THE ROLE OF EPIFAUNAL CRUSTACEANS ON *SARGASSUM* SPP. AT MAGNETIC ISLAND, GREAT BARRIER REEF, AUSTRALIA.

Thesis submitted by
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the Department of Marine Biology at
James Cook University of North Queensland.

"Ecology is the science that seeks to understand the distribution and abundance of life on earth. It is both an environmental and an evolutionary science, since it works to discover the ways in which environmental resources are divided among individuals of different species. In this process species are forged and kept distinct, males are separated from females and numbers are so regulated that the common stay common and the rare stay rare." Paul A. Colinvaux,

"To see a World in a Grain of Sand,
And a Heaven in a Wild Flower,
Hold Infinity in the palm of your hand,
And Eternity in an hour."
Auguries of Innocence, William Blake

Frontispiece. An insect of the sea? A juvenile *Cymodoce* forages on a *Sargassum* frond.

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ABSTRACT

Generalisations about the community ecology of invertebrates associated with plant surfaces have been developed largely from studies on terrestrial insect-plant systems and by limited studies on temperate marine macroalgal systems. This study was designed to quantify the seasonal variation in populations of a tropical macroalga and its associated epifauna, to investigate the causal factors producing the phenological patterns and to relate these findings to the general area of plant-arthropod relationships. The system investigated was four sympatric species of the brown alga *Sargassum* and their mobile epifauna, living at Magnetic Island, Queensland, Australia (19°10'S, 146°50'E).

Over two annual cycles all species of *Sargassum* showed pronounced seasonality in size and reproduction but not in density; three of four species grew annual laterals from perennial axes in spring, reached maximum size in summer, reproduced and subsequently senesced, while the fourth species showed the opposite phenology. Epiphytic algae on the surface of *Sargassum* were primarily absent during the spring and summer periods of *Sargassum* growth but attained high abundance during the winter on the residual portions. Epifauna was diverse and abundant on all species of *Sargassum*, being dominated numerically by gammarid amphipods, sphaeromatid isopods, tanaids, errant polychaetes and gastropods. There were few significant differences between abundance of epifauna on different species of *Sargassum* and few or no representatives of the reef cryptofauna: this suggested that the epifauna was a distinct algal-associated community. All epifaunal taxa also showed distinct, repeated seasonal changes in abundance. Gammarid amphipods, sphaeromatid isopods, tanaids and polychaetes – together with many of the less abundant taxa – had abundance maxima in winter and minima in summer. Conversely, only one dominant taxon, gastropods, and two less abundant taxa had summer maxima and winter minima. At finer temporal scales, epifaunal abundance was consistent over a time scale of hours and days, and moderately variable over a scale of weeks. There were few significant day-night variations in abundance of epifauna.

Manipulative experiments were run to test hypotheses about factors influencing the abundance of epifauna. Recolonisation experiments showed that the populations of epifauna were extremely dynamic in space and time, equilibrial communities being re-established on defaunated plants in approximately two weeks. The influence of predation by fishes was examined with an eight-week exclusion experiment: no effect

of predation was detected although cage artifacts may have obscured abundance changes of small magnitude. The influence of habitat complexity and heterogeneity was examined using artificial plants with and without epiphytic algae: a very significant positive correlation was found between the abundance of epiphytic algae and the abundance of many taxa of epifauna. Analysis of the results at the community level revealed that communities became increasingly similar over the eight weeks of the experiment, as epiphytes accumulated on the originally epiphyte-free artificial plants. It is suggested, therefore, that the seasonal patterns of abundance of epifauna, both at the community and taxon level, are driven primarily by fluctuations in the abundance of epiphytic algae.

A detailed study of the sphaeromatid isopods was conducted to determine whether the above results and hypotheses were applicable at the species level, as opposed to the family or community level. Resolution of the seasonal pattern of abundance for the sphaeromatid family revealed that each of three common genera had distinct, unimodal phenologies: *Cerceis* and *Cymodoce* showed autumn maxima while *Neonaesa* had a winter maximum. Size-frequency distributions of all genera suggested that reproduction occurred continuously over extended periods of time and that adults emigrated from *Sargassum* upon reaching a certain size. For these isopods the *Sargassum* and epiphytes acted as a nursery habitat for juveniles, providing habitable space and a potential food source. A series of laboratory and field experiments with artificial substrata revealed that various aspects of habitat structure (size and colour) and habitat architecture (number, size and arrangement of habitable spaces) were important determinants of colonisation by *Cymodoce*. It is suggested that the observed patterns of abundance for sphaeromatid isopods on *Sargassum* were produced by the selective colonisation of epiphytes by juveniles in response to a complex set of habitat criteria.

Although complicated at a local scale, broad scale patterns in the *Sargassum*-epifauna system are similar to those in temperate macroalgal-epifauna interactions. *Sargassum* and its associated epifauna, in common with these other systems, appears to be a 'passive' system, wherein associations are facultative and unspecialised. This contrasts strongly with 'active' terrestrial systems where plants and arthropods commonly have highly specialised, often obligate relationships. Thus, paradigms developed from terrestrial systems about the role of factors such as habitat structure or secondary compounds will need to be revised before they can be applied to marine plant-arthropod interactions.

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I owe an enormous debt of gratitude to Ben who has provided ideas, helped with field work, brought in pastries to the lab. and even kept me up all night counting coral larvae – go forth and vanquish the nibble-pibblies!!

To my parents and thanks for being there; I love you very much.

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Infromation derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

K.M. Martin-Smith

This day: 27·1·94

CHAPTER 1

INTRODUCTION: THE ARTHROPOD/PLANT INTERFACE

"Ecological relationships of higher plants and animals are universal, of fundamental importance, and paradoxical...plant and animal relationships influence the composition of entire communities." Henry F. Howe and Lynn C. Westley, Ecological Relationships of Plants and Animals.

1.1 HISTORICAL BACKGROUND

The plant-animal interaction has traditionally received far less attention than either animal-animal or plant-plant interactions. This has perhaps been the result of the artificial distinction between the scientific disciplines of botany and zoology or the cryptic nature of many of the interactions, or maybe because we just didn't look! Only within the last 30 years have we come to realise that there is a vast spectrum of hitherto unrecognised interactions involving both plants and animals. Curiosities such as carnivorous plants and ant-plant relationships were documented by early natural historians (e.g. Belt 1874), but detailed quantitative measurements on such seminal topics as herbivory, pollination or seed dispersal were neglected (see McIntosh 1985). Major ecological theories have been proposed based on the terrestrial insect-plant relationship, including explanations of species diversity (see summaries in Matthews and Kitching 1984, Howe and Westley 1988), the role of plant secondary compounds (Feeny 1970, Coley *et al.* 1985) and the development of ecological strategies and the habitat templet (Southwood 1977).

The marine plant-animal relationship has had a much shorter history and far less investigation has been performed (Parsons 1980). The reasons for this are manifold – difficulties associated with working in the marine environment, lack of knowledge of the biology of the interacting organisms and the low economic importance of marine plants and their associated animals. However, marine plant-animal interactions provide an opportunity to test the generality of paradigms developed in terrestrial systems and have the potential to generate alternative hypotheses about the nature of the plant-animal relationship. In the rest of this chapter I intend to detail some of the important aspects of the terrestrial insect-angiosperm relationship, the marine crustacean-macroalga relationship, comparisons and contrasts between the two and finally to describe how the investigation of the *Sargassum*-epifauna system can help with understanding these systems.

1.2 THE TERRESTRIAL SYSTEM: INSECTS AND ANGIOSPERMS

The terrestrial environment is dominated in terms of species richness and abundance by two groups of organisms: angiosperms ('flowering plants' of the division Magnoliophyta) and insects. Some 235 000 angiosperm species are currently recognised although the true number may be much higher (Woodland 1991), while estimates of insect species diversity run from 4-10 million (Lovejoy 1974) to upwards of 30 million (Erwin 1983) representing 72% of extant animal species (Ride 1978). The association between the groups has a long history – insects have been interacting with vascular plants for at least 250 million years (New 1988) and with angiosperms since their evolution in the Jurassic period (c. 150 Ma B.P.). It is probably true to say that no species of angiosperm completes its life cycle without interacting with at least one insect species, and many insects and plants live in obligate associations, either mutualistically or antagonistically. The history and frequency of the insect-plant contact leads New (1988) "...to suggest that the basic principles of community ecology can best (and probably only) be understood adequately from studying the biology of insects on plants".

How do insects interact with plants? Theoretically there are nine possible classes of interaction, representing all the possible combinations of negative, neutral and positive responses by each partner in the association (Table 1.I). However, while examples of all of these types of interaction may be found, they are not all of the same ecological or evolutionary importance. The most important classes of association found between insects and angiosperms are mutualistic (pollination) and antagonistic (herbivory and parasitism). Pollination of gymnosperms by beetles is hypothesised to have arisen in the Triassic period, c. 200 Ma B.P. (Baker and Hurd 1968) before the origin of the angiosperms. The subsequent rise and radiation of angiosperms appears to have gone hand-in-hand with the radiation of the four major pollinating orders of insects (Coleoptera, Diptera, Hymenoptera and Lepidoptera). Herbivory (phytophagy) is also an ancient trait, thought to have arisen in the Carboniferous period c. 350 Ma B.P. and many of the earliest plant fossils show insect damage (Swain 1978). Today, phytophagous insects represent over half the extant insect species (Matthews and Kitting 1984); this is by far the most common mode of insect nutrition.

Within the gamut of insect-angiosperm interactions there are varying degrees of specialisation and dependence of the participating organisms. Associations range from ubiquitous, polyphagous insects such as cockchafers and wireworms feeding casually

Interaction	Effect on plant	Effect on animal	Frequency of occurrence	Example
COMPETITION	Negative	Negative	Rare/Never	–
AMENSALISM	Negative	Neutral	Common	transmission of plant pathogens (viruses etc.)
HERBIVORY/ PARASITISM	Negative	Positive	Very common	aphids on bean, gall wasps
AMENSALISM	Neutral	Negative	Common?	digestibility reducers in leaf fall
NEUTRALISM	Neutral	Neutral	Rare/Never?	casual encounters between insect and non-host
COMMENSALISM	Neutral	Positive	Common	cryptic moths on tree bark
PREDATION/ CARNIVORY	Positive	Negative	Occasional	pitcher plants
COMMENSALISM	Positive	Neutral	Common?	frass deposition by saprophagous insects
MUTUALISM	Positive	Positive	Very common	pollination, ant plants

Table 1.I. Types of interactions between insects and plants

on a wide range of hosts (Edwards and Wratten 1980) to extreme specialisation and obligate dependence as in fig wasps and various *Ficus* species where one species cannot reproduce without the other (Ramirez 1974). The general trend appears to be that both insects and angiosperms are specialised to a quite high degree. There is an evolutionary advantage to an angiosperm having a specialist insect pollinator since this will ensure less wastage of pollen and hence greater fertilisation success (Matthews and Kitting 1984). This is exemplified by the highly specialised orchids, such as *Ophrys*, which induce male bees of one particular species to copulate with their flowers by mimicking females of that species, in order to achieve pollination (Yeo 1972). However, the majority of pollinators are oligolectic or polylectic (visiting several or many taxa), an evolutionary consequence of periodic flowering behaviour and the relatively long life span of the pollinator compared to the flower (Howe and Westley 1988). With regard to herbivory, polyphagous insects appear to have much longer development times (i.e. they grow more slowly) than oliphagous species: this may be a consequence of having to invest more resources in enzyme systems to detoxify a wide range of plant secondary compounds, rather than a specialist system to overcome a single type (Scriber 1983, 1984).

The role of plant chemistry in mediating the insect-angiosperm interaction is repeatedly stressed by many workers (e.g. Edwards and Wratten 1980, Howe and Westley 1988). Angiosperms have a wide variety of so-called 'secondary' compounds, whose function appears to be primarily defensive (Harborne 1977, Rosenthal and Janzen 1979). The variety and abundance of these compounds and of specialist insect herbivores which feed on them led to the development of the 'co-evolution' hypothesis, first put forward by Ehrlich and Raven (1964). They proposed that a "stepwise reciprocal selective response" occurred, whereby increasingly effective chemical defences in plants leads to increasing specialisation by insects and *vice versa.* A plant with a novel compound or an insect with the ability to detoxify it would enter a new adaptive zone, rapidly generating new species. This hypothesis has been used to try and explain the diversity of both insects and angiosperms: it envisages an evolutionary 'arms race' where plant and animal are continually struggling to overcome herbivory or chemical defence. The theory has since been modified (e.g New 1988) to account for suites of similar, co-occurring herbivores and plants, with continual minor changes in both plant and insect ('diffuse co-evolution').

In addition to interactions played out over evolutionary time, insects and angiosperms also interact significantly over ecological time. Insects can influence the population dynamics of plants (Harris 1972, Wallner 1987); equally, plants can influence the population dynamics of insects (Van Emden and May 1972, Rhoades 1985). The former case has been more intensively studied, from casual observations

on insect plagues which can destroy local plant populations (examples in New 1988) to detailed quantitative studies on the effects of specific insects on their hosts (see Crawley 1983). Harris (1972), in a literature review, found that insects could (a) increase plant abundance (b) have no effect or (c) decrease plant abundance. Pollination is obviously essential in increasing the abundance of most flowering plants, however, herbivory can also stimulate sexual and vegetative reproduction or vegetative growth of plants. Putting the case for the neutral interaction Harris (1972) states that "...most insect species, most of the time, have little effect on plant abundance" and provides a couple of examples. Finally, there are cases where insects can dramatically decrease the abundance of plants, the best examples being biological control situations such as the decline of the cactus *Opuntia* following the introduction of the cactus moth *Cactoblastis cactorum* (Wilson 1960). With regard to the effect of plants on the population dynamics of insects, there is a growing body of evidence to suggest that plants can have a significant effect. The following table summarises the hypothesised factors controlling insect abundance in 27 forest studies (in Berryman 1988):

Factor	No. of studies where factor hypothesised to be important in controlling insect population (out of 27*)
Predation/Parasitism	12
Food value/host stress	11
Food availability†	10
Weather	8
Migration	2
Interspecific competition	1
Mutualism with nematode which causes tree stress	1

*Total is greater than 27 because some studies indicated more than one controlling factor.

†Most studies suggested that food availability was equated with intraspecific competition.

Table 1.II. Factors hypothesised to control insect abundance in some forest studies.

Food availability and food value, both potentially controlled by the plant, are the constraining factors for insect populations in half of these studies. Although most of the plants involved in these interactions are gymnosperms, there is no reason to

suppose that angiosperm-insect interactions would be any different (merely less quantitatively studied).

To summarise: insect-angiosperm interactions dominate the terrestrial environment. These interactions can be of many different types, the most common and important being mutualism (pollination and seed dispersal) and herbivory. Specialisation of both interacting groups is often high and there are important consequences to both groups over ecological and evolutionary time.

1.3 A MARINE SYSTEM: CRUSTACEANS AND MACROALGAE

In the euphotic zone of the ocean macroalgae are normally the dominant phytal component of the ecosystem, especially in temperate waters (Chapman 1974, Schiel 1988). Angiosperms (seagrass) and microscopic or coralline algae are also important in certain areas (Cribb 1981, King 1981). The diversity and abundance of animal life in the marine environment is not concentrated in a single phylum as is the case on land. Diversity is high in a number of marine phyla especially Mollusca (> 100 000 species), Crustacea (> 30 000 species) and Annelida (approx. 10 000 species) (Barnes 1980). However, this diversity is at least one, if not two, orders of magnitude less than that of the insects. Hay *et al.* (1987b, 1990a) have compared phytal amphipods to terrestrial insects justifying this in terms of influences on populations, and the ecological role of the alga and the amphipod. Further to this, Phaeophyta (brown algae) approach vascular plants in terms of their degree of organisation of vegetative tissue (Raven *et al.* 1981) – this differentiation means that an appreciable amount of structural complexity of habitat is present, an important consideration in terms of the animal-plant interaction

There are some 1500 species of brown algae which are hypothesised to have arisen c. 500 Ma B.P. in the late Cambrian (Banks 1970, Meyen 1987). The radiation of the brown algae into the groups we see today probably occurred in the Ordovician or Silurian periods (500-395 Ma B.P.) since fossils resembling laminarians and fucaleans are found in the Devonian (Banks 1970). The crustaceans also arose in the Cambrian, however the higher groups, those which are today intimately associated with algae, did not arise until the Devonian and extensive radiation of these groups took place in the Carboniferous period (Briggs and Clarkson 1990, Clarkson 1993). Thus, it seems that crustaceans and algae have been interacting for at least 350 million years. The initial malacostracan crustaceans were carnivores or scavengers; it seems that the herbivorous condition arose later (Briggs and Clarkson 1990).

As with insects and angiosperms there are nine possible types of interactions between macroalgae and crustaceans. The types and frequency of occurrence of these interactions are given in Table 1.III. The most common and ecologically important of these interactions are commensalism by crustaceans and herbivory. There are very few documented examples of mutualisms between macroalgae and crustaceans, in contrast to the terrestrial system. This is not surprising given the absence of animal-mediated pollination in the marine environment. However, commensalism has a far greater role in the marine environment. The aquatic medium is rich in food particles, both living and inanimate, in contrast to the terrestrial atmosphere; thus, many marine species have become adapted to filter-feeding in the water column. Barnes (1980) states "at least some representatives of almost every order [of crustaceans] are filtering suspension feeders, eating plankton and detritus". The other important interaction in the sea is herbivory with the mouthparts of crustaceans being able, in many cases to chew algal tissue.

There is also a paucity of knowledge on the degree of specialisation exhibited in marine macroalga-crustacean relationships. Although there are examples of extreme host plant specialisation – the amphipod *Pseudamphithoides incurvaria* only lives on a few related *Dictyota* species (Hay *et al.* 1990a) – this appears to be a rare situation: Hay and co-workers have stated "...feeding specialisation among marine herbivores is rare" (Hay *et al.* 1989). Hay and Fenical (1992) hypothesise that the degree of specialisation should vary with the mobility of the herbivore. Crustaceans are considered intermediate in mobility between herbivorous fishes (most mobile) and gastropods (least mobile). This hypothesis would then predict that crustaceans (and other invertebrates) would show higher specialisation than fishes and this is borne out, to a limited extent, by studies of amphipods, polychaetes and fishes feeding on *Dictyota* (Hay *et al.* 1987a, 1988c, 1990a).

As in terrestrial systems the chemistry of the host plant plays an important role in mediating the plant-animal interaction, although this has only recently been recognised (see reviews by Hay and Fenical 1992, Steinberg 1992, Paul 1992). Secondary metabolites have been assumed to play a defensive role against herbivores although rigorous testing has often not been applied. The effect of each compound appears to be specific and can vary against different herbivore groups (Hay and Fenical 1992) and geographically (Steinberg 1992). However, since most marine herbivores are generalists, coevolution is unlikely to occur, since a single herbivore will not depend on a single species of food (Hay and Fenical 1992). The model of plant apparency, both as originally proposed (Feeny 1976, Rhoades and Cates 1976) and as modified to concentrate on resource availability (Coley *et al.* 1985) does not appear to fit the marine system: polyphenolics production does not correspond with apparency

Interaction	Effect on plant	Effect on animal	Frequency of occurrence	Example
COMPETITION	Negative	Negative	Rare/Never	–
AMENSALISM	Negative	Neutral	Rare/Never	transmission of pathogens?
HERBIVORY/ PARASITISM	Negative	Positive	Common	isopods on kelp
AMENSALISM	Neutral	Negative	Rare/Never	–
NEUTRALISM	Neutral	Neutral	Common	casual encounters between crustaceans and hosts
COMMENSALISM	Neutral	Positive	Common	filter feeding or domicolous amphipods
PREDATION/ CARNIVORY	Positive	Negative	Rare/Never	–
COMMENSALISM	Positive	Neutral	Rare/Never	–
MUTUALISM	Positive	Positive	Occasional	removal of epiphytes by epifauna

Table 1.III. Types of interactions between crustaceans and plants

(Steinberg 1992), the costs of different types of compound are not significantly different (Hay and Fenical 1988) and the division between toxins and digestibility reducers does not appear to be clear-cut (Hay *et al.* 1987a). It is emerging that the chemical ecology of marine systems is very different to terrestrial systems.

As with terrestrial systems, herbivores may have ecological impacts on plant populations and *vice versa*. Lubchenco and Gaines (1981) address both of these impacts in their review paper, although there are few studies which concentrate on crustacean impacts. Algal abundance may increase, remain the same or decrease with herbivory, the impact being dependent on the size of the herbivore population and its food preference (Lubchenco and Gaines *loc. cit.*). The reverse situation, the effects of the algae on the herbivore population, has not been addressed. Obviously the dynamics of specialist herbivores such as *Pseudamphithoides* will be affected by the abundance and distribution of the host (Hay *et al.* 1990a) but what of the typical case, the generalist herbivore? It is often assumed that the populations of these organisms are independent of the dynamics of algae, since they can switch food sources, but this has not been rigorously tested. It remains to be seen, therefore, what effect algal populations have on crustacean populations.

To summarise macroalgal-epifauna relationships: again, many different types of interaction are found, the most common being commensalism by epifauna on the macroalga. Mutualism is rare and most epifauna are facultative generalists associated with numerous hosts.

1.4 COMPARISONS AND CONTRASTS: ARE CRUSTACEANS THE INSECTS OF THE SEA?

The two sections above have briefly summarised some aspects of insect-angiosperm and crustacean-macroalga interactions. This section will attempt to synthesise the two bodies of knowledge and address the question 'are crustaceans the insects of the sea?'. This question is only one way of comparing the two systems, but there is a far broader knowledge base about the insect-plant interaction upon which to draw; thus it seems logical to phrase the question in this manner. Some of the important characteristics of both sets of interactions are listed in Table 1.IV. Other researchers, most notably Mark Hay and co-workers (e.g. Hay *et al.* 1987a, b, 1988a, b, c, 1989, 1990a, b) have posed this question and Hay *et al.* (1987a) say "...thus it appears that some species of small, relatively immobile marine invertebrates [amphipods] may be ecologically similar to terrestrial insects" although this has been challenged by Bell (1991). Is this hypothesis justified?

CHARACTERISTIC	INSECT	CRUSTACEAN
(A) ENVIRONMENTAL		
SURROUNDING MEDIUM:	Air	Water
VARIABILITY:	High	Moderate
PREDICTABILITY:	Variable	Variable
STABILITY:	Variable	High
HOST:	Usually angiosperm, occasionally lower plant	Usually alga or angiosperm (seagrass)
(B) PHYSIOLOGICAL		
EXOSKELETON:	Chitinous integument	Calcified integument
LOCOMOTION:	Flying or crawling	Swimming or crawling
MOUTHPARTS:	One pair of mandibles, one pair of maxillae, labium (formed from fused second maxillae), often highly modified	One pair of mandibles, two pairs of maxillae, sometime modified
LIMBS:	Uniramous, often slightly modified (grasping, collecting etc.)	Biramous, often highly modified (grasping, cutting etc.)
NERVOUS SYSTEM:	Well-developed, capable of fast co-ordinated reaction	Well-developed, capable of fast co-ordinated reaction
SENSE ORGANS:	Eye compound, many types of sensillae, chemoreceptors, sometimes tympanic organs	Eye simple (nauplius) or compound, proprioceptors, statocysts, chemoreceptors
DIGESTIVE TRACT:	Straight, cecae present, ventriculus secretes digestive enzymes	Straight, cecae present, hepatopancreas secretes digestive enzymes
RESPIRATION:	Spiracles and trachae	External gills
DEVELOPMENT:	Incomplete (e.g. thrips) or complete (e.g. butterflies) metamorphosis	Various modifications of nauplius–zoea–postlarva–adult
(C) ECOLOGICAL		
LIFESPAN OF HOST:	Variable	Short
LEVELS OF EPIPHYTES ON HOST:	Low	Variable, often high
CUES FOR LOCATION OF HOST:	Chemical or visual	Unknown
CLOSENESS OF ASSOCIATION:	Some generalists Many specialists	Very few specialists Many generalists
DIET:	Often host	Sometimes host, often epiphytes or filter-feeding in water column
DISPERSAL ON TO NEW HOSTS:	Winged adults and selective oviposition	Planktonic juveniles in many species, mobile adults
DIVERSITY OF SPECIES	Very high	Moderate
ADULT RESPONSE TO ENVIRONMENTAL STRESS:	Diapause (if environmental variation predictable), migration (if unpredictable)	Limited local migration

(continued on next page)

HOST DEFENSIVE ADAPTATIONS:		
(A) CHEMICAL:	Digestibility reducers (e.g tannins) or toxins (e.g. alkaloids)	Digestibility reducers (e.g. polyphenolics) or toxins (e.g. terpenes)
(B) MORPHOLOGICAL:	Tough cuticle, lignification, trichomes (either hooked or glandular)	Calcification, tough thalli
(C) OTHER:	Spatial or temporal escape	Spatial or temporal escape
ANIMAL DEFENSIVE ADAPTATIONS:		
(A) CHEMICAL:	Toxins (sequestered from plant or produced by insect), Stings	None known
(B) MORPHOLOGICAL:	Tough exoskeleton, spines, protuberances etc.	Tough exoskeleton, spines, protuberances etc.
(C) OTHER:	Behavioural adaptations, crypsis and camouflage, Batesian and Müllerian mimicry	Behavioural adaptations, crypsis and camouflage
POPULATION CONSTRAINTS:	Predation, food, host and mate location, reproductive success, interspecific competition, environmental stress	Predation, food, host and mate location, reproductive success, interspecific competition

Table 1.IV Comparisons and contrasts between plant-associated insects and crustaceans

Some of the similarities between insect and crustacean communities are striking, others are subtle. Both types of organisms are small arthropods, often abundant and diverse on a phytal habitat. Oak trees may have up to 300 insect species living on them at densities of greater than 100 individual m^{-2} foliage (Feeny 1970), while Coyer (1984) found at least 100 species of crustacean on *Laminaria* and Mukai (1971) found over 200 000 crustacean individuals on a single *Sargassum* plant. The size and diversity of these populations may be controlled by the same factor(s) – predation, host chemistry or habitat constraints (Hay *et al.* 1987a, refs. in Berryman 1988, Hacker and Steneck 1991). Herbivory by arthropods can defoliate enormous areas of vegetation e.g. 1700 km^2 of defoliated *Eucalyptus* forest caused by a stick insect (Neumann *et al.* 1977) or large areas of kelp forests denuded by an amphipod (Tegner and Dayton 1987). Another important ecological similarity is the ability to disperse from one habitat to another at some stage of the life cycle (winged adults in insects and planktonic juveniles or swimming adults in crustaceans). In evolutionary terms the possession of multiple appendages (Barnes 1980) which can be adapted for grasping, cutting, piercing etc. is important; this allows adaptive radiation to take place to exploit different ecological niches.

However, there are important differences between phytal-associated insects and crustaceans which have a bearing on the comparison of the two groups. Perhaps the most important difference is the degree of dependence exhibited between the arthropod and its host. The majority of insects are specialists, living and feeding on a few species of plants (Futuyma and Gould 1979, Strong *et al.* 1984), whereas crustaceans appear to be more generalist, being found on a wide variety of hosts (Lubchenco and Gaines 1981, Hay and Fenical 1988). This difference may be artifactual – the mere presence of an organism on a host does not prove that it is the preferred habitat of that species. It is also possible that the specificity of crustacean-algal interactions has not been investigated enough to make generalisations. However, from the knowledge base available the insect-plant relationship is more host-specific than the crustacean-algal case. The ecological implications of this are many – generalists are less dependent on the population dynamics of their hosts and have the potential to attain larger populations (Wallner 1987) but may grow more slowly because of trade-offs in performance (Futuyma and Moreno 1988). Another major difference between the insect-plant and crustacean-macroalga interactions in the relative frequencies of commensalism and true herbivory (where the organism eats the host). Many crustaceans are specialised to filter-feed in the water column using setae (e.g. Barnard 1976, Aoki and Kikuchi 1990) and debate has raged over the relative importance of epiphytic organisms as food (comment by Bell 1991 on paper by Hay *et al.* 1987a and subsequent reply by Duffy and Hay 1991a). These two modes of feeding, collecting

material from the surrounding medium and feeding on epiphytes, are not important in the insect-plant relation: instead, feeding on the host is the norm. This also has consequences in terms of the limiting factors controlling population abundance – food limitation has been seldom demonstrated to control marine epifaunal populations (review by Orth *et al.* 1984) whereas insect populations are often food-limited (refs. in Berryman 1988).

1.5 DEFINITION OF TERMS

To avoid later confusion some of the specialised terms used in the description of the crustacean-macroalga interaction are defined below. In the context of the rest of this work, I propose to use the following definitions:

Epibiosis – association between two organisms, the **basibiont** and the **epibiont**, whereupon the latter lives on or in close association with the former. The basibiont is sessile, the epibiont may be sessile or mobile; either may be plant or animal. The association is usually facultative in so much as the epibiont is not physiologically dependent on the basibiont. However, in natural systems it may not be possible to find one without the other i.e. the association is ecologically obligate.
Basibiont – sessile substrate, host to the epibiont.
Epibiont – organism living on or in close proximity to the basibiont. If the organism is a plant, it is an **epiphyte**, if an animal it is an **epizoan** (or **epizoite**). Collectively the epizoans are called the **epifauna**. Epifauna may be sessile/attached (e.g. hydroids) or mobile/free-living (e.g. amphipods). Unless otherwise stated epifauna will be taken to mean mobile epifauna.

These definitions are rather different to those given by Wahl (1989) in a review paper on marine epibiosis. However, he was considering macromolecules, bacteria and sessile organisms only. The other term which has had considerable confusion over its meaning is **symbiosis**. Abercrombie *et al.* (1980) define symbiosis as "(1) Association of dissimilar organisms whatever the relationship between the two partners. (2) Association of dissimilar organisms to their mutual advantage". I propose to use the definition (1) for symbiosis and to use **mutualism** for case (2).

1.6 THE *SARGASSUM*-EPIFAUNA SYSTEM: MACROALGAL-CRUSTACEAN INTERACTIONS IN THE TROPICS

The specific system which was chosen to test some of the paradigms and hypotheses about arthropod-plant relationships was the association between various species of the large brown alga *Sargassum* and mobile epifauna. Some of the reasons for choosing this system were:

- *Sargassum* is a widespread and abundant genus, extending geographically into tropical and temperate waters all around the world (Nizamuddin 1970). This makes extrapolation from the study to other systems more valid. The dominance of *Sargassum* on tropical fringing reef systems in many parts of the world (e.g. Wanders 1976, De Wreede 1976, Ang 1986) mean such interactions are of high local importance.

- There were large populations of *Sargassum* and epifauna at Magnetic Island, allowing replicated, repeated sampling.

- The system was easy to manipulate: it was possible to perform removal, defaunation, exclusion and recolonisation experiments without severe logistical difficulties.

- Other studies had shown rapid changes in epifaunal populations (e.g. Howard 1985) suggesting that experimental manipulations could be carried out over short time scales, appropriate to a time-limited study such as this.

- Preliminary data was available (Vacamoce 1987) showing significant seasonal biomass and size changes in *Sargassum* populations. Thus a 'natural experiment' was already in operation with seasonal habitat changes and the consequent effects on epifaunal populations

This study of this *Sargassum* system set out to help in the elucidation of aspects of the arthropod-plant interaction. The existence of sympatric species of *Sargassum* allowed the degree of specialisation of various groups of the epifauna to be ascertained, the temporal changes in animal and plant populations were used to investigate the closeness of the relationship and the ability to manipulate the system allowed the population fluctuations to be investigated with a view to determining the relative importance of particular causal factors.

1.7 AIMS AND OBJECTIVES

Having descended from the general to the specific, I would like to explicitly state the aims of this project. Within each subsequent chapter the pertinent aims will be further detailed, but as an overview of the project rationale the following objectives were set (see Figure 1.1):

(1). To quantify the broad temporal pattern of four species of *Sargassum* growing at Magnetic Island in terms of growth, reproduction, demography and epiphyte loads. This objective was concerned with a large temporal scale of months and seasons, rather than shorter-term variations.[Chapter 2].
(2). To concurrently quantify the populations of mobile epifauna associated with those four species of *Sargassum* in the context of holistic ecology (i.e. examining broad taxonomic grouping rather than individual species). Again this was concerned with temporal patterns on a large time scale. [Chapter 3].
(3). To relate the temporal patterns of *Sargassum*, epiphytes and epifauna to each other.[end of Chapter 3].
(4). To quantify the short-term temporal variation in epifaunal populations, examining population fluctuations on a scale of hours and days up to a couple of weeks. [Chapter 4].
(5). To investigate the short-term spatial variation of epifaunal populations, through recolonisation of defaunated substrata over time. [Chapter 4].
(6). To generate hypotheses to explain the causal factors underlying the seasonal temporal patterns in epifaunal populations. [Chapter 5].
(7). To test hypotheses by experimental manipulations of the system, specifically the role of habitat complexity and predation by fishes [Chapter 6].
(8). To compare the holistic ecology of one broad taxonomic group, the sphaeromatid isopods, with the population fluctuations of species groups within it, and to discuss the consequences for sampling strategies. [Chapter 7].
(9). To further investigate the role of aspects of habitat complexity on sphaeromatid isopods [Chapter 7].
(10). To synthesise all of the findings from the study into a general view of the crustacean-macroalga relation and to relate it back to the field of arthropod-plant relations [Chapter 8].

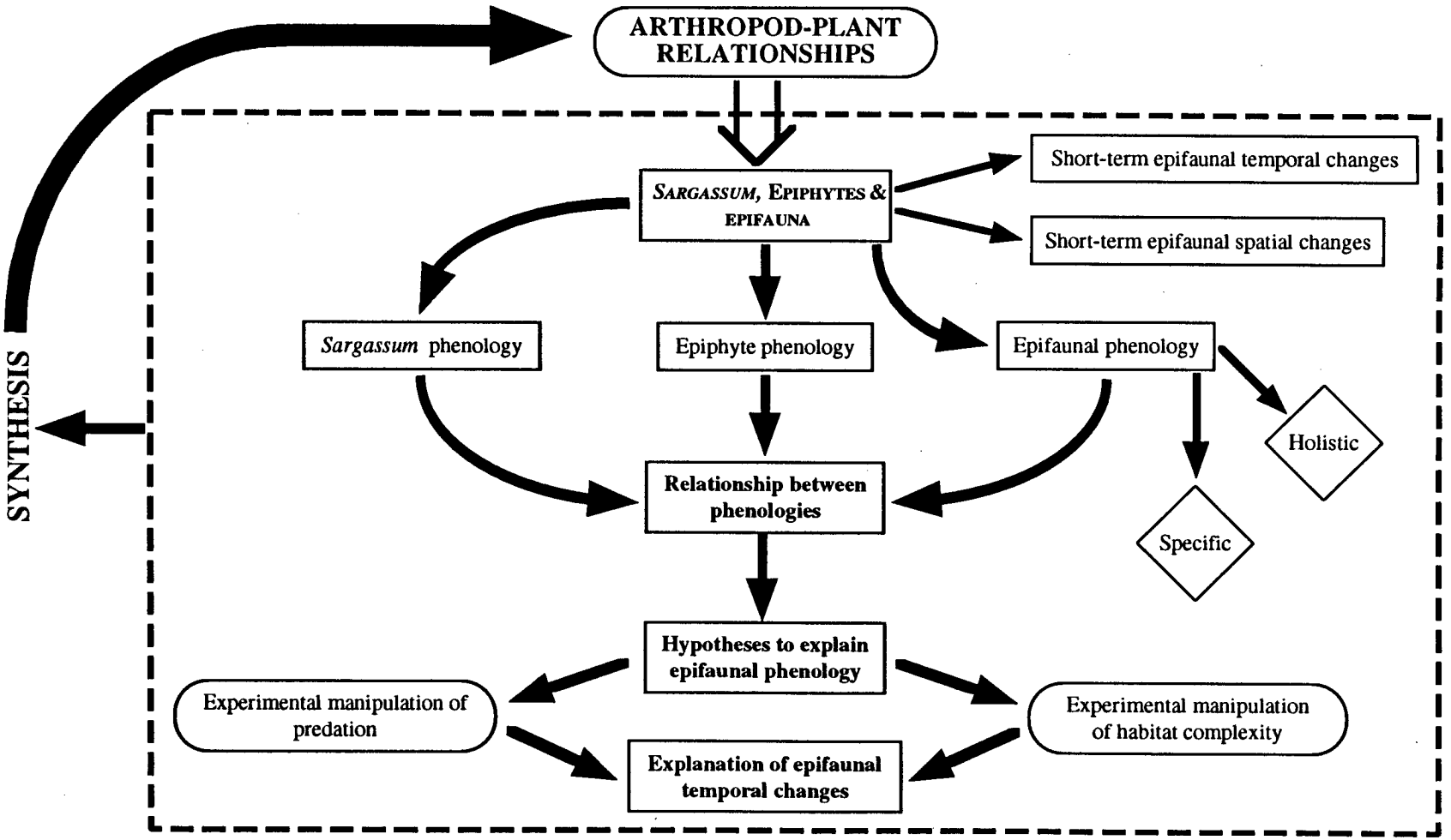

Figure 1.1. Perceived relationships between aspects of study on *Sargassum*-epifauna system.

CHAPTER 2

THE PHENOLOGY OF FOUR SPECIES OF *SARGASSUM**

"παντα ρει, ουδεν μενει" *(translation: All is flux, nothing is stationary)*
Heracleitus

2.1 INTRODUCTION

The genus *Sargassum* (Phaeophyta: Fucales) is diverse, widespread and abundant (Nizamuddin 1970). Some 400 species have been described (Yoshida 1983 cited in Kilar *et al.* 1992), although the true number of species is estimated to be approximately 200 (Womersley 1987). *Sargassum* is normally found growing intertidally or in the shallow sub-tidal, although species have been reported growing to 200 m depth (Magruder 1988). Diversity of the genus is high in both tropic and temperate regions (Nizamuddin 1970). The ubiquitous nature of *Sargassum* over such a wide geographical range allows interesting comparisons to be drawn between growth patterns and their causal factors, since different species face a wide variety of environmental and biotic conditions. Direct comparisons can be made on species with wide distributions (e.g. the work of Díaz-Piferrer 1967, 1970, 1974 on *S. cymosum* and *S. filipendula*) or indirectly with related species (e.g. McCourt 1984).

As with many other fucalean genera, growth and reproduction in *Sargassum* is highly seasonal, in both the tropics and in temperate regions (Table 2.IA and B respectively). For temperate species the general phenological pattern which emerges is a period of maximum growth in late winter or spring followed by peak biomass in spring or summer. There appears to be a continuum of phenologies in tropical species of *Sargassum* with maximum standing crops in spring (e.g. Paula and Oliveira F° 1980), summer (e.g. Raju and Venugopal 1971), autumn (e.g. Ang 1985a, b) or winter (e.g. De Wreede 1976). This data only partially support a hypothesis proposed by Conover (1964) that plants in the tropics are adapted as either 'summer' or 'winter' plants. More species have biomass peaks in winter than any other season, partial support for an alternative hypothesis proposed by Mathieson and Dawes (1974), that tropical algae should have peak growth at cooler times of year, but again there are numerous exceptions.

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* This chapter is reported in the paper: Martin-Smith, K. M. (1993a). The phenology of four species of *Sargassum* at Magnetic Island, Australia. Bot. Mar. **36**: 327-334.

Study	Species	Location	Maximum Growth Rate	Maximum Biomass
Ang (1985a, b, c)	*S. siliquosum*, *S. paniculatum*	Philippines	Summer Summer	Autumn Summer
Chauhan & Krishnamurthy (1971)	*S. swartzii*	India	Winter	Winter
Chennubhotla (1982)	*S. ilicifolium*, *S. myriocystum*	India	Summer-Autumn	Winter
De Ruyter van Steveninck & Breeman (1987)	*S. polyceratium*	Curaçao	Summer	Summer-Autumn
De Wreede (1976)	*S. polyphyllum*, *S. echinocarpum*, *S. obtusifolium*	Hawaii	late Summer-Autumn	Winter-Spring
Doty (1971a)	*S. oligocystum*	Hawaii	not given	none
Durairatnam (1966)	*S. cervicone*	Sri Lanka	not given	Winter
Heijis (1985)	*S. oligocystum*	Papua New Guinea	Winter	Spring
Lawson (1957)	*S. vulgare*	Ghana	not given	Winter
Misra (1966)	*S. tenerrimum*, *S. plagiophyllum*, *S. cinereum*	India	not given	Winter
Murthy *et al.* (1978)	*S. swartzii*	India	Autumn	Winter
Neal (1930)	*S. polyphyllum*, *S. oligocystum*	Hawaii	not given	Winter
Ngan & Price (1980)	*S. oligocystum*	Queensland	Spring	Summer
Paula & Oliveira F° (1980)	*S. cymosum*	Brazil	Winter	Spring
Raju & Venugopal (1971)	*S. plagiophyllum*	India	Spring	Summer
Santelices (1977)	*S. polyphyllum*, *S. echinocarpum*	Hawaii	not given	Winter Spring
Sivalingham (1978)	*S. grevillei*	Malaysia	not given	Winter
Svedilius (1906)	*S. cristaefolium*	Sri Lanka	not given	Winter-Spring
Trono & Lluisma (1990)	*S. crassifolium*, *S. cristaefolium*, *S. oligocystum*, *S. polycystum*	Philippines	not given	Winter
Tsuda (1972)	*S. cristaefolium*	Guam	Winter-Spring	Spring
Tsuda (1974)	*S. granuliferum*	Guam	Autumn	Winter
Tsuda (1976)	*S. crassifolium*	Ulithi & Kayangel Atolls	not given	Summer
Umamaheswararao & Sreeramulu (1964)	*S. ilicifolium* *S. tenerrimum* *S. turneri* *S. vulgare*	India	Winter	Winter
Vacamoce (1987)	*Sargassum spp.*	Queensland	not given	Summer

Table 2.I A. Summary of literature concerning seasonality in growth and standing crops for tropical *Sargassum*.

Study	Species	Location	Maximum Growth Rate	Maximum Biomass
Conover (1964)	*S. filipendula*	Texas	Spring	Summer
Croley & Dawes (1970)	*S. filipendula* *S. pteropleuron* *S. polyceratium*	Florida	not given	none none Spring
Deysher (1984)	*S. muticum*	Japan	Spring	Summer
Edgar (1983a)	*S. verruculosum*, *S. bracteolosum*	Tasmania	Spring-Summer	Summer
Gunnill (1980a)	*S. muticum*	California	Spring	Summer
Jephson & Gray (1977)	*S. muticum*	U.K.	Spring	Summer
Koh & Ahn (1985)	*S. confusum*	Korea	Spring	Summer
Koh & Shin (1990)	*S. lorneri*	Korea	Spring	Summer
Littler *et al.* (1979)	*S. agardhianum*	California	early Summer	late Summer
McCourt (1984b)	*S. johnstonii*, *S. herporhizum*, *S. sinicola*	California	Winter	Spring
Mukai (1971)	*S. serratifolium*	Japan	Autumn	Winter
Ohno (1979)	*S. piluliferum*	Japan	Winter-Spring	Spring
Prince (1980)	*S. polyceratium*	Florida	Autumn	Winter
Prince & O'Neal (1979)	*S. pteropleuron*	Florida	Summer	Autumn
Schiel (1985)	*S. sinclarii*	New Zealand	Spring	Summer
Shepherd & Womersley (1970)	*S. bracteolosum*	South Australia	Spring	Summer
Tseng & LuBaoren (1988)	*S. polycystum*	China	not given	Spring
Umezaki (1983)	*S. miyabei*	Japan	Spring	Summer
Umezaki (1984a)	*S. horneri*	Japan	Winter	Spring
Umezaki (1984b)	*S. hemiphyllum*	Japan	Winter	Spring

Table 2.I B. Summary of literature concerning seasonality in growth and standing crops for sub-tropical and temperate *Sargassum*.

This chapter presents data on the seasonal fluctuations of biomass, length and reproductive periodicity of four species of *Sargassum* growing on an inshore reef in Australia and the changes in density and rates of loss of adult plants from a mixed species community. Since the majority of previous studies were conducted in the northern hemisphere with little work in tropical southern hemisphere waters (Morrissey 1980, Heijis 1985, 1987) it is interesting to compare and contrast the findings of the current study with results from other species from the tropics. The paucity of phenological studies on algae from the tropics makes it very difficult to generalise about seasonality, thus, it is hoped, the following work can contribute to and expand this body of knowledge.

It is not surprising, given the wide range of phenologies exhibited by *Sargassum* (Table 2.I), that a number of different hypotheses have been advanced to try and explain the causal factors and/or cues for this behaviour. Most hypotheses have centred on seasonal variation in physical environmental variables: low (De Wreede 1976) or high (Prince and O'Neal 1979) water temperatures, high nutrient levels (Prince and O'Neal 1979, Ang 1985) or desiccation and rainfall (Tsuda 1974). Little attention appears to have been paid to biotic interactions between species apart from a study by Santelices (1977) and the influence of genetic control of phenology remains largely uninvestigated.

Macroalgae invariably act as hosts for a plethora of epiphytic organisms, both plant and animal, sessile and motile (Chan 1981, Seed and O'Connor 1981, Edgar 1991a). The concurrent variations in mobile epifauna living on *Sargassum* are the subject of the next chapter, but it is important to note here that the phenology of the host must be ascertained before any understanding of the population fluctuations of organisms inhabiting the plant can be attempted. Unless the variation in habitat (alga) is quantified any explanation of epifaunal variation is invalid. In addition, the amounts and types of algae growing epiphytically are also known to vary seasonally (D'Antonio 1985, Arrontes 1990a) which can have important consequences for both the plant and the epifauna living on it. For example, Howard and Short (1986) have shown decreased growth and survival of seagrass leaves with high levels of epiphytes, similarly D'Antonio (1985) found that epiphytes significantly increased the probably of axis breakage in *Rhodomela larix*; however the epiphytes were grazed by epifaunal gastropods and amphipods. Stoner (1979), Johnson and Schiebling (1987), Hall and Bell (1988) and Schneider and Mann (1991a) have all shown positive correlations between populations of epifauna and epiphytic biomass Thus, it was also necessary to quantify the levels and types of epiphytes living on *Sargassum* to gain a full understanding of the seasonal variation in both the host and its motile inhabitants.

2.2 AIMS AND OBJECTIVES

Previous work (Morrissey 1980, Vacamoce 1987) had demonstrated significant seasonal variation in intertidal *Sargassum* populations growing at Magnetic Island. However, information was still lacking on the phenologies of individual species of *Sargassum* within the general population and on subtidal species. Thus, the explicit aim of this part of the study was to elucidate and quantify the phenologies of four species of subtidal *Sargassum*, namely *S. fissifolium*, *S. linearifolium*, *S. oligocystum* and *S. tenerrimum*. A further aim was a quantification of the temporal variation in the levels and types of epiphytes living on each of these species, due to their postulated importance to both host and motile epifauna. Three of the above species, *S. fissifolium*, *S. oligocystum* and *S. tenerrimum*, are found in large mixed-species aggregations. A final aim was, therefore, to assess some of the demographic parameters (loss rates and densities) of these aggregations. The justification for this was that the epifauna living on the plant (Chapter 3) may not have been host-specific and thus responded to the overall community phenological pattern.

2.3 STUDY SITE DESCRIPTION

2.3.1 Species Identification

The genus *Sargassum* is speciose and considerable taxonomic uncertainty exists both between and within 'species' (Kilar and Hanisak 1988, Kilar *et al.* 1992). Taxonomy is complicated by, among other factors, temporal changes in morphology (Womersley 1954, Kilar and Hanisak 1988), environmentally-induced variation (Critchley 1983a, b) and geographical variability (Jephson and Gray 1977). The taxonomic status of *Sargassum* at Magnetic Island has been the focus of work by Edyvane (unpublished) and currently eight species are recognised. Brief descriptions of these species are given below:

S. fissifolium (Mertens) J. Agardh 1848. Discoid holdfast with rounded or slightly flattened distinct primary axis. Plants often have 'bushy' appearance with numerous laterals. Leaves generally undulate, characteristically dichotomous with pronounced yellowish tips. Non-divided leaves may be present but new leaves almost always divided. Vesicles scattered, large, 4-8 mm diameter. Plants monoecious. Found mid-subtidal extending down to 5-8 m.

S. linearifolium (Turner) C. Agardh 1820 (see Womersley 1987). Discoid-conical holdfast bearing 1-6 dark brown thalli. Primary branches 10-45 cm long covered throughout their length with short secondary branches 2-5 cm long. Leaves linear to lanceolate, entire margins. Vesicles few, scattered, small. Plants monoecious. Found on the tops of rock boulders; shallow low-intertidal to subtidal species (to 3 m).

S. oligocystum Montagne 1845 (see Trono 1992). Holdfast small, discoid. Stem short. Primary branches strongly flattened, especially at basal portions, 3-4 mm across, smooth, up to 80 cm long; secondary branches distichous, alternately arranged on primary branches. Leaves large, linear-lanceolate, up to 7 cm long, with very short stalks. Vesicles scattered, few, 2.5-7.5 mm long, 1.0-5.0 mm wide (smaller in fertile plants). Plants dioecious. Found shallow subtidal down to 5 m.

S. opacum J. Agardh 1848. Description almost exactly similar to *S. polycystum* but has discoid holdfast. Intertidal to shallow subtidal.

S. polycystum C. Agardh 1824 (see Chiang *et al.* 1992, Trono 1992). Thallus to 90 cm. Holdfast rhizoidal at Magnetic Island. Primary branches crowded at distal end of short (10-20 mm) stem, terete, lumpy with many simple or Y-shaped short processes. Leaves broadly lanceolate to linear-lanceolate. Vesicles numerous, clustered, very small, 1.5-2.5 mm long and 1.0-2.0 mm wide. Plants dioecious. Intertidal to shallow subtidal.

S. siliquosum J. Agardh 1848 (see Trono 1992). Shield-shaped to massive amorphous holdfast. Stem to 24 mm long; primary and secondary branches terete to slightly compressed, lumpy in young plants. Leaves variable in shape, lanceolate to oblong on secondary branches, large (to 80 mm). Vesicles scattered, large (6-10 mm diameter). Plants dioecious. Subtidal, deepest occurring species (to 9 m).

S. spinifex C. Agardh 1824. Numerous primary axes bearing densely clustered, very small, ovate leaves (less than 5 mm). Plant small with discoid holdfast, vesicles few or absent. Occurs in intertidal to uppermost sublittoral in exposed habitats.

S. tenerrimum J. Agardh 1848 (see Misra 1966). Distinct primary axis, rounded, yellowish-brown, possessing discoid holdfast. Often long internodes between laterals, giving 'spindly' appearance. Leaves linear or linear-lanceolate. Vesicles stalked, spherical, singly or in small groups. Plants have been described as monoecious or as dioecious females only. Occurs in mid-subtidal extending down to 5 m.

2.3.2 Study Site Location and Species Distribution

This work was carried out at Magnetic Island, Queensland, Australia. The island is located within the semi-enclosed Cleveland Bay, about 8 km north of Townsville. The physical setting has been described in detail by Morrissey (1980), Walker (1981a,b), Walker and O'Donnell (1981) and Bull (1982). Briefly, the climate in the Townsville region varies seasonally with respect to temperature and rainfall. Air temperature is minimum in winter (mean in July of 19.9°C) and maximum in summer (mean in January of 27.6°C); however, 80% of the average rainfall (111 cm) falls in summer (December-March) (Morrissey 1980). Walker (1981a) measured salinity in Cleveland Bay and found lowest salinities at times of maximum run-off. Collins (1978) reports salinities of as low as 17‰ in Nelly Bay (adjacent to one of the study sites) after cyclonic rain. Winds are generally south-easterly (Trade Winds) and vary both seasonally and diurnally. Morrissey (1980) reports that winds are stronger in winter – over the period 1990-1992 there was little seasonal predictability in wind velocity, varying about a mean value of approximately 10 kmh^{-1} (Townsville Bureau of Meteorology). Diurnal variation is also evident in wind speed, with higher velocities in the afternoon resulting from the development of an on-shore sea breeze. The tides in Cleveland Bay are semi-diurnal with pronounced diurnal inequality. Spring tides occur during the night in summer and in the afternoon in winter with a mean range of 2.5 m, while neap tides have a mean range of 0.8 m. Average Secchi disc transparency for Nelly Bay is 1.8 m indicating high turbidity (Collins 1978).

Biotically, the island has well developed fringing reefs supporting a mixed community of corals and macroalgae (Morrissey 1980, Bull 1982). Three bays were chosen as representative of the eastern side of Magnetic Island. Florence Bay is the northernmost bay (19°7'S, 146°53'E) and has an extensive carbonate reef on the northern side of the bay (Plate 2.I). *Sargassum spinifex* is found on subtidal boulders, *S. polycystum* in slightly deeper water to 1-2 m where multispecific stands of *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* occur. These communities give way to the deepest living species, *S. siliquosum*, at about 6-8 m. Alma Bay (19°9'S, 146°52'E) is about 3 km SSE of Florence Bay and does not have a carbonate reef, rather boulders descend steeply to a sandy bottom at about 4 m on both sides of the bay which slopes off gently to about 6-7 m in the middle of the bay (Plate 2.II). *Sargassum spinifex* grows intertidally on boulders between +1 and 0 m where it is replaced by dense monospecific stands of *S. linearifolium* which persist down to 3-4 m. At the base of the boulders and on any stable substratum on the

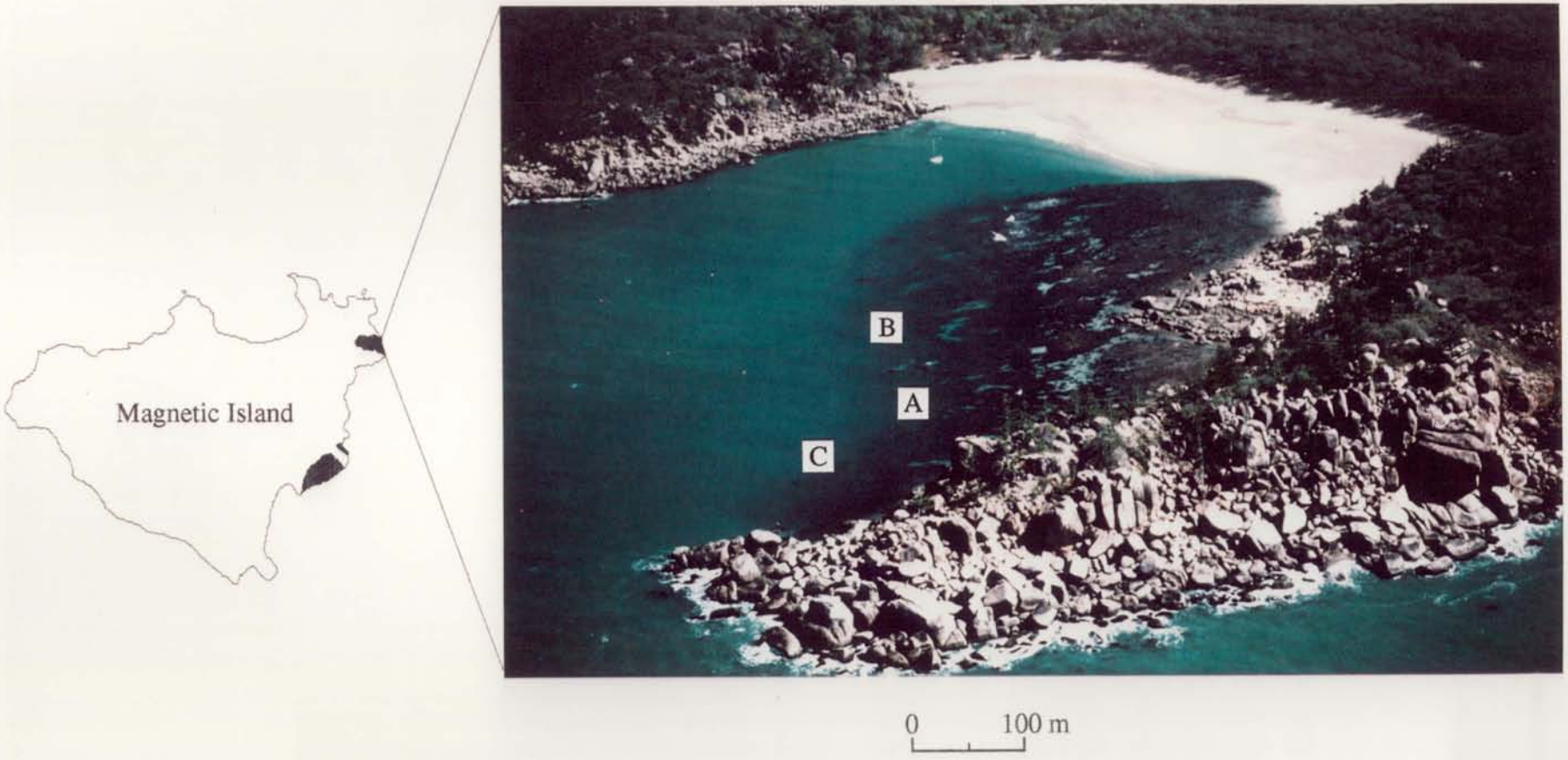


Plate 2.I. Photograph of Florence Bay to show location of reef and sampling sites. Sites are shown by letters on photograph.

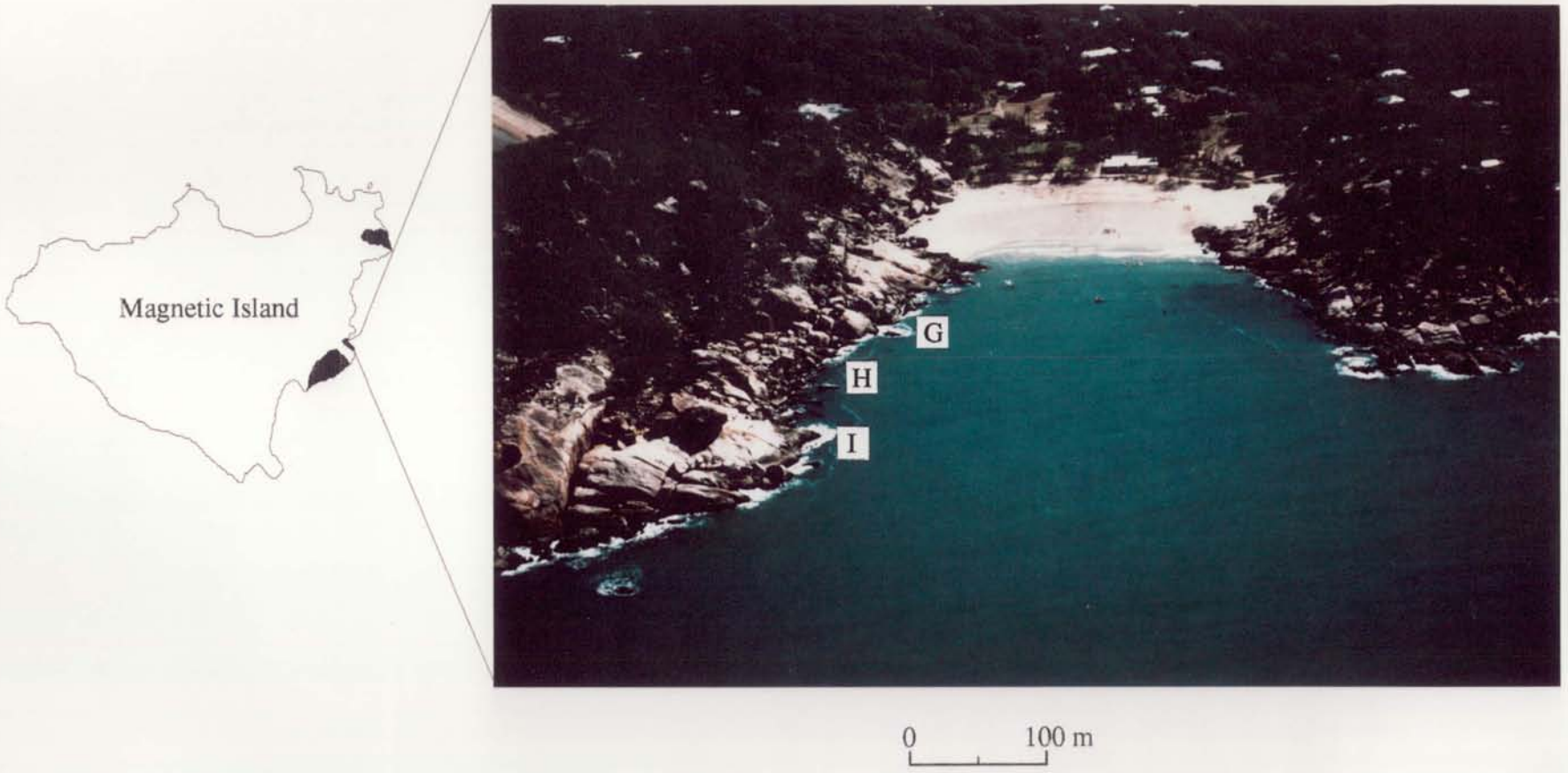


Plate 2.II. Photograph of Alma Bay to show location of reef and sampling sites. Sites are shown by letters on photograph.

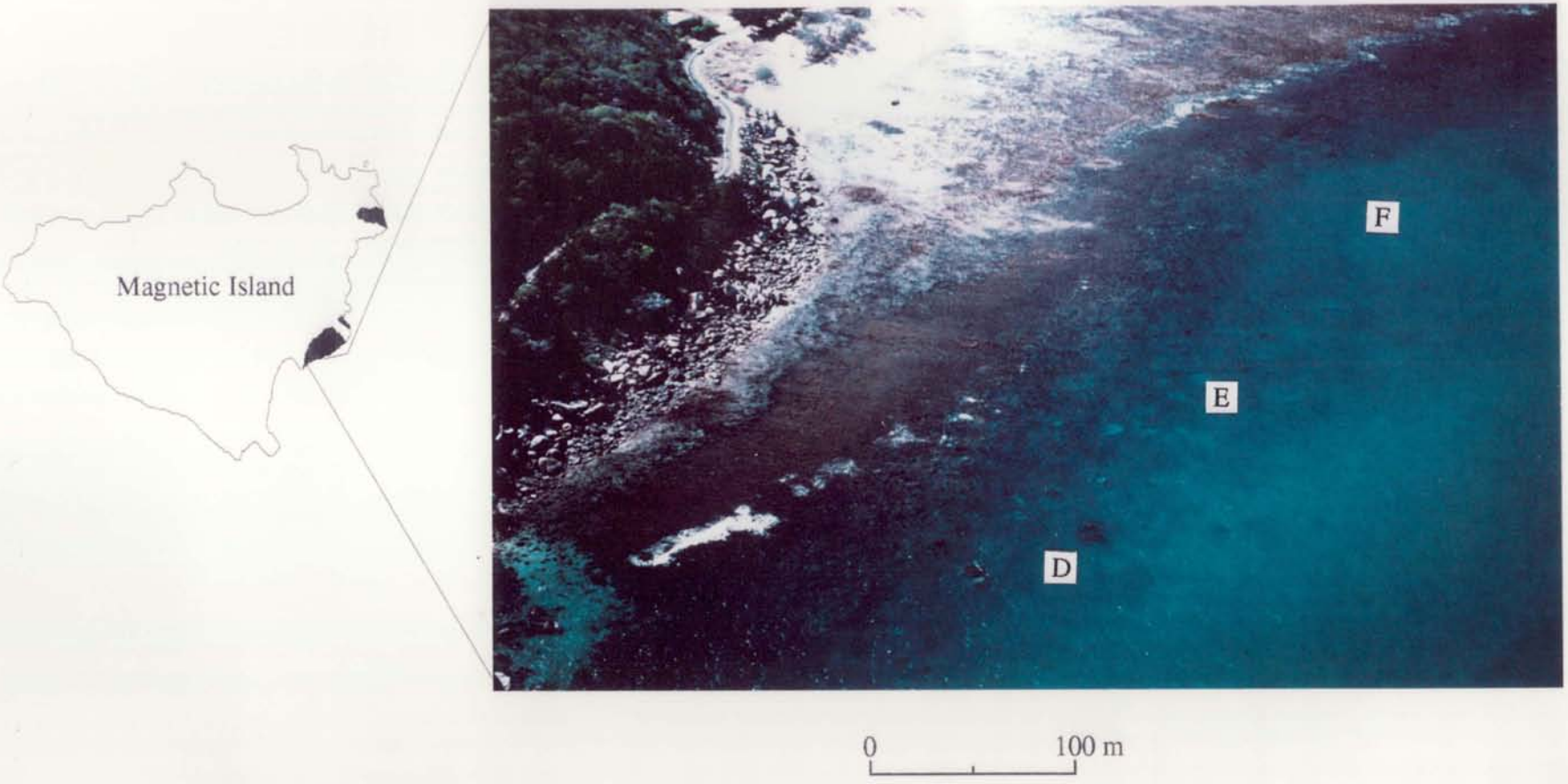


Plate 2.III. Photograph of western end of Geoffrey Bay to show location of reef and sampling sites. Sites are shown by letters on photograph.

sand, there are mixed patches of *S. fissifolium* and *S. tenerrimum*. Geoffrey Bay is found another 500 m S (19°9'S, 146°52'E). There is an extensive carbonate reef across the entire width of the bay extending to a maximum of 800 m offshore and a depth of 8 m (Plate 2.III). *Sargassum* is abundant both on the reef flat and the reef slope, growing on any stable substratum (coral rubble or moribund areas of living coral) – *S. polycystum* is found in the shallow subtidal giving way to dense multispecific stands of *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* in the depth range 1-7 m. *Sargassum tenerrimum* is the shallowest-occurring of these species and *S. fissifolium* the deepest-occurring. Representative diagrams of the patterns of occurrence of *Sargassum* in the three bays are shown in Figures 2.1-2.3.

2.4 MATERIALS AND METHODS

2.4.1 Sampling dates

Initial samples of *Sargassum* were collected in March 1990, followed by further collections in May and July. These samples were part of a pilot study to design and perfect an apparatus for collection of a plant and associated epifauna at the same time (see section 3.3.1). Quantitative sampling was commenced in Florence and Geoffrey Bays in August 1990 and in Alma Bay in January 1991 at sites A-I (shown on Plates 2.I-2.III). Monthly collections were taken continuously from August 1990 to September 1992 with the exception of November 1990, February 1991 and June 1992 when weather conditions prevented collection.

2.4.2 Destructive phenological measurements (species phenologies)

From August-December 1990 ten individual plants were collected from mixed species patches of *S. fissifolium*, *S. oligocystum* and *S. tenerrimum*. Individuals were haphazardly selected, sealed inside a large plastic bag, then the holdfast was prised from the substratum. The samples were returned to the laboratory where the following measurements were taken:

(1). Wet weight of plant after spinning for 60 seconds in a salad spinner to remove excess moisture.

(2). Maximum length of primary axis (or longest axis in species with no distinct primary axis).

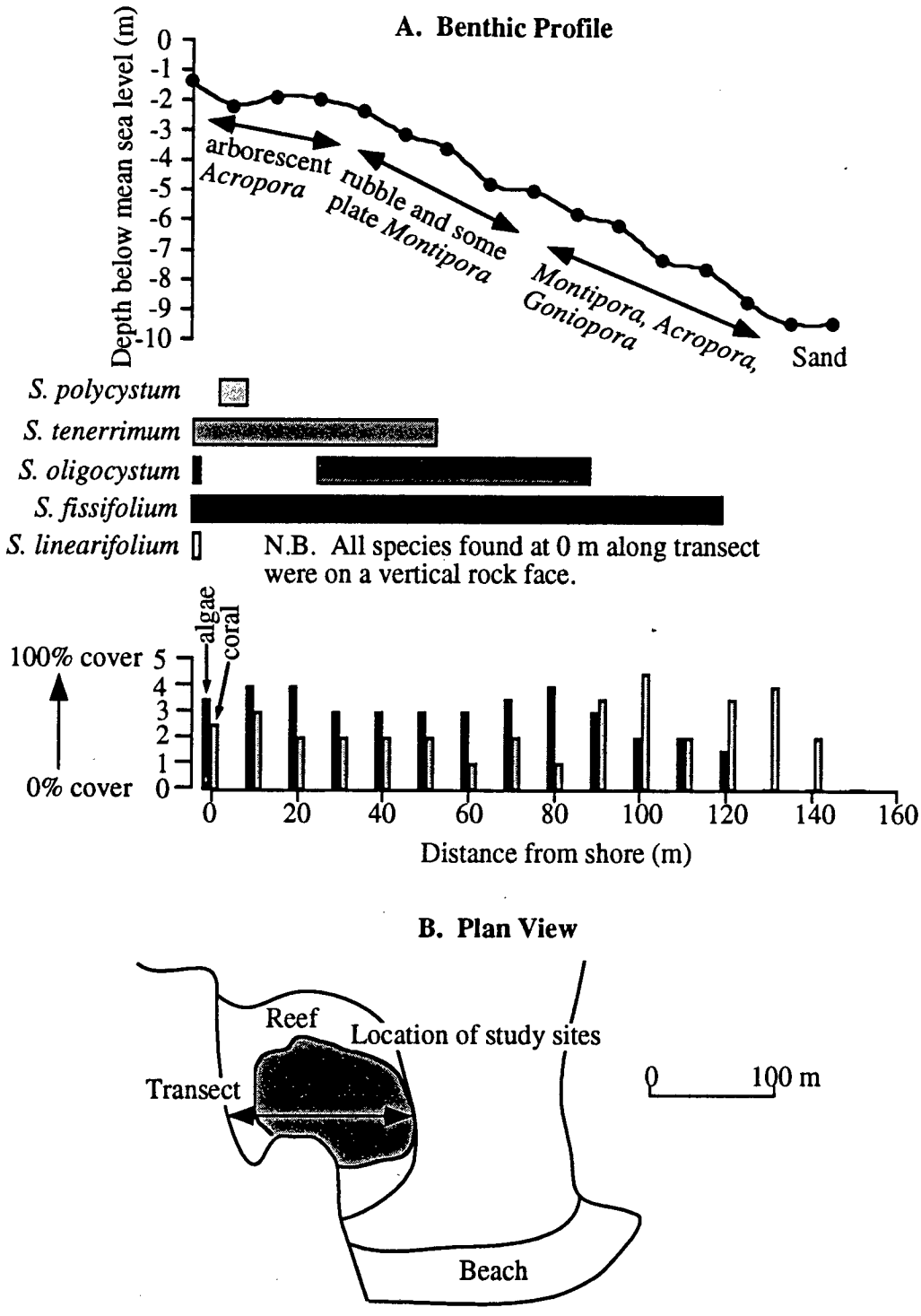


Figure 2.1. Summary diagram of some aspects of study location in Florence Bay. A. Depth profile and distribution of *Sargassum* species with estimation of abundance of coral and algae. B. Plan view of area.

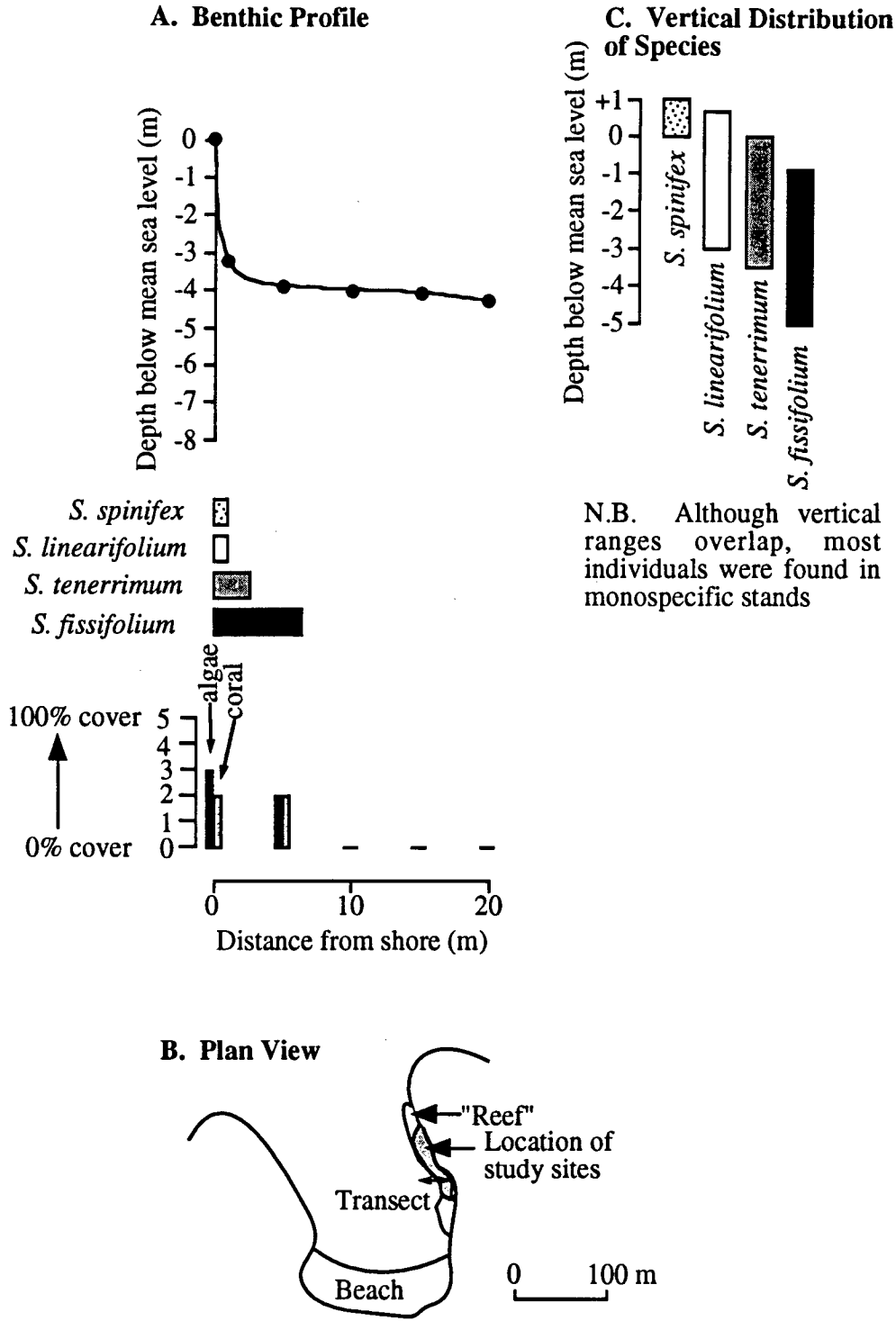


Figure 2.2. Summary diagram of some aspects of study location in Alma Bay. A. Depth profile and distribution of *Sargassum* species with estimation of abundance of coral and algae. B. Plan view of area. C. Vertical distribution of *Sargassum* species on boulders.

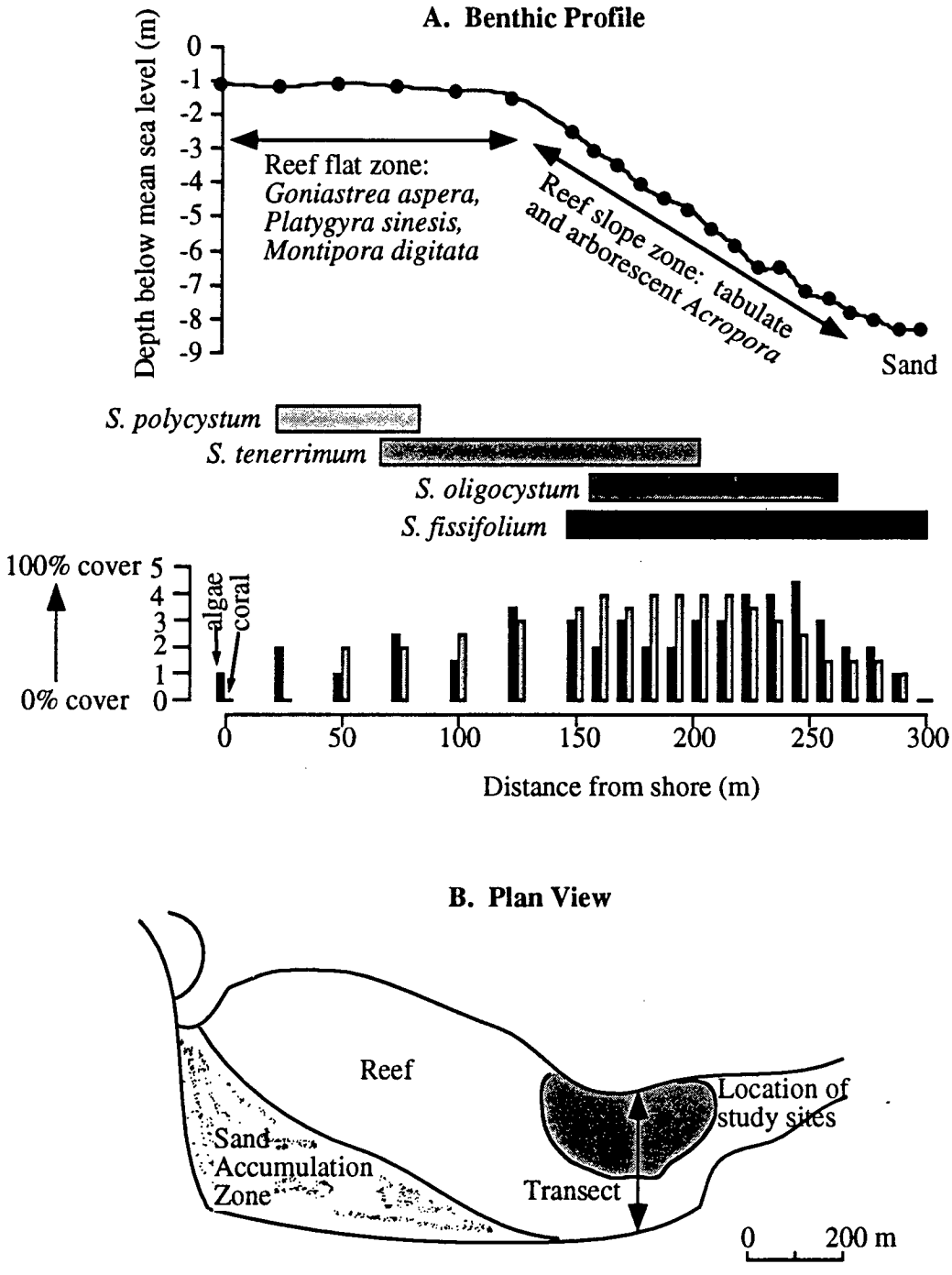


Figure 2.3. Summary diagram of some aspects of study location in Geoffrey Bay. A. Depth profile and distribution of *Sargassum* species with estimation of abundance of coral and algae. B. Plan view of area.

(3). Presence or absence of receptacles.

(4). Species identification (following dichotomous key of Edyvane – *unpub.*).

(5). [From August 1991 onwards] Levels of epiphytic algae and sessile epifauna on each plant. An arbitrary scoring system (modified from the Blaun-Blanquet scale) from 0-5 was given to the levels on both the axis and the blade with the scores estimated as follows:

SCORE	DESCRIPTION OF EPIPHYTE COVER	APPROXIMATE COVER OF EPIPHYTES
0	Pristine	0-5 %
1	Rare	5-25 %
2	Few-Moderate	25-50 %
3	Moderate-Abundant	50-75 %
4	Abundant-Total Cover	75-100 %
5	Total Cover-Superabundant	100+ %

Table 2.II. Estimation of epiphyte cover on *Sargassum.*

A more detailed examination of the types of epiphytes was carried out on samples from September, December 1991, March and July 1992. Epiphytes were classified into one of four major groupings – geniculate red algae (e.g. *Amphiroa, Galaxaura*), filamentous red algae (e.g. *Hypnea, Laurencia*), brown algae (e.g. *Colpomenia, Dictyota, Dictyopteris, Hydroclathrus, Padina*) or sessile invertebrates (bryozoans, hydroids). Each class of epiphyte was given a score from 0-5 for the total plant as above.

In January 1991 the sampling design was changed somewhat with the inclusion of samples from Alma Bay. Seven individuals of each of the 4 species *S. fissifolium, S. linearifolium, S. oligocystum* and *S. tenerrimum* were collected. This meant that individuals of the same species were collected from different bays (with the exception of *S. linearifolium* which was only found in Alma Bay). Justification for this was obtained by running a MANOVA on the data from August-December 1990 with factors SITE (bay), TIME (sampling date) and SPECIES. Significant differences in wet

weight and length were found for both TIME, SPECIES and TIME*SPECIES ($p<0.05$) due to seasonal variations in plant size; however, no significant difference was found between bays for any of the species.

2.4.3 Non-destructive (in situ) phenological measurements (population measurements)

Field estimates of plant density and size for mixed-species populations were also made between August 1990 and September 1992. The number of adult plants and the maximum length of the primary axis of each were measured in each of nine haphazardly placed 1 m^2 quadrats in Geoffrey and Florence Bays. The time necessary to examine each plant in conditions of low visibility and high surge for much of the year precluded the identification of each individual. Measurement of the densities of *S. linearifolium* in Alma Bay was hampered by the vertical attitude of the boulders to which it was attached along with the high wave exposure experienced. Additionally, since mixed-species aggregations of the same species of *Sargassum* were not present in Alma Bay, direct comparison with the results from Geoffrey and Florence Bays would have been meaningless, therefore it was decided not to attempt to measure plant density here.

Labelled individuals were used to monitor the loss of plants from the population: in November 1991 four groups of 50 adult plants in mixed species patches of *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* (the identity of each individual was not ascertained) in Geoffrey Bay were tagged with plastic "Dymo" labels which were affixed to the plants with plastic-coated wire. The labels were placed on the axes of the plants as close as possible to the holdfast. Twenty control labels of the same construction as the above were attached in the same manner to a 12 mm polyethylene rope held in the water column by a polystyrene float. The number of labels remaining were counted in December 1991, January, February, March and May 1992. In May 1992 a further 200 labels were deployed in each of Florence and Geoffrey Bays (in four groups of 50 with 20 controls) and counted in August 1992 (both bays), October 1992 (Geoffrey Bay only) and January 1993 (Florence Bay only). Since the 3 species tagged have a single distinct stem (Trono 1992) the loss of a label was assumed to indicate the loss of an entire plant.

2.4.4 Temperature measurements

Temperature is the factor that has received the most attention as a cue or causal factor determining algal phenology. Temperature data for Cleveland Bay for 1991 were obtained from the Australian Institute of Marine Science from a submersible data logger and temperature probe which was at a depth of approximately 2 m attached to a marker indicating the shipping channel to Townsville port (about 1 km east of the sampling locations). From November 1991 onwards temperature was recorded in Geoffrey Bay itself at a depth of approximately 5 m using a similar logger attached to a buoyed rope place at the edge of the reef slope. Daily means were calculated from hourly temperature readings.

2.5 RESULTS

2.5.1 Phenology of individual Sargassum *species*

2.5.1.1 Standing crop and growth

There was pronounced seasonality in the size of all four species of *Sargassum* (Figures 2.4 and 2.5). *S. fissifolium* , *S. oligocystum* and *S. tenerrimum* all had length and wet weight maxima in summer (December-February) and minima in winter (June-July). *Sargassum fissifolium* and *S. tenerrimum* had almost identical temporal patterns while *S. oligocystum* had a slightly later peak of wet weight and length. *Sargassum linearifolium* had a length and wet weight maximum in late summer/early autumn (August-November) and a minimum in spring (March-May). Minimum lengths and weights of all species were similar but maximum lengths and weights were different (Table 2.III). This confirms the observation that the overwintering basal parts of each species were similar. Interannual variation was shown in the size of mean wet weight maxima for *S. fissifolium*, *S. linearifolium* and *S. tenerrimum* but minimum values were consistent between years. The data for the standing crop given above can be used to calculate average growth rates for each species between sampling dates. These estimates of growth rate show that maximum growth for each species occurred 1-2 months before the maximum for standing crop (Figures 2.6 and 2.7). 'Negative' growth rates corresponded to loss of axes as senescence set in.

All four species showed significant ($p<0.001$) positive regressions between maximum length of the primary axis and wet weight (Table 2.IV). Data were log-transformed, since mass and length do not normally scale linearly in biological systems. However, R^2 values for all regressions were low (<0.5), despite large

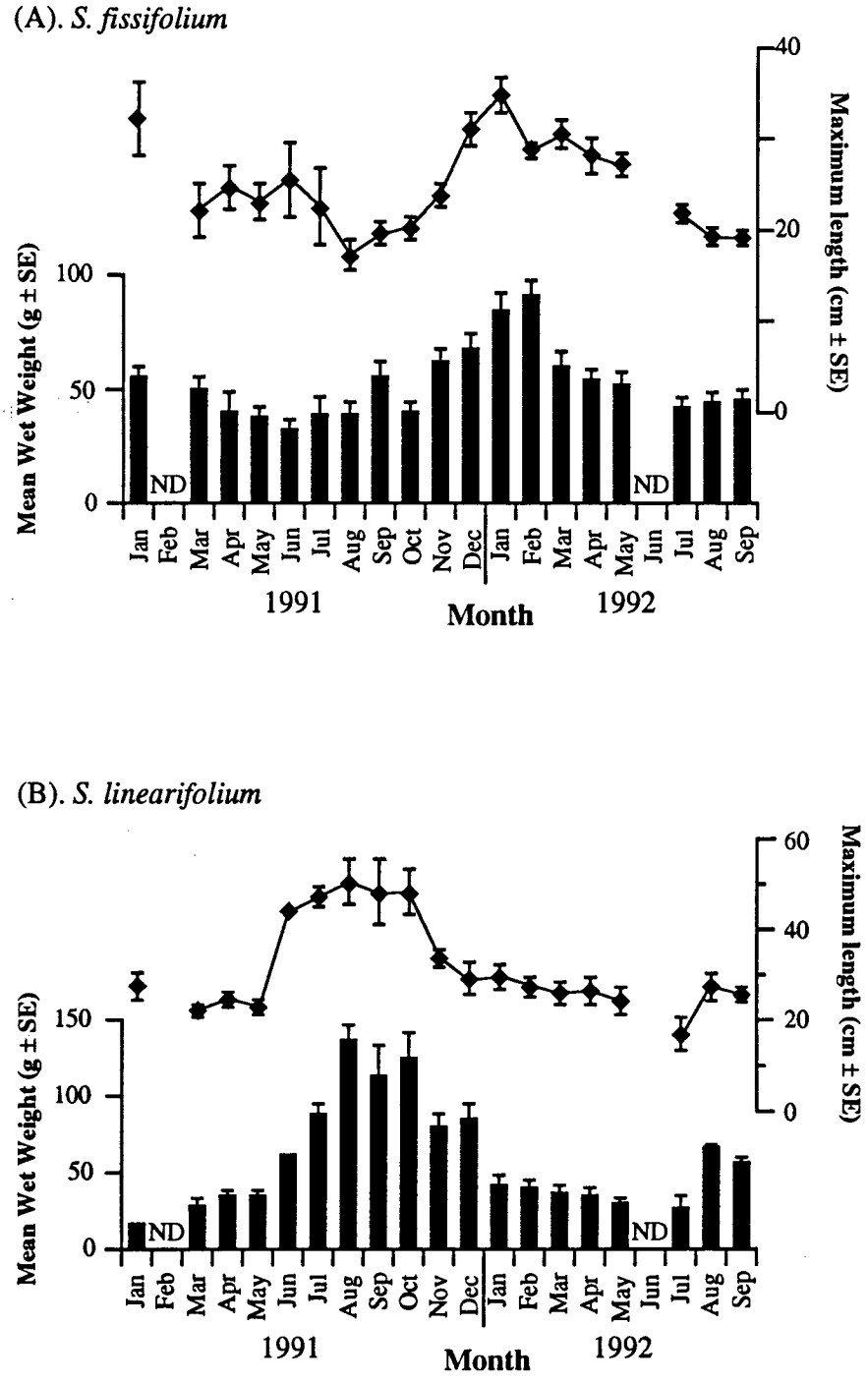
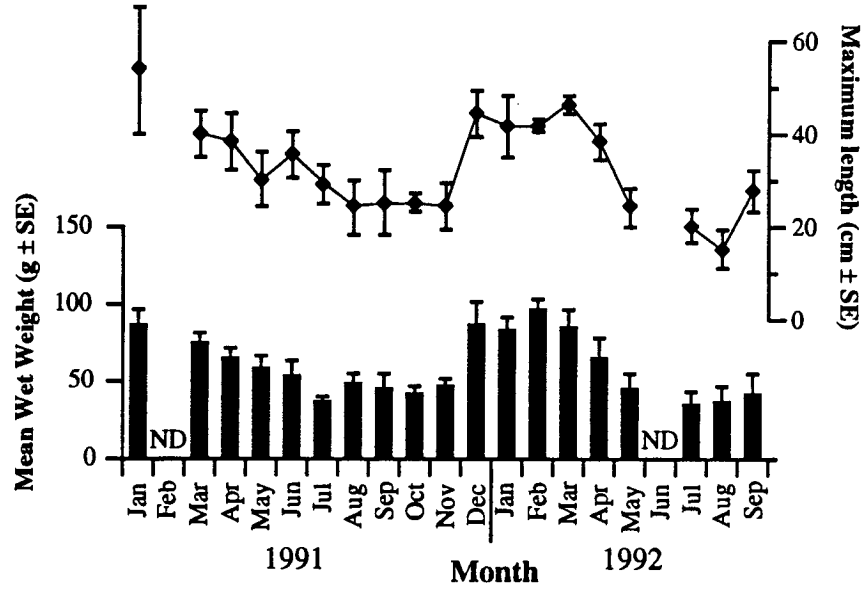


Figure 2.4. Monthly variation in mean biomass and maximum length of (A) *Sargassum fissifolium* (B) *S. linearifolium*. n=7 for each point. ND=no data.

(A). *S. oligocystum*



(B). *S. tenerrimum*

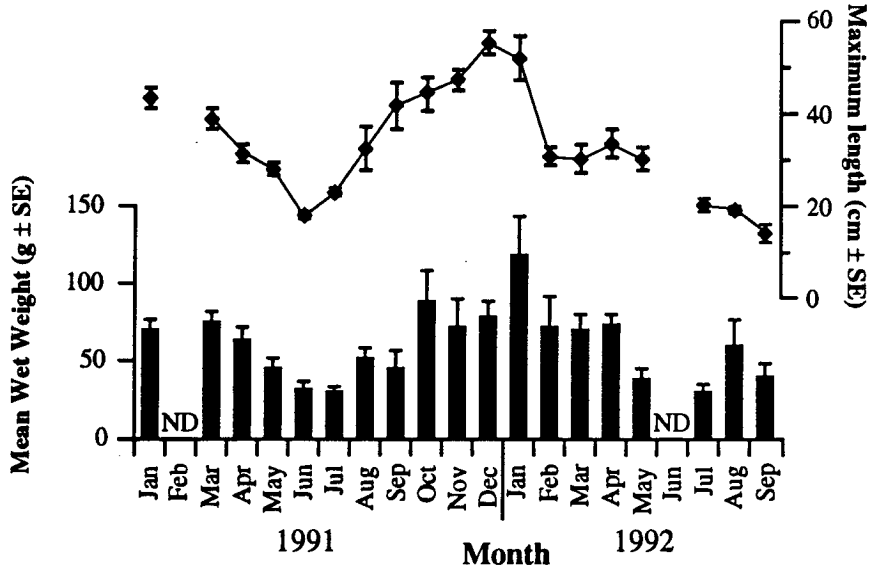


Figure 2.5. Monthly variation in mean biomass and maximum length of (A) *Sargassum oligocystum* (B) *S. tenerrimum*. n=7 for each point. ND=no data.

Species	Maximum Weight (g)	Date	Maximum Length (cm)	Date
S. fissifolium	186.6	Feb. 92	57	Mar. 92
S. linearifolium	156.5	Oct. 91	61	Sep. 91
S. oligocystum	291.7	Mar. 92	77	Mar. 92
S. tenerrimum	230.3	Jan. 92	80	Jan. 92
Species	Minimum Weight (g)	Date	Minimum Length (cm)	Date
S. fissifolium	10.6	Sep. 91	8	Aug. 92
S. linearifolium	15.2	Jan. 91	12	Jan. 91
S. oligocystum	12.6	Jun. 91	8	Aug. 92
S. tenerrimum	9.3	Jun. 91	14	Jun. 91

Table 2.III. Magnitude and times of wet weight and length maxima and minima for *Sargassum* species.

Species	Regression Equation	R^2	Probability
S. fissifolium	L=0.157 W + 15.6	0.40	<0.001
S. linearifolium	L=0.206 W + 15.6	0.49	<0.001
S. oligocystum	L=0.167 W + 26.3	0.35	<0.001
S. tenerrimum	L=0.160 W + 23.4	0.22	<0.001

Table 2.IV. Regression equations for wet weight against length for *Sargassum* spp. L=maximum length of primary axis, W=wet weight (both variables log-transformed).

