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# Feeding studies on potential fish predators of post-settlement *Acanthaster planci*

## Final report prepared for the Great Barrier Reef Marine Park Authority

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## Executive Summary

### Background to interpretation of gut contents

- Digested remains of adult and juvenile *A. planci* are easily recognised with the use of a dissecting microscope.

- In the only systematically documented instance of predation by a lethrinid - one *L. nebulosus* had four arms from an adult *A. planci* - is not likely to have been fatal. It remains possible that several fish often attack the same starfish.

- Most of the contents of a lethrinid's gut have been consumed in the preceding 24 h. A small fraction of the food consumed in the preceding 24 h will have passed already. Thus recording the number of *L. miniatus* with *A. planci* present in gut contents will give a slight (~ 15%) underestimate of the number of fish that have consumed Crown of thorns starfish in the previous 24 h.

### Estimates of the impact of fish predation on *A. planci* populations

- Experiments removing arms from starfish have shown that, while effect of damage is variable, minor damage causes little mortality in the short term.

- While minor damage is not usually fatal, it does cause reduced gonad development by around 10%. There is evidence of reduced gonad size in damaged arms and arms adjacent to damaged arms in both sexes. This means that predators that inflict sub-lethal damage may lower reproductive output of *A. planci* populations.

- For control programs, even cutting a Crown of thorns starfish in half was not reliably fatal.

- A concerted fishing effort targeting lethrinids within a short distance of high densities of adult Crown of thorns starfish found no evidence that *L. miniatus* prey on adults on the basis of a sample of 95 fish. Estimates of predation rates from gut samples are imprecise because they are themselves products of several estimates (predator density, prey numbers), leading to propagation of errors.

- Variation in gut fullness with time of capture suggested that *L. miniatus* do feed after dusk and so their feeding does coincide with times when juvenile *A. planci* would be out feeding on coral and hence accessible to predators.

- When juvenile *A. planci* were offered to lethrinids in aquaria no starfish were eaten.

- When juvenile *A. planci* were offered to lethrinids in the field, two species did eat some of them. However this occurred in a minority of cases and in no instance were all the available individuals consumed. Starfish that were consumed were often bitten and spat out by several fishes before being swallowed. Lethrinids were unenthusiastic predators of juvenile *A. planci*.

- A predator exclusion experiment using juvenile *A. planci* in a site where putative predators were present found that total predatory mortality was very low relative to levels required by population models. Large fish predators could account for only a fraction of this predation. This did not support the hypothesis that commercially exploited fishes are important predators of juvenile *A. planci*.

- An attempt to repeat this experiment at another site was frustrated.

## 1: General Introduction

The Crown-of-thorns starfish, *Acanthaster planci*, has attracted attention in several areas of the Indo-Pacific by causing extensive damage to coral communities (Potts 1981, Moran 1986, Birkeland & Lucas 1990). Numerous hypotheses have been put forward to account for the sudden population increases, ranging from natural processes (Moore 1978), through amplification of natural processes by human activity (Nishihira & Yamazoto 1974; Pearson 1975) to direct human interference. One of the first of these hypotheses involving human interference was that starfish population outbreaks were caused by the removal of predators, specifically collection of the giant triton, *Charonia tritonis*, for sale to tourists (Endean 1969). Potts (1981) referred to this as the "predator removal hypothesis". Tritons eat adult *A. planci* but consumption rates have been found to average about one starfish per week (Chesher 1969, Pearson & Endean 1969) and many starfish are only partially eaten and so survive and regenerate lost arms (Chesher 1969). The natural density of *C. tritonis* and the potential impact on populations of *A. planci* have never been quantified, but their low consumption rates and apparent rarity argue against their ability to control large outbreaks.

The general question that prompted this study was whether human exploitation of the fish predators of *Acanthaster planci* may lead to increased frequency of outbreaks on the GBR. This variant of the predator removal hypothesis is also originally put forward by Endean (1976), who recorded remains of juvenile (10 cm) *A. planci* in the gut of a Queensland groper, *Epinephelus* (=*Promicrops*) *lanceolatus*, and suggested that fishing may remove predators and so increase the likelihood of outbreaks. This hypothesis was revitalised in the late 1980s as a result of population modelling by McCallum (1987, 1988) which suggested that the kind of population dynamics shown by *A. planci*: general low density occurrence but with unpredictable outbreaks, could be produced by a non-specialist predator showing a Type III (accelerating) functional response (typical of vertebrates) attacking the post-settlement stages of a prey species with planktonic larvae (so heavily depleted populations could be replenished from other reefs). He suggested that a predatory mortality rate of about 1.5% of starfish per day would prevent outbreaks (McCallum 1988). The hypothesis changed in other ways about that time: attention focussed on Lethrinidae, particularly *Lethrinus miniatus* (= *L. chrysostomus*), and to a lesser extent on maori wrasse, *Cheilinus undulatus*. These commercially exploited fishes feed largely on benthic invertebrates, including echinoderms (Walker 1978, Randall et al. 1978), and are associated with areas of coral. Secondly, the life-stage where fish predators may exert a regulatory effect is that of post-settlement juvenile starfish, since these are seen to be more vulnerable to fish predators than are adult *A. planci*.

Ormond et al. (1990) modelled the predator-*A. planci*-coral interaction and supported their predictions by correlating predator densities with the incidence of outbreaks. The model used minor modifications of the standard logistic population equations. The consumption rates and functional response of the model predators were specified with lethrinid fishes in mind, though some critical variables, such as the predators' switching coefficient, could only be guessed. The resulting estimates suggested that densities of 5-20 lethrinids per 100 m of reef front could control high recruitment pulses of up to 2 x $10^4$ starfish at a time over a similar spatial scale. At lower predator densities or higher recruitment rates there was an increasing chance of such starfish populations escaping predator control to a level limited by food. Surveys of lethrinid densities at 10 reefs on the Great Barrier Reef (GBR). Reefs that had experienced recent outbreaks of Crown-of-thorns starfish had lower densities than lightly affected reefs. Lethrinid densities on outbreak reefs were less than 5 per 100 m of reef front; minor impact reefs had densities at or above that threshold. All the GBR sites had much lower fish densities than the sites in the eastern Red Sea, where *A. planci* occurs but outbreaks have never been recorded. One of numerous differences between GBR sites and Red Sea sites was that fishing activity was minimal at many of the latter.

A number of conditions must hold for over-fishing to affect the frequency of outbreaks of Crown-of-thorns starfish. First fishes, particularly exploited fishes, must be significant predators of *A. planci*. Second, there should be evidence of reduction in predator populations due to fishing. Most aspects of this study address the first point. In the rest of this section I will review the evidence for fish predation on Crown-of-thorns starfish and introduce the questions I addressed in the experimental work.

**Table 1.1.** Data from Marine Bio Logic (1990) survey of anecdotal accounts of predators of *Acanthaster planci*.

| | Size of starfish | | | | |
|---|---|---|---|---|---|
| **Predator species** | **< 15** | **15-30** | **> 30** | **not known** | **Total** |
| *Cheilinus undulatus* | - | 11 | - | 6 | 17 |
| *Lethrinus miniatus* | 1? | 1? | - | 10 | 12 |
| *Lethrinus nebulosus* | 1? | - | - | - | 1 |
| *Thalasoma lunare* | - | - | - | 2? | 2 |
| *Balistoides viridescens* | - | 1 | - | - | 1 |
| *Euxiphipops sexstriatus* | - | - | - | 1 | 1 |
| *Arothron hispidus* | - | 3 | 1 | 1 | 5 |
| unspecified "toadfish" | - | 1 | - | 5 | 6 |
| "Giant groper" | - | - | - | 1 | 1 |

N.B. One "Sweetlip Emperor" appears to have been put in with *L. nebulosus* in the original report - I included it with *L. miniatus*.

### Which are the exploited fishes?

The human activity that is most likely to result in fewer fish predators is fishing. Commercial Fisheries data from the Queensland Fish Board to 1981 (summarised by Steven [1988]) and creel surveys by GBRMPA (Craik and Fallows [1979], Fallows and Craik [1980]) suggest that both commercial anglers and amateurs catch two main taxa from coral reefs (as opposed to inter-reefal areas): three species of Coral Trout and two species of lethrinid: *Lethrinus nebulosus* and *Lethrinus miniatus* (formerly *L. chrysostomus*), with smaller catches of other serranids and Maori wrasse, *Cheilinus undulatus*. All commercial fisheries statistics include a vague category "mixed reef fillets" which constitutes a considerable proportion of the catch. This probably includes a number of wrasses and snappers that feed on benthic invertebrates and potentially are predators of juveniles. In the southern section of the reef, "parrot" (*Choerodon* spp., and other wrasses) are caught in considerable numbers by both classes of anglers. These tuskfishes do forage by turning over rubble and so are possible predators of young juveniles.

If outbreaks of *A. planci* are generally influenced by over-fishing then the fishes that are involved are likely to be those that are taken in large numbers. All evidence from gut contents (Choat 1968, Hiatt & Strasburg 1960) as well as morphology and behaviour suggests that coral trout are piscivores and are unlikely predators of *A. planci* of any age. The most likely candidates are lethrinids and wrasses.

### Fishes that are known to eat *A. planci*.

There are many reports of fishes attacking adult *A. planci* (see Moran 1986), most of these are anecdotal and it is often unclear whether or not the attacks were staged by the observers. Some of the most convincing (e.g. Owens [1971], Ormond and Campbell [1974]) concern triggerfishes and pufferfishes which are unlikely to suffer fishing pressure or other human interference (arguments of Ormond et al. 1990 not withstanding). A survey (Marine Bio Logic [1990]) of anecdotal reports of predation from the GBR recorded the fish predators shown in Table 1.1.

There is only one fully documented report from the GBR of an exploited coral reef fish with *A. planci* remains in its gut: Birdsey (1988) found a *L. nebulosus* that had eaten part of an adult *A. planci*. From elsewhere, Randall *et al* (1978) report a personal communication from W.A. Starck who kept detailed records of stomach contents and "removed an *A. planci* from the stomach" of a 45 kg *C. undulatus* at Eniwetak.

From these data, *C. undulatus* and lethrinids, particularly *L. miniatus*, are the most frequently recorded predators that are subject to fishing pressure. These species are taken by amateur and commercial anglers. Lethrinids are taken in large quantities. The wrasses are caught in lower numbers but they also occur at lower densities and are considered desirable by anglers.

### Studies of gut contents of lethrinids

Toor (1964) looked at *Lethrinus lentjan* in size-classes between 25 and 525 mm TL and found that a large proportion (44-96%) of individuals between 150 and 450 mm TL had eaten 'echinoderms.'

Walker (1975) found that asteroids made up 1.9% of the diet of *Lethrinus miniatus* (= *chrysostomus*) (n=299) by species and 0.6% the diet of *L. nebulosus* (n=52). None of these asteroids was *A. planci* (personal communication with G.R. Russ). *Lethrinus miniatus* differs from *L. nebulosus* in being associated more with areas of hard substrate; *L. nebulosus* is much more a fish of sandy lagoons and inter-reefal areas. Walker states that his results "indicate that *L. nebulosus* forages for food on sandy bottoms associated with coral more than *L. chrysostomus* [= *miniatus*] which forages for food more in the associated coral rubble."

Birdsey (1988) looked in detail at the stomach contents of 26 *L. nebulosus* and 22 *L. miniatus* caught by charter vessels on reefs with a recent history of *A. planci* infestation. The only asteroid remains found were some arms of an *A. planci* in one *L. nebulosus*, though echinoids made up 24% of the diet of *L. nebulosus* and 9% of the diet of *L. miniatus* by volume.

These studies show that various members of the Lethrinidae eat benthic invertebrates including echinoderms. The general lack of records of *A. planci* remains cannot be interpreted as negative evidence because, with the exception of Birdsey's (1988) samples, fishes have been collected from areas where the status of *A. planci* populations was unknown. In this study *L. miniatus* were collected for gut analysis from the immediate vicinity of current outbreaks (Section 5).

Assessing predation on juveniles is more problematic. First, very few outbreaks have been identified when the animals were small. Second, while the remains of adult *A. planci* may be distinctive, the skeletal elements of small juveniles in gut samples would be easy to overlook if well digested. The appearance of skeletal elements after digestion is examined in Section 4. Because of the absence of areas with high densities of juveniles in nature, predation rate was estimated in a field experiment using laboratory-reared animals (Section 6).

## Predation on adults and juvenile *A. planci*

It is generally held that juvenile Crown-of-thorns starfish are more susceptible to predation by fishes than are adults. This is largely based on logic: lethrinids and other benthic feeding fishes consume echinoderms of the size of 1-2 year old juvenile *A. planci* and juveniles lack the pungent spines of adult starfish. There are two anecdotes concerning fish predation on juveniles: Endean's (1969) finding of a small *A. planci* in the guts of a Queensland groper and an observation by R. Bell, quoted by Ormond et al. (1990), who saw a lethrinid eat a small *A. planci* that had just been exposed by a diver. McCallum et al. (1989) recorded incidence of damaged starfish in an outbreak population of *A. planci* and found circumstantial evidence in a non-significant negative relationship between mean size of starfish in transects and the proportion of them that were damaged.

While adult Crown-of-thorns starfish are found on the surface of the coral day and night, juveniles are cryptic by day and are often buried deep (30 cm) in coral rubble (Doherty & Davidson 1988, Yokochi & Ogura 1987). For fish to be potential predators they must feed at night. There are no published data to show when *L. miniatus* feeds. *L. miniatus* and *L. nebulosus* can be seen picking at rubble areas and sandy substrates respectively in daylight (pers. obs., Jones *et al.* 1992), but their nocturnal activities are unquantified. This is addressed in Section 5.

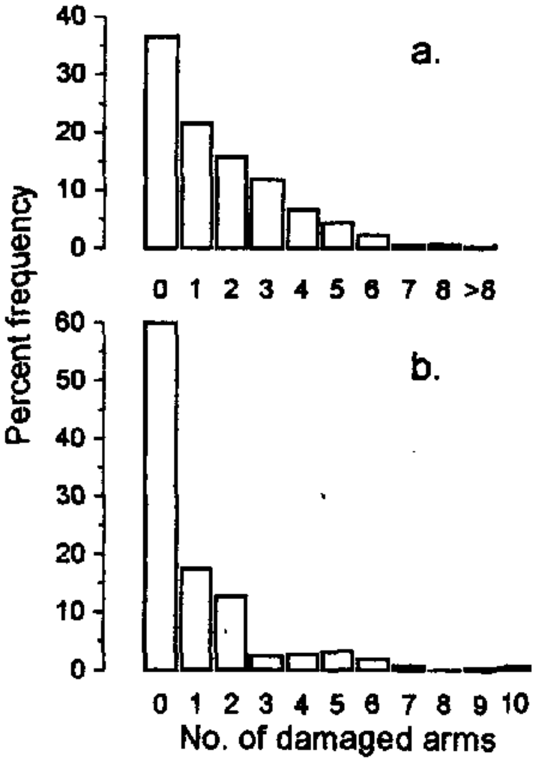
### Estimating predation rates on *A. planci* from gut contents of fishes.

Estimates of predation rates involve two stages: the first is estimating the rate of predatory encounters and the second is assessing the rate of outright mortality from the prey remains.

In order to assess the rate of predation from gut analyses, gut transit times must be estimated. The contents of the gut represent remains of food items ingested over a certain period related to the total gut transit time. Gut transit time estimates for meals containing remains of *A. planci* for *L. miniatus* are given in Section 4.

With the exception of large *Cheilinus undulatus*, fish predators generally ingest only part of an adult Crown-of-thorns starfish: the *L. nebulosus* found by Birdsey (1988) had four arms of an adult, 40 cm in diameter, in its gut. While it is probable that a damaged starfish will be attacked by several fish, each of which consumes a portion, studies of natural populations have found that many apparently healthy individuals are missing arms, parts of arms and even sections of the oral disk (Moran 1986, Table VII; Fig 1.1) and this is usually attributed to partial predation. Echinoderms are famous for their ability to survive damage and regenerate tissue and it is clear that many predator attacks do not result in death. The question of how much damage is fatal is addressed in Section 2. While the high incidence of starfish that are missing arms shows that not all predatory attacks are fatal, healing and regeneration must have an energetic cost, which may divert energy from other functions, such as reproduction. The relationship between damage, regeneration and gonad development is considered in Section 3.

**Figure1.1:** Frequency of damaged *A. planci* in natural outbreak populations. **a.** from Helix and Keeper Reefs (B.T. Kettle, unpubl.), **b.** Data from Holbourne Island (McCallum et al. 1989).



## 2: Experimental Investigations of the Ability of Adult Crown-of-Thorns Starfish to Survive Physical Damage.

### Summary

1. Groups of adult *A. planci* were held in cages without food and subjected to several levels of damage in four experiments spanning two years.
2. Levels of damage ranged from handling controls to removal of half or two thirds of the starfish. Some animals were starved prior to experiments.
3. Results were very variable, ranging from minimal mortality of any treatment in two weeks to substantial mortality even of the control animals. In general starvation had little effect and more extensively damaged animals showed higher mortality.
4. There was no seasonal trend in mortality, nor any apparent effect of the population aging.
5. Minor experiments found no evidence that crowding increased mortality and no differences between sexes, though these were not powerful tests.
6. The only way to ensure mortality of *A. planci* is to cut it into more than four pieces across the oral disc or remove it from the water.

### Introduction

One of the ways in which human activities may have influenced the incidence of outbreaks of Crown-of-thorns starfish is through the removal of predators. Commercial and recreational fishing are obvious human impacts on the Great Barrier Reef and it has been suggested that exploited fishes may be predators of *A. planci*. Recent advocates of the predator removal hypothesis consider predation on juveniles more likely to be important than predation on adults. This is based on logic and one anecdote quoted by Ormond *et al.* (1990) in which a lethrinid ate a small juvenile that was dug out of rubble by a diver.

There are more records of fishes preying on adults, though most are anecdotal field observations: Ormond and Campbell (1974) report at least one instance of a triggerfish, *Balistoides viridescens*, attacking *A. planci* in a natural encounter. They found that the puffer fish *Arothron hispidus* and the triggerfishes *Pseudobalistes flavimarginatus* and *B. viridescens* attacked adult *A. planci* when these were made available by divers. In a majority of cases, *A. hispidus* ate all of the starfish except the aboral dermis and spines. Triggerfishes tended to turn the starfish over and concentrate their feeding around the base of the arms where the gonads are located.

