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Feeding biology of the Crown-of-Thorns Starfish, *Acanthaster planci* (Linnaeus)

Thesis submitted by

John Kenneth KEESING BSc(Hons)

in March 1990

for the degree of Doctor of Philosophy in

the Department of Zoology at

James Cook University of North Queensland

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ABSTRACT

Field and laboratory studies were undertaken to examine aspects of the feeding biology of _Acanthaster planci_ (Linnaeus) in the central region of the Great Barrier Reef. Day and night surveys were carried out to examine feeding periodicity, and measurements of feeding and movement rates were made by monitoring tagged animals. Diet and feeding preferences were assessed in the field and laboratory studies were undertaken to assess the importance of nutritional quality of food in governing feeding preferences.

Small starfish feed nocturnally and remain cryptic during the day. Large starfish are primarily diurnal feeders and are rarely cryptic. Starfish are most mobile around dawn and dusk. It is proposed that the observed behaviour patterns have evolved as a predator avoidance strategy with large starfish achieving a refuge in size. These size dependent behavioural patterns, together with changes in population size structure, have important implications for assessing the numbers of starfish remaining undetected in _A. planci_ survey and control programs.

Rates of movement in _A. planci_ are dependent on food availability. These are about 1 $m.day^{-1}$ in areas of high coral cover and about 4 $m.day^{-1}$ in patches of low coral cover. Starfish in extensive areas of depleted coral cover move at rates of about 10 $m.day^{-1}$.

Feeding rates in _A. planci_ are dependent on starfish size and season, being greatest prior to the summer spawning season. Starfish at Davies Reef in summer averaged 1.5 feeds per day, killing about 300 cm^2 of coral cover or 15 g DW (dry weight) of soft coral tissues per day. Biomass utilization is about 4 g DW or 90 kJ per day. Feeding rates in winter are about half those of summer.

Feeding rate measurements were applied to ecological and physiological considerations in A. planci. The magnitude of changes to coral communities in terms of area and biomass of coral killed during A. planci outbreaks is substantial. Outbreaking populations (ca. 100000 starfish per reef) will kill thousands of square metres of coral; equivalent to hundreds of kilograms dry weight of soft tissues per day. Feeding rate measurements were used to predict a threshold population level of about 1000 starfish per km^2 which would cause minimal damage to coral communities on the Great Barrier Reef. It is evident that large scale fluctuations in A. planci populations can occur without causing extensive coral mortality. Comparison of physiological requirements with feeding rates confirms that, despite increased feeding rates in large adults, growth is determinant and senility of large A. planci can be expected. As suggested in previous studies, this occurs because as the starfish grows its capacity to feed cannot meet the demands of metabolising tissue.

The diet of A. planci is almost exclusively scleractinian corals (90 - 95 %). Non-coral prey are taken in increasing abundance in areas of low coral availability. A. planci exhibits strong feeding preferences in both the field and the laboratory. The scleractinian families Acroporidae and Pocilloporidae are most favoured. Non-preferred prey are taken in increasing abundance in areas depleted of favoured species. The nutritional value of different species of coral prey was assessed and related to the observed feeding preferences. Several attributes may affect a coral species suitability as food; these are surface area complexity, biomass, nutritional value and abundance. Prey preference was more closely related to a general assessment of food suitability than to the absolute predictions of optimal diet theory. It is proposed that the ability to feed more efficiently on certain prey types is the most important factor giving rise to observed and published patterns of prey selection.

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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. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

J K Keesing
7 March 1990

CHAPTER ONE

GENERAL INTRODUCTION

Acanthaster planci: the crown-of-thorns starfish

Acanthaster planci (Linnaeus) is a large, predatory asteroid which feeds almost exclusively on scleractinian corals. The species is distributed on coral reefs throughout the Indo-Pacific region but is absent from the Caribbean and other parts of the Atlantic. Population outbreaks of A. planci have led to concern amongst the public and scientific communities due to the resultant extensive coral mortality.

As a result of this notoriety, A. planci has become one of the most studied coral reef organisms, being the subject of several hundred recent scientific papers and numerous reviews. The most recent, and comprehensive of these reviews is that of Moran (1986) (see also Moran, 1988).

Debate about the reasons behind population outbreaks of A. planci has generated much of this literature. However, whatever the cause of the observed large scale fluctuations in population size, it is fundamentally the feeding behaviour of the animal that constitutes the basis of our concerns. Other echinoderms exist at high population densities in tropical areas, i.e. some other asteroids (Oreaster reticularis 2 - 7 m^{-2}; Scheibling, 1980; Archaster typicus up to 160 m^{-2}; Mukai et al., 1986), echinoids (Echinometra mathaei 30 m^{-2}; Downing and El-Zahr, 1987; Diadema antillarum 71 m^{-2}; Sammarco, 1980) and holothuroids (Holothuria leucospilota up to 14 m^{-2}, H. atra up to 6 m^{-2}; Massin and Doumen, 1986); yet they do not generate the same consternation. This is due to differences in the trophic interactions between other echinoderms, such as those above, and their mainly detrital or algal food sources and

A. planci and its prey, the scleractinian corals. Because A. planci is the only carnivorous coral reef echinoderm, with the potential to outbreak (increase population size rapidly and dramatically) and devastate coral communities, study of its feeding biology and ecology is fundamental to understanding its influence on coral reef ecosystems.

Asteroid feeding biology and ecology

Asteroids and echinoids make up the most researched groups of echinoderms (Sloan, 1980) and many of these studies have involved the feeding biology of asteroids. Studies such as those of Paine (1966; 1969; 1971), Mauzey et al. (1968), Dayton et al. (1974), Birkeland (1974), and Menge (1972) have established the importance of asteroids in determining and regulating the structure of benthic communities.

It is the predatory nature of asteroids which constitutes their importance in the organisation of benthic communities. Not only do predators limit the range and population size of their prey, but the interaction between the predator and its prey is important to the maintenance of populations of other components of the community (Paine, 1966). As such, much research has been directed at examining the effects of asteroid feeding on the environment and the organisation of benthic communities (Menge, 1982).

Predatory asteroids

Analysis of the review of asteroid diets by Jangoux (1982a) reveals that, of 236 asteroids, 184 (78 %) were primarily predatory carnivores. Most of the remainder were detritivores (Goniopectinidae and Porcellanasteridae), substrate feeders (mainly Ophidiasteridae), algivores (some Asterinidae) or scavengers. In an earlier review, Sloan (1980) examined the diets of 112 species of asteroids. Only

19 of these were not primarily predatory in their feeding behaviour.

Experimental removal of asteroid predators has demonstrated the profound effect they have on community structure. Paine (1971) showed how removal of an important asteroid predator, *Stichaster australis*, resulted in a 40 % increase in the area occupied by the asteroid's principal prey (a mussel) and a 30% reduction in species richness of other fauna in the habitat. Similarly, when *Pisaster ochraceus* was removed from a rocky intertidal habitat, its principal prey, a mussel, expanded its range and excluded algae; the lack of which in turn displaced grazing molluscs from the habitat (Paine, 1966). Where asteroids are predators upon other asteroids (tertiary consumers) then more complex patterns of population regulation occur in the community. One such case is *Tethyaster vestitus*, which regulates populations of other asteroids and hence, in turn, their molluscan prey (Penchaszadeh and Molinet, 1983).

Large increases in the population size of predatory asteroids can also have a significant effect on community structure. *Asterias forbesi* (north-east USA) and *A. rubens* (northern Europe) undergo large scale changes in population size and are regarded as pests due to extensive aggregative feeding on oyster beds (Sloan, 1980). Despite the importance of *Asterias* species, few studies of their impact on subtidal community structure have been undertaken. Lubchenco and Menge (1978) found *A. forbesi* to be an important predator in the lower intertidal zone and Menge (1982) produced some evidence, although equivocal, that *A. forbesi* regulates mussel populations in subtidal areas. Anger *et al.* (1977) examined the diet and feeding rate of *A. rubens* at very high population densities (up to 800 m^{-2}) and concluded that this species was a significant predator of benthic organisms. Unfortunately, they provided little information on the impact of such feeding on the environment.

Amongst those asteroids which undergo large scale fluctuations in population density, and whose feeding activities have a profound effect on community structure, A. planci is by far the best studied (see above). The impact of feeding by outbreak populations of A. planci has been described as an ecocatastrophe (Endean and Cameron, 1985). Reports of coral mortality as a result of A. planci predation are widespread (see Moran, 1986 for review). These typically document drastic reductions in both coral cover and diversity. Whilst some studies have shown that coral recovery is relatively rapid and complete 10 - 15 years following outbreaks (Pearson 1981; Colgan, 1982, 1987), other research has suggested that the slower growing components of the reef community (e.g. poritids and faviids) may take from several decades to a century in recovering to pre-outbreak levels (Endean et al., 1988; Done et al., 1988).

Changes to components of coral reef biota other than hard corals have been recorded in the wake of A. planci outbreaks. A reduction in fish species richness, particularly obligate coral feeders and coral dwellers, has been recorded as a consequence of A. planci depredation of coral reefs (Sano et al., 1984, 1987; Williams, 1986). Sano et al. (1987) demonstrated significant reductions in numbers of species and individuals of all trophic groups of fishes two years after reef devastation by A. planci.

Diets of predatory asteroids

Asteroids have been found to feed on most groups of benthic organisms (see Sloan, 1980; Jangoux, 1982a for reviews of asteroid diets) and even some nektonic animals (Mauzey et al., 1968, Anger et al., 1977). Ten asteroid species are known to feed on hard corals. The reviews of Sloan (1980) and Jangoux (1982a) list eight of these. Other than A. planci, only Culcita novaeguinea feeds primarily on hard corals (Goreau et al., 1972) and Glynn and Krupp (1986) noted that selective feeding by C. novaeguinea may have an influence on coral reef communities. No other asteroid species appear to be important corallivores. Culcita schmideliana is known to prey upon hard corals, but is generally omnivorous, feeding on algae, sponges, soft corals and ascidians (Thomassin, 1976). Observations of Linckia laevigata feeding on hard corals are limited to two observations by Laxton (1974). It is unlikely that L. laevigata has the potential to be a significant corallivore due to its small stomach size and lack of prehensile ability resulting from a rigid body wall (Birkeland, 1989). Yamaguchi (1975) found an Asterina species feeding in aggregation on Acropora echinata and the other asteroids recorded as feeding on coral are Tessellaster nobilus and Plinthaster dentatus (Jangoux, 1982a), Pharia pyramidata (Dana and Wolfson, 1970) and Nidorellia armata (Glynn and Wellington, 1973). Two other species, Nardoa variolata and Echinaster purpureus, are recorded as feeding on coral mucus (Thomassin, 1976). Sloan (1980) cites Toponce (1973) as referring to Oreaster occidentalis feeding on corals. In fact, the popular article by Toponce makes reference only to feeding on algal fragments.

The small number of corallivorous asteroids is surprising considering the comparatively large number of other predatory asteroids with specialized diets, such as those feeding on other echinoderms, bivalve molluscs and sponges (Sloan, 1980). In contrast to A. planci being the only obligate coral feeding asteroid, there are numerous asteroid predators of sponges. Sloan (1980) lists 29 species of starfish as feeding on sponges, seven of these from tropical waters.

Whilst *A. planci* has been considered a highly specialized predator (Cameron, 1977) due its almost solely scleractinian diet and ability to digest wax-based energy resources in corals (Benson *et al.*, 1975), other asteroids are in fact far more specialized with regards to diet. *Acanthaster planci* is known to feed on many species of corals, and indeed many genera (Pearson and Endean, 1969; Ormond *et al.*, 1976), whilst some asteroids feed almost exclusively on one prey species. *Perkinaster fuscus antarcticus* for example feeds almost solely on one species of sponge (Dayton *et al.*, 1974).

Feeding mechanisms

Whilst non-predatory asteroids are mostly extra-oral feeders, eg. the deposit feeder *Oreaster reticularis* (Scheibling, 1980; 1982), predatory starfish can be either intra- or extra-oral feeders. Some species can feed utilizing both mechanisms (Jangoux, 1982a).

McClintock *et al.* (1983) described extra-oral feeding as an advanced attribute and Jangoux (1982a) has split extra-oral feeders into two categories: those bivalve mollusc feeders which can evert their stomach between the valves of prey after forcing them apart, and those which can only feed on encrusting organisms or those with their tissues exposed. *Acanthaster planci* is clearly in the latter class of extra-oral feeders, feeding by everting its stomach through the oral cavity and spreading it over the surface of the coral using its tube feet (Barnes *et al.*, 1970). Jangoux (1982a) noted that the stomach of *A. planci* was "extraordinarily large", implying that *A. planci* has a greater feeding capacity than other asteroids. *Culcita novaeguinea* has a smaller stomach and a lower feeding rate than *A. planci* despite having a similar biomass (Glynn and Krupp, 1986;

Birkeland, 1989). This suggests that different energetics or feeding efficiencies occur between these species; however, this remains to be investigated.

Feeding behaviour

i. Feeding rhythms

Daily and seasonal patterns of activity have been recorded for many species of asteroids. Daily behavioural patterns are generally governed by tidal cycles or by phototactic behaviour.

Soliman et al., (1986) showed that feeding activity in Asterina minor was governed primarily by tidal cycles, with temperature and light having little influence on behaviour. However, many asteroids are nocturnal feeders. Astropecten latespinous is nocturnal, remaining buried during day, and emerging to forage at night (Nojima and Doi, 1977). Similar behaviour has been observed in Luidia sarsi (Fenchel, 1965). Other asteroid species are crepuscular (e.g. Astropecten polyacanthus; Mori and Matsutani, 1952). These behaviours may have evolved in response to patterns of prey availability. For example, Luidia clathrata was conditioned to associate darkness with food (McClintock and Lawrence, 1982). Lawrence (1987) has also suggested that predator avoidance may play a role in governing daily behaviour patterns; this has been demonstrated for the sea urchin, Centrostephanus coronatus (Nelson and Vance, 1979) and suggested for some tropical holothurians (Hammond, 1982).

Due to a lack of detailed empirical data on diel feeding behaviour, there is considerable conjecture as to whether A. planci shows any clear feeding periodicity. Much of the literature suggests that the daily mode of feeding is dependent on starfish density. Pearson and Endean (1969) and Endean (1974) stated that A. planci on the Great

Barrier Reef generally feed during the day when present in high densities, but that in "normal" (low density) populations *A. planci* remain cryptic during the day and feed mainly at night. Chesher (1969) and Cheney (1974) observed similar behaviour of *A. planci* in Guam and Branham *et al.* (1971) noted that "the majority" of *A. planci* were actively feeding during the day in an aggregated population in Hawaii. However, none of the above authors presented any quantitative data on the proportions of animals feeding during the day and night.

Conflicting reports on the feeding mode of *A. planci* have come from the Red Sea area, Australia and California. Goreau (1964) described *A. planci* as a "nocturnal predator" with feeding sometimes continuing to 0900 hours, and Ormond and Campbell (1974) found *A. planci* to be nocturnally active independent of density, whilst diurnal feeding of *A. planci* has been observed among low density populations both in western Australia (Wilson and Marsh, 1975) and the Gulf of California (Dana and Wolfson, 1970).

There are few records of observations of behaviour of juvenile *A. planci* in the field. Zann *et al.* (1987) noted that juveniles in Fiji remained cryptic and fed nocturnally until they were about 20 months old, at which time feeding became aggregative and diurnal.

Seasonal patterns of behaviour in some species of asteroids have been recorded. Seasonal patterns in feeding are influenced mainly by temperature, salinity, food availability or reproductive activity. Menge (1972) found that the feeding rate of *Leptasterias hexactis* decreased in winter months and that seasonal changes in diet also occurred. These changes were found to be related to food availability, with *L. hexactis* feeding more selectively when food was abundant (Menge, 1972). MacKenzie (1969) noted that *Asterias forbesi* increased its feeding rate from winter to summer and he demonstrated that feeding rate was related to water temperature. MacKenzie (1969) also noted a brief decrease in feeding rate associated with summer spawning in A. forbesi. Similar behaviour has been observed in Asterina minor which has been shown to undergo a seasonal decrease in feeding rates during winter and its summer spawning period (Soliman et al., 1986).

Seasonal variability in behaviour in A. planci has not been studied. However, Wilson and Marsh (1975) noted that low rates of feeding observed amongst starfish in summer, in shallow water, may have been due to thermal stress.

ii. Aggregative feeding

Although some echinoderms form aggregations during spawning, most aggregations are related to feeding (Reese, 1966). Feeding aggregations have been recorded in both predatory and non-predatory asteroids.

Scheibling (1980) noted feeding aggregations up to 7 individuals m^{-2} of the deposit feeder, Oreaster reticularis. Under these conditions animals overlapped and there was competition for the organically rich sediments. Amongst predatory asteroids several exhibit high density feeding on mussel beds (e.g. Asterias rubens at 300 - 400 individuals m^{-2} [Dare, 1982]). Anasterias rupicola also participates in aggregative feeding (up to 171 m^{-2}), although this species is unusual in that such aggregations may involve a number of individuals feeding on a single prey item (usually a limpet) (Blankley, 1984; Blankley and Branch, 1984).

Sloan (1980) reviewed information on aggregation in A. planci and suggested that a number of biological and physical factors may act synergistically to bring about large aggregations of A. planci. Aggregation in A. planci has been linked to both reproductive behaviour and feeding.

Beach et al. (1975) suggested a spawning pheromone may be responsible for attracting conspecifics during the reproductive season. Acanthaster planci is known to be attracted to coral tissue extracts (Ormond et al., 1973) and Ormond and Campbell (1974) found that A. planci was strongly attracted to the feeding activity of other starfish. Dana et al. (1972) suggested that A. planci may aggregate in response to food shortages following severe storm damage of reefs.

Food perception, prey preference and optimal foraging theory

Unlike the rheotactic responses of filter feeding echinoderms, such as crinoids, asteroids appear to rely very little on physical stimuli to detect food (Sloan and Campbell, 1982). Gustatory stimuli upon prey encounter and olfactory chemical stimuli are thought to be the most important agents of food perception in asteroids (Sloan and Campbell, 1982). Castilla and Crisp (1970) demonstrated how A. rubens showed attractant and avoidance responses to water currents passed over prey and predator species, respectively. Much of the work carried out on chemoreception in asteroids has been done on A. planci. Brauer et al. (1970) were able to induce a feeding response (stomach eversion) in A. planci using crude coral extracts. Later, Collins (1974; 1975a; 1975b) and Hanscomb et al. (1976) isolated from corals various protein fractions that would produce a series of feeding and avoidance responses in A. planci.

Food perception is also related to prey choice and learned behaviour. Little is known of the role of "ingestive conditioning" (Wood, 1968), whereby an animal's food preferences are related to previous experience. This has been demonstrated in some species of asteroids (Landenberger, 1968; Castilla, 1972) including A. planci.

Ormond *et al.*, (1976) showed that *A. planci* would accept a normally non-preferred prey genera (*Fungia*) over its preferred prey (*Acropora*) after the starfish had been "conditioned" on *Fungia* for two months. The authors noted that the "ingestive conditioning" they observed could be responsible for giving rise to observed preference of *A. planci* for the most common coral prey species in the field (Red Sea). Ormond *et al.* (1976) suggested that nutritional value and nematocyst defences of prey may also be important in determining prey preferences. Thus, some studies have shown that *A. planci* preferentially selected prey species that were uncommon. Branham *et al.* (1971) found that *A. planci* in Hawaii fed preferentially on *Montipora verrucosa* although this species comprised only 5% of the available coral cover. The conflicting results of Ormond *et al.* (1976) and Branham *et al.* (1971) suggest that both "ingestive conditioning" and nutritional value of prey may be important in determining food preferences. For example, in the study of Branham *et al.* (1971) although the preferred prey species made up only 5% of the total coral cover this was still the second most abundant species (*Porites compressa*). Ormond *et al.* (1976) believed *Porites* to be of low nutritional value. Glynn and Krupp (1986) found that the preferred coral prey species of *Culcita novaeguinea* was the species that could be best utilized by the starfish in terms of tissue extraction.

Several studies have been carried out to examine the importance of nutritional value of prey type on feeding preferences in asteroids, and have tried to relate this to cost-benefit analysis or optimal foraging theory (MacArthur and Pianka, 1966) [Schoener (1971), Krebs (1978), Hughes (1980) give reviews of the theory of optimal foraging]. Several asteroids have been shown to exhibit characteristics of behaviour consistent with optimal foraging theory. Most of these studies have been carried out on predatory asteroids, although the deposit feeder

Oreaster reticularis has been shown to optimize its distance and direction of movement to maximize food utilization (Scheibling, 1981). Prey species selection in Asterias rubens (Allen, 1983) and prey size selection in Pisaster ochraceus (McClintock and Robnett, 1986) have been demonstrated to be "cost-benefitting" feeding behaviours. Functional response to food availability (density dependent predation) in asteroids has also been demonstrated (e.g. L. clathrata, McClintock and Lawrence, 1981).

There have been few field studies of optimal foraging in asteroids with the exception of Scheibling (1981) and Campbell (1984). The latter author found that movement in Asterias forbesi was random and did not comply with optimal foraging theory. However, Campbell (1984) did not examine other aspects of foraging in A. forbesi, such as prey selection.

Reese (1966) reviewed the early work on learned behaviour in echinoderms and concluded that at least temporary behaviour modification in response to experience had been demonstrated. Much of this work involved inducing avoidance behaviour in certain situations through "punishment" and did not relate to feeding behaviour. More recently Valentincic (1983) demonstrated that Marthasterias glacialis would learn to avoid a food model which delivered a mild electric shock when the starfish approached to feed.

The work of Ormond et al., (1976) on learned response in A. planci and its relationship to food selection is discussed above; however, little is known about the "memory" or learned retention period in echinoderms.

Feeding rate and digestion

Studies of feeding rates in asteroids (see Jangoux, 1982a for recent review) have generally been expressed in terms of the number of prey items per starfish per day, or as a weight fraction of the starfish biomass per day. The former method is of limited use as it does not allow for interspecific comparisons and does not account for the contribution of prey size or mixed species prey diets to variability in feeding rates. Feeding rates in terms of biomass are far more meaningful; however, potential differences in food value between prey species place limitations on the use of this method in interspecific comparisons. Feeding rates in terms of energy or net carbon transfer would allow more meaningful interspecific comparisons and more useful intraspecific analysis of predator size/age effects on feeding rates. Lawrence (1984) has expressed the need for physiological and feeding studies on echinoderms to use common units (energy) to allow direct comparisons between species.

To date the feeding rate in A. planci has been expressed in terms of the planar area "coral cover" eaten in the field (Pearson and Endean, 1969; Dana and Wolfson, 1970; Glynn, 1973) or weight of coral skeleton from which the tissue is eaten in the laboratory (Yamaguchi, 1974). Feeding rates in terms of "coral cover" may be of use in calculating the extent of damage caused by A. planci, but have little biological meaning and coral skeletal weight measurements are unlikely to permit comparisons between coral prey of different morphologies or skeletal densities. A far more useful approach would be the measurement of feeding rate in terms of biomass of coral tissue or energy ingested.

Digestion time in extra-oral feeding asteroids has been defined as "the interval between stomach eversion and the release of indigestible remains" (Jangoux, 1982a). Digestion in A. planci has been recorded as taking several hours (Goreau, 1964); however, there is no information on the effect of prey size or type on digestion time in A. planci. Predictably, prey size has been shown to affect digestion times in asteroids. Rosenthal and Chess (1972) found that *Dermasterias imbricata* took longer to digest large urchins than smaller prey of the same species. Prey (bivalve) size was also found to be an important factor affecting digestion time in *A. rubens* (Anger *et al.*, 1977), and Jangoux (1982a) noted that temperature is likely to affect digestion times in asteroids, but this is yet to be demonstrated.

Digestion of coral tissue by *A. planci* takes place externally with the stomach secreting digestive enzymes over the area covered by the stomach. Jangoux (1982a) stated that digestion time in extra-oral feeding asteroids should vary with the amount of substrate able to be covered by the stomach. The digestive enzymes of *A. planci* (mainly wax esterases) have been described by a number of workers. Moran (1986) has reviewed these descriptions in detail.

This study

This study seeks to expand our present knowledge of the feeding biology of *A. planci*. The first objective was to identify any daily behavioural patterns. This was done by making detailed day and night observations of starfish within one population. The conjecture about daily behaviour patterns in *A. planci*, referred to above, has resulted from lack of such detailed observations. Temporal variation in behaviour characteristics was also examined. Other potential factors affecting behaviour, such as food availability, depth and starfish distribution, were also examined and the mechanisms giving rise to observed behaviour patterns are discussed.

The second major objective of this study was to measure feeding rates in *A. planci* in the field. This was done by monitoring the behaviour of tagged starfish which were subsequently subjected to minimal disturbance. Feeding rates were measured in terms of biomass and energy, as well as the (more usual) area of coral eaten. This has enabled the ecological and physiological implications of feeding rates to be considered.

The field studies on behaviour and feeding rate provided a large sample description of diet and feeding preferences. This was analysed to assess the influence of food availability on diet and feeding preferences. The nutritional quality of different coral prey species was then examined with the aim of relating this to feeding preferences and assessing the importance of this factor in governing prey preferences.

The ecological and management implications arising from the research are discussed and suggestions are made for future research into the complex behaviour and feeding ecology of this extraordinary starfish.

CHAPTER TWO

Temporal patterns in the feeding and emergence behaviour of Acanthaster planci.

INTRODUCTION

Despite numerous studies on the biology and ecology of Acanthaster planci there is conjecture in the literature as to whether feeding activity is diurnal, nocturnal or continuous. Additionally there is little information on the main factors governing behaviour of individuals or populations.

The majority of studies portray A. planci as a nocturnal predator remaining cryptic during the day when present on reefs at normal, or low densities, but that in aggregated, outbreaking populations feeding takes place day and night (Pearson and Endean, 1969; Chesher, 1969; Branham et el, 1971; Endean, 1974; Cheney, 1974). However, there have been few studies undertaken at night and information conflicting with the above general view has been presented by a number of workers. Ormond and Campbell (1974) found feeding activity in A. planci to be nocturnal and independent of density in the Red Sea. Moreover, diurnal feeding of A. planci has been observed among low density populations in western Australia (Wilson and Marsh, 1975), Mexico (Dana and Wolfson, 1970) and Panama (Glynn, 1973).

Few of the above authors presented any quantitative data on the proportions of animals feeding during the day and night and only Ormond and Campbell (1974) monitored individual starfish over a 24 hour period (see also Crump (1971) in Roads and Ormond, 1971). There have been few observations of behaviour of juvenile A. planci in the field. However, Zann et al. (1987) noted that a large population of juvenile A. planci in Fiji remained cryptic and fed nocturnally until they were about 20 months old when feeding became aggregative and diurnal.

This study sought to identify temporal patterns of behaviour in A. planci and the factors governing these at a population level.

MATERIALS AND METHODS

Field Studies

Wheeler Reef (18° 47' S, 147° 28' E) in the central Great Barrier Reef region (figure 1) was studied because of the presence of large numbers of A. planci and reasonably good coral cover, thus guaranteeing the persistence of the starfish population for the duration of the study.

Surveys of starfish behaviour were made during October 1986, January and June 1987. SCUBA assisted surveys were made along the back (leeward side) and flanks of the reef (see figure 1) at different times of the day and night over three to six day periods. Eight surveys were conducted in October, 13 in January and 9 in June. During each survey, one or two pairs of divers carefully searched an undefined area around the boat collecting data on as many starfish as possible. Each dive was made in a different area to those previous to ensure no starfish disturbed in previous dives were included in the samples. All A. planci encountered were measured (maximum diameter, to nearest cm) and their activity (feeding, stationary or moving) and behaviour (cryptic or non-cryptic) was recorded. Starfish were regarded as feeding if their stomach was everted over coral or other substrate and moving if active locomotion was observed when the starfish was encountered. Starfish were judged cryptic if they were located in crevices, under coral or ledges or deep in staghorn thickets. Non-cryptic starfish were those located out in the open or generally visible from above. Habitat data such as depth and reef substratum type were also recorded for each starfish, and live coral abundance in the immediate area (ca. 5 m radius around starfish) was visually assessed and placed into one of six categories [after Crown of thorns study (1985)]; i.e., 0, none; 1, a little, 1 - 10 %; 2, some, 10 - 30 %; 3 nearly half, 30 - 50 %; 4, more than half, 50 - 75 %; and 5, almost all, 75 - 100 %. The distribution of the starfish was also recorded. Starfish were designated: solitary if there were no others within view in the area; evenly distributed, if more than one was visible; or aggregated if two or more starfish were within one metre of each other.

During the January expedition light levels were measured at different times of the day and at different depths during the surveys using a submersible selenium photocell instrument (Drew, 1983) calibrated with a photometer (model LI-188B, Li-Cor Inc.).

Statistical procedures

Starfish were allocated to one of three size categories < 20 cm, 20 - 39 cm and $\geq$40 cm, for analyses of activity patterns. There were physiological and growth considerations in selection of these size classes. Maturity occurs at about two years or 20 cm (Lucas, 1984; Yamaguchi, 1974a) and there is evidence from laboratory studies that senility occurs in older adult (large) A. planci (Lucas, 1984). Because age is not always related to size, and growth is known to slow in adult A. planci (Lucas, 1984), it was thought that choosing $\geq$40 cm as a size class would ensure these starfish were at least three and probably more than four years old, thus separating young and older adults.

For statistical comparison of diver search efficiency and the levels of feeding and cryptic activity between day and night, samples (dives) were divided into four groups: morning, 0400 - 0800 h; day, 0800 - 1600 h, evening, 1600 - 2000 h and night, 2000 - 0400 h. Due to time limitations and unfavourable weather in October 1986 and June 1987, only one morning sample and two evening samples were made in each of these months. For this reason, analyses were mostly limited to day/night comparisons. Unless specified otherwise, comparisons were made with analyses of variance (ANOVA's) and Student's t-test. Tukey's HSD test (Zar, 1984) was used to contrast significant factors from the ANOVA. Where main factors in the analyses were subsumed in significant interactions, multiple comparisons were made using ANOVA and tested at Bonferroni levels of significance (two levels of comparison) or Tukey's HSD test (greater than two levels). Cochran's C test (Winer, 1971) was used to compare group variance. Any transformations required to ensure homoscedasticity are outlined in the analyses. Data which could not be satisfactorily transformed to meet the assumptions required for parametric testing were analysed using Kruskal-Wallis and Mann-Whitney tests (Conover, 1980).

Due to the small numbers in some groups requiring comparison, analysis of factors affecting behaviour patterns (i.e. food availability, depth and starfish distribution) were carried out using Chi-square analyses (Snedaker and Cochran, 1967) for analyses with continuous variables and a G-test (Sokal and Rohlf, 1981) where more than two ordinal variables were involved.

Aquarium Studies

Light levels

The fine scale effects of light levels (i.e. small changes in light intensity) on starfish behaviour are difficult to assess in the field because few animals can be observed at one time and light levels change rapidly during the critical crepuscular periods. Thus, the behaviour of animals during this period was examined in aquaria. Two round ponds, 3 m in diameter and 0.6 m deep, with flow-through sea water were used in the experiment. A 1 m^2 area of shelter raised 12 cm off the pond floor was placed in the centre of the pond to provide shaded refuge. Experiments were carried out under natural light which was monitored using the instruments described above. Live coral was placed in the ponds, around the shelter. _Acanthaster planci_ ranging in sizes from 7 - 24 cm (N = 15) and 29 - 37 cm (N = 9), respectively, were introduced to each of the ponds and their activity (feeding, stationary or moving) and location in the pond were recorded at least hourly (but continuously during crepuscular periods) over three days. Night observations were made with a torch covered with a heavy red filter.

Day length manipulation

Behaviour of _A. planci_ was also monitored under conditions of altering day length. Eight 180 litre flow-through sea water aquaria under artificial lighting were used for the experiment. The initial light regime was 11.5 h dark/11.5 h "day-light" (200 $\mu E\ m^{-2}\ sec^{-1}$) with each period of light preceded and followed by 0.5 h "twilight" (5 $\mu E\ m^{-2}\ sec^{-1}$). After two and a half full 24 h cycles, the day length regime was altered to periods of 4 h light and 4 h dark (including a 0.5 h "twilight" period between) for a further 24 h. Lights were controlled by automatic timers.

One A. planci (12 - 18 cm) in diameter was introduced to each aquarium which also contained shelter in the form of 10 cm diameter plastic piping. Starfish were recently collected from the field, but no food was provided during the experiment. Starfish activity and position were monitored in each aquarium once every hour and more frequently immediately prior to, during and after lights turned on or off. Activity was categorised as moving or stationary and position as in or out of shelter.

The percentage frequency of each type of behaviour for each starfish was calculated and then compared with each of three theoretical models of behaviour (see results for details).

RESULTS

Population Size Structure

Population size frequency histograms for each of the three sampling periods are shown in figure 2. Size distribution changed markedly over the nine month course of the study. In October the distribution was bimodal, with peaks of 17 and 47 cm and a mean size of 34.7 cm. In January the size frequency distribution was less strongly bimodal with peaks of 22 and 42 cm and a mean size of 28.6 cm. By June the size structure was unimodal (mean 29.1 cm) with starfish < 20 cm and ≥40 cm making up only 6.6 % and 4.9 % of the population, respectively (table 1.). Comparisons of the mean size of A. planci between consecutive samples required carrying out an approximate t-test (Sokal and Rohlf, 1981) as an F-test revealed unequal variances between samples. The mean size of A. planci differed significantly between October and January ($p < 0.001$) but not between January and June ($p > 0.10$, see also table 1).

Search Efficiency

The number of starfish found per hour of searching time was tested for biases between day and night which may have occurred as a result of differential efficiencies in locating A. planci. As interactions between the months and between size classes were not of interest, a one-way ANOVA was used to test the hypothesis that the number of starfish in each size class found per hour search time was independent of time of day. Significant bias was found only among the <20 cm A. planci in October and January ($p < 0.05$) indicating this size class of starfish was being under-represented in day samples in those months (table 2).

Diel Patterns in Cryptic Behaviour

The proportion of A. planci cryptic in each size class in day and night samples from each month is shown in figure 3 which reveals a size related pattern of cryptic behaviour during the day. At least 80 % of A. planci specimens < 20 cm were cryptic during the day in all months. Indeed, as searching efficiency for these small starfish was significantly less competent during the day than at night, the actual proportion of cryptic small starfish would have been even higher. A large proportion of starfish 20 - 39 cm was cryptic during the day in January (73 %) and June (48 %), but not in October, more than 60 % of animals being non-cryptic during both day and night. Large A. planci (≥40 cm) showed no clear pattern of diel behaviour with most being non-cryptic day and night (see also appendix figures I - III).

The importance of starfish size, time (day/night) and month sampled on cryptic behaviour in A. planci were examined using a three-way fixed factor ANOVA. This model explained most of the variation in cryptic behaviour of A. planci (80.6 % sums of squares accounted for, table 3) .

Starfish size and time (day/night) effects

Starfish size and day/night effect had the greatest influence on cryptic behaviour (table 3). During the day A. planci specimens <20 cm were significantly more cryptic than 20 - 39 cm starfish, which in turn were significantly more cryptic than those ≥40 cm. There was no difference in the extent of cryptic behaviour between sizes at night. Starfish < 40 cm were significantly more cryptic during the day than at night, but there were no diel differences in the cryptic behaviour of starfish ≥40 cm.

Effects of month sampled

The main factor of month sampled had no significant effect on cryptic behaviour, but was subsumed in a highly significant 1st-order interaction with time of day. This interaction is due to monthly changes in the population size structure and not behaviour, as confirmed by the significance and uniformity of the size dependency above. Thus, in any month the trend for all size classes pooled will tend to reflect the trend for the most abundant size class. Overall extent of cryptic behaviour did not vary between months for either day or night samples.

Analysis of within day variation in cryptic behaviour was carried out using a G-test on pooled data within each time period due to the small number of morning and evening samples. Table 4 shows that the proportions of A. planci cryptic (all sizes pooled) varied significantly between morning, day and evening in all months ($p < 0.001$). Starfish were least cryptic in the morning in January and June whilst in October starfish were generally more cryptic in the mornings than during the day. Only animals in

January showed a consistent response over the three size classes, being least cryptic in morning samples (table 4, see also appendix figure IV).

Figure 4 shows the apparent population size structure of *A. planci* at Wheeler Reef during the three months sampled. The apparent population is that proportion which is not cryptic at a particular time. This is typically the proportion of the population able to be observed by a rapid survey technique such as "manta" towing. Figure 4 shows that the proportion of the population cryptic changes over the course of a day and varies between months for a given time of day. For example at 1200 h the proportion of the population cryptic was about 80 %, 35 % and 50 % in October, January and June, respectively. This tends to reflect the combination of size dependant diel behaviour and the changing size structure of the population over time.

Diel Patterns in Feeding Behaviour

Figure 5 suggests a transition from predominantly nocturnal feeding in juvenile *A. planci* to diurnal feeding in large adult ($\geq$40 cm) starfish in the October and January samples (see also appendix figures V, VI and VII). There was an overall reduction in the proportion of starfish < 40 cm feeding in June (large adults were rare at Wheeler Reef in June).

A three-way fixed factor ANOVA was carried out to assess the effect of size, time (day/night effect) and month sampled on feeding behaviour. The model used fitted the data reasonably well, explaining 76 % of the total variance (table 5), but there was a highly significant 2nd order interaction explaining nearly half the variation attributable to the model. All three main effects were significant and two of the 1st order interactions were significant, however only the main effect of month sampled explained more than 10 % of the total variance.

The small number of <20 cm and ≥40 cm A. planci in the June samples and the large variance associated with these samples (see appendix figure VII) may have confounded interpretation of patterns of feeding behaviour. Thus a second three-way ANOVA was carried out on just the October and January data (table 6) whilst between month comparisons were limited to starfish 20 - 39 cm (see table 7). The model fitted in the three factor ANOVA to the October and January data accounted for 79.8 % of the variance and the variance attributable to the second order interaction was reduced to 2.2 % (see table 6).

Starfish size and time (day/night) effects

Although the main factor of starfish size was not significant, it was subsumed in a highly significant 1st order interaction which when broken down revealed significant differences in both size and time within different levels of each (table 6). During the day A. planci ≥40 cm fed at a significantly greater level than those <40 cm. The reverse was true at night with A. planci <40 cm feeding significantly more than larger animals. The proportion of <20 cm A. planci feeding at night was significantly greater than during the day. No significant differences in behaviour between day and night were detected for the 20 - 39 cm size class. Acanthaster planci ≥40 cm were found to feed at a significantly greater degree during the day than at night (table 6).

Effects of month sampled

For all size classes combined there was a significant reduction in the level of day feeding by A. planci between October and January (table 6). Examination of 20 - 39 cm starfish only (table 7) indicates a general reduction in feeding from October through to June. Acanthaster planci in October fed at a significantly greater level than those in both January and June during the day, whilst at night feeding levels in both October and January were significantly greater than June. Significant diel differences in the level of feeding in 20 - 39 cm A. planci were only detected in January.

Diel Patterns in Movement

Figure 6 shows the proportion of A. planci actively moving every half hour over a 24 h period, for the October, January and June samples. Clear pulses of movement around dawn and dusk are evident in all months. The proportions of A. planci moving during morning and evening in January were significantly greater than those during the day and night ($p < 0.001$). Significant differences were also detected in other months (table 8). There were no consistent differences in movement patterns between size classes (see appendix figure VIII).

These periods of active movement correspond to the daily change over between periods of feeding and non-feeding for A. planci. Figure 7 demonstrates this as well as the close relationship between feeding and emergence behaviour.

Factors affecting feeding and emergence behaviour

To analyse the effects of depth, food availability and spatial distribution of starfish on behaviour in A. planci, separate analyses were carried out for each size class and for both day and night samples. This was done because the strong size and day/night effects established above may otherwise mask any significant effects due to other factors, if present. Analyses were carried out on data from

January 1987 only as this was the largest data set and represented all three size classes adequately.

Depth

In an analysis of the effect of depth on the behaviour of A. planci, observations were split into four depth categories; < 3, 3 - 6, 6 - 9 and > 9 meters. No significant effect of depth on cryptic behaviour was detected (table 9, see also appendix figure IX). Incidence of feeding decreased significantly with an increase in depth (sizes pooled, both day and night, table 10, see also appendix figure X).

Assessing the importance of depth effects on starfish behaviour is confounded by the significant inverse relationship between live coral cover and depth found at Wheeler Reef ($p < 0.001$, figure 8). Thus although starfish showed a greater incidence of feeding in the shallower areas, these were the areas with the greatest level of food availability. The size distribution of starfish was also found to be depth dependent ($p < 0.001$) with starfish size increasing directly with depth (figure 9).

Live coral cover (food availability)

The influence of live coral cover on behaviour of A. planci was assessed at < 10 %, 10 - 30 % and > 30 % levels of live coral cover. Starfish tended to be less cryptic in areas of high coral cover, although these effects were only significant for starfish < 40 cm in night samples (table 11, see also appendix figure XI).

Starfish > 40 cm tended to feed at a greater level in areas of high coral cover, but this was only significant in the night sample (all sizes pooled, table 12, see also appendix figures XII).

Starfish distribution (aggregation)

Aggregated starfish tended to be more cryptic than non-aggregated starfish. This effect was only significant among small starfish in night samples (table 13, see also appendix figure XIII), and may reflect a tendency for juveniles to feed concealed within staghorn coral thickets at night. There was no significant difference in the level of feeding in aggregated and non-aggregated starfish (table 14, see also appendix figure XIV).

Light

Ambient light during sunny, cloudless conditions in January 1987 (figure 10) indicate that ambient light at the water surface was about 2000 μE m^2 sec^{-1} in the middle of the day and reduced to about 1200 μE m^2 sec^{-1} at 1 m depth and about 500 μE m^2 sec^{-1} at 12 m depth. The most rapid changes in light levels occurred in the mornings between 0630 and 0900 h and in the evenings between about 1600 and 1800 h. During the crepuscular periods (around 0600 and 1830) there was very little difference in light levels between depths. As the greatest movement activity was found to occur around these times it is unlikely that differences in behaviour with depth during the day will result from different light levels at different depths.

In aquaria the activity cycle of starfish closely followed that of the ambient light (figure 11). Starfish began searching for food and feeding immediately following sunset. Light was not detectable (< 0.1 μE m^{-2} $sec-^{1}$) in the tanks after 1800 h on both nights studied. From 1800 to 1900 h on the first night activity of the large starfish increased from 22 % to 100 %. At the same time the rate of activity of the smaller starfish increased from 6.6 % to 60 % with 93 % of starfish active by 2300 h. All small <u>A.</u>

planci were feeding by 0115 h, about seven hours after sunset. The large starfish were a little slower to reach 100 % feeding on the second night (3 hours) but in general the trend was the same.

