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A Holocene Vegetation Record from Wrights Creek Valley, New South Wales

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Borehole sediments, together with a radiocarbon-dated pollen and charcoal diagram, allow inferences concerning mid and late Holocene vegetational history in the environs of Wrights Creek, part of the Hawkesbury River system. Estuarine mud infilling Wrights Creek Valley was replaced by increasingly freshwater organic deposits from c. 4,000 BP. Prior to this time *Aegiceras* succeeded *Avicennia* in the riparian flora, and after it Poaceae and Cyperaceae came to dominance in valley-floor wetland vegetation that previously had a saltmarsh component. Local geomorphic and sedimentary, or hydrologic factors were probably the most likely cause of these changes. However, the palaeovegetational data hint at a regional fall in relative sea level from a height above that of today. Wet sclerophyll forest, dominated by *Eucalyptus* and *Casuarina*, covered most of the lower valley slopes throughout the period represented, with dry sclerophyll woodland clothing much of the upper slopes and plateau above. Sub-tropical rainforest, now confined to sheltered gullies in the upper part of the valley, was floristically more diverse and widespread prior to 4,000 BP. The expansion of rainforest may have been a response to the combined effects of fire and of a seasonally warmer and annually wetter climate. Its decline could have been associated with a less effective precipitation regime.

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KEYWORDS: Holocene, palaeovegetation, Wrights Creek, New South Wales, pollen, charcoal, wetland, forest, sea level.

INTRODUCTION

This paper is a contribution to a series of studies of Holocene forest and wetland dynamics in the Sydney region (Kodela and Dodson 1988; Jones 1990; Dodson and Thom 1992; Devoy et al. 1994). These studies have had three main aims. Firstly, to establish whether the current diverse and highly endemic sclerophyll flora of this area has existed throughout the last 10 millennia. Secondly, to investigate the former extent of sub-tropical rainforest, now confined to sheltered, mesic sites in this coastal sector of New South Wales. Thirdly, to provide a biostratigraphic basis for the interpretation of relative sea level change, the pattern of which had hitherto been deduced largely from geomorphic and lithostratigraphic evidence in the region.

Previous data from this research indicate that the character of the sclerophyll vegetation has remained largely unaltered during the Holocene, but within the region it is also evident that rainforest has expanded and contracted its distribution over this timespan. Information concerning movements of relative sea level during the Holocene is equivocal. There is support for the hypothesis of Thom and Roy (1983) of a rapid marine transgression in the early Holocene. However, the date of the termination of the rise in relative sea level in this region is controversial, as is the notion of Thom and Roy that since this time a sea surface height equivalent or very close to that of today has persisted (Young et al. 1993).

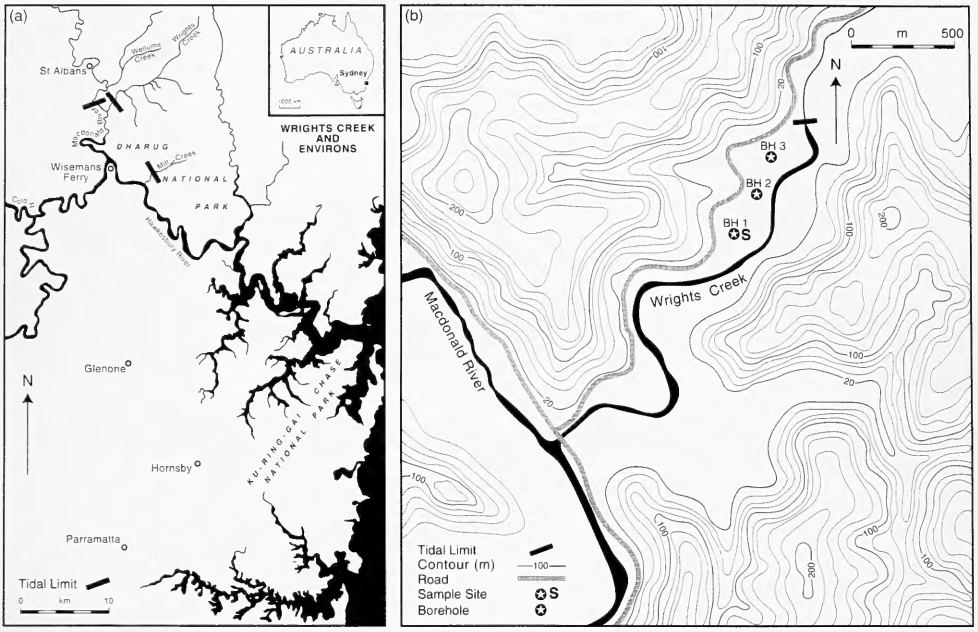


Figure 1. (a) Location of the study area (b) The lower part of Wrights Creek Valley showing the sample site

The main focus of this paper is a mid and late Holocene local vegetation history near the present tidal limit, and its implications for possible climatic and sea level oscillations.

THE STUDY AREA

Wrights Creek is located about 60 km north of metropolitan Sydney. It is a tributary of the Macdonald River, joining this south of St Albans, some 16 km from its confluence with the Hawkesbury River at Wisemans Ferry. The tidal limit of the Macdonald River is just above its junction with Wrights Creek (Fig. 1).

The freshwater to estuarine Hawkesbury catchment is large, deeply incised, tectonically stable and possesses a thick sedimentary sequence (Roy and Thom 1981; Thom and Roy 1985; Devoy et al. 1994). Wrights Creek (Fig. 1b) occupies a small valley which drains about 100 sq km of plateau north of the Hawkesbury River (Figs 1a and 1b). It was mainly excavated during the Tertiary, in sandstones and shales of the Triassic Hawkesbury Sandstone and underlying Narrabeen Group. The former, exposed over 95% of the catchment, is the more resistant. The softer sandstones and shales of the Narrabeen Group outcrop in the deeper valleys. Fluvial incision was also active at times of low sea level in the Pleistocene. Bedrock in the valley is about 20 m below current sea level. Late Pleistocene and Holocene eustatic sea level rise led to the drowning of the valley. In the estuarine environment which developed, a thick sequence of sand and mud was laid down. During the later episode of infilling, estuarine deposits were succeeded by swamp sediments and sandy riverine material. Small alluvial fans at the confluence of tributaries with the valley have been instrumental in impeding drainage and promoting the development of wetland on its floor (Watkins 1982). Soils on Hawkesbury Sandstone are of low fertility. The regolith on moderate inclinations normally has leached soils, while steeper slopes are characterized by heavily eroded regolith and shallow soils. Narrabeen Group sediments typically have clayey and loamy soils of higher fertility and water-holding capacity (Benson 1986).

Climatic statistics for Glenorie (168 m AHD) (Fig. 1a) indicate that mean maximum temperature is 28°C and mean minimum 16°C in January; the July equivalents being 16°C and 5°C respectively. Annual rainfall averages 973 mm, with January receiving most precipitation and September the least (Bureau of Meteorology 1975). As Dodson and Thom (1992) point out, the deeply incised valleys (such as that occupied by Wrights Creek) have a local climate which is more humid than that of the surrounding plateau.

Pidgeon (1937–1941) referred the plant communities of the Hornsby Plateau to a mixed *Eucalyptus* forest association consisting of scrub forests and low scrub in less favourable localities, and of high forest and increasingly mesophytic vegetation in more propitious ones. Beadle (1981) recognized two major types of vegetation on Hawkesbury Sandstone in this area, *Eucalyptus* woodland and forest developed mainly on impoverished soils, and tall *Eucalyptus* forest restricted to soils of higher fertility. Benson (1986) has provided a detailed account of the vegetation in this part of the Sydney region. The Hawkesbury Sandstone plateau has open forest, low woodland and open scrub plant communities which exhibit local floristic and structural characteristics, mainly in response to topography, aspect and drainage. On sheltered hillsides and in shallow valleys, open forest dominated by *Eucalyptus piperita* and *Angophora costata*, with a diverse understorey of sclerophyllous shrubs and a ground cover with numerous graminoids, is typical. Ridges and spurs are usually covered by low woodland in which *Angophora costata*, *A. bakeri, Eucalyptus gummifera, E.eximia, E.haemastoma, E.punctata* and *E.racemosa* are prominent. A diverse shrub understorey accompanies these and includes *Banksia, Hakea, Pultenaea, Dillwynia, Epacris, Leucopogon, Boronia, Eriostemon, Leptospermum* and *Acacia* species. The ground layer is composed mainly of sclerophyllous monocotyledon genera such as *Lomandra, Xanthorrhoea* and *Restio*.

Deeply incised valleys are able to support more mesic, wet sclerophyll vegetation. In this tall open forest *Eucalyptus deanei, E.acmenoides, Angophora floribunda, Syncarpia glomulifera, Acmena smithii, Casuarina torulosa* and *Ficus rubiginosa* are present. *Cyathea australis*, a tree fern, also occurs, as do *Acacia prominens* and *Backhousia myrtifolia*. The ground is covered mainly by ferns such as *Doodia* and *Culcita* (*Calochlaena*), grasses including *Imperata cylindrica* and *Themeda australis*, together with *Lomandra* spp. Associated with wet sclerophyll vegetation, usually in the deepest and most sheltered gullies with a southerly or easterly aspect within the upper part of valleys, is sub-tropical rainforest. It has a patchy distribution, and is of closed canopy type with emergent eucalypts. *Ceratopetalum apetalum, Doryphora sassafras, Acmena smithii* and *Livistonia australis* are its commonest trees, while *Backhousia myrtifolia, Trochocarpa laurina, Tristaniopsis collina* and *Wilkiea huegliana* frequent the tall-shrub component. Climbers, notably *Smilax* and *Cissus*, are characteristic of this forest, which has a ground layer dominated by *Blechnum cartilagineum, Culcita* (*Calochlaena*) *dubia* and *Doodia aspera*.

Wetland vegetation on the valley floor of Wrights Creek in the vicinity of the site investigated is dominated by *Phragmites australis, Juncus kraussii* and Cyperaceae species. *Triglochin procera* and *Sporobolus virginicus* are also present in plant communities which reflect the influence of both fresh and saline water.

METHODOLOGY AND PROBLEMS OF INTERPRETATION OF LITHOSTRATIGRAPHIC AND BIOSTRATIGRAPHIC DATA

Lithostratigraphy and Radiocarbon Dating

A SW–NE transect of three boreholes was made using a 'Russian' pattern hand-operated sampler along about 500 m of swamp, commencing c. 1,500 m from the confluence of Wrights Creek and the Macdonald River. A lack of bench marks in the area did

not allow the precise elevations of the borehole surfaces to be ascertained in relation to AHD. However, as the present tidal limit is some 200 m upstream of BH3, their heights must be close to high-water mark and thus c.+2 m AHD (Fig. 1b). Each borehole revealed a similar gross stratigraphy, which comprises of up to 0.50 m of silty organic mud underlain by highly minerogenic silty clay. The tenacity of the latter prevented penetration below 2.50 m in all boreholes. Samples for pollen and charcoal analysis and radiocarbon dating were obtained from the thickest (hence potentially oldest) sedimentary sequence. This core (BH1), located close to the centre of the 400 m-wide valley floor, was also advantageous in that the contribution of dry-land pollen from vegetation on the nearest parts of the valley sides should have been minimized, and a more representative estimate of the airborne pollen rain from the catchment of the site obtained. A 2 cm thick sample spanning the boundary between the silty organic mud and silty clay gave a radiocarbon age of 3710±110 BP (SUA-2791) (Fig. 2). The organic content of the silty clay was too low to permit radiocarbon assay of a sufficiently thin slice of sediment to give a meaningful age.

Pollen and Charcoal Analysis

Samples of about 1 cm^3 of sediment, taken at 0.10 m intervals throughout the core, were prepared using KOH and HF digestion, and acetolysis (Moore et al. 1991). Known quantities of *Alnus rugosa* pollen were added to the samples in order to obtain concentration (absolute) values for pollen and charcoal. Residues were mounted in silicone oil. Quaternary pollen and spores were abundant and well preserved at almost all levels. Thus in spite of a small component of degraded, reworked Permo-Triassic palynomorphs in a number of samples, significant redeposition of those of Quaternary age (by water as a result of riverbank erosion, for example) seems unlikely. At least 300 grains and spores of terrestrial taxa (excluding exotic pollen) were counted at each level, and formed the sum for the percentage calculations. Charcoal frequencies were obtained using the point count method (Clark 1982). Both percentage and concentration pollen data were obtained. Separate pollen diagrams (Figs 3 and 4) were drawn using the TILIA computer package of E.C. Grimm, Illinois State Museum, and both were zoned independently by

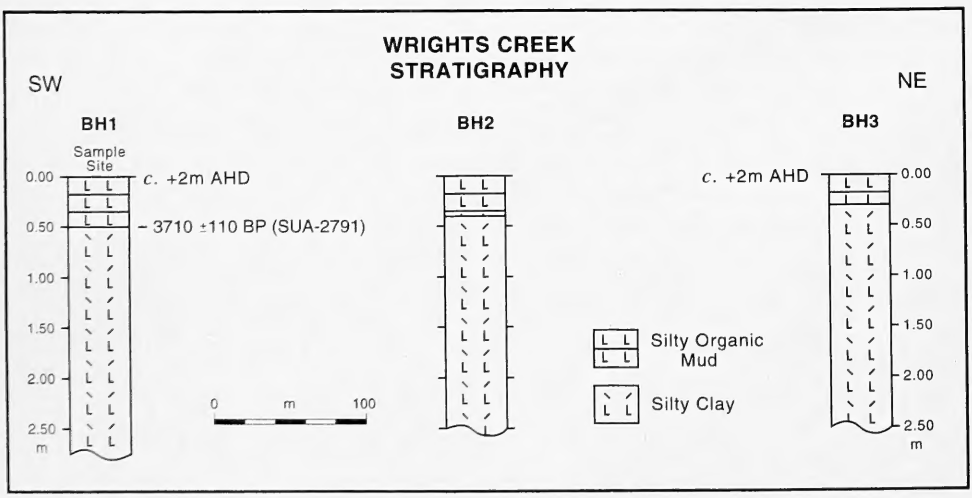


Figure 2. Borehole stratigraphy

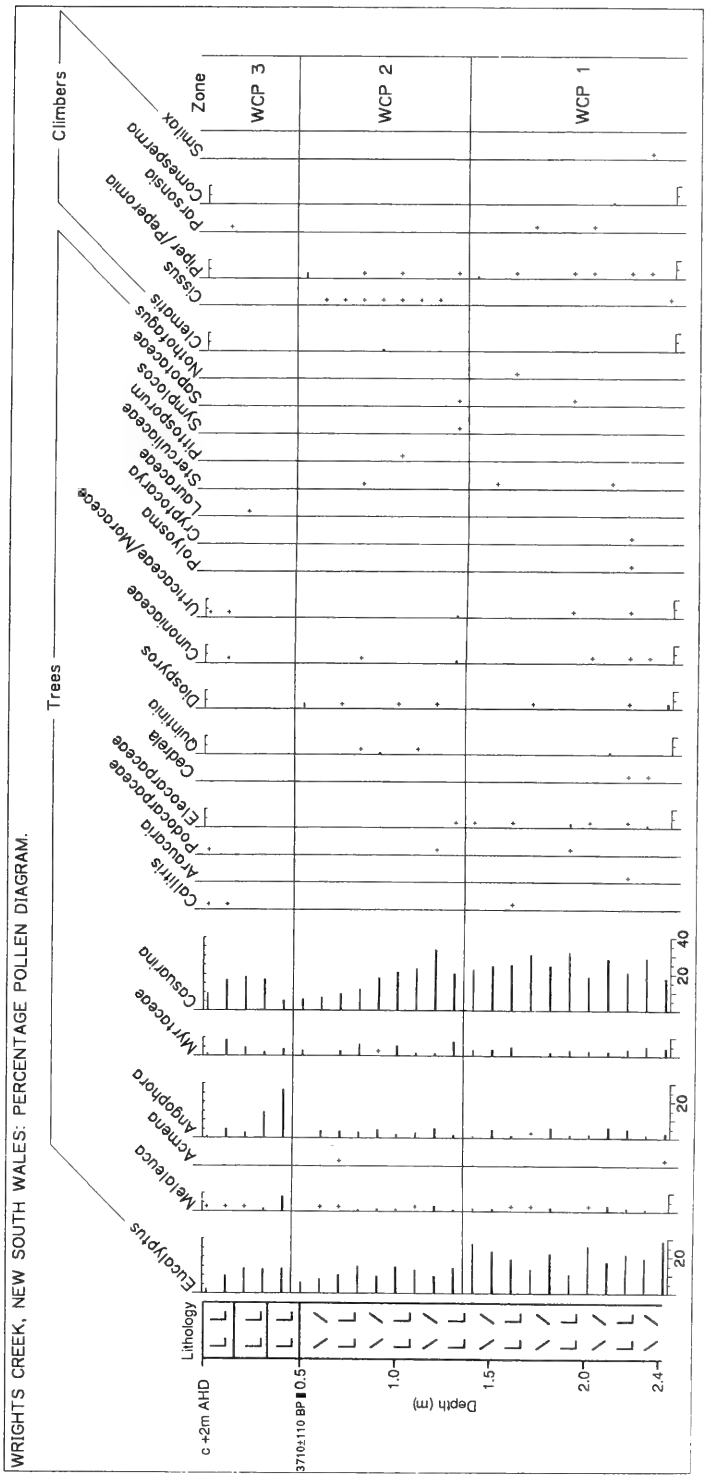
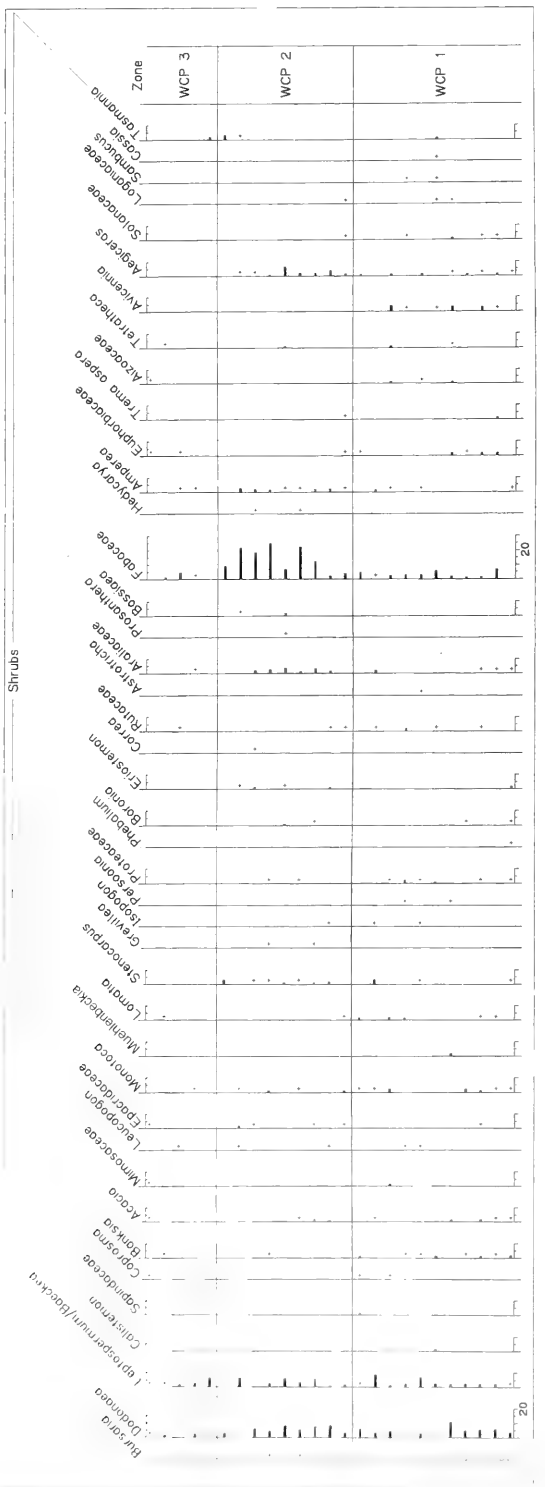
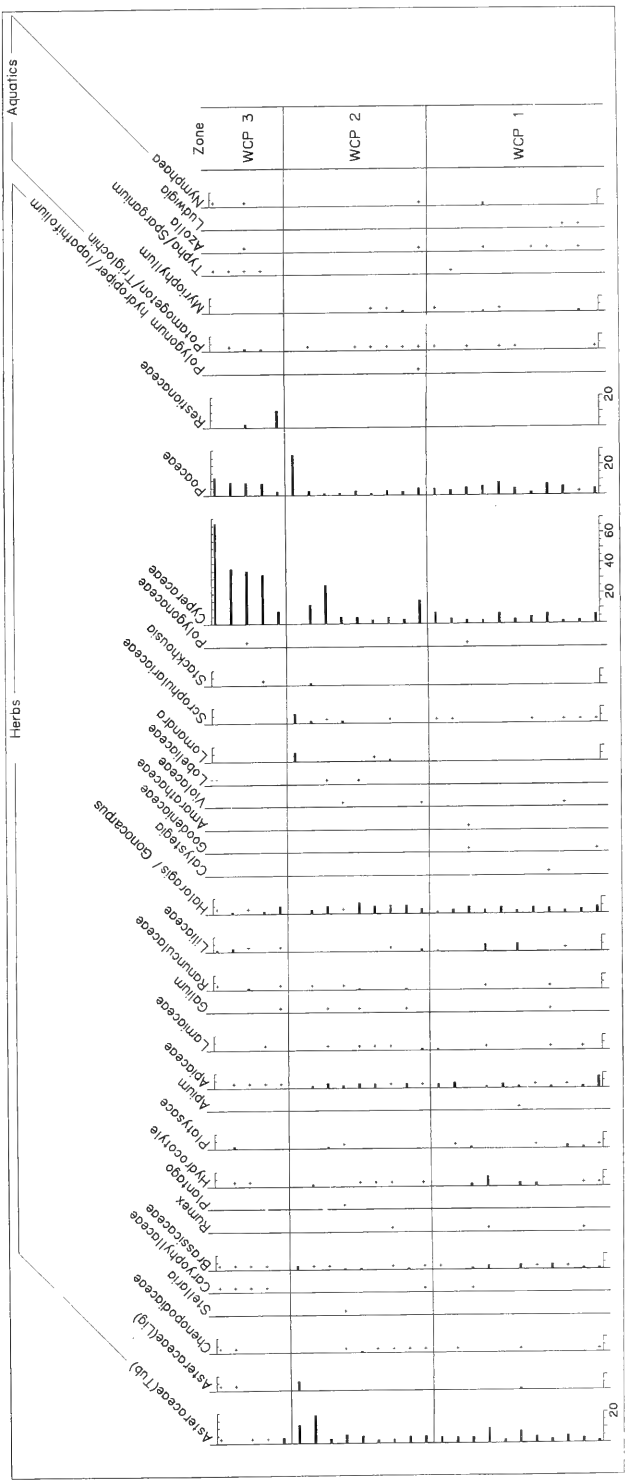
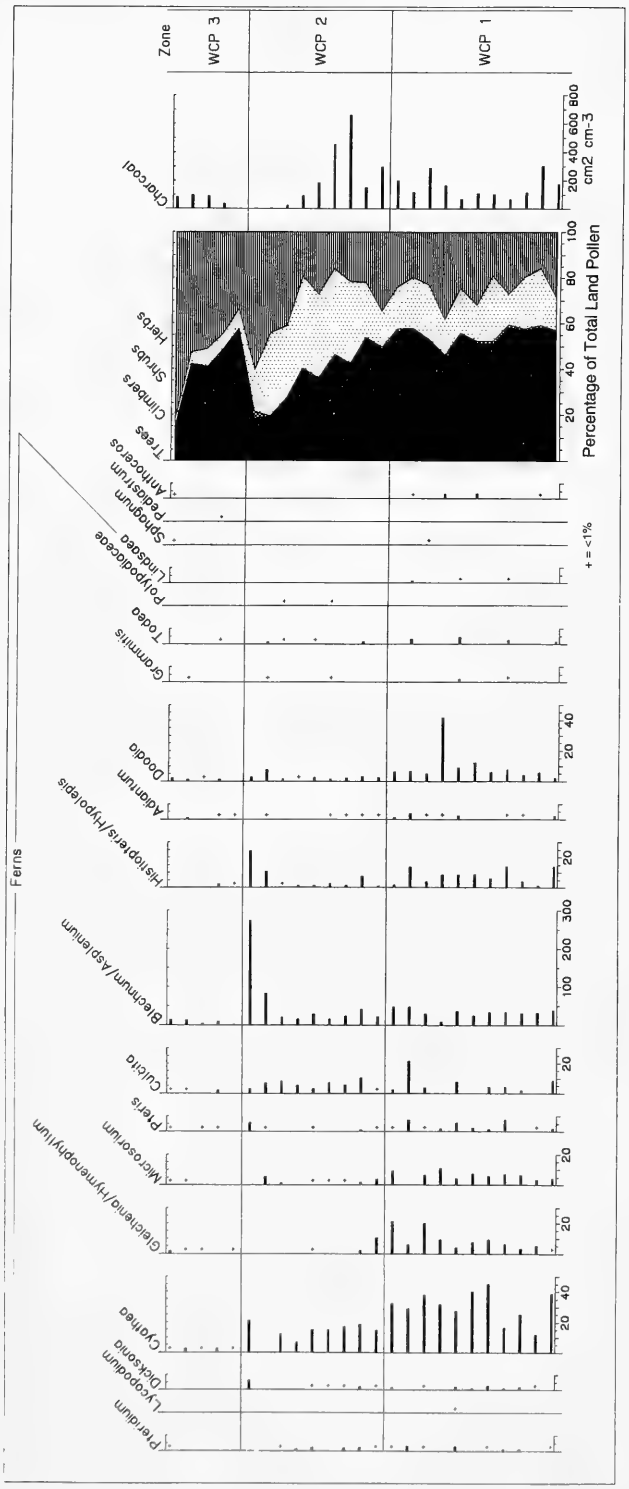


Figure 3. Percentage pollen diagram


Zone
WCP 3
WCP 2
WCP 1
Shrubs
Eucalyptus/Eucalyptus
Callistemon
Sapindaceae
Corrosma
Banksia
Acacia
Myrtaceae
Leucopogon
Ericaceae
Monotoca
Muehlenbeckia
Lomatia
Stenocarpus
Grevillea
Isopogon
Persoonia
Proteaceae
Phebalium
Boronia
Eriostemon
Correa
Rutaceae
Astrotricha
Araliaceae
Prostanthera
Bossiaea
Fabaceae
20
Hibbertia
Amperea
Euphorbiaceae
Trema aspera
Urticaceae
Ficus
Avicennia
Ageratum
Solanaceae
Logania
Santalum
Casuarina
Casuarinaceae
Dodonaea
Blue sedge
20


Aquatics
Herbs
Zone
WCP 3
WCP 2
WCP 1
Asteraceae(Tub)
Asteraceae(Lig)
Chenopodiaceae
Stellaria
Caryophyllaceae
Brassicaceae
Rumex
Plantago
Hydrocotyle
Plotyscce
Apium
Apiaceae
Lomiaceae
Galium
Ranunculaceae
Liliaceae
Hoitorgis / Gonocarpus
Calystegia
Goodeniaceae
Ammannia
Violaceae
Lobeliaceae
Lomandra
Scrophulariaceae
Stackhousia
Polygonaceae
Cyperaceae
Poaceae
Restionaceae
Polygonum
Hydrocotyle / Oppositifolium
Myriophyllum
Typha/Sparganium
Azolla
Ludwigia
Nymphaeae
20
20
20
40
60


Zone
WCP 3
WCP 2
WCP 1
Charcoal
200 400 600 800
cm2 cm-3
Percentage of Total Land Pollen
Trees
Climbers
Shrubs
Herbs
Ammocer-os
Pedicstrum
Sphagnum
Polypodiaceae
Cnidaceae
Todea
Gramnnis
Dodia
Adiantum
Histiopteris/Hypolepis
Blechnum/Asplenium
Cuthra
Pteris
Microsorium
Gleichenia/Hymenophyllum
Cyathea
Dicksonia
Lycopodium
Pteridium
Ferns
+ = <1%

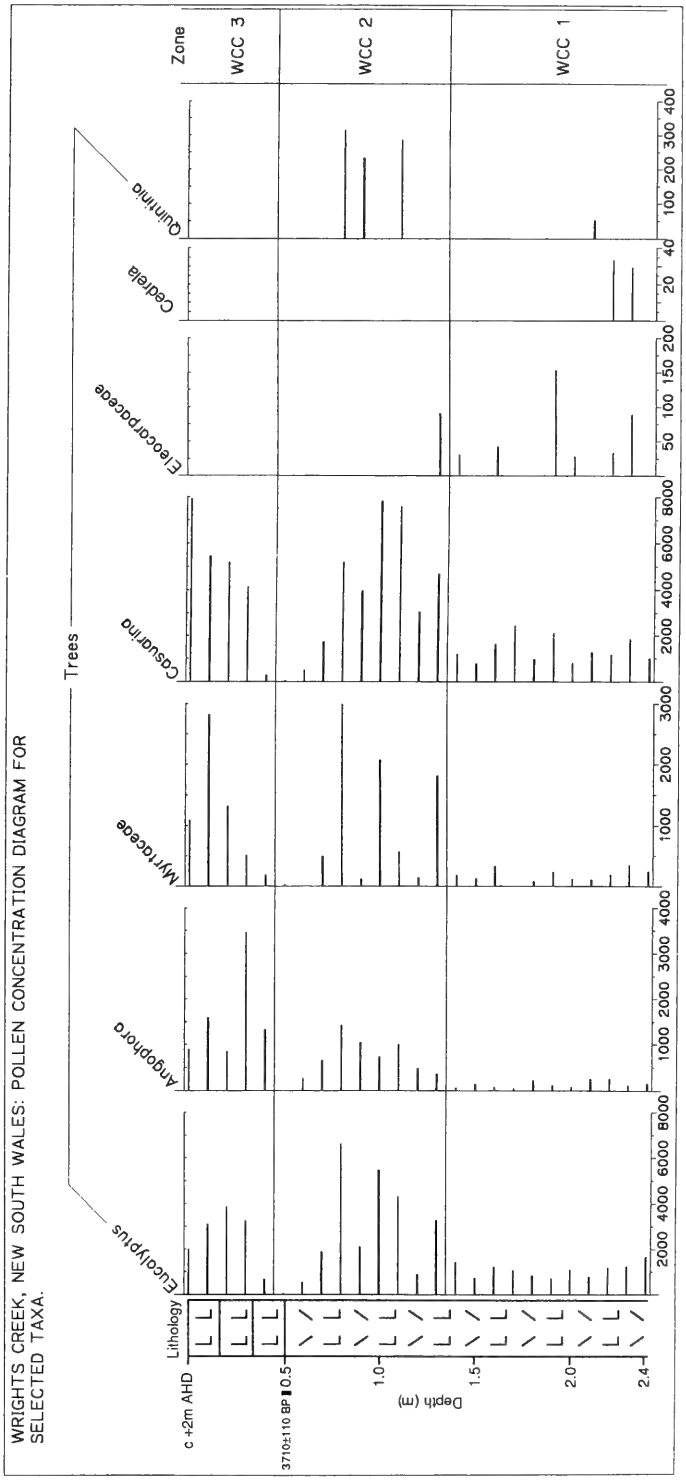
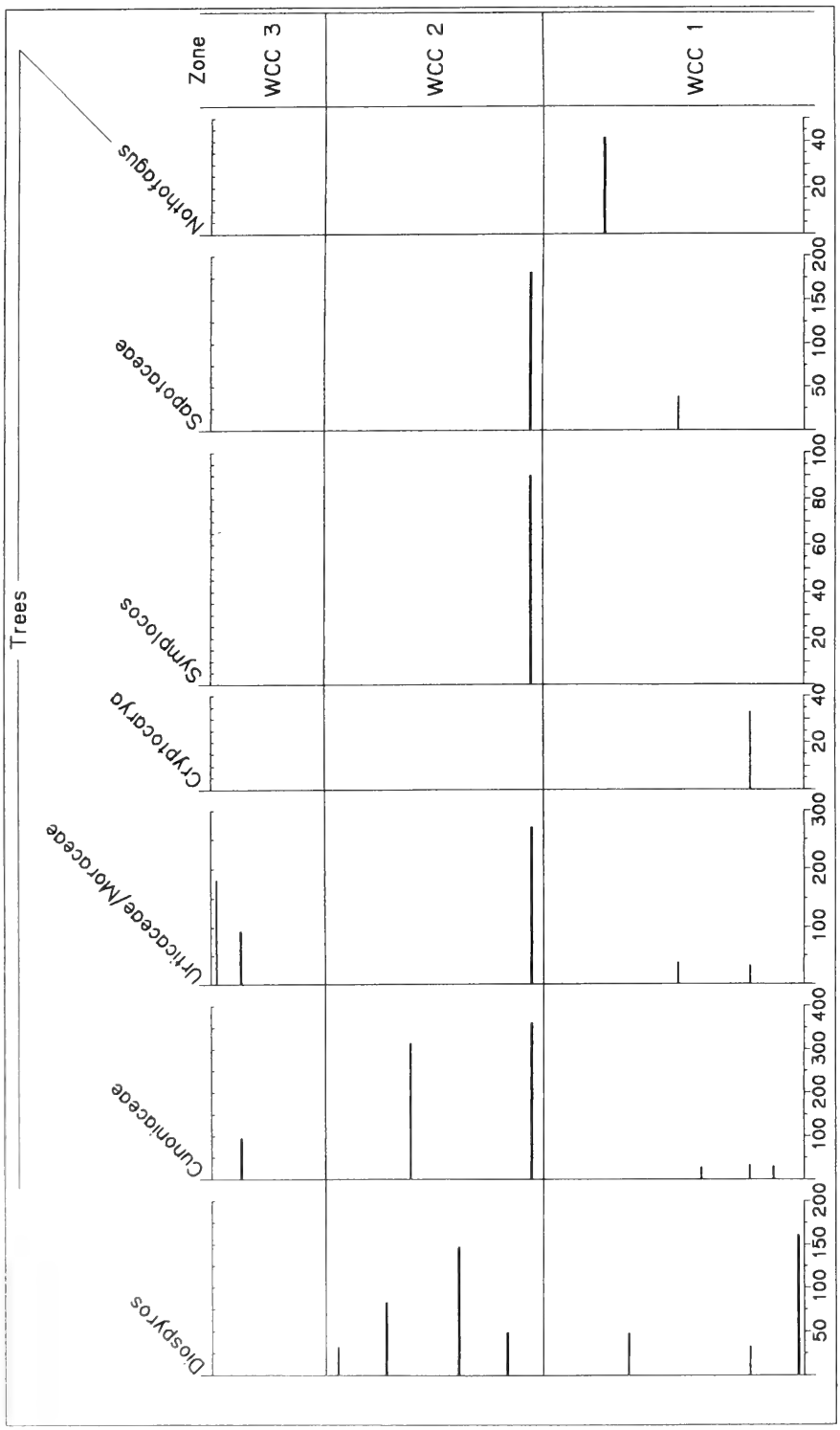
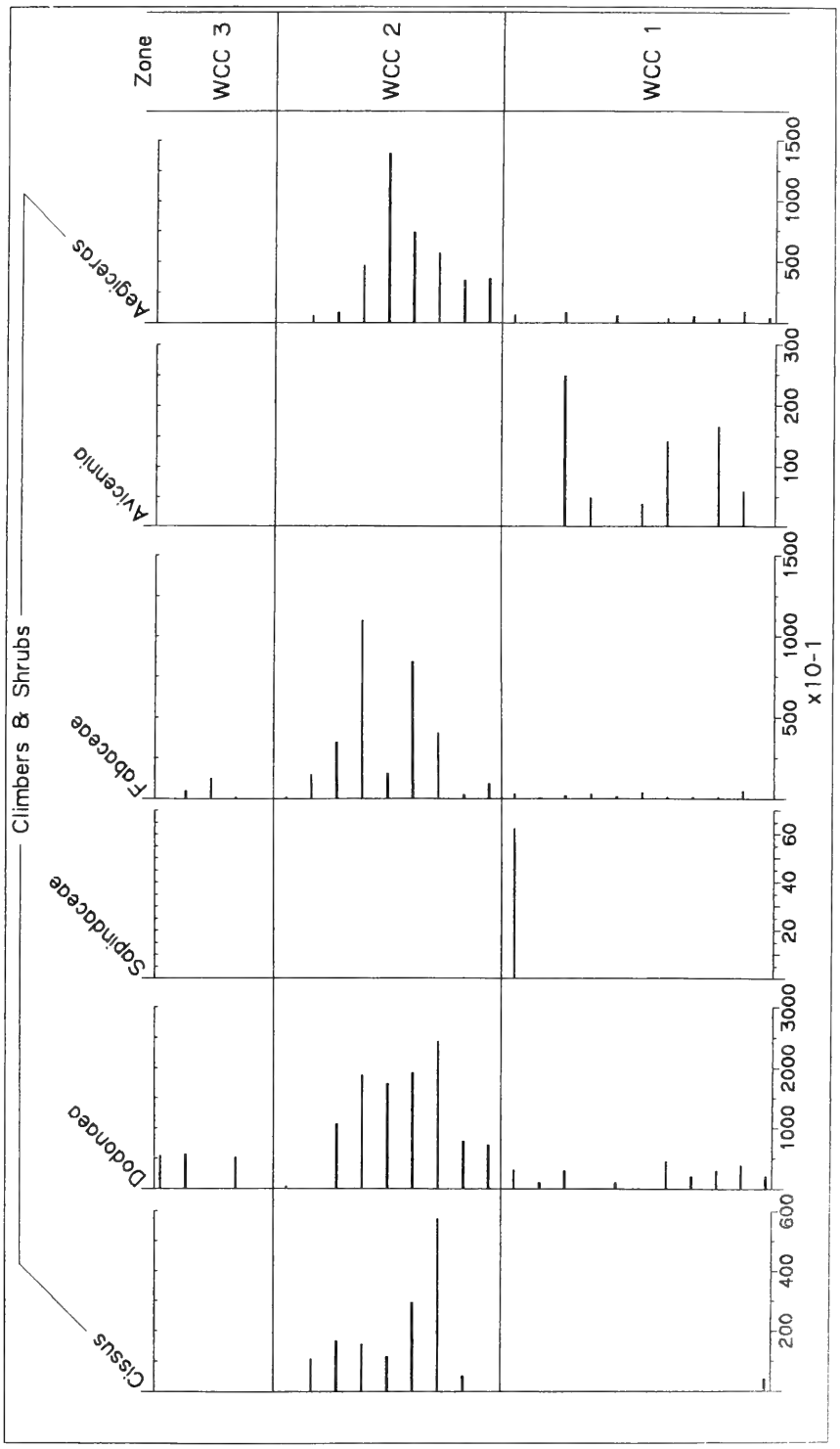
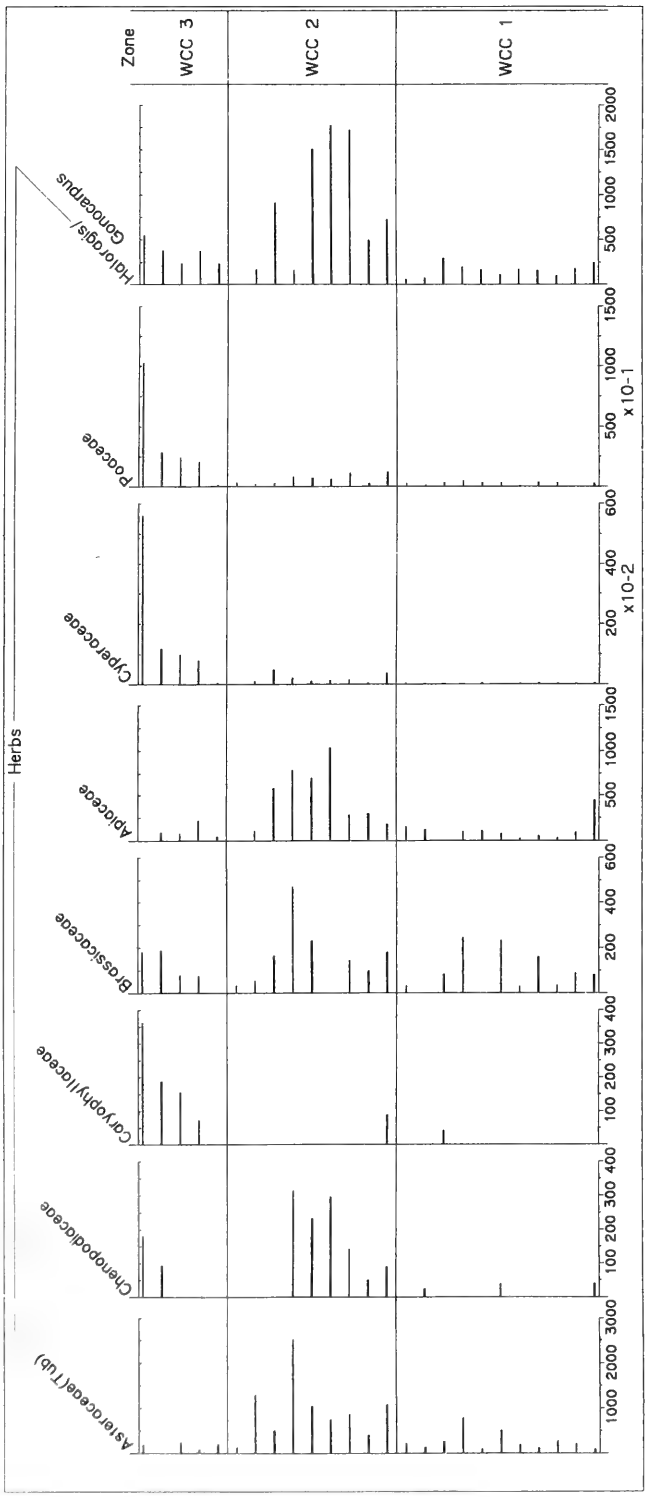
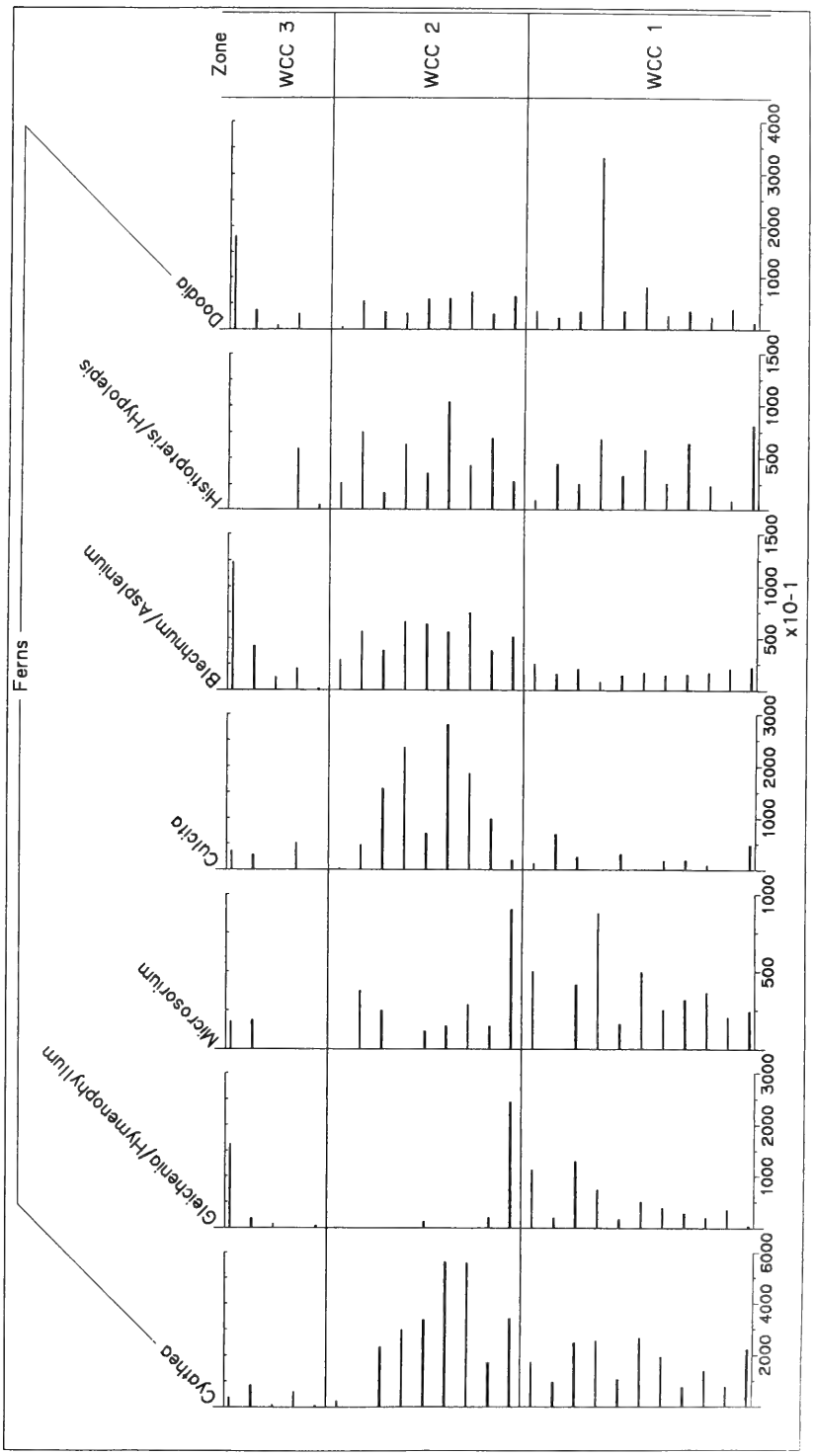


Figure 4. Pollen concentration diagram for selected taxa


Zone
WCC 3
WCC 2
WCC 1
Trees
Nothofagus
Sapotaceae
Symplocos
Cryptocarya
Urticaceae/Moraceae
Cunoniaceae
Diospyros
20 40
50 100 150 200
20 40 60 80 100
20 40
100 200 300
100 200 300 400
50 100 150 200


Climbers & Shrubs
Zone
WCC 3
WCC 2
WCC 1
Aegiceras
Avicennia
Fabaceae
Sapindaceae
Dodonaea
Cissus
500 1000 1500
100 200 300
500 1000 1500
x10-1
20 40 60
1000 2000 3000
200 400 600


Zone
WCC 3
WCC 2
WCC 1
Herbs
Asteraceae(Tub)
Chenopodiaceae
Caryophyllaceae
Brassicaceae
Apiaceae
Cyperaceae
Poaceae
Haloragis/
Gonocarpus
x10-1
x10-2


Zone
WCC 3
WCC 2
WCC 1
Ferns
Doodia
Histiopteris/Hypolepis
Blechnum/Asplenium
Cuicita
Microsorium
Gleichenia/Hymenophyllum
Cyathea
x10-1

eye. The concentration diagram shows only the major taxa germane to the palaeovegetational interpretation. On it, varying scales are used to highlight different concentrations. Each diagram has three assemblage biozones with boundaries located in the same positions. Although there is a considerable degree of consistency in the composition of the percentage and concentration biozones, certain important differences are also evident.

The distribution of present vegetation types and their representation in the surface (modern) sample of the pollen rain (Figs 3 and 4) suggest that plants growing either in the wetland near to the site, or on the adjacent valley sides, were its principal contributors. The results of more extensive surface pollen sample analyses from the Hawkesbury Valley are indicative of analogous circumstances (Dodson and Thom 1992). It thus seems reasonable to assume that the fossil pollen spectra emanated mainly from similar sources. In addition to wind, palynomorph transport in water must have occurred to this riverine locality. Although it is not possible to quantify the relative contribution of each component, that of an aerial nature is likely to have been greatest. The estuarine regime would have lead to both upstream (fresh) and downstream (saline/brackish) waterborne components in the pollen record. The upstream component, from a water catchment of about 100 sq km is therefore likely to have included representatives of the plateau flora. Elements of the vegetation around the fringes of the 40 km of Hawkesbury Estuary seaward of Wrights Creek are probably reflected in the downstream (tidal) component. Moreover, it is clear that certain changes in the pollen record from Wrights Creek Valley are associated with changes in sedimentation, and may be due to a diminution in waterborne pollen in favour of other sources (see below).

DESCRIPTION AND INTERPRETATION OF POLLEN ASSEMBLAGE BIOZONES

WCP 1 and WCC 1

The percentage and concentration data are fairly consistent. *Eucalyptus, Casuarina, Dodonaea, Avicennia* and Fabaceae pollen, and *Cyathea* spores, dominate the spectra. There are also scattered occurrences in low values of Eleocarpaceae, *Cedrela, Quintinia, Diospyros*, Cunoniaceae, Urticaceae/Moraceae, *Polyosma, Cryptocarya*, Sterculiaceae, Sapotaceae and *Nothofagus*. Substantial values of *Gleichenia/ Hymenophyllum, Microsorium, Culcita, Blechnum/Asplenium, Histiopteris/Hypolepis* and *Doodia* occur.

These data allow the inference of a vegetation cover in the environs of Wrights Creek which included a considerable amount of wet sclerophyll forest in the damper areas of the valley sides. In this forest, *Eucalyptus* and *Casuarina* (presumably, as today, *C.torulosa* although its pollen was inseparable from that of *C.glauca*) probably would have been overstorey trees, while *Cyathea* was important in its understorey, where *Dicksonia* also occurred. The ground flora is likely to have contained a large component of ferns. However, it should be noted that fern spores are characteristically over-represented when waterborne and that this method of palynomorph transport was likely to have been important during estuarine sedimentation in Wrights Creek Valley. The Eleocarpaceae–*Nothofagus* group of taxa are indicative of rainforest. Except for *Nothofagus*, a cool-temperate type (whose pollen probably arrived by long-distance transport), these trees are found in sub-tropical rainforest in south-eastern Australia today (Beadle 1981). Investigations by Kodela (1990) have demonstrated that rainforest in the Sydney region at present is characterized by low and intermittent pollen production. Thus rainforest pollen are probably under-represented in fossil spectra. Low frequencies and sporadic occurrences are likely to reflect the continued existence of more than isolated occurrences of rainforest constituents in the vegetation mosaic. Therefore, the implication is of sub-tropical rainforest possibly with a fern-rich ground layer within

the pollen catchment of the sample site. As now, its main development is likely to have been in the most sheltered and mesic locations within the valley, associated with wet sclerophyll forest. Also, a present site for sub-tropical rainforest in this area is alluvial flats flooring sheltered valleys. Here *Cedrela australis, Acmena smithii* and *Cryptocarya glaucescens* are characteristic members of the flora. However, the number of such localities has been much reduced by recent vegetation clearance (Benson 1986). All three trees are present in WCP 1 and WCC 1, and may have been growing in rainforest developed on spreads of alluvium deposited by Wrights Creek. *Smilax* and *Piper/Peperomia*, whose pollen are also present, could have been climbers in either or both wet sclerophyll and rainforest. Today, wet sclerophyll often has rainforest species in its understorey. If this vegetation remains unburnt, it will revert to rainforest (Ashton 1981). It is thus possible that such vegetation change formerly took place in Wright Creek Valley.

While most of the *Eucalyptus* and *Angophora* pollen together with that of other Myrtaceae, *Dodonaea*, Fabaceae and a number of additional shrubs, is likely to have been produced by vegetation on adjacent valley sides, some could have come from sclerophyllous woodland on the drier, more exposed, upper valley slopes and plateau beyond. Dodson (1983) has shown that pollen of many understorey shrubs of sclerophyll forest and woodland in south-eastern Australia are poorly dispersed, and hence are almost certainly under-represented in fossil spectra. As open sclerophyll woodland and forest dominates the plateau in the area today, a similar extensive development of it at this time is envisaged.

Avicennia and *Aegiceras* pollen indicate the growth of mangroves in the local riparian vegetation during the time represented by WCP 1/WCC 1. *Avicennia* pollen is distributed close to its source (Flenley 1979). The river mangrove, *Aegiceras corniculatum* has a low pollen productivity and poor dispersal capacity (M.K. Macphail in litt.). Thus small quantities of its pollen may indicate fairly extensive growth of the plant close to the sample site. Mangroves are intertidal and estuarine in habitat (Adam 1992). Today, *Aegiceras corniculatum* extends further up the Hawkesbury River than the grey mangrove (*Avicennia marina*), the latter having a higher tolerance of salinity (Beadle 1981). Therefore, water of greater salinity than currently reaches the environs of the sample site (where neither mangrove species grows today) is thought to have been present at this time. It should be observed, however, that as mangroves are merely tolerant of saline conditions rather than requiring them, competition is the main determinant of their distribution and that other hypotheses than higher salinity are possible. A component of the herbaceous pollen flora implies the existence of saline-brackish lagoonal and marsh habitats in the valley not far from the sampling point. Certain species of Cyperaceae, Asteraceae (*Cotula*), and Chenopodiaceae now live in maritime saline conditions in this region, and representatives of the latter taxon are currently absent from its other vegetation types. Some Poaceae (notably *Phragmites australis*), *Apium, Potamogeton, Triglochin, Typha, Myriophyllum* and *Hydrocotyle* species can tolerate a brackish environment (Beadle 1981). However, the presence of *Azolla, Nymphaea* and *Ludwigia* confirm the existence too of ponded freshwater and associated wetland nearby. *Gonocarpus* may also have grown in this wetland. It should be noted though that pollen of *Gonocarpus* cannot be separated from that of *Haloragis*, species of which occur in numerous dryland communities in south-eastern Australia (Galbraith 1977).

Today, mangroves are usually found in front of saltmarsh vegetation along estuaries in south-eastern Australia, with alluvial flats landward of the saltmarsh. Stands of *Casuarina glauca* and *Eucalyptus*, together with *Leptospermum* and *Melaleuca*, are typical of such flats (Beadle 1981). Although a relatively narrow valley such as that containing Wrights Creek is unlikely to have developed extensive zones of mangroves, saltmarsh and alluvial-flat forest, they each seem to have been present in its lower reaches, and would have attained greater extent in the nearby and considerably larger valley of the

Macdonald River (Fig. 1b), where these plant communities are present today. The palynological data also suggest that the wetland flora included ferns. Species of *Blechnum, Gleichenia* and *Lindsaea* presently grow in such habitats. However, spores of these taxa are very common constituents of waterborne assemblages (G.S. Hope pers. comm.), and thus may have had an extra-local provenance.

Although the quantification of pollen-slide charcoal provides poor spatial and temporal resolution of fire regimes, it can be useful for demonstrating periods of high versus low fire importance in a single core. Charcoal fragments of the size present on pollen slides will travel a few hundred metres from their source if lifted several metres off the ground. If they reach higher elevations, they do not begin to be deposited until about a kilometre from their source (Clark 1988). Sustained and quite high charcoal concentrations (Fig. 3) thus indicate that substantial burning of vegetation took place during WCP 1/WCC 1. All sclerophyllous forest and woodland in the region is currently particularly prone to fire, and burning is an integral part of wet eucalyptus forest ecosystems, being fostered by dry spells. Burnt stands of wet sclerophyll vegetation are susceptible to invasion and replacement by rainforest species growing nearby within two centuries. The higher the rainfall, the less likely this sequence is to be interrupted by fire (Ashton 1981). The resolution of the pollen samples is not fine enough to allow discrimination between fire regimes which may have either enhanced closed forest succession or supported eucalypt scrub. As burning was likely to have decreased the amount of rainforest, it was probably confined to sclerophyll areas. Rainforest in gullies could have largely escaped burning. Today, gullies are fire shadows. Fires sweep up ridges and over plateaux, jumping over protected gullies where fire-sensitive species may survive in an otherwise fire-prone environment (Ashton 1981).

The age of these pollen spectra is undetermined. However, a radiocarbon date of c. 4,000 BP from organic sediment 1 m higher in the stratigraphy, allied with comparable radiocarbon-dated pollen spectra from the nearby Mill Creek Valley (Dodson and Thom 1992; Devoy et al. 1994) places the events in a mid-Holocene context. No quantitative estimates of former Holocene climates have yet been made for the Sydney region and none are possible from this localized and temporally constrained study. However, fossil pollen data from Victoria indicate an expansion of cool-temperate rainforest 7,000–4,000 BP. A bioclimatic prediction model applied to these data indicates that over this timespan, summer temperatures were about 2°C lower and winter temperatures c. 1C higher than those of today, and that effective precipitation was greater year-round (McKenzie and Busby 1992). Analogous methods have lead to similar predictions of mid Holocene climates in Tasmania (Markgraf et al. 1986) and Queensland (Kershaw and Nix 1988). Fossil pollen evidence from montane southern New South Wales indicates a less continental climate before about 4,000 BP (Martin 1986). If the climate of New South Wales was comparable with that in other areas, it could have favoured rainforest development.

WCP 2 and WCC 2

There is considerably less accord between the percentage and concentration data of these biozones. The percentages indicate reductions in *Eucalyptus, Casuarina, Angophora* and (except in the upper two levels) in ferns. Rainforest elements occur in similar percentages to those of WCP 1. Percentages of *Dodonaea*, Fabaceae and *Aegiceras* are increased, and of herbaceous taxa analogous, to those of WCP 1. The concentrations indicate increases then declines in *Eucalyptus, Angophora, Casuarina* and a number of rainforest trees. Concentrations of *Dodonaea*, Fabaceae and *Aegiceras* exhibit similar trends to their percentages. Increase followed by decline is also characteristic of the concentrations of *Cyathea, Culcita, Blechnum/Asplenium* and *Histiopteris/Hypolepis*. *Microsorium* and *Doodia* concentrations are similar and those of *Gleichenia/Hymenophyllum* reduced, compared with those of WCC 1. Pollen concentrations of the

major herbaceous taxa, and charcoal concentrations (Fig. 3), also rise to a maximum, then fall sharply.

As pollen concentrations are independent for each taxon, they avoid the limitations associated with percentages, and should provide a more reliable estimate of vegetation composition (Birks and Birks 1980). However, pollen concentration values are influenced by factors other than the make-up of plant communities, notably rates of sedimentation. In WCC 2, some taxa have fluctuating concentrations, while others have more consistent ones. The former phenomenon implies that the sedimentation rate may have varied rapidly, the latter that it was either consistent or changing smoothly. Pollen concentration can be enhanced if the rate of deposition of its embedding medium is reduced. Devoy et al. (1994) have demonstrated that sedimentation rates in the Hawkesbury system were reduced during the middle and late Holocene. In Wrights Creek Valley, only 0.50 m of sediment has accumulated during the last 4,000 years. An alternative explanation for fluctuating pollen concentrations may be non-uniform rates of pollen production, perhaps related to climatic variability.

Against such a backdrop, the episode of vegetation development represented in WCP 2/WCC 2 seems initially to have involved the extension of upper estuarine *Casuarina* (presumably, as today, *C.glauca* although its pollen was inseparable from that of *C.torulosa*) dominated swamp-forest on alluvial flats, increased representation of *Angophora*, Myrtaceae, *Dodonaea* and Fabaceae in dry sclerophyll forest and woodland, and further expansion of sub-tropical rainforest at the expense of wet sclerophyll. As noted above, rainforest is today confined to the upper part of the valley occupied by Wrights Creek. While earlier in the Holocene, as now, it was likely to have developed discontinuously and mainly in sheltered gullies, the implication being of an extended distribution down-valley, with alluvial flats bordering the creek perhaps also having more patches of rainforest in their most mesic parts than during WCP 1/WCC 1. The frequencies of *Cyathea* and *Culcita*, in particular, demonstrate the continued importance of both wet sclerophyll and rainforest in the area. Records of *Cissus*, mainly a rainforest climber, are largely confined to WCP 2/WCC 2.

The causes of these trends, which on the basis of the c. 4,000 BP radiocarbon date from the site and comparable pollen data noted above, may have occurred c. 6,000–5,000 BP, could have been similar to those operational during the initial period of the record. Of particular relevance may be a corresponding peak in charcoal frequency (Fig. 3), indicating a heightened regime of burning of sclerophyll. A greater frequency of fires would have led to the extension of the understorey shrub component of open forest on the upper valley slopes and plateau. The decline phase of the trees and shrubs in these trends is not accompanied by high charcoal frequencies. This suggests that burning was probably not the main agent responsible for their demise. A climate shift may offer an alternative explanation. If, as noted above, the climate of New South Wales became more continental c. 4,000 BP, lower quantities of precipitation may have been a contributory factor in the decline of forests requiring substantial amounts of moisture. Interpretation of this event is further complicated because a reduction in burning would encourage the spread of rainforest and wet sclerophyll forest at the expense of woodland and shrubland.

Percentages and concentrations of pollen likely to have come from plant communities closer to the sample site show better accord in WCP 2/WCC 2. Of especial significance may be peaks then declines of *Aegiceras* and Chenopodiaceae. These are likely to reflect the maximum extension, then a reduction, in river mangrove and saltmarsh vegetation. Similar trends in the Asteraceae and Apiaceae records may also relate to these vegetation changes. However, as species from these families occur elsewhere in the region, it is not possible to be certain that they were represented in the saltmarsh flora. The absence of *Avicennia* indicates lower water salinity. Nonetheless, the pollen flora demonstrates the presence of an intertidal environment, where salinity levels at first were greater than those which exist today in that part of Wrights Creek Valley near the sample

site. A further reduction in salinity is first evident just before 4,000 BP. There could have been a number of causes of reduced salinity, acting either individually or in combination. The silty clay below 0.50 m is estuarine. It passes conformably upwards into silty organic mud. Prolonged levee development could have caused areas to be isolated from peak tides. In such areas, more organic paludic sedimentary infill would subsequently have occurred in a mainly freshwater environment. An increased influx of freshwater from the Wrights Creek catchment could also have either initiated or assisted a change from haloseral to hydroseral conditions in this locality. Impeded drainage due to alluvial fan formation in the valley (Watkins 1982) would have enhanced the formation of freshwater wetland. While these events need not have been associated with a fall in relative sea level from a height above that of today, the palaeovegetation record suggests that the latter cannot be excluded as a possible cause of reduced salinity. However, evidence from more sites and firmer dating control are necessary before inferences can be made concerning a regional trend in relative sea level. The peak of *Haloragis/ Gonocarpus* pollen (see above) is interesting. If the pollen is from *Gonocarpus micrantha*, it may have been growing in *Casuarina-Melaleuca* swamp-forest as it does today (Beadle 1981). Its decline late in WCP 2/WCC 2 accompanies that of *Casuarina*, and thus could also signal the decline of upper estuarine swamp-forest in this locality. Its maximum values however, also coincide with the earlier charcoal peak. Therefore, the possibility that this wide-ranging taxon expanded then as a result of burning in dry sclerophyll communities cannot be excluded.

WCP 3 and WCC 3

These biozones exhibit the closest agreement between percentages and concentrations. Among tree and shrub taxa, the main features are a resurgence in *Eucalyptus* and *Casuarina* values, substantial increases in *Angophora* and other Myrtaceae, and a very limited rainforest component (Cunoniaceae, Urticaceae/Moraceae, Lauraceae) with a highly intermittent occurrence. This suggests a revival in wet sclerophyll forest at the expense of rainforest. *Cyathea*, *Culcita* and *Doodia* frequencies rise, supporting this notion. *Angophora* and other myrtaceous trees and shrubs probably achieved greater representation in dry sclerophyll forest on the upper valley slopes and plateau. Charcoal is present and increases in frequency throughout this zone (Fig. 3), but overall quantities of it are lower than in the previous zones. This allows the inference that while fire continued to have a role in plant community dynamics, it was reduced. The most marked and consistent increases in herbaceous taxa are of Cyperaceae, Poaceae, Caryophyllaceae, Brassicaceae, and *Haloragis/Gonocarpus* species. Restionaceae pollen is confined to this zone, as are colonies of the freshwater alga *Pediastrum*. The ferns *Blechnum/Asplenium* and *Gleichenia/Hymenophyllum* rise in frequency. While a number of the herb taxa contain species able to tolerate brackish conditions, and there is little doubt that these continued to exist near to the sample site (as they do over a limited area close to the creek today), the overall impression from the pollen flora is of increased freshwater conditions in a riverine swamp over the last four millennia. Continued effects of one or more of the possible causes discussed in relation to WCP 2/WCC 2 could have accounted for this development.

DISCUSSION

Data comparable with those from Wrights Creek Valley are available at three other localities within the Hawkesbury catchment. The closest palaeovegetation record is that from Mill Creek Valley (Dodson and Thom 1992; Devoy et al. 1994), some 10 km to the south-east (Fig. 1a). A composite radiocarbon-dated sequence from two cores shows that

c. 8,000–2,500 BP, *Eucalyptus* and Casuarinaceae pollen dominates, and there are several rainforest taxa, together with abundant fern spores. The vegetation was dominated by sclerophyll forests. A maximum of rainforest occurred from about 6,000 BP until 2,800 BP. It is possible that an upper estuarine *Casuarina glauca* forest occurred and had declined by around 4,450 BP. Charcoal frequencies are high until c. 2,800 BP, suggesting that fire played an important part in maintaining the mosaic of vegetation. A freshwater swamp existed in this locality, and indications of mangrove and saltmarsh vegetation are slight.

M.K. Macphail (in litt.) has obtained palynological data from the Hawkesbury River and Colo River valleys, about 20 km south-west of Wrights Creek (Fig. 1a). Holocene forests on the valley sides in this area have been dominated by *Eucalyptus/Angophora* and *Casuarina*. Rainforest, either local and restricted in its spread, or more extensive and distant (or both), has been part of the vegetation. Ferns have formed an important component of these forests. Mangrove and saltmarsh vegetation developed alongside freshwater plant communities from about 8,000 BP in the Colo. Mangroves ceased to grow after c. 6,000 BP, and saline conditions were gradually reduced until about 3,350 BP, since when freshwater plant communities have predominated. Diatom studies of the same cores examined by Macphail have been reported by Devoy et al. (1994). A strong marine-brackish water influence is indicated around 7,800 BP, reflecting the rise in relative sea-level along the coast. An expansion of brackish water diatoms occurred after c. 6,700 BP. This probably indicates a reduction in the rate of relative sea-level rise, coupled with substantial sedimentary infill of the Hawkesbury Valley. The latter phenomenon would have restricted the penetration of saline water upriver. A short-lived episode of heightened marine influence, detected around 6,000 BP, was suggested to correlate with the peak in Holocene relative sea level. Since c. 6,000 BP, freshwater riverine diatoms have dominated the record. The pollen and diatom records from the Mill Creek and Hawkesbury-Colo Valleys appear to corroborate the hypothesis of Thom and Roy (1983) that the sea had become established at or very close to its present level along the New South Wales coast by c. 6,500 BP.

Anomalies between the Mill Creek and Hawkesbury-Colo sites and the Wrights Creek Valley site could be explicable in terms of local environmental factors. The Mill Creek Valley site seems to have been able to impede the ingress of saline water throughout the Holocene. Perhaps levee development in the main valley blocked the tributary. Significant marine influence was present at the Hawkesbury-Colo sites until c. 6,000 BP. Their locations suggest that since this time they could have been receiving a greater influx of freshwater from the catchment than would have been possible to Wrights Creek Valley. Also, if relative sea level was above that of today and this persisted later than 6,000 BP, the position further inland of the Hawkesbury-Colo sites than that in Wrights Creek Valley could account for reduced marine influence in the former areas. Conclusions regarding forest history are more consistent between these sites. The continued dominance of a mixture of wet and dry sclerophyll forest and woodland is clear, as is a greater extent of sub-tropical rainforest than at present. The rôle of burning in these forest and woodland communities is evident. Differences in the rate and timing of similar vegetation changes could be related to local conditions, with considerable lags operational at the most protected sites. Finally, it must also be borne in mind that some of the palaeobotanical records are fragmentary, and that radiocarbon dates are not available for certain episodes. Assumptions of age, necessary against such a backdrop, have further decreased the temporal resolution of these studies.

Kodela and Dodson (1988) have described vegetational history over the last 6,000 years on Hawkesbury Sandstone in Ku-ring-gai Chase National Park, close to the mouth of the Hawkesbury River (Fig. 1a). Here, dry sclerophyll heath and woodland, of similar composition but changing relative abundance, has persisted, with burning identified as an integral element in vegetation dynamics. The enduring nature of the vegetation was

thought to be a reflection of its adaptation to harsh local habitat conditions (such as nutrient-poor soils, drought and high insolation) and insensitivity to minor modifications in the regional (especially climatic) environment. However, organic matter accumulation, which began 6,000–5,000 years ago, seems to have been in response to enhanced rainfall, perhaps consequent upon the rise in Holocene relative sea level.

The nearest comparable study in an estuarine environment is from Terragong Swamp, located beside the Minnamurra River, c. 100 km south of the Hawkesbury Estuary (Jones 1990). A mixture of wet sclerophyll forest and sub-tropical rainforest has dominated the dryland vegetation for most of the past five millennia. Between about 4,300 and 2,500 BP, tidal flat and saltmarsh communities extended further inland than they do today, probably in response to a higher relative sea level. The replacement of saline by freshwater wetland vegetation c. 2,500 BP was likely to have reflected a fall in relative sea level towards that of the present. Dated geomorphic, lithostratigraphic and biostratigraphic evidence from coastal localities about 20 km north of the Minnamurra Estuary has identified that the sea reached its present level about 7,000 years ago. It then continued to rise to at least 2 m above that of today, and probably remained at this level until c. 1,500 BP (Jones et al. 1979; Young et al. 1993). This hypothesis contradicts that of Thom and Roy (1983), stated above.

CONCLUSIONS

The fossil pollen and charcoal data above are interpreted as a sequence of vegetation records as follows:

1). Wet sclerophyll forest dominated by *Eucalyptus* species and *Casuarina torulosa*, and probably rich in ferns, as today, has been the most widespread plant community on the lower slopes of Wrights Creek Valley for in excess of 4,000 years BP. Over the same timespan, the upper parts of the valley and the plateau above have mainly carried open, dry sclerophyllous woodland, of which *Eucalyptus* and *Angophora* have been important constituents, the latter especially since c. 4,000 BP. This woodland has had a well developed shrub understorey.

2). Associated with wet sclerophyll forest, mainly in sheltered gullies but probably also on protected alluvial flats, there have been discontinuous stands of sub-tropical rainforest, which also probably possessed a significant component of tree and ground ferns. The most floristically diverse and extensive patches of rainforest developed prior to 4,000 BP, ranging further down the valley than they do today. The combined effects of burning of wet sclerophyll and of a climate which may have been warmer in winter and wetter throughout the year than that of the present, was perhaps responsible for rainforest composition and expansion. A decline in both the floristic diversity and extent of rainforest took place shortly before 4,000 BP. Burning does not seem to have been a major factor in this decline, a possible contributory factor to which may have been a less effective precipitation regime.

3). Mangroves, saltmarsh and *Casuarina glauca* dominated swamp-forest comprised the bulk of the riparian vegetation in the lower part of Wrights Creek Valley until about 4,000 BP. These communities are extant where the creek joins the Macdonald River today and are maintained by water of a higher salinity than currently enters the creek.

4). Since c. 4,000 BP, mangroves have not grown along the banks of Wrights Creek in the environs of the sample site, while saltmarsh and swamp-forest have gradually disappeared from that sector of its valley floor. Notwithstanding the maintenance of restricted areas of brackish wetland beside the watercourse, the lowest sector of which remains tidal, the last four millennia have witnessed the progressive expansion to dominance of freshwater swamp vegetation on the valley floor. In this vegetation, Gramineae (probably mainly *Phragmites australis*) and Cyperaceae species have been of most importance.

Local geomorphic and sedimentary changes may provide the most plausible explanation for the spread of freshwater at the expense of saline habitats. However, the data also hint at a fall in relative sea level from a height above that of today, identified elsewhere in coastal New South Wales during the late Holocene, as a contributory factor to this change.

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REFERENCES

Adam, P. (1992). 'Australian rainforests'. (Oxford University Press: Oxford).

Ashton, D.H. (1981). Tall open-forests. In, 'Australian vegetation' (Ed. R.H. Groves) pp. 121–151 (Cambridge University Press: Cambridge).

Beadle, N.C.W. (1981). 'The vegetation of Australia'. (Cambridge University Press: Cambridge).

Benson, D.H. (1986). The vegetation of the Gosford and Lake Macquarie 1:100 000 vegetation map sheet. *Cunninghamia* **1**, 467–489.

Birks, H.J.B. and Birks, H.H. (1980). 'Quaternary palaeoecology'. (Edward Arnold: London).

Bureau of Meteorology (1975). 'Climatic averages Australia'. (Department of Science and Environment: Canberra).

Clark, J.S. (1988). Particle motion and the theory of charcoal analysis: source area, transport, deposition and sampling, *Quaternary Research*, **30**, 67–80.

Clark, R.L. (1982). Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et Spores* **24**, 523–535.

Devoy, R.J., Dodson, J.R., Thom, B.G. and Nichol, S. (1994). Holocene environments in the Hawkesbury Valley, New South Wales: a comparison of terrestrial and marine records. *Quaternary Science Reviews* **13**, 241–256.

Dodson, J.R. (1983). Modern pollen rain in southeastern New South Wales, Australia. *Review of Palaeobotany and Palynology* **38**, 249–268.

Dodson, J.R. and Thom, B.G. (1992). Holocene vegetation history from the Hawkesbury Valley, New South Wales. *Proceedings of the Linnean Society of New South Wales* **113**, 121–134.

Flenley, J.R. (1979). 'The equatorial rain forest: a geological history'. (Butterworths: London).

Galbraith, J. (1977). 'A field guide to the wild flowers of south-east Australia'. (Collins: Sydney).

Jones, B.G., Young, R.W. and Eliot, I.G. (1979). Stratigraphy and chronology of receding barrier-beach deposits on the northern Illawarra coast of New South Wales. *Journal of the Geological Society of Australia* **26**, 255–264.

Jones, R.L., (1990). Late Holocene vegetational changes on the Illawarra coastal plain, New South Wales, Australia. *Review of Palaeobotany and Palynology* **65**, 37–46.

Kershaw, A.P. and Nix, H.A. (1988). Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. *Journal of Biogeography* **15**, 589–602.

Kodela, P.G. (1990). Pollen-tree relationships within forests of the Robertson-Moss Vale region, New South Wales, Australia. *Review of Palaeobotany and Palynology* **64**, 273–279.

Kodela, P.G. and Dodson, J.R. (1988). A late Holocene vegetation and fire record from Ku-ring-gai Chase National Park, New South Wales. *Proceedings of the Linnean Society of New South Wales* **110**, 317–326.

Markgraf, V., Bradbury, J.P. and Busby, J.R. (1986). Palaeoclimates in southwestern Tasmania during the last 13,000 years. *Palaios* **1**, 368–380.

Martin, A.R.H. (1986). Late Glacial and Holocene alpine pollen diagrams from the Kosciusko National Park, New South Wales, Australia. *Review of Palaeobotany and Palynology* **47**, 367–409.

McKenzie, G.M. and Busby, J.R. (1992). A quantitative estimate of Holocene climate using a bioclimatic profile of *Nothofagus cunninghamii* (Hook.) Oerst. *Journal of Biogeography* **19**, 531–540.

Moore, P.D., Webb, J.A. and Collinson, M.E. (1991). 'Pollen analysis'. (Second edition. Blackwell Scientific Publications: Oxford).

Pidgeon, I.M. (1937–1941). The ecology of the central coastal area of New South Wales. I (1937). The environment and general features of the vegetation. II (1938). Plant succession on the Hawkesbury Sandstone. III (1940). Types of primary succession. IV (1941). Forest types on soils from Hawkesbury Sandstone and Wianamatta Shale. *Proceedings of the Linnean Society of New South Wales* **62**, 315–340; **63**, 1–26; **65**, 221–249, **66**, 113–137.

Roy, P.S. and Thom, B.G. (1981). Late Quaternary marine deposition in New South Wales and southern Queensland - an evolutionary model. *Journal of the Geological Society of Australia* **28**, 471–489.

Thom, B.G. and Roy, P.S. (1983). Sea level change in New South Wales over the past 15 000 years. In 'Australian sea levels in the last 15 000 years: a review' (Ed. D. Hopley) pp. 64–84. (Monograph Series Occasional Paper 3. James Cook University of North Queensland: Townsville).

Thom, B.G. and Roy, P.S. (1985). Relative sea levels and coastal sedimentation in Southeast Australia in the Holocene. *Journal of Sedimentary Petrology* **55**, 257–264.

Watkins, J. (1982). 'Sand resources of the St. Albans area. Stage 1: Wrights Creek and Wellums Creek'. (Geological Survey of New South Wales Department of Mineral Resources Report GS1982/552. Geological Survey of New South Wales: Sydney).

Young, R.W., Bryant, E.A., Price, D.M., Wirth, L.M. and Pease, M. (1993). Theoretical constraints and chronological evidence of Holocene coastal development in central and southern New South Wales, Australia. *Geomorphology* **7**, 317–329.

History of the Vegetation at Burraga Swamp, Barrington Tops National Park, Upper Hunter River Region, New South Wales

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SWELLER, S. AND MARTIN, H. (1996) History of the vegetation at Burraga Swamp, Barrington Tops National Park, Upper Hunter River Region, New South Wales. *Proceedings of the Linnean Society of New South Wales*, **118**, 23–50.

Burraga Swamp is set in a small enclosed basin in temperate *Nothofagus* rainforest with areas of eucalypt forests nearby and subtropical rainforest along the watercourses. The swamp sediments consist of 3.35 m of lake clay overlain by 2.65 m of peat. The base of the peat has been dated at 6,500 years and the base of the clay is possibly about 12,000 years B.P.

The vegetation was open and grassy, with few trees, until 6,500 years B.P., during the lake phase, and the lake supported periodic blooms of *Myriophyllum*. Towards the top of the lake phase, *Dicksonia* became common. The transition from a lake to a peat swamp was accompanied by an increase in *Nothofagus* pollen and temperate rainforests occupied the site from about 6,000 years B.P. to the present. Eucalypts remained relatively low throughout the whole of the time, hence eucalypt forests were only a minor component of the vegetation at the site. Woody myrtaceous swamp shrubs, e.g. *Leptospermum,* were sometimes abundant over the swamp.

The history of the vegetation at Burraga shows similar trends to those of other sites on the Barrington Tops studied by Dodson and colleagues. The *Nothofagus* forests expanded westwards about 6,000 years B.P., when the climate was slightly warmer and wetter, and there has been only minor variation since.

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KEYWORDS: Holocene, Palynology, *Nothofagus*, Barrington Tops, History of the vegetation.

INTRODUCTION

The Barrington Tops is an isolated plateau 1,000 to 1,500 m ASL in the Eastern Highlands (Fig. 1). Burraga Swamp is set in a small enclosed basin located at 985 m, below the plateau surface on the Mount Allyn Range, one of ridges leading up to the southern scarp of the plateau. The swamp is surrounded by temperate rainforest with *Nothofagus moorei* dominant, but there are areas of *Eucalyptus* forests close by and subtropical mixed rainforest on the protected slopes and in the gullies. With three major types of vegetation close by, any changes in distribution should be recorded in the swamp sediments.

Dodson and co-workers studied mire development and have reconstructed the vegetation history of a number of swamps from the plateau above 1,000 m (Dodson et al. 1986, Dodson 1987, see Fig. 2). Dodson et al. (1994) have also studied 2 cores from Burraga Swamp with a maximum depth of 35 cm and a maximum age of 2,140 years B.P. to assess the human impact on the palaeoenvironment. Dodson and Myers (1986) studied the modern pollen rain of the Barrington Tops and Upper Hunter River regions to define the pollen signature of the different types of vegetation. This latter study, together with other similar studies (e.g. Dodson 1983), show that most Australian pollen types travel in quantity only a few tens of metres from their source. Swamp sediments are thus likely to record a predominantly local history of the vegetation. This study of a 6 m core

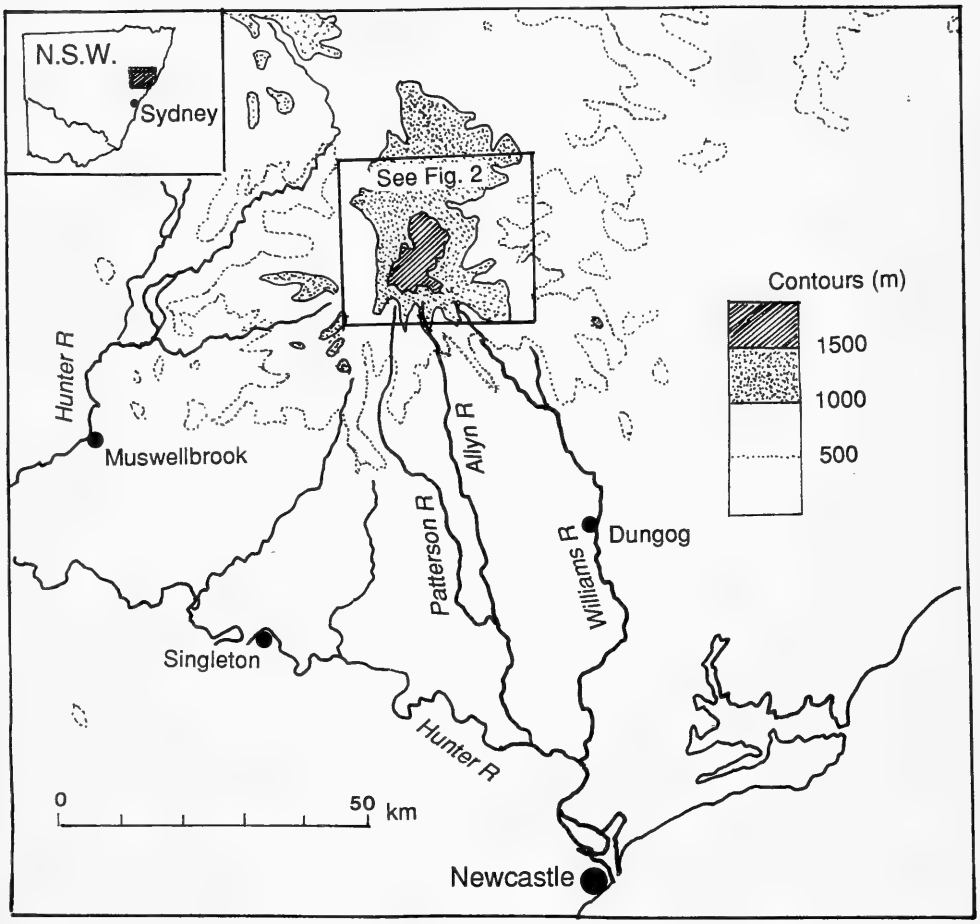


Figure 1. Location of Barrington Tops.

from Burraga Swamp, with an age of probably 12,000 years B.P., adds yet another locality for a more comprehensive picture of the history of the vegetation.

Frazer and Vickery (1937, 1938, 1939) made detailed studies of the vegetation of the Williams and Allyn River regions and Turner (1976) studied an altitudinal transect in rainforest some 3 km to the northwest of Burraga Swamp. These authors note that there are no small individuals of *Nothofagus moorei* within the mature *N. moorei* forests, but coppicing is widespread and may be the normal means of reproduction within the forests. Turner (1976) suggests that *N. moorei* is migrating upwards, and Frazer and Vickery (1938) conclude that *N. moorei* is invading the lower eucalypt forests. This study may provide some evidence about the migration of *N. moorei* during the Holocene.

THE ENVIRONMENT

The Barrington Tops massif is largely Permian granite, folded and faulted Carboniferous and Devonian sediments with an eroded Tertiary basalt capping. The plateau surface is gently undulating and the sides are steeply sloping to the south and

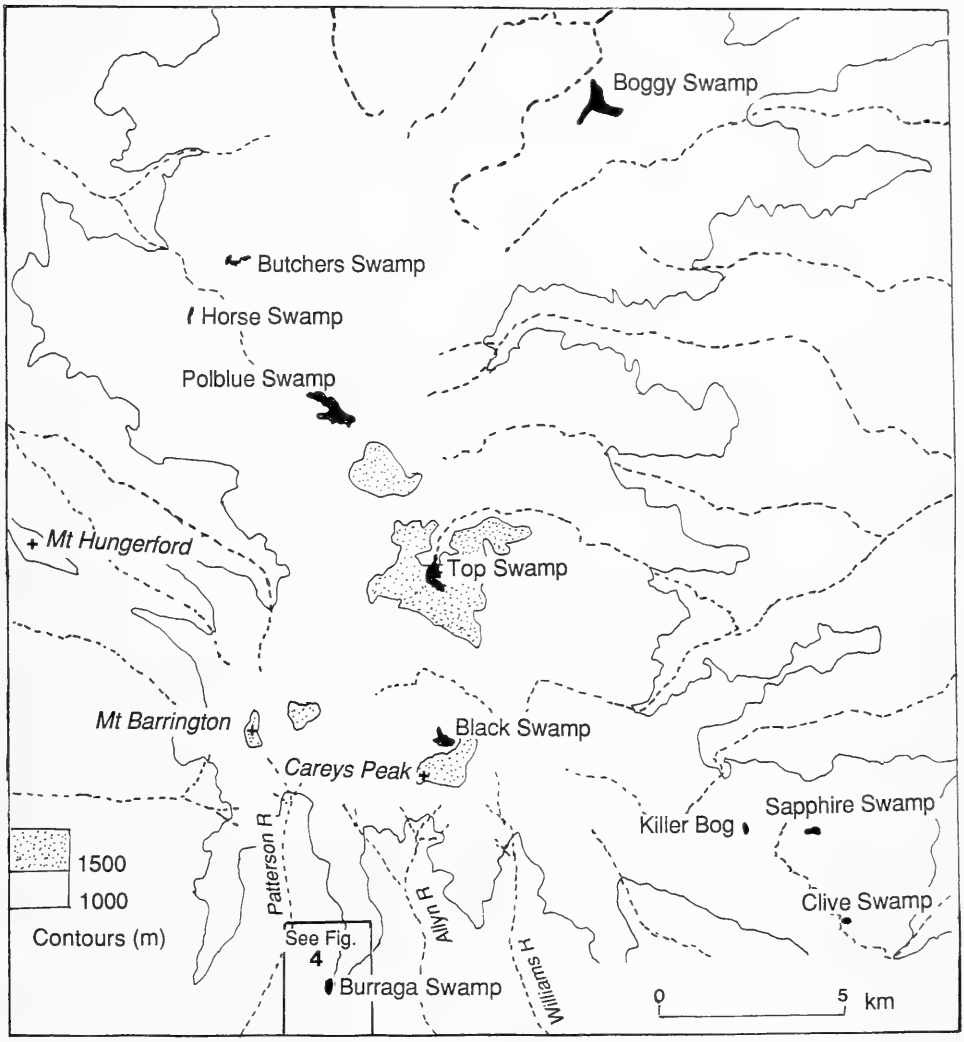


Figure 2. Location of Burraga Swamp in relation to the sites studied by Dodson (1987) and Dodson et al. (1986).

west, but more gently sloping to the north. For an excellent summary of the geomorphology and soils, see Dodson and Myers (1986).