Analyses of gut contents are potentially an important source of information on natural predation by fishes. Reports of *A. planci* remains in the guts of any fishes are rare; among exploited species Randall *et al.* (1978) report a whole adult *A. planci* in the guts of a large *Cheilinus undulatus* and Birdsey (1988) found four arms of an *A. planci* about 40 cm in diameter in the gut of a *Lethrinus nebulosus*. While total ingestion must be fatal, the loss of four arms is harder to interpret. A proportion of predatory encounters are not fatal for it is well documented that *A. planci* of all sizes frequently have damaged and regenerating arms (Fig. 1.1, McCallum *et al.* 1989, Yokochi & Ogura 1987, Zann *et al.* 1987, references in Moran 1986). An adult *A. planci* would represent a large prey item for all but the largest fishes and gastropods; a knowledge of the rate of survival associated with various extents of damage would assist with estimations of mortality from gut content analysis.

Knowledge of the extent of damage that is likely to be fatal to starfish is also relevant to starfish control programs. Physical cutting of starfish seems to have been avoided as a control method for fear that the animals will regenerate damaged parts, survive and even multiply (Birkeland & Lucas 1990). Other control measures may be more reliable but they are either more laborious, such as removing the starfish and drying them on the shore, or involve injection of toxic substances. This requires equipment of varying sophistication, careful handling and may entail risks to other reef organisms as well as to the operators themselves.

This study set out to investigate the extent of damage that would be fatal to adult starfish.

## Methods

All fieldwork was carried out at Davies Reef (18° 50'S, 147° 38'E), a mid-shelf reef near Townsville, North Queensland, Australia. The crown-of-thorns starfish population on Davies Reef was declared an outbreak in summer 1986-87 when a large cohort reached maturity (age 3+). Further cohorts matured in the following two years (R. Stump, pers comm.). There were four experiments: Experiment 1 in winter 1991, Experiment 2 in summer 1991, Experiment 3 in winter 1992 and Experiment 4 in summer 1992. In all experiments, adult crown-of-thorns starfish were collected by snorkellers and held in a 1000 l tank with running seawater on the deck of the research vessel for up to 24 h before processing.

The Experiment 1 ran from 1-15 May. One hundred starfish were collected. Groups of five individuals were selected haphazardly and each individual was randomly allocated to one of five treatment groups. After collection and transfer to the holding tank, all starfish received the following handling: They were lifted out of the tank placed on a flat surface, and then placed in another tank for transportation to the experimental cage. This was all the handling that Control starfish received; three other groups were treated similarly except that when they were placed on the flat surface, two, four or eight adjacent arms were cut off with a diving knife at the point where the arm joined the oral disc. A final group was treated similarly except that starfish were cut in half across the oral disc and one half was discarded. These treatments were based on the studies of natural populations showing that few animals had more than six damaged arms (Fig. 1.1).

The 20 members of each treatment group were then placed in a pen of 12 mm square mesh (welded fabric) which was approximately oval and with a circumference of 12 m. The walls were 1.1 m high. Initially, the pen did not have a roof but the walls had an overhang that curved inwards for about 0.6 m, following the design of Bell et al. (1987). Dead rubble was put in the pen to provide cover. After seven days, the starfish were counted and the top of the pen was sealed with mesh. The starfish were counted again after 14 days and released.

Since very few starfish died in the first experiment, the treatments were made more drastic in those that followed. There had been elevated densities of starfish at Davies Reef for some years, but the population there had not formed local concentrations that decimate all the coral locally and so might lead to malnutrition. For this reason, animals that were less healthy due to starvation were included in future experiments to simulate a situation where high densities of starfish eat the coral near to extinction. The extent of starvation was based on a study by Kettle (1991), who took *A. planci* from an area with abundant coral and kept them in aquaria without food for 22 weeks, by which time more than half had died. He followed their decline in condition by measuring the percentage of the total calorific value of the animal represented by the pyloric caeca. Pyloric caeca are storage organs, so this may represent loss of reserves. Kettle found that about half the total loss of calorific value occurred in six weeks. On this basis, 108 starfish were collected in mid-October 1991 and kept in cages without any live coral for six weeks prior to the summer 1991 experiment. Ninety-seven animals survived after six weeks.

Experiment 2 was set up 6-14 December. There were two other differences beside the inclusion of a starvation treatment. Firstly, the damage treatments were also changed by omission of the loss of two arms and addition of a treatment where two thirds of each starfish (based on number of arms) was removed. By the end of the experiment, animals that were cut in half could not be distinguished reliably from those that had two thirds of their arms removed, so the two categories were combined for analysis. Secondly, the design of the holding cages was different: rather than having a single pen, rectangular cages 3.5 x 1.5 x 0.45 m made of 12 mm-square mesh were used. Each cage was divided into two compartments so that the starved and unstarved animals were kept separated but close together, so as to be subjected to the same conditions. Twenty-five animals were put in each compartment. When the cages were full, they were wrapped on three sides with black polythene sheet to give the starfish cover. Animals in the first two cages to be filled suffered high mortality in the first week. Before the covers were put on, these cages were holed by large puffer fish, *Arothron stellatus*, that attacked some captive *A. planci* and possibly allowed others to escape. The remaining animals were omitted from analyses. To compensate, twenty-five more unstarved starfish were processed and placed in another cage on 14 December. Cages were checked on 21 December (7-15 days) and the experiment ended 3 January 1992 (20-27 days).

Experiment 3 was set up 25-29 May 1993 and was similar to the preceding experiment and involved the same damage levels for newly collected starfish. Once again, animals that were cut in half were combined for analysis with those that had two thirds of their arms removed. One hundred and twelve *A. planci* were collected six weeks prior to the experiment, but many died during the period of starvation. The 25 remaining starved animals were put in one cage and allocated to only two treatments: undamaged controls and loss of eight adjacent arms. One hundred animals were collected just prior to the experiment and 20 were allocated to each of the same damage treatments as in Experiment 2, though once again the bisected and trisected categories were combined for analysis.

An additional, low density treatment was added to test the possibility that the high experimental densities exaggerated mortality by enhancing conditions for transmission of pathogens. Four cages were set up, each containing five unstarved starfish in each of two treatment groups: controls and -8 arms.

The cage design evolved again: cages were made of heavier mesh to resist puffer fish and each cage consisted of a single compartment measuring 1.2 x 2.0 x 0.4 m with a hinged lid to allow easy examination of survivors. Starved and newly collected animals were kept in separate but adjacent cages. Cages were wrapped on three sides with blue plastic tarpaulins. The experiment finished 12 June (14-17 days).

In Experiment 4, one group was collected 21-22 October 1992 and held in cages in the field for more than a month without food and the other was collected just prior to the experiment. Experimental cages were established 26-28 November. Because of the relatively low numbers of *A. planci* in that season at Davies Reef, the experiment included only three levels of damage: animals that had four arms removed, animals that were cut in half across the middle of the oral disc and a control group that were handled but not damaged intentionally. Another, smaller, group of unstarved animals were collected, sexed and tested to see if there were gender differences in susceptibility to damage. Few female starfish were found so only two damage treatments were used: controls and -4 arms. All experimental animals were held without food in cages in the field and checked after 19 days. There were three cages for each treatment and all cages were kept within 20 m of each other so that they experienced similar conditions.

In all experiments, the counts of survivors after approximately 15 days were used for analysis. At the end of each experiment, the starfish were inspected individually to determine which treatment group they belonged to before release. This was not always obvious because the body wall may contract to seal wounds causing an animal to assume contorted shapes. Also, necrotic tissue may form along the edge of wounds so it may become hard, for example, to distinguish animals cut in half from those that lost eight adjacent arms. In Experiment 2 , the animals were checked visually at 7-15 days through the cage, though they were handled and inspected individually at the end of the experiment. Counts from the

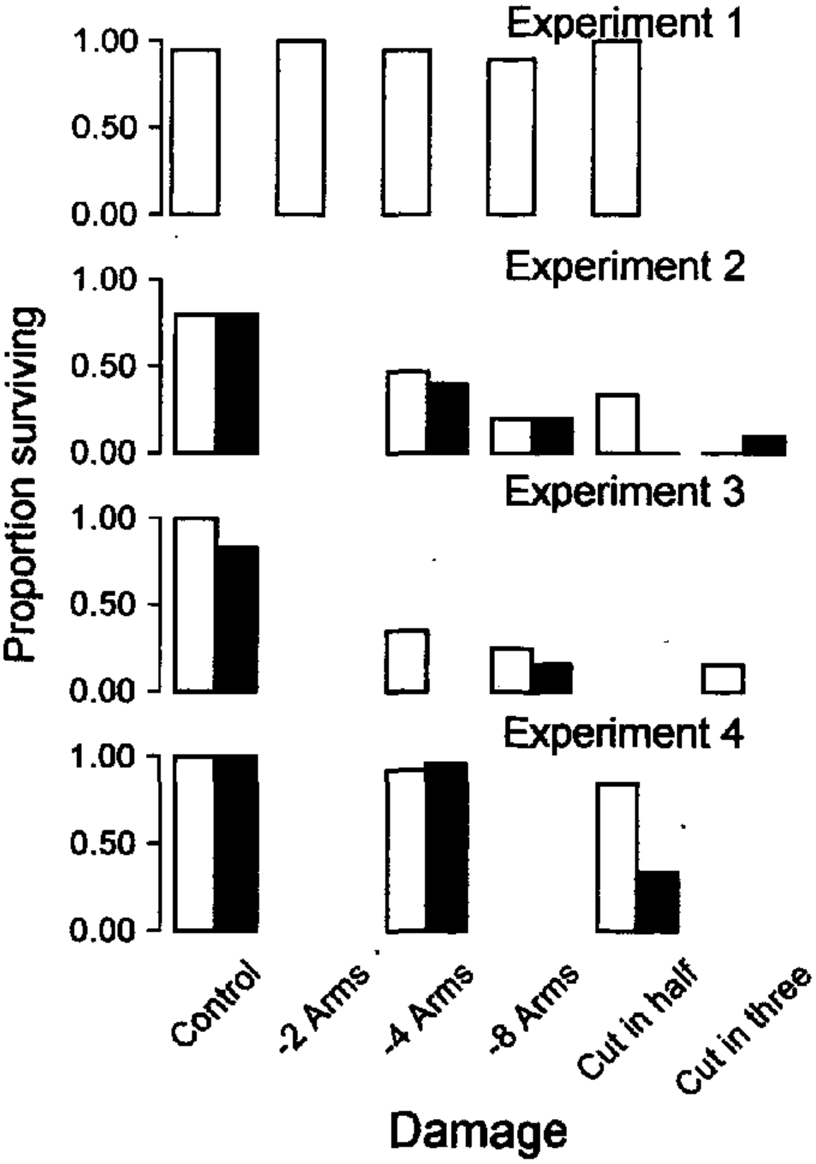


**Figure 2.1:** Percent survival of starved and unstarved *A. planci* subject to various amounts of damage. Hollow bars denote unstarved animals, filled bars denote starved animals.

7-15 day census were used for analysis but they were adjusted where they were incompatible with the final census. The probability of survival was related to experimental variables by logistic regression. The levels of damage can be viewed as a linear series of increasing intensity or as a series of categories whose relative intensities are unspecified.

## Results

### Effects of damage

When freshly collected, apparently healthy, animals were considered, the effects of increasing arm loss varied among the experiments (Fig 2.1). The most obvious difference is between Experiment 1, in which there was practically no mortality, and Experiments 2 and 3, where mortality was substantial in the higher damage classes. Mortality in Experiment 4 was intermediate. When damage treatments were treated as a linearly increasing series (e.g. -8 arms is twice as severe as -4 arms) the data were overdispersed: a linear model did not describe the relationship between mortality and damage level satisfactorily. When the damage treatments were treated as categories, the logistic model was more appropriate, but there was a significant interaction (Table 2.1) reflecting the variation in effects of damage treatments among experiments. Because of this the experiments will be considered separately.

There was no significant difference in survival among the groups of damaged

**Table 2.1:** Effect of damage on survival of freshly collected *A. planci.* Analysis of deviance table for Experiments 1 - 4. Damage treatments coded as categories, -2 arms and -8 arms omitted, -½ and -¾ combined. I= intercept, D = damage, E = experiment.

| Model | Deviance | df | Difference | $\delta$df | component | p |
|---|---|---|---|---|---|---|
| I+E | 72.59 | 10 | $d_{I+D+E} - d_{I+E} = 61.22$ | 2 | D | 0.000 |
| I+D | 107.14 | 10 | $d_{I+D+E} - d_{I+D} = 95.80$ | 3 | E | 0.000 |
| I+D+E | 11.34 | 6 | $d_{I+D+E+DxE} - d_{I+D+E} = 11.34$ | 6 | DxE | 0.078 |

animals in Experiment 1 (Fig 2.1a, damage was considered to be a linear factor: logistic regression, slope not significantly different from zero, $\chi^2_1 = 0.23$, $p = 0.63$). By contrast in Experiment 2, survival tended to decrease with increasing arm damage for unstarved *A. planci* (Fig. 2.1b, logistic regression, slope deviates from zero, $\chi^2_1 = 16.82$, $p<0.001$). In Experiment 3, survival did not decrease linearly with increasing extent of the damage (Fig. 2.1c). When damage treatments were treated as a linear series the data were overdispersed. When treatments were entered as categories, damage was shown to affect survival ( $\chi^2_1 = 49.74$, $p \ll 0.001$). In Experiment 4 the statistical evidence for a linear effect of damage on survival was marginal with the reduced number of treatments (Fig 2.1d, $\chi^2_1 = 3.86$, $p = 0.049$).

### Seasonal effects of damage

A possible explanation for differences among Experiments is that there are seasonal effects. Crown-of-thorns starfish breed in summer so it is possible that the energetic cost of producing gametes or the physiological changes involved in reproduction make them more susceptible to damage. The data do not support

**Table 2.2:** Effect of starvation on survival of damaged *A. planci*. Analysis of deviance table for Experiments 1 - 4. Two groups of damage treatments (Control vs [-8 arms or more]). I= intercept, D = damage, E = experiment and S = starvation.

| Model | Deviance | df | Difference | $\delta$df | component | p |
|---|---|---|---|---|---|---|
| I+D+S | 88.16 | 7 | $d_{I+D+E+S}-d_{I+D+S}$<br>$= 77.15$ | 1 | E | 0.000 |
| I+D+E | 57.90 | 7 | $d_{I+D+E+S}-d_{I+D+E}$<br>$= 46.89$ | 1 | S | 0.000 |
| I+E+S | 24.36 | 7 | $d_{I+D+E+S}-d_{I+E+S}$<br>$= 13.35$ | 1 | D | 0.000 |
| I+D+E+S | 3.87 | 6 | $d_{I+D+E+S+DxS+SxE+DxE}-$<br>$d_{I+D+E+S}$<br>$= 11.01$ | 3 | DxS + SxE + DxE | 0.100 |
| I+D+E+S+DxE+ DxS+SxE | 4.77 | 3 | $d_{I+D+E+S+DxS+SxE+DxE+DxSxE}$<br>$-d_{I+D+E+S+DxS+SxE+DxE}$<br>$=0.00$ | 3 | DxSxE | 0.189 |
| I+D+E+S+DxE+ DxS+SxE+DxSxE | 4.77 | 2 | $= 4.77$ | 2 | variance | 0.092 |

**Table 2.3:** Effect of density and damage on survival of freshly collected *A. planci*, Experiment 4. Analysis of deviance table. Damage treatments: Controls vs. -4 arms. I = intercept, Dmg = damage, Dns = density.

| Model | Deviance | df | Difference | δdf | component | p |
|---|---|---|---|---|---|---|
| I+Dmg+Dns | 5.33 | 1 | $d_{I+Dmg+Dns+DmgxDns} - d_{I+Dmg+Dns} = 5.33$ | 1 | DmgxDns | 0.021 |

this. Considering freshly collected, unstarved starfish, damaged animals survived relatively well in two of the experiments: Experiment 1 (winter) and Experiment 4 (summer) (Fig 2.1). This lack of a seasonal pattern was reflected in overdispersion of the data when a model including a seasonal term was fitted.

**Effect of starvation and damage**

Experiments 2 - 4 included starved starfish in the experimental design though reduced availability of animals meant that not all damage treatments were included in each experiment (Fig 2.1). Because of this, there were not enough data points to fit a model containing terms for damage level, starvation, experiment number and all the associated interactions. However, if any comparisons are going to show an effect of damage and starvation, it will be those comparing mortality rates

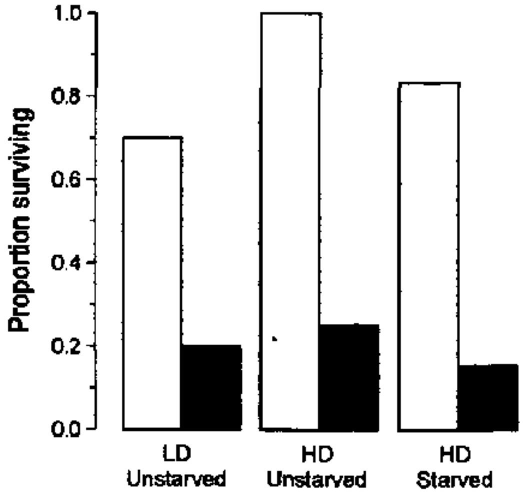


**Figure 2.2:** Effects of density and starvation on survival of *A. planci* over 14 days. Hollow bars = unstarved; filled bars = starved; LD = low density (10 per cage); HD = high density (25 per cage).

