Adey + Farrier, 1989

The Biology, Ecology and Mariculture of Mithrax spinosissimus, Utilizing Cultured Algal Turfs

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PREFACE

This publication consists primarily of an integrated set of papers treating the efforts of the Marine Systems Laboratory from 1983-1986 to develop a low cost, itinerant fishermen mariculture for Mithrax spinosissimus, the West Indian Red Spider Crab or Caribbean King Crab. Efforts to develop such a mariculture derive directly from our increasing understanding of the potential for the utilization of cultured marine algae in coastal Caribbean waters. A discussion of the biology and culture methods developed for algal turfs, as well as methods for feeding this algal production to Mithrax spinosissimus crabs, is also presented along with the biology, ecology and mariculture of the crab itself.

For many decades, it has been accepted that primary production on shallow water tropical coral reefs is among the highest of any natural community on earth. Indeed, at a level of 5-25 g dry m^{-2} d^{-1}, it generally exceeds that of the best agriculture (Lewis, 1977; Adey and Steneck, 1985). Since most coral reefs occur in seas with extraordinarily low nutrient concentrations, it has generally been assumed that rapid recycling processes, or perhaps local input of nitrogen and phosphorus is occurring to allow such high levels of production (Adey, 1987). Unfortunately, given both the recycling requirement, as well as the sensitivity of coral reef communities to perturbations of any nature, including fishing and elevated nutrients, it has seemed unlikely to most reef scientists and mariculturists that high reef production was of more than academic interest.

During the past decade, a series of laboratory studies, with coral reef microcosms, and field studies, using a variety of techniques, have demonstrated that the source of high primary production is in the dense algal turf mat that covers a major part of most shallow water reef substratum. These studies have also shown that elevated production levels are real (i.e., not an artifact of methodology), can be harvested and under the high physical energy environmental conditions common to coral reefs, are indefinitely sustainable under low nutrient conditions (Adey, 1982, 1983, 1987; Adey and Steneck, 1985; Adey and Goertemiller, 1987). Algal turfs are highly diverse (20-30 species on a single square meter screen), and a typical, cultured community includes taxa of most major algal groups. Polyculture harvest of algal turfs is appealing as a potential mariculture because it avoids the built-in disadvantages (particularly inherent instability) of monocultural agriculture (Doyle, 1985).

The possibility of a mariculture based on the relatively simple and low cost artificial substratum-grown algal turf technology was quite interesting in terms of potential adaptability to local populations in third world, tropical countries. During early 1983, support from the Bioenergy

Council, Earthwatch and the United States Department of State for the potential development of a low technology mariculture in Caribbean waters led to the Agency for International Development's (AID) interest in developing a low cost algal turf mariculture.

Earlier Marine Systems Laboratory microcosm and field work had identified several turf grazers within reef environments which could have mariculture potential. One of these, <u>Mithrax spinosissimus</u> (the West Indian Red Spider Crab or Caribbean King Crab), a large and tasty animal, is a gourmet fishery item of low volume interest in several Caribbean and South American countries. It has been the subject of some previous research (Munro, 1974; Hazlett and Rittschoff 1975; Bohnsack, 1976; Brownell <u>et al</u>., 1977; and Provenzano and Brownell, 1977). While all of these authors had investigated <u>Mithrax spinosissimus</u> for potential fishery or mariculture utilization, the general conclusion was that the animal was not abundant enough to form a fishery and grew too slowly to have viable mariculture potential. Based on Marine Systems Laboratory preliminary research in both the field and laboratory, <u>M. spinosissimus</u> was deemed hardy, both in the wild and in microcosm culture, with growth rates exceeding those presented in the literature (Bohnsack, 1976). With regard to Bohnsack's studies, and MSL follow up studies partially described herein, there was and still remains some concern that the Florida population is a separate species or sub-species.

In 1983, the Marine Systems Laboratory submitted a proposal to AID and was eventually funded by that agency, specifically to attempt to develop a low cost, itinerant fishermen mariculture in several Caribbean countries.

This treatise summarizes the information available to date regarding this species and its preferred food, algal turfs. It also presents the results of a three-year effort in a variety of Caribbean locations and environments on the biology, ecology and mariculture of the Caribbean King Crab. The approaches presented here are not the only possibilities for a mariculture of this animal. We specifically avoided any extensive efforts to develop a mariculture that appeared to have limited value for an itinerant fishermen mariculture or did not utilize algal turfs as a food source. Commercial modifications to the methods described herein would appear to have considerable potential.

Mithrax spinosissimus is a large spider crab that is primarily a herbivore. In the wild, it feeds mostly on algal turfs and, like a number of similarly adapted crabs, has specially-developed claws for handling these small algae (Coen, 1987). It also posesses specialized grinding teeth in a "gizzard" or anterior stomach. In addition, larval rearing is brief (40-72 hours to settling at megalops and 70-90 hours to first crab) and relatively simple (planktonic feeding regimes and required conditions for such feeding appear to be unnecessary).

As adults these crabs also have a harem-type social structure in which excessive aggressive behavior is generally avoided. It is relatively docile in character. Its primary defenses lie in nocturnal behavior, an ability to cling tightly to the substratum and its large adult size. The latter two characteristics provide strong and extensive body musculature (i.e., considerable body meat). When crowded, juvenile Mithrax crabs sometimes kill many of their cohorts, perhaps in response to a common tendency for heavy local settlement when conditions for propagation are ideal. This may provide an area of concern for mariculture. On the other hand, fecundity is very high, each female brooding about 300,000 eggs during her reproductive life.

In culture, growth rates for M. spinosissimus are relatively high (12-15 months to maturity). Considering the highly cryptic nature of immatures of the species, it would appear that rapid growth is to a large extent genetically determined and achieves a major species survival element in the large size of the adults.

M. spinosissimus populations vary widely from locality to locality, suggesting minimum gene transfer and a relative plasticity in a shallow water organism with a very short planktonic phase. Since the animal breeds easily in captivity, stock improvement with breeding seems assured.

All of these characteristics together suggest considerable mariculture potential without the great difficulties that accompany culture in most crabs and lobsters.

INTRODUCTION

The basis for the Mithrax spinosissimus (Caribbean King Crab) mariculture described in this set of papers lies in the screen culture of algal turfs. There is little question that the production of a highly diverse algal turf, at a level of 8-18 g dry m^{-2} d^{-1}, is routinely possible at a wide variety of Caribbean sites at which Mithrax crab mariculture can be practiced. Algal production is affected by the characteristics of the screen material and by the way in which it is oriented in the water column. It is affected strongly by turbulence (the strength of ambient current and surge), depth, harvest rate and continuity as well as atmospheric cloudiness. These factors are now reasonably well understood in field practice by MSL. The role of carbonate sedimentation in limiting algal turf production is now better understood and managed (in terms of site selection and harvest criticality) on more of a qualitative basis. A more quantitative understanding of the role of sedimentation in limiting algal turf culture is needed.

Carbon levels appear low (15-20%) in algal turfs cultured in open Caribbean waters and nitrogen levels (6-8%) are relatively high. Low carbon content is also a characteristic of many of the individual species that make up the turf. Blue-green algae have largely proteinaceous walls and diatoms have siliceous frustules. Both of these groups are major turf components. On the other hand, laboratory cultured turfs with few diatoms have relatively high levels of carbon (28-30%). Carbonate siltation is certainly a factor in low organic carbon, though, it does not explain the low carbon levels occurring in samples of individual plant components. Preparation and preservation procedures for these "volatile" plants is strongly suspect and should be further examined.

In any case, algal turfs are highly productive, rich in protein and generally lack protective "toxic" compounds and the tough walls and skeletons that characterize many macroalgae. They also appear to be preferred by Mithrax spinosissimus, as well as a wide spectrum of vertebrate and invertebrate grazers. The high growth rates consistently found in culture and given below for juvenile Mithrax spinosissimus are based primarily on algal turf feeding. Work currently underway at Grand Turk using pure algal turf cultures have given similar high growth rates that point to to an adult crab in 12-15 months.

In order for this new form of algal production to be used as fodder, an efficient transfer method from algal culture to grazer culture is essential, regardless of the absolute level of plant production available. The system that we have devised and describe in detail in this set of papers averages a transfer rate of about 5-8 screens (0.5 m^2 each, cultured for 12 days) every three to four days for 50 older juvenile crabs (greater than 30 mm). This process is labor intensive; however, the development of a "low tech," low capital cost mariculture was a primary objective of this project. Considerable improvements can be made in the transfer process. For example, the current transfer methods can certainly be improved greatly through the mass movement of screens using specially-designed small outboard-powered boats (catamarans, e.g.) equiped with simple power winches such as those that are used widely in lobster fisheries.

Mithrax spinosissimus is a large, tasty, meat-rich animal that already forms the basis of a small gourmet fishery in several Caribbean countries. At most Caribbean sites for which we have adequate population data, average adult males exceed 1.5 kg in weight and average adult females exceed 1 kg in weight. Antigua crabs are a little smaller and Florida crabs are much smaller. Some negative comment has been received by MSL from North American crustacean marketing specialists with regard to the color, thickness and encrusted nature of the carapace, which they feel may prevent it from being an "ideal" or top value restaurant product. However, these observations refer to the Florida collected crabs that are more greenish brown in color (and are a much smaller animal). They also refer to an adult animal that is on the average several months post-molt. Cultured Caribbean crabs are quite red in color and have rather thin shells. Since, in culture, they would be harvested relatively soon following a molt, they would lack encrustations.

In the Caribbean/West Indian region, wild Mithrax spinosissimus crab populations, rather uniform at each site vary widely from island to island. At most locales, the collection process has been extensive and varied. It is highly unlikely that the population characteristics derive from sampling bias. This variation most likely results from their short larval time and therefore limited gene transfer from pool to pool. Florida "Mithrax spinosissimus," somewhat isolated from the Caribbean populations and subject to very different yearly weather and mean habitat conditions, is much smaller than its Caribbean counterparts. It differs more subtly in a wide variety of ways and may be a different species or subspecies. In any case, because breeding is so easily accomplished with Mithrax spinosissimus, the possibility of considerable stock "improvement" in the future certainly exists.

Mithrax spinosissimus populations tend to have a weak "harem" type of social structure, with scattered or even sparsely distributed "colonies" of a few to many females accompanied by several males. These animals are nocturnal and tend to remain close to their home crevice or cave. "Bachelor" males wander more widely and, while still crevice and nocturnally oriented, they are frequently found alone on open pavement. Our observations on hundreds of adults from several sites show that this species as adults accomodates well to cage culture. While some "jostling" for space and male competition for females occurs, it seems clear that adult intra-species aggression is not an important mortality consideration. There appears to be juvenile mortality during molts resulting from crowded conditions in cages and we are now in the process of developing shore based experimental systems at Grand Turk, so as to allow careful observation of growing dense juvenile populations.

Mithrax spinosissimus mate in the hard shell state, after the molt to maturity. It seems likely that multiple fertilizations, as well as routine sperm storage, do occur. In captivity, an average female produces four to five broods with a mean of 60,000 eggs each. The female is ovigerous for about 30 days, producing a brood about every two months. Experience with hundreds of animals from several sites has demonstrated that with 20-25 adult crabs, roughly 70-80% female, a hatch per week can be routinely achieved and easily managed in a cage culture system. The methods for accomplishing this process are described in detail in the text.

Many thousands of hatchlings have been raised in cage culture in this project to 100-120 days of age in a standard two-step process that is described in detail. Most recently, 200-300 animals per hatch were routinely produced at 120 days, in a procedure that at Buen Hombre, Dominican Republic, was easily understood and managed by the local fishermen working with the project. Considering the ease by which this can be accomplished, this is certainly sufficient at this time for a successful itinerant fishermen mariculture. In any case, steady improvement in the survival rate has been attained and we predict that 500-600 animals per hatch at 120 days of age can be achieved for this crab, with present methods. In the text, we discuss several problems and the steps by which this improvement can be achieved. For a commercial mariculture or a government supported fisherman mariculture, a hatchery process can probably be developed which would improve considerably 100-day survivorship.

In the last six months of the project, we routinely achieved growth rates of about 0.21 mm/day (carapace length) in a growout from first crab through seven to nine instars at 100 days. From that time to about 300 days, mean growth rates of about 0.35 mm per day were achieved through another six to seven instars. These crabs were fed primarily algal turfs with an occasional supplement of a variety of macroalgae. Recent work at Grand Turk has achieved the same growth rates with a diet of pure algal turf. We have little statistically significant data from that point on, but these rates strongly indicate that for a marketable adult of 120 mm carapace length, 360-500 days would be required. We believe that growout to a marketable adult can be routinely achieved in an itinerant fishermen cage culture in about 400 days, though this has yet to be demonstrated in large numbers.

Steady mortalities of about 80% per 100 days have reduced the prepubertal crabs that we have raised in cage culture to a few individuals at the molt to adult. There are no indications of serious disease or nutrition factors involved in these mortalities. Ryther, et al. (1987) found disease a serious problem in culture. However, nitrate levels of 35 mg/l (compared with typically 1 to 7 X 10^{-3} mg/l in the wild) indicate serious water quality problems. At two sites, Carriacou and Grand Turk (in the 1983-1987 period), logistics, finances and timing prevented crab growout beyond a three to six month period. Nonsuch Bay, Antigua was our only environmentally poor site, where we were restricted in the later stages of growout, also for reasons not related to crab biology or mariculture management. At Buen Hombre, Dominican Republic sufficient time was available to gain minimum experience in the 300-500 day range and some crabs were brought to reproductive maturity by local fishermen participating in the project. However, even here, logistic and political problems minimalized that experience.

Our successful experience and continual improvement in reducing mortalities in bringing 200 to 300 Mithrax spinosissimus per hatch to 100 days in open water cage culture is promising. We are continuing to work on providing in cage molt protection in a variety of forms and a more efficient turf transfer process. It seems likely that a survivorship of greater than 50% per 100 days can be achieved from 100-400 days. This would render the process successful, at least on a minimal basis. With more experience in managing the details of the culture process, it is likely that within a relatively short period of time, 30% survivorship can be achieved from first crab to 100 days (to produce 600 juveniles per hatch for adult growout), as well from that time to market size (for a total of 180 market animals per hatch). This is sufficient to provide a successful and competitive process for the itinerant fisherman who can easily produce a hatch several times per month.

We feel strongly that all indicators remain positive for the completion of a successful itinerant fishermen mariculture of Caribbean King Crab, based on algal turf culture. Success is likely to lie in improving the details of cage structure and operation (the removal of waste without predator introduction and in providing molt protection for individuals against their cohorts and rough weather) and in the improved management of algal screen transfer. Ultimately, low-cost, mass-produced plastic cages would greatly reduce the time and cost to the individual fisherman.

Note that in this volume we chose to measure carapace length (CL) rather than carapace width (CW), which is the standard for crab biology. This was done to provide a more accurate measurement for this species when hundreds of individuals, some quite small need to be sized. A relationship for CW = f (CL) is provided in figure 5 (Biddlecomb, et al., this volume).

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SECTION I: ALGAL TURF PRODUCTION

THE COMPOSITION AND PRODUCTION OF TROPICAL MARINE ALGAL TURFS IN LABORATORY AND FIELD EXPERIMENTS

THE COMPOSITION AND PRODUCTION OF TROPICAL MARINE ALGAL TURFS IN LABORATORY AND FIELD EXPERIMENTS

W. H. Adey and J. M. Hackney

Abstract

Laboratory and field studies in the Caribbean region with cultured algal turf communities have demonstrated consistent primary production levels of 8 to over 15 g (dry)/sq. m/day. A wide variety of environmental factors that control this production, including wave action, current, harvest rate and substratum type, are discussed in detail.

Tropical screen-cultured algal turfs are highly diverse (typically 30-40 species). Algal screens are dominated by benthic diatoms, during early development. At maturity, under a 7-20 day harvest regime, blue-green and red algae, with epiphytic diatoms, come to dominate the community.

Carbon percentages, as measured by CHN analyses, are relatively low (14-30%) in algal turfs, in large part due to the siliceous cell walls of diatoms and the proteinaceous cell walls of blue-green algae. Also, in the field, even properly-managed algal turf screens contain some carbonate silt. On the other hand, protein levels are high (8-10%) in algal turfs and the high growth and reproduction rates of crabs fed pure algal turf suggest that the problems that terrestrial grazers face in degrading and utilising higher plant cellulose are greatly reduced with turf grazers in the marine environment.

INTRODUCTION

Most traditional fisheries and maricultures are based on phytoplankton production. Recent world-scale analyses of primary production demonstrate that this floating and mostly pelagic community has low efficiency, well below most land communities, but nevertheless is the dominant component of total oceanic biological energy conversion (Bunt, 1975; Ryther, 1959, 1969; Adey, 1987a). On the other hand, coral reefs often have been regarded as the most productive of world ecosystems (Lewis, 1977;

Sournia, 1977; Adey and Steneck, 1985), and the source of that production has been attributed mostly to a thin, low biomass, grass-like layer of algae on the reef surface. Unfortunately, little serious effort has been made to understand the mechanisms of this particular type of primary production and how it might be used. It is now strongly suspected that these diminutive reef algae can consistently achieve high levels of plant production and are generally not limited by the factors that typically restrict phytoplankton production (Adey, 1987a). It has become common practice to refer to this assemblage of reef algae as "turfs". This paper examines a series of laboratory and field experiments on primary production by a coral reef algal turf assemblage.

The term "algal turf" has been employed frequently without reference to any particular morphological, ecological, or systematic definition. Most authors have regarded turf as a collection of short filamentous or foliose algae that grow to form a thick, dense mat (Dahl, 1972; see also review by Stewart, 1982), a group definition that remains applicable to a range of plant associations. Neushul and Dahl (1967) utilized the term to describe subtidal algae that varied from delicately branched forms such as _Griffithsia_, _Antithamnion_, and _Pterosiphonia_, to considerably larger species of foliose _Halymenia_ and the more heavily branched _Botryocladia_. These algae grew both as epiphytes of kelps and as cover on hard or soft substrata beneath a macroalgal canopy. The authors reported that this turf form displayed marked seasonal changes in distribution and composition in temperate Pacific waters. Algal turf also has been identified as a major component of the intertidal. Stephenson and Stephenson (1972) noted its presence throughout most of the temperate and tropical regions of their survey. These turfs encompassed blue-green filaments, crustose forms, articulated corallines, and a diversity of fleshy macroalgae that included *Bostrychia*, *Codium*, *Cryptonemia*, *Dictyota*, *Gelidium*, *Gigartina*, *Laurencia*, *Plocamium*, *Pterocladia*, *Rhodymenia*, and *Turbinaria*. Turfs from the low intertidal of temperate and subtropical waters were described by Stewart (1982) as composite structures of various anchor species (e.g., *Corallina*, *Lithothrix*, *Hypnea*, and *Pterocladia*), as well as, epiphytic species (e.g., *Ceramium*, *Laurencia*, *Chondria*, *Heterosiphonia*). The anchor taxa in these turfs, though often multi-generic composites, displayed similar morphological characteristics and persisted throughout the year, while the epiphytic species tended to fluctuate seasonally. Aggregate assemblages of a few algal species have been labeled turfs on shallow coral reef flats and slopes (Hay, 1981, referred to *Dictyota*, *Halimeda*, and *Laurencia*), and on temperate intertidal rocky shores (Taylor and Hay, 1984, referred to *Corallina*, *Lithothrix*, *Gelidum*, and *Rhodoglossum*,). These algae possess both prostate and upright branches that form a tightly compacted morphology which is capable of resisting both desiccation, occuring during periodic emersion in either environment, and intense herbivory encountered on coral reefs. These factors probably also prevent epiphytism by more productive species. Lower portions of the coral reef turf thalli exhibit decreased rates of apparent photosynthesis and dark respiration, which enables persistance as resting stages during periods of physical stress and maintains substratum coverage by the individual populations (Hay, 1981). Species forming turfs in the temperate environment are able to adjust the degree of thalli compaction under varied levels of environmental stress (Taylor and Hay, 1984).

In addition to the wide variety of turf forms of the examples cited above, investigators have begun to recognize a turf assemblage on coral reefs that is distinguished less by characteristic morphologies or systematics than by a high efficiency in solar energy capture and growth. Whole-system estimates of daily coral reef gross primary productivity have ranged from 3.4-20.0 (mean = 10) g C m^{-2} d^{-1} (see reviews by Lewis, 1977, and Sournia, 1977), with yearly estimates ranging from 1800-4200 g C m^{-2} yr^{-1}. Gordon and Kelly (1962) have reported a maximum of 11,680 g C m^{-2} yr^{-1} gross primary productivity for a fringing reef in Hawaii, which rivals systems under intense agricultural management. Algal assemblages that have been described as turfs have been identified as providing the major portion of the carbon fixation occurring on coral reefs (Odum and Odum, 1955; Borowitzka _et_ _al_., 1978; Borowitzka, 1981). As much as 70-80% of the total productivity of reefs (Brawley and Adey, 1977; Adey and Steneck, 1985) have been attributed to algal turfs. Though the importance of algal turf to the coral reef ecosystem and the great magnitude of its productivity have been acknowledged in the last decade, the literature has not recognized yet a specific description of the community most responsible for these productivity levels.

For the past several years, the Marine Systems Laboratory has studied the dominant plant assemblage of the Caribbean and western tropical Atlantic coral reefs in field, microcosm, and productivity chamber studies. We refer to this assemblage as a coral reef algal turf. We have demonstrated that this turf is capable of high rates of productivity both in the wild and in culture. We describe here the various characteristics which we feel distinquish it from assemblages that are more broadly defined in the literature.

The Coral Reef Algal Turf Assemblage

In this paper, a coral reef algal turf is a multi-specific association of benthic, subtidal, free-living algae subjected to emersion only during extremely low tides. The assemblage typically persists as coverage of dead coral colonies, loose rubble, interstitial surfaces, and other areas of reefs that are subjected to high levels of grazing. Although seasonal shifts in biomass and abundance occurs in this assemblage (Adey and Steneck, 1985), the lack of more pronounced seasonal changes on submerged portions of tropical coral reefs renders inappropriate a distinction of annual vs. perennial forms. These turf species are predominately unicells, uniseriate filaments, simple branching filaments or weakly corticated filaments that generally range in height from a few mm to a maximum of several cm. The height of this assemblage at any point in space and time depends largely on the intensity of grazing by herbivores. Smaller members of more anatomically complex macroalgae having pseudo-parenchymatous thalli are generally less important but persistent members of this assemblage.

In a similar grouping on an Australian fringing reef, Morrissey (1980) noted an imprecise boundary between turf species and larger macroalgae, particularly those genera with early developmental stages of short stature. An additional distinquishing characteristic for many of these turf species is the frequent presence of an extensive, stoloniferous basal system that supports multiple, upright axes (Brawley and Adey, 1977). In this regard, this assemblage closely resembles the herpophytes, described by Setchell (1924) as minute, crawling algae with prostrate axes that attach to the substratum by fascicles or rhizoids and bear erect or ascending lateral branchlets. A similar classification, the Hemichamaephyceae, was made by Nasr (1946) for perennial tropical algae of this form that possess apical growth zones (see also Feldman, 1966).

The thalli arising from this stoloniferous basal system conform generally to the Littler and Littler (Littler *et al*., 1980; Littler *et al*., 1983) and the Steneck and Watling (1982) filamentous functional-form groups as commonly uniseriate or multiseriate, lightly corticated filaments. However, composition of this coral reef turf assemblage is fairly complex and includes many species which do not fit any one particular functional-form or anatomical group classification. A number of diatoms (centrate, pennate, unicellular, and filamentous), coccoid and filamentous blue-green algae, and benthic dinoflagellates dominate in early stages of turf development and persist generally through later stages, adhering to a thin layer of detrital scum which persists among the basal holdfasts. Such components of the turf probably contribute to formation of the scum by mucilage production. A variety of bacteria, protozoans, and occasional metazoans (e.g., nematodes, small annelids, microcrustaceans) are also associated with this scum layer. Tubular or sheet-like species of *Enteromorpha*, which attach to the substratum with a single holdfast, are often present, though only in small size. With the reduced stature of this assemblage, epiphytes are limited to blue-green algae, diatoms, or minute branching filaments such as Asterocytis or Erythrotrichia.

Table 1 contrasts the diversity of species that are found consistently in this assemblage with those genera that most frequently composed the remainder of the benthic flora in surveys of a number of Caribbean/West Indian coral reefs (Adey et al., 1979; Adey and Goertemiller, 1987; Adey and Steneck, 1985; Connor and Adey, 1977; Peyton et al., 1987). Each genus in this table is categorized as: 1) including species that are common, persistent components of the coral reef turf assemblage; 2) including both the turf species listed and other species which do not persist within the turf assemblage; or 3) including no persistant turf species and considered as either an encrusting coralline or a macroalga in this study. The genera are divided further into a series of anatomical groupings ranging from simple, single-celled forms to the more tightly packed cellular arrangement of parenchymatous thalli. A category of pseudo-parenchymatous construction was designated in this summary to account for those algae which lack extensive three dimensional cellular division, yet achieve some mass and degree of morphological complexity by cortication and other differentiation about a basically filamentous form.

As defined by the organization of Table 1, the coral reef algal turf assemblage encompasses genera of simpler anatomical organization in each of the phylogenetic groups. The unicellular forms representing green, brown and red algae are limited to spores which are observed often to adhere to the mucilagenous scum layer at the base of the assemblage. Among the filamentous eucaryotic components, branched forms predominate generally and, as defined here, include the common Licmophora, a diatom cell complex supported on repeatedly branched mucilaginous stalks. Those turf genera that achieve a pseudo-parenchymatous thallus construction through multiseriate, polysiphonous, or corticated growth are predominately members of the Rhodophyceae, a class with an essentially filamentous organization. These more complexly corticated red algal species are often in genera that contain other species not persistent within the turf assemblage. In such cases, the turf elements tend to be more minute species of the genus (e.g., Gelidium pusillum, Laurencia caraibica, Amphiroa fragillissima, Jania capillacea). Species in this assemblage from "turf/non-turf" genera are organized clearly with greater thallic structural support than simpler filamentous turf algae, but they have mature thallus diameters that are limited to under 300 uM. This is less than the diameter achieved by certain uniseriate turf elements such as Cladophora. On the other hand, larger examples of simple anatomies (e.g., Valonia, Dictyosphaeria, certain species of Chaetomorpha and Cladophora) are rarely encountered among the turf assemblage. On this basis, we have concluded that it is a small adult plant stature, rather than a strictly anatomical or systematical classification, that is the primary factor determining composition of the coral reef turf assemblage. The ability to grow rapidly, to enter reproductive cycles quickly and to withstand repeated grazing through basal structures or rapid spore settlement are necessary for successfully exploiting a small adult stature of this nature.

Grazing Pressures and Turf Maintenance

A more unified definition of coral reef algal turf composition is provided by examining the macroherbivore grazing pressures which are encountered normally in reef communities and contribute to maintenance of this assemblage. (Macroherbivores are defined here to include fish, gastropods, urchins, and larger crustaceans such as crabs.) In brief, the turf is composed primarily of those algae which successfully withstand the high levels of grazing by rapid growth, rapid reproduction and basal persistence rather than by protective mechanisms such as toxicity or thallus strength. The reduced thallus size within this assemblage generally has allowed minimal differentiation of photosynthetic tissue to structural material. Since allocation of materials to structural components increases with the increase of structural complexity (Littler and Arnold, 1980), high grazing pressure would maintain surviving plants in a generally early stage of regrowth and increase the proportion of photosynthetically active cells in the corticated or partially calcified turf species included in Table 1. Such high ratios of photosynthetic tissue to structural material would provide for high biomass-specific rates of productivity and growth (Littler and Littler, 1980; Littler et al., 1983). The extensive basal holdfast systems of algal turfs often persist after upright axes have been grazed, since macroherbivores, even parrot fish, face increased energy expenditures after removal of a certain quantity of plant material and substratum (Brawley and Adey, 1981). Many of the algal species composing this turf persist by vegetative reproduction through fragmentation of thalli, while others display very short cycles of sexual reproduction.

Each of these factors would assist a rapid regeneration of the turf following grazing, and it is likely that the generally resistant, prostrate growth form has enabled survival of the assemblage under intense macroherbivore grazing (Dethier, 1981; Hixon and Brostoff, 1981). Indeed, it is now understood that macroherbivore grazing actually benefits the coral reef algal turf assemblage, much as the grazing of large mammals can maintain grassland. In this case, it enables the turf to maintain its commonly widespread coverage of dead portions of coral colonies, loose rubble and various interstitial areas. (Odum and Odum, 1955; Dahl, 1972; Wanders, 1976a; Morrissey, 1980).

Among the turf algae, listed in Table 1, are a number of macroalgae which, once established, may be able to escape grazing with structural or chemical defenses (Ogden et al., 1973; Ogden, 1976; Ogden and Lobel, 1978). Certain of these macroalgae, which often display appparent parenchymatous thallus construction, often maintain a scattered, non-persistant distribution amidst the turf assemblage. However, sporeling or germling stages of these plants are often consumed indiscriminately by reef macroherbivores that graze among the turf assemblage. Since these immature stages lack adaptations for rapid recovery from such disturbance, this grazing decreases macroalgal recruitment while increasing short-term fitnesses of turf species (Sammarco, 1982; Carpenter, 1981, 1984). Consequently, such grazing pressure promotes the observed persistence of this turf assemblage over large portions of substratum and maintains the benthic algal component of coral reefs in a characteristic high-turnover, early successional stage with a low standing crop of small stature and patchy distribution (Hatcher and Larkum, 1983; Ogden and Lobel, 1978; Dahl, 1972; Marsh, 1976).

The experimental removal of macroherbivore grazing commonly results in temporary increases in the biomass of algal turf (Randall, 1961; Carpenter, 1981, 1984). However, the simple, filamentous growth form predominant in this assemblage lacks the structural support necessary for the development of large standing stocks. The dense packing of thalli that quickly develops from lack of grazing eventually decays from senescence, as a result of self-shading and reduced circulation of surrounding seawater (Stephenson and Searles, 1960; Wanders, 1977; Carpenter, 1984). Following this decomposition, upright thalli may regenerate from persisting holdfasts to maintain the assemblage in an unstable stage of transition, but eventually the turf is displaced by the slower growing, more heavily corticated or parenchymatous macroalgae listed in Table 1 (Sammarco, 1982; Sammarco *et al*., 1974; Ogden and Lobel, 1978; Hatcher and Larkum, 1983; Carpenter, 1981, 1984). Large standing crops of such macroalgae (e.g., *Gracilaria*, *Halimeda*, *Padina*, *Sargassum*, *Turbinaria*) often develop naturally on coral reef algal ridges and wave-swept flats or pavements, where wave surge prevents easy access by macroherbivores (Wanders, 1976b; Adey, 1978; Adey *et al*., 1977; Connor and Adey, 1977).

The diversity of benthic algal species on Caribbean coral reefs has been shown to decrease eventually during an absence of macroherbivore grazing (Sammarco, 1982, 1983; Carpenter, 1981, 1984). Relatively few macroalgae can come to dominate the community. On the other hand, extremely heavy grazing pressures can also decrease diversity by allowing the replacement of both the turf assemblage and larger macroalgae with encrusting coralline genera (see Table 1 and Brawley and Adey, 1977; Hay, 1981; Sammarco, 1982; Carpenter, 1984). These responses by the benthic algal component suggest that macroalgae are prevented from excluding (through eventual overgrowth and shading) the smaller, more prostrate turf species by intermediate levels of generalist macroherbivore grazing, a pattern encountered frequently in the marine intertidal (Lubchenco, 1980). McNaughton (1984) reviews such changes in species composition, diversity and growth form as a consequence of grazing common to both marine and terrestrial ecosystems. The coral reef algal turf might be further compared to terrestrial grassland assemblages which require either regular biological or physical disturbance (most frequently grazing and fire, respectively) to prevent eventual exclusion by larger shrubs and woody plants (see Pellew, 1983).

The algal turf assemblage is subjected also to grazing by certain microherbivores, which compound the effects that have been discussed thus far. Brawley and Adey (1981) have demonstrated that an amphipod crustacean found on Caribbean reefs is capable, when undeterred by predation, of heavily exploiting the assemblage, eventually clearing the substratum for growth by a larger macroalga of a later successional stage. The macroalga in these experiments, _Hypnea_ _spinella_, was protected from microherbivore grazing by its large size. On coral reef substrata inaccessible to fish, due to experimental caging or wave surge, the eventual displacement of turf species by macroalgae may therefore be further facilitated by the grazing of such microherbivores (see also Fenwick, 1976; Lobel, 1980; Kennelly, 1983).

Algal Turf in Water Quality Control

Coral reef algal turfs have played an important role in maintaining a series of marine and estuarine microcosms and mesocosms established by the Marine Systems Laboratory (Adey, 1983; Williams and Adey, 1983; Tangley, 1985; Adey, 1987b). The development of these functioning closed model ecosystems has required the balancing of diel community metabolic processes. Many shallow water communities often have overall P/R (photosynthesis/respiration) ratios of 1.0 or less. Even when P/R is 1.0 or greater, considerable daily deviation from this value can occur with non-conservative metabolites. For example, in a study of community metabolism on Robin Reef, St. Croix, Adey and Steneck (1985) measured a respiration rate at sunset of approximately 2 g O_2 m^{-2} h^{-1} at a depth of approximately 1 m. Even when waters overlying the reef are supersaturated with oxygen during the day, it is evident that with this magnitude of community respiration, an oxygen debt would be incurred by the reef within a few hours of darkness. However, with the cessation of photosynthetic activity each evening, turbulent mixing of ocean water provided by trade winds and water currents replenishes oxygen, preventing community stress. Simple diffusion across a still air-water interface could not supply the demonstrated oxygen demand by itself (Smith and Marsh, 1978). Equally important, metabolic products such as CO_2 or ammonia would be expected to accumulate to toxic levels without the flushing provided by exchange with the open ocean. These considerations likely contribute to the frequency of well-developed shallow water coral reefs on the windward side of their adjacent landforms (Adey and Burke, 1976). The requirement for support of a benthic ecosystem by ocean, or open river or bay waters is even more pronounced in ecosystems that show a consistent P/R less than 1.0 due to the import of organic materials from other ecosystems (or mud flat, for example).

Attempts to establish aquaria or microcosms of ecological communities in enclosed aquaria have for the most part simulated this open ocean exchange through traditional means of water quality control, i.e., bacterial or mechanical filtration with subsidiary water sterilization. However, these water treatments are inadequate for all but the smallest of microcosm systems and essentially extend the basic degenerative processes of respiration without proper restoration of the oxygen concentrations or pH values or nutrient levels required to prevent community deterioration. Unfortunately, the more obvious strategy of an open aquarium system that provides continual circulation of fresh seawater is hindered often by poor water quality due to the siting of the laboratory or to the changes that result from pumping, transport, or storage of the water supply.

The critical problem of matching high quality open waters in microcosm and mesocosm maintenance can be solved by circulating water through a sub-unit of the system where photosynthetic activity is promoted during hours of darkness to counteract the high rate of community respiration (Adey, 1983). This supplemental photosynthesis, which clears respiratory products from the water column while restoring pH and oxygen concentrations, can be most efficiently supplied by cultures of algal turfs. The utilization of this turf form provides numerous advantages over alternative plant assemblages. Phytoplankton cultures are difficult to maintain in adequate densities and would require continuous filtration from the seawater being recycled to the microcosm. Cultures of larger macroalgae would display generally lower rates of carbon fixation and being "leaky" would likely release a variety of dissolved organic compounds into the water column (Khailova and Burlakova, 1969; Sieburth and Jansen, 1969; Spotte, 1979). The algal turf assemblage, on the other hand, being opportunistic, with little stored food, is not characterized by "leakiness." Also, it is established in culture easily on an inexpensive, uniform substratum of plastic-coated fiberglass screening which provides porous substratum for the algal bases. When grown in shallow "sea tables" and provided with intense metal halide irradiance, a continuous circulation of water, and protection from grazing, the very productive turf assemblage provides a highly efficient, controllable and easily harvested unit of biological water quality control. We refer to these separate water quality control units as "algal turf scrubbers" (Adey, 1987). The growth of the algal turf assemblage upon a section of scrubber screen is represented in Figure 1.

In addition to providing homeostatic control of the physical and chemical parameters of microcosm water, when utilized for coral reef microcosm management, the algal turf cultures are employed on the reef itself to maintain a balance in the trophic exchange that occurs with the system. Coral reef microcosms maintained in this way are self-supporting communities in which negative diel variation is controlled by metal-halide irradiance and algal turfs. The primary productivity occurring within the reef and lagoon tanks of this system is consumed by grazers on several trophic levels and is distributed amongt more than 300 species of consumers in many of the same energy exchange patterns observed on natural coral reefs. The only external organic input provided is a daily addition of a very small quantity of brine shrimp and dried krill, to simulate an open-ocean input to the diet of the fish and some invertebrates. The periodic (seven day) harvest of the coral reef algal turf culture compensates for the addition of this biomass to the microcosm, develops a balanced import/export ratio, and maintains the scrubber culture in an early, more highly productive stage of successional growth.

Wave Surge and Cultured Turf Productivity

As benthic plants attached to either natural reef substrata or fiberglass screening, algal turfs would be expected to demonstrate productivity which responds to the strength and form of passing currents (Gerard and Mann, 1979; Wheeler, 1980, 1982; Norton *et al.*,1982; Madsen and Sondergaard, 1983). Such currents replenish nutrients in the water overlying these stationary plants and reduce boundary layers, which enhances cellular exchange and promotes efficient plant metabolism (Wheeler, 1980, 1982). Preliminary scrubbers designed to provide simple continuous flow demonstrated relatively low harvest production and proved ineffective in controlling nutrient levels within a reef microcosm. Later, scrubbers were provided with wave action. Examination of the continously recirculated seawater of one scrubber (Figure 2) illustrates the relationship between oxygen production and wave action. As shown, the blocking of the wave bucket to provide a simple continuous flow of seawater results in a decreased rate of oxygen production. This trend is reversed as wave action is restored and production increases until the original rate is attained. This oxygen production pattern, with an absence of an overshoot, suggests that wave surge is not acting simply to dislodge gas accumulating around algal filaments, but is instead promoting photosynthesis to the maximum rate possible given the physiological constraints imposed by the micro-environment of this scrubber.

Nutrients and Plant Production in the Ocean

Adey (1987a) recently reviewed the basis of our understanding of marine primary production and the role of nutrients, waves, currents and light in determining the level of that production by algal turfs. In this section, for continuity, that discussion is briefly summerized.

In an examination of the "Potential Productivity of the Sea", Ryther (1959) concluded that a net "production of organic matter of some 10-20 g (dry) m^{-2} d^{-1} may be expected" in the oceans. He suggested that a maximum of about 25 g (dry) m^{-2} d^{-1} could be attained under ideal conditions, without nutrient limitation and with maximum irradiance. Later work by Ryther and others (e.g., Goldman et al., 1975) established that actual productivity approaching 50% or more of these proposed maximal rates can be achieved in large-scale culture when the critical parameters, especially nutrient availability and mixing, are optimized.

Traditionally, it has been accepted that net phytoplankton production in the sea ranges from about 0.3-2.0 g (dry) m^{-2} d^{-1} (0.15-1.0 g C m^{-2} d^{-1}), with the lowest values applying to tropical open seas. More recent physical and chemical oceanographic investigations have suggested that ^{14}C-based studies of ocean primary production are in error and underestimate production by 5-10 times. Epply (1982) set a maximal level for net plankton production in tropical and subtropical oligotrophic seas at about 1-2 g (dry) m^{-2} d^{-1} (0.5-1 g C m^{-2} d^{-1}).

Ryther (1959), accepting severe nutrient limitation of phytoplankton production, questioned such limitation in benthic communities: "The fact that they (nutrients) are continually being replenished as the water moves over the plants probably prevents their ever being limiting." While later studies have shown a large production potential for benthic algae (e.g., La Pointe and Tenore, 1981), unrestricted nutrient availability has been regarded as crucial.

A recent review of coral reef primary productivity by Lewis (1977) revealed a wide range of gross primary production (GPP) rates, covering nearly an order of magnitude (3.4-20.0 g C m^{-2} d^{-1}). Kinsey (1979) took 7 g C m^{-2} d^{-1} as the modal rate of organic carbon production for reef systems in general. Adey and Steneck (1985) demonstrated that under ideal conditions (determined by the state of geological development, wave and current action and intense continuous irradiance), considerably higher rates of GPP (20-30 g C m^{-2} d^{-1}) are routinely possible. Data that corresponds closely to published values has been obtained in recent studies of large reef communities (Atkinson and Grigg, 1984) when various modeling techniques are combined with primary productivity rates based upon standard oxygen production data and known rates of predation.

With regard to potential nutrient limitations on primary production in coral reefs, some studies have shown that reefs actually can export nitrogen (Wiebe et al., 1975). Other researchers have been able to demonstrate that certain benthic communities rich in heterocystic blue-green algae are able to fix nitrogen (Wilkinson and Sammarco, 1983). While older studies suggested a "tight recycling" or retention of phosphorus, more recent studies carried out across very broad reef flats have indicated phosphorus uptake and depletion from the overflowing ocean water (Atkinson, 1981).

In spite of these well-known facts, it often has been accepted in recent years that reef communities are strongly nutrient limited, which has lead to numerous studies for identifying potential sources of nutrient input (e.g., D'Elia et al., 1981; Andrews and Gentien, 1982; Meyer et al., 1983; Andrews and Muller, 1983).

Growth of Algal Turfs on Artificial Substrata in Tropical Seas

For several years, the Marine Systems Laboratory has grown algal turfs on artificial substrata in a wide variety of marine environments, most frequently employing plastic screens in a range of sizes, shapes, colors, pore sizes and densities. This work has been concentrated in the waters of the Caribbean and southwestern tropical Atlantic, where nutrient concentrations of nitrate/nitrite rarely exceed 0.5 ug-at/l and often are below 0.1

ug-at/l. Algal harvests obtained from these screens generally indicate the extraordinary levels of productivity previously implied by whole-system coral reef community metabolism studies. More typically, harvests reach roughly 50% of gross primary production by the reef. When in-situ losses due to community respiration, thalli fragmentation, and micro-grazing are considered, these values are quite reasonable and confirm previous estimates of high reef production. More importantly, in the context of the present volume, these harvests are attained repeatedly in situations where significant recycling is either impossible or highly unlikely.

Given intense solar energy input to an environment with considerable wave-induced turbulence, it seems clear that high rates of metabolic exchange and production are possible. Since algal turfs have the ability for efficient extraction at low concentrations of the required nutrients, it is conceivable that only a depletion of nutrients from the overlying water column could lead to limited production. With generally constant, strong seawater flow in trade wind seas generated by both equatorial currents and local wave action, nutrient depletion is rarely a serious factor in production limitation.

Algal Turf Research

In this paper several years of research both in the laboratory and the field are summarized, particularly with regard to turf community structure, succession and productivity as controlled by a wide variety of environmental factors and by the characteristics of the artificial substrata used.

MATERIALS AND METHODS

LABORATORY STUDIES

These studies were conducted on a side loop of a 12 kl coral reef microcosm (Adey, 1983; 1987a). A series of attached sea-tables were constructed of polyester-coated plywood to provide shallow wave surge tanks for the cultivation of the experimental algal turf assemblage. One end of these algal turf scrubbers supports a trough-like wave bucket (approximately three liters volume) designed to fill with a continuous inflow of water pumped from the microcosm. The wave buckets tip into the sea-tables on off-centered axes, and create a periodic surge of seawater which crosses the table to drains that direct the return of the outflow back to the microcosm. These drains are fitted with standpipes so that a 2 cm column of seawater is maintained in the bottom of each scrubber during periods between wave generations. Two squares of plastic-coated fiberglass window screening (0.5 m^2, 1 mm mesh) are mounted in plexiglass frames across the bottom of each scrubber, which divides the bottom surface area into an upstream screen, nearest the wave bucket, and a downstream screen of equal area. Each screen is positioned beneath a 400 watt multivapor, high intensity metal halide lamp providing ca. 1000 $uEin/m^2/sec$ to the screen surface. With the intense irradiance and continuous circulation of coral reef microcosm water through the scrubbers, algal spores, zygotes and vegetative fragments settle quickly and grow on the screens. The passage of each generated wave oscillates sharply the algal filaments, though wave intensity diminishes markedly towards the far end of the scrubber, providing a weaker surge for the turf on the downstream screen. The design of the scrubbers was described in general by Adey (1982).

Standard Conditions of Turf Growth. During the period of study, the salinity of the microcosm water ranged from 35.0-36.0 parts per thousand, temperature from 25-28^{o}C, pH from 8.2-8.3, and dissolved oxygen from 5.5-8.3 mg/l. The concentrations of nitrate/nitrite averaged 1.0-1.5 ug-at/l, somewhat higher than the 0.1-1.0 ug-at/l common to many Caribbean reefs (Adey and Steneck, 1985; Adey and Goertemiller, 1987). Typically, nitrogen concentrations increase sharply within the system following the introduction of blocks of reef carbonate containing organisms or fish from field collections and lower gradually with continued removal of biomass from the scrubbers (see below). High nutrient concentrations for experimental work were induced by including a number of large Mithrax spinosissimus in a 800 l tank interconnected with the reef microcosm.

The primary production of turf algae growing on upstream and downstream screens was monitored over a period of several months to assess the influence of different factors in the scrubber environment. During this period of study, a set of scrubber parameters was selected as standard for purposes of comparison and included a 12 day harvest period, a light intensity of 1000 uEin/m^2/sec, a 2 cm depth of water overlying the screens, a screen pore size of 1 mm, and a flow of 13.5 l/min to the wave buckets. The standard photoperiod provided to both the reef tanks and the algal scrubbers was 14 h light/10 h dark. The light period for the scrubbers commenced as the various lamps over the reef exhibit began to switch off, providing essentially inverse photoperiods. The length of the light period is typical of a trade wind/tropical summer day. While the scrubber light intensities of 1000 uEin/m^2/sec were somewhat below those encountered typically on a Caribbean coral reef flat at approximately 1 m depth, the total incoming energy on a daily basis is about the same.

Measurement of Primary Production. Primary production of the algal turf community was determined during this study as the weight of biomass harvested every 12 days. During harvests of the turf assemblage, the screens were placed in a shallow plexiglass collecting tray and scraped with a beveled plexiglass blade. Scraping of the screens in this manner removed the major portion of the upright filaments while the basal holdfasts or rhizoids remained attached to the inner surfaces of the mesh pores (Brawley and Adey, 1981). In addition to the material collected by scraping the screens, any biomass growing on the sides and bottom surface areas of each scrubber also was removed at time of harvest for purposes of microcosm management. However, only that portion removed from the circular area of screen directly beneath the halide lamp reflectors was employed in production calculations. After harvest, the collected biomass was drained briefly, dried to constant weight (approximately four days at 35°C) and weighed to determine production as g dry wt m^{-2} d^{-1}.

For comparison, the biomass-specific primary productivity of the algal turf also was measured as the rate of carbon fixation in a series of short-term incubations (Hackney, 1984). Samples of screening with attached algal turf were divided into 4 cm^2 squares and incubated for 2 h under metal halide irradiance (1000 uEin/m^2/sec) in filtered, constantly stirred seawater with added 14C-$NaHCO_3$ (5 x 10^{-3} uCi/ml). Following incubation, the turf squares were dried, weighed and converted to g dry wt biomass after subtracting the standard weight of a square of cleaned screen. Individual turf squares were oxidized by the method of Van Slyck _et al_. (1951) to $^{14}CO_2$, which was reduced to soluble ion by passage through a 1.0 N solution of KOH. Replicate aliquots of base from each oxidation were counted by liquid scintillation, with average counts converted to rates of total carbon fixed during incubation (mg C/h/g).

Turf Composition. Prior to each of the screen harvests in this study, three randomly placed samples of the turf assemblage were removed with tweezers and preserved in 5% formalin. Samples from each of the screens were combined and examined periodically to identify the various species of algae that compose the turf assemblage.

Long-term Observations. For a series of observations covering a period of eight months, parameters were established in each of seven separate scrubbers to conform to the above standards with the exception of one of the following substitutions (i.e., the test conditions): 1) a variation in the depth of water overlying the screens (1 or 4 cm); 2) a shortened harvest period (7 or 10 days); 3) an increased light period (16 h light: 8 h dark); 4) a varied screen pore size (210, 710, or 1400 um) and 5) a change in intensity of irradiance (800 or 1200 uEin/m^2/sec). The intensity of light received by scrubber screens, as measured by an integrating photometer (Li-Cor Model LI-188B) at the water surface, was varied by raising or lowering the position of the metal halide lamps above the scrubbers.

Paired Scrubber Studies. In addition to the long-term observations, two scrubbers were paired for a series of tests lasting 5-11 weeks to compare concurrent 12 day harvests under varying flow rates. The adjustment of flow rates to the scrubbers affected directly the frequency of wave generation, although one comparison employed a shallower wave bucket (approximately 2 l volume) to examine the impact of two different frequencies under a single high rate of flow.

Blockage of Wave Surge. The effect of totally blocking wave generation was tested directly in one scrubber that otherwise shared the standard parameters described above. For a period of six weeks, seven day periods of harvest were monitored with a functional wave bucket provided for one week, alternated by a week during which the bucket was blocked from rotation to create a continuous flow of water that spilled across its leading edge. This design tested the effect of providing an identical flow rate in both the presence and absence of wave generation and controlled for any unaccounted environmental parameters that might affect biomass production within these scrubbers.

Monitoring of Nutrient Concentrations. Effects of changing nitrate/nitrite concentrations on production were observed by monitoring a series of harvests from one scrubber after collections of invertebrates were introduced to the reef microcosm. As part of this examination, the productions of both scrubber screens, subjected to standard parameters, were recorded over a 26-week period as N-(NO_2 + NO_3) concentrations fell from nearly 20 uM to less than 2 uM.

FIELD STUDIES

Mayaguana. The studies undertaken at Mayaguana were published by Adey and Goertemiller (1987). To provide continuity to this volume, that work is summarized here.

The waters off Mayaguana Island (22° 20' N; 773° W), in the southeastern Bahamas (Figures 3, 4) were chosen as a site because they provided a well-developed coral reef that faces open, deep and incoming North Equatorial Current water. In addition, this site was logistically feasible, with minimum expense and was not subjected to winter extratropical swell. During most of the year, Mayaguana lies within the outer trade wind belt (Adey 1978). Abraham Bay reef on the south side of the island provides low nutrient concentration lagoonal waters and open ocean waters within close proximity.

During the course of the project, no significant differences in nutrient concentration between lagoon and open ocean waters could be discerned. The maximum concentration of nitrate/nitrite was 0.13 ug-at/l, and on some occasions was below detection limits.

The surfaces supporting algal turf growth were 1 m^2 plastic screen material of either single or double layers. The bottom of the double screen was made of black polypropylene screen (1.6 x 4.8 mm mesh), while the upper layer was polyester (1 mm^2 mesh). Both layers of the double screen were sewn together with fine plastic filament to increase strength. The single screens were standard polypropylene (1.6 x 4.8 mm).

The turf screens were attached to individual rafts made of 7.6 cm diameter PVC plumbing pipe and were suspended at 15, 30 and 40 cm depth. The pipes at the top of the frames were sealed shut to allow flotation. Water entered through holes drilled in the legs and bottom sections of the frame to serve as ballast and prevent capsizing (Figure 5). A set of three double-screen rafts, one for each depth (15, 30 and 45 cm), was placed at both the lagoon and open ocean sites. A similar arrangement was developed for single screen rafts, with two replicates of the single screen set for both the lagoon and the open ocean sites.

Another two sets of single fiberglass and polypropylene screens (0.5 m x 0.5 m) were suspended directly on anchored line rather than on rafts. These open ocean screens were suspended between the reef and the oceanic drop-off in a water depth of about 17 m (Figure 6). Placing of these screens allowed examination of variation in algal turf production with depth in an area with a much deeper bottom.

After three weeks of initial algal turf growth, all screens were scraped and harvested. A regular scraping interval of seven days began at the end of these three weeks. All scrapings were done as described above. The top and bottom of each screen was harvested and the results pooled. The algae were oven dried until weight variation over a 12 h period was less than 0.5 g (total). A variation in screen design was provided by attaching the screen directly to a polyester-resined plywood sheet. It was not successful, but is mentioned here and briefly discussed below because it has interesting implications.

Grand Turk. The algal turf studies undertaken at Grand Turk have been separately prepared in manuscript form and are now in review for publication (Peyton et al., 1987). To provide continuity in this volume, this paper also is summarized briefly. At Grand Turk, additional testing with regard to the effects on algal turf production of a variety of additional factors (e.g., screen type, irradience level and harvest rate) was undertaken.

From January to September, 1984, an algal turf production study was conducted from the R/V Marsys Resolute in the reef lagoons adjacent to Grand Turk Island (Figures 3, 7). The island, which is well within the trade wind belt (Adey 1978), is 3.2 km wide by 13 km long and is oriented north to south. The lagoon used for these studies lies on the eastern or windward side of the island, and is approximately 10 km long (north to south) by 2 km wide. The east lagoon faces directly into the North Equatorial Current and is protected partially from the trade wind sea by a patch or boiler-type complex of coral reefs and algal ridges. The impinging waters can be characterized as essentially tropical open ocean. Silver Bank and Mouchoir Bank lie to the east, which is south of the general equatorial flow to

Grand Turk. The lagoon is 1-4 m deep, with scattered small patch reefs, while the remaining bottom is covered by calcareous sand (approximately 50% of total area) and seagrass (approximately 45%, primarily Thalassia). The floating rafts used to support the algal screens were essentially the same as those described above. The controls consisted of white polyester monofilament screens (1000 um pore size) hung at 30 cm depth.

Three study sites were established in lagoonal waters off the east and southeast sides of the island. A study of the effect of screen types was conducted at site 1 (Figure 7) in 4.0 m water depth, over the partially sandy bottom of a patch reef grazing halo. Four of the seven screen types tested were white polyester monofilament (500, 710 and 1000 um (control) pore size). Other substrata tested included nylon weave (200 um pore size), blue multiweave (2mm thick) and a black polypropylene molded screen (2 X 3 mm pore size).

The harvest rate study and turf community study were conducted at site 2, at 4 m water depth. The bottom consisted of sandy sediment sparsely covered with siphonaceous green algae. Screens were harvested at 4, 7, 12 and 20 day intervals.

The development of the turf community upon two screens (1000 um pore size) was studied under controlled conditions. One screen was harvested every 12 days, while the other was never harvested. With the exception of black polypropylene screens of 2 X 3 mm mesh, all screens in this study were sampled at each harvest for the first 97 days to observe possible variation in community development among screens.

Site 3 was located between an algal ridge and a Thalassia bed in 2.3 m water depth, over a white calcareous sandy bottom. The effects of irradiance (see light measurement) on biomass production as a function of water depth was investigated at this location. Six screens of blue and white multiweave (2 mm thick) screens were hung at the surface (0-3 cm) and at 10, 20, 30, 40 and 100 cm water depth, and harvested every seven days. In addition, single, double and triple-layered black polypropylene screens (1 X 3 mm mesh) were suspended at 30 cm water depth and harvested every seven days. Multilayered screens were sewn together with monofilament fishing line.

At Grand Turk Island, algal turf was harvested as described above. Due to differences in irradiance received by the top and underside of the screen, the turf scrapings were processed separately. Harvested biomass was oven dried at 80°C for three days and transfered to a 100° C drying oven for 24 hours or until the variance in weight between hourly weighings was less than 0.1 g.

Prior to harvesting, four 1.0 cm samples were collected randomly from the screens. Samples were collected from each side of the screen and preserved in 3% buffered formalin to determine the turf algal species composition and relative abundances of algal genera for each screen substratum. Both the direct count method and point counts were used in these calculations.

Photosynthetically active radiation (PAR) was measured on cloudless days using a LI-COR Model 511 photometer with a flat-topped cosine corrected sensor (Licor, Inc.), which averaged PAR over a 10 sec period. Irradiance values of incident light and of light reflected from the bottom were recorded every 10 cm through the water column at each study site. Incident and reflected PAR at 30 cm below the surface were noted every hour from sunrise to sunset on four occasions. Incident and reflected light also were measured through a screen supporting seven days of algal turf growth and again immediately after harvesting.

Irradiance was measured in specific wave bands at site 3 using an IL 1500 series photometer with a SEA015 detector (International Light, Inc.).

Concentrations of nitrate/nitrite and orthophosphate were determined by standard methods using a Beckman DU-2 spectrophotometer. Salinity, temperature, and pH of ambient water were recorded also. All samples were collected at 30 cm water depth at each study site.

Antigua. From February to July, 1985, experimental studies of algal turf growth were conducted in the easternmost part of Nonsuch Bay, Antigua (17° 5'N; 61° 41'W; Figures 8, 9). The basic methods and equipment used were the same as those employed at Grand Turk.

In addition to seeking corroboration of previous results at an entirely different, high island site, the work at Antigua further extended the study of the effect of different screen characteristics, specifically screen color (i.e., black or white), on algal turf production. Depth and protection factors also were examined further, along with the effect of screen orientation (i.e., horizontal vs. vertical). In this section, turfs were harvested every seven days to maximize the number of test events.

Nonsuch Bay is a relatively narrow, steep-sided, east-west oriented bay cut into shelf limestones raised during the late Tertiary (Figure 9). It is protected to the east by a bank barrier reef, which blocks much of the constant easterly trade wind swell at this latitude. There are two main passes into the Bay from the east, one running diagonally north/south through the reef and the other running over a submerged reef south of Green Island and entering west of Green Island. There are no significant exits to the south-west or north. As a result of this configuration, water flow forced by trade winds over the reefs into Nonsuch Bay can exit only back into the general equatorial current. Antigua is a moderately elevated island and has greater rainfall and run-off than Mayaguana and Grand Turk. Thus, the inner end of Nonsuch Bay is somewhat stagnant and highly turbid with suspended sediment. The outer end of the bay, where the experimental work was conducted, is significantly clearer, though even at this site turbidity is greater under certain conditions than at previous algal turf research sites.

Screen sets were placed 1) at Rat Island; 2) in the lee of Bird Island; 3) at Devils Bridge and 4) to the north of Green Island. One set of single thickness black polypropylene screens (2 X 3 mm mesh) were placed at each of the sites to examine the effects of location (i.e., availability of protection, amount of suspended sediment) on production. A double set of screens was placed at Devils Bridge. All other testing was carried out at the Green Island site in 3 m of water, over a light sand bottom.

The Rat Island site had intermediate protection, providing relatively turbid water and turbulence from waves generated within the bay itself. The site lay at 6 m watere depth over a silty sand bottom. The Bird Island site, at 3 m water depth, was slightly less turbid than Rat Island. The lee side of Bird Island had a small patch of mangroves that indicated considerable protection from intense wave action. However, this site was subject to moderate currents that changed with tide and wind direction. Screens at the Devils Bridge site were placed at 3 m water depth in clear water overlying patch reefs and a coral rubble bottom. Turbulence at this site generally was intense due to waves coming at a variety of angles around the patches and reflecting off limestone cliffs to the northwest.

The Green Island site was the standard work area for the studies in Antigua. This site received moderate wave-driven surge and flow over the reef at most times, thus sharing characteristics with the Grand Turk and Mayaguana sites. However, due to the protection provided by Green Island, the site on occasion could be relatively calm.

Since previous tests on the effects of screen color (i.e., potential reflection or absorption of light and/or heat) were inconclusive, additional testing was conducted at the Green Island site. Sets of single layer black polypropylene (2 X 3 mm mesh) and white polyester monofilament (2 mm mesh) were paired and placed at the surface, and at 0.1, 0.2, 0.4, 1.0 and 2.0 m water depth and monitored for a period of 14 weeks.

At the Green Island site, additional testing of multilayered black polypropylene screens (2 X 3 mm mesh) was conducted using double, triple and quadrupal layers for a period of nine weeks. Single layers of these same screens also were placed horizontally at 30 cm and observed for nine weeks. These were placed on standard float lines, similar to those used for feeding crabs (see below).

Carriacou, Grenada. From March thru June, 1986, algal turf production studies on standard plastic screen substrata were carried out in Grand Bay, Carriacou (12 ^{o}, 28' N; 61^{o}, 26' W; Figures 8, 10). As a relatively high energy study site, interest in algal turf studies here was directed towards comparing findings with data from Mayaguana, Grand Turk and Antigua.

Carriacou lies on the large and moderately deep Grenadines Shelf. It is subject to trade winds of high constancy and relatively high velocity (Adey, 1978). The shelf is characterized also by strong tidal flows. Grand Bay is oriented north to south and the east and south sides are protected by a nearly continuous bank barrier reef, the crest of which lies near or slightly below mean low water. Continuous waves of approximately 0.2-0.6 m height occur on the reef apron that lies adjacent to the outer lagoon. The primary reef lagoon pass is located near the island in the southwest corner of Grand Bay. Though a well-developed lagoon, the reef apron site at Grand Bay is nevertheless one of the most turbulent lagoon sites in the eastern Caribbean.

Work at Grand Bay was carried out at five sites. Two of these lay in the more turbulent eastern part of the bay. Site 1 was situated on the reef apron itself, while site 2, located immediately off the apron, was adjacent to a patch reef. Both sites were in very clear water over coarse sands, with a water depth of about 5m.

The remaining sites lay in the western half of the bay on the island sediment apron. Site 3 lay near the eastern margin of the apron in fairly clear and moderately turbulent water, overlying fine sand at a water depth of about 8m. Sites 4 and 5 lay nearer inshore on the island sediment apron, at water depths of 5 and 4 m, respectively. At these sites, the water was quite turbid. While waves were slightly higher on average at the inner sites, total water flow from waves and tide-driven currents was less.

Standard harvest procedures were employed at Carriacou, as described above. All screens used at this site were black polypropylene (2 X 3 mm mesh). Standard screens (0.92 m^2) were placed horizontally at 30 cm water depth and vertically, with the top at 10 cm below the surface. In addition, smaller screens (0.57 m^2) were placed horizontally and vertical arrays of eight screens were fitted in a cage size frame.

<u>Buen Hombre, Dominican Republic</u>. Extensive algal turf productivity studies were not carried out at Buen Hombre (19 °, 40' N; 71°, 20' W; Figure 11). However, since extensive crab mariculture studies were carried out at the Buen Hombre site, a limited number of comparative algal turf production studies were undertaken there from May thru September, 1985. These studies were conducted using the standard mariculture float/feed lines and black polypropylene screens (2 X 3 mm mesh) (see below) that were placed vertically. The harvest and drying procedures were standard. All screens were double-layered and 0.56 m^2 (0.61 X 0.92 m). Four screens were anchored by a single attachment point, four were anchored by two attachment points, and two

screens were hung one over the other (tandem).

Experimental screens grown in the wild at one locality show wide and synchronous variation in algal turf production that is a function primarily of wave action, current and available light (cloudiness). Because of this synchronous variation, demonstrations of the significance of other variables is often difficult to demonstrate with available statistical techniques, even when a plot of the data clearly shows a visually significant difference. On four test lines of 10 screens each recently established in Grand Turk lagoon (May-September, 1987), each test line was successively examined for the sign of change (+,-) relative to each other line with each harvest. The results were: 34/11; 37/8; 35/10 and 37/8 (change in same direction as line tested/change in opposite direction). This procedure clearly demonstrates that much of the variation against which significance is tested is due to synchronous and not random variations. In the following presentation of results and discussion, where tests of significance are negative but close and where the plotted data indicate the likelyhood of a difference, the results are simply stated along with the nature of the test.

RESULTS

LABORATORY STUDIES

Scrubber Turf Composition. Thirty (36) species of algae were identified as consistently present in the scrubber turf (Table 2). As in the field turf assemblage, the scrubber turf is a complex of species from each of the major benthic algal groups. At any one time, observations indicated that 30-50% of the biomass of this turf was composed of blue-green algae, most frequently species of *Calothrix*, *Oscillatoria*, and *Schizothrix*. The eukaryotic genera most dominant in the community were *Ceramium*, *Cladophora*, *Ectocarpus*, *Enteromorpha*, and *Polysiphonia*. *Smithsoniella earleae*, a persistent, occasionally common component of the scrubber turf assemblage, is encountered rarely in the field. Vegetative fragments of non-turf, macroalgal species were found frequently to have settled within the scrubber assemblage. Without periodic harvests, these fragments are capable of maintaining active growth on the scrubber screens.

Long-term Observations. The harvests in the long-term observations provided production values ranging from 0.3-21.6 g m^{-2} d^{-2} (mean = 7.2, ±4.0 S.D., n=277 harvests from seven scrubbers). The lowest productions were measured in the first harvests of the study, following introduction of screens to the scrubbers, and typically increased over a two-three week period as the turf assemblage became fully established upon the screens. The C/H/N ratios for samples of scrubber algal turf were determined by using a Perkin-Elmer Model no. 240 elemental analyzer. Mean compositions of 25.9% carbon (±3.0, range = 17.0-31.2, n = 61 replicates from 27 turf samples) and 2.7% nitrogen (±0.5, range = 1.4-3.4, n = 61) were calculated. When combined with harvest data from this study, the carbon composition value would indicate that 0.8-5.6 g C m^{-2} d^{-1} are fixed by algae in these scrubbers. In comparison, rates of carbon fixation measured during ^{14}C incubations averaged 5.32 mg C/h/g dry wt (±3.46, range = 1.35-23.45, n = 216 samples from 12 incubations). When these data are calculated alternately in units of areal production by employing the value of 4 cm^2 for each sample of turf-covered screen, a range of 0.15-0.64 g dry m^{-2} h^{-1} is obtained (mean = 0.28, ±0.09).

The harvests of both upstream and downstream screens from all scrubbers undergoing long-term observation were compared to examine the impact of wave surge upon turf biomass production. Mean production of downstream screens, 4.5 g dry m^{-2} d^{-1} (±1.88, n = 98 harvests from 5 scrubbers) was significantly lower (paired t-test, $P < 0.01$) than the mean upstream screen production, 8.5 g dry m^{-2} d^{-1} (±3.8, n=99).

Harvests from screens of varying pore size demonstrated that pore size may be decreased (fiber surface area may be increased) to a point where carbonate accumulation is promoted, which interferes in the establishment and subsequent growth of the turf assemblage. As a result, screens of 210 um pore size failed to support adequate biomass accumulation and were subsequently discontinued. While it has been observed that turf growth may decline on the decreased surface area provided by markedly larger pore sizes, no significant differences were detected between harvests from standard screens (1000 um) and 710 or 1400 um screens.

There were no significant differences detected between scrubber treatments when water depth, harvest schedule, photoperiod, or light intensity were varied within the scrubbers. However, it is likely, based on field studies, that insufficient parameter variation was applied.

Paired Scrubber Studies. The summary of data from the series of concurrent harvests (Table 3) shows that in the first test the two scrubbers provided with flow rates of 5.5 and 16.0 l/min produced significantly increased biomass on both upstream and downstream screens under the higher flow. Furthermore, under the 16.0 l/min flow rate, average productions from both screens were equal statistically (comparison of 1 c to 1 d, paired t-test, $p < 0.05$). In the second test, average upstream harvests under 13.5 l/min (2a) were equal statistically to average harvests from both screens receiving 16.0 l/min in the preceeding tests (1c and 1d each compared to 2a, $P < 0.05$). However, an increase to 32.5 l/min led to greater harvests on downstream screens only (2d), which resulted in a mean production value that equaled statistically the average upstream production under either flow rate (2d compared to both 2a and 2c, $P < 0.05$). In the third test, the increase from 13.5 to 32.5 l/min resulted in no significant increase for either screen. This test employed a smaller wave bucket at the higher flow rate, creating a 5 sec wave period. The average downstream production in this test, lower than observed on upstream screens at both flow rates, was lower statistically than average downstream production under the same flow rate in the preceeding test (comparison of 3d to 2d, $P < 0.05$).

Blockage of Wave Surge. The results of the blocked wave surge tests (Figure 12) illustrate that, while production varied considerably throughout the six weeks of harvests, the blockage of wave surge affected significantly lower production for both the upstream and downstream screens (paired t-test, $P < 0.01$). The production of downsteam screens was consistently lower than that of upstream screens in both the presence and absence of wave surge.

Monitoring of Nutrient Concentrations. Nitrate/nitrite concentrations measured during the 12 days prior to each harvest varied by over an order of magnitude, from 0.8-20.2 ug-at/l (Figure 13). Although there was no statistically significant relationship detected between the nutrient data and harvest, production averaged 11.2 g dry m^{-2} d^{-1} ($N = 18$) at N concentrations < 2.0 ug-at/l, 7.2 g dry m^{-2} d^{-1} (N =10) at concentrations of 2-7 ug-at/l, and 5.0 g dry m^{-2} d^{-1} (N = 2) at concentrations of > 15 ug-at/l. If there is a relationship, it is an inverse one.

FIELD STUDIES

Mayaguana. Plywood-based screens tended to accumulate fine carbonate sediment and produced algal turf growth very slowly. These screens lacked the constant animal activity of a hard reef surface, and were not subjected to cycloidal wave currents. Consequently, these screens resembled broad patches of protected reef pavement and contained more turf-bound sediment than the largely sediment-free open carbonate surfaces that characterize more irregular and/or turbulent reef sites. These rafts were eventually discontinued and detailed data are not presented. The experiments are mentioned because they demonstrate that the nature of the substratum by itself may limit production significantly even when potential production is very large. Subsequent studies have shown that finer screens (less than 0.5 mm mesh) also can accumulate significant fine carbonate sediment in some lagoonal sites, particularly on upper surfaces (see below), resulting in greatly reduced algal production. In the Mayaguana study, microscope observations on selected sample scrapings indicated the existence of only a very small proportion of sediment.

Data from the remainder of the screens is given in Table 4. The screens reached maturity, or sub-climax production, after four to six weeks of harvesting (Figure 14). Both the single layered black polypropylene (1.6 X 4.8 mm mesh) and the attached plastic-coated fiberglass window screen initially appeared to have the same potential for supporting algal growth. The single screen, however, lacked the support and protection of double layers and tended to degenerate, a process that ultimately lead to the tearing and loss of entire pieces of screen in rough water.

About 50% of the turf species identified on the reef were also found on mature raft screens (Table 5), although a long term study would probably lead to identification of further species. A number of diatom species, belonging to several genera, constituted the first algal colonizers. The diatoms appeared within a few days and developed to form a heavy, white-yellow fuzz within several weeks. After five to seven weeks, and several harvests, a mixture of blue-green algae and diatoms dominated the screens. After seven to eight weeks, the typical screen turf assemblage consisted of roughly equal quantities of blue-green algae and red algae, with only epiphytic diatoms and very few filamentous browns.

It is obvious that screen depth is critical to harvest production (Figure 15). As one might expect, algal turf production generally declines with depth. However, on the 1 m^2

screens, production also clearly declines near the water surface, displaying a consistent production peak at about 30 cm water depth. In all of the major raft localities (both lagoon and ocean), screens were placed at 15, 30 and 45 cm. At all non-lagoon sites for which harvests at all three depths were conducted, the peak of mean harvest production occurred at 30 cm, with marked reductions at both 15 and 45 cm (Figure 16). Also, out of 34 harvests conducted at all three depths, 19 showed peak production at 30 cm while 15 showed peak production at 45 cm. In only one case did the peak occur at 15 cm, and this was on a single screen raft, the most unstable design type. A two-way analysis of variance on a randomized block design revealed a highly significant difference between production at 15 and 30 cm ($P < 0.01$). The difference between 30 and 45 cm is significant at a probability of 0.05. However, the very consistent and smooth drop in production levels on screens placed in deeper, open ocean water indicates a pattern of production that peaks near 30 cm and declines with increased depth. Simple comparisons of standard deviation bars tend to cover up the wide and parallel production variation over time.

Even though there were significant and consistent differences in harvest values between the lagoon and open ocean sites for all shallow depths of screen placement, the patterns of increase or decrease over time are quite similar in both areas.

For example, in 27 out of 33 instances, harvests of the deeper (45 cm) and shallower (15 cm) screens followed both increases and decreases of harvests from screens placed at 30 cm water depth. On the other hand, lagoon and open ocean harvests seemed to be uncoupled. After the screens matured, the change in lagoon harvest production over time was obvious and consistent on each raft. Harvest was high in April, low in May, and high again in June (Figure 16).

Grand Turk.

Species Composition. Algal taxa from the Rhodophyta (reds), Cyanophyta (blue-greens), Chlorophyta (greens), and Chrysophyta (golden browns) were observed in the screen algal turf assemblages (Table 6). Spatial distribution and attachment of species observed in the intial 168 days of screen turf development can be divided into three ecological types: 1) the mat forming species which occur as mucilagenous colonies, on stalks, or as chains or filaments of cells (primarily Chrysophyta and Cyanophyta); 2) filamentous plants growing through the matted layer and producing a canopy of erect and creeping species with holdfasts, prostrate branches, and rhizoidal outgrowths entangled around the screen mesh (almost exclusively Rhodophyta) and 3) conspicuous epiphytes, growing on the canopy plants, primarily Chrysophyta and a few Cyanophyta. Two distinctive communities developed, due to differences in incident light between the top and underside of the screen. Although each side had similar species composition, percent composition of those species varied (Figure 17, 18). Benthic diatoms colonized the screens within 24 hours after they were placed in the lagoon and during the initial two months, diatoms continued to dominate the pioneer community. After one week, both sides had developed a layer of mucilage. This sticky layer consisted primarily of diatoms, bacteria and their secretions, which included some detrital matter. Thus, a bio-adhesive layer, on the basal plastic screen substratum, preceeded spore setttlement of most green, brown and red algae.

All major diatom species were present after 10 days on the top sides of the screens. Eighty percent of the turf community was the genus Syneda sp.B. Development on the bottom side was slower and included a greater number of diatom species, including those of Tabelaria sp, Licmophora sp, Synedra sp.A and a single unidentified species.

A notable successional pattern occured over the first 25 days on the top side of the harvested screen and about 50 days on the bottom. On the top, the growth of the dominant Synedra sp.B was followed by that of Licmophora and finally Tabellaria. The same pattern occured on the bottom, except that during the 25-50 m day interval, two new species settled and successively developed into major components. Growth of Synedra sp.A was followed by that of an unidentified diatom. For the first 25 days, the field count percentages and generic composition did not significantly differ between the harvested and unharvested screens. By the 84th day, coccoid and filamentous red and blue-green algae appeared in significant numbers. For the first 69 days, diatoms dominated the top side of the screens, representing 55% of the community and over the next 30 days their numbers decreased to 40% of the community. Later epiphytic diatoms, representing 60% of the community and largely growing on the red canopy, dominated the remaining 78 days of the study.

On the underside of the harvested screens the diatom colonization stage ended at 54 days, representing 34% of the community. At this point, the diatoms were succeeded by blue-greens, primarily Anacystis. For the next 50 days, the blue-greens fully dominated the underside. Finally, reds with a thick cover of epiphytic diatoms became primary elements. Mature screens discussed in this paper, have a whitish/yellow color on the upper side and a reddish brown color on the bottom side, which indicate the relative importance of the diatoms and the red algae.

On the top sides of the unharvested test screen, diatoms decreased from 60% at 49 days to 41% at 64 days. Cyanophyta increased in point count percentages from 7% at 49 days to 20% at 60 days. There was no significant change in composition of red algae between 49 days (20%) and 64 days (19.6%). Rhodophyta began to dominate the community, increasing from 23% at 49 days, to 39% at 59 days, to 55% five days later. Macrophytes, such as _Laurencia_ sp. and _Dasyopsis antillarium_, dominated the unharvested community for the remainder of the study, clearly demonstrating that the relationships between harvested and unharvested screens are similar to those of wild reefs.

Unfortunately, poor substratum material (1000 um, single layered screen) was chosen to model potential turf community development. Due to the relative thinness (0.5 um thick) of the 1000 um screen, algal holdfasts were frequently removed on harvest, which resulted in a poorly developed canopy structure. In the screen type and depth array studies, the multiweave screen had a high surface area to screen thickness (2000 um) ratio which allowed for sufficient unscraped surface area for holdfast development. The 1000um mesh screens maintained high diatom concentrations. With each harvest the mat layer was almost entirely removed from the substratum, except for small quantities which were forced between the pores of the mesh. Thus, the substratum was partly re-exposed and diatom colonization began again.

