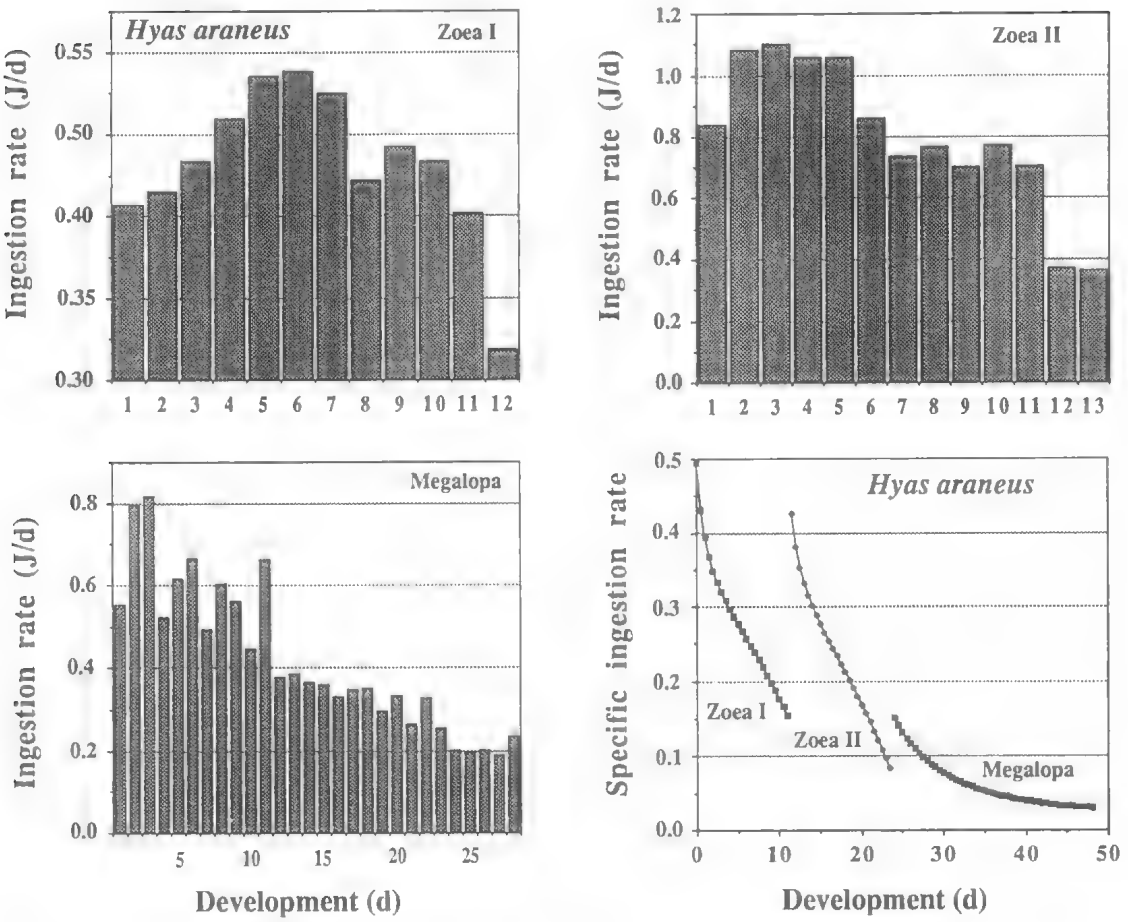

FIG. 2. *Hyas araneus*. Changes in individual and energy-specific ingestion rates during larval development (units: Joules· individual^{-1}·d^{-1}; and fraction ·d^{-1}, respectively) (data from Anger *et al.*, 1989b.)

periments with *Hyas araneus* larvae confirmed these findings, with maximum ingestion rates occurring progressively earlier in subsequent larval instars (Fig. 2). Similar patterns in $\dot{F}$ were found when phytoplankton instead of *Artemia* was given as food (Harms *et al.*, 1991), suggesting an indirect endocrine control of feeding activity via the moult cycle. In the zoeal instars of *H. araneus*, they were described with quadratic equations, in the megalopa as an exponential function of time (t) (Anger *et al.*, 1989b):

$$\dot{F}=\dot{F}_0 + a\cdot t - b\cdot t^2 \qquad \text{(zoea I, II)} \qquad \text{[eq. 5]}$$

$$\dot{F}=\dot{F}_0\cdot e^{-mt} \qquad \text{(megalopa)} \qquad \text{[eq. 6]}$$

The constant F_0 represents an estimate of the initial ($t = 0$) feeding rate, and the fitted parameters a, b, and m define the curvature of these functions.

When specific ingestion rates, $\dot{F}_0$/E (that is: $\dot{F}$ expressed as a fraction of larval energy content, E [both in Joules]), are plotted against time of development, decreasing values are found, not only within individual moult cycles but, on the average, also in successive larval instars (Fig. 2). According to these experiments, early spider crab zoeae may ingest up to almost one half of their own energy content per day, whereas the same instars eat much less (<20%· d^{-1}) in late premoult. The megalopa shows very low $\dot{F}$/E rates throughout the moult cycle, still decreaseing before metamorphosis (Fig. 2). However, it remains uncertain how general these patterns in decapod larvae are, until

data with a comparably high temporal resolution are available for more species.

Most 'average' ingestion rates reported in the literature (Table 1) are based on single measurements made in an unspecified stage of the moult cycle, in some cases even without specifying the larval instar. Thus, such values must be treated with much reservation, as well as gross growth and assimilation efficiencies calculated from those feeding rates (see below).

While the measurement of F suffers from great methodological difficulties, this applies even more to the determination of faecal and other losses summarised as L (Fig. 1). Consequently, most authors did not measure L directly, but estimated it from difference, F-A (eq. 2). Since measurements of F are not precise, the same must be true for indirect estimates of L. Among the authors listed in Table 1, only Logan and Epifanio (1978) determined faeces production directly in decapod larvae.

Respiration (R)

Respiration rate is usually measured as oxygen consumption (µg O_2·individual^{-1}·h^{-1}, or d^{-1}) which can then be converted to metabolic energy loss, with an equivalent of 14.06 Joules per mg O_2 (Gnaiger, 1983a). Besides integrated respiratory losses (R, in Joules per individual), I will distinguish here: (1) individual respiration rate (in µg O_2 or Joules·individual^{-1}·h^{-1} or d^{-1}), for which I will use the widely accepted symbol $\dot{V}O_2$ (instead of '$\dot{R}$'; Gnaiger, 1983b); (2) weight-specific respiration rate ($\dot{Q}O_2$; in µg O_2·individual^{-1}·h^{-1}, or d^{-1}, per unit [mg] of dry weight). The latter is a measure of the intensity of tissue metabolism. It can be expressed also as an energy-specific rate (related to energy accumulated in biomass; dimension: fraction·d^{-1}). The term 'respiration rate' will indiscriminately refer to both $\dot{V}O_2$ or $\dot{Q}O_2$. Values given in the literature represent usually an undefined rate, somewhere between basal and active metabolism, normally considered as 'routine metabolism'. This applies also to all studies listed in Table 1.

Changes of respiration during individual larval moult cycles were studied in only a few decapod species. In first-instar larvae of a freshwater prawn, *Macrobrachium olfersii*, McNamara *et al.* (1980) found slightly decreasing metabolic rates. However, this example is very specific, as these larvae reveal lecithotrophic development from the egg to the second zoeal instar. Also in the megalopa of the hermit crab *Pagurus bernhardus*, which shows secondary lecithotrophy (Anger, 1989), decreasing respiration was measured during the moult cycle (Dawirs, 1984; Anger *et al.*, 1990). Like most other decapod larvae, the zoeal instars of the hermit crab, as well as lobster (*Homarus americanus*) and crab larvae (*Hyas araneus*, *H. coarctatus*, *Libinia ferreirae*), take up food during their entire development, and their respiration increases during the course of each moult cycle (Sasaki *et al.*, 1986; Jacobi and Anger, 1985; Anger *et al.*, 1989a, b). No general correlation, however, was found between metabolism and feeding rate (Anger *et al.*, 1989b) or activity of digestive enzymes (Hirche and Anger, 1987; Harms *et al.*, 1991).

The general patterns that were found in both *Hyas araneus* and *H. coarctatus* larvae are illustrated, with the former species as an example, in Fig. 3: linear increase of respiration with time of development in the zoeal instars, but a cyclical pattern in the megalopa, with substantial increase during each ecdysis. In the zoeal instars of *Pagurus bernhardus*, a linear increase (zoea I, II), or a fairly constant respiration rate (zoea III, IV) was also measured (Anger *et al.*, 1990). Unfortunately, no data with a high temporal resolution are available for other decapod larvae, so that a generalisation of these patterns is not possible at present.

In *Hyas* spp. larvae $\dot{Q}O_2$ shows patterns of change during development that are different from those in $\dot{V}O_2$: high values after each ecdysis (postmoult) are followed by low rates throughout the intermoult and early premoult phases, and sometimes by another increase during late premoult (Fig. 3). The same patterns were observed also in larval lobsters (Sasaki *et al.*, 1986), as well as in spider crab (*Libinia ferreirae*) and hermit crab (*Pagurus bernhardus*) larvae (Anger *et al.*, 1989a, 1990). These cyclic changes in the average metabolic activity of tissues may occur generally in crustacean larvae. They should be a result of particularly energy-consuming processes of integumental growth and differentiation taking place shortly before, during, and after ecdysis (see below: mechanisms of growth).

Average $\dot{Q}O_2$ values decrease in most instances like during development from the first to the last larval instar. Only in larval lobsters was an increasing tendency observed (Sasaki *et al.*, 1986). The former trend is consistent with the general relationship of decreasing $\dot{Q}O_2$ with increasing body weight in animals (Zeuthen,

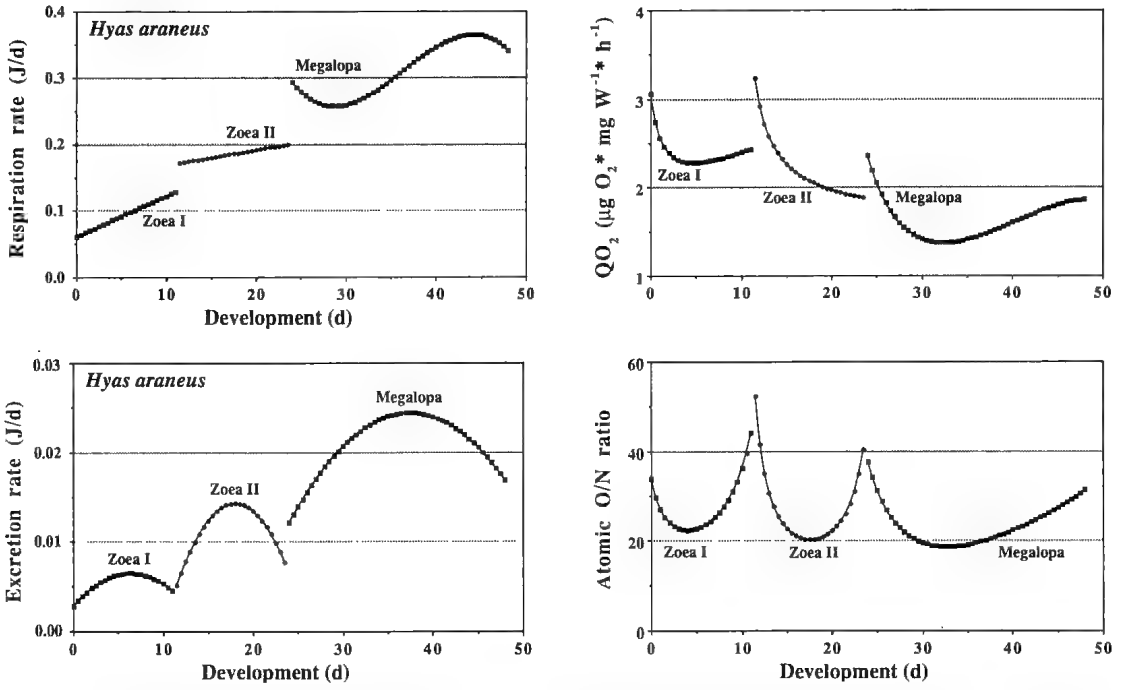

FIG. 3. *Hyas araneus*. Changes during larval development in: rates of individual respiration ($\dot{V}O_2$; *Joules* ·individual^{-1}.d^{-1}), weight-specific respiration ($\dot{Q}O_2$; µg O_2.[mg dry weight]$^{-1}$·h^{-1}), nitrogen excretion ($\dot{U}$; *Joules* ·individual^{-1}.d^{-1}), and in the atomic O/N ratio (data from Anger *et al.*, 1989b).

1947). This relationship was quantified in larvae of various decapod species (Logan and Epifanio, 1978; Schatzlein and Costlow, 1978; Anger and Jacobi, 1985). However, the patterns shown in Fig. 3 demonstrate that the respiration-weight relationship is superimposed by developmental events that are not necessarily associated with growth.

Nitrogen Excretion ($\dot{U}$)

Ammonia is assumed to be the major excretory product of larval decapods (Logan and Epifanio, 1978; Capuzzo and Lancaster, 1979; Johns, 1982). Dawirs (unpubl.) found, in addition, some traces of urea production in *Carcinus maenas* megalopa. Phosphate excretion has been measured only in some unidentified larvae isolated from plankton samples (Ikeda *et al.*, 1982; values mucher lower than in N excretion) but no data from decapod larvae maintained under controlled conditions are available. Thus, the following review will deal exclusively with the excretion of nitrogenous waste products, namely ammonia, which is assumed to represent the major part of total excretion. It can be converted to energy with a factor of 24.87 J/mg ammonia-N (Elliot and Davison, 1975).

Most investigators did not measure $\dot{U}$ as a part of the energy budget in larval decapods (Table 1). Some authors considered it as a part of faecal loss, which is not correct (it belongs to A: Fig. 1; Warren and Davis, 1967). The authors who measured it (Logan and Epifanio, 1978; Johns, 1982; Anger *et al.*, 1989b) found, however, that it constituted only a minor energy flow. In spider crab (*Hyas araneus*) larvae, we found cumulative excretory energy losses of 2–5% of A (Fig. 7). These measurements suggest that nitrogen excretion increases during larval development, not only in absolute terms (per individual) but also in relation to the other energy flows.

During individual moult cycles, excretion curves for spider crab larvae consistently showed a maximum approximately in the middle (intermoult and early premoult stages) of the moult cycle (Fig. 3). Since almost no comparable information is available from other taxa, it is not known if these patterns are typical of brachyuran larvae. Data given by Sasaki *et al.* (1986) suggest that at least larval lobsters may

exhibit quite different patterns, with low excretion rates in intermoult.

O/N Ratio

The atomic O/N ratio may be used as an indicator of the relative significance of protein as an energy source (Mayzaud and Conover, 1988). Capuzzo and Lancaster (1979) and Sasaki *et al.* (1986) found lower O/N ratios in stage IV lobsters than in earlier instars, suggesting an increasing protein catabolism during larval development. Decreasing average values were also observed during the development of spider crab larvae, however, superimposed by variation during individual moult cycles (Fig. 3). According to these data, protein catabolism in *Hyas araneus* larvae is at a maximum during intermoult, whereas lipid and/or carbohydrates play a major role in the premoult and postmoult stages.

Growth (G)

Larval growth has been studied in many decapod species (Kurata, 1962; Rice, 1968; Hartnoll, 1982; Gore, 1985; McConaugha, 1985), but different units of measurement have been used: size, moult cycle duration, fresh weight, dry weight, ash-free dry weight, carbon, nitrogen, hydrogen, protein, lipid, or energy (measured by microcalorimetry or estimated from biochemical or elemental composition).

Dawirs (1981, 1983), Anger and Dawirs (1982), and Sasaki *et al.* (1986) showed that fresh weight is a very poor measure of growth in crustaceans, as it does not reflect actual changes in living biomass during development or in relation to nutritional conditions. It should never be used as a reference unit for biochemical data (although some authors did this). Dry weight and ash-free dry weight are certainly better measures of biomass. Carbon and nitrogen measurements proved to be especially accurate and reproducible. They show highly significant relationships with the energy content (Salonen *et al.*, 1976) and with the major biochemical components, protein and lipid (Anger and Harms, 1990). These different measures of biomass can be converted into each other, either using such empirical relations or a stoichiometric model (Gnaiger and Bitterlich, 1984).

Not only different measures of biomass have been used, but also conflicting models of growth. Probably the most frequently used is 'Dyar's rule' or 'Brook's law' (Kurata, 1962). It describes an increase in size or biomass as an exponential function of the number of instars; however, several authors used it to describe growth as a function of time. Empirical data on instantaneous growth rates (see below) show that this is an erroneous use of the exponential model.

Anger and Dawirs (1982) expressed zoeal biomass in *Hyas araneus* (dry weight, C, N, H, or energy [µg or Joules· individual^{-1}]; in the latter case is: biomass = E) as a power function of time (t; [d]) within a given instar:

$$E = E_0 \cdot (t+1)^m \qquad \text{[eq. 7]}$$

E_0 is an estimate of initial ($t = 0$) energy, and m is a fitted constant (the regression coefficient of the linearized form of the equation). This model was later applied also to other larval brachyurans, *Carcinus maenas* (Dawirs, 1983), *Hyas coarctatus* (Jacobi and Anger, 1985), *Inachus dorsettensis* (Anger, 1988), *Liocarcinus holsatus* (Harms, 1990), and lobsters, *Nephrops norvegicus* (Anger and Püschel, 1986).

Another model, a second-order polynomial equation, was applied to describe megalopa growth in *Hyas* spp., where biomass reaches a maximum in the middle of the moult cycle and then decreases, prior to metamorphosis (Anger and Jacobi, 1985; Jacobi and Anger, 1985).

$$E = E_0 + a \cdot t - b \cdot t^2 \qquad \text{[eq. 8]}$$

E_0 (as in eq. 7), a, and b are fitted constants. Dawirs *et al.* (1986) suggested that this model might be better suited than eq. 7 for describing zoeal growth patterns, since they observed in *Carcinus maenas* zoeae a decrease in biomass during late premoult. The same was found also in the zoeal instars of the anomuran crabs *Pagurus bernhardus* (Anger, 1989; Anger *et al.*, 1990) and *Galathea squamifera* (Anger, unpubl.), and in the larvae of the European lobster, *Homarus gammarus* (Messerknecht, pers. comm.).

Both models predict that growth rate (G, defined as change of biomass per unit of time, that is the first derivation of eqs. 7 and 8, respectively) will decrease during each larval instar:

$$G = dE/dt = E_0 \cdot m \cdot (t+1)^{m-1} \qquad \text{[eq. 9]}$$

$$G = dE/dt = a - 2bt \qquad \text{[eq. 10]}$$

G has the dimension [Joules·individual^{-1}·d^{-1}]. Eq. 9 gives a hyperbolic, eq. 10 a linear pattern of decrease (Fig. 4). Further data from more species is required to decide which model is a better description of larval growth patterns, if a universal pattern exists. The parabola-shaped bi-

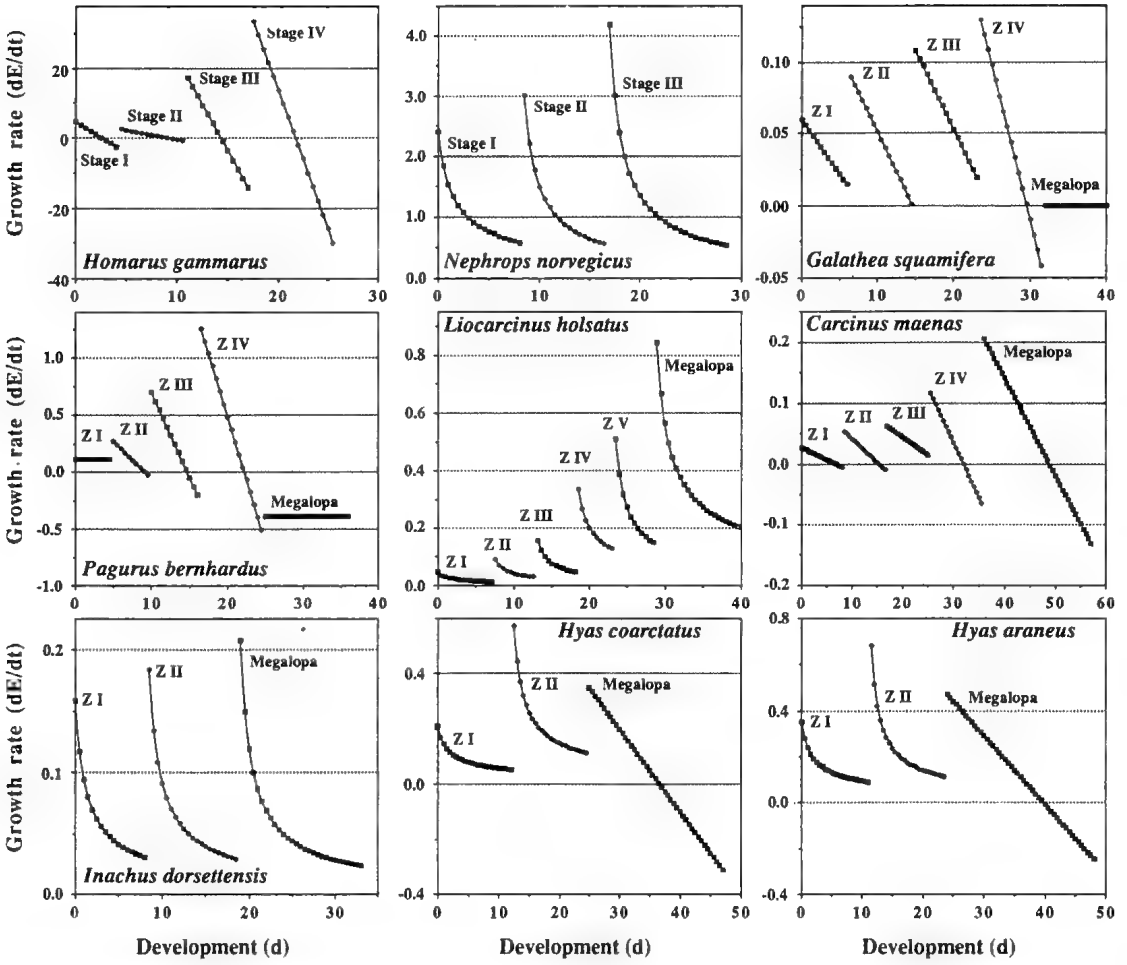

FIG. 4. Changes in individual growth rates (G, Joules ·individual^{-1}· d^{-1}) of decapod crustacean species during larval development. (sources of data: Messerknecht, pers. comm. (*Homarus gammarus*); Anger and Püschel, 1986 (*Nephrops norvegicus*); Anger, unpubl. (*Galathea squamifera*); Anger *et al.*,1990 (*Pagurus bernhardus*); Harms, 1990 (*Liocarcinus holsatus*); Dawirs *et al.*, 1986 (*Carcinus maenas*); Anger, 1988 (*Inachus dorsettensis*); Jacobi and Anger, 1985 (*Hyas coarctatus*); Anger *et al.*, 1989b, Anger and Harms, 1989 (*H. araneus*)).

omass curve (with a final decrease) described by eq. 8 might be an artifact (although I do not consider this very likely) that could be caused by weak, slow-growing larvae that are proportionally more frequent in samples taken very late (after the onset of moulting) from a culture.

Although the curvature of growth curves may remain uncertain, Fig. 4 shows one universal tendency in all nine decapod species and in a total of 34 (out of 37) instars considered: larval growth decreases during the course of individual moult cycles. Only in the zoea I and megalopa of *Pagurus bernhardus* and in the megalopa of *Galathea squamifera*, was a linear change in biomass, i.e. a constant growth rate ($\dot{G}$), found (a negative value in the secondarily lecithotrophic hermit crab megalopa); in no case was an increase observed in $\dot{G}$.

This is important to note, as some authors attempted to estimate 'average' growth rates in plankton populations of decapod larvae, applying an exponential model (see above) that predicts a progressively increasing $\dot{G}$ with time of development (Incze *et al.*, 1984; Lindley, 1988; Paul *et al.*, 1990). Since this model describes only gross biomass changes in a series of subsequent instars as a function of instar number, not as a function of time, it has very

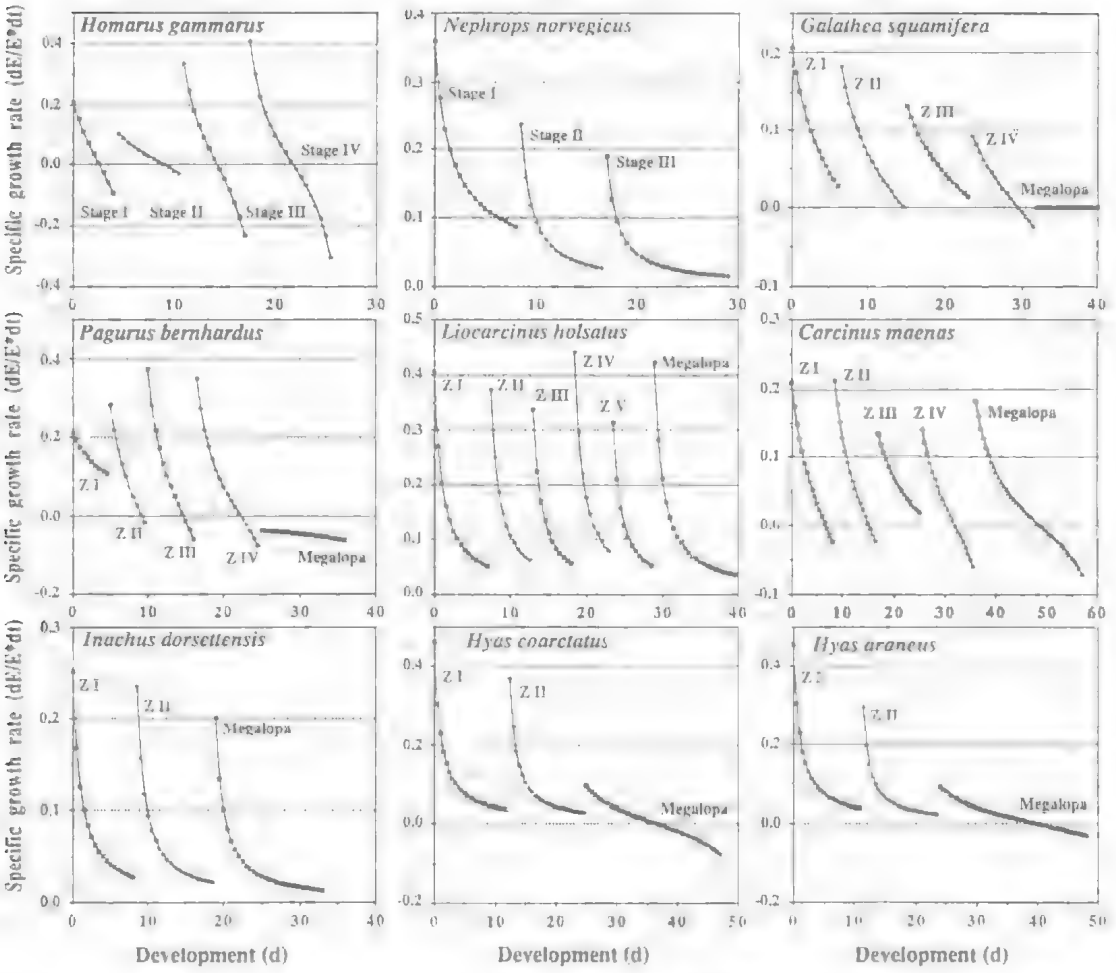

FIG. 5. Changes in energy-specific growth rates (G/E; fraction $\cdot d^{-1}$) of decapod crustacean species during larval development (sources of data: as in Fig. 4).

poor predictive power when growth within specific instars is studied. Thus, 'average' growth rates calculated from it are likely to be physiologically unrealistic (Fig. 4). Such rough estimates, however, may be useful as overall indices of growth, when only a comparison of different environmental conditions is attempted (Paul *et al.*, 1990).

Naturally, the absolute growth rate (dE/dt) depends also on the specific size of a larva: for instance, a late lobster larva may gain 100 times more energy per day than an early portunid crab larva (Fig. 4). Thus, it is useful for direct comparison to calculate specific growth rates:

$$\frac{G}{E} = \frac{dE}{E \cdot dt} = \frac{[eq.9]}{[eq.7]} \quad [eq.\ 11],$$

or

$$\frac{G}{E} = \frac{dE}{E \cdot dt} = \frac{[eq.10]}{[eq.8]} \quad [eq.\ 12],$$

respectively

Specific growth rates have the dimension of a fraction (or %) of E [d^{-1}]. Fig. 5 shows that post-moult G/E varies in most species and instars between 0.15 and 0.40 (or 15–40 %). It decreases dramatically during later moult cycle stages, often reaching negative values. The average level of daily specific growth in subsequent larval instars remains constant or it decreases. In no moult cycle or series of instars were increasing rates observed.

Crustacean growth is further complicated by a partial independence of the moult cycle from morphogenesis and growth (McConaugha, 1985). This is particularly obvious in caridean shrimp larvae, where moulting frequency may remain unaltered under suboptimal conditions, while morphogenesis and growth cease, resulting in a highly variable number and morphology of larval instars (Reeve, 1969; Knowlton, 1974).

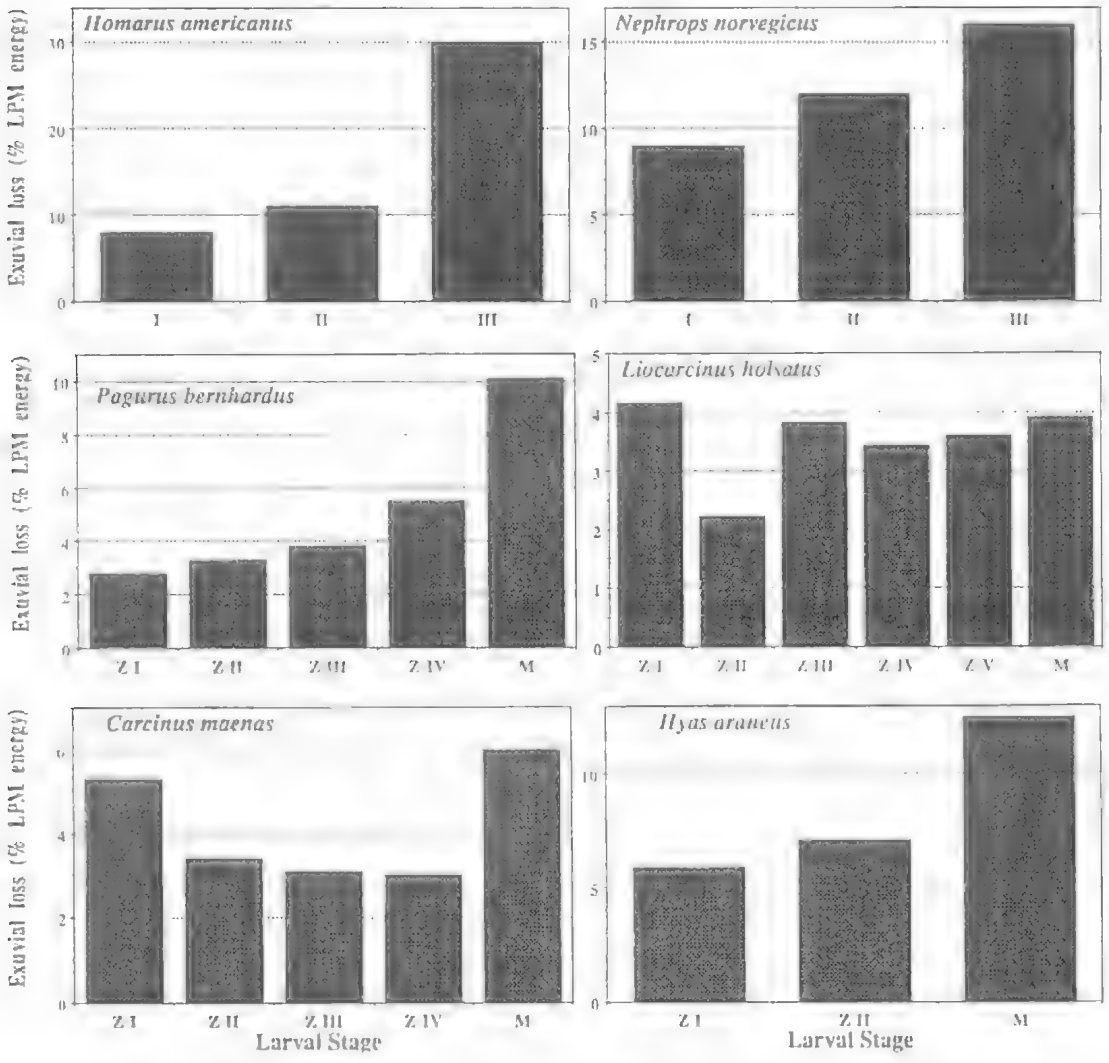

FIG. 6. Exuvial loss (% of late premoult, LPM, energy) in successive larval instars of decapod crustaceans; Z I, II etc.= zoeal stages; M= megalopa, (sources of data: Logan and Epifanio, 1978 (*Homarus americanus*), Dawirs, 1983 (*Carcinus maenas*), Anger, 1989 (*Pagurus bernhardus*); others as in Fig. 4).

EXUVIA PRODUCTION (G_E)

The exoskeleton is an integral part of crustacean growth, but equally a loss, as it is cast when ecdysis occurs (Fig. 1). Like total biomass, its absolute quantity (in Joules per individual) increases in successive larval instars at an exponential rate (Anger, 1984, 1989; Harms, 1990).

In Fig. 6 data are compiled on exuvial loss in larvae of decapod species, where measurements of late premoult biomass are available as a reference basis. It shows that anomuran and brachyuran zoeae shed *c.* 3–7% of their total late premoult energy, whereas the megalopa instar, as well as lobster larvae, lose higher percentages with their exuviae. Except in portunid crab species, there is a clear increasing trend not only in absolute (per individual), but also in percentage exuvial loss of subsequent larval instars (Fig. 6).

Among the species compared in Fig. 6, *Hyas araneus* reveals intermediate G_E values. During its complete larval development it casts <6% of total energy ingested as exuvial matter (Anger and Harms, 1989), two thirds of this loss occurring in the final (metamorphic) moult from the megalopa to the juvenile crab. In relation to total

energy assimilated, the exuvial loss amounts here to 5–9% per instar (Fig. 7).

The fraction of total growth (G) that is lost as exuvial energy, increases in *Hyas araneus* larvae from 9% (zoea I) to 13% (zoea II), and eventually 35% (megalopa). Similar or higher losses were found in larval *Menippe mercenaria* (Mootz and Epifanio, 1974), *Homarus americanus* (Logan and Epifanio, 1978), *Rhithropanopeus harrisii* (Levine and Sulkin, 1979), *Carcinus maenas* (Dawirs, 1983), and *Nephrops norvegicus* (Anger and Püschel, 1986). Lower values (mostly <5%) were reported for *Cancer irroratus (Johns, 1982), Liocarcinus holsatus* (Harms, 1990), and *Pagurus bernhardus* (Anger, 1989). In general, the data reveal that G_E tends to increase during larval development both in absolute terms, and as a percentage of either late premoult biomass G

Summary Budgets and Efficiencies

Quantitative information on uptake of food (F) and on losses that occur prior to assimilation ($L = F\text{-}A$; eq. 2), is in general considered unreliable (see above). Thus, changes that may occur during development in assimilation efficiency (A/F) and gross growth efficiency (K_1; eq. 3) will not be discussed here in detail, since both indices of food conversion are seriously affected by low precision of F measurements (Pechenik, 1979). Some possible patterns of developmental change were discussed recently by Anger and Harms (1989).

For cumulative budgets of complete larval development of decapod crustaceans, Mootz and Epifanio (1974), Logan and Epifanio (1978), Levine and Sulkin (1979), Johns (1982), and Anger and Harms (1989) calculated A/F values ranging from 45–81%. Lower assimilation efficiency (22%) was found by Dawirs (1983).

Cumulative K_1 values of complete larval development were found in most species to range from 27–30% (Mootz and Epifanio, 1974; Logan and Epifanio, 1978; Levine and Sulkin, 1979; Johns, 1982; Anger and Harms, 1989), whereas Dawirs (1983) observed a cumulative K_1 of only 3% in *Carcinus maenas* larvae .

The overall partitioning of assimilated energy (A) is exemplified with data from *Hyas araneus* (Fig. 7). In this species, the portion of A that is channelled into growth (K_2) decreases in subsequent instars from 59–26%, while respiratory (R) and excretory losses (U) increase from 39–69%, and 2–5%, respectively. Within G, exuvial loss (G_E) increases in successive instars, whereas tissue production (G_T) decreases.

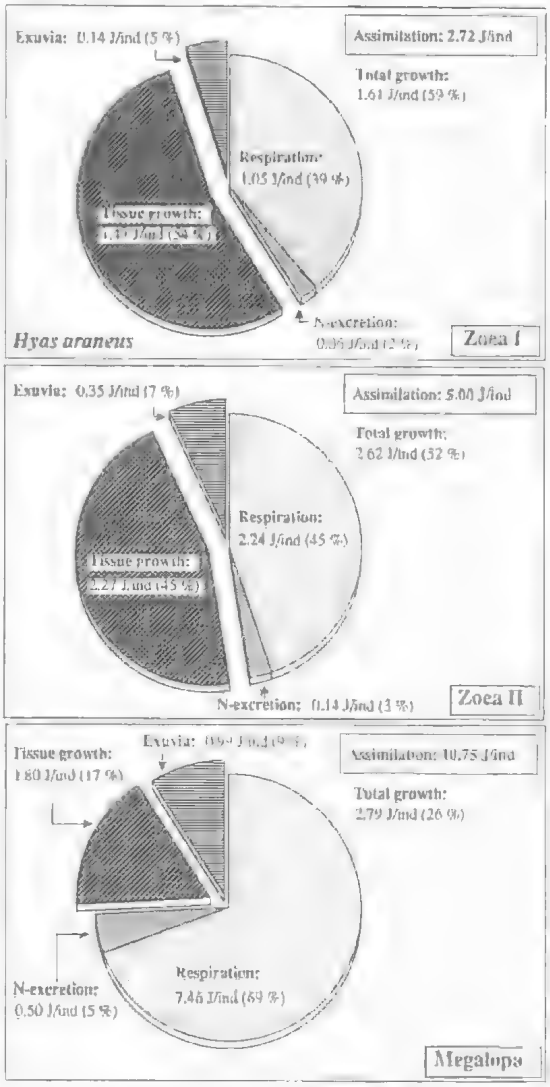

FIG. 7. *Hyas araneus*. Partitioning of assimilated energy (A) in successive larval instars (Joules, individual^{-1}, and % of A) (data from Anger *et al.*, 1989b; Anger and Harms, 1989).

With respect to changes in K_2 during larval development, some authors (compiled by McConaugha, 1985; Stephenson and Knight, 1980) found an increasing tendency from instar to instar, whereas Reeve (1969) and a number of other authors (Fig. 8) observed the opposite trend. Since K_2 decreases during larval development in most species for which sufficiently precise data with a high temporal resolution is available (Fig. 8), this may be considered more likely as a general pattern in decapod larvae.

The discrepancy between K_2 values of early

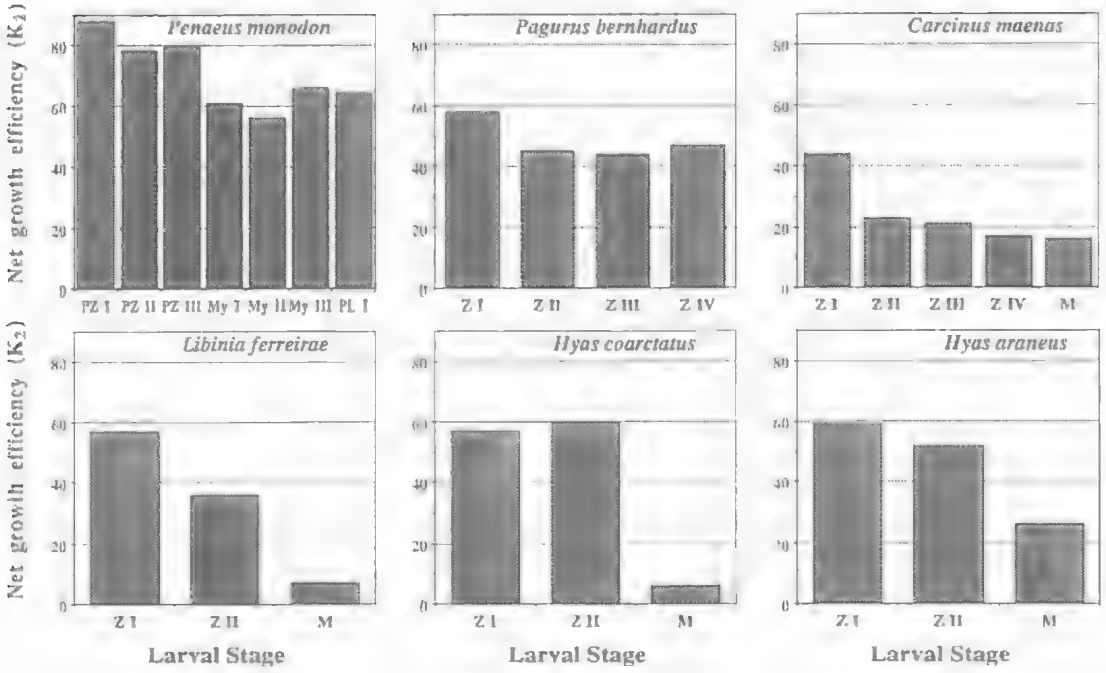

FIG. 8 Net growth efficiency (K_2; G % of A) in successive larval instars of decapod crustaceans; PZ= protozoea; My= Mysis; PL= postlarva; Z I, II etc.= zoeal stages; M= megalopa (sources of data: Kurmaly *et al.*, 1989 (*Penaeus monodon*); Dawirs,1983 (*Carcinus maenas*); Anger *et al.*, 1989a (*Libinia ferreirae*); others as in Fig. 4).

and late developmental instars appears particularly great in spider crab larvae. It is caused mainly by events that take place during the premoult (premetamorphic) phase of megalopa development, with feeding activity becoming very low (Fig. 2), and metabolic intensity of tissues remaining high (Fig. 3). As a consequence of $\dot{F}<\dot{V}O_2$, growth becomes negative ($\dot{G}<0$; Figs 4, 5). These patterns may be interpreted as signs of an increasing degree of lecithotrophy in the final instar. The ultimate degree, 'secondary lecithotrophy' (Anger, 1989), is found in hermit crab (*Pagurus bernhardus*) megalopa. No more feeding occurs here ($\dot{F}=0$), and thus development to metamorphosis depends exclusively on energy accumulated by the preceding zoeal instars. This phenomenon is associated with a switch in life style, from pelagic to benthic, and it may be interpreted as an adaptation to an extremely specialised habitat requirement, in this case the need to find a gastropod shell after settlement and metamorphosis. Secondary lecithotrophy should increase the chance to find such a particular habitat, as no time and energy must be sacrificed for feeding activity.

The degree of decrease in K_2 may thus reflect the degree of food independence, i.e. the degree of secondary lecithotrophy, in a late developmental stage. Since the ability to develop independently of food through metamorphosis should in general be more important for species that depend on very particular habitats, rather than in opportunistic settlers, the degree of lecithotrophy may represent a measure of ecological specialisation.

There is a decrease not only in average K_2 of successive larval instars (Fig. 8), but also in instantaneous values during the course of individual moult cycles (Fig. 9). The tendency of decreasing growth and K_2 values with time of development corresponds to the finding that very young, post-natal organisms tend to have particularly high net growth efficiencies (ranging from *c.* 50–80% in most poikilotherms; Calow, 1977). Each ecdysis is, in principle, comparable to hatching, i.e. to 'birth' of a larval instar, and the following moult cycle is characterised by processes of growth, morphogenesis, and physiological aging, accom-

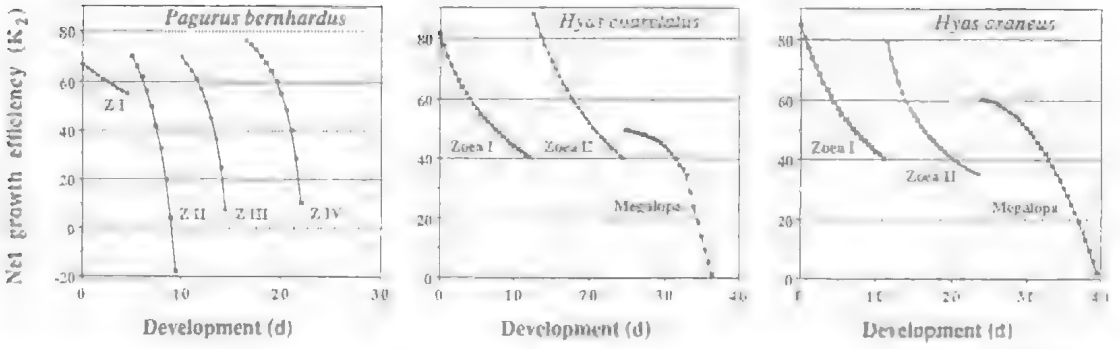

FIG. 9. Changes in instantaneous net growth efficiency (K_2) during larval development of decapod crustaceans: Z= zoeal instars (sources of data as in Fig. 4).

panied by decreasing growth efficiency. Ecdysis initiates the next cycle, beginning again with higher K_2 values (Fig. 9). Since development proceeds and the absolute age of larvae increases with each subsequent instar, a decreasing trend should be expected also in average efficiencies of successive instars. Thus, it is hypothesised that tendencies of decreasing K_2 during development (Figs 8, 9) may be a typical bioenergetic pattern in decapod larvae.

When different taxa are compared, highest average K_2 values (56–88%) were found in larvae of a penaeid prawn, lower values in anomuran zoeae (44–58%; the entirely lecithotrophic hermit crab megalopa is excluded from this comparison), and lowest in crab larvae (6–60%) (Fig. 8). It is interesting to note that this sequence might reflect a phylogenetic tendency of decreasing net growth efficiency, from more primitive toward more advanced groups (for taxonomy of Decapoda see Bowman and Abele, 1982). Since low growth efficiencies are expected in partially lecithotrophic instars or species, this would suggest a phylogenetic tendency in the Decapoda toward an increasing degree of lecithotrophy and thus, of increasing ecological specialisation. This presumption is corroborated by differences in the average chemical composition of decapod larvae belonging to different infraorders (Fig. 10; see below). However, special adaptations to environmental (including biotic) factors such as life of hermit crabs in a mollusc shell, can occur in any taxonomic group and thus, there should be many exceptions to this hypothetically postulated rule.

Mechanisms of Growth and Concluding Remarks

Available data suggest that the decreasing trends in growth rate (both per individual and per unit of biomass energy), as well as in net growth efficiency during development, may be a bioenergetic rule in larval decapods. These trends have clearly been observed during individual moult cycles (Figs 4, 5, 9), and they occur in sequences of larval instars (Fig. 8). They may be seen also in phylogenetic development, from primitive toward more advanced groups (see above: K_2). Presumably, the existence of such general patterns raises the question as to what mechanisms of growth may be involved and how these may change during larval development.

Data on elemental and biochemical composition of decapod larvae reveal recurrent patterns of developmental change that are illustrated, again with *Hyas araneus* as a well-documented example (Fig. 10). The carbon/nitrogen (C/N) ratio which is frequently used as an indicator of the lipid/protein ratio, shows here in all larval moult cycles an initial increase, followed by a transitory maximum, and a final decrease. When patterns of instantaneous growth rates in C and N are compared (dC/dt, dN/dt), the following tendencies may be discerned: (1) an initial phase with high G. It is characterised by particularly strong gain in C (i.e. lipid) and maximum C/N ratios approximately at the end of the intermoult (stage C) phase of the moult cycle. (2) The rate of accumulation in C (reflecting the lipid fraction) decreases dramatically, whereas that in N (protein) decreases more slowly. In late megalopa development, these differential slopes of instantaneous growth curves cause a reversal of biochemical patterns, with accumulation of N eventually exceeding that of C (Fig. 10).

These two distinct phases of growth correspond to those of an obligatory and a facultative

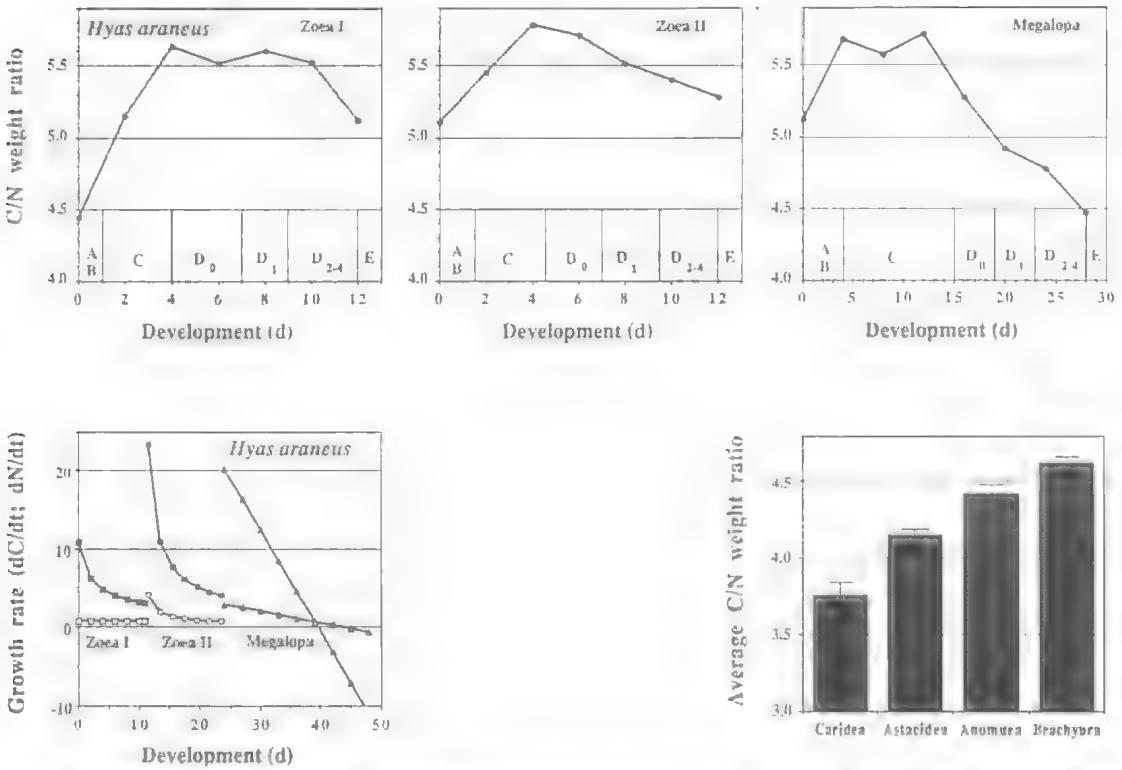

FIG. 10. *Hyas araneus*. Changes in the C/N weight ratio and in carbon- and nitrogen-specific growth rates (dC/dt, closed symbols; dN/dt, open symbols; µg individual^{-1} d^{-1}) during larval development. A–E, stages of larval moult cycles (after Drach, 1939; Anger, 1983); data from Anger and Hirche, 1990. Lower right: average C/N weight ratio (x ±95% confidence intervals) in larvae belonging to different decapod infraorders (taxonomic position after Bowman and Abele, 1982; data from 3 species of Caridea, 2 Astacidea, 2 Anomura, and 10 Brachyura after Anger and Harms, 1990).

feeding period, the latter in principle being independent of food (Anger, 1987). Thus, one can say that the final phase of the moult cycle (premoult) reveals a high degree of secondary lecithotrophy, as further development is possible with energy reserves that have been accumulated during earlier stages (postmoult, intermoult). The critical point that must be reached to allow autonomous development (the 'point of reserve saturation'; Anger and Dawirs, 1981; Gore, 1985; Dawirs, 1986), was identified as the transition between intermoult (stage C) and early premoult (stage D_0) and hence, was termed 'D_0 threshold' (Anger, 1987).

Although larvae will continue to eat when food is available, the facultative feeding period is characterised, independent of feeding conditions, by low rates of food uptake (Fig. 2) and growth (Figs 4, 5), high metabolic loss (Fig. 3), and consequently, low net growth efficieny (Fig. 9). Apparently, morphogenetic reconstruction processes and other physiological and anatomical preparations for ecdysis ('qualitative growth') have during this developmental phase priority over mere accumulation of energy ('quantitative growth'), and their completion is secured by an increased degree of lecithotrophy.

In a recent study on nucleic acids in *Hyas araneus* larvae, Anger and Hirche (1990) suggested that these two phases of growth may differ also in the relative significance of two major mechanisms of growth: cell enlargement (hypertrophy) and cell multiplication (hyperplasy). Assuming constant amounts of DNA per cell and neglecting interstitial materials, the former type of growth may be measured as an increase in the DNA content per individual, the latter as a C/DNA ratio, and synthetic activity of tissues may be indicated by the RNA/DNA ratio (Fig. 11).

Mitoses take place continuously from hatching of the zoea I to premoult of the megalopa instar, whereas maximum synthetic activity of tissues and an increase in average cell size were observed mainly in the initial (postmoult) peri-

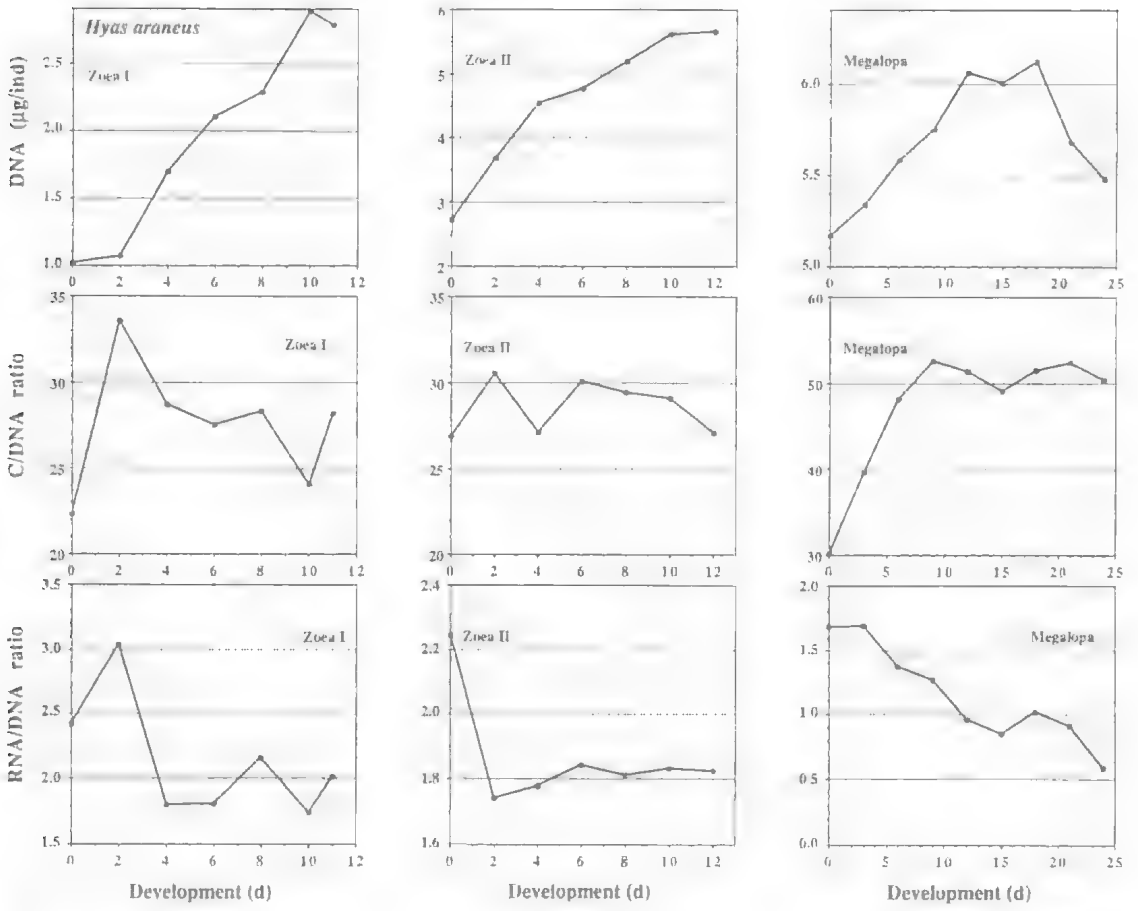

FIG. 11. *Hyas araneus*. Changes in DNA content (µg individual^{-1}), and in the carbon:DNA (C/DNA) and RNA/DNA weight ratios during larval development (data from Anger and Hirche, 1990).

ods of larval moult cycles (Fig. 11). High initial rates of synthesis are suggested also by measurements of adenosine nucleotides in *Carcinus maenas* larvae (Harms *et al.*, 1990b). They suggest a high turnover rate of ATP during postmoult and early intermoult, leading to a minimum adenylate energy charge in stage C, in spite of increasing ATP concentrations (Fig. 12). Ultrastuctural evidence (Storch and Anger, 1983), shows that this initial accumulation of energy reserves (mainly of lipids) takes place in R-cells of the larval hepatopancreas, where fat vacuoles are enlarged. Protein synthesis may be associated mainly with epidermal enlargement and reconstruction processes, and with hyperplasy rather than hypertrophy (McConaugha, 1985, and earlier papers; Freeman, 1986, 1990, 1991; Freeman *et al.*, 1983). The latter processes become independent of further external energy supply, when sufficient internal reserves of energy and essential substances have been accumulated to allow autonomous development. This energetic status is normally reached in late stage C of the moult cycle, and it may may set the signal for increasing ecdysteroid production in the larval Y-organs which then gives the stimulus for development through the premoult phase (Spindler and Anger, 1986; Anger and Spindler, 1987).

Even when food is available, the premoult stages are characterised by signs of an increasing degree of lecithotrophic development, with catabolism of lipid reserves (Fig. 10), no further increase in average cell size (Fig. 11: C/DNA), and decreasing ATP concentrations (Fig. 12). Like morphogenesis (Anger, 1987), these trends may be fairly independent of feeding or starvation commencing after the D_0 thre-

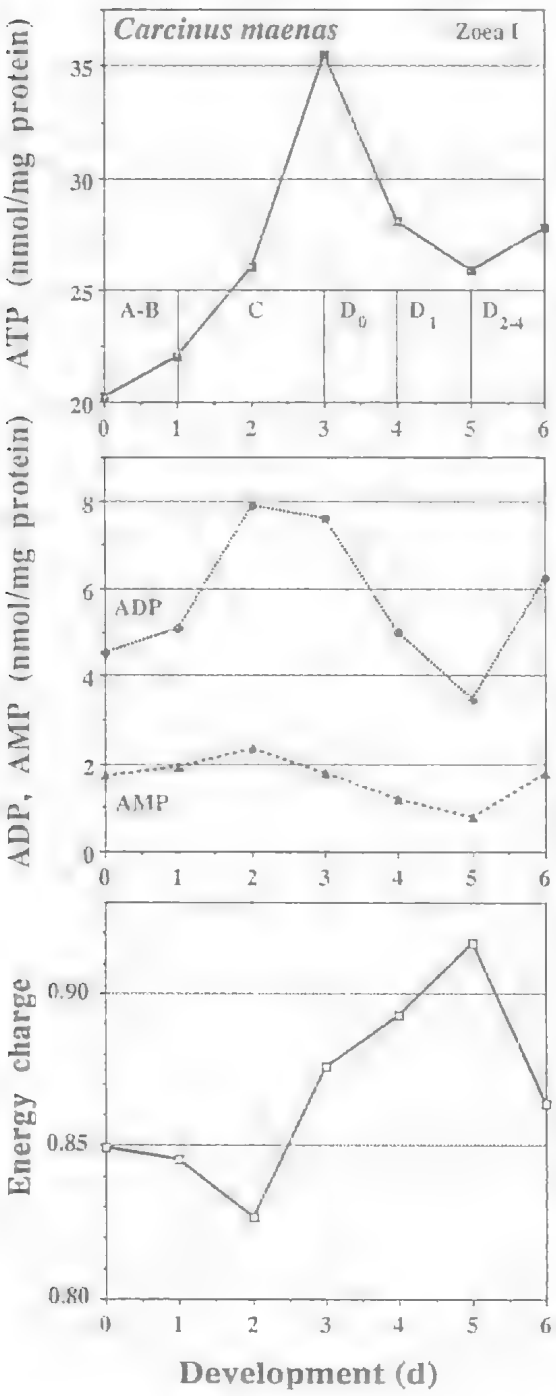

FIG.12 *Carcinus maenas*. Changes in adenosine nucleotide concentrations (ATP, ADP, AMP; nmol ·[mg protein]$^{-1}$) and adenylate energy charge during the moult cycle stages (A–E, cf. Fig. 10) of the zoea I instar (after Harms *et al.*, 1990).

shold (Dawirs, 1983; Anger and Spindler, 1987; Freeman, 1990, 1991; Harms *et al.*, 1990). In the megalopa of *Hyas araneus*, the premetamorphic phase shows particularly strong signs of autonomous development, with reconstruction processes that are associated with drastic losses in the lipid fraction (C/N; Fig. 10), and probably with cell lysis (DNA; Fig. 11).

If high C/N ratios are considered as indicators of a high lipid content and hence, an increased ability to develop without external energy supply, then this index suggests significant differerences in the degree of lecithotrophy among higher taxa of the Decapoda. In Fig. 10, larvae belonging to different infraorders were grouped in a sequence of increasingly advanced taxonomical position (Bowman and Abele, 1982). They show in this order a significant increase in average C/N ratios. This agrees with the tendency of decreasing net growth efficiencies in the same sequence (see above; Fig. 8). Caridean shrimps should reveal, on the average, the lowest degree of lecithotrophy, brachyuran crabs the highest. This tendency corresponds to a decreasing number and variability of instars passed during larval development, and an increasing degree of morphological change in each moult cycle. The latter trend suggests that, as in insects, there may be an evolutionary tendency toward increasingly metamorphic development. While Caridea can respond to unsuitable environmental factors with additional moults and reduced morphogenesis (Knowlton, 1974), the Brachyura are only moderately able to vary their number and morphology of developmental instars, and hence depend more on sufficient energy reserves necessary for drastic reconstruction processes. Thus, bioenergetic traits of larvae may reflect phylogenetic trends, with an increasing degree of lecithotrophy, increasing ecological specialisation, and an increasingly metamorphic type of development in the evolution of the Decapoda.

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GROWTH AND MORPHOGENESIS IN CRUSTACEAN LARVAE

JOHN A. FREEMAN

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Crustaceans grow in a step-wise manner that is a function of the tissue growth during the moult cycle combined with stretch at ecdysis, moult increment, and moult cycle duration. In larvae, growth of the epidermis is also involved in the morphogenesis of integumental structures. To understand the mechanism and regulation of growth and integumental morphogenesis, tissue growth was studied in *Palaemonetes* larvae and *Artemia* metanauplii. Increase in carapace length in *Palaemonetes* larvae is proportional to the growth of the underlying epidermis. Moreover, growth in the epidermis is highly correlated with that of the muscle. Both tissues show the greatest amount of growth during the first third of the moult cycle. Tissue growth and carapace size were not affected by rearing temperature or exposure to the moulting hormone (20-hydroxyecdysone), factors that strongly affect moult cycle duration. Another factor, feeding regime, markedly affected tissue and carapace growth. The most critical period for food intake is the first third of the moult cycle. It is uncertain, however, whether nutritional state controls tissue growth directly or through other physiological processes. At ecdysis, hydrostatic pressure, under the control of the neurosecretory center, expands the new integument to a point equal to the amount of new tissue generated during the previous moult cycle. Although eyestalkless larvae grew more in carapace length than intact larvae, there is no difference in the amount of growth of the epidermis between the two groups. Uptake of water at ecdysis, then, serves to expand the new cuticle but, under normal conditions, does not affect tissue growth. Studies on segment morphogenesis in *Artemia* reveal that patterned cell replication is involved in growth and shape of the thoracic integument and, as a morphogenetic force, leads to regional differences in cell density that are integral to formation of the arthrodial membrane and the thoracopod limb bud. The cell replication pattern may, in fact, be an initial step in cell differentiation. Thus, epidermal growth and morphogenesis in crustacean larvae is a function of both the nutritional state of the organism and cellular events that control development. □ *Crustacea, larvae, growth, morphogenesis.*

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The presence of a restrictive exoskeleton in larval and adult crustaceans limits expansion of the integument to periods of ecdysis. The corresponding growth curve appears to rise in a step wise manner (Hartnoll, 1982; Botsford, 1985). The growth curve is a function of the time between ecdyses, or moult cycle duration (MCD), and the amount of linear growth that takes place at ecdysis, or moult increment (MI). These factors have been recently reviewed in depth by Hartnoll (1982) and Gore (1985). The growth curve is generally species-specific and defines the relationship between larval size and duration of the larval period. Variation in the curve can result from sexual maturation, environmental factors (chiefly temperature), nutritional stress, and parasitism (Hartnoll, 1982).

Crustacean larvae undergo a series of larval moult cycles, hereinafter referred to as instars, before metamorphosis to the juvenile form. For each species, the number of instars may be constant or may vary under certain environmental conditions (Broad, 1957b; Knowlton, 1974). Some degree of morphogenetic change is observed at each instar, and the schedule of the changes is in most cases so invariant that the morphogenetic state defines that particular instar (Broad, 1957a; Williamson, 1982). Development may be gradual (direct) with slight change at each ecdysis (e.g. *Homarus*, *Artemia*) or there may be one or more major changes in body form (indirect), as exhibited by barnacles and penaeid shrimp (Walley, 1969; Williamson, 1982). For each larval instar, the organism grows in size and changes form. Although these changes are manifested at ecdysis, the tissue changes occur continuously throughout the moult cycle. The constancy of growth and morphogenesis in the larval instars would suggest that both processes are interrelated and may be regulated by a common mechanism. However, this mechanism has yet to be elucidated.

In our studies of the control of growth and morphogenesis in crustacean larvae, we have examined the process of growth in larvae of the caridean shrimp, *Palaemonetes pugio*, and growth and morphogenesis in larvae of the brine shrimp, *Artemia*. Since linear dimension is a function of the cuticle and the epidermis, growth in this tissue was used as a tool to differentiate between the factors that regulate moulting and MCD and those that control MI (Fig. 1A,B). The larval epidermis is a two dimensional monolayer of cells whose primary role is to carry out the cyclical degradation of the old cuticle and synthesis of the new cuticle. The cells actively participate in this function throughout most of the moult cycle with only a brief resting (intermoult) period (Freeman and Costlow, 1980; McConaugha, 1985; Christiansen, 1988). In addition to its role in cuticulogenesis, the epidermal cell replicates to increase the area of the monolayer and differentiates to form specific integumental structures.

MOULT CYCLE DURATION

A primary component of growth is the moult cycle duration (MCD). The length of the moult cycle is temperature dependent, relatively constant, and species-specific in the larval phases, while the juvenile and adult moult cycles increase in length with age. Although the regulation of the length of each stage of the moult cycle remains unclear, it is widely accepted that the endocrine system controls the onset of premoult and ecdysis. During most of the intermoult period, the onset of moulting is blocked by moult-inhibiting hormone (MIH), a peptide secreted by the eyestalk neurosecretory centers (Chang, 1985; Skinner, 1985). Cessation or reduction in production of MIH are presumed to initiate the onset of proecdysis. This has been shown for adults (Skinner, 1985) but has not been consistently observed in larvae. Eyestalk removal did not stimulate moulting in crab larvae (Costlow, 1966a,b) and shrimp larvae (Little, 1969). A more frequent observation schedule revealed that eyestalk removal was effective in shortening the moult cycle (Freeman and Costlow, 1980). The findings from these studies clearly show that the larvae are traversing the moult cycle at a rapid rate that can be only slightly accelerated.

Promotion of the onset of premoult is controlled by ecdysone and 20-hydroxyecdysone (20HE)(Skinner, 1985). This regulatory step was demonstrated for larvae in barnacles (Freeman and Costlow, 1983a), and crabs (McConaugha and Costlow, 1981; Freeman and Costlow, 1984) when larvae exposed to 20HE entered premoult prematurely. Recently, ecdysteroid levels have been determined in lobster larvae (Chang and Bruce, 1981) and in crab zoeas (Spindler and Anger, 1986; Anger and Spindler, 1987). In both studies the hormonal titres resembled those of adults in that the concentration declined following postmoult, remained at a basal level for the short period of intermoult and then peaked during mid premoult. Moreover, by comparison to hormone profiles in adult crustaceans, the premoult rise appears to begin earlier than stage D_0 in some instars. Chang and Bruce (1980) also showed that the profile was similar during multiple, shortened moult cycles in eyestalkless lobster juveniles. The titre increased at the onset of premoult, which began earlier, suggesting that the titre can undergo normal cycles even in the absence of MIH. Thus, the regulation of moulting hormone levels may be under the control of more factors than just MIH.

Temperature has been shown to be a strong regulator of moult cycle duration in crustacean larvae. There is generally an inverse relationship between temperature and MCD (Knowlton, 1974; Hartnoll, 1982). At the lower temperature range the MCD will be several times longer than that seen at the optimal temperature. In some cases, the larvae will never moult. At the higher temperature range, the MCD will reach a point where it cannot be further accelerated.

To find if the amount of growth during an instar was dependent on the MCD, temperature was used to control the MCD in instar II *Palaemonetes* larvae. The MCD was inversely proportional to a temperature range of 15–30°C with larvae at the lowest temperature (15°C) demonstrating moult cycles of almost seven days compared to a two day MCD for those at 30°C (Freeman, 1990b). The MI, however, was greatest at 20 and 25°C with the least amount of growth at 30°C. The results show that growth of the carapace then was dependent on temperature but it was independent of the MCD. Moreover, since all moult cycle stages were lengthened or shortened proportionately by these treatments, there does not appear to be one phase of the moult cycle that must be of a certain minimum duration in order for growth to occur.

Moulting hormones accelerate the onset of the premoult period and thereby shorten the intermoult period in larvae of all crustaceans examined (Skinner, 1985; Christiansen, 1988).

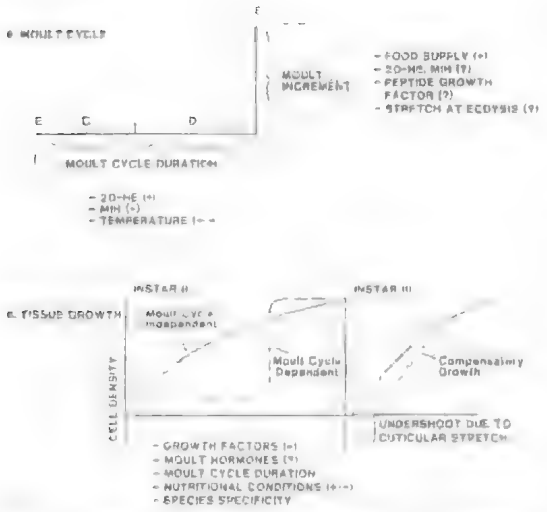

FIG. 1. Model of the growth process in crustacean larvae. A, Factors that control growth during one moult cycle, shown as part of a growth curve. The moult cycle is the period between ecdyses (E) and is divided into postmoult and intermoult (C) and premoult (D) after Drach (1944). Factors that control moult cycle duration include 20-hydroxyecdysone (20HE), moult-inhibiting hormone (MIH), and temperature. The amount of growth at ecdysis, or moult increment, is affected by food supply, stretch at ecdysis, and possibly moulting hormones and growth factors. B, Growth of tissues during the moult cycle. Growth could be moult cycle stage dependent if it occurs primarily during one stage of the moult cycle, or moult cycle stage independent if it occurs throughout the moult cycle. Here for example, the growth occurs during early premoult. When growth of the epidermis is seen as change in cell density, the density will increase during the molt cycle and then return to a basal level at ecdysis, as shown here for the change at ecdysis to instar III. After ecdysis, the density will again increase. If a greater than normal amount of stretch occurs, the density value will fall below the basal level (undershoot). The tissue may (compensatory growth) or may not be able to obtain the same density. Tissue growth is influenced by nutritional conditions, genetic factors (species specificity), and, possibly, growth factors, moult controlling hormones and moult cycle duration.