**Table 2.4:** Effect of gender and damage on survival of freshly collected *A. planci*, Experiment 4. Analysis of deviance table. Damage treatments: Controls vs. -4 arms. I= intercept, D = damage, S = sex.

| Model | Deviance | df | Difference | $\delta$df | component | p |
|---|---|---|---|---|---|---|
| Mean | 3.71 | 3 | $d_{I+D+S} - d_I = 2.51$ | 2 | D + S | 0.285 |
| I+S | 1.45 | 2 | $d_{I+D+S} - d_{I+S} = 0.25$ | 1 | D | 0.617 |
| I+D | 3.48 | 2 | $d_{I+D+S} - d_{I+D} = 2.28$ | 1 | S | 0.131 |
| I+D+S | 1.20 | 3 | $d_{I+D+S+DxS} - d_{I+D+S} = 1.20$ | 1 | DxS | 0.273 |

of the more severe damage treatments (-8 arms, cut in half) with the controls. Such models suggest that there are significant differences due to severe damage, due to starvation and to differences among experiments (Table 2.2).

**Effect of experimental density and damage**

Comparison of the two damage levels (Control and -8 arms) that were present at the two densities in May 1992 showed evidence that the effect of damage depended on density (significant interaction, Fig 2.2, Table 2.3) but the difference was a matter of degree rather than a qualitative difference. More importantly, survival was lower at the low density (Fig. 2.2). There was no evidence that the experimental density increased mortality by favouring pathogens.

**Effect of gender and damage**

Comparison of the survival of starfish of different genders found no statistical evidence for a difference (Fig 2.3, Table 2.4), but the small numbers involved mean that this is a weak test.

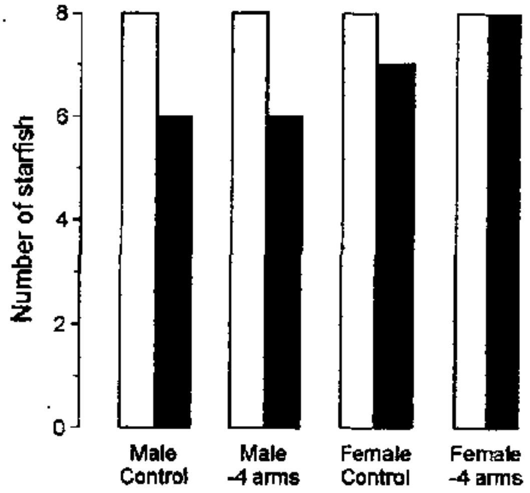


**Figure 2.3:** Effects of gender and damage on survival of *A. planci*. Hollow bars = initial numbers; filled bars = survivors after 19 days.

## Discussion

The aim of this sub-project was to determine the degree of arm damage that is fatal to adult crown-of-thorns starfish. The results of the four experiments are inconsistent in this regard, particularly because of the contrast between the May 1991 experiment, when there was practically no mortality over the experimental period for any of the levels of damage, and the other three experiments. There are two obvious sources of variation among experiments: seasonal changes in reproductive condition and progressive aging of the main cohort of the population. Neither of these are supported by the experiments: there was no seasonal trend and age effects can be dismissed because survival of unstarved animals was higher in the first and the last experiments. In spite of a systematic experimental approach and relatively large numbers of animals it is only possible to conclude that extensive damage and starvation do reduce survival, but the relationships are not very clear. The inclusion of estimates of condition as assessed by examination of the pyloric caeca may reduce the variation, but even larger numbers of animals would be required, with associated expenses in collection and processing time.

However the differences among experiments came about, the results of the experiment in May 1991, showing that even animals that were cut in half showed little mortality, makes it impossible to be sure that any level of damage up to loss of half of the animal is necessarily lethal. This conclusion is conservative because the population at Davies Reef was mainly composed of large adults (35-45 cm diam.) and it is likely that larger animals will be more vulnerable to damage because of their lower skeletal content which makes it difficult to seal wounds (Birkeland & Lucas 1990). Predation is only certainly lethal if the whole starfish is taken, though this may be achieved by several predators acting together.

These experiments were based on the assumption that any mortality would be rapid and that a 15 day period would be adequate. This seemed to be the case in the later experiments. Prolonging the experiments would mean that starvation in the experimental period would become more significant, which raises the logistical problem of having to provide quantities of coral. There are two pieces of anecdotal evidence that heavily damaged animals did not die after the end of the experiment in May 1991. In October 1991 a starfish that had been cut in half was found within 50 m of the site of the pen. The wound had healed but no regeneration was apparent. In November 1991 an animal missing eight adjacent arms was seen near the site of the experiment. It too had healed but no regeneration was evident.

Other anecdotal reports of healing and regenerative abilities of *A. planci* suggest that animals usually survive the loss of a few arms, but consequences of more extensive damage are inconsistent. Pearson and Endean (1969) kept three individuals (16, 23 and 31 cm) alive for at least a month after cutting off one arm. Owens (1971) cut two arms off six animals (size unspecified) and released them. He recovered one 50 days later and found the wound had healed but there was no regeneration. Pearson and Endean (1969) cut two large adult animals in half and found that they were dead the next day. Owens (1971) cut a 35 cm individual in half and found that the halves appeared to be rejoining seven days later. He separated them again and, a month later, the wounds of each half had healed and the two animals were feeding. Apart from the differences in size among animals, Owens' animals were kept in cages in the sea while Pearson and Endean used tanks. Birkeland and Lucas (1990) cite a report by G. Walker that 92 *A. planci* were cut into quarters and released in Okinawa. An intensive search 28 days later found two quarter-starfish that had apparently healed. The fate of the other 394 quarters is unknown, but clearly *A. planci* can survive such treatment under some circumstances. In Guam, H. Moore put 300 *A. planci* in a cage at high densities and found that animals that sustained any damage developed infections and died though undamaged individuals survived for "several months" without food, implying that they were in good condition at the start (Birkeland & Lucas 1990). In summary, the extent of physical damage that *A. planci* can survive seems very variable and can be very severe. Though size may be important, there are clearly other unknown factors involved.

## 3: The effects of sub-lethal predation on gonad development in *A. planci*

### Summary

1. The relationship between gonad development and size, number of damaged arms, and regeneration was examined in 148 starfish collected from aggregations at two reefs near Townsville.
2. Total gonad weight was less in male animals with evidence of damage (after correction for size). Females showed the same trend but this could not be tested.
3. Total weight of gonads was negatively correlated with number of missing arms but showed no relationship with the extent of regeneration.
4. There was evidence that damaged arms supported smaller gonads than undamaged arms of the same starfish. This was true to a lesser extent for undamaged arms neighbouring damaged arms.
5. Populations with high incidence of sublethal damage should have a lower reproductive output *per capita* than populations with few damaged individuals.

### Introduction

Echinoderms are famous for their powers of survival and regeneration. Natural populations of *A. planci* commonly contain sizeable proportions of animals with arms that show evidence of damage and regeneration (Fig 1.1). This is taken as evidence of sub-lethal predation. This is often assumed that fishes are responsible for such damage (e.g. McCallum *et al.* 1989) though the Giant Triton (*C. tritonis*) may also be responsible. Pearson & Endean (1969) observed tritons to clamp some arms of the starfish between the foot and the scalloped rim of the aperture of the shell and reach in between arms and rasp out tissue with the radula. The more the snail eats, the less remains for it to grip so that eventually the starfish may escape (R.C. Babcock, pers. comm).

While sub-lethal predatory activity does not reduce the size of the existing population, it may reduce the rate of population growth because healing and regeneration requires energy, so damaged individuals may have to divert energy from reproduction.

Conand (1975) found a linear relationship between gonad weight and fecundity in *A. planci*, implying that gonad weight is an indicator of fecundity. This section examines the relationship between damage, regeneration and gonad weight in animals from natural populations of *A. planci* from two reefs near Townsville.

## Methods

### Field work

One hundred and forty eight starfish were collected by snorkellers 16-25 November 1991. Ninety-six starfish were collected from Lynch's Reef (18-091) and 52 from Davies Reef (18-096). The starfish at Lynch's Reef were smaller than those at Davies and there was a preponderance of males (Fig. 3.1). This was about one week before the first spawning of the year at Davies Reef (R. Babcock, pers. comm.), so their gonads were well developed.

Starfish were held in 1000 l tanks on the deck of the research vessel prior to

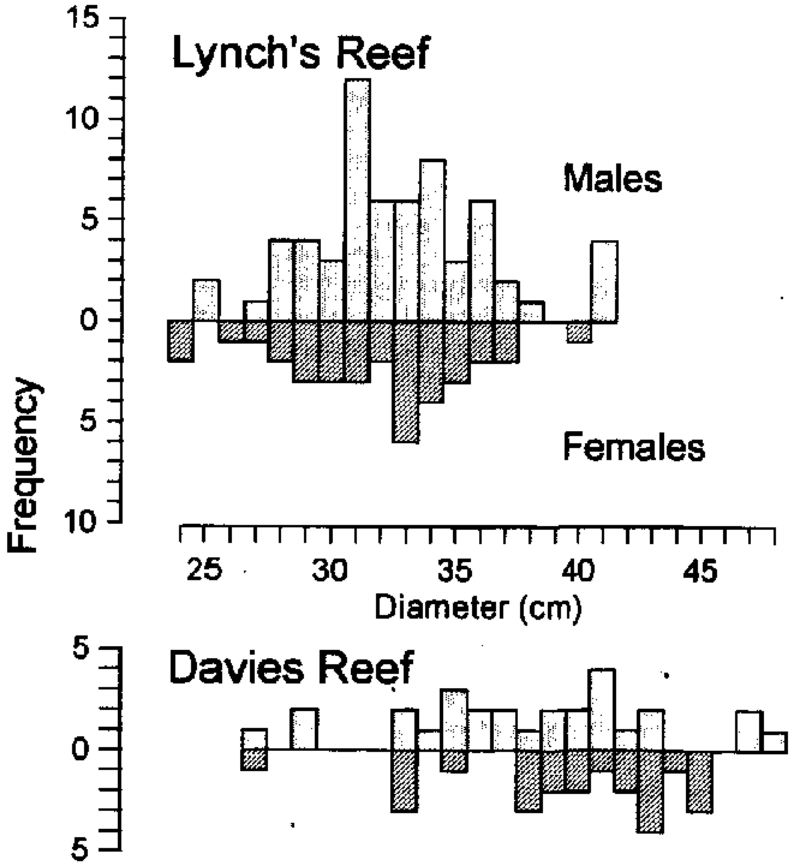


**Figure 3.1:** Size frequency by gender for 148 A. planci collected from Lynch's and Davies reefs.

dissection. Starfish were lifted from the water, held for two to three seconds to drain off surface water and then placed in a plastic tray and weighed to the nearest gram on a parallel balance. The draining period was short enough that the coelomic membrane did not burst, so initial weight included coelomic fluid. The gonads were then removed through dorsal incisions. Initially, the gonad tissue from each arm was placed in a separate marked plastic bag. For animals collected later, the gonad material from each **side** of each arm was placed in separate bags. Arms of *A. planci* are delimited by septa, each of which has pairs of gonadal lobes associated with it. Thus the development of gonad lobes attached to one septum of an arm might be more similar to lobes on the other side of the same septum (but in the adjacent arm) than to lobes on the other septum of the same arm. Gonads were kept frozen until processed.

The starfishes' arms were examined carefully and classified by amount of damage and extent of regeneration (as a proportion of initial arm length) as evident from differences in length, thickness, spine-length, etc. The carcass was then shaken to remove excess water and weighed to give a somatic weight of

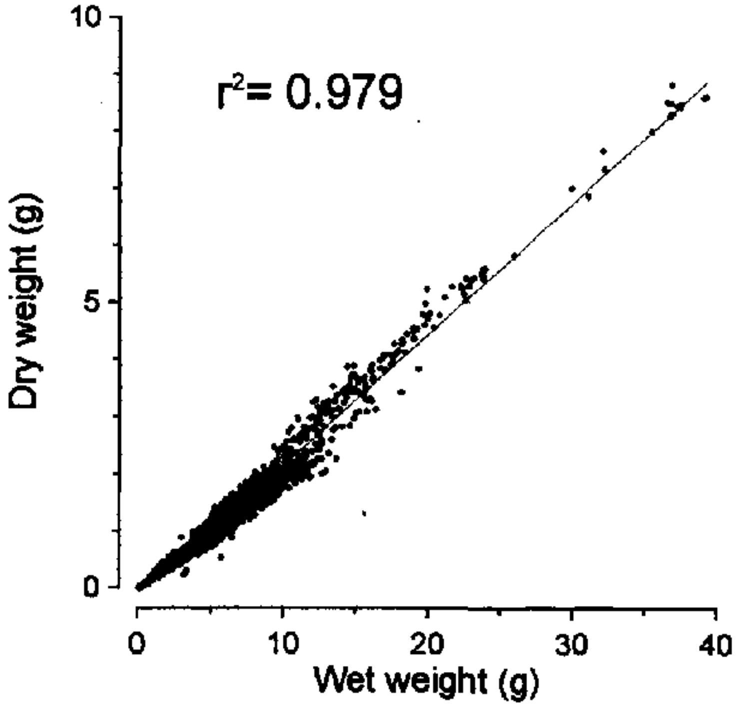


**Figure 3.2:** Relationship between wet and dry weights for 1441 gonad samples from individual arms of 80 *A. planci*.

tissues less gonads and coelomic fluid. This somatic weight was then adjusted upwards to allow for tissue lost to sub-lethal predation. Since it was rare that animals showed evidence of damage to the oral disc, I assumed that the loss of 100% of an arm (the entire portion beyond the oral disc) represented half of the fraction of the whole starfish associated with that arm. For instance, one missing arm from a starfish with 20 arms represented half of one twentieth of the undamaged somatic weight (2.5%).

**Laboratory work**

Initially the gonads were dried in an oven at 50°C prior to weighing. Trials showed that it could take 13 days drying for the gonad tissue from a single arm of a large mature starfish to show a change in weight less than 100µg per day. Samples approached a stable weight asymptotically and a series of curves was constructed to allow estimation of the times required for gonads of different sizes to come within 5% of their final asymptotic weight. Samples dried using these curves showed that there was a linear relationship between wet and dry weights (Fig. 3.2) so the laborious drying process was discontinued and wet gonad weights were used in analyses.

One starfish was omitted from any analyses because its gonads were very small and an abnormal dark colour. Some other samples were omitted from some analyses because of lost samples or because labelling errors led to uncertainty in matching samples with particular arms.

**Table 3.1:** Analysis of covariance table for male *A. planci* with and without damaged arms. Test for heterogeneity of slopes, p = 0.264. Log transformed data.

| Source | SS | d.f. | MS | F | p |
|---|---|---|---|---|---|
| Size (Covariate) | 296719.1 | 1 | 296719.1 | 104.9 | 0.000 |
| Damage | 13122.7 | 1 | 13122.7 | 4.640 | 0.035 |
| Error | 180997.2 | 64 | 2828.1 | | |

## Results

### The effect of damage on total gonad weight

In a first analysis, animals were categorised as having evidence of damage (and hence having borne energetic costs of healing and varying degrees of regeneration) or not. It was necessary to include a covariate to correct for size of animal; I used the somatic weight adjusted for arm-damage. Damaged males showed a statistically significant decline in total gonad weight (Table 3.1, Fig. 3.3). Though damaged females generally had smaller gonads (Fig. 3.3), such an analysis was inappropriate because the assumption of equal slopes of the regression lines was dubious (p = 0.064). The enormous spread in gonad weights for larger damaged females (Fig. 3.3) shows that simple presence or absence of damage does not account for much of the variability in total gonad weight.

In order to incorporate a measure of the extent of damage into the model,

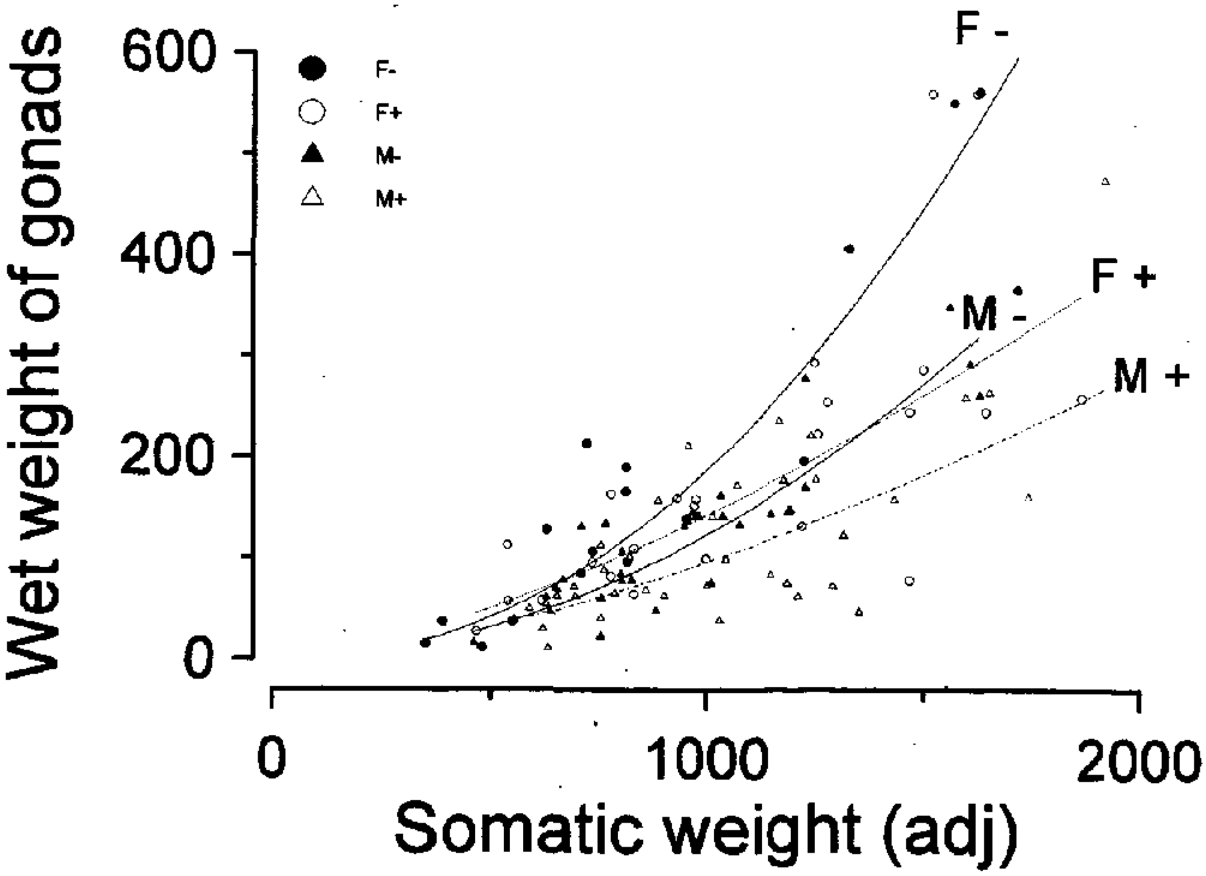


**Figure 3.3:** Relationship between total gonad weight (g) and adjusted somatic weight (g). Fitted lines are power curves. F = female, M = male; + = with evident damage, - = without evident damage.