It appears that the onset of even very low levels of light will act to inhibit active behaviour (feeding and foraging) in A. planci. Light was first detected (by the equipment used) at 0630 on both mornings and one hour after this the activity rate of small starfish had fallen from 73.3 % to 6.6 %. The large starfish were slower to end their activity period. These patterns were repeated for both large and small starfish on the second morning of the experiment. Starfish which were not feeding generally returned to the shelter when light was first detected, whilst those that were still feeding usually took longer.

Artificially controlled daylength

The responses of A. planci in aquaria to changes in day length were examined and compared to three theoretical patterns of behaviour (figure 12). These were:

I. a pattern of cryptic and emergence behaviour resulting exclusively from light avoidance; i.e. starfish would emerge and forage in periods of darkness and remain hidden in shelters during periods of light. This pattern would be maintained regardless of the length of the lightness and darkness periods.

II. a pattern of cryptic and emergence behaviour governed endogenously, but not independent of periods of light and dark; i.e. starfish would maintain the pattern of behaviour observed under natural lighting levels emerging from shelter to forage around dusk and returning to shelter around dawn, but would respond to any abnormal changes in light levels by avoiding such light.

III. a pattern of cryptic and emergence behaviour governed endogenously, independent of periods of light and dark; i.e. starfish would maintain the pattern of behaviour observed under natural lighting levels emerging from shelter to forage around dusk and returning to shelter around dawn regardless of any changes in ambient light regime.

The rationale of this experiment was to examine whether activity patterns in A. planci are exogenously or endogenously controlled, and to determine whether changes in ambient light patterns would disrupt an endogenous rhythm if present.

Comparing the data to the models

It was predicted that starfish would show their normal nocturnally active behaviour pattern under periods of normal daylength. This was tested over 60 hours of artificially controlled "normal" (12 hour "day"(light)/"night"(dark) cycles before manipulations of day length (4 hour light / 4 hour dark) were introduced.

The normal periods of 12 h dark / 12 h light

As predicted, most starfish remained outside their shelters or actively searched for food during dark periods (88 - 98 % total agreement [TA][1] with models, figure 12) or remained inside their shelter during light periods for the two and a half normal day/night cycles (60 to 69 % TA). Model agreement during the light periods was lower than expected and this was because some starfish moved to the top corners of the tanks, where light levels were only about 30 to 50 $\mu E\ m^2\ sec^{-1}$, for their periods of inactivity, instead of inside shelters.

First period of 4 hours light

After 2.5 normal day/night cycles, what would have normally been a 12 h period of light was limited to only 4 h. All models predicted normal "day" behaviour for this period and the experimental data showed a 63 % TA.

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[1] Percent total agreement (TA) refers to the degree of match between predicted and actual. Percent total disagreement (TD) refers to the degree that the experimental data contradicted that predicted; i.e. if the model predicted animals should be stationary and hidden and 25 % were actively moving in the open, then TD = 25 %.

First period of 4 hours dark

This change occurred four hours into what was a normal "day" period. The experimental data most closely fitted models 2 and 3 (62 % TA). Starfish behaviour did not change as predicted by Model I (starfish should become active if their behaviour was governed by external light levels). 62 % of experimental data was in total disagreement (TD) with model I. The only agreement with model I was due to two animals spending their inactive period outside the shelter. It was concluded that these data provided sufficient grounds to discard model I (exogenous control of behaviour).

Second period of 4 hours light

This period coincided with the last four hours of a "normal" day period. The models predicted standard "day" behaviour, and there was 50 % TA with models II and III and 16 % TD.

Second period of 4 hours dark

This period of darkness coincided with the first four hours of a "normal" night period. Thus, models 2 and 3 predicted standard nocturnal behaviour and the data showed 88 % TA.

Third period of 4 hours light

This period was the first to expose starfish to light during a "normal" night period. Model II predicted standard day behaviour due to light avoidance, whilst model III predicted no change in behaviour, i.e. a continuance of foraging behaviour. The data showed 25 % TA with model II and 75 % TA with model III. Total disagreement with both models was 25 %.

Third period of 4 hours dark

Normal nocturnal behaviour continued following the change to this period (94 % TA with all models).

Thus, model III was the most predictive of A. planci behaviour, indicating strong endogenous control of daily activity patterns which was not over-ridden by light avoidance behaviour. However the data showed that the dark to light changes did cause some behavioural response, probably indicating disturbance.

DISCUSSION

Population Size Structure

The size structure of the A. planci population in the study site at Wheeler Reef changed markedly over the October 1986 to January 1987 period. This was caused by the loss of large starfish from the population and the growth of juvenile animals (<20 cm) into the adult population. Growth of A. planci at Wheeler Reef, as indicated from modal shifts in size frequency, compared very closely with the laboratory growth of reared animals measured by Lucas (1984). After reaching 17 cm (the October 1986 mode in this study) Lucas' animals grew to 24 cm in three months and 30 cm after nine months. Over the same time periods in this study A. planci at Wheeler Reef grew to modal sizes of 22 cm and 27 - 32 cm respectively. Although survey sites were limited mostly to the leeward side of the reef, there was no evidence to suggest that the size structure of the population was different at other sites on the reef. However, rough weather in June 1987 prevented even cursory examination of other sites. Investigation of the cause of the large starfish's disappearance was not the object of this study and has not been further examined. However, rapid change in size structure of an outbreaking A. planci population has been observed previously on the Great Barrier Reef by Moran et al. (1985). Kettle (pers. comm.) observed the same trends in an outbreaking population on Helix Reef and attributed the decline in large animals during summer to mortality, possibly arising from post-spawning morbidity.

Diel patterns of activity in Acanthaster planci

Behaviour of A. planci in this study was found to be strongly size dependant. Small starfish (< 20 cm) were highly cryptic during the day, emerging to feed at night, whilst large starfish (≥ 40 cm) fed diurnally and showed little tendency for cryptic behaviour. Intermediate sized starfish showed a varied response suggesting a transition period. Zann et al. (1987) recently noted a similar change in behaviour of a cohort of A. planci in Fiji as they grew. Previous reports of the times of feeding in A. planci have tended to be conflicting (see Introduction). This has probably resulted from a lack of detailed night observations or consideration of size related and temporal variability.

Asteroids in general show a variety of behavioural patterns. Many species are nocturnal (i.e. Astropecten latespinosus; Nojima and Doi, 1977), some are crepuscular (Astropecten aranciacus and others; Ferlin-Lubini and Ribi, 1978). Still others show no clear patterns of behaviour (i.e. Marthasterias glacialis; Savy, 1987) or their behaviour patterns correspond to tidal cycles (i.e. Asterina minor; Soliman et al., 1986). However, all tend to show characteristics such that observations without a temporal component or size consideration can result in misleading conclusions. For example, Asterias rubens is clearly nocturnal in summer, but becomes mostly inactive in winter when water temperatures fall below 6°C (Thain, 1969); and small A. aranciacus have a much shorter foraging period than large animals (Burla et al., 1972). Behaviour of starfish can also vary between populations of the same species (Ferlin-Lubini and Ribi, 1978) and this possibility cannot be discounted for A. planci on the basis of the data presented here.

Data presented in this study shows daily pulses in the active mobility of A. planci during crepuscular times and these are consistent with the beginning and end of periods of foraging behaviour. This has not been recorded previously for A. planci, although it is known in other asteroids (Burla et al., 1972; Ferlin-Lubini and Ribi, 1978).

Factors affecting behaviour in A. planci

The daily pattern of feeding and emergence behaviour in A. planci was found to be strongly dependent on starfish size. Differences in the behaviour of A. planci between the sampling dates suggested a reduction in feeding rate over the study period rather than a change in pattern of activity. Thus, size dependant and temporal factors explained about 80 % of the observed variability in A. planci behaviour. Other factors considered to affect the behaviour of A. planci are food availability and physiological condition, starfish density and distribution, seasonal effects (e.g. temperature, reproduction), age, exposure to wave energy and light levels (Moran, 1986). The effects of food availability, starfish distribution (aggregative behaviour), depth and light levels on behaviour were examined in this study. An analysis of seasonal effects appears later in this study.

Depth, live coral cover and aggregation were found to have little direct effect on behaviour of A. planci in this study. There were significant trends for greater incidence of feeding in shallower and higher coral areas. However, these two environmental factors are correlated making separation of the effects of each difficult. It is likely that food availability is more important in influencing feeding behaviour than has been possible to demonstrate in this study. Acanthaster planci is highly mobile and there is great difficulty in locating sites where the behaviour of animals from one population can be studied in extremes of low and high coral. The effect of live coral cover on rates of movement is examined later in this study (see chapter 4).

Aggregated A. planci tended to be more cryptic than non-aggregated animals. Cheney (1972) noted that dispersed or isolated A. planci exhibited photonegative behaviour whereas aggregated animals showed no light avoidance behaviour. However, Cheney's observations were based on more than one population, with differing size distributions. Kenchington and Morton (1976) noted that cryptic behaviour in A. planci seemed to be independent of density. The dependence of cryptic behaviour on starfish distribution found in this study may reflect the observation that a large number of aggregated A. planci found in this study were located within large staghorn Acropora colonies. It has been suggested previously that live coral abundance may affect within-reef distribution of A. planci (Moran et al., 1985).

Age of A. planci cannot be accurately determined and is likely to be related to size only over a very large size range (Kettle and Lucas, 1987). As such, it was not possible to determine the effect of age on starfish behaviour. However, differing behaviour between similar sized (intermediate size class) animals suggests an age-effect when the size structure of the population in the different months is compared. Acanthaster planci 20-39 cm in October 1986 and June 1987 showed little diel variability in behaviour. However, in January 1987 when smaller starfish had grown into the 20 - 39 cm size class the behavioural pattern was primarily nocturnal. This suggests a change in behaviour from mainly nocturnal to mainly diurnal occurs at about 30 cm, or some time during the third year of life.

Influence of light levels on behaviour

Behaviour of A. planci in the laboratory was closely related to ambient light levels. A sudden onset of activity of A. planci was observed when light levels fell below detectable limits (0.1 $\mu E\ m^{-2}\ sec^{-1}$) and similarly, the lowest levels of light were sufficient to stimulate starfish to end their foraging and return to shelter. Astropecten latespinosus shows a similar behaviour pattern with a rapid increase in activity after dusk (Nojima and Doi, 1977). In the field the greatest periods of movement in A. planci were during crepuscular periods and thus coincide with low light levels. Previously, Rosenberg (1972) noted that there was a threshold level of light which triggered photonegative behaviour in A. planci, but did not provide details.

In view of the demonstration of strong endogenous control of behaviour in (at least small) A. planci (figure 12), the correlation between light levels and levels of activity in A. planci in the field and laboratory suggest an evolved response to natural light cycles rather than light avoidance behaviour. These results contrast with those of Thain (1969) who found that the diel behaviour of the normally nocturnal Asterias rubens in the laboratory was almost totally light dependant (exogenously controlled). In a similar experiment to that conducted here, Thain was able to stimulate the beginning and cessation of activity simply by turning the lights off and on.

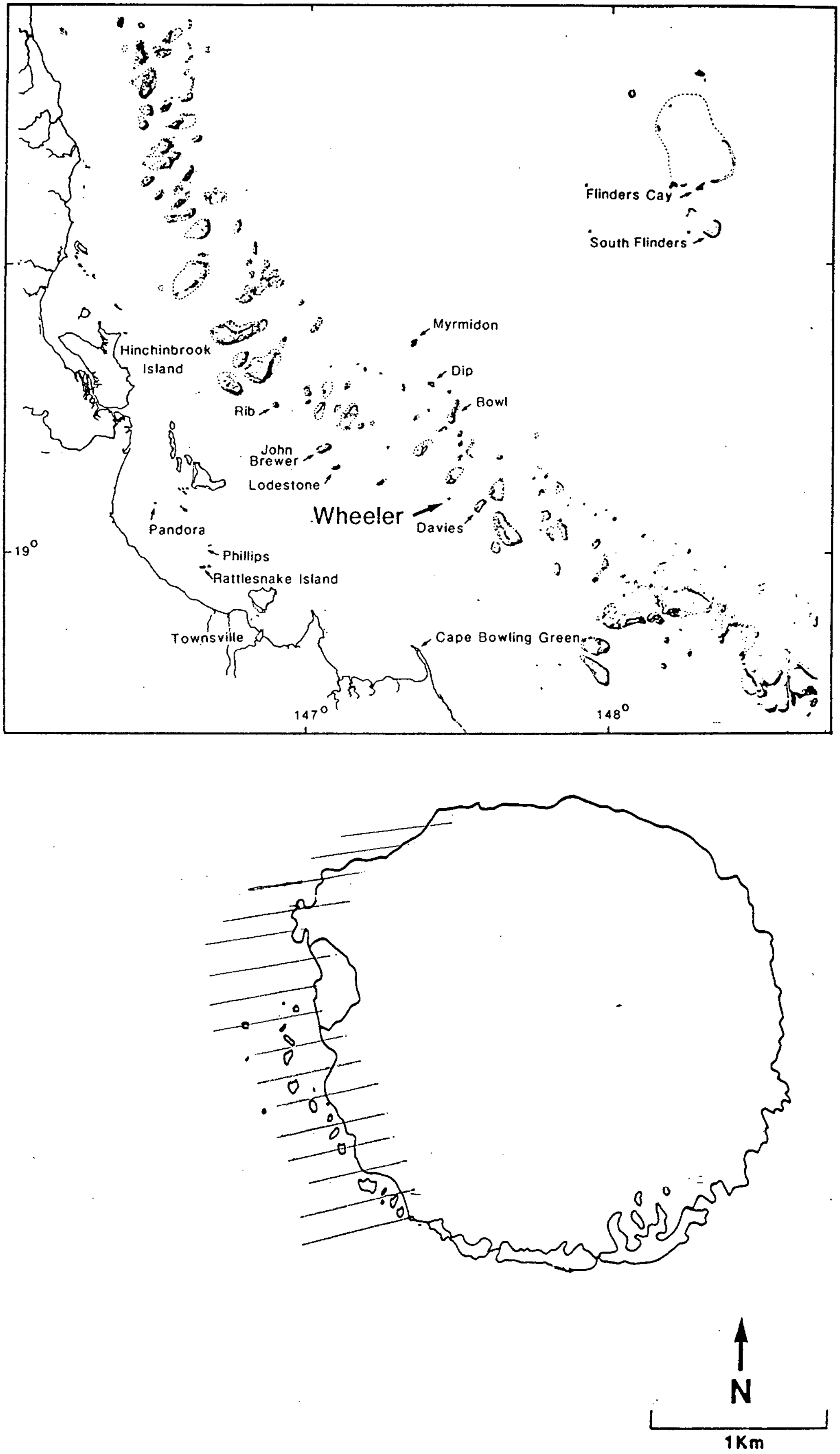

Figure 1. Location of Wheeler Reef and survey sites. The shaded area indicates extent of survey sites.

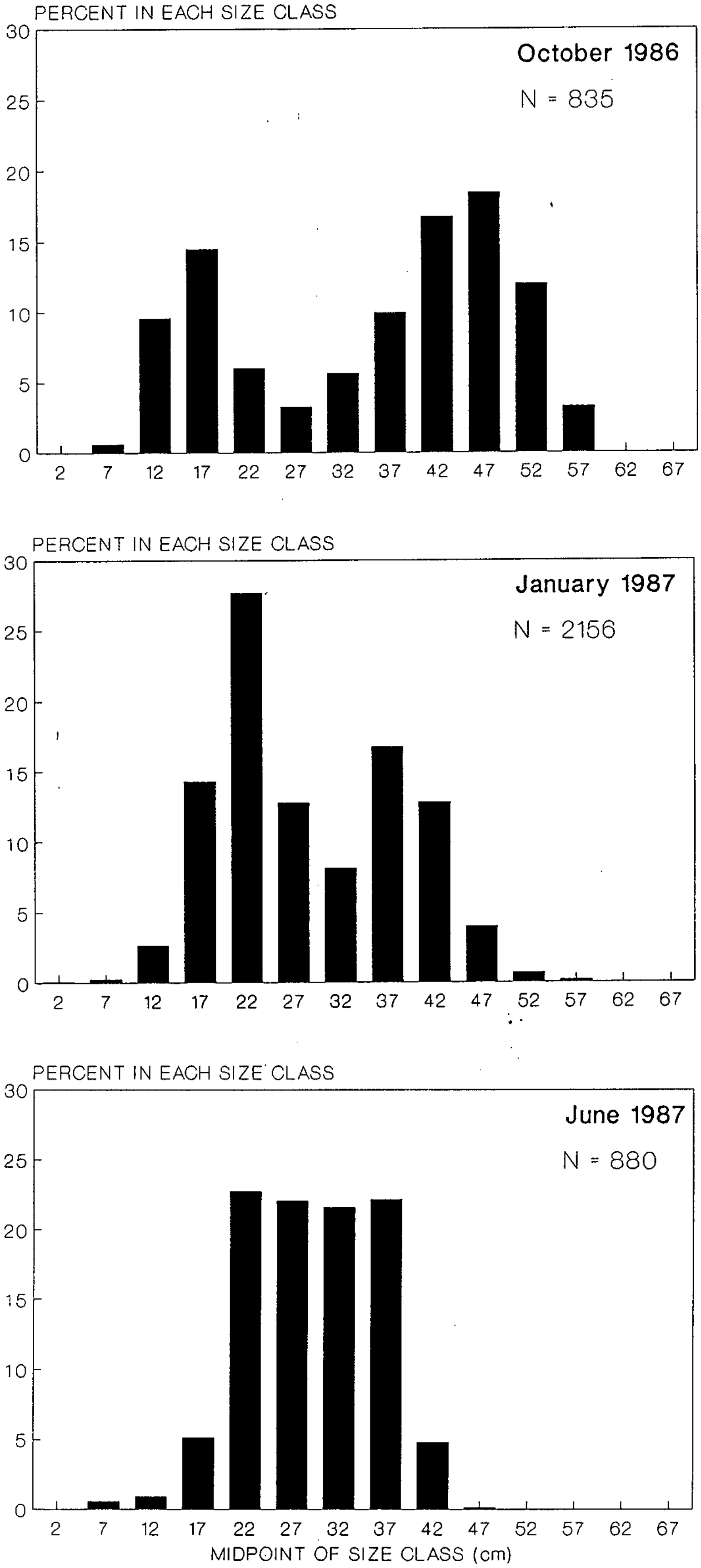

Figure 2. Size frequency distribution of the *Acanthaster planci* population at Wheeler Reef for October 1986, January 1987 and June 1987.

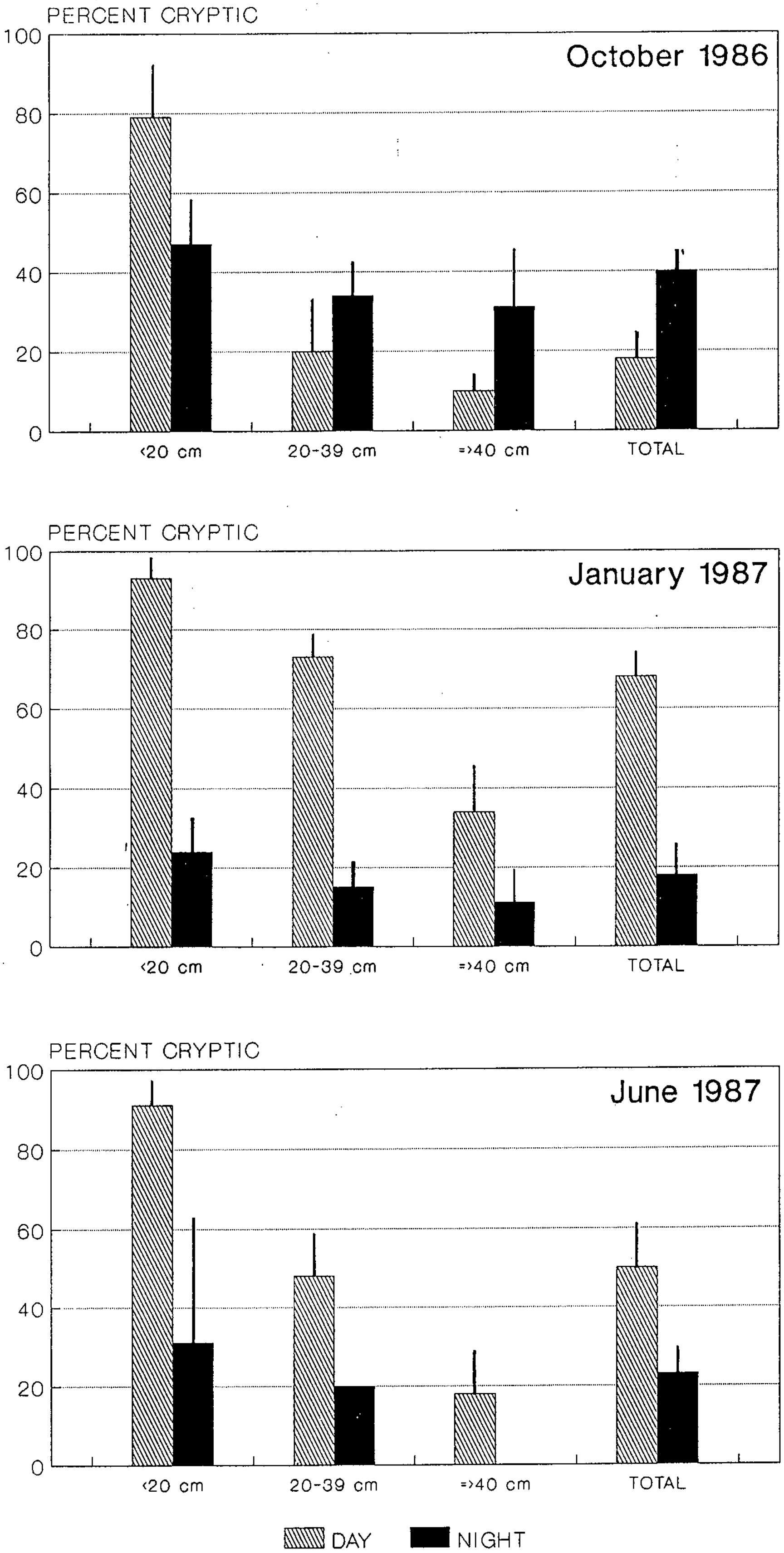

Figure 3. The proportion of <u>Acanthaster</u> <u>planci</u> cryptic in each size class during day and night samples at Wheeler Reef in October 1986, January 1987 and June 1987. Sample sizes are; October: day=3, night=2; January: day=5, night=4; June: day=4, night=2.

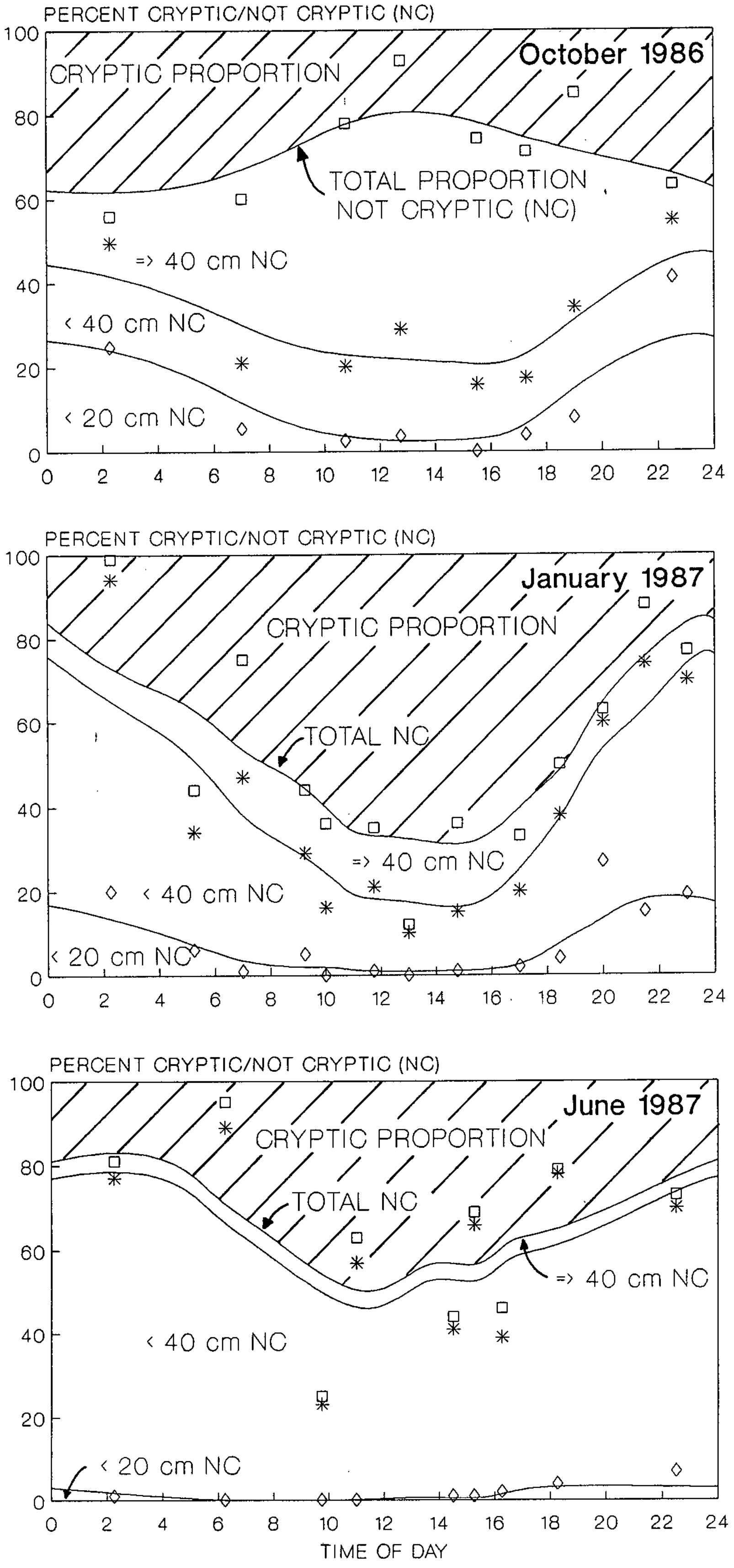

Figure 4. The <u>apparent</u> population size structure of <u>Acanthaster planci</u> at Wheeler Reef in October 1986, January 1987 and June 1987. See appendix figures I, II and III for details of sample size and curve fitting. NC = not cryptic.

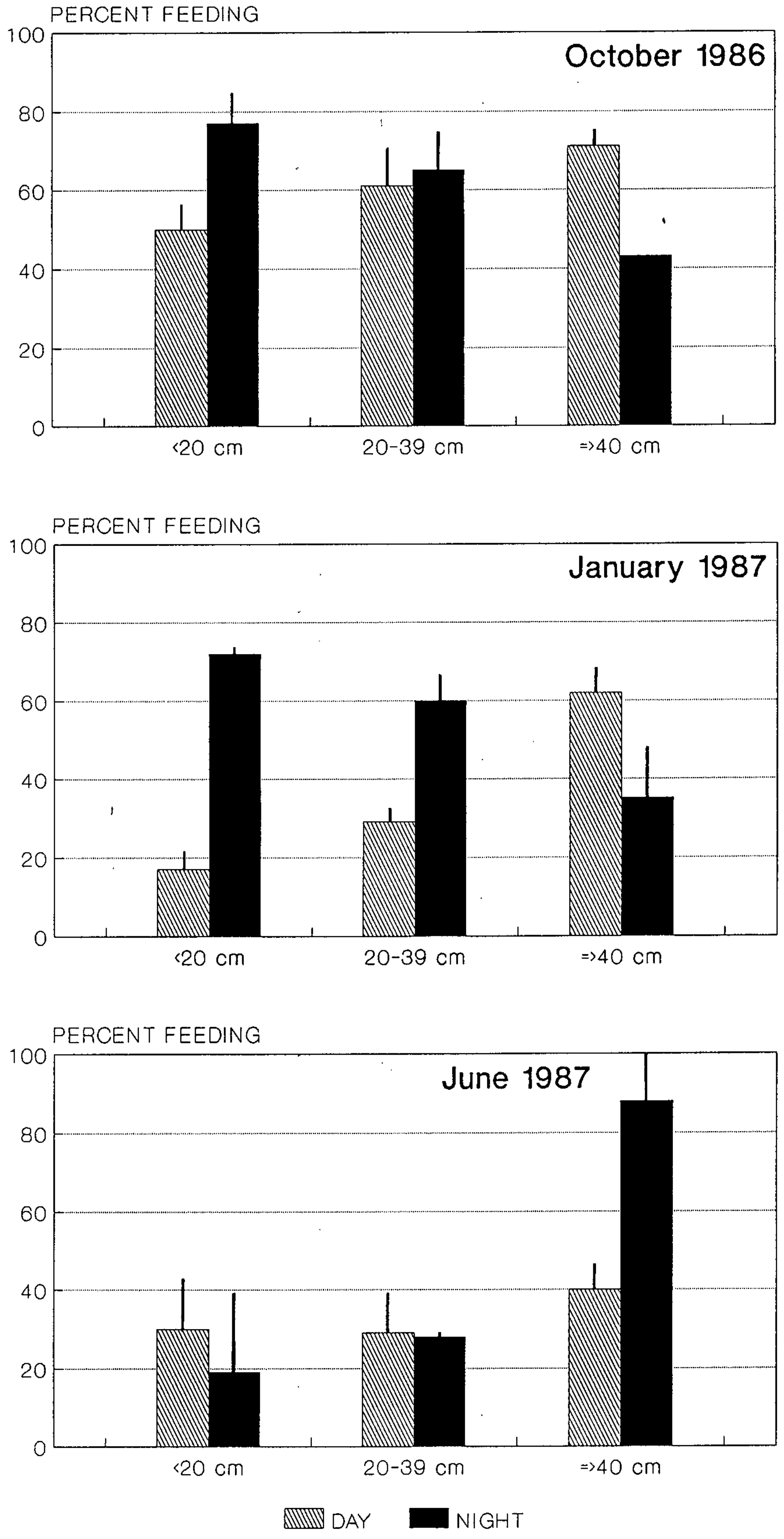

Figure 5. The proportion of Acanthaster planci feeding in each size class during day and night samples at Wheeler Reef in October 1986, January 1987 and June 1987. Sample sizes are; October: day=3, night=2; January: day=5, night=4; June: day=4, night=2.

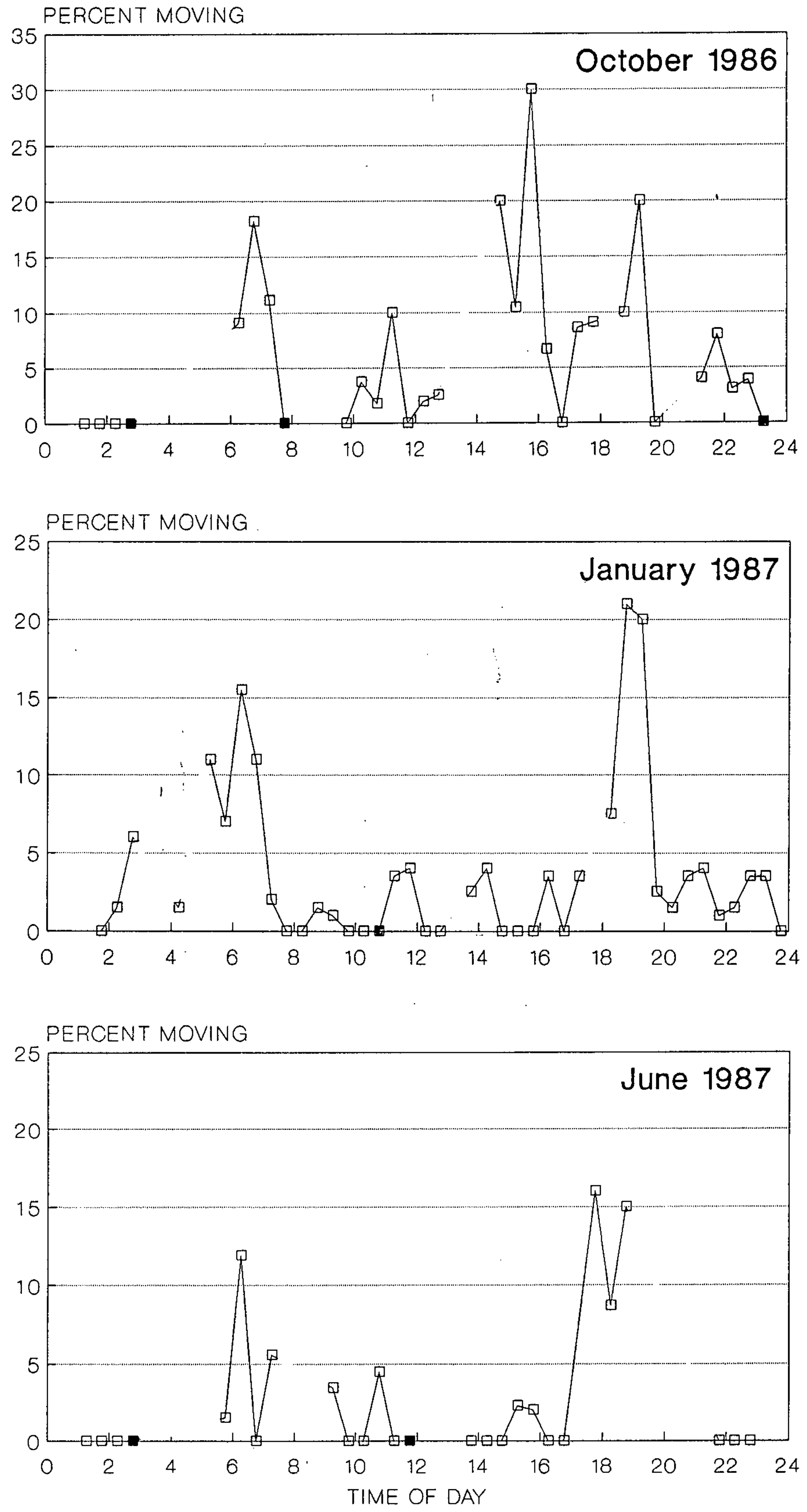

Figure 6. Morning and evening pulses of movement in Acanthaster planci at Wheeler Reef in October 1986, January and June 1987. Each data point represents percentage of animals (each N is 3 ≤ 130) actively mobile during half hour intervals. Filled boxes indicate where N < 10.

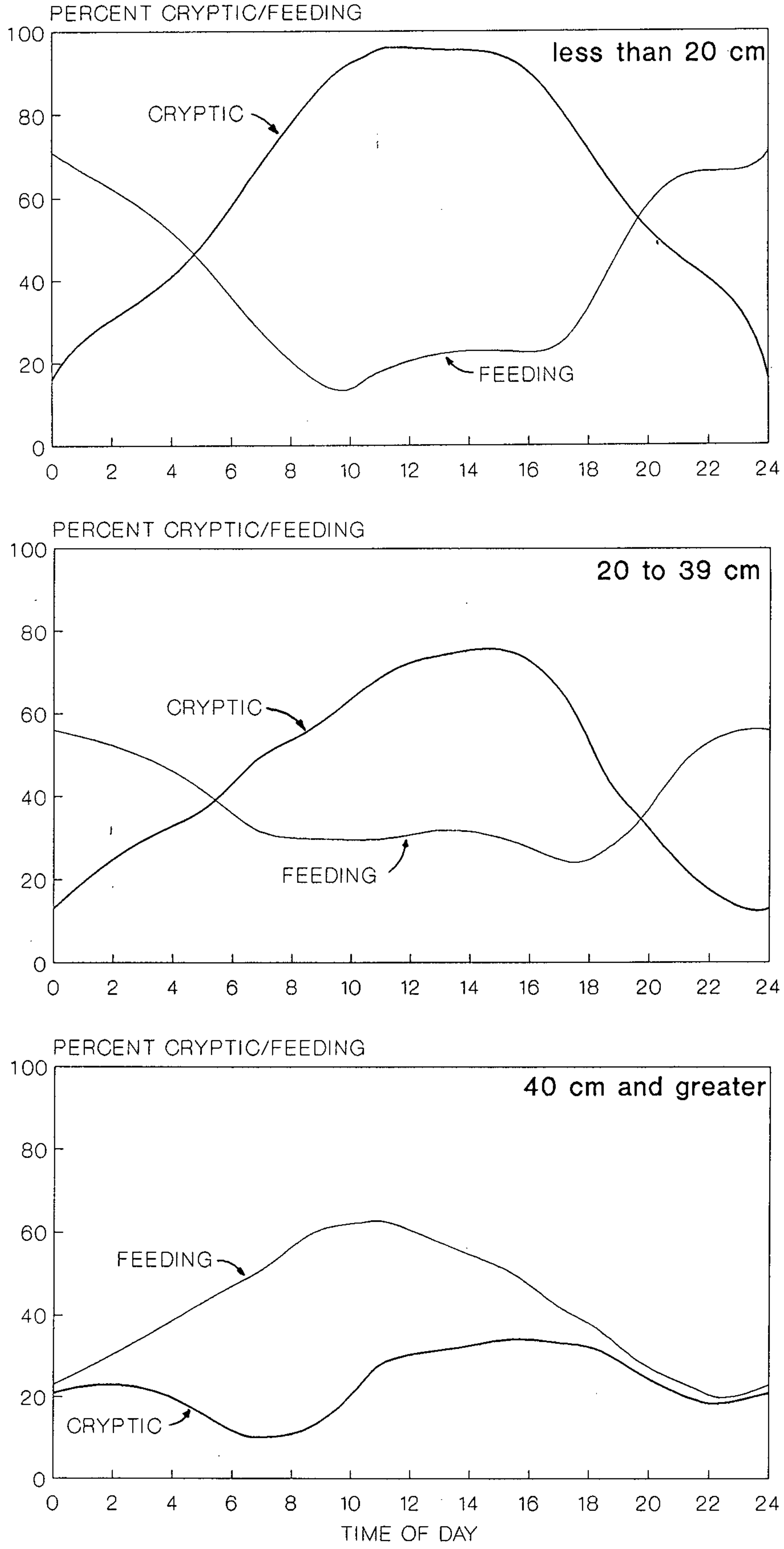

Figure 7. Relationship between cryptic and feeding behaviour in Acanthaster planci at Wheeler Reef in January 1987. See appendix figures II and VI for details of sample size and curve fitting.

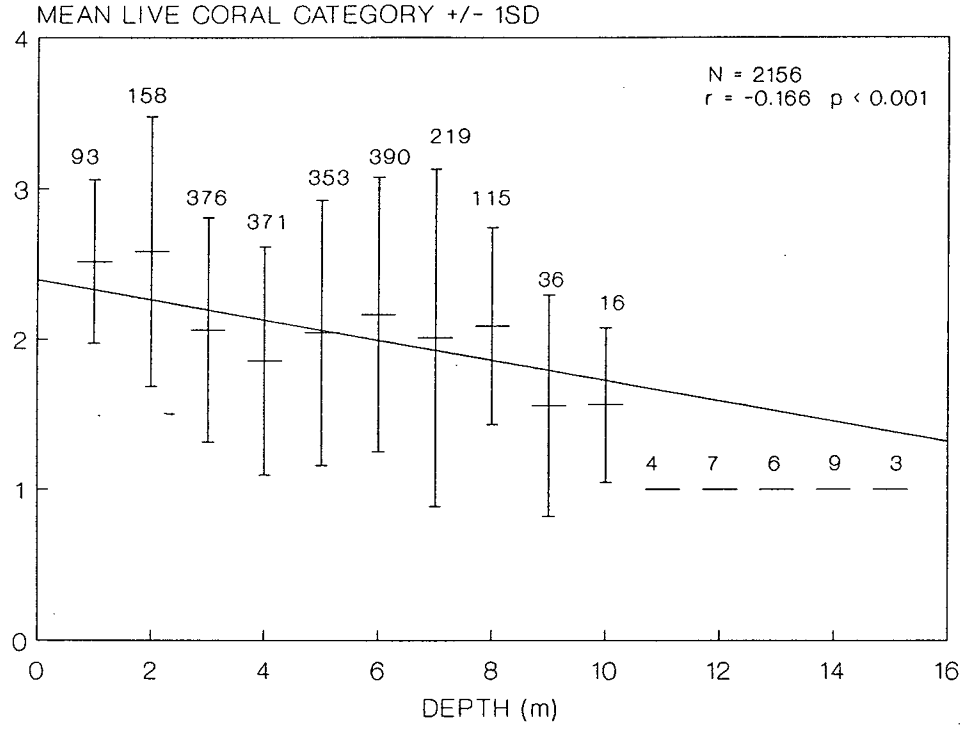

Figure 8. Relationship between depth and mean live coral cover at Wheeler Reef in January 1987.

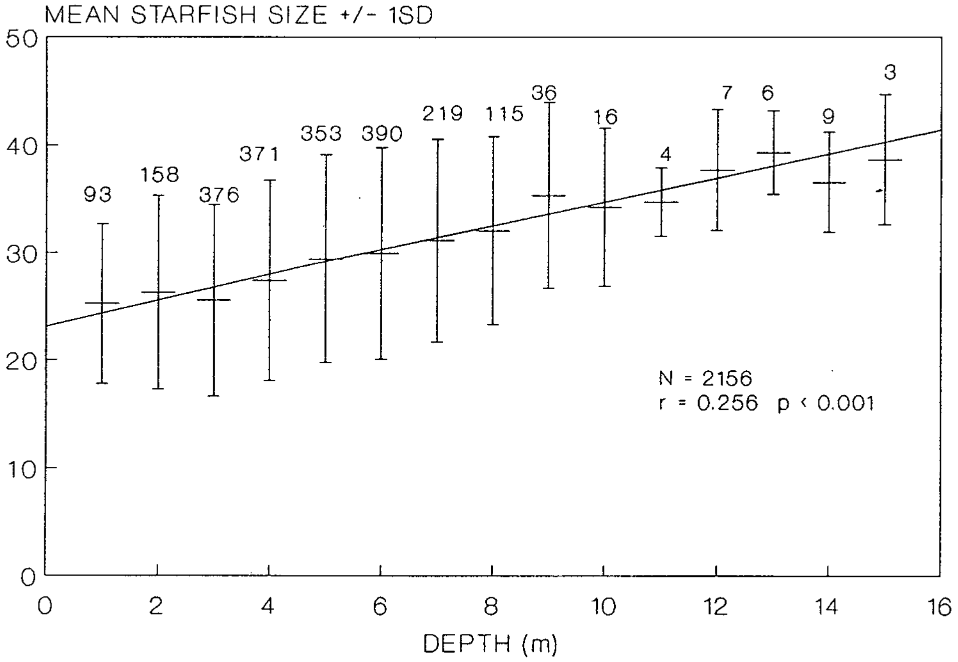

Figure 9. Relationship between depth and size of _Acanthaster_ _planci_ at Wheeler Reef in January 1987.