Treatment with 20HE was used as a method to shorten the MCD in order to further examine the relationship of MCD and growth and to explore the role of moulting hormones in the growth process (Freeman, 1990b). Exposure of instar II *Palaemonetes* larvae to 20HE shortened the postmoult and intermoult periods by 33% but did not noticeably affect the duration of premoult. There was no difference in carapace length of the control and hormone-exposed larvae. These findings support the contention that growth in crustacean larvae is not dependent on the MCD. The results also suggest that moulting hormone does not have any direct influence on growth of the larvae. The endocrine system, then, controls the moult cycle and the rate at which intermoult tissue growth is realised at ecdysis. However, the moulting hormone may possibly play a permissive role in growth by establishing conditions conducive to growth of the epidermal cells, e.g. cell division in late premoult.

The conditions tested (2 day MCD, temperature control; 36 hr intermoult stage C, 20HE control) did not permit a continuous attenuation of the MCD below a certain point. At some point in the abbreviation process, the larva would probably lose the ability to accumulate food reserves. At that point the synchrony of the complex cellular events would be disrupted, which would lead to decreased growth. Since one day of feeding is required to successfully moult (Freeman, 1990b), this may be the critical duration although even lesser periods may be possible at higher temperatures.

An obvious candidate for regulation of MCD is the quality and quantity of the food. Many studies have examined the role of nutrition in crustacean growth, metamorphosis and survival (Broad, 1957b; Knowlton, 1974; Hartnoll, 1982; Gore, 1985; McConaugha, 1985). As expected, low rations of food limit growth. This result is confirmed during studies on the effect of feeding regime in shrimp larvae (Freeman, 1990a). Several studies have clearly shown that normal MCD and morphogenesis is controlled by the nutritional condition of the larva (Broad, 1957b; Anger *et al.*, 1981; McConaugha, 1982; Anger, 1984; West and Costlow, 1988).

MOULT INCREMENT

Although increase in linear dimension is observed at ecdysis, the growth process occurs throughout the moult cycle (Frank *et al.*, 1975; Sulkin *et al.*, 1975; Anger *et al.*, 1989). These data, obtained primarily from biochemical analyses, contain little information on the actual growth of the tissues. In this section I consider factors that: 1) play a role in the moult increment (MI) in the organism and influence growth of the tissues during the moult cycle, and 2) control expansion at ecdysis.

Any consideration of a growth mechanism must begin at the level of the gene. The disparate sizes are obviously a function of the genetic

mechanism that controls the MI and, to a lesser degree, the MCD. For each species, there appears to be a process that establishes a basal MI under normal conditions (Rice, 1968; Hartnoll, 1982; Gore, 1985; Freeman, 1990b). External factors may act on this process directly or may control the rate at which the system operates. Future efforts aimed at understanding the genetic control of growth will greatly contribute to general knowledge of growth in crustaceans and other organisms.

Built into the growth controlling system in larvae is the ability to somehow recognise their size or 'growth state' and to grow accordingly. A larva which is smaller than the mean size for that species/instar/cohort may grow more than larger larvae of similar age, and vice versa. This has been shown for *Palaemon* (Hartnoll and Dalley, 1981), barnacle (West and Costlow, 1987), and *Palaemonetes* (Freeman, 1990b). The manner in which this system functions is not understood.

Temperature appears to affect growth by controlling metabolism. There is an optimum temperature at which food conversion and anabolic processes take place and, as mentioned above, an optimum temperature for progression through the moult cycle. Growth probably occurs most efficiently at a temperature where the optima coincide. For larvae of *Palaemonetes pugio* this optimum is 25°C.

Growth controlling hormones may include those that regulate moulting (mentioned above) and the hormone(s) that regulate hydromineral content. Eyestalk removal in crustaceans has been shown to significantly decrease the intermoult period under conditions where the moult cycle progression is carefully monitored, indicating the presence of MIH in larvae. In addition to regulating the MCD, MIH could actually affect the growth behaviour of the cells, although no evidence of such a role for MIH has been presented. Growth does not appear to be affected by MCD and the neurosecretory system is incomplete in early larval instars. Thus, it is unlikely that MIH participates in growth regulation other than the control of the MCD.

In addition to moult cycle acceleration, eyestalk removal results in a postmoult size that is larger than the comparable value for intact animals. This has also been shown to be true for eyestalkless larvae of *Rhithropanopeus* (Kalber and Costlow, 1966; Freeman *et al.*, 1983), *Homarus* (Charmantier *et al.*, 1984; Snyder and Chang, 1986), and *Palaemonetes* (Okazaki *et al.*, 1989; Okazaki, pers. comm.). The increased size is thought to be due to enhanced uptake of water as a result of loss of the hormone that controls hydromineral balance (Mantel and Farmer, 1985). The higher than normal hydrostatic pressure stretches the new, soft integument beyond the limits established by tissue growth during the previous instar. Thus, the stretch before hardening of the cuticle supercedes the growth potential.

The mechanism of tissue growth under the conditions of supranormal haemolymph hydrostatic pressure is beginning to be studied. Freeman *et al.* (1983) found that the density of the epidermal cells of juvenile *Rhithropanopeus harrisii* that had undergone four or five moult cycles following eyestalk removal during the larval period was greater than that of intact animals although the carapace was much larger. These results indicated that the epidermal tissues of eyestalkless larvae somehow compensated for increased cuticle area after ecdysis by increasing cell growth and replication. Conversely, Okazaki *et al.* (1989) found that the increased stretch in eyestalkless larval and adult shrimp was not accompanied by compensatory growth of the cells. Instead, the density remained lower than that of the intact animals. Comparable studies with different species are needed to find 1) the most common growth process for crustaceans, and 2) if the response to stretch differs between stages of the life cycle within a single species.

Not unexpectedly, nutritional state is a strong regulator of growth. Many studies have shown that food deprivation or differences in food quality has a marked effect on growth (Hartnoll, 1982; McConaugha, 1985; Anger, this volume). Recently, the feeding regime was used to examine the growth processes in *Palaemonetes* larvae (Freeman, 1990a). Feeding during the first two thirds of the moult cycle did not markedly affect the MI, indicating that sufficient food was stored during the intermoult and early premoult periods. Feeding only on the first or second days of the instar, however, resulted in levels of growth that were intermediate between starved and continuously fed controls with more growth observed in those larvae fed on day 1 of the instar. These findings indicate that feeding during the first third of the moult cycle is critical for successful growth. This period corresponds to the 'point of reserve saturation' (Anger and Dawirs, 1981) or the threshold for growth and development (West and Costlow, 1988), while feeding on day 2 may be sufficient to reach the

'D_0 threshold' and moult, but with only slight growth (Anger, 1987). The first third of the moult cycle is clearly a period in which food assimilation is somehow monitored and translated into actual tissue growth or stored for further growth and morphogenesis. Why this phase should be so essential is not obvious. Several studies have shown that tissue growth occurs at this time (Frank *et al.*, 1975; Sulkin *et al.*, 1975; West and Costlow, 1987; Anger *et al.*, 1989; Harms *et al.*, 1990). Feeding may become more active because apolysis and premoult changes have not yet begun. Interestingly, in the *Palaemonetes* feeding study, some growth occurred in starved larvae that survived instar II. This growth may have been fueled by food reserves accumulated during the previous instar or may have resulted from tissue catabolism.

CELLULAR BASIS OF INTEGUMENTAL GROWTH IN CRUSTACEAN LARVAE

To comprehend growth of the cuticle, it is necessary to understand how the process occurs in the underlying epidermis. This is best accomplished by considering the cell cycle with respect to the moult cycle. Following the beginning of premoult, the epidermis increases in cell number by mitosis (Tchernigovtzeff, 1965; Halcrow, 1978). In some larvae mitosis may occur in periods of the moult cycle other than premoult (Le Roux, 1978; Freeman, 1986). In either case, cell replication slightly increases the area of the epidermis. Cell replication and growth may occur to the extent that, in transverse section, the epidermis appears to be folded (Skinner, 1962; Freeman and Costlow, 1980). At ecdysis, the uptake of water (DeFur *et al.*, 1985) expands the new integument to a point that will equal its new size (Freeman, 1990b).

Little information exists on the control of the cellular processes by external and internal factors. To establish a conceptual framework, a model of the system relating tissue growth and the moult cycle is shown in Fig. 1B. The instar II larva of *Palaemonetes pugio* is well-suited for this model since the epidermal cells of dorsal carapace exist as a monolayer which is spatially restricted so that its growth can be compared to change in the carapace dimensions (Fig. 2).

The epidermal cell density is found to increase only during the first day of the moult cycle in normal larvae (Freeman, 1990b) (Fig. 3). At the end of this period the predicted growth can be determined from the cell density. This is also the period when maximal growth of the muscle occurs (Schaff and Freeman, unpubl.). Preliminary findings show that the increase in cell density is a result of enlargement of certain cells within the epithelium. The cells that enlarge appear to be cells that have divided during premoult of the previous instar. Their expansion slightly compresses other cells in the monolayer, and results in the enhanced cell density.

Factors that affect MI do so through the growth of the epidermis. Growth of the epidermis in *Palaemonetes* is greatest at the optimum temperature of 25°C (Freeman, 1990b). Larvae exposed to moulting hormone show no differences in the epidermal growth, as was the case for MI. The strong effect of nutrition on MI is reflected in the cellular growth. An example of this relationship is shown in Fig. 4. Starved larvae underwent little growth in the epidermis while larvae fed on day 1 demonstrated cell growth that was intermediate between fed and starved larvae. A direct correlation was observed between the increase in density by day two of the instar and the MI (Freeman, 1990b)

The tissue, then, is able to respond to the nutritional state (or food storage) very rapidly by growth of some cells leading to increased density. Since the density does not increase as much in starved larvae, the process of enlargement (G1 growth ?) may be controlled by sufficient uptake of food or uptake of certain compounds. The other growth phase is the premoult period when cell division takes place. Little is known of how this phase is controlled by food uptake. One possiblity is that the cell cycle is controlled by nutritional state such that a cell will make a decision to continue through S, G2 and mitosis as a result of some signal propagated after feeding. Alternatively, a certain number of cells are stimulated to cycle during the feeding-sensitive period but that other factors, generated during the remainder of the moult cycle, would control their division. Several control points in the eukaryotic cell cycle have been shown to exist. A major point is the G1-S (or G1a-G1b) transition (Pardee, 1989). In the shrimp epidermis this may be seen as the enlargement of a few cells. Another control point is the G2-M transition (Murray and Kirschner, 1989). Since mitosis is most often seen in premoult, this decision may be one that is independent of the transition to S phase. These intriguing hypotheses must be empirically tested to determine how the epidermal cells are regulated by food intake and nutrition.

From our preliminary studies it is clear that only

FIG. 2. Nuclei of the dorsal epidermis of live instar II *Palaemonetes pugio*. The nuclei are vitally stained with a nuclear fluorochrome bisbenzimide (Hoechst, 33342).Fluorescence image. Bar = 50 µm.

certain cells, or a certain number of cells replicate during the moult cycle. This has been found to be true for *Palaemonetes* larvae where the positions of dividing and enlarging cells appear to be constant. Moreover, positional information may be used to determine if a cell is to divide or remain in the non-cycling compartment. Within the monolayer some cells will leave the cycling population as growth and morphogenesis proceed. How nutritional state effects the regulation of these events is not understood.

GROWTH AND MORPHOGENESIS

The crustacean epidermis represents an unusual example of cell differentiation in that the function of cuticulogenesis is fully developed at hatching but the cells must also form the morphologically different regions of the integument. In this process, they will further differentiate to a more specialised type of epidermal cell. Among the specialised cells are setal cells, tendinal cells, transport cells, and, in developing nauplii of some species, the neuroblast cells (Freeman, 1989a). Each of these cell types begins as a cell in the general larval epithelium. As the tissue grows and develops, the cell changes and differentiates. Following differentiation, the cell may not grow further or, if it is part of a growing region of the integument, it may continue to divide as the region grows in proportion to other areas of the integument. For many species of crustaceans another dramatic change will occur when the larva undergoes metamorphosis. In some instances, this change involves only a transformation from a caridoid to a cancroid form. In others, an extreme change takes place, e.g. the barnacle cyprid (Walley, 1969). While a discussion of all of the cellular and regulatory processes is beyond the scope of this review, the process of cell growth is essential to the generation and maintenance of form and shape of the integument and will be discussed here.

Crustacean larvae hatch from the eggs at different stages of larval development (Williamson, 1982; Gore, 1985). Some may be advanced and undergo little postembryonic development (e.g. *Homarus*), while others may hatch at the nauplius, the least developed larval form of the Crustacea. At each ecdysis some amount of growth occurs and developmental complexity increases. For the nauplius, this is seen as the process of segmentation in the thorax and abdomen, while in the zoea it involves development of limbs in segments that are already formed.

Morphogenesis in decapod crustaceans, the group for which most studies have been accomplished, includes continued development of the

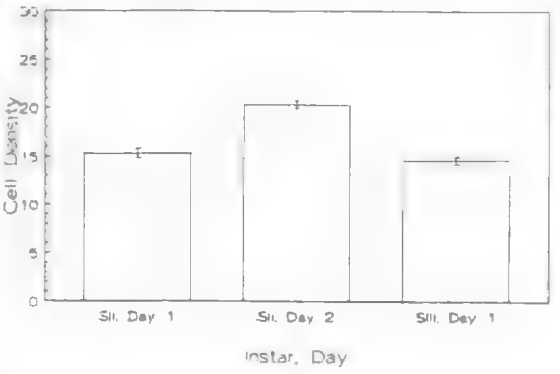

FIG. 3. Change in density of the epidermal cells in the dorsal carapace of live *Palaemonetes pugio* during the second instar. The density increased by approximately five cells during the first day of the instar and returned to the basal level at ecdysis to instar III.

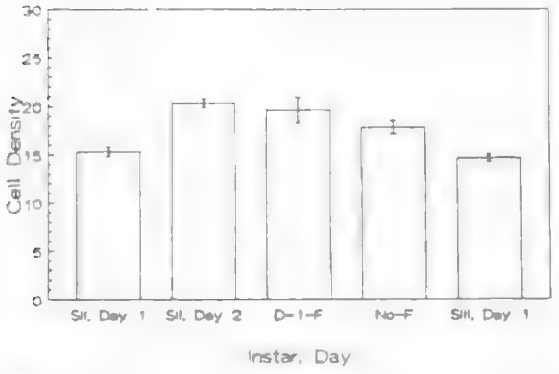

FIG. 4. Change in cell density of the epidermis under different feeding conditions that are known to affect the molt increment (Freeman, 1990a). The density at the beginning of the instar was similar for all groups (SII, Day 1). Fed control larvae underwent the normal increase in density by the end of day 2 (SII, Day 2) while larvae fed only on day 1 (D-1-F) or starved (No-F) showed less growth of the epidermis during the same period. All larvae that moulted to instar III demonstrated the same density early on day 1 (SIII, Day 1), indicating that the larvae that were fed only on day 1 or starved grew less during the instar.

abdominal segments and thoracic legs (Williamson, 1982). The changes are moderate and expand on an already segmented state in which most of the cell types and tissues has been formed. A major transformation ensues at metamorphosis in crabs when the integument changes from a laterally to a dorso-ventrally compressed form.

Segment formation in the nauplius of *Artemia* begins when the pattern of cell replication changes from one that maintains a longitudinal file of epidermal cells to that of a transverse file (Freeman, 1986, 1989a,b). The first transverse file is positioned ventro-laterally in the middle of the presumptive first thoracic segment (Fig. 5). Segmentation proceeds in a anterior-posterior gradient beginning at segment 1 (Weisz, 1946, 1947; Anderson, 1967; Benesch, 1969; Freeman, 1989a,b). The maxillae (cephalon) develop at about the same rate as the first two segments. The first major segregation of integumental regions is the formation of the arthrodial membrane (AM) and the thoracopod bud. Cells of the limb bud continue to divide transversely at a faster rate than the AM cells until a well defined difference in the cell density is established early in instar II (metanauplius 1). This difference in the spatial arrangement of the cells is essential for the evagination process (Freeman, 1989b,c). Within two hours of achieving the differential cell density the AM cells change shape and undergo apolysis earlier than the posterior regions. As a result of the combination of these events the AM region invaginates as the thoracopod bud region evaginates and segment one is defined.

Formation of the thoracopod continues over the next several instars. Throughout this period the spatial and temporal manner of the cell replication is important for 1) outward expansion of the bud, 2) growth of the exopodites, endopodites, and epipodites, and 3) placement of cells for differentiation (Freeman, unpubl.). Special cell types differentiate during this period. The major tendinal cell forms at the end of instar II (Fig. 6) while smaller tendinal cells differentiate in concert with the segmental muscles during instars IV, V, and VI (Freeman, 1989a). The neural precursors leave the epithelium during

FIG. 5. The pattern of epidermal cell nuclei in the ventral epidermis of fixed instar II *Artemia* larvae. Nuclei are stained as described in Figure 2. Anterior is to the top. A longitudinal file is indicated by single arrowhead. The first transverse file of the first segment is indicated by paired arrowheads. (M= midline; Seg 1 = segment 1). Bar = 50 μm.

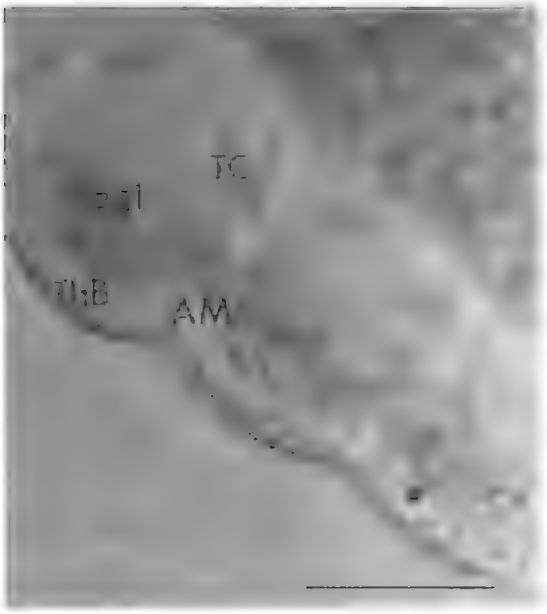

FIG. 6. The segmenting region of the presumptive thorax of live instar II *Artemia* larvae. The thoracopod limb bud (ThB) and the arthrodial membrane region (AM) of segment 1 (Seg1) are shown. The tendinal cell (TC) supports the invaginated AM region. Bar = 50 µm.

instar III or IV and their position within the epidermis may be identified as early as instar II. Finally, the setal cells differentiate during instar VI as the thoracopod is completed. Thus, growth in crustacean larvae leads not only to increased size at ecdysis, but also to segmental structures.

Although numerous papers have described the development of the larval appendages, none have investigated the cellular basis of this development. We must presume that the changes are, in general, similar to the kinds of morphogenetic changes observed in the thoracopod of brine shrimp. As a comparison, the AM region would correspond to the joints of the limbs and the tendinal and setal cells would develop in conjunction with the muscles and integumental structures, respectively. The control of this process is not understood at this time. The events may be preprogrammed within the developing epidermis, or, alternatively, the cells may be responding to extrinsic elements. Although the pattern of segmental development is relatively constant, there is some plasticity within the epidermis. This is demonstrated by the limb regeneration process in which non-limb epidermal cells can generate the entire limb within two moult cycles (Adiyodi, 1972).

Cellular activities other than growth and differentiation are involved in larval development and metamorphosis. Programmed cell death occurs in the antennae of barnacle cyprids following attachment and in the spines of crab zoeas during metamorphosis to the megalopa stage (Walley, 1969; Freeman and Costlow, 1983a,b). This cellular state appears to be developed during the larval period and is activated by hormonal mechanisms. Exactly how growth sets the stage for these events is unknown.

SUMMARY

The integument of the crustacean larva grows and assumes form by a pattern of epidermal cell replication and differentiation that is regulated in a spatial and temporal manner. Growth is independent of the moult cycle duration and moult-controlling hormones. Nutritional state is a strong determinant of cellular growth. The cells grow to a point that determines the growth potential that is realised at ecdysis when the new cuticle expands. Segmentation and limb formation result from the spatial pattern of cell replication within the epidermis. Future endeavors will explore the basis of the cellular events involved in integumental growth and development and the regulatory mechanisms that are involved in these processes.

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FEEDING AND GROWTH IN MERO-PLANKTONIC LARVAE OF *CALLINECTES SAPIDUS* (CRUSTACEA: PORTUNIDAE)

Capture of sufficient numbers of quality prey to meet the demands of metabolism and growth is a major factor in determining larval survival and recruitment success. Capture of prey is a function of prey density, predator and prey swimming speeds, and handling time. Handling time is related to prey type, size, and natural defences. Feeding rates were determined for the larval stages of the portunid crab, *Callinectes sapidus*, using laboratory and natural prey. Feeding was examined in both light and dark. Using laboratory determined values for energy efficiencies the proportion of daily standard metabolism and growth was determined.

Materials and Methods

Ovigerous *C. sapidus* were collected from the Chesapeake Bay. Upon hatching, the zoea were raised in 1000 ml culture bowls and fed with a diet of 15 000 *Branchionus plicatus*/L and 5000 *Artemia salina*/L. The zoea were transferred into fresh seawater and fed daily.

Prey were counted and placed into 500 ml bottles containing 200 ml of seawater with three replicates of each concentration of prey. A single replicate, without a zoea was used as a control. Prey included *A. salina*, (5, 25, 50, 100/L), *B.plicatus* (25, 50, 125, 250/L), and *Acartia tonsa* (25, 50, 125/L). Zoea of the appropriate stage were added and the bottles incubated at 25°C. After 10–12 hours illumination each zoea was transferred to a new bottle with the same concentrations of prey and incubated at 25°C in the dark. After each segment of the experiment the contents of each bottle were preserved and the remaining prey enumerated.

Wild *C. sapidus* megalopae were collected from plankton samples onboard the NOAA R/V Albatross IV. Prey items were sorted from additional plankton samples and identified to species and developmental stages. Shipboard feeding studies range in duration from 7–9 hours.

Feeding Experiments

When fed a combination of rotifers and *Artemia* nauplii, first and second stage larvae fed exclusively on rotifers. Visual observations suggest that the size of *Artemia* nauplii was the selection criteria. Ingestion of rotifers increased at the second stage and remained relatively stable through the megalopae stage. Third stage zoea occasionally captured *Artemia* nauplii, there was a significant increase in ingestion rates of *Artemia* by the fourth through sixth stage zoeae. A second increase during the last zoeal and the megalopa stage was also evident. Total carbon ingested was low through zoeal stage 3 then increased in parallel with the increase in ingestion of *Artemia* nauplii. Our original hypothesis was that small prey would be dropped from the diet or be captured in reduced number by late stage larvae due to handling costs. These data indicate that small prey contribute to the energetics of all stages. Consumption of *A. tonsa* nauplii was sufficient to meet 25–100% of energy needs for zoeal stages 1–6, but less than 50% of the needs of megalopae (Table 1)

TABLE 1. Daily ingestion of *Acartia tonsa* Stage 1 nauplii by *C. sapidus* larvae.

CONC/L	STAGE						
	1	2	3	4	5	6	Meg
25	5.3	4.9	3.8[1]	3.2[2]	5.7[3]	5.4[3]	5.4[3]
50	5.3	6.3	8.5	4.6[2]	11.6[3]	11.2[3]	9.9[3]
125	11.5	14.0	19.6	8.6[3]	28.6	36.2	33.5[3]

%Std Metabolism
1 — 50% < Std > 100%; 2 — 25% > Std > 50%; 3 — Std < 25% all others > 100% Std.

Wild megalopae fed the sixth copepodite stage of *Acartia tonsa* demonstrated a linear increase in feeding with concentration. In contrast, consumption of male and female *Centropages hamatus* displayed a sharp plateau at 25/L. Consumption of *C. hamatus* nauplii (I, II) plateaued at 50 to 100/L. Megalopae fed cladocerns, *Penilla* and *Evadne*, displayed a linear increase in feeding through the highest concentrations tested (100/L). Consumption of *Uca* sp. zoea plateaued at 25/L. The observed feeding rates are undoubtedly a function of prey size, handling time, and satiation. Based on the model of Gerritsen and Strickler (1979) larger prey were encountered, and captured less frequently. Handling time increases with size and natural defenses, i.e. spines of *Uca* zoea. Smaller first stage *C. sapidus* zoea with shorter spines are readily consumed by *C. sapidus* megalopae.

Diurnal Feeding Patterns

All zoeal stages fed at higher rates at night. Sulkin *et al.* (1979) demonstrated that swimming speeds of *C. sapidus* larvae followed a diurnal pattern with up to 60% increased swimming speeds at night. Based on the Gerritsen and Strickler (1979) model increased nighttime feeding can be explained by changes in swimming speed. Actual feeding rates for various concentrations of prey were equal to or less than predicted values. Lower observed rates may reflect prey handling time. Megalopae fed at higher rates during daylight hours when offered small prey (rotifers and *A. tonsa* nauplii). No difference in feeding rate was noted when large prey (*Artemia* nauplii) were offered. Calculation of Manly's (1974) B index for prey selection indicates that megalopae weakly select for *Artemia* nauplii during daylight hours. Selection for *Artemia* nauplii was enhanced at night. These data suggest that megalopae can consume small prey but rely more on visual prey identification than zoeal stages.

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ECOLOGICAL PHYSIOLOGY OF LARVAL EUPHAUSIIDS, *EUPHAUSIA SUPERBA* (EUPHAUSIACEA)

ROBIN M. ROSS AND LANGDON B. QUETIN

Ross, R.M. and Quetin, L.B. 1991 09 01: Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiacea). *Memoirs of the Queensland Museum* **31**: 321–333. Brisbane. ISSN 0079-8835.

Studies of the effects of environmental variability on the physiology of the early life history stages of the Antarctic krill, *Euphausia superba*, suggest that there are several critical periods during the first year of life that will affect survival, and thus recruitment of young krill into the adult population. The first critical period occurs during development of the non-feeding stages. Results of a collaborative modelling study suggest that release of embryos over warm deep water (250–400 m) is advantageous for these early larval stages. The geographical distribution of spawning populations combined with the observed pattern in sinking rates of embryos during development form a reproductive strategy that maximises survival of the early non-feeding stages. The first winter is the second critical period. Physiological condition (condition factor, lipid content, and growth rate) of larvae and juveniles is an index of their nutritional history and ability to survive and enter the adult population the following summer. Significant differences were found in the physiological condition of larvae collected during two winters which differed primarily in the degree of ice cover. Larvae in the heavy ice winter had higher growth rates, higher condition factor and more lipid. Although phytoplankton in the water column were scarce in both winters, ice biota were an additional possible source of food during the heavy ice winter. □ *Larval euphausiids, reproductive strategy, recruitment, physiological condition, critical period.*

Robin M. Ross and Langdon B. Quetin, Marine Science Institute, University of California at Santa Barbara, Santa Barbara, California 93106, USA; 11 February, 1991.

The most abundant euphausiid in the world's oceans, *Euphausia superba* Dana, the Antarctic krill, lives only in the Southern Ocean. This one species is often the dominant herbivore, unlike the case in most other oceans where copepods are the important grazers of phytoplankton primary production (Clarke,1985). Although Antarctic krill have a circumpolar distribution, high concentrations are found in only a few locations (Marr,1962; Laws, 1985).

Because krill are concentrated within the area of strong seasonal variation in pack ice cover, many investigators have postulated a close coupling between sea ice and krill populations due to associated food sources (Laws,1985; Quetin and Ross,1991). Sea ice provides a habitat in which microscopic plants and animals can live and grow. In addition fresh water from melting sea ice in the spring promotes water column stability and ice-edge blooms of phytoplankton several months before the open water blooms (Smith *et al.*, 1988). The annual advance and retreat of sea ice involves about 16 million km^2 of ocean surface, advancing from a minimum of 4 million km^2 in summer to a maximum of more than 20 million km^2 in late winter (Garrison and Siniff, 1986).

Growth and reproductive cycles of krill are keyed to the extreme seasonal cycle of primary production in the Antarctic caused by lack of light in the fall and winter (Quetin and Ross, 1991). Phytoplankton concentrations in the water column are also very low during these periods (0.1 to 0.2 µg chl a l^{-1} (Ross *et al.*, 1987; McClatchie, 1988)). Krill are long-lived for a pelagic crustacean, with an estimated maximum life span of seven or eight years (Ettershank, 1984; Siegel, 1987; Berman *et al.*, 1989). They probably begin to reproduce in their third summer. Although the ovary begins to mature in September and October, embryos are not released until the summer months, unlike most other Antarctic zooplankton that spawn in the spring. *E. superba* releases multiple batches of embryos throughout the spawning season if food supplies are sufficient (Ross and Quetin, 1983, 1986; Cuzin-Roudy, 1987). Spawning intensity will thus depend on regional environmental conditions. Once released, krill embryos sink rapidly out of the surface layers, hatching at 600 to 1000 m after 4.5 to 6 days (Marschall and Hirche, 1984; Quetin and Ross, 1984; Ross and Quetin, 1985). The newly hatched larvae then begin their ascent to the surface. The nonfeeding naupliar stages are usually found below 250 m, but Calyptopis 1 (C1), the first

larval stage with a mouth and feeding appendages, are usually found in the lighted surface layer with their food source – phytoplankton (Marschall, 1985). Embryos released in mid- to late December appear in the surface layers as Calyptopis I in early to mid-January, about the same time as the summer phytoplankton bloom. Thus, production of embryos and larvae is timed so CIs usually encounter food once they arrive at the surface. Larval developmental times through the three calyptopis and six furcilia stages depend on temperature and food availability. Estimates range from four months with excess food (Ikeda, 1985) to 10–11 months (mid-November) under winter conditions of low food and temperatures (Ross *et al.*, 1987; Elias, 1990).

Euphausia superba is a 'keystone' species in the Antarctic food web. Because of their high biomass and long life span, Antarctic krill provides a year-round food source. In fact they are often the primary food source for predators in this ecosystem (Laws, 1985). Turnover rates and recruitment success of *E. superba* are of particular interest because of its integral role in the dynamics of the Antarctic ecosystem and the possible impact of the commercial fishery for krill.

Fisheries researchers have long recognised that there are periods during early larval life that are critical to survival and to the recruitment success or failure of the year class (Hjort, 1914; May, 1974). More recently the same concept has been applied to crustacean larvae (Anger and Dawirs, 1981; Dawirs, 1987; Ross and Quetin, 1989). Identification of these critical periods and the possible consequences will allow us to predict variability in recruitment success from pertinent environmental factors.

In this paper we describe recent research that focuses on several factors that influence inter-annual variability in recruitment success of *E. superba*. By recruitment we mean the abundance of the age class 1+, the youngest subadults, at the beginning of their second summer. Clearly both reproductive output of adults, termed 'recruitment potential', and survival of the embryos and larvae impact the size of the year class, and are the sources of annual and geographical variability in recruitment. We will focus on two studies relevant to the success of early life history stages. Each study identifies one critical period in the first year of life. The approaches used avoid several of the logistical and theoretical problems inherent in sampling a mobile species with an ocean-wide and patchy distribution (Hamner *et al.*, 1983, 1984; Kanda *et al.*, 1982). These approaches yield valuable insight into recruitment dynamics and population maintenance, and are valuable techniques for those wishing to understand processes underlying variability in recruitment of other pelagic crustaceans.

The first study is a coupled biological/physical model that integrates laboratory measurements of the physiology and behaviour of the embryos and non-feeding larval stages and the actual vertical temperature structure of the waters near the Antarctic Peninsula (Hofmann *et al.*, in press). The objective was to simulate the descent/ascent cycle under different environmental conditions to explore questions about the relative success of spawning in different hydrographic regimes. The second study documents the effects of inter-annual variability in winter conditions on the physiological condition and thus survival of larvae and juveniles during their first winter (Quetin *et al.*, in press). Results from these two studies have helped us understand how environmental variability can lead to success or failure of a year class in *E. superba*.

DESCENT/ASCENT MODEL OF EARLY LIFE HISTORY

The first critical period in *E. superba*'s life history occurs during the descent/ascent cycle immediately after release of the embryo. Because the embryos and early larvae depend solely on internal reserves until C1 (Quetin and Ross, 1989), the reserves remaining at metamorphosis to C1 is a function of environmental temperature and its effect on metabolism and development. From our laboratory studies of starvation tolerance during this first feeding stage, we know that the point-of-no-return (PNR) ranges from 10 to 14 days (Ross and Quetin, 1989). After the PNR, even if food does become available, larvae are unable to recover from the effects of prolonged starvation. They fail to develop normally and eventually die. Thus the level of initial reserves, how fast they are used, and whether food is available shortly after the C1 reaches the surface determine larval success in this first critical period.

Time- and Temperature-Dependent Model

A time- and temperature-dependent model (Hofmann *et al.*, in press) was developed to answer several questions relevant to the use of internal reserves in the embryos and early larvae: (1) how do water mass characteristics affect the use of reserves?, (2) what are the hatching depths

and thus the depth from which the larvae have to ascend?, and (3) what reserves are still available when the larvae reach the surface? The model simulates the descent/ascent physiology and behaviour of embryo and early larval stages under different hydrographic conditions.

Development and definition of parameters of the model included careful consideration of the biology and physiology of the embryos and larvae of *E. superba*. Temperature affects developmental and metabolic rates (Ross *et al.*, 1988; Quetin and Ross, 1989), and also has a direct effect on the survival of the early life history stages. Embryos and larvae reared at -1°C do not continue development past the C1 stage (Ross *et al.*, 1988). We suggest that there may be a temperature sensitive period at some point during early development, and that a necessary developmental process does not take place at negative temperatures. Older stages survive and grow at these low temperatures, so we believe that it is only very early in development that exposure to low temperatures has deleterious effects. We also incorporated the effects of temperature and developmental stage on larval ascent rates (Ross *et al.*, 1985).

Because sinking rates of the embryos are critical to hatching depths, one important aspect of the model was to simulate the sinking rate pattern of the embryos during development (Quetin and Ross, 1984; Ross and Quetin, 1985). Changes observed in sinking rates imply changes in the density of the embryo during development. Initially embryos sink rapidly, 175 to 200 m d^{-1}. After about 24 h, however, sinking rates decrease to 50 to 60 m d^{-1}. Just prior to hatching, sinking rates increase to near initial rates. The sinking rate pattern was clear. What was not clear was whether this pattern was important in the life cycle of Antarctic krill, and what, if any advantages such a pattern would confer on the species. High initial velocities serve to remove embryos from schools of feeding adult krill, a probable predator, but the advantages of the subsequent decrease in sinking rates were not apparent.

With the model we derived depth profiles of the embryo and larva, and calculated the decrease in carbon during development under different temperature regimes. The simulated descent and ascent patterns are primarily a result of the effect of temperature on the developmental times of early life history stages. Development in *E. superba* is equiproportional, i.e. each developmental stage occupies the same proportionate amount of time relative to other stages at any constant temperature (Ross *et al.*, 1988). Because development in Antarctic krill is equiproportional, the biological processes included in the model are formulated in terms of fraction of total developmental time (Hofmann *et al.*, in press).

Simulations

Simulations of the descent/ascent cycle were run for constant temperatures and for actual vertical profiles from the waters west of the Antarctic Peninsula, particularly at locations around the South Shetland Islands and in the Bransfield Strait (Hofmann *et al.*, in press). In some parts of this region warm Circumpolar Deep Water (CDW), warmer than 0°C, is found between 200 and 600 m (Fig. 1). Except for seasonal warming of the surface waters, waters above and below the CDW are less than 0°C.

Simulations with constant temperatures show the role of temperature in determining the depth of hatching and the total time for the descent/ascent cycle (Hofmann *et al.*, in press). Longer developmental times affect the total sinking period and the time at high sinking rates. In addition, larvae swim more slowly at colder temperatures and have to ascend from deeper water, increasing the use of energy reserves before reaching the surface. Over deep cold water embryos hatch at depths >1000 m, and metamorphose to C1 within the lighted surface layer. At warmer temperatures krill larvae reach the surface well before metamorphosis into the first feeding stage, so have a longer time at the surface to find food before passing the PNR. However, even at -1°C less than 20% of the total carbon was used during the descent/ascent cycle (Hofmann *et al.*, in press), far less than the 50% level for the PNR (Ross and Quetin, 1989).

The simulations show that under no conditions do larvae pass the PNR before reaching the surface. However, if the underlying water is cold, larvae arrive at the surface with less time before they need to feed.

Simulations of the descent/ascent cycle with observed vertical temperature structures emphasised the role of temperature in controlling the hatching depth, the time spent on the bottom before hatching, and the amount of carbon used during the cycle (Hofmann *et al.*, in press). In regions characterised by warm CDW at depth, such as north of the South Shetland Islands where water warmer than 0°C is found at all depths greater than 150 m, embryos arrive in waters greater than 1°C about 1.5 d after release.

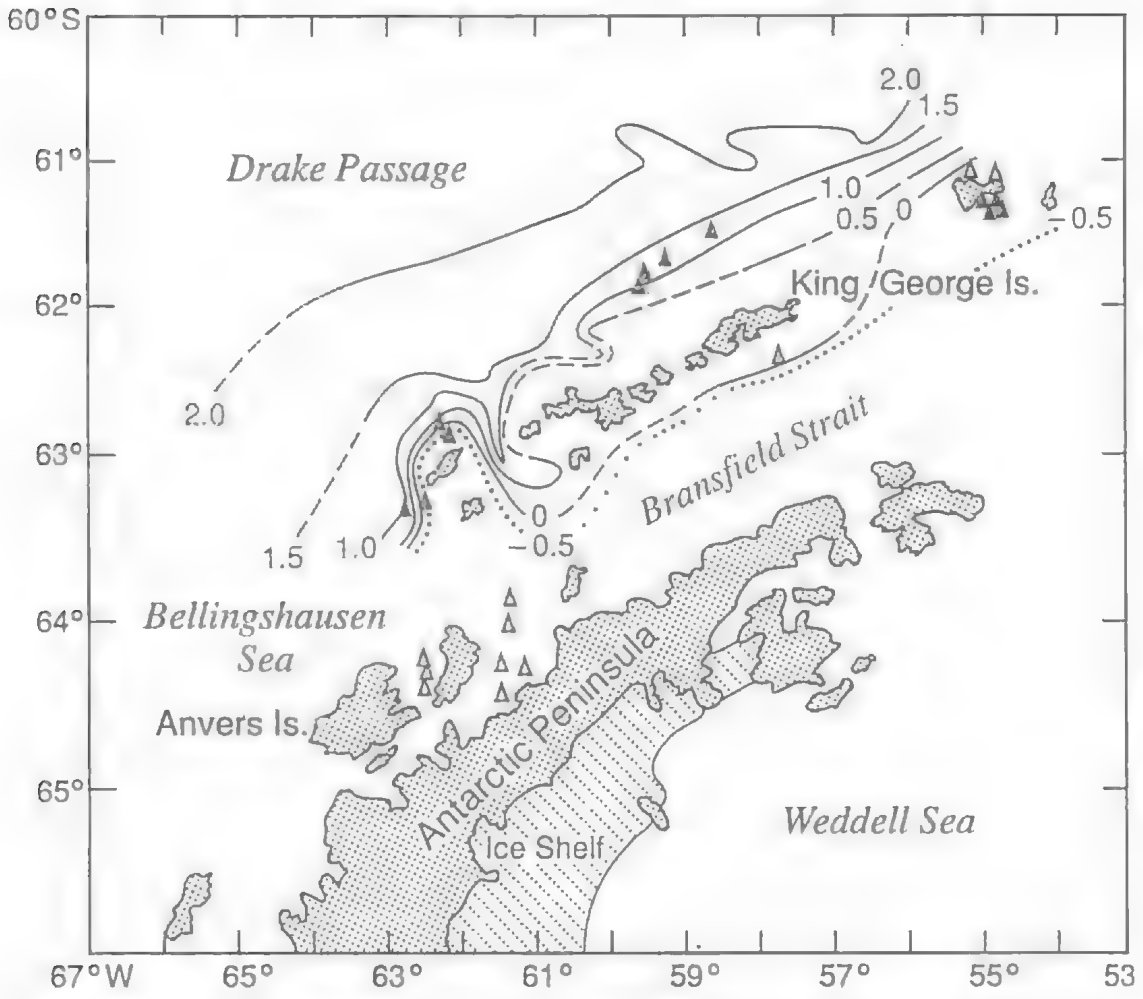

FIG. 1. Composite temperature distribution at 500 m in area of study. The distributions were constructed using historical temperature data collected during the last ten years from XBT and CTD observations. Contour interval is 0.5°C. Dashed lines indicate extrapolation of the temperature (data from Hofmann *et al.*, in press). Distributions of krill schools in 1982 containing gravid (▲) and nonreproducing females (Δ) are plotted (Quetin and Ross, 1984).

Because sinking rates are very low during the few days, embryos remain in this CDW until hatching, about 5 d after release and at 680 m (Fig. 2a). In the eastern Bransfield Strait, waters are less than -1°C at all depths. Hatching time is almost 10 days. Slower developmental times mean that the period of high initial sinking rates lasts longer, and embryos reach about 500 m before slowing down. Embryos hit bottom at 1000 m 2 days before hatching, and about 20% of embryonic development occurs on the bottom (Fig. 2b). In contrast embryos released north of the Shetland Islands hatch before they reach bottom. North of the South Shetland Islands, larvae complete their ascent in about 13 days, bringing the total descent/ascent cycle to 18 days. Total carbon use is about 2 µg C, 13% of initial values (Fig. 2c). Ascent rates in the eastern Bransfield Strait, however, are slower so larvae take about 25 days to complete the ascent, for a total descent/ascent time of 35 days, about twice as long as in the area north of the South Shetland Islands (Fig. 2d). Total carbon use throughout the descent/ascent cycle is about 26% of the initial carbon content of the embryo, again twice as much as for the area over CDW. This carbon usage brings the larvae much closer to the PNR of 7.5 µg C, or a 50% decrease, and gives the larvae fewer days in which to find food.

These simulations show firstly that embryos

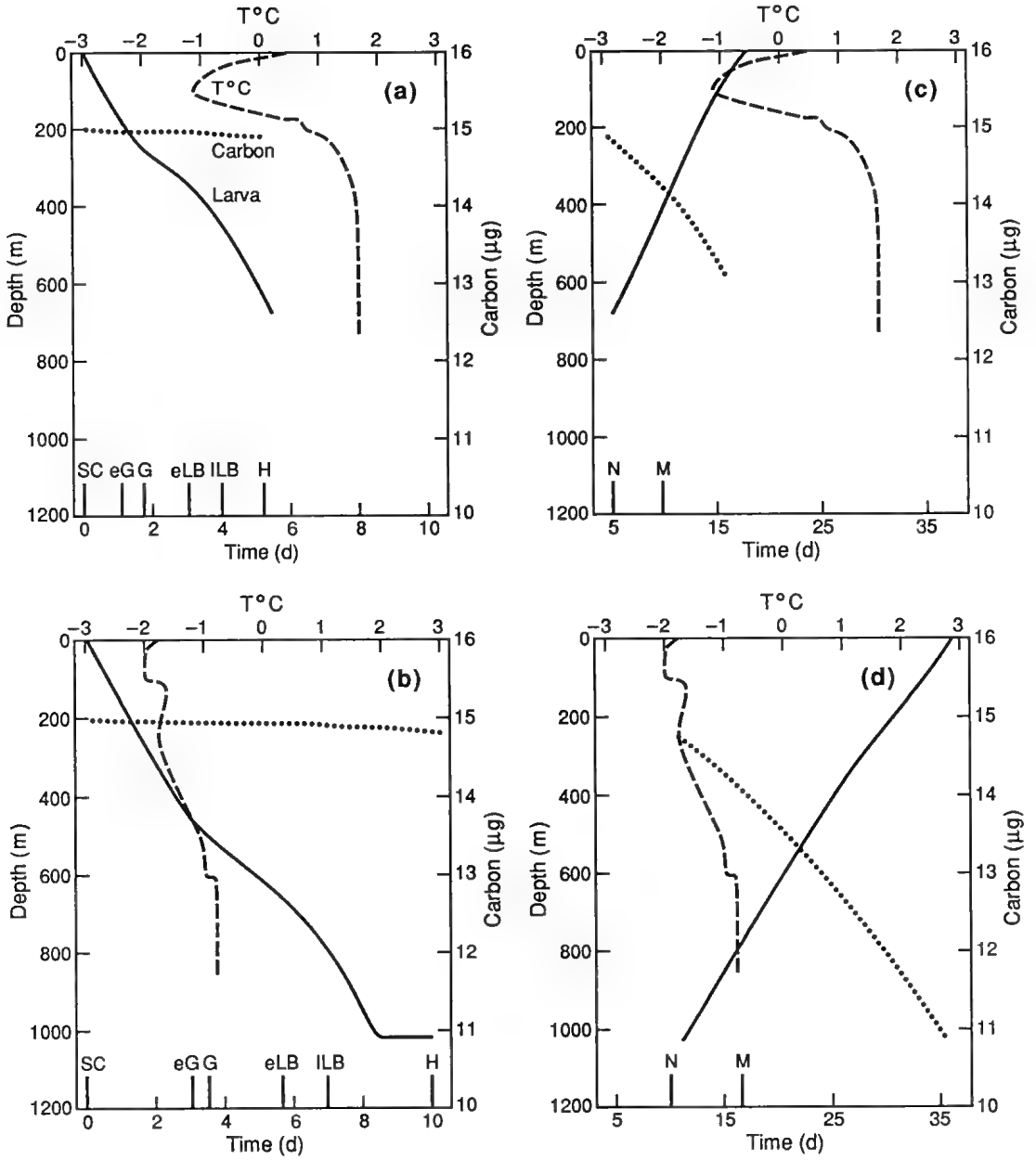

FIG. 2. Simulation of descent/ascent cycle of the embryos and larvae of *Euphausia superba* with vertical temperature structures typical of the region west of the Antarctic Peninsula and north of Anvers Island: temperature profile (dashed line), depth profile (solid line) and carbon content (dotted line) of the embryo or larva. a, descent of embryo, north of King George Island (60.8°S, 58.5°W). b, descent of embryo, eastern Bransfield Strait (63.5°S, 61.4°W). c, ascent of larva, north of King George Island (60.8°S, 58.5°W). d, ascent of larva, eastern Bransfield Strait (63.5°S, 61.4°W). (SC= single cell; eG= early gastrula; G= gastrula; eLB= early limb bud; lLB= late limb bud; H= hatch; N= nauplii; M= metanauplii) (from Hofmann *et al.*, in press).

developing at cold temperatures may spend some of their developmental time on the bottom, where they may be eaten by benthic animals or buried in sediment. Secondly, that larvae which complete the descent/ascent cycle at cold temperatures have less time after reaching the surface to find food before passing the PNR. And lastly, that most of early development in these regions with no CDW takes place at negative temperatures, so the probability is high that the early stages have been exposed to cold temperatures during the temperature sensitive period, and will never develop past C1. Embryos released in regions with CDW at depth will thus encounter more favourable conditions for continued development and maximising the reserves available after reaching the surface.

Reproductive Strategy

Several investigators have suggested that waters over the continental slope, and not shallow waters, are favourable spawning areas because early larval stages are regularly abundant on the continental slope and not on the shelf (Ichii, 1990). In addition gravid females are generally found in areas along the continental slope of the Antarctic Peninsula with high chlorophyll a concentrations (Quetin and Ross, 1984b; Endo *et al.*, 1986; Siegel, 1988; Capella *et al.*, in press). The energetic requirements of spawning suggest that food availability is a limiting factor for reproduction (Ross and Quetin, 1986) so the co-occurrence of spawning populations and high food concentrations is not surprising.

Since the spawning distribution of *E. superba* is spatially restricted relative to the distribution of the species, and the distribution of adult krill changes seasonally (Siegel, 1988), the question arises as to whether this spawning distribution is defined by hydrographic conditions as is true of many fishes (Sinclair, 1988). Siegel (1988) suggested that adult krill might actively migrate during summer into offshore waters, and back into shelf waters in the fall. Siegel speculated that this horizontal migration might reduce intraspecific food competition between adults and larvae. The results of the time- and temperature dependent model of the descent-ascent cycle provide an alternate hypothesis: spawning in regions with CDW at depth confers a reproductive advantage on the population and is thus part of a reproductive strategy.

In our study region west of the Antarctic Peninsula and northeast of Anvers Island, most schools of reproducing females are associated with CDW (Fig. 1 for 1981–82 season; Capella *et al.*, in press). Selection of particular waters by spawning krill cannot be thought of as fortuitous, particularly as the presence of mature females in continental slope waters over CDW appears to involve a seasonal horizontal migration. We suggest that a reproductive strategy has evolved in krill in response to its environment that is composed of at least two elements: the sinking rate pattern of the embryos, and the specific geographic pattern in population structure.

Fisheries scientists first recognised that reproductive strategies, including restricted spawning locations and horizontal migrations, play a definite role in population maintenance and persistence of a species in the late 1800s (Sinclair, 1988). Recently, these restricted distributions have been perceived in several groups of fishes as interactions between reproductive strategies and oceanographic conditions (Parrish *et al.*, 1981; Sherman *et al.*, 1986). The general concept is that the life cycle and structure of the population has evolved in response to specific oceanographic or spatial conditions to take advantage of features in the environment that enhance the survival of the early life history stages (Sinclair, 1988).

In the case of *E. superba*, the hypothesised reproductive strategy confers three advantages. (1) the depth of hatching and time on the bottom is minimised; (2) carbon use before metamorphosis into C1 is minimised, with obvious advantages in increasing the time before passing the PNR; and (3) the embryo and early larvae spend a minimal time in sub-zero waters, where they may be exposed to very cold temperatures during the postulated temperature sensitive period. Recruitment might be affected in several ways if embryos are not released above CDW, as may happen in years when changes in circulation patterns shift the surface distributions of adult krill in summer away from CDW (Capella *et al.*, in press). Mortality of both the larvae and embryos will be increased, because of the temperature sensitive period, deep hatching depths, and greater use of energy reserves. Those larvae that do reach the surface will be less tolerant of subsequent periods of low food availability.

In 1983–84 krill biomass in the study region (Fig. 1) was very low, as documented by the many researchers involved in SIBEX (Second International BIOMASS Experiment). This low biomass has been attributed to large scale population displacement due to hydrographic changes, and not to severe mortality in the adult population or to poor recruitment several years previously (Priddle *et al.*, 1988). The one area

where gravid females were consistently found was the Gerlache Strait (Capella *et al.*, in press). In this year when gravid females were few relative to other years, and not found in the traditional spawning locations over continental slopes and CDW, spawning success as judged by the abundance of the early life history stages was poor (Witek and Kittel, 1985).

PHYSIOLOGICAL CONDITION DURING THE FIRST WINTER

The second critical period is during the first winter, when larvae must survive a six-month period of very low food availability in the water column after a brief summer in which to build up energy reserves. Three lines of evidence suggest that low food conditions in the winter may present difficulties for the young-of-the-year who winter over primarily as late furcilia stages or early juveniles (Guzman, 1983; Ross *et al.*, 1987). First, unlike the adults who satisfy a significant portion of their winter energetic requirements with their lipid reserves (Quetin and Ross, 1991), the small amount of lipid accumulated by the larvae is not enough to contribute significantly to energetic requirements. In the fall about 2% of the wet weight of furcilia 6 and juvenile krill is lipid, compared to 6–8% for adults (Quetin and Ross, 1991; unpubl.). Second, furcilia do not have the same starvation capabilities as adults, supporting the evidence of low lipid reserves. Elias (1990) found that the mean survival time of late furcilia under starvation conditions varied with the age of the larvae (Table 1). The older larvae survived longer than younger larvae, but no stage could survive a winter with no food, unlike adults that can starve at least as long as 211 days (Ikeda and Dixon, 1982). Third, when furcilia larvae are maintained at food concentrations representative of the range of winter chlorophyll a concentrations in the water column west of the Antarctic Peninsula, larvae at the minimum concentrations (0.09 μg chl a L^{-1}) turned to cannibalism while larvae at maximum concentrations (0.28 μg chl a L^{-1}) did not (Elias, 1990). The lowest food concentrations appear to have triggered a change in nutritional mode, whether due to a change in behaviour of the larvae or a growing inability of the larvae to escape predation. In the field, however, cannibalism is less likely to occur than in the confined experimental vessels in the laboratory, and larvae may need to find other food sources. These results all suggest that if phytoplankton is the only food source, larvae and early juvenile krill will not be able to meet their energetic requirements in open water in the winter when phytoplankton levels are at or near winter minimum concentrations. Their continued development during the winter in the field, inability to tolerate long periods of starvation, and lack of lipid reserves all suggest that larvae need to feed in winter and must utilise a food source other than the phytoplankton in the water column.

TABLE 1. Starvation tolerance of late furcilia stages of *Euphausia superba*. Larvae were collected in April, and kept at ambient food and temperature for 2.5 months. In July individuals were isolated and maintained in filtered seawater until they died (Elias, 1990).

Stage at Collection	Mean Survival Time (Days)
Furcilia 4	29
Furcilia 5	59
Furcilia 6	84

Many have speculated about the role of ice and the ice-biota in the winter-over existence of *E. superba* (references in Quetin and Ross, 1991). But quantitative estimates of the importance of the sea ice as either a food source or a refuge from predation, and its impact on recruitment are lacking. We do know, however, that larvae and juveniles feed on the under side of the ice in areas of annual or smooth ice both winter and spring (Guzman, 1983; Kottmeier and Sullivan, 1987; Quetin and Ross, 1988; Daly and Macaulay, 1988; Marschall, 1988). If larval and juvenile krill are dependent on ice-biota in the winter, then their ability to survive the winter in good condition is indirectly dependent on the timing and extent of pack ice development during the winter. We hypothesise that the condition of the larval and juvenile krill and their winter over survival will be higher in years of greater pack ice when food availability is also greater.

Inter-annual variation in the maximum extent of pack ice in the winter is substantial (Zwally *et al.*, 1983; Smith *et al.*, 1988), and can be dramatic in the region west of the Antarctic Peninsula (Quetin and Ross, 1991). Timing is also variable. In some years pack ice is present by July, but in others not until late August. These inter-annual variations in pack ice extent allow us to test predictions based on our hypothesis. The impact of the first winter on recruitment of any one year class into the subadult population will depend on mortality due to either physiological factors or predation. Although quantifying winter-over

survival or recruitment into the subadult population is difficult, we can quantify the physiological parameters that affect survival probabilities. If predation on these young-of-the-year is low, physiological condition and survival should depend on many of the same environmental factors and be well correlated. Because most known predators select the larger size fraction of krill, predation pressure on the furcilia and juveniles will be low (Croxall *et al.*, 1988; Lowry *et al.*, 1988).

Physiological Condition

We define physiological condition as a group of three measurements that depend on the nutritional history of the larva: instantaneous growth rate, condition factor, and lipid content (Quetin *et al.*, in press). Instantaneous growth rate experiments are conducted on board ship for four days immediately after collection (Quetin and Ross, 1991). The brevity of the experiment ensures that these growth rates reflect the immediate previous nutritional history, and are not a laboratory artifact. Condition factor, a measure of organic matter per unit body volume, is more frequently used as an index of nutritional history for fish (Ehrlich *et al.*, 1976), but has occasionally been used for pelagic crustaceans (Omori, 1970; Durbin and Durbin, 1978). Condition factor (μg carbon per length cubed) is higher under better nutritional conditions. Lipid is commonly used by crustaceans as an energy reserve. Both condition factor and total lipid reflect longer term nutritional history than growth rate. These factors allow us to evaluate the relative 'fitness' of the larvae in the field and to distinguish good years from bad.

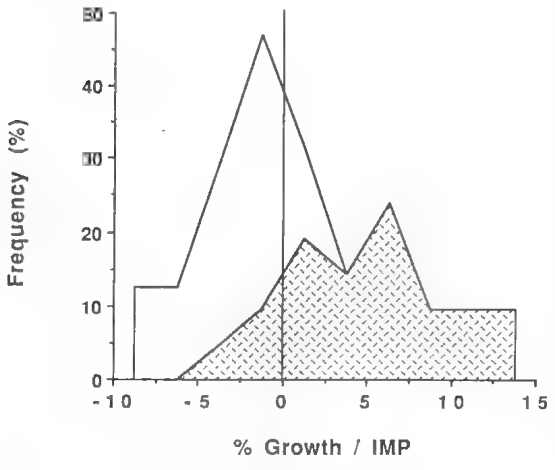

FIG. 3. Distribution of growth increments per intermolt of larvae of *Euphausia superba* in the winters of 1987 (flecked), with heavy pack ice, and 1989 (no fill), with light pack ice. The vertical line is the no-growth line.

Physiological condition of larval krill from the region west of the Antarctic Peninsula was measured in two winters that differed greatly in pack ice extent (Quetin *et al.*, in press). Pack ice was heavy in the winter of 1987 (9/10 and 10/10 over most of the region), but nearly non-existent in 1989 (Quetin and Ross, 1991). Other possible significant environmental variables were similar in the two years. Chlorophyll a concentrations in the water column were about 0.10 μg chl a L^{-1} in both years, but temperatures were slightly lower in the heavy ice year (-1.6 to -1.8°C *versus* -0.2 to -1.8°C). Larval krill were collected from open water with paired meter nets on a bongo frame with 505 μm mesh, and by divers from under the ice when ice was present. Stages collected ranged from furcilia 3 to 6 to small juvenile young-of-the-year.

Growth rates were positive in the heavy ice year, but negative in the light ice year (Fig. 3) (Quetin *et al.*, in press). Growth was 5.43 % per intermoult period in the heavy ice year (n = 21, SD = 4.95, 5 experiments), and -3.42% per intermoult period in the light ice year (n = 8, SD = 3.45, 3 experiments). Intermoult periods in the winter of light ice were twice those during the winter of heavy ice. Although these longer intermoult periods minimised actual shrinkage per day, growth rates were still zero or negative in winters of low ice.

Condition factor and lipid content were both significantly higher for all larval stages collected during the heavy ice year than during the light ice year (Fig. 4) (Quetin *et al.*, in press). The differences were greater for lipid than for condition factor. Total lipid in larvae from the light ice year was only about half that in the heavy ice year, whereas condition factors differed by about 20%. Thus in the winter of heavy pack ice larvae were in better physiological condition: they were growing, and contained more organic matter per volume and more lipid, some of which could presumably be used to meet energetic demands. Shrinkage, and use of lipid and body protein are all mechanisms used by adult krill to survive a winter of low food availability (Quetin and Ross, 1991). In the light ice year larvae appear to be using some of the same mechanisms to supply their energetic requirements as adults do in all years. However, we know that larvae cannot survive starvation for as long as adults. If very low food concentrations continue for the entire winter, the

larvae will continue to deplete their body lipid and protein, and may pass the PNR. Once past the PNR these larvae will not recruit into the juvenile and subadult population in the late spring and early summer.

Although the mechanisms underlying these correlations are still largely unknown, the difference in physiological condition in larvae from a heavy and a light ice winter suggests that enhancement of winter-over survival is mediated by the presence of pack ice. The most probable cause is the presence of an alternate food source which allows the young-of-the-year to continue to grow and develop throughout the winter without using their body reserves to meet energetic requirements.

INTER-ANNUAL VARIABILITY IN RECRUITMENT

Variability in recruitment of a zooplankton population in any one region is caused by a number of factors. The abundance of any one year class is dependent on both the number of embryos actually released and how many of those embryos survive the first year. Spawning intensity in the region varies with the number of reproducing females and the number of embryos each produces. Thus spawning intensity in *E. superba* will depend not only on large scale hydrographic changes that cause regional changes in population structure (Priddle *et al.*, 1988), but also the amount and timing of food availability (Ross and Quetin, 1986). We will term this factor in the recruitment equation 'recruitment potential'. Mortality of the young-of-the-year is the other major factor.

There is evidence for significant inter-annual variability in 'recruitment potential' of *E. superba* in the region west of the Antarctic Peninsula and north of Anvers Island. Brinton *et al.* (1986, 1987) reviewed available information on early larval and gravid female abundance and distribution, and suggested that eight of the twelve years from 1965 to 1984 for which we have information have been successful spawning years for *E. superba*. In the years with poor 'recruitment potential' one or more of the following was observed: gravid females were rare in the area (1982–83; 1983–84); spawning was delayed (1977–78; 1983–84); or larval development was retarded (1966–67). Larval abundance in one of the 'successful' years during this period (1980–81) was much greater than in either 1983–84 (Brinton *et al.*, 1987) or 1976 or 1978 (Hempel, 1985). The 1980–81 year

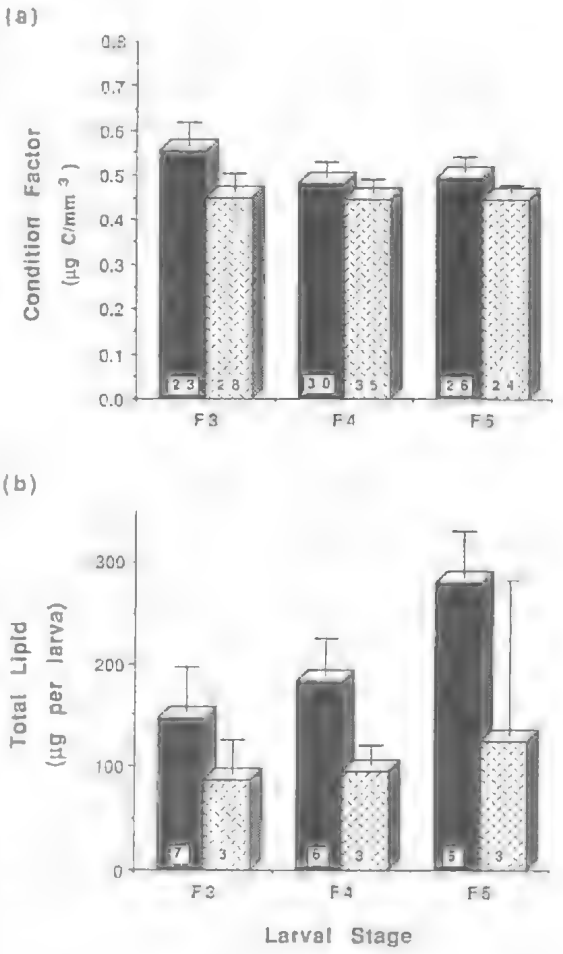

FIG. 4. Condition of the three late furcilia stages of *Euphausia superba* in the winters of 1987 (solid), with heavy pack ice, and 1989 (flecked), with light pack ice. a, condition factor in µg carbon mm^{-3}. b, total lipid in µg $larva^{-1}$. Lipid content of a group of 5 to 8 individuals of the same stage was determined with a charring technique (Marsh and Weinstein, 1966). Error bars represent standard deviations. Numbers in bars are numbers of individuals for condition factor or number of samples of groups of five to eight of the same stage for total lipid.

of high 'recruitment potential' followed a cold winter, as evidenced by extremely cold air temperatures in this region (Rakusa-Suszczewski, 1988) and heavy winter pack ice in the Weddell sector (Zwally *et al.*, 1983) (Fig. 5). The poor 'recruitment potential' years appear to coincide or lag one year behind El Nino Southern Oscillation (ENSO) events (1965–66; 1972–73; 1976–77; 1982–83 (Sahrhage, 1988)) and occur after warmer winters.

Evidence for interannual variability in mortality of the later larval stages is scarce. With a long-lived species such as *E. superba*, only when recruitment fails in several years in succession will we be able to detect differences in absolute abundance (Priddle *et al.*, 1988). However, age-specific differences in mortality rates will lead to predictable changes in length-frequency distributions. For instance, high mortality rates for young-of-the-year in the winter would lead to a length-frequency distribution dominated by older, larger krill the following summer, and low mortality rates to a high-proportion of the population as juveniles or sub-adults. Using such an analysis to separate out the effects of 'recruitment potential' and winter-over survival, however, requires a good estimate of spawning intensity. Siegel (1988) attempted to follow certain year classes from an analysis of the length-frequency distribution of krill catches. Siegel (1988) suggested that larvae from the 1979–80 season were scarce in later years, but larvae from the 1980–81 season were abundant the following year. The first winter for both these year classes, i.e. the winters of 1980 and 1981, was cold with heavy ice pack (Fig. 5). Yet recruitment differed significantly. One possible factor is that mean air temperatures in this region in the winter of 1979 were warmer than usual, and reflect the low ice cover that winter and spring (Zwally *et al.*, 1983). Thus winter and spring conditions were not favourable for 'recruitment potential' in 1979–80, yet were favourable in 1980–81. The year class of 1980–81 had high 'recruitment potential' and probably high winter-over survival.

The existing evidence thus suggests that 'recruitment potential' and winter-over survival both vary from year to year, and that both appear to be correlated with environmental conditions during the winter and early spring. However, a decrease in one is not necessarily followed by a decrease in the other. 'Recruitment potential' reflects environmental conditions before the spawning season, and winter survival reflects conditions the winter after the spawning season.

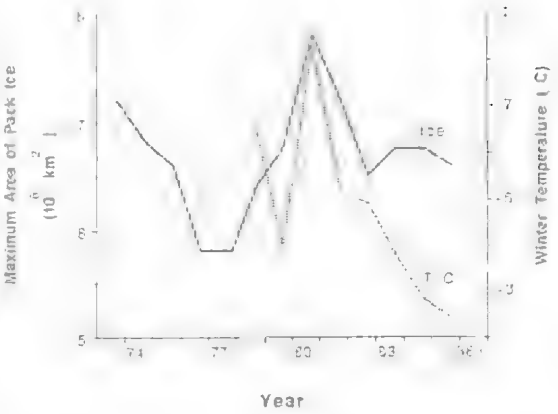

FIG. 5. Maximum extent of pack ice in the Weddell Sea sector (September, October) (Zwally *et al.*, 1983; Smith *et al.*, 1988) and mean winter (June, July, August and September) air temperatures at Admiralty Bay, King George Island (Rakusa-Suszczewski, 1988) from 1973 to 1986.

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The contributions of our collaborators in these research efforts were invaluable. E. Hofmann and J. Capella created the time-and temperature-dependent model with physiological and behavioral data provided by ourselves, and first recognised the connection between the presence of Circumpolar Deep Water and spawning populations. M. Amsler is a valued member of our research team, and was of enormous assistance in organising and conducting the field work in both winters. The work would not have been possible without the assistance of volunteers on both cruises: 1987, D. Martin, M. Elias, W. Connelly, 0. Schofield, D. Steinberg, J. Hydanus; 1989, A. Martinez, E. Stephens, D. Martin, R. Clark IV, J. Aldstadt, C. Stenler, W. Brock, D. Boylan. We also thank the captains and crews of the Polar Duke during two winter cruises. The research reviewed was supported by NSF, Division of Polar Programs, with grants to E. Hofmann (DP-85-15486) and to R. Ross and L. Quetin (DPP-85-1 8872).

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A SATELLITE TRACKED DRIFTER WITH A VERTICALLY MIGRATING DROGUE FOR STUDIES OF LARVAL DISPERSAL

Potential larval dispersal is a function of time in the plankton and hydrographic regimes. This is further complicated by the interaction between environmental cues and larval responses which dictate changes in vertical distribution of the larvae within that hydrographic milieu. These changes in distribution can be ontogenetic, cyclic (diurnal or tidal) or a combination of both. The vertical distribution of the larvae is usually measured by discrete sampling over a very short time frame (Rimmer and Phillips, 1979; Rothlisberg, 1982). Because long-term, vertically-stratified sampling of larvae and known environmental stimuli are impracticable, the advection of larvae is extrapolated from these limited observations using a mean larval behaviour and a fixed circulation (Phillips and Williams, 1986) or estimated from models of both the larval behaviour and hydrographic regime (Rothlisberg *et al.*, 1983). A more direct approach to estimating dispersal pathways and potential is a device that mimics the larval behaviour in situ and can be monitored continuously, remotely and over the length of the planktonic larval life. This was the motivation for the satellite-tracked drifter with a vertically migrating drogue.

The current drifter was designed to estimate the larval dispersal of the ornate rock lobster *Panulirus ornatus*, in the northern Coral Sea and Gulf of Papua. We have used the behaviour of *P. cygnus* larvae (Rimmer and Phillips, 1979) as there have been no studies of the larval ecology of *P. ornatus*. Phyllosomes of *P. cygnus* undergo diurnal vertical migrations of 100 to 150 m, are planktonic for periods up to one year and potentially disperse over oceanic basins. The drogue has a fixed diurnal migration pattern, activated by light intensity, migrating at 10 m min^{-1}, between the surface at night and 130 m by day. The drogue is fitted with a sensor so its depth can be monitored. The drifter uses solar power to operate the winch and control electronics while the telemetry transmitter uses dry cell batteries for power. The life span of the drifter, as dictated by battery capacity, is approximately one year. The geographic position of the drifter, the depth of the drogue, surface temperature, sea state and battery voltage are transmitted 6 to 8 times per day by CLS-Argos tracking telemetry. Sea trials of the device are underway and deployment in the Gulf of Papua is planned for December 1990.

Future models of the drifter will 'react' to the environment and will be able to 'behave' more realistically. They will be programmed with taxon specific behaviour regimes and ontogenetic changes in behaviour will also be possible. An *in situ* temperature sensor will monitor the environment and control the 'growth rate' of larvae and their attendant behaviour. An *in situ* light meter will allow the drogue to follow isolumes and react to variable light intensity and penetration. An echo sounder will allow the drogue to migrate near the bottom, permitting movement through shallow water and entrance into nursery grounds.

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METABOLIC RESPONSES OF SOME ESTUARINE CRUSTACEAN LARVAE TO SALINITY VARIATION

Estuarine systems, characterised by large variations in environmental parameters, are widely recognised both as areas of high productivity and as rearing grounds for a variety of marine and freshwater crustaceans. In order to become successfully adapted to this special environment, larval crustaceans must be able to tolerate such variations, specially in salinity. Although the influence of environmental parameters on the metabolic rate of adult crustaceans has been the subject of several studies, few papers have dealt with larvae.

This paper presents data on some crustacean larvae which inhabit estuarine waters along the coast of the State of Sao Paulo, Brazil, the adults of which live in very different biotopes. The metabolic rates of these larvae were determined in different salinities (0.2, 7, 14, 21, 28 and 35 ppt) at 20°C, using Cartesian diver microrespirometers. Larvae of the oligohaline or freshwater species showed salinity independent metabolic rates over the salinity range 7–28 ppt while larvae of the mesohaline species regulate metabolism over a higher salinity range, 14–35 ppt. Larvae of the marine species (euhaline), however, regulated metabolism over the salinity range 21–35 ppt. Such results indicate that the larvae of these species, although developing in the same biotope, respond differently to salinity variations, revealing in some cases, greater metabolic regulation in the salinity range approximating that of the adult environment.