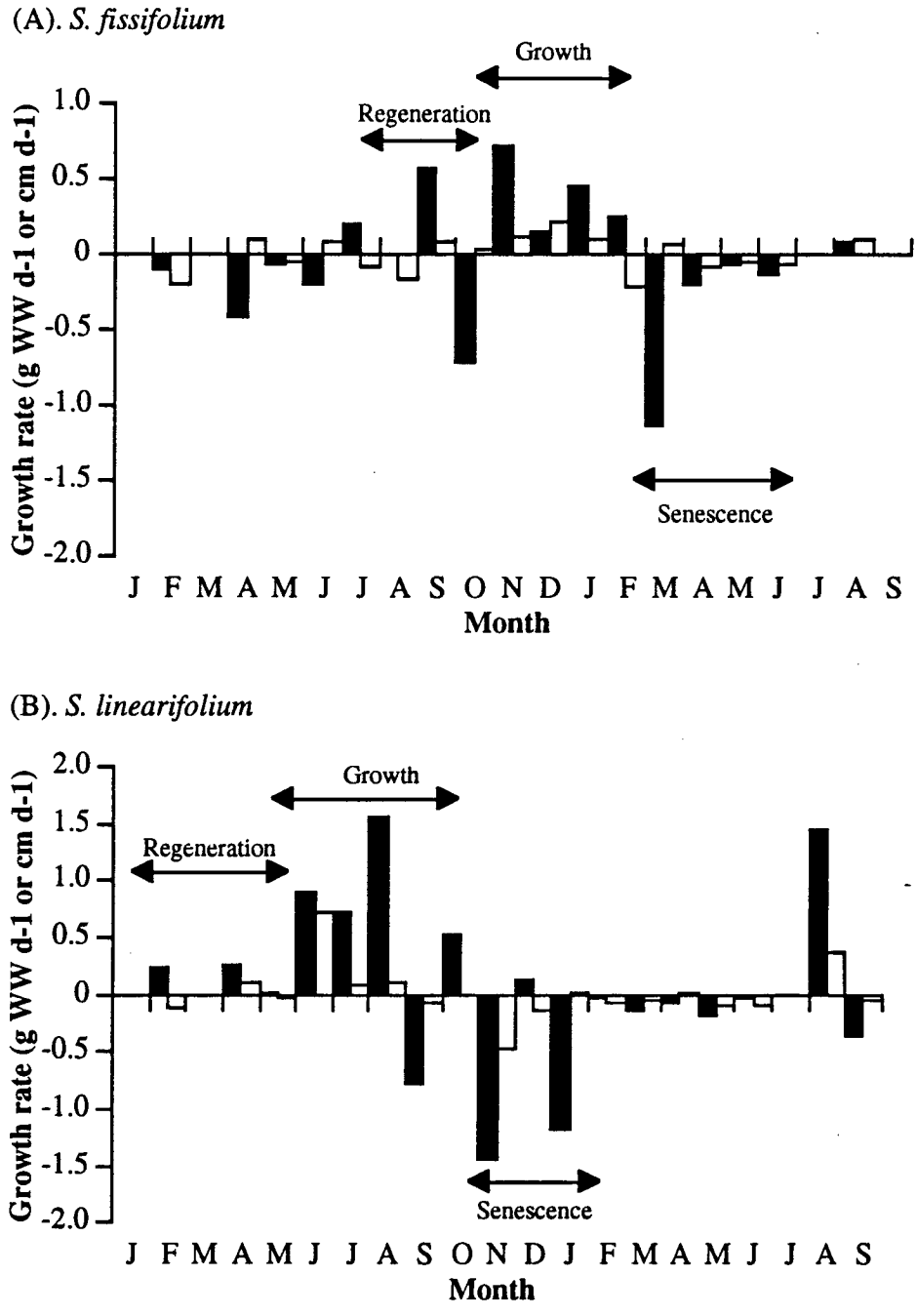
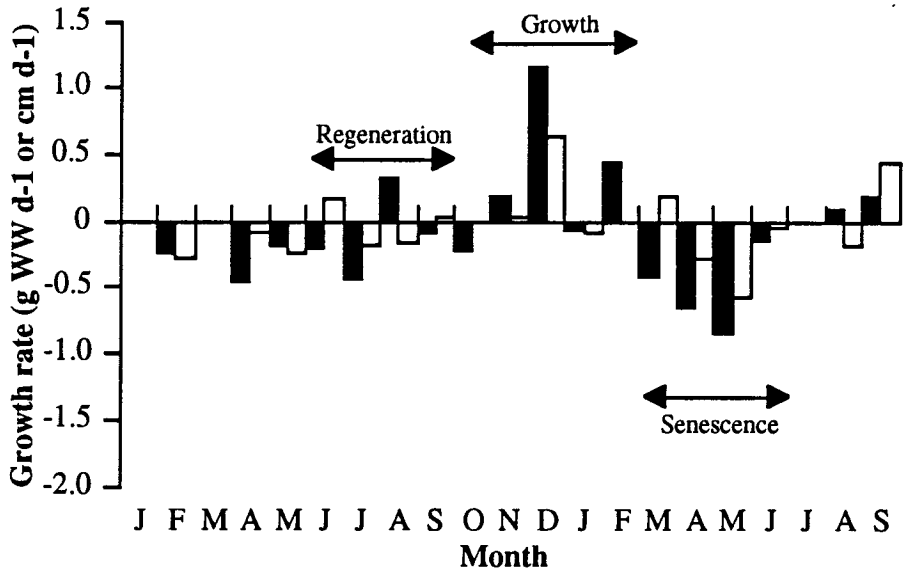


Figure 2.6. Monthly variation in growth rates of (A) *Sargassum fissifolium* (B) *S. linearifolium*. Growth rates expressed as changes in wet weight (■) and maximum length (□). Growth rates calculated from mean values displayed in Figure 2.4.

(A). *S. oligocystum*



(B). *S. tenerrimum*

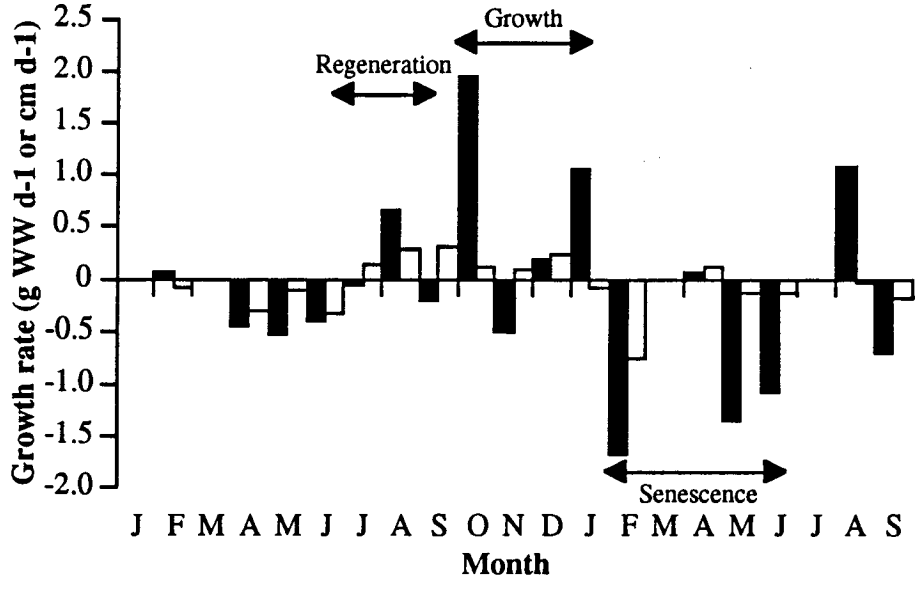


Figure 2.7. Monthly variation in growth rates of (A) *Sargassum oligocystum* (B) *S. tenerrimum*. Growth rates expressed as changes in wet weight (■) and maximum length (□). Growth rates calculated from mean values displayed in Figure 2.5.

sample sizes (n=133). This implies that the morphology of each species was highly variable: although *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* had single stems, the number of axes varied widely. *Sargassum linearifolium* had the least variable morphology of the species studied, with a correspondingly higher R^2 value. Since the regression was performed on the total data set ontogenetic changes in morphology could have lead to 'spread' of data points (Kilar and Hanisak 1988 found quantitative changes in morphology through the growing season).

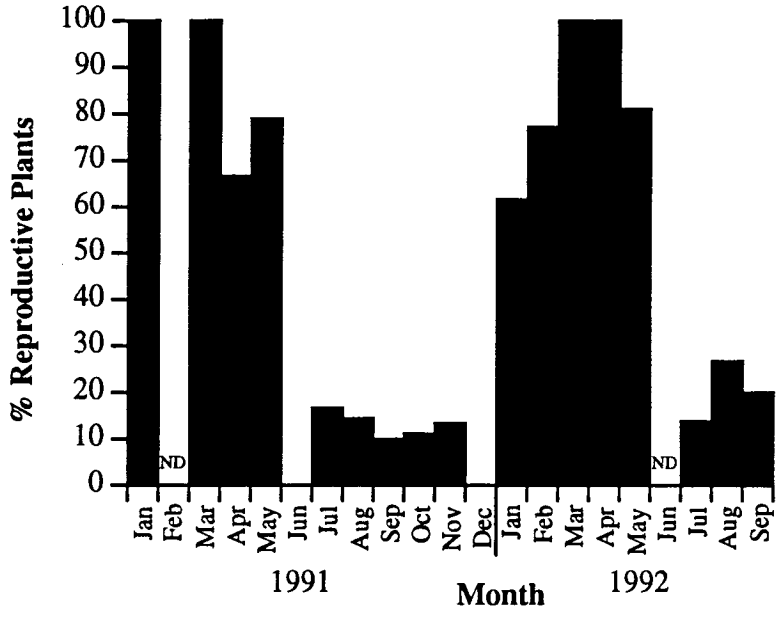
2.5.1.2 Reproduction

Reproduction of all species was also markedly seasonal (Figures 2.8 and 2.9). Reproductive maxima for the populations of *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* all occurred in February-May, shortly after size maxima. None or very few plants were reproductive from June-December The reproductive maximum for *S. linearifolium* was in September/October which reflects the pattern of its earlier size maximum and there was little reproduction between February and July. It is possible that the proportion of reproductive plants was overestimated, if very small, non-reproductive plants were not among the samples collected; however, plants of all sizes were observed to be reproductive. The reproductive maxima shown represent estimates generated from the presence or absence of receptacles on plants: De Wreede (1978) demonstrated that embryo development in tropical *Sargassum* takes 1-2 months, thus the release of embryos is likely to have shown more restricted maxima.

2.5.1.3 Epiphyte loads

Epiphyte loads varied seasonally with highest cover during periods of little or no growth for all species (Figures 2.10-2.13). There were consistently more epiphytes on the axes of the plants than on the leaves for all species but the patterns of abundance of epiphytes were the same for both leaves and axes. Epiphyte cover was highest on *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* during the winter (August-September), lowest in summer (January-February) whilst epiphytes were most abundant on *S. linearifolium* during the autumn (April-May) and least abundant in spring (October-November). Seasonal changes in epiphyte loads were most pronounced on *S. linearifolium*, some plants having no epiphytes in November and December, whilst seasonal changes were least pronounced on *S. fissifolium*. There were also differences in the type of epiphytes on different *Sargassum* species (inset graphs on Figures 2.10-2.13). *Sargassum fissifolium* and *S. oligocystum* had large

(A). *S. fissifolium*



(B). *S. linearifolium*

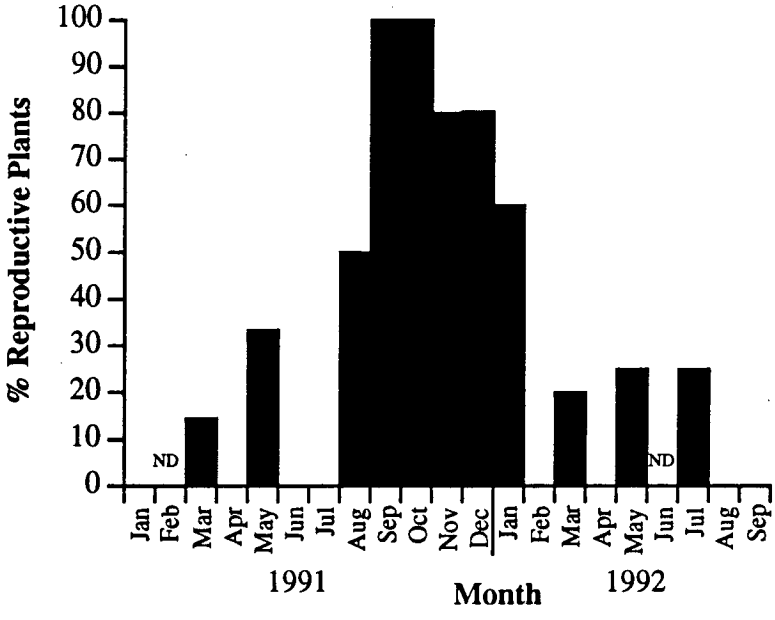
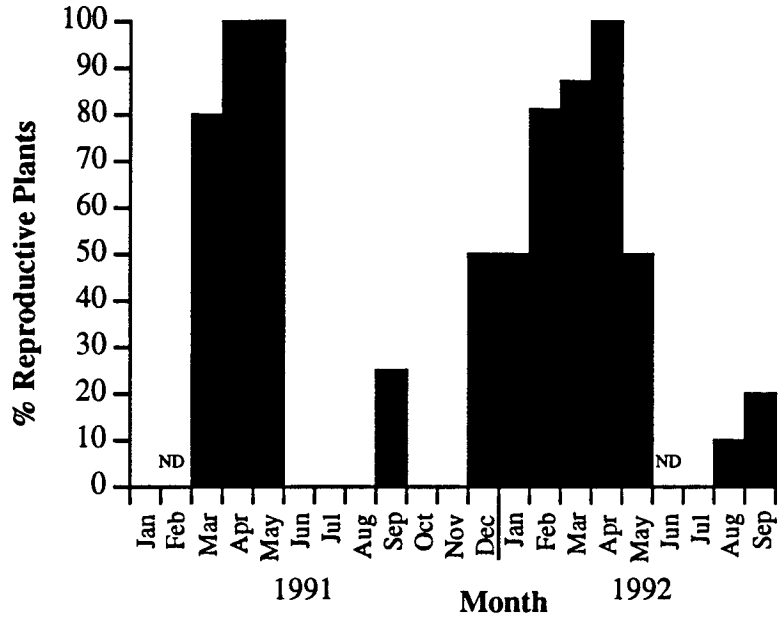


Figure 2.8. Monthly variation in percentage of reproductive plants of (A) *Sargassum fissifolium* (B) *S. linearifolium*. n=7 for each point. ND=no data.

(A). *S. oligocystum*



(B). *S. tenerrimum*

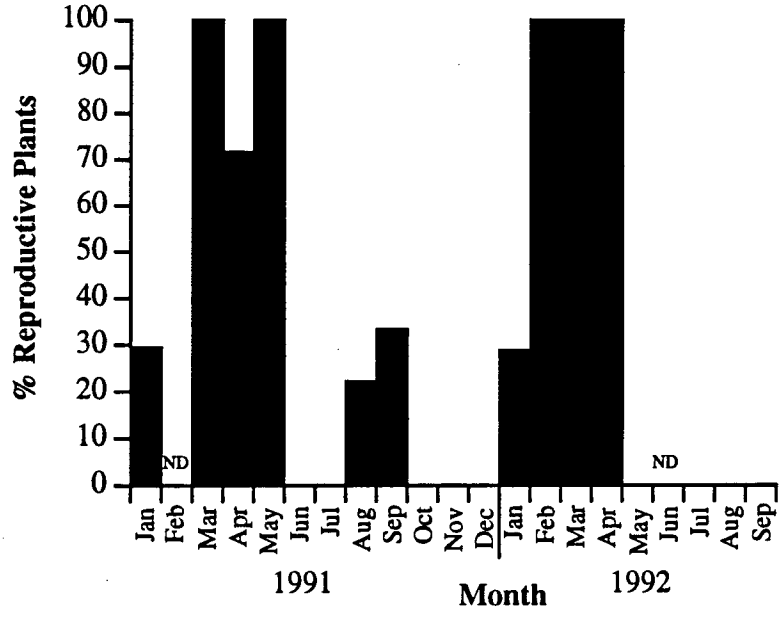


Figure 2.9. Monthly variation in percentage of reproductive plants of (A) *Sargassum oligocystum* (B) *S. tenerrimum*. n=7 for each point. ND=no data.

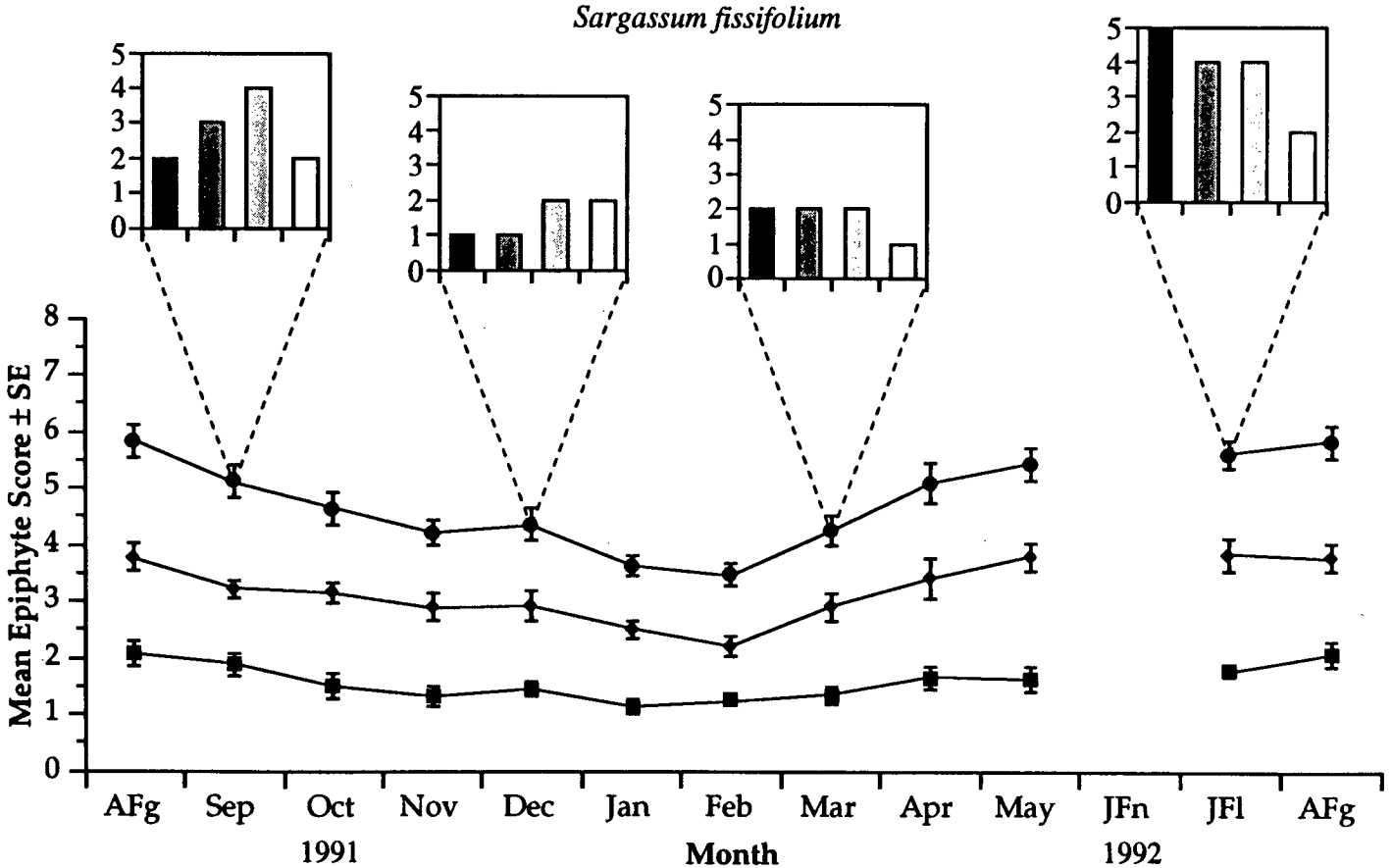


Figure 2.10. Epiphyte loadings on leaves (■), axes (◆) and total *Sargassum* plants (●). n=7 For each point. Inset graphs show abundance of geniculate coralline algae (■), filamentous red algae (▩), brown algae (□) and sessile invertebrates (□) on arbitrary abundance scale.

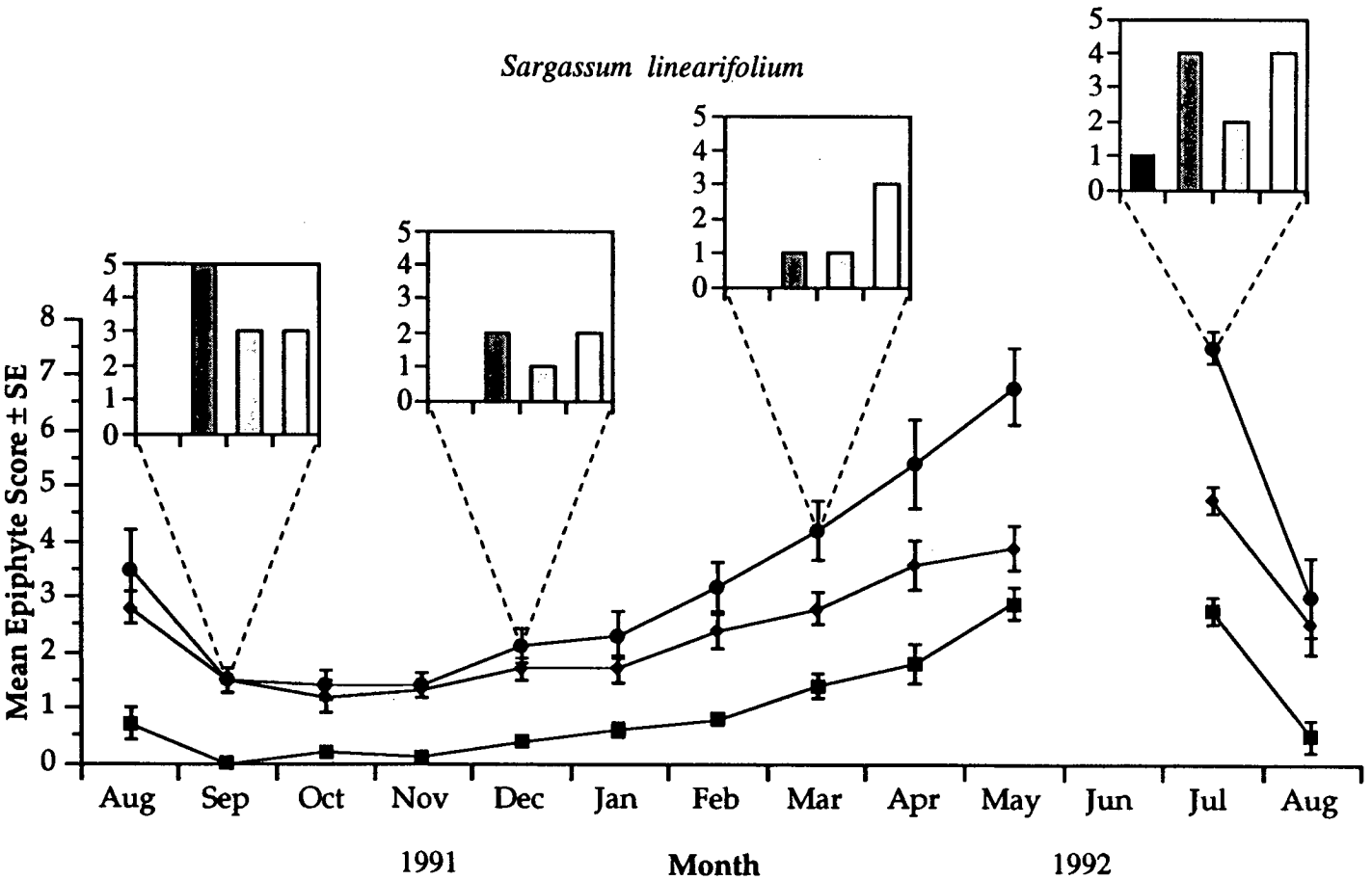


Figure 2.11. Epiphyte loadings on leaves (■), axes (◆) and total *Sargassum* plants (●). n=7 for each point. Inset graphs show abundance of geniculate coralline algae (■), filamentous red algae (▨), brown algae (□) and sessile invertebrates (□) on arbitrary abundance scale.

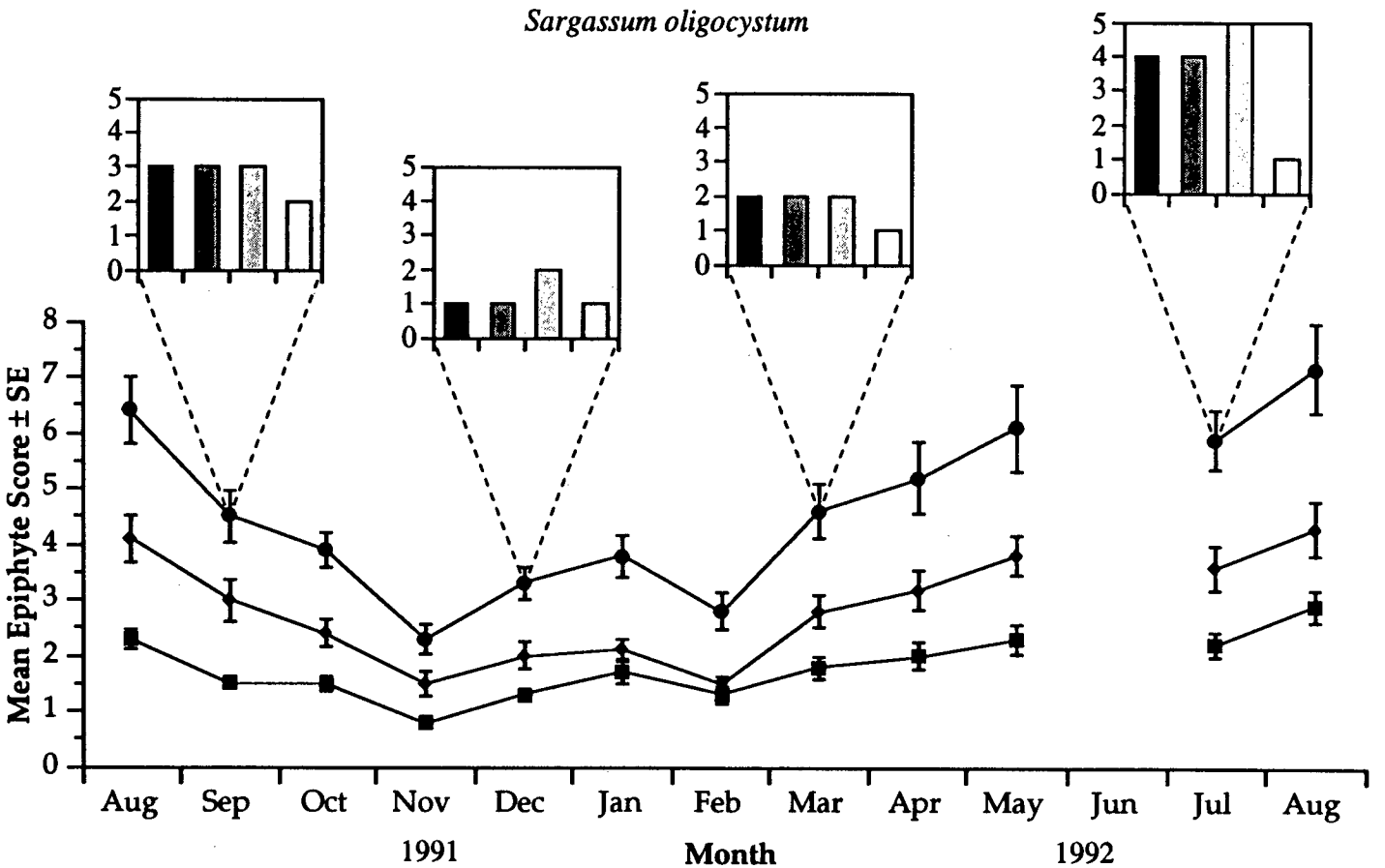


Figure 2.12. Epiphyte loadings on leaves (■), axes (◆) and total *Sargassum* plants (●). n=7 for each point. Inset graphs show abundance of geniculate coralline algae (■), filamentous red algae (▣), brown algae (□) and sessile invertebrates (□) on arbitrary abundance scale.

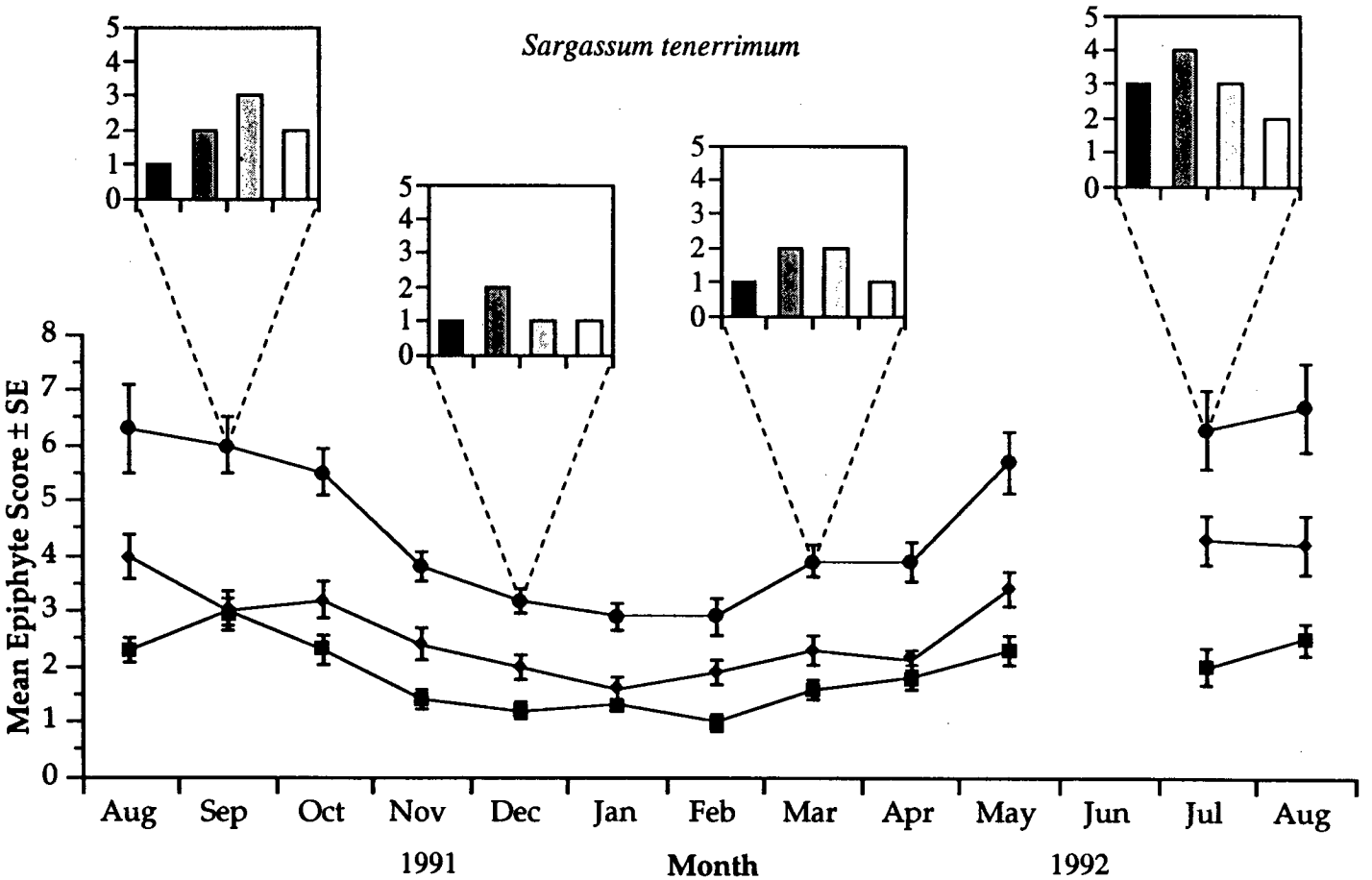


Figure 2.13. Epiphyte loadings on leaves (■), axes (◆) and total *Sargassum* plants (●). n=7 for each point. Inset graphs show abundance of geniculate coralline algae (■), filamentous red algae (▣), brown algae (□) and sessile invertebrates (□) on arbitrary abundance scale.

amounts of geniculate red algae during the winter (July) in contrast to *S. linearifolium* which always had low levels. Filamentous red algae were present on all species at all times, but were especially abundant during the winter. Brown algae were also found on all species at all times of year but appeared to be generally less abundant on *S. linearifolium.* Epiphytic brown algae reached highest levels of abundance in July and September. Sessile invertebrates were fairly aseasonal on *S. fissifolium*, *S. oligocystum* and *S. tenerrimum*, generally present but in low abundance, while they were present in higher abundance on *S. linearifolium*, reaching a maximum value in July. For some individuals of *S. fissifolium* and *S. tenerrimum* during the winter, the biomass of the epiphytes was greater than the biomass of the plant.

2.5.2 Population demographic parameters

2.5.2.1 Standing crop and growth

Distinct seasonal variation in mixed species populations of *Sargassum* was evident (Figure 2.14). *In situ* length measurements showed summer maxima in January-March in both 1991 and 1992, followed by minima in July-September. Pooled wet weight data from *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* showed a similar pattern. Growth rates calculated from length data showed a similar pattern to those for the individual species (Figure 2.15). Growth rates were highest in autumn, some time before maximum biomass was attained, followed by senescence of annual axes in late summer-early spring, then a resting phase and subsequently regeneration in winter. Year-to-year variation in the size of plants and the calculated growth rates was not very pronounced.

2.5.2.2 Loss rates and density

Loss of adult plants occurred throughout the year (Figure 2.16) but the rates of loss changed through the season (Table 2.V). No control labels were lost during either of the two monitoring experiments so it was assumed that any lost label was due to the loss of a plant. Despite the changes in loss rates between different sampling periods there were no significant differences between these rates (1-way ANOVA, $p>0.05$). There was also no significant difference between rates of loss in Florence and Geoffrey Bays (1-way ANOVA, $p>0.05$). Concurrently, there were no discernible patterns in the density of adult plants in mixed stands (Figure 2.17). Maxima and minima were attained at different times in the two bays and were not

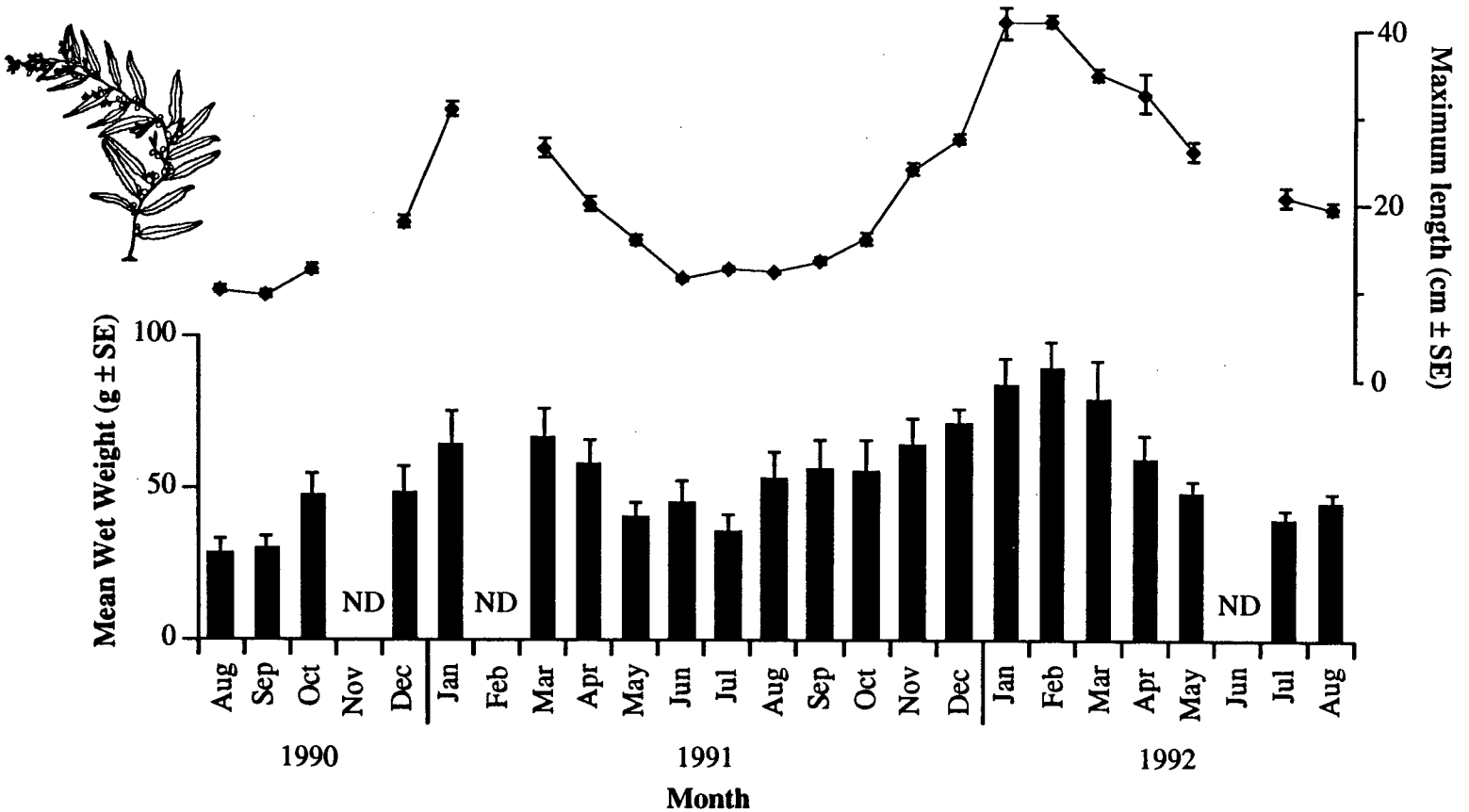


Figure 2.14. Monthly variation in mean *Sargassum* biomass and maximum length (data for all species combined). n=20 for Aug.-Dec. 1990, n=28 from January 1991 onwards. ND=no data.

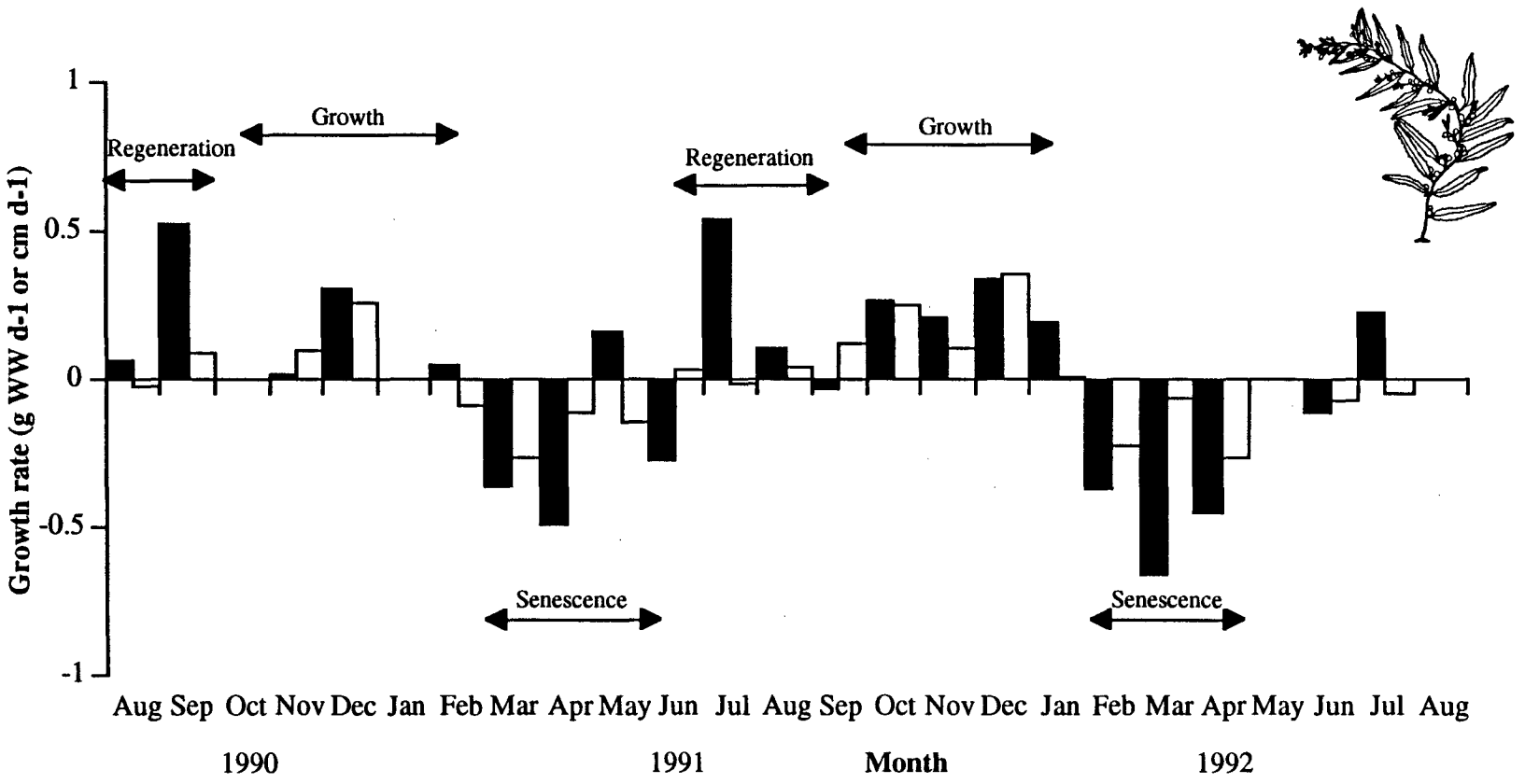


Figure 2.15. Monthly variation in growth rates of *Sargassum* population (all species combined), calculated by change in wet weight (■) and change in length (□). n=20 for Aug-Dec 1990, n=28 from Jan 1991 onwards

consistent between locations or sampling dates for the period 1990-1992. Plant densities varied between 16 and 41 plants m^{-2}. Plants could only be detected in the field once they had reached a certain size (approximately 2-3 cm in length), thus very small plants would have been missed.

Period	Mean Rate of Plant Loss (plants day^{-1}) ± SE
Nov-Dec 1991	0.095 ± 0.014
Dec 1991-Jan 1992	0.147 ± 0.047
Jan-Feb 1992	0.194 ± 0.028
Feb-Mar 1992	0.259 ± 0.080
Mar-May 1992	0.123 ± 0.031
May-Aug 1992	0.143 ± 0.018
Aug-Oct 1992	0.170 ± 0.031
Aug 1992-Jan 1993	0.150 ± 0.010

Table 2.V. Mean rates of tagged *Sargassum* loss from November 1991 to Jan 1993.

2.5.3 Seasonal variation in water temperature

Daily mean temperature varied from a minimum of 22°C in June to a maximum of 32°C in January (Figure 2.18). Daily mean temperatures remained high for three months over the summer (December-March), but low temperatures only persisted for less than a month. The most rapid changes in temperature occurred in August (increasing) and March-April (decreasing).

2.6 DISCUSSION

The four *Sargassum* species investigated in this study all showed pronounced seasonality with respect to growth and reproduction. *Sargassum fissifolium*, *S. oligocystum* and *S. tenerrimum* all showed biomass and length increase in the austral spring followed by a summer peak in size and subsequently reproduction, whilst *S. linearifolium* showed late winter growth followed by a spring peak in size and reproduction. There have been a number of studies of *Sargassum* seasonality in the tropics but no general phenological pattern has emerged (Table 2.IA). Within the 22 species reported in the studies in Table 2.IA examples of almost any phenological pattern can be found: 4 show standing crop maxima wholly in summer, 1 in autumn, 10 in winter, 3 in spring, 3 over more than one season and 1 shows no pattern. Temperate and sub-tropical species have much more consistent phenological patterns

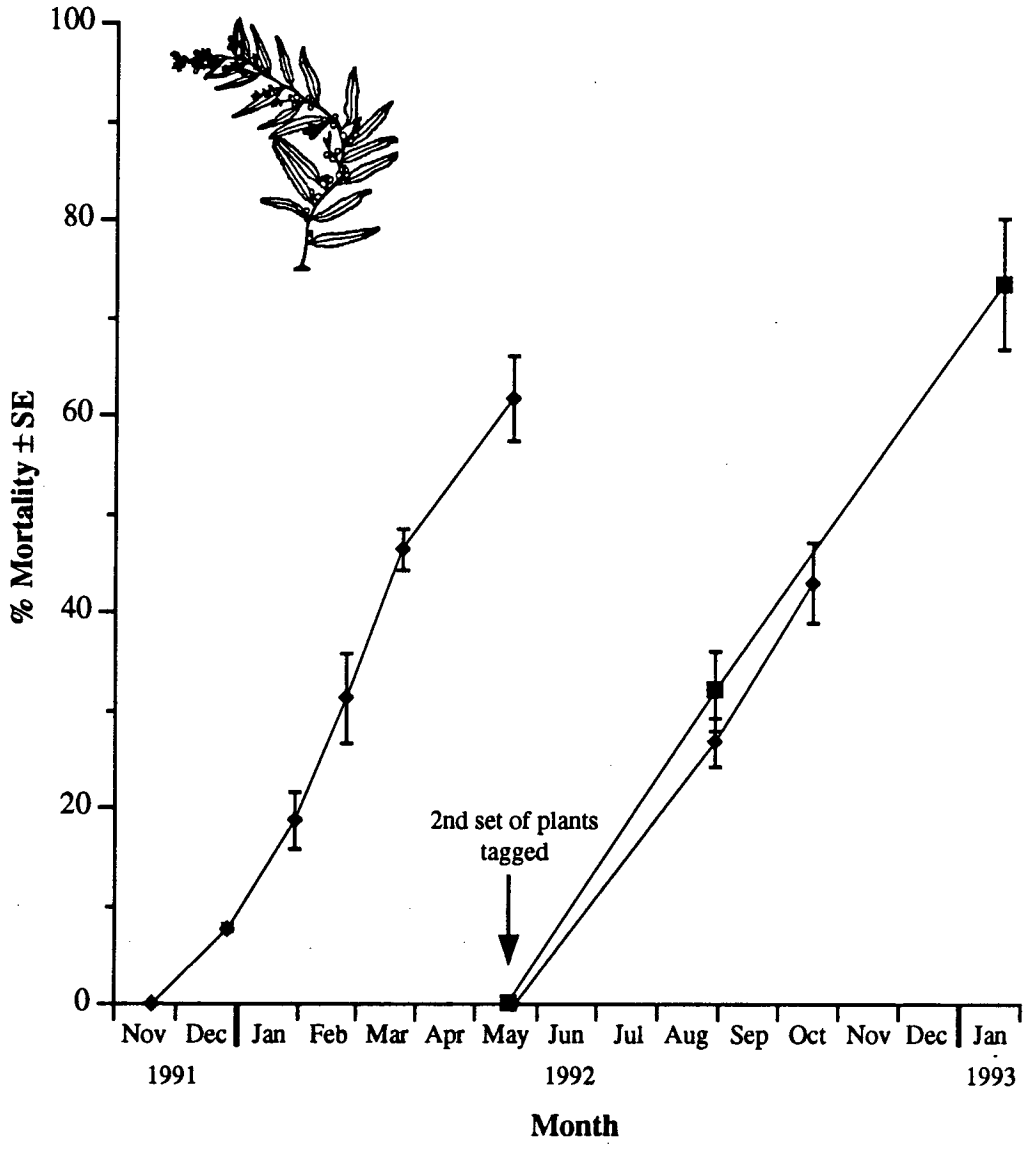


Figure 2.16. Cumulative mortality curves for tagged *Sargassum* from Geoffrey (◆) and Florence (■) bays. n=4 groups of 50 plants for each point.

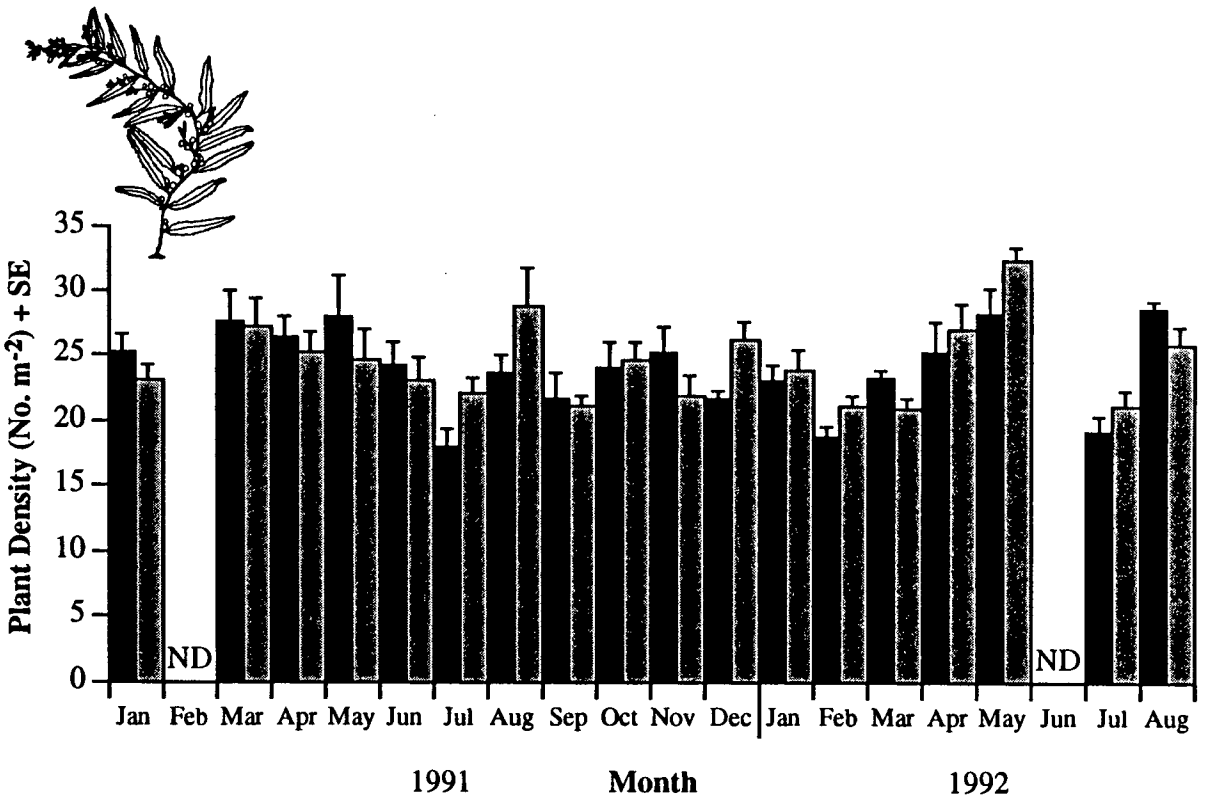


Figure 2.17. Mean *Sargassum* density from Geoffrey (■) and Florence (▣) Bays. n=9 for each point. ND=no data.

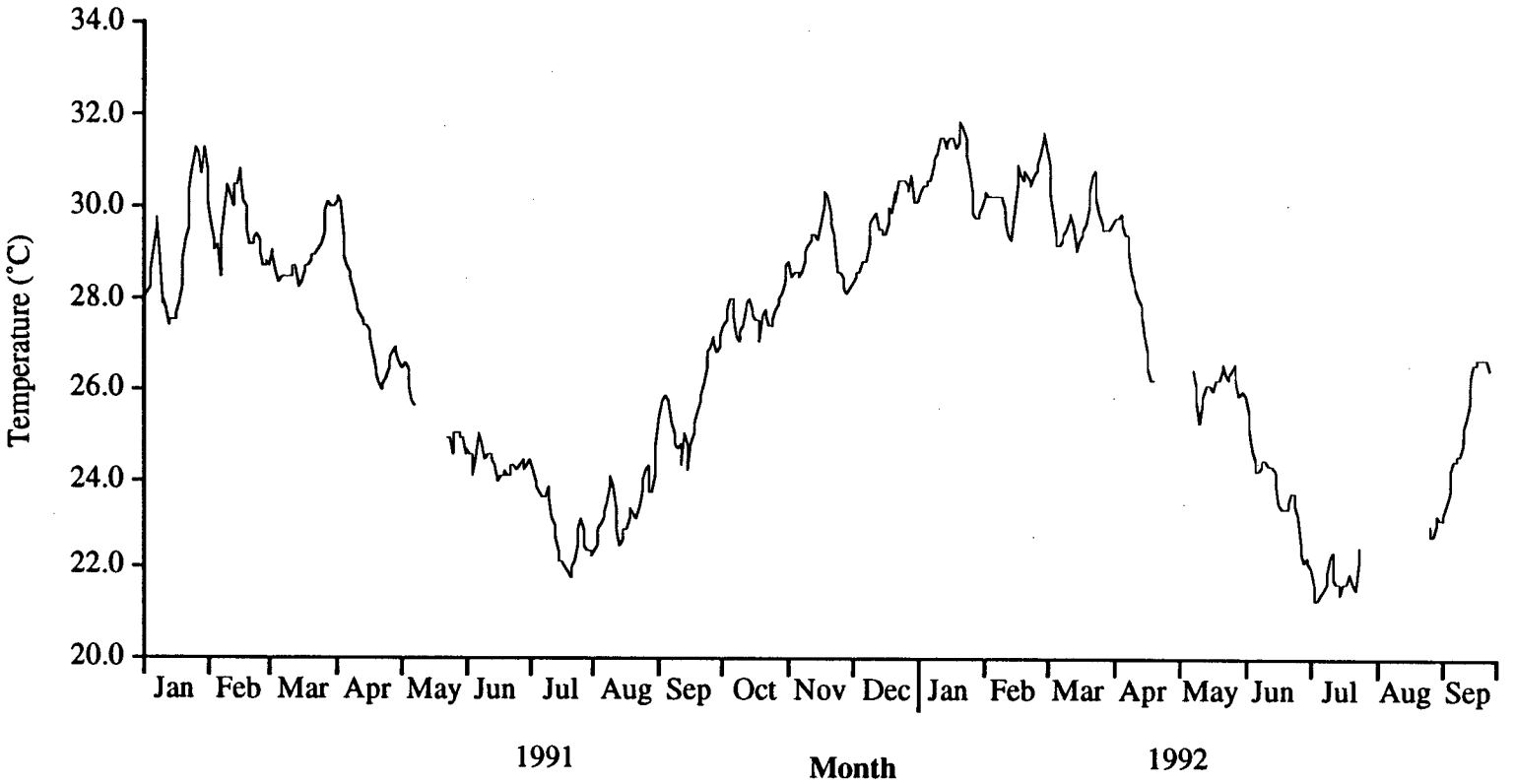


Figure 2.18. Mean daily sea water temperatures in Cleveland Bay from January 1991-August 1992 (calculated from hourly readings). Data courtesy of AIMS (to November 1991) and Ben Stobart (November 1991 onwards).

with a general standing crop maximum in spring/summer (of the 20 species in Table 2.IB, 18 show this pattern). The phenologies of two of the species studied here, *S. oligocystum* and *S. tenerrimum*, have been investigated previously. Misra (1966) found maximum biomass of *S. tenerrimum* in winter in India, while maxima for *S. oligocystum* have been reported to occur in spring, in summer and not at all (Heijis 1985, Ngan and Price 1980 and Doty 1971 respectively).

Periods of maximum growth rates do not necessarily correspond with maximum standing crops as pointed out by Prince and O'Neal (1979). In fact for the majority of reviewed studies it appears that maximum growth rates occurred 1-2 months before maximum biomass was attained. This appears to be the case in the present study, for although growth of individual plants was not measured directly, the average growth rates was calculated from mean values each month (as in Prince 1980). These show that maximum increase in biomass occurred for *S. fissifolium* in October, for *S. linearifolium* in May, for *S. oligocystum* in November and for *S. tenerrimum* in September (Figures 2.6 and 2.7).

That three of these maximum growth rates occur at times of increasing water temperature (Figure 2.18) tends to support the first hypothesis of De Wreede (1976) that high seawater temperatures are not detrimental to the growth of adult *Sargassum.* Seemingly contrary to De Wreede's second hypothesis, maximum fertility in three of the four species studied here (*S. fissifolium*, *S. oligocystum* and *S. tenerrimum*) occurred at times of highest water temperature. However, given that embryo development takes 1-2 months (De Wreede 1978) and that the fertility peaks of the above species tended to persist into April-May (Figures 2.8 and 2.9), the actual period of release and settlement of embryos may have occurred during periods of low water temperature (May-June). Temperatures at Magnetic Island in March-April are around 31°C (Figure 2.18) which is the temperature at which poorest embryo growth occurred in laboratory studies (De Wreede 1976), while temperatures in May-June are 22-24°C, the optimum temperature for embryo growth in the above study. Given the paucity of studies in the Southern Hemisphere tropics (Ngan and Price 1980, Heijis 1985, Vacamoce 1987) it is difficult to ascertain whether reproduction generally occurs at times of low or high seawater temperatures.

Alternative hypotheses to explain phenology based on seasonal variation of physical factors such as tide heights and nutrient levels (Prince and O'Neal 1979, Ang 1985a) or desiccation and rainfall (Tsuda 1974) have been proposed (see review by Doty 1971b). The local changes in salinity and nutrients have been investigated for Cleveland Bay by Walker (1981a, b) and Walker and O'Donnell (1981). Salinity was found to decrease in late summer, correlated with river run-off during the wet season

(Walker 1981a) and nitrate and phosphate levels were correlated with wind-driven resuspension events, but not with salinity (Walker and O'Donnell 1981). The pronounced difference between the phenology of *S. linearifolium* and the other species studied would seem to cast doubt on the hypothesis that the phenology of *Sargassum* is adaptive towards a particular set of local physical conditions since at least two distinct phenological patterns were observed (with *S. oligocystum* perhaps displaying a third pattern).

Interestingly, *S. linearifolium* is described in "The Benthic Flora of South Australia" (Womersley 1987) as having temperate affinities with a winter-maximum phenology in temperate waters. Thus, this species may be displaying seasonal growth determined by historical and genetic considerations. Steinberg *et al.* (1991) found that tropical *S. linearifolium* (from Magnetic Island) was very similar chemically and ecologically to temperate *S. linearifolium* in herbivory experiments: evidence for close genetic similarity. Further evidence for a genetic basis for *Sargassum* phenology comes from comparison of this study with previous studies on the same species in the Northern Hemisphere. *Sargassum tenerrimum* displays a winter-maximum phenology in India (Umamaheswararao and Sreeramulu 1964, Misra 1966) but a summer-maximum phenology at Magnetic Island. Studies on *S. oligocystum* have produced conflicting results with respect to its phenology (Neal 1930, De Wreede 1976, Ngan and Price 1980, Trono and Lluisma 1990, this study), however there is taxonomic confusion over the status of *S. oligocystum* which may be responsible for this (De Wreede 1976 states that what he calls *S. oligocystum* should be referred to as *S. echinocarpum* until the taxonomy is clarified). If the phenology of *S. oligocystum* and *S. tenerrimum* was genetically controlled and populations of these species came from a common source then the seasonal pattern could be a 'biological ghost' (Diamond 1990) and not necessarily adaptive. Ang and Trono (1987) and Kilar and Hanisak (1988) report seasonal patterns of morphological variability within *Sargassum* species which are, to a large extent, genetically determined. Long distance transplant experiments would be required to demonstrate such genetic control of phenology.

Conover (1964) proposes the hypothesis that there are 'summer' and 'winter' plants in the subtropics, these strategies being different adaptive solutions to the same environmental factors, an hypothesis which can be extended to the tropics following work on adjacent populations of *S. pteropleuron* and *S. polyceratium* in Florida (Prince 1980) and the present study. Under this classification *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* would be 'summer' plants while *S. linearifolium* would be a 'winter' plant. Another hypothesis, proposed by Mathieson and Dawes (1974), suggests that maximum growth of algae in the tropics should occur during

periods of low water temperature. There is support for this hypothesis – for example, most of the species investigated by Price (1989) show maximal growth during periods of low temperature. Whether the *Sargassum* community at Magnetic Island is just a notable exception to this hypothesis or an example of a wider geographical pattern remains to be determined.

Biological interactions between the species may be important – Santelices (1977) also found that different species of *Sargassum* had different seasonal patterns in the same location: *S. polyphyllum* showed a positive correlation between biomass and seasonal patterns of water movement and a negative correlation with light intensity, whereas *S. echinocarpum* showed a seasonal cycle of biomass change not correlated with any of four physical factors (temperature, light intensity, water movement and salinity) but negatively with that of *S. polyphyllum.* Trono and Saraya (1987) found biotic interactions to be important in determining the abundance of species associated with *Sargassum.* Whilst the four species in this present study co-occur on a macroscopic scale, *S. linearifolium* is not found admixed with the other species on a micro-scale. This could indicate that it is competitively excluded by the other species from coral areas, but is competitively dominant on boulders. The slight differences between the phenology of *S. oligocystum* and those of *S. fissifolium* and *S. tenerrimum* could also be indicative of niche differentiation within mixed species areas. Manipulative work is needed to investigate the importance of such biotic interactions.

Loss rates in this study are high compared to the rates of Edgar (1983b) who estimated mortality at 20-25% of labelled individuals per year for *S. bracteolosum* and *S. verruculosum* in Tasmania. Extrapolating from measured rates of loss of labelled plants would give a value of 80+% for the present study (Figure 2.16). This could reflect actual loss (De Ruyter van Steveninck and Breeman 1987 lost 100% of plants in 2-4 months following storm surge) or could be due to experimental artifacts to some extent if, for example, plants with labels were more susceptible to breakage or labels were lost with annual axes while the perennial holdfasts persisted. The three *Sargassum* species living in mixed species aggregations would appear to be pseudoperennial with some individuals surviving as basal holdfast systems and producing new annual laterals each year, comparable to published reports of *Sargassum* longevity (Chauhan and Krishnamurthy 1971, Tsuda 1972, De Wreede 1976, Ang 1985b).

'Fouling' (*sensu* Wahl 1989) is an important consideration for *Sargassum* individuals. Epiphytes may increase the probably of detachment and hence mortality (D'Antonio 1985, Hay 1986), reduce photosynthesis (Bulthuis and Woelkerling

1983) or have other negative effects on plant growth (Hay 1986); however they may be preferentially grazed by epifauna which would otherwise be forced to eat their host (Brawley and Fei 1987). Epiphytism is lowest on *Sargassum* during periods of rapid growth, which could result from inhibition of epiphyte settlement by newly-produced *Sargassum* tissue or simply that the epiphytic community develops more slowly than the *Sargassum* grows (Arrontes 1990a). Over periods of little or no *Sargassum* growth epiphytes accumulate to very high levels (>100% surface cover and biomass). The apparent decrease in levels of epiphytes when growth commences could be artifactual, resulting purely from the appearance of new, uncolonized tissue or could result from axis loss. The levels of epiphytes are consistently higher on the *Sargassum* axes than on the leaves. The axes represent a more 'apparent' resource (*sensu* Feeney 1976) since they persist for a longer time than an individual leaf and it is probable that leaves with very high epiphyte loads break off and are lost from the plant.

In conclusion, there are interesting phenological differences between species of *Sargassum* from the same location. It remains unclear whether these differences indicate different responses to abiotic environmental factors, historical genetic legacies, biotic interactions such as competition and niche differentiation or a combination of these factors. These patterns warrant further investigation into the causes and cues for the seasonal behaviour of algae in the tropics.

CHAPTER 3

PHENOLOGY OF MOBILE EPIFAUNA ASSOCIATED WITH *SARGASSUM**

"Populations living in a seasonal environment are exposed to regular or systematic changes in resource quality and abundance... the size of populations living in a seasonal environment usually varies in a systematic fashion." Steven D. Fretwell, Populations in a Seasonal Environment.

3.1 INTRODUCTION

Macroalgae, including *Sargassum*, invariably support large populations of epifaunal organisms of numerous taxa (e.g. Fine 1970, Mukai 1971, Tararum and Wakabara 1981, Edgar 1983b, 1991a, Duffy 1990). These organisms are often classified as either meiofauna or macrofauna, according to their size – meiofauna are usually defined as 63 mm-1 mm in size and macrofauna as greater than 1 mm (McIntyre 1969, Gibbons and Griffiths 1986). Henceforth I shall use the term 'epifauna' to refer solely to macrofauna, although I acknowledge that meiofauna are more abundant than macrofauna and may be important as secondary producers (Koop and Griffiths 1982, Gibbons and Griffiths 1986). Using the above definition of epifauna, the most abundant members of the epifaunal community are normally peracarid crustaceans, molluscs or polychaetes, in both tropical and temperate systems. In the tropics for example, Stoner (1985) found that epifauna on *Penicillus* was dominated by tanaids, amphipods and isopods and Vacamoce (1987), in a study of *S. polycystum* at Magnetic Island, found large numbers of harpacticoid copepods, tanaids, gammarids, ostracods and polychaetes with isopods and gastropods common. Tararum and Wakabara (1981) collected large numbers of gammarid amphipods, with significant numbers of copepods, isopods and caprellids, as well as high numbers of polychaetes and molluscs from *S. cymosum* in sub-tropical Brazil. Mukai (1971) found that copepods, amphipods and isopods were dominant on *S. serratifolium* in Japan and Duffy (1990) found that amphipods made up 97% of macroscopic animals on *S. filipendula* in the USA.

Most marine organisms are characterised by high temporal variability in abundance, a generalisation which can be extended to populations of epifauna (e.g. Nelson *et al.* 1982, Lewis 1987, Arrontes and Anadon 1990b). These changes in

* Some of this chapter and the preceding chapter are reported in: Martin-Smith, K. M. (in press). Seasonal variation in tropical benthic *Sargassum* and associated motile epifauna. Proc. 7th Int. Coral Reef Symp.

abundance can be enormous and occur very rapidly – Arrontes and Anadon (1990) found a 15-fold increase in the density of isopods within a month and an equally sharp decrease two months later. These changes may occur synchronously with changes in the biomass or abundance of the macrophyte host, especially in temperate systems – for example, Edgar (1983b) demonstrated maximal faunal abundance in late summer, 1-2 months after maximal crops of four macroalgae in Tasmania and Aoki (1990) found maximal abundance of caprellids 1-2 months before maximal *Sargassum* biomass in Japan. Heck (1979) and Nelson (1979) have reported similar seasonal patterns for epifauna living on seagrass in tropical and subtropical regions. Most epifaunal organisms appear to have annual population fluctuations (e.g. Healy and O'Neill 1984, Salemaa 1979, Arrontes and Anadon 1990) despite fairly short development times and brooded young for many epifaunal crustacean species (Barnard 1976, Caine 1979, Salemaa 1979, Holdich and Jones 1983). There have been numerous hypotheses presented to explain abundance changes in epifauna which will be discussed in Chapter 5; however, a sound database of these changes is an essential prerequisite before the generation and testing of such hypotheses can be undertaken. Thus, this chapter will be concerned with the sampling and presentation of abundance changes in mobile epifauna inhabiting *Sargassum* over a period of two years.

The nature of the symbiosis between the host macrophyte and the epifauna which live on it is another area of controversy. Various authors have suggested the relationship is commensal, mutualistic or antagonistic. The macroalgae may be simply be selected as a habitable environment (Hacker and Steneck 1990) alternatively it may be a refuge from predation (Hay *et al.* 1990) or from wave action (Fenwick 1976). These systems would all be described as a commensal relationship. However, if the epifauna are feeding directly on the macroalga removing photosynthetic tissue or new, growing tissue (D'Antonio 1985, Duffy 1990) then the relationship is antagonistic. It has also been shown that the epifauna can be beneficial, removing epiphytes that overgrow the host (Brawley and Adey 1981a, b, D'Antonio 1985, Brawley and Fei 1987). Duffy (1990) found that both mutualistic and antagonistic effects were found within one epifaunal community on *S. filipendula* and that the net result was determined by the relative contributions of the different species of epifauna. The documentation of patterns of epifaunal abundance in relation to patterns of host abundance can help to suggest which kind of interaction is occurring in a particular system.

3.2 AIMS AND OBJECTIVES

The aims of this part of the project were:

- To develop a method for the reliable capture of mobile epifauna associated with individual *Sargassum* plants.

- To identify the dominant mobile organisms living on *Sargassum* (in terms of abundance and biomass).

- To quantify populations of the important taxa of mobile organisms over an extended period of time. This was to be done concurrently with phenological measurements from the *Sargassum* population.

- To synthesise the patterns of population change in both the *Sargassum* and the mobile epifauna in order to generate hypotheses about structuring forces acting upon the community.

3.3 MATERIALS AND METHODS

3.3.1 Development of sampling method

Initial studies were conducted between March and July 1990 to determine a suitable method for collection of mobile epifauna from *Sargassum.* The first method which was used was simply to enclose individual *Sargassum* plants in a large (100 x 60 cm) plastic bag underwater, remove the plant from the substratum, seal the bag and subsequently take the bag to the laboratory, where a small amount of 40% formalin solution was added to the seawater surrounding the plant and the contents of the bag emptied through a 200 mm plankton mesh sieve (Edgar 1983b, Stoner 1985). However this method involved the laborious transport of large amounts of seawater with the possibility of bag breakage and subsequent loss of epifauna and the time involved could have resulted in the loss of epifauna due to predation. To minimise these problems it was decided to try and develop a method whereby epifauna could be separated from the plant in the field, as soon as possible after collection.

To do this a 'cod end' was designed and attached to a plastic bag so that water could be flushed through the sample but the epifauna would be retained (Figure 3.1). The cod end was constructed of a tube of 200 mm plankton mesh attached by a stainless steel hose clamp to a 90 mm diameter PVC tube with a screw-off PVC base. A 60 mm diameter hole was drilled in this base and covered with plankton mesh. The

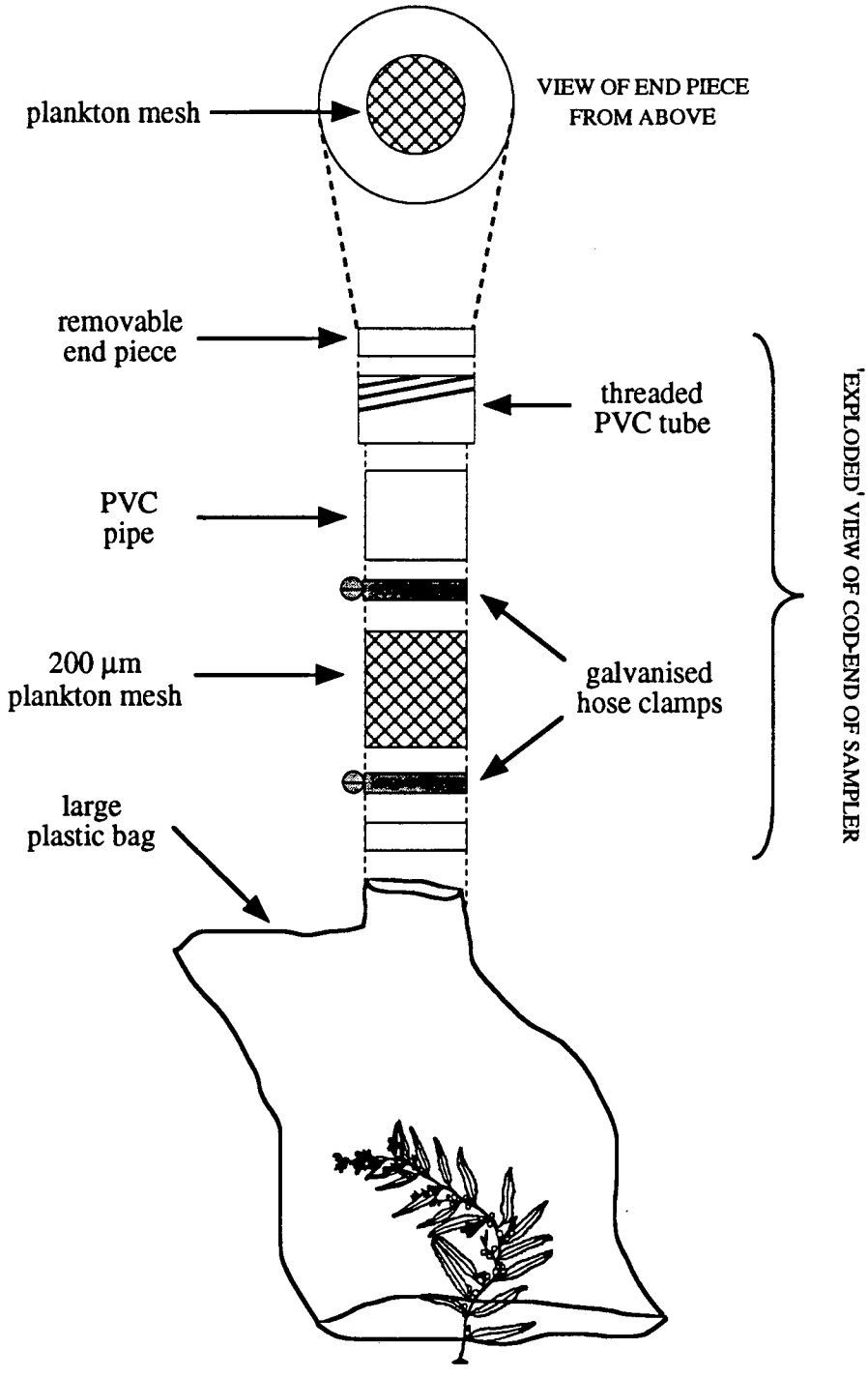


Figure 3.1. Schematic diagram of sampler used to collect *Sargassum* and associated epifauna.

whole apparatus was attached to the bag by another hose clamp. The procedure to collect samples of epifauna was as follows:

(1). The plastic bag was placed over a haphazardly-selected *Sargassum* plant and held sealed around base of plant as close as possible to the holdfast.

(2). The holdfast was prised off the substratum with a knife and pushed into the bag which was held closed during return to the boat.

(3). When the bag was lifted up the water drained out through the plankton mesh. Seawater was run through the bag twice more to dislodge all epifauna.

(4). The plant was removed from the bag and sealed in a smaller, labelled bag.

(5). Epifauna was washed down off the plankton mesh tube into the base of the cod end with wash bottles.

(6). The base of the cod end was unscrewed and the epifauna washed off with seawater into a small amount of 40% formalin solution.

Plants were washed a further two times in the laboratory although epifaunal recovery from the *in situ* field wash was determined to be ≥90% ($\bar{x}$ = 92%, SD = 12, n = 20). Inspection of plants using a hand lens revealed almost no epifauna remained after washing.

3.3.2 Sample collection

Samples of epifauna were taken from all *Sargassum* plants collected from August 1990-September 1992 (see sections 2.4.1 and 2.4.2). Ten samples were taken from unidentified *Sargassum* from August-December 1990, thereafter 7 samples were taken from each of the four species of *Sargassum*. No samples were taken in November 1990, February 1991 and June 1992. All epifaunal samples were extracted as described in the previous section.

3.3.3 Epifauna identification

Since the aim of this study was to investigate the response of the epifaunal community to temporal changes in *Sargassum* populations and given the paucity of taxonomic information about tropical species, it would have been both inappropriate

and highly time-consuming to attempt to identify every individual (or even a subsample) to the species level. Thus a value judgement was made to concentrate on obtaining and processing enough samples to look at epifaunal communities rather than laboriously identify every individual of a necessarily much smaller sample set, an approach which has been taken by previous workers examining similar material (Doherty and Preston *in press*). Epifauna were identified into broad taxonomic groupings of the level of Order or Suborder (taxonomy mostly as in Barnes 1980, but Crustacea and Chelicerata elevated to phylum status rather than subphylum) as follows:

Phylum Crustacea
- Class Malacostraca
  - Superorder Peracarida
    - Order Amphipoda –
    - Group (1) Suborder Gammaroidea (gammarids)
    - Group (2) Suborder Caprellidea
    - Order Isopoda –
    - Group (3) Suborder Flabellifera (sphaeromatids)
    - Group (4) Other Isopods
    - Group (5) – Order Tanaidacea
    - Group (6) – Order Cumacea
  - Superorder Eucarida
    - Group (7) – Order Decapoda

Phylum Annelida
- Group (8) – Class Polychaeta

Phylum Mollusca
- Group (9) – Class Gastropoda

'Minor' taxa:

Phylum Echinodermata
- Group (10) – Class Stelleroidea, subclass Ophiuroidea

Phylum Cnidaria
- Group (11) – Class Anthozoa

Phylum Chelicerata
- Group (12) – Class Pycnogonida

Caprellids, tanaids and other isopods were initially grouped together as "other crustaceans" but were categorised separately from July 1991 onwards. The validity of these groupings and detailed treatment of one of the groups, sphaeromatid isopods, is examined in Chapter 7.

3.3.4 Epifaunal community data analysis

A total of 21 time points were sampled between August 1990 and August 1992 (see section 3.3.2 above). For each time point the epifaunal community was represented by an array of numbers for the abundance of each taxon. Since plant size varied considerably during the year (Chapter 2) these numbers were standardised to densities per 100 g wet weight (100 g^{-1} WW) of plant material. For multivariate analyses, data were log (x+1) transformed to deal with the differences in abundance between taxa (Hurlbert and White 1993) and produce multivariate-normal data (verified using Levine's test). Firstly a 2-way, orthogonal multiple analysis of variance (MANOVA) was performed with the factors TIME (i.e. sampling date) and SPECIES (i.e. *Sargassum* species) on data from January 1991 onwards. Where a significant MANOVA result was obtained (Pillai's Trace, $p<0.05$) data were then analysed using Canonical Discriminant Analysis (CDA). CDA plots data on perpendicular axes of best fit through the data cloud, standardised to unit within-sample variance. It is a pattern-seeking multivariate technique rather than a hypothesis-testing technique and so the interpretation of the output is very much subjective.

Abundance data for univariate analyses were not log (x+1) transformed, provided they were normally distributed (verified using Cochran's test). There were no *a priori* questions about inter-bay differences and so data were pooled from Florence, Geoffrey and Alma, provided there were no differences between *Sargassum* species. Where there were significant differences between species of *Sargassum* data were analysed both pooled and by individual *Sargassum* species.

3.4 RESULTS

3.4.1 Epifauna community composition

A large number of different taxa of epifauna were found on *Sargassum*. The taxa which were found regularly in large numbers were:

Phylum Crustacea – gammarid and caprellid amphipods, sphaeromatids, anthurids and other isopods, tanaids, cumaceans and decapods. Ostracods were found in smaller numbers. Occasionally stomatopods were found. Copepods were regularly sampled, but never in large numbers. These were not quantified due to their small size and thus the possibility that only larger individuals were being sampled.

Phylum Mollusca – large numbers of gastropods were found (mainly shelled meso- or neogastropods). Regular low numbers of shell-less opistobranchs were found and on rare occasions cephalopods were collected. Bivalves were also found regularly in moderate numbers.

Phylum Annelida – large numbers of errant polychaetes were found (sedent polychaetes were not enumerated). Lower numbers of oligochaetes.

Other mobile taxa which were found regularly but in low numbers were:

Phylum Cnidaria – the swimming anemone *Boloceroides murrichii.*

Phylum Platyhelminthes – tubellarian flatworms .

Phyla Nematoda and Rhynchocoela – marine "worms".

Phylum Chelicerata – small numbers of pycnogonids and acarinds were found.

Phyla Sipuncula and Echiura – lesser protostome "worms".

Phylum Echinodermata – ophioroids were found in moderate numbers and holothurians were occasionally found.

Phylum Chordata – fish (apogonids and blennies) were caught rarely.

3.4.2 Epifaunal community analysis by sampling date

MANOVA of the epifaunal community revealed a significant effect of both TIME and SPECIES (Pillai's Trace, $p<0.001$). The difference between epifauna on different species of *Sargassum* is discussed in section 3.4.4, all of the results in this section and section 3.4.3 are from analyses conducted on pooled data from all species. To determine the pattern of community change over time CDA was used and this technique revealed significant directional shifts in community structure (Figure 3.2). The first 3 canonical variables explained 84% of total sample variation and were assumed to represent the important biological changes. Plots of both can 1 against can 2 and can 1 against can 3 showed a cyclical pattern of community change (Figure 3.2). Samples from the same time of year were close together whereas samples from different seasons were widely separated. Summer & winter and autumn & spring samples were diametrically opposed on the CDA plots. The important taxa which produced this separation are shown in the bi-plots for each of the two CDA plots and these are discussed in the following section on univariate data.

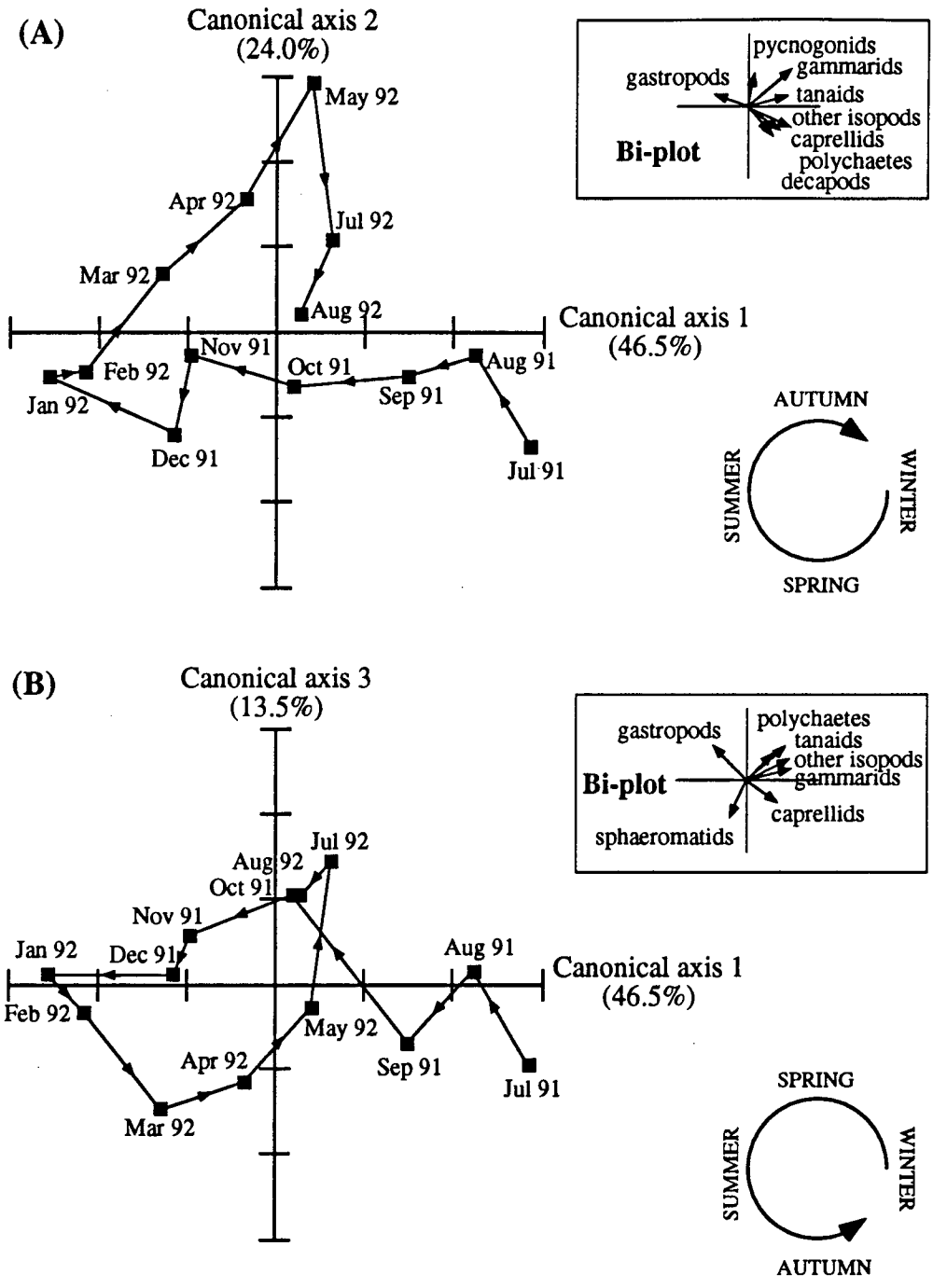


Figure 3.2. Results of CDA on epifaunal communities on *Sargassum* from July 1991-August 1992 (A) can 1 vs can 2 (B) can 1 vs can 3. Bi-plots show taxa contributing to separation between points, arrows show summary of community shifts through the year. 95% error clouds are circles of unit diameter. n=28 for each point.

3.4.3 Phenology of epifauna on all Sargassum *spp combined*

(i) Total abundance

Total abundance of all epifauna on *Sargassum* varied considerably from month to month (Figure 3.3A). Highest numbers of organisms were found during the winter months from June-August 1991 and May-July 1992 and lowest numbers during the summer in January 1991 and from January-March 1992. These patterns of a winter peak in abundance and a summer minimum were consistent between years of the study. Maximal values of epifaunal abundance were ≈1000 individuals 100 g^{-1} WW of algae and minimal values were ≈150 ind. 100 g^{-1} WW, almost an order of magnitude difference. For most of the sampling period crustaceans comprised 70-90% of all organisms collected from *Sargassum* (Figure 3.3B), thus the pattern described above for total organisms was also displayed by total crustaceans, i.e. a winter maximum and summer minimum. Again there was an order of magnitude difference between minimal and maximal abundance values (between January and August 1991 respectively).

(ii) Crustacean abundance (by taxon)

All of the crustacean taxa enumerated displayed seasonal peaks in abundance (Figures 3.4-3.7). The dominant groups within the crustaceans for the sampling period were gammarid amphipods (Figure 3.4A), sphaeromatid isopods (Figure 3.4B) and tanaids (Figure 3.6A). These three groups together constituted 80-95% of all crustaceans collected. The most abundant group, gammarid amphipods, had maximal abundance in winter from May-July and minimal abundance in summer from December-March (Figure 3.4A). The maximum abundance value was ≈600 ind. 100 g^{-1} WW in May 1992 and the minimum was ≈30 ind. 100 g^{-1} WW in January 1991. The patterns of abundance were consistent between 1991 and 1992 although values were significantly lower in 1990.

Sphaeromatid isopods displayed significant variation between sampling dates with abundance peaks in autumn from March to May and minima in winter from July to August (Figure 3.4B). However, seasonal peaks were not as pronounced with sphaeromatids and there were 'minor' maxima at other times of the year, in autumn (September-November). There was approximately a 6-fold difference between minimal values of 25 ind. 100 g^{-1} WW and maximal values of 150 ind. 100 g^{-1} WW. Peak sphaeromatid numbers occurred just before or just after the peak in gammarid abundance.

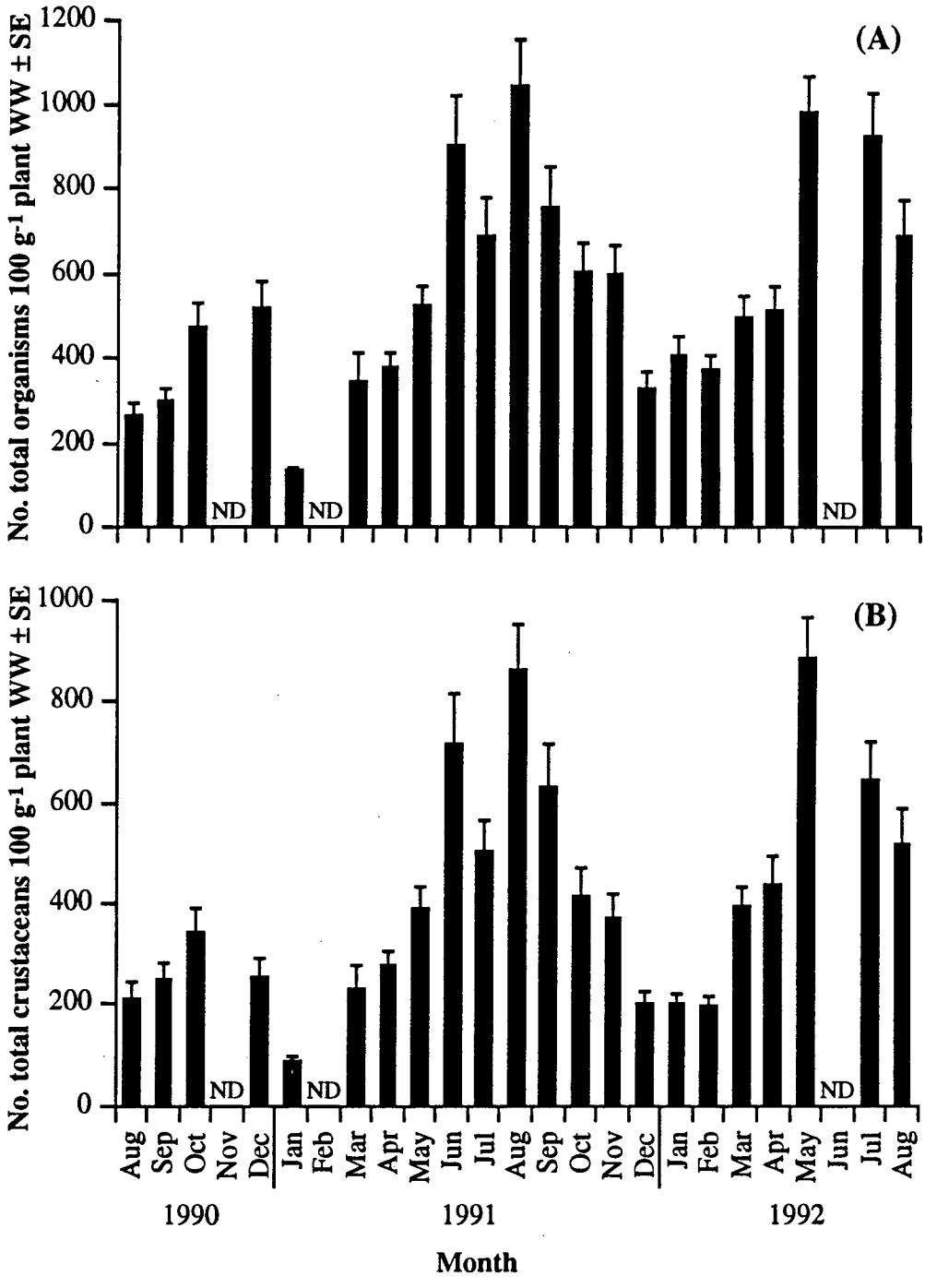


Figure 3.3. Mean abundance of (A) total organisms (B) total crustaceans collected from *Sargassum* plants from August 1990-August 1992. n=28 for each month. ND indicates no data.

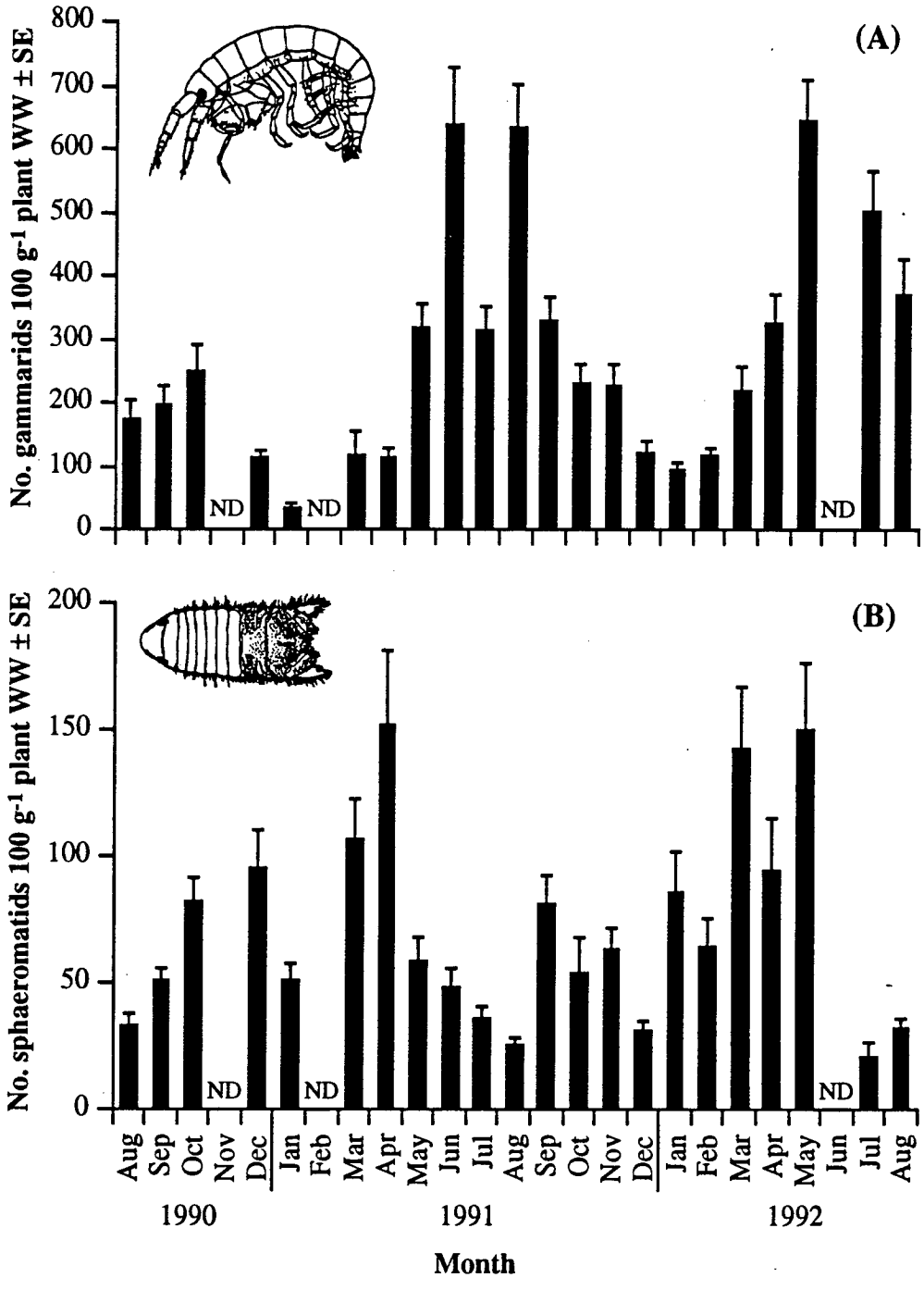


Figure 3.4. Mean abundance of (A) gammarids (B) sphaeromatids collected from *Sargassum* plants from August 1990-August 1992. n=28 for each month. ND indicates no data.

Decapods showed a rather indistinct phenological pattern, with a single large peak in abundance in December 1990 and a much smaller peak in November-December 1991 (Figure 3.5A). For the rest of the sampling time abundance of decapods were consistently low (<10 g^{-1} WW). Cumaceans, on the other hand, showed a much clearer seasonal pattern with high abundance in the winter from June-August and low abundance over the summer and spring from December-April (Figure 3.5B). There was an order of magnitude difference between minimal and maximal values (3 and 35 ind. 100 g^{-1} WW respectively). Patterns were reasonably consistent between years, although abundance was generally lower in 1992.

Tanaids and other isopods (non-sphaeromatids) also showed winter maximum-summer minimum phenologies (Figures 3.6A and 3.6B). Tanaids showed an order of magnitude difference in abundance between 15 ind. 100 g^{-1} WW in March 1992 and 170 ind. 100 g^{-1} WW in September 1991 (Figure 3.6A). Data were not available to discuss inter-annual variation. Other isopods had a very similar pattern to tanaids with maximal values of 30 ind. 100 g^{-1} WW in August 1990 declining to 3 ind. 100 g^{-1} WW in January-April 1992 (Figure 3.6B). Finally, the abundance of caprellid amphipods was generally very low (<10 ind. 100 g^{-1} WW) for most of the sampling period except for a single peak of ≈40 ind. 100 g^{-1} WW in August 1991 (Figure 3.7A).

(iii) Non-crustacean abundance (by taxon)

Pycnogonids were absent from *Sargassum* plants for much of the year, with a brief autumn/winter period (March-August) when they were collected (Figure 3.7B). Despite the fact that the period when pycnogonids appeared was the same from year to year the data values are too low to ascribe significance to the peak abundance. Errant polychaetes showed abundance peaks in July 1991 and 1992 and minima in January 1991 and April 1992 (Figure 3.8A). Again, approximate an order of magnitude difference was detected between maximal abundance of 150 ind. 100 g^{-1} WW and minimal abundance of 20 ind. 100 g^{-1} WW. In contrast, gastropods displayed a summer maximum phenology in both 1990 and 1991 with a dramatic increase in abundance in December 1990 and November 1991 to levels of ≈220 ind. 100 g^{-1} WW (Figure 3.8B). Autumn minima of ≈20 and 40 ind. 100 g^{-1} WW occurred in April 1991 and April 1992 respectively. The phenological pattern for gastropods was slightly different in 1992 when abundance increased much earlier in the year (in July-August) than in the previous two years.