Substratum Area and Type. The screen mesh size studies conducted at site 1 indicated a relationship between substratum type, algal community, and biomass production. Of the seven single layered mesh types tested, the multiweave screen had the highest mean production rates at 10.6 g dry m^{-2} d^{-1} (see Table

7). While not significantly different (using ANOVA at 5% level) than the multiweave screen, screening with a finer mesh (125, 500, 710 um) had a lower mean production (7.8, 7.7, 7.8 g dry m^{-2} d^{-1}, respectively). The course black screen (2x3 mm) produced at levels close to the multiweave screen when in a single layer, but produced at much higher levels when doubled and tripled.

Site 1 at Grand Turk was protected from the prevailing trade winds. However, a shift in wind direction to the southeast would result in carbonate silt and detrital matter settling on the top sides of the screens. This silt coating hindered algal turf development and growth, especially on the finer mesh screens, and lowered production rates. The screens with greater porosity, had less of a build-up of silt and so algal turf production was much greater. Although mean production rates in the finer mesh screen were lower during the initial harvests, ultimately they reached production values equal to that of coarser screens for the same harvest period (200 um mean - 14.6 g dry m^{-2} d^{-1}; multiweave mean - 14.5 g dry m^{-2} d^{-1}).

Due to the silt problem at site 1, site 3 was chosen for a multilayered (single, double, triple) screen study. There were significant differences in biomass production between the single layered screen and both the double and triple layered screens (Scheffe Procedure at the 5% level). Although no significant differences were recorded between the double and triple layered screens, the triple layered screen yielded a higher mean production (17.8 g dry m^{-2} d^{-1}) than the double layered screen (14.7 g m^{-2} d^{-1}).

Small, double layered, black (2x3 mm) screens were introduced at site 3 to examine the possibility that edge to surface area ratios affects the biomass production, possibly due to water motion around the edges of artificial substrata (Borowitzla, et al., 1978). A 0.25 m^2 screen averaged 5.1 g dry m^{-2} d^{-1}, while a similar screen of 0.75 m (introduced and harvested at identical intervals) averaged 12.2 g dry m^{-2} d^{-1}. Biomass production based on edge to surface area ratios was to be the inverse of what was expected.

Harvest Rate. In order to determine harvest rates at which algal turf production could be optimized, biomass was collected from the screens at varied intervals. The mean biomass produced during 4, 7, 12 and 24 day harvest regimes was 5.3, 7.4, 7.6, 9.4 g dry m^{-2} d^{-1}, respectively.

Depth and Light. In depth/production studies, mean biomass yields increased with an increase in water depth from the surface (9.7 g dry m^{-2} d^{-1}) up to 30 cm depth, with no significant differences between 30, 40 and 100 cm depth (maximum 16.0 g dry m^{-2} d^{-1}; Table 9, Figure 19). The highest production values for a given harvest occurred at 30 cm (29.5 g dry m^{-2} d^{-1}) and 40 cm (28.9 g dry m^{-2} d^{-1}). Mean biomass production on the top side of the screen at 30, 40 and 100 cm water depth was not significantly different, while the shallower screens placed at the surface and 10 and 20 cm below the water surface had lower biomass values on average. Average underside production showed little variation with depth (3.5-4.6 g dry m^{-2} d^{-1})

The peak irradiance for incident and refected PAR, measured over 13 h, from sunrise to sunset (0630 - 1830 HRS), occured between 1130 and 1330, with incident light averaging 1700 uEin/m^2/sec. Reflected light averaged 200 uEin/m^2/sec in 2.0 m water depth, overlying a sandy bottom. Average incident PAR over the 13 h was 986 uEin/m^2/sec and average refected PAR was 100 uEin/m^2/sec. The spectral quality of available light over the top one meter of the water column in which the depth/production studies were carried out is shown in Figure 19.

At 30 cm water depth, incident PAR measurements were reduced to 655 uEin/m^2/sec when made through a 1000 um mesh screen. PAR was reduced further by 40%, when made through a similar screen, with seven days of turf growth. Harvesting the screen did not significantly change the incident PAR intensity (400uEin/m^2/sec), which passed through the screen.

Nutrients. Nutrient analyses were done in July and August at Grand Turk. At site 1, mean nitrite/nitrate was 0.06 ug-at/l, site 2 the mean averaged 0.25 ug-at/l and at site 3 the mean was 0.12 ug-at/l. These results are consistent with the flow pattern of equatorial currents over the reef and through the lagoon, which gradually pick up nitrogen released from the lagoon sediments. At all raft locations, orthophosphate concentrations were less than 0.03 ug-at/l below the detectable limits of the method used.

Antigua. Algal community structure was not formally tallied at Antigua. It was apparent, however, that the typical pattern of successive diatom, blue-green, red algal dominance was followed as a succession with time. However, it is the opinion of all observers at Antigua that algal diversity on the screens was markedly lower than at other sites.

Mean algal turf production with time is shown in figure 20 for both black polypropylene (2 X 3 mm mesh size) and white polyester monofiliment ($2mm^2$ mesh size) screens. The same data are plotted with depth in figure 21. It is apparent that the white screens show a significant increase in production (approximately 15% increase). This difference appears consistently when considering time, as well as depth. With depth, there is a clear production peak levels at 30-40 cm, with a sharp rise from surface values of about 75% of the peak and then with a slow drop off in algal growth with greater depth.

Table 10 shows the results of the location, multilayer and horizontal/vertical tests at Antigua. At dry weight production means of 7.3 g m^{-2} d^{-1} and 4.2 g m^{-2} d^{-1}, the protected sites of Rat Island and Bird Island, respectively, are significantly below the dry weight production mean of 18.2 g m^{-2} d^{-1} found in the more open and turbulent Green Island and Devils Bridge sites. The more protected sites were also characterized by gradual sediment deposition and a general degeneration of production with time to virtually zero values at 100 days.

The use of double-layered screens over single screens significantly increases algal production, as has been demonstrated at a number of sites. At Antigua, the increase in production from single screens to double layered screens was over 50%. On the other hand, triple and quadruple layers of screening reduced production. Algal growth was significantly lower when the quadruple layered screens were employed.

The vertical single screens tended to produce at mean levels of about 12% below that of the horizontal screens, which is consistent with earlier studies. However, the variation with time was typically large and, as a result, the difference is not statistically significant. The screens that were placed vertically developed an intermediate community between the typical diatom dominated top and red/blue-green dominated bottom communities.

As discussed below, apparent production levels were larger at the Antigua Green Island site than at any other location. This resulted in large measure from a high volume of included sediment.

Carriacou. Thirty-five algal species were tallied on the turf test screens at Carriacou (Table 11). While this is more or less typical of sites previously tallied, it is probably low because of the relatively short time that work was carried out at this site.

The productivity data collected at Carriacou are shown in Table 12 and plotted with time in Figure 22. The pooled means taken at each site included the small and vertical screens, since they did not provide harvests that were significantly different from the standard screens. The results from the tandem arrangement are omitted from the means at sites 1 and 2, since they provided mature harvests well below the stand alone screens.

The mean mature screen harvests for outer lagoon sites (sites 1 and 3) with maximum flow and turbulence, are 16.3 and 14.7 g $m^{-2}.d^{-1}$ respectively. These values are significantly higher than other sites, except for Antigua with its heavy sediment load, and reflect the greater turbulence levels in Grand Bay. Wind levels (taken three times/day on the ship's anemoneter) at Carriacou generally averaged above 15 knots. However, during the 40-53 day interval, wind speeds averaged below 10 knots. This is reflected in the general production dips for sites 1 and 3 at 45 and 55 days. It is also probably responsible for the apparent peaks in production on the island apron sites due to settled sediment during the calm period.

The Island apron sites, with less turblence in general showed production levels of 12.9, 8.6 and 9.7 g m^{-2} d^{-1}, which are significantly below those in the outer lagoon and reef apron.

Buen Hombre, Dominican Republic. The harvest production levels achieved at Buen Hombre are shown in Table 13. The mean value for all screens was 9.1 g m^{-2} d^{-1}, which is to be expected from this moderately quiet site. Additional factors in the moderate production level are a relatively short harvest interval and vertically oriented screens. No significant difference between the separate tests could be discerned. The prime interest in the data is that it extends through the summer period, a time when continuous data from other sites is not available.

DISCUSSION

LABORATORY WORK

The results of the laboratory experiments suggest, that given adequate light levels, of all the variables tested, turbulence is the primary factor controlling biomass production within the algal turf scrubbers. When provided with standard flow (13.5 l/min.), scrubber biomass production rates ranged above 20 g dry m^{-2} d^{-1}, indicating carbon fixation rates of over 6 g C m^{-2} d^{-1}. Assuming a 14 h light period and a set proportion of carbon lost to dark respiration each day, the range of these harvest data coincides well with ^{14}C-based specific productivity rate estimates of 0.15-0.64 g C m^{-2} h^{-1}. These biomass productivity rates were not significantly affected by the tested ranges of variation for most of the factors in this study. Water depth appears irrelevant to scrubber production so long as screens are continually submerged, though increases past a certain depth might interfere with turbulent mixing. There is also some indication that water depth may control the impact of UV toxicity in the field (see below). Although self-shading undoubtedly decreases rates of weight-specific productivity, results here suggest that for a period of between one and two weeks the exact harvest schedule is not critical to biomass production. While longer scrubber light periods conceivably could encroach upon the light cycle of the reef tanks, resulting in increased competition for carbon dioxide and other nutrients between scrubber and reef algae, no such hinderance to production was evident with the 2 h increase tested here. Scrubber light levels tested here are approximately 60% of the values recorded at levels of maxium turf production in the western tropical Atlantic and are probably well below saturation levels (Carpenter, 1985). It would be be expected, therefore, that increased irradiance would promote turf production in the scrubbers. The lack of a discernable response in this study probably reflects the narrow range of intensities tested, a limitation of the light source employed.

In contrast, adjustment to flow rate appears to directly affect biomass production within the scrubber environment by controlling the frequency of wave generation. This conclusion is based upon the disparate production values separating upstream and downstream screens, the harvests contrasting production under presence and absence of wave action, and the responses of production to increased flow rate.

Within the confines of the scrubbers, the cyclical dumping of the trough-like wave buckets is viewed most accurately as generating three liter displacements of water which cross the turf assemblage in the form of pulses, or waves. As this displaced water travels across the scrubber, it encounters friction in contacting algal filaments and quiescent water and converts in part to an oscillating flow that travels across the surface of the turf increasing disturbance of the boundary layer (Nowell and Jumars, 1984).

Diffusion gradients form continually within the boundary layers surrounding the thalli of metabolically active alga as a result of the low coefficients of molecular diffusion in water (Leyton, 1975; Norton _et_ _al_., 1982). Thus, any disturbance to these boundary layers, particularly an oscillating disturbance, will increase molecular exchanges between the plant cells and the surrounding water, ultimately influencing metabolic rates. By increasing the rates of simple, unidirectional currents in laboratory cultures of various aquatic plants, investigators have succeeded in reducing the thickness of boundary layers and raising rates of respiration, photosynthesis, nutrient uptake, and growth (e.g., Dromgoole, 1978a, b; Madsen and Sondergaard, 1983). However, turbulent flow, more typical of that encountered in the field, is particularly effective for disruption of boundary layers (Anderson and Charters, 1982). It is now recognized that certain marine algae may even have adaptive morphologies that serve to generate disruptive eddies as water flows across their thalli (Anderson and Charters, 1982; Norton et al., 1982).

Since the waves provide a turbulent flow that lessens in intensity with passage, the metabolic efficiency of a turf alga could be expected to vary with location in the scrubber. In addition, because diffusion gradients undoubtedly are re-established between wave passages, production would be influenced further by wave frequency, which results directly from flow rate. The importance of magnitude and frequency of wave surge most likely explains the significantly higher rates of production observed generally on upstream screens, specifically when wave action was restored.

In a preliminary examination of potential nutrient limitation within a scrubber receiving the standard flow rate (13.5 l/min), the nitrate/nitrite concentrations measured in upstream water filling the wave bucket and downstream water entering the drain pipe demonstrated a constant drop from about

1.0 to 0.75 ug-at/l. Similar measures of orthophospate failed to detect significant differences. While such data indicate an ability for rapid clearance of nitrogen, it appears doubtful that the availability of these particular nitrogen forms is a major controlling factor in turf biomass production. Based upon a 2.7% nitrogen composition, the mean value for upstream production of 8.53 g dry m^{-2} d^{-1} represents a requirement of about 16.3 mmole N/m^2/day. In comparison, under the standard flow rate and photoperiod (14 h illumination/day), the nitrate/nitrite clearance in the monitored scrubber indicates an uptake of only about 4.7 mmole N/m^2/day. The plot of production values against nitrate/nitrite concentrations also suggests that these species may not represent the major source of nitrogen and may have negligible control of biomass production within these scrubbers. With the exception of the one point that represents the lowest production and the highest nitrate/nitrite concentration, a possible outlier value, these data form a nearly vertical plot, indicating no relation between production and nitrogen concentrations over the ranges of concentration studied. Should the outlier be included within the analysis, an inverse relation is suggested. A relationship which these data clearly do not represent is the conventional interpretation of limitations to marine productivity, i.e., a decreased production under lower nutrient levels.

The scrubber turf algae may rely predominately upon an alternate source of nitrogen, ammonium, which has been measured at levels of around 0.3 ug-at/l within the microcosm. This concentration, appreciably higher than those which typify shallow Caribbean reefs (Meyer et al., 1983; Williams, 1984), undoubtedly reflects accumulation due to the closed system circulation and probably serves as a major nutrient source that is present at consistently high levels. However, an analysis of the specific ammonium clearance within an individual scrubber has yet to be performed. Fixation of atmospheric nitrogen by blue-green algae, an important turf component, might provide another source that is distributed through micrograzer activity or pathways. Should such fixation occur, it probably could provide large amounts of nitrogen to the assemblage, given the mixing enabled by shallow depths and wave surge within the scrubbers.

The results of the paired harvests under varied flow rates (Table 3) require some analysis to determine whether the wave frequency or the nutrient supply limits production. Increased harvests for both screens and equal productions between screens were observed under the higher flow rate of the first test. Under even more greatly increased flow in the second test, harvests increased on downstream screens to equal the upstream harvests under either flow rate. When considered together, these results suggest that any limit to production by flow rate past the upstream screens would be alleviated with a flow of around

13-16 l/min. The increase in downstream productions with 32.5 l/min regime to equal those upstream screens which remained unchanged, indicate that nutrients were not a limiting factor for production on the upstream screens at either flow rate in the second test. Similarly, the lower downstream production under the 13.5 l/min flow likely resulted from wave frequency that was too low to maintain as effective a disruption of diffusion gradients downstream, given the lowered turbulence reaching this portion of the scrubber.

The third test of 13.5 and 33.5 l/min, with a smaller wave bucket at the higher flow rate, resulted in no significant increases for either screen. Again, production on upstream screens may have neared the maximum for this scrubber environment under a flow rate of 13.5 l/min. A wave bucket with 1/2 the normal volume decreased the amount of disruption provided even further, by each wave that reached the downstream turf. Such decreased disruptive wave surge might have prevented a higher production on downstream screens, even with the greatly increased flow and resulted in the significantly lower value when compared to the mean obtained under the same flow rate in the second test. Thus, both volume and frequency appear to affect the disruptive capacities of wave surge. As particularly suggested by the wave generation test, where lack of surge flow nearly equalizes the differences between upstream and downstream screens, the nutrient supply aspect of flow rate does not appear as a significant factor limiting production in the scrubbers.

While the results of the six week study that examined the effect of intermittently blocked wave generation clearly support the contention that wave surge is the primary controlling factor in turf production, a decreased production nevertheless persisted on the downstream screen despite the maintenance of constant flow (13.5 l/min). A close examination of flow patterns arising from blocked wave buckets shows that they fail to provide a continuous advance of seawater across the width of the scrubber, allowing patches of reduced flow to develop over portions of the downstream screen. These relatively stagnant areas develop as the flow follows paths of least resistance towards the sides (or unharvested portions) of the scrubbers and probably explains the decreased production on downstream screens.

FIELD WORK

The mature algal turf community that develops on cultured, harvested screens in turbulent Caribbean waters is quite diverse, with over 30 species typically present. Except in the case of a few widespread and common species such as *Centroceras clavulatum*, *Sphacelaria tribuloides*, *Polysiphonia sphaerocarpa* and *Wrangelia argus*, the turfs do not generally have common species from site to site. That this is a real difference, in that species have been selected from stable but different population pools at each site, seems unlikely. It seems more likely that the pattern is a result of either widespread geographic and time variability in turf species throughout the region, morphological variation that makes accurate identification difficult, or real problems in taxonomy at the species level. In any case, at the generic level, there is considerable uniformity from site to site. Genera that tend to be common on the screens at most sites are: the diatoms, Licmophora and Navicula; the blue-greens, Anacystis, Oscillatoria and Schizothrix; the greens, Bryopsis, Cladophora, Derbesia and Enteromorpha; the browns, Giffordia and Sphacelaria and the reds, Callithamnium, Centroceras, Ceramium, Polysiphonia, Herposiphonia, Lophosiphonia, Wrangelia, Griffithsia, and Laurencia.

Diatoms are the primary early colonizers of algal turf screens at all sites. In most cases, they are largely replaced by blue-greens and early members of the canopy-forming reds and greens by 30 days. After that time, the diatoms that remain are primarily epiphytic. At Grand Turk, diatoms persisted as a major biomass element for longer than other sites but this may relate to the type of screen used for those particular tests and overharvesting. The percentage diatom composition varied for screen types tested, with benthic diatoms responsible for 30 to 50% of the biomass yielded. This suggests that diatoms can be as productive in the tropics as they are considered to be in the temperate zones. In a recent mangrove system study, Littler, _et al_. (1985) reported that a gelatinous species of naviculoid diatom was a major primary producer in the total community productiviy. Further, certain diatom species have demonstrated a resistance to ultraviolet light which could make them particularly suited for growth on screens suspended near the surface.

Perhaps the greater abundance of diatoms on the harvested screens as compared to the unharvested test screens and the wild reef was partially due to a shorter (4-12 days) harvest schedule on the screens. Harvesting would expose new substratum continuously, hinder red algal development, and allow benthic diatoms to proliferate. Benthic diatoms which initially colonized the screening also rapidly respond to harvesting (grazing pressure). Diatom dominance, although not quantitatively sampled, was noted to be particularly obvious at the four day harvest interval. Also, community structure tests were performed on single layered screens which resulted in overharvesting or, in ecological terms, high disturbance levels.

It would be difficult to quantify the biomass attributed to the major algal groups as the screens develop without major time expenditure. However, experience at all sites, with screen appearance and in tallies on microscope slides, indicates that there is an intermediate time from about 20-40 days in which blue-green algae dominate in biomass. After that time, it is typically the species of red algae that dominate in biomass as well as diversity (Figure 23). It is almost invariably the case that on the undersides of the horizontal screens the turf takes on a dark red brown color. On the topside of the screen, diatoms and blue-greens remain importent, resulting in a more light brown color. The green and brown algae, although almost invariably present on mature screens, are rarely important in terms of biomass.

Production of algal turfs on screens, as a function of depth, was examimed at Mayaguana, Grand Turk and Antigua. In all cases, production levels at or near the water surface were lower than at a depth of several tens of centimeters. At Mayaguana, the peak production level was at 20-30 cm and at Antigua, it was 30-40 cm with lower production in deeper water. At Grand Turk, however, no decline in production could be discerned up to a depth of 1 m.

Reduced algal turf production at the shallowest depths, with peak production occurring somewhat deeper, is to be expected because of ultraviolet toxicity, as described in phytoplankton studies. However, the tropical ocean/plankton production peak typically occurs at 10-30 meters (Steemann-Nielsen, 1955). For example, in Oscillatoria thiebautii (a blue-green phytoplankton in the Caribbean Sea), peak production occurs between 300 and 600 uEin/m^2/sec (Li et al., 1980), whereas in the algal turfs investigated here, it occurred over 1600 uEin/m^2/sec. Carpenter (1985) found similar results in chamber studies of coral reef algal turfs.

It is apparent from observations of algal turfs in a wave surge environment that the position of any given cell relative to incoming light is constantly changing, and that in most cases, individual cells are receiving widely varying light levels. The apparent increased resistance to ultraviolet radiation, with a concomitant ability to utilize most of the available visible radiation, may derive in part from the shading/light-flashing effects on individual algal cells in a regime of alternating wave surge (Falkowski, 1984). As we discussed above, with regard to the laboratory studies and with further consideration below, there is little question of the close association between high algal turf production and turbulence, including both current and wave surge.

Successive harvest production rates on the topsides of the screens were least variable at 100 cm depth. However, production in intense irradiance regimes ranging from the surface to 40 cm, revealed a high variability in biomass production from harvest to harvest. The turf community at less than 40 cm, while adapted to intense PAR and relatively high UVB was perhaps less photosynthetically efficient, and therefore, relatively more sensitive to weather related fluctuation in irradiance values.

The two ends of the spectrum, red/infrared and ultraviolet A + B, show significant reductions in intensity in the upper 30-40 cm (Figure 19B) and this corresponds with lower topside biomass production levels at the same depths. Recent work by Jokiel and York (1984) suggests that ultraviolet light should be considered as a photoinhibitor of primary productivity. However, Carpenter (1985) reported minimal UV effects on coral reef algal turf respiration rates. The algal community on screens may well have developed a chromatic adaptation to ultraviolet light. Certain species of diatoms (mostly from tropical waters) have been shown to have a resistance to ultraviolet radiation (Jokiel and York Jr., 1984), and several species of Rhodophyta (Tsujino and Saito, 1961; Yoshida and Sivalingam, 1970) and Cyanophyta (Shibata, 1969) contain ultraviolet absorbing substances.

At Mayaguana, a maximum algal production of 19.6 g dry m^{-2} d^{-1} was achieved with a mean of 12.6 g dry m^{-2} d^{-1} for 30 cm depth, double layered screens. Applying the same approach to Grand Turk, with similarly low nutrient concentrations, a maximum yield of 30.8 g dry m^{-2} d^{-1} was produced with mean biomass of 18.0 g dry m^{-2} d^{-1}. The increase in production at Grand Turk as compared to Mayaguana, in large part derives from an increased screen thickness and spatial heterogeneity, thereby preventing overharvest.

Algal turf production, on individual screens, varied significantly over time, apparently with no distinctive pattern, and often exhibiting dramatic fluctuations in production from one harvest to the next. However, production rates of the depth array screens, at both Mayaguana and Grand Turk, introduced at the same site and harvested on the same days, had consecutive peaks and troughs of production for individual screens. This continuity of biomass production among screens, from one harvest to the next, is quite similiar to that shown by simultaneously harvested screens at all sites, and suggests a real and consistent photosynthetic sensitivity to short term changes in physical parameters such as irradiance and water motion.

When the biomass production rates of the topside and the underside of the screens were considered separately, it is evident that the topside produced a higher proportion of the biomass values. For all screens tested at Grand Turk, the underside was consistent, as it yielded a mean of 5 g dry m^{-2} d^{-1}, with only a small deviation from the mean. Although the species composition of the underside screen community was more diverse, many of the same species were identified on both sides. The species composition of turf algae cultivated on screening did not seem to have a significant effect on the variations in turf biomass production.

Visually, the topside of most horizontal screens can be distinguished from the characteristically darker underside, which receives less PAR (as refected and transmitted light) than the topside. At 30 cm, with 1700-1800 $uEin^{-2}$ sec^{-1}, being received on the top side of the screens, approximately 400 $uEin^{-2}$ sec^{-1} would be transmitted through a standard black screen to the bottom side. With 200 $uEin^{-2}$ sec^{-1} being reflected back from the bottom at 4m (over a sand bottom) the bottoms of the screens are receiving nearly 50% of that received on the topside. In the Grand Turk experiments, where top and bottom production was separated, the bottoms developed 50% of surface production at 20 cm depth and 30% at 30-40 cm depth. Algae can vary photosynthetic pigment ratios or the total amount of pigments as chromatic adaptation for various irradiance intensities. Under reduced irradiance, the plants are more photosynthetically efficient and yeild lower but more consistant production values, regardless of long term irradiance fluctuation.

At Nonsuch Bay, Antigua, a 100 day study provided a consistent and significantly higher level of production on white translucent screens, as compared to the standard black screens. Based on the above discussion, this is clearly the result of increased transmission of PAR through the substratum screen.

In the screen type study at Grand Turk, both single-layered screens and finer mesh screens produced significantly less than multilayered and complex mesh screens. As discussed above, overharvesting as a result of insufficient substratum surface on single-layer screens and therefore protection for algal rhizoids and attachments seems to be clearly responsible. On the other hand, the finer mesh screens tend to accumulate fine carbonate sediment, which may initially result in relatively large apparent harvests. Eventually however, depending upon the availability of wave energy to remove the superficial sediment settling on the screens, sedimentation reduces turf production to low levels and in some cases to virtually no algal production at all.

The most significant and obvious difference in algal harvest at Mayaguana was that observed between ocean and lagoon rafts. Average production of the mature double lagoon screens at 30 cm depth was 13.8 g dry m^{-2} d^{-1}, over 2 1/2 times the ocean double screen production of 5.0 g dry m^{-2} d^{-1} for the same depth. The "ocean array" system likewise achieved lower production levels.

As mentioned above, nitrogen concentrations tested both in our laboratory and in an independent laboratory were in the range of 0.100-0.130 ug-at/l over a period of several weeks in April/May. No significant difference between ocean and lagoon could be found. While it is possible that another source of nitrogen is available in the lagoon (e.g., NH_4^+), it is unlikely to be a limited factor independent of phosphorus, particularly considering that abundant nitrogen fixation on these screens is quite likely. It is also unlikely that another source of moderate to elevated nitrogen would be available in the absence of higher concentrations of nitrate.

At Mayaguana, "ocean"/shelf sea conditions are only moderate for trade wind seas because of the partial protection offered by the East/West trending island. It is unfortunate that no open ocean or open shelf production data are available at other sites to assess offshore trade wind sea production levels. However, what is most important in this context is that at Mayaguana, the trade wind sea, when driven over the reef by wave action, greatly increases in turbulence and in flow rate, due to depth compression.

In the course of the three year investigation, some current meter readings were taken with a Marsh McBirny, electromagnetic meter that measures both current and surge. However, without continuous readings over many months, energy quantification is of little value. On the other hand, the very process of working algal screen lines on a daily basis provides a qualitative measure of energy levels available at each site. Thus, the direct relationship between production and wave and current energy, as shown in figure 24, can be regarded as a reasonable semi-quantitative measure. The single anomalously high value for Green Island, Antigua deserves further comment.

The harvest biomass of maximum production screens (lagoon doubles), at Mayaguana, had a mean of 15.5% carbon (C) (S.D = ±1.97; N = 22), based on C/H/N analysis. This compares to a figure of 19.8% (S.D. = ±3.62; N = 14) for all turf algae (including blue-greens, greens and browns, but not diatoms) provided by Atkinson and Smith (1983). The somewhat lower carbon value for Mayaguana could be related to sediment inclusion, though little could be seen on microscopic examination of turf samples. On the other hand, the Mayaguana "ocean" equivalent screens had a mean carbon level of 14.7% (S.D. = ±0.71; N = 8), not significantly below the lagoon value. If sediment were a contributing factor to apparent production in this case, and it might be argued that this is the reason for the lower "ocean" production, "ocean" carbon values would be significantly higher. Blue-green algae, with their largely proteinaceous cell walls, are a major component of algal turfs; this is undoubtedly partially responsible for the relatively high protein content (8-10%) of algal turfs. Likewise, diatoms with siliceous walls are major elements of the turfs. With these factors in mind, the relatively low carbon percentages do not appear unreasonable. It is likely that insufficient drying and/or dry storage aboard ship for several months in the tropical climate provided for some fungal and bacterial respiration losses in the samples. The upstream, mature laboratory algal turfs subjected to C/H/N analysis provided much higher carbon percentages (C = 27.9%; S.D. = ±1.29; N = 16), even at relatively low ambient nitrogen levels (near 1 uM). Diatoms are a much smaller part of the laboratory turf flora, and this is likely partially responsible for the higher carbon percentages; laboratory levels are also well above the values obtained by Atkinson and Smith (1983) for field turf species. However, a general preparation problem of algal turfs with regard to low carbon percentage cannot be ruled out. It is to be further noted that the data of Atkinson and Smith show no significant difference for carbon percentage in algal turf and small algae for low nutrient and high nutrient waters.

The carbon percentage values provided by Atkinson and Smith (1983) show means of 19.8% for algal turfs, 30.3% for small macro algae (e.g., Ulva, Dictyota, and Hypnea) and 33-35% for large algae (e.g., Sargassum) and marine flowering plants. The relatively low carbon values probably result in part from less structural carbon in walls (cellulose and its algal relatives). They may also result in part from greater difficulty in perserving organics intact (considering the larger surface areas) until analysis is performed. Laboratory turf samples with a quite similar algal community, though perhaps significantly lacking in diatoms, showed carbon percentages close to that for macroalgae. The subject needs further investigation.

Unfortunately C/H/N analyses were not performed on the Antigua harvests. It is clear from visual and microscopic observations that levels of carbonate sediment in the Green Island samples were high, and this could account for the anomalously high weights. On the other hand, it has been our experience from other sites (Grand Turk, Carriacou) that where low energy and a corresponding increased sediment deposition is involved, that algal production is very low. Also, it was found that screens placed vertically as compared to screens placed horizontally (which should greatly reduce sediment settlement) at the same site at Antigua, provided harvests only about 12% lower.

Nonsuch Bay, Antigua, unlike all other sites, has no ready lagoon outflow down wind. Waters that are driven over the reef with their accumulated carbonate sediment as well as water and sediment derived from land run-off, must largely depart from the Bay through two channels, both trending eastward into the tradewind sea. As a result, the waters of Nonsuch Bay are generally more turbid than other sites that were utilized in this investigation. Even though wave energies and current flow are moderate at the Green Island reef site, suspended fine sediment is typically high. Thus, it is tentatively concluded that increasing sediment loads generally reduce algal turf production (real and apparent) in cultured screen situations. Where both moderate wave and current energy are available and high loads of fine sediment also are present, sediment is driven into and imbedded in the basal, blue-green and diatom, mucilagenous layers that comprise the algal turf community. As long as the sediment is fine-grained and moderate in abundance, turf production is not significantly decreased, but simple dry weight algal production is increased. Judging by the considerable difficulties in sustaining the growth of grazing crabs and in reducing crab mortality at this site, as compared to other sites, the sediment load in the screens under these special circumstances appeared to provide a significant problem for these animals. This matter is discussed in greater detail under Mariculture (this volume).

General Discussion

Unfortunately, quantitive algal turf production work was undertaken only during the Winter, Spring and Summer periods, between the months of February to August. Based on the coral reef production work of Adey and Steneck (1985) at St. Croix, reductions in algal turf production are to be expected during the relatively cloudy calm and radiation minimum autumn period. Qualitatively, this early "winter" reduction was experienced at several sites, in terms of the utilization of turf production to feed grazing crabs. However, a more interesting characteristic of the long term production of algal turfs on plastic screens, which cannot be substantiated by quantitative studies at this time, is the apparent tendency for continuously used screens at some sites to accumulate coralline algal crusts and sometimes bryozoans, anemones and ascidians. Unfortunately, this results in a lowered algal production. This problem appeared to be more characteristic of the lower energy, more turbid sites (Antigua, Buen Hombre) than the clearer more turbulent areas. Brief drying and re-stringing of the turf screen lines quickly solves the problem. In addition, at all sites, continuous harvest, in the 10-20 day range, is essential to keep the screens highly productive with algal turfs. Screens, un-harvested for several months tend to develop a patchy macroalgal growth, often including species characterized by toxic compounds (e.g., Laurencia, Acanthophora) and by significantly increased attached epifauna. These screens have greatly lowered production rates (presumably equivalent to that of a mature forest community) and greatly reduced value for feeding grazers (much as results when a forest replaces grazing farm land). Unfortunately, it is very difficult to return such screens to mature algal turf production levels. Thorough drying and scraping is the only method that we recognize at this time.

In cases where relatively low algal production was experienced, variability with time was also considerably less. Also, production rates often continued to slowly rise throughout these studies. This phenomenon occurred at the deep ocean sites at Mayaguana, the protected sites at Carriacou and the moderate energy situations at Buen Hombre. The reasons for these relationships and the level of the eventual peak values that could be obtained under these conditions are not known and should be further investigated.

CONCLUSIONS

There is little question that given adequate wave and current motion and intense solar irradiance, reef algal turf communities on artificial screen-type substrata, in nutrient poor seas, can consistently produce at harvest rates of 8 to over 15 g dry m^{-2} d^{-1}. A number of physical and biotic variables are involved in determining the level of this production. These include: 1) overharvest potential as related to substratum type and harvest frequency; 2) underharvest potential as related to colonization by macroalgae and animals; 3) water depth, screen type and screen orientation as related to ultraviolet and/or perhaps infrared radiation and to the transmittance and reflectance of light and 4) sedimentation level and quality as related to wave action.

While mat-forming benthic diatoms are the primary colonizers of these substrata and remain important elements in all cases, mat-forming blue-green algae and finally "canopy"-forming red algae become critical biomass-producing elements as the screens mature. Red algae become the dominant producers in the presence of some shading and where short term harvesting is not carried out.

Wild, screen-cultured algal turfs are highly diverse with approximately 30-40 species of algae typically being significant elements of the community as it develops and matures. This diversity could very well be of critical importance to the stability of biomass production for mariculture, as it is unlikely to be disturbed significantly by disease or micro predation. The tendancy for human agriculture to heavily pursue monocultures and to use a battery of modern tools to reduce genetic diversity has considerable implications with regard to a general sensitivity to large scale crop failure.

Carbon percentages based on C/H/N analyses are relatively low in field algal turfs as compared to laboratory algal turfs, macro algae and flowering marine plants. This relates only partially to included carbonate silt levels. Algal turfs are rich in blue-green algae with proteinaceous walls and are therefore relatively rich in protein as compared to cellulose. Dried algal turfs arre also rich in silica as a result of high diatom abundances. Sample preparation and preservation may also be a critical factor. The very nature of the algal turf, in which species compete by rapid growth and reproduction with little investment in structure or defense through armor or toxic compounds, suggests a composition subject to rapid breakdown by fungi and bacteria and alternatively easily available for utilization as a food source. Also, many grazing animals, including the _Mithrax_ crab, discussed in the depth in this volume, appear to prefer algal turfs and are adapted to their harvest, even when in the wild this results in a digestive system that is rich in sediment and detritus.

Most important, numerous and repeated successful broodings of _Mithrax_ females utilizing algal turfs have occured in this study (see Reproduction, this volume). In addition, and probably more critical, _Mithax_ _spinsosissimus_ fed pure algal turfs or algal turfs supplmented with small quantities of wild macro algae in culture have provided considerably higher growth rates (see Morphology, this volume) than crabs fed on diets of macro algae, meat and commercial feeds (Ryther, et al., 1987) This indicates that algal turf is a rich food source for this predominantly herbivorous animal and is likely a similarly rich food source for other reef grazers.

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LEGENDS

FIGURE 1. Typical laboratory/mesocosm algal turf growing on a one mm^2 mesh screen. The plastic strands of the screen are 330 um in diameter. Present on this screen, as drawn are: the diatoms, *Licmophora* sp. and *Navicula* sp.; the blue greens, *Anacystis dimidiata*, *Calothrix crustacea* and *Oscillatoria submembraanacea*; the greens, *Cladophora fascicularis*, *Smithsoniella earleae* and *Derbesia vaucheriaeformis*; the browns, *Ectocarpus rhodochortonoides* and *Sphacelaria tribuloides*; and the reds, *Asterocytis ramosa*, *Ceramium corniculatum*, *Polysiphonia havanensis* and *Herposiphonia secunda*.

FIGURE 2. Oxygen concentration of seawater undergoing direct, continuous recirculation through an algal turf scrubber versus elapsed time of incubation. Note change in rate of oxygen production as wave action blocked and restored.

FIGURE 3. Location of Mayaguana Island, Bahamas.

FIGURE 4. Abraham Bay, Mayaguana research site. Depths in fathoms show sharp drop off near rafts. Local trade winds and currents constantly bring ocean water to the experimental site.

FIGURE 5. Standard pvc pipe raft used to hold screens for algal culture. The screen dimensions are 1 m^2 and the PVC pipe is 7.6 cm dia.

FIGURE 6. "Ocean Array" of 1/4 m^2 screens established to determine rates of algal production with depth.

FIGURE 7. Grand Turk shelf, reef and research sites. See figure 3 for the location of Grand Turk.

FIGURE 8. Eastern Caribbean sea, showing islands with field research sites.

FIGURE 9. Detail of Nonsuch Bay, Antigua study sites 1-4.

FIGURE 10. Detail of Grand Bay, Carriacou and field study sites 1-5.

FIGURE 11. North Coast of Monte Christi Province, Dominican Republic, showing the location of the Barrier Reef, Buen Hombre and the algal research site.

FIGURE 12.	Scrubber biomass production rates for one week harvest periods under the presence or absence of disruptive wave surge. Production rates indicated for upstream (triangles) and downstream (circles) screens within one scrubber that had wave action blocked during alternate weeks.
FIGURE 13.	Scrubber biomass production rates for 12 day harvest periods vs. N-(NO_2 + NO_3) concentrations in circulating microcosm water. Values plotted for upstream screens (triangles) and downstream screens (circles) for one scrubber. Values correspond to average of nitrogen concentrations measured during harvest period. Range in measured concentrations indicated, when possible, by bars.
FIGURE 14.	Mean harvest production rates of screens at Mayaguana with time (harvest every seven days).
FIGURE 15.	Harvest production rates of screens with depth (harvest every seven days; means beginning with forth week for one meter screens; means beginning with fifth week for ocean array).
FIGURE 16.	Relative abundance of diatoms on test screens at Grand Turk for the first 41 days of algal turf development.
FIGURE 17.	Relative abundance of major algal groups on test screens at Grand Turk for 48-168 days.
FIGURE 18.	Biomass production of algal turf as a function of water depth and screen size at Grand Turk. Also, included is a typical, mid day solar energy spectrum as a function of depth.
FIGURE 19.	Algal turf production with time on white (translucent) screens and black screens at the same site on Antigua.
FIGURE 20.	Algal turf production on white (translucent) and black screens as related to depth at Antigua.
FIGURE 21.	Algal turf production with time and site on standard screens at Carriacou. Dashed lines indicate period of heavy sedimentation on island apron screens.
FIGURE 22.	Number of species of major algal groups on algal turfs as a function of time at Grand Turk.

FIGURE 23. Qualitative relationship between turbulence (wave and current energy) and mean harvest production at research sites. This is the result of an independent survey taken of scientists who spent a considerable amount of time working with algal screens at at least several of the sites in question.

TABLE 1. Algal genera consistently present in various surveys of Caribbean and western tropical Atlantic coral reefs. Species listed within genera are common, persistent components of the coral reef algal turf assemblage. Genera designated by parentheses contain no persistent turf components and are classified as encrusting coralline or macroalgae in this study. Asterisks designate genera that contain both the listed turf component species and other species which do not persist within the assemblage. Plus signs designate calcareous genera.

TABLE 2. Common, persistent components of the coral reef algal turf assemblage in microcosm scrubbers. Species were identified using Taylor (1960), Humm and Wicks (1980) and Sears and Brawley (1982).

TABLE 3. Biomass production rates calculated from 12 day, concurrent harvests of paired scrubbers. Mean production rates, ±S.D., range and harvest numbers listed for both upstream and downstream screens in each of three flow rate comparisons.

TABLE 4. Algal turf harvest with time, depth and screen type at Abraham Bay, Mayaguana, Bahamas Islands.

TABLE 5. Turf Algae of Mayaguana

TABLE 6. Algal species identified on turf culture screens at Grand Turk, Turks and Caicos Islands.

TABLE 7. Screen type study at site 1 and site 2, Grand Turk.

TABLE 8. Results of harvest rate study at site 2, Grand Turk.

TABLE 9. Results of depth array study at site 3, Grand Turk.

TABLE 10. Algal production (g m^{-2} d^{-1}) in location and screen type tests in Nonsuch Bay, Antigua.

TABLE 11. Algal species tabulated on turf growth rafts at Grand Bay, Carriacou, Grenada.

TABLE 12. Algal turf production (g m^{-2} d^{-1}) as a function of location, screen type and time at Grand Bay, Carriacou.

TABLE 13. Algal Harvest Data from Buen Hombre, Dominican Republic.

Figure 1

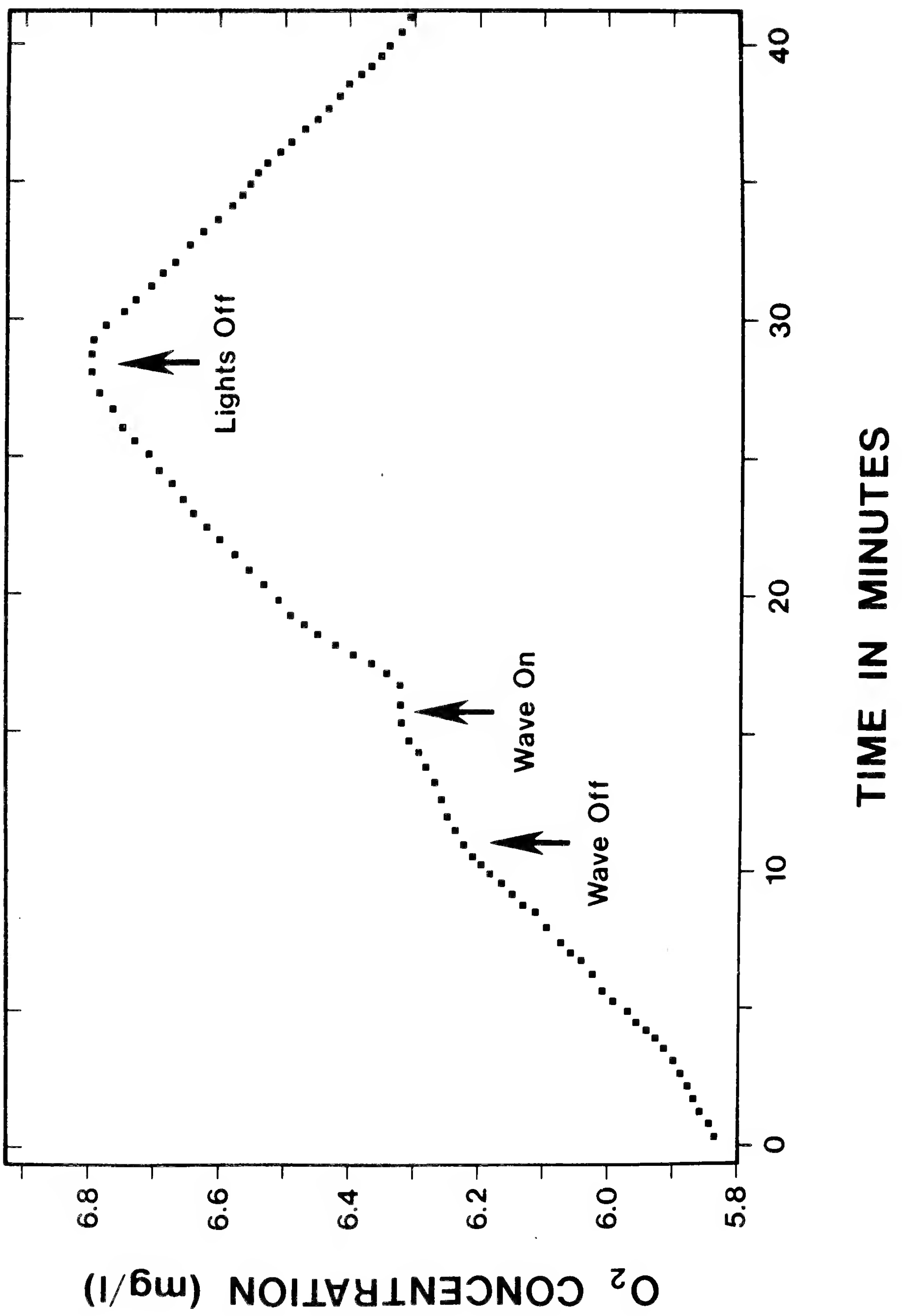

O$_2$ CONCENTRATION (mg/l)
6.8
6.6
6.4
6.2
6.0
5.8
Lights Off
Wave On
Wave Off
0
10
20
30
40
TIME IN MINUTES

Figure 2

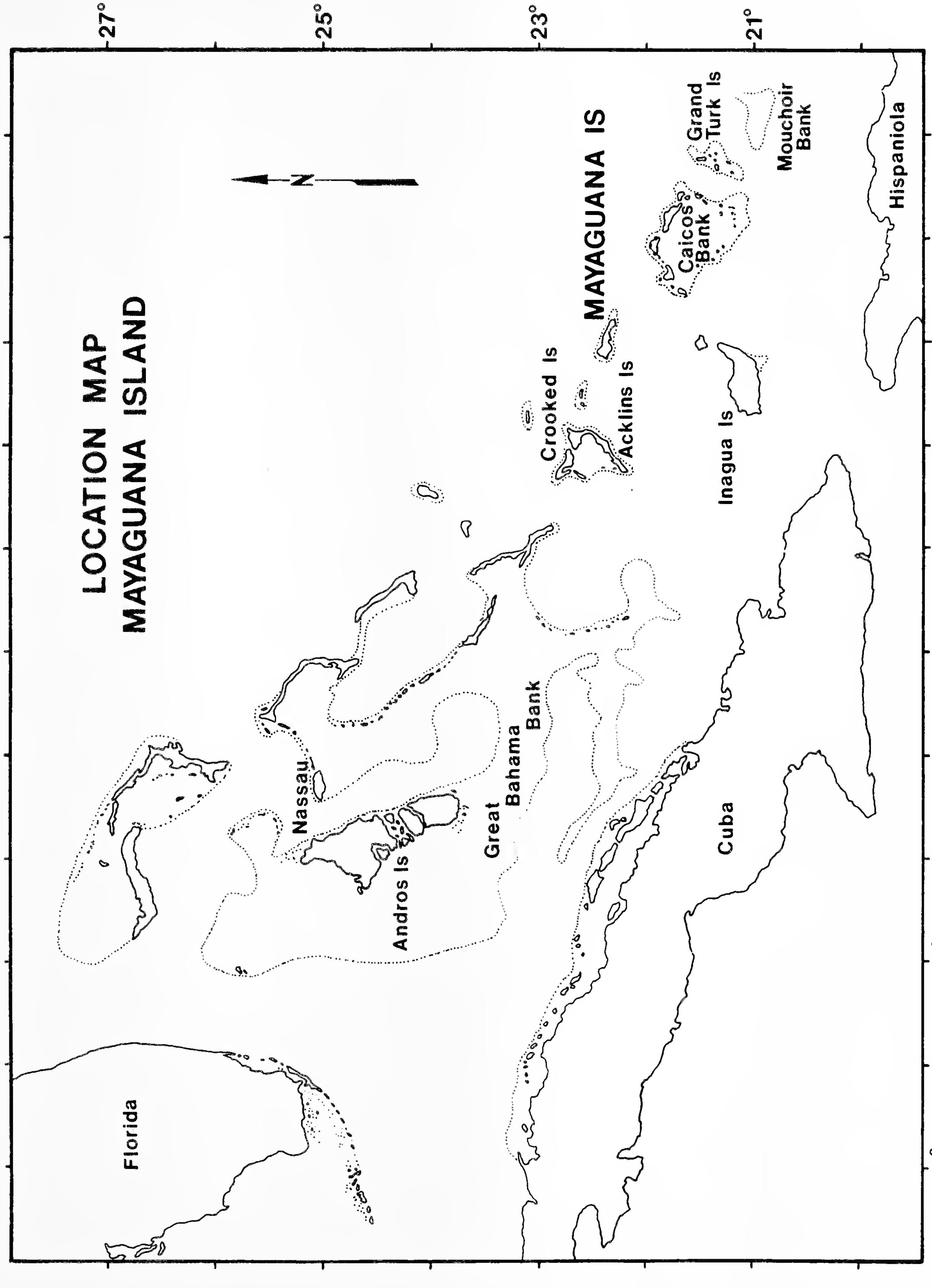

LOCATION MAP
MAYAGUANA ISLAND
N
Florida
Andros Is
Nassau
Great Bahama Bank
Cuba
Crooked Is
Acklins Is
Inagua Is
MAYAGUANA IS
Caicos Bank
Grand Turk Is
Mouchoir Bank
Hispaniola
27°
25°
23°
21°
71°
73°
75°
77°
79°
81°

Figure 3

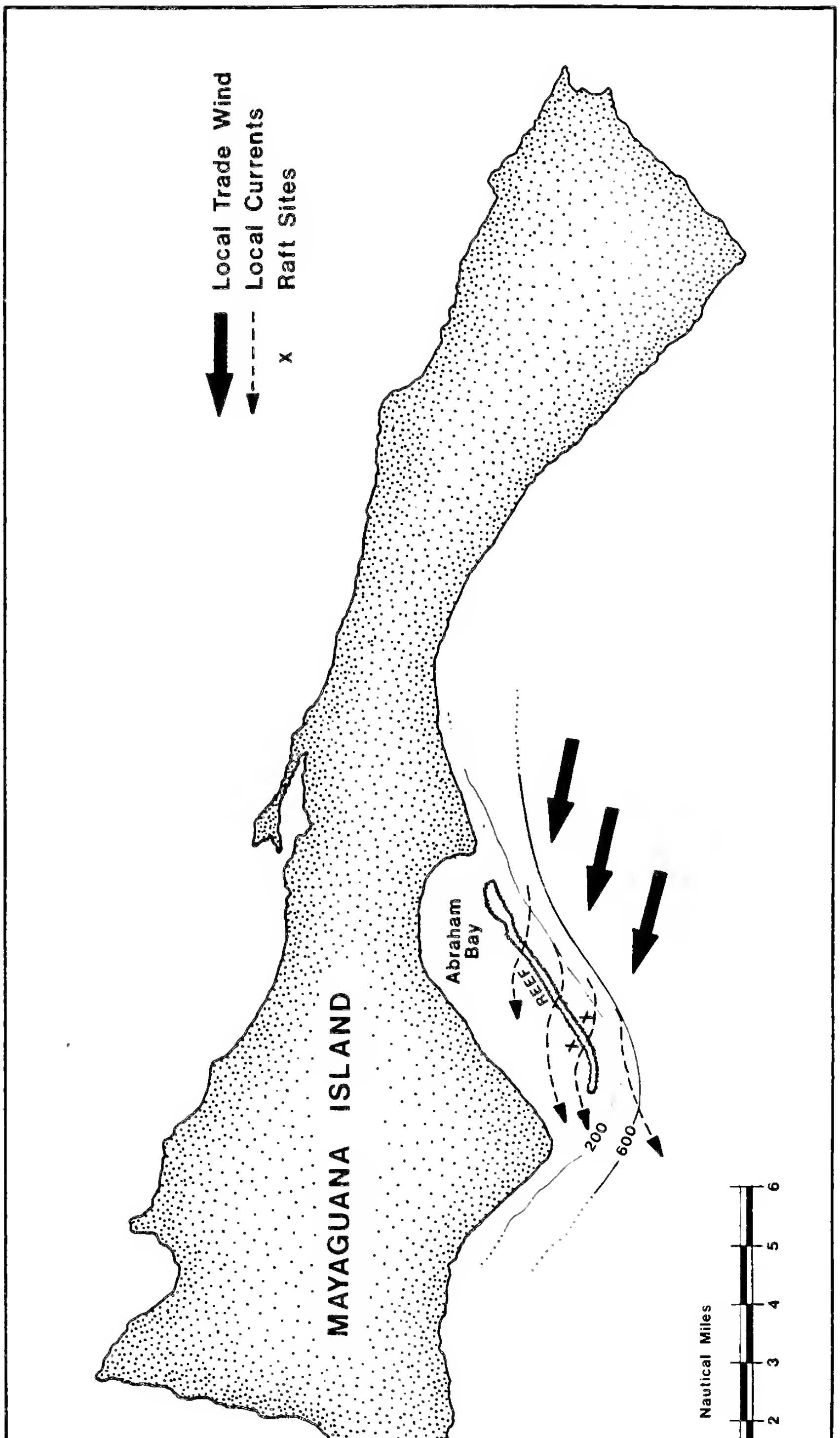

Local Trade Wind
Local Currents
x Raft Sites
MAYAGUANA ISLAND
Abraham Bay
REEF
200
600
N
Nautical Miles
0
1
2
3
4
5
6

Figure 4

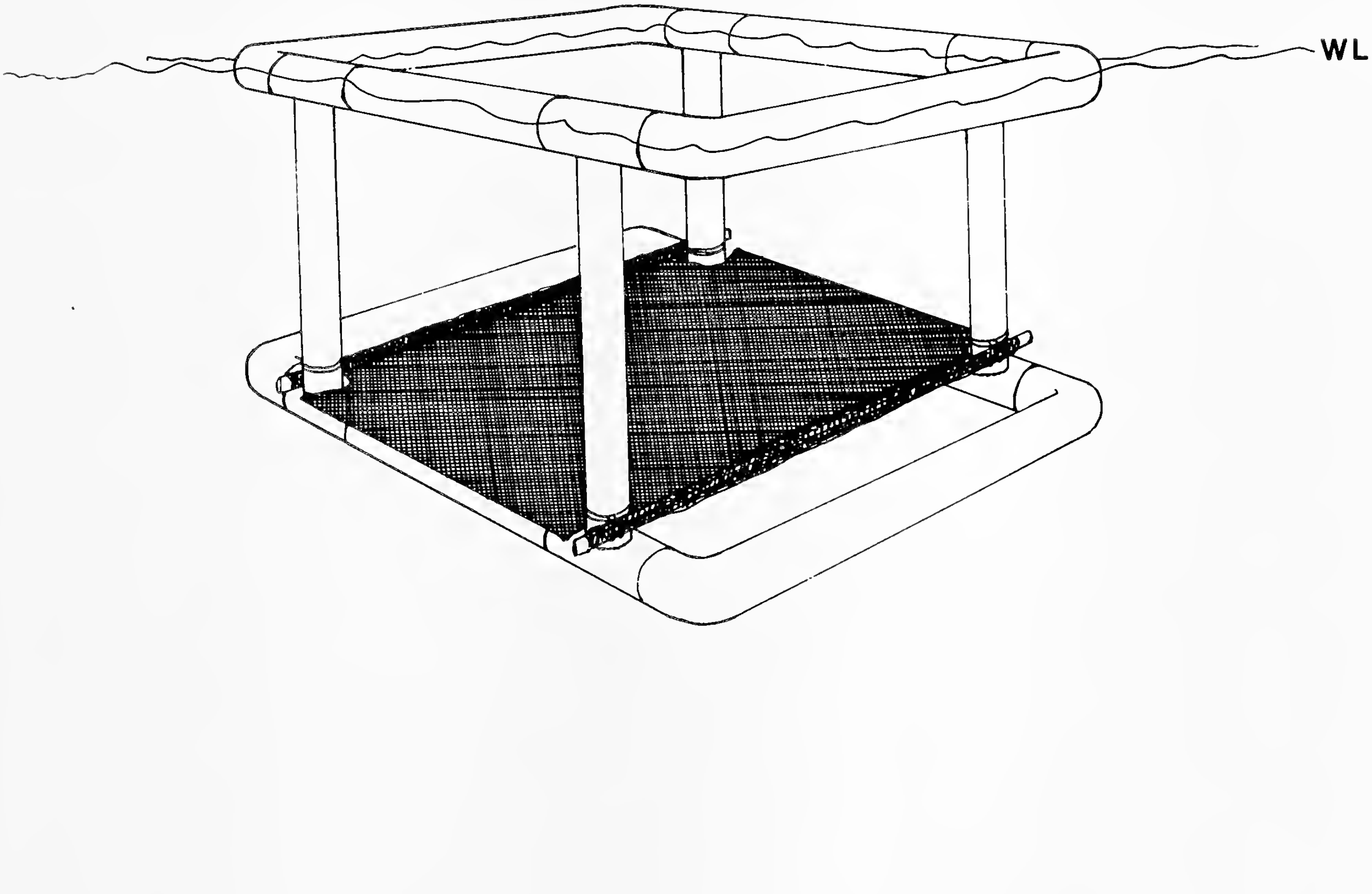


Figure 5

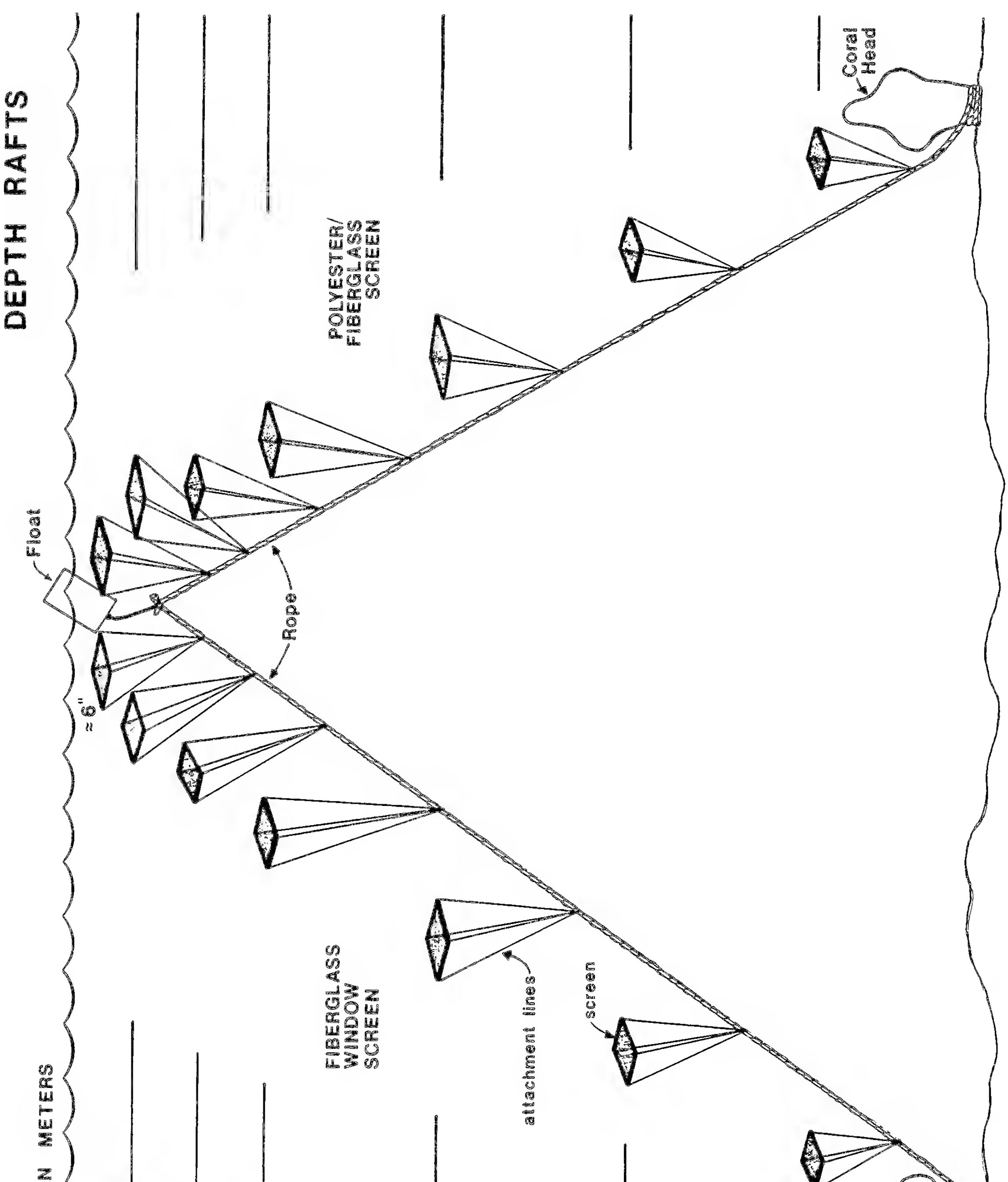

DEPTH RAFTS
DEPTH IN METERS
1
2
3
6
9
12
FIBERGLASS WINDOW SCREEN
POLYESTER/ FIBERGLASS SCREEN
Float
Rope
≈6"
attachment lines
screen
Coral Head

Figure 6

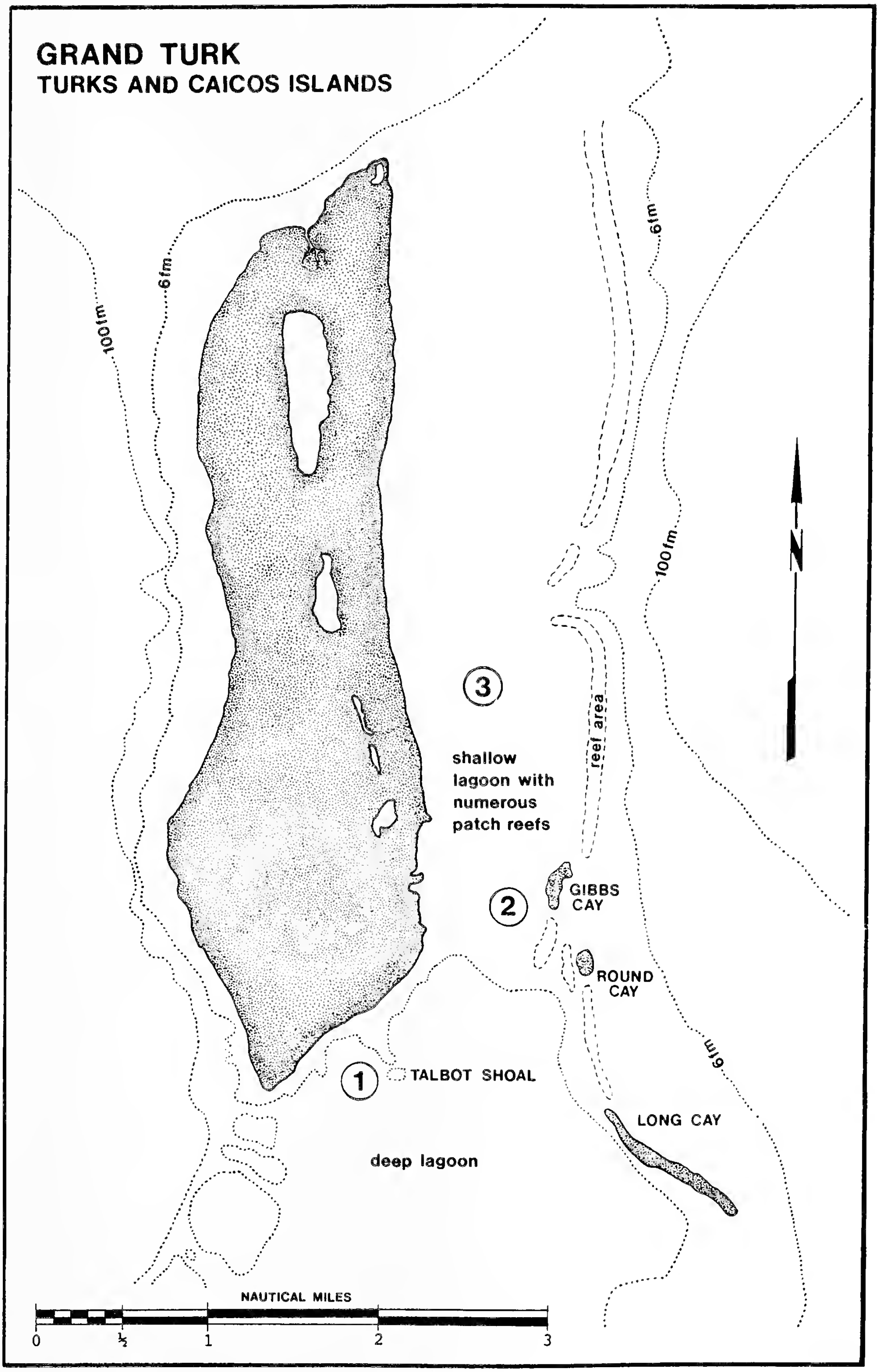

GRAND TURK
TURKS AND CAICOS ISLANDS
100fm
6fm
6fm
100fm
3
shallow lagoon with numerous patch reefs
reef area
2
GIBBS CAY
ROUND CAY
1
TALBOT SHOAL
6fm
LONG CAY
deep lagoon
N
NAUTICAL MILES
0
½
1
2
3

Figure 7

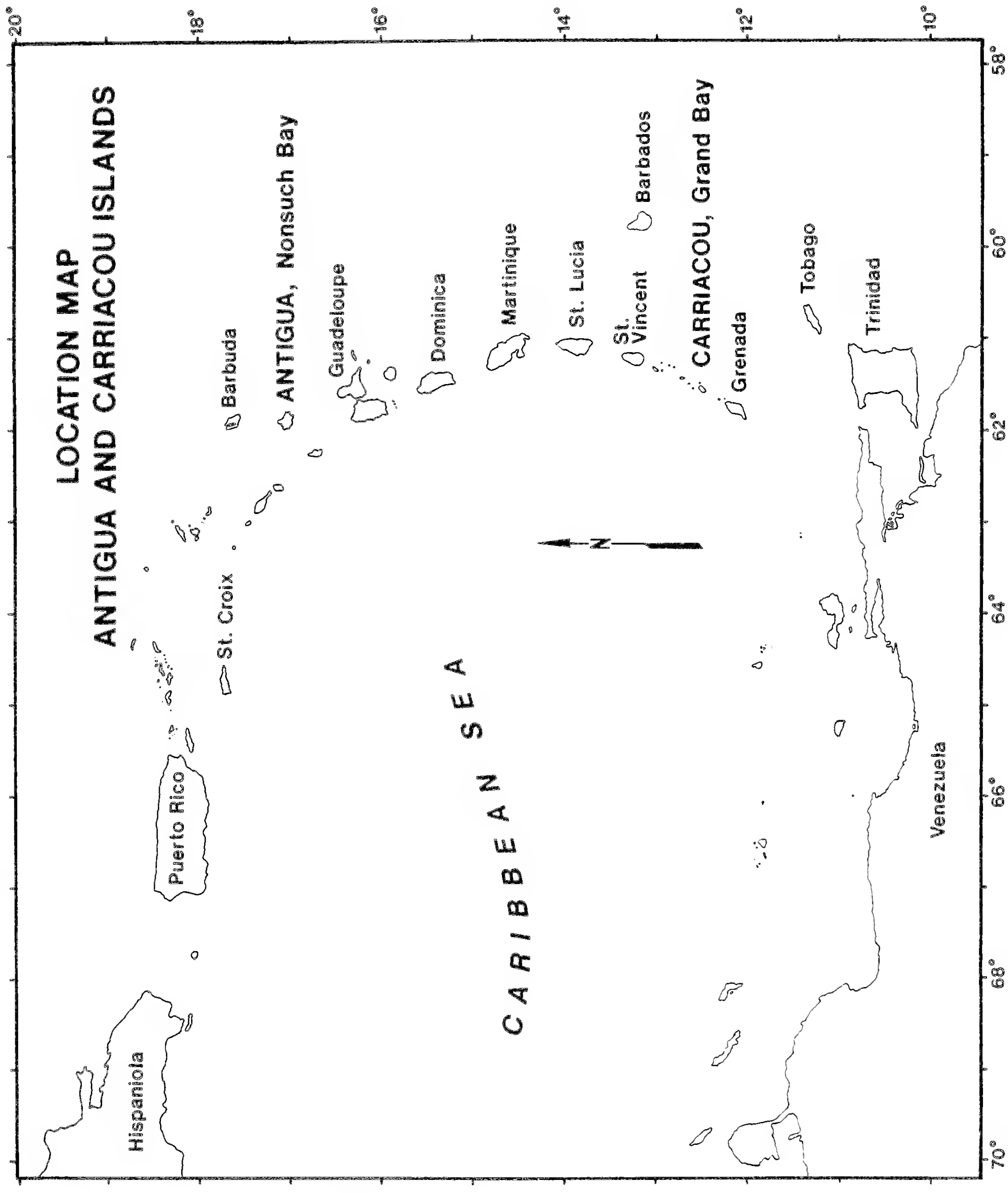

LOCATION MAP
ANTIGUA AND CARRIACOU ISLANDS
Hispaniola
Puerto Rico
St. Croix
Barbuda
ANTIGUA, Nonsuch Bay
Guadeloupe
Dominica
Martinique
St. Lucia
St. Vincent
CARRIACOU, Grand Bay
Grenada
Barbados
Tobago
Trinidad
Venezuela
CARIBBEAN SEA
N
20°
18°
16°
14°
12°
10°
58°
60°
62°
64°
66°
68°
70°

Figure 8

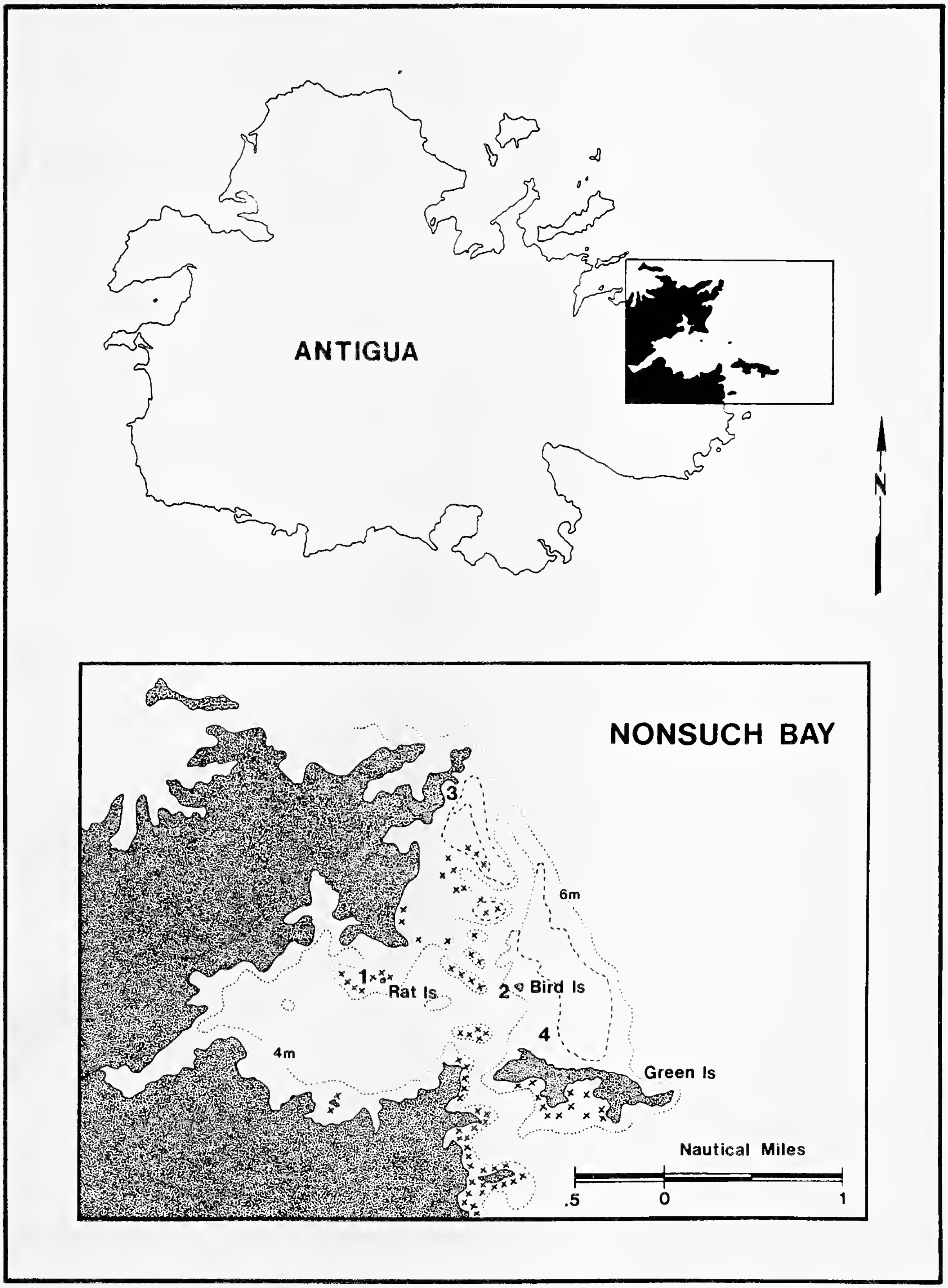

ANTIGUA
N
NONSUCH BAY
3
6m
1
Rat Is
2
Bird Is
4
4m
Green Is
Nautical Miles
.5
0
1