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FACETOTECTA ('Y-LARVAE'): ONE DAY'S CATCH IN OKINAWA, JAPAN (CRUSTACEA: MAXILLOPODA)

The Facetotecta ('nauplius y' and 'cypris y,' adults unknown) is classified together with the Cirripedia and Ascothoracida in the maxillopodan subclass Thecostraca. These 'Y-larvae' were considered rare curiosities until Itô began a series of reports on the estimated 30 species he has found in Tanabe Bay, Honshu, Japan. Itô's (1986, 1987a, b, 1990, in press) are the only previously published descriptions of Pacific Facetotecta. In order to confirm whether y-larvae are similarly abundant and diverse elsewhere, I have been collecting them in Okinawa in the Ryukyu Islands.

Methods

Four plankton samples were taken with a small, fine-mesh net during a 24-hour period on 31 Aug and 1 Sept 1989 from the pier of the Sesoko Marine Science Center on Sesoko-jima, Okinawa (26°38.5'N, 127°51.5'E). All y-larvae were immediately pipetted into a common holding dish and, after the last sample, fixed in formalin. Later the nauplii were processed for SEM: dehydration in ethanol, critical point drying from liquid CO_2, mounting on stubs, coating with gold. Most of the 'long-tailed' specimens were lost, so 15 similar ones from a sample taken on 5 Sept 1989 were substituted. In all, 103 nauplii were examined in a Hitachi S-510 scanning electron microscope and most were photographed.

Results and Discussion

Fifteen distinct 'forms' of nauplius y (1–22 specimens each), some with two or three putative instars, were recognised. Facetotectans are thus diverse and abundant in Okinawa, and Tanabe Bay is not unique in this regard. However, not every 'form' may represent a distinct species and instars may not have been surely discriminated. Such determinations require the rearing of individual larvae through all their stages (Itô, in press).

Of the 15 Okinawan 'forms', perhaps five also occur in Tanabe Bay. Two correspond to two supposed instars of nauplius y Pacific type I (Itô, 1986), that probably actually belong to distinct species. These and three undescribed but similar 'forms' are the only likely planktotrophs in the lot. One 'form' corresponds to nauplius y type VIII-c (Itô, 1987b). Two of the three 'long-tailed forms' may correspond to nauplius y type XI (Itô, 1987a) and an unnamed type (Itô, in press: fig. 1), but this is less certain. Of the six other undescribed Okinawan 'forms,' four 'whale-shaped' ones may represent as few as one or two species.

Itô (1990, in press) shows that at least five naupliar instars may be expected, but no more than three were recognised for any 'form' here.

Some morphological observations may be important in defining the Facetotecta. Three of the present 'forms' have few or no cuticular ridges on the cephalic shield; however, many ridge pattern elements are clearly common to all the other 'forms.' Only the five supposedly planktotrophic 'forms' have a dorsocaudal organ. Frontal filaments are absent except possibly as a pair of swellings in two 'forms,' and rudimentary maxillules are also absent.

This is the first extensive SEM survey of the nauplii of any crustacean group.

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ORIGIN AND BEHAVIOUR OF POST-LARVAL PENAEID PRAWNS IN TWO ESTUARIES ON THE NATAL COAST OF SOUTH AFRICA

The northern Natal coast is the southern limit of commercially viable populations of penaeid prawns on the east coast of Africa. The major centres of abundance are the St Lucia lakes and Richards Bay and the offshore Tugela Bank. The major commercial species are *Penaeus indicus*, *Metapenacus monoceros* and *P. monodon*.

The Natal fishery is associated with soft substrata and turbid water conditions. This type of habitat is relatively common in Natal estuaries but is less common in the offshore habitat where the shallow Tugela Bank is separated from the Mocambique grounds by some 400 km of deep, clear water overlying sandy substrata.

Links between Mocambique and Natal prawn stocks are unclear. The southward flowing Agulhas current could provide a larval input which would influence population fluctuations in Natal. There is however, no information on the occurrence of post-larvae in this part of the Agulhas current. As there does not appear to be any indication that post-larvae are capable of selecting specific estuaries it was assumed that larvae migrating into estuaries are representative of offshore populations. Plankton samples were taken overnight during spring flood tides at St Lucia on the northern edge of the Tugela Bank and also at the Agulhas dominated Kosi Bay just south of the Mocambique border. Some ebb tide sampling was also done to provide comparative data on tidal behaviour in the turbid St Lucia and clear Kosi systems.

Post-larvae of *P. japonicus*, a commercially unimportant species in Natal, totally dominated samples at Kosi Bay. Similar densities of this species were recorded at St Lucia but it was matched by the numbers of *P. indicus* while *P. monodon*, *P. semisulcatus* and *M. monoceros* were also regularly present. The numbers of *P. japonicus* at St Lucia suggest a possible influence of the Agulhas current on recruitment but the other species recorded in this system indicate an additional larval source. It is significant that the additional species are commercially important and that these appear to be derived from Natal waters rather than further north.

Only *P. japonicus* occurred in sufficient numbers to allow comparison of post-larval tidal behaviour in both areas. This psammophilic species was present in the water column over flood and ebb tides in the muddy St Lucia system but in negligible numbers over ebb tides in the sandy Kosi estuary. Movement into the water column thus seems to be influenced not only by the presence of tidal currents but also by the nature and suitability of the substratum.

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LABORATORY REARED LARVAL STAGES OF A MANGROVE CRAB, *SESARMA EDWARDSI* DE MAN 1887 (DECAPODA : GRAPSIDAE)

The complete larval development of a mangrove crab, *Sesarma edwardsi*, has been described from animals reared under laboratory conditions at a temperature of 26 ± 1°C and a salinity of 25 p.p.t. Larvae were fed freshly hatched *Artemia* nauplii daily. Four zoeal stages and a megalopa appeared prior to metamorphosis to the first crab stage. Development time through to this stage was 16 days, intervals between zoeal stages being 2 days except the final zoea (3 days) and megalopa (7 days). Unlike other species of *Sesarma*, brightly coloured chromatophores throughout the body in all larval stages are characteristic of *S. edwardsi*. The setal formula of 0, 0, 6 on the endopod of the second maxilliped of zoeal stages, and the presence of 4 lateral setae on the telson separate *S. edwardsi* from others of the genus so far described.

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PENAEID PRAWN RECRUITMENT: GEOGRAPHIC COMPARISON OF RECRUITMENT PATTERNS WITHIN THE INDO-WEST PACIFIC REGION

D.J. STAPLES

Staples, D.J. 1991 09 01: Penaeid prawn recruitment: geographic comparison of recruitment patterns within the Indo-West Pacific region. *Memoirs of the Queensland Museum* 31: 337–348. Brisbane. ISSN 0079-8835.

Despite many years of study, the basic seasonal dynamics and life-history parameters, such as longevity and generation time, still remain poorly understood for many penaeid prawns. Even in the better known commercially important species, considerable controversy still exists as to whether the generation time is one year or six months. This confusion appears to arise mainly from the extreme variability seen both between species and within species in the seasonal dynamics of migrations, growth and abundance which underlies the seasonal cycles of spawning and recruitment at the population level. These in turn have been modified, in many cases, by the impact of fishing, making comparisons of natural cycles extremely difficult. In an attempt to understand this variability, trends in the timing of the main life history events were related to factors which change with increasing latitude (and depth). An equatorial pattern of two generations per year provides the basis for the description of many of the variants seen throughout each species range. Farther from the equator, one or other of the generations tends to dominate, resulting in what is essentially a one year generation time. In more temperate waters, most penaeids become strictly annual with one spawning period and one recruitment period each year. A study of these changes with latitude in *Penaeus merguiensis* is used as an example to demonstrate these latitudinal differences. □ *Penaeids, recruitment, life history, Indo-West Pacific.*

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The world's yield of penaeid prawns is now in excess of 700,000 tons (Garcia, 1988) and forms one of the world's most valuable fisheries. Despite this important position, the outlook for the fishery as a whole is not good. The high price of prawns on the export market during the 1970s and 1980s has stimulated rapid development with inadequate controls. This has lead to excessive fishing effort, over capitalisation, excessive production costs and in some cases depleted stocks. Because many of these fisheries operate in developing countries, reliable stock assessments are few but those available have indicated that the stocks are overexploited resulting in less than optimal returns for the effort expended in their capture. Growth overfishing (capture of individuals at size too small to produce the optimal yield) is common and despite earlier assumptions concerning the resilience of prawn stocks to fishing pressure, recruitment overfishing (fishing effort at a level which will depress future spawning stocks and recruitment) has also been detected in several stocks (Penn and Caputi, 1985). Management measures addressing these problems include the limitation of fishing in space and time (area and seasonal closures) and limitation of effort through input controls. Both the detection of overfishing and subsequent remedial action require detailed knowledge of the dynamics of the prawn's life history in terms of the distribution of the different life-history stages in both space and time. This information is not readily available for many of the world's prawn stocks.

The basic life cycle of penaeid prawns appears to be relatively uniform across the family; all shed eggs directly into the water column, pass through a relatively short larval life consisting of three stages (nauplius, protozoea, and mysis), and develop through postlarval, juvenile, subadult and adult stages. In contrast, the spatial and temporal distribution of these stages is extremely variable. Although many of the more commercially important species spawn at sea and spend their postlarval and juvenile stages in estuarine and nearshore coastal waters, there is a broad continuum of cycles ranging from species which are entirely estuarine to those which are entirely marine (Kutkuhn, 1966; Dall *et al.*, 1990). The temporal variability appears to be even greater.

In this paper I will concentrate on the temporal dynamics of penaeid life histories, starting with

a detailed examination of one species (*Penaeus merguiensis*) in Australia, moving on to a comparison of life history patterns of other species throughout the world and finally give a brief account of a comparative study on the seasonality of (*P. merguiensis*) across the Indo-West Pacific. In this way, I hope to provide an assessment of the current knowledge of penaeid life histories as well as future research needed in this field.

PENAEUS MERGUIENSIS IN AUSTRALIA

Munro (1975) provided the first detailed account of the life history of *P. merguiensis* in the Gulf of Carpentaria, Australia, based on field sampling of adult prawns in the south eastern Gulf and juveniles in one of the adjacent mangrove estuaries. Because Munro observed spawning and immigration of postlarvae to occur only in spring, he concluded that the cycle was essentially annual. In a more detailed analysis of *P. merguiensis* from a range of locations, Staples (1979) showed that a simple annual cycle as suggested by Munro, could not explain the rather complex geographical differences in the seasonal timing of postlarval and juvenile prawns that occurred in different areas of the Gulf. Four areas in the Gulf, each characterised by its own pattern of seasonality were recognised and it was suggested that these geographical differences could be explained on the basis of semi-annual cycle of spawning, with peaks in spring and autumn. This pattern of spawning was later confirmed by Crocos and Kerr (1983). Geographical differences in the differential survival of these generations in different areas of the Gulf suggested that the life cycle in the north was dominated by the survival through to juveniles of the autumn spawning whereas the life cycle in south was more influenced by the higher survival of the spring generation. A further complicating factor was that juvenile *P. merguiensis* emigrate out of the estuary to offshore waters mainly during periods of rain (Staples and Vance, 1986) and because rainfall is extremely seasonal in the Gulf of Carpentaria (only one wet season each year) only one pulse of prawns recruit each year into offshore waters.

Based on more recent evidence the life history pattern was reviewed by Rothlisberg *et al.* (1985). In the southern Gulf, larvae from the spring spawning period reach the estuaries as postlarvae 2–3 weeks after hatching and spend 2–4 months as juveniles before emigrating offshore during the summer wet season. After approximately 2 months migration offshore, subadult prawns recruit into the offshore fishery (4–7 months old) and form the basis of the autumn fishery. A proportion of these young recruits become sexually mature and spawn giving rise to the autumn larvae. Most of these larvae never reach the estuarine nursery areas (Rothlisberg *et al.*, 1983) and it is the prawns which escape the autumn fishery and survive through to the next spring which provide the spawning stock to repeat the cycle (Fig. 1). In the north the spring component of the cycle is similar but many more larvae produced from the autumn spawning recruit into the estuaries. More recent information on the seasonal distribution of postlarvae in the northern areas, suggests that the strength of the spring generation of postlarvae and juveniles may have been underestimated in previous studies (Vance *et al.*, 1990) but the general conclu-

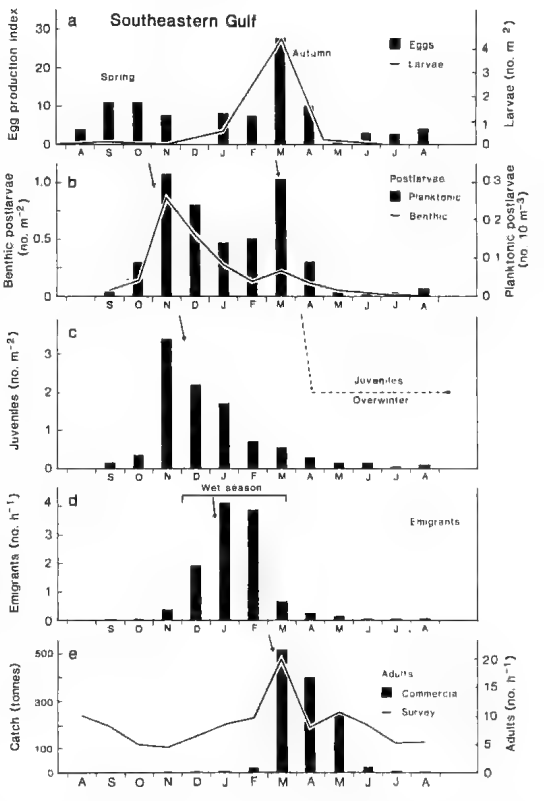

FIG. 1, Seasonal dynamics in the abundance of the main life-history stages of *Penaeus merguiensis* in the southeast Gulf of Carpentaria (from Rothlisberg *et al.*, 1985).

sions have remained unchanged. Because of the unimodal rainfall pattern and offshore recruitment, autumn juveniles contribute less to the offshore fishery than those from the spring generation (Fig. 2).

Rothlisberg *et al.* (1985) suggest that the life history seen in the Gulf was derived from a basic pattern of two equal spring and autumn populations, each contributing to the next generation 6 months later with some survivors of this group contributing again in 12 months, i.e. two interlocking cycles of 6 and 12 months. This implies two wet seasons per year and two periods of offshore recruitment. Another notable feature of *P. merguiensis* in the Gulf is the mismatch between the size of the spawning population and the size of its contribution to the next generation. This is especially apparent in the southern Gulf where the extremely small spring population of females gives rise to the large number of postlarvae and the subsequent offshore fishery. Garcia (1988) has argued that because of the extremely heavy exploitation of *P. merguiensis*, (approximately 80% of the population is caught in the 2 months following recruitment (Lucas *et al.*, 1979), this represents a severe distortion of the basic life cycle, and without fishing the spring spawning would constitute the main reproductive input.

Because the life history of *P. merguiensis* is composed of two interlocking cycles with periods of 6 months and 12 months, there has been some controversy in the literature about the generation time for this species and penaeids in general. At an individual level, generation time is defined as the time between egg and first spawning is 6 months. At the population level, Garcia (1988) argues that the generation time should be defined as the time between the average date of birth of the main generation and the average date of birth of the main group of offspring from the generation. Using this definition, the main generation in the Gulf is obviously the spring generation and the generation time is 12 months.

REVIEW OF WORLD LIFE HISTORY PATTERNS

The life span of most coastal penaeids is between 1 and 2 years in the tropics but is probably longer in temperate waters. The length of time spent in the different life history stages is a function of the growth rate. Environmental factors such as temperature that vary with season,

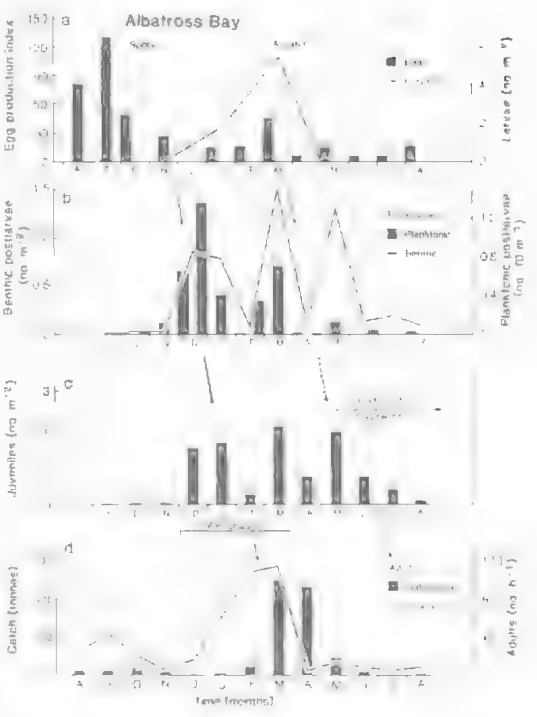

FIG. 2, Seasonal dynamics in the abundance of the main life-history stages of *Penaeus merguiensis* in Albatross Bay, northeast Gulf of Carpentaria (from Rothlisberg *et al.*, 1985).

latitude and depth, therefore, also control the time to first maturity, and consequently the generation time. Latitudinal trends reflecting changes in temperature and rainfall patterns, therefore, are extremely important in considering penaeid life history patterns. Similar trends in life-history parameters will also occur with changes in depth. In an attempt to standardise for these effects, I will consider the three latitudinal zones: equatorial (±5°, tropical/subtropical (5–25°) and temperate (>25°), recognising that this is a oversimplification and will not account for areas influenced by local events such as upwellings. However, despite these local events, the classification does assist in the interpretation of observed life-history patterns.

Equatorial Pattern

Little information is available on penaeids in equatorial regions. However, close to the equator, individual prawns appear to be capable of spawning all year round (Hall, 1962), although seasonal cycles in abundance in prawns will

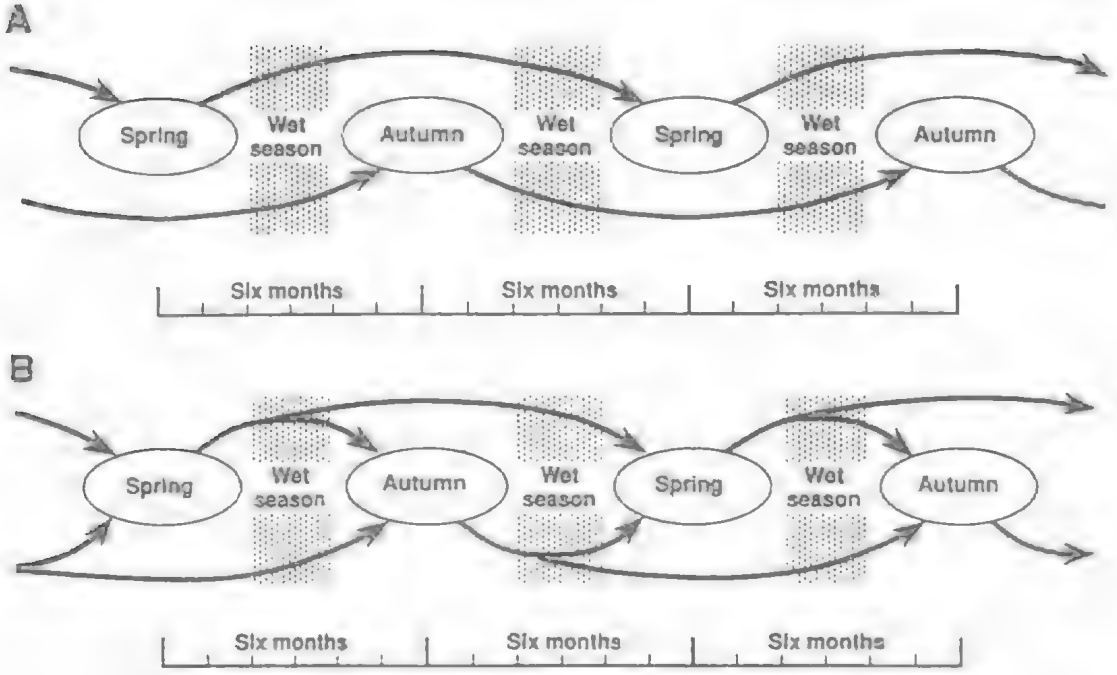

FIG. 3. Schematic life histories of equatorial penaeid prawns. A, alternation of annual generations. B, interlocking six-monthly and yearly generations (from Dall *et al.*, 1990).

result in seasonal spawning activity at the population level (Garcia, 1977). Population cycles are affected by seasonal rainfall, often associated with seasonal monsoons or seasonal temperature changes brought about by the seasonal shifts in the winds, especially in localities close to continental land masses. At the population level, this appears to result in two main periods of increased spawning in each year, even in populations close to the equator (Hall, 1962; Pauly *et al.*, 1984; Staples and Rothlisberg, 1990). These periods of increased spawning tend to occur during the intermonsoonal months of September – November and March – May, periods characterised by decreased winds and currents. By analogy with temperate regions, these periods will be called spring and autumn.

Hall (1962), suggested that this bimodal pattern of spawning was maintained by an alternation of the generations in which the generation time is one year; the spring generation gives rise to the spring generation of the following year and the same for the autumn generation (Fig. 3A). It must be stressed that this interpretation of penaeid life histories is based on an assumption that it took the main species observed, *Metapenaeus moyebi*, one year to reach maturity. We know from the work of Crocos and Kerr (1983) that *Penaeus merguiensis* can mature in 6 months in a sub-tropical area, and a more likely interpretation is that the equatorial penaeids exhibit combinations of 6-monthly and 12-monthly cycles as suggested as a basic scheme for *P. merguiensis* by Rothlisberg *et al.* (1985). This concept has been extended to produce hypothetical scheme for an equatorial pattern which has equal contributions from both the 6-monthly and 12-monthly cycles (Fig. 3B). Obviously more research on equatorial populations is required including more information on the size and age of first maturity and the proportion of the two generations which mature and spawn within their first 6 months of life. The next section of this paper describes a study in the Indo-West Pacific aimed at providing some of this information.

The hypothetical equatorial pattern, although substantiated with few data at this time, does serve as a useful conceptual model for discussing other latitudinal patterns. All of the patterns seen in both the tropical and temperate regions can be derived by the removal or modification of appropriate links.

Tropical/Subtropical Pattern

Bimodal spawning and recruitment are also extremely common in the slightly higher latitudes,

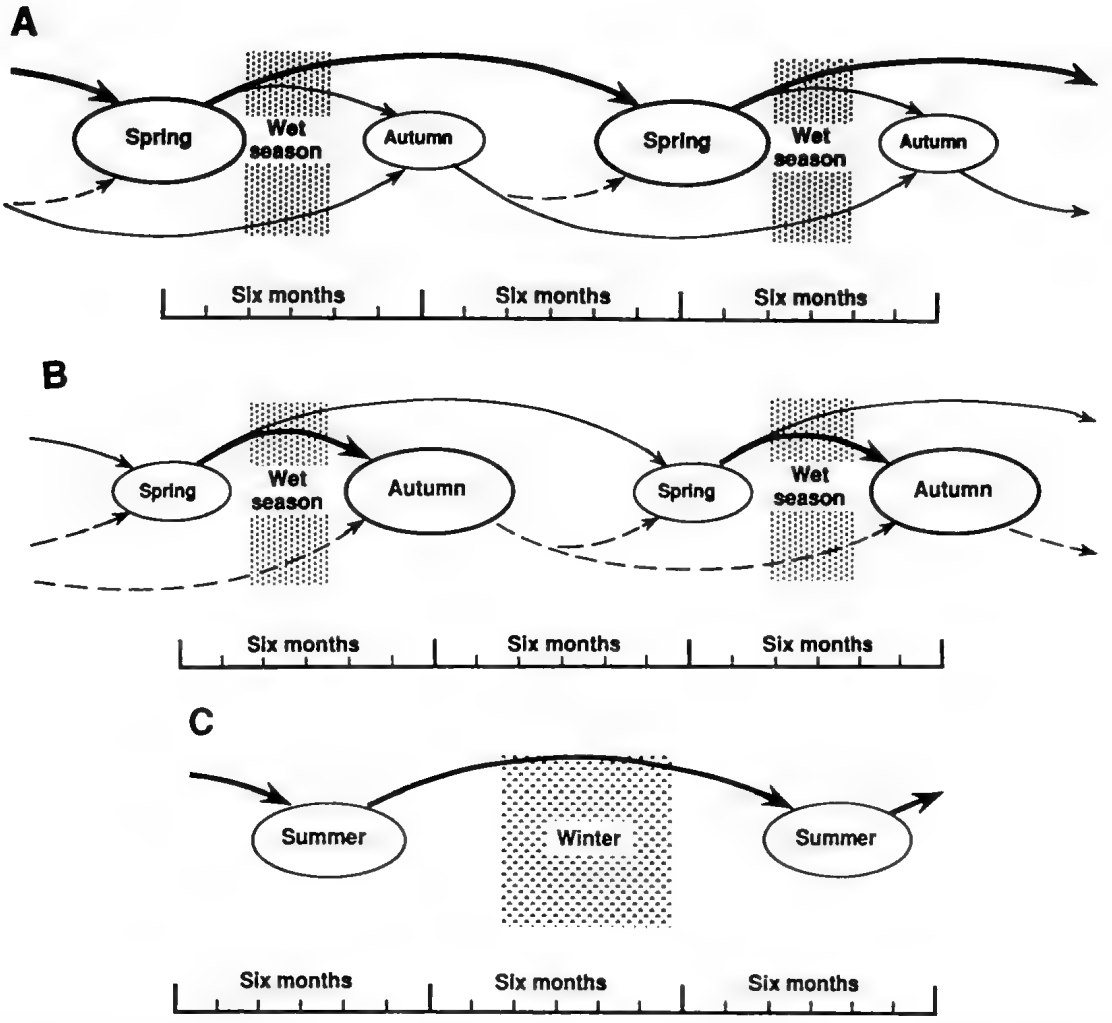

FIG. 4. Schematic life histories of tropical and temperate penaeids. A, 'typical' tropical *Penaeus* pattern (after Garcia, 1985). B, *Penaeus merguiensis* in southeast Gulf of Carpentaria (after Rothlisberg *et al.*, 1985). C, temperate pattern with summer spawning (from Dall *et al.*, 1990).

but in contrast with the equatorial pattern, it appears that seasonal rainfall and lower winter temperature results in either the spring or autumn generation being dominant in the offshore phase. *Penaeus merguiensis* in Gulf of Carpentaria fits into this pattern but is rather extreme in its asymmetry (Fig. 4B). Other examples include *P. notialis* in Senegal (Garcia, 1977; Lhomme and Garcia, 1984), *P. semisulcatus* and *M. affinis* in Kuwait (Mathews *et al.*, 1987), *P. semisulcatus* in northern Australia (Crocos, 1987; Somers, 1987), *P. indicus* in Madagascar (Le Reste, 1971, 1978; Le Reste and Marcille, 1976) and *M. dobsoni*, *P. indicus* and *Parapenaeopsis stylifera* in India (Kurup and Rao, 1975), *P. notialis* and *P. schmitti* in Cuba (Perez *et al.*, 1984a, b). Bimodal postlarval recruitment patterns have been recorded for *P. merguiensis*, *P. japonicus*, *P.semisulcatus* and *P. monodon* in the Philippines (Motoh, 1981) and *P. japonicus* in Natal (Forbes and Benfield, 1986), in Japan (Mito, 1972) and in Korea (Pyen, 1974). Similarly, seasonal postlarval patterns of *M. brevicornis*, *M. dobsoni*, *M. monoceros*, *P. monodon*, *P. semisulcatus*, and *P. indicus* have been reported for several estuaries along the coast of India. A summary of these presented by Babu and Babu (1987) shows that despite considerable local variability, all species show two peaks of increased postlarval abundance within the year in most locations. Bimodal recruitment into offshore fisheries which link to

the bimodal pattern of postlarval abundance in India has also been reported by several authors (Kurup and Rao, 1975).

Pérez Farfante (1969), provides a comprehensive summary of the life history of several western Atlantic species. In the tropical/subtropical regions, *P. aztecus*, *P. duorarum* and *P. setiferus* are known to have both spring and autumn generations. This fact has caused considerable confusion in earlier interpretations of Gulf of Mexico prawn life histories. For example, Baxter and Renfro (1967) reported that the postlarval peak in abundance was 6 months out of phase with the peak of larval abundance observed by Temple and Fischer (1967). On the basis of this mismatch, Temple and Fischer suggested that *P. aztecus* must overwinter in the postlarval stage. A more likely interpretation is that one group of workers had observed the spring generation while the other had observed the autumn generation.

Because a life history pattern with disproportionate spring and autumn generations appears to be common in the tropics, Garcia (1985) suggested that this was the typical pattern for the genus *Penaeus* as a whole (Fig. 4A). In this scheme he describes a large spring spawning peak which produces a strong spring generation which recruits into the adult population the following autumn and spawns again the following spring to give a generation time of 1 year for this main generation. A small proportion of the new recruits spawn in autumn giving rise to a small more intermittent autumn generation (Fig. 4A). Garcia, in proposing this model accepted that it may be an oversimplification but that it provided a stimulus for discussion. The literature shows that several *Penaeus* species do not fit the Garcia model. *P. merguiensis* , for example, although having an apparently overall pattern, differs in one important point (compare Fig. 4A and 4B). The proportion of prawns spawning during autumn is much greater and as a result the autumn spawning becomes the major event. Several other studies have also reported that this is the case, including *P. semisulcatus* and *M. affinis* in Kuwait (Mathews *et al.*, 1987), *P. notialis* in north Senegal (Lhomme and Garcia, 1984), *P. notialis* and *P. schmitti* in Cuba (Perez *et al.*, 1984 a, b). Garcia, however, argues that spring phytoplankton blooms are a global occurrence and as a result of increased larval food at this time, natural selection would favour a larger spring spawning biomass. Because all the examples given above are heavily fished stocks, he suggests that in these cases, the spring spawning population may have been severely reduced as a result of fishing the autumn recruits and the populations do not truly reflect the pre-fishing situation. More research on the seasonal dynamics of phytoplankton throughout the tropics would help resolve this debate.

Temperate Pattern

The influence of temperature on the life history dynamics becomes much more obvious further from the equator. There is a trend for the bimodal spawning pattern seen in many species in the tropics to become unimodal in temperate latitudes. This is usually associated with one well-defined period of recruitment into the offshore fishery each year and the species becomes truly annual with a generation time of 1 year (Fig. 4C). In many species the spawning season shifts to the summer period when temperatures are similar to those experienced during the spring or autumn in more tropical areas of the species distributions. Reported examples of this trend occur in both *P. aztecus* and *P. duorarum* in the western Atlantic. *Penaeus aztecus* spawns both in spring and autumn in Florida Bay, but there is only summer spawning further north along the Carolina coast (Pérez Farfante, 1969). *Penaeus japonicus* is another species with wide geographic range which shows a strong geographical trend in its life history dynamics. Spawning is bimodal over much of its range (as described above) but is confined to the summer months in the Mediterranean (Tom and Lewinsohn, 1983), in Japan (Hudinaga, 1942) and in Korea (Lee and Lee, 1970). In Australia, *P. latisulcatus* has all year-round spawning with two peaks in northern regions, which becomes reduced to a single peak in southern Australia (Penn, 1980). *Penaeus merguiensis*, although exhibiting bimodal spawning over most of its range, is unimodal in the south China Sea with a peak of spawning in spring (Liu, 1986).

Several species with geographical ranges restricted to the temperate zone also have spawning seasons restricted to one period each year. *Penaeus setiferus* shows a unimodal pattern over its entire range. In the Pohai Sea (37°–45°N), *P. chinensis* [= *orientalis*] exhibits an extreme adaptation to a cool temperate climate (Chang Cheng, 1984). Adults spawn in shallow water in early spring at 13°C and juveniles begin leaving the nursery grounds of the Pohai Sea in summer and migrate into deeper waters, where after overwintering offshore they return to the Pohai Sea as mature adults to spawn. In some other cases,

prawns spawn in late summer or autumn and it is the juvenile stage which overwinters in the nursery grounds, e.g. *P. plebejus*, Ruello, 1975; *M. macleayi*, Glaister, 1978; *M. bennettae*, Coles and Greenwood, 1983.

As expected, several penaeid species have been shown to have depth related changes in their life history which parallel those seen in changes with latitude. *Penaeus aztecus*, in the Gulf of Mexico, spawns from spring to early winter at 27m depth, with a period of greatest activity from October–December and a smaller peak from March–May. At greater depths, spawning is more or less continuous (Cook and Lindner, 1970).

PENAEUS MERGUIENSIS IN THE INDO-WEST PACIFIC

As seen from the above review several issues require further research. These include:

1. Does the hypothetical life history pattern of interlocking 6-monthly and 12-monthly cycles exist in the equatorial region?
2. Can the life history pattern of penaeids throughout their range be derived from this hypothetical model?
3. In tropical penaeids, is the seasonality of spawning adapted to the seasonality of phytoplankton production where the spring spawning event is the main spawning season as suggested by Garcia (1985)?
4. As a result of 3, is the generation time always one year (defined as the average date of birth of the main generation and the average date of birth of the offspring from this generation)?
5. What other environmental factors are responsible for the variability in life-history patterns seen across a species geographical range?

In an attempt to answer these questions and to provide a better management-orientated research programme for several countries across the Indo-West Pacific region, the Penaeid Recruitment Program (PREP) was established in 1988 under the auspices of the Intergovernmental Oceanographic Commission (IOC) and the United Nations Food and Agriculture Organisation (FAO). By selecting study sites in 6 countries (Philippines, Thailand, Malaysia, Indonesia, Papua New Guinea and Australia) the life history dynamics of *Penaeus merguiensis* can be compared across a range of latitudes, climatic regimes and fishing activities. Additional sites in Brunei, Darussalam and Peoples Republic of China are soon to be included. In all sites, we are attempting to collect data on the seasonal abundance of the major life history stages of *P. merguiensis* and then to compare them across the region.

A full description of the study has been published by Staples and Rothlisberg (1990). Spawning follows a bimodal pattern in most countries (not all countries are able to collect spawning data) during periods roughly coinciding with the temperate spring and autumn seasons. Most data for subadult and adult prawns come from commercial catch sampling and although many other interpretations are possible, it is assumed at this stage that these show seasonal trends in abundance and hence reflect recruitment into the offshore area (Fig. 5). Close to the equator at the Malaysian site the catch per unit effort (CPUE) is high in all months with higher catch rates being recorded from March–May and from September–December (Fig. 5C). Further from the equator at the Indonesian and Thailand sites, recruitment becomes more asymmetrical with the September–December peak dominating. In Papua New Guinea, asymmetry also occurs but the peak is in April–July. At higher latitudes, in the Philippines and Australia, recruitment into the offshore fishery resulted in one major peak in catch rate from October–January in the Philippines and from February–April in Australia.

To date, the programme has demonstrated a clear latitudinal trend from a bimodal recruitment pattern near the equator to an unimodal pattern at higher latitudes. There is also general agreement in the timing of recruitment peaks across the region. Unlike the 'typical' pattern of the genus *Penaeus*, however, the autumn recruitment is not always dominant. An interesting example is that of Indonesia and PNG where although both sites are situated on 8°S, the peaks in recruitment are several months out of phase. Because of the strong correlation between the timing of rainfall and the emigration of juvenile prawns out of the estuary (Staples and Vance, 1986) in Australia, the seasonal timing of rainfall in the six sites was examined to determine whether this factor alone could account for the variability in the pattern of recruitment seen across the region. In general, the seasonal pattern in the CPUE closely followed the seasonal pattern of rainfall in all sites (Figs 5, 6). Australia is the extreme example where the one distinct wet season forces an extremely distinct seasonal pulse in recruitment. In the Indonesian and PNG cases, the phase shift in the recruitment timing

also appears to be related to the phase shift in rainfall, with a September–December peak in rainfall in the Indonesian site and a May–July peak in PNG.

In Fig. 7A, the hypothetical equatorial pattern is represented by a bar diagram which joins the two main generations from their time of spawning to their time of recruitment into the offshore region 6 months later. Superimposed on these progressions is a bimodal seasonality of rainfall which coincides with the periods of spawning and subsequent recruitment. Of the 6 PREP study sites, the Malaysian site is the closest representative to the hypothetical equatorial situation. Unfortunately, we do not have spawning data yet, but juveniles and adults appear to closely follow the hypothetical pattern with a bimodal recruitment pattern coinciding with the two wet seasons. In Indonesia and Thailand, a marked asymmetry in both rainfall and recruitment occurs. In both these localities, tracing the two recruitment pulses back to their spawning origins, shows that in both cases the main recruitment event (spring in Indonesia and autumn in Thailand) originated from the smaller of the two spawning peaks (shown as narrow bars in Fig. 7C, E). In Australia and the Philippines, with only one main wet season, one generation is lost almost entirely from the population.

From these preliminary results we can start to answer the questions posed above. It would appear that the different life history patterns seen in *P. merguiensis* across the Indo-West Pacific can be derived from modifications of the hypothetical equatorial scheme. It would also appear that the hypothetical pattern can be found close to the equator in areas experiencing two equal wet seasons each year such as that observed in west Malaysia. More research is needed to establish whether the two generations show a true alternation of generations as suggested by Hall (1962), or whether the pattern is

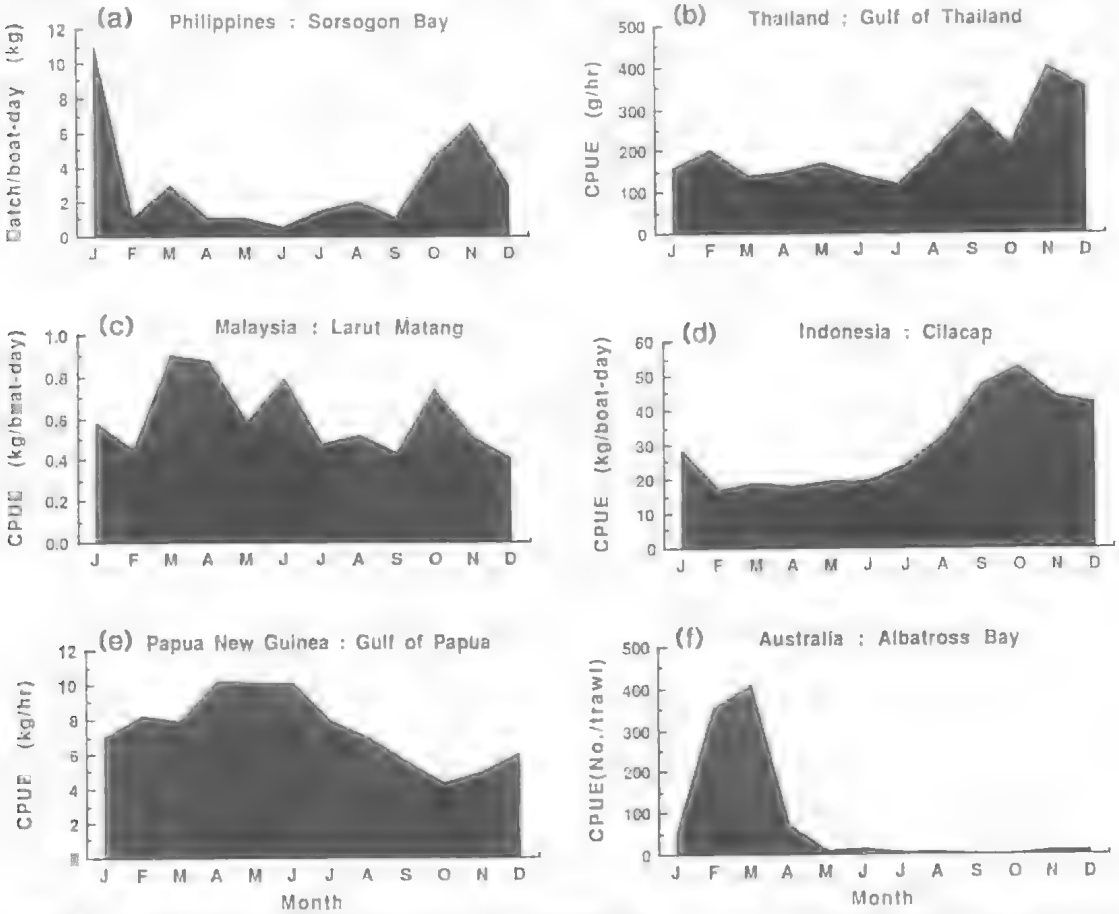

FIG. 5. Seasonal distribution of catch per unit effort (CPUE) of *Penaeus merguiensis* from six localities across the Indo-West Pacific (from Staples and Rothlisberg, 1990).

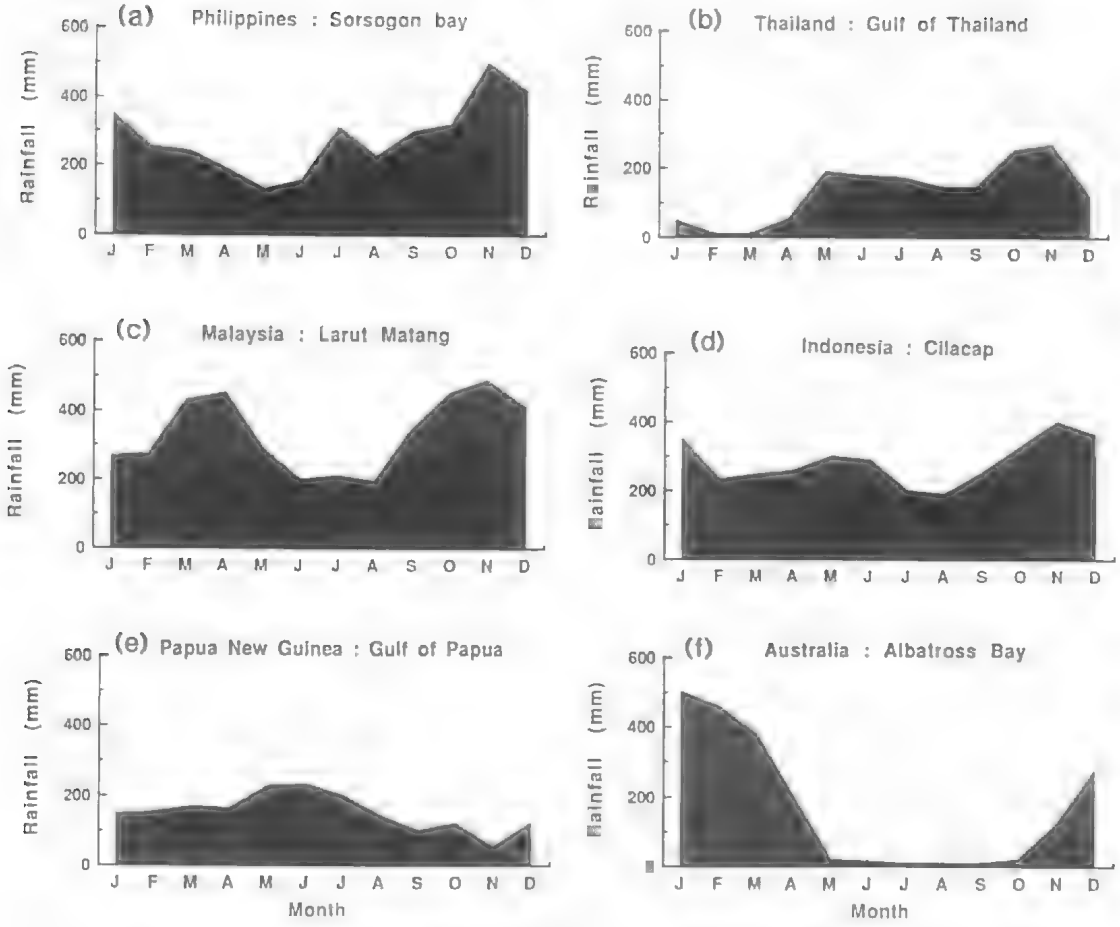

FIG. 6. Seasonal distribution of rainfall at six localities across the Indo-West Pacific (from Staples and Rothlisberg, 1990).

an interlocking of 6-monthly and 12-monthly cycles. Based on the Australian results I suggest that the latter is most likely. Without seasonal phytoplankton results it is also not possible to determine whether the seasonal spawning dynamics is in phase with phytoplankton biomass as suggested by Garcia (1988). However, from the limited data available it does seem likely that the major spawning can occur in either spring or autumn. An obvious reason for the shift is that for *P. merguiensis* the spawning intensity at the population level is greatest at the time of maximum recruitment (large number of small ripe females). This appears to be true in both Thailand and Indonesia, for example, the main spawning season (spring and autumn, respectively) occurs during the time of major recruitment, this event itself being under the influence of rainfall. A testable hypothesis is that the major spawning occurs during or following the major wet season (as a result of major recruitment). This may also link with increased phytoplankton productivity, but not necessarily a spring bloom.

CONCLUSIONS

1. *Penaeus merguiensis* in Australia exhibits a rather unusual life history pattern with two spawning seasons each year, but the main generation of prawns in autumn arising from a rather minor peak of spawning in spring. In some areas of the Gulf of Carpentaria, offspring from the large autumn spawning do not contribute significantly to the subsequent offshore population because of high larval and postlarval mortality.

2. There are many examples of bimodal spawning within the year in tropical penaeids,

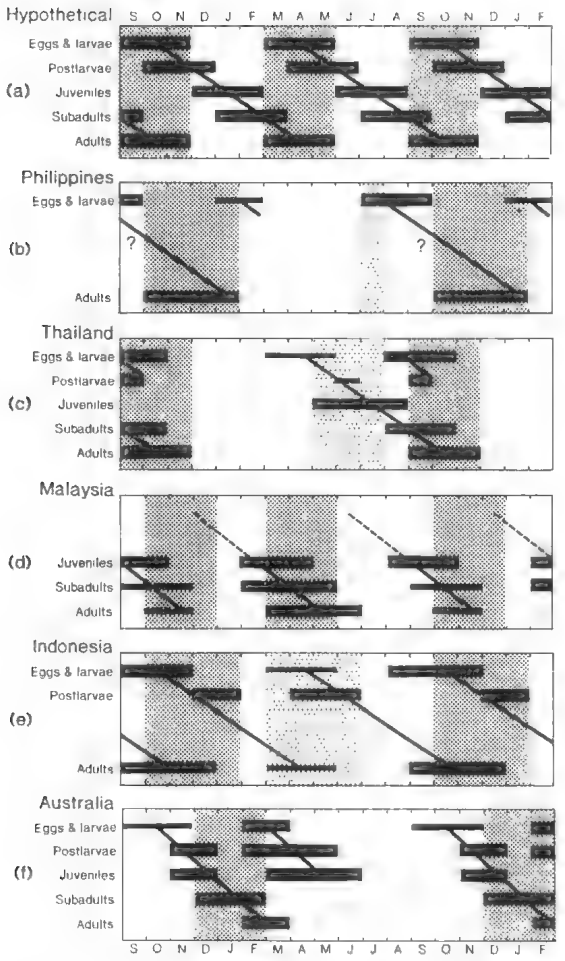

FIG. 7. Seasonal life-history dynamics of *Penaeus merguiensis* as indicated by the cycles of abundance of the main life history stages from five sites across the Indo-west Pacific shown together with a hypothetical equatorial pattern. Light and heavy shaded areas denote minor and major wet seasons (from Staples and Rothlisberg, 1990).

and in many cases a disproportionate survival produces one main and one subsidiary generation (it can be either spring or autumn, but commonly spring). In these cases, description of the generation time is difficult and depends largely on the definition used.

3. It is hypothesised that all these asymmetrical life history patterns are derived from a symmetrical equatorial pattern where both generations interlock in 6-monthly and 12-monthly cycles.

4. In higher latitudes, the bimodal spawning pattern becomes reduced to a single spawning season and the generation time is definitely one year.

5. By comparing the life history dynamics of *P. merguiensis* across the Indo-West Pacific, the derivation of the many variants seen in local life-history patterns can be derived from the hypothetical equatorial scheme.

6. Further research on the factors affecting recruitment strength and timing is needed across a broad geographic range before the basic life history dynamics of penaeids is fully understood.

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SPATIAL AND TEMPORAL PATTERNS IN RECRUITMENT FOR AMERICAN LOBSTER *HOMARUS AMERICANUS* IN THE NORTHWESTERN ATLANTIC

ROBERT W. ELNER AND ALAN CAMPBELL

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The lobster, *Homarus americanus*, is a long-lived crustacean that has been heavily exploited along the northeast coast of North America for over 100 years. Catches revived markedly in many lobster fisheries during the 1980s after prolonged declines from peaks at the turn of this century. Because of high exploitation rates, the increased yields are assumed to reflect real changes in lobster abundance, although there is no consensus on why recruitment should have improved. Geographic comparisons of time series of landings, larval surveys and oceanography have indicated tentative stock boundaries but there is little understanding of stock-recruitment relationships. To-date, none of the numerous biotic and abiotic factors that have been hypothesized as controlling lobster recruitment have proven reliable for forecasting yields. Work on the behavioural ecology of the cryptic early benthic stages has invoked various density-dependent mechanisms as population controls in local areas; however, these mechanisms may not account for larger-scale recruitment events. Changes in climate, and to a lesser extent, reduced exploitation rates in the last 20 years may have caused a general increase in recruitment, producing yields to match historic highs in some lobster fisheries. There are implications for both traditional fisheries models and management if lobster stocks are dominated by 'supply-side' recruitment dynamics under the control of an unpredictable climatic phenomenon. □ *Lobster, life history, fishery, density-dependence, recruitment mechanisms, research approach.*

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The American lobster, *Homarus americanus*, is the largest and most abundant species of 'true' or clawed lobster (Nephropoidea). Some specimens have been reported to achieve a live weight over 19 kg (Wolff, 1978). The species has a largely boreal distribution along the northeastern coast of North America, from the Strait of Belle Isle through the Gulf of St. Lawrence, and the Gulf of Maine to Wilmington, North Carolina (Williams, 1984). The Gulf Stream around Cape Hatteras, North Carolina appears to present a thermal barrier at the southern limit (Fig. 1). The total range of the species extends over 15 degrees of latitude. Lobster (Note: throughout the text lobster refers to the American lobster, *H. americanus*, unless indicated otherwise) usually occur within 20–25 km of the coast at depths shallower than 50 m; however, populations exist on the continental shelf and offshore banks, extending to depths of over 700 m in the canyons of the continental slope.

Before commercial exploitation began, American lobster was common even in intertidal areas and collected for food by Indians and, later by the early European settlers. Lobster was so abundant it was reportedly used for agricultural fertilizer (DeWolf, 1974). Lobster fisheries have been of major economic and cultural importance for over one hundred years. Commercial harvesting started in Massachusetts in the early 1800s and had reached Maine by 1840 (Herrick, 1911). Lobster fishing in Canadian waters expanded rapidly after the introduction of canneries to Nova Scotia in 1851. Lobster landings began in Quebec in 1871, Newfoundland in 1874 and the Magdelen Islands in 1875; the Canadian fishery was considered to be fully developed by the 1890s (Robinson, 1980; Pringle *et al.*, 1983). Monitoring and regulation of the various lobster fisheries began as early as 1873, biological research soon after (Herrick, 1896). Although American lobster appears one of

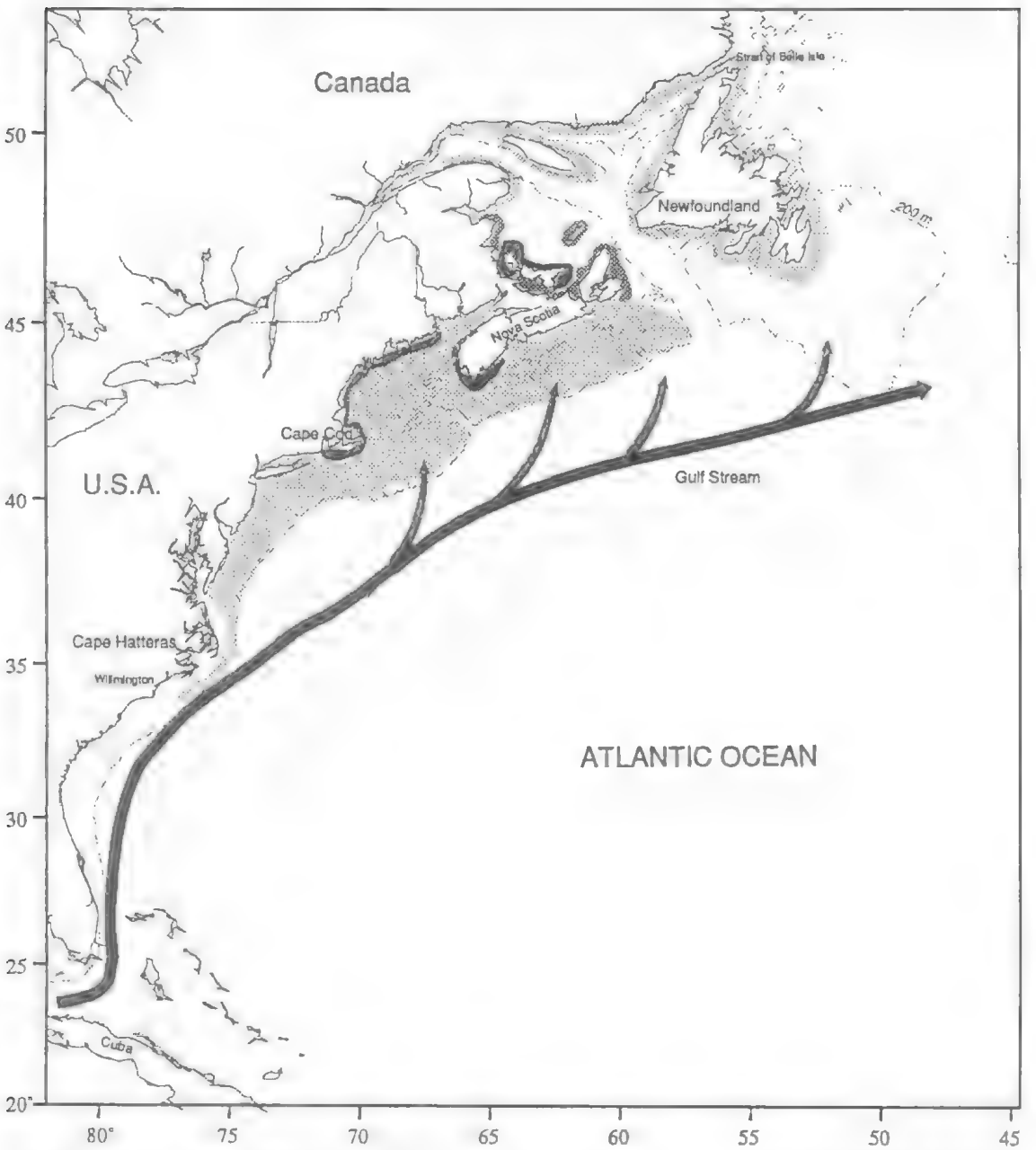

FIG. 1. The geographical distribution of American lobster, *Homarus americanus* (shaded) along the coast of North America; note, major fishing areas (black).

the most intensively studied and popularly recognized marine crustaceans there remain large gaps in understanding of its life history and the ecological mechanisms controlling abundance. Consequently, powers to predict recruitment are limited, and determining the consequences of fisheries management initiatives is problematic. The present paper reviews the biological basis to recruitment, the development of the commercial fishery and postulated recruitment mechanisms. Progress in describing lobster life history dynamics and understanding the factors that influence recruitment patterns is argued to have been hindered by the lack of an effective postlarval collector, long-term data sets on oceanographic events and the overall scientific approach.

BIOLOGICAL BASIS TO RECRUITMENT

A female lobster carries between 7,000 to 97,000 eggs, depending on body size and origin, on her abdominal pleopods for 9–12 months. Brooding time is strongly related to temperature (Templeman, 1940a; Perkins, 1972). Ovigerous females undertake seasonal depth migrations that appear associated with maximizing degree days needed for egg development: hatching eggs in relatively shallow, warm water increases survivorship of larvae by decreasing development time to the benthic stage (Campbell, 1986a, 1990a; Campbell and Stasko, 1986). The eggs hatch during summer (July – September) and the four stages of free-living pelagic larvae remain in the water column for 1–2 months, depending on temperature (Templeman, 1940b). Stage IV larvae become benthic in late summer, settling into preferred substrates such as gravel (Cobb, 1971, 1977; Cobb *et al.*, 1983,1989). Mortality during the larval stages is probably high, due to predators, starvation and physical factors (Scarratt, 1964, 1973; Caddy, 1979; Harding *et al.*, 1982). Early postlarvae are cryptic and burrow into preferred substrates where they are less susceptible to predation and may filter feed (Pottle and Elner, 1982; Lavalli and Barshaw, 1986, 1989; Barshaw and Lavalli, 1988). There is uncertainty whether the few inshore settlement sites that have been discovered should be considered 'nurseries' (areas preferentially selected for settlement) *per se* or merely areas with appropriate bottom characteristics where postlarval survival and, hence, density, is higher than other settlement sites. Lobster above approximately 40 mm carapace length (C.L.) frequently forage outside their burrows, roaming progressively further afield as they become larger and mature (Lawton, 1987). However, substrate characteristics, particularly size and availability of shelters, continues to strongly influence lobster distribution and abundance (Scarratt, 1968; Cobb, 1971; Cobb *et al.*, 1986; Hudon, 1987).

Recruitment-related variables such as growth rate, size at maturity and spawning characteristics vary with environmental conditions, notably temperature (Aiken and Waddy, 1986). Lobster attain the current legal minimum size, for most grounds around Nova Scotia, of 81 mm C.L. after five to eight years. In some areas, such as the Gulf of St. Lawrence, 'canner' lobsters of 64 mm C.L. are fished and recruitment into the fishery may occur at an even earlier age. In addition, summer temperatures over much of the southern Gulf of St. Lawrence may be sufficiently high to permit two moults per year, instead of the usual one, for newly recruited lobster. Offshore lobster also grow relatively fast, attaining fishable size after 4–5 years, as compared to the 7–12 years required for those on some nearshore grounds (Cooper, 1977). Most lobster reach fishable size before attaining sexual maturity (Ennis, 1986; Cobb and Wang, 1985). Although tagging and laboratory studies have provided extensive information on moulting and growth for immature and early adult stages (Miller *et al.*, 1989), estimating the age of older adults is problematic, as the intermoult period becomes longer and less predictable after the onset of maturity. Aging is further complicated because mature females can delay moulting in order to extrude a further batch of eggs (Waddy and Aiken, 1986).

There is no consensus on the natural life-span for lobster. Cooper and Uzmann (1977) computed a von Bertalanffy growth equation, using L_∞ values of 270 mm C.L. (males) and 240 mm C.L. (females), that provided maximum estimates of 100 years for offshore specimens. Estimates by Campbell (1983a) suggest more rapid growth whereby males and females reach 200 mm C.L. in 20 and 30 years, respectively.

For American lobster, as for most marine invertebrates, critical linkages between oceanography and larval life-history phases are lacking, and the existence of a stock-recruitment relationship is largely a matter of faith (Cobb and Wang, 1985). Sources of recruitment and larval mixing are only superficially understood, and consequently so are mechanisms for variability in recruitment patterns. Development of predictive models has been slow. Studies in the Northumberland Strait (Scarratt 1964, 1973) have failed to demonstrate a correlation between abundance of stage I lobster larvae and the parent stock or a predictive relationship between the production of stage IV larvae and subsequent recruitment into the fishery (but see Fogarty and Idoine (1986) for a re-evaluation). However, Campbell (1990b) derived a prerecruit abundance index from commercial traps to predict recruitment for lobster grounds off southwestern Nova Scotia 1–2 years later.

For the purposes of this paper, a stock is defined as 'a population of organisms which, sharing a common gene pool, is sufficiently distinct to warrant consideration as a self-perpetuating system that can be managed' (Larkin, 1972). We define recruitment broadly as survival from

some earlier life-history stage to the minimum legal size for the commercial fishery. The continuity of the stock in time and space depends on the larvae or a later life-history phase returning to the brood area to complete the genetic cycle. Egg hatching locations are often far from habitats favorable to juveniles, which, in turn, may differ from areas preferred by adults. If a species has not evolved a reproductive strategy that returns recruits to the fishing grounds regularly, the stability of the stock cannot be assumed and it will be practically impossible to predict recruitment.

The delineation of stocks and the mechanics of stock-recruitment relationships are problems fundamental to fisheries science. Presumably if stocks can be identified, effective management regimes can be imposed to optimise exploitation of the resource. Ennis (1986) detailed five requirements for determining a stock-recruitment relationship:

1. a population that is more or less discrete, both geographically and biologically (i.e. a stock);

2. measure of stock size over a time period when abundance ranged widely;

3. measure of recruitment to the stock which coincides with the same time period;

4. understanding of the effect of variation in factors other than stock size on recruitment variability; and,

5. understanding of recruitment processes for the stock.

Although components of all five have been studied for *H. americanus* there has been no concerted attempt to integrate results and re-define management areas. Campbell and Mohn (1983) examined historical catch data from the Canadian Maritime Provinces and Maine and defined broad geographic population boundaries for lobster on the basis of coherence in temporal trends in landings over several decades. A similar exercise performed by Harding *et al.* (1983) suggested the same major groupings. Although morphometric studies have indicated some segregation of inshore and offshore lobster (Saila and Flowers, 1969) the movement patterns of mature lobster and the propensity for larval exchange suggest that genetic mixing occurs at least within the Gulf of Maine system (Campbell and Stasko, 1985, 1986). To date, attempts to delineate lobster stocks on the basis of parasites (Uzmann, 1970; Boghen, 1978; Stewart, 1980; Brattey and Campbell, 1986) have had only limited success. Protein electrophoresis indicates that American lobster from various areas are genetically similar, with the exception of a single enzyme that allows discrimination between lobsters from Prince Edward Island and south of Cape Cod (Tracey *et al.*, 1975).

Mark-recapture studies in Canada (Miller *et al.*, 1989) have shown that while immature commercial-sized lobster travel only short distances (Campbell, 1982), mature lobsters undertake extensive movements (> 100 km) and tend to return to the location where they were initially marked (Pezzack and Duggan, 1986; Campbell, 1986a). This homing behaviour may involve a round trip movement of up to 400 km in one year (Campbell, 1989). In addition, short, seasonal inshore-offshore, or shallow-deep, migrations have been noted in the Gulf of Maine, on Georges Bank and off the Magdelen Islands (Saila and Flowers, 1968; Dow, 1974; Cooper and Uzmann, 1980; Krouse, 1980; Campbell and Stasko, 1986). The movements appear associated with maintaining maximum local temperatures (Cooper and Uzmann, 1971; Campbell and Stasko, 1986). In comparison, tagging studies off eastern Nova Scotia, around Newfoundland and, generally, in the Gulf of St. Lawrence have revealed only small-scale movements (< 15 km) (Ennis, 1984).

Movement patterns for lobster larvae are poorly known and investigators have usually related larval pathways to residual surface currents. Various attempts have been made to elucidate larval sources for the Nova Scotian Atlantic coast and the rich inshore fishing grounds off southwestern Nova Scotia. While Stasko (1978) hypothesised that Browns Bank was the source of larvae for southwestern Nova Scotia, Harding *et al.* (1983) suggested the larvae originate from Georges Bank (but see also Harding and Trites, 1988, 1989; Pezzack, 1989). Dadswell (1979), on the assumption that circular currents retain larvae within an area while longitudinal currents carry larvae away, proposed that there are six lobster-recruitment cells for the Canadian Maritimes. More recent work has shown that lobster larvae exhibit pronounced diurnal vertical migration behaviour and should not necessarily be considered passive surface drifters (Harding *et al.*, 1987). If lobster larvae resemble other decapod larvae, this behaviour may maintain their position (Sulkin, 1986). Lobster larvae were collected only at the surface and only with onshore winds during a study in a nearshore area off Newfoundland, also suggesting that a nearshore retention mechanism exists (Ennis, 1983).

THE FISHERY

For over 100 years, American lobster have been predominantly caught by traps, both in Canada and the U.S.A.. Prior to the late 1860s lobster were captured by a variety of methods including hooks, spears and hoop nets (DeWolf, 1974; Dow, 1980). The majority of offshore fisheries use large traps but in some offshore areas of the U.S.A. otter trawling has occasionally supplemented trapping (Dow, 1980; Fogarty *et al.*, 1982; Pezzack and Duggan, 1983). The various inshore and offshore lobster fisheries are partitioned into management areas based on socioeconomic considerations rather than biological criteria (Dow, 1980; Pringle *et al.*, 1983; Campbell, 1989). Depending on the area involved, conservative management of these lobster fisheries has included a combination of regulations : minimum and maximum sizes, protection of ovigerous females, effort restrictions through license and trap limitations and season openings and closures, plus quota restrictions for the offshore fishery (Dow, 1980; Fogarty *et al.*, 1982; Pezzack and Duggan, 1983; Pringle *et al.*, 1983; Campbell, 1986b, 1989). Without adequate empirical stock-recruitment data determining whether these regulations have been effective conservation tools is impossible.

Historically, landings have fluctuated considerably (Fig. 2) but in recent years they have generally risen for most areas (Fig. 3). Total North American landings exceeded 60,000 t (Ennis, 1986) and Canadian lobster landings reached over 45,000 t per annum in the last century. Record lows in the 1960s and 1970s have been followed by all time highs in the 1980s; total Canadian lobster landings doubled between 1977 and 1986 and in some areas rose by an order of magnitude. The main reason for the rise appears to be an increase in the absolute abundance of lobster (Miller *et al.*, 1987). Although there has been some increased fishing effort and expansion to new grounds, catch rates have also increased. In addition, management measures, including more stringent enforcement of regulations and a reduction in the number of licenses, have helped sustain the recovery in Canada.

Historical fishing effort trends are not as well known as landings for the American lobster. Fishing effort can fluctuate with many factors such as market demand (Dow, 1980) and increases in fishing gear efficiency; also, trapability can vary from location to location depending on lobster activity and physiological condition (McLeese and Wilder, 1958; Elner, 1980). However, because effort is high (currently, there are about 10,000 licensed lobster vessels in Canada and exploitation rates have been estimated at

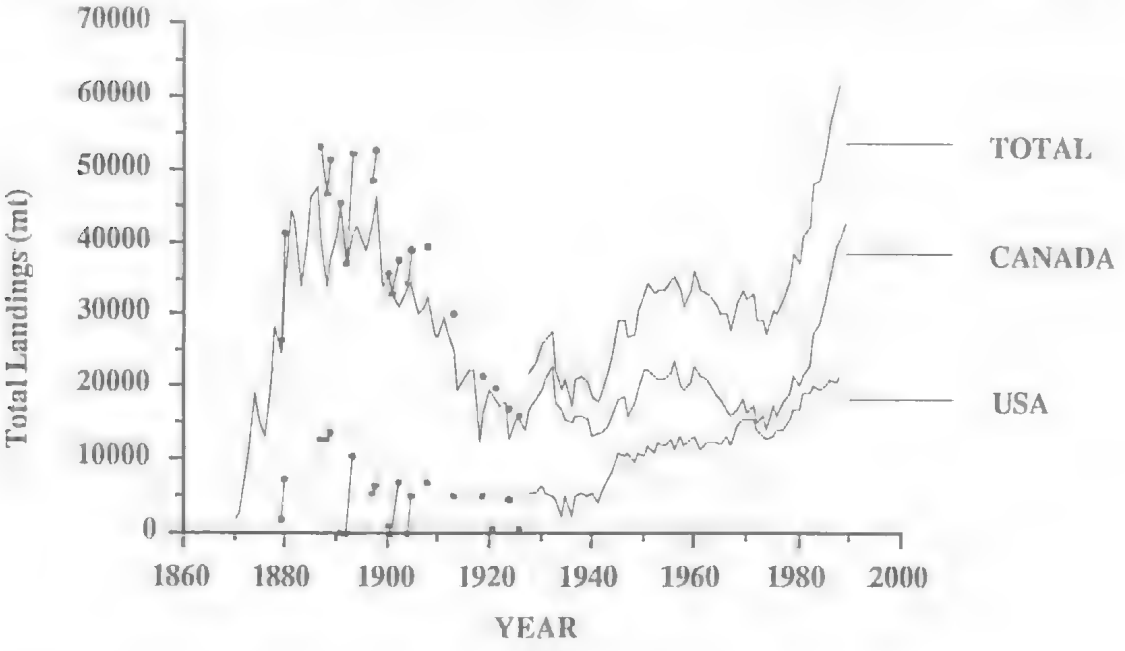

FIG. 2. Annual landings of American lobster for Canada and the U.S.A., 1870–1989.

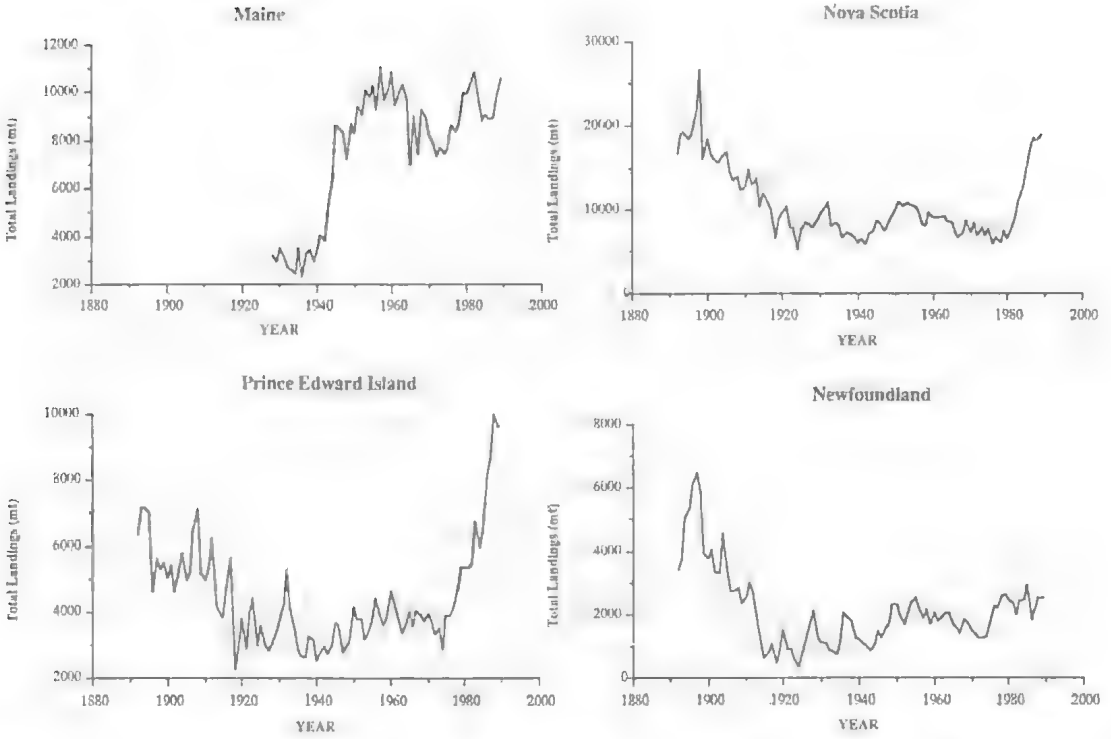

FIG. 3. Annual landings of American lobster for Maine, Nova Scotia, Prince Edward Island and Newfoundland, from the late 1880s–1989.