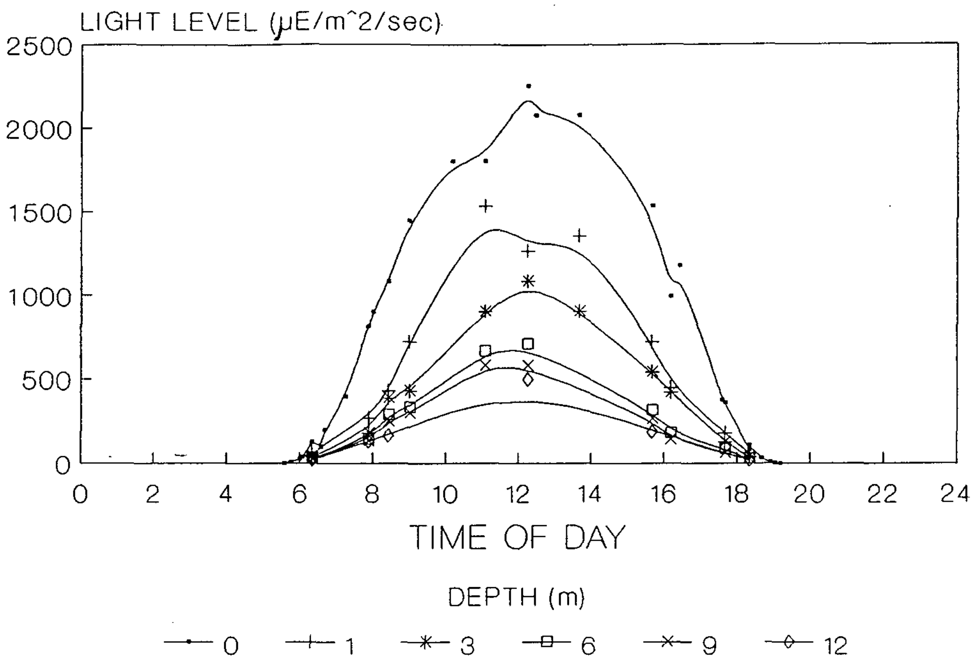

Figure 10. Ambient light measurements at surface and various depths over a 24 hour period at Wheeler Reef in January 1987.

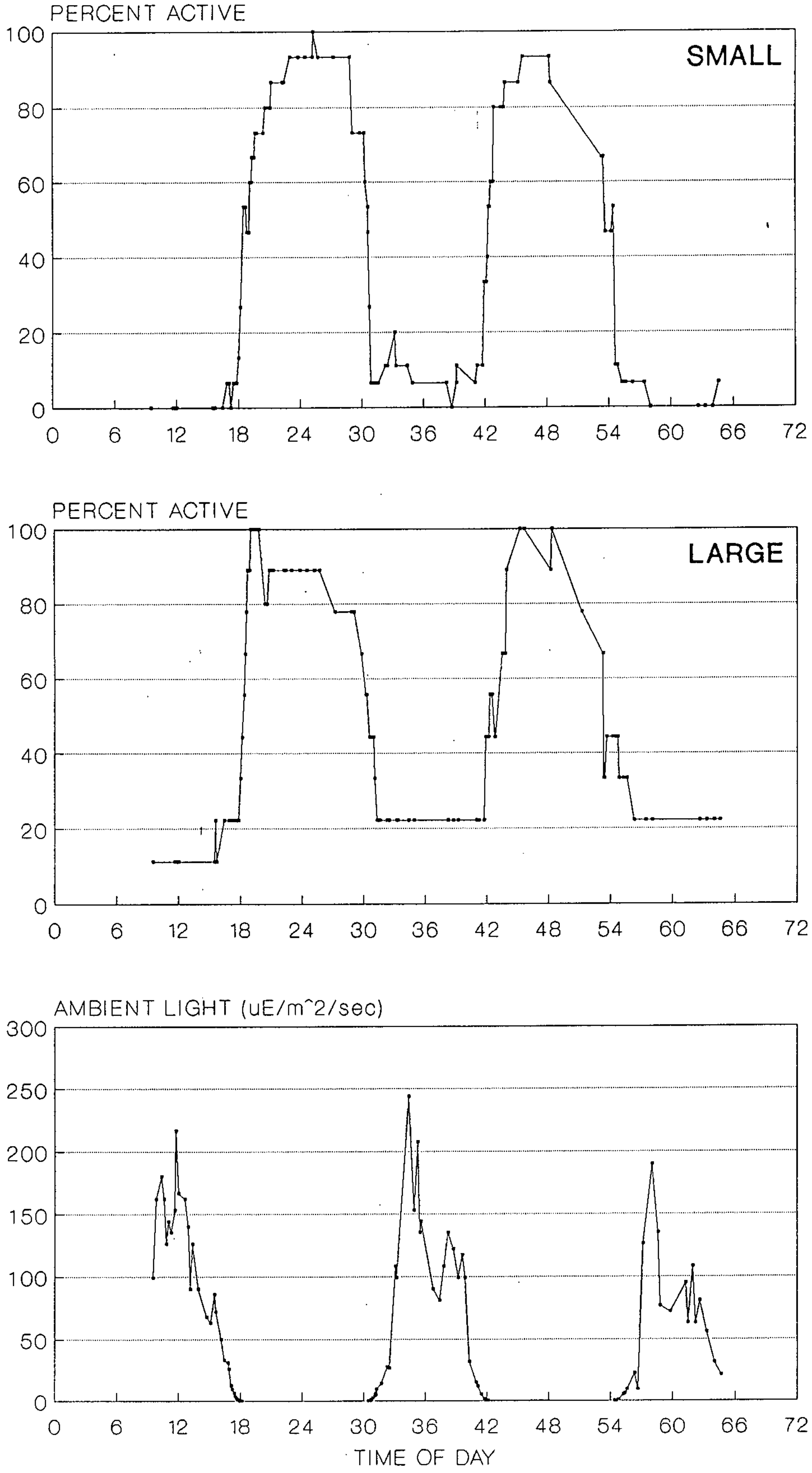

Figure 11. Activity patterns of small (7 - 24 cm) and large (29 - 37 cm) Acanthaster planci in aquaria and ambient light levels over a three day period in June 1987.

Figure 12 is located in the folder
at the back of the thesis

Figure 12. Experimental data and three theoretical responses of _Acanthaster planci_ to alteration of daylength regimes.

Month	Starfish Size	N	% of Total	Mean Size	s.d.
Oct'86	<20 cm	206	24.7	14.8	2.6
	20-39 cm	207	24.8	30.3	6.5
	≥40 cm	422	50.5	46.6	4.5
	TOTAL	835	100.0	34.7	14.0
Jan'87	<20 cm	371	17.2	16.6	2.5
	20-39 cm	1407	65.3	27.9	6.4
	≥40 cm	378	17.5	43.1	3.1
	TOTAL	2156	100.0	28.6	9.6
Jun'87	<20 cm	58	6.6	16.3	3.3
	20-39 cm	779	88.5	29.4	5.6
	≥40 cm	43	4.9	41.4	1.3
	TOTAL	880	100.0	29.1	6.9

Table 1. Proportion, mean size and standard deviation of *A. planci* in each size class at Wheeler Reef in October 1986, January 1987 and June 1987.

Month	Starfish Size	Time of day	#/hr	P	sig.
Oct'86	<20 cm	D	3.4	0.016	*
		N	24.0		
	20-39 cm	D	8.7	0.488	NS
		N	11.8		
	≥40 cm	D	23.6	0.062	NS
		N	4.5		
	TOTAL	D	35.7	0.751	NS
		N	40.2		
Jan'87	<20 cm	D	5.4	0.012[1]	*
		N	16.7		
	20-39 cm	D	24.4	0.140[2]	NS
		N	35.4		
	≥40 cm	D	7.7	0.322	NS
		N	4.9		
	TOTAL	D	37.5	0.085	NS
		N	57.0		
Jun'87	<20 cm	D	2.4	0.348	NS
		N	1.5		
	20-39 cm	D	32.6	0.354	NS
		N	23.2		
	≥40 cm	D	1.6	0.495	NS
		N	0.8		
	TOTAL	D	36.7	0.272	NS
		N	25.6		

[1] log transformation used to homogenize variances
[2] Kruskal-Wallis procedure used

Table 2. Summary of analyses comparing numbers of *A. planci* found per hour search time during the day and night samples at Wheeler Reef during each month. Sample sizes are; October: day=3, night=2; January: day=5, night=4; June: day=4, night=2.

Summary of ANOVA

Source of variation	df	SS	%SS	P	sig.
Month sampled (M)	2	625.7	1.0	0.3594	NS
Starfish size (S)	2	22216.8	34.4	0.0001	****
Time of day (T)	1	15489.8	24.0	0.0001	****
M x S	4	1787.3	2.8	0.2201	NS
M x T	2	6006.3	9.3	0.0003	****
S x T	2	5230.2	8.1	0.0007	****
M x S x T	4	613.3	1.0	0.7258	NS
Error	42	12528.1	19.4		
Total	59	64497.2	100		

Multiple comparisons

Analysis of Month x Time of day interaction

Month	Time of day	Mean
Oct'86	Day	36.2
	Night	36.9
Jan'87	Day	66.6
	Night	16.8
Jun'87	Day	52.2
	Night	17.0

Within Month

	P	sig.
Oct'86	0.961	NS
Jan'87	<0.001	****
Jun'87	0.045	NS

Within Time of Day

	P	sig.
Day	0.105	NS
Night	0.071	NS

Analysis of Starfish size x Time of day interaction

Starfish size	Time of day	Mean
<20 cm	Day	88.7
	Night	31.4
20-39 cm	Day	51.4
	Night	21.0
≥40 cm	Day	22.5
	Night	13.3

Within Starfish size

	P	sig.
<20 cm	<0.001	****
20-39 cm	0.008	**
≥40 cm	0.317	NS

Within Time of Day

	P	sig.
Day	<0.001 i.e.<20>20-39>≥40	****
Night	0.157	NS

Table 3. Three-way ANOVA table summarising analysis of the effects of starfish size, time of day and month sampled on the level of cryptic behaviour in <u>A. planci</u> at Wheeler reef.

Month	Starfish Size	Time of day			G	P	sig.
Oct'86	<20 cm	E	D	M	2.51	>0.250	NS
	20-39 cm	D	M	E	5.06	>0.050	NS
	≥40 cm	D	E	M	8.11	<0.025	NS
	TOTAL	D	E	M	21.39	<0.001	****
Jan'87	<20 cm	M	E	D	20.00	<0.001	****
	20-39 cm	M	E	D	43.12	<0.001	****
	≥40 cm	M	E	D	15.30	<0.001	****
	TOTAL	M	E	D	58.26	<0.001	****
Jun'87	<20 cm		E	D	2.35	>0.250	NS
	20-39 cm	M	E	D	110.97	<0.001	****
	≥40 cm	E	M	D	4.55	>0.100	NS
	TOTAL	M	E	D	122.38	<0.001	****

Table 4. Summary of G-test analyses on numbers of *A. planci* cryptic during morning, day and evening samples from Wheeler Reef in October 1987, January 1987 and June 1987. Samples are ranked from least cryptic to most cryptic and lines join times which are not significantly different. All tests were made at Bonferoni levels of significance (i.e. $\alpha = 0.05 / 12 = 0.004$).

Summary of ANOVA

Source of variation	df	SS	%SS	P	sig.
Month sampled (M)	2	4858.5	15.5	0.0001	****
Starfish size (S)	2	1790.4	5.7	0.0113	*
Time of day (T)	1	2244.4	7.1	0.0010	***
M x S	4	1966.4	6.2	0.0409	*
M x T	2	778.6	2.5	0.1235	NS
S x T	2	3084.3	9.8	0.0007	**
M x S x T	4	9162.4	29.2	0.0001	****
Error	42	7528.8	24.0		
Total	59	31423.8	100		

Table 5. Three-way ANOVA table summarising analysis of the effects of starfish size, time of day and month sampled on the level of feeding activity in A. planci at Wheeler reef.

Summary of ANOVA

Source of variation	df	SS	%SS	P	sig.
Month sampled (M)	1	2501.4	13.2	0.0001	****
Starfish size (S)	2	162.4	0.9	0.5355	NS
Time of day (T)	1	1699.0	9.0	0.0010	***
M x S	2	211.6	1.1	0.4453	NS
M x T	1	784.8	4.2	0.0189	*
S x T	2	9279.1	49.2	0.0001	****
M x S x T	2	411.2	2.2	0.2157	NS
Error	30	3819.1	20.2		
Total	41	18868.9	100		

Multiple comparisons

Analysis of Month x Time of day interaction

Month	Time of day	Mean
Oct'86	Day	60.5
	Night	61.4
Jan'87	Day	36.2
	Night	55.5

Within Month

	P	sig.
Oct'86	0.898	NS
Jan'87	0.028	NS

Within Time of Day

	P	sig.
Day	0.004	**
Night	0.568	NS

Analysis of Starfish size x Time of day interaction

Starfish size	Time of day	Mean
<20 cm	Day	29.5
	Night	73.7
20-39 cm	Day	41.3
	Night	61.3
≥40 cm	Day	65.0
	Night	37.4

Within Starfish size

	P	sig.
<20 cm	<0.001	****
20-39 cm	0.034	NS
≥40 cm	0.004	**

Within Time of Day

	P	sig.
Day	0.001	***
	i.e.<20=20-39<≥40	
Night	0.001	***
	i.e.<20=20-39>≥40	

Table 6. ANOVA table summarising the effects of starfish size, time of day and month sampled on the level of feeding activity in *A. planci* at Wheeler reef. October 1986 and January 1987 data only.

Summary of ANOVA

Source of variation	df	SS	%SS	P	sig.
Month sampled (M)	2	3200.9	44.9	0.0010	***
Time of day (T)	1	1030.0	14.4	0.0152	*
M x T	2	1012.5	14.2	0.0495	*
Error	14	1887.6	26.5		
Total	19	7131.0	100		

Multiple comparisons

Analysis of Month x Time of day interaction

Month	Time of day	Mean
Oct'86	Day	61.1
	Night	64.6
Jan'87	Day	29.4
	Night	59.6
Jun'87	Day	28.6
	Night	27.6

Within Month

	P	sig.
Oct'86	0.783	NS
Jan'87	0.001	***
Jun'87	0.948	NS

Within Time of Day

	P	sig.
Day	0.013	*
	i.e. Oct>Jan=Jun	
Night	0.021	*
	i.e. Oct=Jan>Jun	

Table 7. Two-way ANOVA table analysing the effects of time of day and the month sampled on the level of cryptic behaviour in 20 - 39 cm <u>A. planci</u> at Wheeler reef.

Month	Time of day	G	P	sig
Oct'86	M E D N	12.04	<0.01	*
Jan'87	E M N D	78.97	<0.001	***
Jun'87	E M D N	16.08	<0.01	*

Table 8. Summary of tests of independence (G - test, Sokal and Rohlf, 1981) to determine whether rates of movement are independent of time of day. Times are ranked from greatest degree of movement to least and lines join times which are not significantly different ($\alpha = 0.05 / 3 = 0.017$). M, morning; D, day; E, evening; N, night.

Starfish Size	Day		Night	
	P	sig.	P	sig.
<20 cm	0.488	NS	0.034	NS
20-39 cm	0.550	NS	0.366	NS
≥40 cm	0.343	NS	0.248	NS
TOTAL	0.338	NS	0.396	NS

Table 9. Summary of chi-square analyses on frequencies of *A. planci* cryptic at different depths during day and night samples from Wheeler Reef in January 1987. Values are the probability of a significant difference between depth classes (0 - 3 m, 3 - 6 m, 6 - 9 m and > 9 m). All tests were made at Bonferoni levels of significance (i.e. $\alpha = 0.05 / 8 = 0.006$).

Starfish Size	Day		Night	
	P	sig.	P	sig.
<20 cm	0.186	NS	0.457	NS
20-39 cm	0.036	NS	0.034	NS
≥40 cm	0.033	NS	0.384	NS
TOTAL	0.002	*	<0.001	**

Table 10. Summary of chi-square analyses on frequencies of *A. planci* feeding at different depths during day and night samples from Wheeler Reef in January 1987. Values are the probability of a significant difference between depth classes (0 - 3 m, 3 - 6 m, 6 - 9 m and > 9 m).All tests were made at Bonferoni levels of significance (i.e. $\alpha = 0.05 / 8 = 0.006$).

Starfish Size	Day		Night	
	P	sig.	P	sig.
<20 cm	0.345	NS	0.005	*
20-39 cm	0.068	NS	0.005	*
≥40 cm	0.045	NS	0.241	NS
TOTAL	0.483	NS	<0.001	**

Table 11. Summary of chi-square analyses on frequencies of *A. planci* cryptic at different categories of live coral cover during day and night samples from Wheeler Reef in January 1987. Values are the probability of a significant difference between live coral categories (0 - 10 %, 10 - 30 % and > 30 %). All tests were made at Bonferoni levels of significance (i.e. α = 0.05 / 8 = 0.006).

Starfish Size	Day		Night	
	P	sig.	P	sig.
<20 cm	0.951	NS	0.304	NS
20-39 cm	0.090	NS	0.009	NS
≥40 cm	0.009	NS	0.361	NS
TOTAL	0.127	NS	0.002	*

Table 12. Summary of chi-square analyses on frequencies of *A. planci* feeding at different categories of live coral cover during day and night samples from Wheeler Reef in January 1987. Values are the probability of a significant difference between live coral categories (0 - 10 %, 10 - 30 % and > 30 %).All tests were made at Bonferoni levels of significance (i.e. α = 0.05 / 8 = 0.006).

Starfish Size	Day		Night	
	P	sig.	P	sig.
<20 cm	0.101	NS	0.001	*
20-39 cm	0.221	NS	0.016	NS
≥40 cm	0.626	NS	0.420	NS
TOTAL	0.020	NS	<0.001	**

Table 13. Summary of chi-square analyses on frequencies of aggregated and non-aggregated _A. planci_ showing cryptic behaviour in day and night samples from Wheeler Reef in January 1987. All tests were made at Bonferoni levels of significance (i.e. $\alpha = 0.05 / 8 = 0.006$).

Starfish Size	Day		Night	
	P	sig.	P	sig.
<20 cm	0.013	NS	0.825	NS
20-39 cm	0.905	NS	0.678	NS
≥40 cm	0.796	NS	0.556	NS
TOTAL	0.186	NS	0.622	NS

Table 14. Summary of chi-square analyses on frequencies of aggregated and non-aggregated _A. planci_ feeding in day and night samples from Wheeler Reef in January 1987. All tests were made at Bonferoni levels of significance (i.e. $\alpha = 0.05 / 8 = 0.006$).

CHAPTER THREE

Feeding Rate of Acanthaster planci in the field

INTRODUCTION

Considering that it is the extent of coral destruction by A. planci that has given the starfish so much notoriety, it is surprising that so little information is available regarding actual feeding rates of the starfish.

Some information is available from the field studies of Chesher (1969), Pearson and Endean (1969) and Glynn (1973). These authors provided gross feeding rate estimates from measurements of coral cover killed and density of A. planci. Estimates of individual feeding rates have come from caging starfish in the field (Pearson and Endean, 1969) and from the laboratory studies of Yamaguchi (1974b). These studies recorded feeding rates in terms of area or weight of coral skeleton killed and provide information on community impact of feeding but convey less information about the feeding biology of the starfish than feeding rates expressed in terms of biomass or energy. Information on daily and seasonal characteristics of feeding rate as well as individual variation is lacking in particular for A. planci.

The importance of feeding rate to physiological considerations such as growth in A. planci has received little attention. However, Lucas (1984) found that growth rates of laboratory reared A. planci slowed after sexual maturity and identified a "senile" stage after about three years of age when shrinkage and gonadal decline were observed. This was associated with a decline in feeding rate. Lucas (1984) suggested that the mass of metabolizing tissue in these large A. planci outstrips the feeding capacity of the animals to maintain such a biomass. Lucas suggested that this physiological condition played a role in determining maximum size in A. planci and would eventually lead to senility and death. This senile phase is yet to be identified in field based populations. Yamaguchi (1974a) and Kettle and Lucas (1987) have provided information on respiration rates of A. planci, but presently available data on feeding rate are insufficient to determine how feeding rates of starfish compare with the maintenance requirements of the starfish.

The purpose of this section of the study was to:

(1) measure the feeding rates of individual, undisturbed animals in the field,

(2) determine whether feeding rate varied seasonally,

(3) examine any size dependent influences and,

(4) provide feeding rate measurements in units useful for both community impact assessment and the physiological consideration of A. planci.

MATERIALS AND METHODS

Monitoring individual feeding behaviour in the field

Monitoring of feeding behaviour of individual A. planci was carried out during October 1987, January 1988, June 1988 and October 1988 at Davies Reef (Lat. 18°50'S, Long. 147°39'E) in the central Great Barrier Reef (fig. 1). Approximately 20 starfish were tagged on each expedition by placing an individually numbered piece of plastic sheeting 2 cm^2, with a central 2 mm punched hole over one of the large spines on the disc of the starfish. Although these tags are eventually shed by the starfish, trials confirmed that quadruple tagging would ensure starfish remained recognizable for the duration of the four to five day monitoring period. The location of each tagged starfish was marked with a coloured flag and the site was marked with a surface buoy. Any recent scars in the vicinity of the tagged starfish were marked with coloured tape and/or crayon to ensure any further feeding was not confused with previous scarring.

Subsequent daily monitoring included locating the starfish, recording its activity, measuring the distance of any movement, marking the new position and identifying any new feeding scars. The size of freshly eaten colonies and the extent of scarring was measured and the eaten colony or a sample was collected for later identification. Habitat characteristics of the site such as live coral cover (see page 18 for method), depth and location were recorded for each new feeding scar found.

Analysis of feeding rates

In total four different measurements of feeding rate were able to be made:

i. the number of feeding events per day,
ii. the one dimensional area of coral (planar surface area [PSA] or coral cover) killed per day,
iii. an estimate of the mass of coral tissue consumed per day,
iv. an estimate of the energy consumption per day.

Measurements of the number of colonies damaged and killed per day as well as an estimate of the real or actual coral surface area (RSA)[1] and coral biomass killed per day[2] by A. planci were also made.

Measurements of feeding rate in terms of the number of feeding events per day and coral cover killed per day were made from records collected in the field. A number of laboratory procedures had to be undertaken to enable these field measurements to be converted to measurements in units of real coral surface area (RSA), biomass and energy.

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[1] Real coral surface area (RSA) takes into account the surface complexity of the prey species, in contrast to coral cover or planar surface area (PSA) which may not vary between encrusting and branching coral growth forms. See text on page 65 for details.

[2] Because some tissue is always left behind in the skeleton of coral colonies preyed upon by A. planci coral biomass killed will always be greater than coral biomass consumed. This varies between prey species, see text on pages 64 and 65 for details.

Laboratory Procedures

Samples of 16 coral species (see appendix table VII for species names) were collected from Davies Reef and Nelly Bay, Magnetic Island (Lat. 19o 10'S, Long. 146o 51'E) in the central Great Barrier Reef region. Approximately 20 specimens of each species was taken and half of these were immediately frozen. The remaining half were transported live to the Australian Institute of Marine Science. Following removal of commensals, live coral colonies were placed on the floor of a 3 m diameter, 0.8 m deep pool. A continuous flow of fresh seawater was maintained through the pool. Fifteen _A. planci_ which had been starved for 7 days to standardize hunger were introduced to the pool which contained a central raised shelter area. Feeding generally took place at night and each morning the eaten specimens of coral were removed and frozen.

Coral soft tissue biomass

The eaten and uneaten frozen coral samples were oven dried at 70°C to constant weight (determined after 1 hours' cooling at room temperature). During the drying process any loose coral pieces, coral symbionts and algae were removed from the specimens. Samples were weighed on a Sartorius electronic balance; ± 1mg. The weighed samples were then bleached for two days in 2.5 % sodium hypochlorite to remove all coral tissue. Some samples (mainly _Fungia_ and _Lobophyllia_) required longer to completely remove all tissue. Samples were then rinsed in running fresh water for one day before re-drying and weighing. The dry weight of soft coral tissue was then calculated by difference for each sample.

The weight of soft coral tissues lost from each sample by bleaching was converted to weight lost per unit of RSA (see below) (i.e. g $DW.cm^{-2}$). The mean difference in weight loss between uneaten and eaten samples of each species provided an estimate of biomass consumption. Biomass lost from the uneaten samples during bleaching provides an estimate of coral biomass killed in each prey species during feeding.

Coral surface area measurements

The area that each of the above samples would contribute to coral cover, or planar surface area (PSA), was also measured. This was done by tracing around the outline of the sample when viewed from above and then cutting out the resultant shape and measuring the area on a LICOR LI-3000 Leaf Area Meter.

The real surface area (RSA) of the coral specimens was measured using the technique described by Hoegh-Guldberg (1989) whereby coral skeletons sealed with varnish are coated with methylene blue dye and the dye adhering to the coral is then washed off into a known volume of water. The amount of dye in the water is proportional to surface area (calculated from standard geometric shapes[1]) and can be measured by colorimetry.

---

[1] Surface area standards were constructed from wooden blocks and from bleached and dried staghorn coral, Acropora nobilis, cut into cylindrical shapes. The correlation between absorbance and known surface area for both the wooden standards and the coral standards was highly significant ($r^2 = 0.966$) indicating that the technique was very accurate. However, for wooden and coral standards of the same surface area, as calculated from their geometry, the coral standards had a 40 % greater surface area as calculated by the Hoegh-Guldberg technique. It is expected that the surface irregularity (unevenness and corallite structures) of the Acropora coral standards would account for this. Surface area calculations for the coral samples were made based on the wooden standards.

The ratio of RSA to PSA was calculated for each of the samples and the mean ratio for each of the species was used to convert feeding rate in terms of PSA to RSA[1] (see appendix table VI for summary of RSA to PSA ratios).

Coral soft tissue energy content

The energy content of coral soft tissues was calculated from two samples of each species for which biomass data was collected. Coral tissue was removed from the skeleton using a water pik (Teledyne brand, model WP-30A). The water pik delivers a high pressure jet of water and the sample (in this case 100 ml) was recycled to increase the concentration of tissue in the sample (see Johannes and Wiebe, 1970). This method of coral tissue removal results in a small amount of skeletal material being removed. This was separated from the tissue by decanting the slurry after it had stood for several minutes. The resultant tissue slurry was refrozen and dried in a Dynavac vacuum freeze dryer at -70°C. The samples of the freeze dried tissue (about 1 - 2 g) were split into two and each portion was accurately weighed on a Mettler H54AR balance; ± 0.1 mg. One half of the sample was ashed in a muffle oven at 500°C for 4 hours to determine ash free (organic) dry weight (AFDW).

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[1] The species and growth forms of corals used in these analyses were representative of most of the species preyed upon by tagged A. planci in the field. Where data for a specific species or genus of prey eaten in the field were not available, then values for a similar species/genus were substituted. For example, values of surface area and biomass content for Goniastrea retiformis were used when the actual prey items were Montastrea or Favites.

Ashed and unashed samples of the dried coral tissue was then analysed for carbon content using a LECO CHN-600 carbon-hydrogen-nitrogen determinator. The energy content of the coral tissue was then estimated on a kJ.g^{-1}AFDW basis from an organic carbon to energy conversion relationship:

$$\mathrm{kJ}\ g_{AFDW}^{-1} = 11.5\ (1 - W_{H_2O}) - 66.27 \times W_C\ ,$$

where W_{H_2O} is the residual water fraction of ash free dry weight (AFDW) and W_C is the organic carbon fraction in AFDW [equation 6; Gnaiger and Bitterlich (1984)].

Starfish biomass

A sample of 20 A. planci over the 24 to 45 cm size range was collected from Davies Reef in May 1989 and transported live to AIMS where they were held in aquaria before being measured (maximum diameter) and weighed (whole wet weight, after Kettle and Lucas, 1987). Starfish were oven dried at 70°C to constant weight. The allometric relationships for wet weight and dry weight with diameter were then calculated.

Statistical procedures employed

Some tagged animals were not found each day, so only data from animals monitored for greater than two days were used in the analyses to ensure any day to day irregularities in feeding behaviour did not confound calculation of overall feeding rates.

Unless stated otherwise, statistical procedures used to compare feeding rates between size and between months were standard analyses of variance (ANOVA) and analyses of covariance (ANCOVA). Cochran's C (Winer, 1971) was used as the test statistic for homogeneity of group variances and a square root transformation was necessary to correct variance structure in some samples for ANOVA to be valid.

Regression analyses were undertaken to determine whether there is a direct relationship between starfish size and feeding rate over the size range examined. Analyses of covariance (ANCOVA) were used to examine between-month differences where significant linear relationships existed between size and feeding rate. This technique allows more accurate separation of significant month effects than the gross comparisons above where sizes were pooled, as it corrects for the variation due to the size co-variate.

Least significant difference (LSD) was used to contrast adjusted means from the ANCOVA, following the procedure of Snedaker and Cochran (1967). Significance of linear regressions was tested using ANOVA (Zar, 1984).

RESULTS

Feeding rates of _Acanthaster_ _planci_ in the field

Between 16 and 21 _A. planci_ were able to be monitored for greater than two days each of the months sampled. Most starfish were able to be monitored for the full four or five days of the experiments. The larger two of the three size classes characterized in the previous chapter (i.e. 20 - 39 cm and $\geq$40 cm) were able to be monitored at Davies Reef. Starfish monitored varied between 20 and 60 cm in maximum diameter and the mean sizes during each expedition are shown in table 1.

There was no significant difference in mean size of _A. planci_ between months among $\geq$ 40 cm starfish or the total (all sizes pooled) sample ($p > 0.05$). Among _A. planci_ <40 cm, only starfish in the October 1987 and June 1988 samples differed in size significantly ($p < 0.05$).

i. Number of feeding events per day

The seasonal trend in the mean number of feeding events of tagged A. planci per day recorded at Davies Reef during four visits between October 1987 and October 1988 is shown in figure 2. The mean number of feeds per day in June 1988 was 0.71. This was significantly less than the values in all other months which averaged over 1.5 feeds per day ($p < 0.05$). This pattern was consistent in both size classes of starfish examined ($p < 0.05$). Starfish $\geq$ 40 cm fed on average more times per day than those < 40 cm in diameter in October 1987 and January 1988 ($p < 0.05$).

ii. Area of coral cover killed per day

The mean planar area of coral cover killed varied between 129 and 301 cm^2/day (figure 3) and was significantly lower in June 1988 than in both October samples ($p < 0.05$). Large starfish ($\geq$ 40 cm) killed significantly more coral than smaller starfish in all months except June 1988 ($p < 0.05$).

iii. Real surface area of coral killed per day

Real surface area of coral skeleton killed per day by A. planci varied between 436 cm^2 in June 1988 and 1368 cm^2 in October 1987 (figure 4). Both size classes showed similar trends to the overall data with the June 1988 rate significantly less than both October samples. Significant differences between sizes were found in all samples except June 1988 ($p < 0.05$).

iv. Tissue biomass killed per day

The seasonal pattern shown in other feeding rate parameters was repeated for coral biomass killed (figure 5). The mean mass of coral tissue killed per starfish per day was in excess of 12.6 g DW in both October samples compared with 5.4 g DW in June 1988 and 8.2 g DW in January 1988. Small A. planci killed significantly less coral tissue than those $\geq$ 40 cm in all months ($p < 0.05$). Both size classes showed a similar seasonal trend to the overall sample (figure 5).

v. Tissue biomass consumed per day

Estimates of the actual tissue consumed or utilized during feeding by the tagged A. planci are shown for all months sampled in figure 6. Biomass consumed was at its lowest in June 1988 at 1.7 g DW per A. planci per day compared with 2.8 g DW in January 1988 and over 3.8 g DW in both October samples. Starfish $\geq$ 40 cm consumed significantly more coral tissue than smaller starfish in all months except June 1988 ($P < 0.05$, see figure 6).

vi. Energy value of food consumed per day

Mean daily energy consumed ranged from 89.7 kJ in October 1987 and 35.9 kJ in June 1988 (figure 7). Energy intake was significantly greater in A. planci $\geq$ 40 cm than in smaller animals in all months except June 1988.

vii. Coral colonies eaten and killed per day

The mean number of coral colonies eaten and the number killed totally by A. planci during feeding by the tagged starfish is shown in table 2. Overall, starfish fed on and killed significantly less colonies in June 1988 (0.6 eaten and 0.2 killed per starfish per day) than in any other month ($p < 0.05$). Mean rates for all the other months were 1.5 - 1.6 eaten and 0.9 - 1.0 killed per starfish per day. However, there were no significant differences between months in the number of colonies killed outright by starfish. The overall mean number of coral colonies killed per starfish per day was 0.8.

Relationship between starfish size and feeding rate

Table 3 shows the results of regression analyses of feeding rate against size for each of the units calculated in each month. Analyses of covariance were made for the coral cover killed, biomass utilized and energy uptake data, as significant regressions existed between size and rate in all months (table 3) and these are the most useful measuring units in ecological and physiological terms. The relationships are shown graphically in figures 8, 9 and 10. Square root transformation of all data sets was required for the analyses. The analyses of covariance confirm the broad seasonal patterns shown above for the pooled size comparisons with the summer (October 1987 and 1988, January 1988) feeding rates being significantly greater than those in winter (June 1988). These analyses also revealed a significant depression in feeding rate between the two October samples and the January sample. Summary statistics for these analyses of covariance are shown in tables 4, 5 and 6.

Weight specific feeding rate

Whole wet weight and dry weight of starfish collected in May 1989 were significantly correlated to starfish size (figure 11) and fitted the relationships:

$$\ln\,[\text{whole wet wt. (g)}] = 2.495.\ln\,[\text{size (mm)}] - 7.025,\ r^2 = 0.886$$

$$\ln\,[\text{dry wt. (g)}] = 2.320.\ln\,[\text{size (mm)}] - 8.213,\ r^2 = 0.878$$

The size of the tagged starfish from the four expeditions was converted to weight and the weight specific feeding rate (mg DW coral utilized/g body weight/day) for each was calculated. Regression analyses were performed to examine for significant relationships between body weight/size and weight specific feeding rate. Only the October 1988 sample showed a significant relationship (see figure 12). A 25 cm (1000 g) A. planci consumes about 2 mg DW coral tissue per gram whole wet body weight (WW) per day (0.2 % of body WW) and the rate for a 55 cm (6000 g) starfish would be about 0.8 mg DW/g WW (0.08 % of body WW). In dry weight terms similar sized animals would consume 1.7 and 0.8 % of their whole body dry weight per day, respectively.

Feeding rate and metabolic requirement

Yamaguchi (1974a) and Kettle and Lucas (1987) have provided data on the respiration rate of A. planci. The relationship for respiration rate versus starfish whole wet weight:

$$\ln [\text{ml } O_2.\text{hr}^{-1} \text{ @ } 25^{\circ}\text{C}] = 0.870.\ln [\text{g wet wt.}] - 3.328,$$

from Kettle and Lucas (1987) was used in this study to estimate respiratory requirements of A. planci in the field. Adjustment for differing water temperature in this study to that of Kettle and Lucas (1987) was made using data in Yamaguchi (1974b). Respiration rates were transformed into energy requirement by multiplying by Ivlev's conversion value:

$$1 \text{ ml } O_2 = 4.8 \text{ cal} = 21 \text{ J}, \text{ (Pamatmat, 1983)}.$$

Energy requirement due to respiration was assumed to be 80 % of total metabolic requirements[1] and the predicted metabolic energy requirements were calculated for the tagged starfish from October 1988 in order to examine how energy consumed related to energy required. The relationship between ratio of energy utilized to energy required and size approached significance ($r = -0.423$, $p = 0.063$, line A; figure 13).

The small number of A. planci < 30 cm in the sample and the likelihood that some animals were feeding at less than their potential capability probably prevented a significant effect being detected. Thus it was reasoned that a relationship probably does exist.

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[1] Energy requirements for and losses due to excretion in asteroids are difficult to measure and have only been studied in detail by Shirley and Stickle (1982) for Leptasterias hexactis. These workers calculated energy expenditure (loss) due to excretion between 13 and 18 %. Greater losses of absorbed energy have been recorded in some echinoids (Lawrence and Lane 1982).

To examine the ramifications of this possible relationship to growth and maximum size in A. planci, the amount of energy available for metabolism and somatic growth was calculated by subtracting the proportion of energy channelled into gonads[2] and recalculating the ratio of energy utilized to energy required. Once this adjustment for energy being channelled into gametes had been made it was found that there was a highly significant effect of size on the ratio of energy consumed to that required ($p \leq 0.001$). Figure 13 shows this relationship versus size and predicts that energy requirement for metabolism will outstrip energy intake between 42 and 70 cm leaving no scope for growth.

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[2] Kettle and Lucas (1987) have provided a relationship for the proportion of total body energy content for gonad tissue. This is a size dependent relationship:

$$\% \text{ energy in gonad} = 0.0003 \times (\text{Whole Wet Wt.})^{1.515}.$$

This value was calculated using animals up to 41 cm (2800 g, from table 1, Kettle and Lucas, 1987) only. This gives a maximum gonad energy component of 50 %. Extrapolating to the 50 cm A. planci found in this study suggests an energy component in excess of 100 %, which is clearly impossible. For this study two sets of calculations were made using ceilings of 50 and 90 % total energy component of gonad.

DISCUSSION

Measurements of feeding rate

Measurements of feeding rate in A. planci described previously are 378 cm^2 coral/day (Chesher, 1969); 116 - 187 cm^2 coral/day (Pearson and Endean, 1969), 150 cm^2 coral/day (Glynn, 1973) and the area of a starfish's disk per day (Laxton, 1974). As feeding rate in this study was found to vary seasonally and with starfish size, direct comparisons of the above rates with those of this study are difficult, however all fall within the range of mean values found in this study (66 cm^2 coral/day, < 40 cm, June 1988, and 478 cm^2 coral/day, $\geq$ 40 cm, October 1987). Feeding rates in units other than area of coral cover, or weight of coral skeleton, have not previously been presented for A. planci. However, Glynn and Krupp (1986) provided data showing Culcita novaeguinea consumed about 0.26 g DW organic matter of Pocillopora damicornis tissue per day (about 28 cm^2 coral or 6.14 kJ) in Hawaii and suggested that this was about one-fifth of what was consumed by A. planci. This study shows it to be an even greater difference, on the Great Barrier Reef at least. Depending on size and season A. planci consumed between 1 and 7 g DW of coral tissue or about 15 to 150 kJ daily.

Seasonal differences in feeding rate

Clear seasonal differences in feeding rates of A. planci, consistent over the size range examined (20 - 60 cm) were demonstrated in this study. Starfish monitored in June fed at about half the rate of those in October and January indicating a profound winter - summer effect. Water temperatures during these two periods were 24 and 28 - 29 °C respectively.

Seasonal differences in feeding rate have not been recorded previously for A. planci, although Wilson and Marsh (1975) attributed a low "incidence" of feeding in a group of A. planci in western Australia to thermal stress from high surface water temperatures in summer. This was in line with the findings of Yamaguchi (1974b) who noted a strong effect of temperature on metabolic rate in A. planci and cessation of feeding in thermally stressed animals. It is likely that the winter-summer differences in feeding rate observed in A. planci in this study were related to water temperature.

Whilst significantly greater than in winter, the January feeding rate was significantly depressed when compared to the October samples. This within-summer reduction in feeding rate follows the mid-summer spawning season of A. planci and suggests that feeding rate is high leading up to the spawning season, i.e. during the period of intense gametogenesis and gonad growth (Lucas, 1973), and slows following spawning. The reduction in feeding rate following spawning may relate to the reduced energy requirement at that time and possibly a cause or consequence of post-spawning morbidity which is suspected in very large A. planci (Kettle, pers. comm.; Lucas, pers. comm.).

Identical patterns of behaviour are known from other asteroids. Both Asterias forbesi (MacKenzie, 1969) and Asterina minor (Soliman et al., 1986) were found to increase their feeding rate from winter to summer and both showed a reduction in feeding rate during the summer spawning season. MacKenzie (1969) was also able to show that feeding rate was related to water temperature.

Size/Weight specific feeding rate

A. planci was found to consume between 0.8 and 1.7 % of their body (dry) weight in coral tissue per day. The weight specific feeding rate decreased with an increase in size. It is well known that juvenile asteroids may feed at a greater relative rate than adults (Jangoux, 1982a). A reduction in weight specific feeding rate with an increase in body size has been recorded for a number of echinoderms and this is consistent with a reduction in weight specific respiration rates with increase in body size (Lawrence and Lane, 1982). Lawrence (1987) suggested that this may mean that somatic growth requires a greater amount of respiratory energy than gonadal growth. However, weight specific respiration in A. planci decreases as a function of weight, even in juveniles prior to the onset of gametogenesis (Kettle and Lucas, 1987). The reduction in weight specific feeding rate in large A. planci may be offset by partitioning of energy towards reproduction at the expense of the body wall as recorded by Kettle and Lucas (1987).

Feeding rate and growth

Further evidence for determinate growth in A. planci (Yamaguchi, 1974a) is provided in this study. Previously there has been debate regarding this (Kenchington, 1977). Laboratory studies of Yamaguchi (1974a) and Lucas (1984) indicate a slowing of growth, following sexual maturity, up to a maximum size of about 35 cm and yet field sightings of A. planci up to 73 cm (source cited in Lucas, 1984) have been made. Lucas (1984) reasoned that maximum size was likely to be variable, dependent on food availability and genotypic variation, but nevertheless determinate due to the way the mass of metabolizing tissue exceeds the starfish's capacity to feed (see also Birkeland, 1989) and the increasing proportional commitment of energy to reproduction. This study shows that despite increased feeding rates in large A. planci in areas of abundant food, energy requirements will still exceed intake capacity and thus growth must cease. Ultimate sizes predicted in this study are consistent with that of maximum starfish sizes observed in the field, ie. typically 45 - 60 cm, but up to 70 cm. The maximum size a starfish will reach is probably determined by the food availability during the exponential phase of its growth (Lucas, 1984).

Whilst senility of A. planci has not been identified in animals in the field, the results of this study indicate that such a state is inevitable. However, such individuals are likely to be very rare in the field where they would be susceptible to disease and predation.