Figure 9

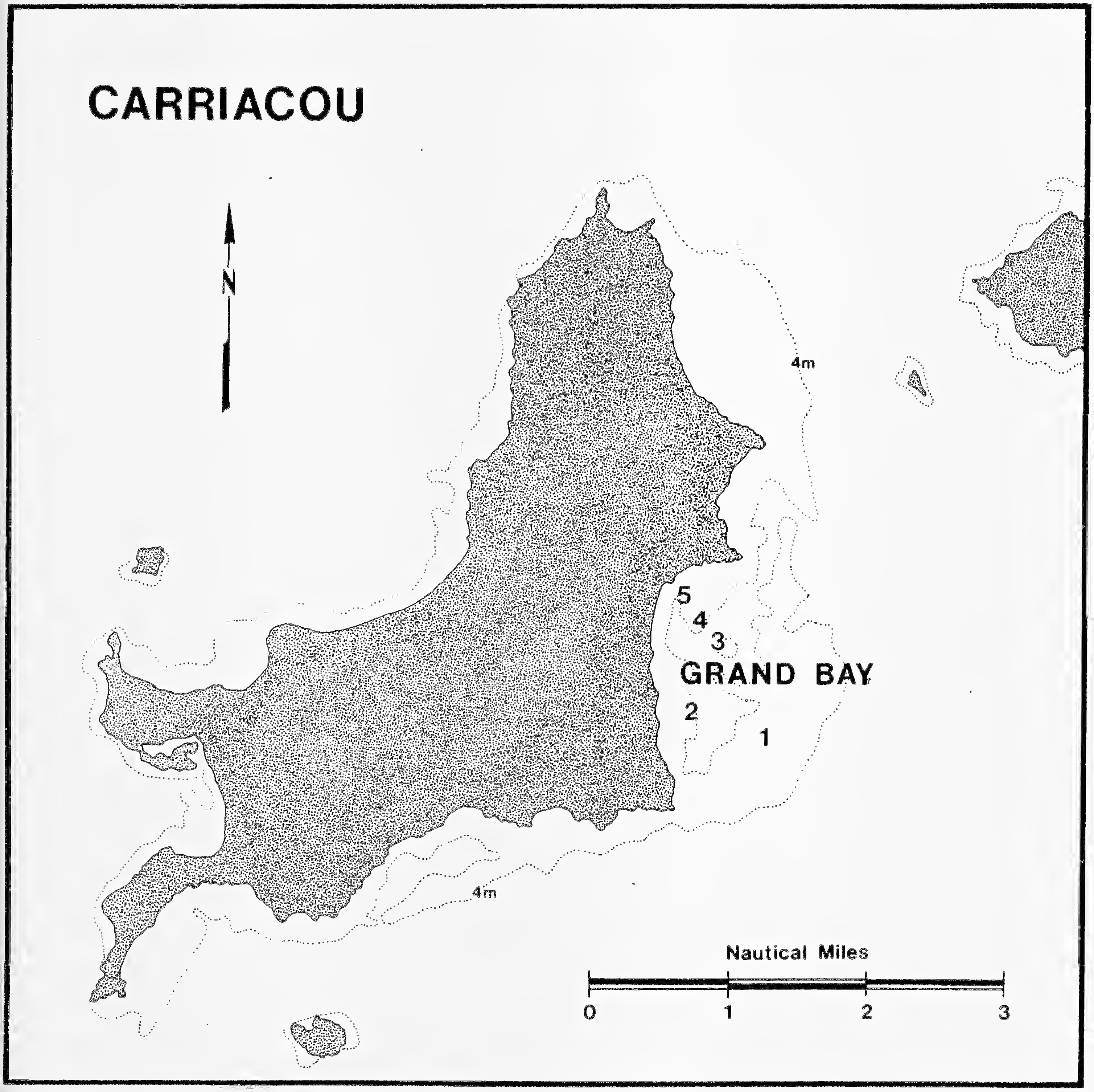


Figure 10

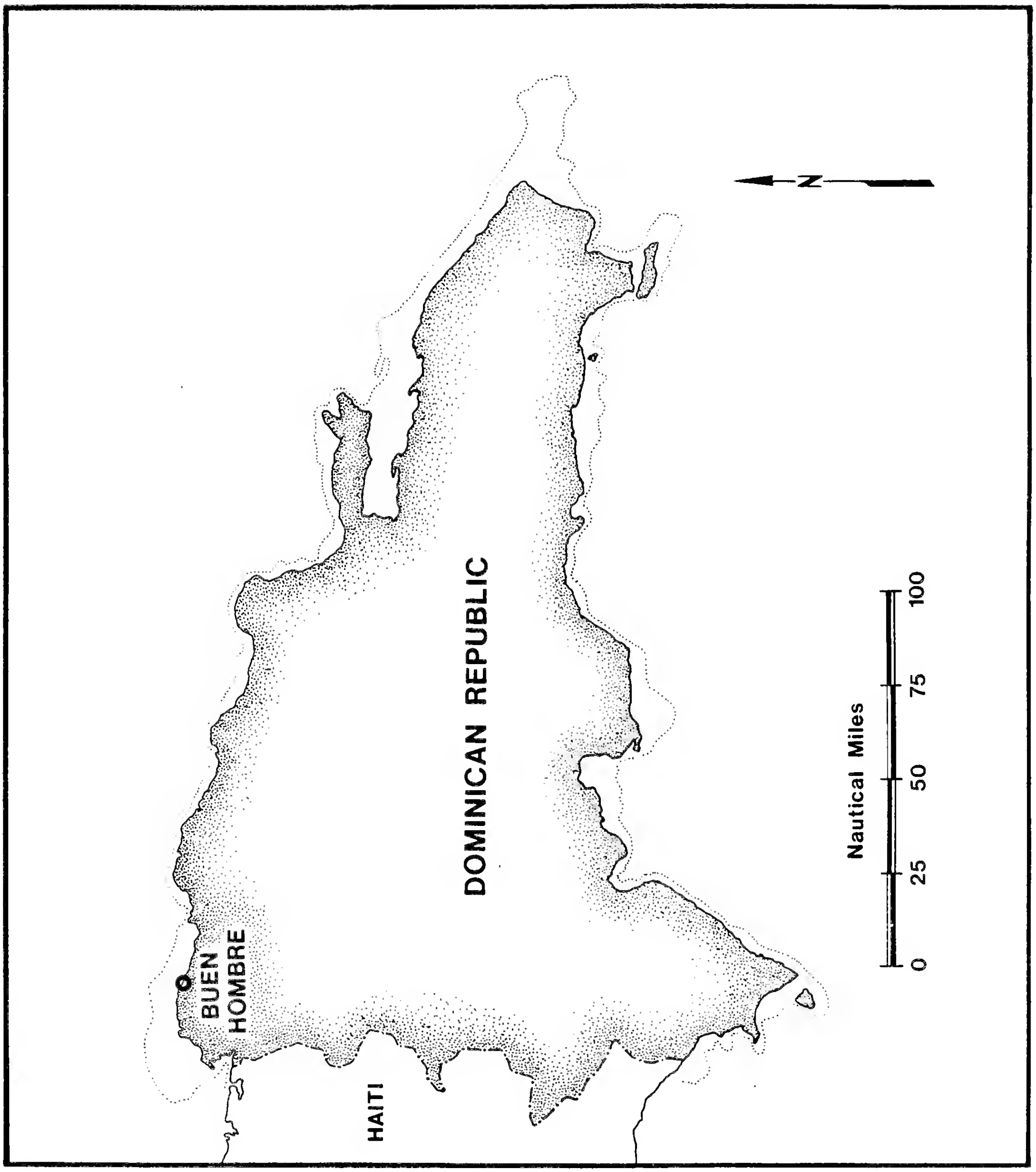

BUEN HOMBRE
HAITI
DOMINICAN REPUBLIC
N
Nautical Miles
0
25
50
75
100

Figure 11

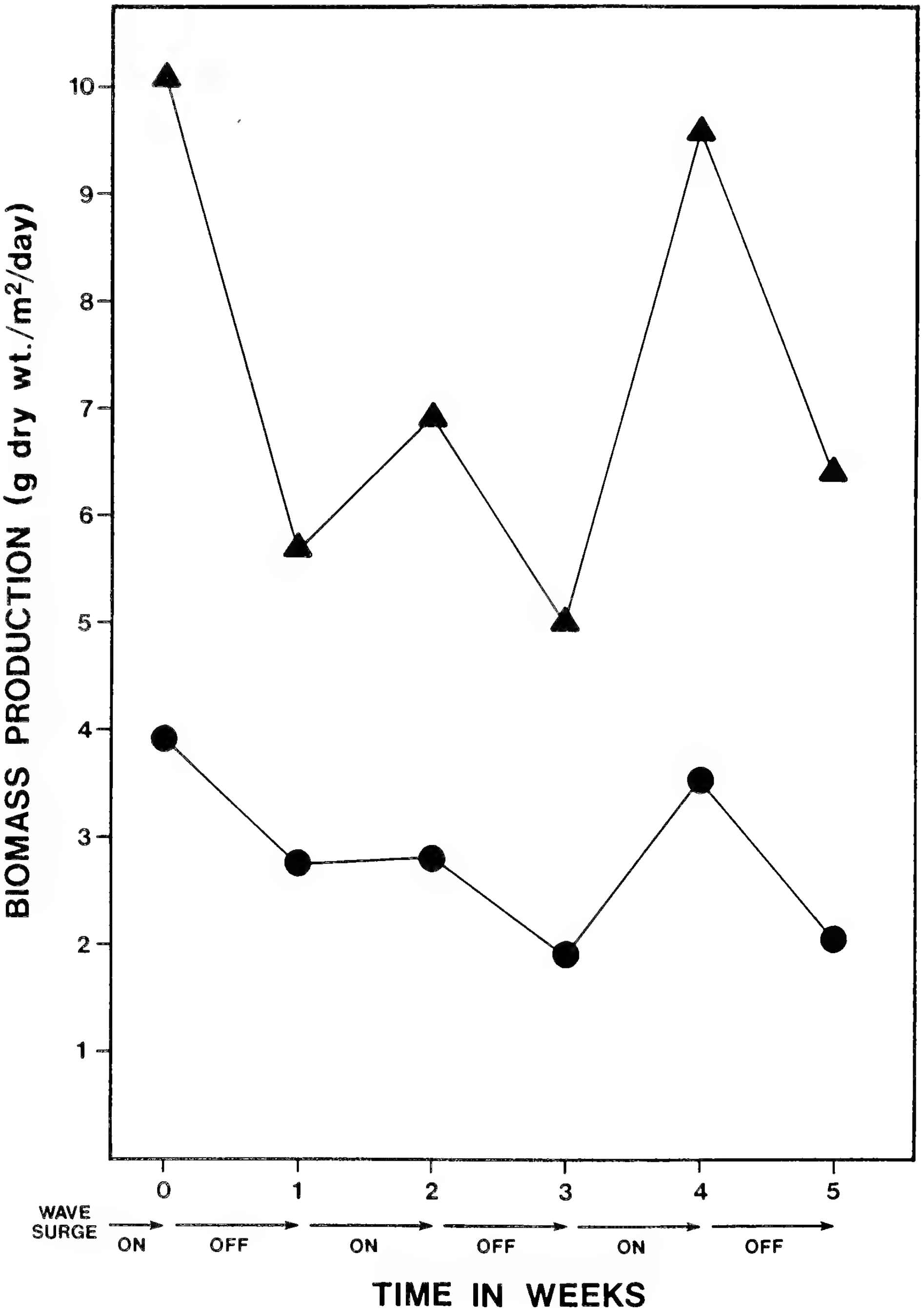

BIOMASS PRODUCTION (g dry wt./m²/day)
10
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
WAVE SURGE
ON
OFF
ON
OFF
ON
OFF
TIME IN WEEKS

Figure 12

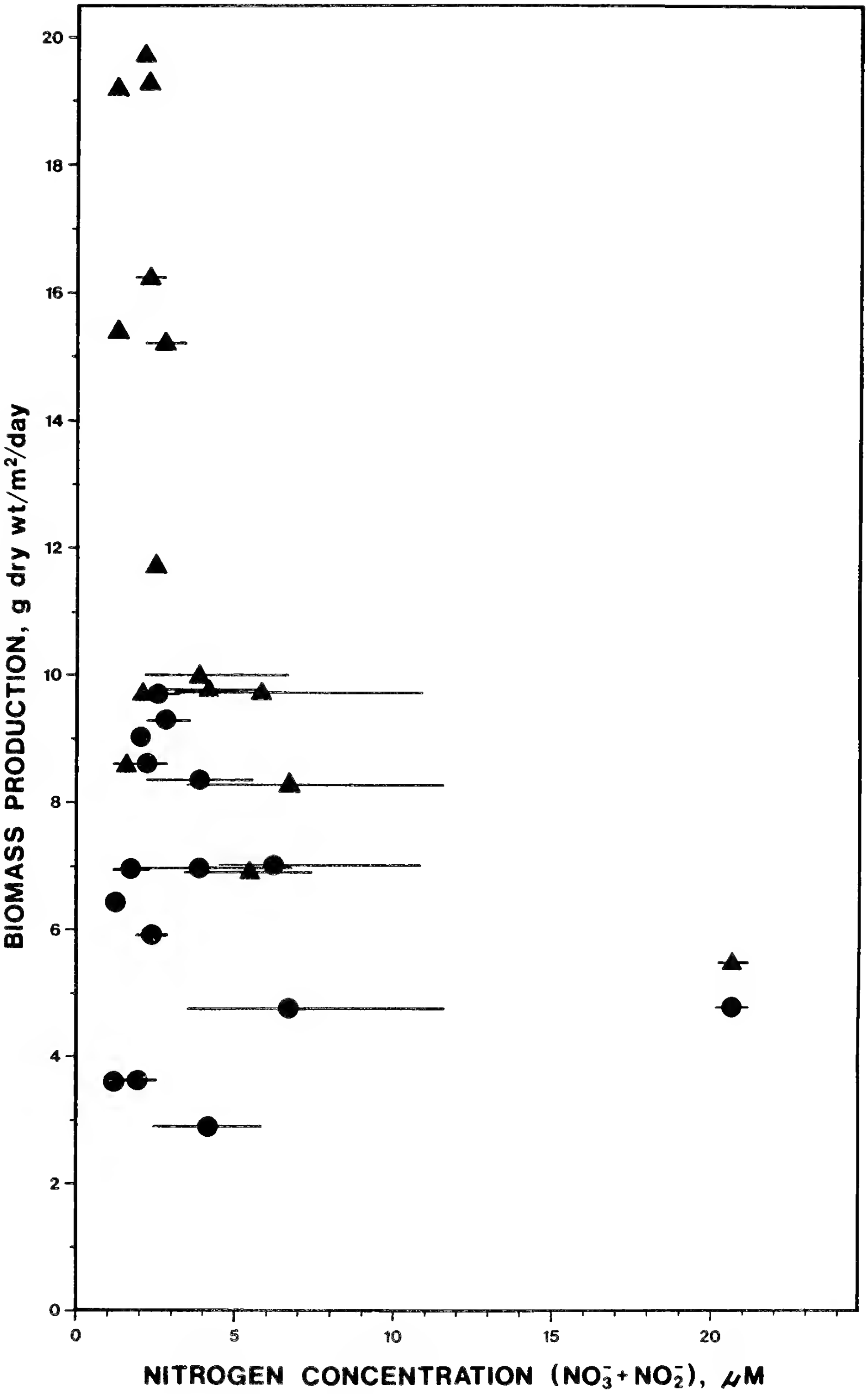

BIOMASS PRODUCTION, g dry wt/m²/day
0
2
4
6
8
10
12
14
16
18
20
0
5
10
15
20
NITROGEN CONCENTRATION (NO₃⁻+NO₂⁻), μM

Figure 13

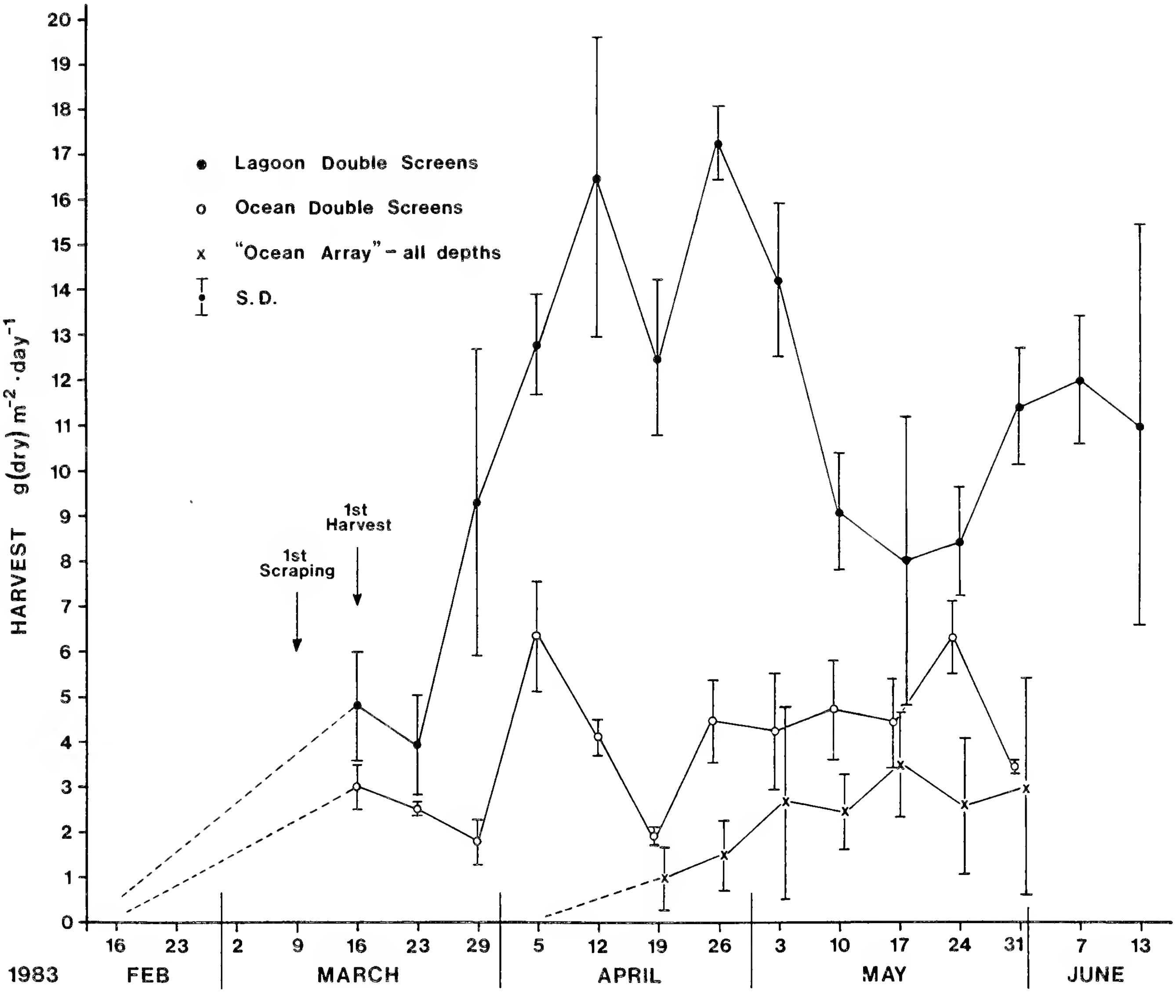

20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
HARVEST g(dry) $m^{-2} \cdot day^{-1}$
● Lagoon Double Screens
o Ocean Double Screens
x "Ocean Array" - all depths
S.D.
1st Scraping
1st Harvest
16
23
2
9
16
23
29
5
12
19
26
3
10
17
24
31
7
13
1983
FEB
MARCH
APRIL
MAY
JUNE

Figure 14

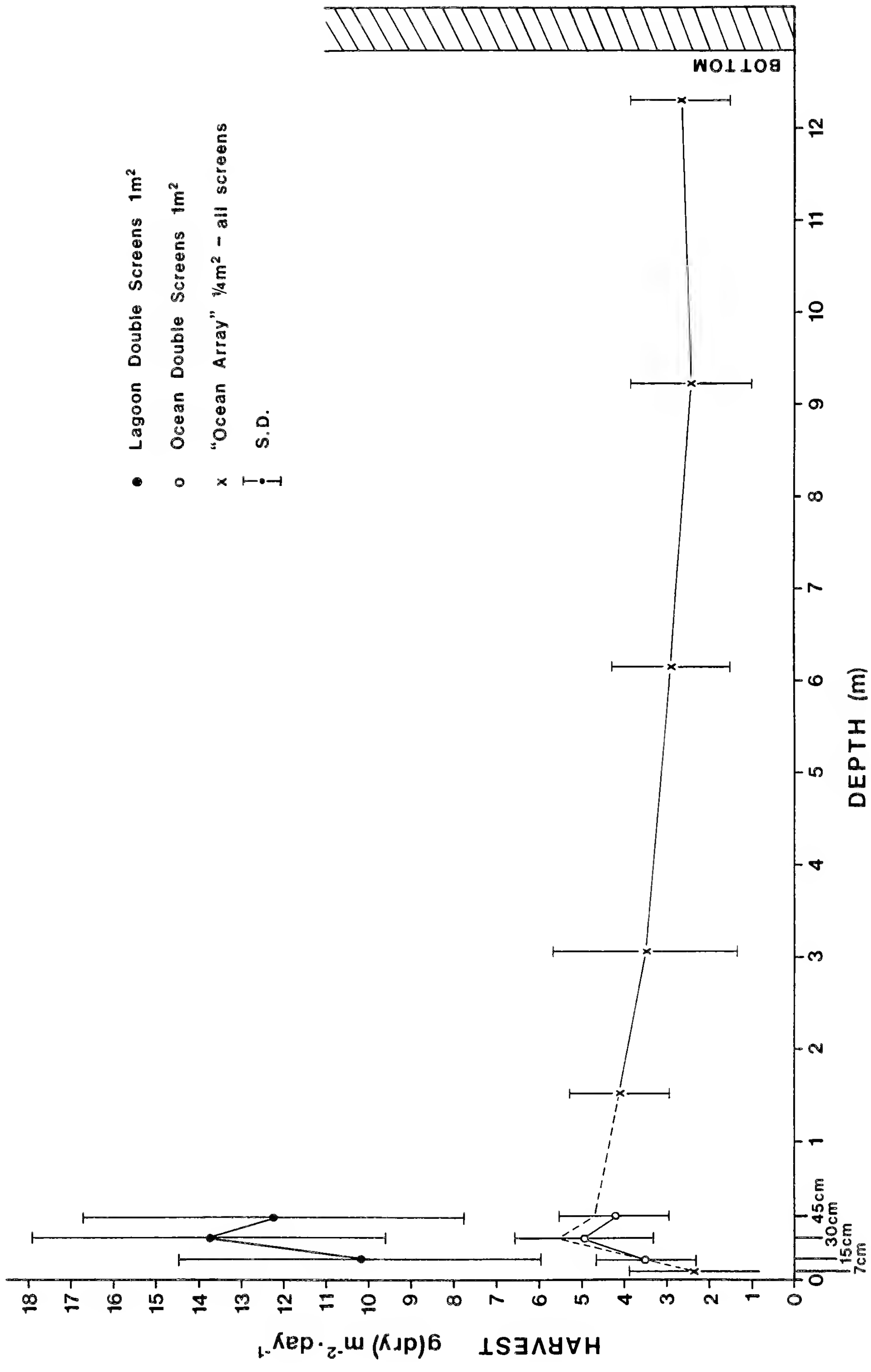

● Lagoon Double Screens 1m²
○ Ocean Double Screens 1m²
x "Ocean Array" ¼m² – all screens
S.D.
HARVEST g(dry) m⁻²·day⁻¹
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
DEPTH (m)
7cm
15cm
30cm
45cm
BOTTOM

Figure 15

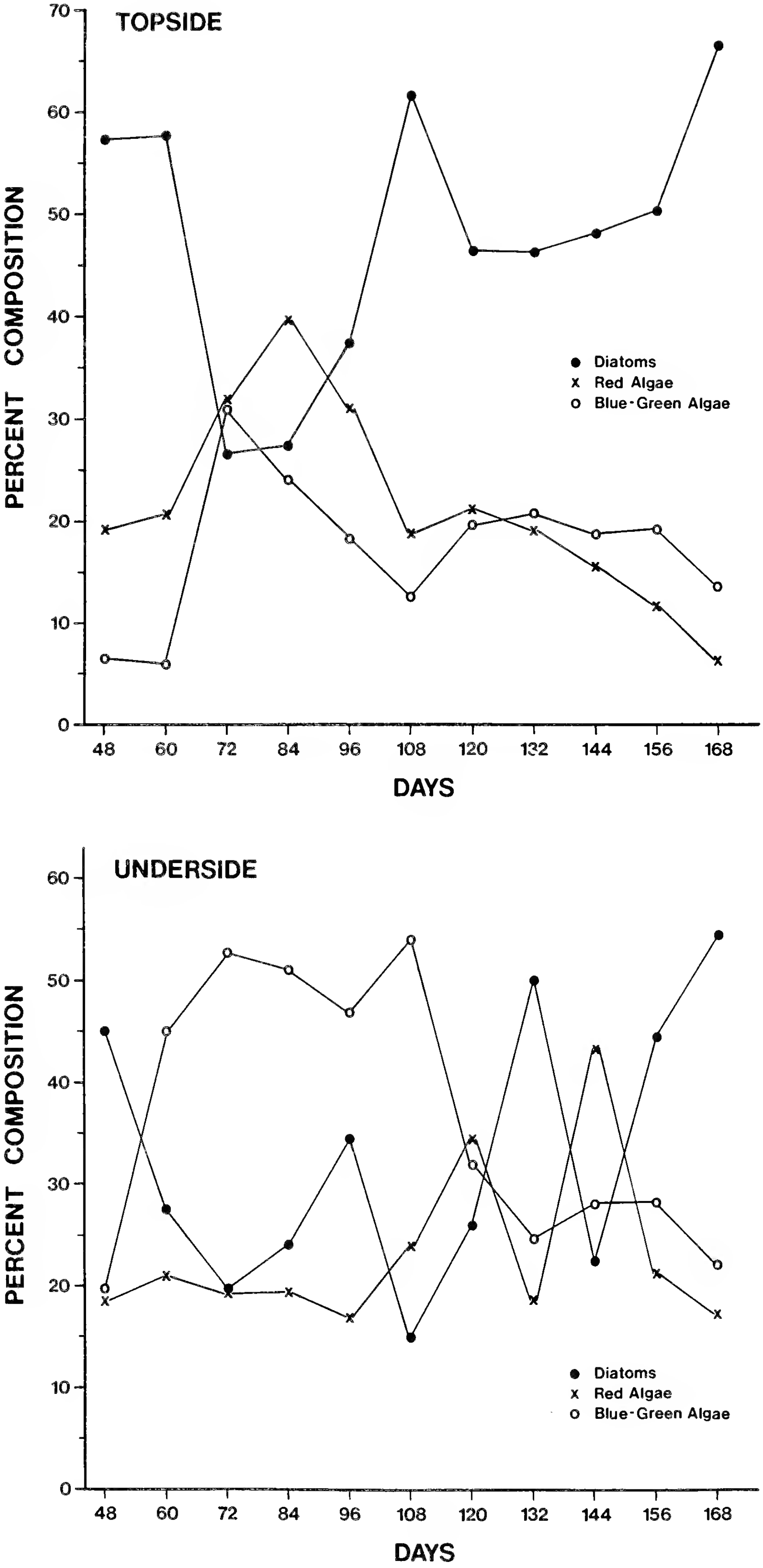

TOPSIDE
PERCENT COMPOSITION
70
60
50
40
30
20
10
0
DAYS
48
60
72
84
96
108
120
132
144
156
168
● Diatoms
x Red Algae
o Blue-Green Algae
UNDERSIDE
PERCENT COMPOSITION
60
50
40
30
20
10
0
DAYS
48
60
72
84
96
108
120
132
144
156
168
● Diatoms
x Red Algae
o Blue-Green Algae

Figure 16

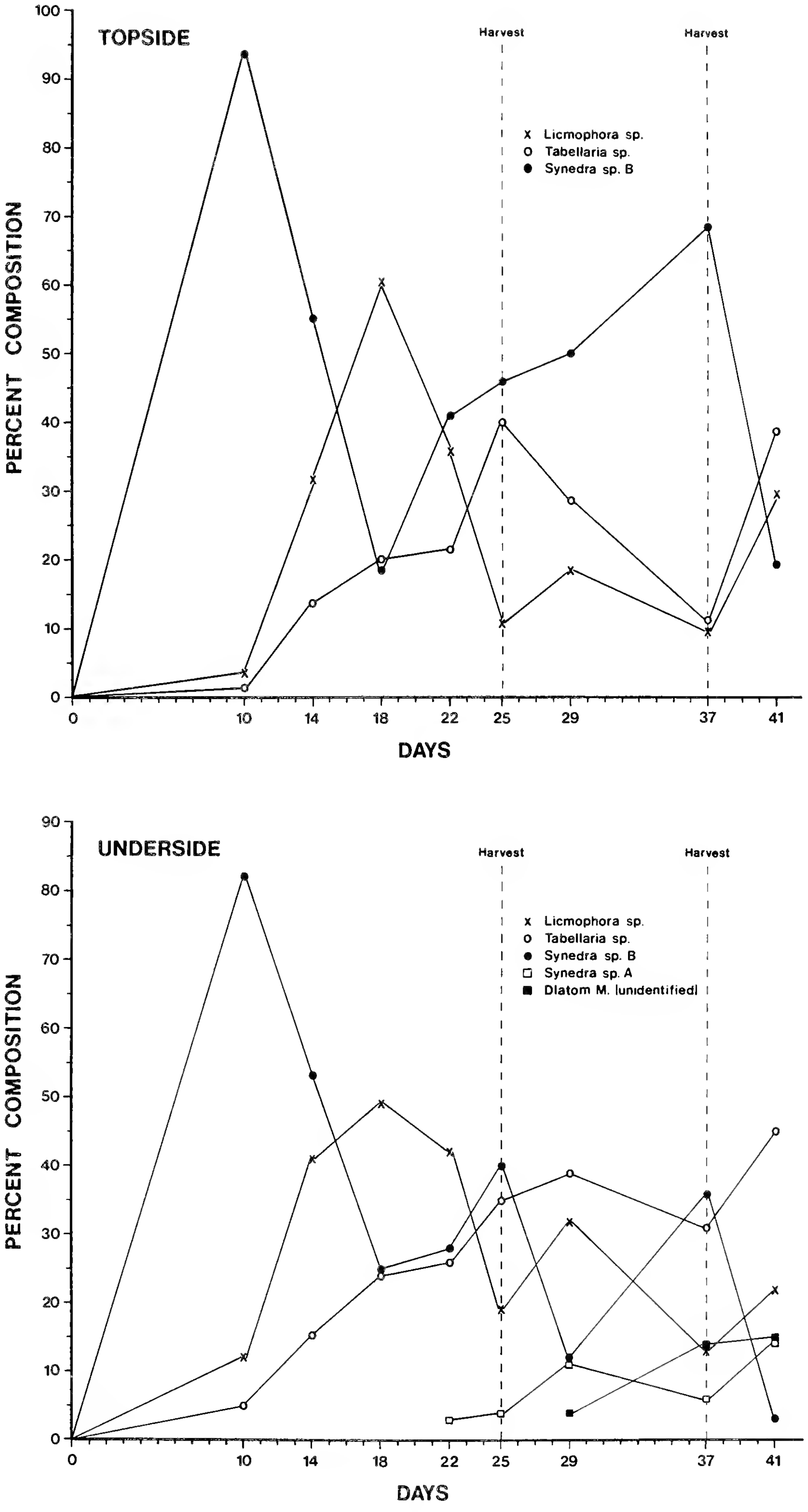
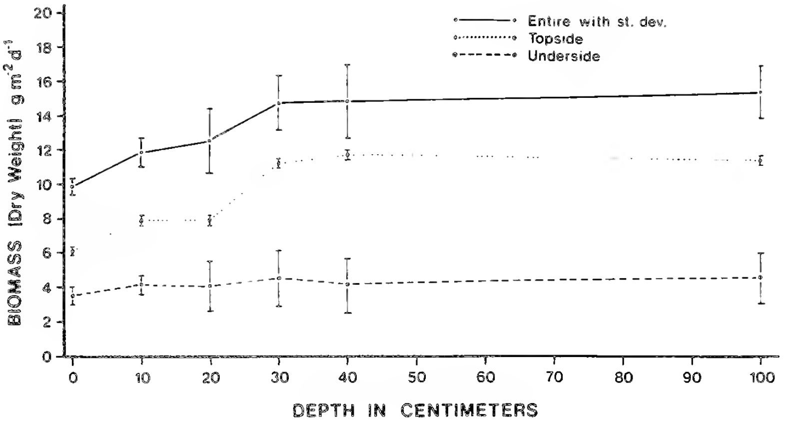
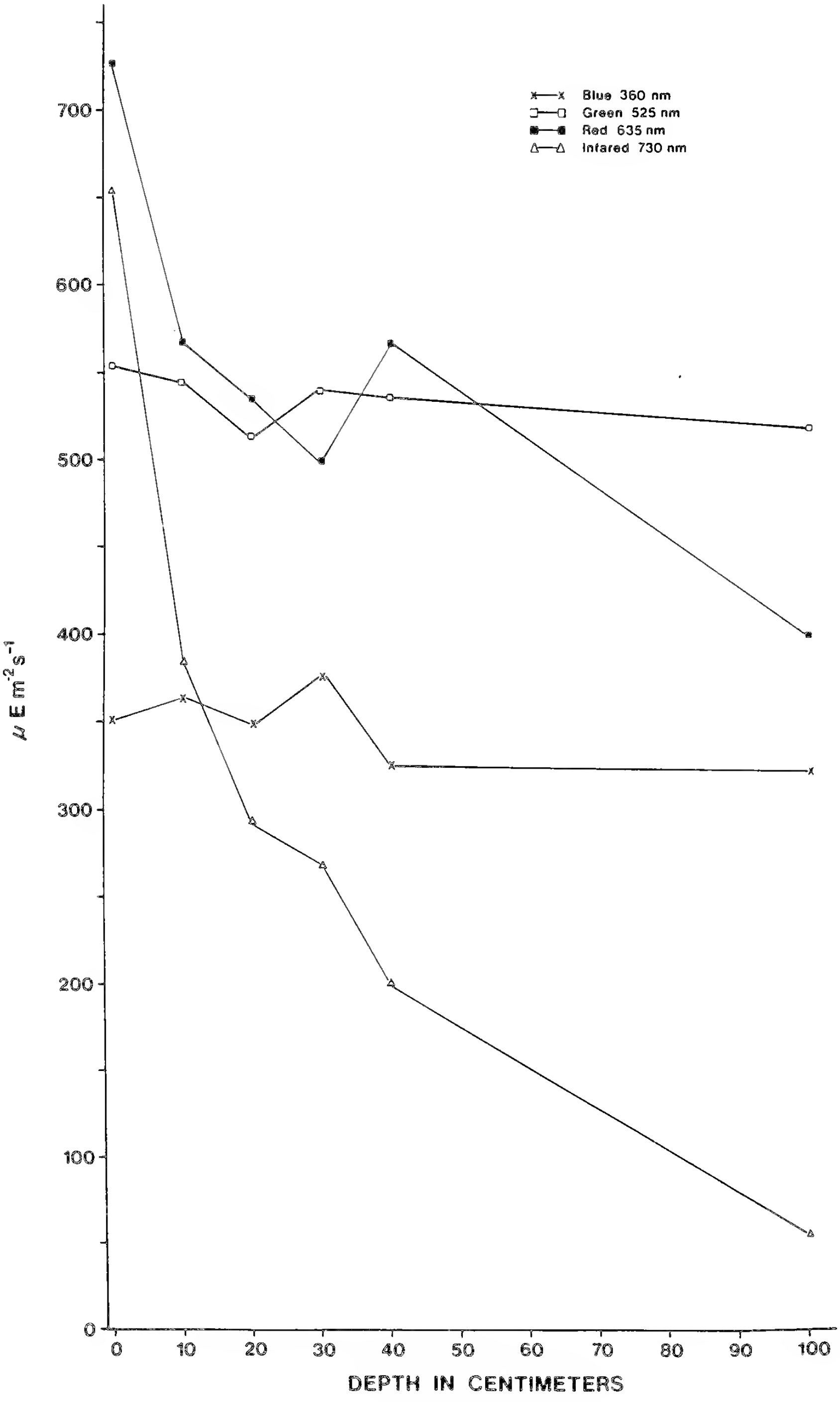

TOPSIDE
Harvest
Harvest
x Licmophora sp.
o Tabellaria sp.
● Synedra sp. B
PERCENT COMPOSITION
100
90
80
70
60
50
40
30
20
10
0
0
10
14
18
22
25
29
37
41
DAYS
UNDERSIDE
Harvest
Harvest
x Licmophora sp.
o Tabellaria sp.
● Synedra sp. B
□ Synedra sp. A
■ Diatom M. (unidentified)
PERCENT COMPOSITION
90
80
70
60
50
40
30
20
10
0
0
10
14
18
22
25
29
37
41
DAYS

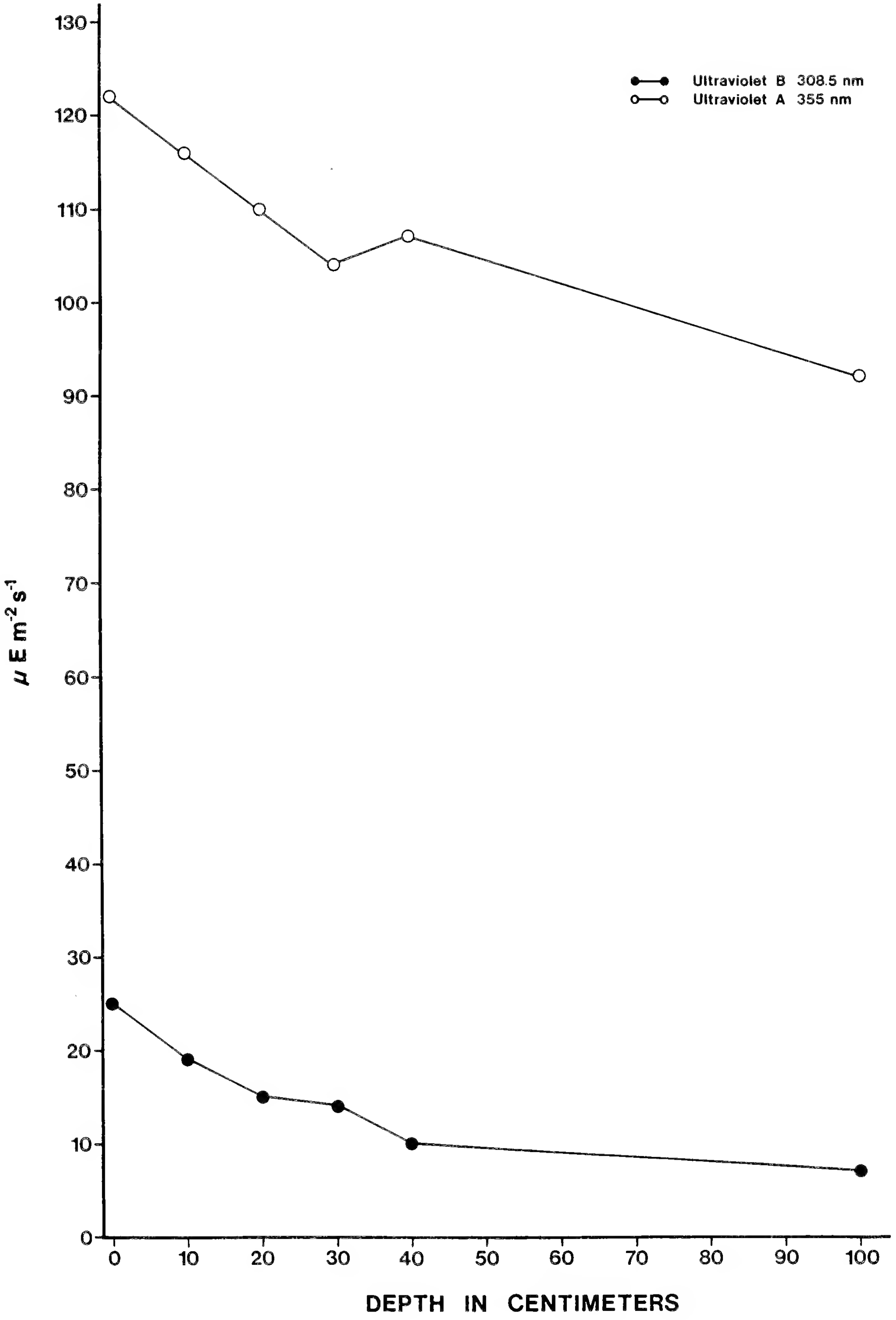
Figure 17



Entire with st. dev.
Topside
Underside
BIOMASS (Dry Weight) g m^{-2} d^{-1}
0
2
4
6
8
10
12
14
16
18
20
0
10
20
30
40
50
60
70
80
90
100
DEPTH IN CENTIMETERS



Blue 360 nm
Green 525 nm
Red 635 nm
Infared 730 nm
μ E m^{-2}s^{-1}
0
100
200
300
400
500
600
700
0
10
20
30
40
50
60
70
80
90
100
DEPTH IN CENTIMETERS


Ultraviolet B 308.5 nm
Ultraviolet A 355 nm
μ E m⁻² s⁻¹
130
120
110
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
DEPTH IN CENTIMETERS

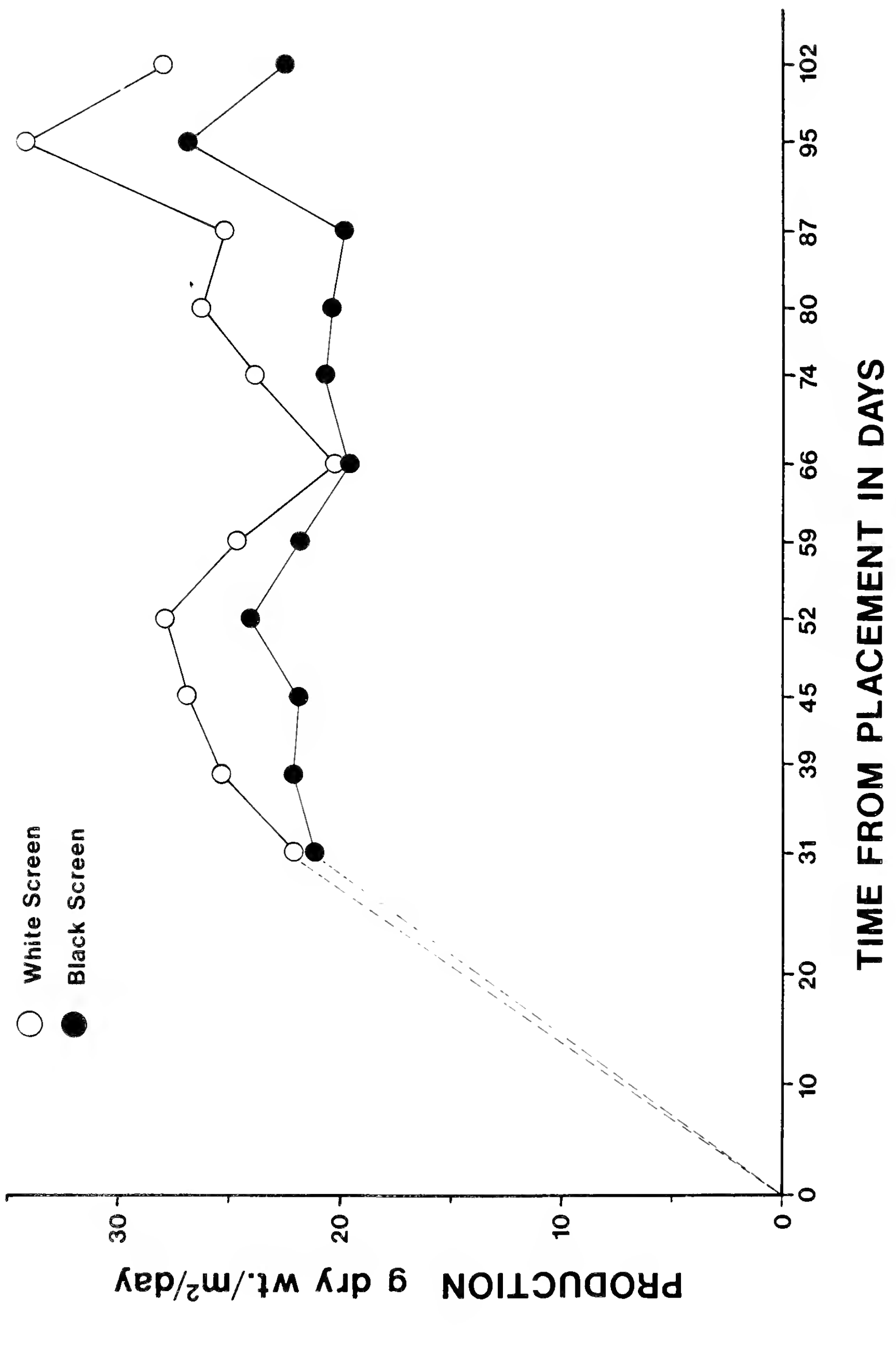

White Screen
Black Screen
PRODUCTION g dry wt./m²/day
0
10
20
30
TIME FROM PLACEMENT IN DAYS
0
10
20
31
39
45
52
59
66
74
80
87
95
102

Figure 19

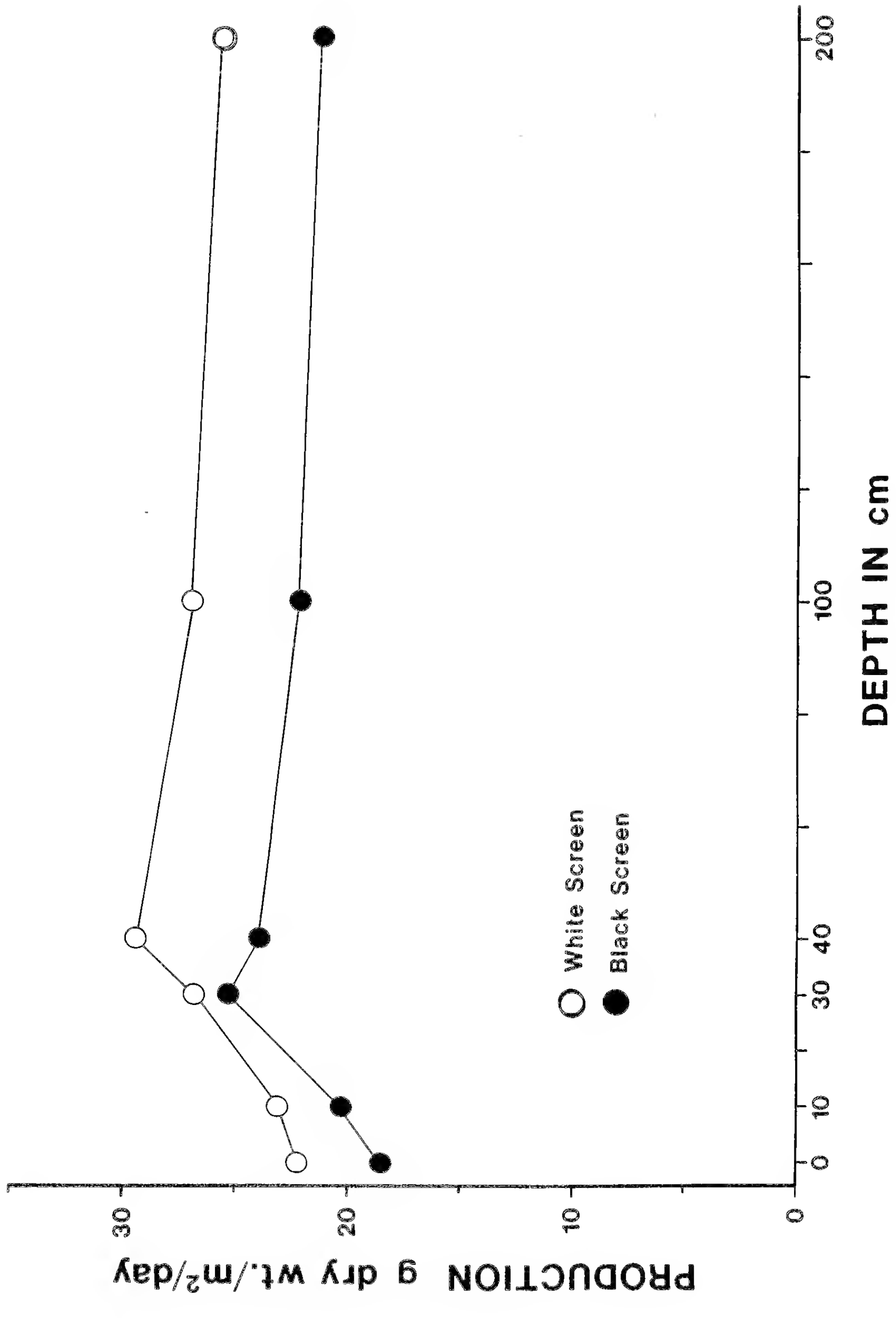

PRODUCTION g dry wt./m²/day
0
10
20
30
DEPTH IN cm
0
10
30
40
100
200
White Screen
Black Screen

Figure 20

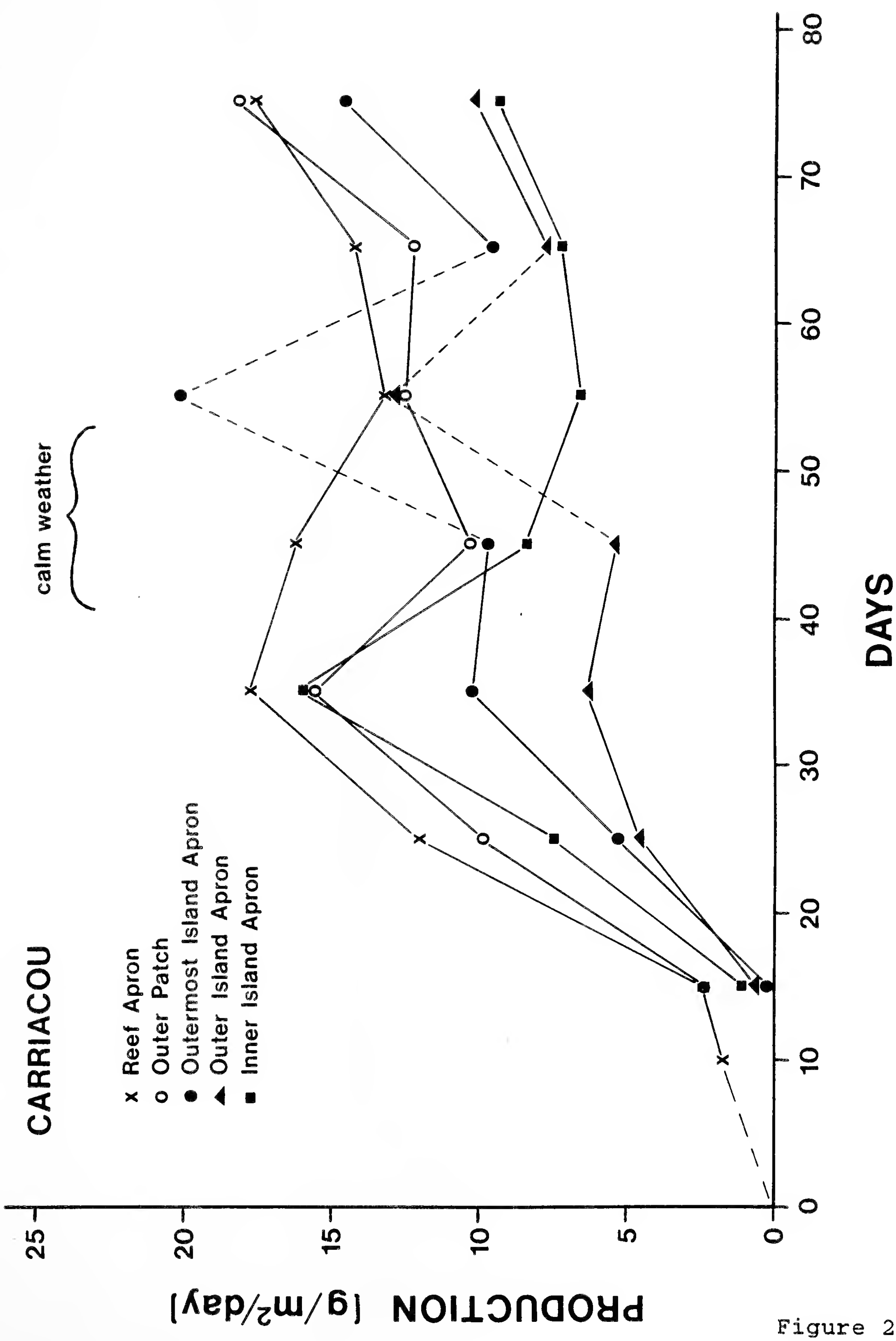

CARRIACOU
x Reef Apron
o Outer Patch
● Outermost Island Apron
▲ Outer Island Apron
■ Inner Island Apron
calm weather
PRODUCTION [g/m²/day]
0
5
10
15
20
25
DAYS
0
10
20
30
40
50
60
70
80

Figure 21

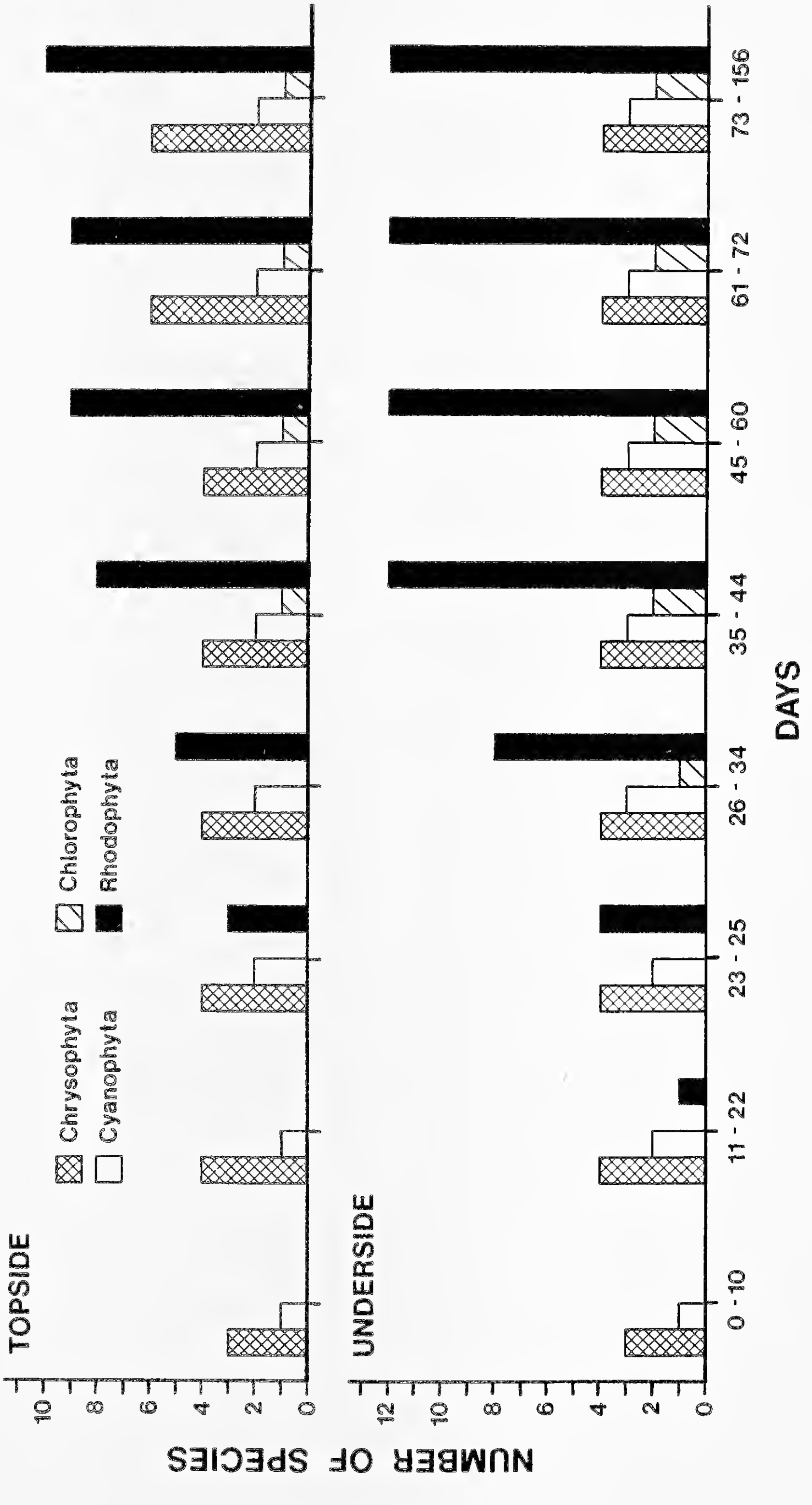
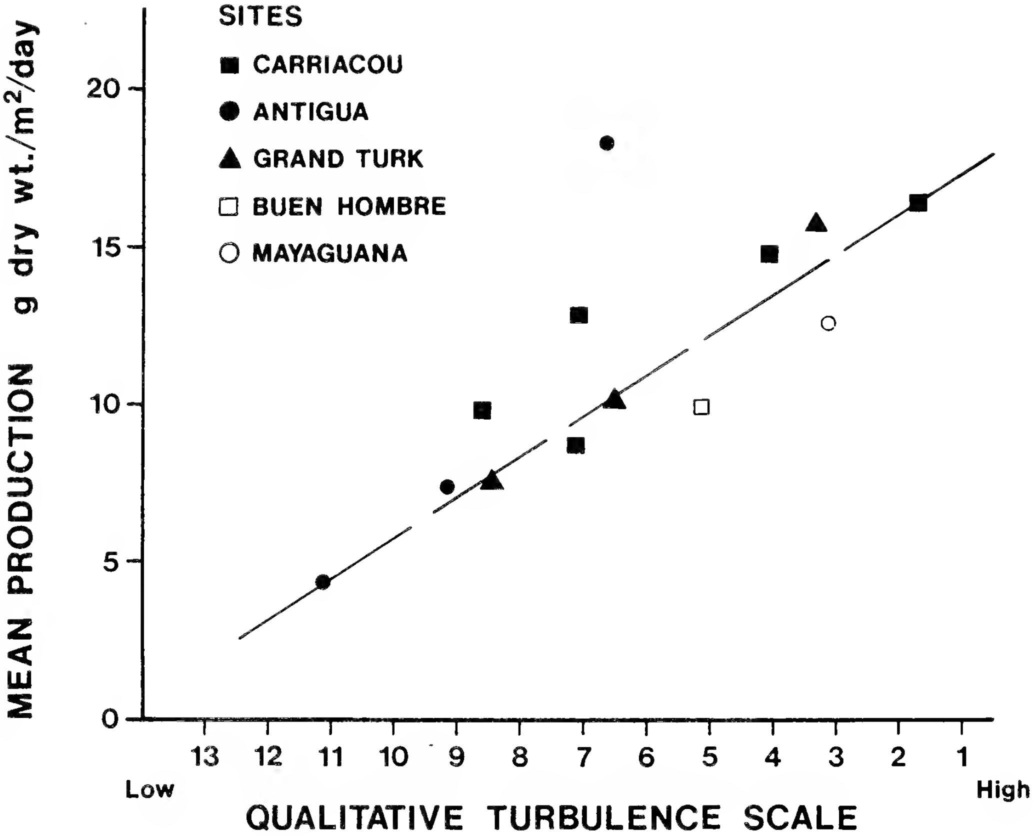

TOPSIDE
UNDERSIDE
Chrysophyta
Cyanophyta
Chlorophyta
Rhodophyta
NUMBER OF SPECIES
0
2
4
6
8
10
12
DAYS
0 - 10
11 - 22
23 - 25
26 - 34
35 - 44
45 - 60
61 - 72
73 - 156

Figure 22



SITES
■ CARRIACOU
● ANTIGUA
▲ GRAND TURK
☐ BUEN HOMBRE
○ MAYAGUANA
MEAN PRODUCTION g dry wt./m²/day
0
5
10
15
20
13
12
11
10
9
8
7
6
5
4
3
2
1
Low
High
QUALITATIVE TURBULENCE SCALE

Figure 23

TABLE 1. Algal genera consistently present in surveys of Caribbean and western tropical Atlantic coral reefs. Species listed within genera are common, persistent components of the coral reef algal turf assemblage. Genera designated by parentheses contain no persistent turf components and are classified as encrusting coralline or macroalgae in this study. Astericks designate genera that contain both the listed turf component species and other species which do not persist within the assemblage. Plus signs designate calcareous genera.

	UNICELLULAR	FILAMENTOUS		PSEUDO-PARENCHYMATOUS		PARENCHYMATOUS
		SIMPLE	BRANCHING	MULTISERIATE, POLYSIPHONOUS OR WEAKLY CORTICATED	COMPLEXLY CORTICATED	
CYANOPHYCEAE (BLUE-GREEN ALGAE)	Various coccoid forms Anacystis dimiduata	Anabaina oscillarioides Calothrix crustacea Entophysalis sp. Microcoleus lynbyacea Rostoc spumigena Osillatoria submembranacea Schizothrix calcicola S. mexicana	Scytonema hofmannii			
CYANOPHYCEAE (DIATOMS)	Isthima sp. Navicula sp. Hitzchia sp. Synedra sp.	Thalassionema sp. Tabellaria sp.	Licmophora sp.			
CHLOROPHYCEAE (GREEN ALGAE)	Various spores Pseudotetraspora antillarum	Chaetomorpha* minima (Valonia)	(Acetabularia) (Avrainvillea)+ Bryopsis pennata B. sp. (Chamaedoris) Cladophora laetevirens C. montageana C. vageunda Cladophoropsis* macromeres C. membranacea (Codium) Derbesia marina (Ernodesmus) (Neomeris)+ (Penicillus)+ Pseudobryopsis spp. (Rhizoclonium) (Struvea) (Udotea)+	Enteromorpha chaetomorphoides E. sp. Protoderma marinum		(Caulerpa) (Dictyosphaeria) (Halimeda)+ (Ulva)
PHAEOPHYCEAE (BROWN ALGAE)	Spores		Bachelotia antillarum Ectocarpus elachistaeformis Giffordia rallsiae	Sphacelaria furcigera S. fusca S. tribuloides S. sp.		(Colpomenia) (Dictyopteris) (Dictyota) (Dilophus) (Lobophora) (Padina) (Sargassum) (Turbinaria)
RHODOPHYCEAE (RED ALGAE)	Spores	Erythrotrichia carnea	Acrochaetium spp. Antithamnion antillarum A. sp. Asterocytis ramosa Bangiopsis subsimplex Callithamnion halliae C. sp. Crouania attenuata Dohrniella antillarum Goniotrichum alsidii Grallatoria reptans Griffithsia barbata G. globulifera G. schousboei Gymnothamnion elegans Halodictyon mirabile Pleonosporium caribaeum Spermothamnion investiens	(Archeolithothamnium)+ Bangia atropurpurea Ceramium brevizonatum C. byssoideum C. comptum C. corniculatum C. cruciatum C. fastigiatum C. flaccidum C. leptozonum C. leutzelburgii C. nitens Dasya* rigidula D. sp. Dasyopsis antillarum Falkenbergia hillebrandii Herposiphonia pecten veneris H. secunda H. tenella H. sp. Heterosiphonia wurdemanni (Hydrolithon)+ (Hypoglossum) (Lithophyllum)+ (lithothamnium)+ Lophosiphonia cristata (Martensia) (Neogoniolithon)+ (Paragoniolithon)+ Polysiphonia atlantica P. binneyi P. denudata P. exilis P. ferulacea P. flaccidisima P. sphaerocarpa P. subtilissima (Porolithon)+ (Spyridia) Taenioma nanum (Tenarea)+ Wrangelia argus W. penicillata	(Acanthophora) Amphiroa+* fragillisima A. sp. (Asparagopsis) (Bryothamnion) Centroceras clavulatum Champia parvula Chondria* collinsiana Coelothrix irregularis Digenia simplex (Eucheuma) (Galaxaura)+ Gelidiella* trinitatensis G. sanctarum Gelidiopsis intricata Gelidium* pusillum (Gracilaria) (Halymenia) (Hypnea) Jania+* adherens J. capillacea J. pumila J. rubens Laurencia* caraibica (Liagora)+ (Lomentaria) (Meristotheca) (Pterocladia) Wurdemannia miniata	

Table 1

TABLE 2. COMMON, PERSISTENT COMPONENTS OF CORAL REEF ALGAL TURF ASSEMBLAGE IN MICROCOSM SCRUBBERS. SPECIES WERE IDENTIFIED USING TAYLOR (1960), HUMM AND WICKS (1980) AND SEARS AND BRAWLEY (1982).

Bacillariophyta

Licmophora sp.
Navicula sp.
Nitzschia sp.
Thalassiothrix sp.

Cyanophyta

Anacystis dimidiata (Kutzing) Drouet and Daily
Calothrix crustacea Schousboe and Thuret
Entophysalis sp.
Microcoleus lyngbyaceus (Kutzing) Crouan
Oscillatoria submenbranacea Ardissone andd Strafforella
Schizothrix sp.

Chlorophyta

Bryopsis hypnoides Lamouroux
Cladophora crystallina (Roth) Kutzing
Cladophora delicatula Montagne
Derbesia vaucheriaeformisa (Harvey) J. Agardh
Derbesia sp.
Enteromorpha lingulata J. Agardh
Enteromorpha prolifera (Muller) J. Agardh
Smithsoniella earleae Sears and Brawley

Phaeophyta

Ectocarpus rhodocortonoides Borgesen
Giffordia rallsiae (Vickers) Taylor
Pylaiella antillarum (Grunow) De Toni
Spacelaria tribuloides Meneghini

Rhodophyta

Acrochaetium sp.
Asterocytis ramosa (Thwaites) Gobi
Bangia fuscopurpurea (Dillwyn) Lyngbye
Callithamnion sp.
Centroceras clavulatum (C. Agardh) Montagne
Ceramium corniculatum Montagne
Ceramium flaccidum (Kutzing) Ardissone
Erythrocladia sudintegra Rosenvinge

Erythrotrichia carnea (Dillwyn) J. Agardh
Gymnothamnium elegans (Schousboe) J. Agardh
Herposiphonia secunda (C. Agardh) Ambronn
Polysiphonia havanensis Montagne
Spyridia sp.

TABLE 3. BIOMASS PRODUCTION RATES CALCULATED FROM 12 DAY, CONCURRENT HARVESTS OF PAIRED SCRUBBERS. MEAN PRODUCTION RATES ±S.D., RANGE AND HARVEST NUMBERS LISTED FOR BOTH UPSTREAM AND DOWNSTREAM SCREENS ON EACH OF THREE FLOW RATE COMPARISONS.

FLOW RATE COMPARISONS	BIOMASS PRODUCTIONS ($g\ m^{-2}\ d^{-1}$)	
	UPSTREAM SCREENS	DOWNSTREAM SCREENS
#1 5.5 1/min (1 wave/70 sec)	a. X=6.7 (±1.4 S.D.) Range=5.3-8.5 N=4 harvests (12 days growth per harvest period)	b. X=2.9 (±1.3) 1.4-4.3 N=4
vs.		
166.0 1/min (1 wave/23 sec)	c. X=11.4 (±3.4) * 8.8-16.2 N=4	d. X=12.6 (±2.2) * 9.7-14.7 N=4
#2 13.5 1/min 1 wave/27 sec	a. X=11.9 (±3.4) 6.4-15.4 N=5	b. X=5.5 (±1.3) 3.6-6.8 N=5
vs.		
32.5 1/min 1 wave/10 sec	c. X=13.7 (±3.3) 10.9-19.3 N=5	d. X=12.4 (±3.9) * 6.0-16.8 N=5
#3 13.5 1/min 1 wave/27 sec	a. X=8.9 (±2.1) 5.5-11.8 N=7	b. X=5.5 (±2.0) 2.9-8.3 N=7
vs.		
32.5 1/min 1 wave/5 sec, wave bucket 1/2 normal volume	c. X=10.6 (±2.4) 7.3-14.1 N=7	d. X=5.6 (±1.0) 3.9-6.6 N=7

* = statistical significance between harvests on the same screen within the comparison, $P < 0.05$

TABLE 5. TURF ALGAE OF MAYAGUANA

Chlorophyta (Green Algae)
Ulotrichales
    Ulvaceae
        *_Enteromorpha_ _chaetomorphoides_ Borgesen

Cladophorales
    Cladophoraceae
        *_Cladophora_ _laetenvirens_

Siphonocladiales
    Valonniaceae
        Cladophoropsis _macromeres_ Taylor
        Cladophoropsis _membranacea_ (C. Agardh) Borgesen

Siphonales
    Derbesiaceae
        Derbesia _marina_ (Lyngbye) Kjellman

    Bryopsidaceae
        Bryopsis sp.
        *_Bryopsis_ _pennata_ Lamouroux
        *_Pseudobryopsis_ sp.

Phaeophyta (Brown Algae)
Ectocarpales
    Ectocarpaceae
        *_Giffordia_ sp.

Sphacelariales
    Sphacelariaceae
        *_Sphacelaria_ sp.
        *_Sphacelaria_ _tribuloides_ Meneghini

Rhodophyta (Red Algae)
Gelidiales
    Gelidiaceae
        *_Gelidium_ sp.
        *_Gelidium_ _pusillum_ (Stackhouse) Le Jolis

Cryptonemiales
Corallineae
*Amphiroa sp.
*Amphirea fragilissima (Linnaeus) Lamouroux
*Jania sp.
Jania adherens Lamouroux
Jania capillacea Harvey
Jania pumila Lamouroux
Jania rubens (Linnaeaus) Lamouroux
Rhodymeniales
Champiaceae
Coelothrix irregularis (Harvey) Borgesen

Ceramiales
Cerramiaceae
Crouania attenuata (Bonnemaison) J. Agardh
*Grallatoria reptans Howe
*Antithamnion sp.
Dohrniella antillarum (Taylor) Feldman-Mazoyer
Wrangelia argus Montagne
*Wrangelia pencillata C. Argardh
*Callithamnion sp.
Callithamnion halliae Collins
*Mesothamnion caribaeum Borgesen
*Griffithsia globulifera Harvey
Spermothamnion investens (Crouan) Vickers
*Ceramium sp.
*Ceramium flaccidum (Kutzing) Acdissm
Ceramium nitens (C. Agardh) J. Agardh
Ceramium breizonatum H.E. Petersen V. Caraibica
*Centroceras clavulatum (C. Agardh) Montagne

Delesseriaceae
Taenioma macrourum Thuret

Dasyaceae
*Dasya sp.
Dasya rigidula (Kutzing) Ardissone
Heterosiphonia wurdemanni (Bauley ex Harvey) Falkenberg
Halodictyon mirabile Zanardini

Rhodomelaceae
Falkenbergia hillebrandii (Bornet) Falkenberg
(This is the tetrasphorophyte stage of Asparagopsis armata)
Polysiphonia sp.
Polysiphonia atlantica Kapraun and Norris
Polysiphonia binneyi Harvey

Polysiphonia _denudatum_ (Dillwyn) Kutzing
Polysiphonia _exilis_ Harvey
Polysiphonia _ferulaceae_ Shur
Polysiphonia _flaccidisma_ Hollenberg
Polysiphonia _sphacerocarpa_ Borgesen
Polysiphonia _simplex_ (Wulfen) C. Agardh

Herposiphonia sp.
*_Herposiphonia_ _pectin-veneris_ (Harvey) Falkenberg
*_Herposiphonia_ _secunda_ (C. Agardh) Ambronn
Herposiphonia _tenella_ (C. Agardh) Ambronn
*_Lophosiphonia_ _cristata_ Falkenberg
*_Laurencia_ sp.
Laurencia _microcladia_ (Kurtzing)

Cyanophyta (Blue-Green Algae)
    Nostocacceae
        *_Calothrix_
        *_Nostoc_
        *_Anabaena_
Oscillatoriaceae
        *_Oscillatoria_
        *_Schizothrix_

Chrysophyta
    Bacillariophyceae (diatoms)
    (several genera and species occuring particularly on young screens - not tabulated)

* Occurs on algal turf rafts

TABLE 6. ALGAL TURF SPECIES IDENTIFIED ON TURF CULTURE SCREENS AT GRAND TURK

CHRYSOPHYTA	
Navicula sp.	mat forming & epiphytic
Nitzschia sp.	mat forming & epiphytic
Synedra sp. A	mat forming & epiphytic
Synedra sp. B	mat forming & epiphytic
Tabellaria sp.	mat forming & epiphytic
Diatom M (unidentified)	mat forming & epiphytic
Licmophora	mat forming & epiphytic
CYANOPHYTA	
Anacystis sp.	mat forming
Schizothrix calcicola (C. Agardh) Gomont	epiphytic
Schizothrix mexicana Gomont	mat
CHLOROPHYTA	
Cladophora sp.	canopy
coccoid green	mat
RHODOPHYTA	
Asterocytis ramosa (Thawaites) Gobi	mat forming & epiphytic
Centroceras clavulatum (C. Agardh)	canopy
Montagne	canopy
Ceramium sp.	canopy
Ceramium byssoideum Harvey	canopy
Ceramium comptum Borgesen	canopy
Ceramium cruciatum Collins & Harvey	canopy
Ceramium fastgiatum (Roth) Harvey	canopy
Champia sp.	canopy
Dasyopsis antillarum Howe	canopy
Chondria collinsiana Howe	canopy
Dohrniella antillarum (Taylor) Feldman-Mazoyer	canopy
Griffithsia Schousboei Mantage	canopy
Herposiphonia sp.	mat forming
Laurencia sp.	canopy
Laurencia obtusa (Hudson) Lamouroux	canopy
Laurencia Poitei (Lamouroux) Howe	canopy
Polysiphonia sp. A (unidentified)	canopy
Polysiphonia sphaerocarpa Borgesen	canopy
Wrangelia sp.	canopy
Wrangelia argus Montagne	canopy
Wrangelia penicillata C. Agardh	canopy

TABLE 7. SCREEN TYPE STUDY AT SITE 1 AND SITE 2

PORE SIZE (um)	MEAN (g m^{-2} d^{-1})	STD ERROR
MONOFILAMENT WOVEN SCREENS AT SITE 1		
200	7.4	1.298
500	7.9	1.415
710	7.7	0.644
710[1]	8.8	0.783
1000u	8.6	0.582
multiweave	11.3	0.820
MULTILAYER EXTRUDED BLACK SCREENS 2 X 3 mm SITE 3		
single layer	10.1b	0.872
double layer	14.8a	0.996
triple layer	17.8a	1.812

a,b values with same subscript are not significant at 5% level using Scheffe procedure

[1] coarser screen (monofilament wider diameter)

TABLE 8. RESULTS OF HARVEST RATE STUDY AT SITE 2, GRAND TURK.

HARVEST RATE (days)	MEAN (g m^{-2} d^{-1})	STD. ERROR
4 day[a]	5.3	0.449
7 day[a,b]	7.4	0.672
12 day 1[a,b]	7.8	0.762
12 day 2[a,b]	7.2	0.614
12 day 3[a,b]	7.9	0.922
20 day[b]	9.4	1.200

a,b means with same superscript are not significantly different at 5% level using Scheffe procedure

TABLE 9. RESULTS OF DEPTH ARRAY STUDY AT SITE 3

DATA IN g m^{-2} d^{-1}

DEPTH CM	TOPSIDE MEAN	TOPSIDE RANGE	UNDERSIDE MEAN	UNDERSIDE RANGE	ENTIRE MEAN	ENTIRE RANGE	NUMBER HARVESTS
sur	6.1	4.1-9.1	3.5	2.9-4.6	9.7	7.1-12.0	9
10	7.9	5.2-16.5	4.2	3.0-5.8	12.1	8.2-21.8	10
20	7.9	3.0-15.9	4.1	3.2-4.9	12.0	6.8-20.8	9
30	11.2	5.6-22.0	4.5	3.2-7.5	15.7	9.5-29.5	10
40	11.7	3.7-23.7	4.2	2.7-5.5	15.9	8.8-28.9	10
100	11.4	6.4-19.2	4.6	3.4-6.1	16.0	14.2-24.0	9

TABLE 10. Algal production in location and screen type tests in Nonsuch Bay.

		5/8	5/16	5/22	5/29	6/5	6/12	6/20	6/26	7/3	7/11	7/18
BIRD ISLAND		12.2	13.0	6.9	3.9	3.5	1.6	0.05	0.5	0.3	0.0	-
RAT ISLAND		15.4	15.6	6.8	7.6	6.5	5.0	2.9	8.4	4.6	0.6	-
GREEN ISLAND		-	-	15.7	14.2	16.0	15.3	11.3	12.5	30.0	25.2	23.8
DEVIL BRIDGE	1	15.3	20.3	15.3	16.5	17.9	26.6	15.1	13.9	20.8	23.4	21.2
	2	19.3	-	17.2	15.2	16.2	22.3	-	13.7	-	-	-
MULTI LAYER	2X			27.7	27.3	32.4	25.5	27.2	26.9	27.3	27.4	-
	3X			31.7	25.8	27.4	23.2	25.8	26.3	23.2	25.8	-
	4X			22.3	24.3	26.66	21.7	17.2	18.9	18.4	10.2	-
APPLETON	V		11.9	21.5	23.3	20.3	13.9					
HORIZONTAL	H		26.2	19.4	22.1	22.5	22.7					
VERTICAL	V		34.2	20.3	26.1	18.0	11.5					

TABLE 11. ALGAL SPECIES TABULATED ON TURF GROWTH RAFTS AT GRAND BAY, CARRIACOU, GRENADA.

Chlorophyta
- *Cladophora sp.*
- *Cladophora fascicularis*
- *Cladophoropsis sp.*
- *Halicystus osterhoutii*
- *Bryopsis plumosa*

Phaeophyta
- *Dictyota dentata*
- *Dictyota ciliolata v. bermudensis*
- *Dictyota dichotoma*
- *Giffordia mitchellae*
- *Padina vickersiae*

Rhodophyta
- *Ceramium byssoideum*
- *Ceramium subtile*
- *Callithamnion sp.*
- *Griffithsia globulifera*
- *Laurencia sp.*
- *Acanthophora spicifera*
- *Polysiphonia subtilissima*
- *Polysiphonia denudata*
- *Lophosiphonia sp.*
- *Wranglia penicillata*

Chrysophyta (bacillariophyceae)
- *Asterionella sp.*
- *Cosinodiscus sp.*
- *Isthemia sp.*
- *Nitzschia sp. A*
- *Nitzschia sp. B*
- *Licmophora sp.*
- *Striatella sp.*
- *Thalassionema sp.*
- *Grammatophora sp.*

Cyanophyta
- *Anabeana sp.*
- *Anacystis sp.*
- *Lyngbya sp.*
- *Nostoc sp.*
- *Oscillatoria sp.*
- *Schizothrix mexicana*

TABLE 12. Algal turf production as a function of location, screen type and time at Grand Bay, Carriacou, Grenada.