60–90% (Anthony, 1980; Campbell, 1980; Miller *et al.*, 1987)) catches mainly comprise lobster that are newly-recruited to commercial size and the assumption is that landings are a reliable indication of the total fishable biomass. Therefore, major fluctuations in recruitment (lobster molting into the fishery) will be reflected in the landing trends. Recent increases in exploitation of large mature lobster, an important source of recruits, concurrent with high exploitation of newly recruited lobster in the inshore fishery has caused concern that the amplitude of landing fluctuations could increase until recruitment failure occurs (Campbell, 1989).

RECRUITMENT MECHANISMS

Throughout their extensive geographical distribution American lobster are found in a diverse array of habitats, from the intertidal zone to a variety of coastal sublittoral habitats to the canyons of the continental slope (Cooper and Uzmann, 1977). Because physical and biological factors vary widely (e.g. temperature can be from 0°C to 25°C) their influence on recruitment will change in time and space (Aiken and Waddy, 1986); thus, understanding recruitment mechanisms is a challenging task. After a century of research fundamental factors such as the relationships between the seasonal movements of adult lobster, distribution of brood stock, larval recruitment processes and oceanographic features are still unclear. The numerous attempts to explain fluctuations in lobster abundance have included factors and mechanisms such as:

— Temperature variation (Flowers and Saila, 1972; Dow, 1977; Fogarty, 1988) which acts strongly to regulate activity and trapability of commercial-sized lobster (McLeese and Wilder, 1958) and the growth rates of all life-history stages. The probability of moulting is strongly temperature related and the proportion of lobster that moult can decrease by nearly 50% in cold years (Campbell, 1983b).

— Freshwater river discharge (Sutcliffe, 1973) which influences food production and, hence, larval survival. Other workers (Sheldon *et al.*, 1982) suggest that increased discharge intensi-

fies stratification, causing higher heat retention, faster larval development and improved survival.

– Excessive exploitation rates, which reduce eggs per recruit (Robinson, 1979; Campbell and Robinson, 1983) causing recruitment failures and declines in landings. Egg predators (Campbell and Brattey, 1986; Fogarty and Idoine, 1986) and anthropogenic factors (Aiken and Waddy, 1986) have also been hypothesised as reducing eggs per recruit.

– Ecosystem productivity changes (Wharton and Mann, 1981) and competition with sea urchins for space (Garnick, 1989) which affect recruitment.

We do not intend to account for all the hypotheses that have arisen (Ennis, 1986), but rather describe the general history and progress of research to elucidate lobster recruitment patterns.

In the 1970s, during the period of collapsed lobster landings along the Atlantic coast of Nova Scotia, workers suggested several causes for the slump: recruit overfishing (Robinson, 1979), ecosystem deterioration due to a population explosion of sea urchins triggered by overfishing lobster (Wharton and Mann, 1981) and closing the Strait of Canso blocking an important source of larvae (Dadswell, 1979). Subsequently, the recruitment failure was attributed by Harding *et al.* (1983) to all three scenarios: excessive fishing of immature lobster between the 1890s and 1920 depleted the breeding stock and caused the initial decline in landings; climatic cooling and the closure of the Strait of Canso further reduced lobster stocks and, in the absence of predation by lobster, destructive grazing of macroalgal beds by sea urchins reduced the carrying capacity of the environment for lobster. None of these explanations was subjected to thorough scientific testing and each had its proponents and critics (McCracken, 1979; Pringle *et al.*, 1982; Elner and Vadas, 1990). Meanwhile, apart from reducing the number of licensed vessels, fisheries managers took little action and, from either inertia or their conservative nature, were still considering the situation when landings started to recover during the early 1980s. The sea urchins suffered mass mortality from disease and macroalgal beds recovered while landings increased (Miller and Colodey, 1983; Miller, 1985a; Scheibling and Raymond, 1990). The cause of the upturn is as enigmatic as explanations for the decline, especially with respect to the role of macroalgae. However, no reliable evidence links lobster production to macroalgae (Miller, 1985b; Elner and Campbell, 1987). Indeed, lobsters responsible for the increased landings in the early-to-mid 1980s spent their pre-recruit years during the mid-1970s on the urchin barrens. The appearance and virulence of the sea urchin pathogen in 1980 has been linked to unusually warm seawater temperatures (Scheibling and Stephenson, 1984; Miller, 1985a; Margosian *et al.*, 1987). Possibly urchin die-offs and revived lobster landings are caused by the same environmental factor(s) (Fig. 4).

The dramatic turnabout in the lobster fishery during the 1980s was a surprise given the arguments that inshore stocks should, in theory, have been exhausted by the high exploitation rates and low survival to maturity. Only the existence of refugia for reproductive lobster was thought to prevent collapses in many areas (Anthony and Caddy, 1980). To-date, only two hypotheses have been advanced for the recruitment pulse : 1) a large-scale climatic change; and 2) a decrease in fishing mortality during the 1970s. However, there has been no testing of postulated mechanisms. More recent studies have concentrated on larval transport problems (Hudon *et al.*, 1986; Harding and Trites, 1988, 1989) and the ecology of early benthic stages (Hudon, 1987; Hudon and Lamarche, 1989). The current debate centers partly on the behavioural ecology of the cryptic early benthic stages and possible density-dependent controls in local areas. Various mechanisms linking lobster larval settlement and subsequent recruitment into the fishery have been postulated (Aiken and Waddy, 1986). Several authors have stressed the importance of protective habitat availability for juveniles to lobster population dynamics (Cobb *et al.*, 1986; Fogarty and Idoine, 1986; Garnick, 1989). Thus, limited suitable bottom may be a 'bottleneck' that stabilises and strengthens the resilience of the fishable stock, but, also, limits recruitment into the fishery. A similar scenario has been advocated for settling larvae of Norway lobster, *Nephrops norvegicus* (Hill and White, 1990).

Fogarty and Idoine (1986) applied their arguments on shelter-mediated, density-dependent regulation of prerecruit lobster to ecological theory for animals with complex life cycles (Wilbur, 1980). American lobster may be considered K-selected strategists (life-history characterised by low fecundity, large egg size, parental investment in brooding eggs, repeat spawning in successive seasons, large body size, late sexual maturity, and longevity) which typically have low recruitment variability and are adapted for exploiting physically stable environments controlled largely by density-dependent

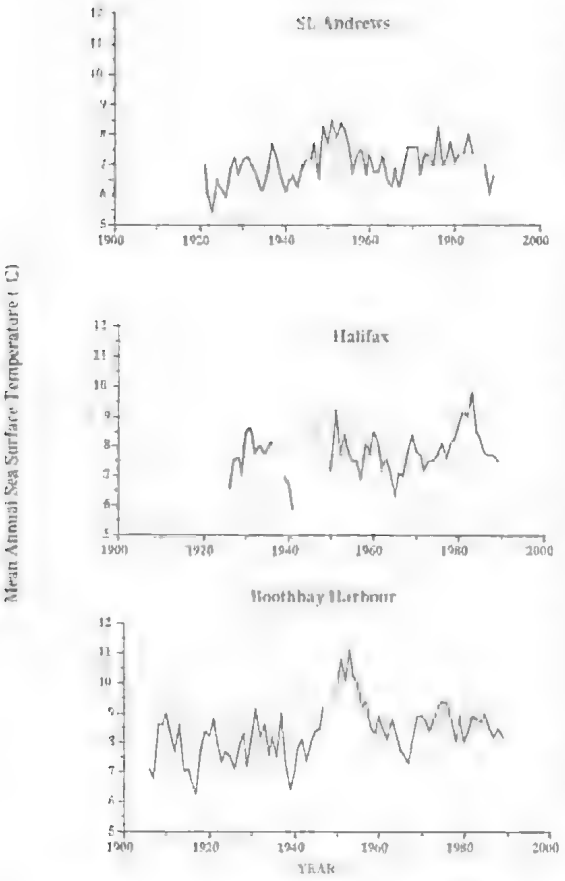

FIG. 4. Mean annual sea surface temperature profiles for St. Andrews, New Brunswick; Halifax, Nova Scotia; and Boothbay Harbor, Maine; note generally elevated values in late 1970s/ early 1980s.

forces (Barnes and Hughes, 1982). In contrast, other crustaceans such as shrimp with small bodies, rapid growth, early sexual maturity and high fecundity are opportunistic, r-selected, organisms adapted to physically unstable environments and subject to wide fluctuations in recruitment. Applying Wilbur's (1980), criteria, the American lobster could be classified by 'Density-Dependent Regulation Only During the Larval Stage'. Theoretically, the adult population varies with the productivity of the larval habitat (substitute early-stage, benthic, juveniles in the case of lobster), and if adults are long-lived, the age structure would reflect the relative 'larval' success of recent year classes. However, while such theory may have been suitable for guiding research on lobster recruitment mechanisms in the 1970s, the current improved recruitment trend is more reminiscent of an r-selected strategist, and accepted life-history theory appears to have little application. Rather, the scenario seems akin to the current 'supply-side' paradigm where recruitment levels can change internal controls normally operating within a system (Gaines and Roughgarden, 1985; Lewin, 1986; Underwood and Fairweather, 1989).

American lobster yields have always been geographically variable. Although landings improved in all fishing areas during the 1980s, yields from some increased far more than in the traditionally stable areas off Maine and Newfoundland (Fig. 3). Pezzack (in press) distinguished areas stable between 1947–1986, including Maine, Newfoundland, Grand Manan, southwestern Nova Scotia, the Gulf of St. Lawrence, Quebec, northeastern Cape Breton and Massachusetts. The areas which have exhibited wide fluctuations in landings are the eastern shore of Nova Scotia and southeastern Cape Breton. Lobster fishing grounds along the Atlantic-coast of Nova Scotia have displayed differing degrees of response to the improved recruitment of the 1980s (Fig. 5). Inter-ground stability differences could be due to differences in continental shelf area, which effect retention of larvae and substrate and food availability for juveniles, as well as physical environment.

DISCUSSION

Although a fundamental appreciation of the American lobster's life history was achieved early in this century with classic studies by Herrick (1896, 1911) and Hadley (1906, 1908) the subsequent history of research into stock-recruitment relationships has been somewhat *ad hoc*, apparently suffering from a lack of a concerted approach. Research thrusts seem to have changed opportunistically with ecological fads (Abrahamson *et al.*, 1989) rather than doggedly addressing fundamental questions until they were solved. Work during the 1940s and 1950s focussed mainly on growth and movement of lobster that had already recruited into the fishery in an effort to prevent growth overfishing (Wilder, 1947, 1948, 1958). During the 1960s to mid-1970s there were various attempts both to identify stocks (Saila and Flowers, 1969; Barlow and Ridgeway, 1971; Cooper and Uzmann, 1971; Tracey *et al.*, 1975) and to explain trends in landings through environmental influences such as temperature (Dow, 1961) and river discharge (Sutcliffe, 1973). Lobster research from the mid-1970s to early 1980s was influenced by

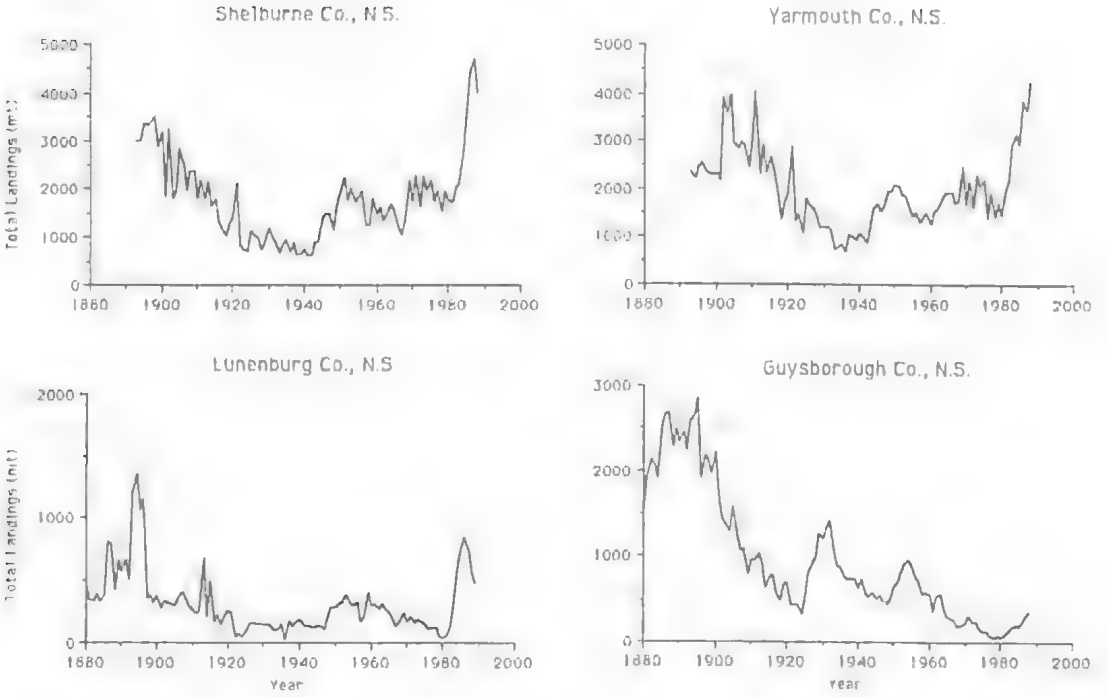

FIG. 5. Annual landings of American lobster for representative historically stable (Shelburne County, Yarmouth County) and collapsed (Lunenburg County, Guysborough County) fishing grounds along the Atlantic coast of Nova Scotia, to illustrate various degrees of response to the general increase in yield during the 1980s; for geographic areas that have remained more stable throughout see profiles for Maine and Newfoundland (Fig. 3).

vigorous arguments over the impact of the causeway across the Strait of Canso (McCracken, 1979) and the ecological implications of destructive grazing by sea urchins (Elner and Vadas, 1990). The controversy subsided without clear resolution as landings recovered, and the emphasis of research changed again. Recent investigations focus on larval transport and the movement of adult lobsters although work on the population ecology of early life-history stages has continued. While the numerous studies on *H. americanus* over the past century provide a valuable general understanding, they reach no consensus on the major factors influencing recruitment.

The recent recruitment pulse and major increase in landings in Canada started around 1981 and has unshackled both the Sutcliffe model correlating Quebec lobster landings and river run-off (Drinkwater *et al.*, in press) and stock discrimination based on historical landings patterns (Campbell and Mohn, 1983). We believe that the causitive mechanism(s) must be very powerful to have effected virtually all lobster fisheries. Landings increased more or less in unison throughout coastal Nova Scotia and the southern Gulf of St. Lawrence, but in varying degrees in local areas, suggesting that large environmental force(s) may have acted during the same general time period to influence recruitment. The various density-dependent mechanisms invoked as population controls of the cryptic early benthic stages of lobster in local areas are unlikely to account for large-scale recruitment events. Changes in climate coupled, perhaps, with decreased exploitation rates in the last 20 years are a more probable cause. We speculate that larval and early juvenile survival was enhanced during several years in the late 1970s-to-early-1980s through increased growth and food availability probably due to an increase in water temperature (Fig. 4). Also, low fishing mortality in some areas during the late 1970s could have allowed more females to produce eggs and the increased number of eggs per recruit may have swollen recruitment into the fishery 5–8 yr later (Campbell, 1990b). Subsequently differential individual growth rates spread this cohort into the fishery over several years, resulting in 3–5 years of record landings. Coupled with increased lobster abundance, fishing effort and total mortality

of lobster increased dramatically in some areas (Campbell, 1990b).

'Supply-side' lobster recruitment controlled by an unpredictable climatic phenomenon has profound implications for fisheries management. Most management initiatives are based on the understanding that fishing mortality can have a strong impact on annual recruitment and that regulation of fishing pressure can preempt recruitment problems. If, as the events with lobster in the northwestern Atlantic over the past 10 years suggest, recruitment can be independent of fishing pressure then proactive management becomes essentially impotent, with managers only being able to react to changes in stock abundance as they occur. The situation would make recruitment predictions largely dependent on understanding and forecasting the causative environmental mechanism(s). Traditional fisheries models based on concepts such as surplus production and stable recruitment would be largely redundant.

While much is known about the biology of American lobster a conspicuous inability to understand recruitment remains compared to the successes achieved for the western rock lobster, *Panulirus cygnus* (Caputi and Brown, 1986; Phillips, 1986). Progress appears to have been hindere'd by three factors. First, the numerous attempts to develop a passive collector to intercept and index the recruitment strength of American lobster postlarvae at settlement have all failed. Instead, trial collector designs have succeeded in capturing early benthic stages of the commercial rock crab, *Cancer irroratus* (Beninger *et al.*, 1986). Second, comprehensive long-term data sets on oceanographic events (other than sea surface temperature and river discharge), prerequisites to exploratory correlation analysis and effective generation of hypotheses on physical controls on lobster recruitment, have not been available. Thirdly, the overall scientific approach appears to lack rigor. Although numerous explanations for recruitment patterns in American lobster have been advanced there has been little actual experimental testing of actual hypotheses and no concerted attempt to sequentially advance by 'strong inference' (Elner and Vadas, 1990). We believe that only by effectively addressing these three factors together can a realistic model of a biological lobster stock, integrating physical and oceanographic parameters with the complete life-cycle and ecology in a defined area through time, be achieved. Such a model of the whole system is required before the various system components can be viewed in context, their relative influences explored, and predictive models developed.

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LIFE HISTORY CHARACTERISTICS OF *LITHODES FEROX* (ANOMURA: LITHODIDAE) OFF NAMIBIA

Lithodes ferox (Filhol) is a deep water anomuran crab that lives on the upper continental slope off West Africa. It constitutes an important by-catch of the demersal hake fishery (Abelló and Macpherson, 1986) and of the red crab trap fishery (Melville-Smith, 1982) in Namibia. Despite its abundance and its potential as a fishery resource, little is known of its biology and ecology.

L. ferox was sampled off Namibia in the Benguela upwelling region during ten fishery research cruises performed between 1983 and 1989 on board freezer-trawlers. The study area was between latitudes 23°S and 30°S and depths between c. 50 and 500 m. Some deeper trawls were occasionally performed. The area was divided into strata of one degree latitude and 100 m depth.

Sex, carapace length, presence of eggs or egg remains on the female pleopods, and occurrence of a rhizocephalan parasite were noted for all crabs. Occurrence of epibionts was also noted in some cruises. Sex-ratio analysis was performed when more than 10 individuals were caught in a trawl. Fecundity was calculated from recently extruded eggs from dry weight proportions.

Distribution

Some interesting features have been identified in the distribution patterns of *L. ferox*: (1) Occurrence of a seasonal bathymetric migration. The species rarely occurs at depths less than 400 m in summer, while there is a dispersion of the population towards shallower waters (<300 m) in winter. These movements appear to be related to: (a) The reproductive biology of the species: Almost all of the females occurring in the shallowest strata (300–400 m) in winter are ovigerous, the proportion clearly decreasing with depth; and (b) Upwelling-related hydrographic events. Oxygen levels on the bottom show seasonal decreases (Chapman and Shannon, 1985; Mas-Riera *et al.*, 1990). Lowest levels are found in summer. (2) Recruitment to the adult population takes place in deep water. Juvenile crabs are found almost exclusively in areas deeper than those inhabited by the adult population. The mean size of both males and females decreases with depth. (3) Sex-ratio patterns. Sex-ratio distribution shows a clear tendency for the species to form unisexual groups. Males tend to be captured with other males and females with other females.

Reproductive Biology

As stated above, the seasonal movements performed by the population can be partially considered as a reproductive migration. A high proportion of ovigerous females is found in all seasons. Most adult females are ovigerous. The size of female sexual maturity, calculated from the occurrence of ovigerous females, lies between 75 and 90 mm carapace length (CL). The number of eggs carried by ovigerous females is related to size and fluctuates between 2500 and 8000. The mean diameter of recently extruded eggs is 1.97 mm.

The patterns of epibiosis by the pedunculate barnacle *Poecilasma kaempferi* indicate several features related to the reproductive and moulting biology of the host: (a) different moulting patterns occur between the sexes; (b) the approximate size of puberty moult lies between 80–90 mm CL in males and between 70–80 mm in females; (c) males do not have a terminal moult; (d) females apparently have a terminal moult; (e) there is a close match of the ovigerous/size pattern with the epibiosis/size pattern.

Reproductive and epibiosis patterns suggest that (a) puberty moult coincides with terminal moult in females. This would imply (b) that females would accordingly only undergo one reproductive cycle.

A small proportion of adult crabs is infested by the rhizocephalan *Briarosaccus callosus*: 2.6% females and 4.3% males. These crabs are not able to reproduce.

Discussion

Several features of the life history of *L. ferox* may be inferred. Ovigerous females migrate in winter towards shallower (300–400 m) waters, where hatching presumably occurs. Larvae may then be carried to the surface by the upwelling waters and dispersed northwards and offshore by the Benguela current. Recruitment takes place in deeper waters, as happens in other deep-water crabs (Wigley *et al.*, 1975). As crabs grow they move into shallower waters, as shown by size frequency distributions and mean size per trawl. Adult crabs then segregate into unisexual groups in the main habitat (muddy bottoms, 300–500 m depth). In summer, the population moves into deeper waters, presumably in relation to the seasonal decrease in bottom oxygen levels.

Puberty moult apparently coincides with terminal moult in females, but not in males. Females could accordingly only undergo one reproductive cycle. A small part of the population is parasitized by a rhizocephalan and would not therefore be able to reproduce.

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SPATIAL AND TEMPORAL RECRUITMENT PATTERNS OF DUNGENESS CRAB IN THE NORTHEAST PACIFIC

GLEN S. JAMIESON AND DAVID A. ARMSTRONG

Jamieson, G.S. and Armstrong, D.A. 1991 0901: Spatial and temporal recruitment patterns of Dungeness crab in the northeast Pacific. *Memoirs of the Queensland Museum* **31**: 365–381. Brisbane. ISSN 0079-8835.

The Dungeness crab, *Cancer magister*, is the main crustacean species exploited in the northeastern Pacific from central California to Kodiak, Alaska. Abundance along the coast south of British Columbia has fluctuated in a generally cyclical manner which a number of studies have tried to explain, but several unrefuted competing hypotheses currently remain preventing resolution of this question. A combination of mechanisms seems a likely possibility and additional data appears necessary before understanding is achieved. There is general agreement that fluctuation in catch is a reflection of variable year-class strength and recent studies of larval and 0+ crab have investigated the importance of abiotic and biotic factors. Dungeness crab are regionally unique in that while many of their pelagic larvae move tens of kilometres offshore, they must return to shallow water to survive as juveniles. Oceanographic and meteorological conditions seem to be particularly influential in determining the magnitude of dispersal and onshore movement, and the conditions which allow successful settlement off Vancouver Island have now been described. Strong settlement does not necessarily equate with a strong year class at harvesting, though, and biotic factors primarily determine survival of juvenile crab. Finally, there is increasing evidence that the crab population in Georgia Strait and Puget Sound, i.e. in the 'inland sea' inside of Vancouver Island, may be a distinct stock with dispersal, recruitment and population dynamics characteristics unique from the population found on the open outer coast. Comparison of common features between the two stocks is allowing evaluation of the relative importance of major factors influencing population abundance and ultimately, landings. □ *Dungeness crab, Cancer magister, fishery, recruitment, larvae, dispersal, population dynamics, northeast Pacific.*

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Studies of larval and juvenile stages of commercial Decapoda have generally been done for purposes of describing ecology, reproductive biology, population dynamics, habitat requirements, and predator/prey relationships. While quantitative studies of catch-per-unit-effort (CPUE) and density have been used to estimate the next year's recruitment for incorporation into fisheries management plans, data have been rarely amenable for accurate predictions in excess of one year (Cobb and Caddy, 1989). Although predictive capability is a desirable aspect for management, in the case of Decapoda, this is often frustrated because of high seasonal and spatial variability, as well as tremendous interannual variability, caused by a suite of biotic and abiotic factors (Jamieson, 1986a, b; Botsford *et al.*, 1989). This is particularly the case for quantitative data on larvae, and such data are typically of limited use in definition of stock-recruitment relationships or prediction of ultimate year-class strength in the fishery.

Only a few attempts have been made to estimate adult abundance from measures of larval abundance and female fecundity. Nichols *et al.* (1987) calculated female stock biomass of *Nephrops* lobster in the Irish sea from estimates of larval production and female fecundity and incorporated these data into a multi-species model of lobster and cod interaction. Application of this same technique was used by Nichols and Thompson (1988) to estimate stock size of the edible crab, *Cancer pagurus*. Similarly, Incze *et al.* (1987) accounted for significant differences in interannual densities of larval tanner crab (*Chionoecetes opilio*) based on quantitative changes in number of adult females. However, their suggested relationship did not hold in all years of their study, nor did it apply well to a congener, *C. bairdi*.

Use of indices of juvenile abundance in Decapoda to predict adult spawning stocks or relative strength of fisheries have only been developed successfully in a few instances. Relative year-class strength of juvenile rock lobster (*Panulirus cygnus*), as measured by an index of puerulus

settlement, was correlated to the strength of commercial fisheries four years later (Caputi and Brown, 1986; Phillips, 1986; Phillips and Brown, 1989). A similar approach was used in stock-recruitment analyses of blue crab (*Callinectes sapidus*) populations in Chesapeake Bay (Tang, 1985). A more thorough study was recently presented by Lipcius and Van Engel (1990) based on a thirty year time series of data, from which they concluded that a significant correlation exists between juvenile abundance and spawning stock size.

In this paper, we review recruitment of Dungeness crab, *Cancer magister* Dana, considering all three major life stages: embryo, larvae and juveniles. We define recruitment as abundance change between consecutive life history stages, culminating ultimately in an annual increase in abundance of the fished population since larger crabs only moult once annually. We emphasise recruitment to both larvae and juvenile life history stages, since these are periods of great mortality, and generally the times when relative year-class strengths at recruitment to the fishery are typically established for this species. Events progressively occurring throughout the life history cycle are discussed as these will bear on the abundance of crabs at each successive life history stage leading to recruitment to the fishery. We also consider recruitment in four major geographic regions: 1) the outer coast from San Francisco, California, to Cape Flattery, Washington; 2) off the west coast of Vancouver Island; 3) north of Vancouver Island to Kodiak Island, Alaska; and 4) the Georgia Strait–Puget Sound (GS–PS) complex. These specific locations were selected on the basis of broad-scale oceanographic boundaries, unique oceanographic singularities, and available data on local Dungeness crab population dynamics.

DUNGENESS CRAB LIFE HISTORY

Dungeness crab ranges from the Pribilofs Islands to Magdalena Bay, Mexico, in the northeastern Pacific (Hart, 1982; Jensen and Armstrong, 1987) and is commercially exploited from northern California to Kodiak, Alaska. This spatial distribution overlaps generally recognised oceanographic domains (Dodimead *et al.*, 1963; Thomson, 1981; Ware and McFarlane, 1989) for coastal areas of the northeastern Pacific Ocean, and this probably influences observed recruitment patterns and makes causative generalisations inappropriate for the coast as a whole.

Dungeness crab have a relatively long pelagic larval period, with five zoeal stages and one megalopal stage before settlement to the benthos. Total larval period is about 110 days at ambient temperatures (Poole, 1966; Lough, 1976; Reilly, 1983), with about 28 days spent as megalopae (Hatfield, 1983). It is somewhat unique among nearshore benthic species in that a portion of its larvae is commonly found considerable distances offshore, with later stage zoea and early stage megalopae tending to be found furthest offshore (Reilly, 1983; Jamieson and Phillips, 1988; Jamieson *et al.*, 1989). Late intermoult stage megalopae are found in abundance progressively closer inshore (Hatfield, 1983; Jamieson and Phillips, 1988), but mechanisms which would bring megalopae located more than about 30–40 km offshore to appropriate nearshore locations (<64 m depth) for enhanced survival as juveniles (Carrasco *et al.*, 1985) have not yet been satisfactorily determined (Jamieson *et al.*, 1989). Offshore movement presumably facilitates larval dispersal, but it may be that most nearshore settlement results from those larvae which remained shoreward of region-specific, mostly as yet undetermined, oceanographic boundaries.

Most larval settlement is typically in May and June along the outer coast, with settlement in both estuarine and nearshore locations. Much recent study in Washington (Gunderson *et al.*, 1990) has been focused on the relative importance of some of the region's major estuaries (Willipa Bay and Grays Harbor, Washington), compared with the area shoreward of the 50 m isobath along the outer coast, in terms of their habitat contribution to overall regional recruitment. Juvenile dynamics of Dungeness crab in both these locations have been relatively well described, and it has become evident that considerable annual variation can occur. Female crab extrude their first egg mass as 2 y-olds at about 115 mm, notch-to-notch carapace width (CW), while males are larger than females at puberty and begin mating successfully at about 140 mm CW (3-y olds). Males mostly recruit to the fished population at 3–4 y of age.

THE PHYSICAL ENVIRONMENT

Regional Circulation

The general surface current pattern over the continental shelf has been described by a number of recent reports, including Hickey (1979, 1989), Freeland *et al.* (1984), and Thomson *et al.* (1989). The west coast of Vancouver Island borders the bifurcation zone of the Subarctic Current, an extensive, albeit poorly defined, zonal flowing, cross-Pacific surface current (Fig. 1). Seaward of the continental shelf, this current

splits into the pole-ward flowing Alaska Current and the equator-ward flowing California Current. Direct observation of a persistent northward near-surface flow off Vancouver Island indicates that the offshore circulation there is dominated by the Alaska Current (Thomson *et al.*, 1989). Dungeness crab occur in two of the three principal oceanographic domains recognised by Ware and McFarlane (1989), namely the Coastal Upwelling and the Coastal Downwelling Domains (Fig. 2). The former extends from Baja California to the northern tip of Vancouver Island and is defined by the normal summer pattern of wind stress curl and Ekman divergence, i.e. upwelling (Parrish *et al.*, 1981). Generally northwest winds from May to September result in a southward-flowing Shelf-Break Current (SBC) centred on the outer margin of the continental shelf. This causes upwelling of intermediate depth, cold water onto the continental margin and offshore transport. Southwest winds dominate this Domain during the winter, causing downwelling, onshore transport and poleward transport of surface waters in a seasonal current called the Davidson Current. The annual transition between the predominantly upwelling and downwelling seasons occurs in the spring (Mar.–Apr.) and fall (Sept.–Oct.) with the seasonal reversal in prevailing alongshore winds and currents (Thomson *et al.*, 1989).

The Coastal Downwelling Domain extends from the northern tip of Vancouver Island northward along the coast of southeast Alaska and then westward along the Aleutian Islands. The Alaska Current flows adjacent to the coast of North America seaward of the coastal margin, being driven by a wind stress curl and augmented by freshwater addition and an along-shore, wind-induced sea level gradient. Freshwater runoff causes a poleward flowing coastal current, extending to about 40 km offshore. The transition in prevailing coastal winds in the spring is weak, but due to the general behaviour of the cyclonic meteorological systems in the region, wind stress tends to augment the baroclinic component of the coastal circulation by confining it close to shore. As a consequence, from central British Columbia north to about Kodiak Island, there is a generally persistent downwelling except for a few months in the summer (Ware and McFarlane, 1989). The southern boundary of this Domain is not sharply defined from a strictly oceanographic viewpoint.

The continental shelf off Vancouver Island, although not a recognised Domain itself, being part of the Coastal Upwelling Domain, has a unique oceanographic feature which for Dungeness crab makes this area intermediate between the two Domains discussed. The outflow from Juan de Fuca Strait, being of lower density runoff from rivers entering the GS–PS complex, forms the source of the Vancouver Island Coastal Current (VICC). This is a persistent pole-ward flowing coastal current, confined mostly landward of the 100 m isobath on the continental shelf, that extends to about the northern tip of Vancouver Island (Thomson *et al.*, 1989). After the spring transition, this current flows counter to the prevailing northwesterly winds along the outer coast and the Shelf-break Current while after the fall transition, it flows with and merges with the Davidson Current.

Topography

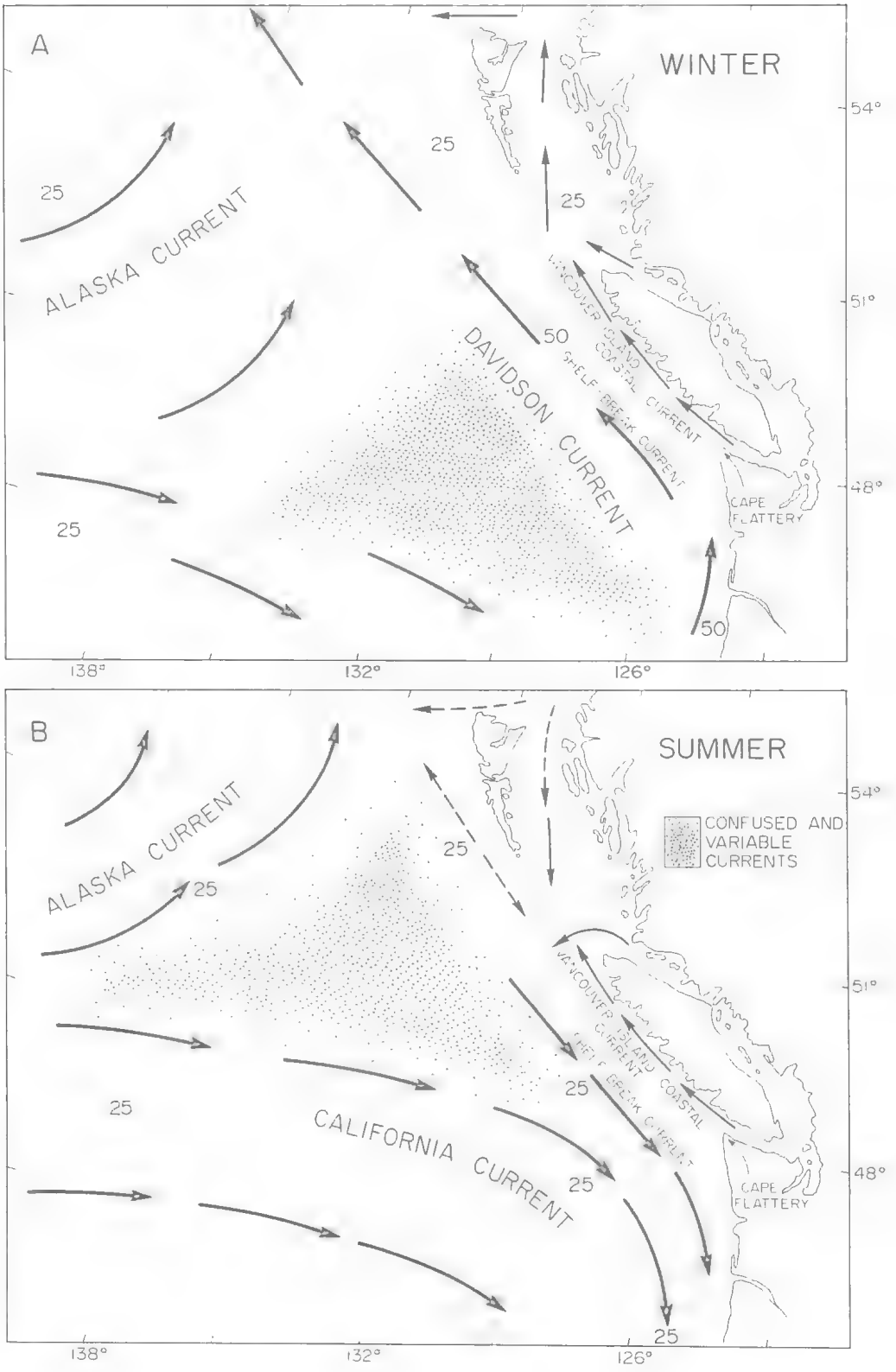
Washington, Oregon and California typically have broad, extensive, sandy beaches extending for scores of kilometres, with few bays or headlands. The coast of British Columbia and southeast Alaska is mostly rocky and fjordal, with many headlands, islands, small bays, and relatively small, crescent-shaped beaches. Dungeness crab most commonly occur in a habitat of extensive sand, and so available optimal habitat is generally less north of Washington State.

Georgia Strait and Puget Sound consist of a variety of habitats, with fjordal inlets predominant on the eastern side in Canada and gently sloping, gravel-sand bottoms predominant in Puget Sound and the southeastern side of Vancouver Island. The Gulf and San Juan Islands are in the middle of this region and have mostly steep, rocky shores, which are of marginal suitability the Dungeness crab.

LIFE HISTORY STAGES AND THEIR RECRUITMENT

Parent Population and Fecundity

The extensive pelagic larval duration of Dungeness crab in areas of strong along-shore ocean currents apparently prevents development of discrete, genetically distinctive populations on the outer coast (Soulé and Tasto, 1983). There is no evidence to suggest that crab larvae have the navigational ability to 'home' and return to the specific location where they were hatched. In the Coastal Upwelling Domain, larvae hatch in January–February during a period of strong, northward-flowing nearshore currents, which about two months later typically reverse to flow equally strongly in a southerly direction. With an approximately four month larval period, this may result in extensive larval dispersal. Larvae hatching off northern California could theoretically move as far north as British Columbia before currents reverse. Similarly, larvae hatch-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CALIFORNIA CURRENT
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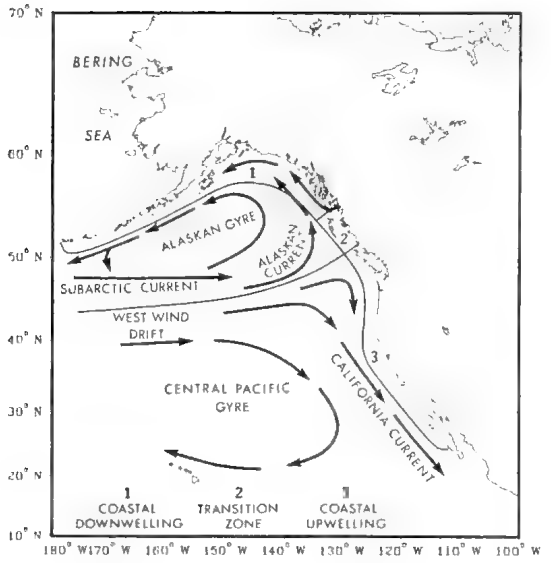

FIG. 2. Approximate areas of oceanic domains and prevailing current directions in the northeast Pacific Ocean (modified from Ware and McFarlane, 1989).

ing near the southern boundary of the Coastal Downwelling Domain could move to its northern boundary, while larvae hatching in the northern part of the Coastal Upwelling Domain could move into the Coastal Downwelling Domain, entirely because of passive transport. The consequence is that considerable mixing of progeny hatched at different sites probably occurs, making it impossible to clearly identify the parent population of juveniles that recruit at any particular location. As discussed by Jamieson (1986a), the extent to which a local population may contribute to local recruitment is unknown, but it appears with available data to be slight.

It is illegal to harvest female Dungeness crab in Alaska, Washington, Oregon and California. Although this can legally be done in British Columbia if females exceed the minimum legal size (MLS) of 155 mm CW (= 165 mm, spine-to-spine carapace width), in practice, few are harvested because of poor market demand, since meat yield is less, and there is a general lack of sufficiently large female crab. The size limit for males, although not known to be based on any documented biological data, presumably allows successful mating to regularly occur since in most locations many female crab caught during the winter carry extruded, fertilised eggs (Jamieson and Armstrong, unpubl.). Jamieson (1986a) discussed in detail the available data supporting assumptions relating to crab fecundity, and concluded that if maximising reproductive potential is an identified goal, then insufficient data are presently available to establish what relative level of progeny production is being achieved. Nevertheless, although commercial landings have varied substantially over time (Fig. 3), detailed surveys of larval occurrence (Jamieson and Phillips, 1988; Jamieson *et al.*, 1989; Jamieson, unpubl.) have consistently found widespread high levels of larval abundance over the continental shelf off Vancouver Island and Washington, and in Georgia Strait in the five years studied to date. Annual settlement of larvae has varied substantially during this period (Jamieson *et al.*, 1989), suggesting that factors other than overall larval production are the major determinants in establishing year-class strengths.

Larval Settlement

Some Dungeness crab larvae occur at great distances offshore and while this no doubt facilitates and/or is the result of species dispersal, there is always the risk of larval wastage in that many larvae may never return successfully to geographic areas favourable to juvenile survival. It has not been established how far offshore most larvae which do settle and survive have actually gone, but the relative lack of early-stage megalopae, in abundance, in close proximity to shore in outer coast areas, at least off British Columbia and Washington (Jamieson *et al.*, 1989; Jamieson, unpubl.), does suggests that movement in at least the kilometre scale can be expected. Assumed aspects relating to this have been discussed in detail by Jamieson *et al.* (1989), and they, along with Jamieson and Phillips (1988), have demonstrated that juvenile recruitment patterns off the outer coast of Vancouver Island, British Columbia, are substantially different from that off Washington, Oregon and California (Fig. 3).

Outflow from rivers emptying into the GS–PS complex is predominantly through surface outflow in Juan de Fuca Strait, and this outflow, the VICC, subsequently moves northward adjacent to the coast of Vancouver Island. Crab megalopae are virtually absent in this current and are concentrated on its seaward boundary (Jamieson and Phillips, 1988; Jamieson *et al.*, 1989). It thus apparently acts as a barrier to the movement of plankton to shore (Thomson *et al.*, 1989), and

FIG. 1. Prevailing surface circulation off the British Columbia–Washington coast. A, winter. B, summer. Broken arrows indicate uncertain currents. Numbers give speeds (cm s^{-1}) (modified from Thomson, 1981).

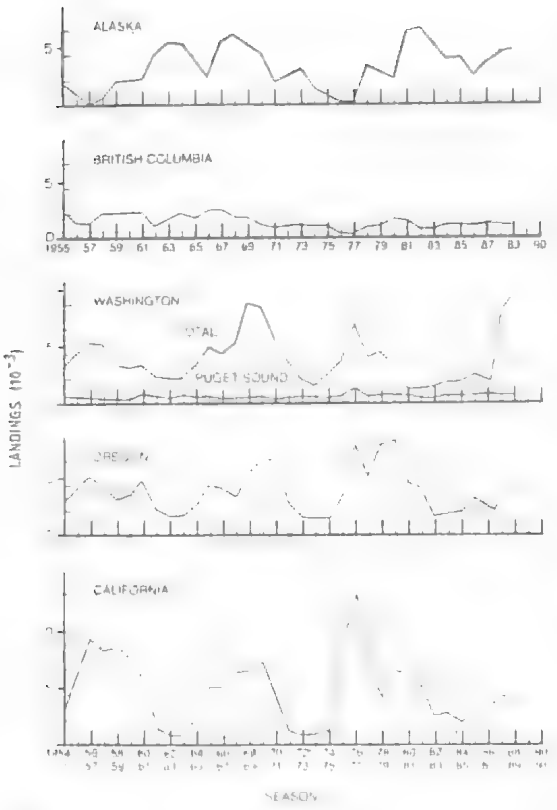

FIG. 3. Dungeness crab landings by political jurisdiction off western North America.

recent study by Jamieson and Thomson (unpubl.) indicates that megalopae are being concentrated in an area of upwelling and/or seaward surface current movement of relatively low velocity (1–5 cm sec^{-1}) between the VICC and the SBC (Fig. 4). Shoreward movement of surface waters is associated with southerly winds (Fig. 5) but unless sufficiently intense or prolonged, such movement is only to the seaward boundary of the VICC. The presence of the VICC seems to direct most up-welled water offshore, while because of the shallow depth of the nearshore portion of the continental shelf, no shoreward movement beneath the VICC is possible. The only apparent opportunity for substantial movement to the shore is when the VICC temporarily breaks down because of cessation of the surface outflow in Juan de Fuca Strait, which is typically associated with sustained, strong southerly winds. This is accompanied by a rise in mean coastal sea level, enhanced wind and convective mixing of surface waters and the cessation of upwelling — events similar to those which occur during and after the Fall Transition (Thomson *et al.*, 1989). From a crab recruitment, major recruitment on the west coast of Vancouver Island is thus only possible when appropriate meteorological events occur when megalopae are present and ready to settle, namely May and June (Jamieson and Phillips, 1988). This does not always occur, and since 1983, major crab settlements at Tofino, British Columbia, were only observed in 1983 and 1989 (Smith and Jamieson, 1989a; Jamieson, unpubl.). Little settlement occurred from 1985 to 1987, while there was only limited settlement in 1988.

South of Cape Flattery, located at the southern, seaward end of Juan de Fuca Strait, the absence of a 'barrier' current adjacent to the coast means that settlement is not physically impeded by nearshore currents, although years of excep-

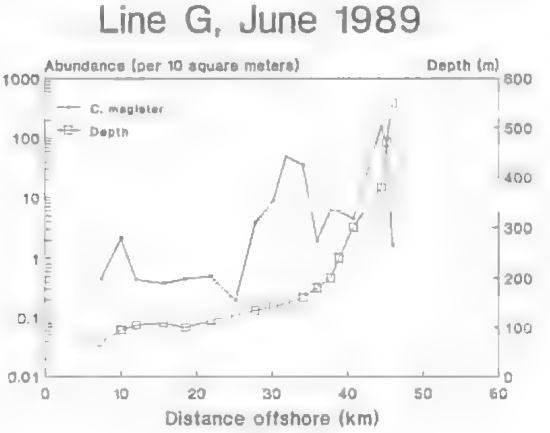

FIG. 4. Abundance of Dungeness crab megalopae in across-shelf transects in relation to depth. The north-flowing Vancouver Island Coastal Current is mostly shoreward of 100 m depth, with the south-flowing Shelf-Break Current on the seaward side.

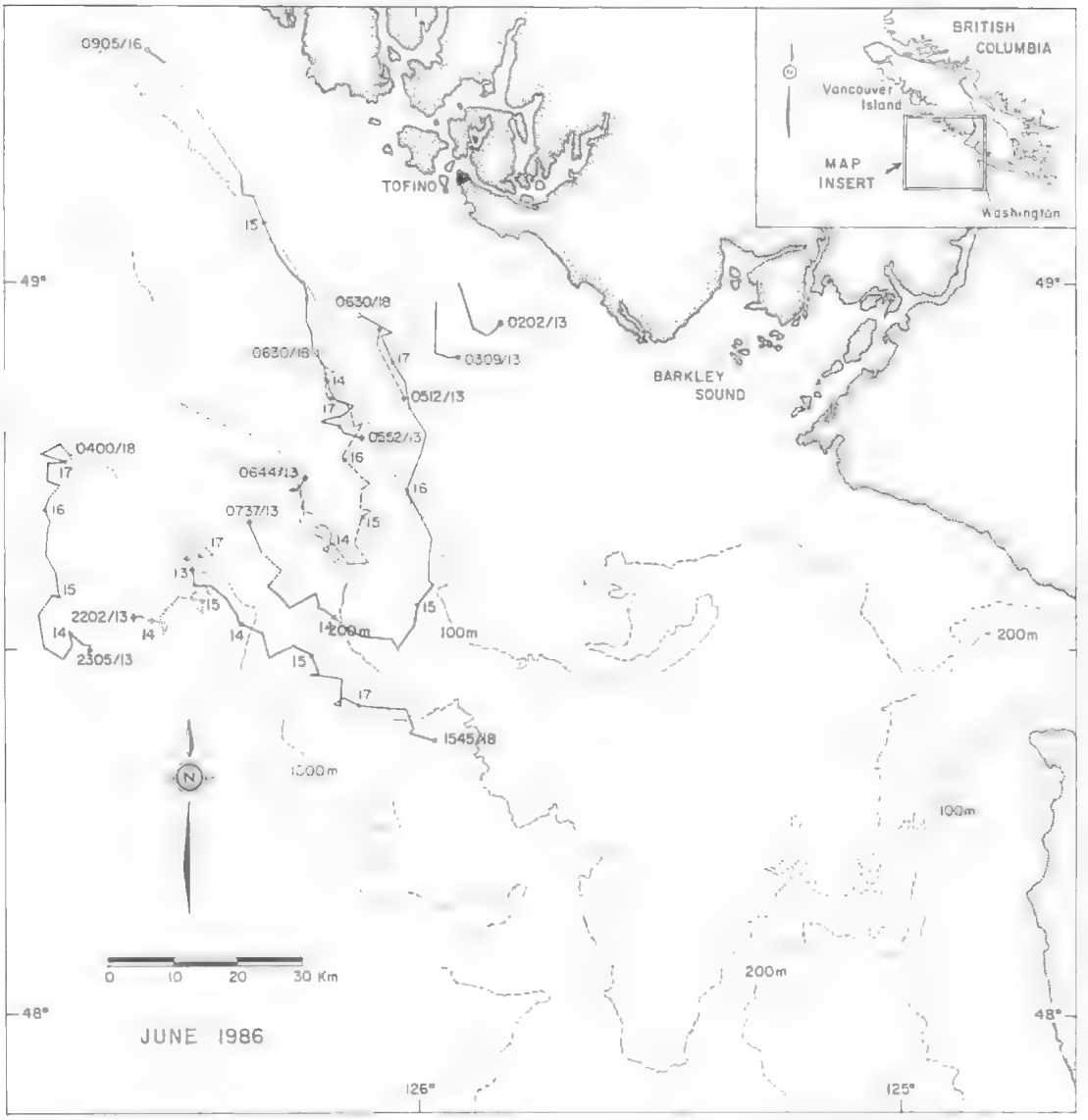

FIG. 5. Tracks of 9 drifters deployed along a transect off Tofino, British Columbia, on June, 1986. Marks along each track indicate the position of each drifter at noon on the day (the adjacent 2-digit number) indicated. Four-digit numbers refer to the hour the drifter was deployed and or retrieved (from Jamieson *et al.*, 1989).

tional settlement are also typically sporadic. The temporal pattern of settlement along the American coast has shown an annual variability in magnitude of about ten-fold, with no obvious similarity to that off Vancouver Island. Major landings have occurred about every 9–10 y (Fig. 3) and causative mechanisms have been hypothesised and discussed extensively (Jamieson, 1986a; Methot, 1989; Botsford *et al.*, 1989). A satisfactory explanation has yet to be fully established. While larvae have been observed in abundance over most of the continental shelf, some data suggest (R.A. McConnaughey, Univ. Washington, Seattle, WA, pers. comm.) that in years of major settlement off Washington, most larvae may never move far from shore. This, coupled with that area's extensive favourable habitat, increases larval survival at settlement.

There have been no studies of relative larval distribution and abundance off Alaska. Annual commercial landings (Fig. 3) do not show the same pattern evident off British Columbia or

further south, but this may be because, like the crab fishery in British Columbia (Jamieson, 1985), regional landings are the composite of a number of distinct regional fisheries (Koeneman, 1985; Kimker, 1985; Merritt, 1985; Eaton, 1985). Recruitment patterns in each region may be largely disconnected, giving no clear pattern for the region as a whole.

Larval settlement patterns in the GS–PS complex are different from those along the outer coast. Megalopae settle in abundance mostly later in the year (August–September), are smaller in size, and show some minor, although perhaps significant, morphological differences (DeBrosse *et al.*, 1990). Recent studies of megalopal spatial and vertical distribution (Jamieson and Phillips, unpubl.) in Georgia Strait indicate that in July, megalopae are found in high abundance throughout the Strait but that their vertical distribution during daylight seems to differ from that found off the outer coast (Fig. 6). In the Strait, megalopae appear to descend to depths of about 150 m while offshore, they are seldom found in quantity below about 40 m (Jamieson *et al.*, 1989). While megalopae have been caught below 100 m on the outer coast (Jamieson, unpub.data), they have been late intermoult stage, suggesting they may have been in the process of settling. Dungeness crab megalopae have been caught as deep as 273 m in coastal inlets in epibenthic sled tows (Jamieson and Sloan, 1985), a depth where they are unlikely to survive as juveniles.

This difference in megalopal diel migration behaviour has interesting consequences, particularly if zoea from the two regions show similar differences as well. Since summer water temperatures below about 50 m in most of the Strait are 7–8°C (Thomson, 1981) [temperatures on the outer coast at 25–50 m depth are about 12–14°C (Thomson *et al.*, 1989)] and daylight in July is about twice as long as darkness, growth rate would be reduced, thereby probably extending the larval period and possibly resulting in their smaller size at settlement. It also could result in stock isolation, since the surface water of Juan de Fuca Strait, the main connection between the GS–PS complex and the Pacific Ocean, flows predominantly seaward (Fig. 7) while water below about 80–100 m flows predominantly shoreward (Thomson, 1981). Georgia Strait megalopae, which may spend most of their time at depth, would thus tend to be retained within the GS–PS complex while outer coast megalopae, which are mostly near the surface, would generally be prevented from entering the Strait. Sustained southerly winds can, though, temporarily stop the outflow of surface water in

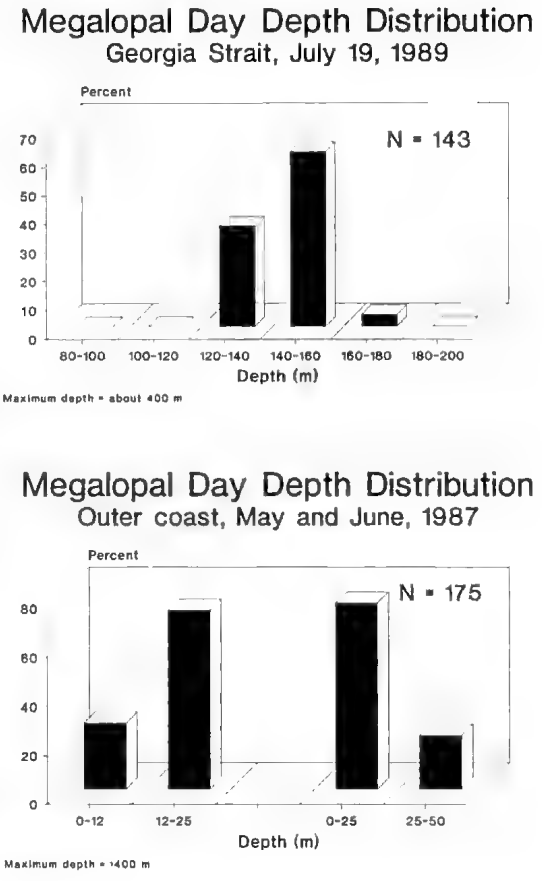

FIG. 6. Daytime depth distributions of megalopae off the outer coast (modified from Jamieson *et al*,. 1989) and Georgia Strait. Data collected with Tucker trawls in 1987 and 1989, respectively.

Juan de Fuca Strait and the penetration of outer coast water (Fig. 8), sometimes containing megalopae (P. Dinnel and D. Armstrong, unpubl.), has been documented (Thomson, 1981; Thomson *et al.*, 1989). However, for reasons described later, this is mostly on the American side of the Juan de Fuca Strait and relatively few outer coast megalopae would seem likely to penetrate into the Canadian waters of Georgia Strait.

Juvenile Survival

Upwelling Domain: Megalopae settle to the benthos and metamorphose to first instar juvenile crabs primarily between May and June along the coast from Northern California through Washington State (Botsford *et al.*, 1989). Most studies of juvenile crab populations in this area have been descriptive portrayals of distribution and abundance, growth and size-at-instar

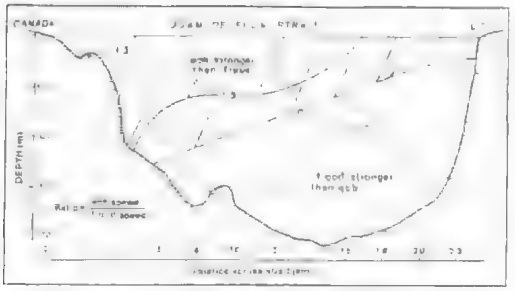

FIG. 7. Average direction of water flow in cross-section of Juan de Fuca Strait from Pillar Point (USA) to Port Renfrew (Canada). Shaded is a seaward flow, no shading is a landward flow (from Thomson, 1981).

(Cleaver, 1949; Poole, 1967). There have been few quantitative surveys that provided estimates of mortality or indices of year-class strength, but those done indicate that considerable differences in survival occur within a region, depending on both abiotic and biotic factors. It is important to briefly discuss these factors in considering how recruitment is mediated.

Although larvae may occur in abundance offshore, juveniles for the most part seem to survive only in nearshore locations, in water generally shallower than 40 m (Gotshall, 1978; Carrasco *et al.*, 1985). Estimated density increases approximately 20- to 50-fold as depth decreases from 41–70 m to 16–40 m (Carrasco *et al.*, 1985; McConnaughey and Armstrong, unpubl.). Even inside of the 40 m isobath, density of 0+→0+ crab fluctuates appreciably because of substrate type. It is highest on well sorted sand and lowest on gravel-cobble (Fig. 9). Trawl samples off Grays Harbor, Washington, in 1985 showed 0+ crab densities as high as 30,000 crab/ha on sand, compared to only about 200/ha on gravel. Post-settlement crab growth on the outer coast from June through September is typically relatively slow, and young-of-the-year are only usually about third instar (13 mm CW) by September (Fig. 10; Gunderson *et al.*, 1990). This is due in large part to bottom water temperatures of less than 10°C in this upwelling system. As a consequence of small size, crab mortality is high, since they remain susceptible to many predators (Reilly, 1983) through the winter. Even numerically strong year-classes at settlement, such as that of 1985 (Gunderson *et al.*, 1990), can have their abundance depleted sufficiently through their first winter to become unexceptional at recruitment to the fishery.

Quantitative data of sufficient 0+ →0+ y-class

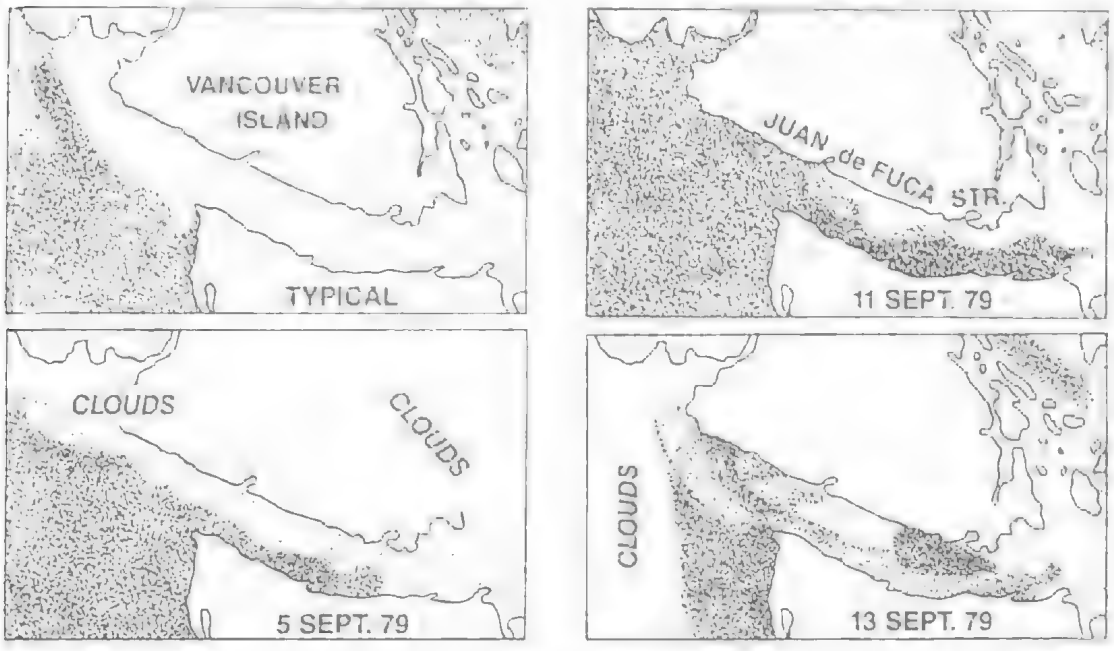

FIG. 8. Drawings based on infrared satellite images of sea-surface temperatures, showing a sequence of warm-water intrusion (heavy stippling) into Juan de Fuca Strait from the Pacific Ocean in September, 1979. Intrusion was confined to the southern half of the Strait and reached a maximum of 135 km from the entrance. Four days after the cessation of the causative southwest winds, the seaward estuarine circulation was reestablished and the intrusion began to be advected out of the Strait (from Thomson, 1981).

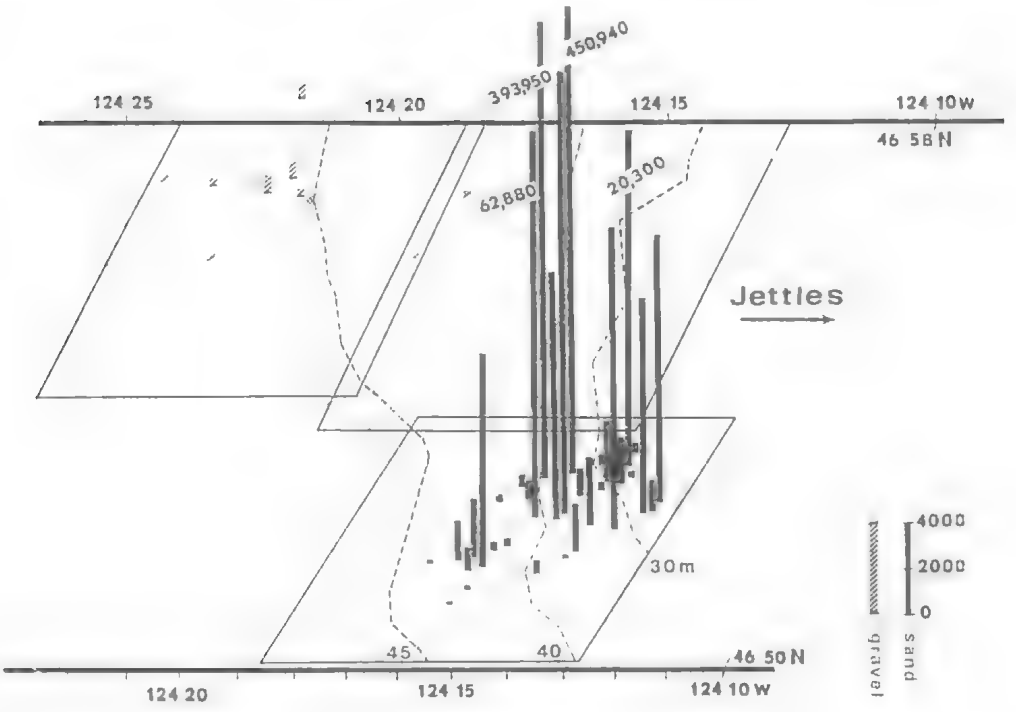

FIG. 9. Dungeness crab density (number ha^{-1}) offshore of Grays Harbor, WA, June 1985.

survival over sequential years to construct indices of year-class strength and determine spawner-recruit relationships are non-existent. Gotshall (1978) found no correlation between an index of 0+ crab abundance and commercial landings 3.5 y later, based on cursory coastal and estuarine surveys in northern California. However, Warner (1987) measured 0+ crab density in fall trawl surveys off northern California from 1972 through 1985 and noted that a 20-fold greater density for the 1972 year-class subsequently resulted in a near-record commercial fishery in 1976 (11,300 t). Tasto (1983) and Reilly (1983), who estimated the abundance of benthic juveniles and larvae in central California, respectively, both observed relatively strong year-classes in 1975 and 1977, which were consistent with an increase in commercial landings for California in 1978–80 (Methot, 1989; PMFC, 1989).

The most comprehensive study of 0+ Dungeness crab recruitment and survival has been done along the southern Washington coast between 1983 to 1989 (Armstrong and Gunderson, 1985; Gunderson *et al.*, 1990). While they found that high interannual variability in estimated abundance of 0+ crab did not equate well to the strength of future fisheries, measures of 1^{+} y-old crabs did. The high abundance of 1+ crab in 1985 (1984 year-class; Fig. 11) led to a record high fishery in excess of 10,000 t in 1987/88 and 1988/89 (Fig. 3). Unique to the 1984 year-class was unusually rapid growth of the coastal cohort (Armstrong and Gunderson, 1985), which re-

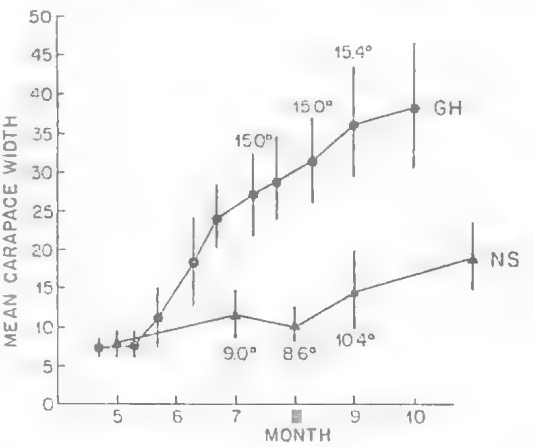

FIG. 10. Comparison of $0^{+} \rightarrow 0+$ Dungeness crab growth during their first summer inside an estuary (Grays Harbor, GH) and on the outer coast in nearshore waters near the estuary (NS). Numbers indicate mean bottom water temperature (°C.); bar = 1 SE) (from Armstrong and Gunderson ,1985).

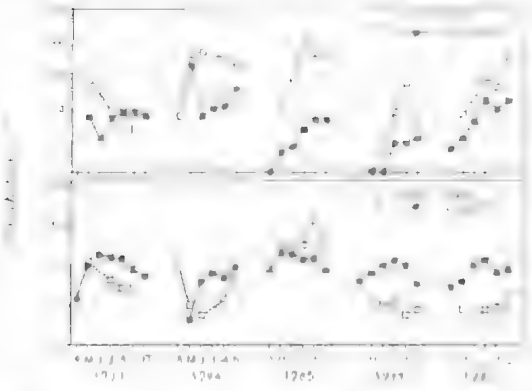

FIG. 11. Population estimates for 0+ and 1+ →0|← 1+ Dungeness crab by month and year on the outer coast and adjacent estuaries off Washington. Estuarine data for 1983–84 are for Grays Harbor only, but include Willapa Bay for 1985–87 (from Gunderson *et al.*, 1990).

sulted in a mean size, by fall, of about 22 mm CW. Gunderson *et al.* (1990) speculated that the more rapid growth of this year-class increased survival over fall and winter and, in turn, a strong 1+ cohort in 1985 (Fig. 11). The cause of more rapid growth in 1984 seemed to be a combination of early settlement and unusually warm bottom water temperatures in May and June, 1984, compared to other years during the study.

Another aspect of settlement along the open coast in the Upwelling Domain is direct recruitment of juveniles to coastal estuaries (Fig. 12). Settlement there can be high in both intertidal and subtidal areas, although in the subtidal, mortality is relatively high and newly settled crab quickly disappear (Dumbauld and Armstrong, 1987; Gunderson *et al.*, 1990). Optimal habitat in the intertidal has a large quantity of bivalve shell, notably of cultured oyster (*Crassostrea gigas*) or wild softshell clam (*Mya arenaria*) (Armstrong and Gunderson, 1985; Dumbauld and Armstrong, 1987). Estuarine crab also benefit from higher temperatures and accelerated growth (Fig. 10). By September, estuarine 0+ crab are approximately 35 mm CW, in contrast to the approximately 13 mm CW of outer coast juveniles. During the summer, intertidal crab gradually move to the subtidal, where they are now able to avoid most predators by virtue of their greater size (Reilly, 1983). However, despite high intertidal estuarine abundances of 0+ 1+ crab abundance, annual 1+ y-old subtidal estuarine populations are fairly constant and fluctuate only about two-fold (Fig. 11; Gunderson *et al.*, 1990). This had led to speculation that estuaries provide a relatively stable recruitment source to the fishery, representing a significant proportion of the long-term average landing in coastal fisheries. Contrary to original hypotheses of Armstrong and Gunderson (1985), estuaries may thus not be the source of particularly strong year-classes that cause peaks in cycles of fisheries landings (Fig. 3). Such peaks instead seem to be the result of high survival of 0+ crab that settle and recruit directly in outer coast areas (Gunderson *et al.*, 1990).

DOWNWELLING DOMAIN: As previously noted, this region is topographically quite different from most of the Upwelling Domain region. General life history and fishery information on the species has been summarised by Koeneman (1985) for southeast Alaska. There is no reason to assume that aspects of life history and habitat requirements are any different for Dungeness crab in this area, but the timing of seasonal life cycle events is different. Settlement of larvae is later and typically occurs in August and September. Although fisheries landings do not show cycles of the same magnitude as reported along the coast from Washington to California, substantial fluctuations in catch probably reflect variability in year-class size, attributable to the same suite of biotic and abiotic factors hypothesised to affect the species elsewhere in its range (Botsford *et al.*, 1989). The downwelling features of this area, as previously described, may serve to retain larvae nearshore rather than encourage long distance transport in the Alaska Current. Larvae may thus be produced and retained in a smaller geographical scale and progeny may recruit to areas near where they were hatched. No systematic, quantitative long time series of data exist for juvenile Dungeness crab recruitment and survival in this Domain.

GEORGIA STRAIT/PUGET SOUND: As noted earlier, oceanographic features in the inland sea of the GS–PS complex, which extends across the border between Canada and the United States, lead to unusual conditions that may result in maintenance of a separate stock distinct from that on the outer coast. Based on timing of settlement and size of first instar juveniles, P. Dinnel and D. Armstrong (unpubl.) have defined at least two cohorts of 0+ crab recruiting to Puget Sound in May through September. The first cohort settles in May and June and juveniles are approximately 7–8 mm CW, comparable in size with outer coast crab juveniles (Gunderson *et al.*, 1990). This outer coast cohort is identical in size to cohort 'a' reported by Orensanz and Gallucci (1988). Coastal zoeae or megalopae apparently enter the GS–PS complex through the Strait of Juan de Fuca, probably either in surface waters when surface outflow temporarily ceases (Fig.

FIG. 12. Schematic of generalized movement and distribution of megalopae, 0+ and 1+ y-old juvenile crabs between the nearshore coast and Grays Harbor estuary.

8), as discussed earlier, or at depth in the compensating inward flow of more dense water. Because of the across-Strait tilt in the boundary line separating net seaward flow at the surface and net landward flow in the lower layer (Fig. 7) due to the combined effects of the Coriolis force and channel curvature (Thomson, 1981), outflow favours the Canadian side and inflow the American side. This explains why most settlement of outer coast crabs in the Strait and GS–PS has been observed in American waters.

The second cohort identified by P. Dinnel and D. Armstrong (unpubl.) settles in late July and August and is substantially smaller, with a first instar size of <5 mm CW. Because of settlement later in the summer, this 'Puget Sound' cohort (synonymous with cohort 'b' of Orensanz and Gallucci, 1988) grows relatively little in its settlement year and typically overwinters in the intertidal. Settlement by the Puget Sound cohort two months after the 'outer coast' group is probably due to slow growth caused by cold water temperatures in the central part of the GS–PS complex. Tidal flow among the American San Juan Islands and Canadian Gulf Islands brings to the surface the denser, colder lower water layer, and this vertical mixing of the water column results in surface water temperatures which are colder there than found on the outer coast. Such conditions do not apply in the central part of Georgia Strait and in the southern, low current parts of Puget Sound.