Mt. Lumeah to the north west of Burraga Swamp has a basalt capping and large boulders may be found between the two sites. Smaller boulders and cobbles of basalt may be found throughout the forests.

The region receives both summer rain from the north and winter rain from the south, but in any one year, either climatic type may predominate. The plateau surface receives mean values of over 2,000 mm (Dodson and Myers 1986), and the general precipitation patterns over the region are illustrated in Fig. 3. Mists and fogs may be common in favourable topographic regions and desiccating winds from the west occur mainly in late summer to autumn and in early spring (Frazer and Vickery 1937).

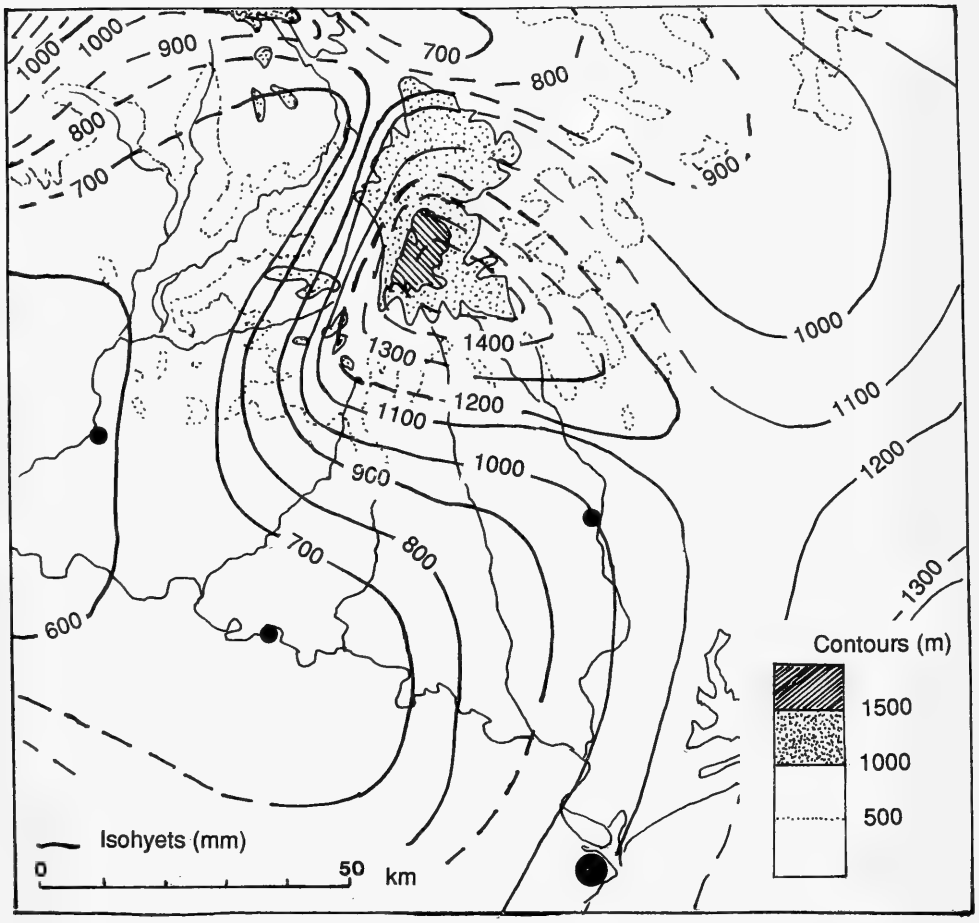


Figure 3. Reconstructed isohyets, from Turner (1981). Broken lines signify uncertainty.

Mean winter minimum temperatures fall below zero and maxima rise to 9–10°C, while summer equivalents of 8–9°C and 22–23°C occur. Maximum temperatures at the base of the plateau are some 5–6°C higher. Snow and frost is common on the plateau (Dodson and Myers 1986).

METHODS

Vegetation

The forest surrounding the swamp was examined in detail and all species encountered were collected and identified. A site 11 km away in riverine subtropical rainforest was studied also, for comparison with the temperate rainforest around the swamp. The vegetation over the swamp was mapped by visual estimation of the percentage cover of the dominant species in 1 m square plots. The author citation of all plant names may be found in Harden (1990–1993).

Stratigraphy of the swamp sediments

Cores along two intersecting transects were studied for stratigraphy. The sediments were described using the Troels-Smith method (Birks and Birks 1980) and seeds were collected for identification. A core from the deepest part of the swamp, approximately in the centre, was sampled at 10 cm intervals for pollen analysis. A Hiller corer was used throughout.

Samples for radiocarbon dating were taken from a hole close to that sampled for pollen analysis. The Department of Main Roads kindly loaned a soil sampling auger for this purpose. Samples were submitted to the Radiocarbon Dating Laboratory, Department of Nuclear and Radiation Chemistry, University of New South Wales.

Modern Pollen Deposition

Samples of moss polsters on the surface of the soil or sediment were collected to assess modern pollen deposition. Collection sites were located on the swamp surface and in the forest surrounding Burraga Swamp. For comparison, Polblue Swamp, some 15 km north, on the plateau surface (Fig. 2) and within subalpine eucalypt forest, was sampled.

Treatment of samples

The carbon content of the sediments was estimated from loss of weight by ignition at 450°C. A subsample of 0.2 gm of sediment was spiked with *Alnus* pollen of 2.76×10^4 grains/mm^3 concentration for the estimation of pollen concentration. The samples were treated with hydrofluoric acid to remove mineral matter, dispersed with 10% sodium hydroxide (heated in a water bath for 10 mins), disaggregated with ultrasonic vibration and sieved through an 85 mesh (0.18 mm) sieve, followed by standard acetolysis (Moore et al. 1991). The residues were dehydrated and mounted in silicone oil. Surface samples were treated in the same way.

Pollen reference samples were treated with acetolysis, dehydrated and mounted in silicone oil.

Pollen analysis

A known volume of a suspension of exotic *Alnus* grains was added to the sediment samples to enable the calculation of the fossil pollen concentration. At least 200 fossil grains, the *Alnus* grains found with the fossils and microscopic charcoal particles were counted. The size of the charcoal particles were mainly 5–65 μm in diameter, i.e. about the same size range as that of spores and pollen. Very few particles larger than 65 μm were encountered. The total concentration of pollen and the concentration of charcoal particles in the sediment were calculated. Pollen concentrations for the most abundant pollen types and percentages for all types were calculated. Individual pollen concentrations are independent of all the others and hence prove a useful aid to the interpretation of the percentages. The total spore and pollen count was used as the pollen sum in the percentage pollen diagrams. The 0.95 confidence limits for the percentages were computed using the methods of Maher (1972). The surface pollen counts are treated in the same way as that of the core.

RESULTS

Vegetation

A map of the general vegetation of the area is presented in Fig. 4. The swamp is within temperate rainforest but there are stands of eucalypt forest within 100 m and sub-

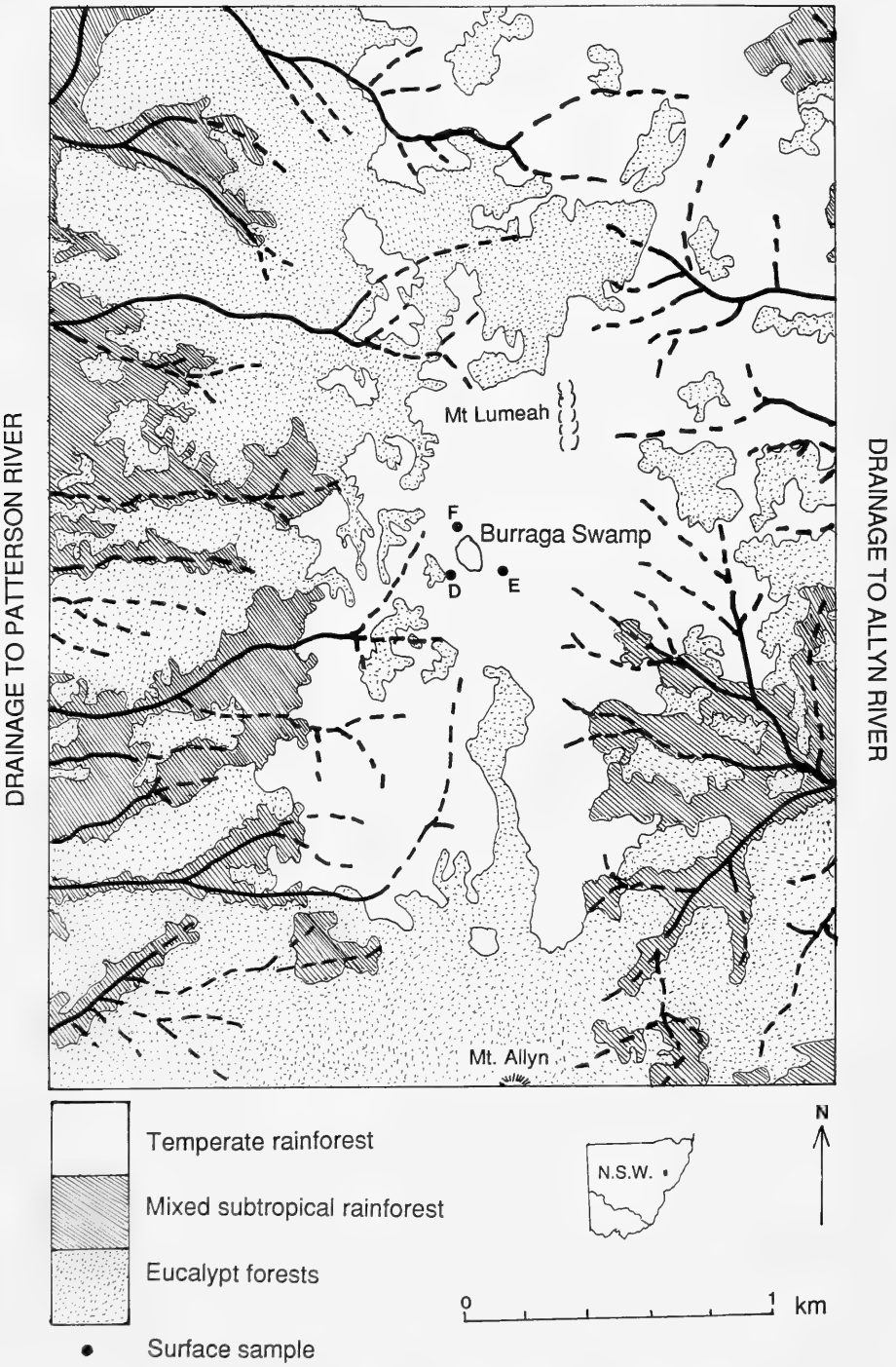


Figure 4. The vegetation of the area around Burraga Swamp, modified from the Boonabilla Management Area Map (Forestry Commission of N.S.W. 1983). For Dominant species, see Table 1. For the vegetation and sites of surface samples on the swamp, see Fig. 5.

tropical rainforest is about a half km away. The chief dominants are shown in Table 1 (Forestry Commission of N.S.W. 1983)

The temperate rainforest around the swamp has a tree stratum 10–30 m tall with a foliage projective cover of more than 70%. This layer has *Nothofagus moorei* dominant. Other species present are *Acmena smithii, Caldcluvia paniculosa, Diospyros australis, Doryphora sassafras, Eucalyptus laevopinea, Orites excelsa, Quintinia sieberi, Rapanea howittiana* and *Schizomeria ovata. Tristaniopsis laurina* and *Tristaniopsis collina* may be found in disturbed areas.

A small tree stratum 2–10 m tall is composed of *Coprosma quadrifida, Solanum* sp, *Hymenanthera dentata* and *Duboisia myoporoides.* The tree fern *Dicksonia antarctica* is usually over 2 m tall. There may be shrubs less than 2 m, viz *Coprosma quadrifida, Rubus rosifolius* and around the swamp, *Rubus hillii* and the introduced stinging nettle, *Urtica urens.*

TABLE 1

Forest types around Burraga Swamp. Modified from the Boonabilla Management Area, Map (Forestry Commission of N.S.W. 1983).

Temperate Rainforest

Dominants:

Nothofagus moorei
Eucalyptus laevopinea
Orites excelsa
Schizomeria ovata

Ferns and vines present

Mixed Subtropical Rainforest

Dominants:

Eucalyptus laevopinea

Variable:

Caldcluvia paniculosa
Diploglottis australis
Elaeocarpus grandis
Orites excelsa
Citronella moorei
Toona ciliata
Schizomeria ovata
Litsea reticulata
Dysoxylum fraserianum
Cinnamomum oliveri
Cryptocarya erythoxylon

Also present:

Tristaniopsis collina
Dendrocnide excelsa

Eucalyptus forests

Main dominants:

Eucalyptus laevopinea
E. campanulata
E. saligna
E. quadrangulata
E. acmenoides
E. canaliculata
E. punctata

Understorey: dry or moist

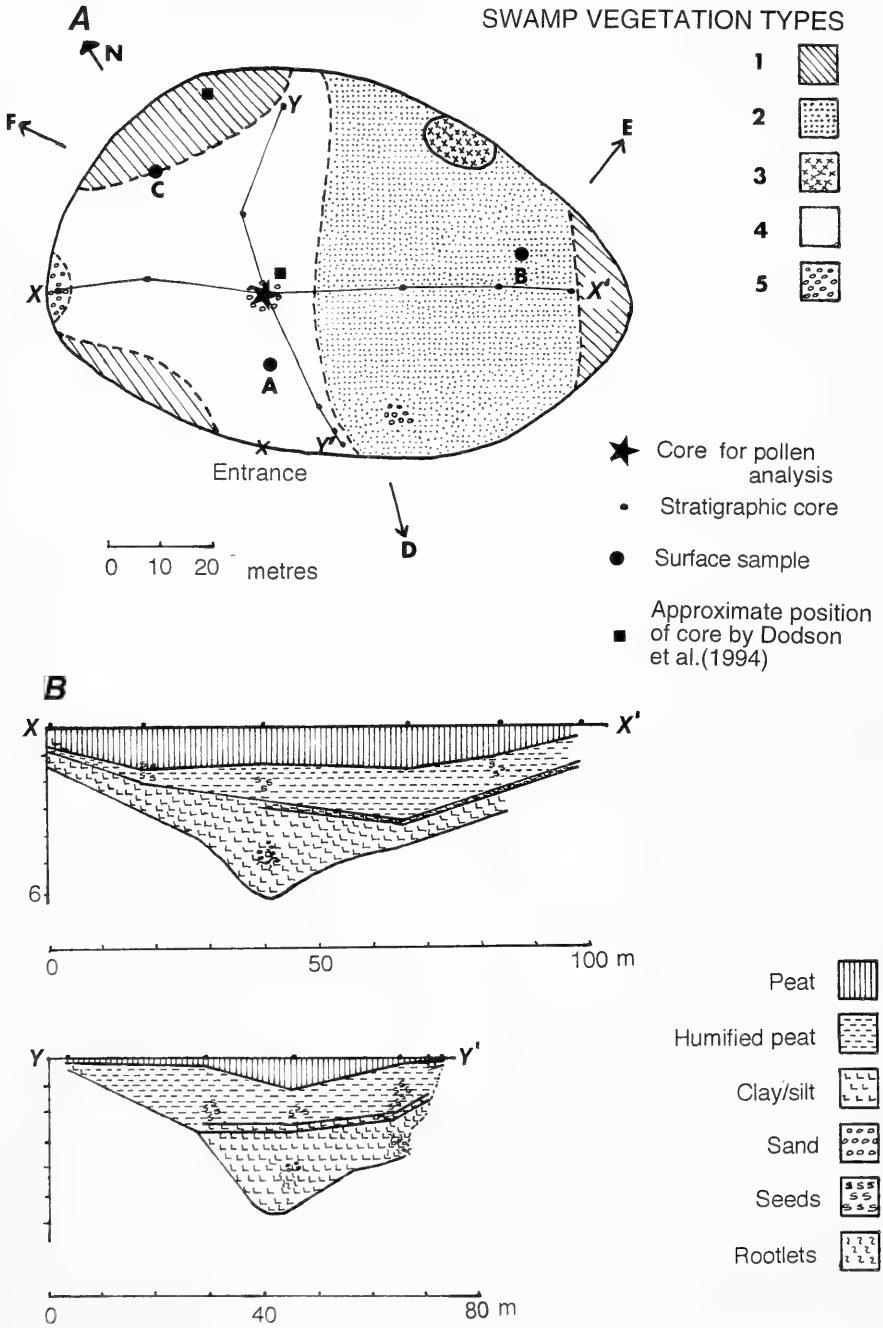


Figure 5. A. Burraga Swamp showing vegetation, core for pollen analysis, swamp surface sample sites and direction of forest surface sample sites. The approximate position of the cores studied by Dodson et al. (1994) are shown. 1). Dense *Phragmites australis* community: 40–50% P. *australis*, 60–50% *Cyperus lucidus*. 2). Patchy *P. australis* community with *P. australis, C. lucidus, Glyceria australis,* mosses and *Lastreopsis microsora.* Very hummocky. 3). *Glycera australis* community with 70% *G. australis,* 15% *Cyperus lucida,* 10% moss and 5% *L. microsora.* 4). *Glycera australis, Phragmites australis* community with 50% of each one and some moss. 5). Mainly bare ground with a moss cover and a little *G. australis.* B. Profiles of the swamp.

Ground-covering plants are found mainly in the higher light intensities of the canopy gaps and are usually herbaceous and less than 1 m tall. *Carex appressa, Hydrocotyle tripartita, Dianella* sp, *Juncus usitatus* and *Lomandra spicata* are found here. Trailing or twining plants include *Morinda jasminoides, Pandorea pandorana, Parsonsia staminea, Polygonum subsessile, Polygonum decipiens, Dioscorea sp.* and *Cayratia clematidea.*

Ferns are common in the ground cover also. The species include *Hymenophyllum flabellatum, Pellaea falcata, Lastreopsis microsora, Hypolepis* sp. and marginal to the forest, *Pteris* sp. The epiphytic ferns *Microsorum diversifolium, Microsorum scandens* and *Arthropteris tenella* are present also.

The swamp vegetation is mapped in Fig. 5. The main dominants are *Phragmites australis, Cyperus lucidus* and *Glyceria australis*. Five communities have been defined and these are shown on Fig. 5.

The species identified from the surface sample sites are found in Table 2 and a list of all species identified in the study area is given in Appendix 1.

TABLE 2

Species identified from the Surface Sample Sites (see Fig. 5.)

Swamp sites

A: *Glyceria australis*, *Phragmites australis*, mosses

B: Patchy distribution of *Phragmites australis*, *Cyperus lucidus*, *Glyceria australis*, mosses and the fern *Lastreopsis microsora.*

C: *Cyperus lucidus*, *Phragmites australis*

Forest sites

D: Junction of *Eucalyptus laevopinea* and *Nothofagus* forests.
Eucalyptus laevopinea, Nothofagus moorei, Caldcluvia paniculosa, Schizomeria ovata, Orites excelsa, Syzygium australe, Doryphora sassafras, Daphnandra tenipes, ground ferns.

E: South East Forest, Burraga Swamp
Nothofagus moorei, Orites excelsa, Doryphora sassafras, Syzygium australe, Caldcluvia paniculosa, Daphnandra tenipes, Citriobatus sp., *Dicksonia antarctica*, ground and tree creeper ferns. *Hymenanthera dentata, Symplocos* sp., *Cryptocarya* sp.

F: North Side Forest, Burraga swamp
Nothofagus moorei, Caldcluvia paniculosa, Syzygium australe, Schizomeria ovata, Diploglottis australis, ground and tree creeper ferns

Swamp stratigraphy

The location of the transects and cores in the swamp are shown on Fig. 5A. The profiles of the swamp along the transects are shown in Fig. 5B.

There is a root mat at the surface overlying fibrous peat. Seeds, pieces of wood and charcoal fragments may be encountered in the peat. Clayey peat underlies the peat, with a grey clay and silt layer beneath the clayey peat. Thin layers of peat with roots may be encountered in this latter layer. The peat and clay layers thin out towards the edges of the swamp and are thickest in the centre. The stratigraphy of the core sampled for pollen analysis is shown in Fig. 6. The carbon content (Fig. 7) is lower in the clay/silt layer and higher in the peat, as expected.

Seeds collected from the peat were identified as *Eleocharis sphacelata*, cf *Scirpus* sp, *Carex fascicularis* and *Carex brownii* (K. Wilson pers. comm.).

The radiocarbon dates are given in Table 3 and their place in the stratigraphy on

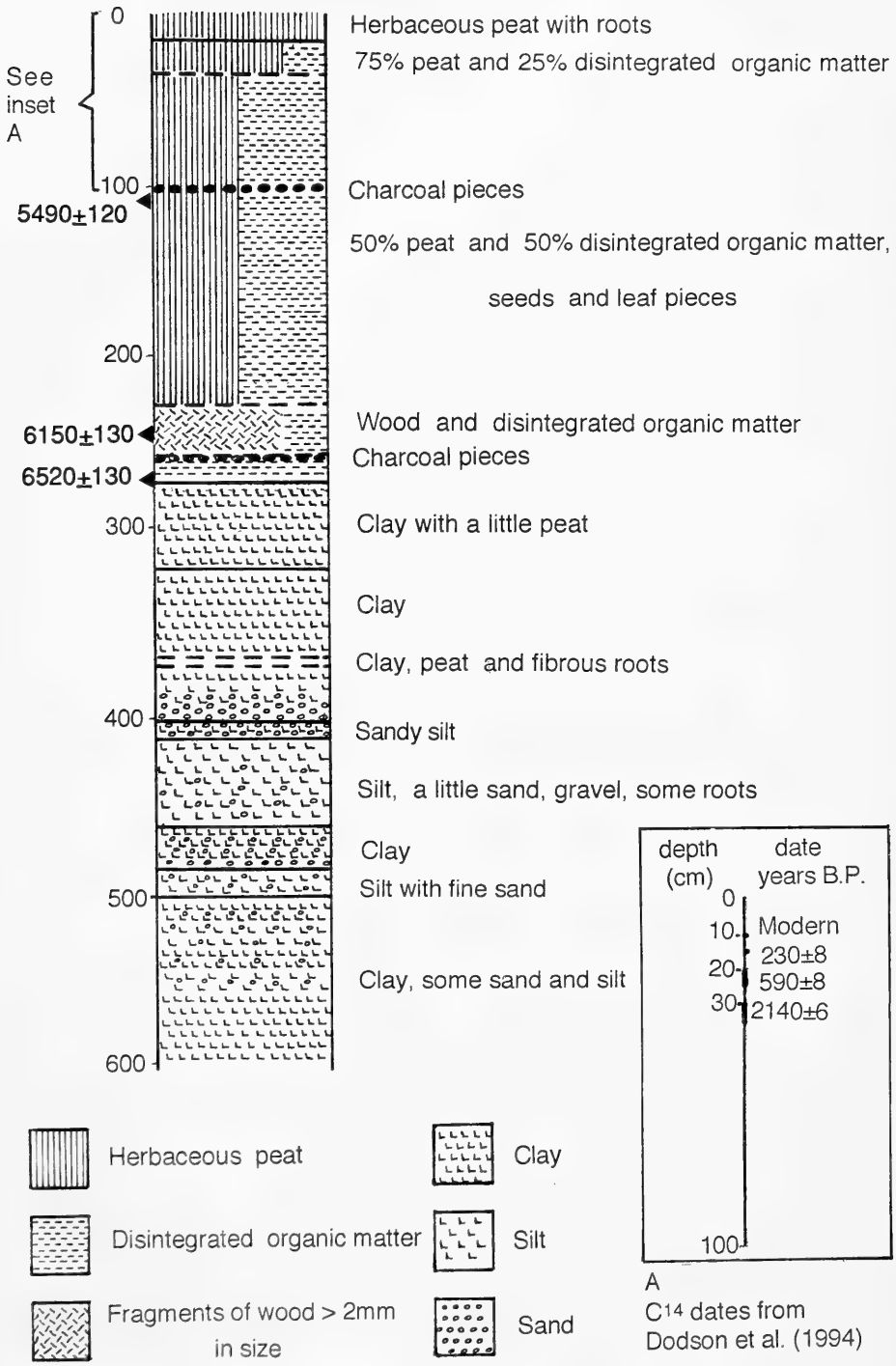


Figure 6. The stratigraphy of the core sampled for pollen analysis. The radiocarbon dates from the core in the centre of the swamp, studied by Dodson et al. (1994), are shown also.

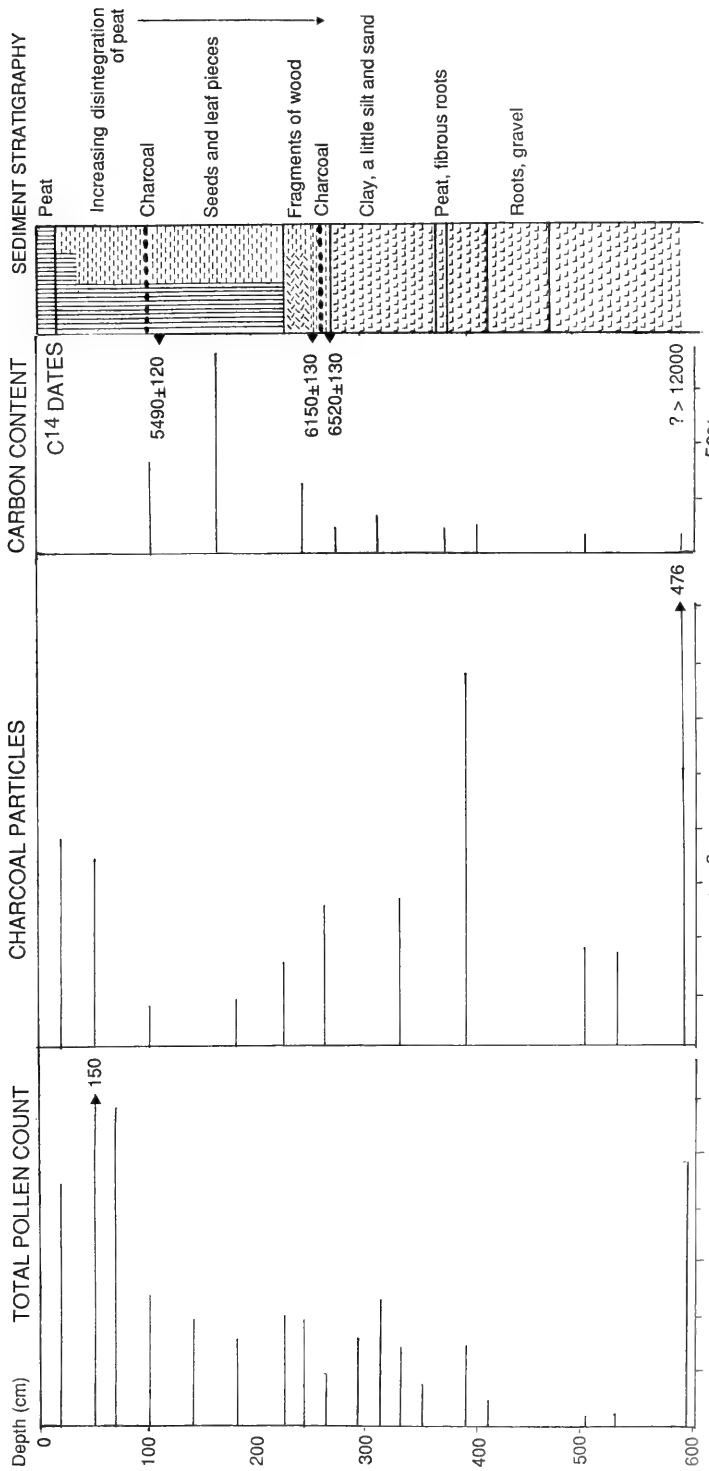


Figure 7. Total pollen concentrations, microscopic charcoal particles and carbon content. The symbols on the sediment column are the same as those for Fig. 6.

Fig. 6. They show that the base of the peat layer is 6,500 years old. The clay contained insufficient carbon for dating, but if the average rate of accumulation of the peat is extrapolated, then the base of the clay would be about 12,000 years old. Other possibilities and the reasons for this assumption are discussed further, below.

TABLE 3

Radiocarbon age of the sediments

Depth (cm)	Reference No.	Age (years BP)
100–110	NSW 345	5490 ± 120
240–250	NSW 348	6150 ± 130
260–270	NSW 347	6520 ± 130

Initially, the swamp was a lake which accumulated clays, washed in from the surrounding slopes. Being an enclosed basin, sediments originated only from erosion of the slopes. Occasionally, some high energy event, such as a rainstorm, transported some sand or gravel into the lake, but such events were uncommon and minor. The thin layers of peaty clay with roots show that the lake had become shallow and the surface was colonised by swamp vegetation for a short time. Throughout its history, the lake was probably never very deep.

At 265 cm, the change of the sediments from clay to organic material shows lake levels had fallen again and the surface was covered with swamp vegetation. This change occurred about 6,500 years ago and the surface has remained vegetated ever since. The substantial amount of wood in the sediments at 220–250 cm suggests that trees, or at least woody shrubs grew on the swamp surface, for there is no evidence of the transport of wood from the forest to this site in the middle of the swamp. Some high values of a small-grained Myrtaceae pollen occur with the wood, hence woody myrtaceous swamp shrubs, which are not present there now, are a possibility. Dodson et al. (1994) identified a substantial amount of *Leptospermum* pollen from the centre of Burraga Swamp, thus woody myrtaceous swamp shrubs have grown at the site. Pieces of leaves and seeds are found throughout the peat. The charcoal layers bear testimony of fires over the surface of the swamp.

The peat accumulated at a rapid rate, approximately 150 cm in 1,000 years, initially. The rate of accumulation after 5,500 years ago has been slower, 110 cm in 5,500 years, assuming that deposition has been continuous to the present, and the surface has not been eroded. The radiocarbon dates from the centre of the swamp core studied by Dodson et al. (1994), where the 15–20 cm level is 230 years old and the 30–35 cm level is 2,140 years old, supports the assumption that there has been no erosion of the surface.

Pollen analysis

There is a high concentration of pollen at the base of the profile (Fig. 7). The 400–590 cm section has a very low pollen concentration and there were too few grains to count from 420–500 cm. The section from 100–400 cm has moderate concentrations, with higher concentrations from 0–100 cm. Charcoal particle values are variable, with higher values in the clay/silt layer and the lower values in the peat. The lowest concentration of charcoal particles, from 100–200 cm depth, coincides with the highest frequencies of *Nothofagus* pollen. A comparison of pollen concentration and percentages (Fig.

8) for the major pollen types show that both methods produce generally parallel patterns, with some minor deviations, especially in the peat. Substantial deviation from essentially parallel trends are seen with Poaceae and *Myriophyllum* in the clay, where the percentages show an inverse relationship, i.e. where Poaceae is high, *Myriophyllum* is low and vice versa, which is not reflected in the pollen concentrations. A similar pattern may be seen in *Nothofagus* above 100 cm, where percentages decrease but concentrations increase.

The pollen diagram for both surface and core samples is shown on Fig. 9. A definition of all the pollen taxa on the diagram with their distribution in the vegetation is given in Appendix 2.

The frequency of *Nothofagus* pollen is low in the clay, increasing from the base of the peat. The level at which values comparable to those of the surface samples are reached, is about 200 cm. The values for Myrtaceae are moderate through most of the profile, with some high values in the peat. The high values all result from increases in the small grain group (Fig. 10), with the *Eucalyptus* content remaining fairly constant, except for the very top. The base of the clay also has a somewhat higher value than the rest of the profile. *Casuarina* pollen is relatively low throughout and is probably the result of long distance dispersal. These three pollen groups would account for most of the tree pollen.

A separate analysis of the Myrtaceae pollen (Fig. 10) identifies three groups: *Eucalyptus/Syzygium, Melaleuca* and a small grain group, size < 14 μm, probably consisting of *Tristaniopsis, Backhousia, Baeckea* and possibly *Acmena* (see Appendix 2). Fig. 10 shows moderate frequencies of *Eucalyptus/Syzygium* at the base of the profile followed by mostly low values upwards and a maximum at the surface. *Melaleuca* is sporadic and low throughout. The small grain group frequencies are low to moderate through most of the profile with occasional high values in the upper part. The high values of total Myrtaceae (Fig. 9) are thus almost entirely due to increases in this small grain group. As discussed above, myrtaceous swamp shrubs, e.g. *Leptospermum* (identified by Dodson and Myers 1986), would fall within this small grain group.

Frequencies of Cyperaceae are moderate to low in the basal clay with higher values in the upper peat. Poaceae, however, shows opposite trends with higher values in the clay, reaching a maximum at 340–370 cm, and lower frequencies in the peat. Fig. 11 shows the analysis of size frequencies of Poaceae from some levels in the profile and suggests that different species are involved. *Myriophyllum* shows variable frequencies, in both clay and peat. The other herbaceous taxa (Fig. 9) have low values, varying only a little through the profile.

The tree fern *Dicksonia* shows low frequencies with the exception of higher values at 280–310 cm, the top of the clay. The other fern spore groups all have low to moderate frequencies throughout, with only small variation.

The pollen spectra may be divided into two major zones, an open, grassy Zone 1, coinciding with the lake phase and clay deposition and a forested Zone 2, coinciding with the swamp phase and peat deposition. Each zone may be further subdivided, as shown on Fig. 9.

Zone 1, 265–600 cm.

Throughout the zone, eucalypts were virtually the only trees. In subzone A, there is an exceptionally high content of *Myriophyllum* and low frequencies of practically every other pollen type. In subzone B, Poaceae and *Myriophyllum* have high values, but in an inverse relationship, i.e when Poaceae is high, *Myriophyllum* is low. The other herbaceous pollen types are low, but some of the fern spore groups may have somewhat higher values. In subzone C, *Dicksonia* increases to a peak at the top of the zone. The herbaceous taxa *Ranunculus* and *Hydrocotyle,* and some of the fern spore groups have higher values also.

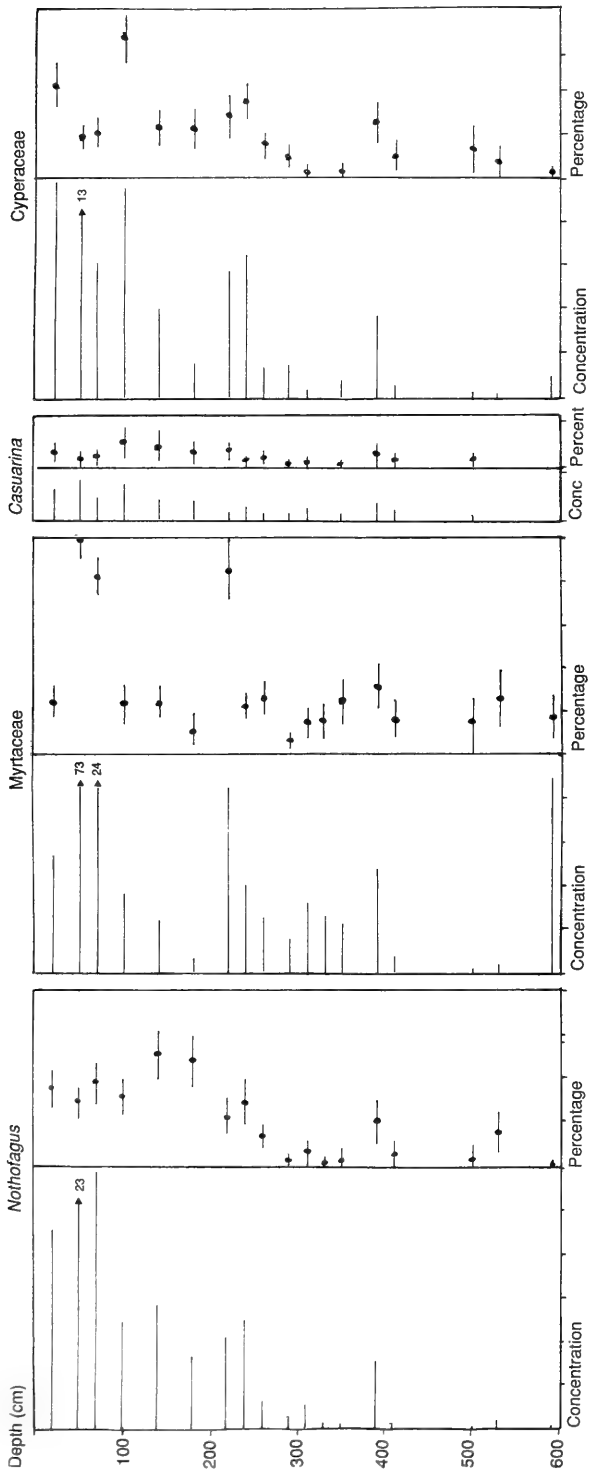
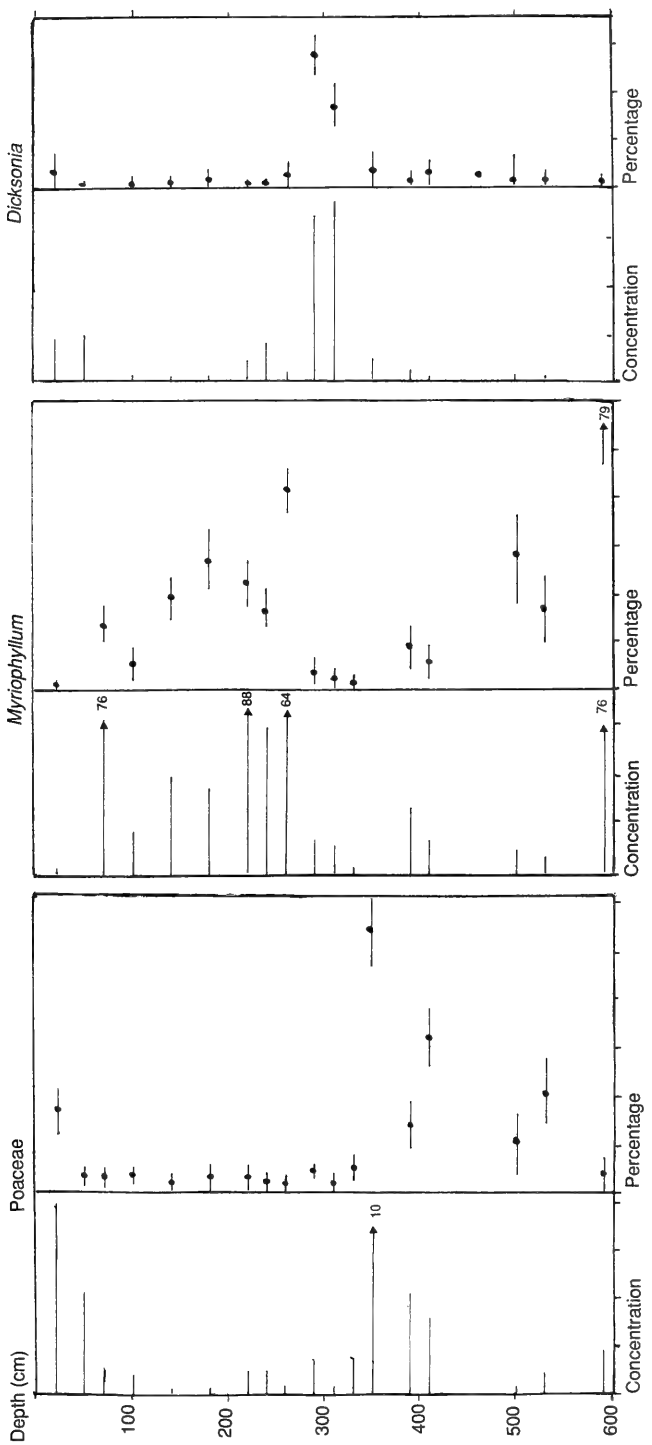


Figure 8.
A comparison of pollen concentrations and percentages. Scales: Pollen concentrations, one division=$2x10^3$ grains/gm. Percentages, one division=10% of total spore and pollen count.


Depth (cm)
100
200
300
400
500
600
Poaceae
Concentration
Percentage
10
Myriophyllum
Concentration
Percentage
76
88
64
76
79
Dicksonia
Concentration
Percentage

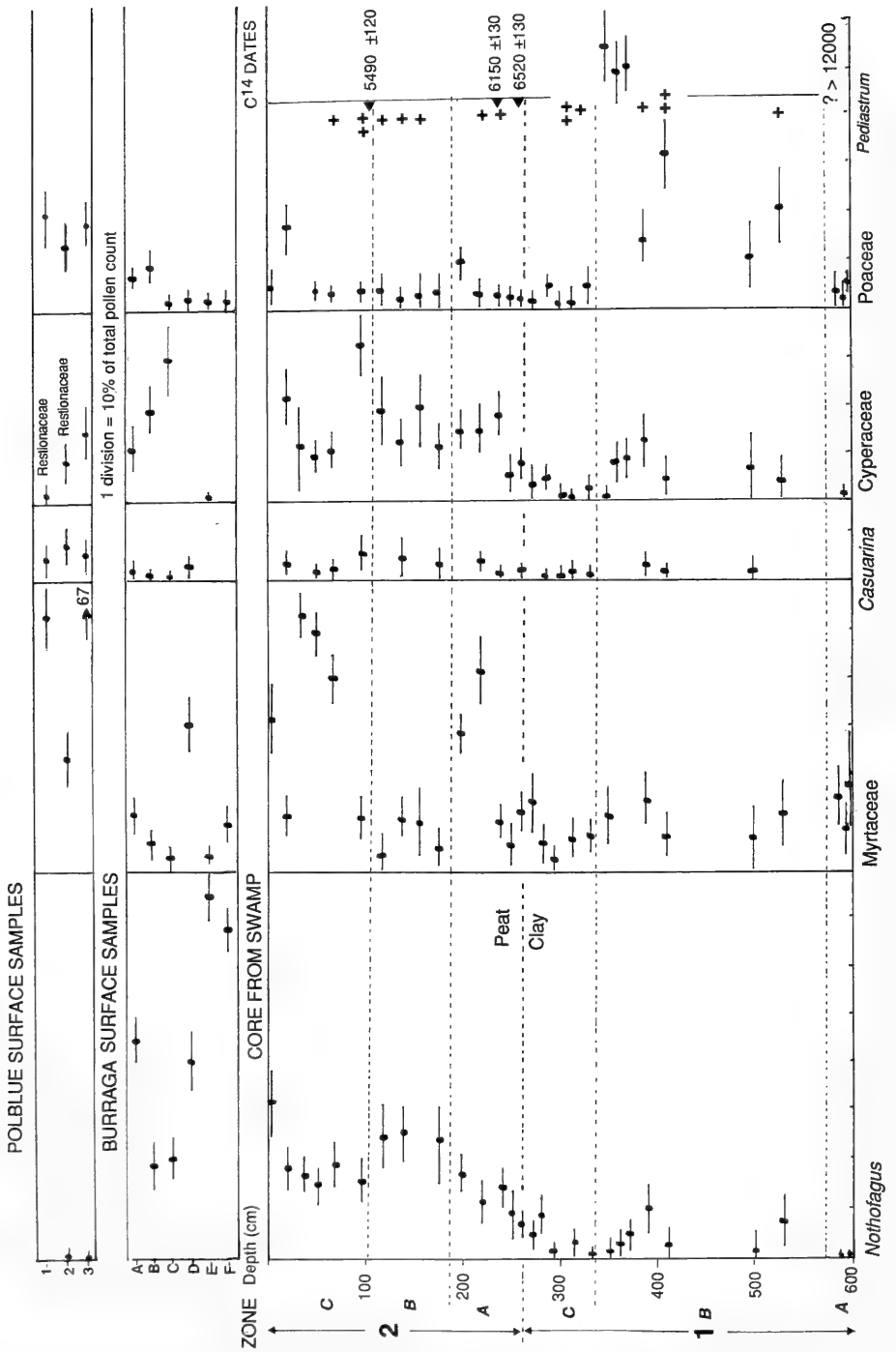
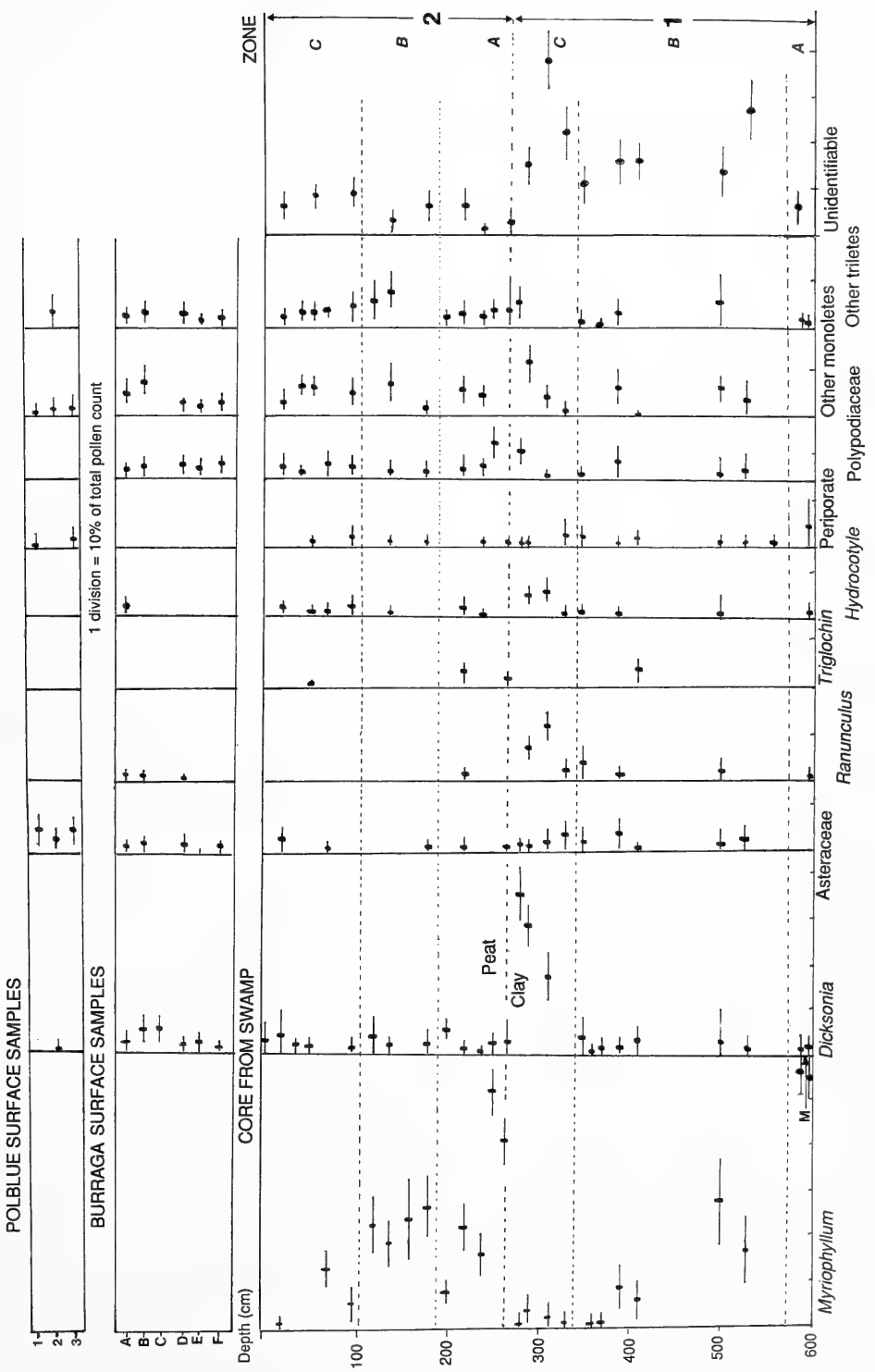


Figure 9. Pollen Diagram. The Polblue surface samples are as follows: 1, Eucalypt forest. 2, *Sphagnum* swamp. 3. Eucalypt forest. For the position of the Burraga surface samples, see Fig 5. For *Pediastrum*, + = present and ++ = abundant. The unidentifiable group records degraded, crumpled and distorted grains. M, The arrow indicates 79% of *Myriophyllum*.


POLBLUE SURFACE SAMPLES
1
2
3
BURRAGA SURFACE SAMPLES
A
B
C
D
E
F
1 division = 10% of total pollen count
Depth (cm)
CORE FROM SWAMP
ZONE
C
B
2
A
C
B
1
A
Peat
Clay
100
200
300
400
500
600
M
Myriophyllum
Dicksonia
Asteraceae
Ranunculus
Triglochin
Hydrocotyle
Periporate
Polypodiaceae
Other monoletes
Other triletes
Unidentifiable

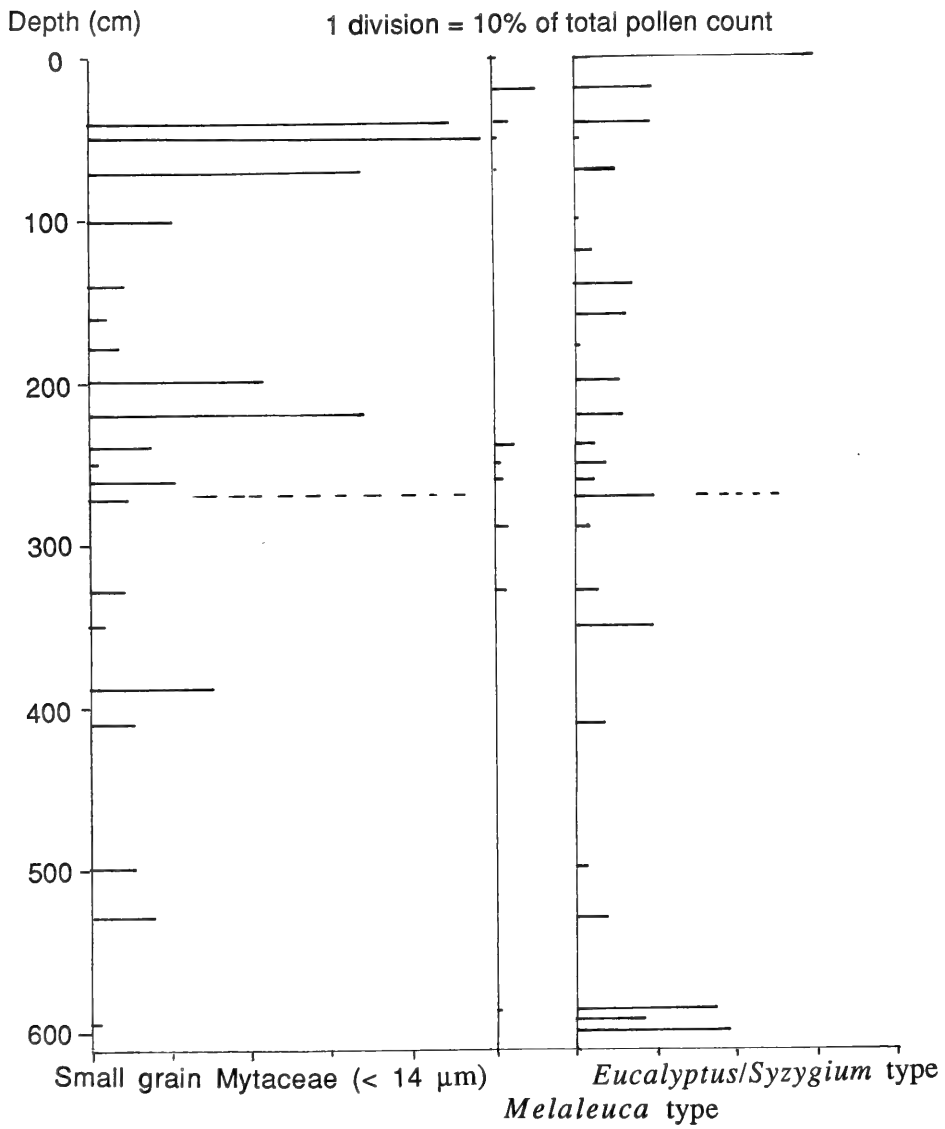


Figure 10. Analysis of Myrtaceae pollen.

Zone 2, 0–265 cm.

The base of the zone coincides with the transition from clay to peat. *Nothofagus* frequencies increase in a transitional subzone (2A), followed by relatively high and stable values (2B) and then a slight fall with a subsequent rise at the very top (2C). Subzone 2A has fluctuating values for Myrtaceae and *Myriophyllum*, whereas subzone 2B has relatively low and stable values for Myrtaceae and high stable values for *Myriophyllum*. Subzone 2C has fluctuating values for Myrtaceae and low values for *Myriophyllum*. Throughout the zone, Cyperaceae has high values, and Poaceae and *Dicksonia* are low.

The small amount of *Nothofagus* pollen in the lake phase (Fig. 9), suggests either long distance transport or a very small stand nearby. *Nothofagus* pollen has a reputation for being over-represented and capable of long distance transport, but in Victoria, only 1–2% of *Nothofagus cunninghamii* pollen disperses more than 70 m from the edge of small stands (K. Harle pers. comm.). In New Zealand, pollen of *Nothofagus menziesii* is under-represented and not as widely distributed when compared with that of the *fusca* species (McKellar 1973). *Nothofagus moorei*, the species of this study, has the same pollen type as *N. cunninghamii* and *N. menziesii*, and our surface samples show its distribution is fairly localised. In view of the evidence about pollen dispersal, *Nothofagus* would have been very minor in the vegetation around Burraga during the lake phase, if present at all. This small amount of pollen may have come from *Nothofagus* growing to the east (Dodson et al. 1986), discussed further below.

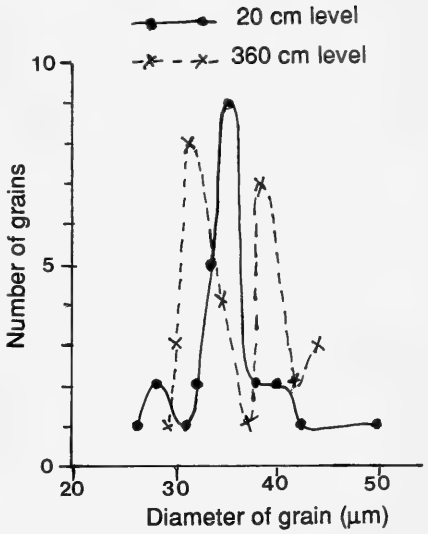


Figure 11. An analysis of the size of Poaceae grains from two levels show that different species are probably involved. There are probably two species represented in the 360 cm level.

Nothofagus increased from about 6,500 years B.P. to a position in the vegetation comparable with that of today at about 6,000 years B.P. There have been fluctuations after that time, but all of the values above the 220 cm level, i.e. about 6,000 years age, fall within those of the surface samples (Fig. 9). The fluctuations would thus fall within the variability seen in the forests today.

The Myrtaceae at the base of the profile is almost entirely *Eucalyptus. (Syzygium* is considered unlikely in this pollen spectrum). The low level of eucalypt pollen throughout the profile is lower than that of surface samples (this study and Dodson and Myers 1986), hence eucalypt forests were probably not dominant at any time, at this locality. In the lake phase, prior to 6,500 years B.P., the trees were probably found in sparse clumps occupying suitable habitats. Other myrtaceous taxa were sometimes common, especially in the peat phase, after 6,500 years B.P. Dodson and Myers (1986) characterize the subtropical rainforests by an abundance of *Backhousia* pollen, which would fall within the small grain group of this study. In the peat above 100 cm, when the small grain group of Myrtaceae increases, *Nothofagus* decreases, hence these changes may reflect some increase/decrease of the subtropical rainforests if *Backhousia* is responsible for the large increase in the small grain group. On the other hand, the small grain group may also contain pollen from myrtaceous swamp shrubs, such as *Leptospermum* and *Baeckea*, both of which are found associated with swamps on the Barrington Tops today (Dodson et al. 1986). The wood in the sediments and the identification of *Leptospermum* pollen from Burraga (Dodson et al. 1994) suggests that the swamp shrubs were involved, and the possibility of changes in the subtropical rainforest is only conjectural.

Cyperaceae became prominent once peat started accumulating. The species have changed with time, for the identifications from seeds do not match any of the species growing there today. Poaceae, however, declined once peat started accumulating, suggesting that swamp grasses, such as *Phragmites australis*, were not a major part of the swamp vegetation until recent time. The species of Poaceae have changed during the history of the swamp, as suggested by the grain size analysis (Fig. 11). At times,

Myriophyllum was abundant in both the lake and peat phases, but this pollen type represents species which grow both in water and on mud (see Appendix 2). The variability of the grains suggests that more than one species was involved.

When the lake first formed, it contained an abundance of *Myriopyllum*. In the subsequent subzone, *Myriopyllum* fluctuated, and when low, there were more Poaceae. There may have been some Poaceae in swamp vegetation around the edge of the lake, but most of the Poaceae would have been growing in the dryland environment. This apparent inverse relationship of Poaceae and *Myriopyllum* may be an artifact of the percentage method where the total must always be 100%. If the lake periodically produced a bloom of *Myriopyllum* while the rest of the vegetation remained the same, the high frequencies of *Myriopyllum* pollen would depress percentages of the other pollen types, and Poaceae, the other pollen type with high percentages, would be depressed the most. Examination of the pollen concentrations (Fig. 8), which do not parallel the frequencies in the clay, suggests the latter explanation.

Dicksonia reaches a peak in the clay, just before the transition to peat, at a time when the tree cover would have been slight, and then remains low in the forested phase. In forests of the Barrington Tops, *Dicksonia antarctica* is most abundant in damp hollows (Turner 1976) and the highest frequencies of spores may reflect high moisture, before the forest cover occupied the site with a consequent rise in evapotranspiration. In Tasmania today, it occurs under canopy gaps and expands rapidly when the rainforest is disturbed (Macphail 1979). It colonizes abandoned fields and forest clearings, and being able to migrate freely, is a logical precursor to rainforest (G.S. Hope pers. comm.). The peak of *Dicksonia* in Burraga Swamp thus heralds the transition to temperate rainforest.

With the change from a lake to swamp environment, there was an initial transition period (subzone 2A) when *Nothofagus* increased and the forests occupied the site. The small grain type of Myrtaceae was abundant near the top of the transitional subzone, and *Myriopyllum,* either growing in water or on mud, was common. Then followed a period (subzone 2B) with maximum *Nothofagus* and less Myrtaceae. In subzone 2C, the percentages of *Nothofagus* suggest a slight decline, but the pollen concentrations are higher. The extremely high levels of Myrtaceae thus depressed the percentages of *Nothofagus*. This subzone has very high total pollen. These changes within the forests, however, are relatively minor.

In summary, during the lake phase, the vegetation around the site was open and grassy with sparse eucalypts, probably restricted to suitable habitats. About 6,500 years ago, peat started accumulating and the *Nothofagus* forests developed. Since about 6,000 years ago, there have been fluctuations in the forests at Burraga but they probably do not exceed the variability seen in the forests of the region today. There is a possibility that woody shrubs were once common in the swamp, whereas they are not present today.

DISCUSSION

During the last glacial period, about 26 to 12.5 thousand years, the climate was drier and very windy, with high evaporation and colder temperatures (Hope 1994). At the height of the last glacial period, the mean temperature was about 9°C lower than those of today in the Snowy Mountains (Galloway 1965). There were very few lakes and rivers trickled intermittently (Dodson 1992). The vegetation was open and herbaceous or shrubby, with few trees (Kershaw 1981, Dodson 1992, Hope 1994). The record in the Burraga Swamp sediments probably starts at the end of this glacial period, at a time when the severe climatic conditions were moderating and surface runoff became sufficient to form the lake.

It is unfortunate that the basal clay of the swamp has not been dated. Extrapolation of the average rate of sedimentation of the upper, dated sediments arrives at an approxi-

mate date of 12,000 years, but there is no reason to assume a uniform rate of sedimentation. The dated section of peat shows clearly that the rate of sedimentation was not uniform, with rapid accumulation in the lower half and slower accumulation in the upper part. Lake clays usually accumulate at slower rates than peats. In the study of the swamps at higher altitudes on the Barrington Tops (Dodson 1987), several swamps had a basal clay layer with overlying peat. All of the clays show a slower rate of accumulation, viz., 0.06 to 0.12 mm/yr for clay compared with 0.88 to 2.00 mm/yr for peat. Some of the clays started accumulating before 11,000 years, the oldest dates obtained by Dodson (1987). Most upland sites in southeastern Australia do not extend back beyond 11,000 years, due to gravels and soils underlying swamp and lake sediments (Hope 1994). In view of this evidence, the assumption that the base of the sediments at Burraga are approximately 12,000 years old is not unreasonable.

Changes in the swamp sediments are frequently accompanied by changes in the pollen spectrum. The major change, from Zone 1 to Zone 2 occurs at the clay/peat boundary, hence changes in hydrology occurred at the same time forests developed. The section from 420–500 cm, with too few grains to count, is gravelly and the high energy required to transport gravel is not conducive to pollen sedimentation. The thin peaty layer with roots in the clay at 350 cm depth is accompanied by very high Poaceae values, suggesting that grasses may have been important in this brief interlude of swamp vegetation in the lake phase. About 40 cm above both of the macroscopic charcoal layers in the peat, there is an increase in the pollen concentrations of *Nothofagus*, Myrtaceae and Cyperaceae (see Figs 6 and 8), suggesting that these taxa may have been stimulated by fire. The stimulation by fire of Myrtaceae, most likely *Leptospermum* in this case, is well known. After burning, *Nothofagus* probably regenerated by coppicing, and it may have taken some years before they flowered. Howard (1973) found that trees of *N. cunninghamii* from coppices had both a higher growth rate and an earlier seed production than those from seed. Mass flowering of the *Nothofagus* coppices probably coincided with the peak in the Myrtaceae pollen production.

The history of the swamp sediments at Burraga show similar patterns to the sites on the plateau studied by Dodson (1987). Clay underlies most of the peats and the oldest dates in the clay are more than 11,000 years B.P. The age at which peat starts accumulating is variable. The oldest peat, at Killer Bog, is a thin layer in the clay, dated at 8,230 years B.P. At the other sites, the beginning of peat accumulation starts later, with dates between 4,830 and 740 years B.P., and peat swamps are still forming on the plateau (Dodson 1987).

The pollen diagram shows two major vegetation types: an open grassland with sparse eucalypts, from about 12,000 to 6,500 years, followed by temperate *Nothofagus* forest, from about 6,500 to the present. The pollen analysis of Burraga Swamp may be compared with those studied by Dodson et al. (1986) for the Barrington Tops. Today, the plateau above 1,000 m supports a mosaic of sub-alpine grasslands, montane eucalypt forests, wet eucalypt formations, cool temperate rainforests and wetland communities. The open vegetation prior to 6,500 years at Burraga is similar to that described for about 11,000 years B.P. on the Barrington Tops, except that this latter study found a high Asteraceae (Tubuliflorae) content, whereas this pollen type is minimal at Burraga.

A number of sites on the plateau register *Nothofagus* in the profile (Dodson et al. 1986) and Fig. 12 compares the *Nothofagus* content of Burraga Swamp with that of the others on the Barrington Tops. Black Swamp, the closest to Burraga, has a very similar pattern of *Nothofagus* frequencies. Killer Bog, the most easterly of the sites and with extensive *N. moorei* forests around the site, would have been forested 9,000 years ago. These patterns suggest that the *Nothofagus* forests expanded westward about 6,000 years ago. Boggy Swamp, on the northeast of the plateau, shows a peak at roughly the same time. All the other sites on the higher and more westerly parts of the plateau, where there is little *Nothofagus* today, show relatively little *Nothofagus* pollen which may have been from long distance dispersal, or at most, from small, isolated local stands.

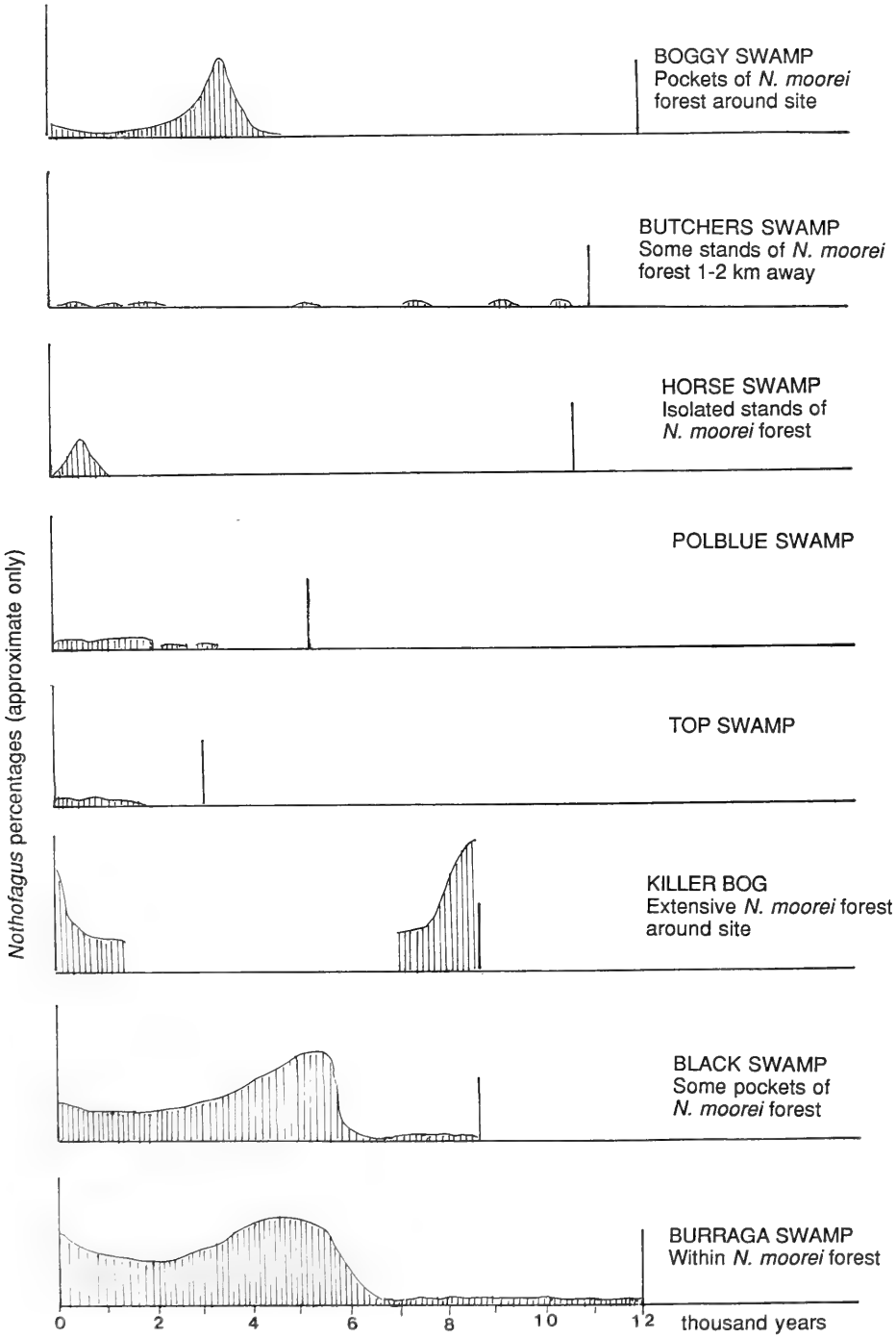


Figure 12. A comparison of the *Nothofagus* content of Burraga Swamp with that of the sites studied by Dodson et al. (1986). All sites are plotted to a uniform time scale and the percentages of *Nothofagus* are approximate only. For location of the sites, see Fig. 2

Dodson et al. (1986) found that all of the vegetation types had become established on the plateau by 9,000 years B.P. There was an expansion of wet eucalypt forests in the west and temperate rainforest in the south and east about 6,500 to 3,500 years, when *Nothofagus* moved into the Burraga site, most likely due to a change in climate. It is thought that an increase in temperatures, perhaps by 1–2°C (Dodson et al. 1994), accompanied by increased summer rainfall from the east and south, allowed this expansion of *Nothofagus*. There followed a contraction of these forests from about 3,500 years, thought to be the result of a slight cooling, and another expansion of the temperate forests about 1,500 years B.P. (Dodson et al. 1986). These latter trends are recorded in Burraga Swamp also.

Dodson et al. (1994) studied two cores with a maximum depth of 35 cm and age of 2,140 years from Burraga Swamp, to assess the effect of human impact. The core from the centre of the swamp registers an appreciable *Leptospermum* content and in the core from the edge, a little of the *Baeckea* type pollen. Relatively little change in the proportions of the temperate and eucalypt vegetation is indicated. Human impact is relatively slight, but there is an increase in the rate of erosion in the catchment at the beginning of the historical period (Dodson et al. 1994).

Ecological studies (Frazer and Vickery 1938, Turner 1976) note the lack of regeneration in mature stands of *Nothofagus moorei* and the occurrence of seedlings and saplings in the adjoining vegetation and conclude that the forest is migrating. Dodson et al. (1986) conclude that *Nothofagus* is expanding its distribution in the west but not in the east. Decreased charcoal input, probably as a result of fire control, may in part account for the small spread in *Nothofagus*. These changes have been going on for over the last 1,000 years (Dodson et al. 1986). In this study, the changes of *Nothofagus* parallel those of Dodson et al. (1986), but they fall within the variability seen in the forests today.

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REFERENCES

Birks, H.J.B. and Birks, H.H. (1980). 'Quaternary Palaeoecology'. (Edward Arnold: London).

Dodson, J.R. (1983). Modern pollen rain in southeastern New South Wales. *Review of Palaeobotany and Palynology* **38**, 249–286.

Dodson, J.R. (1987). Mire development and environmental change, Barrington Tops, New South Wales. *Quaternary Research* **27**, 73–81

Dodson, J.R. (1992). Dynamics of environment and people in the forested crescents of temperate Australia. In 'The Naive Lands. Prehistory and environmental change in Australis and the south-west Pacific' (Ed. J.R. Dodson) pp 115–159 (Longman Cheshire: Melbourne).

Dodson, J.R., Greenwood, P.W. and Jones, R.L. (1986). Holocene forest and wetland vegetation dynamics at Barrington Tops, New South Wales. *Journal of Biogeography* **13**, 561–585.

Dodson, J.R. and Myers, C.A. (1986). Vegetation and modern pollen rain from the Barrington Tops and Upper Hunter River regions of New South Wales. *Australian Journal of Botany* **34**, 293–304.

Dodson, J.R., Roberts, F.K. and De Salis, T.(1994). Palaeoenvironments and human impact at Burraga Swamp in montane rainforest, Barrington Tops National Park, New South Wales, Australia. *Australian Geographer* **25**, 161–169.

Forestry Commission of N.S.W. (1983). Map of the Boonabilla Management area (unpublished).

Frazer, L. and Vickery, J.W. (1937). The ecology of the upper Williams River and Barrington Tops districts. I. Introduction. *Proceedings of the Linnean Society of New South Wales* **62**, 269–283.

Frazer, L. and Vickery, J.W. (1938). The ecology of the upper Williams River and Barrington Tops districts. II. The rainforest formations. *Proceedings of the Linnean Society of New South Wales* **63**, 139–184.

Frazer, L. and Vickery, J.W. (1939). The ecology of the upper Williams River and Barrington Tops districts. III. The Eucalypt forests and general discussion. *Proceedings of the Linnean Society of New South Wales* **64**, 1–33.

Galloway, R.W. (1965). Late Quaternary climate in Australia. *The Journal of Geology* **73**, 603–618.
Harden, G.J. (1990–1993). 'Flora of New South Wales, Vols 1–4'. (New South Wales University Press: Sydney).
Hope, G.S. (1994). Quaternary vegetation. In 'History of the Australian Vegetation: Cretaceous to Recent'. (Ed. R.S. Hill) pp 268–389 (Cambridge University Press, Cambridge).
Howard, T.M. (1973). Studies in the ecology of *Nothofagus cunninghamii* Oerst. I. Natural regeneration on the Mt. Donna Buang Massif, Victoria. *Australian Journal of Botany* **21**, 67–78.
Kershaw, A.P. (1981). Quaternary vegetation and environments. In 'Ecological Biogeography of Australia' (Ed A. Keast) pp 81–102 (W. Junk: The Hague).
Macphail, M.K. (1979). Vegetation and climates in southern Tasmania since the last glaciation. *Quaternary Research* **11,** 306–341.
Maher, L.J. Jr. (1972). Nomograms for computing 0.95 confidence limits of pollen data. *Review of Palaeobotany and Palynology* **13**, 85–93.
McKellar, M.H. (1973). Dispersal of *Nothofagus* pollen in Eastern Otago, South Island, New Zealand. *New Zealand Journal of Botany* **11**, 305–310.
Moore, P.D., Webb, J.A. and Collison, M.E. (1991). 'Pollen Analysis Second Edition". (Blackwell Scientific Publications: London).
Turner, J.C. (1976). An altitudinal transect in rain forest in the Barrington Tops area, New South Wales. *Australian Journal of Ecology* **1**, 155–174.
Turner, J.C. (1981). The distribution of Australian rainforests. In 'Rainforest Conference, May 1981' pp 6–20. (Geographical Society of N.S.W. Conference Papers No. 1: Sydney).
Wakefield, N.A. (1955). 'Ferns of Victoria and Tasmania'. (Field Naturalists Club of Victoria: Melbourne).

APPENDIX 1

Species identified in the study area. Sample sites are: 1 = the swamp surface, 2 = *Nothofagus* forest around the swamp, and 3 = Riverine subtropical forest, 11 km from the swamp. Notes in the species list are: d = disturbed areas, e = edge of forest, l = in light breaks.

SAMPLE SITES:	1	2	3
Mosses			
Campylopus introflexus	+		
Dicronoloma dicarpum	+		
Holomitrium perichaetate		+	
Papillaria sp.		+	
Pteridophytes			
Arthropteris tenella		+	
Dicksonia antarctica		+	
Hymenophyllum sp.		+	
Hypolepis sp.		+	
Lastreopsis microsora	+	+	
Microsorum diversifolium		+	
M. scandens	+	+	
Pellaea falcata		+	
Pteris sp.	+		
Angiosperms			
Apiaceae: *Hydrocotyle tripartita*	+	+	
Apocynaceae: *Parsonsia straminea*		+	
Asteraceae: *Gnaphalium gymnocephalum*	+		
Bignoniaceae: *Pandorea pandorana*		+	
Boraginaceae: *Ehretia* sp.			+
Brassicaceae: *Cardamine hirsuta*	+		
Casuarinaceae: *Casuarina* sp.			+
Cunoniaceae: *Caldcluvia paniculosa*		+d	
Schizomeria ovata		+	
Cyperaceae: *Carex appressa*		+l	
C. inversa	+		
C. lobolepis	+		
Cyperus lucidus	+		
Scirpus inundata	+		
Dioscoreaceae: *Dioscorea* sp.		+	
Ebenaceae: *Diospyros australis*		+	
Escalloniaceae: *Quintinia sieberi*		+	

Euphorbiaceae: *Croton verreauxii*			+
Fabaceae: *Acacia melanoxylon*			+
Cassia sp.			+
Fagaceae: *Nothofagus moorei*		+	
Juncaceae: *Juncus usitasus*		+	
Lauraceae: *Cryptocarya* sp.		+	
Malvaceae: *Hibiscus* sp.			+
Meliaceae: *Synoum glandulosum*			+
Monimiaceae: *Doryphora sassafras*		+	
Moraceae: *Ficus coronata*			+
Myrsinaceae: *Rapanea howittiana*		+	
Myrtaceae: *Acmena smithii*		+	
Backhousia sp.			+
Eucalyptus laevopinea		+	
Syzygium australe		+	+
Tristaniopsis collina		+d	
Onagraceae: *Epilobium* sp.	+		
Orchidaceae	+		
Pittosporaceae: *Citriobatus* sp.		+	
Poaceae: *Agrostis avenacea*	+		
Echinopogon ovatus	+		
Glyceria australis	+		
Microlaena stipoides	+		
Phragmites australis	+		
Polygonaceae: *Polygonum subsessile*		+	
P. decipiens		+	
Proteaceae: *Orites excelsa*		+	
Rosaceae: *Rubus hillii*		+d	
R. rosifolius		+e	
Rubiaceae: *Coprosma quadrifida*		+	
Morinda jasminoides		+	
Rutaceae: *Melicope micrococca*			+
Sapindaceae: *Diploglottis australis*		+	
Scrophulariaceae: *Gratiola peruviana*	+		
Solanaceae: *Duboisia myoporoides*		+	
Solanum sp.		+	
Sterculiaceae: *Commersonia* sp.			+
Symplocaceae: *Symplocos* sp.		+	
Violaceae: *Hymenanthera dentata*		+	
Vitaceae: *Cayratia clematidea*		+	
Xanthorrhoeaceae: *Lomandra spicata*		+	

APPENDIX 2

The species represented by the pollen type.

Pollen type on pollen diagram	Plant species represented by pollen type	Distribution in vegetation
Nothofagus	*N. moorei*	restricted to rainforest
Myrtaceae	all species in Appendix A and any probable	all types of forest
Eucalyptus/ *Syzygium* type	all *Eucalyptus* spp. and *Syzygium australe*	a few eucalypts scattered in the rainforest, but mostly in mixed rainforest and eucalypt forest. *Syzygium* in rainforest to riverine forest
Small grain Myrtaceae (< 14 μm)	mostly probably *Tristaniopsis*, possibly *Backhousia* sp., maybe *Baeckea gunniana*, some *Acmena smithii*	*Tristaniopsis* in mixed rainforest. *Acmena* in *Nothofagus* forest, *Backhousia* in riverine forest. *Baeckea* not currently in area.
Melaleuca type	similar to *Melaleuca quinquenervia*	not currently in area
Casuarina	probably a mixture of *Casuarina* species	at least 11 km distant from swamp
Poaceae	all species in Appendix A	swamp surface
Cyperaceae	all species in Appendix A	swamp surface and in light breaks in *Nothofagus* forest
Hydrocotyle sp.	probably *Hydrocotyle tripartita*	swamp surface and rainforest
Ranunculus	*Ranunculus* spp.	swamp surface
Triglochin	*Triglochin* spp.	swamp surface
Periporate	*Polyporina granulata* Martin 1973, ?Caryophyllaceae	not sited in region at present
Asteraceae	probably 3 species but mostly *Gnaphalium gymnocephalum*	swamp surface
Myriophyllum spp.	probably *M. pedunculatum, M. varifolium, M. verrucosum*	currently not represented, but *M. pedunculatum* is found in the mud, other two found in water
Dicksonia	*Dicksonia antarctica*	rainforest and tall eucalypt forest
Other trilete	probably a mixture of *Hymenophyllum* sp., *Pellaea falcata, Pteris* sp.	rainforests

Polypodiaceae	probably *Microsorum scandens* and *M. diversifolium*	swamp surface and rainforest
Other Monolete	mostly *Lastreopsis microsora* and *Hypolepis* sp.	swamp surface and rainforest
Unidentifiable	all grains which could not be placed into a taxonomic group owing to its crumpled or broken or degraded state	

The Stratigraphic Palynology of Bores Along the Darling River, Downstream From Bourke, New South Wales.

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The palaeovalley of the Darling River has been interpreted as a series of small en echelon basins or shallow grabens, with Tertiary fill overlying the Early Cretaceous basement. A saline aquifer is trapped at some depth and where deflected upwards, discharges into the river in places, such as near Glen Villa, downstream from Bourke. The palynology shows that the base of the Tertiary sediments is late Eocene at Tilpa and late Oligocene–early Miocene from Louth to 'Jandra'. The basement is earliest Early Cretaceous and may be of marine or freshwater origin.

The vegetation was probably a mixture of rainforest and Casuariaceae forests through the Tertiary, indicative of a much higher precipitation than that of today. In the late Pliocene-Pleistocene the forests had disappeared and the vegetation had become open, indicating a reduced precipitation, but it was considerably higher than that of today. The palaeoenvironments recorded by the Tertiary sediments suggest freshwater deposition. The high salinities have developed subsequent to the early Pleistocene.

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KEYWORDS: Palynology, Tertiary, Darling River, saline groundwaters, history of the vegetation.

INTRODUCTION

When Charles Sturt explored the Darling River, he discovered unpotable saline water, downstream of Bourke. In certain places, saline water is discharged into the river from a thick, saline aquifer in the Tertiary sediments that fill the ancient valley. The Darling River (Fig 1) follows an ancient fracture zone of the Darling River Lineament (Mount 1992). The Tertiary sediments southwest of Bourke fill a series of discontinuous shallow basins that are potentially favourable for pollen preservation. To be preserved, pollen must be buried sufficiently to escape the destructive effects of a fluctuating watertable. Outside of the Murray Basin, with its active though slight tectonism (Brown 1989), where Tertiary pollen assemblages are commonly encountered (Martin 1984a, 1984b, 1993, Macphail and Truswell 1989, 1993), few such Tertiary assemblages have been found west of the Western Slopes of New South Wales.

Tertiary palynofloras in these inland arid regions are of special interest for they assist in the understanding of the evolution of the arid vegetation. They may also provide some evidence of the development of saline groundwaters as the microplankton content may indicate the water quality at the time of deposition. This paper presents the palynology of the Tertiary sediments of the Darling River palaeovalley and the underlying Cretaceous basement, where encountered.

MATERIALS AND METHODS

Samples used in this study are cuttings as core samples were not available. The possibility of contamination is greater with cuttings, both from carry down with the circulating

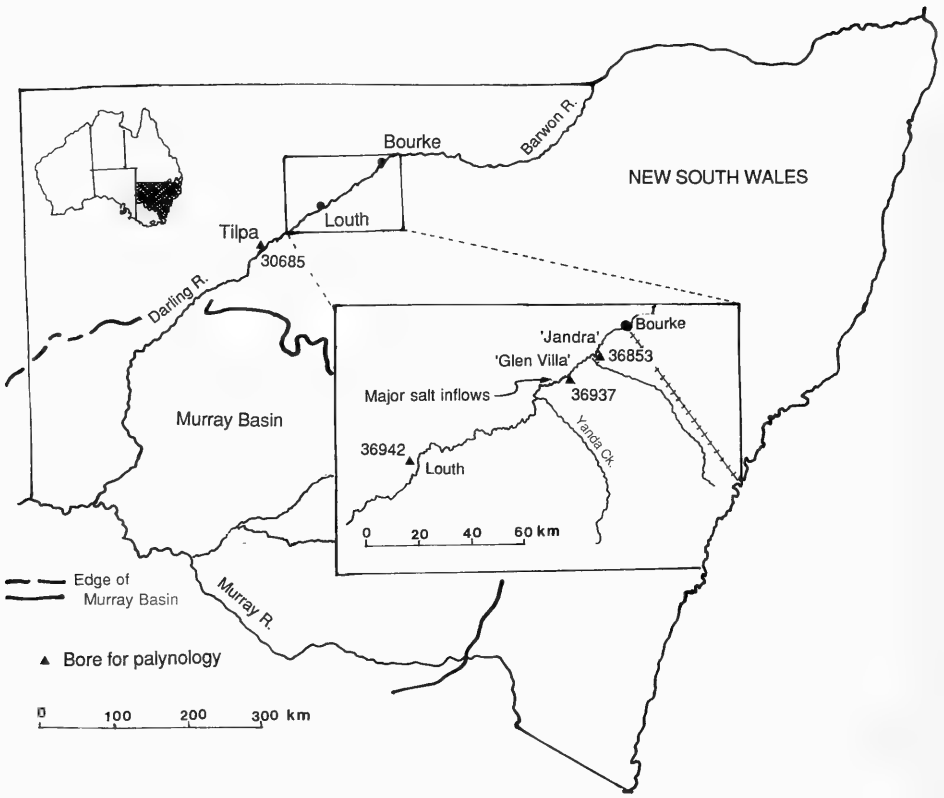

Figure 1. Locality map.

mud and from cavings, but with proper drilling and sampling procedures, relatively uncontaminated samples may be obtained. For investigative drilling, the mud is circulated until it is clean of the coarse fraction and this practice greatly reduces contamination. Contamination may be assessed from bores that penetrate both the Tertiary sediments and the Cretaceous basement, where Tertiary contamination is either absent or minimal in the Cretaceous assemblages, thus increasing confidence in the reliability of the samples. Barren samples may occur anywhere in the sequence and these would not be possible with appreciable contamination. While the possibility of contamination can not be ruled out completely, cuttings produce consistent patterns, repeated in bore after bore, and this consistency would not be possible with appreciable contamination. There is thus reasonable confidence that these samples produce reliable results (Martin 1984c).

Preparation techniques used hydrochloric and hydrofluoric acids to remove the mineral material, controlled oxidation with cold Schultz solution, and potassium carbonate to clear the residues which were then mounted in glycerine jelly.

GEOLOGY

The Darling River Lineament (Mount 1992) defines the junction between outcrops of the Lachlan Fold Belt to the southeast and the Great Artesian Basin to the north. The palaeovalley of the Darling River was formed partly by the downwarping and block col-

lapse of an older surface, possibly a peneplain, and partly by concurrent erosional incision. The basins forming the palaeovalley of the Darling River have been interpreted as a chain of en echelon grabens, to approximately 150 m depth, strung out along the Darling River Lineament. These grabens have been formed in response to alternating sinstral, but predominantly dextral strike-slip movement, probably in the upper mantle, along the Darling River Lineament (Mount 1992). The Cainozoic valley deposits form a linear belt along the lineament.

Two main units are recognised in the Tertiary valley fills:

(1) An upper grey, silty clay of the modern floodplain, approximately 7–10 m thick, which is probably equivalent to the Shepparton Formation in the Murray Basin, of Pliocene-Quaternary age. In places, the river has cut through this unit.

(2) A main aquifer zone below the 'Shepparton Formation' equivalent. It consists of an upper sand layer, two main cycles of coarse sand and fine gravels in the middle and towards the base, carbonaceous muds containing wood fragments. This unit is thought to be equivalent to the upper part of the Palaeogene Renmark Group of the Murray Basin (Mount 1992) but this study shows that it is mid-late Tertiary and possibly early Pleistocene in age.

Individual bores showed minor grey clay lenses through the second unit. The grey and carbonaceous clays are best for palynology, but pollen recovery has been sporadic. The lithologic logs of the bores are shown in Table 1.

TABLE 1

Lithologic logs. The ages given for the palynological samples are from this study.