		DAYS (g m^{-2} d^{-1})							
STATION		10	15	25	35	45	55	65	75
REEF APRON 5 m depth	ST1	1.63	1.54	7.55	17.09	10.27	14.63	12.86	17.70
	ST2	1.74	5.54	14.69	23.51	10.58	16.17	13.31	18.04
	1BF	-	1.93	18.90	18.00	19.63	12.21	15.53	17.45
	1BH	-	.47	6.87	17.09	25.15	13.95	15.02	17.08
	1T	-	4.99	11.55	13.24	-	9.32	-	-
	X	1.7	2.4	12.0	17.8	16.4	13.3	14.2	17.6
OUTER ISLAND APRON 8 m depth	ST3	-	0.24	6.63	9.59	9.21	19.77	8.17	13.98
	ST4	-	0.40	4.08	11.21	10.22	20.56	11.02	15.52
			0.3	5.4	10.4	9.7	20.2	9.6	14.7
PATCH 5 m depth	ST5	-	2.11	15.42	14.50	7.32	13.77	14.45	18.86
	ST6	-	1.86	7.35	18.94	7.73	13.72	17.42	21.84
	3BF	-	2.59	11.61	16.23	14.49	16.39	15.41	17.97
	3BH	-	3.30	5.16	12.83	11.81	14.38	11.88	14.52
	3T	-	4.07	3.73	9.47	-	10.39	-	-
			2.5	9.9	15.6	10.3	15.3	14.8	18.3
ISLAND APRON 5 m depth	ST7	-	0.51	6.76	6.46	5.94	13.02	9.74	11.43
	ST8	-	0.41	2.7	6.82	5.06	13.20	5.89	8.73
			0.5	4.7	6.6	5.5	13.1	7.8	10.1
INNER ISLAND APRON 4 m depth	ST9	-	1.12	7.21	16.44	9.24	6.07	8.40	10.79
	ST10	-	1.30	7.75	15.52	7.54	7.38	6.33	8.52
			1.2	7.5	16.0	8.4	6.7	7.4	9.7
COMBINED STATIONS 1 AND 3			2.5	10.9	16.7	13.4	14.3	14.5	18.0

TABLE 13. Buen Hombre, Dominican Republic Algal Harvest Data. Each value represents two pooled screens of area 0.56 m^2 each. Growth time equals seven days.

TOTAL DRY HARVESTS (all 2 screens pooled)

	g m^{-2} d^{-1}	SV	SH	T	DH	DV	
6/10	6.7	67	43	42	-	59	
6/17	8.2	55	62	61	75	70	
6/24	10.3	84	83	75	74	82	
7/1	6.6	51	54	58	51	45	
7/8	8.5	63	69	68	60	72	
7/15	8.6	58	67	70	67	77	
7/22	10.0	105	61	81	64	77	
7/29	8.2	88	88	38	-	42	
8/5	9.4	72	80	72	55	89	
8/12	9.0	73	73	58	67	81	
8/19	9.6	50	86	91	72	76	
8/26	8.8	98	56	61	61	70	
9/2	12.3	85	95	89	101	112	
9/9	10.2	69	83	85	82	79	
		72.7	71.4	67.8	69.9	73.6	Mean harvest
		9.3	9.1	8.6	8.9	9.4	Mean daily production.

SUMMATION OF ALL HARVESTS

70.98 g for 7 days; X = 9.1 g m^{-2} d^{-1}, S.D. = ±2.0, N = 68

SECTION II: BIOLOGY AND ECOLOGY OF MITHRAX SPINOSISSIMUS

MORPHOLOGY AND RELATIVE GROWTH OF MITHRAX SPINOSISSIMUS (DECAPODA: BRACHYURA: MAJIDAE)

MORPHOLOGY AND RELATIVE GROWTH OF MITHRAX (MITHRAX) SPINOSISSIMUS (DECAPODA: BRACHYURA: MAJIDAE)

A.H. Biddlecomb, M.P. Craig and J.M. Iglehart

Abstract

In this study of *M. spinosissimus* collected on the reefs of Antigua, B.W.I., twelve instars from first crab stage (1.5 mm CL) to instar 15 (83.0 mm CL) are identified from culture. All 15 stages were obtained by rearing eggs taken from berried females caught from the reef environment. Measurements of ventral propodus length, carapace length and carapace width were used to define the growth phases of *M. spinosissimus*. The average growth per molt for crabs less than 80 mm CL is 35.7%, and 23.7% for those greater than 80 mm CL.

In this work, the point at which the molt of puberty occurs (±105 mm CL) is decidedly different from the results of a study in the Florida Keys (±80 mm CL) (Bohnsack, 1976). It is suggested that there are several morphologically distinct post-pubertal male instars and the molt of puberty is not the terminal molt.

INTRODUCTION

Mithrax (*Mithrax*) *spinosissimus* (Lamarck, 1818) is placed in the Family Majidae (infraorder Brachyura), commonly known as the spider crabs. Milne-Edwards (1832) amended the taxonomic classification to the present genus and specices, from the previously classified *Maia spinosissima* (Lamarck, 1818). The genus *Mithrax* designates crabs as being characterized by long slender walking legs, a nearly oval shaped carapace with the front formed of two small often pointed rostral horns. The orbital margins are generally more or less spinous or tuberculate, and the merus of the external maxillipeds are broad.

The abdomen of the male is formed of seven free segments. *M. spinosissimus* is sometimes referred to as the West Indian Red Spider Crab or, because of its large size, the Caribbean King Crab. In this investigation, we have succeeded in obtaining a number of successive developmental stages of this species. These collected specimens have served as the basis for describing the life history and growth phases of *M. spinosissimus*.

Morphology of Adults

Mithrax spinosissimus is distinct from other tropical Majids because of its large size. It is the largest species in the genus; the largest adult previously reported had a carapace length (CL) of 167 mm (Rathbun, 1925) and larger animals are reported in this study. Considerable size variation does, however, occur throughout the geographic range (see Iglehart, *et al*., this volume). *M. spinosissimus* is distinguished from other Caribbean/tropical Atlantic species by the presence of eight to nine spines on the dorsal edge of the manus, the presence of two spines on the basal part of the antennae and its nearly naked carapace. The hepatic and cardiac regions of the carapace are distinctly delimited.

The carapace of an adult *Mithrax spinosissimus* is large, naked and approximately equal in width and length. The entire carapace is rough with short spines. In the center, the spines are blunt, while elsewhere they are sharp. With a deep cervical suture, the rostral horns are narrow, truncate at the tips and are separated by a U-shaped sinus of equal length and breadth. *Mithrax spinosissimus* is strongly sexually dimorphic. The chelipeds of mature males are larger and longer than their walking legs. A large tooth-like structure emanates from the male dactyl (Figure 1). Spines on the chelae of old males tend to be blunt and tuberculiform, while those on the merus tend to retain their spiny character. Chelipeds of both sexes are armed with numerous stout spines. Chelipeds of the mature female are no longer and not much stouter than their first walking legs. The manus tapers distally and the fingers are narrowly gaped with numerous denticles on the inner edges. The tips of the chelae are hollowed and spoonlike with serrated edges in both sexes, thus allowing the animals to feed on the abundant algal turfs and small macroalgae present in reef environments.

The male abdomen is triangular through abdominal segments 1, 2 and 3, and nearly rectangular through segments 4, 5, 6 and 7 and hangs loosely in mature males. The abdomen of the male covers only a small portion of the width of the sternum, while the abdomen of the mature female is broad and nearly covers the entire sternum.

Morphology of Juveniles

Rathbun (1925) described medium sized juveniles as having a carapace much longer than wide and covered with setae. At this age, the spines are sharper than the spines of adult crabs, including the tips of the rostral horns which also curve slightly inward. Both sexes, as juveniles, have small chelipeds with a gape extending one-half the length of the fingers.

In younger individuals, spines appear sharper than those of older juveniles and longer in relation to carapace size. The rostral horns are also longer, one-fifth as long as the carapace. There are two spines on the suborbital margin outside the antennal segment. The chelipeds of the young are no longer or stouter than the first pair of legs.

Morphology of Larvae

Provenzano and Brownell (1977) described the larval and first crab stages. Wilson, *et al*. (1979) discussed morphological differences and similarities in larvae of *M*. *forceps*, *M*. *spinosissimus* and *M*. *pleuracanthus* (Yang, 1967). The latter species was fully described by Goy, *et al*., (1981), in which the authors proposed a reassessment of the genus because of similarities between *M*. *forceps* and *M*. *pleuracanthus* (of separate subgenera), both of which differ from *M. spinosissimus*. Goy, *et al*. (1981) states that larval *M*. *spinosissimus* are "clearly less related" to other Mithracinae. Other developmental descriptions of larval stages for species in the genus are for _M_. _coryphe_ (Scotto and Gore, 1981), _M_. _hispidus_ (Fransozo and Hebling, 1982) and _M_. _verrucosus_ (Bolanos and Scelzo, 1981).

Relative Growth of the Chelae

The process of reaching maturity, the size at maturity and the presence or absence of a terminal molt are significant elements in considering the mariculture potential of _M. spinosissimus_. Physical and sexual maturation bring about changes in the relative growth between various body parts. An aspect of the relative growth of _M_. _spinosissimus_ with biological and economic significance is the large size of the chelipeds of mature male instars. Useable meat to total weight ratios are considerably higher for mature males with the largest chelae. At the molt of puberty, chelae of the male _M_. _spinosissimus_ become substantially larger, while in the females the abdomen increases in width so as to cover the sternum, thereby making a protected brooding space. In addition, gonads in both sexes begin to mature. The female pleopods, gonopores and abdominal locking mechanism also noticably change at the molt of puberty (see Craig, _et_ _al_., this volume). By relating the "claw length" (VPL) to the carapace width of the crabs collected in Florida, Bohnsack (1976) suggested that male _M_. _spinosissimus_ molted to maturity at approximately 80 mm CW, because at this point the chelae length increases at a proportionately higher rate than carapace length.

Tessier (1935), Vernet-Cornubert (1958) and Hartnoll (1963, 1965) compared ventral propodus length (VPL) and carapace length (CL) or width (CW) on a log-log plot to determine specific changes in allometry, especially at maturation. These three authors all concluded that in the Majidae, ecdysis and therefore growth during molt ceases after the molt to puberty.

Hartnoll (1965) investigated the life history of five tropical spider crab species. He concluded that the molt to maturity was the terminal molt based on: 1) evidence of pre-pubertal instars molting in captivity, i.e., observations of several dissected pre-pubertal instars preparing to molt and the lack of molting or indications of molting among the post-pubertal instars; 2) pre-pubertal instars developed limb buds upon losing an appendage, while post-pubertal instars with autotomized appendages formed calcified stumps and were not observed to form limb buds; and 3) the "epifauna of the integument," which attach as larvae (i.e., barnacles and serpulid worms), was observed to be more abundant and older on post-pubertal instars, indicating at least, a much longer intermolt period.

Tessier (1935) described a critical molt in male instars of the species Maia squinado prior to the molt of puberty. The molt, called the molt of pre-puberty, marked the first differentiation of relative growth rates between sexes. In Pisa tetraodon, Vernet-Cornubert (1958) was able to show that the pre-pubertal instar has a great range of carapace lengths, and the molt of puberty may be from one to three instars after the first pre-pubertal instar. Tessier (1935) showed the molt of pre-puberty to occur at approximately 70 mm CL in Maia squinado and the molt of puberty to occur three instars later. The first slight proportional increase in growth of the chelae over the carapace was considered by Tessier (1935), Vernet-Cornubert (1958) and Hartnoll (1963) to be the beginning of the range of carapace lengths where the molt of pre-puberty occurs in the species they studied. Hartnoll (1963) gives extensive consideration and discussion to a pre-pubertal molt in the "Manx" spider crabs, but the Majids he studied in Jamaica are not mentionned (Hartnoll, 1965).

Hartnoll (1965) found a wide size range of post-pubertal Majids in both sexes. From samples of Mithrax sculptus, differences in post-pubertal CL were calculated showing that the largest mature female was 162% larger than the smallest mature female, and the largest mature male was 314% larger than the smallest mature male (Hartnoll, 1965).

In most Majids there is only a single type of post-pubertal male instar. However, Hartnoll (1963) and Vernet-Cornubert (1958), found that among Pisa tetraodon, Pisa gibbsi and Inachus leptochirus, there are two morphologically distinct types of post-pubertal males which vary in chela length (the latter two) and in chelae breadth (all three), so that the two distinct types in each species have different levels of allometry, i.e., separate phases of maturity.

Hartnoll (1974, 1978) described the growth of organs functioning as primary or secondary sexual characteristics relative to carapace growth by the allometric growth equation, $y=Bx^a$ where y = variable dimension (organ size); x = reference dimension (carapace length or width); a = the regression coefficient (or rate of growth); and B = y intercept (or proportional difference between organ and body). The allometric growth equation expressed logarithmically is: $\log y = \log B + a \log x$. The relative growth of Brachyuran chela, abdomen and first pleopods may then be compared by using the regression coefficient, "a", or the level of allometry (Hartnoll, 1974). These changes in levels of allometry at specific instars indicate important changes in the function of particular body parts relative to sexual maturation.

In a comparison of the positive allometry levels of the adult male chela and the female abdomen, Hartnoll (1974) also found a positive allometry in the pre-pubertal male phase and considerable size increases at the pubertal molt. At the molt of puberty, the relative growth of the male chela increases to a higher level of positive allometry as does the relative growth of the abdomen of the female whose terminal molt coincides with the molt of maturity. In those females that continue to molt after the molt of puberty, the abdomen width to the carapace length decreases isometrically.

METHODS

From 1985-1986, 157 M. spinosissimus were collected with standard West Indian lobster traps off the eastern coast of Antigua in the Caribbean/tropical Atlantic (Lat. 17° 10' N, Long. 61° 43' W). In addition, 107 measured crabs were reared from larvae at NonSuch Bay in eastern Antigua (see Porter, et al., this volume). The cultured crabs were reared from broods generated by captured animals from wild populations. Nearly all crabs less than 80 mm were cultured. Photographs of post-larval instars 1-15 are presented from culture.

Ventral propodus length (VPL) was measured from the most distant tip of the fixed finger to the end adjacent to and projecting slightly below the carpal hinge (A/B Figure 1). All measurements were made to the nearest 0.1 mm using precision dial calipers. Plots of the measurements of CL vs VPL were used to identify size at maturity. Measurements were taken from the right cheliped unless it was missing, in which case, the left was used. Carapace length (CL) was measured, exclusive of rostral horns, from the middle of the rostral sinus to the most posterior edge of the carapace. Carapace length is a more precise measurement than the width due to its ease of measurement and standardization of measurement procedure in terms of replication. Carapace width (CW), measured from just in front of the fourth branchial spines, was also taken to compare CW to CL and provide a reference to previous work. A least squares regression was used to determine the relationship between CW and CL.

RESULTS

Of 264 crabs measured in Antigua, 107 were cultured and 157 were captured locally. The crabs ranged in size from 19.8 to 146.5 mm CL. The VPL and CL data for individual crabs given in figure 2 shows that males and females are dimensionally indistinguishable up to approximately 55 mm CL. Up to that size, both sexes are showing a slight positive allometry or proportional increase of the propodus relative to the carapace. At that point, however, sexual dimorphism begins to be evident with the males showing proportionally even longer chelae. At 75 to 80 mm CL there is a distinct inflection in the relationship between ventral propodus length and carapace length for pre-pubertal males with even greater chela elongation. Beginning at about 100 mm CL, the VPL of mature males increases markedly relative to carapace size. This point marks the instar size at which the cheliped becomes longer than the carapace in approximately 85% of the post-larval instars in the 100-120 mm CL range. Finally, at about 130 mm CL, the allometry of the VPL decreases slightly for mature males. These allometric relationships are rigidly adhered to in the crab population we studied. A single male, 114.8 mm CL, 76.4 mm VPL, had both chelae equivalent in length to females of the same carapace size.

The relationship between ventral propodus length and carapace length of females is also positively allometric (+1.17), except for a number of the largest adults, which tend to show relatively "shortened" chelae, or a slightly negative allometry, like the oldest males. A study of the allometric relationships of the abdomen width would probably show roughly inverse male/female relationships.

Examination of the percent incease in carapace length increment at each molt shows a total mean increase of 30.4% (S.D. ±9.4%; N=44) (Figure 3). The data were separated at 80 mm CL because of the definite differentiation of males from females at this point as determined from figure 2. The mean CL increment of instars less than 80 mm CL is 35.7% (S.D. ±6.8 %, N=26), and above 80 mm CL, 23.7% (S.D. ±5.8%, N=18).

Eleven, wild, immature crabs molted in captivity in Antigua. Four of the seven males and each of the four females molted to maturity. The females averaged a 24.6% increase in CL and an average of 31.1% increase in VPL. Of the four females that molted to maturity, the largest pre-pubertal instar was 86.2 mm CL, 53.3 mm VPL and the smallest post-pubertal instar was 94.4 mm

CL, 64.3 mm VPL. The males that molted to maturity were among the largest of the immature crabs captured but they molted only to the lower end of the range of mature males, from means of 101.4 mm CL, 76.6 mm VPL to 119.3 mm CL, 114.6 mm VPL, (averages). The males averaged a 17.7% increase in CL and a 49.9% increase in VPL. The other three males molted to a size somewhat larger than the pre-pubertal size of those that became mature. They experienced an average increase of 26.1% in CL and 39.7% in VPL. These relationships are plotted as means on figure 2.

Of the 264 M. spinosissimus examined, the relative growth of the chela of pre-pubertal males exhibit a positive allometry that is higher than that of the pre-pubertal females, especially between 80 and 105 mm CL (Figure 4) (Table 1). The male VPL significantly increases at the molt to maturity as represented by the break in the distributions, with a subsequently higher level of positive allometry. The female VPL, however, appears to have nearly isometric chelar growth in relation to the CL for specimens greater than 105 mm CL. Photographs of the maturation of male and female chalae are shown in figure 6.

The relationship between CL and CW (Figure 5) (CW = -4.84 + 1.06 CL; $P < 0.005$) depends on the stage of development. At the early post-larval instars, CL is greater than CW, whereas in adult M. spinosissimus, CW exceeds CL. The transition from the elongated body shape (CL > CW) of the juvenile poost-larval instars to the anteriorly-posteriorly flattened body shape (CW > CL) of the adults occurs at approximately 80.7 mm CL. At approximately 80.7 mm, CW is equal to CL. Simply stated, the juvenile carapace is longer than wide. At 80.7 mm CL as the crabs enter full puberty, it is virtually round. Finally, as a sexually mature adult, the carapace becomes wider than long.

Developmental Morphology

All the developmental stages observed were obtained by rearing larvae from eggs obtained from gravid females caught in the reef environment. Fifteen successive instars, from first instar to the last pre-pubertal instar are depicted in figures 7-25. The terminal part of the first post-larval instar is similar to the megalops stage as the telson is loosely tucked to the abdomen. From the second post-larval instar to the eighth post-larval instar (Figures 8 to 13), additional spines become apparent and existing spines increase in length. Also, the orbital region initially increases in size in relation to the body, and then proportionally decreases in size through those instars as the portion of the carapace shielding the eyes diminishes in size. At instar 4, the second rostral horns develop. The carapace becomes more oval shaped and wider posteriorly through instars 5-7. In addition, the carapace shows increased spine development, with the third branchial spine bifurcating. The orbital region shortens and the rostral horns turn in slightly at the tips through instar 8. From instar 9 (Figure 14), which generally occurs from 14 to 24 mm CL, the basic form and shape of the adult carapace has been assumed, and the species is easily distinquished. Prior to instar 9 or 10, M. spinosissimus is similar in appearance to the adult Mithrax acuticornis and juveniles of other Mithrax species such as Mithrax verrucosus. Sex is readily determined at instar 10, although the abdomen does not achieve its mature shape until the pubertal molt. The third branchial spine is longer while the rostral horns are noticeably thicker and shorter in proportion to the carapace length. At instar 11, there is a shortening of the orbital region and the L/W ratio approximates 1.08 which remains constant or decreases slightlty through the rest of the instars. Instar 13 (Figure 20) lacks hooked setae on the carapace. On the dorsal region of the carapace, these setae are absent but are present along the carapace edges. The propodus and dactyl segments of the walking legs have abundant setation even on mature crabs. The chelipeds and abdominal regions exhibit marked allometric growth from the fourteenth instar. At instars 14-16 the spines on the carapace become shorter and more rounded. There are fewer setae on the carapace.

DISCUSSION

Accompanying growth in *Mithrax spinosissimus* are changes in carapace and limb proportions. When very young, the juveniles are slightly elongated and quite spiny. Prior to about instar 7 they are decorators and very difficult to see in an algal environment. As they approach pre-puberty, they become slightly wider than long and the sharp setae gradually become blunter. The mean increment of molt size increase of approximately 30.4% for carapace length is of little value in the morphometics of growth. This increment although highly variable is clearly larger (approximately 35%) in young juveniles and decreases and narrows in range in older juveniles. In pre-pubertal crabs, the molt interval drops to about 25% and finally, as the terminal molt approaches, extends below 20%. The development of the chelae in the males is slightly allometric as young juveniles becomes strongly allometric and proportionally larger at the molts of pre-puberty. Hartnoll (1965) determined that the sharp alteration in relative size of the chelae in male spider crabs is the primary and most reliable index of the the molt of puberty. Thus, in *M. spinosissimus* the relationship between ventral propodus length and carapace length indicated by the sharp inflection and break in the line at approximately 105 mm CL indicates the point at which the male molt of puberty occurs. Figure 6 shows the chelae of a male and female through a series of molts. Though the relationship between ventral propodus length and carapace length becomes sharply allometric in males at about 100 mm CL, and becomes isometric in females at about 80-90 mm CL, as both apparently molt to even larger sizes, growth becomes negatively allometric and cheliped size shortens relative to the body length. Although the primary growth and morphological relationships seem quite clear through the young adults in the Antiguan population, the post-puberty patterns and the relationship of the Antiguan crabs to those elsewhere in the Caribbean leave some questions.

The relationship between VPL and CL from M. spinosissimus collected in Antigua indicates that the morphological relationships shown in figure 4 are significantly different from those previously sampled in Florida (Bohnsack, 1976). There appears to be some Caribbean-wide regional variation in morphological characteristics as mature crabs caught at other sites were larger than those in Antigua, which in turn were considerably larger than the Florida population (see Bohnsack, 1976).

Very large pre-pubertal and post-pubertal male instars were collected in the Dominican Republic, measuring 131.0 and 180.0 mm CL respectively. The largest pre-pubertal and post-pubertal female instars were collected in Grand Turk, measuring 105.6 and 158.2 mm CL respectively. This coincidental trend suggests that the large pre-pubertal crabs molt to the largest adults. The large immature male (131.0 mm CL) had morphologically immature chelae, and after molting, it measured 153.3 mm CL (no VPL was recorded for this crab).

The molt increment data in figure 4 indicates a sharply decreasing trend in molt increments for crabs molting at a CL longer than 80 mm. A general decrease in increment might be attributed to conditions of culture since much of this data is derived from crabs cultured from eggs. However, the low molt increments are consistent with that found from wild crabs only observed in culture for short periods. Also, this relationship, as expressed by the "Hiatt Growth Diagram," is well known for other crabs (Mauchline, 1976).

The observed molt increments suggest that it is improbable for an Antiguan crab to molt from the largest CL in the size range of pre-pubertal crabs to the largest in the size range of post-pubertal crabs. This would be a carapace length increase of about 34% for males, whereas we predict an increase in CL increment at each molt of only about 15-20% based on figure 3 and the molts achieved after capture. Comparable figures are available for Hyas coarctatus (brachyura) with an average increase in CL among laboratory specimens (n=8) of 21.5 (Hartnoll 1963a). With regard to carapace/propodus relationships, female maturation is not so clear. Based on those animals that did molt to maturity in captivity, a 25% increment is found, and this essentially agrees with figure 3. On the other hand, the required female CL molt increment would have to be 37.4% between the largest pre-pubertal instar (92.4 mm CL, 59.0 mm VPL) and the largest post-pubertal instar (127.0 mm CL, 81.1 mm VPL).

It is suggested that the terminal molt may not occur at the molt to maturity in female Mithrax spinosissimus as evidenced by the wide variation in range of carapace length for mature females and the consistent variation in molt increments for crabs of the same carapace length. On the other hand, the wide variation in carapace length observed in cultured crabs at the same instar and the inability to be certain whether some females have indeed achieved the full reproductive state make it very difficult to establish the state of some crabs. Also, great differences in size increase between crabs that molted to maturity and the increments predicted based on the distribution, may occur due to environmental variables, such as temperature, light, amount and type of food available, and competition for food and space. The difference may also be due to genetic variation, in which case the cited crabs that molted to maturity in captivity are an insufficient sample.

Until recently the majid crab Chinoecetes opilio (the snow crab) was thought not to have a terminal molt at the molt to maturity (Davidson, et al., 1985). While it has now been demonstrated otherwise, it is to be noted that in that species there is considerable overlap in male carapace size between the pre-pubertal animals and the adults (Watson, 1980). This differs significantly from the data found for M. spinosissimus in this study (Figure 2). In addition, from Figure 2, there is an apparent reduction in positive allometry for those males over 130 mm VPL. Males with a VPL greater than 130 mm are offset from and slope slightly less than the smaller mature males. Thus, in this species there remains considerable doubt that the terminal molt always occurs at the molt to maturity, at least as that maturity is evidenced by the size of the propodus.

Juvenile instars of 80 mm CL exhibit positive chelar allometry. Allometry levels calculated from logarithmically transformed values for ventral propodus length and carapace length of instars show the relative growth of Mithrax spinosissimus to be similar to other Brachyurans (Hartnoll, 1974). The allometry level of VPL for the pre-pubertal male of this species and for pre-pubertal male Brachyurans in general is respectively, 1.27 and 1.26. Post-pubertal Mithrax spinosissimus males have a higher level of allometry than post-pubertal Brachyurans (1.73 to 1.53, respectively). The VPL allometry level for pre-pubertal females is also higher than that for their Brachyuran counterparts, 1.17 and 1.11, respectively. However, the VPL allometry level for post-pubertal females decreases considerably from that calculated for other mature Brachyuran females, 0.97 compared to 1.10.

Hartnoll (1965) states that mature majids do not molt based on evidence of epizoeal growth. However, the post-pubertal M. spinosissimus were relatively clean of epizoal growth. Because of this, observations of the growth of epizoal organisms to gauge relative age of the exoskeleton may not be easily applicable for these crabs. When collected, the mature Antiguan crabs had very little epizoeal growth on the carapace. During captivity, however, all crabs developed epizoal organisms and some eventually attained very well developed red crustose algae on the carapace. In addition, gooseneck barnacles developed around the base of the chelipeds.

CONCLUSIONS

The morphometric characteristics of mithrax spinosissimus change considerably from first crab, through juvenile and pre-pubertal instars to adult. The shape and growth, relative to the carapace, of the chelipeds provides a standard morphological reference point for Mithrax spinosissimus. Maturity is reached in 16 or 17 molts. The size range of carapace length among individual populations from different geographic locations throughout the Caribbean/West Indian region varies widely, although it is rather narrow within populations. Different mean carapace sizes at each study site may be the result of specific ecological effects perhaps including available burrow size, available food, predation pressure and temperature in the case of

Florida. However, considering the extremely short swimming period of the larval stages and the great depths of water present between many Caribbean Islands, genetic differences between isolated populations must be suspected.

From our observations, we cannot establish with certainty that the molt of puberty is the terminal molt. It appears that the expected molt increment of 20-25% is too small to allow for all pre-pubertal instars to molt to the largest post-pubertal instars. In addition, at Antigua the lack of attached epifaunal growth on the carapace of all post-pubertal instars coupled with the observation of male crabs with slightly enlarged chelipeds molting lead us to suggest that another instar can occur after the pubertal molt, that being the terminal molt.

Except for the Florida populations, which in mariculture might molt to non-commercial sizes, Mithrax spinosissimus appears to offer maximum potential for marketing in that a choice could be made between relatively small, low meat to weight ratio females, the large, high meat to weight ratio males and an even larger size male post-larval instar. Unfortunately, we have no information at this time on the time interval to a second adult molt. It may or may not be consistent with the later molts of pre-puberty and the molt to adult.

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LEGENDS

Figure 1. Position of male chelar VPL measurement (A to B.)

Figure 2. VPL vs CL in mm for wild and cultured *Mithrax spinosissimus* from Antigua. Solid lines represent average increment increase of A) four males that molted to maturity, B) three males that molted to pre-pubertal instar and C) four females that molted to maturity.

Figure 3. Relationship of increase in size of *Mithrax spinosissimus* carapace length (CL) as a function of pre-molt carapace length.

Figure 4. Growth phases for juvenile and adult *Mithrax spinosissimus*. CL=carapace length; CW=carapace width; VPL=ventral propodus length. Log/log plot.

Figure 5. Relationship of *Mithrax* *spinosissimus* carapace width to length (mm).

Figure 6. Chelae of immature and mature male and female *Mithrax spinosissimus*.

Figure 7. Zooea, megalops and first crab (instar I) of *mithrax spinosissimus* hatched in culture. 1) Pre-zooea, 2) Zooea 1, 3) Zooea 2, 4) Megalopa, 5) first crab (Instar I, CL = 1.5 mm).

Figure 8. Instar 2, 2.5 mm CL. The extended carapace eye shields are gone and a spine on the eyestalk is more prominent.

Figure 9. Instar 4, 5.0 mm CL. The second rostral horns and carapace spines are more developed.

Figure 10. Instar 5, 5.7 mm CL. The carapace is noticeably spinier.

Figure 11. Instar 6, 7.9 mm CL. The posterior width of the carapace is more pronounced.

Figure 12. Instar 7, 10.3 mm CL. Greater spine development.

Figure 13. Instar 8, 13.8 mm CL. The orbital region is shortened and the rostral horns are turned in slightly at the tips.

Figure 14. Instar 9, 14.8 mm CL. Pronounced lengthening of the third branchial spine.

Figure 15. Instar 10, 21.5 mm CL. Rostral horns are thicker and shorter and the carapace is more round.

Figure 16. Instar 11, 28.5 mm CL. Rostral horns have become more truncate and turn slightly inward.

Figure 17. Instar 11, ventral.

Figure 18. Instar 12, dorsal view, 34.5 mm CL. The carapace is rounder.

Figure 19. Instar 12, ventral.

Figure 20. Instar 13, 48.0 mm CL. Rostral horns have become thicker and shorter in proportion to CL.

Figure 21. Instar 14, 60.5 mm CL. An increase in spines on top of the carapace.

Figure 22. Instar 15, 83.0 mm CL. The carapace is wider in proportion to the CL and the spines on top of the carapace are low and rounded.

Figure 23. Instar 16, 101.2 mm CL.

Figure 24. Detail of immature *Mithrax spinosissimus* showing limb buds that form upon loss of an appendage.

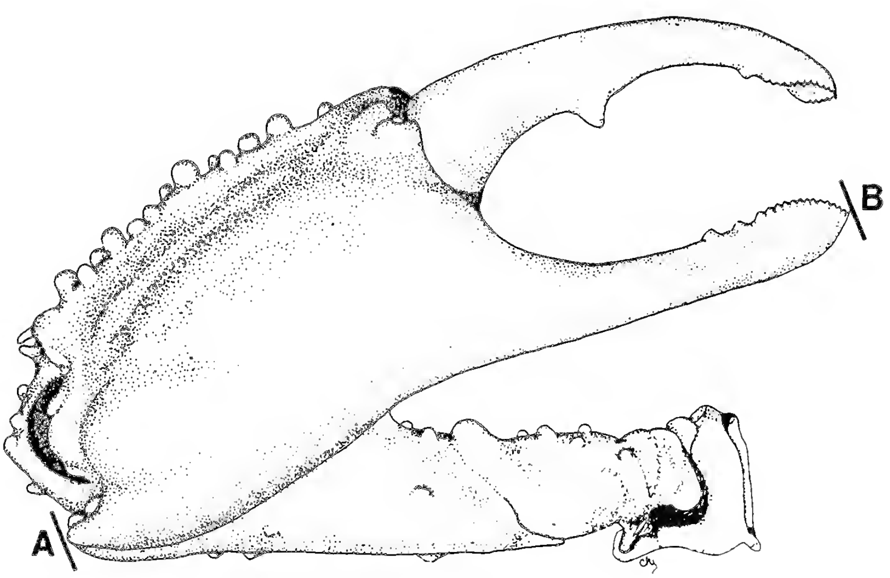


Figure 1

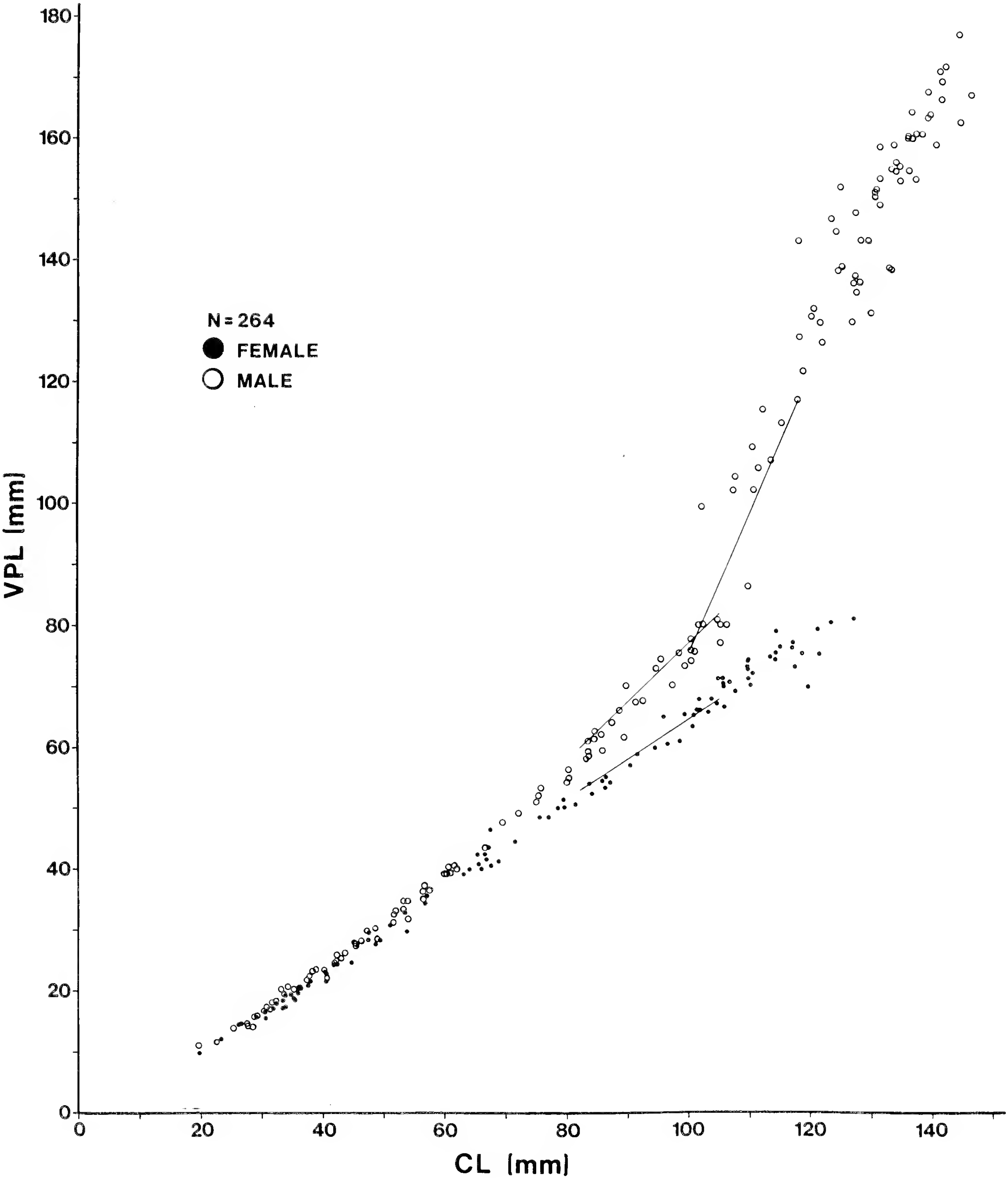


Figure 2

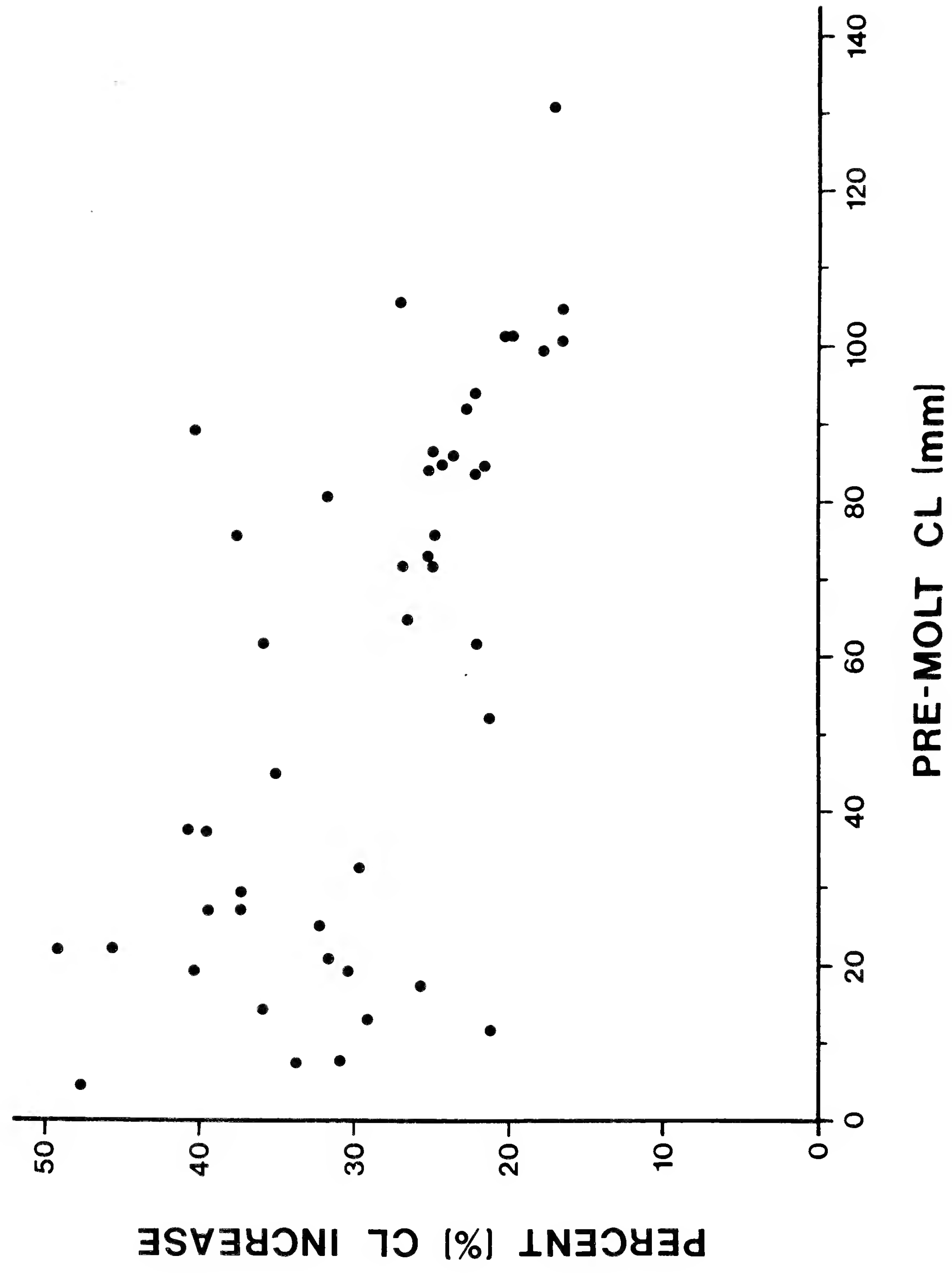

PERCENT (%) CL INCREASE
0
10
20
30
40
50
PRE-MOLT CL (mm)
0
20
40
60
80
100
120
140

Figure 3

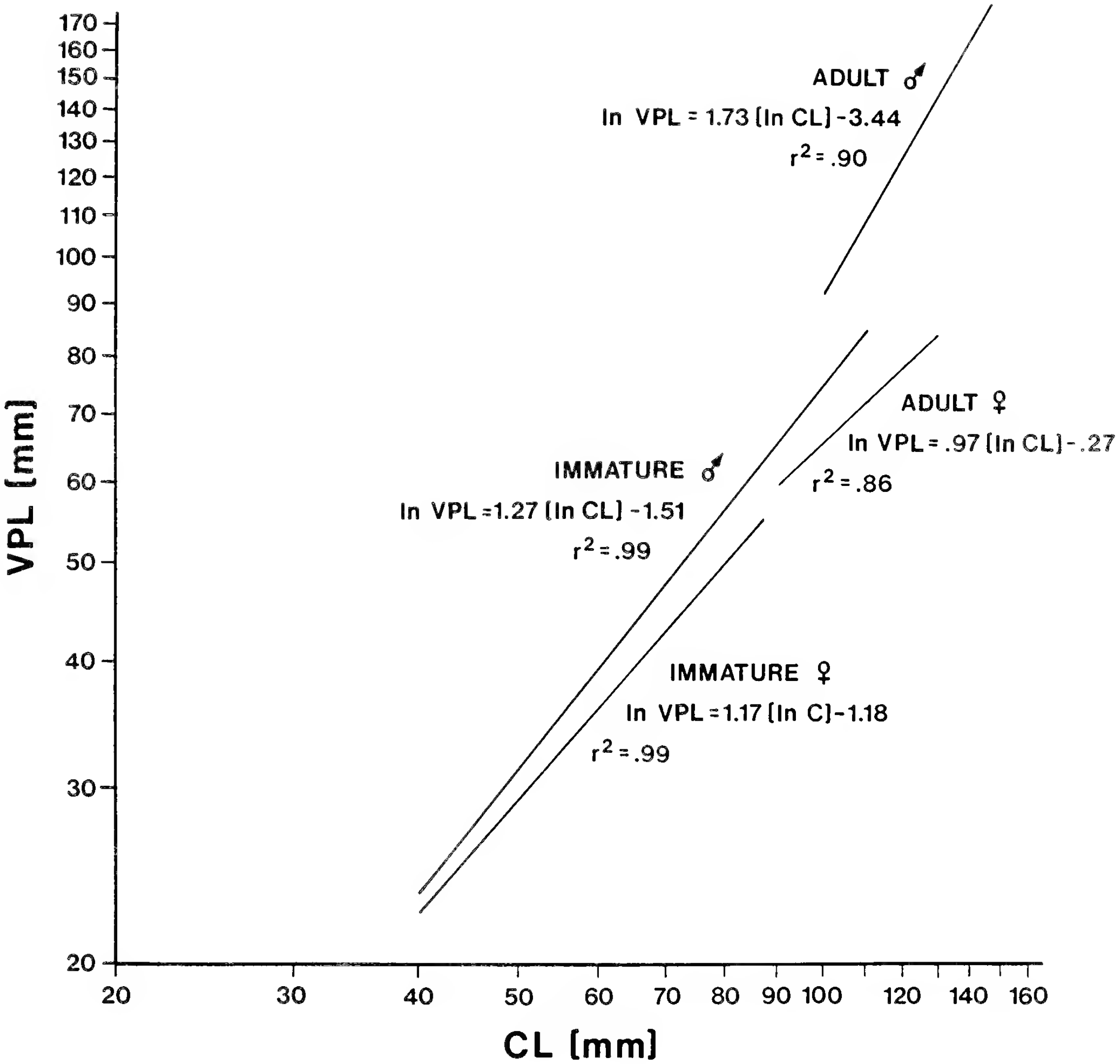

ADULT ♂
ln VPL = 1.73 (ln CL) -3.44
r^2 = .90
ADULT ♀
ln VPL = .97 (ln CL) -.27
r^2 = .86
IMMATURE ♂
ln VPL = 1.27 (ln CL) -1.51
r^2 = .99
IMMATURE ♀
ln VPL = 1.17 (ln C) -1.18
r^2 = .99
VPL (mm)
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
CL (mm)
20
30
40
50
60
70
80
90
100
120
140
160

Figure 4

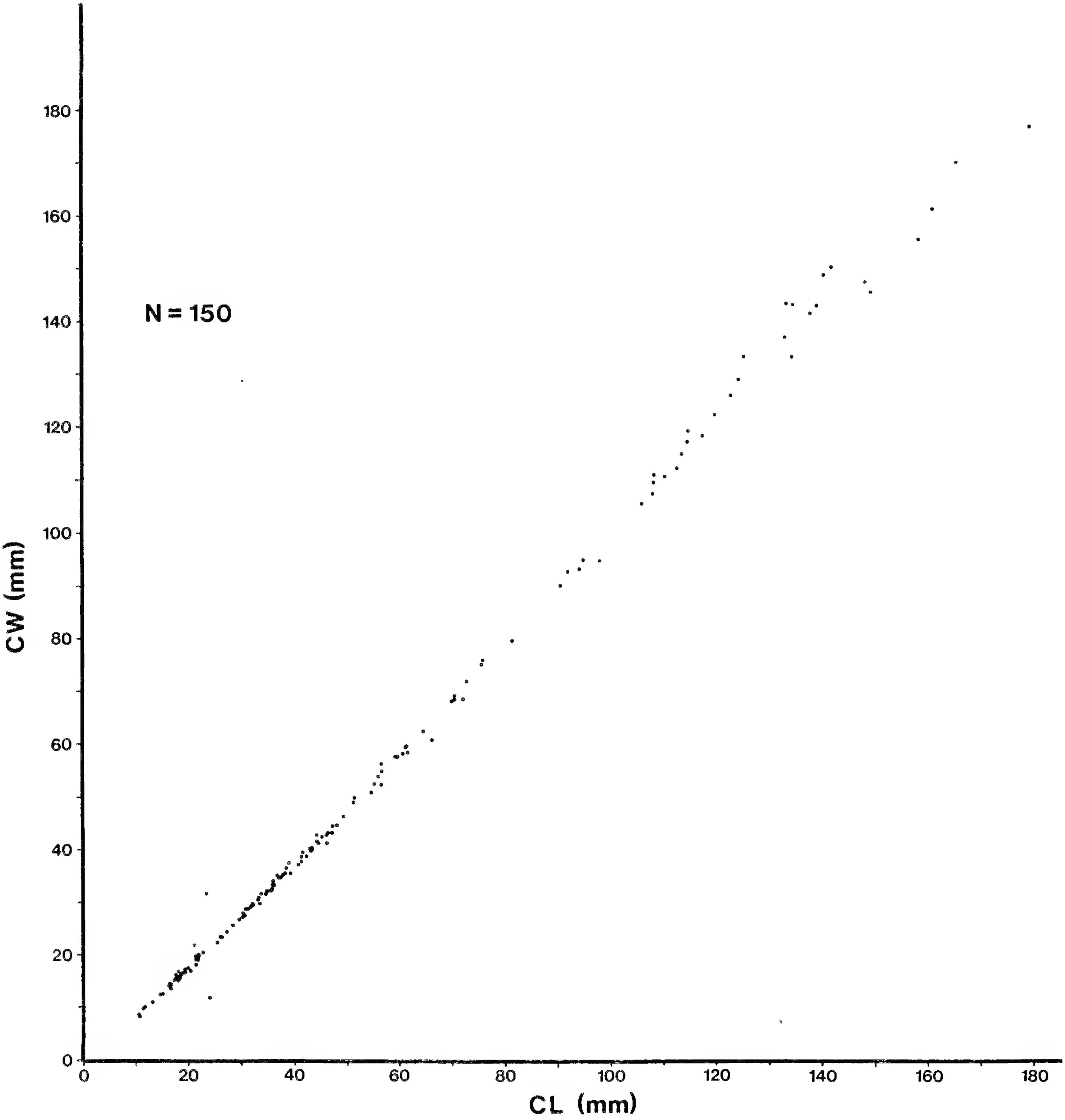

N = 150
CW (mm)
CL (mm)
0
20
40
60
80
100
120
140
160
180
0
20
40
60
80
100
120
140
160
180

Figure 5

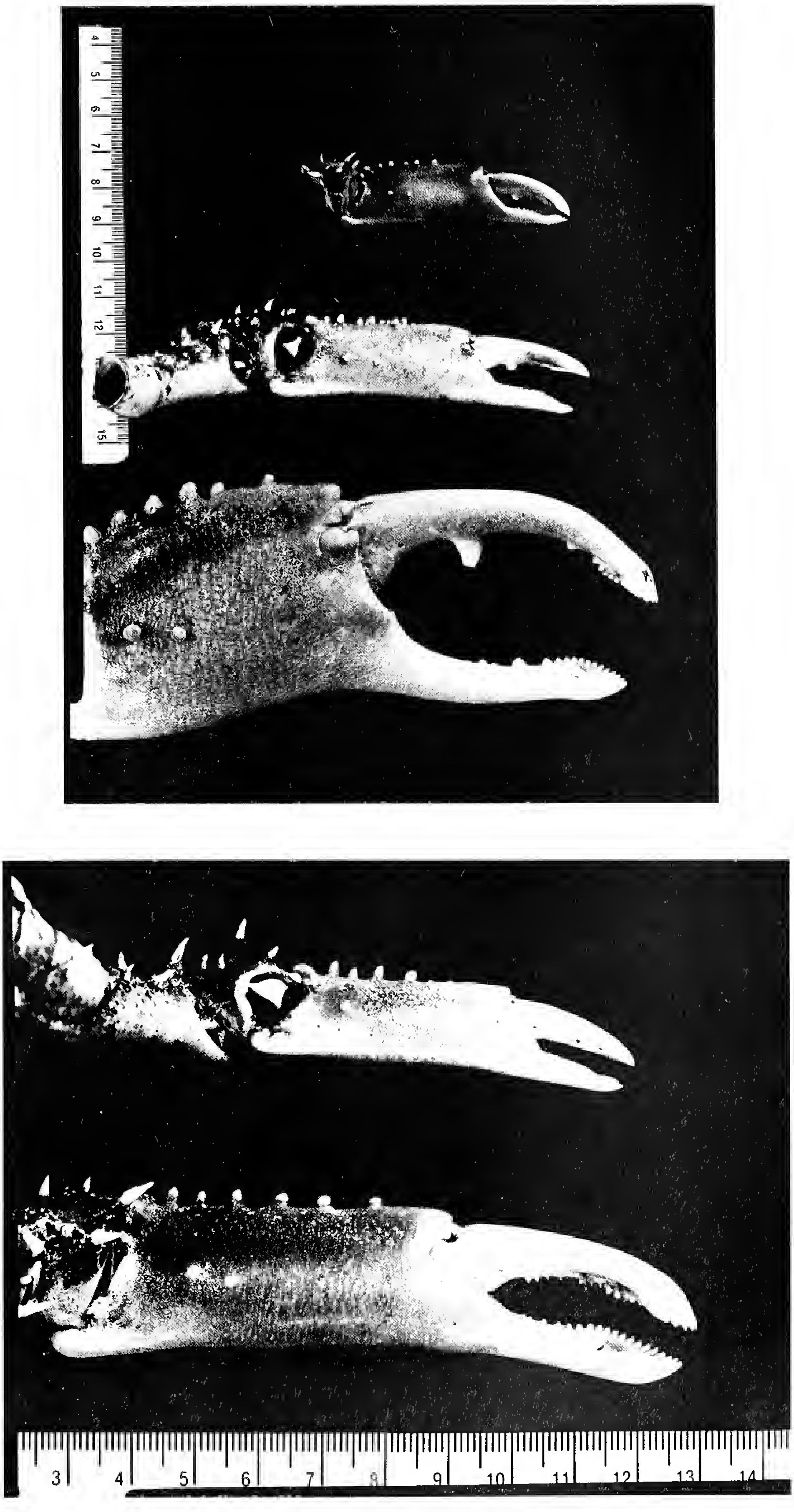
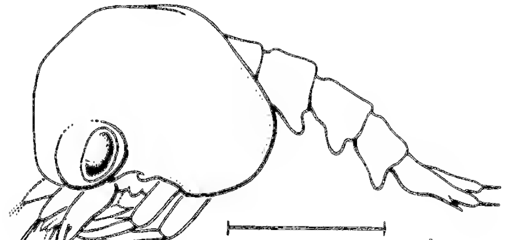


Figure 6



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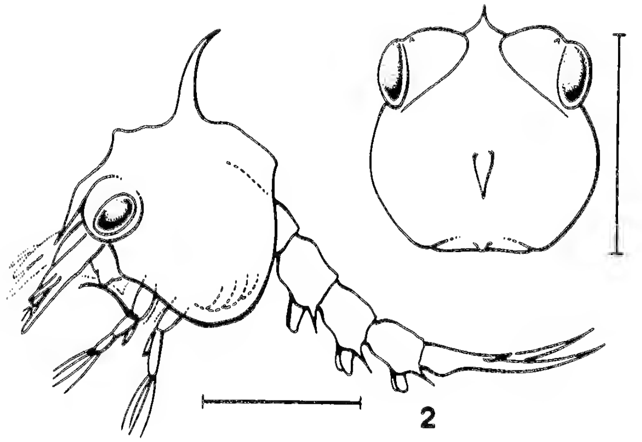

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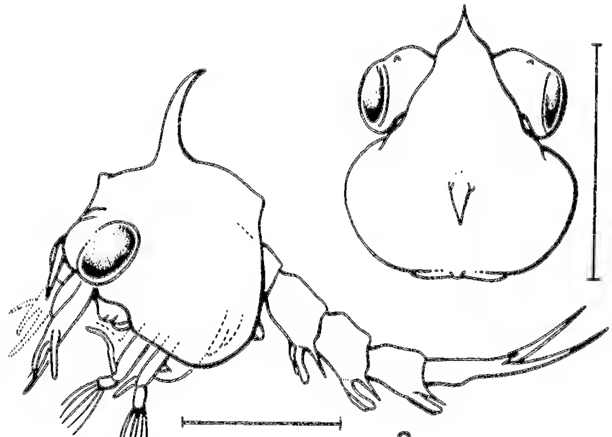

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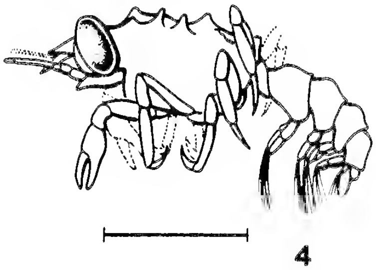

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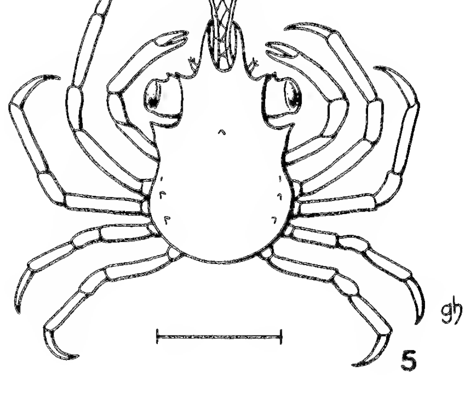
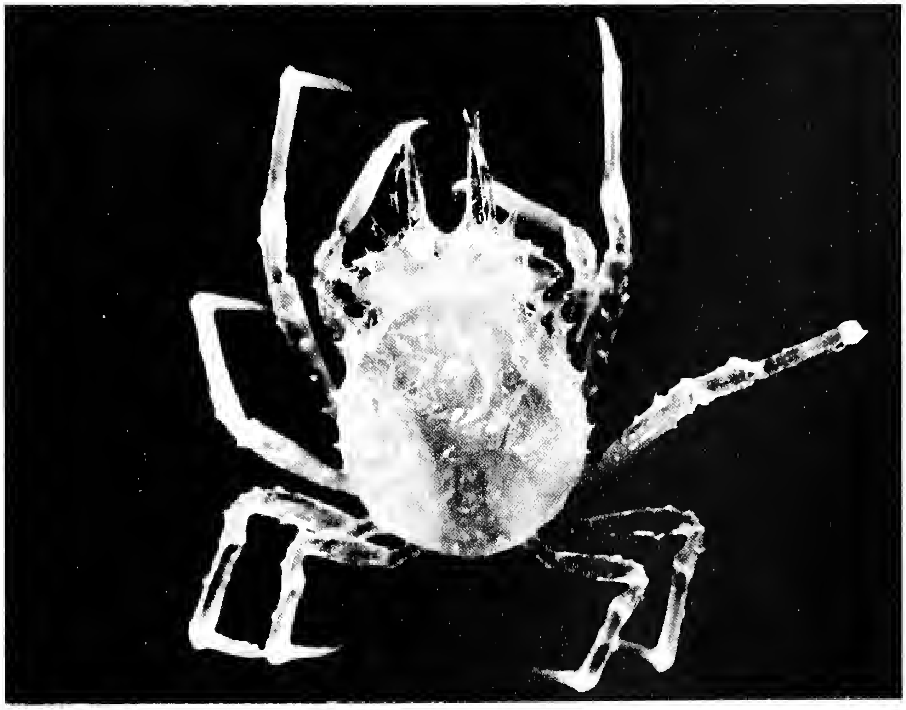


5

scale bars : 1mm

Figure 7



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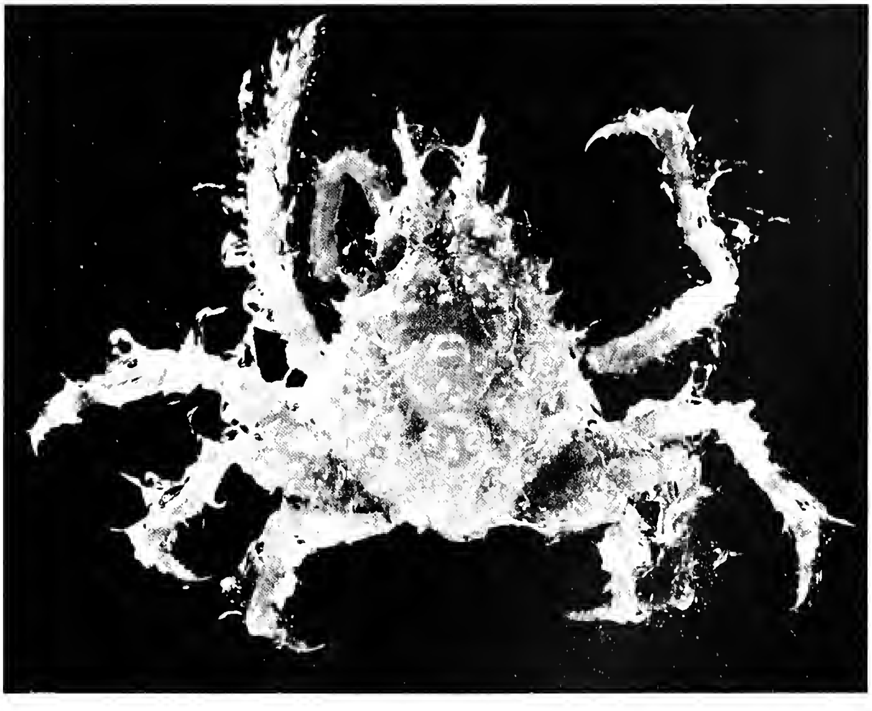

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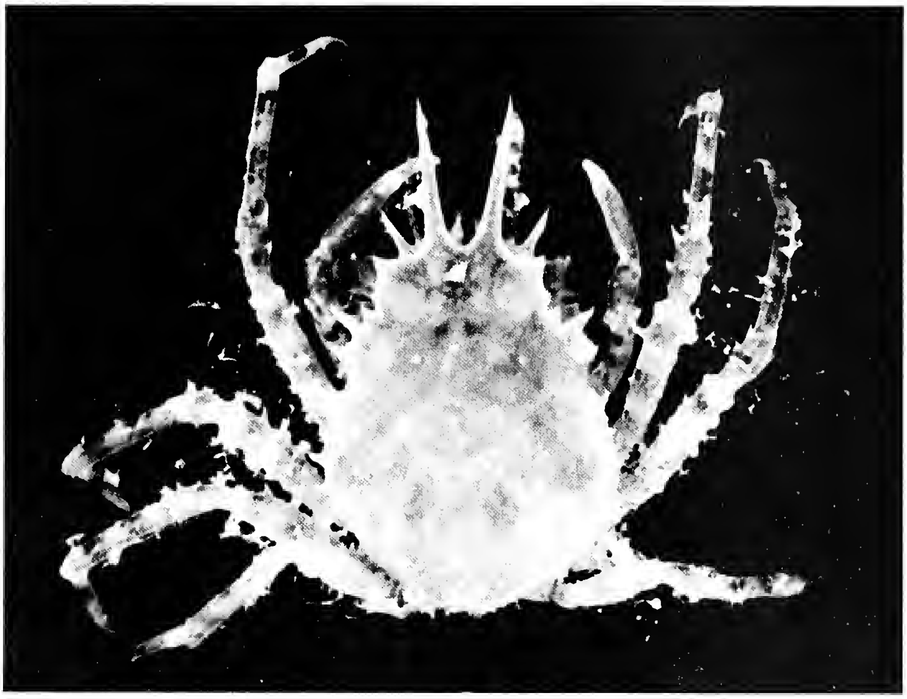

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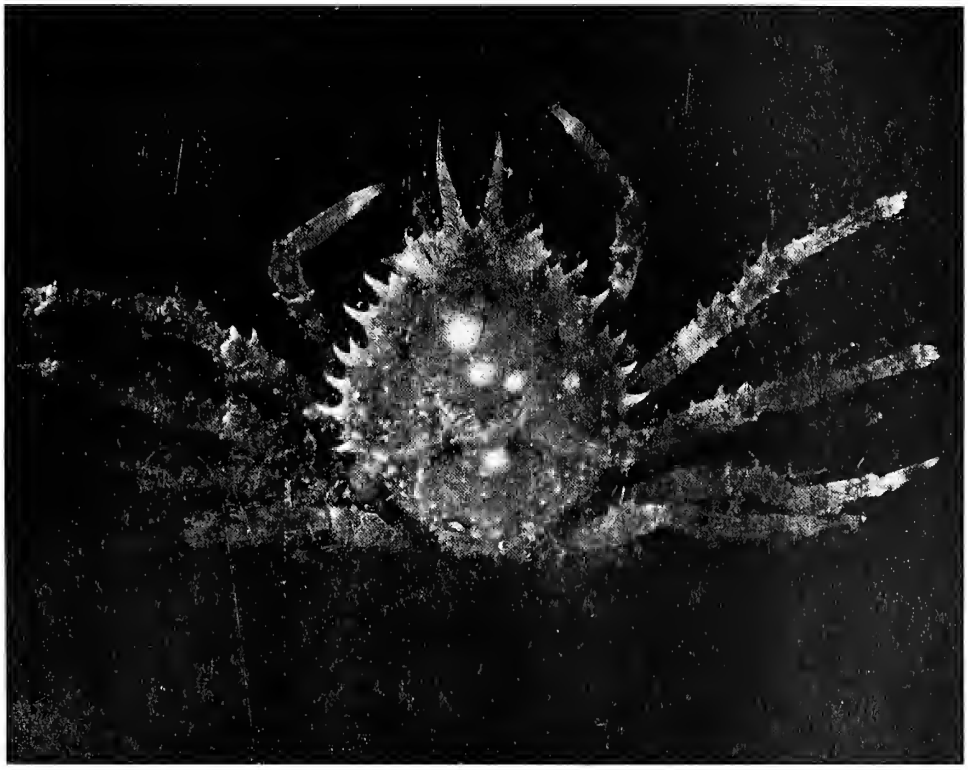

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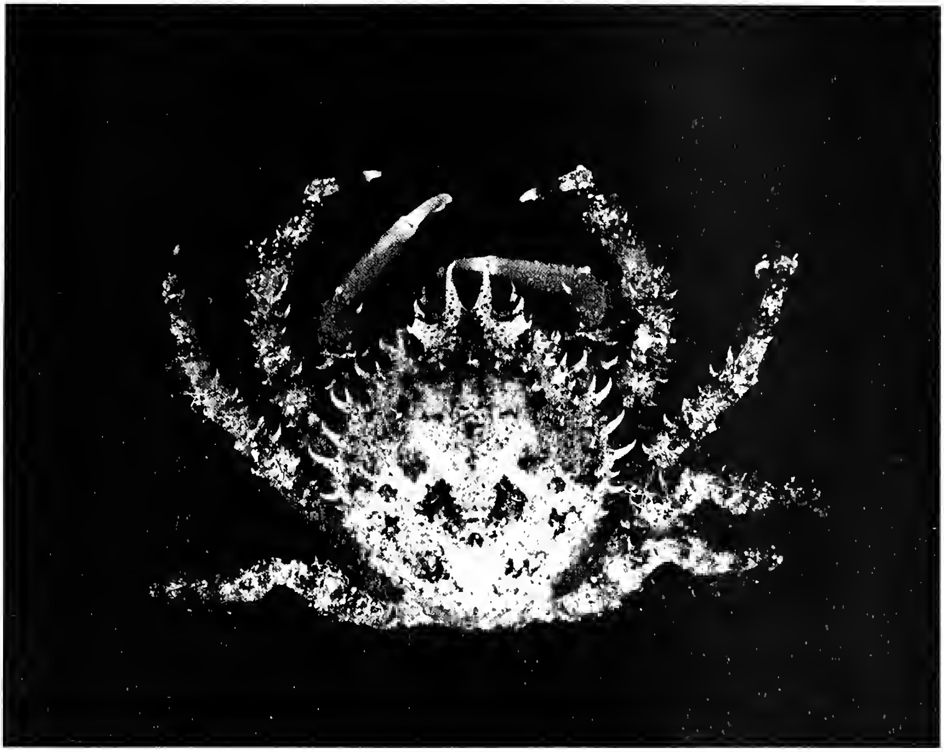


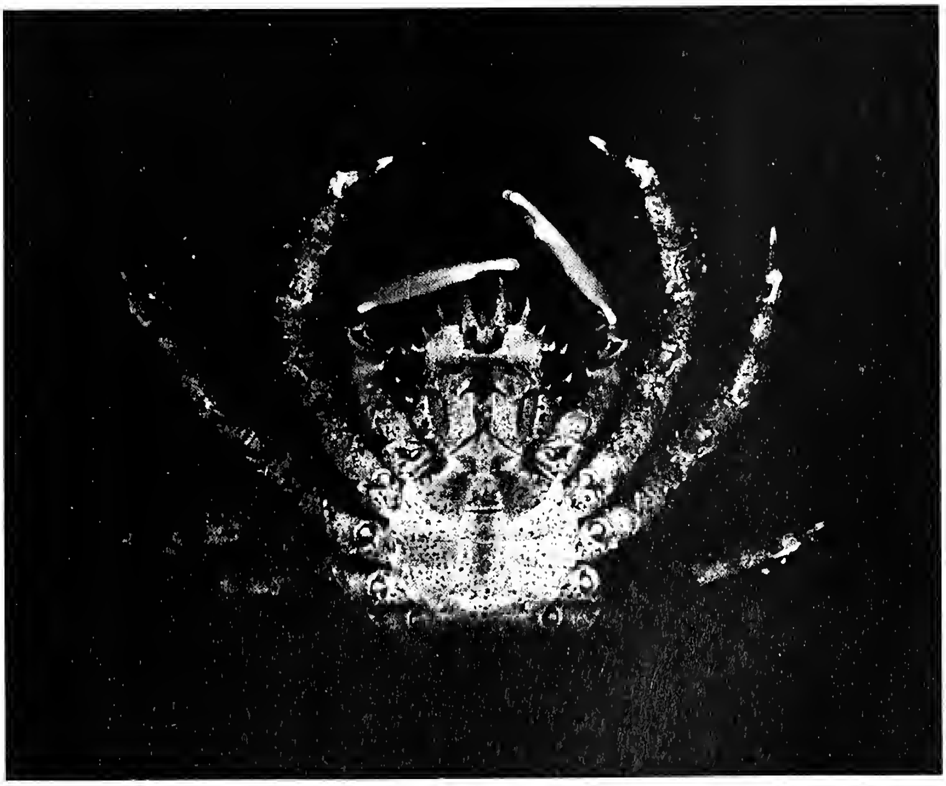
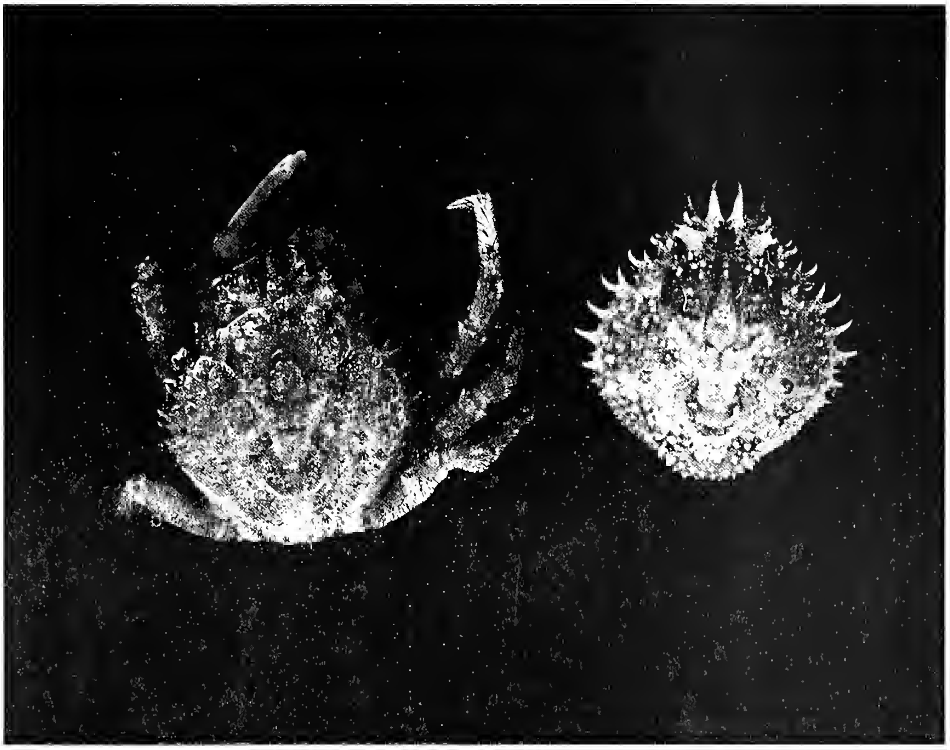


Figure 16 & 17



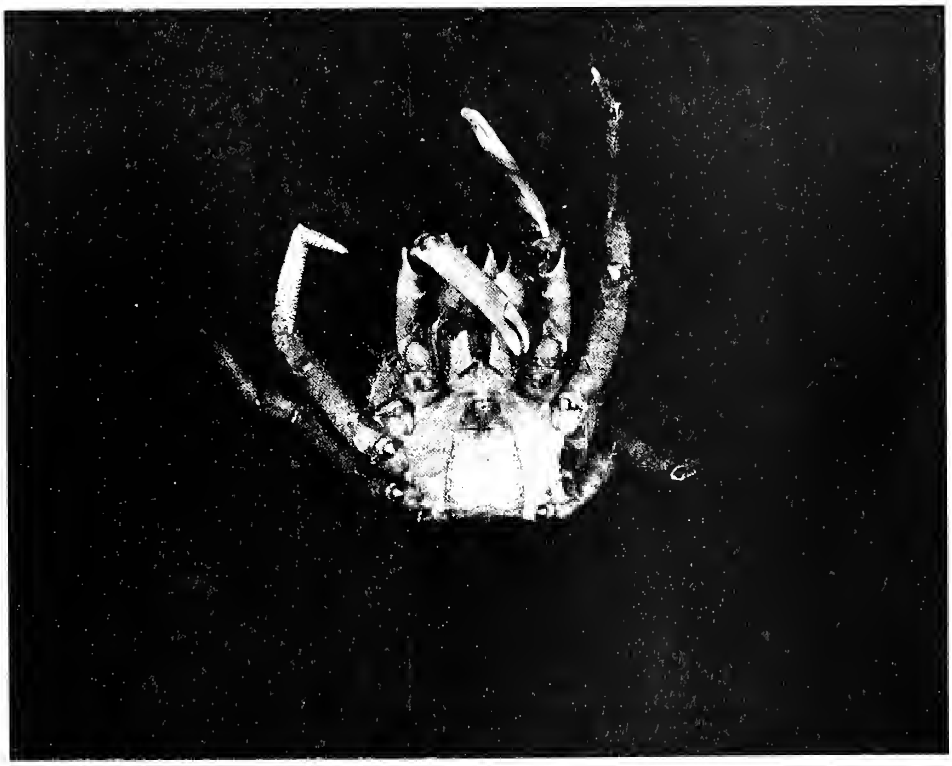


Figure 18 & 19

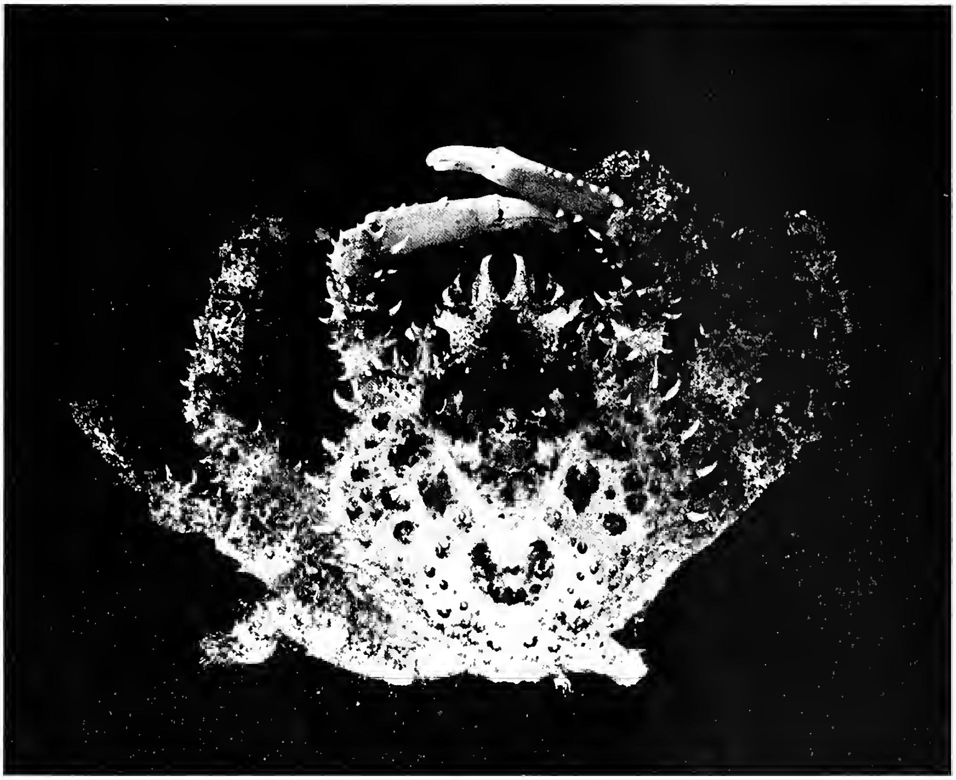
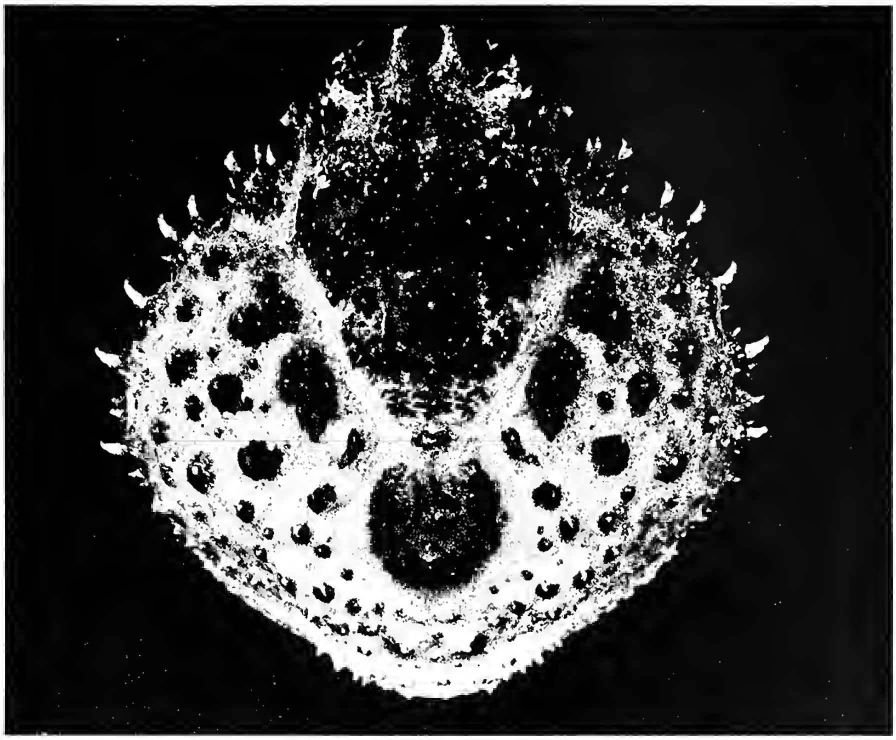


Figure 20 & 21



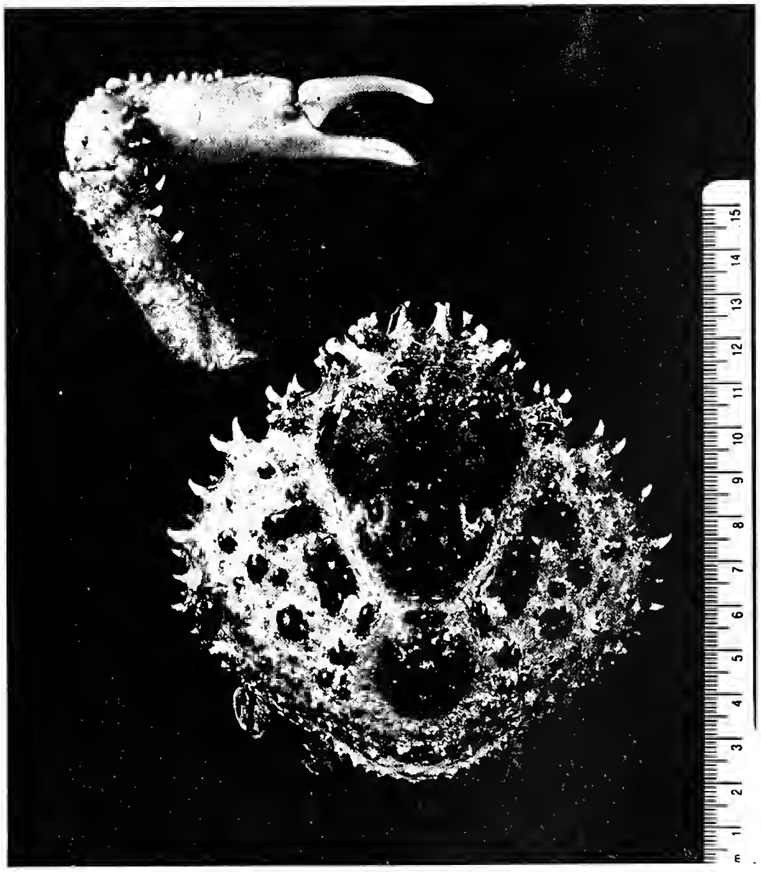


Figure 22 & 23

Figure 24

SECTION II: BIOLOGY AND ECOLOGY OF *MITHRAX SPINOSISSIMUS*

POPULATION DENSITY AND STRUCTURE OF *M. SPINOSISSIMUS* AT SIX CARIBBEAN SITES AND THE FLORIDA KEYS.