**Table 3.2** Partial correlation analysis of the relationship between gonad weight and proportion of damaged arms and extent of regeneration in Crown of thorns starfish of each sex after correction for initial size.

| | Partial correlation coefficient | *p* |
|---|---|---|
| Females (n = 41) | | |
| Proportion of arms damaged | 0.3031 | 0.057 |
| Sum of regeneration | 0.1600 | 0.324 |
| Males (n = 67) | | |
| Proportion of arms damaged | 0.3876 | 0.001 |
| Sum of regeneration | 0.0821 | 0.512 |

partial correlations were used. I assumed that the cost of an arm being damaged was more or less independent of the amount of lost tissue because there would be the basic cost of sealing off the body cavity, however much of an arm was lost. On the other hand, the cost of regeneration would vary with the amount of an arm that was replaced. Only starfish that had apparent damage were included in the analysis for obvious reasons. After correcting for the initial size of the animal using adjusted somatic weight, the partial correlation between gonad weight and proportion of arms that had been damaged was negative for both sexes (Table 3.2). However the partial correlation between gonad weight and amount of regeneration was non-significant (Table 3.2). This implies that the number of damaged arms has an effect on gonad development while the amount of tissue lost is less important. When an animal is damaged, it must heal the wound to seal the body cavity as soon as possible so as to retain coelomic fluids, nutrients, etc., so an immediate investment of energy is essential for survival. When partial correlations between total gonad weight and total regeneration were calculated after correcting for both size (adjusted somatic weight) and extent of damage, the results are counter intuitive. The coefficients were positive in both sexes and in males the correlation is significant (Table 3.2).

**Does damage affect local gonad development?**

If healing and regeneration of damage by predators involves diversion of resources from gonad development, this effect might be most strongly manifest in tissues closest to the wound: in the gonads of the damaged arm itself. To test this possibility, gonad weights for damaged arms were compared with those of undamaged arms selected at random from the same starfish. Two levels of damage were considered: first all arms with any damage were included, then only cases where more than 25% of the arm had been lost were used. One damaged and one undamaged arm was selected from each starfish. Damaged and undamaged arms were selected using a random number generator and 10 sets of samples were drawn and compared using a paired t-test.

When arms that show any damage at all were considered, undamaged arms did contain more gonad material on average than did damaged arms in male starfish. The mean difference was in the predicted direction in all 10 random sets, though it was only significantly different from zero in 4 sets. When the differences between arms of individual starfish in each of the sets were examined, the damaged arm

**Table 3.3:** Results of random pairings of gonad weights from damaged and undamaged arms of the same starfish, all amounts of damage included. Data from 45 males and 32 females. Ctrl - Dmg gives the mean difference in gonad size as a percentage of the undamaged value. Ctrl > Dmg gives the percentage of pairs of arms where gonad in damaged arm weighed less than that in the undamaged arm. *p* is the one-tailed probability from a paired t-test.

| | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| **Run** | **Ctrl - Dmg** | **Ctrl > Dmg** | ***p*** | **Ctrl - Dmg** | **Ctrl > Dmg** | ***p*** |
| 1 | 11.9% | 60.0% | 0.03 | 11.8% | 56.3% | 0.04 |
| 2 | 5.2% | 51.1% | 0.18 | -2.1% | 56.3% | 0.43 |
| 3 | 8.5% | 55.6% | 0.04 | 12.9% | 59.4% | 0.02 |
| 4 | 8.2% | 60.0% | 0.04 | 13.1% | 68.8% | 0.01 |
| 5 | 12.3% | 55.6% | 0.03 | 16.8% | 71.9% | 0.00 |
| 6 | 6.5% | 48.9% | 0.17 | 8.9% | 68.8% | 0.08 |
| 7 | 6.9% | 51.1% | 0.17 | 13.1% | 53.1% | 0.04 |
| 8 | 8.5% | 48.9% | 0.10 | 14.5% | 65.6% | 0.01 |
| 9 | 9.1% | 46.7% | 0.07 | 7.3% | 53.1% | 0.17 |
| 10 | 2.2% | 51.1% | 0.36 | 22.4% | 68.8% | 0.00 |
| | **mean** | | | **mean** | | |
| | 7.9% | | | 11.9% | | |

had a larger gonad than the undamaged arm in 40 - 53% of individuals (Table 3.3), so the pattern was not consistent at the level of the individual. Given that the sample size was limited, the consistency of the overall pattern implies that there is a biological effect. For female starfish, more of the differences were greater than zero but in one case the mean size of gonads from damaged arms exceeded that from undamaged arms. Once again, gonads from damaged arms exceeded those from undamaged arms in a significant proportion of individuals (Table 3.3) but the overall effect was consistent.

Increasing the criterion for damage to at least 25% of an arm having been affected made little difference in the overall results: the mean difference between damaged and undamaged arms increased in males. The difference was significantly greater than zero in more random sets from males than before, but fewer sets from females. Randomly selected damaged arms had larger gonads

**Table 3.4:** Results of random pairings of gonad weights from damaged and undamaged arms of the same starfish, only arms that had lost > 25% of their length included in damaged category. Data from 37 males and 26 females. Ctrl - Dmg gives the mean difference in gonad size as a percentage of the undamaged value. Ctrl > Dmg gives the percentage of pairs of arms where gonad in damaged arm weighed less than that in the undamaged arm. *p* is the one-tailed probability from a paired t-test.

| | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| **Run** | **Ctrl - Dmg** | **Ctrl > Dmg** | ***p*** | **Ctrl - Dmg** | **Ctrl > Dmg** | ***p*** |
| 1 | 10.4% | 67.6% | 0.15 | 16.2% | 61.5% | 0.02 |
| 2 | 14.7% | 62.2% | 0.02 | -0.3% | 53.9% | 1.00 |
| 3 | 12.5% | 70.3% | 0.01 | 8.7% | 61.5% | 0.12 |
| 4 | 14.2% | 70.3% | 0.01 | 12.8% | 46.2% | 0.06 |
| 5 | 12.7% | 62.2% | 0.02 | 13.3% | 61.5% | 0.01 |
| 6 | 13.7% | 62.2% | 0.05 | 17.4% | 69.2% | 0.01 |
| 7 | 12.8% | 54.1% | 0.03 | 11.0% | 73.1% | 0.03 |
| 8 | 7.7% | 62.2% | 0.24 | 4.8% | 57.7% | 0.35 |
| 9 | 6.2% | 56.8% | 0.29 | 7.7% | 50.0% | 0.28 |
| 10 | 14.7% | 70.3% | 0.02 | 9.7% | 57.7% | 0.13 |
| | **Mean** | | | **Mean** | | |
| | 12.0% | | | 10.1% | | |

than undamaged arms in more than one third of all individual starfish of either sex in all sets of data (Table 3.4), but the overall pattern of decrease with damage was consistent.

### Does arm damage affect gonad development in adjacent arms?

Since gonads of *A. planci* are in the form of lobes arranged on both sides of the septa between arms, it is possible that mobilisation of resources for healing and regeneration away from gonad production in one arm may also lead to reduced gonad production in adjacent arms through reduced development of the gonadal lobes attached to the septum separating the two. To test this, an undamaged arm adjoining a damaged arm and an undamaged arm without adjacent damaged arms were selected at random from each starfish. These samples were then compared

**Table 3.5:** Results of random pairings of gonad weights from undamaged arms and arms adjacent to damaged arms of the same starfish, all amounts of damage included. Data from 54 males and 37 females. Ctrl - Nbr gives the mean difference in gonad size as a percentage of the undamaged value. Ctrl > Nbr gives the percentage of pairs of arms where gonad in damaged arm weighed less than that in the undamaged arm. *p* is the one-tailed probability from a paired t-test.

| | | **Males** | | | **Females** | |
|---|---|---|---|---|---|---|
| **Run** | **Ctrl - Nbr** | **Ctrl > Nbr** | ***p*** | **Ctrl - Nbr** | **Ctrl > Nbr** | ***p*** |
| 1 | -7.1% | 40.7% | 1.000 | 6.4% | 62.2% | 0.055 |
| 2 | -6.0% | 37.0% | 1.000 | 9.5% | 54.1% | 0.062 |
| 3 | -0.3% | 46.3% | 1.000 | 4.3% | 45.9% | 0.233 |
| 4 | 0.7% | 46.3% | 0.438 | -15.5% | 40.5% | 1.000 |
| 5 | -7.5% | 51.9% | 1.000 | 11.1% | 70.3% | 0.014 |
| 6 | 7.6% | 55.6% | 0.057 | 0.1% | 51.4% | 0.493 |
| 7 | 8.7% | 51.9% | 0.034 | 13.5% | 54.1% | 0.008 |
| 8 | 4.5% | 51.9% | 0.120 | 1.7% | 54.1% | 0.388 |
| 9 | -2.3% | 50.0% | 1.000 | 0.4% | 43.2% | 0.459 |
| 10 | -1.2% | 48.1% | 1.000 | 11.2% | 56.8% | 0.018 |
| | **Mean** | | | **Mean** | | |
| | -0.3% | | | 4.3% | | |

**Table 3.6:** Results of random pairings of gonad weights from undamaged arms and arms adjacent to damaged arms of the same starfish, only arms that had lost > 25% of their length included in damaged category. Data from 47 males and 32 females. Ctrl - Nbr gives the mean difference in gonad size as a percentage of the undamaged value. Ctrl > Nbr gives the percentage of pairs of arms where gonad in damaged arm weighed less than that in the undamaged arm. *p* is the one-tailed probability from a paired t-test.

| | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| **Run** | **Ctrl - Nbr** | **Ctrl>Nbr** | ***p*** | **Ctrl - Nbr** | **Ctrl>Nbr** | ***p*** |
| 1 | 2.5% | 53.2% | 0.296 | 2.1% | 59.4% | 0.288 |
| 2 | 1.8% | 51.1% | 0.352 | -1.8% | 50.0% | 1.000 |
| 3 | 2.5% | 59.6% | 0.298 | 2.7% | 40.6% | 0.335 |
| 4 | 7.2% | 57.4% | 0.112 | 3.3% | 50.0% | 0.206 |
| 5 | 6.4% | 57.4% | 0.250 | 1.6% | 46.9% | 0.356 |
| 6 | 0.2% | 48.9% | 0.477 | 6.5% | 53.1% | 0.071 |
| 7 | 2.2% | 57.4% | 0.321 | 10.6% | 65.6% | 0.017 |
| 8 | 11.7% | 57.4% | 0.073 | 0.9% | 46.9% | 0.392 |
| 9 | 11.2% | 59.6% | 0.081 | 12.9% | 65.6% | 0.009 |
| 10 | 0.7% | 42.6% | 0.429 | -6.1% | 43.8% | 1.000 |
| | **Mean** | | | **Mean** | | |
| | 4.6% | | | 3.3% | | |

using paired t-tests as before.

Considering any level of damage, evidence for an effect of damaged arms on gonad development in neighbouring undamaged arms was limited and inconsistent. Males showed less evidence of an effect than females: only one set of random samples from males showed a mean decrease significantly greater than zero and in five of the sets, the gonads in arms adjacent to damaged arms were on average larger than those of undamaged arms. The overall mean difference was practically zero. In females, three sets of random samples showed a mean decrease significantly greater than zero (two others being marginally non-significant, Table 3.5). In only one random set were gonads in arms adjacent to damaged arms *larger* on average than those of undamaged arms. In the data from both sexes, gonads in neighbouring arms were larger than those in undamaged arms in a large proportion of the pairs in each set. The same was substantially true when only arms with higher levels of damage were considered (Table 3.6). Overall, the differences in gonad size between undamaged arms and those adjacent to damaged arms were less than between damaged and undamaged arms, but, given the limited data, the consistency of the pattern suggests a biological effect.

## Discussion

Conand (1975) estimated fecundity in *A. planci* by releasing oocytes from weighed gonad fragments using Gilson's fluid and counting volumetric subsamples. There was a linear relationship between gonad weight and fecundity (though no statistical analysis was given). This implies that gonad weight is an indicator of fecundity. This extensive study has shown that gonad weight is very variable among starfish of similar size. Gonad development also varies among the arms of an individual starfish.

Rather little of this variability can be explained by costs of healing and regeneration. There are several possible reasons for this. Variation among arms of individual starfish may not be closely related to damage because the supply of energy in the form of the products of digestion are transported to the tissues in the coelomic fluid. If this moves freely in the body cavity then gradients in concentration of metabolites are unlikely. This would mean that differences in gonad development arise from the process of development itself rather than from competition for metabolites.

Gonad development and regeneration are most likely to be in competition for resources at the level of the whole starfish, since the total energy intake must be partitioned among these and other functions. There was evidence for this in the lower total gonad size of males with damage, though there was much variability in gonad development of undamaged animals of similar size making differences hard to detect. Some sources of this variability can be predicted. First, estimates of extent of damage and regeneration have never been substantiated; not all damage and regeneration may be equally easy to detect and there may well be errors in the estimates. Second, these analyses take no account of the time since the damage occurred. It is not clear how much control the starfish have over whether to regenerate or not; it is possible that wounds have been healed in previous reproductive seasons and no extra metabolic cost has been involved if no regeneration has occurred recently. On present knowledge there is no basis for estimating the time since damage occurred and any estimates would be very dubious. These problems could only be resolved by following animals and recording histories of damage and regeneration. This would be an enormous task given the problems of marking animals in the field or maintaining them in captivity for long periods.

The question of interest to managers is: Do starfish populations with high proportions of damaged individuals (due to large numbers of predators or to control programs) have a lower reproductive output than populations of undamaged individuals? The answer is that the reproductive output is likely to be lower on average. Given the general lack of stock-recruitment relationship in organisms with pelagic larvae and the prodigious numbers of larvae produced by individual starfish, partial predation levels seem likely to have only a limited effect on future recruitment. The direct effects of partial predation on reproductive output may be smaller than indirect effects of predators such as their presence causing aggregations to disperse, hence lowering fertilisation rates. Ormond & Campbell (1974) observed large triggerfishes to disperse an aggregation in the Red Sea.

# 4. Laboratory studies of digestion in *Lethrinus miniatus*.

## Summary

1. Gut transit times of *L. miniatus* were estimated in winter and summer. Transit times were very variable and the mean seasonal difference appears to be slight, in spite of a difference of 5°C in water temperature.
2. Simulations using the experimental gut transit times suggest that the number of fish with *A. planci* remains in their guts will be a slight (5%) underestimate of the numbers that have eaten *A. planci* in the preceding 24 h. The effect of increasing transit times would be to make this an overestimate.
3. Remains of adult *A. planci* were abraded but easily recognisable after passage through the gut.
4. Remains of juvenile *crown-of-thorns starfish that were fed to the fish* consisted of a bolus of recognisable but tiny skeletal elements resembling fine sand to the naked eye; the body wall was completely digested.
5. The experimental *L. miniatus* ignored small living juvenile *A. planci* when these were put into their tanks.

## Introduction

Two kinds of information are required in order to interpret gut samples collected in the field: first it is important to confirm that remains of *Acanthaster planci* of varying sizes can be recognised in various stages of digestion in stomachs and intestines of fishes. If small juvenile *A. planci* (2.5 cm diam.) are treated with bleach, the remaining skeletal remains resemble a small quantity of very fine sand. There is the potential for erosion of larger elements by digestive acids. Second, gut transit times are important for estimating rates of predation, which are needed for modelling the predator-prey interaction. The gut contents represent the food taken over a period of time which is related to the gut transit time. I approached both these questions by feeding skeletal elements of *A. planci* to fishes caught by hook and line and kept in large aquaria. I chose to use *Lethrinus miniatus* because this species has repeatedly been identified as a possible predator of Crown-of-thorns starfish. Because digestion rate was thought to be influenced by water temperature, fishes were tested in summer and in winter.

## Methods

*Lethrinus miniatus* were caught by hook and line on midshelf reefs near Orpheus Is. in early January and early August 1992. In order to minimise pressure changes, they were caught in not more than 20 m of water and were brought to the surface at as slow a rate as was compatible with keeping them on the hook. Even so, fishes exhibited severe stress: though they looked normal when brought to the surface, within five minutes they developed distended swimbladders and floated upside down in the holding tanks. This was relieved by puncturing with a hypodermic needle through the flank. In January only three of more than 20 survived more than 48 h. About one month after capture, these fish in turn developed large ulcers in their mouths, presumably originating from hook wounds, and stopped feeding. To prevent repetition of this, fish that were caught in August were held in a dilute solution of 2-Phenoxy-ethanol (1 $cm^3$ in 60 l) in the boat, which kept them mildly sedated. Prior to putting them in the experimental tanks, they were injected with tetracycline (100 $mg.kg^{-1}$). This appeared to improve survival (6 out of 12).

In summer, each fish was held in a rectangular raceway (5.1 x 0.85 x 0.5 m) with a small shelter and supplied with flow-through seawater. In winter the raceways were divided in half with 75 mm mesh and two fish were kept in each. The tops of the raceways were covered with plastic birdmesh to prevent the fish from jumping out. The water temperature varied by 2 - 4 degrees over the day, ranging from 22.0 to 25.5°C in August and 26.5 to 32°C in January/February.

Parts of the bleached skeletons of several adult *A. planci* (>35 cm diam.) were fed to the fishes by sewing them into sacs of squid which were bought frozen as bait. The parts were mainly of three types: oral ossicles and first ambulacral ossicles (Walbran 1987, plate 4; 1 and 2) and primary abactinal ossicles (Walbran 1987, plate 7; 3 and 4). The oral and first ambulacral ossicles were similar in size and shape, each consisting of an irregular plate with a projection, and measured about 1 cm in their longest dimension. Here I refer to these as jaws. Primary abactinal ossicles are the bases of the large spines and were more or less cylindrical. Those used varied in length from about 15 to 24 mm and from 2.4 to 2.8 mm in diameter. These will be referred to as spine bases. On two occasions fish were fed secondary abactinal ossicles: the spine tips.