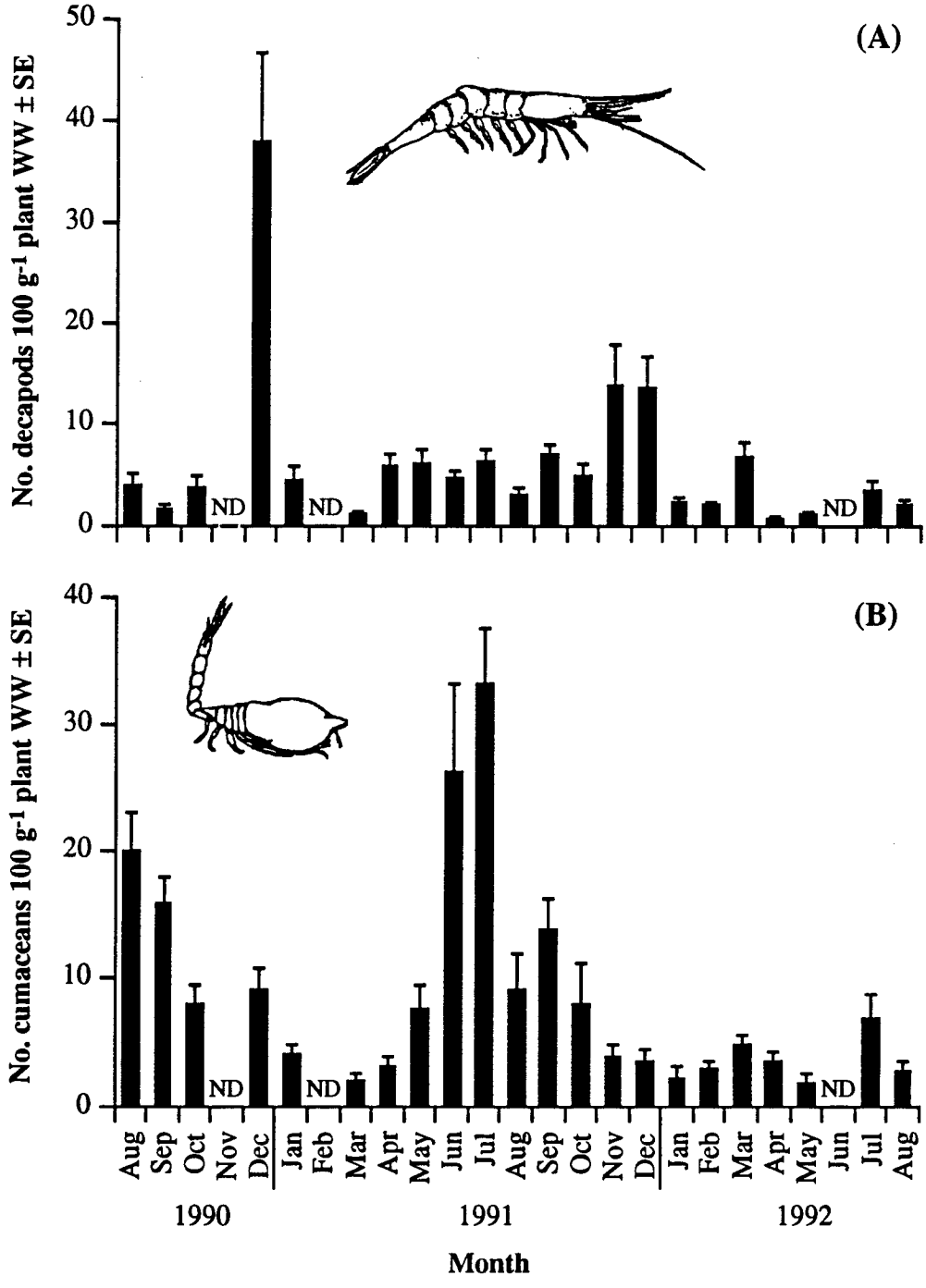


Figure 3.5. Mean abundance of (A) decapods (B) cumaceans collected from *Sargassum* plants from August 1990-August 1992. n=28 for each point. ND indicates no data.

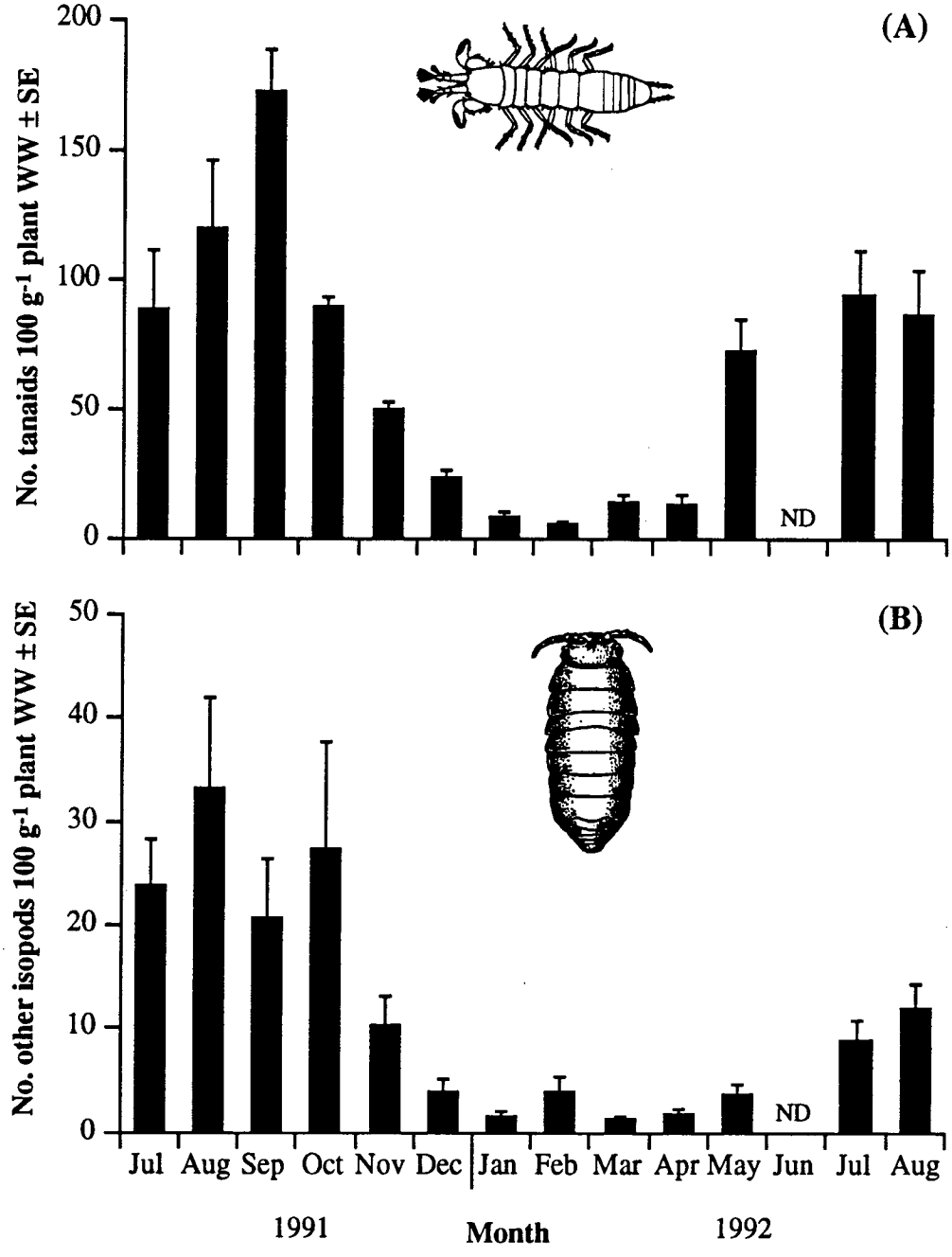


Figure 3.6. Mean abundance of (A) tanaids (B) non-sphaeromatid isopods collected from *Sargassum* plants from July 1991-August 1992. n=28 for each point. ND indicates no data.

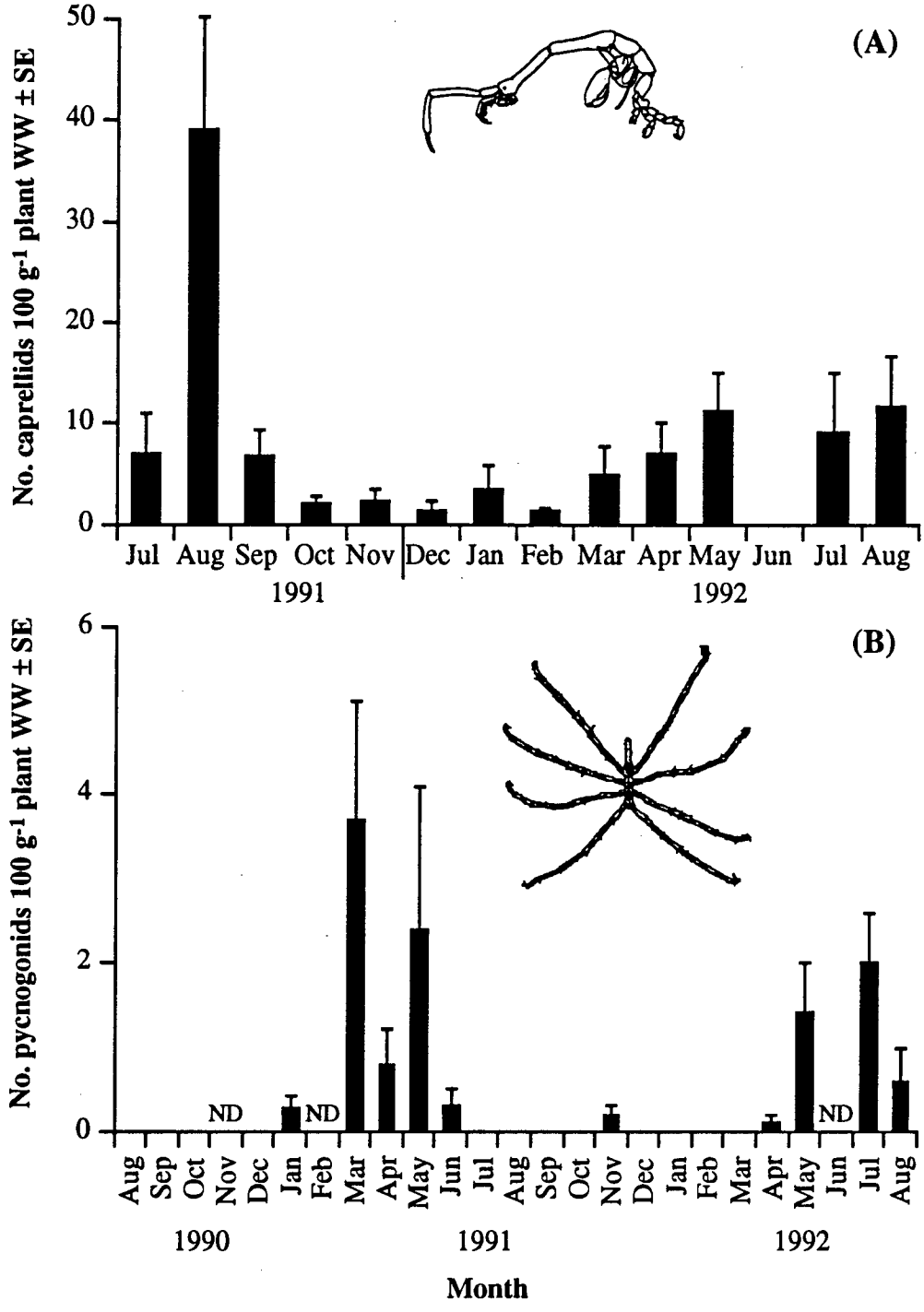


Figure 3.7. Mean abundance of (A) caprellids (B) pycnogonids collected from *Sargassum* plants from July 1991-August 1992 (for caprellids) and August 1990-August 1992 (for pycnogonids). n=28 for each point. ND indicates no data.

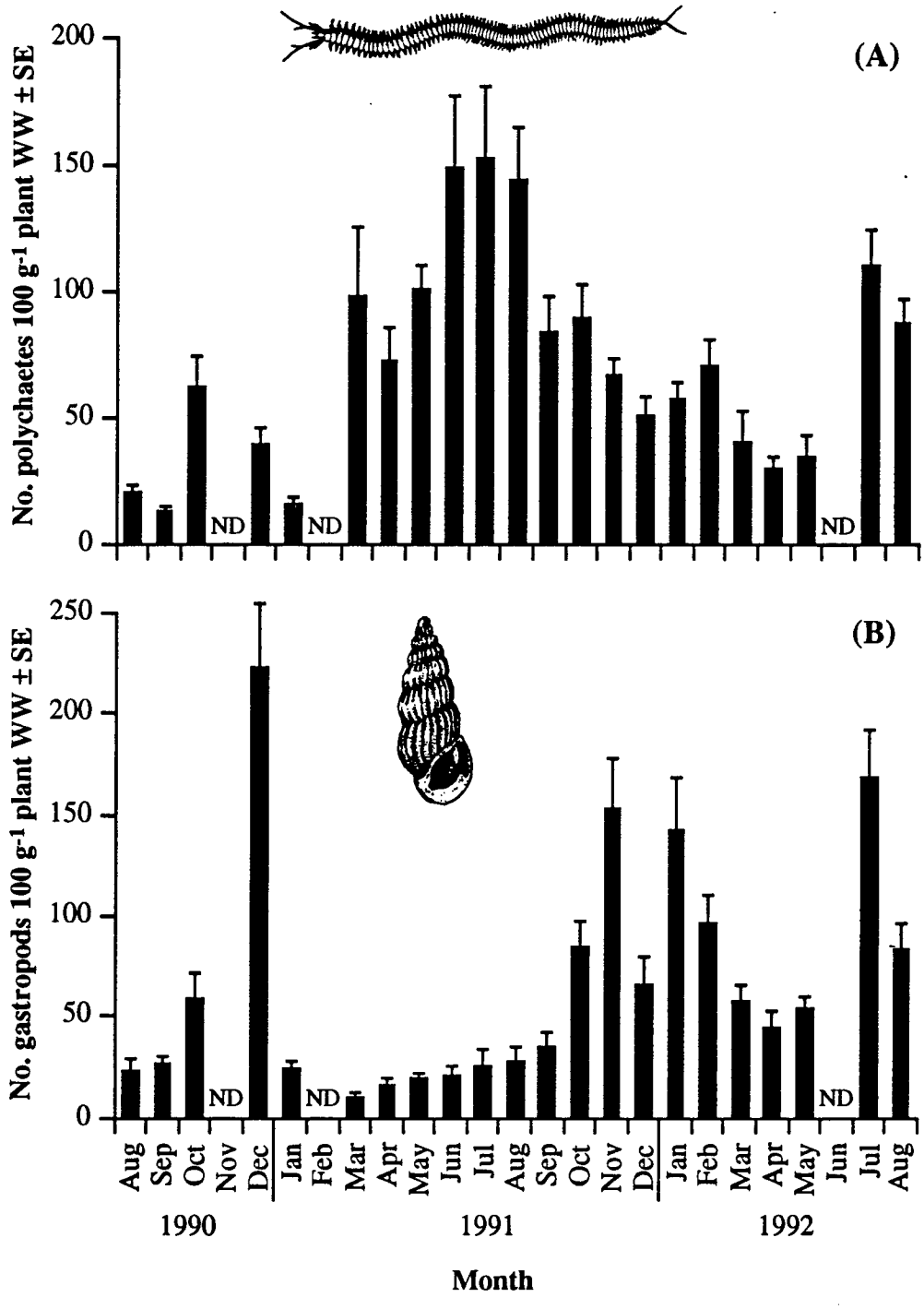


Figure 3.8. Mean abundance of (A) polychaetes (B) gastropods collected from *Sargassum* plants from August 1990-August 1992. n=28 for each point. ND indicates no data.

The two final taxa, ophiuroids and anemones, also displayed seasonal patterns of abundance (Figure 3.9). Ophiuroids had maximal abundance in winter from June-August of 15 ind. 100 g^{-1} WW and minimal abundance in summer from December-February of 4 ind. 100 g^{-1} WW (Figure 3.9A). Anemones (exclusively *Boloceroides murrichi*) showed abundance peaks in late winter/spring from August-December with maximal values of 10 ind. 100 g^{-1} WW and minima in autumn/early winter when they were absent (Figure 3.9B). A summary of the phenological patterns of all the taxa examined is given in Table 3.I. For all of the individual taxa abundance changes were an order of magnitude between maxima and minima and for some taxa changes were almost two orders of magnitude.

3.4.4 Comparison between epifaunal communities on different species of Sargassum

There were significant differences between the communities of epifauna on different species of *Sargassum*, as shown by CDA (Figure 3.10). The most important biological information is probably contained in the first two canonical variables which together explain 93.2% of total sample variation (Figure 3.10A). This plot shows that the epifaunal communities on *S. fissifolium* and *S. tenerrimum* were extremely similar (there was overlap between the 95% confidence circles for these two means). Furthermore the epifaunal community on *S. oligocystum* was reasonably similar to that on both the former species and the community on *S. linearifolium* was most different from the others, evidenced by its wide separation from the other three species. The important taxa which contributed to the differences between species are shown in the bi-plots for the CDA.

When data were examined at the taxon level it emerged that some taxa consistently had differences in abundance between species of *Sargassum* and that others only showed occasional differences (Table 3.II). It was assumed that if abundance was different between *Sargassum* species for more than a third of the samples that this represented a real biological phenomenon, whereas the other differences were assumed to be random 'noise'. The two taxa which showed consistent differences between *Sargassum* species were caprellid amphipods and sphaeromatid isopods. Data for these two groups were thus analysed by species. Caprellids were found on all species of *Sargassum* but abundance was always much higher on *S. linearifolium* than on any other species (Figure 3.11). For much of the time almost no caprellids were found on *S. fissifolium*, *S. oligocystum* or *S. tenerrimum* , but significant numbers were found on *S. linearifolium* for all sampling dates except for February 1992. The general pattern shown in Figure 3.7A

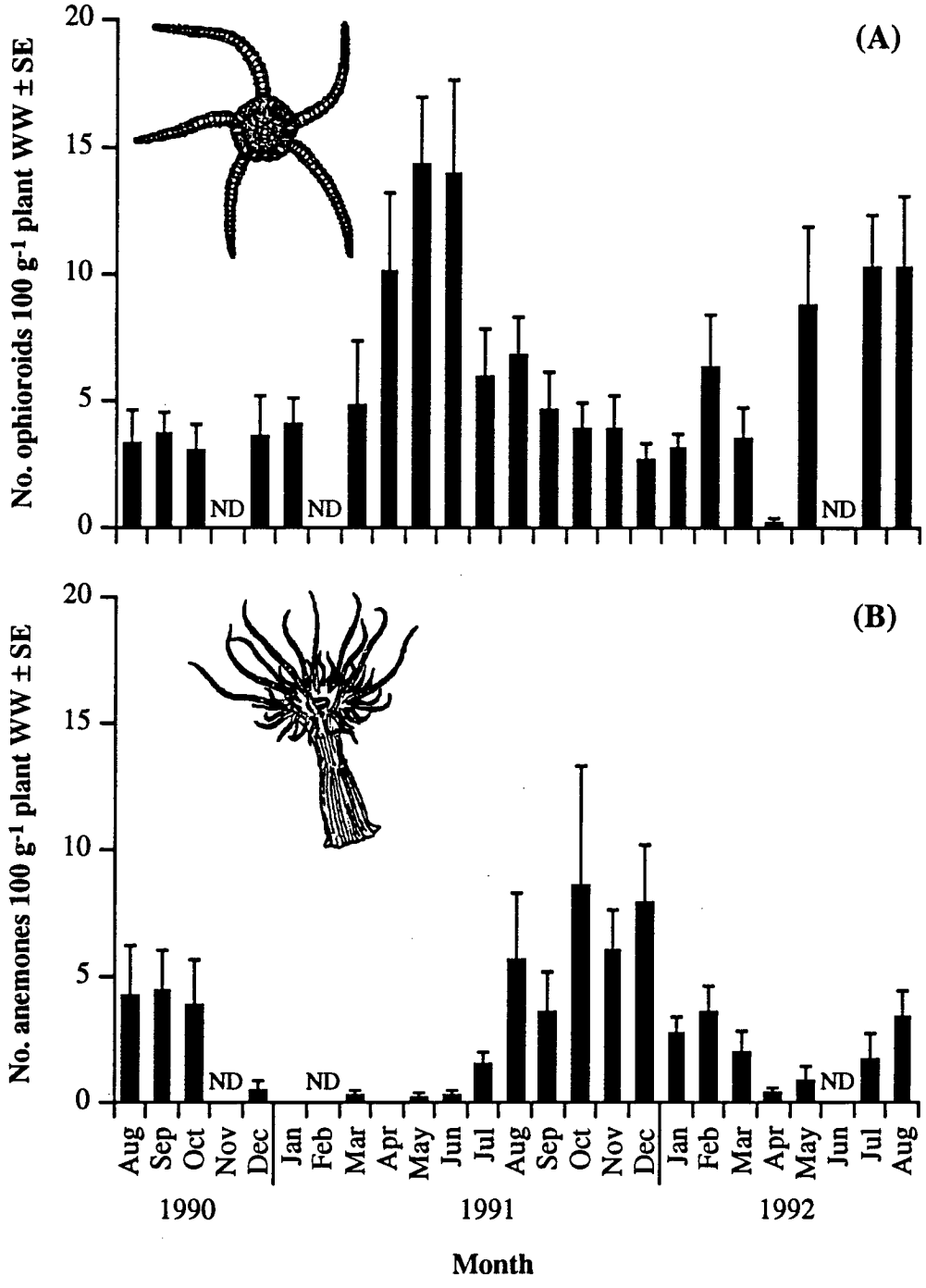


Figure 3.9. Mean abundance of (A) ophiuroids (B) anemones collected from *Sargassum* plants from August 1990-August 1992. n=28 for each point. ND indicates no data.

Taxon	Time of maximum abundance	Time of minimum abundance	Maximal value (nos. 100 g^{-1} plant WW)	Minimal value (nos. 100 g^{-1} plant WW)	Magnitude of difference
Total organisms	May-August	December-February	1050	265	4.0
Total crustaceans	May-August	December-February	890	90	9.7
Crustaceans:					
Gammarid amphipods	May-August	December-February	640	35	17.9
Caprellid amphipods	August?	rest of year	40	1.5	27.9
Sphaeromatid isopods	March-May	July-August	150	20.5	7.3
non-Sphaeromatid isopods	August	January-March	35	1.5	25.4
Tanaids	September	January-February	170	5.5	31.3
Cumaceans	June-July	December-February	35	2.0	18.3
Decapods	November-December?	rest of year	40	1.5	26.7
Other taxa:					
Polychaetes	June-August	March	150	13.5	11.3
Gastropods	November-January	rest of year	220	2.5	96.5
Ophiuroids	May-June	January-February	15	0.2	71.5
Anemones	October-December	January-April	10	0	–
Pycnogonids	March-July?	rest of year	5	0	–

Table 3.I. Times and magnitudes of maximal and minimal abundance of epifaunal taxa from *Sargassum*.

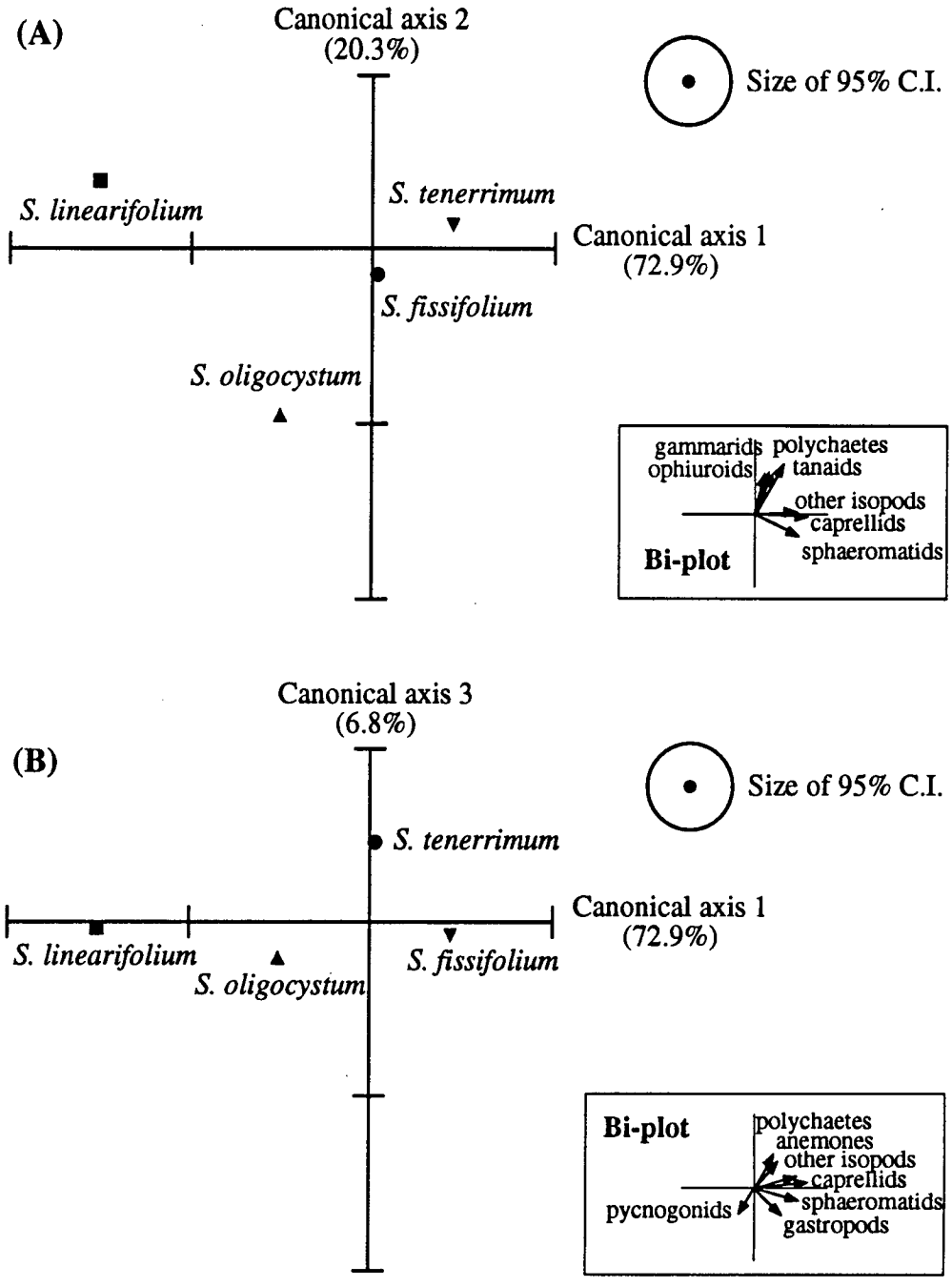


Figure 3.10. Results of CDA on epifaunal communities on *Sargassum* from July 1991-August 1992 by *Sargassum* species (A) can 1 vs can 2 (B) can 1 vs can 3. Bi-plots show taxa contributing to separation between points. n≈80 for each point.

Date	Gammarids	Caprellids	Sphaeromatids	Other Isopods	Tanaids	Cumaceans	Decapods	Polychaetes	Gastropods	Ophiuroids	Anemones	Pycnogonids
Jan 91	+		–			–	–	+	–	–	–	–
Feb 91	No data available											
Mar 91	+		–			–	+	+	–	–	–	–
Apr 91	–		–			–	–	–	–	–	–	–
May 91	–		+			–	–	–	–	+	–	–
Jun 91	+		–			–	–	–	–	+	–	–
Jul 91	–	–	–	–	–	–	–	–	–	–	–	–
Aug 91	–	–	–	–	–	–	–	–	–	–	–	–
Sep 91	–	+	+	–	–	+	–	–	–	–	–	–
Oct 91	–	+	–	–	–	–	+	–	+	–	–	–
Nov 91	–	+	+	+	–	+	–	–	–	–	–	–
Dec 91	–	–	–	–	–	–	–	–	–	–	+	–
Jan 92	–	+	+	+	–	–	–	–	–	–	+	–
Feb 92	–	–	+	–	+	–	–	+	+	–	–	–
Mar 92	+	+	+	–	+	+	–	+	–	–	–	–
Apr 92	No data available											
May 92	+	+	+	–	–	–	–	–	+	+	–	–
Jun 92	No data available											
Jul 92	–	+	–	–	–	–	–	–	–	–	–	–
Aug 92	–	–	+	–	+	–	–	–	–	+	–	–
Total	**5/17**	**7/12**	**8/17**	**2/12**	**3/12**	**3/17**	**2/17**	**4/17**	**3/17**	**4/17**	**2/17**	**0/17**

Table 3.II Summary of MANOVA significance for effect of *Sargassum* species on abundance of epifauna. + indicates significance at $p<0.05$, - indicates no significant effect.

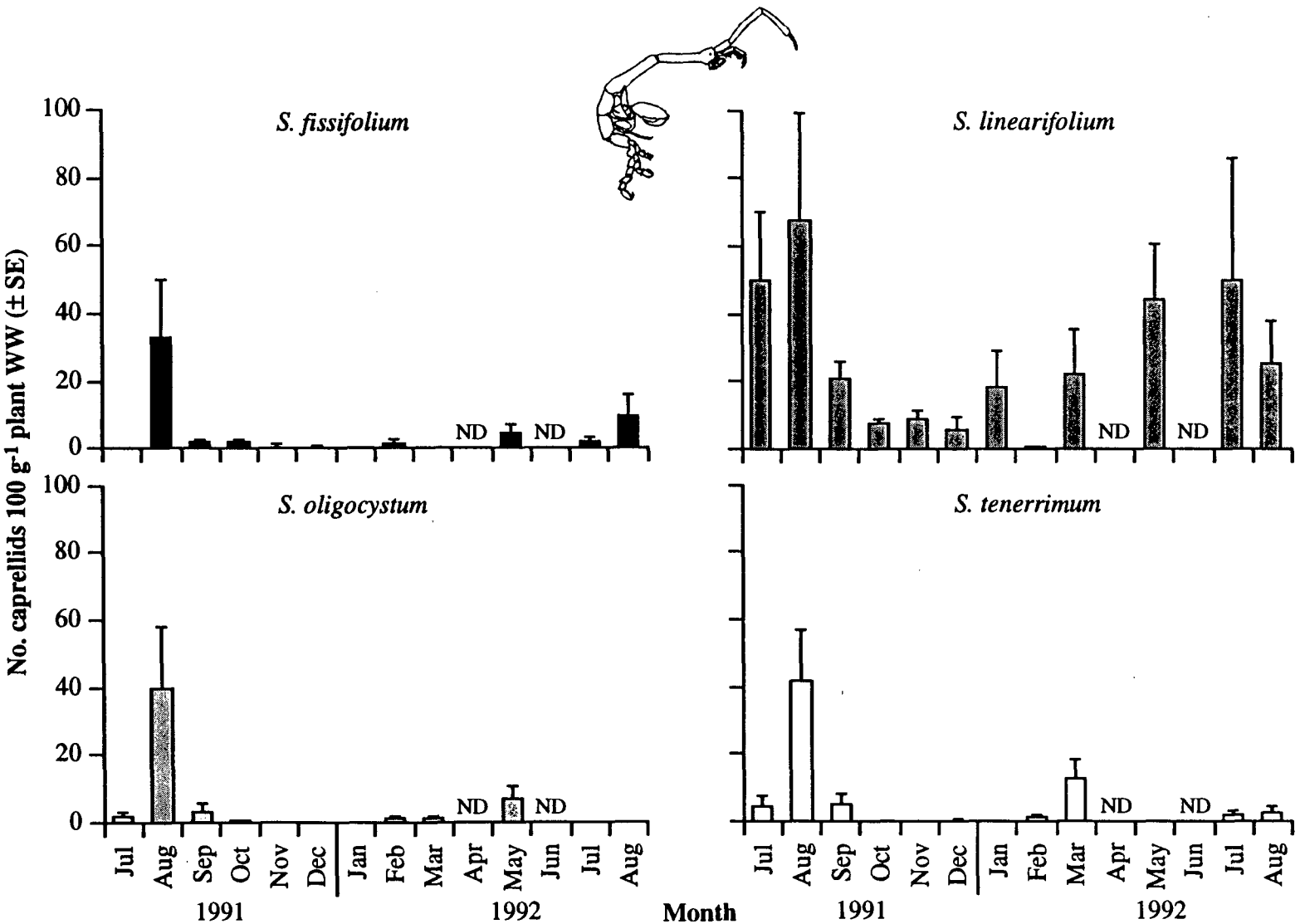


Figure 3.11. Mean abundance of caprellids on each species of *Sargassum* from July 1991-August 1992. n=7 for each point. ND = no data.

is largely driven by the caprellids living on *S. linearifolium*. Caprellids on all four species of *Sargassum* showed maxima at the same time (August 1991) and the phenological patterns appeared to be generally similar between species. Abundance on *S. linearifolium* was 2-5 x greater than on any other species with a maximal value of 65 ind. 100 g^{-1} WW.

In contrast to caprellids, there was consistently lower abundance of sphaeromatids on *S. linearifolium* than on the other species throughout the year, never attaining more than 50 ind. 100 g^{-1} WW (Figure 3.12). Sphaeromatid populations on *S. fissifolium* and *S. oligocystum* both showed autumn peaks, although abundance was consistently higher on *S. fissifolium*, reaching levels of 220 g^{-1} WW in contrast to peak levels of 110 ind. 100 g^{-1} WW on *S. oligocystum*. Sphaeromatids on *S. tenerrimum* also showed an autumn population peak (in April 1991 and May 1992) and they reached high abundance of 160 ind. 100 g^{-1} WW in spring (September-November 1991).

3.5 DISCUSSION

3.5.1 Epifaunal phenology

The numerical abundance of crustaceans on *Sargassum* throughout the year was not unexpected. Crustaceans are frequently dominant on temperate species of algae including *Sargassum* (for example Fine 1970, Mukai 1974, Edgar 1983b, Gunnill 1983, Wakabara *et al.* 1983, Aoki 1990, Duffy 1990). Tropical species of algae have been studied far less but, again, crustaceans are commonly found (Lewis 1987, Russo 1987, 1990, Vacamoce 1987). Gastropods and polychaetes, the other major taxa living on *Sargassum* in this study, are also common epifaunal organisms on macroalgae (Nagle 1968, Fine 1970, Edgar 1983a, b, 1990e). The ubiquitous nature of crustaceans as epifauna in numerous different systems, in different physical environments, on plants varying in structure, chemical composition and morphology suggests that these organisms possess attributes which are particularly suited to life on the plant surface. Some of these characteristics include the possession of multiple grasping limbs which allow the organism to maintain itself on the plant, swimming ability which facilitates dispersal to new hosts (a very important consideration for peracarid crustaceans which brood their young) and mouthparts with the evolutionary plasticity to adapt to numerous modes of feeding.

Most marine organisms including invertebrate epifauna have populations which are characterised by large seasonal fluctuations in abundance (e.g. Mukai 1971,

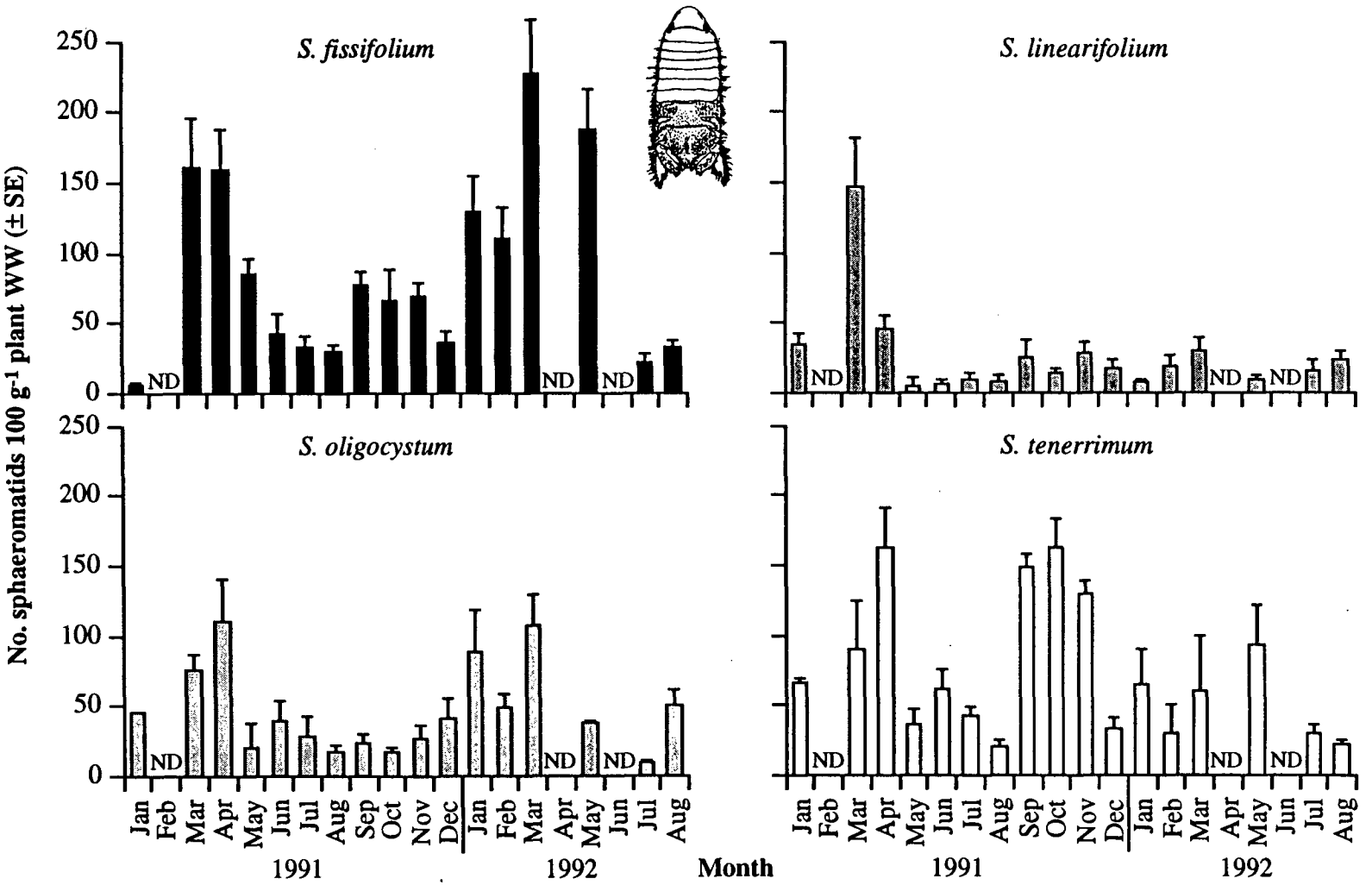


Figure 3.12. Mean abundance of sphaeromatids on each species of *Sargassum* from January 1991-August 1992. n=7 for each point. ND = no data.

Nelson *et al.* 1982, Edgar 1983b, Gunnill 1983). Whether on macroalgae or seagrass, in the tropics or in temperate regions abundance can change dramatically over the course of a few weeks. The general pattern which emerges from the literature is that epifaunal populations are usually largest during the summer months. This has been shown for temperate macroalgae (Aoki 1990, Arrontes and Anadon 1990), temperate seagrass (Marsh 1973, Schneider and Mann 1991a) and tropical seagrass (Heck 1977) but there appear to be no studies on seasonal variation of abundance of epifauna on tropical macroalgae. The magnitudes of the population fluctuations in most of these studies is approximately one order of magnitude, which gives some grounds for believing there to be some commonality of mechanisms underlying the changes.

3.5.2 Comparison between epifaunal and Sargassum *phenologies.*

The most surprising finding of the present study was the unexpected seasonal peak of crustacean numbers and density during winter months when *Sargassum* plants were smallest. Aoki (1990) found a winter maximum of caprellid amphipods on *S. patens* in Japan, but this was in response to peak *Sargassum* biomass during the winter. Other studies on *Sargassum* have recorded high epifaunal populations at times of high algal biomass: Mukai (1971) recorded a spring maximum of copepods and amphipods at the time of greatest algal biomass, Edgar (1983) found that phytal animals peaked in late summer/early autumn just after peak biomass of algae was reached and Duffy (1990) reported a summer peak in amphipod abundance in response to increased algal biomass.

Seasonal patterns of epifaunal abundance have been documented for temperate fucoid algae (Holmlund *et al.* 1990) and for subtropical (Nelson 1979b, Lewis 1987) and tropical seagrass (Heck 1979). These studies showed a summer/autumn peak in epifaunal abundance which correlated with maximum biomass of the macroalga or seagrass. For the present study this appeared to be true only for the gastropod and anemone epifauna which had clear summer peaks. Hypotheses as to why there should be high abundance of epifauna during periods of low *Sargassum* biomass are discussed and tested later (Chapters 5 and 6); however it seems clear that abundance of organisms was not determined by the amount of algae. It is further suggested that the animals were either not feeding on the *Sargassum* or that food limitation was not responsible for their changes in abundance. This counter-intuitive pattern was remarkably consistent over the two year period of the study, with almost all taxa

showing very similar patterns across years. All of this evidence points to the presence of a strong 'structuring force(s)' which determined population abundance.

An interesting pattern to emerge was the distinct preferences demonstrated by the sphaeromatids and caprellids for different species of *Sargassum* (Figures 3.10 and 3.11 respectively). Caprellids showed the same seasonal pattern for all four species of *Sargassum* but there were consistently higher numbers on *S. linearifolium*. An explanation for this difference could be the correlation between body morphology of caprellids and the shape of the leaves of *S. linearifolium*. Hacker and Madin (1991) demonstrated that two species of shrimps living in pelagic *Sargassum* showed camouflage and part-plant mimicry and modified behaviour to take advantage of these morphological attributes. Caprellids have a specialized body architecture with elongated, laterally-compressed bodies (their common name is "skeleton shrimps") and *S. linearifolium* has long, narrow leaves: hence mimicry and crypsis should be more effective for a caprellid living on *S. linearifolium* than on other *Sargassum* species.

Sphaeromatids also had differing distributions among the four species of *Sargassum*; however seasonal patterns were not identical for the populations living on each species. Again, camouflage and crypsis may have been involved in determining changes, since abundance was consistently lower on *S. linearifolium* and sphaeromatids have a short, dorsally-flattened body shape. There appear to be no studies relating body shape of sphaeromatids to habitat preference although Arrontes (1990b) and Arrontes and Anadon (1990a) have found that distribution patterns of isopods on macroalgae in Europe were related to diet and Arrontes and Anadon (1990b) showed that seasonal population fluctuations of three species of sphaeromatid were related to reproductive biology. Further work needs to be done on the reasons for the difference in populations of caprellids and sphaeromatids between the different species of *Sargassum*.

In conclusion, this chapter has demonstrated that there is a diverse and abundant fauna which lives associated with benthic *Sargassum* at Magnetic Island. This fauna is dominated numerically (and in terms of biomass) by crustaceans, particularly gammarid amphipods, sphaeromatid isopods and tanaids. All of the twelve taxonomic groupings enumerated showed large and predictable changes in abundance over the course of two years. Of these twelve taxa, ten showed peaks in winter to some degree or form, while only two showed peaks in summer. These changes were inversely correlated with the biomass and size of their *Sargassum* host but positively correlated with levels of epiphytes.

CHAPTER 4

SHORT-TERM TEMPORAL AND SPATIAL DYNAMICS OF EPIFAUNA

"Acts in...the 'ecological theatre' are played out on various scales of space and time. To understand the drama, we must view it on the appropriate scale." Joseph A. Wiens, Spatial Scaling in Ecology.

4.1 INTRODUCTION

The preceding work has been concerned with variation in *Sargassum* and epifauna populations on the temporal scale of months to years. However, such observed patterns may simply be a function of the scale of measurement. To validate temporal or spatial patterns it is necessary to obtain an estimate of the level of variation at other scales. If daily or weekly fluctuations in abundance are greater than monthly variation, then a perceived 'seasonal' pattern can be generated by random stochastic events on the day of sampling. Similarly, true patterns can be obscured by the same processes. The sampling and experiments described in this chapter were designed to examine whether monthly sampling provided an accurate representation of seasonal epifaunal population changes. The effects of scaling are often not considered nor acknowledged, prompting Wiens (1989) in his essay review to pose the question "Why have ecologists been so slow to recognize scaling?". Wiens (*loc. cit.*) gives a number of examples of ecological patterns (e.g. organism distribution) which are different or even reversed between different spatial scales. Although the choice of scale may eventually be arbitrary, constrained by logistical or other factors, it is essential to define that scale – Meentemeyer and Box (1987) have called for scale to be an explicitly stated variable in ecological analyses. Wiens (1989) goes further and states that "ecologists therefore need to adopt a multiscale perspective...studies conducted at several scales will provide a better resolution of domains, of patterns and their determinants, and of the interrelationships among scales".

To further elucidate the role of the epifauna on *Sargassum* it was important to know their short-term spatial dynamics. While most epifauna have well developed locomotory abilities (Barnes 1980), did they regularly move short distances from plant to plant? The rate of exchange of individuals within the system will determine how quickly new habitats are located and colonised and how long it takes to establish equilibrium. An *a priori* assumption was that these processes would occur on a time scale of less than a month, hence shorter scale experiments would be needed to ascertain colonisation rates.

A final point about terminology used in discussions of scaling: 'extent' refers to the overall area or time encompassed by the study and 'grain' is the magnitude of individual units of observation.

At any particular scale, there are three possible approaches to examining spatial and temporal variation – spatial variation is traditionally measured by keeping time constant and sampling at various points in space, temporal variation is measured by keeping location constant and sampling at various time points and finally both can be measured simultaneously. It is axiomatic that it is normally impossible to measure spatial and temporal variation over all scales comprehensively. In the monthly sampling programme described in Chapter 3, temporal variation was measured on a scale of months and years and spatial variation on a scale of tens of metres to kilometres (intra- versus inter-bay sampling). Smaller scale spatial sampling would have involved sub-sampling individual plants and was considered of dubious ecological importance. However, the population dynamics on a smaller temporal scale, that of hours to weeks, was important in interpretation of the larger scale patterns of seasonal variation. The following section reviews approaches which can be taken to investigate these smaller scale patterns:

(1). Short-term* observational studies. It appears that individual organisms within a population of epifauna are very mobile and that turnover is rapid. This was demonstrated elegantly by Howard (1985) who used an *in situ* staining method to look at turnover of crustaceans and gastropods in seagrass beds. He found turnover rates of >50% in 3 hours for one caridean shrimp, and most taxa he investigated (amphipods, shrimps, gastropods) showed >25% turnover of individuals in 6 hours. Although the turnover of individuals may be high, the effects the population is dependent on the synchronicity of the movement of individuals (i.e. whether they all immigrate or emigrate concurrently). Synchronous diel population movements have been observed for a wide variety of taxa inhabiting a wide variety of substrata. Zooplankton are commonly observed to move into the water column at night (e.g. Alldredge and King 1977, 1980, Jacoby and Greenwood 1988) and macrofauna associated with seagrass beds are predictably more abundant at night (Livingston 1976, Greening and Livingston 1982, Howard 1987). Kitting (1984) used a non-destructive approach (photography) to look at distributions and feeding of organisms on seagrass beds over 24 hour periods and found increased abundance and activity of gastropods and shrimps at night. Edgar (1983d) found that populations of amphipods on *Zonaria* decreased at night, but that populations on *Sargassum verruculosum* did

* I propose to use 'short-term' here to describe studies with an extent of hours to days and a grain size of minutes to hours. This is an arbitrary definition based on the reviewed study with the smallest grain size (Kitting 1984)

not change predictably over a 24 hour period. Fincham (1974) found that 80% of amphipods in a light trap were epifaunal species, however the area from which these were sampled was unknown. Ledoyer (1969) and Montouchet (1979) found increased abundance of epifauna on macroalgae at night due to immigration by benthic species. Thus, there did not appear to be a general hypothesis with regard to the abundance of epifauna over the time scale of days and no *a priori* assumptions about abundance of epifauna of tropical *Sargassum* over the same period were generated.

(2). Short-term* manipulative studies. Generally recolonisation of defaunated plants occurred very rapidly; in all studies reviewed, some epifauna had recolonised at the first sample time. Stoner (1985) found 6 species of crustacean at levels of 15 g^{-1} DW on *Penicillus* only 1hr 20 mins after defaunation, Edgar (1983d) had recolonisation rates of amphipods of 1.7-3.0% overnight and Virnstein and Curran (1986) found gastropods, amphipods and copepods on artificial seagrass 12 hours after deployment. Similarly, maximal abundance were achieved rapidly in most studies e.g. after 72 hours in Stoner (1985) and 4 days in Virnstein and Curran (1986). Bell and Devlin (1983) found that macrofauna had returned to control abundance 7.5 hrs after defaunation of soft sediment and DeWitt (1987) also measured high rates of amphipod colonisation in similar sediments. The question of whether equilibrium was reached or how long it took is more contentious, certainly Schoener (1974) found her species-time curve reached an asymptote at 31 days and Virnstein and Curran (1986) found no increase in species number between 8 and 16 days. It seems that the willingness of the observer to believe in equilibrium is the determining factor in interpretation of these results!

Of course, consideration of many of the aspects of the biology of epifauna on *Sargassum* is dependent on the assumption that organisms found on the plant are indeed epifauna, not vagrant species or representatives of the reef cryptofauna. If this assumption was invalid then population dynamics of organisms found on *Sargassum* could have been dependent on processes occurring elsewhere in the reef system. Thus, a sampling programme was conducted to examine whether 'epifauna' were found in the reef substratum and/or emerged from the substratum on to *Sargassum.* A related point of interest was the fate of epifauna on detached *Sargassum* plants or axes. Kingsford and Choat (1985) showed that the fauna on drift algae in New Zealand (*Carpophyllum, Sargassum* and *Durvillea*) was largely the result of colonisation from open water and that epifauna quickly left detached axes. Similarly Aoki (1990) showed that the caprellid fauna of floating *Sargassum patens* was very different to that

* Again 'short-term' is defined arbitrarily, referring to experiments occurring over an extent of hours to weeks with a grain size of hours to days.

of benthic plants. Brief sampling of floating *Sargassum* was performed to investigate the situation at Magnetic Island.

4.2 AIMS AND OBJECTIVES

More detail on the rationale for each of the sampling observations and experiments is given in each section. However, the general aims of the work in this chapter were:

- To describe the community of epifauna found on detached *Sargassum* axes and to compare it with the concurrent benthic community.

- To ascertain the specificity of epifauna to a phytal habitat as opposed to chance presence on *Sargassum* at the time of sampling.

- To describe the diel fluctuations in abundance of epifauna and the subsequent implications for a purely diurnal sampling strategy.

- To quantify variation in abundance and composition of populations of epifauna over time scales of hours to weeks.

- To monitor the recolonisation of epifauna on to uninhabited plants and to provide an estimate of the time course for subsequent experiments involving colonisation of defaunated substrata (see Chapter 6).

4.3 SAMPLING OF DRIFT *SARGASSUM*

4.3.1 Introduction and Method

In February-April, soon after the onset of reproduction, a dramatic decline was found in the biomass of the *Sargassum* population (Figures 2.4, 2.5 and 2.14). Much of this decline was attributable to the loss of annual axes. In addition, entire plants were lost throughout the year by wave dislodgment from the substratum (Figure 2.16). This material may survive for some time, floating free in the ocean, before eventually senescing or being washed ashore. Two species of *Sargassum* in the Atlantic, *S. fluitans* and *S. natans* have become adapted to an entirely pelagic existence, trapped in the gyre of the Sargasso Sea, proving the potential of such a mode of existence. This pelagic *Sargassum* supports large numbers of specialised epifauna and fish (Weis 1968, Fine 1970, Hacker and Madin 1991). The aim of this

part of the study was to quantify the epifauna living on drift *Sargassum* since this material represents a potential method of dispersal to new habitats. However, previous studies have shown that epifauna can quickly perceive and respond to the detachment of their host, emigrating within 5 minutes of detachment (Kingsford and Choat 1985).

In both December 1991 and May 1992 ten floating *Sargassum* plants were collected from the waters on the eastern side of Magnetic Island. The first ten individuals encountered which were at least 40 g WW were sampled. The plants were collected in the same way as described in Section 3.3.1. Data for the abundance of epifauna were compared with samples taken from benthic *Sargassum* at the same time. A 2-way MANOVA on log (x+1) transformed data revealed significant DATE * TYPE (benthic or pelagic) interaction so CDA was used to separate the four different categories of sample; Dec. benthic, Dec. drift, May benthic, May drift.

4.3.2 Results and Discussions

Individuals of most taxa that were collected from benthic *Sargassum* were also found on drift *Sargassum*. However, abundance was significantly lower for most taxa on drift samples (Figure 4.1, 1-way ANOVA on untransformed data, $p<0.01$, 9 df). The only taxon which was not significantly less abundant was caprellids in December – these were slightly more abundant on the drift samples than on the benthic samples, though not significantly so (1-way ANOVA, $p>0.05$, 9 df). In general abundance of all organisms was very low on drift *Sargassum* indicating that most epifauna had left the plant on detachment from the substratum or at some subsequent point. For 8 of the 9 taxa enumerated there were lower numbers on the drift samples in May than in December (the exception being sphaeromatids), and the difference in abundance between drift and benthic samples was more pronounced in May also (Table 4.I). This lower abundance on the May drift *Sargassum* could indicate that the plants had been adrift for a longer period of time, or that the rate of loss of epifauna from them was greater. In addition to epifauna, most of the pieces of drift *Sargassum* had up to a dozen small fish (apogonids and blennioids) associated within them.

In general the communities remaining on the drift *Sargassum* were similar to each other despite the changes in epifaunal abundance on the benthic *Sargassum* between December and May (Figure 4.2). CDA showed that drift communities were not significantly different at the two sampling dates whereas benthic communities had significant differences in community abundance and composition.

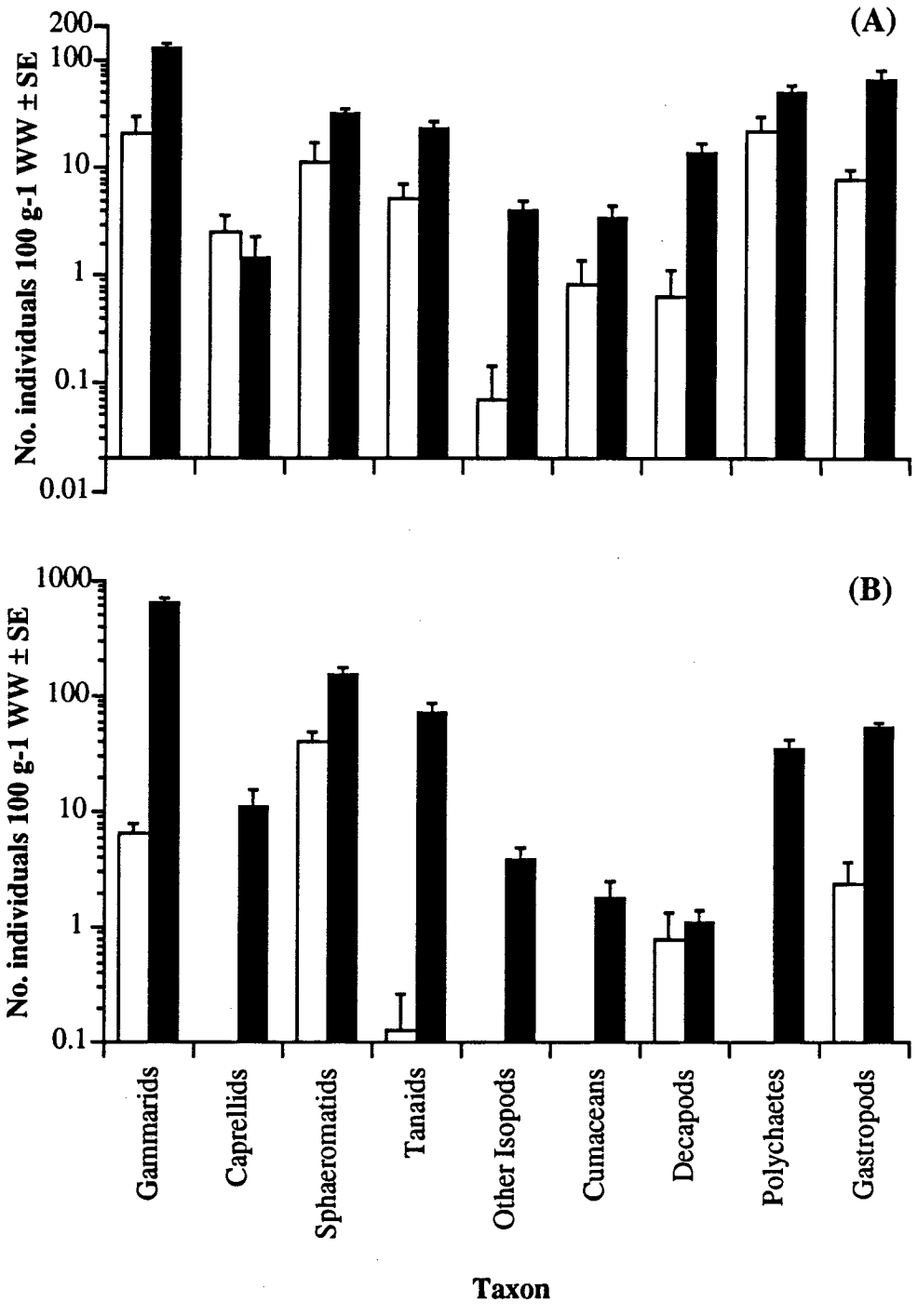


Figure 4.1. Mean abundance of epifaunal taxa on benthic (■) and drift (□) *Sargassum* in (A) December 1991 (B) May 1992. Note log abundance scale. n=27 for benthic *Sargassum*, n=10 for drift *Sargassum*.

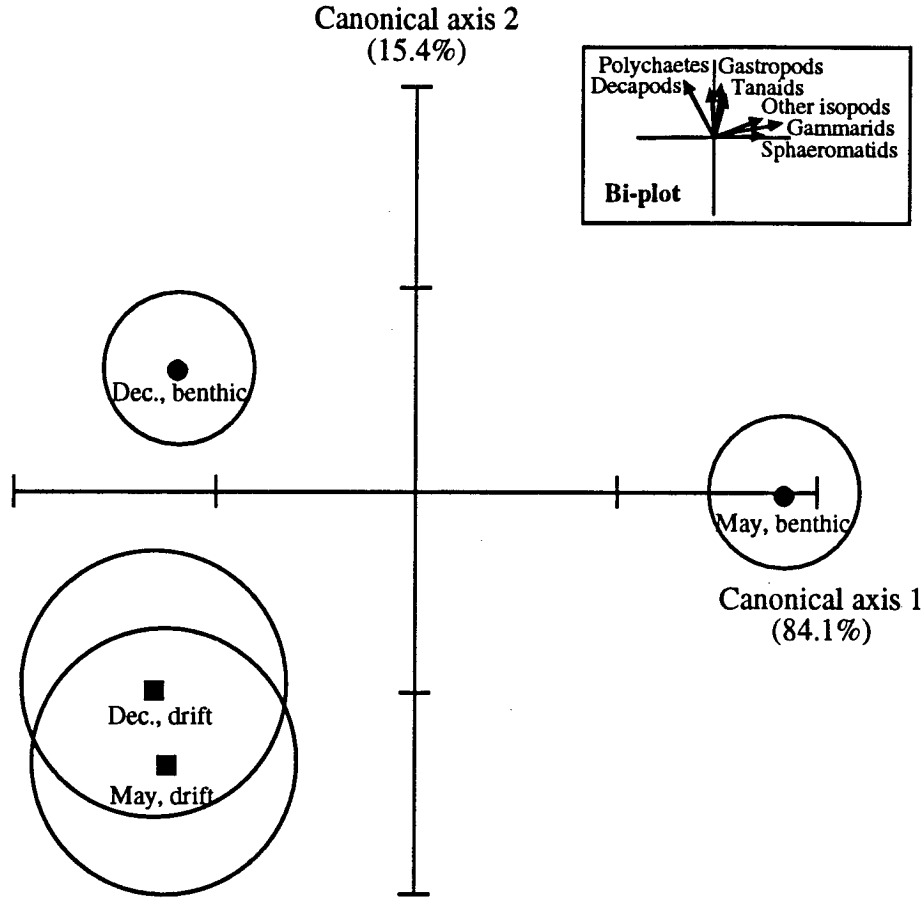


Figure 4.2. Plot of first two canonical axes for epifaunal communities on drift and benthic *Sargassum* collected in December 1991 and May 1992. Circles represent 95% C.I. about mean. Bi-plot shows taxa contributing to separation between points. n=27 for benthic samples, n=10 for drift samples.

Taxon	% Abundance of taxon on drift compared to benthic *Sargassum* in December 1991	% Abundance of taxon on drift compared to benthic *Sargassum* in May 1992
Gammarids	17.3	1.0
Caprellids	175.7	0
Sphaeromatids	36.9	26.3
Other Isopods	21.9	0.2
Tanaids	1.7	0
Cumaceans	24.0	0
Decapods	4.5	69.0
Polychaetes	43.5	0
Gastropods	12.2	4.5

Table 4.I Mean abundance of epifaunal taxa on benthic and drift *Sargassum.*

The conclusions from this brief sampling programme are that the drift material did not represent a favourable resource for epifauna. Kingsford and Choat (1985) showed that epifauna actively 'bailed out' from artificially detached macroalgae in New Zealand. They found that drift algae had large numbers of open-water shrimps, crab megalopa and fish associated with it and small numbers of epifauna. The situation at Magnetic Island appears similar with 'bail out' the most likely explanation for low epifaunal abundance on drift algae. In addition the predation risk to epifauna may be substantially higher on drift material, especially since the clumps appeared to act as fish aggregation devices (Kulczycki *et al.* 1981). *Sargassum fluitans* and *S. natans* in the Sargasso Sea support large populations of epifauna, including amphipods, isopods, decapods, polychaetes and gastropods (Weis 1968, Fine 1970) so this mode of existence is obviously possible. However many of these are specialized forms with adaptations for such existence (Hacker and Madin 1991) which are not represented in the benthic *Sargassum* epifauna.

4.4 EMERGENCE TRAP SAMPLING

4.4.1 Introduction and Method

Sargassum is frequently found growing on coral rubble, a complex substratum known to have numerous organisms living in the interstices (Peyrot-Clausade 1980, Klumpp *et al.* 1988). Klumpp *et al.* (*loc. cit.*) found that the most abundant cryptofauna in some Australian reefs were harpacticoid copepods, gammarids, syllid

polychaetes and gastropods: thus, it was possible that the '*Sargassum* epifauna' was merely a subset of organisms normally living in the rubble. In addition, it was not known to what degree epifauna left *Sargassum* at night. The subsequently described collection was designed to quantify the organisms emerging from the rubble and to directly measure the epifaunal emigration from *Sargassum* (in contrast to the indirect measurement of section 4.5).

Emergence traps are a common tool used to study organisms which live in complex substrata, but leave to forage at certain times (Alldredge and King 1977). The trap consists of an enclosure which funnels to a narrow opening at the top, to which is attached a collection device permitting one-way passage of organisms. The emergence trap used in the current experiment was designed and built by Dr. M. Jones (Great Barrier Reef Marine Park Authority) and is shown in Figure 4.3. Each trap consisted of a perspex tetrahedron, the base covering 0.25 m^2, leading into an inverted funnel and collection vessel. Three traps were deployed between 1630 and 1730 hrs on each of 15, 16, 17 December 1991 and collected the next morning between 0830 and 0930 hrs. One of each set of three traps was placed over bare substratum and the other two over substratum and attached *Sargassum.* In addition nine *Sargassum* plants were sampled on each morning when the traps were collected for comparison with emergence trap samples. Data for each type of sample (*Sargassum* alone, emergence trap over bare substratum and emergence trap over *Sargassum*) from the three nights' collections were pooled for presentation.

4.4.2 Results and Discussion

Abundance of epifauna from emergence traps is given in Figures 4.4 and 4.5. Absolute numbers of individuals collected are shown in Figure 4.4, whilst Figure 4.5 shows epifaunal abundance standardised to 'plant equivalents' (since emergence traps covered more than a single plant, numbers of organisms were divided by 6.6 – the mean number of plants per 0.25 m^2). The most abundant epifauna found in emergence traps were decapods, particularly shrimps, which were found in densities of up to 580 individuals per trap. There were more decapods from traps over *Sargassum* than from traps over bare substratum or from *Sargassum* plants. This indicates that there were decapods present both as epifauna on *Sargassum* and living in the rubble, which is supported by the fact that the numbers of decapods per plant equivalent in the traps over *Sargassum* was almost exactly equal to the sum of the number from *Sargassum* plants alone and traps over bare substratum (Figure 4.5).

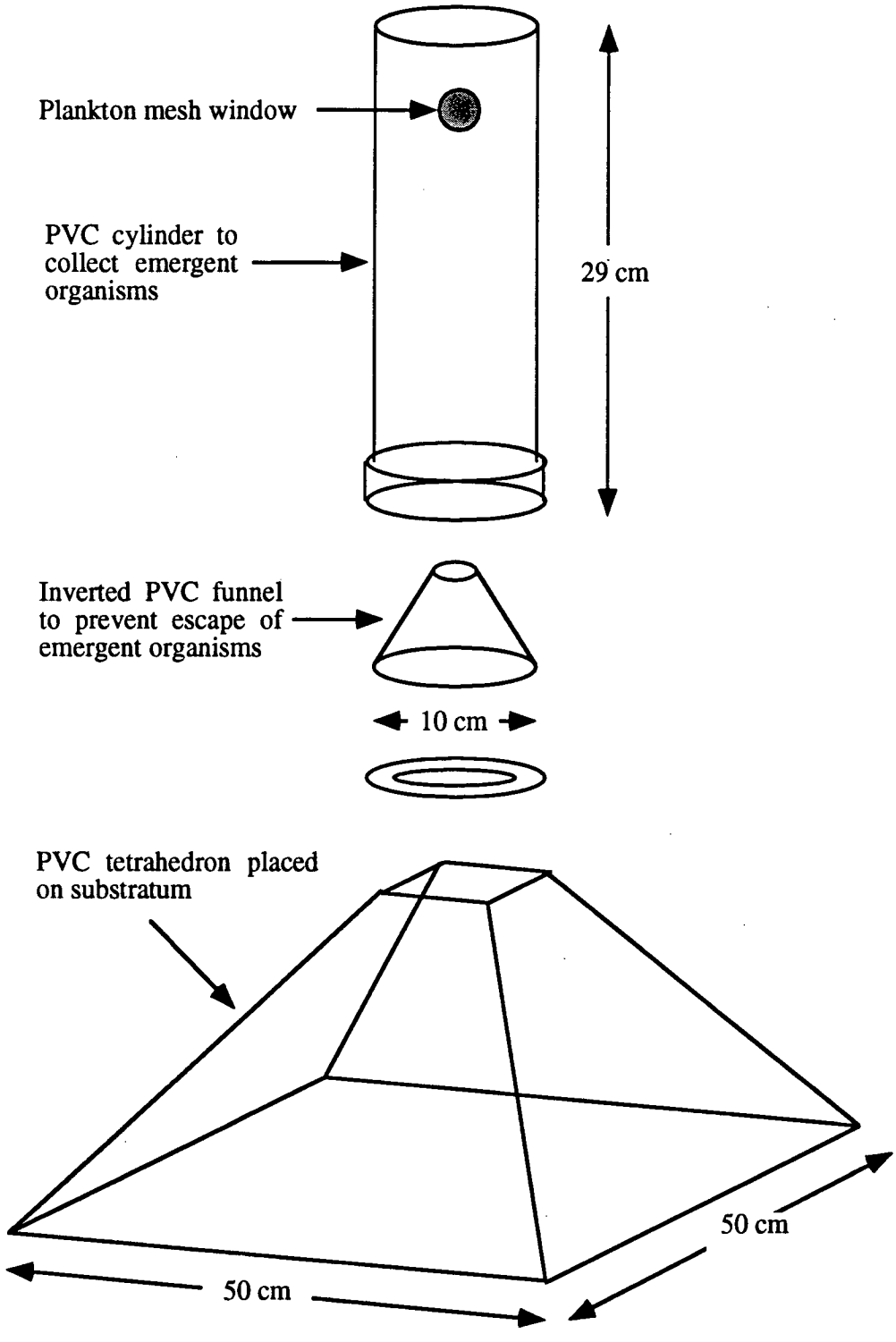


Figure 4.3. Exploded diagram of emergence trap (built by M. Jones, Great Barrier Reef Marine Park Authority).

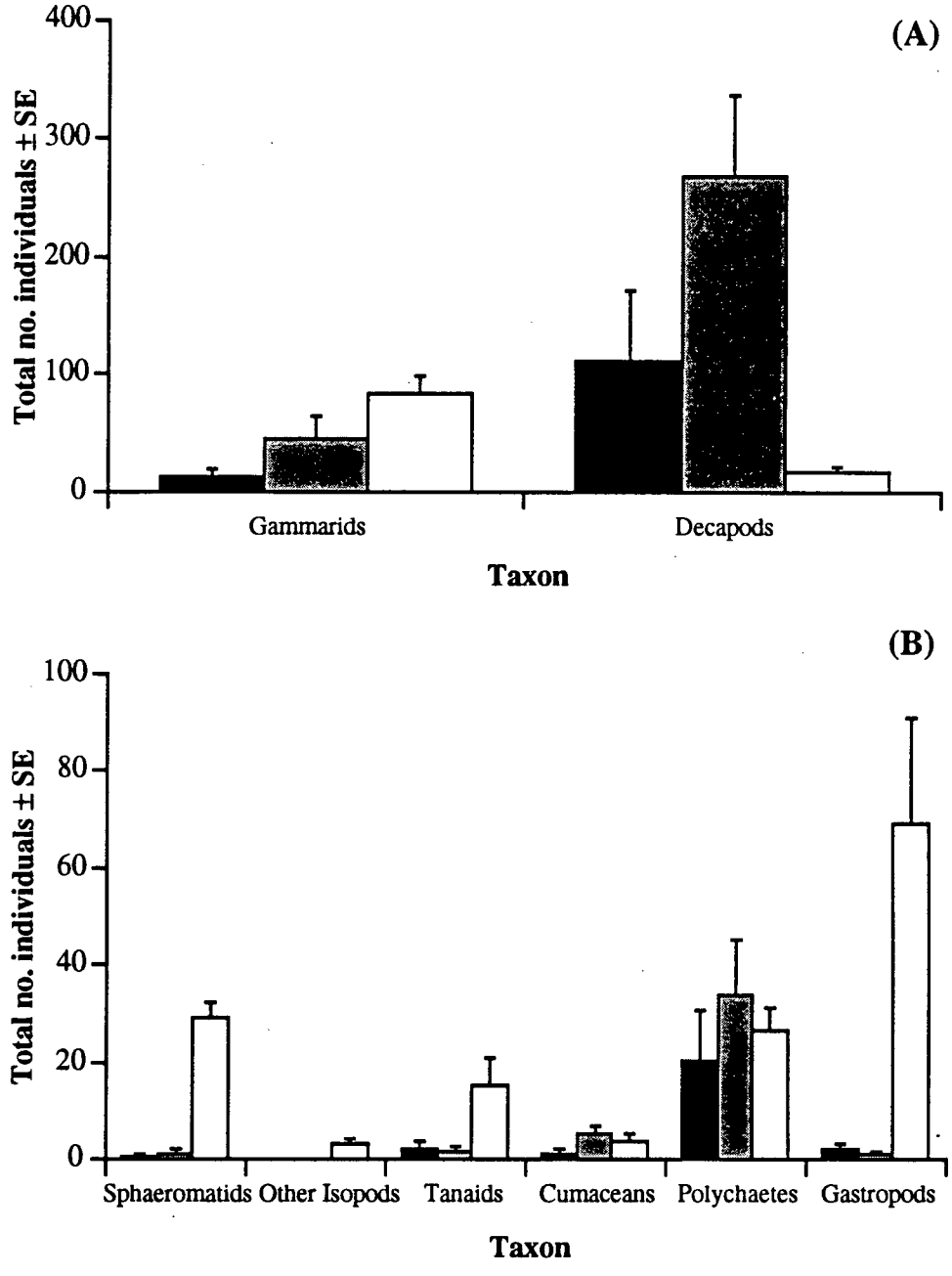


Figure 4.5. Mean abundance of invertebrates from *Sargassum* plants alone (□), emergence traps over bare substratum (■) and emergence traps over *Sargassum* and substratum (▩), raw numbers. Data from nights of 15.12-17.12.91 combined. n=3 for emergence traps alone, n=6 for emergence traps over *Sargassum* and n=9 for *Sargassum* plants.

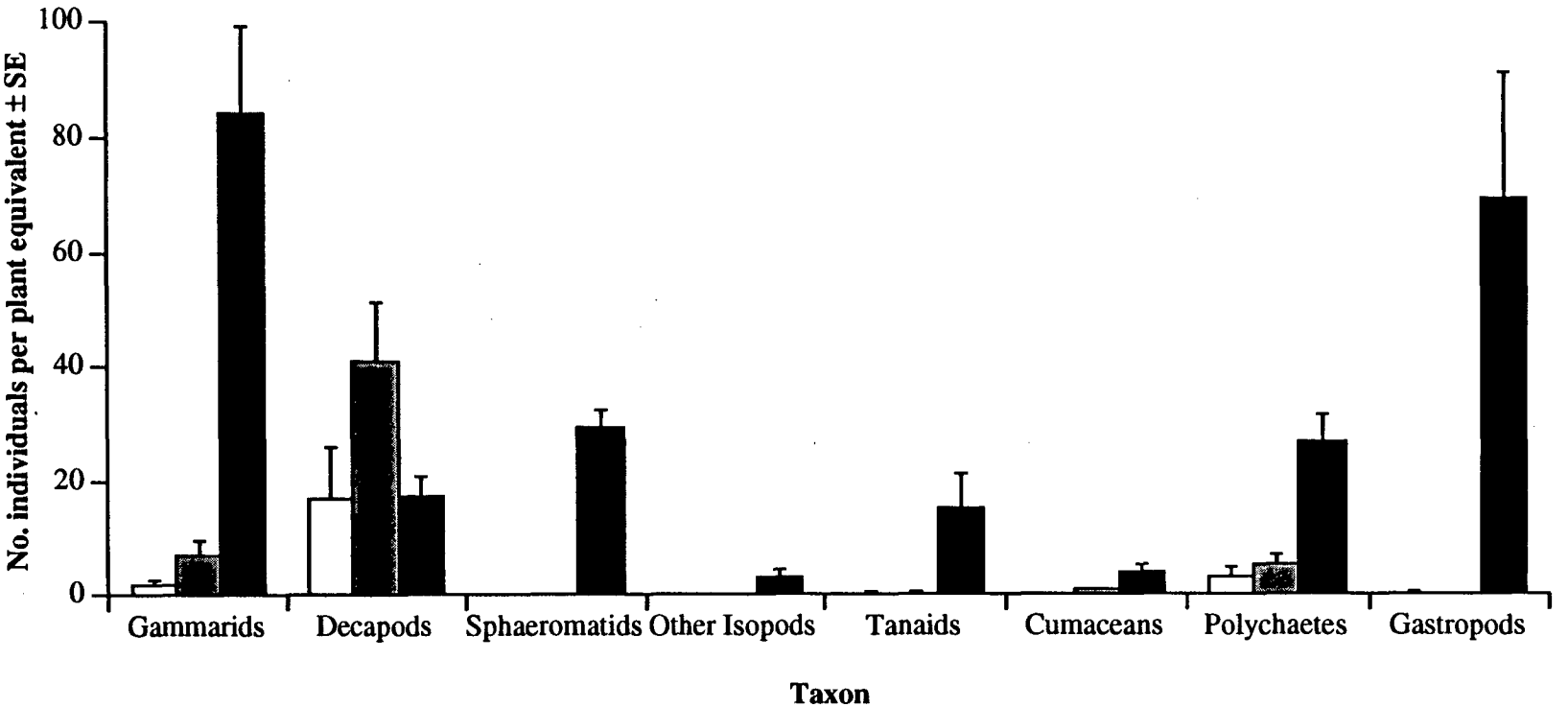


Figure 4.5. Mean abundance of invertebrates from *Sargassum* plants alone (□), emergence traps over bare substratum (■) and emergence traps over *Sargassum* and substratum (▣) standardised to 'plant equivalents'. Data from nights of 15.12-17.12.91 combined. n=3 for emergence traps alone, n=6 for emergence traps over *Sargassum* and n=9 for *Sargassum* plants.

For all taxa, apart from decapods, the proportion of 'epifauna' which was found to inhabit the rubble was very low (Figure 4.5).

The conclusions from this are that the 'epifauna' (i.e. organisms which inhabited the region in and around a *Sargassum* plant) formed a distinct and separate community from the 'cryptofauna' (i.e. the organisms which inhabited the rubble and sediment areas). For most taxa, densities of individuals which emerged (numbers cm^{-2}) in the present work were one or two orders of magnitude smaller than Klumpp *et al.* (1988) found actually living in the substratum, although decapods were an order of magnitude greater. This suggests that decapods were the only components of the cryptofauna which moved from the rubble habitat into the water column which were also found regularly on *Sargassum*. Other studies on the Great Barrier Reef have generally found that harpacticoid and calanoid copepods dominate the emergent fauna and that levels of other crustaceans are low (Alldredge and King 1977, 1980, McWilliam *et al.* 1981, Jacoby and Greenwood 1988). Harpacticoid copepods were found in emergence traps at Magnetic Island in very large numbers but were never abundant on *Sargassum* plants. A further piece of evidence about the nature of the cryptofauna are casual observations which were made whilst searching for adult female sphaeromatid isopods (see Chapter 7). Two large plastic basins were placed in hollows made in the coral rubble on the reef flat, filled with rubble and left for c. 2 months. Almost no gammarids, tanaids or isopods were found when the rubble was agitated and washed through 200 mm plankton mesh. It would appear justifiable to treat the epifauna as a discrete community in the study of the invertebrate fauna of the reef at Magnetic Island rather than as a subset of a wider community.

4.5 DIEL EPIFAUNAL SAMPLING

4.5.1 Introduction and Method

It is known that there can be very significant differences in abundance and composition of faunal communities, especially crustaceans, between day and night (Livingston 1976, Greening and Livingston 1982, Howard 1987). Many invertebrates are known to be more active at night, leaving the substratum to forage or exhibiting increased activity levels (e.g. Reynolds and Casterlin 1979, Kitting 1984). Various scenarios of habitat use by epifauna could be hypothesised:

(1). Decreased epifaunal abundance at night, due to epifauna leaving the plant to forage elsewhere.

(2). Increased epifaunal abundance at night, due to infauna from the substratum emerging to forage on the *Sargassum* .

(3). No diel differences in epifaunal abundance, from a combination of the above or because of no diel preferences.

The aim of this work was thus to quantify the diel variation in epifaunal abundance, which would allow assumptions about the generality of monthly sampling and experimental manipulations (involving only diurnal sampling) to be made.

Samples were collected in Geoffrey Bay on 18/19 March 1991. Nine plants and associated epifauna were collected as described in section 3.3.1 at the following times: 1500 hrs 18.3, 2100 hrs 18.3, 0300 hrs 19.3 and 0900 hrs 19.3. Sunrise on 19.3 was approximately 0530. Abundance data were log (x+1) transformed and analysed by 1-way MANOVA with fixed factor TIME followed by *a posteriori* SNK tests on raw abundance data for each taxon.

4.5.2 Results and Discussion

Comparison between sampling times, using MANOVA, revealed no significant effect of time of day on the community composition (Pillai's Trace, p=0.175). Abundance of individual taxa varied with time of day (Figure 4.6) but unpredictably so in most cases. There were no significant differences in abundance of gammarids, sphaeromatids, polychaetes and gastropods at different times of day (Table 4.II). Cumaceans and decapods both had significant greater abundance at night than during the day, greatest abundance occurring at 0300 hrs and lowest abundance at 0900 hrs (Table 4.II).

Taxon	Significance of Sampling Time	Abundance of epifauna 100 g^{-1} in decreasing order of magnitude (bars connect time points which are not significantly different)
Gammarids	NS	0300 1500 2100 0900
Sphaeromatids	NS	0300 1500 0900 2100
Cumaceans	$p < 0.002$	0300 > 2100 > 1500 > 0900
Decapods	$p < 0.001$	0300 > 2100 > 1500 0900
Polychaetes	NS	0300 1500 2100 0900
Gastropods	NS	0300 2100 1500 0900

Table 4.II. Results of *a posteriori* SNK tests on abundance data in diel sampling.

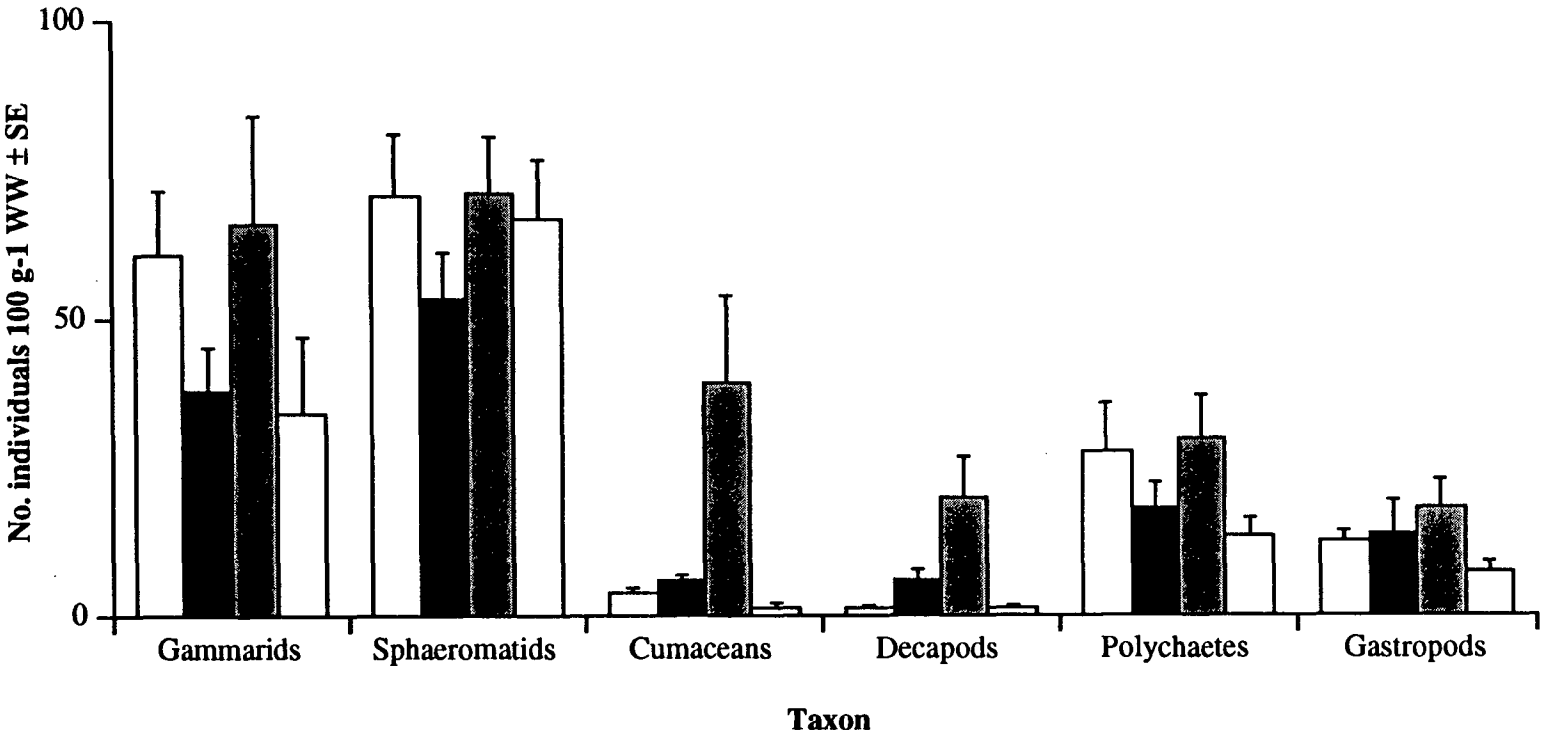


Figure 4.6. Mean abundance of epifauna at 1500 (□), 2100 (■), 0300 (▩) and 0900 (□) hrs on 18.3-19.3.91. n=9 for all samples.

Therefore, although there were diel changes in the abundance of organisms on *Sargassum*, these changes were small in comparison with sample variability, hence the non-significant MANOVA result. The taxa which showed significant diel changes were decapods and cumaceans. The change in the abundance of decapods with time of day is not surprising – many previous studies have shown the same result. For example Livingston (1976) found significant increases in trawled decapods at night, as did Greening and Livingston (1982) with seagrass-associated decapods in Florida. Increase in cumacean abundance at night was even more pronounced but there appears to be no literature documenting this.

It is proposed that most of the epifauna inhabiting *Sargassum* do not undergo diel migrations from the plant. If diel changes did occur then they involved behavioural shifts rather than immigration or emigration. Feeding and foraging behaviour are likely to increase during the night (Kitting 1984) but epifauna continued to be associated with the plant. Although epifauna can be captured in large numbers at night over macroalgal beds (Fincham 1974) such collections can result from the movement of only a small proportion of the epifauna from each plant. Edgar (1983d) found that populations of amphipods on *Sargassum verruculosum* did not change predictably over a 24 hour sampling period although populations on *Zonaria* decreased at night. Montouchet (1979) found increased abundance of epifauna on *S. cymosum* at night due to immigration by benthic species, a similar situation to that postulated for cumaceans and decapods at Magnetic Island.

4.6 RECOLONISATION EXPERIMENTS

4.6.1 Introduction

Much of the rationale for performing these experiments was given in section 4.1. To recapitulate, recolonisation experiments provide a means of measuring both the short-term temporal dynamics of populations of epifauna (through comparisons of control populations through time) and the short-term spatial dynamics (through comparisons between control and experimental populations through time). Colonisation or recolonisation experiments have been carried out on a number of different time scales in marine systems, ranging from approximately 12 hours (Edgar 1983d) through to 11 months (Schoener 1974). Most of the experiments which have been performed on epifauna have used time scales in the order of hours to days (e.g. Gunnill 1982b, Stoner 1985, Virnstein and Curran 1986, Schneider and Mann 1991b), which seemed appropriate for the present study.

Although distinctive seasonal patterns were observed in the present system, the extent of day-to-day and week-to-week variability was not known, making the predictability of such results uncertain. Thus, it was necessary to quantify shorter-term variations in abundance and composition of epifauna. Additionally, manipulative experiments were planned (Chapters 6 and 7) and it was necessary to know what temporal scale such experiments should be carried out on, in order to maximise the detection of significant results.

4.6.2 Methods

Methods which have been used to study short-term spatial dynamics of epifauna include the defaunation of plants in fresh water (e.g. Gunnill 1982b) or some other narcotising agent such as $MgCl_2$ solution (e.g. Omori and Fleminger 1976) or staining of epifauna with dye and subsequent recapture (e.g. Howard 1985). However, the results of the study by Howard (1985) suggested that this latter method was only of use on short time scales of up to about 24 hours. It was decided to defaunate plants using fresh water to narcotise the epifauna. Two experiments were performed to investigate spatial dynamics of epifauna on different, short-term time scales, but the defaunation methodology was the same for both: individual *Sargassum* plants were removed haphazardly from the substratum and placed in buckets of sea water on board the research vessel. Plants were transferred to a bucket of fresh water and left for 5 minutes, then transferred to a second bucket of fresh water for 5 minutes before being returned to buckets of seawater pending reattachment to the substratum. Six plants were placed in plastic bags for examination in the laboratory to test the efficacy of the defaunation method. For replacement on the substratum, plants were tied, close to their holdfasts, on to 40x25x15 cm plastic mesh baskets using plastic-coated wire. Six plants were attached to each basket, which was then placed in the area from where the plants had initially been taken. The basket was secured by hammering a 100 cm piece of steel reinforcing rod through the handle at either end and by placing pieces of coral rubble inside the basket. For each time point in an experiment plants were selected using random number tables and collected as per the method in section 3.3.1. Unmanipulated control plants were taken haphazardly from the same area at the same time. The experimental design for both experiments is given in Table 4.III. The abundance of five taxa (gammarids, sphaeromatids, decapods, polychaetes and gastropods) were enumerated in experiment 1 while the abundance of ten taxa (gammarid and caprellid amphipods, sphaeromatid and other isopods, tanaids, cumaceans, decapods, polychaetes, gastropods and anemones) were enumerated in experiment 2.

EXPERIMENT 1 (SHORT TERM): 14.3.91-20.3.91		
Treatment	Defaunated (Experimental)	Control
No. Plants	3	3
Times Sampled	0, 6, 12, 24, 48 hours 4, 6 days	0, 6, 12, 24, 48 hours 4, 6 days
EXPERIMENT 2 (MEDIUM TERM): 17.2.92-16.3.92		
Treatment	Defaunated (Experimental)	Control
No. Plants	9	9
Times Sampled	0, 1, 2, 14, 21, 28 days	0, 1, 2, 14, 21, 28 days

Table 4.III. Experimental design for recolonisation experiments.

Both univariate and multivariate analyses were performed on abundance data from recolonisation experiments. The multivariate abundance data from both experiments were log (x+1) transformed to homogenise their variances (Hurlbert and White 1993) and were subsequently analysed using a 2-way MANOVA with fixed factors TREATMENT (control or defaunated) and TIME (time since start of experiment). To examine the patterns at the entire community level a Canonical Discriminant Analysis (CDA) was performed on the data set for each experiment. This procedure allows multivariate data to be visualised in a reduced set of dimensions determined by the perpendicular axes of best fit through the group centroids, standardised to the within-group variances. Univariate plots of untransformed data were used to show the recolonisation patterns of individual taxa and the data for particular time points were tested, where appropriate, with *post-hoc* Bonferroni-Dunn tests with reduced significance levels.

4.6.3 Results

The MANOVA for the experiment 1 showed significant effects of TIME, TREATMENT and the interaction between them (Pillai's Trace $p<0.001$). Thus CDA was used to try and visualise the processes involved at the community level. Plots of the first three canonical axes (representing 74.5, 10.2 and 9.2% of total sample variation) showed clear separation between control and defaunated treatments (Figure 4.7). The greatest variation was shown along canonical axis 1, wherein large

positive values represented high abundance of gammarids, isopods, polychaetes and gastropods (shown by the bi-plots in Figure 4.7 and the bubble plots of Figures 4.8 and 4.9). Little separation was evident between communities along canonical axes 2 and 3. Control communities were very similar to each other over the 6 day course of the experiment, the CDA means for each time point clustering closely together, while the defaunated communities showed a directional shift over the course of the experiment along canonical axis 1 as abundance of all taxa increased (Figures 4.7-4.9).

MANOVA of the data from experiment 2 also showed significant effects of TIME, TREATMENT and their interaction (Pillai's Trace, $p<0.001$) so again CDA was used. CDA plots of the first three canonical variables (representing 51.3, 16.9 and 13.4% of total sample variation) showed separation between control and defaunated treatments initially (from 0-2 days). However, over the longer time scale of this 2nd experiment, these differences became smaller and control and defaunated communities were similar at 14, 21 and 28 days (Figure 4.10). The comparison of the two treatments was complicated by the directional movement exhibited by the control communities over the four weeks of the experiment. Control communities for 0, 1 and 2 days were clustered together but changes in abundance of various taxa led to separation between the 14, 21 and 28 day communities (Figure 4.10 and bubble plots of Figures 4.11 and 4.12). My interpretation of the CDA for the 2nd experiment is that there was increasing similarity between control and defaunated communities, overlaid on top of a common, 'seasonal' community change which occurred for both treatments.

Within the multivariate community response there were two distinct univariate patterns (Figures 4.13-4.20). The first type of recolonisation pattern ('Type I') was a steadily increasing abundance from the time of defaunation until control levels were attained – 'asymptotic approach'. This was shown by gammarids (Figure 4.13) and polychaetes (Figure 4.14) in both experiments and by other isopods (Figure 4.18B), tanaids (Figure 4.19A), cumaceans (Figure 4.19B) and anemones (Figure 4.20) in the medium-term experiment. The second type of pattern ('Type II') involved rapid colonisation initially, with abundance increasing to significantly higher levels than the controls followed by a subsequent decline below controls and recovery to control abundance – 'overshoot'. This response was shown by sphaeromatid isopods (Figure 4.15) in both experiments and by decapods (Figure 4.16B) and caprellids (Figure 4.18A) in the 2nd experiment. There was some evidence of overshoot in decapod abundance in the short-term experiment (Figure 4.16A) but there was very high variability in abundance. To test the significance of the overshoot phenomenon, abundance at these time points were tested with a *post hoc* Bonferroni-Dunn test with

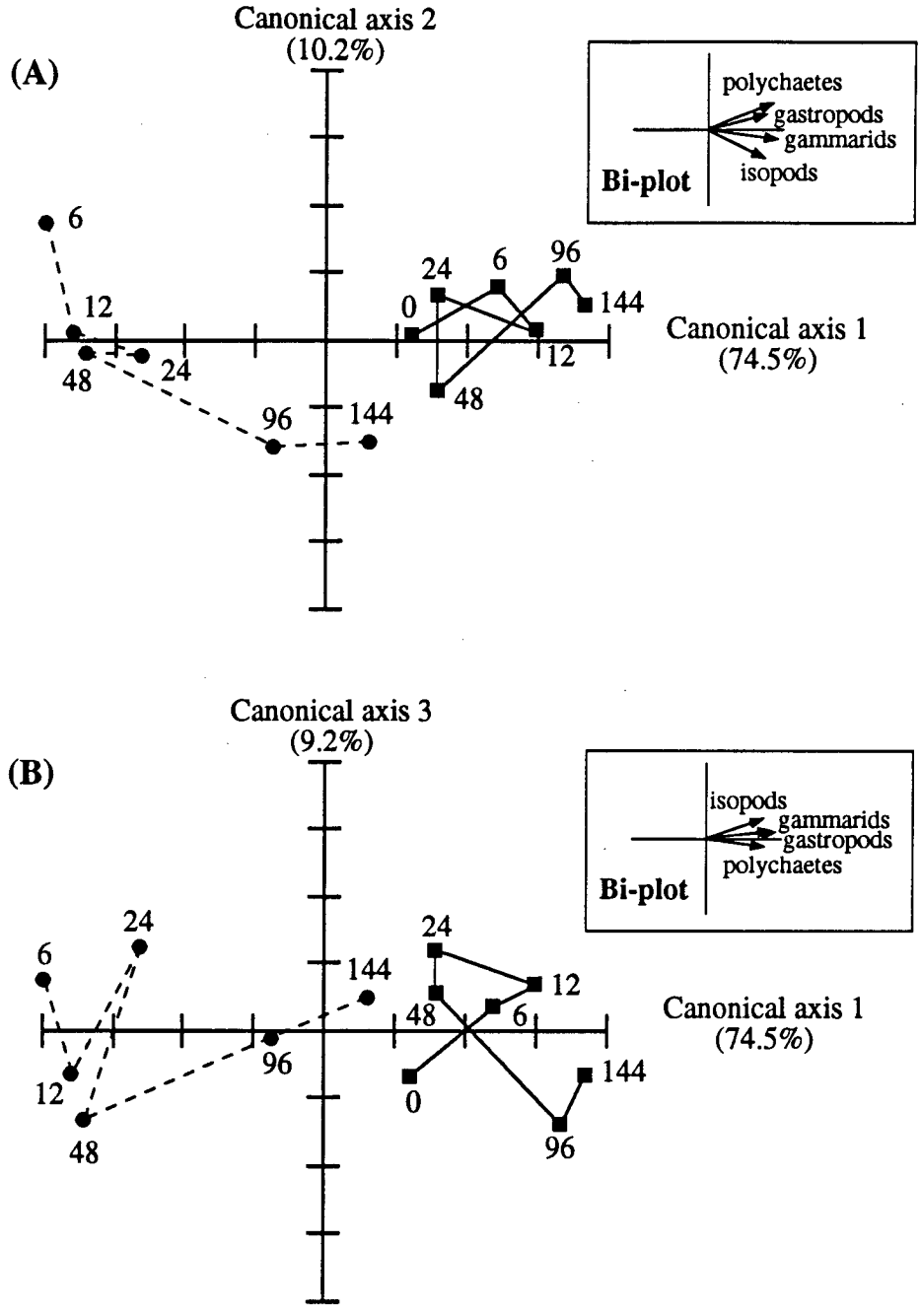


Figure 4.7. Canonical Discriminant Analysis for epifaunal communities in recolonisation experiment 1 (0-6 days). (A) Can 1 vs Can 2 (B) Can 1 vs Can 3. Bi-plots show taxa influencing distribution of points. Each point represents mean (n=3) for each time point (given in hours). Control (■) and defaunated plants (●).