As occurs along the outer coast, juvenile crab predominantly occur in shallow water habitats

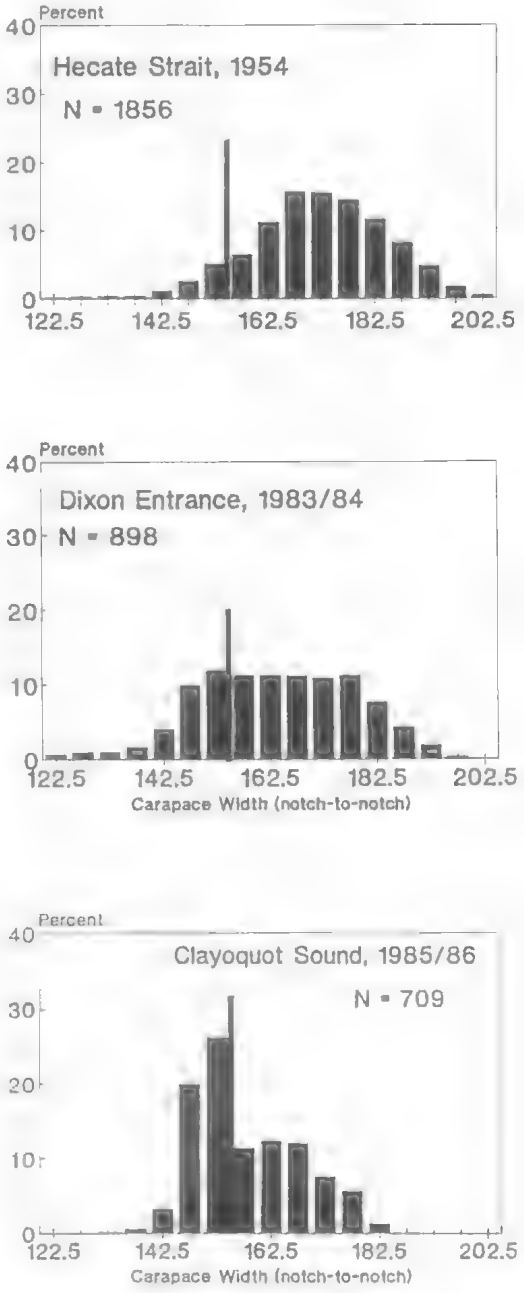

FIG. 13. Commercial catch size distributions of Dungeness crab, showing the reduction in relative proportion of large crabs as fishing has intensified over time. The narrow vertical bar indicates the minimum legal size limit, modified to show the notch-to-notch measurement. Hecate Strait data modified from Butler (1960); remaining data modified from Smith and Jamieson (in press).

characterised by sand and small cobble, often with eelgrass (*Zostera marina*) or overlying mats of algae such as *Ulva* sp. At a number of intertidal locations throughout Puget Sound, Dinnel *et al.* (1987) reported high densities of 0+ crab in cobble-sand, with densities highest if macrophytes were present (Dinnel *et al.*, 1986). Predictably, refuge availability is an important element determining the carrying capacity of an area, but in contrast to the outer coast where bivalve shell is important (Armstrong and Gunderson, 1985), algae and eelgrass provide most cover in the GS–PS complex. As measured by trends in the fishery, overall recruitment and survival of juvenile stages appears to be more constant and stable within the GS–PS complex compared to the outer coast, and is probably limited in magnitude to a great extent by availability of appropriate refuge habitat for early juvenile instars at settlement.

Pre-recruit Survival

Pre-recruits are defined here as the size cohort that will recruit to the exploitable cohort in the next subsequent year, and for Dungeness crab, this implies male crab in the size interval of about 130–159 mm CW (Smith and Jamieson, 1989b). The conventional assumption is that since male crab greater than 140 mm show evidence of previous matings by abrasion marks on their chelipeds (Butler, 1960; Smith and Jamieson, in press), current minimum size limits (155–159 mm CW, depending on jurisdiction) should protect many crab from capture for at least one breeding season prior to their recruitment to the exploitable size range. The rationale and data used to justify existing size limits were never documented, but in the early 1900s when size limits were first introduced, it is hypothesised that most crab populations were less heavily exploited than at present and that a relatively large proportion of crab significantly exceeded the minimum size limit adopted. In 1954, the mean size of crab sampled by Butler (1960) in Hecate Strait, the location of the largest fishery at that time, was about 173 mm CW, with many crab exceeding 190 mm CW (Fig. 13). Crab this size are seldom caught today in any significant fishery in British Columbia (Fig. 13), although large crab are caught on the outer coast of Washington [mean = about 175 mm CW (S. Barry, Washington State Dept. Fish., Montesano, WA, pers. comm.)] and even larger crab are caught in Alaska. Merritt (1985) reported that the mean CW of commercial crab caught at Bluff Point, Cook Inlet, AK, from 1973–75 ranged from 190–200 mm, but that the very large crab (230+ mm CW) caught when the fishery first began

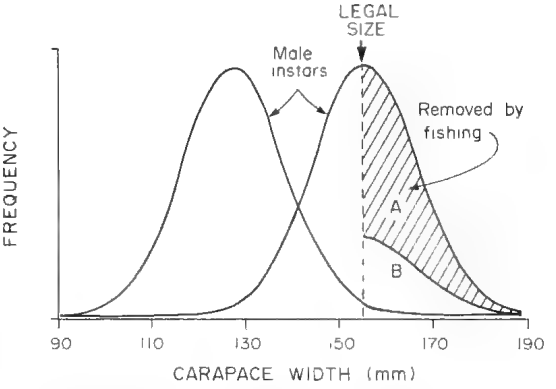

FIG. 14. Diagrammatic depiction of a male crab instar size distribution in relation to the minimum legal size limit, and the effect of fishing removal on the apparent instar composition of a size frequency distribution. Two instars from Clayoquot Sound, 1985–86, are shown: adjacent μ = 129 mm CW ($\pm$12 mm CW) and μ = 156 mm CW ($\pm$13 mm CW) instars (from Smith and Jamieson, 1989b).

there in 1973 had disappeared. Crab landed in Kachemak Bay, adjacent to Bluff Point and which has been exploited for most of the century, averaged 15% smaller than Bluff Point crabs between 1978–83.

In an intensive study of the Tofino, British Columbia, crab fishery, Smith and Jamieson (1989a, b) reported that the recruiting instar size distribution was nearly halved by the minimum legal size (MLS) (Fig. 14). Forty-two percent of this cohort were pre-recruits, and hence unavailable to the commercial fishery that year. What was surprising, though, was that there was considerable evidence (Smith and Jamieson, 1989a) that these pre-recruits had a high natural mortality (M=2.9–4.5), with less than 10% ultimately surviving to legal size. Thus, about 40% of this recruiting cohort apparently never recruited.

It is not known if this was a phenomenon unique to the relatively small geographic area involved (about 60 km^2) and/or that particular time period (1985–86). Further study, both at Tofino and elsewhere, is currently under way, but because of a lack of settlement at Tofino in recent years and logistic difficulties in conducting an appropriate study in a larger geographic area, these results have not been confirmed elsewhere to date. Smith and Jamieson (1989a) suggested this apparentlyy high mortality might be a result of having recruits being removed from the population in this year-round fishery virtually as fast as they recruit (F=5.1–6.9); only 9–16% of recruits are expected to survive more than 90 days. Continuous trapping and release of

pre-recruits while fishing for recruits (current escape port size is not optimal; Jamieson, unpubl.) may have increased their mortality substantially, or there may be some, as yet undetermined, biological explanation.

A final consideration is the growth history of the recruiting cohort. In the Tofino instance described above, the MLS divided the recruiting cohort almost equally, but this may not always occur. In some years, mean instar sizes may be such that the MLS falls between distinct, adjacent instars, rather than over one instar specifically, resulting in almost the entire pre-recruit instar recruiting with its next moult. Any scenario between the above two extremes may occur, resulting in up to a two-fold difference in recruitment of year-classes of similar absolute abundance. This may mostly explain the large average size of recruited crab in the outer coast Washington fishery (175 mm CW) relative to that in the Tofino fishery (about 165 mm CW; Smith and Jamieson, 1989a).

SUMMARY

The prediction of relative year-class strength at recruitment to the fishery for Dungeness crab, and probably for most species, is not a trivial matter. Limited mobility, pronounced spatial differences in abundance, and a variable environment result in sufficient unpredictability that future estimation of year-class abundance of Dungeness crab to a fishery can only be made with acceptable accuracy from 1+ y-olds. Female abundance, in the absence of any fishery for them and little data on their occurrence because of the use of escape ports, is unavailable. The ultimate settlement location of larval production is also unknown. Consequently, traditional stock-recruitment relationships are effectively meaningless for management and have not been determined for this species. Research emphasis is currently focusing on determining and describing the critical environmental conditions (currents, temperature, winds, refuge availability), behaviour (larval distribution in the water column), and population dynamics (growth rate, survival and causes of mortality) in coastal areas having significant regional fisheries.

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UNUSUALLY RAPID GROWTH OF COASTAL 0+ DUNGENESS CRAB MAY LEAD TO STRONG FISHERIES

Dungeness crab, *Cancer magister*, is the primary crustacean fishery along the west coast of the United States from northern California through Washington, and is characterised by cyclic landings with a periodicity of 9 to 10 years (Botsford *et al.*, 1989). Despite numerous hypotheses to suggest a suite of biotic and abiotic factors as explanations for such cycles, no cause-and-effect relationship has been demonstrated as responsible for high or low year class abundance. Although larval production, transport, and settlement to nearshore areas are assumed to be critical for high juvenile abundance, year class strength is often not determined until the 1+ age class since mortality of early benthic instars is very high. In previous hypotheses, Armstrong and Gunderson (1985) believed that estuarine recruitment of juveniles was essential to production of a strong year class because growth is more rapid in these systems than along the colder (upwelling) open coast, and estimated abundance of 1+ juveniles is usually greater in estuaries compared to the coast.

Since 1983 we have measured timing of settlement, growth rates, movement, and relative abundance of juvenile Dungeness crabs along the southern Washington coast in a stratified survey program intended to contrast population dynamics across several habitats within the estuaries of Grays Harbor and Willapa Bay and along the nearshore (inside 70m) coast. During this time we have measured at least two very strong year classes as 1st instar, 0+, crab; one of which had very low subsequent survival and produced an average fishery, and one that produced a record fishery 4 years later.

Megalopae settle along the nearshore coast and in estuaries, and mortality is generally rapid in both systems. Estimates of 0+ juveniles within the survey areas shown by Gunderson *et al.* (1990) have varied by at least 14 times, and in most years initial summer survival seems to be highest in estuarine intertidal shell habitat. As a consequence of estuarine settlement, 1+ abundance is typically high the following year and this cohort is joined by siblings that immigrate to the estuary from the open coast, thereby decreasing the summer abundance of juveniles in colder coastal waters. Summer estuarine abundance has varied by only about 2 times between 6 to 12 million crabs in a system like Grays Harbor.

Year class strength as reflected in the fishery was discernible during the period of our study. Six of the worst commercial years on record occurred between 1980 and 1987 (1,400–1,800 t), but some of the largest landings for Washington state were in 1988 (7,500 t) and 1989 (10,000 t) which corresponds to a 3.5 and 4.5 year lag back to the 1984 year class (YC) that entered the fishery over a two year period. Reasons for this strong YC are not based on extraordinary events in the estuaries where 1+ abundance was consistent with values from all other years. Rather, the coastal cohort of the 1984 YC was exceptionally strong and survived well for two apparent reasons. Firstly, the YC settled in strength early that year in May whereas other YC's typically do not fully recruit until late June to early July. The effect of early settlement was essentially a longer growing season. Secondly, bottom water temperatures in May and June were about 1.5°C warmer than six year monthly averages. As a result, 0+ crab of the 1984 YC were about 22–25mm carapace width (CW) by September compared to a range of 12–14mm CW in most years. Substantially larger size by the end of summer protected the 1984 YC from continued high predation that usually decimates a coastal 0+ population by the following spring.

Measured as 1+ abundance in spring the year after settlement, the 1984 YC ranged in abundance from 29–100 million juveniles along the coast compared to 1–10 million in other years. Thus coastal fisheries of low to moderate yield may be largely based on fairly stable estuarine production of juveniles, but very large fishery peaks that characterise Dungeness crab could result from auspicious coastal conditions and early settlement that, in this case, led to accelerated growth of coastal 0+ juveniles in 1984. Related to this observation is the perspective that strong onshore larval abundance and subsequent settlement do not often equate to a strong YC since 0+ mortality is extremely high. Larval retention and/or transport onshore is only a first-stage ingredient for a strong YC that is also based on survival of 0+ juveniles.

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ASPECTS OF THE BIOLOGY OF THE HAIR CRAB, *ERIMACRUS ISENBECKII*, IN THE EASTERN BERING SEA (CRUSTACEA: DECAPODA: ATELECYCLIDAE)

The hair crab, *Erimacrus isenbeckii*, is a medium-sized brachyuran in the family Atelecyclidae. The development of an United States fishery for hair crab in 1979, and the substantial decline of the eastern Bering Sea (EBS) population from 1981 to 1984 prompted an analysis of hair crab data collected by the National Marine Fisheries Service (NMFS) during trawl surveys in the summers of 1979–1984, and in February 1983 and 1985. Pertinent Japanese literature on the worldwide distribution, reproduction, and moulting of hair crab is summarised.

In the eastern Bering Sea, *Erimacrus isenbeckii* is distributed from the north shore of the Alaska Peninsula to the Pribilof Islands, and north to St. Matthew Island. It also occurs along the Aleutian Archipelago. In the West Pacific, it is distributed along the east coast of Korea, both coasts of Japan and Hokkaido, and along the Kurile Islands to the Kamtchatka Peninsula (Rathbun, 1930; Vinogradov, 1947). According to NMFS surveys, the estimated population in the eastern Bering Sea was about 23 million crabs from 1979 to 1981, but declined sharply to 4.4 million by 1984 (Otto *et al.*, 1985). The majority (67%) of the population occurred in the Pribilof Islands area. Male crabs occurred at a mean temperature of 3.4°C and depth of 66 m, whereas females occurred at a mean of 2.4°C and 64 m. There was no significant difference in mean depths between males and females, but there was a significant difference in mean temperatures at which male and female hair crab were found. Some reproductive information was collected from females, which comprised only 8% of the total survey catch. Ovigerous females were 65–87 mm in carapace length and carried from 34,000–160,000 eggs. Females' gonopores were open, closed with a proteinaceous plug of male origin, or closed with a swollen membrane similar to an arthrodial membrane, depending on reproductive state of the female. Moulting was much more apparent during the February 1983 cruise than the other cruises; 30% of the females and 20% of the males were either softshell or in the process of moulting. The mean length of males was 96 mm and the mean weight was about 714 g. The mean size of females was much smaller than for males; they averaged 66 mm in length and 197 g in weight. Hair crab have been fished around Japan and Korea for more than 60 yrs (Kawakami, 1934). The United States fishery began in 1979 and occurred incidental to the Bering Sea tanner crab fishery during the months of March through June. The Pribilof area contributed 94–98% of the catch (Griffin and Dunaway, 1985), which was taken with commercial king and tanner crab pots.

The decline of the Bering Sea hair crab population coincided with the substantial declines of king and tanner crabs. These declines may have resulted from changes in the environment, increased predation, increased incidence of disease, or vulnerability to fishing pressure. Additional information on maturity, growth, and mortality is important for a more complete understanding of the biology of the hair crab.

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THE IMPACT OF STAGHORN SCULPIN PREDATION ON NEWLY SETTLED DUNGENESS CRAB

During late spring/early summer, vast numbers of Dungeness crab (*Cancer magister*) megalopae reach estuaries and settle on intertidal flats, and during the next two months the crab population is rapidly culled by predation and cannibalism. Crab without appropriate refuge habitat are highly vulnerable to predation by fish and birds and accordingly survival of young crab is highest in shell and eelgrass beds. Staghorn sculpin (*Leptocottus armatus*) known to be generalist, opportunistic predators with large gapes, have high estuarine abundance, and are distributed throughout estuaries as crabs settle and moult to 1st instar. The objective of this study was to assess the potential impact due to staghorn sculpin predation on newly settling Dungeness crab in the Washington coastal estuary of Grays Harbor.

Staghorn sculpin and Dungeness crab population dynamics have been followed by monthly trawl surveys from April to September in 1983 through 1989. Young sculpin are found in the upper reaches of the subtidal channels and creeks, and migrate to deeper channels of the bay as they grow. Sculpins sampled by our gear ranged in size from 60 to 230 mm TL, and all sculpin greater than or equal to 80 mm TL were found to be capable of consuming newly settled crabs which comprised similar proportions of the diet of two size groups of sculpin in our samples.

The summer diet of staghorn sculpin composition was assessed by a series of 6 trawling trips in April through August, 1989. Stomach contents of sculpin from these monthly collections were analysed by a modified Index of Relative Importance (Stevens *et al.*, 1982). The sculpin's diet consisted of amphipods (46%), crangonid shrimp (24%), and small fish (12%) in April and *Callianassa* sp. (45%) and nereid polychaetes (37%) in May before crab settlement. In early June as crab became available, sculpin switched to nereid polychaetes (60%) and Dungeness crab (23%) as their primary food. In July and August, *Callianassa* and *Upogebia* sp., two species of mud shrimp, and *C. magister* were the three major items of diet. By pooling the results of all stomach content analyses from April to August, it was determined that *C. magister* formed 9% of the total summer diet of staghorn sculpin in Grays Harbor. It should be noted that the IRI index is a composite of frequency of occurrence, numerical and gravimetric percentages and thus a conservative measure of dietary importance in this case.

Staghorn sculpin are opportunistic feeders. This is shown by shifts in monthly diet that reflect prey availability. These fish have relatively high food requirements for rapid estuarine growth during warm summer months when water temperatures reach 14–16°C. Percent gut fullness (by visual assessment) was routinely high (>50% to distended) and mean gut contents were calculated at 7% of dry fish body weight. Interannual variability in sculpin populations was examined from 1983 to 1988 and peak summer populations ranged from 1 to over 3 million sculpin, with a six year mean estimated to be 2 million fish.

To assess the potential impact of sculpin predation on crabs, energetic requirements were used to derive an estimate and then field data were used to substantiate the parameters. An average size sculpin of 120 mm TL (20.4 g wet wt, 4.1 g dry wt) would consume 7% of its body weight per day (0.3 g dry wt) as a daily ration. If 10% of the total summer diet is Dungeness crab, then sculpin would consume 0.03 g crab dry weight per day. Gutermuth and Armstrong (1989) calculated the dry weights of Dungeness crab instars. Thus the daily ration of crab is equivalent to either 2 first instars, 1 second instar or 0.5 third instars. This pattern and frequency were substantiated by examining the number and stage of crab consumed by sculpin from early June to late July. As the instar size increased the number of instars eaten per fish decreased. Two scenarios of sculpin impact took into account variation in crab settlement period, crab moult frequency, proportion of daily ration composed of specific crab instars, and numbers of resident sculpin. Extremes in the different scenarios predicted staghorn sculpins could consume between 158 and 180 million newly settled Dungeness crab during June and July. Armstrong *et al.* (1987) have estimated that the average estuarine population of newly settled Dungeness crab is about 400 million which is reduced to between 20 and 40 million juvenile crab by the end of the summer. Thus, of the 360 million crab lost during summer, staghorn sculpin predation accounts for approximately 44 to 50% of the loss.

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SOME BIOLOGICAL ASPECTS OF THE GIANT ISOPOD, *BATHYNOMUS GIGANTEUS* (A. MILNE-EDWARDS) (ISOPODA: CIROLANIDAE), OFF THE YUCATAN PENINSULA

Specimens of the giant isopod, *Bathynomus giganteus* (A. Milne-Edwards), were collected on the continental slope off the Yucatan Peninsula, Mexico, in October 1985 (74 isopods), February 1986 (70), August 1986 (64), August 1989 (163) and February 1990 (1280). The isopods were collected with traps baited with skipjack tuna and large carangids. Depth of collection ranged from 350 to 730 m. In the deepest station, only mancas and juveniles were obtained. Size distribution ranged from 4.4 cm to 36.5 cm total length. A 36.5 cm male is the largest specimen of this species so far recorded. Male-female ratio varied in each collecting date, from 0.8:1 to 1.7:1. Mature males and females were obtained in every collecting date. Length-weight and length-width relationships were obtained. Specimens collected in August 1989 and February 1990 were studied in more detail. In August, 35% of the males had appendices masculinae, and 14% of the females showed fully developed oostegites. In February, these percentages were 50 and 45, respectively. Both the smallest mature male and female measured 21 cm. No ovigerous females were caught in any cruise. An ovarian development scale was designed, ranging from stage 1 (quiescent ovaries) to stage 5 (spent ovaries with ovocites in resorption). In August, a large percentage of females showed ovaries in intermediate stages 2 and 3, while in February, the ovaries of most of the females were in stages 1 and 4. These results suggest a differential distribution of life stages on the bottom. An exponential relationship between body length (BL) and body weight (BW) was found (Log. BW.= -1.43 (BL) + 2.96; n = 515, r = 0.998). Although males with appendices masculinae and females with developed oostegites were found from every collecting date, the analysis of ovarian development indicates that in August most females are preparing for reproduction, while in February most of this reproduction has taken place. The large number of mancas (554) collected in February also support this idea.

In gut content analysis, the following groups were identified: fish, cephalopods, decapods, isopods, sponges, echinoderms, nematodes and tunicates. No differences were found in the diet composition between sexes. *B. giganteus* is reported as a scavenger, but these results show that it also feeds on some sessile organisms on the bottom. A large female was found in the stomach of a tiger shark, *Galeocerdo cuvierii*.

In regard to epizoans, the cirriped *Octolasmis aymonini geryonophyla* was found in a large percentage of isopods from every cruise. In February 1990, the gastropod *Mitrella rushii* was found in large quantities inside the oostegites of a number of females, but also on the coxal plates and pleopods of some males. This is the first record of this association, but their relationship is not clear. Epizoans were more abundant on females than on males which suggests that they have a lower moult rate than males.

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GROWTH AND REPRODUCTION OF TWO SPECIES OF SPIDER CRAB (BRACHYURA: MAJIDAE)

Brachyuran crabs, and decapod Crustacea generally, display a great diversity of growth-reproductive patterns (Hartnoll, 1985). The Majidae are more constrained than most other brachyuran groups, as the females are limited to a single mature instar (Hartnoll, 1963, 1985). The processes of growth and reproduction are therefore temporally separate. These species are not, however, fully semelparous as females may lay several egg batches in the terminal instar. This study considers the female life history of two majids, *Hyas coarctatus* and *Inachus dorsettensis*. Reproduction in the field and growth in the laboratory have been studied in relation to the known phenology of their life-cycles. A life history strategy model currently applied to a different species is described also, to which the results of this study are to be applied.

Animals were collected at sites where the two species co-exist in the Irish Sea, 54° N. The offshore water temperature there is at a minimum between February and March and at a maximum between August and September. The two species have contrasting life histories. *H. coarctatus* females start to mature their ovaries in January, prior to the terminal moult which occurs mainly between May and July. Mating and egg laying follows immediately. After 9–11 months, the following March to April, eggs are hatched and the females which survive then lay a second batch. *I. dorsettensis* females mature their ovaries only after the terminal moult, which occurs between July and September. After a short delay for ovarian maturation the first egg batch is laid in autumn. Egg development time is relatively short, allowing a second batch to be laid in early spring. Egg development is not synchronised with the seasons in this species.

Fecundity of the females was assessed using a dry method. In *H. coarctatus* a strong relationship was found between egg number and the cube of carapace length. *I. dorsettensis* had a double fecundity curve. Samples taken in the autumn, when most animals would have been carrying their first batch of eggs, gave a shallow curve. In the spring, when the animals would have been carrying their second or subsequent batch, a significantly steeper curve was obtained. It would appear therefore that fecundity is low for the first batch of eggs, despite the animal delaying ovarian maturation until the final and largest instar.

The growth experiment was performed in the laboratory over 500 days, with the temperature mimicking that of the sea through the seasons. The results, in the form of the percentage moult increment and intermoult period, were analysed in relation to the size of the animal and the temperature, treating juveniles and animals moulting to maturity separately where appropriate.

In *H. coarctatus* the mean percentage increment was significantly smaller for maturity moult than for juvenile moults. This may be related to the early diversion of resources to reproduction in this species. Percentage increment showed a significant negative correlation with temperature, but only for juvenile moult. Intermoult period was positively related to carapace length and negatively correlated with temperature.

In direct contrast, *I. dorsettensis* had a greater percentage increment at the maturity moult than at its juvenile moults. This may be tentatively interpreted as a strategy for maximum body size in the final instar, in which to develop its ovaries. The maturity moult was undergone at a significantly higher temperature than the juvenile moults, a result which agrees well with the known phenology of this species. Intermoult period was found to be negatively related to temperature but unrelated to carapace length.

These results will be applied to the model of Hartnoll and Gould (1988). At present this model describes the life history of a crab species which continues moulting after puberty. It is aimed to predict how lifetime egg production varies with the precocity of reproduction and lifespan, both measured as the number of instars. A second aim is to observe the change in optimal strategy, with respect to lifetime egg production, when the mortality assumptions are varied. Application of the spider crab data to the model will allow a comparison of predicted optima with the observed natural life history and the investigation of the effect of mortality on life history strategy.

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ROLE OF FILTER-FEEDING CRUSTACEAN ZOOPLANKTON IN DUTCH LAKES OF VARYING DEPTH AND TROPHY

Most freshwater lakes in The Netherlands are man-made, small (area 50–200 ha), shallow (mean depth 1–2 m) and highly eutrophic. The major symptoms of the eutrophication are: 1) high standing crop of seston (phytoplankton and detritus) (10–20 mg DW.L^{-1}) comprised mainly of filamentous blue-green algae; 2) high chlorophyll a levels (100–300μgL^{-1}); and 3) poor under-water light climate (Secchi-disc transparency, 30–50 cm). The mesotrophic lakes, which are relatively less common are, on the other hand, deep and exhibit summer stratification; they have much lower algal and detrital concentrations, and the light penetrates to deeper layers. Recently, attempts have been made to restore some of the eutrophic lakes (Loosdrecht Lakes) by reducing the external phosphorus loading (Van Liere *et al.*, 1990). In many other smaller lakes biomanipulation has been attempted as a lake rehabilitation measure (Gulati, 1990a, b). These restoration measures offered a good opportunity to follow the course of changes in the structure and grazing of crustacean zooplankton.

Results and Discussion

There are major differences between the two trophic categories of these lakes in the composition, size structure and grazing activities of the crustacean zooplankton. In the shallow, eutrophic category larger-bodied crustacean filter-feeders, *viz. Daphnia* species (>1.5 mm), are generally scarce, or even absent; instead, the smaller-bodied, filter-feeding crustaceans, (*Bosmina longirostris, B. coregoni, D. cucullata* and *Chydorus sphaericus*) are abundant, besides 3–5 species of cyclopoid copepods. It is puzzling, however, that one *Daphnia* species, *D. hyalina*, which invariably coexists with *D. cucullata* in both the eutrophic lakes and mesotrophic lakes, is absent in several other eutrophic lakes (Gulati, 1990b). The calanoid copepod *Eudiaptomus gracilis* is an important indicator of trophic status, being sparse or absent in eutrophic lakes. The limnetic zooplankton of the eutrophic lakes is dominated by rotifers which, with their mean densities of *c.* 4000 ind.L^{-1} outnumber the crustaceans by 9 to 1. The size structure of crustacean community also differs: in the mesotrophic lakes the mean crustacean size is larger (3–11 μg C.ind^{-1}) than in the eutrophic lakes (0.65 μg C.ind^{-1}). Biomass relationships between the crustaceans and their sestonic food (< 150 μm) indicates a Monod type of relationship with an initial part of the curve in which the zooplankton responds linearly to the seston increase to about 2 mg C.L^{-1}, observed in the mesotrophic and biomanipulated lakes. At seston levels of 3–4 mg C.L^{-1}, the zooplankton mass (0.4 mg C.L^{-1}) reaches a saturation level. At higher seston levels (4–10 mg C.L^{-1}), the food is dominated by blue-green algae, so that zooplankton mass tends to decrease rather than increase, possibly due to the inhibitory effects of the food. The structural differences between the crustaceans in these lakes are attributable to differences in the intensity of the size-selective predation or on the larger-bodied crustaceans by planktivorous fish. These fishes, especially bream (*Abramis brama*), and other young-of-the-year planktivorous fish, are far more abundant in the eutrophic lakes than in the mesotrophic and biomanipulated lakes. Experimental biomanipulation, i.e. artificial reduction in planktivorous fish, or alternatively increase in piscivorous fish, in some of the smaller eutrophic waters has led to the appearance of and dramatic increases in large-bodied *Daphnia* species. These changes generally go hand in hand with corresponding differences in the grazing pressure of the filter-feeders. The specific filtering rates (filtering rates per unit body weight, l.mg^{-1} zoop. C) in the deep mesotrophic lakes (1–3.5 l.mg zoop. C.L^{-1}) are 2 to 5 times higher than in the eutrophic lakes. The crustacean zooplankton is thus an important causal factor in the phytoplankton mortality in deeper lakes. In the eutrophic lakes, on the contrary, the seston standing crop is high, dominated by filamentous blue-greens which are poorly edible. The smaller-sized crustacean zooplankton which dominate in the eutrophic lakes is much less effective in grazing down the food than the larger-bodied species in the mesotrophic lakes. To eliminate the daily phytoplankton primary production in the eutrophic lakes (e.g. Lake Breukeleveen in the Loosdrecht area) about 525 ind.L^{-1}.d^{-1} of the crustacean grazers are required, compared with only about one-tenth of this number needed to remove the daily production in the mesotrophic and biomanipulated lakes.

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NATURAL DIET OF *CALLINECTES ORNATUS* (BRACHYURA: PORTUNIDAE) IN BERMUDA

Foregut contents of 56 specimens of *Callinectes ornatus* (8.8-51.8 mm carapace length) collected from Mullet Bay, Bermuda in 1981 and 1988 were examined. Foreguts which were ≥ half full (91.1%) contained more prey items per gut (X = 4.67) than did guts ≤ half full (X = 2.73). Dietary analysis was based on two methods; (1) the index of relative importance (IRI), which combined frequency of occurrence (FO), percentage of total biomass (GC), and percentage of total numbers consumed (NC), and (2) weighted points (PTS), which combined FO and estimated relative volumes of each prey item. No significant differences were revealed in relative proportions of foregut contents between males and females, or between adult and juvenile crabs.

This crab is an opportunistic predator of slowly moving benthic macroinvertebrates, specifically gastropod molluscs. Diet was related to prey availability. *Modulus modulus*, a cerithiacean gastropod that grazes algae and *Thalassia*, dominated the diet, accounted for 21.1% of the total IRI. Two other cerithiaceans collectively ranked second (19.9% of total IRI). All species were common in Mullet Bay. Carbonate substrate was the most frequently occurring category (51.79%) and ranked third in IRI (17.2% of total). While many studies of crustacean diet relegated such entities to a non-nutritional status, other papers documented the presence of diverse microscopic and meiobenthic organisms in coral sand substrates. Because the biomass can be relatively high in such substrates, they should be regarded as a potentially important food source, and considered part of the diet. Plant material, crustaceans, nereid polychaetes, fish, and bivalve molluscs ranked fourth through eighth in IRI. The PTS index is better suited for foods consisting of a high proportion of soft tissue; FO is appropriate for most foods, but tends to elevate the importance of unidentifiable material, sand, and small animals occurring frequently, but in small amounts. Errors due to accumulation of material that is digested or cleared slowly occurs in both methods. While no one quantitative method is ideal for assessment of dietary analysis in brachyurans, the IRI value has a great deal of merit. Because IRI is based on three other indexes, it is possible to determine the relative impact that each component index has on the total IRI for the dietary items, and because the PTS method has been widely accepted, it is recommended that future dietary studies of brachyurans be designed to incorporate all indexes.

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THE LIFE HISTORIES OF THE TASMANIAN FRESHWATER CRAYFISHES OF THE GENUS *ASTACOPSIS* (DECAPODA: PARASTACIDAE)

The life histories of the two poorly understood members of the Tasmanian endemic freshwater crayfish genus *Astacopsis* were studied in their natural habitats. *A. gouldi*, the world's largest freshwater crayfish, and therefore freshwater crustacean, is capable of reaching very large size (3 to 4 kg) and is restricted to the rivers of the north of Tasmania while the smaller *A. franklinii* (up to 1 kg) is widespread in rivers and lakes throughout the state (Swain *et al.*, 1982). Both species are generally associated with swift and cool riverine or highland lacustrine habitats.

Male and female seasonal reproductive and moulting cycles, mating, spawning and larval development, were investigated through intensive monthly sampling and mark-recapture programme from September 1985 to May 1987 (Hamr, 1990). A portion of each catch was preserved for subsequent gonad analysis in the laboratory.

Results

Mature females of *A. gouldi* mate and spawn in April–May, eggs are carried over winter, hatch in January, and young stay attached until late into the following summer (March–April). After the release of their broods females overwinter, then moult in mid-summer (January–February) and mate and spawn again in autumn, two years after their previous mating. Similarly, *A. franklinii* mate and spawn in April–May, eggs are carried over winter, hatch in January, and young stay attached until well into the following autumn (April–May). Adult females of *Astacopsis* therefore exhibit a biennial breeding and moulting cycle. This strategy results in two distinct female reproductive groups: 1. reproductive, or those moulting, mating and spawning in a given summer and, 2. non-reproductive, or those incubating young and larvae in a given summer. These two groups can be easily separated on the basis of ovary development, presence of eggs or young, moult stage and the condition of secondary sexual characters such as glair glands and gonopore and pleopodal setation. Representatives of the two reproductive groups occurred in collections throughout the duration of the study. In males of both species, sperm was found within the vasa deferentia from February to May. Sperm tubes began forming in February, their number peaking in early May and then decreasing through the winter. Unlike females, males appear to breed every year. The gonads of reproducing females and males therefore show synchronous cyclic development with peak development occurring just prior to the mating season. The postembryonic development in *Astacopsis* consists of four morphologically distinct larval stages and appears to be significantly different from other parastacids as well as astacids/cambarids. The development sequence is considered to be primitive in having retained some of the ancestral marine larval characters in particular the four developmental stages, and early differentiation of swimming appendages in the form of a tail fan.

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IMMIGRATION OF *METAPENAEUS STEBBINGI*, *M. AFFINIS* AND *M. MONOCEROS* JUVENILES IN THE CREEKS AND BACKWATERS NEAR KARACHI

Metapenaeus stebbingi, *M. affinis* and *M. monoceros* inhabit the northern Arabian Sea and contribute significantly to the Pakistani fishery. The immigration and life cycles of these species were studied in four localities: Korangi Creek, Bhambore Sandspit and Hab Delta during 1979. These are all muddy, mangrove areas near Karachi City, with a temperature range of 16°–33°C . Salinities were generally high during winter (December–January) and spring (37–39 ppt) due to the prolonged dry season. Lower salinities (29–30 ppt) in summer were caused by southwest monsoon rains and in winter due to the occasional northeast monsoon. The growth rates in the four species were determined by rearing these in the laboratory so as to know their age when caught.

M. stebbingi were caught round the year in Korangi Creek with a peak from July to September and secondary peaks during February–March and November (early winter), a July peak in Hab Delta and a November peak at Sandspit. In general larger 10–14 mm C.L. individuals were abundant during winter and smaller 3–9 mm during spring and summer. Recruitment generally occurred during late summer (July–October) and early winter (November–December). Juveniles of this species are abundant in areas where high salinity prevails, like Korangi Creek and Mekran coasts, but are insignificant in areas where there is great variations (0–40 ppt) as in the Indus Delta (Hassan, 1989). The species spawns throughout the year with a peak during May–July.

Peaks of abundance in *M. affinis* occur during summer at the four localities, with highest in Korangi Creek and lowest at Sandspit. Larger 8–12 mm were more frequent during winter (January–February) and late summer (September–October), and smaller 3–7 mm during spring (April) and summer. This species in less abundant in areas where high salinity prevails (30–36 ppt) but recorded in very large numbers further south in the Indus Delta where there are great variations in salinity (0–40 ppt, Hassan 1989). The species spawns throughout the year with peaks during February–March and recruitment generally occurring from April to July.

M. monoceros juveniles were present in the study area in smaller numbers than other species at the four localities, and only during April to October, with a peak during May–June. The species spawns from January to July with recruitment occurring during summer. It is typically abundant off the coast of Pakistan (Golobov and Grobov, 1969; Zupanovic, 1971). It seems that juveniles of this species prefer low or moderate salinities as George (1971) reported great abundance in low saline estuaries and paddy-fields in India.

A temporal partitioning is apparent between *M. affinis*, *M. monoceros* and *M. stebbingi* related to spawning cycles. In the former the spawning is in spring and in the latter summer. This is similar to *M. endeavaouri* and *M. dalli* in Dugong River (Coles and Long, 1985) and to *M. bennetae* and *M. macleayi* in Moreton Bay (Young, 1978; Dall, 1958).

Life Cycle

Metapenaeus spawn at sea and enter the creeks and backwaters when 15–20 days old and 1 mm C.L. They continue to move to and fro with tidal currents and generally settle at one month old and 3 mm C.L. (Hassan, 1983, 1987b, 1989). Juveniles grow for about 4 months before migrating back to sea at 12–16 mm. Sub-adults spend about a month in the deeper waters of the same locality, or shallower shelf, and attain 20 mm. They continue to grow and mature as they spread into deeper waters and spawn when 7 months old (20–30 mm). However, the bulk of the cohort spawn at 30–35 mm C.L., when 10–12 months old (Zupanovic, 1971; Garcia, 1985).

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GREGARIOUS SETTLEMENT BY PORCELAIN CRABS, *PETROLISTHES* (ANOMURA: PORCELLANIDAE)

The planktonic larvae of many marine invertebrates settle in response to specific cues (Meadows and Campbell, 1972; Scheltema, 1974), but the means by which postlarvae of decapod Crustacea identify and select appropriate habitats are largely unknown. A series of field and laboratory experiments were conducted to examine settlement patterns by megalopae of the porcelain crabs *Petrolisthes cinctipes* and *P. eriomerus*, which often display distinct, non-overlapping intertidal distributions when they co-occur. The adult vertical distributions are due to abiotic factors; sensitivity to thermal stress during aerial exposure confines *P. eriomerus* to the low intertidal, while the distribution of *P. cinctipes* is correlated with substrate composition (Jensen, 1990). These patterns are maintained in part through gregarious settlement by megalopae of both species; megalopae were induced to settle in response to caged conspecific adults transplanted above or below their normal range (Jensen, 1989). Subsequent investigations have focused on the means by which conspecific adults are located, and possible post-settlement benefits of associating with adults.

In a field experiment, adult *P. eriomerus* were confined to chambers placed beneath concrete patio blocks. These chambers were screened in a manner that prevented either tactile or visual contact by megalopae, while similar chambers without crabs served as controls. Significantly more megalopae occurred on the treatment blocks as compared to interspersed controls, suggesting that a waterborne cue is involved.

Laboratory observations revealed that contact with adults initiates a sequence of behavioural and morphological changes including a loss of forward swimming behaviour, changes in color, and degeneration of the pleopods, all features consistent with ensuing metamorphosis to first instar. *Petrolisthes cinctipes* megalopae (obtained by holding zoeae caught in plankton tows) placed individually in containers with adults completely settled within 2–4 days while those in control treatments without adults continued to swim strongly for 2 weeks; in some individuals the swimming response persisted for as long as 3 weeks (Fig. 1). This suggests an extended period of competency to settle, an important consideration since upon moulting from a zoea into the megalopa stage an individual could be anywhere from tens of metres to tens of kilometres from shore. After settlement, juveniles continue to remain intimately associated with conspecific adults for at least a year, hiding beneath them or between their legs. Clustering with adults probably reduces predation by intertidal fishes, as the megalopae of these species are relatively slow moving and do not demonstrate other defensive tactics such as burying in the substrate. In a laboratory experiment, juveniles with conspecific adults suffered significantly less predation compared to those with adult congeners or in controls with no adults.

There are indications that two species of porcellanids of the genus *Pachycheles* also behave in a similar manner (Jensen, 1990), and while adult-mediated settlement in these filter-feeding species is admittedly a special case, gregarious settlement could be widespread among deposit-feeding or herbivorous decapods. Species that are likely candidates should meet 3 criteria that are compatible with this type of selective settlement: 1) adults and juveniles occur together; 2) they should have relatively specialised habitat requirements; and 3) a minimal risk of cannibalism. Gregarious settlement could be advantageous even among potentially cannibalistic species, provided the benefits of proper habitat selection outweigh the risks, or settling postlarvae are too small to elicit attack. It is unknown to what extent the benefits of such close association with adult populations may be offset by increased intraspecific competition.

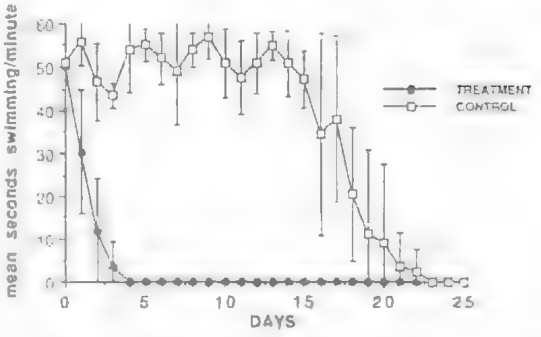

FIG. 1. Mean swimming times (seconds/minute; 1 sd) for *P. cinctipes* megalopae confined with adults (treatment) or held alone (control).

This study provides evidence of a settlement competency period for porcellanid megalopae, and subsequent benefits of gregarious settlement. More importantly, it demonstrates settlement in response to a specific cue, a widespread phenomenon in other invertebrate larvae but not previously demonstrated for decapod crustaceans.

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VERTICAL MIGRATION OF THE EDIBLE CRAB, *CANCER PAGURUS* (CRUSTACEA: DECAPODA: BRACHYURA), ON ROCKY SHORES OF THE SOUTH COAST OF NORWAY

Crustacean foraging activity in the intertidal zone during high tides, and sheltering in subtidal areas during low tides, has been noted on numerous occasions by many authors. Besides the study by Robles *et al.* (1989) on diel variation of intertidal foraging by *Cancer productus* L. in British Columbia, Canada, there exist only a few quantitative studies of temporal variations of such habits (Robles *et al.*, 1989).

It has been known for many years that *Cancer pagurus* L. (the only commercial crab in Norway) makes diurnal vertical movements on rocky shores of the Norwegian Skagerrak coast during the summer and early autumn (Nordgaard, 1912; Bjerkan, 1927; Dannevig and Gundersen, 1982). According to Dannevig and Gundersen, many crabs move to shore level at night to forage, and angling for crabs with flash light and scoop net on summer nights has a long tradition. This kind of cyclical movement of *C. pagurus* has not been reported from other parts of the crab's range, from the Mediterranean to northern Norway (Christiansen, 1969), nor has a close study of this activity been previously undertaken. Here we describe skin-diving surveys of cyclical movements of *C. pagurus* during the night, and throughout the year, on rocky shores on the Norwegian Skagerrak coast.

Study Area and Results

The study area was a small unsheltered rocky islet between Grimstad and Lillesand *c.*150m from the mainland (58°16'19"N, 8°32'33"E) The islet is *c.* 290 m in perimeter, and a maximum of 100 m across. The whole field area covered *c.* 3700 m^2, bounded in depth by the upper limit of *Laminaria digitata* (Hudson) (3–5 m), and the water line. The common mussel, *Mytilus edulis* L., occupied a broad zone in the study area. The survey reported here was carried out between March and December 1980. Temperature, salinity, water level, height of waves, directions of current and wind, and light conditions were recorded during all surveys. The difference in tide at the study area is 17 cm.

No crabs were seen on the first night-survey (30 March), nor were any individuals observed at night on the two next surveys (1 and 3 May). On 24 May, and until the last survey on 11 December, crabs were observed on all 30 nights of survey. On all surveys, crabs were observed eating *M. edulis*, and random examinations showed that the crab stomachs usually were filled with fragments of the mussel. A maximum of 237 crabs were counted during a survey on 22 June. In contrast only 1 crab was observed during the night survey on 7 August. This low number may be due to the moulting and mating processes which occur at this time of the year.

In late August surveys were carried out every fourth hour throughout 24 hours. Only 2–3 crabs were observed during day time, whereas the highest number, 91 crabs, was counted between two and three hours after sunset. Surveys were also carried out during the daytime on 9 different days, but only 0 to 4 crabs were observed on these surveys.

Carapace width throughout the investigation period varied between 50–190 mm for females and 50–200 mm for males, with the highest number between 130–150 mm and 120–140 mm, respectively. Females were regarded as sexually mature at 130 mm, but females with eggs were never observed in the study area. According to the literature (Edwards, 1979; Dannevig and Gundersen, 1982) crabs with a carapace width of 115 mm should be about 5 years old, and older individuals may be up to 300 mm in carapace width.

Tagging of crabs was done while swimming in the field area. Of 542 tagged crabs, 136 (25%) were recaptured from 1 to 7 times at the islet or within a 0.5 km radius, during the study period. In addition, 44 crabs (8.1%) were found between 0.5 and 28 km from the islet. Two of these had earlier been recaptured at the islet. The last recapture of a long-distance migrant crab was two years after tagging. The percentage of recaptured individuals at the islet was highest for males, whereas a higher percentage of females was recaptured more than 0.5 km from the islet. That females of *C. pagurus* make extensive migrations has previously been mentioned by several authors (Edwards, 1979).

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SPATIAL STRUCTURE IN A STONE CRAB POPULATION (BRACHYURA:XANTHIDAE) AND THE INTERPLAY WITH RESOURCE MOSAICS

For large, motile, den-dwelling decapods (e.g. clawed and spiny lobsters) habitat should be considered a mosaic of resource patches. Patchiness affects access to resources which, in turn, affects mating patterns within populations (Emlen and Oring, 1977). For some small brachyurans, patchiness of refuge or premium burrowing sites factors into male mating success (Christy, 1983; Diesel, 1986; Abele *et al.*, 1986). We asked if population structure of commercially important stone crabs would vary with refuge patchiness sufficiently to exclude alternative mating strategies as defined by Christy (1987).

Methods

Refuge spatial patterns were manipulated as a split-plot experimental design for a population of hybrid stone crabs (*Menippe mercenaria* x *M. adina*) in the northeastern Gulf of Mexico. Six interspersed treatment plots each contained 36 prefabricated reef modules in either a widely spaced (60m), uniform pattern, a closely spaced (2m) uniform pattern, or an intermediate, mixed pattern, i.e. 6 widely spaced clusters, each with 6 closely spaced modules. In September and October, 1987, 12 randomly selected modules were non-destructively sampled on each plot. In late August and early October, 1987, one block of treatment plots was exhaustively but non-destructively sampled (n = 36 modules/plot). That same block was exhaustively sampled monthly from August 1988 through July 1989. Data for each crab included specific den location, tag identification, sex, carapace width, and phenotypic index according to Bert and Harrison (1988)

Summary of Results

Phenotypically, this hybrid population most closely resembled *M. mercenaria*. In 1987, widely spaced modules harboured more crabs than did closely spaced modules or those in an intermediate, mixed pattern. Widely spaced and mixed modules also tended to harbour larger males and females, although differences were not significant for every sampling period. Sex ratios did not differ among treatments, yet widely spaced modules harboured more mated pairs than expected from the distribution of males among plots

Crabs left the study site during late summer and fall 1988 as *Octopus vulgaris* invaded plots. Treatment effects re-emerged following spring 1989 recolonisation by adult crabs. Crabs tagged in 1989 were not long-term den residents, but resightings were greater than expected by chance on the wide plot. Females were resighted more often than males. Only 5 of 100 tagged males were resighted, three resighted just once, and two large males (122 mm and 110 mm CW) found repeatedly in different wide-plot modules with different females.

Discussion

Differences in crab abundance may be explained by differential prey depletion on soft-bottom as a function of refuge spacing and distance from refuge (Lindberg *et al.*, in press, Frazer and Lindberg, unpubl.). Refuge value apparently changes with access to prey, and the resultant mosaic then influences residency patterns by size and sex.

Low site fidelity by males compared to females and multiple male occupancy of modules (Wilber, 1989a; and herein) precludes a resource-centred male mating strategy. Protracted mate guarding (Wilber, 1989b) also impugns an encounter-rate-competition male strategy. The greater per capita mating success of males on wide plots, and resightings of few large males amidst numerous females is consistent with either a female-centred, patrol-and-defend strategy or a search-and-defend strategy influenced by patterns of food and refuge.

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SPATIAL AND TEMPORAL DISPERSAL AND RECRUITMENT PATTERNS OF DECAPOD CRUSTACEA IN THE NORTHWESTERN ATLANTIC

Larval dispersal and postlarval recruitment are vital processes affecting the maintenance of ecologically and economically significant populations of decapod crustaceans. Vertical positioning of larvae and postlarvae in the water column plays a major role in the particular strategies of retention or expulsion with immigration that are employed.

The present study was undertaken to investigate variations in vertical distribution of prejuvenile decapod crustaceans according to temporal (diel), spatial (estuarine, transitional, oceanic), ontogenetic (larval stages, postlarvae) and various environmental factors (light, temperature, salinity, wind, tidal cycles). Furthermore, effects of vertical positioning on dispersal and recruitment were examined.

Three stations were established for the present study: York River mouth (estuarine) (37°12'N, 76°16'W); Chesapeake Bay mouth (transitional) (36°58'N, 76°07'W); Chesapeake Light Tower (offshore) (35°54'N, 75°43'W). Each station was occupied for a continuous 72 hour period in late summer over six tidal cycles. Quantitative plankton samples were collected every three hours from the following depths: Neuston (0.1 m), 1m, 3m, 6m, epibenthos (11–13 m). A total of 375 samples were obtained (125 from each station). Non-parametric methods of statistical analysis were used, except where normality was not critical.

Collectively, 41 decapod species, 160 developmental stages and an estimated 6,000,000 specimens were obtained. A large majority of the total catch (86%) came from the offshore location. True crabs (Brachyura) accounted for 53% of the species, 50% of the stages and 92% of the specimens. Anomurans, thalassinideans and shrimps were also found. *Callinectes sapidus* (87% of the total), *Uca* spp. (3%) and *Panopeus chaetopterana* (2%) were the most commonly collected species.

Of the 160 developmental stages, 56 were present in sufficient quantities for data analysis (Maris, 1986). Fifteen different distributional groups were formed based on statistical comparisons of abundances with depth.

Results indicated that proximity to the estuary greatly affects vertical positioning. Overall day-night mean depths (m) for collective specimens were: estuarine, 5.96–4.24; transitional, 7.49–3.19; offshore, 1.86–1.41. Light was proposed as the major factor governing distribution, with temperature, salinity and tidal cycles having no significant effects.

Six dispersal-recruitment patterns were established for collected genera based on temporal and spatial distributions: retained estuarine (*Neopanope, Palaemonetes, Panopeus*), retained estuarine-transitional (*Callinassa, Panuxa, Pinnotheres, Upogebia*), retained transitional-nearshore (*Eucrramus, Hexapanopeus, Pagurus*), retained offshore (*Emerita, Libinia, Ovalipes*), expelled with estuarine spawning (*Uca*) and expelled with transitional spawning (*Callinectes*).

Vertical positioning greatly influences larval dispersal and postlarval recruitment of decapod crustaceans. Certain estuarine and transitional species accomplish retention by consistently maintaining a vertical location near the bottom, while some vertically migrate over short intermediate distances, presumably to the depth of no net motion. Others maintain constant intermediate depths, while various species vertically migrate over long distances. Offshore, individuals are typically retained on the continental shelf by maintaining shallow-intermediate depths.

Larval abundance correlations with ebb tides (promoting flushing) and flood tides (promoting retention) in small inlets have been presented by Cronin and Forward (1982), Lambert and Epifanio (1982), and Brookins and Epifanio (1985). In the present study, the general lack of correlation between tidal influence and vertical distribution possibly indicates that different mechanisms are in effect in large systems as compared to small inlets.

Even though tidal effects were found to be minimal, larvae likely utilise the net flow patterns of the bilayered system for movement. Transport mechanisms typically consist of near-bottom estuarine concentrations with upper layer affinities maintained offshore.

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AGE STRUCTURE OF ANTARCTIC KRILL (*EUPHAUSIA SUPERBA*) POPULATIONS AS DETERMINED BY AGE-PIGMENT ANALYSIS AND BY SIZE-FREQUENCY ANALYSIS

Morphometric measurements and size frequency analysis have conventionally been used to assess the age structure of crustacean populations. Certain crustaceans have, however, not proven amenable to such analyses. For example, laboratory studies have shown that the Antarctic krill *Euphausia superba* can live for 7–8 years (Ikeda and Thomas, 1987), a life-span far in excess of that predicted from morphometric determinations. Furthermore, this species may decrease in size during periods of low food availability (Ikeda and Dixon, 1982) thus obscuring the relationship between measurements of body size and age. In response to these problems, an age-determination technique was developed for *E. superba* which was based on the measurement of levels of age-pigments (FAPs) in the animals (Ettershank, 1983, 1984a, b, 1985).

Early work on FAPs held promise (Ettershank, 1983, 1984a, 1985) but subsequent studies demonstrated methodological problems (Nicol, 1987). Studies examining FAPs in other organisms have yielded equivocal results (Hill and Radtke, 1988; Hirche and Anger, 1987) but the utility of this technique for aging populations of the species for which it was originally proposed — *Euphausia superba* — is yet to be proven.

A population of juvenile *E. superba* was maintained under constant laboratory conditions. A sample of the population was removed at the start of the experiment and the animals were frozen individually in liquid nitrogen. The surviving animals from the original population were frozen in liquid nitrogen one year later. The two sets of samples were analysed for FAPs (Ettershank, 1984b) and the mean fluorescence peak heights of the two groups were compared. The results of the fluorescence technique were compared with those of a more conventional weight-frequency analysis.

The mean fluorescence (expressed as relative fluorescence or as weight specific relative fluorescence) of the year 2 group was significantly greater than that of the year 1 group. In contrast, the mean weight of the individuals in the population decreased significantly over the course of the year (Table 1). The weight and relative fluorescence data were pooled, simulating the normal field situation of a series of frequency data from which peaks must be discerned. In this instance the number of year classes and the mean peak heights were known so the results from the frequency analyses could be compared to the expected (real) case. An analysis of the weight specific relative fluorescence data by the Macdonald-Pitcher method yielded a best fit for two modal peaks, the means of which were not significantly different to the known means for the two year classes. The weight-frequency analysis also yielded a best fit for two peaks but in this case the correspondence between the means of the predicted and known weight groups was not so precise or accurate.

TABLE 1. The mean values and predicted mean values for the weight specific relative fluorescence and the dry weight of the animals in each sample.

	Year 1	Year 2
Fluorescence	133.286	213.873
Mean wt. specific fluorescence	10.625 (9.53)	21.10 (20.42)
Mean dry weight	13.286 (19.34)	9.926 (9.65)
number of samples	37	23

Comparison between mean weight specific fluorescence in year 1 and year 2: $t = -7.586$, 58 df, $p < 0.0001$.
Comparison between mean dry weight in year 1 and year 2: $t = 2.522$, 58 df, $p = 0.014$.
Values in brackets are predicted means from Macdonald-Pitcher analyses of combined year 1 and year 2 data sets.

These results show that under laboratory conditions it is possible to separate year groups of *E. superba* by FAP quantification and that the accumulation rate over a period of one year is great enough that the year groups can be discriminated even when the data are pooled. We have also shown that FAPs can be used to demonstrate year group separation and predict which group is older when size-frequency analysis gives the wrong answer.

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ESTIMATION OF GROWTH PARAMETERS OF THE VELVET SWIMMING CRAB (*LIOCARCINUS PUBER*) (BRACHYURA: PORTUNIDAE) AT PLYMOUTH, S.W. ENGLAND.

Liocarcinus puber (L.) (formerly *Macropipus puber*) is a locally abundant portunid crab on rocky coasts of Western Europe. Recent overfishing in Spain and continued demand has allowed an export fishery to develop from the UK being centered in N.W. Scotland. Anecdotal information suggests that there may be significant variations in the growth format between Spain and N.W. Scotland, however management parameters for the UK fishery have been based largely on data from Spain.

Approximately 4,000 specimens were sampled by hand from the intertidal, and via SCUBA, nearshore sub-littoral areas, from November 1985 to December 1987. Size frequency analysis from monthly samples readily described the growth of juveniles, attaining a mean model size of 40–45 mm Carapace Width at an age of 1 y. Sexual maturity occurs at *c.* 1 y (= 46.5, = 40.6 estimated from allometric growth of chela and abdomen) (Norman, 1989). Adult modes showed no clear definition into year classes.

Examination of moult stages of adults from monthly samples showed a marked peak in early post-moult crabs (soft and paper-shell stages) in June/July for males and in August for females and a smaller peak in autumn. Laboratory rearing under simulated natural conditions, showed similar moult periodicity, with large adults (>60 mm, >50 mm CW) moulting annually, males in June and females in July/August, whilst smaller adults moulted at corresponding times to larger adults and again between September and December. Male growth curve showed close agreement with other methods, whilst females showed reduced growth from >55 mm CW (Fig. 1); this probably being due to increased reproductive effort.

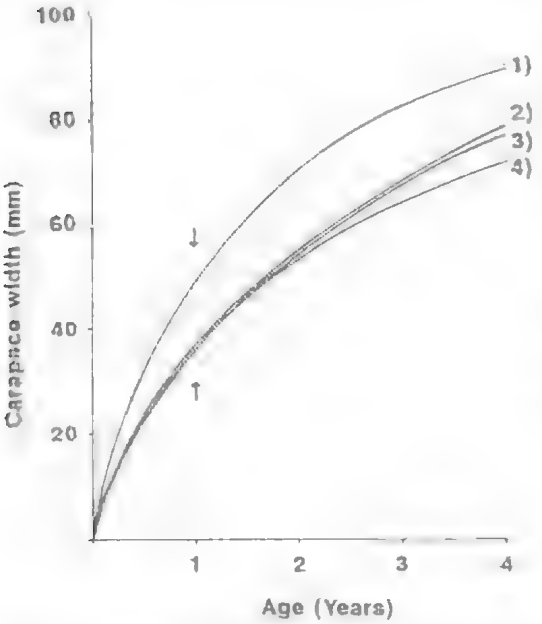

FIG. 1. Von Bertalanffy growth curves for female *Liocarcinus puber* from 1) Spain (González Gurriarán, 1985) and 2), 3) and 4) this study, ELEFAN, probability paper technique and laboratory rearing respectively. Arrows demark size at 1 year old.

ELEFAN (Pauly, 1987), a programme which fits a continuous growth curve to monthly size frequency data via a least squares optimisation process showed clear optimisation of parameters, but low agreement between actual and estimated parameters due to the discontinuous nature of crustacean growth as well as the natural variation within the sample. The probability paper technique (Cassie, 1954) due to the difficulty in distinguishing moult classes from year classes and requirement of subjective assessment, was felt to be less robust than other methods. Estimates for the growth constant (K) between the three methods ranged from, for male 0.28 to 0.34, and female 0.35 to 0.45, and for the asymptotic length (L_∞), for male 107 to 114, and female 91 to 98.

Size frequently analysis from Spain (González Gurriarán, 1985) gave higher estimates of K (0.65, 0.67), but comparative L_∞ (= 109, = 96). In both studies age of sexual maturity is approx. 1 year, but at correspondingly different sizes (Fig. 1). The validity of this difference in size of sexual maturity is further endorsed by measurements from allometric growth, the size of smallest ovigerous female and size at which 50% of sample have mature ovaries, for each, estimates from Spain are consistently larger, by approx. 10 mm, than for Plymouth (González Gurriarán, 1985; Norman, 1989).

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SPAWNING BEHAVIOUR OF *SERGIA LUCENS* (HANSEN) (DECAPODA: SERGESTIDAE)

The 'Sakura-ebi' *Sergia lucens* (Hansen) has provided the base of an historic fishery in Suruga Bay, on the south coast of Honshu, since 1894. Today, the annual catch totals 2500 to 3000 metric tons, more than US$20 million in landed value. Research on the shrimp is well advanced (Omori, 1969; Omori *et al.*, 1973).

Sergia lucens completes its life cycle in Suruga Bay. Spawning occurs at 1 year of age, from June to the middle of November. One female produces about 2000 eggs. The eggs are primarily spawned near the mouth of the rivers at the head part and the western part of the bay. The eggs are planktonic, and are distributed mostly at depths ranging from 20–50 m, where the temperature is higher than 18°C, which is the lower limit of the optimal temperature range (18°–25°C) for spawning and larval development (Omori, 1971; Omori and Jo, 1989). Eggs hatch into nauplii after 24–36 hrs under normal environmental temperature conditions. The larvae attain a length of 20–25 mm and recruit to the fishery at 3–4 months old. The fishery is based on a species with a lifespan of only 1.5 years, and the recruitment is instrumental in determining year-class strength.

In 1985 and 1986, frequent sampling of the 0–50 m water column by vertical tow net was conducted at 2 stations at the head of the bay for July, August and September. In addition, samples were obtained once a month from June to October at 8 stations in the entire bay. The abundance and distribution of eggs and larvae were analysed in relation to possible causes of the temporal and spatial variations.

Daily fluctuation in egg abundance was considerable. The coefficient of variation in July varied from 81–269% (Bishop *et al.*, 1989). In 1985 spawning occurred from the beginning of July, whereas in 1986 it occurred after the middle of July. In August when the seasonal thermocline is particularly marked and the optimum temperature zone narrow, spawning was reduced.

The possibility of a second peak of spawning was suggested in September 1985. In 1986 spawning activity did not recover at the head of the bay, as the principal spawning area seemed to have shifted from the head to the western part. Under favourable conditions, *S. lucens* may produce two broods in one season with a considerable interval between.

Many external and internal factors may be involved in the spawning activity of *S. lucens*. Among them, temperature seems to be the most important. The start of heavy spawning is roughly associated with the warming of the surface water to 24°C and vertical oscillation of the 18°C-isotherm depth. The temperature around 40 m rapidly increases to 18°C, 3–7 days before the spawning peaks. Temperature at 20–50 m depth affects the abundance and growth of the larvae, whereas food is abundant and would not have great a effect. Correlations between spawning and lunar period were not significant. In general, the potential size of stock for the following year is largely affected by the production and survival of eggs and larvae during the early spawning season. There is a positive relation ($r<0.01$) between year-class strength and yearly average width of the optimum temperature zone from June through to August at the head of the bay (Nakamura, 1982).

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CATASTROPHIC MORTALITY OF BREEDING TROPICAL ROCK LOBSTERS

In August–September each year many 3–4 year old subadult *Panulirus ornatus* emigrate from Torres Strait, northeastern Australia, into the Gulf of Papua; some migrate as far as Yule Island at the eastern side of the gulf, appearing in breeding condition on shallow coastal reefs by mid-January (Moore and MacFarlane, 1984; MacFarlane and Moore, 1986; Bell *et al.*, 1987). There is a seasonal artisinal fishery for these breeding lobsters, but it lasts only a few months. The breeding lobsters are in poor condition and it has been hypothesised that they invest so much energy in the migration and in reproduction that death is inevitable (Trendall and Prescott, 1989). However, the population could also decline as a result of fishing pressure or emigration from the fishing grounds. These alternative explanations of the annual decline of the breeding population were investigated in early 1989.

Methods

In order to distinguish between the three hypotheses it was necessary to estimate natural and fishing mortality, and immigration and emigration rates. A variety of methods were used to estimate these parameters; (a) tangle nets were deployed in deep water adjacent to the coastal reefs to reveal the extent of movements on and off the reefs, (b) the catch and effort of the fishery were analysed to indicate trends in abundance, (c) lobsters were tagged and their recapture rate was monitored to provide an estimate of population size and loss rates, and (d) the water content of samples of digestive gland was measured to show trends in physiological condition.

Results and Discussion

The Yule Island fishery followed a typical pattern over the period January–March 1989, with two major peaks in catch following monsoonal storms before waning through March. The sex ratio of the first peak was close to unity whereas prior to this the catch consisted mostly of males and the second peak comprised almost entirely females.

The tangle nets caught lobsters in two pulses in synchrony with the January and February full moons. However, these pulses were considered not to indicate emigration because (i) catch rates from the reef top peaked immediately afterwards, (ii) several animals tagged from the nets were caught later by the fishery, and (iii) through March, when the catch of the fishery declined rapidly, no associated movement of lobsters off the coastal reefs was revealed by the nets. Instead, the pulses were interpreted as lunar hatching excursions as they comprised almost entirely females with evidence of recently hatched broods.

Analysis both of the tagging and catch data indicated extraordinarily high total loss rates ($Z = 10–12$) compared with lobsters in Torres Strait ($Z < 1$); indeed, of the 20,000–30,000 lobsters estimated to be present at the beginning of the study more than 95% disappeared during the following few months. The tag return rate was high indicating that fishing pressure was responsible for much of the decline ($F = 3–4$), but the natural mortality rate over the period was even higher ($M = 7–8$) possibly as a result of the stress of migration and breeding.

This interpretation is supported by trends in the water content of the digestive gland. The water content (60% in healthy lobsters) increased steadily to 80% by early March after which it declined slightly; this apparent recovery may have resulted from animals with the highest water content dying at a faster rate. The degree of deterioration was greater in females and the recovery was more marked in the very few males remaining in the fishery at this time. Prior to this physiological recovery, recently moulted lobsters were very rare. However, in the final weeks of the fishery nearly all males caught had moulted recently and their mortality rate had reduced to an unmeasurable level. In contrast, moulting was not observed in females and their mortality rate remained very high throughout the study.

It is clear that lobsters breeding on coastal reefs near Yule Island do not survive to breed again in subsequent years. This raises the question of the generality of this phenomenon among other breeding populations of *P. ornatus* that have been discovered recently in deep water adjacent to the far northern Great Barrier Reef of Australia.

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REPLENISHMENT OF CRUSTACEAN ASSOCIATES OF CORAL ISOLATES IN THE CENTRAL REGION OF THE GREAT BARRIER REEF

Most coral reef habitats support a rich fauna of crustacean associates (Bruce, 1976). These associations range from the use of corals as one of a range of habitats (Coles, 1980) through to obligate species feeding on coral mucus (Knudsen, 1967). Although previous ecological studies have revealed local and regional variations in species composition and abundance of coral dwelling crustaceans (Abele, 1976) there have been few attempts to quantify distributions, abundances and species replenishment systematically at any scale.

The present study was a four year survey of the crustacean fauna associated with live and dead *Pocillopora verrucosa*. The crustaceans were sampled systematically from isolated corals placed at coral reefs located on a transect spanning the width of the continental shelf in the central region of the Great Barrier Reef. The location of the reefs and the sampling methods used are described in detail in Preston and Doherty (1990).

The results of this study demonstrated pronounced cross-shelf patterns in the species composition and abundance of crustaceans that colonised cleared corals. These patterns persisted throughout the four year study.

Among the microcrustaceans copepods were the dominant taxa found on live and dead corals in the mid-shelf and outer shelf reefs. Tanaids and cumaceans were more dominant on the inner shelf reef particularly on back reef sites. The total abundance of microcrustaceans was significantly greater on the mid-shelf than on the inner or outer shelf.

Live and dead corals from the mid-shelf reefs yielded significantly greater numbers of agile shrimps than those located at the inner or outer shelf reefs. On all reefs the shrimp fauna on live corals was dominated by a single species; *Periclimenes amymone*. However, monthly comparisons of community structure and faunal similarity revealed regional variation in species replenishment following disturbance of live corals. By contrast, the agile shrimp associates of dead corals showed a more even distribution of individuals among species and a more regular pattern of regional species replenishment.

Destructive sampling at the end of the survey revealed that live corals on all reefs supported a common group of sedentary macrofaunal associates. However, there were significantly fewer of these associates on the inner shelf reef. On dead corals there were similar numbers of sedentary macrofaunal associates at all locations but pronounced cross-shelf patterns in species composition.

The results of this study suggest that the amount of space available is not necessarily a limiting resource for crustaceans that have formed an association with living corals. Nor is it the case for free-living species that inhabit dead corals. Consistently lower yields of agile shrimps and microcrustaceans from standard sized units of live and dead corals at the inner and outer shelf reefs compared with the mid-shelf reefs indicate that the former sustain relatively depauperate populations of these crustacean associates. Relatively low rates of replenishment by recruitment or migration apparently maintain this cross-shelf pattern.

Regional variation in replenishment of live corals by obligate species probably reflects the regional population density of the host corals. In order to establish if a similar link exists between the distribution and abundance of free-living species and concurrent patterns of particular habitats we need to know more about the connection between these species and their habitats.

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REPRODUCTIVE BEHAVIOUR OF *CARDISOMA CARNIFEX* (HERBST, 1794) (BRACHYURA: GECARCINIDAE) AT LIZARD ISLAND, GREAT BARRIER REEF

The land crab, *Cardisoma carnifex*, was first found at Lizard Island by Peter Davie of the Queensland Museum in June 1987. The closest previous record was Murray Island in the Torres Strait (Türkay, 1974).

The populations studied were located in Watson's Bay and Mermaid Cove on Lizard Island (14°40'S, 145°27'E). The Watson's Bay study site included two areas of approximately 400 sq m with over 300 obviously active burrows. The Mermaid Cove site is smaller comprising 300 sq m and 200 burrows. The burrows were located on the edge of the mangroves near the high-water mark in a community of grasses dominated by the saltwater couch, *Sporobolus virginicus*.

Reproductive behaviour and periodicity were studied between October 1987 and June 1990. The female crabs spawned by migrating from their burrows to the ocean. In Watson's Bay they migrated from their burrows on the landward edge of the mangroves, over a 5m high spinifex covered sand dune to the ocean or followed Ferrier's Creek to its mouth. The crabs entered the sea and swam a maximum of 15m from shore to depths of 0.1–3m. Hatching was induced when the egg laden abdomen was submerged and the female flicked her abdomen. The egg cases immediately ruptured and the zoea swam free. Each 300–400g crab released between 350,000 and 450,000 eggs. Egg mass was related to body weight.

Evidence from captures of berried females, tracks on the beach at Watson's Bay and Mermaid Cove, and observations of spawning, indicated that spawning was highly seasonal and tied to lunar phase on Lizard Island. In October 1988 tracks from 10 crabs were observed on the beach at Watson's Bay indicating that in at least some years spawning may begin as early as October (the austral spring). No berried females or tracks were observed in November in any of the study years. Spawning migrations occurred primarily three nights before full and new moons in December 1989 and January 1990. Spawning migrations were observed on 11–13 December 1989 (approximately 30 crabs per night at Mermaid Cove; 20 crabs per night at Watson's Bay) and 8–10 January 1990 (approximately 20 crabs at Mermaid Cove; 30 crabs at Watson's Bay), both periods occurred during the three days prior to full moon. No migrating males were observed. Also tracks from 60–70 spawning crabs were observed on 12 December 1989 in Watson's Bay and from 25–30 crabs at Mermaid Beach. Tracks from approximately 50 crabs were observed on the strand line on the new moon on 29 January 1989. There was no evidence of spawning in February 1990.

An ovigerous female was captured by the burrows on December 1989. The undifferentiated yolky eggs developed into zoea and hatched in 13 days. The timing of zoea release coincided with the December spawning migration.

Vision plays an important role in the migration. Crabs that had just released eggs were captured. Some crabs eyes were covered blocking vision; the eyes of others were left unobstructed. When released the visually impaired crabs were disorientated. Non visually impaired crabs would immediately move up the beach and seek cover. Migrating crabs would stop if a light or large shadowy object was near them.

A sample of the migrating crabs were caught and tagged by etching the carapace with a hacksaw. Although *Cardisoma guanhumi* is known to spawn several times in a season (Lutz and Austin, 1983), none of the tagged spawning females were recaptured during subsequent spawning migrations.

During the 2 3/4 year study a total of nine copulations were observed — six between October to January and two during the last week of May. Three female crabs collected in late May/early June were dissected. Two of these were post copulatory, In all three, the brown ovaries were undeveloped and weighed 0.7, 0.9 and 1.4g.

The period between copulation and spawning in *Scylla serrata* can extend up to 7 months under unfavourable conditions of temperature and nutrition (DuPlessis, unpubl. in Heasman *et al.*, 1985). It is possible that copulation in *Cardisoma carnifex* occurs 1–5 months prior to spawning.