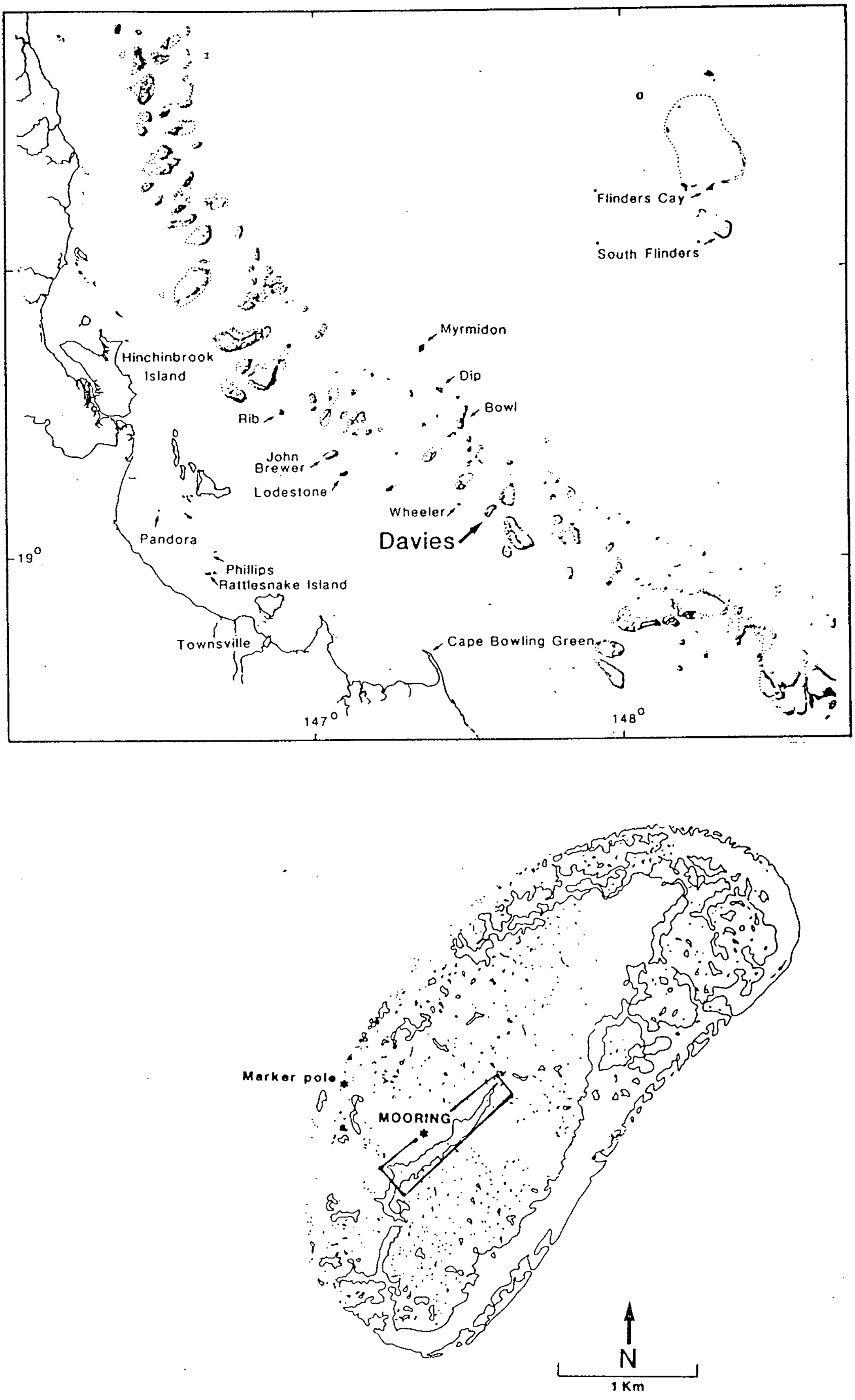
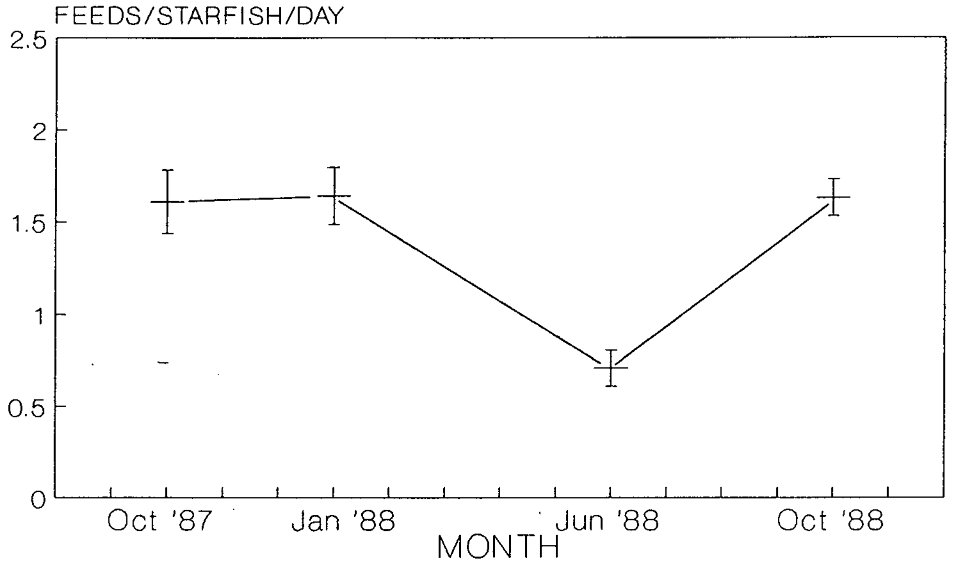


Figure 1. Location of Davies Reef within the central Great Barrier Reef. Location of the study site is indicated by the boxed area.



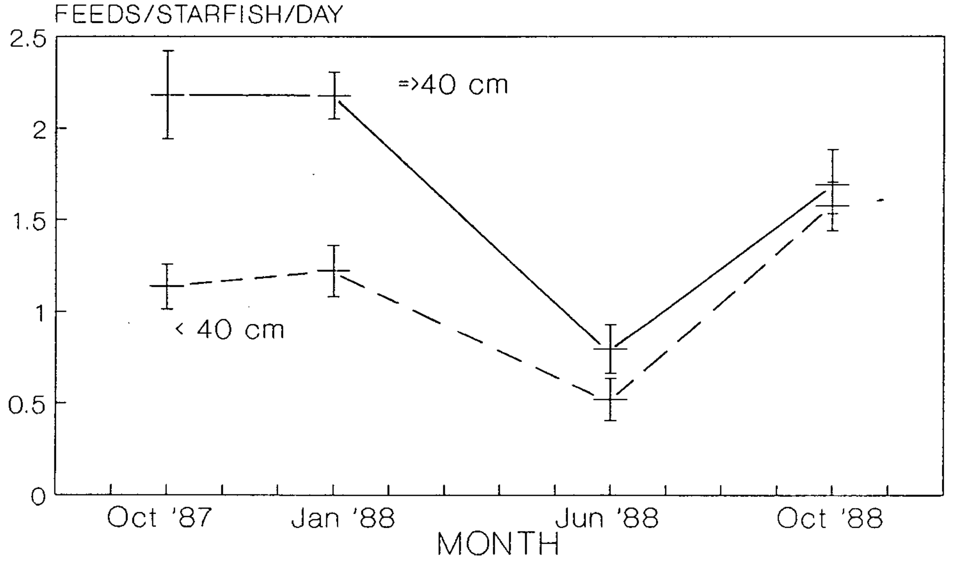
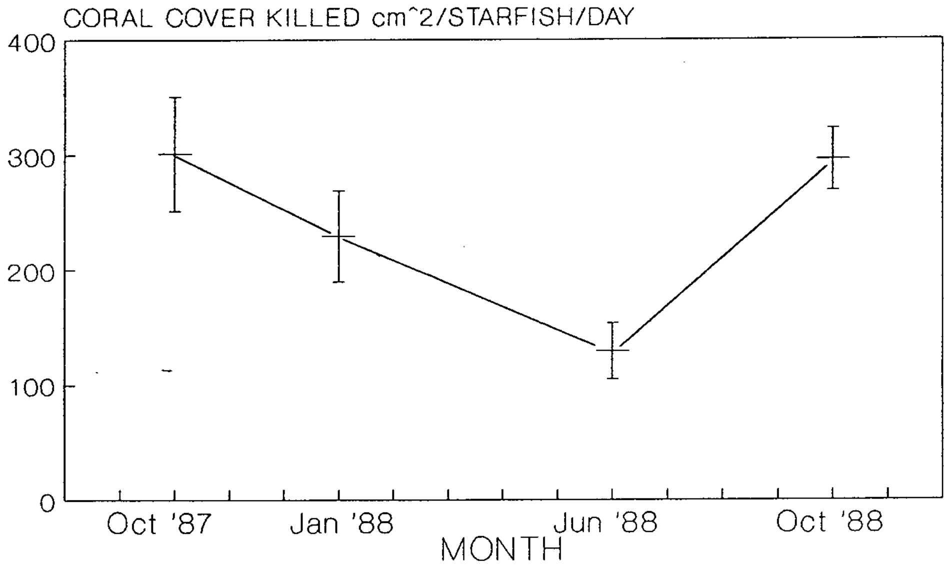


Figure 2. Mean number of feeding events per starfish per day ± 1S.E. at Davies Reef in October 1987, January 1988, June 1988 and October 1988. Upper figure is total sample, lower figure is split into two size classes. Sample sizes are given in table 1.



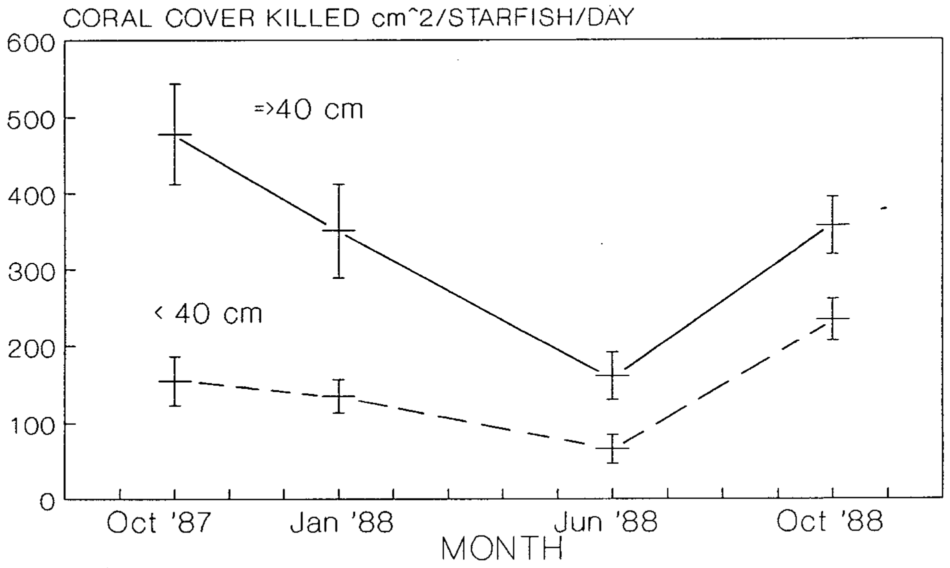
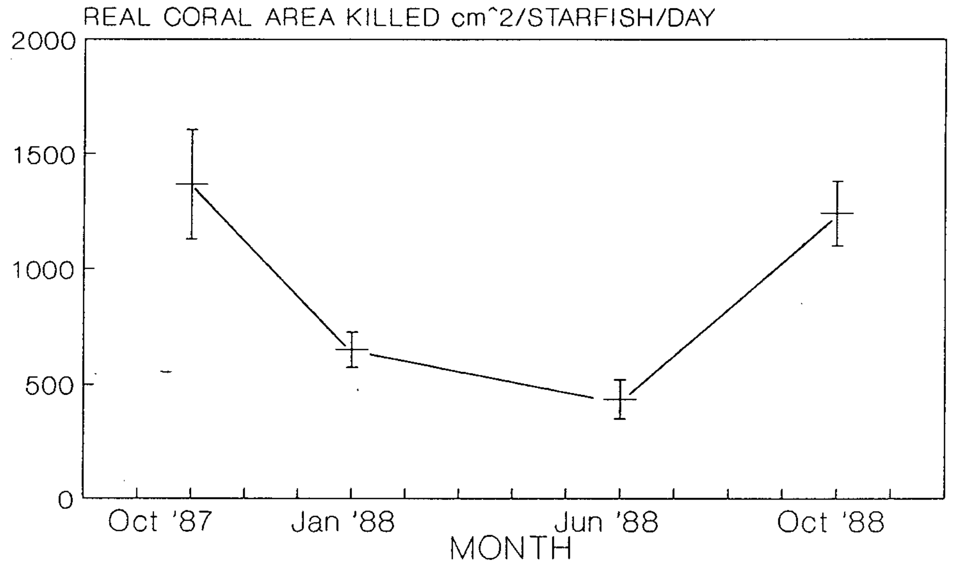


Figure 3. Mean area of coral cover killed (cm^2) per starfish per day ± 1S.E. at Davies Reef in October 1987, January 1988, June 1988 and October 1988. Upper figure is total sample, lower figure is split into two size classes. Sample sizes are given in table 1.



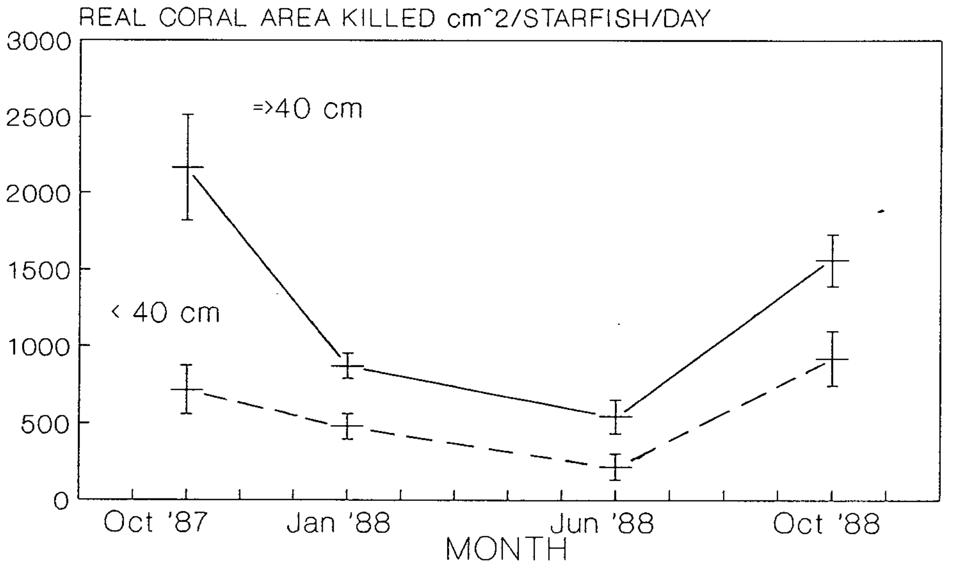
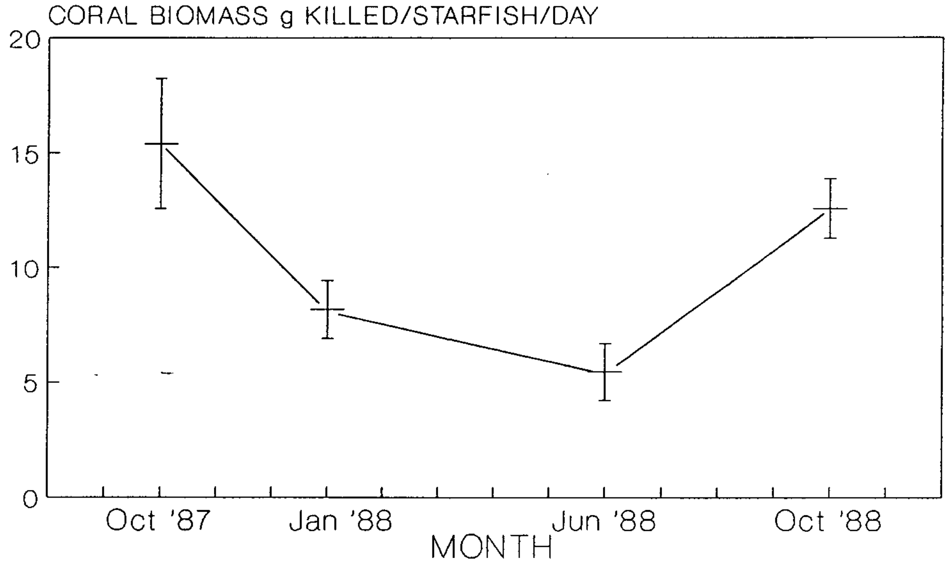


Figure 4. Mean of real coral surface area killed (cm^2) per starfish per day ± 1S.E. at Davies Reef in October 1987, January 1988, June 1988 and October 1988. Upper figure is total sample, lower figure is split into two size classes. Sample sizes are given in table 1.



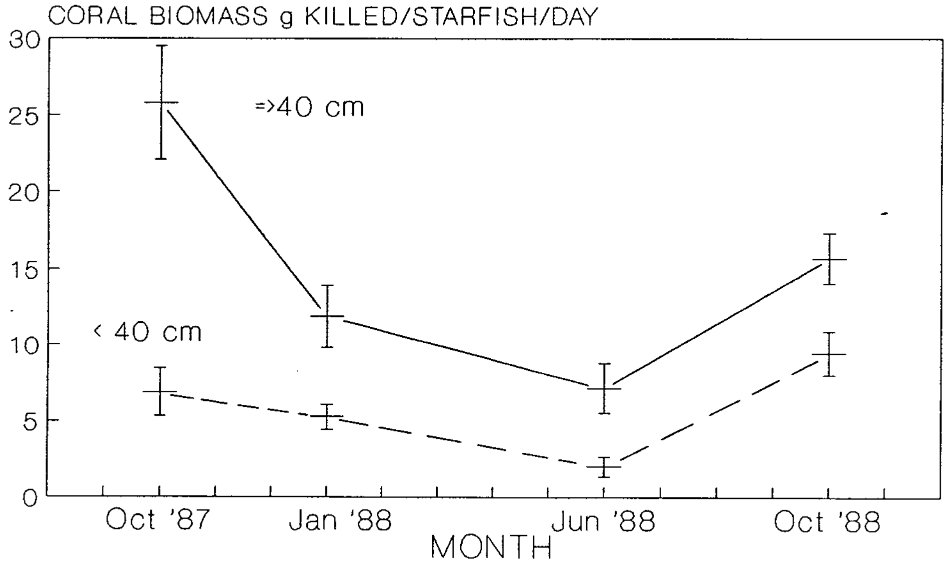
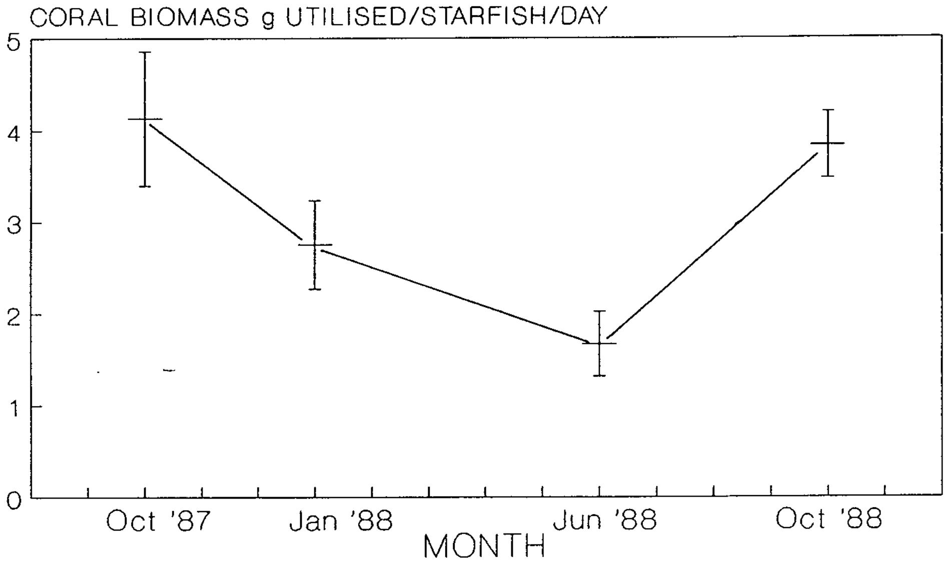


Figure 5. Mean coral tissue biomass killed (g DW) per starfish per day ± 1S.E. at Davies Reef in October 1987, January 1988, June 1988 and October 1988. Upper figure is total sample, lower figure is split into two size classes. Sample sizes are given in table 1.



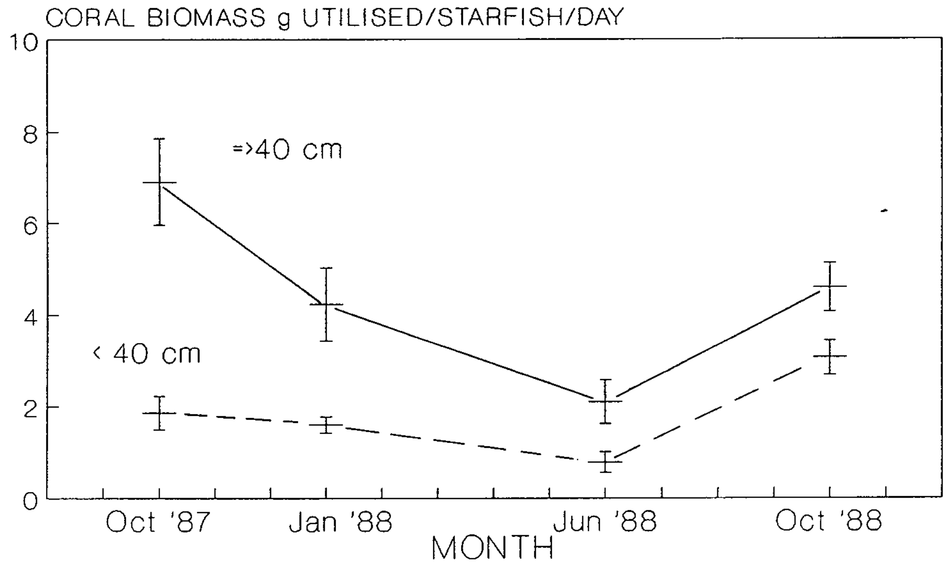
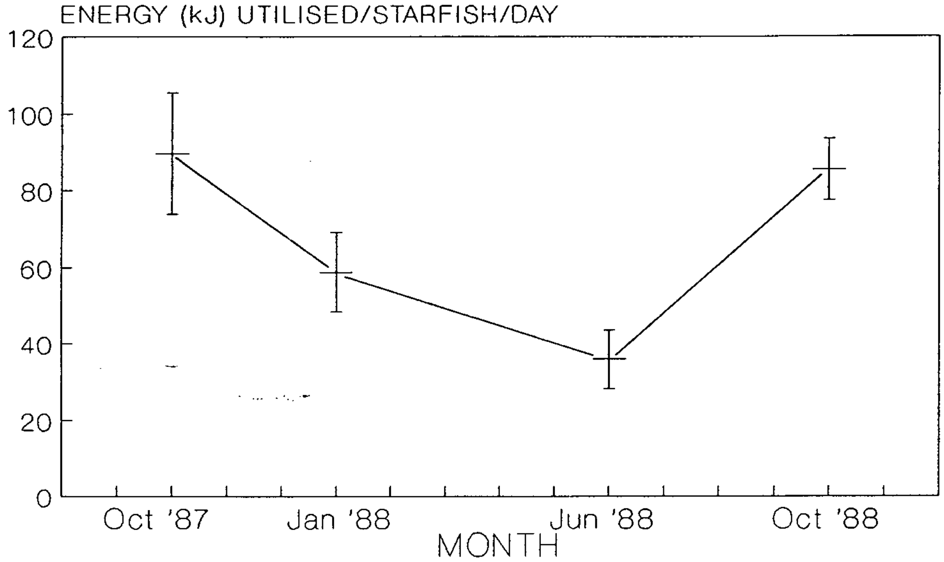


Figure 6. Mean coral tissue biomass consumed or utilized (g DW) per starfish per day ± 1S.E. at Davies Reef in October 1987, January 1988, June 1988 and October 1988. Upper figure is total sample, lower figure is split into two size classes. Sample sizes are given in table 1.



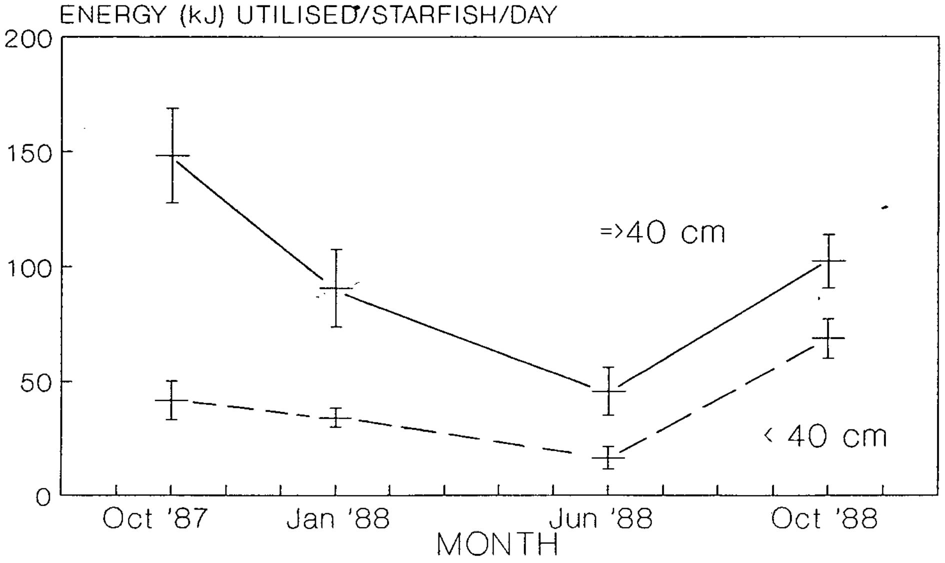


Figure 7. Mean energy value of tissue consumed (kJ) per starfish per day ± 1 S.E. at Davies Reef in October 1987, January 1988, June 1988 and October 1988. Upper figure is total sample, lower figure is split into two size classes. Sample sizes are given in table 1.

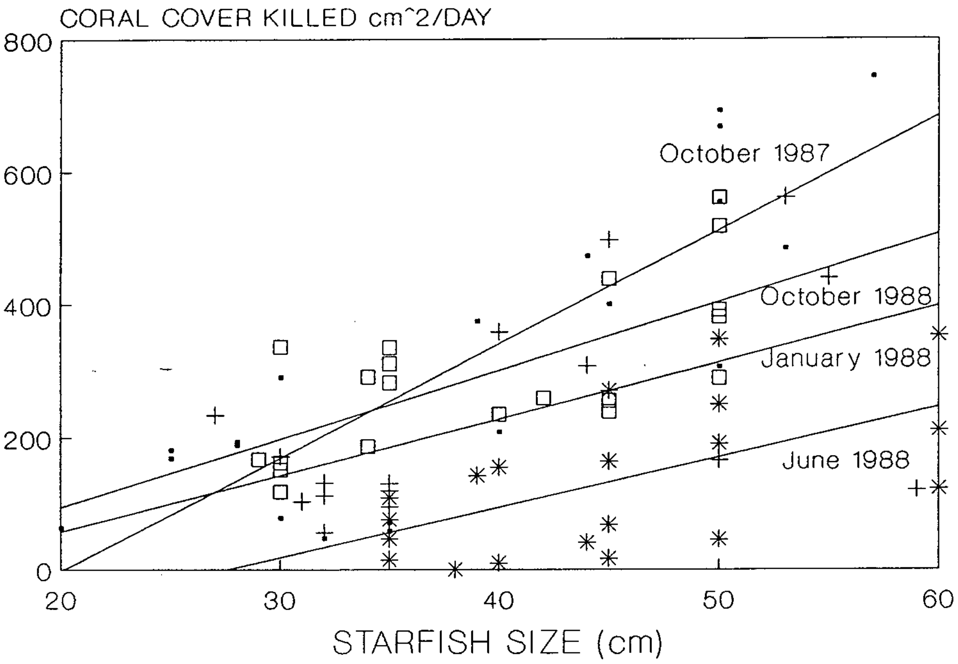


Figure 8. Relationship between starfish size and mean area of coral cover killed (cm^2) per day at Davies Reef in October 1987, January 1988, June 1988 and October 1988.

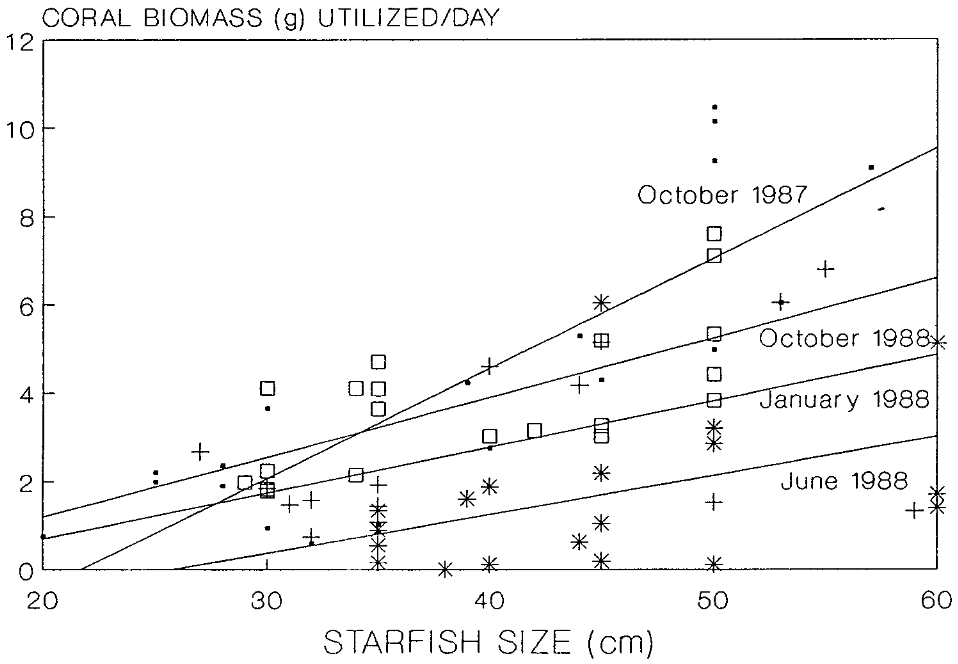


Figure 9. Relationship between starfish size and mean coral tissue biomass utilized (g) per day at Davies Reef in October 1987, January 1988, June 1988 and October 1988.

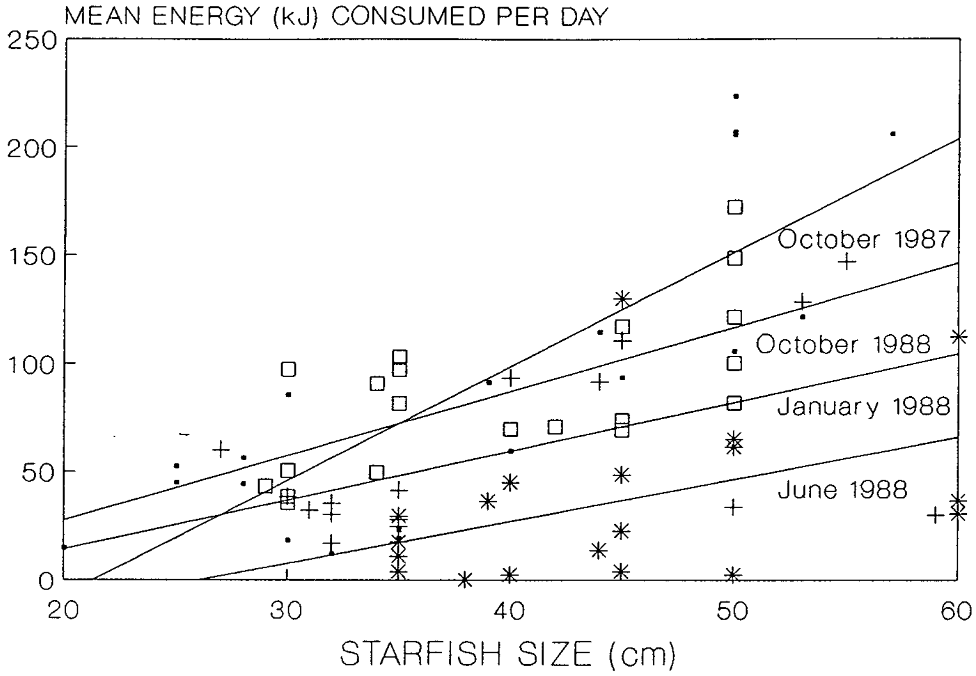
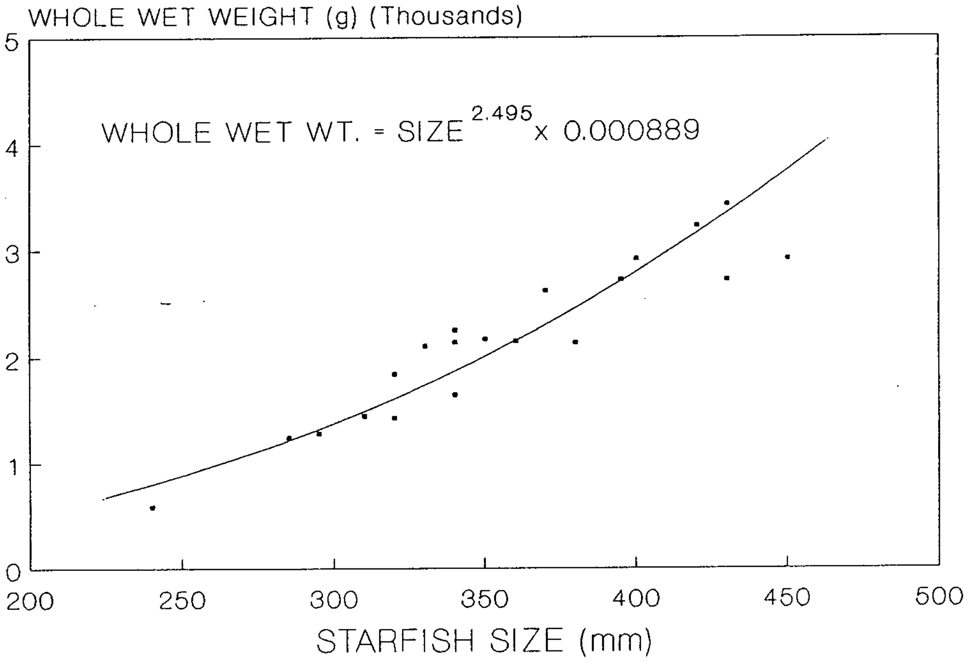


Figure 10. Relationship between starfish size and mean energy uptake (kJ) per day at Davies Reef in October 1987, January 1988, June 1988 and October 1988.



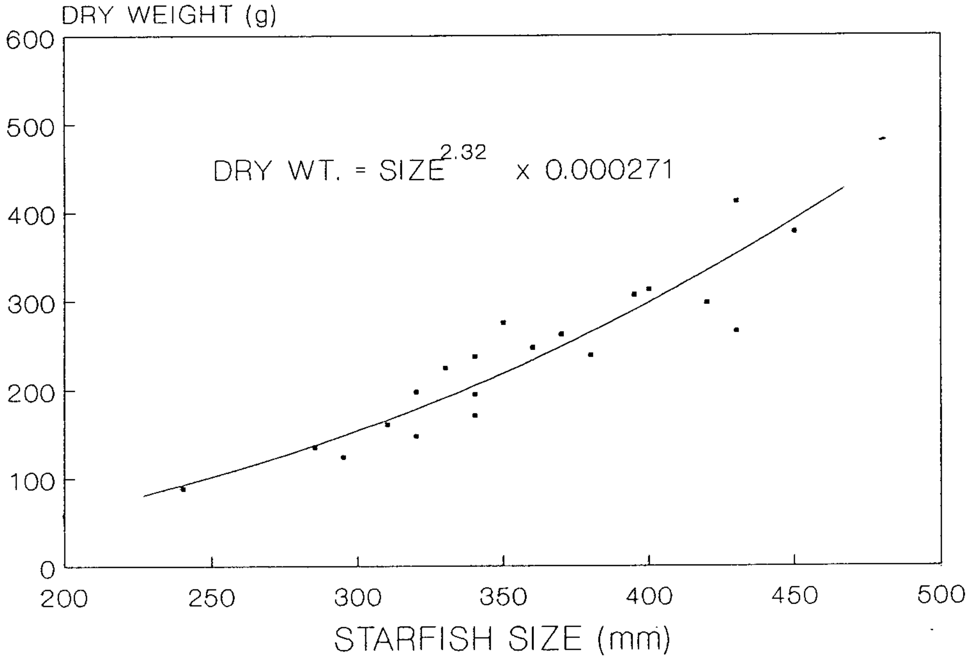
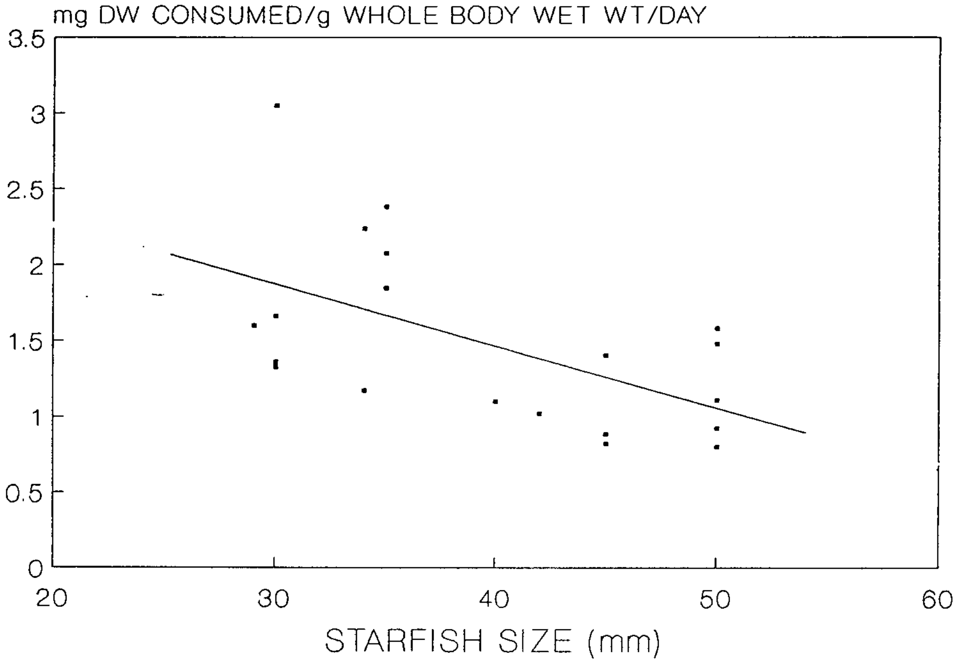


Figure 11. Relationship between diameter and wet weight (upper figure) and dry weight (lower figure) of A. planci collected from Davies Reef in May 1989.



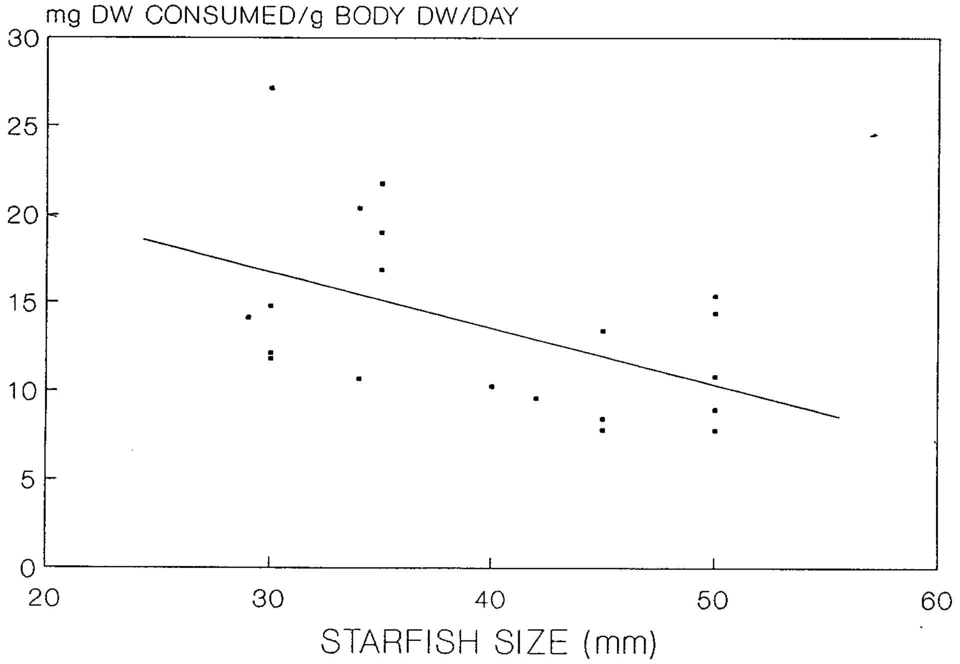


Figure 12. Relationship for weight specific feeding rate per day (g DW coral tissue utilized/g starfish wet wt. [upper figure] and dry wt. [lower figure]).

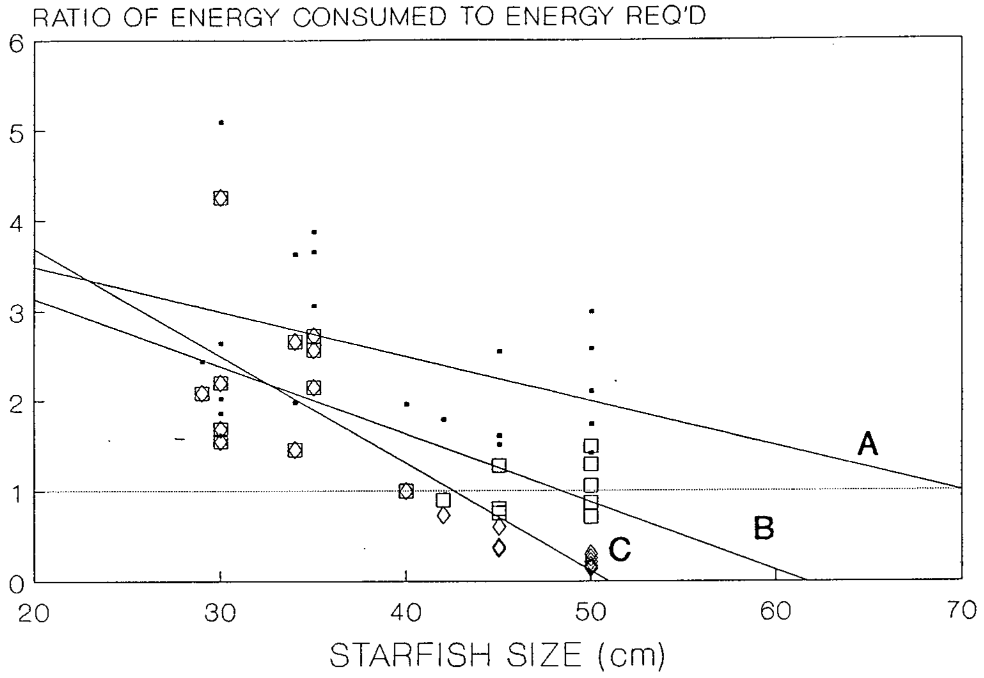


Figure 13. Relationship between starfish size and the ratio of energy consumed to energy required. Where the regression lines intercept with ratio = 1, this predicts maximum size for: **A.** negligible energy shunt to gonad; **B.** size dependent energy shunt to gonad up to maximum of 50 %; **C.** size dependent energy shunt to gonad up to maximum of 90 %. See text for further details of calculations.