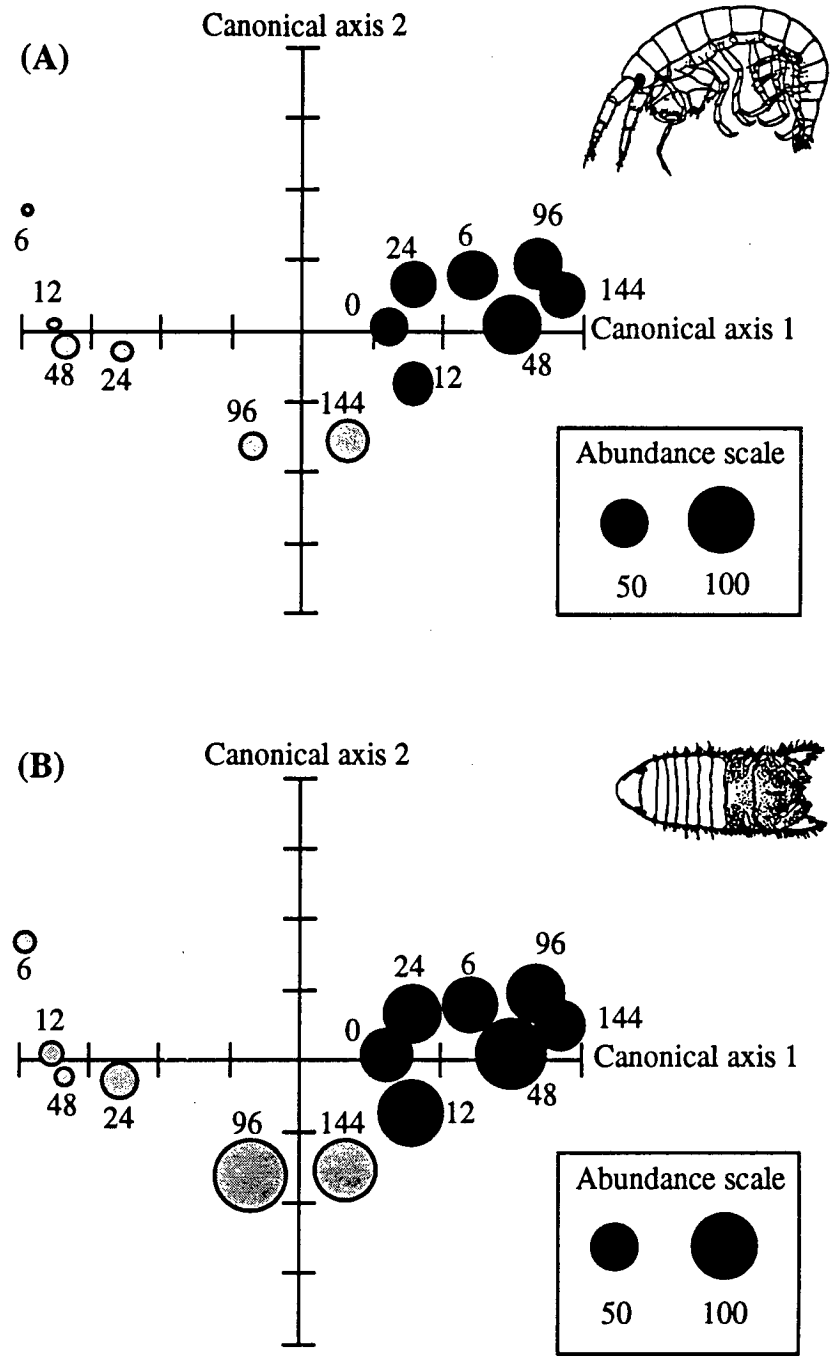


Figure 4.8. Abundance of (A) gammarids and (B) sphaeromatids in recolonisation experiment 1, superimposed on CDA plot from Figure 4.7. Size of bubbles is proportional to abundance and number indicates time in hours from start of experiment. Control (●) and defaunated (◎) plants with time . n=3 for each point.

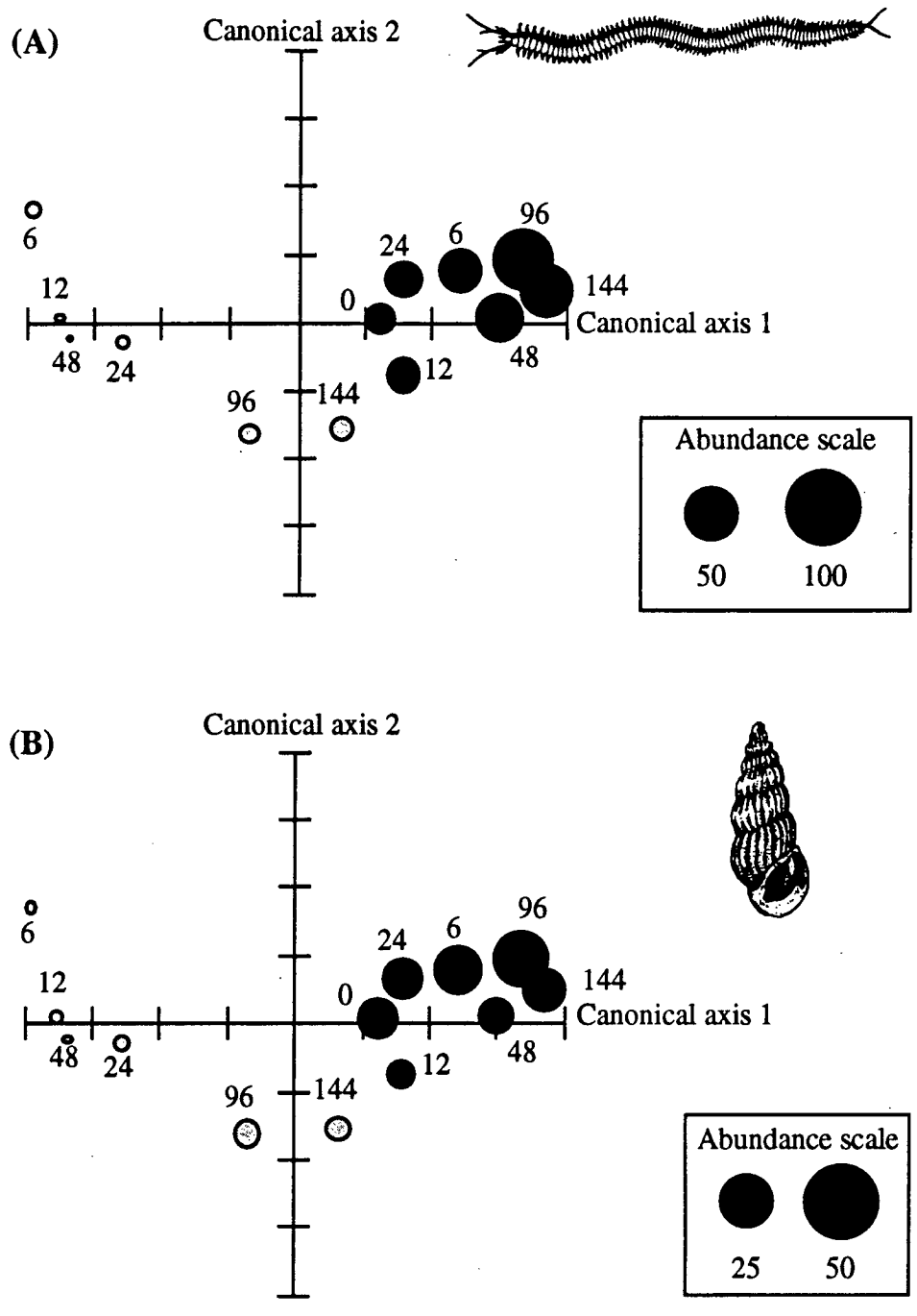


Figure 4.9. Abundance of (A) polychaetes and (B) gastropods in recolonisation experiment 1, superimposed on CDA plot from Figure 4.7. Size of bubbles is proportional to abundance and number indicates time in hours from start of experiment. Control (●) and defaunated (◉) plants with time . n=3 for each point.

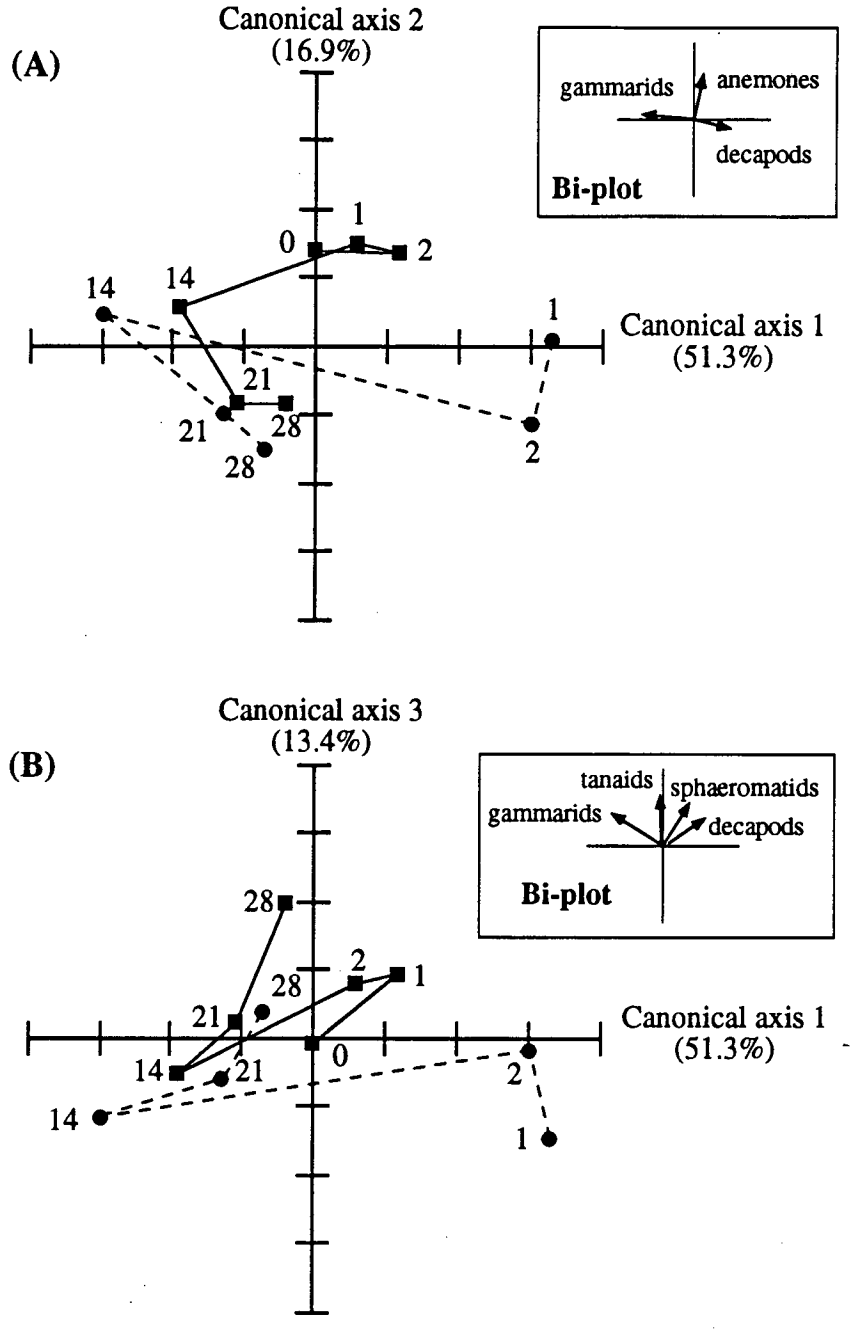


Figure 4.10. Canonical Discriminant Analysis for epifaunal communities in recolonisation experiment 2 (0-28 days). (A) Can 1 vs Can 2 (B) Can 1 vs Can 3. Bi-plots show taxa influencing distribution of points. Each point represents mean (n=9) for each time point (given in days). Control (■) and defaunated plants (●)

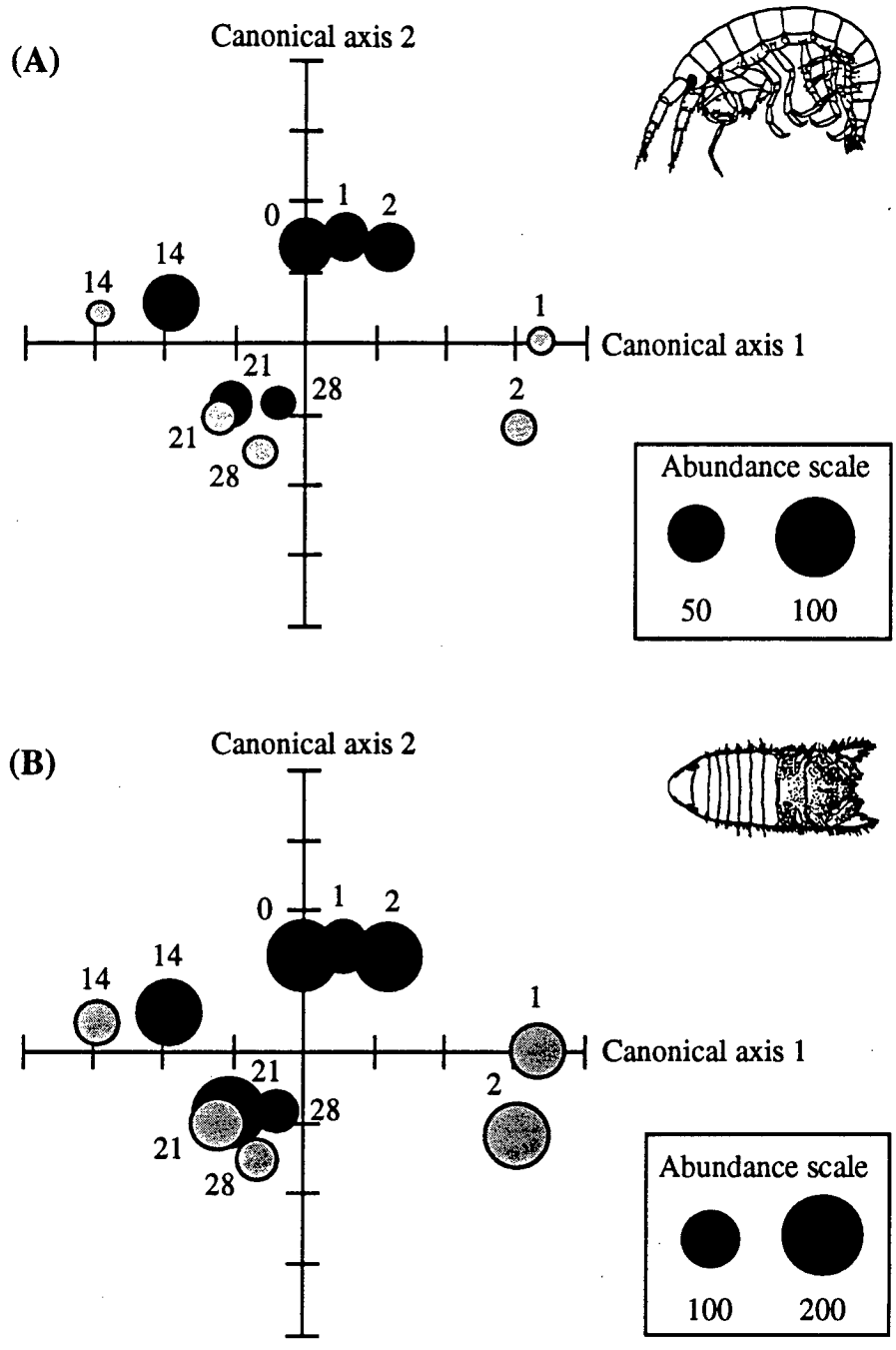


Figure 4.11. Abundance of (A) gammarids and (B) sphaeromatids in recolonisation experiment 2, superimposed on CDA plot from Figure 4.10. Size of bubbles is proportional to abundance and number indicates time in days from start of experiment. Control (●) and defaunated (◉) plants with time . n=9 for each point.

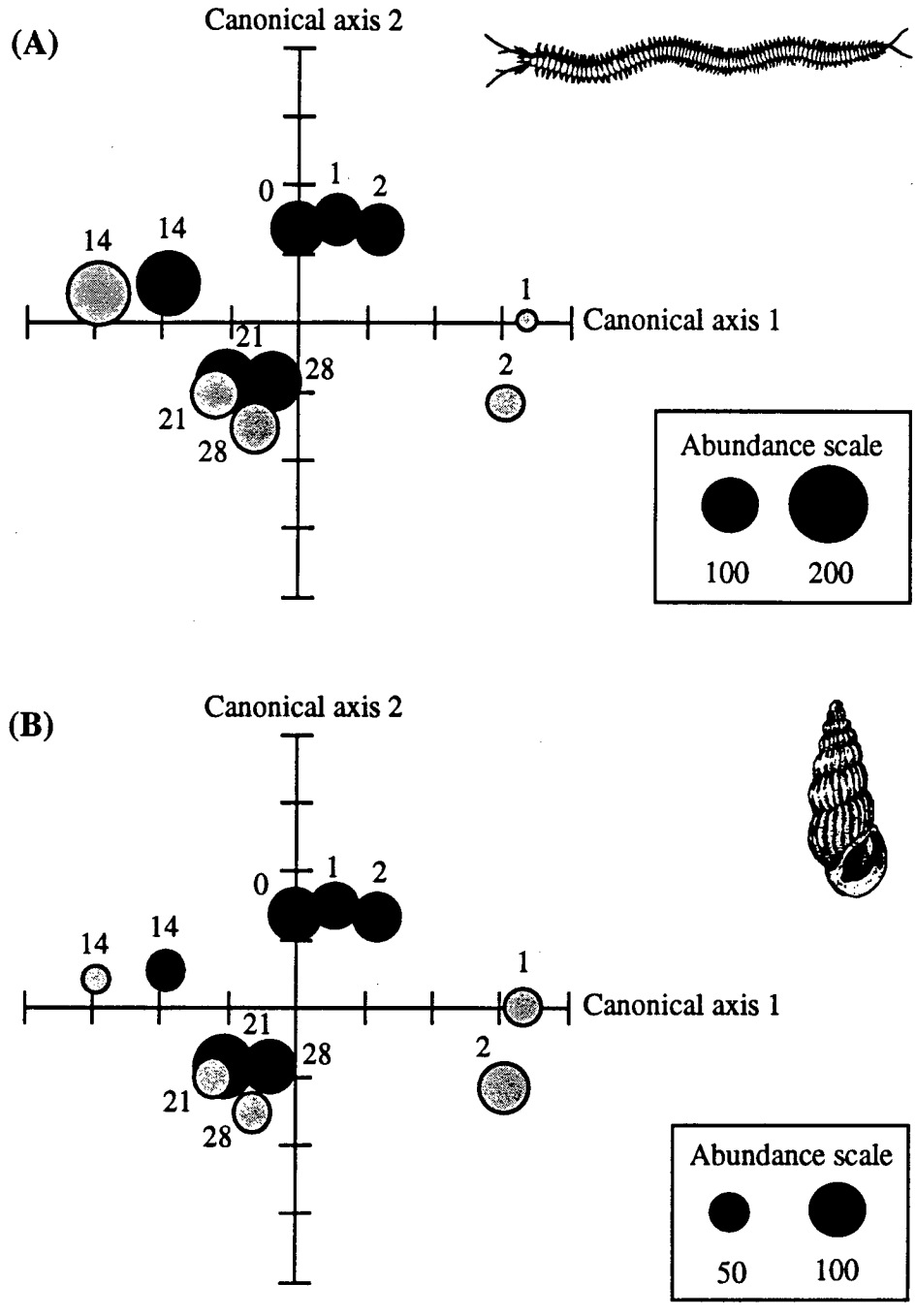


Figure 4.12. Abundance of (A) polychaetes and (B) gastropods in recolonisation experiment 2, superimposed on CDA plot from Figure 4.10. Size of bubbles is proportional to abundance and number indicates time in days from start of experiment. Control (●) and defaunated (◎) plants with time . n=9 for each point.

a reduced level of significance to account for the number of sampling points. These tests showed that the overshoot of caprellids and decapods in the 2nd experiment were significant, but that of the sphaeromatid isopods in the 1st experiment was not, perhaps due to the low sample size and reduced significance level ($p<0.007$ demanded by the Bonferroni-Dunn test). Finally gastropod abundance showed what appeared to be a type I pattern in the short-term experiment and a rather variable pattern in the medium-term experiment and so the overall pattern was uncertain. A summary of these recolonisation patterns in given Table 4.IV.

Taxon	Type of recolonisation	Type II significance?
Gammarids	Type I	n/a
Caprellids	Type II	+
Sphaeromatids	Type II	–
Other Isopods	Type I	n/a
Tanaids	Type I	n/a
Cumaceans	Type I	n/a
Decapods	Type II	+
Polychaetes	Type I	n/a
Gastropods	uncertain	n/a
Anemones	Type I	n/a

Type I pattern: increased abundance with time, control abundance approached asymptotically.
Type II pattern: rapid increased abundance, experimental abundance overshot control levels, declined, then stabilised at control levels.

Table 4.IV. Summary of recolonisation patterns of epifaunal taxa.

4.6.4 Discussion

Recolonisation of epifauna on to defaunated *Sargassum* plants occurred very rapidly (Figures 4.13-4.20), with some individuals of all taxa found within 6 hours of defaunation. This indicates that populations of epifauna were very dynamic and immigration and emigration rates from individual plants were high. This concords with previous studies such as those of Howard (1985) who found high rates of turnover within populations of seagrass epifauna or Stoner (1985) who found rapid rates of recolonisation by macroalgal epifauna. It appears that the taxa of epifauna recolonised in two ways – the asymptotic Type I pattern and the overshoot Type II pattern (Table 4.IV). Sphaeromatid isopods, caprellids amphipods and decapods

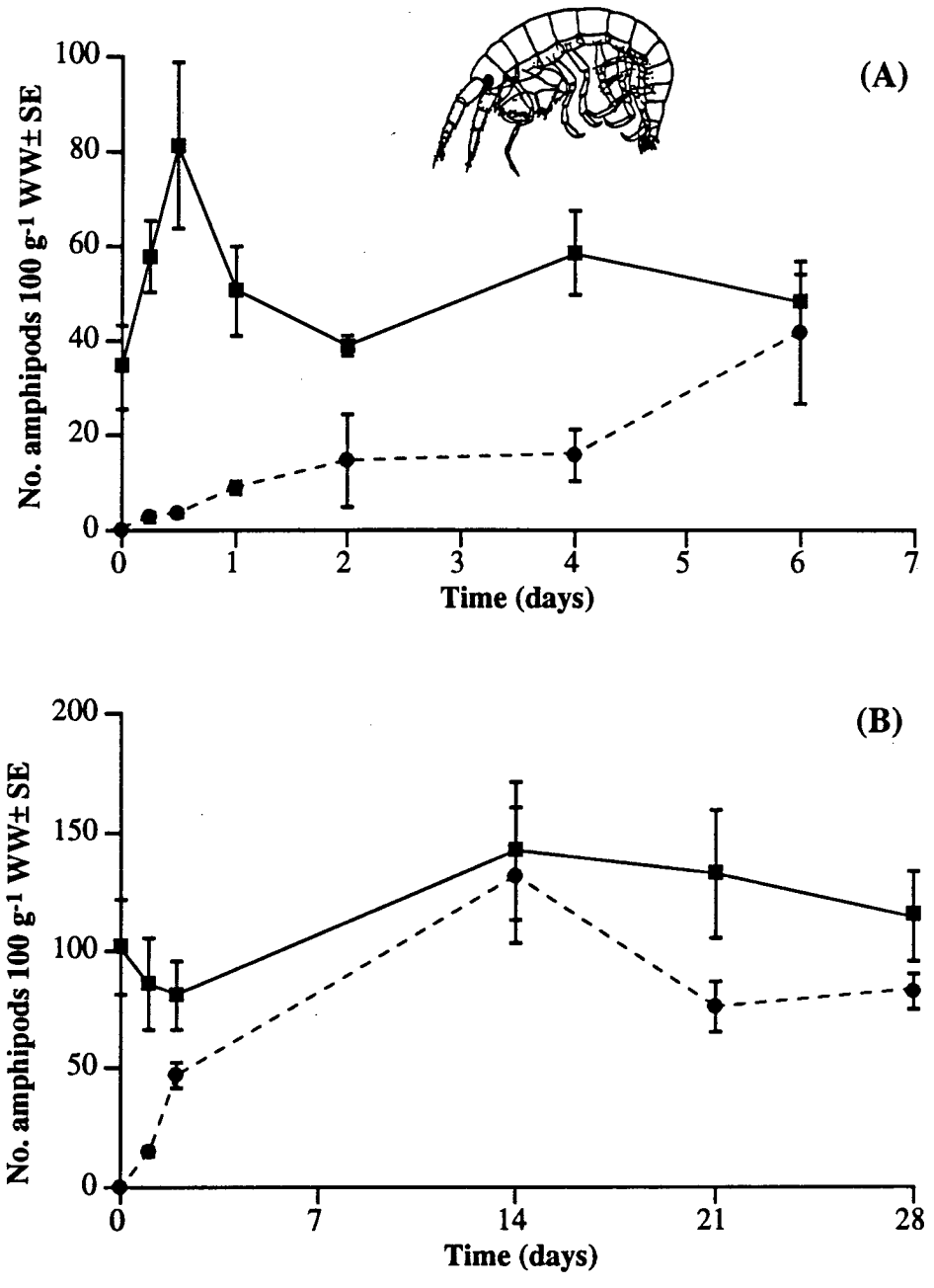


Figure 4.13. Mean abundance of gammarids in recolonisation experiments. (A) Experiment 1 (0-6 days) n=3 plants per time point (B) Experiment 2 (0-28 days) n=9 plants per time point. Controls (■) and defaunated plants (●).

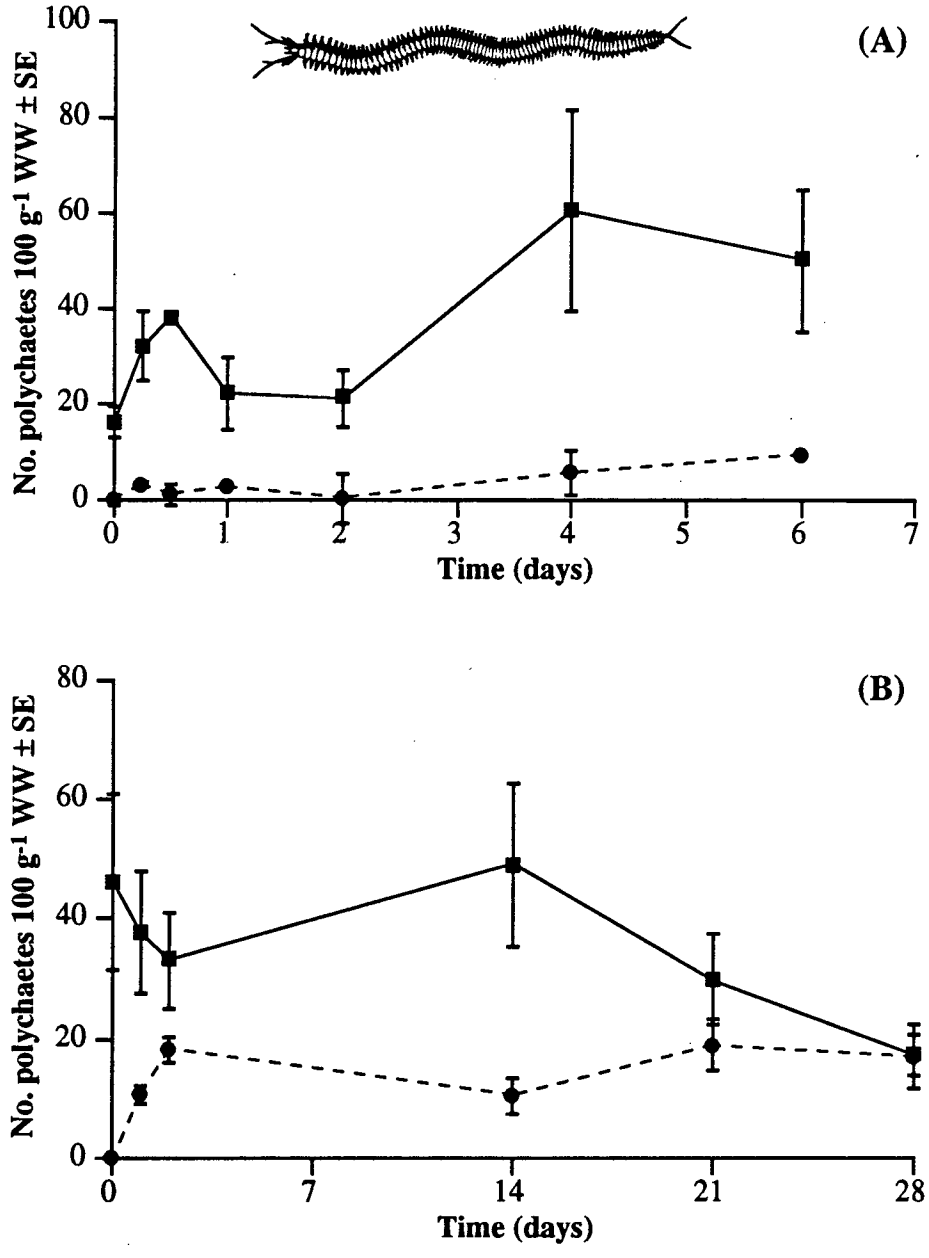


Figure 4.14. Mean abundance of polchaetes in recolonisation experiments. (A) Experiment 1 (0-6 days) n=3 plants per time point (B) Experiment 2 (0-28 days) n=9 plants per time point. Controls (■) and defaunated plants (●).

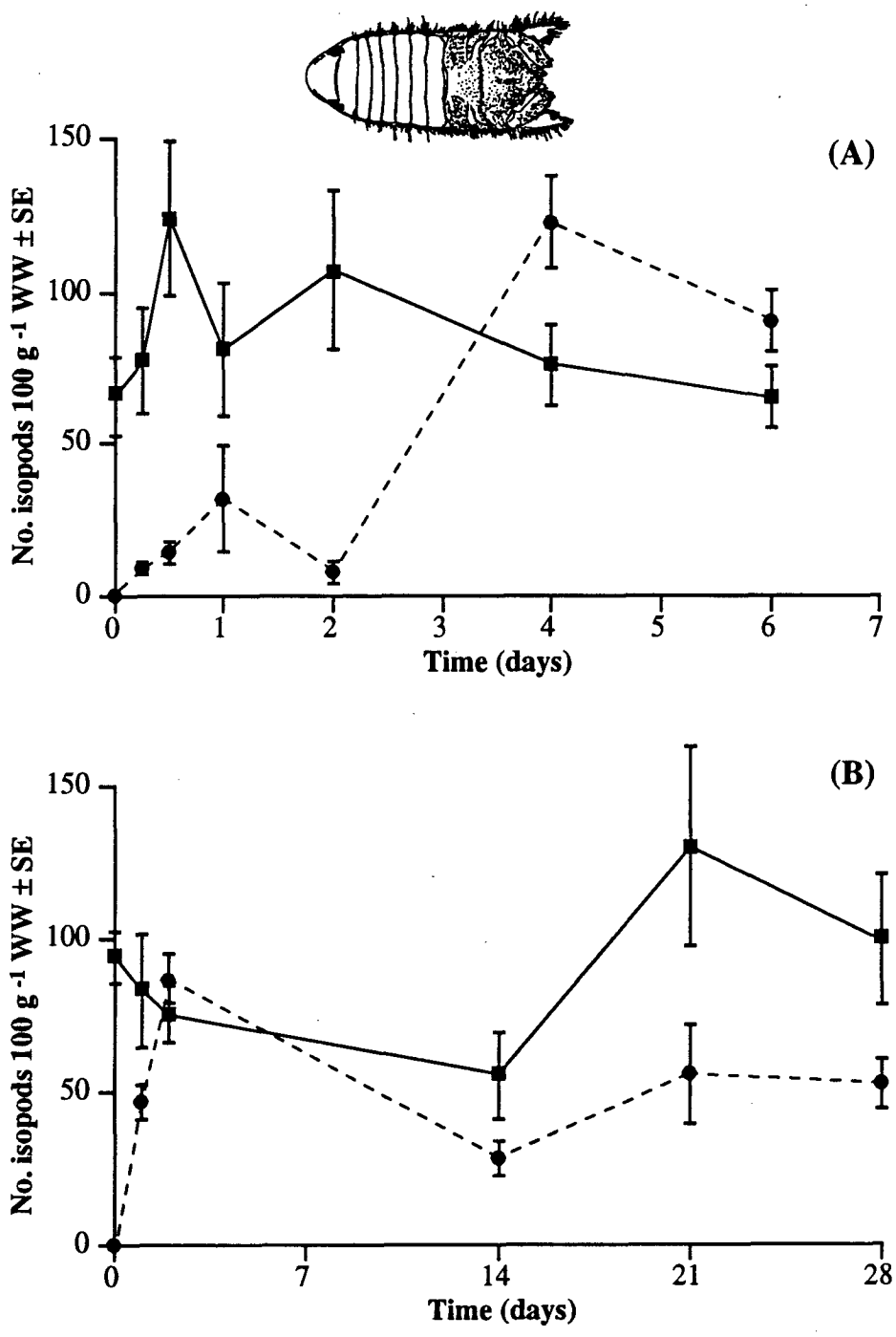


Figure 4.15. Mean abundance of sphaeromatids in recolonisation experiments. (A) Experiment 1 (0-6 days) n=3 plants per time point (B) Experiment 2 (0-28 days) n=9 plants per time point. Controls (■) and defaunated plants (●).

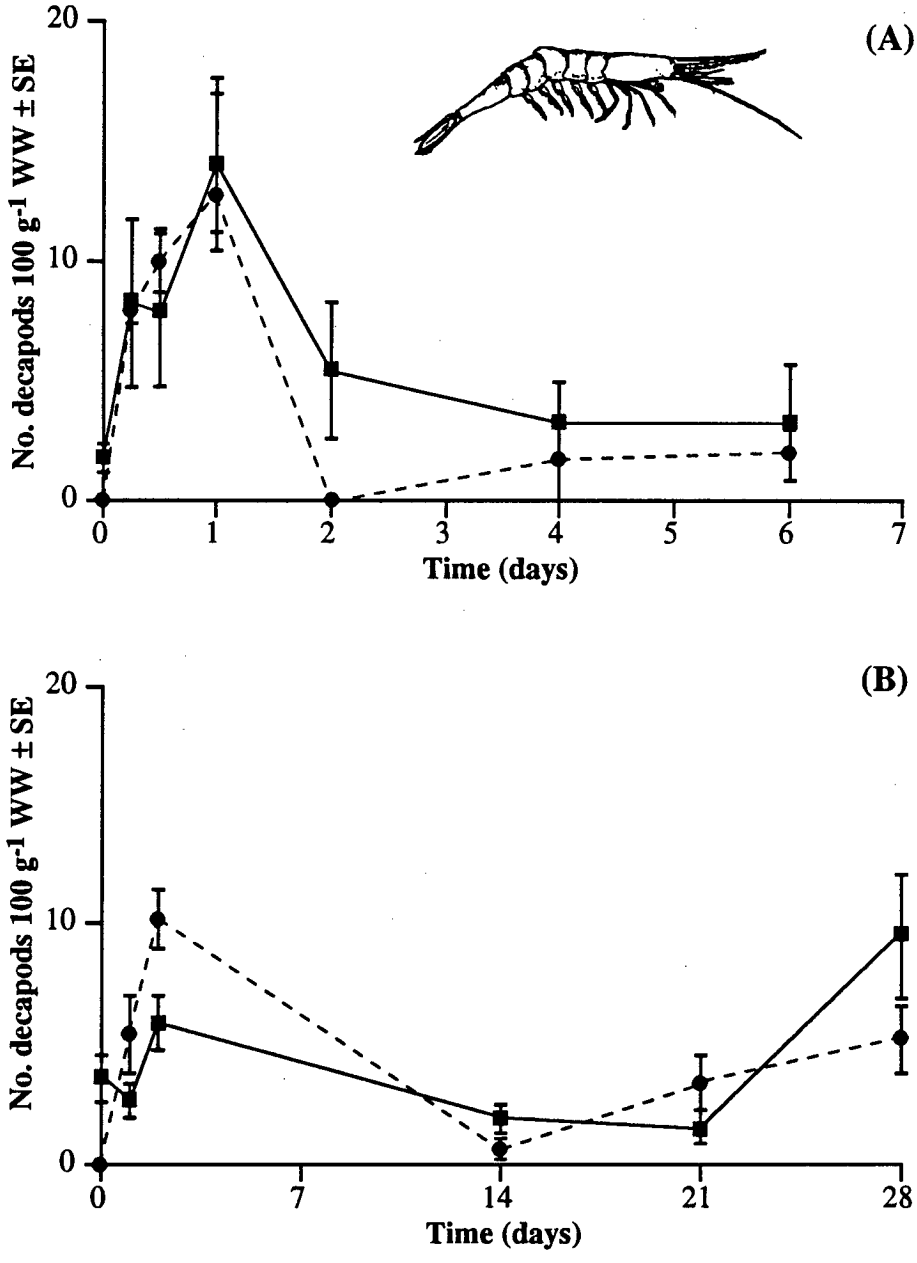


Figure 4.16. Mean abundance of decapods in recolonisation experiments. (A) Experiment 1 (0-6 days) n=3 plants per time point (B) Experiment 2 (0-28 days) n=9 plants per time point. Controls (■) and defaunated plants (●).

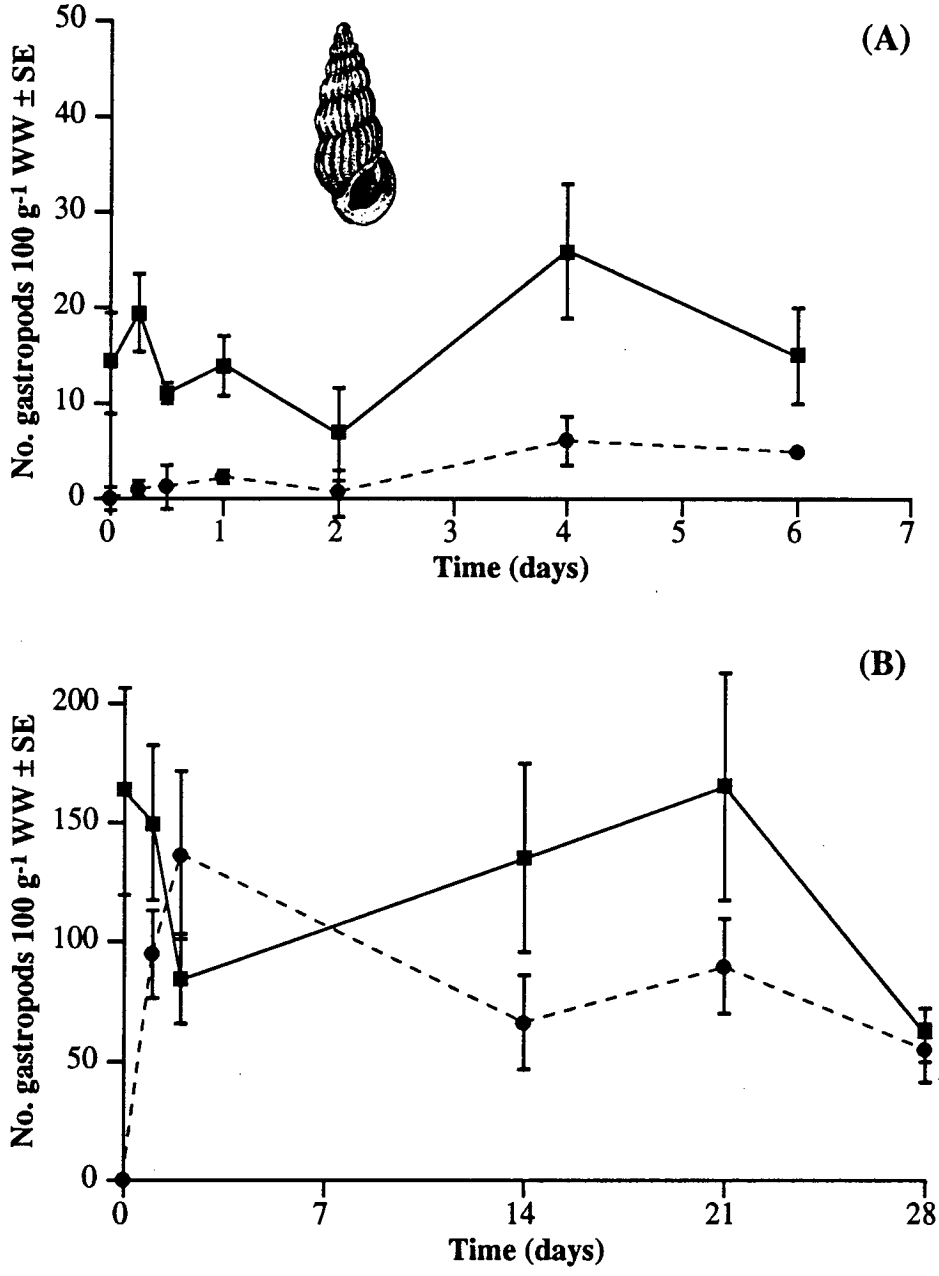


Figure 4.17. Mean abundance of gastropods in recolonisation experiments. (A) Experiment 1 (0-6 days) n=3 plants per time point (B) Experiment 2 (0-28 days) n=9 plants per time point. Controls (■) and defaunated plants (●).

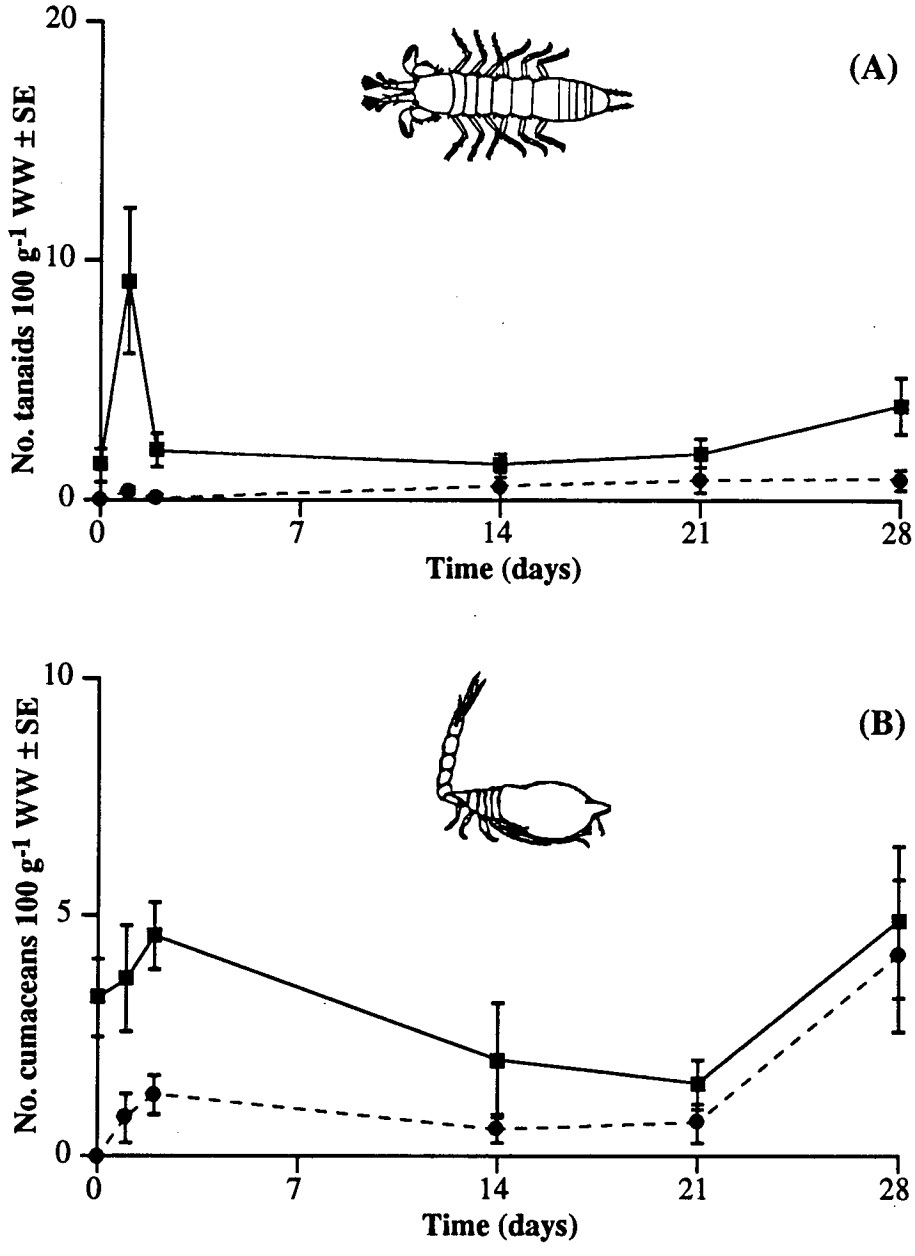


Figure 4.18. Mean abundance of (A) tanaids (B) cuamceans in recolonisation experiment 2 (0-28 days). n=9 plants per time point. Controls (■) and defaunated plants (●).

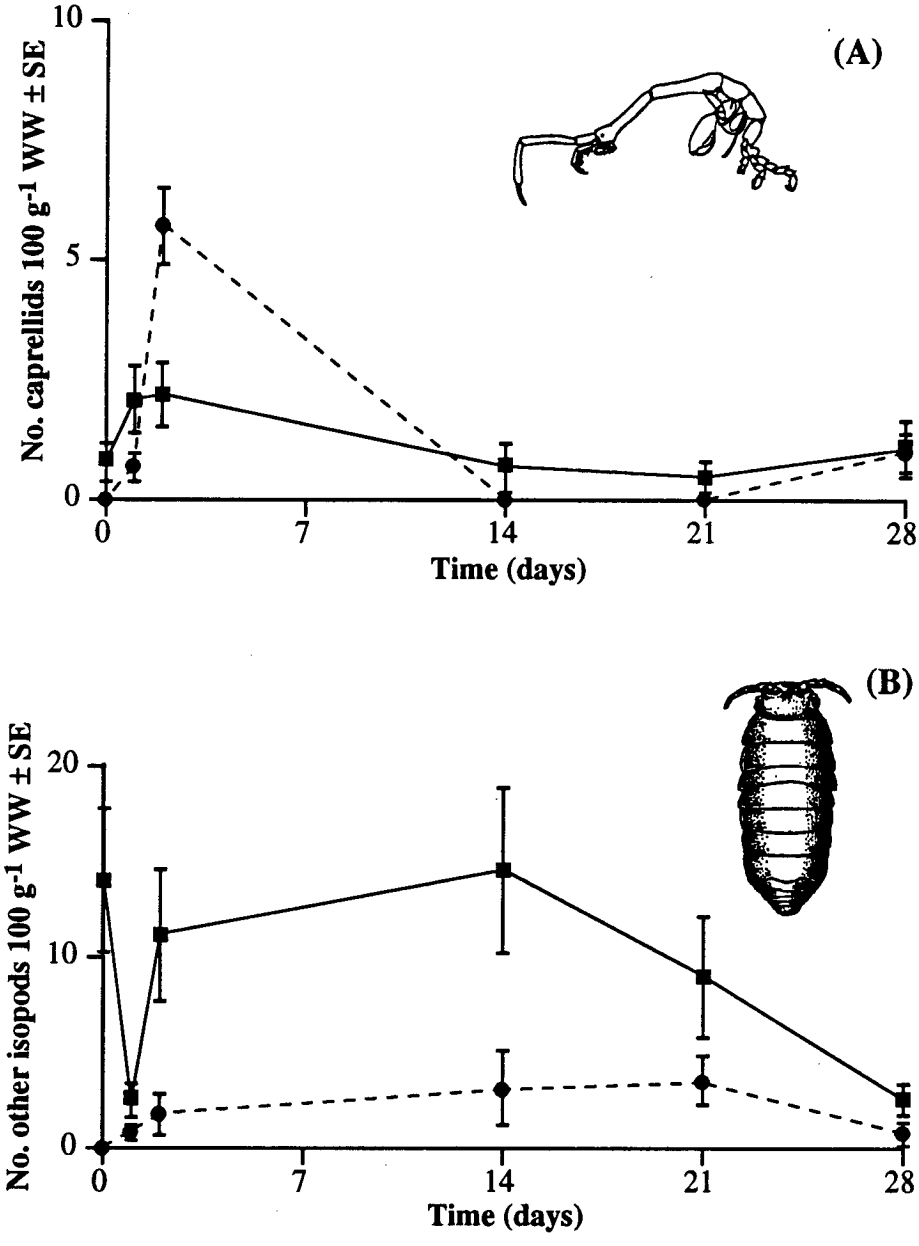


Figure 4.18. Mean abundance of (A) caprellids (B) other isopods in recolonisation experiment 2 (0-28 days). n=9 plants per time point. Controls (■) and defaunated plants (●).

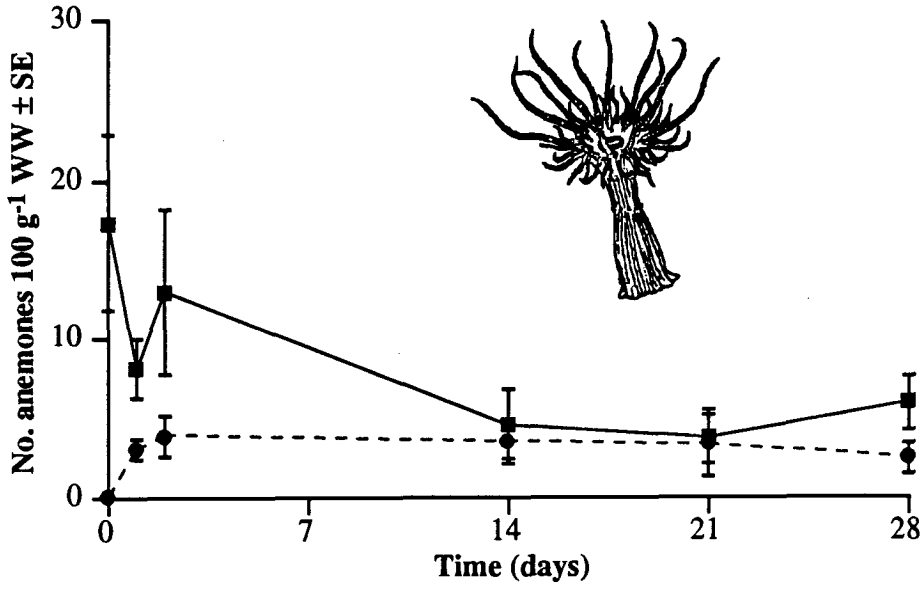


Figure 4.20. Mean abundance of anemones in recolonisation experiment 2 (0-28 days). n=9 plants per time point. Controls (■) and defaunated plants (●).

(mostly shrimps) recolonised at much faster rates (comparing experimental and control abundance) than other taxa. Are there any common features among these taxa which would provide an explanation for this? One obvious explanation would be a difference in locomotory abilities between the taxa. Sphaeromatids and decapods have well-developed swimming behaviours (Barnes 1980), however so do gammarids and polychaetes (*loc cit.*) which do not colonise as rapidly, and caprellids, a rapidly colonising taxon, are described by Barnes (1980) as being "...adapted for climbing" and by Krapp-Schickel (1993) as good swimmers over short distances between plants. Thus, it would appear that locomotory differences were not responsible for the two types of recolonisation patterns.

An alternative hypothesis is that behaviour was different between the taxa – the rapidly colonising taxa had greater turnover rates among plants. 'Investigation' of new habitats (i.e. periodic immigration and emigration behaviour) could be more pronounced in sphaeromatids, caprellids and decapods, resulting in the faster location of unoccupied habitats. This could be investigated by a short-term *in situ* staining experiment comparable to that of Howard (1985). Another hypothesis, assuming that epifauna actively search for suitable habitats, is that different taxa use different cues for locating habitats and that a defaunated plant initially either lacked a specific cue for slow-colonising taxa, or produced a specific cue for fast-colonising taxa. Synergism between taxa could be important if, for example, a chemical cue from one taxon influenced the settling behaviour of conspecifics or individuals of another taxon. It has been shown that sphaeromatid isopods exhibit aggregative settling behaviour (Holdich 1976, Shuster 1990) and this may have been the reason for their rapid recolonisation. There is still not enough information about the behaviour of epifauna to distinguish between these hypotheses.

The phenomenon of overshoot of populations has a theoretical basis in the ecology of succession (e.g. Odum 1975, Gutierrez and Fey 1980, Colinvaux 1986). Gutierrez and Fey (1980) state that "...the overall successional mode of behaviour can be characterized as growth followed by equilibrium, with possibly biomass and diversity temporarily overshooting their climax values before settling down to their equilibrium levels in the long run". Virnstein and Curran (1986) found that populations of the gastropod *Bittium varium* and the amphipod *Cymadusa compta* on defaunated plants both overshot their respective final abundance, although there is no control data to show what population fluctuations occurred on unmanipulated plants. There is evidence that the same thing occurred with total crustacean individuals on defaunated *Penicillus* (Stoner 1985), although again there are no control plants and the experiment was terminated after only 4 days.

Finally, the question arises as to whether equilibrium was attained in the experiments. The communities in the medium-term experiment were similar at 14, 21 and 28 days on two of the first three canonical axes (Figure 4.10) and showed the same directional shifts in abundance. This suggests that equilibrium on the defaunated plants may have been attained as early as 14 days after the beginning of the experiment. Schoener (1974) suggested that equilibrium in communities of invertebrates living in sponges was reached about a month after deployment but Gunnill (1982b) found similar species richness and abundance of controls and defaunated plants between 7 and 18 days in an experiment with *Pelvetia fastigiata* and Bell and Devlin (1983) found recolonisation of invertebrates in sediments to control levels within 25 hours of defaunation. The time scale of recolonisation in the present work is thus consistent with previous studies. Given that the equilibrium state is a defined (MacArthur and Wilson 1967) as a dynamic balance between the opposing forces of immigration and emigration (ignoring birth and death rates over the short times of the experiments) and that immigration and emigration rates were very high (the former measured directly in the short-term experiment, the latter inferred from this) it seems reasonable to conclude that equilibrium was established in 2-4 weeks.

4.7 CONCLUSIONS

Although this chapter has dealt with a number of discrete experiments they provide a context into which the phenological data (Chapter 3) and the manipulative studies (Chapters 6 and 7) can be placed. Specifically the following sets of questions and answers were generated:

(1). Was the population of epifauna specific to benthic *Sargassum*?

- The epifauna was a primarily a phytal fauna, not a subset of the invertebrates living both on *Sargassum* and in the reef matrix.
- Drift *Sargassum* did not represent a utilisable resource for epifauna.

(2). Over periods of months and years communities of epifauna showed distinct and predictable changes in abundance and composition. What were the changes in abundance and composition of epifauna over different time scales?

- Over a time scale of 24 hours the magnitude of changes in abundance of most epifauna were small (less than 1x) and the community composition showed a small change from day to night attributable to individuals emerging from the substratum.

• Over a time scale of 6 days the magnitude of changes in abundance of epifauna were greater than that shown over 24 hours (in the order of 1-3x) but still small. Changes in composition of epifauna were small and unpredictable.

• Over a time scale of 28 days the magnitude of changes in abundance of epifauna was still in the order of 1-3x, significantly less than the order of magnitude changes shown over a year. Changes in the composition of epifauna were larger and were probably predictable, given appropriate seasonal data.

Thus, it appears that the patterns of seasonal abundance changes presented in Chapter 3 represented true differences, not merely artifacts generated by the time of day, week or month when the sample was taken, given the disparity in the magnitudes of these changes between the different time scales.

(3). What were the short-term spatial patterns of epifaunal populations with respect to their colonisation of bare, available habitats?

• Rates of movement of epifauna were very high and colonisation occurred rapidly on to 'new' habitats. Equilibrium communities appeared to have been established within 28 days.

These results and verify that the epifauna on *Sargassum* was indeed a discrete and structured community which exhibited real and distinctive phenological patterns and provided a basis for the design of manipulative experiments to test hypotheses to determine the processes underlying these seasonal changes.

CHAPTER 5

HYPOTHESES TO EXPLAIN EPIFAUNAL PHENOLOGY

"A theory attempts to identify the factors that determine a class of phenomena and to state the permissible relationships among the factors as a set of viable propositions. A purpose is to simplify our education by substituting one theory for many facts. A good theory points to possible factors and relationships in the real world that would otherwise remain hidden". Robert H. MacArthur & Edward O. Wilson, The Theory of Island Biogeography.

5.1 INTRODUCTION

Chapter 3 demonstrated that, for the majority of epifaunal taxa living on *Sargassum*, maximum abundance occurred during periods of minimum host biomass. This is a surprising result: a literature survey reveals that epifaunal abundance are usually high during periods of high host biomass and *vice versa* (Table 5.I). Of ten studies reviewed which collected data simultaneously on host and epifauna, seven showed maximum epifaunal abundance at or around the time of maximum host abundance with only one study (Nelson *et al.* 1982) that suggested that epifaunal abundance was not correlated with host abundance. A further 6 studies showed a correlation between epifaunal abundance and the biomass of the host or epiphytic algae although the seasonality of the phytal component was not specifically stated.

However, in the *Sargassum*-epifauna system, it seems inescapable that epifaunal abundance was not dependent simply on the presence and abundance of *Sargassum* but were controlled by some other factor(s). A number of hypotheses were devised to account for the observed pattern and these are detailed below. The list is by no means exhaustive, reflecting the most likely possibilities and the focus of previous work. Briefly, the factors controlling epifaunal abundance could have been:

(1). Predation by fish and/or larger invertebrates.
(2). Habitat complexity and availability.
(3). Competition between epifaunal taxa.
(4). Reproductive periodicity of epifauna.
(5). Seasonal variation in physical parameters (temperature, salinity etc.).
(6). Algal defensive chemistry.
(7). Combinations of the above acting synergistically or antagonistically.

Reference	Type	Locality	Epifaunal taxon studied	Time of maximum phytal biomass and/or correlation with abundance	Time of maximum epifaunal abundance
Ansari *et al.* (1991)	SG	Arabian Sea	POLY AMPH ISO	ND A/B corr.	ND
Aoki (1990)	MA	Japan	AMPH	April	March
Arrontes & Anadon (1990b)	MA	Spain	ISO		May-July
Charvat *et al.* (1990)	Sand	Florida	AMPH	ND	May-August
Choat & Kingett (1982)	Turf	New Zealand	AMPH OST POLY	ND	December (AMPH) April (POLY)
Duffy (1990)	MA	North Carolina	AMPH	ND	Feb-Apr (1987) May-Jun (1988)
Dugan & Livingston (1982)	SG	Florida	DEC	ND	July-Nov
Edgar (1983b)	MA	Tasmania	AMPH TAN GAST POLY	Dec-Mar	Feb-Mar
Edgar (1990f)	SG	West Australia	AMPH POLY GAST	Mar-Sep	Feb-May
Fine (1970)	MA	Sargasso Sea	DEC AMPH POLY	ND	May
Fredette *et al.* (1990)	SG	Virginia	ISO AMPH DEC GAST	ND	Aug-Nov (ISO) May (AMPH)
Gore *et al.* (1981)	SG	Florida	DEC	April, July, Jan	April, July
Gunnill (1983)	MA	California	AMPH COPE	ND A/B corr.	July-Sep
Hall & Bell (1988)	SG	Florida	COPE AMPH NEM	ND A/B corr. with epiphytes	
Heck (1977)	SG	Panama	DEC GAST	ND	July-Sep
Heck (1979)	SG	Florida	DEC GAST	ND	April, June, Nov
Heck & Wetstone (1977)	SG	Panama	DEC GAST	ND A/B corr.	ND
Johnson & Scheibling (1987)	MA	Nova Scotia	COPE NEM ACAR	ND A/B corr. with epiphytes	June-Jul
Lewis (1984)	SG	Florida	AMPH DEC	ND A/B corr.	ND
Lewis (1987)	SG, MA	Florida	AMPH DEC	various	May-June
Marsh (1973)	SG	Virginia	AMPH ISO GAST	June-July	July-Sep

(continued on next page)

Reference	Type	Locality	Epifaunal taxon studied	Time of maximum phytal biomass and/or correlation with abundance	Time of maximum epifaunal abundance
Mukai (1971)	MA	Japan	COPE NEM AMPH	Feb-Mar	Feb-Mar
Nagle (1968)	MA	Cape Cod	GAST AMPH	ND	June-July
Nelson (1979b)	SG	North Carolina	AMPH	July-Aug	Feb, Sep
Nelson *et al.* (1982)	SG	Florida	AMPH	June-July (Eiseman *et al.* 1974)	variable
Schneider & Mann (1991a)	SG	Nova Scotia	AMPH GAST	ND A/B corr. with epiphytes	July-Sep
Stoner (1980b)	SG	Florida	AMPH	July	Feb-May, Nov
Stoner (1983)	SG	Florida	AMPH TAN	July	July
Wakabara *et al.* (1983)	MA	Brazil	AMPH	ND	May
Young (1981)	SG	New South Wales	AMPH DEC	ND	random

Table 5.I Summary of literature on basibiont/epifaunal phenology.

Legend:

Type

MA = macroalga
SG = seagrass

Taxon

AMPH = amphipod
COPE = copepod
DEC = decapod
ISO = isopod
OST = ostracod
TAN = tanaid

ACAR = acarinid
GAST = gastropod
NEM = nematode
POLY = polychaete

Time of maximum phytal biomass

ND = No data
A/B corr. = correlation between abundance of ep biomass of alga/seagrass & epifauna

It was also entirely possible that abundance of the different epifaunal taxa (or even species within a defined group) were controlled by different factors. However, given the similar patterns exhibited by most taxa and the extreme difficulty in separating differential effects in time and space between taxa, it was decided to concentrate on a single hypothesis at a time. More detailed consideration to each hypothesis is given below:

5.2 HABITAT COMPLEXITY AND HETEROGENEITY

An important factor in controlling populations of organisms is habitat complexity (see review by McCoy and Bell 1991).. A summary of literature on the role of habitat complexity in marine epifaunal systems is given in Table 5.II. A large number of studies have inferred the effect of habitat complexity on abundance and species composition from correlative data only, but of the manipulative studies reviewed, 14 out of 15 found positive effects of habitat complexity on the abundance of mobile epifauna. In these studies a general increase in habitat complexity or heterogeneity led to increased abundance or species diversity of epifauna. No studies were found which manipulated habitat complexity in the tropics, the only studies being correlative.

Habitat availability is not simply a function of phytal biomass but depends also on spatial and structural architecture (Hacker and Steneck 1990). In fact, apparent discrepancies between some previous studies may have resulted from different methods of estimating habitat complexity and availability. Some authors have taken biomass as a simple measure of habitat complexity (Heck and Wetstone 1977, Gunnill 1982b, Stoner 1985), others have used surface area (Stoner and Lewis 1985, Dean and Connell 1987a, b), still others have used surface area/volume ratios or more complicated thallus/canopy volume measurements (Hacker and Steneck 1990). Most measurements of surface area are based on the method of Harrod and Hall (1962) which uses the weight of a detergent film to measure surface area. However, the method is normally used to generate a regression line of surface area on biomass from which sample surface area is estimated for the remainder of the samples – thus, this method is only a measurement of biomass. Measurements of habitat architecture are more useful when dealing with plants of widely varying morphology (Hacker and Steneck 1990) rather than plants of similar morphology, which, by definition, will have similar architectural characteristics. Of the four species of *Sargassum* collected in this study three had very similar morphologies, evidence of which is given by the similar coefficients for length/biomass regressions (Table 2.IV). The fourth species, *S. linearifolium*, had slightly different epifaunal patterns (Figures 3.11 and 3.12).

Reference	Type	Locality	Epifaunal taxon studied	Type of experiment used	Habitat complexity effect detected
Bell & Westoby (1986a)	SG	New South Wales	DEC	Leaf height and density reduction	YES
Bell & Westoby (1986b)	SG	New South Wales	DEC	Leaf height and density reduction with exclusion cages	YES
Brook (1978)	SG	Florida	DEC GAST POLY	Observation only	NO (INFERRED)
Coull & Wells (1983)	MA	New Zealand	AMPH COPE	Lab. and field manipulations of density	YES
Dean & Connell (1987b)	MA	California	AMPH GAST POLY	Lab. and field manipulations of biomass and surface area of natural and artificial plants	YES
Edgar (1983b)	MA	Tasmania	AMPH GAST POLY	Observation only	YES (INFERRED)
Greening & Livingston (1982)	SG/MA	Florida	DEC GAST	Observation only	YES (INFERRED)
Gore *et al.* (1981)	SG/MA	Florida	DEC	Observation only	YES (INFERRED)
Gunnill (1982b)	MA	California	AMPH COPE	Observation only	YES (INFERRED)
Hacker & Stenenck (1990)	MA	Maine	AMPH	Artificial plants	YES
Hall & Bell (1988)	EPI/SG	Florida	AMPH COPE NEM	Defaunation and recolonization of artificial and natural seagrass and epiphytes	YES
Heck (1979)	SG	Panama, Florida	DEC	Observation only	NO (INFERRED)
Heck & Thoman (1981)	SG	Maryland	DEC	Lab. manipulations and tethering experiments	NO
Heck & Wetstone (1977)	SG	Panama	DEC GAST	Observation only	YES (INFERRED)
Hicks (1980)	MA	England	COPE	Observation only	YES (INFERRED)
Leber (1985)	SG	Florida	AMPH DEC GAST POLY	Lab. manipulation of density and field observation	YES
Lewis (1984)	SG	Florida	AMPH DEC	Observation only	YES (INFERRED)
Main (1987)	SG	Florida	DEC	Lab. observation of prey behaviour	PARTIAL
Mukai (1971)	MA	Japan	AMPH COPE NEM	Observation only	YES (INFERRED)
Nelson *et al.* (1982)	SG	Florida	AMPH	Observation only	NO (INFERRED)
Orth *et al.* (1984)	SG	various	various	Review	YES
Russo (1990)	MA	Hawaii	AMPH	Observation only	PARTIAL

(continued on next page)

Reference	Type	Locality	Epifaunal taxon studied	Type of experiment used	Habitat complexity effect detected
Schneider & Mann (1991b)	EPI/SG	Nova Scotia	AMPH DEC GAST	Lab. and field experiments with artificial plants	YES
Stoner (1980a)	SG/MA	Florida	AMPH	Lab. manipulations of macrophyte density	YES
Stoner (1983a)	SG	Florida	AMPH TAN	Observation only	YES (within sp.) NO (between sp.)
Stoner (1985)	MA	Puerto Rico	AMPH DEC ISO TAN	Observation only	YES (INFERRED)
Stoner & Lewis (1985)	SG/MA	Venezuela	AMPH ISO TAN	Field manipulations of density and biomass	YES
Virnstein & Howard (1987a)	SG	Florida	AMPH DEC GAST	Observation only	NO (INFERRED)
Virnstein & Howard (1987b)	MA/SG	Florida	AMPH DEC GAST	Observation only	NO (INFERRED)

Table 5.II Summary of literature on habitat complexity in marine epifaunal systems. Legend as in Table 5.I

However, subsequent manipulative experiments on habitat complexity were performed in mixed-species patches of *S. fissifolium*, *S. oligocystum* and *S. tenerrimum* only – thus simple measurement of biomass as an index of habitat architecture of *Sargassum* was justifiable.

Although *Sargassum* biomass was not correlated with abundance of epifauna at Magnetic Island, there was a positive correlation between the amount of epiphytes and populations of epifauna. As shown in Figures 2.10-2.13 *Sargassum* plants became heavily epiphytised over the winter when populations of most epifaunal taxa increased. Epiphytes may add an additional level of habitat complexity if their morphology differs from that of the host. In addition a diverse epiphytic community will increase the heterogeneity of the habitat. This has been recognised in the studies of Johnson and Scheibling (1987), Hall and Bell (1988) and Schneider and Mann (1991a), all of whom found correlation between epifaunal abundance and epiphytic biomass (as opposed to host biomass). Thus, one *a priori* hypothesis which was generated was that abundance of epifauna was controlled by additional habitat complexity provided by epiphytes. This was tested by the use of artificial *Sargassum* plants with different levels of epiphytes.

5.3 PREDATION

Historically, predation has been assumed or hypothesised to be the most important factor controlling the populations of numerous taxa in many different ecosystems (see review by Sih *et al.* 1985). Many manipulative studies have been performed and have demonstrated predation effects on prey populations: Sih *et al.* (*loc. cit.*) reviewed 138 studies from 20 years of literature, 132 of which demonstrated effects of predation. The study of predation effects has been much more limited in the marine environment than on land or in freshwater systems – only 24 studies reviewed in Sih *et al.* (*loc. cit.*), all of which showed predation effects.

A summary of literature on predation in marine epifaunal systems in given in Table 5.III. Many of these studies rely purely on observation data for their conclusions about the structuring role of predation; this is correlation only, not causality. Thirteen studies manipulated predator densities (usually by the use of exclusion cages): of these 8 showed that predators were important in controlling the abundance of one or more epifaunal taxa.

The major predators in epifaunal systems have been assumed to be fishes and decapods, usually determined by gut contents analysis or observation of feeding (for

Reference	Type	Locality	Epifaunal taxon studied	Type of experiment used	Predation effect detected
Aoki (1990)	MA	Japan	AMPH	Exclusion cages	YES
Choat & Kingett (1982)	Turf	New Zealand	AMPH OST POLY	Exclusion cages	NO
Duffy & Hay (1991b)	MA	North Carolina	AMPH	Observation only	YES (INFERRED)
Edgar (1983b)	MA	Tasmania	AMPH GAST POLY	Observation only	YES (INFERRED)
Edgar (1983d)	MA	Tasmania	AMPH	Size-frequency distributions	YES (INFERRED)
Edgar (1990f)	SG	West Australia	GAST	Exclusion cages and consumption rate calculations	YES
Heck (1979)	SG	Panama, Florida	DEC	Observation only	YES (INFERRED)
Holmlund *et al.* (1990)	MA	North Carolina	AMPH	Exclusion and inclusion cages	NO
Jones (1965) reported in Bernstein & Jung (1979)	MA	California	ISO	Observation only	YES (INFERRED)
Kennelly (1991)	MA	New South Wales	AMPH OST	Exclusion cages	NO
Kneib (1982)	*Spartina*	North Carolina	AMPH	Transplantation	NO
Kneib (1988)	*Spartina*	Georgia	COPE GAST OLIGO POLY	Inclusion cages	generally NO, YES for few taxa
Leber (1985)	SG	Florida	AMPH DEC GAST POLY	Exclusion and inclusion cages	YES
Nelson (1979a)	SG	North Carolina	AMPH	Laboratory experiments and observation data	YES (INFERRED)
Nelson (1979b)	SG	North Carolina	AMPH	Exclusion and inclusion cages	NO (exclusion) YES (inclusion)
Nelson (1980a)	SG	Florida to Nova Scotia	AMPH	Observation only	YES (INFERRED)
Nelson (1981)	SG	Florida	AMPH DEC GAST ISO POLY TAN	Laboratory experiments and inclusion cages	NO (fish and crab) YES (prawns)
Nelson *et al.* (1982)	SG	Florida	AMPH	Observation only	YES (INFERRED)
Stoner (1980b)	SG	Florida	AMPH	Observation only	YES (INFERRED)
Summerson & Peterson (1984)	SG	North Carolina	AMPH GAST	Exclusion cages	NO
Tegner & Dayton (1987)	MA	California	AMPH	Observation only	YES (INFERRED)
Vince *et al.* (1976)	*Spartina*	Massachusetts	AMPH GAST	Exclusion fences	YES
Young *et al.* (1976)	SG	Florida	AMPH GAST POLY	Exclusion cages	YES

Table 5.III Summary of literature on predation in marine epifaunal systems. Legend as in Table 5.I

example Nelson 1981, Aoki 1990, Holmlund *et al.* 1990). Large, predatory decapods were never captured in large numbers on *Sargassum* and the only species which were found consistently were spider crabs and various shrimps which are primarily detritus and algal feeders (Barnes 1980). Conversely, there is a large and varied fish fauna living in and around *Sargassum.* A preliminary study of fish fauna at Magnetic Island (A. Green, *pers. comm.*) suggested that wrasses, especially *Halichoeres* spp., were the principal epifaunal predators. This was confirmed by Randall *et al.* (1990) who state – "*Halichoeres*...feed mainly on small benthic crustaceans and molluscs.".

Aoki (1990) suggests that wrasse predation on caprellids caused their drastic decline 2 months before decline of host *Sargassum* and Taylor and Jones (*unpub.*) suggest an effect of predatory wrasses on epifaunal populations living on temperate macroalgae. Thus, an alternative hypothesis that fish predation was causing the observed temporal variations in epifaunal abundance, either through greater perception and capture of epifauna in summer or through increased predator populations. This hypothesis was tested using exclusion cages to reduce predation on epifaunal populations.

5.4 INTERACTION OR SYNERGISM BETWEEN HABITAT COMPLEXITY AND PREDATION

It is often difficult to separate the effects of predation from habitat complexity in determining abundance patterns or species compositions of communities. The intensity of predation may be reduced through reduced foraging success in areas of greater habitat complexity, occasionally following some simple function (review by Orth *et al.* 1984) or more often with a 'threshold' below which predation is not affected (Nelson 1979, Gotceitas and Colgan 1989). In these situations predation is still the determining factor controlling abundance but it is modified by the interaction with habitat structure. Hixon and Menge (1991) have modelled the effect of increasing habitat complexity (refuges) within the framework of competing sessile epibenthic species. They consider 4 different "prey-diversity response" curves and the effect of increasing predation – increasing habitat diversity significantly affects the shape of these curves. Empirical support for some of their predictions is given in Brock (1979), Hixon and Brostoff (1983, 1985) and Menge *et al.* (1985, 1986).

It can also be difficult to determine proximate from ultimate factors determining abundance of organisms. Reaka (1985) found that stomatopods showed no response to reduced predation (caging) but responded to increased habitat availability (more available rubble). However, with the presence of barriers to immigration/emigration

from the system a predation effect was found. She concluded that the population of stomatopods consisted of some individuals with territories and some "floaters" – following removal of an individual from its territory, this was immediately colonised by a floater. Thus, although the proximal cause for population fluctuation was habitat complexity, the underlying causal force was in fact predation.

Selection for habitats of increased complexity may be a direct result of past evolutionary predation pressure. Intense predation pressure would ensure that organisms which selected for increased habitat complexity (and associated lowered probability of mortality) would have a selective advantage. Subsequent reduction in predation intensity could leave habitat complexity as the determining factor in population abundance.

5.5 COMPETITION

Despite much scepticism about the role of interspecific competition (e.g. Connell 1975) there are still many studies which have found competition effects (reviewed in Schoener 1983). Competition is obviously important in marine systems – Schoener (*loc. cit.*) found 33 studies showing some sort of competition effect. However, Hairston *et al.* (1960) proposed a theory which was later developed later by Menge and Sutherland (1976) which suggested that the relative importance of predation and competition should be dependent on the trophic level of the interacting organisms. They predict that organisms in low trophic levels (herbivores/omnivores) should have their populations regulated by predation not competition and that competition should only be important at higher trophic levels (carnivores). Despite the dearth of natural history on the *Sargassum* epifauna it can reasonably be assumed that most of the species are herbivores, detritivores or filter-feeders (considered herbivores by Menge and Sutherland *loc. cit.*) through examination of the small body of literature for the tropics (Barnard 1976) or analogous literature in temperate systems (e.g. Fauchald and Jumars 1979, Zimmerman *et al.* 1979, Steneck and Watling 1982, Holdich and Jones 1983). Thus, it would be predicted that epifauna on *Sargassum* would not compete. Although Schoener's (1983) review of the literature showed only weak support for this hypothesis in marine systems, significance of the analysis rises substantially with the removal of herbivorous fishes (which generally do compete).

Recently Graham Edgar has proposed that populations of epifauna are constrained by quantifiable resource ceilings (Edgar 1990g, 1993, Edgar and Aoki 1993). This hypothesis has generally been rejected in the past (e.g. Orth *et al.* 1984). However, through the use of artificial habitats in *Sargassum* beds and experimental

field microcosms Edgar has shown that secondary production remains constant in diverse habitats with similar photosynthetic production (Edgar 1990a, b, f, 1991a, b, 1993) and he concludes "if this 'production ceiling' hypothesis is correct then diffuse competition is generally more important than predation or environmental disturbance in restricting the growth of mobile epifaunal populations" (Edgar 1993). Diffuse competition is extremely difficult to measure, however. Although attractive, this hypothesis does not easily lend itself to experimental manipulation in the *Sargassum*-epifauna system and so was not pursued.

5.6 OTHER HYPOTHESES

5.6.1 Recruitment

Although extrinsic forces (biotic or abiotic) may be involved in determining abundance of organisms, intrinsic population cycles may be equally important. Stoner (1980b) looked at amphipods associated with tropical seagrass and found that reproductive cycles governed abundance for most of the abundant species. Arrontes and Anadon (1990) investigated 3 species of isopod inhabiting macroalgae in Spain and concluded the same thing. Jones *et al.* (1992) manipulated the predation pressure on infaunal molluscs in a reef lagoon – as part of their study they examined the population size structure of the molluscs. They found that a number of the common species exhibited a summer peak due to an influx of a cohort of juveniles. It is interesting that the gastropod epifauna in the present work shows a summer peak in abundance (Figure 3.8B); this may have been due to an analogous recruitment event.

Despite the potential importance of epifaunal reproductive dynamics in controlling population abundance this factor is difficult to demonstrate. Manipulative studies are impossible, leaving correlational studies using the presence of reproductive individuals or the size-frequency distribution of the population only. Absolute reproductive output will be important only if juvenile mortality is density-independent, if it is density-dependent, then the causal factor(s) determining population abundance will be the causes of mortality.

The population dynamics of one group of epifauna, the sphaeromatid isopods were examined in detail, including determination of reproductive individuals and the measurement of size-frequency distributions (Chapter 7). Although useful in looking at the factors controlling the abundance of this group, such a treatment would have been prohibitively time-consuming for the entire epifauna.

5.6.2 Abiotic Environmental Factors

Abundance of epifauna would only be directly controlled by abiotic factors if the organisms were living near their physiological tolerance limits. Organisms may use changes in such factors as cues for the initiation of reproduction, for example, which could indirectly lead to population abundance changes. However, direct control of abundance by temperature- or salinity-induced mortality is unlikely. Both Nelson (1979a) and Stoner (1980b) suggest that physical factors are unimportant in the abundance changes of amphipods associated with seagrass. Indeed Stoner (1980b) states that "most of the amphipods in this study appear to be euryhaline and are reproductively active over a wide temperature ranges".

Van Dolah (1978) tested the physiological tolerances of temperate amphipods and found that only freezing stress would cause significant mortality in the range of conditions experienced. He also concluded that abiotic factors were not responsible for population fluctuations in this system. The range of conditions experienced by epifauna at Magnetic Island can be considered 'benign' (*sensu* Saunders 1968) with daily mean temperatures ranging from 24-32°C (Figure 2.18) and salinity ranges of 26-36‰ (Walker 1981a). It seems unlikely that these relatively small fluctuations could physiologically stress the epifauna, despite the hypothesis that organisms in the tropics have a narrower range of environmental tolerance (Stevens 1989). Abiotic factors are difficult to manipulate in field experiments and laboratory experiments suffer from justifiable criticism as to their ecological relevance. Thus, it was decided not to attempt to manipulate abiotic factors.

5.6.3 Defensive Chemistry

Tropical *Sargassum* is known to contain secondary metabolites (polyphenols) hypothesised to be chemical defences against herbivores (Steinberg and Paul 1990) although such metabolites may only be present in low concentrations or may even be attractants for invertebrates (Hay *et al.* 1988a, b, Hay and Fenical 1988). However there does not appear to be data on the temporal variation of the levels of these compounds in tropical brown algae which could be correlated with epifaunal abundance. There are some data available for seasonal variation in polyphenols in temperate fucalean algae: Munda (1962) and Joshi and Gowda (1975) (both reported in Ragan and Jensen 1978) found no seasonal variation in polyphenols from two *Sargassum* species, but Ragan and Jensen (1978) found significant variation in

polyphenol content of *Fucus vesiculosus* and *Ascophyllum nodosum* which was correlated with algal reproduction. A similar increase in the concentration of defensive chemicals in *Sargassum* during the summer could explain the epifaunal temporal pattern if the polyphenolics caused epifaunal mortality or reduced reproduction and the epifauna were deriving most of their nutrition from eating *Sargassum*. If, as commonly assumed, most tropical epifauna obtain their food by periphyton grazing, filter feeding in the water column (Barnard 1976) or feeding on epiphytes (D'Antonio 1985) it seems unlikely that defensive chemistry was responsible for epifaunal phenology.

5.7 HYPOTHESIS TESTING: PREDATION AND HABITAT COMPLEXITY

It is clear from the above discussion that there were numerous possible explanations for the epifaunal temporal patterns observed. However, time and logistics precluded the exhaustive testing of all the hypotheses. Thus, it was decided to concentrate on predation and habitat complexity initially, as likely structuring forces in this community. Two large-scale manipulative experiments were performed, one examining the effect of predation using exclusion cages and the other the role of epiphytic secondary habitats using artificial plants. Not only did this attempt to answer questions about the forces structuring epifaunal communities, it provided information on the relative importance of the predation and habitat complexity, something which has rarely been done.

CHAPTER 6

THE ROLE OF HABITAT COMPLEXITY AND FISH PREDATION IN CONTROLLING EPIFAUNAL ABUNDANCE: HYPOTHESIS TESTING*

"In an experiment, we dare nature to come up with some unknown factor that would foil our preconception about how things should work." Thomas Schoener, Field Experiments on Interspecific Competition.

6.1 INTRODUCTION

How important are habitat complexity and predation in a tropical marine macroalgal ecosystem?. This question is the fundamental basis for the work subsequently described in this chapter. Habitat complexity and predation have been considered major processes affecting the abundance of organisms in vegetated marine habitats (Heck and Orth 1980a, b, Choat 1982). Recent studies which have demonstrated that aspects of habitat complexity were important in determining patterns of abundance of epifauna and/or size-frequency distributions include Dean (1981), Stoner and Lewis (1985), Hall and Bell (1988) and Hacker and Steneck (1990). Likewise Duffy and Hay (1990) state 'mesograzer populations are usually maintained at low densities by predation' and their findings are echoed by, amongst others, Nelson *et al.* (1982), Sih *et al.* (1985), Aoki (1990) and Edgar (1990e). Habitat complexity and predation may be very closely linked, with complexity mediating predation through reduced foraging success by predators (see review by Orth *et al.* 1984, Russo 1987 and Holmlund *et al.* 1990) or by modifying the interaction between predation and competition (Hixon and Menge 1991). However, the relative importance of habitat complexity and predation have seldom been explicitly assessed for the same system (but see Bell and Westoby 1986c). A common assumption has been that if predation is demonstrated to be important that habitat complexity is unimportant and *vice versa*, however both or neither may be the determinant of community composition and abundance.

Why might we expect populations of epifauna to be influenced by habitat complexity and predation? Tropical epifaunal communities associated with macroalgae appear likely candidates for the influence of habitat complexity and predation since both of these factors have been hypothesised to play a highly significant role in the tropics. Structural complexity of both the biological and physical components of reef

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systems are high (Bradbury and Loya 1978) and associated species appear to respond to habitat on a finer scale in the tropics (Spight 1977, Stevens 1989). *Sargassum* is one of the most structurally complex of all algae, with tissue differentiation into blades, vesicles, stems and holdfast (Kilar *et al.* 1992), individual plants grow to large size (Nizamuddin 1970, Chapter 2) and epiphytic growth of algae and sessile invertebrates can provide large amounts of additional, structurally diverse, habitat (Dean 1981, Edgar 1983c, D'Antonio 1985, Schneider and Mann 1991b). This means that a *Sargassum* plant potentially provides abundant, diverse habitat niches for epifaunal organisms. Similarly, predation pressure appears to increase along a latitudinal gradient from temperate to tropical regions (Vermeij 1978, Wallerstein and Brusca 1982) and appears to be more temporally homogeneous in the tropics, denying the possibility of temporal escape (Menge and Lubchenco 1981). Menge and Sutherland (1976) theorise that organisms from lower trophic levels should experience greater effects of predation: invertebrate epifauna are important lower order prey items for larger invertebrates and fish (Leber 1985, Jones *et al.* 1991). Thus, there were strong *a priori* reasons for believing that habitat complexity and predation were important in the *Sargassum*-epifauna system and that detection of these processes, should they be occurring, would be possible.

The next problem to be addressed was how to test these hypotheses that habitat complexity and/or predation were producing the observed patterns of epifaunal abundance. As demonstrated in section 2.5.1.3 *Sargassum* plants became heavily epiphytised during the winter (Plate 6.I). The positive correlation between levels of epiphytes and abundance of epifauna suggested that epiphytic habitat complexity was important. Therefore it was decided to manipulate levels of epiphytes. This was difficult to perform on *Sargassum* for a number of reasons – the damage caused to the plant in removing or reducing levels, the confounding effect of inter-plant variability which was known to be high, both specifically at Magnetic Island (Chapter 2) and generally (Kilar *et al.* 1992), and the autocorrelation of a number of factors if experiments were performed at different times of year on plants with different natural levels of epiphytes. To try and reduce the number of confounding variables I decided to use plastic *Sargassum* mimics, which separated effects of *Sargassum* from the effects of epiphytes, allowed manipulation of epiphytes without physical trauma to the host and allowed standardisation of plant size.

The use of artificial substrata to overcome such problems as spatial heterogeneity or precise quantification of particular aspects of a habitat has a long history: Schoener (1974) and Shuster (1992) used artificial sponges to investigate island biogeography and the reproductive behaviour of an isopod respectively, Barber *et al.* (1979), Bell *et al.* (1985) and Virnstein and Curran (1986) all used artificial seagrass for epifaunal

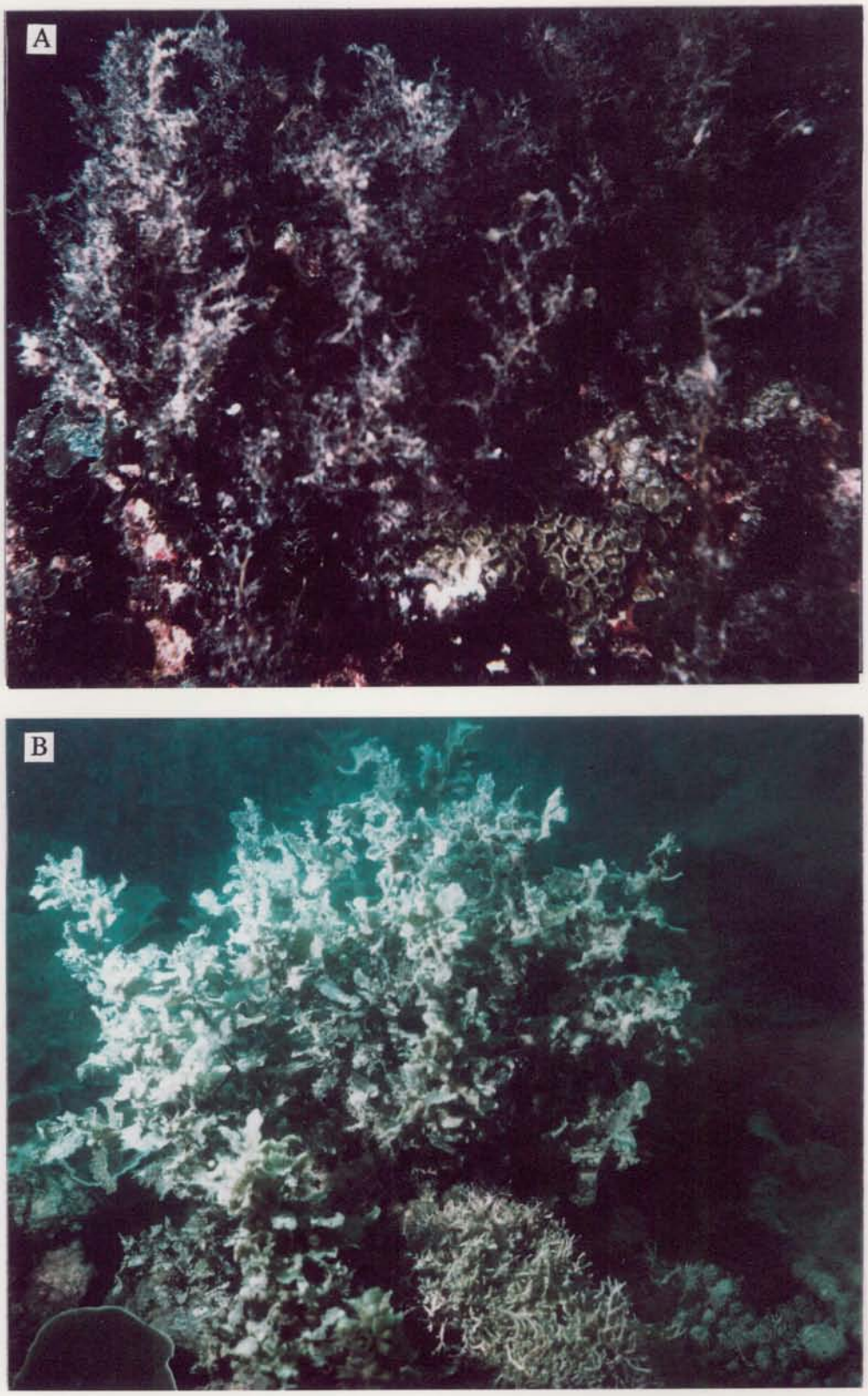


Plate 6.I. Temporal variation in levels of epiphytes on *Sargassum fissifolium*. (A). Winter (June 1991). (B). Summer (late November 1991).

sampling while Myers and Southgate (1980), Dean and Connell (1987b) and Edgar (1991a, b) used artificial algae of various morphologies to investigate cryptofauna and epifauna. The usefulness of such substrata has been demonstrated on numerous occasions – most of the above studies found similar abundance and species compositions of organisms on artificial substrata to natural substrata within a short time. Edgar (1991a) discussed the use of artificial algae as analogues of natural algae and concluded, both from his own work on *Sargassum* and from the literature, that artificial algae have "...considerable potential as tools in benthic sampling programs", especially in view of the significantly lower coefficient of variation he found for artificial plants. The main caveat to the use of artificial plants is that they will not sample organisms which are obligate specialists on the real plant. However, as discussed in Chapter 1, the majority of epifaunal organisms have been found to be generalists and careful design of the experiment to include control *Sargassum* plants allowed the validity of the experiment to be tested (see later). Edgar (1991a) only found one species, which was rare, that did not recruit on to artificial *Sargassum.*

Similarly, a number of approaches have been used to demonstrate and manipulate the effect of predation (summarised in Choat 1982 and Jones *et al.* 1991). Unfortunately the problems associated with the experimental manipulation of predation tend to be more severe and intractable that those associated with habitat complexity. Jones *et al.* (1991) provide a review and critique of the different methodologies which have been used. A number of studies have investigated correlations between abundance of fishes and invertebrates (e.g. St. John *et al.* 1989) or calculated the rate of biomass removal by fishes (e.g. Alheit 1981, Alheit and Scheibel 1982) but these approaches do not do more than suggest further lines of investigation. The experimental approaches which have been used and some of their associated problems include:

(1). Exclusion experiments (e.g. Menge and Lubchenco 1981, Lubchenco *et al.* 1984, Jones *et al.* 1988). These continue to be the preferred tool of many researchers but suffer from a number of problems, chief of which is artifacts introduced by the physical structure. No matter how carefully designed, any object provides additional structure which changes environmental parameters such as water flow, light regimes sedimentation etc. etc. (Jones *et al.* 1988, Kennelly 1991) The conventional way to try and separate these effects from predation effects is to use partial exclusion structures which provide physical structure but allow access by predators. However, there may still be differences attributable solely to the differences in structure between cages or fences and partial controls. Despite this, valuable data have been provided by cage experiments (e.g. Doherty and Sale 1985, Jones *et al.* 1992).

(2). Removal of predators or other organisms (e.g. Lobel 1980). Due to the high mobility and [often] large numbers of invertebrate-feeding fishes on reefs, this technique is only really valid over very short time scales or if very large numbers of fish are killed (something unacceptable to most researchers and regulatory bodies). Lobel (1980) removed damselfish (which guarded territories of algae containing significantly higher densities of invertebrates than surrounding areas) and found a consequent decline in invertebrate abundance.

(3). Inclusion experiments (e.g. Gilinsky 1984, Fitzhugh and Fleeger 1985, Leber 1985). The density of predators within an exclusion cage can be precisely controlled and so threshold densities can be identified. However, as with exclusion cages, there is the problem of experimental artifacts due to cage structure alone. In addition there is no control for any behavioural changes in the predators due to their confinement or higher-order trophic interactions (i.e. predation on the predators). Despite these problems, Fitzhugh and Fleeger (1985) showed significant effects of predation by gobies on meiofauna and Leber (1985) successfully demonstrated a predation effect on a number of taxa in a sparsely vegetated seagrass habitat.

(4). Experimental microcosms and artificial reefs (e.g Brock 1979, Wolf *et al.* 1985, Taylor and Jones *unpub.*). Extrapolation of results from artificial microcosms and substrata to natural substrata is complicated by artifacts associated with artificial systems. Although it has been shown that artificial substrata can quickly accumulate an invertebrate community very similar to a natural situation (Myers and Southgate 1980, Edgar 1991a) this has not been demonstrated for fish communities (Wolf *et al.* 1985). The behavioural responses of fishes to novel substrata are often very different (Bohnsack 1989) and the time taken for a large structure such as an artificial reef to equilibrate with the surrounding environment is likely to be orders of magnitude greater than a 30 cm plastic plant.