DEPTH (M)	DESCRIPTION
Bore 30685	**Tilpa**
0–11.3	Grey sandy clay
11.3–21.6	Sandrock
12.6–26.2	Grey clay
26.2–37.5	Grey clay and sandrock Sample for palynology, 30.5 m, barren
37.5–59.4	Grey clay
59.4–70.1	Grey sandy clay
70.1–212.7	Dark green shale with hard bands. Sample for palynology, 72.6 m, late Eocene Sample for palynology, 91.4 m, Early Cretaceous
212.7–214.8	Dark green shade Sample for palynology, 213.4 m, Early Cretaceous
Bore 36942	**Louth**
0–9	Yellow grey, grey brown and light grey clay and silty clay
9–15	Grey to yellow quartz sand with gravel at the base
15–22	Light to mid grey clay with wood at the base Sample for palynology, 20–22 m, late Pliocene–early Pleistocene
22–24	Quartz sand with some fine gravel
24–30	Grey clay, silty clay and gravelly clay
30–32	Quartz sand with some clay and wood

32–41	Light grey clay with minor mottles, laminations and silty bands
41–46	Quartz sand with minor yellow silt
46–47	Quartz gravel and yellow clay
47–48	Silcrete, fine gravel and siliceous sandstone
48–59	Mid to dark grey clay with minor carbonaceous bands 2 samples for palynology, 49–50 m and 50–51 m, Early Cretaceous
59–60	Fine grained quartzose sandstone with minor mid to dark grey siltstones Sample for palynology, 59.2 m, Early Cretaceous
Bore 36937	**Glen Villa**
0–12	Pale grey and pale brown clay and silt, some mottling
12–13	White kaolinitic sand
13–49	Sand in a pale grey to white and pale yellow to yellow clay matrix
49–56	Gravelly coarse sand, quartzitic
56–57	Lignitic dark brown humus with peaty wood chips. Sample for palynology, 56–57 m, late Oligocene–early Miocene
57–61	Sand, pale grey
61–69	Sand and gravel, pale grey
Bore 36853	**'Jandra'**
0–10	Grey brown and yellow brown clay
10–17	Fine sand, light yellow brown
17–19	Sandy clay, blue green and light grey
19–21	Quartz gravel with light grey clay
21–27	Grey clay Sample for palynology, 21–23 m, late Pliocene–early Pleistocene
27–35	Light yellow brown clay
35–47	Sand with light grey and yellow brown clay
47–55	Dark grey clay with some sand
55–71	Sand, carbonaceous in places Sample for palynology, 61–63 m, ?mid–late Miocene
71–139	Quartz gravel with minor sand layers, light grey
147	Shale, dark grey to black Sample for palynology, 147 m, Early Cretaceous
147.4	Shale and sandstone

Salt inflows are located in the bed of the river and are controlled by the geological structure. A saline aquifer is trapped beneath the 'Shepparton' clays and a ridge of bedrock at 'Jandra' functions as a subsurface 'dam' and impedes the southwesterly movement of the groundwater. The work of Mount (1992) has developed a model for saline groundwater inflows to the River in terms of geological and structural control of the saline aquifer, especially the regional lineaments and the en echelon graben geometry of the Tertiary basins along the Darling River (Mount 1992).

STRATIGRAPHIC PALYNOLOGY

Early Cretaceous

'Jandra' bore 36853 at 147 m, Louth bore 36942 at 49–59 m and Tilpa bore 30685 at 91–213 m (Table 2)

TABLE 2

Cretaceous species identified. References: (1) Dettmann 1963, (2) Helby et al. 1987, (3) Backhouse 1978, (4) Lentin and Williams 1989, (5) Morgan 1980, (6) Playford and Dettmann 1965.

Locality	Jandra	Louth			Tilpa	
Bore (DWR)	36853	36942			30685	
DEPTH m	147	49–50	50–51	59.2	91.4	213.4
SPORES						
Aequitriradites spinulosus 1			+			+
A. *verrucosus* 1			+			
Baculatisporites comaumensis 1	C	+	+	+	+	+
Ceratosporites equalis 1	+	+	+	+	+	+
Cicatricosisporites australiensis 1						+
C. ludbrookii 1				+		
Coptospora striata 1						+
Couperisporites tabulatus 1						+
Crybejosporites stylosus 1	+	+			+	
Cyathidites australis 1	+	+	C	+	+	+
C. concavus 1		+				
C. minor 1	+	+			+	+
Cyclosporites hughesii 1	+					
Dictyophyllidites pectinataefornis 1			+			
Dictyotsporites complexis 1	+			+		
D. speciosus 1	+					
Foraminisporis dailyi 1	+					+
F. wonthaggiensis 1						+
Foveosporites canalis 1				+		
F. parviretus 1		+				
Gleicheniidites circinidites 1	+	C	+		+	+
Ischyosporites punctatus 1	+					
Klukisporites scaberis 1		+				
Krauselisporites linearis 1	+					
Leptolepidites verrucatus 1		+		+	+	+
Lycopodiacidites asperatus 1	+					
Murospora florida 1						+
Neoraistrickia truncatus 1	+	+	+	+		+
Osmundacidites wellmanii 1	+	+	+	C	+	+
Pilosisporites notensis 1	+				+	+
P. parvispinosus 1						+

Polycingulatisporites sp 6	+					
Reticuloidosporites arcus 1	+					
Retitriletes (=Lycopodiumsporites) austroclavatidites 1, 2	+		+	+	+	+
R. circomlumensus 1, 2	+	+	+	+	+	+
R. eminulus 1, 2		+			+	+
R. facetus 1, 2		+				
R. nodosus l, 2	+			+	+	+
R. reticulumsporites 1, 2				+		
R. watherooensis 3		+	+			
Retitriletes spp		C	+	+		
Rouseisporites sp 1			+			
Sestrosporites pseudoalveolatus 1				+	+	
Stereisporites antiquasporites 1	+	+	+		+	+
Triletes cf *T. tuberculiformis* 1	+	+	+			
GYMNOSPERMS						
Araucariacites australis 1	C	+	+	+	+	C
Alisporites grandis 1	+				C	C
A. similis 1					C	C
Alisporites spp		C	C	C		
Corallina torosa (= Classopollis classoides) 1, 3	+	+	+	+	+	+
Ginkgocyadophytus nitidus 1				+		
Microcachryidites antarcticus 1	C	C	C	C	C	C
Podocarpidites spp 1	C	C	C	C	C	C
Podospirites microsaccatus 1	+				+	
DINOGLAGELLATES AND ACRITARCHS						
Adanatosphaeridium sp 4	+					
Canningia sp A of Morgan 4, 5					+	
Cleistosphaeridium ancoriferum 4					+	+
Cribroperidinium edwardsii 4					+	
C. perforans 4						+
Diconodinium cf. *D. davidii* 4					+	
Hesterotonia cf. *H. stricta* 4					+	
Heterophaeridium sp 4	+					
Kiokansium polypes 4	+					
Leptodinium episomum 4					+	
Micrhystridium sp	+				C	+
Muderonga cf. *M. staurota* 4						+
Nummus monoculatus 4	+					
Oligosphaeridium complex 4	+					
O. pulcherrimum 4	+					+
Spiniferites spp 4	+				+	
Tenua hystrix 4	+				C	
Trichodinium sp 4					+	
Zone	*C. hughesii*		*C. australiensis*		*C. hughesii*	

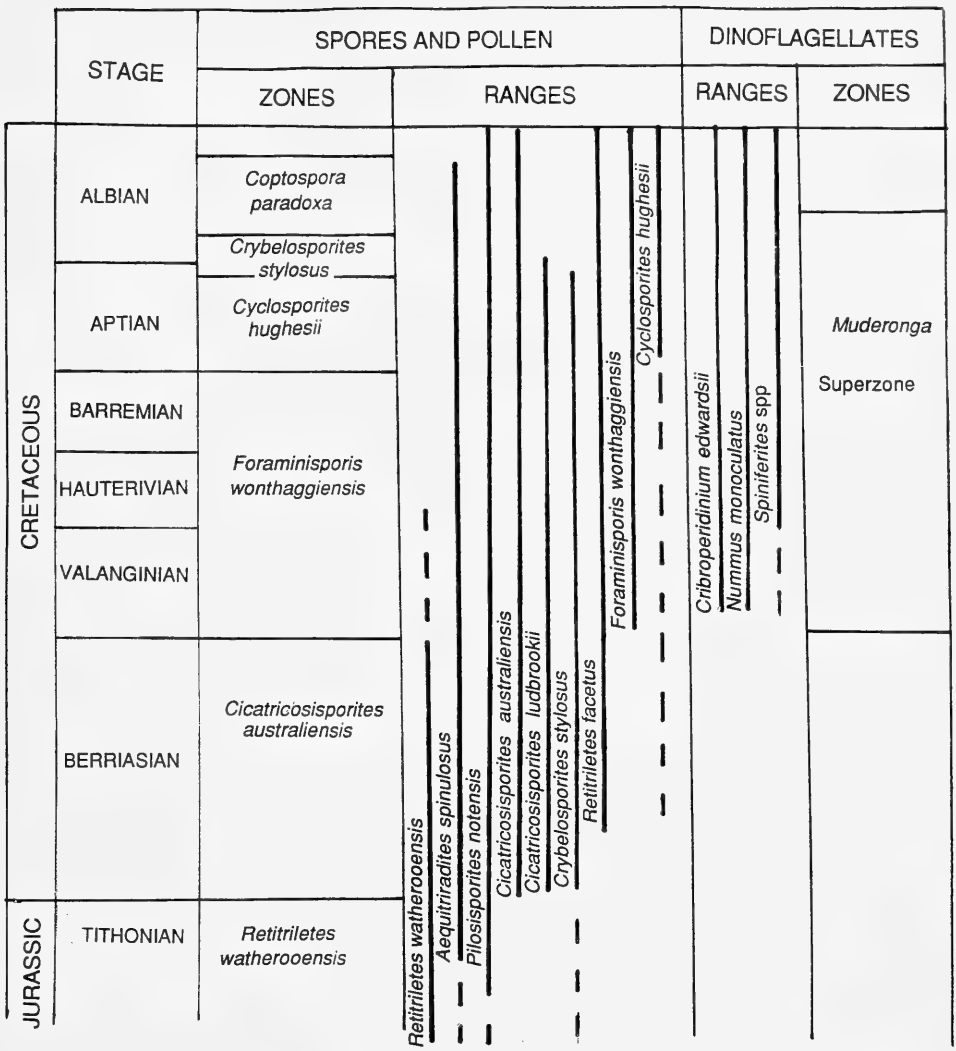

Figure 2. Early Cretaceous palynological zones and the ranges of diagnostic species. From Helby et al (1987) and Dettmann and Playford (1969).

The assemblages have a rich diversity of species. The gymnosperms *Microcachryidites antarcticus, Podocarpidites* spp and *Alisporites* spp are common and characteristic of the *Microcachryidites* Superzone of Berriasian into Albian age (Fig. 2). The diagnostic species *Crybelosporites stylosus* and *Cicatricosisporites ludbrookii* indicate the *Cicatricosisporites australiensis* Interval Zone of Berriasian age, in bore 36492, 49–51 m, at Louth (see Fig. 1 for bore locations). *Pilosisporites notensis* indicates the *Cyclosporites hughesii* Interval Zone of Aptian age in bore 30685, 91–213 m, at Tilpa. Bore 36853, 147 m, at 'Jandra' has the diagnostic species *Cyclosporites hughesii*, indicative of the *C. hughesii* Interval Zone (Fig. 2).

Dinoflagellates are present in two of the bores The assemblages are very limited,

but the diagnostic species *Cribroperidinium edwardsii* and *Spiniferites* spp are both present in the upper level of bore 30685, Tilpa, and their first appearance indicates the *Muderonga* Superzone (Helby et al 1987). The diversity is too limited for a more specific zone determination. Bore 36853, 'Jandra' has *Nummus monoculatus* and *Spiniferites* sp, also indicative of the *Muderonga* Superzone of Valangian-Albian age. The spore/pollen *Cyclosporites hughesii* Zone, of Aptian age, falls within the Valangian-Albian, as shown in Fig. 2.

These dinoflagellates, together with good spore/pollen assemblages, indicate deposition under marginal marine conditions. Early Cretaceous deposition was thus marginal marine during the younger Aptian *C. hughesii* Interval Zone in bore 36853 at 'Jandra' and 30685 at Tilpa, and freshwater during the older Berriasian *C. australiensis* Interval Zone in bore 36942 at Louth.

Cainozoic

(Table 3, Fig. 3)

TABLE 3

Tertiary spores and pollen. References: (1) Stover and Partridge 1973, (2) Dettmann 1963, (3) Martin 1973a, (4) Alley and Broadbridge 1992, (5) Martin and McMinn 1993, (6) Harris 1965, (7) Cookson and Pike 1954, (8) Pocknall and Mildenhall 1984, (9) Truswell et al. 1988, (10) Macphail and Truswell 1989, (11) Germeraad et al. 1968, (12) Martin 1973b, (13) Macphail and Truswell 1993, (14) Mildenhall and Crosbie 1979, (15) Martin 1974, (16) Cookson 1953, (17) Van Geel and van der Hammen 1978.

Locality	Jandra	Louth		G. Villa	Jandra		Tilpa
Bore (DWR)	36853	36942		36937	36853		30685
Depth	21–22	20–21	21–22	56–59	61–62	62–63	72.6
SPORES							
Baculatisporites disconformis 1					1.5	0.7	
Ceratosporites equalis 2							0.4
Cingulatisporites bifurcatus 3		0.7					
Cyatheacidites annulatus 1				+			
Cyathidites australis 1				0.7			+
C. paleospora 4			0.7	0.7	5.9	3.5	
Gleicheniidites circinidites 3	2					+	
Klukisporites lachlanensis 3				0.7	+	0.7	
Laevigatosporites ovatus 3					+	0.7	
Polypodiaceoisporites sp 5				0.7	0.7	1.4	
Polypodiidites sp 3					0.7		0.4
Reticulatisporites cowrensis 3/ *Rugulatisporites micraulaxis* 1		2.0	0.7		+	0.7	
Reticulatisporites echinatus 3		0.7					
Rouseisporites sp 3	+	4.0	2.7	1.3	0.7		
Rugulatisporites trophus 1					0.7	+	
Todisporites sp 3					0.7	1.4	
GYMNOSPERMS							
Araucariacites australis 3	4	0.7	2.0	1.3	7.3	5.7	0.9
Cupressaceae 3			0.7	0.7			0.4

Dacrycarpites australiensis 3				1.3	2.2	3.6	
Dilwynites granulatus 6				0.7			0.4
Lygistepollenites florinii 1					2.2		4.0
Pavisaccites catastus 1							0.4
Phyllocladidites palaeogenicus 7				+			
P. mawsonii 1							0.4
Podocarpidites spp 2			0.7	1.3	14.0	11.4	2.7
Podosporites microsaccatus 2						0.7	
ANGIOSPERMS							
Acaciapollenites myriosporites 8	1	4.0	4.0				
Anacolosidites acutullus 1							+
A. sectus 1							0.4
Banksieaidites arcuatus 1							0.9
B. elongatus 1	1					0.7	
Canthiumidites cf *C. oblatus* 8						0.7	
Chenopodipollis chenopodiaceoides 9	9	2.7	4.0	0.7			
Convolvulaceae (panporate)				+			
Corsinipollinites sp 10				3.4		0.7	
Cupaneidites orthoteichus 1				0.7	0.7	2.1	
Cyperaceaepollis 9		0.7	1.3	0.7			
Dodonaea sphaerica 3		0.7					
Fenestites sp 11	3						
Graminidites monoporites 3	10	3.4	2.0				
Gyrostemonaceae 9		0.7					
cf *Hakea*		1.3	1.3				
Haloragacidites haloragoides 3	5	8.8	10.8				
H. harrisii 1	7	20.0	20.3	37.8	20.6	23.6	39.8
Liliacidites sp 1					1.5		
Malvaceae sp 1			0.7				
Malvaceae sp 2			0.7				
Malvacearumpollis sp 9						0.7	
Malvacipollis sp 1						0.7	1.8
Montia sp 12	1						
Myriophyllum sp		2.0	4.0				
Myrtaceidites eucalyptoides 3	8	1.3	3.4	2.7	3.7		0.9
M. cf *M. eucalyptoides*			4.7	1.3			
M. parvus 3	1	0.7		1.3	2.2	4.3	2.9
M. verrucosus 1							+
Myrtaceae unidentified	1	6.7	7.4	8.1			0.4
Nothofagidites asperus 1				0.7	2.2	0.7	
N. emarcidus 1				9.4	8.8	17.1	14.5
N. falcatus 1					1.5	1.4	0.9
N. vansteenisii 1					0.7	0.7	2.7
Nusipollenites sp *(Dodonaea triquetra)* 9					+		

Perfotricolpites digitatus 11				+			
Periporopollenites demarcatus 1							0.9
P. vesicus 1							0.4
Polyorificites oblatus 3				0.7			8.6
Polyporina granulata 3		0.7	0.7				
Propylipollis ivanhoensis					0.7		0.4
Proteacidites pseudomoides 1					0.7		
P. rectomarginis 1							+
P. reticuloscabratus 1							0.9
P. symphyonemoides 1				+	0.7		
Proteacidites sp		0.7			0.7	1.4	
Rhoipites ampereaformis 13						0.7	
Santalumidites cainozoicus 1							0.4
Sapotaceoidaepollenites rotundus 6							4.1
Simplicepollenites meridianus 1							0.9
Sparganiaceaepollenites barungensis 6		1.2		2.7			
S. sphericus 14					2.9	+	
Tricolporites substriatus 3/*T. paenestriatus* 1				0.7	0.7		
Tricolporopollenites endobalteus 15					0.7	1.4	1.8
Tubulifloridites antipodica/simplis 3	24	29.0	23.0				
T. pleistocenicus 3	15						
Unidentified monosulcates		1.3					
Unidentified tricolpate/tricolporates	7	4.7	8.8	19.6	14.6	11.0	3.6
Unidentified triporates							1.8
ALGAE							
Botryococcus 16				+	+		
Debarya 17	+						
Pediastrum 16				+	C		
SUMMARY OF MAJOR POLLEN GROUPS							
Spores	3	7.4	4.0	4.0	11.0	8.5	0.9
Gymnosperms	4	0.7	2.7	5.4	26.5	21.4	9.9
Casuarinaceae	7	20.0	20.3	37.8	20.6	23.6	39.8
Myrtaceae	8	8.8	15.5	13.5	5.9	4.3	5.0
Nothofagus				10.1	13.2	20.0	18.1
Asteraceae	42	29.0	23.0				
Cyperaceae		0.7	1.3	0.7			
Poaceae	10	3.4	2.0				
Chenopodiaceae/Amaranthaceae	9	2.7	4.0	0.7			
Age		Late Pliocene–early Pleistocene		L. Oligo early Mio	Mid–late Miocene		Late Eocene

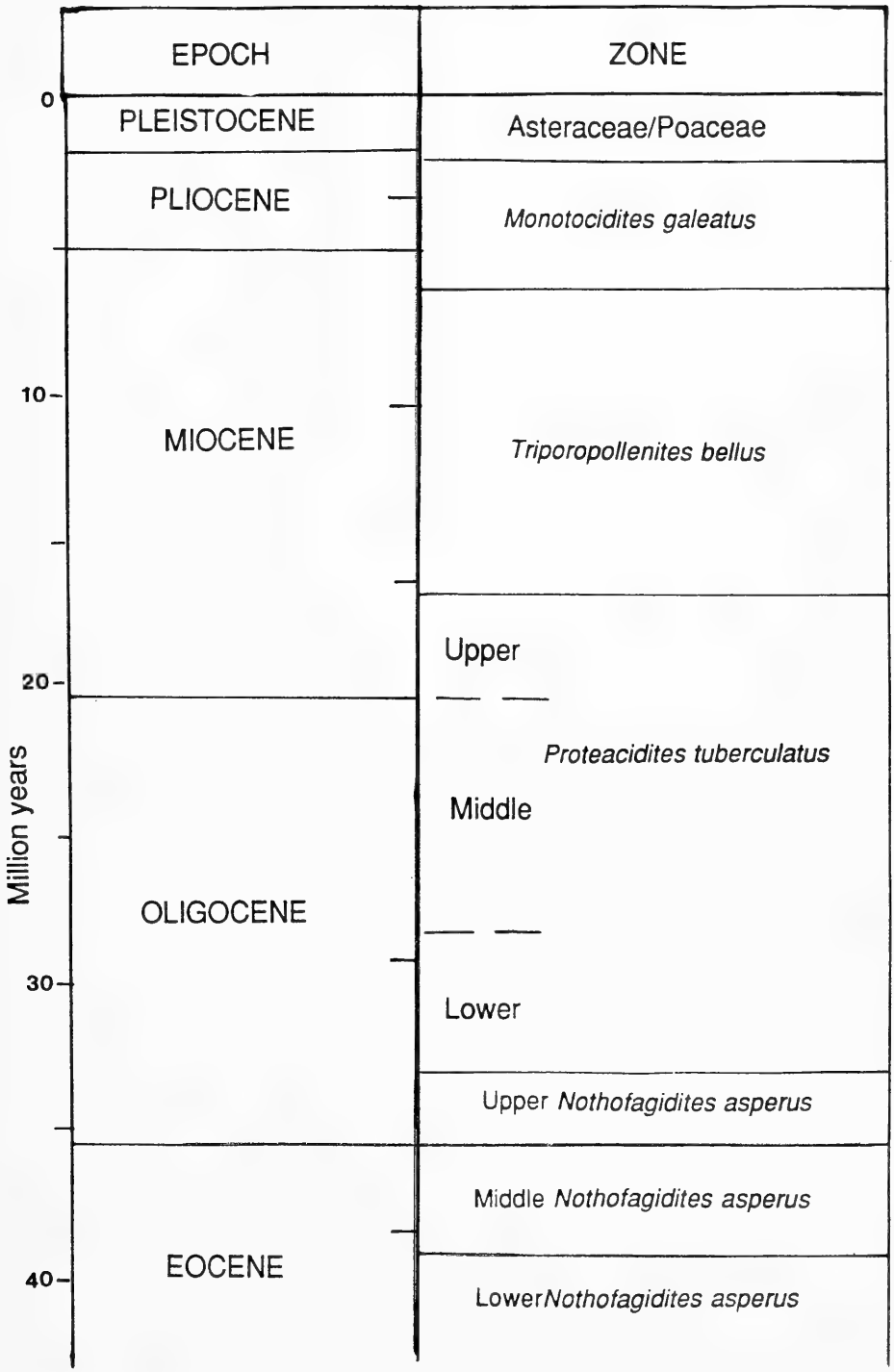

Figure 3. Cainozoic palynological zonation. From Stover and Partridge (1973), Macphail and Truswell (1993) and Martin (1987).

1). Late Eocene Middle *Nothofagidites asperus* Zone, Tilpa, bore 30685 at 72.6 m

The diagnostic species *Anacolosidites sectus* is restricted to the late Eocene Middle *N. asperus* Zone (Stover and Partridge 1973). *Banksieaidites arcuatus* and *Proteacidites reticulscabratus* are commonly found in the late Eocene and the ranges of *Santalumidites cainozoicus* and *Simplicepollenites meridianus* end at the top of the Middle *N. asperus* Zone. This assemblage is thus a correlative of the Middle *N. asperus* Zone (Stover and Partridge 1973, 1982).

Haloragacidites harrisii (Casuarinaceae) is abundant with lesser amounts of *Nothofagidites* spp and when compared with many other late Eocene assemblages, frequencies of the proteaceous pollen type (*Propylipollis* spp and *Proteacidites* spp) are unusually low. Other angiosperm pollen types are well represented, especially *Sapotaceoidaepollenites rotundus* and *Polyorificites oblatus.*

2). Late Oligocene-early Miocene, the upper part of the *Proteacidites tuberculatus* Zone, 'Glen Villa', bore 36937 at 56–59 m

The assemblage lacks diagnostic species of the latest early-mid Miocene *Triporopollenites bellus* Zone hence is placed in the underlying upper part of the *P. tuberculatus* Zone of late Oligocene-early Miocene age. *Acaciapollenites myriosporites* first appears in the early Miocene (Stover and Partridge 1973) but it is not present here, hence a late Oligocene age cannot be excluded. This pollen type, however, is rare in the early Miocene, hence its absence does not signify this assemblage is not of this age. *Cyatheacidites annlatus* and *Corsinipollenites* sp demonstrate the interval is no older than the *P. tuberculatus* Zone

Haloragacidites harrisii is abundant and there are lesser amounts of *Myrtacidites* spp and *Nothofagidites* spp. The relative abundances of spores and gymnosperms (see Table 3) are low and there is a rich diversity of low frequency angiosperms.

3). Mid-late Miocene, *T. bellus* Zone, 'Jandra', bore 36853 at 61–63 m

The diagnostic species *Proteacidites symphyonemoides* and *Reticulatisporites cowrensis* first appear in the latest early-mid Miocene *T. bellus* Zone (Stover and Partridge 1973). *Rhoipites ampereaformis*, also present, first appears in the late Miocene-early Pliocene *M. galeatus* Zone (Macphail and Truswell 1993), but only one specimen was found and diagnostic species may occaisionally be found earlier than their accepted first appearance, and it may be a contaminant from the drilling mud. The relatively high abundance of the gymnosperms and *Nothofagus*, especially the *brassopora* species (*N. emarcidus*, *N. falcatus* and *N. vansteenisii*), are typically that of the *T. bellus* Zone. There are no other features which would definitely indicate the *M. galeatus* Zone, hence this assemblage is assigned to the latest early-mid Miocene *T. bellus* Zone.

4). Late Pliocene-early Pleistocene, Asteraceae-Poaceae phase, Louth, bore 36942 at 20–22 m and 'Jandra', bore 36853 at 21–22 m.

The abundance of *Tubulifloridites* spp with some *Graminidites monoporites* indicates the Asteraceae/Poaceae phase of late Pliocene-early Pleistocene (Martin 1987). *Polyporina granulata* and *Tubulifloridites pleistocenicus* first appear in the late Pliocene-early Pleistocene also.

The two assemblages from bore 36942 lack *T. pleistocenicus*, have lower frequencies of *Graminidites monoporites* and more *Haloragacidites harrissii* than in bore 36853, hence they present a somewhat older aspect than the higher frequencies of *T. pleistocenicus* in bore 36853 that are usually found in younger early Pleistocene assemblages.

In all of these Cainozoic assemblages, no dinoflagellates or any other indication of marine conditions are present. The algae recorded occaisionally (see Table 3) may all be found in fresh water to brackish environments.

DISCUSSION

Fig. 4 presents a summary of the palynology. In so far as pollen has been recovered, the Tertiary sediments overlying the Early Cretaceous basement are late Eocene at Tilpa and late Oligocene-early Miocene at Louth to 'Jandra'. Mid-late Miocene and late Pliocene-early Pleistocene assemblages are present also, further up the sequence. The Early Cretaceous basement may be either marine or non-marine, but the Tertiary sediments are all fresh water to brackish.

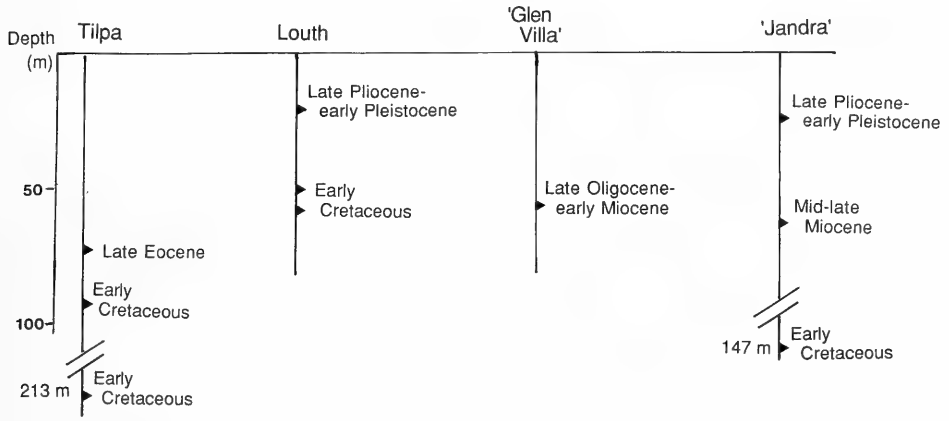

Figure 4. Summary cross section of the bores along the Darling River. For location of bores, see Fig. 1.

TABLE 4

Botanical affinities of the Tertiary spores and pollen.

Fossil Name	Botanical affinity
SPORES	
Baculatisporites disconformis	Osmundaceae
Ceratosporites equalis	*Sellaginella*
Cingulatisporites bifurcatus	Anthocerotae
Cyatheacidites annulatus	
Cyathidites spp	*Cyathea*
Gleicheniidites circinidites	*Gleichenia*
Polypodiaceoisporites sp	*Pteris*
Rouseisporites sp	Hepatic
Todisporites	Osmundaceae
GYMNOSPERMS	
Araucariacites australis	Araucariaceae
Cupressaceae	Cupressaceae
Dilwynites granulatus	Araucariaceae
Lygistepollenites florinii	*Dacrydium*
Pavisaccites catastus	*?Dacrydium*
Phyllocladites mawsonii	*Lagarostrobos franklinii*
P. palaeogenicus	*Phyllocladus*
Podocarpidites sp	*Podocarpus sens. lat.*

ANGIOSPERMS

Acaciapollenites myriosporites	*Acacia*
Anacolosidites spp	*Anacolosa*
Banksieaeidites spp	Banksieae
Canthiumidites cf C. *oblatus*	Rubiaceae
Chenopodipollis chenopodiaceoides	Chenopodiaceae/Amaranthaceae
Convolvulaceae (panporate)	Convolvulaceae
Corsinispollinites	*Ludwidgia*
Cyperaceaepollis	Cyperaceae
Dodonaea sphaerica	*Dodonaea*
Fenestrites	Asteraceae, Liguliflorac
Graminidites media	Poaceae
Hakea	*Hakea*
Haloragacidites haloragoides	*Haloragis*
H. harrisii	Casuarinaceae
Liliacidites	?Liliales
Malvaceae	Malvaceae
Malvacearumpollis	Malvaceae
Malvacipollis sp	*Austrobuxus/Dissiliaria*
Montia	*Montia*
Myriophyllum	*Myriophyllum*
Myrtaceidites eucalyptoides	Angophora/bloodwood eucalypt type
M. cf *M. eucalyptoides*	Other eucalypts
M. parvus	*Tristania/Backhousia/Baeckea*
M. verrucosus	*Archirhodomyrtus/Rhodomyrtus*
Myrtaceae unidentified	Myrtaceae
Nothofagidites emarcidus	*Nothofagus brassii type*
N. falcatus	*Nothofagus brasssii* type
N. vansteenisii	*Nothofagus brasssii* type
Nuxipollenites sp *(Dodonaea triquetra)*	*Dodonaea triquetra*
Perfotricolpites digitatus	*Merrimia*
Periporopollenites demarcatus	—
P. vesicus	—
Potyorificites oblatus	*Austrobuxus/Dissilaria*
Propylipollis ivanhoensis	*Helicia/Orites*
Proteacidites rectomarginis	—
P. reticuloscabratus	—
Santalumidites cainozoicus	*?Santalum*
Sapotaceoidaepollenites rotundus	Sapotaceae
Simplicepollis meridianus	—
Sparganiaceaepollenites barungensis	Sparganiaceac
S. sphericus	Sparganiaceae
Tricolporopollenites endobalteus	*Macaranga/Mallotus*
Tubulifloridites antipodica/simplis	Asteraceae
T. pleistocenicus	Asteraceae
Unidentified monosulcates	Monoctyledons, probably some palms
Unidentified tricolpate/tricolporates	Dicotyledons
Unidentified triporates	Dicotyledons

Casuarinaceae and to a lesser extent, *Nothofagus* (see Table 4 for botanical affinities) are the predominant pollen types in the late Eocene palynofloras. There is an unusually low content of the proteaceous pollen type but other rainforest angiosperms, such as Sapotaceae and *Austrobuxus/Dissiliaria* are well represented. There is a diversity of rainforest gymnosperms and under-represented angiosperms. The vegetation was a mixture of forests, probably mostly Casuarinaceae forests with limited patches of *Nothofagus* forests and possibly other rainforest types within the catchment. The rainfall was relatively high, above 1,500 mm p.a., the lower limit for rainforest (Martin 1987).

Vegetation in the late Oligocene-Miocene and mid-late Miocene was a mixture of forest types where Casuarinaceae, *Nothofagus* and gymnosperms were common. The Glen Villa site probably represents a backswamp where *Ludwidgia* (*Corsinipollinites*) grew. Previous studies on the Miocene vegetation show that there was considerable variation (Martin 1990). The rainfall would have been much the same as above.

The late Pliocene-early Pleistocene palynofloras, with their high content of herbaceous taxa (Asteraceae, Poaceae, Cyperaceae and Chenopodiaceae) indicate open vegetation, implying that the forests had disappeared. Casuarinaceae and the eucalypts would have been the main trees in a sparse cover. The minor quantities of the gymnosperm Araucariaceae could have come from long distance dispersal or from very minor, relictual stands. The rainfall had decreased considerable, below 1,000 mm, the lower limit for wet sclerophyll forest (Martin 1987), but it would have been above that of today. A study of the hydrology of the Plio-Pleistocene megalake, Lake Bungunnia, which extended over the confluence of the Murray and Darling Rivers, lead Stephenson (1986) to conclude that the precipitation of this time was considerably more than at present over the catchment of the Murray Darling River system.

The algae present (see Table 3) indicate a freshwater to brackish environment (Pentecost 1984) at the time of deposition, from the late Oligocene to late Pliocene-early Pleistocene. Today, the water from the Jandra bore has a salinity about that of sea water. It is likely that the higher rainfall during the late Tertiary would have assisted flushing salt out of the catchment, but precipitation is not the only factor to be considered. A similar situation is found in the Tresco bore in northwest Victoria, where groundwater about twice the salinity of sea water originates from late Pliocene-early Pleistocene sediments that were deposited under freshwater conditions (Knight and Martin 1989).

The geological structure (Fig. 5) has facilitated the accumulation of highly saline groundwater. The en echelon arrangement of shallow grabens along the Darling River Lineament function as 'blind' compartments that inhibit flushing of the aquifers by nor-

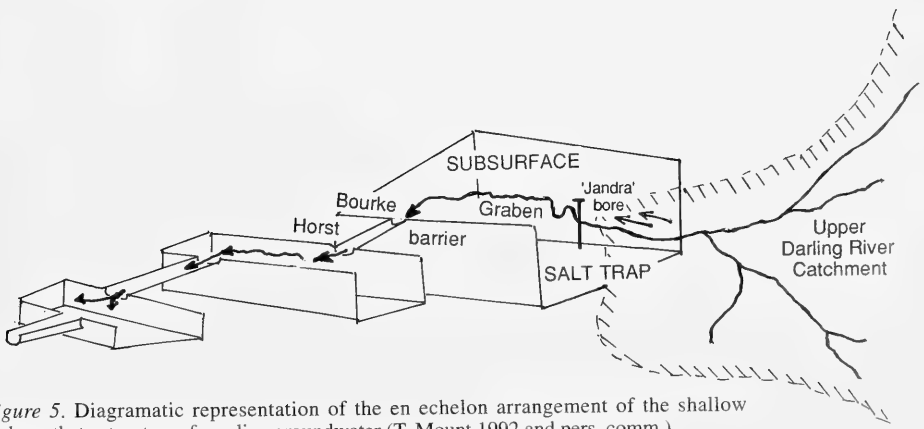

Figure 5. Diagramatic representation of the en echelon arrangement of the shallow grabens that act as traps for saline groundwater (T. Mount 1992 and pers. comm.).

mal downstream movement of groundwater. The bedrock ridges, or horsts, dividing the compartments, have provided effective barriers to groundwater movement, allowing salt to accumulate. The source of the salt can be found in the upper Darling River catchment, above Bourke (from air lofted marine spray, weathered rock and evaporation). The Bourke Graben (T. Mount, pers. comm. and 1992), being the first compartment in the series, is interpreted as the primary trap for the upper catchment salt.

Aridity has increased since the late Pliocene-early Pleistocene, the youngest of the pollen assemblages reported here. During the last 500,000 years, the decreasing rainfall and increasing evaporation, effectively assisted in the build-up of salts (Bowler 1988). The glacial phases of the glacial/interglacial cycles combined low rainfall with strong winds and high evaporation. Freshwater lakes became saline, and if they dried up, the winds spread the salt-laden dust around. When the climate moderated in the interglacial periods, the rainfall increased and the lakes filled with freshwater, but it did not mix well with the saline water which would then recharge the groundwater (Bowler 1988). Though this mechanism may explain much of the salinity problem in inland southeastern Australia today (e.g. the Tresco bore discussed above), the special geological circumstances of the Darling River are probably the major cause of the problems there, but other factors may be involved as well.

ACKNOWLEDGEMENTS

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REFERENCES

Alley, N.F. and Broadbridge, L.M. (1992). Middle Eocene palynofloras from the One Tree Hill area, St Vincent Basin, South Australia. *Alcheringa* **16**, 241–267.

Backhouse, J. (1978). Palynological zonation of the Late Jurassic and Early Cretaceous sediments of the Yarragadee Formation, central Perth Basin Western Australia. *Geological Survey of Western Australia Report* **7**, 1–43

Bowler, J.M. (1988). Environmental and salinity history of the Murray Basin in the last 500, 000 years. In 'Abstracts Murray Basin 88 Conference" (Eds C.M. Brown and W.R. Evans). *Bureau of Mineral Resources, Geology and Geophysics Record* **1988/7,** 19–20.

Brown, C.M., (1989). Structural and stratigraphic framework of groundwater occurrences and surface discharge in the Murray Basin, southeastern Australia. *BMR Journal of Australian Geology and Geophysics* **11,** 127–146.

Cookson, I.C. (1953). Records of the occurrence of *Botryococcus braunii*, *Pediastrum* and the Hystrichosphaerideae in Cainozoic deposits of Australia. *Memoirs of the National Museum, Melbourne* **18**, 107–123.

Cookson, I.C. and Pike, K.M. (1954). The fossil occurrence of *Phyllocladus* and two other podocarpaceous types in Australia. *Australian Journal of Botany* **2**, 60–68.

Dettmann, M.E. (1963). Upper Mesozoic microfloras from south-eastern Australia. *Proceedings of the Royal Society of Victoria* **77**, 1–148.

Dettmann, M.E. and Playford, G. (1969). Palynology of the Cretaceous: a review. In 'Stratigraphy and Palaeontology: Essays in Honour of Dorothy Hill' (Ed. K.S.W. Campbell) pp 174–210. (Australian University Press: Canberra).

Germeraad, J.H., Hopping, C. and Muller, J. (1968). Palynology of Tertiary sediments from tropical areas. *Review of Palaeobotany and Palynology* **6**, 189–348.

Harris, W.K. (1965). Basal Tertiary microfloras from the Princetown area, Victoria, Australia. *Palaeontographica B* **115**, 75–106.

Helby, R., Morgan, R. and Partridge, A.D. (1987). A palynological zonation of the Australian Mesozoic. *Memoir of the Association of Australasian Palaeontologists* **4,** 1–94.

Knight, M.J., and Martin, H.A., (1989). Origins of groundwater salinity near Tresco, northwest Victoria. *BMR Journal of Geology and Geophysics* **11**, 285–289.

Lentin, J.K. and Williams, G.L. (1989). Fossil dinoflagellates: Index to genera and species 1989 edition. *American Association of Stratigraphic Palynologists, Contribution Series* **20**, 1–473.

Macphail, M.K. and Truswell, E.M. (1989). Palynostratigraphy of the central west Murray Basin. *BMR Journal of Australian Geology and Geophysics* **11**, 301–331.

Macphail, M.K. and Truswell, E.M. (1993). Palynostratigraphy of the Bookpurnong Beds and related Late Miocene-Early Pliocene facies in the central west Murray Basin, part 2: Spores and pollens. *BMR Journal of Australian Geology and Geophysics* **14**, 383–409.

Martin, H.A., (1973a). The palynology of some Tertiary Pleistocene deposits, Lachlan River Valley, New South Wales. *Australian Journal of Botany, Supplementary Series* **6**, 1–57.

Martin, H.A., (1973b). Upper Tertiary palynology in southern New South Wales. *Geological Society of Australia, Special Publication* **4**, 35–54.

Martin, H.A., (1974). The Identification of some Tertiary pollen belonging to the family Euphorbiaceae. *Australian Journal of Botany* **22,** 271–291

Martin, H.A., (1984a). The stratigraphic palynology of the Murray Basin in New South Wales. II. The Murrumbidgee area. *Journal and Proceedings of the Royal Society of New South Wales* **117**, 35–44.

Martin, H.A. (1984b). Stratigraphic palynology of the Murray Basin in New South Wales III. The Lachlan area. *Journal and Proceedings of the Royal Society of New South Wales* **117**, 45–51.

Martin, H.A., (1984c). The use of quantitative relationships and palaeoecology in stratigraphic palynology of the Murray Basin in New South Wales. *Alcheringa*, **8**: 253–272.

Martin, H.A., (1987). The Cainozoic history of the vegetation and climate of the Lachlan River Region, New South Wales. *Proceedings of the Linnean Society of New South Wales* **109,** 214–257.

Martin, H.A., (1990). Tertiary climate and phytogeography in southeastern Australia. *Review of Palaeobotany and Palynology* **65,** 47–55.

Martin, H.A., (1991). Tertiary stratigraphic palynology and palaeoclimate of the inland river systems in New South Wales. In 'The Cainozoic of Australia: a re-appraisal of the evidence' (Eds M.A.J. Williams, P. De Dekker, and A.P. Kershaw). *Special Publication of the Geological Society of Australia* **18,** 181–194

Martin, H.A. (1993). The palaeovegetation of the Murray Basin, late Eocene to mid Miocene. *Australian Journal of Systematic Botany.***6,** 491–531.

Martin, H.A. and McMinn, A. (1993). Palynology of Sites 815 and 823: the Neogene vegetation history of coastal northeastern Australia. *Proceedings of the Ocean Drilling Program, Scientific Results* **133**, 115–125.

Mildenhall, D.C. and Crosbie, Y.M. (1979). Some porate pollen from the upper Tertiary of New Zealand. *New Zealand Journal of Geology and Geophysics* **22**, 499–508.

Morgan, R. (1980). Palynostratigraphy of the Australian Early and Middle Cretaceous. *Memoirs of the Geological Survery of New South Wales, Palaeontology* **18,** 1–153.

Mount, T.J. (1992). Yanda Creek salt inflows project, Bourke, N.S.W Hydrological framework studies 1991–1992. *Department of Water Resources, Technical Services Division*, T.S. 92.032.

Pentecost, A. (1984). 'Introduction to freshwater algae'. (Richmond Publishing Co.: England.)

Playford, G. and Dettmann, M.E. (1965). Rhaeto-Liassic plant microfossils from the Leigh Creek coal measures, South Australia, *Senekenbergiana Lethaea* **46**, 127–181.

Pocknall, D.T. and Mildenhall, D.C. (1984). Late Oligocene-early Miocene spores and pollen from Southland, New Zealand. New Zealand *Geological Survery Palaeontological Bulletin* **51**, 1–66.

Stephenson, A.E. (1986). Lake Bungunnia — a Plio-Pleistocene megalake in southern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **57**, 137–156.

Stover, L.E., and Partridge, A.D., (1973). Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin southeastern Australia. *Proceedings of the Royal Society of Victoria* **85**, 237–286.

Stover, L.E., and Partridge, A.D., (1982). Eocene spore-pollen from the Werillup Formation, Western Australia. *Palynology* **6**, 69–95.

Truswell, E.M., Sluiter, I.R. and Harris, W.K. (1985). Palynology of the Oligocene-Miocene sequence in the Oakvale-1 corehole, western Murray Basin, South Australia. *BMR Journal of Australian Geology and Geophysics* **9**, 267–295.

Van Geel, B. and van der Hammen, T. (1978). Zygnemataceae in Quaternary of Columbian sediments. *Review of Palaeobotany and Palynology* **25**, 377–392.

The Composition of the Bee (Apoidea: Hymenoptera) Fauna Visiting Flowering Trees in New South Wales Lowland Subtropical Rainforest Remnants

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Native and exotic bees were sampled visiting mass-flowering rainforest trees in lowland subtropical rainforest remnants in the Manning Valley, on the New South Wales north coast. The number of bee species varied between individual rainforest sites and native bee taxa exhibited differential occurrence at individual plant species and in different rainforest subformations. Bees exhibited increased recruitment responses to peak-phase flowering of individual trees. Flowers visited by bees exhibited a number of different floral morphologies. Colletidae-Hylaeinae was the most diverse native bee group collected but individual taxa were in general not restricted to single plant species. Exotic *Apis mellifera* were most abundant at flowers during peak-phase flowering. *Apis mellifera* foraged at most plants sampled and foraging activities resulted in disturbance to small native hylaeine bees on flowers. Native *Trigona carbonaria* bees were recorded on fewer species of flowering trees than was *Apis mellifera*.

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INTRODUCTION

The popular awareness of plant-pollinator interactions is largely focused on the role of 'specialised' bees, especially that of the honey bee *Apis mellifera* (Paton 1993; Seeley 1983), in the pollination of both wild and horticultural plants. However, bees exhibit great ecological diversity as pollinators (Roubik 1989). Bees, and in particular the neotropical Euglossini, have been the subject of numerous pollination ecology studies (e.g., Cruden 1972; Frankie et al. 1976; Armbruster and Webster 1979; Ackerman 1983; Kevan and Lack 1985; Appanah, Willemstein and Marshall 1986; Roubik and Ackerman 1987; Snow and Roubik 1987; Roubik 1989; Armbruster and Berg 1994). Bees are not always pollinators of the various flowering tropical rainforest plants from which bee visitation has been recorded, and may consume nectar and pollen, and destroy flowers, without any benefit to plant reproduction (Bullock 1994; Roubik 1989; Williams and Adam 1994).

Although records exist for bees visiting plants in sclerophyllous habitats (e.g., Exley 1968a, 1968b; Houston 1975, 1981; Armstrong 1979; Houston et al. 1993) little is known about bee-plant interactions in Australian rainforest communities. Gross (1993), however, recorded bee pollination of the pioneer tropical Australian rainforest shrub *Melastoma affine* (Melastomataceae), principally by buzz-pollinating Anthophoridae. Additionally, Heard (1993) recorded native *Trigona* bees pollinating the subtropical rainforest tree *Macadamia integrifolia* (Proteaceae) cultivated as an orchard crop.

The pollination ecology of lowland subtropical rainforest trees was studied, from

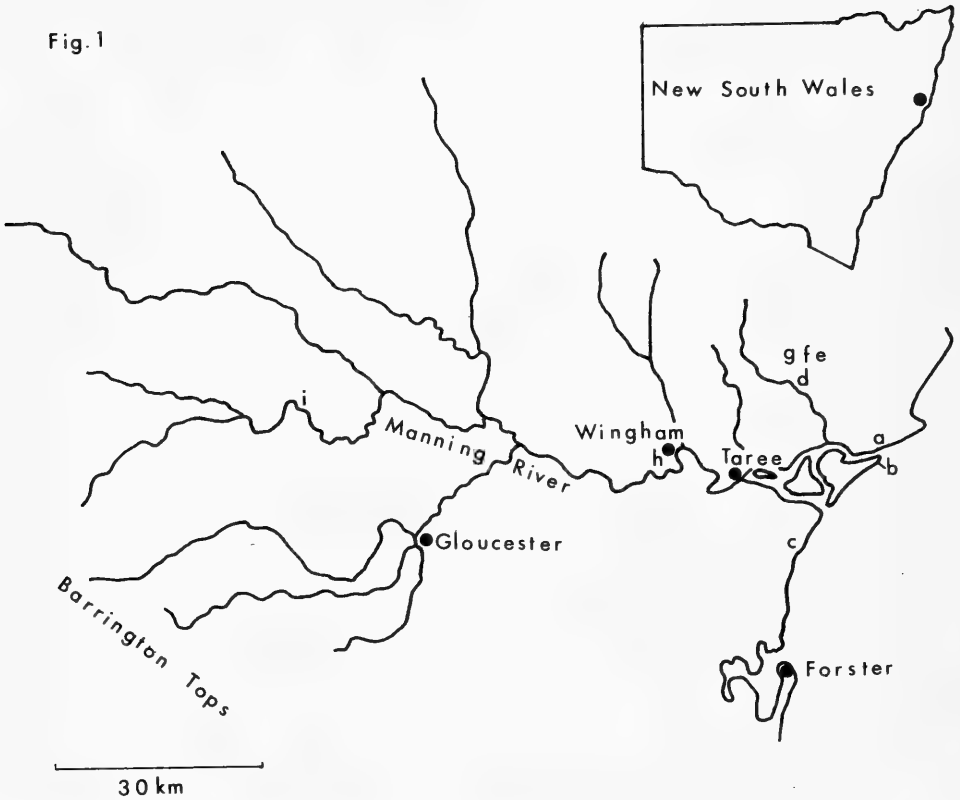


Figure 1. Study sites (rainforest subformation/class definition incorporates structural-physiognomic classification of Webb [1978]). **a.** Harrington (32°52′30″S, 152°41′00″E) (littoral rainforest; mixed notophyll vine forest). **b.** Manning Point (31°53′30″S, 152°40′00″E) (littoral rainforest; mixed notophyll vine forest). **c.** Saltwater Reserve (32°00′30″S, 152°33′45″E) (littoral rainforest; mixed notophyll vine forest). **d.** Lansdowne Reserve (0.5km SE Lansdowne) (31°47′30″S, 152°32′30″E) (riverine rainforest; notophyll vine forest). **e.** Lorien Wildlife Refuge (3km N. Lansdowne) (31°45′00″S, 152°32′30″E) (submontane rainforest; notophyll-notophyll evergreen vine forest). **f.** Lorien Wildlife Refuge (wet sclerophyll forest). **g.** Kenwood Wildlife Refuge (4km NNW Lansdowne); (31°44′45″S, 152°31′30″E) (submontane rainforest-mixed wet sclerophyll forest). **h.** Wingham (31°52′40″S, 152°22′00″E) (riverine + riparian rainforest; notophyll vine forest/complex notophyll vine forest). **i.** Woko National Park (approximately 24km NNW Gloucester) (31°49′00″S, 151°47′00″E) (riverine + riparian rainforest; notophyll vine forest).

1990 to 1994, in rainforest remnants located in the Manning Valley on the north coast of New South Wales (G. Williams unpubl. data) (Fig. 1). The sites have also been subject to intensive invertebrate surveys, especially since 1979 (Williams 1993). An additional number of rainforest tree species in rainforest–wet sclerophyll forest ecotones were also sampled. This was a broad-based study of the rainforest community primarily designed to investigate the incidence of generalist versus specialist plant-pollinator relationships in subtropical rainforests, and to identify putative pollinators. It resulted in the collection of more than 60,000 insects of which bees formed a small proportion (<5%). Although no attempt was made to measure the efficiency of individual insect species as pollinators (e.g., foraging patterns, pollen deposition and resultant seed set) field observations suggested that insects visiting entomophilous flowers were capable of achieving some level of pollination; irrespective of the pollen loads they were capa-

ble of transporting, the frequency with which they contacted stigmas or the distance that they travelled within plant populations. However, bees are of ecological interest, and the aim of this paper is to describe the bee fauna collected from 17 species of mass-flowering rainforest trees during this study (Table 1). There is morphological variation between the flowers of these species but all conform to the entomophilous flower syndrome (Armstrong 1979; Faegri and van der Pijl 1979). All flowers were open in structure, and readily accessible, with little depth effect in the perianth. Flowers were coloured white, or creamish white, except for those of *Tristaniopsis laurina* which were yellow. None of the flowers possessed obvious nectar guides. Although there was variation in foraging behaviour, temporal and spatial constancy to available blossoms and placement and carriage of pollen on their bodies, most bees appeared to be generalist pollinators. However, further studies are needed to define the pollination ecology of individual bee taxa. Bees were not recorded from 6 understorey and subcanopy trees that have specialised pollination ecologies (*Wilkiea huegeliana, Daphnandra micrantha*–Monimiaceae, *Eupomatia laurina*–Eupomatiaceae, *Endiandra muelleri*–Lauraceae, *Rapanea howittiana, R. variabilis*–Myrsinaceae). These possess more specialised flowers (except for *D. micrantha*) that generally deny bee access and, with the exception of *E. muelleri* (whose pollinators are unknown), are pollinated by thrips (*W. huegeliana, R. howittiana, R. variabilis*), weevils (*E. laurina*) or Nematoceran flies (*D. micrantha*) (G. Williams unpubl. data).

There has been no previous systematic collection of the regional rainforest bee fauna. A number of substantial range extensions to previously known distributions are listed in the appendix.

STUDY SITES AND METHODS

Most study sites were located in the floodplain, lower valley and maritime zone of the Manning Valley. However, the Woko National Park site is situated in the western extreme of the valley, approximately 80 km inland from the coast. Sites a-h (Fig. 1) ranged from 10–150 metres above sea level but the Woko site (i) was at approximately 300 metres a.s.l.

Definitions of subtropical rainforest follow Adam (1987, 1992). Definitions of riparian, riverine and littoral subtropical rainforest subformations in the Manning region follow Williams (1993). Floristic composition of sites and the regional physical environment are discussed in Williams (1993).

Trees were sampled by hand netting throughout their flowering period. Insects respond positively to increased availability of floral resources (Sands and House 1990; Augspurger 1980) but insect activity is also influenced by temperature, humidity, shading of flowers and foliage, wind and rainfall (Cruden 1972; Stiles 1977; Primack 1978; Wolda 1978; Real 1981; Kevan and Baker 1983; Armbruster and Berg 1984; Matthews and Kitching 1984; Frith and Frith 1985; Inouye and Pyke 1988; Read 1989; Roubik 1989; Basset 1991; Gross 1993). Consequently, sampling was avoided during cool, rainy periods, periods of moderate to strong wind, and in shaded situations (very few Hymenoptera were active on shaded flowers; large insects, generally, were absent)–conditions that reduce insect activity and abundance.

Crown height of the study trees was generally low (normally less than 10m). Inflorescences were sampled using an extendible 6.2m hand held net, with a mouth diameter of 46 cm. A fine nylon, sailcloth re-enforced, net was attached to the net frame. The size of the net mesh prevented escape of insects >0.2 mm. As far as possible, two trees of any single species, from each study site, were sampled each day of collection (between 0900–1500 hrs). This was to maximise the range of anthophilous (flower frequenting) taxa captured during the period of greatest insect activity.

However, flowers of *Acradenia euodiiformis* (Rutaceae) were sampled every two hours from 0800 hrs until 2000 hrs, and weather conditions noted (Table 3), as an investigation of daily fluctuations in numbers of foraging anthophilous insects (this was only intended as a preliminary investigation of foraging patterns). Other species were generally sampled only once in the morning and afternoon, on any collection day. Although there may be variation in the daily cycle of available floral rewards offered by subtropical rainforest trees, *A. euodiiformis* did not appear to deviate from the overall pattern of nectar production by generalist mass-flowering trees included in the study. General insect visitation to individual tree species was also observed, at all sites except Woko, between sunrise and two hours after sunset, for a minimum of 8 hours (range 8–>10hrs). Bees were not active at night. Individual trees and tree species failed to flower each year and, consequently, it was not possible to sample each tree species over each of the three seasons (1990–91, 1991–92, 1992–93). However, increased sampling at individual tree species did not necessarily result in increases in the number of bee taxa collected. For example, *Alphitonia excelsa* (Rhamnaceae) sampled ('n', number of samples, =160) at Kenwood Wildlife Refuge in 1992, resulted in the collection of 10 bee species, but *A. excelsa* at Harrington, sampled (n=590) intensively over three seasons (1990–1993), yielded only 7 species (Table 1). The flowering phenology of populations also varied, thus the duplication of samples was an attempt to maximise collection of the visiting insect taxa.

On individual days of collection ten inflorescences from each tree were sampled (randomly across the crown face) by quickly placing the net over individual flower masses and briskly shaking. The net mouth was closed by quickly rotating the handle to minimise loss of fast flying insects. Inflorescence sets were not necessarily resampled each day due to factors such as variation in shading and netting damage to flowers. Collectively, approximately 3,000 inflorescences were sampled by this method during the 1990–91, 1991–92 and 1992–93 study seasons, but the number of samples collected from individual tree species varied between years due to differences in phenology (see Table 2). Insect taxa in samples, collectively, were dominated by Coleoptera, Diptera and Hymenoptera generally; but overall bees (although often conspicuous) were relatively uncommon.

Following the collection of each sample the net bag was detached, placed in a plastic container, sprayed with commercial pyrethroid insecticide and sealed. After 10–20 minutes the contents were emptied into individual labelled containers. These were later sorted separately to remove extraneous floral segments (e.g., stamens, petals), and then freeze-stored in labelled Petri dishes for later counting of numbers of species and individuals, measuring, identification and mounting of representative specimens.

The hand net collection method could not be used during and after heavy rain as wet foliage and flower surfaces quickly saturated the net bag, to which small insects readily adhered. The netting technique was also limited when flowers were sparse or held below foliage. For this latter group of trees (i.e., *Diospyros australis, Abrophyllum ornans*) collection using malaise intercept traps (placed on forest margins adjoining or below trees), or hand netting of individual insects as they landed on flowers, was undertaken. No bees were collected in malaise traps set during this study though numerous aculeate wasps were collected by this method. This divergence in trapping methods restricts quantitative comparisons between plant species but does permit a qualitative indication of potential pollination agents. Large insects in general do not behave as inert objects moving in constant and linear patterns, and some large Hymenoptera (e.g., Scoliidae) are able to navigate around malaise intercept traps (Campbell and Brown 1994). Of interest, however, the large halictid bee *Nomia aurantifera* was frequently collected in malaise traps during biological surveys of floodplain rainforest remnants in the Manning Valley (G.Williams unpubl. data) but otherwise was not collected or observed on flowering plant species included in this study.

Field estimation of recruitment cues and potential floral resources

Anthophilous insects are principally recruited to blossoms by visual and olfactory cues (Williams and Dodson 1971; Proctor and Yeo 1975; Armstrong 1979; Kevan and Baker 1983; Papaj and Prokopy 1989; Bell 1990). Inflorescence movement is also thought to stimulate visual recruitment of insects (Bell 1990).

The measurement of potential floral resource availability at various times in the flowering of individual rainforest plants allows an assessment of the change in recruitment stimulus to pollinators (Kearns and Inouye 1993).

A simple field technique was devised to investigate relationships between abundance and richness of bees and potential resources indicated by numbers of open flowers. The technique entailed an estimation of the blossom (or bud) to leaf surface ratio (BLS) on each of the trees being sampled. The estimation was based on 3 points of reference (left, centre, right) across the horizontal visual field of each plant to be sampled, immediately prior to sampling. These three values were summed and a mean value determined.

Flower or floret opening is rarely synchronous and inflorescences normally consist of fully open flower buds, partially open buds and senescent or fructescent flowers. These patterns are a fundamental and necessary consequence of inflorescence structure. A relative estimate of percentage available buds (PAB) was obtained by counting buds on inflorescence subsections, total bud numbers on individual inflorescences or solitary flowers. Minimum numbers of buds counted ranged from total numbers, for species with large but relatively sparse flowers (i.e., *Rhodomyrtus psidioides*) to more than 300, on a minimum of 10 inflorescences, for species with numerous small flowers (e.g., *Euroschinus falcata*). The available bud (PAB) value is a relative measure, because the finite number of initially available buds gradually diminishes due to carpel development, abortion of flowers or herbivore attack.

Both BLS and PAB values are influenced by environmental cues (e.g., day length, temperature, rain), leaf phenology, herbivore damage, number of florets in the inflorescence, inflorescence structure etc., and are not necessarily constant throughout the period of anthesis. However, the two measures provided a useful, though crude, field estimation of potential floral resources against which to investigate bee recruitment (Tables 2 and 3, Figs 4c and 4d).

Several flaws are inherent to the methods. BLS ratios are estimated horizontally at eye level but a declination estimate would probably yield a higher blossom surface value, and one more approximately comparable to the visual cue perceived by insects in flight. In mass-flowering species such as *Tristaniopsis laurina* (Myrtaceae) the inflorescences are partly obscured by leaves and BLS values are biased in favour of leaf surface. In such instances flowers may actually be obscured to insects. BLS values will never reach 100%, this being a consequence of the presentation of flowers and leaves, so that peak recruitment responses in tabulated data are indicated at BLS values $\geq 50\%$.

PAB values may be similarly biased as it is difficult to evaluate values for upper canopy inflorescences.

RESULTS AND DISCUSSION

Fidelity of bee taxa to plant species

A summary of the bee species collected is provided in Table 1. We were unable to identify a number of small Euryglossinae collected primarily on flowers of *Waterhousea floribunda* and *Tristaniopsis laurina.* These are not considered in this paper and reference specimens are lodged with the CSIRO, Division of Entomology (Canberra). Records in Table 1 are derived primarily from bees collected in netted samples, but observations of several additional bee species, not collected in samples, are also included

TABLE 1

Numbers of bee taxa (Apoidea) collected from flowering rainforest trees in lowland subtropical rainforest remnants and mixed wet sclerophyll forest, Manning Valley, northern New South Wales (plants are listed alphabetically by family; '—' no netted samples taken; numbers in brackets, following plant spp. and sites, represent cumulative totals of bee taxa from each plant species or site).

Plant Species

Anacardiaceae
1. *Euroschinus falcata* (24)

Cunoniaceae
2. *Caldcluvia paniculosa* (5)
3. *Schizomeria ovata* (3)

Ebenaceae
4. *Diospyros australis* (11)

Escalloniaceae
5. *Abrophyllum ornans* (3)
6. *Cuttsia viburnea* (7)

Euphorbiaceae
7. *Drypetes australasica* (3)

Flacourtiaceae
8. *Scolopia braunii* (11)

Lauraceae
9. *Cryptocarya microneura* (1)

Myrtaceae
10. *Acmena smithii* (19)
11. *Rhodomyrtus psidioides* (7)
12. *Tristaniopsis laurina* (46)
13. *Waterhousea floribunda* (41)

Rhamnaceae
14. *Alphitonia excelsa* (17)

Rutaceae
15. *Acradenia euodiiformis* (16)

Sapindaceae
16. *Alectryon coriaceus* (14)
17. *Guioa semiglauca* (7)

Sites

A. Harrington(24)
B. Manning Point (13)
C. Saltwater Reserve (20)
D. Lansdowne Reserve (10)
E. Lorien Wildlife Refuge (rf.) (36)
F. Lorien Wildlife Refuge (wet s.f.) (48)
G. Kenwood Wildlife Refuge (7)
H. Wingham Brush (40)
I. Woko National Park (10)

Month of Collection

S(Sept.), O(Oct.), N(Nov.) D(Dec.), J(Jan.), F(Feb.), M(Mar.)

Plant code	1	1	2	3	4	4	5	6	7	8	8	9	10	10	10	10	11	11	12	12	13	13	14	14	15	16	16	17	Coll.
Site code	A	C	F	F	D	F	E	E	B	A	F	E	A	B	D	I	D	F	F	H	E	H	A	G	E	A	B	A	Mths.
Number of samples	180	160	30	70	–	–	–	80	10	30	20	20	150	70	30	70	10	40	60	90	90	280	590	160	220	120	110	260	
Anthophoridae																													
Amegilla bombifrons																			1										D
Amegilla sp. nr. bombifrons																			1										J
Amegilla ?pulchra																		1											D
Exoneura lawsoni																							1						J
Exoneura spp.						1			1					2	1	1			3		1				3		2		SONDJ
?Exoneura sp.																											1		D
Lestis aeratus						1																1							D
Thyreus lugubris																			1										J
Thyreus nitidulus						1																							D

Apidae																											
Apis mellifera	1	1			1	1		1		1			1	1		1		1	1	1	1		1	1	1		1	SONDJFM
Trigona carbonaria		1					1								1		1					1	1				SONDF
Trigona ?carbonaria								1																			D
Colletidae-Colletinae																											
Callomelitta ?fulvicornis							1																				D
Leioproctus alleynae								1																			D
Leioproctus amabilis																		1									ND
Leioproctus ?amabilis																	1										D
Leioproctus carinatus																	1										N
Leioproctus cristatus																										1	ND
Leioproctus ?cristatus	1																		1			1			1		NJF
Leioproctus ?irroratus	1																										N
Leioproctus sp. nr. irroratus																	1		1		1						SNDF
Leioproctus spp.							1						1		1	3		1	2								NDJ
Paracolletes sp.																1			1								DJ
Colletidae-Euryglossinae																											
Euryglossa ephippiata													1			1	1	1	1								NDJ
Euryglossa sp. nr. occidentalis																			1								D
Euryglossa subsericea																1	1										DJ
Euryglossa ?subsericea																		1	1								ND
Euryglossa terminata																1											D
Euryglossa spp.		1											1				2	2	4								NDJ
?Euryglossa sp.		1																									N
Euryglossella spp.		1	1																								N
?Euryglossella sp./?spp.		1											1			1											NDJ
Euryglossina spp.			1																								N
Pachyprosopis sp.													1				1		1								NDJ
?Pachyprosopis sp.																					1						F
Sericogaster fasciata													1			1											NDJ
Colletidae-Hylaeinae																											
Amphylaeus nubilosellus	1	1						1												1		1	1	1	1	1	SONDJF
Amphylaeus ?nubilosellus	1										1											1					SN

Hemirhiza melliceps					1																		1			DJ
Heterapoides sp.nr. exlexae	1	1		1				1				1	1					1		1			1	1	1	NDJF
Heterapoides nigriconcava			1																							N
Heterapoides ?nigriconcava	1																									N
Heterapoides spp.						2						1			1			2			1	2			1	SONDF
?Heterapoides sp.		1				1																				N
Hylaeus amiculiformis								1																		O
Hylaeus amiculinus																			1							N
Hylaeus cyanophilus																				1						JF
Hylaeus ?cyanophilus	1																									N
Hylaeus sp. nr. cyanophilus		1														1										NJ
Hylaeus elegans																	1		1							DJ
Hylaeus euxanthus																	1		1							D
Hylaeus sp. nr. euxanthus																			1							D
Hylaeus foveatus									1																	N
Hylaeus ?jacksoniae																				1						F
Hylaeus microphenax		1							1			1														N
Hylaeus ?microphenax	1																									N
Hylaeus nubilosus																	1					1				OJ
Hylaeus sp. nr. nubilosus																	1									D
Hylaeus ofarrelli			1	1					1									1								N
Hylaeus ?ofarrelli															1											N
Hylaeus perhumilis		1																1								N
Hylaeus primulipictus	1	1							1	1			1			1	1	1	1							ONDJ
Hylaeus ?primulipictus					1												1									D
Hylaeus proximus																	1									J
Hylaeus rotundiceps	1																1		1	1						NDJF
Hylaeus turgicollaris				1																						SN
Hylaeus spp.	1	2						1	1						1		1		2			1		1		SONDJ
Meroglossa sulcifrons									1																	N
Palaeorhiza sp.					1																					D
Halictidae																										
Homalictus brisbanensis			1													1		1			1	1				SNDF

Homalictus ?brisbanensis																		1	1	1							NDJ
Homalictus sp. nr. brisbanensis																						1					S
Homalictus flindersi	1																				1			1	1	1	NDJ
Homalictus ?flindersi																								1			J
Homalictus sp. nr. flindersi																				1							ND
Homalictus megastigmus	1						1	1			1										1			1	1		SONJF
Homalictus ?megastigmus	1																										N
Homalictus sp. nr. megastigmus	1																										N
Homalictus punctatus																			1								D
Homalictus sphecodoides													1														N
Homalictus ?sphecodoides																										1	D
Homalictus spp.											1														1		NJ
Lasioglossum bicingulatum																	1	1	1	1							NDJ
Lasioglossum ?bicingulatum																	1			1							DJ
Lasioglossum polygoni				1																							D
Lasioglossum spp.	1			1					1				1				3	4	1	2		1	2				SNDJF
?Lasioglossum sp./?spp.																	1		1			1					NDJF
Nomia spp.	1																			1							ND
Megachilidae																											
Chalicodoma deanii																		1									D
Chalicodoma lucidiventris																	1	1									DF
Chalicodoma punctata													1														D
Megachile maculariformis																	1										D
Megachile ?mystacea (sp.1)					1												1										D
Megachile ?mystacea (sp.2)																	1										D
Megachile pictiventris				1	1	1																					D
Megachile ?pictiventris																	1										D
Megachile punctata																	1										J
?Megachile sp.																				1							D
Total spp.	13	20	5	3	6	7	3	7	3	5	7	1	1	9	4	10	1	6	31	24	22	30	10	7	16	8	10	7

Fig. 2a

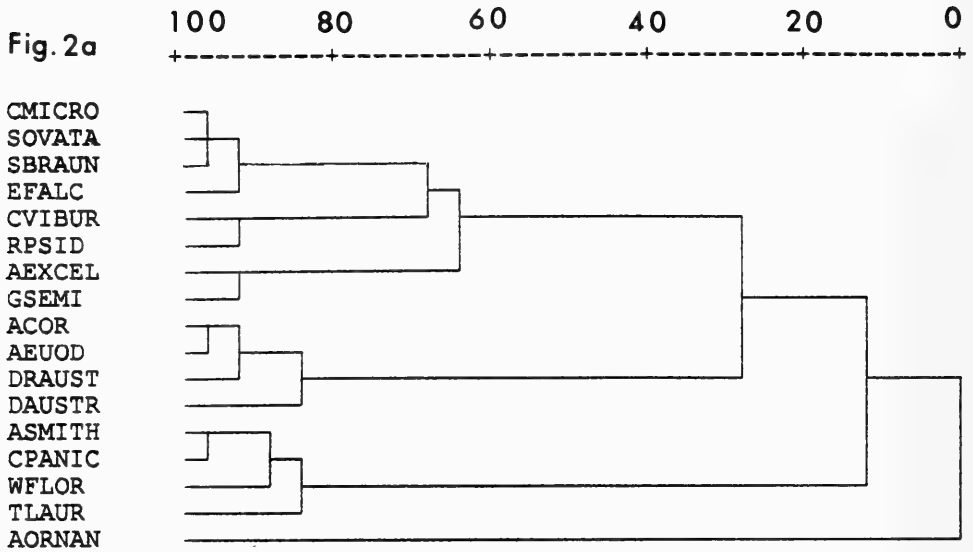
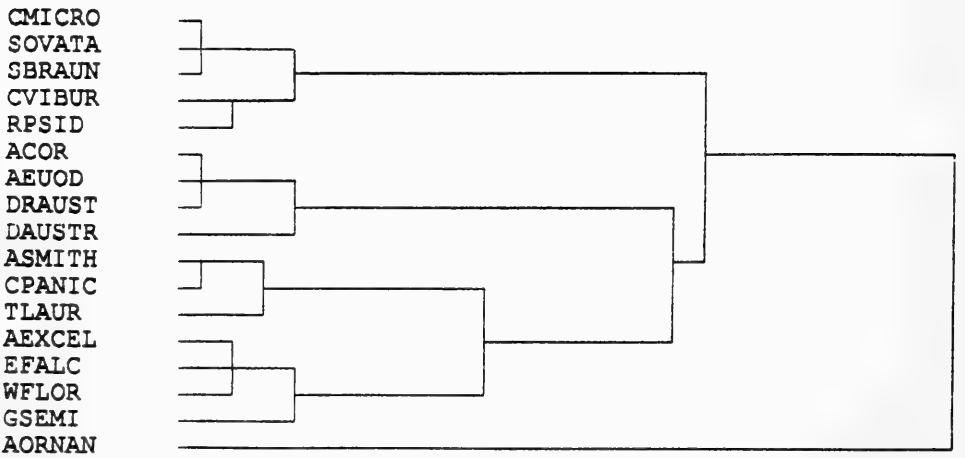


Fig. 2b



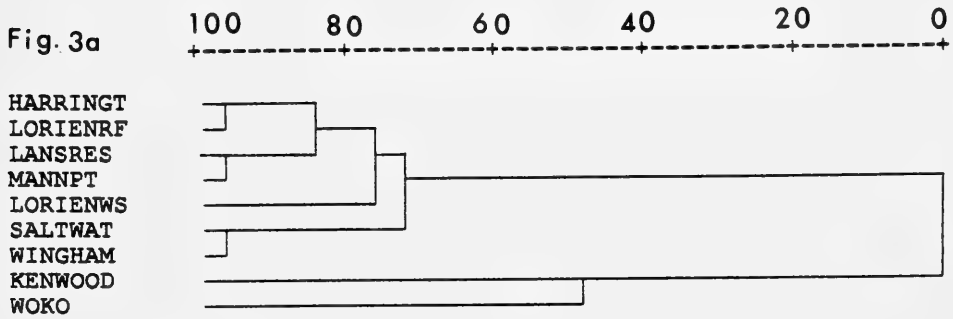
Figures 2a, 2b. Dendrograms of clustering of plant species on the basis of bee assemblages (a, all bee species; b, excluding *Apis*). Code: ACOR = *Alectryon coriaceus*, AEUOD = *Acradenia euodiiformis*, AEXCEL = *Alphitonia excelsa*, AORNAN = *Abrophyllum ornans*, ASMITH = *Acmena smithii*, CMICRO = *Cryptocarya microneura*, CPANIC = *Caldcluvia paniculosa*, CVIBUR = *Cuttsia viburnea*, DAUSTR = *Diospyros australis*, DRAUST = *Drypetes australasica*, EFALC = *Euroschinus falcata*, GSEMI = *Guioa semiglauca*, RPSID = *Rhodomyrtus psidioides*, SBRAUN = *Scolopia braunii*, SOVATA = *Schizomeria ovata*, TLAUR = *Tristaniopsis laurina*, and WFLOR = *Waterhousea floribunda*.

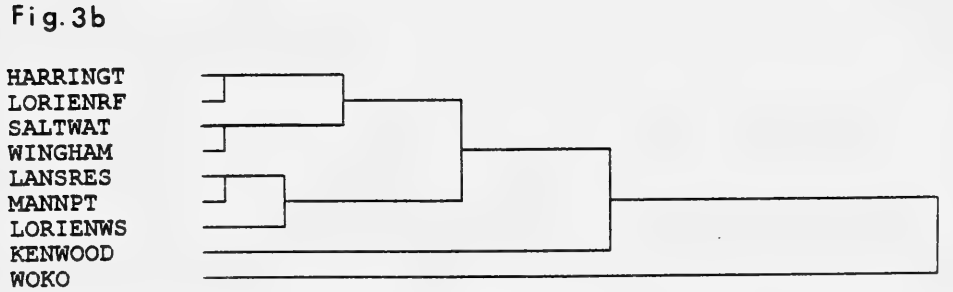
for completeness. No commercial *Apis mellifera* hives were located near the study sites and although honey bees may fly more than 8 km to forage (Roubik 1989, and references therein) all records for *Apis mellifera* are considered to be from feral populations. Although we did not attempt to locate and assess the number of feral colonies at any of the study sites estimates of feral *A. mellifera* hive density in tropical and semi-arid environments have been given as from 6 to more than 100 per km^2 (see Oldroyd et al. 1994).

The structure of the data in Table 1 was examined to determine whether plant species and/or sites could be characterised on the basis of assemblages of bee taxa. Agglomerative hierarchal cluster analysis (Ward's Method) was performed using the SPSS statistical package (Norusis/SPSS Inc. 1993). The raw data used were the number of bee species in each family, except for Colletidae, where subfamilies were recognised; data were standardised prior to analysis. Clustering was carried out both on the total data set and on the native species only (i.e., removing the widespread and abundant *Apis mellifera*).

Clustering of plant species (Figs 2a and 2b) showed that, in terms of bee utilisation, *Abrophyllum ornans* was very distinctive. This may reflect the small number of taxa recorded from the species, which was a function of the sampling technique. However, daily observation (x2) of *A. ornans* flowers (undertaken between 0730–2300 hrs), during the period of greatest flower availability, indicated that visits by bees were fewer than one every hour. The other plant species fall into a number of clusters (which differ in composition depending on whether *Apis* was included in the analysis). However, these clusters do not obviously reflect either taxonomy or flower morphology.

The site analysis (Figs 3a and 3b) indicates the presence of distinct assemblages of bees at Woko and Kenwood but the majority of sites are generally similar. The separation of the Woko assemblages, although collected from a single taxon (*Acmena smithii* var. 'minor'), is not surprising given that the site is at a higher elevation and further inland than the others. The general similarity of the Manning lowland sites suggests that within a limited geographic area stand structure and composition has a relatively minor influence on the bee assemblage.





Figures 3a, 3b. Dendrograms of clustering of study sites on the basis of bee assemblages (a, all bee species; b, excluding *Apis*). Code: HARRINGT = Harrington, KENWOOD = Kenwood Wildlife Refuge, LANSRES = Lansdowne Reserve, LORIENRF = Lorien Wildlife Refuge [rainforest site], LORIENWS = Lorien Wildlife Refuge [wet sclerophyll forest site], MANNPT = Manning Point, SALTWAT = Saltwater Reserve, WINGHAM = Wingham, WOKO = Woko National Park.

The observed recruitment and visitation of bees to most trees appeared to be greatly influenced by density of available blossoms. For example, trees of *Alectryon coriaceus* (Sapindaceae) possessing few flowers, or with many senescent flowers and developing fruit, were visited only occasionally by bees (usually *Exoneura* spp. or Hylaeinae). Isolated, often shaded, sparsely flowering *Acradenia euodiiformis* trees generally did not recruit bees even though densely flowering conspecific trees nearby were visited by large numbers of *Trigona carbonaria* and *Apis mellifera* (see Tables 2 and 3).

TABLE 2

Summary of bee recruitment to mass-flowering rainforest trees (plants listed alphabetically by family). Bees collected in netted samples; each daily record is derived from a composite of 10 inflorescence samples. Variation in number of daily samples and number of trees sampled is due to variation in flowering patterns. Number of native individuals: number of native taxa given in brackets "( )", number of *Apis mellifera* unbracketed. Samples collected during morning "m" or afternoon "a" indicated separately; "—" = no data/samples collected; "@" = approximate numbers only. Blossom: Leaf Surface ratio and relative estimate of Percentage Available open Buds indicated as "BLS:PAB"; "f" = no longer flowering.

ANACARDIACEAE					
Euroschinus falcata					
Harrington					
male tree					
date	19.11.90	26.11.90	3.12.90		
m	18(0:0)	0(3:3)	1(0:0)		
BLS:PAB	<40:<50	>40:<50	<10:f		
male tree					
date	6.11.91	13.11.91	19.11.91		
m tree1	23(17:@7)	0(2:2)	0(4:3)		
a	0(7:2)	0(0:0)	0(1:1)		
BLS:PAB	50:<50	40:50	40:>70		
male tree					
date	6.11.91	13.11.91	19.11.91	26.11.91	2.12.91
m tree2	24(12:5)	6(0:0)	0(0:0)	0(0:0)	0(4:2)
a	—	0(1:1)	0(2:2)	0(0:0)	0(5:1)
BLS:PAB	50:<50	50:<10	40:<10	<50:<5	<30:>95
Saltwater Reserve					
female tree*					
date	12.11.91	19.11.91	26.11.91	3.12.91	
m tree1	0(28:7)	8(16:8)	6(24:8)	0(1:1)	
a	0(16:7)	6(4:4)	5(13:4)	0(0:0)	
BLS:PAB	40:<5	50:30	50:>80	<30:100	
* not sampled 10.12.91 due to cessation of flowering					
male tree**					
date	19.11.91	26.11.91	3.12.91	10.12.91	
m tree2	3(9:2)	0(56:4)	0(1:1)	0(5:2)	
a	0(14:6)	0(7:4)	0(1:1)	0(2:2)	
BLS:PAB	60:<5	>60:10	70:<10	60:<10	
** not sampled 12.11.91 due to lack of open flowers					

ESCALLONIACEAE

Cuttsia viburnea

Lorien Wildlife Refuge

date	6.12.91	9.12.91	16.12.91	22.12.91
m	0(0:0)	0(6:3)	1(17:4)	1(0:0)
a	1(7:2)	0(2:1)	1(3:2)	0(0:0)
BLS:PAB	30:>50	30:>60	50:>90	50:100

date	12.12.92	23.12.92	28.12.92
no bees collected during this period			

MYRTACEAE

Acmena smithii

Harrington

date	19.11.90	26.11.90		
	19.11.92	27.11.92	7.12.92	14.12.92
no bees collected during these periods				

Lansdowne Reserve

date	6.11.90	12.11.90	15.11.90
m	0(4:4)	0(5:3)	0(2:2)
BLS:PAB	>30:100	>60:100	<40:100

Manning Point

date	3.11.90	18.11.90	15.11.90
m tree1	0(10:5)	0(10:3)	0(1:1)
BLS:PAB	<40:<10	>40:—	>30:f

date	8.11.90	15.11.90
m tree2	0(10:3)	0(1:1)
BLS:PAB	>40:—	>70:f

Woko National Park

date	25.11.90	5.12.90
m tree1	0(0:0)	0(1:1)
a	1(5:5)	—
BLS:PAB	>30:<50	40:5

date	25.11.90	5.12.90
m tree2	0(0:0)	0(2:2)
a	1(1:1)	—
BLS:PAB	>30:>50	35:f

date	5.12.90
m tree3	0(1:1)
BLS:PAB	70:>50

Tristaniopsis laurina

Wingham

date	17.12.90	24.12.90
m tree1	0(2:2)	0(13:5)
BLS:PAB	<20:<50	30:60

date	17.12.90	24.12.90	(24.12.90, duplicate)
m tree2	0(0:0)	0(5:4)	0(18:8)
BLS/PAB	<20:>60	30:40	30:40

date	17.12.91	24.12.91
m tree1	7(1:1)	0(13:7)
a	1(1:1)	0(1:1)
BLS/PAB	10:>90	<10:100

date	24.12.91	2.1.92
m tree2	7(4:3)	4(9:6)
a	11(8:7)	1(10:9)
BLS/PAB	40:100	<30:100

date	2.1.92	7.1.92
m tree3	0(11:5)	4(10:4)
a	0(22:13)	3(4:4)
BLS:PAB	40:100	<30:100

Lorien Wildlife Refuge

date	26.12.91	3.1.92	6.1.92
m	1(10:9)	0(3:3)	0(5:1)
a	2(9:6)	0(27:@20)	1(4:3)
BLS:PAB	30:>40	40:80	40:>90

Waterhousea floribunda

Wingham

date	14.11.90	22.11.90	29.11.90
m tree1	5(16:7)	5(10:5)	1(8:4)
BLS:PAB	<30:<30	40:>95	<20:f

date	22.11.90	29.11.90	6.12.90
m tree 2	0(30:@6)	1(14:8)	1(20:10)
BLS:PAB	>50:>90	>60:>70	10:f

date	19.11.91	27.11.91	3.12.91	10.12.91	
m tree1	6(18:5)	0(2:2)	4(15:7)	0(2:1)	
a	2(25:15)	3(10:8)	8(4:4)	1(1:1)	
BLS:PAB	60:50	>70:>90	60:100	<10:100	

date	19.11.91	27.11.91	3.12.91	10.12.91	17.12.91
m tree2	2(7:5)	6(5:4)	7(11:5)	3(50:11)	20(11:8)
a	2(9:6)	7(7:6)	9(12:8)	5(9:7)	3(17:9)
BLS:PAB	50:45	70:45	70:50	>70:>90	<20:100

date	17.12.91	24.12.91
m tree3	1(18:7)	2(18:9)
a	3(6:6)	1(5:3)
BLS:PAB	70:100	70:100

Lorien Wildlife Refuge

date	1.12.90
m	1(0:0)
BLS:PAB	>50:>50

date	29.11.91	5.12.91
m tree1	2(29:18)	0(1:1)
a	3(23:4)	1(10:5)
BLS:PAB	30:50	<30:>90

date	29.11.91	5.12.91
m tree2	3(24:16)	2(11:6)
a	1(20:11)	3(17:13)
BLS:PAB	30:70	40:>90

RHAMNACEAE

Alphitonia excelsa

Harrington

date	3.1.91	11.1.91	19.1.91	25.1.91	1.2.91	
m tree1	0(0:0)	0(0:0)	0(0:0)	0(0:0)	1(0:0)	cont.
BLS:PAB	>30:<1	40:<30	40:50	30:<40	30:>80	

date	9.2.91	14.2.91	22.2.91
m tree1	1(0:0)	0(0:0)	0(0:0)
BLS:PAB	30:>90	<30:f	<10:f

date	3.1.91	11.1.91	19.1.91	25.1.91	1.2.91	
m tree2	0(0:0)	0(0:0)	1(0:0)	2(0:0)	1(0:0)	cont.
BLS:PAB	>30:<5	40:<30	60:>50	50:>50	<40:>70	

date	9.2.91	14.2.91	22.2.91
m tree2	1(0:0)	0(0:0)	0(0:0)
BLS:PAB	20:f	<10:f	30:>90

date	3.2.92	12.2.92	20.2.92	28.2.92	6.3.92	12.3.92
m tree1	0(0:0)	3(0:0)	39(0:0)	11(1:1)	0(0:0)	0(0:0)
a	1(0:0)	12(2:2)	38(0:0)	9(0:0)	9(0:0)	0(0:0)
BLS:PAB	30:<10	50:30	>50:>60	50:90	30:>99	<10:f

date	3.2.92	12.2.92	20.2.92	28.2.92	6.3.92	12.3.92
m tree2	2(0:0)	15(1:1)	63(1:1)	24(0:0)	14(0:0)	0(0:0)
a	0(0:0)	21(0:0)	20(0:0)	18(0:0)	16(0:0)	0(0:0)
BLS:PAB	30:<10	40:30	>50:>50	>60:>95	40:>95	<20:f

date	28.1.93	4.2.93	11.2.93	1.3.93
m tree1	3(16:1)	9(14:1)	2(17:1)	1(0:0)
a	0(1:1)	6(9:1)	1(5:1)	0(0:0)
BLS:PAB	40:20	40:30	—	<10:80

date	28.1.93	4.2.93	11.2.93	1.3.93
m tree2	0(0:0)	0(0:0)	2(6:1)	3(0:0)
a	0(8:1)	2(7:1)	4(3:2)	2(0:0)
BLS:PAB	<20:<10	<20:<20	—	<30:>90

Kenwood Wildlife Refuge

date	6.2.92	13.2.92	22.2.92	29.2.92
m tree1	3(0:0)	2(0:0)	0(0:0)	5(0:0)
a	4(0:0)	4(0:0)	14(2:2)	6(2:2)
BLS:PAB	30:<5	<30:<20	40:50	30:>90

date	6.2.92	13.2.92	22.2.92	29.2.92
m tree2*	15(0:0)	0(0:0)	0(0:0)	0(0:0)
a	1(2:1)	17(9:4)	10(0:0)	1(0:0)
BLS:PAB	40:20	40:>60	30:>90	30:>90

* tree shaded each morning

RUTACEAE

Acradenia euodiiformis

Lorien Wildlife Refuge

date	18.9.91	19.9.91	25.9.91	2.10.91
0800hrs	—	2(0:0)	0(0:0)	0(0:0)
1000hrs	8(8:5)	13(8:3)	6(29:5)	0(10:5)
1200hrs	10(10:6)	—	7(43:5)	0(9:3)
1400hrs	3(3:1)	—	9(69:6)	0(3:1)
1600hrs	1(0:0)	—	0(13:3)	0(0:0)
1800hrs	0(0:0)	—	0(0:0)	0(0:0)
2000hrs	0(0:0)	—	0(0:0)	0(0:0)
BLS:PAB	50:35	"	60>70	50:<5

SAPINDACEAE

Alectryon coriaceus

Manning Point

date	17.12.91	27.12.91
m tree1	0(19:<8)	0(2:1)
a	0(1:1)	0(0:0)
BLS:PAB	40:f	30:f

date	27.12.91	2.1.92
m tree3	3(17:@4)	2(0:0)
a	1(0:0)	1(1:1)
BLS:PAB	40:50	50:f

date	2.1.92
m tree4	2(5:@2)
a	3(2:1)
BLS:PAB	50:f

Harrington

date	7.1.93	11.1.93	18.1.93
m tree1	0(0:0)	3(3:1)	2(0:0)
a	2(0:0)	1(0:0)	1(0:0)
BLS:PAB	<30:>60	40:>70	>30:>70

date	7.1.93	11.1.93	18.1.93
m tree2	1(0:0)	2(1:1)	1(0:0)
a	1(0:0)	3(1:1)	1(0:0)
BLS:PAB	<30:>60	<20:>70	<20:100

Guioa semiglauca

Harrington

date	6.11.90	12.11.90	19.11.90	26.11.90	3.12.90
m tree1	1(0:0)	22(0:0)	60(0:0)	66(0:0)	27(0:0)
a	—	—	6(1:1)	—	—
BLS:PAB	—	50:—	>50:>80	50:>80	>20:>90

date	6.11.90	12.11.90	19.11.90	26.11.90
m tree2	15(0:0)	36(0:0)	23(0:0)	39(0:0)
a	—	4(1:1)	—	—
BLS:PAB	—	50:40	<70:>50	<60:—
date	26.11.90			
m tree3	5(1:1)			
BLS:PAB	60:>40			
date	19.11.92	27.11.92	7.12.92	14.12.92
m tree1	0(0:0)	2(3:1)	31(8:2)	3(0:0)
a	0(1:1)	0(0:0)	0(5:1)	0(0:0)
BLS:PAB	<10:<5	<30:<20	<20:>80	<10:100
date	14.12.92	21.12.92	25.12.92	
m tree2	6(0:0)	1(1:1)	2(1:1)	
a	5(1:1)	0(0:0)	1(0:0)	
BLS:PAB	<10:<20	<10:50	<10:100	

The abundance of individuals was generally highest during peak flowering, but the peak in abundance is more pronounced in relation to BLS than PAB (Tables 2 and 3, Figs 4c and 4d). There were no clear trends in the number of species in relation to availability of resources (Figs 4c and 4d), although over the season numbers of individuals and species show a similar pattern with peaks in November/December (Figs 4a and 4b). Floral morphology did not appear to strongly influence recruitment. High numbers of visiting bee taxa were obtained from *Euroschinus falcata* (13 spp. Harrington–20 spp. Saltwater), *Acradenia euodiiformis* (16 spp. Lorien), *Tristaniopsis laurina* (31 spp. Lorien–24 spp. Wingham) and *Waterhousea floribunda* (22 spp. Lorien–30 spp. Wingham) (Table 1). These trees include species both with open dish-like corollas with half inferior ovaries (*T. laurina, W. floribunda*) and those with superior ovaries (*E. falcata, A. euodiiformis*). The latter group are often visited by eusocial Apidae whilst unadapted or semi-specialised (see Faegri and van der Pijl 1979) Colletidae characterise the bee visitors to the former. The greatest cumulative number of bee species was collected from *Tristaniopsis laurina* (46 spp.) and *Waterhousea floribunda* (41 spp.) (Table 1). However, both species were sampled at the Wingham and Lorien sites, which also possessed the richest bee faunas (Tables 1 and 2), and the high bee numbers recorded for *T. laurina* and *W. floribunda* may reflect site influences.