POPULATION DENSITY AND STRUCTURE OF MITHRAX SPINOSISSIMUS

J.M. Iglehart, R.V. Ruark and K.H. Koltes

Abstract

The population density and structure of the Caribbean King Crab, Mithrax spinosissimus, was examined for mariculture purposes at seven sites from the Florida Keys to the eastern coast of Antigua. A significant size difference was found in the carapace length when comparing Florida crabs to the Caribbean populations. Individuals from the Florida Keys were smaller, with a greener coloration and a relatively thinner carapace. Temperature differences, fishing pressure and the species short planktonic stage may contribute to the variation in crab density, size and sex ratios found between sites and seasons. The differences observed between sites, particularly Florida versus all other sites, suggests that present-day populations have been isolated for a long period of time, and represent separate stocks of the same species.

INTRODUCTION

In response to the declining Alaskan King Crab fishery, based primarily on Paralithodes camtschatica, investigations of crab species suitable to support mariculture projects and fisheries have increased (Idyll, 1971). Preliminary studies have included investigations of the West Indian giant spider crab, or Caribbean King crab, Mithrax spinosissimus (Munro, 1974; Hazlett and Rittschof, 1975; Bohnsack, 1976, Provenzano and Brownell, 1977; Porter, et al., in review). The crab is found throughout the tropical Western Atlantic from the Florida Keys and Bahamas to the West Indies, Venezuela and Nicaragua (Williams, 1984) at depths of 2-200 meters (Colin, 1978). A reported range of Mithrax spinosissimus extending as far north as the Carolinas (Rathbun, 1925) seems unlikely.

Two populations have been described previously. Munro (1974) conducted a survey of 212 Mithrax spinosissimus caught in traps off the Jamaican coast. In that study, males outnumbered females almost 2:1 and had a mean carapace width (CW) of 133.4 mm. Females had a mean CW of 122.8 mm.

The Florida population was sampled by Hazlett and Rittschof (1975) and by Bohnsack (1976). Bohnsack (1976) reported carapace widths of 96 mm (male) and 86 mm (female) for crabs in the South Florida Keys, with females outnumbering males 2:1. Hazlett and Rittschof (1975), sampled 115 crabs from a canal at Little Torch Key, Florida and found none to exceed 110 mm CW.

Little information exists concerning seasonal trends in the relative abundance of Mithrax spinosissimus. However, crabs have been collected every month of the year. Munro (1976) found a seasonal variation in crab abundance based on a two-year survey of trapping rates in Jamaica. Catches were zero or negligible in January and February, 1970, 1971 and 1972. Catch rates reached a maximum in March or April, June or July and November or December, 1970 and 1971. Catch rates were generally greatest in areas of intensive fishing pressure.

Several factors appear to affect the local abundance of crabs. Hazlett and Rittschof (1975) and Bohnsack (1976) found that crab density was directly proportional to crevice density in their studies of the Florida population. Patterns of activity and size of home range were found to differ between males and females in these studies (Hazlett and Rittschof, 1975) and may influence both sex ratios and overall abundance.

This paper reports results of field studies conducted in the Florida Keys, the southeastern Bahamian archipelago and in several Antillean sites from the Dominican Republic to Antigua. The purpose of these investigations was to identify and define parameters of Mithrax spinosissimus populations throughout the region. Conclusions about population characteristics are drawn from both these data and from previous studies.

METHODS

Seven sites in the Caribbean were investigated (Figure 1). Site 1, in the Florida Keys ($24^{o}80$'N; $81^{o}05$'W), was surveyed in January, 1984, July, 1986 and July, 1987. The census was conducted along manmade canal walls and old quarries particularly at Grassy Key. One canal at Big Pine Key and three canals at Little Torch Key also were surveyed in July, 1987. These data were combined with those from Grassy Key. Site 2 was located at the main reef off Abraham Bay along the south coast of Mayaguana, Bahamas (22^{o} 0' N; 73^{o} 0' W) and was surveyed between February 1983 and May, 1983. Site 3, located at the east end of the

Caicos Bank, just west of Long Cay, South Caicos, Turks and Caicos Islands, British West Indies (22°05'N; 71°30'W), was repeatedly surveyed from December, 1984 to May, 1986. Site 4 was situated at the reef drop off, on the western side of Grand Turk, Turks and Caicos (21°90'N; 68°80'W). Crab population surveys there were conducted between January 1984 and March 1985. An active crab research program continues at Grand Turk and data from this site include information collected through the summer of 1987. Site 5 crabs were collected from the inner and outer reefs, off the north coast of the Dominican Republic, at Buen Hombre (19°10'N, 71°20'W) from March 1985 to September, 1986. The crabs from Site 6, located on the south coast of the Dominican Republic, at Azua (18°20'N; 70°50'W), were collected over the same time period. Site 7 crabs were collected from reef areas along northeast Antiqua, WI (61°43'W; 17°10'N), between May, 1985 and July, 1986. With the exception of sites 1 and 5, crabs were surveyed by sampling all individuals in a 3.05 m diameter circle (area = 7.3 m^2) established at random during diving operations.

Crabs were collected by three methods. Those at site 1 were collected at night from the shore using a pole net or by free diving. At sites 2, 3, 4, 5 and 7, SCUBA was used to conduct surveys of crab populations and to collect individuals. Isolated coral heads, rubble and shoal areas and drop offs were examined from depths of 3-35 meters. Most dives were conducted at dusk or in the early morning hours. Lights were used to illuminate crevices and caves. Wire mesh traps also were used to catch crabs at sites 5, 6 and 7. At sites 2, 4, 5 and 7, extensive, less formal searches were carried out by snorkel.

Approximately 600 crabs were sampled in this investigation. Carapace length (CL) (distance from the rostral sinus to the most posterior point of the carapace) and weight were measured. In addition, crabs were sexed and state of maturity determined. Males were considered adult if the ventral propodus length (VPL) was equal to or greater than the CL, based on VPPL = f(CL) (see Biddlecomb, et al., this volume). VPL is the ventral distance of the propodus from the tip of the chela to the posterior end of the socket containing the carpal hinge (see Figures 1 and 2; Biddlecomb et al., this volume). Females whose abdomen covered the entire sternum were considered adult. Lost appendages and other physical characteristics also were recorded. Captured crabs were used to determine population parameters for each site and to establish the percentage of individuals with a number of missing appendages. Data on trapped crabs from Sites 5 and 7 were used to determine seasonal fluctuations, sex distribution and reproductive status.

CL measurements on male and female crabs from six of the seven sites (Site 6 was omitted) were used in an analysis of variances to test for differences between sexes. Data from crabs trapped at Sites 5 and 7 were used to determine sex ratios (t-tests) and seasonal patterns in crab abundance. Data from both trapped and hand caught crabs at Sites 5 and 7 were also used for histogram plots of the CL (mm) for adult males and females. Pooled data (all sites) were used to compare the percentage loss of appendages for adult crabs. Chelae loss was considered separately from loss of walking legs because of their importance in overall body weight and their presumed role in aggression and/or courtship (particuarly in males).

RESULTS

General Population Characteristics

Significant variation in the size of male and female *Mithrax spinosissimus* was observed both within and between populations at the seven sites (Table 1). Overall mean CL for adult males (N = 166) was 136.5 mm (S.D. = 17.5) with a range of 79.6 mm CL (Site 1) to 190.5 mm CL (Site 2). Adult females (N = 281) averaged 120.4 mm CL (S.D. = 16.4) with a range of 65.7 mm CL (Site 1) to 165.0 mm CL (Site 2). More than 50% of the wild caught females were gravid at the time of capture.

Results from an analysis of variance (Table 2) showed a significant difference (F TEST; $P < 0.05$) between sites. The greatest difference was observed between the Florida (Site 1) and Caribbean populations (Sites 2-7). Florida crabs were significantly smaller (X = 98.8 mm CL for males; X = 83.5 mm CL for females) than those at all other sites (Duncan's Multiple Range; P <0.05).

Antiguan (Site 7) crabs (both male and female) were the smallest of the Caribbean population (Sites 2-7) with males averaging 131.4 mm CL and females 108.2 mm CL, while crabs from Mayaguana (Site 2) were the largest (X = 166.9 mm CL for males; X = 140.6 mm CL for females). Males from the Turks and Caicos Islands (Sites 3 and 4) and from Buen Hombre (Site 5) were similar in size (with Grand Turk males averaging slightly larger) and intermediate among the populations. Females from Grand Turk were slightly smaller in size than Mayaguana (site 2) females, the largest females among the sites. South Caicos (site 3) and Buen Hombre (site 5) females were intermediate in size.

The distribution of CL (Figure 2, 3) for adult males and females from Sites 5 and 7 showed some overlap in size between the sexes, but males were consistently larger than females at all sites (Table 2), (t-test; P<0.001). An interesting observation in the population from Site 5 is that an abrupt attenuation in CL distribution for females occurs at the 135 mm CL size class (Figure 2). The reason for this is not known, but it suggests either differential mortality or catch rates (primarily trapping) at the higher size classes. It could also represent a bimodal curve with two overlapping adult instars.

The range of CL of immature crabs overlapped the range of adult CL for both males and females for all sites except Site 4 (females; N = 2) and Site 6 (females; N = 3), probably due to the small number of individuals collected. At Site 7 (N = 42) there was a bimodal distribution of CL for juvenile males (Figure 4) indicating two instars in the juvenile size range. These sizes correspond with those found for instars 14 and 15 (Biddlecomb _et al_., this volume).

Individual Sites

Site 1: Florida, Grassy Key

A total of 87 crabs were collected at Site 1 using a pole net or by free diving. Ten adult males and 18 adult females had a mean CL of 98.8 and 83.5 mm respectively. The remaining 59 crabs were immature.

The average size of adults was smaller than those determined for all other sites. Except for the large mean carapace length among Mayaguana crabs (unfortunately with a low N; N=11), the size range between all non-Florida sites was only about one-half of that between the Florida sites and the next nearest non-Florida site (in size). The Florida crabs also displayed other characteristics which differed from the Caribbean/West Indian populations. They had a dull dark green color and in some adult males, the chela had a bluish hue. Offspring of these crabs in culture displayed a coloration similar to that of the adults as well. The females were much hardier than the males when maintained in cages. Other differences included a relatively thinner carapace and the absence of male chela puncture scars on the female crabs.

Five juveniles at Site 1 were found feeding in the shallows with adult females in January, 1984. Their feeding movements and algal species preference were identical to the adult females. However, when pursued, they moved more rapidly and with more direction than the adults.

Site 2: Bahamas, Mayaguana

At Site 2, a total of 30 crabs were captured using SCUBA of which 12 were measured. CL averaged 166.9 mm (N = 6) for adult males, and 140.6 mm (N = 5) for adult females. The largest male measured 190.5 mm CL, while the largest female measured 165.0 mm CL. Only one juvenile was captured, a female measuring 54.0 mm CL. An extensive search for juveniles or small adults was carried out throughout the lagoon and reef areas by snorkel and diving. Approximately 100 man-days of effort was devoted to this search, and a number of coral heads of various spatial arrangements were totally dissected.

Thirty hours of post-sunset/night SCUBA surveys were conducted on the Abraham Bay reef , along the forereef spur and groove region, at depths of 20-32 m. The grooves or sand channels 13-18m wide, extended between the spurs to a wide sand plain (30 m) at the top of the dropoff. The high, porous and sometimes cavernous spurs ran perpendicular to the reefcrest. The overlying substratum was covered by live corals (*Montastrea sp.*) and gorgonians. Macroalgae dominated areas of eroded limestone. Macroalgal species included *Halimeda sp.*, *Lobophora sp.*, *Microdictyon sp.*, *Dictyosphaeria cavernosa*, *Valonia sp.*, *Padina sp.* with occasional *Sargassum sp.* The currents were predominantly longshore. Water temperatures ranged from 25.2 - 29.8° C during the period of study.

Twenty-two of the 30 crabs caught during the study period were taken from a single cave at the seaward end of a spur (25 m water depth). The cave was large and cavernous, approximately 2.5 x 10 m with small (0.8m x 1.2m) interconnecting crevices hollowed out of the coral rock. These, and other smaller crevices led further in to and out of the spur. Light levels in the cave were low. Many of the crabs clung to the cave ceiling, but when approached by divers, retreated into crevices. Approximately 30-35 large crabs were observed in this cave and adjoining crevices. Four others were captured from the dropoff wall while grazing on algae, and one adult male was found in the shallow forereef (1 m water depth).

Site 3: Turks and Caicos, Caicos Bank, Long Cay

Forty crabs were captured at Site 3 by free diving and SCUBA. Nine adult males ($\bar{X}$ = 138.3 mm CL) and 26 adult females

(X = 114.2 mm CL) were taken. Five juveniles were also captured.

Site 3 adults were characterized by a heavy growth of encrusting algae on the carapace. Carapace color was a light venous red, with blue in the chela of the older adult males. Carapace thickness was relatively moderate. The crabs were very docile, and easily handled.

During 12 hours of underwater survey, approximately 25 coral heads were examined. Two coral heads were found with large populations of crabs. One small head (approximately 35 m^2) contained well over 50 crabs, mostly females and juveniles. On surrounding heads, single males were common but females were rarely encountered. The second head, not quite as densely populated, was located some 300 m away. Again, crabs were sparse on the surrounding heads. Most of the surrounding heads were similar in size and coral composition. Local fishermen do not normally harvest crabs. This site was visited on numerous occasions over a two-year period and the pattern of crab distribution remained static.

Site 4: Turks and Caicos, Grand Turk

A total of 74 crabs were captured at Site 4 using SCUBA and free diving. The 25 adult males had a mean CL of 146.8 mm (largest = 180.0 mm), and the 59 adult females a mean CL of 136.5 mm (largest = 158.2 mm).

The carapace and appendages were a deep venous red and had little or no calcareous encrustation. The adult males had comparatively large chela and although intimidating in appearance, they were very docile. Generally scarless, the chitin was relatively thicker than all but the Site 5 population. Most were caught in >20 m water depth.

SCUBA Survey, site 4

A SCUBA survey was conducted along the west coast of Grand Turk (Figure 5). A deep vertical coral covered "wall" parallels the coast. Starting with the spur and groove region at a depth of 10-20 m at the wall crest, it drops to a small shelf at approximately 100 m before dropping down to a depth of more than 1 km. The current flow is primarily offshore.

The wall was surveyed in two sectors, one north and one south of the island's main shipping point (South Dock). The northern sector (Figure 5; a) was 4 km in length. Approximately 50 hours of survey were conducted using SCUBA. This section of the wall included areas of rubble, Montastrea sp., dense soft corals (gorgonia forests), open areas with small caves and mixed coral populations. All crabs were located between depths of 17-35 m and 16 of the 24 caught were found in a fairly open area (aI), with many small, interconnected caves. This area, approximately 50 m in length, was the only one of its kind along both the north and south sectors. Crabs were found either at the entrances to crevices, or just inside them. No two crabs were found in the same crevice.

The southern sector (Figure 5; b) ran 3 km south from South Dock. Forty seven hours of SCUBA were used to survey this section. Shoreward of the wall, the reef community was dominated by Montastrea sp.. This gave way to a diversified coral reef community along the edge of the wall. The wall itself drops vertically and is characterized by a mixed community of sponges and gorgonians.

All 15 crabs were found between depths of 15-28 m, along a 300 m section (bI) of a diverse coral community dominated by Montastrea sp. Crabs were located in small crevices in the wall, between plates of the deeper Montastrea sp. and in small heads at the edge of the drop-off. In two instances, female pairs were found together in a small head. No other crabs were found together and no other crabs were found outside the 300 m section.

Juveniles were seen on numerous dives. Compared to adults, they were extremely quick and agile. All were observed on or in coral and numerous molt shells (<40 mm CL) were found at the base of small coral heads. Extensive search patterns by snorkel and diving were also carried out through the east lagoon area for juveniles and adults.

Site 5: Dominican Republic, Buen Hombre

A total of 201 crabs were collected at Site 5 by SCUBA and trapping over an 18-month period. The 57 adult males had a mean

CL of 140.2 mm and mean CL for the 125 adult females was 122.9 mm. Fourteen juvenile males and five juvenile females were captured. The largest male and female measured 168.4 mm CL and 141.7 mm CL, respectively.

Male chela were not proportionately as large as those at other sites; however, the chitin was extremely thick. It was common for males to have one or more puncture wounds on both the chela and legs. These males were more aggressive than those found at any of the other sites. About 20% of the females had puncture scars. They too, were more aggressive than females found at other sites. There appears to be a large crab predator population at Site 5, which includes hogfish, groupers, and humans. Newly molted adults at Site 5 have a carapace which is dark, dull red in color. The new spines are light colored with white tips. In both sexes, the carapace is soon encrusted with crustose or coralline algae, serpulid worms, and soft algae. All crabs captured at the site, except two newly molted individuals, had small barnacles encrusting the carapace at the gill outlet.

Trapping, Site 5

Among the total number of crabs trapped, adult females outnumbered adult males 3.5 : 1, and 81.7% were gravid at capture. The percentage of gravid females varied from a low of 55.6% in July to a high of 100% in April. Juvenile males made up 3.8% and juvenile females 1.3% of the total. Catches varied from a low of six crabs in November to a high of 34 in March. No crabs were caught during the months of December and January because of unfavorable weather conditions or technical difficulties.

SCUBA survey, Site 5

In Buen Hombre, 105 hours of SCUBA were spent examining 130 coral heads over an area divided into nine sectors (Fig. 6). The heads in sectors A, B, C and D rose from an average depth of 18 m to an average depth of approximately 12 m below the surface. These heads were approximately 50-60 m^2, and covered with macroalgae and a few soft corals present. Sectors E and F contained numerous heads with an area of approximately 70-80 m^2. These heads rose from a sandy bottom at 11-14 m and were covered with heavy coral growth, reaching up to an average depth of 3 m below the surface. Sectors G and H contained heads similar in size and growth to sectors A, B, C and D, but rose from a grassy bottom at 11-14 m. Area I contained a large diversity of heads and shoal areas in depths ranging from 3-10 m. Of the 130 coral heads examined, 19 were found to be occupied by M. spinosissimus crabs. A total of 65 crabs were found over the entire area of sectors A - I.

In the 13 coral heads found to contain adult males, there were only two instances in which more than one male was present (Table 3). In the 11 heads with a predominantly female population, seven contained more than one male. Of the six juveniles located, four were found on heads with other juvenile crabs, but only one was found on a head with adult males. Three heads (two in sector B; one in sector I) had large crab populations, but with the exception of sector I, could not be relocated. A head in sector I was revisited on numerous occasions and several adult crabs were removed for study.

Three crabs were found dead and a fourth dying. All four were adult, one was male, and all were found at different locations and times. All had apparently died where they were found. One female was on a ledge outside a crevice, the other three crabs were out in the open, more than a meter from cover. The chelae on all four were extremely worn. The chela (one chela was missing) on the moribund crab was worn to points. Upon dissection and examination of the dying individual, complete atrophication of the musculature had occurred.

In one dive outside of the nine sectors, five large males (140+) were found wandering in a sandy plain (>1 ha.) littered with dispersed small (10 m^2) heads. No females were observed.

As at Site 4, juveniles were located on numerous dives. They too, were observed to be extremely quick and agile. All were found on and in coral with the exception of one, which was (~35 mm CL) found on a gorgonian at night. Numerous molt shells (<40 mm CL) were found at the base of small coral outcrops. Molt shells were also located along the forereef area at this site, but in no particular pattern. Numerous small crabs (15-30 mm CL) were found in grouper stomachs.

In addition to the above formal search processes and trap catches, numerous snorkel searches were undertaken throughout the extensive lagoon/mangrove complex. These were undertaken primarily in a search for appropriate macroalgal feed, but any *M. spinosissimus* crabs sighted were taken.

Site 6: Dominican Republic, off Azua

At Site 6, 47 adult females, three juvenile females, and 12 juvenile males captured in traps were brought to the laboratory. The adult females had a mean CL of 122.0 mm, and the largest was 141.1 mm CL. Data for trapped adult males was unobtainable because they were marketed by the fishermen.

Crabs at this site resembled Site 5 crabs in color, but generally lacked scars. The crabs surveyed had an encrusting growth of barnacles on the carapace.

Site 7: Antigua, northeast reefs

A total of 168 crabs were collected at Site 7 by SCUBA and trapping over a 15 month period. Of 105 males, 45 were juveniles. The 60 adults had a mean CL of 131.4 mm. Forty-four adult females averaged 108.2 mm CL. There were 16 juvenile females caught. The largest male and female measured 157.4 mm CL and 127.0 mm CL respectively.

The mean of Site 7 crabs were slightly smaller in size compared to the Site 3 crabs. The VPL for adults having undergone normal molting was significantly longer than CL. Coloration was deep, venous red. Carapaces were usually free of significant encrustation by coralline algae. Epifaunal species consisted of bryozoans, small serpulid worms, an occasional sponge, and a few goose barnacles along the gill areas. Chela wear was negligible, and carapace spines were sharp. Males were generally slow, quite docile, and easily handled. Females often exhibited strong defensive behaviors, using legs and body movements to aid chelae effectiveness.

Trapping, Site 7

Of the total 168 crabs collected, 148 were caught in traps. Trapped adult males outnumbered adult females by 1.07:1. A large segment of the total were juveniles: 29.7% male and 10.1% female. A high percentage (62.8%) of the adult females were gravid and ranged from zero (N=3) caught in May to a high of 84.6% of those caught in November. No crabs were caught during the months of August and September for logistic reasons. The greatest number were caught in November (N=19), with females outnumbering males about 2:1.

SCUBA Survey, Site 7

Over 120 hours of SCUBA and skin diving surveys were conducted at several locations around Site 7. Crabs or crab remains were sighted at all locations except in algal ridges due east. Three small "pockets" of crabs were found northeast, north and west of the island. At the northeast area inside the mouth of Parham Sound (15-25 m depth), five males and one female (all adult) were captured on a 15-25 m length of an old algal ridge (dead coral) with 2-3 m (diameter) boulders. The water was turbid. At nearby spur and groove formations, no crabs were found. In a trapping area leeward of the well-developed algal ridge, two crabs were found dead in traps, but none were seen on the ridge, or in the mounds of dead Acropora sp and Montastrea sp.

At the northern end of the island, shallow (1-3 m depth) patch reefs were examined. Six males were located among the patches of Acropora sp. and Millepora sp.

On the west coast of Antigua, shallow boulders have fallen from a cliff face fronting the sea at Dickerson Bay, providing a refuge for M. spinosisimus. In the 1-2.5 m crevices in these boulders, five males and one female were captured. The area experiences strong wave action along with wakes from boating activity associated with nearby resorts.

These three small "pockets" of crabs produced a total of 16 males and two females. Crabs were not captured by SCUBA at any other locations, although four were sighted, two in a single coral head.

Seasonal Variation

Trapping results by month at Sites 5 and 7 (N > 140) showed variation in catch rates by month, sex and site (Fig. 7). At Site 5, peak catches of females occurred in March, May and November. Male catch rates were lower overall and varied less than those for females with modest peaks in March and August.

A somewhat different pattern occurred at Site 7. Overall, male catches exceeded female catches, with peaks in April, June and December. Female catches peaked in November.

Sex Ratios

Data on trapped crabs from Sites 5 and 7 showed a high degree of variation in the sex ratio between populations (see Figure 7). Females were significantly more abundant than males (t-test; $P<0.01$) at Site 5 by a factor of 3.5:1 (115 females:33 males). No significant difference (t-test; $P>0.10$) was found in the ratio of females to males (46 females:46 males) at Site 7.

Appendage Loss

Three hundred twenty five of the crabs sampled were recorded as to the total number of appendages present. Appendage loss in populations from all sites ranged from zero (complete) to six (Table 4). Of the 197 females recorded, 67 (34%) had all appendages present and of the 128 males recorded, 38 (29.7%) had all appendages present. Female crabs missing one appendage

(N=68) were 3% lighter than the complete female crabs. Those missing two appendages were 7.5% lighter. Chelae loss was considered separately from loss of walking legs in males. Males with all appendages present (N=38) had a mean CL of 137.4 mm (weight = 1607 g). They were 2.2% heavier than males with one missing leg (N=25) and 14.8% heavier than males missing both a walking leg and a chelae (N=7). We found that 26.6% of all males recorded were missing at least one cheliped (N=34).

DISCUSSION

Archaeological studies indicate a long-term presence of Mithrax spinosissimus in the Caribbean region. Collins and Morris (1976) found evidence of Mithrax spinosissimus in Pliocene and Pleistocene formations in Barbados while Rathbun (1923) found shell fragments of M. spinosissimus in Pleistocene formations in Haiti. The present-day distribution of M. spinosissimus is somewhat in question, particularly in regard to the northern limit of its range. Rathbun's (1925) description of two chelipeds found at an undetermined locality in North or South Carolina do not agree with the known ranges from these and previous studies. The possibility that these chelipeds were transported from a more southerly site should be considered.

Results from this study showed a high degree of variability in the populations of Mithrax spinosissimus throughout its range, and yet a rather narrow range of characteristics within a population. This suggests that fishing pressure, geographic isolation, genetic drift and adaptation to local conditions have played an important role in shaping the characteristics of the individual populations. Differences were particularly evident between the Florida and Caribbean populations where the Gulf Stream may act as a barrier to dispersal of crabs from the southern populations, particularly given the brief planktonic stage. While samples taken in Florida and South Caicos might have been biased by limited collection time, searches at the other sites were extensive, and it is highly unlikely that major segments of the M. spinosissimus populations could have been totally overlooked.

Despite the small sample size for some sites, results showed that the Florida population was unique in several aspects from all other populations investigated. Crabs from South Florida taken in this study were similar in size to those of previous studies (Hazlett and Rittschof, 1975; Bohnsack, 1976) and were significantly smaller than those at all other sites. Additionally, Florida crabs were different in coloration and carapace thickness. These physical characteristics may be attributed to lower water temperatures and/or different habitats, particularly adaptation to living in crevices in turbid waters.

Crabs also appear to exhibit different behavior in the

Florida vs. Caribbean populations. Hazlett and Rittschof (1975) reported that in cases of multiple occupation by crabs of a crevice in South Florida, pairs most often consisted of a male and a female and least frequently of a female and female. Bohnsack (1976) recalculated these data, correcting for small sample size, and concluded that female pairs were not rare, but male-female pairs were still more common. Bohnsack's (1976) own data agree with those of Hazlett and Rittschof (1975) in determining male-female pairs to be the most common, but he found significantly more multiple occupations of crevices by females. Pairs of males were rare. This finding differs from our observations in the Caribbean populations (Sites 2-7) in which the most common pair or group consisted of multiple females with none or a few males. These large phenotypic and behavorial differences between the Florida and Caribbean populations suggest the Florida crabs may be a subspecies.

The sizes of Caribbean crabs (Sites 2-7) found in this study were consistent with Monroe's (1974) data from Jamaica where the mean size of males was 133.4 mm CW (=130.4 mm CL) and 122.8 mm CW (=120.4 mm CL) for females. Jamaican crabs were intermediate in size among those investigated in this study and were not significantly different from the populations at Antigua (males) or Buen Hombre (females). Size does not seem to be directly related to temperature since the largest (Site 2) and the smallest (Site 7) crabs found in the Caribbean region were at the northern (cooler) and eastern (warmer) extremes respectively. However, between Mayaguana and Antigua, mean minimum temperatures are not likely to be more than a degree or two centigrade. Florida crabs were consistently smaller than any of the Caribbean crabs. They would also be subjected to winnter temperatures on the order of 5°C lower than the Caribbean sites.

Density of crabs varied by site, season and sex. Crab densities appear to be correlated with both habitat (resource availability) and social factors. In the Florida population, where crabs occupy canal wall crevices, crevice density appears to be the limiting factor in crab abundance (Hazlett and Rittschof, 1976; Bohnsack, 1977). Our studies suggest that "crevice" availability may be important in at least some areas where competition for space exists.

Fishing pressure may account for some of the observed variation in population density. In areas experiencing heavy fin-fishing pressure, crab abundance was found to be greater. Intensive fishing pressure occurs in the Dominican Republic (Site 5), Antigua (Site 7) and along the Caicos Banks (Site 3) where a commercially important fishery for spiny lobster exists. Fishing pressure may reduce crab predator abundance as suggested by Munro (1974) for Jamaica, or reduce competition for other resources such as crevice availability or food resources. By contrast, crab densities were low in areas experiencing little fishing pressure such as that found along the west coast of Grand Turk (Site 4), an area protected from fishing. While large adult crabs, as nocturnal grazers, are probably relatively free from heavy fish predation, few juveniles are likely to recruit to adults when fish predation is heavy.

Seasonal variation in trapped crab abundance has been observed by Munro (1974) for Jamaican crabs and at Sites 5 and 7 in this study. Munro (1974) found higher catches for crabs in March/April, June/July and November/December over a two year trapping period. Catches at Sites 5 and 7 showed seasonal fluctuations, particularly at Buen Hombre (Site 5). Part of the fluctuation at site 5 is due to the shift by fishermen in Buen Hombre to agricultural and other landbased occupations in the fall and winter (Stoffle, 1986). The decline in catch rates, particularly for females, probably reflects this declining effort by the fishermen versus an actual seasonal variation in the population density.

Results from trapping studies at Site 5, in which females were caught at a rate of 3.5:1, indicate a bias towards females in this population. Assuming a 1:1 sex ratio at recruitment, this suggests that there is a differential mortality rate for the sexes at this site or that "excess" males move away from the area. Hazlett and Rittschof (1975) found in the Florida population that males moved more frequently, had a larger home range and a greater activity radius than females. In our studies, "bachelor" males were more often found far from their crevices, generally alone. Trap effect may also account for some of the variability if inter-male aggression influences the probability of more than one male entering the trap. Only one recorded instance of two males in a trap occurred at Site 5, although Munro (1974) reports several males captured at a time in his Jamaican trap study.

Not all sites showed the same sex ratios. There was no difference found in the sex ratio at Antigua (Site 7) and males outnumbered females almost 2:1 in trap catches in Jamaica (Munro, 1974). Variation in the sex ratio between sites suggests other factors such as fishing pressure or intraspecific competition contribute to a population's sex ratio. Fishing pressure may be of particular importance in the Dominican Republic and South Caicos where large male M. spinosissimus are locally marketed.

M. spinosissimus is generally gregarious, usually with pairs or several individuals occupying a cave or crevice. Bohnsack (1976) found that about 55% of the occupied holes in his study contained crabs in clusters of 2-11 individuals. On the basis of his results, he suggested that agression occurs between males since only one of 42 clusters examined had more than one male. Hazlett and Rittschof (1975) found a negative relationship between average day-to-day movement for males and male density, a relationship not observed for females. Our studies also support the concept of a gregarious social structure with males apparently holding a "harem" of one to several females. Multiple occupation of crevices by females was commonly observed at Sites 2, 3, 4 and 5. At Site 5, female-female pairs were encountered most often, with as many as five females found in a crevice. Males were found more than one to a crevice in only two instances: the cave at Site 2, and a large hole (1 m x 2 m) on head I1, Site 5. Divers examining "harem" heads after trapping commonly found continued high female populations, with three or four females sharing a small coral outcrop. At one of these heads, a single unbaited trap was placed at the edge of the grazing ring, resulting in seven females (six gravid) caught after a two-day set. Females were seldom caught individually, but as previously noted, two males in a trap were rare.

Mariculture experiments at Sites 4, 5 and 7 showed little aggression in the captive populations. Crabs were reared from egg and stocked in large growout cages (1.3 m x 1.3 m x 2.6 m) with as many as 25-35 crabs per cage. Brood stocks of wild crabs were maintained in holding cages (1.3 m x 1.3 m x 0.75 m) and were stocked with 10-12 crabs, usually consisting of one male and several females. One instance of mortality assumed to have resulted from aggression was noted at Grand Turk, when a recently introduced male was found dead in a holding cage containing one male and several females. Otherwise, aggression was not observed in the captive adult populations.

A considerable percentage (66% females; 69.1% males) of the adult population is found without walking legs and/or chelipeds, suggesting some non-mortal predation and the ability to continue with less mobility and feeding potential. The frequency of highly worn claws and encrusted shells and algae suggests a relatively long life span once an animal has reached adulthood. A relatively large number of old, apparently moribund crabs also suggests moderate predation of adults. The population data occasionally suggest a second molt in males.

The differences observed among the populations in this study suggest that present-day populations have been isolated for a long period of time and represent separate stocks of this species. The large differences between the Florida (Site 1) and Caribbean (Sites 2-7) populations may be the result of environmental, geographic and hydrologic factors coupled with the species short planktonic stage. The Caribbean region is characterized in general, by volcanic islands (Antillean), or groups of islands on broad, shallow banks (Bahamian) separated by deep channels such as that between South Caicos (Site 3) and Grand Turk (Site 4) and between these sites and the Domincan Republic (Site 5). These natural barriers presumably restrict interchange between the populations.

The possibility of larval exchange between the populations is limited by the short duration (< 125 hr) of the free-swimming planktonic stage (Provenzano and Brownell, 1977; Porter _et_ _al_., 1987) which permits little opportunity for dispersal of the larvae over long distances. Sastry (1983) states that restocking of benthic crustacean populations generally occurs from the larvae retained within the geographic range of the species. Given the extremely brief planktonic stage of this species and limited movement of the benthic population, it seems likely that restocking of _M. spinosissimus_ populations generally occurs from larvae retained within the restricted range of each individual population.

Recruitment, then, must come from the offspring of the local adult population. At all sites, juveniles were found to inhabit the same areas as adults. They were abundant at Sites 5, 6 and 7, where trapping of crabs was successful. Scarcity of juveniles reported in previous studies such as those of Munro (1974) may be due to the cryptic nature of the juveniles. Juvenile _M. spinosissimus_ smaller than 20 mm CL generally decorate their carapaces with algae and inhabit small crevices, making them difficult to detect. Munro (1976) failed to locate juveniles by diving or capture in traps but reported the occurrence of several juveniles in the stomachs of the red hind _Epinephelus guttatus_. Juveniles were located in the stomachs of groupers (Site 5) in this study. Traps were generally successful for capturing larger (> 60 mm CL) juveniles, but were used only at three sites.

Our studies show that variation in size, sex, social structure, abundance and presumably recruitment of M. spinosissimus must be considered for individual populations in any fishery model of this crab in the Caribbean. The variation observed throughout the region suggests little exchange between the populations. If each population is a separate stock, the potential exists for rapid decline in local populations experiencing heavy exploitation. On the other hand, the crabs are easily bred, and considerable opportunities exist for stock "improvement."

CONCLUSIONS

Information on the size, sex ratio, abundance and ecology of M. spinosissimus has been reported. A high degree of variation, particularly between the Florida (Site 1) and Caribbean (Sites 2-7) populations, was observed. This suggests populations have been isolated for a long period of time and little genetic exchange occurs between the separate stocks. The Florida population is significantly smaller than any other population sampled and differs from Caribbean/West Indian M. spinosissimus in a number of morphological and behaviorial features.

In the Caribbean/West Indian region, adult Mithrax spinosissimus populations are bimodally distributed with males approximately 15-25% larger (CL) than females. These nocturnal crabs inhabit caves or crevices in coral reef habitats and usually consist of a single male with a "harem" of several females. In spite of this social structure, serious adult inter-male aggression seems rare, even when confined to cages.

Crab abundance varies by site, sex and season. Factors affecting abundance appear to be crevice availability (directly proportional) and fishing pressure (inversely proportional). A large number of females are found gravid year-round. Juveniles are rarely seen in the wild, probably due to their cryptic habits and in the earliest instars algal decoration.

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LEGENDS

FIGURE 1. Map of Caribbean, showing seven study sites. 1 = Grassy Key, Florida; 2 = Mayaguana, Bahamas; 3 = South Caicos, Turks and Caicos, B.W.I.; 4 = Grand Turk, Turks and Caicos Islands, B.W.I.; 5 = Buen Hombre, Dominican Republic; 6 = Azua, Dominican Republic; 7 = Antigua, W.I.

FIGURE 2. Histogram plot of CL (mm) for adult male and female crabs from Buen Hombre, Dominican Republic (site 5).

FIGURE 3. Histogram plot of CL (mm) for trapped adult male and female crabs from Antigua, W.I. (site 7).

FIGURE 4. Histogram plot of CL (mm) for immature trapped crabs from Antigua, W.I. (site 7).

FIGURE 5. Map of Grand Turk, showing survey areas along western wall; a = "north sector"; b = "south sector." a = 11 females, 10 males captured; a_2 = 3 females captured; b_1 = 6 females, 9 males captured.

FIGURE 6. Map of coral reef (forereef, reef crest and back reef) area around Buen Hombre, Domincan Republic showing nine sectors surveyed by SCUBA (site 5). (Sectors A-D: 18 meters depth; E-H: 12 meters depth; I: 10 meters) See text for description of sectors.

FIGURE 7. Number of trapped male and female crabs by month at sites 5 and 7.

TABLE 1. Number, S.D., and range of CL for each site.

TABLE 2. Results of ANOVA.

TABLE 3. Results of SCUBA survey.

TABLE 4. Percent appendage loss.

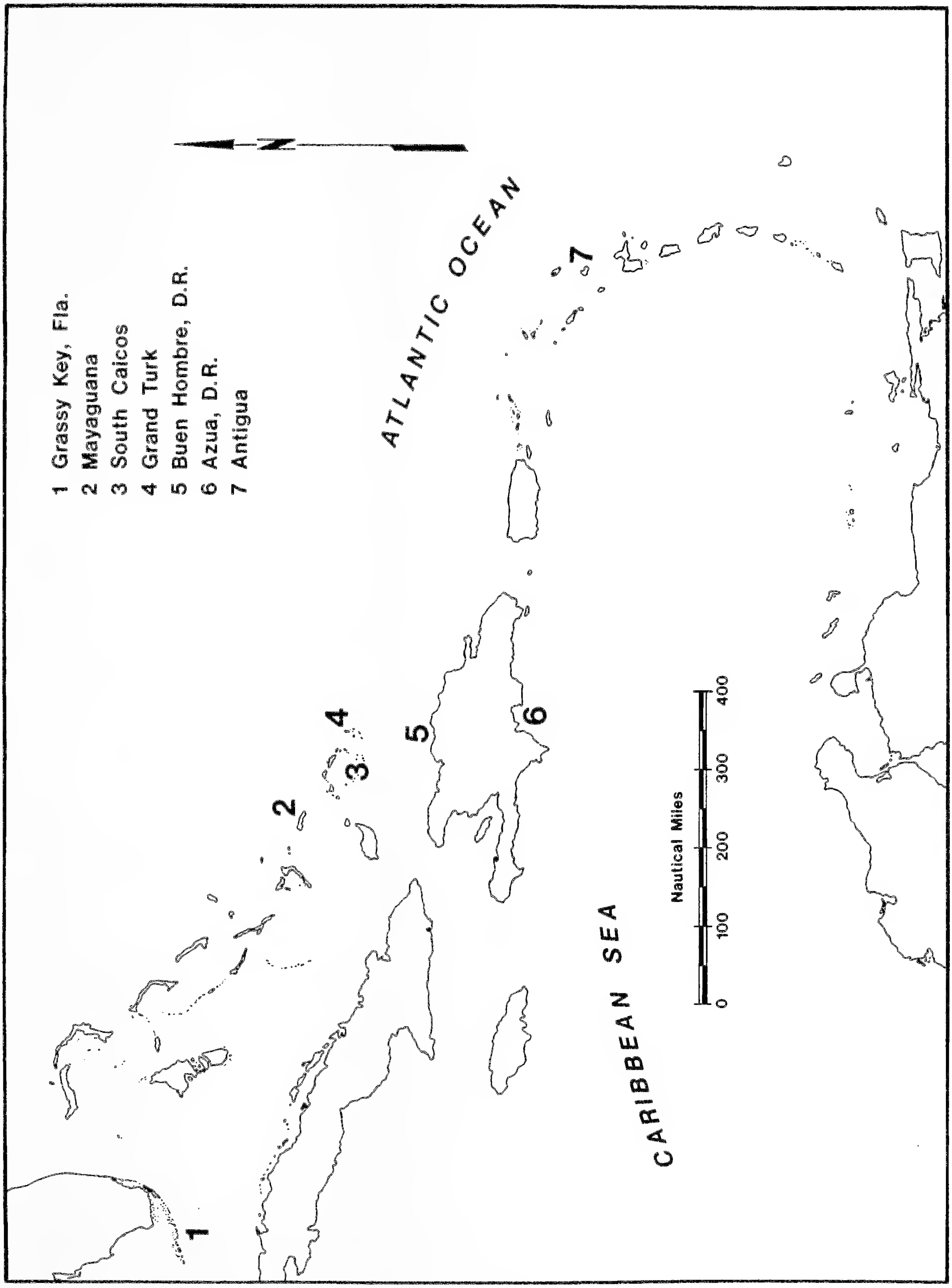

N
1 Grassy Key, Fla.
2 Mayaguana
3 South Caicos
4 Grand Turk
5 Buen Hombre, D.R.
6 Azua, D.R.
7 Antigua
ATLANTIC OCEAN
CARIBBEAN SEA
Nautical Miles
0
100
200
300
400
1
2
3
4
5
6
7

Figure 1

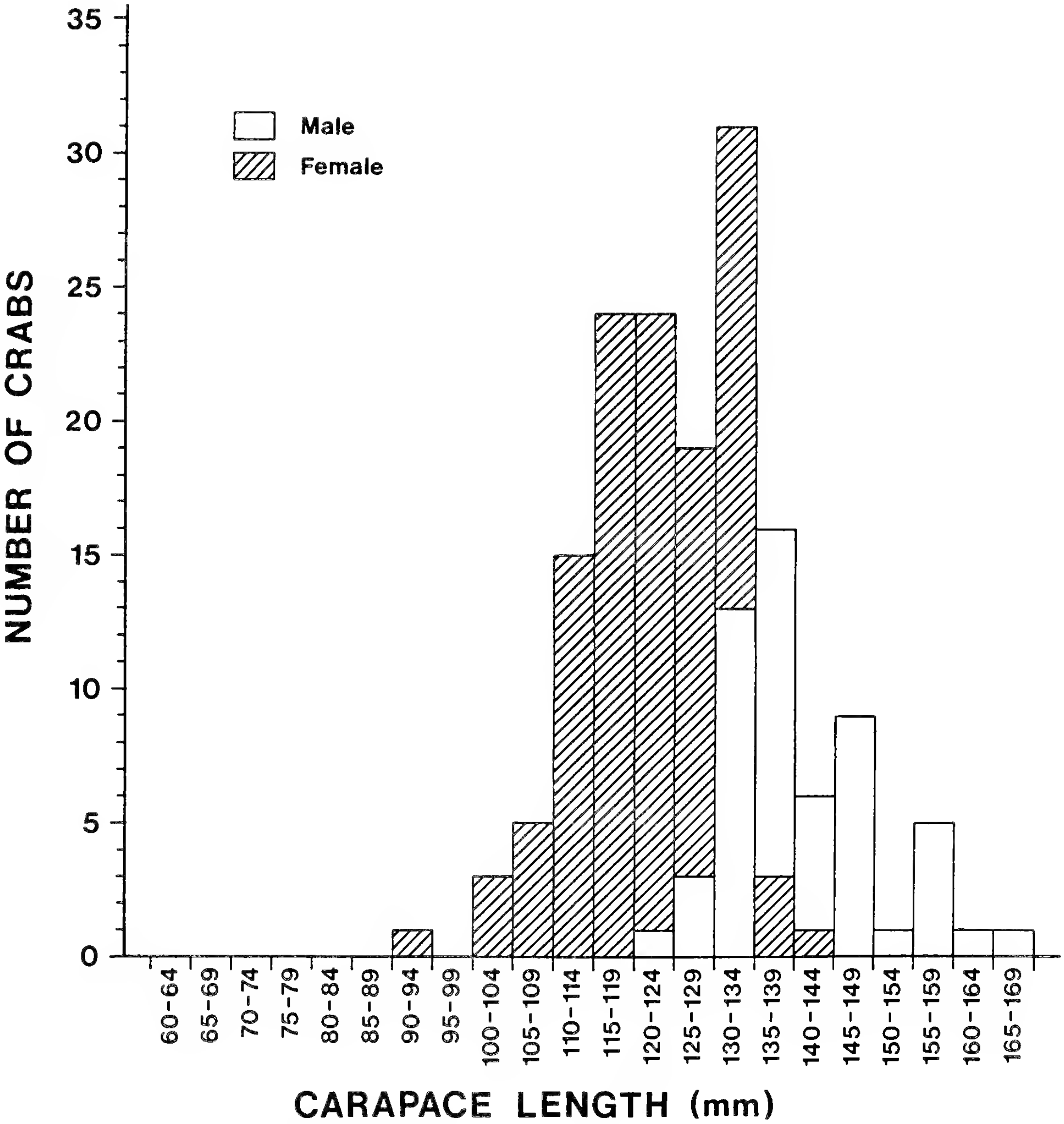

NUMBER OF CRABS
35
30
25
20
15
10
5
0
Male
Female
60-64
65-69
70-74
75-79
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144
145-149
150-154
155-159
160-164
165-169
CARAPACE LENGTH (mm)

Figure 2

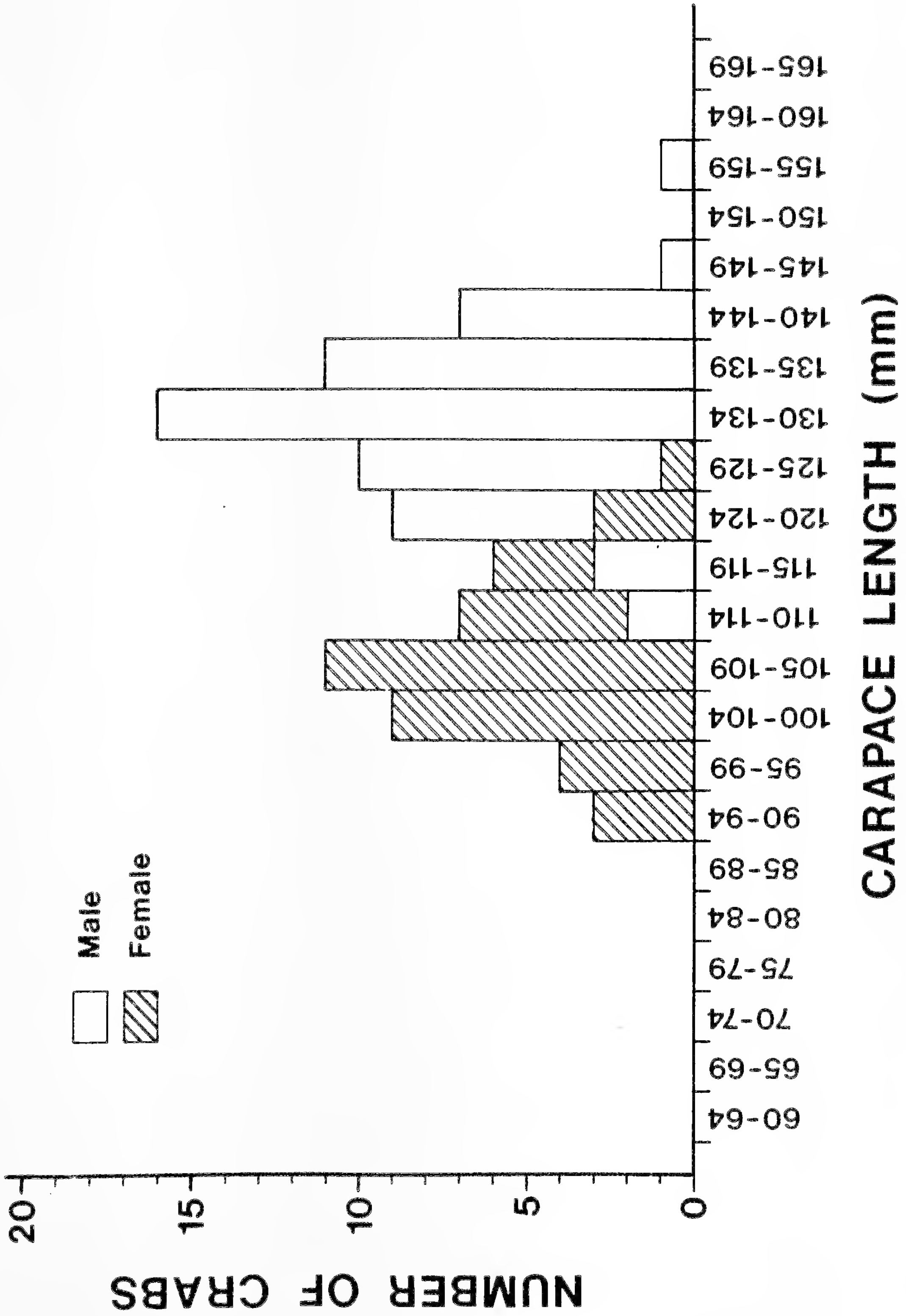

NUMBER OF CRABS
20
15
10
5
0
Male
Female
60-64
65-69
70-74
75-79
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144
145-149
150-154
155-159
160-164
165-169
CARAPACE LENGTH (mm)

Figure 3

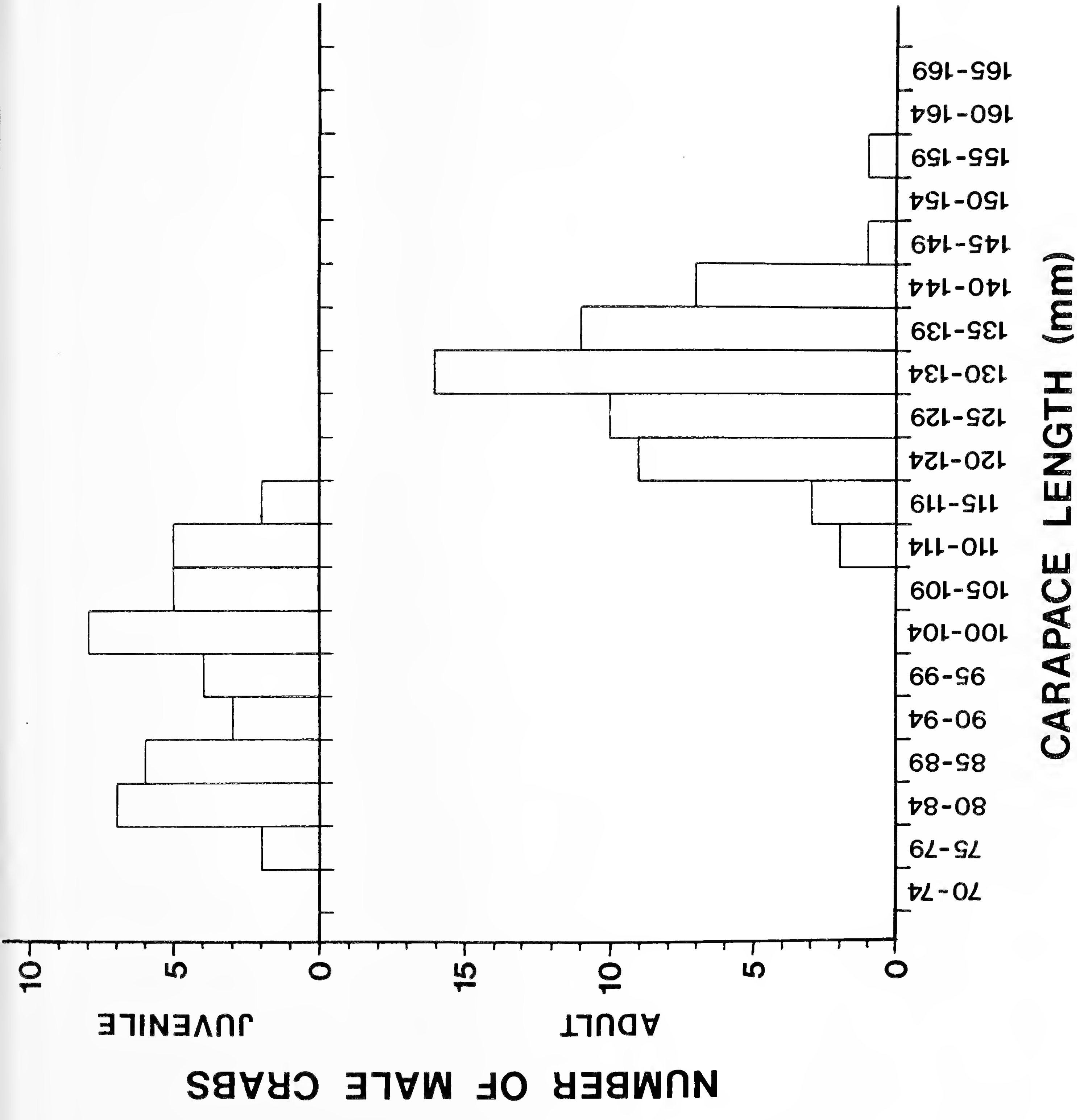

CARAPACE LENGTH (mm)
70-74
75-79
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144
145-149
150-154
155-159
160-164
165-169
NUMBER OF MALE CRABS
ADULT
0
5
10
15
JUVENILE
0
5
10

Figure 4

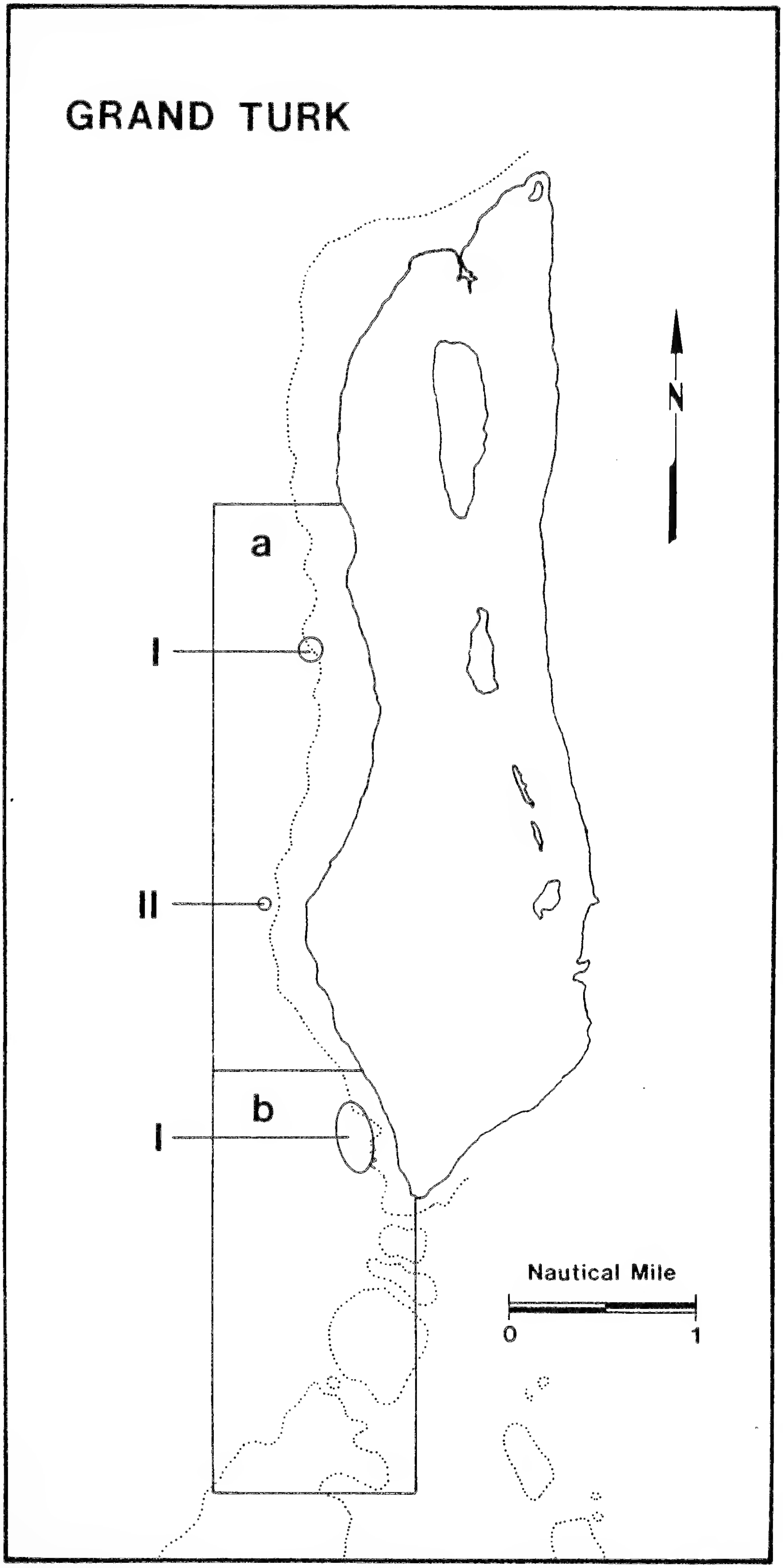


Figure 5

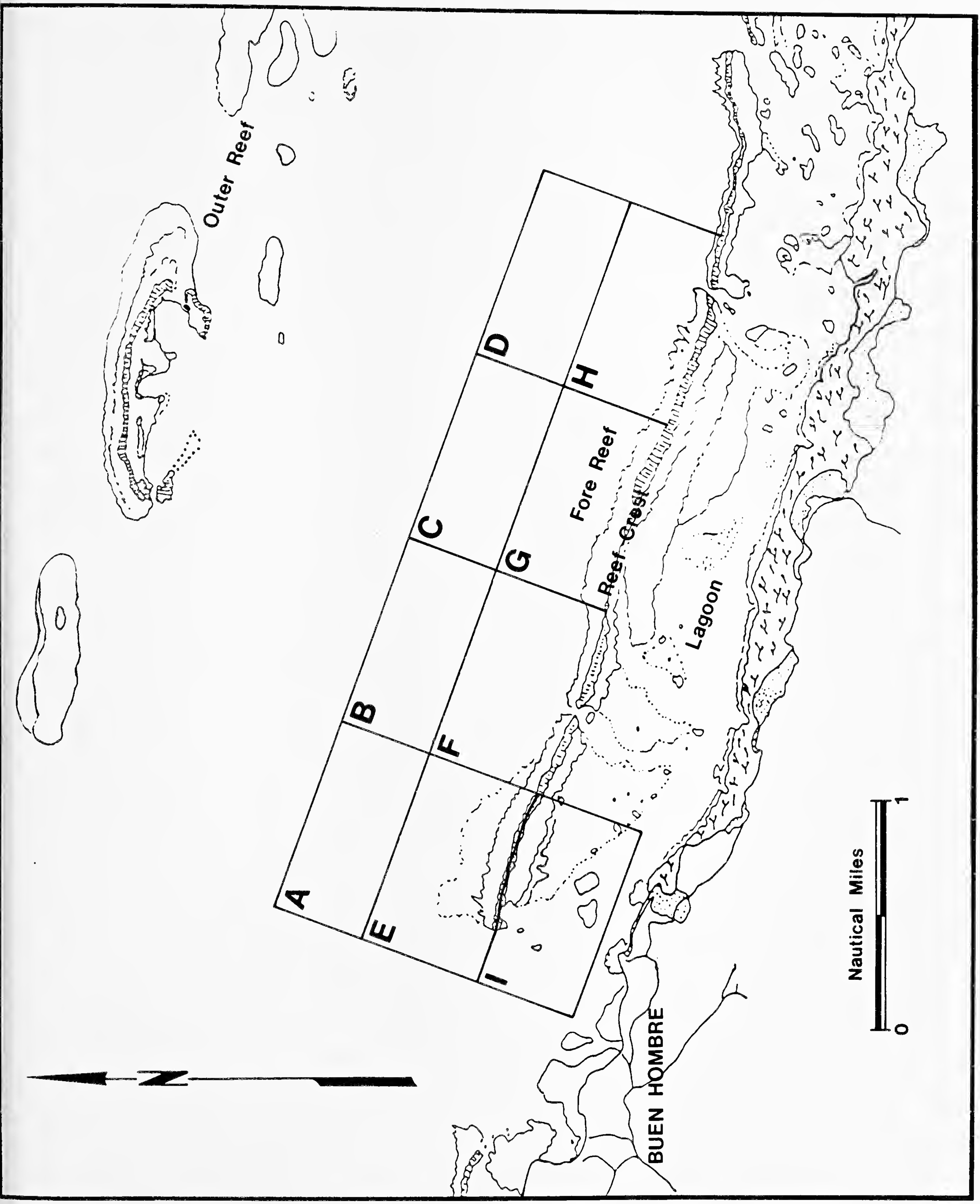
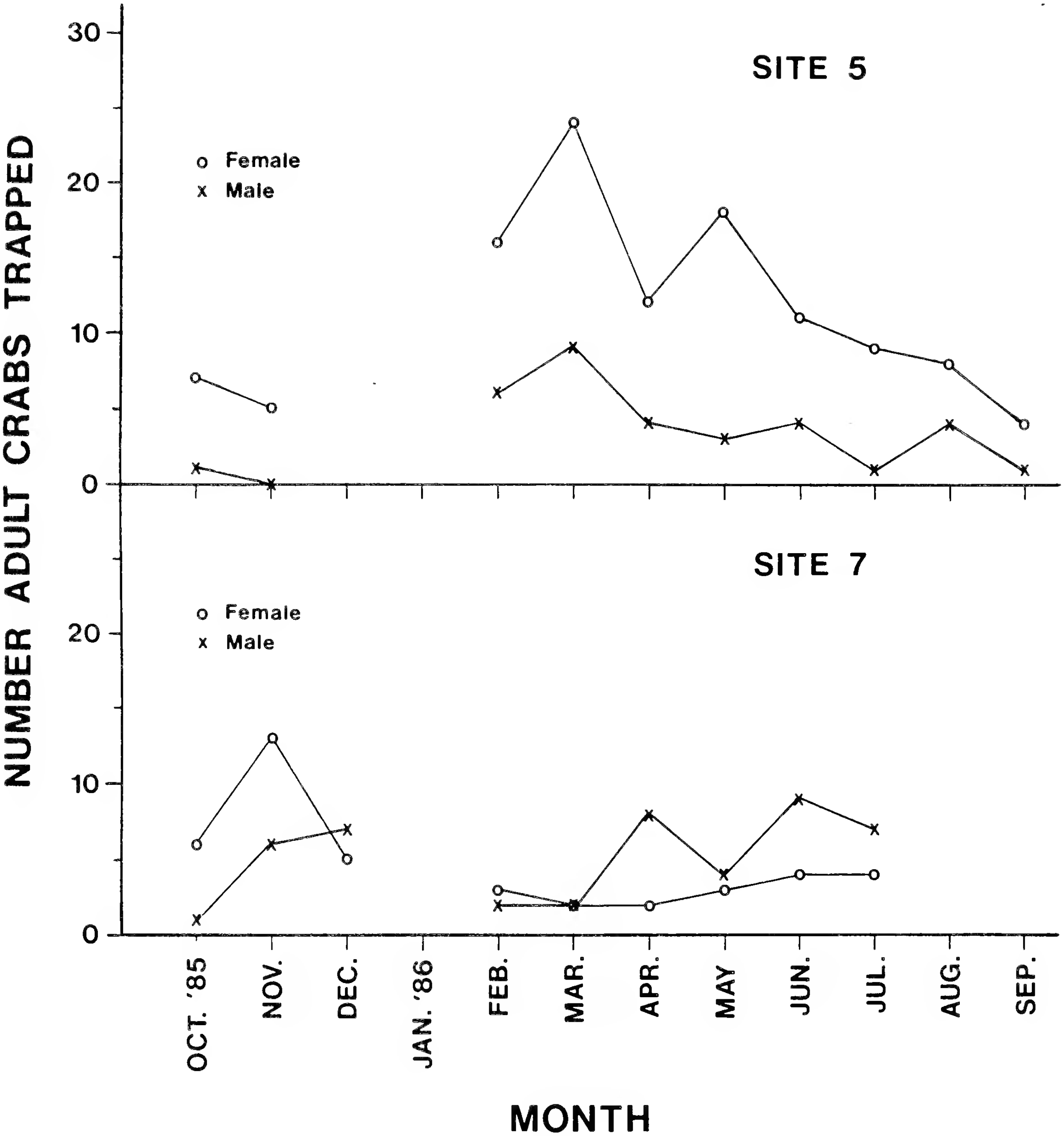

Outer Reef
A
B
C
D
E
F
G
H
I
Fore Reef
Reef Crest
Lagoon
BUEN HOMBRE
N
Nautical Miles
0
1

Figure 6



NUMBER ADULT CRABS TRAPPED
30
20
10
0
SITE 5
o Female
x Male
SITE 7
o Female
x Male
20
10
0
OCT. '85
NOV.
DEC.
JAN. '86
FEB.
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP.
MONTH

Figure 7

TABLE 1. Mean, S.D. and range of CL (mm) for adult male and female *Mithrax spinosissimus* for each site. See text for description of sites.

Site	sex	N	mean (mm)	SD	Range (mm)
1	M	10	98.8	14.8	79.6 - 110.0
	F	18	83.5	9.9	65.7 - 94.9
2	M	6	166.9	17.3	141.0 - 190.5
	F	5	140.6	20.9	114.3 - 165.0
3	M	9	138.3	8.3	127.0 - 148.0
	F	26	114.2	10.0	93.8 - 136.6
4	M	25	146.8	22.0	104.1 - 180.0
	F	59	136.5	9.7	114.6 - 158.2
5	M	56	140.4	9.7	121.0 - 168.4
	F	126	122.9	8.9	91.6 - 141.7
6	F	47	122.0	8.7	106.3 - 141.1
7	M	60	131.4	8.7	112.1 - 157.4
	F	44	108.2	8.7	90.3 - 127.0

TABLE 2. Results of analysis of variance used to test for differences in CL (mm) for adult males and females between sites (excluding site 6). Subsets (S) with different letters are significantly different (Duncan's multiple range; $P< 0.05$); DF=5. An asterisk (*) indicates that males and females within a site are significantly different in size (t-test; $P< 0.05$).

	MALE		FEMALE	
Sites	Mean	S	Mean	S
1	98.8	A*	83.5	A*
2	166.9	B*	140.6	B*
3	138.3	C*	114.2	C*
4	146.9	D*	136.5	D*
5	140.4	C*	122.9	E*
7	131.4	E*	108.2	F*

TABLE 3. Results of 105 hours of SCUBA survey in Buen Hombre, Dominican Republic (site 5).

SECTOR	# OF CORAL HEADS	MALES	FEMALES	JUVENILES	TOTAL CRABS
A	1	1	1	-	1
	2-17	-	-	-	0
B	1	-	8	1	9
	2	-	3	-	3
	3	1	1	-	2
	4	-	3	1	4
	5	1	3	-	4
	6	1	7	-	8
	7	3	1	-	4
	8	1	-	-	1
	9-29	-	-	-	0
C	1	1	-	-	1
	2	1	-	-	1
	3	1	-	-	1
	4-27	-	-	-	0
D	1-2	-	-	-	0
E	1	1	2	-	3
	2	-	-	-	0
F	1	-	1	1	2
	2-13	-	-	-	0
G	1	1	-	-	1
	2	-	-	1	1
	3-28	-	-	-	0
H	1-2	-	-	-	0
I	1	9	7	1	17
	2	1	-	-	1
	3	-	-	1	1
	4-10	-	-	-	0
Total:	130	23	37	6	65

TABLE 4. Percent appendage loss for adult male and female crabs from all sites. Chelae and walking legs are treated separately for males only.

CRAB	N	% CHELAE LOST		% WALKING LEGS LOST						
		1	2	0	1	2	3	4	5	6
MALE	128	20.3	6.3	29.7	23.4	16.4	2.3	1.6	--	--
FEMALE	197	--	--	34.0	35.0	16.8	9.1	4.6	--	0.5

SECTION II: BIOLOGY AND ECOLOGY OF MITHRAX SPINOSISSIMUS

REPRODUCTIVE BIOLOGY, FECUNDITY AND EMBRYONIC DEVELOPMENT OF M. SPINOSISSIMUS.

REPRODUCTIVE BIOLOGY, FECUNDITY AND EMBRYONIC DEVELOPMENT OF MITHRAX SPINOSISSIMUS

M.P. Craig, K.L. Porter, R.V. Ruark and J.M. Iglehart

Abstract

The reproductive morphology, size of female and clutch at maturity, fecundity, seasonality of reproductive effort, embryogenesis and duration of egg incubation were investigated for the tropical Majid crab, Mithrax spinosissimus. Crabs were collected from the Dominican Republic, Antigua, the Turks and Caicos Islands, and the Florida Keys.

Mithrax spinosissimus is sexually dimorphic. The male prepubertal instar ranges in carapace length (CL) from 80.0-115.0 mm. The mean CL of ovigerous crabs ranges from 83.5-137.5 mm depending on the study site. The mean CL of mature males ranged from 93.9-146.7 mm. Reproductive capability was determined to be year round. Captive crabs were observed to mate during the intermolt period while positioned ventrally to each other. Female M. spinosissimus have the capability to store spermatazoa for long periods of time. Mean clutch size is 6.0639 X 10^4 eggs (S.E.=3025; N=20).

Embryogenesis is divided into five distinctly observed stages which develop over a mean time period of 29.5 days (S.D=0.5; N=4). All larvae were hatched within 12-16 hours. The mean interval of time between hatching of eggs and the spawning of a new batch was 61.9 days (S.D.=19.6; N=247). Each female had an average 3.75 hatches over a 10 month period in captivity. It is concluded that the reproductive capacity of Mithrax spinosissimus appears relatively unaffected by conditions of captivity. All reproductive characteristics of M. spinosissimus are suitable for mariculture.

INTRODUCTION

The molt of puberty or maturation molt denotes reproductive capability in Majidae (Hartnoll, 1963; Ingle, 1983) and may be attained after 16-20 postlarval molts in Brachyura (e.g., Callinectes sapidus or blue crabs: Van Engel, 1958). Hartnoll

(1965) found female members of the Majidae from tropical waters (including Mithrax sculptus) only able to physically mate and reproduce after the maturation molt. Terminal anecdysis or the cessation of molting is said to coincide with the maturation molt in Majidae (Hartnoll, 1963, 1965, 1974). In Mithrax sculptus, the maturation molt (Hartnoll, 1965a) is accompanied by distinct external morphological changes in the chelae of males and by a variety of changes in the shape and function of the abdomen, pleopoda, sternum and gonopores of females. An internal change occurs in the males' sperm ducts, the posterior part of the genital tract. They characteristically appear pale and translucent when immature, whereas in mature males, the sperm ducts become swollen and assume an opaque white appearance indicating the presence of mature sperm. In females, the maturation of the ovaries is evident by marked changes in the developing ova. The diameter of the ova increases as much as eight times before spawning and the color changes as the yolk is deposited (Hartnoll, 1965a).

Usually, maturation of the gonads is considered to coincide with the development of certain anatomical characteristics. However, Hartnoll (1965b) mentions that some of the larger prepubertal Mithrax sculptus and Microphrys bicornutus, both Majids, had partly swollen sperm ducts which contained ripe sperm. In males of the Majid crabs Inachus and Macropodia and in females of Pisa tetraodan, the gonads of some prepubertal crabs were maturing before the maturation molt and in Hyas coarctatus the females' gonads always began to mature prior to the maturation molt (Hartnoll, 1963, 1965b). Little information has been published concerning maturation of M. spinosissimus, but it has been assumed to be characteristic of the order and family.

Teissier (1935) describes a critical molt preceeding the maturation molt in Maia squinado and considered this "molt of pre-puberty" or the pre-pubertal instar, to mark the first differentiation of relative growth rates between the sexes. The final molt, the maturation molt occurs three molts later. In Pisa tetraodan, Vernet-Cornubert (1958) was able to show that the maturation molt occurs over a range of carapace lengths (CL) and may be from the first to third molt after the pre-pubertal instar. In a boreal crab Hyas coarctatus the maturation molt occurs during particular seasons of the year. Where mating occurs only during a particular season, Hartnoll (1963) found the time of year and the size of the individual at the instance of molting contributing factors in determining whether a crab will make a further normal molt after pre-pubertal instar or will undergo the maturation molt directly. Crabs of similar size were found to undergo a normal molt or reach the pre-pubertal instar at the same time, indicating that other factors may contribute to the timing of the maturation molt. In four Majid species Hyas coarctatus, Inachus dorsettensis, Macropodia rostrata and

Microphrys bicornutus, it was found that at the same time and within the same population of each species, specimens of very different size were undergoing the maturation molt (Hartnoll, 1963).