(5). Transplant experiments (e.g. Bakus 1964, Neudecker 1977, 1979). These experiments can demonstrate that organisms can or cannot survive outside their normal distribution range, but any conclusions about the role of predation are only correlative.

(6). Tethering experiments (e.g. Heck and Thoman 1981, Heck and Wilson 1987). There are logistical constraints on tethering experiments in that the tethered organism must be relatively large (such as decapod crustaceans). The tethering procedure may disrupt some of the behavioural abilities of the organism and its susceptibility to predation. This technique is not suitable for animals smaller than 5 cm.

(7). Combinations of the above (e.g. Reaka 1985). Ideally experimental manipulations to examine predation pressure should involve combinations of the

above techniques so that the shortcomings of one approach can be offset or answered by another method. This is the conclusion of Jones *et al.* (1991) – "we believe that progress will only made in this area if individual workers apply a range of techniques". However, the ever-present constraints of time and logistics must be balanced against the thoroughness of the investigated to be performed.

I therefore decided to attempt to manipulate predation with exclusion cages, which, despite their shortcomings, appeared to be most suitable for the *Sargassum*-epifauna system.

6.2 AIMS AND OBJECTIVES

The subsequent parts of this chapter describe two experiments performed to test hypotheses about processes concerning abundance of mobile epifauna on *Sargassum.* Explicitly stated these hypotheses were:

(1). Abundance of mobile epifauna was determined by selection of additional habitat complexity provided by epiphytes growing on the surface of *Sargassum.*

(2). Abundance of mobile epifauna was determined by mortality produced by fish predation.

One point to note is that these hypotheses were not necessarily exclusive of each other if interaction occurred between the two processes. The aims of the habitat complexity experiment were:

- To produce artificial plants with different levels of epiphytes.
- To defaunate these mimics and place them available for colonisation by epifauna.
- To sample the epifaunal communities at various time intervals after defaunation in order to monitor the abundance and composition of epifauna on the two experimental treatments.
- To concurrently sample real *Sargassum* plants to determine the validity of results from the experimental samples.

The aims of the exclusion experiment were:

- To exclude all fish predators larger than approximately 10 mm from areas of *Sargassum.*

- To sample the epifaunal communities at various time intervals over a period of a few weeks to monitor the effects of predator exclusion.
- To assess the effects of exclusion structures in order to separate the effects of structure from the effects of exclusion.

6.3 METHODS

6.3.1 Effects of habitat complexity

Additional habitat complexity which may determine abundance of epifauna may be provided by epiphytes living on the surface of *Sargassum*. To test for the effects of this habitat complexity on abundance and composition of epifauna, an experiment was designed using artificial plants with different amounts of epiphytes (for experimental design see Figure 6.1). The use of artificial plants removed any biological variability between individual *Sargassum* plants as a confounding variable in interpretation of results. It also allowed the levels of epiphytes to be manipulated without physical removal, which was found in preliminary experiments to be both damaging to the plant and extremely time-consuming. Two morphologies of artificial *Sargassum* were used: the first mimic consisted of partially-unravelled 12 mm polyethylene rope (mean length 30 ± 2 cm) and the second mimic consisted of 4 'leaves' of green plastic shade cloth (1 mm woven nylon mesh), of dimensions 25 x 5 cm, bound together near the base. Forty mimics of each kind were attached to 40 x 25 x 15 cm plastic baskets and anchored to the reef for 100 days (from 12.5.92 to 20.8.92) to develop an epiphytal community, while forty mimics of both types were left in seawater in the laboratory for the same period (to control for any leaching effects from the plastic). The mimics with epiphytes were designated "epi +", those without "epi -".

After 100 days the epi + mimics were brought to the surface, removed from the baskets and defaunated by two 5 minute periods of submergence in fresh water. Four random individuals of each type of mimic were selected and sealed in plastic bags for later determination of the efficacy of the defaunation treatment. Three defaunated epi + and three epi – mimics were tied to each of 13 plastics baskets, which were then reattached to the reef using 1 m lengths of steel reinforcing rod. The recolonisation experiments of Chapter 4 suggested that equilibrium communities of epifauna were established 2-4 weeks after defaunation. These results, together with the assumption that epi – plants would be accumulating epiphytes which could possibly confuse interpretation, led to the *a priori* designation of sampling times at 2, 4 and 8 weeks after defaunation (3.9.92, 17.9.92 and 9.10.92 respectively). At each of these times 9 individuals of each treatment were randomly selected and collected in the

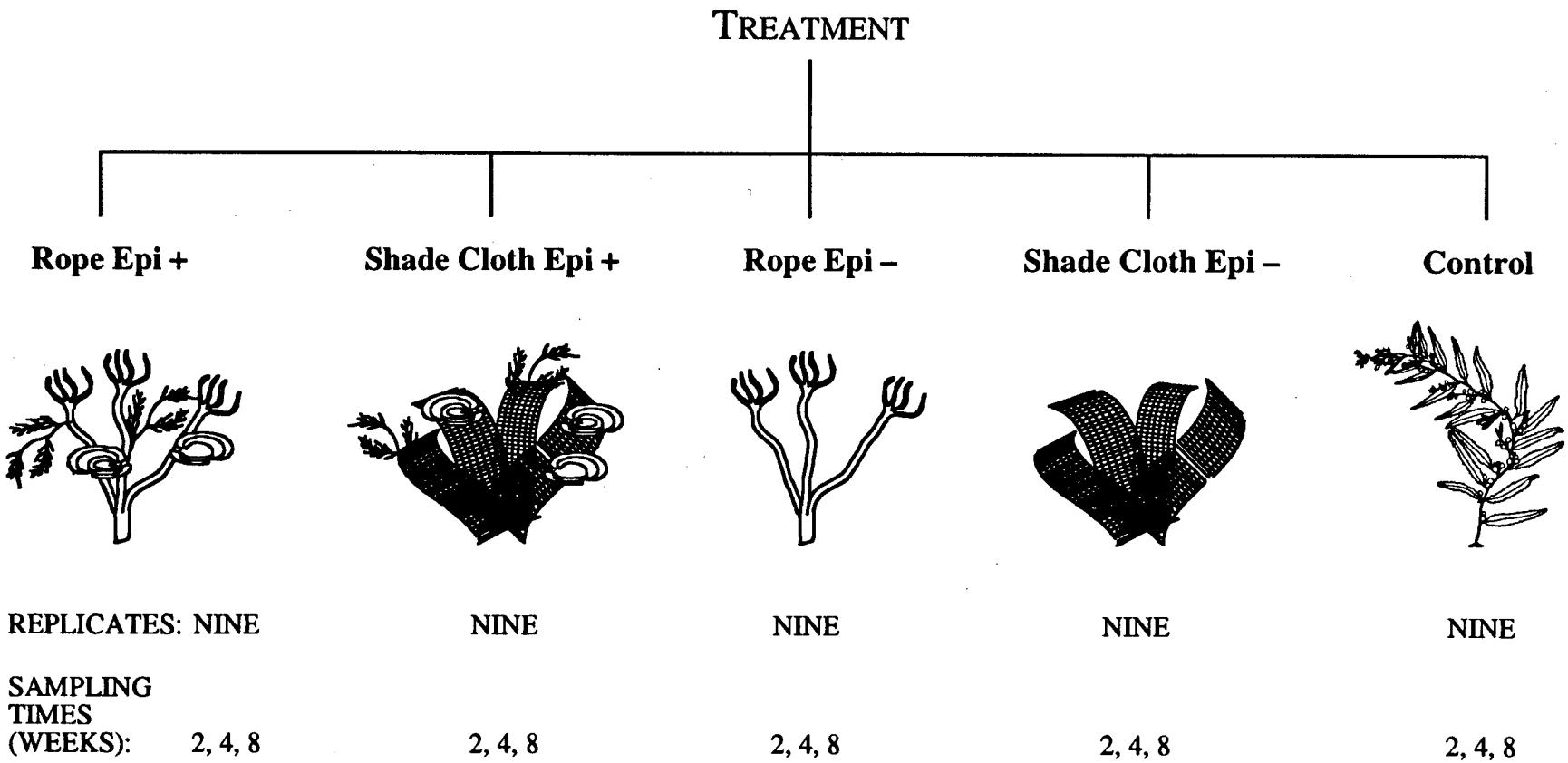


Figure 6.1. Experimental design to test effects of added habitat complexity on abundance of epifauna.

manner described in section 3.3.1. Nine control *Sargassum* plants of approximately the same size were also collected at the same times to compare communities between real and artificial plants.

Abundance of epifaunal taxa was log (x+1) transformed to homogenise variances and were analysed with a 3-way MANOVA after stepwise discriminate analysis with TIME, TYPE (real plant, rope mimic or shade cloth mimic) and TREATMENT (epi + or epi -) considered as fixed factors. Pillai's Trace revealed significant 2 and 3 way interactions between factors ($p<0.0002$) so data were subsequently analysed using Canonical Discriminant Analysis (CDA). In addition to this examination of the community response, abundance of individual taxa was also plotted and, where appropriate, analysed with 3-way ANOVA (on untransformed data) and *post hoc* SNK tests to determine which treatment was significantly different.

6.3.2 Effects of Predation by Fishes

A preliminary survey of some of the fish fauna at Magnetic Island was performed by Alison Green in August 1991. Many of these fish species common at Magnetic Island are known to feed primarily on benthic invertebrates or ingest them with plant material or detritus (Table 6.I). The most common fish in the study areas which are known to feed on invertebrates appeared to be wrasses of the genus *Halichoeres*, thus 20 individuals of these fish were caught, killed and their guts examined. To test the effects of predation by these fish on mobile epifauna a caging experiment was used (for experimental design see Figure 6.2). The design of cages was dictated by a number of factors: the small size of the fishes and their tendency to investigate areas of disturbance (such as when sediment is suspended or plants are agitated), uneven topography for attachment and the necessity to isolate large areas of *Sargassum* in order to include enough plants for repeated sampling. The smallest individual wrasses caught were approximately 20 mm standard length and about 10 mm body depth so cages were constructed of 6 mm square galvanized steel fencing mesh. Cages were of dimensions 1.5 x 0.9 x 0.5 m and so isolated approximately 40 individual plants within one cage. These were attached to the substratum using 0.9 m lengths of steel reinforcing rod. To ensure that fish could not move into the cage from underneath each cage had a 'skirt' of black plastic attached around the bottom edge which was spread out over the substratum and anchored using pegs and coral rubble. Cages were scrubbed underwater once a week to remove detritus and fouling organisms to minimize caging effects on water movement and light attenuation – most of this material was resuspended by the surge and washed

Family	Species	Food items*
Serranidae	*Cephalopholis microprion*	Small fishes, crustaceans
	Epinephalus quoyanus	
Apogonidae	*Apogon fasciatus*	Fish, small crustaceans & other invertebrates
	Apogon cookii	
	Apogon spp.	
Lutjanidae	*Lutjanus carponotatus*	Fishes, crabs, prawns & gastropods
Lethrinidae	*Lethrinus variegatus*	Crabs, prawns and other sand-dwelling invertebrates
	Lethrinus spp.	
Mullidae	*Parupeneus indicus*	Sediment-dwelling invertebrates
Chaetodontidae	*Chaetodon aureofasciatus*	Live coral, benthic algae and invertebrates
	Chaetodon lineolatus	
	Chaetodon spp.	
Pomacanthidae	*Chaetodontoplus spp.*	Algae, detritus, sponges, invertebrates
	Pomacanthus spp.	
Pomacentridae	*Abudefduf whitleyi*	Algae, small crustaceans, plankton
	Acanthochromis polyacanthus	
	Neopomacentrus azysron	
	Pomacentrus molucensis	
	Pomacentrus wardi	
	Stegastes apicalis	
Labridae	*Choerodon cynodus*	Benthic invertebrates, small crustaceans, gastropods, polychaetes, plankton
	Choerodon graphicus	
	Choerodon schoenleinii	
	Coris aureolineata	
	Halichoeres dussumieri	
	Halichoeres miniatus	
	Halichoeres nebulosus	
	Halichoeres margaritaceus	
	Hemigymnus melapterus	
	Stethojulis interrupta	
	Thalassoma lunare	
Scaridae	*Scarus rivulatus*	Benthic algae
Acanthuridae	*Acanthurus xanthopterus*	Benthic algae
Siganidae	*Siganus lineatus*	Algae & seagrass

Table 6.I. Summary of feeding habits of some common fish at Magnetic Island (*after Hiatt and Strasburg 1960 and Randall *et al.* 1990).

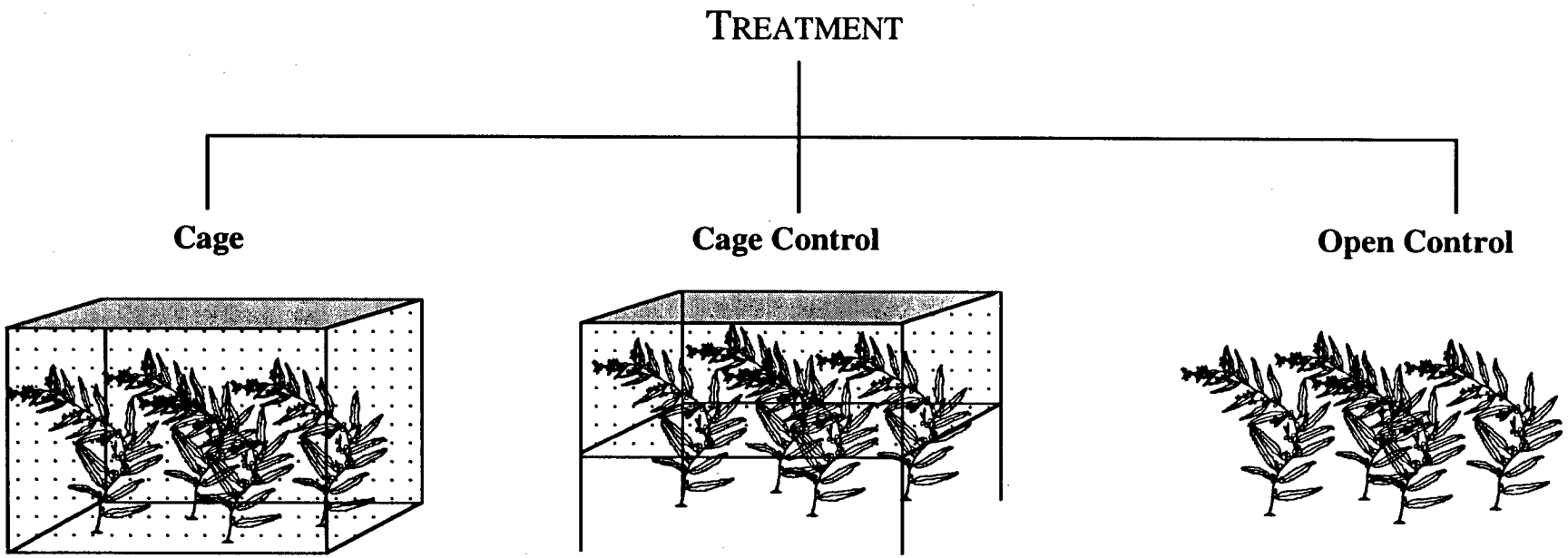


Figure 6.2. Experimental design to test the effects of predator exclusion on abundance of epifauna.

away. Cage controls had an identical construction but lacked side panels. Open control areas of undisturbed *Sargassum* were also established close to cages. Four replicates of each treatment (cage, cage control and open control) were established.

As with the habitat complexity experiment, sampling times were decided *a priori*: in this case the sampling times were 0 (pre-treatment), 2, 4 and 8 weeks after cage deployment (12-13.10.91, 28.10.91, 11.11.91 and 3.12.91 respectively). These sampling times were designated following previous studies (e.g. Leber 1985), the results of the recolonisation experiment of Chapter 4 and its implications for the rates of community response and to try to minimise caging artifacts. Each sample consisted of 3 haphazardly selected plants from each treatment and collected as in section 3.3.1. Cage samples were collected after tipping the cage sideways following removal of the rubble and pegs holding the skirt down and any obviously disturbed areas were avoided. Cage control samples were sampled by reaching through the open panels on the side and collecting haphazardly selected plants from within and open control plants in the usual monthly sampling manner. At each time all treatments were examined for approximately 10 minutes to observe the behaviour of fish in and around cages although these data were not quantified. At 4 weeks three juvenile apogonid fish were observed inside one of the cages; these were caught and their gut contents revealed little or no epifauna. At 8 weeks cages were starting to show signs of deterioration with breaks appearing in the mesh of two. Fish were observed feeding inside these cages, so results for this time were excluded from analyses. Over the period during which this experiment was performed an attempt was made to quantify abundance and feeding rates of *Halichoeres* in the *Sargassum* areas. Visual censuses of the number of *Halichoeres* were conducted on 13.10.91, 24.10.91, 27.10.91 and 17.12.91 by swimming along a 30 or 40 m fibreglass tape laid parallel to the shoreline and counting the number of fish individuals within 1 m either side of the tape. Between 9 and 20 censuses were performed between 1415 and 1630 hrs at a depths ranging from 2 to 7 m below mean sea level. A brief quantification of feeding rates of *Halichoeres* was performed at 1530 hrs on 27.10.91 at 2-3 m depth by following individual fish for as long as possible (usually less than 2 minutes) and counting the number of bites which they took in that period.

Again log (x+1) transformed abundance of the epifaunal taxa was analysed using MANOVA after stepwise discriminate analysis, using a 3-way fixed factor design with factors TIME, TREATMENT (cage, cage control or open control) and SITE (since individual plants from each cage could not be considered as independent). Pillai's Trace revealed significant ($p<0.0003$) interactions between factors at both 2 and 3 way interactions, so data were then analysed using CDA. Responses of

individual taxa to experimental manipulations were analysed using a 3-way ANOVA with the same factors as given above.

6.4 RESULTS

6.4.1 Effects of Habitat Complexity

The effect of epiphytes on abundance of epifauna was striking. CDA revealed significant community differences across treatments and times (Figures 6.3 and 6.4). The first three canonical axes in the analysis represented 40.7%, 28.5% and 12.9% of the total sample variation while the other 7 canonical axes together represented the remaining 17.9% with no individual axis greater than 6%. It was assumed, therefore, that the most important biological differences were represented in the first three canonical axes, hence only these have been displayed. A plot of the first two canonical axes (Figure 6.3) showed clear separation between epi + communities and epi – communities, especially early in the experiment (2 and 4 weeks). All of the epi + points were clustered in the top right-hand quadrant of the plot, while the epi – points were generally diametrically opposed, in the bottom left-hand quadrant except for the 8 week samples. The bi-plot in Figure 6.3 shows the taxa whose abundance affected the distribution of the points – this indicates that epi + communities had higher abundance of gastropods, gammarids and tanaids than epi – communities, which is confirmed by the bubble plots of Figures 6.5-6.7. Epi + and control communities had greater similarities over the course of the experiment, indicated by their tight clustering, while epi – communities showed directional movement. There seemed to be relatively little difference in the composition and abundance of epifauna between the two types of mimic, since the epi + and epi – points for each time point were close (except for rope epi – at 8 weeks which had unusually high levels of caprellid amphipods and hence a large negative value on canonical axis 1). A final point to note is that control communities were different from both epi + and epi – communities, at least for the first 4 weeks. A similar set of patterns was found for the plot of the 1st and 3rd canonical axes in Figure 6.4. Again, clear separation was evident between epi + and epi – points, and the type of mimic did not strongly affect the results; however, clustering among all epi + and all epi – treatments over time was approximately the same on this plot.

Examination of the univariate data showed that different taxa had different responses to type, treatment and time (Figures 6.8-6.14), hence the significant value for Pillai's Trace in the MANOVA. The one consistent pattern displayed was a general decline in abundance over the course of the experiment on all treatments

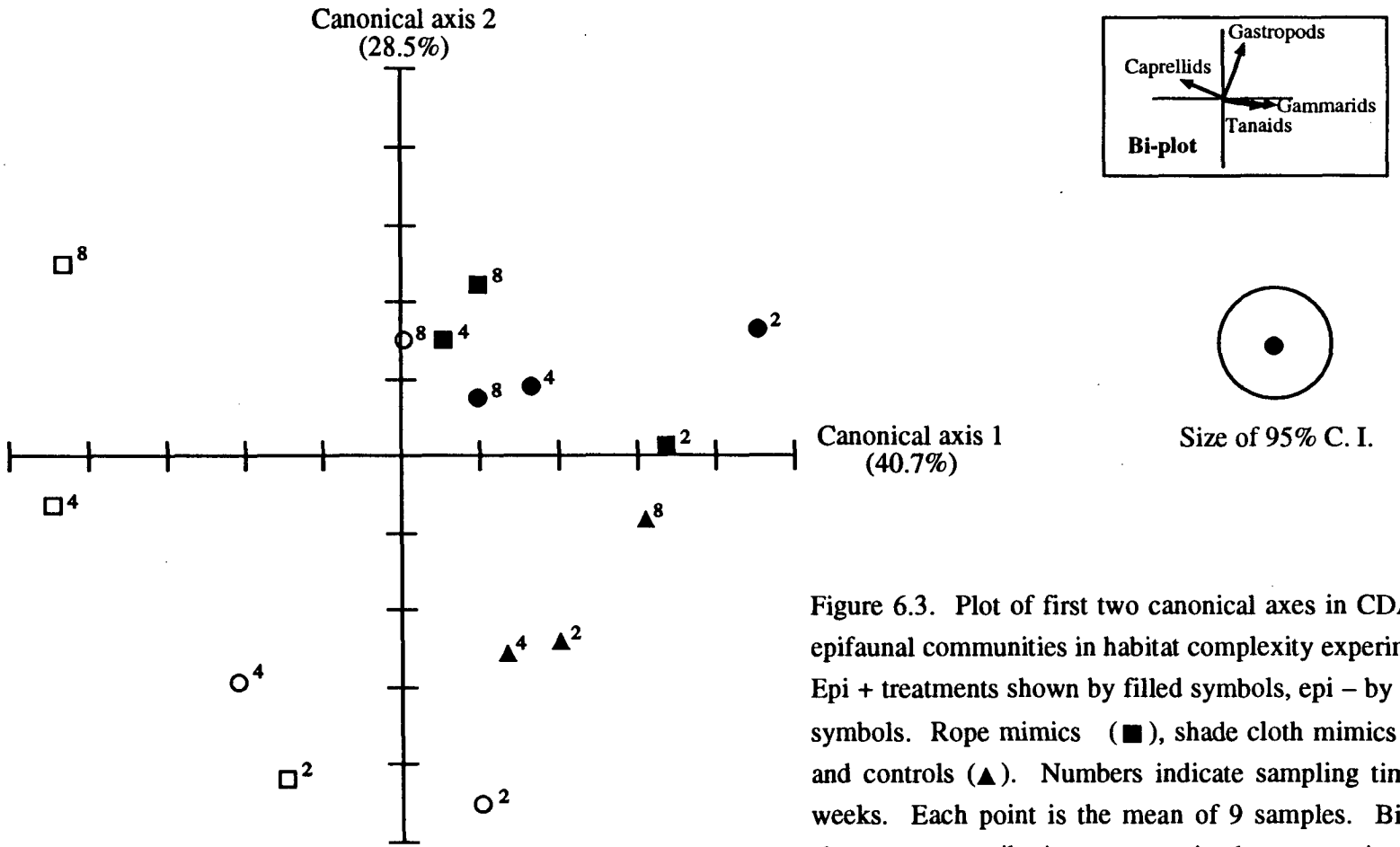
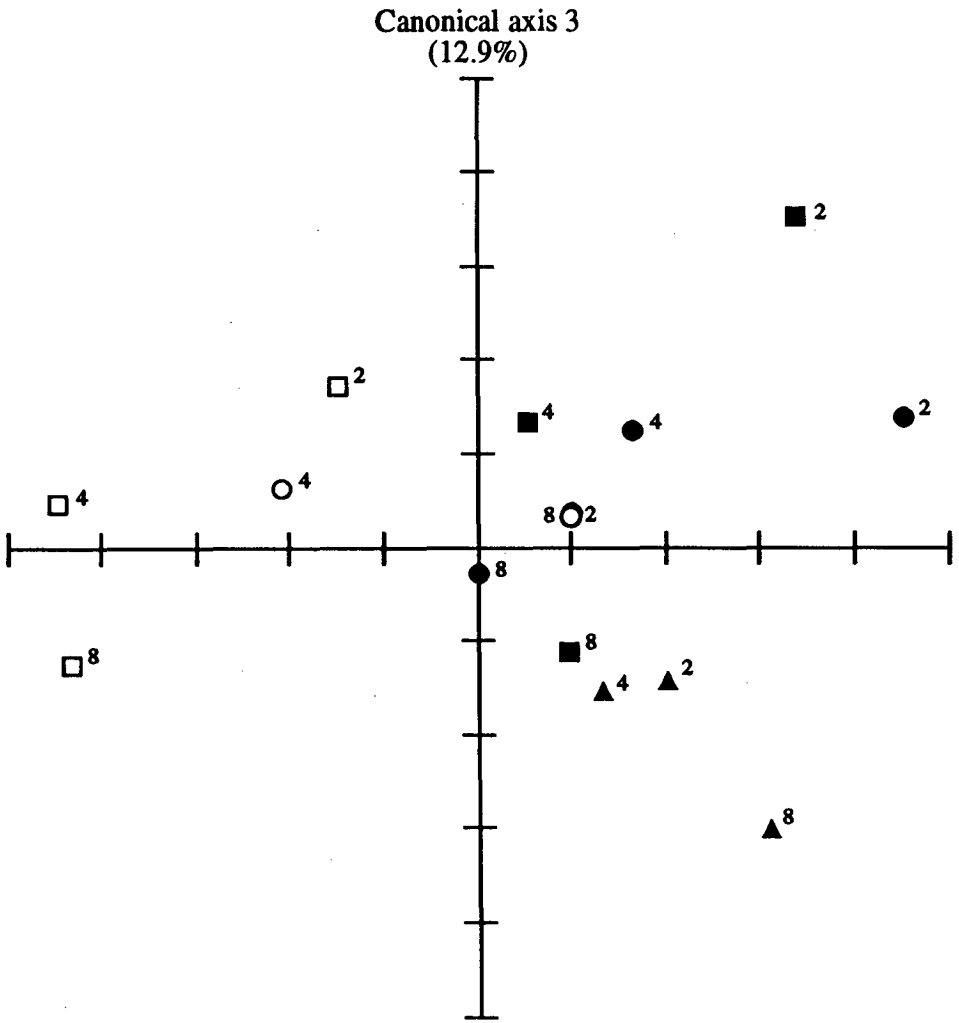
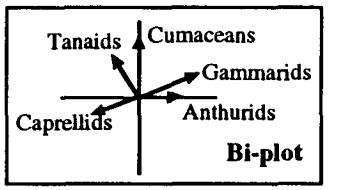


Figure 6.3. Plot of first two canonical axes in CDA on epifaunal communities in habitat complexity experiment. Epi + treatments shown by filled symbols, epi – by open symbols. Rope mimics (■), shade cloth mimics (●) and controls (▲). Numbers indicate sampling time in weeks. Each point is the mean of 9 samples. Bi-plot shows taxa contributing to separation between points.





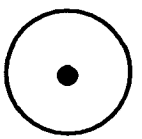


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Figure 6.4. Plot of canonical axes one and three in CDA on epifaunal communities in habitat complexity experiment. Epi + treatments shown by filled symbols, epi – by open symbols. Rope mimics (■), shade cloth mimics (●) and controls (▲). Numbers indicate sampling time in weeks. Each point is the mean of 9 samples. Bi-plot shows taxa contributing to separation between points.

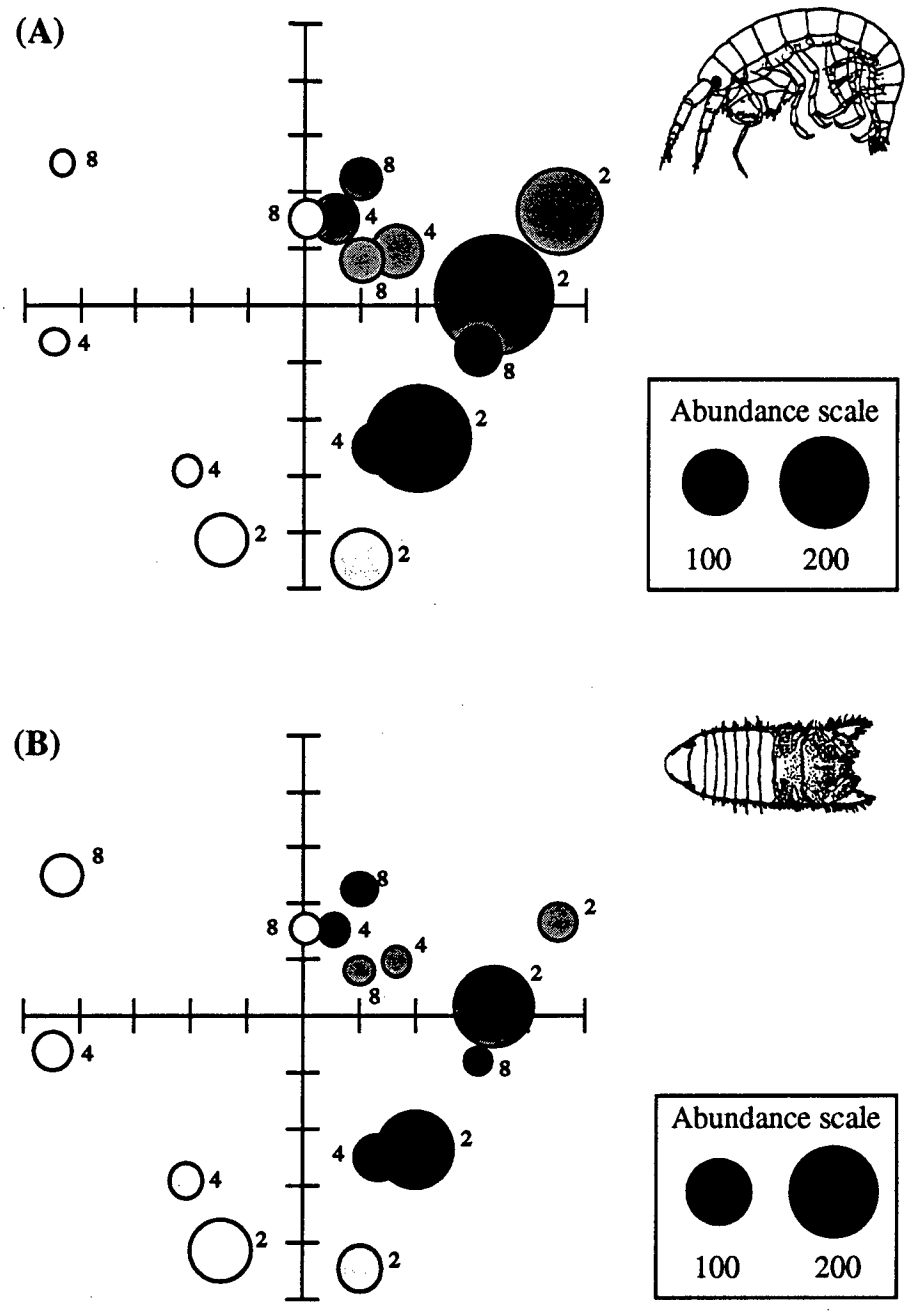


Figure 6.5. Abundance of (A) gammarids and (B) sphaeromatids superimposed on CDA plot from Figure 6.3. Size of bubbles is proportional to abundance. Rope epi + (●), rope epi – (○), shade cloth epi + (◉), shade cloth epi – (○) and control (●). n=9 for each point.

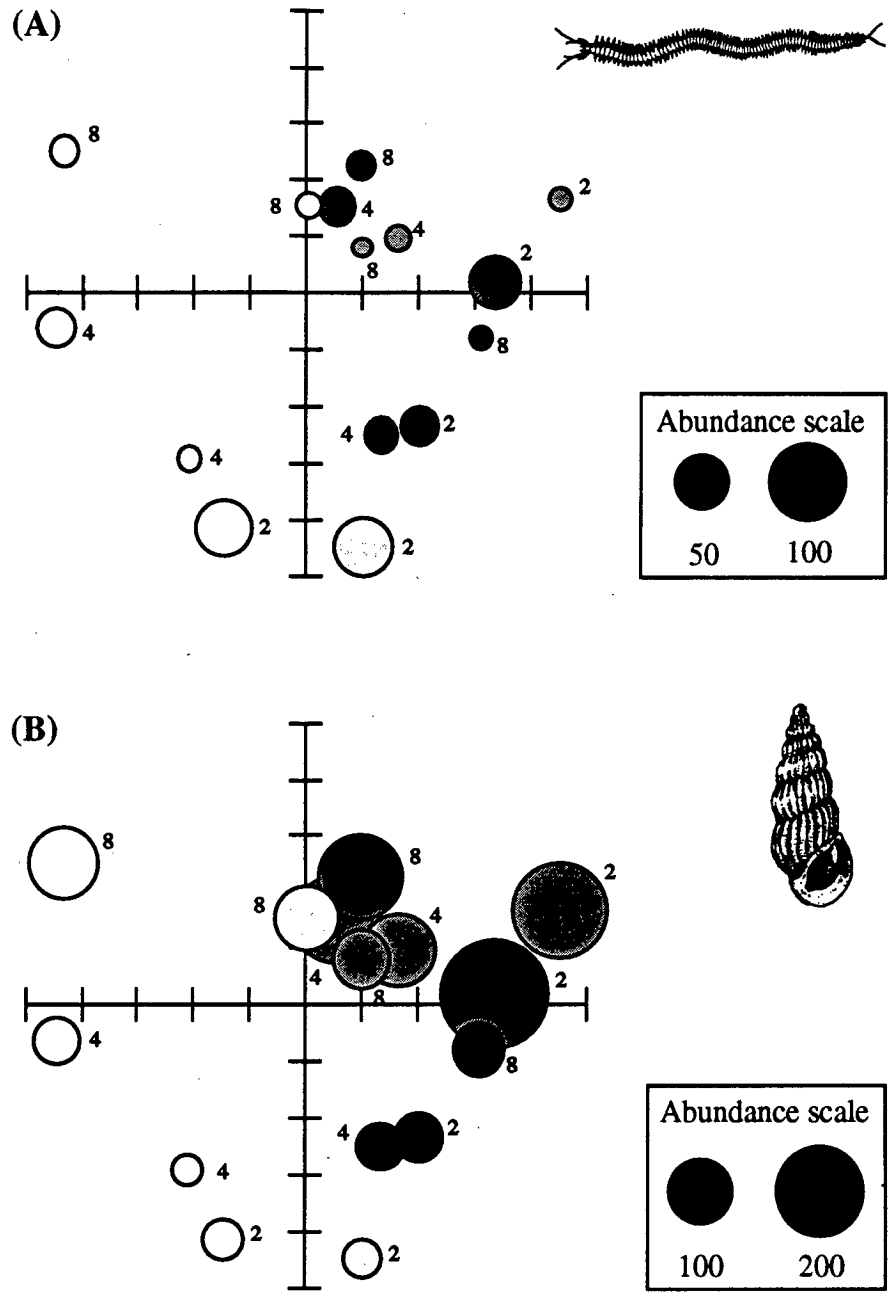


Figure 6.6. Abundance of (A) polychaetes and (B) gastropods superimposed on CDA plot from Figure 6.3. Size of bubbles is proportional to abundance. Rope epi + (●), rope epi – (○), shade cloth epi + (◍), shade cloth epi – (○) and control (●). n=9 for each point.

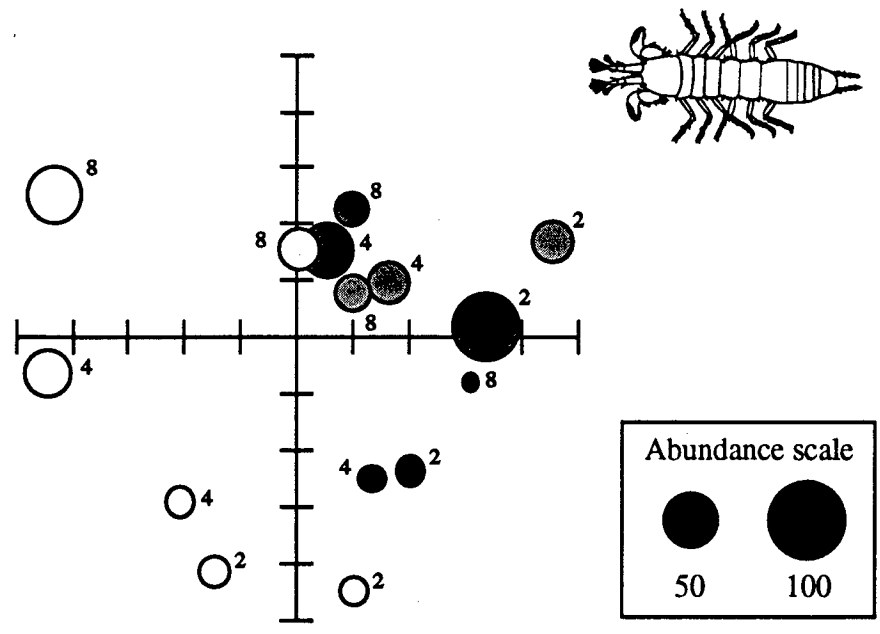


Figure 6.7. Abundance of tanaids superimposed on CDA plot from Figure 6.3. Size of bubbles is proportional to abundance. Rope epi + (●), rope epi – (○), shade cloth epi + (◍), shade cloth epi – (○) and control (●). n=9 for each point.

including controls, shown clearly for the 5 most abundant taxa in the bubble plots of Figures 6.5-6.7. This probably represents the seasonal patterns of abundance superimposed over the experimental responses, since the experiment was performed over the period during which abundance of crustaceans drop rapidly (September-November, see section 3.4). A taxon-by-taxon treatment of results is given below:

(1) Gammarids (Figure 6.8). Epi + treatments were significantly preferred over epi – treatments at all time points. This was most pronounced at 2 weeks, but still apparent at 4 and 8 weeks. There were no consistent differences between the types of mimic. Abundance on epi + treatments was never significantly different from control levels.

(2) Sphaeromatids (Figure 6.9). It appears that rope mimics were preferred over shade cloth mimics at all time points, although this difference was only significant at two weeks. There were no significant differences between epi + and epi – treatments except at 2 weeks when epi + was preferred over epi –. Abundance of sphaeromatids on both treatments was comparable to control abundance at all time points

(3) Tanaids (Figure 6.10). Epi + mimics were significantly preferred over epi – mimics at 2 and 4 weeks and there is some evidence at both these times for preference of rope over shade cloth. High abundance of tanaids was found on rope epi – mimics at 8 weeks. Abundance on both experimental treatments was equal or greater than control abundance at all time points.

(4) Caprellids (Figure 6.11). Abundance of caprellids was very low throughout the experiment, except for rope epi – at 4 and 8 weeks, which had significantly greater abundance than any other treatment.

(5) Other isopods (Figure 6.11). There were no significant differences between types or treatments at any time point.

(6) Cumaceans (Figure 6.12). Again, there were no significant differences between types or treatments, except for consistently higher abundance on mimics than on real *Sargassum* at 2 and 4 weeks.

(7) Decapods (Figure 6.12). Epi + mimics were significantly preferred over epi – mimics at 2 weeks, thereafter there were no significant differences. Abundance on both treatments was equal or greater than control abundance at all times.

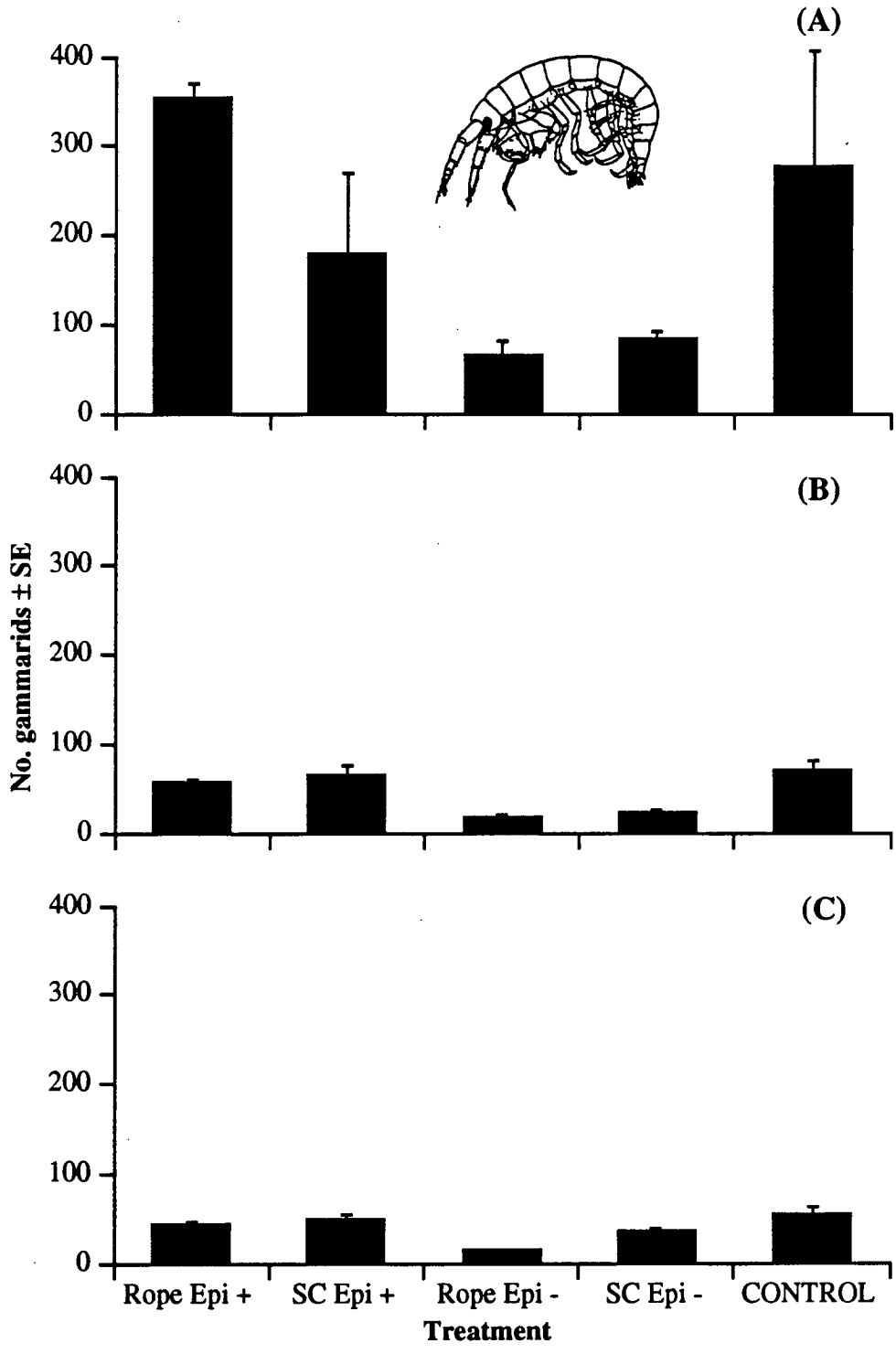


Figure 6.8. Mean abundance of gammarids in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

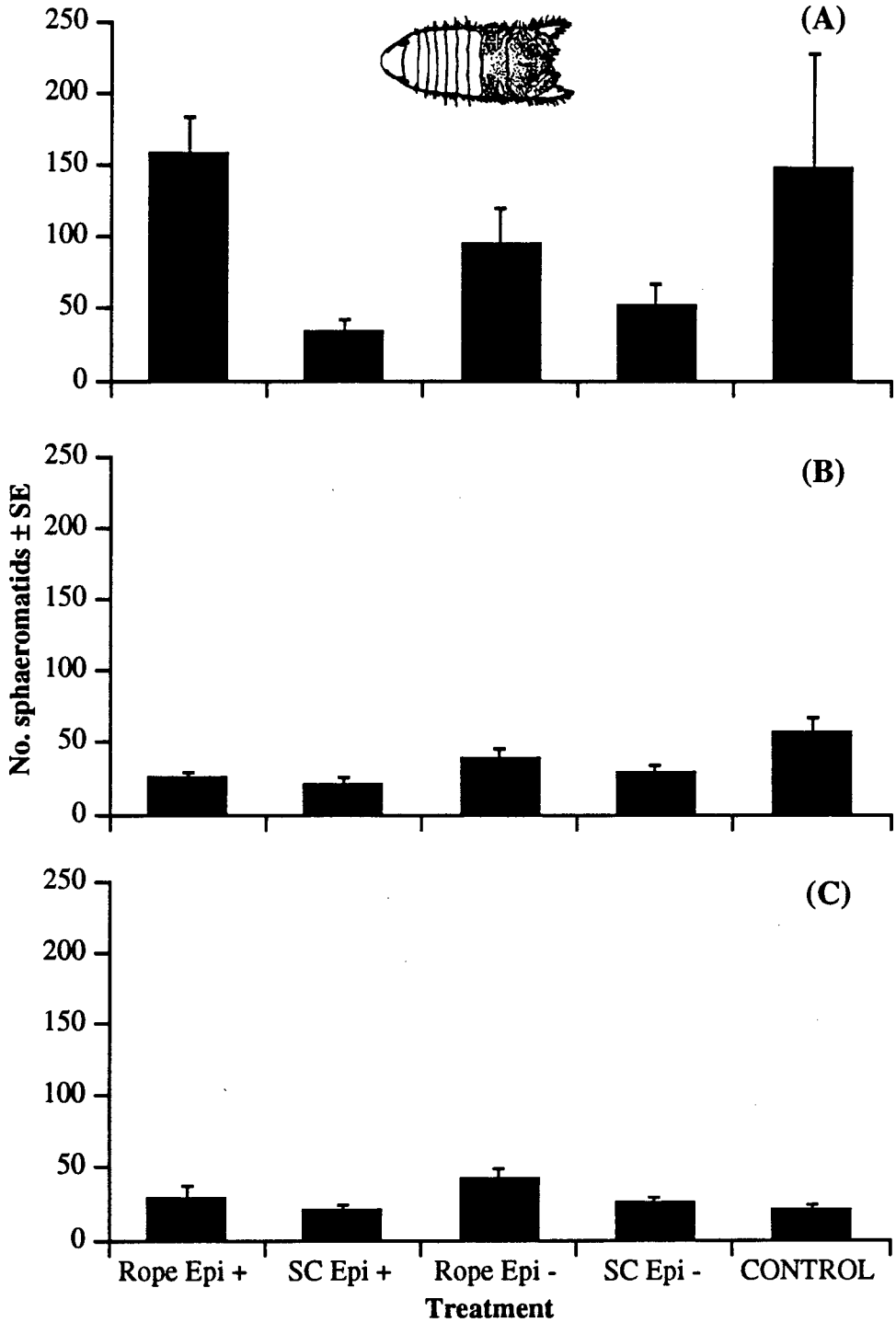


Figure 6.9. Mean abundance of sphaeromatids in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

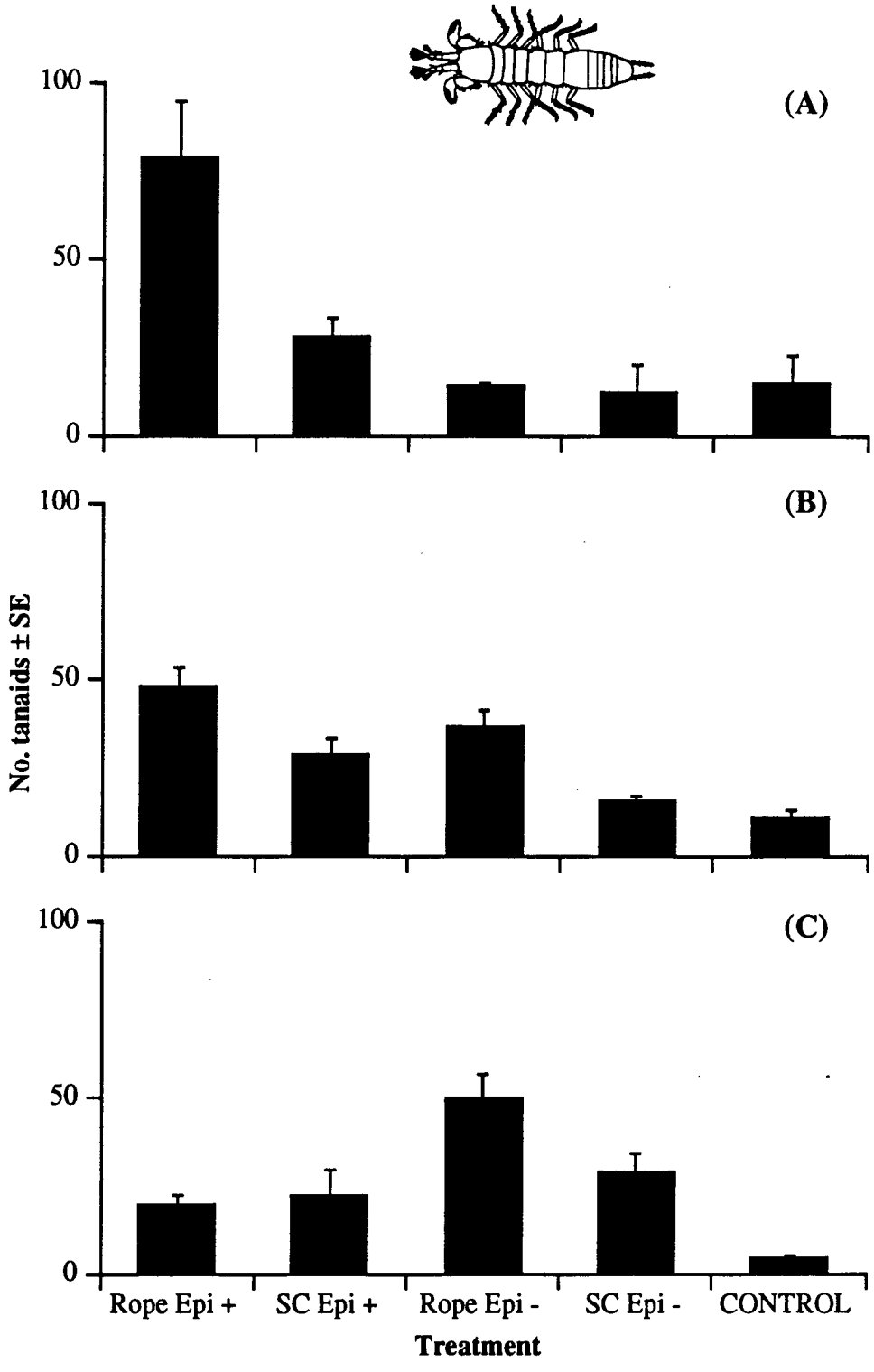


Figure 6.10. Mean abundance of tanaids in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

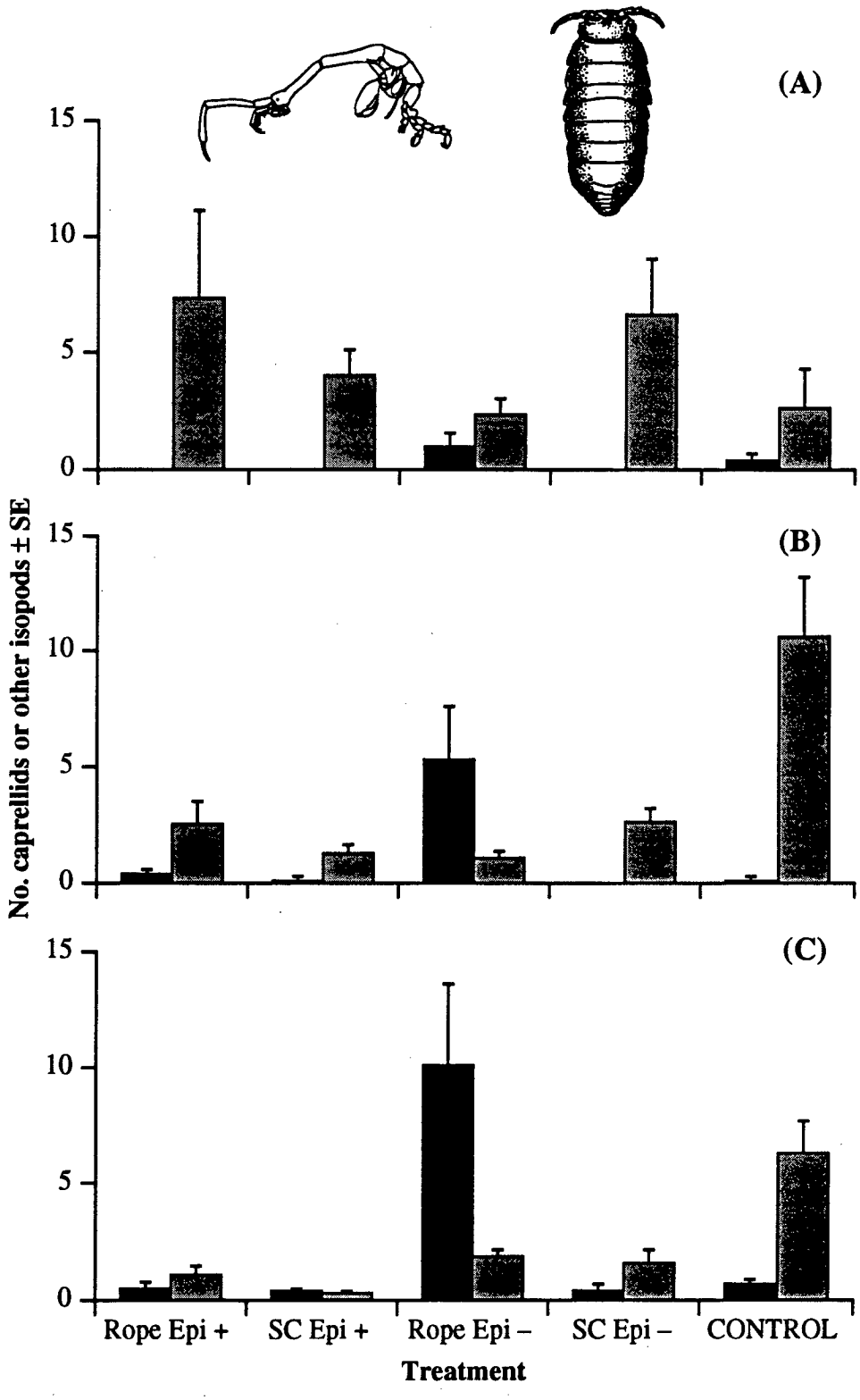


Figure 6.11. Mean abundance of caprellids (■) and other isopods (▩) in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

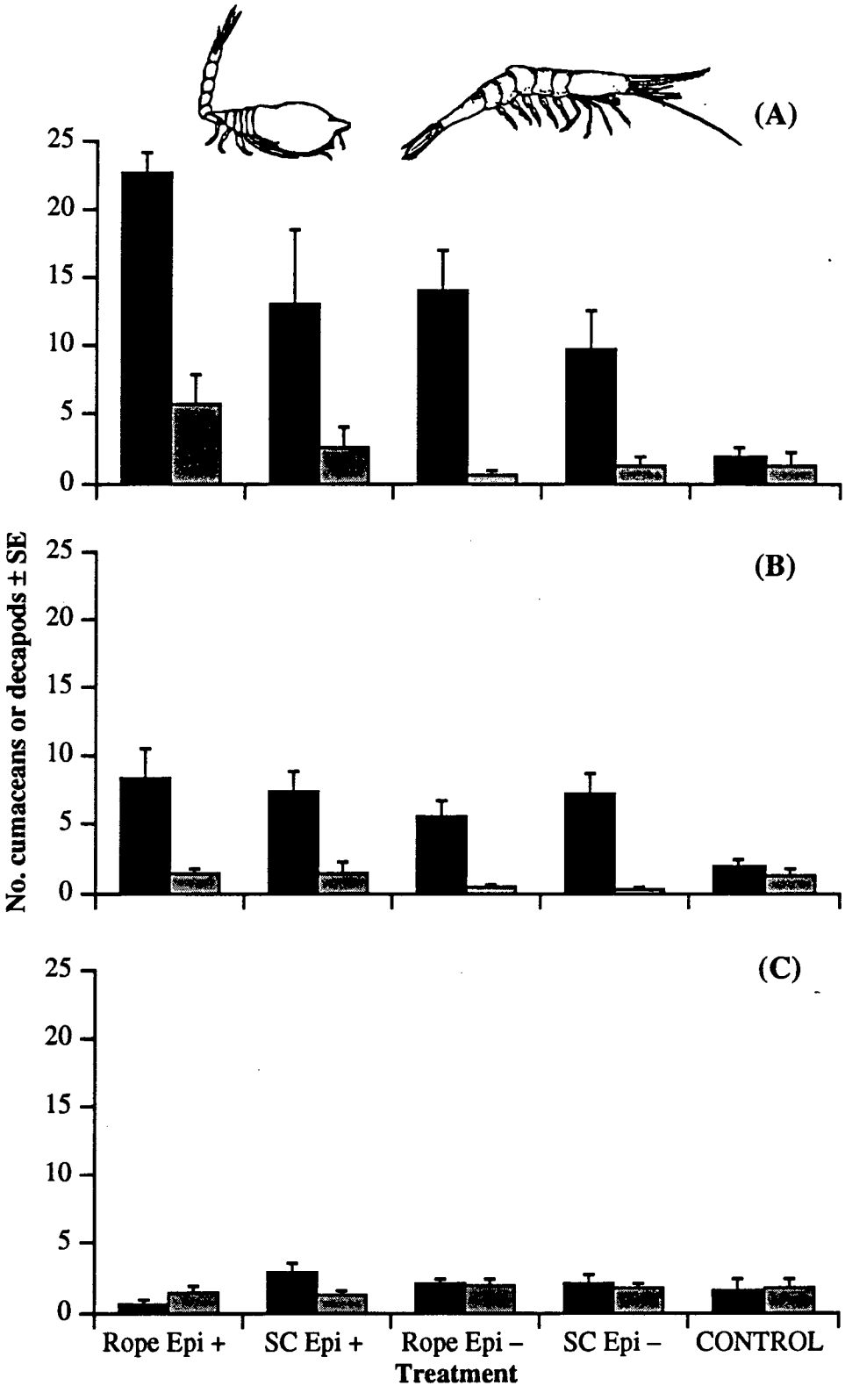


Figure 6.12. Mean abundance of cumaceans (■) and decapods (▨) in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

(8) Polychaetes (Figure 6.13). Abundance of polychaetes was extremely variable. Rope was significantly preferred over shade cloth at 4 weeks but no effect of epiphytes was observed.

(9) Gastropods (Figure 6.14). Epi + treatments were significantly preferred over both epi – and control treatments at 2 and 4 weeks, with no significant differences at 8 weeks. No effect of type was detected.

All of the taxa enumerated had equal or greater abundance than control plants suggesting that colonisation on to artificial plants was extremely rapid. It appears that different taxa responded to the shape of the mimic and/or its levels of epiphytes in different ways; however 5 of the 9 taxa, including both of the most abundant (gammarids and gastropods) showed increased abundance on epi + treatments, indicating that this was a general response.

6.4.2 Effects of Predation by Fishes

It appeared from the initial survey in August 1991 that there were a number of potential epifaunal predators living on the reef at Magnetic Island (Table 6.I). During the whole of the study period of this work (August 1990-August 1993) I have observed a number of different fish species feeding on epifauna. The most obvious of these fish have been labrids, especially *Halichoeres*. Data from visual censuses of this fish are given in Figure 6.15. This shows that *Halichoeres* are indeed abundant at Magnetic Island, with abundance of up to 5 individuals 10 m^{-2}. This may an underestimate of their true abundance because of the cryptic nature of some of the species and my inexperience as an observer. Over the depth range surveyed (2-7 m below mean sea level) there appeared to be no differences in the abundance of *Halichoeres* (Figure 6.15A) although other unquantified observations indicate that they are not present at the bottom of the reef slope at depths of >7 m. It is not possible to draw any conclusions from the temporal variation in abundance (Figure 6.15B) due to insufficient samples – these values are intended merely as an estimate of the magnitude of the fish abundance. Observation of 20 individual fish on 27.10.91 gave a feeding rate on epifauna of 2.79 bites min^{-1} (± 0.48 SE), again not as a definitive value, but as an estimate. That *Halichoeres* feed on epifauna is confirmed by the gut contents which showed large amounts of amphipods, copepods and miscellaneous other crustaceans (Table 6.II).

Continuing on to the exclusion experiment, there were no discernible patterns of community response (Figures 6.16 and 6.17). The first three canonical axes of the

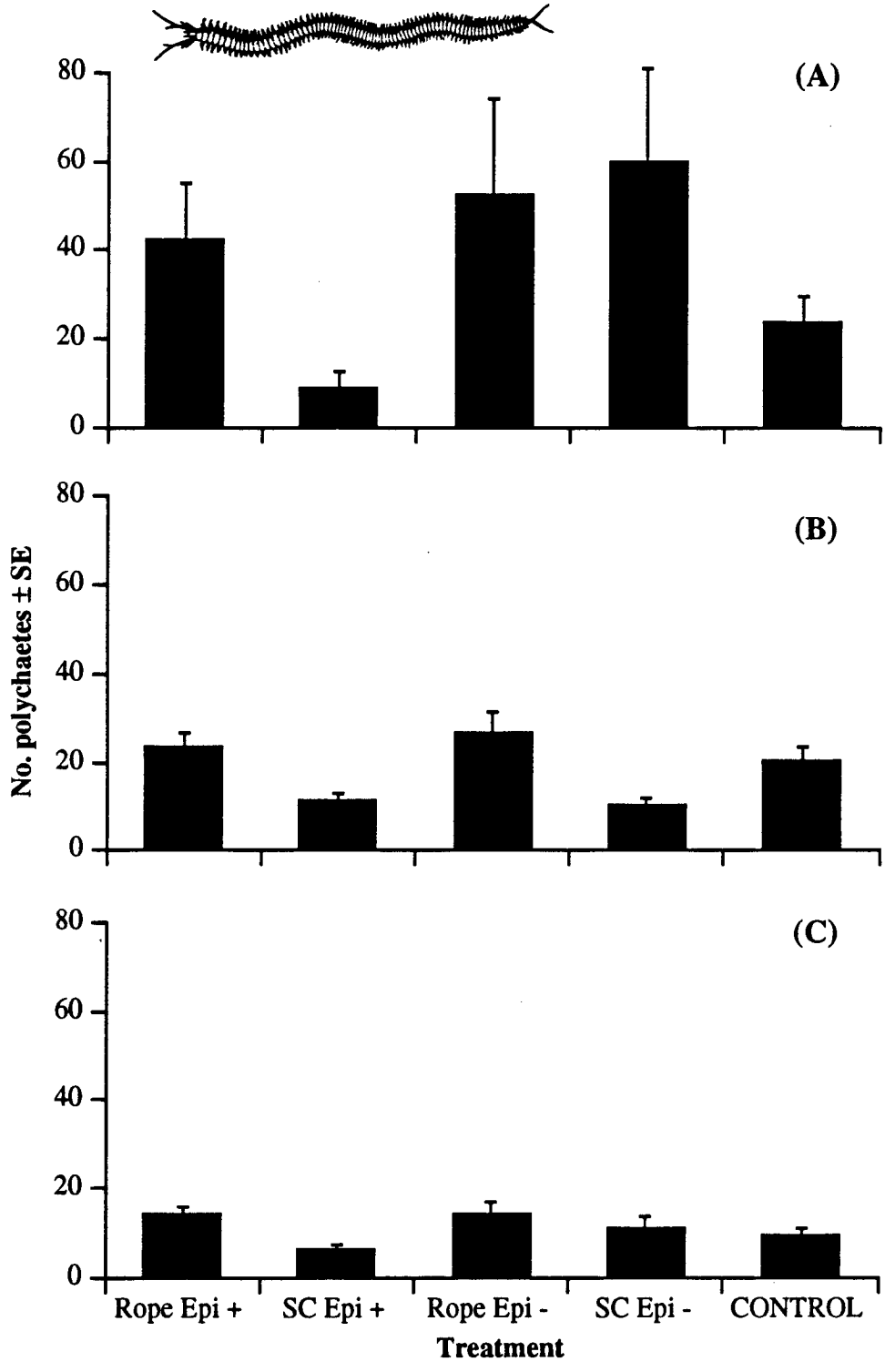


Figure 6.13. Mean abundance of polychaetes in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

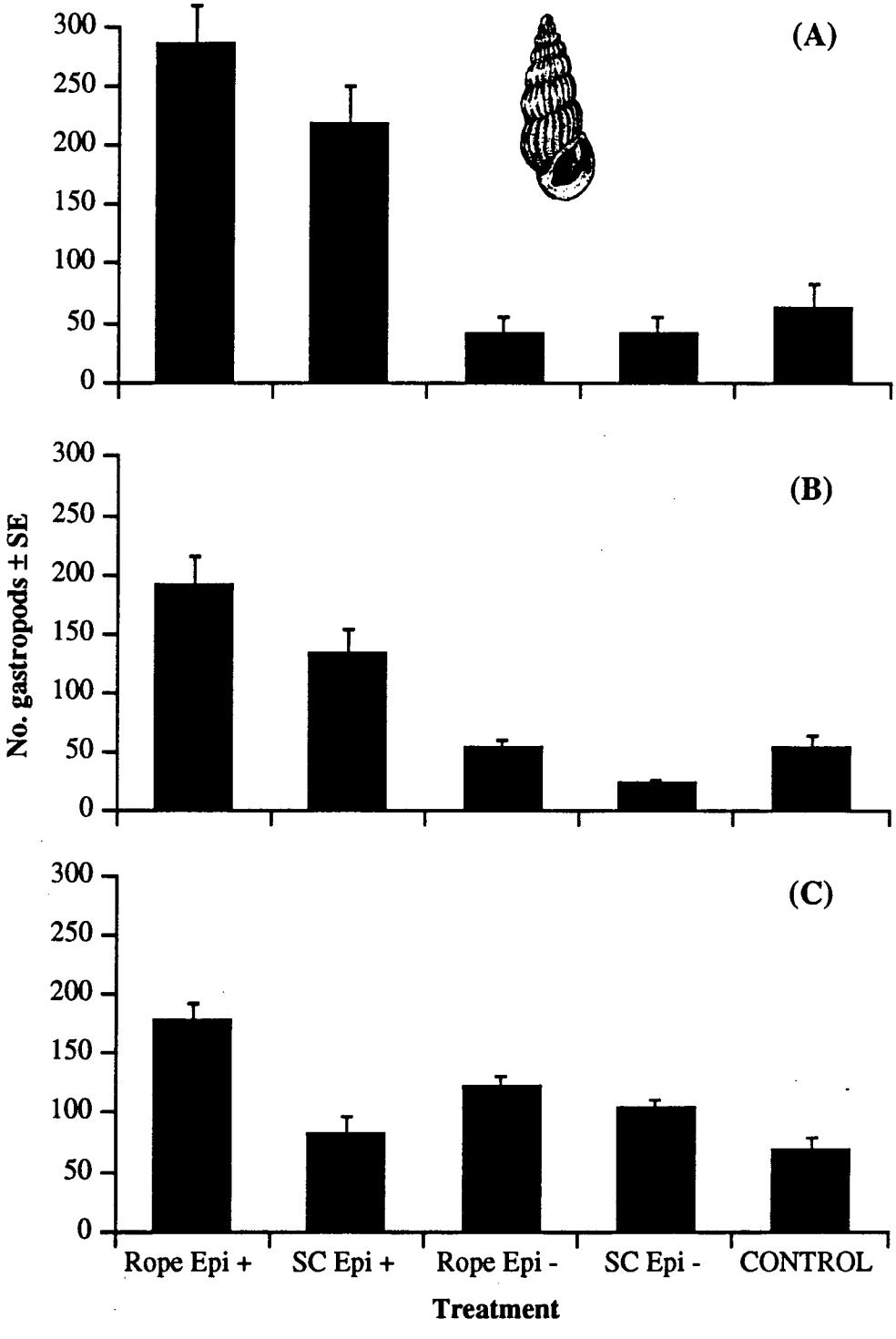


Figure 6.14. Mean abundance of gastropods in habitat complexity experiment at (A) 2 weeks (B) 4 weeks (C) 8 weeks. n=9 for each sample.

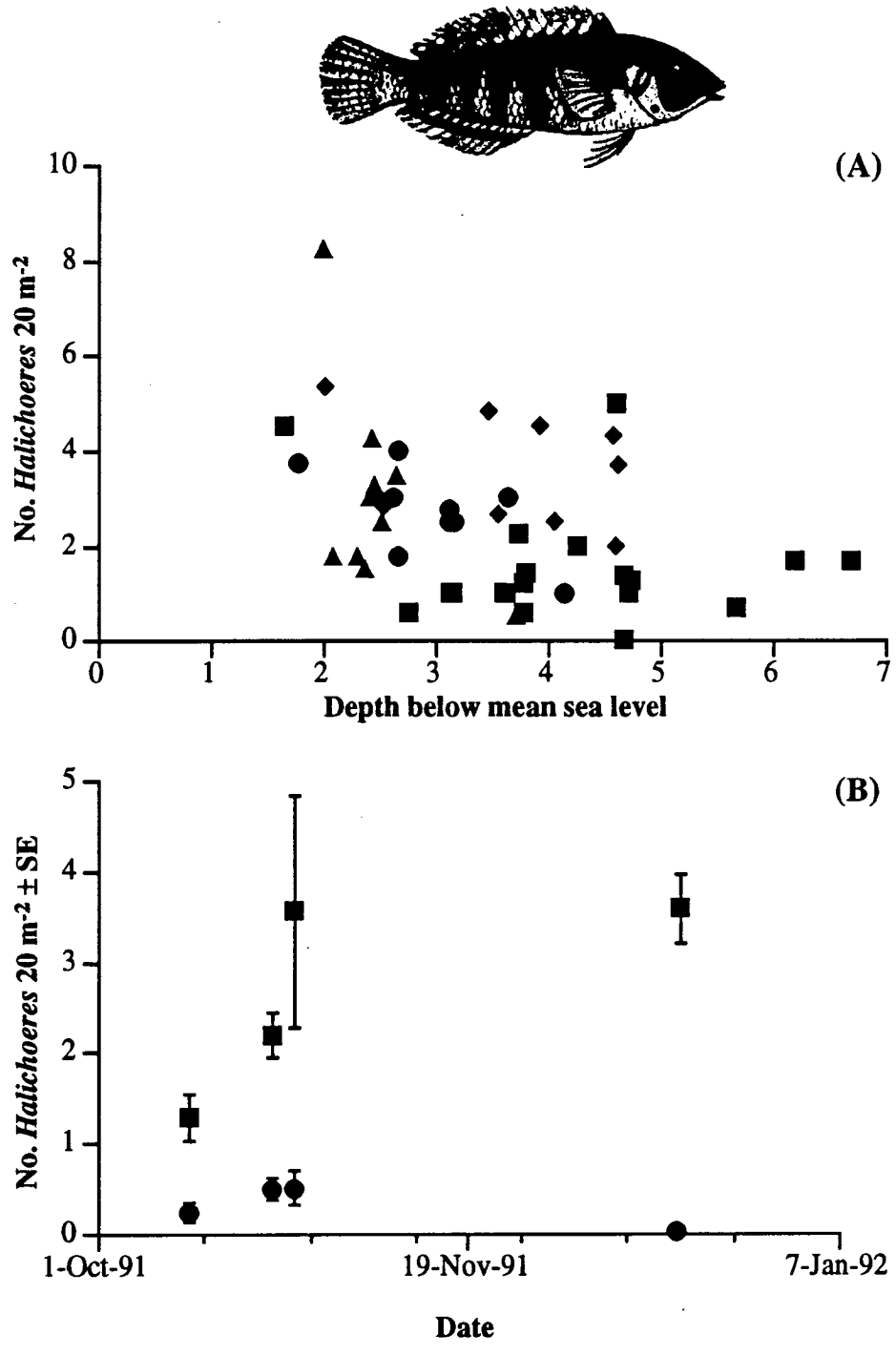


Figure 6.15. (A) Abundance of *Halichoeres spp.* at different depths. Different symbols represent different sampling dates. (B) Mean abundance of *Halichoeres dussumieri* (■) and *H. miniatus* (●) at four dates during and after exclusion experiment.

Fish species	No. examined	Gut contents		
		Food item	Approximate % of total food	% of fish containing item
Halichoeres dussumieri	10	Gammarids	50	100
		Sphaeromatids	5	50
		Copepods	15	100
		Miscellaneous crustaceans	5	100
		Polychaetes	10	70
		Gastropods	5	10
		Unidentified fragments	10	100
Halichoeres miniatus	10	Gammarids	45	100
		Sphaeromatids	10	80
		Copepods	5	70
		Miscellaneous crustaceans	15	100
		Polychaetes	10	60
		Gastropods	5	30
		Unidentified fragments	10	100

Table 6.II. Gut contents of *Halichoeres dussumieri* and *H. miniatus* collected from Nelly Bay on 20.8.91

CDA analysis explained 41.0%, 16.5% and 12.6% of total sample variation with the other 7 canonical axes explaining the remaining 29.9% (with no axis greater than 8.9%), so again only the first three canonical axes were considered. The only pattern evident in the plot of the first two canonical axes (Figure 6.16) is that the open control communities were grouped more closely together than either cage or cage control samples, which indicates that these communities had greater self-similarity. There appear to be no other groupings by time or treatment. The same lack of pattern is shown in the plot of canonical axes 1 and 3 (Figure 6.17), again indicating the lack of any overall community response to time or treatment.

Thus to determine the responses to experimental manipulation, the univariate data for each taxa were examined (Table 6.III and Figures 6.18-6.25). Again each taxon is discussed individually:

(1) Gammarids (Table 6.III and Figure 6.18). No change in abundance of open controls was observed. A significant decrease in abundance of gammarids in both cage and cage controls compared to open controls was observed at 4 weeks, but no differences between cages and cage controls was detected.

(2) Caprellids (Figure 6.19). There was no significant difference in abundance between any combination of time and treatment and abundance at all times was extremely low.

(3) Sphaeromatids (Table 6.III and Figure 6.20). There were no significant differences over time in open control areas, but a significant decrease in abundance in both cages and cage controls (which were not significantly different from each other).

(4) Other isopods (Table 6.III and Figure 6.21). Other isopods increased significantly in open control areas from 0 to 2 weeks and thereafter remained the same, whereas abundance in both cages and cage controls decreased significantly over the same period.

(5) Tanaids (Table 6.III and Figure 6.22). There were no significant changes in abundance in cages and cage controls, but abundance increased significantly in open control areas from 0 to 2 weeks.

(6) Cumaceans and decapods (Figure 6.23). Abundance of both taxa remained the same in open control areas, but decreased significantly in cages and cage controls.

(7) Polychaetes (Table 6.III and Figure 6.24). There were no significant changes in abundance in any treatment over time.

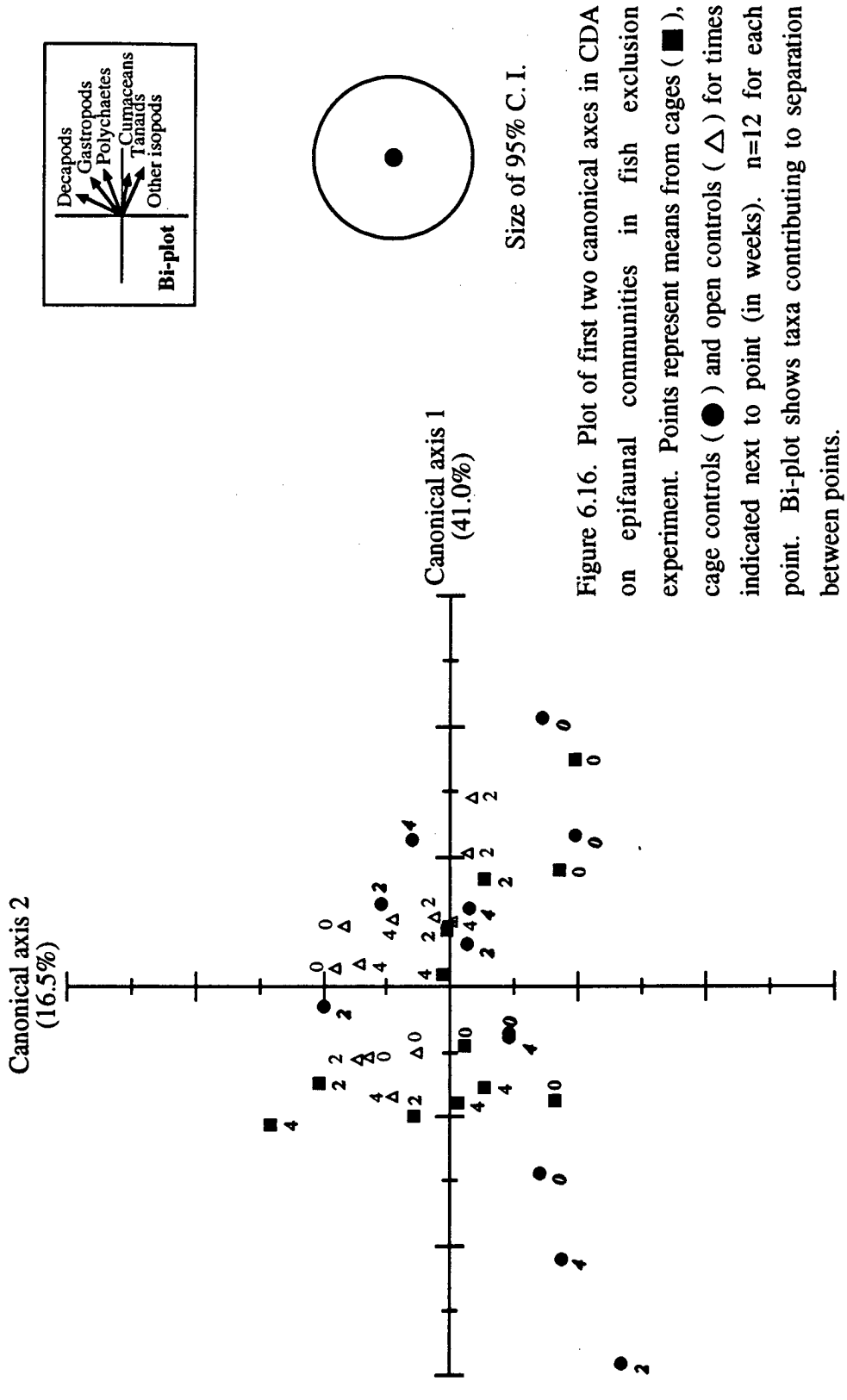


Figure 6.16. Plot of first two canonical axes in CDA on epifaunal communities in fish exclusion experiment. Points represent means from cages (■), cage controls (●) and open controls (△) for times indicated next to point (in weeks). n=12 for each point. Bi-plot shows taxa contributing to separation between points.

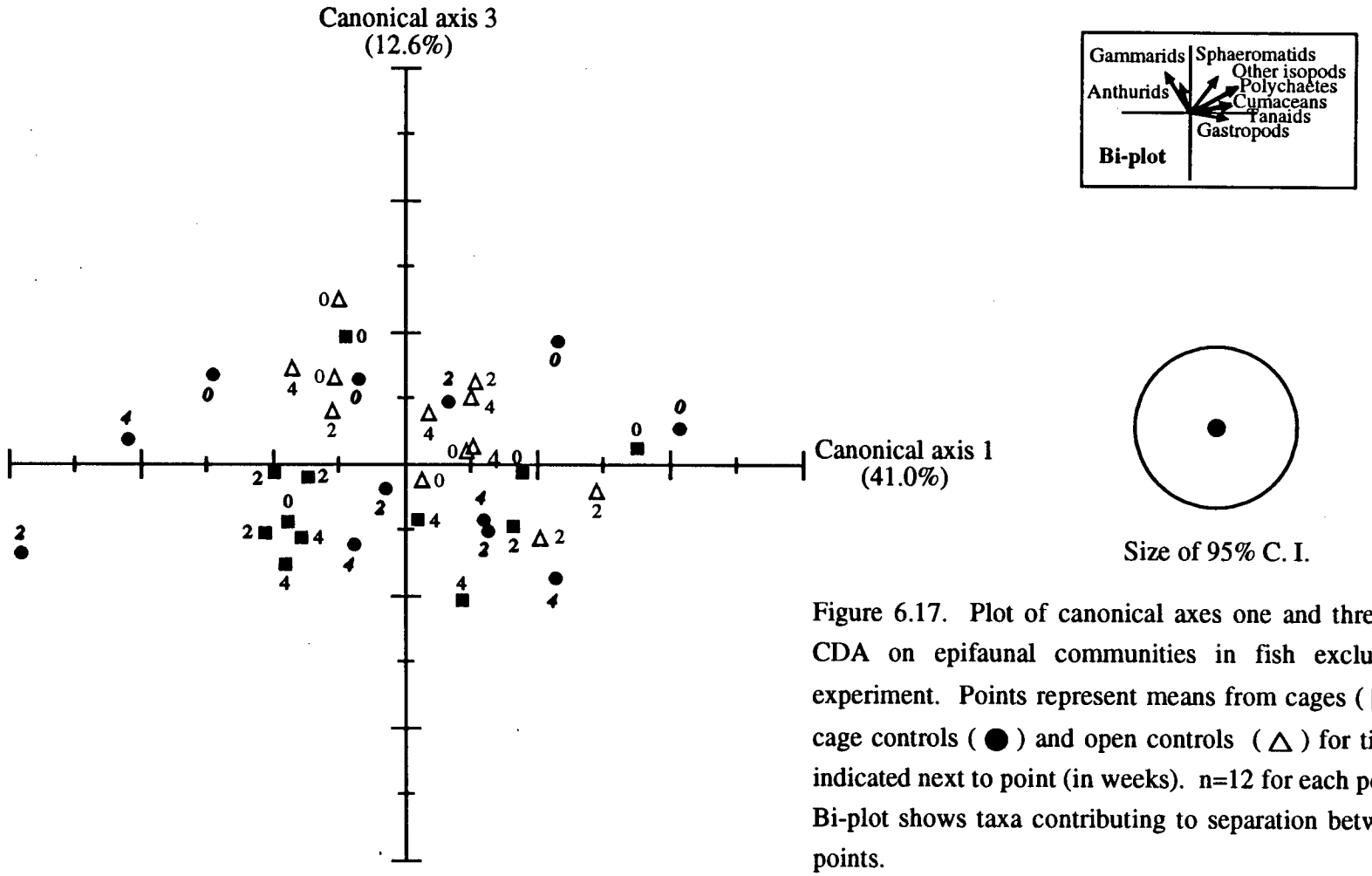


Figure 6.17. Plot of canonical axes one and three in CDA on epifaunal communities in fish exclusion experiment. Points represent means from cages (■), cage controls (●) and open controls (△) for times indicated next to point (in weeks). n=12 for each point. Bi-plot shows taxa contributing to separation between points.

A Treat.	TAXON						
	Gammarids	Sphaeromatids	Other Isopods	Tanaids	Total Crustaceans	Polychaetes	Gastropods
CA	0 4 2 *	0 2 4 **	0 2 4 ***	ns	0 2 4 *	ns	ns
CC	4 0 2 *	0 2 4 **	0 2 4 ***	ns	0 2 4 ***	ns	0 4 2 *
OC	ns	ns	0 2 4 *	0 2 4 *	ns	ns	ns
B Time (weeks)							
0	ns	CC CA OC *	CA CC OC ***	CA CC OC *	ns	CA CC OC *	ns
2	ns	ns	CA CC OC ***	ns	ns	ns	ns
4	CA CC OC **	CA CC OC ***	CA CC OC *	CA CC OC *	CA CC OC ***	ns	ns

Table 6.III. ANOVA results for effects of predation on epifauna. **A.** Time effects on treatments. **B.** Treatment effects through time. CA = cage, CC = cage control & OC = open control. Bars connect abundances that are not significantly different. Probability levels: ns = not significant ($p > 0.05$), * = $0.05 < p < 0.01$, ** = $0.01 < p < 0.001$, *** = $p < 0.001$.

