WORKSHOP SERIES No 18

The Possible Causes and Consequences of Outbreaks of the Crown-of-Thorns Starfish

Edited by
Udo Engelhardt
and
Brian Lassig

Proceedings of a workshop held in Townsville, Queensland,
Australia, 10 June 1992
at the Sheraton Breakwater Casino Hotel

GREAT BARRIER REEF MARINE PARK AUTHORITY
CROWN-OF-THORNS STARFISH RESEARCH COMMITTEE

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Great Barrier Reef
Marine Park
Authority

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Contributed papers

Preface

The following papers and abstracts were presented at a workshop on *"The Possible Causes and Consequences of Outbreaks of the Crown-of-thorns Starfish"*, held on 10 June 1992 in Townsville, Australia. The workshop was hosted by the Crown-of-thorns Starfish Research Committee (COTSREC) and the Great Barrier Reef Marine Park Authority (GBRMPA) with a view to:

- Presenting recent research findings about the crown-of-thorns starfish relevant to determining the possible causes and consequences of outbreaks;
- Reviewing the current status of the COTSREC research program; and
- Discussing and recommending possible future research directions.

Selected papers from the workshop held the previous year appeared in volume 43/3 of the Australian Journal of Marine and Freshwater Research which has been reprinted under the title *"Crown-of-thorns Starfish on the Great Barrier Reef: Reproduction, Recruitment and Hydrodynamics"*, C Johnson (ed).

Papers in this proceedings represent projects funded by the Authority through the COTSREC research program over the last three years. During that time Professor John M Swan has acted as Chairman of the Crown-of-Thorns Starfish Research Committee. Professor Swan also chaired the Authority's previous crown-of-thorns starfish advisory committee (COTSARC) from 1985 to 1989. He has been a major influence on the direction and conduct of crown-of-thorns starfish research for about 7 years. It is with deep regret (from all parties involved) that Professor Swan has decided to stand aside from his position because of personal and family commitments. The papers of this proceedings (together with others before and yet to come) stand as testimony to his drive, dedication and global perspective. The following introductory paper demonstrates some of these qualities. Thanks John.

Brian Lassig
Co-ordinator Crown-of-Thorns Starfish Research Program
Great Barrier Reef Marine Park Authority

Weather, climate and starfish populations

John M Swan
Chairman, COTSREC

The weather-climate dilemma is familiar. Over days or weeks the weather patterns can vary widely, especially in temperate zones. Melbourne has four seasons - often all on the one day.

But how do we assess climate, and especially climate change, within this envelope of weather variability? When finally do we conclude from a succession of hot days, or hot years, that, yes, the world is warming, the climate is changing? This is the classic problem of time scales, and it is one that concerns ecologists as well as meteorologists. When (and how) does "natural" biological variability over a short timeframe lead to a "cataclysmic" event such as a population explosion or a species extinction over a much longer time frame? What is short and what is long?

Perhaps one of the most valuable decisions made by COTSREC and its predecessors was to support regular annual monitoring of a large number of reefs over a wide extent of the Great Barrier Reef (GBR). It is not always easy to persuade scientists that "routine monitoring" is sometimes more worthy of funding than the exploration of an exciting and novel idea. But amid all the controversy surrounding crown-of-thorns starfish (COTS) outbreaks, it was clear that only a long-maintained record of coral cover, starfish densities, coral destruction by other agencies (cyclones, coral bleaching, *Drupella*), and the rates of coral recovery after damage, could provide a basis for ecological understanding of the COTS phenomenon. Further extension of this record will include water quality parameters and the densities of certain fishes.

Weather and climate have very different time scales. What are the time scales of COTS outbreaks? Are we observing a unique, grossly exceptional event with human causes? Or are the outbreaks, when viewed on a long time frame, episodic events which are a part, possibly an important part, of the natural history of coral reefs ?

The pattern of outbreaks of crown-of-thorns starfish along the GBR since 1966 has now been well documented and analysed (Moran *et al.* 1992). Population models have been developed on the basis of hydrodynamics, larval dispersal and juvenile recruitment (Scandol and James 1992, James *et al.* 1990, Dight *et al.* 1990a, b). Johnson (1992) has well documented the hypotheses proposed to explain causality, and especially the underlying recruitment processes. These are that primary outbreaks arise from (1) mass settlement of larvae emanating from "natural" stochastic events independent of anthropogenic interference, (2) mass settlement as a result of terrestrial runoff enhancing larval survival, (3) increased post-settlement survival as a result of reduced predation rates on juvenile and sub-adult starfish, and (4) aggregation of adult animals of a variety of ages.

But when is a primary outbreak big enough to initiate a wave of subsequent and expanding secondary populations? Here we encounter another problem facing the statistician. Predicting the frequency of "exceptional" events is one thing, predicting their intensity is quite another. There is a strong tendency for individuals and communities always to assume that the hottest recorded day, the largest flood, the most powerful earthquake or the biggest plague of starfish is somehow a true maximum. But the very next such event might dwarf the previous "maximum" by a power of 10, or more. How big is big?

This concern is no excuse for doing nothing. In the long run, even more devastating starfish irruptions might well occur on coral reefs than those recorded around the Indo-Pacific over the last 30 years. But as Lord Keynes was fond of saying "in the long run we are all dead". If we want to understand and preserve coral reefs, we should be conservative in our definitions of "exceptional events", and try to understand them.

This is where the problems start for managers. What level and range of understanding of the COTS phenomenon is required before direct intervention would be justified? How "serious" does a problem have to be before the clamour to intervene is irresistible? Can we indeed "fight these infestations"?

Preliminary findings of a long-term study by Leon Zann of GBRMPA has now shown that COTS outbreaks since the 1950s have occurred on reefs throughout the Pacific and have been a common feature of coral reefs rather than rare catastrophes. The outbreaks have affected reefs separated by thousands of kilometres. Zann suggests that there is a link between outbreaks and ocean-scale influences rather than separate independent local causes. But his study also indicates that outbreaks are often more serious on reefs affected by human activity than on undisturbed reefs. So while outbreaks may be "natural", their intensity, and hence the degree of damage to the coral, could well be exacerbated by anthropogenic factors such as discharge of sewage from towns or nutrient runoff from agricultural land. The management of water quality factors is certainly conceivable and is now under intensive study within the GBRMPA.

In view of the common belief that the remote islands of the Pacific are still pristine and idyllic, it is sad to learn from a recent article (Zann 1992) that there are now many reefs within the island systems in which population pressure, fishing pressure, terrestrial runoff and pollution are extreme. Suva, Fiji's capital, has the highest concentrations of tributyl tin of any port in the world. Pagopago, the capital of American Samoa, has very high levels of heavy metals and fishing has been banned in the harbour area. Apia, Western Samoa, has high siltation, nutrients, eutrophication, faecal bacteria etc, and the adjacent reefs have structurally and functionally collapsed. The list goes on ... Within the GBR the population pressures are generally low in magnitude and, according to Zann, it has so far not been possible to establish any clear evidence of human impacts through experimentation and monitoring. But studies must certainly be continued.

I would like to pose a final question in relation to the management of complex ecosystems. Certainly we must try to eliminate gross human disturbance and particularly the input of noxious chemicals and high levels of nutrients. But if we can be satisfied on this score, then given the diversity and resilience of coral reefs, would we not be better advised to allow nature to restore any "imbalances" (COTS predation, cyclone damage, coral bleaching, etc) and do any healing that may be required? Culling the starfish seems to this observer to be highly problematic.

Some two years ago at a meeting of the GBR Consultative Committee I drew an analogy between COTS damage to coral reefs and the destruction of trees in an African National Park by herds of elephants. Another elephant story has come my way. Trevor (1992) has described how the combined impact of drought, floods and elephants had destroyed most of the vegetation that fringed the Tsavo River in Kenya a decade earlier. The call came to cull the elephants "to save the park". But particular local conditions made this "solution" impossible to carry out. The result has been, not the wholesale destruction of the Tsavo National Park, but a new lease of life. The natural cycle has now reached the dense bushland phase that people remember from the fifties. And the evidence is that it was the elephants, not humans, that created the conditions for regeneration. Indeed, Trevor's article is entitled Elephant as Architect. I recommend it to all my crown-of-thorns colleagues.