Approximately 80 percent (n=78) of the bee records were from three or fewer plant species or individual locations (Table 1). Only *Heterapoides* sp. near *exleyae* (Colletidae) and the introduced honey bee *Apis mellifera* (Apidae) were recorded from 10 or more of the plants sampled. *Apis mellifera* was collected from all but five plant species (*Caldcluvia paniculosa, Schizomeria ovata, Abrophyllum ornans, Drypetes australasica, Cryptocarya microneura; Apis mellifera* was recorded from sites at which these species were in flower), which nevertheless, do not possess flowers, flowering strategies, or offer floral resources of a nature that would appear to preclude *Apis* foraging. The bee fauna of individual tree species frequently differed between sites, and these differences were expressed both where trees were sampled in floristically and topographically different forests (e.g., *Tristaniopsis laurina* at Wingham Brush and Lorien Wildlife Refuge), as well as floristically related subformations (e.g., *Euroschinus falcata* in littoral rainforests at Harrington and Saltwater Reserve).

TABLE 3

Changes in bee activity on *Acradenia euodiiformis* (Lorien Wildlife Refuge) during the course of the day. Key to weather conditions: C=cold; f=scattered clouds; R=rain; T=twilight; c=cool; h=warm-hot; S=sunny; W=gusting, strong winds; d=dark; H=very hot; s=dappled light on tree; w=light wind, breeze; F=fine; HU=humid; sh=tree shaded.

	800	1000	1200	1400	1600	1800	2000	/	800	1000
18–19.9.91										
No. of individuals										
Apis mellifera	—	8	10	3	1	0	0		2	13
Trigona carbonaria	—	4	6	3	0	0	0		0	6
misc. native bees	—	4	5	0	0	0	0		0	2
total bees	—	16	21	6	1	0	0		2	21
total insects (incl. bees)	—	88	112	71	143	412	93		75	105
No. of taxa										
other Apoidea	—	4	5	0	0	0	0		0	2
total bees	—	6	7	2	1	0	0		2	4
total insects (incl. bees)	—	38	47	41	60	72	40		47	47
BLS:PAB 50:>30										
weather condition	n/a	sWF	SWF	SWF	shWF	CWFT	cwF		sCw	Sf
25.9.91										
No. of individuals										
Apis mellifera	0	6	7	9	0	0	0			
Trigona carbonaria	0	23	35	57	10	0	0			
misc. native bees	0	6	8	12	3	0	0			
total bees	0	35	50	78	13	0	0			
total insects (incl. bees)	142	280	259	284	190	198	182			
No. of taxa										
other Apoidea	0	4	4	5	2	0	0			
total bees	0	6	6	7	3	0	0			
total insects (incl. bees)	31	46	44	42	43	40	22			
BLS:PAB 60:>70										
weather condition	cshF	sf	Swh	Sshw	shcwf	cwT	cWd			
02.10.91										
No. of individuals										
Apis mellifera	0	0	0	0	0	0	0			
Trigona carbonaria	0	2	4	3	0	0	0			
misc. native bees	0	8	5	0	0	0	0			
total bees	0	10	9	3	0	0	0			
total insects (incl. bees)	271	86	30	69	35	83	71			
No. of taxa										
other Apoidea	0	4	2	0	0	0	0			
total bees	0	5	3	1	0	0	0			
total insects (incl. bees)	37	18	17	18	10	11	16			
BLS:PAB 50:<5										
weather condition	cshF	Shw	SHw	SshHW	shcW	cfwT	Fd			

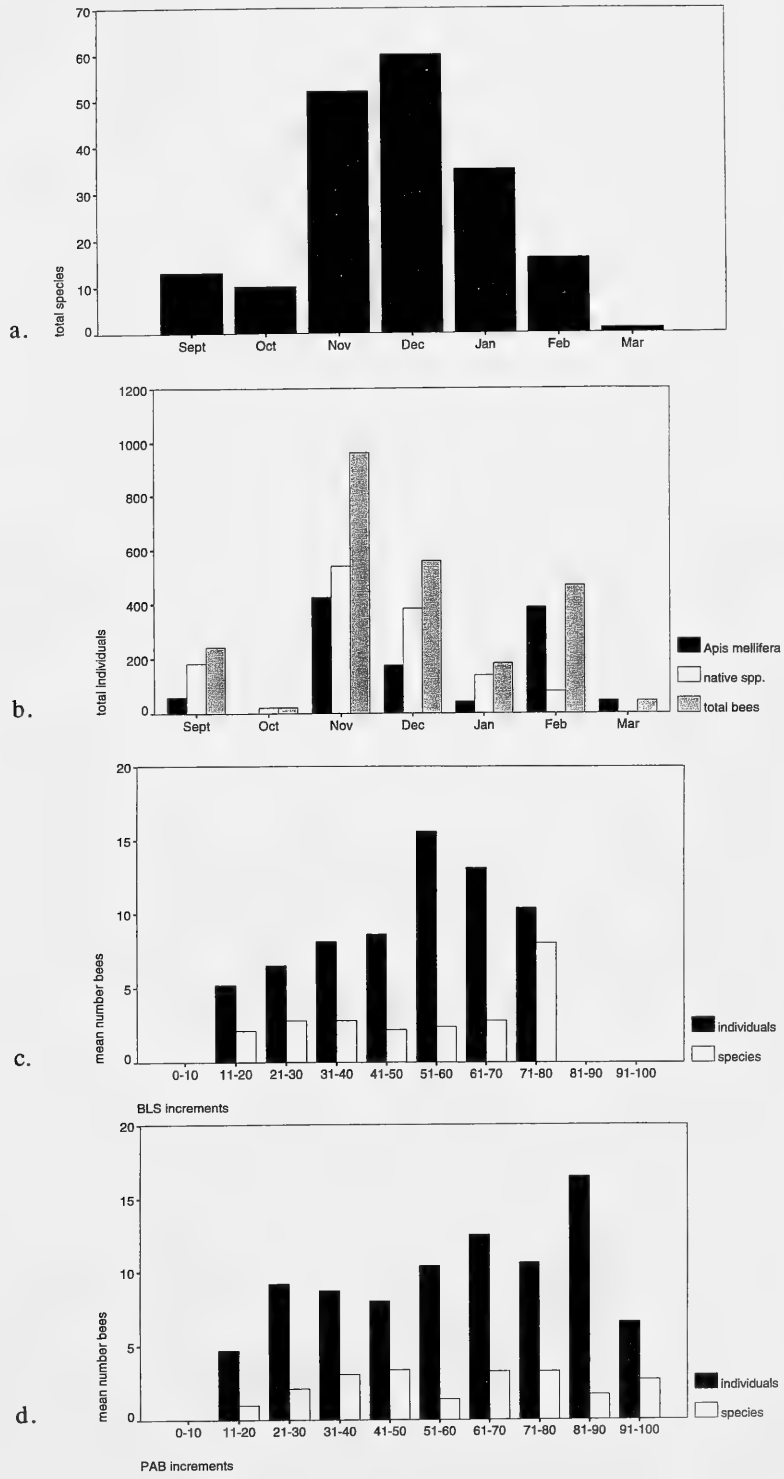


Figure 4. a). Monthly numbers of bee species, b). Monthly numbers of bee individuals, c). Mean number bee taxa and individuals in 10% increments of BLS, d). Mean number bee taxa and individuals in 10% increments of PAB.

At both the family and generic level bees exhibited a broad polytropic response within the spectrum of trees sampled (Table 1). However, more extensive sampling is required to assess the plant fidelity of individual bee species to particular plant species. Where bee genera were recorded from single, or few, plant species this may be due to actual rarity in rainforest, rather than a close plant-pollinator mutualism. Conversely, if populations of individual bee taxa occur (or forage) as spatial or temporal mosaics within rainforest communities then our sampling may have biased against their collection.

Anthophoridae were collected from Ebenaceae, Euphorbiaceae, Myrtaceae, Rhamnaceae, Rutaceae and Sapindaceae but many of these records are represented solely by the genus *Exoneura*. At least two anthophorid genera, *Lestis* and *Amegilla*, foraged in a traplining manner (see Janzen 1971; Roubik 1989; Gross 1993) (G. Williams pers. observ.).

Only two apids occur in the region; introduced *A. mellifera* and the native *Trigona carbonaria*. *Apis mellifera* can dominate the flower-frequenting insect fauna in fragmented forests (Aizen and Feinsinger 1994), competes with native pollinators for floral resources (Anderson 1989), and may modify the pollination ecology of native plants (Pyke and Balzer 1982; Paton 1985; Pyke 1990; Sugden and Pyke 1991). *Apis mellifera* was common at all sites and foraged on species of Anacardiaceae, Ebenaceae, Escalloniaceae, Flacourtiaceae, Myrtaceae, Rhamnaceae, Rutaceae and Sapindaceae. However, *A. mellifera* generally restricted its foraging activity to inflorescences in full sunlight. *Trigona carbonaria* was collected from fewer tree taxa (Anacardiaceae, Escalloniaceae, Myrtaceae, Rhamnaceae, Rutaceae) but did not forage on mass-flowering *Waterhousea floribunda* at Wingham and Lorien Wildlife Refuge even though it commonly foraged at other mass flowering trees at these sites. *Trigona carbonaria* was recorded from only one littoral rainforest site (Saltwater Reserve) where it co-foraged with *A. mellifera* on *Euroschinus falcata* flowers. *Trigona* species have not been recorded from two other littoral rainforest sites, Harrington and Manning Point, which have been subject to intensive invertebrate surveys since 1975 (Williams 1993). *Trigona carbonaria* generally only foraged at large or concentrated blossom resources, rather than isolated blossoms or inflorescences.

Halictidae were recorded from Anacardiaceae, Cunoniaceae, Ebenaceae, Euphorbiaceae, Flacourtiaceae, Myrtaceae, Rhamnaceae, Rutaceae and Sapindaceae. However, of the two principal halictid genera, *Homalictus* and *Lasioglossum*, individuals of *Homalictus* are more abundant at littoral rainforest sites and are common foragers on the flowers of many adjoining dune plants (e.g., *Scaevola, Hibbertia*). *Lasioglossum* is a distinctive and characteristic genus of the bee fauna of mass-flowering Myrtaceae in lowland rainforests.

Megachilidae were more restricted in their occurrence and were only collected from Ebenaceae, Escalloniaceae and two species of Myrtaceae (*Tristaniopsis laurina, Waterhousea floribunda*). Megachilids were encountered as either occasional 'rare' visitors or as episodic 'flushes' of larger numbers of taxa and individuals at single peak-flowering trees, such as at Lorien Wildlife Refuge in January 1991 when large numbers of *Chalicodoma lucidiventris* and *Megachile* spp. occurred on *T. laurina* during a three day period of peak flower availability.

Of the families collected Colletidae were represented by the largest number of species but a number of genera were restricted in ecological and geographic range within the study area. *Paracolletes* (Colletinae), *Pachyprosopis* and *Sericogaster* (Euryglossinae) and *Palaeorhiza* (Hylaeinae) were only collected in riverine and riparian rainforests and their adjoining ecotones. *Meroglossa* (Hylaeinae) was only recorded from a rainforest ecotone at the Lorien site. Most Colletinae, predominantly species of *Leioproctus*, were collected from Myrtaceae, but were also recorded from Anacardiaceae, Escalloniaceae, Rhamnaceae, Rutaceae and Sapindaceae. Euryglossinae were principally collected on Myrtaceae and, with the exception of *Euryglossa,*

Euryglossella and *Euryglossina* species from Saltwater Reserve, were otherwise not collected from littoral rainforest. High species richness of *Euryglossa* (Euryglossinae), in combination with *Leioproctus* (Colletinae), was a characteristic of the *Waterhousea floribunda* bee fauna.

Hylaeinae, principally species of *Hylaeus*, contained the greatest number of species (Table 1) and characterised the native bee fauna of mass-flowering littoral rainforest trees. The greatest number of hylaeine species was recorded in rainforest remnants at Harrington, Wingham and Lorien Wildlife Refuge (Table 1) but this may reflect the greater numbers of samples collected at these three sites. The subfamily was recorded from all plant families but was particularly numerous on Myrtaceae. Most genera appear to be polytropic, at best, oligotropic, in their fidelity to mass-flowering rainforest plants and *Heterapoides* and *Hylaeus*, in particular, were collected from a broad spectrum of flowering rainforest trees (12 and 13 spp. respectively) (Table 1). However, Hylaeinae were not observed on specialised (e.g., Orchidaceae) or semi-specialised (e.g., Commelinaceae, Zingiberaceae, Papilionaceae) zygomorphic rainforest plant flowers examined opportunistically at the study sites. Hylaeinae were often the only bees observed visiting isolated, partially shaded or understorey flowers of otherwise massed, crown-flowering rainforest trees. *Hemirhiza melliceps*, for example, preferentially foraged on shaded, often isolated, flowers of *Alectryon coriaceus* (Sapindaceae) and *Diospyros australis* (Ebenaceae). *Palaeorhiza* sp. also foraged on shaded *D. australis* flowers. Consequently, hylaeine species may contribute to pollination of spatially-restricted, small blossom clusters.

In addition to the hylaeine records given in Table 1 two species of the genus *Hyleoides* were observed in the study region. *Hyleoides* sp. near *concinna* visited flowers of *Brachychiton acerifolius* (Sterculiaceae) (at Coocumbac Island Nature Reserve, Taree) and *Hyleoides concinna* foraged on orchard plantings of exotic pomegranate *Punica granatum* (Punicaceae) at Lorien Wildlife Refuge. Both plants possess vivid red flowers that, although broadly 'tubular' in shape, possess no obvious nectar guides and are readily accessible to bees. The two *Hyleoides* records are particularly interesting because they indicate foraging constancy (neither species was observed on other flowering plants) and represent a departure from the 'bird' pollination syndrome (see Williams and Adam 1994) suggested by the red-coloured flowers of *B. acerifolius* and *P. granulatum*. Additionally, bees have an inability to see red (Barth 1991).

Hylaeine visitation to a phylogenetically diverse mass-flowering subtropical rainforest flora follows the broad polytropic response by Hylaeinae, and Colletidae generally, to plant species in less mesic habitats (see records in Houston 1975, 1981; Armstrong 1979). The unifying theme of plant visitation by Hylaeinae appears be one of blossom morphology, rather than shared phylogeny, in which visited plant species generally possess allophilic (with no structural characters for guiding visitors) or hemiphilic (intermediately adapted) blossoms (see Faegri and van der Pijl 1979) capable of being pollinated by relatively short-tongued and semi-specialised anthophilous insects. The ecological distribution of Hylaeinae appears to be diverse, and hylaeines represent a potential source of generalist pollination vectors upon which rainforest trees with unspecialised 'generalist' pollination requirements may be able to draw.

Influence of flower availability on bee activity

Bees respond to increased availability of floral resources (Augspurger 1980; Roubik 1989). The greatest numbers of bee species and individuals were recorded in November and December (Table 1, Figs 4a and 4b) a period when a greater number of tree species were sampled. The numbers recorded for February and March (Figs 4a and 4b) are largely derived from *Alphitonia excelsa*.

The bee data from 2-hourly netted inflorescence samples of *Acradenia euodiiformis*,

and selected daily samples from other flowering trees (due to absence of bees in some samples, and very short flowering periods of some plant species) are summarised in Tables 2 and 3.

Abundance and diversity of bees were influenced by daily changes in weather conditions (e.g., cloudiness, wind, and possibly increases in temperature) but increased foraging frequency by individuals and increased number of bee species at flowers was generally associated with increased blossom to leaf surface ratios (BLS) and increased bud opening (PAB) (Tables 2 and 3, Figs 4c and 4d). Decreased foraging frequency and reduction in taxonomic diversity of the bee fauna generally corresponded with reduction in available floral resources reflected in decreases in BLS ratios as a result of reduction or senescence of available blossoms — this being a direct consequence of floret abscission and senescence.

Diel responses by bees, with maximal recruitment patterns generally between 1000–1400 hrs, are seen in data for *Acradenia euodiiformis* (Table 3); the patterns of all bees are concordant in terms of trends in daily abundance (i.e. *Apis, Trigona* and other native bees). The visitation of other insects to *A. euodiiformis* varied over longer daily time periods but there seemed to be no consistency in the abundance patterns of total insects (including bees) (Table 3). *Apis mellifera* foraging is maximal at mid to peak-phase while *Trigona carbonaria* and other native bees commence or continue to forage during diminished resource phases (Table 3). Similarly, *Trigona* foraged on late phase *Archontophoenix cunninghamiana* flowers in March 1993 at Lorien Wildlife Refuge when *A. mellifera* numbers were greatly reduced.

Data for *Euroschinus falcata*, *Guioa semiglauca*, *Waterhousea floribunda*, *Tristaniopsis laurina* and *Alphitonia excelsa* (Table 2), species exhibiting longer flowering periods, also demonstrate fluctuations in bee frequency and diversity that generally corresponded with increases and reductions in available floral resources. Reduced abundance of bees in these samples also corresponded with onset of rain or shading of the tree crown during part of the day.

Additionally, preferential visitation to particular trees within populations and, in dioecious spp. (e.g., *E. falcata*), preferential foraging at either female or male plants was observed. At the Saltwater site on the 26th November 1991 *Trigona carbonaria* was common on male *E. falcata* trees but *Apis mellifera* was absent. In contrast, *Apis* was very common throughout the day at the single flowering female tree. *Apis mellifera* was absent or an uncommon forager at male flowers throughout the sampling of *E. falcata* at Saltwater Reserve. *Trigona carbonaria* foraged in large numbers at both male and female trees, and significantly (for potential pollination contributions) foraged at both male and female trees throughout the *E. falcata* flowering episode.

Concentration of *Apis* foraging activity, within peak flowering periods, was also marked in *Alphitonia excelsa* (1992, 1993) and *Guioa semiglauca* (1990, 1992) at Harrington (Table 2). Relative foraging constancy by *A. mellifera*, however, occurred throughout the flowering period of *Waterhousea floribunda* at both the Wingham and the Lorien sites. *Apis* showed no preferential foraging at *Tristaniopsis laurina*, being frequently absent in samples, contrary to the putative bee adaptation suggested by the yellow colouration of its flowers.

Interaction between *Apis mellifera* and *Trigona carbonaria*

Interactions between the eusocial apids *Apis mellifera* and *Trigona carbonaria* are of interest because of the possible resource competition between the two species and the potential for displacement of native 'stingless' bees (*Trigona* and *Austroplebeia* spp., Cardale 1993) by feral *Apis* populations.

Apis mellifera is recorded as a common visitor to tropical, subtropical and cool temperate Australian rainforest plants (Hopper 1980; House 1985; Crome and Irvine

1986; Ettershank and Ettershank 1990; Gross 1993; Heard 1993) and honey bees were common at all our study sites. During this study *Trigona carbonaria* was sampled from *Euroschinus falcata* (Saltwater), *Rhodomyrtus psidioides*, *Abrophyllum ornans*, *Acradenia euodiiformis* (Lorien Wildlife Refuge), *Tristaniopsis laurina* (Wingham), *Alphitonia excelsa* (Kenwood Wildlife Refuge), and possibly *Cuttsia viburnea* (Lorien Wildlife Refuge) (see Table 1), but was common only on *E. falcata* and *A. euodiiformis* flowers. *Trigona carbonaria* was also common (>10 m^{-2}) at *Archontophoenix cunninghamiana* (Arecaceae) flowers at Lorien Wildlife Refuge and synchronously, mass-flowering *Austrosteenisia blackii* (Papilionaceae) vines in the riverine rainforest remnant at Lansdowne Reserve.

Interaction was observed between *A. mellifera* and other native bee genera. Foraging activity of *Apis mellifera* readily disturbed co-foraging native Hylaeine (which flew off when touched by *Apis*) on all occasions when *Apis* and hylaeines were present on flowers. Ettershank and Ettershank (1990) noted reduced native insect numbers near Tasmanian bee-keeping sites but did not observe interactions between native insects and *Apis*.

No direct interaction, displacement or avoidance movement between introduced *Apis* and native *Trigona* bees was observed during fieldwork. Although there are considerable differences in size between the species (*Apis* >9 mm, *Trigona* <6 mm) *Trigona* individuals continued to forage, apparently undisturbed by the presence of *Apis*. These observations, however, were made when *Apis* occurred at only moderate numbers (approx. <10 m^{-2}) or when *Apis* exhibited preferential visitation to single-sexed trees in dioecious populations as on *E. falcata* at Saltwater.

Additional observations (over a number of seasons since 1991) also suggest an absence of displacement or interference interactions between *Apis* and *Trigona* on *Cordyline stricta* (Agavaceae), *Alocasia brisbanensis* (Araceae), *Archontophoenix cunninghamiana* (Arecaceae), arboretum plantings of male *Rhodosphaera rhodanthema* (Anacardiaceae) and domestic and horticultural crops adjoining the Lorien study site, and on plantings of *Banksia ericifolia* (Proteaceae) at Bulahdelah in 1991 (G. Williams pers. observs.).

This apparent lack of disturbance or displacement of *Trigona* cannot be interpreted as evidence for no adverse impact from the foraging of introduced *Apis mellifera* on other native pollinators. McAlpine (1988) notes disturbance by *Apis mellifera* of *Trigona* ?*carbonaria* and *Neurochaeta inversa* (Diptera) taking pollen from *Alocasia brisbanensis* (as *A. macrorrhiza*) in southeast Queensland. *Apis* readily disturbed the foraging activities of native Diptera (i.e. Syrphidae, Lauxaniidae, Drosophilidae) and Coleoptera (Nitidulidae, Chrysomelidae, Scirtidae) on flowering *Archontophoenix cunninghamiana* palms at Lorien Wildlife Refuge and native insects generally on flowering *Guioa semiglauca* trees at Harrington (G. Williams pers. observ.). *Apis mellifera* may compete with native fauna for nest hollows (Oldroyd et al. 1994) and, as suggested elsewhere (Williams 1993), critical population displacement of *Trigona* may occur at prospective hive/nest sites (i.e. tree hollows) rather than the food source. *Trigona* may be particularly vulnerable at nest establishment because founding of *Trigona* colonies is by way of initial establishment by young queens in concert with small numbers of workers rather than the massed swarms utilised by *Apis* (Michener and Houston 1991). Such small founding colonies are potentially readily overwhelmed. Additionally, old *Trigona* queens are unable to vacate nests, as can *Apis* queens (Michener and Houston 1991), so that destruction or loss of nest sites (e.g., through fire) may involve loss of the hive's means of re-establishment at an alternative site.

Managing rainforest so as to preserve or sustain a diverse pollinator guild may be critical to the long-term viability of individual plant populations and the ecosystem in general. A diverse pollinator guild may be important in that it provides flexibility and resilience in breeding systems in the face of environmental change (Williams and Adam

1994). Williams and Adam (1994) suggest that a reduction in the total pollinator guild may result in the loss of subsets of species required for pollination of particular plants.

Potential threats to pollinator guild diversity (and flexibility in plant reproductive ecology) are posed by the increasing fragmentation of habitat and the monopolising of floral resources, important to some pollinators, by introduced *Apis mellifera*. Although there is always a large array of anthophilous insects on subtropical rainforest trees, within which native bees are not a numerically dominant element, bees may nevertheless play an important role in pollination ecology in rainforests.

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REFERENCES

Ackerman, J.D. (1983). Diversity and seasonality of male euglossine bees (Hymenoptera:Apidae) in central Panama. *Ecology* **64,** 274–283.

Adam, P. (1987). 'New South Wales rainforests : the nomination for the World Heritage List.' (National Parks and Wildlife Service: Sydney).

Adam, P. (1992). 'Australian rainforests'. (Oxford University Press: Oxford).

Aizen, M.A. and Feinsinger, P. (1994). Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano". *Ecological Applications* **4**, 378–392.

Anderson, J.M.E. (1989). Honeybees in natural ecosystems. In 'Mediterranean Landscapes in Australia'. (Eds J.C. Noble and R.A. Bradstock) pp. 300–304. (CSIRO: Melbourne).

Appanah, S., Willemstein, S.C. and Marshall, A.G. (1986). Pollen foraging by two *Trigona* colonies in a Malaysian rainforest. *Malayan Nature Journal* **39**, 177–191.

Armbruster, W.S. and Berg, E.E. (1994). Thermal ecology of male euglossine bees in a tropical wet forest: fragrance foraging in relation to operative temperature. *Biotropica* **26**, 50–60.

Armbruster, W.S. and Webster, G.L. (1979). Pollination of two species of *Delechampia* (Euphorbiaceae) in Mexico by euglossine bees. *Biotropica* **11**, 278–283.

Armstrong, J.A. (1979). Biotic pollination mechanisms in the Australian flora: a review. *New Zealand Journal of Botany* **17**, 467–508.

Augspurger, C.K. (1980). Mass-flowering of a tropical shrub (*Hybanthus prunifolius*) : influence on pollinator attraction and movement. *Evolution* **34**, 475–488.

Barth, F. G. (1991). 'Insects and flowers: the biology of a partnership'. (Princeton University Press: Princeton).

Basset, Y. (1991). The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecological Entomology* **16**, 265–278.

Bell, W.J. (1990). Searching behaviour patterns in insects. *Annual Reviews in Entomology* **35**, 447–467.

Bullock, S.H. (1994). Wind pollination of neotropical dioecious trees. *Biotropica* **26**, 172–179.

Campbell, A.J. and Brown, G.R. (1994). Distribution of parasitoids of scarab larvae in relation to remnant vegetation: a preliminary analysis. *Memoirs of the Queensland Museum* **36**, 27–32.

Cardale, J.C. (1993). 'Zoological catalogue of Australia. Volume 10. Hymenoptera: Apoidea'. (Eds W.W.K. Houston and G.V. Maynard) (Australian Government Publishing Service: Canberra).

Crome, F.H.J. and Irvine, A.K. (1986). "Two bob each way" : The pollination and breeding system of the Australian rainforest tree *Syzygium cormiflorum* (Myrtaceae). *Biotropica* **18**, 115–125.

Cruden, A.W. (1972). Pollinators in high-elevation ecosystems : relative effectiveness of birds and bees. *Science N.Y.* **176**, 1439–1440.

Ettershank, G. and Ettershank J.A. (1990). Insects associated with flowers of Tasmanian leatherwoods (*Eucryphia* spp.). *Proceedings of the Tasmanian National Rainforest Conservation Program* — Report No.1, 65–71.

Exley, E.M. (1968a). Revision of the genus *Brachyhesma* Michener (Apoidea: Colletidae). *Australian Journal of Zoology* **16**, 167–201.

Exley, E.M. (1968b) Revision of the genus *Euryglossula* Michener (Apoidea: Colletidae). *Australian Journal of Zoology* **16**, 203–217.
Faegri, K. and van der Pijl, L. (1979). 'The principles of pollination ecology'. (Pergamon: Oxford).
Frankie, G.W., Opler, P.A. and Bawa K.S. (1976). Foraging behaviour of solitary bees : implications for outcrossing of a neotropical forest tree species. *Journal of Ecology* **64**, 1049–1057.
Frith, C.B. and Frith, D.W. (1985). Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology* **10**, 237–248.
Gross, G.L. (1993). The breeding system and pollinators of *Melastoma affine* (Melastomataceae); a pioneer shrub in tropical Australia. *Biotropica* **25**, 468–474.
Heard, T.A. (1993). Pollinator requirements and flowering patterns of *Macadamia integrifolia*. *Australian Journal of Botany* **41**, 491–497.
Hopper, S.D. (1980). Pollination of the rainforest tree *Syzygium tierneyanum* (Myrtaceae) at Kuranda, Northern Queensland. *Australian Journal of Botany* **28**, 223–237.
House, S.M. (1985). Relationships between breeding and spatial pattern in some dioecious tropical rainforest trees. PhD Thesis. Australian National University, Canberra.
Houston, T.F. (1975). A revision of the Australian Hylaeine bees (Hymenoptera: Colletidae). 1. Introductory material and the genera *Heterapoides* Sandhouse, *Gephyrohylaeus* Michener, *Hyleoides* Smith, *Pharohylaeus* Michener, *Hemirhiza* Michener, *Amphylaeus* Michener and *Meroglossa* Smith. *Australian Journal of Zoology. Supplementary Series* **36**, 1–135.
Houston, T.F. (1981). A revision of the Australian Hylaeine bees (Hymenoptera: Colletidae). II. *Australian Journal of Zoology Supplementary Series* **80**, 1–128.
Houston, T.F., Lamont, B.B., Radford, S. and Errington, S.G. (1993). Apparent mutualism between *Verticordia nitens* and *V. aurea* (Myrtaceae) and their oil-ingesting bee pollinators (Hymenoptera: Colletidae). *Australian Journal of Botany* **41**, 369–380.
Inouye, D.W. and Pyke, G.H. (1988). Pollination biology in the Snowy Mountains of Australia: comparisons with montane Colorado, USA. *Australian Journal of Ecology* **13**, 191–210.
Janzen, D.H. (1971). Euglossine bees as long-distance pollinators of tropical plants. *Science N.Y.* **171**, 203–205.
Kearns, C.A. and Inouye, D.W. (1993). 'Techniques for Pollination Biologists'. (University Press of Colorado: Niwot).
Kevan, P.G. and Baker, H.G. (1983). Insects as flower visitors and pollinators. *Annual Reviews in Entomology* **28**, 407–453.
Kevan, P.G. and Lack, A.J. (1985). Pollination in a cryptically dioecious plant *Decaspermum parviflorum* (Lam.) A.J. Scott (Myrtaceae) by pollen-collecting bees in Sulawesi, Indonesia. *Biological Journal of the Linnean Society* **25**, 319–330.
McAlpine, D.K. (1988). Studies in upsidedown flies (Diptera: Neurochaetidae). Part II. Biology, adaptations, and specific mating mechanisms. *Proceedings of the Linnean Society of New South Wales* **110**, 59–82.
Matthews, E.G. and Kitching, R.L. (1984). 'Insect ecology.' (University Queensland Press: St. Lucia).
Michener, C.D. and Houston, T.F. (1991). Apoidea. In 'The insects of Australia. A textbook for students and researchers'. 2nd edit. (CSIRO) pp. 993–1000. (University of Melbourne Press: Melbourne).
Naumann, I.D. (1991). Hymenoptera. In 'The insects of Australia. A textbook for students and researchers'. 2nd edit. (CSIRO) pp. 916–1000. (University of Melbourne Press: Melbourne).
Norusis, M.J./SPSS Inc. (1993). 'SPSS for Windows. Professional statistics, release 6.0'. (SPSS Inc.: Chicago).
Oldroyd, B.P., Lawler, S.H. and Crozier, R.H. (1994). Do feral honey bees (*Apis mellifera*) and regent parrots (*Polytelis anthopeplus*) compete for nest sites? *Australian Journal of Ecology* **19**, 444–450.
Papaj, D.R. and Prokopy, R.J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Reviews in Entomology* **34**, 315–350.
Paton, D.C. (1985). Impact of introduced honeybees on the abundance and behaviour of honeyeaters and their potential impact on seed production by *Callistemon macropunctatus*. *Australasian Pollination Ecologists Society Newsletter* **10**.
Paton, D.C. (1993). Honeybees in the Australian environment. *BioScience* **43**, 95–103.
Primack, R.B. (1978). Variability in New Zealand montane and alpine pollinator assemblages. *New Zealand Journal of Ecology* **1**: 66–73.
Proctor, M. and Yeo, P. (1975). 'The pollination of flowers'. (Collins: London).
Pyke, G.H. (1990). Apiarists versus scientists: a bittersweet case. *Australian Natural History* **5**, 386–392.
Pyke, G.H. and Balzer, L. (1982). The effects of the introduced honeybee (*Apis mellifera*) on Australian native bees. Report to NSW National Parks and Wildlife Service.
Read, J. (1989). Phenology and germination in some rainforest canopy species at Mt. Field National Park, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **123**, 211–221.
Real, L.A. (1981). Nectar availability and bee foraging on *Ipomoea* (Convolvulaceae). *Biotropica Supplement* **13**, 64–69.
Roubik, D.W. (1989). 'Ecology and natural history of tropical bees'. (Cambridge University Press: Cambridge).
Roubik, D.W. and Ackerman J.D. (1987). Long-term ecology of euglossine orchid-bees (Apidae:Euglossini) in Panama. *Oecologia (Berl.)* **73**, 321–333.
Sands, D. and House, S. (1990). Plant/insect interactions, food webs and breeding systems. In 'Australian Tropical Rainforests'. (Eds L.J. Webb and J. Kikkawa) pp. 88–97. (CSIRO: Melbourne).

Seeley, T.D. (1983). The ecology of temperate and tropical honeybee societies. *American Scientist* **71**, 264–272.

Snow, A.A. and Roubik, D.W. (1987). Pollen deposition and removal of bees visiting two tree species in Panama. *Biotropica* **19**, 57–63.

Stiles, G. (1977). Co-adapted competitors : the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science N.Y.* **198**, 1177–1178.

Sugden, E.A. and Pyke, G.H. (1991). Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Australian Journal of Ecology* **16**, 171–181.

Webb, L.J. (1978). A general classification of Australian rainforests. *Australian Plants* **9**, 349–363.

Williams, G.A. (1993). '*Hidden Rainforests: subtropical rainforests and their invertebrate biodiversity*'. (New South Wales University Press -The Australian Museum: Sydney).

Williams, G.A. and Adam, P. (1994). A review of rainforest pollination and plant-pollinator interactions, with particular reference to Australian subtropical rainforests. *The Australian Zoologist* **29**, 177–212.

Williams, N.H. and Dodson, C.H. (1971). Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution* **26**, 84–95.

Wolda, H. (1978). Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* **47**, 369–381.

APPENDIX

Range extension records

A number of bee species collected from the study sites represent new distribution records and are listed below.

Colletidae

Callomelitta ?fulvicornis. C. fulvicornis is known only from type locality 'Jamberoo' (NSW) (Cardale 1993).

Euryglossa terminata. Only published localities 'Brisbane, near Emu Vale (Qld), and Patonga (NSW)' (Cardale 1993).

Hemirhiza melliceps. Previously recorded from southern Queensland (Cardale 1993).

Hylaeus amiculiformis. Previous published records 'Mackay, Brisbane' (Qld) (Cardale 1993).

Hylaeus amiculus. Recorded from Western Australia, South Australia, Victoria and western New South Wales (Cardale 1993); range extension to northern New South Wales.

Hylaeus cyanophilus. Only published records 'Mackay, Redlynch and Goodna' (Qld) (Cardale 1993).

Hylaeus foveatus. Only published localities Jamberoo and Lorne, New South Wales (Cardale 1993).

Hylaeus jacksoniae. Only published localities Mt Coot-tha (Brisbane, Qld) and 'near Woodenbong' (NSW) (Cardale 1993).

Hylaeus microphenax. Previously only known from type locality 'Mackay' (Cardale 1993).

Hylaeus primulipictus. Known only from type locality 'Mackay' (Qld) (Cardale 1993).

Hylaeus proximus. Recorded from Murray-Darling Basin (NSW?), South Australia and Western Australia (Cardale 1993).

Palaeorhiza sp.. Probable new species (T. Houston pers. comm.), genus previously recorded from Queensland and Northern Territory (Cardale 1993).

Sericogaster fasciata. Only published localities 'Mackay, Birkdale, near Stanthorpe [Qld] and Gosford [NSW]' (Cardale 1993).

Halictidae

Lasioglossum polygoni. Range extension from Noosa (Qld) (K. Walker pers. comm.).

Megachilidae

Chalicodoma punctata. Previously only recorded from 'New Holland', exact distribution unknown (Cardale 1993).

Megachile deanii. Range extension from southern Queensland (Cardale 1993).

Megachile pictiventris. Range extension from far north coast, New South Wales (Cardale 1993).

Stomatopod Crustacea of the Macleay Museum, University of Sydney

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The stomatopod crustaceans in the Macleay Museum are documented for the first time. The collection includes 96 specimens, representing 7 families (Gonodactylidae, Odontodactylidae, Pseudosquillidae, Lysiosquillidae, Harpiosquillidae, Squillidae, Takuidae). The 13 genera include 21 species, grouped as follows: *Gonodactylaceus* (3), *Gonodactylinus* (1), *Gonodactylus* (3), *Neogonodactylus* (3), *Mesacturus*(1) *Odontodactylus* (2), *Pseudosquilla* (1), *Pseudosquillana* (1), *Lysiosquilla* (2), *Harpiosquilla* (1), *Alima* (1), *Oratosquilla* (1), *Oratosquillina* (1). These stomatopods form part of larger natural history collections made last century by the Macleays and associates. The stomatopod collection is significant for its inclusion of material from both the western Atlantic and the Indo-West Pacific. Several rare Indo-West Pacific species are represented and much of the western Atlantic material is unique in Australia. The presence of *Gonodactylaceus falcatus* in north-eastern Australia is confirmed. *Gonodactylus chiragra* and *G. platysoma* are newly reported from Lord Howe Island. *Gonodactylinus viridis* is reported from Samoa, *Oratosquilla calumnia* is reported from Fiji and *Pseudosquillana megalophthalma* is reported from the Moluccas for the first time.

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Keywords: *Gonodactylaceus falcatus, Gonodactylinus viridis, Gonodactylus chiragra, Gonodactylus platysoma, Pseudosquillana megalophthalma*, Macleay, stomatopod.

INTRODUCTION

Among the most pugnacious and aggressive crustaceans are the mantis shrimps. They are the 'thugs of crustaceandom' (Schmitt 1965) and comprise the order Stomatopoda, the only extant representatives of the subclass Hoplocarida (Schram 1986). Stomatopods occur in most tropical marine habitats and always occupy a burrow or shelter. All are active predators and many species are flamboyantly coloured. Characteristic features of stomatopods are the large and powerful raptorial appendages; prey is captured by 'spearing' or 'smashing', depending on whether the raptorial dactylus is extended or folded during the strike.

The stomatopod collection in the Macleay Museum, although small, is significant for the several rare species represented. From an Australian perspective, much of the western Atlantic material is significant inasmuch as it is the only material of its kind in the country.

The crustacean collection probably began with material acquired or collected by William Sharp Macleay while stationed in Havana, Cuba (1825–1836). Further additions include an extensive collection of "Annulosa" from the Cape of Good Hope (Macleay 1838); other specimens were collected at sea enroute to Australia in 1838 (Fletcher 1929). After W.S. Macleay's death in 1865, the collections were inherited by his cousin William John Macleay who expanded the collections to include vertebrate and ethnographical specimens.

Professional collectors, donations and Linnean Society collecting trips all contributed to the collections. The 1875 'Chevert' Expedition to New Guinea, however, provided the best single opportunity to collect new material. Today, most of these specimens remain to be documented and provide the best example of the continuing legacy of the Macleays.

MATERIALS AND METHODS

Synonymies are not intended to be complete. They are restricted to the most significant works or those available to us at the time of writing. Some specimens lack collection data and the position of the Chichester Reefs (C7, C8, C32) is presently indeterminate. Those records are nevertheless included for completeness. The location of the Chichester Reefs will likely be known in the future, particularly through ongoing historical study of the Macleays.

Since most specimens were preserved dry, the overall length could not be measured consistently. Therefore, measurements were restricted to carapace length. Carapace length (CL) was measured along the midline of the carapace to the nearest tenth millimetre (mm). Other abbreviations: Is. (island); R.(river); indet. (indeterminate); NSW (New South Wales); NT (Northern Territory); QLD (Queensland).

The collections comprise 57 dry specimens (C1–57) and 39 wet specimens (C58–96) stored in 70% alcohol.

SYSTEMATIC ACCOUNT

Superfamily GONODACTYLOIDEA Giesbrecht, 1910

Family GONODACTYLIDAE Giesbrecht, 1910

Gonodactylaceus falcatus (Forskal, 1775)

Cancer falcatus Forskal 1775: 9.
Gonodactylus falcatus — Holthuis 1967: 31, 41 — Manning 1978a: 4, 5, 13, figs 1, 2a, 9, 1991: 3 — Manning and Lewinsohn 1986: 7–10 — Moosa 1989, 1991: 156–157.
Gonodactylaceus falcatus — Manning 1995: 42–43.

Material

C20, male, CL 11.0mm, Palm Is., QLD, fragmented, 'Chevert' Expedition, 13 August 1875; C22, male, CL 9.0mm, locality and collector unknown; C24, female, CL 8.3mm, locality and collector unknown; C37, female, CL 14.7mm, Endeavour R., QLD, coll. E. Spalding, 1874; C39, 40, New Caledonia, purchased by J. Brazier, 12 September 1874: C39, male, CL 7.5mm; C40, female, CL 9.5mm; C68–72, Sue Is., Torres Strait, 'Chevert' Expedition, 26 June 1875: C68, male, CL 11.0mm; C69, female, CL 10.6mm; C70, female, CL 9.2mm; C71, female, CL 8.6mm; C72, female, CL 7.2mm.

Remarks and Distribution

Manning (1978a) remarked that all records of *G. falcatus* require verification since much of what was previously referred to as this species actually comprises a species complex, all bearing five longitudinal carinae on the telson. Further some species are difficult to distinguish without reference to colour in life. *Gonodactylaceus falcatus* is known with certainty from the Red Sea (Holthuis 1967, Manning 1978a, Manning and

Lewinsohn 1986), but has also been reported from Japan (Moosa 1989), Australia (Manning 1966, Stephenson and McNeill 1955) and New Caledonia (Moosa 1991). One of us (STA) has observed live material (to be reported on elsewhere) from the northern Great Barrier Reef which match published descriptions of *G. falcatus* from the Red Sea (Holthuis 1967, Manning and Lewinsohn 1986). Material reported here is morphologically identifiable with, and is considered conspecific with, *G. falcatus* on the basis of its confirmed occurrence in Australian waters. *Gonodactylaceus falcatus* may prove to be widely distributed in the Indo-West Pacific but we concur with Manning (1991) that such records still require verification. *Gonodactylus falcatus*, reported by Stephenson and McNeill (1955), from Lord Howe Island may refer to a similar species, *G. mutatus* (Lanchester, 1903) which occurs there (Ahyong unpubl.).

Gonodactylaceus glabrous (Brooks, 1886)

Gonodactylus glabrous Brooks 1886: 62, pl.14: fig.5, pl.15, figs. 7, 9 — Manning 1978a: 5, figs. 3, 10 — Manning and Lewinsohn 1986: 9–10[list] — Moosa 1991: 157–158.
Gonodactylaceus glabrous — Manning 1995: 42–45, fig.12.

Material

C73, male, CL 9.7mm, Moluccas, collector unknown.

Distribution

Gonodactylaceus glabrous is widely distributed in the Indo-West Pacific, from the Red Sea, Vietnam, Indonesia and New Caledonia.

Gonodactylaceus graphurus (Miers, 1875)

Gonodactylus graphurus White 1847: 85 [part; nomen nudum].
Gonodactylus graphurus Miers 1875: 344 [part, White's material only] — Kemp 1913: 169–170 — Stephenson 1952: 12, 1953: 47 — Stephenson and McNeill 1955 — Stephenson 1962: 35 — Manning 1966: 108–9 — Manning 1978a: 5 — Manning and Lewinsohn 1986: 9 [list].
Gonodactylaceus graphurus — Manning 1995: 42–43.

Material

C29, female, CL 8.0mm, Cape York, 'Chevert' Expedition, 18–26 June 1875; C36, female, CL 13.6mm, locality and collector unknown; C41–43, 95, Cape Grenville, QLD, 'Chevert' Expedition, 12–17 June 1875: C41, sex indet., fragmented, CL 6.9mm; C42, sex indet., fragmented, CL 7.7mm; C43, sex indet., fragmented, CL 6.4mm; C95, female, CL 15.5mm.

Remarks

The transverse abdominal grooves are a good recognition character for *Gonodactylaceus graphurus* which otherwise closely resembles *G. falcatus*.

Distribution

Gonodactylaceus graphurus is known only from Australian waters where it is most common subtidally on coral reefs.

Gonodactylinus viridis (Serène, 1954)

Gonodactylus viridis Serène 1954: 6, 7, 10, 74, 75 — Dingle *et al* 1977: 16 — Manning 1978: 4, fig. 2a–c — Moosa 1985: 381–2, 1989: 226.
Gonodactylinus viridis — Manning 1995: 66–68 pl. 4, figs. 8c, d, 9c, 10e, 11c, 25a.

Material

C87, female, CL 11.8mm, locality unknown; C92–94, Navigator Is., Samoa, coll. Rev. G. Brown, [18 March 1875]: C92, male, CL 10.5mm; C93, male, CL 9.0mm; C94, female, CL 10.0mm.

Distribution

The known range of *Gonodactylinus viridis* includes Japan, Vietnam, Thailand, the Philippines, New Caledonia and now Samoa.

Gonodactylus chiragra (Fabricius, 1781)

Squilla chiragra Fabricius 1781: 515.
Gonodactylus chiragra — Kemp 1913: 155, pl.9, fig.107 [synonymy] — Manning 1966: 113–114, 1968: 43–44 — Dingle et al. 1977: 17–18 — Manning 1991: 3 — Moosa 1985: 381, 1991: 155–156 — Manning 1995: 68–75, pl.5–8, figs.8e, f, 9a, b, 10a, 11a, 27a, 28–30.

Material

C17, 18, Palm Is., QLD, 'Chevert' Expedition, 31 May-3 June, 1875: C17, female, CL 16.9mm; C18, male, CL 20.3mm; C21, sex indet., thoracic somites damaged, CL 9.8mm C33–35, Torres Strait, 'Chevert' Expedition, 1875: C33, sex indet., fragmented, CL 9.8mm; C34, sex indet., fragmented, CL 11.0mm; C35, female, CL 19.0mm; C44, female, CL 11.3mm, New Caledonia, coll. J. Brazier, 20 April 1874; C47, female, fragmented, CL 18.3mm Low Is., QLD, 'Chevert' Expedition, 7 June, 1875; C49, female, CL 15.2mm, fragmented, Cape Grenville, QLD, 'Chevert' Expedition, 12–17 June 1875; C50, male, CL 14.6mm, locality unknown, coll. W.S. Macleay; C51, male, CL 11.5mm, locality unknown, coll. W.S. Macleay; C52, male, CL 10.5mm, locality unknown, coll. W.S. Macleay; C53, female, CL 17.3mm, locality unknown, coll. W.S. Macleay; C56, female, CL 11.3mm, locality unknown, coll. W.S. Macleay; C62, male, CL 14.1mm, Moluccas, collector unknown; C63, female, CL 14.0mm Moluccas, collector unknown; C64, male, CL 10.5mm, Moluccas, collector unknown; C65, male, CL 7.5mm, Moluccas, collector unknown; C77–79, Port Darwin NT, coll. E. Spalding, September 1877: C77, male, CL 11.4mm; C78, female, CL 11.4mm; C79, female, CL 9.4mm; C82, female, CL 17.3mm, Lord Howe Is., NSW, 'Herald' Expedition; C84, male, CL 13.5mm, locality and collector unknown; C85, male, CL 14.7mm, locality and collector unknown; C86, female, CL 12.3mm, locality and collector unknown.

Distribution

Gonodactylus chiragra occurs on coral reefs and is apparently widely distributed throughout the Indo-West Pacific from Japan, Indonesia, New Caledonia, Australia, the Red Sea and South Africa. This species has not been previously reported from Lord Howe Island.

Gonodactylus platysoma Wood-Mason, 1895

Gonodactylus platysoma Wood-Mason 1895: 11, pl.3, figs. 3–9 — Manning 1966: 110–111, 1968: 44 — Dingle et al. 1977: 17–19 — Cappola and Manning 1994: 277.

Gonodactylus chiragra var *platysoma* — Kemp 1913: 161–162, 1915: 180 — Holthuis 1941: 28.

Gonodactylus chiragra — Stephenson and McNeill 1955: 250 [part] — Manning 1995: 68, 75–76, pls. 9, 10, figs. 9d, 10b, 11b, 27b, 31.

Material

C45–46, Mauritius, coll. J. Brazier, 22 April 1874: C45, female, CL 16.0mm; C46, male, CL 14.5mm; C55, female, CL 14.7mm, locality unknown, coll. W.S. Macleay; C57, male, CL 12.3mm, locality unknown, coll. W.S. Macleay; C66–67, Mauritius, purchased by J. Brazier, 22 April 1874: C66, female, CL 18.8mm; C67, female, CL 16.8mm; C83, female, Lord Howe Is., NSW, CL 16.5mm, 'Herald' Expedition; C88, male, CL 17.7mm, locality and collector unknown; C89, male, CL 18.2mm, locality and collector unknown.

Distribution

This species is known from the Indo-Pacific — western Indian Ocean, Indo-Malayan region, Japan, Australia and the central Pacific from shallow tropical reefs. *Gonodactylus platysoma* has not previously been reported from Lord Howe Island.

Gonodactylus smithii Pocock, 1893

Gonodactylus smithii Pocock 1893: 475, pl. 20B, fig.1 — Manning 1966: 112–113, 1968: 44–45 — Dingle et al. 1977: 19 — Manning 1991: 4 — Moosa 1991: 160 — Cappola and Manning 1994: 277–8 — Manning 1995: 76–80, pls.11, 12, figs. 9e, 10c, 11d, 27c, 32–35.

Material

C12–16, 19, 21, Darnley Is., Torres Strait, 'Chevert' Expedition, 13 August 1875: C12, female, CL 12.0mm; C13, male, CL 16.0mm; C14, male, CL 16.0mm; C15, female, CL 13.2mm; C16, male, CL 14.0mm; C19, female, fragmented, CL 11.6mm; C23, female, CL 11.2mm, locality and collector unknown; C38, female, CL 14.7mm, Endeavour R., QLD, coll. E. Spalding, 1874; C48, female, CL 17.0mm, Low Is., QLD, 'Chevert' Expedition, 7 June, 1875; C54, male, locality unknown, CL 14.0mm, coll. W.S. Macleay; C90, female, Port Moresby, CL 17.0mm; C91, female, Port Moresby, CL 14.8mm.

Distribution

Gonodactylus smithii occurs in the western Indian Ocean, the Indo-Malayan region, New Caledonia and Australia, from the shore to 80m (Moosa 1991). In Australian waters, *G. smithii* is frequently encountered foraging over the reef flat at low tide.

Neogonodactylus bredini (Manning, 1969a)

Gonodactylus bredini Dingle 1969a: 108 [*nomen nudem*].
Gonodactylus bredini Manning 1969a: 315 — Camp 1973: 53–71 — Gore and Becker 1976:171–172 — Schotte and Manning 1993: 567–8.
Neogonodactylus bredini — Manning 1995: 80.

Material

C25, 30–31, Cuba, coll. W.S. Macleay, 1825–36: C25, female, CL 10.3mm; C30, female, CL 8.0mm; C31, male, CL 8.9mm.

Distribution

Neogonodactylus bredini is a common shore species occuring in the tropical western Atlantic, from Bermuda, through the Caribbean and off the coast of South America (Manning 1969a).

Neogonodactylus oerstedii (Hansen, 1895)

Gonodactylus Oerstedii Hansen 1895: 65, footnote [part].
Gonodactylus oerstedii — Manning 1969a: 325–334 [synonymy] — Gore and Becker 1976: 173–6 — Schotte and Manning 1993: 570.
Neogonodactylus oerstedii — Manning 1995: 80.

Material

C26–27, Cuba, coll. W.S. Macleay, 1825–1836: C26, female, CL 10.6mm; C27, female, CL 9.2mm.

Remarks

Neogonodactylus oerstedii and *N. bredini* are two of the commonest shore species in the tropical western Atlantic.

Distribution

This species is known from Bermuda and southern Florida, to Tobago in shallow water (Schotte and Manning 1993).

Neogonodactylus torus (Manning, 1969)

Gonodactylus torus Manning 1969a: 335, 1970: 111 [discussion] — Manning and Hart 1981: 711 [discussion].
Neogonodactylus torus — Manning 1995: 80.

Material

C28, sex indet., glued to card, CL 4.0mm, Cuba, coll. W.S. Macleay, 1825–1836.

Remarks

The single specimen is in rather poor condition (glued to card and slightly fragmented). The abdominal and thoracic appendages are damaged, preventing determination of sex. *Neogonodactylus torus* is a small species (total length less than 33.7mm) inhabiting relatively deep water, usually more than 50m (Manning 1969).

Distribution

Neogonodactylus torus is common in the tropical western Atlantic and has previously been reported from Cuba (Manning 1969).

Family ODONTODACTYLIDAE Manning, 1980

Odontodactylus japonicus (de Haan, 1844)

Gonodactylus japonicus de Haan 1844, pl. 51, fig.7; 1849: 225 [text].
Odontodactylus japonicus — Kemp 1913: 139 — Kemp and Chopra 1921: 297 [listed] — Holthuis 1941: 276 — Stephenson and McNeill 1955: 248 — Stephenson 1960: 61, 1962: 35, 1965: 260 — Manning 1967: 7–10 fig.2, 1968: 41–42 — Graham et al. 1993: 73 [list].

Material

C7, male, badly fragmented, CL 32.9mm, Chichester Reefs, Pacific; C8, male, badly fragmented, CL 32.8mm, Chichester Reefs, Pacific, coll. Dr Raynor.

Remarks

Although both specimens are substantially fragmented, the telson, raptorial claws, uropods and cephalon are sufficiently intact to allow positive identification.

Distribution

Odontodactylus japonicus is widely distributed in the Indo-West Pacific from Japan, Australia, westwards to Madagascar. In Australia, *O. japonicus* has been reported from Exmouth Gulf and Broome in the west (Stephenson 1962), the Capricorn Group in the east and off the Clarence River, N.S.W (Graham et al. 1993).

We could not locate the Chichester Reefs, but the known distribution of *O. japonicus* suggests a western Pacific location.

Odontodactylus scyllarus (Linnaeus, 1758)

Odontodactylus scyllarus — Kemp 1913: 135 — Stephenson 1953: 46 — Stephenson and McNeill 1955: 248 — Stephenson 1962: 35 — Manning 1967: 10, fig.3 — Dingle et al. 1977: 12, 13 fig.6c–e — Moosa 1991: 163 — Manning 1995: 82–85, pl. 13, figs. 35, 37, 38a, b.

Material

C3, male, CL 29.9mm, Mauritius, purchased by J. Brazier at auction, 22 April 1874; C58, male, CL 29.0mm, locality and collector unknown; C59, male, CL 29.0mm, Cardagos, collector unknown.

Distribution

This species is distributed throughout the Indo-West Pacific from Japan, Australia and westwards to Madagascar. Moosa (1991) recently reported this species from New Caledonia. On the eastern coast of Australia, *O. scyllarus* occurs as far south as the Solitary Islands, northern New South Wales.

Family PSEUDOSQUILLIDAE Manning, 1977

Pseudosquilla ciliata (Fabricius, 1787)

Pseudosquilla ciliata — Kemp 1913: 96–100, 196, 1915: 172 — Holthuis 1941: 261 — Stephenson 1953: 44, 1962: 34 — Holthuis 1967:15, 16 — Manning 1969a: 264–271 fig.74 — Gore and Becker 1976: 177 — Manning 1977: 100–103 fig.30, 31 — Dingle et al. 1977: 12, fig. 6a, b — Moosa 1985: 385 — Manning and Lewinsohn, 1986: 12 — Moosa 1991: 169–170.

Material

C9, female, CL 18.0mm, Darnley Is., Torres Strait, coll. W.J. Macleay, 'Chevert' Expedition, 13 August 1875; C10, female, CL 12.0mm, fragmented, Cape Grenville, QLD, 'Chevert' Expedition, 12–17 June 1875; C11, male, CL 13.7mm, New Caledonia, purchased by J. Brazier, 12 September 1874; C74–76, Navigator Is., Samoa, coll. Rev. G. Brown: C74, male, CL 10.8mm; C75, male, CL 11.3mm; C76, male, CL 11.4mm; C80, female, CL 11.5mm, Lord Howe Is., NSW, 'Herald' Expedition.

Remarks

Stephenson (1962) referred to a Macleay specimen from Lord Howe Island as a New South Wales record — presumably C80. In all specimens, the intermediate denticle of the telson is spined and the uropodal endopod is evenly rounded distally. They thus correspond to the "forme claire" of Serène (1951).

Distribution

Pseudosquilla ciliata is among the most widely distributed of stomatopods, occurring in all tropical oceans except the eastern Pacific. This species is common in many habitats, from coral rubble to seagrass flats, and is known from coral reefs as far south as Lord Howe Island, eastern Australia.

Pseudosquillana megalophthalma (Bigelow, 1893)

Pseudosquilla megalophthalma Bigelow 1893: 101 — Kemp 1913: 3, 10, 96, 103 - Holthuis 1941 — Manning and Lewinsohn 1986: 12, 15 — Moosa 1991: 174.
Pseudosquilla richeri — Moosa 1991: 175–176, fig.5.
Pseudosquillana megalophthalma — Cappola and Manning 1994: 283.

Material

C81, female, Moluccas, CL 7.9mm.

Remarks

The present specimen agrees with published accounts for material of its size (eg. Holthuis 1941). The dorsal carinae of the telson are well developed and match the type description. The intermediate spines of the sixth abdominal somite do not bear a secondary, inner spine as described for adults, and the cornea, though expanded, is not yet distinctly bilobed.

The length of the raptorial dactylus exceeds the carapace length, and the posterior margin of the claw when folded is in line with the posterior margin of the carapace. The number of movable spines on the opposable, proximal margin has not been reported in the literature for *P. megalophthalma* and in the present specimen, there are 3. The raptorial propodus does not bear a distal tooth and the anterior margin of the rostral plate is more evenly rounded than as figured by Cappola and Manning (1994: fig.4) for the holotype. *Pseudosquillana megalophthalma* as currently recognized, may prove to be composite (Manning, pers. com.).

Distribution

Although relatively rare, *P. megalophthalma* is widely distributed throughout the Indo-West Pacific, from the Red Sea, the western Indian Ocean, Somalia, New Caledonia and now from the Moluccas, Indonesia.

Family TAKUIDAE Manning, 1995

Mesacturus furicaudatus (Miers, 1880)

Gonodactylus furicaudatus Miers, 1880: 124 — Kemp, 1913: 176–177.
Mesacturus furicaudatus — Manning, 1969d: 151–153 — Manning, 1995: 119.

Material

C32, sex indet., fragmented, CL 5.4mm, Chichester Reefs, Pacific, coll. Dr Raynor.

Remarks

Although the telson and thorax are damaged, careful examination allows positive identification. The exact position of the Chichester Reefs could not be determined, except that they are somewhere in the western Pacific (see remarks under the account of *Odontodactylus japonicus* (de Haan)).

Distribution

Mesacturus furicaudatus is known from the Indonesia, Polynesia and the Borodino Islands, south of Japan (Manning, 1969d).

Superfamily LYSIOSQUILLOIDEA Giesbrecht, 1910

Family LYSIOSQUILLIDAE Giesbrecht, 1910

Lysiosquilla capensis Hansen, 1895

Lysiosquilla capensis Hansen 1895: 74 — Barnard 1950: 856, fig.4e — Manning 1969c: 5, fig.1, 1978b: 3, fig.11, 1995: 125–126.

Material

C2, female, CL 17.9mm, off Cape of Good Hope, tow-net, coll. W.S. Macleay, 1839.

Distribution

Lysiosquilla capensis is known only from southern African waters, from the shore to 90m (Manning 1978b).

Lysiosquilla scabricauda (Lamarck, 1818)

Squilla scabricauda Lamarck 1818:188.
Lysiosquilla scabricauda — Manning 1969a: 24–34 [American specimens only].

Material

C1, male, fragmented, CL 46.0mm, Antilles.

Distribution

Lysiosquilla scabricauda is a large and common western Atlantic species, recorded from Bermuda, through the Caribbean to southern Brazil (Manning 1969).

Superfamily SQUILLOIDEA Latreille, 1803

Family HARPIOSQUILLIDAE Manning, 1980

Harpiosquilla harpax (de Haan, 1844)

Squilla harpax de Haan 1844, atlas, pl.51, fig.1; 1849: 222, text — Tiwari and Biswas 1952: 358, figs.3b, d, f.
Squilla raphidea — Kemp 1913: 88, pl.7, fig.77 [part] — Holthuis 1941: 256 [part] — Stephenson and McNeill 1955: 239 [part]. [All not *S. raphidea* Fabricius] — Stephenson 1962: 34.
Harpiosquilla harpax — Manning 1968: 15–18, fig.4 — Tirmizi and Manning 1968: 33–35, fig.13 — Manning 1969b: 25–33, figs. 28–38, 1969c: 7 — Moosa 1985: 390 — Manning 1991: 8 — Manning 1995: 148, 153–158, pl.28, figs. 90a, 92b, 93, 95, 96.

Material

C6, male, fragmented, CL 31.5mm, Indian seas, collector unknown.

Remarks

The specimen is highly fragmented but may be recognized by the remaining cephalon, telson and uropods. The angled, inferior margin of the raptorial dactylus indicates that the specimen is an adult male (Manning 1969b).

Distribution

Harpiosquilla harpax is the most widely distributed species of the genus, occurring in the Red Sea and throughout the Indo-West Pacific including Australia. In Australia, it is known as far south as Botany Bay, New South Wales.

Family SQUILLIDAE Latreille, 1803

Alima laevis (Hess, 1865)

Squilla laevis Hess 1865: 170, pl. 7, fig. 22 — Kemp 1913: 40 pl. III, figs.35–37 — Stephenson 1952: 6, 1953: 40 — Stephenson and McNeill 1955: 242 — Stephenson 1960: 61, 1962: 33 — Manning 1966: 98–99.
Alima laevis — Moosa 1991: 188.

Material

C4–5, 60, Port Jackson, NSW, coll. Brazier or Macleay, 1874; C4, female, CL 20.2mm; C5, female, CL 19.9mm; C60, male, CL 28.0mm.

Distribution

Alima laevis is the most frequently encountered stomatopod in southern Australian estuaries. It has been reported from Broome in the west (Stephenson 1962), southwards around the continent and north to Queensland. Moosa (1991) reported this species from New Caledonia.

Oratosquilla calumnia (Townsley, 1953)

Squilla calumnia Townsley 1953: 410, figs 8, 9.
Oratosquilla calumnia — Manning 1971: 4–6, fig.1 — Moosa 1991: 210–211.

Material

C61, male, CL 22.5mm, Fiji, coll. A. Boyd, 9 February 1876.

Remarks

The specimen agrees well with Manning's (1971) diagnosis of *O. calumnia*: the dorsal surface is rugose and the anterior lobe of the lateral process of the seventh thoracic somite is sharp. The anterior lobe of the lateral process of the sixth thoracic somite is more slender as in *O. oratoria*, but not as slender as in *O. mauritiana* (Manning, 1968). Abdominal carinae are spined as follows: submedian 4–6, intermediate 1–6, lateral 1–6, marginal 1–5.

Distribution

Originally described from Hawaiian waters, *O. calumnia* has also been reported from New Caledonia (Moosa 1991). The present new record from Fiji further suggests that *O. calumnia* may be widely distributed in the central and western Pacific.

Oratosquillina asiatica (Manning, 1978)

Squilla fabricii — Stephenson 1962: 33 [not *Squilla fabricii* Holthuis 1941].
Oratosquilla asiatica — Manning 1978: 10–12, fig. 4 — Moosa and Cleva 1984: 78–79.
Oratosquillina asiatica — Manning 1995: 225, 227.

Material

C96, female, CL 19.4mm, Moluccas.

Remarks

The specimen largely agrees with the type description (Holthuis 1941) differing in the bearing additional abdominal spines, and an indistinct rostral carina. The abdominal spination is as follows: submedian 3–6, intermediate 2–6, lateral 1–6, marginal 1–5. Stephenson (1962) referred this specimen to *Squilla fabricii* Holthuis.

Distribution

This species is known from Taiwan, the Philippines, Indonesia and Irian Jaya (Manning 1978, 1995). The present record is within the known range for the species.

DISCUSSION

The bathymetric distributions of stomatopods represented in the Macleay collections imply that collecting efforts were largely restricted to intertidal and shallow sublittoral zones. Four species were collected from the Caribbean (5% of the Western Atlantic fauna) and 17 species from the western Pacific and southern Africa (7% of the Indo-West Pacific fauna). The Caribbean specimens are not taxonomically remarkable, but are significant since many are the only stomatopods from that region presently in Australia.

Several rare or seldom reported Indo-West Pacific species are included in the collection: *Pseudosquillana megalophthalma*, *Oratosquilla calumnia*, *Oratosquillina asiatica* and *Mesacturus furicaudatus* (see remarks under accounts of those species). Of these, *P. megalophthalma* and *O. calumnia* are newly reported from the Moluccas and Fiji respectively.

The Lord Howe Island records of *Gonodactylus chiragra* and *G. platysoma* are new. The Australian record of *Gonodactylaceus falcatus* extends its known range to well outside of the Red Sea where it was believed endemic (Manning and Lewinsohn 1986).

The handful of new distribution records from this small collection points to the fact that many more stomatopod species may be more widely distributed than presently known. More intense collecting effort will likely alter our zoogeographical understanding of many species and their radiations.

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REFERENCES

Barnard, K.H. (1950). Descriptive list of South African stomatopod Crustacea (mantis shrimps). *Annals of the South African Museum* **38**, 838–864.

Bigelow, R.P. (1893). Preliminary notes on the Stomatopoda of the Albatross collections and on other specimens in the National Museum. *Johns Hopkins University Circulars* **12**, 100–102.

Camp, D.K. (1973). Stomatopod Crustacea. *Memoirs of the Hourglass Cruises* **3**, 1–100.

Cappola, V. and Manning, R.B. (1994). Research on the coast of Somalia: Crustacea Stomatopoda. *Tropical Zoology* **7**, 271–291.

de Haan, W. (1833–50). Crustacea. In *'Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jusse et auspiciis superiorum, qui summum in India Batavia Imperium tenent, suscepto, annis 1823–1830 collegit, notis observationibus et adumbrationibus illustravit'* (Ed. P.F. Von Siebold) pp.1–243 (Lugdunum Batavorum: A. Arnz)

de Lamarck, J.B.P.A.(1818). 'Histoire naturelle des animaux sans vertebres, presentant des caracteres generaux et particuliers de ces animaux, leur distribution, leur classes, leurs families, leurs genres, et la citation des principales especes qui s'y rapportent; precedee d'une introduction offrant la determination des caracteres essentiels, de l'animal, sa distinction du vegetal et des autres corps naturelles, enfin, l'exposition des principes fondamentaux de la zoologie'. (Deterville, Paris).

Dingle, H. (1969). Ontogenetic changes in phototaxis and thigmokinesis in stomatopod larvae. *Crustaceana* **16**, 108–110.

Dingle, H., Caldwell, R.L. and Manning, R.B. (1977). Stomatopods of Phuket Island, Thailand. *Phuket Marine Biological Centre Research Bulletin* #20.

Fabricius, J.C. (1781). *Species Insectorum exhibentes eorum differentias specificas, synonymy auctorum, loca natalia, metamorphosin adjectis observationibus, descriptionibus* i-viii + 1–552. Carol. Ernest Bohnii, Hamburgii et Kolonii.

Fletcher, J.J. (1929). The society's heritage from the Macleays Part 2. *Proceedings of the Linnean Society of New South Wales* **54**, 185–272.

Forskal, P. (1775). *Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium* 1–164.

Giesbrecht, W. (1910). Stomatopoden. *Fauna Flora Golf. Neapel* **33**, 1–239.

Gore, R.H. and Becker, L.J. (1976). Studies on stomatopod Crustacea from the Indian River region of Florida. II. An annotated check list of the mantis shrimps of the central eastern Florida coast. *Proceedings of the Biological Society of Washington* **89**, 147–184.

Graham, K.J., Liggins, G.W., Wildfoster, J. and Kennelly, S.J. (1993). *Kapala Cruise Report* No. 112.

Hansen, H.J. (1895). Isopoden, Cumaceen and Stomatopoden der Planktonexpedition. *Ergebnisse Planktonexpedition Humbolt-Stiftung* **2**, 1–105.

Hess, W. (1865). *Beitrage zur Kenntniss der Decapoden-krebse Ost-Australiens* 1–47. Bonn.

Holthuis, L.B. (1941). The Stomatopoda of the 'Snellius' Expedition. No.XII (in) Biological Results of the 'Snellius' Expedition. *Temminckia* **6**, 241–294.

Holthuis, L.B. (1967). The Stomatopod Crustacea Collected by the 1962 and 1965 Israel South Red Sea Expeditions. The Second Israel South Red Sea Expedition Report No.1. *Israel Journal of Zoology* **16**, 1–45.

Ingle, R.W. (1971). On the nomenclature of *Gonodactylus graphurus* White, 1847 (Nomen Nudum), Miers, 1875 (Stomatopoda, Gonodactylidae). *Crustaceana* **21**, 220–221.

Kemp, S. (1913). An Account of the Crustacea Stomatopoda of the Indo-Pacific Region, based on the Collection in the Indian Museum. *Memoirs of the Indian Museum* **4**, 1–217.

Kemp, S. (1915). On a collection of stomatopod Crustacea from the Philippine Islands. *Philippine Journal of Science, Section D* **10**, 169–187.

Kemp, S. and Chopra, B. (1921). Notes on Stomatopoda. *Records of the Indian Museum* **22**, 297–311.

Macleay, W.S. (1838). *Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa."* London.

Manning, R.B. (1966). Notes on some Australian and New Zealand stomatopod Crustacea, with an Account of the Species Collected by the Fisheries Investigation Ship Endeavour. *Records of the Australian Museum* **27**, 79–137.

Manning, R.B. (1967). Review of the Genus *Odontodactylus* (Crustacea: Stomatopoda). *Proceedings of the United States National Museum* **123**(3606), 1–358.

Manning, R.B. (1968). Stomatopod Crustacea from Madagascar. *Proceedings of the United States National Museum* **124**(3641), 1–61.

Manning, R.B. (1969a). 'Studies in Tropical Oceanography No, 8: Stomatopod Crustacea of the Western Atlantic'. (University of Miami Press: Florida).

Manning, R.B. (1969b). A review of the genus *Harpiosquilla* (Crustacea, Stomatopoda), with descriptions of three new species. *Smithsonian Contributions to Zoology* **36**, 1–37.

Manning, R.B. (1969c). Notes on some stomatopod crustacea from southern Africa. *Smithsonian Contributions to Zoology* **1**, 1–17.

Manning, R.B. (1969d). Notes on the *Gonodactylus* section of the family Gonodactylidae (Crustacea, Stomatopoda), with descriptions of four new genera and a new species. *Proceedings of the Biological Society of Washington* **82**: 143–166.

Manning, R.B. (1970). Nine new American stomatopod crustaceans. *Proceedings of the Biological Society of Washington* **83**, 99–114.

Manning, R.B. (1971). Keys to the species of *Oratosquilla* (Crustacea: Stomatopoda) with descriptions of two new species. *Smithsonian Contributions to Zoology* **71**, 1–16.

Manning, R.B. (1977). A monograph of West African Stomatopod Crustacea. *Atlantide Report (Copenhagen)* **12**, 25–181.

Manning, R.B. (1978a). Notes on some species of the *Falcatus* Group of *Gonodactylus* (Crustacea: Stomatopoda: Gonodactylidae). *Smithsonian Contributions to Zoology* **258**, 1–15.

Manning, R.B. (1978b). Synopses of the Indo-West Pacific species of *Lysiosquilla* Dana, 1852 (Crustacea: Stomatopoda: Lysiosquillidae). *Smithsonian Contributions to Zoology* **259**, 1–16.

Manning, R.B. (1980). The superfamilies, families, and genera of recent stomatopod Crustacea, with diagnoses of six new families. *Proceedings of the Biological Society of Washington* **93**, 362–372.

Manning, R.B. (1991). Stomatopod Crustacea collected by the Galathea Expedition, 1950–1952, with a list of Stomatopoda known from depths below 400 meters. *Smithsonian Contributions to Zoology* **521**, 1–18.
Manning, R.B. and Hart, C.W. (1981). *Gonodactylus lightbourni*, a new stomatopod crustacean from Bermuda. *Proceedings of the Biological Society of Washington* **94**: 708–712.
Manning, R.B. and Lewinsohn, Ch. (1986). Notes on some Stomatopod Crustacea from the Sinai Peninsula, Red Sea. *Smithsonian Contributions to Zoology* **433**, 1–19.
Miers, E.J. (1875). On some new or undescribed species of Crustacea from the Samoa Islands. *Annals and Magazine of Natural History* series 4, **16**, 341–317.
Miers, E.J. (1880). On the Squillidae. *Annals and Magazine of Natural History* **5**:108–127.
Moosa, M.K. (1985). Resultats des Campagnes Musorstom I & II, Philippines. 11. Stomatopod Crustacea. *Memoires Museum National D'Histoire Naturelle, Serie A, Zoologie* **133**, 367–416.
Moosa, M.K. (1989). Some Stomatopods (Crustacea: Stomatopoda) from Japanese waters, with description of a new species. *Bulletin of the National Science Museum, Tokyo, Series A* **15**, 223–229.
Moosa, M.K. (1991). The Stomatopoda of New Caledonia and Chesterfield Islands. In *'Le Benthos des fonds meubles des Lagons de Nouvelle-Caledonie, Vol.1 Etudes and Theses ORSTOM'* (Ed. B. Richer de Forges) pp.149–219. (ORSTOM: Paris).
Moosa, M.K. and Cleva, R. (1984) Stomatopod Crustacea collected by the mission Corindon II in the Makassar Strait, Indonesia. *Marine Research in Indonesia* **24**: 73–82.
Pocock, R.I. (1893). Report upon the stomatopod crustaceans obtained by P.W. Bassett-Smith, Esq., Commander W.U. Moore. *Annals and magazine of Natural History 6* **11**, 473–479.
Schmitt, W. (1965). *Crustaceans*. (University of Michigan Press: Ann Arbor).
Schram, F. (1986). *Crustacea*. (Oxford University Press: Oxford).
Schotte, M. and Manning, R.B. (1993). Stomatopod Crustacea from Tobago, West Indies. *Proceedings of the Biological Society of Washington* **106**, 566–581.
Serène, R. (1951) Observations sur deux *Pseudosquilla* d'Indochine. *Treubia* 21(1): 11–25.
Serène, R. (1954). Observations biologiques sur les stomatopodes. *Memoires Institude oceanographe Nhatrang*, **8**, 1–93.
Stanbury, P. and Holland, J. (1988). *'Mr Macleay's Celebrated Cabinet'*. (The Macleay Museum: Sydney).
Stephenson, W. (1952). Faunistic records from Queensland. Part I- General Introduction. Part II-Adult Stomatopoda (Crustacea). *Zoological Papers of the University of Queensland* **1**, 1–15.
Stephenson, W. (1953). Notes on the Australian Stomatopoda (Crustacea) in the collections of the Queensland Museum. *Memoirs of the Queensland Museum* **13**, 40–49.
Stephenson, W. (1960). Notes on Queensland Stomatopoda (mantis prawns). *Queensland Naturalist* **16**, 61.
Stephenson, W. (1962). Some Interesting Stomatopoda — Mostly from western Australia. *Journal of the Royal Society of Western Australia* **45**, 33–43.
Stephenson, W. and McNeill, F. (1955). The Australian Stomatopoda (Crustacea) in the collections of the Australian Museum, with a check list and key to the known Australian species. *Records of the Australian Museum* **23**, 239–265.
Tirmizi, N.M. and Manning, R.B. (1968). Stomatopod Crustacea from West Pakistan. *Proceedings of the United States National Museum* **125**(3666), 1–48.
White, A. (1847). *'List of species of Crustacea in the collection of the British Museum'*. (British Museum: London).
Wood-Mason, J. (1895). 'Figures and descriptions of nine species of Squillidae from the collections in the Indian Museum'. (Indian Museum:Calcutta).

Lepidopsocidae, Trogiidae, Myopsocidae and Psocidae (Insecta: Psocoptera) from the Mount Royal Area, New South Wales

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SMITHERS, C.N. (1997). Lepidopsocidae, Trogiidae, Myopsocidae and Psocidae (Insecta: Psocoptera) from the Mount Royal Area, New South Wales. *Proceedings of the Linnean Society of New South Wales* **118**, 111–121.

Two species of Lepidopsocidae, two Trogiidae, two Myopsocidae and twelve species of Psocidae (including *Lasiopsocus hollowayi* sp.n., *Kaindipsocus emarginatus* sp.n. and *K. marksae* sp.n.) are recorded from the Mount Royal area in the Hunter Valley, New South Wales. The female of *Blaste bistriata* Schmidt and Thornton (Psocidae) is described and *Ptycta cornigera* New synonymised with *P. emarginata* New (Psocidae).

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KEYWORDS: Psocoptera, Trogiidae, Lepidopsocidae, Myopsocidae, Psocidae, *Lasiopsocus*, *Kaindipsocus*, *Blaste*, *Ptycta*, Mount Royal.

INTRODUCTION

This paper is based on Lepidopsocidae, Trogiidae, Myopsocidae and Psocidae (Insecta: Psocoptera) collected during a faunal survey of Tuglo Wildlife Refuge (34°14′N, 151°16′E) near Mount Royal, Hunter Valley, New South Wales. Myopsocids, psocids and lepidopsocids are nearly all inhabitants of bark. The two trogiids are common in buildings but are also found on bark. Months in which each species was collected are indicated in brackets. This is the final descriptive paper of a series which brings the total number of species recorded from the Refuge to 77.

PSOCOPTERA RECORDED FROM TUGLO WILDLIFE REFUGE

Lepidopsocidae

Echmepteryx (Loxopholia) brunnea Smithers (May, June, August, September, October, December) (common)
Echmepteryx (Thylacopsis) picta Smithers (April) (uncommon)

Trogiidae

Cerobasis guestfalica (Kolbe) (April) (common in house)
Lepinotus inquilinus Heyden (April, May, December) (common in house)

Myopsocidae

Myopsocus australis (Brauer) (April, May, June, August, October) (common)
Myopsocus incomptus Smithers (April, May, December) (uncommon)

Psocidae

Amphigerontiinae
Blaste bistriata Schmidt and Thornton (April, May) (few specimens)
Blaste lignicola (Enderlein) (April) (one specimen)
Blaste taylori New (January, March, May, June) (common)
Blaste tillyardi Smithers (January, August) (few specimens)
Lasiopsocus hollowayi sp. n. (May, December) (few specimens)
Cerastipsocinae
Sigmatoneura formosa (Banks) (January, November) (few specimens)
Psocinae
Clematostigma maculiceps (Enderlein) (March, April, May, June, October, November, December) (very common)
Kaindipsocus emarginatus sp.n. (March) (one specimen)
Kaindipsocus marksae sp.n. (May) (few specimens)
Ptycta campbelli Schmidt and Thornton (March, April, May, June, August, September, October, November) (very common)
Ptycta emarginata New (= *Ptycta cornigera* New **syn. nov.**) (June, August) (few specimens)
Ptycta umbrata New (April, June) (few specimens)

DESCRIPTIONS AND SYNONYMY

Blaste bistriata Schmidt and Thornton, 1992. *Mem. Mus. Vict.* 53(2):192, Figs 176–180.

Female material of this species was not available when Schmidt and Thornton (1992) described it. Two females from Tuglo are here referred to this species on the basis of the distinctive head and wing patterns and protruding eyes which are similar to those of *B. bistriata* males collected at the same locality.

Female

Colouration (in alcohol). As in male (Schmidt and Thornton, 1992:192).

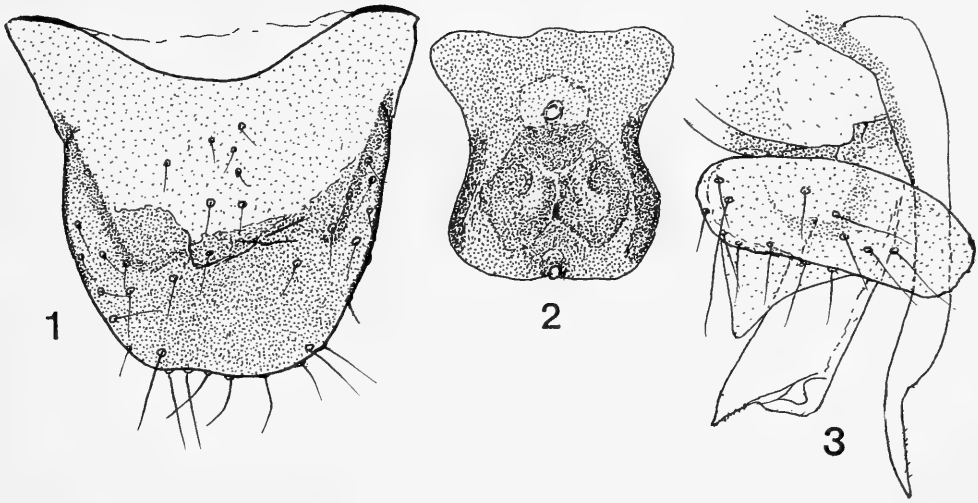
Morphology. Length of body: 3.5 mm. Median epicranial suture distinct to ocellar tubercle. Vertex at suture a little lower than laterally. Length of first flagellar segment: 0.65 mm. Antennae very fine, scape and pedicel short and broad. Eyes large, strongly protruding from dorso-lateral part of head capsule. IO/D: 2.0; PO: 0.83. Measurements of hind leg: F: 0.75 mm; T: 1.56 mm; t1: 0.57 mm; t2: 0.16 mm; rt: 3.5:1; ct: 23, 3. Legs long and slender. Fore wing length: 3.7 mm; width: 1.35 mm. Fore wing form and venation as in male but Rs and M meet in a point instead of being fused for a short length. Sc evanescent, ending free in costal cell, as in male. Epiproct (Fig. 1) large and well sclerotised, held somewhat erect. Paraproct with large, circular trichobothrial field. Subgenital plate with short, glabrous posterior lobe which has a transverse hind margin. Gonapophyses (Fig. 3) with broad ventral valve, distally narrow and finely spiculate. Dorsal valve broad, ending in spiculate extension. External valve well developed, consisting of an elongate-ovoid setose lobe and a tapering postero-dorsal glabrous lobe. Ninth sternite (Fig. 2) very heavily sclerotised around entrance to spermatheca.

Material examined

2 females, Tuglo Wildlife Refuge, 48 km north of Singleton, New South Wales, 7–13.v.1974, A.S. Smithers. 2 males, same locality, 15.iv.1984, A.S.Smithers.

Discussion

The female of *B. bistriata* has a distinctive head and wing pattern similar to that of the male (Schmidt and Thornton, 1992: Fig. 176). The gonapophyses resemble those of



Figures 1–3. Blaste bistriata Schmidt and Thornton. Female. (1). Epiproct. (2). Ninth sternite. 3. Gonapophyses.

B. lignicola (Enderlein) (Schmidt and Thornton, 1992: Fig. 189) but in that species the ventral valve is narrower and the pointed apex of the dorsal valve is more pronounced. There is considerable difference in the shape of the epiproct (Schmidt and Thornton, 1992: Fig. 187). The subgenital plate and gonapophyses of *B. bistriata* are similar to those of *B. tillyardi* but the sclerifications of the ninth sternite are different. (Smithers, 1969: Fig. 198).

Lasiopsocus hollowayi sp. n.

Female

Colouration (in alcohol). Head cream with pale brown marks. Irregular confluent spots on the epicranial plates except for a pale median band from epistomial suture to posterior part of plate. Frons pale brown. Postclypeus with parallel pale brown striae from epistomial suture to anterior margin. Anterior margin almost black. Genae pale. Antennae pale. Eyes black. Ocelli on dark brown tubercle. Maxillary palps pale, distal segment pale brown, darker than other segments. Legs pale brown. Fore wings (Fig. 4) hyaline with pale brown pattern as in figure.