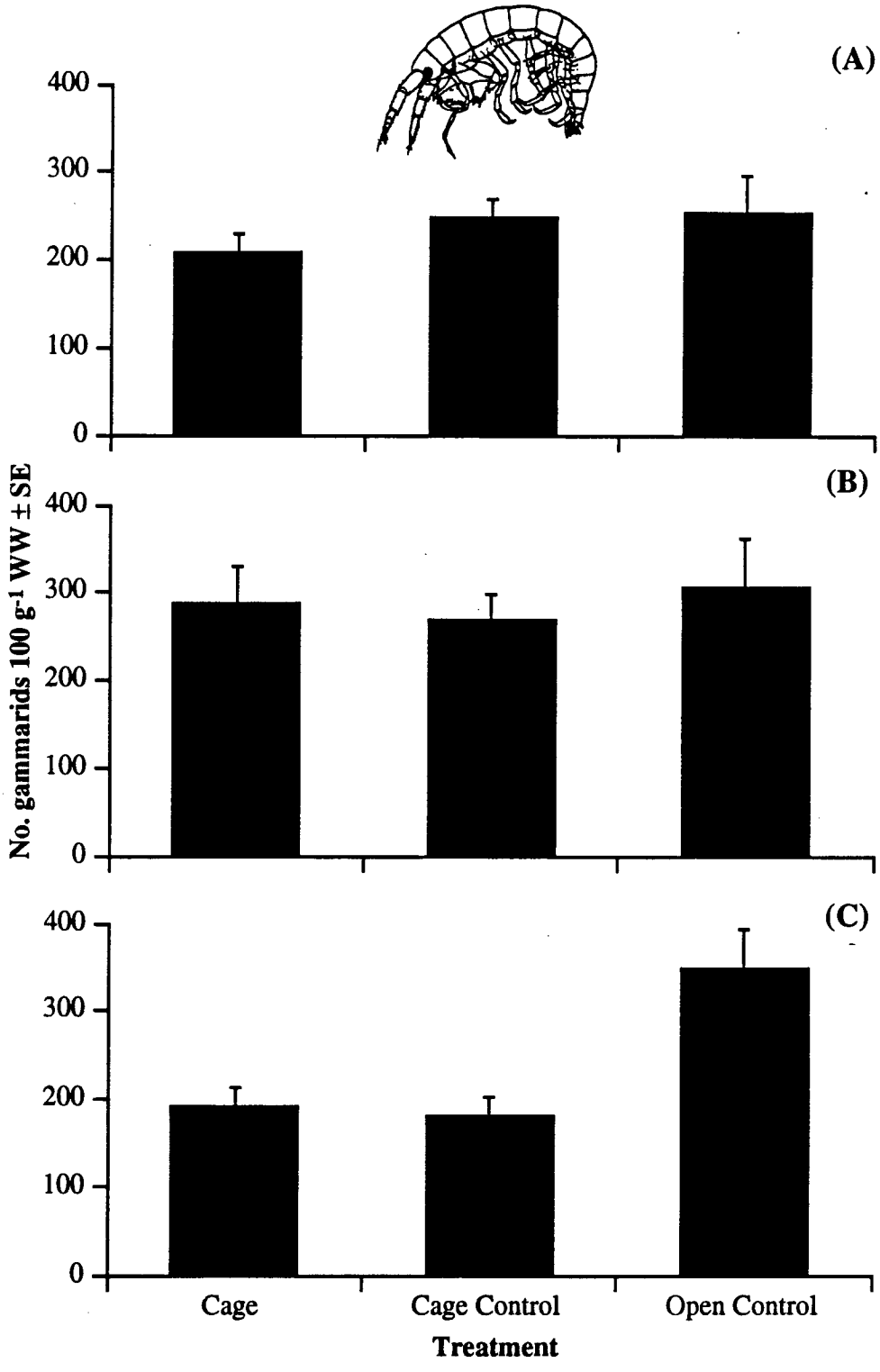


Figure 6.18. Mean abundance of gammarids in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

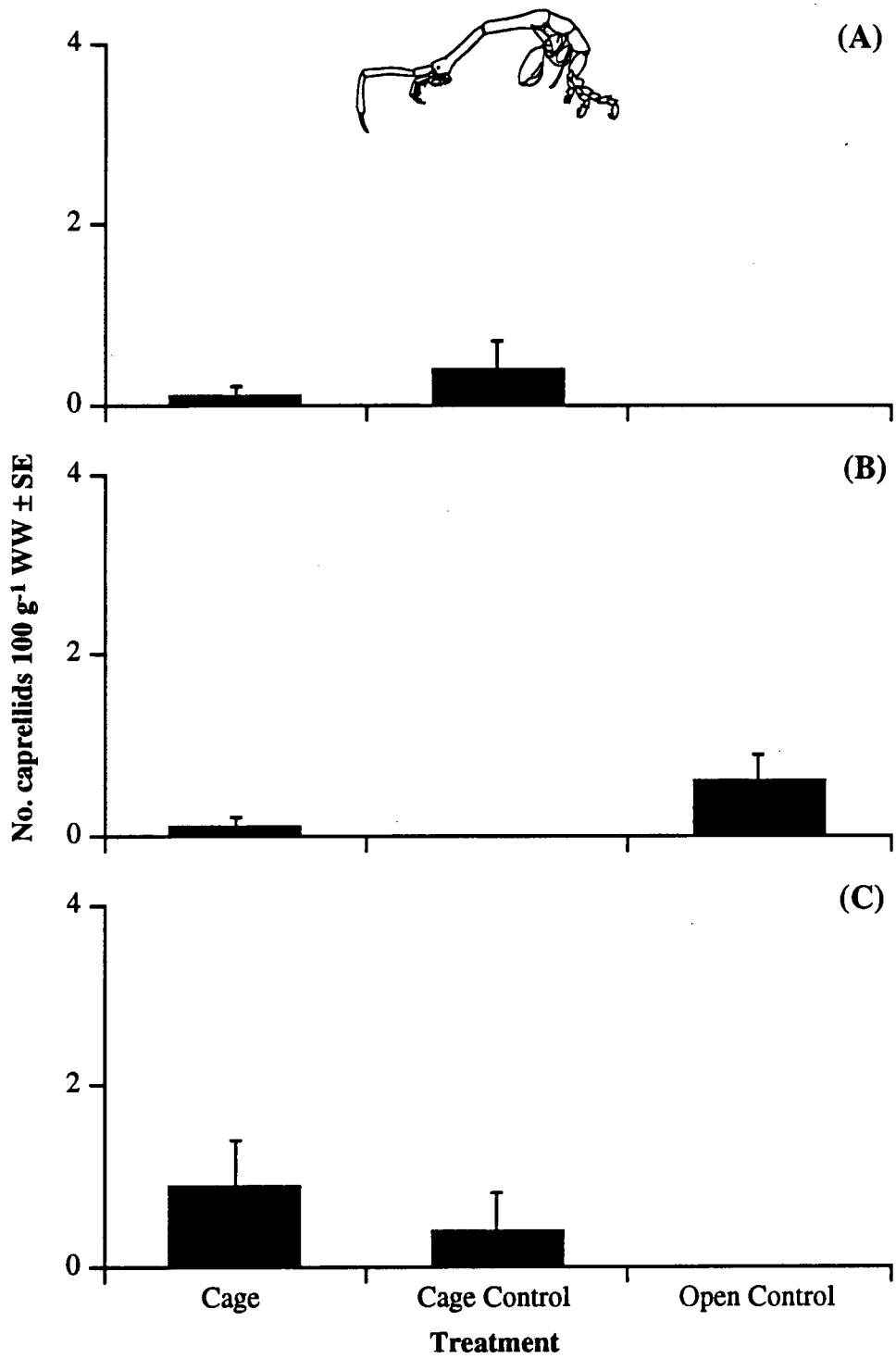


Figure 6.19. Mean abundance of caprellids in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

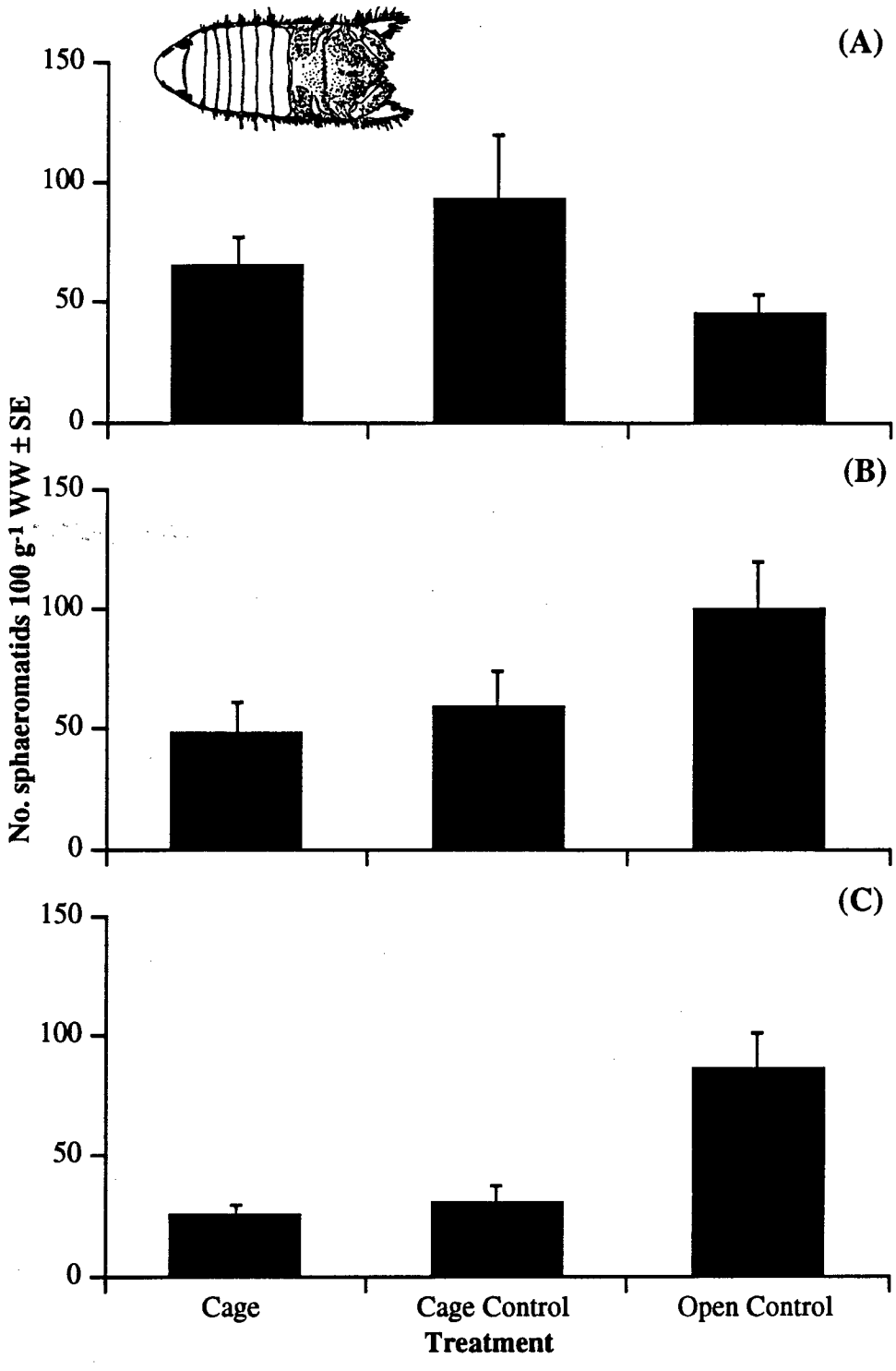


Figure 6.20. Mean abundance of sphaeromatids in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

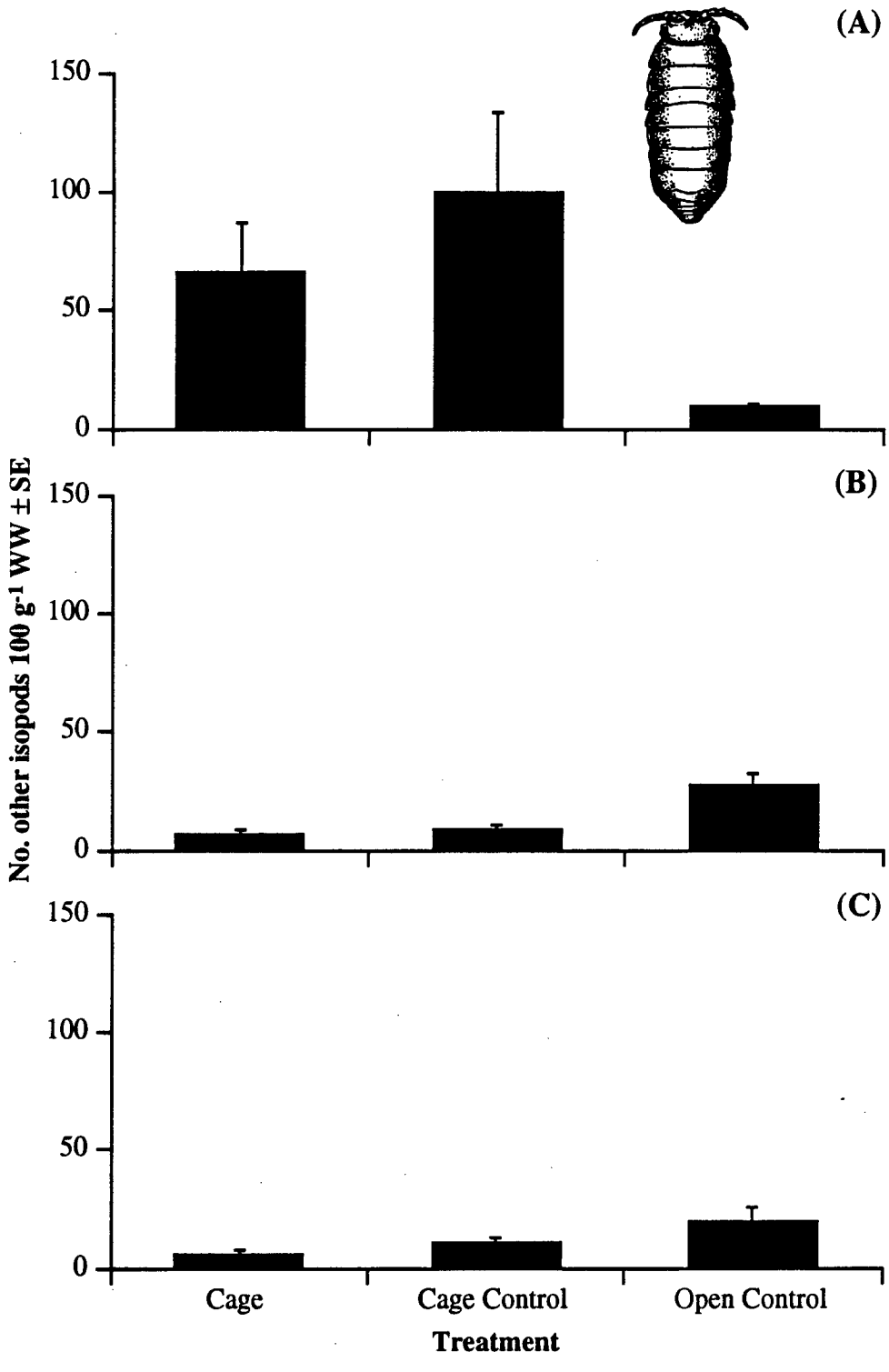


Figure 6.21. Mean abundance of other isopods in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

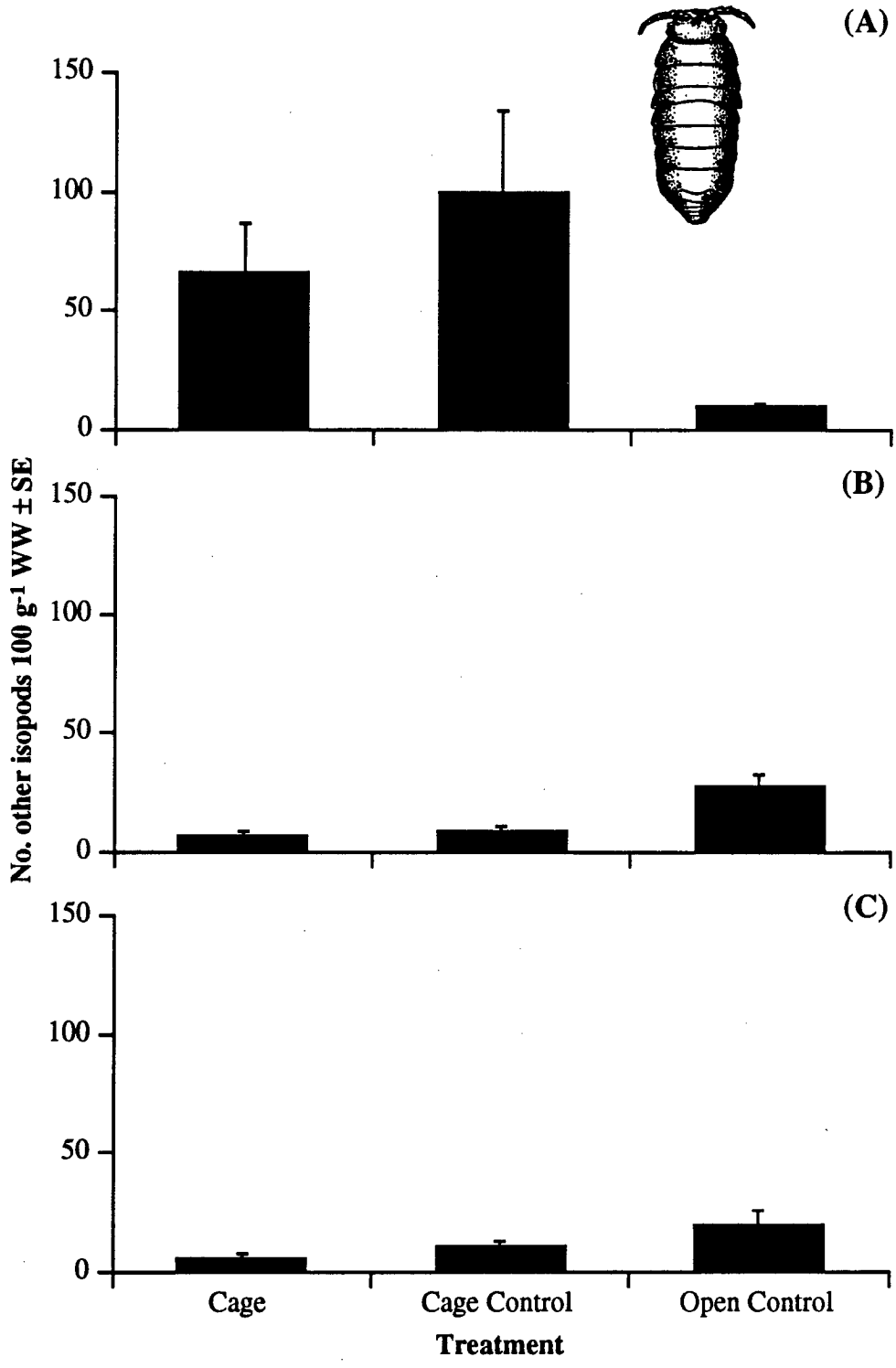


Figure 6.21. Mean abundance of other isopods in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

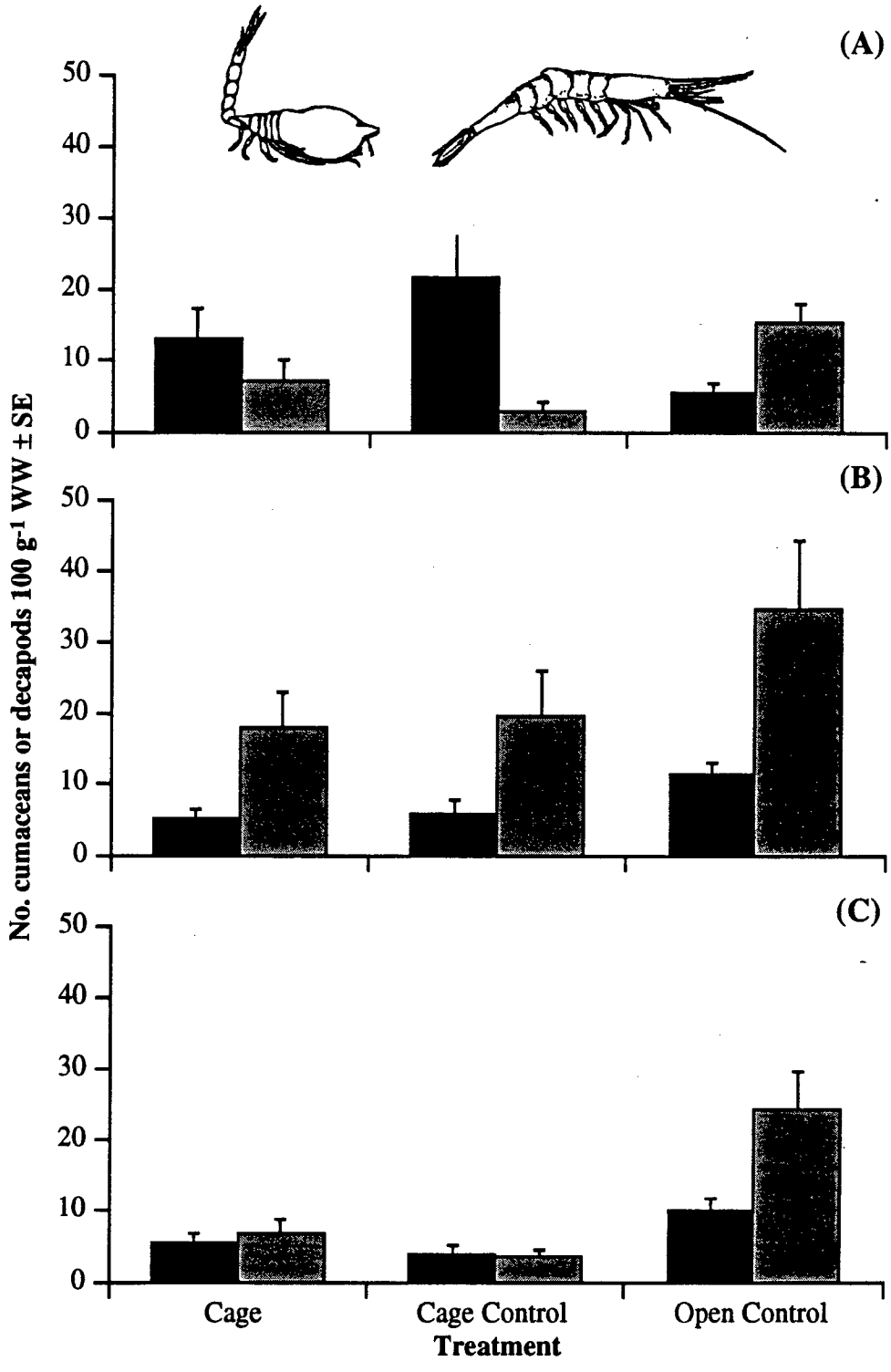


Figure 6.23. Mean abundance of cumaceans (■) and decapods (▣) in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

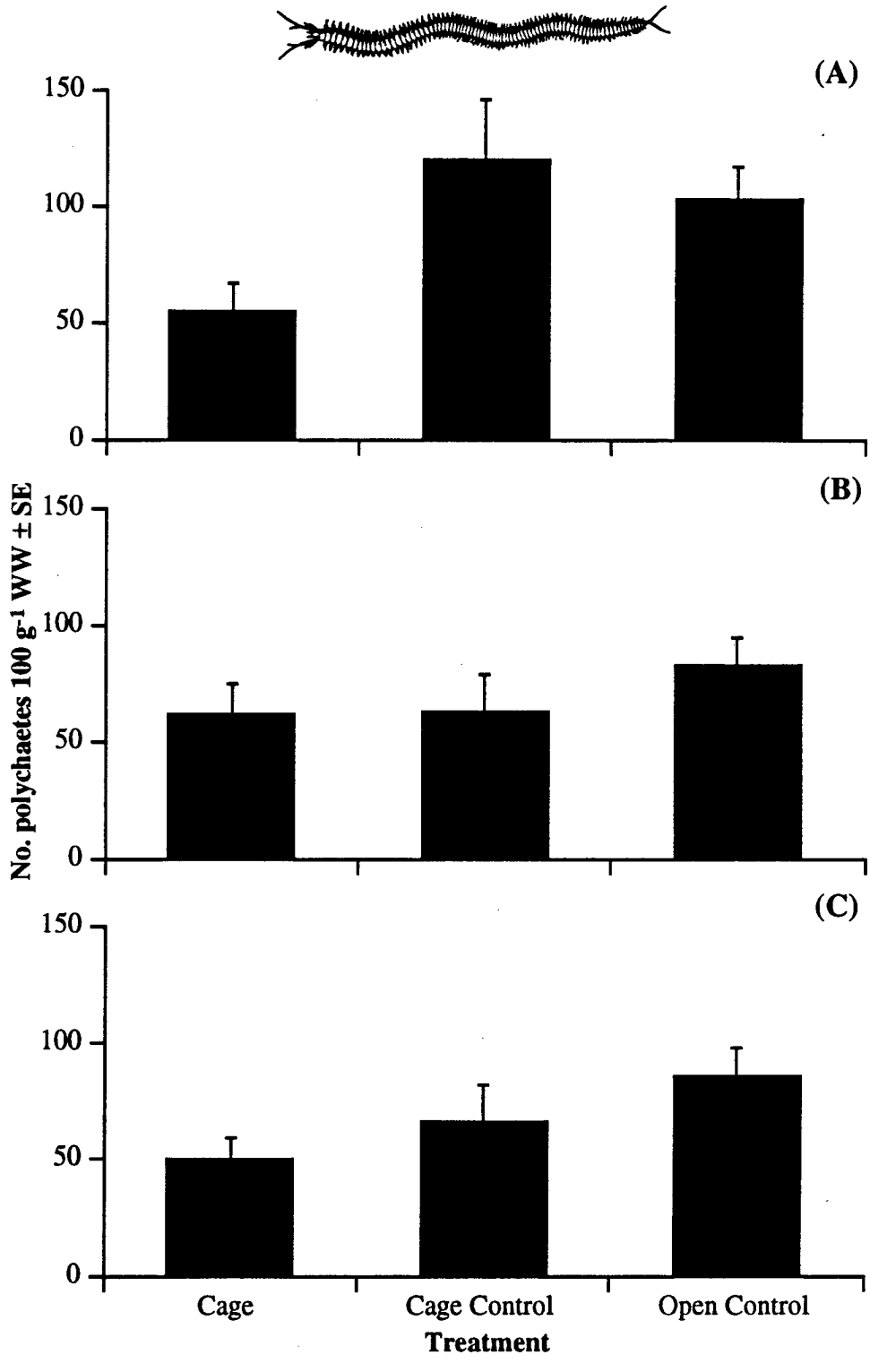


Figure 6.24. Mean abundance of polychaetes in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

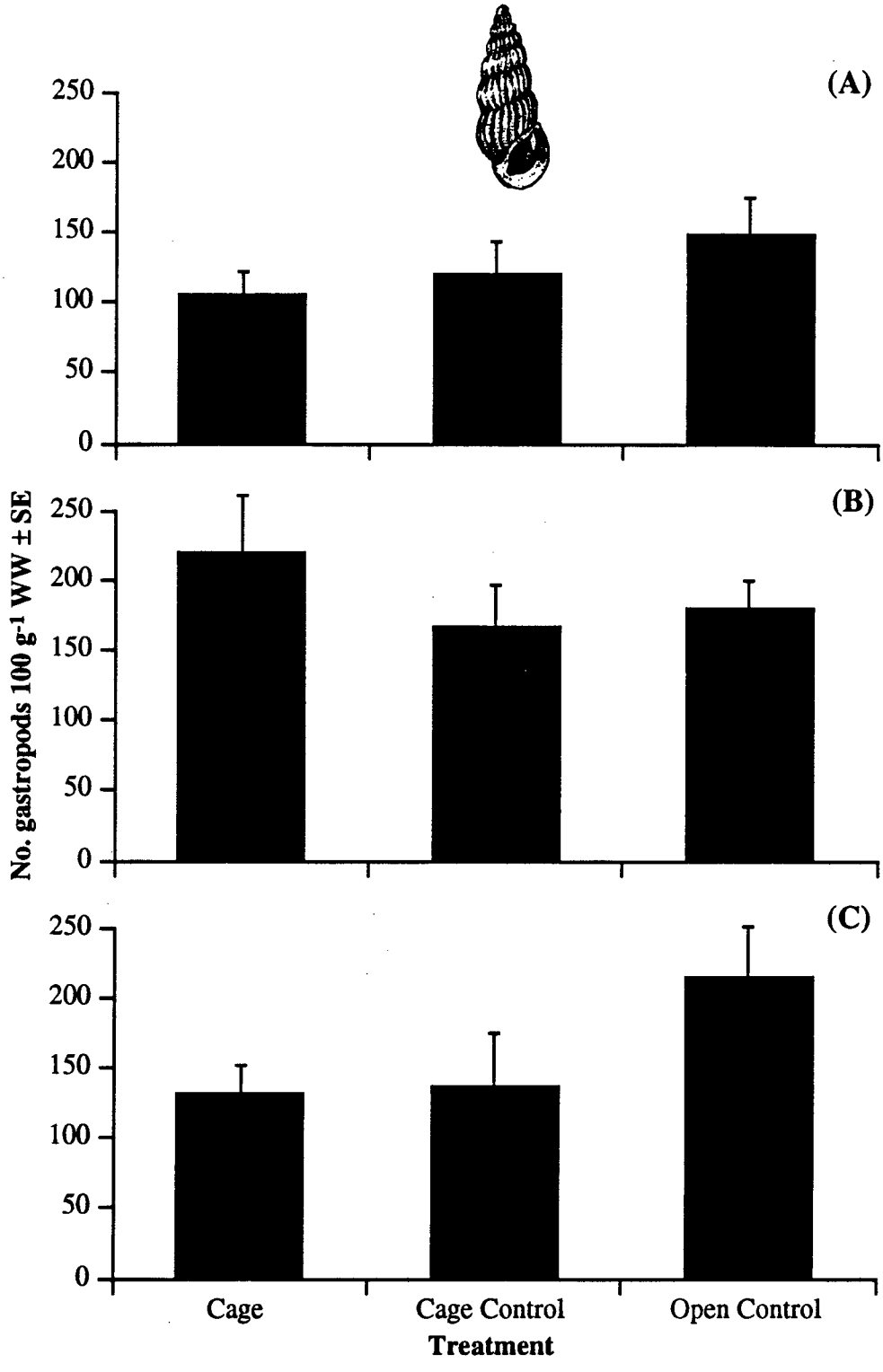


Figure 6.25. Mean abundance of gastropods in predation experiment at (A) 0 weeks (pre-treatment) (B) 2 weeks (C) 4 weeks. n=12 for each sample.

(8) Gastropods (Table 6.III and Figure 6.25). Again, there was no significant changes in abundance in any treatment over time.

A general pattern which emerges from this examination of the individual taxa is that there was a general decrease in abundance over 4 weeks in cage and cage control areas. This is shown by 5 of 9 taxa, 1 further taxon showed the same relative change (i.e. open control abundance becoming greater than cages and cage controls) and the remaining 3 taxa all showed no changes at all. During these 4 weeks of the experiment abundance of all taxa in open control levels remained constant or increased. There were only two significant increases in abundance in cages (gammarids from 0 to 2 weeks and gastropods over the same period and only one point where cages and cage controls were significantly different (polychaetes at 0 weeks).

Observation data from all times demonstrated that fishes could be found in cage control treatments, although their use of these areas was not quantified and could well have been different from that of open control areas.

6.5 DISCUSSION

The experimental work presented above demonstrated a significant community response, in terms of increased abundance, to habitat complexity provided by epiphytes. Significant decreases in abundance were demonstrated in predator exclusions although my interpretation is that this was an experimental artifact produced by the physical structure of the cages. Both habitat complexity and predation hypotheses have been studied in epifaunal systems with no general result emerging and debate has raged over the relative importance of the two processes. Bell and Westoby (1986c) state that "abundance of macrofauna in dense seagrass is due to habitat preference, not predation", and response to habitat complexity is considered an important process by Stoner and Lewis (1985), Hall and Bell (1988) and Schneider and Mann (1991b). However, Heck and Thoman (1981), Nelson *et al.* (1982) and Virnstein and Howard (1987a, b) inferred or detected no effect of habitat complexity. Similarly, Young *et al.* (1976), Leber (1985) and Edgar (1990e) demonstrated negative effects of predation on epifaunal abundance but Choat and Kingett (1982), Summerson and Peterson (1984), Holmlund *et al.* (1990) and Russo (1991) detected no effects of predation. A problem with the interpretation of some of the above studies is that only one of a number of possible alternative hypotheses has been tested and thus the **relative** importance of other processes can only be inferred. As Jones *et al.* (1991) point out, if a study sets out to demonstrate that predation occurs, the

answer will normally be yes since "predators, without a doubt, consume prey!", a rather trivial solution. They suggest that a more appropriate question is "How important is the impact of fish on benthic communities in relation to other processes and how does this importance vary from place to place and time to time?". Although, I have not addressed the spatial and temporal component of this question, I hope that I have gone part of the way to answering the question concerning relative importance of habitat complexity and predation in the *Sargassum*-epifauna system.

The presence of epiphytic algae had a very marked effect on the epifaunal taxa, both as a community (Figures 6.3 and 6.4) and on each individual group (Figures 6.5-6.14). It is clear from the multivariate analysis that epi + and epi - communities were different initially and that these differences tended to disappear through time as epiphytes accumulated on the previously pristine mimics (Figures 6.3 and 6.4). The rapid rates of colonization by epifauna onto unoccupied substrata confirms the assertions of Chapter 4 that rates of immigration in this system were high. That the abundance of all taxa at two weeks for one or both of the experimental treatments was equal or greater than abundance on real *Sargassum* plants suggests that the time scale of the sampling intervals was adequate. This also supports the contention of Chapter 4 that equilibrial communities could be established as early as two weeks after defaunation.

It is not known whether immigration by epifauna was by active selection of a habitat, the epifauna responding to distant visual and/or chemical cues or by passive accumulation with the habitat acting as a "sampling net" in the water column (Dean and Connell 1987c). If immigration was an active process, then the epiphytes acted as some kind of settling cue for epifauna. Host chemistry has been implicated in active selection of habitats by epifauna (Hay *et al.* 1990a) and this hypothesis could be extended to encompass chemotactic responses to epiphytes. However, this appears to be specialized behaviour for epifauna that are obligately associated with a particular host and that visual cues for location of habitats are more widespread since epifauna will colonize totally artificial habitats which lack appropriate chemical cues (Myers and Southgate 1980). Distant visual cues could involve colour or shape and architecture of epiphytes, but work on these type of behavioural responses in epifauna is extremely scarce and it is difficult to separate pre-settlement cues from post-settlement responses. Hacker and Steneck (1990) have shown in the laboratory that phytal amphipods select for the spatial component of habitat architecture and they concluded that predation, disruption by waves and competition are not causal processes involved in determining demographic patterns of these amphipods. However Russo (1987) showed in the laboratory that amphipods did not select for increased complexity but those that were

in more complex habitats had greater rates of survival. Whether these laboratory patterns reflect processes in the field is unknown.

If immigration was a passive process then there is no *a priori* reason to suppose that it should have been higher on an epi + than an epi - treatment; the sampling efficiency of the epi + may have been slightly higher than the epi - plants but certainly not by the order of magnitude difference detected in the abundance of some taxa. If it is assumed that rates of immigration onto the two treatments were similar then the reason for differences in abundance was either higher post-settlement mortality and/or greater rates of emigration on epi - treatments. Increased mortality could result from greater predation of epifauna on epi - plants and this could be tested by a multifactorial experiment involving exclusion of predators from epi + and epi – treatments, although the power of the experiment would have to be high to cope with caging artifacts. Increased emigration could result from a behavioural response to chemistry, food availability or habitat once settlement had occurred. Whether immigration or emigration was responsible for the observed differences in abundance would be difficult to test experimentally. An attempt was made to do this, in the specific study of the sphaeromatid isopod *Cymodoce* (described in Chapter 7) by 'seeding' habitats with isopods and comparing these with 'unseeded' habitats. To do this for an entire epifaunal community would be very complicated and fraught with potential problems, but alternative procedures such as laboratory observation of behaviour are also open to criticism.

There was a general decline in the abundance of crustaceans and polychaetes from all *Sargassum* controls and most experimental treatments. This decline is almost certainly part of the seasonal pattern displayed by these groups. In both 1990 and 1991 regular monthly sampling showed decline in abundance of crustaceans and polychaetes from August through to October (Chapter 3, Figures 3.3-3.9). This seasonal pattern, which prompted the manipulative experiments in the first place, is overlaid on top of the responses to different experimental treatments. This result stresses the importance of the real plants as controls in the experiment – without this data it might be concluded that the observed decline from 2 weeks to 4 weeks was an artifact of the experimental procedure, as with the exclusion experiment. It is absolutely crucial to any work of these kind on organisms whose abundance fluctuates markedly that regular seasonal patterns are documented in order to correctly interpret any experimental work.

Moving on from general community patterns to those of individual taxonomic groups of epifauna, there were interesting differences between taxa in their response to the type of mimic and/or the presence of epiphytes (Figures 6.8-6.14). Gammarids,

other isopods, cumaceans, decapods and gastropods did not seem to exhibit any preferences for one type of mimic or the other, but the remaining groups all showed some kind of preference at one or all time points. Sphaeromatid isopods and tanaids preferred rope mimics over shade cloth mimics (Figure 6.9 and 6.10 respectively), as did polychaetes at 4 weeks (Figure 6.13), while caprellids showed a strong preference for rope epi – mimics over all other treatments (Figure 6.11). These differences may represent important biological differences in the way that the different groups perceive and respond to their environment. The arrangement of habitable spaces of the mimics themselves varied and the distribution and types of epiphytes were also different between the mimics, although these were not quantified. Hacker and Steneck (1990) have shown that an amphipod, *Gammarellus angulosus*, responded to both structure and space, and it seems likely that some of the groups studied here did the same thing. The high abundance of caprellids on rope epi – treatments is difficult to explain, especially since the difference increased with time. If the caprellids were gaining cryptic advantage from resembling the strands of the rope mimic then it would be expected that the difference would decrease over time as epiphytes accumulated. These conundrums will only be solved by detailed examination of the ecology of the different taxa, a study beyond the logistical and temporal scope of this study.

The exclusion experiment performed in the present study did not demonstrate effects of predation by fishes on abundance of epifauna. Predation by fishes obviously occurred: fishes have been observed at many times over the period 1990-3 feeding on epifauna and the limited gut analyses performed showed epifauna in the guts of all *Halichoeres* examined (Table 6.II). Invertebrate-feeding fishes were also abundant – the censused abundance of *Halichoeres* (Figure 6.15) was probably underestimated, but even so, it is considered high (Alison Green *pers. comm.*) However, there were no detectable effects in treatments with reduced predation (Figures 6.17 and 6.18 and Table 6.III). It is possible that there was a effect of predation but it was masked by artifacts introduced by the use of cages. Kennelly (1991) found significant caging artifacts on some species very soon after the deployment of exclusion cages. Jones *et al.* (1988) found it difficult to distinguish between the biological effects of predator exclusion and the physical effects associated with caging (increased sediment deposition, decreased light levels etc.). They argued extreme caution with regard to interpretation of results from caging experiments. A problem with any caging experiment is that the cage controls used may not have the same level of artifacts associated with them as full cages. This was addressed in detail by Schmidt and Warner (1984) who used 3 different types of cage control, as well as full cages and open controls to try and separate out the artifacts associated with

particular designs of cage control. They found different responses by different species to light attenuation or reduced current speed. In the present study the current flow through cage controls was likely to have been greater than through full cages but light attenuation was presumed to be of similar magnitude in both and of less significance than the pronounced day-to-day variations in light intensity produced by wind-driven resuspension of sediment (Walker and O'Donnell 1981).

There was only one taxon at one time point where cage and cage control samples were significantly different and this was due to pre-treatment variability (polychaetes at 0 weeks). The fact that for all other taxa over the course of the experiment, cage and cage control treatments were not significantly different in community composition or individual taxon abundance, suggested that either caging effects were much greater in magnitude than any effects of predation or that there was no real effect of predation on these epifaunal communities. It can be argued that the use of cage control areas by fishes is different to both open and fully enclosed areas and little work has been done to address this problem: however, Jones *et al.* (1992) found no significant difference between feeding rates in partial cages and open areas. Although fish were observed feeding in cage control areas in the present study no quantitative data were taken. It is possible, therefore, that the close correspondence between cage and cage control communities of epifauna were produced by differential use by fishes and/or different levels of artifacts between the treatments.

Choat and Kingett (1982) investigated the role of predation by fishes in determining the abundance of invertebrates living in an algal turf and found no qualitative (species composition) and few quantitative (abundance of species) differences between exclusion and control areas. They concluded that predation by fish, despite the circumstantial evidence pointing towards its structuring role (e.g. the high proportion of turf-inhabiting amphipods and polychaetes in the guts of juvenile sparid and mullid fish) was not important in determining temporal changes in abundance in their temperate subtidal system, similar to results presented here for a tropical system.

The responses displayed by epifaunal taxa to cages and/or reduced predation appeared to be more homogeneous than in the habitat complexity experiment. All of the abundant crustacean taxa – gammarids, sphaeromatids, other isopods, tanaids, decapods and cumaceans – displayed declines in abundance relative to open controls over the course of the experiment (Figures 6.18-6.23). The only crustacean taxon which did not display this pattern was caprellids, whose abundance was so low that it is impossible to draw any conclusions from the patterns shown. Polychaetes and gastropods also displayed a decline in caged areas (Figures 6.24 and 6.25) indicating

a general effect on all taxa. Thus, either biological differences between the taxa were obliterated by an overwhelming caging effect or that there were few of these differences in this manipulation.

Predation and habitat complexity may be intimately linked. It has been shown that the demographic patterns of epifauna may not be the product of choice of habitat by an organism but rather are caused by differential effects of habitat complexity on its predators (refs. in Orth *et al.* 1984). It is difficult to determine whether prey select for 'predator-free' habitats or if they are removed by predation from untenable space, since the processes involved are dynamic. Selection of complex habitats also may be an evolutionary response to predation. Thus, although predation was not demonstrated directly, the results of the habitat complexity experiment could have been driven by either present or past predation.

6.6 CONCLUSIONS

This chapter has described the formulation of hypotheses concerning the processes controlling epifaunal abundance, the subsequent testing of those hypotheses with experimental manipulations and the implications of the results. What are the general conclusions from this and how does this fit into the overall seasonal pattern of abundance of epifauna? My interpretation of the experimental results is that habitat complexity provided by epiphytes is much more important in determining patterns of epifauna than predation. Although, the exclusion experiment was by no means conclusive as to the role of predation, the habitat complexity experiment, backed up by the phenology of epiphytes (Chapter 2) leads me to believe that it is this aspect of the system which is important to epifauna. Furthermore this leads to the conclusion that *Sargassum* is relatively unimportant in the dynamics of the mobile invertebrate epifauna, a rather surprising, counter-intuitive proposal. If this is so, then it is very important to consider the epiphytic component of the habitat when studying epifauna. This has been recognised by Bell (1991) who suggests that "small epiphytic plants on macroalgae may be the more appropriate scale to judge feeding preferences" and that epiphytes are the preferred food of amphipods. The degree of specialisation of particular epifaunal species may be hidden because of this 'extra' level of the system – a 'generalist' found on many species of macroalgae may be associating only with a particular species of epiphyte or a 'specialist' on one species of macroalgae may be encountering a diverse range of epiphytes. The role of epiphytes as food, in particular, has been stressed by a number of authors (e.g. Zimmerman *et al.* 1979,

D'Antonio 1985, Gunnill 1985, Brawley and Fei 1987, Hay *et al.* 1987a) although the relative importance compared to the macroalgal host has been debated (see Hall 1991 and Duffy and Hay 1991a).

A final interesting point is the extent to which epiphytes have determined the phenology of epifauna in other studies. In the *Sargassum* system which I have studied, the suggestion that epiphytes were important was prompted by the 'decoupling' of the phenologies of *Sargassum* and its epiphytes. If the epiphytes followed the same temporal abundance pattern as the host, then it might be assumed that the pattern of host abundance determined epifaunal abundance. Although, this has been recognised by some authors (e.g. Johnson and Scheibling 1987, Hall and Bell 1988), others have either neglected to investigate or report on the epiphytic component of the system (e.g. Nelson 1979a, Gore *et al.* 1981).

CHAPTER 7

SPECIFIC VS HOLISTIC ECOLOGY: SELECTION OF TAXONOMIC SCALE AND HABITAT STUDIES ON SPHAEROMATID ISOPODS

"O wonder! How many goodly creatures are there here!" William Shakespeare, The Tempest.

7.1 INTRODUCTION

7.1.1. Taxonomic scale in ecological studies

The concept of scale in ecological systems was introduced and discussed in Chapter 4. However, one aspect of scale that was not considered was that of taxonomic scale. The detection of pattern in community ecology is often determined by the taxonomic scale which is employed (Dayton and Tegner 1984, O'Neill *et al.* 1986, Sale and Guy 1992). Obviously, it would be ideal to collect all data at the specific level, statistical techniques could then be employed to determine the ecologically relevant domains of scale (Wiens 1989). However, this approach is often not possible due to problems of taxonomy (i.e. species cannot be identified reliably) or logistics (i.e there is not enough time or resources to resolve data to this level). This is especially true in tropical systems where taxonomy is often absent or patchy and species diversity very high (Barnard 1976, Connell 1978, Stevens 1989).

There are advantages and disadvantages associated with examining community responses at high and low taxonomic levels. Species-abundance curves for most systems show that few species generally make up most of the individuals and biomass for a particular community (e.g. Marsh 1973, Gunnill 1982b, Stoner 1985, Kang and Yun 1988). The majority of species are therefore present at low abundances and thus the study of these is much more likely to be affected by random factors or under-sampling (Andrew and Mapstone 1987). Many parametric statistical procedures demand data above a particular level of abundance and many multivariate techniques are sensitive to large numbers of zero values (the so-called 'horseshoe' effect whereby widely separated communities group together due to their commonality of many low numbers). However, when higher taxonomic units are used the population fluctuations of highly abundant species may obscure different patterns displayed by the less abundant species. It can be argued that highly abundant species are to all intents and purposes 'the community', this is a philosophical arena which I do not propose to enter. Competition may be more difficult to detect at higher taxonomic

levels if niche overlap is greater within taxonomic units than between them, but congeneric species may have different requirements (Cooks and Streams 1984). Both approaches have yielded valuable results, from those communities responding at the order level (e.g. Stoner and Lewis 1985) to those responding at the specific level (e.g. Schneider and Mann 1991a) down to intra-specific size- or sex-based responses (e.g. Hacker and Steneck 1990).

The previous chapters have been concerned with response at the family or order level (i.e. high taxonomic groupings). To test the generality of these results it was decided to perform a detailed investigation of one of these groupings. The group that was selected for study was the family Sphaeromatidae within the order Isopoda, for a number of reasons. Firstly crustaceans were the most abundant component of the epifauna living on *Sargassum* and the questions posed and comparisons drawn throughout this thesis have been concerned with arthropod/plant relationships. Throughout most of the sampling period sphaeromatids were present in large numbers, ranking in the top four abundances at family level across all crustaceans, so they were obviously an ecologically important part of the epifauna. Perhaps most importantly, there were only a moderate number of species present, the taxonomy of which has been revised recently (Harrison and Holdich 1982, 1984) and the distinguishing characteristics between genera are relatively simple to diagnose compared to the other potential groups for this sort of study (various families within the gammarid amphipods). Thus, this work was designed to compare the results obtained by examining abundance at the taxonomic scale of family with that at the genus or species level.

As with all the epifauna which were collected from *Sargassum* the sphaeromatid isopods showed pronounced seasonal variation (section 3.4.3). These isopods showed variable responses to habitat complexity and a negative response to predator exclusion (sections 6.4.1 and 6.4.2), neither experiment providing a definitive explanation for their seasonal fluctuations. Arrontes and Anadon (1990b) stated that the populations of the isopods *Cymodoce* and *Dynamene* populations on macroalgae in Spain were strongly influenced by reproductive periodicity as did Shafir and Field (1980) in South Africa with the isopod *Cirolana* . Both of these studies used size-frequency analysis to generate these hypotheses, a technique suitable for the analysis of sphaeromatid populations in the present study. Thus, size-frequency as well as abundance data were collected. Furthermore, the identification of reproductive individuals during the collection of these data was possible, an important additional piece of information in the interpretation of seasonal patterns.

7.1.2. Habitat structure and epifaunal crustaceans

Habitat structure, or the arrangement of physical objects in space, is an important component of ecological studies. There has been confusion over the precise definitions of habitat structure which was addressed in detail by McCoy and Bell (1991). They propose that habitat structure can be described by the axes heterogeneity (relative abundance of different structural components), complexity (absolute abundance of each structural component) and scale (size of area or volume used to measure heterogeneity and complexity). Accepting that there are many different terms for describing habitat structure, important effects on populations of marine invertebrates are evident (see review by Sebens 1991). Specifically for epifaunal crustaceans, Hacker and Madin (1991) have demonstrated the importance of colour and shape to shrimps living on pelagic *Sargassum* , Stoner and Lewis (1985) the effects of size, density and type of habitat to amphipods and tanaids and Hacker and Steneck (1990) and Holmlund *et al.* (1990) the effects of various aspects of habitat architecture (number, size, shape etc. of habitable spaces) on phytal amphipods.

The importance of habitat structure provided by epiphytes to crustaceans on *Sargassum* was demonstrated in the previous chapter. These effects were measured at the community level and it was not known which aspects of the structure made epiphytised habitats attractive to crustaceans. Given that sphaeromatid isopods showed some ambiguous responses to this gross level of habitat manipulation it was decided to try and identify important components of habitat structure to which they responded. A number of different aspects of habitat structure were identified and tested in a series of field and laboratory experiments (Figure 7.1). To separate biological factors (food value, defensive chemistry etc.) from purely physical aspects of structure it was decided to use artificial habitats. Identical artificial habitats can be constructed to ensure precise replication and manipulation, which cannot necessarily be achieved with natural habitats. The efficacy of such artificial habitats has been amply demonstrated for crustaceans (e.g. Myers and Southgate 1980, Coull and Wells 1983, Edgar 1991a).

Aspects of habitat structure which were tested were size and colour of habitat and the number and size of habitable spaces within a habitat. There were a number of *a priori* reasons for presuming these aspects of habitat structure to be important to sphaeromatid isopods. Larger habitats which provide more habitable spaces can accommodate more individuals, although the exact shape of the size/abundance curve (linear, asymptotic, exponential etc.) depends on interactions between size and other factors such as predation or competition (Crowder and Cooper 1982, Orth *et al.* 1984, Stoner and Lewis 1985, Sebens 1991). Colour of the habitat is important to many

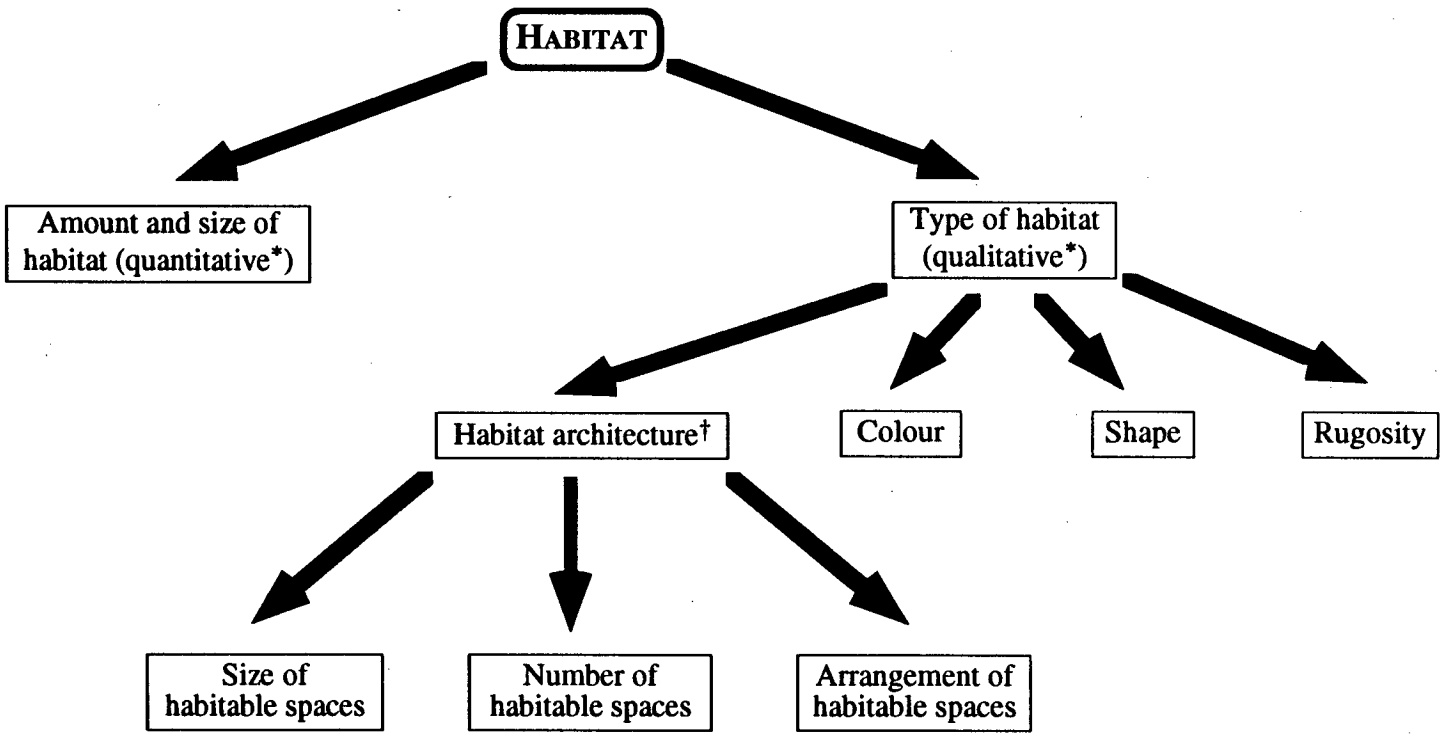


Figure 7.1. Some components of habitat complexity which may influence the composition and abundance of epifaunal populations.
* *sensu* Stoner and Lewis 1985, † *sensu* Hacker and Madin 1990.

crustaceans through crypsis – Hacker and Madin (1990) showed that a yellow shrimp, *Latreutes* from pelagic *Sargassum* preferred artificial yellow habitats and Hay *et al.* (1990b) demonstrated increased survivorship of the camouflaged crab *Thersandrus* when associated with the green alga *Avrainvillea.* Some of the sphaeromatid isopods, especially *Cymodoce*, from *Sargassum* at Magnetic Island are cryptically coloured (Plate 7.I) so it seemed reasonable to test colour of habitat. Many isopods, including sphaeromatids, are known to inhabit cavities at certain stages of their life cycles (Holdich 1976, Upton 1987, Shuster 1992), thus the role of the number and size of habitable spaces (holes) appeared to be an appropriate aspect of habitat complexity to investigate.

7.2 AIMS AND OBJECTIVES

As discussed above there were two components in the study of sphaeromatid isopods on *Sargassum* at Magnetic Island, the first the observation of the seasonal patterns of the isopods, the second the manipulation of their habitat structure. Accordingly the aims were, firstly:

- To determine the seasonal patterns of abundance for individual isopod genera within the family Sphaeromatidae.

- To compare and contrast generic and family data.

- To determine the size-frequency distribution of each genus for each month, with a view to elucidating their reproductive patterns.

Following on from this, the aims of the experimental manipulation were:

- To investigate the effects of different elements of habitat complexity on abundance of sphaeromatids, specifically aspects of habitat size, colour and the size and number of habitable spaces.

7.3 METHODS: OBSERVATIONAL DATA

7.3.1 Identification of sphaeromatid isopods

Identification of sphaeromatid isopods was initially performed using Kensley and Schotte (1989) to obtain the genera of most individuals. Representative

Plate 7.I. A juvenile *Cymodoce* isopod feeding on a young *Sargassum fissifolium* frond.

specimens were sent to Dr. Niel L. Bruce at the Queensland Museum, Brisbane* who provided identification to species level. All the common species of sphaeromatids found belonged to one of two subfamilies, the Sphaeromatinae (hemibranchiates) or the Dynameninae (eubranchiates) and were as follows:
Subfamily Sphaeromatinae.
Genus *Cymodoce* Leach 1814.
Species: *C. tribullis* Harrison and Holdich 1984, *C. bipapilla* Holdich and Harrison 1984.
Subfamily Dynameninae.
Genus *Cerceis* Milne-Edwards 1840.
Species: *C. pravipalma* Harrison and Holdich 1982, *C. tridentata* Milne-Edwards 1840, *C. pustulosa* Harrison and Holdich 1982, *C. aspericaudata* Miers 1884.
Genus *Neonaesa* Harrison and Holdich 1982.
Species: *N. rugosa* Harrison and Holdich 1982.

All of these species except *Neonaesa rugosa* have been collected from Magnetic Island; indeed, the type specimens of *Cymodoce tribullis*, *C. bipapilla* and *Cerceis pustulosa* were all collected around Magnetic Island, from dead or living *Sargassum*. *N. rugosa* has been collected primarily from offshore coral reefs and islands, however it is an ubiquitous species. Little is known about the ecology and natural history of these organisms, although work has been done on congeneric species in temperate areas (Arrontes 1990b, Arrontes and Anadon 1990b).

7.3.2 Seasonal patterns of sphaeromatid isopods

The collection of monthly epifaunal samples is described in section 3.3.2. From each of the monthly samples from Geoffrey Bay the sphaeromatid isopods were separated from the rest of the crustacean epifauna and identified to genus. Adult males were identified by the presence of densely setose pleotelson regions and elongated uropodal exopods (for *Cerceis* and *Neonaesa*) or endopods (for *Cymodoce*) (Harrison and Holdich 1982, 1984). Ovigerous females can be identified by the presence of öostegites on the coxae of the pereopods and the form of the pleotelson (Niel Bruce *pers. comm.*, Harrison and Holdich 1982, 1984). Difference in abundance between months was tested with a 1-way ANOVA with fixed factor SAMPLING DATE. To determine whether abundance of different genera of isopods was different between *Sargassum* species a 1-way analysis of covariance (ANCOVA) was performed on the data with SAMPLING DATE as a covariate and *SARGASSUM* SPECIES as a fixed factor.

* Now Curator of Crustacea, Zoological Museum, University of Copenhagen.

Size-frequency distributions were obtained by the use of a computer image-analysis system. For sampling dates with less than 100 isopods of a particular genus, all individuals were measured; for samples with more than 100 isopods a subsample of approximately 100 was taken and the results appropriately scaled up. Isopods were placed on black background under an Olympus CH2 dissecting microscope which was connected to a video camera. Because of the curvature induced in the isopods by fixation, all individuals were placed laterally. Images were taken from the video camera using an Apple Macintosh IIci computer with Frame Grabber 1.3 software. The curved body length (CBL) of each individual (from ventral tip to pleotelsonic notch) were measured in millimetres using Image 1.44 software after appropriate calibration for the magnification used. Size-frequency distributions were compared using correspondence analysis (CA). This technique is used for pattern detection (as with CDA in previous chapters) from R x C contingency tables. The procedure generates a two-dimensional point for each row and each column which can be plotted separately or overlaid on the same graph. Unfortunately, there do not appear to be any *a posteriori* tests which can be performed to indicate what elements of the contingency table are responsible for the separation of points.

7.4 RESULTS: ISOPOD SEASONAL PATTERNS

7.4.1. Seasonal patterns of abundance of isopods

Seasonal fluctuations of total sphaeromatid isopods were pronounced but difficult to interpret (see section 3.4.3, total sphaeromatid abundance presented again in Figure 7.2). However, when individual genera of isopods were examined patterns of abundance became clearer (Figures 7.3 and 7.4). The absolute number of individuals per plant is shown in Figure 7.3 and the number standardised to 100 g wet weight of plant material in Figure 7.4; both show basically the same patterns although slight differences are apparent in the relative sizes of abundance peaks. *Cerceis* showed peaks in abundance in late summer/autumn (February-May) in both years although the magnitude of the peaks were markedly different, and abundance was low throughout the rest of the year (Figures 7.3A and 7.4A). Some individuals of *Cerceis* were collected at every sampling date and the largest single collection of sphaeromatid isopods was due to a very high number of *Cerceis* (>900 individuals in May 1992). Abundance peaks for *Cymodoce* were not as distinct as for *Cerceis* and *Neonaesa* but there was a peak in autumn 1991 (April) and again in autumn 1992 (February-May) with a minor peak in October 1991 (Figures 7.3B and 7.4B). Again individuals were found at all sampling dates and the maximum number of individuals

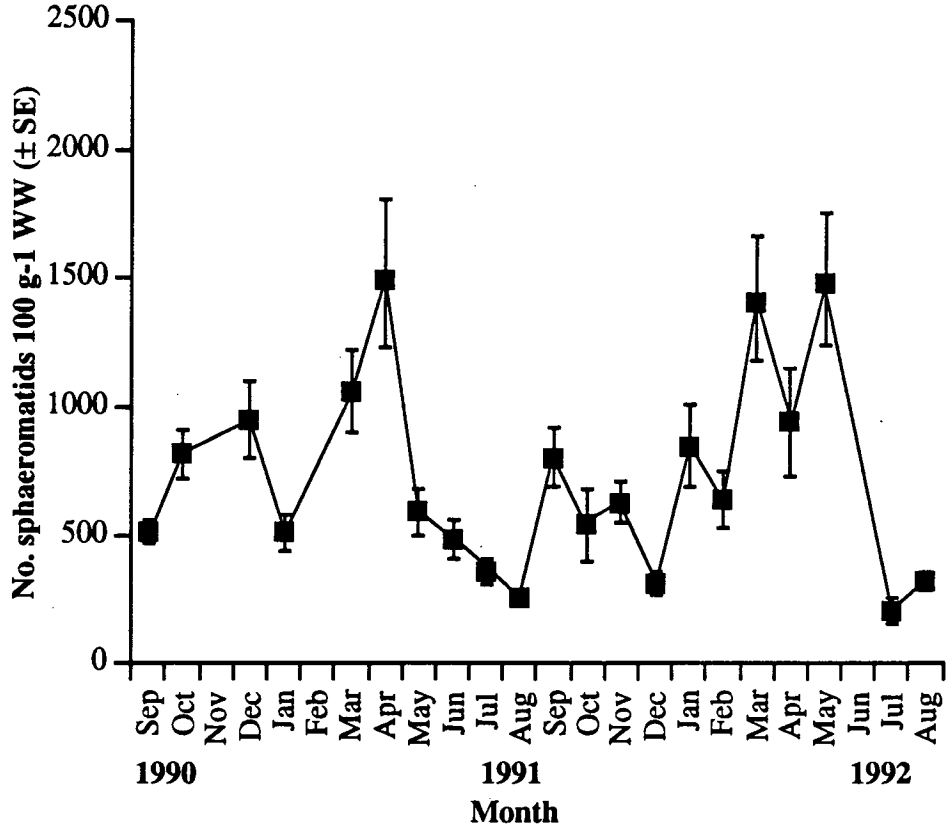


Figure 7.2. Mean abundance of sphaeromatid isopods collected from *Sargassum* from September 1990-August 1992. n=27 for each point.

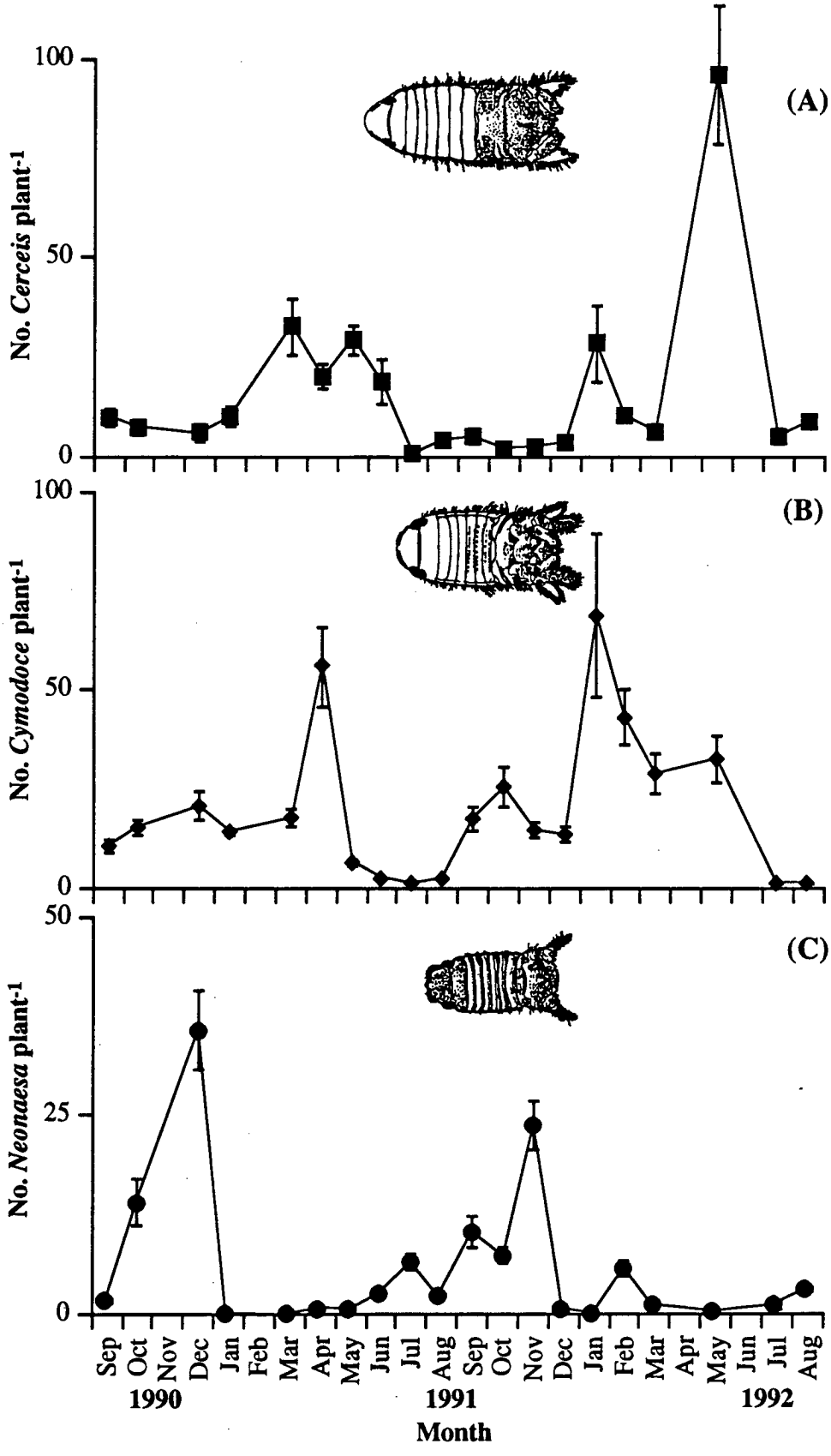


Figure 7.3. Mean abundance of (A) *Cerceis* (B) *Cymodoce* (C) *Neonaesa* from Sep. 90-Aug. 92. No data for Nov. 90, Feb. 91, Apr. and Jun. 92. n=9 for each point.

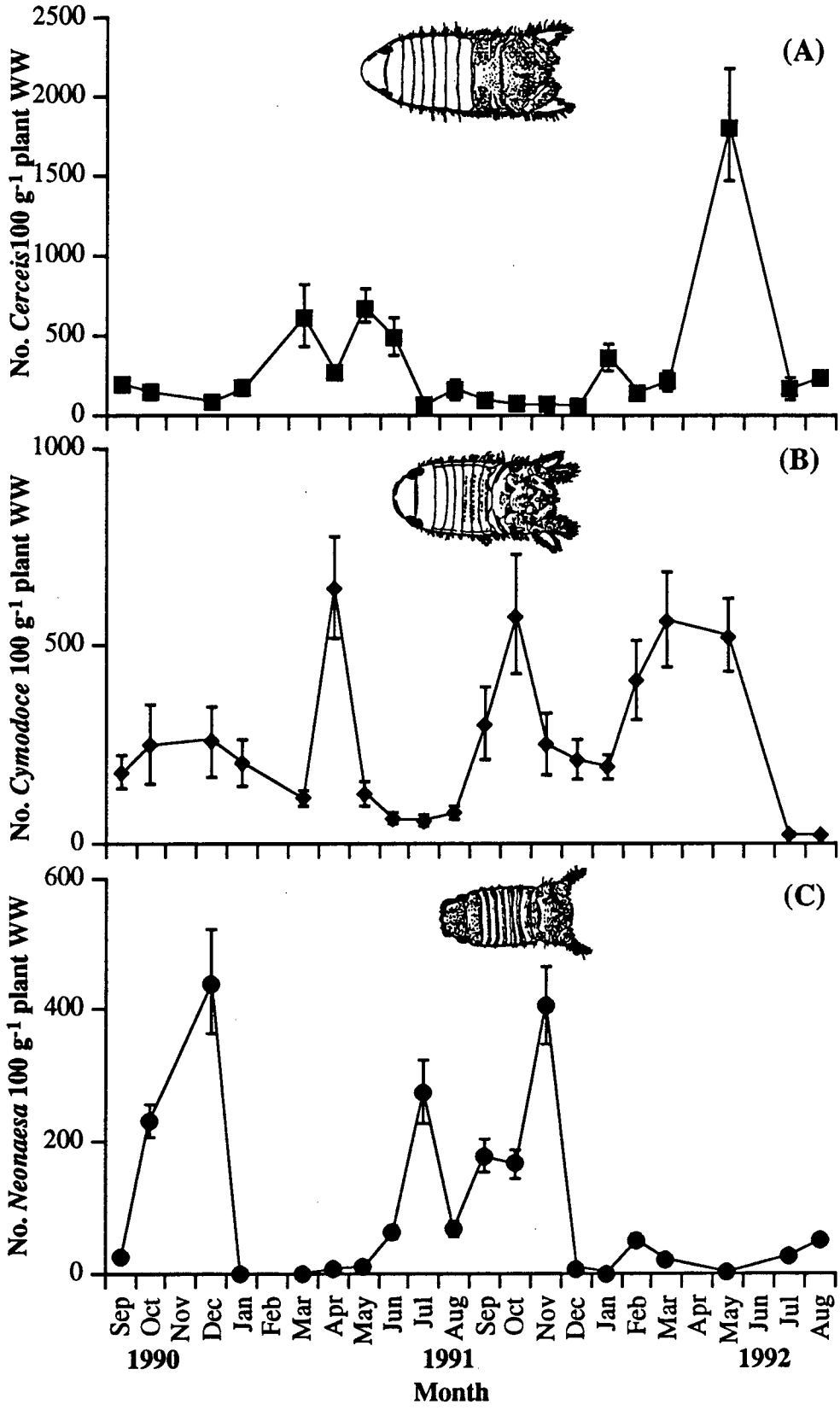


Figure 7.4. Mean abundance of (A) *Cerceis* (B) *Cymodoce* (C) *Neonaesa* from Sep. 90-Aug. 92. No data for Nov. 90, Feb. 91, Apr. and Jun. 92. n=9 for each point.

was approximately 500 in April 1991. *Neonaesa* had abundance maxima much earlier in the year than the other two genera with peaks in abundance in early summer both years (October-December 1990 and September-November 1991) and very small populations for the rest of the year (Figures 7.3C and 7.4C). No individuals of this genus were collected at a number of sampling dates (January and March 1991 and January 1992). ANCOVA showed that there were no significant differences in the abundance of isopods on different species of *Sargassum* ($p>0.05$).

7.4.2. Seasonal patterns of reproductive individuals and size-frequency distributions

Adult male *Cerceis* were present throughout most of the year, only consistently absent from collections in winter (September 1990, August and September 1991, July and August 1992) whereas adult males of the other two genera were more seasonal in their appearance (Table 7.I). Adult male *Cymodoce* were generally present in collections in winter, just before abundance peaks (October, December 1990, March 1991 and September and November 1991) while adult male *Neonaesa* were also present in winter collections and absent from summer collections (September and October 1990, June, July, October and November 1991 and August 1992) (Table 7.I).

Size-frequency distributions for *Cerceis* were self-similar for almost the entire sampling period except for January 1992 (Figures 7.5 and 7.6). The distributions were skewed towards the smaller size classes with a consistent modal size of 2-3 mm CBL. The only exception to this pattern was January 1992 which had a pulse of very small (0-1 and 1-2 mm CBL) individuals. Size-frequency distributions for *Cymodoce* were also similar for much of the sampling period, again skewed towards smaller size classes and with a modal size of 1-2 mm CBL (Figures 7.7 and 7.8). *Neonaesa* individuals were generally smaller than either *Cerceis* or *Cymodoce* but their size-frequency distributions showed similar patterns to both with high numbers of individuals in smaller size classes (1.0-1.5 mm CBL) (Figures 7.9 and 7.10).

Correspondence analysis showed that most of the size-frequency distributions were very similar (Figure 7.11). There were two outliers on the CA plot for *Cerceis*, for September 1991 and January 1992 (Figure 7.11A). The overlay graph shows that these size-frequency distributions were different from the others because of high proportions of large individuals in September 1991 and high numbers of the smallest size class in January 1992. For *Cymodoce* the pattern was even more pronounced with all size-frequency distributions very similar except for September 1991, which again had a high number of individuals in the smallest size class (Figure 7.11B).

Month	Adult Male *Cerceis* present	Adult Male *Cymodoce* present	Adult Male *Neonaesa* present
September 1990	–	–	+
October	+	+	+
December	+	+	–
January 1991	–	–	–
March	+	+	–
April	–	–	–
May	+	–	–
June	+	+	+
July	+	–	+
August	–	–	–
September	–	+	–
October	+	–	+
November	–	+	+
December	+	–	–
January 1992	+	–	–
February	+	–	–
March	+	–	–
May	+	–	–
July	–	–	–
August	–	–	+

Table 7.I. Presence of adult male isopods on *Sargassum* from September 1990-August 1992

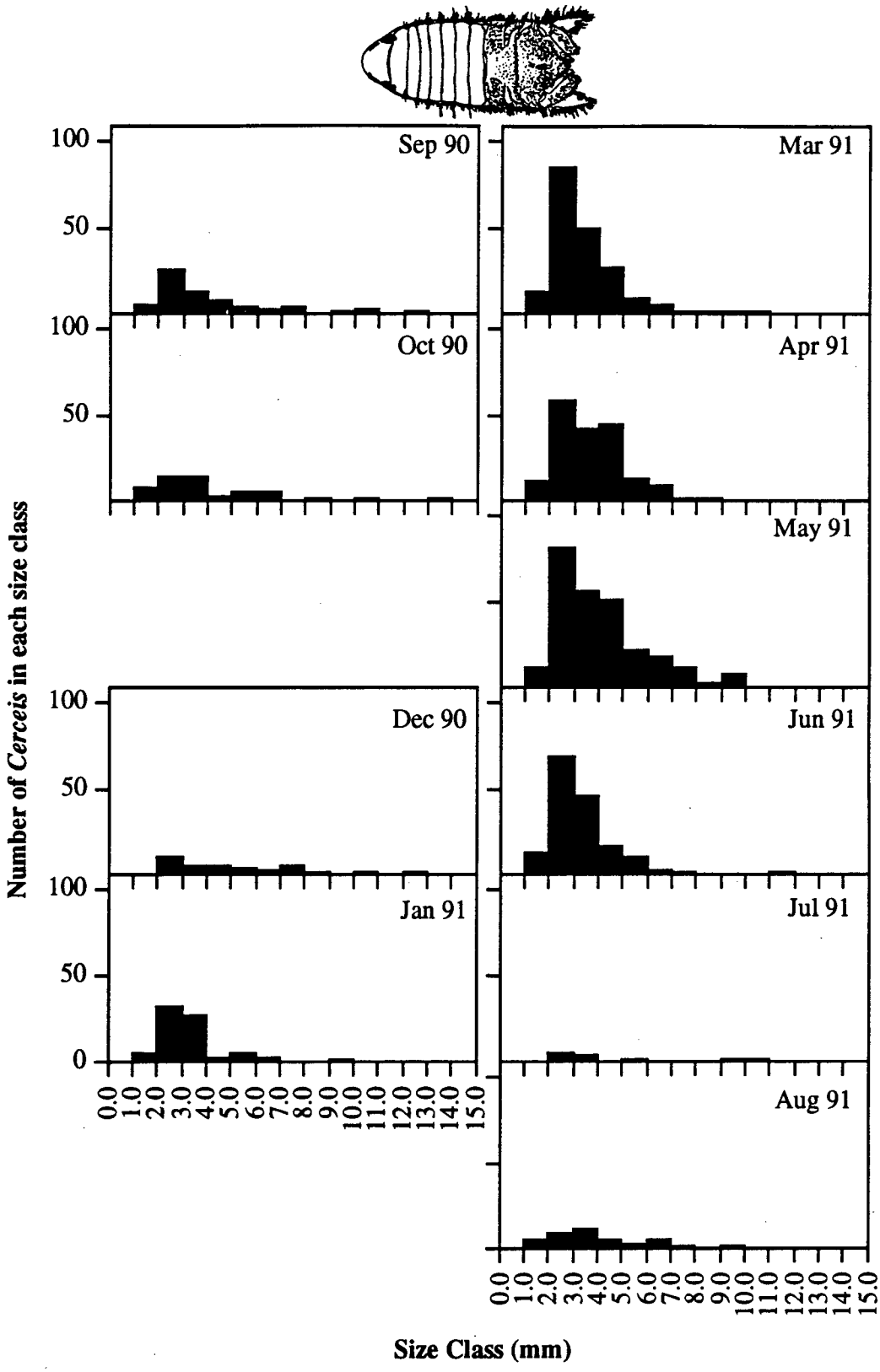


Figure 7.5. Size frequency distributions of populations of *Cerceis* for 1990–1. No data for November 1990 and February 1991.

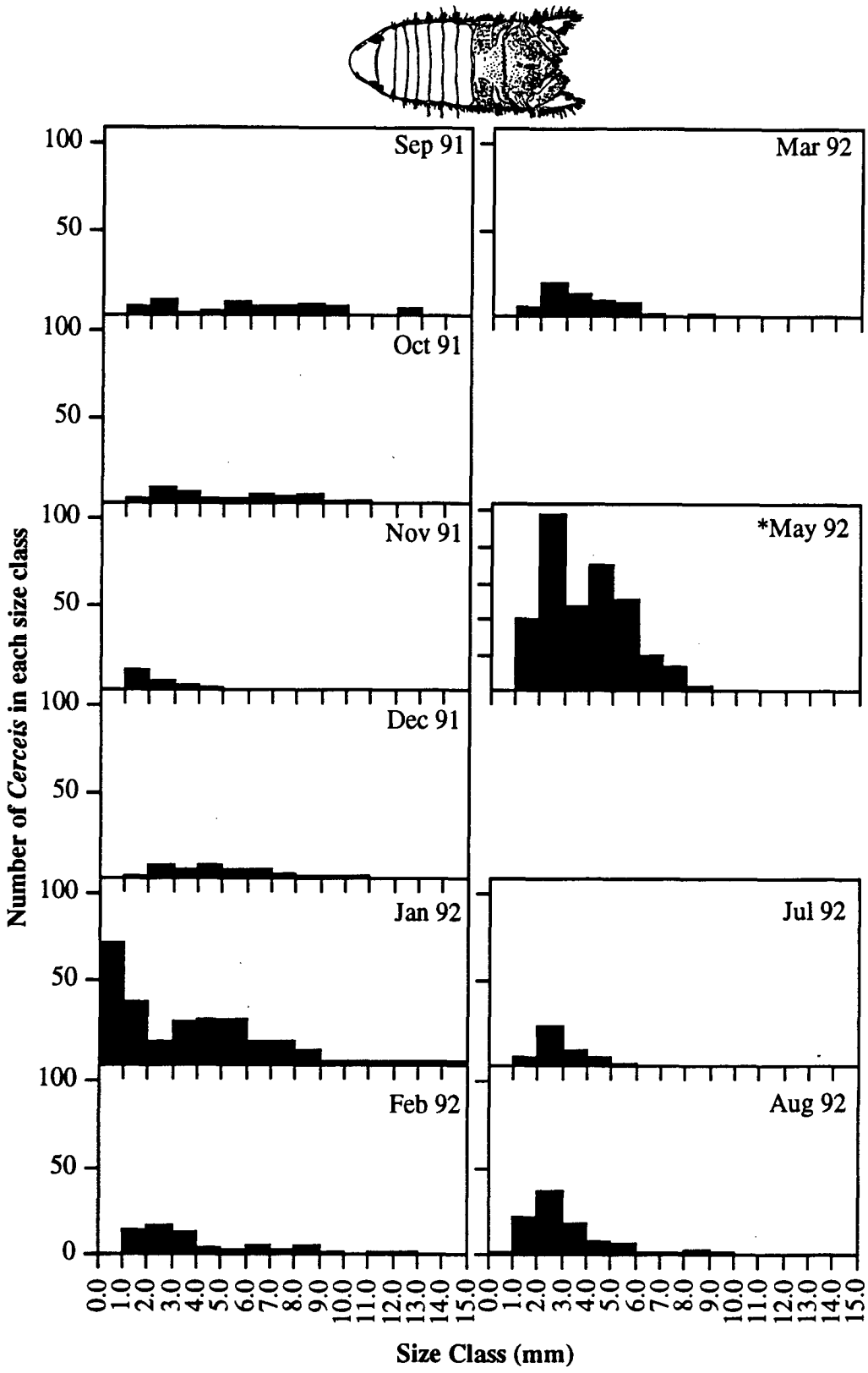


Figure 7.6. Size frequency distributions of populations of *Cerceis* for 1991–2. *Scale for May 92 is 0-250 not 0-100 as in all other distributions. No data for April and June 1991.

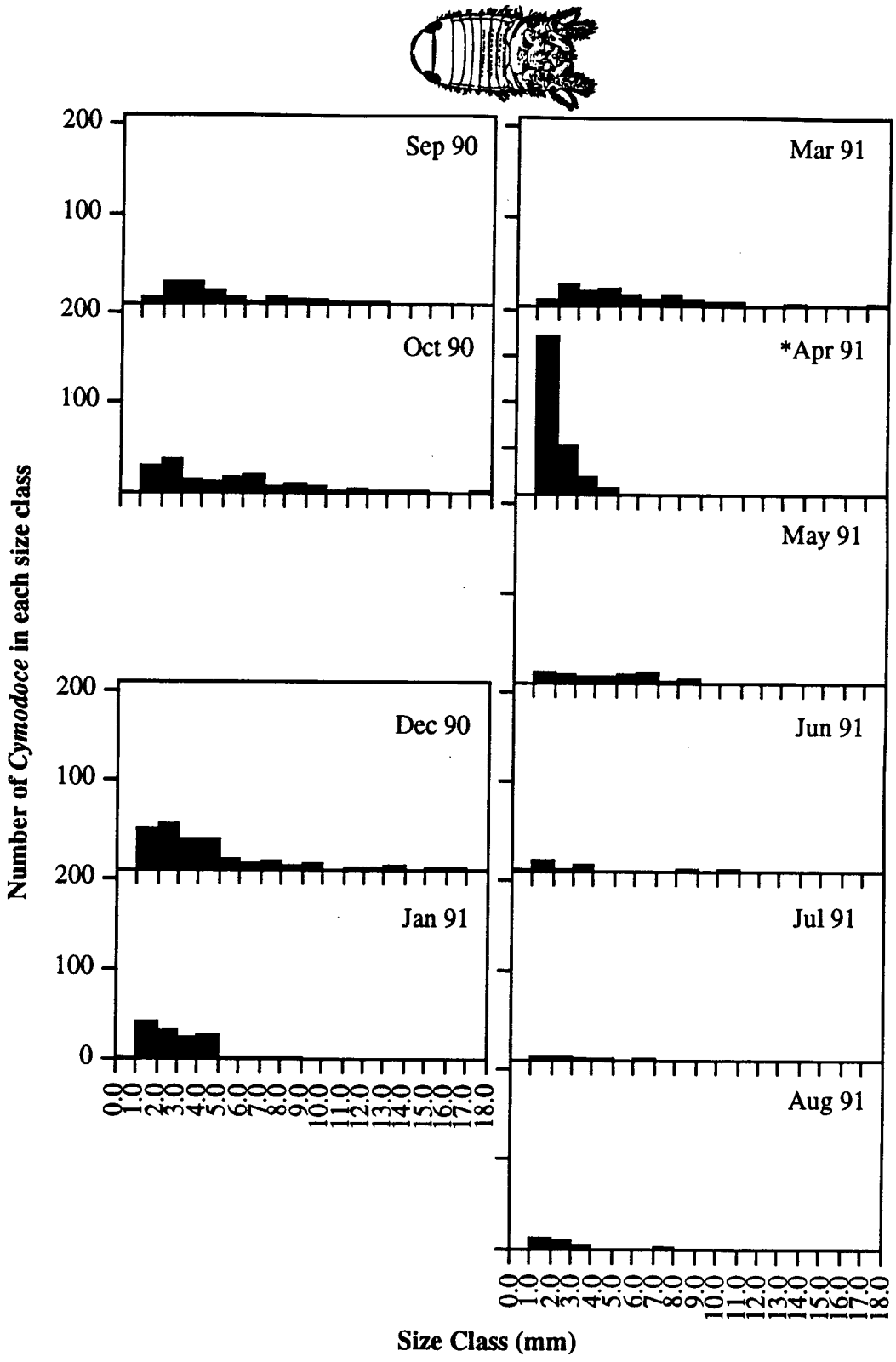


Figure 7.7. Size frequency distributions of populations of *Cymodoce* for 1990–1. *Scale for April 91 is 0-400 not 0-200 as in all other distributions. No data for November 1990 and February 1991.

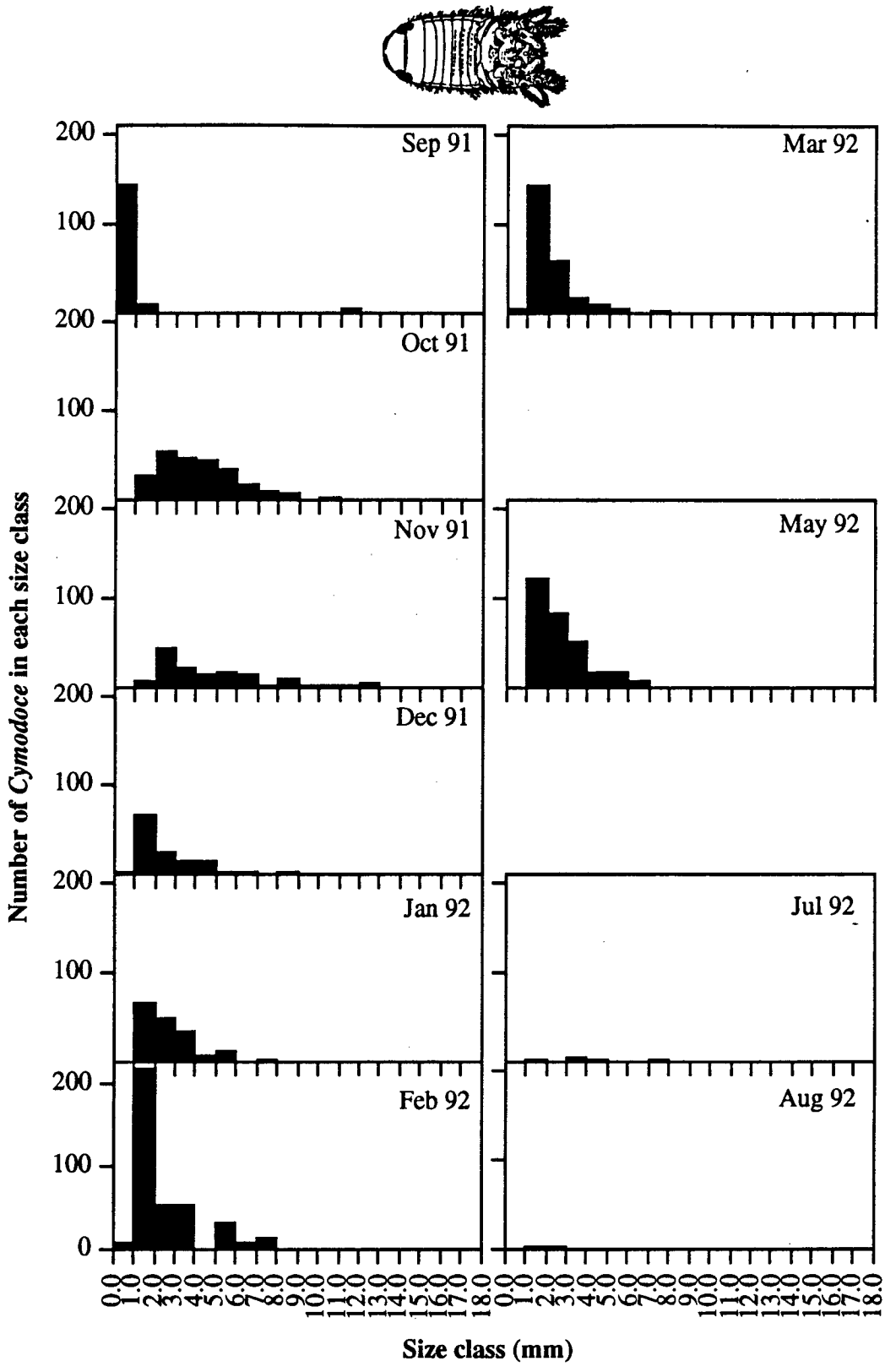


Figure 7.8. Size frequency distributions of populations of *Cymodoce* for 1991–2. No data for April and June 1992.

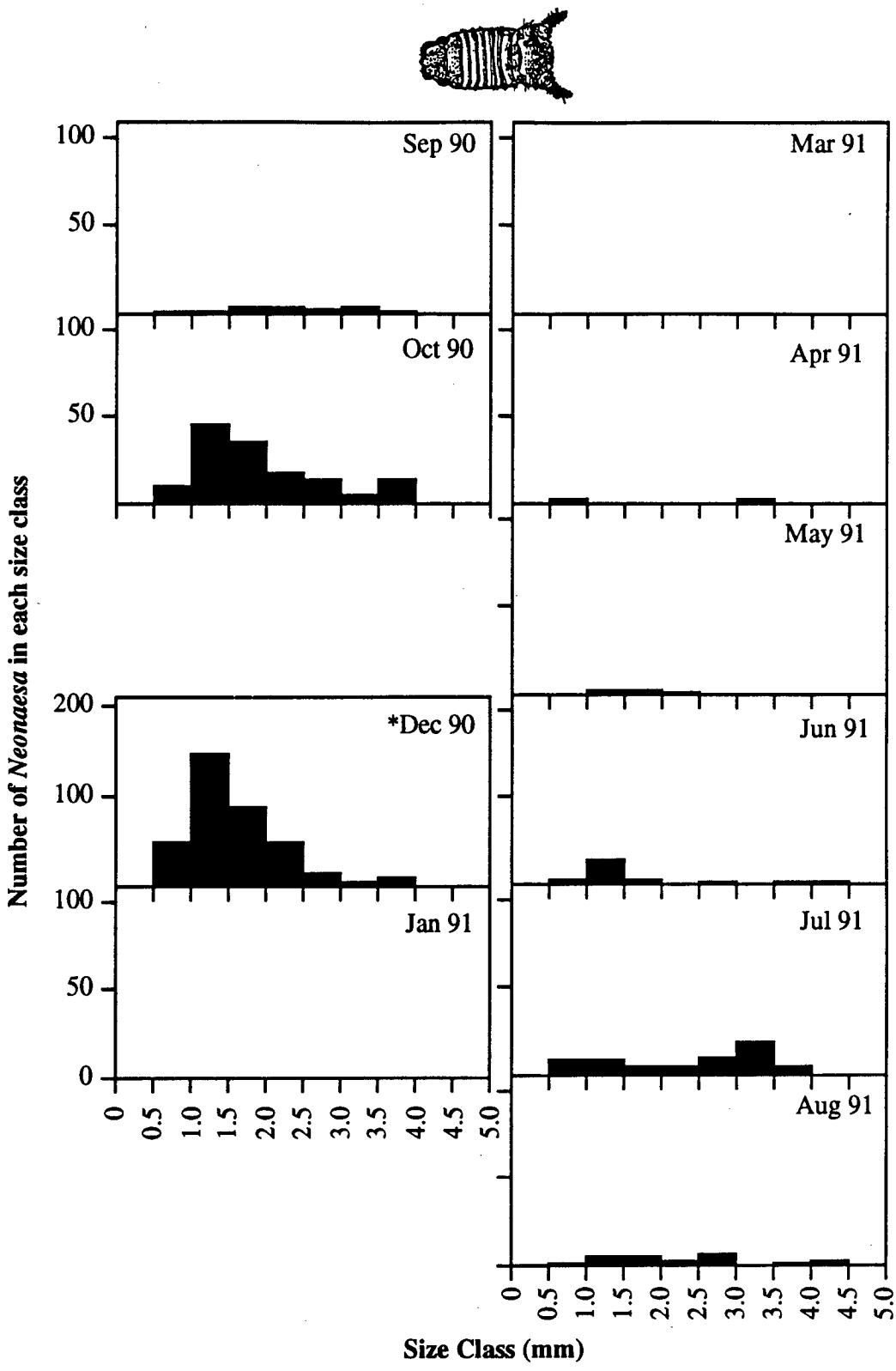


Figure 7.9. Size frequency distributions of populations of *Neonaesa* for 1990–1. *Scale for December 90 is 0-200 not 0-100 as in all other distributions. No data for November 1990 and February 1991.

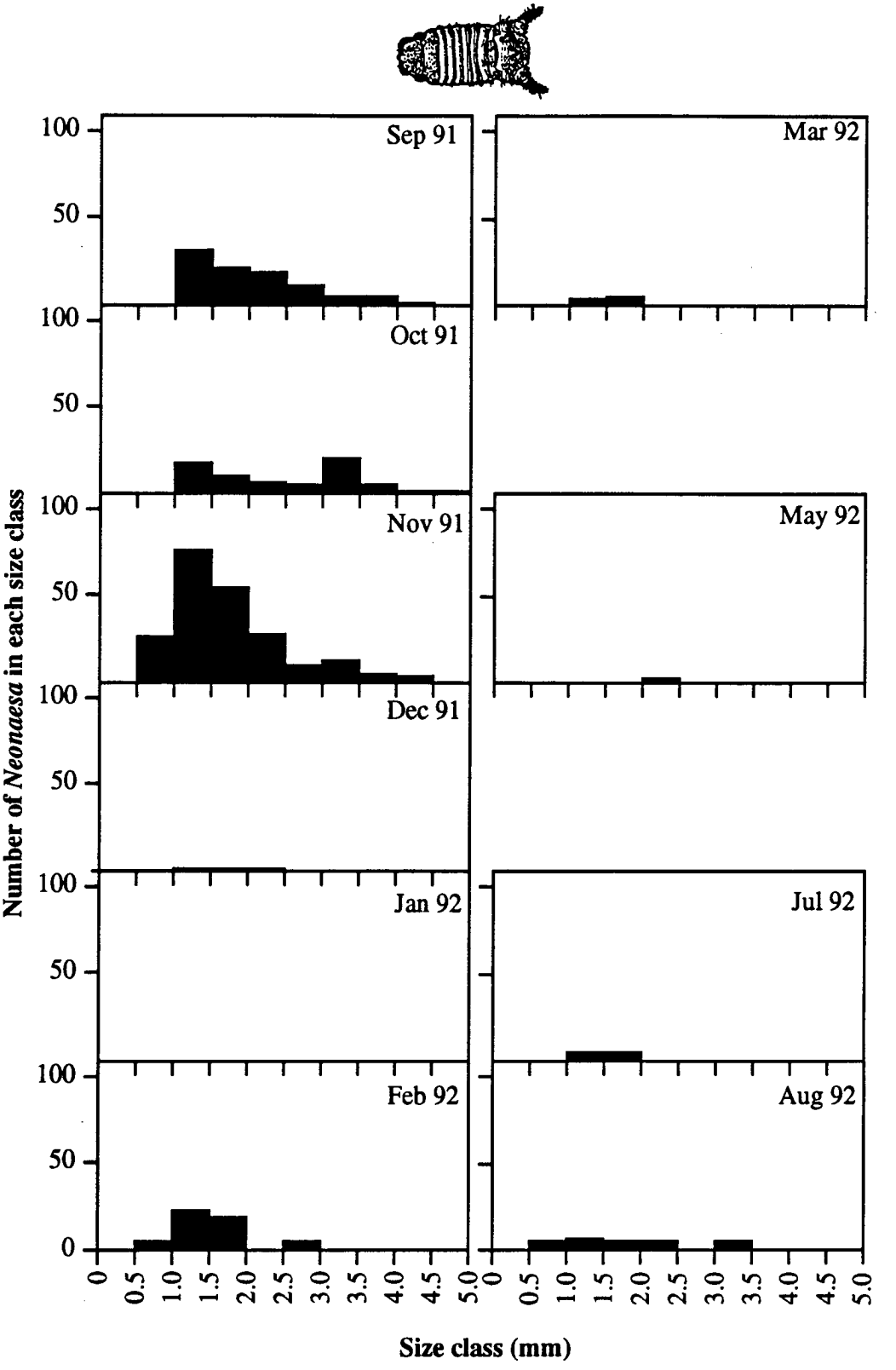
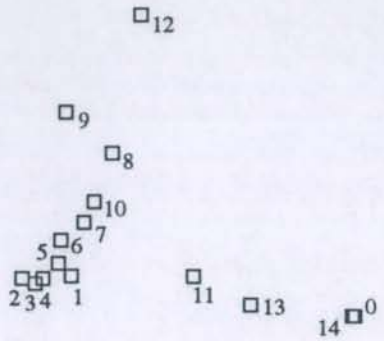


Figure 7.10. Size frequency distributions of populations of *Neonaesa* for 1991–2. No data for April and June 1992.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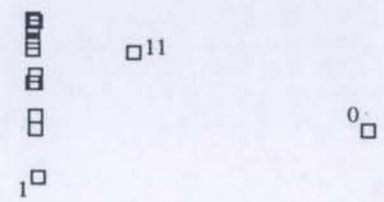
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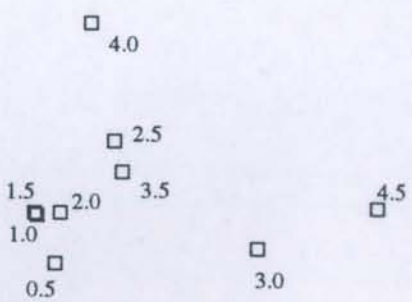
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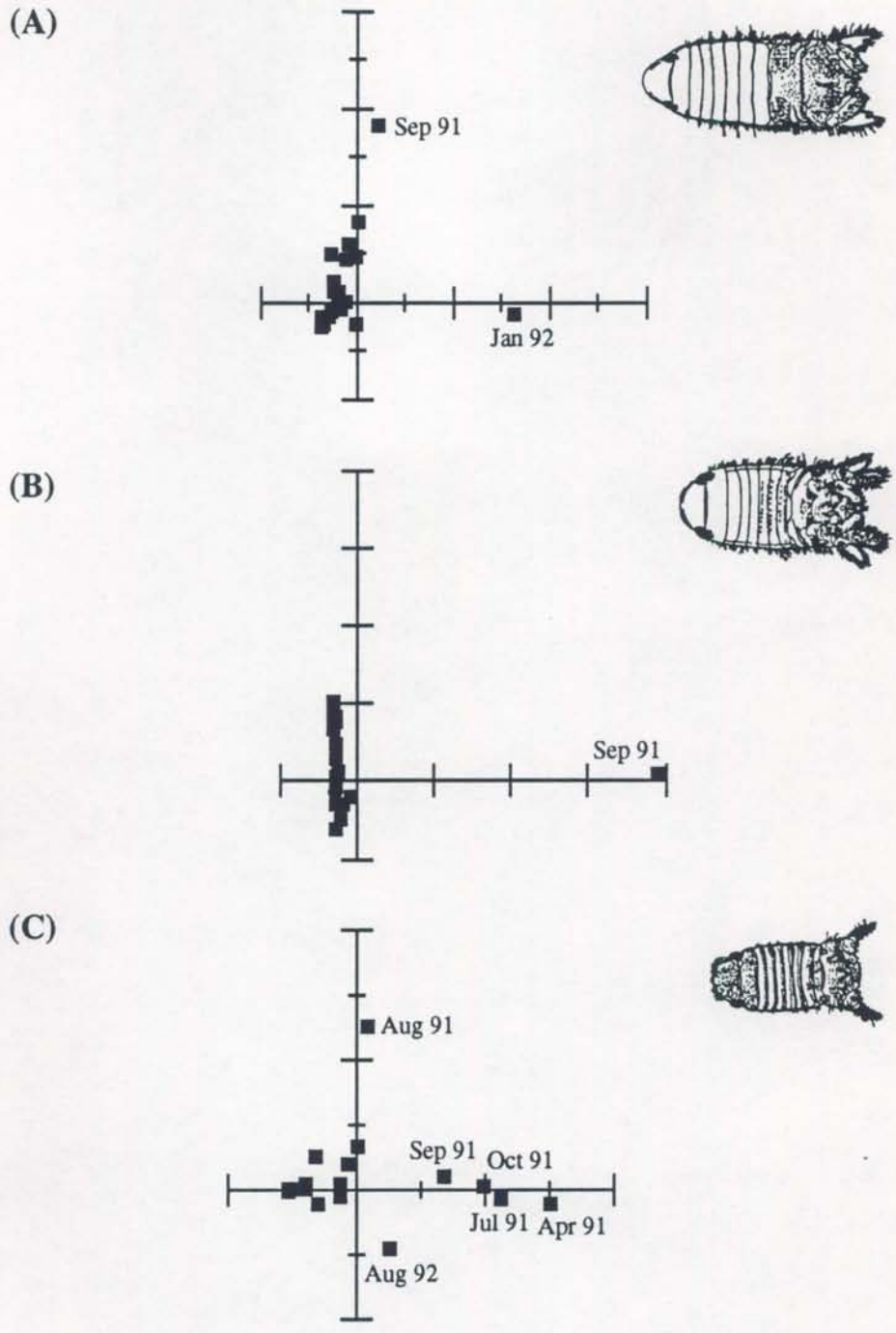


Figure 7.11. Results of Correspondence Analysis conducted on size-frequency distributions of (A) *Cerceis* (B) *Cymodoce* and (C) *Neonaesa* plotted by date. Dates for some points have been omitted for clarity. Overlay shows size classses contributing to differences between months.

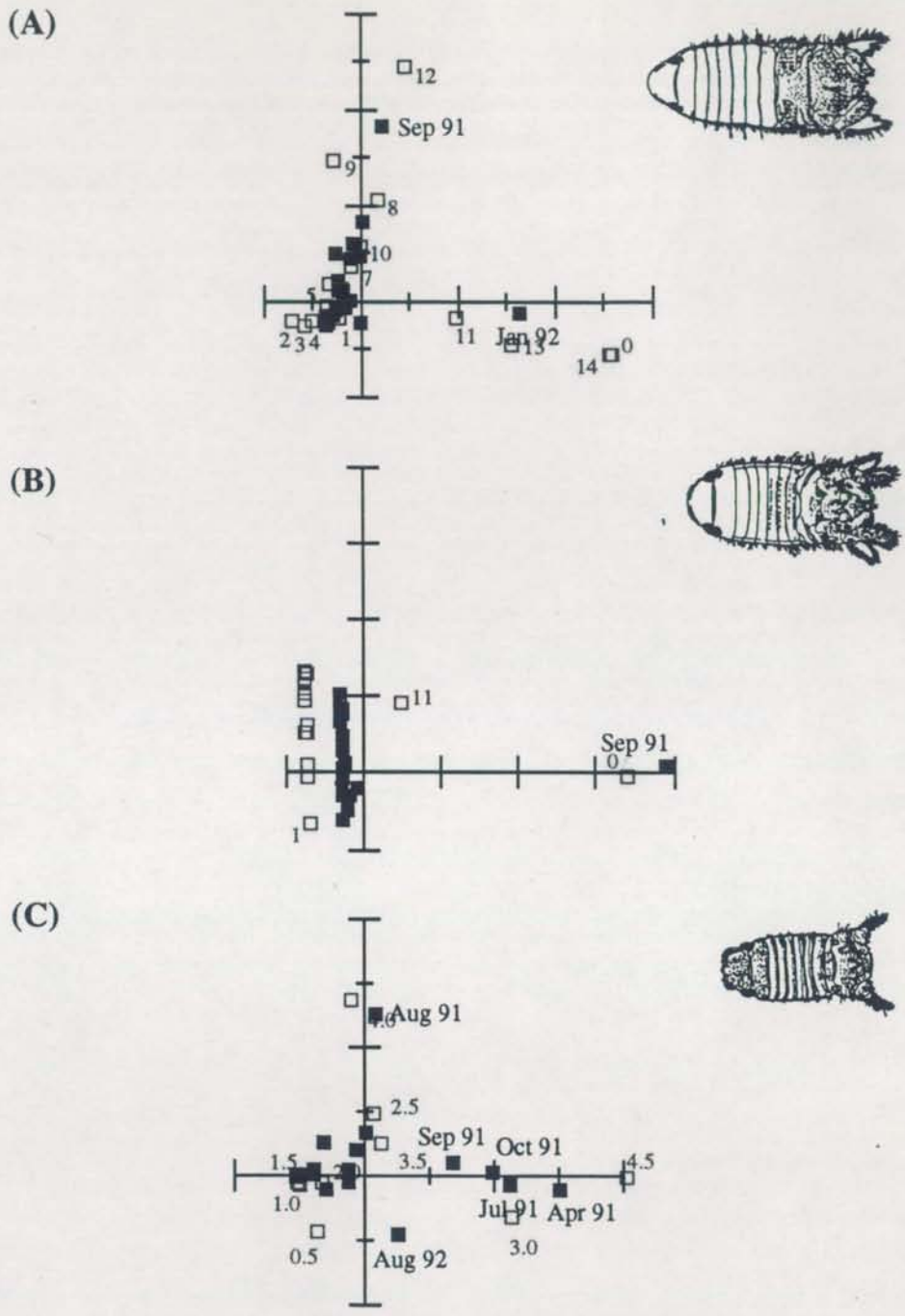


Figure 7.11. Results of Correspondence Analysis conducted on size-frequency distributions of (A) *Cerceis* (B) *Cymodoce* and (C) *Neonaesa* plotted by date. Dates for some points have been omitted for clarity. Overlay shows size classses contributing to differences between months.