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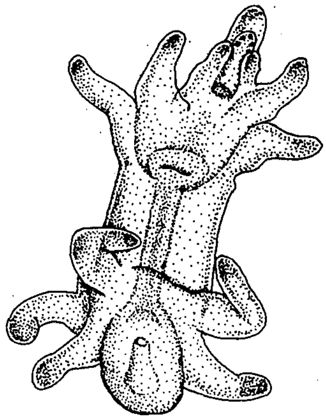
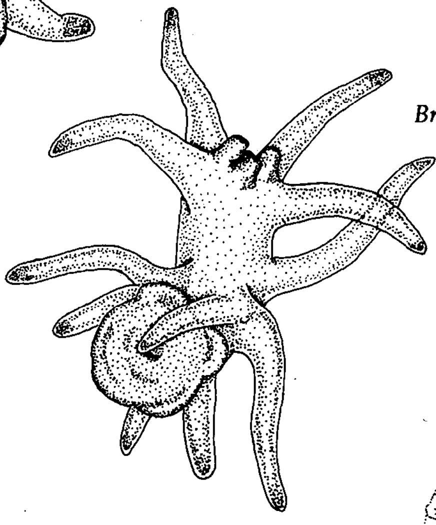
PROGRAM AND LIST OF PARTICIPANTS



Bipinnaria larva



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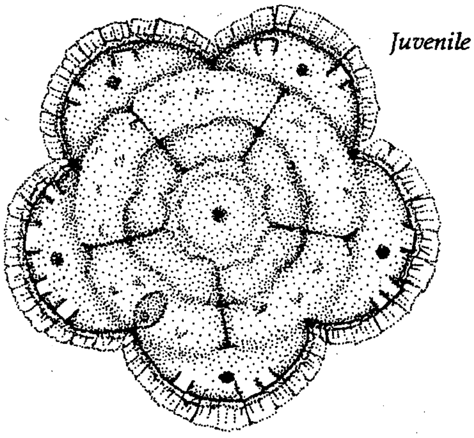

Juvenile Starfish

Program

Objectives of the workshop:

1. *To present recent research findings about the crown-of-thorns starfish relevant to determining the possible causes and consequences of outbreaks.*
2. *To review the current status of the research program.*
3. *To discuss and recommend possible future research directions.*

WEDNESDAY 10 JUNE 1992

0830 **Opening Address**
Mr Graeme Kelleher (Chairman GBRMPA)
Prof John Swan (Chairman COTSREC)

SESSION 1: THE POSSIBLE CAUSES OF OUTBREAKS

*(Chair: **Dr William Gladstone** / GBRMPA)*

0845 "Seasonal changes in fertility and fecundity in *Acanthaster planci*".
Dr Russ Babcock & Mr Craig Mundy (AIMS)

0905 "Resource availability to the larvae of the crown-of-thorns starfish in Great Barrier Reef waters: an overview".
Dr Tenshi Ayukai (AIMS)

0925 "Is *Acanthaster planci* able to utilise dissolved organic matter (DOM) to satisfy the energetic requirements of larval development?".
Dr Ove Hoegh-Guldberg (USYD)

0945 "*In situ* rearing of crown-of-thorns larvae."
Mr Ken Okaji (JCU)

1005 "Field measurement of survival rates of juvenile *Acanthaster planci*: techniques and preliminary results".
Dr John Keesing & Mr Andrew Halford (AIMS)

1025 "An experimental investigation of the ability of adult crown-of-thorns starfish to survive physical damage".
Dr Hugh Sweatman & Mr Ian Butler (JCU)

1045 **MORNING TEA**

1100 "Are crown-of-thorns starfish populations chaotic ? Would it matter if they were ?
Dr Hamish McCallum (UQ)

1120 "Are the hydrodynamics guilty of causing or stimulating outbreaks of crown-of-thorns starfish on the Great Barrier Reef ?"
Dr Kerry Black et al. (VIMS)

1140 "Some perspectives on the *Acanthaster* phenomenon".
Dr Leon Zann (GBRMPA)

1200 "Life history characteristics of *Acanthaster planci* (L.) populations, potential clues to causes of outbreaks".
Mr Richard Stump (JCU)

1220 ***Discussion on the possible causes of outbreaks.***

1245 **LUNCH**

SESSION 2: THE CONSEQUENCES OF OUTBREAKS

*(Chair: **Dr Leon Zann** / GBRMPA)*

1345 "*CotSim*: Scientific visualisation and gaming-simulation for the *Acanthaster* phenomenon".
Mr James Scandol (JCU)

1405 "Consequences of outbreaks: relationships between spatial scales of outbreaks and temporal scales of recovery".
Dr Craig Johnson & Ms Ann Preece (UQ)

1425 "Long-term response of herbivorous fish to crown-of-thorns starfish outbreaks".
Mr Tony Hart (AIMS)

1445 "Effects of *Acanthaster* predation on bioerosion: design and preliminary results".
Ms Barbara Musso (JCU)

1505 ***Discussion on the consequences of outbreaks.***

1530 **AFTERNOON TEA**

SESSION 3: MANAGEMENT OPTIONS AND THE FUTURE OF THE COTS PROGRAM

*(Chair: **Mr Simon Woodley** / GBRMPA)*

SUGGESTIONS FOR FUTURE RESEARCH

1545 Measuring settlement rates of COTS larvae.
Dr John Keesing (AIMS)

1555 Future research into predation on COTS.
Dr Hugh Sweatman (JCU)

COTS CONTROLS:

1605 "The history of crown-of-thorns starfish controls on the Great Barrier Reef and an assessment of future needs for controls".
Dr William Gladstone (GBRMPA)

1620 "A management approach to the COTS question".
Mr Graeme Kelleher (GBRMPA)

1635 "The need for a crown-of-thorns starfish contingency plan".
Dr Brian Lassig (GBRMPA)

1650 ***General Discussion***

1720 **END OF WORKSHOP**

List of workshop participants (*in alphabetical order*):

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Dr Russ Babcock	AIMS
Ms Valonna Baker	AIMS
Ms Debbie Bass	AIMS
Dr Kerry Black	VIMS
Mr Jon Brodie	GBRMPA
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Mr Udo Engelhardt	GBRMPA
Dr William Gladstone	GBRMPA
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Mr Dave Johnson	AIMS
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Ms Barbara Musso	AIMS
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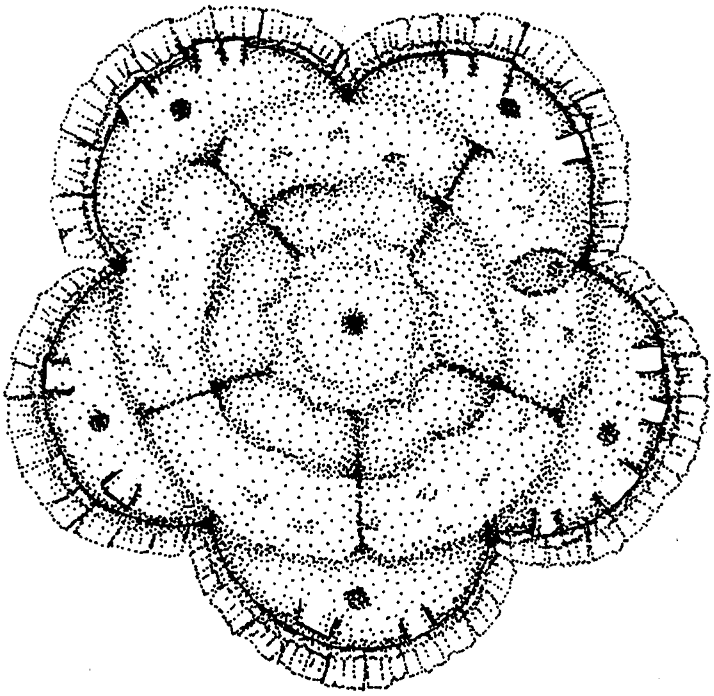
Mr Simon Woodley	GBRMPA
Dr Leon Zann	GBRMPA

Institutions and organisations:

Australian Institute of Marine Science (AIMS)
Crown-of-Thorns Starfish Research Committee (COTSREC)
Great Barrier Reef Marine Park Authority (GBRMPA)
James Cook University (JCU)
Queensland Department of Primary Industries (QDPI)
University of Queensland (UQ)
University of Sydney (USYD)
Victorian Institute of Marine Sciences (VIMS)

SESSION 1

THE POSSIBLE CAUSES OF OUTBREAKS



Juvenile Starfish-Early post-settlement stage

Chair: Dr William Gladstone (GBRMPA)

Seasonal changes in fertility and fecundity in *Acanthaster planci.*

RC Babcock and CN Mundy
Australian Institute of Marine Science,
PMB No. 3, Townsville MC QLD 4810

Abstract

Changes in fecundity, measured as gonad index, and fertility, measured as fertilisation rate, were monitored over the recorded spawning season of A. planci at Davies Reef on the central Great Barrier Reef (GBR) from 1990-1992. This starfish has been observed spawning in the field from December to January on the GBR, with most observations being made in January. In contrast both gonad index and fertility peak early in the season, declining to low levels by late January. These observations indicate that the majority of successful reproductive events will take place early in the spawning season, before the onset of the monsoonal wet season. The timing of spawning may need to be considered in evaluating the importance of terrestrial runoff as a possible causal factor in outbreaks on the GBR.