On six occasions in August the fishes were fed juvenile *A. planci* that had been freshly killed by freezing. Two of these were whole (26-27 mm diam.), four were cut in half (51 mm diam.). They were presented enclosed in squid in the same way.

The guts of *L. miniatus* often contain remains of more than one type of prey item implying that they eat several times per day. As well as the experimental meals of squid, fishes were also offered fish (pieces of Western Australian pilchards, minus the head) *ad libitum* each morning and evening. After each feeding I checked that the squid had been eaten and that the ossicles had not been rejected. The raceways were then scrutinised at irregular intervals for faeces containing skeletal remains. Transit time was estimated from the time of feeding to the end of the intervals between checks in which the ossicles were defecated. No further ossicles were given to the fish until those from previous experimental meals had been recovered.

**Feeding experiments with living *A. planci* juveniles**

On the afternoon of 25 August, five pairs of one small juvenile (about 25 mm diam.) and one larger juvenile (about 50 mm diam.) were placed in the raceways along with a small piece of living staghorn *Acropora*. The juveniles were checked on the afternoon of 29 August.

**Table 4.1:** Frequency of captive *L. miniatus* passing remains of *A. planci* in the first bolus.

| Proportion of ossicles in first bolus | Summer 1992 | Winter 1992 |
|---|---|---|
| All | 7 (29%) | 19 (49%) |
| More than half | 12 (50%) | 10 (26%) |
| About half | 2 (8%) | 2 (5%) |
| Less than half | 3 (13%) | 8 (21%) |
| Total | 24 | 39 |

## Results

**Transit times:** In January, 24 measures of gut transit time were made on the three fish. Two fish stopped feeding in the course of the experiment so the numbers of observations on each fish varied (Fish 1: 5, Fish 2: 12, Fish 3: 7). In August, 45 observations were made on six fish (Fish 4: 11, Fish 5: 8, Fish 6: 8, Fish 7: 5, Fish 8: 4, Fish 9: 9).

The shortest estimated times between ingestion and the appearance of the first ossicle were less than 6.5 h in summer and 11.5 h in winter. In about 75% of the feeding occasions in each period, the fishes passed most of the ossicles from each experimental meal in the first bolus (Table 4.1). In 50% of all observations in January, the fish passed at least one ossicle within 14 h. In 95% of cases, all ossicles were passed within 43 h (Table 4.2). For interpretation of data on the presence or absence of *A. planci* remains in fishes' guts, the maximum transit time is the relevant value because, with careful sorting, single ossicles can be found and identified.

The estimates of gut transit time were similar in winter and summer. When comparing transit times for meals containing similar ossicle loads (5 Jaws in summer *vs* 5 Jaws + 5 Bases in winter [Fig. 4.1]), the maximum estimates for passing all ossicles were not significantly different between the seasons ($F_{(1, 30)}$ = 0.92, ns.). Within the experimental range, there was no evidence that the quantity

**Table 4.2**: Gut transit times for *Lethrinus miniatus* in summer and winter. Number of hours for 50 and 95% of individuals to defecate the first ossicle and all ossicles from an experimental meal.

| | **50%** | **95%** |
|---|---|---|
| **Summer 1992** | | |
| First bolus | 15 | 38 |
| All ossicles | 26 | 43 |
| **Winter 1992** | | |
| First bolus | 21 | 34 |
| All ossicles | 24 | 37 |

of ossicles in a meal affected gut transit time (Fig. 4.1, One-way ANOVA: Summer $F_{(1,14)} = 0.1$, ns; Winter (juveniles omitted) $F_{(2,42)} = 2.3$, ns.)

**Appearance of *A. planci* remains after digestion**

After passing through the gut, ossicles of adult starfish were usually deeply scratched and sometimes broken into two or three pieces, presumably by pharyngeal teeth. They were not obviously eroded externally by acidic conditions and were easily recognisable by their colour and the surface texture.

The digested remains of juvenile *A. planci* were very similar in appearance to bleached specimens: all the connecting tissue was digested but the skeletal elements remained distinct. Most of the skeletal remains were passed in one bolus coated with mucus. Only a very few ossicles were passed later. This shows that *L. miniatus* are able to digest juvenile *A. planci* and their remains would be easy to recognise in gut contents using a dissecting microscope.

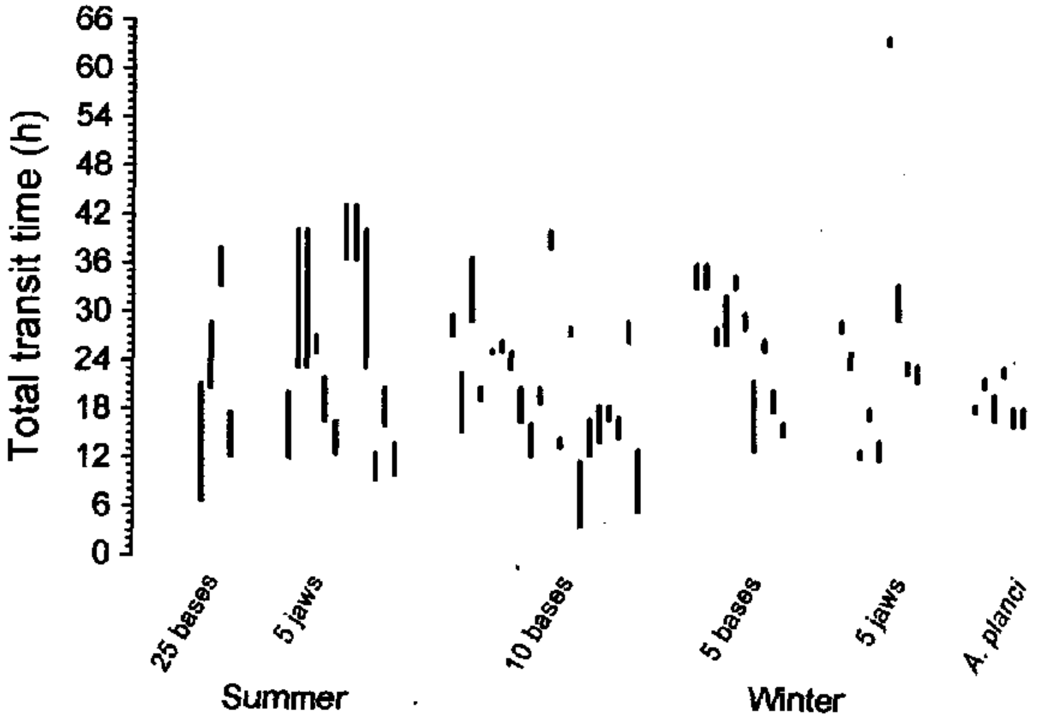


**Figure 4.1:** Total gut transit times for meals with different ossicle loads in summer and winter. "Jaws " and "Bases" are similar in size. "A. planci" denotes juvenile starfish.

**Feeding experiments with living *A. planci* juveniles**

Most of the juvenile *A. planci* abandoned the coral and moved around the raceway at night and hid in the fishes' shelter during the day. They were always easily accessible. The *L. miniatus* were fed their normal pilchards and squid during this time. No juvenile starfish had been eaten after four days.

**Estimation of a daily consumption rate**

Gut transit time is very variable in *L. miniatus*. In the absence of any statistical evidence of seasonal differences or differences due to ossicle loads, I combined the data within each season to give distributions of transit times (Fig 4.2). I used simulation to estimate the number of fish that consume *A. planci* in a day from presence/absence data. I assumed that fishing was haphazard: there is no pattern

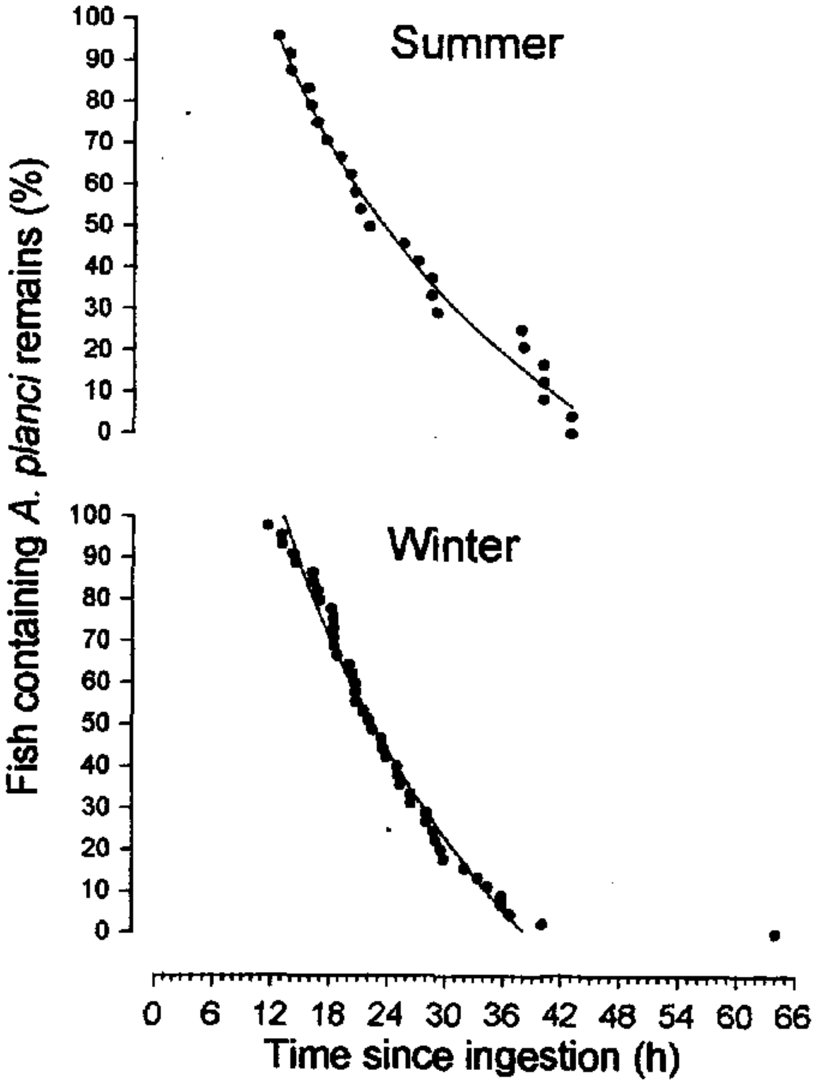


**Figure 4.2:** Frequency distribution of all gut transit times of *L. miniatus* in each season.

in the timing of the fishes' feeding relative to the time of their capture. I generated sets of uniform random numbers between zero and 24 to represent a distribution of intervals between food ingestion and capture in a 24 h period. I then paired these with an equal sample of total transit times from the values observed in both seasons combined. These were drawn randomly with replacement. I scored the number of pairs in which the random intervals between ingestion and capture exceeded the transit time. This is an estimate of the frequency that fishes have eaten *A. planci* in the preceding 24 h, but have already passed all remains by the time of capture. Fifty samples of 1000 pairs of values indicated that this was likely to have occurred in about 15% of fishes caught haphazardly (Table 4.3).

Some of the observed transit times were greater than 24 h, so some *A. planci* in gut samples could have been consumed on the previous day or earlier. To estimate the proportion of remains present in the guts that had been eaten in the preceding 24 h, I drew maximum transit times at random from the combined observed values, as before. For each transit time, I then drew a uniform random number between zero and that transit time to represent the time since ingestion. This assumes haphazard fishing, as before. The proportion of cases where the time since ingestion was 24 h or less gives the proportion consumed (but not completely digested) in one day. Fifty samples of 500 values indicated that about 90% of starfish recorded in guts of *L. miniatus* are likely to have been ingested within the previous 24 h (Table 4.3).

**Table 4.3:** Results from simulations giving the breakdown of remains in guts by time of ingestion for different estimates of transit time and a correction factor to apply to presence absence data. Figures in parentheses are standard errors.

| Transit time | Percent ingested in 24 h and passed before sampling | | Percent ingested less than 24 h before sampling | | Correction factor |
|---|---|---|---|---|---|
| Observed values | 14.2 | (0.015) | 88.9 | (0.009) | 1.05 |
| Extend by 10% | 9.8 | (0.009) | 85.6 | (0.011) | 0.97 |
| Extend by 25% | 5.8 | (0.011) | 79.4 | (0.011) | 0.86 |

Other simulations were run to look at the effect of increasing transit times. The experimental transit time values were simply multiplied by the appropriate factor and simulations proceeded as before.

## Discussion

This simple technique for estimating total transit times has limitations, particularly in that the resolution depends on the frequency with which the raceways were checked. This was generally higher in the winter observations, which may mean that transit times are over-estimated in summer. However, the figures are compatible with published results: Magnuson (1969) found that 1.6 kg skipjack tuna, *Katsuwonus pelamis*, feeding on fish at 23-26°C had total gastric evacuation times of about 12 h. Pierce (1936) measured gastric evacuation time of the tropical snapper *Ocyurus chrysurus* to be 30 h when eating fish at 24°C. Reshetnikov et al. (1972) measured the gastric evacuation rates of several tropical Atlantic snappers to be 5-27 h when feeding on fish at 28-30°C. Since all these are gastric evacuation rates, the total gut transit time should be correspondingly longer. Lane & Jackson (1969) tested 20 species of teleost at temperatures ranging from 19-25°C and found that, on average, voidance was complete in 48 h. In a review, Fange & Grove (1979) found that the average voidance time for species tested at 20-30°C was 29 h. These figures involve many species, trophic groups and experimental methods.

Large indigestible particles have been shown to pass more slowly than small particles or digestible fractions of food (Dos Santos & Jobling 1991). If the sacs of squid were stuffed with too many ossicles the fish would reject them, setting a limit to the range of calcareous material that could be tested. There was no evidence that the meals containing five jaws passed more quickly than those with eight or ten jaws or 25 spine bases (Fig. 4.1). Four complete arms of an adult *A. planci* (as found by Birdsey [1988] in the guts of a *L. nebulosus*) would contain 10-100 times more calcareous material than the experimental meals, but most ossicles are smaller than the ones used in experiments. It seems likely that meals of adult *A. planci* would pass more slowly than the experimental meals.

The simulations to apply the information on transit times to presence or absence of prey in guts are also based on a number of assumptions. The most critical of these is that of haphazard fishing. If the fish have a distinct feeding time of day in which food is likely to be ingested and they are likely to be caught at a particular time (through the behaviour of fish or fishers), this will not hold. The values for transit times may also be biased, the method of checking the tanks at intervals means that transit times will be overestimated. The relatively low calcareous content of the experimental meals may lead to underestimation of transit times. . increasing the transit time will mean that the number of fish with remains of *A. planci* in their guts will be increasingly an overestimate of the numbers that have eaten *A. planci* in the previous 24 h. With increasing transit time, the proportion of fishes that eat *A. planci* and digest and pass the remains before being caught will decrease. An increased proportion of fishes with remains in their guts will have eaten them more than 24 h prior to capture.

There are many methods of determining gut transit times of fishes that could give more precise estimates for individual meals. All have problems: either they require very large numbers of experimental fishes (e.g. periodic sacrifice and dissection) or frequent handling (e.g. feeding fishes X-ray dense meals and following their progress through a series of radiographs [Talbot & Higgins, 1983; Jorgensen & Jobling, 1988]). Given the difficulties of obtaining experimental animals and keeping them in aquaria, and the fivefold range in gut transit times, the chosen method was adequate and has provided information for the interpretation of gut contents in *Lethrinus miniatus*.

## 5. Are commercially exploited reef fishes predators of adult Crown-of-thorns starfish ?

### Summary

1. Analysis of guts of 95 *Lethrinus miniatus* and 3 *L. nebulosus* that were caught within 0.5 km of outbreak densities of adult *A. planci* found no evidence of predation by these fish species.
2. With the size of samples obtained the possibility of predation by fishes at low levels cannot be excluded on statistical grounds.
3. An analysis of the relative fullness of fishes' guts over the day suggests that *L. miniatus* feeds most in the early part of the night. This means that *L. miniatus* would be likely to encounter juvenile *A. planci* if they were present.

### Introduction

Among the first hypothetical explanations for the incidence of outbreaks of Crown of thorns starfish was that human activities had reduced populations of predators. Recently attention has focussed on Lethrinidae, particularly *Lethrinus miniatus* (= *L. chrysostomus*), and to a lesser extent on maori wrasse, *Cheilinus undulatus*. These commercially exploited fishes feed largely on benthic invertebrates, including echinoderms (Walker 1978, Randall et al. 1978), and are associated with areas of coral rather than sand. Population modelling by McCallum (1988) suggested that the kind of population dynamics shown by *A. planci*: general low density occurrence but with unpredictable outbreaks, could be produced by a non-specialist predator showing a Type III (accelerating) functional response (typical of vertebrates) attacking the post-settlement (but pre-reproductive) stages of a prey species with planktonic larvae. He suggested that a predatory mortality rate of about 1.5% of starfish per day would prevent outbreaks.

Information on fish predators comes from anecdotal field observations and from studies of gut contents. There are many anecdotal accounts of predation on adult *A. planci* by fishes (Ormond & Campbell 1974, Owens 1971, Wilson et al. 1974, Endean & Cameron 1990, Marine Bio-Logic 1990, Ormond et al. 1990). Many involve pufferfishes or triggerfishes; it is hard to argue convincingly that these have been reduced in number by human activity on the GBR. Gut contents can reveal whether certain prey items are taken and frequency of consumption can be estimated. Guts of a number of species of potential predators of starfish have been examined (Toor 1964, Walker 1978, Randall et al 1978, Birdsey 1988), but very few occurrences of *A. planci* have been recorded. Most such data have dubious relevance for assessing predation on *A. planci* because few samples have been collected from sites where *A. planci* was known to be present, so fish may not have had the opportunity to eat *A. planci*. The only relevant study is by Birdsey (1988) who examined gut contents of fishes caught at reefs that were known to have outbreak densities of adult starfish. Even then, outbreaks affect only part of a reef at a time; whether fishes were caught close to the particular areas of high starfish density was not recorded. Birdsey examined 26 *Lethrinus nebulosus* and 22 *L. miniatus*. One *L. nebulosus* contained part of an adult *A. planci*. There is one published report of a maori wrasse, *C. undulatus*, with an entire adult *A. planci* in its gut (Randall et al. 1978).