No precopulatory observations were made. Copulation occurred intermoult near burrows of females. Copulation occurred with crabs ventrally juxtaposed by the entrance to the female's burrow. There was little motion. The female was not constrained by the male nor were there other males in the vicinity. Copulation terminated within 1–10 minutes after being spotted. The female quickly entered a burrow while the male slowly moved away.

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FOOD AND DIURNAL BEHAVIOUR OF DEEPWATER PRAWNS

Penaeidean and caridean prawns provide most of the crustacean catch in a demersal trawl fishery for prawns and scampi on the North West Slope of Australia. The main penaeidean prawns are *Aristaeomorpha foliacea*, *Aristeus virilis*, *Haliporoides sibogae* and *Plesiopenaeus edwardsianus*, and the main caridean prawns are *Heterocarpus sibogae* and *H. woodmasoni*. Catch rates of all six prawn species are greater during the day than at night.

Foregut contents in trawl-caught prawns were analysed, and broad dietary groups used to indicate the habitats in which the prawns were feeding. Prey groups considered to indicate midwater feeding included siphonophores, chaetognaths, heteropods and pteropods; prey groups indicating benthic feeding included sponges, polychaetes, bivalves and echinoderms. In all prawn species, the majority of the foregut contents consisted of decapod crustaceans and fish, most of which was unidentifiable or was not classifiable as necessarily having a midwater or demersal origin. Significant quantities of foraminiferans and squid were also ingested.

Aristeus virilis, *Haliporoides sibogae* and *Plesiopenaeus edwardsianus*, which ate mainly benthic or demersal animals, had mean catch rates between 1.4 and 2.0 times greater during the day than at night. *Aristaeomorpha foliacea* and *Heterocarpus sibogae*, which ate both midwater and demersal animals, and *Heterocarpus woodmasoni*, which ate mainly midwater animals, had mean catch rates between 2.6 and 10.5 times higher during the day than at night. Decreased catch rates of these species probably reflect nocturnal migration into midwater. Catch rates of *A. foliacea* peaked around mid-day, suggesting that a substantial proportion of the population may still be in midwater during daylight hours. Catch rates of *Heterocarpus sibogae* and *H. woodmasoni* varied little during daylight hours but changed rapidly around dawn and dusk, suggesting that their diurnal behaviour is strongly dependent on ambient light levels. Studies on midwater populations are proposed to determine the importance of midwater feeding in the diurnally migratory prawn species.

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MICROPROCESSORS AND FIELD INSTRUMENTATION FOR CRUSTACEAN BIOLOGY

Micropower microprocessors are making possible the gathering of data, and its transmission, from situations where direct observation is either impossible or would influence the phenomena under study. This paper proposes two examples of field instrumentation, designed around microprocessors, which will address otherwise refractory questions in two areas of crustacean biology: larval transport/recruitment, and behavioural-physiological ecology.

The highest mortality in life cycles of marine Crustacea occurs during planktonic larval stage, yet little is understood about the phenomena that control mortality, transport, dispersion, and especially eventual recruitment. Experimental testing of hypotheses is made difficult by the minute size of the dispersing larval stages. Sampling of either the larvae themselves, or of the current regimes they would encounter as they migrate vertically, at the relevant spatial scale, is prohibitive. The Lagrangian approach requires intensive sampling from many vessels, with subsequent sorting of high numbers of plankton samples, the Eulerian approach demands unreasonable numbers of current meters.

To experimentally test theories of larval transport and recruitment, we are developing a microprocessor-controlled Lagrangian drifter that behaves like a larva but can be tracked remotely. A buoyancy adjustor under microprocessor control will allow the device to mimic larval behaviour, relevant to the species under study, in response to time, depth and other environmental cues, e.g. temperature, light, salinity. Initially these buoys will be programmed to mimic larvae of *Rhithropanopeus harrisii* and *Callinectes sapidus*, based on behaviours observed in laboratory and field, and used to examine how those behaviours contribute to retention in estuaries (*R. harrisii*) or export to continental shelf waters with subsequent re-invasion of estuaries (*C. sapidus*). A similar approach is applicable to replenishment of benthic faunas on isolated islands. The devices could also be programmed with hypothetical behaviours to examine the consequences of such behaviours for transport in various natural hydrographic regimes.

Another difficult area for study is the physiological and behavioural ecology of species inhabiting estuaries. Direct observation by divers is difficult and often impossible because the subjects are highly mobile, and live under very turbid conditions. Laboratory observations cannot be relied upon to provide relevant behavioral data, particularly for species that range over spatial scales orders of magnitude larger than the laboratory can accommodate.

To relay complex behavioural data from unrestrained animals in natural environments, we have designed microprocessor-based multichannel ultrasonic biotelemetry transmitters. The devices monitor up to eight different phenomena (e.g., muscle potentials, limb positions). At any change of input state, the microprocessor awakens and transmits the current state of its inputs, thus marking the beginning and end of an event at any input. The information is encoded either as pulse width, or as a frequency-shift-keyed (FSK) serial data word. All ultrasonic frequencies are synthesised by the microprocessor, which also drives the piezoelectric transducer directly. Power consumption is held to levels supportable with small batteries by operating the microprocessor with low duty cycles, putting it into 'sleep' (power down) mode when idle. The initial application of these transmitters will be to explore predator-prey and predator-predator interactions among *C. sapidus* and prey patches of small clams in Chesapeake Bay.

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SIZE AND ASSORTATIVE MATING IN THE SHORE CRAB, *CARCINUS MAENAS*

Mating in the common shore crab, *Carcinus maenas*, can only occur when the female has recently moulted. Males find females about to moult by free search, and guard them until they moult. When mating occurs, they will subsequently guard the female until her new carapace hardens. Males will compete aggressively over receptive females, and it is generally assumed that the larger, stronger males will be able to mate with the largest, and presumably, most fecund females. This would be expected to result in a homogamous mating pattern, which we, and others have observed in this species. This type of mating pattern is also seen in other brachyuran species.

The behavioural hypothesis for homogamy rests on a number of assumptions: that a large male will win a fight against a smaller male; that the males are capable of recognizing the relative size of a female, and that there are no other factors affecting a females desirability, e.g imminence of moult, and hence reduced guarding time.

We tested each of these assumptions in the laboratory using artificial conflicts between chosen individuals, taken from mating pairs on the shore.

Firstly, the largest male does not always win in a two male conflict. Out of 85 conflicts between two males over a single female, the smaller male won 36% of the time. Successful smaller males ranged from 2mm to 12mm smaller than their opponent. Similar results were found for groups of males with a restricted number of females (smaller crabs were successful 38% of the time).

In a second set of experiments, one male crab was offered a choice of two females, one large (50–58mm carapace width), the other small (38–43mm). In 57 trials the male chose the smaller female 49% of the time. Similar results were found for groups of males offered an excess of large and small females with 48% of the males mating with the smaller females.

We found that the males did not appear to choose a female according to the imminence of her moult. Field collections showed that there was a slight tendency for large males to be found paired with females further from their moult than small males. In the laboratory single males offered a choice between two females chose the female furthest from her moult approximately 50% of the time.

It would appear that large male *Carcinus* are incapable of discerning a relatively large female or one closer to her moult, and may not win a fight to mate with her even if he did.

A second possible explanation for the observed homogamy in the field is mechanical constraints. We collected over 500 mating pairs of crabs and in no case was the female larger than the male, and usually at least 6mm smaller. During pre-copulatory guarding, the male carries the female under him. It may be difficult or impossible for him to move with a female which is larger than himself. After she has moulted and grown this problem will be exacerbated, which may explain why males tend to pair with females at least 6mm smaller. A second possible factor is that very large males (carapace width > 70mm) rarely mate with females more than 35mm smaller than themselves. This may be due to difficulty in either carrying, or in actually copulating.

We have developed a computer model using the population results found on the shore, in which each male is paired at random with any female within the bounds described. No pairing if the female is within 6mm carapace width of the male or if she is more than 35mm smaller than him. The resulting, simulated, population of mating pairs also shows a distinct positive relationship between male and female size, which is very similar to the field population.

It seems likely, therefore, that homogamy, in this species, is a result of mainly mechanical constraints, and not conflict between males over the 'best' females. This interpretion is supported by the field study. Over 50% of the mating females had moulted within two tidal cycles of capture, which may suggest that if the males were capable of exercising choice they would have very little time in which to do so. Furthermore, in this location there are less females than males, and only a fraction of those will be moulting, and hence available to mate, at any one time. Provided that the available females are sufficiently rare, in both time and space, it would seem likely that the best strategy for an individual male, having found or won a receptive female, would be to remain with her and to mate with her. There is clearly a trade-off between the increased reproductive success of mating with an optimally large female and the amount of time spent finding her. It would seem likely that male *Carcinus* would only adopt a strategy of picking and choosing females, if they were sufficiently common to justify this.

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LIFE HISTORY OF THE BEAR PRAWN, *PENAEUS SEMISULCATUS*, IN COASTAL WATERS OF SOUTHWEST TAIWAN

To establish an effective system for prawn stock enhancement in Taiwan, the Tungkang Marine Laboratory selected the coastal waters along southwest Taiwan as an experimental area and conducted a series of ecological studies on commercially important prawns from July 1982 to December 1987. This paper reviews the life history of the bear prawn, *Penaeus. semisulcatus*, in this area. A strategy for stock enhancement for this species is proposed.

Distribution

The prawns occurred mainly from November to March in waters between Fonbitou and Fangliao at depths of 20–40 m, and in July, between the estuary of Linpien River and Fangliao at depths of 20–30 m. Larger prawns in general occurred in deeper offshore waters (Su and Liao, 1984; Su, 1988).

Reproduction

The prawns seem to spawn throughout the year with a peak season from December to March. The main spawning ground lies in waters between Dapong Bay and the mouth of Linpien River at depths of 20–40 m (Su and Liao, 1984; Su, 1988).

Emigration from Nursery Grounds

The prawns emigrated from Dapong Bay to open coastal waters from July to December, mostly during the new moon or full moon phase, 1–2 months after the rainy season. The mean carapace length of emigrating prawns ranged from 20.7–33.6 mm for females, and 20.4–29.6 mm for males. Early emigrants were usually the smaller ones which migrate mainly from June to August (Su and Liao, 1987).

Food and Feeding

Based on frequency of occurrence the food items were, in order of relative importance, crustaceans, molluscs, detritus and sand granules for prawns from Dapong Bay; and detritus, sand granules and crustaceans for prawns from the open coast. Volumetrically, the order was the same as that described above (Su, 1988).

Growth

The growth rate was 3.21 mm in CL and 5.6 g in body weight per month for females, and 1.8 mm in CL and 3.14 g in body weight per month for males.

Life History and Stock Enhancement

By integrating the above information, the life history model of *P. semisulcatus* is summarised as shown in Fig. 1. For stock enhancement, it is recommended that: (1) postlarvae should be released into Dapong Bay from January to March to enhance the recruitment in the nursery life phase; (2) juveniles should be released into coastal waters to supplement the recruitment in the offshore life phase; and (3) juveniles should be released when they are 10–15 mm in CL, optimally during March to May, and ideally in the nearshore waters between Tungkang and Linpin.

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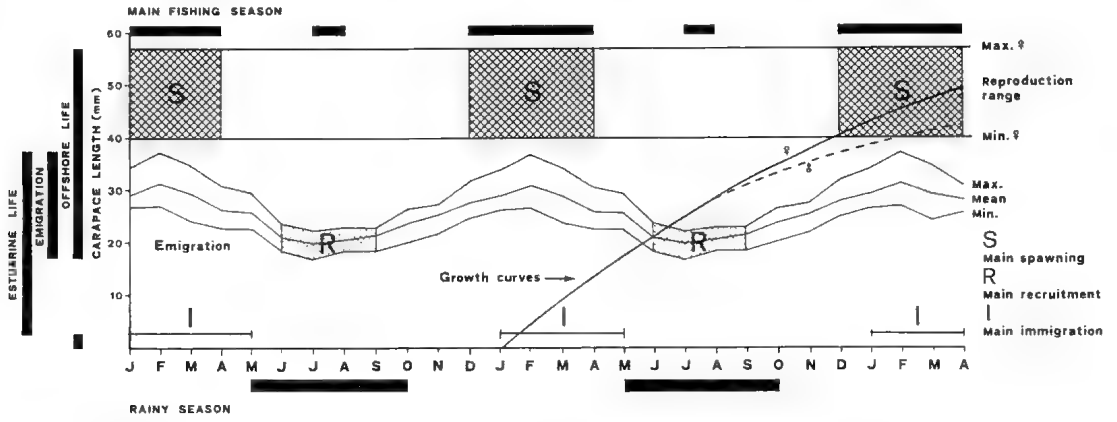

FIG. 1. Model of the life-history of *P. semisulcatus* in the coastal waters of southwest Taiwan.

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PATHOLOGY AND FINE STRUCTURE OF *AMESON* SP., A MICROSPORIDIAN FROM THE BLUE SAND CRAB, *PORTUNUS PELAGICUS*

Microsporidian parasites of crabs were first described by Perez (1904) in the muscle and haemolymph tissues of the common shore crab, *Carcinus maenas* (L.). To date, only 11 microsporidians representing 6 genera have been reported or described from brachyuran crabs. The few reports of microsporidian infections in crabs may be a result of their low prevalence in host populations, the low abundance or crypticism of certain host populations, a lack of expertise in identifying the disease, and/or a lack of proper fixatives in field situations (Shields, pers. obs.). In 1989 the authors found a microsporidian parasite in the musculature of *Portunus pelagicus*. Characteristics of the parasite placed it firmly in the genus *Ameson* (diplokaryotic meront, moniliform sporont, unikaryotic spore, isofilar polar tube, microtubules projecting from the exospore of the sporoblast and spore). *Ameson* sp. from *P. pelagicus* is the twelfth microsporidian reported from a brachyuran host; a full description is in preparation (Shields, unpubl.).

The prevalence of *Ameson* sp. in the observed population of *P. pelagicus* was approximately 3.0% (N ~ 205 crabs). The protozoan caused massive destruction of infected muscle which was flaccid, and had a milky appearance common to this disease. Necrotic muscles contained meronts, sporoblasts, and spores. *Ameson* sp. spores were also found in the blood cells and the ovaries. The parasite was found intracellularly in the sarcoplasm of host muscle cells. Microtubules found on the exospore of sporoblasts and spores were in close proximity to host mitochondria, and may be used to transport nutrients into the cytoplasm of the parasite. Adjacent uninfected muscle was largely unaffected.

Attempts were made to maintain the life cycle of the microsporidian in the laboratory. Infected muscle tissues were macerated and mixed thoroughly in a mixture of one part seawater to two parts freshwater. The supernatant was injected directly into the axilla of the fifth pereiopod of 9 crabs (0.5 mL supernatant/crab). An additional 4 crabs were injected with the seawater-freshwater solution as a control. Infected muscle was also fed to seven crabs that had been without food for 3 weeks.

Crabs injected with spores developed acute disease in approximately 21 days. Spores were detected in injected crabs after 7 days. Crabs that were fed infected tissues did not develop the disease. *Ameson michaelis* from *Callinectes sapidus* is transmitted via cannibalism of infected hosts (Overstreet, 1978). The failure of this route of infection with *Ameson* sp. from *P. pelagicus* may have resulted from the poor quality of meat that was presented to experimental crabs.

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DAILY AND MONTHLY SETTLEMENT PATTERNS OF BRACHYURAN MEGALOPAE ON ARTIFICIAL SUBSTRATES

Postlarval recruitment appears to be a major factor that determines density of adult stocks for several crustacean species. If the population dynamics of marine species are driven by recruitment, then an understanding of recruitment processes and associated spatial and temporal variability is important if accurate predictions of population size are to be achieved. The objectives of the present study were: 1) to compare the temporal patterns of postlarval brachyuran settlement in a South Carolina estuary with settlement patterns in other estuaries that are separated over a broad geographic scale; and 2) to relate settlement peaks to periodic (lunar, tidal, light phase) and chance (wind) events.

Megalopae were collected every 5 days from artificial substrates at a site in Charleston Harbor, South Carolina from July 1987 through October 1988. In 1989, daily samples were taken from July through November at the same site, as well as in the York River and Tangier Island, Virginia (by Robert Orth and Jacques Van Montfrans, Virginia Institute of Marine Science) and in Delaware Bay (Charles Epifanio, University of Delaware) as part of a regional settlement study.

At the South Carolina site, 19 taxa settled on the artificial substrates, with *Callinectes sapidus*, *Uca* spp., and *Panopeus herbstii* numerically dominating collections. Although megalopae were present year-round, except during March, the greatest settlement of blue crab occurred from August through October. Settlement patterns were highly episodic and suggested a pulsed recruitment to the study area. Considerable variability in the magnitude of settlement was observed among years. Temperature and wind direction were the only factors which related to increased number of megalopae. Megalopae were significantly more numerous at night and displayed a semi-lunar pattern of settlement with peak numbers occurring on quarter moons.

When the temporal settlement patterns observed in 1989 were compared among sites, a coherent pattern of settlement on a broad spatial scale emerged, with a major peak in the first week of September. What appears to be more variable and less predictable than the timing of settlement is its magnitude, which differs considerably among years and locations and has implications for variability in fishery stock size among the regions. Data from the regional study suggest that large-scale climatic and hydrographic conditions may be influencing settlement. The spatial and temporal dynamics associated with settlement events can provide insights into factors structuring blue crab populations and may actually indicate limits to year-class strength.

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VARIATION IN THE REPRODUCTIVE STATUS OF SWARMS OF ANTARCTIC KRILL.

The swarming behaviour of Antarctic krill, *Euphausia superba*, is central to its biology. The biological composition of adjacent krill swarms expressed through characteristics such as mean length, sex-ratio and stages in the moult cycle of krill may be very different, e.g. Watkins 1986. In addition the size range of krill in swarms may be restricted in comparison to the local population (Marr, 1962; Hamner, 1984; Watkins, 1986). Such observations have given rise to proposals for sorting mechanisms based on differential swimming or sinking rates (Mauchline, 1980; Kils, 1981). Here we consider the maturity and size composition of animals in 38 swarms to see if a size-related sorting mechanism could account for observed distribution of maturity stages.

Results and Discussion

Swarms were sampled with a large Longhurst Hardy plankton recorder (Bone, 1986) during a 14 day period in February and March 1985 from an area approx 50 km square between Elephant Island and King George Island. The length and sexual maturity stage were measured on up to 100 krill from each swarm (Morris *et al*., 1988).

The sex composition of swarms was highly variable, male and female krill were found in all swarms but the relative proportions in the individual swarms varied greatly (proportion male 19–98%). The swarms were also either virtually all adult or contained a large proportion of subadults. In only 11 swarms was the proportion of adults less than the population average (83%), reaching a minimum of 37% in one swarm. The relative frequency of occurrence of the individual maturity stages within the swarms varied considerably. The two adult male stages were found in all swarms, but no single female maturity stage occurred in every swarm. There was also variation in the number of maturity stages in a swarm: some swarms contained every maturity stage while in others as few as two stages were present. Animals of similar maturity often occurred together as indicated by the significant correlations between all the immature maturity stages and also between the more mature adult stages.

The difference between the length of the largest and smallest krill within each swarm varied greatly (11–30 mm; median 15 mm). The size range in the swarms was significantly more restricted than would be expected if the distribution of size range was random (Kolmogorov-Smirnov test $p<0.001$). Mature krill tend to be larger than immature krill although there is some evidence of size regression after spawning. In addition, the mean size of each particular maturity stage varied between swarms. In some swarms the mean lengths of each maturity stage were longer than average while in others they were shorter than average.

Could these patterns of maturity stage arise as a result of this size-related sorting? Associated maturity stages were not necessarily of a similar size. There was no correlation ($r = 0.175$; $P>0.1$) between the size difference of each maturity stage and the degree of association between maturity stages. Thus, for example, subadult male krill (MS1, MS2 and MS3) were usually found together but the mean sizes of these stages ranged from 42.8–48.4 mm. In contrast, subadult male krill (MS3) and adult male krill (MA2) were negatively associated but the difference between the mean size of these stages was 0.1 mm. It also seems unlikely that differences in sex ratio of the swarms could be explained simply by size differences in the maturity stages because the size differences between the equivalent male and female maturity stages (e.g. MA2 and FA4) were usually small, although sometimes statistically significant.

Passive sorting mechanisms based on size-dependent swimming or sinking speeds and differential growth may explain the inter-swarm differences in krill size, however, they appear to account for little of the inter-swarm variation in sex and maturity stage. The very low numbers of maturing females found without attached spermatophores suggests that mating must occur rapidly after each moult. Because of the very uneven numbers of males and females in many swarms it is likely therefore that active behavioural responses are important in bringing male and female krill together to mate. Thus the swarms containing only mature males may be actively searching for aggregations of mature female krill. However, the actual mechanisms for producing the observed swarm distributions of reproductively active and inactive maturity stages have still to be determined.

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THE RESPONSE OF MYSID SHRIMPS TO PHYTOPLANKTON DISTRIBUTION IN A HIGH ENERGY SURFZONE

Visible accumulations of the diatom, *Anaulus australis*, are characteristic of the surfzone along the Sundays River beach, South Africa. Generally the beach is characterised by active rip systems separated by welded bars. Diatom accumulations are relatively close inshore adjacent to rips and these occur at a frequency of 2 per running kilometre of beach (Talbot and Bate, 1987). At the breakpoint 250–300 m from the swashline, wave height ranges from 1–6 m. Median particle size of beach sand is c. 260 µm. Tides are semi-diurnal, subequal; with a maximum spring tide range of 2.1 m. Water temperatures range from 15–24° C.

Despite this physically harsh environment, two species of mysids are commonly encountered. In the breaker-zone, the bentho-planktonic *Gastrosaccus psammodytes* occurs in numbers of up to 200 m^{-2}. Behind the breakers, the gregarious *Mesopodopsis slabberi* has been recorded in numbers of up to 15,000 m^{-3}.

During the day, *Gastrosaccus psammodytes* is confined to the white-water zone where it exhibits a well defined pattern of intra-specific zonation. Brooding females are significantly more abundant within 10–20 m of the swashline, while males and immatures become progressively more abundant further distant from the beach. Advantages which accrue to brooding females are mostly linked to less frequent disturbance from the substrate as a result of reduced wave turbulence. Inter-alia, physical loss of larvae from the brood pouch is reduced. *Gastrosaccus psammodytes* is a tidal migrant and the pattern of intra-specific zonation is maintained over the tidal cycle.

Close inshore, mysids utilise a rich, but localised phytoplankton food source. Diurnally, alongshore abundance of adult mysids was significantly greater in areas of phytoplankton accumulations (adjacent to rips) on four of five occasions when patches were visible (Chlorophyll-a concentration > 40–100 mg m^{-3} (Campbell, 1988)). On all occasions, adults were dominated by brooding females. Water currents must play a role in dictating mysid distribution, but under relatively calm surf conditions, the distribution of adults is interpreted as a response to the food concentration gradient. This allows maximisation of food intake as mysids (particularly brooding females) undergo forays into the water column. As the energy state of the surfzone increases, water currents feeding into rips must play a progressively more important role in determining mysid distribution. Alongshore distribution of immature mysids is often different to the adult pattern. Since swimming ability of juveniles is weaker compared to adults, threshold water velocities would be less with respect to the influence currents exert on dispersion patterns. Although adults may respond to a food concentration gradient, prevailing current velocities may be sufficient to act as the main forcing function in determining distribution of immature mysids relative to the rips (Wooldridge, 1989).

Although *Anaulus australis* accumulations are generally closely associated with rip currents, cells are continually being added to and eroded from patches as a result of water currents. Cells eroded from patches may be entrained in rips and transported seawards. In the cases of major rip activity, phytoplankton may also be transported behind the breaker line. Here, the lack of air-bubble formation (cell buoyancy is due to attachment to air bubbles) results in the sinking of cells which then accumulate near the bottom of the water column. Re-entry into the breaker zone will occur if wave energy increases, which effectively stirs up the bottom and advects cells shorewards as waves begin to break further offshore (Talbot and Bate, 1988).

Anaulus australis also exhibits a well defined pattern of temporal variability. In the late afternoon, cells become psammophyllic, adhering to sand grains as a result of anatomical changes at the surface of the cell's frustule (Talbot and Bate, 1928). Consequently, *Anaulus* disappears from the water column and is not available to mysids foraging close inshore after dark.

The non-availability at night of phytoplankton in the inner surfzone results in a concomitant change in the feeding behaviour of *Gastrosaccus psammodytes*. The brooding component of the population remains inshore where they become more carnivorous, feeding in the shallows on planktonic and benthic organisms. The more pelagic component of the mysid population migrates offshore where they exploit the accumulated food source behind the breakers. They remain planktonic for the remainder of the night, returning to their inshore habitat at dawn.

A second species of mysid, *Mesopodopsis slabberi* also utilises the accumulated food source behind the breakers at night. Since it is a pelagic species, it seldom ventures into the white-water zone where it would be vulnerable to the more turbulent conditions experienced there. *Anaulus australis* is therefore not available as a food source during the day. Instead, *M. slabberi* remains in deeper water during daylight where it is less visible to predators feeding in the water column. Off Sundays River beach, swarms of this species are encountered at about 15 m depth where they remain in close proximity to reefs. After dark, there is a general migration onshore where they remain until dawn feeding behind the breakers (Webb and Wooldridge, 1990).

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LIFE HISTORY AND BIOLOGY OF *SACCULINA CARCINI* (CIRRIPEDIA: RHIZOCEPHALA) PARASITISING *LIOCARCINUS HOLSATUS* (DECAPODA: BRACHYURA)

Among the six Rhizocephala families, the Sacculinidae comprise the largest number of species. *Sacculina carcini* has been reported to infect species of grapsid, xanthid and portunid crabs, the latter including *Liocarcinus holsatus* (Boschma, 1955). In this study, samples of *Liocarcinus holsatus* were obtained from a beam trawl (2m wide with a 19mm mesh net and a 9.5mm cod-end) at approximately monthly intervals from a depth of 3–20m around the Gower Peninsula, South Wales, U.K. (15°35'N, 04°07'W). Each trawl, at a speed of 3–4 knots, was of 20 to 30 minutes duration. All crabs were examined for infection by *Sacculina carcini* and some of the infected ones (>200) were tagged and maintained in recirculating seawater systems for observations on *Sacculina* growth and reproduction.

Results and Discussion

Of a total of 976 male and 1166 female crabs caught, 35.7% of the males and 38.6% of the females were infected by *Sacculina carcini*. Double and triple externae infections were low (<2%) and occurred mainly in males. The time and magnitude of peak abundance of the different stages of infection differed between years. However, the timing and sequence of the life history events of *Sacculina* was very much related to that of its host (Day, 1935; Heath, 1971; Lützen, 1984).

Externae started growing as early as February or March but the growth of these in the autumn cohort was slow when compared with those which emerged and grew in summer. Externae grew from emergence to 3mm in width in about a week but many did not grow beyond this size unless impregnated by male cyprids, and eventually died leaving a scar. Emergence of externae occurred without the host having to moult. Overall externae growth rate (temperature dependent) was 5.5 ± 2.1 S.E. mm/month in the field and 8.3 ± 1.7 mm/month in the laboratory. Eggs were present in the mantle cavity throughout the year but were most abundant in winter and again in summer. In the field, eggs began hatching in March or early April, reached a peak between June and August and stopped in late October or early November. In the laboratory, two broods of eggs (5–12 x 10^4 each), at an interval of about one month during April–October and four months during December–March, were produced. Both the eggs in the mantle cavity, and the nauplii produced, were of two size classes; the smaller being the females. The length of the internal phase of *Sacculina* infecting *L. holsatus* was estimated to be between 5 and 12 months (x = 8.3 months) and the externae were estimated to live between 6 and 13 months (x = 8.0 months).

Only adult crabs (≥ 20mm CW) could be classified as being highly feminised. These resembled females in their external morphology and behaviour (Choy, 1986). Apart from imposing metabolic stress upon the host, *Sacculina* impairs if not completely stops its growth and reproduction (Lawler and Shepard, 1978; Rubiliani, 1983). Infection by *Sacculina* decreased growth rates by up to 30% in males and 25% in females for each year of infection. During this period, egg production was reduced by up to 62%. For commercially important portunid crabs such as *Necora*, *Ovalipes*, *Portunus*, *Scylla* and *Thalamita*, infection by *Sacculina* can have a disastrous effect on the fishery. Weng (1987) has shown that the normal management practice of protecting smaller crabs can result in higher infection by *Sacculina*. Under these circumstances, management strategies will need to be modified.

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DISTRIBUTIONAL ECOLOGY OF THE VELVET SWIMMING CRAB, *NECORA PUBER* (DECAPODA, BRACHYURA, PORTUNIDAE)

Around the Gower Peninsula (South Wales, UK), *Necora puber* is found mainly on rocky or stony substrata extending from the lower mid-shore down to a depth of about 20 metres below chart datum (Choy, 1988). Routine monthly samples of *N. puber* were taken between October, 1983 and September, 1985 at Langland Bay (51°32'53"N, 4°1'18"W) and between November, 1983 and April 1985 at Worms Head Sound, Rhossili (51°33'42"N, 4°18'16"W), both on the Gower Peninsula. In the intertidal zone, crabs were caught by hand while searching (for 15 minutes at each station of stratified design, and corresponding to different tidal heights) under boulders and rocks during different phases of the tidal and diurnal cycles. Sublittoral samples (to a depth of 20m) were obtained by SCUBA or snorkelling.

Results and Discussion

Catch rate was positively correlated to water temperature ($P<0.05$). The increase in the catch rate of crabs in the intertidal zone between March and November was a result of more newly settled juveniles (<10mm CW) and migrant adults (>40mm CW). Adult crabs did not remain in the littoral zone permanently (Choy, 1988). Crabs migrated onshore either to feed or moult during these warmer months (Crothers, 1968); many adults were in mating pairs. Adult females were ovigerous mainly between January and March, but not between September and November (Choy, 1988).

During winter most of the crabs (especially the adults) were found in the sublittoral zone where the temperature and salinity were more stable. However, complete emigration to the sublittoral zone did not take place as some large crabs were still found on the shore even during the cold months, particularly during low tides which occurred in the mornings. Such a pattern has also been reported for *C. maenas* (Naylor, 1962; Crothers, 1968).

Higher catches were obtained at Rhossili than at Langland Bay ($P<0.01$). There was also a marked difference in the size composition of crabs from the two localities; crabs from Langland Bay being larger ($P<0.01$). At Rhossili, newly settled juveniles appeared in mid-June and continued to do so until the end of July; there were also some in September. During July, August and September, densities of up to 30 juveniles m^{-1} were recorded. There was a progression of the 2.5mm modal width from June until January when the crabs reached about 27mm CW. At Langland Bay, newly settled juveniles (the early crab instars) were never observed although the later instars (7–15mm CW) were. Perhaps larval settlement does not take place here as a result of siltiness, the strength of tidal streams, unsuitable substratum or some other unidentified factor. However, if settlement does occur, it is likely that the numbers are very low and the crabs escape detection or they are immediately predated on.

Boulders at Rhossili were smaller than those at Langland Bay ($P<0.05$) and the size of crabs found under the boulders was correlated to boulder size ($P<0.05$). However, the shape of the boulders was also important: flat boulders sheltered more crabs, especially when these boulders overlaid smaller ones. This partially explains the difference in the size composition of crabs found at Langland and at Rhossili. *N. puber* was never found under otherwise suitable shelters which had decaying organic material or anoxic substrate under them.

During summer, smaller crabs were more abundant in the *Fucus* zone (mid-littoral, LWN–ELWN); the large ones found here were mainly males that were moulting or were about to moult. Very few crabs were found in this zone during winter. Ovigerous females and copulating pairs were found only in the *Laminaria* zone (lower littoral, LWS–ELWS). During winter, the size composition of crabs in the intertidal zone differed depending on the time of day of sampling and the tidal phase. Larger crabs (mainly males) were caught during low tides that occurred during the morning. During the summer large crabs were caught at all low tides irrespective of when these tides occurred.

During the warmer months, increased exploitation of crabs for bait and associated disturbances of the boulders resulted in lower abundance of crabs in the intertidal zone. It was estimated that three to four tidal cycles were required for replenishment of exploited stocks in this zone.

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THE COMMUNITY ECOLOGY OF THE PARASITES AND SYMBIONTS OF *PORTUNUS PELAGICUS*: EVIDENCE FOR POSITIVE AND NEGATIVE INTERACTIONS

Portunus pelagicus possessed a diverse community of parasites and symbionts. In 1989, over 200 crabs were dissected and examined for parasites and symbionts. The common symbiont fauna was comprised of 6 protozoans [*Operculariella* sp., *Lagenophrys* sp., *Acineta* sp. (ciliates), *Thelohania* sp., *Ameson* sp.(microsporidians), *Nematopsis* sp. (gregarine)]; 5 helminths [planocercoid turbellarian, *Levinseniella* sp. (metacercaria), *Polypocephalus moretonensis* (cestode), tetraphyllid cestode, *Carcinonemertes mitsukurii* (nemertean)]; 4 crustaceans [*Choniosphaera indicus* (copepod), *Sacculina granifera*, *Octolasmis cor*, *Chelonibia* sp. (cirripedes)], and 6–7 fouling organisms from other phyla. A few rare parasites were found (*Paranophrys* sp., *Hematodinium* sp.).

The sand crab may possessed an interactive community of parasites and symbionts. There were 11 pairs of interactions/associations between species measured by prevalence (X^2) or by log-intensity (ANOVA on presence/absence, and linear regression). Three pairs of interactions were between protozoa and metazoa. Five pairs in the log-intensity data were reciprocals, i.e. there were significant interactions between both species. There were 3 negative associations (*Carcinonemertes vs Sacculina*, *Polypocephalus* (a lecanicephalid) *vs Levinseniella* (a microphallid), and *Octolasmis cor vs Opercularielle* sp.); the remaining associations were positive. Since association may not be a result of direct species interaction, methods to substantiate the significant associations are being investigated.

The rhizocephalan barnacle, *Sacculina granifera*, had a marked effect on the assemblage of fouling species. Since sacculinised crabs do not moult, there was a notable increase in the diversity of fouling species that live in the branchial chamber and on the external surfaces of the host. The rhizocephalan also had negative effects on other symbionts. The egg predator, *Carcinonemertes mitsukurii* (Nemertea), was commonly found on the gill lamellae of post-ovigerous female crabs (Prevalence ~ 53%). In the sacculinised female host, *C. mitsukurii* was absent. Further, rootlets os *S. granifera* were observed in contact with recently dead *P. moretonensis*, and *Levinseniella* sp. The statistical analyses, however, showed no significant association between the rhizocephalan and these two helminths.

Positive associations were numerous and may have resulted from prey finding abilities (planocercoid turbellarian *vs* branchial and external symbionts), host food preferences (*P. moretonensis vs* tetraphyllid cestode), or association with other host behaviours.

Here, I show that symbionts may interact within and between different microhabitats (guilds?) of the host. The host may mediate the interaction between certain species, especially those that are pathogenic, e.g. *S. granifera vs C. mitsukurii*, because these species do not overlap in their respective host microhabitats but do overlap in their host resource use, e.g. reproductive products. Lastly, the community of parasites and symbionts in *P. pelagicus* did not fit the current definitions and models of communities and community interactions that predict few interactions between species in between guilds in 'isolationist' communities (Holmes and Price, 1986)

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THE JAPANESE MARKET FOR CRUSTACEANS

PERRY SMITH, ANTHONY KINGSTON AND TONY BATTAGLENE

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The Japanese food market is undergoing major changes. Some of the factors influencing these changes on the Japanese seafood market are examined. These include supply-side developments, such as the impact of the rapid development of aqua-culture-sourced products and the changing availability of seafood from capture fisheries. On the demand side, they include the increased 'westernisation' of Japanese culture, changes in the demographic characteristics of the population, increasing incomes and wealth and improvements in the availability of alternative products. Results of recent ABARE studies of Japanese seafood demand are drawn upon, with an emphasis on those results relevant to crustaceans. Price relationships between seafoods, and between seafoods and meats are discussed, as is the growth in consumption in different market segments. ☐ *Japanese market, demand trends, prawn market.*

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Japan's limited agricultural base and its proximity to highly productive seas has resulted in its long recognised dependence on fisheries products as a source of protein. The importance of fisheries products in the Japanese diet increased significantly in the 1950s and 1960s. In 1960 fisheries products supplied almost three-quarters of the total intake of animal protein in Japan (ABARE, 1988: 277).

While consumption of all fisheries products has continued to increase, there have been major changes in the types of seafood consumed and in the factors influencing their consumption. The most apparent of these changes has been in crustacean consumption, which has increased from largely ceremonial and festivity use to more widespread general consumption.

To examine these changes in the Japanese market for crustaceans and the factors behind them, it is useful to first examine the changing demand and supply relationships between fisheries products and other foods before examining those factors specific to crustacean markets.

SUPPLY DEVELOPMENTS

Domestic Production

Although fisheries products were an obvious source of protein for the Japanese people, it is only since the Second World War that fisheries products have been consumed in very large quantities. Fisheries products were the main source of animal protein until the 1960s, as their domestic production could be expanded to meet nutritional needs without the country having to use scarce foreign currency reserves to purchase imports of other foods.

As part of government efforts to improve dietary standards, the fishing industry was encouraged to expand into offshore and distant water operations. It did so successfully, and these fisheries provided Japan with the majority of its fisheries products and were the main source of growth in landings during the 1960s. However, in the 1970s two oil price shocks forced a rationalisation of distant water fishing (ABARE, 1988: 273). Reduced access to foreign waters resulting from the introduction of the exclusive economic zone regime over the period 1977–1980 reinforced this trend.

Despite an increase in production levels between 1970 and 1984 (Fig. 1), Japanese supplies of domestically landed fisheries products used directly for human consumption have remained relatively static. There have been significant changes in the catch composition, with an increase in the importance of lower valued pelagic species landed from offshore fisheries (10–200 nautical miles from shore). Sardine catches were negligible in 1970 but represented 42% of total catches in 1986. These species have not generally been used to meet consumer demand for fish, rather they have been used for processing — sardines into fishmeal, and others into fish-based consumer products such as surimi. Because of the increasing importance of these

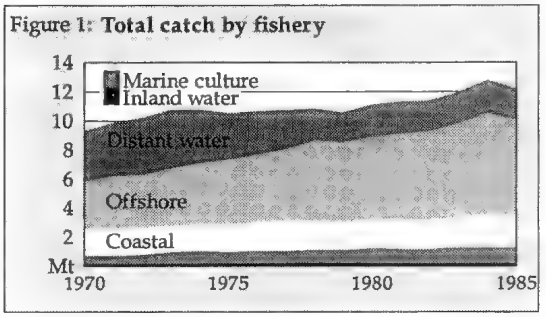


FIG. 1. Total catch by fishery.

species, the amount of domestically caught fish used directly for food has remained static since 1975 (ABARE, 1988: 268).

While representing only a very small component of total Japanese landings, production of crustaceans has shown a similar growth pattern, with output increasing during the late 1950s and the 1960s (Table 1) before stabilising at around 150 kt. Crab has been the main crustacean produced by Japan. Since 1970, crab landings have varied around 90 kt, with gazami (blue crab) and king crab the most valuable species per unit weight. Japanese spiny lobster production has been stable at around 1.1 kt. Prawn catches have varied around 60 kt. The most valuable species of prawns caught in Japanese waters are the white prawn taisho ebi (*Penaeus orientalis*) and a black striped prawn, kuruma ebi (*P. japonicus*), the latter because of its ceremonial importance. The other main crustaceans which are highly valued for traditional use are gazami, snow crabs and Japanese spiny lobster.

There are limited prospects for increased domestic landings of crustaceans from capture fisheries. There has been considerable effort to increase domestic production through culturing of a number of crustacean species in Japan during the 1980s, and a culture industry has been established focussing on the market for live kuruma prawns (Fishery Journal, 1989). However, while much of the culture technology adopted worldwide was developed in Japan, the results of crustacean culture in Japan have been less successful than elsewhere, while in contrast the Japanese aquaculture industry based on fish and mollusc species has prospered.

Fisheries Trade

With the rapid expansion in fishing operations, Japan was a net exporter of fisheries products until the mid-1970s. However, during the 1970s imports of fisheries products increased rapidly, their value increasing threefold between 1975 and 1979 to over US$4077m, while exports increased more slowly to around US$700m. Since 1977, Japan has been the largest single importer of fisheries products, accounting for over 25% of the total value of world imports.

There was a number of demand and supply factors behind these changes. These included strong growth in demand for some high value products, due in part to increasing incomes and

TABLE 1. Japanese landings of crustaceans (liveweight).

	1960 t	1965 t	1970 t	1975 t	1980 t	1985 t
Prawns						
– Freshwater	3 200	2 500	3 300	6 840	5 846	4 816
– Kuruma	3 100	3 100	nas	3 831	3 853	6 020
– Northern	–	–	–	1 996	1 609	–
– Other	57 300	63 400	66 300	63 340	45 524	48 971
Crab						
– Gazami	4 100	1 300	nas	4 229	2 807	5 227
– King	–	25 900	17 600	1 823	56	351
– Snow	9 400	16 400	19 100	24 187	21 314	10 322
– Other	33 900	20 000	53 300	46 030	53 382	83 737
Lobster						
– Japanese spiny	1 300	1 600	1 500	1 086	1 065	1 118

nas = Not available separately.
Source: FAO (1989).

TABLE 2. Japanese imports of edible fisheries products 1970–86: Product weight.

Product	1970 kt	1980 kt	1981 kt	1982 kt	1983 kt	1984 kt	1985 kt	1986 kt
Fresh, chilled or frozen fish								
– Tuna	36.6	108.4	110.2	137.0	149.2	120.3	156.7	157.6
– Other fish	54.6	232.3	346.4	425.8	450.4	530.8	614.4	748.0
Total	91.2	340.7	456.6	562.8	599.6	651.1	771.1	905.6
Fresh, chilled or frozen crustaceans and molluscs								
– Prawns	57.2	144.7	163.4	152.3	149.6	170.0	184.3	215.5
– Squid, cuttlefish, clams, abalone and oysters	57.3	177.4	189.3	103.8	215.3	230.4	232.8	173.1
– Other crustaceans and molluscs	0.9	68.5	71.7	70.3	77.6	97.1	109.2	214.6
Total	115.4	390.6	424.4	326.4	442.5	497.5	526.3	603.2
Processed fish, crustaceans and molluscs (salted, smoked or dried)								
– Fish and roes	9.4	45.0	49.1	53.0	30.8	58.6	56.4	58.3
– Crustaceans and molluscs	12.4	18.8	20.6	20.8	20.9	30.0	36.0	46.6
Total	21.8	63.8	69.7	73.8	51.7	88.6	92.4	104.9
Total imports	229.6 (88)	796.2 (681)	951.6 (808)	963.6 (976)	1 095.2 (944)	1 237.8 (878)	1 390.4 (1 146)	1 614.7 (1 071)

Excludes seaweed, agar-agar, oils and fats, pearl, live fish and shellfish, preparations not in airtight containers, corals, home aquarium fish, fingerlings for culture, caviar, sponges, shells, offal, wax and glue. nas = Not available separately.
Note: Figures in parentheses indicate value in billion yen.
Sources: JETRO (1981); Japan Tariff Association (1986).

in part to their improved availability from overseas sources, and reduced domestic industry competitiveness due to lower resource availability and the appreciation of the yen.

Trade restrictions have also shaped Japanese fisheries trade, in two main ways. Firstly, there have been significant restrictions on imports of potential substitute products, such as beef (ABARE, 1988). Secondly, the types and quantities of fisheries products imported have been strongly influenced by quota and tariff restrictions. Quotas are imposed on four groups of fisheries products (ABARE, 1988: 30) while tariffs apply to most fisheries products. Tariffs applied to crustaceans range from 3% for frozen prawns to 6% for crabs. Higher tariffs are applied to processed products to encourage domestic processing of imported fisheries products.

The rapid growth in imports of fisheries products has had a major impact on Japanese markets over the 1980s. In 1970 imports supplied 5.3% of the 5.6 Mt total of fisheries products used for food. By 1985 this had grown to 22.4% of a total of 8.4 Mt . The main growth in the period 1970 to 1985 was in imports of fresh and frozen fish, which increased eightfold to 770 kt. Crustacean and mollusc imports increased fivefold to 525 kt in the same period. The main single product in this category was prawns, imports of which increased from 57kt in 1970 to 185 kt in 1985 (Table 2).

Imports of fisheries products have continued to rise strongly since 1985. Total imports of fisheries products have increased by 12% a year to 2661 kt in 1988, providing 30% of total seafood consumed in Japan (MAFF, 1990: 38). Prawn imports have increased at an average annual rate of just under 10% a year, reaching 263 kt in 1989. Crab and lobster imports, while much lower, have also recorded strong growth over this time (Table 3). However, the total value of

TABLE 3. Japanese imports of crustaceans.

Type	1985		1986		1987		1988		1989	
	t	¥'000	t	¥'000	t	¥'000	t	¥'000	t	¥'000
Prawns										
— Live	nas	nas	1685	5089	2775	7831	nas	nas	nas	nas
— Frozen	182 912	314 511	212 805	306 722	245 892	334 864	258 232	327 202	263 422	310 657
Crab										
— Fresh	nas	nas	nas	nas	nas	nas	2 192	1324	2 312	1 626
— Frozen	33 887	33 531	44 418	37 736	60 024	53 456	53 786	56 269	54 691	56 802
Rock lobster										
— Frozen	8 707	21 046	9 249	18 513	10 737	20 796	11 991	22 467	12 224	24 726
— Live	nas	nas	nas	nas	nas	nas	1 908	6 095	2 342	7 739
Total	225 506	369 088	268 157	368 060	319 428	416 947	328 109	413 357	334 991	401 550

nas = Not available separately.
Source: National Marine Fisheries Service (1990).

crustacean imports has risen only 2% a year over this period, to ¥400 million in 1989.

Prawn Imports

The rapid growth in supplies of imported prawns has dominated market prospects for crustaceans since 1985 and is likely to continue to do so through the next decade. In 1960, imports of prawns were only 0.6 kt but in only 30 years this has grown to well in excess of 250kt. However, the recent strong growth in imports has been mainly due to significantly lower prices. Since 1985 the unit value of Japanese prawn imports has fallen by an average of 7% a year (Fig. 2).

The growth in Japanese prawn supplies has been due to increased imports from three sources:

- aquaculture production;
- increased commercial fishing for prawns for export in preference to domestic (often subsistence) consumption; and
- increased concentration of the world prawn trade on the Japanese and, to a lesser extent, the US market.

Aquaculture has had a spectacular impact on world prawn supplies. Total cultured prawn production has grown from around 30kt in 1975 (2.3% of world supplies) to about 560kt in 1988 (26% of world supplies), an average annual growth rate of over 25%. Most of this growth in production has occurred in Asia, with large increases initially in Taiwan, China, Indonesia, the Philippines and, more recently, Thailand (Table 4).

Japan has been the most important market for cultured prawns, for a range of reasons. These include the close proximity to the main prawn culture growth areas in Asia, and the Japanese market acceptance of black tiger prawns (the main cultured species) because of its similarity to kuruma and brown tiger prawns. The strength of the yen against other currencies, particularly the US dollar, has also allowed export returns to be maintained at high levels while Japanese wholesale prices have fallen. Without this appreciation of the yen it is unlikely that the Japanese market would have been able to sustain these growth rates.

The rapid growth in cultured prawn imports by Japan has had a number of important effects on the prawn market. These include major changes in the species composition and in the seasonality of supplies, and a major buildup in stock levels.

Changes in Species Composition

It is estimated that in 1989 Japan imported 118 kt of cultured prawns, some 45% of total prawn imports. Black tiger prawns were most important, with 86 kt, sourced mainly from: Indonesia (30.8 kt), Thailand (29.5 kt) and the Philippines

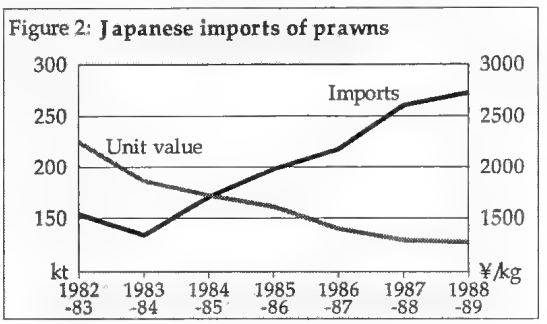


FIG. 2. Japanese imports of prawns.

TABLE 4. Cultured shrimp production in Asia, 1975–1988.

Country	1975 kt	1980 kt	1984 kt	1985 kt	1986 kt	1987 kt	1988 kt
China	0	2.0	22.0	35.0	70.0	153.0	180.0
Taiwan PC	0.3	5.0	17.0	33.3	65.0	75.0	45.0
Indonesia	10.0	28.0	33.0	39.0	48.0	55.0	82.5
Thailand	3.3	10.0	14.5	15.0	16.0	30.0	70.0
Bangladesh	4.0	7.0	11.5	12.5	13.5	14.5	18.0
India	4.0	12.0	14.0	16.7	18.4	22.0	23.5
Philippines	1.0	1.5	26.3	26.5	27.9	35.4	33.6
Vietnam	1.0	4.0	7.0	7.0	7.0	15.0	25.0
Sub-total	23.6	69.5	145.3	185.0	265.8	399.9	477.6
Other regions	16.7	20.5	29.7	25.0	39.2	100.0	82.4
World total	40.3	90.0	175.0	210.0	305.0	500.0	560.0

p = Preliminary. *Source*: Ferdouse (1989).

(16.5 kt), while the remaining 32.2 kt was of white prawns, mainly from China (Ferdouse, 1989).

The development of aquaculture has caused a major change in the species composition of imports. The Japanese market was previously heavily segmented on the basis of particular species and sizes for specific uses. Tiger prawns were largely restricted to use in functions which required a red striped colour for presentation purposes. The increase in supplies has resulted in their more widespread use in a range of other outlets which were previously supplied by other, less favoured, prawn types and sizes which had less demanded characteristics. This has, in turn, placed pressure on suppliers of other prawn types to try to maintain their own market position.

Cultured prawns have also drastically altered the size composition of supplies on the Japanese market. While the large majority of cultured prawns were previously of medium and small counts, technological changes in feeding and breeding technologies used have allowed culture operations to increase the size of prawn produced to take advantage of the higher prices for larger prawns. The consequence of this high grading is that price relativities between species and sizes have altered.

Seasonality of Supplies

The growth of cultured prawn supplies has drastically altered the seasonality of supplies on the Japanese market, particularly as a result of the instability of production of the main prawn exporters over the past four years. Prior to the adoption of aquaculture, Japan had developed a pattern of stock buildup prior to the main periods of consumption (March to May and October to December). Imports and stock levels are now coming to be driven more by production considerations. This appears to be particularly the case with Chinese production and supplies from some other Asian countries where cold storage facilities are not available. Fig. 3A shows the imports of prawns by month for the past two years for the

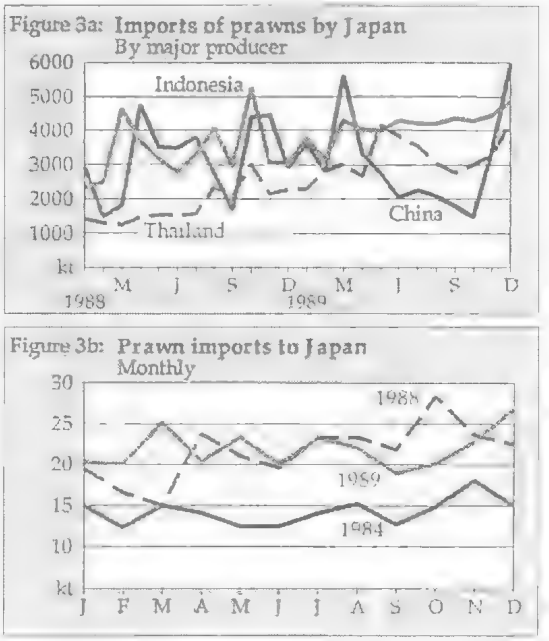


FIG. 3. Imports of prawns to Japan. a, by major producer; b, monthly.

TABLE 5. Consumption of fish and meat per person in Japan.

Year	Fish and shellfish	Meat				Total fish and meat
		Pork	Poultry	Beef and veal	Total	
	kg	kg	kg	kg	kg	kg
1960	27.8	1.1	0.8	1.1	3.0	30.8
1965	29.2	2.7	1.9	1.6	6.2	35.4
1970	31.8	4.7	3.7	2.0	10.4	42.2
1975	34.9	7.3	5.3	2.6	15.2	50.1
1980	34.8	9.6	7.7	3.9	21.2	56.0
1981	34.1	9.6	7.9	4.1	21.6	55.7
1982	33.4	9.5	8.3	4.3	22.1	55.3
1983	34.2	9.6	8.6	4.6	22.8	57.0
1984	35.7	9.7	9.0	4.8	23.5	59.2
1985	35.8	10.3	9.2	4.9	24.4	60.2
1986	37.1	10.5	9.8	5.3	25.6	62.7
1987	38.1	11.2	10.3	5.6	27.1	65.2
1988	38.3	11.4	10.6	6.2	28.2	66.5

Source: ABARE (1988); MAFF (1989).

three largest exporters of prawns to Japan. Fig. 3B shows the total prawn imports by month for the past two years compared with 1984 to illustrate the changes which have occurred in import patterns.

Cold storage Holdings

A key feature of the Japanese market since the early 1980s has been the rapid buildup of prawn stocks in cold storage (Fig. 4). While initially stocks were held to match the seasonality of supplies with demand, the excess supplies on the Japanese market have resulted in growth of stocks to a level where they are likely to have a significant impact on prices paid to exporters.

DEMAND FOR FISHERIES PRODUCTS

Aggregate Consumption Patterns

Fundamental changes have taken place in the dietary patterns of the Japanese people. While the amount of food consumed per person has not altered greatly — average calorie intake per person growing only moderately, from 2200 calories per day in 1960 to around 2500 calories per day in 1980 (Kester, 1980) — the composition of their food intake has changed considerably. Meat and seafood consumption has more than doubled since 1960 (Table 5). Consumption of carbohydrates, predominantly rice, has steadily fallen, from 115kg per person in 1960 to 88kg in 1975 and 73kg in 1986 (ABARE, 1988).

While consumption of fisheries products has continued to increase since 1965 it has done so at a slower rate — though from a higher base — than has consumption of meat products, with the result that fisheries' contribution to average daily intake of animal protein has fallen from 74% in 1965 to around 45% in 1988.

There are a large number of factors influencing the demand for a particular food, including its price, prices of substitute products, incomes, taste preferences, demographic factors and traditions. All of these factors have been important ele-

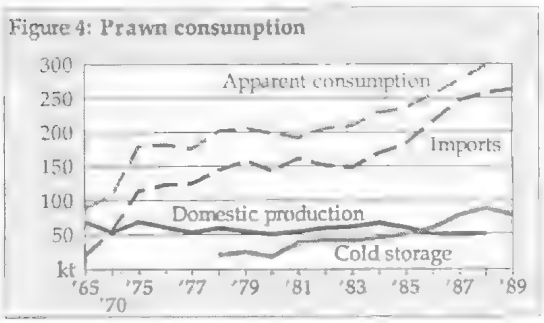


FIG. 4. Prawn consumption.

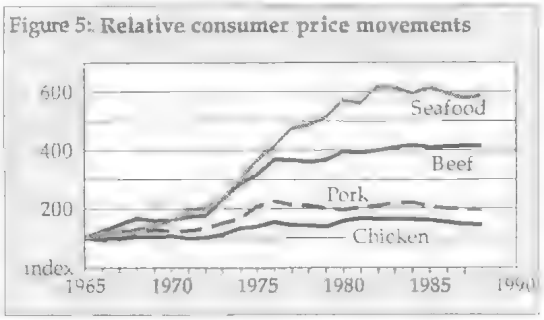


FIG. 5. Relative consumer price movements.

ments behind changes in consumption of fisheries products.

Fisheries products have become more expensive relative to pork and chicken (Fig. 5) and the changes in market shares may reflect consumer reaction to these changes in relative prices. Income levels have risen strongly over the period and changes in consumption may reflect an ability and willingness to purchase more desirable foods. Changes in lifestyle associated with increasing 'westernisation' of Japanese culture will also have influenced food demand.

To better identify the relative importance of the major factors behind changes in consumption of fisheries products, ABARE developed a model to analyse the implications of these changes on the demand for seafood (Kingston, Smith and Beare, 1990). Though a number of models of Japanese meat and seafood demand relationships have been developed in the past, most of these are now likely to be of limited relevance to the current situation in view of the changes which have occurred. (Summaries of the results of a number of these studies are provided in Coyle (1983) and in Dyck (1988).) Another major problem of earlier models is that they aggregate numerous seafood types, inevitably reducing the rigor of the analysis (Kester, 1980). More importantly from the perspective of people interested in a particular group of seafood products such as crustaceans, aggregated models do not provide the level of detail required to address the key issues, such as those associated with rapidly increasing prawn supplies.

The first aspect examined by Kingston *et al.* was the source of growth in consumption. Demand was examined at three levels: aggregate demand, household demand and demand outside the home. An important effect of Japan's increasing prosperity and 'westernisation' is that a high proportion of the increased quantities of meat and seafood eaten have been consumed outside the home. This pattern is consistent for each of the six commodities included in the study: beef, pork, chicken, tuna, other fish, and crustaceans (Fig. 6).

JETRO (1987) attributes this increase in eating-out partly to increased leisure time and increased disposable incomes. Another possible reason for the increased consumption outside the household is the fact that there are more working women in the workforce. Williams (1989) supports this claim, and notes that with the recent trend of working wives re-entering the workforce, most shopping is now done after work and more meals are being consumed at restaurants in shopping centre areas. This trend has also resulted in a greater proportion of seafood being consumed in restaurants.

Estimated Price Relationships

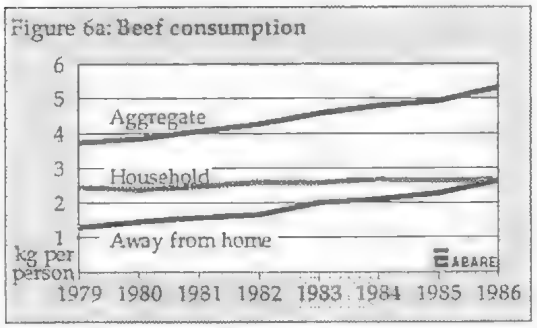
To establish the price relationships between the commodities a two stage demand system approach was used. In the first stage the demand relationships between the three meats and seafood were examined; in the second stage the seafood group was disaggregated into three commodities — crustaceans, tuna and other fish.

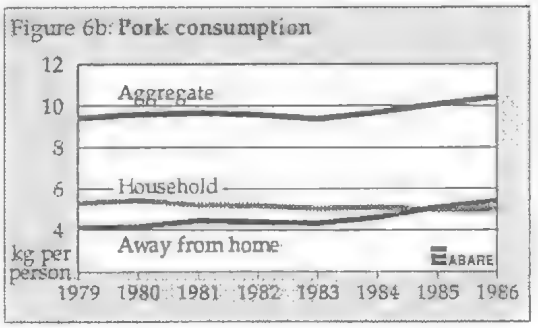
Tables 6 and 7 contain the estimates of the responsiveness of demand to changes in prices of these commodities in the market as a whole and in the household sector of the market. The t-ratios given below the estimates were calculated using Monte Carlo simulations of the parameter estimates using the variance-covariance matrix of the estimates.

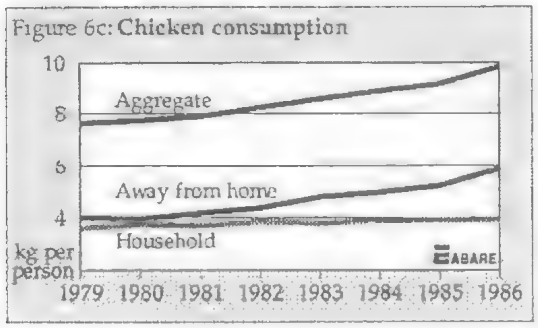
The results obtained from the aggregate model suggest that the demand for seafood in total is relatively unresponsive to changes in its price but nevertheless more price responsive than are the other meats examined. Over the total Japanese market a 10% increase in seafood prices would be expected to result in an 8% reduction in consumption of seafoods and a boost to consumption of alternative meats, mainly chicken (up 6%) and beef (up 4%).

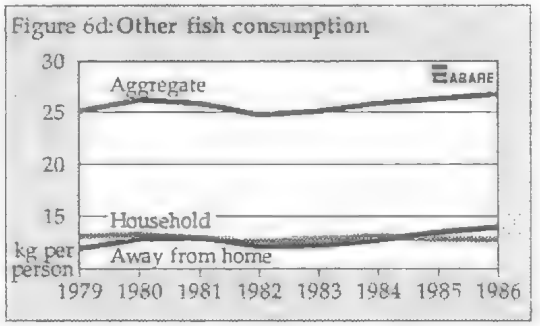
In the aggregate market the demand for individual seafoods (Table 6B) was found to be less responsive to price changes than was the demand for seafood in total (Table 6A), with a 10% increase in the 'own price' expected to result in a 4% fall in consumption of crustaceans, a 4.5% fall in tuna and a 6% fall in fish consumption. A surprising aspect of the results was the indication of a complementary relationship among the seafood commodities. For example, a rise in fish prices appears to have a similar downward effect on demand for crustaceans as on the demand for fish.

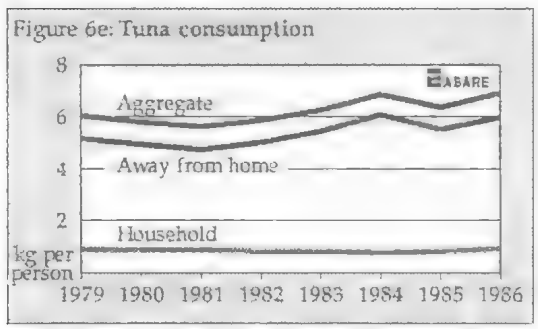
The household sector results (Table 7A) were consistent with expectations. The demand for beef was found to be highly responsive to changes in its price, a result consistent with its luxury status, while pork and seafood were less responsive. There was a strong substitution relationship between beef and seafood (meaning that an increase in the price of one commodity will lead to less consumption of that food and more consumption of the other), with the effect of seafood prices on beef demand much stronger











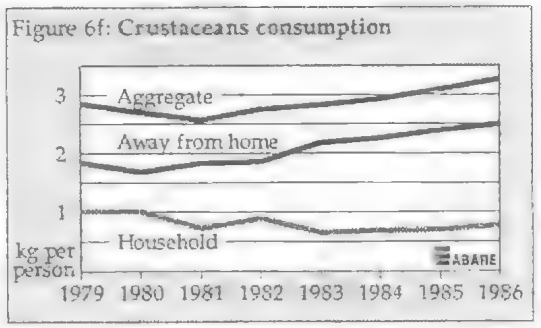


FIG. 6. Consumption of the six major commodity types. a, beef. b, pork. c, chicken. d, other fish. e, tuna. f, crustaceans.

than that of beef prices on seafood. A 10% rise in seafood prices was estimated to result in a 4% increase in beef demand while a similar rise in beef prices would only result in a 2% rise in seafood demand.

In the household sector the demand for crustaceans was found to be very strongly responsive to changes in prices (Table 7B) with a 10% fall in prices leading to a 32% increase in consumption. Tuna demand was also found to be strongly responsive to price changes, while other fish, being more of a staple food, was much less responsive to price changes in the household sector. It is relevant to note that the demand for crustaceans was found to be far more responsive to changes in fish prices than was the demand for fish.

The difference in results between the home and aggregate analysis indicates that consumer behaviour is quite different in the household and away-from-home sectors. In particular, the lower price responsiveness in the aggregate seafood system, and implicitly in the away-from-home sector, suggests that factors other than

TABLE 6A. Aggregate meat and seafood system.

Response of demand for	with respect to change in price of Beef	Pork	Chicken	Seafood
Beef	-0.62	0.24	-0.10	0.36
	(3.6)	(2.0)	(1.0)	(1.9)
Pork	0.18	-0.52	-0.10	0.15
	(1.8)	(4.3)	(1.0)	(1.0)
Chicken	-0.09	0.06	-0.57	0.61
	(1.0)	(0.5)	(3.2)	(2.5)
Seafood	0.12	0.07	0.26	-0.77
	(1.7)	(1.0)	(3.2)	(4.5)

Source: Kingston *et al.* (1990). Figures in parentheses are t-ratios.

TABLE 6B. Aggregate seafood system.

Response of demand for	with respect to change in price of Crustaceans	Tuna	Fish
Crustaceans	-0.39	-0.20	-0.54
	(2.8)	(2.0)	(3.0)
Tuna	0.01	-0.45	0.02
	(0)	(5.6)	(0)
Fish	-0.14	-0.10	-0.58
	(3.5)	(2.5)	(6.4)

TABLE 7A. Household meat and seafood system.

Response of demand for	with respect to change in price of Beef	Pork	Chicken	Seafood
Beef	-1.1	0.14	0.04	0.42
	(7.2)	(1.4)	(0.5)	(2.3)
Pork	0.16	-0.4	-0.01	-0.2
	(1.6)	(2.7)	(0.1)	(1.0)
Chicken	0.11	-0.01	-0.39	-0.13
	(0.5)	(0)	(1.0)	(0.5)
Seafood	0.19	-0.04	-0.01	-0.43
	(3.2)	(0.5)	(0)	(2.4)

Source: Kingston *et al.* (1990).

TABLE 7B. Household seafood system.

Response of demand for	with respect to change in price of Crustaceans	Tuna	Fish
Crustaceans	-3.17	0.62	2.17
	(9.6)	(2.4)	(8.0)
Tuna	0.54	-1.15	0.07
	(2.3)	(3.5)	(0)
Fish	0.24	0.02	-0.68
	(8)	(0)	(14)

price, such as tradition, are important influences on aggregate seafood consumption. At the household level, the demand for individual seafood commodities, particularly crustaceans, shows strong price responsiveness. Significant substitution effects between the three seafoods were also identified.

Any fall in crustacean prices should increase overall crustacean consumption, with the greatest growth occurring in the household sector. Trade information supports this view, for although the household market accounted for only 25% of total crustacean consumption in 1986, around half of the increase in prawn supplies in 1988 was reportedly being sold through supermarkets for household consumption (FAO, 1990). There appears to be considerable potential to increase household crustacean consumption, though the substitution relationships in the household sector suggest that some of this increase will be at the expense of reduced tuna and other fish consumption.

Relationship Between Seafood and Beef

Particularly since the recent decision to liberalise the Japanese beef industry, an understanding of the relationship between the seafood and beef markets is of concern to the aquaculture and prawn fishing industries. Beef supplies are forecast to increase rapidly, and by 1991 consumption is expected to be 15% above current levels.

The results suggest that any fall in beef prices following the increase in supplies will lead to a less than proportional increase in total beef consumption, and that growth will take place in both the household and away from-home-sectors of the market. However, no significant relationship was found between beef prices and seafood consumption at the aggregate level, suggesting that seafood consumption may not fall substantially with increasing beef consumption. There is some substitution between beef and seafood in the household sector, but changes in the price of seafood appear to have a far greater influence on beef demand than *vice versa* (an expected result, in view of their relative importance in consumption).

It should be noted that the consumption relationships were estimated in times of very rigid beef import restrictions. The magnitude of the expected change in beef supplies following trade liberalisation may be sufficient to alter existing consumption behaviour. However, it does seem that any resulting changes in seafood consumption will occur primarily at the household level. Since most crustacean consumption occurs on the away-from-home market, it seems unlikely that the changes taking place in beef trade will have a strong impact on crustacean markets

Income Growth

Growth in income levels has been postulated as one of the main factors behind the changes in Japanese food consumption patterns. Japanese

economic growth remained consistently high in the 1960s and 1970s, with average annual increases in gross domestic product of 7.2% between 1960 and 1983, the highest of any OECD member (the average for all OECD countries was 3.7%). Even though Japan's savings rate is higher than in most other western industrialised countries, growth in private consumption expenditure in Japan was stronger than for other OECD countries with average growth of 5.1% per year over the same period (ABARE, 1988: 20–23).

Previous studies suggest that the influence of increasing incomes on consumption of prawns is likely to be very low. A study of prawn consumption from 1959 to 1981 showed that a 10% increase in per person income resulted in a 0.6% increase in prawn consumption, while the effect of prices was much stronger, with a 10% fall in prices resulting in an 8% rise in consumption (Rackowe *et al.*, 1983). While this study is now dated, the continued high importance of price factors suggest that the influence of consumer income on prawn consumption is still low.

Impact of Aquaculture on Seafood Demand

Prawns are the dominant crustacean output from the aquaculture industry at the moment, but it seems inevitable that techniques will be developed to enable large scale farming of a wide range of fish and shellfish species. The consequences of such developments are likely to be substantial, significantly altering prices for those and substitute products.

As the results outlined indicate that Japanese demand for seafood in general, both in the aggregate market and in the household sector, is responsive to changes in seafood price, it would appear that increased supplies from aquaculture will result in a more than proportional fall in prices in order to stimulate consumption sufficiently to absorb those increases.

For aquaculture species of prawns, however, at current supply levels, import prices will largely be determined by the household market, as this is the marginal market for these prawns in Japan. The household market for crustaceans is extremely price sensitive, and a small fall in prices will lead to a very much larger percentage increase in household consumption. As a result this market may in future act as a buffer to further major falls in price. (Conversely, if there were any significant increase in retail crustacean prices, due to a reduction in imports or a weakening of the yen, the household market is likely to contract sharply to absorb those increases.)

The segmentation of the Japanese market, based on species characteristics, has weakened as a result of the strong growth of cultured supplies of black tiger and taisho prawns. There is now much greater emphasis on relative prices, and considerable substitution between farmed and captured prawns. With the continued strong growth in supplies of cultured prawns and ongoing marketing problems, a key issue for capture fisheries will be to protect their specific market niches. The price differentials between species and counts which existed prior to the expansion of aquaculture have changed considerably with the changes in species composition, and this trend will continue, with pressure to substitute black tiger prawns for more highly valued species with similar characteristics.

FUTURE PROSPECTS

The key influence on prospects for the Japanese prawn market is the likely future growth in supplies. While the large majority of capture fisheries are either at full exploitation levels or overexploited, there remain two potential areas of growth in supplies to the Japanese market — an increase in aquaculture production, and an increase in the proportion of production entering international trade.

Though a slowdown in growth is expected in the 1990s, it is nonetheless anticipated that cultured prawn production will be between 800kt and 1300kt by the mid-1990s. With capture fisheries largely fully exploited, this growth in cultured prawns will result in an increase in world supplies of between 11 and 33% to between 2300kt and 2800kt in the mid 1990s. The differences in these available estimates are crucial in examining the long term prospects for prawns, and point to the need for reliable monitoring of supply developments.

There are several factors which suggest that the recent downturns in prawn prices will result in only a minor slowing in the rate of increase in prawn supplies to Japan. Prawn exports have increasingly been encouraged as a means of raising foreign exchange earnings. This has resulted in a high emphasis on development of aquaculture operations geared to export markets, while in many capture fisheries it has meant a transfer from subsistence fishing to commercial operations, with a consequent increase in fishing effort and catches. It has also resulted in a higher proportion of total catches entering world trade.

As trade relations have improved in Asia,

prawn exports have been seen as one means of financing increased imports of manufactured goods. Both China and Vietnam have entered arrangements with Japan which have involved the transfer of fishing technology and vessels in exchange for prawns.