	< 40 cm	≥ 40 cm	Total
Oct 87	29.7 ± 1.6 (11)	48.8 ± 1.7 (9)	38.3 ± 2.4 (20)
Jan 88	32.1 ± 0.9 (9)	49.4 ± 2.3 (7)	39.7 ± 2.5 (16)
Jun 88	36.0 ± 0.6 (7)	48.9 ± 1.8 (14)	44.6 ± 1.8 (21)
Oct 88	32.2 ± 0.8 (10)	46.7 ± 1.2 (10)	39.4 ± 1.8 (20)

Table 1. Mean size ± 1S.E. of *A. planci* monitored in each month at Davies Reef. Bracketed figures are sample sizes.

Colonies eaten per day (in part or total)

	< 40 cm	≥ 40 cm	Total
Oct 87	0.9 ± 0.3 (11)	2.5 ± 0.2 (9)	1.6 ± 0.3 (20)
Jan 88	1.0 ± 0.2 (9)	2.1 ± 0.3 (7)	1.5 ± 0.2 (16)
Jun 88	0.4 ± 0.1 (7)	0.7 ± 0.1 (14)	0.6 ± 0.1 (21)
Oct 88	1.2 ± 0.2 (10)	1.2 ± 0.2 (10)	1.5 ± 0.2 (20)

Colonies killed outright per day

	< 40 cm	≥ 40 cm	Total
Oct 87	0.4 ± 0.2 (11)	1.6 ± 0.3 (9)	1.0 ± 0.2 (20)
Jan 88	0.6 ± 0.2 (9)	1.5 ± 0.3 (7)	1.0 ± 0.2 (16)
Jun 88	0.2 ± 0.1 (7)	0.2 ± 0.1 (14)	0.2 ± 0.1 (21)
Oct 88	0.7 ± 0.2 (10)	1.1 ± 0.2 (10)	0.9 ± 0.1 (20)

Table 2. Mean number of coral colonies eaten and killed ± 1S.E. per day by _A. planci_ monitored in each month at Davies Reef. Bracketed figures are sample sizes.

Measure of feeding rate	Month	r^2	$P_{(r=0)}$	sig.
No. of feeds	Oct '87	0.466	0.001	***
	Jan '88	0.434	0.005	**
	Jun '88	0.135	0.101	NS
	Oct '88	0.040	0.396	NS
Coral cover	Oct '87	0.700	<0.001	****
	Jan '88	0.290	0.031	*
	Jun '88	0.349	0.005	**
	Oct '88	0.493	0.001	***
Real surface area	Oct '87	0.560	<0.001	****
	Jan '88	0.217	0.069	NS
	Jun '88	0.134	0.103	NS
	Oct '88	0.350	0.006	**
Biomass killed	Oct '87	0.676	<0.001	****
	Jan '88	0.262	0.043	*
	Jun '88	0.176	0.058	NS
	Oct '88	0.496	0.001	***
Biomass utilized	Oct '87	0.692	<0.001	****
	Jan '88	0.290	0.031	*
	Jun '88	0.210	0.037	*
	Oct '88	0.457	0.001	***
Energy uptake	Oct '87	0.676	<0.001	****
	Jan '88	0.268	0.040	*
	Jun '88	0.217	0.033	*
	Oct '88	0.461	0.001	***

Table 3. Summary results of regression analyses of size versus feeding rate.

	Test Statistic	df	P	sig.
Test for homogeneity of group variance	C=0.40	20,k=4	>0.05	NS
Test for homogeneity of slopes	F=1.304	3,69	0.280	NS
Test for difference between adjusted means	F=20.885	1,72	<0.001	****
Rank of adjusted means	1	2	3	4
	Oct'88	Oct'87	Jan'88	Jun'88

Table 4. Summary statistics of ANCOVA comparing significant lines of regression (size of *A. planci* versus coral cover killed) between month sampled.

	Test Statistic	df	P	sig.
Test for homogeneity of group variance	C=0.43	20,k=4	<0.05	*[1]
Test for homogeneity of slopes	F=2.000	3,69	0.122	NS
Test for difference between adjusted means	F=19.149	1,72	<0.001	****
Rank of adjusted means	1	2	3	4
	Oct'88	Oct'87	Jan'88	Jun'88

[1] The Cochrans C test was slightly significant ($C=0.43, C_{crit}=0.42$) at the 0.05 level. It was decided to proceed with the ANCOVA and test for significant differences between adjusted means using the LSD at the 0.01 level (C is NS at $\alpha=0.1$) to keep the Type I error rate at the same level as a test at $\alpha = 0.05$. [See Underwood (1981) for the validity of this procedure].

Table 5. Summary statistics of ANCOVA comparing significant lines of regression (size of *A. planci* versus biomass utilized) between month sampled.

	Test Statistic	df	P	sig.
Test for homogeneity of group variance	C=0.43	20,k=4	<0.05	*[1]
Test for homogeneity of slopes	F=1.731	3,69	0.169	NS
Test for difference between adjusted means	F=19.709	1,72	<0.001	****
Rank of adjusted means	1	2	3	4
	Oct'88	Oct'87	Jan'88	Jun'88

[1] The Cochrans C test was slightly significant ($C=0.43, C_{crit}=0.42$) at the 0.05 level. It was decided to proceed with the ANCOVA and test for significant differences between adjusted means using the LSD at the 0.01 level (C is NS at $\alpha=0.1$) to keep the Type I error rate at the same level as a test at $\alpha = 0.05$. [See Underwood (1981) for the validity of this procedure].

Table 6. Summary statistics of ANCOVA comparing significant lines of regression (size of A. planci versus energy uptake) between month sampled.

CHAPTER FOUR

Foraging behaviour of Acanthaster planci

INTRODUCTION

Foraging behaviour relates feeding biology to the ecology of an animal and includes consideration of the way its environment affects or governs the width of its diet, feeding preferences and movement in relation to feeding.

Aspects of foraging behaviour of A. planci have been examined previously in qualitative studies of diet (Dana and Wolfson, 1970; Chesher, 1969; Laxton, 1974) and feeding preferences (Garlovsky and Berguist, 1970; Branham et al., 1971; Glynn, 1974; Ormond et al., 1976). The large scale and qualitative nature of these studies has been described as inadequate in assessing feeding preferences (Moran, 1986), because the effects of small scale patchiness of the coral reef habitat on foraging are ignored. Moran suggested a more quantitative approach which took small scale phenomena such as localized food availability into account. Both abundance and quality of food are important in this regard.

Moran (1986) listed several factors likely to influence feeding preferences in A. planci, these were; nematocyst or commensal defences of corals, release of chemical attractants by corals, learnt behaviour and nutritional state of starfish, environmental conditions and abundance, morphology, accessibility and nutritional value of corals. Of these the importance of nutritional value of the prey species to prey preference has received little attention. Collins (1975c), Huxley (1976), and Ormond et al. (1976) have demonstrated that A. planci exhibits learnt behaviour or "ingestive conditioning" (Wood, 1968) whereby the more familiar prey items are selected (see also chapter 1). This may account for the apparent preference of A. planci for the commonly occurring Acropora species (Pearson and Endean, 1969; Ormond et al., 1973, 1976); however, some studies have shown A. planci preferring locally rare food types (Branham et al., 1971, Glynn, 1974) suggesting that other factors such as nutritional quality of food may be important in prey selection (Ormond et al., 1976).

This possibility has been pursued in this study. The approach taken was to: (i) examine prey selection in the field (taking into account the precautions suggested by Moran, 1986); (ii) compare this with that exhibited under controlled conditions of prey availability in aquaria; (iii) compare the nutritional value of preferred and non-preferred prey types.

There have been several reports of rates of movement in A. planci (Pearson and Endean, 1969; Ormond and Campbell, 1974) and some on distances moved during foraging (Barham et al., 1973; Aziz and Sukarno, 1977). These studies provided little information on differences within and between populations in contrasting areas of food availability and similarly no information on temporal variability within populations. The range of movement in individual foraging animals and the dependence of movement on food availability was further examined in this study.

Thus, this section of the study addresses several aspects of the foraging characteristics of A. planci:

1. the composition of the diet of A. planci observed in the field and the effect of food availability on diet.

2. movement of A. planci in relation to feeding and food availability.

3. prey preference in the field and the laboratory and the influence of food availability on prey preference.

4. how prey preference in A. planci may be related to food value of its prey.

MATERIALS AND METHODS

Field Studies

Fieldwork for this aspect of the study was carried out at Wheeler Reef, Davies Reef and Little Broadhurst Reef; all in the central section of the GBR. Data on diet and the effect of food availability on diet were collected at Wheeler Reef during the behaviour pattern surveys (see chapter 2) and information on feeding preferences and foraging movements was collected in conjunction with the feeding rate studies at Davies Reef (see chapter 3). Monitoring tagged starfish at Little Broadhurst Reef (Lat. 18° 58' Long. 147° 42') in October 1987 provided data on foraging on a reef with depleted coral cover in contrast to the situation at Davies Reef.

Feeding preferences

Data on feeding preferences were collected during monitoring of tagged A. planci at Davies Reef on four occasions between October 1987 and October 1988 (see chapter 3). The technique used was the "nearest neighbour" method used by Dr. P. Moran in his study on feeding preferences in A. planci (Moran, 1985). This technique entails identification and measurement of the five nearest coral colonies and their distance from the A. planci prey colony.

Each coral colony was identified to genus level and the percentage of each genera taken as prey and available as prey was calculated. To assess preferred and non-preferred prey, an index of prey preference (PPI) for each available prey genera (i) was calculated as follows:

$$PPI_{(i)} = \frac{\text{no. of genus (i) eaten / total no. prey eaten}}{\text{no. genus (i) available / total no. prey available}}$$

Indices greater than one indicate genera that were taken in proportions greater than their availability (preferred). Values less than one indicate that those genera were non-preferred.

Foraging movements

Data on movement rates of tagged A. planci were determined at Davies Reef and Little Broadhurst Reef. Simple measurements of daily distances moved were carried out on all four visits to Davies Reef, whilst data on direction and displacement[1] of starfish during foraging were collected only in October 1988. Movement rates at Little Broadhurst Reef were collected only in October 1987.

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[1] Displacement refers to the absolute distance moved as opposed to the total distance moved. i.e. movement of 1 m to the left followed by 1 m to the right is a total distance of 2 m moved but the absolute distance moved or displacement is 0 m.

Starfish were monitored once or twice per day at Davies Reef for periods of up to five days and every three hours at Little Broadhurst Reef for two days only. The position of each tagged starfish was marked with coloured surveyor's tape at the time of each observation and the distance between tapes was measured.

The ratio of displacement to total distance moved was used as an index of directional movement. Thus movement consistently in one direction will displace the starfish a greater distance from its origin (ratio nearer to one) than would random movement over the same time (ratio nearer to zero). The method of measurement assumes direct movement between each observation, thus probably underestimating the total distance covered during foraging.

Aquarium Studies

Feeding preferences

Feeding preferences of A. planci under controlled conditions of food availability in the laboratory were investigated for comparison with field observations. Ten specimens each of 11 coral species were distributed haphazardly on the bottom of a 3 m diameter pond with flowing seawater. Ten A. planci (ca. 35 cm) were introduced to the tank after five days without food and feeding behaviour was observed over 12 nights. Corals were removed as they were eaten. The frequency of predation on each species in relation to its availability was then calculated.

Time taken to feed (digestion time)

Measurements of time taken to feed were made in the 3 m diameter pond for A. planci feeding on several species of coral. Starfish were monitored from the time they climbed onto the coral and began feeding until they moved off. Checks were made periodically using a mirror to ensure stomach eversion and thus feeding was taking place. Measurements were made with freshly collected starfish to exclude hunger as a factor in the experiment.

Comparison of food value of different species of coral

Because A. planci feeds extra-orally, several factors are important in assessing the comparative food values of different coral species. Probably the most important of these are surface complexity of the coral, biomass of corals (per unit area), the nutritional (energy and protein) value of the tissue and the ability of the starfish to extract the tissue.

Tissue availability was calculated in terms of grams dry weight per unit area of coral skeleton and the nutritional value of different coral species was calculated in terms of kilojoules per gram dry weight of coral tissue. The methods of assessing coral tissue biomass, calorific value and surface area have been outlined in the previous chapter along with a description of the technique for analysis of feeding efficiencies of A. planci on different species. Protein content of coral tissue was calculated stoicometrically from the nitrogen composition of coral tissue (Gnaiger and Bitterlich, 1984; see also chapter 3).

RESULTS

Characteristics of foraging

Field studies

Diet

Over 1600 observations of A. planci feeding were made at Wheeler Reef during the three visits to the reef in 1986 and 1987. Table 1 summarises the observed prey items. Scleractinian corals made up over 90 % of prey items during all three months sampled, with Acropora species constituting a large component of these. The main non-scleractinian food items were alcyonarian soft corals, zoanthids and coralline algae. Inspection of A. planci feeding on non-animal prey usually revealed only partial stomach eversion. Starfish tagged at Davies Reef were only seen to prey on scleractinian corals (403 observations), of which 52.8 % were Acropora (appendix table I).

i. Effects of food availability on diet

The availability of prey species affected both the coral species and non-coral species components of the diet in A. planci. Non-acroporan corals were taken in much greater proportions than Acropora spp. in low coral areas (70 - 90 % of prey items) compared with 25 - 50 % in high coral areas. In turn the proportion of non-coral prey species was highest in low coral areas (4 - 10 % of prey items) compared with high coral areas (0 - 2 %)(appendix figures XV, XVI and XVII).

Feeding Preferences

Preferred corals were those taken in greater proportions than their abundance. These included the common genera Acropora, Seriatopora, and Stylophora. Common genera which were non-preferred included Porites, Favites, Goniastrea, Cyphastrea and Pocillopora. Another common genus, Montipora, was taken as prey in similar proportions to its availability (appendix table I). Figure 1 groups prey preference indices by family and indicates that pectinids and acroporids were highly preferred, being taken in proportions 1.5 - 1.7 times their abundance, whilst pocilloporids were slightly preferred and faviids, poritids and mussids were non-preferred. Predation was not recorded on all families present.

i. Effect of food availability on prey species preference

At very high levels of live coral cover (> 50 %) the only preferred genera were Stylophora and Acropora. At lower levels of live coral cover a greater proportion of available genera were preferred. Seven genera, including those above, were preferred at < 10 % coral cover (appendix table II). The effect of low levels of food availability on prey selection is most evident at the family level (figure 2). Acroporids were the only family preferred at all levels of live coral cover. Pocilloporids were preferred at all levels of live coral cover less than 50 %. Faviids were taken in greater proportion to their abundance only at live coral cover levels less than 10 % and poritids were never among the preferred families.

The abundance of acroporids available as prey decreased directly with live coral cover. Faviids and poritids were only more abundant than acroporids and pocilloporids at levels of live coral cover less than 10 % (figure 3).

Foraging movements

i. Distance

The mean daily movement for tagged starfish at Davies Reef over the four field trips was 2.8 m per day (see table 2). There was no significant difference in the mean rate of movement between months (ANOVA, $p > 0.05$).

ii. Direction

The mean ratio of displacement to total distance moved was 0.61 (sd = 0.28) for average daily movements and 0.38 (sd = 0.30) for movement over the five 4 - 5 day periods of observation. These means are significantly different (paired t-test, $p = 0.001$); however, neither are significantly different from 0.5 and both are significantly different from 0 and 1 (one tail t-test, $p > 0.1$). These data are limited to observations of 17 tagged A. planci from October 1988 at Davies Reef, but they suggest that foraging movement is at least partially directional on a day to day basis, tending toward randomness over greater periods of time.

iii. Effect of food availability on movement

Food availability was found to affect mobility in A. planci with animals in areas of > 30 % live coral cover moving at a lesser rate (1 m.day^{-1}) than those in areas with poorer coral cover (3 - 4 m.day^{-1}, see table 3) (ANOVA on log transformed data, $p < 0.001$). Analyses of tagged starfish movement data also revealed that small-medium sized A. planci (< 40 cm) are significantly less mobile than larger animals (1.4 m.day^{-1} compared with 4.2 m.day^{-1}, see table 2, t-test on log transformed data, $p < 0.001$) and tend to be found in areas of higher coral cover (see table 3, ANOVA, $p < 0.001$). Movement in the low density Davies Reef population was less than that found at Little Broadhurst Reef (table 3) where the _A. planci_ were an order of magnitude denser and coral cover on the entire reef was very low.

Laboratory studies

Feeding Preferences

Of the species offered to _Acanthaster planci_ in the laboratory the two _Acropora_ species were the first taken and thus most highly preferred. These species were followed by _Seriatopora_ and _Stylophora_. _Porites_ colonies were only consumed when most other genera had been depleted (appendix table III). Figure 4 shows the pattern of prey selection at the family level for acroporids, pocilloporids, faviids and poritids. These laboratory data agree strongly with those found from the field tagging studies with a clear order of preference of acroporids > pocilloporids > faviids > poritids (see figure 1).

Prey recognition time

Prey recognition time is difficult to assess and was determined to be the time taken to reject non-preferred prey. On numerous occasions during experiments carried out to assess time taken to feed (digestion time) starfish were seen to mount prey in typical feeding fashion, only to move off some minutes later, leaving the coral apparently unharmed. This was observed only with non-preferred genera such as _Porites_, _Goniastrea_, and _Fungia_, and exceeded five minutes only on one occasion (7 minutes).

Time taken to feed

The time taken to feed by Acanthaster planci on the coral colonies offered ranged from 0.5 to 11 hours; however digestion time was dependent on prey size and prey type. There was a significant relationship between prey size and time taken to feed ($p < 0.05$) for Acropora sp., Acropora carduum, Seriatopora hystrix and Stylophora pistillata (appendix figure XVIII). The mean digestion time per unit area was calculated for each sample and differences between species and between family were examined. Time taken to feed varied from 3.2 min/cm^2 for A. carduum to only 1.0 min/cm^2 for Porites lutea. More time is spent in consuming acroporids than either the pocilloporid or poritid families (appendix table IV).

Mean time taken to feed was correlated with ash-free dry weight absorbed for the seven species examined where corresponding data on feeding efficiency were available (table 4) (Spearman rank correlation, $r_s = 0.739$, $p < 0.05$). This indicates that the amount of food absorbed is directly proportional to time spent feeding for prey of uniform size.

Feeding efficiency

The efficiency of tissue extraction by A. planci during feeding varied between 0 and 57 percent of available tissue depending on the prey species (appendix table V). The magnitude of the error estimates and variability in coral tissue ash content (see later) preclude statistical comparisons between species; however, in general terms A. planci fed much less efficiently on Porites than on other species examined. Qualitative observation of freshly eaten colonies both in the field and the laboratory indicated that large amounts of tissue remained in the skeletons of Porites, faviid and fungid prey when compared to Acropora, Stylophora and Seriatopora. Examination of colonies broken in half reveals that the living layer of tissue in the latter genera extends only one or two mm into the skeleton compared with 3 - 5 mm or more in Porites, faviids and fungids.

Prey characteristics

i. Surface area

The ratio of real surface area (RSA) to apparent or planar surface area (PSA) is an index of the complexity (IC) of available surface on which the starfish has to feed[1]. The branching and tabulate Acropora species had the greatest IC (5.2 - 5.6) followed in turn by the branching pocilloporids (4.0 - 5.1), the massive growth form corals (mussids, faviids and poritids 3.0 - 3.8) and the foliose and encrusting forms (1.3 - 2.1)(appendix table VI).

ii. Biomass

Coral biomass was calculated in terms of ash free dry weight (AFDW) per unit area (PSA and RSA) for each of the species examined. The massive growth form corals, mussids, faviids and poritids, had the greatest biomass (10 - 25 $mg.cm^{-2}$ RSA) compared with 3 - 6 $mg.cm^{-2}$ RSA in acroporids and pocilloporids (appendix table VII). Ash content of coral tissue varied between 29 % in Pocillopora damicornis and 62 % in Porites lichen. Ash content of pocilloporids was consistently at the lower end of the range (29 - 34 %) but varied greatly in other families; ie 35 - 56 % for acroporids and 38 - 62 % for poritids (appendix table VIII).

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[1] see chapter 3 (materials and methods) for explanation and calculation of RSA and PSA.

iii. Energy content

The energy content of the coral species examined varied between 17.5 - 23.7 kJ.g^{-1} AFDW (4.18 - 5.66 kcal.g^{-1} AFDW). Species of Acropora generally had the highest energy content 19.3 - 23.7 kJ.g^{-1} AFDW, with pocilloporids ranging between 21.6 and 22.7. The species with the lowest energy content were Porites lichen (17.5) and P. lutea (18.0)(appendix table IX).

iv. Protein content

Protein content of coral tissue varied between 40 and 60 % of AFDW. The pocilloporid species along with Fungia had the highest protein content (56.8 - 59.9 %) whilst the Porites species were at the lower end (40.6 - 50.1 %)(appendix table X).

Comparison of food value of different corals to A. planci

i. Tissue absorption

Table 4 compares the absorption of AFDW coral tissue by A. planci feeding on similar sized colonies of different species. This takes into account the biomass of the different species, tissue ash content and tissue extraction efficiency (see also appendix table V). The acroporids, pocilloporids and fungids allow the highest degree of absorption (68 - 81 %) for A. planci and the poritids, mussids and faviids the least (0 - 44 %).

ii. Energy and protein value

Table 5 shows the calculated energy and protein obtained by A. planci feeding on similar sized colonies of different species. Food values ranged from minimal return in Porites cylindrica and P. lichen to 91 kJ and 2232 mg protein in Lobophyllia hemprichii. The most commonly eaten food items, i.e. Acropora and Stylophora provide a feeding A. planci with about 20 - 40 kJ and 400 - 1000 mg Protein per 100 cm^2 coral eaten.

iii. Food value as a function of time

For species where time taken to feed by A. planci was proportional to prey size, energy consumption was 5 - 10 $kJ.h^{-1}$ and protein consumption 133 - 282 mg $protein.h^{-1}$ (table 6). These values were for acroporids and pocilloporids. Porites lutea and Fungia had potentially higher rewards per unit time. However, the high variability in digestion times and their independence of prey size indicate that some feeds may be unsuccessful. In such cases, food value of these species will be variable, and may perhaps dependent on experience or the hunger of the starfish.

The comparative food value of different prey to A. planci is greatly affected by search time and the relative abundance of different coral types (table 7). For example for search times of 0.5 hours in areas of low (< 10 %) coral cover Porites lutea provided 2.5 times the rate of energy uptake than Acropora carduum, but only 1.2 times more when the search time was 10 hours. At high levels of food availability (> 50 % coral cover) A. carduum provided a greater rate of energy uptake than P. lutea at all but the shortest of search times (see table 7).

iv. Overall food potential of prey

Table 8 broadly summarises the prey characteristics for the common scleractinian families listed in order of prey preference by A. planci. This takes into account surface area complexity, biomass, absorption efficiency, energy and protein value. The comparative abundance of each family of corals at the Davies Reef study site is also shown. The table suggests that the preferred families (acroporids and pocilloporids) have the theoretically favourable traits of high abundance, high surface area complexity and are at the higher end of the food value measurements when compared to non-preferred families such as poritids. The favoured families have the lowest biomass; however, this appears to be countered by the starfish being able to extract tissue more readily from these species.

DISCUSSION

Diet

As found elsewhere _A. planci_ is primarily a corallivore (Jangoux, 1982a) feeding almost exclusively on scleractinians. Despite this apparent specialization, _A. planci_ feeds on a large number of different species. Prey from eight families and seventeen genera of hard corals were recorded in this study. Non-coral prey are rarely taken but the incidence of non-coral prey increases in response to low levels of food availability. This response has been suggested previously (Chesher, 1969), but here it has been quantified. In this study other coelenterates (alcyonarian soft corals and zoanthids) were the usual non-coral foods as well as some algae. Moran (1986) listed algae, some molluscs and other coelenterates as previously recorded non-coral foods of _A. planci_ in the field.

Movement in relation to feeding

Acanthaster _planci_ is known to move up to 80 m in a day (Ormond and Campbell, 1974) but normal foraging distances are much less. The mean daily movement rate of 2.8 m/day found in this study for A. planci in low density and in areas of adequate food supply (Davies Reef) is the same as that observed in the Red Sea by Ormond and Campbell (1974), but lower than that observed in Mexico (8.9 m/day) by Barham et al. (1971). Aziz and Sukarno (1977) recorded foraging movements of 0.3 - 8 m/day in Indonesia. Starfish density and food availability are likely to account for differences in movement rates in relation to foraging by A. planci. In this study animals in a high density population with low food availability (Little Broadhurst Reef) moved on average 10.3 m/day. Within the Davies Reef population starfish in areas of similar low coral cover (< 10 %) moved on average 4.3 m/day, which is more than in areas of coral cover greater than 30 % (1.0 m/day), but still less than that at Little Broadhurst Reef. This difference may reflect the urgency dictated by competition and the overall low coral cover at Little Broadhurst Reef which in turn may have resulted in poor nutritional condition of the starfish. At Davies Reef a foraging starfish can move in and out of areas of high and low food availability and would rarely encounter intra-specific competition for food. Variability in movement rates inversely correlated with coral availability was also noted by Barham et al. (1973) in the Gulf of California.

Time taken to feed

Digestion time in A. planci has not been recorded previously, but was known to take several hours (Goreau, 1964). Digestion times recorded in this study were found to be species dependent, and size dependent for some coral species. There was no relationship between time taken to feed and size for Porites or Fungia indicating that in some cases feeding on these non-preferred corals may be unsuccessful. Tissue absorption and time taken to feed were directly related in the species examined indicating that a short feeding time for some prey species may not be an attribute favouring predation of that species.

Prey preference

Acroporid and pocilloporid corals were preyed upon by *A. planci* in preference to others. There was clear rejection of the other two common families at the study site: faviids and poritids. Faviids joined acroporids and pocilloporids as preferred groups in areas of low coral cover when the latter two were less common than in high coral areas. An aquarium experiment under controlled conditions reinforced this trend with acroporids being selected first, followed by pocilloporids and then faviids. Poritids were only taken in proportions greater than their availability toward the end of the experiment when other prey sources were scarce. These findings are consistent with those of earlier studies on feeding preference in *A. planci* in the Red Sea (Brauer *et al.*, 1970; Collins, 1975c; Ormond *et al.*, 1976) and the qualitative field observations of Pearson and Endean (1969) and Branham *et al.* (1971) in Australia and Hawaii, respectively. These workers determined acroporid and pocilloporid corals were preferred prey and corals such as *Porites* were avoided. This conflicts with studies in the eastern Pacific where *Porites* has been found to be taken in preference to *Pocillopora* (Dana and Wolfson, 1970; Glynn, 1974). The genus *Acropora* does not occur in Mexico and Panama where this work was done (Veron, 1986). In these areas *Pocillopora* is the most common genus. Although *Pocillopora* makes the greatest proportion of the prey of *A. planci* in Panama (Glynn, 1974), predation by *A. planci* on *Pocillopora* is limited by commensal crabs which repel foraging starfish (Glynn, 1980). This may be an important factor in determining that *A. planci* in the eastern Pacific must feed on less abundant corals. The most favoured of these seem to be *Porites*, agaricids and siderastreids (Glynn, 1974).

Prey preference and nutritional value of prey

Ormond et al. (1976) first suggested that nutritional quality of food may be important in determining prey preferences in A. planci. This followed reports of selection of rare prey species by A. planci despite clear evidence for ingestive conditioning from their own studies and those of Collins (1975c) and Huxley (1976). Allen (1983) has previously related food value (AFDW obtained) of bivalve prey to feeding preference in Asterias rubens.

The preferred prey families of A. planci (Acroporidae and Pocilloporidae) were amongst those with the highest energy and protein content of corals examined in this study. The most non-preferred group, Porites, had the lowest energy and protein content. However, relating feeding preference to food value for an animal feeding on a large number of species in such a complex environment as a coral reef requires more than an assessment of absolute nutritional content of food. For example, there was variability within coral groups in terms of nutritional content of tissues and the non-preferred family Faviidae had similar nutritional content to the preferred families. In addition, biomass was hardly related to prey preference, with the main four non-preferred families poritids, mussids, faviids and fungids having far greater biomass than either of the preferred families.

The non-preferred, but potentially high nutritional value corals are less common than acroporids and pocilloporids except where coral cover is low, as a result of selective predation. Thus, their relative rarity and the increased search time for predators may outweigh the higher food value when it comes to influencing prey selection. Indeed, there was evidence for this in this study. The rate of energy uptake was related to prey preference when comparative search times at different levels of food availability were considered. The strongly favoured Acropora coral provided the greatest rate of energy uptake in high coral areas where the less favoured Porites was comparatively rarer, but in areas of poor food availability where there was less difference in the relative abundance of the two genera, Porites provided a greater rate of energy uptake than Acropora. This may explain the observation of a greater rate of acceptance of Porites as prey in low coral areas compared to areas of abundant alternative prey. These results suggest that A. planci has at least some response consistent with that predicted by optimal foraging theory (see Morse, 1980, Sibly and Calow, 1986). However, Porites remained a non-preferred genus even at very low levels of live coral cover, indicating that other factors may be more important in determining prey preference.

Laboratory experiments have shown that starfish exhibit some behavioural characteristics consistent with optimal foraging theory. These include prey species selection (Allen, 1983) and prey size selection (McClintock and Robnett, 1986). However, the only demonstration of optimal foraging by an asteroid in the field is for Oreaster reticulatus, a detrital feeder occupying a very uniform habitat (Scheibling, 1981).

The other important factor will be the ability of A. planci to feed on the tissue. In this regard two elements are important: the area which can be covered with the stomach and the efficiency with which it can extract tissue.

Jangoux (1982b) has described A. planci as having an "enormous", well-developed stomach, thus enabling it to cover a large area when feeding. Despite this, lateral expansion of the stomach rarely exceeds the dimensions of the body disc when feeding (pers. obs.), thus effectively limiting the area which can be fed upon at any one time.

However, within this constraint the expansion of the stomach is great, meaning that most available surface area beneath the disc can be utilized. As such, prey with a complex branching structure should provide a greater surface area for feeding than encrusting forms of the same diameter or planar dimensions. This was borne out in this study. Analysis of surface area complexity showed that branching forms of coral such as the favoured acroporids and pocilloporids may have more than four times the utilizable area of encrusting forms and one and a half times more than massive growth forms.

Efficiency of tissue absorption was found to vary greatly with the preferred acroporids and pocilloporids being amongst the most efficiently fed upon groups. This may be related to superficial position of the tissues in these groups. Glynn and Krupp (1986) suggested that "tissue accessibility" in Pocillopora was related to effective utilization of organic matter by Culcita novaeguinea. Glynn and Krupp found that C. novaeguinea showed a preference for Pocillopora over Montipora, Porites and Fungia. Thus, both Glynn and Krupp (1986) and this study have found a relationship between prey preference and tissue extraction efficiency in the major corallivorous asteroids. However, this still does not provide a conclusive link between prey preference and nutritional value of food. This is because when all factors such as surface area complexity, biomass, tissue absorption efficiency and nutritional content are taken into account there is little difference in the actual energy and protein absorbed between preferred and non-preferred groups (refer table 5).

It appears that if nutritional value is an important factor in determining prey preference in A. planci, then factors such as the location of energy reserves in corals may be important. Recent and ongoing work has suggested that lipid reserves in hard corals are deep within the mesenteries of the coral polyp (M. Stafford-Smith, pers. comm.). If this is the case, then lipid reserves in massive growth form corals such as poritids, faviids and mussids, which have polyps penetrating further down into the skeleton than in acroporid and pocilloporid species, will be more inaccessible to the feeding mechanism of A. planci. Thus feeding efficiency and the "trade off" between longer feeding times to enable digestion of deep tissues versus search time to locate alternative prey could explain the preference for acroporid and pocilloporid corals in areas of abundant food availability and increasing acceptance of faviids and poritids as other prey types become rarer. This would also explain why time taken to feed on the high biomass genera Porites and Fungia was so variable in laboratory experiments.

The importance of the ability to feed efficiently rather than absolute energy value of food is best documented for herbivorous marine invertebrates. Vadas (1977) found that food preference in three species of echinoids was inversely related to energy content but strongly correlated to absorption efficiency. Also Himmelman and Carefoot (1975) found that the chiton Katherina tunicata selected the nutritionally inferior of two species of algae, being able to digest this three times faster.

Other factors are likely to affect, or have been found to affect, prey preference in A. planci. These include prey availability and coral defence in terms of nematocysts (Goreau et al., 1972) or commensals (Glynn, 1983). The last two can be included in factors which affect the efficiency of feeding, whilst the first is implicit in the establishment of ingestive conditioning (Ormond et al., 1976). It seems then, that being able to feed effectively on a common food resource would be a favourable evolutionary trait and may have been important in the development of prey preference patterns in A. planci.

The efficiency of assimilation of nutrients into growth by *A. planci* may also influence prey preference on an evolutionary scale, as preferences for food sources which promote better growth may be selected for. There are no data on assimilation efficiencies in *A. planci*; however, Yamaguchi (1974a) found that juvenile *A. planci* consumed more *Acropora nasuta* than *Pocillopora damicornis* (in terms of skeletal weight) for the same weight gain.

To more effectively weigh up the relative importance of nutritional value of prey and ingestive conditioning to prey preferences in *A. planci* it will be necessary to carry out ingestive conditioning and prey preference experiments on juvenile *A. planci* that have no previous experience of corals. This should include examination of growth of such animals on different prey types and the resultant growth efficiencies as more precise measures of the actual nutritional value of each to the starfish.

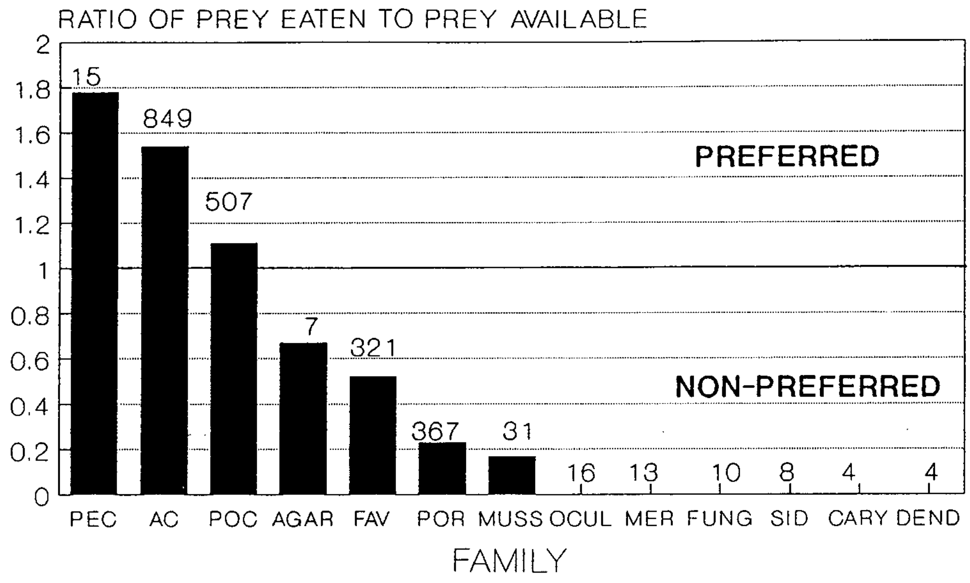

Figure 1. Ratio of number of each prey family eaten and number of each family available. Ratios greater than one indicate preferred prey families, ratios less than one indicate non-preferred families. Data from tagged Acanthaster planci from Davies Reef, October 1987 - October 1988. N is total number available.

Key to families: PEC; Pectinidae, AC; Acroporidae, POC; Pocilloporidae, AGAR; Agaricidae, FAV; Faviidae, POR; Poritidae, MUSS; Mussidae, OCUL; Oculinidae, MER; Merulinidae, FUNG; Fungidae, SID; Sidastreidae, CARY; Caryophyllidae, DEND; Dendrophyllidae.

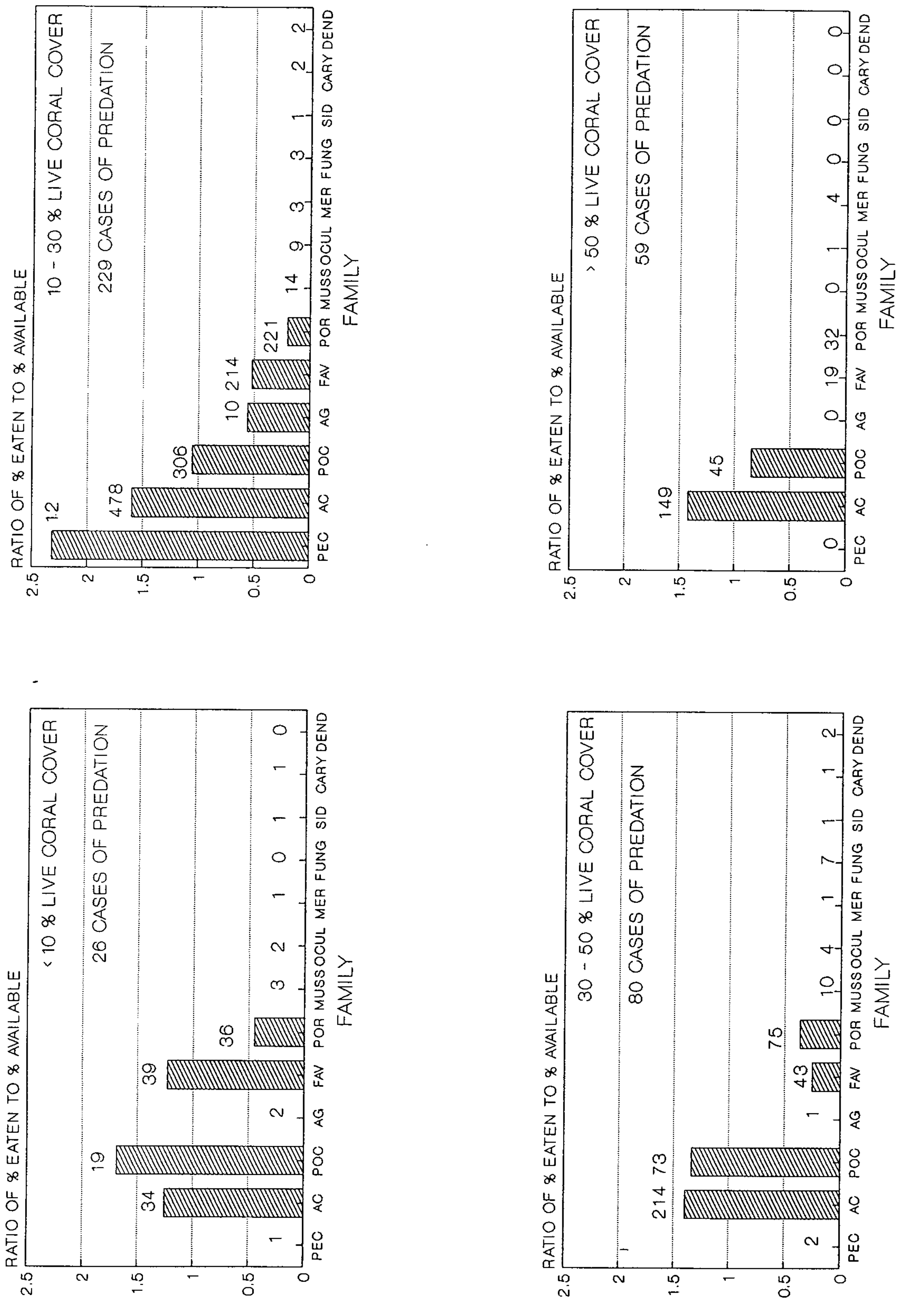

Figure 2. Ratio of the number of colonies of each prey family eaten to the number of colonies of each family available at different categories of live coral cover. Ratios greater than one indicate preferred prey families, ratios less than one indicate non-preferred families. Data from tagged <u>Acanthaster planci</u> from Davies Reef, October 1987 - October 1988..Family name abbreviations are as for figure 1. N = total number of each family available (indicated above each bar).

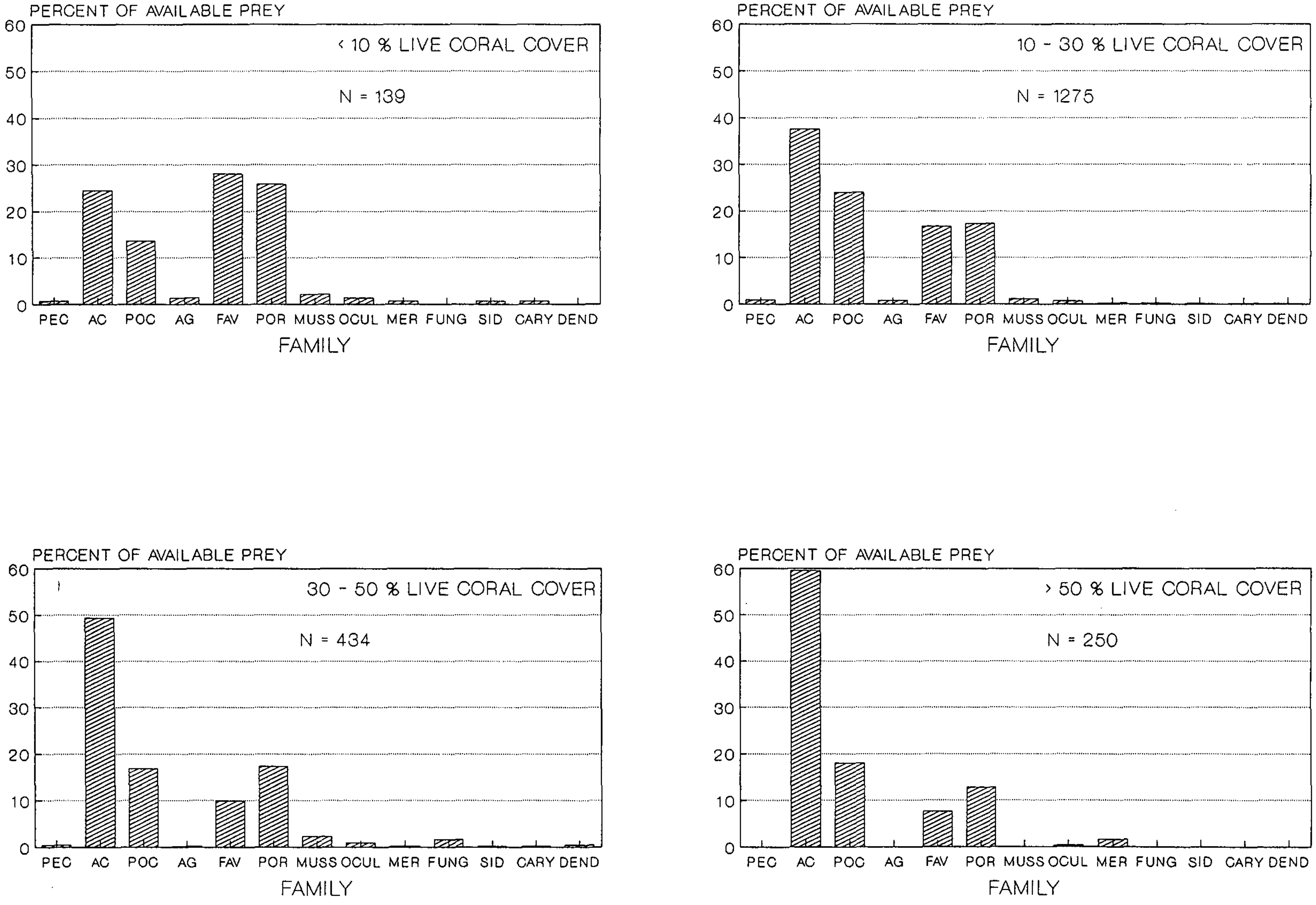

Figure 3. Percentage of total number of colonies of each prey family available at different categories of live coral cover. Data from tagged *Acanthaster planci* from Davies Reef, October 1987 - October 1988. Family name abbreviations are as for figure 1.