Introduction

Since the beginning of debate concerning outbreaks of the crown-of-thorns starfish the potential importance of reproductive phenomena in population fluctuations has been recognised (Cheney 1974). For example Vine (1973) considered variations in fertilisation success to be a central feature of the natural causes hypothesis. Since that time other hypotheses have also been based, at least in part, on reproductive events. The terrestrial-runoff hypothesis (Birkeland 1982) suggested that if populations of A. planci spawned at around the time of major storms which washed large amounts of nutrients into the sea, more larvae would survive than might normally be the case, and that this could result in the establishment of an outbreaking population. In order to effectively evaluate this hypothesis it is necessary not only to have records of weather and the occurrence of outbreaks, but also to possess certain critical biological information about the crown-of-thorns starfish. For instance it is important to know whether the larvae of *Acanthaster* are actually limited by lack of food before we can judge whether increased nutrients or algae can significantly influence their survival in the plankton. Research by Olson (1987) indicated that, in the waters of the Great Barrier Reef lagoon, lack of food is not a limiting factor in the survival of larvae to settlement. In more oligotrophic seas nutritional factors may be more critical, but this question has yet to be addressed experimentally. It is also important to know the length of larval life and the timing of spawning in relation to the timing of terrestrial runoff, since the availability of nutrients input into the reef system may be limited in space and time (eg. Furnas and Mitchell 1986, for central GBR).

In the course of research conducted on the GBR into fertilisation rates, larval nutrition and other hypotheses concerning *A. planci,* it became apparent, that as the spawning season progressed, raising numbers of larvae through to settlement became more and more difficult (Olson, *pers. comm.*, Moran, *pers. comm.*, Keesing, *pers. comm.*). Fertilisation rates also appeared to decline. This study was designed to address specific questions about the reproduction and development of *A. planci* which would improve our understanding of general aspects of the crown-of-thorns phenomenon. We conducted a series of experiments to determine whether there was a systematic decrease in fertility and egg viability in *A. planci* through the known reproductive season. Gonad index and observational data were collected in parallel with these experiments. The results of this research were then used to provide a more detailed assessment of the relationships between terrestrial runoff and numbers of crown-of-thorns starfish on the GBR.

Materials and Methods

Gonad indices

Animals were collected at irregular intervals between August 1990 and January 1992. Sampling was infrequent during the winter non-spawning period, but was as frequent as once per week during the spawning season. At each sampling 10 male and 10 female animals were collected and dissected to provide data for gonad indices. Gonad index was determined as total weight of gonads divided by total wet weight of starfish (water was allowed to drain from surface of animals for 3 seconds before weighing). During the winter the total gonad weight was determined from gonad weights of three arms. In this procedure gonads from each of the three arms were weighed individually and their weights averaged. The average weight of gonads was then multiplied by the number of arms, providing a value for total gonad weight. During the peak of spawning season (Nov. - Dec.), all gonads were dissected from starfish, since ripe gonads could not be assigned to a particular arm with a high degree of confidence.

Fertilisation rates and developmental success

Fertilisation rates and developmental success were examined on seven occasions between October and the end of January during the 1991-92 spawning season. Starfish were collected from Davies Reef and all experiments were conducted within five days of collection. Five male and five female starfish were identified by syringe biopsy for each experiment. A small amount of gonad (1-3 gm) was dissected from each animal and placed in 50 ml $1x10^{-4}M$ 1-MeAde in seawater for 30 minutes. At the end of this time the gonads were removed from the solution and the concentration of gametes remaining (eggs and sperm) was determined in each of the containers. Counts of sperm were obtained using haemocytometers, while for eggs small plankton sorting trays were used to count aliquots from the original suspension. These data were then used to produce suspensions of eggs and sperm at the same concentration for each animal. The desired concentrations were 3x 10^3 ml^{-1} sperm and 3x 10^2 ml^{-1} eggs, levels which where designed to produce high levels of fertilisation (J Benzie, *pers. comm.*), yet not to create an oversupply of sperm which would result in polyspermy or swamp any differences in sperm viability. The design of each fertilisation trial was an orthogonal (5x5) matrix which resulted in sperm from each male being crossed with eggs of each female. Controls for sperm contamination were prepared using eggs alone with no additional sperm added. For each cross eggs, or eggs and sperm, were placed into three replicate 20 ml glass scintillation vials. This procedure enabled us to conduct fertilisation trials under conditions which standardised sperm and egg concentrations both among the starfish in each experiment and among the several trials conducted throughout the spawning season.

The proportion of fertilised eggs was scored 2 hours after the addition of sperm. All eggs with fertilisation membranes were scored as "fertilised". Approximately 100-150 eggs were counted. The vials containing the eggs were then resealed and re-counted 24 hours later. Eggs or embryos (100-150) were scored as either "gastrula" if they had developed a definite archenteron, or "non-gastrula", where this invagination was lacking or where fertilisation had not occurred.

All experiments were conducted under laboratory conditions either on land or on board a research vessel. During the course of the season it was noted that fertilisation rates often appeared to be lower during shipboard experiments and accordingly we set up a trial at the end of the season (27 Jan. 1992) in which the normal experimental design was replicated with seawater that had just been brought from Davies Reef, and with local coastal sea water (AIMS aquarium system). The only difference between this paired trial and the other trials was that for each starfish four vials were prepared, two containing reef water and two containing coastal water.

Results

Gonad indices

Gonad indices for the 1991-92 reproductive season peaked between late November and early December (*Fig. 1*). Gonad index values for the population prior to spawning were similar in both years, the only exception being the high values for the population in 1990-91 just before a major spawning. The decline in gonad index took place within one week of a similar drop after spawning in the 1990-91 season, and appeared to be rather more rapid in the second season than during the first season, reaching levels of less than 5% in early January.

The two largest falls in gonad index occurred at the times when the largest spawning events were observed in the population. During the 1991-92 spawning season four spawning events were observed in the Davies Reef population. Spawning was first seen on Dec. 11, at 1630 hr (Eastern Daylight Savings Time). The animal was an isolated female. One hour later two males, part of a group of around 50 starfish, were observed releasing small amounts of sperm. Other starfish in the group were displaying spawning-related behaviour (climbing, arching), but no gametes were released. The following day, Dec 12, one female and eight male starfish were seen releasing gametes at 1930 hr. These animals were part of the group seen on the previous day in which the two males had spawned, and once again many animals which were not spawning were displaying spawning-related behaviour. Since observations on this evening only commenced at 1930 hr it is possible that many of these starfish had ceased spawning before observations began. Further spawning was also seen on the next night, Dec. 13, when a single male was observed releasing sperm at 2030 hr. Spawning-related behaviour among other members of the population was reduced relative to previous nights. Prior to these spawning observations the populations displayed spawning-related behaviour at the same time as a major spawning of several bivalve species was observed (Dec. 10). The only other spawning of *Acanthaster planci* seen at Davies in the 1991-92 season was on Jan. 23. When observation commenced at 2030 hr many starfish were in exposed situations such as at the top of dead staghorn thickets, and two males were seen releasing gametes, though only from gonopores on a few arms. The 1990-91 spawnings have been reported in detail elsewhere (Babcock and Mundy 1992).

Fertilisation rates and development success

Fertilisation rates and development success both declined significantly between mid-October and the end of January (*Fig.* 2). Although they were variable, fertilisation rates were significantly lower for the last experiment (55%) than they were at the beginning of the season (87%). They were also lower for the second and fourth trials, both of which were conducted at Davies Reef. Development success decreased more steadily over the season, from a high of 80%, to around 20% by the end of December and decreasing to 13% near the end of January. Development success from late December to January was significantly lower than for trials earlier in the season.

Direct comparison of fertilisation and development success using Davies Reef and inshore water demonstrated that both fertilisation and development were significantly higher in inshore water (*Fig.* 3). Type of seawater was a major source of variation in both fertilisation and development for experiments conducted throughout the season.