Finally, CA for size-frequency distributions of *Neonaesa* showed separation between some months, but most of this separation was due to the presence of a few (in some cases only one) individuals in the larger size classes when sample size was very small (Figure 7.11C). Overall, CA of the size-frequency distributions of all the genera of isopods is consistent with the null hypothesis of no difference between samples.

7.5 DISCUSSION: ISOPOD SEASONAL PATTERNS

The abundance patterns of sphaeromatid isopods as a group were quite difficult to interpret, due to the presence of multiple abundance peaks at different times of year, but a general pattern of greatest abundance during late summer/early spring was detected (section 3.4.3). This pattern was resolved to a greater extent when the data were re-examined by individual genus of sphaeromatid (Figures 7.3 and 7.4). Some of the multiple abundance peaks for the group as a whole were revealed to be discrete abundance peaks for each genus. The overall pattern of a late summer peak was produced by late summer abundance of *Cerceis* and *Cymodoce* and the minor peaks in early summer were shown to be peaks in the abundance of *Neonaesa* rather than random 'noise'. There were also considerable differences in the magnitude of maximal abundance of *Cerceis* and *Cymodoce* from year to year which it was not possible to determine from the data for the group as a whole.

The seasonal patterns of tropical isopods remain almost entirely unknown. The few published studies of tropical sphaeromatids have been concerned with descriptions of new species and taxonomy (e.g. Harrison and Holdich 1982, 1984, Kensley and Schotte 1989) with brief notes on the location and habitat from which specimens were collected. Other studies which have examined seasonal patterns of isopods are exclusively temperate (see references in Table 7.II). For almost all species in studies which have explicitly enumerated population densities maximal abundance has occurred in summer-early autumn (Table 7.II). In the present study *Neonaesa rugosa* had an early summer population maximum, comparable with *Ligia dilatata* in South Africa (Koop and Field 1980) or *Dynamene magnitorata* in Spain (Arrontes and Anadon 1990b) while *Cerceis* and *Cymodoce* had late summer/early autumn maxima comparable to *Idotea baltica* and *I. chelipes* in the Baltic (Salemaa 1979) or *Dynamene bidentata* in Spain (Arrontes and Anadon 1990b). Kang and Yun (1988) reported highest densities of 8 species of isopod inhabiting surf grass (including *Cymodoce*) in April in Korea. Thus it would appear that seasonal patterns of abundance of sphaeromatid isopods are consistent between temperate and tropical regions.

Study	Location	Species	Time of maximum abundance	Time of minimum abundance	Release of juveniles
Amanieu (1969)	France	*Cyathura carinata*	not given	not given	July-Aug.
Arrontes & Anadon (1990)	Spain	*Dynamene bidentata*	Aug.-Oct.	Dec.-Apr.	continuous
		D. magnitorata	May- June	Aug.-Mar.	Apr.-May
		Cymodoce truncata	June-July	Aug.-Mar.	Apr.-May
		C. emarginata	variable	variable	not given
		Paranthura nigropuctata	Sep.-Oct.	Dec.-Mar.	not given
		Synisoma spp.	Nov.-Dec.	Mar.-Jul.	not given
Daguerre de Hureaux (1979)	France	*Sphaeroma serratum*	not given	not given	continuous (peak in June-Oct.)
Harvey (1968)	Wales	*Campecopea hirsuta*	not given	not given	July-Aug.
Healy & O'Neill (1984)	Ireland	*Idotea pelagica*	June-July	Oct.-Mar.	continuous (peak in Dec.-Aug.)
		I. granulosa	variable	variable	continuous (peak in Jan.-Apr.)
Heath & Khazaeli (1985)	England	*Sphaeroma rugicauda*	Aug.-Sep.	June-July	July-Sep.
Holdich (1976)	France	*Dynamene bidentata*	not given	not given	continuous
		D. magnitorata			
Jansen (1971)	New Zealand	*Isocladus armatus*	not given	not given	Dec.-Jan
		I. calcareus			Feb.-Apr.
		Exospheroma obtusum			Feb.-Mar.
		Dynamenopsis varicolor			Mar.-May
		Dynamenella huttoni			Feb.-May
		D. cordiforaminalis			Apr.-June
		Cymodocella egregia			continuous (peak in Mar.-May)
		Amphoroidea media			Oct.-Dec, Feb.-Apr.
		Scutuloidea maculata			Feb.
Johnson (1976)	California	*Cirolana harfordi*	not given	not given	continuous
Jones (1974)	England	*Jaera nordmanni nordica*	not given	not given	continuous (peak in July-Aug.)

(continued on next page)

Study	Location	Species	Time of maximum abundance	Time of minimum abundance	Release of juveniles
Koop & Field (1980)	South Africa	*Ligia dilatata*	Dec.-Jan.	May-Oct.	Oct.-Nov.
Salemaa (1979)	Baltic	*Idotea baltica*	Oct.	Aug.-Sep.	July-Aug.
		I. chelipes	Oct.	Aug.-Sep.	July-Aug.
		I. granulosa	not given	not given	July-Aug.
Shafir & Field (1980)	South Africa	*Cirolana imposita*	not given	not given	continuous (peak in Nov.-Dec.)
Tully & Ó Céidigh (1986)	Ireland	*Idotea emarginata*	Apr.-Nov.	Dec.-Feb.	Jul.-Nov.
		I. baltica	Apr.-Nov.	Dec.-Feb.	Jul.-Nov.
		I. neglecta	June-Aug.	Dec.-Feb.	Jul.-Aug.

Table 7.II. Summary of literature on isopod phenology and population dynamics.

Arrontes and Anadon (1990b) suggest that the reason for the observed population fluctuations of *Dynamene* and *Cymodoce* was related to their reproductive biology with macroalgae acting as a habitat for juveniles which then migrate from the algae when mature. This is similar to the present data in that most of the sphaeromatids collected from *Sargassum* were juveniles with very few adult males and no adult females present. Holdich (1976) reports that juvenile *Dynamene* were collected from *Sargassum* and *Cystoseira* but adults were found among colonies of hydroids, under rocks and in empty barnacle tests. I have conducted brief investigations of similar habitats at Magnetic Island but have failed to locate ovigerous females or adult males (*pers. obs.*). Other isopods show a shift in habitat from juveniles to adults e.g. *Eurydice pulchra* (Fish 1970), *Idotea baltica* (Salemaa 1979) and *Ligia pallasii* (Carefoot 1973) and this may be a general phenomenon. This 'migration' hypothesis is supported by examination of the size-frequency data for the different genera (Figures 7.5-7.10), although the disappearance of larger size classes could have been due to predation. Individuals in the largest size classes for all genera (invariably adult males) were never present in large numbers.

The seasonal patterns for all three genera of sphaeromatids were remarkably consistent between the two years of the study (Figures 7.3 and 7.4). Maximal abundance occurred for short periods of time (1-2 months) at the same times in 1991 and 1992. One interesting result is the difference in the timing of these seasonal peaks, which may indicate that temporal partitioning of the habitat was occurring. *Neonaesa* had a seasonal pattern almost diametrically opposed to the other two species and almost negligible numbers during the periods of *Cerceis* or *Cymodoce* abundance. Although *Cerceis* and *Cymodoce* had broadly similar patterns of abundance there were subtle differences which may indicate the processes controlling the relative abundance of the two genera. Both *Cerceis* and *Cymodoce* juveniles have been observed to eat young portions and receptacles of *Sargassum* (*pers. obs.*) and maximal populations occurred at times of decreasing *Sargassum* biomass, so resource competition for food could have occurred (cf. Gunnill 1984, 1985). Alternatively, in concordence with results from the previous chapter, either resource or interference competition for epiphytes as food or shelter could have occurred. Further work could manipulate populations of *Cerceis*, *Cymodoce* and *Neonaesa*, either in the field or in the laboratory to investigate these possibilities.

Sex-ratios and brood pouch measurements are usually used to ascertain breeding cycles of isopods (Table 7.II). The lack of ovigerous females in the present samples precluded direct estimation of the release of juveniles into the population. However, Arrontes and Anadon (1990b) used size-frequency data to elucidate the breeding patterns of *Dynamene* although no ovigerous females were found. Similar to their

patterns for *D. bidentata* there appeared to be an extended breeding period for *Cerceis*. In 1990-1 the size-frequency distributions were very similar from month to month, especially over the period March-July 1991. This could be interpreted in a number of ways – the most parsimonious explanation would be that the population did not change over these months. However, given the reported growth patterns of isopods (Amanieu 1969, Johnson 1976, Daguerre de Hureaux 1979, Shafir and Field 1980) this seems unlikely. Another possible explanation is that breeding took place over an extended period of time and consequently juveniles were being released continually into the population. Combined with continual loss of larger size classes, either by emigration or mortality, these processes would produce the observed patterns. In 1991-2 there appeared to be a burst of juveniles in January 1992 which may have been picked up again in March. Unfortunately, due to missing samples, further interpretation is not possible.

The size-frequency distributions of *Cymodoce* were similar to those of *Cerceis* which could indicate the same kind of reproductive behaviour. Large numbers of small isopods were found for extended periods of time, again suggesting continual or prolonged reproduction. CA confirmed that there was little or no difference in the size-frequency distributions of both *Cerceis* and *Cymodoce*. There was some evidence that *Neonaesa* had a more restricted period of reproduction since there were periods of time with no individuals at all. During the periods when *Neonaesa* was present in large numbers CA again showed that there was little pattern between months. If it is assumed that juveniles of this species only inhabit *Sargassum* at Magnetic Island, then it is hypothesised that reproduction in *Neonaesa* occurred during the period September-December. The presence of adult males from each genus may have linked with periods when reproduction occurred, alternatively their collection could have been a random event. If the former were true then *Cerceis* and *Cymodoce* would appear to have had extended breeding periods through much of the year, while *Neonaesa* had a more restricted breeding period during the winter/spring (June-November). Some of the problems with the interpretation of these results could be overcome by the acquisition of data about life-spans and laboratory studies of the growth of individuals would allow estimation of the transition times between size classes.

The conclusion to the above discussion is that *Sargassum* was a 'nursery' habitat for sphaeromatid isopods, similar to the role of macroalgae in temperate regions (Holdich 1976, Arrontes and Anadon 1990b). It remains to be ascertained where adults of these isopods are found although *Neonaesa* has been found inhabiting coral, both live and dead (Harrison and Holdich 1982, N.L. Bruce *pers. comm.*). It is interesting that the same situation should pertain in both the tropical and temperate regions despite the very great differences in both physical and biological environments. There may be strong selective pressures, such as predation, which restrict these isopods to *Sargassum* as juveniles, alternatively genetic legacies may be responsible.

Despite the additional information obviously obtained by the study of individual genera within the sphaeromatid isopods, the dilemma discussed earlier still remains – is it better to look at one group in great detail or to try and work with higher taxonomic groups at reduced resolution? In the case of the sphaeromatids presented above, resolution to generic level provided information that was otherwise unattainable about the phenology of *Neonaesa*. However, it was possible to obtain most of the other information about *Cerceis* and *Cymodoce* by considering the group as a whole. The solution to the dilemma is to let the question which the research is trying to answer drive the selection of taxonomic scale of the investigation. This is perhaps intuitive, but, like many such ideas, needs to be tested in a situation such as this to confirm it. The *Sargassum*-epifauna system was and remains little studied, the questions which this research hoped to answer involved community dynamics and there will always be logistical constraints on any work undertaken. As such, the broad-scale taxonomic approach adopted for the majority of this thesis was clearly appropriate.

7.6 METHODS: EXPERIMENTAL MANIPULATION OF HABITAT ARCHITECTURE

7.6.1 Determination of a suitable experimental system

In order to separate habitat effects from potentially confounding biologically effects artificial habitat units (AHUs) were used. AHUs were constructed in the form of small plastic cages (20 x 25 mm Nylex "Tree Guard" mesh), buoyed at the top with a 30 mm plastic float, open at the bottom to allow introduction of the habitat material and attached by nylon twine to large baskets for attachment to the substratum. Two sets of AHUs were constructed, both roughly cylindrical, the first with a diameter of 70 mm, height 80 mm (thus volume enclosed ≈ 300 mL), the second

with a diameter of 70 mm, height 140 mm (thus volume enclosed ≈ 540 mL). A trial of 8 AHUs of each type with the same material inside showed no significant difference in the number of *Cymodoce* which colonised (1-way ANOVA, $p>0.05$). A preliminary experiment was run from 9.10.92 to 23.10.92 to evaluate a range of artificial habitats as substrata for sphaeromatid isopods. Materials which were tested were: completely unravelled 8 cm lengths of 12 mm diameter polyethylene rope, 8 x 5 x 0.5 cm pieces of green plastic dish-cleaning sponge, 8 x 5 cm pieces of green nylon scouring pad and small volumes of "AquaFluff" aquarium filter material. Two natural habitats were also used to evaluate the efficacy of artificial vs real habitats: ≈ 5 cm pieces of *Padina* and red filamentous (RF) algae. The thallus volume (*sensu* Hacker and Steneck 1990) of habitat material was determined by the displacement of fresh water in an appropriate-sized measuring cylinder. Three AHUs of each of the six habitat materials were deployed on 9.10.92, two of each set of three were collected on 16.10.92 and the remaining AHUs collected on 23.10.92. AHUs were collected by placing each in a 'zip-lock' bag underwater, then cutting the nylon twine securing the AHU and sealing the bag. The contents of each bag were emptied through a 200 mm sieve and washed into a pot of 10% seawater-formalin. The habitat material was also placed in seawater-formalin for later microscopic examination.

7.6.2. Importance of size and colour of habitat and the presence of conspecifics

The results of the preliminary experiment (see section 7.7.1) showed that plastic dish-cleaning sponge was a suitable artificial habitat for sphaeromatid isopods, particularly *Cymodoce*. This material was used in a series of experiments designed to investigate the role of habitat size, colour and the presence of conspecific individuals on colonisation by *Cymodoce*. In the first experiment two colours of sponge (green and yellow) and a number of sizes (20, 50, 100, 150, 200, 400 cm^2) were tested in a 2 factor, orthogonal design (Figure 7.12A). Two replicates of each combination of size and colour of sponge were placed in AHUs and deployed on 26.11.92, along with 4 controls consisting of the AHU only with no habitat material inside. All AHUs were collected on 4.12.92 by the method described in the previous section. Size-frequency data on individuals colonising the green sponge was collected to determine if there was a size-specific response to habitat size. In a second experiment only green sponge was used with a different range of habitat sizes (100, 200, 300, 400, 500 cm^2) (Figure 7.12B). Four replicate AHUs with each size of sponge as well as four controls AHUs were deployed on 12.1.93 and collected on 19.1.93.

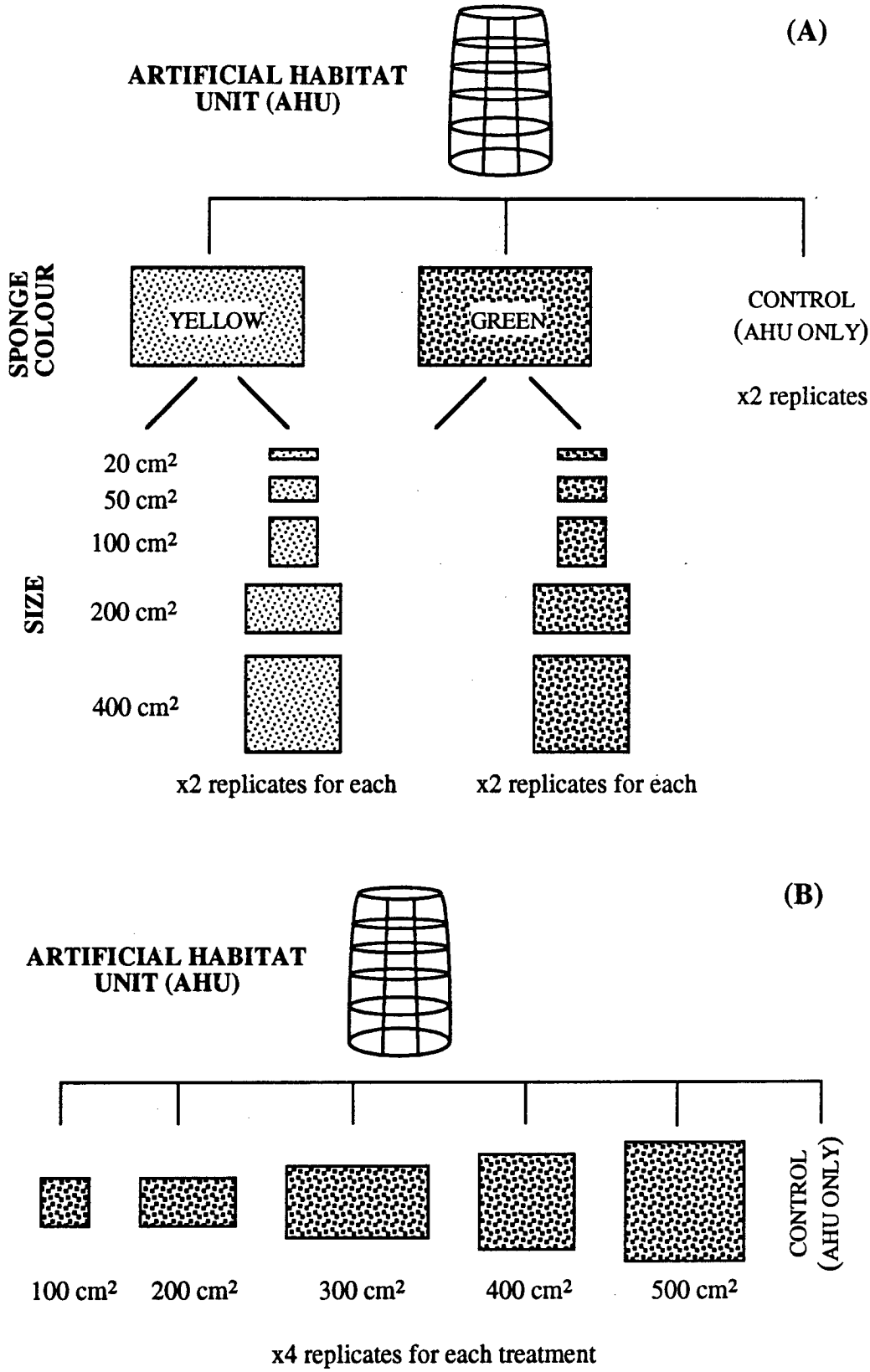


Figure 7.12. Experimental designs to test the effects of (A) colour and size of habitat (B) size of habitat on colonisation by *Cymodoce*.

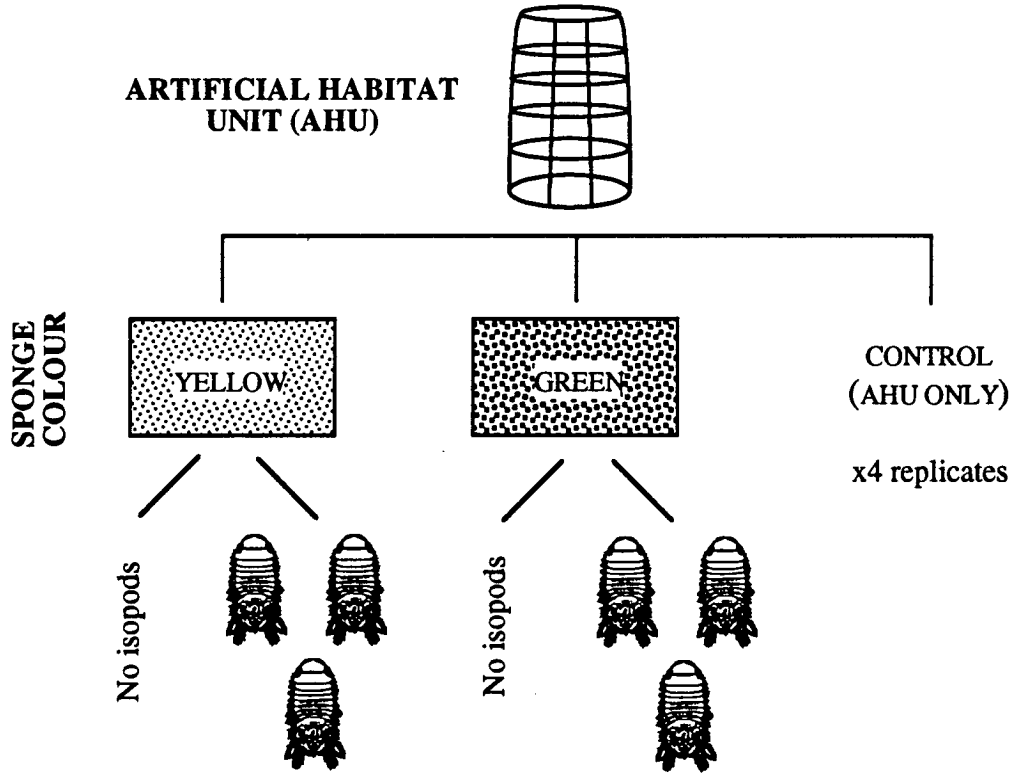


Figure 7.13. Experimental design to test effects of colour of habitat and presence/absence of conspecifics on colonisation by *Cymodoce.*

Sphaeromatids are known to exhibit aggregative settling behaviour (Shuster 1990), so it was decided to test the effects of conspecifics on colonisation. A third experiment was performed from 12.1.93-19.1.93 with an orthogonal design testing colour (green or yellow), sampling time (1, 2 or 7 days) and presence/absence of conspecifics (Figure 7.13). Forty-eight 200 cm^2 pieces of green and yellow sponge (24 of each colour) were placed in AHUs, along with 9 control AHUs only. Twelve AHUs for each colour of sponge were placed in plastic bags containing seawater. *Cymodoce* individuals were collected by washing a number of *Sargassum* plants in multiple changes of seawater and then 10 individuals were pipetted into each of the bagged AHUs which were then sealed using cable ties. These were designated as 'seeded' treatments, the other AHUs as 'unseeded' treatments. Both sets of AHUs were then attached randomly to baskets which were secured on to the substratum with 1 m lengths of reinforcing rod. All AHUs were then left for 2 hours to acclimate the isopods on the seeded treatments, after which time the cable ties were cut and the plastic bags removed. The plastic bags were subsequently examined to determine if any isopods had not settled on the sponge. AHUs were collected 1, 2 and 7 days after deployment (13.1, 14.1 and 19.1.93 respectively).

Abundance data for the numbers of *Cymodoce* in the first experiment were analysed using a two-way ANOVA with fixed factors COLOUR and SIZE. A regression of abundance against size of habitat was performed for each colour. For the second experiment involving habitats of green sponge only, data were analysed using a one-way ANOVA with fixed factor SIZE, followed by a regression of abundance against size of habitat. For the third experiment data were analysed using a three-way ANOVA with fixed factors TIME, COLOUR and PRESENCE OF ISOPODS.

7.6.3. Importance of holes to Cymodoce

All previous experiments were conducted using plastic sponge with a random array of hole sizes and distributions. To examine the effect of number of holes and hole size, artificial habitats were created with different numbers and sizes of holes. Expanded polystyrene was used instead of sponge, since it was easier to make suitable holes. Treatments were an orthogonal combination of small and large holes (4 and 6 mm nominal diameter respectively) and few or many holes (4 or 20 respectively) (Figure 7.14). Holes were created using steel drill bits pressed through 8 x 5 cm pieces of polystyrene. Six replicate AHUs of each treatment were deployed along with four control AHUs and left in the field from 13.4-20.4.93, then collected in the

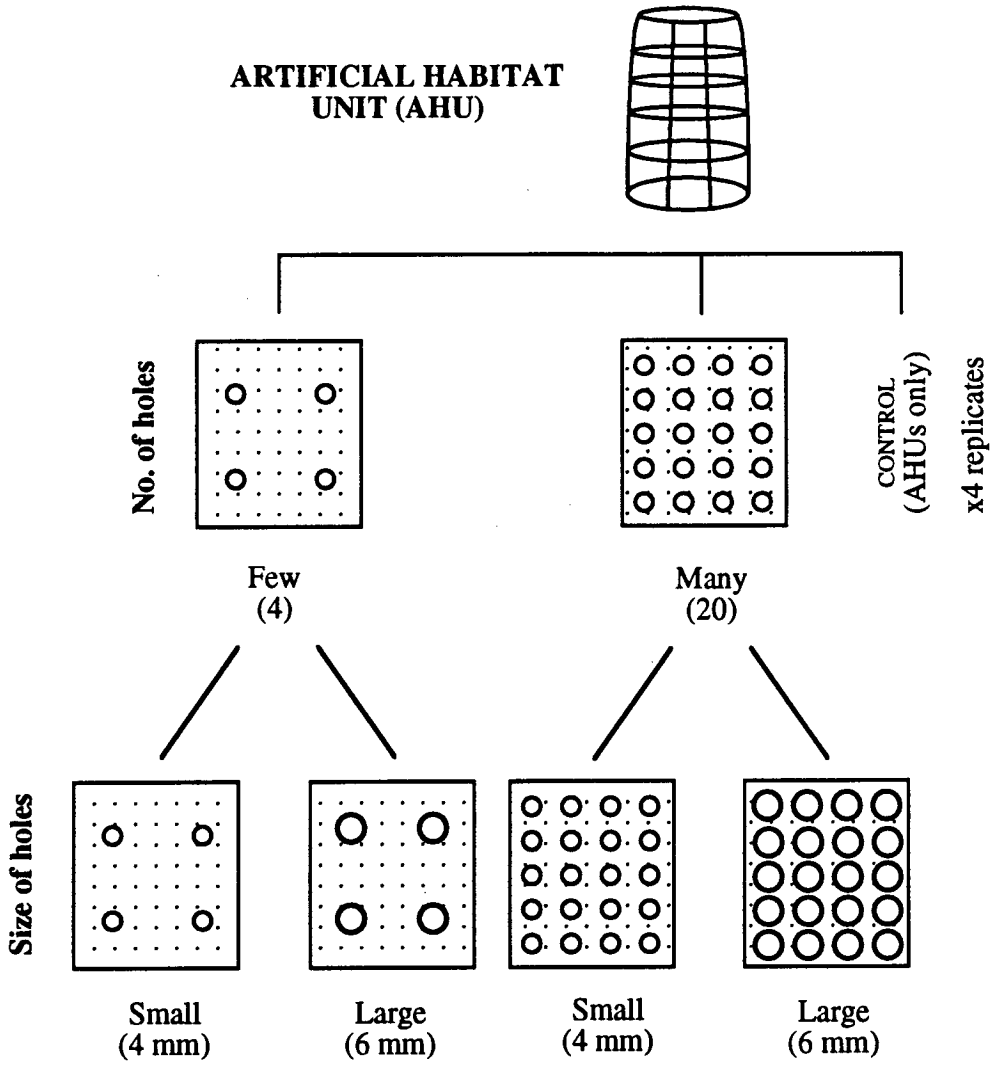


Figure 7.14 Experimental design to test the effect of number of holes and hole size on colonisation of expanded polystyrene by *Cymodoce*

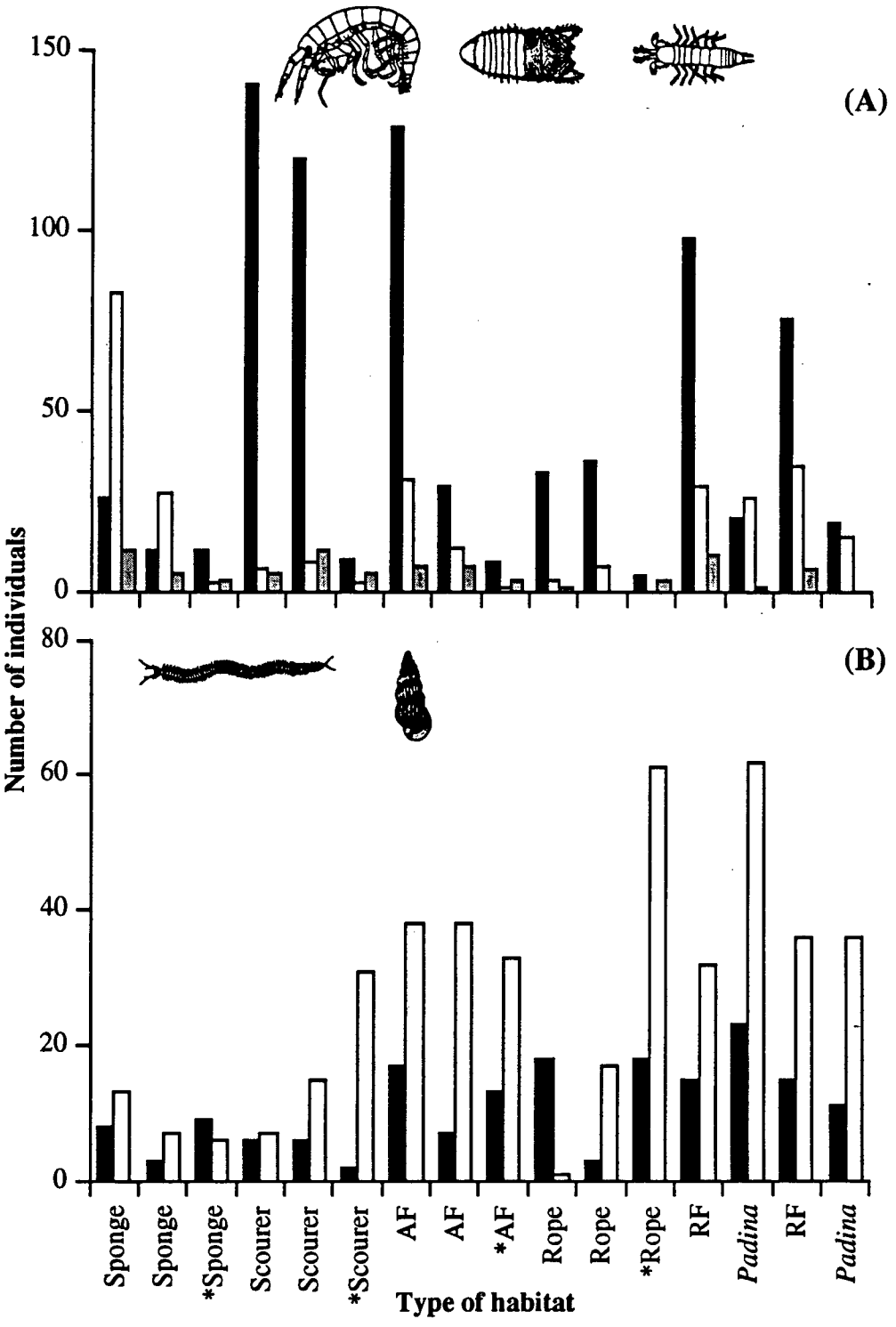


Figure 7.15. Numbers of (A) gammarids (■), sphaeromatids (□) and tanaids (▩) and (B) polychaetes (■) and gastropods (□) in preliminary artificial habitat experiment. All samples marked with * collected 2 weeks after deployment, 1 week for all others. AF=aquarium filter material, RF=red filamentous algae.

usual manner. The size-frequency distribution of *Cymodoce* collected was determined by video analysis as described in section 7.3.2.

The abundance data were analysed using 2-way ANOVA with fixed factors SIZE OF HOLES and NUMBER OF HOLES. Size-frequency data were analysed by correspondence analysis

7.7 RESULTS: EFFECTS OF HABITAT ARCHITECTURE

7.7.1 Preliminary experiment

Different taxa were attracted to different artificial habitats (Figure 7.15), although replication was too low in this experiment to make any statistical comparisons between habitats. Gammarids were found on all treatments and in especially high abundance on scourers (at 1 week only), on AquaFluff and on red filamentous algae (Figure 7.15A). Sphaeromatids were found in highest abundance on the 1 week sponge samples and in the red filamentous and *Padina* and tanaids were found generally on all habitats (Figure 7.15A). Polychaetes and gastropods were also found on all habitats, with highest abundance generally on AquaFluff, rope, red filamentous algae and *Padina* (Figure 7.15B). Most of the samples taken at 2 weeks had fewer crustaceans than the samples taken at 1 week. There was little correlation between thallus volume and the abundance of individuals of any taxon, either between or within artificial habitat types.

7.7.2 Effects of colour and size of habitat and presence of conspecifics

In the first experiment both colour and size significantly affected the number of *Cymodoce* which colonised the sponge habitats (Figure 7.16). There were significantly more *Cymodoce* individuals on green sponge of all sizes than yellow and there were increasing numbers of *Cymodoce* with increasing size of habitat regardless of colour (Table 7.III). Significant linear relationships were found between the number of *Cymodoce* and the size of habitats for both colours of sponge (Figure 7.16). However the R^2 value for yellow was low (due to high variability within replicates and the loss of some samples) and the regression for green was driven primarily by a single point with high numbers of *Cymodoce* (400 cm^2 size). There was no interaction between colour and size (Table 7.III) indicating a similar response to size of habitat from both colours, despite the difference in the slope of the regression lines. It appears that there may have been a 'threshold' size of habitat

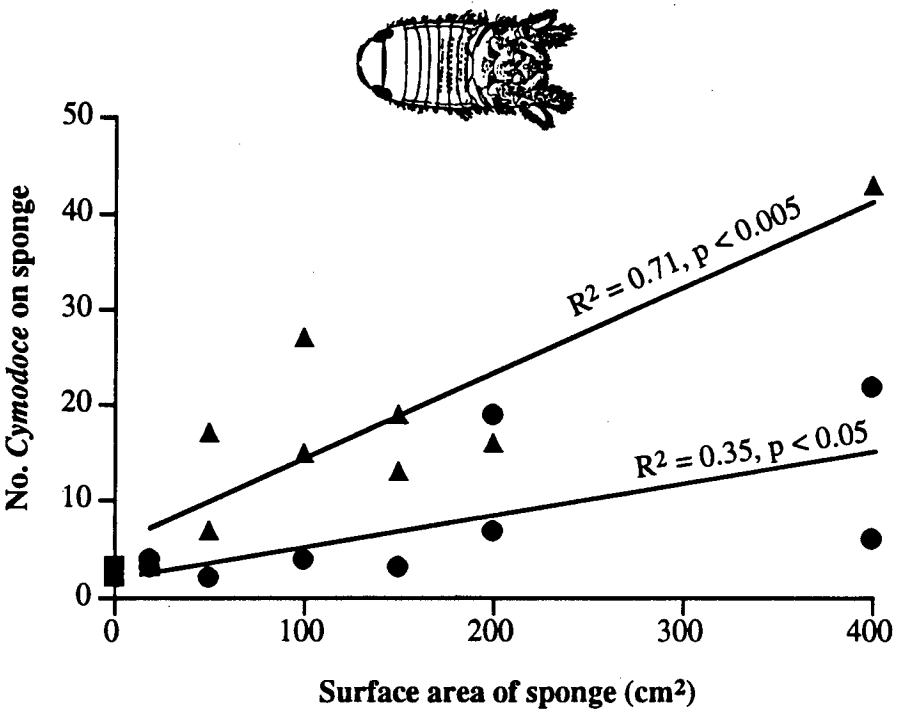


Figure 7.16. Number of *Cymodoce* colonising green (▲) and yellow (●) sponge habitats of differing sizes, with fitted linear regressions. Control AHUs (■).

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Colour	1	684.500	684.500	15.919	.0040
Size	5	1106.952	221.390	5.149	.0208
Colour * Size	5	418.952	83.790	1.949	.1916
Residual	8	344.000	43.000		

Dependent: No. *Cymodoce*

Table 7.III. Results of 2-way ANOVA performed on number of *Cymodoce* colonising green and yellow sponges of various sizes with fixed factors COLOUR and SIZE.

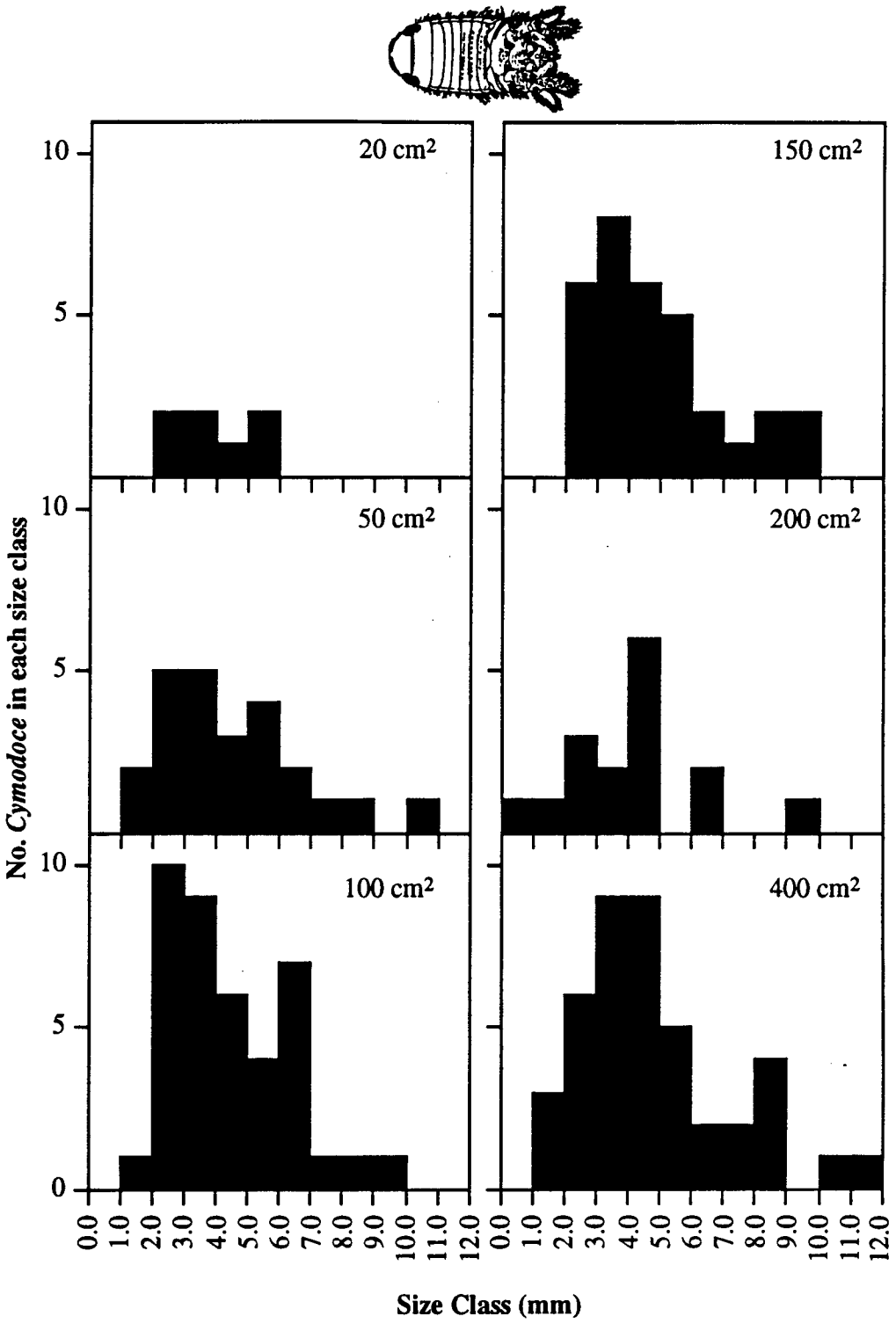


Figure 7.17. Size-frequency distributions of *Cymodoce* colonising green sponge habitats of differing sizes (size of habitat given in top left hand corner of each distribution).

required since numbers on 20 cm^2 and 50 cm^2 habitats were little different to controls. Unfortunately, due to high variability between samples and the (unexpected!) difference between colours there was not sufficient power to perform *a posteriori* tests between controls and experimental samples.

The size-frequency distributions of *Cymodoce* from green sponges of different sizes were similar (Figure 7.17). Most distributions were skewed towards the smaller size classes but the modal size was generally greater than for size-frequency distributions from *Sargassum* plants at a similar time of year (3-5 mm CBL as opposed to 2-3 mm CBL in Figures 7.6 and 7.7). CA showed that the size-frequency distributions between the different sizes of sponges were fairly similar, only the 200 cm^2 samples being greatly different from the others, probably due to low sample size (Figure 7.18).

When the experiment was repeated with green sponge only and higher replication, there were again higher numbers of *Cymodoce* on larger sizes of habitat (Figure 7.19), a result which was statistically significant (Table 7.IV). A significant linear relationship was again found between number of *Cymodoce* and size of habitat but the R^2 value was low (Figure 7.19). *A posteriori* SNK tests showed that the only significant differences between means from different sizes of sponge were between the 100 cm^2 sponge and the others. Numbers were lower on habitats of comparable size in the second experiment when compared with the first.

In the final experiment to investigate the effects of colour and the presence of conspecifics there was no significant effect of colour or of seeding the habitats* (Figure 7.20). A significant time effect was found with higher numbers of isopods after 7 days than at 1 or 2 days (Table 7.V). None of the interaction terms between the three factors were significant indicating similar responses over time to yellow and green and seeded and unseeded sponges (Table 7.V). Again, numbers of *Cymodoce* were low compared with comparable sized sponge from the first experiment.

7.7.3 Effects of size and number of holes in habitat

There was no significant effect of size of holes on abundance of *Cymodoce* but there were significantly more individuals on treatments with more holes (Figure 7.21 and Table 7.VI). There was no significant interaction between size and number of holes, the same relationship being evident between treatments despite the differences

* Data for T_0 was omitted from the analysis since there was an *a priori* specified difference between treatments

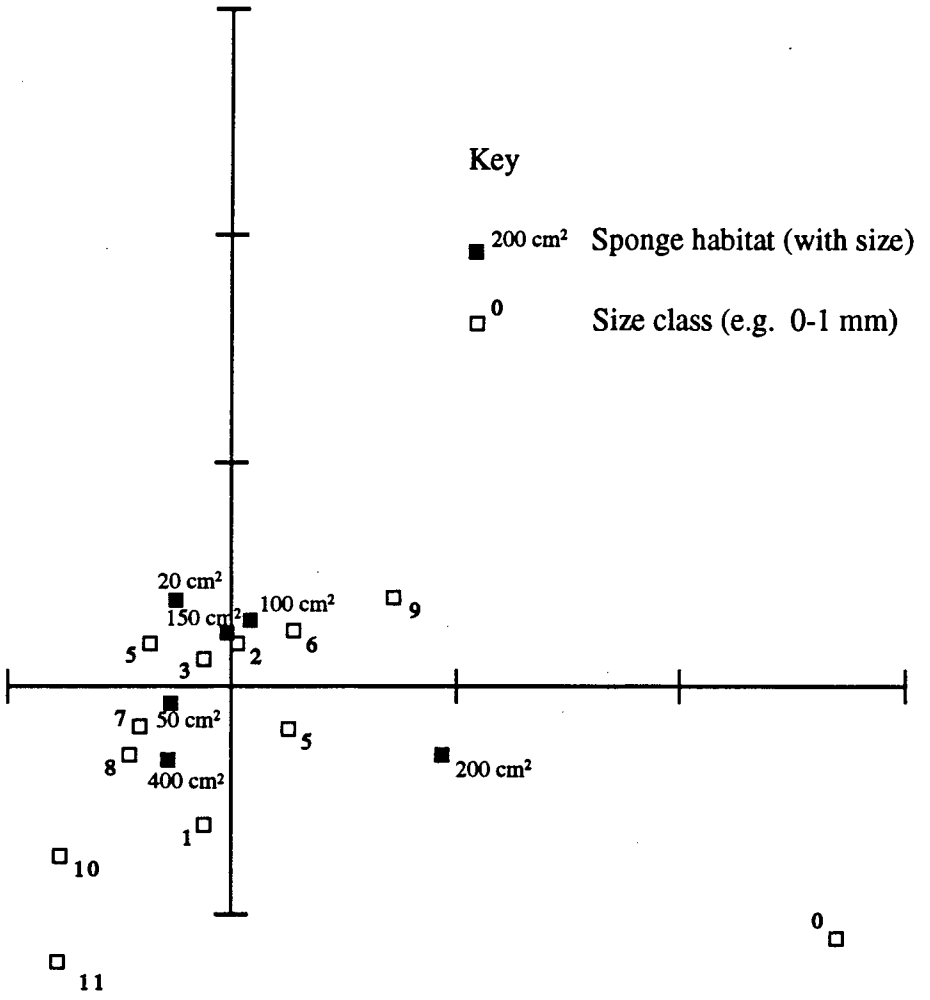


Figure 7.18. Results of correspondence analysis on size-frequency distributions of *Cymodoce* from green sponge habitats of various sizes.

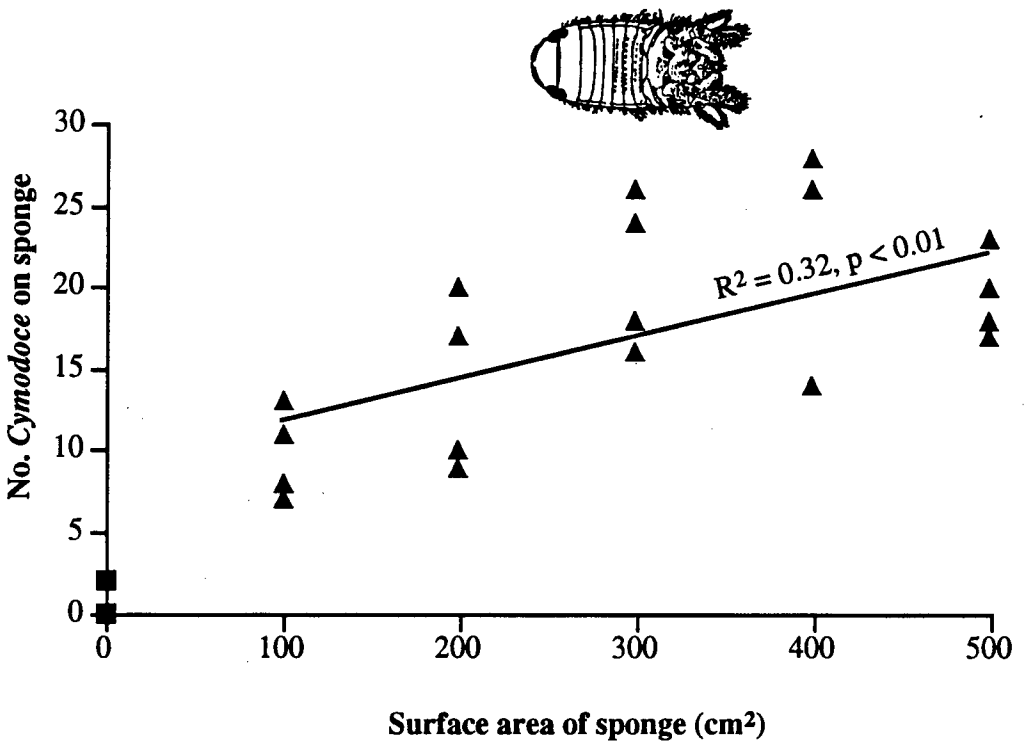


Figure 7.19. Number of *Cymodoce* colonising green sponge (▲) of differing sizes with fitted linear regression. Control AHUs (■).

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Size	4	384.200	96.050	3.907	.0228
Residual	15	368.750	24.583		

Dependent: No. *Cymodoce*

Table 7.IV. Results of 1-way ANOVA performed on number of *Cymodoce* colonising green sponge of various sizes with fixed factor SIZE.

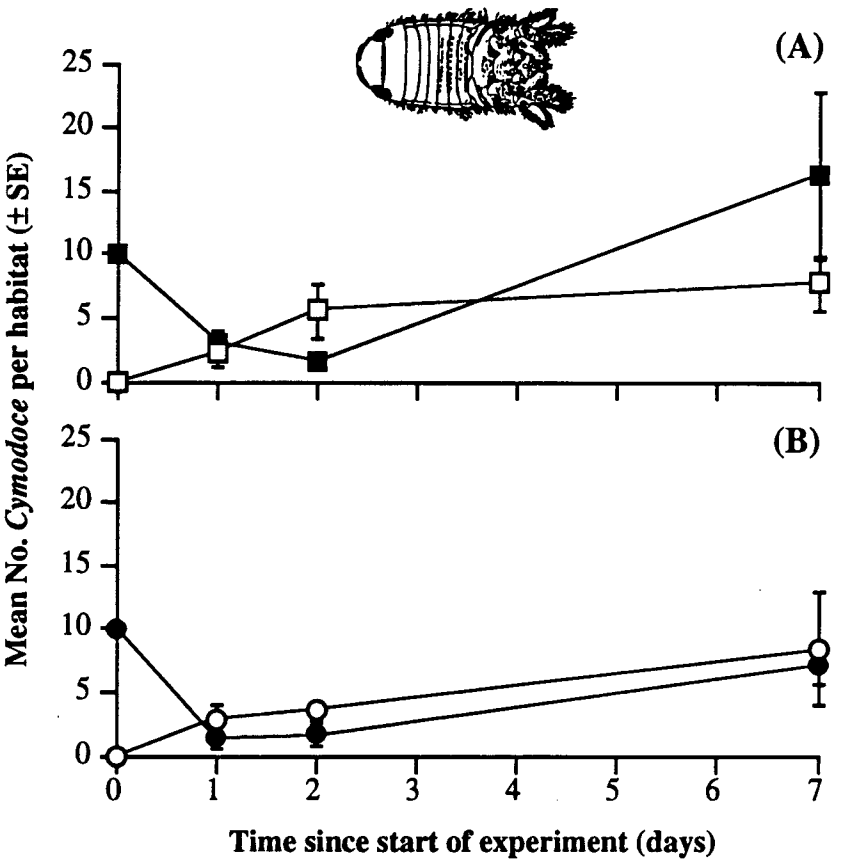


Figure 7.19. Mean numbers of *Cymodoce* colonising (A) yellow (B) green sponge habitats. Filled symbols indicate habitats were initially seeded with 10 *Cymodoce* individuals, open symbols were not seeded. n = 4 for each time point.

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Day (D)	2	465.596	232.798	13.970	.0001
Colour (C)	1	40.573	40.573	2.435	.1288
Seeding (S)	1	.446	.446	.027	.8710
D * C	2	22.826	11.413	.685	.5116
D * S	2	71.796	35.898	2.154	.1330
C * S	1	25.335	25.335	1.520	.2268
D * C * S	2	60.859	30.429	1.826	.1779
Residual	31	516.583	16.664		

Dependent: No. *Cymodoce*

Table 7.V. Results of 3-way ANOVA performed on data plotted above with fixed factors DAY, COLOUR and SEEDING.

in numbers (Table 7.VI). The modal size of *Cymodoce* on habitats with large holes was greater than that for habitats with small holes (Figure 7.22). However, there were a few large individuals on treatments with small holes. This was shown in the CA by the wide separation of all four treatments, each treatment being influenced by different size classes of isopod (Figure 7.23).

7.8 DISCUSSION: IMPORTANCE OF HABITAT STRUCTURE TO *CYMODOCE*

Habitat structure was obviously important to sphaeromatid isopods. The first interesting point which emerged was the specificity of colonisation of all of the habitats by *Cymodoce* rather than *Cerceis*. Although concurrent seasonal data on abundance of both were not available, data from the two previous years showed that both were abundant over the period during which the experiments were performed (winter/spring). However, in none of the field experiments performed, were there more than 2 *Cerceis* individuals per AHU, and more often than not there were none at all. *Cerceis* and *Cymodoce* may have responded differently to the artificial habitats – sponge was specifically chosen because of its porous structure, based on the habitat preferences of sphaeromatids from temperate regions (Holdich 1976, Shuster 1992). *Cerceis* may choose habitats based on spaces larger or differently-shaped to those offered by sponge, or respond to thallus thickness or shape (Hacker and Steneck 1990). Another hypothesis to explain the lack of *Cerceis* on artificial habitats could be due to differential swimming behaviour between the two genera. The AHUs floated in the water column and therefore presumably sampled swimming individuals, this behaviour being well-known in sphaeromatid isopods (Jones and Naylor 1970, Fish and Fish 1972) and *Cymodoce* was observed to swim often in basins. If *Cerceis* exhibited lower levels of this behaviour then it would consequently have been less abundant in collections. A further hypothesis could invoke competition between the two genera whereby *Cymodoce* excluded *Cerceis* from the holes in the habitat. Additional behavioural experiments would be needed to test these hypotheses.

Colonisation by *Cymodoce* was rapid in all experiments with large numbers of individuals usually present within 7 days of deployment. The only experiment to explicitly test the effect of time (experiment 3) showed an increase over time from 1 and 2 days to 7 days after deployment. This is very similar to the pattern found by Edgar (1991a) with the colonisation of artificial turf habitats in a *Sargassum* bed in Japan by an unidentified sphaeromatid. Interestingly the abundance of the sphaeromatid declined from 8 days onwards in Edgar's experiment as was found with sphaeromatids between 1 and 2 weeks in the preliminary experiment. Stoner (1985)

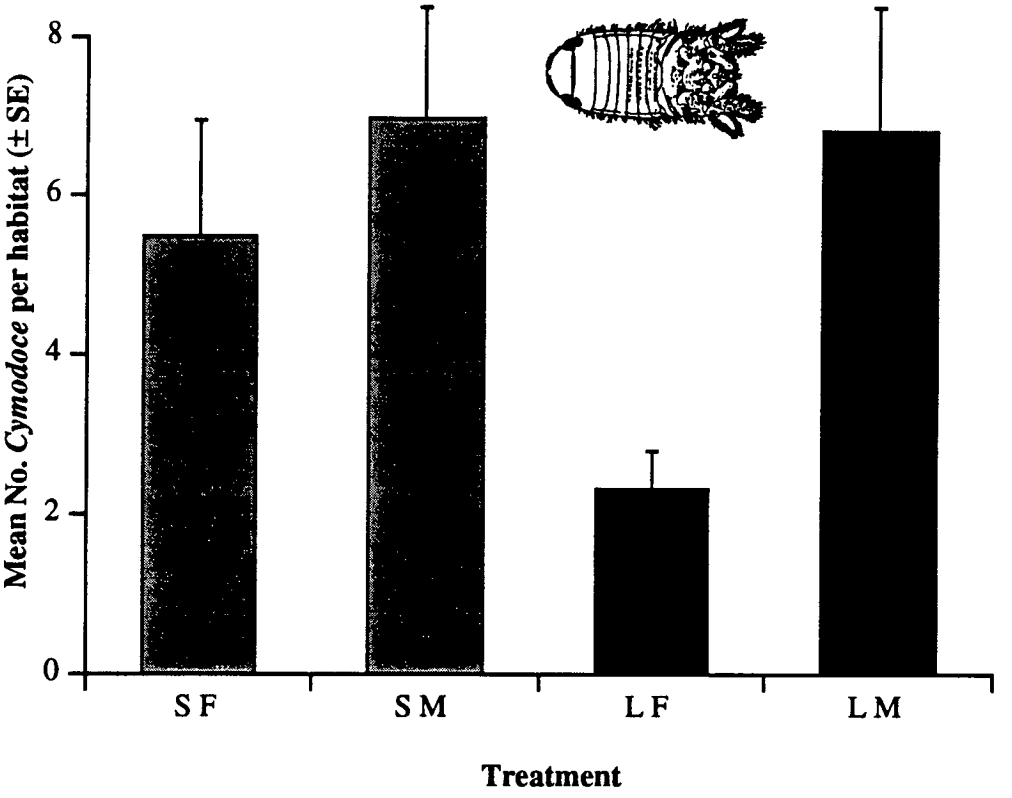


Figure 7.21. Mean numbers of *Cymodoce* colonising polystyrene with small, few (S F), small, many (S M), large, few (L F) or large, many (L M) holes. Small = 4 mm nominal diameter, large = 6 mm, few = 4, many = 20. n = 6 for each treatment.

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Size of Hole (S)	1	16.667	16.667	1.669	.2111
No. of Holes (N)	1	54.000	54.000	5.409	.0307
S * N	1	13.500	13.500	1.352	.2586
Residual	20	199.667	9.983		

Dependent: No. *Cymodoce*

Table 7.VI. Results of 2-way ANOVA performed on data plotted above with fixed factors SIZE OF HOLE and NUMBER OF HOLES.

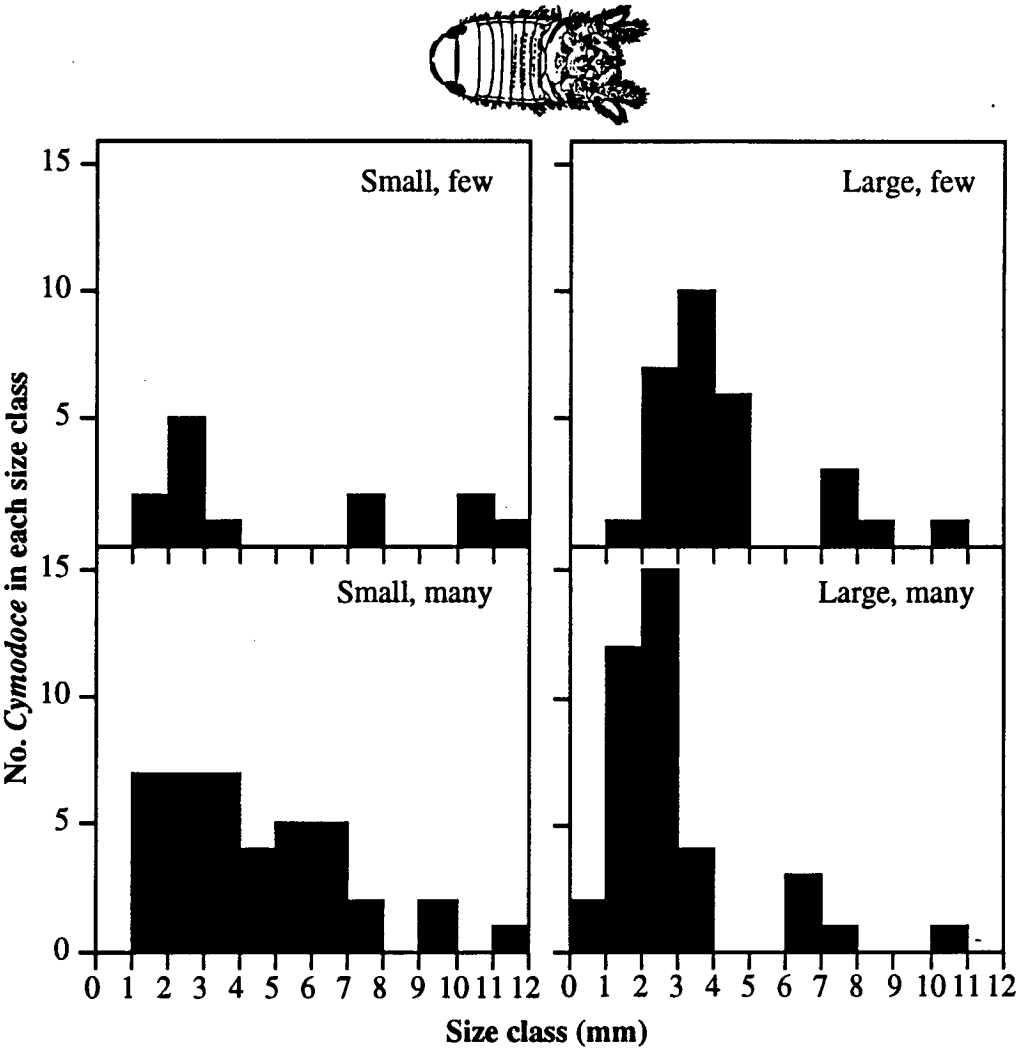
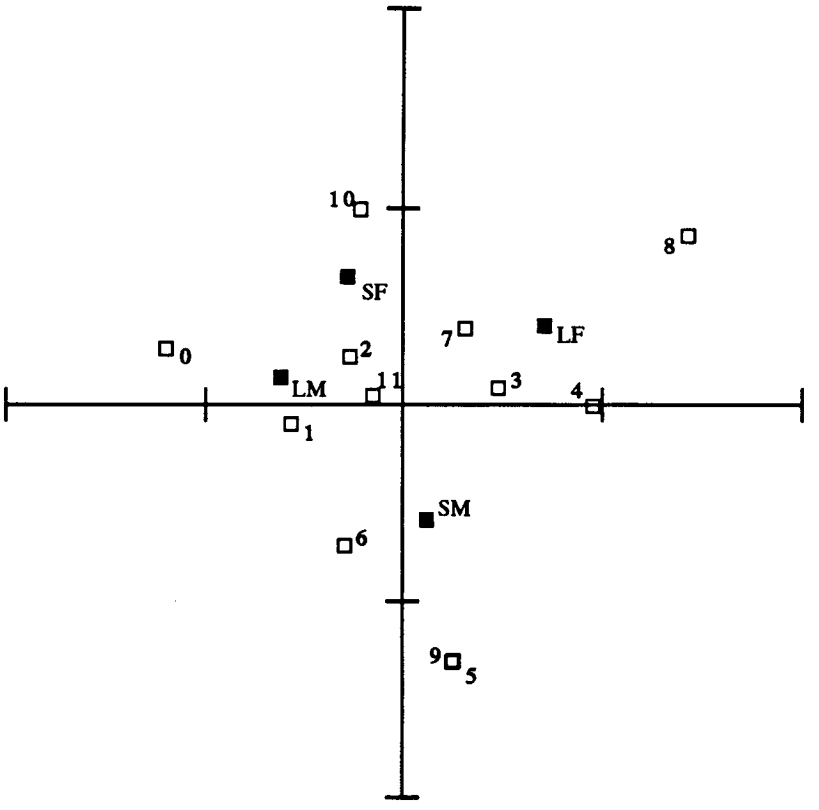


Figure 7.22. Size-frequency distribution of *Cymodoce* colonising polystyrene habitats with holes. Small = 4 mm nominal diameter, large = 6 mm, few = 4, many = 20.



Key

■ LF Polystyrene habitat (with treatment)

□ 0 Size class (e.g. 0-1 mm)

Figure 7.23. Results of correspondence analysis on size-frequency distributions of *Cymodoce* from polystyrene habitats with small, few (SF), small, many (SM), large, few (LF) or large, many (LM) holes.

also found that an isopod, *Bagatus stylodactylus,* colonised defaunated *Penicillus* very quickly, increasing in abundance from its appearance 3 hours after defaunation up to 96 hours when the experiment was terminated.

Cymodoce responded to most of the aspects of habitat structure that were tested. The size of habitat was obviously an important variable in colonisation by this isopod – more *Cymodoce* were found on larger habitats in all experiments. This was probably not because of the probability of encounter, since all the habitats were contained in AHUs of the same size and presented similar surface areas. Although significant linear regressions were fitted to all the data the goodness-of-fit was low. This indicates that abundance of isopods was not responding linearly to the size of habitat. There appeared to be a 'threshold' level of <100 cm^2 surface area of habitat below which the habitat was too small for colonisation and a 'ceiling' level of 300-500 cm^2 where abundance of isopods remained constant. Very small habitats may have rendered isopods susceptible to predation (the mesh of the AHU was large enough to allow entry by fish) or may not have been visible to a searching isopod. Portions of increasingly large habitats within a fixed volume AHU may not have been available for occupation or increasing density of *Cymodoce* could have led to interspecific competition. The analysis of size-frequency distribution supports the idea that there were no size-specific responses by the isopods to the size of habitat.

Colour of the habitat was very important in the first experiment performed, with isopods significantly preferring green sponge, but this effect was not evident when the experiment was repeated. This could be a statistical artifact resulting from a Type I error in the first experiment or a Type II error in the second or could reflect a real difference caused by some other factor differing between the sampling dates. Hacker and Madin (1991) showed a significant preference by the shrimp *Latreutes* for yellow artificial algae although another shrimp tested, *Hippolyte,* showed no colour preference. In laboratory trials Hay *et al.* (1990b) found that the green crab *Thersandrus* consistently chose its normal green algal host *Avrainvillea* over other green seaweeds and that this was not related to the secondary metabolites of the alga. *Cymodoce* are similar in colour to *Sargassum* (Plate 7.I) which suggests that colour of habitat may be important , but interpretation of the results from the present study remains equivocal.

Higher numbers of *Cymodoce* were found on habitats with larger number of holes, which suggests that these isopods preferentially inhabit crevices (see Holdich 1976, Shuster 1992). The size of hole was not important in terms of the numbers of isopods which colonised but it did strongly influence the sizes of those isopods. The modal size of isopods inhabiting habitats with large holes was greater than that of

those inhabiting habitats with small holes, suggesting that *Cymodoce* select holes which match their body size. Shuster (1992) demonstrated that a-males of the sphaeromatid *Paracerceis sculpta* preferred sponge oscula which closely matched their body size and Steger (1985) showed that stomatopods occupy cavities of particular sizes. It appears, therefore, that these isopods can find and discriminate between these type of structural aspects of their habitat.

A summary of the findings of the experiments which were performed is shown schematically in Figure 7.24 along with possible explanations for the results.

7.9 CONCLUSIONS: PATTERNS AND PROCESSES WITHIN POPULATIONS OF SPHAEROMATID ISOPODS

How does the results of this chapter fit together to describe the role of sphaeromatids on *Sargassum*? It seems that the *Sargassum* acts as a substrate for the growth of epiphytic algae which provide the appropriate habitat for colonisation by juvenile sphaeromatids. These individuals grow and mature on the plants and then leave again when sexually mature. *Sargassum* has an ecological role towards the sphaeromatids as a nursery habitat, while the reciprocal interaction is probably mutualistic or commensal with respect to the effect of the sphaeromatids.

Although *Cymodoce* was observed in the laboratory to feed on *Sargassum*, this antagonistic behaviour is probably of little ecological consequence. Arrontes (1990b) found that the most common dietary items of *Cymodoce* were newly settled sponges and detritus, while no information is known about *Cerceis* or *Neonaesa*. Nicotri (1980) noted that *Idotea baltica* preferentially selected large brown algae as habitats but he attributed this to protection from predation by fishes, earlier work having shown that grazing losses of cultured macroalgae were of little consequence (Nicotri 1977). Hootsman and Vermaat (1985) also found that *Idotea* grazed periphyton, rather than seagrass blades, and that this behaviour was mutualistic with increased growth rates of the seagrass in the presence of the isopod. Edgar and Robertson (1992) showed that a number of epifaunal species, including isopods, declined in abundance with epiphyte removal. No work has been performed on *Sargassum* at Magnetic Island to determine whether (a) photosynthesis is light-limited or (b) shading by epiphytes and periphyton is of greater consequence than reduction in light levels caused by wind-driven resuspension of sediment (Walker and O'Donnell 1981). Such work would be needed to determine whether the *Sargassum*-sphaeromatid interaction is commensal or mutualistic.

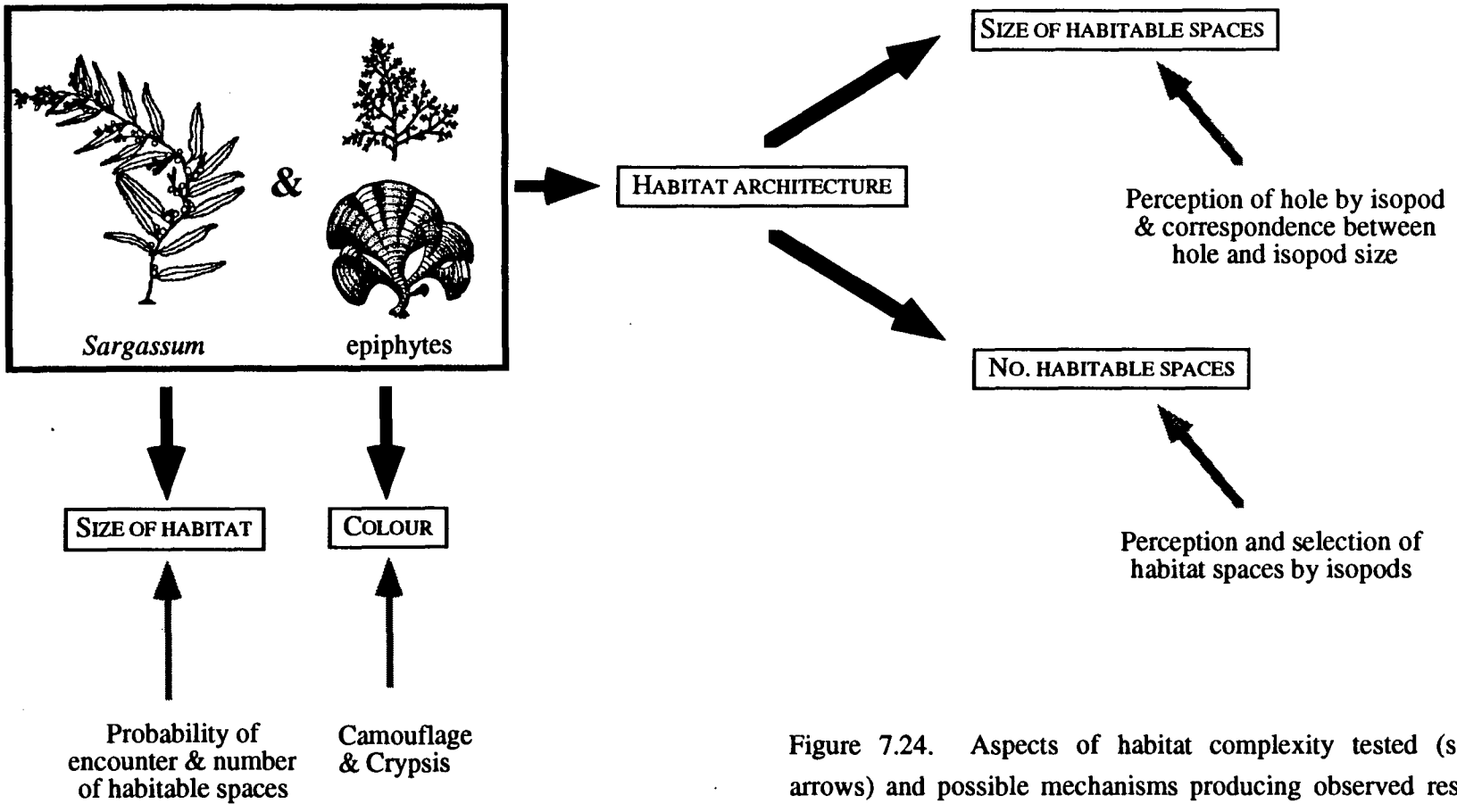


Figure 7.24. Aspects of habitat complexity tested (solid arrows) and possible mechanisms producing observed results (shaded arrows).

CHAPTER 8

LIFE ON THE PLANT SURFACE: CONCLUSIONS FROM THE *SARGASSUM*-EPIFAUNA SYSTEM

"It is the great beauty of our science that advancement in it, whether in a degree great or small, instead of exhausting the subject of research, opens the doors to further and more abundant knowledge, overflowing with beauty and utility."
Michael Faraday.

The aim of this chapter is to integrate the results from the study of the *Sargassum*-epifauna system into present perceptions of animal-plant relationships. This will be done on three levels of increasingly generality: firstly, at a local level, what I consider to be the situation pertaining in this particular system; secondly, at a regional level, comparing and contrasting tropical and temperate marine macroalgal-epifauna relationships; and finally, a return to the concepts of Chapter 1, the relationships and paradigms of marine versus terrestrial arthropod-plant interactions. The perceived relationships between these levels of discussion are shown in Figure 8.1. Some of this material will be speculative, but this is deliberate in the hope of stimulating discussion or research about these topics.

8.1 SPECIFIC PATTERNS AND PROCESSES

At the local level, what, briefly, are the most important findings of this study?

• An obvious point, which should be mentioned at this early stage is that the *Sargassum*-epifauna system is an important element of the benthic biota at Magnetic Island. For much of the year *Sargassum* makes a significant contribution to primary production and standing crop of the reef system. Common perceptions of reef systems is that they are clear-water communities dominated by scleractinians with very low biomass of macroalgae. While this is true for mid- and outer-shelf reefs on the Great Barrier Reef, many inshore reefs, especially those in areas of terrigenous run-off, have large amounts of macroalgae (Morrissey 1980, Mather and Bennett 1993). Research from other parts of the world shows these mixed macroalgal-scleractinian reefs to be common and of high local importance (e.g. De Wreede 1976, Wanders 1976, Cordero 1981, Ang 1985b). Paradigms developed from reefs with low amounts of macroalgae should only be applied to such systems with caution.

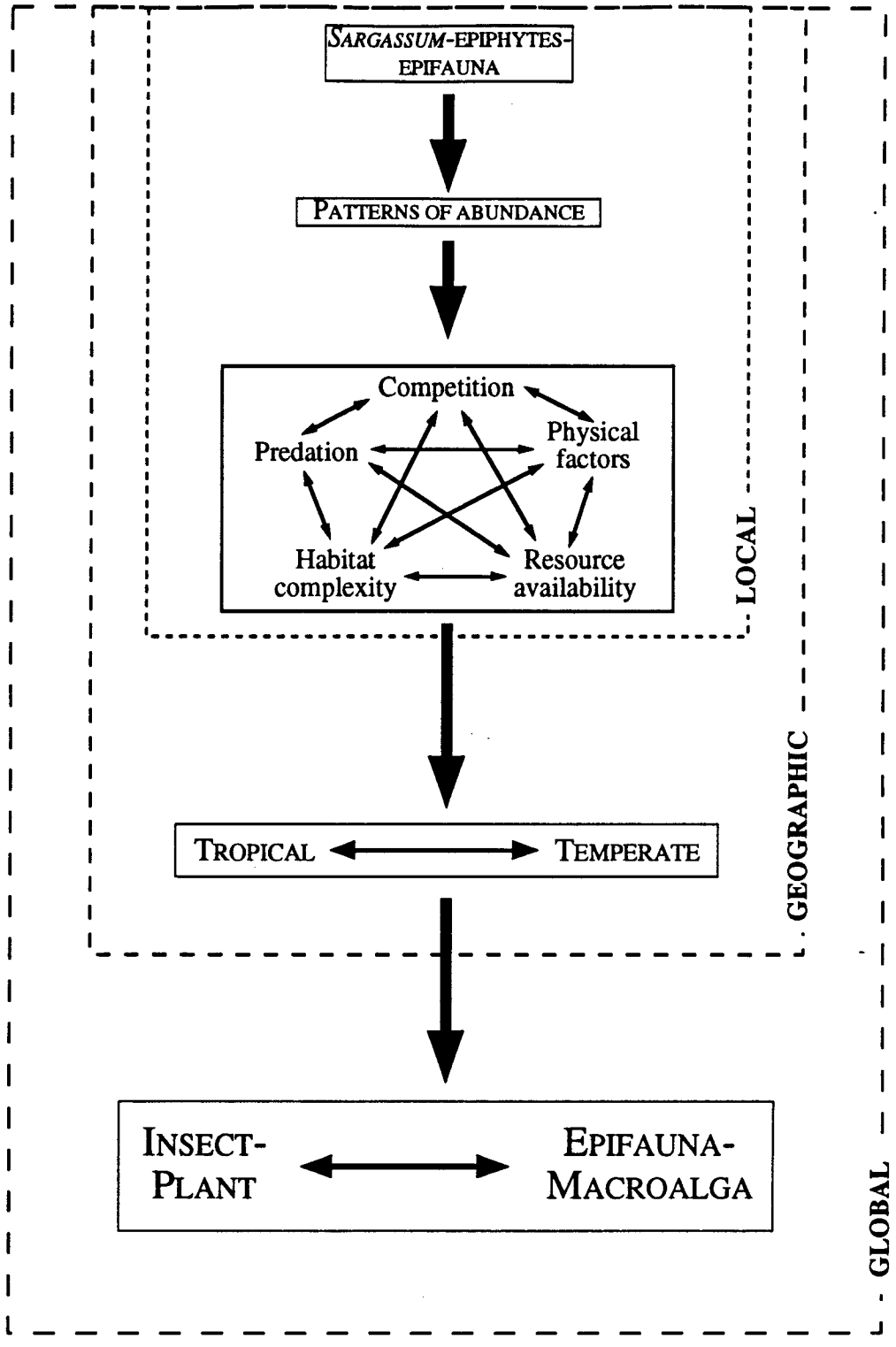


Figure 8.1. Factors and relationships with regard to *Sargassum*-epifauna system

• Despite large changes in abundance and composition of communities from month to month, such changes were highly predictable. This indicates that there were seasonally varying factors which controlled (a) the phenology of *Sargassum* and (b) the abundance of epifauna.

• The *Sargassum* and epifauna formed a distinct ecological community. All *Sargassum* species except *S. linearifolium* showed synchronous changes in size, biomass and reproduction. Parallel to this, epiphytes and most taxa of epifauna showed synchronous changes in abundance. Such changes were not species-specific in most cases and appeared to be controlled by the same factor(s). Thus, to a large extent both plant and invertebrate communities behaved as predictable, congruent units.

• Both *Sargassum* population characteristics and abundance of epifauna were highly variable at a time scale of months. Abundance changes of up to an order of magnitude were found between sampling dates 4 weeks apart. Variability decreased as the time scale of measurement was decreased. Thus, epifaunal abundance was moderately variable at the scale of weeks and reasonably constant at the scale of days. Inter-plant variability was high and not predictable at any particular temporal or spatial scale.

• Two hypotheses concerning the nature of these factors were tested with respect to abundance of epifauna. Predation was not demonstrably important; habitat structure and heterogeneity, both at a gross level (presence or absence of epiphytes) and at a finer scale (aspects of architecture and structure) were important to whole communities and to individual species. The time scales and experimental procedures of all these experiments were roughly comparable so it is suggested that these were real effects.

These findings can be combined into an overview of the entire seasonal pattern of the *Sargassum* -epifauna system:
Sargassum had a predictable seasonal pattern with growth in spring and summer, followed by reproduction, loss of annual axes and a 'static' winter period. Epiphytes colonised *Sargassum* in autumn and attained maximal abundance in winter. Most epifauna reached peak abundance in winter and had minimal populations in summer. Changes in epifaunal abundance was related primarily to the amounts of epiphytes on the surface of the *Sargassum*. The epifauna colonised the epiphytes in response to habitat structure and architecture cues which may be taxon-specific.

It was apodictic that additional habitat complexity was extremely important in determining epifaunal abundance:- there was high abundance of epifauna on habitats with increased complexity and *Cymodoce* isopods were shown to colonise artificial

sponges with particular habitat attributes. My interpretation of the role of epiphytic habitat complexity is conceptualised in the following model (Figure 8.2):

(1). Assume that epifauna have a predetermined set of criteria which defines a suitable habitat space.

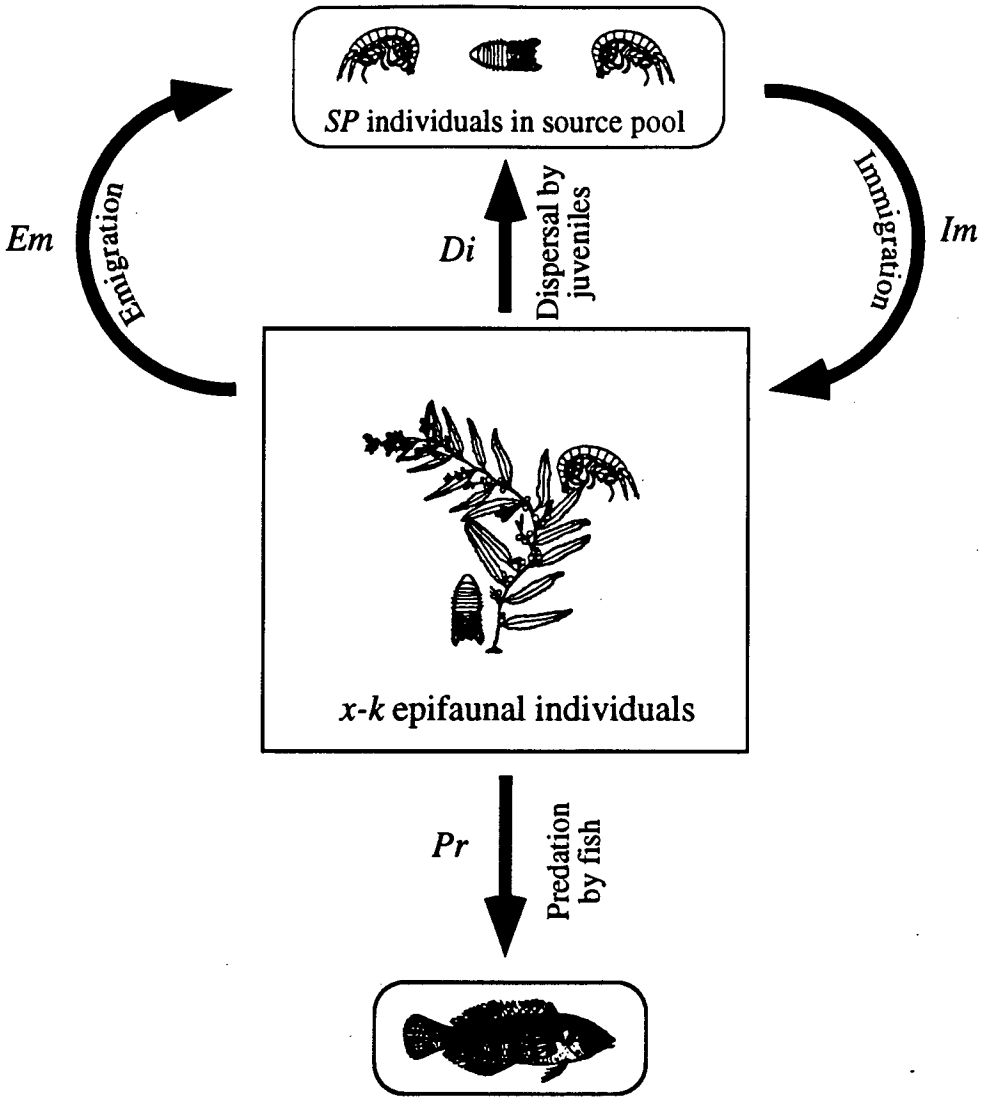
(2). An unoccupied *Sargassum* plant and associated epiphytes will have x habitat spaces. Accumulation of individuals will occur until there are x-k individuals on the plant where k represents the number of unoccupied suitable spaces.

(3). Emigration can occur through dispersal of juveniles (*Di*), or through adult movement to find food or a mate (*Em*). Removal of individuals from a plant can also occur through predation (*Pr*). Immigrating individuals (*Im*) come from a small source pool of individuals in the water column or elsewhere (*SP*).

(4). At equilibrium the following relationships will hold: $x\text{-}k = Im - Em - Pr - Di$ and $SP = Di + Em - Im$ where *Im, Em, Pr, Di* are all measured per unit time.

This model may help to explain why no effect of reduced predation was detected. Although a reduction in the value of *Pr* was obtained by the use of exclusion cages, this could have been balanced by an decreased value of *Im,* since individuals would not have been removed from the plant so rapidly. The only detectable effect would be a increase in the number of individuals in the source pool, *SP*, something very difficult to measure. The source pool would act as a buffer, absorbing the abundance changes produced by reduced predation. This model would predict that an increase in fish predation would be balanced by an increase in the immigration rate and a consequent reduction in the numbers in the source pool, but that x-k would remain constant. The counter-intuitive decrease in abundance in both cages and cage controls could have resulted from a reduction in the number of habitable spaces due to shading or other cage effects. Although intra- and interspecific resource competition for the habitat spaces x could be postulated as the driving force behind the abundance of individuals, this is not strictly necessary if not all of the habitable spaces are occupied.

Circumstantial evidence exists to support this model: low numbers of individuals were captured in emergence traps but colonisation of defaunated plants, both artificial and real, was very rapid. This suggests that the source pool of individuals not on the plant was quite small, in accordance with the few quantitative studies performed on emigration of amphipods from their preferred habitat (Stretch 1985, Ambrose 1984, 1986) but that movement from this source pool on to the plant



At equilibrium: $x - k = Im - Em - Pr - Di$

$SP = Di + Em - Im$

Figure 8.2. Model of population dynamics of epifauna on *Sargassum*.

was highly favoured. Individuals of many crustacean taxa from different habitats are known to display periodic swimming behaviour (e.g. Fincham 1970, Jones and Naylor 1970, Ambrose 1986) and dispersal by juveniles is a necessary consequence of the marsupial development of peracarids (Barnard 1976). A testable prediction from the model is that an increase in the number habitat spaces will produce an increase in abundance of epifauna, regardless of predator exclusion. A bi-factorial experiment along these lines was attempted using artificial plants with and without epiphytes, in and out of exclusion cages, but unfortunately the cage structures were destroyed by bad weather.

Another question of primary importance is why the epifauna should associate with *Sargassum* in the first place and what effect the various partners in the relationship had on each other. Did the epifauna use *Sargassum* or epiphytes as food or purely as a habitable space in which to live? What effect did epifauna have on the *Sargassum* and epiphytes? The relationship, I believe, was that the epifauna were facultatively commensal on *Sargassum*. As such, the relationship was not exclusive between *Sargassum* and epifauna (i.e. both could exist without the other) and there were no significant detrimental effects to *Sargassum* due to the presence of the epifauna. The evidence for this conclusion includes:

(1). Epifauna were positively associated with epiphytes, both in observational and experimental data, rather than with the *Sargassum* plant itself.
(2). There were very few significant taxon-specific differences between the different species of *Sargassum* which would be expected if there was obligate mutualism between the plant and the epifauna. Almost all species of epifauna were found on all species of *Sargassum*.
(3). Epifauna colonised artificial habitats rapidly to the same abundance as natural plants.
(4). Although sphaeromatid isopods were observed to feed on *Sargassum* (an antagonistic behaviour), they also colonised sponge which would have had no nutritional value.
(5). Observations of *Sargassum* for over two years during sampling trips never revealed plants which had noticeable grazing scars, including detailed examination of all sampled plants.

It is possible that some taxa were facultatively mutualistic, removing epiphytes which were decreasing the photosynthetic ability or increasing the possibility of axis breakage of the *Sargassum* (D'Antonio 1985, Howard and Short 1986, Arrontes 1990a). However, members of most taxa colonised artificial habitats without epiphytes and these organisms were presumably feeding on the bacterial and diatom

film which quickly develops on surfaces underwater (Wahl 1989) or filter-feeding in the water column (e.g. Barnard 1976, Aoki and Kikuchi 1990). Thus, although particular species or individuals may have had different forms of relationship with the plant, the overall **community** interaction was a commensal one, the *Sargassum* providing a substrate for the growth of an epiphytic habitat. The exact nature of the relationship between particular taxa of epifauna and epiphytes remains unknown. With regard to feeding activities - many of the gammarid amphipods on *Sargassum* were nestlers or tube-dwellers, described by Barnard (1976) as mainly particulate-feeding with some herbivores, tanaids are described by Holdich and Jones (1983) as "...raptorial feeders consuming detritus and its associated micro-organisms" and Naylor (1972) states that isopods have "...acquired a raptorial method of feeding in which they macerate large pieces of food". Of the abundant crustaceans it would seem that only sphaeromatids could have fed on *Sargassum.* Although there are numerous different feeding modes in the polychaetes, Fauchald and Jumars (1979) state "...the largest number of polychaetes are microphagous" which includes diatom grazers, filter-feeding and deposit-feeding. The gastropods on *Sargassum* were also probably diatom grazers and scrapers (Steneck and Watling 1982).

Finally it is interesting to speculate on the trophic position of all components of the system within the general reefal community. Since the epifauna appeared to be confined to the *Sargassum*, it is probable that there was limited trophic exchange between the two parallel primary production systems i.e. scleractinian corals and their zooxanthellae on one hand and *Sargassum* and epifauna on the other (Figure 8.3). The limited gut contents analysis performed, as well as behavioural observations, would seem to indicate that some members of the ichthyofauna, particularly *Halichoeres,* were also isolated within the *Sargassum* trophic system and that trophic exchange may only have taken place on this reef at the highest levels with secondary and tertiary carnivores. The epifauna on *Sargassum* were shown in this study to be abundant for much of the year, in addition Klumpp *et al.* (1988) and Riddle (1988) have demonstrated that the reef cryptofauna of bare sand and both living and dead coral are both abundant and productive. Benthic secondary production was thus split between epifauna and cryptofauna. The total trophic structure of reefs such as those at Magnetic Island with significant macroalgal primary production and epifaunal secondary production is likely to be very different to mid- and outer-shelf reefs.

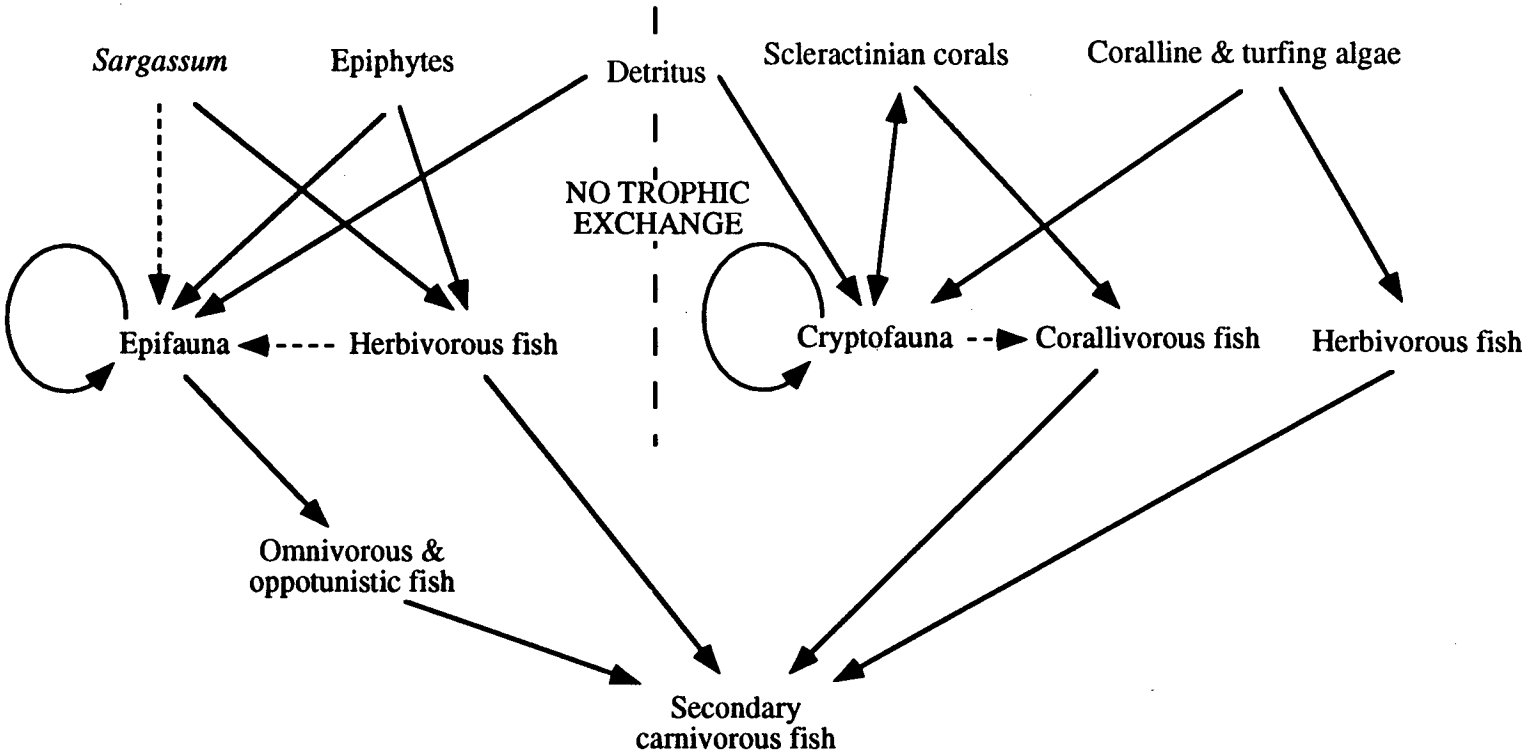


Figure 8.3. Some possible trophic relationships on a mixed algal/scleractinian reef at Magnetic Island. Arrows indicate energy flow, dotted arrows indicate possible but insignificant energy flow.

8.2 THE GENERALITY OF FINDINGS ABOUT THE *SARGASSUM*-EPIFAUNA SYSTEM: TROPICAL/TEMPERATE COMPARISONS

As has been stressed throughout this thesis, most previous studies of marine macroalgae-epifauna relationships were conducted in temperate regions of the world. What are the major differences that exist between macroalgal communities in tropical and temperate regions and how do these relate to the *Sargassum*-epifauna system which was investigated in the present study? A general tendency for species richness to increase with decreasing latitude has been documented since the 'voyages of discovery' of Darwin and Wallace (Wallace 1878) to the present day (Pianka 1966, MacArthur 1972, Colinvaux 1973, Ricklefs 1973, Krebs 1985, Stevens 1989). However, this general relation does not hold true for the macroscopic brown algae. Laminarians (kelps) and most of the genera of the Fucales (wracks) have maximum diversity and abundance in northern hemisphere cool temperate waters with far fewer genera and species in tropical waters (see references in Womersley 1981). *Sargassum, Turbinaria* and some genera of the Dictyotales are the only diverse and abundant Phaeophyta in the tropics. Similarly gammarid amphipods are also an exception to the rule of increasing diversity in the tropics, again with higher diversity in northern temperate and boreal waters (Barnard 1976, Barnard and Karaman 1991).

However, there are important similarities between *Sargassum*-epifauna and temperate macroalgae-epifauna systems despite differences in species composition and diversity. Some of these include:

- Presence of a distinct epifaunal community, which behaved as an ecological unit.
- Similarity of dominant organisms at the order level.
- Pronounced and repeated seasonal patterns of abundance and dominance.
- Magnitude of abundance changes from month to month.
- Relationship of epifaunal phenology to epiphyte phenology.

Whilst in contrast, the important differences include:

- Timing of seasonal changes.
- Relationship of epifaunal phenology to macroalgal phenology.

In temperate macroalgal systems, there appears to be a general case of a spring or summer maximum in epifaunal abundance (see Table 5.I for references); in the tropics very limited information is available but summer maxima have been reported for macroalgal epifauna in the subtropics (Stoner 1983, Lewis 1987) and for seagrass in the tropics (Heck 1977, Gore *et al.* 1981). Although the present study showed a winter maximum for epifaunal abundance, there is not enough information on long-

term seasonality in the tropics to conclude a general case. In addition a strong positive correlation between epiphytes and epifaunal abundance was found, similar to temperate systems (Gunnill 1983, Johnson and Schiebling 1987, Schneider and Mann 1991a).