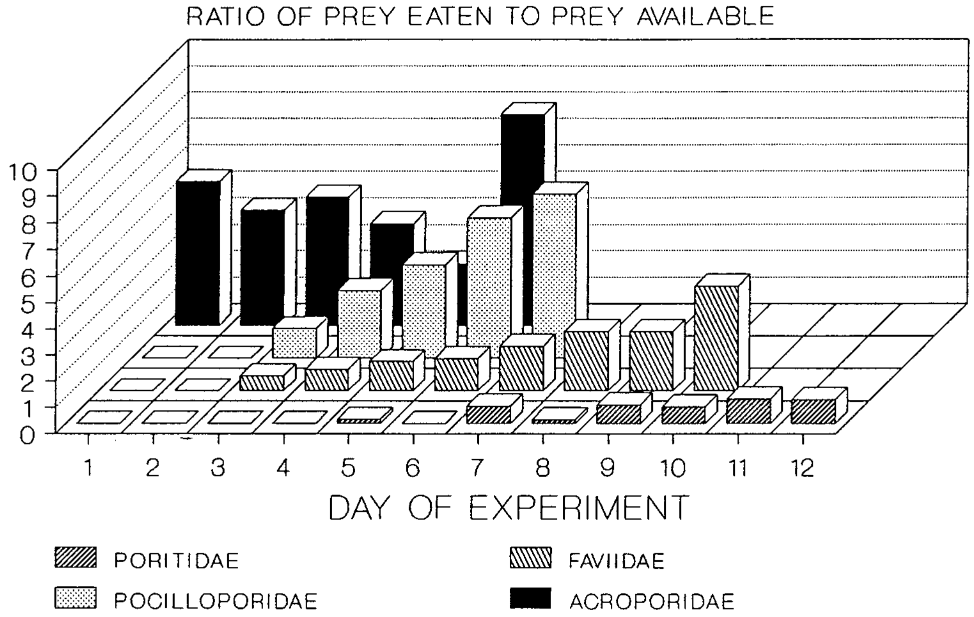

Figure 4. Sequential preference of four families of coral prey when offered in equal proportions to <u>Acanthaster planci</u> in the laboratory. The higher the ratio, the more preferred the family.

Prey item	Oct '86		Jan '87		Jun '87	
	#	%	#	%	#	%
Total hard coral	477	95.2	814	95.6	267	91.5
Soft coral	10	2.0	6	0.7	5	1.7
Zoanthids	2	0.4			3	1.0
Other fauna			1	0.1	0	0.0
Coralline algae	7	1.4	24	2.8	2	0.7
Other algae	3	0.6	3	0.4	7	2.4
Unknown	2	0.4	3	0.4	8	2.7
Total	501	100	852	100	292	100

Table 1. Prey item categories for A. planci observed feeding at Wheeler Reef.

month / size class sampled	$\bar{X}$	sd	range	N
October 1987	2.7	2.4	0.0 - 9.6	20
January 1988	1.2	1.2	0.0 - 4.5	12
June 1988	3.2	3.0	0.1 - 8.4	20
October 1988	3.6	2.3	0.2 - 6.7	17
20 - 39 cm	1.4	1.4	0.0 - 6.6	34
≥ 40 cm	4.2	2.6	0.5 - 9.6	35
Total (pooled)	2.8	2.5	0.0 - 9.6	69

Table 2. Mean movement rates (m day^{-1}) of tagged *A. planci* during foraging.

Live coral cover	$\bar{X}$	sd	range	N
Movement (m day^{-1})				
Davies				
< 10 %	4.3	2.5	0.9 - 8.4	16
10 - 30 %	3.1	2.5	0.1 - 9.6	34
> 30 %	1.0	0.8	0.0 - 2.7	19
Little Broadhurst				
< 10 %	10.3	9.3	0.0 - 37.2	21
Starfish size (cm)				
Davies				
< 10 %	45.7	8.1	30 - 60	16
10 - 30 %	42.1	9.3	25 - 60	34
> 30 %	32.7	6.9	20 - 50	19

Table 3. Mean movement rates (m day^{-1}) and size of tagged *A. planci* in areas of contrasting food availability (live coral cover) during foraging.

Species	utilized mg AFDW	available mg AFDW	% feeding efficiency
Acropora carduum	1974	2450	80.6
Pocillopora damicornis	1459	1818	80.3
Fungia fungites	1350	1985	68.0
Seriatopora hystrix	748	1475	50.7
Stylophora pistillata	1586	3314	47.8
Acropora nasuta	1088	2341	46.5
Lobophyllia hemprichii	4196	9573	43.8
Porites lutea	1941	4566	42.5
Echinopora lamellosa	861	2238	38.5
Porites lichen	270	1547	17.4
Porites cylindrica	0	2383	0.0

Table 4. Feeding efficiency of *A. planci* on various coral species in terms of ash-free dry weight. Biomasses in table have been calculated for a 100 cm^2 colony of each species from appendix tables V, VI, VII and VIII.

Species	kJ obtained	mg Protein obtained
Lobophyllia hemprichii	91.26	2232
Acropora carduum	40.17	1046
Stylophora pistillata	34.26	939
Pocillopora damicornis	33.08	829
Fungia fungites	27.94	809
Porites lutea	35.02	788
Acropora nasuta	24.70	558
Echinopora lamellosa	18.25	451
Seriatopora hystrix	16.96	442
Porites lichen	4.72	110
Porites cylindrica	0.00	0

Table 5. Food value of several coral species in terms of energy and protein obtained from a feeding bout on a 100 cm^2 colony. Figures obtained by calculations using data from table 4 and appendix tables IX and X.

Species	kJ obtained per hr ± 1SE	mg Protein per hr ± 1SE
Porites lutea	14.59 - 48.86	328 - 1099
Stylophora pistillata	10.28 ± 1.51	282 ± 41
Acropora carduum	7.53 ± 0.73	196 ± 19
Acropora nasuta	6.17 ± 0.54	140 ± 12
Seriatopora hystrix	5.08 ± 0.97	133 ± 34
Fungia fungites	2.29 - 20.70	66 - 599
Porites lichen	0.69 - 3.78	31 - 89

Table 6. Food value of several coral species in terms of energy and protein obtained per hours feeding time from a feeding bout on a 100 cm^2 colony. Figures obtained by calculations using data from table 4 and appendix tables IV, IX and X. Values with error estimates are for species in which there was a significant linear relationship between time taken to feed and prey size (see appendix figure XVIII). Otherwise ranges are given.

> 50 % coral cover

	search time in hours*			
Species	0.5	1	5	10
Porites lutea	**9.0**	5.6	1.4	0.7
Stylophora pistillata	6.9	5.2	1.7	0.9
Acropora carduum	6.9	**6.4**	**3.9**	**2.6**
Acropora nasuta	5.5	4.9	2.7	1.8
Seriatopora hystrix	3.4	2.6	0.9	0.5
Fungia fungites	0.9	0.4	0.1	<0.1

< 10 % coral cover

	search time in hours*			
Species	0.5	1	5	10
Porites lutea	**17.3**	**14.0**	**5.6**	**3.2**
Stylophora pistillata	8.2	6.7	2.8	1.6
Acropora carduum	6.9	6.4	3.9	2.6
Acropora nasuta	5.5	4.9	2.7	1.8
Seriatopora hystrix	4.0	3.3	1.4	0.8
Fungia fungites	2.0	1.1	0.2	0.1

Table 7. Comparative rates[1] of energy uptake by *A. planci* feeding on different coral species at two levels of food availability when search time is taken into consideration. Bolded values are the highest rates of energy uptake for a given search time. Rates can only be compared within each level of food availability, not between levels. *These are the theoretical range of times it would take a starfish to locate the most abundant type of coral (in this case *Acropora*).

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[1] rates of energy uptake (R) calculated as: $R = E / T_s + T_f$,

where E is the amount of energy gained after T_f hours feeding and T_s hours search time [after Sibly and Calow (1986)]. In each case E is the value of energy (kJ) obtained from a feeding bout on a 100 cm^2 colony of that species (table 5) and T_f is the feeding time taken to obtain E kJ (from table 6). T_s is calculated by multiplying the theoretical search times indicated in the above table by the relative abundance of the each species group when compared to the most abundant group (*Acropora*) from figure 3.

e.g. for *S. pistillata* at > 50 % coral cover and 1 h search time

energy obtained from a 100 cm^2 colony = 34.2 kJ (from table 5)
time taken to consume colony = 34.2 / 10.3 (from table 6) = 3.3 h
relative abundance of pocilloporids to acroporids in areas of
> 50 % coral cover at Davies Reef = 60 / 18 = 3.33
search time x relative abundance = 1 h x 3.33 = 3.33

i.e. $R = E / T_s + T_f = 34.2 / 3.33 + 3.3 = 5.2$

Table 8. Qualitative assessment of coral prey characteristics. RSA/PSA is an index of coral surface area complexity (see page 107 for details).

Family	RSA/PSA ratio	biomass AFDW	absorption efficiency	energy content of tissues	protein content of tissues	comparative abundance
Acroporidae	high	low - med	med - v. high	moderate	high	abundant
Pocilloporidae	med - high	low - med	med - v. high	moderate	high	very common
Faviidae	low - med	high	med	moderate	high	common
Poritidae	low - med	high	low - med	low	low	common
Mussidae	med	v. high	med	moderate	high	uncommon
Fungidae	low	high	high	moderate	high	rare

<u>RSA/PSA ratio</u>

1 - 3 = low
3 - 5 = medium
> 5 = high

<u>biomass AFDW mg/cm^2</u>

< 5 = low
5 - 10 = medium
10 - 20 = high
> 20 = very high

<u>absorption efficiency</u>

< 25 % = low
25 - 50 % = med
50 - 75 % = high
> 75 % = very high

<u>energy content of tissues</u>

< 20 kJg^{-1} = low
> 20 kJg^{-1} = moderate

<u>protein content of tissues</u>

< 50 % = low
> 50 % = high

<u>comparative abundance</u>

< 1 % of available = rare
1 - 10 % of available = uncommon
10 - 20 % of available = common
20 - 30 % of available = very common
> 30 % of available = abundant

CHAPTER FIVE

General Discussion

This chapter discusses the general contribution of this study to knowledge of the biology of Acanthaster planci and the implications for our understanding of the Acanthaster phenomenon.

Size dependent behavioural patterns in Acanthaster planci: Implications for survey and control programs.

Population surveys

A number of surveys have been undertaken to determine the distribution of A. planci populations and their impact on coral reefs (Pearson and Endean, 1969; Endean and Stablum, 1973; Pearson and Garrett, 1975, 1978; Kenchington and Morton, 1976; Nash and Zell, 1982; Johnson et al., 1988). These surveys have included swim searches along reef perimeters, spot checks at different sites on the reef and "manta" tows around the perimeter of reefs or a combination of these techniques.

This study has identified four notable characteristics of A. planci populations which have important implications for surveys such as these:

1. Population size structure can change markedly over the course of an outbreak.

2. Acanthaster planci exhibits strong size dependent patterns of emergence and cryptic behaviour.

3. Feeding rates are depressed in winter.

4. Feeding rates are size dependent.

The combination of these factors results in a number of problems (see table 1), which will not only influence the reliability of counts of starfish, but will make temporal comparisons within and between reefs difficult.

Problems of observer limitations and bias in such surveys have been the subject of detailed examination (Kenchington, 1978), but there have been few considerations of the affect of starfish behaviour on survey reliability. However, the problem has been recognized previously. Kenchington and Morton (1976) noted that their survey was biased against juveniles and that starfish camouflage and cryptic behaviour would influence results. Nash and Zell (1982) suggested that a combination of starfish counts and amounts of dead coral could be used to correct for biases due to cryptic behaviour of starfish. However, extensive coral mortality is not necessarily associated with the density of <u>A. planci</u> (Kenchington and Morton, 1976) and coral mortality can result as a consequence of other agents such as bleaching (Glynn, 1983), extreme low tides (Loya, 1976), warm water currents (Glynn, 1984) and predation by the gastropods <u>Drupella</u> (Moyer <u>et al.</u>, 1982) and <u>Coralliophila</u> (Brawley and Adey, 1982). Cyclones also cause considerable coral mortality (Randall and Eldredge, 1977; Harmelin-Vivien and Laboute, 1986).

Given the many biases involved with visual surveys and the enormous task of surveying many reefs spread over a wide geographic range, it is important that such surveys be seen as tools for long term monitoring of (macroscale), and detecting gross changes (mesoscale) in, coral reef ecosystems. Efforts to quantify the techniques by elaborate corrections for a myriad of factors are probably futile.

However, an awareness of the effects of changes in population size structure and other temporal phenomena will assist in interpretation of broadscale survey data.

Control programs

Zann and Weaver (1988) determined that control programs on A. planci have been largely unsuccessful. Yamaguchi (1986) concluded that an extensive and expensive control campaign in the Ryukyu islands had failed because too many starfish remained uncollected and continued to cause coral mortality. An important implication of the behaviour patterns of A. planci described in this study is that control exercises which are carried out during the day will miss large numbers of juveniles, and indeed many adults, which are cryptic during the day.

For a control program to be successful it must be carried out before considerable coral mortality has occurred and it must remove or kill enough starfish to ensure that those which remain cannot cause further significant damage to the coral community. Yamaguchi (1986) lamented the failure of control programmes to work to reducing populations to these "tolerable" levels.

Ideally contemporary control methods for A. planci, such as copper sulphate injection (Kenchington and Pearson, 1981), should be carried out when starfish are exposed in greatest numbers i.e. at night. However, control at this time is impractical for logistic reasons and since darkness will in turn reduce the efficiency of the control efforts through patches of starfish being missed. However, it is recommended that control operations should include night surveys of the area to show starfish accumulation and give a better idea of juvenile numbers. As juvenile distribution on reefs has been found to be patchy (Pearson and Endean, 1969; Moran et al, 1985; Zann et al, 1987) night surveys may expose concentrations of juveniles which can be controlled at night or thorough searching during the day. It is also important that control programs be repeated over the same area, in order to remove starfish which were initially missed, if "tolerable" levels (Yamaguchi, 1986) are to be achieved.

Control programs carried out in summer are also more likely to be successful than in winter as feeding rates are higher and starfish emerge from hiding to feed more frequently in summer. Thus, control programs would be best carried out in the warmer months but preferably before the spawning period so as to reduce reproductive output from the population.

Size Dependant behaviour in Acanthaster planci as a predator avoidance strategy.

This study showed that juvenile Acanthaster planci have a nocturnal pattern of emergence which is related to feeding and that large adults are rarely cryptic. The diel behavioural pattern of juveniles is endogenously tied to the natural day/night rhythm.

Daily rhythms in animal behaviour have evolved in response to their survival needs. Basically these needs are to eat and avoid being eaten. Echinoderms show daily behaviour rhythms in response to both prey availability and predators. Ebling et al., (1966) suggested that the urchin Paracentrotus lividus avoided predation by the nocturnal starfish, Marthasterias glacialis, and crabs by feeding diurnally. Centrostephanus coronatus leave their crevices to forage nocturnally, thus avoiding contact with their diurnally active fish predators (Nelson and Vance, 1979). Entrainment through experience will give rise to such behaviour patterns. Several demonstrations of behaviour modification in asteroids have been made (Valentincic, 1983). McClintock and Lawrence (1982) found that Luidia clathrata learned to associate darkness with food availability and that this response was strengthened by reinforcement. Such responses operating over evolutionary time would give rise to behaviour rhythms, particularly if such behaviour enhanced survival.

The availability of food to Acanthaster planci, as a predator of sedentary scleractinian corals, is not affected by diel differences in accessibility. Thus, it is most likely that nocturnal behaviour has evolved in response to threat of predation. The diel pattern of nocturnal feeding and diurnal concealment is typical of some echinoids which have been shown to demonstrate predator avoidance behaviour (see Nelson and Vance, 1979). It is also of interest to note that Acanthaster brevispinis, a non-venomous, short spined deep water species is capable of moving whilst digesting its mollusc prey (pers. obs.). Acanthaster planci is thought to have evolved from an A. brevispinis like ancestor (Lucas et al., 1985) and may have developed long venomous spines for protection during its more sedentary feeding mode.

There are several indications that A. planci is subject to predation pressure. There is a high incidence of sublethal arm damage in A. planci populations (Moran, 1986) and the animals are heavily armoured with movable venomous spines which show a response well adapted to defence (Watanabe, 1983). Known predators of A. planci include the giant triton, Charonia tritonis and several fish species (Endean, 1973; Ormond and Campbell, 1974); however most recorded observations of predation are of adults. The type of predator most likely to enforce a predator avoidance response in A. planci could be one or more species of generalist fish predators which feed on benthic invertebrates (see Randall, 1967 for details on diets of predatory coral reef fishes). Most families of coral reef fish which feed on benthic invertebrates are diurnal (Hobson, 1965; 1974).

The fact that large adult A. planci do not show the same diel activity pattern as juveniles and are rarely cryptic suggests that large starfish achieve a refuge from predation in size. Kettle and Lucas (1987) found that small A. planci partition energy toward rapid somatic growth and inferred that starfish try to out-grow predators before partitioning energy into gonad development at the expense of body wall maintenance.

Size refuge from predation in asteroids is not unknown. Birkeland et al. (1982) found that two species, Solaster stimpsoni and Dermasterias imbricata which have a refuge in size from their principal predator, were more abundant than two smaller species of starfish. They suggested that the refuge in size was important in allowing the species to persist by protecting the reproductive stock residing with the large, slow growing and long lived animals. However, the behaviour pattern in A. planci is similar to that in echinoids not subject to predator pressure. Lawrence (1975) noted that Diadema setosum is nocturnally active; but it remains concealed during the day in subtidal areas where predators are present, while in shallow areas they will remain exposed during the day. Continuous activity in D. setosum was also noted in a "predatorless" environment (newly built port) by Fricke (1974) when compared to a normal reef habitat. McClanahan and Muthiga (1989) found large Echinometra mathaei were subject to less predation pressure than smaller animals.

Alternative reasons for a change in behaviour by large A. planci could be that either refuge space for large starfish is limiting, or that large starfish must feed more often. Only the latter reason is plausible, in that large A.

planci feed at a greater frequency than small animals. However, this does not explain why large starfish were found to feed significantly more during the day than at night.

Feeding Rates in Acanthaster planci

Ecological and management implications

Estimates of feeding rates in A. planci under natural conditions are provided for the first time. Variability in feeding rates dependent on starfish size and season are also given. These data allow an assessment of impact (coral mortality) in terms of coral cover and colony number. For example depending on size and season, the magnitude of damage by 100 000 A. planci feeding is estimated at:

20 000 - 100 000 colonies killed per day
1 000 - 5 000 m^2 coral cover killed per day
250 - 2500 kg coral soft tissue killed per day

Such figures not only more accurately define what has previously been termed devastation (Done, 1985) and eco-catastrophe (Endean and Cameron, 1985), but allow prediction of likely effects following population surveys of the type undertaken by Johnson et al., (1988).

Calculations of projected coral mortality which consider feeding rate, population size and coral cover are shown in figure 1. The model assumes an average daily feeding rate of 300 cm^2 per starfish per day for 10^0 - 10^5 A. planci per km^2. Typical average coral cover of 20 - 50 % was used for the model following examination of the results of surveys on the Great Barrier Reef (Moran et al., 1989). It is apparent that, regardless of initial coral cover, significant coral mortality only occurs when starfish densities exceed 1000 per km^2. The often quoted nonoutbreak density of 0.06 A. planci per ha (6 per km^2) (Endean, 1974) is two orders of magnitude below this "critical threshold" (1000 per km^2). Glynn (1973) reckoned that serious damage to the coral community in Panama would not occur below 6500 per km^2 (normal = 2600 per km^2), however, A. planci in

Panama only fed at half the rate of animals in this study[1] and Glynn's model included coral regrowth. Glynn (1973) predicted that rapid coral destruction would occur at densities of 26000 per km^2.

Both models suggest A. planci populations can undergo dramatic increases in population size before significant damage occurs. These findings have implications for understanding why large numbers of A. planci skeletal elements are found in reef sediments (Walbran et al., in press), without the abundance of elements being related to whether reefs have suffered damage from A. planci (Moran et al., 1986).

More complex models which take into account continuing growth of existing coral, seasonal and starfish size dependent effects could be developed for individual reefs to assess "carrying capacity" if required.

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[1] This is consistent with the findings of Yamaguchi (1974a) who found that juvenile A. planci killed twice as much Acropora as Pocillopora for the same weight gain. Starfish in Glynn's (1973) study consumed primarily Pocillopora, whilst Acropora was found to be the major food of A. planci in this study. Yamaguchi (1974a) suggested that Glynn's model may not be applicable to Acropora dominated reefs in the western Pacific.

There has been difficulty in classifying populations as outbreaking or not (Moran, 1986). This is because population sizes and impact vary. The above model suggests that, above a threshold level, different types of outbreak effects can occur as a result of variability in live coral cover. There are probably four critical factors determining the severity of the effects from an _A. planci_ population fluctuation:

1. magnitude of recruitment - this is probably the most important factor as it determines the potential for significant impact.

2. survival of post-settlement starfish - if survival is density dependent, then this factor will be important in determining the impact significance.

3. coral cover - will determine the length of time until significant impact. Coral community structure and coral growth rates may affect this.

4. reef size - if recruitment level is independent of reef size then time to significant impact will be greatly affected by reef size.

Models using feeding rate to predict rate of coral mortality also allow the worth and likely success of control programs to be assessed in advance. The calculation of critical or "tolerable " population levels (Yamaguchi, 1986) may be calculated for a given reef size. Knowledge of such critical levels could save considerable expense if the goal can be to control to threshold densities instead of zero density.

Other ecological implications arise from detailed measurements of feeding rate of A. planci. The magnitude and rapidity of the space made available by coral death and the enormous change in the structure of trophic pathways on coral reefs following A. planci outbreaks can now be appreciated. One m^2 of dead coral surface will provide between 1.3 and 5.7 m^2 of utilizable area for algae and encrusting and boring organisms. This space becomes available in a very short period of time as outbreaks may be over in a matter of months (Moran et al., 1985). The mass of soft tissue biomass killed during this time can amount to hundreds of tonnes dry weight, which may be consequently completely lost from the reef.

Before outbreaks occur, reefs have a large amount of biomass in the form of coral tissue. This tissue constitutes a substantial deposit of energy and organic matter. Extensive predation results in the death of most of this deposit. Some goes directly into detrital pathways, but most (depending on coral species) is absorbed by the starfish. As starfish are known to disappear from reefs as rapidly as they appear (Moran et al., 1985) the biomass transferred from coral to starfish may be lost from the reef if starfish move off reefs after outbreaks as suggested by the observations of Endean (1969) and Fisk et al. (1988). In the event that starfish die on the reef the biomass will be transferred to detrital pathways. Mass mortality of A. planci is unknown and considering that movement rates in this study were found to be greater in areas of depleted coral cover, and A. planci is known to live for at least four months without food (Endean, 1969), it seems unlikely that mass mortalities would occur. Either way there is a large shift in biomass structure of the reef (Bradbury and Mundy, in press) as the vast areas of dead surface are colonised initially and for long periods by algae, which has a relatively low protein content, and which are grazed extensively and subject to fragmentation. Corals normally transfer very little biomass through trophic pathways on the reef except to some corallivorous fish (Harmelin-Vivien and Bouchon-Navaro, 1983) and by mucus release (Davies, 1984). This contrasts with high trophic exchange between algae and grazers (Klumpp and Polunin, 1989). Also Klumpp and McKinnon (1989) showed that epilithic algae, rather than other producers like coral, are the main suppliers of carbon to non-symbiotic consumers on the Great Barrier Reef. Thus a complete change in reef primary productivity and trophic structure results. Previous research on reef metabolism has been preoccupied with examining how nutrient budgets on reefs are balanced (Johanssen _et al._, 1972) but the impact of _A. planci_ outbreaks on this is unknown.

A. planci consumes about the same amount of food as other asteroids, i.e. 1 - 2 % of their body DW per day (see Lawrence, 1987 for some comparisons); but because the coral food source has such a low biomass (tissue + skeleton), _A. planci_ must kill large quantities of coral to satisfy its nutritional requirements. Lawrence and Glynn (1984) made this same conclusion for the corallivorous echinoid _Eucidaris thouarsii_. This requirement for large quantities of food in _A. planci_ results in far more significant impact on reefs during outbreaks than from population fluctuations of other coral reef echinoderm species which are largely algivorous (echinoids) or deposit feeders (holothurians).

Physiological implications

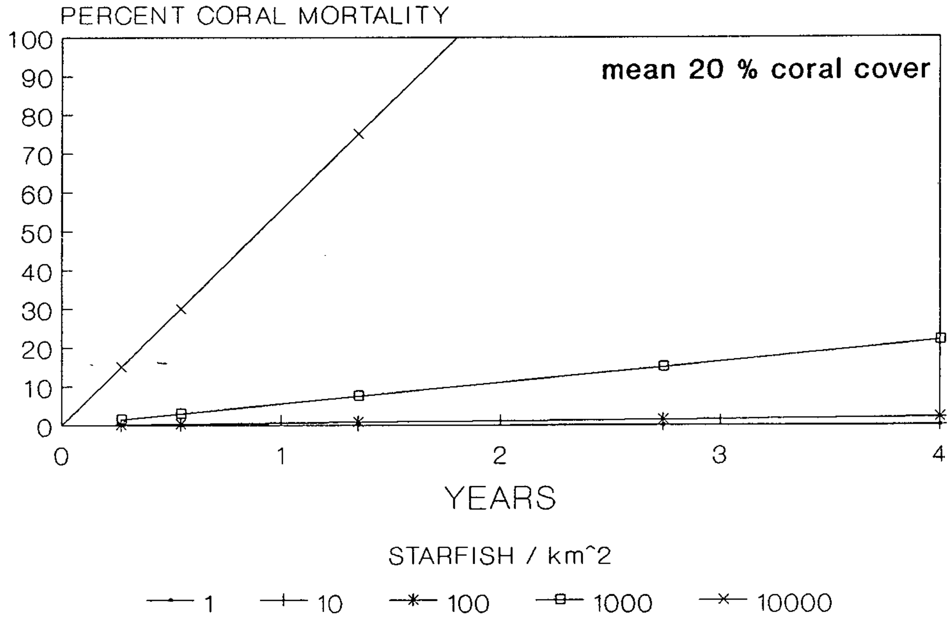
Because of the need to kill large amounts of prey to achieve nutritional requirements (as discussed above) the starfish has evolved a large stomach, probably from a bivalve feeding ancestor, (Lucas _et al._, 1985). However, despite having such a large stomach, feeding capacity in relation to body size decreases and thus body size is determinate and senility will result as the requirements for gonadal development and biomass maintenance exceed intake capacity (Lucas, 1984). Debate regarding determinate growth has centred around the existence of very large adults in the field (Kenchington, 1977) and the fact that senility has not been observed in the field (Lucas, 1984, Moran, 1986) Further evidence for determinant growth and senility is provided from application of feeding rate measurements in this study to physiological requirements of A. planci. Despite increased feeding rates in large adults, the weight specific feeding rate decreases and growth must slow as energy is directed into gonadal growth. Eventually metabolic demands will result in an energy deficit and growth will cease and senility and death will follow.

Foraging characteristics of Acanthaster planci

As in previous studies A. planci was found to exhibit strong feeding preferences. Animals with feeding preferences have the potential to influence community structure. Porter (1972; 1974) proposed that selective predation on abundant species by low level populations of A. planci may enhance species diversity. However, Glynn (1974) found no evidence to support this theory, noting that A. planci feed preferentially on locally rare species in the eastern Pacific. Since that time Porter's ideas have received little attention. Acanthaster planci in this study was found to feed preferentially on the two most abundant genera. Coral diversity on the Great Barrier Reef is much greater than in the eastern Pacific (Veron, 1986). Thus the predictions made by Porter (1972) merit further study.

This study failed to find unequivocal evidence for a strong influence of nutritional quality of food governing feeding preferences. Feeding preferences are probably influenced by a large number of factors (Moran, 1986) but feeding preferences are still likely to develop from ingestive conditioning and evolve from a factor such as nutritional quality of food. Discussion of results in this study suggests that the important attribute may be efficiency of feeding. Such an attribute could be selected for in the event that such food is abundant or provides superior energy assimilation for growth and reproduction. The ability to feed proficiently not only encompasses tissue absorption efficiency but also overcoming deterrents such as prey symbionts, nematocyst defences and physical attributes affecting accessibility. Experiments to separate the importance of ingestive conditioning and nutritional food quality using artificially reared animals with no learning history are proposed in chapter 4. Such experiments may also provide an insight into the extent that behavioural attributes are learnt or passed on genetically.

Present data suggest that feeding efficiency and familiarity are more important to food preferences than an absolute assessment of energy gained per unit time. However, A. planci behaviour does show some response consistent with optimal diet theory (Morse, 1980, Sibly and Calow, 1986). But further examination of search time in relation to prey availability and measurements of growth efficiencies on different coral prey types are required before conclusive statements can be made regarding whether A. planci does conform to the predictions of optimal foraging theory.



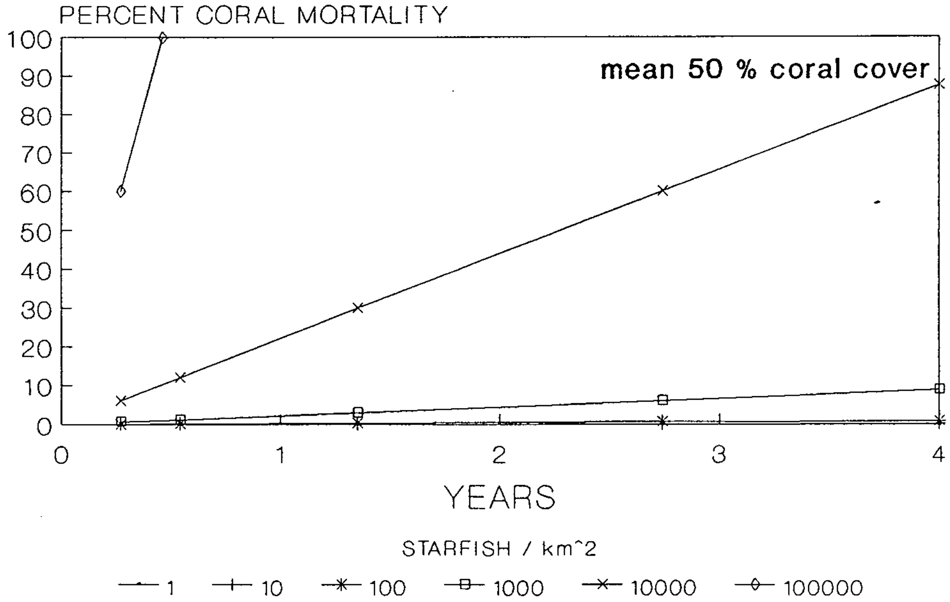


Figure 1. Model of predicted percent coral mortality in a 1 km^2 area over four years from feeding activities of different densities of Acanthaster planci. Model assumes daily feeding rate of 300 cm^2 per starfish per day.

Problem	1	2	3	4	5	6
Comparison						
Within reef	*	*				
Between reefs			*	*		
Within reefs (temporal)		*	*	*	*	
Between reefs (temporal)			*	*	*	
Between reefs (spatial)			*	*	*	*

Problem

1. Underestimation of population size.

2. Large juvenile population may be missed.

3. Variation in population size structure results in different proportions of population being visible.

4. Variation in coral mortality as a result of difference in population size structure (caused by size-dependent feeding rates).

5. Variation in coral mortality caused by seasonal differences in feeding rate.

6. Variation in coral mortality caused by temperature effects on feeding rate at different latitudes.

Table 1. Potential problems in within and between reef comparisons of visual survey data of Acanthaster planci distribution and abundance and coral mortality, which may result from ignoring size related and temporal variability in starfish behaviour.

APPENDIX

Figures and Tables

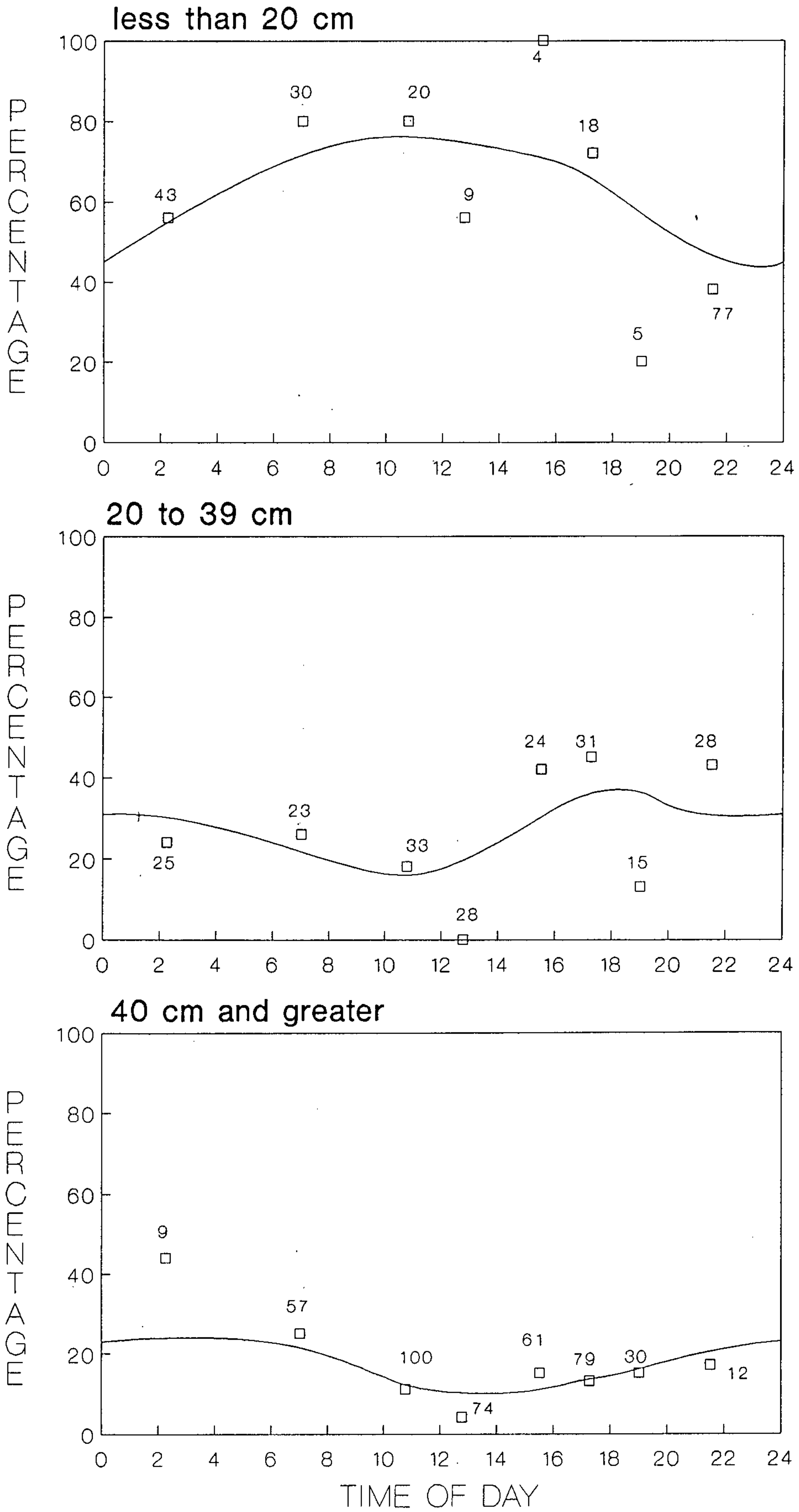


Figure I. The cryptic proportion of each size class of <u>A. planci</u> versus time of day at Wheeler Reef during October 1986. Sample size is indicated at each data point. Each fitted curve is a three point moving weighted average (after Tukey, 1977).

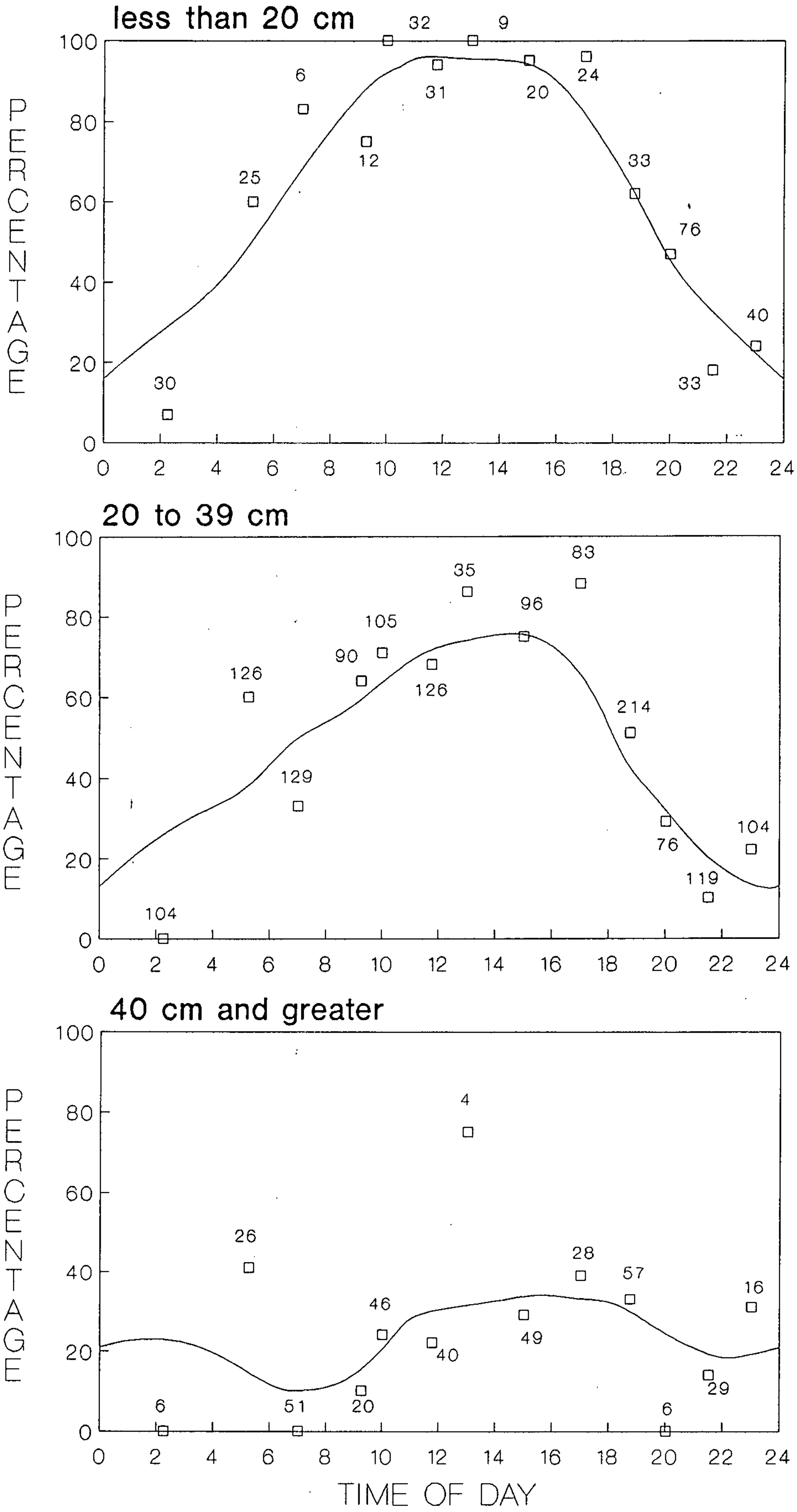


Figure II. The cryptic proportion of each size class of A. planci versus time of day at Wheeler Reef during January 1987. Sample size is indicated at each data point. Each fitted curve is a three point moving weighted average (after Tukey, 1977).

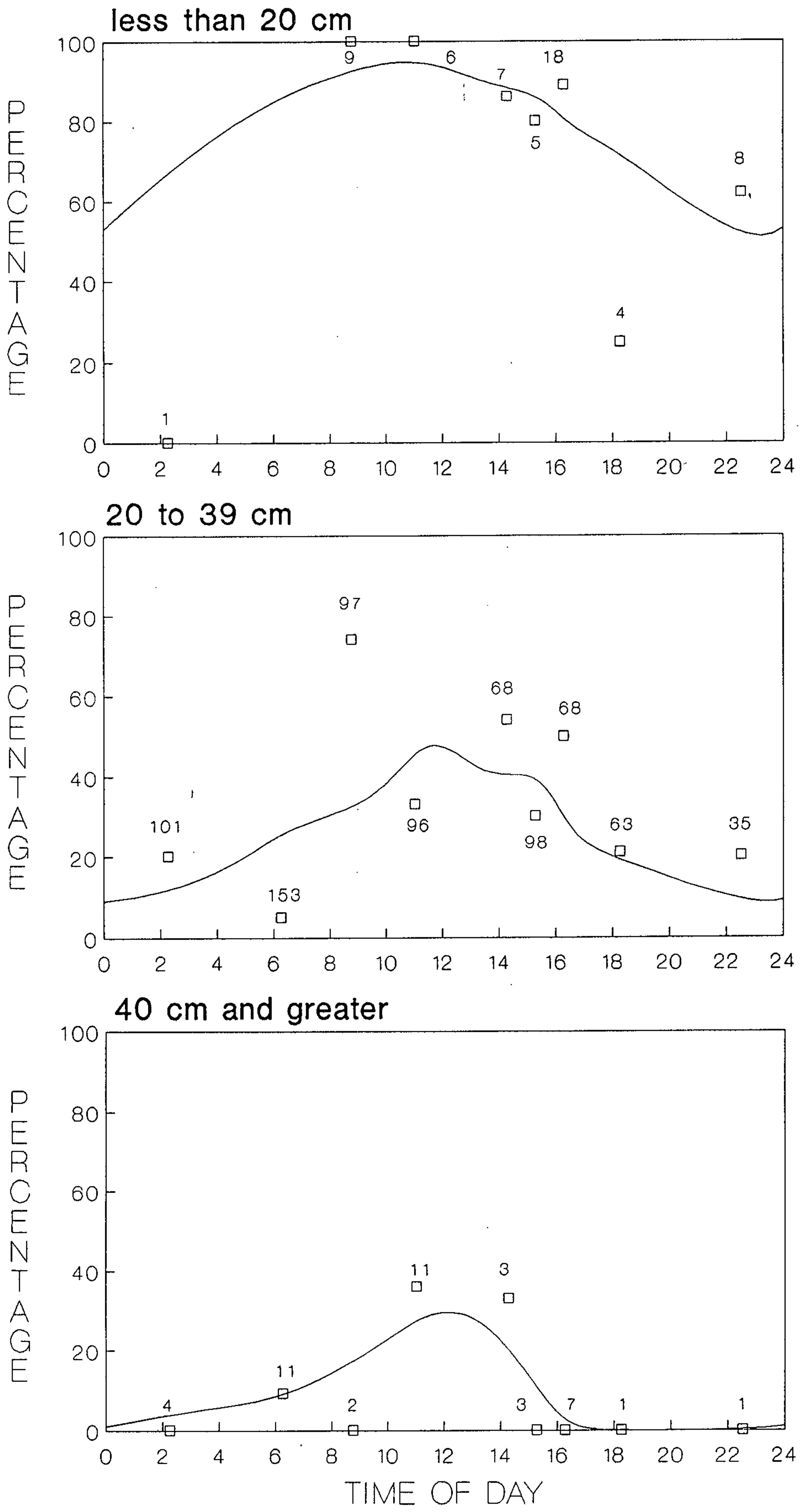


Figure III. The cryptic proportion of each size class of _A. planci_ versus time of day at Wheeler Reef during June 1987. Sample size is indicated at each data point. Each fitted curve is a three point moving weighted average (after Tukey, 1977).