Morphology. Length of body: 4.5 mm. Medial epicranial suture very distinct as far as ocellar tubercle, anterior arms absent. Length of flagellar segments: f1: 0.67 mm; f2: 0.55 mm. Eyes fairly small, not reaching level of vertex. IO/D: 3.3; PO: 0.77. Anterior ocellus much smaller than lateral ocelli. Epistomial suture very distinct, curving forwards a little anterior to ocellar tubercle. Measurements of hind leg: F: 0.95 mm; T: 1.67 mm; t1: 0.40 mm; t2: 0.16 mm; rt: 2.5:1; ct: 15, 0. Ctenidiobothria with basal combs hardly developed. Fore wing length: 3.6 mm; width: 1.24 mm. Fore wings (Fig. 4) with Rs and M fused for a length. M+Cu_1 slightly widened just basad of separation of M and Cu_1. R_{2+3} slightly sinuous. First section of Cu_{1a} barely longer than second and at slight angle to it. Veins and wing margin glabrous. Hind wing glabrous. Epiproct (Fig. 5) large, with lateral sclerotised strengthening bars in basal half. Hind margin of tergite anterior to

epiproct strongly sclerotised for a length opposite anterior corners of epiproct. Posterior margin of 9th tergite laterally well sclerotised to form a conspicuous, narrow band running down to base of gonapophyses. Paraprocts (Fig. 6) very lightly sclerotised with circular field of spaced trichobothria, one seta without basal rosette. Inner face of paraproct appears to be sculptured with densely packed lenticular rugosities in posterior region. Subgenital plate (Fig. 9) with long setose posterior lobe. Base of lobe glabrous. Gonapophyses (Fig. 8) long. Ventral valve long, narrow, ending in a short, sharply pointed apophysis. Dorsal valve broad, apically rounded, lightly sclerotised with field of fine papillae in distal quarter. External valve very lightly sclerotised in form of a divided lobe only one half of which is setose, the other long and apically narrowed, more than half the length of the dorsal valve. Sclerification of ninth sternite (Fig. 7) consists of two heavily sclerotised, irregularly ovoid plates and two very small sclerotised spots flanking entrance to spermatheca.

Male

Colouration (in alcohol). Body pattern similar to that of female but fore wing pattern not discernible.

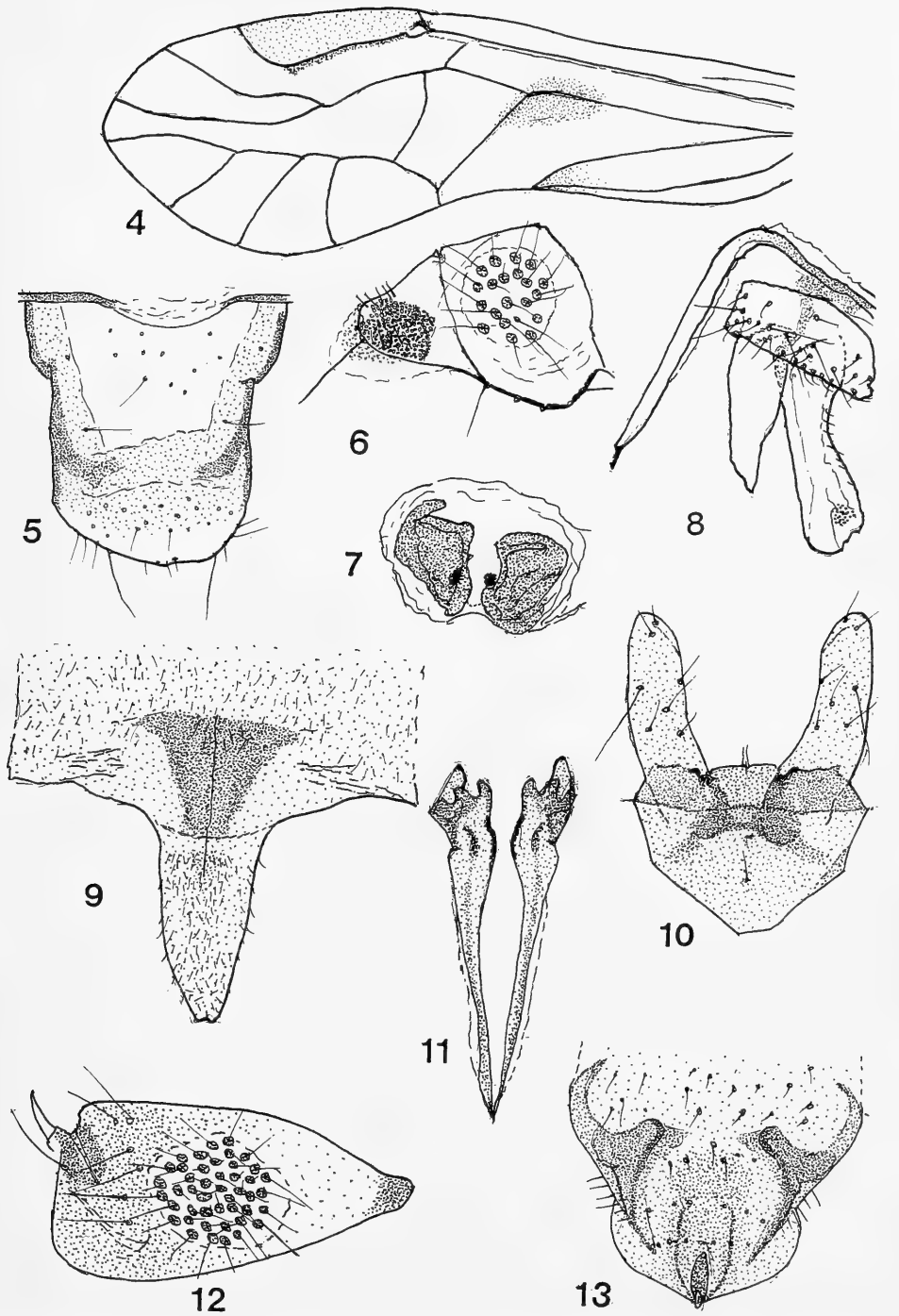
Morphology. Length of body: 4.3 mm. Medial epicranial suture as in female. Postclypeus with very strongly sclerotised anterior margin, as in female. Eyes large, reaching well above level of vertex. IO/D: 0.71; PO: 0.85. Ocelli large, median ocellus a little smaller than lateral ocelli. Measurements of hind leg: F: 0.57 mm; T: 1.3 mm; t1: 0.35 mm; t2: 0.11 mm; rt: 3.2:1; ct: 20, 2. Fore wing length: 3.5 mm; width: 1.4 mm. Fore wing as in female but Rs meets M in a point. Thickening of distal section of $M+Cu_1$ present but less pronounced than in females. First section of Cu_{1a} shorter than second, curved in opposite directions to one another so that the margin of the areola postica is strongly sinuous. Wings glabrous. Epiproct (Fig. 10) small, with a small median lobe and pair of elongated, erect, curved lobes, sparsely setose, the ends of which are entire. Paraprocts (Fig. 12) lightly sclerotised, simple, narrow basally, broadened distally with a large circular field of trichobothria, elsewhere sparsely setose. Postero-dorsal angle with a strong spur arising from a heavily sclerotised area of integument. Hypandrium (Fig. 13). Phallosome (Fig. 11) of two posteriorly diverging bars, broadest distally with the posterior end divided into several lobes.

Material examined

2 females (holotype and paratype), Tuglo Wildlife Refuge, 48 km north of Singleton, New South Wales, 7–13.v.1974, A.S.Smithers. 1 male paratype, same locality, 10.xii.1981, G.A. Holloway. Holotype and paratypes in the Australian Museum. This species is named for Geoff Holloway, in appreciation of his collecting Psocoptera over many years.

Discussion

When Enderlein (1907) erected the genus *Lasiopsocus* for *L. michaelseni* from Western Australia he gave as one of its obvious distinguishing features the presence of setae on the veins and wing margin of the fore wing. There are relatively few species in the large family Psocidae in which the fore wings are not glabrous. Smithers (1983) described a second species of *Lasiopsocus*, *L. simulatus* Smithers, based on a New South Wales specimen which had previously been misidentified as *L. michaelseni* and in which the setae on the fore wing are few and very small, being difficult to see except in the prepared specimen. A third species, *L. dicellus* Smithers (1984) was described from South Australia in which there are very few tiny wing setae. Other morphological features leave no doubt that the three species are congeneric. Although obvious in the type species, wing setae are clearly not a constantly obvious feature of the genus. In *L. michaelseni*, the largest species, with wing length in the male of 7.0 mm, both sexes have



Figures 4–13. Lasiopsocus hollowayi sp.n. Figs 4–9. Female. (4). Fore wing. (5). Epiproct. (6). Paraproct. (7). Ninth sternite. (8). Gonapophyses. (9). Subgenital plate. Figs 10–13. Male. (10). Epiproct. (11). Phallosome. (12). Paraproct. (13). Hypandrium.

hyaline wings without obvious colour pattern other than the usual darkening of the pterostigma. Some of the females have relatively short wings. In the type series Enderlein gave a wing length of 4.7 mm for the female. In *L. hollowayi* the wings are 3.5 mm (male) and 3.6 mm (female), hyaline in males and with a small area of pale brown just basal to the separation of Cu_1 and M the female (Fig. 4). In *L. dicellus* both sexes have wings of about 5.0 mm, larger than in *L. hollowayi*, without colour in the males. In the female wing there is a broad, dark, broken brown band at the basal third and brown membrane adjacent to the Rs and M meeting point. The female of *L. simulatus*, unfortunately, is not known but males of *L. simulatus* and *L. dicellus* are very similar, being distinguishable only on small differences in the proportions of their genitalia. It is likely that their females will also be similar to one another. Males of both species can be distinguished from *L. hollowayi* on wing size. The phallosome of *L. hollowayi* is distinctive and would not be confused with that of any other described species in the genus.

Kaindipsocus emarginatus sp. n.

Female

Colouration (in alcohol). Head, body and appendages creamy yellow. A pattern of irregular brown bands on front of head (Fig. 15) and two bands across genae, one at level of antenna base and the other below antenna. Fore wings (Fig. 14) hyaline with faint brownish pattern. Hind wings (both incomplete on available specimen) hyaline.

Morphology. Length of body: 3.5 mm. Head (Fig. 15) elongate. Dorso-lateral angles of head capsule protruding, forming incipient eye stalks. Vertex curved downwards between eyes. Median epicranial suture distinct, anterior arms absent. Epistomial suture very distinct. Anterior margin of postclypeus heavily sclerotised as a marginal band. Antennae with short, broad scape and pedicel. Flagellum very fine, bearing only a few fine, scattered setae. Apex of first flagellar segment slightly but distinctly swollen at joint with second. Length of flagellar segments: f1: 1.1 mm; f2: 1.08 mm. Eyes large (Fig. 15), of unusual, somewhat conical shape with medio-ventral edge emarginate. Seen from above inner margins diverge posteriorly, pigmented area reniform, emarginate medially. IO/D: 1.63; PO: 1.0. Ocelli small, median ocellus smaller than lateral ocelli. Lacinia similar to that of *K. marksae* (Fig. 21) and *K. mixtus* Smithers and Thornton. Distal segment of maxillary palp long, sides almost parallel, tapering distally to a rounded end. Metascutellum with mere suggestion of median apophysis. Measurement of hind leg: F: 1.1 mm; T: 2.3 mm; t1: 0.81 mm; t2: 0.16 mm; rt: 5:1; ct: 31, 3. Ctenidiobothria with small basal combs and long, fine setae. Claws long and slender, slightly curved near apex, with small preapical tooth. Legs very long and slender. Coxa of hind leg with well developed Pearman's organ. Fore wing length: 4.8 mm; width: 1.8 mm. Sc ends free in costal cell. Pterostigma strongly concave proximal to hind angle, which is acute and bears an obvious spurvein. Rs and M joined by a crossvein. R_{4+5} approaching M. Veins R, $M+Cu_1$, 1A and basal section of hind margin of wing as far as nodulus, thickened. Cu_1 strongly arched where it forms the proximal margin of the discoidal cell. Areola postica tall, with narrow apex. Basal section of Cu_{1a} at angle to second. Hind wings incomplete in only available specimen. Epiproct damaged in preparation, but similar to that of *K. marksae*. Paraproct (Fig. 16) lightly sclerotised, with large field of trichobothria and a ventral, posteriorly directed apophysis. Subgenital plate (Fig. 17) with posterior median lobe, glabrous end rounded. Inner surface with sclerotisation. A transverse fold present at base of posterior lobe. Gonapophyses (Fig. 18). well sclerotised, the ventral valve narrow with an even narrower distal section. Dorsal valve broad with a narrow apical section. External valve setose with a posterior, small, glabrous lobe. Sclerotisation of ninth sternite (Fig. 19).

Male

Unknown.

Material examined

1 female (holotype), Tuglo Wildlife Refuge, 48 km north of Singleton, New South Wales, 31.iii.1975, A.S.Smithers. Holotype in the Australian Museum.

Discussion

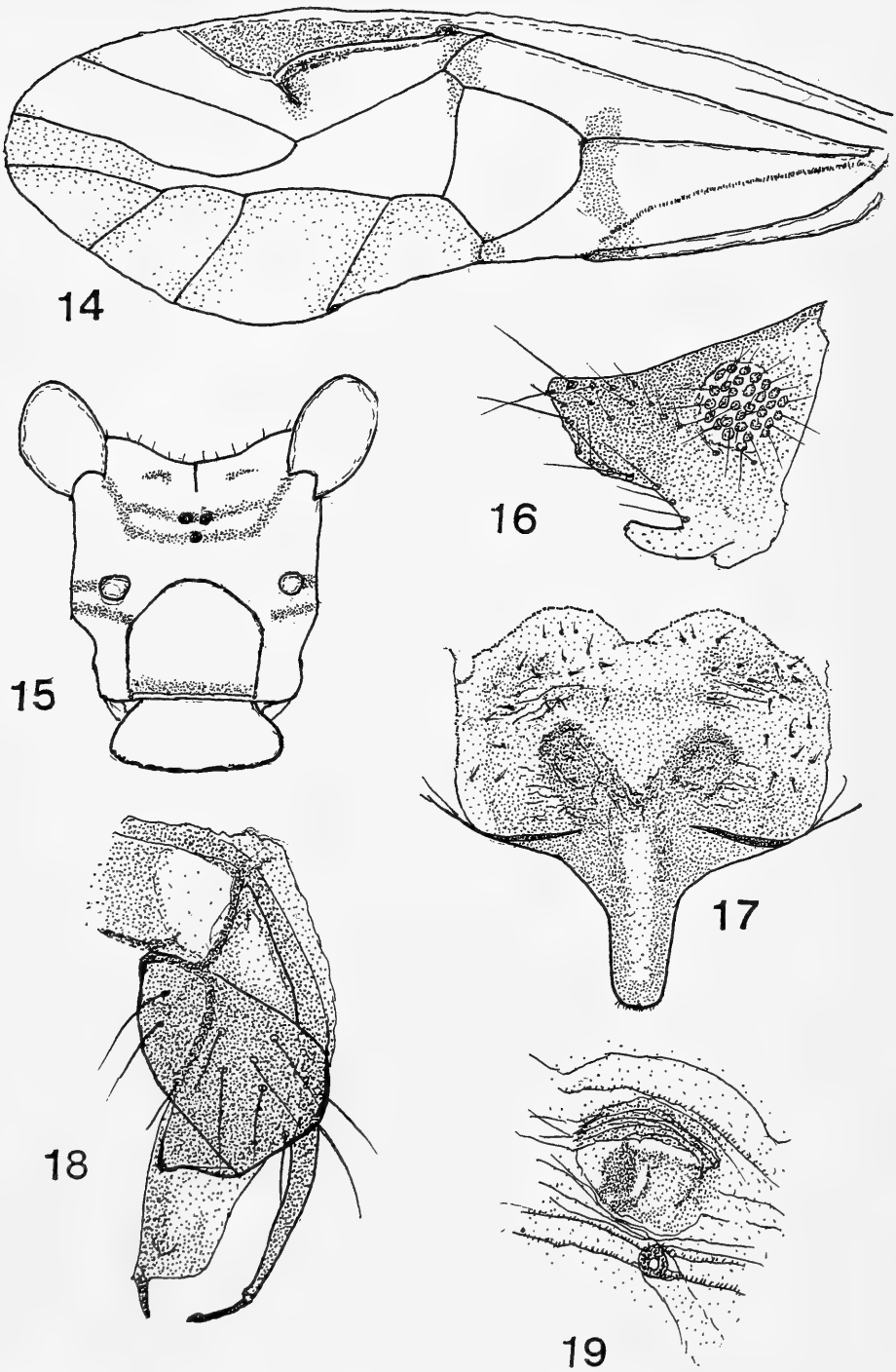
K. emarginatus differs from *K. marksae* in being bigger and in having a facial pattern. It is about the same size as *K. mixtus*. It differs most obviously from both *K. mixtus* and *K. marksae* in having Cu_1 very strongly curved where it forms the posterior proximal margin of the discoidal cell so that the cell is strongly convex along the proximal edge and in the almost conical shape of the eyes. All three species have the eyes somewhat protruding at the dorso-lateral angles of the head. The shape of the sclerotisations at the entrance to the spermatheca are distinctive. The discovery of two species of *Kaindipsocus* at the northern edge of the Hunter Valley in New South Wales is unexpected, the genus having been previously known only from a few specimens from high altitudes in New Guinea. At present its distribution elsewhere is not known but its close relationship to other genera in New Guinea, such as *Elytropsocus* Smithers and Thornton, suggests that it might be a relatively recently-arrived invasive element of that part of the Australian fauna which has a northern origin.

Kaindipsocus marksae sp. n.

Female

Colouration (in alcohol). Head, body and appendages pale creamy yellow. Eyes pale brown. Fore wings (Fig. 20) hyaline with faint brown areas.

Morphology. Length of body: 2.5 mm. Head somewhat elongated, widened dorsally. Eyes large, almost spherical, placed high at dorso-lateral angles of head, the vertex between them very slightly downcurved. IO/D: 1.6; PO: 0.9. Median epicranial suture distinct, anterior arms absent. Epistomial suture very well developed. Flagellum of antenna very fine in relation to somewhat enlarged scape and pedicel, setae few and very fine. Ocelli small. Apex of lacinia (Fig. 21) with very well developed outwardly curved outer tine which is apically rounded. Fourth segment of maxillary palp long, widest at about 2/3rds of length from base, beyond which it tapers to end in a rounded apex. Meso- and metascutellum heavily sclerotised, median plate only slightly raised into a suggestion of an apically rounded apophysis. Legs, especially those of metathorax, long and slender. Pearman's organ well developed on hind coxae. Measurement of hind leg: F: 0.89 mm; T: 1.78 mm; t1: 0.62 mm; t2: 0.14 mm; rt: 4.4:1; ct: 29, 2. Ctenidiobothria with small basal combs and long, fine setae. Claws long, narrow, only slightly curved distally, with small preapical tooth. Fore wing length: 3.2 mm; width: 1.3 mm. Fore wing (Fig. 20) glabrous. Sc ends free in costal cell. Pterostigma strongly concave basal of apex, slightly convex distal to apex, which has a short but not obvious spurvein in some wings. Rs and M joined by a long crossvein. R_{2+3} straight, R_{4+5} strongly sinuous, approaching M closely in basal part. Cu_1 slightly curved, giving a slightly convex proximal margin to the discoidal cell. M almost straight beyond Rs-M crossvein. Areola postica tall. Basal section of Cu_{1a} straight, longer and at a strong angle to second section so that the areola postica is tall with a narrow apex. M_1 and M_3 curved, M_2 straight. Hind wing with Rs and M fused for a length. Terminal abdominal structures lightly sclerotised. Epiproct (Fig. 22) elongate, tapering to narrower, rounded, hind margin, laterally reinforced by more heavily sclerotised sinuous bars. Paraproct (Fig. 23) with large, circular field of



Figures 14–19. Kaindipsocus emarginatus sp.n. Female. (14). Fore wing. (15). Head. (16). Paraproct. (17). Subgenital plate. (18). Gonapophyses. (19). Ninth sternite.

densely packed trichobothria and with large, posteriorly-directed, elongate ventral lobe which is dorsally curved towards distal end. Subgenital plate (Fig. 25) with elongate posterior lobe, posteriorly rounded without setae. At base of lobe the plate has a transverse fold anterior to which the plate is sparsely setose with fine setae. Gonapophyses (Fig. 26). Sclerotisation of the ninth sternite (Fig. 24) well developed, complex.

Male

Unknown.

Material examined

4 females, including holotype, Tuglo Wildlife Refuge, 48 km north of Singleton, New South Wales, 7–13.v.1974, A.S.Smithers. Holotype and paratypes in the Australian Museum. This species is named for Heidi Marks in appreciation of her help in taking care of a Malaise trap used in the Tuglo survey during my absence.

Discussion

Kaindipsocus marksae is clearly congeneric with *K. mixtus*, described from New Guinea. It is similar in wing venation and in wing pattern, genitalia, unusual form of the lacinial tip, presence of a ventral lobe on the female paraproct, sclerotisation of the ninth sternite, in having the posterior lobe of the subgenital plate glabrous and the unusual development of raised areas on the meso- and metascutellum. The unusual, presumably stridulatory, structure of the meso- and metascutellum is similar to that found in *Kaindipsocus mixtus* (cf. Smithers and Thornton 1981:959, Figs 97–99) but is very much smaller and less conspicuous than in that species. It differs from *K. mixtus* and *K. emarginatus*, in being smaller (forewing length 3.2 mm, cf. 4.6 mm in *K. mixtus* and 4.8 mm in *K. emarginatus*), in having differences in the wing pattern and in having a relatively longer and narrower posterior lobe to the subgenital plate. Although there is apparently no facial colour pattern in this species, *K. mixtus* does have a dark line from the eye to the anterior margin of the postclypeus on each side and *K. emarginatus* has dark bands across the front of the head. It is possible that *K. marksae* has a facial pattern which has been lost during storage in alcohol. There seems to be some degree of correlation between development of characteristic and unusual facial patterns and presence of large, protruding compound eyes in the Psocoptera, e.g. as seen also in the Australian species *Blaste macrops* Smithers and *B. tillyardi*.

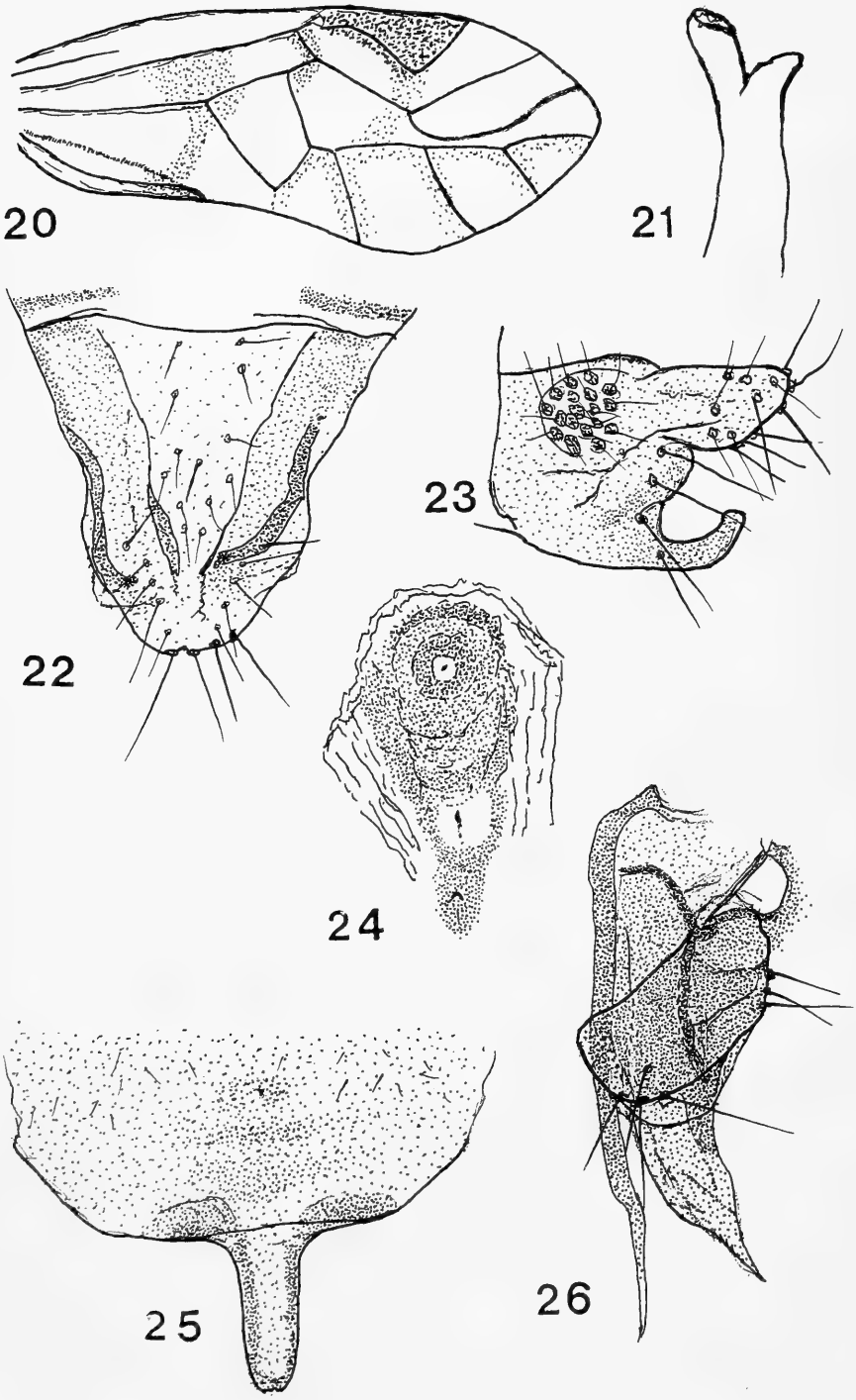
Ptycta emarginata New

Ptycta emarginata New, 1974. *J. Aust. ent. Soc.* 13:299, Figs 48–50 (female).
Ptycta cornigera New, 1974. *J. Aust. ent. Soc.* 13:301, Figs 54–57 (male) (**syn. nov.**).

New (1974) described *Ptycta emarginata* (female only) and *P. cornigera* (males only) from Jandakot, Western Australia. Ten females and five associated males in the Tuglo material identifiable as *P. emarginata* and *P. cornigera* respectively leave no doubt that they represent the two sexes of the same species. *Ptycta cornigera* is, therefore, considered to be a synonym of *Ptycta emarginata* (**syn. nov.**).

ACKNOWLEDGMENTS

Nearly all the Psocoptera in the survey of Tuglo Wildlife Refuge have been collected by my wife, without whose continuous help the survey could not have been made. I would also like to thank Geoff Holloway, Max Moulds, Larry Watrous, Barbara Duckworth and Roger de Keyzer for collecting some of the specimens recorded in this paper and Graeme Smithers and Heidi Marks for taking care of a Malaise trap in my absence.



Figures 20–26. Kaindipsocus marksae sp.n. Female. (20). Fore wing. (21). Lacinia. (22). Epiproct. (23). Paraproct. (24). Ninth sternite. (25). Subgenital plate. (26). Gonapophyses.

REFERENCES

Enderlein, G. (1907). Copeognatha. In 'Die Fauna Südwest-australiens. Ergebnisse der Hamburger Südwest-australischen Forschungsresise 1905' pp. 233–250 (W. Michaelsen and R. Hartmeyer: Jena).

New, T.R. (1974). Psocidae (Psocoptera) from southern Australia. *Journal of the Australian Entomological Society* **13**, 285–304.

Schmidt, E.R. and Thornton, I.W.B. (1992). The Psocoptera (Insecta) of Wilsons Promontory National Park, Victoria, Australia. *Memoirs of the Museum of Victoria* **53**, 137–220.

Smithers, C.N. (1969). The Psocoptera of New Zealand. *Records of the Canterbury Museum* **8**, 259–344.

Smithers, C.N. (1983). A new species of *Lasiopsocus* Enderlein (Psocoptera: Psocidae) from New South Wales. *Australian Entomological Magazine* **10**, 61–63.

Smithers, C.N. (1984). The Psocoptera of South Australia. *Records of the South Australian Museum* **18**, 453–491.

Smithers, C.N. and Thornton, I.W.B. (1981). The Psocidae (Insecta: Psocoptera) of New Guinea, including a New Coleopteriform genus from high on Mount Wilhelm. *Australian Journal of Zoology* **29**, 921–969.

Lower Devonian (Emsian) Microfauna from the Gamilaroi Terrane at Glenrock in the Southern New England Orogen, New South Wales

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METCALFE, I., AITCHISON, J.C. AND STRATFORD, J.M.C. (1997). Lower Devonian (Emsian) microfauna from the Gamilaroi Terrane at Glenrock in the southern New England Orogen, New South Wales. *Proceedings of the Linnean Society of New South Wales* **118**, 123–130.

Radiolarians and conodonts extracted from ribbon-bedded tuffaceous chert and interbedded limestones and shales of the Frog Hollow Formation (Gamilaroi Terrane) at Bralga Tops, Glenrock Station indicate a Lower Devonian (Emsian) age. The radiolarian fauna includes *Helenifore laticlavium* Nazarov and Ormiston, *Palaeoscenidium cladophorum* Deflandre, *Ceratoikiscum* sp., *Trilonche hindea* (Hinde), *Trilonche vetusta* Hinde, *Trilonche echinata* (Hinde), and *Trilonche elegans* (Hinde) which represents the Emsian *Helenifore laticlavium* assemblage. The conodont fauna includes *Polygnathus* cf. *serotinus* Telford, *Ozarkodina* cf. *prolata* Mawson and *Pandorinellina expansa* Uyeno and Mason? which suggest an upper Emsian age.

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KEYWORDS: Devonian Radiolarians Conodonts Gamilaroi Terrane, New England Orogen New South Wales.

REGIONAL SETTING

The microfossils described in this study were collected from the Siluro-Devonian Gamilaroi Terrane (Flood and Aitchison 1988, Aitchison and Flood 1994), the westernmost terrane in the New England Orogen. This terrane comprises a complex association of volcaniclastic sediments, tuffs, volcanic rocks and minor carbonates formed in an intra-oceanic island-arc setting (Aitchison and Flood 1994, Stratford and Aitchison 1996) which accreted to the eastern margin of Gondwana sometime during the Late Devonian (Flood and Aitchison 1992). Unconformably overlying Upper Devonian to Carboniferous sedimentary and volcanic rocks which formed along the continental margin of Gondwana are interpreted as an overlap assemblage which developed on top of the Gamilaroi Terrane after its accretion to the Gondwana margin. The Gamilaroi Terrane and its overlying Carboniferous volcano-sedimentary overlap assemblage are often together referred to as a structural entity, the Tamworth Belt (Korsch 1977).

Gamilaroi Terrane strata in the southern New England Orogen have an arcuate distribution pattern throughout northeastern NSW over a distance of approximately 450 km. Local lithostratigraphies have been developed in several areas of Gamilaroi Terrane outcrop and a lithostratigraphic succession within the terrane was first described from Nundle (Crook 1961; Cawood 1983). With varying success, formations within the Tamworth Group can be traced along strike for approximately 120 km from Attunga through Tamworth to Nundle. The terrane can be followed further southeast to the Upper Barnard River catchment where a different local lithostratigraphic subdivision has been

developed (Stratford and Aitchison in press). Tamworth Group lithostratigraphy cannot easily be traced to this area due to inherent variations in sedimentation patterns in the Gamilaroi Terrane depositional setting. Lithostratigraphic units recently described from the Upper Barnard catchment southwest of Nundle (Aitchison and Stratford in press, Stratford and Aitchison in press) can be traced from Barry through Glenrock to Pigna Barney (approx. 100 km). The microfauna reported herein comes from localities within the Frog Hollow Formation. This formation is the lowest sedimentary unit and overlies the Pitch Creek Volcanics which form the basement to the terrane.

The sampled outcrops occur within the Gamilaroi Terrane at Glenrock station. The sequence in which the limestones occur is incompletely exposed and their relations to adjacent strata cannot be confirmed. They appear to overlie altered felsic volcanic rocks of the Pitch Creek Volcanics but the possibility of an allochthonous origin cannot be excluded. The limestones lie on the east side of a fault which cuts through the low pass between the fossiliferous outcrops. The fault lies entirely within the Gamilaroi Terrane and is marked by serpentinite. Total displacement is indeterminate. On the west side of the fault highly altered purple coloured pillow basalts are overlain by tuffaceous radiolarian-bearing cherts (Figure 1).

RADIOLARIAN FAUNA

Several rock chip samples, of approximately 300 g each, were collected from a large, 20 m wide, road cutting outcrop of ribbon-bedded tuffaceous chert in the Frog Hollow Formation (Stratford and Aitchison in press) at Bralga Tops (Glenrock 1:25000 NSW CMA mapsheet 9134–I-S GR 543957; Fig. 1).

A diverse, well preserved radiolarian fauna was recovered from three samples (Plates 1, 2). The fauna includes *Helenifore laticlavium* Nazarov and Ormiston, *Palaeoscenidium cladophorum* Deflandre, *Ceratoikiscum* sp., *Trilonche hindea* (Hinde), *Trilonche vetusta* Hinde, *Trilonche echinata* (Hinde), and *Trilonche elegans* (Hinde). Unfortunately many other radiolarians present are entactiniids which are only referable to as *Trilonche* spp. or *Stigmosphaerostyla* spp. Precise diagnosis of these fossils depends on examination of internal detail which is almost invariably lacking.

CONODONT FAUNA

Conodonts were extracted from a single large (22.5 kg) channel sample (No. 1131) of limestone collected from an approximately 10 m thick section of interbedded limestones and shales exposed in a ditch and road cutting (Glenrock 1:25000 NSW CMA mapsheet 9134–I-S GR 545958; Fig. 1) at Bralga Tops on Glenrock Station, approximately 90km northeast of Scone, NSW.

The following conodont elements were recovered from the sample:

Ozarkodina cf. *prolata* Mawson	Pa	27
Panderodus unicostatus Branson and Mehl	Sa	1
Pandorinellina expansa Uyeno and Mason?	Pa	1
Polygnathus cf. *serotinus* Telford	Pa	1
Neopanderodus aequabilis Telford	Sa	3
	Sb	1
	M	2
unidentified	Pb	2
unidentified	Sc	2
unidentified fragments		25
TOTAL		65

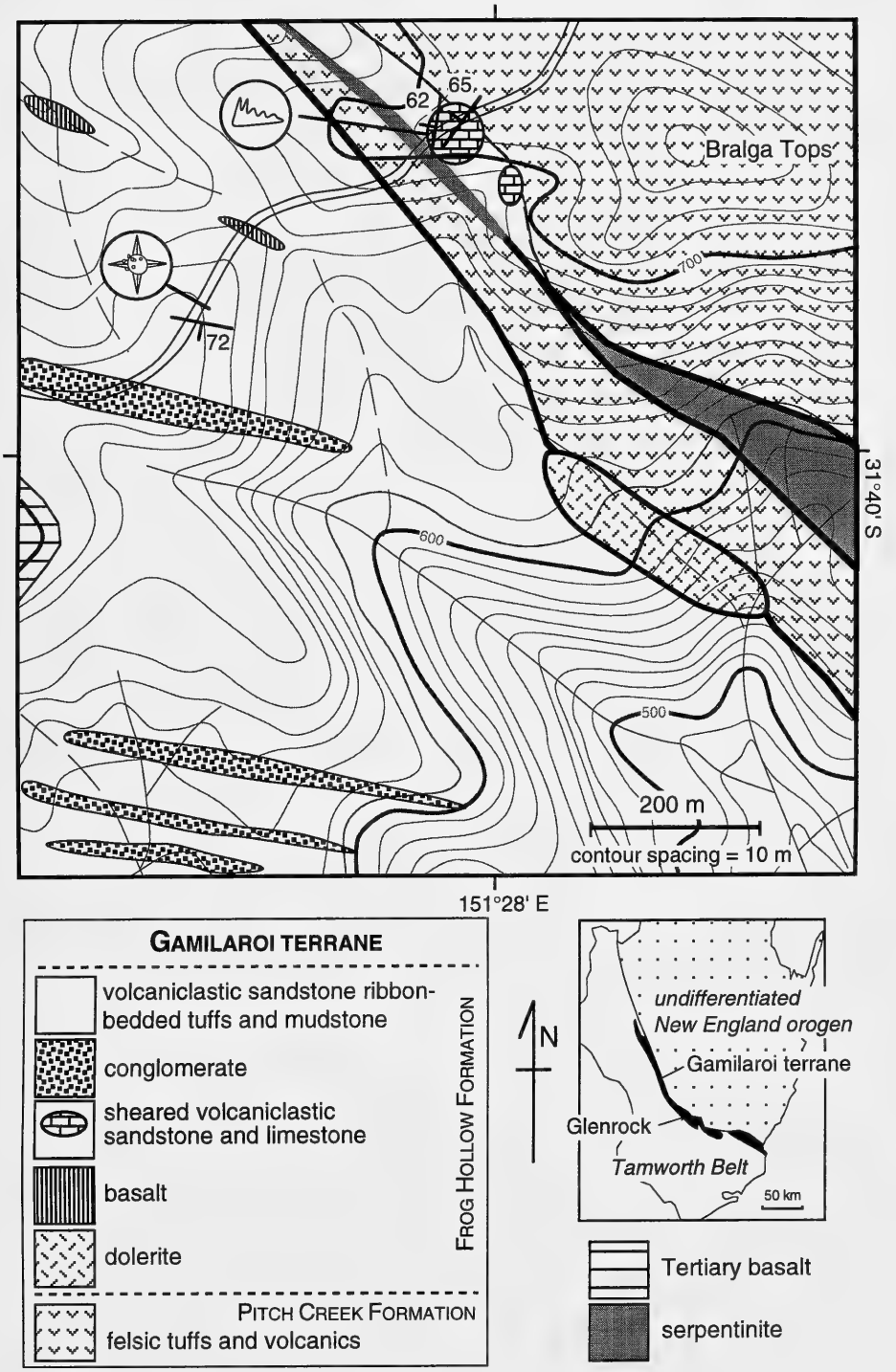

Figure 1: Distribution of Gamilaroi Terrane lithologies in the Bralga Tops locality showing the location of fossil radiolarian and conodont samples.

Conodont Colour Alteration Index

The conodonts exhibit a Conodont Colour Alteration Index (CAI) of 4 which indicates that the conodont elements have been heated to between 190°C and 300°C (Epstein et al. 1977).

AGE OF THE FAUNAS

The single Pa element of *Polygnathus* cf. *serotinus* Telford is morphologically close to *Polygnathus serotinus* except that the lip on the outer side of the basal cavity is not well developed. This specimen may be a transitional form between *Polygnathus serotinus* and its ancestral species *Polygnathus inversus* Klapper and Johnson, suggesting a late Emsian age. The twenty-seven elements of *Ozarkodina* cf. *prolata* Mawson are morphologically close to *Ozarkodina prolata* Mawson and have the same shape and position of the basal cavity. However, the anterior-most denticles of the blade are not as high as those of *Ozarkodina prolata* Mawson. An Emsian age is again indicated by this form. The one specimen of *Pandorinellina* is tentatively identified as *Pandorinellina expansa* Uyeno and Mason but the denticles of the blade are broken precluding confirmation of this assignment. The position and shape of the basal cavity is however consistent with *Pandorinellina expansa* Uyeno and Mason. This species is known from the late Emsian *Polygnathus costatus patulus* and *Polygnathus serotinus* zones (Mawson et al. 1995). A Late Emsian age is therefore suggested by the conodont elements recovered. The presence of *Panderodus unicostatus* Branson and Mehl, which has a stratigraphical range from Middle Ordovician to Middle Devonian, and *Neopanderodus aequabilis* Telford, which occurs in the Lower and Middle Devonian, is consistent with an Emsian age.

Radiolarians are equivalent to those found elsewhere in lowermost stratigraphic portions of the Gamilaroi Terrane in southern New England and are equated with the Emsian *Helenifore laticlavium* assemblage of Stratford and Aitchison (1996, 1997).

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REFERENCES

Aitchison, J.C. and Flood, P.G. (1994). Gamilaroi Terrane: a Devonian rifted intra-oceanic island arc assemblage, NSW, Australia. In 'Volcanism associated with extension at consuming plate margins' (Ed. J. L. Smellie) pp. 155–168. Geological Society, London Special Publication 81.

Aitchison, J.C. and Stratford, J.M.C. (in press). Geology of the Upper Barnard Region, New England Orogen, eastern NSW, Australia. *Australian Journal of Earth Sciences.*

Cawood, P.A. (1983). Modal composition and detrital clinopyroxene chemistry of lithic sandstones from the New England Fold Belt (east Australia): a Paleozoic forearc terrane. *Bulletin of the Geological Society of America* **94**, 1199–1214.

Crook, K.A.W. (1961). Stratigraphy of the Tamworth Group (Lower and Middle Devonian), Tamworth-Nundle District, N.S.W. *Journal and Proceedings of the Royal Society of New South Wales* **94**, 173–188.

Epstein, A.G., Epstein, J.B. and Harris, L.D. (1977). Conodont color alteration — an index to organic metamorphism. *U.S. Geological Survey Professional Paper* **995**, 1–27.

Flood, P.G. and Aitchison, J.C. (1988). Tectonostratigraphic terranes of the southern part of the New England Orogen. In 'New England Orogen Tectonics and Metallogenesis' (Ed J. D. Kleeman) pp. 7–11. (University of New England, Armidale).

Flood, P.G. and Aitchison, J.C. (1992). Late Devonian accretion of the Gamilaroi Terrane to eastern Gondwana: provenance linkage suggested by the first appearance of Lachlan Fold Belt-derived quartzarenite. *Australian Journal of Earth Sciences* **39**, 539–544.

Korsch, R.J. (1977). A framework for the Paleozoic geology of the southern part of the New England Geosyncline. *Journal of the Geological Society of Australia* **25**, 339–355.

Mawson, R., Talent, J.A. and Furey-Greig, T. (1995). Coincident conodont faunas (late Emsian) from the Yarrol and Tamworth belts of northern New South Wales and central Queensland. *Courier Forschunginstitut Senckenberg* **182**, 421–445.

Stratford, J.M.C. and Aitchison, J.C. (1996). Devonian intra-oceanic arc rift sedimentation — facies development in the Gamilaroi terrane, New England orogen, eastern Australia. *Sedimentary Geology* **101**, 173–193.

Stratford, J.M.C. and Aitchison, J.C. (1997). Lower to Middle Devonian radiolarian assemblages from the Gamilaroi terrane, Glenrock Station, NSW, Australia. *Marine Micropaleontology* ***30***, 225–250.

Stratford, J.M.C. and Aitchison, J.C. (in press). Devonian Lithostratigraphy of the Gamilaroi terrane in the upper Barnard River, NSW. *Australian Journal of Earth Sciences*.

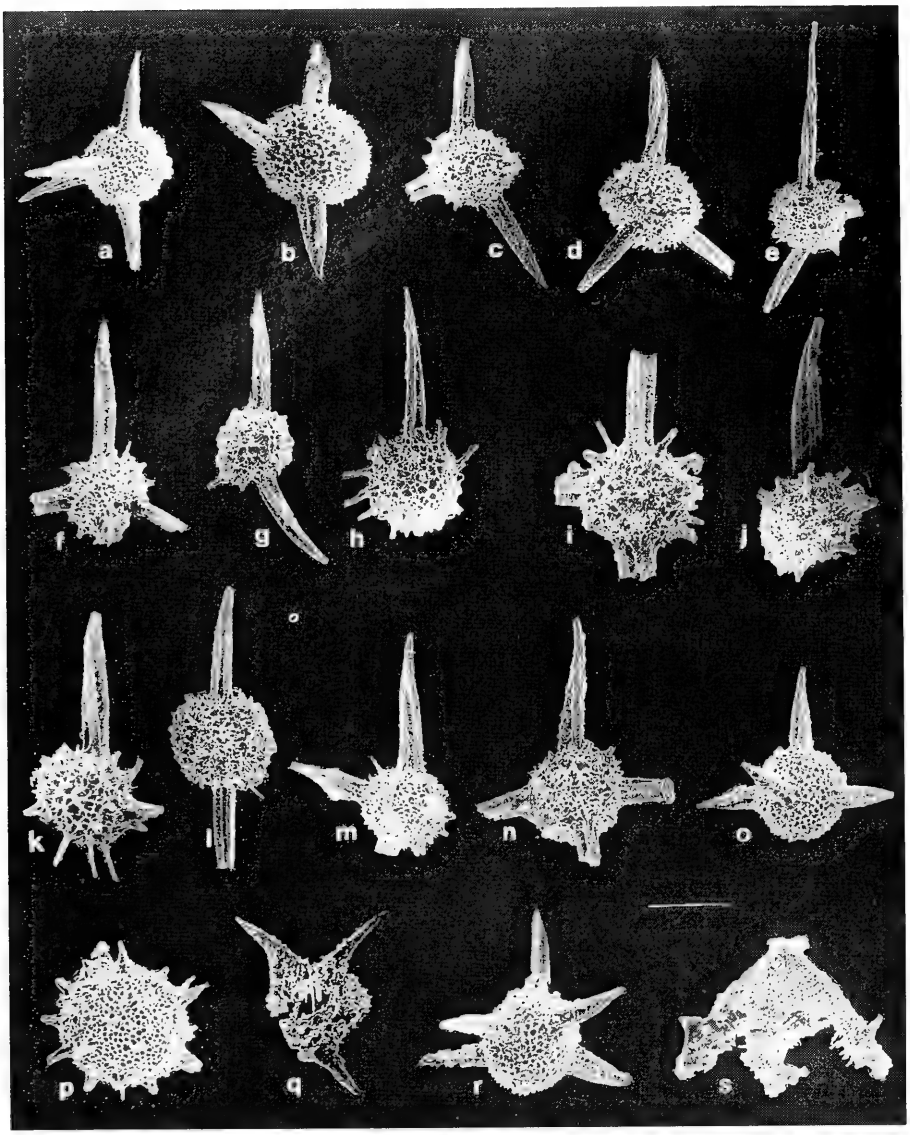

Plate 1: Emsian radiolarians from the Frog Hollow Formation exposed at Glenrock GR543957, Bralga Tops, Glenrock Station, NE NSW. All specimens are housed in the collections of the Department of Earth Sciences, University of Hong Kong. Specimen number and length of scale bar is indicated in parentheses.
***Ia**: Trilonche* sp. cf. *T. elegans* (Hinde); (HKUDES96/001, 120 μm), ***Ib**: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/002, 150 μm), ***Ic**: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/003, 150 μm), ***Id**: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/004, 150 μm), ***Ie**: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/005, 160 μm), ***If**: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/006, 140 μm), ***Ig**: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/007, 160 μm), ***Ih**: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/008, 125 μm), ***Ii**: Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/009, 100 μm), ***Ij**: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/010, 125 μm), ***Ik**: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/011, 120 μm), ***Il**: ?Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/012, 140 μm), ***Im**: Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/013, 140 μm), ***In**: Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/014, 125 μm), ***Io**: Trilonche* sp. cf. *T. elegans* (Hinde); (HKUDES96/015, 90 μm), ***Ip**:* Entactinid gen. et sp. indet.; (HKUDES96/016, 100 μm), ***Iq**: Ceratoikiscum* sp.; (HKUDES96/017, 80 μm), ***Ir**: Trilonche* sp. cf. *T. elegans* (Hinde); (HKUDES96/018, 100 μm), ***Is**: Palaeoscenidium cladophorum* Deflandre; (HKUDES96/019, 50 μm)

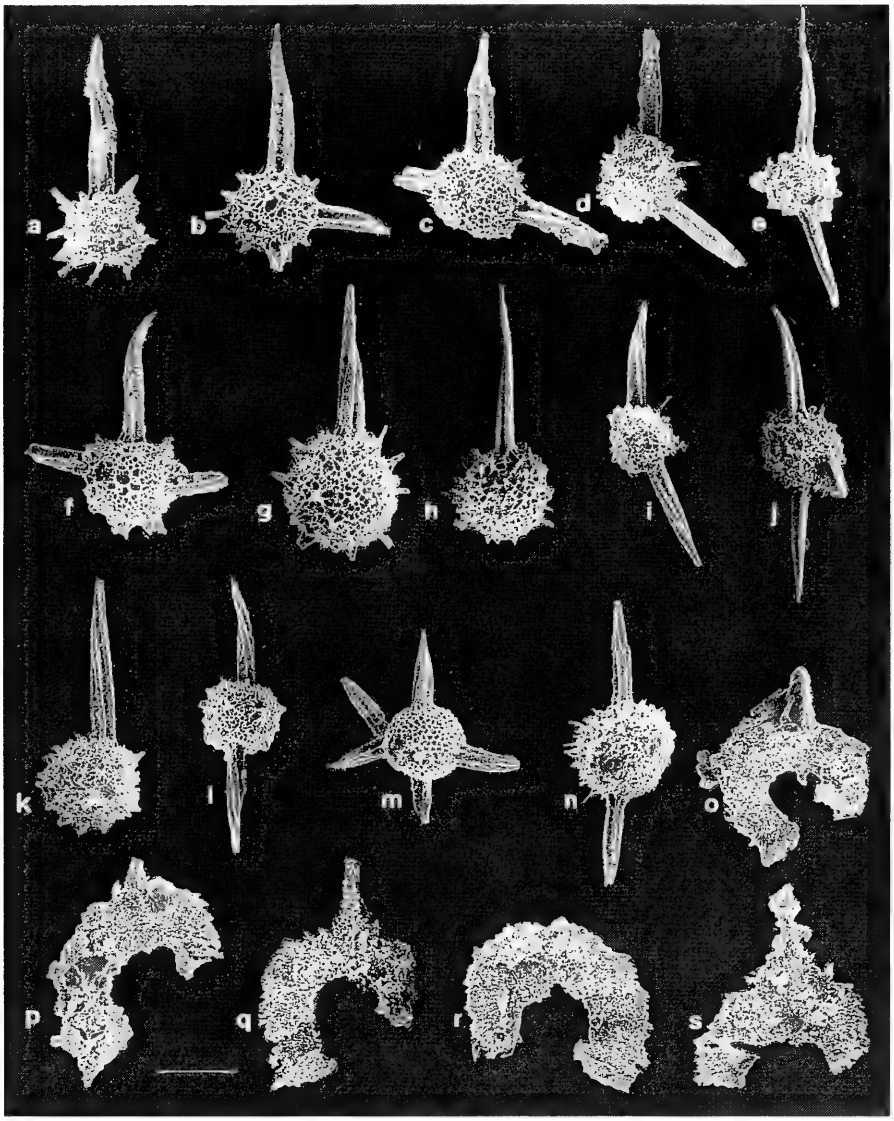

Plate 2: Emsian radiolarians from the Frog Hollow Formation exposed at Glenrock GR543957, Bralga Tops, Glenrock Station, NE NSW. All specimens are housed in the collections of the Department of Earth Sciences, University of Hong Kong. Specimen number and length of scale bar is indicated in parentheses.
2a*:* Entactinid gen. et sp. indet. (HKUDES96/020, 140 μm), ***2b****: Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/021, 125 μm), ***2c****: Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/022, 125 μm), ***2d****: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/023, 150 μm), ***2e****: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/024, 160 μm), ***2f****: Trilonche* sp. cf. *T. hindea* (Hinde); (HKUDES96/025, 125 μm), ***2g****: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/026, 100 μm), ***2h****: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/027, 140 μm), ***2i****: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/028, 160 μm), ***2j****: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/029, 150 μm), ***2k****: Trilonche* sp. cf. *T. echinata* (Hinde); (HKUDES96/030, 125 μm), ***2l****: Trilonche* sp. cf. *T. vetusta* Hinde; (HKUDES96/031, 150 μm), ***2m****: Trilonche* sp. cf. *T. elegans* (Hinde); (HKUDES96/032, 125 μm), ***2n****: Trilonche vetusta* Hinde; (HKUDES96/033, 140 μm), ***2o****: Helenifore laticlavium* Nazarov (HKUDES96/034, 80 μm), ***2p****: Helenifore laticlavium* Nazarov (HKUDES96/035, 80 μm), ***2q****: Helenifore laticlavium* Nazarov (HKUDES96/036, 80 μm), ***2r****: Helenifore laticlavium* Nazarov (HKUDES96/037, 80 μm), ***2s****: Helenifore laticlavium* Nazarov (HKUDES96/038, 80 μm)

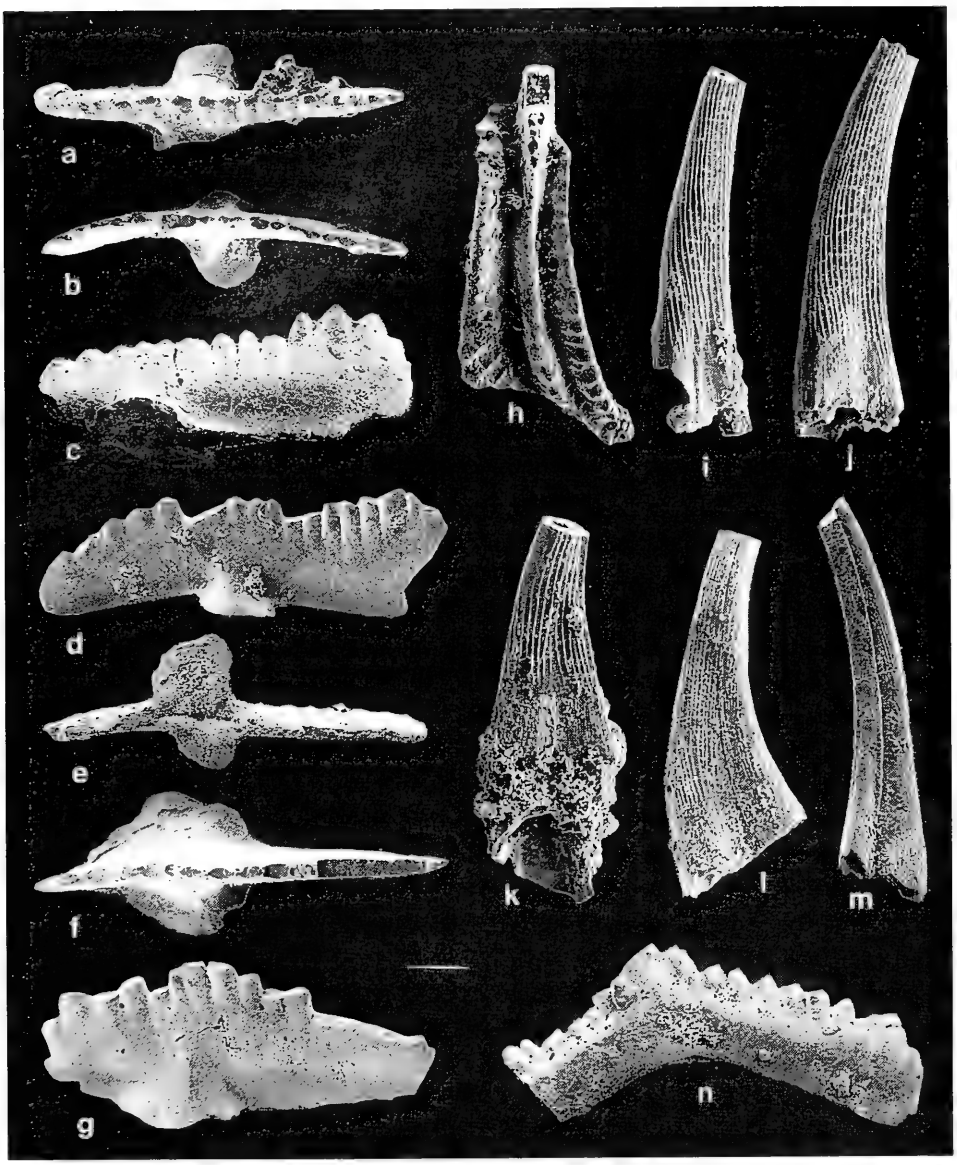

Plate 3: Emsian conodonts from the Frog Hollow Formation exposed at Glenrock GR543957, Bralga Tops, Glenrock Station, NE NSW. All conodont specimens are housed in the collections of the Australian Museum, Sydney. Specimen number and length of scale bar is indicated in parentheses.
***3a**: Ozarkodina* cf. *prolata* Mawson Pa, upper view (AMF.100254, 100 μm), ***3b**: Ozarkodina* cf. *prolata* Mawson Pa, upper view (AMF.100255, 100 μm), ***3c**: Ozarkodina* cf. *prolata* Mawson Pa, lateral view (AMF.100256, 100 μm), ***3d**: Ozarkodina* cf. *prolata* Mawson Pa, lateral view (AMF.100257, 100 μm), ***3e**: Ozarkodina* cf. *prolata* Mawson Pa, basal view (AMF.100258, 100 μm), ***3f**: Pandorinellina expansa* Uyeno and Mason? Pa upper view (AMF.100259, 117 μm), ***3g**: Pandorinellina expansa* Uyeno and Mason? Pa lateral view (AMF.100259, 117 μm), ***3h**: Polygnathus* cf. *serotinus* Telford Pa, upper view (AMF.100260, 100 μm), ***3i**: Neopanderodus aequabilis* Telford Sa, lateral view (AMF.100261, 100 μm), ***3j**: Neopanderodus aequabilis* Telford Sa, lateral view (AMF.100262, 100 μm), ***3k** Neopanderodus aequabilis* Telford Sb, lateral view (AMF.100263, 125 μm), ***3l**: Neopanderodus aequabilis* Telford M, lateral view (AMF.100264, 125 μm), ***3m**: Panderodus unicostatus* Branson and Mehl Sa, lateral view (AMF.100265, 100 μm), ***3n**:* Unidentified Pb element, lateral view (AMF.100266, 100 μm)

Reproductive Biology of the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Poorly known aspects of external dimorphism, maturation, early development and the annual reproductive cycle of *Euastacus spinifer* have been investigated in populations south of Sydney (Georges River, Hacking River, Loddon River). Setal development surrounding gonopores is a reliable field indicator of maturity in females and the degree of inflation of genital papillae is a useful maturity indicator in males.

Females commence maturing at 65 mm carapace length (CL), but many don't mature until 70–75 mm CL; a majority spawn once each year after reaching maturity. Two groups of reproductively functional males were identified in Loddon River populations; normal males became functionally mature at 45–55 mm (CL), but small 'precocious' individuals were mature at 12–20 mm CL.

The robust spermatophore structure is considered to be related to the protracted period (4–6 weeks) between mating and release of the ellipsoid, yolky eggs (means 3.5, 2.7 mm); fecundity increased with size (268 at 73.1 mm CL to 1299 at 109.4 mm CL). Early embryonic development and the three juvenile stages between hatching and release are similar to those of other parastacids; development of offspring on individual *E. spinifer* females is synchronised.

In the Loddon River mating occurs in late May or early June when water temperatures fall rapidly below 15°C. Most breeding females are carrying spermatophores in early June and eggs by early July; incubation extends for 110–140 days over winter. Juveniles remain with the parent for a further 28–70 days before release in early December (water temperatures 20–24°C). Timing of events in this annual cycle is known to vary in different river systems; however, *E. spinifer* is clearly a winter brooder. The selection mechanisms, that may have produced the precocious males remain unknown.

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KEYWORDS: Reproduction, *Euastacus spinifer*, dimorphism, maturation, development, seasonality.

INTRODUCTION

Australia's freshwater crayfish fauna is diverse but poorly known (Merrick 1993) and detailed studies of the group have been restricted (largely) to a few species that are significant in recreational fisheries or have commercial culture potential (Merrick and Lambert 1991). Aside from original descriptions and isolated natural history comments there is virtually nothing published on most mainland species — many of which have restricted ranges in the eastern highlands and coastal drainages (Merrick 1993, 1995).

As part of an extended program on growth and population structure in *Euastacus spinifer* several aspects of reproduction were investigated; the only other *Euastacus* species whose reproductive biology has been studied comprehensively are *E. armatus* (Geddes 1990; Geddes et al. 1993; Morgan 1986) and *E. bispinosus* (Honan and Mitchell 1995a, b, c). Table 1 provides selected reference data for 18 *Euastacus* species.

TABLE 1

Selected reproductive data for *Euastacus* species, aside from *E. spinifer* (from Honan and Mitchell 1995a; Jones and Morgan 1994; Merrick 1993, 1995; Merrick and Lambert 1991; Morgan 1986, 1988, 1997; Turvey 1980).

Species	Size at maturity (CL in mm)*	Fecundity (Egg size in mm)†	Mating & Spawning Season	DEVELOPMENT		
				Incubation (Period)	Larval Period	Release
E. armatus	40 (♀)	300–800	May–June	June–October (4–5 months)	October–November (3–4 weeks)	November–December
E. australasiensis	30–40 (♀)	44–155 (3.0, 2.0)	Autumn	May–October (4–5 months)	September–November	September–January
E. balanensis	~30 (♀)			Winter		
E. bispinosus	55–85 (♀)	63–812 (<4.1 long)	April–May	June–October (6–7 months)	October–November (4 weeks)	November–December
E. crassus	50–60 (♀) 30–40 (♂)			November–March	February–April	
E. gumar	>30 (♀)			September		
E. hystricosus	~60 (♀) ~40 (♂)		Autumn	May–September		
E. keirensis (now synonymised with *E. hirsutus*)	30–40 (♀)	55–184	Autumn	May–November	Summer	
E. kershawi	65–70 (♀) ~50 (♂)	1000–1200				
E. reductus	~30 (♀)			September–October	January	
E. robertsi	60 (♀)			September		
E. setosus	30 (♀)			October		
E. sulcatus	40 (♀) 30 (♂)		Autumn	Winter		
E. suttoni	40 (♀) 20 (♂)		Spring		Summer	Late Summer
E. valentulus	>40 (♀)			May–October	October–November	
E. woiwuru	40 (♀)			September		
E. yanga	30–50 (♀)	43–164		October–November		
E. yarraensis	~40 (♀)			September–November		

*These carapace lengths are rounded and indicate minimum size at sexual maturity; these values are equivalent to the commonly quoted OCL. Some species mature over a wide size range and maturity sizes vary in different populations.

†Where eggs are described they are ovoid or ellipsoid.

Dimorphism, Maturation, Early Development and the Annual Cycle

The sexual dimorphism seen in many decapods (Barnes 1987) is not marked in parastacids. The external reproductive morphology of parastacids, has been described previously in taxonomic works (Riek 1969, 1972); gonopores of females are located on the coxae of the third pereopods, while male gonopores are produced into papillae on the coxae of the fifth pereopods. In several larger *Euastacus* species females are reported to have broader abdomens and males to have larger chelae (Jones and Morgan 1994); these differences conform to the patterns of differential allometric growth, between the sexes, described in other crayfishes (Lowery 1988).

In order to relate variation in *E. spinifer* growth rates to sex and size, it was essential to reliably determine (in the field) the state of maturity of captured individuals without harming them. Mature females of other parastacids have been identified by the presence of attached eggs during the breeding season (Shipway 1951a,b), or by the presence of egg-bearing setae on the pleopods (Morrissy 1970). Mature males have not been reported to exhibit external maturity features; however, Shipway (1951a) noted that the genital papillae of male *Cherax tenuimanus* become more erect during the mating season. In small samples of large *Euastacus* females Ryder (1972) noted that gonopores were surrounded by setae and, at the commencement of this study, considerable variation was observed in the degree of inflation of genital papillae of *E. spinifer* males.

Unpublished observations on spermatophore structure in *Cherax destructor* are available (Johnson 1979), but aside from several general comments by Honan and Mitchell (1995a), there are no published studies of *Euastacus* spermatophores. The few observations of *Euastacus* eggs describe them as being maroon, reddish-brown or orange in colour and ovoid or ellipsoid in shape; egg colour is also reported to change during development (Merrick 1993; Morgan 1988; Turvey 1980).

Aspects of the reproductive cycle have been described for a few species in several other parastacid genera (Hamr 1990, 1995; Lake and Newcombe 1975; Morrissy 1970, 1975; Suter 1977); however, except for *E. bispinosus* (Honan and Mitchell 1995a), there has been no systematic investigation of *Euastacus* relating major physicochemical environmental influences to gonadal maturation, breeding or early development over several annual cycles. Parastacid breeding cycles have been recently discussed by Hamr and Richardson (1994) and Honan and Mitchell (1995a).

This paper is the first in a series on the biology of the Sydney crayfish *Euastacus spinifer.* Objectives of the studies reported here are: to establish whether the development of setae surrounding the gonopores can be used as a reliable field indicator of female maturity; to ascertain whether the degree of inflation of genital papillae in males can be used as a field indicator of maturity; to relate phases of reproduction or development with major environmental parameters and demonstrate factors which may influence the reproductive cycle; and to discuss the overall life cycle strategy of *Euastacus spinifer.*

MATERIALS AND METHODS

Observations were made on several populations; however, most data were derived from the Loddon River population. Crays were captured using baited drop-nets and individual size determined by measuring carapace length (CL) to the nearest 0.1 mm, from the posterior margin of the orbit to the middle of the dorsal posterior carapace margin; all CL, gonopore and egg dimensions were measured with dial calipers. Captured specimens were marked for recognition by removing distal portions of the abdominal pleura and tail fan, according to the system illustrated in Turvey and Merrick (1997a).

Study Area

The Loddon River is the most eastern tributary of the Nepean River system and forms part of the catchment of the Cataract Dam under the jurisdiction of Sydney Water; public access is restricted and most of the catchment is in a natural condition. The Loddon originates on the plateau behind the Illawarra escarpment in a shallow basin, with an area of approximately 13 km^2 at elevations of 360–380 m (lat. 34°17′S: long. 150°54′E).

The river commences as a series of small, semi-permanent channels draining the sedge swamp which covers much of the basin and overlies Hawkesbury sandstone. This swamp is thought to have been in its present state for a long period (Davis 1936), maintained by a combination of high rainfall and high water table resulting from slow evaporation rates, the local soil structure and vegetation, as well as the presence of furrows (at intervals of 0.9–1.8 m) at right angles to the normal drainage slope. The soil layer is deep, (up to 5.0 m) with an acid pH and high humus content.

The main watercourse commences abruptly, in the south-western sector of the swamp, as a series of large pools connected by shallow riffles and narrow channels. The area sampled comprised the first eight of these pools, extending approximately 500 m downstream but with little gradient. The pools (30–100 m in length, up to 30 m in width), consist of channels excavated through the sedge swamp to the bedrock at depths of 4 m or more. Banks are characteristically almost vertical, extending from less than 1 m above water level to depths of 3 m, and flow rates are negligible except during times of flood.

The stream bed consists of flat shelves of sandstone, irregular outcrops and boulders, interspersed with areas of sand and gravel. The bottom was typically clean in appearance; plant debris was sparsely and patchily distributed, with substantial accumulations in restricted areas. The only conspicuous vegetation consisted of dense, but narrow, stands of the aquatic angiosperm *Triglochin procera* (ribbon weed) along the edges of some pools with less steep banks.

Aside from a typical assemblage of insects, the only aquatic macroinvertebrates observed were the shrimp *Paratya australiensis* and another small crayfish, *Euastacus keirensis* (now synonymised with *E. hirsutus* by Morgan (1997)). The two major fish species present were mountain galaxias and Macquarie perch.

Maturation

Females

Females (CL range 20–100 mm) were collected from the study area in 1976, 1977, and 1978 during May and June, just prior to spawning. These specimens were returned to the laboratory, anaesthetised by chilling, and weighed (to nearest 0.1 g); ovaries were then removed under a dissecting microscope. Adherent blood vessels were cut away and oviducts severed at the points at which they turned ventrally around the lateral margins of the hepatopancreas. The gonads were drained briefly on tissue paper and weighed (nearest 1 mg); the contribution of reproductive tissues to body weight was expressed for each crayfish as a 'gonosomatic index' of the form:

$$[\text{gonad weight}/(\text{body weight} - \text{gonad weight})] \times 100.$$

Changes in gonosomatic index associated with body weight were determined.

The second left pleopod and coxa of the third left pereopod were also removed from each dissected female and fixed in formol-alcohol (Humason 1972). Major types of setae surrounding the gonopores and on the pleopods were described, classified according to Thomas (1970), and distributions recorded. Three patterns of setal distribution (Stages 0, 1 and 2) were proposed and each cray allocated to a stage from observation of the gonopore.

All females examined were allocated to CL classes (5 mm increments) and percentages of individuals in each size class at each setal Stage calculated. Confidence limits (95%) for values on repeated sampling were estimated for each percentage using a normal approximation for samples exceeding 30 individuals, in each size class (Snedecor and Cochran 1967), or from tables based on the binomial distribution (Crow 1956) for smaller samples.

Another 20 females (in Stages 1 and 2) were examined in the laboratory during November or early December in 1976 and 1978. Numbers in each stage with developing, yolky oocytes and immature oocytes were determined and Stage 1 was further sub-divided. These laboratory results were supplemented with field data; females examined in the field were considered mature when they were known to have spawned, but the mark-recapture records also provided setal allocations of immature females. Setal stages were compared between captures for each individual that was captured more than once and inconsistencies in allocations, that could not be explained by transitions at moulting from Stage 0 to Stage 1 or Stage 1 to Stage 2, were noted.

The maximum diameter (to nearest 0.1 mm) of the left gonopore was measured for each of a series of females.

Males

Males in the range 20–90 mm CL were collected from the study area in 1976, 1977 and 1978 in May, during the mating period; these individuals were anaesthetised by chilling and weighed (nearest 0.1 g). Both testes and vasa deferentia were removed, under a dissecting microscope, after cutting away adhering blood vessels and severing the vasa deferentia close to the gonopores. Gonads were drained briefly on tissue paper, weighed (nearest 1 mg), fixed for one hour in alcoholic Bouin's solution (Humason 1972), and stored in 70% alcohol. Gonosomatic indices were calculated as for females. Paraffin sections 10 μm thick were taken at several places along the posterior lobes of the testis and stained in Delafield's hematoxylin and eosin by the regressive method (Humason 1972). Mature males were identified by the presence of sperm in open spermatic cysts and ducts in the testis.

Males were divided into three groups on the basis of the degree of genital papilla inflation and the relationships between papilla inflation, maturity and gonosomatic index were investigated. All males captured were size classed (using 5 mm CL increments) and further classified by papilla development status; percentage abundances of each inflation state, related to size, were examined.

Records of marked individuals, that were captured more than once, were examined for variability in the degree of inflation of genital papillae through time.

Spermatophores, Fecundity and Early Development

The appearance of spermatophore material was described before and after its attachment to females, and the structure of attached spermatophores was examined from sections (0.5 mm thick) of fresh material.

Eggs, egg attachment, juvenile stages and juvenile attachment were briefly described. Maximum and minimum diameters (to nearest 0.1 mm) of 10 eggs from each of five females were measured for estimates of egg size. The relationship between egg number and the size of females was estimated as the linear regression of egg number on carapace length for 10 individuals.

Annual Reproductive Cycle

Events in the annual reproductive cycle of *E. spinifer* were described from the condition of mature females captured each month as part of the mark-recapture study of

growth. Mature females were identified upon capture and rated according to whether they were carrying spermatophores, eggs, or first, second or third stage juveniles. Individuals were assigned a brooding state and specimens with each state tabulated for each month; combined raw data for the three years were compared.

Average water temperatures were recorded for each monthly sampling at two of the pools for the period May 1977 to December 1978. Periods during which mating, spawning and release of juveniles occurred were compared with the annual water temperature regime.

RESULTS

Maturation

Females

Ovary Structure

The ovary of *E. spinifer* is located ventral to the heart, dorsal to the hepatopancreas, mid- and hindgut, and posterior to the gastric mill, extending slightly into the first abdominal segment. Each ovary consists of two elongate, tubular sacs joined by a single, broad commissure towards the anterior end, adjacent to the points of exit of the oviducts. As oocytes mature prior to spawning, the ovary increases in size to occupy much of the posterior cephalothoracic lumen. The yolk of mature oocytes is a maroon to dark maroon colour; white oocytes observed have been classed as non-yolky.

Setation

Setae surrounding the female gonopores are mostly of the pappose type (Fig. 1); each seta consists of a thick, tapering shaft with numerous, distally-directed setules distributed irregularly around the shaft circumference. By contrast, the setae on pleopod margins are of two types, plumose setae and oosetae (Fig. 1). Each plumose seta comprises a shaft of moderate thickness bearing numerous, long, distally-directed setules arranged in opposing pairs, in the same plane as flat surfaces of the pleopod. Each ooseta consists of a long, filament-like shaft bearing a number of minute setules over its distal quarter; these setules are barely visible even at 400x magnification.

Females were allocated to one of three stages on the basis of the patterns of setae around the gonopores (Fig. 2). Crayfishes in Stage 0 lack obvious setae around the gonopores. Basipodites of the pleopods are free of obvious setae, while all margins of both endopodites and exopodites carry a continuous fringe of evenly-spaced plumose setae. Stage 1 is recognised by partial encirclement of each gonopore by a narrow band of pappose setae. Setae are typically distributed sparsely within this band, although in some individuals they are arranged in dense but narrow clumps for short intervals, particularly around the posterior gonopore margins; both plumose setae and oosetae are present on the pleopods. Oosetae and a few plumose setae are present on the medial margin of the basipodite, the lateral margin of the near-proximal exopodite, as well as medial and lateral margins of the near-proximal endopodite; otherwise both endopodite and exopodite carry the complement of plumose setae typical of Stage 0. The presence of oosetae usually corresponds to a reduction in the number of adjacent plumose setae in Stage 1 females.

Stage 2 individuals have complete encirclement of each gonopore by a band of pappose setae (Fig. 2). These setae are frequently longer posteriorly, and the band of setae is narrower anteriorly in some smaller individuals. Otherwise, setae are densely packed to form a continuous band up to several millimetres wide around each gonopore; in large specimens, a dense belt of setae frequently extends anteriorly over the surface of the coxa.

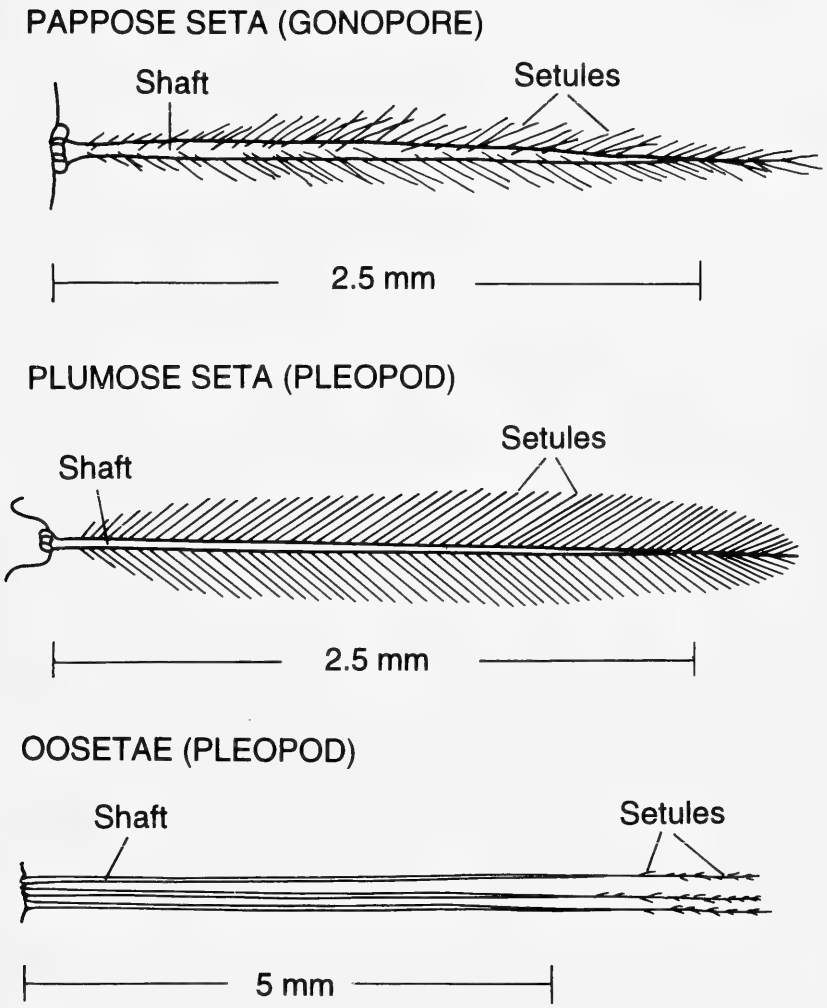

Figure 1. Major types of setae surrounding gonopores and on the pleopods of mature *E. spinifer* females.

Dense beds of long oosetae are conspicuous on pleopods of Stage 2 females. Oosetae are best developed on the medial margin of the basipodite, lateral and medial margins of the proximal endopodite and lateral margin of the proximal half of the exopodite. Plumose setae are either very sparse or absent in these areas and oosetae are typically twice the length of plumose setae elsewhere on the pleopods. Shorter oosetae are usually present on the central third of the lateral margin and proximal two-thirds of the medial margin of the exopodite, as well as all margins of the distal endopodite except the tip.

The presence of oosetae in these areas corresponds to a reduced density of plumose setae similar to that described for Stage 1 females, while the very tip of the endopodite and distal third of the exopodite carry plumose setae typical of Stage 0. The described oosetal patterns are applicable to most individuals in Stages 1 and 2; however, oosetal development in some Stage 1 specimens was indistinguishable from Stage 2.

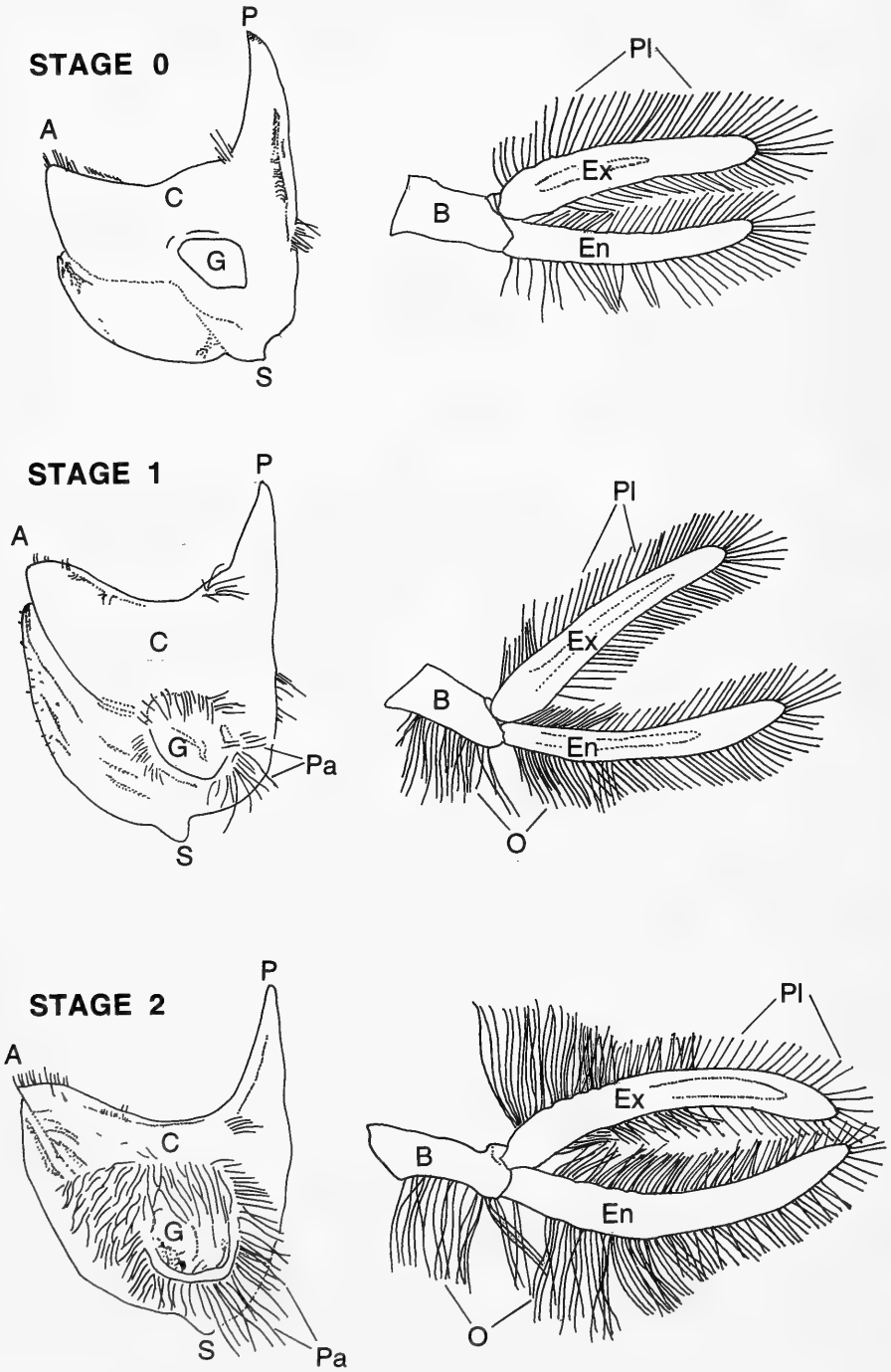

Figure 2. Patterns of setae around gonopores and setal distributions on the pleopods of female *E. spinifer*. Left field: ventral view of the coxa of the left third pereopod; right field: anterior view of the left second pleopod. Key to abbreviations: A = anterior articulation of coxa with basis (or basipodite); B = basipodite; C = coxa; En = endopodite; Ex = exopodite; G = gonopore; O = oosetae; P = posterior articulation of coxa with basis; Pa = pappose setae; Pl = plumose setae; S = articulation of coxa with sternum.

Gonosomatic Index

This index, ovarian maturity, and setal stage were clearly related for females examined just prior to spawning. Data were plotted with indices scaled in $\log_{10}$ to provide approximately linear relationships with body weight (Fig. 3). All Stage 0 and Stage 1 individuals had immature ovaries, while in nine of the ten Stage 2 females the ovaries were mature. Oocytes in the other Stage 2 female were normal in appearance and light yellow-orange in colour, indicating early stages of yolk deposition, so the ovary was classified as developing. The gonosomatic indices of Stage 0 and Stage 1 females formed a continuous, approximately exponential progression with body weight from approximately 0.02 at ~10 g, to approximately 0.3 at a body weight of 300 g. In contrast, gonosomatic indices of Stage 2 females were much higher and, on average, constant with body weight (2.5–3.0); the index of the Stage 2 female with a developing ovary was similar to indices of Stage 1 individuals of similar size.

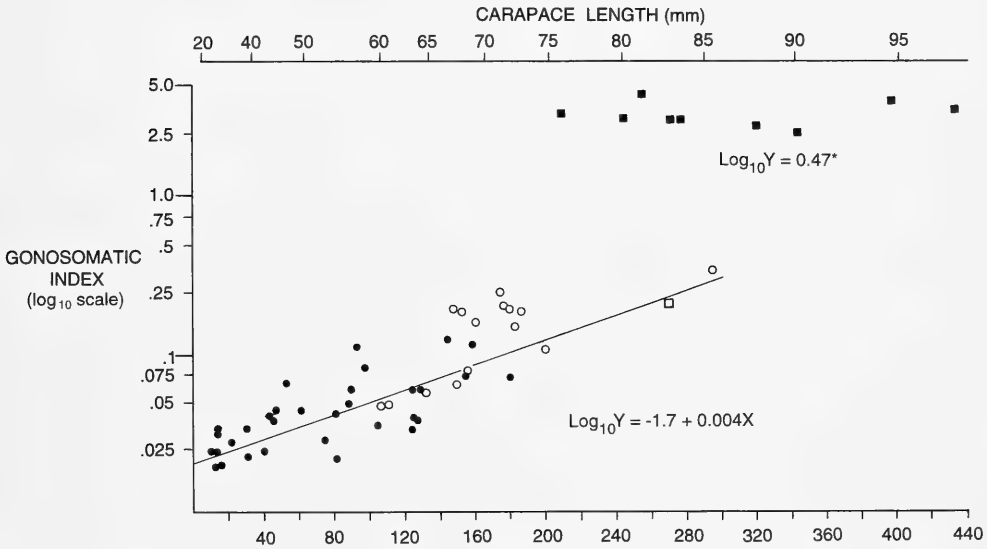

Figure 3. Relationship between gonosomatic index, ovarian maturity, setal stage and body weight in female *E. spinifer*. Key to symbols: ● = Setal Stage 0, ovary immature; ❍ = Setal Stage 1, ovary immature; ❑ = Setal Stage 2, developing ovary; ■ = Setal Stage 2, mature ovary. * slope of regression for mature individuals not significantly different from zero ($p >> 0.5$), but slope of regression for immature individuals significantly different from zero ($p << 0.001$).

In addition, 71 mature females were examined in the field. In 69 instances individuals were allocated to Stage 2 and the other two were allocated to Stage 1; but both of these females had been allocated to Stage 2 on several other occasions. There were also occasional inconsistencies in the field allocation of females to Stages 0 and 1. Of 112 records of Stage 0 individuals, that were captured more than once, there was a single inconsistent allocation of an otherwise Stage 0 female to Stage 1; out of 31 captures of Stage 1 females there was also a single allocation of a Stage 1 specimen to Stage 2.

Among females captured and dissected during November to December, all eight Stage 2 individuals and eight of the 12 Stage 1 specimens had ovaries containing yolky, developing oocytes; remaining Stage 1 animals had ovaries containing non-yolky, immature oocytes. It was not possible to distinguish between the Stage 1 females with developing and immature oocytes according to the density of the setal bands surrounding the gonopores.

These Stage 2 females were carrying offspring and the maturity of the gonads indicated that they would probably spawn again in the following season; further evidence of spawning in successive years was obtained from mark-recapture records. Of six Stage 2 females with capture records in the brooding periods of 1977 and 1978, five carried eggs in both years; the other individual carried eggs in 1977, but only a spermatophore in 1978.

Body weights of Stage 0 and Stage 1 females examined in the laboratory (Fig. 3) overlapped in the 110–180 g range (60–72 mm CL) while Stage 1 and Stage 2 females overlapped in the 200–300 g range (75–85 mm CL). Similar trends were evident when frequencies of Stage 0, 1 and 2 were combined for all catches during the study period (Table 2), confirming the overlap in sizes of Stage 1 and 2 females suggested by the laboratory results. Substantial numbers of females in both stages occurred in the range of 70–95 mm CL, with the relative abundance of Stage 1 decreasing with increasing size.

In contrast to the results for gonosomatic index, ovarian maturity and setal stage, there was no apparent change in the relationship between gonopore diameter and carapace length. Gonopore diameters increased linearly in the range 50–90 mm CL ($Y = -0.027 + 0.044 X$, $n = 28$), but considerable variability was evident.