Although complicated on a local level, it seems that macroalgae-epifauna systems share a high degree of similarity over different geographical locations. Despite the very great differences in physical environment between tropical Australia and temperate Europe, for example, patterns of diversity and abundance of sphaeromatid isopods are remarkably similar (cf. Chapter 7 and Arrontes and Anadon 1990b). There are differences in the timing of abundance maxima but the size, duration and repeatability of seasonal patterns are consistent across large latitudinal gradients.

It is predicted, however, that seasonality will be found in populations of epifauna in the tropics, but that the timing of this seasonality may vary from location to location. My reason for this prediction is the contention that epifaunal seasonality is primarily determined by biological interactions. The seasonality of algae, both epiphytic and benthic, has been hypothesised to be driven by physical factors e.g. light, temperature, nutrients etc. (Tsuda 1974, De Wreede 1976, Prince and O'Neal 1979, Ang 1985a); but at the epifaunal level it seems clear that the population dynamics are driven by biological factors, a logical extension of their trophic position as consumers (i.e. at the most basic level they require food provided by another organism). Even in temperate regions it has not been suggested that abundance of epifauna are controlled by physical stress-induced mortality, where organisms are under the severest physical conditions.

With so little literature available about epifauna in the tropics the study of Arrontes and Anadon (1990b) is especially interesting, since two of the species they investigated, *Cymodoce truncata* and *C. emarginata* , are congeneric with species of isopod investigated in the present study. Thus, here are data on very similar species from both temperate and tropical macroalgae. There was remarkable similarity between the seasonal pattern of abundance of *Cymodoce* in Spain and at Magnetic Island, despite the differences in location. The abundance maxima for both populations occurred from March to July, although this represents spring-summer in Spain and autumn-winter in Australia. Even the absolute magnitude of the density maxima of both populations were almost identical (1600 m^{-2} in Spain and 1500 m^{-2} at Magnetic Island when converted from per plant numbers to per area values). Another notable similarity was that females with eggs were never found in either population and adults males only infrequently. This indicates that macroalgae in both

places was performing the same ecological role as a nursery habitat for juveniles. Although the patterns of abundance were so similar, populations of *Cymodoce* in Spain showed marked differences in size structure to those at Magnetic Island (cf. Arrontes and Anadon 1990b p.237 with Figures 7.7 and 7.8). In Spain it would appear that the abundance maxima were produced by influxes of juveniles from a limited period of reproduction, whereas reproduction was almost continuous at Magnetic Island with juveniles continually entering the population, and that habitat factors were responsible for the observed seasonality. This one example where data are available for comparable temperate and tropical marine systems supports the contention that it is the biological interactions that are important to epifauna. However, it also reveals that patterns and underlying cause are not necessarily related. It would be interesting to see if the same causal factors operated on similar isopods in other macroalgal habitats e.g tropical *Sargassum* in the Philippines (Ang 1985a, Ang and Trono 1987) or even temperate *Sargassum* in the U.S.A. (Duffy 1990) or Australia (Edgar 1983a).

Differences in the chemical ecology of both host and epiphytes is a potential reason for differences between temperate and tropical systems. There is significant evidence to suggest that temperate algae have different levels and types of secondary compounds (Steinberg 1985, Steinberg and Paul 1990), hypothesised to be chemical defences against both vertebrate and invertebrate herbivores (Hay *et al.* 1988b, Hay and Fenical 1988, Hay 1991). If these compounds act as feeding deterrents (Hay 1991) or feeding attractants (Hay *et al.* 1988a, b) toward epifauna or as chemical cues for locating a host upon which an organism will be protected by associational defence (Hay *et al.* 1990a) then latitudinal differences in host chemistry could influence epifaunal community composition and abundance. For example, Steinberg *et al.* (1991) have shown that *Sargassum* species from Magnetic Island contained significant lower levels of polyphenolics than temperate *Sargassum* (except for *S. linearifolium* which is found in both temperate and tropical regions). Seasonality in the chemistry of various algae has been documented (Ragan and Jensen 1978) which could affect epifaunal community processes. When the chemical ecology of the epiphytic algae is added to the equation it can be seen that there are numerous potential levels at which secondary algal compounds can affect epifauna, predators or both.

8.3 PLANT-ANIMAL RELATIONSHIPS REVISITED: IMPLICATIONS AND SPECULATIONS

The major proposition which I wish to present from this investigation of the *Sargassum*-epifauna system is that macroalgae play a 'passive' role with regard to the organisms associated with them, whereas angiosperms adopt an 'active' role. This contention has profound implications about many aspects of the plant-arthropod relationship including species diversity and abundance, specialisation, speciation and evolutionary pathways.

First of all, let me define what I mean by passive and active in the two systems. The active role adopted by terrestrial angiosperms is perhaps more easily defined. It is envisioned as a conflict between plants and insect populations which are capable of consuming them, or as an attempt to flag down a pollinator or seed-disperser. Some of the important characteristics of the active role are:

- Production of physical defences e.g. trichomes, lignin (Maxwell and Jennings 1980)
- Production of chemical defences e.g. toxins, digestability reducers (Rosenthal and Janzen 1979)
- Rewards offered for pollination or seed dispersal (Howe and Westley 1988)
- Obligate relationships (both mutualistic and antagonistic) between plant and insect common (Edmunds and Alstad 1978, Schupp 1986)
- High physical complexity of plant (Lawton 1983) and high levels of specialisation of insects (Matthews and Kitching 1984, Bernays and Graham 1988).

The passive role of marine macroalgae towards epifauna is considered to be less of a conflict to avoid potential defoliation or to attract a pollinator for reproduction; instead it represents a casual, chance encounter.. It, in turn, is characterised by:

- Low structural complexity of macroalgae (Littler and Littler 1980).
- Many facultative relationships between macroalgae and epifauna (Lubchenco and Gaines 1981).
- Low levels of specialisation of epifauna (Lubchenco and Gaines 1981, Hay *et al.* 1990a, b).
- Low levels of physical defence and ineffectiveness of chemical defence towards epifauna (Littler and Littler 1980, Hay *et al.* 1987b, Hay *et al.* 1988b).

Cause and effect are difficult to separate but a major reason for the dichotomy between active and passive strategies is the nature of the surrounding medium. Water over the continental shelf (where almost all macroalgae grow) is usually rich in nutrients and particulate matter close to shore (Larkum 1981). Detritus and phytoplankton in the water column can provide large amount of energy for primary consumers (i.e. epifauna). In addition, the nutrient-rich status of the water is ideal for the growth of bacterial and diatom films and larger epiphytic organisms which invariably cover underwater surfaces within a very short period of time (Wahl 1989). Conversely, in terrestrial environments, bacterial and fungal growth on leaf surfaces is normally low (Fokkema and Van den Heuvel 1986) and epiphytism is the exception rather than the rule except in some tropical forests (Benzing 1990). Thus terrestrial plants are effectively isolated as food sources with no other material with which to tempt would-be consumers. Marine plants can offer extraneous food sources or act as a platform for the exploitation of the water column. It is axiomatic that to fully exploit a terrestrial environment dominated by angiosperms insects had to evolve to consume and live intimately with plants, a condition not imposed on marine epifauna. Given that angiosperms possess a range of chemical and morphological defences there has been selective pressure on insects to specialise.

Support for this view comes from the fossil record. Major radiations of both angiosperms and insects occurred simultaneously in the Cretaceous and Tertiary periods leading Wootton (1990) to state "...it is clear from palaeontology and from our knowledge of extant ecosystems that the importance to insect evolution of the rise of the angiosperms cannot be overemphasized". Wootton (*loc. cit.*) further asserts that "the enormous diversification of species reflects the fact that very many of these phytophagous insects are mono- or oligophagous". Radiation of malacostracan crustaceans occurred in the early Carboniferous period (Briggs and Clarkson 1990), well after radiation of macroscopic algae in the Ordovician period (Banks 1970) and many fossil crustaceans are hypothesised to be unspecialised generalist feeders (Briggs and Clarkson 1990).

Insects have short generation times and minimal learning capacity, allied with advanced sensory systems, therefore they can perceive small changes in their environment but cannot adapt behaviourally to them. It is suggested that they adapt genetically to their environment and thus speciation occurs (Matthews and Kitching 1984). Further changes in plant chemistry or structure can promote 'co-evolution' and even greater speciation – first proposed by Ehrlich and Raven (1964), see discussions in Matthews and Kitching (1984) and New (1988). In marine systems, with a wider potential food base, lower structural and chemical complexity, the pressure to

specialise is not as great. Furthermore "detritus food-chains have relatively little diversifying influence...this is simply because dead organic matter does not defend itself, and no coevolution can occur except among the consumer species themselves through competition, and between the consumers and micro-organisms" (Matthews and Kitching 1984), an important consideration with respect to the evolution of epifauna feeding in the water column or on bacterial films.

From the point of view of an amphipod, a *Sargassum* plant is a passive, three-dimensional object which is colonised by an array of epiphytic algae providing appropriate habitat spaces. The dominant perception of epifauna is the physical habitat structure, hence the colonisation of entirely artificial substrata. Although insects perceive and respond to physical habitat structure (New 1988) they are also assailed by a complex mosaic of chemical signals which are designed to attract or deter – the plants' active arsenal. In the words of Daniel Janzen (1978) – "the plant world is not colored green; it is colored morphine, caffeine, tannin...saponin and L-dopa". A specialised herbivorous insect is unable to complete its life cycle without a particular small group of host plants which are actively trying to avoid the insect. The important cues used to find the plant must act at a distance and be host-specific, a property of secondary compounds, thus the interaction is primarily chemically mediated. Matthews and Kitching (1984) estimate that greater than 72% of Australian insects show a high degree of host specificity, whilst very few epifaunal species have been shown to be specialists (Lubchenco and Gaines 1981, Hay *et al.* 1987a, 1988b, 1990a). Generalists do not need long distance cues to locate particular habitats.

While not denying the demonstrable effects of secondary compounds produced by some marine plants on some invertebrate epifauna as shown by Hay, Paul, Steinberg and co-workers (Steinberg 1985, Hay *et al.* 1987a, b, 1988a, b, 1990a, b, Paul *et al.* 1987) I would argue that in a passive association the physical characteristics of the habitat are more important. Epifauna, both in the present work and in previous studies, have been shown to respond to habitat structure alone, without any chemical cues. It is surely no coincidence that artificial plants are seldom used by entomologists compared to their frequent use by workers on epifauna (e.g. Virnstein and Curran 1986a, b, Edgar 1991a, Schneider and Mann 1991b). Entomologists often use pheromone traps to sample populations (review by McNeil 1991), demonstrating the importance of chemical cues for insects. Adequate simulation of the physical habitat is often all that is needed for colonisation and subsequent growth and reproduction by marine invertebrates, whereas insects demand precise levels of particular compounds allied with complex habitat architecture.

There are many aspects of architectural specialisation shown by terrestrial plants which are not shown by the structurally simple marine algae. Herbs and algae may be structurally equivalent – with stems, leaves and reproductive parts – but the diversity of niches within even the simplest tree is much higher than is shown by any marine plant. Heterogeneity is also important in habitat structure – a tropical rainforest has very high plant species diversity (Connell 1978, Hubbell 1979) and will consequently offer a much higher range of microhabitats and niches than a monospecific seagrass or macroalgal bed. However, despite the greater structural complexity of, for example, an oak forest compared to a kelp bed, it is the **relative** response of the arthropods to the complexity which is important. Although habitats are more diverse and structurally complex on land, the physical structure may actually be less important than in the sea.

Lawton and Schröder (1977) and Lawton (1983) have shown that more architecturally diverse habitats support larger numbers of species of phytophagous insects. This holds true across comparisons between annual herbs, perennial herbs and shrubs (Lawton and Schröder 1977), between congeneric species with different leaf shapes (Lawton and Price 1979), between seasons with the same species (Lawton 1978) and over time with the same species (Banerjee 1981). These kinds of comparisons have performed in a much more limited way in marine environments – Abele (1974) showed that the number of species of decapods was greater in more structurally complex environments, while Heck and co-workers (Heck and Wetstone 1977, Heck 1979, Heck and Orth 1980b) have considered a variety of aspects of tropical and temperate seagrass beds and have shown that biomass but not seagrass species diversity was important to decapod species richness. There is a need for criteria that define habitat architecture to be developed (see discussion in McCoy and Bell 1991) and a comparison of species lists between marine algae with different, quantified aspects of habitat architecture to address this problem.

The same argument can be applied to the abundance of individual species as well as to total species diversity. Both Lawton (1983) and Wallner (1987) give examples where habitat structure is important in determining abundance of insect species on land, as do Bell and Westoby (1986a, b) for seagrass fauna. Hacker and Steneck (1990) and the present study have shown that the abundance of epifauna on macroalgae and on artificial plants are dependent on habitat structure.

Finally, a brief consideration of the mechanisms which may be involved in the promoting species abundance or diversity in more structurally complex habitats:

- Increased provision of niches. If organisms are specialised this will promote species diversity, if ubiquitous then abundance will increase. Increased provision of niches can ameliorate the effects of competition, allowing populations of organisms to attain higher abundance.
- Increased immigration to or decreased emigration from habitat. Given that the population on a plant is a dynamic balance between the processes of immigration and emigration, if the magnitude of one is changed then the position of equilibrium will shift.
- Moderation of physical factors such as wave action which would remove organisms from the habitat.
- Increased provision of refuges which provide protection from predation. These refuges can be permanent, created by additional habitat structure in which predators cannot forage, or temporary, created by habitat heterogeneity where predators chose one particular habitat type in which to forage at any one time.

The conclusion to this discussion is that increased habitat structure and heterogeneity positively affect abundance and species diversity of arthropods living on the plant surface, both on the land and in the sea. Furthermore, I propose the hypothesis that this aspect of the plant is relatively more important in marine systems than on the land.

Populations of organisms are never stable, because of differential mortality, reproduction, immigration and emigration, but community ecologists like to be able to predict the magnitude, direction and temporal scale of changes in abundance. How predictable or random are populations of plant-associated organisms and does this differ between marine and terrestrial environments? The *Sargassum*-epifauna system appears to have high predictability in the direction and temporal scales of abundance with lower predictability about the magnitude of a population at any particular time. Similarly, other marine studies which collected seasonal data over more than one year have shown that population changes can be highly predictable (Mukai 1971, Livingston 1976, Arrontes and Anadon 1990). The species involved in these studies could be described as having a stable equilibrium population for any particular point in time or alternatively as 'non-outbreaking' populations (following the terminology of Wallner 1987). Occasionally populations of marine epifauna have displayed unpredictable outbreaks or crashes (Bernstein and Jung 1979, Tegner and Dayton 1987) but these fluctuations are especially notable because of their infrequency. In contrast, there are a much higher number of documented cases of insect outbreaks involving large unpredictable changes in abundance (see review by Wallner 1987, New 1988). Part of the reason for this is undoubtedly the anthropogenic

establishment of terrestrial monocultures and/or manipulation of natural predators or competitors. However, Turnock (1977) quoted in Wallner (1987) found that natural populations of a number of species of phytophagous insects on Canadian prairies displayed outbreaking patterns and New (1988) cites a number of examples of outbreaks in natural populations of insects in Australia. Tropical insects display cycles of abundance of comparable magnitude to temperate insects (Wolda 1983) but are predicted to have fewer outbreaks (Young 1979).

Wallner (1987) lists a number of factors which control or promote outbreaks, namely weather, habitat quality and natural enemies (predators, parasites and disease). Weather is considered particularly important since "insects with periodic outbreaks occur especially in areas that are physically severe" (Wallner *loc. cit.*). In this context, it is notable that the outbreaks of isopods reported in Bernstein and Jung (1979) and amphipods reported in Tegner and Dayton (1987) both followed periods of significant environmental change associated with El Niño events. It appears that the effect of unusual weather is mediated by some change in the regulatory ability of the system, such as increased levels of amino acids in host trees (White 1969) or decreased levels of usual predators (Bernstein and Jung 1979, Teyner and Dayton 1987). To test this theory, it would be pertinent to investigate whether populations of tropical epifauna showed large and unpredictable fluctuations in abundance following a major, random event such as a cyclone.

Predation has been implicated as a strong organising force in many marine systems, especially in the intertidal (e.g. Connell 1970, Dayton 1975, Paine 1976, Peterson 1979, Garrity and Levings 1981, Menge and Lubchenco 1981, Lubchenco 1983), but the present study did not demonstrate any significant effects of predation by fishes on populations of epifauna on *Sargassum.* Why was this so and what is the relative importance of predation in marine epifaunal and terrestrial plant-insect systems? Sih *et al.* (1985) conclude from an extensive review of manipulative studies on predation that "...predation paradigms emerging from the intertidal or from lakes may not hold as well elsewhere because predation is not as strong elsewhere". They attribute this conclusion to the structural simplicity of lakes and the rocky intertidal, supporting the idea of habitat complexity as an important force in organising other communities. The review of Sih *et al.* (*loc. cit.*) reveals a number of other important comparisons when examining the effects of predation:

- At the level of the study (i.e. all the experiments in one paper) almost all studies which looked for predation effects found some and the effects were consistent regardless of latitude, system (marine, terrestrial, lentic, lotic), predator trophic level or predator taxon.

• At the level of the individual comparison (i.e. each taxon within an experiment) there was no effect of latitude, herbivores had greater effects than carnivores and non-arthropod predators had greater effects than arthropods. Although the effect of latitude was non-significant the authors suggest that the paucity of studies in the tropics may be partially responsible, since there was a trend towards increasing effects of predation in the tropics.

Thus the predictions from the review of Sih *et al.* (1985) would be that predation is equally important to marine epifaunal communities and to terrestrial phytophagous insect communities. Plant-associated arthropods from marine and terrestrial systems both occupy the same trophic positions and usually have vertebrate predators (fishes or birds and mammals). At the level of the comparison, effects of predation were demonstrated in only 48.6% of non-intertidal marine systems and 55.8% terrestrial systems, so it is perhaps not so unexpected after all that the present study did not demonstrate fish predation on epifauna, despite strong circumstantial evidence. A final consideration about predation with regard to the *Sargassum*-epifauna system is the possibility of 'unexpected' effects (usually when experimental increase in predation brings about an increase in prey abundance or *vice versa*). Unexpected effects are normally attributed to the 'keystone' predator effect (Paine 1966) where a predator reduces the population of a competitively dominant prey item or to 'three-trophic-level' effects when one predator consumes another predator thus releasing the bottom trophic level from predation (Sih *et al.* 1985). Predation in the *Sargassum*-epifauna system may be more important as an evolutionary force than as an ecological force, e.g. Wallerstein and Brusca (1982) attribute the decreased body size and increased ornamentation of idoteid isopods in lower latitudes to the effects of increasing predation by fishes.

A further factor which may contribute to the regulation of species abundance and diversity is competition. Intraspecific competition will act to regulate abundance while interspecific competition will act on species diversity. Intraspecific competition may be more important to insects they have a higher proportion of outbreaking species as abundance will be attained where competition becomes the dominant factor. In non-outbreaking populations, abundance may be maintained at lower levels by other factors, such that intraspecific competition plays only a minor role. Certainly, intraspecific competition has been demonstrated for both phytophagous insects (see review by Klomp 1964) and for marine fauna (Ambrose 1986) but is generally not assumed to be of general importance (Nelson 1979a, Zimmerman *et al.* 1979). The idea of interspecific competition, conversely, has generated fierce argument as to its presence and importance (see reviews by Connell 1975, Lawton and Strong 1981, Schoener 1982, 1983, Sih *et al.* 1985). There has certainly been a shift in ecological

thinking from the belief that competition is the key force in structuring communities (MacArthur 1965, Ricklefs 1973) towards the role of other factors (see refs. in Sih *et al.* 1985).

For terrestrial herbivorous insects Lawton and Strong (1981) are firmly of the opinion that "...interspecific competition is too rare or impuissant to regularly structure communities of insects on plants". They present a couple of studies where interspecific competition has been clearly demonstrated (McClure and Price 1975, 1976, Stiling 1980) but conclude that these are the exceptions rather than the rule. The alternative view that Lawton and Strong (1981) offer is that "...autecological factors of a harsh and changing climate, host plant phenology, seasonal sequences of chemical and physical change in host tissue and patchiness of food plant resources are obviously of great importance to phytophages. Natural enemies...frequently combine with autecological factors to lend what regulation of numbers we do see among insects on host plants".

Interspecific competition has been shown to be important in marine rocky-shore communities (e.g. Connell 1961, Underwood 1978, Peterson 1979) but there is not a single study on epifaunal systems to be found in the reviews of Schoener (1983) and Sih *et al.* (1985). This may be because of the difficulty of demonstrating competition in such systems or assumptions that competition in not important. Clearly studies need to be initiated on interspecific competition in marine epifauna, although I predict that the same general conclusions will be reached about its importance as Lawton and Strong (1981) concluded about insects. Edgar (1993) has recently introduced the idea that populations of organisms in benthic habitats, in particular the epifauna of seagrass and macroalgae, are limited by resources. If this is the case, then competition will be of much greater importance than has been previously thought. It remains to be seen whether Edgar's demonstration of a fairly constant metabolic-rate index really reflects resource limitation and there is ample opportunity for careful manipulative experiments to test the hypothesis.

8.4 CONCLUSIONS AND FUTURE DIRECTIONS

Hopefully, the above discussion will have provided an insight into where the community patterns of epifauna observed during this study fit into the local and global views of community ecology. Mindful of the risks of oversimplifying, I wish to present a brief summary of my conclusions:

- Local scale: *Sargassum*, epiphytes and epifauna all had seasonality. Epiphytes provided habitat for epifauna, hence epiphyte seasonality determined epifaunal seasonality. Predation by fishes was not directly important in determining community abundance.
- Geographic scale: predation and habitat complexity are important determinants of community composition and abundance in both tropical and temperate regions. The phenology of epifauna in any system will be determined by the local biotic interactions rather than seasonal physical changes.
- Global scale: community regulation of species abundance and diversity is determined by the interaction of a number of factors, their relative importance being different between terrestrial plant-insect systems and marine macroalgae-epifauna systems. Terrestrial systems involve active association between plants and insects, while passive interactions are prevalent in marine systems. The relative importance of predation/parasitism, habitat complexity, competition and autecological factors is system-specific.

Finally, I wish to suggest applications for this work and research which may help further unravel this complex, interactive system:

- The responses of the epifaunal community to changes in their habitat and environment have been shown to be very rapid. Re-establishment of the community from complete defaunation took about 2 weeks, and significant colonisation of both natural and artificial habitats only took a few days. Thus, given sufficient data on natural abundance fluctuations, either the entire epifaunal community or a particular portion of it, have enormous potential as monitoring tools. With the last 20 years many marine organisms have been shown to be effective and reliable indicators of changes in their environment, particularly pollution (see Phillips and Rainbow 1993 for a comprehensive review). Long generation times and slow population dynamics of some of the traditional reef bioindicators, such as scleractinian corals, suggest that environmental impact studies might be better focussed on epifauna (Thomas 1993).
- Artificial habitats have proved an invaluable tool in the present research. The ability to manipulate aspects of habitats quickly, easily and repeatably suggest that these

structures could be gainfully used in a number of situations e.g. biogeographic studies on organisms from a wide diversity of habitats. Edgar (1993) has used a similar approach to sample epifauna from Micronesia to the Antarctic and produced a global theory of resource limitation and carrying capacity of benthic habitats, a good example of the application of such a technique.

- The natural history and taxonomy of the epifaunal organisms from most tropical habitats is usually either lacking or in a confused state. Without such information conclusions about many factors of importance will remain speculative. Although, a plea probably issued by every worker on tropical invertebrates, I should just like to re-iterate that more taxonomic and basic life-history work is needed.
- To complement the present study on the numerical abundance of epifauna it would be useful to have data on the biomass of the various taxa. With a detailed picture of abundance available, point sampling at only a few times during a year would be all that was necessary, followed by separation of the epifauna into size classes through nested sieves and quantification of the biomass of each fraction. This could then be used to form estimates of the secondary production of the system.
- A bi-factorial experiment to test both habitat structure and predation would be necessary to test the predictions of the model presented in section 8.2. Ideally, 3 or 4 different levels of epiphytes and predator inclusion as well as predator exclusion would be required.
- Tropical/temperate comparisons could be addressed by standardised collections of *Sargassum* and epifauna, or the use of artificial plants, from various areas around the world, especially other tropical areas.

REFERENCES

Abele, L. G. (1974). Species diversity of decapod crustaceans in marine habitats. Ecology **55**: 156-161.

Abercrombie, M., Hickman, C. J., Johnson, M. L. (1980). The Penguin Dictionary of Biology 7th Edition. Penguin Books, Middlesex.

Alheit, J. (1981). Feeding interactions between coral reef fishes and the zoobenthos. Proc. 4th Int. Coral Reef Symp. **2**: 545-552.

Alheit, J., Scheibel, W. (1982). Benthic harpacticoids as a food source for fish. Mar. Biol. **70**: 141-147.

Alldredge, A. L., King, J. M. (1977). Distribution, abundance and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. **41**: 317-333.

Alldredge, A. L., King, J. M. (1980). Effects of moonlight on the vertical migration patterns of demersal zooplankton. J. exp. mar. Biol. Ecol. **44**: 133-156.

Amanieu, M. (1969). Variations saisonnières de la taille et cycle reproducteur à Arcachon de *Cyathura carinata* (Kröyer). J. exp. mar. Biol. Ecol. **4**: 79-89.

Ambrose, W. G. (1984). Increase emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. J. exp. mar. Biol. Ecol. **80**: 67-75.

Ambrose, W. G. (1986). Experimental analysis of density dependent emigration of the amphipod *Rhepoxynius abronius*. Mar. Behav. Physiol. **12**: 209-216.

Andrew, N. L., Mapstone, B. D. (1987). Sampling and the description of spatial patterns in marine ecology. Oceanogr. Mar. Biol. Ann. Rev. **25**: 39-90.

Ang, P. O. (1985a). Phenology of *Sargassum siloquosum* J. Ag. and *S. paniculatum* J. Ag. (Sargassaceae, Phaeophyta) in the reef flat of Balibago (Calatagan, Philippines). Proc. 5th Int. Coral Reef Congress, Tahiti **5**: 51-57.

Ang, P. O. (1985b). Regeneration studies of *Sargassum silquosum* J. Ag. and *S. paniculatum* J. Ag. (Phaeophyta, Sargassaceae). Bot. Mar. **28**: 231-235.

Ang, P. O. (1985c). Studies on the recruitment of *Sargassum* spp. (Fucales: Phaeophyta) in Balibago, Calatagan, Philippines. J. exp. mar. Biol. Ecol. **91**: 293-301.

Ang, P. O. (1986). Analysis of the vegetation structure of a *Sargassum* community in the Philippines. Mar. Ecol. Prog. Ser. **28**: 9-19.

Ang, P. O., Trono, G. C. (1987). The genus *Sargassum* (Phaeophyta, Sargassaceae) from Balibago, Calatagan, Philippines. Bot. Mar. **30**: 387-397.

Ansari, Z. A., Rivonker, C. U., Ramani, P., Parulekar, A. H. (1991). Seagrass habitat complexity and macroinvertebrate abundance in Lakshadweep coral reef lagoons, Arabian Sea. Coral Reefs **10**: 127-131.

Aoki, M. (1990). Factors affecting population fluctuations of caprellid amphipods inhabiting *Sargassum patens* bed. Abstr. 5th Int. Congress Ecol., Tokyo 373.

Aoki, M., Kikuchi, T. (1990). Habitat adaptations of caprellid amphipods and the importance of epiphytic secondary habitats in a *Sargassum patens* bed in Amakusa, southern Japan. Publ. Amakusa Mar. Biol. Lab. Kyushu Univ. **10**: 123-134.

Arrontes, J. (1990a). Composition, distribution on host and seasonality of epiphytes on three intertidal algae. Bot. Mar. **33**: 205-211.

Arrontes, J. (1990b). Diet, food preference and digestive efficiency in intertidal isopods inhabiting macroalgae. J. exp. mar. Biol. Ecol. **139**: 231-249.

Arrontes, J., Anadon, R. (1990a). Distribution of intertidal isopods in relation to geographical changes in macroalgal cover in the Bay of Biscay. J. mar. biol. Ass. U.K. **70**: 283-293.

Arrontes, J., Anadon, R. (1990b). Seasonal variation and population dynamics of isopods inhabiting intertidal macroalgae. Sci. Mar. **54**: 231-240.

Baker, H. G., Hurd, P. D. (1968). Intrafloral ecology. Ann. Rev. Entomol. **13**: 385-414.

Bakus, G. J. (1964). The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Found. Publ. **27**: 1-29.

Banerjee, B. (1981). An analysis of the effects of latitude, age and area on the number of arthropod pests of tea. J. Appl. Ecol. **18**: 339-342.

Banks, H. P. (1970). Evolution and Plants of the Past. Fundamentals of Botany Series (Jensen, W. A., Kavaljian, L. G. eds.). Macmillan Press, London.

Barber, W. E., Greenwood, J. C., Crocos, P. (1979). Artificial seagrass - a new technique for sampling the community. Hydrobiologia **65**: 135-140.

Barnard, J. L. (1976). Amphipoda (Crustacea) from the Indo-Pacific tropics: a review. Micronesica **12**: 169-181.

Barnard, J. L., Karaman, G. S. (1991). The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Rec. Aust. Mus. Suppl. **13**:

Barnes, R. D. (1980). Invertebrate Zoology. 4th Edition. Saunders College, Philadelphia & Tokyo.

Bell, J. D., Steffe, A. S., Westoby, M. (1985). Artificial seagrass: how useful is it for field experiments on fish and macroinvertebrates? J. exp. mar. Biol. Ecol. **90**: 171-177.

Bell, J. D., Westoby, M. (1986a). Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. J. exp. mar. Biol. Ecol. **104**: 249-274.

Bell, J. D., Westoby, M. (1986b). Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. J. exp. mar. Biol. Ecol. **104**: 275-295.

Bell, J. D., Westoby, M. (1986c). Abundance of macrofauna in dense seagrass is due to habitat selection, not predation. Oecologia **68**: 205-209.

Bell, S. S. (1991). Amphipods as insect equivalents? An alternative view. Ecology **72**: 350-354.

Bell, S. S., Devlin, D. J. (1983). Short-term macrofaunal recolonization of sediment and epibenthic habitats in Tampa Bay, Florida. Bull. Mar. Sci. **33**: 102-108.

Bell, S. S., Woodin, S. A. (1984). Community unity: experimental evidence for meiofauna and macrofauna. J. Mar. Res. **42**: 605-632.

Belt, T. (1874). The Naturalist in Nicaragua. J. Murray, London (reprinted by the University of Chicago Press 1985).

Benzing, D. H. (1990). Vascular Epiphytes. General biology and related biota. Cambridge University Press, Cambridge.

Bernays, E. A. and Graham, M. (1988). On the evolution of host specificity in phytophagous arthropods. Ecology **69**: 886-892.

Bernstein, B. B., Jung, N. (1979). Selective pressure and coevolution in a kelp canopy community in Southern California. Ecol. Monogr. **49**: 335-355.

Berryman, A. A. (1988) (ed.). Dynamics of Forest Insect Populations. Plenum Press, New York.

Bohnsack, J. A. (1989). Are high densities of fish at artificial reefs the result of habitat limitation or behavioural preference? Bull. Mar. Sci. **44**: 631-645.

Bradbury, R. H., Loya, Y. (1978). A heuristic analysis of spatial patterns of hermatypic corals at Eilat, Red Sea. Am. Nat. **112**: 493-507.

Brawley, S. H., Adey, W. H. (1981a). The effect of micrograzers on algal community structure in a coral reef microcosm. Mar. Biol. **61**: 167-177.

Brawley, S. H., Adey, W. H. (1981b). Micrograzers may affect macroalgal density. Nature **292**: 177.

Brawley, S. H., Fei, X. G. (1987). Studies of mesoherbivory in aquaria and in an unbarricaded farm on the Chinese coast. J. Phycol. **23**: 614-623.

Briggs, D. E. G., Clarkson, E. N. K. (1990). The late Paleozoic radiation of malaecostracan crustaceans. In: Taylor, P. D., Larwood, G. P. (eds.) Major Evolutionary Radiations. Systematics Association Special Volume **42**: 165-186

Brock, R. E. (1979). An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. Mar. Biol. **51**: 381-388.

Brook, I. M. (1978). Comparative macrofaunal abundance in turtlegrass (*Thalassia testudinum*) communities in Florida characterized by high blade density. Bull. Mar. Sci. **28**: 212-217.

Bull, G. D. (1982). Scleractinian coral communities of two inshore high island fringing reefs at Magnetic Island, North Queensland. Mar. Ecol. Prog. Ser. **7**: 267-272.

Bulthuis, D. A., Woelkerling, W. J. (1983). Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. Aquat. Bot. **16**: 137-148.

Caine, E. A. (1979). Population structures of two species of caprellid amphipods (Crustacea). J. exp. mar. Biol. Ecol. **40**: 103-114.

Carefoot, T. H. (1973). Studies on the growth, reproduction, and life cycle of the supralittoral isopod *Ligia pallasii*. Mar. Biol. **18**: 302-311.

Chan, S. O. (1981). Species diversity and zonation of epiphytes on two species of *Sargassum*. Proc. 4th Int. Coral Reef Symp., Manila **2**: 385-392.

Chapman, A. R. O. (1974). The ecology of macroscopic marine algae Ann. Rev. Ecol. Syst. **5**: 65-80.

Charvat, D. L., Nelson, W. G., Allenbaugh, T. A. (1990). Composition and seasonality of sand-beach amphipod assemblages of the east coast of Florida. J. Crust. Biol. **10**: 446-454.

Chauhan, V. D., Krishnamurthy, V. (1971). Ecology and seasonal succession of *Sargassum swartzii* (Turn.) C. Ag. in Indian waters. Phykos **10**: 1-11.

Chennubhotla, V. S. K. (1982). Seasonal changes in growth and alginic acid and mannitol contents in *Sargassum ilicifolium* (Turner) J. Agardh and *S. myriocystum* J. Agardh. Indian J. Mar. Sci. **11**: 195-196.

Chiang, Y-M, Yoshida, T., Ajisaka, T., Trono, G. C., Tseng, C. K., Lu, B. (1992). Distribution and variation in *Sargassum polycystum* C. A. Agardh (Fucales, Phaeophyta). In: Abbott, I. A. (ed.) Taxonomy of Economic Seaweeds. With reference to some Pacific and Western Atlantic Species. Volume III. California Sea Grant College, University of California, La Jolla, California.

Choat, J. H. (1982). Fish feeding and the structure of benthic communities in temperate waters. Ann. Rev. Ecol. Syst. **13**: 423-449.

Choat, J. H., Kingett, P. D. (1982). The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. Oecologia **54**: 88-95.

Clarkson, E. N. K. (1993). Invertebrate Palaeontology and Evolution 3rd Ed. Chapman and Hall, London.

Coley, P. D., Bryant, J. P., Chapin, F. S. (1985). Resource availability and plant antiherbivore defense. Science **230**: 895-899.

Colinvaux, P. A. (1986). Ecology. John Wiley and Sons, Inc., New York.

Collins, J. D. (1978). A study of the interactive biology of corals. PhD. thesis, James Cook University of North Queensland.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**: 710-723.

Connell, J. H. (1970). A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. **40**: 49-78.

Connell, J. H. (1975). Some mechanisms producing structure in natural communities. In: Cody, M. L., Diamond, J. M. (eds.) Ecology and Evolution of Communities pp. 460-490. Belknap, Cambridge, Mass.

Connell, J. H. (1978). Diversity of tropical rainforests and coral reefs. Science **199**: 1302-1310.

Conover, J. T. (1964). The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. Bot. Mar. **7**: 4-41.

Cooks, W. L., Streams, F. A. (1984). Fish predation on *Notonecta* (Hemiptera): relationship between prey risk and habitat utilization. Oecologia **64**: 177-183.

Cordero, P. A. (1981). Eco-morphological observations of the genus *Sargassum* in central Philippines, including notes on their biomass and bed distribution. Proc. 4th Int. Coral Reef Symp., Manila **2**: 399-409.

Coull, B. C., Wells, J. B. J. (1983). Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology **64**: 1599-1609.

Coyer, J. A. (1984). The invertebrate assemblage associated with the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California: a general description with emphasis on amphipods, copepods, mysids and shrimps. Fishery Bull. **82**: 55-66.

Crawley, M. J. (1983). Herbivory. University of California Press, Berkeley.

Cribb, A. B. (1981). Coral reefs. In: Clayton, M. N., King, R. J. (eds.) Marine Botany: an Australasian Perspective pp. 329-345. Longman Cheshire, Melbourne.

Critchley, A. T. (1983a). The establishment and increase of *Sargassum muticum* (Yendo) Fensholt populations within the Solent area of Southern Britain. I. An investigation of the increase in number of population individuals. Bot. Mar. **26**: 539-545.

Critchley, A. T. (1983b). The establishment and increase of *Sargassum muticum* (Yendo) Fensholt populations within the Solent area of Southern Britain. II. An investigation of the increase in canopy cover of the alga at low water. Bot. Mar. **26**: 547-552.

Croley, F. C., Dawes, C. J. (1970). Ecology of the algae of a Florida Key. I. A preliminary checklist, zonation and seasonality. Bull. Mar. Sci. **20**: 165-185.

Crowder, L. B., Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63**: 1802-1813.

Daguerre de Hureaux, N. (1979). Etude du cycle biologique annuel d'une population de *Sphaeroma serratum* (Isopode, Flabellifere, Sphaeromatidae) du Bassin d'Arcachon. Crustaceana **37**: 85-99.

D'Antonio, C. (1985). Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: Negative effects on the host and food for herbivores? J. exp. mar. Biol. Ecol. **86**: 197-218.

Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algae community. Ecol. Monogr. **45**: 137-159.

Dayton, P. K., Tegner, M. J. (1984). The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price, P. W., Slobodchikoff, C. N., Gaud, W. S. (eds.) A New Ecology. Novel approaches to interactive systems pp. 457-481. Wiley, New York.

Dean, R. L., Connell, J. H. (1987a). Marine invertebrates in an algal succession: I. Variations in abundance and diversity with succession. J. exp. mar. Biol. Ecol. **109**: 195-215.

Dean, R. L., Connell, J. H. (1987b). Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. J. exp. mar. Biol. Ecol. **109**: 217-247.

Dean, R. L., Connell, J. H. (1987c). Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. J. exp. mar. Biol. Ecol. **109**: 249-273.

Dean, T. A. (1981). Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. J. exp. mar. Biol. Ecol. **53**: 163-180.

De Ruyter van Stevenick, E. D., Breeman, A. M. (1987). Population dynamics of a tropical intertidal and deep-water population of *Sargassum polyceratium* (Phaeophyceae). Aquat. Bot. **29**: 139-156.

DeWitt, T. H. (1987). Microhabitat selection and colonization rates of a benthic amphipod. Mar. Ecol. Prog. Ser. **36**: 237-250.

De Wreede, R. E. (1976). The phenology of three species of *Sargassum* (Sargassaceae, Phaeophyta) in Hawaii. Phycologia **15**: 175-183.

De Wreede, R. E. (1978). Growth in varying culture conditions of embryos of three Hawaiian species of *Sargassum* (Phaeophyta, Sargassaceae). Phycologia **17**: 23-31.

Deysher, L. E. (1984). Reproductive phenology of newly introduced populations of the brown alga, *Sargassum muticum* (Yendo) Fensholt. Hydrobiologia **116/117**: 403-407.

Diamond, J. M. (1990). Evolutionary biology: biological effects of ghosts. Nature **345**: 769-770.

Díaz-Piferrer, M. (1967). Effectos de las aguas de afloramiento en la flora marina de Venezuela. Carib. J. Sci. **7**: 1-13.

Díaz-Piferrer, M. (1970). Adiciones a la flora marina de Venezuela. Carib. J. Sci. **10**: 159-198.

Díaz-Piferrer, M. (1974). The genus *Sargassum* in Western Atlantic: a biogeographical approach. Proc. 8th Int. Seaweed Symp., Bangor 307-312.

Doherty, P. J., Preston, N. P. (in press). Cross-shelf patterns in the community structure of coral -dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. Mar. Ecol. Prog. Ser.

Doherty, P. J., Sale, P. F. (1985). Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs **4**: 225-234.

Doty, M. S. (1971a). Antecedent event influence on benthic marine algal standing crops in Hawaii. J. exp. mar. Biol. Ecol. **6**: 161-166.

Doty, M. S. (1971b). Physical factors in the production of tropical benthic marine algae. In: Costlow, J. D. (ed.) Fertility of the Sea pp. 99-121.

Duffy, J. E. (1990). Amphipods on seaweeds: partners or pests? Oecologia **83**: 267-276.

Duffy, J. E., Hay, M. E. (1990). Seaweed adaptations to herbivory. BioScience **40**: 368-375.

Duffy, J. E., Hay, M. E. (1991a). Amphipods are not created equal: a reply to Bell. Ecology **72**: 354-358.

Duffy, J. E., Hay, M. E. (1991b). Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology **72**: 1286-1298.

Dugan, P. J., Livingston, R. J. (1982). Long-term variation of macroinvertebrate assemblages in Apalachee Bay, Florida. Est. Coast. Shelf Sci. **14**: 391-403.

Durairatnam, M. (1966). Quantitative survey of *Sargassum* along the south-west coast of Ceylon. Bull. Fish. Res. Sta. Ceylon **19**: 11-12.

Edgar, G. J. (1983a). The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. J. exp. mar. Biol. Ecol. **70**: 129-157.

Edgar, G. J. (1983b). The ecology of south-east Tasmanian phytal animal communities. II. Seasonal changes in plant and animal populations. J. exp. mar. Biol. Ecol. **70**: 159-179.

Edgar, G. J. (1983c). The ecology of south-east Tasmanian phytal animal communities. III. Patterns of species diversity. J. exp. mar. Biol. Ecol. **70**: 181-203.

Edgar, G. J. (1983d). The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of amphithoid amphipods among algae. J. exp. mar. Biol. Ecol. **70**: 205-225.

Edgar, G. J. (1990b). The use of size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. J. exp. mar. Biol. Ecol. **137**: 195-214.

Edgar, G. J. (1990b). The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. J. exp. mar. Biol. Ecol. **137**: 215-240.

Edgar, G. J. (1990c). Predator-prey interactions in seagrass beds. I. The influence of macrofaunal abundance and size-structure on the diet and growth of the western rock lobster *Panulirus cygnus* George. J. exp. mar. Biol. Ecol. **139**: 1-22.

Edgar, G. J. (1990d). Predator-prey interactions in seagrass beds. II. Distribution and diet of the blue manna crab *Portunus pelagicus* Linnaeus at Cliff Head, Western Australia. J. exp. mar. Biol. Ecol. **139**: 23-32.

Edgar, G. J. (1990e). Predator-prey interaction in seagrass beds. III. Impacts of the western rock lobster *Panulirus cygnus* George on epifaunal gastropod populations. J. exp. mar. Biol. Ecol. **139**: 33-42.

Edgar, G. J. (1990f). Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass. J. exp. mar. Biol. Ecol. **144**: 205-234.

Edgar, G. J. (1991a). Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese *Sargassum* bed. Hydrobiologia **226**: 111-118.

Edgar, G. J. (1991b). Distribution patterns of mobile epifauna associated with rope fibre habitats within the Bathurst estuary, south-western Tasmania. Est. Coast. Shelf Sci. **33**: 589-604.

Edgar, G. J. (1992). Patterns of colonization of mobile epifauna in a Western Australia seagrass bed. J. exp. mar. Biol. Ecol. **157**: 225-246.

Edgar, G. J. (1993). Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. Oecologia **95**: 115-121.

Edgar, G. J., Aoki, M. (1993). Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. Oecologia **95**: 122-133.

Edgar, G. J., Robertson, A. I. (1992). The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australia *Amphibolus* bed. J. exp. mar. Biol. Ecol. **160**: 13-31.

Edmunds, G. F., Alstad, D. N. (1978). Coevolution in insect herbivores and conifers. Science **199**: 941-945.

Edwards, P. J., Wratten, S. D. (1980). Ecology of Insect-Plant Interactions. Studies in Biology no. 121. Edward Arnold, London. 60pp.

Ehrlich, P. R., Raven, P. H. (1964). Butterflies and plants: a study in coevolution. Evolution **18**: 588-608.

Erwin, T. L. (1983). Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: Sutton, S. L., Whitmore, T. C., Chadwich, A. C. (eds.) Tropical Rain Forest: Ecology and Management p. 73. British Ecological Society, Oxford.

Fauchald, K., Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. Oceangr. Mar. Biol. Ann. Rev. **17**: 193-284.

Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**: 565-581.

Feeny, P. (1976). Plant apparency and chemical defence. Recent Adv. Phytochem. **10**: 1-40.

Fenwick, G. D. (1976). The effect of wave exposure on the amphipod fauna of *Caulerpa brownii*. J. exp. mar. Biol. Ecol. **25**: 1-18.

Fincham, A. A. (1970). Rhythmic behaviour of the intertidal amphipod *Bathyporeia pelagica*. J. mar. biol. Ass. U.K. **50**: 1057-1068.

Fincham, A. A. (1974). Periodic swimming behaviour of amphipods in Wellington Harbour. N.Z. J. Mar. Freshwat. Res. **8**: 505-521.

Fine, M. L. (1970). Faunal variation on pelagic *Sargassum*. Mar. Biol. **7**: 112-122.

Fish, J. D., Fish, S. (1972). The swimming rhythm of *Eurydice pulchra* Leach and a possible explanation of intertidal migration. J. exp. mar. Biol. Ecol. **8**: 195-200.

Fish, S. (1970). The biology of *Eurydice pulchra* (Crustacea: Isopoda). J. mar. biol. Ass. U.K. **50**: 753-768.

Fitzhugh, G. R., Fleeger, J. W. (1985). Goby (Pisces: Gobiidae) interactions with meiofauna and small macrofauna. Bull. Mar. Sci. **36**: 436-444.

Fokkema, N. J., Van den Heuvel, J. (1986). Microbiology of the phyllosphere. Cambridge University Press, Cambridge.

Fredette, T. J., Diaz, R. J., Van Montfrans, J., Orth, R. J. (1990). Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in Lower Chesapeake Bay. Estuaries **13**: 431-440.

Futuyma, D. J., Gould, F. (1979). Associations of plants and insects in a deciduous forest. Ecol. Monogr. **49**: 33-50.

Futuyma, D. J., Morano, G. (1988). The evolution of ecological specialization. Ann. Rev. Ecol. Syst. **19**: 207-233.

Garrity, S. D., Levings, S. C. (1981). A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecol. Monogr. **51**: 267-286.

Gibbons, M. J. (1988). Impact of predation by juvenile *Clinus superciliosus* on phytal meiofauna: are fish important as predators? Mar. Ecol. Prog. Ser. **45**: 13-22.

Gibbons, M. J., Griffiths, C. L. (1986). A comparison of macrofaunal and meiofaunal distribution and standing stock across a rocky shore, with an estimate of their productivities. Mar. Biol. **93**: 181-188.

Gilinsky, E. (1984). The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology **65**: 455-468.

Gore, R. H., Gallaher, E. E., Scotto, L. E., Wilson, K. A. (1981). Studies on decapod crustacea from the Indian River Region of Florida. XI. Community

composition, structure, biomass and species-areal relationships of seagrass and drift algae-associated macrocrustaceans. Est. Coast. Mar. Sci. **12**: 485-508.

Gotceitas, V., Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia **80**: 158-166.

Greening, H. S., Livingston, R. J. (1982). Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities. Mar. Ecol. Prog. Ser. **7**: 147-156.

Gunnill, F. C. (1980). Recruitment and standing stocks in populations of one green alga and five brown algae in the intertidal zone near La Jolla, California during 1973-1977. Mar. Ecol. Prog. Ser. **3**: 231-243.

Gunnill, F. C. (1982a). Macroalgae as habitat patch islands for *Scutellidium lamellipes* (Copepoda: Harpacticoida) and *Amphithoe tea* (Amphipoda: Gammaridae). Mar. Biol. **69**: 103-116.

Gunnill, F. C. (1982b). Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigiata.* Mar. Biol. **69**: 263-280.

Gunnill, F. C. (1983). Seasonal variations in the invertebrate fauna of *Pelvetia fastigiata* (Fucaceae): effects of plant size and distribution. Mar. Biol. **73**: 115-130.

Gunnill, F. C. (1984). Differing distributions of potentially competing amphipods, copepods and gastropods among specimens of the intertidal alga *Pelvetia fastigiata.* Mar. Biol. **82**: 277-291.

Gutierrez, L. T., Fey, W. R. (1980). Ecosystem Succession. Massachusetts Institute of Technology Press, Cambridge, Massachusetts.

Hacker, S. D., Madin, L. P. (1991). Why habitat architecture and color are important to shrimps living in pelagic *Sargassum*: use of camouflage and plant-part mimicry. Mar. Ecol. Prog. Ser. **70**: 143-155.

Hacker, S. D., Steneck, R. S. (1990). Habitat architecture and the body-size-dependent habitat selection of a phytal amphipod. Ecology **71**: 2269-2285.

Hairston, N. G., Smith, F. E., Slobodkin, L. E. (1960). Community structure, population control, and competition. Am. Nat. **94**: 421-425.

Hall, M. O., Bell, S. S. (1988). Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. J. Mar. Res. **46**: 613-630.

Harborne, J. B. (1977). Introduction to Ecological Biochemistry. Academic Press, London.

Harris, P. (1972). Insects in the population dynamics of plants. In: Van Emden, H. F. (ed.) Insect/Plant Relationships pp. 201-209. Symposia of the Royal Entomological Society of London: Number Six. Blackwell Scientific Publications, Oxford.

Harrison, K., Holdich, D. M. (1982). New eubranchiate sphaeromatid isopods from Queensland waters. Mem. Qld. Mus. **20**: 421-446.

Harrison, K., Holdich, D. M. (1984). Hemibranchiate sphaeromatids (Crustacea: Isopoda) from Queensland, Australia, with a world-wide review of the genera discussed. Zool. J. Lin. Soc. **81**: 275-387.

Harrod, J. J., Hall, R. E. (1962). A method for determining the surface areas of various aquatic plants. Hydrobiologia **20**: 173-178.

Harvey, C. E. (1968). Distribution and seasonal population changes of *Campecopea hirsuta* [Isopoda: Flabellifera]. J. mar. biol. Ass. U.K. **48**: 761-767.

Hay, M. E. (1986). Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. Am. Nat. **128**: 617-641.

Hay, M. E. (1991). Marine-terrestrial contrasts in the ecology of plant chemical defenses against herbivores. Trends Ecol. Evol. **6**: 362-365.

Hay, M. E., Duffy, J. E., Pfister, C. A., Fenical, W. (1987b). Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology **68**: 1567-1580.

Hay, M. E., Duffy, J. E., Fenical, W. (1990a). Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology **72**: 733-743.

Hay, M. E., Duffy, J. E., Fenical, W., Gustafson, K. (1988a). Chemical defense in the seaweed *Dictyopteris delicatula*: differential effects against reef fishes and amphipods. Mar. Ecol. Prog. Ser. **48**: 185-192.

Hay, M. E., Duffy, J. E., Paul, V. J., Renaud, P. E., Fenical, W. (1990b). Specialist herbivores reduce their susceptibility to predation by feeding on the chemically defended seaweed *Avrainvillea longicaulis*. Limnol. Oceanog. **35**: 1734-1743.

Hay, M. E., Fenical, W. (1988). Marine plant-herbivore interactions: the ecology of chemical defense. Ann. Rev. Ecol. Syst. **19**: 111-145.

Hay, M. E., Fenical, W. (1992). Chemical mediation of seaweed-herbivore interactions. In: John, D. M., Hawkins, S. J., Price, J. H. (eds.) Plant-Animal Interactions in the Marine Benthos pp. 319-337. Clarendon Press, Oxford.

Hay, M. E., Fenical, W., Gustafson, K. (1987a). Chemical defense against diverse coral-reef herbivores. Ecology **68**: 1581-1591.

Hay, M. E., Pawlik, J. R., Duffy, J. E., Fenical, W. (1989). Seaweed-herbivore-predator interactions: host-plant specialization reduces predation on small herbivores. Oecologia **81**: 418-427.

Hay, M. E., Renaud, P. E., Fenical, W. (1988b). Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia **75**: 246-252.

Healy, B., O'Neill, M. (1984). The life cycle and population dynamics of *Idotea pelagica* and *I. granulosa* (Isopoda: Valvifera) in South-East Ireland. J. mar. biol. Ass. U.K. **64**: 21-33.

Heath, D. J., Khazaeli, A. A. (1985). Population dynamics of the estuarine isopod *Sphaeroma rugicauda*. Est. Coast. Shelf Sci. **20**: 105-116.

Heck, K. L. (1977). Comparative species richness, composition and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panama). Mar. Biol. **41**: 335-348.

Heck, K. L. (1979). Some determinants of the composition and abundance of mobile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows. J. Biogeog. **6**: 183-200.

Heck, K. L., Orth, R. J. (1980). Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay - decapod crustacea. Estuaries **3**: 289-295.

Heck, K. L., Orth, R. J. (1980). Seagrass habitats; the role of habitat complexity, competition and predation in structuring associated fish and mobile macroinvertebrate assemblages. In: Kennedy, V. S. (ed.) Estuarine Perspectives. Academic Press, New York.

Heck, K. L., Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. J. exp. mar. Biol. Ecol. **53**: 125-134.

Heck, K. L., Wetstone, G. S. (1977). Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J. Biogeog. **4**: 135-142.

Heck, K. L., Wilson, K. A. (1987). Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. J. exp. mar. Biol. Ecol. **107**: 87-100.

Heijis, F. M. L. (1985). The macroalgal component in monospecific seagrass beds from Papua New Guinea. Aquat. Bot. **22**: 291-324.

Heijis, F. M. L. (1987). Community structure and seasonality of macroalgae in some mixed seagrass beds from Papua New Guinea. Aquat. Bot. **27**: 139-158.

Hiatt, R. W., Strasburg, D. W. (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. **30**: 65-127.

Hicks, G. R. F. (1980). Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. J. exp. mar. Biol. Ecol. **44**: 157-192.

Hixon, M. A., Brostoff, W. N. (1983). Damselfish as keystone species in reverse: Intermediate disturbance and diversity of reef algae. Science **220**: 511-513.

Hixon, M. A., Brostoff, W. N. (1985). Substrate characteristics, fish grazing, and epibenthic reef assemblages off Hawaii. Bull. Mar. Sci. **37**: 200-213.

Hixon, M. A., Menge, B. A. (1991). Species diversity: prey refuges modify interactive effects of predation and competition. Theoret. Pop. Biol. **39**: 178-200.

Holdich, D. M. (1976). A comparison of the ecology and life cycles of two species of littoral isopods. J. exp. mar. Biol. Ecol. **24**: 113-149.

Holdich, D. M., Jones, J. A. (1983). Tanaids - keys and notes for the identification of the species. Synopses of the British Fauna (New Series) No. 27. Cambridge University Press, Cambridge & London.

Holmlund, M. B., Peterson, C. H., Hay, M. E. (1990). Does algal morphology affect amphipod susceptibility to fish predation? J. exp. mar. Biol. Ecol. **139**: 65-83.

Hootsman, M. J. M., Vermaat, J. E. (1985). The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. Aquat. Bot. **22**: 83-88.

Howard, R. K. (1985). Measurements of short-term turnover of epifauna within seagrass beds using an *in situ* staining method. Mar. Ecol. Prog. Ser. **22**: 163-168.

Howard, R. K. (1987). Diel changes in the abundance of epifauna associated with seagrasses of the Indian River, Florida, USA. Mar. Biol. **96**: 137-142.

Howard, R. K., Short, F. T. (1986). Seagrass growth and survivorship under the influence of epiphyte grazers. Aquat. Bot. **24**: 207-302.

Howe, H. F., Westley, L. C. (1988). Ecological Relationships of Plants and Animals. Oxford University Press, Oxford.

Hubbell, S. P. (1979). Tree dispersion abundance and diversity in a tropical dry forest. Science **203**: 1299-1309.

Hurlbert, S. H., White, M. D. (1993). Experiments with freshwater invertebrate zooplanktivores: quality of statistical analyses. Bull. Mar. Sci. **53**: 128-153.

Jacoby, C. A., Greenwood, J. G. (1988). Spatial, temporal, and behavioural patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. Mar. Biol. **97**: 309-328.

Jansen, K. P. (1971). Ecological studies on intertidal New Zealand Sphaeromatidae (Isopoda: Flabellifera). Mar. Biol. **11**: 262-285.

Janzen, D. H. (1978). Complications in interpreting the chemical defenses of trees against tropical arboreal plant-eating vertebrates. In: Montgomery, G. D. (ed.) The Ecology of Arboreal Folivores pp. 73-84.. Smithsonian Institution Press, Washington, D. C.

Jephson, N. A., Gray, P. W. G. (1977). Aspects of the ecology of *Sargassum muticum* (Yendo) Fensholt in the Solent region of the British Isles. I. The growth cycle and epiphytes. In: Keegan, K. F., Ó Céidigh, P., Boaden, P. J. S. (eds.) Biology of Benthic Organisms. Proceedings of the 11th European Symposium on Marine Biology, Galway, Ireland pp. 367-375. Pergamon Press, Elmsford, N.Y.

Johnson, S. C., Scheibling, R. E. (1987). Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. **37**: 209-227.

Johnson, W. S. (1976). Biology and population dynamics of the intertidal isopod *Cirolana harfordi*. Mar. Biol. **36**: 343-350.

Jones, D. A., Naylor, E. (1970). The swimming rhythm of the sand beach isopod *Eurydice pulchra*. J. exp. mar. Biol. Ecol. **4**: 188-199.

Jones, G. P., Ferrell, D. J., Sale, P. F. (1991). Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. In: Sale, P. F. (ed.). The Ecology of Fishes on Coral Reefs pp. 156-179. Academic Press, San Diego.

Jones, G. P., Ferrell, D. J., Sale, P. F. (1992). Fish feeding and dynamics of soft-sediment mollusc populations in a coral reef lagoon. Mar. Ecol. Prog. Ser. **80**: 175-190.

Jones, G. P., Sale, P. F., Ferrell, D. J. (1988). Do large carnivorous fishes affect the ecology of macrofauna in shallow lagoonal sediments?: a pilot experiment. Proc. 6th Int. Coral Reef Symp., Townsville **2**: 77-82.

Jones, I. G. (1965). Canopy grazing at southern Point Loma. Kelp Habitat Improvement Project Annual Report, 1 Feb. 1964-31 March 1965 pp. 62-63. W. M. Keck Laboratory of Environmental Health and Engineering, California Institute of Technology, Pasadena, California.

Jones, M. B. (1974). Breeding biology and seasonal population changes of *Jaera nordmanni nordica* Lemercier [Isopoda, Asellota]. J. mar. biol. Ass. U.K. **54**: 727-736.

Joshi, G. V., Gowda, C. A. (1975). Seasonal variations in chemical composition of *Sargassum ilicifolium* Grun. and sea water. Indian J. mar. Sci. **4**: 165-168.

Kang, Y. J., Yun, S. G. (1988). Ecological study on isopod crustaceans in surfgrass beds around Tongbacksun, Haeundae, Pusan (in Korean). Ocean Research **10**: 23-31.

Kennelly, S. J. (1991). Caging experiments to examine the effects of fishes on understory species in a sublittoral kelp community. J. exp. mar. Biol. Ecol. **147**: 207-230.

Kensley, B. F., Schotte, M. (1989). Guide to the Marine Isopod Crustaceans of the Caribbean. Smithsonian Institute Press, Washington, D.C.

Kilar, J. A., Hanisak, M. D. (1988). Seasonal patterns of morphological variability in *Sargassum polyceratium* (Phaeophyta). J. Phycol. **24**: 467-473.

Kilar, J. A., Hanisak, M. D., Yoshida, T. (1992). On the expression of phenotypic variability: why is *Sargassum* so taxonomically difficult? In: Abbott, I. A. (ed.) Taxonomy of Economic Seaweeds. With reference to some Pacific and Western

Atlantic Species. Volume III. California Sea Grant College, University of California, La Jolla, California.

King, R. J. (1981). Marine angiosperms: seagrasses. In: Clayton, M. N., King, R. J. (eds.) Marine Botany: an Australasian Perspective pp. 200-210. Longman Cheshire, Melbourne.

Kingsford, M. J., Choat, J. H. (1985). The fauna associated with drift algae captured with a plankton-mesh purse seine net. Limnol. Oceanog. **30**: 618-630.

Kitting, C. L. (1984). Selectivity by dense populations of small invertebrates foraging among seagrass blade surfaces. Estuaries **7**: 276-288.

Klomp, H. (1964) Intraspecific competition and the regulation of insect numbers. Ann. Rev. Entomol. **9**: 17-40.

Klumpp, D. W., McKinnon, A. D., Mundy, C. N. (1988). Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. Mar. Ecol. Prog. Ser. **45**: 95-108.

Kneib, R. T. (1982). Habitat preference, predation, and the intertidal distribution of gammaridean amphipods in a North Carolina salt marsh. J. exp. mar. Biol. Ecol. **59**: 219-230.

Kneib, R. T. (1988). Testing for indirect effects of predation in an intertidal soft-bottom community. Ecology **69**: 1795-1805.

Koh, C. H., Ahn, I. (1985). Community structure and productivity of phytobenthos in Juckdo (eastern coast of Korea): 3. Growth pattern and productivity of *Sargassum confusum* (Phaeophyta). Korean J. Bot. **28**: 119-126.

Koh, C. H., Shin, H. C. (1990). Growth and size distribution of some large brown algae in Ohori, east coast of Korea. Hydrobiologia **204/205**: 225-231.

Koop, K., Field, J. G. (1980). The influence of food availability on population dynamics of a supralittoral isopod, *Ligia dilatata* Brandt. J. exp. mar. Biol. Ecol. **48**: 61-72.

Koop, K., Griffiths, C. L. (1982). The relative significance of bacteria, meio- and macrofauna on an exposed sandy beach. Mar. Biol **66**: 295-300.

Krapp-Schickel, G. (1993). Do algal-dwelling amphipods react to the 'critical zones' of a coastal slope? J. Nat. Hist. **27**: 883-900.

Krebs, C. J. (1985). Ecology: The Experimental Analysis of Distribution and Abundance 3rd. Ed. Harper and Row, New York.

Kulczycki, G. R., Virnstein, R. W., Nelson, W. G. (1981). The relationship between fish abundance and algal biomass in a seagrass-drift algae community. Est. Coast. Shelf Sci. **12**: 341-347.

Larkum, A. W. D. (1981). Marine primary productivity. In: Clayton, M. N., King, R. J. (eds.) Marine Botany: an Australasian Perspective pp. 369-385. Longman Cheshire, Melbourne.

Lawson, G. W. (1957). Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. J. Ecol. **45**: 831-860.

Lawton, J. H. (1978). Host-plant influences on insect diversity: the effects of space and time. Symp. R. Entomol. Soc. Lond. **9**: 105-125.

Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. Ann. Rev. Entomol. **28**: 23-39.

Lawton, J. H., Price, P. W. (1979). Species richness of parasites on hosts: agromyzid flies on the British Umbelliferae. J. Anim. Ecol. **48**: 619-637.

Lawton, J. H., Schröder, D. (1977). Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature **265**: 137-140.

Lawton, J. H., Strong, D. R. (1981). Community patterns and competition in folivorous insects. Am. Nat. **118**: 317-338.

Leber, K. M. (1985). The influence of predatory decapods, refuge and microhabitat selection on seagrass communities. Ecology **66**: 1951-1964.

Ledoyer, M. (1969). Écologie de la faune vagile des biotopes Méditerranéens accessible en scaphandre autonome. V. Étude des phénomènes nycthéméraux. Les variations nycthémérales des populations animales dans les biotopes. Téthys **1**: 291-308.

Lewis, F. G. (1984). Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substratum. Mar. Ecol. Prog. Ser. **19**: 101-113.

Lewis, F. G. (1987). Crustacean epifauna of seagrass and macroalgae in Apalachee Bay, Florida, U.S.A. Mar. Biol. **94**: 219-231.

Littler, M. M., Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am. Nat. **116**: 25-44.

Littler, M. M., Murray, S. N., Arnold, K. E. (1979). Seasonal variation in net photosynthetic performance and cover of intertidal macrophytes. Aquat. Bot. **7**: 35-46.

Livingston, R. J. (1976). Diurnal and seasonal fluctuations of organisms in a north Florida estuary. Est. Coast. Mar. Sci. **4**: 373-400.

Lobel, P. S. (1980). Herbivory by damselfishes and their role in coral reef community ecology. Bull. Mar. Sci. **30**: 273-289.

Lovejoy, T. E. (1974). World wildlife fund: new granting emphasis. Assoc. Syst. Coll. Newsletter **2**: 13-14.

Lubchenco, J. (1983). *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology **64**: 1116-1123.

Lubchenco, J., Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst. **12**: 405-437.

Lubchenco, J., Menge, B. A., Garrity, S. D., Lubchenco, P. J., Ashkenas, L. R., Gaines, S. D., Emlet, R., Lucas, J., Strauss, S. (1984). Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). J. exp. mar. Biol. Ecol. **78**: 23-73.

MacArthur,. R. H. (1965). Patterns of species diversity. Biol. Rev. **40**: 510-533.

MacArthur, R. H. (1972). Geographical Ecology. Harper and Row, New York.

MacArthur, R. H., Wilson, E. O. (1967). The theory of island biogeography. Princeton University Press, Princeton, N.J.

Magruder, W. H. (1988). *Sargassum* (Phaeophyta, Fucales, Sargassaceae) in the Hawaiian Islands. In: Abbott, I. A. (ed.) Taxonomy of Economic Seaweeds: with reference to some Pacific and Caribbean species. Vol. 2. pp. 65-87. California Sea Grant College Program, University of California, La Jolla, California.

Main, K. L. (1987). Predator avoidance in seagrass meadows: prey behavior, microhabitat selection and cryptic coloration. Ecology **68**: 170-180.

Marsh, G. A. (1973). The *Zostera* epifaunal community in the York River, Virginia. Chesapeake Sci. **14**: 87-97.

Martin-Smith, K. M. (1993a). The phenology of four species of *Sargassum* at Magnetic Island, Australia. Bot. Mar. **36**: 327-334.

Martin-Smith, K. M. (1993b). Abundance of mobile epifauna: the role of habitat complexity and predation J. exp. mar. Biol. Ecol. **174**: 243-260.

Martin-Smith, K. M. (in press). Seasonal variation in tropical benthic *Sargassum* and associated motile epifauna. Proc. 7th Int. Coral Reef Symp., Guam

Mather, P., Bennett, I. (1993). A Coral Reef Handbook 3rd Ed. Surrey Beatty and Sons, Sydney.

Mathieson, A. C., Dawes, C. J. (1974). Ecological studies of Floridian *Euchuema* (Rhodophyta, Gigartinales). II. Photosynthesis and respiration. Bull. Mar. Sci. **24**: 274-285.

Matthews, E. G., Kitching, R. L. (1984). Insect Ecology. 2nd Edition. University of Queensland Press, Brisbane. 211 pp.

Maxwell, F. G., Jennings, P. R. Breeding Plants Resistant to Insects. John Wiley and Sons, New York.

McClure, M. S., Price, P. W. (1975). Competition among sympatric *Erythroneura* leaf hoppers (Homoptera: Cicadellidae) on American sycamore. Ecology **56**: 1388-1397.

McClure, M. S., Price, P. W. (1976). Ecotope characteristics of coexisting *Erythroneura* leaf hoppers (Homoptera: Cicadellidae) on sycamore. Ecology **57**: 928-940.

McCourt, R. M. (1984a). Niche differences between sympatric *Sargassum* species in the northern Gulf of California. Mar. Ecol. Prog. Ser. **18**: 139-148.

McCourt, R. M. (1984b). Seasonal patterns of abundance, distributions and phenology in relation to growth strategies of three *Sargassum* species. J. exp. mar. Biol. Ecol. **74**: 141-156.

McCoy, E. D., Bell, S. S. (1991). Habitat structure. Habitat structure: the evolution and diversification of a complex topic. In: Bell, S. S., McCoy, E. D., Mushinsky, H. R. (eds.) The physical arrangement of objects in space pp. 3-27. Chapman and Hall, Melbourne.

McIntosh, R. P. (1985). The Background of Ecology. Cambridge University Press, Cambridge.

McIntyre, A. D. (1969). Ecology of marine meiobenthos. Biol. Rev. **44**: 245-290.

McNeil, J. N. (1991). Behavioural ecology of pheromone-mediated communication in moths and its importance in the use of pheromone traps. Ann. Rev. Entomol. **36**: 407-430.

McWilliam, P. S., Sale, P. F., Anderson, D. T. (1981). Seasonal changes in resident zooplankton sampled by emergence traps in One Tree Lagoon, Great Barrier Reef. J. exp. mar. Biol. Ecol. **52**: 185-203.

Meentemeyer, V., Box, E. O. (1987). Scale effects in landscape studies. In: Turner, M. G. (ed.) Landscape Heterogeneity and Disturbance pp. 15-34. Springer-Verlag, New York.

Menge, B. A., Lubchenco, J. (1981). Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol. Monogr. **51**: 429-450.

Menge, B. A., Lubchenco, J., Ashkenas, L. R. (1985). Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. Oecologia **65**: 394-405.

Menge, B. A., Lubchenco, J., Ashkenas, L. R. (1986). Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. J. exp. mar. Biol. Ecol. **100**: 225-269.

Menge, B. A., Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. Am. Nat. **110**: 351-369.

Meyen, S. V. (1987). Fundamentals of Palaeobotany. Chapman and Hall, London.

Minello, T. J., Zimmerman, R. J. (1983). Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. J. exp. mar. Biol. Ecol. **72**: 211-231.

Misra, J. N. (1966). Phaeophyceae in India. Indian Council Agr. Res. (E.C.A.R.), New Delhi, 1-203.

Montouchet, P. C. G. (1979). Sur la communauté des animaux vagile associés à *Sargassum cymosum* C. Agardh, à Ubatuba, État de São Paulo, Brésil. Stud. Neotrop. Fauna **14**: 33-64.

Morrissey, J. (1980). Community structure and zonation of macroalgae and hermatypic corals on a fringing reef flat of Magnetic Island (Queensland, Australia). Aquat. Bot. **8**: 91-139.

Mukai, H. (1971). The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. Mar. Biol. **8**: 170-182.

Munda, L. (1960) Der Einfluss von Chlorinität auf die chemische Zusammensetzung, Wachstum und Fruktifizierungstätigkeit von einigen Fucaceen. Norsk Inst. for Tang- og Tareforsk. Foreløbige Rapp. No. 111.

Murthy, M. S., Bhattacharya, M., Radia, P. (1978). Ecological studies on intertidal algae at Okha (India). Bot. Mar. **21**: 381-386.

Myers, A. A. (1993). Dispersal and endemicity in gammaridean Amphipoda. J. Nat. Hist. **27**: 901-908.

Myers, A. A., Southgate, T. (1980). Artificial substrates as a means of monitoring rocky shore cryptofauna. J. mar. biol. Ass. U.K. **60**: 963-975.

Nagle, J. S. (1968). Distribution of the epibiota of macrobenthic plants. Contrib. Mar. Sci. **13**: 105-144.

Naylor, E. (1972). British Marine Isopods - keys and notes for the identification of the species. Synopses of the British Fauna (New Series) No. 3. Academic Press, London.

Neal, M. C. (1930). Hawaiian marine algae. B. P. Bishop Mus. Bull. **67**: 1-84.

Nelson, W. G. (1979a). Experimental studies of selective predation on amphipods: consequences for amphipods distribution and abundance. J. exp. mar. Biol. Ecol. **38**: 225-245.

Nelson, W. G. (1979b). An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. J. exp. mar. Biol. Ecol. **39**: 231-264.

Nelson, W. G. (1980). A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bull. Mar. Sci. **30**: 80-89.

Nelson, W. G. (1981). Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar. Ecol. Prog. Ser. **5**: 141-149.

Nelson, W. G., Cairns, K. D., Virnstein, R. W. (1982). Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River lagoon, Florida. Bull. Mar. Sci. **32**: 121-129.

Neudecker, S., (1977). Transplant experiments to test the effects of fish grazing on coral distribution. Proc. 3rd Int. Coral Reef Symp., Miami **1**: 317-323.

Neudecker, S. (1979). Effects of grazing and browsing fishes on the zonation of corals in Guam. Ecology **60**: 666-672.

Neumann, F. G., Harris, J. A., Wood, C. H. (1977). The phasmatid problem in mountain ash forests of the central highlands of Victoria. Bulletin no. 25, Forests Commission, Victoria.

New, T. R. (1988). Associations Between Insects and Plants. New South Wales University Press, Sydney.

Ngan, Y., Price, I. R. (1980). Seasonal growth and reproduction of intertidal algae in the Townsville region (Queensland, Australia). Aquat. Bot. **9**: 117-134.

Nicotri, M. E. (1977). The impact of crustacean herbivores on cultured seaweed populations. Aquaculture **12**: 127-136.

Nicotri, M. E. (1980). Factors involved in herbivore food preference. J. exp. mar. Biol. Ecol. **42**: 13-26.

Nizamuddin, M. (1970). Phytogeography of the Fucales and their seasonal growth. Bot. Mar. **13**: 131-139.

Odum, E. P. (1975). Ecology 2nd Ed. Holt Rinehart and Winston, London, New York.

Ohno, M. (1979). Culture and field studies of *Sargassum piluliferum*. Rep. Usa. Mar. Biol. Inst. Kochi. Univ. **0**: 25-32.

Omori, M., Fleminger, A. (1976). Laboratory methods for processing crustacean zooplankton. In: Steedman, H. F. (ed.) Zooplankton Fixation and Preservation. UNESCO, Paris.

O'Neill, R. V., De Angelis, D. L., Waide, J. B., Allen, T. F. H. (1986). A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, N.J.

Orth, R. J., Heck, K. L., Van Montfrans, J. (1984). Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**: 335-350.

Paine, R. T. (1966). Food web complexity and species diversity. Am. Nat. **100**: 65-75.

Paine, R. T. (1976). Size-limited predation: an observation and experimental approach with the *Mytilus-Pisaster* interaction. Ecology **57**: 858-873.

Parsons, T. R. (1980). The development of biological studies in the ocean environment. In: Sears, M., Merriam, D. (eds.) Oceanography: The Past p. 540-550. Springer-Verlag, New York.

Paul, V. J. (1992). Ecological Roles of Marine Natural Products. Comstock Publishing Associates, Ithaca, N. Y.

Paul, V. J., Hay, M. E., Duffy, J. E., Fenical, W., Gustafson, K. (1987). Chemical defense in the seaweed *Octodes secundiramea* (Montagne) Howe (Rhodophyta):

effects of its monoterpenoid components upon diverse coral-reef herbivores. J. exp. mar. Biol. Ecol. **114**: 249-260.

Paula, E. J., Oliveira Fº, E. C. (1980). Phenology of two populations of *Sargassum cymosum* (Phaeophyta-Fucales) of São Paulo state coast, Brazil. Bol. Bot. Univ. São Paulo **8**: 21-39.

Peterson, C. H. (1979). The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. Oecologia **39**: 1-24.

Peyrot-Clausade, M. (1980). Motile cryptofauna of Tuléar reef flats. Mar. Biol. **59**: 43-47.

Phillips, D. J. H., Rainbow, P. S. (1993). The Biomonitoring of Trace Aquatic Contaminants. Elsevier, London.

Pianka, E. R. (1966). Latitudinal gradients in species diversity. Am. Nat. **100**: 33-46.

Price, I. R. (1989). Seaweed phenology in a tropical Australian locality (Townsville, North Queensland). Bot. Mar. **32**: 399-406.

Prince, J. S. (1980). The ecology of *Sargassum pteropleuron* Grunow (Phaeophyceae, Fucales) in the waters off South Florida. II. Seasonal photosynthesis and respiration of *S. pteropleuron* and comparison of its phenology with that of *S. polyceratium* Montagne. Phycologia **19**: 190-193.

Prince, J. S., O'Neal, S. W. (1979). The ecology of *Sargassum pteropleuron* Grunow (Phaeophyceae, Fucales) in the waters off South Florida. I. Growth, reproduction and population structure. Phycologia **18**: 109-114.

Ragan, M. A., Jensen, A. (1978). Quantitative studies on brown algal phenols. II. Seasonal variations in polyphenol content of *Ascophyllum nodosum* (L.) Le Jol. and *Fucus vesiculosus* (L.). J. exp. mar. Biol. Ecol. **34**: 245-258.

Raju, P. V., Venugopal, R. (1971). Appearance and growth of *Sargassum plagiophyllum* (Mert.) C. Agardh on a fresh substratum. Bot. Mar. **14**: 36-38.

Ramirez, W. (1974). Coevolution of *Ficus* and *Agaonidae*. Annals Missouri Bot. Garden **61**: 770-780.

Randall, J. E., Allen, G. R., Steene, R. C. (1990). Fishes of the Great Barrier Reef and Coral Sea. Crawford House Press, Bathurst, Australia.

Raven, P. R., Evert, R. F. and Curtis, H. (1981). Biology of Plants. 3rd Edition. Worth Publishers, New York.

Reaka, M. L. (1985). Interactions between fishes and mobile benthic invertebrates on reefs: the significance of motility vs. defensive adaptations. Proc. 5th Int. Coral Reef Symp., Tahiti **5**: 439-444.

Reynolds, W. W., Casterlin, M. E. (1979). Diel activity of the pink shrimp *Penaeus duorarum*. Hydrobiologia **66**: 223-226.

Rhoades, D. F. (1985). Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. Am. Nat. **125**: 205-238.

Rhoades, D. F., Cates, R. G. (1976). Towards a general theory of plant antiherbivore chemistry. Rec. Adv. Phytochem. **10**: 168-213.

Ricklefs, R. E. (1973). Ecology. Nelson, London.

Riddle, M. J. (1988). Patterns in the distribution of macrofaunal communities in coral reef sediments on the central Great Barrier Reef. Mar. Ecol. Prog. Ser. **47**: 281-292.

Ride, W. D. L. (1978). Towards a national biological survey. Search **9**: 73-82.

Rosenthal, G. A., Janzen, D. H. (1979). Herbivores. Their interaction with secondary plant metabolites. Academic Press, New York and London.

Russo, A. R. (1987). Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods. Mar. Ecol. Prog. Ser. **36**: 101-105.

Russo, A. R. (1990). The role of seaweed complexity in structuring Hawaiian epiphytal amphipod communities. Hydrobiol. **194**: 1-12.

Russo, A. R. (1991). Do predatory fishes affect the structure of an epiphytal amphipod assemblage on a protected algal reef in Hawaii? Hydrobiologia **224**: 185-192.

Sale, P. F., Guy, J. A. (1992). Persistence of community structure: what happens when you change taxonomic scale? Coral Reefs **11**: 147-154.

Salemaa, H. (1979). Ecology of *Idotea* spp. (Isopoda) in the Northern Baltic. Ophelia **18**: 133-150.

Santelices, B. (1977). Water movement and seasonal algal growth in Hawaii. Mar. Biol. **43**: 225-235.

Schiel, D. R. (1985). Growth, survival and reproduction of two species of marine algae at different densities in natural stands. J. Ecol. **73**: 199-217.

Schiel, D. R. (1988). Algal interactions on shallow subtidal reefs in northern New Zealand: a review. N.Z. J. Mar. Freshwat. Res. **22**: 481-489.

Schmidt, G. H., Warner, G. F. (1984). Effects of caging on the development of a sessile epifaunal community. Mar. Ecol. Prog. Ser. **15**: 251-263.

Schneider, F. I., Mann, K. H. (1991a). Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlation studies. J. exp. mar. Biol. Ecol. **145**: 101-117.

Schneider, F. I., Mann, K. H. (1991b). Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. J. exp. mar. Biol. Ecol. **145**: 119-139.

Schoener, A. (1974). Experimental zoogeography: colonization of marine mini-islands. Am. Nat. **108**: 715-737.

Schoener, T. W. (1982). The controversy over interspecific competition. Am. Sci. **70**: 586-595.

Schoener, T. W. (1983). Field experiments on interspecific competition. Am. Nat. **122**: 240-285.

Schupp, E. W. (1986). *Azteca* protection of *Cecropia*: Ant occupation benefits juvenile trees. Oecologia **70**: 379-385.

Scriber, J. M. (1983). Evolution of feeding specialization , physiological efficiency, and host races in selected Papilionidae and Saturnidae. In: Denno, R. G., McClure, M. (eds.) Variable Plants and Herbivores in Natural and Managed Systems p. 373-412. Academic Press, New York.

Scriber, J. M. (1984). Host-plant suitability. In: Bell, W. J., Carde, R. T. (eds.) Chemical Ecology of Insects p. 159-204. Chapman and Hall, New York.

Sebens, K. P. (1991). Habitat structure and community dynamics in marine benthic systems. In: Bell, S. S., McCoy, E. D., Mushinsky, H. R. (eds.) Habitat structure. The physical arrangement of objects in space pp. 211-234. Chapman and Hall, Melbourne.

Seed, R., O'Connor, R. J. (1981). Community organization in marine algal epifaunas. Ann. Rev. Ecol. Syst. **12**: 49-74.

Shafir, A., Field, J. G. (1980). Population dynamics of the isopod *Cirolana imposita* Barnard Crustaceana **39**: 185-195.

Shepherd, S. A., Womersley, H. B. S. (1970). The sublittoral ecology of West Island, South Australia. I. Environmental features and the algal ecology. Trans. Roy. Soc. S. Aust. **94**: 105-137.

Shuster, S. M. (1990). Courtship and female mate selection in a semelparous isopod crustacean (*Paracerceis sculpta*). Anim. Behav. **40**: 390-399.

Shuster, S. M. (1992). The use of artificial sponges as breeding habitat by *Paracerceis sculpta* (Holmes) (Crustacea: Isopoda). J. exp. mar. Biol. Ecol. **165**: 75-89.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeier, K. (1985). Predation, competition and prey communities: a review of field experiments. Ann. Rev. Ecol. Syst. **16**: 269-311.

Sivalingham, P. M. (1978). Biodeposited trace metals and mineral content studies of some tropical marine algae. Bot. Mar. **21**: 327-330.

Sokal, R. R.; Rohlf, F. J. (1981). Biometry. The principles and practice of statistics in biological research 2nd Ed. W. H. Freeman, San Francisco.

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? J. Anim. Ecol. **46**: 337-365.

Spight, T. M. (1977). Diversity of shallow-water gastropod communities on temperate and tropical beaches. Am. Nat. **111**: 1077-1097.

Steger, R. (1987). Effects of refuges and recruitment on gonodactylid stomatopods, a guild of mobile prey. Ecology **68**: 1520-1533.

Steinberg, P. D. (1985). Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecol. Monogr. **55**: 333-349.

Steinberg, P. D. (1992). Geographical variation in the interaction between marine herbivores and brown algal secondary metabolites. In: Paul, V. J. (ed.) Ecological Roles of Marine Natural Products. Comstock Publishing Associates, Ithaca, N. Y.

Steinberg, P. D., Edyvane, K., De Nys, R., Birdsey, R., Van Altena, I. A. (1991). Lack of avoidance of phenolic-rich brown algae by tropical herbivorous fishes. Mar. Biol. **109**: 335-343.

Steinberg, P. D., Paul, V. J. (1990). Fish feeding and chemical defenses of tropical brown algae in Western Australia. Mar. Ecol. Prog. Ser. **58**: 253-259.

Steneck, R. S., Watling, L. (1982). Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Mar. Biol. **68**: 299-319.

Stevens, G. C. (1989). The latitudinal gradient in geographical range: how so many species can coexist in the tropics. Am. Nat. **133**: 240-256.

Stiling, P. D. (1980). Competition and coexistence among *Eupteryx* leafhoppers (Hemiptera: Cicadellidae) occurring on stinging nettles (*Urtica dioica* L.). J. Anim. Ecol. **49**: 793-805.

St. John, J., Jones, G. P., Sale, P. F. (1989). The distribution and abundance of soft-sediment meiofauna and a predatory goby in a coral reef lagoon. Coral Reefs **8**: 51-57.

Stoner, A. W. (1979). Species-specific predation on amphipod crustacea by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. Mar. Biol. **55**: 201-207.

Stoner, A. W. (1980a). Perception and choice of substratum by epifaunal amphipods associated with seagrasses. Mar. Ecol. Prog. Ser. **3**: 105-111.

Stoner, A. W. (1980b). Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. Contrib. Mar. Sci. **23**: 63-77.

Stoner, A. W. (1983). Distributional ecology of amphipods and tanaidaceans associated with three sea grass species. J. Crust. Biol. **3**: 505-518.

Stoner, A. W. (1985). *Penicillus capitatus*: an algal island for macrocrustaceans. Mar. Ecol. Prog. Ser. **26**: 279-287.

Stoner, A. W., Lewis, F. G. (1985). The influence of quantitative and qualitative aspects of habitat complexity in tropical seagrass meadows. J. exp. mar. Biol. Ecol. **94**: 19-40.

Stretch, J. J. (1985). Quantitative sampling of demersal zooplankton: reentry and airlift dredge sample comparisons. J. exp. mar. Biol. Ecol. **91**: 125-136.

Strong, D. R., Lawton, J. H., Southwood, Sir R. (1984). Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific Publications, Oxford and London.

Summerson, H. C., Peterson, C. H. (1984). Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar. Ecol. Prog. Ser. **15**: 63-77.

Svedelius, N. (1906) Über die Algenvegetation eines Ceylonischen Korallenriffes mit besonderer Rucksicht auf ihre Periodizität. In: Kjellman, F. R. (ed.) Sartryck ur Bataniska Studier tillagnade pp.184-220. Uppsala.

Swain, T. (1978). Plant-animal coevolution: a synoptic view of the Paleozoic and Mesozoic. In: Harborne, J. B. (ed.) Biochemical Aspects of Plant and Animal Coevolution pp. 3-20. Academic Press, New York.

Tararum, A. S., Wakabara, Y. (1981). The mobile fauna - especially Gammaridea - of *Sargassum cymosum*. Mar. Ecol. Prog. Ser. **5**: 157-163.

Tegner, M. J., Dayton, P. K. (1987). El Niño effects on Southern California kelp forest communities. Adv. Eco. Res. **17**: 243-279.

Thomas, J. D. (1993). Biological monitoring and tropical biodiversity in marine environments: a critique with recommendations, and comments on the use of amphipods as bioindicators. J. Nat. Hist. **27**: 795-806.

Trono, G. C. (1992). The genus *Sargassum* in the Philippines. In: Abbott, I. A. (ed.) Taxonomy of Economic Seaweeds. With reference to some Pacific and Western Atlantic Species. Volume III. California Sea Grant College, University of California, La Jolla, California.

Trono, G. C., Lluisma, A. O. (1990). Seasonality of standing crop of a *Sargassum* (Fucales, Phaeophyta) bed in Bolinao, Pangasinan, Philippines. Hydrobiologia **204/205**: 331-338.

Trono, G. C., Saraya, A. (1987). The structure and distribution of macrobenthic algal communities on the reef of Santiago Island, Bolinao, Pangasinan, Phil. J. Sci. Monogr. **17**: 63-81.

Tseng, C. K., Lu Baoren (1988). Studies on Chinese species of zygocarpic *Sargassum*. In: Abbott, I. A. (ed.) Taxonomy of Economic Seaweeds. With reference to some Pacific and Caribbean Species. Volume II. California Sea Grant College, University of California, La Jolla, California.

Tsuda, R. T. (1972). Morphological, zonational and seasonal studies on two species of *Sargassum* on the reefs of Guam. Proc. 7th Int. Seaweed Symp. 40-44.

Tsuda, R. T. (1974). Seasonal aspects of the Guam Phaeophyta (brown algae). Proc. 2nd Int. Coral Reef Symp, Brisbane **1**: 43-47.

Tsuda, R. T. (1976). Occurrence of the genus *Sargassum* (Phaeophyta) on two Pacific atolls. Micronesica **12**: 279-282.

Tully, O., Ó'Céidigh, P. (1986). The ecology of *Idotea* species (Isopoda) and *Gammarus locusta* (Amphipoda) on surface driftweed in Galway Bay (West of Ireland). J. mar. biol. Ass. U.K. **66**: 931-942.

Turnock, W. J. (1977). Adaptability and stability of insect pest populations in prairie agricultural ecosystems. Tech. Bull. Agric. Exp. Stn. Univ. Minn. **310**: 89-101.

Umamaheswararao, M., Sreeramulu, T. (1964). An ecological study of some intertidal algae of the Visakhapatnam coast. J. Ecol. **52**: 595-616.

Umezaki, I. (1983). Ecological studies of *Sargassum miyabei* in Maizura Bay, Japan Sea. Bull. Jpn. Soc. Sci. Fish. **49**: 1825-1834.

Umezaki, I. (1984a). Ecological studies of *Sargassum horneri* in Obama Bay, Japan Sea. Bull. Jpn. Soc. Sci. Fish. **50**: 1193-1200.

Umezaki, I. (1984b). Ecological studies of *Sargassum hemiphyllum* in Obama Bay, Japan Sea. Bull. Jpn. Soc. Sci. Fish. **50**: 1677-1684.

Underwood, A. J. (1978). An experimental evaluation of competition between three species of intertidal prosobranch gastropods. Oecologia **33**; 185-202.

Upton, N. P. D. (1987). Asynchronous male and female life cycles in the sexually dimorphic, harem forming isopod, *Paragnathia formica* (Crustacea: Isopoda). J. Zool. **212**: 677-690.

Vakamoce, V. C. (1987). Seasonal changes in the large brown algal vegetation and the associated marine invertebrates on a fringing reef, Magnetic Island, GBR region, Australia. MSc Thesis, James Cook University of North Queensland, Australia.

Van Dolah, R. F. (1978). Factors affecting the distribution and population dynamics of the amphipod, *Gammarus palustris*, in an intertidal salt marsh community. Ecol. Monogr. **48**: 191-217.

Van Emden, H. F., May, M. J. (1972). Host plants in the population dynamics of insects. In: Van Emden, H. F. (ed.) Insect/Plant Relationships pp. 181-200. Symposia of the Royal Entomological Society of London: Number Six. Blackwell Scientific Publications, Oxford.

Vermeij, G. J., 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press, Cambridge, Mass.

Vince, S., Valiela, I., Backus, N., Teal, J. M. (1976). Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution. J. exp. mar. Biol. Ecol. **23**: 255-266.

Virnstein, R. W., Curran, M. C. (1986). Colonization of artificial seagrass versus time and distance from source. Mar. Ecol. Prog. Ser. **29**: 279-288.

Virnstein, R. W., Howard, R. K. (1987a). Motile epifauna of marine macrophytes in the Indian River lagoon, Florida. I. Comparisons among three species of seagrasses from adjacent beds. Bull. Mar. Sci. **41**: 1-12.

Virnstein, R. W., Howard, R. K. (1987b). Motile epifauna of marine macrophytes in the Indian River lagoon, Florida. II. Comparisons between drift algae and three species of seagrass. Bull. Mar. Sci. **41**: 13-26.

Wahl, M. (1989). Marine epibiosis. I. Fouling and antifouling: some basic aspects. Mar. Ecol. Prog. Ser. **58**: 175-189.

Wakabara, Y., Tararum, A. S., Takeda, A. M. (1983). Comparative study of the amphipod fauna living on *Sargassum* of two Itahaém shores, Brazil. J. Crust. Biol. **3**: 602-607.

Walker, T. A. (1981a). Seasonal salinity variations in Cleveland Bay, Northern Queensland. Aust. J. Mar. Freshwater Res. **32**: 143-149.

Walker, T. A. (1981b). Dependence of phytoplankton chlorophyll on bottom resuspension in Cleveland Bay, Northern Queensland. Aust. J. Mar. Freshwater Res. **32**: 981-986.

Walker, T. A., O'Donnell, G. (1981). Observations on nitrate, phosphate and silicate in Cleveland Bay, Northern Queensland. Aust. J. Mar. Freshwater Res. **32**: 877-887.

Wallace, A. R. (1878). Tropical Nature and Other Essays. Macmillan, London.

Wallerstein, B. R., Brusca, R. C. (1982). Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). J. Biogeog. **9**: 135-150.

Wallner, W. E. (1987). Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. Ann. Rev. Entomol. **32**: 317-340.

Wanders, J. B. W. (1976). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles) II: Primary productivity of the *Sargassum* beds on the north-east coast submarine plateau. Aquat. Bot. **2**: 327-335.

Weis, J. S. (1968). Fauna associated with pelagic *Sargassum*. Am. Midl. Nat. **80**: 554-558.

White, T. C. R. (1969). An index to measure weather-induced stress of trees associated with psyllids in Australia. Ecology **50**: 905-909.

Wiens, J. A. (1989). Spatial scaling in ecology. Func. Ecol. **3**: 385-397

Wilson, F. (1960). A review of the biological control of insects and weeds in Australia and Australian New Guinea. Tech. Commun. Conmmonw. Inst. biol. **1**.

Wolda, H. (1983). "Long term" stability of tropical insect populations. Res. Popul Ecol. Suppl. **3**: 112-126.

Wolf, N. G., Bermingham, E. B., Reaka, M. L. (1985). Relationships between fishes and mobile benthic invertebrates on coral reefs. In: Reaka, M. L. (ed.)

Ecology of deep and shallow coral reefs pp. 69-78. NOAA Undersea Res. Prog., Rockville.

Womersley, H. B. S. (1954). Australian species of *Sargassum* subgenus *Phyllotrichia*. Aust. J. Bot. **2**: 337-354.

Womersley, H. B. S. (1981). Biogeography of Australasian marine macroalgae. In: Clayton, M. N., King, R. J. (eds.) Marine Botany: an Australasian Perspective pp. 292-307. Longman Cheshire, Melbourne.

Womersley, H. B. S. (1987). The Marine Benthic Flora of Southern Australia. South Australian Government Printing Division, Adelaide.

Woodland, D. W. (1991). Contemporary Plant Systematics. Prentice-Hall, New Jersey.

Wootton, R. J. (1990). Major insect radiations. In: Taylor, P. D., Larwood, G. P. (eds.) Major Evolutionary Radiations. Systematics Association Special Volume **42**: 187-208.

Yeo, P. F. (1972). Floral allurements for pollinating insects. In: Van Emden, H. F. (ed.) Insect/Plant Relationships pp. 51-58. Symposia of the Royal Entomological Society of London: Number Six. Blackwell Scientific Publications, Oxford.

Yoshida, T. (1983). Japanese species of *Sargassum* subgenus *Bactrophycus* (Phaeophyta, Fucales). J. Fac. Sci. Hokkaido Univ. Ser. 5 (Botany) **13**: 99-246.

Young, A. M. (1979). Notes on a population outbreak of the beetle *Uroplata* sp. (Coleoptera: Chrysomelidae) on the tree *Bunchosia pilosa* (Malpighiaceae) in Costa Rica. J. NY Entomol. Soc. **87**: 289-298.

Young, D. K., Buzas, M. A., Young, M. W. (1976). Species density of macrobenthos associated with seagrass: a field experimental study of predation. J. Mar. Res. **34**: 577-592.

Young, P. C. (1981). Temporal changes in the vagile epibenthic fauna of two seagrass meadows (*Zostera capricornii* and *Posidonia australis*). Mar. Ecol. Prog. Ser. **5**: 91-102.

Zimmerman, R., Gibson, R., Harrington, J. (1979). Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. **54**: 41-47.