Hartnoll (1965a) observed throughout the Majidae studied that the maturation molt occurred over a large range of carapace lengths. Among a group of Mithrax sculptus, differences in mm CL between the largest and the smallest postpubertal crab, represented as the largest being a percentage of the smallest, was 162% for females and 314% for males (min 8 mm, max 13 mm; min 7 mm, max 22 mm). The length of post-pubertal specimens has been shown to vary between separate populations of a species within the same region (e.g., Hyas coarctatus Leach around the Isle of Man) but even when a single population was studied from a very limited area (e.g., Microphrys bicornutus in Kingston Harbor, Jamaica), these same large variations were still apparent (Hartnoll, 1965b). Munro (1974) found ovigerous Mithrax spinosissimus females from Jamaica to average 125.3 mm carapace width (CW) and he believed this to be the mean size after the maturation molt.

A considerable increase in chelae size relative to carapace length occurs during the maturation of M. spinosissimus males, but is not noted in the females. Bohnsack (1976) decided that Mithrax spinosissmus males from a Florida canal population may be mature based on increased cheliped size, once carapace width (CW) is near 80.0 mm, though he did not examine sperm ducts for mature sperm. Brownell, et al. (1977) reported a 94 mm CL male specimen from Venezuela with small chelae to be sexually active before it molted to a 115 mm CL having proportionally larger chelae.

Courtship in the Brachyura may involve a series of visual, tactile, auditory and/or chemical signals. The male distinquishes a female from a potential aggressor male crab by the female cheliped size and more than likely, also by olfactory signals or pheromones which are released by the sexually receptive female (Warner, 1977).

Copulation in Brachyuran crabs occur during different phases of the molting cycle, the phases being species specific. Females of Carcinus maenas and Cancer pagurus, Cancrid crabs, copulate soon after molting while their integument is soft. Females of Hyas coarctatus and Maia squinado, both Majids, mate in either the soft or hard shelled state (Hartnoll, 1965b). Other Majid crab species, i.e., Pisa tetraodon and P. corystes, mate when hard shelled (Hartnoll, 1963, 1969; Ingle 1983).

In matings where both male and female have hard exoskeletons, duration of copulation is measured in minutes rather than in days, a characteristic of those species copulating only when the female has just molted (Hartnoll, 1969). Corystes cassivelaunus, a Corystid crab, can only mate for a 12-20 day period during the intermolt when the opercula of the gonopores become decalcified (Hartnoll, 1968b). No data is available in the literature with regard to the conditions required for Mithrax spinosissmus mating.

During copulation, many crabs face each other ventrally, generally with the male clasping the female. The male is positioned so that the posterior of his body is between the females abdomen and sternum. His abdomen is unfolded and his first pleopods are inserted into the genital openings of the female (Warner, 1977). In Brachyurans, the female may receive spermatozoa as packets or spermatophores for storage in spermathecae. Consecutive egg broods can be fertilized using the stored sperm. For example, one female Mithrax hispidus was observed to have laid three batches of eggs in the absence of a male of that same species (pers. obs.). Van Engel (1958) found sperm to survive for at least one year in the seminal receptacles of several crab species. Moreover, females of Corystes cassivelaunus can store sperm for a year and then mate again (Hartnoll, 1968b). Munro (1974) suggested, due to the capability of Mithrax spinosissimus to store spermatozoa in spermathecae for multiple fertilizations of egg broods, it may only be necessary for mating to occur only once in its lifetime. Hartnoll (1965b), suggested for the Majids he studied, one copulation can fertilize a succession of spawnings and is probably sufficient for all the eggs a female will produce during her lifetime.

The potential number of batches of eggs carried during a year is related to the incubation time and the time interval between spawnings. The interval between mating and spawning may range from days (Corystes cassivelaunas) to months (Cancer pagurus) (Ingle, 1983). Luachus and Macropodia, Majid crabs, incubate eggs for approximately three months and breed continuously, producing at least three sets of eggs per year (Hartnoll, 1963).

There was no indication of seasonal breeding activity in the five Jamaican Majids studied by Hartnoll (1965a). In nearly every sample collected from December to July, all of the post-pubertal females were ovigerous. He also suggests there is continuous breeding in these tropical Majids, with a succession of incubations extending from the maturation molt to the death of the crab. In four of the five species where successive sets of eggs were recorded (during an undescribed part of an eight month experiment), he found Macrocoeloma trispinosum to have three sets with an incubation time of 13 to 14 days each; Microphrys bicornutus, four sets with 10 to 13 days incubation; Mithrax sculptus, two sets with 11 to 13 days incubation; and Stenorhynchus seticornis, three sets with 12 days incubation. There was little delay between hatching and spawning.

Maia squinado, a boreal crab of similar carapace length to Mithrax spinosissimus, carries only one batch of eggs per year (Hartnoll, 1963). However, Mediterranean populations of Pisa tetraodon have been observed to carry six to eight batches of eggs per year (Vernet-Cornubert, 1958; Ingle, 1983). Brownell, et al., (1977) observed an individual M. spinosissimus female to produce three consecutive broods of eggs at one month intervals while in captivity.

Several authors report observing ovigerous M. spinosissimus during particular months of the year. Ovigerous crabs were observed in January (Brownell and Provenzano, 1977); February to August (Brownell, et al., 1977); May and June (Rathbun, 1925); August through November (Bohnsack, 1976); and year-round (Munro, 1974).

For some tropical crabs, usually land crabs, reproduction follows the lunar cycle (29.5 days between full moons or 14.8 days between spring tides) with larval hatching timed to coincide with spring tides (Warner, 1967; Gifford, 1962).

Majid crabs generally produce large numbers of eggs. A 130 mm CL specimen of Maia squinado produced approximately 156,000 eggs at its annual spawning (Hartnoll, 1963), while a 127 mm CW specimen of Cancer pagurus, a Cancrid crab, produced 1,000,000 eggs (Edwards, 1978). Munro estimated M. spinosissimus brood size at 50,000 eggs for females of 122.8 mm CW caught in waters off Jamaica (Munro, 1974).

The proteinaceous yolk and lipid vesicles containing carotenoid pigments give crab eggs their characteristic coloration throughout incubation (Anderson, 1982). The eyes and pigment spots appear first, followed by the outlines of the abdomen and cephalothorax (Warner, 1967).

Little published data has been available concerning *Mithrax spinosissimus* size at maturity, reproductive morphology, fecundity, seasonality of reproductive effort, embryogenesis and duration of egg incubation. This study was carried out, in part, to provide answers to these critical questions.

METHODS

The *Mithrax spinosissimus* specimens examined in this study were collected in traps and by SCUBA divers from five study sites with depths ranging from 6-10 meters on the north coast of the Dominican Republic (19° 80' N; 71° 20' W) (Site 1), 1-180 m in Antigua (17° 10' N; 61° 43' W) (Site 2), 10-25 m in Grand Turk (21° 90' N; 71° 10' W) (Site 3), 2-5 meters in South Caicos (21° 80' N; 71° 30' W) (Site 4) and 1-3 meters at Grassy Key, Florida (24° 80' N; 81° 05' W) (Site 5). Each crab was weighed, measured and tagged. For identification, colored plastic cable or "zip ties" were fastened around the merus of one or two walking legs. Lost appendages and other distinctive physical characteristics were recorded, as well. Specimens were sexed and the state of maturity was determined for each crab. For purposes of table and graph construction, male maturity was determined to be the point when ventral propodus length (VPL) becomes approximately equal to or greater than the carapace length (CL) after molting

(Iglehart, et al., this volume). Females were considered mature if their abdomen completely covered their sternum. It was also determined whether or not the mature females were gravid; for gravid crabs the egg mass characteristics were recorded.

After initial data collection, crabs were introduced into 4.0' X 4.0' X 8.0' wooden cages covered with 1/4-1" mesh black plastic screen. The cages floated with their tops at the surface, and were anchored in protected lagoonal or back reef environments. Crabs were fed diets of screen-grown turf algae (Adey and Hackney, this volume).

Non-gravid females were kept with mature males until the females were observed to have eggs. None of the mature females were isolated to determine the number of broods from one copulation. Ovigerous females were transferred to cages without males and egg development was observed to determine the time to hatching. When close to hatching (one to three days), as determined by the egg color, the gravid female was put into a "hatch cage" separate from other females. After hatching, the female was then returned to a cage containing males and other females. Several ovigerous crabs were dissected to examine reproductive structure and to gather data on brood characteristics and egg development.

Brood size was determined by two methods: 1) individually counting all of the eggs in a brood from four individual crabs and 2) by replicate calculations of dry and wet weight determinations of individual eggs and the entire egg mass. Dry weights (24 hours at 80°C) of an entire brood and of five samples of 20 eggs were determined from the egg masses of six more female broods. Wet weight was determined after blotting eggs for 10 seconds. A Mettler electrobalance (model PC 8000) was used for weight determinations. Results were presented as individual egg weights (dry) and total brood egg number, calculated from the total brood dry weight to individual egg weight proportion. A wet weight to dry weight ratio was also determined from mean individual egg wet and dry weights. The egg mass and total number of eggs for 20 females was determined by weighing the females both pre and post hatch. The difference was considered the brood wet weight. The brood size was determined using the calculated wet weight to dry weight ratios and the mean (dry) individual egg weight.

Approximate intervals for marked changes in gross egg characteristics were determined from observations of live and preserved fertilized eggs selected from broods throughout their incubation. Eggs were removed every two days, until the day of hatch, from the broods of several ovigerous females from just after extrusion onto the pleopodal endopodites. These were fixed in 5% buffered formalin and then transferred to 70% isopropyl alcohol. External changes in the eggs were studied using a dissecting microscope.

Duration of egg incubation was determined as the length of time between the exact date of extrusion of the eggs onto the pleopods and the hatch date. Data for time intervals between any successive viable hatches from individual tagged females was used to determine mean interval of time between hatching and spawning of a new batch.

RESULTS

Size at Maturity

Mithrax spinosissimus crabs are sexually dimorphic. The sex of juveniles cannot be determined visually until the crabs grow to a carapace length (CL) of approximately 25 mm. At this size, the females' abdomen begins to be noticeably wider than the males' through the fourth, fifth and sixth abdomenal segments. At first, immature females are characterized by an oblong triangular abdomen that covers a similar proportion of the sternum through each molt. Finally, the female undergoes a molt resulting in the maximum increase in width of the abdomen and at this point, for our purposes, was considered sexually mature, though ovaries of immature and newly molted mature crabs were not examined. Females in captivity reaching this stage of development were never observed to molt again.

Assuming that female *M. spinosissimus* is characterized by a terminal molt of puberty (see discussion Biddlecomb, *et al.*, this volume), it can be concluded that an ovigerous crab is mature and will not molt again. In terms of the allometric growth equation ($y = Bx^a$), as more typically applied to various dimensions of the male chelae (Hartnoll, 1974), the female abdomen compared to carapace length is positively allometric ($a > 1.0$) throughout its juvenile development (beginning at 25 mm CL) and becomes strongly positive at the maturation molt (Figure 1).

Males maintain a uniform abdomen shape throughout their molt history. The allometry of the abdomen in relation to the carapace length is nearly isometric (Figure 2). However, in contrast to females, maturing male crabs are characterized by a significant increase in size and shape of the chelipeds. When comparing log carapace length (CL) to log ventral propodus length (VPL) of Antiguan crabs, the males' VPL, as well as the cheliped in general, gradually begins to become proportionately larger than the females' at approximately 80 mm CL. The VPL then becomes markedly larger at a subsequently increased rate at approximately 105 mm CL (see Biddlecomb, et al., this volume). This first gradual inflection is likely the beginning of the size range for the pre-pubertal instar of this species. The pre-pubertal instar appears to range in CL between 80 mm CL and 115 mm CL. The second inflection, assumed to represent male crabs having undergone the maturation molt, begins as low as 102 mm CL and ends for the Antiguan population at 147 mm CL (Refer to Figure 2, Biddlecomb, et al., this volume). These appendages were observed to aid in agonistic displays and may also aid in courtship communication and defense. Biddlecomb, _et_ _al_. (this volume) discuss the possibilty of a single post pubertal molt in _M. spinosissimus_.

Natural population characteristics categorized by sex, size class, egg bearing state and state of maturity for each of the sites are presented in Table 1. The mean size (CL) of male and female crabs, designated mature, are different at all sites (see Iglehart, _et_ _al_., this volume). Mature male and female crabs were largest from site 3 (Grand Turk, BWI) while those from site 5 (Florida) were smallest. The largest population samples were from the Dominican Republic and Antigua, with 56 and 57 males and 126 and 44 females, respectively. Table 2 and Figure 3 show the size frequency distributions of female crabs caught from the five study sites.

Gravid crabs were caught every month of the year both in traps and by SCUBA divers, indicating reproductive capability throughout the year. The mean percentage of mature ovigerous females caught in traps at the Dominican Republic was 81.3% (S.D.= 12.4%) for February through November (no traps were set in December and January), with a mean of 11.5% (S.D.= 5.8%) mature females caught each month. At the Antigua site 65.7% (S.D.= 17.4%) of crbas trapped were ovigerous with an average of 4.8% (S.D.= 3.4%) ovigerous females per month. No crabs were collected during the months of January, May and November (Figure 4).

Mating

Mating of captive Mithrax spinosissimus while in aquaria was observed on four separate occasions. In each instance, both female and male were hard shelled and the females were barren. The crabs faced each other ventrally, the male dorsal side down and underneath the female. The female's abdomen was opened and outside the carapace of the male, whereas the male's abdomen was only slightly parted from his sternum and the first pleopods were inserted into the gonopores of the female. The female used her legs for support, while the male held the female by interlocking legs and/or by clasping her appendages with his chelae. Crabs were observed to remain in this mating position for less than one hour. The observed matings occurred in January and February.

Reproductive Morphology

The configuration of the ovaries in female Mithrax spinosissimus differs from that of the Brachyuran crabs as described in Warner (1977). Ovaries are paired and anastomose directly posterior to the cardiac stomach. They have lobes leading both anteriorly on each side of the stomach to the frontal margin under the eyes and posteriorly underneath the pyloric stomach, as in other crabs (Figure 5).

Each of two gonopores located on the sternites of the sixth thoracic segment and covered with pliable chitinous flaps, opens to an approximately one cm thin chitinous tube, which ends at the junction of each ovary and each of the paired spermathecae. This configuration, like that in other Majids, is "concave" as described by Hartnoll (1968), with the spermathecae projecting above the ovary-gonopore tube junction, rather than being between the ovary and gonopore tube (Figure 5). From this junction, a section of each ovary runs dorsally to each of the main paired bilobal sections. The spermathecae are barrel shaped with dimensions of approximately 15 X 10 mm in a crab of 106 mm CL. The spermathecae consists of two parts. The dorsal half is composed of two white waxy bodies pressed together, possibly sperm plugs (Hartnoll, 1969), while the ventral half, at the ovary-gonopore tube junction, consists of a more viscous brown/white liquid.

Of the 28 mature female crabs dissected, all had pale orange unfertilized eggs throughout the lobes of the ovaries and all had spermathecae with the anatomy described above, regardless of whether fertile eggs were being actively brooded at the time. In one dissected female (79.4 mm CL) judged to be one or two molts from maturity, the gonopores were barely discernible (pinholes). Chitinous tubes leading to the ovaries from the gonopores did not exist and ovaries and spermathecae were not obvious, as they are in mature females. Protrusions on the fifth thoracic sternite fit into sockets in the sixth abdominal segment in this immature crab. Pleopodal setae were only slightly developed and sparse as compared to those on mature females.

The eight pleopods of mature females have very setose exopods that cover the area between the abdomen and sternum when the abdomen expands as the brood develops. The setae on the endopodite of each pleopod are stouter, spirally organized and more sparse than those on the exopods. There are approximately 100 sets of three to six setae on each of eight endopodites. Each encased fertile egg has an individual strand that runs along a portion of each clumped set of setae and then twists around the set at the junction of the strand and egg. The strands of a clump of eggs may also twist around each other before separating and running along the set of setae (Figure 6).

Male reproductive structure was examined in less detail. In the largest mature males, spermataphores which appear as white waxy bodies (closely resembling those found in the spermathecae of the female) were observed in each of the paired sperm ducts, probably indicating the presence of mature sperm. The sperm ducts of smaller "mature" males and those of immature males were not found.

Clutch Size

Clutch size in M. spinosissimus was determined using dry and wet weights and weights of samples of individual eggs from those masses. The mean dry weight of five replicate samples of 20 eggs from each of six females was 4.7×10^{-3} gms (S.E.= 0.07×10^{-3} gms; range = $4.3 - 5.1 \times 10^{-3}$ gms; n=30), which yields a mean dry weight of 0.23×10^{-3} gm/egg. The mean wet weight of these samples was 19.7×10^{-3} gms (S.E. = 0.09×10^{-3} gms; n= 30). Based on this estimate, each dry-weight gram of Mithrax spinosissimus egg mass contains about 4348 eggs, assuming that the egg clutch is filled with eggs of uniform size and weight. However, the egg mass ordinarily contains some interfollicular connective tissue, as well as a very small portion of eggs at various stages of embryogenesis. The wet weight of the above samples is 4.2 times the dry weight.

Twenty ovigerous crabs were weighed pre and post hatch. The difference in weight was taken to be the total egg mass wet weight. Using the calculated wet weight to dry weight ratio and the egg number per dry weight gram, the total egg number per wet brood was estimated. Mean clutch size was 6.0639×10^4 eggs for crabs with a mean CL of 125.5 mm (SE = 3025: range = 55,249 - 66,026; N=20). The linear regression of the crab carapace length to derived clutch size was determined ($r = 0.65$; $p < .05$; N=20) and plotted (Figure 7).

Counting the eggs in four broods, using the two methods described, from four females of differing carapace lengths revealed a mean total of 7.1446×10^4 eggs per brood. From the wet weights of these four broods and the wet weight to dry weight ratio, the dry weight of each brood was estimated and the number of eggs expected from the dry weights calculated using 4348 eggs/g (dry wt.). The predicted and actual brood number varied less than 1000 eggs in each of the four cases.

Embryogenesis

Unfertilized eggs in the ovaries are usually pale orange. After spawning the fertilized eggs (about one mm in diameter) are attached to the pleopods and are orange in the early stages of development. Subsequently, they change to orange-red, red, amber-red and at the day of hatching, they change from clear-amber to a translucent opaque white color. From a sample of four female crabs, where the exact dates of spawning and subsequent larval release are known, incubation time was 29.5 days (S.D.= 0.5).

Minor differences in egg color were observed depending on the collection site of crabs. The "red" eggs from Antiguan crabs are actually dark red or raspberry color, while the "red" in eggs from Dominican Republic and South Caicos crabs are light red or strawberry color.

The development of the eggs up to hatching has been divided into the five most distinctly observed stages from visual and microscopic examination of the eggs of seven female crabs (Figures 8, 9).

Stage I

At the time of spawning, the yolk is pale to bright orange. Over the next six to nine days, the yolk divides into oblong cells and the color gradually changes to a red color (Figure 8a).

Stage II

After 10-12 days, the yolk, 95% of the egg, is prominent and composed of large oblong red cells with small rounder red cells closest to the developing larva. The larva appears as a small amber-clear segmented line. As the egg develops up to hatching, the yolk cells become smaller but they do not completely disappear. The eye spots are not yet visible. The heartbeat is not present at the beginning of this stage (Figure 8b).

Stage III

By the 15-18th day, the eyes (not yet full ovals as in later stages), thorax, abdomen, telson, appendage buds and beating heart are obvious. The yolk, now comprising 50% of the egg, appears microscopically as four contiguous lobes around the cardiac region and, in reference to the larval portion, appears visually as a dorsolaterally positioned solid crescent shape. A few black, orange or yellow chromatophores around the cardiac region and along the abdomen are also visible (Figures 8c-8g).

Stage IV

From 19-27 days, the yolk still appears dorsolaterally, as a solid crescent and coloration continues to disappear gradually as the larva develops up to and through this stage, so that the colored yolk encompasses only 25-30% of the egg. Yolk cells without color are noticeably smaller than those with color. The now fully oval eyespots are pink-red and the thoracic appendages become more developed, though still not extended (as in the hatched zoea). To the unaided eye, the larval portion is clear-amber with both a few very small chromatophores and the eyespots visible (Figure 9a-9c).

Stage V

At 26 -27 days, three to four days prior to hatching, the yolk color separates at the dorsal midline into distinct spheres on each side of the cardiac region. At the beginning of this stage the yolk occupies 10-15% of the egg. The thoracic appendages are clearly visible and periodically beat rapidly. Haemolymph can be seen rushing with each heartbeat around the inside of the larva. The cardiac region has been seen in healthy eggs to beat as fast as 250 beats/minute. The larva portion is still amber-clear to the unaided eye. Visually, the eyespots are pink and can be confused with the colored portion of the remaining yolk until the day of hatching, when little or no yolk color is visible in the morning and no yolk color is visible by dusk. Occasionally, healthy larvae strongly flex their abdomens during the few days prior to hatching. At the day of hatching, the egg cases change subtly from clear-amber to translucent opaque white (Figure 9d-9k).

Hatching

Nocturnal hatching was the norm, usually beginning at dusk or early evening. Several hatches occurred in the afternoon but rarely as early as 1400 hours. Eggs removed and put into a beaker of seawater during the day prior to the night of hatching would hatch only after dusk. The occurrence of hatching in relation to its proximity to the new or full moon was examined with no apparent pattern observed. For all sites combined, hatches occurred on any given day of the year regardless of the time of the month.

Throughout incubation, females were occasionally observed to lower their abdomen and pleopods as one unit and then successively raise each layer of pleopods (four layers). They would start with the innermost layer, followed by the next layer, until the abdominal flap itself returned to its original closed position, at which point they would then repeat the pumping action. At hatching, the abdomen and pleopods are pumped continuously in the same manner to expel the prezoea. In addition, those larvae that are able to do so, swim out of the brood space. Occasionally, one or both of the chelae were observed to be briefly placed into the brood space. Complete hatching time varies from two hours to as long as 36 hours, but usually was complete for viable hatches between 12-16 hours.

Results of the occurrence of captive crab hatches are summarized in Table 3. Thirty-eight crabs held in captivity for two months averaged 1.03 hatches each and four crabs held in captivity 10 months averaged 3.75 hatches each.

Of a sample of 26 females collected in Antigua, 70% were gravid when caught. Of the 30% not gravid when caught, 87% became gravid within 30 days. Forty-seven percent of crabs caught gravid or becoming gravid within 30 days (12 crabs) had three or more hatches while in captivity. Of those 47%, 70% died before having a fourth hatch. One female produced seven successful hatches over the course of a year in captivity.

The mean interhatch interval for 37 individual females studied was 61.9 days (S.D. = 19.6, n = 247). Samples not included were those where hatches failed due to the brooding females death prior to hatching or that were aborted. The shortest interval was 33 days, only three days from the hatch to the extrusion of her subsequent brood. Another female had a new brood the day after hatching but the new eggs were not attached and washed out easily when the crab was handled. The longest interval of time between release of an egg brood and the spawning of a new batch of eggs was 127 days. Sixty percent of the intervals ranged between 50-70 days.

DISCUSSION

A noticeable change occurs in the relationship between male ventral propodus length (VPL) and carapace length (CL) at the pre-pubertal instar. Most importantly, chelae begin to enlarge prior to the pre-pubertal instar and continue to enlarge significantly at an increased rate up to the maturation molt. This indicates a single maturation molt to adult morphology occurs in male *Mithrax spinosissimus*, although the increase in cheliped size during the pre-pubertal instar suggests sexual activity prior to the maturation molt. Brownell, *et al.*, (1977), mentions an immature crab being sexually active prior to molting to maturity and Hartnoll (1963) presents evidence from his observations that males of different Majid species, including *Mithrax sculptus*, have developed some mature sperm prior to the maturation molt. Since there was no data collected on the internal morphology of pre-pubertal instars and mature male crabs, we have no evidence other than external characteristics to suggest there may also be sperm maturation prior to the maturation molt. Future reproductive studies should focus on the necessity for collecting information on male internal anatomy at a variety of morphological stages.

We have little evidence to indicate that females mature during the pre-pubertal range, since external changes are not evident and specific examination of eggs from immature females was not conducted. An examination of an immature female of 79.4 mm CL showed no obvious internal reproductive structures. It is possible, however, that the duct between the gonopore and spermathecae-ovary junction was soft and so separated from the carapace upon examination. This duct may become chitinous only at the maturation molt. This limited evidence suggests females do not sexually mature internally and do not obviously mature externally until the maturation molt.

We have never observed a female to molt once the abdomen reached maximum width or if she was ever gravid. When dissected, mature females always had eggs at some stage of development in their ovaries and may direct their energy into egg production rather than to prepare for further ecdysis and subsequent growth. This suggests females have a terminal molt to maturity. With males, however, the evidence is not as clear. We have observed only one apparently mature male crab greater than 120 mm CL to molt (131.0 mm CL to 153.3 mm CL); the individual was collected in the Dominican Republic where unusually large immature male, as well as female crabs, were recorded. Though the percent change of molt increments generally decreases after 80 mm CL (see Biddlecomb _et_ _al_., this volume), there is one example of a male crab molting from 89.0 mm CL to 125.0 mm CL, which is an increase of 43%. Hartnoll (1963) also presents evidence that the Majids which generally have a terminal molt, often have a wide range between the smallest and the largest mature crabs.

On the other hand, as discussed in detail in Biddlecomb, et al. (this volume), the percentage size increase in CL of recorded moltings constantly drops from a mean of over 35% to a mean of 23% or less at the maturation molt. Considering the discontinuity in data at the maturation molt and the slight decrease in VPL allometry of the largest adult males, a second molt after the maturation molt may be indicated. This may not occur for a year or more and may not occur in all surviving males. Further investigation is necessary to support this theory.

Ninety-five percent of mature females collected in Antigua produced eggs while in captivity. Forty-seven percent of a sample of 26 crabs collected from Antigua had three or more hatches. All dissected females brooding fertilized eggs were also developing another batch of eggs in their ovaries, thus if caught gravid, we could expect at least two hatches. Moreover, the occurrence of three or more hatches while captive suggests that adequate nutritional material was being made available using the standard algal turf feeding process, supplemented occasionally with various macroalgae. The occurrence of one crab having seven broods in captivity appears rather exceptional. The relationship between the frequency and the number of hatches per crab is shown in Figure 7. Four to five hatches are the normal maximum to be expected from a mature female Mithrax spinosissimus.

The broods of crabs gravid or becoming gravid soon after collection were large and healthy. In some cases, the ensuing broods were smaller while in others, a greater number of undeveloped eggs were noticed. Whether this suggests decreasing or deteriorating internal sperm stores or deteriorating culture conditions is not known. Though we did not record pre-and post-hatching weights consistently for females, general observations of relative brood size for captive crabs appeared to be consistent for successive broods, except for the last brood before the death of the crab where the last brood tended to be unusually small. Since a reduction in fecundity with time is not apparent in captivity, it would appear that the conditions of cage life, including feeding quantity and quality are adequate for a mature crab producing approximately 5-10% of her body weight in eggs.

The broods of several females kept in closed aquaria for two to four weeks became infested with filamentous epiphytes, microscopic isopod-like animals running around the egg surface, as well as various Ciliophorans. If infested early during incubation, most or all eggs in a brood would die and appear opaque-brown. One brood infested approximately nine days prior to the expected time of larval hatching appeared quite viable but died by the expected hatch date. However, one brood with infestation obvious at only four to six days prior to hatching, survived well. Broods of females kept in open water cages never became infested. The few broods (3) that died while in open cages occurred in ovigerous females collected by fishermen and had been inappropriately transported, i.e., out of water or lying in bilge water. These broods appeared opaque grey-white, and subsequently decayed in the abdomen space, turning pleopods black. Subsequent broods from these females were not affected.

In the Dominican Republic, a mean of 81.3% of mature females caught in traps over a 10 month period were ovigerous. If this percentage is representative of the wild population, it suggests that mature females are consistently reproducing throughout the year, i.e., seasonality does not affect reproduction and females constantly reproduce throughout their adult life. If the percent becoming gravid within 30 days, as determined from a sample of Antiguan crabs, is applied to the Dominican Republic population, then we might expect an additional 16% of the total collected females to become gravid within 30 days. This large number of wild gravid crabs or crabs becoming gravid shortly after collection (97%) strongly suggests that the consistent egg production rates observed in captivity could represent a natural characteristic of the species.

The mean interval between brood release and spawning of the next brood was 61.9 days with a standard deviation of 19.6 days. The large variation in this interval is due to a number of factors. Of 14 female crabs tranported to Carriacou in aquaria with constant sea water exchange, seven had intervals greater than 80 days between the initial hatch and their next hatch. The mean intervals for these is 105.0 days (S.D. = 20.4). Of the remaining seven, five had a mean interval of 61.4 days (S.D. = 7.4) for that particular interval. The last two females died before their next hatch after transport. These rare and unusually long intervals, and the death of two of the transported females before successfully hatching, suggests stress due to the process of transportation. The hatches of those crabs surviving the pre- and post- transportation interval were successful. The mean for all intervals recalculated without those seven individuals is 58.4 days (S.D. = 14.2).

Of the 37 females examined to determine intervals, a specific group of 11 females, having more than two hatches consistently produced hatches whose individual intervals varied within by a range of 10 days. For example, one female's intervals were 53, 62 and 59 days. This consistency suggests that a fertile female, healthy and well fed, will produce eggs at a specific biologically determined interval. The variance in intervals among 11 females examined was much greater than the variance within each female (mean = 51.5 days; S.D.= 5.1, n = 22). That is, while one female's intervals may vary consistently with a mean of 50 days, another female's may vary at 60 or 40 days.

No relationship between lunar cycle and hatch times was noted, though the mean incubation time is 29.5 days and the mean between brood interval is 61.9 days, suggesting that hatching could potentially correlate with the lunar cycle. On the other hand, the large variation in time interval, if representative of the species in the wild, suggests no correlation to any definite cycle. Since the ovaries of both brooding and non-brooding females were always full of eggs, presumably developing, the time intervals may solely be due to the genetically determined unspawned egg maturation time, specific to each female. However, some variation in the maturation time is probably due to energetic and/or nutritional constraints. If food supply is limited, it may affect yolk deposition into the unspawned eggs.

The few times mating was observed, both male and female *Mithrax spinosissimus* were in the hard shell state with the female dorsal to the male. In adult *Mithrax spinosissimus* the gonopores are covered by a moveable flap and it is likely that copulation can occur at any time after maturation. The similar shape and texture of the white, waxy bodies found in the spermathecae of the female (two in each) and in the male reproductive tract (one in each) suggest that spermatophores are generally present in the spermathecae of mature females.

It appears that egg bearing capacity increases with crab size as measured by carapace length. However, the variance in the measured crabs was quite high and is attributed to the difference in egg mass weight due to the state of embryonic development, the number of spawnings since mating and the condition of the female.

The pre-hatch larvae or embryo changes drastically during the second week of development from what appears to be a mass of yolk to a distinct larva. The percentage of yolk color present is a characteristic that can be used to determine the approximate time to hatching, but only during the last week can the hatch date be predicted within a day. When the yolk appears to split into two colored spheres, it is usually three days before hatching. Crabs from Antigua had darker red eggs, suggesting phenotypic variation between populations. Darker eggs make determination of the hatch date considerably easier.

Eggs observed in a beaker during the day prior to a night of hatching, hatched at dusk. This suggests that hatching is controlled at least partially by the larvae. Also, the subtle change in egg case color on that same day could indicate internal chemical changes initiated by the larvae. The strong flexing of larvae prior to hatch suggests they help to liberate themselves from their cases. However, synchronization of the liberation of entire broods within two to twelve hours may indicate at least some internal biological control or biological rhythm by the female as to the hatch date and duration.

CONCLUSIONS

Aspects of the reproductive biology of *Mithrax spinosissimus* have been examined and the results reported. As with some other Majids, this species appears to have a prepubertal instar just prior to the maturation molt at least in males. Females appear to cease molting after the maturation molt. Our evidence is not conclusive for males; some indications for a second molt exist and are discussed in Biddlecomb *et al*. (this volume). Limited evidence suggests the male may begin to mature prior to the maturation molt. At the maturation molt the male's chelae significantly increase in size and the female's abdomen increases in width to cover the sternum.

The reproductive morphology and mating behavior is similar to other described Majidae. A female can store sperm in spermathecae and potentially fertilize many and perhaps all spawnings during its reproductive life from one mating. As well, it appears capable of multiple matings once mature.

Like other tropical Majids, this species was found to be ovigerous throughout the year with no obvious seasonality and can reproduce continuously, approximately every 62 days, throughout its mature life. The maximum potential reproductive life of the female appears to be one to one and a half years after the maturation molt. Incubation of eggs attached to the pleopods requires approximately 30 days to mature and hatch.

From the pattern of embryogenesis, exact hatch dates can not be determined until the last week of incubation. Based on morphological evidence presented in this paper, an estimate can be made at that time to within a day. Hatching in the sea, in cages, can be very reliable with no indication of disease problems.

More comprehensive data are needed, such as, 1) examination of the internal male reproductive anatomy at a variety of morphological stages; 2) positive determination of a second molt after the maturation molt in male Mithrax spinosissimus; 3) the weights of successive hatches from newly mature to death to indicate reproductive potential and effects of captivity; 4) the weights of females themselves through time in captivity; 5) an accurate determination of numbers of hatches from a fertilized but isolated female; 6) a determination of the age of mature crabs at the time of collection to indicate reproductive life span; and 7) determinations of any variations in fecundity with changes in environmental and geographical parameters.

From the present study, we can conclude that Mithrax spinosissimus appears relatively unaffected by conditions of captivity, with a large percentage of mature females consistently producing viable broods. The fecundity of this species may actually be enhanced in an open water mariculture facility by stable feeding conditions, protection of larvae from predators, and a thorough understanding of the reproductive biology and embryonic development.

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LEGENDS

FIGURE 1. Adult female ventral and posterior view indicating abdomen size difference and appearance of the inside of the abdomen with eggs on the pleopods.

FIGURE 2. Adult male ventral and posterior view.

FIGURE 3. Histogram plot of number of ovigerous females captured pooled from all sites.

FIGURE 4. Percent of total females trapped from the North coast of the Dominican Republic (site 5) and the Northeast coast of Antigua (site 7) for the year beginning October 1985.

FIGURE 5. Illustration of the paired ovaries, and the gonopore tube-spermathecae-ovary complex. The outlines of the carapace and sternum are of the dorsal view.

FIGURE 6. Examples of incubating eggs attached to the clumped setae of the endopodites of the pleopods.

FIGURE 7. Relationship between the carapace length of *M. spinosissimus* and potential clutch size in thousands of eggs. Based on size specific dry weight of total egg mass and mean dry weight of individual eggs (0.0047 gm/20eggs : S.E. = 0.0007 gm; n = 20).

FIGURE 8. Stages I - III of incubating eggs.

FIGURE 9. Stages IV and V of incubating eggs.

TABLE 1. The mean carapace length of mature males and females by sites and source of collection. Carapace width (CW) is approximately 1.05 carapace length (CL) in adult Caribbean populations.

TABLE 2. The frequencies of ovigerous females captured by study site and 10 mm carapace length increments.

TABLE 3. The average number of hatches per crab for specific time intervals of captivity. Data for (N) crabs is from 49 total females observed.

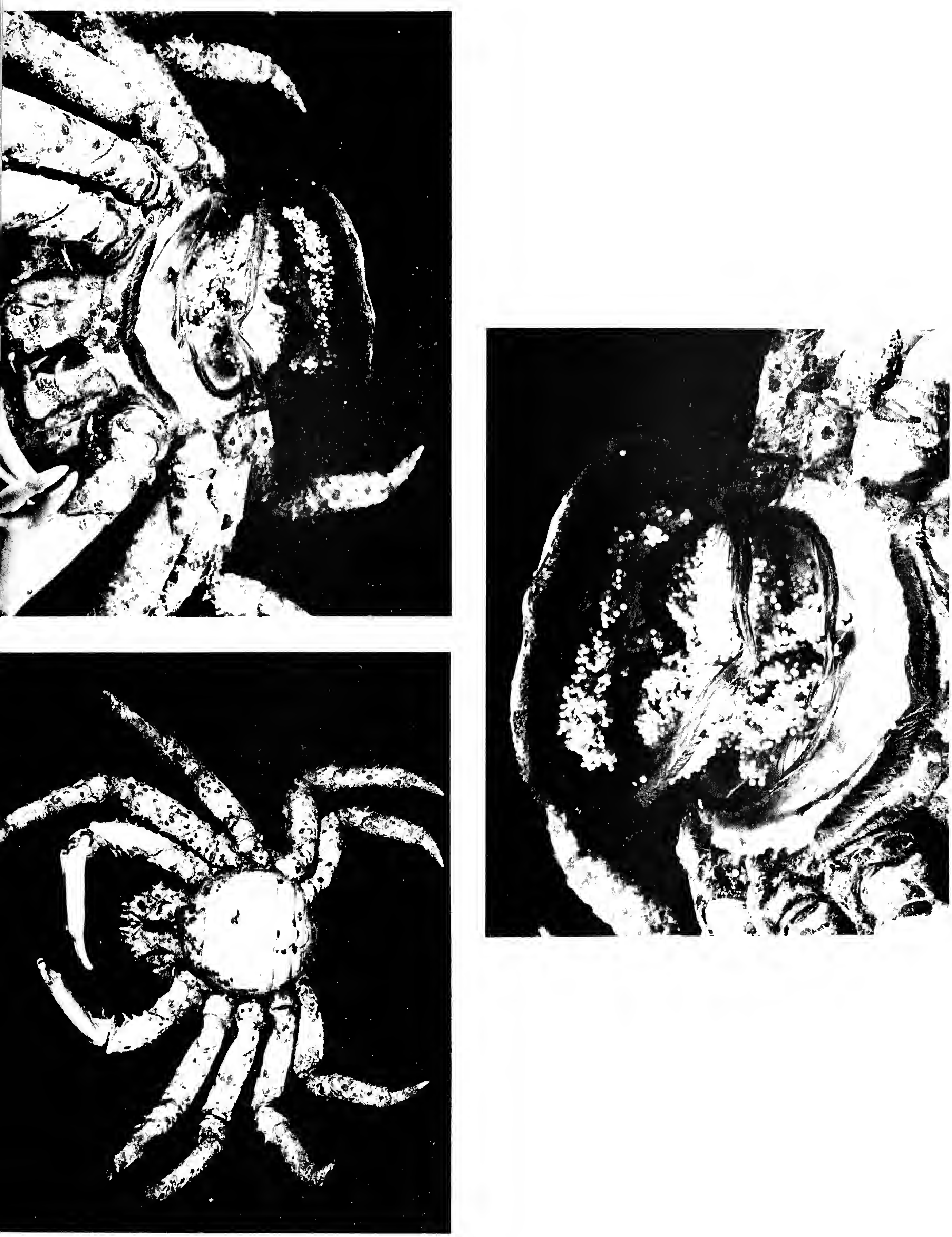

Figure 1

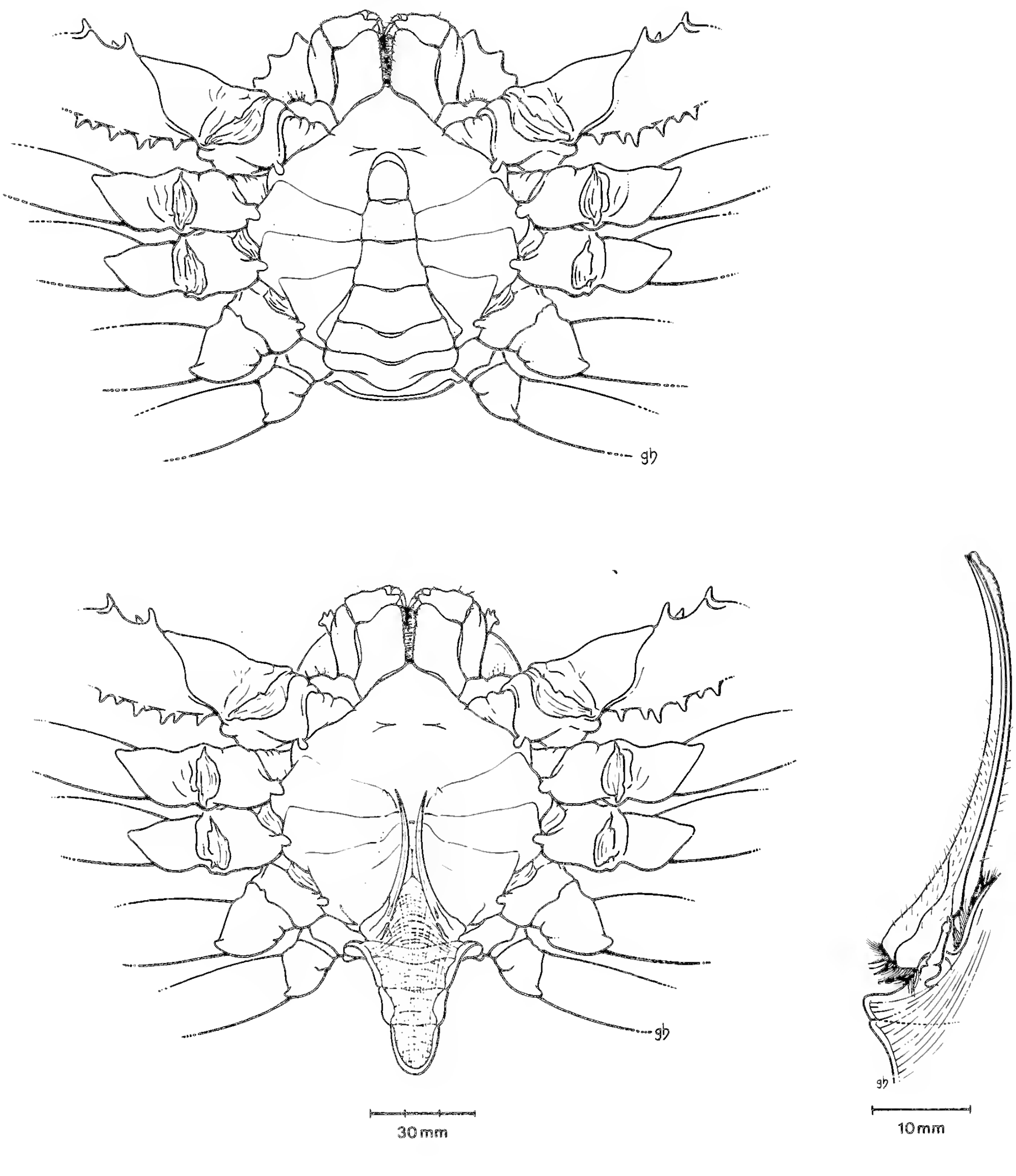

Figure 2

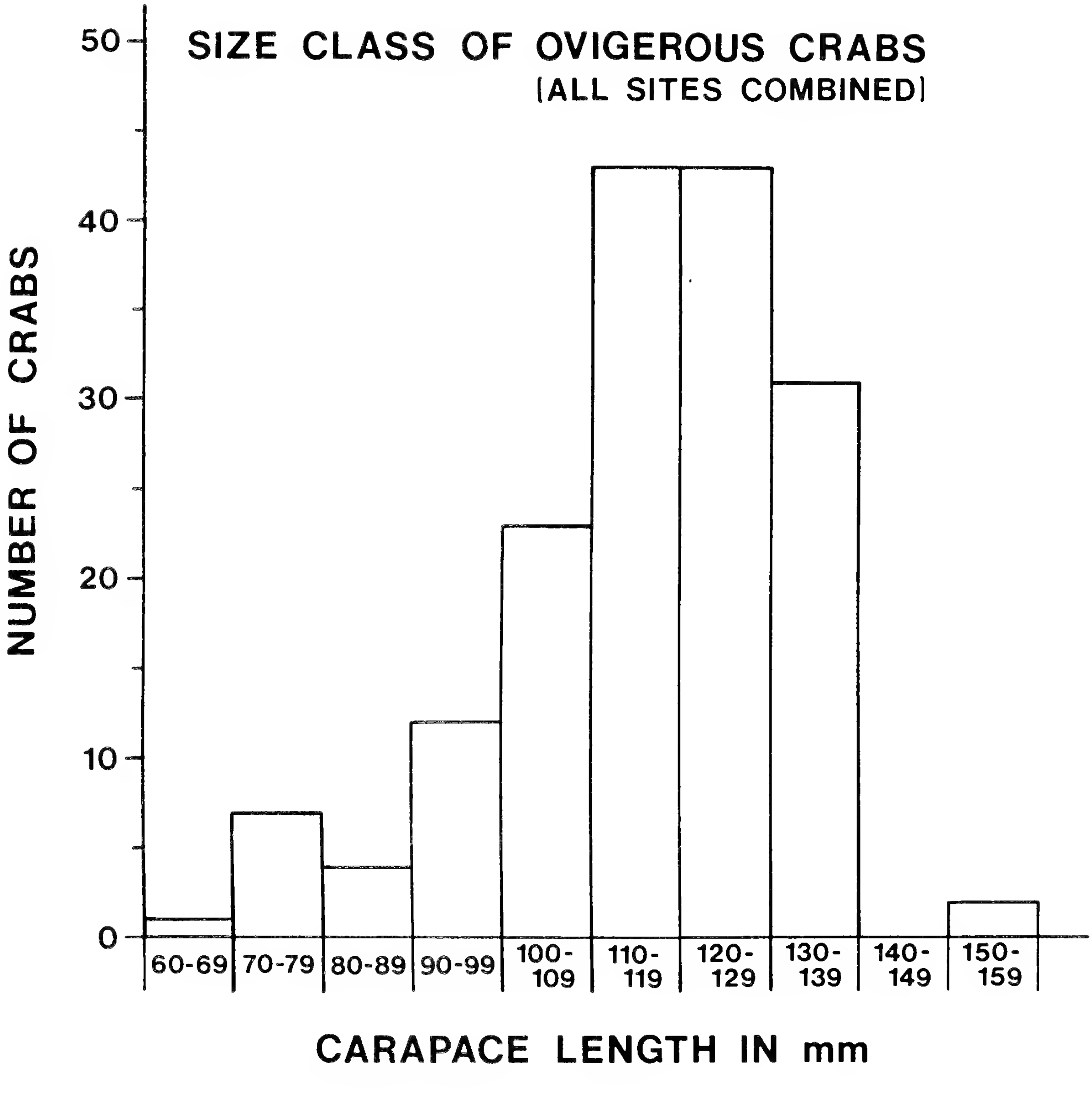
SIZE CLASS OF OVIGEROUS CRABS
(ALL SITES COMBINED)
NUMBER OF CRABS
50
40
30
20
10
0
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
CARAPACE LENGTH IN mm

Figure 3

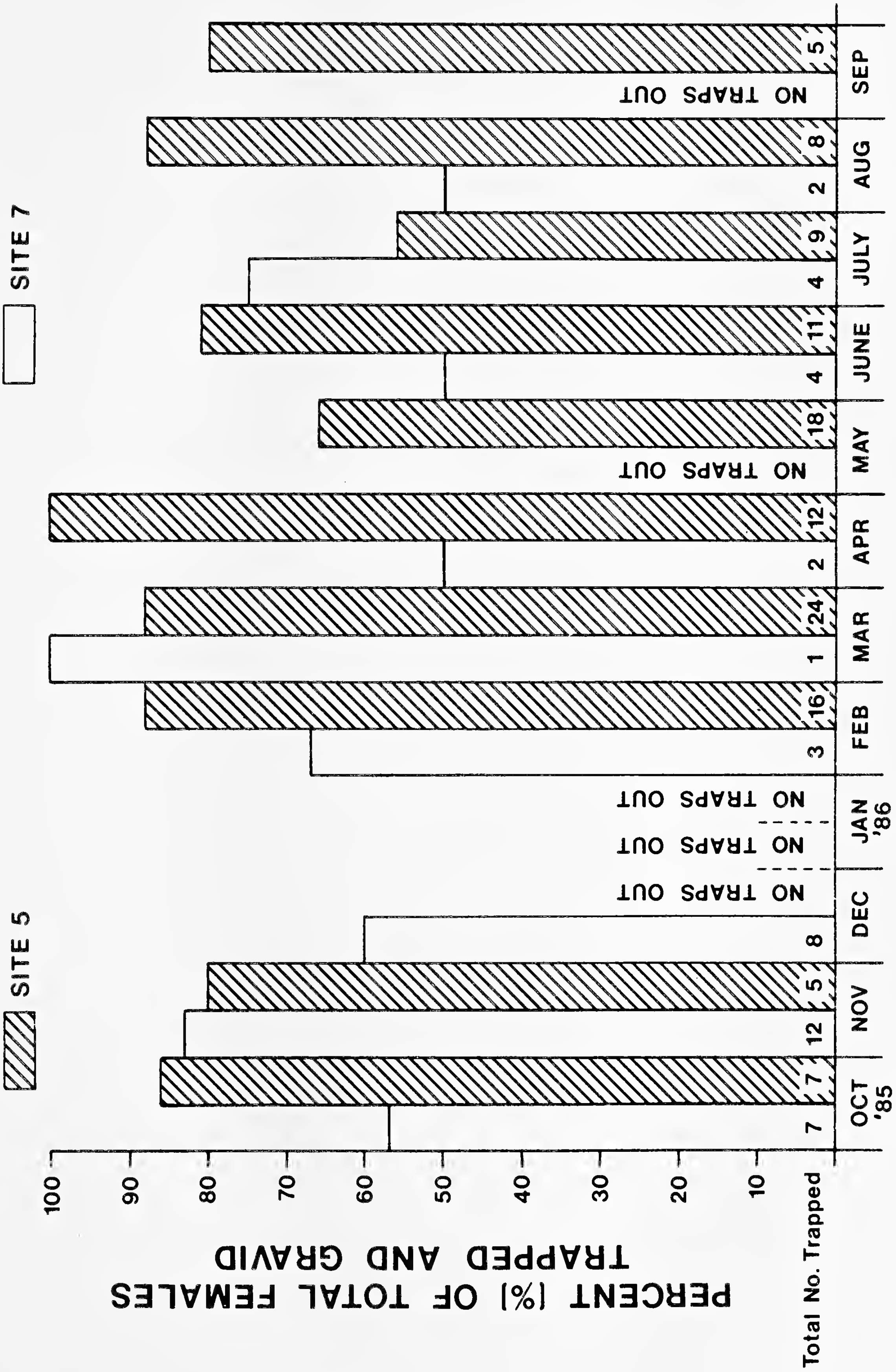
SITE 5
SITE 7
PERCENT (%) OF TOTAL FEMALES TRAPPED AND GRAVID
100
90
80
70
60
50
40
30
20
10
Total No. Trapped
7
7
OCT '85
12
5
NOV
8
DEC
NO TRAPS OUT
NO TRAPS OUT
JAN '86
NO TRAPS OUT
3
16
FEB
1
24
MAR
2
12
APR
NO TRAPS OUT
18
MAY
4
11
JUNE
4
9
JULY
2
8
AUG
NO TRAPS OUT
5
SEP

Figure 4

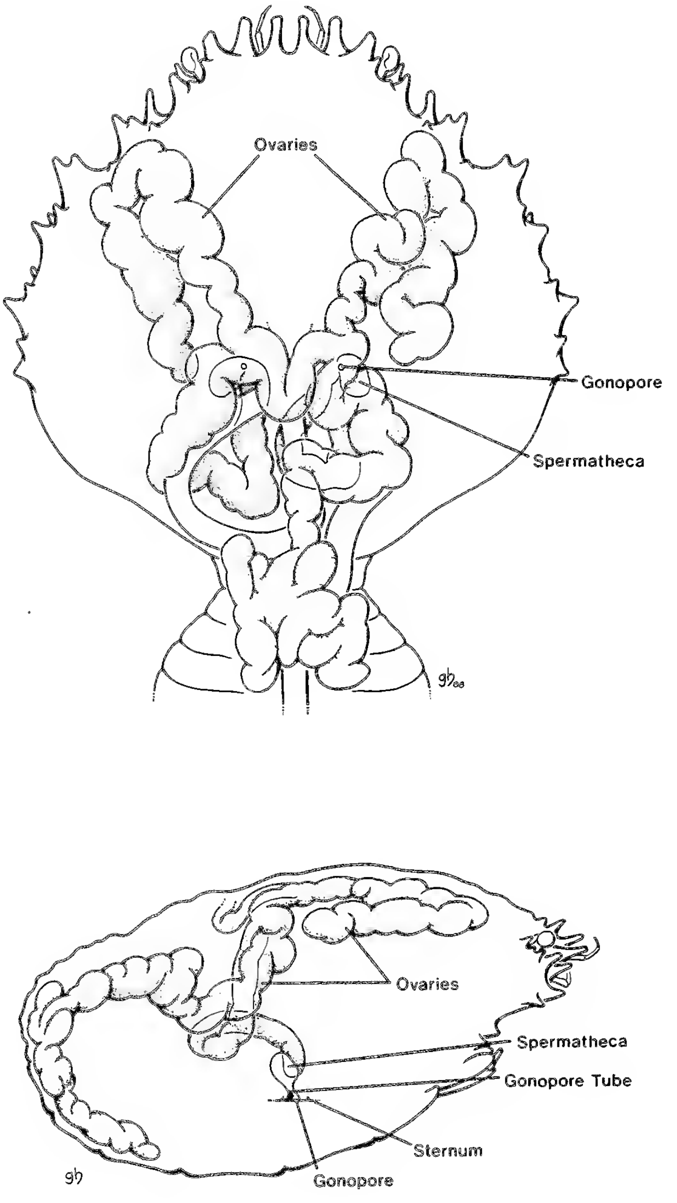
Ovaries
Gonopore
Spermatheca
gb88
Ovaries
Spermatheca
Gonopore Tube
Sternum
gb
Gonopore

Figure 5

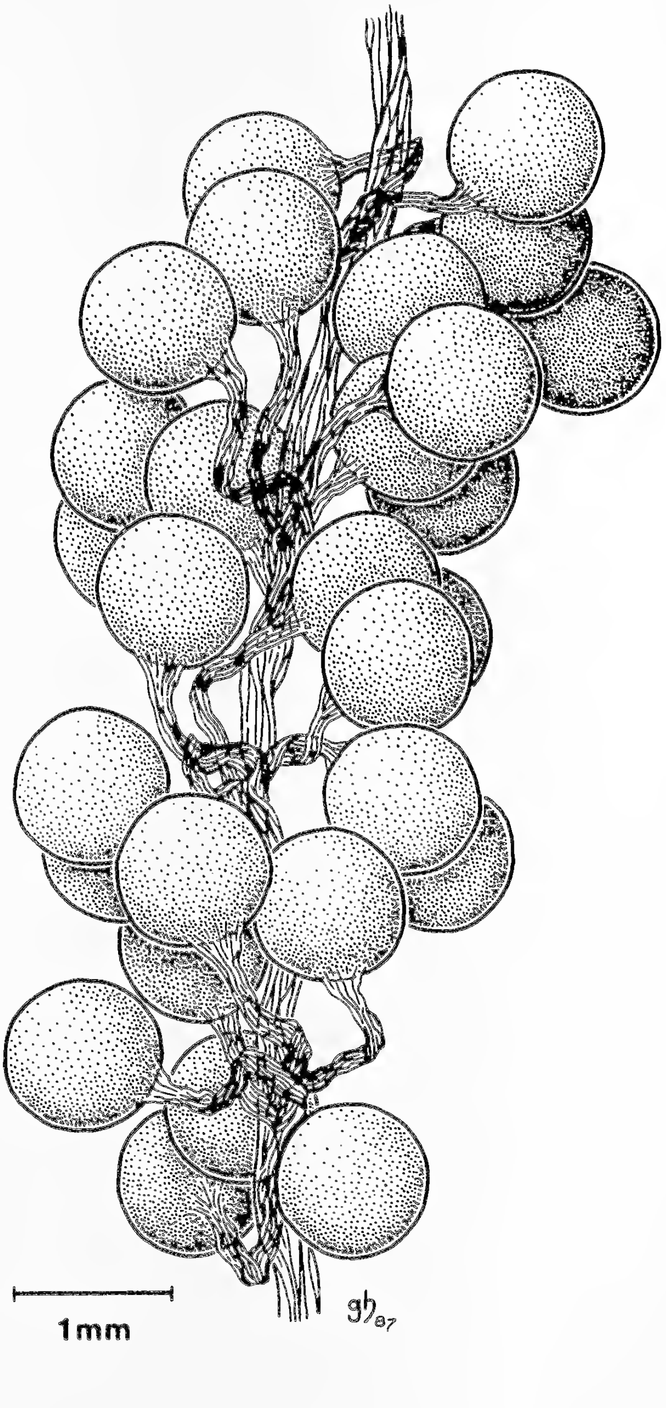

Figure 6

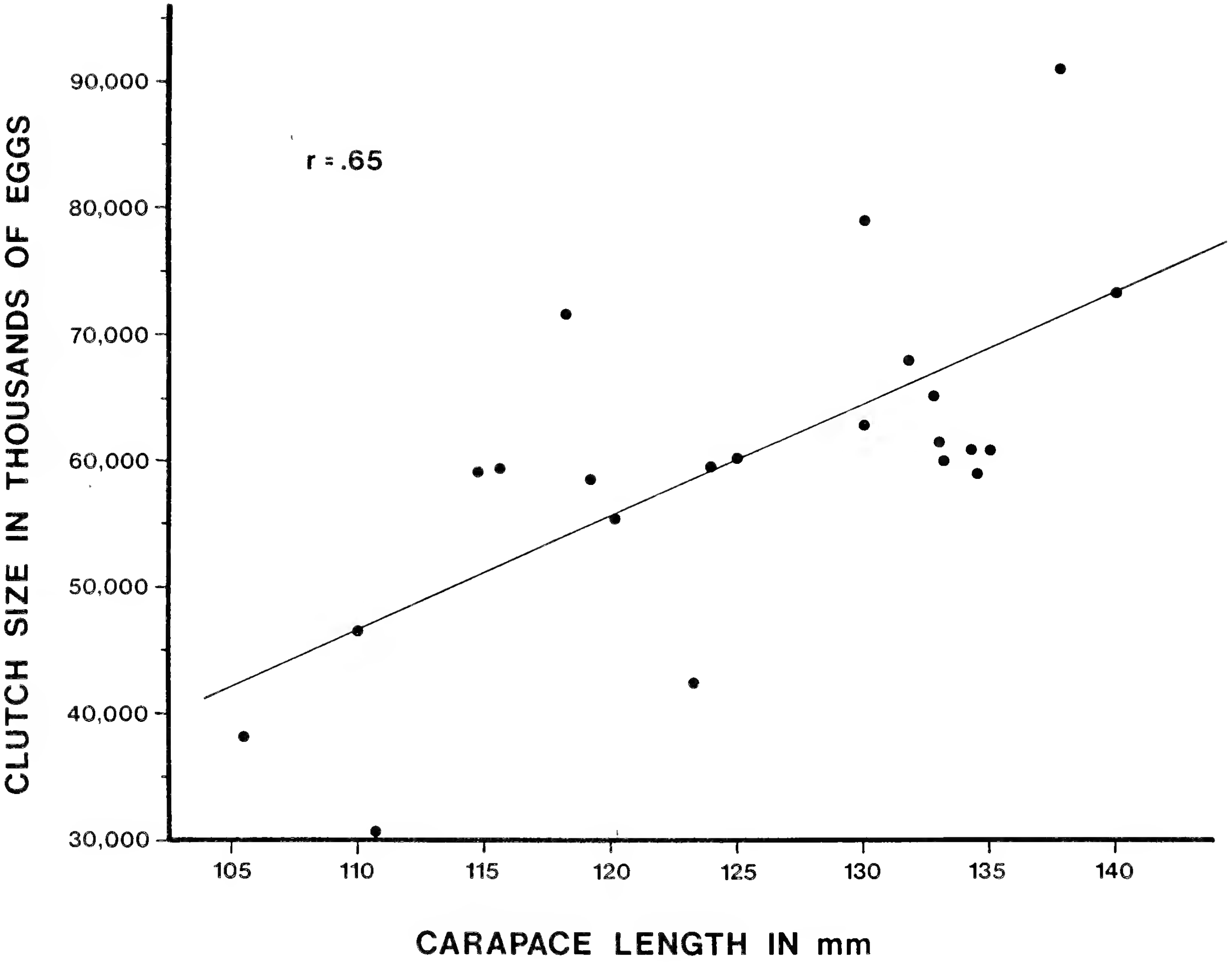
r = .65
CLUTCH SIZE IN THOUSANDS OF EGGS
90,000
80,000
70,000
60,000
50,000
40,000
30,000
105
110
115
120
125
130
135
140
CARAPACE LENGTH IN mm

Figure 7

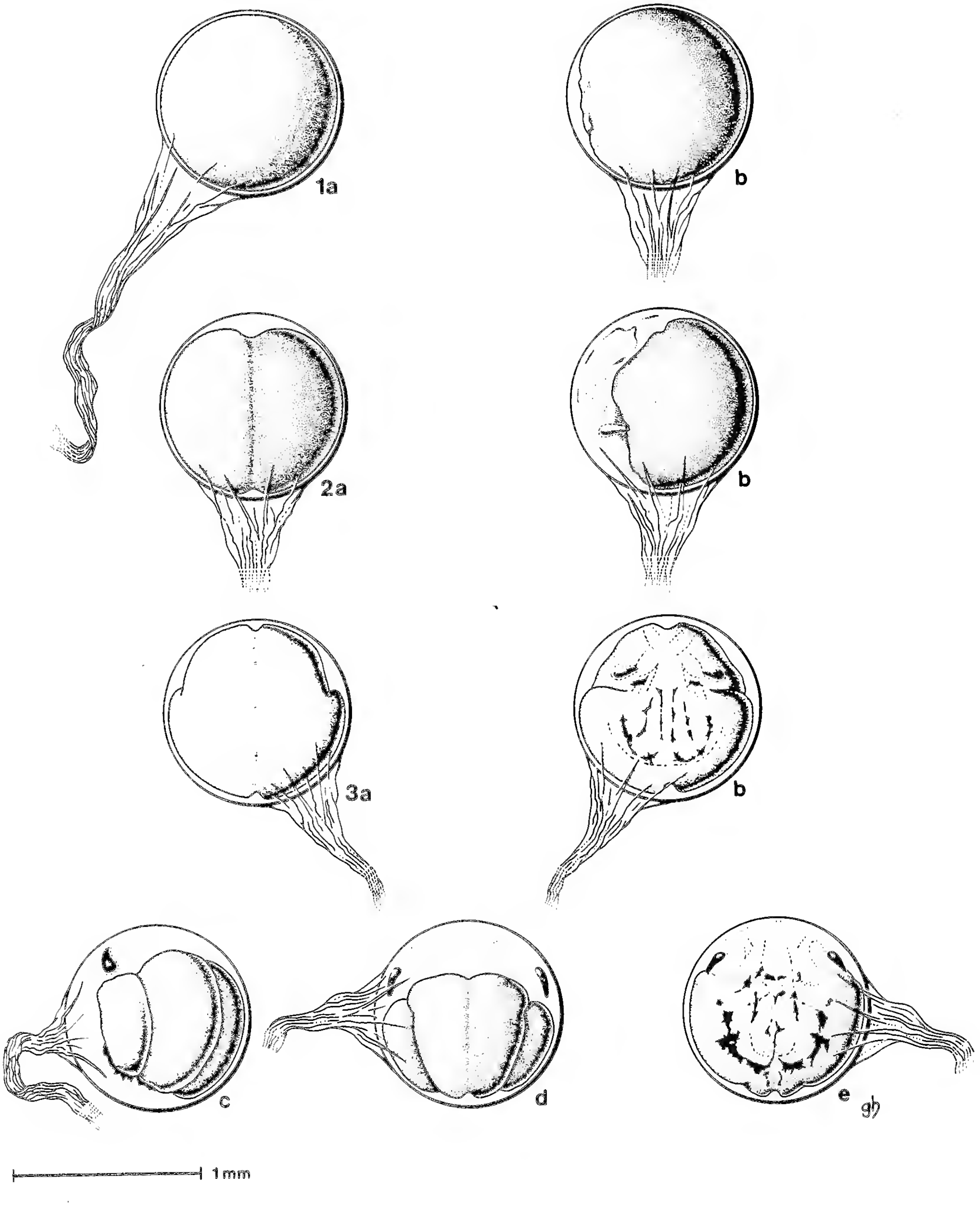

Figure 8

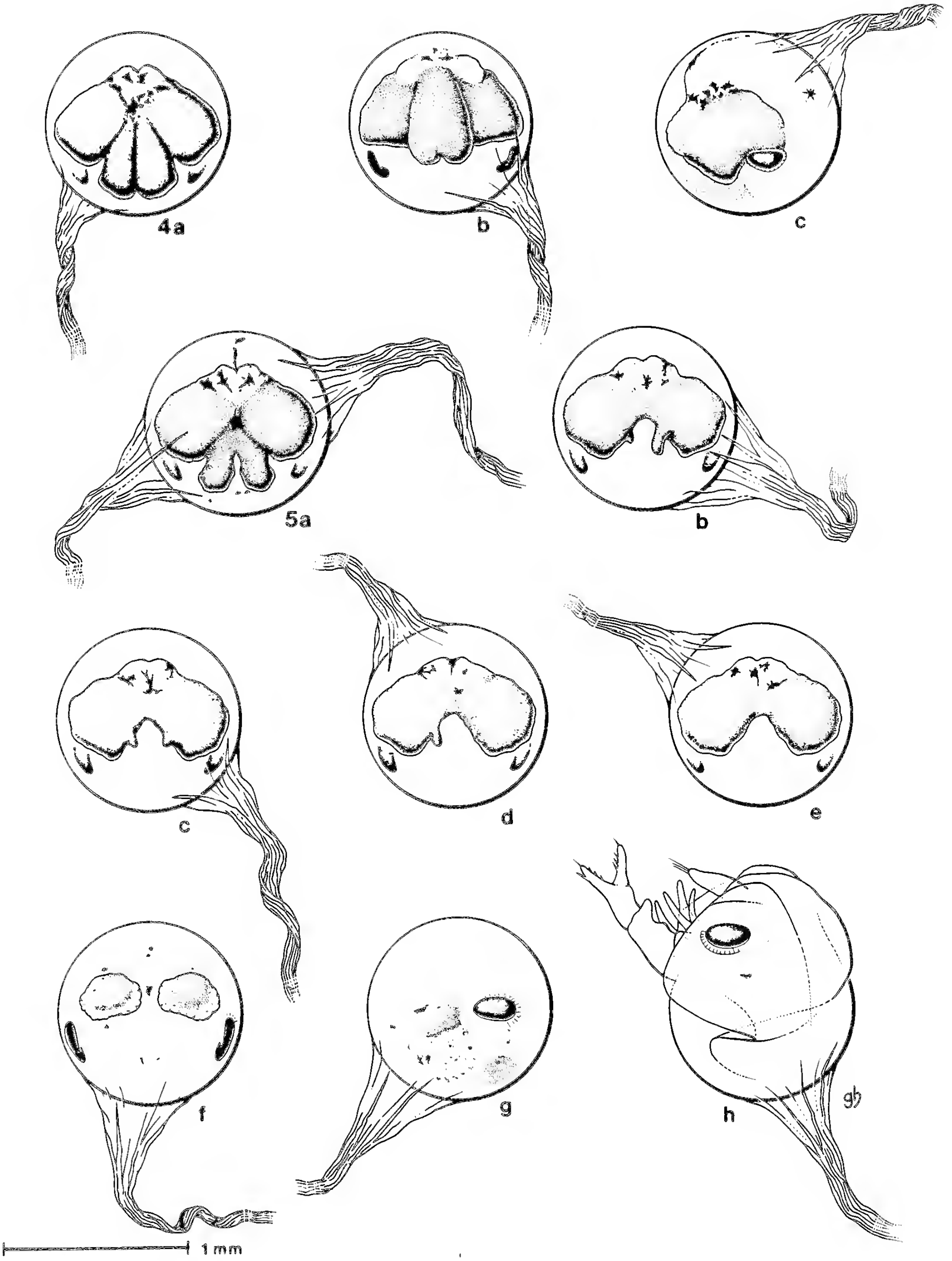

Figure 9

TABLE 1: The mean carapace length of mature males and females by sites and source of collection. CW = 1.05 CL for all adults except from Florida.

MEAN SIZE OF CRABS (MM CL)

LOCATION	ALL ADULT (FEMALES)	GRAVID (MATURE FEMALES)	MATURE (MALES)	SOURCE	TOTAL POP. SAMPLE
DOMINICAN REPUBLIC	122.7 +/- 0.8 N=126	122.5 +/- 0.9 N=97	140.8 +/-1.4 N=56	THIS STUDY	203
ANTIGUA	107.8 +/- 1.3 N=44	108.6 +/- 1.6 N=27	131.2 +/- 1.2 N=57	THIS STUDY	162
GRAND TURK	140.2 +/- 2.5 N= 19	137.5 +/- 3.7 N=10	146.7 +/- 6.1 N=15	THIS STUDY	44
SOUTH CAICOS	113.7 +/- 1.9 N=27	113.7 +/- 3.2 N=12	135 +/- 3.7 N=10	THIS STUDY	39
FLORIDA	81.7 +/- 3.6 N=33	83.5 +/-5.1 N=18	93.9 +/- 4.6 N=11	THIS STUDY	86
JAMAICA	125.3(CW) N=71	122.8(CW) N=35	133.4(CW) N=141	MUNRO (1974)	212
FLORIDA	86.0(CW) N=73		96.0(CW) N=28	BOHNSACK (1976)	103

TABLE 2: The frequencies of females captured ovigerous by study site and 10 mm. carapace length increments.

SIZE CLASS OF OVIGEROUS FEMALES BY STUDY SITE

SIZE CLASS CL (MM)	GRAND TURK	SOUTH CAICOS	DOMINICAN REPUBLIC	FLORIDA	ANTIGUA	TOTALS
60-69				1		1
70-79				6		6
80-89				4		4
90-99		1	1	7	3	12
100-109		3	6		14	23
110-119		4	31		8	43
120-129	3	3	34		3	43
130-139	5	1	25			31
140-149						0
150-159	2					2
TOTALS	10	12	97	18	28	

TABLE 3: The average number of hatches per crab for specific time intervals of captivity. Data for (N) crabs is from 49 total females observed.

<u>NUMBER OF HATCHES FROM CAPTIVE FEMALE CRABS</u>

MONTHS IN CAPTIVITY	AVG # OF HATCHES/ CRAB	NUMBER OF CRABS (N)	% OF TOTAL	TOTAL HATCHES
1	0.6	49	100	27
2	1.03	38	77. 5	39
4	1.85	33	67.3	61
6	2.70	21	42.8	56
8	3.23	13	26.5	42
10	3.75	4	8.2	15
12	7	1	2.0	7

SECTION II: BIOLOGY AND ECOLOGY OF *MITHRAX SPINOSISSIMUS*

POST-LARVAL GROWTH OF CULTURED *M. SPINOSISSIMUS*

POST-LARVAL GROWTH AND SURVIVORSHIP OF CULTURED MITHRAX SPINOSISSIMUS

K.L. Porter, J.M. Iglehart, R.V. Ruark, M. Craig, A. Biddlecomb,
and W.H. Adey

Abstract

Mithrax spinosissimus rearing studies were conducted to develop simple and inexpensive hatching and growout techniques. Crabs were hatched in 0.25 cubic meter cages enclosed by 0.5 mm plastic mesh. Post larval crabs were transferred to larger cages upon reaching carapace lengths of 10 mm and again at 20-25 mm. Initial post-larval first crab (Instar I) densities are estimated at 2000/0.25 cubic meter cage.

Fed on an experimental diet of primarily cultured algal turfs, a total of 56 hatched egg broods were reared through 100 days post hatch or longer. Crab growth ranged from 0.11-0.19 mm/day at 60 days post-hatch to 0.10-0.21 mm/day at 100 days post-hatch and to over 0.5 mm/day at 280 days post-hatch. Crab survivorship averaged 22% to 60 days, 23.6% from 60-120 days and 18.5 % from 120 to 300 days.

Growth rate and feeding data strongly indicate that under optimum environmental conditions in cages, growth rates are high and molt stages largely pre-determined. The relatively high mortalities in this study may result in part from under-feeding, but more likely result from a complexity of factors including predation by intruders in the cage environment, wave damage during molting and aggressive behavior by some individuals. Proper cage construction and management can likely greatly reduce juvenile mortality.

INTRODUCTION

The tropical western Atlantic crab Mithrax spinosissimus is not extensively exploited by commercial fishermen, due in large part to its scattered distribution and relatively low population levels (Munro, 1974), though it forms an important gourmet restaurarnt food in some Caribbean countries. On the other hand, its brief larval life (90-140 hours to first crab, (Provenzano and Brownell, 1977; Porter, *et al*., in review), herbivorous lifestyle (Coen, 1987; Colin, 1978), high fecundity, and potential economic value make it an ideal choice for mariculture (Brownell *et al*., 1977).

Little has been known of the growth rate of *M. spinosissimus* either in the wild or in captivity. Laboratory rearing studies have been limited to describing the morphology of the larval stages (Provenzano and Brownell, 1977). Brownell, *et al*., (1977) conducted a single experiment of *M. spinosissimus* juvenile crab culture in a fine meshed (0.363 mm) open water cage which resulted in rates of growth of 0.06 mm/day CL. The authors suggested conditions in the cage adversely affected the juvenile crabs and depressed their rate of growth. The attached algal microflora on the screen mesh surface served as the sole food supply. A single crab was grown at a rate of 0.11 mm/day CL for over 175 days in the laboratory (Brownell, *et al*., 1977).

In a field study of crabs grown in unattended screened cages for 60 days (similar to the methods of Brownell, *et al*., 1977) Porter, *et al*. (in review) found crab growth (at a mean of 0.11 mm/day CL) to be much greater than in the earlier work by Brownell. Iglehart, *et al*. (1987) found that crab growth under conditions of supplemental feeding of cultivated algal turfs in cages increased crab growth rates to 0.17 - 0.20 mm/day CL for 100 day cultures.

The objective of our work was to develop baseline growth information that would allow the development of simple and inexpensive rearing techniques for post-larval crabs. It was hoped that such techniques could be used by itinerant fishermen in under-developed Caribbean nations. The effects of crab density, diet and rearing systems on the growth and survival of juveniles of the Caribbean King Crab, *M. spinosissimus* in open water cage culture are described.

MATERIALS AND METHODS

Crabs

In this investigation, crab culture was carried out, "in situ", in cages in tropical Caribbean coastal lagoons at ambient water conditions. The field study sites, occupied at various times from 1984-1986, were 1) Buen Hombre, northwestern Dominican Republic (19° 80' N, 71° 20' W); 2) Nonsuch Bay, eastern Antigua (17° 10' N, 61° 43' W); and 3) Carriacou, Grenada (12° 60'N, 61° 40'W) (Figure 1). In this investigation, 154 ovigerous *M. spinosissimus* were collected from the coastal waters of the study sites. Gravid crabs nearing hatch release were placed in separate cages. The procedures for managing breed stock and egg development in the ovigerous female are discussed in detail by Craig, *et al*. (this volume). The ovigerous female crab was removed from the cage upon completion of the hatching process and the larvae were left undisturbed until they settled out as post larval instar I or first crabs. Survival of larvae from egg to the first post-larval crab stage has averaged 3.0% in earlier studies (Iglehart, et al., in manuscript). The rate of survival is based on the mean brood size of female crabs (6.0639×10^4 eggs; S.E. ± 3025: Craig, et al., this volume) and the resulting survival rate as found in hatch cages similar to those used in this study. Therefore, initial post-larval crab densities in the hatch cages in this study are assumed to be approximately 2000 crabs/cage (Porter et al., in review). Crabs were reared in cages throughout the experiment. All survivorships are calculated from first crab or from the stated interval.