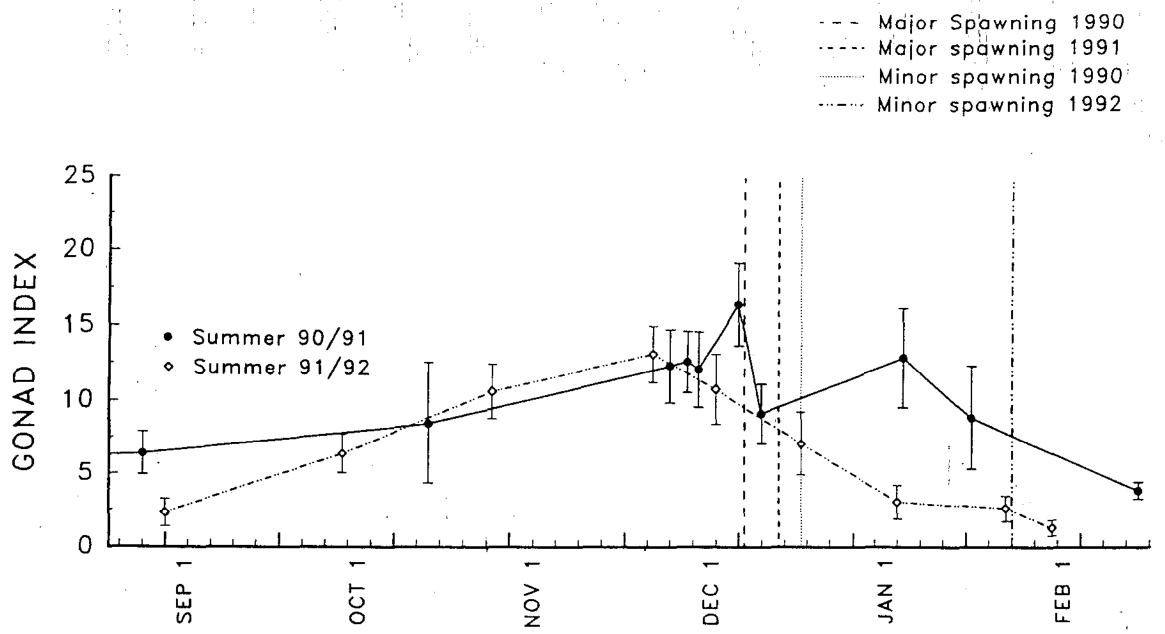


Figure 1: Gonad indices for *Acanthaster planci* population at Davies Reef, 1990-1992. Data are for females and males combined, presented as means and 95% confidence intervals. Vertical lines indicate dates on which spawning was observed at Davies Reef.

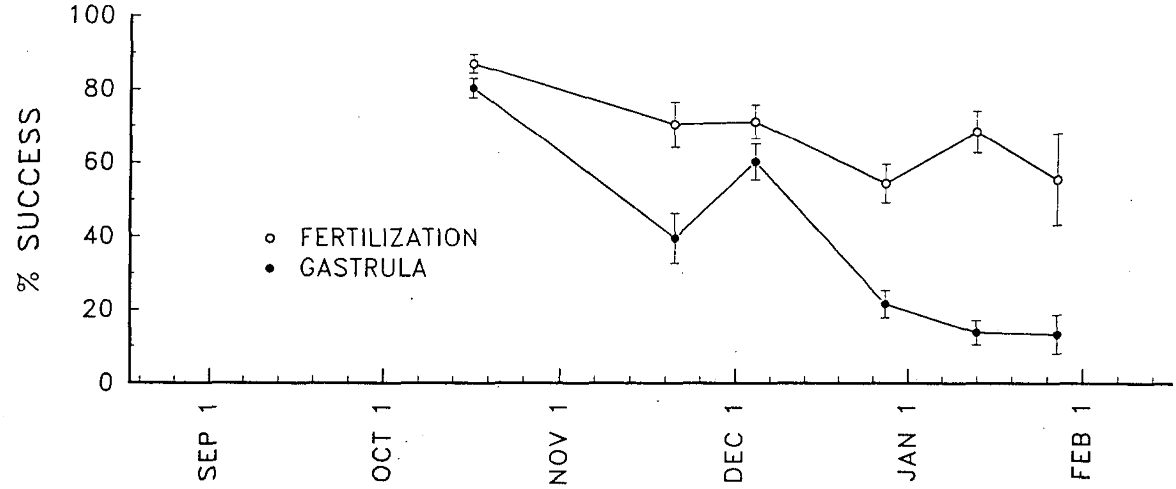


Figure 2: Fertilisation rate and developmental success of *Acanthaster planci* eggs *in vitro*. Data for fertilisation trials are presented as means and 95% confidence intervals. Fertilisation trials marked by asterisks were conducted at Davies Reef. Significance of downward trends in the data over the season were analysed by regression of the means. Slopes were significantly different from zero both for fertilisation rate (slope = -0.27, R-Square = 0.35, $p < 0.01$) and for developmental success (slope = -0.69, R-square = 0.69, $p < 0.01$).

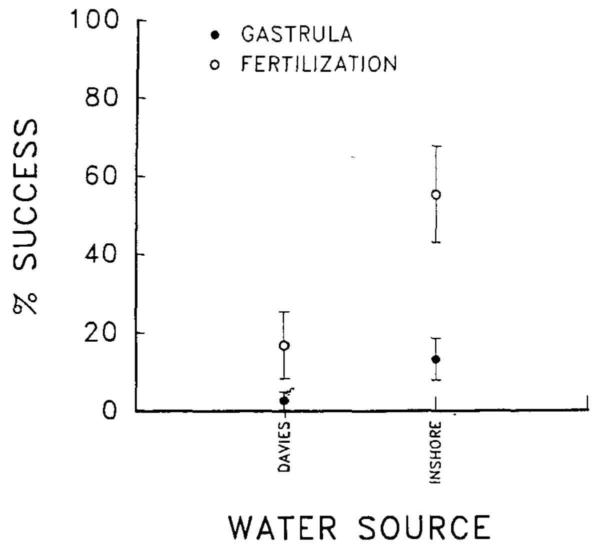


Figure 3: Fertilisation trial comparing seawater from Davies Reef and AIMS seawater system. Means and 95% confidence intervals. Trial conducted 27 January 1992. Differences between water from the two sources were highly significant (T-test; fertilisation T =-5.24, DF = 58, $p < .0001$, development to gastrula T =-3.69, DF = 58, $p < .0005$).

Discussion

Spawning season

Four natural spawnings of *Acanthaster planci* were seen during the course of this study at Davies Reef. Three of these took place during early to mid-December and the fourth was in the latter half of January. The rapid drop in gonad index in the first half of December reflects this pattern in spawning behaviour, and the magnitude of the drop in gonad mass, which is relatively greater in December than in January, indicates that the majority of gametes are likely to be spawned in the first half of the season. There were multiple spawnings in the population, the latest seen on Jan. 23, but later spawnings tended to involve fewer animals and appeared to be less intense. This pattern is reinforced by other observations on the GBR as well as in other parts of the Indo-Pacific. Of the five observations on the GBR involving natural spawnings of more than 10 animals, four took place in the first half of the season (Babcock and Mundy 1992). Populations of starfish from the Ryukyus also displayed the greatest drop in gonad index early in the spawning season, rather than a steady decline over the season (Yokochi and Ogura 1987, Okaji 1991). These observations for *A. planci* indicate that although spawning is repeated and may be spread over several months the bulk of gametes are likely to be released over a much shorter period of time, at least where seasonal temperature variations are marked.

Gamete viability

Seasonal variations in gamete viability were apparent both for fertilisation rate and for the rate of successful development to gastrula. Surprisingly high rates of fertilisation and developmental success were observed in October, well before spawning was observed. At this time seawater temperatures were <26°C, well below the 28°C usually needed before spawning will commence in natural populations (Lucas 1973).

Temperatures at or slightly above this level are optimal for larval survival (Lucas 1973, Yamaguchi 1973). Variation in fertilisation through the season, although largely attributable to artefacts related to the source of experimental seawater, did show a consistent downward trend. A similar but much stronger pattern was evident in the proportion of eggs which successfully developed to the gastrula stage.

The reasons for the differences observed in fertilisation rate and development to gastrula between inshore and reef water remains unclear. It may be due to differences in buffering capacity of the seawater, since pH is well known to affect sperm motility and fertilisation rates for echinoid eggs *in vitro* (Chia and Bickell 1983). Any possible differences in buffering capacity between inshore and offshore water have yet to be examined in detail. In any case the values obtained in this study should be regarded more as an index of fertilisation than as absolute values.

The results of this research indicate that the majority of successful reproduction in *Acanthaster planci* populations on the GBR takes place early in the season, during December. The factors responsible for this are decreased developmental success (and to a lesser extent fertilisation rate) in the latter half of the season, combined with the concentration of spawning activity in the early part of the spawning season. Accordingly, if rainfall is to affect larval survivorship through input of terrestrial nutrients to the marine system, it would be most likely to have a major effect if it fell during the period of greatest larval abundance. Areas of mainland Australia adjacent to the GBR receive their greatest rainfall during the summer months, as part of monsoonal weather activity, but on average the heaviest rain falls in February, well after most of the spawning activity is over. Even in January, the second wettest month, successful larval production is likely to be relatively low. Spawning is most intense, and the probability of successful development are greatest in December however and rainfall during this month is usually relatively low. The population dynamics of *A. planci* on the GBR are therefore most likely to be affected by variations in larval survivorship during the early part of the spawning season.