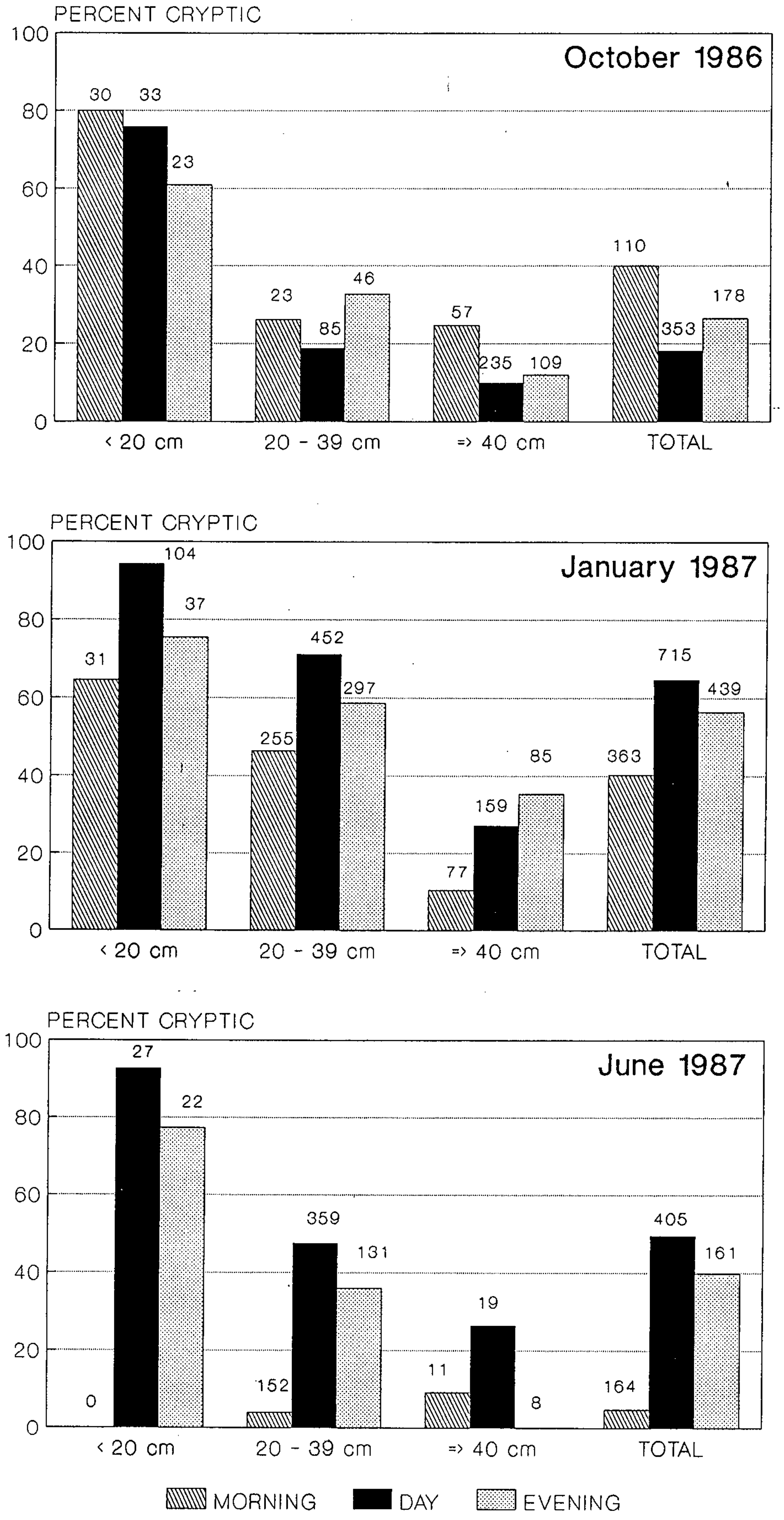


Figure IV. The cryptic proportion of <u>A. planci</u> in each size class during the morning, day and evening samples at Wheeler Reef in October 1986, January 1987 and June 1987. Sample size is indicated above each bar.

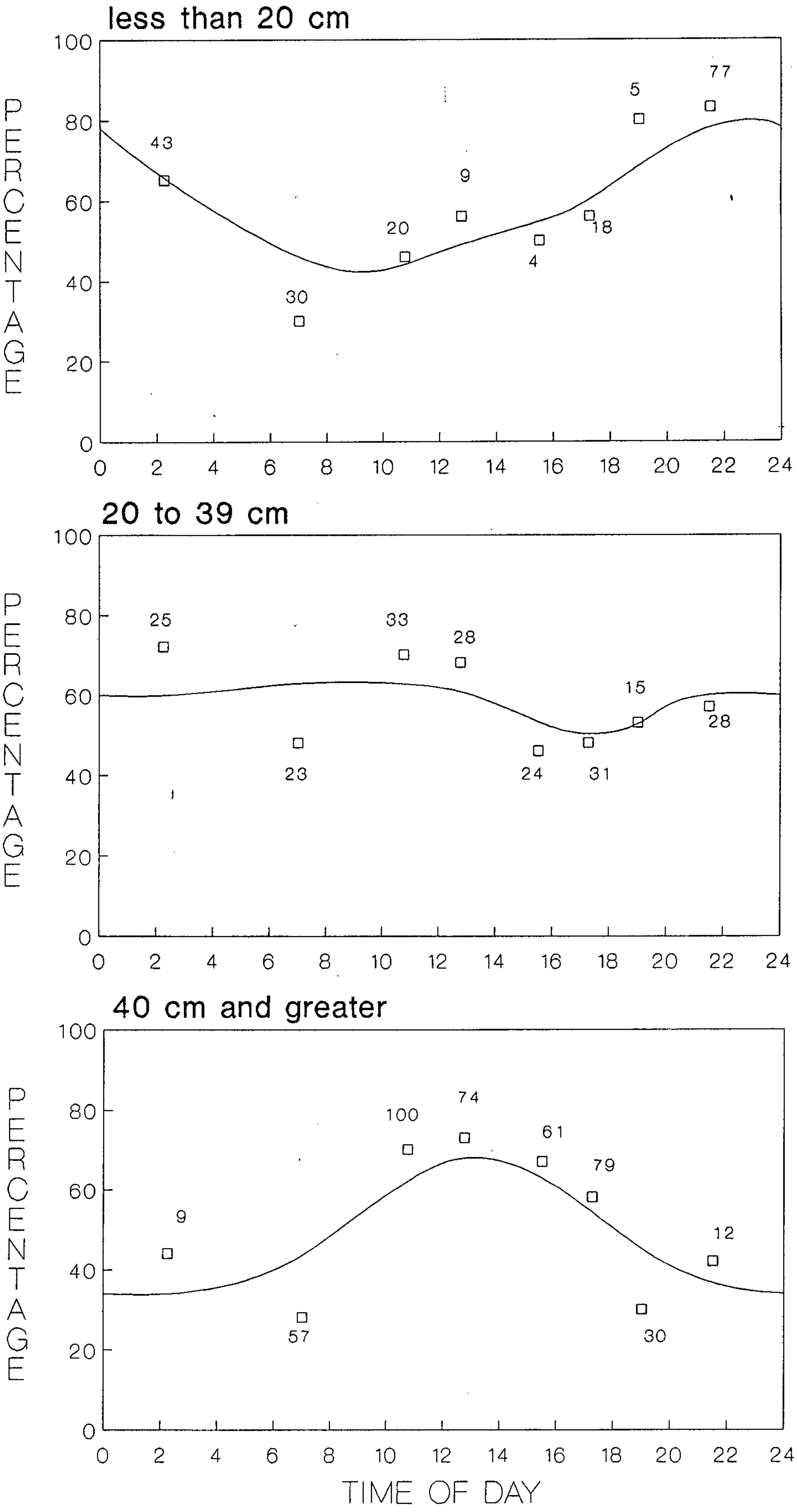


Figure V. The proportion feeding of each size class of A. planci versus time of day at Wheeler Reef during October 1986. Sample size is indicated at each data point. Each fitted curve is a three point moving weighted average (after Tukey, 1977).

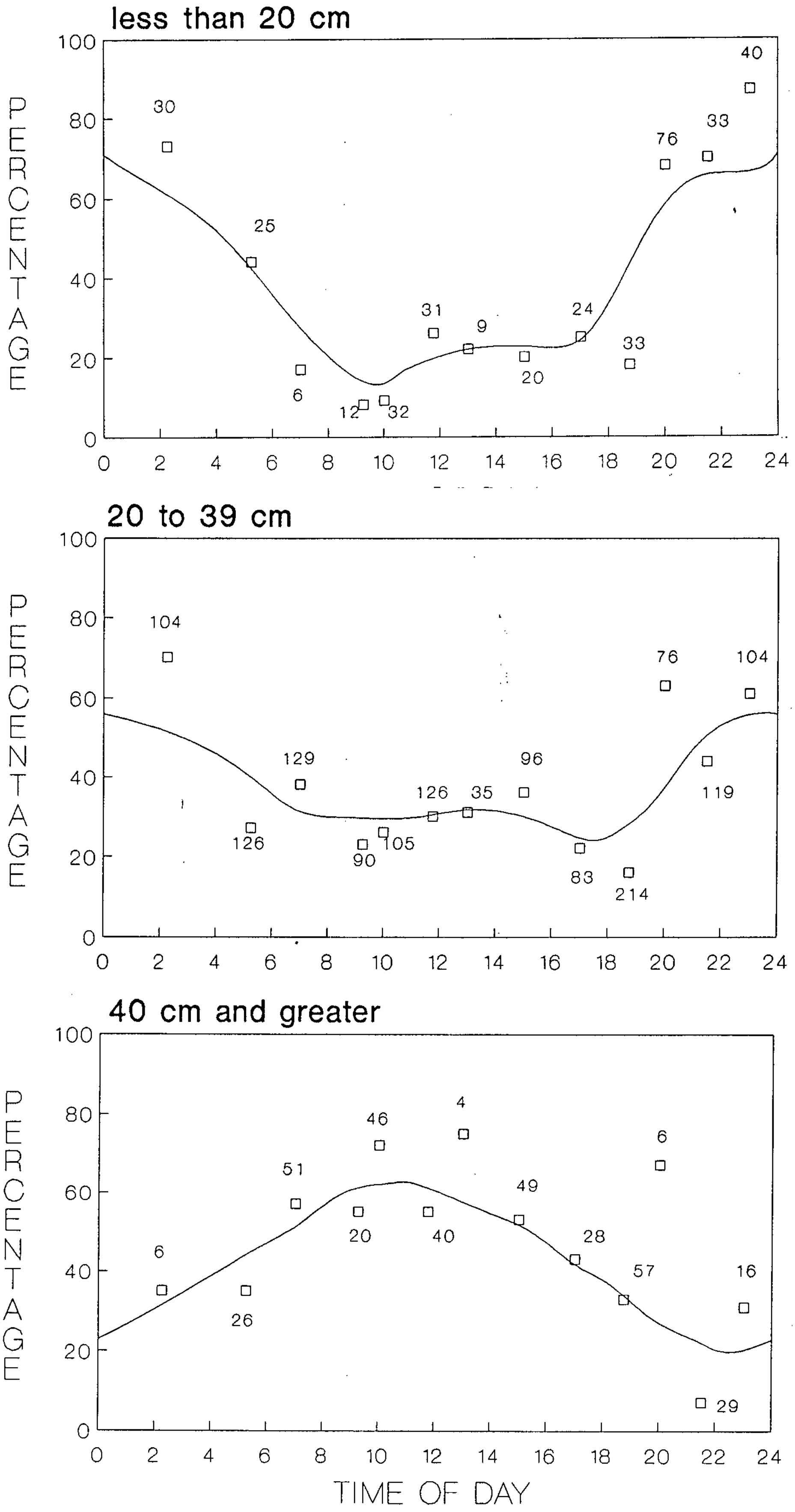


Figure VI. The proportion feeding of each size class of A. planci versus time of day at Wheeler Reef during January 1987. Sample size is indicated at each data point. Each fitted curve is a three point moving weighted average (after Tukey, 1977).

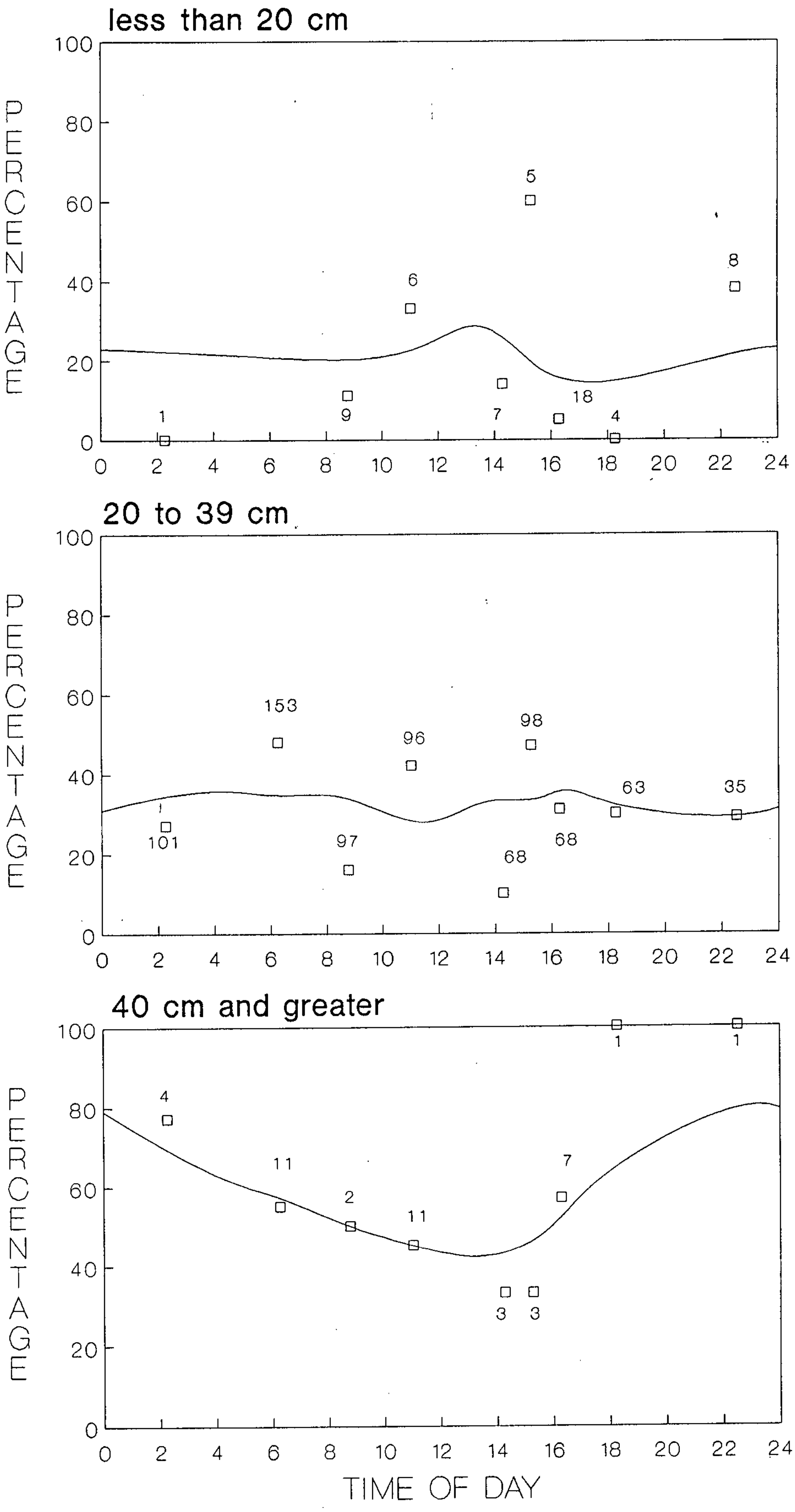


Figure VII. The proportion feeding of each size class of <u>A. planci</u> versus time of day at Wheeler Reef during June 1987. Sample size is indicated at each data point. Each fitted curve is a three point moving weighted average (after Tukey, 1977).

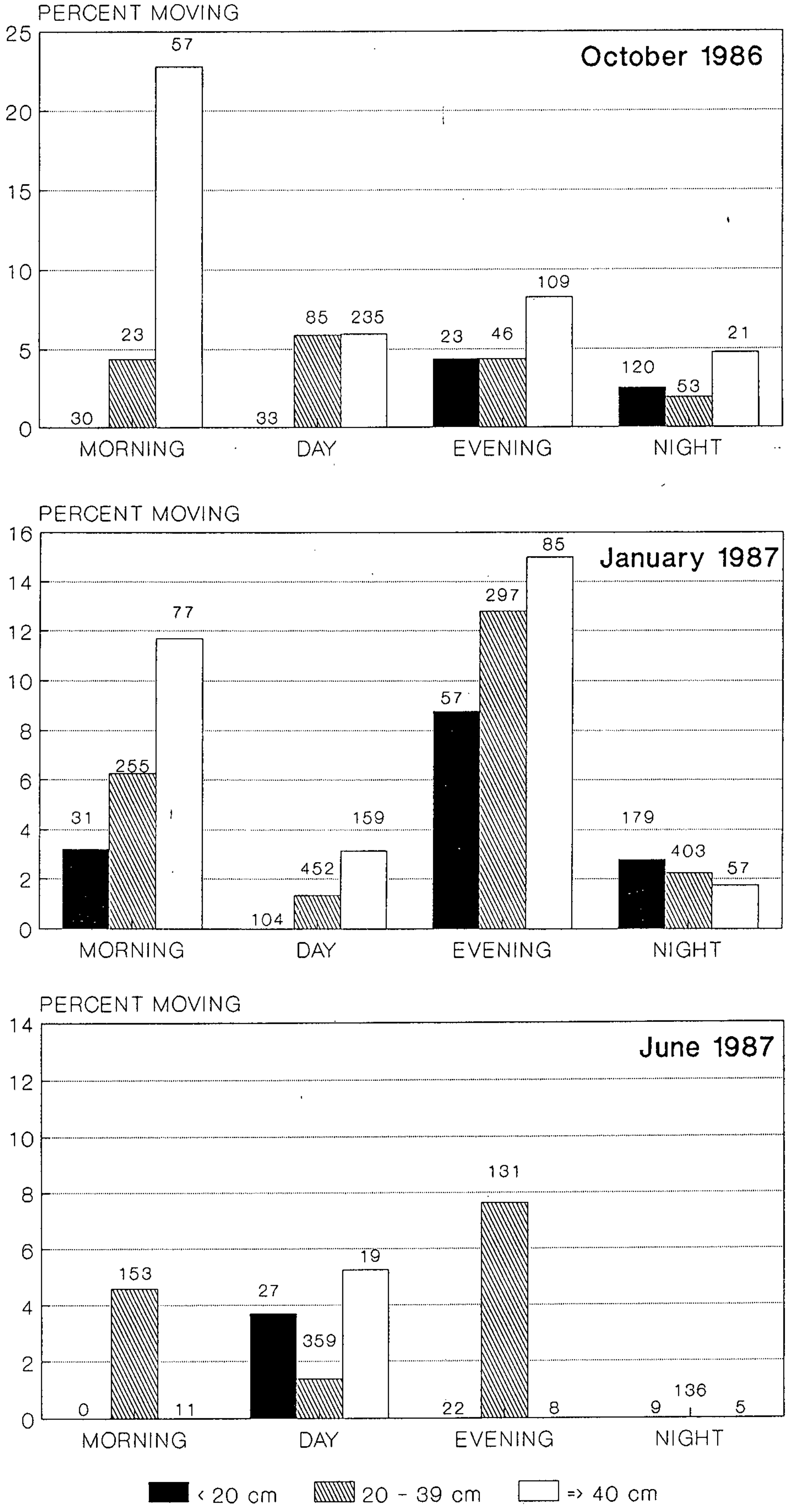


Figure VIII. The proportion of A. planci moving during morning, day, evening and night samples at Wheeler Reef in October 1986, January 1987 and June 1987. Sample size is indicated above each bar.

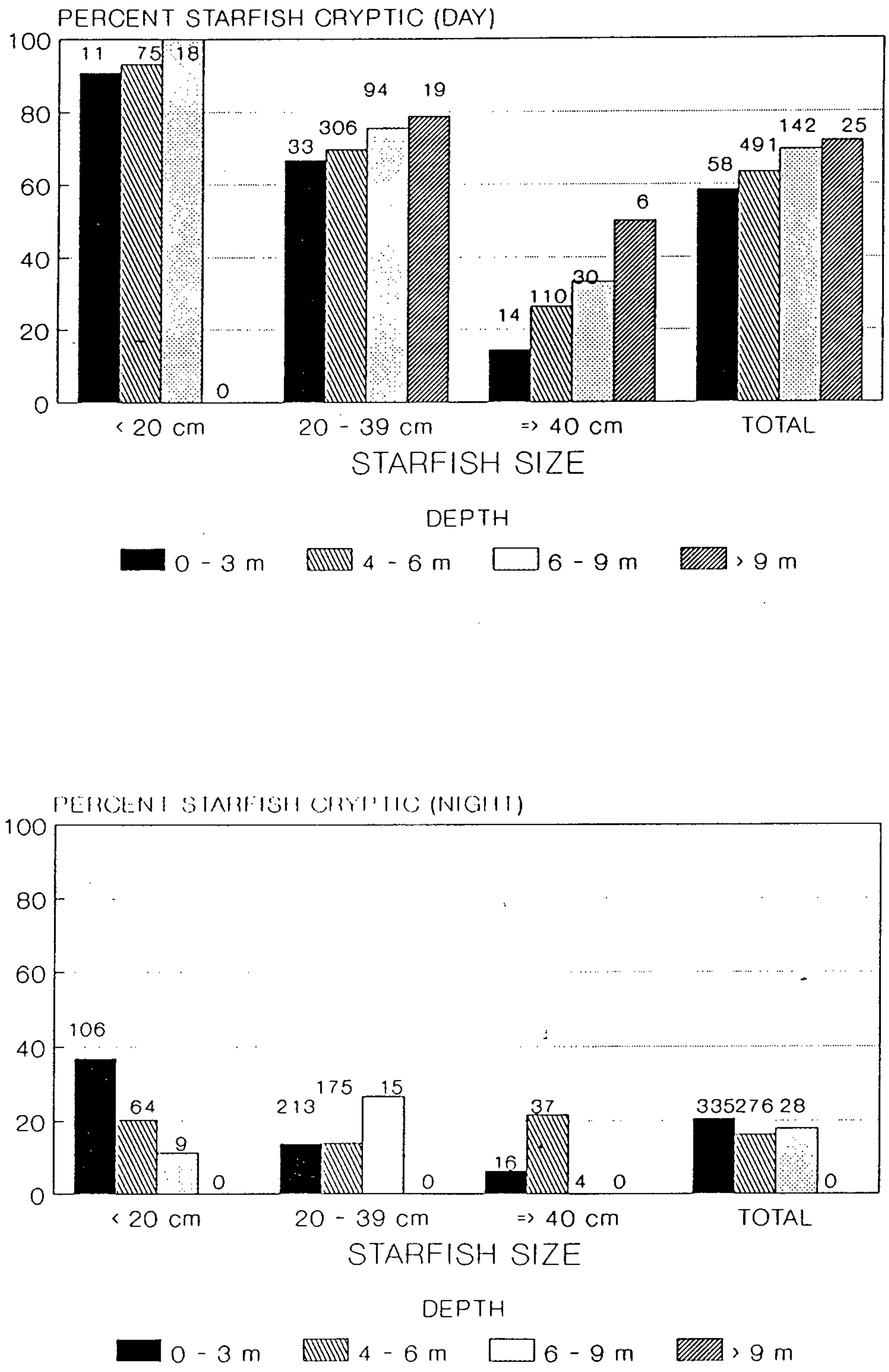


Figure IX. The proportion of A. planci cryptic at different depths at Wheeler Reef in January 1987 day and night samples for each size class. Sample size is indicated above each bar.

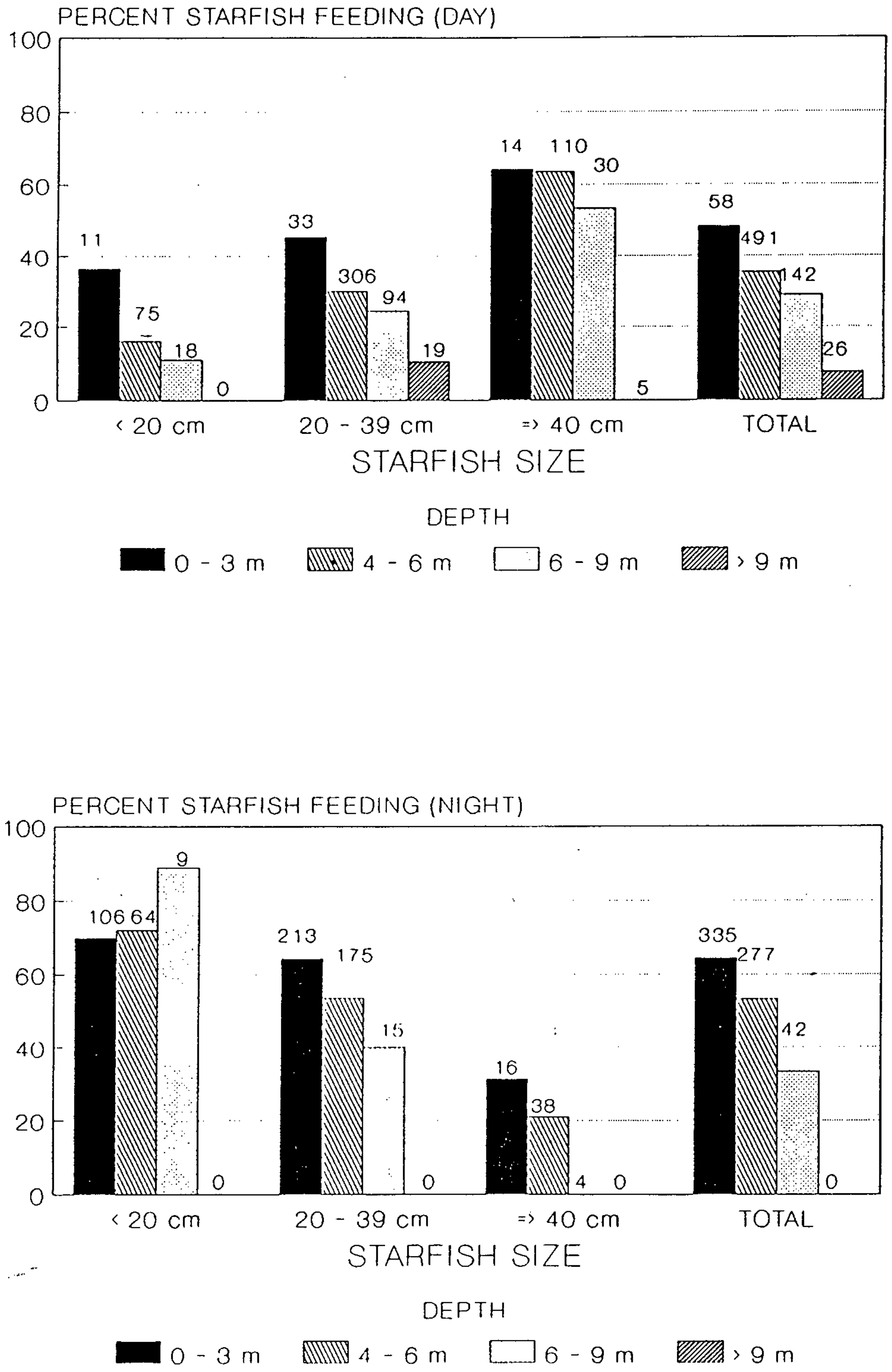


Figure X. The proportion of A. planci feeding at different depths at Wheeler Reef in January 1987 day and night samples for each size class. Sample size is indicated above each bar.

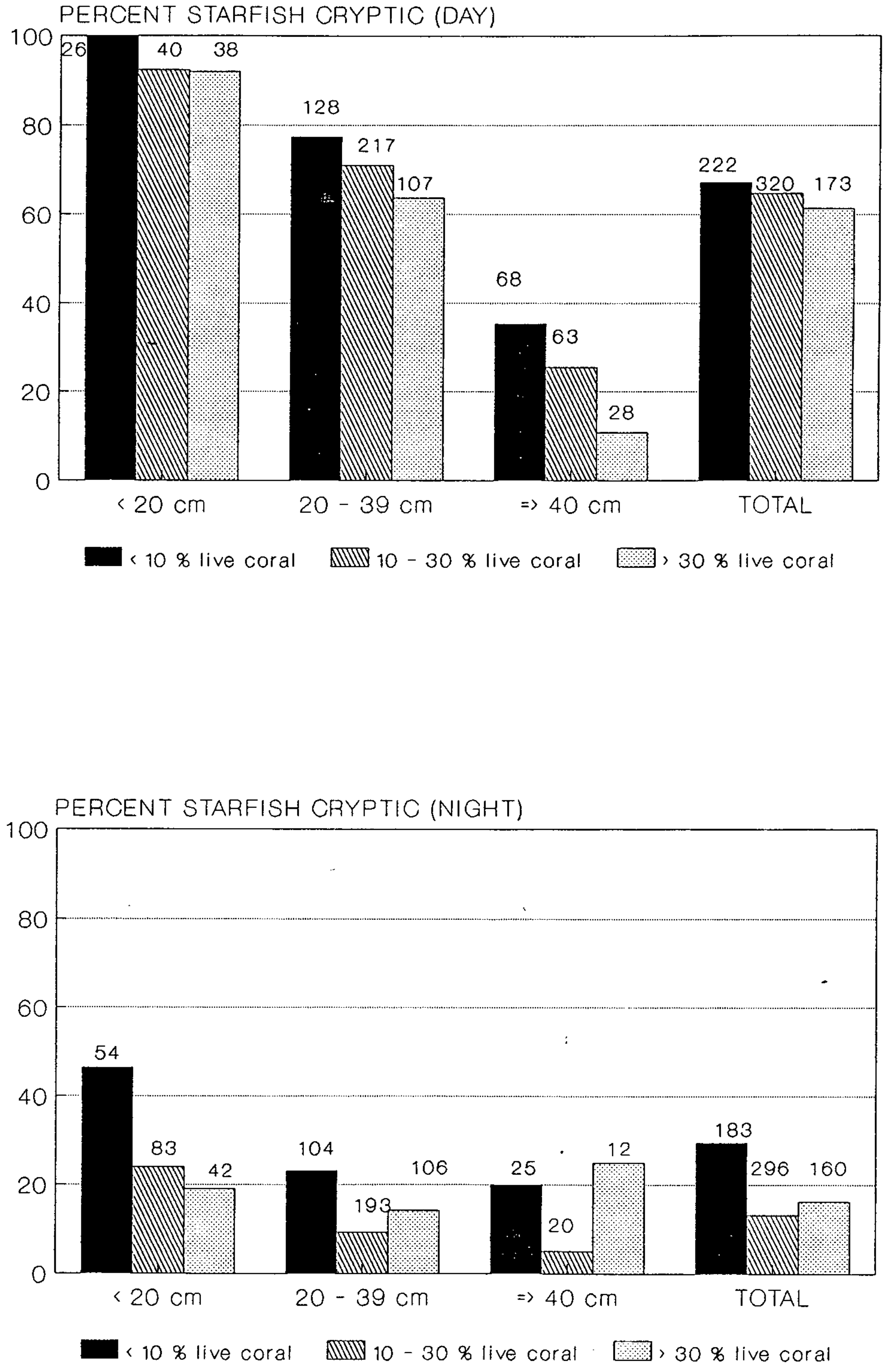


Figure XI. The proportion of <u>A. planci</u> cryptic at different categories of live coral cover at Wheeler Reef in January 1987 day and night samples for each size class. Sample size is indicated above each bar.

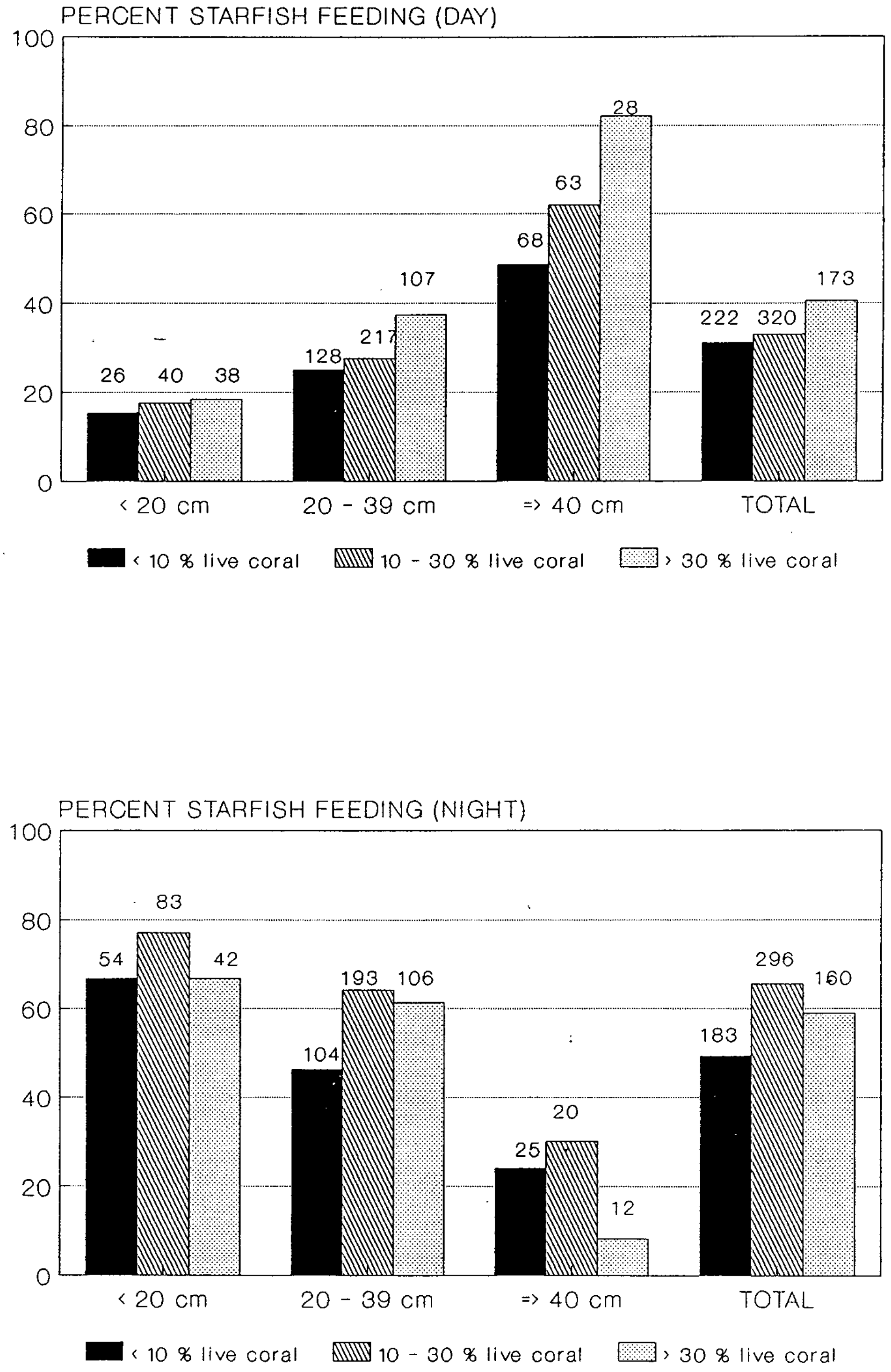


Figure XII. The proportion of A. planci feeding at different categories of live coral cover at Wheeler Reef in January 1987 day and night samples for each size class. Sample size is indicated above each bar.

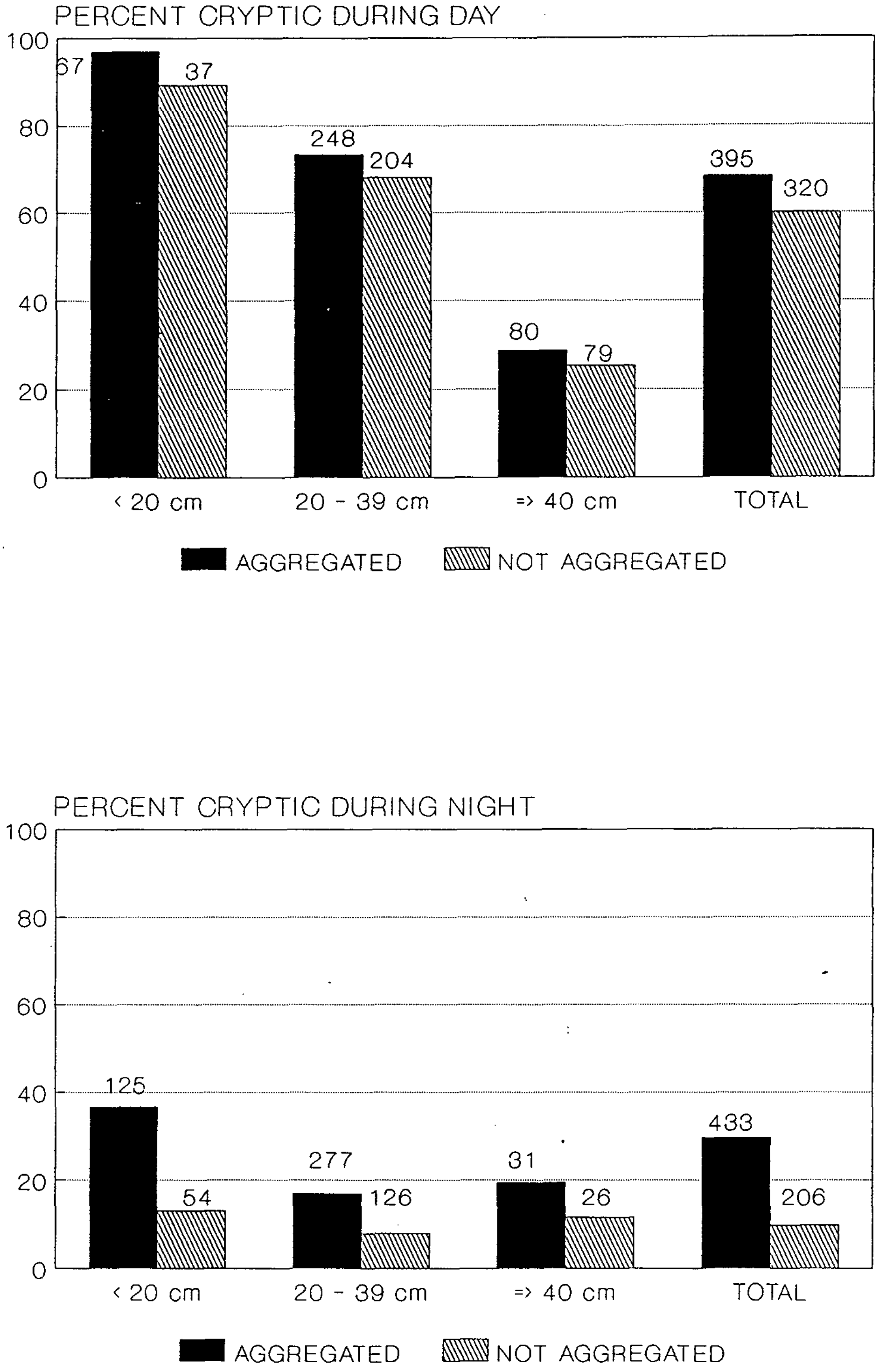
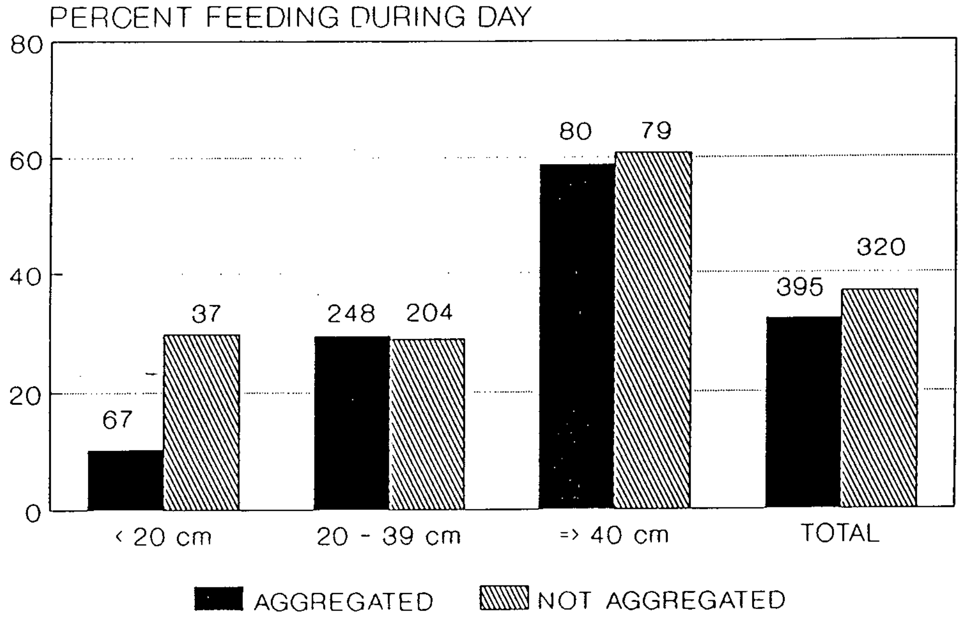


Figure XIII. The proportion of aggregated and non-aggregated A. planci showing cryptic behaviour during day and night samples at Wheeler Reef in January 1987. Sample size is indicated above each bar.