TABLE 2

Relative abundances of female *E. spinifer* in three maturation states (Stages 0,1,2) over the carapace length range recorded in all catches.

Carapace Length Class (mm)	**Maturation Length 0**	**1**	**2**
9.95–14.95	100*		
14.95–19.95	100		
19.95–24.95	100		
24.95–29.95	100		
29.95–34.95	100		
34.95–39.95	100		
39.95–44.95	100		
44.95–49.95	100		
49.95–54.95	100		
54.95–59.95	100		
59.95–64.95	100		
59.95–64.95	85	15	
64.95–69.95	14	82	4
69.95–74.95	4	70	26
74.95–79.95		35	65
79.95–84.95		25	75
84.95–89.95		34	66
89.95–94.95		17	83
94.95–99.95			100
99.95–104.95			100

* Abundance values are proportions of females (%) in each stage.

Males

Testis Structure

Each testis consists of two elongate, whitish lobes, slightly flattened dorso-ventrally, and joined towards the anterior end, adjacent to the points of exit of the vasa deferentia, by a broad commissure. In some individuals a second commissure is present mid-way along the testis length. Each vas deferens consists of two portions. The proximal portion is of constant, relatively small diameter, long, tightly coiled and convoluted to form a compact tubule mass lateral to the central portion of the gonad. The distal vas deferens is initially slightly convoluted, becoming relatively straight and increasing rapidly in diameter (Fig. 4).

In males with uninflated genital papillae (described below), the testes and vasa deferentia are small and inconspicuous, but in males with inflated papillae testes and vasa deferentia are much larger relative to the size of the individual; distal portions of vasa deferentia are noticeably distended over most of their length. In males with highly inflated papillae the testes are of similar relative size (compared with individuals with inflated papillae) and distal portions of vasa deferentia are relatively enormous, occupying much of the posterior half of the cephalothorax. In males with either inflated or highly inflated papillae the distal vasa deferentia contain large quantities of dense, white, glue-like spermatophore material, and account for much of the total gonad weight.

Papilla Structure

The gonopores of male *E. spinifer* are enclosed in membranous papillae on the ventral surfaces of the coxae of the fifth pereopods. Each papilla consists of a smooth membranous area, continuous with the arthrodial membrane of the coxa-basis articulation, and supporting an incompletely sclerotised ring, or crescent; details of structure and the three inflation stages are illustrated in Figures 5 and 6.

Uninflated genital papillae are flush with or only slightly raised above the general contours of the coxa, with the sclerotised ring closely adjacent over most of its length to the body of the coxa. In contrast, inflated genital papillae are distinctly raised above the general contours of the coxae, all membranous areas are distinctly tumid and the sclerotised ring separated from the body of the coxa by an obvious area of membrane. Uninflated and inflated genital papillae are otherwise similar, and some of the inflated papillae that are less tumid resemble uninflated papillae. Highly inflated genital papillae are conspicuous and unmistakable. These papillae are produced into turgid, balloon-like vesicles, often extending laterally past the coxa-basis articulation, with the sclerotised ring relatively small in size, displaced to the anteroventral surface of the papilla, and well-separated from the body of the coxa.

Gonosomatic Index

These results were plotted using a $\log_{10}$ scale for the index to provide an illustration in the same format as used for females. However, there were no clearly progressive relationships between gonosomatic index and body weight, so regression equations were not calculated. There were several distinct grouping of conditions of the genital papillae, gonosomatic index, and testicular maturity (Fig. 7). Males with uninflated genital papillae and body weights less than 45 g had immature testes, and had gonosomatic indices of approximately 0.1; specimens with inflated genital papillae and body weights over 130 g had mature testes as well as a gonosomatic index (0.5–1.5) that was variable but, on average, constant with carapace length. Individuals weighing 45–130 g had mature testes and either inflated or uninflated genital papillae. Animals with uninflated genital papillae had gonosomatic indices similar to those of smaller, immature males; however, indices of similar-sized individuals with inflated genital papillae were substantially greater, varied widely and attained the levels characteristic of larger mature males. Occasional individuals with aberrant numbers of gonopores were recorded.

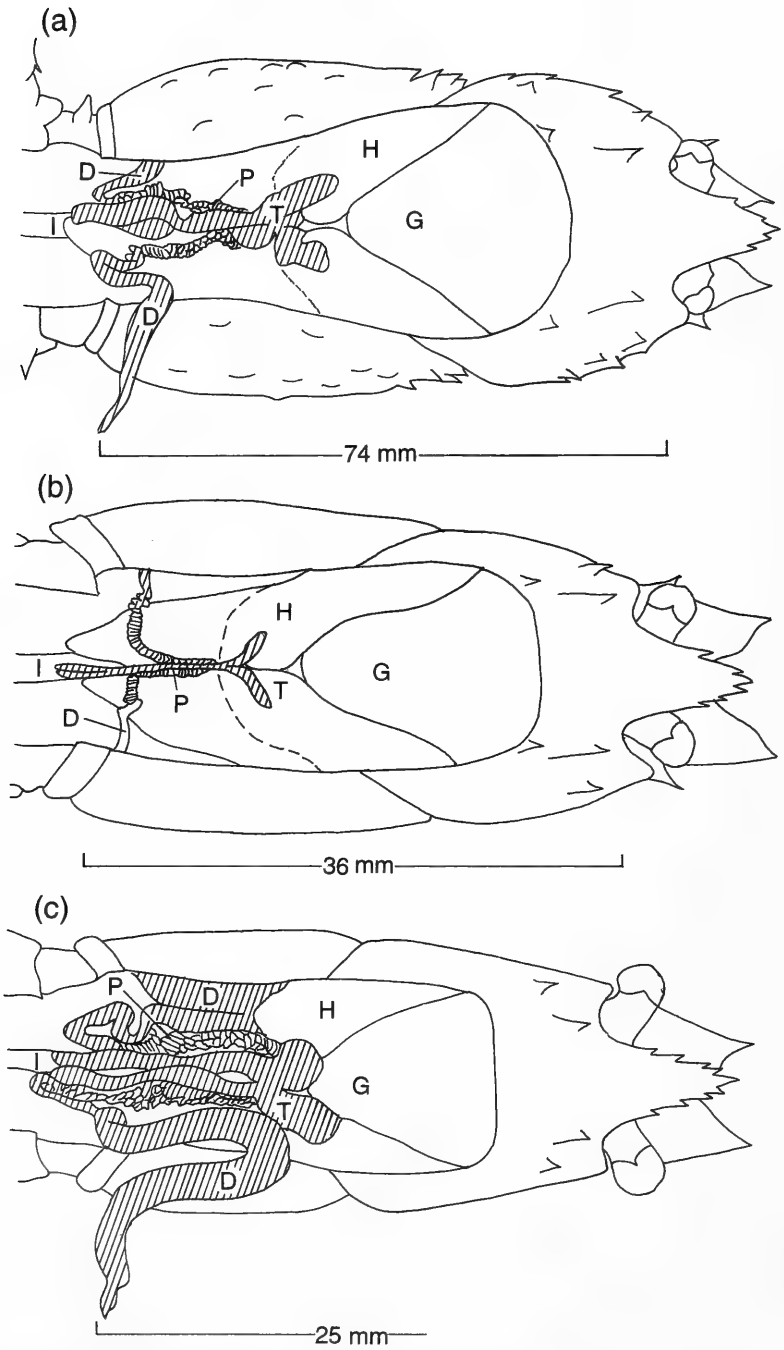

Figure 4. Anterior dorsal views of dissected *E. spinifer* males with different degrees of genital papilla inflation, showing testes and vasa deferentia *in situ*: (a) inflated papillae (normal mature); (b) uninflated papillae (normal immature); (c) highly inflated papillae (precociously mature). The dorsal walls of the carapace and abdominal segments, heart and dorsal blood sinuses, as well as the posterior dorsal gastric mill musculature have been removed. Key to symbols: D = distal vas deferens; G = gastric mill; H = hepatopancreas; I = hindgut; P = proximal vas deferens; T = testis.

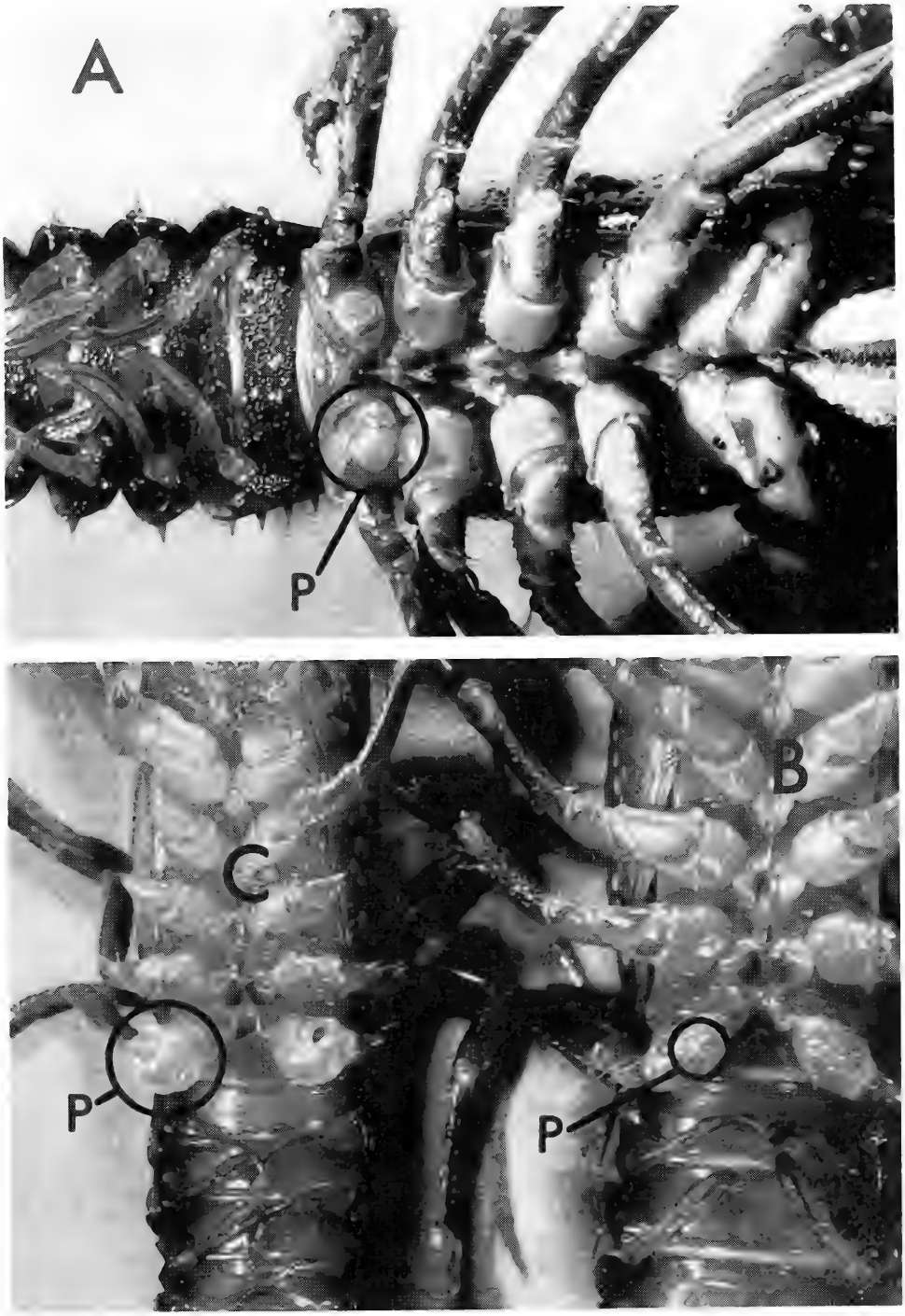

Figure 5. Ventral views of male *E. spinifer*, showing genital papillae: (A) inflated genital papillae (normal mature); (B) uninflated genital papillae (normal immature); (C) highly inflated genital papillae (precociously mature); P = genital papilla.

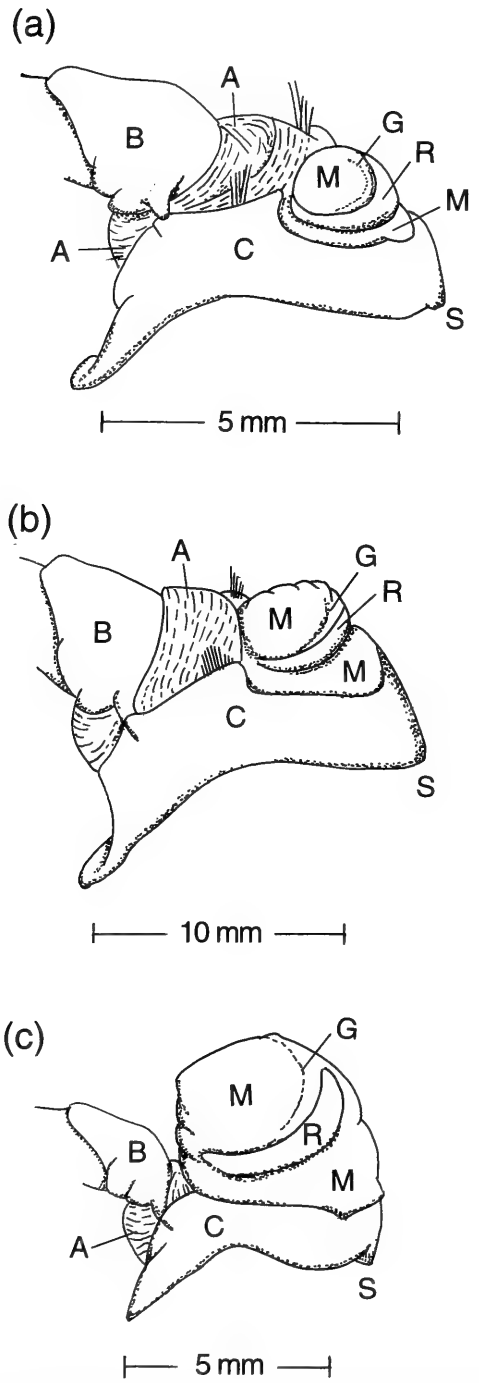

Figure 6. Degrees of inflation of the genital papillae of male *E. spinifer*. Coxa of the left fifth pereopod, anterior view: (a) uninflated (individual 36.6 mm CL); (b) inflated (individual 74.3 mm CL); (c) highly inflated (precocious individual 24.6 mm CL). Key to symbols: A = arthrodial membrane of the coxa - basis articulation; B = basis (or basipodite); C = coxa; G = gonopore; M = membranous part of papilla; R = sclerotised ring; S = articulation with sternum.

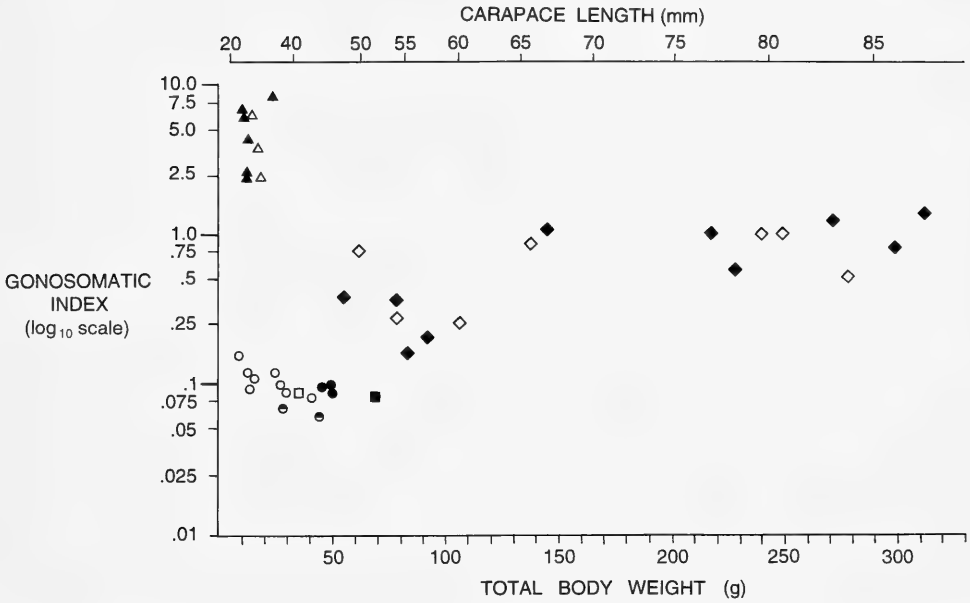

Figure 7. Relationships between gonosomatic index, testicular maturity, inflation of the genital papillae and body weight for male *E. spinifer*. Key to symbols: ● = papillae uninflated, testis immature; ○ = papillae uninflated, testis mature; ◓ = papillae uninflated, testis not examined; ◆ = papillae inflated, testis mature; ◇ = papillae inflated, testis not examined; ▲ = papillae highly inflated, testis mature; Δ = papillae highly inflated, testis not examined; ■ or ❑ = each individual with two male and two female gonopores.

Males with highly inflated genital papillae formed an entirely separate group. They were restricted to weights below 25 g, had mature testes and extremely high gonosomatic indices, two to ten times those calculated for mature individuals. Members of this group were designated as 'precocious' males.

Papilla Inflation and Size

Changes with carapace length in the relative abundances of males with uninflated, inflated or highly inflated genital papillae were similar in laboratory samples (Fig. 7) and all catches combined for the period of study; however, a major difference was that substantial numbers of larger males (CL >55 mm) with uninflated genital papillae were present in combined field data. Percentages of the two inflation categories varied considerably over this range, although variation was within sampling error except in the 60–65 mm size class; no sustained trends with CL were apparent.

Percentages with uninflated and highly inflated papillae were within sampling error at carapace lengths less than 25 mm, although calculations suggested a trend towards an increasing relative abundance of precocious males, over the range 10–25 mm (CL). Above 25 mm CL the relative abundance of males with highly inflated genital papillae decreased markedly and remained low up to the 40–45 mm size class; no males with highly inflated papillae were recorded above that size. The high relative abundance of individuals with uninflated genital papillae over 30–45 mm CL, rapidly decreased corresponding to the appearance of larger males with inflated papillae.

Recapture records (Table 3) indicated that genital papillae of males in the range 20–30 mm CL neither changed from the uninflated to the highly inflated condition nor reverted to the uninflated state. Although fewer data were available there was no evi-

dence of a different situation among larger individuals with highly inflated papillae. By contrast among very small males (<20 mm CL) there was some indication that genital papillae may have changed from uninflated to the highly inflated condition.

TABLE 3

Variation in the degree of inflation of the genital papillae of individual male *E. spinifer* with multiple recapture records.

Carapace Length (mm)	Mean Captures per male	Number of Individuals and Rating*			
		O	HI	I	O/I/HI
<20	2.8	2	6	–	1(O/HI)
20–30	2.5	69	29	–	–
30–40	3.4	63	3	–	–
40–60	4.1	21	1	4	8(O/I)
60+	3.1	2	–	12	6(O/I)

* Rating

O — genital papillae not inflated at all captures.

I — genital papillae inflated at all captures.

HI — genital papillae highly inflated at all captures.

O/I/HI — mixture of records as indicated.

Spermatophores, Fecundity and Early Development

Spermatophores appear as translucent, grey-white, irregularly-shaped masses of tough, gelatinous material; these are distributed patchily over the coxae of the fourth and fifth pereopods and adjacent sternal plates of large females. In section, each spermatophore consists of an amorphous matrix containing an irregularly distributed, highly convoluted tubule (0.05 mm diameter) containing the spermatozoa. Spermatophore material obtained from the distal vasa deferentia is white in colour, of thick but plastic consistency and extremely adhesive, setting rapidly after release.

Eggs are ellipsoid in shape; maximum and minimum diameters of individual eggs (n=50) ranged from 3.2–3.9 mm and 2.4–2.9 mm, with mean values of 3.5 and 2.7 mm. Eggs are attached (individually or in bunches) to the medial margins of the basipodites, all margins of the endopodites except the tips and to the proximal lateral margins of exopodites of all pleopods; attachment is by cords formed by several oosetae twisted together. This egg distribution corresponds to the occurrence of long oosetae, with the majority of eggs carried on the endopodite. Although both plumose setae and oosetae are present on the pleopods of mature females, eggs have not been observed attached to plumose setae.

The relationship between the number of eggs and carapace length for female *E. spinifer* (n=10) was well described by a straight line (Fig. 8). The regression slope was significantly different from zero ($t = 9.2$, d.f. = 8, $p < 0.001$), with carapace length accounting for 91% of the variance in egg number. Numbers of eggs for females from the study area ranged from 268 for an individual of 73.1 mm CL to 779 for a large adult of 103.6 mm CL. Additional data were obtained for five females collected from the Hacking River near Otford, in an adjacent catchment; egg numbers ranged from 534 for a female of 82.9 mm CL to 1299 for a female of 109.4 mm CL.

The maroon yolk of oocytes becomes darker during the later development of fertilised eggs. During early development the blastopore is visible to the naked eye as a small dark spot; later the embryo becomes visible as a white patch at the pole of the egg,

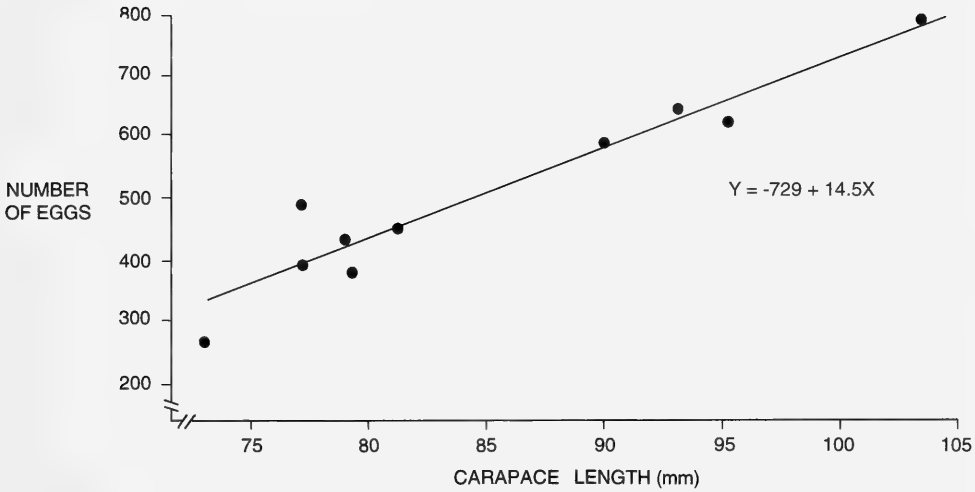

Figure 8. Relationship between the number of eggs and the carapace lengths of female *E. spinifer* (n = 10: 70–105 mm CL).

opposite its point of attachment to the parental pleopod. Early larval development is completed within the egg and young hatch as Stage 1 juveniles; post-embryonic development continues with Stage 1 moulting to become Stage 2 juveniles. With a further moult these become Stage 3 juveniles, identical in form to adults except for the progressive development of body spines and an increase in robustness with size.

Overall morphology of Stage 1 and 2 juveniles is as described for other parastacids (Hamr 1992); and observations of captive stocks (at ~20°C) indicate that Stage 1 juveniles are attached to the egg membrane by a thread running from the telson for a period of at least several hours after hatching. One day after hatching these threads are no longer apparent. Both Stage 1 and Stage 2 juveniles are attached to the setae of parental pleopods by recurved hooks; one hook extends proximally, in the medial plane, from the distal dactylus of the fourth and fifth pereopods. These hooks close onto a series of serrations on the body of the dactylus, firmly gripping the setae.

Brooding females held in captivity began to devour their offspring after periods ranging from several days to several weeks, and offspring had difficulty in hatching and moulting when detached from their mother. It was not possible to accurately estimate duration of stages in a particular brood; however, observations of offspring at different stages, on different females, suggested that development on a given female was synchronised to within a period of several days. Detailed observations on two captive females indicated that all Stage 3 juveniles departed voluntarily from the parent over a period of three to four days, although prior to this many juveniles made short excursions over and away from the parent.

Annual Reproductive Cycle

Periods of the year during which mating, spawning, incubation, hatching and departure of juveniles occurred were inferred from the relative abundances of females in different brooding states. Numbers of females captured at monthly samplings were often small and not all 31 months for the study period (1976–78) were represented; however, available data indicate that trends, in numbers of females at particular brooding states, were similar for each of the three years.

The majority of mature females mated during May, and were observed carrying spermatophores in early June. Spawning typically occurred during June, and the majority of females carried eggs in early July. The percentage of females that retained spermatophores after spawning was initially high at around 60% in early July, declining to zero by early October.

Eggs of most females hatched during October and a majority of mature females carried Stage 1 juveniles in early November. Stage 1 juveniles moulted during early November, and all captured females carried Stage 2 juveniles during mid-November. Stage 2 juveniles moulted during late November, and the majority of females carried Stage 3 juveniles in early December. Of the two non-brooding females captured in early December one had traces of egg attachments on the pleopods. One of the brooding females had already released the majority of her offspring but none of the females captured in mid-late December were carrying juveniles.

These data indicate that reproduction in the *E. spinifer* population at the study area followed a fixed, annual cycle, and events in the annual reproductive cycle of the majority of females were synchronised to within a period of a few weeks. Water temperature also followed an annual cycle (Fig. 9) and events in the annual reproductive cycle coincided with changes in water temperature that were similar for each year. Mating occurred as water temperatures fell rapidly below 14–15°C, spawning occurred as water temperatures approached the annual minimum of 10–11°C, while juveniles were released as water temperatures attained the annual maximum (20–24°C).

DISCUSSION

Study Area

The Loddon River was selected for accessibility, the permanence of the stream and the large crayfish population. Although it may be typical *E. spinifer* habitat, in terms of stream bed topography and substrate types or aquatic vegetation, the site may also be considered atypical in two respects.

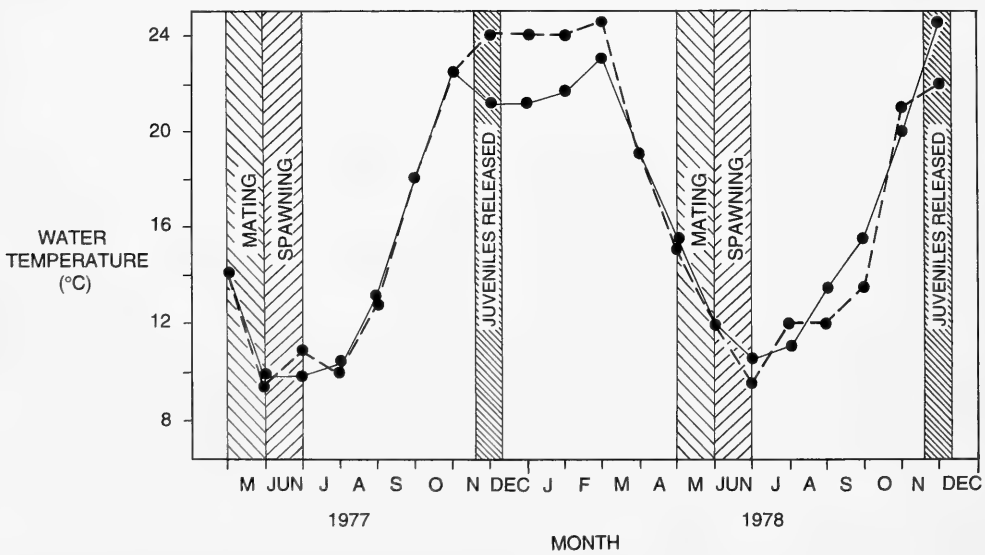

Figure 9. Summary of annual water temperatures related to key events in the annual reproductive cycle of *E. spinifer* from Pool 3 (– –) and Pool 7 (—) on the Loddon River.

Firstly, the terrain is relatively flat and study pools are near the river source. So the flooding that did occur probably had less impact than on typical sandstone streams of the region, which are characteristically steep and flowing through rocky gullies. Secondly, the adjacent swamps and high local rainfall probably provide a more continuous input of water than most streams around Sydney receive; the pools did not have the dramatic reduction in water level associated with many sandstone streams during dry periods. So the hydrologic environment in the study area is abnormally constant over the year.

Maturation

Females

The ovaries of *E. spinifer* are of typical decapod form (Barnes 1987), although the tubular, anterior extensions (additional lobes) lateral to the cardiac stomach, described in *Cherax tenuimanus* (Morrissy 1970) and *C. destructor* (Johnson 1979), have not been observed. Colour and the degree of yolkiness provide a rapid means of assessing the state of development of ovaries and identifying immature as well as incipiently mature or mature females, without histological examination.

Allocation of females to three Stages, on the basis of setal development around the gonopores, during May-June resulted in complete segregation of mature and immature individuals. The immature ovaries and single, linear progression in gonosomatic indices for Stage 0 and 1 females indicated that the initial appearance of setae, around the gonopores, was not related to any immediate change in reproductive condition.

The Stage 2 female captured during May–June with a developing ovary was not considered an example of inconsistent allocation. The ovary of this individual differed from all Stage 1 females captured at the time and was similar to Stage 2 ovaries. Incomplete yolk deposition in this female may have been associated with delayed spawning, or with failure to spawn.

Combined laboratory and field examinations showed a very low incidence of incorrect allocation on setal development; each individual for which inconsistent stages were recorded had also been allocated to the normal stage on other occasions. None of the inconsistencies were related to changes in setal development at moulting; in addition, some gradation in the degree of setal development between stages was noted. Inconsistent allocations of Stage 2 to Stage 1 or Stage 1 to Stage 2 occurred with similar frequencies. So an incorrect allocation could be expected once for every 40 examinations; the single inconsistent allocation of a Stage 0 female to Stage 1 was probably a recording error.

The discussion of Stage 1 females has been based on collections during May-June; however, ovaries of females collected during November-December indicated that a substantial proportion in Stage 1 were incipiently mature and likely to spawn in the next season. Females larger than 55 mm CL (including all those in Stages 1 and 2) were found to moult once per year, during March-April (Turvey and Merrick 1997b). As no Stage 1 females were observed to be carrying eggs, it is concluded that incipiently mature females moulted during March-April and assumed Stage 2 characteristics prior to their first spawning.

The inability to distinguish between immature and incipiently mature females in Stage 1, on the basis of gonopore setae, has several implications. If individuals are examined between the annual moult and the commencement of spawning, then all females likely to spawn in that year will be Stage 2. Similarly, for females captured at other times, all that spawned during the previous season will be in Stage 2. But, given the high proportion of Stage 1 females that were incipiently mature, numbers of Stage 2 females taken outside the period between annual moult and spawning would probably be a gross underestimate of those likely to spawn during the next season.

The overlap in CL ranges of females in Stages 1 and 2 (Table 2) indicates considerable variation in the size at which individuals attain maturity. Only one mature specimen was recorded in the 65–70 mm CL group; however, substantial numbers of mature females were present in the 70–75 mm class. The percentage of mature individuals increased rapidly above this size, but 100% maturity was not attained until females exceeded 95 mm CL.

Variability in the size of females at maturity has also been noted for other parastacids (Honan and Mitchell 1995a; Morrissy 1975); however, maturity in many decapods is not simply a function of size. Chittleborough (1974) concluded that the variable size of female lobsters *(Panulirus longipes cygnus)* resulted from variation in growth rates, with maturity being attained at a specific age. The same may apply to *E. spinifer*, as growth rates did vary, resulting in a wide range of estimated sizes at any given age (Turvey and Merrick 1997c). As it was not possible to determine ages of individual females, the relationship with maturity could not be clarified.

The data suggest that the majority of mature female *E. spinifer* spawned each year after reaching maturity; factors contributing to this conclusion were the percentage of individuals known to have spawned in both 1977 and 1978, as well as the ovarian condition of adults carrying juveniles in November-December. Honan and Mitchell (1995a) reported that over 95% of mature *E. bispinosus* females bred each season.

It was the observations of Ryder (1972), on *E. australasiensis,* that initially stimulated investigation of a possible link between gonopore setae and maturity. During this study gonopore setae, similar to those of *E. spinifer,* were also observed in large female *E. armatus, E. hirsutus, E. hystricosus* and *E. valentulus.* In each instance the full development of gonopore setae (Stage 2) was associated with females carrying eggs. Detailed analyses were not undertaken, but it is suggested that the setal development stages devised for *E. spinifer* might indicate maturity in other species; although, Honan and Mitchell (1995a) did not find setation a reliable maturity indicator in *E. bispinosus.*

The structure of *E. spinifer* oosetae and their distribution on pleopods is similar to that described for other parastacids (Johnson 1979; Morrissy 1975); egg distributions were also similar to those reported previously, with the majority of eggs carried on the endopodites. Despite their small size (requiring microscopic assessment), oosetae must be considered a primary sex characteristic; they performed the function of attaching eggs to pleopods and were present only on mature or incipiently mature females. But in the absence of any observed function, the gonopore setae are probably a secondary sex characteristic.

Gonosomatic indices of mature *E. spinifer* females, collected in May-June, ranged from 2.3–4.2. Johnson (1979) calculated similar indices (from 0.9–3.5) for *C. destructor* with ovaries in the later stages of maturation, but for individuals just prior to spawning, the values exceeded 3.5 (up to 5). So these two species apparently have similar allocations of body tissue to reproduction.

No further comment is possible on quantitative relationships between gonopore size and carapace length; Honan and Mitchell (1995a) used different qualitative features (level compared with coxal surface, calcification, rim incisions) to rate gonopores in relation to maturity in *E. bispinosus.*

Males

The gonads of all males are similar in form, apart from differences in proportions; they are also similar in overall morphology to that reported for other astacuran decapods (Farmer 1974; Johnson 1979).

In normal males there is a progressive acquisition of mature characteristics with increasing size. Initially individuals have a low gonosomatic index, immature testis and uninflated genital papillae. The first sign of incipient maturity is maturation of the testes,

without any substantial increase in gonosomatic index or papilla inflation. This is followed by a simultaneous inflation of genital papillae and rise in gonosomatic index, to a level which is maintained with further increase in carapace length.

In individuals with high gonosomatic indices and inflated genital papillae, the distal vasa deferentia are turgid with large quantities of spermatophore material,and contribute a substantial proportion of the total gonad weight; the increased gonosomatic index is considered to be due to spermatophore production. Only males that produced spermatophore material could be considered reproductively functional. Normal males with mature testes but uninflated genital papillae were designated as immature and inflated papillae were considered to be indicative of functional maturity.

The carapace lengths of functionally mature and immature normal males overlapped in the 55–70 g range (45–55 mm CL) and it is concluded that normal males become functionally mature over this range. Gonosomatic indices typical of large males were generally attained at body weights exceeding 140 g (~65 mm CL), indicating that maximum spermatophore production may not have occurred until individuals were considerably larger than the size at which they first matured.

Individuals with three or four gonopores are not uncommon among Australian parastacids (Horwitz 1990; Johnson 1979) and are often functional males. *E. spinifer* with aberrant gonopores, from the Loddon River, displayed charactersitics typical of males; furthermore, Honan and Mitchell (1995a) found that frequencies of aberrant gonopore configurations varied widely between *E. bispinosus* populations.

Analyses of Loddon River males, collected during the mating season indicate the presence of a second group of 'precocious' functional males (Fig. 7). Gonosomatic indices of precocious males were considerably greater than those of normal males; their vasa deferentia were extremely large (relative to size of animal) and filled with spermatophore material. Precocious males were functionally mature at a size considerably below that of the smallest normal male. Apart from the highly inflated genital papillae, precocious males retained the appearance of small *E. spinifer* of both sexes, showing no external differences either in body proportions or development of spines.

Multiple recapture records (Table 3) indicated that the highly inflated condition of genital papillae was fixed once it had been attained; nor did immature normal males assume the precocious condition at carapace lengths greater than 20 mm, so above this size male *E. spinifer* were dimorphic. They were in either the fixed, precociously mature condition, or were immature, attaining maturity at 45 mm CL or above.

Increases in relative abundance of males (10–20 mm CL) with highly inflated genital papillae suggested that immature normal males may have assumed the precocious condition over this size range. Only a small number of individuals of this size were captured more than once during the study, but the papillae of one are known to have changed from the uninflated to the highly inflated condition. It should also be emphasised that the smallest precocious male captured had a carapace length of 12.0 mm and was among the smallest individuals recorded. It is possible that some males may be precociously mature at smaller sizes.

Dimorphism in the size of males has been recorded for other decapods. In dense populations of the freshwater prawn (*Macrobrachium rosenbergii*), differential growth patterns have been detected and the presence of very small sexually mature individuals has been demonstrated (Barki et al. 1991a,b; Karplus et al. 1991). The only report of male dimorphism in a parastacid is a general comment by Morgan (1997), about small males (with the features of the precocious group) being present in a number of *E. spinifer* populations.

Observations of captive specimens indicated that precocious males were capable of mating with mature females, in the absence of other males (Turvey 1980); however, the contribution of precocious males to successful mating in the Loddon River population is not known. The possible significance of these two male forms for *E. spinifer* is discussed

in population studies (Turvey and Merrick 1997a), which consider sex ratios and overall size structure, relative abundances of both types of functional male as well as recruitment and origins of the precocious group.

Spermatophores, Fecundity and Early Development

E. spinifer spermatophore structure is similar to that described for another local parastacid *(Cherax destructor)* by Johnson (1979). Mason (1970) considered that sperm were released when the spermatophore dissolved during spawning in the astacid *Pacifastacus trowbridgii*, but the mechanism of sperm release for fertilisation in *E. spinifer* is unknown.

As other freshwater crayfishes do, *E. spinifer* produces large yolky eggs which hatch at a late stage of development. *E. spinifer* eggs were similar in shape and size to those of other parastacids (Hopkins 1967; Johnson 1979; Morrissy 1970; Ryder 1972; Shipway 1951a); they were also attached to the pleopods in the same way. An approximately linear increase with carapace length in the number of eggs carried by females has also been described for other parastacid species (Hopkins 1967: Johnson 1979; Morrissy 1970); recorded fecundities are similar to ranges reported for other *Euastacus* (Table 1).

Yolk colour in the eggs of several other parastacids has been reported to change during development (Hopkins 1967; Johnson 1979; Ryder 1972); however, this does not occur in *E. spinifer*, except for a slight darkening.

The early embryonic development as well as larval attachment, morphology and number of juvenile stages after hatching are typical of Australasian parastacids (Hamr 1992; Hopkins 1967; Johnson 1979; Ryder 1972; Shipway 1951a; Suter 1977). The terminal teeth of the chelae and antennal scale spines of Stage 1 and 2 juveniles may have been similar to the 'hooks' described for other parastacids (Clark 1937; Hopkins 1967; Suter 1977), but were not used for attachment in *E. spinifer.*

Development of the offspring on individual females was synchronous to within a few days, up to and including the departure of juveniles from the mother. Females collected in early December had released most larvae indicating that the release of Stage 3 juveniles commenced during late November. Lack of any *E. spinifer* carrying in mid or late December indicated that release of juveniles was normally completed in early December; a similar observation of developmental synchrony has been made for *Cherax destructor* (Johnson 1979).

Annual Reproductive Cycle

The interval between mating and the appearance of eggs indicates that spermatophores may have been carried for a month or longer, before spawning occurs. It is also clear that spermatophores are not completely removed at spawning and may be retained for another month or more. *E. spinifer* differs considerably from *Cherax destructor* (Johnson 1979), in which spawning usually commences within a few hours of mating, and spermatophores are present for no more than a few days. Although the durability of *E. spinifer* spermatophores would be advantageous in preventing loss or damage due to abrasion against rock substrata, the long period between mating and spawning cannot be explained.

Females of a number of *Euastacus* species carrying eggs in early stages of development have been observed during the month of May (Table 1). These observations include *E. spinifer* in the Hacking River, a separate drainage basin north-east of the study area (Turvey 1980). The data available suggest that *Euastacus* typically spawn in late autumn throughout much of the eastern coastal range of the genus; but *E. spinifer* in the Georges River near Campbelltown, in the adjacent catchment north-west of the study area, spawned during early September in both 1975 and 1978 (Turvey 1980).

Female *E. spinifer* incubated eggs for approximately 110–140 days over winter prior to hatching; similar, or longer, incubation periods have been reported for a number of *Euastacus* species (Table 1). From the field records it is estimated, in *E. spinifer*, that the total period between hatching and the departure of juveniles from the mother is between four and ten weeks; Honan and Mitchell (1995a) also reported a larval period of about four weeks in *E. bispinosus.*

Control of reproductive cycles by temperature and/or photoperiod has been proposed for other freshwater crayfishes (Aiken 1969; Merrick and Lambert 1991), but Sastry (1983) suggested that a complex of factors was involved. Honan and Mitchell (1995a) also contend that the breeding pattern is unlikely to be determined by a single environmental variable. Whilst events in the *E. spinifer* cycle, in the study area, were certainly closely associated with water temperatures, they could also be correlated with photoperiod or other environmental parameters showing annual periodicity. Honan and Mitchell (1995a) reported that *E. bispinosus* also mated when water temperatures were 15°C and falling; hatching occurred as temperatures exceeded 15°C and *E. bispinosus* also released juveniles at about 20°C.

Annual reproductive cycles of parastacids generally fall into two groups, those with a relatively short incubation period during the warmer months (summer brooders), and those with a long incubation period over winter (Honan and Mitchell 1995a). Some summer brooders only breed once while others may reproduce for several years (these include the commercial *Cherax* species). Whereas winter brooders may breed annually or biennially for a number of years (Honan and Mitchell 1995a). This study indicates that *E. spinifer* is a winter brooder.

Life Cycle Strategy

Broadly, the reproductive biology of *Euastacus spinifer* conforms to the pattern emerging for the genus. Details of anatomy, egg structure and attachment, fecundities, developmental stages and the timing of the annual breeding cycle are similar to data available for other *Euastacus* species. Small differences include the delay between mating and spawning and the fact that eggs do not change colour as they develop. The most unusual reproductive feature of the Loddon River population was the presence of small, precocious males.

The different life cycle traits exhibited by females or normal males and precocious *E. spinifer* males could be interpreted as separate strategies designed to cope with different sets of environmental conditions. The K-strategy (to maximise the ability to compete and avoid predation) seems to apply to females and normal males. Features associated with this selection include delayed reproduction, large maturity sizes, brood care and individual longevity (Stearns 1976). By contrast, the r-strategy or selection favours increased reproductive output in fluctuating environments; associated features include early reproduction and small size at maturity (Stearns 1976).

So r- selection apparently fits the available results for precocious males. But it is unclear how two sets of traits, selected for by different sets of environmental conditions, could develop and be maintained in one population especially when the previously documented stability of the Loddon River habitat is considered. Perhaps social interaction within the population contributes to the male dimorphism, as it is known to do in *Macrobrachium rosenbergii* (Karplus et al. 1991).

The level of incidence of precocious males in *Euastacus spinifer* populations is unknown and general conclusions about the species have to be based on normal males and females. In summary, the Sydney crayfish *(E. spinifer)* is slow to mature at a relatively large size, breeds annually in a synchronised cycle for each population, has low fecundity and limited recruitment. The success of this life cycle strategy depends on long-lived individuals, breeding repeatedly over a number of years and low natural mortality.

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REFERENCES

Aiken, D.E. (1969). Ovarian maturation and egg-laying in the crayfish *Orconectes virilis*: influence of temperature and photoperiod. *Canadian Journal of Zoology* **47**, 931–935.

Barki, A., Karplus, I. and Goren, M. (1991a). The agonistic behaviour of the three male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (Crustacea, Palaemonidae). *Behaviour* **116**, 252–277.

Barki, A., Karplus, I. and Goren, M. (1991b). Morphotype related dominance hierarchies in males of *Macrobrachium rosenbergii* (Crustacea, Palaemonidae). *Behaviour* **117**, 145–160.

Barnes, R.D. (1987). 'Invertebrate zoology. Fifth Edition'. (CBS College Publishing, Philadelphia).

Chittleborough, R.G. (1974). Western rock lobster reared to maturity. *Australian Journal of Marine and Freshwater Research* **25**, 221–225.

Clark, E. (1937). The life history of the Gippsland crayfish. *Australian Museum Magazine* **6**, 186–192.

Crow, E.L. (1956). Confidence intervals for a proportion. *Biometrika* **43**, 423–435.

Davis, C. (1936). Plant ecology of the Bulli district. Part I: Stratigraphy, physiography and climate, general distribution of plant communities and interpretation. *Proceedings of the Linnean Society of New South Wales* **61**, 285–297.

Farmer, A.S.D. (1974). Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). *Journal of Zoology (London)* **174**, 161–183.

Geddes, M. (1990). Crayfish. In 'The Murray' (Eds N. Mackay and D. Eastburn) pp. 302–307. (Murray-Darling Basin Commission, Canberra).

Geddes, M.C., Musgrove, R.J. and Campbell, N.J.H. (1993). The feasibility of re-establishing the River Murray crayfish, *Euastacus armatus*, in the lower River Murray. *Freshwater Crayfish* **9**, 368–379.

Hamr, P. (1990). Comparative reproductive biology of the Tasmanian freshwater crayfishes *Astacopsis gouldi* Clark, *Astacopsis franklinii,* Gray and *Parastacoides tasmanicus* Clark (Decapoda: Parastacidae). Ph. D. thesis, University of Tasmania, Hobart.

Hamr, P. (1992). Embryonic and postembryonic development in the Tasmanian freshwater crayfishes *Astacopsis gouldi, Astacopsis franklinii* and *Parastacoides tasmanicus tasmanicus* (Decapoda: Parastacidae). *Australian Journal of Marine and Freshwater Research* **43**, 861–878.

Hamr, P. (1995). The reproductive biology of the Tasmanian freshwater crayfish *Parastacoides t. tasmanicus. Freshwater Crayfish* **8**, 331–351.

Hamr, P. and Richardson, A. (1994). Life history of *Parastacoides tasmanicus tasmanicus* Clark, a burrowing freshwater crayfish from south-western Tasmania. *Australian Journal of Marine and Freshwater Research* **45**, 455–470.

Honan, J.A. and Mitchell, B.D. (1995a). Reproduction of *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and trends in the reproductive biology of freshwater crayfish. *Marine and Freshwater Research* **46** (2), 485–499.

Honan, J.A. and Mitchell, B.D. (1995b). Catch characteristics of the large freshwater crayfish, *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and implications for management. *Freshwater Crayfish* **10**, 57–69.

Honan, J.A. and Mitchell, B.D. (1995c). Growth of the large freshwater crayfish, *Euastacus bispinosus* (Decapoda: Parastacidae). *Freshwater Crayfish* **10**, 118–131.

Hopkins, C.L. (1967). Breeding in the freshwater crayfish *Paranephrops planifrons*. White. *New Zealand Journal of Marine and Freshwater Research* **1**, 51–58.

Horwitz, P. (1990). The conservation status of Australian freshwater crustacea. *Australian National Parks and Wildlife Service Report Series* (14), 1–121.

Humason, G.L. (1972). 'Animal tissue techniques. Third Edition'. (W.H. Freeman & Co., San Francisco).

Johnson, H.T. (1979). Reproduction, development and breeding activity in the freshwater crayfish *Cherax destructor* Clark. M. Sc. thesis, University of Sydney.

Jones, D.S. and Morgan, G.J. (1994). 'A field guide to crustaceans of Australian waters'. (Reed, Chatswood).

Karplus, I., Barki, A., Israel, Y. and Cohen, S. (1991). Social control of growth in *Macrobrachium rosenbergii.* II. The "leapfrog" growth pattern. *Aquaculture* **96**, 353–365.

Lake, P.S. and Newcombe, K.J. (1975). Observations on the ecology of the crayfish *Parastacoides tasmanicus* (Decapoda; Parastacidae) from south-western Tasmania. *Australian Zoologist* **18**, 197–214.

Lowery, R.S. (1988). Growth, moulting and reproduction. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 83–113. (Croom Helm Ltd., London).

Mason, J.C. (1970). Egg-laying in the Western North American crayfish, *Pacifastacus trowbridgii* (Stimpson) (Decapoda, Astacidae). *Crustaceana* **19**, 37–44.
Merrick J.R. (1993). 'Freshwater crayfishes of New South Wales'. (Linnean Society of New South Wales, Sydney).
Merrick, J.R. (1995). Diversity, distribution and conservation of freshwater crayfishes in the eastern highlands of New South Wales. *Proceedings of the Linnean Society of New South Wales* **115**, 247–258.
Merrick, J.R. and Lambert, C.N. (1991). 'The yabby, marron and red claw. Production and marketing'. (J.R. Merrick Publications, Sydney).
Morgan, G.J. (1986). Freshwater crayfish of the genus *Euastacus* (Decapoda, Parastacidae) from Victoria. *Memoirs of the Museum of Victoria* **47**, 1–57.
Morgan, G.J. (1988). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda, Parastacidae) from Queensland. *Memoirs of the Museum of Victoria* **49**, 1–49.
Morgan, G.J. (1997). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from New South Wales, with a key to all species of the genus. *Records of the Australian Museum, Supplement* (23), 1–110.
Morrissy, N.M. (1970). Spawning of marron, *Cherax tenuimanus* (Smith) (Decapoda: Parastacidae) in Western Australia. *Fisheries Research Bulletin of Western Australia* **10**, 1–23.
Morrissy, N.M. (1975). Spawning variation and its relationship to growth rate and density in the marron, *Cherax tenuimanus* (Smith). *Fisheries Research Bulletin of Western Australia* **16**, 5–32.
Riek, E.F. (1969). The Australian freshwater crayfish (Crustacea: Decapoda: Parastacidae), with descriptions of new species. *Australian Journal of Zoology* **17**, 855–918.
Riek, E.F. (1972). The phylogeny of the Parastacidae (Crustacea: Astacoidea), and description of a new genus of Australian freshwater crayfishes. *Australian Journal of Zoology* **20**, 369–389.
Ryder, W.G.J. (1972). Some aspects of the biology of freshwater crayfish in the Sydney region. B.Sc. (Hons.) thesis, University of Sydney.
Sastry, A.N. (1983). Ecological aspects of reproduction. In 'The biology of Crustacea Vol. 8'. (Eds F.J. Vernberg and W.B. Vernberg) pp. 179–270. (Academic Press, New York).
Shipway, B. (1951a). The natural history of the marron and other freshwater crayfishes of south-western Australia. Part 1. *Western Australian Naturalist* **3** (1), 7–12.
Shipway, B. (1951b). The natural history of the marron and other freshwater crayfishes of south-western Australia. Part 2. *Western Australian Naturalist* **3** (2), 27–34.
Snedecor, G.W. and Cochran. W.G. (1967). 'Statistical methods'. (Iowa State University Press, Ames, Iowa).
Stearns, S.C. (1976). Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**, 3–47.
Suter, P.J. (1977). The biology of two species of *Engaeus* (Decapoda: Parastacidae) in Tasmania. II. Life history and larval development, with particular reference to *E. cisternarius. Australian Journal of Marine and Freshwater Research* **28,** 85–93.
Thomas, W.J. (1970). The setae of *Austropotamobius pallipes* (Crustacea: Astacidae). *Journal of Zoology, (London)* **160**, 91–142.
Turvey, P. (1980). Aspects of the biology of the freshwater crayfish *Euastacus spinifer* (Heller) (Decapoda: Parastacidae). M.Sc. thesis, University of Sydney.
Turvey, P. and Merrick, J.R. (1997a). Population structure of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume*.
Turvey, P. and Merrick, J.R. (1997b). Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume*.
Turvey, P. and Merrick, J.R. (1997c). Growth with age in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume*.

Population Structure of the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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The structures of *Euastacus spinifer* populations in two pools of the Loddon River (south of Sydney, New South Wales) are described. No significant differences in catchabilities have been detected between the sexes, related to size classes, or between precocious (very small, sexually mature males) and normal males. Sex ratios in both populations show similar long-term trends, although short-term fluctuations are evident. Normal males comprise about 50% of populations up to 25–30mm CL, but above this size the male percentage declines well below 50%. Substantial rises and declines in frequencies of precocious males are noted, although few survive above 30mm CL; however, generally there is a surplus of males in the Loddon populations.

Frequency distributions are skewed to the smallest size classes, with pulses of recruitment detected in spring and summer; numbers of mature adults captured are low, females (3%) and males (6%) from Pool 3. It is suggested that the dominance of smaller size groups at Loddon River sites may be related to lowered predation, especially by eels.

Possible origins of the precocious males are discussed and two hypotheses advanced to explain their observed abundances relative to females; however, the available data do not permit a decision between almost total mortality over a confined size range (25–30mm CL) or recent selective recruitment of precocious males to the study populations.

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KEYWORDS: Population, recruitment, *Euastacus spinifer*, size classes, mark-recapture, frequency, dispersal, sex ratio.

INTRODUCTION

Although a number of studies have been published on stocked or intensively managed populations of commercial crayfishes (Huner 1978; Keller 1993; Morrissy 1979), relatively few detailed sampling programs have been completed on wild populations of non-commercial species. But several general findings are relevant here. Firstly, cray populations comprise a large proportion of the biomass in many aquatic systems; up to 30% in a stream ecosystem has been reported with standing crop estimates of 1345 kg/ha/year (Hogger 1988).

Secondly, the holding capacity of a habitat is more important in controlling population size than pressures such as predation. The two major factors determining holding capacity are the availability of suitable habitat (presence of suitable cover or hides) and the relative abundance of food (Hogger 1988). An impoundment may support a population many times larger than an adjacent lotic waterway and this population may have totally different characteristics, due to modified selection pressures (Hogger 1988). It has also been demonstrated that, although found in a variety of environments, even closely

related species have distinct flow and depth or substrate preferences (Eversole and Foltz 1993; Hogger 1988).

Thirdly, although males often dominate the largest size classes (Honan and Mitchell 1995a), long-lived species have higher mortality in early life stages when growth is most rapid (Momot and Hauta 1995). Finally, maturing males may regulate the growth and mortality rates in other individuals, so restricting the recruitment of juveniles (Momot 1993).

Population studies have been done on a few species in other Australian genera (Hamr 1990; Hamr and Richardson 1994) but, with the exception of recent studies on three Victorian species nothing has been published on *Euastacus*. Barker (1992) reported preliminary surveys of *Euastacus armatus, E. bispinosus* and *E. kershawi*, while Honan and Mitchell (1995a,b) focused more detailed investigations on *E. bispinosus*.

Catchability, Sex Ratios and Population Density.

Catchability varies due to a number of factors. Aside from trap design and density, individual differences in mobility (related to sex or size), behaviour (related to moult or reproductive phase) or distribution (related to preferred habitat and food resources) influence catches (Hogger 1988).

In *E. bispinosus* catchability varied seasonally. This species exhibited most activity in winter, with mature females dominating catches during the winter brooding season (May - November). In summer catch rates were low and male juveniles dominated the samples (Honan and Mitchell 1995a).

Variations in sex ratios with size are widespread among crustaceans, although apart from well-documented instances of sequential hermaphroditism, the origins of these variations are generally unknown (Wenner 1972). But recently social control of growth, particularly inhibition of growth in small individuals, has been demonstrated in another decapod (Karplus et al. 1991, 1992). For most freshwater crays the observed sex ratio changes during the year. In the breeding season adult males are usually caught more frequently, but at other times the ratio reverts to 1:1 (Honan and Mitchell 1995a).

Although previously not reported in parastacids, a separate sub-group of very small but sexually mature males has been detected in some *E. spinifer* populations (Morgan 1997; Turvey and Merrick 1997a). These individuals, characterised by highly inflated genital papillae and high gonosomatic indices, have been designated precocious males; sizes at maturity of female, normal male and precocious male *E. spinifer* are documented in Turvey and Merrick (1997a).

Extreme fluctuations of crayfish numbers in local areas have been recorded and density is known to influence growth rates, reproductive capacity, age at maturity and life-span within a population (Hogger 1988). The density of the *E. bispinosus* population, at one site, was estimated to be one large (>85mm CL) individual for every 2–5m of bank, although many other smaller individuals were also present. The majority of these crays had a home range of less than 75m (Honan and Mitchell 1995a).

The objectives of this paper are: to infer relative abundances in populations of females as well as normal and precocious males of different sizes, from their abundances in catches (on the basis of equal average catchability); to document trends in the structures of cray populations in the study areas, particularly with respect to the occurrence of precocious males; to present two hypotheses to account for the observed abundances.

MATERIALS AND METHODS

Major features of the Loddon River site (lat. 34°17′S: long. 150°54′E) are documented in Turvey and Merrick (1997a), but more details of sampling techniques and marking methods follow. Sampling was conducted at approximately monthly intervals,

during the last quarter and new moon phases of the lunar cycle, when the moon was not visible in the night sky; netting commenced one or two hours after dark and continued for five hours. Net stations were permanently marked with pegs at regular intervals along the length of each pool (every 6m for Pool 3, every 5m for Pool 7). The number of nets deployed at each station was proportional to the width of the pool at that point; at each session nets were placed in the same positions, in a rectangular grid pattern.

The 40 nets set in Pool 3 (54m long, ~770m^2) and 22 nets in Pool 7 (40m long, ~320m^2) were hauled, checked and returned to original positions every 30 minutes. Captured specimens were immediately placed in wet hessian bags until relevant catch data (e.g. time, net station, carapace length (CL), sex, condition) were recorded prior to marking and/or release; all captives were returned to the part of the pool from which they came. Individuals were marked by removing distal portions of the abdominal pleura and tail fan using scissors or a leather punch; these marks were clearly visible after at least one moult (Fig. 1).

Average Catchability

Average catchabilities were estimated from monthly catches (Pools 3, 7) during the mark-recapture study. From mark-recapture records, individuals were considered available for capture during a particular period if they were captured on or before the first sampling, and on or after the last sampling of the period. Proportions of actual captures among total opportunities were used to estimate average catchabilities in selected sex and size groups. Estimates were determined separately for females and normal males in four carapace length classes from Pool 3, and two CL classes from Pool 7, for the periods November 1977-February 1978 and May-August 1978 (Table 1); results for each period and pool were analysed separately.

Initially, average catchabilities of normal males and females within each class were tested for significant differences using chi-squared values calculated from contingency tables; the difference between overall catchabilities (combined for size classes) of males and females was similarly tested. The relationship between catchabilities of males and females was tested for heterogeneity among size classes. An additional comparison between the catchabilities of large males and females (75–100mm CL) was also conducted for the period February-May 1978.

Average catchabilities were recalculated for the combined data (normal males, females) in each size class where, for a particular period and location, there were no significant results in the preceding analysis. Combined average catchabilities of normal males and females were tested for heterogeneity with respect to size class, separately for each period and location, using a variance test for homogeneity of the binominal distribution (Snedecor and Cochran 1967). Average catchabilities of large females (75–100mm CL) from Pool 3 were also included in this analysis. When this overall test indicated significant differences among catchabilities in different size classes, the class with the most obviously different value was removed and the test recalculated.

An attempt was also made to compare catchabilities of precocious and normal immature males; this test was confined to individuals of 20–25mm CL. Data for three sampling periods (12 months, July 1977–June 1978) were combined. To eliminate bias, random samples of normal males were selected so that ratios of normal to precocious males were fixed for each location. Combined data were then used to test for significant differences between precocious and normal males for each of the two locations, using 2 x 2 contingency tables.

Sex Ratios

Catches were initially analysed for changes in relative abundances of females and males of different sizes over the duration of the mark-recapture study. Both sexes were allocated to five length classes (20–30mm, 30–40mm, 40–50mm, 50–70mm, 70–100mm CL);

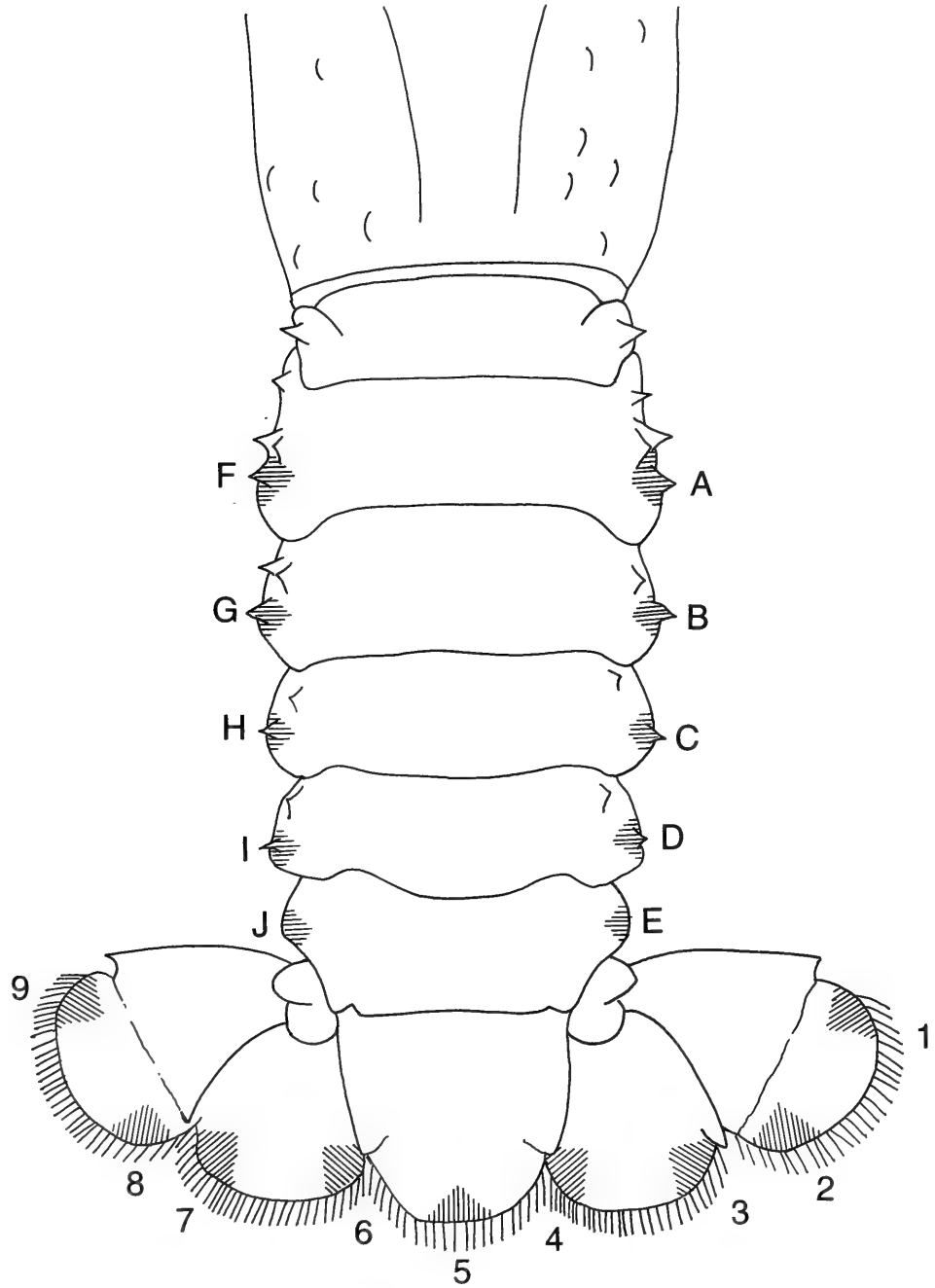

Figure 1. Dorsal view of an *E. spinifer* abdomen with uropods extended. The identification for each individual consisted of a single pleural mark combined with up to four tail fan markings; shaded areas denote the sections removed (e.g. A 13 to I 4679).

separate distributions of percentage of catch with month were constructed for each sex and size class at each location. Differences between the distributions were tested for significance using a Kolmogorov-Smirnov test (Siegel 1956).

To investigate fluctuations, over time, in numbers of normal and precocious males the two groups were allocated to four classes (<20mm, 20–25mm, 25–30mm, 30–35mm CL) at both locations. Total catches of males less than 35mm (CL) were tabulated for the periods May-August 1977, September-December 1977, January-April 1978, May-August 1978, and September-December 1978. The percentage of each catch attributable to precocious or normal males in each class was calculated and percentages plotted as frequency histograms for each period (Fig. 3).

Average sex ratios of crayfish populations in Pools 3 and 7 were determined for the total study period, and interpreted on the basis of catchabilities and variation over time in relative abundances of females, normal and precocious males. The total catch from each location was divided into five classes (from 10mm CL). Percentage frequencies of normal and precocious males (in the total catch for each size class) were calculated, and relationships between frequencies and carapace lengths constructed for both locations. Confidence limits (95%) for mean frequencies with repeated sampling were also plotted, based on tables by Crow (1956) for small sample sizes (≤30), or on a normal approximation for samples of larger size (Snedecor and Cochran 1967). This procedure was also applied to combined catches (June, July, August, and November 1976 from Pool 7) as well as several catches from two other pools.

Size Frequency Classes

Monthly catches from the mark-recapture study were combined for the periods May-August 1977, September-December 1977, January-April 1978, May-August 1978, and September-December 1978, for each sampling location. Size (CL) frequency histograms were constructed for crays in each combined catch (Fig. 6) and changes, over time, in the size structure of catches were noted for both populations.

RESULTS

Average Catchability

There were no significant differences ($p > 0.05$) in the average catchabilities of males or females for the periods of testing, either within any size class, or when classes were combined to provide overall estimates (Table 1); furthermore, there were no instances of significant heterogeneity ($p > 0.05$) among size classes in the relationships between catchabilities of males and females.

When average catchabilities were combined for each sex and tested for homogeneity with respect to size, there was significant heterogeneity for both periods in Pool 3 (Table 2). Removal of the 75–100mm size class from the November 1977–February 1978 series rendered the catchabilities of remaining classes homogeneous ($p > 0.25$); similar results were obtained for May-August 1978 by removing the 30–40 mm class ($p > 0.50$). Catchabilities of each of these classes were aberrant in only one of the two periods. There was no significant heterogeneity ($p > 0.05$) with respect to size in the catchabilities of crays from Pool 7 for either period.

By contrast, there was an apparent difference between observed and expected catches of precocious and normal males from Pool 3 for the period November 1977–February 1978 (Table 3). But separate testing, using a 2 x 2 contingency table, did not confirm this (χ^2 corrected for continuity = 1.42, d.f. = 1, $0.25 > p > 0.1$); the observed and expected catches were extremely close for all other periods, for both locations. On

this basis, the data for the three periods were combined for each location, and no significant differences were detected between the catchabilities of precocious and normal males.

TABLE 1

Comparisons of average catchabilities of female and normal male *E. spinifer*.

Location & Period	Size Class (mm)	Female *P	Female N	Male P	Male N	χ^2 (1 d.f.)	p
Pool 3:	20–30	0.48	104	0.50	104	0.08	>0.25
Nov. 1977–Feb. 1978	30–40	0.31	32	0.42	36	0.79	>0.25
	40–50	0.55	40	0.34	44	3.70	>0.05
	50–75	0.39	36	0.47	32	0.44	>0.50
	Overall	0.45	212	0.45	216	0.01	>0.90
	Heterogeneity $\chi^2 = 5.02$ (3 d.f.)						>0.10
Pool 3:	20–30	0.21	52	0.15	40	0.57	>0.25
May 1978–Aug. 1978	30–40	0.41	132	0.37	112	0.47	>0.25
	40–50	0.18	28	0.13	16	0.22	>0.50
	50–75	0.29	24	0.22	32	0.39	>0.50
	Overall	0.33	236	0.28	200	1.10	>0.25
	Heterogeneity $\chi^2 = 0.55$ (3 d.f.)						>0.90
Pool 7:	20–40	0.18	44	0.14	56	0.28	>0.50
Nov. 1977–Feb. 1978	40–70	0.18	76	0.25	16	0.36	>0.50
	Overall	0.18	120	0.17	72	0.09	>0.50
	Heterogeneity $\chi^2 = 0.56$ (1 d.f.)						>0.25
Pool 7:	20–40	0.61	64	0.57	44	0.18	>0.50
May 1978–Aug. 1978	40–70	0.41	68	0.63	16	2.38	>0.10
	Overall	0.51	132	0.58	60	0.95	>0.25
	Heterogeneity $\chi^2 = 1.61$ (1 d.f.)						>0.10
Pool 3:	75–100	0.14	36	0.08	12	0.25	>0.50
Feb. 1978–May 1978							

*P is the proportion of captures among the total number of opportunities for capture (N) of crayfishes known to be present during the given period.

Sex Ratios

Female and male *E. spinifer* in both locations showed similar overall trends in capture frequency during the mark-recapture study (Fig. 2), although short-term differences were evident. The only evidence of a change through time in the relative capture frequencies of males and females was for crays in the 20–30mm CL class in Pool 7 (Table 4). In this instance the difference between males and females just failed to reach the 5% level of significance (D = 0.168, critical 5% value of D = 0.171), suggesting a trend towards an increasing number of males relative to females in the later part of the study.

Size frequency distributions of precocious and normal males (Fig. 3) indicated that, in Pool 7, there was a substantial increase in precocious male numbers relative to normal

males in the 20–25mm class, during the period May 1977–April 1978. This increase was concomitant with rises in relative numbers of smaller, normal males, and was followed by a sharp increase in relative numbers of precocious males in the 25–30mm class from May-August 1978. Relative numbers of both groups were approximately equal, during September-December 1978, at all sizes except the 30–35mm class from which precocious males were absent. Relative numbers of precocious males also increased in Pool 3 over the same period. Normal males were initially more abundant in the 20–25mm and 25–30mm classes, while approximately equal numbers of precocious and normal males were present in the 30–35mm group. By the end of the mark-recapture study numbers of precocious and normal males were approximately equal, except in the 30–35mm class in which normal males were more abundant. Relative abundances of precocious and normal males also differed considerably between periods twelve months apart at both locations.

TABLE 2

Comparisons of average catchabilities of *E. spinifer* in different size classes — combined for females and normal males.

Location	Size Class	PERIOD Nov 1977–Feb 1978 *P	N	May 1978–Aug 1978 P	N
Pool 3	20–30	0.49	208	0.18	92
	30–40	0.37	68	0.39	244
	40–50	0.44	84	0.16	44
	50–75	0.43	68	0.25	56
	†75–100	0.18	28	0.19	36
	Overall	0.43	456	0.30	472
		Overall Homogeneity $\ddagger\chi^2_c$ =11.4, d.f. = 4		Overall Homogeneity χ^2 = 21.9, d.f. = 4	
		0.025> p >0.01		p <0.005	
		Minus 75–100		Minus 30–40	
	Adjusted	0.45	428	0.20	228
		Remaining Homogeneity χ^2_c = 3.4, d.f. = 3		Remaining Homogeneity χ^2 = 1.5, d.f. = 3	
		p >0.25		p >0.50	
Pool 7	20–40	0.16	100	0.59	108
	40–70	0.20	92	0.45	84
	Overall	0.18	192	0.53	192
		Overall Homogeneity χ^2_c = 0.21, d.f. = 1		Overall Homogeneity χ^2 = 3.19, d.f. = 1	
		p > 0.50		0.1 > p > 0.05	

*P is the proportion of captures among the total number of opportunities for capture (N) of crays known to be present during the given period.

†Females only.

‡Chi-squared corrected for continuity.

TABLE 3

Comparisons of average catchabilities of precocious and normal male *E. spinifer* with carapace lengths of 20–25 mm.

Male Type	SEPARATE PERIODS Jul–Oct 1977			Nov 1977–Feb 1978			Mar–June 1978		
	*C	E	N	C	E	N	C	E	N
				Location — Pool 3					
Precocious	1	1	4	7	4.8	12	3	2.5	8
Normal	3	3	12	12	14.2	36	7	7.5	24
				Location — Pool 7					
Precocious	6	5	16	3	4	16	1	1.5	8
Normal	4	5	16	5	4	16	2	1.5	8

Location	COMBINED PERIODS Precocious		Normal		χ^2_e	p
	P	N	P	N	(1d.f.).	
Pool 3	0.46	24	0.31	72	1.23	>0.25
Pool 7	0.25	40	0.28	40	0	~1

* C is the observed number of captures among the total number of opportunities for capture (N) of crays known to be present during the given period. E is the expected value for C under the null hypothesis that there is no difference between the frequency of capture of precocious and normal males that are known to be present. As in previous tables, P = C/N.

TABLE 4

Summary of Kolmogorov-Smirnov Tests results comparing trends through time in the capture frequencies of male and female *E. spinifer*.

Size Class	Pool 3 F	M	D	p	Pool 7 F	M	D	p
20–30	259	224	11	>0.1	116	140	17	≈0.05
30–40	271	209	11	>0.1	136	67	12	>0.1
40–50	81	78	19	>0.1	24	24	17	>>0.05
50–70	48	74	23	>0.1	117	45	11	>0.1
70–100	28	28	39	>>0.05	17	17	24	>>0.05

F = total catch of females.
M = total catch of males.
D = maximum difference between the cumulative distributions of percent frequency of capture vs. month for males and females.
p = the probability of obtaining a difference equal to or greater than the observed difference D purely by chance, given that the two distributions were from the same population.

Abundances in catches of males, relative to females, varied among the different size classes in Pools 3 and 7 (Fig. 4). In Pool 3, approximately 50% of individuals less than 25mm CL were male, while the 50% occurrence of males extended to 25–30mm CL in Pool 7. At all locations except Pool 3 (Figs. 4 and 5) there was a trend for the percentage of males to remain below 50% among crays greater than 30mm CL. There was evidence of fluctuations (with CL) in percentages of males in these larger classes, but both cyclic percentage changes and irregular variations were within limits of error inherent with the small samples of many size classes.

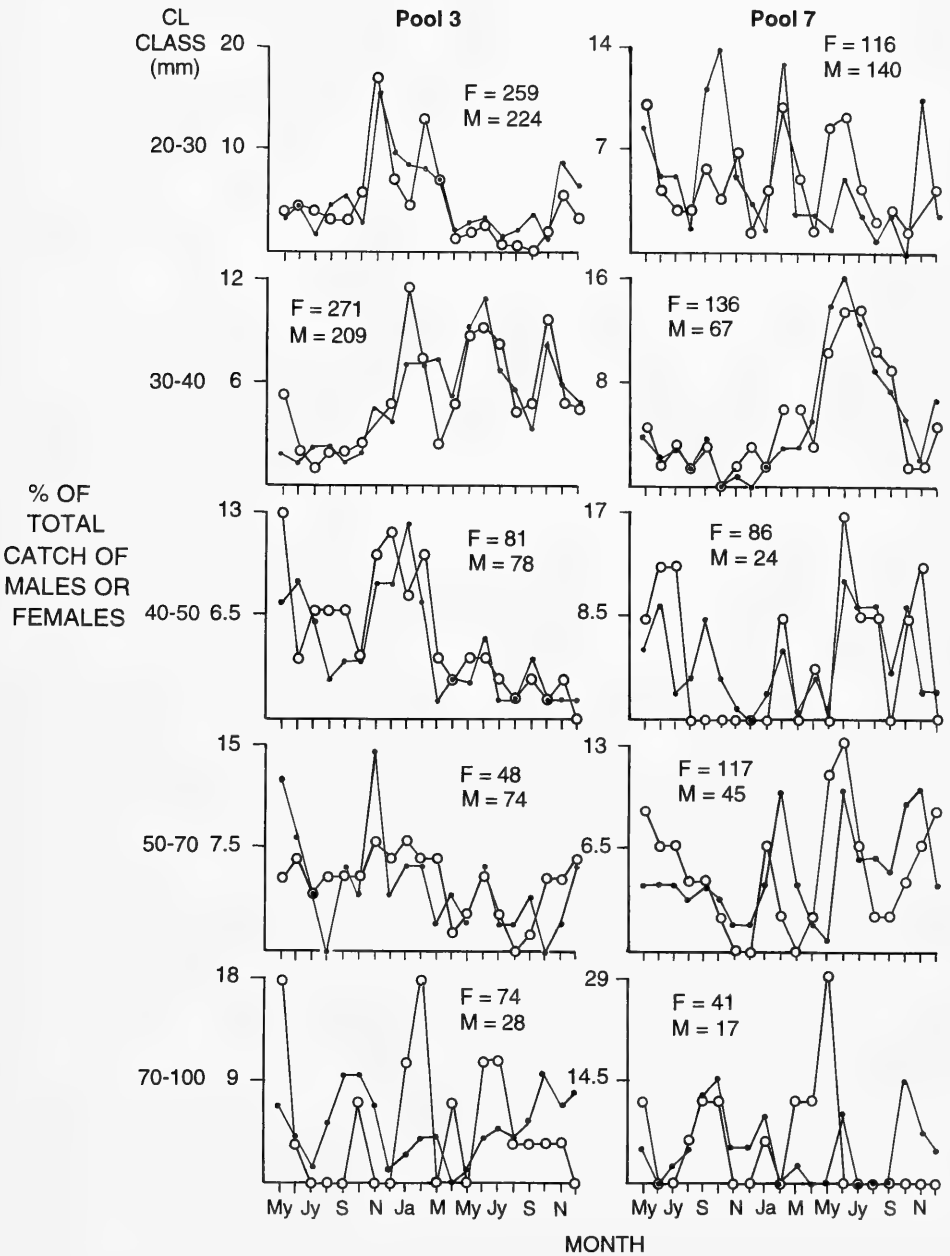

Figure 2. Changes over the mark-recapture study in capture frequencies of *E. spinifer* from two Loddon River pools. Total catches of females and males are included in each graph. Key to symbols: ● = females; ○ = males; ⊙ = both sexes combined.

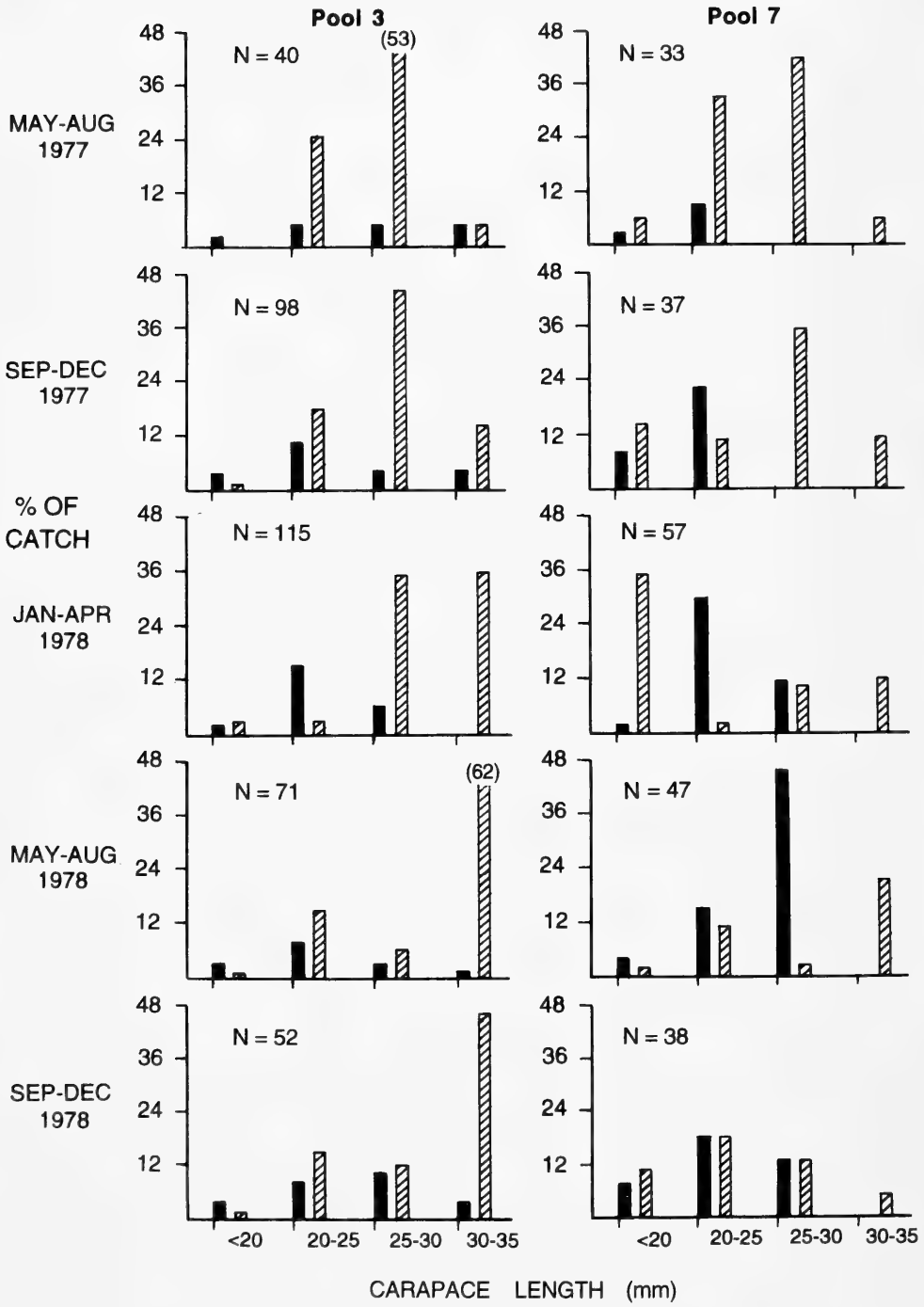

Figure 3. Changes over the mark-recapture study in relative capture frequencies of precocious and normal male *E. spinifer* in the smaller size classes. The total catch of males in all of the included size classes (N) is listed in each graph. Key to symbols: ■ = precocious males; ▨ = normal males.

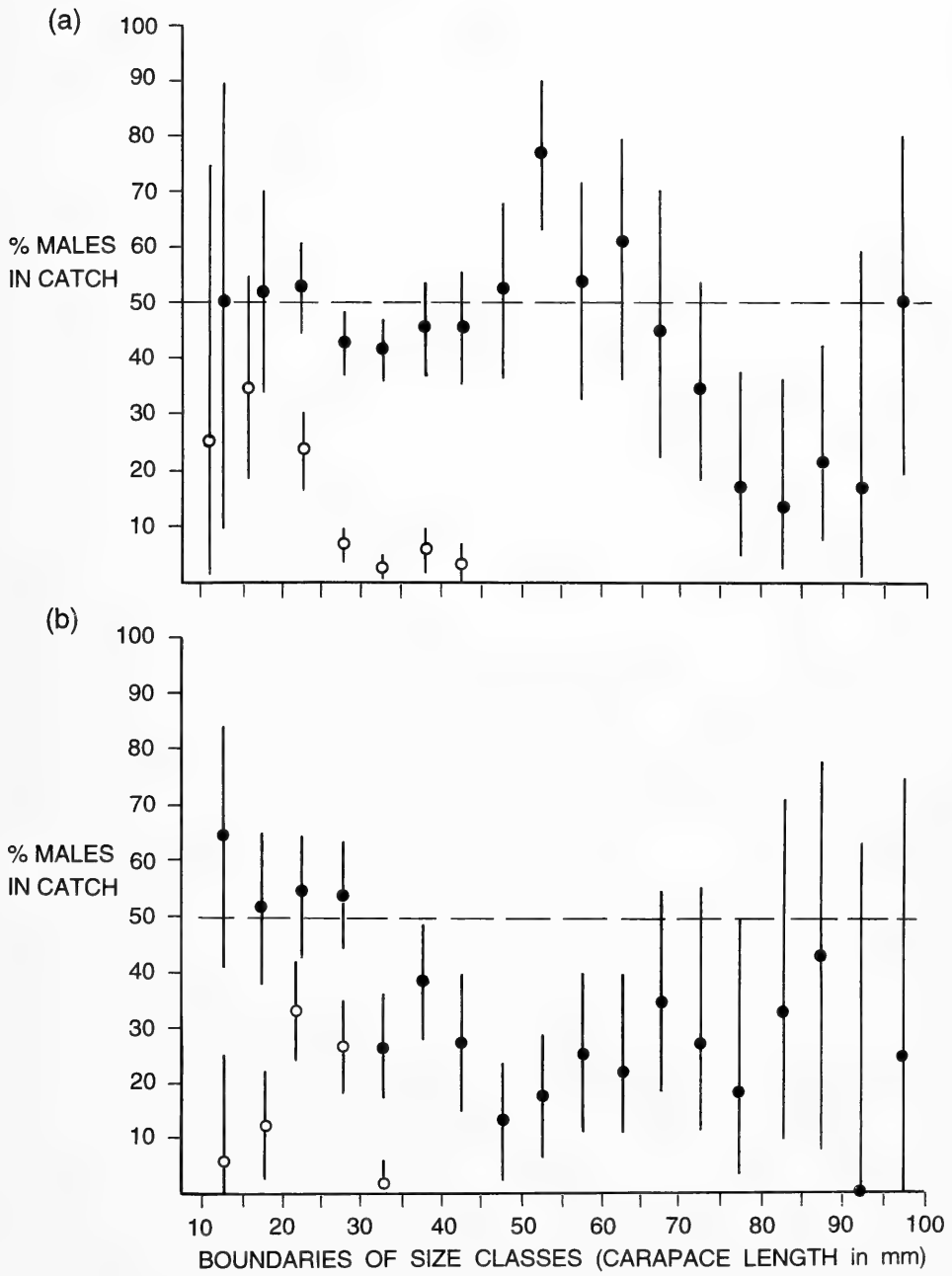

Figure 4. Changes with carapace length in the frequency of capture of male *E. spinifer* relative to females, averaged over the mark-recapture study: (a) Pool 3; (b) Pool 7. Key to symbols: ● = normal males; ○ = precocious males; | = 95% confidence limits for the mean percentage on repeated sampling.