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Resource availability to the larvae of the crown-of-thorns starfish in Great Barrier Reef waters: an overview

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Abstract

Whether or not resource limitation is important in crown-of-thorns starfish (COTS) larvae has been controversial. Lucas (1982) has suggested that the concentration of phytoplankton in GBR waters is usually too low for COTS larvae to achieve normal growth and development. In contrast, in situ rearing of COTS larvae has shown no evidence of starvation under low phytoplankton conditions common in GBR waters (Olson 1985, 1987). Both Lucas and Olson have suggested the possibility that COTS larvae derive their nutrition from resources other than phytoplankton, i.e. dissolved organic matter (DOM) and bacteria. The study of utilization of these two resources by COTS larvae appears to hold the key to compromise the discrepancy between their results. Results from the present study indicate that free-living bacteria are too small to be utilized by COTS larvae. On the other hand, COTS larvae were able to take up dissolved free amino acids (DFAA) that seemingly represent a large proportion of biologically utilizable DOM in seawater. The carbon budget model developed suggests that, even if the contribution of DFAA is taken into account, the starvation of COTS larvae is likely to occur quite commonly in GBR waters.

Introduction

Over the past decades, vigorous urban and agricultural developments have taken place along the NE Queensland coast. There have been claims that increased human activities may have resulted in a significant increase in concentration of nutrients in Great Barrier Reef (GBR) waters (eg. Bell 1991, Bell and Gabric 1991). Although such claims tend to suffer from the low reliability of the data in earlier days, it has developed into wide concern about the effect of elevated nutrient concentration on the crown-of-thorns starfish (COTS) phenomenon. For instance, in reviewing the literature, Brodie (1992) suggested that heavy nutrient inputs from anthropogenic sources may relax resource limitation of COTS larvae, leading to higher recruitment success and to an increase in adult population size (see Birkeland 1982).

There have been two opposing views with regard to the question of whether resource limitation is important in COTS larvae. Lucas (1982) first conducted laboratory experiments to quantify the effect of phytoplankton concentration on the feeding rate and development of COTS larvae. The extrapolation of Lucas' results to the field has suggested that phytoplankton concentration in GBR waters is far below the concentration where COTS larvae can achieve their normal development. Thus any factors that alleviate the degree of starvation of COTS larvae in the field (eg. the drainage of nutrient-rich terrestrial waters, Birkeland 1982) have the potential to increase their survival rate. In contrast to Lucas' results, the results from *in situ* rearing experiments (Olson 1985, 1987) have shown no evidence of larval starvation under low phytoplankton conditions common in GBR waters. One significant consequence of this controversy is a realisation that COTS larvae may be able to exploit non-phytoplankton resources, such as bacteria and dissolved organic matter (DOM) (Olson and Olson 1989, Birkeland and Lucas 1990). Indeed, some workers have suggested that bacteria (or bacteria sized particles) and DOM make significant contributions to the energy requirements of some echinoderm larvae (eg. Rassoulzadegan and Fenaux 1979, Rivkin *et al.* 1986, Stephens 1988, Manahan 1990). Therefore, until the nutritional spectrum of COTS larvae and the availability of individual resources in the field are fully understood, the degree of resource limitation of COTS larvae or the so-called "larval starvation hypothesis" can not be evaluated adequately.

Ayukai and Hoegh-Guldberg (1992) have recently conducted laboratory experiments to assess the role of bacteria and DOM in the nutrition of COTS larvae. This paper briefly describes the results of their experiments and then overviews existing data on the resource availability to COTS larvae in GBR waters.

Nutritional Mode

Suspension feeding

In common with other asteroid larvae (Strathmann 1971), COTS larvae use a single band of cilia to create feeding currents and capture suspended particles. The maximum size of food particles ingested by COTS larvae is approximately 40-60µm and is limited by the diameter of the oesophagus (Yamaguchi 1973). The lower size limit of food particles, on the other hand, has not fully been studied, probably because of the lack of appropriate methods. This seems crucial if the overwhelming dominance of picoplankton (<2µm, Sieburth *et al.* 1978) in the putative environment of COTS larvae is considered. For instance, photosynthetic picoplankton account for up to 90% of the total phytoplankton biomass, with greater contributions being reported for oligotrophic tropical waters (*cf.* Stockner 1988). Heterotrophic bacteria are usually equal to 10-40% of phytoplankton biomass (Ducklow 1983), but can be greater than phytoplankton biomass in oligotrophic waters (Cho and Azam 1990).

Generally, the feeding rate of zooplankton is determined by measuring the change in cell concentration during incubations (Frost 1972). The reliability of data obtained by this method, however, is often hampered by the low precision of cell counting. Considering such an inherent problem in the cell counting method, Ayukai and Hoegh-Guldberg (1992) determined the feeding rate of COTS larvae by directly counting the number of heat-killed, fluorescence labelled cells (FLC) in the gut of individual COTS larvae after short incubations (<15 min.). This method was developed for the study of bacterivory by heterotrophic flagellates (Sherr *et al.* 1987) and later applied for determination of the feeding rate of larger protozoans and rotifers on microalgae (Rublee and Gallegos 1989).

Table 1 summarises the clearance rate of bipinnaria and brachiolaria larvae feeding on five different types of FLC: ie. *Phaeodactylum tricornutum, Dunaliella tertiolecta,* two strains of coccoid cyanobacteria (unidentified and ACMM 326, the culture collection of the Sir George Fisher Centre, James Cook University) and natural bacteria. It clearly shows the effect of cell size on the clearance rate of COTS larvae. For instance, bacteria were not utilised by COTS larvae. COTS larvae were able to utilise both strains of cyanobacteria, but the clearance rates determined were more than one order of magnitude lower than the clearance rates on larger phytoplankton, *P. tricornutum* and *D. tertiolecta.*

For *P. tricornutum* and *D. tertiolecta,* the clearance rate was nearly doubled from 0.277 - 0.292 ml ind^{-1} h^{-1} for late bipinnaria larvae to 0.493 - 0.635 ml ind^{-1} h^{-1} for late brachiolaria larvae. A similar trend has been reported in the earlier study of Lucas (1982).

Table 1: Clearance rate* of bipinnaria (*Bip*) and brachiolaria (*Bra*) larvae of *Acanthaster planci* on 5 different types of heat-killed, fluorescence labelled cells (from Ayukai & Hoegh-Guldberg 1992). ESD: equivalent spherical diameter, nd: not detected.

		Clearance rate (ml ind^{-1} h^{-1})		
Type	ESD(μm)	Late *Bip*	Early *Bra*	Late *Bra*
Phaeodactylum tricornutum	4.7	0.292	0.437	0.635
Dunaliella tertiolecta	5.1	0.277	0.299	0.493
Cyanobacteria, ACMM 326	1.8	0.013	0.018	0.022
Cyanobacteria, small strain	1.0	0.005	0.007	0.008
Natural bacteria	< 0.8	nd	nd	nd

*Clearance rate = Ingestion rate (cells ind^{-1} h^{-1}) /Cell concentration (cells ml^{-1})

Transepidermic uptake of DOM

Dissolved organic matter is defined as organic matter that passes through filters with a 0.45 μm pore-size (Goldberg *et al.* 1952). In the case of dissolved organic carbon (DOC), its quantity in the oceans is generally thought to be at least one order of magnitude greater than that of non-living particulate organic carbon (POC) and two orders of magnitude greater than that of living POC (eg. Williams 1975, Cauwet 1978). A recent study has even suggested that DOC makes up one of the largest carbon pools on the earth (Martin and Fitzwater 1992).

It is worth noting that the enormous advantage of utilising DOM as an energy source was discussed early in this century (Putter 1909, *in:* Jorgensen 1976). However, DOM should not be regarded as an unlimited energy source for marine invertebrates. Ultrafiltration of seawater has shown that at least 50% of the total DOM is in a colloidal phase (approx. 1-100 nm in size or 500 to 100,000 Daltons in molecular weight, eg. Sharp 1973, Ogura 1974). The majority of such high molecular weight DOM is biologically inert (eg. Iturriaga and Zsolnay 1981, Brophy and Carlson 1989). The classes of DOM, of which the transepidermic uptake has been reported, usually represent less than 10% of the total DOM (Williams 1975).

Since a series of experiments by Stephens and Shinske (1957, 1958, 1961), a growing body of evidence has shown that most of soft-bodied marine invertebrates studied are able to take up DOM through their epidermis (dissolved free amino acids, sugars, fatty acids, acetate and nucleosides, *cf.* Stephens 1988, Welborn and Manahan 1990). In these experiments, radio-isotope labelled substances are most commonly used as tracers. The DOM uptake rate determined by this method, however, is not exactly equal to the net absorption rate, because a sizeable fraction of DOM is excreted at the same time (Johannes *et al.* 1969, Stephens 1988). Nevertheless, it has generally been understood that uptake of radio-isotope labelled substances is a good reflection of net absorption (Manahan *et al.* 1982).

Ayukai and Hoegh-Guldberg (1992) studied DOM uptake by COTS larvae using ^{14}C labelled alanine (amino acid) and glucose (sugar) as tracers. The results of their DOM uptake experiments were described by Hoegh-Guldberg (in this proceedings). Briefly, COTS larvae were able to take up both alanine and glucose. The relationship between substrate concentration and uptake rate could be fitted by the familiar Michaelis-Menten equation. The estimated kinetic parameters (ie. the maximum uptake rate, a half saturation constant) suggested that alanine had the potential to make a significant contribution to the energy requirements of COTS larvae, whereas glucose was relatively unimportant as a nutrient resource for COTS larvae.