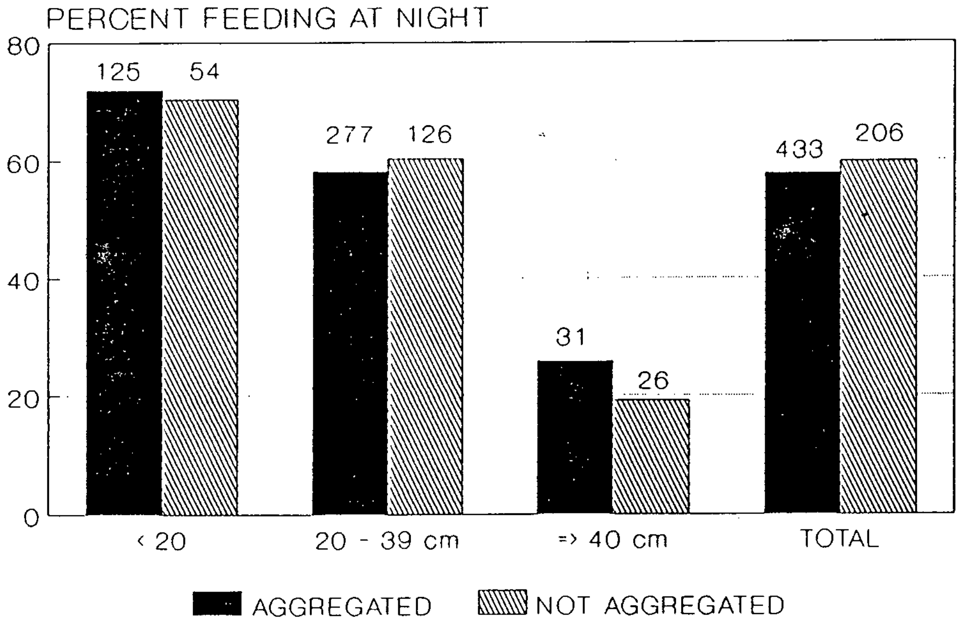


Figure XIV. The proportion of aggregated and non-aggregated A. planci feeding during day and night samples at Wheeler Reef in January 1987.

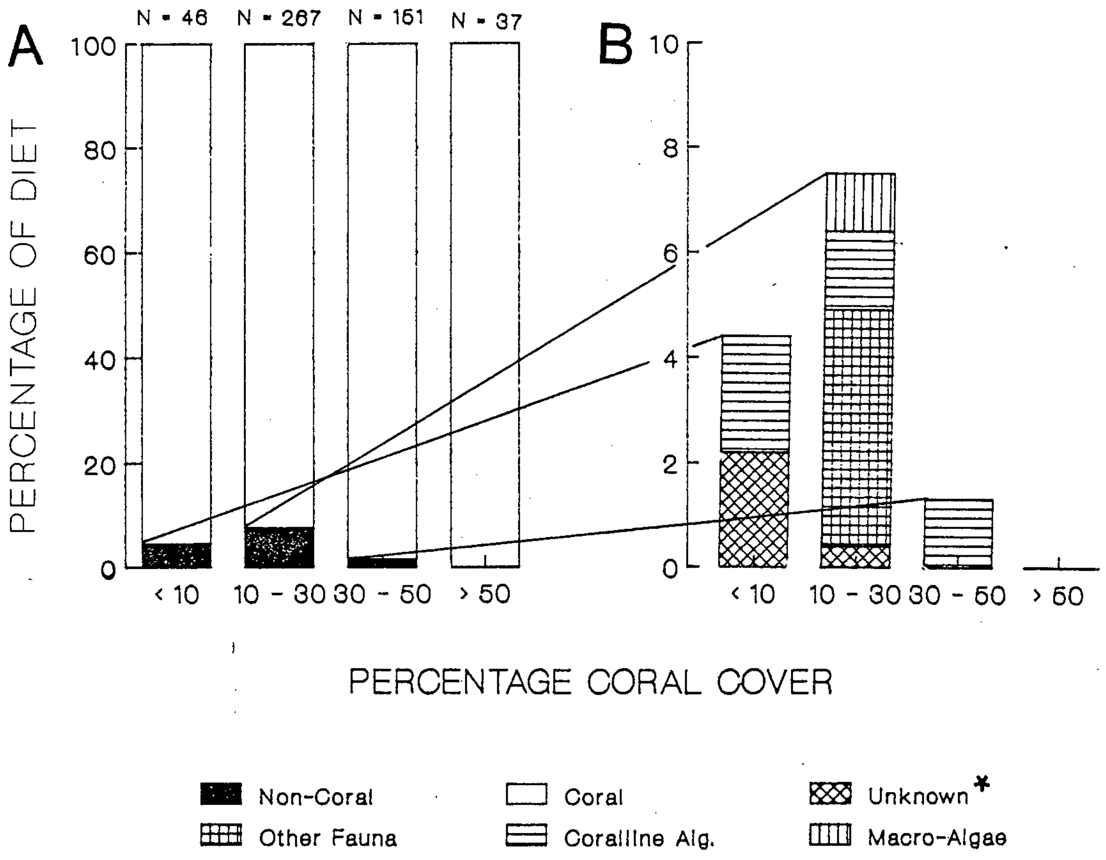


Figure XV. Components of diet of <u>Acanthaster planci</u> in areas of differing live coral cover. A, Proportions of coral and non-coral prey.; B, Detail of non-coral prey components. Wheeler Reef, October 1986.

*Unknown refers to cases where starfish stomach was extruded over reef surface, but actual prey item was unclear.

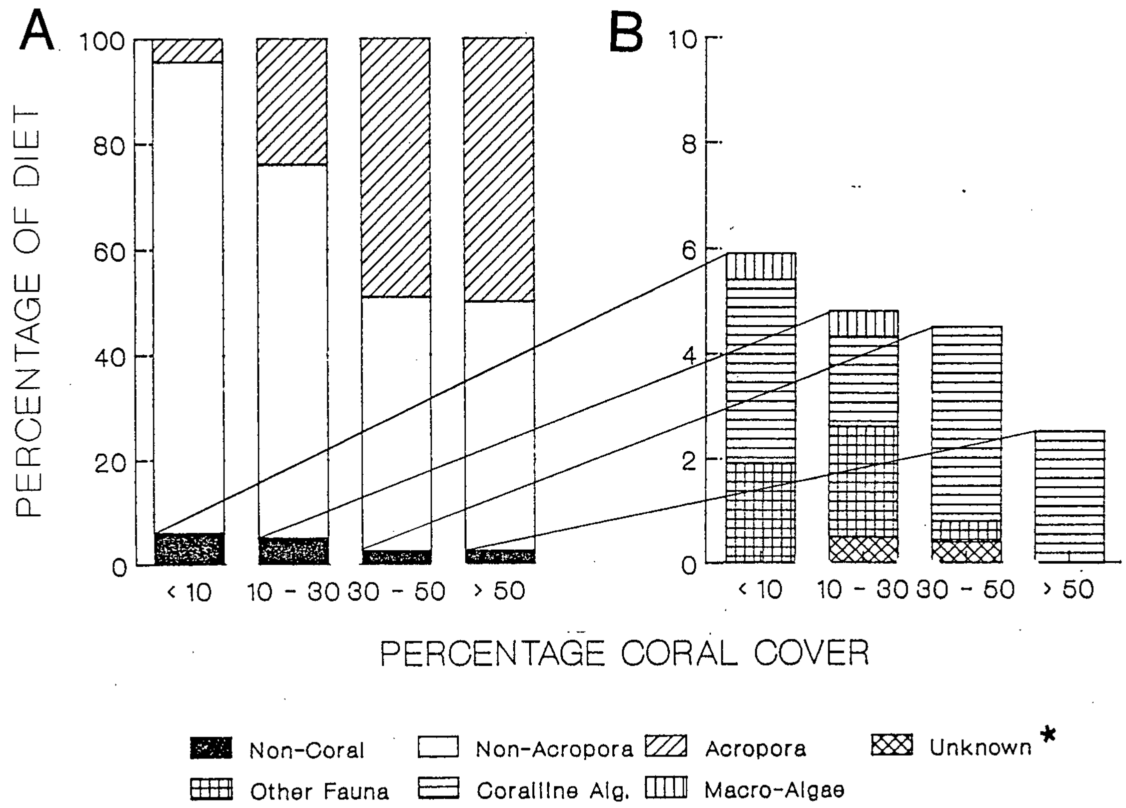


Figure XVI. Components of diet of Acanthaster planci in areas of differing live coral cover. A, Proportions of Acropora coral, other coral and non-coral prey.; B, Detail of non-coral prey components. Wheeler Reef, January 1987.

*Unknown refers to cases where starfish stomach was extruded over reef surface, but actual prey item was unclear.

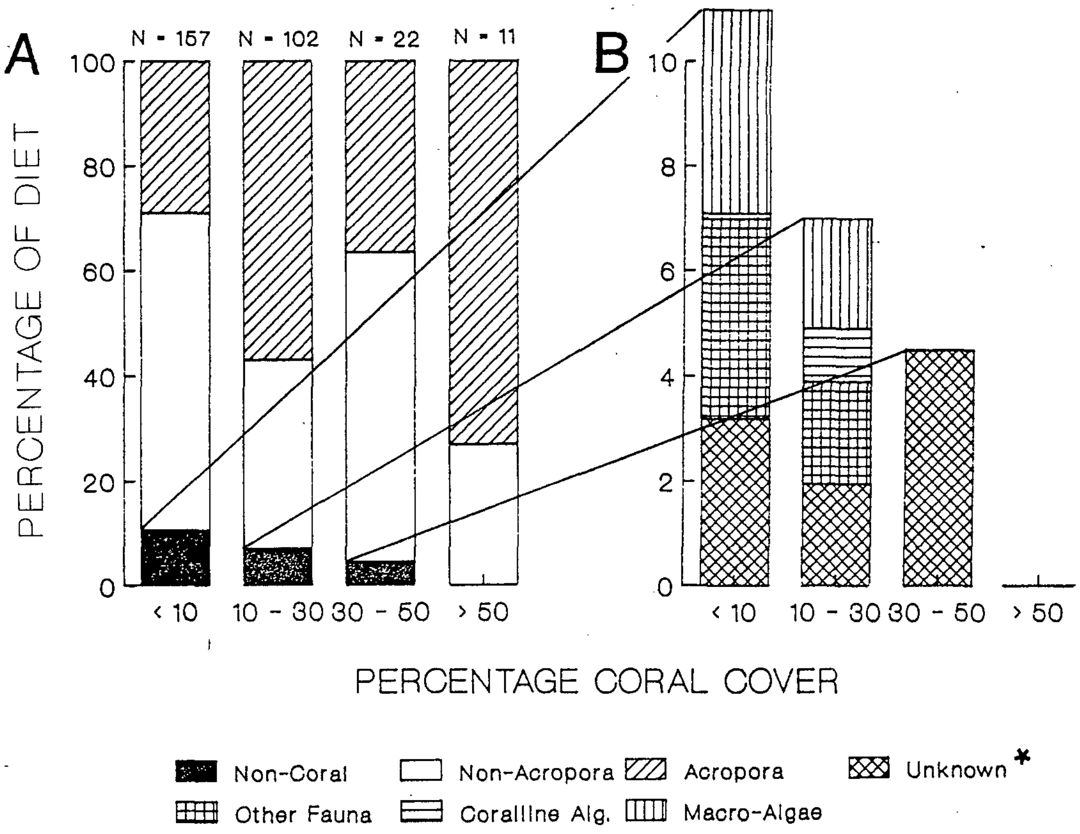


Figure XVII. Components of diet of *Acanthaster planci* in areas of differing live coral cover. A, Proportions of *Acropora* coral, other coral and non-coral prey.; B, Detail of non-coral prey components. Wheeler Reef, June 1987.

*Unknown refers to cases where starfish stomach was extruded over reef surface, but actual prey item was unclear.

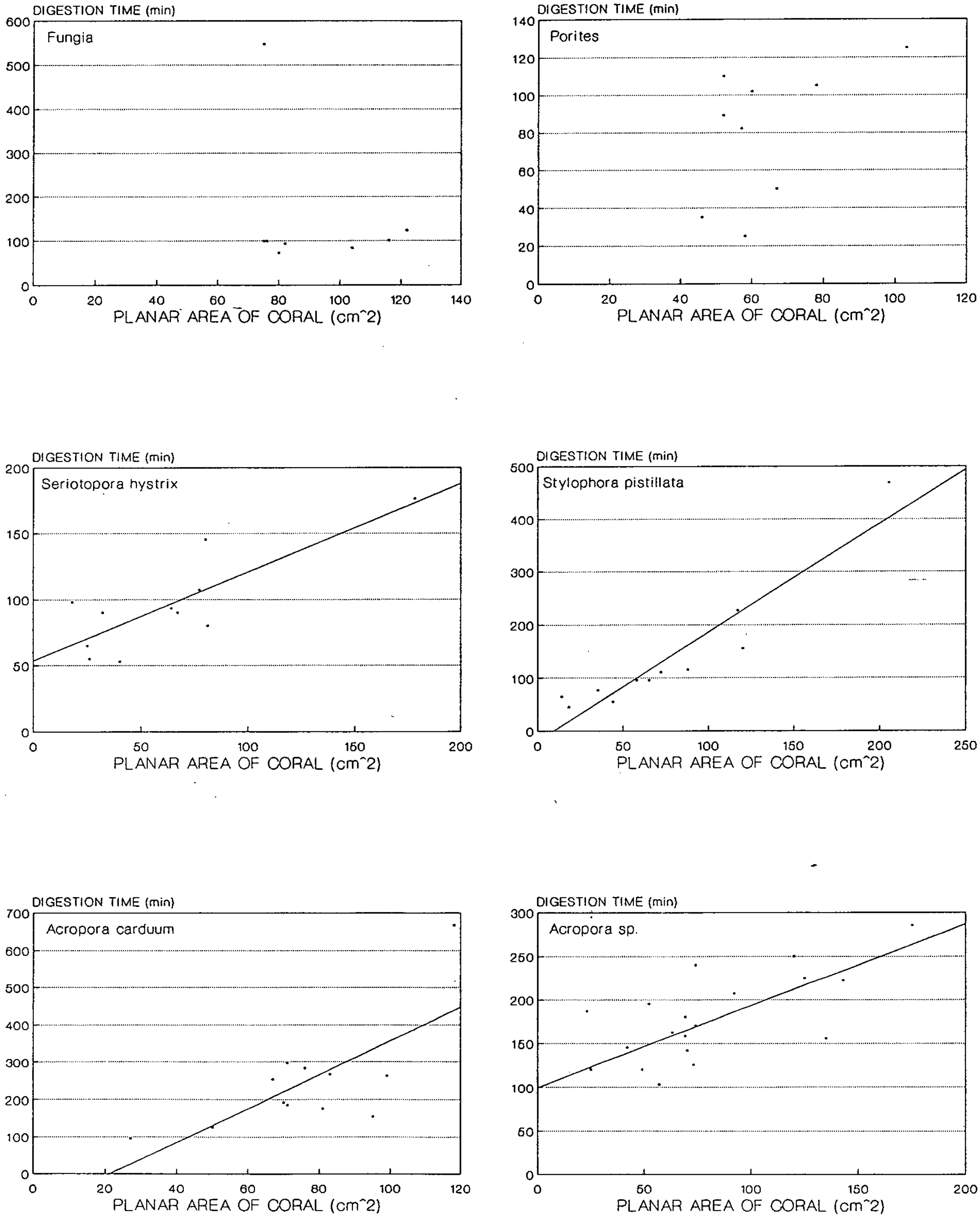


Figure XVIII. Relationship between planar area of coral and digestion time for <u>Acanthaster planci</u> feeding on six species of corals in the laboratory. Regression lines indicate significant linear relationships.

Prey Genus	Number eaten	Percent eaten	Number available	Percent available	Ratio eaten/ available
Mycedium	2	0.50	3	0.14	**3.56**
Acropora	213	52.85	679	31.54	**1.68**
Echinophyllia	3	0.74	11	0.51	**1.46**
Seriatopora	23	5.71	88	4.09	**1.40**
Platygyra	1	0.25	4	0.19	**1.34**
Stylophora	52	12.90	233	10.82	**1.19**
Echinopora	3	0.74	16	0.74	1.00
Montipora	31	7.69	167	7.76	0.99
Pocillopora	30	7.44	186	8.64	0.86
Cyphastrea	13	3.23	82	3.81	0.85
Pavona	1	0.25	8	0.37	0.67
Goniastrea	7	1.74	71	3.30	0.53
Favites	5	1.24	68	3.16	0.39
Symphyllia	1	0.25	16	0.74	0.33
Porites	16	3.97	363	16.86	0.24
Favia	1	0.25	24	1.11	0.22
Montastrea	1	0.25	48	2.23	0.11
Lobophyllia	0	0.00	14	0.65	0.00
Galaxea	0	0.00	13	0.60	0.00
Hydnophora	0	0.00	8	0.37	0.00
Fungia	0	0.00	8	0.37	0.00
Merulina	0	0.00	5	0.23	0.00
Coscinaraea	0	0.00	5	0.23	0.00
Turbinaria	0	0.00	4	0.19	0.00
Diploastrea	0	0.00	4	0.19	0.00
Goniopora	0	0.00	4	0.19	0.00
Oulophyllia	0	0.00	4	0.19	0.00
Astreopora	0	0.00	3	0.14	0.00
Pseudosidastrea	0	0.00	3	0.14	0.00
Acrhelia	0	0.00	3	0.14	0.00
Sandolitha	0	0.00	2	0.09	0.00
Plerogyra	0	0.00	2	0.09	0.00
Euphyllia	0	0.00	1	0.05	0.00
Pectinia	0	0.00	1	0.05	0.00
Scolymia	0	0.00	1	0.05	0.00
Physogyra	0	0.00	1	0.05	0.00
	403	100.00	2153	100.00	

Table I. Prey genus preference data for tagged A. planci from Davies Reef. Observations for four field trips pooled. Values greater than one (bolded) indicate genera that were taken in proportions greater than their availability (preferred). Values less than one indicate that those genera were non-preferred.

Prey Genus	Number eaten	Percent eaten	Number available	Percent available	Ratio eaten/ available
< 10 % Live coral					
Seriatopora	2	7.69	3	2.16	**3.56**
Cyphastrea	3	11.54	5	3.60	**3.21**
Acropora	8	30.77	21	15.11	**2.04**
Echinopora	1	3.85	3	2.16	**1.78**
Stylophora	3	11.54	11	7.91	**1.46**
Goniastrea	3	11.54	11	7.91	**1.46**
Pocillopora	1	3.85	5	3.60	**1.07**
Favia	1	3.85	7	5.04	0.76
Favites	1	3.85	10	7.19	0.54
Porites	3	11.54	35	25.18	0.46
Montipora	0	0.00	13	9.35	0.00
Montastrea	0	0.00	3	2.16	0.00
Lobophyllia	0	0.00	3	2.16	0.00
Galaxea	0	0.00	2	1.44	0.00
Pavona	0	0.00	1	0.72	0.00
Merulina	0	0.00	1	0.72	0.00
Coscinaraea	0	0.00	1	0.72	0.00
Goniopora	0	0.00	1	0.72	0.00
Pseudosidastrea	0	0.00	1	0.72	0.00
Plerogyra	0	0.00	1	0.72	0.00
Pectinia	0	0.00	1	0.72	0.00
	26	100.00	139	100.00	

Table II A. Prey genus preference data for tagged *A. planci* from Davies Reef. Observations for four field trips pooled and presented for contrasting food availability (live coral cover). Bolded genera are preferred groups. Continued over.

Prey Genus	Number eaten	Percent eaten	Number avail-able	Percent avail-able	Ratio eaten/ available
10 - 30 % live coral cover					
Mycedium	2	0.87	3	0.23	**3.78**
Platygyra	1	0.44	3	0.23	**1.91**
Echinophyllia	3	1.31	9	0.70	**1.87**
Acropora	113	49.34	360	28.15	**1.75**
Echinopora	2	0.87	7	0.55	**1.58**
Seriatopora	11	4.80	44	3.44	**1.40**
Montipora	24	10.48	118	9.22	**1.14**
Stylophora	29	12.66	149	11.65	**1.09**
Pavona	1	0.44	6	0.47	0.94
Pocillopora	18	7.86	113	8.84	0.89
Cyphastrea	9	3.93	69	5.39	0.73
Goniastrea	4	1.75	43	3.36	0.52
Favites	3	1.31	39	3.05	0.43
Porites	8	3.49	216	16.89	0.21
Montastrea	1	0.44	34	2.66	0.16
Favia	0	0.00	15	1.17	0.00
Lobophyllia	0	0.00	7	0.55	0.00
Galaxea	0	0.00	6	0.47	0.00
Symphyllia	0	0.00	6	0.47	0.00
Merulina	0	0.00	4	0.31	0.00
Coscinaraea	0	0.00	4	0.31	0.00
Diploastrea	0	0.00	4	0.31	0.00
Oulophyllia	0	0.00	4	0.31	0.00
Hydnophora	0	0.00	3	0.23	0.00
Fungia	0	0.00	3	0.23	0.00
Acrhelia	0	0.00	3	0.23	0.00
Turbinaria	0	0.00	2	0.16	0.00
Pseudosidastrea	0	0.00	1	0.08	0.00
Euphyllia	0	0.00	1	0.08	0.00
Goniopora	0	0.00	1	0.08	0.00
Scolymia	0	0.00	1	0.08	0.00
Physogyra	0	0.00	1	0.08	0.00
	229	100.00	1279	100.00	

Table II B.

Prey Genus	Number eaten	Percent eaten	Number available	Percent available	Ratio eaten/ available
30 - 50 % live coral cover					
Acropora	39	48.75	135	31.10	**1.57**
Stylophora	14	17.50	55	12.67	**1.38**
Seriatopora	4	5.00	18	4.15	**1.20**
Montipora	7	8.75	32	7.37	**1.18**
Pocillopora	9	11.25	44	10.14	**1.11**
Cyphastrea	1	1.25	7	1.61	0.78
Porites	5	6.25	75	17.28	0.36
Favites	1	1.25	16	3.69	0.34
Goniastrea	0	0.00	8	1.84	0.00
Montastrea	0	0.00	7	1.61	0.00
Symphyllia	0	0.00	6	1.38	0.00
Fungia	0	0.00	5	1.15	0.00
Lobophyllia	0	0.00	4	0.92	0.00
Galaxea	0	0.00	4	0.92	0.00
Echinopora	0	0.00	3	0.69	0.00
Astreopora	0	0.00	3	0.69	0.00
Favia	0	0.00	2	0.46	0.00
Turbinaria	0	0.00	2	0.46	0.00
Echinophyllia	0	0.00	2	0.46	0.00
Sandolitha	0	0.00	2	0.46	0.00
Pavona	0	0.00	1	0.23	0.00
Hydnophora	0	0.00	1	0.23	0.00
Pseudosidastrea	0	0.00	1	0.23	0.00
Plerogyra	0	0.00	1	0.23	0.00
	80	100.00	434	100.00	

Table II C.

Prey Genus	Number eaten	Percent eaten	Number avail- able	Percent avail- able	Ratio eaten/ available
> 50 % Live coral					
Stylophora	5	8.47	14	5.60	**1.51**
Acropora	50	84.74	145	58.00	**1.46**
Seriatopora	2	3.39	10	4.00	0.85
Pocillopora	2	3.39	21	8.40	0.40
Porites	0	0.00	30	12.00	0.00
Goniastrea	0	0.00	7	2.90	0.00
Montipora	0	0.00	4	1.60	0.00
Montastrea	0	0.00	4	1.60	0.00
Hydnophora	0	0.00	4	1.60	0.00
Favites	0	0.00	3	1.20	0.00
Echinopora	0	0.00	3	1.20	0.00
Goniopora	0	0.00	2	0.80	0.00
Galaxea	0	0.00	1	0.40	0.00
Cyphastrea	0	0.00	1	0.40	0.00
Platygyra	0	0.00	1	0.40	0.00
	59	100.00	250	100.00	

Table II D.

SPECIES	DAY OF EXPERIMENT											
	1	2	3	4	5	6	7	8	9	10	11	12
Acropora carduum	**5.45**	**4.38**	**3.24**	**4.65**	**4.76**							
Acropora nasuta	**5.45**	**4.38**	**6.48**	**2.58**	0.00	**8.00**						
Seriatopora hystrix	0.00	0.00	**2.27**	**3.88**	**3.57**	**8.00**						
Stylophora pistillata	0.00	0.00	0.00	**1.55**	**3.57**	**4.00**	**6.22**					
Echinopora lamellosa	0.00	0.00	**1.13**	**1.72**	**2.04**	**2.00**	**4.15**	**3.62**				
Fungia fungites	0.00	**3.50**	0.00	0.00	0.53	1.00	**1.78**	**2.89**	0.00	**4.00**		
Goniastrea retiformis	0.00	0.00	0.00	0.00	0.48	0.89	0.78	**2.07**	**2.27**	**4.00**		
Lobophyllia hemprichii	0.00	0.00	0.00	0.00	0.00	0.80	0.00	**1.21**	**1.70**	**1.33**	**1.50**	**2.00**
Porites cylindrica	0.00	0.00	0.00	0.00	0.48	0.00	**1.38**	0.00	0.49	0.67	0.60	**2.00**
Porites lichen	0.00	0.00	0.00	0.00	0.00	0.00	0.62	0.00	**1.13**	0.67	**1.80**	1.00
Porites lutea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.43	0.57	0.50	0.00

Table III. Sequential species prey preference of *A. planci* during laboratory experiment. Table values are ratios of prey eaten to prey available. Values greater than one (bolded) indicate preferred species.

Species	Mean minutes per cm2 of PSA	Standard deviation	N	*
<u>Acropora</u> <u>carduum</u>	3.2	1.1	12	|
<u>Acropora</u> <u>nasuta</u>	2.4	0.9	18	| |
<u>Stylophora</u> <u>pistillata</u>	2.0	1.0	11	| | |
<u>Seriatopora</u> <u>hystrix</u>	2.0	1.3	11	| | |
<u>Porites</u> <u>lichen</u>	1.5	0.5	5	| |
<u>Porites</u> <u>lutea</u>	1.0	0.4	4	|
<u>Fungia</u> <u>fungites</u>**	1.8	2.2	8	
<u>Goniastrea</u> <u>retiformis</u>**	1.6	1.0	2	
Family				
Acroporidae	2.7	1.0	30	|
Pocilloporidae	2.0	1.1	22	| |
Poritidae	1.3	0.5	9	|

Table IV. Mean digestion times per unit area for <u>A. planci</u> feeding on different species of coral in the laboratory.

*lines connect non-significant subsets ($p > 0.05$, Tukey's HSD).

**not included in analyses due to excessive variance contamination (<u>Fungia</u>) and small sample size (<u>Goniastrea</u>).

Species		Feeding efficiency (percent)*	Standard error**
Pocillopora damicornis	psa	57.7	12.5
Acropora nobilus	rsa	50.0	12.5
Acropora carduum	psa	48.9	3.1
	rsa	44.4	6.7
Fungia fungites	psa	31.2	15.2
	rsa	38.9	10.6
Stylophora pistillata	psa	18.6	11.4
	rsa	33.3	11.1
Seriatopora hystrix	psa	37.8	16.4
	rsa	33.3	15.0
Echinopora lamellosa	psa	37.1	17.1
	rsa	26.7	13.3
Lobophyllia hemprichii	psa	36.9	10.1
	rsa	25.6	6.0
Acropora nasuta	psa	14.0	17.7
	rsa	25.0	11.2
Porites lutea	psa	15.6	10.0
	rsa	17.9	7.9
Porites lichen	psa	0.0	-
	rsa	6.7	14.4
Porites cylindrica	psa	0.0	-
	rsa	0.0	-

Table V. Efficiency of tissue extraction for A. planci feeding on different coral species in the laboratory. Percent feeding efficiencies presented for both planar surface area (psa) and true or real surface area (rsa).

* the difference between means of available soft tissue DW and uneaten soft tissue DW (i.e. consumed soft tissue) as a percentage of available tissue

** percent standard error of difference between available tissue and uneaten means multiplied by percent feeding efficiency

i.e. if mean difference = 10 mg and S.E. = 2 mg then %SE = 20
thus if available tissue = 20 mg
then feeding efficiency = 50 %
and error = 20% of 50 = 10
i.e. feeding efficiency = 50 +/- 10 %

Species	mean ratio of RSA/PSA	standard deviation	N
Acropora nasuta	5.65	1.07	21
Acropora hyacinthus	5.43	1.08	12
Acropora carduum	11.15 (above) 5.17 (side)	3.60 0.74	28
Stylophora pistillata	5.12	0.91	27
Seriatopora hystrix	4.01	1.10	22
Lobophyllia hemprichii	3.83	1.15	25
Porites lutea	3.74	0.57	15
Goniastrea retiformis	3.68	0.85	23
Porites cylindrica	3.47 (above) 2.48 (side)	1.22 0.91	21 21
Montipora digitata	3.37 (above) 2.44 (side)	0.91 0.18	5 5
Fungia fungites	2.95 (total) ca. 1.95 (available)*	0.49	20
Echinopora lamellosa	2.15	0.42	22
Porites lichen	1.33	0.37	20

Table VI. Table of surface area complexity indices for different coral species preyed upon by A. planci. Table values are ratios of real surface area (RSA) to planar surface area (PSA). *The bottom of the solitary coral Fungia is usually inaccessible to feeding starfish.

Species	soft tissue biomass (mg DW) per cm^2	sd.	N	soft tissue biomass (mg AFDW) per cm^2
<u>Lobophyllia</u>	156.0 PSA	37.2	9	91.1
<u>hemprichii</u>	42.8 RSA	15.0	9	25.0
<u>Porites</u>	36.2 PSA	6.2	13	13.9
<u>lichen</u>	30.3 RSA	5.8	13	11.6
<u>Porites</u>	104.0 PSA	16.0	11	43.9
<u>lutea</u>	29.0 RSA	4.0	11	12.2
<u>Goniastrea</u>	88.5 PSA	28.1	11	43.2
<u>retiformis</u>	22.9 RSA	5.2	11	11.2
<u>Fungia</u>	48.3 PSA	10.7	9	27.6
<u>fungites</u>	17.8 RSA	2.6	9	10.2
<u>Montipora</u>	53.5 (above)	11.9	5	34.7
<u>digitata</u>	39.2 (side)	2.3	5	25.4
	16.2 RSA	2.1	5	10.5
<u>Porites</u>	43.2 (above)	7.3	7	26.8
<u>cylindrica</u>	33.6 (side)	4.8	7	20.8
	15.5 RSA	2.6	7	9.6
<u>Echinopora</u>	34.8 PSA	8.0	9	24.1
<u>lamellosa</u>	15.0 RSA	3.6	9	10.4
<u>Acropora nobilus</u>	11.7 RSA	3.2	7	5.1
<u>Stylophora</u>	43.3 PSA	9.1	9	30.1
<u>pistillata</u>	9.3 RSA	2.5	9	6.5
<u>Acropora</u>	47.4 PSA	13.4	12	30.6
<u>hyacinthus</u>	8.7 RSA	1.6	12	5.6
<u>Acropora</u>	118.2 (above)	18.9	14	65.1
<u>carduum</u>	45.2 (side)	6.7	14	24.9
	8.6 RSA	1.2	14	4.7
<u>Acropora</u>	43.4 PSA	14.2	9	23.4
<u>nasuta</u>	7.7 RSA	1.3	9	4.1
<u>Seriatopora</u>	24.2 PSA	11.7	13	15.9
<u>hystrix</u>	5.6 RSA	1.5	13	3.7
<u>Montipora aequituberculata</u>	30.8 PSA	3.8	7	16.7
<u>Pocillopora damicornis</u>	25.6 PSA	5.1	5	18.2

Table VII. Soft tissue biomass of different coral species preyed upon by <u>A. planci</u>. Values presented are both; dry weight (DW) and ash-free dry weight (AFDW) for planar surface area (PSA) and true or real surface area (RSA).

Species	% ash	sd.
Pocillopora damicornis	29.0	3.6
Stylophora pistillata	30.4	4.2
Echinopora lamellosa	30.6	1.0
Seriatopora hystrix	34.3	0.2
Montipora digitata	35.1	
Acropora hyacinthus	35.5	2.3
Porites cylindrica	38.0	
Lobophyllia hemprichii	41.6	0.5
Fungia fungites	42.8	3.3
Acropora carduum	44.9	2.3
Montipora aequituberculata	45.7	0.2
Acropora nasuta	46.2	1.7
Goniastrea retiformis	51.2	
Acropora nobilus	56.5	
Porites lutea	57.9	2.1
Porites lichen	61.6	9.2

Table VIII. Ash content of different species of scleractinian corals. Mean values are for two samples (colonies). Values without a standard deviation are for single samples.

Species	$kJ.g^{-1}$ AFDW	sd.
Acropora hyacinthus	23.69	0.15
Acropora nasuta	22.70	0.48
Pocillopora damicornis	22.67	0.25
Seriatopora hystrix	22.67	0.40
Porites cylindrica	22.43	
Montipora digitata	21.89	
Montipora aequituberculata	21.85	0.27
Lobophyllia hemprichii	21.75	1.06
Stylophora pistillata	21.60	1.77
Echinopora lamellosa	21.20	0.61
Fungia fungites	20.70	3.03
Acropora carduum	20.35	0.75
Goniastrea retiformis	20.28	
Acropora nobilis	19.28	
Porites lutea	18.04	1.08
Porites lichen	17.48	

Table IX. Coral tissue energy content for different species of scleractinian corals. Mean values are for samples of two colonies. Values without a standard deviation are for single samples. One outlier for P. lichen (11.0 kJ) was omitted.

Species	% Protein	sd.
Fungia fungites	59.9	0.1
Stylophora pistillata	59.2	5.1
Seriatopora hystrix	59.1	0.3
Pocillopora damicornis	56.8	0.0
Acropora hyacinthus	54.4	3.2
Montipora aequituberculata	54.0	2.5
Lobophyllia hemprichii	53.2	1.6
Acropora carduum	53.0	1.4
Echinopora lamellosa	52.4	8.7
Acropora nasuta	51.3	1.0
Porites cylindrica	50.1	
Goniastrea retiformis	49.6	
Montipora digitata	49.0	
Acropora nobilus	42.6	
Porites lichen	40.8	
Porites lutea	40.6	2.5

Table X. Coral tissue protein content (% of AFDW) for different species of scleractinian corals. Mean values are for samples of two colonies. Values without a standard deviation are for single samples.

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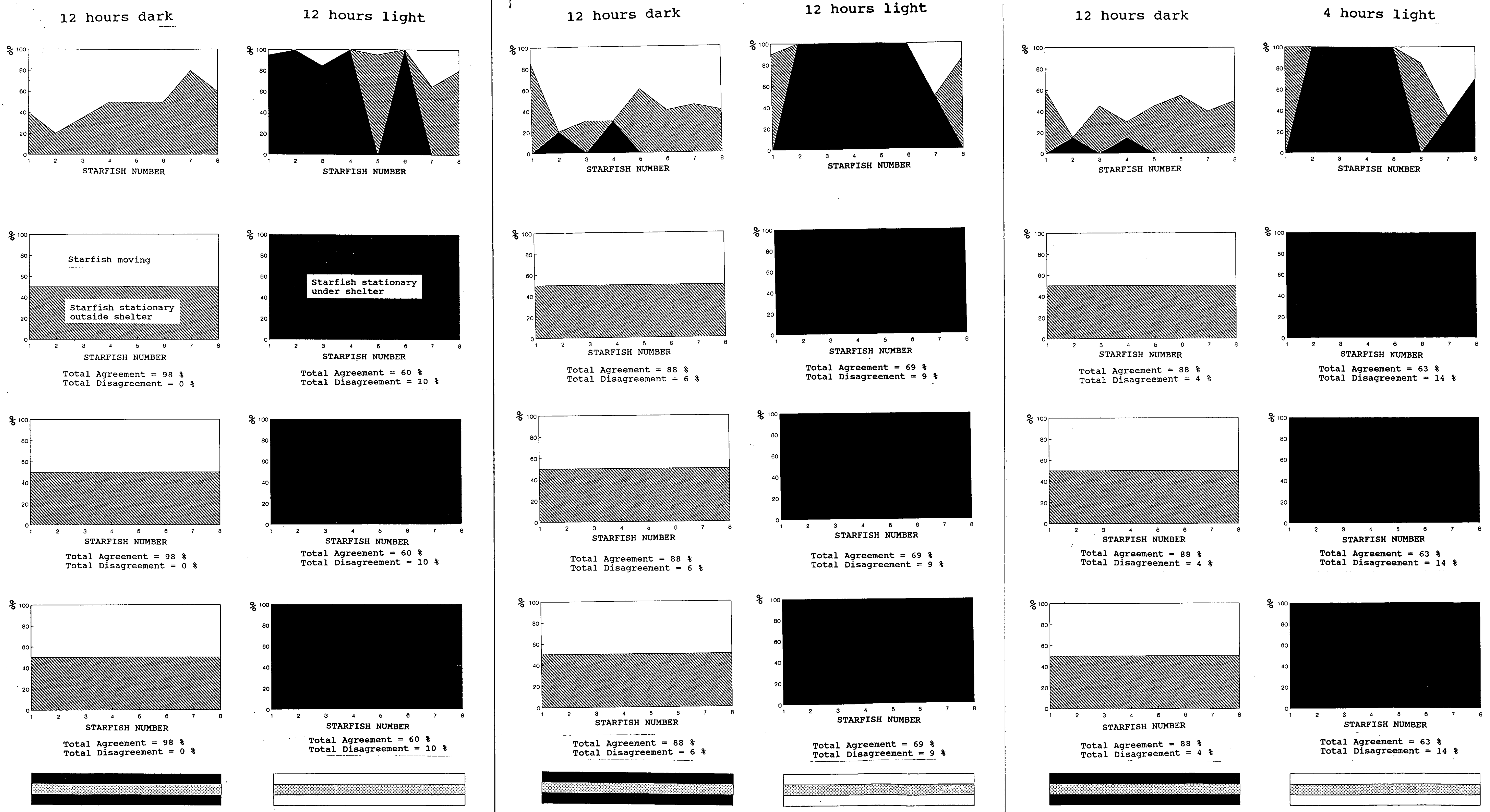
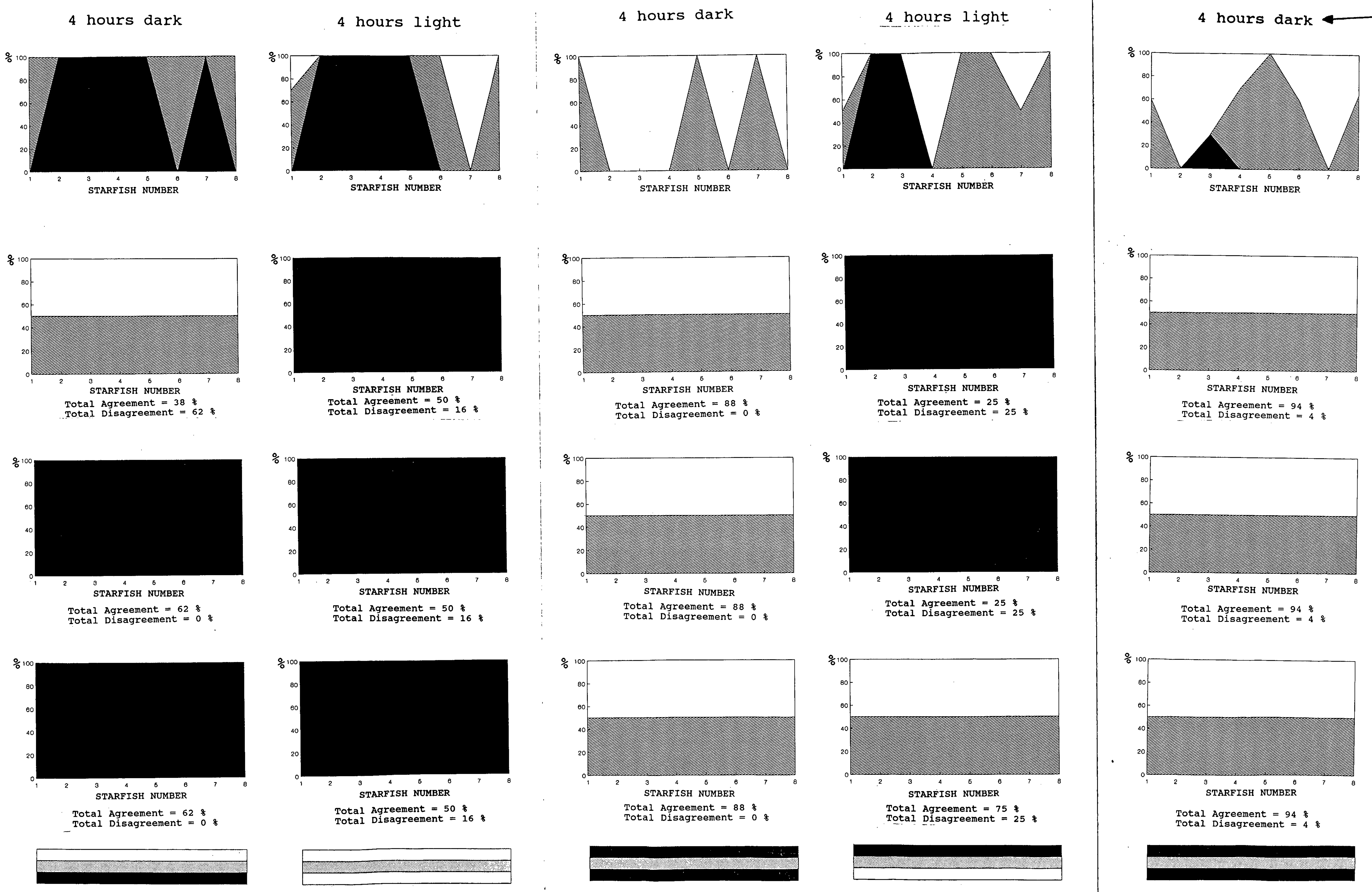


Figure 12. Experimental data and three theoretical responsesof *Acanthaster planci* to alteration of day length regimes. Area charts indicate percent frequency of each behaviour type. See page 30 for explanation.



Duration of light / dark period

Experimental Data

% frequency of each behaviour type for eight *A. planci* during the experimental period

Theoretical model 1

Total light dependent behaviour (negatively phototactic)

Theoretical model 2

Endogenously controlled nocturnal behaviour with light avoidance over-ride (negatively phototactic)

Theoretical model 3

Endogenously controlled nocturnal behaviour with no response to additional photic stimulus

Key to Light Regime

Natural ambient
white=day, black=night

Experimental ambient
white=light, black=dark