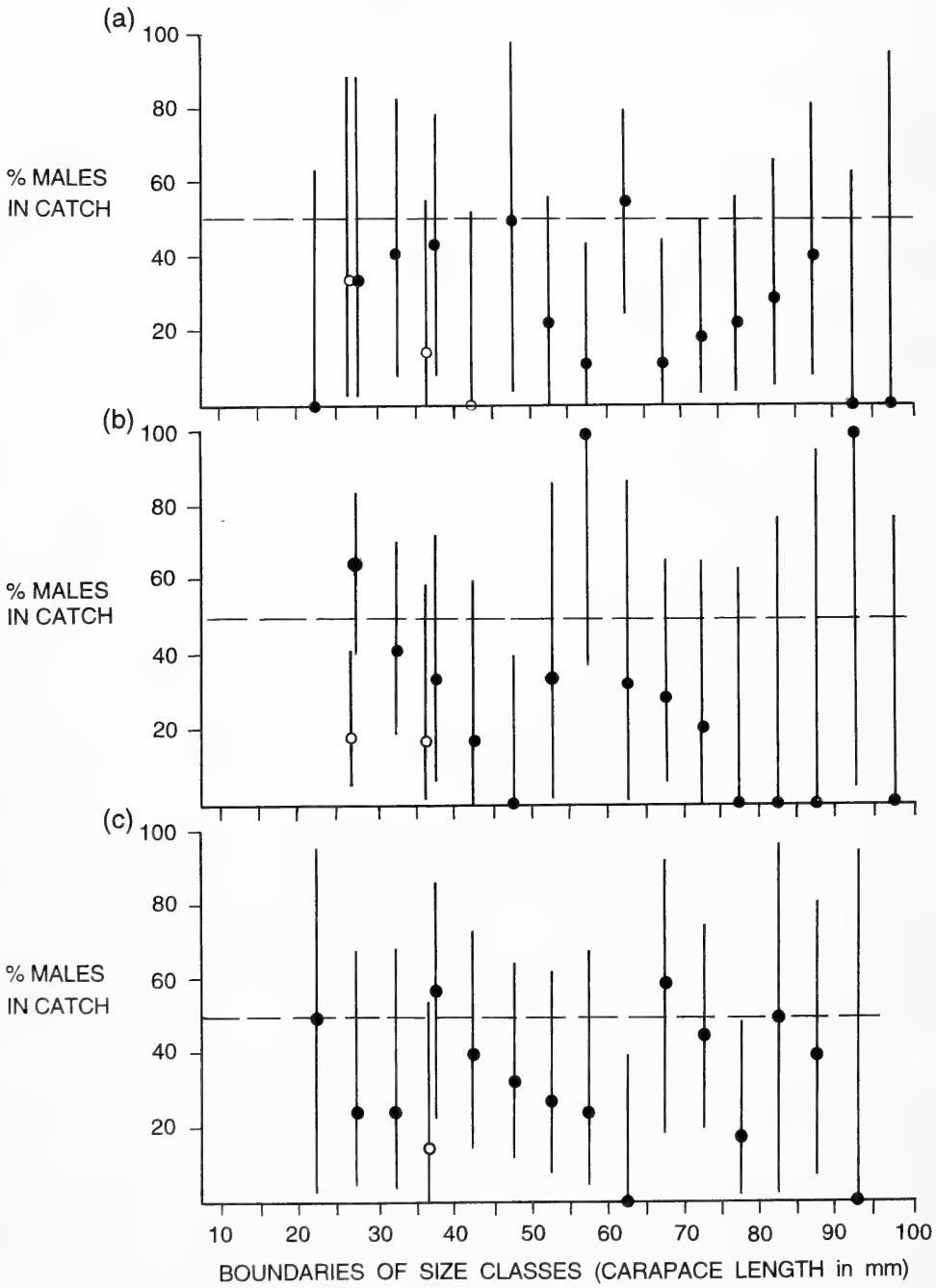

Figure 5. Changes with carapace length in the frequency of capture of male *E. spinifer* relative to females for catches taken in three Loddon River pools: (a) Pool 7, catches during June, July, August and November 1976; (b) Pool 6, catches during December 1977; (c) Pool 8, catches during January and June 1978. Key to symbols: ● = normal males; ❍ = precocious males; | = 95% confidence limits for the mean percentage on repeated sampling.

In Pool 3 (Fig. 4a), the percentage of males was significantly less than 50% ($p < 0.05$) for individuals in both 25–30mm and 30–35mm CL classes. This reduced incidence was followed by an increase to a level significantly greater than 50% ($p < 0.05$) for the 50–55mm class, above this size male occurrence declined to a level well below 50%. In this pool (Fig. 4a), precocious males comprised approximately 25% of catches of small individuals (<25mm CL), although these percentages may have been subject to considerable sampling error. Frequencies of precocious males declined rapidly at sizes above 25mm CL; they remained at a low level up into the 40–45mm class, but above that they were absent.

In Pool 7 (Fig. 4b) there was a significant frequency increase in precocious males from the 15–20mm to the 20–25mm class ($p < 0.05$), while they were captured with equal frequency in the 20–25mm and 25–30mm size classes. The abundance of precocious males declined to a low level from the 25–30mm to the 30–35mm class, above that size they were absent from catches. In both Pools 3 and 7 the decrease in overall abundance of males occurred over the same narrow CL range as the decline in precocious male abundance, although the size ranges at which these events occurred were different for the two locations.

Size Frequency Classes

The frequency distributions of crays captured during the mark-recapture study were skewed towards the smaller size classes (Fig. 6) in both pools, although small individuals (<20mm CL) were only abundant in Pool 7 catches from January-April 1978. The relative capture frequency of the 20–30mm class increased substantially during the period September-December 1977; this size grouping constituted a modal group which progressed into the 30–40mm class by September-December 1978. There was evidence of a similar increase in relative numbers of the 20–30mm class from September-December 1978 in Pool 3, but not in Pool 7. Frequency distributions for May-August 1977 and September-December 1977, in Pool 3, were thus dominated by the 20–30mm class; the same periods one year later were dominated by the 30–40mm class. A similar dominance existed in the May-August catches from Pool 7, but there was no dominant class in September-December 1978 catches corresponding to the 20–30mm cohort of one year earlier.

Of the total number of different individuals captured in Pool 3 during the study, approximately 3% were mature females, 6% were normal mature males, and 9% were precocious males.

DISCUSSION

The sampling techniques were designed to maximise recapture frequency. Preliminary observations had indicated larger catches on moonless nights and nets were deployed at the highest possible densities. To minimise confounding influences, such as dominance behaviour and differential mobility, all captured individuals were retained until the completion of each sampling. Pools were selected for their degree of separation and on size that enabled the whole pool to be fished intensively over a single collection session.

Average Catchability

Overall catchabilities calculated for normal males and females, in Pools 3 and 7, indicated that the null hypothesis (no difference between catchabilities of sexes) should be accepted (at a low level of significance) for each period at each location. Available data provided no evidence of a difference in average catchabilities of males and females over 75mm CL; however, few values were available for males. The average catchability

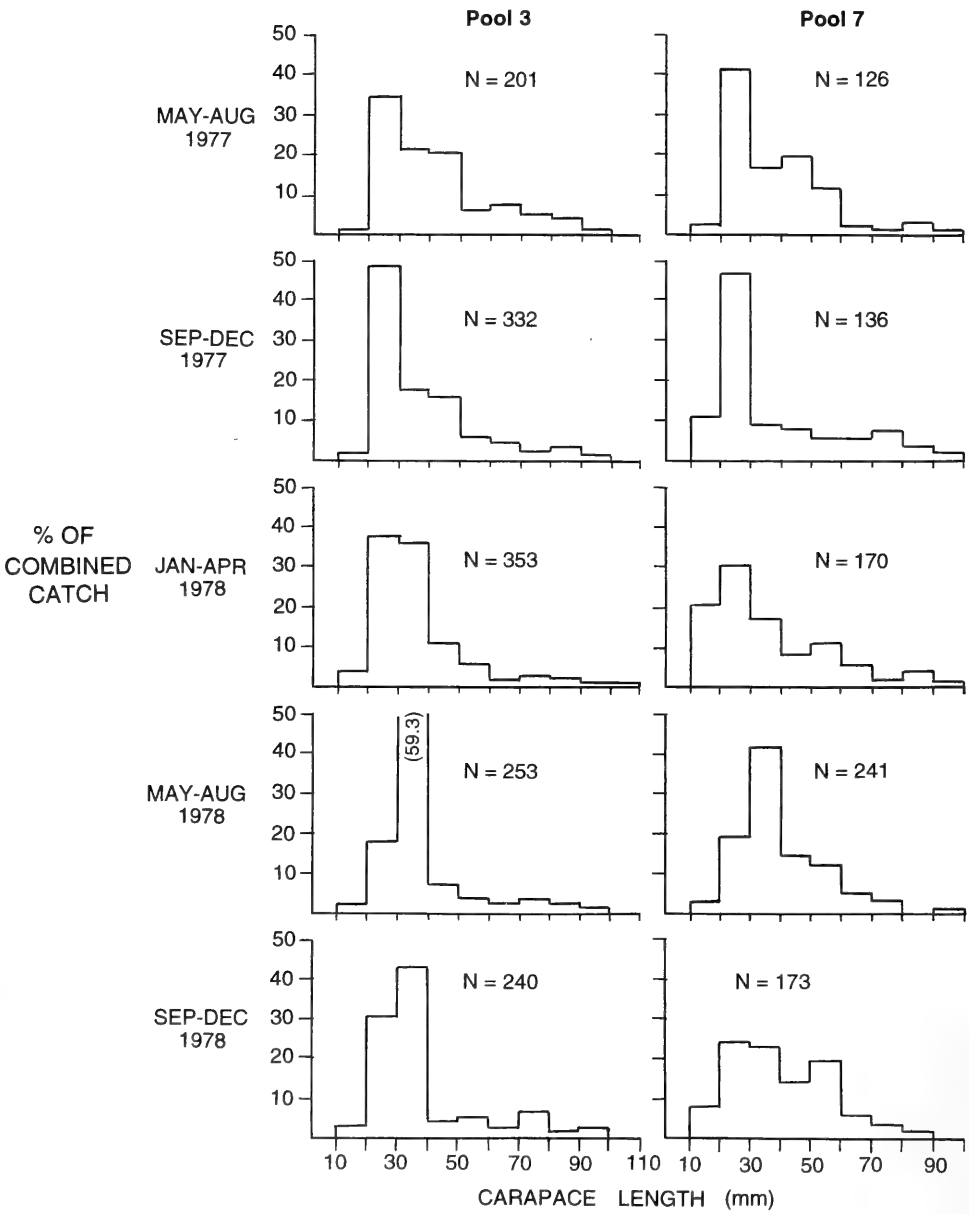

Figure 6. Size frequency distributions of *E. spinifer* captures taken over five periods during the mark-recapture study in Pools 3 and 7 (Loddon River). N = total number of captures for the period; percentage extending off graph is included in parentheses.

of these large females was also similar to that of both sexes in several smaller size classes, during the period May-August 1978. Taking these findings together there is no indication of any difference in catchability between large (>75mm CL) individuals and smaller size classes. The catchability comparison of precocious and normal juvenile males was restricted to a narrow size range, due to the virtual absence of multiple recapture records for precocious males of other carapace lengths. Data for the three sampling periods (July-October 1977; November 1977–February 1978: March-June 1978) were combined because precocious samples were insufficient to test for heterogeneity between periods. There was no evidence that catchability of precocious males differed from that of normal males of similar size when data were combined for 12 month periods. This finding, together with the similarity of actual and expected catches for most shorter sampling periods, suggests that catchabilities of precocious and normal males do not differ.

Extension of this conclusion to the entire *E. spinifer* population throughout the study area cannot be definite; however, the results for most females and normal males for eight months of a year in two pools, precocious male data and the probability that large individuals conformed to patterns for smaller size groups all support the concept of equal average catchabilities within size classes.

Sex Ratios

As capture frequencies for males and females, within different size classes, did not differ over the duration of the study (Fig. 2 and Table 4) relative abundances were estimated by calculating the percentage frequency of males in the total catch (for each size class) over the entire period. These estimations indicated that, in Pool 7, the percentage of males was well below 50% in the range 30–100mm CL (Fig. 4b). Similar results were obtained for Pool 7 catches during the previous year (1976), and for catches from nearby pools in 1977 and 1978 (Figs 5b and 5c).

While there was an increase in the percentages of males of intermediate carapace lengths in Pool 3, the trend towards percentages below 50% was apparent for both large and smaller individuals (Fig. 4a). A scarcity of males over 30mm CL may therefore be typical of the Loddon River population during the study period; while the abundance of intermediate-sized males in Pool 3 may be aberrant. This contrasts with similar abundances of the sexes in smaller size classes in both Pool 3 and Pool 7 (Fig. 4).

Precocious males were also abundant in the small size classes, and the CL at which relative abundance of males decreased coincided exactly with the size range at which precocious males virtually disappeared from catches. Deviations from the 1:1 sex ratio among small *E. spinifer*, as well as the scarcity of large males, were considered due to the respective presence and absence of precocious males. Although smaller size classes were poorly represented in catches from other pools (Figs 5b and 5c) and precocious males were occasionally included in them, the long-term numerical contribution of the precocious group to *E. spinifer* populations remains unclear.

Skewed sex ratios in crayfishes are not unusual and Hogger (1988) reported that in some commercial catches only about 7% were females. That low proportion was considered due to seasonal migrations (from littoral to deep areas) but on the available data no estimates of natural mortality, emigration or recruitment in *E. spinifer* populations are possible.

Size Frequency Classes

Although catches in both Pool 3 and Pool 7 included high percentages of small individuals (Fig. 6), the size composition of catches was not stable over the period. Some of this variability was attributed to differences in average catchabilities at different carapace lengths. For example, the high percentage of the 30–40mm class from May-August 1978 (Fig. 6) would have been partly due to a higher catchability (~2x) that of other sizes

at this time (Table 2). However, as catchabilities were similar over most classes in each period and differences were not sustained in both periods, it is suggested that major catch composition changes are indicative of real trends in population size structure.

This skew towards smaller classes in Loddon River populations contrasts with *E. spinifer* catches taken in nearby catchments using the same techniques. Catches from the Georges River and Hacking River consisted entirely of larger individuals (50–110mm CL). Long-finned eels (*Anguilla reinhardtii*) were frequently observed at both these sites, while only two individual eels were sighted in the Loddon River over the entire study period. It is suggested that the high relative abundance of small crays at the study site may have reflected a low level of eel predation. Higher percentages of large adults have also been reported in a number of populations of three Victorian *Euastacus* (Barker 1992; Honan and Mitchell 1995a), but these values may reflect differing levels of harvesting or selection due to particular trapping techniques.

Increases in the relative numbers of small individuals (20–30mm CL) in Pools 3 and 7 from September-December 1977 (Fig. 6) are taken to represent recruitment of previously smaller crays into this size class. The majority of these individuals had recently moulted at the commencement of growth after winter (Turvey and Merrick 1997b), but this recruitment was neither preceded by, nor simultaneous with, catches of similar numbers of smaller individuals. Individuals in the 20–30mm size class dominated both populations early in the study. This domination was maintained into the 30–40mm class at the end of the study in Pool 3, and until August 1978 in Pool 7. A further pulse of recruitment into the 20–30mm size class may have commenced from September-December 1978 in Pool 3, but there was no evidence of this in Pool 7.

Assuming that catch frequency distributions reflected population size structures, and accepting that precocious males were capable of mating with mature females (Turvey and Merrick 1997a), relative abundances of mature females, precocious and normal mature males were estimated in the intact population of Pool 3. These estimations were designed to indicate the potential contributions of the two types of males to reproductive output. The true percentage for precocious males was probably higher than the calculated value (9%), as these individuals matured at less than 20mm CL and crays of this size were less catchable. The values calculated indicate that: only ~10% were adults (3% mature ♀, 6% normal mature ♂); there was a surplus of males; precocious males may have contributed significantly to successful mating. Furthermore, the large residual percentage of pre-reproductive individuals would suggest a high potential for population growth (Miller 1994).

Origins of the Precocious Group

Sexes becoming functional at different sizes is not unusual among crustaceans but this situation, of a significant proportion of the population comprising a third reproductive (precocious) group, has not been recorded for Australian crayfishes before.

It should be noted that in many areas where *E. spinifer* live, large individuals are sparsely distributed with the streams consisting of small and widely separated pools connected by shallow or ephemeral zones. So there are several potential benefits of developing this condition as a reproductive strategy, in an area with very limited habitat for large individuals. Firstly, the restricted suitable areas could be fully utilised by mature females. With minimal competition for limited resources from males mortality would be lowered and reproductive output maximised. Secondly, precocious males could successfully colonise shallows minimising direct competition with females. Thirdly, an ample supply of functional males would be available for a relatively small number of mature females, maximising successful spawning frequency.

Precocious males may be the result of the kinds of social interaction and inhibition now documented for *Macrobrachium rosenbergii* (Karplus et al. 1991, 1992); however, like other suggestions, relating to selection for male dimorphism (Gadgil 1972) and ran-

dom mortality of large males in small local populations (Ghiselin 1974), the idea of social control of growth was not tested and further discussion is not possible. It is also possible that the precocious male condition is triggered by short-term variability in the physico-chemical environment, but this is inconsistent with the apparent long-term stability of the upper Loddon habitat.

The authors have developed two hypotheses to explain the observed trends in abundance of males to female *E. spinifer*, but before discussing these, two general findings should be considered. Firstly, the reproductive studies (Turvey and Merrick 1997a) indicated that precocious males did not revert to the normal condition; while the reverse was unlikely at carapace lengths exceeding 20mm it may have occurred at smaller sizes. Secondly, it is possible that the high percentages of intermediate-sized males in Pool 3 were due to a chance aggregation.

The first hypothesis is that the decrease, in male abundance with increasing CL, resulted from the failure of initially abundant precocious males to attain a larger size. This also assumes that the relative abundances of females, precocious males and normal males from Pools 3 and 7 (Fig. 4) were typical of previous generations of crays in the study area. For this hypothesis to be acceptable, it is necessary to invoke some factor preventing most precocious males from attaining a size over 25–30mm CL. A cessation of growth alone is unlikely as, without high mortality, it would have resulted in an accumulation of precocious males at ~30mm CL and this was not indicated by the data. Furthermore, there was some evidence that growth rates of precocious males were similar to those of other individuals (Turvey and Merrick 1997b). If this hypothesis holds, then precocious males must have sustained almost 100% mortality over the 25–30mm CL range; this suggestion is supported by the dramatic decline in relative abundance of precocious males of this size in Pool 7 between May-August 1978 and September-December 1978 (Fig. 3).

The second hypothesis is that the increased abundance of males in smaller size ranges was due to a recent influx of precocious males that had not had time to attain a larger size. This implies: that during previous generations females were consistently more abundant than males at all sizes; that equal abundances of males and females in smaller classes during the mark-recapture study were due to the recent inclusion of numerous precocious males, in addition to normal males and at the expense of females. This hypothesis is supported by the increase in abundance of precocious males during the study in Pool 7 (Fig. 3), in association with a possible decrease in abundance of small females (Table 4 and Fig. 2) and by a lesser increase in the relative abundance of precocious males in Pool 3 (Fig. 3).

On the available data, it is impossible to exclude either hypothesis; they are not mutually exclusive when applied to data collected over a relatively short period.

Whilst the life cycle strategy of *E. spinifer* appears to be based on slow-growing large adults breeding for many years (Turvey and Merrick 1997a), the development of the precocious condition could be part of an alternative population survival strategy. In the event of severe environmental disruption and significant mortality of large adults the precocious individuals, in combination with newly maturing females, would potentially enable population numbers to be increased more quickly than if recruitment was based solely on output from slowly maturing adults of both sexes.

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REFERENCES

Barker, J. (1992). The spiny freshwater crayfish monitoring program, 1990. *Fisheries Management Report* (44), 1–31. *Department of Conservation & Environment, Melbourne.*

Crow, E.L. (1956). Confidence intervals for a proportion. *Biometrika* **43**, 423–435.

Eversole, A.G. and Foltz, J.W. (1993). Habitat relationships of two crayfish species in a mountain stream. *Freshwater Crayfish* **9**, 300–310.

Gadgil, M. (1972). Male dimorphism as a consequence of sexual selection. *American Naturalist* **106**, 574–580.

Ghiselin, M.T. (1974). 'The economy of nature and the evolution of sex'. (University of California Press, Berkeley).

Hamr, P. (1990). Comparative reproductive biology of the Tasmanian freshwater crayfishes *Astacopsis gouldi* Clark, *Astacopsis franklinii,* Gray and *Parastacoides tasmanicus* Clark (Decapoda: Parastacidae). Ph.D. thesis, University of Tasmania.

Hamr, P. and Richardson, A. (1994). Life history of *Parastacoides tasmanicus tasmanicus* Clark, a burrowing freshwater crayfish from south-western Tasmania. *Australian Journal of Marine and Freshwater Research* **45**, 455–470.

Hogger, J.B. (1988). Ecology, population biology and behaviour. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 114–144. (Croom Helm Ltd., London).

Honan, J.A. and Mitchell, B.D. (1995a). Catch characteristics of the large freshwater crayfish, *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and implications for management. *Freshwater Crayfish* **10**, 57–69.

Honan, J.A. and Mitchell, B.D. (1995b). Growth of the large freshwater crayfish, *Euastacus bispinosus* (Decapoda: Parastacidae). *Freshwater Crayfish* **10**, 118–131.

Huner, J.V. (1978). Crawfish population dynamics as they affect production in several small, open crawfish ponds in Louisiana. *Proceedings of the World Mariculture Society* **9**, 619–640.

Karplus, I., Barki, A., Israel, Y. and Cohen, S. (1991). Social control of growth in *Macrobrachium rosenbergii.* II. The "leapfrog" growth pattern. *Aquaculture* **96**, 353–365.

Karplus, I., Hulata, G. and Zafrir, S. (1992). Social control of growth in *Macrobrachium rosenbergii.* IV. The mechanism of growth suppression in runts. *Aquaculture* **106**, 275–283.

Keller, M. (1993). Development of a *Astacus astacus* population in Lake Bronnen - a small gravel lake in Bavaria, Germany. *Freshwater Crayfish* **9**, 97–100.

Miller, G.T. Jnr. (1994). 'Living in the environment: principles, connections, and solutions. Eighth Edition'. (Wadsworth Publishing Co., California).

Momot, W.T. (1993). The role of exploitation in altering the processes regulating crayfish populations. *Freshwater Crayfish* **9**, 101–117.

Momot, W.T. and Hauta, P.L. (1995). Effects of growth and mortality phenology on the cohort P/B of the crayfish, *Orconectes virilis*. *Freshwater Crayfish* **8**, 265–275.

Morgan, G.J. (1997). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from New South Wales, with a key to all species of the genus. *Records of the Australian Museum, Supplement* (23), 1–110.

Morrissy, N.M. (1979). Experimental pond production of marron *Cherax tenuimanus* (Smith). *Aquaculture* **16**, 319–344.

Siegel, S. (1956). 'Nonparametric statistics: for the behavioural sciences'. (McGraw-Hill Kogakusha, Ltd., Tokyo).

Snedecor, G.W. and Cochran, W.G. (1967). 'Statistical methods'. (Iowa State University Press, Ames, Iowa).

Turvey, P. and Merrick, J.R. (1997a). Reproductive biology of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Turvey, P. and Merrick, J.R. (1997b). Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Wenner, A.M. (1972). Sex ratio as a function of size in marine crustacea. *American Naturalist* **106**, 321–350.

Diet and Feeding in the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Detailed analyses of gut contents, and field observations of feeding behaviour, clearly indicate that *Euastacus spinifer* is an opportunistic omnivore; diet does not vary with size, age or sex and much of the food is terrestrial in origin. The bulk of the diet comprises partly decomposed woody materials, but decomposing angiosperm macrophytic material is also consumed with occasional diatoms; small aquatic animal prey are actively hunted at times. It is suggested that nutrients are largely derived from fine organic particles associated with detritus, with supplements from scavenging and predation.

The common browsing feeding pattern is not planned or premeditated. A variety of materials can be cropped or gathered in different ways and food particles of widely disparate size are manipulated. The periodic hunting is a premeditated activity involving deliberate stalking of mobile prey and rapid ambush. The occasional bulldozing mode may be a response to scarcity of food but details of preferred food particle size and contributions of specific sources remain unknown.

Preliminary trials demonstrate that both hepatopancreatic fat content and protein concentrations in gastric fluid show wide individual variation, suggesting fluctuating feeding success. Future trials, to test for an index of nutritional state, should be of short duration, with larger samples at a single moult stage. Factors suggested as contributing to variation in feeding success among wild populations include seasonal changes and food availability.

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KEYWORDS: Diet, feeding success, condition, *Euastacus spinifer*, hepatopancreatic fat, gastric fluid protein.

INTRODUCTION

Crustacean nutrition is generally poorly known with most research based on marine prawns or lobsters (Goddard 1988). Studies of crayfish diets and feeding behaviour, both in Australia and elsewhere, have largely focussed on species with commercial potential (Merrick and Lambert 1991). Although qualitative information on natural foods of these cultured species has often been available for some years, detailed quantitative dietary analyses and investigations of nutritional requirements are more recent (O'Brien 1995). Some data are available for several Australian parastacids with no commercial importance, for example, two *Engaeus* species (Suter and Richardson 1977) and *Parastacoides tasmanicus* (Lake and Newcombe 1975). But only a few general comments have been published about the natural diets of *Euastacus* species (Merrick 1993).

Natural Diet, Feeding Behaviour

The unusual polytrophic role of crayfishes in aquatic systems has now been acknowledged (Goddard 1988; Hogger 1988), but a few general findings have emerged

from studies to date and these are listed below. Firstly, their diet consists largely of plant debris, although the prime nutrient source is considered to be micro-organisms and fungi epiphytic on the detritus (Hogger 1988). Secondly, in order to utilise a wide variety of foods, crays possess a complex digestive system (Holdich and Reeve 1988). Thirdly, crayfish biomass is high when compared with other consumers which cannot utilise detritus or living vegetation (Hogger 1988). Fourthly, although other aquatic invertebrates are commonly cited as prey items, cannibalism is also an important aspect of feeding activity (Goddard 1988). Finally, juveniles generally feed more extensively on aquatic invertebrates and show more definite preferences for sizes or species of live foods (Goddard 1988; Warner and Green 1995; Warner et al. 1995).

Nutritional State

Although data on nutritional requirements of crays are still scarce (Goddard 1988) several general points are relevant here. Studies on omnivorous species indicate that good growth is only achieved when dietary protein exceeds 20% (Tsvetnenko et al. 1995) and that food consumption can be high (12–26% body weight/day) in juveniles, declining in adults to 2–3% body weight/day (Musgrove, 1993; Warner and Green 1995). Finally, the seasonal changes detected in lipid, carbohydrate and protein levels of tissues have, for one species, been associated with lowered lipid reserves at the end of the reproductive period (Fernandes et al. 1995).

Growth rates of individuals of *Euastacus spinifer* in the wild population are very variable (Turvey and Merrick 1997a,c). When considered in conjunction with the very patchy distribution of plant debris on the stream bed, the hypothesis was formulated that variation in growth might have related to variable feeding success; however, to investigate feeding success some form of index or measure of nutritional state is required.

In other studies previously reported *E. spinifer* could only be captured in numbers by using baits and this involves interruption of the normal feeding pattern (Turvey and Merrick 1997b). The volume of stomach contents of such animals could not be used as a measure of feeding success and the need for some estimate of average feeding success over a longer period was indicated. Studies of various decapods found that amounts of food consumed over a period affected both the dry weight and fat content of the hepatopancreas (Armitage et al. 1972; Heath and Barnes 1970; Stewart et al. 1967). Dall (1974) also found that hepatopancreatic solids of the spiny lobster *Panulirus longipes* decreased during starvation, but in addition, found that the protein concentration in gastric fluid decreased with decreased feeding, and was a reliable indicator of nutritional state (Dall 1975).

The objectives of the studies reported here are: to document in detail the major components of the diet; to investigate possible relationships between amounts of food consumed over time with fat content of the hepatopancreas and protein concentrations in gastric fluid; to discuss environmental factors that may influence feeding success.

MATERIALS AND METHODS

Natural Diet

For examination of gut contents individuals were fixed in 10% formalin immediately on capture. Samples were collected from several pools at the Loddon River study site (lat. 34°17′S: long. 150°54′E) south of Sydney (Turvey and Merrick 1997a) on three separate occasions (May, June, December) over a 30 month period.

Individuals were separated into four carapace length (CL) classes (20–30 mm,

30–40 mm, 40–50 mm, and 50+ mm). Cardiac stomach contents were removed from each cray and combined for animals in each size class. Each combined sample was separated into two particle-size fractions, by sieving through 0.5 mm mesh, to facilitate examination of constituents. Coarse material was observed using a dissecting microscope while finer material was examined under higher magnification, and the constituents were described qualitatively. With samples taken later in the study the contents of hindguts of five individuals were treated in the same way as stomach contents. Maximum dimensions of some of the smaller particles from both stomach and hindgut were measured using a graduated microscope eyepiece. Results of these analyses were compared with the observed feeding behaviour of captive *E. spinifer* and other species of *Euastacus*.

Feeding Trials

Two feeding trials were conducted and details of both experiments (including design, feeding regimes) are listed in Table 1. In the first trial, crays were allocated so that there were no significant differences between either means or variances of weights of individuals in each feeding group. During acclimation (to aquarium conditions and maintenance routine), the amount of food consumed (by each individual) at each feeding was determined. At the end of the trial the hepatopancreas and carcass (including all fluids released during dissection) were oven dried at 105°C for 24 hours. Moult increments during the experiment were compared with increments in wild crays. Moult increments, in Loddon River populations, were determined by comparing the difference in CL values over a known interval with annual frequencies calculated from the size class (Turvey and Merrick 1997b). Experimental individuals were paired with wild individuals of the same sex and similar carapace length, and the mean of differences between moult increments in each pair was tested for significance using a paired t-test.

TABLE 1

A summary of stocks, treatments and durations of *Euastacus spinifer* feeding trials.

Experiment	Stock (*) Size	Acclimation Period	Experimental Period (▲)
Trial 1	6 ♀(immature)	12 weeks	12 weeks
	+ 6 ♂	Fed 3–4 times per week (†)	Group a — fed every 3 days
	(20–240g)		Group b — fed every 9 days
Trial 2	9 ♀(immature)	2 Weeks	8 weeks
	+ 9 ♂	Fed 5 times per week (▼)	Group a — fed every day or two
	(20–30 mm CL)		Group b — fed every 7 days

* Each experimental individual allocated randomly to glass aquarium (45 l capacity); aquarium aerated, bottom covered with sand from study site, plastic flower pot provided for shelter; all aquaria subject to ambient temperatures and photoperiod.

† During this period all individuals fed with fish pieces, prawns or specially prepared pelletised food (Balazs et al. 1973).

▲ All tanks containing experimental individuals were cleaned and uneaten food removed the morning after each feeding; amount of food consumed calculated as difference between weight of food introduced and weight (adjusted for water uptake) removed.

▼ All individuals fed with earthworms and leaf litter in the evening.

In the second trial, experimental crays were allocated randomly to two feeding groups after acclimation. All individuals were fed on the last night of the experiment, then starved for three days until most of the ingested material had been eliminated from the digestive tract. All the animals were immobilised by immersion in an ice-water slush (30 minutes) and 0.05 - 0.1 ml of gastric fluid was then collected by applying gentle suction to a glass cannula inserted into the cardiac stomach (Vonk 1960). Each gastric sample was centrifuged (3,000 rpm for 2 minutes) and then two sub-samples of supernatant (0.01 ml each) were collected using 'Microcap' micropipettes; each sub-sample was diluted in 0.99 ml of distilled water.

The protein concentration in each 1% solution of gastric fluid was determined spectrophotometrically using the Biuret method (Layne 1957). Mean protein concentrations were calculated for all individuals, and 95% confidence limits for these means were determined using the 'samples' mean square in the analysis of variance (Snedecor and Cochran 1967). Percentages of total variability in protein concentration due to differences between feeding levels, crayfishes within feeding levels, and samples for each crayfish were calculated using the methods of Winer (1971). Moult stages were rated according to the modified universal moult stage notation (Passano 1960); the stages (and rating features) reported in these feeding studies are listed in Table 2.

TABLE 2

Moult stage notations and criteria used in rating experimental individuals and outgroup comparative field samples (based on Passano (1960)).

Notation	Position in Moult Cycle	Physical Characteristics
Ce	Early inter-moult	Branchiostegites deformable under light pressure, no gastroliths, absence of reddish-brown deposits on ventral surface.
C	Intermoult	Exoskeleton firm all over, no gastroliths, slight to heavy deposits on ventral surface.
De	Early pre-moult	Exoskeleton firm all over, gastroliths present, new exoskeleton not obvious, or slight.
Dl	Pre-moult	Branchiostegites deformable under light pressure, large gastroliths, new exoskeleton obvious and well-formed.

Protein concentrations of gastric fluid were also measured from a sample of wild crays captured at the study site shortly after the end of the trial and these values were compared with those of experimental individuals. The wild crays were starved for three days before gastric fluid samples were taken.

Hepatopancreatic fat determinations of experimental crays were based on small samples of hepatopancreas taken at the termination of the trial. This material had been fixed and stored in Bouin's fixative (Humason 1972). Samples were soaked in water for 48 hours and vacuum-dried to constant weight. Fat content was measured as the decrease in dry weight of the samples after refluxing with diethyl ether in a Quickfit 'Soxhlet' extraction apparatus for 16 hours. This fat was expressed as grams per gram of the initial dry weight of each sample and the difference in mean fat content between groups fed at two rates was tested for significance using a t-test. Using identical methods hepatopancreatic fat content was also determined for 13 wild crays (moult stages Ce and De) collected from the study site in August and January. Moult increments of experimental and wild individuals, of a similar CL, were compared as for Trial 1.

RESULTS

Natural Diet

Stomach contents comprised a mixture of particle sizes up to a maximum of 5mm. The largest size grouping (1–5mm) was recognisable as wood, bark and twigs, with occasional severely decomposed fibrous pieces of ribbon weed leaf (*Triglochin procera*). The woody fragments were either weathered, discrete particles, or had been torn, chewed or broken from some larger object. These particles were typically blackened and in a state of partial decomposition.

Most particles were less than 0.5mm (maximum dimensions) and ranged down to 2–10 μm, although small quantities of much finer material were also present. In all samples, a small proportion of particles down to 5 μm were identifiable as elements of woody plant tissue. Apart from very occasional diatoms, no algal material was obvious and, except for a few small sand grains (maximum dimensions of 0.1mm), the remainder of the fine material was unidentifiable.

Hindgut contents were identical to stomach contents except that the largest particles were only 1.0mm; most particles corresponded to the common small category in the stomach (2–10 μm). There was no obvious variation in gut contents with respect to either size of the individual or season.

Feeding Behaviour

The behavioural patterns considered to be associated with feeding have been divided into three categories: browsing or foraging, active hunting and bulldozing.

The feeding mode seen most often was that of browsing or foraging; this involved gathering and ingesting any edible materials that the cray discovered. Extensive field observations and feeding trials with captive *E. spinifer,* using a range of foods, have indicated that these animals will eat food particles of virtually any size from most types of substratum. Pieces may be bitten, scraped, or torn from larger pieces of flesh or plant debris using the mandibles, which are extremely powerful. Smaller particles may be sorted, selected and picked from the substratum using the chelae of the second or third pairs of pereopods and then passed to the mouth parts. Fine materials may be scraped directly from a surface by the mouth parts.

E. spinifer were occasionally observed to actively hunt and capture tadpoles at the study site. At such times, the actions of the crayfish were clearly predatory and capture of the tadpoles was not accidental. Movements of the cray were deliberate and slow, while the substratum was searched cautiously with the antennae. When a tadpole was encountered, the crayfish lunged forward assisted by a rapid extension of the abdomen, and the tadpole was captured using the great chelae. Captive *E. spinifer* were observed to show similar responses to small fishes, earthworms and smaller crays. In addition, wild *E. spinifer* have been observed on two occasions consuming small, live frogs.

The third type of behaviour may not be a feeding mode, but it is logical to report the observations at this point. This behaviour was observed in captive *E. spinifer*, housed in aquaria that had a bottom covered with sand from the study site containing small fragments of blackened, decomposing wood and charcoal. The sand had been sieved previously through 1mm mesh, in order to remove larger food particles that individuals could pick up using their chelae. After several days of starvation, these individuals began to 'bulldoze' the sand. This process involved the individual pressing its mouth and anterior cephalothorax onto the sand, and piling further sand against the anterior cephalothorax using the second and third pairs of pereopods. The crayfish then pushed the pile of sand forward with its mouth buried, propelled by the fourth and fifth pairs of pereopods, and holding the sand in place using the second and third pairs of pereopods and the great chelae.

Feeding Trials

In Trial 1 all foods were at first eagerly accepted by the experimental crays, but in all instances feeding activity declined over the first two months until individuals fed only occasionally, and generally showed little interest in food. During this trial five specimens died during or shortly after moulting; four did not moult, three moulted normally and ten moulted but failed to harden their new exoskeleton. Some individuals which moulted were an abnormal colour and all survivors were lethargic. The hepatopancreas in all survivors was extremely fragile and abnormally coloured when compared with wild stocks. Further analyses of relative hepatopancreatic weight were not considered meaningful and moult increments of experimental stocks were significantly less than increments of wild individuals with similar carapace lengths (Table 3).

TABLE 3

Comparison between the moult increments of wild stocks and experimental *E. spinifer* (Trial 1).

Experiment		Wild		Experiment		Wild	
C.L.*	I.*	C.L.	I.	C.L.	I.	C.L.	I.
61.8	4.7	61.7	4.9	49.4	2.6	49.1	5.0
44.6	2.8	44.4	5.2	49.1	1.3	49.3	4.9
78.2	2.7	74.3	2.6	47.5	3.1	48.6	5.2
53.7	5.9	54.0	5.1	63.7	3.7	64.0	7.9
51.5	5.2	51.4	5.7	73.8	2.9	77.9	5.0
71.5	4.2	73.0	3.9	67.5	3.9	67.1	6.1
60.4	3.9	61.3	7.1				

Paired t-test: $t = 3.76$; d.f. = 12; $p < 0.005$.

Mean difference Wild-Experiment = 1.7mm with 95% confidence limits of ± 1.0mm.

*Pre-moult carapace length (C.L.) and moult increment (I.) in mm.

Similarly in Trial 2, food was eagerly accepted initially but consumption then declined and became irregular. Although apparently in better condition than Trial 1 survivors, sample tests of these Trial 2 stocks indicated reduced levels of parameters measured. The mean hepatopancreatic fat content of individuals fed five days per week (0.054 g/g) was greater than the mean for those fed once a week (0.025 g/g), but wild *E. spinifer* had fat contents of 0.419–0.729 g/g. The level of feeding had no significant effect on protein concentration in gastric fluid of experimental crays, while differences between means for each feeding group, and between samples for each crayfish, were highly significant ($p < 0.005$, Table 4). Among wild *E. spinifer* gastric protein concentration showed considerable variability (Table 5). Again the moult increments of Trial 2 stocks were reduced in comparison with wild stocks.

DISCUSSION

Natural Diet, Feeding Behaviour

Formalin fixation prevented continuing trituration of ingested material by the gastric mill and preserved gut contents. The long intervals between initial and final samplings were planned so that any obvious dietary changes, either with season or more protracted periods, would be detected.

TABLE 4

Analysis of variation in the protein concentration in the gastric fluid of experimental *E. spinifer* (Trial 2).

Results for Individuals			
5 days/week feeding		**1 day/week feeding**	
Moult Stage	**Mean Protein Concentration***	**Moult Stage**	**Mean Protein Concentration***
Ce	166 ± 14	D1	33 ± 14
Ce	110 ± 14	De	204 ± 14
De	52 ± 14	De	48 ± 14
De	77 ± 14	De	371 ± 14
De	102 ± 14	De	73 ± 14
Mean	101 ± 109	Mean	145 ± 109

Analysis of Variance Summary				
Source of Variation	**d.f.**	**M.S.**	**F**	**p**
Feeding Level	1	39117	< 1	n.s.
Crayfish within Level	8	89152	267	< 0.005
Samples within Crayfish	10	335	8.1	< 0.005
Readings within Sample	60	41.3		

*Protein concentration expressed as mg/ml of crystalline bovine serum albumin, with 95% confidence limits based on the relevant Mean Square Errors from the Analysis of Variance.

TABLE 5

Analysis of variation in the protein concentration in the gastric fluid of wild *E. spinifer* (April 1978).

Mean Protein Concentrations for Individuals*	
Moult Stage Ce	**Moult Stage De**
93 ± 21	99 ± 21
49 ± 21	132 ± 21
141 ± 21	152 ± 21
160 ± 21	197 ± 21
81 ± 21	138 ± 21
Mean 105 ± 42	Mean 144 ± 42

Analysis of Variance Summary				
Source of Variation	**d.f.**	**M.S.**	**F**	**p**
Moult Stage	1	30968	2.33	0.25>p> 0.1
Crayfish within Stage	8	13318	19.7	< 0.005
Samples within Crayfish	10	678	18.3	< 0.005
Readings within Samples	60	37		

*Protein concentration expressed as mg/ml of crystalline bovine serum albumin, with 95% confidence limits based on the relevant Mean Square Errors from the Analysis of Variance.

The decision not to accurately quantify stomach contents, either in types of constituents or particle sizes, was made for the following reasons: lack of variation in stomach contents related to either sampling times or body size in *E. spinifer*, the nature of the stomach contents, the effect of the gastric mill in triturating and homogenising ingested material.

The stomach and hindgut contents of wild *E. spinifer* examined indicated that the natural diet consisted mainly of decomposing plant material, and that the larger food particles were almost exclusively woody plant tissues of terrestrial origin. Although *Triglochin procera* was abundant at several sites where specimens were collected, there was no evidence that this aquatic macrophyte was used as a food source, except occasionally when in a decomposed state. This concurred with aquarium observations that *E. spinifer* only consumed living plant material *(Egeria densa*, or filamentous green algae) after being starved for several weeks; then only a small quantity was consumed by a few individuals.

In contrast, both astacids and cambarids from European and North American freshwaters, have been found to consume large quantities of living macrophytes and algae, in addition to decomposing material (Hogger 1988). Locally, three Western Australian *Cherax* species have been reported as very destructive to macrophytes (Shipway 1951). The diet of *E. spinifer* is unusual in that only decomposing plant material is used.

The presence of fragments of woody plant tissue among smaller particles in the stomach, when the function of the gastric mill is considered, indicates that at least a portion of the finer material resulted from mechanical breakdown of larger particles similar to those identified. The gastric mill of *E. spinifer* is large and robust and well-suited for this purpose, but it is also possible that much of the finer material may have been ingested as fine, particulate detritus.

Although not done with the same degree of resolution the gut content analyses of *E. spinifer* yielded similar results to those from recently completed analyses for the Western Australian marron (*Cherax tenuimanus*) by O'Brien (1995). Given the low nutritional value of wood and studies of other species indicating relatively low utilisation of cellulose and fibrous carbohydrates (Lochmann et al. 1995), it is suggested that *E. spinifer* derives most nutrients from fine particulate organic matter associated with detritus. This fraction (particle size <40 μm) would include bacteria, microalgae, protozoans and fungi. The diet is known to be supplemented by predation and in Loddon River populations, which Turvey and Merrick (1997b) report have surplus males, cannibalism could be expected to be significant (Goddard 1988).

The attracting power of fish and meat baits as well as the hunting behaviour indicates that *E. spinifer* is not wholly detritivorous, it may also act as a scavenger or predator. Although, on present evidence, the bulldozing cannot be definitely described as feeding there are several observations indicating an association between available food and this behaviour pattern. In all cases bulldozing was preceded by a period of starvation and after individuals had made numerous, unsuccessful attempts to pick up food particles using the chelae. Immediately after bulldozing individuals release faeces consisting of fine black material. It is therefore suggested that very small particles of wood or charcoal are removed from the sand substrate during bulldozing.

If *E. spinifer* feeds preferentially on larger particles that can be easily manipulated by the chelae then preferred foods may have been in short supply in the Loddon. This suggestion is supported by the absence of obvious macroscopic plant debris in many parts of the stream and the presence of small sand grains among the stomach contents. Pond trials with another local omnivorous parastacid have indicated that good growth and survivorship are only achieved when benthic organic matter exceeds 0.5 kg/m^2 (Chavez and Mitchell 1995). But regardless of specific sources, it is clear that *E. spinifer* contributes significantly to the breakdown of terrestrial plant debris entering the stream. This allochthonous material is the basis of the energy budget in many aquatic systems (Bunn 1986).

Measurements of particle size of hindgut contents indicated that most ingested material was reduced by the gastric mill to a fine sludge. Indeed size ranges of particles measured, both in the stomach and hindgut of *E. spinifer,* were similar to those found in *Cherax tenuimanus* (O'Brien 1995). *E. spinifer* would thus have made incoming plant debris available to smaller detritivores, and greatly increased the surface area for microbial action.

In summary, *E. spinifer* must be considered an opportunistic feeder in the broadest sense, although its normal feeding role at the study site was that of detritivore; this finding is consistent with studies on other parastacids. There was no evidence of juveniles taking a higher percentage of aquatic invertebrates; a difference in diet between juveniles and adults has been suggested as a form of resource partitioning, to decrease competition for limited supplies (O'Brien 1995).

Feeding Trials

The two feeding trials were designed to investigate effects of differing food consumption on levels of gastric fluid protein and condition of the hepatopancreas, related to sex and size, but results were very limited.

The survivors at the end of Trial 1 were obviously in poor condition so no attempt was made to estimate hepatopancreatic fat content or protein concentration in the gastric fluid. The state of the hepatopancreas, inability to re-build exoskeletons and decline in feeding activity, suggest that this stress may have had a nutritional basis. Although Trial 2 stocks remained in outwardly normal condition, hepatopancreatic fat contents were a fraction of those measured in wild samples. Gastric fluid protein levels were highly variable, just as they were in wild specimens and moult increments were reduced. So it has not been possible to establish a relationship between feeding level and either hepatopancreatic fat or gastric protein concentration.

Comparisons and Recommendations

Other studies have shown that a number of decapods appear to use hepatopancreatic lipid as a nutrient reserve and both the dry weight and fat content values obtained for wild *E. spinifer* are similar to those previously reported for other crayfishes. There was considerable variation in the protein concentration of gastric fluid and hepatopancreatic fat content among wild *E. spinifer*, independent of moult stage. This suggests considerable variation in the feeding success of wild *E. spinifer* and food availability is widely recognised as a crucial factor controlling the abundance of crayfish populations (Flint and Goldman 1977; Hogger 1988; Lowery 1988). The difference in fat content of hepatopancreases of wild *E. spinifer* captured in August and January may indicate seasonal variations in feeding success, corresponding to observed seasonal variation in the average size of moult increments of individuals in different locations (Turvey 1980).

Future trials to elucidate relationships between feeding success and either hepatopancreatic fat content or gastric fluid protein concentration, should also take into account the possibility of seasonal changes in lipid or protein content of crayfish tissues, recently documented by Fernandes et al. (1995), as well as the activity of gut bacteria which have been demonstrated to produce a range of amino acids (Syvokiené and Mickéniené 1993). Suggested design features would include: utilisation of much larger experimental samples; commencement with all stocks at the same moult stage, with values from individuals moulting during the trial omitted from final analyses; and short duration, with trial completed before any substantial decrease in feeding activity. It is also suggested that whole fresh hepatopancreatic lobes be used for fat estimations and larger samples of gastric fluid would increase accuracy of protein analyses.

The response of *E. spinifer* to captivity needs further investigation. In contrast to

the experiments described above, juveniles maintained for growth studies appeared to grow normally over 12 months successfully undergoing several moults. Conditions under which these stocks were maintained differed from those in the feeding trials in two respects. The juveniles were only disturbed a few times during the year, and an actively decomposing bed of detritus was maintained in the tank. The success of this rearing system may indicate that *E. spinifer* is metabolically sensitive to repeated disturbance, or that some component of a complex, intact detrital system is necessary for adequate maintenance of physiological condition.

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REFERENCES

Armitage, K.B., Buikema, A.L. and Willems, N.J. (1972). Organic constituents in the annual cycle of the crayfish *Orconectes nais* (Faxon). *Comparative Biochemistry and Physiology* **41A**, 825–842.

Balazs, G.H., Ross. E and Brooks, C.C. (1973). Preliminary studies in the preparation and feeding of crustacean diets. *Aquaculture* **2**, 369–377.

Bunn, S.E. (1986). Origin and fate of organic matter in Australian upland streams. In 'Limnology in Australia' (Eds P. De Dekker and W.D. Williams) pp. 277–291. (CSIRO Junk, Melbourne).

Chavez, J.R. and Mitchell, B.D. (1995). The role of organic matter in semi-intensive pond production of the yabby *Cherax destructor* Clark, using detrital forage. *Freshwater Crayfish* **10**, 435–446.

Dall, W. (1974). Indices of nutritional state in the western rock lobster, *Panulirus longipes* (Milne-Edwards). I. Blood and tissue constituents and water content. *Journal of Experimental Marine Biology and Ecology* **16**, 167–180.

Dall, W. (1975). Indices of nutritional state in the western rock lobster, *Panulirus longipes* (Milne-Edwards). II. Gastric fluid constituents. *Journal of Experimental Marine Biology and Ecology* **18**, 1–18.

Fernandes, M.A.S., Mendonça, M.I.R., Marques, J.C. and Madeira, V.M.C. (1995). Energy and nutrient storage capacity of *Procambarus clarkii* in the lower Mondego River valley (Portugal). *Freshwater Crayfish* **10**, 98–104.

Flint, R.W. and Goldman, C.R. (1977). The effects of a benthic grazer on the littoral zone of Lake Tahoe. *Limnology and Oceanography* **10**, 1–15

Goddard, J.S. (1988). Food and feeding. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 145–166. (Croom Helm Ltd., London).

Heath, J.R. and Barnes, H. (1970). Some changes in biochemical composition with season and during the moulting cycle of the common shore crab, *Carcinus maenus* (L.). *Journal of Experimental Marine Biology and Ecology* **5**, 199–233.

Hogger. J.B. (1988). Ecology, population biology and behaviour. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 114–144. (Croom Helm Ltd., London).

Holdich. D.M. and Reeve, I.D. (1988). Functional morphology and anatomy. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 11–51.(Croom Helm Ltd., London).

Humason, G.L. (1972). 'Animal tissue techniques. Third Edition'. (W.H. Freeman & Co., San Francisco).

Lake, P.S. and Newcombe, K.J. (1975). Observations on the ecology of the crayfish *Parastacoides tasmanicus* (Decapoda; Parastacidae) from South-Western Tasmania. *Australian Zoologist* **18**, 197–214.

Layne. E. (1957). Spectrophotometric and turbidimetric methods for measuring proteins. In 'Methods in enzymology. Vol. 3'. (Eds S.P. Colowick and N.O. Kaplan) pp. 447–454. (Academic Press, New York).

Lochmann, R., McClain, W.R. and Gatlin, D.M. (1995). Responses of the red swamp crayfish, *Procambarus clarkii*, to different quantities and sources of dietary carbohydrates and lipids. *Freshwater Crayfish* **8**, 364–375.

Lowery. R.S. (1988). Growth, moulting and reproduction. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 83–113. (Croom Helm Ltd., London).

Merrick, J.R. (1993). 'Freshwater crayfishes of New South Wales'. (Linnean Society of New South Wales, Sydney).

Merrick, J.R. and Lambert, C.N. (1991). 'The yabby, marron and red claw. Production and marketing'. (J.R. Merrick Publications, Sydney).
Musgrove, R.J. (1993). Energy use and size in juvenile yabbies, *Cherax destructor* Clark (Parastacidae). *Freshwater Crayfish* **9**, 213–225.
O'Brien, B.G. (1995). The natural diet of the freshwater crayfish *Cherax tenuimanus* (Smith 1912) (Decapoda: Parastacidae) as determined by gut content analysis. *Freshwater Crayfish* **10**, 151–162.
Passano, L.M. (1960). Moulting and its control. In 'The physiology of Crustacea, Vol. I. Metabolism and growth'. (Ed T.H. Waterman) pp. 473–536. (Academic Press, London).
Shipway, B. (1951). The natural history of the marron and other freshwater crayfishes of south-western Australia. Part 1. *Western Australian Naturalist* **3** (1), 7–12.
Snedecor, G.W. and Cochran, W.G. (1967). 'Statistical methods'. (Iowa State University Press, Ames, Iowa).
Stewart, J.E., Cornick, J.W., Foley, D.M., Li, M.F. and Bishop, C.M. (1967). Muscle weight relationship of serum proteins, hemocytes, and hepatopancreas in the lobster, *Homarus americanus*. *Journal of the Fisheries Research Board of Canada* **24**, 2339–2354.
Suter, P.J. and Richardson, A.M.M. (1977). The biology of two species of *Engaeus* (Decapoda: Parastacidae) in Tasmania. III. Habitat, food, associated fauna and distribution. *Australian Journal of Marine and Freshwater Research* **28,** 95–103.
Syvokiené, J. and Mickénienė, L. (1993). The activity of gut bacteria of the crayfish, *Pacifastacus leniusculus* (Dana), in producing essential free amino acids. *Freshwater Crayfish* **9**, 235–240.
Tsvetnenko, Y., Santelices, M. and Evans, L.H. (1995). Effect of dietary protein levels and beta-carotene on growth of marron *Cherax tenuimanus* in an intensive culture system. *Freshwater Crayfish* **10**, 611–622.
Turvey, S.P. 1980. Aspects of the biology of the freshwater crayfish *Euastacus spinifer* (Heller) (Decapoda: Parastacidae). M.Sc. thesis, University of Sydney.
Turvey, P. and Merrick, J.R. (1997a). Reproductive biology of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*
Turvey, P. and Merrick, J.R. (1997b). Population structure of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*
Turvey, P. and Merrick, J.R. (1997c). Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*
Vonk, H.J. (1960). Digestion and metabolism. In 'The physiology of Crustacea, Vol. I. 'Metabolism and growth'. (Ed T.H. Waterman) pp. 291–316. (Academic Press, London).
Warner, G.F. and Green, E.I. (1995). Choice and consumption of aquatic weeds by signal crayfish (*Pacifastacus leniusculus*). *Freshwater Crayfish* **8**, 360–363.
Warner, G.F., Wood, J.C. and Orr-Ewing, R.H. (1995). Signal crayfish (*Pacifastacus leniusculus*) feeding on pond snails: optimal foraging? *Freshwater Crayfish* **8**, 352–359.
Winer, B.J. (1971). 'Statistical principles in experimental design. Second Edition'. (McGraw-Hill Book Co., New York).

Moult Increments and Frequency in the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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TURVEY, P. AND MERRICK, J.R. (1997). Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *Proceedings of the Linnean Society of New South Wales* **118**, 187–204.

Euastacus spinifer mark-recapture data have been used to investigate relationships of moulting frequency and moult increments to biological or environmental factors. Small individuals (20–35mm CL) usually moult three times per year (total frequency range 1–6); the medium size class (35–55mm CL) typically moults twice (total frequency range 1–3); large specimens (>55mm CL) moult once per year. No differences have been detected in annual frequencies related to sex or site and it is suggested that moulting is independent of sex and state of maturity.

Moulting seasons for small and medium *E. spinifer* of both sexes are similar but trends for large females and males differ. Moulting activity in the small class commences in September or October and declines in April or May; the medium size class exhibits two periods of activity (October-November, February-May). Large females moult from March to June (with a peak of activity in May); large males moult from November to January. Temperature appears to be the prime environmental regulator of growth and moulting activity at all sizes usually only occurs when water temperatures exceed 14–15°C.

No significant differences in moult increment have been detected between immature females, normal males or precocious males nor have any differences been found between season or location. Increments of mature females are smaller than males of comparable size and reproduction is considered to decrease increment size in females but not in males. Considerable increment variation, at both individual and populational levels, was detected. Food availability and population density are suggested as factors contributing to this variation. Analyses demonstrated an increase in moult increment with rising pre-moult carapace length in the range of 20–55mm, but above this size increments become constant.

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KEYWORDS: Moult increments, moult frequency, *Euastacus spinifer*, annual moult cycle, moult seasonality, pre-moult length, growth factor.

INTRODUCTION

Overall growth in crustaceans is the result of two fundamental components; these are the amount by which an individual increases in size at moulting (i.e., moult increment) and moult frequency (Hartnoll 1983). Variation in growth rate may result from variation in either or both of these components. So in this study, as in others (Bennett 1974; Berry 1971; Kurata 1962; Mauchline 1977), the contributions of moult increment and moult frequency have been analysed separately.

A systematic approach was developed to extract maximum information from mark-recapture data, based on Hepper (1967), Mauchline (1977) and Underwood (1975). Development of this approach involved extensive preliminary analyses, using sub-sets of

Euastacus spinifer data, to assess contributions of different factors to observed variation (Turvey 1980). Early in the study it became clear that information on moult frequency was essential for the interpretation of temporal variations in moult increment, so it is treated first. The time of year during which moulting occurred was also of interest, as it may have reflected the effects of environmental factors on growth, or changes in growth patterns of individuals at different stages of the life cycle. Investigations of moult increment involved a survey to identify the factors that might have affected the growth of individual *E. spinifer*, as preliminary examination of data indicated that moult increments were highly variable for specimens of any given size.

With the notable exception of studies on *E. bispinosus* (Honan and Mitchell 1995) there are no published studies of moult frequency or growth increments in members of the genus *Euastacus*. Objectives of this paper are: to investigate variation in both frequency and seasonality of moulting with respect to sex, size and capture site; to relate the observed moult seasonality to changes in water temperature; to determine if size-independent variation in moult increment is related to sex, season or site; to assess if increment variation resulted from individual variability, effects of pre-moult carapace length, measurement error or other factors; to interpret variation in moult increment with size based on the analyses for size-independent variation.

MATERIALS AND METHODS

The frequency analyses are based on the mark-recapture sampling conducted in Pools 3 and 7 at the study site during the period May 1977 to December 1978. The site and sampling techniques were documented in Turvey and Merrick (1997a,b). Moult stage notation was based on Passano (1960).

Annual Moult Frequency

Total annual growth for individuals 20–55mm CL was estimated as the difference between carapace length measurements of marked individuals taken 12 months apart. These annual growth increments were subdivided into a series of likely moult increments based on the results of Turvey (1980), and the number of moults per year was determined for each cray as the number of consecutive increments.

Where annual growth could not be divided into consecutive moult increments, the contributing number of moults was estimated as follows. Average moult increments were determined for 5mm size classes, commencing at 19.95mm CL, separately for each sex and location. For each individual, the average moult increment (of relevant size class) was added to the length initially recorded to provide a new CL; this process was repeated, until the annual moult frequency could be estimated as the number of average increments providing the final CL closest to that recorded at the end of twelve months.

Annual moult frequencies of individuals exceeding 55mm CL were determined from numbers of consecutive moult increments over periods of 12–15 months. Annual frequencies of all samples were plotted against initial CL. For analysis, the total CL range was divided into three intervals (20–35mm, 35–55mm, and 55–100mm) designated as small, medium and large respectively.

Seasonality in Moulting

Separate criteria were used to determine the commencement and termination of periods of concentrated moulting activity. Initiation of moulting was determined as follows. Captured individuals were classified into moult stages Ce (early intermoult) or C

(intermoult) at each monthly sampling of the mark-recapture study (Turvey and Merrick 1997b); percentages of specimens in each catch that were in moult stage Ce indicated the level of recent moult activity. These values (referred to as percentages of post-moult crayfishes) were calculated separately for small, medium and large individuals of each sex, from each of the two pools. These calculations were plotted against month of sampling. The onset of moulting activity was considered to occur during the month in which the post-moult percentage increased markedly from a previously low value.

Decline in moulting activity was determined in the following way. Using mark-recapture records and supplementary analyses (Turvey 1980) it was possible to determine whether a crayfish had moulted during the period between any two captures, if the interval was two months or more. So a substantial increase in the percentage that definitely did not moult, in any given month, was used to indicate decreasing moult activity. This value (referred to as the percentage of non-moulting crayfishes) was calculated for the same groups as those for which post-moult percentages had been determined.

Moulting Activity and Water Temperature

Moulting in small *E. spinifer* was compared directly with the thermal cycle. Water temperatures recorded at each sampling were plotted on an annual time scale and months during which each moulting season commenced or ceased were also marked.

Moult Increment and Sex, Season or Site

Increments were tabulated separately for males and females from the two pools. These data were further subdivided into classes, based on individual pre-moult CL, for each of several seasons of moulting activity.

Increments of small individuals (20–35mm CL) were compared for the periods May–October 1977, October 1977–February 1978, February–August 1978 and May–October 1978. Moult increments of medium *E. spinifer* (35–55mm CL) were compared for the periods May–November 1977, December 1977–August 1978 and May–November 1978.

The moult increments of these small and medium classes were compared by calculating the linear regressions of increment on pre-moult CL and comparing slopes as well as elevations of the lines using analysis of covariance (Snedecor and Cochran 1967). Where slopes were not significantly different, the differentials between elevations were used to indicate differences in average moult increment. A Student Newman Keuls test (Zar 1974) was used to test for significant differences among elevations.

Initial comparisons were made between the sexes at each season and location. Where regressions for the sexes were not significantly different ($p > 0.05$), data for both sexes were combined and compared between seasons, separately for each location. Where seasonal regressions were not significantly different ($p > 0.05$), data for similar seasons were combined and regressions for the sets of similar seasons were compared between locations. When there were no significant differences between slopes or elevations for a number of groups, the regression line for the combined data has been presented. Where elevations differed significantly but slopes did not, regressions with the pooled slope for all groups (Snedecor and Cochran 1967) have been plotted through the means of each different group.

Seasonal comparisons were not conducted for large individuals (exceeding 55mm CL); comparisons between males and females of 55–70mm CL were treated in the manner described for smaller individuals. Males considered in all the above comparisons were of the normal type, but comparisons were also made between increments of precocious (very small, sexually mature) males, normal males and females (for the size range 20–25mm CL) during the period October 1977 to February 1978 in Pool 3. Where data

were inadequate to allow comparison between sexes for a season, combined data were used for comparison between seasons.

Moult Increment Variation and Other Factors

Mark-capture records were examined for instances where moult increments had been recorded in consecutive seasons for an individual. Data were arranged into classes based on initial CL, location of capture and the two seasons involved. Multiple regressions of moult increment for the second season (Y) on pre-moult CL for the second season (X_1) and increment for the first season (X_2) were calculated for each class. Any correlation between moult increment and previous increment would include an estimate of the extent to which the sizes of consecutive moults of individuals were related. The error variance from the multiple regression was used to estimate the variability in moult increment that was independent of the combined effects of pre-moult CL and consistent differences between individuals.

The variability in moult increment from measurement error was estimated for each group, independently of the multiple-regression analysis, using the variance of the measurement errors that were isolated from the mark-recapture data. Measurement error variance was then expressed as a percentage of the error variance from the multiple regression for each group.

Moult Increment Related to Pre-moult Carapace Length

This relationship was illustrated using final results of the analyses of variation in moult increment with respect to sex, season and location. Regression lines and 95% confidence belts for each of the final sets of seasons for each size class were plotted, together with moult increments of individuals exceeding 70mm CL.

Using the method of Mauchline (1977) moult increment was expressed as a percentage of pre-moult CL, to provide a 'growth factor'. The linear and $\log_{10}$-linear regressions of growth factors on pre-moult CL were then determined. Individuals with moult increments recorded from seasons of maximum growth were allocated to a series of size classes (5mm width), commencing at 19.95mm.

Growth factors were calculated for individuals and linear regressions of growth factor and $\log_{10}$ growth factor on pre-moult CL determined for the whole range of carapace lengths. Correlation coefficients for each relationship were determined and tested for significant departures from zero and each other (Snedecor and Cochran 1967). The same procedure was applied to the combined data for *E. spinifer* over 70mm CL and individuals with increments recorded from seasons of minimum growth.

RESULTS

Annual Moult Frequency

Small individuals (20–35mm CL) were characterised by a moult frequency of three, although a few specimens moulted from one to six times per year. Medium crayfishes (35–55mm CL) typically moulted twice per year, with occasional individuals moulting once or three times; all seven large males and 14 large females recorded had moulted once over 12–15 month periods, another large female moulted twice (see Fig. 1).

All annual frequencies of one were based on actual numbers of moult increments recorded - not on estimates. There were no apparent differences in annual moult frequencies with respect to either sex or location for the small or medium groups. Moult frequencies of large males and females from Pool 3 were similar to each other, and to the single value from Pool 7.

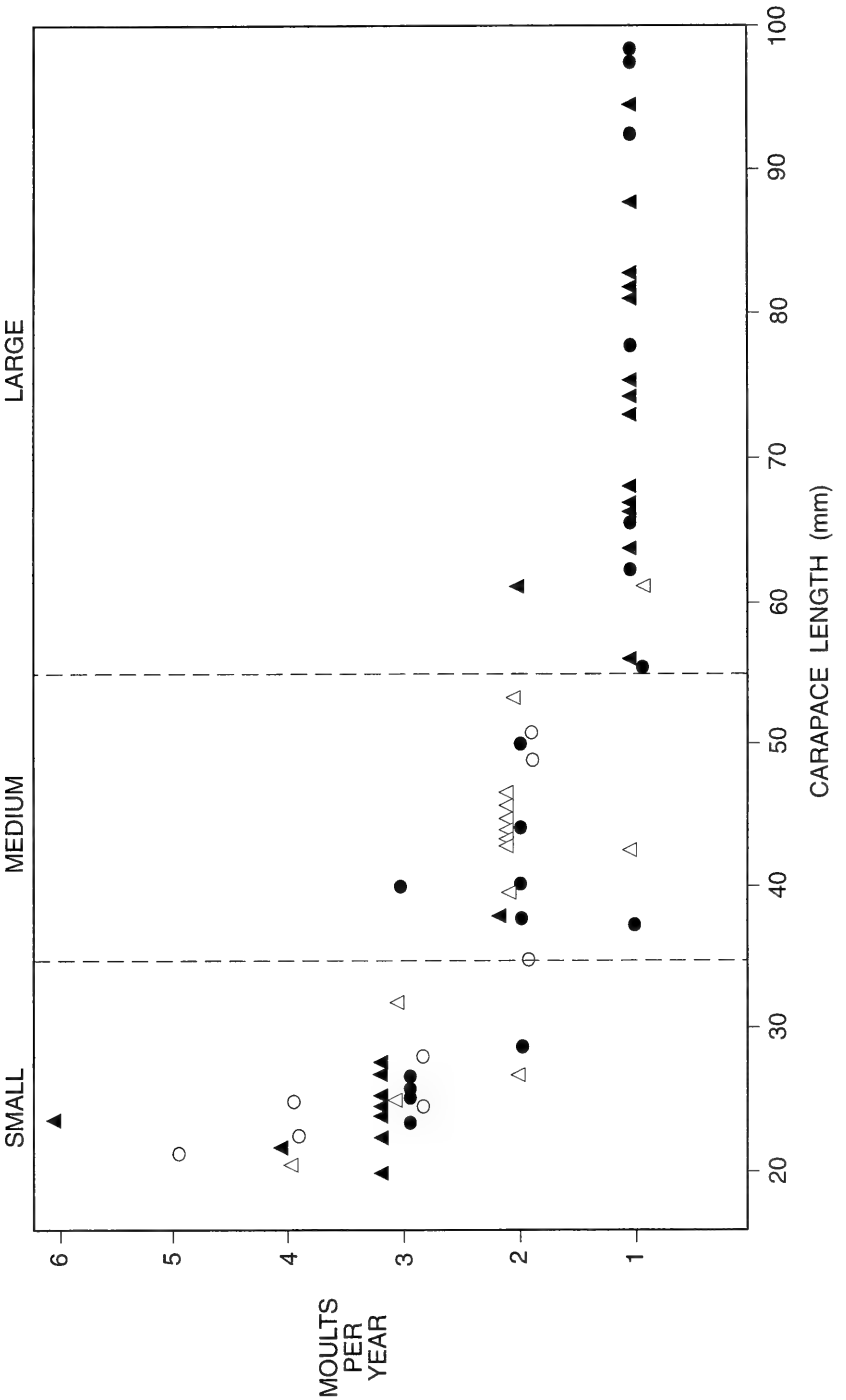

Figure 1. Summary of annual moult frequency related to initial carapace length in *E. spinifer*. Group ranges: small = 20–35mm CL; medium = 35–55mm CL; large = 55–100mm CL. Key to symbols: ○ = Pool 7, male; ● = Pool 3, male; Δ = Pool 7, female; ▲ = Pool 3 female.

Seasonality in Moulting

Trends in percentage of post-moult and non-moulting individuals of small and medium size were similar for males and females in both locations, while trends for large males and females were distinctly different.

Moulting activity among small individuals commenced rapidly during September 1977, decreased rapidly during mid-April to mid-May 1978 and increased rapidly again during October 1978. There was a pronounced decrease in moulting activity in Pool 3 from mid-December 1977 to March 1978, while a less pronounced decrease occurred among small specimens in Pool 7 over the same period.

Two periods of moulting activity per year were evident for medium-sized *E. spinifer* from Pool 3, during the periods October-November 1977 and February-April 1978; moulting activity commenced again during October 1978. Trends for medium-sized specimens in Pool 7 differed in two major respects. Firstly, despite normal sampling, no medium-sized *E. spinifer* were collected from October to December 1977 although this period coincided with a peak of moulting activity in this size class from Pool 3. Secondly, the other major period of moulting in Pool 7 is from March-May 1978 compared with February-April 1978 in Pool 3.

Trends in percentages of large, non-moulting females were similar for both locations. In Pool 7, the increasing percentage of non-moulting individuals, marking the end of the moulting season, occurred in two steps commencing slowly during March-May 1978, followed by a sharp increase in June; while in Pool 3 a single, sharp increase occurred during June 1978. The major peak in post-moult percentage occurred in May 1978 at both sites; by contrast, moulting activity commenced during April in Pool 3 and during February in Pool 7.

Recapture records indicated that the small peaks in percentage of post-moult crays for September 1977 and 1978, in Pool 3, were due to individuals that had not moulted since the previous major peaks of moulting activity. High percentages of both post-moult and non-moulting individuals during May-June 1977 indicated that a period of moulting activity had occurred just prior to this in both pools.

The trends in percentage of large, non-moulting males from the two locations appeared to be of similar configuration; they were also related in the same general manner as those described for females of similar size, although data for Pool 7 were incomplete. Changes over time in percentages of both post-moult and non-moulting males were quite different from those recorded for large females. In Pool 3, the initial increase in percentages of large, non-moulting males indicated the finish of the major period of moulting activity during January 1978; moulting had been initiated during November 1977. Although percentages of large, post-moulting males in Pool 7 were absent for the initial part of this period, values for October 1977 and January 1978 indicated that large males had also moulted in Pool 7 during November-January.

The May 1977 peak in percentage of large, post-moult males in Pool 7 resulted from two specimens (59.4mm, 63.4mm CL); recapture data indicated that both of these individuals had moulted during late 1977 and again during the period January–May 1978.

Moulting Activity and Water Temperature

Variations in water temperature were strongly seasonal; although similar for both pools the 1977–78 summer temperatures for Pool 7 were 2–3°C lower than those for Pool 3 (Fig. 2). Moulting activity of small *E. spinifer* commenced as water temperatures increased to levels substantially greater than 14°C during September 1977 and October 1978, whereas moulting activity ceased as water temperatures decreased below approximately 15°C during May 1978.

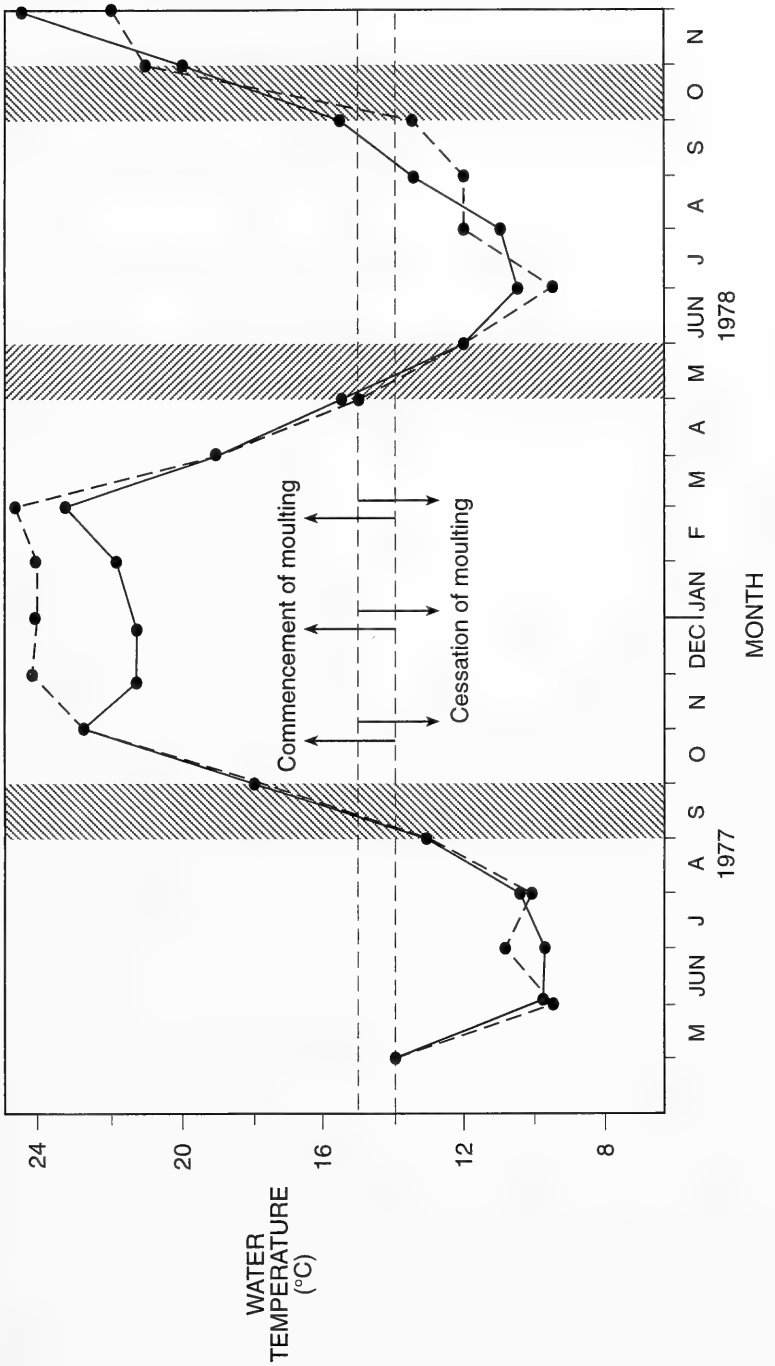

Figure 2. Summary chart of water temperatures in two Loddon River pools and identified moulting activity in small *E. spinifer* (20–35mm CL) over an 18 month period. Key to symbols: — = monthly water temperature for Pool 3; – – = monthly water temperature for Pool 7; ☑ = month for commencement of moulting activity; ☒ = month for cessation of moulting activity.

Moult Increment and Sex, Season or Site

No significant differences were detected between slopes of the regressions of moult increment on pre-moult CL in any of the comparisons for sex, season or location; however, separate regressions (increment on pre-moult CL) for each class at each location for the seasonal periods demonstrated the following. No significant differences were detected among seasons for individuals in Pool 7, but significant differences were present among seasonal regressions for the small class (20–35 mm CL) in Pool 3 ($p < 0.005$). The Student Newman Keuls test indicated that elevations of regressions for May-October 1977 and February-August 1978 were similar ($p > 0.05$), and significantly greater than the elevation of the October 1977– February 1978 regression ($p < 0.001$); for *E. spinifer* of 35–55mm CL in Pool 3, the elevation of the May-November 1977 regression was significantly greater than that of the December 1977– August 1978 regression ($p < 0.005$).

When seasonal regressions (increment on pre-moult CL) are compared between locations, significant differences were detected among elevations for small and medium size classes ($p < 0.005$). For the 20–35mm size class (Fig. 3), the elevations of regressions for all seasons in Pool 7 as well as May-October 1977 and February-August 1978 in Pool 3 were similar ($p > 0.50$), but significantly greater than the elevation of the regression for October 1977–February 1978 in Pool 3 ($p < 0.001$). For the 35–55mm size class (Fig. 4), elevations of regressions for all seasons in Pool 7 and May-November 1977 in Pool 3 were similar ($p > 0.20$); they were also greater than the elevation of the December 1977–August 1978 regression for Pool 3 ($p > 0.005$).

The elevation of the regression of annual moult increment on pre-moult CL for females with carapace lengths of 55–70mm in Pool 7 was significantly greater than that for Pool 3 (Fig. 5, $p < 0.005$). No significant differences were detected among the elevations of the regressions for precocious males, normal males and females with carapace lengths of 20–25mm for October 1977–February 1978 in Pool 3 ($p > 0.05$, Fig. 6).

Moult Increment Variation and Other Factors

The error variance from the multiple regression of moult increment (Y) on pre-moult CL (X_1) and previous increment (X_2) accounted for a uniformly high proportion of the total variance in moult increment for the different groups of *E. spinifer* (Table 1), with values ranging from 64 to 92%. A large proportion of increment variability was thus independent of both pre-moult CL and consistent differences between moult increments of different individuals. Only a small percentage (3–7%) of this independent variability could be accounted for by increment measurement errors.

Moult Increment Related to Pre-moult Carapace Length

Moult increments of individuals with carapace lengths 20–55mm increased with increasing pre-moult CL at a relatively constant rate for seasons of both maximum and minimum growth at moulting (Fig. 7). Increments of larger specimens (55–70mm CL) were approximately constant with respect to pre-moult length in both locations, although 95% confidence belts for the regression slopes were wide. Data were available for two males and an immature female in the 70–95mm CL range, all from Pool 3; increments of these individuals were close to the average moult increment for the 55–70mm class from the same location. Moult increments of mature females were substantially smaller than those of the two males and immature female of similar size; furthermore, increments of both sexes decreased markedly at a pre-moult CL of approximately 95mm (Fig. 7).

Correlation coefficients of the regressions of both growth factor and $\log_{10}$ growth factor on pre-moult CL were not significantly different from zero ($p > 0.9$) for individuals

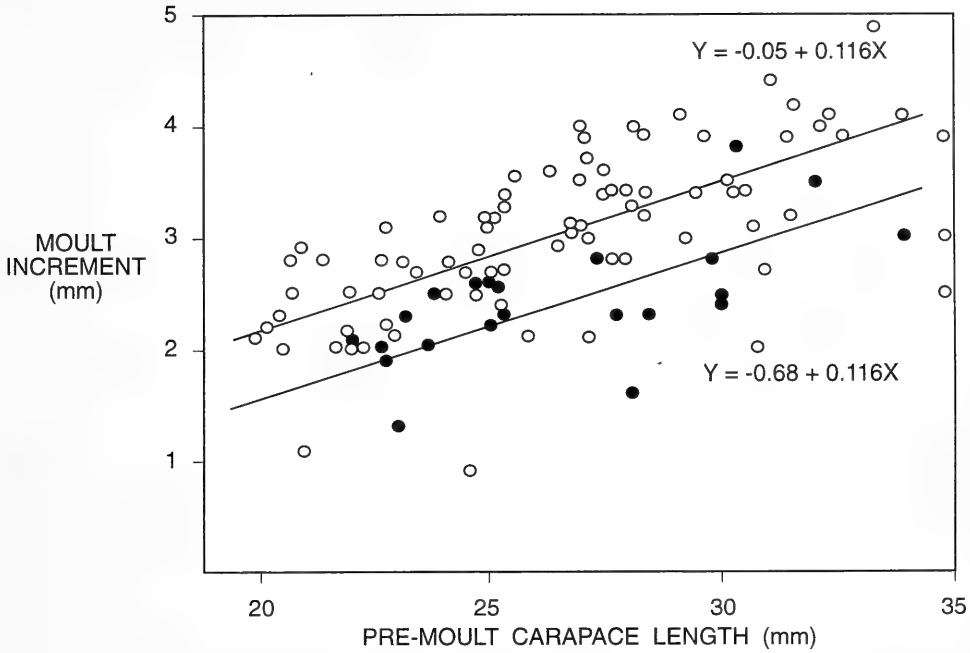

Figure 3. Regressions of moult increment on pre-moult carapace length for small *E. spinifer* (20–35mm CL). Key to symbols: ○ = Pool 3, May–October 1977, February–August 1978 and Pool 7, May–October 1977 and October 1977–February 1978 and February–August 1978 and May–October 1978; ● = Pool 3, October 1997–February 1978.

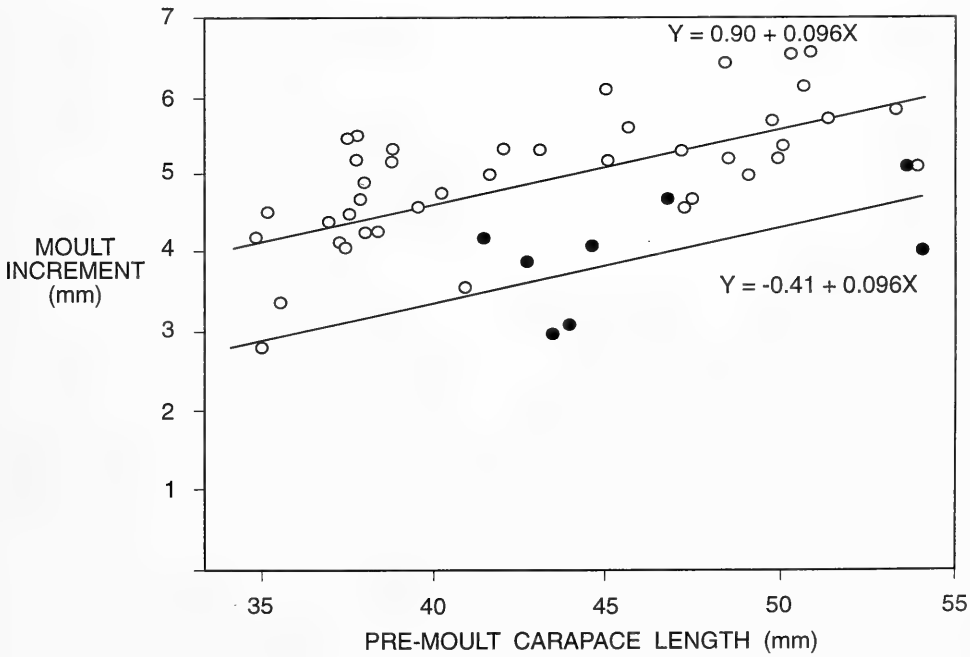

Figure 4. Regressions of moult increment on pre-moult carapace length for medium *E. spinifer* (35–55mm CL). Key to symbols: ○ = Pool 3, May–November 1977 and Pool 7, May–November 1977 and December 1977–August 1978 and May–November 1978; ● = Pool 3, December 1977–August 1978.

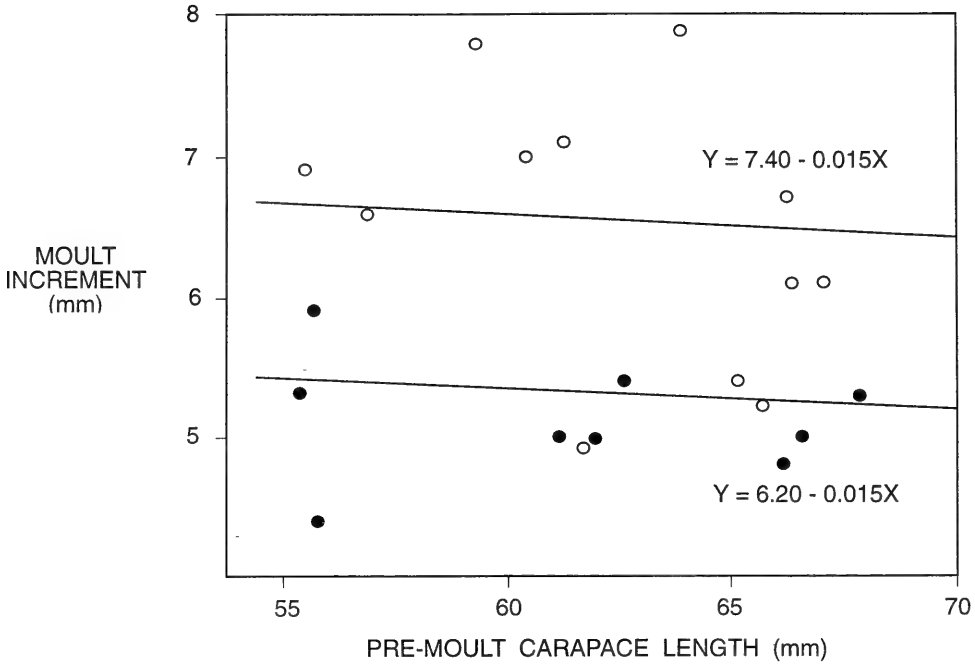

Figure 5. Regressions of moult increment on pre-moult carapace length for large *E. spinifer* (55–70mm CL). Key to symbols: ○ = Pool 7, annual moult increment; ● = Pool 3, annual moult increment.

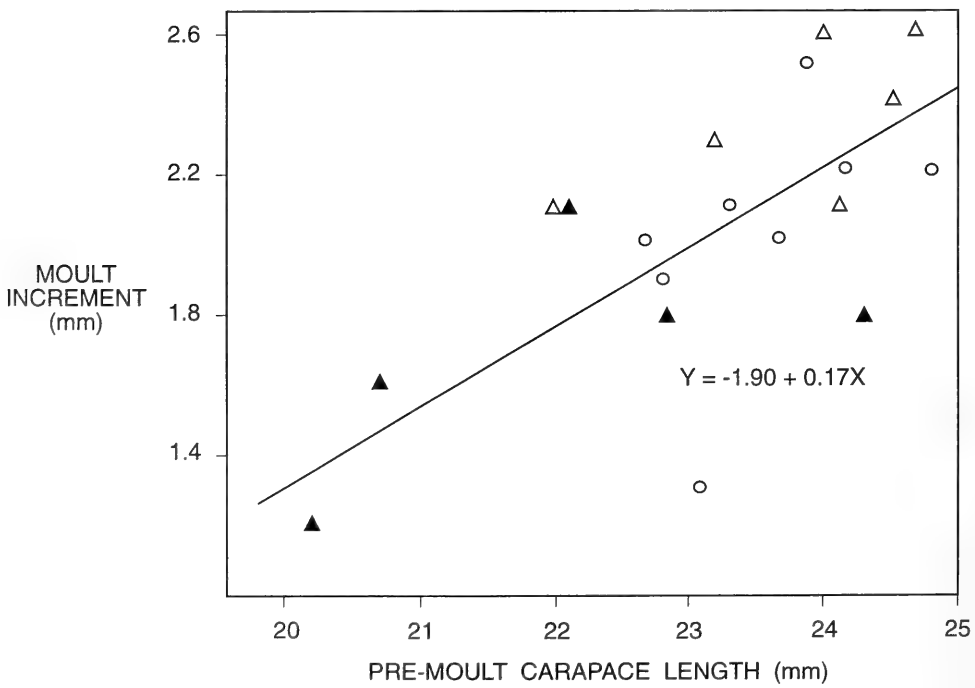

Figure 6. Overall regression of moult increment on pre-moult carapace length for precocious males, normal males and immature female *E. spinifer* (20–25mm CL) from Pool 3 during the period October 1977– February 1978. Key to symbols: ○ = immature female; Δ = normal male; ▲ = precocious male.

that had moulted during seasons of maximum growth at moulting (Fig. 8). Percent increase in carapace length at moulting was thus approximately constant, with respect to pre-moult CL for these crays, at an average value of about 11.5%. The co-efficients derived for stocks that had moulted during seasons of minimum growth at moulting (Fig. 9) were significantly different from zero ($p < 0.001$), but not from each other ($p > 0.6$). Thus there was a significant decrease in growth factors with increasing CL and the linear and log-linear regressions were of equally good fit; although neither curve provided an adequate fit to the growth factors of the largest individuals.

TABLE 1

Contributions of measurement error and unidentified factors to variation in *E. spinifer* moult increment, based on multiple regressions of moult increment (Y) on pre-moult carapace length (X_1) and previous increment (X_2).