Energy requirements

In aerobic metabolism, oxygen consumption is directly related to the amount of food oxidised. Therefore, the minimum energy requirements (= the minimum amount of energy necessary for compensating oxygen consumption) can be estimated by measuring oxygen consumption rates and assuming an appropriate Q_{O2} (respiration quotient) value. Then, if the relationship between food concentration and feeding/assimilation rate is known, it is also possible to estimate the food concentration above which animals can meet the minimum energy requirements and achieve positive growth. This "compensating" food concentration is a basic measure in assessing the resource availability to animals in the field.

In *Table 2*, the minimum carbon requirements of bipinnaria and brachiolaria larvae and the compensating phytoplankton and DFAA (dissolved free amino acids) concentrations were estimated based on the data on the rates of oxygen consumption

(Hoegh-Guldberg *unpubl.*, *in:* Ayukai and Hoegh-Guldberg 1992), feeding and alanine uptake by COTS larvae. Unfortunately, a number of assumptions were made to estimate these values, and at present the validity of some assumptions is not testable. For instance, COTS larvae were assumed not to utilise bacteria. The results of feeding experiments with FLC support this assumption, but do not deny the possibility of utilisation of detritus-attached bacteria, which may account for up to 50% of total bacterial populations in coral reef waters (Sorokin 1974, Moriarty 1979). It is also questionable whether the kinetic parameters determined for alanine uptake can be applied to uptake of other DFAA. Jaeckle and Manahan (1989 a, b) have reported that alanine is among several DFAA that are most readily taken up by larvae. The estimates shown in *Table 2*, therefore, should be regarded as approximate values.

Table 2: Minimum carbon requirements of the bipinnaria and brachiolaria larvae of *Acanthaster planci* and the compensating phytoplankton and dissolved free amino acid (DFAA) concentrations (from Ayukai & Hoegh-Guldberg 1992).

	Minimum carbon	Compensating concentration[b]	
Larval stage	requirements[a] (ngC ind^{-1} h^{-1})	Phytoplankton[c] (µgC l^{-1})	DFAA[d] (µmol l^{-1})
Bipinnaria	2.29	38	1.8
Brachiolaria	7.95	80	4.7

[a] Minimum carbon requirements for compensating respiratory oxygen consumption.

[b] Food concentration, at which the minimum carbon requirements can be met.

[c] Assumptions made to calculate the compensating phytoplankton concentration:
- The percent contribution of picoplankton (<2 µm) to the total phytoplankton carbon concentration (P_{total}, ngC ml^{-1}) is 50% (A) (see *Table* 3).
- Larvae do not utilise picoplankton.
- The clearance rates of bipinnaria and brachiolaria larvae on nanoplankton (>2 µm) are 0.3 and 0.5 ml ind^{-1} h^{-1} (B), respectively (see *Table* 2).
- The assimilation efficiency of larvae feeding on nanoplankton is 40% (C) (Bayne 1983).
- Minimum carbon requirement = $P_{total} \times (A/100) \times B \times (C/100)$

[d] Assumptions made to calculate the compensating DFAA concentration.
- No difference in kinetic parameters among DFAA species.

Resource availability

Phytoplankton

Table 3 shows the average and range of phytoplankton carbon concentration during the

COTS spawning season (October - January) in three areas of the central GBR (the GBR lagoon, mid-shelf and outer-shelf). These data were based on the chlorophyll data obtained during three 1-3 year oceanographic surveys, one of which included measurements of size-fractionated chlorophyll concentration (<2 μm, >2 μm). The conversion of chlorophyll concentration into carbon concentration was made to facilitate direct comparison with the compensating phytoplankton concentration.

Phytoplankton concentration decreases from the GBR lagoon towards outer-shelf area. The comparison of the average phytoplankton concentration in mid-shelf and outer-shelf areas (2.7-9.0 $\mu gC\ l^{-1}$) with the compensating phytoplankton concentration suggests that, in these areas, the energy gains of bipinnaria and brachiolaria larvae from phytoplankton are approximately 7-24% and 3-11% of the minimum carbon requirements, respectively. In the GBR lagoon, the average phytoplankton concentration ranges between 16.8 - 19.2 $\mu gC\ l^{-1}$ and again COTS larvae seem unable to meet even the half of the minimum carbon requirements by utilising phytoplankton. However, it is worth noting that phytoplankton concentration in the GBR lagoon occasionally increases to the level (up to 105 $\mu gC\ l^{1}$), at which both bipinnaria and brachiolaria larvae may be able to achieve positive growth.

Table 3: Summary of the average value and range of phytoplankton carbon concentration[*] ($\mu gC\ l^{-1}$) during the spawning season of *Acanthaster planci* (October - January) in the central Great Barrier Reef. Numbers in parentheses are the percent contribution of picoplankton (<2 μm) to the total phytoplankton carbon concentration.

	GBR lagoon	Mid-shelf area	Outer-shelf area
1975-1978[a]			
Surface layer (0 m)	19.2	10.8	
	3.3 - 82.5	3.3 - 39.0	
Sub-surface layer (7 m)	16.8		
	3.0 - 105.0		
1980-1981[b]			
Surface layer (0 m)		6.6	3.9
		3.6 - 19.2	0.3 - 17.1
Sub-surface layer (10 m)		6.6	4.2
		3.6 - 17.4	1.2 - 16.5
Bottom layer (50 m or bottom)		12.3	9.0
		5.1 - 19.2	0.3 - 61.8
1983[c]			
Surface layer (0 m)		6.9 (50)	3.3 (59)
		1.8 - 15.9	1.8 - 7.2
Sub-surface layer (10 or 25 m)		6.9 (52)	2.7 (67)
		2.1 - 14.1	1.8 - 4.5
Bottom layer (50 m or bottom)		13.8 (41)	7.5 (58)
		5.7 - 48.3	2.7 -16.2

[*] Calculated from chlorophyll concentration using the carbon/chlorophyll ratio of 30 (Parsons *et al.* 1984).

[a] Ikeda *et al.* (1980)

[b] Bellamy *et al.* (1982)

[c] Furnas and Mitchell (1984)

Dissolved free amino acids

DFAA concentration in oceanic waters varies from trace concentrations to 0.15 µmol l^{-1} (*Table* 4). Variations of similar magnitude can be seen also in coastal and reef waters, if the exceptionally high DFAA concentration in Kenyan Reef is excluded. It must be noted that Kenyan Reef is located a few km off the coast and has been subjected to the sewage discharge from Mombasa areas (Done, *pers. comm.*).
Welborn and Hoegh-Guldberg measured DFAA concentration at 10 stations along the transect between Magnetic Island and Myrmidon Reef in the central GBR (*unpubl., in:* Ayukai and Hoegh-Guldberg 1992). The DFAA values (trace -0.17 µmol l^{-1}) of Welborn and Hoegh-Guldberg are in a similar range to those reported for other tropical waters. At these concentrations, COTS larvae are able to meet 10% of the minimum energy requirements at most. To date, however, virtually nothing is known about the variability of DFAA concentration in GBR waters. It is obviously too early to draw any conclusion with regard to the contribution of DFAA to the energy requirements of COTS larvae.

Table 4: Summary of dissolved free amino acid concentration (µmol l^{-1}) in tropical waters.

Oceanic waters		
GBR lagoon	-0.07	Welborn & Hoegh-Guldberg (*unpubl.*)[b]
Equatorial Pacific	0.02-0.06	Lee and Bada (1975)
Sargasso Sea	0.01-0.04	Lee and Bada (1977)
Sargasso Sea	0.02-0.15	Liebezeit *et al.* (1980)
Sargasso Sea	-0.06	Suttle *et al.* (1991)
Coastal and reef waters		
Myrmidon Reef	0.17[a] (*unpubl.*)[b]	Welborn & Hoegh-Guldberg
Bermuda	-0.22 -0.21[a]	Ferrier (1991)
Biscayne Bay (FL)	0.02-0.05	Lee and Bada (1977)
Kenyan Reef, Mombasa	0.86-1.07	Schlichter and Liebezeit (1991)

[a] Samples collected from nearby substrata

[b] *in:* Ayukai & Hoegh-Guldberg (1992)

Discussion

At this stage, COTS larvae seem to derive their energy largely from phytoplankton and in part from DFAA. The average concentrations of these two resources in GBR waters, however, appear too low for COTS larvae to balance the energy expenditure due to respiration. This implies that, in GBR waters, COTS larvae are usually unable to grow and constantly face death from starvation. Overemphasis of the possibility of "chronic starvation", however, is somewhat misleading. Generally, an argument based on the average resource availability implicitly assumes that, although zooplankton and their prey are unevenly distributed in the oceans, this heterogeneity does not have a strong impact on the dynamics of zooplankton populations, because the average individual should effectively experience the average environment over time. This assumption may be valid for relatively long-lived zooplankton, but not for COTS larvae with a planktonic life of only a few weeks. There is a possibility that COTS larvae are dependent for energy on event/local scale phenomena. What "chronic starvation" really suggests is the importance of the temporal and spatial variations in resource availability to the survival and recruitment of COTS larvae.