Experimental food

Algal turfs cultured upon rigid, black plastic screens (0.61 x 0.92 m; 2 x 3 mm mesh) (Figure 2) were introduced as feed to the post-larval crabs. Algal screens were exchanged every two to six days to ensure an adequate supply for crab consumption. Baseline data for algal turf community structure, methodology and productivity are discussed in Adey and Hackney (this volume).

Rearing systems

The rearing system cages were constructed of wood frames enclosed by plastic screening of various mesh sizes. Polyester fiberglass resin was used to coat the wood frames before assembly. The hatch cage (1.0 m L x .35 m W x .70 m H) (Figure

3) was covered by white, 0.5 mm polyester monofilament screen. Cage dimensions varied among the field sites from 0.3 m^3-0.4 m^3 (Tables 1, 3). The cages were anchored and suspended in protected lagoonal waters at 2.5-4 m depths so as to reduce or eliminate any surface wave action from affecting the cage. The intermediate cage (1.0 m L x 1.0 m W x 1.3 m H) was identical in construction to the hatch cage but covered with 1-1.5 mm mesh white polyester monofilament screen and anchored near the hatch cages in reef lagoons at depths of 1-2 meters from the bottom. The growout cage (2.6 m L x 1.0 m W x 1.0 m H) (Figure 4) was 3.5 m^3 covered with 1/4" black polypropylene plastic mesh and anchored so as to float at the lagoon surface. A more complete discussion of cage design, construction, placement and mooring is given in Porter et al. (this volume).

The cage system used for each crab hatch included a hatch cage and a growout cage. Crabs were hatched and reared during early larval stages in unattended cages suspended in the water at field sites 1-3 (Tables 1-3). From approximately 15-25 days post-hatch, cultivated algal turf screens were introduced into the juvenile crab cages on a regular schedule. Juvenile crabs were transferred to a larger cage (Tables 1-3) when the average carapace length of the group was 10 mm or greater. At site 1 an additional intermediate cage was used as crabs were transferred again at 100-125 days (Table 1). At all sites juvenile crabs were transferred to the growout cage when the crabs had attained sizes of approximately 20-25 mm CL.

The crab cages were regularly sampled to determine carapace length, survival rates and to assess general culture conditions. Sixty hatches were examined, 56 carried through 100 days post-hatch, and 22 broods through as many as 280 days of growth in the growout cage. Measurements of 23,000 post-larval crabs over a total span of 472 days were obtained to derive the data discussed herein.

RESULTS

Growth

In this investigation, the mean carapace length (CL) as measured at 20 day intervals up to 280 days post-hatch is plotted for each study site to compare overall growth rate data regardless of location variance. Crab growth rates during the first 60 days (three sampling intervals) ranged from 0.11-0.19 mm/day for all sites, with crabs cultured at site 3 having the highest rate. Carapace length (CL) vs. time up to 280 days post-hatch is shown in figure 5.

Crabs 60 days post-hatch had a mean carapace length in mm of: site 1) 7.76;± 0.49; n=14382; site 2) 6.42; ± 0.25; n=3841 and site 3) 11.6 mm; ± 0.80; n=3000. At 100 days post-hatch the mean CL from site 3 was greatest. The maximum period of culture was 472 days (site 1) where specimens averaged 79.88 mm CL (SE ± 2.43; n =5), with a maximum of 91.0 mm CL. Because the project at Buen Hombre was closing down for the last 100 days, these crabs were poorly fed and growth rates were low. Some cultured crab populations averaged similar or larger sizes (66-84 mm CL) at much earlier periods post-hatch (e.g., 230-318 days post-hatch). At site 2 a mean CL of 76.88 mm CL± (n=5) was measured after a 318 day period of culture. The deviation of crab carapace length from the mean among a population increased with age. For those cultured crab populations with large numbers of measured individuals, from 0-100 days post-hatch the mean growth rate increases from 0.09 mm/day to 0.15 mm/day or greater. Beyond 100 days post-hatch, the mean growth rate began to climb at two of the sites for the remainder of the study period; of 0.31 mm/day (site 1); 0.38 mm/day (site 2); 0.13 mm/day (site 3). Beyond 180 days at sites 1 and 2 (combined) growth rates exceeded 0.50 mm/day.

Experimental Diet

Cultured algal turfs were provided to each cage every two to six days, depending on the algal production rates of each site (see Adey, et al., this volume). Algal turf screens were exchanged more frequently at site 2 (necessitating a larger number of screens per cage) to offset the lower algal turf production levels. Table 1 presents the amount of algae turf fodder provided to crab culture cages per day at each site.

Algal turf growth was greatest at site 3, as was the rate of crab growth. The algal turf growth at sites 1 and 2 was moderate, necessitating an increase in the number of screens per cage and an increase in the number of times that the screens are changed. However, we were unable to construct a sufficient number of plastic screens during the study period to offset the lower algal turf production levels. This is especially evident in the first 120 days of post-hatch growth as the lower levels of algal turf production at sites 1 and 2 depressed early crab growth rates. On the other hand, after 120 days at site 3, the project was closing down, less time was available for feeding and growth rates fell off.

The feeding rate in the growout cages and the intermediate cages was much greater than in the hatch cages and the crab density per cage was greatly reduced, thus increasing the level of survival. These factors promoted rapid growth and a lower relative mortality rates for all crabs in culture from 100 days to 300 days post-hatch. For those reasons, the Carriacou growth rates are used in a composite curve (Figure 6) to 100 days and then the Buen Hombre and Antigua rates are used. The molt intervals are calculated from Biddlecomb, et al. (this volume), figure 3.

Survival

The average gravid female crab carries 60,000 eggs (Craig, et al., this volume) thus the density of zoea in the hatch cages exceeded 45 crab larvae/cm^2 of cage screen surface area, in the best of circumstances. Approximately 2000 crabs survive the larval period to five days post-hatch using the hatch cage techniques employed in this study (Iglehart, et al., in manuscript). Though the larval density greatly affected larval survival to the first post-larval stage, instar I stage (3.3% survival), the non-technical, low cost "in situ" lagoon cage hatchery methods, provided an adequate number of stage I postlarval crabs (n=2000) for continued growout. Mean survival to 100 days in hatches conducted during the beginning of the research study was 4.93% and in the later studies increased to 10.9% (n=11 hatches at site 1).

Upon transferring crabs from the hatch cages to the larger mesh cages, survival rates increased to 64% from 100-150 days post-hatch (site 1); 63% from 100-160 days post-hatch (site 2); and 39% from 80-120 days post hatch (site 3). The mortality rate beyond 150 days post-hatch at all sites is considerably less than in the first 150 days post-hatch. By the 300th day of post larval culture, the number surviving was 16-28% of the total number of crabs initially placed in the growout cage. Of the hatches initiated earlier in the study at site 1, while we were still developing procedural methods for larval rearing, the total number of crabs from each hatch surviving beyond 300 days was not sufficient to analyze statistically.

DISCUSSION

Crabs cultured at site 3 exhibited the greatest rate of early growth, attaining a mean size of 11.6 mm CL at 60 days. In general, when the crabs attained sizes of 10 mm CL or at 80-100 days post-hatch, they were transferred from the hatch cages to larger mesh cages. The larger screen mesh effectively decreased detrital buildup in the cage. At site 3 (compared with sites 1 and 2) crabs were larger throughout the entire culture period of 180 days. Up to 120 days, growth showed a log rate of increase (Figure 7). However, mean growth rates started to fall off after 100 days (less labor was available for feeding). In several cases (4 hatches) at site 3 the cultured crab population achieved growth rates up to 0.40 mm/day CL based solely on algal turf feeding. This can be partly attributed to the greater quality and quantity of algal turf biomass cultivated per screen per unit time and the ensuing benefits derived from higher feeding rates. This suggests that growth in crabs cultured at sites 1 and 2 was retarded through at least 100 days post-hatch. Crab growth rates increased at sites 1 and 2 to a comparable level attained at site 3 after 150-180 days culture, most likely due to lower crab density per cage (31 crabs/ m^2) and greater feeding rates.

Managing young larvae is not particularly time consuming, so that at sites with lower algal turf productivity we suggest that the easiest method to increase crab growth rates may be by splitting hatches into several cages (thereby decreasing crab density/cage), increasing algal turf screen rate of exchange into and out of the cages, and increasing the hatch cage size.

Zoea had metamorphosed to the first post-larval stage crabs by 144 hours post-hatch at all study sites. For the first 20 days post-hatch the fine meshed screen initially allowed adequate exchange of seawater through the cage. Eventually however, the fine meshed screen became clogged with microfloral algal growth as well as detrital material. This apparently decreased the water quality and exchange of clean water into the cage. As the crab biomass increased with time, mortality exponentially increased (Figure 8). In addition, if the algal turf screens that were placed into a cage were not fully grazed, the ungrazed algae then would die and slough off the plastic screen to collect at the cage bottom. This buildup of detrital matter (e.g., algal matter plus crab feces and crab molt shells) is thought to have substantially contributed to the fouling of the cages and increased crab mortality rates in the cages. A cage design allowing the removal of detritus, without damaging crabs, would greatly improve survivorship.

Crabs remained in the hatch cages for as long as 120 days in some cases. The resident crab population in each cage decreased with time. The first 60 days of cage culture resulted in approximately 13-26% survival at all sites. By the 70th day post-hatch, if the crabs were left in the hatch cage, crab mortality greatly increased. This necessitated the development of procedures to transfer crabs from the hatch cage to the larger mesh cages at the 80-100 day mark or at approximately 10 mm CL. The coarser screen mesh greatly enhanced the exchange of seawater through the cage and removal of detrital material from the cage. Crab survival to 100 days post-hatch was 5.29% (site 1); 2.92% (site 2); and 6.7% (site 3).

At site 3 survival decreased by 1/3rd from 60 days (survival = 23%) to 80 days (survival = 14%) post-hatch. It is believed that the greater cultured algal biomass per screen at site 3 contributed to a greater detrital buildup in the cage. The greater quantities of algal turf per crab increased crab survival rates, crab growth rates, and thus greater amounts of metabolic byproducts (feces, molt shells). The total detrital buildup in the cage appeared to reach a saturation point at approximately 60 days post-hatch, when a mass mortality of crabs occurred. Upon opening several cages (site 3) at 60 days post-hatch, 1/4th to 1/3rd of the total crab population was found to be dead, and lying on the bottom of the cages. This reinforces the concept that the waste products, due to increased biomass level (as compared to crab survival and size at sites 1 and 2) at 60 days post-hatch substantially increased the fouling levels of detrital material entrapped by the fine meshed screen. As mentioned above, a new cage designed to reduce detrital material might be critical to increasing survivability. Overall however, the greater number of crabs surviving the first 120 days of culture at site 3 is attributed to the increased feeding rate and earlier transfer of crabs to a larger mesh cage as compared to sites 1 and 2. Crab survival from 120 days post-hatch to the end of the culture period remained at a high level at all sites. Site 2 had the poorest level of survival (12%) from 120 days to 300 days, while the numbers surviving at sites 1 and 3 changed very little from 120-300 days post-hatch. At the end of the culture period the survival rates were 18% (300 days) and 28% (175 days) at sites 1 and 3 respectively.

In the investigation period reported here, growth time was not long enough to bring any crabs to market size, though the largest sizes attained (91.0 mm CL) (site 2) were only one to two molts away. During later unmonitored studies at site 1, several crabs were brought to adult size.

Evaluation of Rearing Systems

The dimensions and therefore surface area of the hatch cages was found to have the greatest influence in terms of success for these mariculture techniques. The initial larval and first post-larval stage crab densities in the hatch cages were much too high for the cage sizes used in this study. Several alternatives exist to ensure adequate feeding rates and space requirements. By enlarging the cage, the screen surface area may be increased. Hatch success therefore depends upon using a larger hatch cage and/or transferring five day post-hatch crabs from the hatch cage to several cages of similar design. This should increase the feeding rate as well as decrease the crab density and lessen the detrital buildup as the crab biomass is greatly reduced. All of these factors increase crab survival and growth rates, allowing the crabs to be transferred to a larger meshed cage at an earlier age.

Following 100 days post-hatch, the culture of crabs in open water cages approached levels of growth and survival necessary for mariculture operations. We suggest that the redesigning of the hatch cage to allow the removal of detrital matter etc., combined with proper, consistent algal turf feeding rates will significantly improve crab survival, as well as allow crab growth rates to attain mean values of 0.30 mm/day CL through 400 days post-hatch as achieved in several individual brood rearings.

Local fishermen were hired to work on the project at Site 1. Their initial level of marine husbandry skills was very low, but as the artisinal fishermen worked on the project, the level of skill and knowledge greatly increased. This is directly evident in Figure 9, where the relationship of the survival of crabs at 100 days post-hatch relates to the advancement of time of the study period. By day 500 of the study period, survival rates had increased by a factor of 10. Using the growth rates of figure 5 and the length to weight ratios developed by Porter _et_ _al_. (this volume), after 100 days cultured crabs double in weight every 25 days.

Although adult crabs in cages show little aggression towards each other, and very few incidents of dismemberment have been encountered, some of the relatively few juveniles kept in aquaria for observation have attacked and dismembered their cohorts. Rarely has such an attacked crab been eaten. The extent of this problem is not known and as a standard practice we have included pvc pipe habitats in cages to provide protection during molting.

It seems clear that if environmental quality is high, *M. spinosissimus* maintain relatively high, probably genetically fixed growth rates. Sometimes in this study the algal feed supplied was insufficient and this may have resulted in relatively low survivabilities. However, the often very high growth rates suggest another mechanism. In spite of the comments of Ryther *et al*. (1987), disease does not seem to be a factor in our work. The level of nitrate at 35 mg/l in the Ryther study is extremely high as compared to the wild environment (approximately 10,000 times higher) and suggests poor environmental conditions in that investigation. Even though adult crabs show little aggression in captivity, there is some evidence for mortal aggression in juveniles (see also Ryther *et al*., 1987). While we have typically provided molt habitats in many of our cages, these may well be inadequate. We are now trying a wide variety of habitat types.

CONCLUSIONS

Using the algal turf feeding methods and crab culture techniques described in this volume for M. spinosissimus, mean growth rates of approximately 0.27 mm/day CL from hatch to at least 280 days were achieved during the last six months of the study. Although from 180 to 280 days, growth rates exceeded 0.45 mm/day, beyond 280 days, data is minimal and only suggests a possible decrease in growth rates. Nevertheless, it should be possible to grow cultured crabs to maturity in less than 400 days.

Crab survivorship averaged 22% to 60 days, 23.6% from 60 to 120 days and 18.5% from 120 to 300 days. Methods of improving survivorship are discussed. In particular, increasing the cultured algal turf quantities available to each juvenile crab, providing a means of periodically and safely removing detritus from the juvenile cages and providing a variety of molt habitats in the adult cages should increase survivorship significantly.

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LEGENDS

Figure 1. Map of Caribbean showing coastal research field sites. Buen Hombre, Dominican Republic (site 1); Nonsuch Bay Antigua (site 2); and Grand Bay, Carriacou, Grenada (site 3).

Figure 2. Plastic screens (0.61 x 0.92 m, 2.0 x 3.0 mm mesh) for algal turf cultivation. Screens suspended vertically in the water column from the float line.

Figure 3. Hatch cage/intermediate cage. Hatch cage dimensions vary from 1.0 L x .35 W x .70 H, to 1.0 L x .60 W x .70 H with 0.5 mm mesh. Intermediate cage(1/4" mesh) identical in design to hatch cage but with dimensions as follows 1.0 L x 1.0 W x 1.3 H.

Figure 4. Growout cage. Dimensions are 2.6 L x 1.0 W x 1.0 H and hold 23 screens. Mesh size is 1/4" - 1/2".

Figure 5. Relationship of carapace length to age showing growth of algal turf fed _M. spinosissimus_ at sites 1-3. Points represent mean CL of n=5745 (site 1); n=2086 (site 2); n=479 (site 3).

Figure 6. Projected growth rate curve based on rates routinely achieved during the last six months of the project. Molt numbers and sizes based on figures 2 and 3 (Biddlecomb, _et al_., this volume) and figure 7 (this section).

Figure 7. Linear relationship of carapace lengths of crabs (site 3) at successive intervals of time (Carapace lengths transformed to logs) ($r = 0.96$); $y = 1.249 + 0.016\,x$; $n=479$).

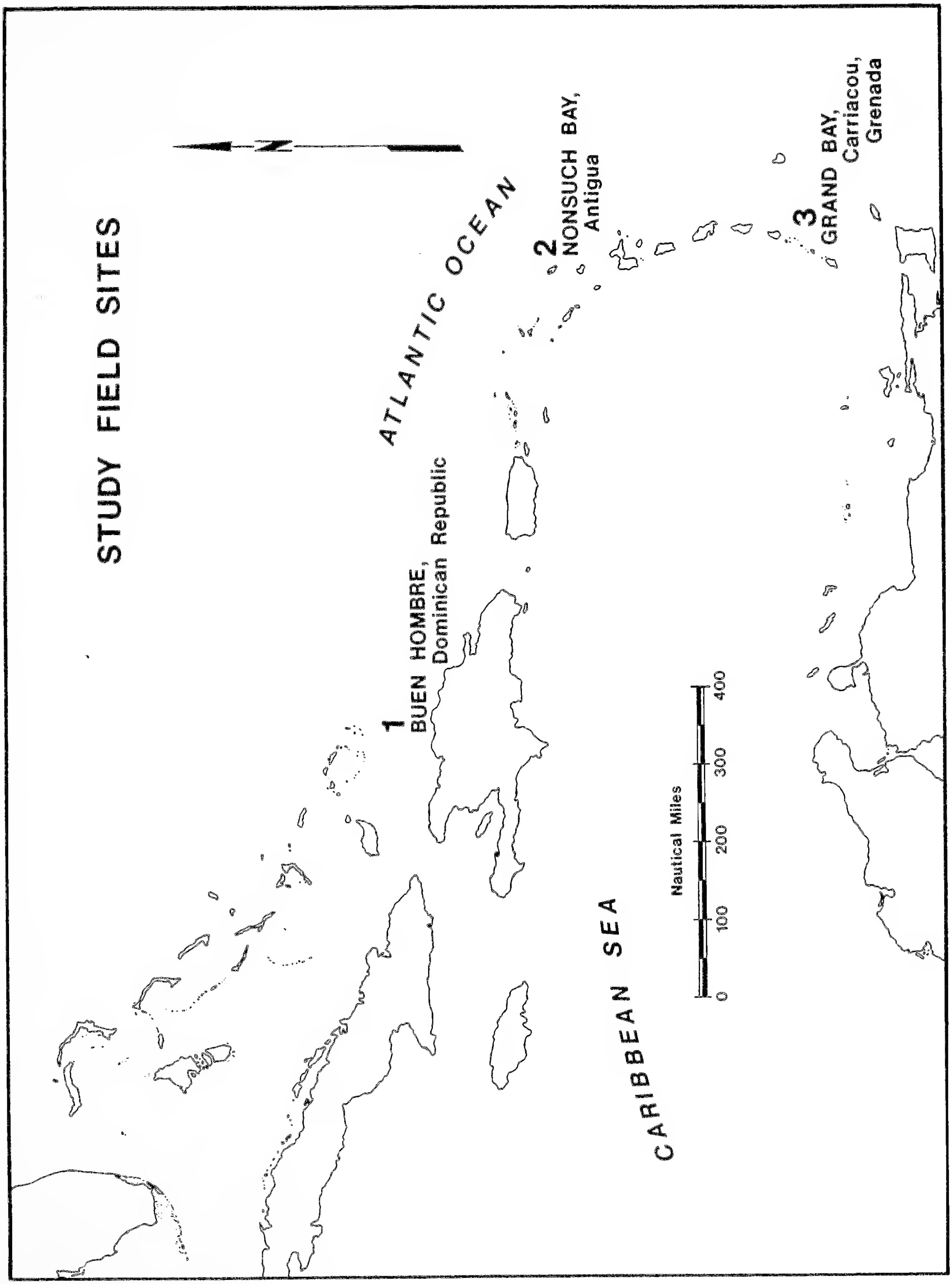
Figure 8. Relationship between age and survival of post-larval crabs. All post-larval crabs transferred to larger mesh cage at 100 days (site 1), 100 days (site 2) and 80 days (site 3). Site 1 crabs transferred again at 125 days. (Dashed lines represent transfer of crabs to new cages).

Figure 9. Relationship showing increase in success of culture technique refinement of post-larval culture of 100 day old crabs. # of hatches = 25; $y = 108.7$; SE ± 22.54

Table 1. Amount of algal turf fodder provided to crab culture cages and crab dimensions. Site 1.

Table 2. Amount of algal turf fodder provided to crab culture cages and crab dimensions. Site 2.

Table 3. Amount of algal turf fodder provided to crab culture cages and crab dimensions. Site 3.



STUDY FIELD SITES

Figure 1

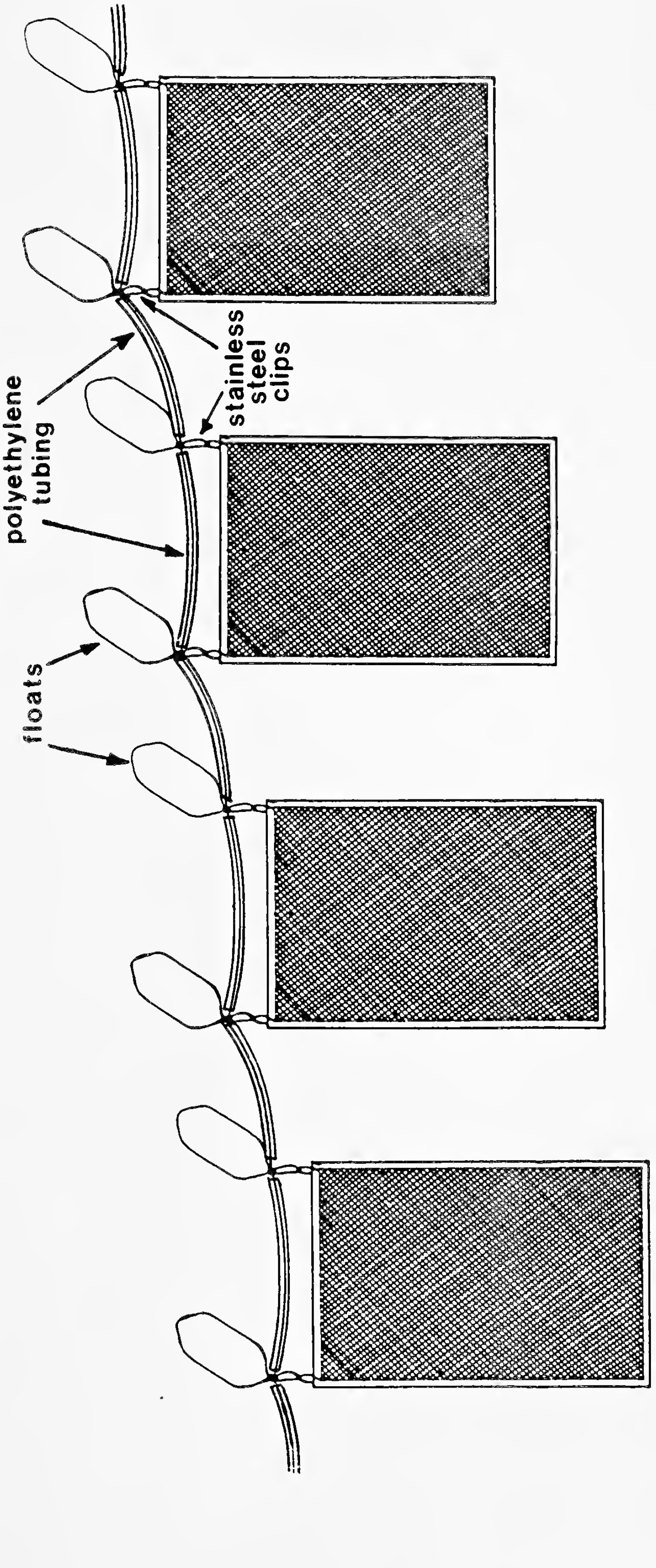
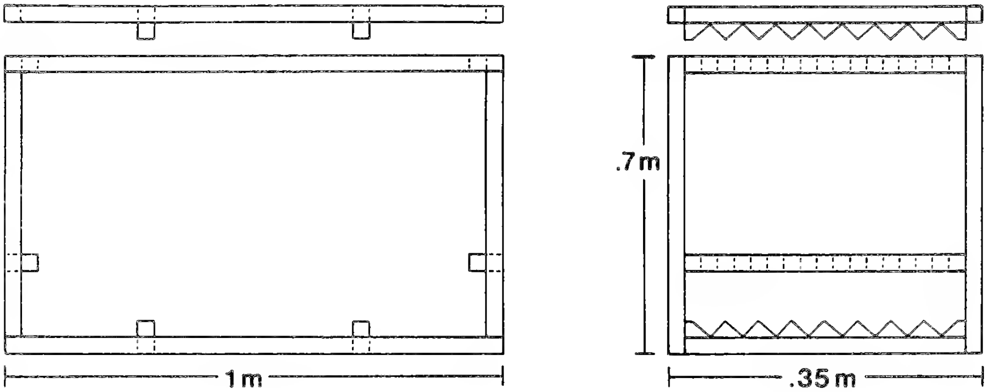
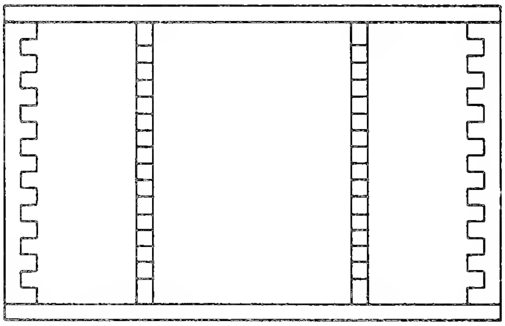


Figure 2



SIDE VIEW WITH LID

END VIEW WITH LID



TOP VIEW

Figure 3

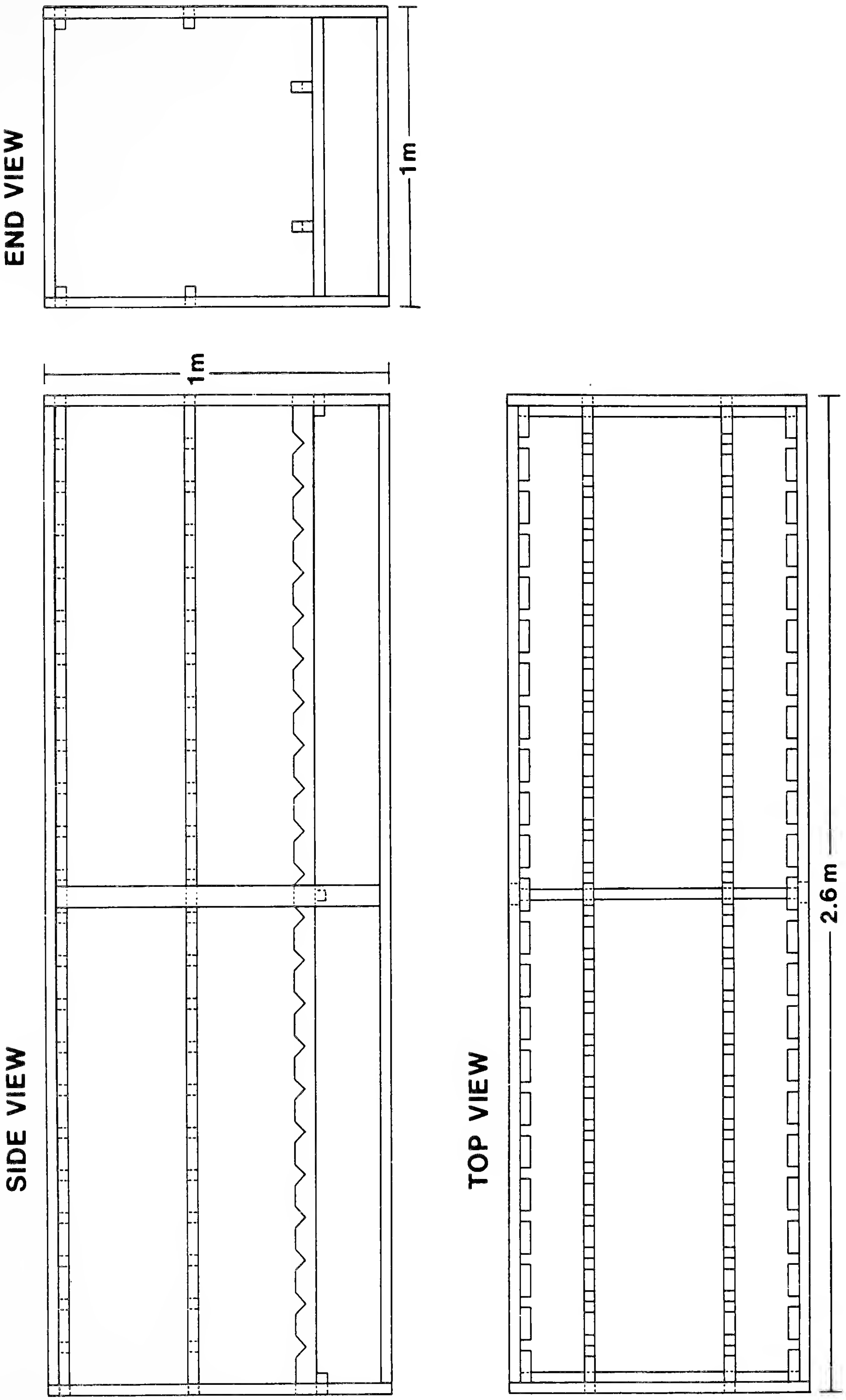


Figure 4

NUMBER OF CRABS MEASURED

■	469	493	488	607	1614	516		1059		274		95		130	
X	212	218	355	307	717	96		124		28		15		14	
●	62	37	269	20	17	52	10	1	11						

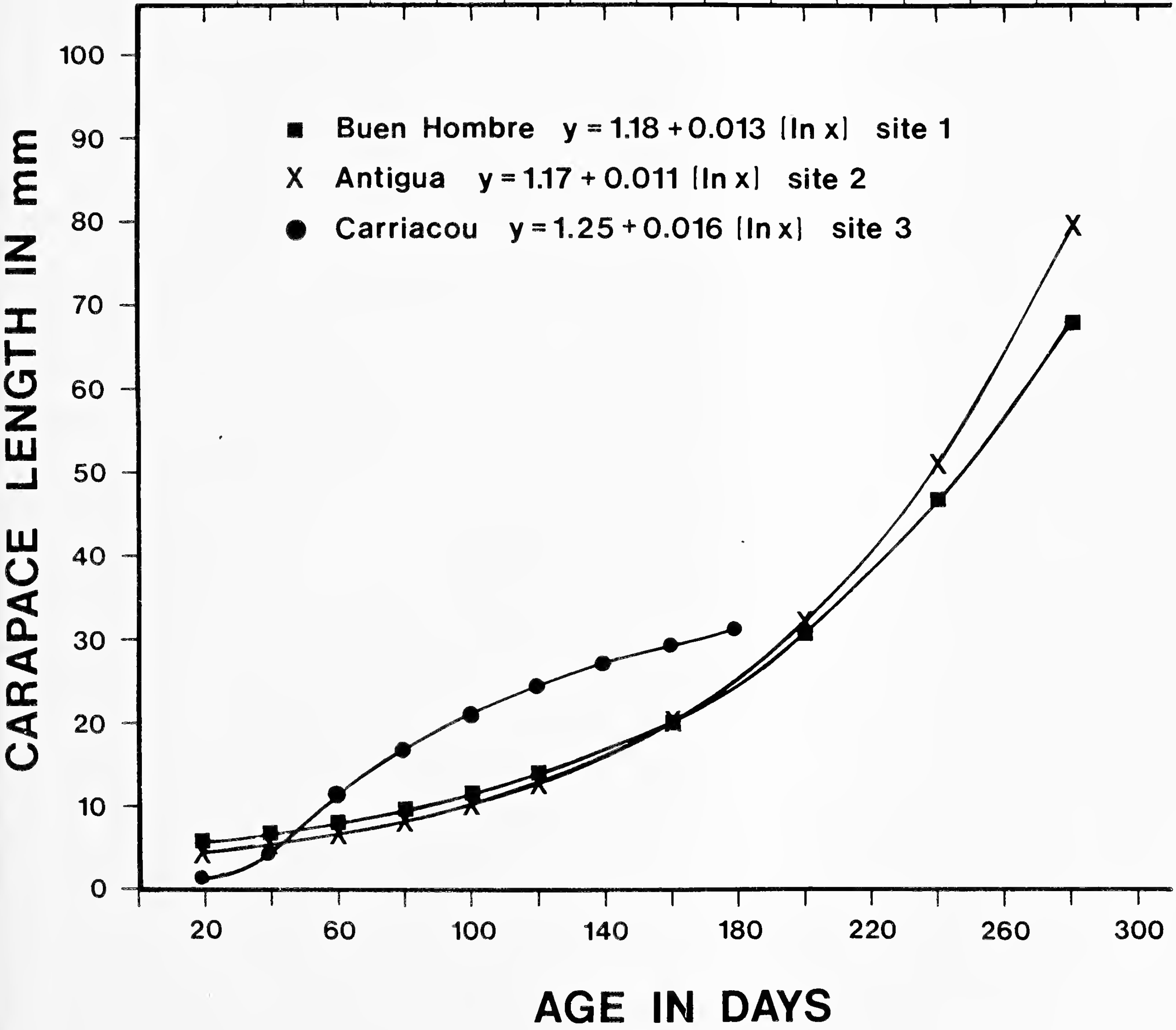


Figure 5

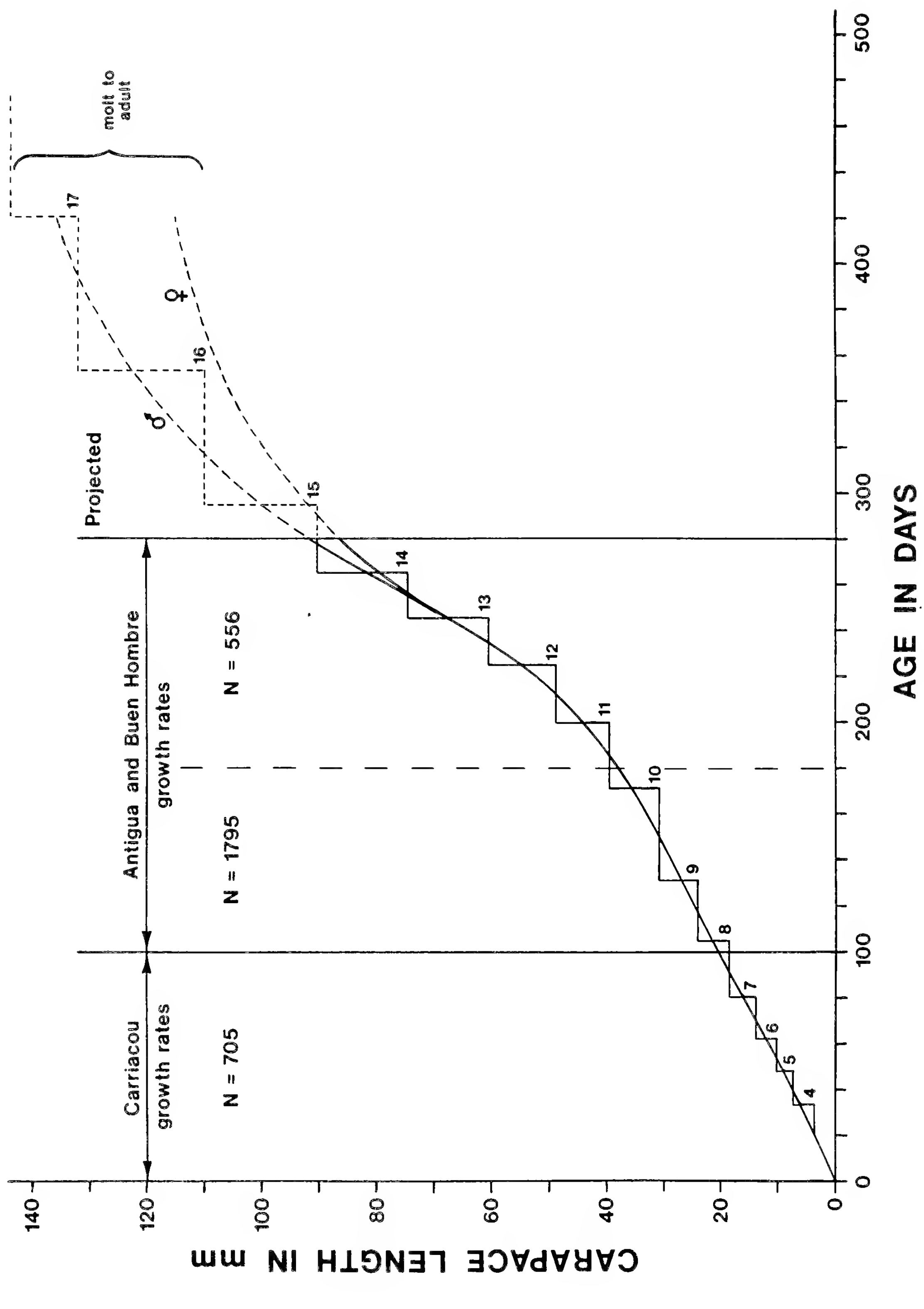

CARAPACE LENGTH IN mm
0
20
40
60
80
100
120
140
AGE IN DAYS
0
100
200
300
400
500
Carriacou growth rates
N = 705
Antigua and Buen Hombre growth rates
N = 1795
N = 556
Projected
molt to adult
♂
♀
4
5
6
7
8
9
10
11
12
13
14
15
16
17

Figure 6

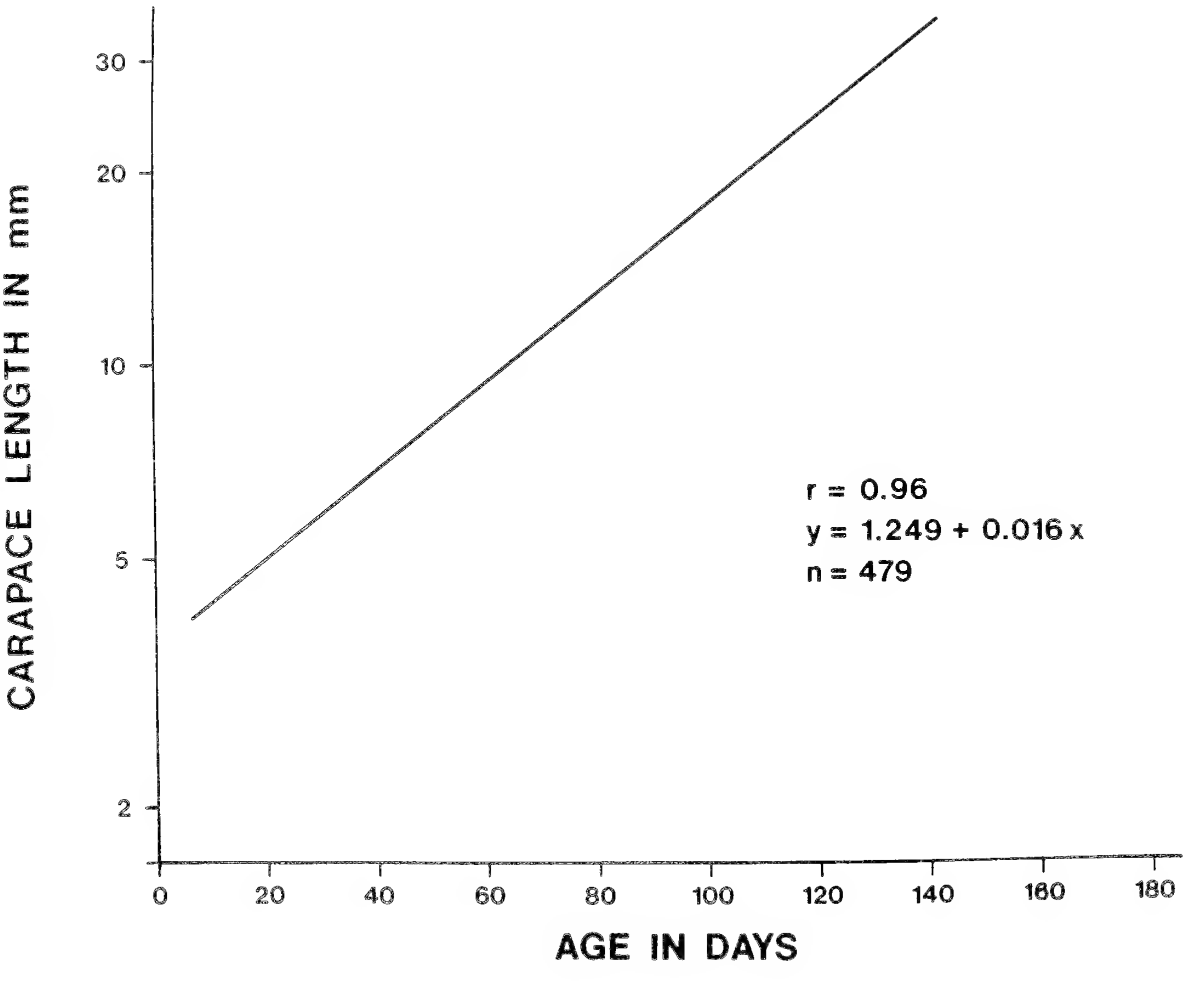

CARAPACE LENGTH IN mm
30
20
10
5
2
0
20
40
60
80
100
120
140
160
180
AGE IN DAYS
r = 0.96
y = 1.249 + 0.016 x
n = 479

Figure 7

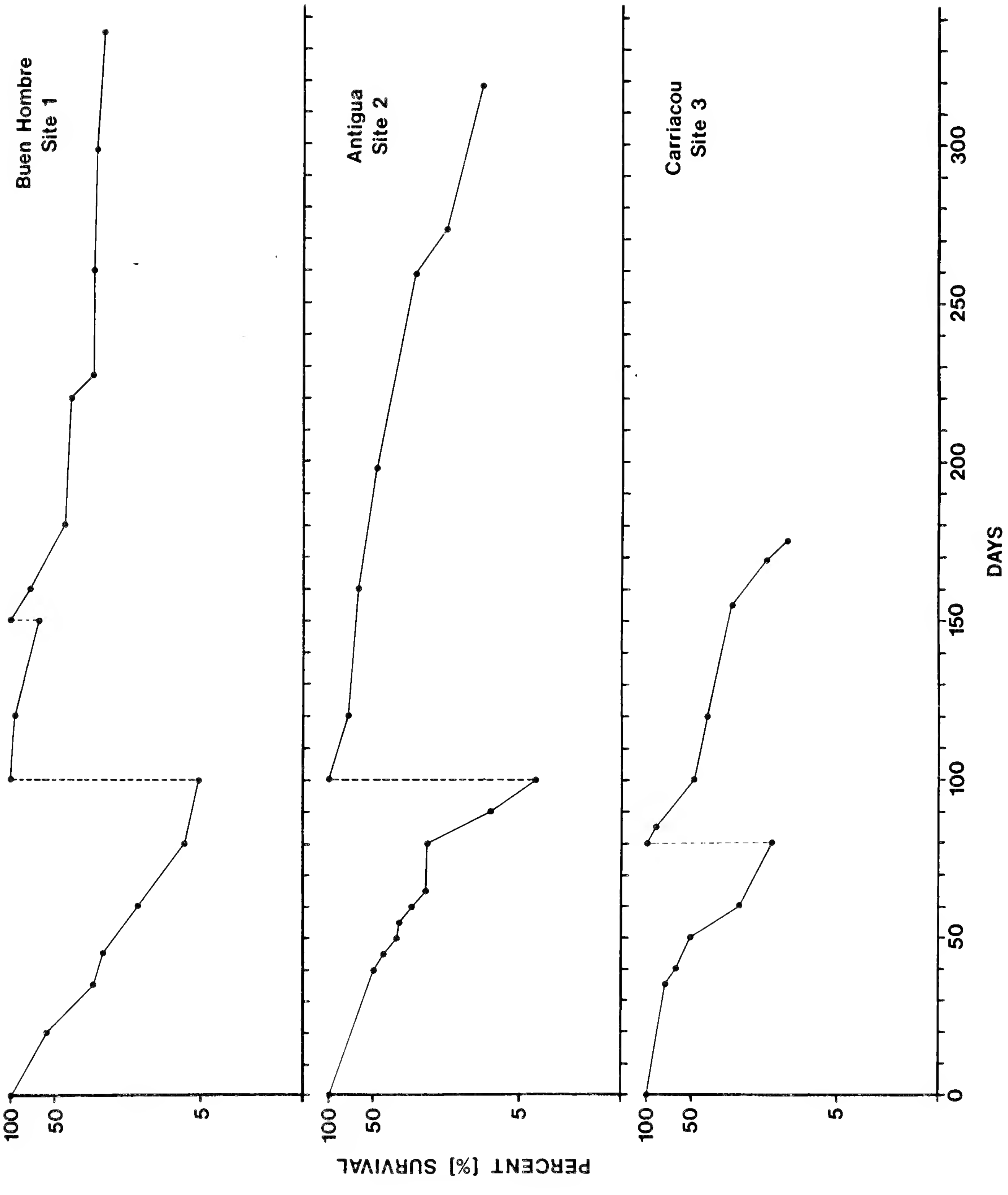

Buen Hombre
Site 1
Antigua
Site 2
Carriacou
Site 3
PERCENT (%) SURVIVAL
100
50
5
DAYS
0
50
100
150
200
250
300

Figure 8

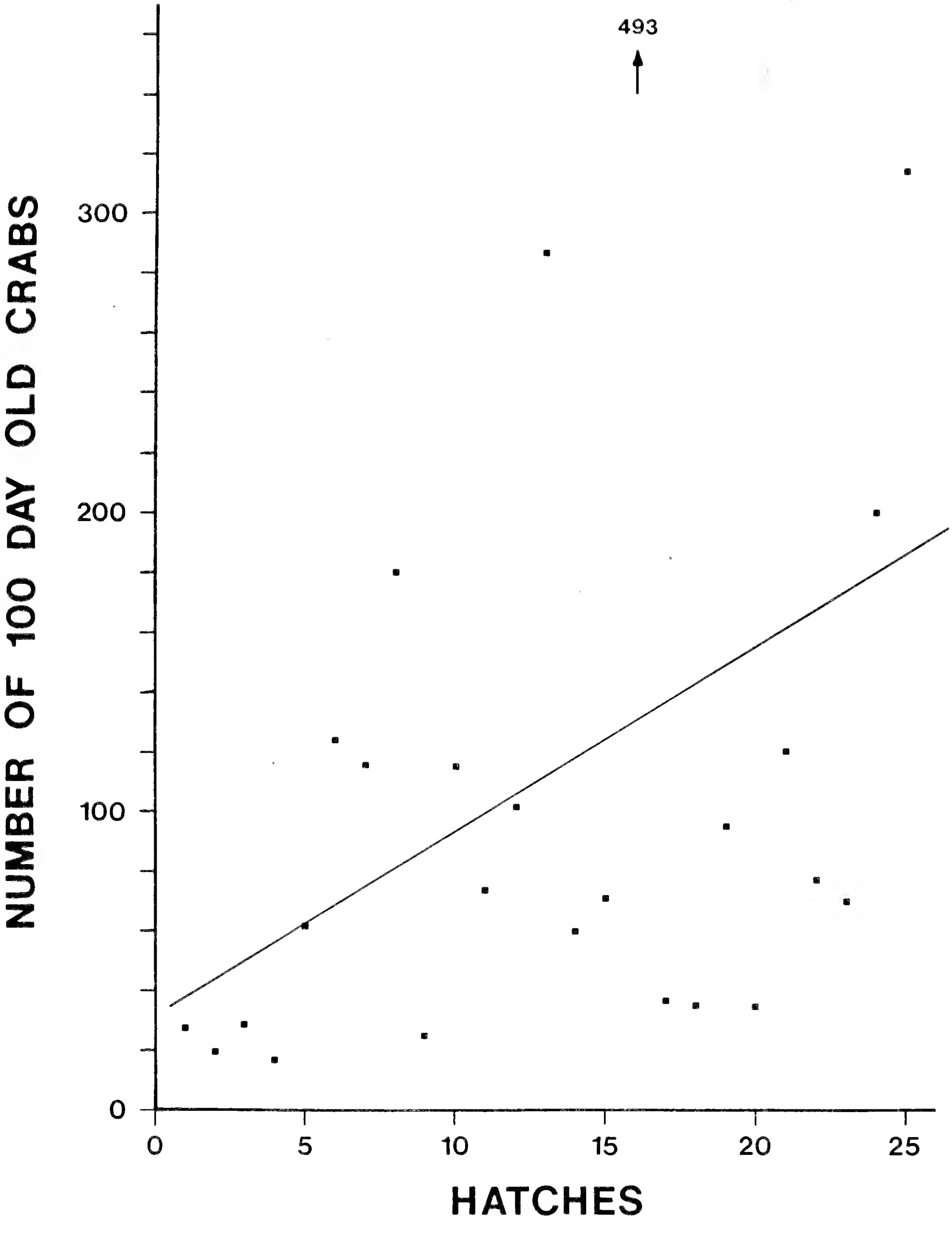

493
NUMBER OF 100 DAY OLD CRABS
300
200
100
0
0
5
10
15
20
25
HATCHES

Figure 9

TABLE 1 SITE 1

AMOUNT OF ALGAL TURF FODDER PROVIDED TO CRAB CULTURE CAGES AND CAGE DIMENSIONS

	Hatch cage	Intermediate cage	Growout
Dimensions (meters)	1.0 x .35 x .70	1.0 x 1.0 x 1.3	1.2 x 1.2 x 2
Cage surface area	2.6 sq. m	7.2 sq. m	13 sq. m
Cage volume	0.3 cu. m	0.5 cu. m	3.6 cu. m
Screen feeding rate	2 screens/ 5 days	6 screens/5 days	4 screens/5 days
Total Algal Turfs	98.3 gm(dry)/5 days	655 gm(dry)/6 days	364 gm(dry)/ days
Initial Algal Feed Rate crab/day	0.05 gm/crab/5 days	6.36 gm/crab/5 days	5.6 gm/crab/ 5 days
Algal Turfs per crab per day	0.01 gm/crab/day	1.27 gm/crab/day	1.1 gm/crab/ day
Initial Density Crabs/area of cage surface	769/sq. m	14.3/sq. m	5/sq. m

TABLE 2 SITE 2

AMOUNT OF ALGAL TURF FODDER PROVIDED TO CRAB CULTURE CAGES AND CAGE DIMENSIONS

	Hatch cage	Growout cage
Dimensions (meters)	1.0 x .35 x .70	2.6 x 1.0 x 1.0
Cage surface area	2.6 sq. m	12.4 sq. m
Cage volume	0.3 cu. m	1.8 cu. m
Screen feeding rate	2 screens/ 3 days*	6 screens/4 days*
Total Algal Turfs	117.9 gm(dry)/3 days	874 gm(dry)/4 days
Initial Algal Feed Rate crab/day	0.06 gm/crab/3 days	15.3 gm/crab/4 days
Algal Turfs per crab per day	0.02 gm/crab/day	3.8 gm/crab/day
Initial Density Crabs/area of cage surface	769/sq. m	4.6/sq. m

* -- Site 2 algal turf production was heavily biased by entrapped sediment, therefore the true algal turf production may be considerably less. See Adey and Hackney in this Volume.

TABLE 3 SITE 3

AMOUNT OF ALGAL TURF FODDER PROVIDED TO CRAB CULTURE CAGES AND CAGE DIMENSIONS

	Hatch cage	Growout cage
Dimensions (meters)	1.0 x .60 x .70	2.6 x 1.0 x 1.0
Cage surface area	3.4 sq. m	12.4 sq. m
Cage volume	0.4 cu. m	1.8 cu. m
Screen feeding rate	3 screens/ 6 days	9 screens/5 days
Total Algal Turfs	305 gm(dry)/6 days	1368 gm(dry)/5 days
Initial Algal Feed Rate crab/day	0.15 gm/crab/6 days	5.0 gm/crab/5 days
Algal Turfs per crab per day	0.03 gm/crab/day	1.0 gm/crab/day
Initial Density Crabs/area of cage surface	581.4/sq. m	22.3/sq. m

SECTION III: MARICULTURE TECHNIQUES

MARICULTURE TECHNIQUES FOR *MITHRAX SPINOSISSIMUS* INCLUDING BROODSTOCK LARVAL AND POST-LARVAL REARING AND GROWOUT TECHNIQUES

MARICULTURE TECHNIQUES FOR MITHRAX SPINOSISSIMUS INCLUDING BROODSTOCK LARVAL AND POST-LARVAL REARING AND GROWOUT TECHNIQUES

K.L. Porter, J.M. Iglehart, M. Craig and W.H. Adey

INTRODUCTION

Innovations developed over the past 50 years in the fishing industry have produced a world fish catch totaling approximately 70 million metric tons annually (Pillay, 1985; 74.8, Simon and Kahn, 1984; 74.0, Brown, 1985). The use of electronic equipment and modern fishing vessels caused a six percent increase per year in the total catch in the 1950's and 1960's. In the last decade, however, the total worldwide fish catch has increased less than one percent per year, accompanied by serious reductions of fish stocks in some important fisheries. This worldwide depletion of the fishing stocks has resulted in a more concerted effort to develop aquaculture and mariculture. Annual worldwide output of aquaculture products now exceeds 10.5 million metric tons (Pillay, 1985).

In the late 1970's and early 1980's, Smithsonian scientists of the Marine Systems Laboratory (MSL), while conducting microcosm research, developed a technique for culturing algal turfs on artificial substrata to manage the water quality in closed systems (Tangley, 1985; Adey, 1983; Adey, 1987). This technique reproduces, in manageable form, the high algal turf production levels that characterize these benthic algae communities in the wild. In these "scrubber" systems, laboratory production levels of five to over 15 g dry m^{-2} d^{-1} are common. Algal turf production levels of 8-18 g dry m^{-2} d^{-1} are attained when similarly designed "algal scrubbers" (in this case, suspended plastic screens) are anchored in turbulent tropical Caribbean waters (Adey and Goertemiller, 1987; Figure 1).

The highly diverse and productive algal turfs are consumed by a wide variety of animal grazers in the wild. However, a direct use of algal turfs for humans has yet to be developed. Many modern maricultures and aquacultures are capital intensive, require considerable technological expertise and utilize expensive industrial food preparations. It was hoped that a system could be developed that would allow local fishermen in underdeveloped countries the means to tap this rich and readily available food source.

Mithrax spinosissimus (Figure 2), a large tropical spider crab, which consumes smaller benthic algae and algal turfs naturally, was chosen as a potential candidate for this new approach to mariculture. A full life cycle mariculture for this Caribbean King Crab has been developed for utilization in developing countries with low technological capabilities. While brooding, hatching and juvenile growout have been quite successful for a "low tech" mariculture based on early pilot studies, late juvenile mortalities have been higher than predicted. Efforts directed at improving late juvenile growout techniques are continuing. No published efforts have been undertaken previously to develop an operational mariculture for Mithrax spinosissimus, although several preliminary biological studies have been carried out. These previous studies are discussed in detail in the earlier sections of this volume.

For the past three years, the development of Mithrax spinosissimus mariculture by MSL has been funded by the United States Agency for International Development. As part of this project, Mithrax spinosissimus cage culture has been conducted in a number of Caribbean/West Indian islands, including the Turks and Caicos Islands, the Dominican Republic, Antigua and in Carriacou, Grenada (Figure 3).

Mariculture production techniques for Mithrax spinosissimus, as developed by MSL, have been separated into care of brooding females, hatching, juvenile, older juveniles and immature adult phases. Gravid females, obtained from the wild and brooded in captivity, have provided a regular and reliable supply of newly hatched juvenile crabs. A gravid female, which produces an average of 60,000 eggs every two months (Craig, et al., this volume), is placed in a sea-cage prior to hatching. Such "hatch cages" (90 X 40 X 110 cm) are made of a wood frame, coated with polyester resin and covered by a fine (0.5 mm) plastic mesh screen. Newly hatched crabs (approximately 2000 first post larval instar crabs at five days post-hatch) are left in the "hatch" cage until 60 days post-hatch. At that time, they are transferred to an identically designed cage, which is covered with a coarser mesh screen for the next 40-60 days. These methods have produced 100-400 juveniles from each hatch surviving to 100-120 days old. Crab growth rates and survival following hatch depend in large part upon the amount of algal food made available and the density of juvenile crabs in relationship to algal turf screen area. Care in construction of cages and in management of stocking and feeding is also required to avoid the introduction of predators or algal turf competitors, which are primarily small invertebrates.

Growout to harvest of Mithrax spinosissimus is carried out in similar wood frame/plastic cages (2.2 X 1.0 X 1.0 m) enclosed with plastic mesh (1/4-1/2"). When the crabs are 100-120 days old, they are transferred to these juvenile/adult growout cages which are designed to hold 30-50 harvestable crabs. To date, our work indicates that a crab requires 12-15 months of growth to reach a harvest size of 0.8-1.3 kgs, though it is quite likely that further refinement can both shorten the time and increase the size of the harvested animals. Crab survival rates in these growout cages need to be about 50%, yielding 50 harvestable crabs per cage to be successful. Chronic mortality has led to a survival rate of 15-25% per 100 days. Small predators in the cages, excessive wave action during molting and aggressive interactions of the crabs appear to be responsible. This last phase to improve survivorship requires additional research effort. It is thought that the problems can be solved by cage design and efforts are underway at Grand Turk to achieve this.

In the MSL mariculture technique, turf algae is the primary food source for cultured *Mithrax spinosissimus* crabs. Though labor intensive, it is replenishable and easily grown as well as highly productive and highly nutritious. Laboratory analysis shows the algal turfs to contain 8-10 grams of protein per 100 grams (dry) of algae.

During the latter part of the early juvenile stage and during the entire growout stage, algal covered plastic mesh screens are fitted into the cages. As the crabs consume the algae, the screens are replaced every three to four days. The algae is cultivated on screens suspended from lines that are floated in turbulent waters. Wave action, current and sunlight in a low nutrient water environment provides optimal conditions conducive to algal turf growth on these plastic screens. Before being placed in a crab cage the plastic screens must have sufficient algal growth, which takes 20-40 days to initiate. However, repeated feedings typically require 7-14 days for sufficient algal re-growth. Algal growth rates are variable during the year due to changes in weather and other environmental factors. Sunny, windy weather, typical of the "trade" wind islands, produces maximum algal growth. Environments consistently rich in suspended carbonate sediment need to be avoided as continual sediment accumulation on the screens must be removed or algal production will suffer.

The changing of screens and the tending of the juvenile crab and growout cages is labor intensive. A one man operation utilizes 24 growout cages with accompanying juvenile and intermediate cages and about 800 screens. The operation requires six to eight man hours per day. However, as in most fisheries and in agriculture, it is desirable to carry out a larger operation using teams.

In several Caribbean countries, including the Dominican Republic and Belize, the wild harvest of Mithrax spinosissimus in traps forms a small but important fishery. This animal is generally regarded as a delicacy and is served in seafood restaurants. Although older crabs often have a tough shell, cultured animals, especially those newly molted to maturity, have a thin shell. The Caribbean King Crab has a sweet, textured meat, concentrated in the outer body, legs and in the large chelae of the males. At 18-35% of total body weight, harvestable meat is considerable.

BIOLOGY OF CULTURED CARIBBEAN KING CRAB

This study treats the species of crab commonly known as both the "West Indian Giant Red Spider Crab" and the "Caribbean King Crab." In Spanish speaking Caribbean countries, it is generally referred to as "Centolla." The species' name is *Mithrax spinosissimus* and it is one of the evolutionarily more advanced members of the *Mithrax* family (Goy *et al*., 1981). The biological and ecological aspects of this species pertaining to mariculture are briefly reviewed.

Caribbean King Crabs are generally found throughout the tropical Western Atlantic, from southern Florida and the Yucatan through the West Indies, to eastern Venezuela at depths of 2-200 meters. Individuals may be encountered at night as they feed on reef or pavement surfaces, during the day they tend to be confined to caves and crevices at depths of 2-30 meters often in small "communities" or harems. In these daytime hideaways, there are usually several females in close proximity to one another, often with one or two males. On the other hand, additional "bachelor" males tend to be isolated and distantly dispersed. The abundance of *Mithrax spinosissimus* in the Caribbean/West Indian area varies greatly from island to island and from site to site. Although a quantitative survey of the entire Caribbean has not been done, it appears that crab distribution and abundance are a function of the availablity of appropriately-shaped caverns or crevices and probably the proximity of good algal feeding grounds. (See notes from population surveys in Jamaica: Munro, 1976; Florida: Bohnsack, 1976; Hazlett, 1975; Dominican Republic, Antigua, Turks and Caicos and Mayaguana: Iglehart, et al., this volume; and Belize: Koltes, personal communication.) It is likely that the abundance of fish, crab and octopus predators are also crucial in determining Mithrax distribution and abundance.

With knowledge of the local reef terrain, Mithrax spinosissimus is most easily obtained by SCUBA from dusk into the evening. Crabs may also be caught in traps. Wild Mithrax spinosissimus population sizes vary from reef to reef (Iglehart, et al., this volume). While the very real likelihood of stock improvement through breeding exists, the initial breed stock is quite important. In this context, crabs from the Florida region are by far the smallest and therefore least desirable (Iglehart, et al., this volume).

The extensive observation of both wild and captured crabs during the process of feeding, the growth and development of the crabs in culture on a diet of algal turfs and the examination of crab stomachs and the structure of both the chela and gastric mill all support the conclusion that M. spinosissimus is a facultative herbivore on smaller algae. In the course of grazing, organic detritus, sediment, coral bryozoans, and other small organisms (eg., amphipods) are almost invariably ingested. While M. spinosissimus is not particularly discriminating in its choice of algae, some macroalgae are strictly avoided. When a wide variety of algal turf, along with some macroalgae are presented on cultured screens, the turfs are almost invariably eaten before the macroalgae. Mithrax spinosissimus will eat meat (conch, urchin, e.g.) when provided. However, it has not been demonstrated that meat is necessary in any way for growth or reproduction. The highest known growth rates and maximum egg production have been achieved on a pure algal turf diet.

The large claws or chelipeds terminate in long narrow fingers with crenulated spoon shaped tips. These aid in the digging and sifting of the substratum for algal material and also provide strong sharp tools for the cutting, tearing and pulling of algal holdfasts and stalks. The paired appendages associated with the endostome "teeth" hold and tear food and assist in respiration (For more information on feeding mechanics, see Coen, 1987)

The gastric mill, located inside the mouth between two stomachs, is well-developed for algal turf feeding. The urocardiac ossicle has a single large "grinding" tooth and two smaller, more pointed ones. The opposing zygocardiac ossicles are ridges and most likely perform crushing and chewing motions. A small row of soft spines are located opposite the urocardiac ossicle side of each zygocardiac ossicle. These are not connected directly to either ossicle and most likely are utilized to transfer food in and out of the gastric mill.

Research to date has not focused on providing phytoplankton to the larval stages. While good planktonic feed might improve their survivorship at 30-50 hours post-hatch, survival of 2000 post-larval crabs from a single brood is normal without special plankton feeding. After settling, they shift over to microbenthic algae in algal turfs (particularly diatoms), through the megalopae and early crab stages. From 1-10 mm CL, the young crabs feed upon diatoms, blue-green algae, organic detritus and smaller turf algae. As they grow to carapace lengths of 10-25 mm CL, the larger algal turfs form the majority of the diet. For crabs above 25 mm to 80 mm CL, the natural diet is primarily composed of larger algal turfs with some included macroalgae. The final period of growth is characterized by a diet including a wide variety of benthic algae, excluding many of the algal species that are mildly toxic, or protected by carbonaceous or similarly tough cortex. Note that similar crabs in Florida and apparently some other areas in the northern and western Caribbean, especially in those growing in mangrove communities, are much smaller (Iglehart, _et_ _al_., this volume). They may be a separate species or subspecies.

In natural waters, Caribbean King Crabs attain carapace lengths of 120-180 mm, weighing 0.8-3 kgs. Under culture conditions, crab growth rates are a function of density and algal turf feeding rates, as well as the food conversion rates of the crabs. The daily linear growth rates of _M._ _spinosissimus_, under conditions of constant algal turf and macroalgal feeding, have been found to be initially 0.10-0.20 mm CL/day ranging up to over 0.50 mm/day at 200 days, thus attaining a mature weight of 0.8-1.8 kgs and 100-150 mm CL at 12-15 months growout (Figure 4). Wild crabs are known to achieve a weight exceeding 2 kgs, probably at an 18th molt. It is not known whether this can be achieved in culture.

M. spinosissimus undergo a molt of puberty which is generally the final molt, wherein both males and females take on their final adult secondary sexual characteristics. There is some question as to whether or not they undergo a second molt. This could be important to the mariculture of very large animals (Biddlecomb, et al., this volume). Copulation has been observed among hardshell crabs that have passed through the molt of puberty.

On average, every 60 days, females produce a batch of eggs. Subsequent egg clutches are fertilized by sperm which are stored in spermathecae. The sperm remains viable in the spermathecae for an extended period of time, though secondary mating may occur. Mating and fertilization occurs easily in captivity in both aquaria and cages.

Crabs may be ovigerous at any time of the year. Egg development requires approximately 30 days, at which time 40,000-70,000 eggs are released (Table 1). In the early stages of development, the fertilized eggs (about 1 mm in diameter) are attached to the female pleopods and are orange in color. As embryogenisis proceeds, they change to an orange-brown, red and finally amber-red color. Towards the end of the egg development cycle, the eggs are actively brooded by the female and the frequency of cleaning and aeration of the brood is increased. Normally, it is possible to determine time of release, within a day or two (Craig, *et al.*, this volume), by sampling and observing the eggs closely. The eggs almost always are released at night. The entire process of maintaining a breeding population and bringing the eggs to a successful hatch in a cage situation in the water is relatively simple and has been accomplished approximately 150 times using the methods outlined below.

Newly hatched *M. spinosissimus* larvae normally develop through: 1) a non-swimming prezoeal stage; 2) swimming first (two hours post hatch) and second zoeal (36-48 hours post hatch) stages; 3) a non-swimming, benthic megalops (40-72 hours post-hatch); and then 4) first crab (70-90 hours post-hatch) (Figure 5).

Crab growth is dependent upon temperature, molt frequency, food quantity and quality and the stage in development. Molting is the primary method of growth. Increments of molt show an average of 30-40% increase of carapace length per molt in the early juveniles decreasing to 10-25% for the pre-adult and adult molts. After the early juvenile stages, considerable overlap in carapace sizes between instar classes occurs.

Growth is rapid in juvenile crabs. Second instar to eighth instar molt frequencies decrease from about 4-6 day intervals (ie., between first and second instar) to 18-20 days by the 60th day post-hatch. Juvenile crabs are spiny, rather elongate and often heavily decorated with algal turfs. Not until the eighth crab instar does the overall appearance resemble that of the immature adult form (Biddlecomb *et al.*, this volume).

Not including "Florida crabs," puberty is estimated to be attained at the 16-17th post-larval molt or under optimum growing conditions, approximately 8-12 months post hatch. Growth of younger juvenile males and females is only slightly, i.e., all the parts increase in size at roughly the same rate. However, as they approach and then become sexually mature, the growth of the males is allometric (with regard to their large chelae) and the females' growth is allometric with regard to their abdomen width. The range of sizes (CL) at which sexual maturity is attained varies considerably. Excluding "Florida crabs" and similar small populations, the mean size of sexually mature females from many sites is 124.5 mm CL, 0.9 kgs; and for males 144.8 mm CL, 1.5 kgs.

SELECTION OF CRAB MARICULTURE SITES

General

Two basic factors are crucial in site selection for *Mithrax spinosissimus* mariculture as described in this paper: 1) a shallow, turbulent (wave and current) and moderately sediment-free locality for growing algal turfs; this should be in reasonable proximity to 2) a moderately quiet lagoon, with some current. We have found that sites where a coral reef breaks the surface at low tide are ideal as they provide sufficient protection of a lagoon area in which both algal turfs and crab cages can be kept and easily worked from small boats.

Ideally, such a site should have a broad back reef flat or sandy reef apron of two to four meters depth with constant wave surge and wave driven currents for algal growth. It is then desirable to locate crab cages in somewhat calmer shallow lagoonal water of two to six meters depth, not too far from the algal screens. Moderate currents are desirable. A sandy bottom substratum allows maximum reflective light for algal turf growth. However, water of relatively high clarity is desired. Excessive suspended sediment entrains within the algal turfs and eventually reduces algal growth. If this occurs only occasionally, under storm conditions, it can be managed by lightly brushing the screens. If it occurs frequently, algal production is considerably reduced. Water temperature should average 23-30°C year round with a salinity of 33-38 ppt. In addition, the more remote a site from boat traffic the better, as the extensive algal turf screen and crab cage system requires a large area.

Numerous sites that fulfill these general requirements exist throughout the Caribbean and West Indies. Of the five sites we have worked at extensively, four were quite good (Mayaguana, Grand Turk, Buen Hombre and Carriacou). Nonsuch Bay, Antigua was generally too turbid.

Requirements for algal turf growth

Mature algal turf screen cultivation results in biomass productivity rates of 8-18 g dry m^{-2} d^{-1} over 7-14 days growth. An appropriate algal turf community develops four to eight weeks after emplacement of the screen on the water. It is desirable to scrape the screens with a hand held piece of plastic once or twice during this period. After the start-up or colonization period, periodic harvesting of the algae every 7-14 days mimics grazing and results in high, continuous biomass production. The harvesting (or grazing in natural, benthic algal turf communities) prevents overgrowth and competition for available space, light and nutrients. Generally, the turf screens must be harvested on a regular basis or undesirable algae and animals colonize the screen. If screens have been allowed to overgrow with undesirable organisms, it may be necessary to remove, dry and clean them before the full efficiency of algal turf growth can be achieved again. If algal turf screens are not to be regularly used for feeding animals, it is necessary to regularly scrape them to keep production level high.

Algal turfs are dense mats of small, anatomically simple algae (usually less than several centimeters in height) belonging to all major groups of benthic marine algae. The algal species, which compose the complex turf associations, tend to be anatomically simple as compared to the more morphologically differentiated macroalgal types, although a few complex miniature macroalgae are important turf elements as well. With almost all cells of the algal thallus participating in metabolite exchange and active photosynthesis, the energy efficiency of algal turfs is higher than in other more complex plants. Since these algae rely on rapid growth and reproduction to survive, they are not characterized by protective skeletons or toxic defense chemicals.

a) Light

Algal turfs in a area of strong current and wave induced oscillatory flow are able to maximize production in high light intensities. However, in these brillantly-lit situations, ultraviolet light levels are also high, and U.V. usually has a detrimental affect on organisms, including algae. Considerable testing (Adey and Hackney, this volume) has demonstrated that algal turf production levels at the surface in tropical seas are well below those at 20-100 cm. Also, since a screen has two sides (equivalent to the extensive surface area of a reef) and production on the underside of horizontal screens is somewhat reduced, the transmission of light through the screen and reflection off shallow sandy bottoms is also critical to maximizing production. It has been shown that white, translucent screens are more productive than black screens. In practice, since horizontally suspended screens must be hung from four points (thus doubling the time required to remove and re-string a screen from a line), the screens are hung vertically. Other factors being equal, algal turf production on vertical screens is slightly less than the production from horizontally suspended screens. However, the time factor involved in the management of the horizontally suspended screens more than outweighs the decrease in algal production.

b) Water Motion

Trade winds and their seas drive ocean water over reefs and across the back reef flats to the lagoon. In addition, the shallowing water in these localities compresses the flow of the equatorial current, raising flow rates from that source. Waves approaching 15-50 cm in height on the backreef or lagoon side, with currents of 5-35 cm/sec, are ideal for growing algal turfs on screens. Yet these conditions are not generally so rough that the maintainence of those screens without serious losses due to overly rough sea conditions is a serious problem.

Screens must be held rigid to some extent in order to force contact with the turbulent water and to maximize algal turf growth. Thus, the screens are hung vertically and perpendicular to the general movement of the waves and currents. A moderately sized weight, such as a piece of 1/4" reinforcing rod, or sand fill in the p.v.c. pipe frame, on the lower side of each screen frame assists in providing "rigidity" against the flow and surge. As the algal turf develops, the screens become more buoyant and gradually lift to about an angle of 45°. Thus, once familiar with the strength of the current at a site, a glance at the angle of the screen line is usually enough to assess the maturity of the algal growth.

c) Sediment

Algal turfs do not require the presence of fine carbonate sediment to provide maximum production rates, and in laboratory culture, with wave surge and lighting (exceeding 1000 $u/m^2/$ sec), production rates of 5-18 g dry m^{-2} d^{-1} have been achieved without significant carbonate inclusion. In reef environments with low sediment loads, production rates near to or slightly higher than those in the laboratory are achieved. At higher concentrations of suspended sediment, apparent algal production rates (as measured by dry weight) initially appear higher (to over 30 g dry m^{-2}/d^{-1}) (Peyton _et_ _al_., in review), but after several weeks to months production tends to drop radically to levels of 3-8 g dry

m^{-2} d^{-1}. At very high sediment loads, real algal production can be virtually nil.

Site Requirements for Crab Growth

As mentioned above, the mariculture of Mithrax spinosissimus can be treated in four distinct phases: 1) breed stock; 2) larval development; 3) juvenile development and 4) adult growout. To some extent, different conditions are required for each of these phases. In all cases, cages should be located in areas of moderate current flow (0.5-5 cm/sec) and minimum sedimentation.

a) Hatchlings

Newly hatched crabs are particularly sensitive to strong wave action. We have found that the damaging effects of waves or chop can be avoided by sinking the hatching cages to several meters depth. Unfortunately, this renders the exchange of algal turf screens difficult, and is to be avoided if possible.

b) Juveniles and Adults

As far as we are aware, the older crab instars (over 20 mm CL) are not particularly sensitive to light wave action and any increased water movement is usually desireable. Larger waves (approximately greater than 30 cm) at molt may cause some mortalities. For growout, practical limit to roughness at sites is determined by the ease of working algal screens and the crabs themselves from a small boat.

Description of Crab Mariculture Research Sites

In the last several years, crab mariculture research has been conducted at a variety of sites in the north central and eastern Caribbean. In the algal chapter of this volume, detailed maps of each of these sites are presented, so they will not be repeated here. However, it would be helpful in terms of analyzing potential crab mariculture sites if we briefly described the advantages and disadvantages of each site for *Mithrax spinosissimus* mariculture. The following is a list of the sites in approximate order of site quality from best to worst:

1) Grand Turk, east lagoon. The water quality at this site is excellent, as it is derived directly from the North Equatorial current. The reef and algal ridge to the east is rather patchy, but continuous enough to force current compression from breaking waves and to block the larger seas. Tidal currents also provide a component of north/south water movement, and the entire east side of the lagoon is sufficiently free from suspended sediment to provide for maximum algal growth. The western portions of this very large lagoon have too much sediment for good algal growth, especially within a few hundred meters of the island itself. Southwest or northwest winds, although quite infrequent, can cause sediment entrainment in turf screens on the east side of the lagoon. The lagoon waters can be rough at times, and

considerable practical working experience is required to learn how to keep lines from becoming seriously frayed or entangled with the combination of moderate seas and rotating tidal currents. Crab cages for both juveniles and adults can be effectively managed anywhere in this lagoon. In the winter, the lagoon seas can sometimes be too rough for hatchling cages and cause mortality in juvenile crabs. However, the protection provided in the lee of the eastern cays provides excellent hatchling andn winter growout localities.