		Site			
		Pool 3	**Pool 3**	**Pool 3**	**Pool 7**
Source of Regression	Size Class (mm)	20–35	20–35	35–55	35–55
	Y Season	Oct 1977–Feb 1978	Feb–Aug 1978	Dec 1977–Aug 1978	Dec 1977–Aug 1978
	X_2 Season	May–Oct 1977	Oct 1977–Feb 1978	May–Nov 1977	May–Nov 1977
	Total (T)*	0.46(9)	0.30(20)	0.63(8)	0.56(7)
Estimates of Variability	Error (E)†	0.32(7)	0.20(18)	0.56(6)	0.52(5)
	%E/T	69	64	89	92
	Measurement (M) ▲	0.010 (66)	0.010 (66)	0.038 (179)	0.019 (92)
	% M/E	3.1	5.1	6.8	3.6

* Total (T) variance in moult increment, with degrees of freedom (d.f.).

† Error (E) variance from the multiple regression of Y on X_1 and X_2, with degrees of freedom (d.f.).

▲ Measurement (M) error variance in Y, estimated from independent data, with degrees of freedom (d.f.).

DISCUSSION

Low catchabilities of very small *E. spinifer* (Turvey and Merrick 1997b) resulted in few data for individuals less than 20mm CL, so descriptions of moulting frequency and increment were confined to individuals above this size. Data were insufficient for the description of moult frequencies of precocious males, although some information on increment size is provided.

Annual Moult Frequency

Direct interpretation from Figure 1 is necessary as data are inadequate for further statistical evaluation. The data indicate that annual moult frequencies are similar for males and females of the same size; this suggestion is supported, for small and medium

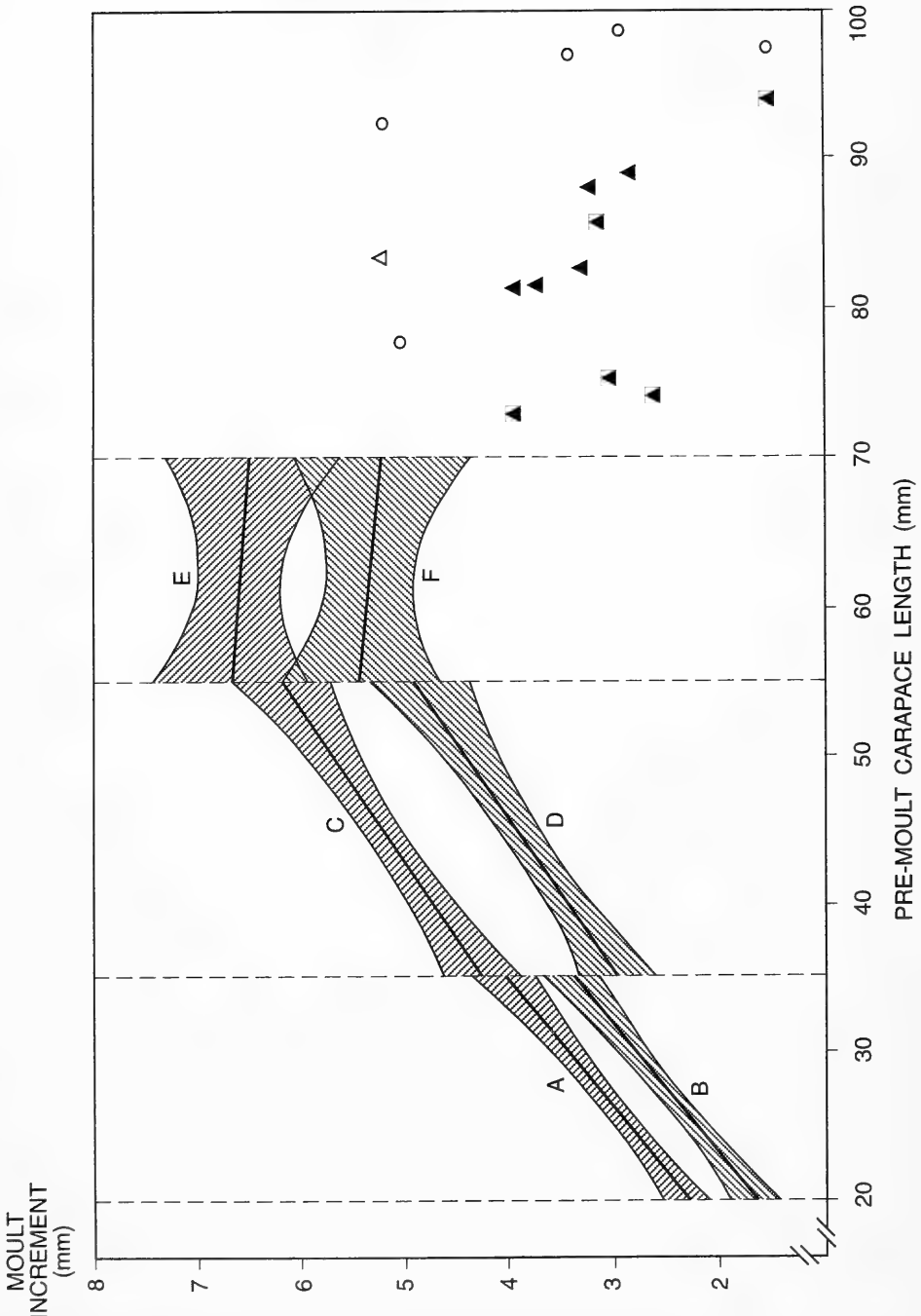

Figure 7. Variation in moult increment with pre-moult carapace length for all *E. spinifer*. Seasons of maximum growth at moulting: A = Pool 7, all seasons and Pool 3, May–November 1977 and December 1977–August 1978; C = Pool 7, all seasons and Pool 3, May–November 1977; E = Pool 7, annual moult. Seasons of minimum growth at moulting: B = Pool 3, October 1977–February 1978; D = Pool 3, December 1977–August 1978; F = Pool 3, annual moult. Key to symbols: ○ = male, Pool 3, annual moult; Δ = immature female, Pool 3, annual moult; ▲ = mature female, Pool 3, annual moult.

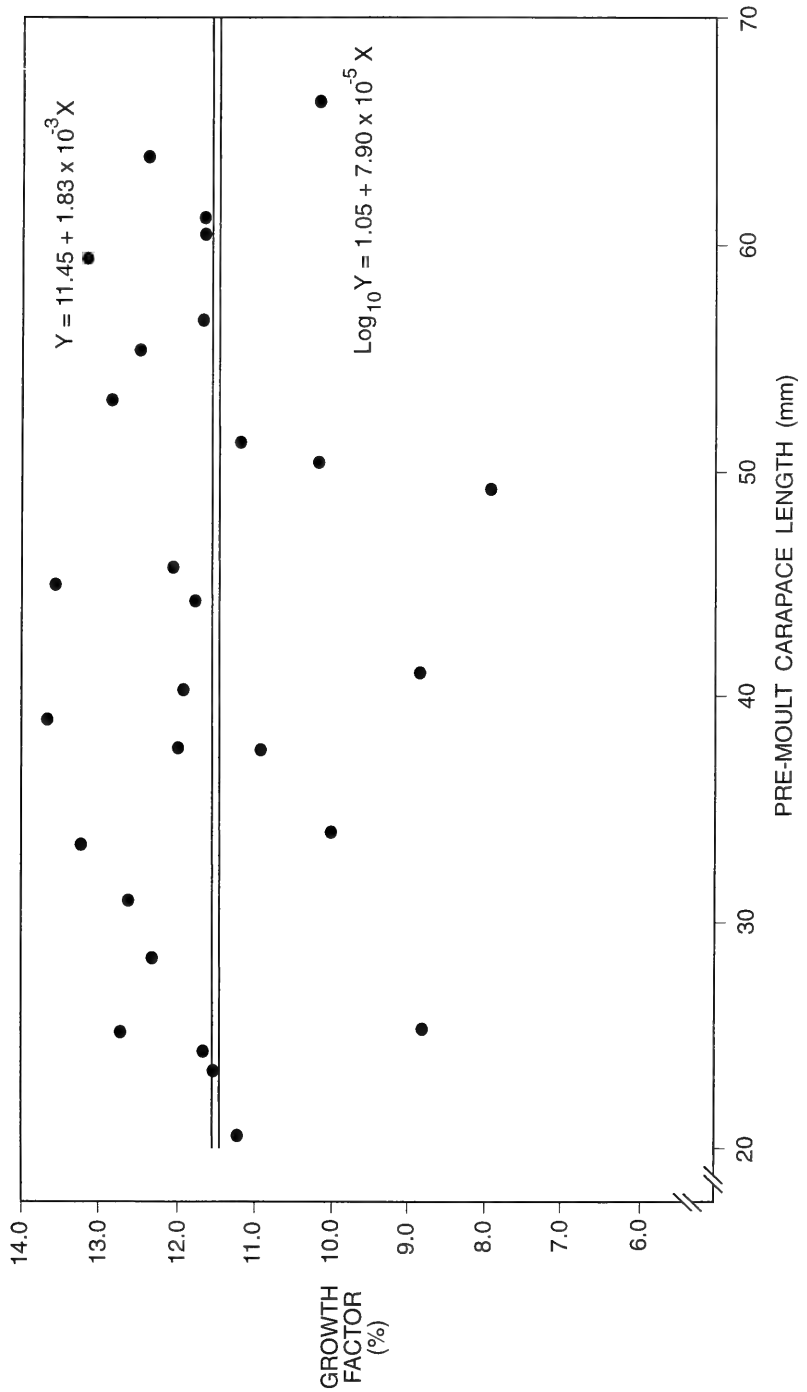

Figure 8. Variation in growth factor with pre-moult carapace length, for male and immature female *E. spinifer* of 20–70mm CL, during seasons of maximum growth at moulting in Pools 3 and 7.

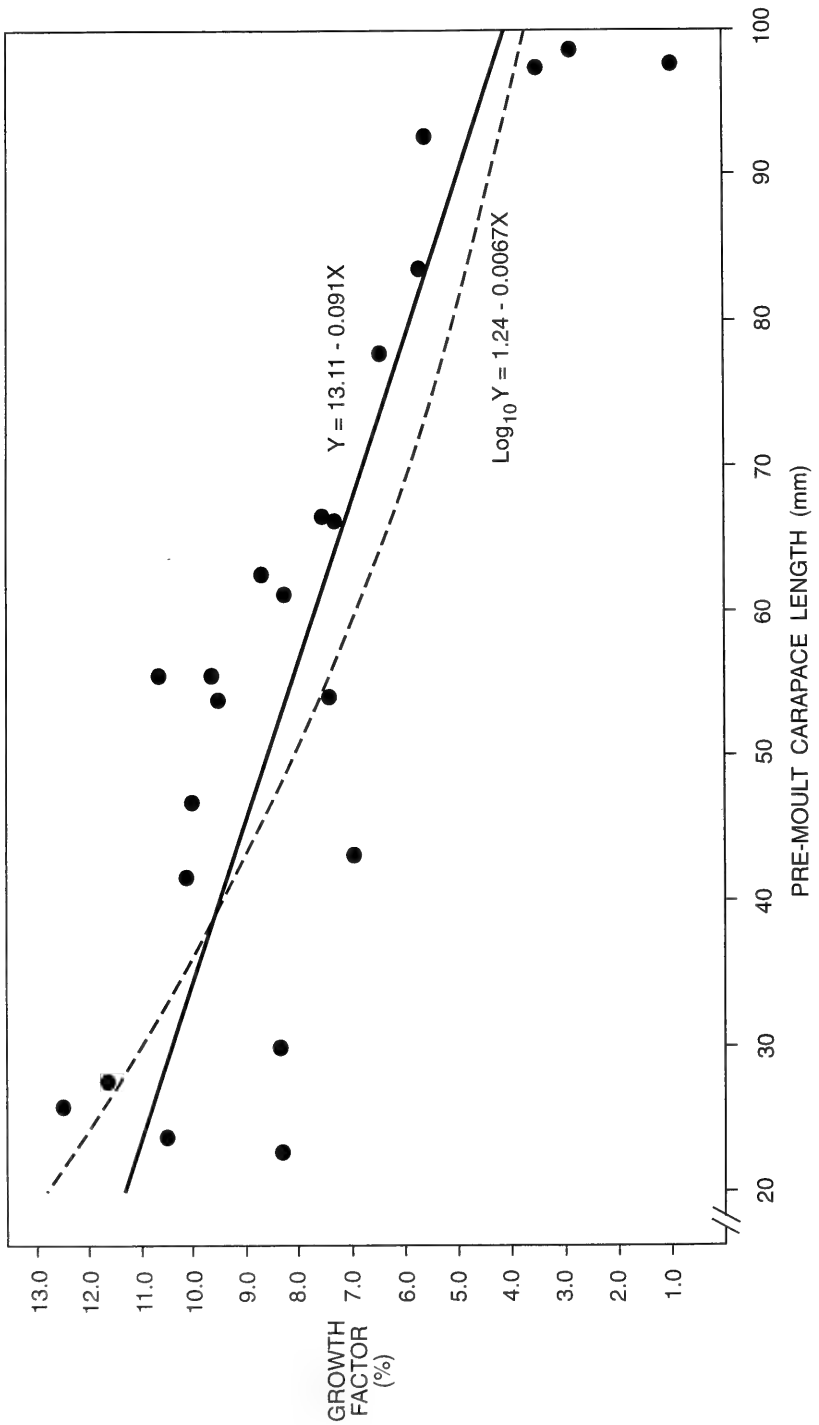

Figure 9. Variation in growth factor with pre-moult carapace length, for male and immature female *E. spinifer* of 20–100mm CL, during seasons of minimum growth at moulting in Pool 3.

classes, by the closeness of seasonal patterns of moulting activity of both sexes. It is also unlikely that there are major differences between moult frequencies of large (>55mm CL) individuals. As 21 out of 22 large specimens moulted once, a single annual moult is probably typical of both sexes.

As normal male *E. spinifer* mature over 45–55mm CL and females at carapace lengths exceeding 70mm (Turvey and Merrick 1997a), annual moult frequencies appear independent of sex and state of maturity. Similarly, Honan and Mitchell (1995) found that growth rates of males and females were not significantly different; they also concluded that *E. bispinosus* up to 50mm CL moulted twice a year, above that size moults became annual.

Although moult frequency in *E. spinifer* is probably independent of sex or maturity, there is clearly a relationship with carapace length. Decreases in frequency with increasing size have been recorded for many large decapods (Kurata 1962). Records for some lobster and crab species (Bennett 1974; Cooper and Uzmann 1971) indicate that this decrease may be continuous over the whole size range of a species, resulting in frequencies of less than one per year in mature individuals. This is not the case for *E. spinifer,* where moulting occurs at a constant frequency of once a year over much of the upper part of the size range. Similar results have been obtained for species in two other parastacid genera (Hopkins 1967a; Shipway 1951; Sokol 1988).

Seasonality in Moulting

Seasonal patterns of moulting activity differ for small, medium and large *E. spinifer* in accordance with differences in annual moult frequency. A different method had to be used to measure decreasing moulting activity because individuals could remain in moult stage Ce for several months after moulting.

Small individuals typically moult three times each year, sometimes more; moulting activity in the field population is continuous, with fluctuations in intensity from early spring to late autumn. The majority of the medium class moult twice a year and moulting activity is largely confined to two discrete periods, one in spring and one in autumn. The annual moult in large individuals is usually confined to a single relatively brief period, early summer for males or late autumn for females. By comparison, Honan and Mitchell (1995) were unable to precisely determine a moulting season for adult *E. bispinosus*. They showed that: *E. bispinosus* moulted between late spring and late autumn; juveniles moulted 11–12 times in their first year to reach ~20mm CL; small individuals (20–30mm CL) moulted 3–4 times in the second year; above this sub-adults typically moulted twice per year until ~50mm CL.

The above generalisations relating to *E. spinifer* were based on the allocation of individuals to arbitrary discrete size classes for the purposes of analysis. In the field average moult frequencies and hence seasonal patterns of moulting activity, probably changed continuously with carapace length until the adoption of a single annual moult. A number of departures from the suggested generalised pattern are possible, including some individuals moulting twice annually when just above 55mm CL.

The different moulting seasons of large males and females contrasted with the simultaneous seasons of smaller individuals and with annual frequencies of the rest of the population. In other crays, males moult at various times, but females typically moult just after the release of juveniles or just before mating (Hopkins 1967a,b; Payne 1972; Weagle and Ozburn 1972). In mature *E. spinifer* females moulting occurred prior to mating in May, rather than after the release of juveniles in December. This proximity of moulting to mating and oviposition may be related to the need for pleopodal setae to be in good condition for egg attachment. But other influences on moult timing would include the long incubation period (precluding moulting) and the need to accumulate large reserves of nutrients for egg production.

Moulting Activity and Water Temperature

The comparison of moulting activity and water temperature was confined to the small class, as they moulted more frequently and changes in patterns of moulting activity provided a more sensitive indication of altered metabolic responses to environmental parameters. Results suggested an association between growth processes and water temperatures, with growth being initiated above 14–15°C. This conclusion contrasts with findings of studies on some North American crayfishes showing that growth is regulated by photoperiod (Aiken 1969; Armitage et al. 1973); although increased moult frequency with increasing temperature has been reported for a number of European and Australasian species (Hopkins 1967a; Lowery 1988). Hopkins (1967a) found that while frequencies decreased during winter for the New Zealand parastacid, *Paranephrops planifrons*, moulting activity did not cease. This suggests a lowering of moulting activity, rather than an absolute threshold below which growth cannot occur. This may also apply to *E. spinifer*, since at least two individuals moulted outside the normal season, with ambient temperatures well below 14°C.

Moult Increment and Sex, Season or Site

There were no significant differences between the moult increments of immature female and normal male *E. spinifer* up to 70mm CL; the increments recorded for the two males and immature female in the 70–95mm CL range were similar in size. In the one instance where data were adequate for testing, there were no significant differences among the moult increments of precocious males, normal males or immature females that could not be accounted for by CL differences.

While there is general similarity between the increments of males (regardless of maturity) and immature females, the increments of mature females are smaller than those of the two males and immature female of comparable size. It is suggested that, for *E. spinifer,* reproduction acts to decrease the size of moult increments in females but not in males; this effect has been recorded in other large crayfishes (Hopkins 1967a; Lowery 1988; Sokol 1988).

Moult Increment Variation and Other Factors

Considerable variation in increments was also present, in all groups of *E. spinifer*, independent of the trends described above. The multiple regression analysis indicated that most of this variability could not be attributed to effects of pre-moult CL or other genetically based differences between individuals. Up to 7% of this independent variation could be attributed to errors in increment measurement; but measurement errors in pre-moult CL and previous increment could only have contributed a proportion of the remaining variation. Some 50–80% of total variability cannot be explained and potential causes of this variation are discussed below.

Firstly, variation in increment has been linked with food availability in *Cherax destructor* (Sokol 1988) and some indirect evidence of fluctuating feeding success has been presented for *E. spinifer* (Turvey and Merrick 1997c). As the major component of the *E. spinifer* diet is decaying plant material of terrestrial origin (Turvey and Merrick 1997c) an erratic supply may have contributed to the observed situation. Substantial input of this allochthonous material only occurred during flooding events, which happened two or three times per year at irregular intervals. Furthermore, once debris entered the watercourse it was distributed unevenly in small isolated deposits. Secondly, moult increments in other parastacids are known to be affected by population density (Morrissy 1975; Sokol 1988); however, in the absence of data on the carrying capacity of the Loddon River habitat or *E. spinifer* population numbers no further comment is possible.

Moult Increment Related to Pre-moult Carapace Length

Growth factors (increments expressed as a percentage of pre-moult CL) ranged from 14% in juveniles to 6–1% for large adult *E. spinifer*, covering a range similar to those recorded for two other parastacids (Hopkins 1967a; Shipway 1951).

Although absolute values of average increments of *E. spinifer* varied with both season and location, the slopes of the relationships between increment and pre-moult CL within a size class were unaffected by such variation (Fig. 7). Hence changes in the slopes of these relationships are likely to be fundamental to the patterns of growth of *E. spinifer* in the area, rather than effects of variable external factors. The change from an increase in moult increment with pre-moult CL for the 20–55mm group to a constant increment for individuals of 55–70mm CL is considered to be both real and general; although confidence limits for the slopes of the latter regressions were wide (Fig. 7). As moult frequency dropped from typically twice to once per year at approximately 55mm CL, there is an association between the onset of a constant moult increment and the adoption of a single moult per year.

Kurata (1962) found that Hiatt growth diagrams of numerous crustaceans were characterised by abrupt changes in slope, which he termed 'inflexions'; these inflexions were frequently independent of gonad maturation. Similar relationships have now been documented for lobsters, cambarid crayfishes and other parastacids (Farmer 1973; Jones 1981; Newman and Pollock 1974; Payne 1972; Weagle and Ozburn 1972). The relationship between increment and pre-moult CL for *E. spinifer* appears to conform to a general decapod growth pattern, with an increase in increment with body size followed by a constant or decreasing moult increment.

On the other hand, the equations relating growth factors and pre-moult CL proposed for decapods by Mauchline (1977) do not closely describe the relationship in *E. spinifer* (Figs. 8 and 9), for moults undergone during similar growing seasons. But this does not imply that *E. spinifer* differs fundamentally from other decapod taxa in its growth patterns. Rather, it suggests that the equations do not adequately describe the relationship between growth at moulting and size over the greater part of the growth history of the species.

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Appreciation is expressed to Sydney Water (formerly the Metropolitan Water Sewerage and Drainage Board) for permission to work in their catchment areas; special thanks are due to Board Rangers Mr. G. Williams and Mr. A. Richards for assistance in selecting the study site. We are grateful to Mr. J. Cleasby, School of Earth Sciences and Miss P. R. Davies, Graduate School of the Environment, Macquarie University for assistance with figure and manuscript preparation respectively. This work was carried out as part of an extended study on *Euastacus spinifer* supported by University of Sydney research grants.

REFERENCES

Aiken, D.E. (1969). Photoperiod, endocrinology, and the crustacean moult cycle. *Science* **164**, 49–55.

Armitage, K.B., Buikema, A.L. Jr. and Willems, N.J. (1973). The effect of photoperiod on organic constituents and moulting of the crayfish *Orconectes nais* (Faxon). *Comparative Biochemistry and Physiology* **44A**, 431–456.

Bennett, D.B. (1974). Growth of the edible crab *(Cancer pagurus* L.) off South-West England. *Journal of the Marine Biological Association of the United Kingdom* **54**, 803–823.

Berry, P.F. (1971). The biology of the spiny lobster *Panulirus homarus* (Linnaeus) of the east coast of southern Africa. *Investigational Report of the Oceanographic Research Institute of South Africa* **28**, 1–75.

Cooper, R.A. and Uzmann, J.R. (1971). Migrations and growth of deep-sea lobsters *Homarus americanus*. *Science* **171**, 288–290.

Farmer, A.S. (1973). Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae). *Marine Biology* **23**, 315–325.

Hartnoll, R.G. (1983). Strategies of crustacean growth. *Memoirs of the Australian Museum* **18**, 121–131.
Hepper, B.T. (1967). On the growth at moulting of lobsters *(Homarus vulgaris)* in Cornwall and Yorkshire. *Journal of the Marine Biological Association of the United Kingdom* **47**, 629–643.
Honan, J.A. and Mitchell, B.D. (1995). Growth of the large freshwater crayfish, *Euastacus bispinosus* (Decapoda: Parastacidae). *Freshwater Crayfish* **10**, 118–131.
Hopkins, C.L. (1967a). Growth rate in a population of the freshwater crayfish, *Paranephrops planifrons* White. *New Zealand Journal of Science* **1**, 464–474.
Hopkins, C.L. (1967b). Breeding in the freshwater crayfish *Paranephrops planifrons*. White. *New Zealand Journal of Marine and Freshwater Research* **1**, 51–58.
Jones, J.B. (1981). Growth of two species of freshwater crayfish (*Paranephrops* spp.) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **15**(1), 15–20.
Kurata, H. (1962). Studies on the age and growth of Crustacea. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* **24**, 1–115.
Lowery, R.S. (1988). Growth, moulting and reproduction. In 'Freshwater crayfish: biology, management and exploitation' (Eds D.M. Holdich and R.S. Lowery) pp. 83–113. (Croom Helm Ltd., London).
Mauchline, J. (1977). Growth of shrimps, crabs and lobsters - an assessment. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **37**, 162–169.
Morrissy, N.M. (1975). Spawning variation and its relation to growth rate and density in the marron, *Cherax tenuimanus*. *Fisheries Research Bulletin of Western Australia* **16**, 1–32.
Newman, G.G. and Pollock, D.E. (1974). Growth of the rock lobsters *Jasus lalandii* and its relationship to benthos. *Marine Biology* **24**, 339–346.
Passano, L.M. (1960). Moulting and its control. In 'The physiology of Crustacea, Vol. I. Metabolism and growth'. (Ed. T.H. Waterman) pp. 473–536. (Academic Press, London).
Payne, J.F. (1972). The life history of *Procambarus hayi*. *American Midland Naturalist* **87**, 25–35.
Shipway, B. (1951). The natural history of the marron and other freshwater crayfishes of south-western Australia. Part 2. *Western Australian Naturalist* **3** (2), 27–34.
Snedecor, G.W. and Cochran. W.G. (1967). 'Statistical methods'. (Iowa State University Press, Ames, Iowa).
Sokol, A. (1988). The Australian yabby. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 401–425. (Croom Helm Ltd., London).
Turvey, S.P. (1980). Aspects of the biology of the freshwater crayfish *Euastacus spinifer* (Heller) (Decapoda: Parastacidae). M.Sc. thesis, University of Sydney.
Turvey, P. and Merrick, J.R. (1997a). Reproductive biology of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*
Turvey, P. and Merrick, J.R. (1997b). Population structure of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*
Turvey, P. and Merrick, J.R. (1997c). Diet and feeding in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*
Underwood, A.J. (1975). Comparative studies on the biology of *Nerita atramentosa* Reeve, *Bembicium nanum* (Lamarck) and *Cellana tramoserica* (Sowerby) (Gastropoda: Prosobranchia) in S.E. Australia. *Journal of Experimental Marine Biology and Ecology* **18**, 153–172.
Weagle, K.V. and Ozburn, G.W. (1972). Observations on aspects of the life history of the crayfish, *Orconectes virilis* (Hagen), in northwestern Ontario. *Canadian Journal of Zoology* **50**, 366–370.
Zar, J.H. (1974). 'Biostatistical analysis'. (Prentice-Hall Inc., Englewood Cliffs, N.J).

Growth with Age in the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Growth with time of different sub-groups in the *Euastacus spinifer* population in two pools of the Loddon River has been measured and assessed. Annual increments of newly released juveniles maintained in captivity match predicted values from the linear regression calculated from large field samples (sub-adults, mature males <55mm CL). No difference in growth related to sex, could be detected and the decline in annual growth (again a linear relationship) for all specimens above 55mm CL is partially due to lowered moulting frequency, to a single annual moult.

Normal males mature at about 5 years (45–55mm CL), while females do not reach maturity until 8 years (~70mm CL) or older. Mean carapace length at age can be estimated with confidence up to at least 8 years; with calculated ages, for the largest specimens recorded at the study site, ranging from 22–39 years. Reports suggest that in some areas *E. spinifer* can attain a size (160mm CL) and weight (1.8kg) which place it among the largest of parastacid species.

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KEYWORDS: Annual growth, size at age, *Euastacus spinifer*, juvenile growth, maximum weight.

INTRODUCTION

The difficulties of determining age in crustaceans have been noted by many authors. But in the absence of ageing structures, growth rates may be determined by identifying age classes in catch size frequency distributions, or by following the growth of marked individuals. For relatively short-lived species, size at age can be estimated directly by the former method (Momot 1967; Weagle and Ozburn 1972) but in larger, long-lived species age classes may be obscured after the first few years by variable or low average growth rates (Bennett 1974; Chittleborough 1976; Farmer 1973). Then information on the age of larger individuals in wild populations can only be obtained through mark-recapture programs.

Size estimates at age can be made by combining the relationships of moult increment and frequency to body size (Bennett 1974; Berry 1971; Mauchline 1977). This combined method involves errors in fitting curves to two data sets and is only realistic when relationships, for moult increment and frequency, can be fitted by a single continuous curve, which is the case with *Euastacus spinifer* (Turvey and Merrick 1997c).

In this study on *E. spinifer*, annual growth rates have been estimated from the linear relationship between final carapace length after a twelve month period and initial carapace length, averaged for a number of individuals of different initial sizes. This estimated true growth may be used to calculate mean size at any age for surviving individuals, if mean

size at one age covered by the calculated relationship is known. The reliability of size estimates drawn from these relationships depends upon the assumption that observed growth rates were typical of rates in previous years. The only other comprehensive studies relating *Euastacus* age to growth have been those on *E. bispinosus* (Honan and Mitchell 1995b). Objectives of this paper are: to measure annual growth rates in newly released juveniles, immature and mature samples of both sexes; to compare rates within and between these population sub-groups; to provide a series of estimates of size at age so that a total growth relationship relating carapace length with age in years can be developed; to relate age estimates with reproductive maturity, maximum individual size and longevity.

MATERIALS AND METHODS

The study site and techniques for sampling the Loddon River populations were documented in Turvey and Merrick (1997a,b). As there were no field recapture data for specimens below 20mm CL, growth at the smallest sizes was estimated from captive juvenile stocks.

Growth of Newly Released Juveniles

Mature females were collected just prior to the release of juveniles (November 1977). Mean CL of juveniles at release was estimated from a random sample (n = 20) measured before moulting, but after release from parents held briefly in aquaria. Females still carrying juveniles were introduced into a new, specially constructed farm dam in the adjacent Hacking River catchment; shelter and leaf litter was provided. In March 1978, 20 juveniles were removed from the dam and transferred to an outdoor tank (2.0 x 1.0m in area: depth 1.0m). The tank was aerated and juveniles supplied with shelters, leaf litter and detritus; small pieces of fish were added occasionally to supplement the diet.

This experimental stock was only disturbed three times during captivity and the tank was subjected to ambient temperature and photoperiod regimes. In November 1978 the trial was terminated and carapace lengths of the eight survivors measured (nearest 0.1mm). The differential between final carapace length (after one year) and initial CL was then compared with the relationship obtained for wild stocks.

Annual Growth Rate and Size at Age in Wild Populations

Annual growth increments, of *E. spinifer* at the study site, were measured using methods described in Turvey and Merrick (1997c). Carapace lengths after 12 months were plotted against initial lengths for annual increments of females and normal males of different sizes from Pools 3 and 7; no distinction was made between the data for males and immature females. Linear regressions of final CL after one year on initial CL were calculated separately for individuals with initial carapace lengths below and above 55mm; confidence limits (95%) for final lengths at any given initial CL were calculated for each regression and plotted as confidence belts. The regression line and confidence belts for individuals in the size range 20–55mm CL were extrapolated back to the estimated initial CL of captive juveniles, and compared with final lengths of these experimental stocks after approximately one year.

Using the mean CL of newly released juveniles as mean CL at age 0, the estimated CL at 12 months (age 1) may be read directly from the regression line described above; mean CL at two years of age may be estimated in a similar manner from the calculated mean size at one year. If the regression is linear, it is of the form,

$$L_{t+1} = a + bL_t$$

where L_{t+1} = final carapace length after one year and L_t = initial carapace length. Then the process of estimating consecutive sizes at age from the regression line generates a relationship of the form,

$$\frac{L_n = a(1 - b^n) + b^n L_0}{1 - b}$$

where L_n = mean carapace length after n years, L_0 = mean carapace length at age 0, providing that $b \neq 1$ (Kurata 1962). Separate equations of this form were constructed from the regression lines for individuals below and above 55mm CL. The first was applied up to and including the first mean CL at age that exceeded 55mm, and the second from this point onwards. Confidence limits (95%), calculated as for CL, were used to estimate approximate ranges of size at age for individuals.

In addition, the maximum carapace length attainable by a crayfish growing at a particular rate may be predicted from the regression line, as the point at which final CL equals initial length (assuming the relationship between the two variables remains unchanged). Maximum attainable lengths (with upper and lower 95% confidence limits), provided estimates of CL at age for individuals growing at the mean, sustained maximum and sustained minimum annual rates. These estimated attainable sizes together with the relationship between mean CL and age were compared to maximum carapace lengths recorded at the study site.

Relationship of Estimated Size at Age and Size Classes in Initial 1977 Catches

Size classes were determined for combined catches taken in May, June, July and August 1977 from both pools; a single size frequency distribution (CL class width 1mm) was constructed. Points of overlap of its constituent size classes were located using the probability paper method of Harding (1949); where feasible, the mean CL of individuals in each size class was calculated. The size distribution was plotted as a frequency histogram; the spacings and mean carapace lengths of contributing size classes were compared with the estimates of mean CL at age that had been derived from the mark-recapture data.

RESULTS

Growth of Newly Released Juveniles

The mean carapace length of juveniles at release was estimated to be 4.46mm ± 0.02mm (95% confidence limits). Carapace lengths of captive juveniles after approximately fifty weeks of growth, from the time of release from their mother were 10.8mm, 12.8mm, 12.8mm, 13.4mm, 14.4mm, 15.5mm, 17.0mm and 20.6mm.

Annual Growth Rate and Size at Age in Wild Populations

The relationship between carapace length after one year and initial length (Fig. 1) was closely approximated by a straight line for both size groups. The majority of final carapace lengths of the reared juveniles were grouped about the regression line for the group of smaller individuals (<55mm CL) and contained within the 95% confidence limits for the population at that point.

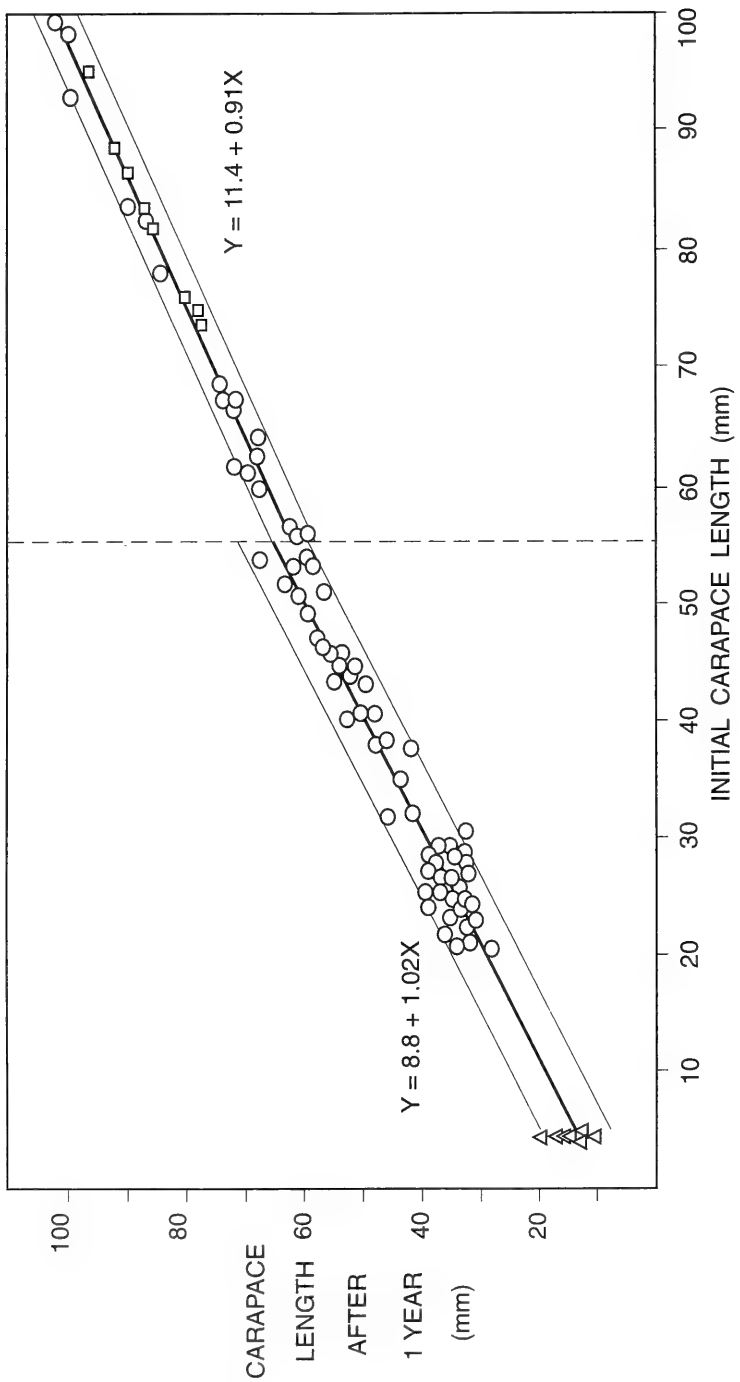

Figure 1. Relationship of carapace length after one year to initial carapace length in *E. spinifer*. Separate regressions have been fitted for individuals above and below 55mm CL; 95% confidence limits are for the population of carapace lengths after one year at any given initial carapace length. Key to symbols: Δ = juveniles raised in captivity; ❍ = wild male or immature females; ❑ = wild mature females.

For individuals with initial carapace lengths exceeding 70mm, the final lengths of females were located on or just below the regression line, while the final lengths of males (and one immature female) were located above the regression line. The single exception was one of the largest males with a final carapace length below the regression line. The estimated maximum carapace lengths attainable by crays growing at the mean and sustained maximum and minimum annual growth rates were 123mm, 159mm and 89mm respectively. The predicted maximum carapace lengths of individuals growing at the estimated maximum and mean rates were both greater than the maximum recorded value at the study site.

Estimated mean carapace lengths increased exponentially with age up to a CL of 60.4mm at an age of six years (Fig. 2); however, the yearly increase in annual growth increments for these latter individuals was slight. For crays of ages greater than six years, annual growth increments decreased each year. The earlier attainment of a CL greater than 55mm, and subsequent adoption of the growth rate predicted for individuals sustaining the estimated maximum rate (60.4mm at 4 years), resulted in asymmetry of the maximum and minimum carapace lengths at age about the mean value for stock more than four years old.

Relationship of Estimated Size at Age and Size Classes in Initial 1977 Catches

The combined size frequency distribution was resolved into six size classes, up to a carapace length of 69mm (Fig. 3). The frequency distribution above this point consisted of a number of small, isolated groups which could not be identified reliably as discrete size classes. The mean CL of the size class containing the smallest crayfish was not calculated, as lower boundaries of this class could not be reliably determined. The spacing of the other size classes was similar to the spacing of the estimated mean carapace lengths of individuals at 3–7 years of age.

Estimated mean CL values at ages six and seven years were within 0.5mm of the size class means for individuals with carapace lengths exceeding 56mm. The mean CL of individuals in the 45–55mm size class was about 1mm less than the estimated mean carapace length for a five year old. The size class mean for specimens of 33–44mm CL was approximately 2mm less than the estimated mean CL for four year olds; the class mean for 25–33mm CL was about 4mm less than the estimated mean CL for 3 year olds.

DISCUSSION

The technique of estimating annual growth by CL differentials (averaged for samples of different size classes) was developed independently in this investigation; however, an earlier study (Hancock 1965) had also reported that this method provided a reliable assessment of true growth, providing that data were drawn from a number of age groups.

Growth

The experimental juveniles were maintained in conditions designed to approximate those in the wild and carapace lengths attained by these captives, after approximately one year, were generally close to the values predicted by the relationship determined for wild stocks. No distinction was made between values for immature females and males since moult increments and annual moult frequencies had been demonstrated to be the same (Turvey and Merrick 1997c). The pattern of differences in CL means, over five size classes and individuals 3–7 years old, conforms to that expected if growth rates during the study were typical of the growth in previous years.

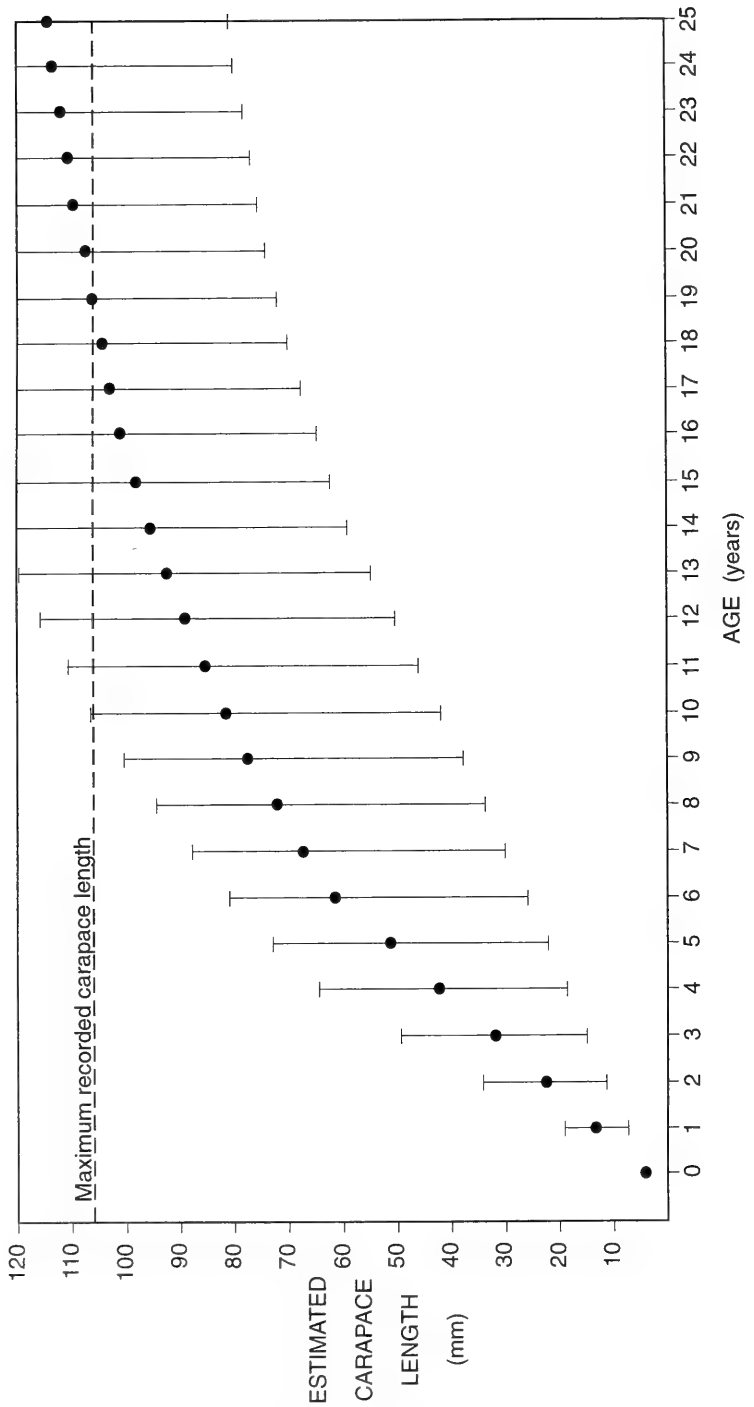

Figure 2. Estimated carapace length at age in *E. spinifer*. Key to symbols: ● = estimated carapace length at age for individuals growing at the mean annual rate; | = estimated carapace length at age for individuals sustaining the estimated maximum or minimum annual growth rate.

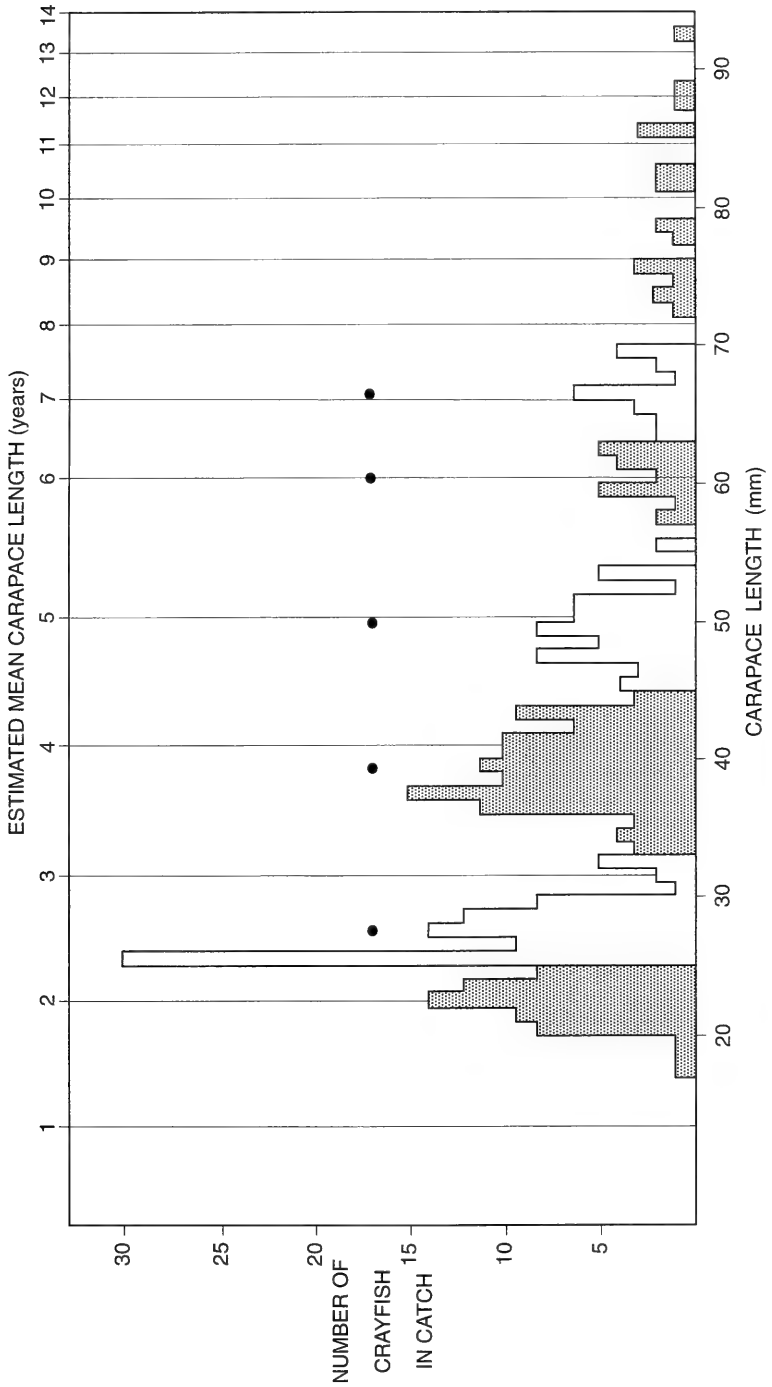

Figure 3. Relationship between estimated mean carapace length at age and size classes of *E. spinifer* in catches. Alternate size classes are distinguished by hatching; the size class containing the smallest individual is incomplete. Key: ● = mean CL of individuals in the size class.

The regressions (for <55mm and >55mm CL) were calculated separately for the following reasons. Individuals with carapace lengths just below 55mm typically moult twice per year, while individuals exceeding 55mm CL almost all moult only once per year. As moult increments of individuals with carapace lengths just below and for a considerable distance above 55mm are similar (Turvey and Merrick 1997c), an abrupt and sustained decrease, by a factor of about 50%, in the annual growth rates occurs at this point (Fig. 1).

The initial 1977 catches were selected for analysis of length classes for the following reasons. Firstly, as individuals rarely moulted during that period of the year (Turvey and Merrick 1997c), catches could be combined to provide a larger sample and more sensitive, reliable analysis. Secondly, the characteristics used to determine absence of moulting were independent of size; furthermore, size classes were determined from catches taken prior to any growth used to estimate annual rates from mark-recapture data.

If the difference between sampling time and end of the growth year is taken into account, the mean carapace lengths at age estimated from growth during the study coincide remarkably well with CL means of classes in 1977 catches. It can also be concluded that annual growth rates observed provide an accurate estimate of annual growth for at least seven years prior to these studies; this finding applies to specimens both greater and less than 55mm CL.

This conclusion has two implications: firstly, that mean CL at age can be confidently estimated for *E. spinifer* up to an age of at least eight years; secondly, that effects of environmental factors on growth were generally constant for at least eight years up to the end of the mark-recapture study.

Turvey and Merrick (1997c) found that sizes of consecutive moult increments were generally not correlated for any individual, so it is unlikely that any crayfish maintained the growth rates estimated from the 95% confidence limits for any protracted period. Sizes at age calculated from these growth rates must therefore be considered as potential maximum and minimum values that are unlikely to have been attained by *E. spinifer* in the study area, although they may have been reached by stocks in other areas.

Although samples of precocious males were too small for meaningful age analyses a brief discussion of preliminary findings is appropriate. The studies by Turvey (1980) indicated that this group, of very small but apparently sexually functional males, matured at ≥12mm (≥12 months age), declined in frequency when two or three years old (25–30mm CL) and a few survivors reached four years of age (~40mm CL). The suggestion that precocious males have similar growth rates to normal *E. spinifer* individuals contrasts with the situation in the freshwater prawn, where very small males are reported to have slow growth relative to other groups (Ra'anan et al. 1991).

Age and Life Cycle

Discussion relating age to life cycle events has to be in terms of estimated mean CL. The spread of carapace lengths about size class means (Fig. 3) indicated that most values in each class were within 5mm of the mean. So the age range for an individual of a given CL is likely to extend one year either side of the value indicated by the mean growth rate, for individuals up to ~60mm CL. This age range may increase as CL rises further due to variability in annual growth rates; but, broadening of the range is unlikely to be great, due to growth compensation. This process describes the interaction between higher growth of smaller individuals in a group and decreasing rates with increasing CL (Fig. 1), which causes a decrease in the spread of carapace lengths about a mean (Ricker 1975).

Average annual growth rates of mature females are typically smaller than those of

males and the immature female of comparable size (Turvey and Merrick 1997c). If the relationship between final carapace length (after one year) and initial CL remained constant for very large individuals (an asymptotic approach to some theoretical maximum size), it is predicted that the maximum CL attainable by individuals growing at the mean rate would be approximately 123mm. This is considerably greater than the largest individual (♀: 105mm CL) measured during the study; however, several larger specimens were captured at the study site, with carapace lengths estimated at 110–120mm, so the predicted maximum size is probably realistic.

Based on the mean annual growth rate, specimens with carapace lengths of 110 and 120mm would be approximately 22 and 39 years of age respectively; an individual of 100mm CL would be 16–17 years old. These predicted ages must, however, be viewed with some caution. Given the probability of dying during any year at any size, it is suggested that individuals surviving to a large size may have been the more rapidly growing individuals. The situation described for *E. spinifer* is similar to that reported for large *E. bispinosus*, where apparently the data don't support either a hyperbolic or linear approach to maximum size (Honan and Mitchell 1995b).

Despite variability due to the above factors, a number of points relating to the age composition of Loddon River populations are clear. Individuals with carapace lengths over 110mm were present and specimens of ~100mm CL were not uncommon. It is unlikely that any of these large *E. spinifer* sustained growth in excess of the maximum rate calculated, for any protracted period, and minimal ages for individuals of 100 or 110 mm CL have been estimated at 10 and 12 years respectively (Fig. 2). This means that *E. spinifer* at the study site regularly reach 10 years of age. While the higher ages estimated for larger individuals are subject to some uncertainty, the considerable period of constant average growth prior to the study suggests that these ages (22–39 years) may not be unrealistic.

The minimum CL at maturity of female *E. spinifer* is approximately 70mm, while normal males mature over the range 45–55mm CL. These carapace lengths indicate ages at maturity of approximately 8 and 5 years respectively, similar to the situation demonstrated in *E. bispinosus* (Honan and Mitchell 1995b). As Table 1 shows, a number of *Euastacus* species apparently have this characteristic slow or late maturity (5–9 years) at a considerable size (CL >40mm).

There are reliable reports of *E. spinifer,* in other catchments near the study site, regularly reaching weights of about 1.8 kg. From the length-weight relationship determined from study samples (Turvey 1980), individuals of this weight would have a CL of approximately 160mm. This is close to the maximum attainable size predicted for sustained growth at the maximum annual rate at the study site. Furthermore, the average maximum size of *E. spinifer* in catches has been observed to vary considerably between locations, so there is no reason to doubt that *Euastacus spinifer* attains the weight range indicated.

As Table 1 shows only eight *Euastacus* species are known to reach 120 mm CL. A weight of 1.8kg would rank *E. spinifer* among the largest known species of freshwater crayfishes in the world, behind *Astacopsis gouldi* (<4.0kg), *Euastacus armatus* (3.0kg), *E. bispinosus* (2.6kg) and *E. hystricosus* (~2.5kg).

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TABLE 1

Summary of size, maturity and age data for 34 *Euastacus* species (from Honan and Mitchell 1995a,b; Merrick 1993; Morgan 1986, 1988, 1989, 1991, 1997).

Species	Maturity Size (Age in years)	Maximum Size (CL in mm; Weight in kg)
Euastacus armatus	♀40 *(6–9)	250 (3.0)
Euastacus australasiensis	♀30–40	~60
Euastacus balanensis	♀~30	35
Euastacus bidawalus	♀>40	50
Euastacus bispinosus	♀55–85 (8–11)	>130 (2.6)
Euastacus brachythorax	♀40–50	~50
Euastacus claytoni	♀40–50	~60
Euastacus crassus	♀50–60; ♂30–40	~60
Euastacus dangadi	♀ 30–40	~45
Euastacus dharawalus	♀~40	~60
Euastacus diversus	♀>40	50
Euastacus eungella	♀>30	50
Euastacus fleckeri	♀>80	130
Euastacus gamilaroi	♀~40	>40
Euastacus gumar	♀>30	>35
Euastacus hirsutus	♀30–40	~45
Euastacus hystricosus	♀~60; ♂~40	200(~2.5)†
Euastacus kershawi	♀65–70; ♂~50	~160
Euastacus neodiversus	♀40	55
Euastacus neohirsutus	♀30–40	~45
Euastacus polysetosus	♀~40	~55
Euastacus reductus	♀25–30	~35
Euastacus rieki	♀40–50	~55
Euastacus robertsi	♀>30	55
Euastacus setosus	♀30	40
Euastacus simplex	♀~40	~55
Euastacus spinichelatus	♀~30	~40
Euastacus spinifer	♀70 (7–8); ♂55 (5–6)	160 (1.8)
Euastacus sulcatus	♀40; ♂30	~120
Euastacus suttoni	♀40–60; ♂20	~80
Euastacus valentulus	♀40	125
Euastacus woiwuru	♀40–60	75
Euastacus yanga	♀30–50	>60
Euastacus yarraensis	♀40	~80

*All CL values are rounded (to nearest 5mm)

†Conservative weight estimate based on comparative size

REFERENCES

Bennett, D.B. (1974). Growth of the edible crab *(Cancer pagurus* L.) off South-West England. *Journal of the Marine Biological Association of the United Kingdom* **54**, 803–823.

Berry, P.F. (1971). The biology of the spiny lobster *Panulirus homarus* (Linnaeus) of the east coast of southern Africa. *Investigational Report of the Oceanographic Research Institute of South Africa* **28**, 1–75.

Chittleborough, R.G. (1976). Growth of juvenile *Panulirus longipes cygnus* George on coastal reefs compared with those reared under optimal environmental conditions. *Australian Journal of Marine and Freshwater Research* **27**, 279–295.

Farmer, A.S. (1973). Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae). *Marine Biology* **23**, 315–325.

Hancock, D.A. (1965). Graphical estimation of growth parameters. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **29**, 340–351.

Harding, J.P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journal of the Marine Biological Association of the United Kingdom* **28**, 141–152.

Honan, J.A. and Mitchell, B.D. (1995a). Reproduction of *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and trends in the reproductive biology of freshwater crayfish. *Marine and Freshwater Research* **46** (2), 485–499.

Honan, J.A. and Mitchell, B.D. (1995b). Growth of the large freshwater crayfish, *Euastacus bispinosus* Clark (Decapoda: Parastacidae). *Freshwater Crayfish* **10**, 118–131.

Kurata, H. (1962). Studies on the age and growth of Crustacea. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* **24**, 1–115.

Mauchline, J. (1977). Growth of shrimps, crabs and lobsters - an assessment. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **37**, 162–169.

Merrick, J.R. (1993). 'Freshwater crayfishes of New South Wales'. (Linnean Society of New South Wales, Sydney).

Momot, W.T. (1967). Population dynamics and productivity of the crayfish, *Orconectes virilis*, in a marl lake. *American Midland Naturalist* **78**, 55–81.

Morgan, G.J. (1986). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda, Parastacidae) from Victoria. *Memoirs of the Museum of Victoria* **47**, 1–57.

Morgan, G.J. (1988). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda, Parastacidae) from Queensland. *Memoirs of the Museum of Victoria* **49**, 1–49.

Morgan, G.J. (1989). Two new species of the freshwater crayfish *Euastacus* Clark (Decapoda: Parastacidae) from isolated high country of Queensland. *Memoirs of the Queensland Museum* **27**, 555–562.

Morgan, G.J. (1991). The spiny freshwater crayfish of Queensland. *Queensland Naturalist* **31**, 29–36.

Morgan, G.J. (1997). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from New South Wales, with a key to all species of the genus. *Records of the Australian Museum, Supplement* (23), 1–110.

Ra'anan, Z., Sagi, A., Wax, Y., Karplus, I., Hulata, G. and Kuris, A. (1991). Growth, size rank, and maturation of the freshwater prawn, *Macrobrachium rosenbergii*: analysis of marked prawns in an experimental population. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* **181**, 379–386.

Ricker, W.E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**, 1–382.

Turvey, P. (1980). Aspects of the biology of the freshwater crayfish *Euastacus spinifer* (Heller) (Decapoda: Parastacidae). M.Sc. thesis, University of Sydney.

Turvey, P. and Merrick, J.R. (1997a). Reproductive biology of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Turvey, P. and Merrick, J.R. (1997b). Population structure of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia.*This volume.*

Turvey, P. and Merrick, J.R. (1997c). Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Weagle, K.V. and Ozburn, G.W. (1972). Observations on aspects of the life history of the crayfish, *Orconectes virilis* (Hagen), in northwestern Ontario. *Canadian Journal of Zoology* **50**, 366–370.

Conservation and Field Management of the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), in the Sydney Region, Australia

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Much of the natural range of *Euastacus spinifer*, in the Sydney region, is now included in the metropolitan and associated urban areas. Whilst a green belt of National Parks provides some reserves, these refuges are known to have been modified to varying degrees and many waterways outside Park boundaries are severely degraded.

Based on current biological knowledge of *E. spinifer* and experience with other *Euastacus* fisheries, a number of management options for this important macro-invertebrate are presented together with specific recommendations. Although effective conservation will require a number of interacting waterway and catchment programs, it is suggested that: recreational harvesting be restricted to the largest individuals (>85 mm CL) with small bag limits (5/person/day); a short annual closure (March-June) be declared; permanently closed areas be established with upgraded monitoring and response systems.

The ease of individual marking, sedentary behaviour, limited physiological tolerances, polytrophic status and longevity are all characteristics enhancing the potential of *E. spinifer* as a biological indicator. The types of catchment features, local habitat characteristics and biotic site data considered important for inclusion in quantitative habitat assessment for this crayfish, are briefly discussed.

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KEYWORDS: Management, conservation, freshwater crayfish, *Euastacus spinifer*, bio-monitor, habitat assessment.

INTRODUCTION

Conservation Status of Australian Crayfishes, Background

Some 33 Australian crayfishes have been reported as needing conservation attention (Horwitz 1995); of these, 14 are *Euastacus* species and one is found in New South Wales. Another, the Murray crayfish (*E. armatus*), is known to have undergone range reduction (Horwitz 1994; Versteegen and Lawler 1997). To date, recovery plans have not been developed for any of the threatened *Euastacus*.

The local situation relating to *Euastacus* in eastern New South Wales, was discussed by Merrick (1995), who also formulated general management recommendations; however, as much of its geographic range coincides with the extensive metropolitan area of Sydney as well as development surrounding the regional centres of Newcastle and Wollongong, the management of *Euastacus spinifer* needs urgent attention. A couple of observations about the exploitation of *Euastacus* are also relevant. Honan and Mitchell (1995) considered that another large species, *E. bispinosus*, with a similar life history could not sustain even moderate mortality rates. When discussing three large Victorian *Euastacus* species, Horwitz (1990) reported that the range of each had declined and implicated fishing pressure.

Fortunately, the acknowledgement of the need for integrative management of whole catchments has been accompanied by detailed studies relevant to local *E. spinifer* habitats. These include: research on soil erosion by Hannam (1995) in steep forested catchments; studies on parts of the Hawkesbury-Nepean System in relation to diversity of riparian vegetation (Benson 1995), its rehabilitation (Benson and Howell 1993), riparian vegetation corridors (Outhet et al. 1995) and their interactions with the waterway (Brooks 1995). Swales (1994) also discussed in-stream flows for fauna in N.S.W. rivers.

Management Options

The broad, commonly accepted management objectives (maintenance of resource sustainablility, maintenance of satisfactory recreation for users), expressed by Barker (1990) for other freshwater fisheries, also apply to *E. spinifer*. But, as Horwitz (1994) points out, effective protection cannot be achieved without adequate policing and intensive education of recreational users.

With recently published biological data (Turvey and Merrick 1997a,b,c,d,e) the potential now exists to define optimal environmental parameters and incorporate *Euastacus spinifer* management into local environmental plans. Furthermore this crayfish, among aquatic macro-invertebrates in the Sydney region, has good potential for long-term bio-monitoring.

Bio-monitoring

The use of biota to assess water quality and optimal criteria for selecting indicator species, as well as ways of assessing or rating impacts are questions still subject to much controversy; the situation in Australia is summarised by Bunn (1995). Bio-monitoring has been approached in a number of ways, using a wide variety of organisms (Norris and Norris 1995); however, several general conclusions can be drawn from experience. These are: that, whilst macro-invertebrates have been the most popular group, different key or indicator species (from widely disparate taxa) are probably necessary in different areas (Wright 1995); that many of the initial indices developed, based solely on biodiversity, have limited value (Norris and Norris 1995); that the most robust predictive systems now being developed involve a suite of contributing environmental and biotic characters (Harris 1995); that, using identified early warning features (such as enzyme change), the future predictive capacity of these models needs to be developed (Bunn 1995; Holdway et al. 1995); that interactive links must now be developed between assessment or monitoring models and field management.

Objectives of this paper are: to summarise biological and environmental baseline data into a series of major management criteria; to discuss management options, in relation to key biological cycles or previous experience with other *Euastacus* species and suggest specific interim measures; to explain the unusual features that make *E. spinifer* particularly suitable as a long-term biological indicator; and to outline types of data that should be incorporated in a quantitative predictive assessment model.

REVIEW AND DISCUSSION

Baseline Data, Life Cycle Strategy

Environmental and biological data, together with population observations, from previous studies are summarised under three major categories of requirements or management phases (Table 1). These criteria form the basis of a number of recommendations as options for any monitoring or conservation program.

Euastacus spinifer has a long-term, low mortality life cycle strategy which depends on individuals reproducing annually for many years (Turvey and Merrick 1997a). A unique feature of some *E. spinifer* populations is the presence of a significant percentage of very small but sexually mature males (Morgan 1997), designated as precocious males (Turvey and Merrick 1997a). The origins and benefits of this group remain unclear but there is evidence that the frequency of small size classes, may be related to the numbers of aquatic predators (Merrick 1995; Turvey and Merrick 1997b). A relatively sedentary nature makes *Euastacus* species susceptible to local predation (which includes over-fishing).

TABLE 1

Selected baseline data listed as major management criteria (summarised from Turvey and Merrick 1997a, b, c, d, e).

Feature	Range/Comment
ENVIRONMENTAL PREFERENCES	
Substrate	Sand or gravel, logs and some rock; decomposing terrestrial detritus (≥0.5 kg/m^2); some steep banks shaded by overhanging natural vegetation.
Macrophytes	Small beds of ribbon weed.
Water Conditions*	Low turbidity, salinity, temps (9–25°C), D.O. >6.0 p.p.m.
BEHAVIOUR PATTERNS, LIFE CYCLE	
Feeding, Mating	Peak activity at night — especially early evening (sunset to moonrise). Juveniles eat same foods as adults. Mating — Autumn (temps ↓15°C)
Non-migratory, Territorial	No dispersal phase, details unknown but home ranges small
Growth and Longevity+	Growth declines with age, males mature at ≥5 years (45–55mm CL), females at ≥8 years (~70mm CL). Individuals may survive for 20–40 years
KEY ANNUAL BIOLOGICAL PHASES	
Moulting†	Throughout warmer months in juveniles; seasonal peaks (Autumn, Spring) in medium-sized sub-adults; summer in large males and large females in Autumn (temps 22–15°C).
Reproduction‡	Spawning — Early Winter (at 10–11°C) Incubation (110–140 days) Larval attachment (28–70 days) in Spring to Early Summer. Juvenile release — Early Summer (20–24°C).

* Water parameters obviously vary (e.g. turbidity increases with flushes or flooding) but these fluctuations are short-term.

\+ Populations appear to support small numbers of large adults.

† Moulting frequency varies with age and is influenced by a number of factors, but most maturing and mature individuals moult at the times stated.

‡ The exact timing of the reproductive cycle may vary in different river systems.

As was found with *E. bispinosus*, environmental modification has probably led to reduction and fragmentation of *E. spinifer* populations; furthermore, Honan and Mitchell (1995) point out that local population sizes of *E. bispinosus* are relatively small. Many *E. spinifer* habitats are also small and only appear to support relatively small numbers of adults, which have a patchy distribution (Turvey and Merrick 1997b). This type of situation can pose special management difficulties in the maintenance of genetic heterogeneity.

Management Options

The Victorian and south-western New South Wales *Euastacus* fisheries have had closures (4–7 years) to allow for assessment and collection of baseline data (Barker 1990). *E. spinifer* fisheries have not been closed, although some of the discussion below draws on the findings of those closure studies mentioned above. As Table 2 indicates, restoring the aquatic system has two major aspects, the watercourse and bank areas. Stream bed restoration, in turn, involves maximising area of aquatic environment (by re-activating natural meandering reaches or subsidiary channels) and increasing diversity of habitats (with respect to features such as flow, substrate or cover). For example, to ensure adequate food and shelter in areas where a watercourse has been de-snagged, some logs or other woody debris should be replaced or allowed to accumulate. Programs for the complete reconstruction and rehabilitation of highly modified urban streams in western Sydney are currently in progress (Schaffer and Maelzer 1996).

Maintenance or establishment of small ribbon-weed beds has two direct benefits for *E. spinifer*. They provide potential cover, especially for juveniles, and macrophytes selectively extract metals and other compounds from water passing over them. So these plants act as in-stream filters. Another way of maintaining optimal water quality, especially high dissolved oxygen (DO) levels, is to increase or stimulate prolonged in-stream flow. This may be achieved in several ways: (a) negotiation with the managing authority of an upstream impoundment for increased releases; (b) restrictions on quantities of water that can be drawn or diverted from the stream; (c) modification or removal of an upstream impoundment structure that is no longer essential for catchment activities.

The importance of intact riparian zones, both for supplying energy and maintaining water quality, has been well documented (Bunn 1986). It has been reported that riparian zones are particularly badly effected by urbanisation (Adam 1995). Over much of the *E. spinifer* range natural riparian vegetation would comprise eucalypt sclerophyll forest or woodland with pockets of rainforest in sheltered situations (Australian Surveying and Land Information Group 1990; McLoughlin 1985); techniques for restoring these floristic complexes have been well developed (Friederich 1991).

The existing regulations relating to the New South Wales *E. armatus* fishery (NSW Fisheries 1994) are a useful framework on which local management can be based; but several specific modifications are necessary. The suggested minimum size (85–90mm) is high, both in relation to normal maturation sizes and maximum lengths attained by the species (Turvey and Merrick 1997a, e). The recommended bag limit is low in comparison with the catch limits set for *E. bispinosus,* which were apparently not effective. If tight controls are imposed initially, in the interests of sharing a limited resource, any subsequent relaxation would generate a positive user response. While the concept of uniform state-wide catch regulations is logical, with 24 *Euastacus* species of widely differing sizes and restricted distributions (Morgan 1997), it is not practical.

In Victorian fisheries *Euastacus* species can only be trapped during the breeding and brooding period, at other times of the year adults are inactive and inaccessible, so breeding season closures are unworkable (Barker 1990). This natural cessation of cray activity does not occur with *E. spinifer* and it can be caught at most times of the year. What is proposed is a short closed season coinciding with the peak moulting and mating activity of harvestable adults. Although researchers have previously suggested removing closures for other *Euastacus* fisheries (Barker 1990), it is strongly recommended that some closed areas be retained for *E. spinifer*. There are several reasons for this: the documented regional variability in the species; the continued existence of large populations only in areas with limited public access and little urban impact; reduction of potential problems in areas difficult to monitor. This type of strategy was also suggested for the giant Tasmanian freshwater crayfish, *Astacopsis gouldi*, which is widespread with a simi-

lar life cycle and subject to the same types of threatening processes and exploitation. Horwitz (1994) proposed adequate reservation by measures such as restricting fishing in National Parks or Forestry reserves.

To take advantage of the nocturnal activity cycle all sampling would be best done in the early evening; however, aside from initial surveys to gather local or populational baseline data, subsequent handling should be minimal to alleviate any risks of physiological stress. As individuals remain in limited areas for long periods of time, mark-recapture projects are recommended; the animals are easily marked (Merrick 1993; Turvey and Merrick 1997b) or externally tagged. Monitoring programs of this kind have already commenced with several Victorian *Euastacus* species (Barker 1992).

Whilst remembering that as many populations should be conserved as possible, to retain genetic heterogeneity (Versteegen and Lawler 1997), the recovery phase for *E. spinifer* may be a long-term process. In areas where populations have been dramatically reduced, or where local extinctions have occurred, culturing and repeated stocking may be necessary for periods of 8–10 years. This will allow for the slow individual growth and sexual maturity and enable natural recruitment to become significant. Techniques for culturing *Euastacus* species are summarised in Merrick (1997).

It may also be necessary to actively control other large carnivorous species in the system. Significant numbers of predators such as eels, cod, cormorants or water rats would negate the benefits of cray stocking or other riparian restorative measures (Barlow and Bock 1984; Sokol 1988). Control could involve culling or regulation of in-stream migrations.

Despite the active involvement of many community groups (such as bush regenerators, anglers, students, naturalists, scouts or youth clubs) in different aspects of management the effectiveness of any initiatives will ultimately depend on comprehensive patrolling. This is unfortunately essential because the areas of concern are accessible and adjacent to large human populations; there is a constant threat of illegal activity (e.g. dumping, arson) or pollution accidents. Whilst many factors can and will impact on these urban or semi-rural *E. spinifer* habitats the author considers the major threats to be fire, chemical pollution and introduced species.

There are two important aspects of fire management that relate to riparian zones. Wet sclerophyll and rainforest communities are particularly badly effected by fire, as they are less resilient in regenerating than other drier communities (Friend 1996). Then, although fire control regimes are still subject to much controversy, it is clear that rapid containment is essential otherwise the intensity of the blaze quickly builds to uncontrollable levels (Adams and Simmons 1996; Incoll 1996).

There are several considerations relating to chemical pollution. The waterways concerned are small (in size, volume, flow rates) and so have limited capacity to buffer or dilute the impacts of intermittent spills or continued small releases. At least some pollutants would lodge in the substrates or sediment and persist in the system, possibly for long periods after release of the toxins was stopped. Details of exact sites are not readily available, but it is known that Sydney and associated long-established areas have a number of pollution 'hot spots'; these pose longstanding and on-going environmental management problems.

A summary of the main pollutants, sources and effects on water quality in local urban waterways is included in Essery (1995). Although some data are available on toxicities and system interactions of a few major industrial pollutants (Chapman 1995), the effects of many other compounds (such as synthetic hormones or related derivatives) have not been considered locally, but problems caused by these substances have been identified elsewhere (Jobling and Sumpter 1993; Jobling et al. 1996).

Introduced species (exotic or non-indigenous forms) pose two major biotic threats; the first is ecological disruption and or direct competition for limited resources, the second is disease. The problems of introductions and translocations of aquatic organisms

have been well documented (Courtenay 1990; Horwitz 1995) and need not be repeated here, but the potential for disease transmission is more insidious. Unfortunately recent research on aquatic diseases indicates that many groups of parasitic micro-organisms can utilise a variety of hosts, transferring from one group to another depending on circumstances (Semple 1995).

It is emphasised that while the detailed, field-oriented suggestions (Table 2) relate specifically to identified local problems, they should be considered in conjunction with broader conservation management initiatives (Merrick 1995).

TABLE 2

Summary of specific management recommendations for *Euastacus spinifer* (based on Barker 1990; Honan and Mitchell 1995; Merrick 1993, 1995; Turvey and Merrick 1997a, b, c, d, e).

1. Initiate research programs on:
   (a) detailed nutritional requirements;
   (b) interactions with *Cherax destructor*;
   (c) the relationship of predation by eels to population structure and recruitment;
   (d) tolerances to major chemical pollutants identified in waterways of range.

2. Restore aquatic habitat by:
   (a) allowing woody debris to accumulate in watercourse, re-establishing selected macrophytes;
   (b) restoration and protection of riparian zones.

3. Improve water quality by:
   (a) identifying and removing sources of pollution;
   (b) modifying structures impeding water flow and aquatic faunal movement (*).

4. Convert the *E. spinifer* fishery to a sport category with strict regulations, including:
   i a high minimum size (e.g. 85–90mm CL);
   ii only males to be retained when catches approach bag limit (e.g. 5 person/day);
   iii berried females to be released immediately;
   iv bans on trapping from mid-March to mid-June (peak moulting, mating period);
   v permanent exclusion zones (closed waters) or refuges in less accessible areas.

5. Establish comprehensive field monitoring and an effective patrolling organisation (with appropriate legal powers) for long-term management.

(*) Maintaining a minimal environmental flow will be critical during severe conditions, such as drought.

Bio-monitoring

A wide range of aquatic organisms have been suggested as bio-indicators of waterway health (Cullen 1990) but, aside from its ecological importance in local fluviatile systems, *E. spinifer* has several special features which make it particularly suitable as a key indicator species in the long-term in the Sydney region.

With relatively narrow tolerances for oxygen and temperature this cray would be sensitive to organic pollution with a high oxygen demand; it would also react to ther-

mal pollution. As a result of its polytrophic role *E. spinifer* is also exposed to accumulated pollutants at all major levels of the aquatic food chain. This large invertebrate is easy to monitor in a confined area, so population disruptions would be a sensitive indicator of point source problems. Furthermore, the work on *E. bispinosus,* indicates that it cannot sustain any significant pressure or mortality. Finally, the longevity of *E. spinifer* makes it an ideal subject for bio-accumulation studies and assessment of sublethal or chronic impacts.

Habitat Assessment Model

Recent fishery management forums and studies have logically placed a high priority on habitat (Cadwallader 1993; Hancock 1993; Lawrence 1991); but the emphasis has been on fishes and their requirements, which do not necessarily coincide with optimal conditions for invertebrates. Chessman (1995) developed an assessment method for macro-invertebrates in the Sydney region but, although useful, this system needs further refinement by inclusion of more environmental factors that are important for crayfishes.

Chessman's assessment is based on standardised collection of a range of aquatic invertebrates from up to six defined stream habitats; a biotic index is then calculated on the basis of sensitivities of taxa (at family level) to common pollutants. The disadvantages of this model, in relation to *E. spinifer*, include the acknowledged interspecific variation in tolerance to particular types of pollutants and potential errors in occurrence ratings, with a favourable small habitat only supporting a small number of large individuals. Although substrates are considered indirectly, cover and food availability (amounts of litter) are not included. Neither flow nor depth, factors known to significantly affect abundance in crayfishes, are considered in detail and levels of natural predation are not assessed. Finally, the states of immediate riparian zones are not included.

Perhaps these parameters could be incorporated in the development of a general regional bioassessment system based on an Index of Biotic Integrity or IBI (Harris 1995) or the River Invertebrate Prediction and Classification System (RIVPACS) concept (Wright 1995). Fortunately the Sydney region is now sufficiently documented (Chessman 1995; Growns et al. 1995) that much of the required reference data would be available.

Although *E. spinifer* is now considered one of the more widespread *Euastacus* species (Morgan 1997) the total natural range also coincides with the most densely populated and highly developed coastal areas in the state. In this instance, there is no alternative to more active management, to upgrade monitoring and protection in existing reserves and to maintain environmental quality in other areas. Opportunities for creating additional reserves in this highly developed region are very limited. So successful conservation programs developed for crayfishes around Sydney will be useful in local sustainable environmental management in many other areas. As Horwitz (1995) points out most fisheries and environmental protection legislation in Australia now contains sections that require relevant authorities to control processes which degrade water quality, so theoretically, many of the threatening processes are controllable; however, for remedial measures to be invoked locally the species has to be recognised as threatened and in need of regulatory protection

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REFERENCES

Adam, P. (1995). Urbanization and transport. In 'Conserving biodiversity: threats and solutions'. (Eds R.A. Bradstock, T.D. Auld, D.A. Keith, R.T. Kingsford, D. Lunney and D.P. Sivertsen) pp. 55–75. (Surrey Beatty & Sons Ltd., Chipping Norton).

Adams, R. and Simmons, D. (1996). The impact of fire intensity on litter loads and understorey floristics in an urban fringe dry sclerophyll forest and implications for management. In 'Fire and biodiversity. The effects and effectiveness of fire management. Proceedings of the Conference held 8–9 October 1994, Footscray, Melbourne'. pp. 21–35. (Department of the Environment, Sport and Territories, Canberra).

Australian Surveying and Land Information Group. (1990). 'Atlas of Australian resources. Third series. Volume 6. Vegetation'. (Australian Government Publishing Service, Canberra).

Barker, J. (1990). Spiny freshwater crayfish management strategy. *Fisheries Management Report* (34), 1–17. *Department of Conservation & Environment, Melbourne.*

Barker, J. (1992). The spiny freshwater crayfish monitoring program, 1990. *Fisheries Management Report* (44), 1–31. *Department of Conservation & Environment, Melbourne.*

Barlow, C.G. and Bock, K. (1984). Predation of fish in farm dams by cormorants, *Phalacrocorax* spp. *Australian Wildlife Research* **11**, 559–566.

Benson, D. (1995). Vegetation interactions with rivers: plant biodiversity associated with riparian and floodplain corridors. In 'Geomorphology and river health in New South Wales'. (Eds G.J. Brierley and F. Nagel) pp. 81–84. (Graduate School of the Environment, Macquarie University).

Benson, D.H. and Howell, J. (1993). 'A strategy for the rehabilitation of the riparian vegetation of the Hawkesbury-Nepean River'. (Royal Botanic Gardens, Sydney).

Brooks, A. (1995). Vegetative interaction with rivers: morphodynamic associations - implication for river health. In 'Geomorphology and river health in New South Wales'. (Eds G.J. Brierley and F. Nagel) pp. 49–66. (Graduate School of the Environment, Macquarie University).

Bunn, S.E. (1986). Origin and fate of organic matter in Australian upland streams. In 'Limnology in Australia'. (Eds P. De Deckker and W.D. Williams) pp. 277–291. (CSIRO/Junk,Melbourne).

Bunn, S.E. (1995). Biological monitoring of water quality in Australia: workshop summary and future directions. *Australian Journal of Ecology*, **20** (1), 220–227.

Cadwallader, P.L. (ed). (1993). 'Freshwater fisheries in Victoria - today and tomorrow. Symposium Proceedings, Radisson President Hotel, Queens Road, Melbourne, 11 October 1992'. (Department of Conservation and Natural Resources, Victoria).

Chapman, J.C. (1995). The role of ecotoxicity testing in assessing water quality. *Australian Journal of Ecology* **20** (1), 20–27.

Chessman, B. (1995). Rapid assessment of rivers using macroinvertebrates: a procedure based on habitat - specific sampling, family level identification and a biotic index. *Australian Journal of Ecology* **20** (1), 122–129.

Courtenay, W.R. Jnr. (1990). Fish introductions and translocations and their impacts in Australia. In 'Introduced and translocated fishes and their ecological effects'. (Ed D. A. Pollard) pp. 171–179. (Australian Society for Fish Biology Workshop, Bureau of Rural Resources Proceeding 8).

Cullen, P. (1990). Biomonitoring and environmental management. *Environmental Monitoring and Assessment* **14**, 107–114.

Essery, C. (1995). Geomorphology and water quality. In 'Geomorphology and river health in New South Wales.' (Eds G.J. Brierley and F. Nagel) pp. 131–136. (Graduate School of the Environment, Macquarie University).

Friederich, R. (1991). Management of rainforest in national parks and equivalent reserves in northern New South Wales. In 'The rainforest legacy. Australian National Rainforests Study. Volume 3'. (Eds G. Werren and P. Kershaw) pp. 216–230.(Australian Heritage Commission, Special Australian Heritage Publication Series 7).

Friend, G. (1996). Fire ecology of invertebrates - implications for nature conservation, fire management and future research. In 'Fire and biodiversity. The effects and effectiveness of fire management. Proceedings of the Conference held 8–9 October 1994, Footscray, Melbourne'. pp. 155–162. (Department of the Environment, Sport and Territories, Canberra).

Growns, J.E., Chessman, B.C., McEvoy, P.K. and Wright, I.A. (1995). Rapid assessment of rivers using macroinvertebrates: case studies in the Nepean River and Blue Mountains, NSW. *Australian Journal of Ecology* **20** (1), 130–141.

Hancock, D.A. (ed). (1993). 'Sustainable fisheries through sustaining fish habitat. Australian Society for Fish Biology Workshop, Victor Harbor, SA, 12–13 August 1992'. (Bureau of Resource Sciences Proceedings, AGPS, Canberra).

Hannam, I. (1995). Soil conservation in steep forested catchments in New South Wales. In 'Geomorphology and river health in New South Wales'. (Eds G.J. Brierley and F. Nagel) pp. 31–39. (Graduate School of the Environment, Macquarie University).

Harris, J.H. (1995). The use of fish in ecological assessments. *Australian Journal of Ecology* **20** (1), 65–80.

Holdway, D.A., Brennan, S.E. and Ahokas, J.T. (1995). Short review of selected fish biomarkers of xenobiotic exposure with an example using fish hepatic mixed-function oxidase. *Australian Journal of Ecology* **20** (2), 34–44.

Honan, J.A. and Mitchell, B.D. (1995). Catch characteristics of the large freshwater crayfish, *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and implications for management. *Freshwater Crayfish* **10,** 57–69.

Horwitz, P. (1990). The conservation status of Australian freshwater crustacea. *Australian National Parks and Wildlife Service Report Series* (14), 1–121.

Horwitz, P. (1994). Distribution and conservation status of the Tasmanian giant freshwater lobster *Astacopsis gouldi* (Decapoda: Parastacidae). *Biological Conservation* **69**, 199–206.

Horwitz, P. (1995). The conservation status of Australian freshwater crayfish: review and update. *Freshwater Crayfish* **10**, 70–80.

Incoll, R. (1996). Asset protection in a fire prone environment. In 'Fire and biodiversity. The effects and effectiveness of fire management. Proceedings of the Conference held 8–9 October 1994, Footscray, Melbourne'. pp. 213–217. (Department of the Environment, Sport and Territories, Canberra).

Jobling, S., Sheahan, D., Osborne, J.A., Matthiesen, P. and Sumpter, J.P. (1996). Inhibition of testicular growth in rainbow trout (*Oncorhynchus mykiss*) exposed to estrogenic alkylphenolic chemicals. *Environmental Toxicology and Chemistry* **15** (2), 194–202.

Jobling, S. and Sumpter, J.P. (1993). Detergent components in sewage effluent are weakly oestrogenic to fish: an in vitro study using rainbow trout (*Oncorhynchus mykiss*) hepatocytes. *Aquatic Toxicology* **27**, 361–372.

Lawrence, B.W. (1991). 'Fish management plan'. (Murray-Darling Basin Commission, Canberra).

McLoughlin, L. (1985). The middle Lane Cove River. A history and a future. *Centre for Environmental and Urban Studies (Macquarie University), Monograph* (1), 1–175.

Merrick J.R. (1993). 'Freshwater crayfishes of New South Wales'. (Linnean Society of New South Wales, Sydney).

Merrick, J.R. (1995). Diversity, distribution and conservation of freshwater crayfishes in the eastern highlands of New South Wales. *Proceedings of the Linnean Society of New South Wales* **115**, 247–258.

Merrick, J.R. (1997). 'Freshwater fish and cray farming in Australia'. (J.R. Merrick Publications, Sydney).

Morgan, G.J. (1997). Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from New South Wales, with a key to all species of the genus. *Records of the Australian Museum, Supplement* (23), 1–110.

Norris, R.H. and Norris, K.R. (1995). The need for biological assessment of water quality: Australian perspective. *Australian Journal of Ecology* **20** (1), 1–6.

NSW Fisheries. (1994). Fisheries Management Act 1994 - Regulation. (Fisheries Management (General) Regulation 1994). (New South Wales Government, Sydney).

Outhet, D., Duckham, J., Stewart, D., Ardill, S. and Holics, M. (1995). Riverine corridor vegetation-Nepean River and tributaries - Wollondilly Local Government Area. In 'Geomorphology and river health in New South Wales'. (Eds G.J. Brierley and F. Nagel) pp. 67–79. (Graduate School of the Environment, Macquarie University).

Schaffer, B. and Maelzer, B. (1996). 'Restoring the waters project'. (Australian Conservation Foundation, Sydney).

Semple, G.P. (1995). Occurrence of pathogenic *Thelohania* (Microsporida: Nosematidae) in the Australian freshwater crayfish, *Cherax quadricarinatus* (Decapoda: Parastacidae). *Proceedings of the Linnean Society of New South Wales* **115**, 225–231.

Sokol, A. (1988). The Australian yabby. In 'Freshwater crayfish: biology, management and exploitation'. (Eds D.M. Holdich and R.S. Lowery) pp. 401–425. (Croom Helm Ltd., London).

Swales, S. (1994). Streamflow requirements for fish in NSW rivers - the role and importance of flushing flows. In 'Proceedings of the environmental flows Seminar, Canberra 25–26 August 1994'. pp. 178–183. (Australian Water and Wastewater Association, Sydney).

Turvey, P. and Merrick, J.R. (1997a). Reproductive biology of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Turvey, P. and Merrick, J.R. (1997b). Population structure of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Turvey, P. and Merrick, J.R. (1997c). Diet and feeding in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Turvey, P. and Merrick, J.R. (1997d). Moult increments and frequency in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Turvey, P. and Merrick, J.R. (1997e). Growth with age in the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. *This volume.*

Versteegen, M. and Lawler, S. (1997). Population genetics of the Murray River crayfish *Euastacus armatus*. *Freshwater Crayfish* **11**, (in press).

Wright, J.F. (1995). Development and use of a system for predicting the macroinvertebrate fauna in flowing waters. *Australian Journal of Ecology* **20** (1), 181–197.

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