Logic suggests that the nutritional value of adult *A. planci* may be seasonal: close to spawning, the body cavity is packed with gonad tissue which, while toxic (Lucas *et al.* 1979) is likely to be rich in lipids and protein. The longest aboral spines are at the bases of the arms, where the main mass of gonads occurs. Ormond & Campbell (1974) recorded that triggerfishes concentrated their feeding at the base of the arms leaving a ring of arm tips. It has also been suggested that starfish, particularly females, are more cryptic close to spawning time (R.C. Babcock, pers. comm.).

The principal aim of this part of my study was to collect as large a sample of putative predators of *A. planci* close to outbreak densities of adults with developed gonads to look for evidence of predation and to assess the *per capita* predatory mortality. A secondary aim was to look for evidence of timing of *L. miniatus* feeding from gut fullness.

## Materials and Methods

Two reefs with current outbreaks of Crown-of-thorns starfish were visited 14-22 February 1994. These were Snake Reef (22-088; 152°08' E, 22°02' S) and Gannet Cay (21-556; 152°29' E, 21°59' S). Areas of high starfish density were located within these reef systems by systematic manta tows and snorkelling. These were marked with buoys.

**Fish sampling**

Three fishermen targeted *L. miniatus* fishing with handlines using squid, WA pilchards and mullet as bait. Fishing activity was all within 500 m of the starfish concentrations. Standard length was recorded for all fish caught. The time of capture (to the nearest hour) was recorded in the majority of cases. The entire digestive tract was removed shortly after capture and preserved in buffered seawater formalin (10%). In the laboratory, entire gut contents were washed out onto fine plankton mesh (17µm). This was left to drain on absorbent paper for 25 min. and then weighed. Gut contents were scrutinised under a binocular microscope for remains of *A. planci* and large items were identified.

Because the fish varied in size, an index of gut fullness was calculated. I assumed that gut volume was related to the volume of the fish. For each fish, I divided the wet weight of gut contents by the cube of the standard length.

**Starfish counts**

The numbers of starfish in outbreak centres were estimated. At Snake Reef, the outbreak covered an extensive area along the edge of a large patch reef and on an adjacent shoal area in about 14 m depth. Initially I planned to count the starfish in a series of dives, each animal being marked with a temporary tag as it was counted. These tags consisted of small (25 mm) lengths of dayglo orange flagging tape which were attached by impaling them on one of the dorsal spines and pushing them down near the base using a 10 cm length of plastic tubing (5 mm internal diameter). Each individual was marked with two tags to reduce the chance of tag loss. There was no indication of tag loss or spine necrosis over the 3 - 4 days of the observations. After tagging 135 individuals, it was clear that the outbreak covered a larger area than was first thought, so tagging was discontinued. The numbers of starfish were estimated by measuring the length of reef edge and the width of the affected area using 50 m tapes. Two divers participated, each counting *A. planci* in a 2 m band on one side of the tape. The width of the area and density of *A. planci* were estimated by swimming transects 5 m wide, starting at the sand and running at a normal to the reef edge. These vertical transects were separated by about 15 m. The width of the infestation was taken to be the distance from the sand to the starfish that was second furthest from the sand. This was to reduce bias due to outlying starfish.

At Gannet Cay, starfish were located in two patches, one small one on the west side of the reef, just south of the Cay, and another larger one just around the corner of the reef on the south face. The starfish were quite localised and so were suitable for tagging as was attempted at Snake Reef.

Small numbers of starfish were collected for examination of their reproductive state.

**Fish counts**

Twenty counts of fish were made at Snake Reef in the vicinity of the Crown-of-thorns starfish outbreak. Lethrinids were counted in 50x10 m transects placed

**Table 5.1** Population estimates for Crown-of-thorns starfish and lethrinids and for predation rates at *Snake Reef and Gannet Cay*. Est. *Population* of lethrinids = estimated numbers of *Lethrinus* spp. within 0.5 km of outbreak; Est. max predation per starfish (means) = percent of starfish population that could have been eaten per day, based on mean estimates for fish and starfish populations; (worst case) percent of starfish population that could have been eaten per day, based on upper confidence interval (C.L.) for fish population and lower C.L. for starfish numbers.

| | Snake Reef | Gannet Cay |
|---|---|---|
| Number of *A. planci* | 434<br>(169 - 699) | 131<br>(min.) |
| No. Lethrinids per hectare | 9.0<br>(0.7 - 17.3) | 8.8<br>(0.9 - 16.6) |
| Est. Population of lethrinids | 414<br>(34 - 794) | 49<br>(5 - 93) |
| Est. max predation per starfish | | |
| (means) | 3.6%<br>(0.9 - 6.5) | 1.4%<br>(0.2 - 2.7) |
| (worst case) | 9.3%<br>(0.8 - 17.9) | |

haphazardly along the reef edge at least 20 m apart, starting at a depth of about 3 m and running down the slope.

At Gannet Cay 16 50x10 m transects were swum along the west face of the reef, starting in about 3 m of water and running down the slope. It was not possible to count fish in the immediate vicinity of the large aggregation because of rough seas and strong currents. At each reef, the numbers of fish were very low, averaging much less than one per transect.

## Results

### Estimates of numbers of *A. planci*

Combining the estimated area of the infestation and the estimated mean density gave a value of over 400 starfish in the infestation at Snake Reef (Table 5.1). These were mainly large adults. One hundred and thirty five starfish were tagged before that method was judged too time consuming; there were certainly many more than that.

At Gannet Cay, a total of 131 adult starfish were tagged and counted in the two aggregations. Although these aggregations appeared well defined this must be taken as a minimum population estimate.

### Reproductive state of *A. planci*

Five males and four females were collected at Snake Reef and four males and two females were collected at Gannet Cay. Gonads varied in development with size of the starfish; when compared with ripe individuals collected immediately prior to spawning from Lynch's and Davies reefs near Townsville (Section 3), many of the starfish in this study had small gonads for their size (Fig. 5.1).

### Fish counts

Low numbers of lethrinids were observed at both sites, with mean densities of less than 0.5 fish per 50x10 m transect (Table 5.1). All the lethrinids seen at Snake Reef were *L. miniatus*; some *Lethrinus atkinsoni* were seen at Gannet Cay. These were included in the fish population estimate because they have been observed to eat juvenile *A. planci* (see Section 6).

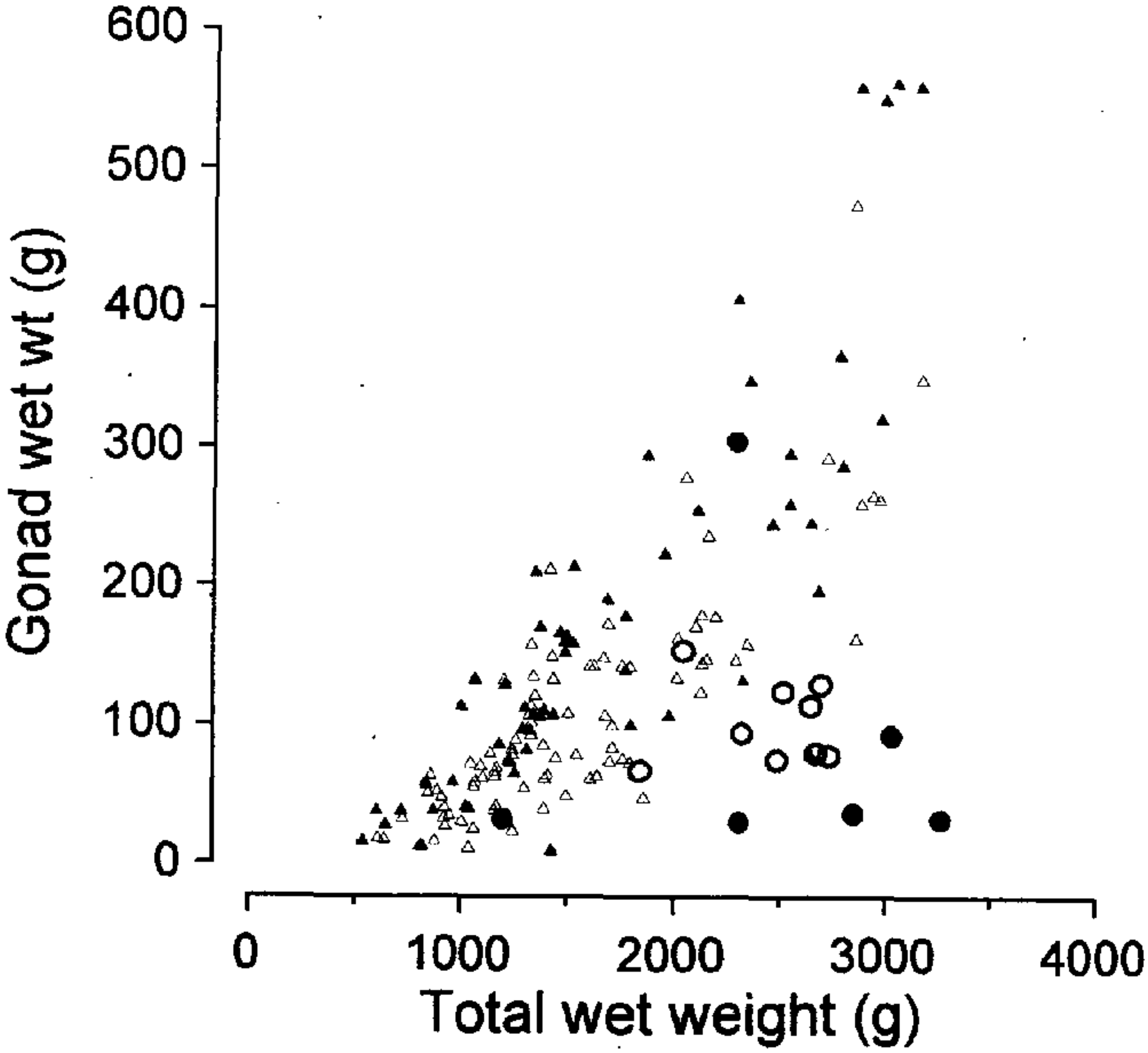


**Figure 5.1:** Relationship between gonad wet weight and size of *A. planci*. Circles = animals from the Swains, triangles = starfish from near Townsville; hollow symbols = males, filled symbols =females.

**Gut contents**

No remains of Crown-of-thorns starfish were found in any of the 95 *L. miniatus* and 3 *L. nebulosus* sampled. There were numerous echinoderm remains (Table 5.2) and one *L. miniatus* had eaten a whole *Linckia* sp. (?*laevigata*) about 50 mm in diameter. Many of the organisms (irregular echinoids, some bivalves, the gastropod *Umbonium guamensis*) live in sandy areas, but the crinoids, ophiuroids, spider crabs and gastropods such as abalone and *Pseudostomatella decolorata* come from hard substrates and suggest that the fishes spend a proportion of their time feeding on the coral and rubble areas.

**Table 5.2:** Numbers of Lethrinids containing recognisable remains of various taxa. Based on a sample of 95 *L. miniatus* and 3 *L nebulosus.*

| | *L. miniatus* | *L nebulosus* |
|---|---|---|
| Chitons | 1 | 1 |
| Bivalves | 13 | 3 |
| Gastropods | 25 | 1 |
| *Aplysia* sp. | 10 | 0 |
| Octopus | 2 | 0 |
| Isopods | 5 | 0 |
| Crabs | 45 | 1 |
| Crinoids | 4 | 0 |
| Ophiuroids | 13 | 0 |
| Asteroids | 2 | 0 |
| Echinoid | 32 | 1 |
| Fish | 32 | 0 |

### The timing of feeding

Neither the fishing effort nor the capture rate was even over the day. There was little fishing effort and few fishes were caught between 23:00 and 06:00 and in the middle of the day. The relationship between the index of gut fullness and time of day (Fig. 5.2) suggests that *L. miniatus* caught between 22:00 and 10:00 tended not to have empty guts. The average value of gut fullness index for the 77 *L. miniatus* whose time of capture was recorded was 0.000162; in 48 cases (62.3%) the index was less than that value. Twenty-eight fish were caught between 22:00 and 10:00; only 11 (39.3%) had less than the mean value of the index. The probability of as few or fewer individuals having low index values by chance was less than 2% (binomial).

### Predation estimates

This study found no evidence of predation by *L. miniatus* on *A. planci*, but how high could the predation rate have been without being detected by such sampling? The maximum estimate for the incidence of predation is represented by the maximum binomial probability whose lower 95% confidence interval includes zero. This gives the maximum proportion of the fish population that could contain *A. planci* remains. All *L. miniatus* collected from both reefs in this study arguably had

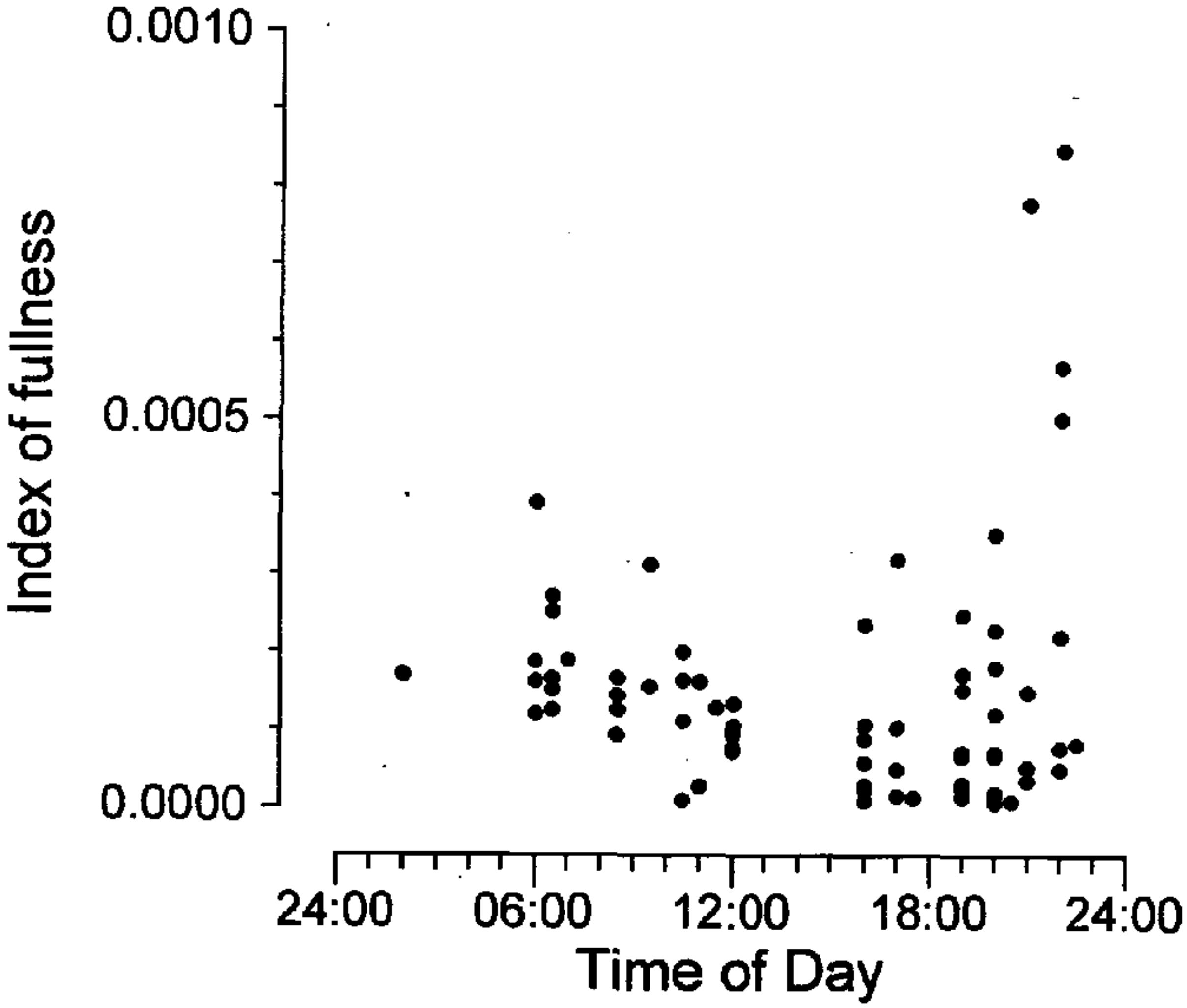


**Figure 5.2:** Index of gut fullness for 77 *L. miniatus* caught at different times of day. Fullness = (wet weight of gut contents / TL$^3$).

had opportunity to eat adult *A. planci*, so collections were combined to give a sample of 95. With a sample of 95 animals, the upper 95% confidence limit for occurrence is 3.81% (binomial). From Section 4, the number of fish with remains of *A. planci* in their guts is a slight underestimate of the number that have consumed *A. planci* This means that the observed rate of occurrence was not statistically different from 3.8% of fishes having eaten *A. planci* in the preceding day.

The population of fishes that was sampled for gut contents was calculated from the estimated population density and a sampling area of 500 m around the aggregations from which fishes were caught for gut analyses. At Snake Reef the starfish were distributed on a 450 m line along the reef edge. Thus the sampling area for fish was taken to be 450 x 1000 $m^2$ plus two semi-circles 500 m in diameter, representing the ends of the sampling area. At Gannet Cay, this area was taken to be a circle 500 m in diameter and an area 50 m long and 1000 m wide with semicircular ends. The resulting estimates of the fish population are shown in Table 5.1.

Combining the estimate of the starfish population size (using the mean density in the case of Snake Reef ) with the maximum predation rate and the estimated numbers of lethrinids within 500 m of the outbreaks based on mean counts, lethrinids could still have been consuming up to 3.6% of starfish per day at Snake Reef and 1.4% at Gannet Cay (Table 5.1).