2) Grand Bay, Carriacou. This was the most turbulent of all our work sites. The constant flow and wave chop across the reef crest provided excellent algal growth. Sea conditions, however, were too rough for hatchling cages and thus these were anchored in the middle of the lagoon at a depth of three meters from the surface. This caused an increase in labor intensity of the hatch phase, but was quite successful. In addition, it was frequently difficult to work the larger crab cages because of the strength of the sea and current, although the sea itself did not appear to affect the juvenile or adult crabs. We feel that a specialized boat, perhaps a small catamaran, could overcome the sea conditions. We understand that a continuing crab mariculture in the somewhat more protected bay just to the North (Watering Bay) has retained most of the algal growth and yet achieved an easier work situation.

3) Buen Hombre, North Coast, Dominican Republic. This very large lagoon is one that could support many crab mariculture operations. It is oriented East/West and as a result, it tends to be rather quiet. The sea conditions are conducive to raising crabs. Winter northers, however, provide rough conditions on occasion, and on many summer afternoons the trade wind combines with onshore winds to provide quite rough seas in the lagoon. However, an adjustment in the work day (i.e., early morning) will offset these conditions. Probably, the most difficult practical situation is that in which the working conditions are generally so good that it is easy to be careless and lose cages and screens on the occasionally very rough days. While this site is certainly a good site, in the quiet lagoon waters' suspended sediment reduces algal growth to moderate levels. The western portion of this 35 mile long reef lagoon might very well be closer to an ideal site.

4) Nonsuch Bay, Antigua. This bay is "closed" against the island itself. The outflow channels are northeast and southeast and they flow back into the trade wind seas, thus restricting the outflow of water from the bay. The sediment load is therefore quite high. Although this site was relatively quiet and easy to work in and there were no direct energy related problems associated with hatchling juvenile or adult cages, the algal production was not good. Furthermore, although initial apparent algal weights were high, due to included sediment, the screens

did not remain even moderately productive for long periods of time. Encrusting animals and undesirable algae provided frequent problems. Nonsuch Bay was an undesirable site. However, the numerous other bays on the northeast side of Antigua would probably provide many suitable sites.

MITHRAX MARICULTURE

Overview

Caribbean King Crab culture, as developed in this project, requires the practice of some critical elements of animal husbandry, as well as the cultivation of algal turf fodder. We have attempted to develop the operation of a low technology mariculture system based on units. The size of the operation determines the number of units required. The operation, which will be briefly described, is based on a single person unit of labor. As in most husbandry, continuous attention to the operation is required and in general two individuals (or two units) would be the normal minimum level of production.

A unit operation consists of three phases, including six hatchery cages, six intermediate cages and 24 growout cages. This process allows for 20-30% downtime for each cage for potential repairs. Six hatchery cages provide space for stocking a crab brood every 32 days. At five days post-hatch, the crab density is thinned by transferring half of the post-larval crabs to a second hatch cage. At 60-80 days post-hatch, juvenile crabs are transferred to the intermediate cage. The amount of crabs produced in the intermediate cages will sufficiently stock two growout cages with 100 crabs (20 mm CL, at 100-120 days age) each month. To achieve a harvest of 100 crabs per month in a unit operation, it is necessary to achieve a survivorship to adult of 50% during adult growout. To achieve one hatch each month, a brood stock of about nine females and three males are required.

Cages stocked with crabs are constructed to accept plastic screens of uniform size. Algal laden screens are exchanged with those in the cage after the crabs have fully grazed the algae from them. These fully grazed screens are then removed from the cage, scraped to remove undesirable algae and then rehung on the float lines at the algal turf growing site. Approximately 10-12 days later, newly developed turf growth reaches a level at which the screens may be exchanged back to a cage. Each crab cage has three to five sets of plastic screens that are rotated. One set of screens is in the cage and the other sets are in various stages of growth. Therefore, with a regular schedule of screen changes, the crabs in the cage are assured of a continual supply of algae. The culture of algae is as important as that of the crabs. To be certain of sufficient feeding it is desirable that some algae remain in each screen when it is removed. If the crabs are "overgrazing" relative to the fed algal turf then either a larger number of screens, a shorter time in the cage or a longer growing period is necessary. In general, it is necessary to manage the algal turf carefully for optimum results. A rigid schedule for screen rotation rather than random selection or visual choice will usually provide maximum production in the long run.

Breeding Stock

Female crabs can be collected using SCUBA or fish traps. Coral reef spur and groove, large coral heads or patch reefs where water depths are 20-100' are likely areas. Controlling reproduction is not necessary, as M. spinosissimus spawn throughout the year. Females bear eggs roughly every two months and are egg-bearing for about 30 days. A typical female bears four to five sets of eggs during her lifetime, although several more are possible. We have found the average breed stock female to bear 2-3 sets of eggs while in captivity. Colored plastic tags facilitate the establishment of an individual code for each crab. Tags can be attached to the legs.

To sustain the requirements of a small operation with 24 large growout cages and a hatch each month, approximately nine mature female crabs are needed. These female crabs should be maintained in several large cages rather than a single one because sufficient feeding to all members of the brood stock can be more easily monitored, making weather and loss of a single cage less crucial. Females crabs should be checked/inspected on a regular basis, at least every five days.

Breed stock cages are the standard adult growout cages. A smaller cage with dimensions of 90 X 78 X 35 cm (Figure 6) can be used for a "female in waiting." This smaller cage is useful as it provides for easier observation of ovigerous crabs. It is constructed of a 2" X 2" wood frame covered with 2 mm screen and fiberglass resined for strength on the wooden framing. Eyebolts from both ends allow several cages to be strung together from one anchor. The tops should be hinged in the center with a simple latch mechanism installed. A crab operation that requires one egg hatch per month should have several broodstock cages containing two to six crabs each.

Special dietary care of Broodstock

Special care is required for successful broodstock production. The female crabs should be fed ample quantities of fully mature cultured algal turfs, as well as periodic supplements of smaller macroalgae that are collected from reefs, pavements or rock ridges. An algal monoculture diet for the crab (i.e., a single species of algae grown in culture), while possible, is extremely risky in terms of potential disease or predation and also is likely to preclude the full reproductive capacity of the species. Algal turfs, by the nature of their community composition (i.e., algal species from nearly every major algal group, forming a community of 30-60 algal species) combine to form a highly nutritious and complete feed.

Breed stock care

Maintained in these cages with ample fresh food supplies, an average female crab will produce two to three consecutive broods in a 200-300 day period. Forty-seven percent of a captive crab population (n = 26) produced three or more broods while in captivity (Craig *et al.*, this volume). Each brood requires three to five weeks to undergo embryonic development. Approximately 60,000 eggs are released by a female (this varies with both the female body size and age). Approximately 70 gms (wet weight) of algae per crab per day should be delivered to each cage. Old or uneaten algae should be discarded at the time that the new algae are put in. Thus, with nine female crabs, each producing two to three broods over a year, one can be assured a hatch every month.

It is critical in this mariculture process to accurately time an impending hatch. Egg brood coloration is the simplest indicator of time to hatch (Table 2). Microscopic examination of individual eggs is a more accurate indicator. An egg brood nearing release (one to three days pre-hatch) will appear clear-amber in color. The individual prezoea will appear active inside the egg and the regular pulsing of the animal circulatory system will be readily apparent. The eyespots will appear predominant while the presence of the brightly-colored yolk will be barely discernible (Craig *et al.*, this volume).

Hatching

Ovigerous female crabs are placed in the fine meshed hatch cages (Figure 7), preferably within 24 hours before hatch. This hatch box, with several bare screens, is placed in the water several days before the female is introduced to allow a fine algal (diatom) growth to begin development. Following hatch, the female crab is removed from the cage. The larvae are then left undisturbed for a period of 5-20 days post-hatch. It is then generally desirable to transfer a portion of the crabs from the hatch cage to another to reduce density. This can be done without handling the very small crabs by simply transferring the bare screens previously placed in the cage. After another 5-20 days, plastic screens containing algal turfs are periodically exchanged to replenish the supply of algae to the young crabs. It is crucial when the *Mithrax* crabs are very small to avoid bringing in potential predators, especially small carnivorous crabs, on the algal feed screens.

Rearing to 60 days and 10 mm CL (Figure 7, 0.5 mm screen)

The rearing cages for crabs to 60 days post-hatch are small, easily handled and labor intensive. The following operational procedures should be observed for managing the rearing system from several days post hatch to 60 days.

1) The post larval crabs should be thinned to separate cages to a density of no more than 500 crabs/m^2 of surface area at 10-20 days post-hatch.
2) Algal screens should be exchanged every four to six days. The grazed screens should be returned to the algal screen float line for a re-growth period of 12-15 days. These screens should be single-layered young screens, rich in diatom growth, that have been in the water no longer than two months.
3) Crabs reaching 10 mm CL should be transferred to the intermediate cage.

Rearing 60-120 days (to approximately 25 mm CL) (Figure 7, 1.5-2 mm screen)

1) Algal feeding rate remains the same.
2) Crab density should be on the order of 50-100/m^2.
3) Upon reaching a size of 20 mm CL crabs are transferred to the adult growout cages. This can be done by gently "flicking" the crabs off the algal feeding screens, where they tend to congregate, or by individually picking them out of the intermediate box where necessary.

Rearing of Juvenile Crabs to Harvest Figure 8, 1/4-1/2" mesh

1) The growout cages are considerably longer (1.0 X 1.0 X 2.6 m) than the hatch and intermediate cages. Crab density therefore is much less (100 when young and 40-50

when grown out).

2) Algal feeding rate is greatly increased, with rates of five to eight double-layered algal screens, every 3-4 days for 30-40 crabs - rate of feeding adjusted by noting remaining algae on screens returning to the line. Some turf should remain to avoid overgrazing.
3) Growout period for 250-400 days, at which point harvestable crabs should attain a size of over 120 mm CL.

CAGE DESIGN, FABRICATION AND MANAGEMENT

The effects of the marine environment on cage, screen line and anchor systems, designs and materials has been examined at six coastal field sites across the northern and eastern Caribbean. Due to the variability of marine conditions at each field site, a unique set of designs and material specifications for mariculture equipment suited to each site has evolved. However, there are many characteristics that are common to all sites and considerable effort has been made to standardize equipment and techniques.

Three types of primary crab cages are used: hatch, intermediate and growout. Small "female in waiting" cages can facilitate the hatching process. The hatch and intermediate cages, with the exception of mesh size, are identical. They are constructed to accept the smaller screens, and their smaller dimensions allow for rapid inspection, removal of material from the cage and ease of handling. The growout cages are larger, more crudely constructed and used to grow crabs from 20-25 mm CL to market size. The three cages are designed to be easily constructed and provide a manageable means of feeding algal turfs to crabs.

The most important factor in the survival of very young Mithrax spinosissimus in an "in situ" mariculture (to 100 days) is the avoidance of predators. This is especially critical in the early stages of growth, when the crabs are essentially defenseless. The presence of competing invertebrate herbivores is also undesireable. Careful cage assembly techniques play the greatest role in prevention of the entrance of other organisms into the cages.

The cages are relatively simple in design. They consist of a frame constructed with wooden 2 x 4"s and 2 x 2"s nailed together with 4" galvanized nails and covered with plastic mesh screen. The lids are removable or hinged and the entire cage is anchored. Slots inside the cage hold the algal turf screens in place. Spaces between the slots allow for movement of crabs between the screens.

Tools necessary to build the cages are common carpenters tools including hammers, saws, pliers, screwdrivers and nails. The cage should be assembled so that all joints are smooth and without gaps. Once assembled, all finished edges of the cage should be sanded smooth to insure a tight fit between the lid and the attached screen. The wood frame should be carefully painted with fiberglass resin to avoid numerous sharp points of hard resin. Any gaps in the wood joints will provide hiding spots for unwanted organisms and so these gaps should be filled.

It is particularly important that the cage lids are well fitted to prevent the entry of unwanted animals into the cage, or the cultured crabs out of the cage. Gaskets must also be fitted on the removable lids of the hatch and intermediate cages. To rigidly hold the lids to the frame on the hatch and intermediate cages, bolts and nuts are necessary. On the larger growout cages, latches should be used.

Hatch cage

The hatch cage is relatively small to allow for easy handling, particularly with regard to the ability to haul it into a small boat. However, it should be as large as possible for maximum crab and screen space. We have generally used cages of 90 X 40 X 110 cm (Figure 7). It is assembled from wood 2 x 2"s nailed together. Assembly of this case requires special care to insure that all joints are exact and tightly fitted so that there are no open spaces between them. Slots or grooves are cut into the inside of the cage frame members to hold four to eight algal turf screens. The wooden framework is then coated with fiberglass resin before the cage is enclosed.

The water-tight frame is covered with a fine plastic screen of 0.5 mm mesh. This prevents newly hatched zoea from escaping and other organisms from entering. If the pore size is any smaller, the flow is restricted unnecessarily. During cage assembly, the enclosing screen mesh should be stretched tight onto the wooden frame work, stapled and then resined directly to the wood surface to form a complete seal of the screen to the cage. After the screen has been resined to the frame, all the gaps between the frame and the screen inside the cage should be filled. When completed there should be no cavities in which predator or competing organisms can hide.

The lid is a separate piece that is fitted and attached to the cage frame by long threaded bolts and nuts. A gasket of silicone plastic sealant is formed by compressing the uncured silicone with the lid to form a complete seal of the cage when the nuts are tightened on the lid. Silicone is used because it retains its shape, does not shrink from the pressure of the bolted lid and lasts for a long time under marine conditions. To form the gasket, the cage lid is prevented from sticking to the silicone by stretching Saran^{R} wrap or similiar plastic over it on the first clamping.

If meticulous care is taken and the cage is well constructed, the screens will fit tightly and easily. There will be no places for intruders to enter or hide and it will provide years of service. Maximizing the number of slots per cage is important so that more screens can be added before handling the screens or crabs that are already in the cage. We have used 24" X 36" screens for this cage and typically have allowed two to four slots. After the basic cage is finished, four eyebolts are put in the bottom and ropes with clips are tied to make two attachment lines. This design tends to reduce pitch and roll when waves or currents affect the cages. This technique also makes the cage pivot at the point of attachment to the anchoring system in a seaway, rather than at the attachment on the cage. Wooden blocks nailed to the cage ends serve as handles.

Hatch Procedures

The ovigerous female should be placed in the hatch cage one to two days before release. She should be adequately fed up to the time of her removal from the breed stock cage. Once in the hatch cage, no algal turf food for the female crab should be introduced, since it may also introduce predators. In any case, the female does not eat on the night of the egg release.

Almost always, at dusk or into the evening, the brooding female will actively release the eggs by flexing her abdomen/pleopods. The entire procedure takes about three to four hours. The spent female crab should be removed from the hatch cage as soon as possible after hatching. The quality of the egg release can be determined by taking a one liter water sample and determining the percentage of viable zoea under the microscope. The larval swimming stages last two to four days.

Viable larval crab densities in these hatch cages should be on the order of 2000 crabs per cage to start. In the instance of a typical size hatch, 2000 1st crabs, of about 1.5 mm carapace length, will remain in the hatch cage at five days post-hatch. From that point until 60 days post-hatch, mortality using these methods will reduce the crab population to 400-600 crabs. Since a nine crab breed stock will provide a hatch a month, this is far more crabs than one fisherman could handle, if they were all to be raised to adults.

At the time that the berried female crab (prior to hatching) is placed in the cage, it is important that the heavy growth of algae or sediment and detritus on and in the hatch cage screen surface be removed. The larval stages need a high exchange rate of sea water through the cage for both adequate supplies of phytoplankton and to carry nitrogenous wastes out of the cage. It has been found that the best way to do this is to remove the hatch cage from the water before the gravid female is placed in it. The hatch cage should be brushed, rinsed and dried to remove all fouling algae from the screen surface both inside and out. The cage should be placed back in the water about five days prior to the gravid female's placement in it. This will allow a light growth of diatom rich turf to develop, providing food for the megalops and early crabs without blocking water flow.

Upon reaching the first crab stage, Mithrax spinosissimus become entirely benthic and settle out on the screen surface. They will consume the diatom turf which has colonized the cage screen surface during the 8-10 days before they reach that state. By about the 10th to 20th day, new cultivated algal turf screens should be emplaced in the cage, as the original growth on the cage itself will be exhausted.

The cage, constructed with four to eight slots should receive two single-layered screens at first, two more, four days later and then two additional screens on the next changing day (remove the first two grazed screens at this time). From that point on, from two to four screens should be placed in the cage at each screen changing date. These should all be singled-layered screens. The grazed screens should be returned to an algal screen line for new growth. Depending upon hatch density and the rate of algal turf growth in a particular locality, hatch cage screens should be changed every four to five days. Hatch cage screens should be young screens, rich in diatom growth that have had no more than eight to ten weeks in the water. After that amount of time, they should be dried and brushed clean.

When algal turf screens are exchanged, the screens that have been in the cage may have many small crabs still attached to the screen, particularly at the earliest changes. Unfortunately, hand removal or brushing increases mortality and is time comsuming. Therefore, the screens should be left in the cage and new screens put in the unused screen slots. If a dense hatch has been achieved, some of these screens and their crabs can be safely and quickly transferred to a second cage, that has been tied up alongside the boat. This procedure will also thin the density of crabs. Each cage should then be provided with a new set of algal laden screens. If a hatch has not been dense enough to justify a split, the older screens can be left in until the next change, at which time most of the young crabs will have moved to the new screens.

The algal turf screens are rich in a resident invertebrate microfauna which can amount to 5-10% of the total screen biomass. Most of these are very small and may well provide some food to the crabs along with the algal turf. However, the larger of these animals must be removed from the screen before it is placed in a cage. It is imperative that exposure of the young *M. spinosissimus* crabs to other invertebrate species be minimized. These unwanted invertebrates may prey on or compete for food with the young *Mithrax spinosissimus* crabs. Eliminating other larger invertebrates can be accomplished by careful inspection, shaking of the screens and if necessary by crushing the animals by rolling a "rolling pin" across the screen surface several times.

After a hatch cage is used and the animals transferred to the intermediate cage, it must be cleaned and reconditioned for use. It should be brushed with a coarse brush inside and outside at the same time, either when quite wet or when completely dry. The cage should then be allowed to dry at least four days, turning it over to be sure of thorough drying. If water has seeped underneath the coating of resin or has saturated the corners, the resin should be peeled off, the wood allowed to dry and the resin replaced. The lid seal should also be checked and redone, especially if drying has warped the top.

Intermediate cage

The intermediate cage design for the second phase is identical for that of the first. Only the cage screen mesh size is different. The mesh size is ideally 1.5-2.0 mm. This promotes a rapid exchange of "green" water through the cage to clean the growing detritus load, while retaining crabs in the cage. The screen must be attached in the same fashion, that is, resined to the framework. Although perhaps not quite so critical, the same care must also be given to the predator control methods. The same gasket type and lid securement is recommended.

Growout cage

Growout cages need to be considerably larger than the hatch or intermediate cages; generally, we have constructed our units with dimensions of 2.4 X 1.0 X 1.0 m. These are also constructed of 2" X 4"s , using the same polyester resin coating. While some care should be taken in cage construction, so that it is able to withstand a sea conditions for several years, joint and screen tightness is not so crucial (Figure 8). These cages hold 20 screens which are oriented vertically and are "guided" by slots cut into the cage structure. Approximately 5" of space between each screen allows the growing juvenile crabs ample feeding space. There is a space (minimum of six inches) under the screens to allow the crabs an area to move from screen to screen. No space is allowed on top of the screens, since the lid is designed to hold the screens tight and to keep them from moving. In the bottom of the cage, "molt" compartments of 1/4" plastic mesh, of 35-90 mm^2 size, are constructed for the crabs.

In the growout cage a double plywood top is used. This provides some darkness and protection from wave chop. It is hinged at the center and opens to one side at a time for screen exchange. There is also a small door cut in one side of the top for easy placement of macro algae supplemental feed. Heavy rope (>3/8"polypropylene) is used for this and rubber strips from used tires serve as hinges.

Because the cages remain in the water for long periods, they are given three coats of fiberglass resin. The cage corners should be reinforced with fiberglass cloth as well. To be able to stock a 20-25 mm CL crab, a mesh size of 1/4-1/2" or less is required. One-quarter inch mesh is ideal. The plastic screening should be attached to the cage with fence nails, then resined and covered with wood or plastic strips for added protection.

Cage Placement

Water flow and quality is the most important condition to consider. Sediments falling from screens, as well as feces, dead crabs, and detritus from inefficient feeding of Mithrax crabs, and other inhabitants, potentially contribute to poor water quality. On the other hand, particularly for hatching crabs, too much flow presses zoea to the screen inside the cage and increases cage maintenance requirements due to racking of the cage structure and chafing of the lines.

In most localities with good flow and wave chop for adult cages and algal screens, nearby areas in the lee of a reef structure or cay can be found to provide the slight additional protection needed for hatch cages. Where this has not been possible, such as at the Carriacou research site, we have achieved the needed hatch cage conditions by submerging them. However, this requires either a diver to enter the water and release them from their anchorage or a system to lower and raise the box.

Anchoring systems

The smaller cages may be anchored either to a chain suspended between two anchors, or anchored individually. The growout cages should be anchored individually, and situated so that the current runs parallel to the screens in the cage. The four lines attached to the cage bolts should tie off to a single heavy line 3/8" or greater, which in turn ties off to a chain from the anchor. The chain is shackled to the anchor. All rope connections are made with hose to reduce line chafe. The line and chain length to depth ratio should be seven to one, or more under particularly turbulent situations.

The water depth in which the cage is placed is critical. A depth that is too shallow increases the effect of waves and swell, which causes the cage to hit bottom, thus exposing the crabs to excessive sand and debris. If current and wave motion are particularly strong, cages should be attached with shackles or 3/8" rope using heavy rubber tubing to prevent chafing from the metal eyebolts on the cage. Alternately, chain can be used throughout, although this greatly increases cost. At the Carriacou research site, where the current was very strong, 1/4" chain was used with six inch longline clips and 1/4" shackles and a chain stretched between two 30 lb. Danforth anchors served as the bottom attachment. Weights were necessary along the chain between cages since the buoyancy of the cages and the strength of the current pulled excessively on the bottom chain. In situations of strong daily reversing tide currents, it is necessary to run the line on the bottom parallel to the current so that opposite anchors will hold alternately as the tide switches.

DISCUSSION

Algal Turf Cultivation

Algal turf growth on plastic screens develops in three distinct phases. The artifical substratum on which the algae grows should be scraped 10 days after being put in the water, and every 10-12 days thereafter. It takes about four to eight weeks for a screen to develop a mature algal turf community. Diatoms and their mucilage sheaths appear in the first week. Shortly before the second scraping (at about 20 days), blue-green algae dominates and appears as soft, sometimes mucilagenous brownish tufted filaments up to two centimeters long. After about three weeks of cultivation, the other algal types, primarily red algae, begin to colonize the screen. If the plastic screen surface is not scraped during this initial period of turf cultivation, the turf will not develop as rapidly or fully. Also, the community may have a disproportionate macroalgal component and gradually develop sponge and calcareous animals that are not palatable to the crabs. Only through a continual scraping/grazing schedule will a high diversity of rapidly growing turf algal growth be established and maintained.

Screen designs and screen fabrication may be tailored to a particular site or to accomodate available materials. Whichever type and size is chosen, it is important that all the screens, for the intermediate and adult cages, are exactly the same dimensions. The algal turf screen mesh size should be no larger than three millimeters and no smaller than one millimeter. We have found a 2 X 3 mm black polypropylene plastic screening material to be adequate. This screen is able to withstand continued scraping from both the initial algal turf cultivation techniques and the crabs. It has been demonstrated that a transparent or translucent screen material significantly increases production. However, a testing program to identify a transparent screen that also has the right mesh and toughness has not been carried out.

For hatch cages, single-layered screens should be used to reduce hiding spaces for predators. For intermediate and adult cages, algal growth is considerably increased by constructing the algal turf screen of two layers of screen material which provides a greater surface area for the algal holdfasts. In addition, optimum algal production is achieved when the plastic screen is rigidly suspended in the water column. A vertical, two point mounting system (Figure 10) optimizes algal production and is easy to handle. The screen frame, constructed of 3/4" PVC pipe is non-corrosive, as well as non-toxic. Filling the lower PVC pipe with sand provides greater rigidity against wave surge and currents. When determining a size for the screen frame, the wet weight of the algae growing on the screen should be considered. A screen measuring two feet by three feet can weigh up to 25 pounds with substantial algal growth; therefore the total surface area of the plastic screen should be kept below one meter. We have used "schedule 40" 3/4" PVC with standard sleeve-type elbows, carefully glued with PVC cement. The plastic screen is wrapped around the ends of the PVC screen frame and tied to it with 60 lb test monofilament fishing line or attached by plastic cable ties. The other two edges of the screen which lay inside the pipe framework are stitched together to prevent tearing. This simply constructed screen and frame is then fitted with 1/4" polypropolene line which extends 12" from each corner of one end of the PVC screen frame. A piece of rubber hose is fitted on the rope so as to prevent the chafing of the rope on the PVC pipe edge. A simple, strong knot such as the "fishermen's" knot should be used, so that the rope loop tightens around the pipe. Due to their air/water tight construction, weight and buoyancy, the screens hang vertically from the water surface with the sand filled pipe weighing the screen down at one end.

Twenty to thirty algal screens typically have been placed on double anchored lines perpendicular to current and wave surge. This "screen" line has regularly spaced tied loops (Figure 11). The length of the screen determines the distance between loops. The distance between screens is approximately one foot. The screens are then simply tied to the "screen lines" with their tie lines. They should be tied as close as possible to the loops to keep them from bouncing into each other. A float at either end of the line marks and supports the ends of the screen line. Anchor lines extend from the floats (Figure 11). The major benefit of this system is its mobility. If the area chosen does not produce expected amounts of algae, or in the advent of a major storm, the line can easily be moved to a better location.

Larval and Post-Larval Rearing and Growout

The 0-60 day or hatching phase is the most critical in the crab's life. The crabs go through metamorphosis from a planktonic zoea to a benthic crab stage and then through several molts. Growth and survival rates are related to initial hatch quality, predation, water quality and flow, food type and availability and handling.

The viability of an egg brood may be discerned by examination of a few eggs prior to hatching. Viable eggs show active larvae with "heart beats" up to 250 bpm and occasional flexing of the abdomen. If the eggs appear cloudy or grey they are usually dead or are of a poor quality and survivability will be reduced.

As the eggs develop, they change colors. As discussed above, examining the eggs as they are brooded can determine just how close they are to hatching and when to put the female into the hatch cage. It is important to minimize the length of time the female is left in the hatch cage, because she is not fed at this time. Eggs may be removed from the brooding crab using forceps and placed in a vial with seawater for later examination.

A female approaching a hatch should be well fed prior to putting her into the hatch cage so that food does not need to be added during her stay there. It is also important that the female be examined for attached predators that could hide in the crevices in her skeleton or among the pleopods or eggs. When transporting the female from the box where she lived to the hatch cage, styrofoam coolers of fresh seawater are ideal.

If the female crab must stay in the hatch cage for more than three days, feedings of macroalgae should be made. However, any such feedings (usually a pressed handful) must be thoroughly checked for invertebrates. Females previously well fed have lasted at least 10 days and have produced successful hatches. Females that have released only part of their hatch can be kept for a second day in the hatch cage, but usually those remaining are not very viable.

After the female has been put in the hatching box with the top sealed and the cage attached, she will eventually position herself in a way that enables her to pump her abdomen which will aerate and eventually liberate the hatched zoea over a two to twelve hour period. On the day after the female was expected to release the eggs the cage should be checked in the late morning or early afternoon. Zoea can be seen through the screen that has begun to accumulate diatoms and sediment. Occasionally, if the female is checked early enough, empty egg cases are left on the pleopods and can be mistaken for unhatched larvae. With a good hatch, many zoea can be easily observed to be swimming about the cage. If a cage is raised and brought to a boat for examination, care should be taken to move it slowly so as to not drive the zoea against the cage screen. It should not be fully lifted from the water, or if absolutely necessary, lifted very slowly for the same reason.

Mithrax spinosissimus starts as a prezoea and goes through two zoeal stages and a megalops stage before metamorphosing into a crab. These stages to first crab last about five days. When examining the contents of the hatching boxes during the planktonic stages one should see larval crabs swimming as well as a mixture of live and dead zoea and empty molts on the cage floor. Often, when removing the female from the cage after hatching, thousands of zoea can be seen on the cage bottom, but this phenomenon doesn't necessarily indicate poor survival. Living zoea may be distinquished by their red eyes, while dead ones and molts have white ones.

The first crab stage is entirely benthic and negatively phototropic. When settled the first crabs space themselves evenly on all of the inner surfaces of the cage, including the top, for the first thirty days. Generally the mortality to the first crab stage from an average brood of 60,000 is 95-97%; the range is dependent on brood fertility, viability and water characteristics. From first crab to 60 days post-hatch, normal mortality will reduce the crab population to 400-600 crabs. The diatoms and other algal spores settling on the cage screen surface provides initial food to the post-larval crabs. But this same settling algae also reduces water flow.

After settling, the crabs will molt at about four, eight and twelve days post-hatch, at which time they have begun to deplete the algae on the inside of the cage. The average growth rates through this 60 day period vary from site to site and seasonally from 0.11 to 0.30 mm CL/day so that the average CL varies from 6 to 12 mm at 60 days. It is not uncommon to see dead crabs at various stages, and it is very common to see molt shells cluttering the bottom of the cage as well as feces and algal debris. Later cage designs have included a valved shute and well at the bottom of the cage to drain off debris with minimum crab loss.

When the algal layer growing on the outside of the cage begins to slough off and it is obvious from looking on the inside of the cage that the algae there has been eaten, then screen feeding should begin. Screen feeding should be initiated at 10-20 days post-hatch. Food preferences appear to be benthic diatoms after settling at megalops, with an increasing emphasis on blue-green algae and by 60 days the red, brown and green algae that dominate a mature algal turf community. Different strategies of feeding have been employed in the first 45 days post-hatch. Ideally, minimum disturbance and handling affords maximum survival, but on the other hand the crabs must be fed. Strategies have ranged from putting one single layer screen into the cage on the day the female was removed after hatching to waiting for 80 days before the first screens were added. Single layer screens added the first day also supply more settling space for first crabs. Generally, screens were first added at 14-30 days. Cages with many screen slots are most desirable since screens can be added for sometime before any are removed, or at least allowed to remain in the cage until most of the small crabs had migrated to newer more algae-laden screens. When screens are added prior to 30 days, they should be assembled with a single layer of screen. This reduces the chance of adding small predators in the folds of the screen.

In the standard hatch cage, after the initial screen or two, screens should be added every four to seven days up to 30 days. These should be primarily colonized by a diatom growth that takes 5-10 days to become established on a new screen. After 30 days and up to 60 days post-hatch, two or more screens should be added on a regular basis of three to five days.

As new screens are added, the older ones are examined for algal growth and the presence of Mithrax crabs. If they have neither, they are removed. Eventually, it will be necessary to remove crabs from the screens being removed. If the screens are single layered, a gentle shake or tapping will remove them easily, especially if no algae is remaining on the screen. If the screens are double layered, holding the screen out of the water for a few seconds then tapping the screen will usually cause the crabs to run towards the bottom of the screen where they will jump off or can be easily removed by hand; alternatively, the screen can be gently agitated in and out of the water to remove them. A cleaner screen affords easy removal by tapping, but a screen with algae still growing on it affords easier removal by hand, since the crabs are not firmly attached.

Another strategy for minimum handling, especially if a hatch is particularly large, is to transfer crab-laden screens from the original hatch cage to an unused cage so that more algae-laden screens can be added to both cages. This technique is also useful if the first cage becomes clogged or too detrital laden.

Intermediate phase

At 60 days post-hatch, the crabs in the hatch cage are transferred to the intermediate cage. This cage (25.5" X 27.5" X 40.5") is identical in design and size to the hatch cage. However, it is covered with a wider screen mesh size of 1.5-2 mm. This greater mesh size allows detritus to fall out of the cage and maintains a high water quality state in the cage. The intermediate cage should be anchored and, if waves and currents are strong, submerged in a manner similar to that of the hatch cages. Algal screens are exchanged into and out of these cages every 3-4 days.

These intermediate cages are stocked with no more than 600 sixty day post-hatch crabs. If the number of crabs surviving from a hatch at 60 days post-hatch is greater than 600, the excess above 600 should be placed in a separate cage. At about 120 days, the crabs should be transferred to the growout cages. A typical mature intermediate cage will yield 100-300 crabs at this point in time, each approximately 25 mm CL. Management of the feeding requires changing algal screens on a routine basis. The intermediate cage screens require a 12-15 day recovery period for optimum algal growth. There should be equal numbers of intermediate and hatch cages.

We have found that survival rates are less and growth rates are slower for crabs left in the original cage for more than 60 days. Crabs greater than 8 mm are large enough to withstand the stress of transfer handling, with only about a 5% population loss. The greatest numbers we have experienced at 60 days is 600 crabs of 10-12 mm. When these crabs molt again, the proportionately large increase in body mass seems to increase the demand for food to a point that exceeds the capacity of the 0.3 cubic meter cage and of the feeding regime (up to 8 screens per week). The subsequent large increase in fecal material, dead crabs, molt and algal debris and the established populations of other organisms, including predators and competitors seems to contribute as well to unfavorable conditions and increased mortality.

Thus, it is necessary to decide to either split the hatch using unused cages similar to the hatch cages or transfer all the crabs to clean intermediate cages with larger mesh size. Either method will work, but a larger mesh size increases water and waste exchange potentially improving growth rate and survival. If the cages are examined carefully at each feeding, predators are not a problem in the intermediate cages of slightly larger mesh sizes. No more than 400 crabs should be placed in each cage of the second phase. Three hundred seems to be ideal. During the next 60 days, after a split hatch, losses of crabs transferred would approach 25-35% so that by 100-120 days post-hatch, 250-300 (20-25 mm) crabs would be left. Another viable strategy, if growth rates are exceptionally high, involves moving only the largest crabs (25 mm CL or more) from the hatch cage directly to the growout cage. Smaller remaining crabs tend to show increased growth rates as competition for food and space is decreased.

In this second phase, algae screens should be changed twice weekly regardless of their condition. These crabs become very selective and sometimes a screen with the appearance of good growth will not be touched or will have been picked over.

Screens on which with bluegreen algae are dominant satisfy most of the intermediate cage crabs for approximately the first three weeks; after that, fully developed algal-turf screens are desirable.

Initially, the screens are placed in the cage four at a time in an six-eight slot cage, so that each set remains for a one week period. If at each change, all the screens are cleaned of growth, then as many screens as possible are changed. By the time the crabs reach 25 mm CL in size, they are able to defend themselves against most small predators that might inadvertantly enter the cage and are able to withstand handling.

Crabs of 20-25 mm or greater, should be transferred into a growout cage. One to two hundred crabs may be transferred to each growout cage. We have found that as the 20 mm CL crabs are removed from the hatch cage and intermediate cages, the remaining crabs are under less competition and reach 25 mm CL in 10-30 days. The intermediate and hatch cages should be removed from the water, cleaned and dried if they have been in the water for more than 80 days.

Growout Phase

The third and final phase involves only variations of previously discussed techniques. The emphasis is on strategies of maximum feeding with attention to increasing varieties of algae fed. Less attention needs to be paid to marine life that may enter the cage. However, on occasion, we have discovered an octopus in our cages. These predators raise havoc with the young crabs.

Screens added to the growout cage are exchanged every rwo to three days. Screens must be scraped after each feeding and returned to the screen line. At times the screens will need to be cleaned, dried and restarted. It seems clear that a source of older juvenile mortality is insufficient feeding. This is best judged by the amount of algae remaining on the screens at the time of removal. If the screens are nearly bare, algal feeding is probably insufficient.

Crabs in the adult growout cages molt another 7-8 times until they reach sexual maturity in about a year. The actual time to maturity can be determined by the growth rate. As the crabs grow they become very easy to handle with little or no risk of damage. Heavy wave action can apparently damage molting crabs, and we are now experimenting with screen annd pipe habitats to provide molting crabs protection against aggressive cage mates.

Wild crabs should not be placed with cultured crabs, since wild ones are often aggressive and may cause mortalities. Mixing sizes even in cultured crabs also may be risky. Because predators do establish themselves and the polyester resin does not keep out all the shipworms, the cages themselves need to be rotated. A cage frame that is pulled out of the water every 12 months, re-resined and repaired should last for at least three years. The effects of hurricanes may be severe if adequate steps are not taken prior to a storm. Important considerations are anchoring methods as well as location and maintenance of gear. During periods of stormy weather, cages may be anchored so as to be submerged beneath the sea surface.

Three of our field sites have been in the direct paths of hurricanes with wind speeds up to 70 knots. The first experience met with cage and crab losses of nearly 30-40%. Subsequent experiences have resulted in minimal losses. These losses have primarily been amongst individual crabs themselves. The design of the cages prohibited the crabs from getting a strong foothold in the cage resulting in many crabs being throwwn about the cages by the motion of the water. Recent cage modifications are expected to prevent these types of losses in the future.

CONCLUSIONS

The mariculture described in this volume was specifically developed in an attempt to utilize a newly found base resource (cultured algal turf) for a local fishermen mariculture. The possiblility of growing <u>Mithrax</u> <u>spinosissimus</u> economically in a sophisticated hatchery and factory growout situation may very well exist. However, we have specifically avoided approaches that seemed unlikely to be adaptable to the itinerant fisherman.

We have repeatedly demonstrated in the Caribbean lagoon environment of the West Indian fisherman that *Mithrax spinosissimus* can be hatched in inexpensive cages "in situ." After working with the itinerant fishermen of Buen Hombre on the northwest coast of the Dominican Republic for nearly a year with this mariculture, we feel confident that these totally uneducated and isolated fishermen are quite capable of carrying out the hatching process as well as the remainder of the mariculture. Indeed after the project was officially closed at this site, the fishermen continued to work with our remaining stock and brought a number of animals to maturity.

Regardless of the likely economics of a *Mithrax* commercial market, a harvest of 1000 adult crabs per year would provide a significant economic boost, or even a total livelyhood for many Caribbean fishermen. Furthermore, this is an environmentally non-destructive process, and with reasonable controls on the adult populations, it is unlikely to be self-destructive. By keeping a breed stock of no more than 20-30 adult crabs in several cages, a hatch rate of from one per week to one per month can be easily achieved. We have accomplished this at all project sites. The keeping of this minimum breed stock is no more than 5% of the total work effort.

Once the vagaries of dealing with wave destruction of the cages and predator control were managed, our results have repeatedly shown that 200-300 crabs per hatch can be raised to 120 days or about 25 mm CL in size. Thus, we have securely demonstrated that in the itinerant fisherman environment, it is reasonably possible to bring roughly 2000-8000 crabs per year, depending upon the number desired, to 120 days of age. Our success at 120 days has continued to improve with time, and it would appear that with the same basic methods, 500-600 crabs per hatch can be routinely achieved at 120 days post-hatch.

If adult growout from 120 days to 12-15 months (approximately 9-12 months in an adult growout cage) can achieve a 30-50% survivorship, the entire algal turf/crab culture method described in this paper would be technially feasible.

To date, we have not achieved this kind of survivorship. Unfortunately, it is very difficult to separate the biology and technology of the process from the very significant logistical and political problems that have beset the project. At our longest running research site, Buen Hombre, research funding has been repeatedly cut off for periods of up to two months, making significant progress extremely difficult. Each site experienced similar or even more difficult problems not related to the basic biological problem of reducing late growout mortality.

At this point, late growout survivorship, despite obvious nonbiological problems, has averaged 18% per 100 days. During the late stages of cage growout, increased mortalities apparently occur at periods of molting. Male/female losses are more or les equal. Intercrab competition may be important during post molt periods, though no extensive evidence of such has been consistently observed. Ryther _et_ _al_., (1987) observed significant dismemberment and death of some animals by "dominant" crabs. However, rarely does cannabalism appear to be a factor. Rough water at molt obviously causes mortalities and modified cage design may greatly increase survivorship. We have developed a new flow-thru sea water system for observing crabs in cage environment and have begun a redesign process for cage microhabitats. Disease may be a possibility for juvenile mortality, though dead animals have been dissected and obvious symptoms or disease sites have not been located. Most important, survivorship has tended to improve throughout the project, suggesting that the answer to a successful itinerant fishermen mariculture utilizing algal turfs lies in continuous improvement of techniques and apparatus.

During the last six months of the project, overall growth rates of about 0.20 mm/day have routinely been achieved to about 100 days, and a mean rate exceeding 0.41 mm/day for potentially a 400 day total growout was achieved at both Buen Hombre and Antigua. Thus, _Mithrax_ _spinosissimus_ mariculture is not likely to be limited by crab growth rates, but rather by survivorship and economics.

We have currently begun an effort at Grand Turk in the Turks and Caicos Islands to concentrate on the problems of late growout mortality. This is certainly one of the best growout sites, so that with a more secure logistic/political situation, the techniques to bring this mariculture to a fully successful conclusion biologically can be developed.

Economically, several hurdles will have to be overcome. While crab sales to local hotels and restaurants would undoubtedly provide some minimum income to the fisherman/entrepreneur, a high volume mariculture would need to develop an export market to North American and perhaps European cities. However, as long as a sufficient source were available, namely enough fishermen working and coordinated in a well-defined market structure, such a market can probably developed fairly easily. Finally, it is necessary for the cost of cage and screen construction to be reduced. This is not an unreasonable goal, and given adequate volume, molded or stamped plastic cages and screens could likely be made cheaply in large numbers. Thus, following biological success, it would be necessary to coordinate development of the supply and marketing process.

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LEGENDS

FIGURE 1.	Screen line commonly used for growing algal turfs in reef/lagoon environments in trade wind seas.
FIGURE 2.	Male *Mithrax spinosissimus*, 10-20 days after final molt and at 1-2.5 kgs, an ideal siize for harvest.
FIGURE 3.	Map of eastern Caribbean showing mariculture work sites for cage culture of *Mithrax spinosissimus*.
FIGURE 4.	Relationship between size (CL) and live weight of *Mithrax spiinosissimus*.
FIGURE 5.	Larval stages showing prezoea, first zoea, second zoea and megalops. (Photos to be added later).
FIGURE 6.	Cage for observing females approaching release.
FIGURE 7.	Hatch cage (0.5 mm screen) and intermediate cage (1.5-2 mm screen).
FIGURE 8.	Growout cage (1/4-1/2" mesh).
FIGURE 9.	Detail of algal screen assembly.
FIGURE 10.	Screen line.
FIGURE 11.	"Mushroom" type anchor design, fabrication and set up.

TABLE 1.	Size and fucundity of *Mithrax spinosissimus*
TABLE 2.	Assumptions to derive cage number and algal turf screens for production level of x crabs/15 months.
TABLE 3.	Essential requirement of hatch cage rearing.

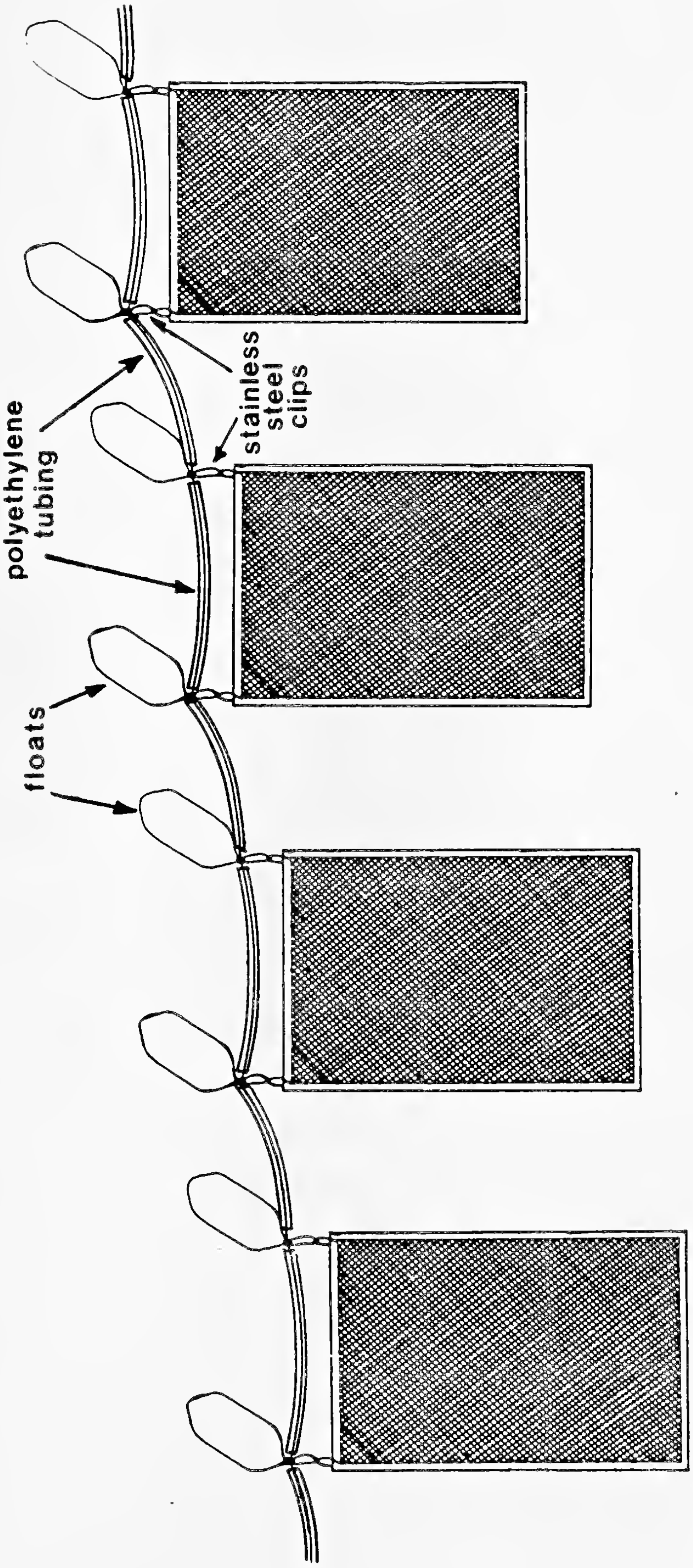

Figure 1

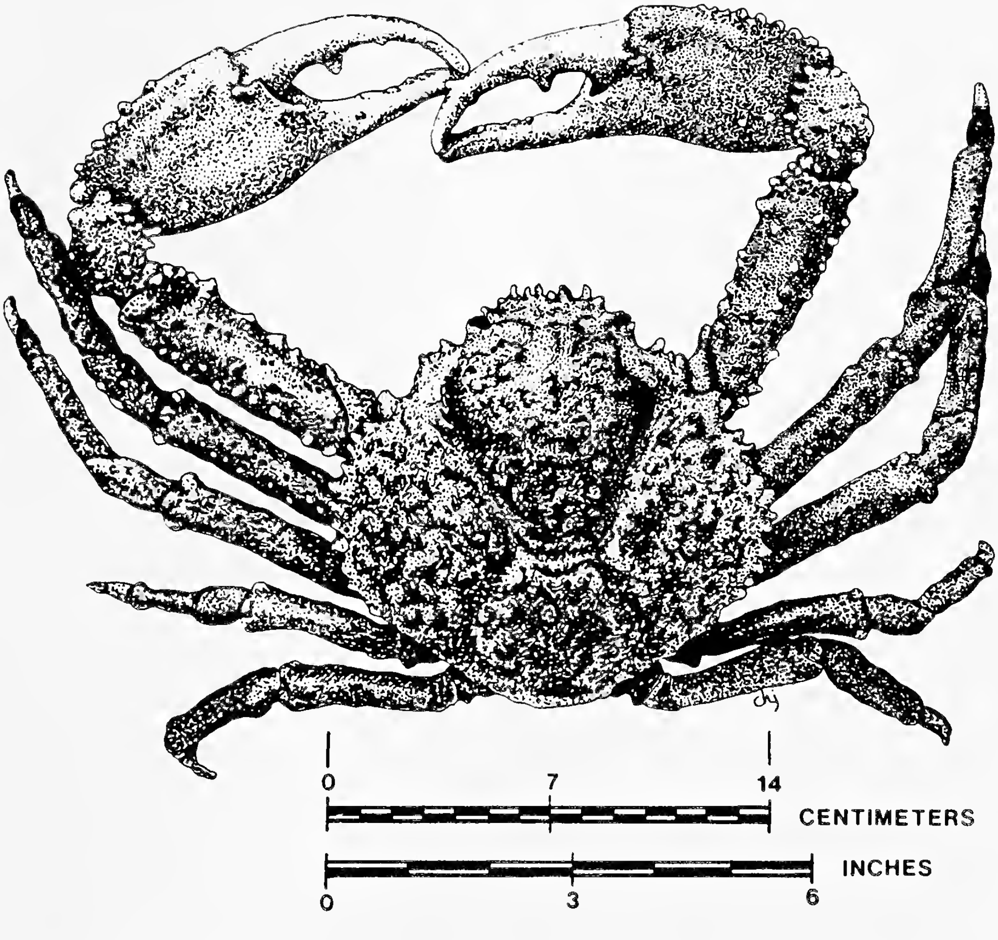

Figure 2

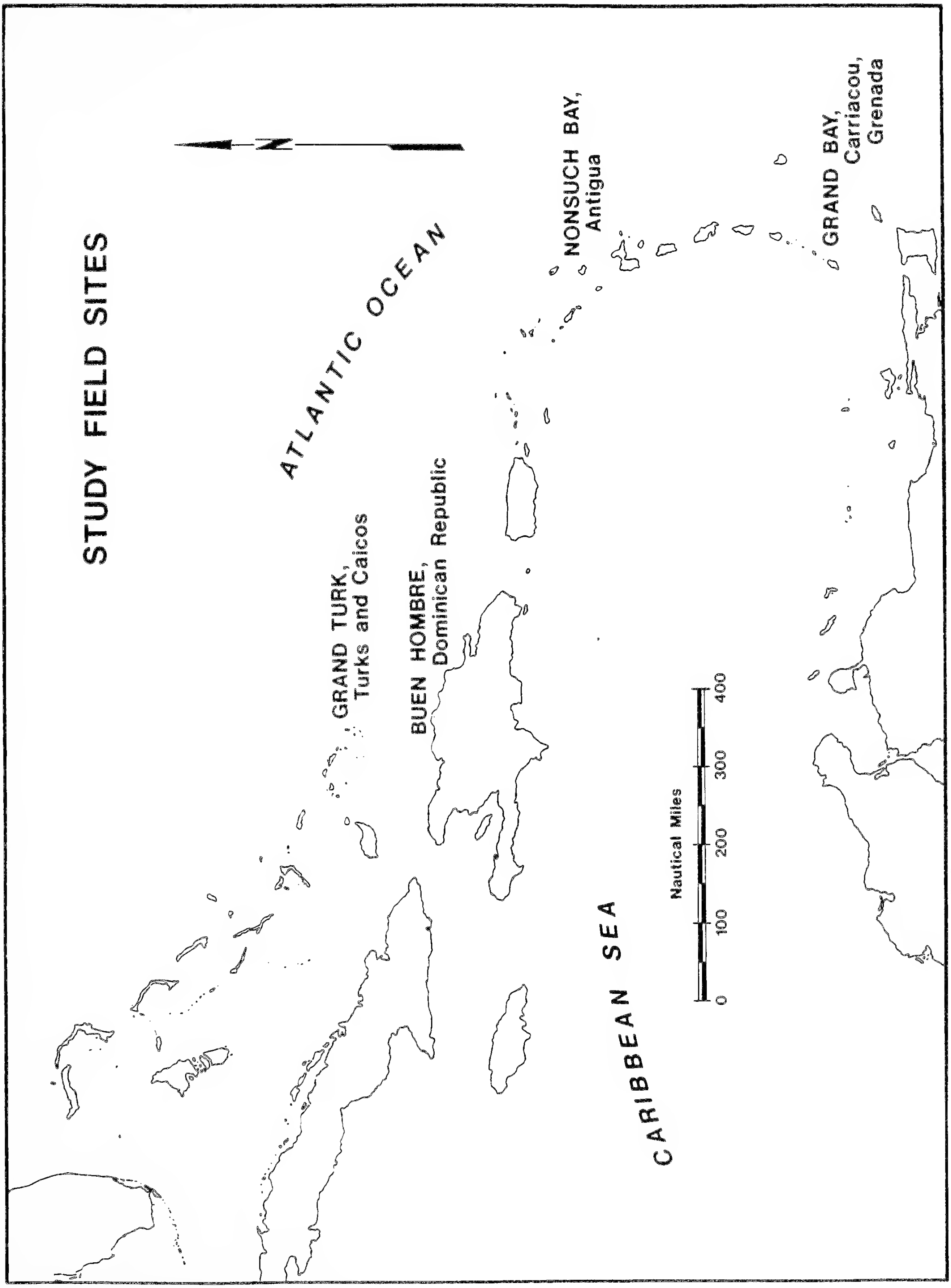
STUDY FIELD SITES
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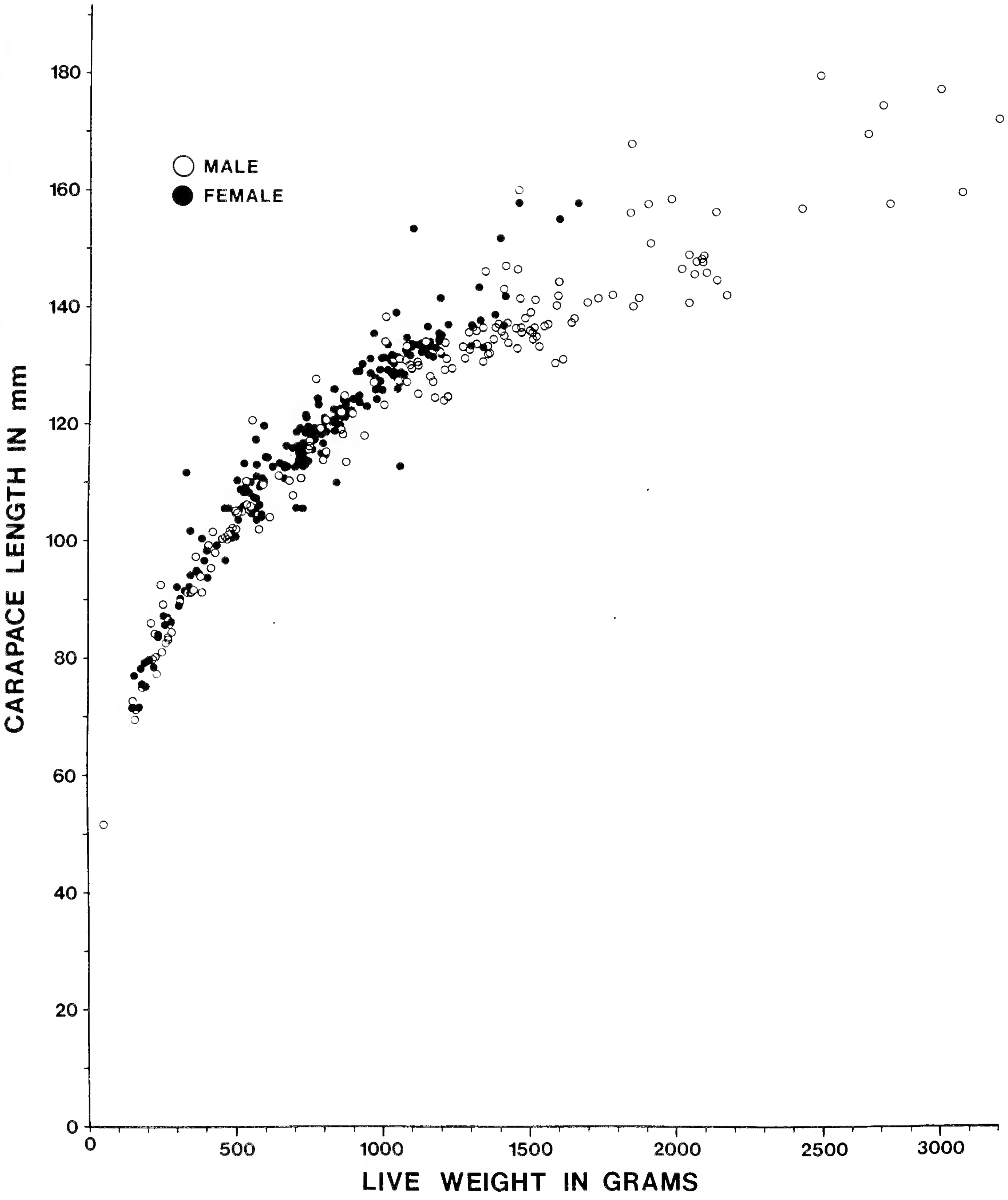
Figure 3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CARAPACE LENGTH IN mm
0
20
40
60
80
100
120
140
160
180
LIVE WEIGHT IN GRAMS
0
500
1000
1500
2000
2500
3000

Figure 4

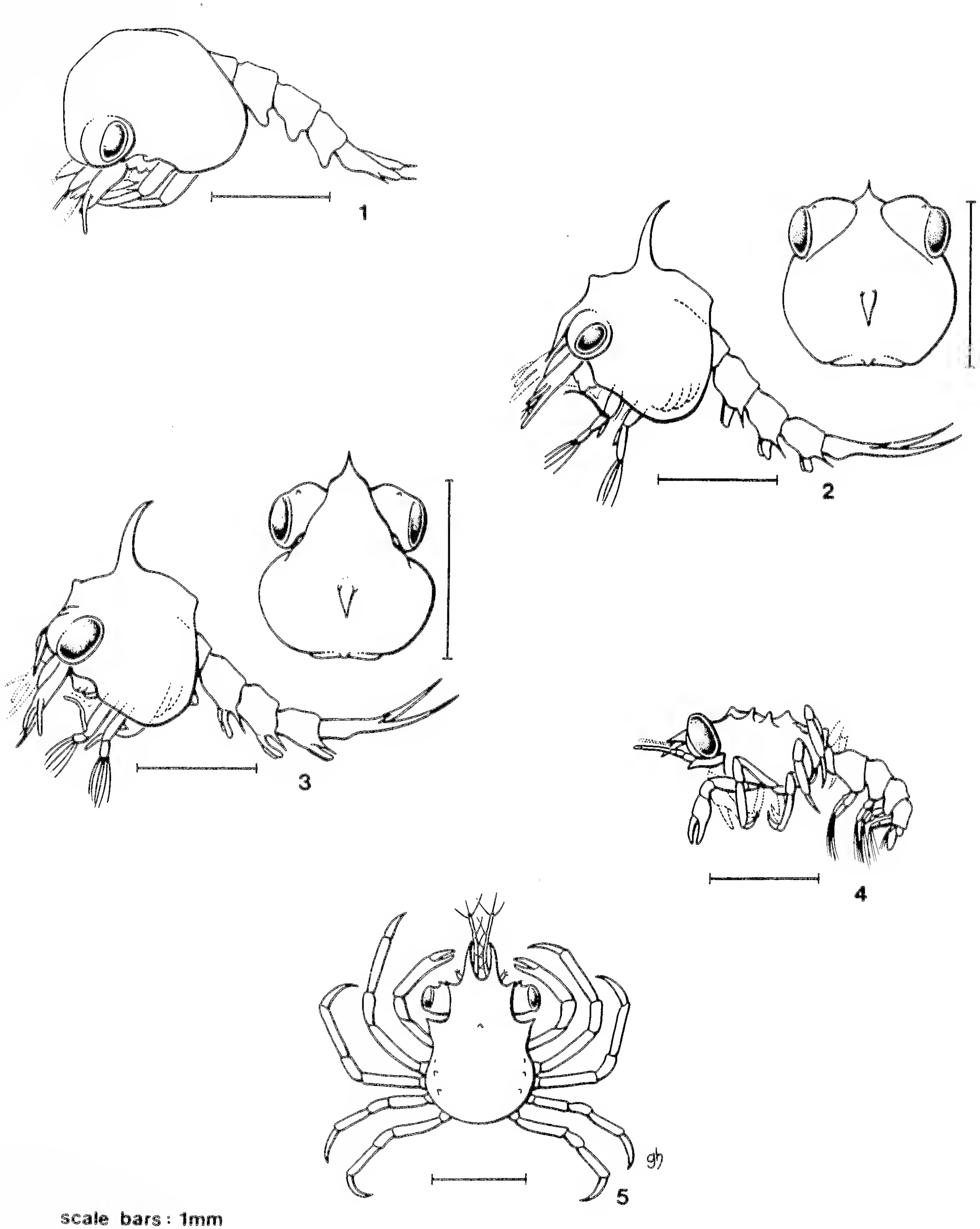


Figure 5

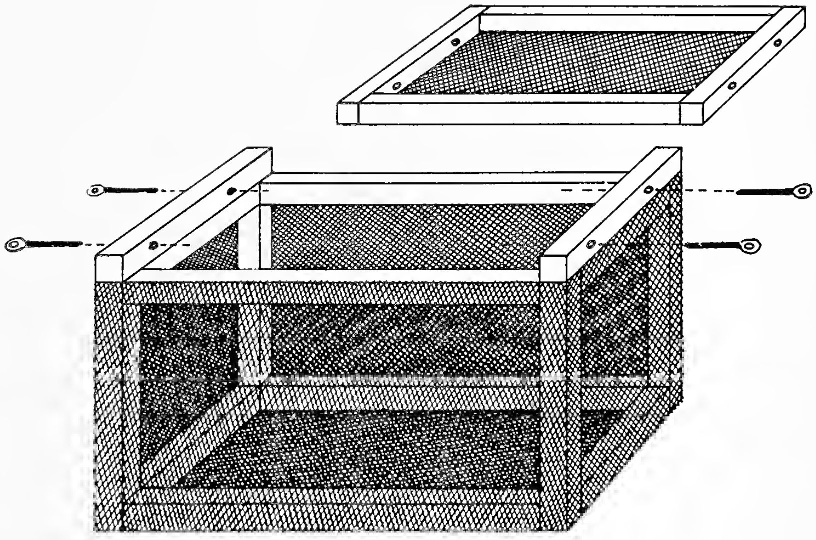
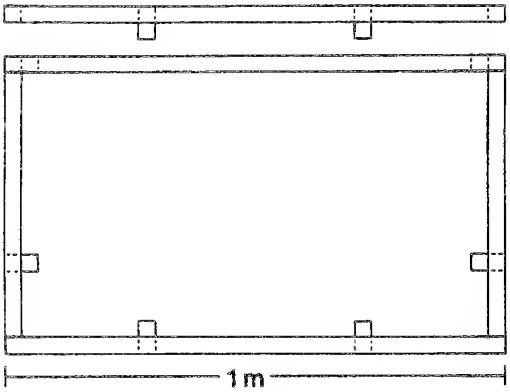
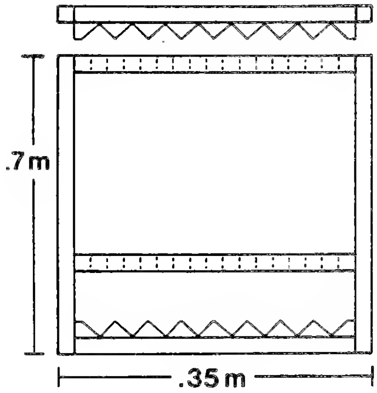


Figure 6

SIDE VIEW WITH LID



END VIEW WITH LID



TOP VIEW

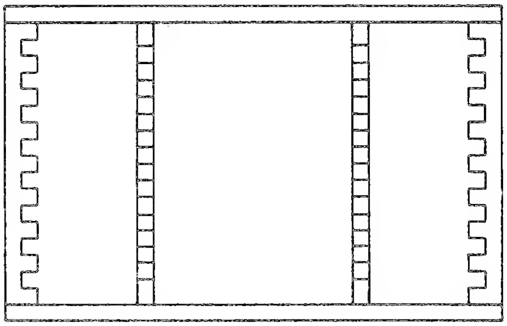


Figure 7

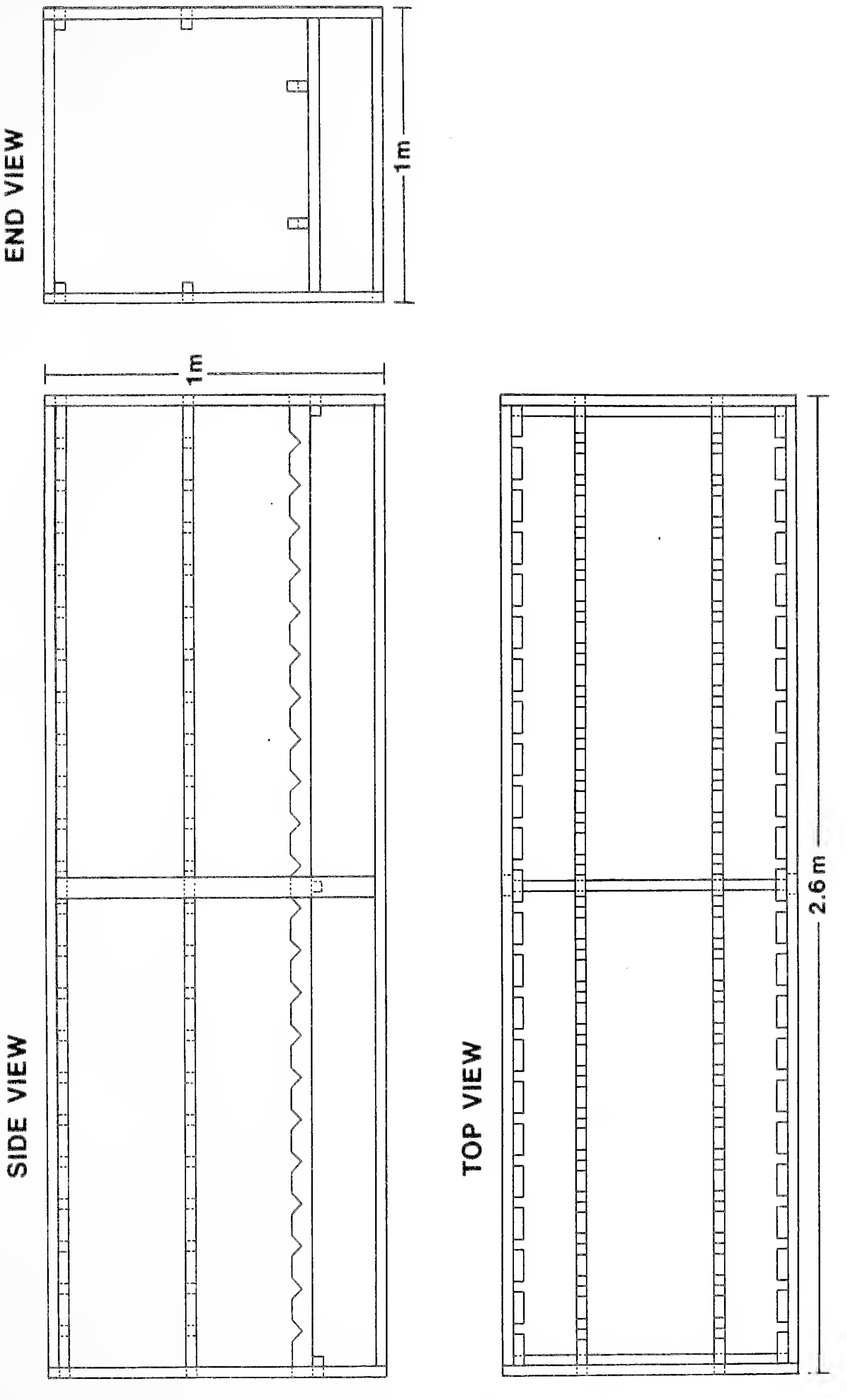
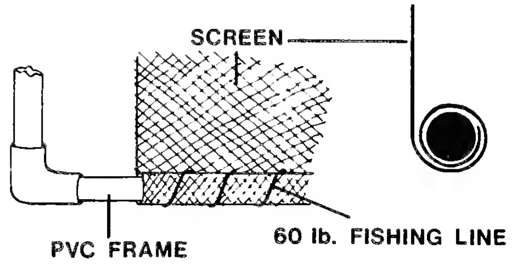
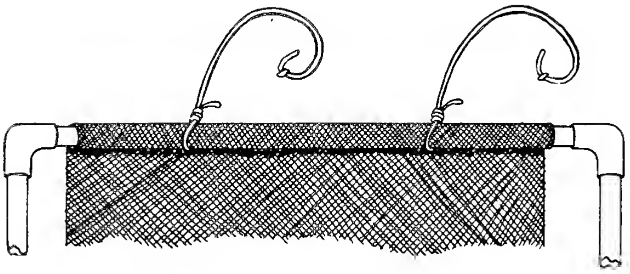


Figure 8


SCREEN
PVC FRAME
60 lb. FISHING LINE



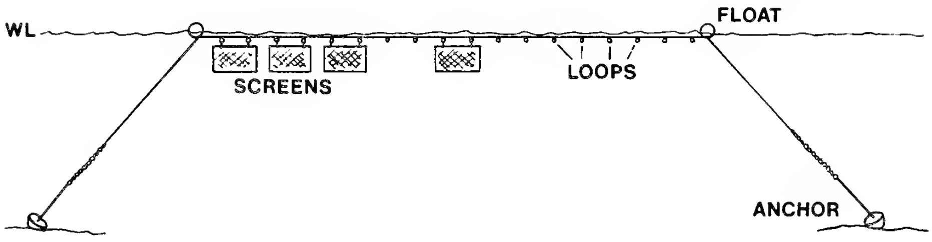

WL
FLOAT
SCREENS
LOOPS
ANCHOR

Figure 9 & 10

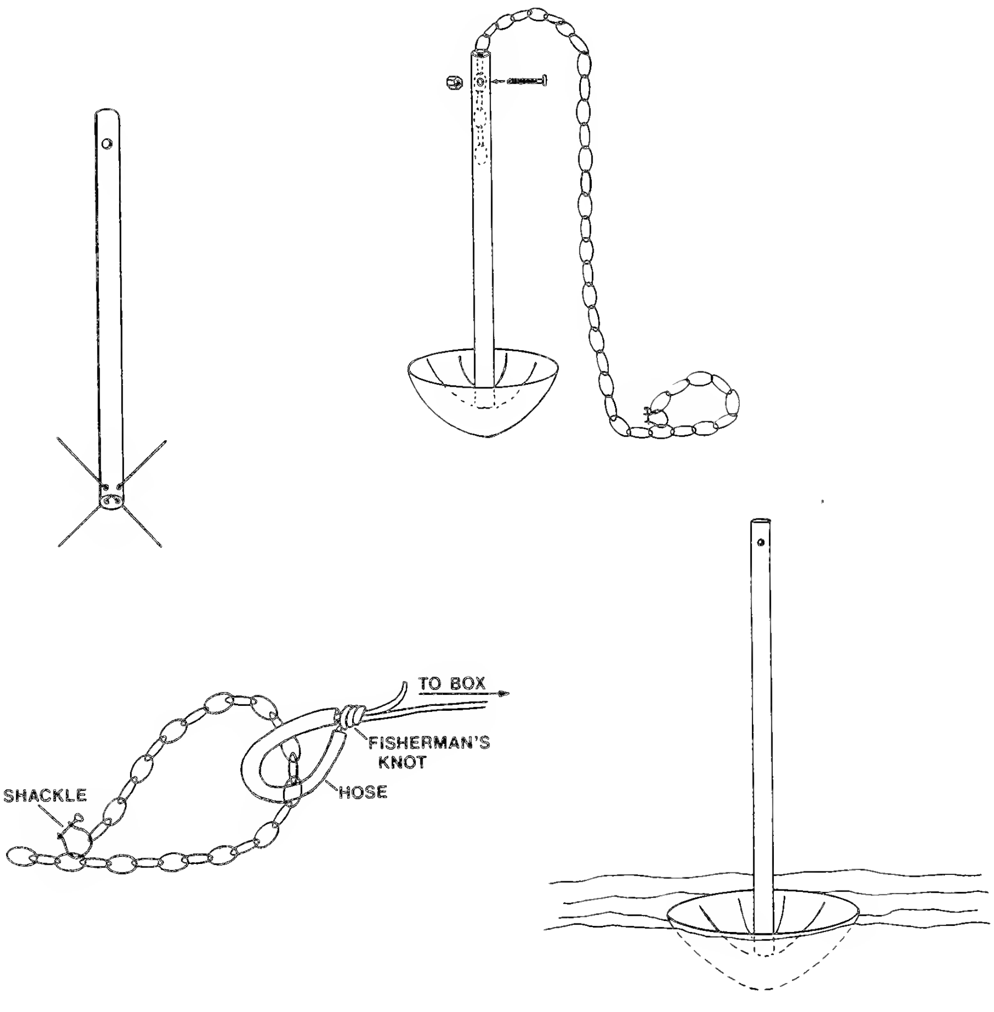


Figure 11

TABLE 1

SIZE AND FECUNDITY OF SELECTED FEMALE _M. SPINOSISSIMUS_

Total CL Length (mm)	Weight of Crabs (gms)	Weight of Egg Mass (gms)	Weight of Crab: Weight of Egg mass	Total Number of Eggs
105	550	40	13:1	42,000
115	800	49	16:1	51,000
125	1090	58	19:1	60,000
135	1400	67	21:1	69,000

*Interpolated from Data in Craig, _et al_., this volume.

TABLE 2.

BASIC BIOLOGICAL CHARACTERISTICS TO DERIVE CAGE NUMBER AND ALGAL TURF SCREEN SETS FOR PRODUCTION LEVEL OF 50+ CRABS PER CAGE PER 15 MONTHS

1. It is a dual system of crab culture and algal turf culture

2. Average female crab produces 60,000 eggs per hatch.

3. Average time between hatches for any one female crab is 60 days.

4. Average female will produce 3-4 broods while in captivity.

5. The initial density of larval crabs is 60,000/sq. m of cage screen surface which is equivalent to 0.2 zoea/cc of cage volume.

6. The rate of survival of larvae is 3.3% (to 5 days post-hatch.

7. The rate of stocking of post-larvae (5-20 days post-hatch) is 500 - 800 crabs/sq. m of cage volume.

8. The rate of survival to 6-10 mm (CL) is 30%(approximately 60 days post-hatch).

9. Algal turf screen sets per hatch cage, number 4 sets of 4 single-layer screens each. Algal feeding rate should be greater than 0.15 gm(dry)/crab/4 day (assuming each screen set is exchanged into the cage for grazing for 4 days and thus is in the lagoon proper undergoing algal regrowth for 12 days). An area of rough, flowing water for growing ample quantities of cultured algal turfs.

10. Young crabs of 10 mm CL or larger are transferred to an intermediate cage of 1-2 mm size mesh.

11. The feeding rate for post-larval crabs of 10 mm CL to 25 mm CL cultured in the intermediate cage is increased to 5-10 gms(dry)/crab/day

12. The rate of survival of rearing young crabs from 10 mm to 25 mm CL is 20-40%

13. Upon attaining 25 mm CL, the crabs are transferred to the growout cages at a stocking density of 8-15 crabs/sq. m. of cage surface area.

14. The number of algal screens required is 60-80, which then comprise a total of 3-4 sets that are periodically exchanged into the cage every 4-6 days.

15. A crab is considered marketable after attaining a size of 120 - 140 mm CL and a weight of 0.8-1.5 kg.

16. The yield of marketable crabs per cage is 50+ at a period of 15 months post-hatch.

TABLE 3

ESSENTIAL REQUIREMENTS OF HATCH CAGE REARING

1) Breedstock crabs in adult cages, fed meticuously.

2) A reasonably calm, well flushed lagoonal area.

3) Hatch cages covered with plastic screening of 0.5 mm mesh openings and meticuously constructed so as to keep unwanted marine life from entering. Calm water or sunken cage.

4) Cultured algal turfs in ample quantities to feed the post-larval crabs up to 60-80 days post-hatch

5) The hatch cage screen mesh should be scrubbed, flushed and rinsed of all algal/detrital material that clogs the screen mesh from previous usage

6) The hatch cage seal should be reinspected to insure its integrity

7) The cage anchoring location should be shallow (10-15') calm or protected, and situated so as to receive clear, highly oxygenated water of 25°C, 34-38 ppt salinity. The shallow pavement area of a backreef is ideal

8) The hatch cage should be anchored 4-5 days prior to the expected hatch to provide the right diatom-rich screen and reduce the potential for presence of predators