Much of the aquaculture industry in South-east Asia has also been developed specifically for the export trade. While it is difficult to assess the alternatives available to culture operations, it is likely that a high proportion of prawn culture operations have few alternative uses, particularly in the short and medium terms. The fall in Japanese prices is likely only to slow the rate of investment in new ventures. The lower costs of production in these countries, particularly in extensive and semi-intensive operations, is expected to ensure continued, but lower, profitability in existing prawn culture activities and only a small slowdown in the growth of supplies.

While there is scope for further increases in Japanese consumption of prawns, these increases will largely be as a result of lower prices to consumers. The results of the ABARE study outlined here suggest that to further stimulate Japanese consumption of prawns, some further falls in prices will be necessary, but these may be less severe than those recently experienced. However, a major contraction of supplies would be required before any recovery of prices on the Japanese market could take place.

ACKNOWLEDGEMENT

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LETHAL EFFECTS OF ACIDIFIED SEAWATER ON *PENAEUS MONODON* AND THE INTERACTION OF SALINITY AND PH ON SUB-LETHAL EFFECTS

Acidification commonly occurs in marine aquaculture systems when ponds are built using acid-sulphate soils containing pyrite (Boyd, 1982). Low salinity can accompany low pH in situations where run-off from acid-sulphate sediments in pond dykes enters ponds during heavy rains.

Low pH can predispose prawns to disease and influence the toxicity of other toxins, eg. ammonia and aluminium, and in acid waters crustaceans may experience impaired ionic regulation (Morgan and McMahon, 1982). The aims of this study were to estimate lethal and 'minimum acceptable' levels of low pH for *Penaeus monodon* in acidified water and to investigate the interactive effects of low pH and salinity on prawn weight gain, moulting frequency, dry matter content and haemolymph osmotic pressure.

Static bioassays were conducted in 70 L aquaria with three replicate aquaria, each containing 10 prawns, for all low pH treatments. pH was adjusted using 10 N HCl and all aquaria were lightly aerated (100 mL min^{-1}) to maintain dissolved oxygen levels above 5.0 mg O_2 L^{-1}. The average individual initial prawn weight was between 4 and 6 g for all experiments. To estimate lethal levels a bioassay was run for 96 h with pH levels of 7.8, 7.0, 6.1, 5.1, 4.1, 3.8 and 3.0. Prawns survived well (>90%) at pH levels of 5.1 or above. The 96 h LC_{50} (95% confidence limits) estimated was 3.7 (3.4, 4.1).

To assess sub-lethal effects a longer term (23 d) growth experiment was conducted. Eight treatments were established; six at 30 ppt with average pH values of 7.8, 7.3, 6.7, 6.1, 5.5 and 4.9 and two others at 15 ppt with average pH values of 7.8 and 5.5. The effects of treatment on survival rate were not significant (P>0.05). Other performance data were analysed using single factor ANOVA (including all eight treatments) or using two factor ANOVA (including data from treatments at pH levels 7.8 and 5.5 for both salinities, 15 and 30 ppt. Growth was depressed at pH ≤ 5.5 at 30 ppt (P<0.05) and although salinity did not affect growth (P>0.05) there was a significant pH/salinity interaction (P<0.05). The absence of a significant difference in growth between 15 and 30 ppt was surprising as prawn farmers in Australia and overseas place great emphasis on maintaining low salinity levels in *P. monodon* ponds. This does not appear necessary in terms of the physiological requirements of *P. monodon* although low salinity could influence other biotic components of pond ecosystems.

The 'minimum acceptable' level was defined as that level which reduced growth by 5% (the EC_5) and was estimated, using two-phase linear regression analysis (Sedgwick, 1979), as being 5.9 pH units for *P. monodon* at a salinity of 30 ppt.

Moulting frequency was highest at pH 4.9 (30 ppt) and was inversely related to salinity, while the interaction was not significant (P>0.05). The dry matter content was depressed at pH 4.9 (30 ppt) but unaffected by salinity or the interaction (P>0.05).

Juvenile *Penaeus monodon* are efficient osmoregulators in the range 15 to 30 ppt with an isosmotic point of between 23 and 25 ppt (Cawthorne *et al.*, 1983). However, a reduction in internal osmolarity at reduced pH had been recorded for a number of freshwater crustaceans and fish (Morgan and McMahon, 1982; Hobe *et al.*, 1983). To investigate whether changes in osmotic pressure might explain the pH/salinity interaction prawns were exposed to combinations of two pH (7.8 and 5.6) and salinity (15 and 30 ppt) levels for three days, sufficient time for osmotic and ionic equilibrium to be reached. At the end of the experiment osmotic pressures in the water and prawn haemolymph were measured and the difference between these two values (Dop) calculated as an indication of osmoregulatory ability. At both salinities (15 and 30 ppt) haemolymph osmotic pressure was closer to ambient osmotic pressure at reduced pH (5.6). Both salinity (P<0.001) and pH (P<0.01) significantly reduced Dop, and there was no interaction (P>0.05). Although the results of this experiment showed that reduced pH lowered osmoregulatory ability in *Penaeus monodon*, they did not confirm the hypothesis that differences in osmoregulatory ability were responsible for the interaction between pH and salinity on weight gain. The interactive effects of pH and salinity on ionic regulation may warrant further investigation.

The estimation of lethal and sublethal low pH levels for *P. monodon* (3.8 and 5.9 pH units respectively) should assist prawn farmers with the management of acidic ponds.

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ECONOMICS OF PRAWN FARMING IN AUSTRALIA

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Hardman, J.R.P., Treadwell, R. and Maguire, G. 1991 09 01: Economics of prawn farming in Australia. *Memoirs of the Queensland Museum* 31: 421–434. Brisbane. ISSN 0079-8835.

The current structure of the prawn farming industry in Australia is defined, the costs of production are estimated and the importance of variation in yield, price, and cost of feed is determined. The importance of economies of size is also demonstrated.

A census conducted in November 1989 indicated that, during 1988–89, there were 25 farms using 249 ha of ponds stocked with marine prawns on the east coast of Australia. Almost all farms were established within the past five years. Total production increased rapidly during the 1980s, and in 1988–89, 351t of prawns (mainly *Penaeus monodon*) were produced.

Costs of production for two separate geographical locations were estimated as follows. First, using a combination of the census data and the opinions of informed growers, characteristics of representative farms were specified. Costs were then assigned to these farms based on actual grower experience. The results indicate that relative to current world prices and prospects, Australian costs of production are high. Sensitivity analyses indicate that farm profitability is very sensitive to price, yield and farm size. Though feed is an important component of total costs (12–38%), it requires a very large reduction in feed costs to significantly reduce the cost of production.

The overriding conclusion from the analysis is the high uncertainty of returns to prawn farming in Australia. Significant reductions in costs may be necessary, in view of the prospect of further price falls with the likely continued expansion of prawn aquaculture in South-East Asia. □ *Prawn farming, prawn aquaculture, profitability, costs of production, prawn farm economics.*

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Marine prawn farming industries have expanded dramatically in many tropical countries, so that by 1989 production from farms accounted for an estimated 26% of total prawn production from fisheries and farms (Rosenberry, 1990). Traditionally, prawns have been farmed in Asia at low stocking densities and with minimal management (less than 1 t/ha/y). However, technology has allowed farmers to increase stocking densities and production intensity to 'semi-intensive' (1–10 t/ha/y) and 'intensive' (more than 10 t/ha/y)(Wickins, 1976). Figures for the eight major prawn farming countries indicate that average yields per hectare are in the low to semi-intensive range (Rosenberry, 1990). Many Asian countries have greatly increased production through expansion of total ponded area and intensification of farming methods (Handley and Moore, 1989). In contrast, prawn farming has remained a small industry in Japan, and has grown slowly in other developed countries such as the United States, where farms are located in warm-temperate areas (Lawrence and Huner, 1987).

In Australia a few unsuccessful prawn farms were established before 1980 (Heasman, 1984). Subsequently, several farms were constructed in the warm-temperate area of northeastern New South Wales, stocked initially with school prawns (*Metapenaeus macleayi*) and later with leader prawns (*Penaeus monodon*). The latter is the main species stocked in farms which have been established in tropical and warm-temperate areas on the east coast of Queensland (Maguire and Allan, in press). Production of Australian farmed prawns rose rapidly to 351 t in 1988/89, and expectations of farmers indicate much greater production in 1989/90 (Potter and Jones, 1990). Despite such progress, the major factors affecting the economic viability of the Australian industry have yet to be analysed.

Several economic analyses have indicated that production costs for farmed prawns vary mark-

edly between countries and with intensity of farming (Shang, 1983). Griffin *et al.* (1986) concluded that prawn farming would be more profitable in a tropical country than in a warm-temperate region. Though many economic assessments have been based on results from experimental rather than commercial prawn farming, those variables which are expected to most affect profitability have been identified. These include unpredictable environmental factors (Griffin *et al.*, 1981), stocking strategies, including density (Pardy *et al.*, 1983), species grown and polyculture (Huang *et al.*, 1984), farm and pond size (Hanson *et al.*, 1985), survival rate (Hollin and Griffin, 1986), use of passively heated nurseries (Juan *et al.*, 1988), and prawn sizes at stocking and harvest (McKee *et al.*, 1989). Most analyses have used deterministic models with single estimates for each variable, although stochastic modelling has been employed (Hansen *et al.*, 1985). This technique uses a range of estimates for each variable and provides a probability value for any particular rate of return. The relevance of risk analysis to prawn farming, particularly in relation to increasing intensity of farming and suboptimal seasons, has also been recognised (Hatch *et al.*, 1987). The collapse of the Taiwanese industry emphasises the importance of risk in prawn farming (Kwei, 1989).

The emphasis in Australian prawn farming research has been on developing appropriate technology rather than on economic analyses. Heasman (1984) adapted a US farm model (Parker and Hayenga, 1979) and applied this to a hypothetical *P. monodon* farm in north Queensland. Hardy (1985) predicted good returns for *M. macleayi* farms in northern New South Wales; Maguire and Leedow (1983) optimised stocking density and feed rate for that species using simple cash flow models. Cook and Lightfoot (1987) predicted attractive returns to farming *P. monodon* in north Queensland, based on model farms of 20 and 100 ha with a low stocking density (7 post larvae/m^2). Yang (1987) adapted a Taiwanese model using Australian cost data and demonstrated the importance of stocking density and survival rate to economic returns.

The approach taken in this study is as follows. First, the current and future market situation is reviewed. Next, the current structure of the prawn industry is determined by means of a census of prawn farmers. This in conjunction with input from farmer groups is used as a basis for specifying the prawn farm models. The models are specified to allow comparison between the tropical and warm-temperate farming regions and between intensities of operation. This is followed by the derivation of the costs of production and rates of return to prawn farming in Australia based on the model prawn farms. Sensitivity testing of results and stochastic analysis of returns are included, not only to demonstrate the risky nature of prawn farming at this stage but also to delineate the major variables which affect profit.

MARKET OUTLOOK

To date, most sales of Australian farmed prawns have been on the domestic market. The Australian prawn market closely follows trends in the international market, because over half of Australian production of wild caught prawns is exported (1988–89 exports being 11.5 kt: ABARE, 1989) and a similar volume is imported. Therefore the prices that Australian prawn farmers receive are largely set in the international marketplace. That market is influenced mainly by demand of the major importer, Japan, and the increasing world supply of cultured prawns. However, domestic prices do fluctuate with seasonal variations in supplies of wild caught prawns.

Asian countries provide more than 80% of the world's supply of cultured prawns. Around half of Asian cultured prawn production is *P. monodon*. In 1989 cultured prawn production by Asia reached 500 kt, almost double that of 1987 (Rosenberry, 1990). This increase was largely due to a rise in production of *P. monodon* by Thailand and Indonesia. China remains the largest producer of cultured prawns with 220 kt in 1989, but, after recent large increases, production in China appears to be stabilising in 1990, reportedly due to disease problems (Anon., 1989). However, total Asian production of cultured prawns is expected to continue to expand and has been forecast to reach 800 kt by the year 2000 (Anon., 1988). Such an increase would continue to put downward pressure on prices.

On the demand side, Japan is the major world importer of prawns and absorbs most of Australia's exports of prawns (around 80%). Australia has very limited influence on the Japanese market, accounting for only about 5% by value of Japanese imports (Battaglene and Kingston, 1990). The major suppliers to the Japanese market are the Asian countries. At the same time

as supplies of prawn have increased, the growth in Japanese consumption of seafood has slowed. Although seafood's share of Japanese meat and seafood consumption has fallen from 74% in 1960 to 44% in 1985 (Kingston *et al.*, 1990), prawn consumption did increase between 1984 and 1987 from 2.5 kg to 3 kg per person a year. However, the increased supply of prawns has exceeded the moderate increase in consumption, the result being a 90% increase in cold storage holdings since 1984 and falling prices on the Japanese market. If prices continue to fall the quantity demanded is likely to rise.

In the longer term there appears to be no relief from lower prices on the Japanese market, because aquaculture production is expected to rise in Asia. Currently, Australian cultured prawns are mainly sold in Australia in bulk through wholesalers, and most production is of *P. monodon*. Thus, these sales would be in direct competition with the Asian cultured prawns, whether on the Australian or world markets. There are options which would enable Australian producers to remain in this very competitive market. Prawn farmers may be able to time production to take advantage of seasonal fluctuations, and thus obtain higher prices by supplying the market when alternative supplies are low. Efforts could be directed to supplying a reliable, high quality, well-presented product, but this would raise marketing costs. Alternatively, management could be directed at producing larger prawns which command a premium in the marketplace. Although 25 g prawns are sold in Australia there is a limited export market for this small size. If production continues to expand, farmers may need to assess the option of larger prawns for the export market. Another option is to supply larger, fresh or live prawns to the restaurant trade, which offers a significant premium over the supermarket or commodity market, particularly in Japan. In addition, farmers could switch production from the commonly produced *P. monodon* to the culture of higher-priced species such as *P. japonicus* or *P. esculentus*. Such a switch in production would require development of appropriate farming methods for these species.

STRUCTURE OF THE PRAWN FARMING INDUSTRY IN AUSTRALIA

The industry is small but expanding rapidly (Fig. 1). Gross value of production could reach $12 million in 1989–90 (O'Sullivan, 1990). Queensland has replaced New South Wales as the major producer of farmed prawns, mainly due to the faster growth rates achievable in the higher water temperatures. Production in other states is negligible.

The majority of Australian farms are < 10 ha, with a few large farms responsible for most of the production. The region between Townsville and Cairns contains 55% of Queensland's farms, while Mackay has 22% and Brisbane region 11%. The greatest growth in farm area is occurring in the Townsville-to-Cairns region.

The data in Table 1 indicate a rapid development process in the prawn industry as evidenced by the following changes from 1988–89 to 1989–90:

- a 23% increase in total ponded area (all within Queensland);
- a 60% increase in total stocked area;
- a 28% increase in stocking density.

The wide range between farms for most of the parameters used for measuring productivity (stocking rate, feed conversion ratio and yield) also indicates the developmental stage of the industry. In addition, the average feed conversion ratio of 2.265:1 (feed weight to product weight) is significantly higher than overseas results which suggest that long term averages of 1.8:1 or better can be achieved (Chen *et al.*, 1989).

Due to the current rapid development phase it is difficult to define a model or average prawn farm for analytical purposes. Regression analysis of farm parameters yielded two statistically significant relationships: as farm size increased, so did pond size ($R^2 = 0.58$, $p < 0.001$) and the number of ponds ($R^2 = 0.59$, $p < 0.001$). No other statistically significant relationships were found in regression analyses including farm parameters such as yield, stocking density and feed conversion ratio ($p > 0.05$). That is, the industry has not developed sufficiently for a clear management pattern to emerge.

With the assistance of prawn farmers, the representative model prawn farm was defined to be six 1 ha ponds as a family farm unit (Table 2). Although this is less than the industry average of 15 ha, the majority of farms are < 10 ha with a few very large farms of up to 95 ha. The 6 ha farm was considered to be representative of most farms, particularly in far north Queensland (FNQ). For comparative purposes the growers in the northern New South Wales/southeast Queensland region (NSW/SEQ) accepted the basic 6 x 1 ha prawn model as defined by FNQ growers, although farms tend to be larger in NSW/SEQ. The most obvious difference between the regions is the number of crops per year, the NSW/SEQ region usually hav-

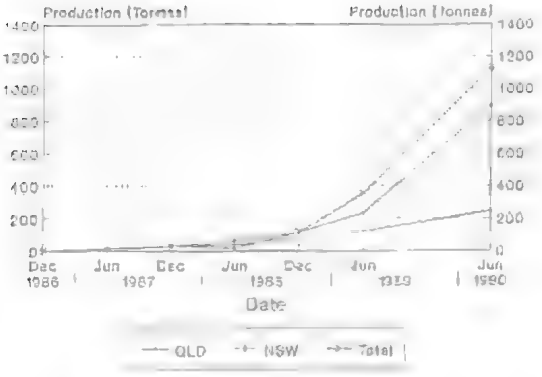

FIG. 1. Production from Australian prawn farms 1986–90. *Source*: Queensland Department of Primary Industries, ABARE and Allan (1989a). *Note*: December 1989 to June 1990 — estimated productions.

ing only one crop a year while two crops a year was considered achievable in FNQ.

Farm operation intensity was defined in terms of stocking density. Two stocking densities, low and high, were accepted as representative. The model low stocking density (8 post larvae (PL)/m^2) falls within the range reported for Australian prawn farms in 1988, of 5–15 PL/m^2 (Robertson, 1988). As is seen from Table 1, stocking density increased again between 1988/89 and 1989/90. The model high stocking density (25 PL/m^2) was chosen to reflect this trend. The low stocking density model was considered by farmers to depict a learning stage rather than a long term farming proposition. For these low densities substantially larger ponds are more appropriate (Scura, 1987)

In the model farms, both survival rates and growth rates declined with increasing stocking density (Table 2). Accordingly, for the lower stocking density the average prawn size at harvest was set higher than for the high stocking density. This relationship between growth and density accords with experimental results reported by Allan and Maguire (1988). However, they concluded that survival rates were not affected by stocking density in their experimental ponds. This indicates that yields may be improved in the future as farmers gain more experience in feeding regimes and pond management.

COSTS OF PRODUCTION

Costs were estimated for the 6 × 1 ha farm model by farmers who attended group assessment meetings held in far north Queensland and northern New South Wales, with additional information from equipment suppliers.

Feed is by far the largest component of annual operating costs, accounting for 57% for the high density model farm in far north Queensland (Table 3). Prawn fry is the other major operating cost, comprising about 20% for the low density farms and 23% for the high density farms.

The major costs of establishment are land and earthworks (Table 4). To achieve six 1 ha ponds a total land area of 12 ha would be required to allow provision of sheds, roadways and channels. The cost of surveying and constructing ponds varies markedly ($12 000–40 000/ha), depending principally on topography, soil type, wall slope and pond configuration. For the model farm of six 1 ha ponds a flat site with a suitable clay base was assumed and a corresponding cost of $20 000/ha used in the analyses. The cost of a pumping system also varies substantially, depending on the level of water exchange required, tidal limitations and the desired speed of filling. It is feasible that farmers could install cheaper pumping systems than those listed in Table 4.

The total establishment cost of around $0.5 million including land purchase (Tables 5 and 6) constitutes a substantial obstacle. However, in the case of sugar cane farmers who enter prawn farming, these capital costs may be considerably reduced through the use of existing surplus land, equipment and possibly underutilised labour. Table 4 outlines costs for a farm of twenty 1 ha ponds. These figures are used below in an investigation of economies of scale.

Total production costs for the low stocking density model are shown in Table 5. In the NSW/SEQ region, the total cost of production, at $15.67/kg, is too high given current market prices and outlook. In far north Queensland, with two crops a year, the production cost is much lower, at $9.38/kg. For the high density farms (Table 6) the difference between regions is much less, with FNQ costs of production $1.54 lower than those in NSW/SEQ. These costs are very close to current market prices. In early 1990 the farm gate price for 25 g prawns varied in the range $8–12/kg, with an average price of $10/kg. Prices increase with the size of prawn, and 30 g prawns fetched about $2/kg more. Therefore, in the analyses prices were varied according to the size of prawn produced (Tables 2, 5 and 6).

Given the possibility of further price falls in the future, it is important to examine the opportunities for reducing costs. The cost of feed may be lowered in two ways: by a drop in the cost of feed per tonne, or by a decrease in the feed

TABLE 1. Prawn Farming Industry: census results.

Variable	Total ponded area	Total number of ponds	Average area of ponds	Stocked area	Stocking density	Feed conversion ratio	Total production	Average yield per unit stocked area(a)
Units	ha	no.	ha	ha	no. PL m^2		t	t/ha.y
1988–89								
Total for all farms	369.9	235		248.55			350.75	
Range for all farms	0.8–95	1–40	0.4–3.5	0.45–50	5–30	1.5–4.6:1	0.4–62	0.07–6.8
Average for all farms	14.8	9.4	1.57	9.94	12.72	2.7:1	14.03	1.41
1989–90								
Total for all farms	455.5	nc		397.1			1130(p)	
Range for all farms	0.8–95	nc	nc	0.8–95	5–35	nc	4–280(p)	1–13.5(p)
Average for all farms	15.16	nc	nc	13.23	16.27	nc	37.67(p)	2.85(p)

Source: Telephone census, November 1989, of all known prawn farmers in Queensland and New South Wales (25 farms). (a) Average yields per stocked area in 1988/89 were mainly based on one crop per year. Only 3 out of 25 farmers double cropped. Average yields per stocked area in 1989/90 are higher than 1988/89 in part because 14 out of 30 farmers indicated their intention to double crop. nc= data not collected. p= projected by Queensland Department of Primary Industries, ABARE and Allan (1989a). PL= post larvae (prawn fry).

TABLE 2. Description of model 6 x 1 ha pond prawn farms.

		Low stocking density		High stocking density	
Item	Units	FNQ	NSW/SEQ	FNQ	NSW/SEQ
Aeration		No	No	Yes	Yes
Number of crops/year	no	2	1	2	1
Average size of prawns	g	27.5	30	25	25
Stocking rate	PL/m^2				
- average		8	8	25	25
- range		6–10	6–10	20–30	20–30
Survival rate	%				
- average		70	50	60	60
- range		80–60	56–50	70–50	60–57
Yield	t/ha/y				
- average		3.08	1.2	7.5	3.75
- range		2.6–3.3	1.0–1.5	7.0–7.5	3.0–4.3
Production	t/6 ha.y	18.48	7.2	45	22.5

Source: Group assessment meetings, South Johnstone, Queensland, and Palmers Island, New South Wales, March 1990. FNQ, Far north Queensland. NSW/SEQ, New South Wales and south-east Queensland.

TABLE 3. Annual operating costs: 6 x 1 ha pond farm model.

Item	Units	Low Stocking Density		High Stocking Density	
		FNQ	NSW/SEQ	FNQ	NSW/SEQ
Number of crops/year	no.	2	1	2	1
Total production	t/y	18.48	7.2	45	22.5
Feed conversion ratio		1.8:1	1.3:1	2.25:1	1.8:1
Feed consumed	t/y	33.26	9.36	101.25	40.5
Total feed cost @ $1500/t	$	49 896	14 040	151 875	60 750
Cost of prawn fry @ 2c	$	19 200	9 600	60 000	30 000
Casual labour	$	8 000	8 000	13 000	10 000
Electricity	$	10 000	3 000	22 000	12 000
Fertiliser	$	3 000	1 500	5 000	1 500
Repairs & maintenance	$	8 000	8 000	10 000	8 000
Miscellaneous	$	3 000	3 000	4 000	4 000

Source: Group assessment meetings: for FNQ, South Johnstone Research Station, Queensland, and for NSW/SEQ, Palmers Island, New South Wales.

conversion ratio. It is evident from the sensitivity tests that it would require a very large saving in feed costs to effect a significant reduction in production costs (Table 7). For example, to effect a saving of about 50c/kg in the total cost of production requires a decrease in feed cost of between 15% (for the FNQ high intensity farm) and 25% (for the low intensity farm in the NSW/SEQ region). Such large cost savings may be difficult to achieve. However, reductions in feed conversion ratios can be effected through more appropriate feed rates (Allan, 1989b).

Yields per hectare may be raised by either increasing the stocking density and/or improving the survival and/or growth rates. The sensitivity tests reported here were based on increasing the stocking density, with feed conversion ratios held constant and no change in survival or growth rates. (The savings in costs would be larger if the same yield increase were achieved at least partly by improved survival and/or growth rates). To achieve a saving of around $1/kg in the total cost of production would require an increase in yield of between 8% (for the low density NSW/SEQ farm) and about 30% (for the high density FNQ farm) (Table 8). This latter increase would imply a yield from two crops totalling 9.8 t/ha/y. Such an increase may be achievable in the future if improved pond management allows higher stocking densities as well as better survival and growth rates.

Economies of size may offer a further option for reducing the unit cost of production. A larger farm of twenty 1 ha ponds with high stocking density was analysed (Table 9). The unit costs of production for the larger farm model are almost 20% lower than for the 6 x 1 ha farm model. This result is not surprising, given that overhead costs comprise 33–46% of total costs for the high density 6 x 1 ha farms (Table 6). Similar size economies are likely for low density farms, for which overhead costs account for an even greater share of total costs.

RATES OF RETURN TO PRAWN FARMING

The previous sections have shown that costs and yields in prawn farming in Australia vary with region and stocking density. Account must also be taken of the high degree of uncertainty surrounding prices, costs and yields for similar farms within the same region. A rate of return based only on the most likely estimates does not fully reflect the nature of returns to prawn farming.

Sensitivity testing over the range of possible values for the uncertain parameters would become unwieldy and difficult to interpret. The alternative approach used in this paper is stochastic investment analysis. This approach is based on the stochastic analysis of returns to new horticultural crops by Treadwell and Woffenden (1984).

The analysis uses the estimated range for each uncertain parameter — that is, for costs, market prices and the parameters set out in Table 2. For each simulation, a value (or a fluctuating time series) was randomly generated for each parame-

TABLE 4. Capital costs for model prawn farms with 1 ha ponds, for both regions.

Item	Total value			Scrap value (c)	Years when purchased (y)
	6 ha farm		20 ha farm		
	Low density ($)	High density ($)	High density ($)		
Earthworks (ponds & channels)	120 000(a)	120 000(a)	300 000(b)	–	0
Pump(s)	15 000	30 000	40 668	10	0,5,10,15
Motor(s)	4 000	8 000	40 667	10	0,5,10,15
Belts, pulleys, pump base, etc.	2 500	5 000	6 665	–	0,3,6,9,12,15,18
Pump shed, valves, filters	10 360	10 360	15 200	–	0
Pipes, gates, screens, boards	24 000	24 000	80 000	–	0
Electric power supply	40 000	80 000	200 000	–	0
Generator (standby)	5 000	10 000	20 000	10	0,10
Rotary hoe	–	3 000	5 000	10	0,10
Spike tooth harrows	1 000	1 000	2 000	10	0,10
Slasher	1 500	1 500	2 000	10	0,10
Bucket	–	1 000	5 000	10	0,10
Blade	1 000	1 000	1 500	10	0,10
Fertiliser spreader	2 500	2 500	2 500	10	0,10
Farm truck (2nd hand)	20 000	20 000	20 000	10	0,10
Tractor (2nd hand)	10 000	10 000	15 000	10	0,10
Motorbike	–	2 000	2 000	10	0,5,10,15
Blower pipe (feed)	1 000	1 000	1 000	–	0,3,6,9,12,15,18
Aeration units	–	33 000	135 000	10	0,5,10,15
Refrig. plant, esky, bins, etc	8 000	14 000	22 000	10	1,11
Ice machine (1 t/day)	13 000	13 000	13 000	10	1,11
Prawn weighing scales	500	1 000	2 500	–	1,4,7,10,13,16,19
Harvest equip (nets/cages)	1 500	2 500	4 000	–	1,4,7,10,13,16,19
Prawn handling area & equip. (washes, trays, loader)	8 000	10 000	10 000		1,11
Farm shed	10 000	15 000	25 000	–	0
Tools	2 000	5 000	10 000	–	0,5,10,15
Test kits	2 000	4 500	4 500	–	0,3,6,9,12,15,18
Boat (2nd hand)	1 500	1 500	2 500	10	0,10
Office equipment	3 000	3 000	3 000	–	0,5,10,15
Miscellaneous	2 000	3 000	5 000	–	0,5,10,15

(a) Plus purchase of 12 ha of land, at $6000/ha in FNQ region and $4000/ha in NSW/SEQ.
(b) Plus purchase of 35 ha of land at same prices as in (a).

ter from its observed distribution. Each such set of parameter values was used to calculate a specific stream of costs and returns, from which the internal rate of return was derived. This procedure was repeated a large number of times (700), to generate a set of internal rates of return (IRR). These were then ranked and their cumulative probability function was calculated. This function gives the probability of the internal rate of return being less than any particular level.

The advantage of this stochastic approach is that it not only produces the expected or mean internal rate or return but also indicates the effect of uncertainty by providing the range of internal rates of return with their corresponding probabilities of occurrence. This procedure avoids the need for sensitivity analysis on individual parameters, as the overall uncertainty is reflected in the probability distribution of internal rates of return. However, individual sensitivity tests can still be undertaken to show the specific effect of variation in a particular parameter.

The stochastic investment analysis was conducted for the four prawn farm models using the

TABLE 5. Cost of production: low stocking density system.

Item	FNQ		NSW SEQ	
PHYSICAL DESCRIPTION				
Number of ponds	6		6	
Area/pond (ha)	1		1	
Total farm area (ha)	12		12	
Production/crop (t/ha)	1.54		1.2	
Number of crops/year (no.)	2		1	
Total production of prawns (t/y)	18.48		7.2	
Feed conversion ratio	1.8:1		1.3:1	
Feed consumed (t/y)	33.26		9.36	
Capital costs of establishment(a)($)	380 360		356 360	
FINANCIAL DESCRIPTION	$ y	$ kg	$ y	$ kg
Gross income	203 280	11.00	86 400	12.00
Operating costs				
— Feed	49 896	2.70	14 040	1.95
— Casual labour	8 000	0.43	8 000	1.11
— Electricity	10 000	0.54	3 000	0.42
— Prawn fry	19 200	1.04	9 600	1.33
— Fertiliser	3 000	0.16	1 500	0.21
— Repairs & maintenance	8 000	0.43	8 000	1.11
— Miscellaneous	3 000	0.16	3 000	0.42
Total operating costs	101 096	5.47	47 140	6.55
Overhead costs				
— Depreciation & interest(b)	40 214	2.18	38 774	5.39
— Allow. for farmer's labour	26 090	1.41	20 872	2.90
— Permanent hired labour	0	0	0	0
— Administrative costs	6 000	0.32	6 000	0.83
Total overhead costs	72 304	3.91	65 646	9.12
Total costs	173 400	9.38	112 786	15.67
Ratio of overhead to total costs (%)		42		58
Return to management	29 880	1.62	-26 386	-3.67

(a) Derived from Table 4 plus land purchase. (b) Assuming real rate of interest 6%.

estimated range in parameter values as set out in previous sections. The analysis was on a pre-tax basis, using private costs and benefits, and was conducted over 20 years, the estimated life of ponds. The analysis was based on the following assumptions.

- Costs do not change relative to prices during the period of analysis — that is, constant (1989–90) values are used.
- The interest rate on money borrowed equals the internal rate of return.
- During the period of analysis, no technical changes occur which result in major increases in yields or substantial changes in the relationship between yields and costs.
- There is no correlation between prices, yields and costs (as Australian prawn farms supply only a minor segment of the market).
- Full production is possible from the first year of operation.
- The farm is well managed and located on a suitable site with ready access to water. There are no disasters such as would cause total loss of crop.

The effects of the last two assumptions, in particular, is that the average internal rates of return generated will be higher than the industry average. The results will reflect more closely the results of more experienced farmers with suitable sites, rather than the average of a new and expanding industry.

The cumulative probability distributions for the four prawn model farms are summarised in Table

TABLE 6. Costs of production: high stocking density system.

Item	FNQ		NSW/SEQ	
PHYSICAL DESCRIPTION				
Number of ponds	6		6	
Area/pond (ha)	1		1	
Total farm area (ha)	12		12	
Production/crop (t/ha)	3.75		3.75	
Number of crops/year (no.)	2		1	
Total production of prawns (t/y)	45		22.5	
Feed conversion ratio	2.25:1		1.8:1	
Feed consumed (t/y)	101.25		40.5	
Capital costs of establishment(a)($)	507 860		483 860	
FINANCIAL DESCRIPTION	($/y)	($/kg)	($/y)	($/kg)
Gross income	450 000	10.00	225 000	10.00
Operating costs				
— Feed	151 875	3.38	60 750	2.70
— Casual labour	13 000	0.29	10 000	0.44
— Electricity	22 000	0.49	12 000	0.53
— Prawn fry	60 000	1.33	30 000	1.33
— Fertiliser	5 000	0.11	1 500	0.07
— Repairs & maintenance	10 000	0.22	8 000	0.36
— Miscellaneous	4 000	0.09	4 000	0.18
Total operating costs	265 875	5.91	126 250	5.61
Overhead costs				
— Depreciation & interest(b)	61 663	1.37	60 223	2.68
— Allow. for farmer's labour	26 090	0.58	20 872	0.93
— Permanent hired labour	37 500(c)	0.83	20 000(d)	0.89
— Administration costs	6 000	0.13	6 000	0.27
Total overhead costs	131 253	2.92	107 095	4.76
Total cost	397 128	8.83	233 345	10.37
Ratio of overhead to total costs (%)		33		46
Return to management	52 872	1.18	-8 345	-0.37

(a) and (b) as for Table 5. (c) Equivalent of 1.5 full-time people. (d) Equivalent of 0.8 full-time person.

10. The highest average internal rate of return is that for the high density farm in north Queensland, followed closely by the low density farm in north Queensland. The uncertainty of the returns is similar for these two types of operation, as is shown by their respective cumulative probability functions (Fig. 2). As noted above, the low stocking density model was considered to be a developmental stage and not a long term proposition. This is certainly true for the NSW/SEQ region, where the low density model did not generate positive returns.

The difference in returns between the two regions is notable, with the internal rates of return for NSW/SEQ falling well below those for FNQ. The higher profitability of the tropical region

FIG. 2. Cumulative probability of IRR: 6 ha prawn farm models.

TABLE 7. Estimated costs of production resulting from decreases in feed cost.

Reduction in feed cost	Low density system		High density system	
	FNQ	NSW SEQ	FNQ	NSW/SEQ
%	$/kg	$/kg	$/kg	$/kg
0	9.38	15.67	8.83	10.37
10	9.11	15.47	8.49	10.10
15	8.98	15.37	8.32	9.96
20	8.84	15.28	8.15	9.83
25	8.71	15.18	7.98	9.69
30	8.57	15.08	7.82	9.56

corresponds with worldwide experience (Griffin *et al.*, 1986). The sensitivity of returns to the number of crops indicates a need to research the necessary requirements (in addition to climate) which facilitate two crops a year. Few farmers produced two crops in 1988/89. Options worthy of consideration include three crops in two years in the FNQ region — with perhaps a larger sized prawn being harvested than is obtainable at two crops a year — or, in the NSW/SEQ region, the production of one prawn crop per year while using the same ponds for other aquacultural products such as oysters in the cooler months (Maguire *et al.*, 1981).

A significant difference between the regions in practice is that prawn farms in NSW/SEQ tend to be larger than those in FNQ, and larger than the 6 x 1 ha pond operation used in this analysis. Therefore, a larger farm of twenty 1 ha ponds was simulated. The expected internal rate of return for the larger farm is more than double that for the small farm. This indicates the existence of significant economies of size in prawn farming. (There may be similar economies in relation to pond size, but that question would require further research which was not possible in this study.)

As in the previous section on costs, the sensitivities of rates of return to a 10% drop in feed costs and a 10% increase in yields were analysed, and the results are summarised in Table 10. Again, the 10% drop in feed costs has a smaller effect on returns than a 10% increase in yields (Fig. 3). For example, for the low density FNQ farm the average rate of return rose by 26% in response to the 10% increase in yield but rose only by 9% given a 10% drop in feed cost.

Another very uncertain factor is the market outlook. Rather than prices remaining constant relative to costs it is probable that relative prices may fall, in view of the continuing expansion of prawn aquaculture, particularly in South-east Asia. If prices were to fall continuously at an annual rate of 1.5%, returns to prawn farming would be expected to fall substantially. For instance, mean returns to the high density NSW/SEQ 6 x 1 ha farm model fell below zero (Table 10). For the twenty 1 ha NSW/SEQ farm model the mean return was less than half that derived with constant prices. However, in the face of a continual price decline prawn farmers would be likely to improve yields and/or reduce costs to offset the effects of the price fall, as has occurred in other primary production activities.

Overall, the simulated distribution of returns to prawn farming indicates that it is a very un-

TABLE 8. Estimated costs of production resulting from an increase in yield.

Yield increase	Low density system		High density system	
	FNQ	NSW/SEQ	FNQ	NSW/SEQ
%	$/kg	$/kg	$/kg	$/kg
0	9.38	15.67	8.83	10.37
10	8.87	14.53	8.45	9.78
15	8.64	14.04	8.29	9.53
20	8.44	13.59	8.14	9.30
25	8.29	13.17	8.00	9.09
30	8.07	12.79	7.87	8.89

TABLE 9. Costs of production for 20 x 1 ha farm with high stocking density.

Item	FNQ		NSW/SEQ	
PHYSICAL DESCRIPTION				
Number of ponds	20		20	
Area/pond ha	1		1	
Total farm area ha	35		35	
Production/crop t/ha	3.75		3.75	
Number of crops/year no.	2		1	
Total production of prawns t/y	150		75	
Feed conversion ratios	2.25:1		1.8:1	
Feed consumed t/y	337.5		135	
Capital costs of establishment(a) $	1 218 200		1 148 200	
FINANCIAL DESCRIPTION	$ y	$ kg	$ y	$ kg
Gross income	1 500 000	10.00	750 000	10.00
Operating costs				
— Feed	506 250	3.38	202 500	2.70
— Casual labour	45 000	0.30	22 500	0.30
— Electricity	73 300	0.49	40 000	0.53
— Prawn fry	200 000	1.33	100 000	1.33
— Fertiliser	16 700	0.11	5 000	0.07
— Repairs & maintenance	15 000	0.10	12 000	0.16
— Miscellaneous	6 000	0.04	6 000	0.08
Total operating costs	862 250	5.75	388 000	5.17
Overhead costs				
— Depreciation & interest(b)	141 937	0.95	137 737	1.84
— Allow. for farmer's labour	26 090	0.17	26 090	0.35
— Permanent hired labour(c)	75 000	0.50	75 000	1.00
— Administration costs	11 000	0.07	11 000	0.15
Total overhead costs	254 027	1.69	249 827	3.33
Total costs	1 116 277	7.44	637 827	8.50
Ratio of overhead to total costs (%)		23		39
Return to management	383 723	2.56	112 173	1.50

(a) Derived from Table 4 plus land purchase. (b) Assuming real rate of interest of 6%. (c) 3 full-time people.

FIG. 3. Cumulative probability of IRR: far north Queensland 6 ha high density prawn farm model.

certain business. For example, the average internal rates of return on the two modelled 6 ha North Queensland farms are 16.8% and 13.8%, but there is a 25% chance that the return could fall below those averages by over a third. In addition, variations in prices, yields, feed costs and the size of farm have very marked effects on returns.

CONCLUSIONS

The principal aim of this study was to provide industry statistics and an analysis of the economics of prawn farming to assist industry, government and researchers to determine future directions. In 1989–90 Australian production of cultured prawns came from 30 farmers with al-

TABLE 10. Internal rates of return to prawn farming: stochastic simulations.

Farm model*		Mean	75% probability that IRR is more than:	75% probability that IRR is less than:
		%	%	%
Low density:	FNQ	13.8	10.0	17.6
	NSW/SEQ	–	–	–
High density:	FNQ	16.8	10.5	22.8
	NSW/SEQ	2.0	–	7.0
Feed costs reduced by 10 percent				
Low density:	FNQ	15.1	11.4	19.4
	NSW/SEQ	–	–	–
High density:	FNQ	20.2	13.8	25.6
	NSW/SEQ	3.6	–	8.4
Yields increased by 10 percent				
Low density:	FNQ	17.4	13.6	21.0
	NSW/SEQ	–	–	–
High density:	FNQ	21.0	15.2	27.4
	NSW/SEQ	5.2	–	10.7
Prawn prices deflated by 1.5% a year				
Low density:	FNQ	6.1	0.2	11.1
	NSW/SEQ	–	–	–
High density:	FNQ	4.2	–	13.3
	NSW/SEQ	–	–	–
20 x 1 ha pond farm, high density				
Constant prices:	FNQ	39.2	30.6	47.2
	NSW/SEQ	15.9	9.6	21.6
Prawn prices deflated by 1.5% a year:				
	FNQ	31.4	20.6	40.2
	NSW/SEQ	6.4	–	14.2

* 6 x 1 ha except where otherwise indicated. — Negative.

most 400 ha of ponds along the east coast. The industry is undergoing rapid change as it expands and develops beyond the infant stage and a clear management pattern has not yet emerged.

The economic analyses were based on a 6 x 1 ha model prawn farm with two intensities of operations in two regions, far north Queensland and New South Wales/south-east Queensland. Given the risks and lead time associated with developing a new industry, the establishment costs of about $0.5 million per farm present a large obstacle. Overhead costs are 33–46% of total costs for the high intensity farm, so it is not surprising that there are substantial economies in operating a larger farm as indicated by the results from a 20 ha model. The costs of production and returns for both intensities of operation are similar in far north Queensland, but there are marked differences between the two regions which reflect the climatic constraint of being able to produce only one crop per year in the more southerly region.

The overriding conclusion to be drawn from the analysis is the high uncertainty of returns and risk involved in prawn farming. At current prices for the product, returns to prawn farming in Australia are adequate, but its profitability is very sensitive to price. With the prospect of further price falls in the future, returns to Australian prawn farmers may be reduced substantially unless savings in production costs can be achieved and/or production is switched to higher priced products. The effect on profitability of production of higher priced products —

such as higher priced species, live prawns or larger prawns — would require further research than was possible in this study. As the industry is still in a developmental stage it may well be possible to effect significant cost savings through increasing yields. The analysis showed that returns were more responsive to changes in yield than to reductions in feed costs. Also, unit costs may be substantially reduced and returns raised by increasing the size of the farm.

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WORLD SHRIMP PRODUCTION

SJEF VAN EYS

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Total world shrimp supply at the end of the 1990's is expected to exceed 3×10^6 t. In 1989, 103 counties were involved in shrimp production; 10 of the top 16 counties were Asian and together produced more than half the worlds production. Tropical shrimps represent 90% of the world shrimp market. The production from wild harvest fishing operations is fully exploited and will remain static at *ca.* 1.5×10^6 t. Shrimp production from aquaculture has shown a dramatic increase over the last 10 years due in part to the development of hatchery techniques and the production of hatchery reared post-larvae. The culture is centred on tropical prawns (*Penaeus* species) grown in Southeast Asia. Latin America has the potential to be a large producer of aquaculture product but its development is hampered by lack of technical expertise and capital. □ *Shrimp, prawn, aquaculture, wild harvest, fisheries, world.*

Sjef van Eys, Infopesca, Adpo. 6–1894, El Dorado, Panamá, RP; 16 January, 1991.

Shrimp are found in all regions of the world in fresh, coastal and oceanic waters. Many species have high value and form the basis of major commercial wild harvest fisheries and culture industries. There are five major market groups of shrimp:

1. Warmwater or tropical marine species. They mature rapidly and often grow to a large size.
2. Coldwater marine species. Inhabit temperate waters, grow slowly and are generally small.
3. Freshwater species. Live in inland water bodies and rivers, mostly in the tropics and often grow to a very large size.
4. Deep sea shrimp. Grow and reproduce slowly and are of limited commercial value.
5. Krill. Landings of Antartic krill (*Euphausia superba)* topped 500,000 t in 1989. The biomass is estimated at 100×10^6 t. New uses of krill by-products and increasing use for human consumption (e.g. in Japan) should encourage more attention to this species.

The world supply of shrimp increased rapidly from 1.09×10^6 t in 1970 to 1.63×10^6 t in 1977 (live weight). Supply of shrimps remained relatively stable until 1981, when landings quickly accelerated to reach about 2.5×10^6 t by 1989.

According to FAO statistics in 1989, 103 countries were involved in the production of shrimp, both wild and cultured. Ten of the top 16 producing countries in 1988 were Asian and together produced 1.6×10^6 t (live weight), equivalent to 65% of the total world production (Table 1). For 1989 this should increase further as a result of continued strong cultured shrimp output.

Estimates reveal that 90% of the total world market supply consists of tropical shrimp.

Coldwater shrimp landings have shown considerable fluctuations, mainly due to incompatible fishing efforts and the natural characteristics of the resource (slow growth and rate of recovery). This has led to major collapses: United States Pacific fishery in early 1980's, Norway

TABLE 1. Sources of shrimp production ($\times 10^3$ t), by principal country.

Country	1980	1985	1986	1987	1988
China	184	367	427	457	584
India	250	232	215	197	237
Indonesia	136	144	157	187	202
USA	162	153	183	165	151
Thailand	133	126	139	150	*150
Taiwan	81	108	137	176	111
Ecuador	17	36	53	79	81
Philippines	26	62	72	68	80
Mexico	77	75	73	84	73
Malaysia	84	69	73	*73	*73
Greenland	36	52	64	64	65
Brazil	48	68	55	55	58
Vietnam	41	54	55	56	*56
Rep. of Korea	27	40	45	48	50
Japan	51	55	48	48	*48
Norway	45	91	57	42	42
Australia	22	21	19	20	20
World Production	1,781	2,298	2,426	2,605	2,763

*Estimated.

TABLE 2. Catches of coldwater shrimps ($x10^3$ t), by selected countries.

Country	1980	1985	1987	1988
Greenland	35.8	52.4	64.4	65.1
Norway	45.3	91.2	42.2	41.7
USA	44.7	19.5	37.8	36.7
Canada	12.0	14.1	25.4	34.5
Iceland	10.0	24.9	38.6	29.6
Denmark	7.0	10.3	16.1	*16.1
USSR	12.1	33.4	12.0	13.7
FR Germany	15.4	17.7	17.0	14.3
Argentina	0.8	10.3	2.8	*2.8
Total	183.1	273.8	256.3	254.5

*Estimated.

and Argentina in 1986. Most of the fisheries appear to have recovered (Table 2) and fishing is now strictly regulated. No major increases are expected for this group and aquaculture has limited potential.

Freshwater shrimp output has remained stable. Initially, demand suffered as marine shrimp supplies increased. However demand is now increasing, due mainly to market demand for large shrimp. Smaller shrimp are used as market subsitutes for small marine shrimp e.g. *Crangon* spp.

The growth in production of cultured shrimp (mainly *Penaeus* species) has been spectacular. In tropical coastal countries, using simple earth ponds, tidal or pumped water supplies, local or hatchery-reared seed, and simple fertilisation or feeding, a marketable crop of 15–30g shrimp can be reared in as little as 3 or 4 months. Annual yields range from 200 to 500 kg ha^{-1} in simple extensive tidal ponds, to upwards of 10 t ha^{-1} in modern intensive systems using formulated feeds, aeration and regular water exchange.

In production terms, the results of the blue revolution have been impressive. In 198l, cultured shrimp accounted for only 2.1% of total world shrimp harvest, while in 1989 this was estimated to have reached 27% with output of 560,000 t, corresponding to a farm-gate market value of about US$2.5 billion. Much of this originates from the developing world, particularly Southeast Asia and Latin America.

As a result of this development, rural coastal land of limited agricultural potential, has acquired a new status. There are also new prospects for income and employment; traditional brackish water fishpond operators have a new source of income; fishing communities can get involved in catching seed shrimp and broodstock; farm and hatcheries in rural areas offer local employment and training for young people. There are new services industries; in Southeast Asia backyard hatcheries have created excellent opportunities for small family-based business, whose earnings in turn give stimulus to local economies. These spin-off benefits can be simply staggering, which is probably a major reason why governments continue to be keen to promote this activity despite the current problems on the marketing level.

The producing countries are discussed on a regional basis below(including the smaller producers, some of which are major suppliers to select markets), followed by an overview of the international trade for shrimp and prospects for future markets.

EUROPE

Capture Fisheries

European Economic Community (EEC)'s dom-

TABLE 3. Cold water shrimp production ($x10^3$ t) from selected countries in the European Region.

Country	1982	1983	1984	1985	1986	1987	1988
Pandalus borealis							
Norway	51.6	78.2	84.0	91.2	57.4	42.0	40.0
Iceland	9.2	13.1	24.4	24.9	35.8	38.6	30.0
Greenland	40.7	41.2	41.5	52.4	64.1	64.1	72.5
Denmark	7.1	10.1	7.3	9.4	10.0	14.3	8.3
Others	7.5	9.2	11.2	13.6	12.1	11.6	*12.0
Total	**116.1**	**151.8**	**168.4**	**191.5**	**179.4**	**170.6**	**162.8**
Crangon crangon							
Germany	19.8	13.4	12.0	17.7	17.0	17.0	*17.0
Netherlands	7.3	7.0	*7.0	*7.0	*7.0	*7.0	*7.0
France	1.4	1.1	1.4	1.0	1.5	1.0	*1.0
UK	1.2	0.8	0.4	0.4	1.0	2.0	1.3
Total	**29.7**	**22.3**	**20.4**	**26.1**	**26.5**	**27.0**	**26.3**

*Estimated.

TABLE 4. Shrimp production ($x10^3$ t) by countries within the European Economic Community.

Country	1982	1983	1984	1985	1986	1987	1988
Germany	19.8	13.4	12.0	17.7	17.0	17.0	14.3
Spain	11.3	11.5	12.2	29.3	23.4	25.1	22.0
Denmark	10.2	12.1	8.1	10.3	11.2	16.2	6.8
Netherlands	7.3	7.0	*7.0	*7.0	*7.0	*7.0	*7.0
Italy	10.3	12.7	17.8	20.2	14.6	12.1	16.4
Greece	2.3	2.4	2.6	3.1	3.7	5.9	4.4
Ireland	0.1	0.1	0.1	0.1	0	0	0
Belgium	2.2	1.0	1.0	0.9	0.6	0.8	0.7
Portugal	0.4	0.7	0.8	0.7	0.2	0.2	0.2
UK	1.2	1.1	0.7	0.8	1.4	2.5	1.6
France	3.2	2.4	2.9	2.1	2.8	2.6	2.3
Total	68.3	64.4	55.2	85.2	81.9	89.4	75.7

*Estimated.

estic production of shrimp increased from 60,000 t in 1981 to over 80,000 t in 1987 (Table 4). Most of this production is made up of *Crangon crangon*, a small coldwater species caught by the fleets of Germany and the Netherlands (Table 3). Spain and Italy contribute *c.* 15,000 t of *Parapenaeus longirostris*, a warmwater species.

From the early 1970's European and North Atlantic catches of *Pandalus borealis* increased steadily from 30,000 t to a peak of 192,000 t in 1985. Since then the landings have declined, due to smaller catches by Norway, to 163,000 t in 1988 (Table 3). Norway used to account for roughly half of the world's *Pan. borealis* landings, but Greenland with 72,500 t in 1988 has become the leader. Iceland's catch of this species tripled between 1983 and 1986. However stock started to decline due to overfishing. Quotas were introduced with the result that catches dropped from 39,000 t in 1987 to 30,000 t in 1988.

Spanish shrimp production reached a peak of 25,000 t in 1985, due to record catches of *Par. longirostris*. Landings then declined to 19,000 t where they have remained. Coldwater shrimp represent a very small proportion of the Spanish shrimp catch. Domestic supply accounts for approximatelty half of the total shrimp consumption in Spain.

UNITED STATES OF AMERICA

Capture Fisheries

The United States domestic shrimp production was 331 x 10^6lbs (150,000 t) in 1988 (Table 5) and comprised about 7% of the world's supply. United States total shrimp landings increased from 192 x 10^6lbs (73,000 t) in 1950 to a record level of 467 x 10^6lbs (216,000 t) in 1977, the result of high landings in the Gulf of Mexico fishery and a record harvest of cold water shrimps production in subsequent years, United States total landings averaged 329 x 10^6lbs (150,000 t) during the period 1980–88, as compared to an average of 391 x 10^6lbs (178,000 t) for the period 1971–79. However the total deflated ex-vessel value of shrimp has shown an overall rising trend during the period 1971–88.

Landings of coldwater shrimp increased rapidly up to 1977, largely as the result of heavy production in Oregon and Alaska. The number of trawlers in the Pacific fishery has since declined. A combination of declining shrimp stocks and reduced prices caused by imports of coldwater shrimp from Norway led to a major drop in Pacific landings during the 1983–85 period. In addition, many production areas in Alaska were closed to permit the resource to recover. Since 1985 catches have improved in Washington, Oregon and California, but a high incidence of small-size shrimp at times has resulted in lower ex-vessel prices. Alaskan stocks show no signs of recovery.

The tropical shrimp fishery has not undergone major fluctuations in recent years. This fishery averaged 253 $x10^6$lbs y^{-1} (115,000 t y^{-1}) during the period 1980–88. Since all major United States shrimping grounds are already exploited to a maximum, the total supply from the warmwater capture fisheries is not expected to increase in the future.

TABLE 5. Shrimp Production ($x10^3$ lbs), by regions, in the United States of America.

Year	Mid Atlantic	South Atlantic	Gulf	Pacific	Total
1971	24,536	31,200	227,367	107,790	390,902
1972	24,461	25,248	228,941	108,811	387,461
1973	20,739	24,557	182,206	152,220	379,722
1974	17,515	27,091	186,208	142,759	373,573
1975	11,655	24,926	170,083	149,067	346,731
1976	2,254	26,108	210,167	167,865	406,394
1977	840	18,021	265,158	192,433	476,452
1978	-	20,138	248,327	154,403	422,875
1979	1,072	32,295	206,564	96,019	335,950
1980	731	32,996	208,280	97,697	339,704
1981	2,271	16,514	268,190	67,496	354,471
1982	3,383	25,580	209,926	44,738	283,627
1983	3,469	26,615	198,457	21,124	249,664
1984	7,114	19,179	254,254	20,807	301,354
1985	9,254	27,970	262,908	33,509	333,641
1986	10,328	23,120	304,051	62,686	400,185

There has been a steady increase in the number of vessels in the fishery for tropical shrimp in the past 10 years. Between 1978 and 1987 the number of shrimp vessels (fishing craft over 5 t gross) in the Gulf of Mexico rose from 3,743 to an estimated 5,800. At the same time, shrimp vessels have become large and more sophisticated.

The Gulf of Mexico shrimp trawlers reportedly operated profitably during the period 1971–80. This trend stimulated the continued expansion in the fleet, despite periodic downturns in shrimp prices and generally rising operating costs. Historically the Gulf of Mexico shrimp fishery has displayed symptoms of overcapitalisation, but regulatory efforts to limit access have generally not been acceptable to the United States industry.

Culture

Total cultured tropical shrimp production was c.1,100 t in 1988. Climate conditions, high labour costs and shortage of suitable land have generally resulted in United States investors going abroad. Initially this was Latin America. Currently the focus of United States investors is Southeast Asia (Thailand, Philippines and Indonesia).

MIDDLE EAST AND NORTH AFRICA

Capture Fisheries

Total shrimp production in Middle East and North African countries was probably between 20,000 t and 30,000 t in 1988. Shrimp is caught both by industrial trawlers and by artisanal fishermen.

The principal shrimp catching countries in the region are Algeria, Bahrain, Egypt, Kuwait, Saudi Arabia and Tunisia (Table 6). Most fisheries for shrimp in the region are considered to be fully exploited. However, there may be scope for increased landings in Algeria, Qatar and the Yemen Arab Republic.

Culture

Although there is some experimental activity in a number of countries in the region, there are no commercial shrimp culture operations.

There are major constraints to the development of shrimp culture, including the availability of suitable species, lack of freshwater, and soil and climatic conditions. In the Middle East countries it is anticipated that little progress will be made, but a country such as Tunisia may be able to develop a shrimp culture industry.

Exports

Total shrimp exports from the Middle East and North Africa were less than 10,000t in 1988.

The principal exporting country in 1988 was Tunisia, which in that year shipped over 3,000 t. Other countries in the region normally export

TABLE 6. Shrimp production (t) from selected countries in the Middle East and North African Region.

Country	1985	1986	1987	1988
Algeria	n/a	5,277	8,750	6,056
Bahrain	1,324	1,733	1,843	1,118
Eygpt	1,939	1,717	2,150	n/a
Kuwait	2,128	1,667	2,443	4,999
Oman	n/a	n/a	200	n/a
Qatar	53	56	61	100
*Saudi Arabia	2,600	1600	2260	2600
Tunisia	1,756	2,279	3,798	3,135
Yemen (P.D.R.)	390	353	275	86
Yemen Arab Republic	320	432	361	273

* Estimated

less than 1,000 t y^{-1}. Export destinations are primarily Europe and Japan.

Outlook

There is little prospect for any increase in supply from the Middle East and North Africa. Most capture fisheries are fully exploited and culture production will be difficult to develop.

Exports from the region have little impact on world trade in shrimp. This situation is not expected to change.

WEST AND EAST AFRICA

Capture Fisheries

Total shrimp catches in West Africa have probably averaged over 30,000 t in the period 1983–86. It is likely that more than 50% was caught by vessels from non-coastal countries.

Of the West African coastal countries, Senegal is the largest producer with over 5,000 t y^{-1} in the period 1983–87. The only other coastal countries to produce consistently over 1,000 t y^{-1} are Nigeria, Morocco and Gabon (Table 7).

Spain is the leading producer of the non-coastal countries, with an average of 8,900 t y^{-1} in the period 1983–86. Its vessels operate under bilateral or EEC negotiated agreements, or joint venture agreements.

Fishing effort in West Africa has tended to concentrate on pink shrimp (*Penaeus notialis*). In several countries, notably Senegal, Cameroon, Sierra Leone and Nigeria, industry sources have expressed concern at decreasing catches and a decline in the size of shrimp caught, which can be taken as a sign of over-exploitation

It is thought likely that local fishing vessels will be directed increasingly towards catching the deepwater rose shrimp (*Par. longirostris*), which has been taken almost exclusively by the Spanish fleet. Local operators will have to invest in certain changes in equipment, notably the winches, to enable their vessels to fish at the depths required.

In East Africa the principal producing countries are Madagascar and Mozambique. In the period 1986–88, over 7,000 t and 5,000 t respectively, were caught annually.

Culture

Shrimp culture activities in Africa are still at an initial stage. While experimental work is being undertaken in several countries, there are as yet no commercial shrimp farms in full operation. Trial production is taking place in Gambia, Madagascar and Tanzania. Madagascar has the best potential.

At this stage it is not clear which shrimp species will be found suitable for culture in West Africa. Currently, West African operations work with imported species (*Pen. monodon* and *Pen. vanamei*), while in East Africa (Madagascar and Mozambique) there is a resource of *Pen. monodon*.

Exports

Western Europe has been the principal outlet for shrimp from West Africa, with France the most important market. African shrimp are very popular due to existing species/taste preference.

Japan is the principal market for exports of shrimp from East Africa (*Pen. monodon* and *Pen. indicus*).

AUSTRALIA

Capture Fishery

Australian fisheries for shrimp produce approximately 20,000 t. All Australian fisheries are managed under systems of limited entry, restrictions on gear and closed seasons.

The northern prawn fishery is the most important with landings of about 10,000 t. The resource is considered to be fully exploited. The principal species caught is the banana shrimp (*Pen. merguiensis*) which, between April and September–October, forms schools in shallow water. Other species caught include white shrimp (*Pen. indicus*), tiger shrimp (*Pen. semisulcatus* and *Pen. esculentus*), endeavour shrimp (*M. endeavouri*), western king shrimp (*Pen. latisulcatus*) and red spot king prawn (*Pen. longistylus*).

The western trawl fishery was originally directed at western school prawns (*M. dalli*). In the 1960's a modern trawl fishery began, for which

TABLE 7. Shrimp production (t) from selected countries in the West and East African Region. Source: FAO Yearbook of Fisheries Statistics and INFOPECHE.

Country	1984	1985	1986	1987	1988
WEST AFRICA					
Coastal Countries					
Morocco	1,400	1,700	1,000	1,300	2,100
Mauitania	300	200	500	600	1,200
Senegal	5,300	5,500	5,600	5,400	n/a
Gambia	500	500	500	500	500
Sierra Leone	700	700	700	n/a	n/a
Cote d'Ivoire	400	500	600	500	600
Chana	200	500	600	1,600	n/a
Nigera	2,300	1,500	1,600	2,200	2,500
Cameroon	900	600	800	800	800
Gabon	1,600	1,700	1,900	2,100	2,000
Non-coastal Countries					
Spain	9,600	10,500	5,800	n/a	n/a
Italy	600	800	1,100	n/a	n/a
Greece	1,800	2,400	2,400	n/a	n/a
EAST AFRICA					
Madagascar	6,052	6,685	7,606	9,020	7,707
Mozambique*	25,845	6,140	5,929	5,570	5,640
Tanzania	294	446	558	1,262	1,324

*Industrial fleet only

the principal species are brown tiger shrimp (*Pen. esculentus*) and western king shrimp (*Pen. latisulcatus*). In recent years catches of these species have declined sharply, leading to the closure of spawning areas. Landings from this fishery account for about 15% of the total Australian catch.

The southern trawl fishery lands only western king shrimp (*Pen. latisulcatus*). The fishery is considered to be fully expoited and has had a system of limited licences since the fishery developed in the mid 1960's.

The eastern shrimp fishery is a complex of sub-fisheries, each targeting a complex of species. The fishery is mainly based on king (*Pen. plebejus, Pen. longistylus* and *Pen. latisulcatus*), banana (*Pen. merguiensis* and *Pen. indicus*), tiger (*Pen. esculentus* and *Pen. semisulcatus*) and endeavour (*M. endeavouri* and *M. ensis*) shrimps offshore and school (*M. macleayi*) and greasyback shrimps (*M. bennettae*) inshore and in estuaries, with some deepwater species such as jack-knife prawn (*Haliporoides sibogae*) and scarlet shrimp (*Plesiopenaeus edwardsianus*) also taken.

Culture

Culture production is limited although some 40 farms are reportedly involved in this activity. Most farms use extensive technology and total production has not exceeded 1,500 t y^{-1}.

The principal culture species is black tiger (*Pen. monodon*), although there are some ongoing trials with other local species. The selection of the black tiger as the principal species puts the entire Australian culture industry in doubt as it is unable to compete nationally and internationally with SE. Asian black tiger supplies because of climatic and lower production costs.

Export

Total exports during 1988/1989 were 11,594 t with Japan as the major outlet. With its market position in Japan seriously challenged by Chinese white, and particularly black tiger, Australian exporters are successfully targeting the Spanish market for head-on shrimp.

Australia is also a significant importer. Imports are mainly from Asian countries, with Thailand, Malaysia and Vietnam the major suppliers. Annual imports are about 11,000 t, and consist primarily of cheaper products.

LATIN AMERICA

Shrimp production in Latin America is summarised in Table 8. In 1988 landings from capture fisheries exceeded 200,000 t (live weight), while cultured production was about half that volume.

The shrimp industry in Latin America developed rather favourably because it supplied a growing United States market, which was also willing to support the industry or at least invest considerable sums of money in it.

The vast majority of facilities are of United States design and are therefore set up to suit its market requirements. This is perhaps also the reason why the Latin American shrimp sector has not been very successful in penetrating other markets.

Capture Fisheries

Mexico is the largest capture fishery in the region with an annual production in excess of 70,000 t y^{-1} (live weight), followed by Brazil with 50,000 t and Argentina which has produced up to 20,000 t. Panama produces about 15,000 t. Other countries in the region normally land less than 100,000t y^{-1}. A drop in production is antic-

TABLE 8. Shrimp production ($x10^3$ t), by countries in the Latin American Region.

Country	1984	1985	1986	1987	1988
Argentina	23.1	10.3	7.0	2.8	18.1
Brazil	67.5	77.7	65.4	62.7	65.5
Chile	3.9	2.9	3.0	4.5	5.0
Colombia	8.1	5.0	6.2	6.7	5.3
Cuba	5.3	5.9	6.0	5.0	4.5
Equador	39.9	36.2	52.8	79.5	81.6
Panama	10.3	15.9	13.1	7.8	6.0
Peru	2.5	3.7	3.4	5.9	4.4
Mexico	79.9	77.9	76.3	87.1	76.9
Venezuela	5.2	6.0	6.6	6.1	5.6

ipated because of significant over-exploitation and poor management.

CULTURE

Except for Ecuador, culture output for the region has been disappointing. Currently the culture sector is passing through a very difficult phase, as a result of:

– limited availability of local and foreign investment capital.

– unfavourable climatic conditions resulting in low wild fry supply and diseases.

– hatcheries not operating or operating on limited scale only with poor results (low output and weak animals due to use of antibiotics resulting in deformities, diseases, slow growth and high mortality in grow out ponds).

– low prices in international markets.

– lack of research and development.

In the Latin American culture industry there are seven countries that deserve to be mentioned: Ecuador, Mexico, Honduras, Brazil, Peru, Panama and Colombia.

Ecuador has accounted for over 75% of the annual production of cultured shrimp in Latin America. Production in 1988 was reportedly about 75,000 t (live weight) but was expected to be approximately 10% less in 1989. No other country in the region produced more than 5,000 t. Yields vary widely. The best managed farms produce more than 2 t $ha^{-1}y^{-1}$, although the average production was estimated by industry sources at 700 kg $ha^{-1}y^{-1}$.

Ecuador is reported to have 124,000 ha of ponds, but in 1989 according to industry sources only 75,000 ha were in operation, owing to shortages of seed. Although there are about 60 hatcheries they have not been able to supply more than 25% of the farmer's need. Thus the industry is still dependent to a great extent on supplies of wild seed, which vary in abundance from year to year.

Shrimp culture in Mexico is conducted extensively in about 10,000 ha of ponds with low yields (350 kg $ha^{-1}y^{-1}$). Potentially there are 100,000 ha of land suitable for culture. Growth in the industry is constrained by lack of investment capital and by legislation reserving the ownership and use of land for cooperative groups of farmers. Nevertheless, this is all set to change from 1990 with private ownership of land and trade in shrimp possible as new legislation comes into effect.

The fastest growth in the region is taking place in Honduras where there were 4,200 ha in use in 1989. It is thought that the total area suitable for shrimp culture is between 20,000–25,000 ha.

In Brazil there are reportedly 3,800 ha of ponds. With a long coastline and a favourable climate, this country appears to have enormous potential for shrimp culture. A number of different species have been tried. Progress has been slow, apparently as a result of technical and administrative difficulties.

The area under cultivation in Peru is estimated to be 3,600 ha from which 2,190 t were reportedly produced in 1988. These figures would indicate an average yield of 600 kg $ha^{-1}yr^{-1}$. The government estimates that 5,000 ha of additional land are available. Shrimp culture is possible only in the extreme northern part of the coast. It is considered that the area under cultivation might increase to 8,000 ha.

The principal species cultured are *Pen. vannamei* (95%) and *Pen. stylirostris* (5%). There are three hatcheries in operation using nauplii from Ecuador.

In Panama 43 shrimp farms with a total area of 3,300 ha are under extensive cultivation. Production was reported to be 2,800 t in 1987 and 3,500 t in 1988. These figures would indicate an average yield of 1,050 kg $ha^{-1}y^{-1}$. Despite the fact that this country was one of the earliest to have major investments in shrimp culture, growth in the industry has been slow, chiefly as a result of lack of technical personnel, poor site selection (especially in relationship to the use of mangrove areas), lack of operating experience and political instability.

Colombia shows potential for development, with the area of ponds and production showing favourable growth. Production has increased from 1,500 t in 1986 to 3,500 t in 1988. Other countries in the region have less than 2,000 ha of ponds each.

If the situation in the capture as well as culture industry does not change quickly (in quantitative and qualitative terms) the industry will continue to lose established market outlets to Asian products. Latin American countries have the advantage of traditional relations and species preference in the United States and certain European markets, but are pressed to compete on price, not to mention consistent supply. For instance, Chinese whites are gaining market support with processors in the United States. Similarly, Australian product is penetrating the Spanish market for head-on shrimp.

ASIA

The shrimp industry in Asia has experienced profound changes over the last 10 years, mainly on account of developments in the culture of marine shrimp (Tables 9,10). These developments have brought about serious socio-economic and ecological repercussions on national and regional levels, and upset traditional world marketing structures.

Asia now accounts for about 60% of the world shrimp production, or in excess of 1.6×10^6 t, due to greatly increased aquaculture output.

The outlook for the Asian shrimp industry is brighter than for any other region because of its competitive position in terms of production costs, and consistent supplies. In addition, the processing sector is gaining the world's esteem because of its efficiency and high output of quality product.

Capture Fisheries

Capture fisheries have reached maximum levels in most countries. Slight increases may still be expected from improved handling and gear. Resource conservation measures are being imposed in the majority of countries

Inland capture of freshwater shrimp for export is limited. Landings appear to be affected by pollution and competition from the more readily available marine shrimp.

Culture

The marine shrimp aquaculture industry has developed rapidly and has reached the stage where mass production is a reality. This has mainly been the result of a production oriented mentality. Governments strongly supported this development as it was considered a potentially important source of foreign exchange and employment, with significant spin-off benefits.

The prime example is Taiwan where large volumes of shrimp were cultured at high profit margins. After initial hesitation and/or a period of adaptation of the culture technology to local conditions, production virtually exploded all over the region. *Pen. monodon* is the prime species cultured with the exception of China where *Pen. orientalis* is the principal species.

In most countries a number of favourable factors allowed rapid development of aquaculture:

- tropical climate
- sound resource of broodstock and/or wild fry.
- positive government support
- suitable species (*Pen. monodon*)
- tradition in culture of aquatic species.

The improving availability of formulated feed and hatchery-reared fry was another significant boost for the development of the sector.

Aquaculture has developed rapidly, particularly in Southeast Asia. On the Indian subcontinent development has been slower, mainly because of bureaucratic constraints and limited local investment capital and knowhow. Systems employed are primarily of an extensive nature.

The development of the culture sector in China shows a number of marked differences from other countries in the region:

- shrimp culture developed in the colder northern region
- the principal species is *Pen. orientalis*
- development is centrally planned
- mostly extensive operations.

Nevertheless, production also increased in China at an accelerated pace, initially due to a rapid increase in pond area. Currently, the culture of *Pen. monodon* in the more temperate southern provinces is also gathering considerable momentum.

The marine shrimp culture industry in Asia has reached a critical point:

- prices have dropped as a result of oversupply on the world market. Although the supply situation has returned to normal, price levels have remained depressed since the end of 1989. Farmers will have to decide whether to continue to increase production with current technology, or concentrate on efforts to improve efficiency in existing operations and develop more cost effective inputs.
- current output is basically limited to two species cultured to medium sizes. Species diversification could result in improved market movement and lower pressure on inputs.
- major investments are needed in research and

TABLE 9. Aquacultured shrimp production (1,000 t) from selected countries in the Asian Region. Source: FAO Yearbook of Fisheries Statistics and FISHDAB.