### Discussion

A sample of 95 *L. miniatus* and three *L. nebulosus* taken from the vicinity of current outbreaks of Crown of thorns starfish failed to show any evidence that the lethrinids were preying on adult starfish. Though my sample size was greater than that of any previous study, it is impossible to exclude the possibility that predation occurs at low rates: a sample of 300 fish is necessary statistically to exclude predation by 1% or more of fishes.

Estimates of the possible predation rate per starfish are very uncertain due to propagation of errors: they are products of estimates of the sampling area (subject to error), estimates of fish density (with error) and estimates of starfish population (with error). All fishing was within 500 m of the marker buoys as estimated by eye and this estimated sampling area take no account of sub-areas that might not be suitable habitat for lethrinids. Since there were no replicate area estimates, confidence intervals cannot be calculated. Counts of lethrinids were replicated but are notoriously unreliable as these fishes are generally shy of divers: it is possible to catch lethrinids with hook and line where none are recorded in concurrent visual surveys (M. Kulbicki, pers. comm.). My density estimates from Snake Reef and Gannet Cay are low compared with mean densities of all *Lethrinus* spp. on seven reefs in the central section of the GBR (Ayling & Ayling, 1994), though these counts varied greatly within reefs. Underestimation of the predator population will tend to underestimate predation rate. The starfish populations were certainly underestimated: Crown-of-thorns starfish are often cryptic and those that are visible may be a small proportion of the total. This would tend to overestimate predation rates.

There is also a problem interpreting the significance of fish predation to the starfish. It would be physically impossible for one lethrinid to consume a whole adult *A. planci*; Birdsey (1988) found four arms in one *L. nebulosus*. The experiments to examine the effects of partial predation suggest that a high proportion of starfish that lose four arms will survive. B.T. Kettle (unpublished) examined 638 starfishes from outbreak populations and found that about 14% of individuals showed evidence of four or more arms having been damaged at some time (Fig. 1.1). It is quite likely that lethrinids would feed in groups and several individuals might consume parts of the same starfish. This is more likely to result in the death of the starfish, but complicates the interpretation of gut contents because several fish consume starfish for each mortality event. The average starfish in Kettle's sample had 16 arms (range: 10-22), thus it would take two lethrinids to inflict a mortal wound and probably at least four to consume a starfish. Taking each occurrence of *A. planci* remains in fish as evidence of a fatal attack is likely to overestimate predation.

The size of these biases cannot be assessed on available information, so assuming that each fish whose guts contain starfish remains corresponds to the death of a starfish and using the mean estimates for fish and starfish populations, daily *per capita* predation rates of 3.6% at Snake Reef and 1.4% at Gannet Cay cannot be refuted on statistical grounds. In the worst case: using the upper confidence limit for the fish population and the lower limit for the starfish population, a daily *per capita* predation rate of 17.9% at Snake Reef is possible. Since the estimate of starfish numbers at Gannet Cay was a simple count without any estimate of error, the corresponding worst case estimate is 2.7% of starfish attacked per day.

Data on spawning seasonality in the Swains area is anecdotal and contradictory: starfish collected at Gannet Cay in mid-December 1991 spawned when transported (I.R. Miller, pers. comm.) but starfish at Reef 22-118, 27 km SW of Gannet Cay had extremely ripe gonads 16 March 1987 (P. Moran, pers. comm.).

Logically the nutritional value of adult *A. planci* should be related to gonad development: Figure 5.2 suggests that the gonads of most individuals sampled in February were not maximally developed but they were not inactive, because some starfish collected at Gannet Cay for other purposes spawned in transportation and most could be induced to spawn artificially.

This part of the study found no evidence of predatory fishes having eaten adult *A. planci* when they had the opportunity. The major thrust of recent arguments about the effects of fish predators on the population dynamics of *A. planci* (Ormond et al. 1990, McCallum 1988) have concerned lethrinids consuming small juvenile starfishes, whose ecology is practically unknown. Attention has focussed on *L. miniatus* because it is a commercially-exploited species that eats benthic invertebrates and inhabits coral areas (as opposed to sandy lagoonal areas). To warrant serious consideration as predator of juvenile *A. planci*, a species must also feed nocturnally, for the starfish are hidden deep in the rubble or the bases of corals during daylight. This study provides the first quantitative evidence of that *L. miniatus* feeds mainly at night. Many prey items are clearly taken from hard substrata so it seems likely that *L. miniatus* would encounter feeding juvenile *A. planci* if these were present. From the experiments with *L. miniatus* in aquaria (Section 4) and from the field feeding trials (Section 6), it appears that *L. miniatus* and other *Lethrinus* spp. will eat juvenile *A. planci*, but do so erratically. The critical question that remains is: what is the predation rate on juvenile *A. planci* due to commercially exploited fishes when high densities occur naturally as at the start of an outbreak? Intensive fishing in the immediate vicinity of high natural densities of juvenile Crown-of-thorns starfish should be given the highest priority.

## 6: Field studies of fish predation on juvenile *Acanthaster planci*

### Summary

1. Laboratory reared juvenile *Acanthaster planci* were placed on small habitat units in an area of a lagoon where a number of species of fish that feed on benthic invertebrates occurred.
2. Predators were excluded from half the units using wire mesh.
3. In 35 days, losses were low and there was no statistically significant difference between caged and uncaged units.
4. The maximum estimate of predatory mortality was much lower than the level that population models indicate would be important in controlling outbreaks. It seems unlikely that predation by large fishes was important in population dynamics of juvenile *A. planci* at that site at the time of the experiment.
5. A second, similar experiment at Bowl Reef was destroyed by weather.
6. When juvenile *A. planci* were presented to lethrinids in the field 13% of juvenile were eaten, but in no presentation did lethrinids eat all the available starfish and those that were eaten were often mouthed and rejected by several fishes before being swallowed.

### Introduction

A recent variant of the hypothesis that removal of predators through human activities has increased the frequency of outbreaks of *A. planci* holds that human exploitation of predatory fishes is responsible. Attention has focussed on Lethrinidae, particularly *Lethrinus miniatus* (= *L. chrysostomus*), and to a lesser extent on maori wrasse, *Cheilinus undulatus*. These commercially exploited fishes feed largely on benthic invertebrates, including echinoderms (Walker 1978, Randall et al. 1978), and are associated with areas of coral. It is also generally held that juvenile starfish are more likely to be susceptible to fish predators than are adult *A. planci*. Population modelling by McCallum (1988) suggested that the kind of population dynamics shown by *A. planci*: general low density occurrence but with unpredictable outbreaks, could be produced by a non-specialist predator showing a Type III (accelerating) functional response (typical of vertebrates) attacking the post-settlement stages of a prey species with planktonic larvae. He suggested that a predatory mortality rate of about 1.5% of starfish per day would prevent outbreaks.

Ormond et al. (1990) summarised a model for the predator-*A. planci*-coral interaction that used minor modifications of the standard logistic population equations. The consumption rates and functional response of the model predators were specified with lethrinid fishes in mind, though some important variables, such as the predators' switching coefficient, could only be guessed. The resulting calculations suggested that densities of 5 - 20 lethrinids per 100 m of reef front could possibly control high recruitment pulses of up to 2 x $10^4$ starfish at a time to the same areas. At lower predator densities or higher recruitment rates there was an increasing chance of such starfish populations escaping predator control to a level limited by food. They surveyed lethrinid densities at 10 reefs on the GBR. Reefs that had experienced recent outbreaks of Crown-of-thorns starfish had lower densities than lightly affected reefs. Lethrinid densities on outbreak reefs were less than 5 per 100 m of reef front; minor impact reefs had densities at or above that threshold. All the GBR sites had much lower fish densities than the sites in the eastern Red Sea, where *A. planci* occurs but outbreaks have never been recorded. One of many differences between GBR sites and Red Sea sites was that fishing activity was minimal at many of the latter.

Ultimately, the impact of fish predators on *A. planci* populations depends on predation rates in the field. Natural concentrations of juvenile *A. planci* have rarely been found so their ecology is poorly known and experiments with natural juveniles have not been possible. Here I report a field experiment comparing the mortality rate for laboratory reared juvenile crown-of-thorns starfish that were exposed to large predatory fishes with that for juveniles protected by cages. I also offered juvenile *A. planci* to lethrinids in the field to see if they would eat them.

## Methods

### Predator Exclusion Experiment

On 17 and 18 October 1992, pairs of small habitat units were built at ten sites along the edge of the lagoon at the south end of Davies Reef (18-096). This area was chosen because a preliminary survey of sheltered areas of Davies Reef found the highest densities of lethrinids there. Each habitat unit consisted of a concrete building block (0.39x0.39x0.19 m) set with the two holes opening vertically. Large dead coral plates were stacked around the block. The holes in the block were partially filled with small pieces of coral rubble and were used to hold erect living pieces of at least three staghorn and corymbose *Acropora* spp. and one or two small colonies of *Seriatopora histrix*.

The back reef generally consisted of a steep drop from the reef flat to a band of rubble and thickets of staghorn coral *Acropora* spp. and then sand. The two units at each site were 3 - 5 m apart and built on sand 2 - 3 m from the edge of the hard substrata. Sites were separated by about 25 m. Depth varied from 3 - 9 m.

On 19 October, 301 cultured *A. planci*, raised at AIMS, were divided into 19 groups of 15 starfish and, unintentionally, one group of 16 individuals. Each group included approximately the same range of sizes, which ranged from 15 - 79 mm in diameter (modal span, arm tip to arm tip). The size distribution was positively skewed and 48% of the experimental animals were < 25 mm in diameter and 80% were < 50 mm in diameter. The value of 15 per habitat unit was chosen as a high natural density based on observations by Pearson & Endean (1969) who found groups of juveniles (26.5-51.5 mm in diameter) at a density of about 10 $m^{-2}$ in colonies of *Acropora echinata*. In the afternoon of 19 October, one group of *A. planci* was placed on each experimental unit, along with one or two pieces of coral

**Table 6.1:** Records of benthic feeding fishes in experimental area 20-23 October. Sites refer to areas between pairs of habitat units. Occ = Number of times one or more individuals of that species was seen (maximum possible = 9), Max = maximum number of individuals seen on any one survey. Right hand columns give mean number seen per survey (area approx. 200 x 5 m) and S.E.

| Area between sites: | 1-2 | | 2-3 | | 3-4 | | 4-5 | | 5-6 | | 6-7 | | 7-8 | | 8-9 | | 9-10 | | | Per Survey | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Occ | Max | Occ | Max | Occ | Max | Occ | Max | Occ | Max | Occ | Max | Occ | Max | Occ | Max | Occ | Max | | | |
| **Lethrinids** | | | | | | | | | | | | | | | | | | | | Mean | SE |
| *Lethrinus atkinsoni* | 1 | 1 | 2 | 1 | 1 | 1 | 0 | - | 4 | 1 | 3 | 2 | 0 | - | 0 | - | 0 | - | | 1.00 | 0.47 |
| *L. miniatus* | 0 | - | 1 | 1 | 0 | - | 1 | 1 | 2 | 2 | 5 | 2 | 4 | 1 | 0 | - | 0 | - | | 1.78 | 0.28 |
| *L. nebulosus* | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 1 | 1 | 2 | 1 | 1 | 1 | 0 | - | | 0.44 | 0.29 |
| *L. obsoletus* | 0 | - | 0 | - | 0 | - | 0 | - | 1 | 1 | 1 | 1 | 0 | - | 0 | - | 0 | - | | 0.22 | 0.22 |
| **Labrids** | | | | | | | | | | | | | | | | | | | ALL | 3.44 | 0.71 |
| *Cheilinus chlorourus* | 1 | 1 | 1 | 1 | 0 | - | 4 | 3 | 2 | 2 | 1 | 1 | 0 | - | 3 | 1 | 2 | 1 | | 1.44 | 0.38 |
| *C. diagramma* | 1 | 1 | 1 | 1 | 0 | - | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | | 1.11 | 0.42 |
| *C. fasciatus* | 7 | 2 | 5 | 5 | 7 | 5 | 6 | 2 | 8 | 9 | 9 | 4 | 4 | 1 | 7 | 4 | 1 | 1 | | 10.67 | 0.69 |
| *C. undulatus* | 0 | - | 0 | - | 1 | 1 | 0 | - | 0 | - | 1 | 1 | 2 | 1 | 1 | 1 | 0 | - | | 0.44 | 0.18 |
| *Choerodon fasciatus* | 6 | 2 | 3 | 2 | 8 | 2 | 7 | 5 | 7 | 4 | 7 | 2 | 8 | 4 | 6 | 3 | 4 | 1 | | 8.78 | 1.00 |
| *Epibulus insidiator* | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | - | 0 | - | 0 | 0 | | 1.56 | 0.50 |
| *Hemigymnus fasciatus* | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 2 | 1 | 1 | 2 | 1 | 1 | | 0.11 | 0.11 |
| *H. melapterus* | 2 | 2 | 5 | 2 | 3 | 2 | 7 | 3 | 7 | 2 | 2 | 2 | 1 | 1 | 3 | 1 | 5 | 2 | | 4.22 | 0.97 |
| **Plectognaths** | | | | | | | | | | | | | | | | | | | ALL | 28.3 | 2.29 |
| *Arothron stellatus* | 1 | 1 | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | | 0.22 | 0.15 |
| *Balistes viridescens* | 1 | 1 | 0 | - | 0 | - | 1 | 1 | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | | 0.22 | 0.15 |
| *Sufflamen chrysopterus* | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 0 | - | 2 | 1 | | 0.11 | 0.11 |
| | | | | | | | | | | | | | | | | | | | ALL | 0.60 | 0.24 |

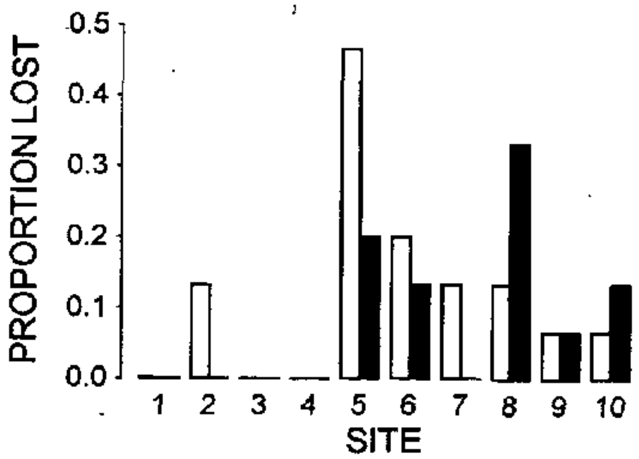


**Figure 6.1:** Proportion of juvenile *A. planci* lost from each habitat unit at each site over the 35 days of the predator exclusion experiment. Hollow bars = uncaged habitat units, filled bars = caged habitat units.

from the holding tank.

One unit at each site was enclosed with a cage of 12.5 mm welded fabric (square wire mesh) approximately 1.4 m in diameter and 0.8 m tall. The edges of the mesh were buried into the sand and the cages were pegged in place with lengths of fencing wire. Since it was important that differences in persistence between caged and uncaged units should be due to predation rather than emigration, slots (50 x 12.5 mm) were cut in the cage at frequent intervals (>50% of the perimeter), 10 - 20 cm above the sand. This would allow starfish that had abandoned the habitat unit and were climbing on the cage to escape. Over the following days the cages were checked and four benthic feeding carnivorous fish (two *Halichoeres trimaculatus* and two *Parapercis hexopthalma*) were removed from the cages at Sites 8 and 9. The caged units at these two sites also were colonised prior to the start of the experiment by some small planktivores: *Dascyllus aruanus*, *Pomacentrus moluccensis* and *Cirrhilabrus punctatus*. These were left in place because removal was judged to be more disruptive to the starfish than their presence.

Potential fish predators were counted at three times of day 20 - 23 October. Two observers snorkelled along the reef edge between the first and last experimental site and counted the number of various categories of benthic feeding fishes between each pair of units in a 10 m wide belt centred on the line where rubble met the sand. The underwater visibility depended to some extent on the angle of the sun, and was generally best in the morning and worst in the late afternoon.

The experiment was visited on 3 and 12 November. The supply of coral was checked. In all cases there was uneaten coral of all types provided. Additional pieces were added each time to ensure a continuing surplus. The sand was inhabited by calianassid shrimps whose burrowing activities sometimes caused small gaps under the edge of the cages allowing *Parapercis* spp., *Coris schroederi* and *H. trimaculatus* to enter the cages. At each inspection, these fishes were chased out and the cage was resealed. The cage at Site 5 was undermined by an adult *Dischistodus perspicillatus*, allowing a sub-adult *Scolopsis bilineatus* and a *Scolopsis margaritifer* into the cage. On no occasion was there a gap more than about 5 cm tall, so fishes >25 cm TL would have been excluded.

On 24 November, all the experimental units were dismantled and each individual piece of rubble was searched independently for juvenile *A. planci* by two divers.

**Feeding experiments**

A series of feeding trials was conducted at Bowl Reef (18-080) in March 1993. The following procedure was followed: A diver located one or more potential predators, usually *Lethrinus* spp., aggregated in staghorn thickets next to sand. Equal numbers (1- 6) of living juvenile *A. planci* (<7 cm diam.) and another small species of starfish, *Fromia elegans* , were placed in a line approximately 0.5 m apart on open sand nearby. The other species was included simply to provide an alternative potential food item. The diver then dropped a live ophiuroid (mostly *Ophiocoma erinaceus*) high in the water column above the line of starfish and withdrew 5 - 10 m to observe. The wriggling ophiuroid attracted the attention of the fishes and usually drew them to the immediate area where the starfishes were. Trials were terminated after 15 minutes because the starfishes generally moved towards cover and hid. If there had been no feeding, the procedure was repeated once more. Observations were made at 16 locations within a shallow (<10 m) area of about 250x200 m.

Four similar trials were made at Davies Reef, 23 - 24 October 1993. The alternative starfish species were either *F. elegans* or juvenile *Linckia laevigata* (<10 cm diam.).

## Results

### Predator counts

The spatial distribution of potential predators, particularly lethrinids and *C. undulatus* was not uniform over the area (Table 6.1). The peaks in occurrence correspond to habitat features such as thickets of staghorn coral where lethrinids sheltered. Large fishes such as lethrinids and *C. undulatus* range over hundreds of metres, thus potential predators did occur near the experimental units.