Although COTS infested reefs are widespread over the GBR, primary COTS outbreaks appear to be a rather local phenomenon. This, in conjunction with the above-mentioned view, tempts to postulate that COTS outbreaks are initiated by a localised, phenomenal increase in resource availability and the resulting high recruitment success of COTS larvae. Our current understanding of the variability of resource availability, however, is insufficient to evaluate this possibility. For instance, the comparison between ambient and compensating phytoplankton concentrations suggests that conditions exist where at least bipinnaria larvae are temporarily able to achieve positive growth by utilising phytoplankton. However, virtually nothing is known about how long such conditions can persist.

Several events are considered to be responsible for a large fluctuation in plankton productivity in GBR waters. Nutrient-rich terrestrial runoff has been described as one of the most dominant events (Revelante and Gilmartin 1982) and its effect on the survival and recruitment of COTS larvae (the "terrestrial runoff hypothesis", Birkeland 1982) has been a matter of concern for more than a decade (Brodie 1992). Events like intrusion of the sub-surface Coral Sea water (eg. Andrew and Gentien 1982, Furnas and Mitchell 1986) and cyclonic disturbance (rainfall, runoff and resuspension of nutrient-rich sediments, Furnas 1989) also cause a massive increase in plankton productivity over a wide area of the GBR shelf. In addition to these rather episodic events, there are less obvious, but more common features of possible importance to the survival of COTS larvae. These include enhanced resource availability within reef lagoons (eg. Furnas *et al.* 1990, Ayukai, *in press*) and the proximity of coral reefs (eg. Revelante and Gilmartin 1982, Wolanski and Hamner 1988). It may be also worth noting that, although the water column in GBR shelf waters is normally isothermal, a significant difference in resource availability is often observed between surface and bottom layers.

Birkeland and Lucas (1990) have stated that the temporal and spatial fluctuations in resource availability seem of little importance in determining the survival and recruitment of COTS larvae. This statement certainly reflects the results of *in situ* rearing experiments (Olson 1985, 1987), which have suggested that resource limitation of COTS larvae is unlikely even in phytoplankton impoverished GBR waters. Olson's approach was unique in the way he attempted to cope with an enormous burden for resolution of the variability of resource availability by rearing COTS larvae *in situ*. As mentioned by Olson himself, however, the environment created within *in situ* chambers appears different from the environment that COTS larvae actually encounter in the field. This occurs not only by keeping COTS larvae stationary in the continuous flow of different water masses, but also by some structural problems of *in situ* chambers (Okaji 1992). This paper suggests the likelihood of resource limitation of COTS larvae and urges the need for further assessment of the degree of resource limitation. As mentioned earlier, this need can be satisfied only by full understanding of the nutrition* of COTS larvae in similar temporal and spatial scales to their life cycle processes.

** 1. The action or process of supplying, or of receiving, nourishment: 2. That which nourishes; food; nutriment (Oxford Dictionary).*

Future Studies

Brodie (1992) has described that the Cairns-Cooktown region is of particular importance from the human / COTS perspective. First, primary COTS outbreaks appear to occur in this region. Second, this region has undergone an amazing development and is expected to grow further. He has then pointed out the proximity of coral reefs in this region to the mainland and a possible link between terrestrial runoff and COTS outbreaks. He has specially refocussed on the Birkeland's (1982) hypothesis that relates heavy nutrient inputs from terrestrial runoff to relaxation of resource limitation and higher recruitment success of COTS larvae and to the occurrence of COTS outbreaks. This paper supports Brodie's view and advocates further studies of the fate of runoff plumes and their influence on resource supplies to COTS larvae.

This paper suggests that, if eutrophication of GBR waters is truly becoming a serious problem, it will influence the magnitude of the recruitment success of COTS larvae by relaxing resource limitation. A recent study has suggested that nitrogen inputs from anthropogenic sources have a minor impact on the annual nitrogen budget for GBR waters (Furnas, *unpubl.*). However, this does not deny the possibility of localised, long-term accumulation of nutrients and its influence on resource supplies to COTS larvae. Thus there is a need for studies that attempt to elucidate the behaviour of nutrients, identify nutrient sinks and forecast the long-term change in nutrient environments. The region of immediate attention in such studies will be again the Cairns-Cooktown region, because of its geographical characteristics and increasing human activities.

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Is *Acanthaster planci* able to utilize dissolved organic matter (DOM) to satisfy the energetic requirements of larval development?

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Abstract

Dissolved organic matter (DOM) is a ubiquitous and plentiful resource in marine environments. Recent work on temperate and polar larvae has highlighted the potential role of DOM in the energy requirements of larval echinoderms. As part of a broader study aiming to define the nutritional biology of the planktotrophic larvae of <u>*Acanthaster planci*</u>*, I examined the role of two important forms of DOM, alanine (neutral amino acid) and glucose (monosaccharide), in the energy requirements of* <u>*A. planci*</u> *during larval development. Glucose was transported by bipinnaria and brachiolaria, but was characterized by a single low affinity transport system. When compared to the metabolic requirements of larval* <u>*A. planci*</u> *(measured using indirect calorimetry), transported glucose appears to be relatively unimportant in the diet of larval* <u>*A. planci*</u>*. Data for alanine, however, present a clearly different situation. Alanine transport was characterized by a biphasic system with the combined features of high binding affinity and high transport capacity. Maximal transport rates for alanine of* <u>*A. planci*</u> *bipinnaria were approximately 5-6 times higher than those of bipinnaria of similar mass cultured from related temperate starfish. This huge increase in the transport capacity for alanine of larval* <u>*A. planci*</u> *is unaccounted for by the effect of temperature on rate processes, and suggests that larval* <u>*A. planci*</u> *have 3 times the number of transport sites for alanine as do temperate relatives. Comparison of alanine transport to larval energy requirements reveals that larval* <u>*A. planci*</u> *can compensate for the requirements of maintenance and growth at alanine concentrations of approximately 2μM. These data are discussed in the context of the nutritional biology of larval* <u>*A. planci*</u> *and preliminary data on the concentration of amino acids in the water column and boundary layers of the Great Barrier Reef.*

Introduction

The nutritional biology of *Acanthaster planci* is central to understanding the potential link between human-driven eutrophication of tropical waters and outbreaks of large numbers of adult starfish. Although much of the nutritional biology of juveniles and adults has been documented, there are still many questions concerning the nutritional biology of the planktotrophic larvae of *A. planci* to be answered. One of these questions has been whether the embryos and larvae of *A. planci* can absorb and use dissolved organic matter (DOM) directly from seawater. DOM has been shown to be effective in supporting the metabolic requirements of a range of invertebrate larvae from temperate waters (Bass *et al.* 1969, Epel 1972, Reish and Stephens 1969, Manahan *et al.* 1983, Jaeckle and Manahan 1989a, Welborn and Manahan 1990). The potential for "non-traditional" food sources like DOM to play a role in the nutrition of the larvae of *A. planci* has been the subject of some speculation (Lucas 1982) but is currently not known.

This present study had four aims: (*i*) to measure the energetic requirements of *A. planci* during larval development, (*ii*) to measure the transport of two representative substrates (glucose and alanine) into the tissues of larvae of *A. planci* as a function of substrate concentration, (*iii*) to measure the concentrations of potential substrates in the waters of the Great Barrier Reef putatively inhabited by the larval stages of *A. planci*, and (*iv*) to produce an energy budget from these data to examine the potential role of DOM for supplying the energy required by *A. planci* during embryonic and larval development. Using this model, the question was asked: Can *A. planci* obtain enough energy from the uptake of DOM to supply a significant proportion of the energy requirements of embryonic and larval development? From this study, it can be shown that DOM does have the potential to provide a significant proportion of energetic requirements of larval development for *A. planci*.

Materials and Methods

Larvae for the experiments described here came from larval cultures (fertilized 17 December 1991) raised as part of the COTSREC juvenile rearing study (Task 6.1.5, Moran and Johnson 1991).

1. Measurement of the energetic requirements of larval development

The potential for DOM to contribute to the energetic requirements of an organism has usually been assessed in relation to energy demand of the organism in question (Johannes *et al.* 1969). Two major sinks for energy during embryonic and larval development are the deposition of energy as biomass during growth (manifested as a change in mass), and the expenditure of metabolic energy as part of maintenance and growth (manifested as instantaneous metabolic rate). In order to estimate the energetic requirements of *A. planci* during embryonic and larval development, both these energy sinks were quantified.