Country	1984	1985	1986	1987	1988	1989
China	22.0	35.0	70.0	153.0	180.0	190.0
Taiwan	5.0	17.0	33.5	65.0	75.0	45.0
Indonesia	33.0	39.0	48.0	55.0	82.5	90.0
Thailand	10.0	14.5	15.0	16.0	40.0	70.0
Bangladesh	11.5	12.5	13.5	14.5	18.0	20.0
India	26.3	26.5	27.9	25.4	33.6	35.0
Vietnam	4.0	7.0	7.0	7.0	15.0	25.0
Malaysia	–	–	–	2.0	3.0	3.0
Others	–	–	–	5.0	6.0	8.0
Total-Asia	145.3	185.0	290.8	408.9	488.6	506.0
Total-World	175.0	210.0	500.0	500.0	560.0	560.0

development to improve efficiency. The need for cheaper and more productive inputs and the current occurrence of various devastating diseases, clearly indicate the need for considerable investment in research and development.

Asia has contributed considerably to improving supplies to major world markets, even to the extent that it is harming its own industry. This situation seems to have resulted in more secrecy and a decrease in the flow of information on actual production estimates. Producers and exporters believe that information on production has a negative effect, basing their arguments on last year's experience. Traders in major markets respond with a wait and see position, resulting in small volumes being moved, little advance buying, little confidence in the future market, and consequently, a continuation of the depressed market prices.

INTERNATIONAL TRADE

Imports

World imports of fresh, chilled and frozen shrimp into the principal market countries during the period 1980–87 increased by 87% in volume and by 134% in value.

The dominant importing countries throughout the period were Japan and the United States. During the period 1980–1987 these two countries maintained their share of world markets, in terms of quantity, at 58%. During 1988 and 1989 imports into both countries have continued to increase although at a more moderate rate. However, the supply patterns by country of origin has experienced considerable changes particularly in the United States market. The EEC is the third largest market, and has shown considerable growth in consumption levels, while its growth potential is rated as impressive.

Growth in imports, by value, in the period 1980–1987 has been notably rapid in countries such as Singapore (1,750%), Italy (319%), Denmark (312%), Hong Kong (238%) and Spain (223%). The rapid growth in imports in such countries as Singapore, Denmark and Hong Kong has to be associated with an important re-export activity which has developed.

Japanese Market

Domestic landings in the period 1984–88 averaged about 50,000 t y^{-1}. Imports, during the period 1985–89 and in 1989 were 44% higher than they had been in 1985.

The share of imports in total supplies to the Japanese market increased from 61% in 1970 to 80% in 1980, while by 1988 it had reached 89%.

For many years India had been the leading supplier to the Japanese market. In 1986 and 1987 Taiwan took the lead, but in 1988 exports from Taiwan dropped by 54% in relation to the previous year and in 1989 only 8,900 t were exported. Indonesia and China assumed the leading position in 1988. In 1989 Indonesia assumed the top position with exports to Japan of 52,000 t (34% more than the second largest supplier, Thailand).

Notable increases in exports to the Japanese market in 1989 (compared to 1987) were achieved by Thailand, Indonesia, Philippines, Vietnam, and China.

The growth in imports during the 1980's has been the result of increased demand, caused by, among others, rising incomes, favourable price levels, together with the movement of the population into urban areas. Since 1985 the strength of the Japanese currency in relation to the United States dollar has also substantially contributed to Japan's strong import performance.

Declining prices have contributed to a signifi-

TABLE 10. Wild shrimp production (1,000 t) from selected countries in the Asian Region. Source: FAO Yearbook of Fisheries Statistics and FISHDAB.

Country	1984	1985	1986	1987	1988	1989*
China	207.1	229.2	200.1	192.5	583.6	580.0
Taiwan	na	100.0	107.7	137.0	126.5	85.5
Indonesia	132.9	144.1	157.3	167.8	167.8	170.0
Thialand	na	136.2	126.3	139.5	150.1	150.1
Bangladesh	61.0	70.0	73.0	74.0	75.0	75.0
India	203.1	232.5	214.7	216.7	216.7	210.0
Vietnam	na	52.0	54.1	55.4	56.0	56.0
Malaysia	na	70.1	69.0	72.9	72.9	72.9
Japan	62.9	55.0	47.9	47.8	47.8	45.0
Total	719.2	1151.1	1122.2	1171.6	1576.0	1519.5

*Estimated.

cant change in the pattern of consumption. In 1982 institutional consumption was reported to account for over 75% of total usage, with the remainder consumed at home. By 1988 home consumption had increased to 55% of the total usage.

Because of increased retail sales the Japanese market was able to expand further in recent years, despite the fact that institutional sales appeared to have reached saturation point.

No major increase in Japanese import and consumption levels are anticipated. The gradually weakening yen, signs of reduced growth in the national economy, increasing competition from other food items, e.g. salmon and beef, and the already high levels of per capita shrimp consumption, are all factors that undermine confidence in the future growth of the Japanese market.

United States Market

Domestic shrimp landings in the period 1985–1988 averaged 162,300 t y^{-1}, live weight. Domestic catches of tropical shrimp have remained stable for many years. Coldwater shrimp landings declined in the early 1980's, but have recently started to recover and in 1988 accounted for 25% of the total domestic landings. Production from domestic shrimp culture is negligible.

Imports increased each year during the period 1985–1988, and in the latter year were 40% higher in volume than they had been in 1985. In 1989 imports remained at the 1988 level. Imports slumped during the last quarter, when the market virtually collapsed due to an oversupply caused by dumping of Asian black tigers and white shrimp, deverted from the Japanese market.

The share of imports in total supplies to the United States market increased from 53% in 1970 to 55% in 1980 and by 1988 had reached 75%.

For many years Mexico was the leading supplier to the United States market, but this country has been unable to maintain its position. In 1987 Ecuador took the lead, but in 1988 was narrowly overtaken by China. Most of the product supplied by China and Ecuador is cultured white shrimp and these two countries together accounted for 37% of the total volume of United States imports in 1989. During 1989 imports from Ecuador dropped by 22% due to problems in their culture industry.

The most significant factor in 1988 was the sharp increase in imports from China (+145%) in relation to the previous year, a position maintained in 1989. Imports from Taiwan (-53%) and Mexico (-23%) declined sharply in 1988 from the previous year, as a result of problems in culture production and lower landings from capture fisheries respectively. During 1989 Mexico maintained this level (+15%) but Taiwan lost more ground as its exports for the year dropped by another 57% compared to 1988.

Headless shell-on shrimp is the predominant product form for imports and in 1988 accounted for 71% of total imports. During the period 1985–88 imports of headless shell-on product grew by 54%, while peeled shrimp imports increased by 18%.

In the period 1970–80 United States consumption of shrimp increased by only 9%. In the period 1980–88, however, it grew by 78% as a result of the increasing popularity of shrimp and improved availability. Still, per capita consumption in 1988 was a modest 1.1 kg (edible meat weight).

The drop in price levels for the medium sizes (20–25 and 26–30) during 1989 was the result of a substantial increase in supply of these sizes, mainly cultured product from Ecuador, China and Southeast Asia. The large sizes (under 15) followed suit as the price gap widened.

The prices for the smaller sizes held up relatively well in 1989 because of increased sales through retail outlets and the fact that imports of these sizes from Ecuador were much below normal (and anticipated) levels.

In recent years the pattern of consumption has changed. It is estimated that about 30% of shrimp is now sold retail, as compared to about 15–20% as recently as 5 years ago. Lower prices have enabled retail outlets to sell shrimp at prices which make it attractive in relation to competing products, and which provide favourable profit margins.

The current United States market can be described as unsettled as nobody seems to have a clear picture of what is happening. There is only scattered news on the production side, which is also mostly based on rumours. As a result trading is generally for immediate use only at depressed price levels. There is definitely no clearly defined direction. The United States market can be expected to have great potential in terms of an increase in imports although the current weakening of the economy will probably have a negative impact on growth. The lower value of the dollar and higher interest rates are additional negative factors. On the other hand, anticipated higher fuel prices could have a negative effect on domestic landings, leaving more room for imports.

European Market

With a total consumption of over 250,000 t in 1988, live weight equivalent, Europe follows Japan and United States as the third largest market for shrimp.

Coldwater shrimp (*Pan. borealis*), which is the major product in the Western and Northern European markets, is mostly supplied by countries from the north Atlantic. Declines in catches by Norway and the USSR have been compensated for by relatively stable landings in Greenland, Iceland, Faeroe Island and Denmark. The proportion of coldwater shrimp in the total shrimp supply to the European market declined from 49% in 1982 to 41% in 1988, although it increased in absolute terms from 81,000 t to 106,900 t during the same period.

Imports of shrimp into European countries in 1988 were 45% higher than they had been in 1985.

The increases in imports of tropical shrimp can also be ascribed, at least partially, to the strength of the European currencies in relation to the United States dollar and the slow growth in the supply of the preferred coldwater species. Price considerations may also have played a role in the growing importance of tropical shrimp.

Contrary to the preference for coldwater shrimp in northwestern Europe, consumption in southern European countries, especially Spain, France and Italy, is primarily directed towards tropical shrimp, and one of the most preferred product forms is head-on shrimp from Africa, the Mediterranean and Latin America. Despite consistent supply and price advantage Asian shrimp have not been able to make inroads in Spain and Italy. Quite the contrary can be said about Western Europe, which can be considered black tiger and chinese white territory by now.

Little impact is expected from the opening up of the eastern European markets in the short term. Incomes are too low.

Judging from the economic preference and current per capita consumption, Europe offers the most promising growth potential. However, it should be kept in mind that shrimp does not occupy the same status and popularity in Europe as it does in Japan and the United States.

Minor Markets

There are a number of important and rapidly growing markets such as Singapore, Hong Kong, Canada and Australia. In addition, the metropolitan areas in developing countries harbour a substantial number of wealthy people who do dine out frequently and like to consume shrimp. Their role in the world shrimp market will become increasingly important. For instance, Brazilian exporters indicate that they could sell the entire national production in the home market, and only export to earn hard currency.

Future Market Prospects

The sharp drop in world shrimp prices during the fourth quarter of 1989 has been a reminder to producers and traders that shrimp, like all traded commodities, is subject to fluctuations in price when the forces of supply and demand are out of balance or when a traditional trading pattern falls apart and uncertainty takes over. The rapid expansion in recent years of cultured shrimp production in Asia and Latin America caused a temporary oversupply on world markets. The sudden fall in prices was inevitable.

Other factors that contributed to the dramatic weakening in market conditions during the last part of 1989 were:

1. the oversupplied and temporarily saturated Japanese market
2. the gradual reduction in prices since early

1988
3. the increasing competition among exporters
4. the switch from a supply to a demand driven market
5. the marketeers in major markets not being ready for the new demand driven market situation.

In considering the future market prospects for shrimp over the next five to ten years it is important to maintain a focus on long term trends and underlying market forces, and to avoid being overly influenced by the recent dramatic events of 1989. To a certain extent this recent crisis has already been overcome, although at considerable cost. During most of 1990 the major markets actually experienced a shortage of certain species and sizes, as a result of production problems and sustained high consumption.

Overall demand for shrimp over the next decade will depend mainly on such factors as population growth rates; increases in disposable income; prices of shrimp; prices of meat, fish, poultry and other substitutes for shrimp; and consumer tastes and preferences. Forecasts of changes in demand for shrimp depend upon anticipated changes in these factors and on the responsiveness of shrimp consumers to these changes.

The World Bank predicts that the population growth rate in industrialised countries during the 1990's will be about 0.3% annually, while that of developing countries will be about 1.8% annually. Overall, the world population is predicted to grow at annual rate of approximately 1.4% during the 1990's. Although total population growth will affect overall shrimp consumption, it will largely depend on the increase in the number of people who can afford to buy shrimp, how much their disposable income will grow and how much of this total disposable income will be spent on seafood (i.e. shrimp).

The World Bank forecasts that the real Gross Domestic Product (GDP) in the industrial and developing countries will increase at average annual rates of 2.6% and 4.9% respectively over the present decade. This suggests a weighted average growth rate of GDP worldwide of approximately 3.5% and an average per capita income growth rate of about 2% annually in the 1990's.

Estimates of the income elasticity of demand for shrimp vary widely from market to market. In our opinion overall income elasticity of demand for shrimp will be less than 1.0. Using the estimate of slightly less than 1.0 as the future income elasticity of demand for shrimp, a worldwide population growth rate of 1.4%, an average growth rate of per capita income worldwide of 2%, and other factors remaining constant, shrimp demand should rise at an estimated annual rate not exceeding 2.5%, up to the year 2000.

With total world shrimp production in 1988 estimated at approximately 2.45 $x10^6$ t with demand expected to continue to grow at about 2.5% annually, the total world production for shrimp will have to rise to about 3.2 $x10^6$ t by the year 2000. It is not expected that there will be any significant increase in landings of shrimp from capture fisheries. A certain proportion of the required supplies will come from reduced post-harvest losses because of better handling and improved yields through new processing technologies and product development. Nevertheless, the major share of the additional supplies will have to come from culture operations which will have to grow from the 1988 level of about 560,000 t to about 1.3 $x10^6$ t in the year 2000. This implies an annual growth rate of cultured shrimp of about 7% over the period until the year 2000. Thus production will have to continue to increase at the 1985–90 rate, resulting in a cultured shrimp production at the year 2000 of 1.5 $x10^6$ t. Such a growth rate of cultured shrimp output appears highly unlikely without either a significant rise in real pond bank prices and profit margins approaching 1988 levels, or a major breakthrough in culture technology that will substantially lower production costs, and/or increase output.

Therefore our forecast is not one of an oversupplied market, although there may be periods of excess supplies, e.g. because of temporary favourable natural conditions. Price levels to the producer/exporter will very much depend on marketeers in major markets successfully promoting shrimp as a tasty, healthy, and value-for-money food item.

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ANALYSIS OF CATCH STATISTICS FROM THE DEEP-WATER PRAWN (*HALIPOROIDES SIBOGAE*) FISHERY OFF NEW SOUTH WALES, AUSTRALIA.

The deep-water trawl fishery for royal red prawns (*Haliporoides sibogae* De Man, 1907) has developed quite recently (mid 1970s) off New South Wales, Australia. Temporal and spatial trends in catch, fishing effort and catch-per-unit effort (CPUE) were analysed using landing statistics from fishermen's cooperatives (1978–1985) and data from a recently introduced logbook system (1985–1988). Fishing effort and CPUE were standardised using (i) a method derived from Gulland or (ii) log-linear regression techniques depending on the quality of data which differed between areas and periods of time. Regression techniques also allowed identification of factors influencing the variability of CPUE. Time of fishing (in terms of three month period) and engine power of vessel explained 79.4 and 20.6% of the variability of CPUE accounted for by the regression model, respectively.

Fishing effort was concentrated within small ranges of latitude (1°) and depth (100 m). Economic and logistic factors, rather than differences in prawn abundance, may be responsible for this geographic concentration of the fishery, suggesting that the royal red prawn stock is not exploited over its full distribution. The absence of obvious temporal and spatial variations in CPUE indicated that royal red prawns caught off central and southern New South Wales belonged to the same stock which was available throughout the year. This apparent temporal and spatial stability of CPUE contrasted with the great variation in CPUE generally observed for coastal prawn species revealing an important difference in the population dynamics between coastal prawns species and deep-water royal red prawns.

From 1979, annual landings have been stable at about 300–350 tonnes and there is at present no apparent reason for concern for the state of the royal red prawn stock off New South Wales. However, the availability of catch and effort data in the present study was limited in space and time. To better understand the relationship between fishing patterns and trends in abundance of prawns it would be necessary to 1) extend the area covered by logbooks, which is limited presently to central and southern New South Wales, and 2) conduct stratified fishing surveys outside the main distribution of the fishery.

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AN APPRAISAL OF TRAWLING AS A TOOL FOR STOCK ASSESSMENT AND DEVELOPMENT OF HARVESTING STRATEGIES IN SOUTH AUSTRALIAN *PENAEUS LATISULCATUS* FISHERIES.

South Australian prawn fisheries are based on a single penaeid species *Penaeus latisulcatus*. Over the last decade, prawn landings in Spencer Gulf have ranged from 1.4 to 2.3 thousand tonnes with a current export value of $50 million. There has been a marked increase in larger prawn grades of the catch attributable to refinement of harvesting strategies. The Spencer Gulf fishery is limited entry (39 vessels) with controls on gear, vessel physical characteristics, amount and direction of effort. Large scale survey sampling is undertaken in conjunction with industry for stock assessment and for development of real time harvesting strategies.

The main objectives of the research are: to develop strategies which minimise the risk of recruitment over-fishing and to optimise the value of the catch. This paper is a brief appraisal of trawl sampling methodology and its application to management.

Trawl sampling is systematic over a wide scale and is primarily based on stratified sampling plans. Inherent problems associated with sampling are apparent. Sampling has a number of functions which in turn require different sampling plans. Owing to environmental gradients, sampling variance can be minimised by sampling across rather than along the gradient. However, cross sampling has practical restrictions: furthermore, information is lost relating to spatial size structure which is necessary for closure delineation. Mixed sampling plans and the value of strategic 'spot' surveys provide a solution to the problem.

The information obtained from survey sampling is used in conjunction with fishermen's log book data for evaluation of the effects of fishing, parameter estimation and development of sequential harvesting strategies. The application of survey data to 'optimal' harvest simulation incorporates a harmonic growth model which enables predictions of biomass and value at different regions in the Gulf. Results show that natural mortality has a large influence on model predictions. Information indicates that biomass and biovalue trends differ depending upon the size composition of the population. However, over all regions, both biomass and biovalue decrease from June to February. Hence, effort reduction from June to March has two advantages: it reduces reproductive depletion attributable to fishing and results in increased value of catch.

The work demonstrates the importance of the participation and cooperation of fishermen in research and management.

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THE BIOCHEMICAL COMPOSITION OF NATURAL FOOD OF *PENAEUS ESCULENTUS* HASWELL (PENAEIDAE: DECAPODA)

The development of artificial diets for penaeid prawn aquaculture has been almost entirely an empirical process, largely driven by the need to provide a diet that gives good growth at minimum cost. Some of the early work was done by Kanazawa *et al.* (1970) and Deshimaru and Shigeno (1972) who formulated artificial diets for *Penaeus japonicus* based on the composition of the short-necked clam, *Tapes* (=*Venerupis*) *philippinarum*. *Penaeus japonicus* grows well on a diet of this clam, but it is not normally eaten in the wild. A more logical approach would be to formulate a diet based on the composition of the natural food of the prawn. Wassenberg and Hill (1987) studied the diet of juvenile *Penaeus esculentus* in seagrass beds and found that the main prey items were small gastropods, bivalves and Crustacea. We have analysed and compared these prey animals together with two commercial prawn feeds.

Materials and Methods

The most abundant known prey of juvenile *Penaeus esculentus* (i.e. 3 species of gastropod, 2 bivalves, 4 crustacea, a polychaete, and ripe and green seeds of *Zostera capricorni*) were collected from an intertidal seagrass (*Zostera capricorni*) bed in Moreton Bay, Queensland. Collections were made in September, February and May when juvenile *P. esculentus* were present. Proximate analyses (water content, ash, lipid, protein and carbohydrate), lipid class, fatty acid and amino acid analyses were carried out on each of the prey species and on 2 commercially produced prawn feeds, one formulated for *P. monodon* and the other for *P. japonicus*.

Results and Discussion

The natural diet contained high levels of ash from the shells and exoskeletons of the prey animals so comparisons with the commercial diets, which contained much lower levels of ash, have been made using the ash-free dry weights. Protein content of the prey animals ranged from 52–76% of ash-free dry weight, lipid 10–20% and carbohydrate 6–21%. *Zostera* seeds, which are eaten seasonally, contained 9% protein, 4% lipid and over 60% digestible carbohydrate. Using the % numerical composition data of the prey animals of the prawns (Wassenberg and Hill, 1987) and the weights and proximate analyses of representative animals, a profile of the natural diet of the prawns was calculated. The profile, expressed in terms of the ash-free dry weight, indicated that the natural diet of the prawns contained 66% protein, 13% lipid and 21% carbohydrate.

The protein contents of the commercial feeds were 51% and 77% of the ash free dry weight, 8% and 16% for lipid and 41% and 8% for carbohydrate. Amino acid composition was fairly uniform in all species and similar to the commercial feeds. Cholesterol was above 4% of ash-free dry weight; phospholipids ranged from 22–80% of total lipid. Saturated fatty acids were mostly less than 45% of total fatty acids and polyunsaturated fatty acids ranged from 24–56% of the total. The *Zostera* seeds contained no fatty acids with a carbon chain length greater than 18. The commercial feeds had a similar saturated fatty acid profile to the prey animals but differed in the mono- and polyunsaturated fatty acids with higher concentrations of C18:1w9 and C18:2w6 and with a lower concentration of C20:4w6, reflecting the presence of vegetable oils.

P. esculentus is a relatively slow growing prawn in both aquarium systems and in aquaculture ponds. The reason for this could be some response to environmental conditions in captivity or an unsuitable diet. The differences between the proximate and fatty acid profiles of the natural diet and the commercial feeds formulated for other penaeid species suggests that growth of *P. esculentus* may be improved by altering the formulation of the feed towards that of the natural diet.

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SPAWNING CONTROL OF THE JAPANESE SPINY LOBSTER

The Japanese spiny lobster, *Panulirus japonicus*, is a very important crustacean in Japan. In this study, the nature of their breeding was investigated as a basis for potential aquaculture of this species. The normal breeding season around Izu Peninsula, Japan, is from June to August. Incubation period was variable and temperature dependent. At normal water temperature on Izu Peninsula in 1989, the incubation period was two months. Phyllosoma larvae were seen toward the beginning of August.

Lobsters were maintained in running sea water aquaria, 142 x 142 x 84 cm, with a capacity of 1,000 L and were fed short-necked clams or fish. Body weight and carapace length of lobsters were 70–440 g and 39–80 mm in females, and 65–450 g and 41–80 mm in males. Beginning in 1983, animals were held at normal, ambient water temperatures or at constant temperatures of 20°C and 25°C.

Paired mature lobsters were transfered to small glass aquaria for observations of copulation and spawning. The mature female lobster grooms the pleopods with the fifth leg before copulation. Body weight and carapace length of lobsters in copulation were 125–310 g and 52–70 mm in females, and 210–360 g and 59–75 mm in males. Males were larger than females among copulating pairs.

Copulation and spawning were observed early in June. Copulation generally occurred at night to early morning. The pre-copulatory phase of the courtship lasted 0.5–3 hours. In copulation, the male embraced the female, belly to belly, for about 20 seconds. With a vigorous extension of the male's abdomen, spermatophores were discharged and deposited on the female's sternum and were stored externally. Frequency of copulation was between one and four times at night.

Within 10–130 minutes after final copulation, spawning, or oviposition began. During oviposition, the female lobster usually assumes a vertical position that will guarantee passage of the eggs from the oviduct opening to the ventral side of the abdomen where the eggs are cemented to the pleopods. Oviposition required 30–50 minutes. Thirty to 550 thousand eggs were deposited. Egg size was about 0.5 mm in diameter. In lobsters held at 20°C and 25°C in the laboratory, spawning was observed in March and April, 1.5–2 months before the start of normal spawning season and spawns in animals held at normal water temperatures. The eggs hatched early in May and June.

Our observations suggest that spawning of the Japanese spiny lobster can be controlled by changes in the water temperature of the rearing aquaria. This may be of great significance in the potential aquaculture of this species.

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EXPERIMENTAL CARAPACE INCREASE IN THE LOBSTER (*HOMARUS AMERICANUS*) FISHERY ON CAPE BRETON ISLAND, CANADA

The Gulf of St. Lawrence lobster population has historically been very productive, landing half of the landed weight of lobsters in Atlantic Canada. While the fishery has experienced fluctuations over the last hundred years, landings in the past fourteen years have steadily increased with the exception of areas in central Northumberland Strait. The Gulf of St. Lawrence lobster fishery captures 75% of lobsters at the commercial 'canner' size (63.5 to 80.9 mm) and 25% at the commercial 'market' size (81.0 mm and greater).

The lobster population of the southern Gulf of St. Lawrence experiences a wide seasonal range of temperature, a range of 0°–20°C is possible at a depth of 10 metres. Under these conditions, some lobsters moult twice a year. Female lobsters become functionally mature at a smaller size (77–80 mm) than in other areas on the Atlantic coast. Recent studies on fecundity have shown that Gulf lobsters carry more eggs at a given size than lobsters from other regions.

In 1987 we promoted an experimental legal carapace size increase programme on the west coast of Cape Breton Island. The purpose was to determine experimentally whether an increase in minimal legal size would enhance yield as predicted by the current models. Over four years the legal carapace size was raised by steps of 1/16" from 2 1/2" to 2 3/4" (63.5 to 70.0 mm). The final increment was completed in 1990. During the carapace size increase programme the size frequency distributions of lobsters caught in the commercial fishery were monitored in the area and in adjacent control areas. Lobster tagging programmes were completed in 1984 and 1988 in the experimental zone to determine if any changes in movement or growth would occur.

To date, the size frequency distributions show only a slight increase in percent frequency for lobsters released during the first three years of the project and presently reaching the new legal size. The experiment will be pursued over a period of five years in order to contrast benefits, if any, of the minimal size increase in the experimental area with the control areas. At this point in time it is not possible to identify any benefits resulting from the carapace size increase despite the model predictions. Landings increased considerably more in one control area than in the experimental area. The tag returns to date do not show significant differences in the growth or movement patterns as seen before the carapace increase programme. It presently appears very difficult to distinguish any changes generated by the minimal size increase from changes generated by natural environmental causes. These results are similar to those encountered by meteorologists confronting predictive modeling and chaos.

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MANAGEMENT AND ENHANCEMENT OF THE STOCK OF *PENAEUS ORIENTALIS* KISHINOUYE IN THE YELLOW SEA AND THE BOHAI SEA

Penaeus orientalis is a large, temperate, migratory species occurring between latitudes 33°30'–41°00'N. It overwinters (December to March) in waters of 60–80 m depth in central and southern areas of the Yellow Sea, and spawns from early May to early June around estuaries of the Yellow Sea and the Bohai Sea. As the shrimp fishery is intensively exploited, recruitment is related to spawning stock, as well as factors such as rainfall, runoff and salinity.

The year class yields of the shrimp in the Bohai Sea have shown periodic fluctuation in recent years. The average yield was 26,580 t in the late 1950s 19,391 t in the 1960s, 30,430 t in the 1970s, 19,297 t in the early 1980s. The maximum yield of 50,653 t occurred in 1979 and a minimum yield of 6,429 t occurred in 1984. Although the average yield in the early 1980s was similar to the 1960s, since then the shortage of spawning stock has led to a decrease of year class recruitment.

The management of shrimp fishery in the Yellow Sea and the Bohai Sea involves two strategies.

1. The protection of spawning stock and postlarvae so as to increase year class recruitment. A regulation forbids their capture along the migration route and in the spawning grounds. In addition, there are regulations which protect postlarvae and juvenile shrimps in the Bohai Sea. This protection includes closed areas and closed periods for the use of nets that could damage postlarvae and juvenile shrimp, and prevention of damage to postlarvae and juvenile shrimp by pumping water for pond culture, salt-making and other industrial usage.

2. The management of the autumn fishery in the Bohai Sea, or the problem of how to utilise and allocate the resources after a year class has matured. Before 1987, the open dates of the autumn shrimp fishery in the Bohai Sea were September 5 for drift nets, September 15 for motor-sailboats equipped with trawls, and October 5 for motor-trawls. From the beginning of the 1988 autumn fishing season, all trawlers have been excluded from the Bohai Sea, and only ships equipped with shrimp drift nets, are permitted to fish in the autumn fishing season in the Bohai Sea.

The major problems of the autumn shrimp fishery involve the huge fishing power employed, high fuel use and poor economic efficiency. Beyond a certain level, fishing mortality (F) does not increase linearly with fishing power. This is due to the limited shrimp fishing areas in the Bohai Sea and over-concentration of fishing vessels. When the number of fishing vessels is beyond a certain limit, fuel consumption rises while fishing coefficient (q), production rate and profit decrease.

The numbers of all major types of nets used in the autumn shrimp fishery in the Bohai Sea and the shrimp catch differs greatly from year to year. From the 1960s to the early 1970s, shrimp catch was largely made by bottom trawls of motor-sailboats and motor-trawlers. In late 1970s, owing to an earlier opening date, the shrimp drift net fishery developed rapidly and shrimp yield from drift nests increased. By 1980s, they began to dominate shrimp fishery, capturing more than 80% of the yield from 1986 to 1987.

Shrimp Stock Enhancement

Shrimp recruitment fluctuated from year to year, ranging from 1.07×10^8 (1985) to 1.40×10^8 (1961). The shrimp resource has had a low recruitment level particularly since early 1980. Hence, the release of hatchery reared larvae can be expected to enhance the shrimp resources in the Bohai Sea and increase yields.

Postlarvae, 30–50mm in length, are regarded as the best size (ecologically and economically) to release. There are many shrimp hatcheries and farms along the coast of the Bohai Sea that are capable of providing seed for release. The waters around the estuaries of the Yellow River, Haihe River and other rivers in the Bohai Sea are ideal release areas with suitable conditions (good water quality with abundant food, and few predators) for shrimp survival.

The best release time is when the sea water is muddy after strong winds, on the ebb, and when water is not being pumped by power plants and salt works. Postlarvae are easily caught by predators immediately after being released as the larvae are weak and stressed by new environmental conditions. Proper selection of release time and sites is therefore of great importance to minimise natural and made-made mortality.

Determination of the optimal quantity of postlarvae for release in a specific sea waters is a complex problem. The optimal quantity depends on the ecological capacity and natural recruitment abundance in the specific waters. Artificial releases can considerably affect ecological balance, interspecific relations and population succession. By using an annual shrimp resources estimation model, the shrimp number required to maximise catch in the Yellow Sea and the Bohai Sea was estimated to be 1.2 billion (food is a major limiting factor to increase of shrimp recruitment).

Since 1984, commercial shrimp postlarvae releases have been carried out in the Bohai Sea, the Yellow Sea and the east China Sea. Good results have been obtained; recapture rate was estimated as *c.* 10%. In the East China Sea, where the original *P. orientalis* population was very small, a natural stock large enough for fishing has grown up after many years of releases. In the inshore waters of the Yellow Sea, where previously natural shrimp populations were small and annual recruitment showed large fluctuation, recruitment has steadily risen after a series of large-scale seed releases. There is still a great potential for artificial seeding the Bohai Sea. The release numbers will be increased in years to come to reach the ecological capacity of the region.

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EVALUATION OF SEASONAL CLOSURES AS A MEANS OF OPTIMISING YIELD FROM A MULTI-SPECIES PRAWN FISHERY

Seasonal closures have been used as a means of optimising yield from Queensland's multi-species coastal prawn fisheries. Field studies and a log book data base have demonstrated that the fishery is supported by six penaeid species, four of which are significant contributors to the fishery. Species composition has varied significantly across distances as little as 100 km, and both the timing and strength of recruitment has varied during the two years (1989-1990) in which sampling took place.

A deterministic model, based upon Thompson and Bell's (1934) yield model, has been used as an initial means of estimating yield (weight of prawn and dollar value) from a given recruitment sequence. The model allows for variable recruitment timing, species composition and mortality. It has the advantages of being mathematically simple, flexible in respect of variability in input parameters, and readily adapted to either spreadsheet or microcomputer programming. Input parameters have been estimated from data obtained in tagging and field sampling programmes (Gribble and Dredge, 1991), or from published literature. There is a wide range of scenarios under which the model can be run. By varying growth and mortality parameters, potential yield from the fishery can be established across normally acceptable ranges of these parameters.

The major role of the model was to test the value of yield under a seasonal closure regime of management. Under a conventional scenario of constant fishing mortality, output from the model suggests that closures had little positive or negative effect upon yield from the fishery. In economic terms, the closure would thus appear to be of little benefit to industry. However, log book data clearly indicate that immediately following the cessation of closures, the fishery undergoes a heavy pulse of effort, which diminishes as the fishing season progresses. Under such a regime of fishing mortality, the model suggests that yield is increased as a consequence of the closures. This is achieved as a consequence of higher exploitation rates of the stocks. The subsequent output from reduced spawning stocks remains to be determined.

The variability of recruitment dynamics in this fishery indicates that seasonal closures are unlikely to optimise yield unless carried out on a regional basis, in conjunction with a detailed sampling programme. The authors intend to investigate the spatial dynamics of the fished species and incorporate these data into an evaluation of spatial closures as an alternative means of optimising the fishery.

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THE WHITE SHRIMP (*PENAEUS SETIFERUS*) FISHERY IN THE CAMPECHE BANK, MEXICO

The white shrimp *Penaeus setiferus* (Linnaeus, 1767) is amongst the most economically important penaeid species in the southwestern Gulf of Mexico, with more than 1000 tonnes caught annually. It supports three different fisheries in the area: an artisanal estuarine fishery, a drift net fishery offshore and the industrial trawl fishery. Relationships between these fisheries were analysed using yield per recruit models. Interaction between sequential fisheries (estuarine artisanal *versus* marine fisheries) is relatively low, as the estuarine fishery on white shrimp is small. Nevertheless, artisanal estuarine exploitation could exert a negative effect on the marine white shrimp fishery if the fishing effort increases inshore. Parallel offshore interaction (drift net and trawling fisheries) is stronger, since the types of gear used in the artisanal marine fishery are very efficient at catching white shrimp. This fishery is selective on large mature shrimp. Catches of the parallel fisheries are inversely related. However, the investment, costs, and benefits of the drift net fishery make this activity highly profitable and competitive with the industrial trawl fishery. A simulation model of the effect of the three fisheries suggested that the 1984 fishing effort was nearing the critical reproductive biomass.

The white shrimp spawns throughout the year, resulting in continuous recruitment. However, seasonal variations in recruitment result in periods of low and high abundance. The relationship between spawning and recruitment did not show a significant correlation ($0.2>P>0.01$) when analysed as biological years. This lack of correlation is attributed to the effect of environmental factors, as well as inter-annual variability of recruitment strength in the main cohorts throughout the year. A Ricker Stock-recruitment relationship ($P>0.001$) was established for dominant cohorts in the 1973–1984 study period. The explained variance increased from 70% to 84% when the model included the rivers' discharge during the previous recruitment month and during the spawning period four months prior. The river discharge has both negative and positive effects on recruitment. Its increase during spawning time can restrict the habitat available for successful establishment of shrimp postlarvae, but on the positive side, a drop in salinity can trigger juveniles to migrate to sea. The recruitment level depends largely upon the carrying capacity of critical nursery habitats. White shrimp adopt an opportunistic strategy to efficiently exploit the seasonal variations in estuarine carrying capacity associated with river discharge.

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COMMERCIAL RECIRCULATING SEAWATER SYSTEMS FOR HOLDING ROCK LOBSTERS IN TASMANIA, AUSTRALIA

Annual production of southern rock lobsters (*Jasus novaehollandiae*) in Tasmania is usually about 1750 - 2250 t with a landed value of $29.2 million in 1987/88. While the majority are sold chilled or frozen, a proportion are held in land-based tanks prior to domestic or export sale at a premium price as live product. In this paper technical aspects which could have influenced mortality in these systems are discussed. Lobsters may be stressed, prior to reaching the holding facility, by being kept out of water for up to five hours in inadequately cooled vans during road transport. Severe swelling occurs around joints and many rock lobsters have to be processed instead. Loss of limbs also reduces product value.

Ideally, a land-based facility should have a continuous seawater supply with a salinity of more than 27‰ and flow-through holding tanks as large amounts of organic matter are released soon after stocking. Accumulation of organic matter in biofilters leads to excessive oxygen demand and ammonia production by heterotrophic bacteria and sulphide production in any poorly exchanged areas (Forteath, 1990). Recirculating systems are used at most facilities and successful inland units rely almost totally on these systems. They are akin to soft crab or freshwater crayfish shedding systems in that the animals are not fed (Malone and Burden, 1988; Manthe *et al.*, 1988) and water should flow through the holding tank, physical filter, biofilter and cooling system in that order. The holding tank is usually a simple fibreglass or concrete tank of 1 m depth. Rapid sand filtration is preferred over dacron filter media although overloading of sand media with organic matter can occur despite backflushing. A separate biofilter tank, containing shell grit for buffering capacity, is preferred to reduce accumulation of organic matter within the biofilter.

Three key environmental variables influencing biofiltration efficiency are: large salinity fluctuation, water temperature and dissolved oxygen levels. Technical problems including inappropriately insulated buildings and inadequate cooling systems have hindered temperature control in Tasmanian systems. Operators usually aim to operate the systems at 10–12°C thereby reducing ammonia production. Ideally the reduction to 6°C, prior to loading of rock lobsters into export packs, should be done in separate systems as the temperature reduction could disrupt biofilter function. The capacity for maintaining dissolved oxygen levels at 2 mgL^{-1} throughout the biofilter, along with flow rate, surface area of medium and bacterial populations, will determine the amount of ammonia that can be converted to nitrate and hence the biological load that the biofilter can accommodate (Manthe *et al.*, 1988). Biofilters which contain partially exposed media and are supplied with seawater via gentle surface sprays may be adopted. Alternatively, if the biofilter medium is fully submerged, airlift pumps should be included to enhance oxygenation of the biofilter (Manthe *et al.*, 1988). The holding tanks are usually aerated with very turbulent surface generate removable organic foam, and may be augmented with occasional inputs of oxygen especially after stocking of rock lobsters as oxygen demand is high. Although separate aeration systems are rarely included in the designs for holding tanks, they should be used as they enhance circulation near the tank bottom and help ensure that water is well oxygenated before entering the biofilter.

Operators may maintain a small population of rock lobsters or fish in the holding systems to help establish or maintain appropriate bacterial populations e.g. *Nitrosomonas* and *Nitrobacter*, prior to bringing rock lobster densities up to commercial levels in the holding tanks (about 60 kg m^{-3}). Alternatively, commercially available bacteria may be added. However, the biological load should be increased progressively, i.e. no more than 10% per day (Malone and Burden, 1988). Even when high bacterial densities have become established (up to six weeks after initiation of biofilter), sudden increases in loading will exceed the capacity of the biofilter thereby leading to stressful levels of ammonia and nitrite. Unfortunately, as large numbers of rock lobsters become available, the holding systems are subject to sudden changes in loading and often pH, ammonia and nitrite levels are not adequately monitored. However, operators are reducing losses by minimising holding periods for rock lobsters within their systems. At a research level, more information is needed on biofilter design, appropriate biological loads, maintenance of bacterial populations and toxicity of ammonia and nitrite. The use of chemical sources of ammonia and nitrite for conditioning biofilters appears promising (Manthe and Malone, 1987). We were able to condition a tropical marine biofilter in 18 days without a biological load by using commercial bacteria and chemical sources of ammonia and nitrite (NH_4Cl and $NaNO_2$).

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PRELIMINARY RESULTS FROM A STUDY OF A CENTRAL QUEENSLAND COASTAL PRAWN FISHERY

As part of an evaluation of seasonal closures, an ongoing study is being carried out to determine the species composition, spatial and temporal distribution, recruitment, growth, and mortality in the multi-species penaeid prawn fishery in the Bowen–Mackay region.

Analysis of QFMA and a restricted number of research log books show that tiger, king and banana prawn are the dominant commercial species 'groups' caught in the region. Bananas and tigers are taken in large numbers inshore throughout the region with the kings coming from the near reef and inshore at Mackay. In 1988 and 1989 fishing effort peaked immediately after the seasonal closure ended and dropped to a very low level by the following December.

Results from night-time research trawls show both spatial and inter-annual differences in species composition and recruitment timing. In January–May 1989 the tiger prawns, *Penaeus esculentus* and *P. semisulcatus* comprised 41.3% and 31.4% respectively of commercial species caught at the Bowen site. At Mackay, 100 km to the south, the catch consisted of 60.3% *P. esculentus* and only 4% *P. semisulcatus*. Banana prawns *P. merguiensis*, were caught at both sites but numbers were highly variable. Western king prawns, *P. latisulcatus*, were most abundant off Mackay. Endeavour prawns *Metapenaeus ensis* and *M. endeavouri* made up the remainder of the catch at both sites.

In 1988/89, *P. esculentus* displayed a single prolonged recruitment apparently peaking in late spring and summer. *P. semisulcatus* appeared to have two recruitment pulses, one in spring and a second in late summer to early autumn. *P. latisulcatus* appeared to have one spring/summer pulse while *P. merguiensis* displayed a number of possible recruitment pulses. In 1989/90, the recruitment pulses of all species appeared to be reduced and delayed.

Von Bertalanffy growth parameters have been estimated for the two tiger prawn species from tagging studies. The pattern of tag recaptures suggest a slow dispersal rather than definite migration of these prawn. The pattern of fishing effort as shown in the research logbooks was relatively even with areas of peak effort matching the areas of highest tag recapture. Further tagging studies of the king and banana stocks are being carried out at present.

Net selection was investigated using the 'alternate haul' method to compare the 39 mm stretch mesh nets used in the research trawls with both a 19 mm mesh and the commercially used 52 mm mesh. A similar technique was used to compare the research beam trawl gear with the industry standard otter board gear.

These data have been used as parameter estimates for a preliminary yield per recruit model of this fishery, described in a companion paper (Dredge and Gribble, 1991).

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LABORATORY VALUATIONS OF THE EFFECT ON THE EASTERN ROCK LOBSTER, *JASUS VERREAUXI* (H. MILNE EDWARDS), OF TAGGING WITH EXTERNAL OR INTERNAL TAGS OR MARKINGS

Three types of anchor tag (toggle, T-anchor and dart) and a mark (V notch in the right uropod) were assessed under controlled conditions for the effects of tagging on the mortality in eastern rock lobsters (*Jasus verreauxi*). In each of six pens in a 1 x 10^6L pool were five lobsters (75–120mm C.L.) from each sex chosen at random. An equal number of untreated lobsters were placed in two remaining pens. After 84 weeks the experiment was terminated. The null hypothesis that there was no difference between treatments in lobster mortality or tag and mark loss was tested using the χ^2 test. We found no difference in mortality between lobsters that were tagged or marked. The mortality among untagged control lobsters was greater however than that of the tagged or marked lobsters. There were no differences between external tag types in the number of tagged lobsters that lost their tag. None of the marked lobsters lost their mark. We found no differences in apparent mortality (mortality plus tag loss) between lobsters tagged with different types of external tags. The apparent mortality among marked lobsters was less than that among those tagged with external tags.

In another experiment in the same pool, 40 lobsters, chosen at random were tagged with visual implant tags and placed in a pen adjacent to one containing an equal number of untagged controls. The experiment was terminated after 48 weeks. The null hypothesis that there was no difference in mortality between lobsters tagged with visual implant tags or untagged controls was tested using the χ^2 test. No differences in mortality between tagged and untagged lobsters were found. However, 43% of the tagged lobsters lost their tag.

We concluded that no one type of external tag tested was better than the others. In a field marking experiment we would expect a greater proportion of lobsters to survive and retain their mark up to 84 weeks than if a similar experiment were done using the types of external tag tested in our experiment. The visual implant tag has potential especially for experiments under controlled conditions. However, tagging techniques need to be improved so that the rate of tag loss can be reduced.

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RECRUITMENT AND STOCK ENHANCEMENT OF THE CHINESE SHRIMP, *PENAEUS ORIENTALIS* KISHINOUYE (DECAPODA, CRUSTACEA)

Hatchery reared juvenile Chinese shrimp, *Penaeus orientalis*, have been restocked into Chinese coastal waters since the early 1980s so as to increase natural stocks. Surveys of the physico-chemical and biological environments have been conducted, to take advantage of natural productivity and resources. The data obtained from Jiaozhou Bay area in the Yellow Sea during 1981–1988 indicated that the released shrimp grew quickly, migrated out of the Bay to the shallow open sea, and could thus be fished during the autumn shrimping season before the start of the over-wintering migration to the deeper part of southern Yellow Sea.

The recruitment of the Chinese shrimp in the Yellow Sea is unimodal (in contrast with multimodality of tropical species) and occurs from June to September with a peak in July and August. The recruitment in July constitutes over 40–50% of the annual recruitment. The total number of shrimp estimated using ELEFAN (Electronic Length Frequency Analysis) for August of 1981–1988 was indicative of the annual stock size and might be used to evaluate and predict the effects of our restocking experiments. The stock size of the shrimp in the Bay was increased to more than 25,000 (41,500 in 1985) for years of commercial restocking (Table 1), which was about 4.5 times the maximum stock size estimated for non-stocking years (1981). The success of the releasing experiments is also reflected in the 2–4 fold increase of local shrimp catch compated with 1981.

The average survival rate of the released juvenile shrimp was estimated between 32.0–35.6%. Based on these figures and data on biological productivity and availability of natural food organisms (mainly benthic animals), the authors recommend that 70–100 x 10^6 juvenile shrimp be released for Jiaozhou Bay area.

Juvenile shrimp have been released in different parts of northern, eastern and southern China Sea based on the findings of these and other similar experiments. To date promising results have been achieved from these stockings.

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TABLE 1. Density and stock size of *Penaeus orientalis* in Jiaozhu Bay in August 1981–1988

Year	Commercial release (10^3 ind.)	Experimental release (10^3 ind.)	Average density (ind km^{-2})	Stock size (10^3 ind.)	Stock size (10^3 kg)	Total Qingadao catch (ton)
1981	0	0	14,110	5,644	225.8	300
1982	0	0	1,335	534	21.4	–
1983	0	280	8,396	3,385	134.3	–
1984	37,000	2,500	66,209	26,484	741.6	640
1985	120,000	7,000	103,716	41,486	1,161.6	900
1986	200,00	47	75,725	30,290	848.1	1,140
1987	0	14	5,181	2,072	58.0	50
1988	180,000	18	63,125	25,249	707.0	840

EFFECT OF DIETARY PROTEIN ON SEXUAL MATURITY AND EGG PRODUCTION IN THE ECONOMICALLY IMPORTANT RIVERINE PRAWN, *MACROBRACHIUM NOBILII*

The effect of dietary protein on sexual maturity and egg production was studied by feeding juvenile *M. nobilii* on one or the other of five isocaloric diets containing 10, 15, 25, 35 or 50% protein for a maximum period of 460 days. The juveniles attained sexual maturity on attaining a body weight of 600 mg after 321, 280 and 240 days, when fed on 15, 25, 35 and 50% protein diet, respectively. Thus the high protein diets (>35%) advanced the onset of maturation. Those fed the 10% protein diet died before reaching sexual maturity. The interspawning period was 45, 33, 24 or 21 days when the prawns were fed with 15, 25, 35, or 50% protein diet respectively. During the experimental period, prawns fed a high protein diet underwent 8 adult moults, carried 5 clutches and produced an average of 4375 eggs, compared to 5 adult moults, 3 clutches and production of 2088 eggs by the group fed on 15% protein diet. Energy content of the eggs produced by the groups fed >35% protein diet was 0.76 J/egg, which is significantly more than that (0.69 J/egg) spawned by the prawns fed on the 15% protein diet.

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CONSEQUENCES OF THE MORTALITY OF DISCARDED SPANNER CRABS (*RANINA RANINA*) IN A TANGLE-NET FISHERY — LABORATORY AND FIELD EXPERIMENTS

In response to evidence of decreasing catch rates, the effects of disentanglement from commercial tangle-traps on the mortality of undersize, discarded spanner crabs, *Ranina ranina* (Linnaeus), was examined for a fishery in New South Wales, Australia. Firstly, the amount of damage sustained by discarded crabs was quantified. Three main methods of disentanglement were used by commercial fishermen: careful removal, causing no damage; quick removal, where any entangled dactyli are broken off (average 3.95 dactyli per crab); and the fastest method whereby crabs are pulled off and entangled limbs and dactyli are broken off (average 2.9 dactyli and 0.8 limbs per crab). The effects of these various kinds of limb damage on the mortality of undersize *R. ranina* were tested in an aquarium experiment in which replicate crabs were damaged in the ways described above and compared to undamaged controls. In addition, a similar (though shorter-term) experiment was performed in the field using enclosures buried in the substratum near the commercial fishing grounds.

The results showed quite significant rates of mortality due to disentanglement: 60–70% of crabs with one or more dactyli removed died within 50 days, whilst 100% of crabs which lost whole limbs (after being pulled off nets) died after 8 days. The data also show that 75% of crabs that are caught by commercial tangle traps are less than the minimum legal size, and that sexual dimorphism in this species means that 85% of females are smaller than this legal size.

The results have implications on the effect of this mortality on subsequent exploitable stocks, the fecundity of the population, the usefulness of current size restrictions and the need for a better method of capture.

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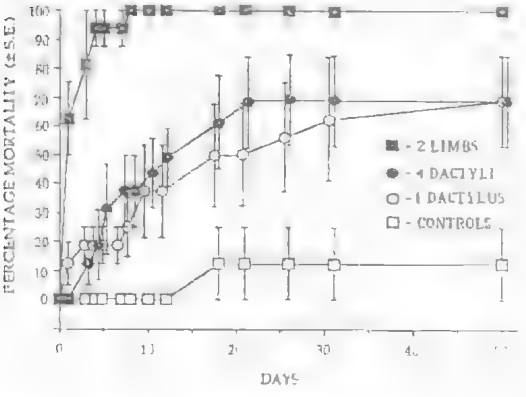

FIG. 1. Mortality of damaged spanner crabs in aquaria.

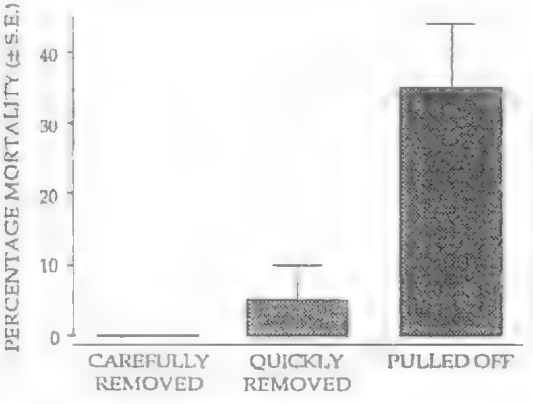

FIG. 2. Mortality of damaged spanner crabs in the field over 24 hours.

ALTERNATIVE AERATION SYSTEM FOR INTENSIVE PRAWN PONDS

An alternative aeration system was designed and used for intensive prawn production in the Southern Philippines. Four ponds were used for two crops with a stocking density of 23–39 post-larvae per sq.m. Dissolved oxygen, salinity and temperature were monitored. D.O. fluctuated from 3.5–10 ppm; salinity from 15–25 ppt; and temperature from a minimum of 27°C to a maximum of 32°C. Readings on nitrates, H_2S and ammonia were not taken. Survival rates after 130 days of culture for pond No. 2 were 79% (first cropping) and 85% (second cropping). Pond No. 1 had low survival rates due to the failure of the blower (human error) to operate at the scheduled time.

Artificial aeration such as the Air-lift System appears to be feasible in high intensive prawn farming. The cost of installation and maintenance appear to be the key to its adoption.

The results of the two croppings in each pond showed that this artificial aeration system working hand in hand with a good water system, will give good harvest results. The system appears to be able to maintain a D.O. level above the 4 ppm needed for ideal rearing.

Considering the cost of materials, energy (power) consumption, maintenance and acquisition costs of major equipment, this alternative has great potential for larger scale application in the aquaculture industry.

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THE LARVATRON: A COMPUTER CONTROLLED APPARATUS FOR REARING PLANKTONIC ANIMALS

Traditionally, workers studying the physical and biological requirements of planktonic animals have used manual methods for feeding the animals and maintaining the specific experimental conditions in each container (Kuban *et al.*, 1985; Diaz, 1987). However when factorial experiments are involved, with large numbers of experimental conditions, there are many problems with this approach. Changing the water, monitoring, and adding food, is labour intensive, and this limits the feasible size of the experiment. There may be gradients in temperature or light intensity within environmental cabinets or water baths, which can cause variation in growth and survival of the experimental animals. Manual handling during water changes may injure some animals and contribute to variation in results. For these reasons, experimental results can be variable and difficult to repeat (Wilkenfeld *et al.*, 1983). Therefore we have developed a method of automating the ongoing maintenance of larval cultures used in large-scale factorial experiments. The new system has the following advantages: minimal labor requirements, no variability due to manual handling; no position effects; and complete flexibility in experimental design, since the treatments are specified only by software.

All operations of the Larvatron are controlled by a personal computer. The rearing vessels travel around a circular track, driven by an electric motor. One tenth of the culture medium in each vessel is withdrawn and replaced on each circuit. Experimental conditions in each rearing vessel are defined in a computer file and the culture medium is made up as it is required for each rearing vessel, with the appropriate salinity, temperature and food concentration. Extensive monitoring and error-checking procedures are included in the computer software. This prototype was tested in two experiments studying growth and survival of penaeid larvae, while salinity, temperature, food density and larval density were varied. In favourable experimental conditions, survival to Mysis I was greater than 80%. In general, variation between replicates of a treatment was low and significant differences between treatments were evident.

Now that the prototype has been tested successfully, we have commenced construction of a full-scale version of the Larvatron, capable of handling 200 experimental culture vessels.

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DEEPWATER FISHERY FOR PRAWNS AND CARIDS OFF WESTERN AUSTRALIA

Deepwater prawns and carids have been fished commercially on the continental slope off northwestern Australia since 1985. The fishery operates by licence under a Commonwealth Development Plan. Operating from Port Hedland and Broome, the fishery (area 490,000 km^2) includes the waters from the 200 m isobath to the outer Australian Fishing Zone. Fishing is by demersal trawlers, with greatest catches in the 400–450 m depth range. Two species of carids and four species of penaeids are caught, totalling 850 t in the 1987/88 logbook year.

The red prawn, *Aristaeomorpha foliacea* (Decapoda: Aristeidae), dominates the catch in weight and commercial value. In 1987/88, 420 t of this species were caught; catch rates were usually between 25 and 75 kg hr^{-1}. *A. foliacea* is caught in a limited area south of Rowley Shoals, in large daytime aggregations. The size composition of the catch is being studied to determine growth rate and life span. Males have a petasma which is recognised at >17 mm carapace length (CL); development of sperm ducts occurs at >21 mm CL. Female reproductive maturity is marked by the presence of a sperm plug (at >26 mm CL) and the caudal extension of the ovarian lobes. Males in reproductive condition and females with sperm plugs are present throughout the year. The size-distribution of males is unimodal; that of females is polymodal, with at least three recognisable year-classes. Females usually outnumber males in samples and at sizes >40 mm CL, females dominate the catch.

Other commercial species are distributed over a greater geographical area than *A. foliacea*; these include *Aristeus virilis* and *Plesiopenaeus edwardsianus* (Aristeidae), *Penaeopsis eduardoi* (Penaeidae), *Haliporoides sibogae australis* (Solenoceridae) and the carid species *Heterocarpus sibogae* and *Heterocarpus woodmasoni* (Pandalidae).

Deepwater prawn fisheries in other parts of the world use baited traps (e.g. tropical Pacific Islands) and trawl nets (e.g. off Spain, north-west Africa, Italy, and south-west India). By comparison with these fisheries, the slope of northwestern Australia provides favourable catch rates and a variety of commercial crustacean species.

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A CALANOID COPEPOD FOR INTENSIVE CULTIVATION

Reliable provision of suitable food for larvae has been an obstacle to successful cultivation of many marine fish species (Kahan *et al.*, 1981/82; Bromage *et al.*, 1988). Small fish larvae require food which, as well as being nutritionally adequate and of appropriate size, elicits a feeding response by its active movement. Artificial foods do not, at present, meet all of these criteria (Wanatabe 1988). Nauplii of *Artemia* and some species of rotifers are used as live food items but copepods, especially copepod nauplii, may be more suitable for very small fish larvae. Copepods are probably important natural food items for many fish, they are naturally rich in essential fatty acids (Stottrup *et al.*, 1986) and are abundant in many parts of the sea. Although cultivation of marine copepods has been successfully achieved (Klein Breteler and Gonzalez, 1986) the animals are not widely available at low cost. Our work with *Gladioferens imparipes* suggests that this species is ideal for intensive low cost cultivation. Animals can be made available as live food, as ecotoxicological test organisms or for research. This contribution describes those aspects of the biology of *G. imparipes* which makes the animal suitable as live food in aquaculture.

Gladioferens imparipes is physiologically robust. Populations occur in estuaries of southwestern Australia which are characterized by marked seasonal changes in salinity and conspicuous vertical salinity discontinuities. Vigorous populations can occur both at low salinity (2 ppt) and in hypersaline conditions (38 ppt.) and in the full range of temperatures (12–28°C) which occur in these estuaries. In culturing these animals, there is no need to maintain physical conditions within close limits. We have deliberately changed the salinity of our cultures from 35 ppt to 5 ppt to rid the cultures of harpacticoid copepods and we regularly separate *G. imparipes* from other estuarine fauna by exploiting this tolerance of rapid salinity change.

G. imparipes feeds by filtering phytoplankton from water. In their natural estuarine habitat dense populations of the copepod follow high phytoplankton productivity when the seasonal run off ceases. In the laboratory, our copepod cultures have thrived on various small phytoplankton species which are easily maintained. We have successfully used strains of *Isochrysis* sp., *Pavlova* sp., *Phaeodactylum tricornutum* and several unidentified estuarine species as food. Dense copepod cultures rapidly clear algal cells from the water and cultures thrive if algae are added twice daily at densities such that water is cleared in a few hours and few old algal cells remain to contribute to reduction of water quality. *G. imparipes* is capable of rapid population growth. This is typical of ecological pioneer species which exploit newly available resources. At 22°C, females are able to reproduce *c.* 14 days after hatching. They then produce egg masses of 25–45 eggs at intervals of 2–4 days. Reproductive activity is affected by temperature and food availability, both of which can be easily manipulated in the laboratory.

G. imparipes have been maintained in our laboratory through 28 generations in 18 months. Comparisons between animals bred for 18 generations in the laboratory and first generation laboratory animals showed no diminution of reproductive activity but a slight reduction in age at maturity for the 18th generation animals.

G. imparipes eggs are carried by females until nauplii hatch. An egg carrying female presents both a conspicuous visual target and a valuable food item to a predator. For animals in cultivation, we have developed a quick method for determining whether a population is reproducing to capacity. An index of fecundity is obtained by examining about 15 living females and giving each a score based on presence or absence of an egg mass, size of the egg mass and whether or not the uterus is full of eggs. The index of fecundity has been shown to relate closely to the level of food provided and therefore permits us to adjust rations by biological criteria.

G. imparipes nauplii exhibit moderately strong phototactic behaviour. We have designed a trap to regularly remove nauplii from our culture containers. Nauplii are attracted to a point source of light and then removed from the culture by siphon. An arrangement of air lift pumps and time switches permits regular automatic operation of the nauplius trap. We have recorded daily production in excess of 20,000 nauplii from a 15 litre culture.

G. imparipes nauplii have a mean body length of 128.5µm on hatching. They grow through nauplius and copepodite stages to *c.* 800µm metasome length when mature. We have shown that nauplii can be taken as food by Dolphin fish (*Coryphaena hippurus*) and we have grown Sea Horses (*Hippocampus angustus*) from hatching to 40mm using nauplii, then copepodites and adults as food. It is likely that other fish species would grow successfully on the same diet.

G. imparipes is ideally suited for relatively low cost intensive cultivation and may, therefore, be useful in marine fish aquaculture.

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EFFECT OF ESSENTIAL AMINO ACID SUPPLEMENTATION OF CASEIN AND SARDINE POWDER ON THE PROTEIN REQUIREMENTS OF THE PRAWN, *PENAEUS JAPONICUS*

Protein requirements of the prawn *Penaeus japonicus* has been extensively studied using purified diets based on casein (Deshimaru and Yone, 1978; Teshima and Kanazawa, 1984), but little work has been done on the essential amino acid balance required by prawn. Application of information on protein requirements to commercial practice will require an understanding of the effects of amino acid balance in the diet on growth. The present study investigates the effects on prawn growth of supplementing sardine powder and casein with essential amino acids.

Material and Methods

Seven purified diets containing varying levels of sardine powder, casein and crystalline amino acids were prepared. Diet 1 (control) contained 50% casein and a total of 53% amino acid. Diets 2, 3 and 4 contained 40, 35 and 30% casein, and this was adjusted to 50, 45 and 40% total amino acid respectively using essential amino acids. Diets 5, 6 and 7 contained 50, 45 and 40% sardine powder and were adjusted to 50, 45 and 40% total amino acid respectively. Amino acids were added individually to adjust the essential amino acid profile of the diet to that of a standard diet based on the composition of prawn muscle. All diets contained 8% gluten-M and 3% CMC as binders. There were two replicates.

Twenty juvenile prawns of 0.41–0.52g body weight were placed in 30L tanks with a recirculating salt water system. Water was maintained at 25±1°C and aerated continuously. Prawns were fed twice daily with a dry diet at 5–10% of body weight.

Results and Conclusion

Weight gain was increased ($P<0.05$) by supplementing the casein with essential amino acids (0.28g, 0.38g and 0.44g in groups 4, 3 and 2 respectively), and by the lowest level of supplementation of sardine powder (0.36g) (Table 1). With the lower levels of sardine powder weight gain (0.20g) was less than for the control diet (0.27g).

Food efficiency ratio was higher with the high level of amino acid supplemented diets, 0.27 in diet 2 and 0.25 in diets 3 and 5. Results showed a linear increase in the food efficiency ratio with level of total amino acids ($r=0.98$ and 0.97 in casein and sardine powder groups respectively).

Protein efficiency ratios were increased by amino acid supplementation and were higher for diets based on casein (0.44, 0.48, 0.44 in groups 2, 3 and 4) than for those based on sardine powder (0.41, 0.29 and 0.20 in groups 5, 6 and 7).

We conclude that growth was higher on casein than on sardine powder based diets. Addition of essential amino acid to diets containing casein and sardine powder increased the weight gain of prawns. The addition of essential amino acid improved the quality of the diet as measured by the food and protein efficiency ratios.

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TABLE 1. Weight gain, food intake, food efficiency and protein efficiency ratio of the prawn, *Penaeus japonicus* as affected by protein source and essential amino acid level.

Base Protein	Diet Intake (g/prawn)	Increase in Body (g)	Food Efficiency	Protein Efficiency Ratio
Casein				
1(Control)	1.54	0.27	0.17	0.33
2	1.62	0.44	0.27	0.44
3	1.57	0.38	0.25	0.48
4	1.40	0.28	0.20	0.44
Sardine Powder				
5	1.46	0.36	0.25	0.41
6	1.54	0.25	0.16	0.29
7	1.68	0.20	0.12	0.20

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ASPECTS OF THE BIOLOGY OF COMMERCIAL PENAEID PRAWNS IN TORRES STRAIT

The Torres Strait Project, which is funded by the Queensland state government, was initiated in July 1985 to investigate the movement and distribution of the commercial prawn species in Torres Strait and to assess seasonal and area closures to ensure that they are being applied in the most effective way. The findings of the research project are of international importance as the Torres Strait prawn fishery is jointly fished and managed by Australia and Papua New Guinea.

Data from monthly otter and beam trawl samples taken between January 1986 and December 1989, and prawn tagging, are being used to investigate the life cycles of the brown tiger (*P. esculentus*), endeavour (*M. endeavouri*) and red spot king (*P. longistylus*) prawns in Torres Strait. Due to tidal constraints in Torres Strait it was necessary to use a daytime water jet beam trawl to sample the seagrass nursery areas on the Warrior Reefs.

An unusual feature of the Torres Strait prawn fishery is that the juvenile seagrass nurseries are located on coral reef platforms (mainly the Warrior Reefs) rather than coastal estuarine mud-flats.

Data indicate that brown tiger prawns move off the seagrass nurseries on the Warrior Reefs into the shallow silty waters to the west of the reefs, at a very small size, then grow and migrate from the closed area west of the Warrior Reefs, eastward into the fishery.

Spawning in brown tiger prawns in Torres Strait occurs year round with three distinct peaks of activity that vary considerably in intensity and duration between years. The yearly spawning pattern produces a series of age classes within each year that results in a complex pattern of recruitment into the fishery. Due to the complexity of the recruitment pattern it is difficult to set an optimal seasonal closure period. As the fishing fleet is highly mobile, a difference in closure timing to that in other areas could result in an extreme 'pulse fishing' effect that may negate any beneficial effect of the closure.

Industry believes that the seasonal closure in Torres Strait opened too late this year thus missing the main recruitment into the fishery. Catches have been much lower than usual this year. Brown tiger prawns tagged in a closed area to the west of the fishery, moved to the eastern side of the fishery before being recaptured. This indicates that the season may have opened later than the optimal time to harvest that particular pulse of recruiting prawns.

Data indicate that areas with high densities of undersized prawns are restricted to the western side of the fishery so an extension of the area closures may be a more appropriate management strategy than a total area seasonal closure. The whole system of area and seasonal closures for both Torres Strait and the east Queensland Coast are currently being reviewed at meetings involving representatives of industry, management and research.

Future research will be aimed at investigating spawning and recruitment patterns of endeavour and red spot king prawns and using fisheries simulation models to assess various closure strategies for the Torres Strait fishery.

The findings of the first three years of the project are detailed in a QDPI Information Series publication, Q190018, titled 'Torres Strait Prawn Project: A Review of research 1986–88'. Editor J.E. Mellors.

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THE FISHERY FOR ANTARCTIC KRILL (*EUPHAUSIA SUPERBA*)

The catch of Antarctic krill in the Southern Ocean in 1989/90 was 395,470 tonnes. This represents 83% by weight of the total catch of all marine species from Antarctic waters; makes the operation for Antarctic krill the world's largest single-species crustacean fishery; and puts the krill harvest among the world's top 30 fisheries by tonnage (FAO 1989).

Antarctic krill are currently being caught predominantly in the Atlantic sector of the Southern Ocean: the Antarctic Peninsula, South Georgia and the South Orkneys but the area of operation of the krill fleets is likely to expand in the near future. Fish are still being caught in the South Georgia, Antarctic Peninsula and Kerguelen Island regions but catches are low (104,405 tonnes in 1989/90) due to over-fishing. The krill fishery has displayed considerable catch fluctuations but is likely to be the mainstay of the Southern Ocean fishery in the foreseeable future.

Estimates of the stock size of Antarctic krill range between 55 and 7000 million tonnes (Miller and Hampton, 1989). The krill population is circumpolar though certain areas are richer in krill than others. Evidence to date suggests that the krill population is not separated into stocks (Fevolden and Schneppenheim, 1989).

The Soviet Union which has more than 100 large (90m+) freezer trawlers operating in the Southern Ocean accounts for 76% of the krill catch. Japan takes 20% of the krill and Poland, S. Korea and Chile are responsible for the other 4%. Some additional countries may enter the fishery if the economic climate becomes favourable.

Antarctic krill is caught in mid-water trawls and processed on board freezer trawlers. Catches of between 3–10 tonnes per hour are aimed for to ensure product quality and to avoid swamping the processing capacity of the vessel. Areas with catch rates of less than 50 tonnes per day are avoided. Krill spoil rapidly because of active proteolytic enzymes and are unfit for human consumption unless processed within 3 hours of capture. After 8 hours they are unfit for use in animal feed. Over 50% of the krill catch is now used for human consumption. Some of the Japanese catch is frozen whole and some is boiled then frozen. Most of the catch is peeled then frozen. Krill shells are extremely rich in fluoride and this migrates out of the shell and into the flesh on death (Christians and Leinemann, 1980). Whole krill have very high fluoride levels because of this — up to 1800 ppm 4 times the EEC allowable limit for animal feed — so peeling is the best approach to obtain a quality product. The yield of tail meat from krill produced by roller peelers is 10–25% of the wet weight of whole krill (Budzinski *et al.*, 1985). Meal is produced from the excess low-quality krill.

Consideration is being given to processes which can utilise the waste material from the krill fishery. Valuable by-products which could be extracted from krill waste include: carotinoid pigments, chitin, proteolytic enzymes and vitamins. The fishery is currently only marginally economic and the extraction of high value chemicals from krill waste may increase the worth of the krill catch and encourage new entrants to the fishery (Nicol, 1989).

Exploitation of the resources of the Southern Ocean is controlled by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) which meets annually in Hobart, Tasmania. Its 20 members include all the nations involved in fishing in the Southern Ocean and all the Antarctic treaty signatories. CCAMLR first met in 1982 but it was not until the 1989 meeting of CCAMLR that management of the krill fishery made it onto the agenda. Management of the krill fishery is necessary since krill occupy the pivotal role in the Antarctic ecosystem and over-exploitation could have disastrous results. The information required to scientifically manage the krill harvest is not yet available. In the absence of such information it should still be possible to protect krill and their predators by introducing interim catch limits. At present these limits could be set high enough that the fishing nations would have considerable room for expansion yet low enough that the Southern Ocean ecosystem would remain undamaged. Whether krill can be the first successfully managed fishery resource in the Southern Ocean will depend on the negotiations over management plans that take place over the next few years.

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AN ALTERNATIVE STOCK MANAGEMENT FOR SNOW CRAB, *CHIONOECETES OPILIO* (BRACHYURA, MAJIDAE), BASED ON THE PRESENCE OF A TERMINAL MOULT

The snow crab, *Chionoecetes opilio*, is the most important commercial crab in Canada. In the southern Gulf of St Lawrence, the landings decreased drastically from 32 000 t in 1982 to 7880 t in 1989, at which point the fishery was prematurely closed due to a high incidence of newly moulted 'white' crabs in the commercial catch.

The description of a terminal moult in male as well as female crabs (Conan and Comeau, 1986) has generated a new interpretation of the life cycle of the species. This new knowledge has important management implications for rebuilding the commercial potential of the stock.

In the Gulf of St Lawrence, processors rely on hard shell terminal moult males which moulted one year or more prior to the short ten week fishing season. At an early state of exploitation, most individuals captured in the southern Gulf were in the terminal moult phase. The catch resulted from the accumulation of 3 to 4 year classes of the terminal moult crabs. As the fishery developed, old terminal moult males were fished out and the proportion of individuals which had recently moulted immediately prior to the fishing season increased in the commercial catch. These recently recruited (called 'whites' by the fishermen) have a low commercial value and are mostly discarded at sea with a subsequent high fishery induced mortality. The harvest became based almost entirely on annual recruitment of newly moulted terminal moult individuals. Such a catch would have been ultimately of low commercial processing quality and extremely sensitive to annual fluctuations of recruitment.

The newly discovered patterns of life history are now being used for designing management strategies of the fishery. Newly moulted males have no chance to mate before a complete hardening of their carapace. The mating of terminal moult males with hard shell multiparous females takes place shortly after the spring moulting season and at the beginning of the spring and early summer fishing season, therefore only the males which reached the terminal moult one year earlier can mate efficiently. Management strategies were designed for avoiding the harvest of recent moulters. The catch would be optimised both in terms of yield per recruit and quality if only the males which have reached the terminal moult at least 12 months earlier were harvested. This can be achieved either by using traps selectively inaccessible to the less aggressive non terminal moult males, or by introducing a gauge identifying terminal moult males as a function of allometry of their larger claw size respective to carapace size.

Using geostatistical mapping techniques subareas likely to contain high densities of recently moulted males can be identified during a prefishing period survey. The geographic concentrations of recently moulted males frequently differ from the concentrations of hard shell ones and specific zones can be closed selectively prior to the fishing season in order to protect the recent moulters.

In order to rebuild the stock and stabilise the commercial landings, the protection of the annual recruitment of soft shell crabs as well as catch limitations of hard-shell terminal moult crab are required. It appears that an age group reaches the terminal moult over a series of successive years. A major, still unresolved issue is to determine whether a non terminal *C. opilio* will opt for the terminal moult over a moult period. The answer would have major implications for management since many crabs reach terminal moult at a size smaller than the existing minimal legal size.

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