### Predator Exclusion Experiment

More than 90% of the experimental starfish were recovered after 35 days. There were differences among sites, but caging had no significant effect on the mortality rates (Fig. 6.1; Table 6.2). Overall loss rates in this experiment averaged

**Table 6.2:** Analysis of variance table for predator exclusion experiment.

| Source | df | SS | MS | F | p |
|---|---|---|---|---|---|
| Site | 9 | 5.50 | 0.61 | 3.99 | 0.026 |
| Cage | 1 | 0.16 | 0.16 | 1.04 | 0.334 |
| Error | 9 | 1.38 | 0.15 | | |
| Total | 19 | 7.04 | | | |

0.34% of individuals per day. The difference in losses between caged and uncaged experimental units, which could have been due to predation, averaged only 0.13% per day (Table 6.3). The power of the experiment to detect predatory effects was inversely related to the rate of non-predatory losses. If the true mean non-predatory loss rate had been 0.56% individuals per day (the upper 95% confidence limit of the observed mean rate for caged units, Table 6.3), this experiment would still have detected predatory mortality at a conservative rate (relative to McCallum's (1988) critical value) of 1% individuals per day with better than 88% probability (following Cohen (1988) for factorial designs, using Laubscher's (1960) square root approximation).

**Table 6.3:** Loss rates from caged and uncaged habitat units.

| | Caged | Uncaged |
|---|---|---|
| Mean Losses per day | 0.28% | 0.41% |
| 95% Confidence Limits | 0.0 - 0.40 | 0.0 - 0.57 |

The differences in the proportions of starfish lost from uncaged units and uncaged units at sites 2 - 9 showed no significant positive correlation with the total number of occurrences of benthic feeding fishes (Table 6.1) in the two adjoining 25 m sections of the experimental area (r = .38, p = 0.17, one-tailed). Nor was there a significant correlation between differences in proportion lost and total number of occurrences of commercially exploited species (the four *Lethrinus* spp. and *Cheilinus undulatus*; r = 0.15, p > 0.35, one-tailed).

**Feeding experiments**

At nine of the 16 sites at Bowl Reef, one or more starfish was taken into a fish's mouth. Individual *L. miniatus* also investigated juveniles by blowing water at them but without taking them into their mouths at another two sites. One or more juvenile crown-of-thorns starfish was eaten on three occasions, but on no occasion were all the available juvenile *A. planci* eaten. Individual starfish were often mouthed and spat out by several fish before being swallowed. *Lethrinus miniatus*, *L. atkinsoni* and *Monotaxis grandoculis* mouthed juveniles, but starfish were only swallowed by the two *Lethrinus* spp. In total, eight were swallowed in 61 opportunities (13%). Only one (1.6%) of an equal number of *F. elegans* was swallowed.

Lethrinids came close (<2 m) to the starfish in four trials at Davies Reef. In only one trial did a *L. miniatus* eat the ophiuroid. The same fish blew water at one juvenile *A. planci* without taking it into its mouth.

## Discussion

The main findings of this study are two-fold: first, when small juvenile starfish were presented in a semi-natural setting in an area where suspected fish predators were present, losses attributable to predation were low: an order of magnitude less on average than the level that population models suggest would be important in population regulation. Second, when small juvenile *A. planci* were made unnaturally accessible to the putative predators, some (though never all) juveniles were consumed.

The choice experiments at Bowl Reef showed that lethrinids will eat juvenile *A. planci* under certain circumstances. The small proportion consumed and the number of times starfish were tried but rejected before being swallowed suggests that juvenile *A. planci* are not a favoured food. The ophiuroids were eaten at nearly every presentation at Bowl Reef, so the fish were not all satiated.

This study was designed to estimate predation rates on juvenile starfish in the field. McCallum (1988) suggested that a predation rate of 1.5% of individuals per day would be significant for population dynamics of *A. planci*, as this would certainly hold starfish populations below outbreak levels. In this study I estimated predation on juvenile *A. planci* in one area of Davies Reef, the mean predation rate by all animals excluded by the cages was 0.13% of individuals per day. The mean predation by exploited fish species can not have been greater than that. The only similar data is from a study by Keesing & Halford (1992) who measured mortality of smaller (mean = 16 mm diam.) cultured *A. planci* at another site at Davies Reef 15 mo. previously and also found little effect of predation. They exposed five batches of 10 starfish for 13 days in boxes of rubble without cages and recorded no mortality, though 11 starfish emigrated. These data represent the situation in one place at one time and so should be generalised with caution. They do suggest that fish predation at Davies Reef around the time of this study was light.

The finding that predation rate was low in the experimental situation is robust statistically because of the power of the experiment. The wider relevance of the experiment depends on how well the experimental procedure conforms to juvenile biology. Very little is known about the behaviour and distribution of juvenile *A. planci* in nature. Small juveniles (< 50 mm) have generally been found under rubble in the day, sometimes buried to 30 cm, and at a variety of water depths from the intertidal reef flat down to 15 m on exposed reef fronts and in protected areas (Moran et al. 1985; Yokochi & Ogura 1987; Zann et al. 1987, 1990; Doherty & Davidson 1988; Sweatman pers obs), though some have been found in the bases of living coral colonies (Pearson & Endean 1969). During daylight, the experimental starfish were completely hidden in the habitat units. When the habitat units were checked after about 2 weeks, there was evidence of tissue having been eaten for some centimetres up from the base of the staghorn corals, showing that juveniles came out at night to feed as has also been observed in nature (J. Keesing, pers. comm.). Juvenile *A. planci* eat coralline algae initially, so may remain continuously hidden in rubble or reef cavities. Laboratory observations suggest that they begin to feed on coral at the age of about six months (10 mm diameter) (Yamaguchi 1974) at which point they must spend time on the surface of the reef, at least at night. On this basis it is reasonable for substantial numbers of juveniles to become available to nocturnal fish predators in an area over a short period. In summary, the experiment was compatible with what little is known of the ecology of juvenile *A. planci*.

This experimental design did not include any controls for the effects of cages. The results of the comparison of mortality on caged and uncaged habitat units would be erroneous if cages caused non-predatory mortality or emigration from caged habitat units that compensated for the predatory mortality on uncaged units. The most likely caging artefacts were shading and reduced water flow leading to sedimentation. These could adversely affect the shelter characteristics of the units and the health of the coral food supply, which might promote emigration. There was no obvious reduction in shelter by sediment except at Site 5 where both habitat units were built on very loose sand. Both units subsided a little with the activities of *D. perspicillatus*. The only evident mortality of coral colonies was due to feeding by the experimental juveniles and food was maintained in excess. Statistical significance aside, the upper 95% confidence limit for losses from all sources (predatory and non-predatory mortality plus emigration) for units without cages (Table 6.3) was less than half the predicted biologically significant level of predatory mortality alone (about 1.5% of individuals per day [McCallum 1988]). Potential caging artefacts were not important to my conclusion.

The density of putative predators at the experimental site ranked low among values reported by Ormond et al. (1990). The experimental area was approximately 200 m long, so lethrinids occurred at about one third of the hypothetical density (Table 6.1) required to control a large recruitment of starfish in one population model (Ormond et al. 1990). Davies Reef is open to fishing and populations may be low for that reason, though there are no relevant data. Note that one third of the predator density corresponded to mean losses due to predation of about ten percent of the biologically significant predation rate estimated by McCallum (1988).

Davies Reef has had elevated densities of adult *A. planci* since 1987. If the predator removal hypothesis is true, this implies that predator populations have been inadequate to control the starfish populations in the past. From back calculations based on spine banding (Stump & Lucas 1990), most of the population at Davies Reef settled early in 1985 and 1986 with minor pulses early in 1987 and 1988 (R. Stump, pers. comm.). At the time of the experiment it was 3.5 years since the youngest identifiable cohort of starfish was the size of the experimental animals. Given the variability in recruitment to reef fish populations, no conclusions can be drawn about predator populations at the time and place of the experiment.

A less artificial test of the role of fish predators in the population dynamics of *A. planci* would involve quantitative studies of gut contents of potential predators from areas where high densities of juvenile starfish occurred naturally. This could be combined with values for gut transit times (Section 4) to estimate rates of consumption. *Per capita* predation rates could then be estimated from the densities of starfish and of predators. Concentrations of natural juveniles are rarely found; studies using laboratory reared juveniles offer an alternative approach, which in this case did not support the predator removal hypothesis. Whatever approach is used, estimates of predation rates are required from a number of locations, particularly reefs that are closed to fishing, before any general conclusions may be drawn.

**NOTE**: A similar experiment was set up at Bowl Reef (18-080) on 3 February 1993 in a back reef area of low density staghorn thickets on sand (see Fig 6.2). Bowl Reef is closed to fishing and lethrinids of several species including *Lethrinus miniatus* were more common in this experimental area than at Davies Reef. When I returned a month later, all except one of the cages had been dislodged and had demolished the caged habitat units, and sometimes the nearby uncaged units as well, in the process. Very few juvenile *A. planci* could be found as a result and no further experiments were possible. The site at Bowl Reef was subject to stronger currents than were found in Davies lagoon and more pegs were used to secure the cages initially. Cyclone "Oliver" passed southwards in the Coral Sea in that period so there may have been storm swells.

In summary, Bowl Reef is a very suitable site for such experiments, but because of its exposed location, cages need to be secured very firmly.

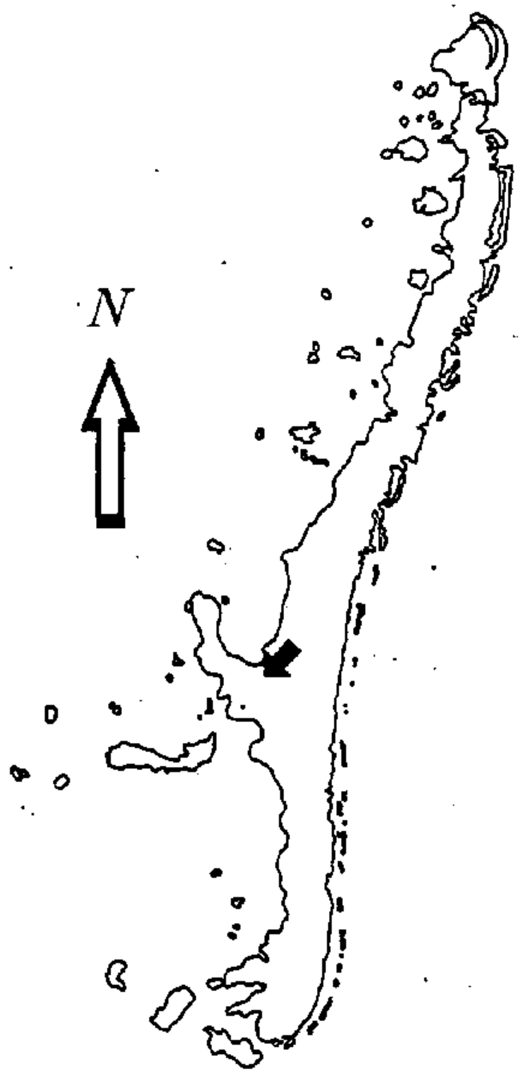


**Figure 6.2:** Map of Bowl Reef showing the experimental site.

## 7: Searches for juvenile *A. planci*

### Summary

Concerted searches were made at six reefs in the study but very few juveniles were found.

### Introduction

Current versions of the predator removal hypothesis hold that settled juveniles will be most susceptible to fish predators (McCallum 1988, Ormond et al. 1990). Tests of the hypothesis require estimates of predation rates when juveniles occur at high densities and evidence that fishes are significant predators, so finding areas with high natural densities of juveniles would allow many relevant observations. Early in the project I invested considerable effort in trying to locate concentrations of juveniles. I surveyed three reefs near Townsville that were considered most likely to have concentrations of juveniles and I made three trips to investigate reports of sightings of juvenile *A. planci*.

#### Surveys of reefs near Townsville, October 1991

I surveyed reefs near Townsville simply for ease of access and economy of ship time. The three reefs that were surveyed were chosen on the following basis. P.J. Moran (pers. comm. and Moran *et al.* [1985]) has found local pulses of recruitment subsequent to the occurrence of high densities of adult *A. planci* in an area, perhaps indicative of self-recruitment. Second, hydrodynamic modelling by Black & Moran (1991) showed good correspondence between initial sites of outbreaks on reefs and predicted areas of reefs where neutrally buoyant particles should be retained under hydrodynamic conditions typical of the summer spawning period. Small juveniles feed on coralline algae and may remain well hidden in areas of rubble, but juveniles in the 1+ age class that are starting to feed on coral are easier to find because they leave small feeding scars. In late 1991, the highest densities of 1+ individuals should have been in retention areas on reefs that supported high densities of adults in the 1989-90 summer spawning season. These included Davies Reef (18-096), Lynch's Reef (18-091) and Little Broadhurst Reef (18-106). Models were not available for these reefs at that time, but predicted retention cells for reefs in the region generally are on the N and S faces (K. Black, pers comm.). Searches were concentrated in these area of the three reefs. Searching consisted of a dive team of three people moving systematically along the reef edge looking for areas of rubble. Superficial pieces of rubble were turned over and examined for juveniles. Searches were generally limited to <8 m depth to avoid decompression problems.

In eight days of diving on Davies Reef (N & NE), Lynch's (NE & SE) and Little Broadhurst (N & S), only two juvenile *A. planci* were found: a 15 mm individual at 8 m under rubble on the north face of Davies and a 105 mm individual at 18 m on surface of rubble covered with coralline algae on the south face of Little Broadhurst. When each juvenile was found, searching effort was redoubled in the immediate area, but no additional animals were located.

### Rib Reef, May 1991

In April 1991, a member of a party from AIMS who was surveying permanent quadrats for fish recruits at Rib Reef (18-032), found two juvenile *A. planci* measuring 7.5 and 14 mm. One came from a marked site (D. Williams' Site III) which is on the false front of the reef in front of the light, the second came from a group of bommies near where the best anchorage is. The diver who found both animals was a volunteer with little experience of reefs. I made a day trip on the Queensland National Parks patrol boat *Stylaster*. Four divers spent one dive turning over rubble near Williams' study site but found no juveniles. Similarly, no animals were found in a dive at the bommies behind the reef.

### Hardy Reef August 1991

In July 1991, the AIMS crown-of-thorns survey team reported high densities of juveniles along the wall of Hardy Reef next to Hook Reef. In August 1991 I made a trip to Hardy Reef to examine the possibilities for experimental work. Twelve person-days of systematic searching (3 dives per day) along the channel wall produced 26 large juvenile *A. planci* 11 - 20 cm in diameter. The animals were scattered so the collection rate was uneconomical to provide subjects for experimental work. All individuals were in shallow water (3 - 4 m) just below the reef crest and all were feeding on staghorn *Acropora*, a habitat that could be reproduced easily in experiments elsewhere.

### Bowl Reef April 1993

Two small *A. planci* were collected in the course of experimental work at Bowl Reef (18-080) in early February (12 cm) and early March 1993 (8 cm) near the site of the second predator exclusion experiment (Fig 6.2). The demise of the cultured starfish at AIMS in early March meant that an alternative source of juveniles was needed for any further experiments. The site was revisited in late April and four divers searched the general area intensively including making night dives. No *A. planci* were found.

## 8: Implications of the results of this project for the Predator Removal Hypothesis

This project has found little evidence to support the predator removal hypothesis. A concerted effort found no evidence that lethrinids, the most likely commercially exploited taxon, ate adult Crown of thorns starfish when these were available. While the sample size was larger than in some previous studies, low rates of predation might still not have been detected. This study differed from previous gut analyses in that the fishes were collected from the vicinity of active starfish outbreaks. This continues a pattern of complete lack of direct evidence that human activities have significantly reduced predation on adult *A. planci.*

Most current versions of the predator removal hypothesis concern predators of juvenile *A. planci* . To date all evidence has been circumstantial and correlative because of the great lack of information on the ecology of juveniles. Two findings of the study are relevant here: *L. miniatus*, the favoured putative predator does appear to do most feeding at night, which is the only time that small juveniles are likely to be accessible to fishes. However, when small juveniles were made artificially accessible to these fishes both in aquaria and in the field, lethrinids appeared to be unenthusiastic predators.

The ideal approach to testing this hypothesis would involve experimental observations and manipulations of predation on natural juveniles at outbreak densities to assess both the total predation rate and that attributable to exploited fishes. A complementary approach would be to assess predation rates from gut contents of commercially exploited fishes that had the opportunity to prey on outbreaks of juveniles, though on their own such estimates suffer from propagation of errors. The main problem has been a lack of opportunity: outbreaks have very rarely been detected before the starfish were adults. A second problem is that juveniles grow very rapidly once they begin to feed on coral, so experimental programs must be implemented rapidly. Very few juveniles of any kind were found in searches made during this study.

An alternative approach is assess predation using cultured juvenile starfish placed in semi-natural situations. The scarcity of information on the ecology of juveniles under natural conditions, particularly habitat preferences and behaviour, means that this approach requires caution because of the possibility of making the experiment unrepresentative of the natural situation. One experiment at one carefully chosen site did not support to the predator removal hypothesis: total predation rate was low compared with the critical values suggested by population models. Predation by exploited fishes presumably constituted only a fraction of that total. The experiment was conclusive in that it had a high probability of detecting low predation rates had they occurred. This approach must be repeated at several sites before any generalisations can be made.

**Recommendations for future research:**

Predator exclusion experiments in the field with cultured juvenile *A. planci* offer the most reliable approach for assessing predation rates. At least one more and preferably several more sites with high densities of commercially exploited fishes would be required to claim generality. It may be possible to say conclusively that fish predation is not important if future predator exclusion experiments also find low predation rates. At least one suitable site exists at Bowl Reef which is closed to fishing.

It is important to follow up all reports of natural occurrences of juvenile *A. planci* because these provide opportunities to gather general ecological information such as habitat preferences, prey preferences, activity patterns, movement patterns which are important for designing realistic tests of the hypothesis. If juveniles are detected over some area, then a fishing program could give the first direct evidence of natural predation by commercially exploited fishes as well as an estimate of predation rate. In the ideal situation, predator exclusion experiments may be possible using natural juveniles in their natural habitat. The rapid growth rate of juveniles means that research must be implemented rapidly.

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