(a) Changes in dry organic weight

Ash-free dry organic mass was determined for *A. planci* at various stages of embryonic and larval development using a mass-calibrated Mettler microbalance (Mettler components: Model numbers BA25, BE22, ME22). Eggs, embryos or larvae (200-500 individuals used per determination) were rinsed in isotonic ammonium formate solution (3.4%, 0.2-µm filtered) and added to small aluminium dishes (pre-ashed at 500°C for 6 h) prior to being dried at 58°C to constant mass (which occurred between 3 and 10 days). Samples were weighed (total dry mass), and then ashed at 458°C for 6 hrs, and weighed again (ash). Biomass was calculated as the difference between the total dry mass and the ash mass.

(b) Metabolic rate of growing and differentiating larvae

The metabolic rate of embryos and larvae was measured for *A. planci* at various stages during development. Polarographic respirometry was done using the Strathkelvin Instruments oxygen monitoring system (Strathkelvin Instruments, Glasgow, U.K., OM780 and SI1302) connected to a data acquisition and analysis system (DATACAN IV, Sable Systems, Los Angeles, CA). Two chambers were run at the same time. Temperature was controlled to within ± 0.02°C by a temperature-controlled water circulator (Lauda, RC6-D, Germany) connected to the water jacket of each micro-respirometer cell each of which contained a micro-cathode oxygen electrode. Temperature was monitored during the experiment using a Pt thermistor (and associated electronics) connected to one channel of the data acquisition system. Total integrated energy use during development was calculated by integrating the instantaneous metabolic rates of *A. planci* over the entire course of embryonic and larval development.

2. *The uptake of alanine and glucose*

The uptake of alanine and glucose was studied by measuring the uptake of radioisotope labelled substrates. The uptake of radio-labelled compounds by larvae (and embryos) has been demonstrated to be due to the larva (or embryo) and not due to contaminating bacteria (Langdon 1983, Manahan *et al.* 1983, Davis and Stephens 1984), and to be a good reflection of net uptake rates (Manahan *et al.* 1982). In this study, alanine and glucose transport kinetics of the larvae of *Acanthaster planci* at various stages of development were investigated using the silicone-oil methodology of Jaeckle and Manahan (1989, a).

Larvae were washed (by resuspending several times) in filtered seawater (0.2m filtered, Nalgene, USA; hereafter referred to as FSW) prior to use in experiments. Glass vials (20 ml) that contained larvae suspended in 5 ml of FSW (concentration of larvae: 80-300 ml^{-1}, depending on larval size) were placed in tight-fitting wells in an aluminium heating block connected to a water circulator (Lauda, RC6-D, Germany) prior to the experiment. After equilibration (30 min.), the substrate (alanine or glucose) and its ^{14}-C labelled analogue were added to the vials and the experiment started. Each vial received 1 Ci of ^{14}-C labelled alanine (L-U-^{14}-C alanine, Amersham, United Kingdom) or glucose (D-U-^{14}-C glucose, Amersham, United Kingdom). To determine K_t and J_{max}, substrate concentrations were varied between vials, with final concentrations ranging between 0.1 µM and 300 µM (after correcting for the substrate added with the ^{14}-C labelled analogue). Following the addition of the substrate and its ^{14}-C labelled analogue, three 100 µl samples were removed from each vial (after gentle mixing) for specific activity measurements. Immediately following this, 1 ml samples were removed from the vials. The samples were placed over 0.5 ml silicone oil (F50, GE Silicones, USA) in a plastic micro-centrifuge tube and centrifuged for 45 sec. (Beckman Model E centrifuge). Centrifugation caused the larvae in each subsample to pass through the oil, leaving the incubation medium (FSW, substrate and radio-labelled analogue) behind. Following centrifugation, the vials were inverted and the silicone oil plus incubation medium discarded. After draining, the bottom of the centrifugation tubes (which still contained the larvae) were cut off and placed in 0.5 ml of tissue solubilizer (Scinti-Gest, Fisher Scientific). Eight samples were taken at approximately 1.5 min intervals from each vial. The larvae were left in the tissue solubilizer for 24 hours with occasional vortexing. Scintillation fluid was added to the vials and the sample radioactivity counted using a scintillation counter. After correcting the data for quenching using internal standards (Beckman), the rate at which the larvae became radioactively labelled during an experiment was investigated by least squares regression analysis of the 8 data points from each experiment. The slope (as DPM larva^{-1}min^{-1}) was converted to a measure of the absolute rate of substrate uptake using the measured specific activity.

3. *The concentration of dissolved free amino acids from the water column of the central Great Barrier Reef*

Samples were taken from the water column at 16 sites across the central Great Barrier Reef using a transect established by Dr. P. Doherty (A.I.M.S.). Three replicate 1.5 ml samples were taken at 10 m depth at 5 sites within the Great Barrier Reef lagoon, and at 5 and 20 m at 6 sites in the Magnetic Passage and 5 sites in the Coral Sea. Samples were also collected from sites 1 cm above algal covered rock substratum. Samples from the water column were collected using acid-washed Niskin bottles by individuals wearing gloves, to avoid contamination of samples by human-derived "DOM", while samples from near the bottom were collected by divers using plastic syringes. Immediately after collection, samples were filtered using 0.2 µm polycarbonate syringe filters (Nalgene) and were stored at -80°C for HPLC analysis using the method of Mopper and Lindroth (1982).

Results

1. *Changes in dry organic weight and metabolic rate during embryonic and larval development*

The mass of embryos and larvae increased from 0.817 µg egg^{-1} to 2.4 µg larva^{-1} (competent brachiolaria). Oxygen consumption by embryos and larvae increased from 37.4 2.19 pmol(O_2) larva^{-1}h^{-1} after 12 hours of development, to 662.4 119.40 pmol(O_2) larva^{-1}h^{-1} just prior to settlement and metamorphosis (*Fig. 1*). The total use of oxygen by *A. planci* during embryonic and larval development was calculated by integrating the instantaneous metabolic rate over the entire course of development. The total amount of oxygen used by *A. planci* to complete development from fertilized ova to competent larva was 78.165 nmol larva^{-1}.

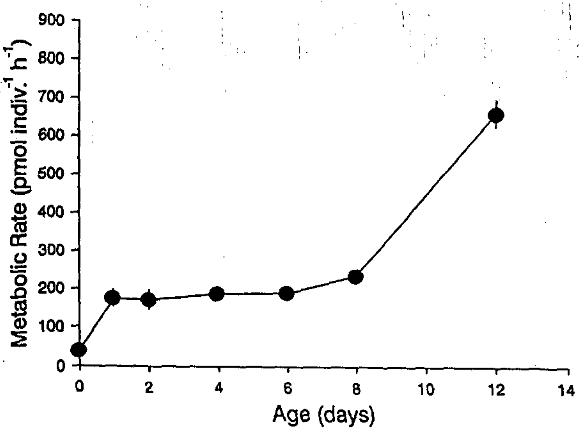

Figure 1: Metabolic rate of *Acanthaster planci* as a function of age. Larvae had reached competence by end of 13 days. Standard error of the means are shown where not obscured by the symbol.

2. *Influx of alanine and glucose*

Both alanine and glucose were taken up by *A. planci* larvae. Rates for both alanine and glucose were saturable, suggesting a carrier-mediated transport system. There were, however, quite striking differences in the kinetic parameters describing the transport of the two substrates.

(a) Kinetic parameters of alanine transport

The rate at which radioactively-labelled alanine entered the tissues of larval *A. planci* was rapid and linear for the first 10 minutes (*Fig. 2A*). Transport rates plotted as function of alanine concentration exhibited Michaelis-Menten kinetics and stage specific changes in transport (*Fig. 2B*). Eadie-Hofstee plots of the kinetic data (*Fig. 3 A,B,C; Table 1*) revealed evidence of biphasic transport kinetics (two sets of linear data), with a high affinity system having a K_t of about 2-3 μM, and a low affinity system having a K_t of about 30-60 μM. Gastrula did not show biphasic kinetics and appeared to have a K_t intermediate between these two values (*Fig. 2A, Table 1*). The transport capacity ($J^{in}{}_{max}$) of the high affinity system increased with larval size, in concert with mass and metabolic demand (*Fig 6A*).

Table 1: Kinetic parameters describing the transport of alanine and glucose into larvae of *Acanthaster planci* as a function of developmental stage (age). Values are given as pmol (substrate) larva^{-1}h^{-1} (for $J_{max}{}^{in}$) or μM (for K_t).

	High affinity system		Low affinity system	
	$J_{max}{}^{in}$	K_t	$J_{max}{}^{in}$	K_t
Alanine				
Gastrula (25 h)	38.7	11.8		
Bipinnaria (97 h)	172.7	3.1	360.7	66.0
Brachiolaria (264 h)	350.0	2.7	506.5	30.2
Glucose				
Early bipinnaria (57 h)			57.9	119.0
Brachiolaria (288 h)			32.0	55.0

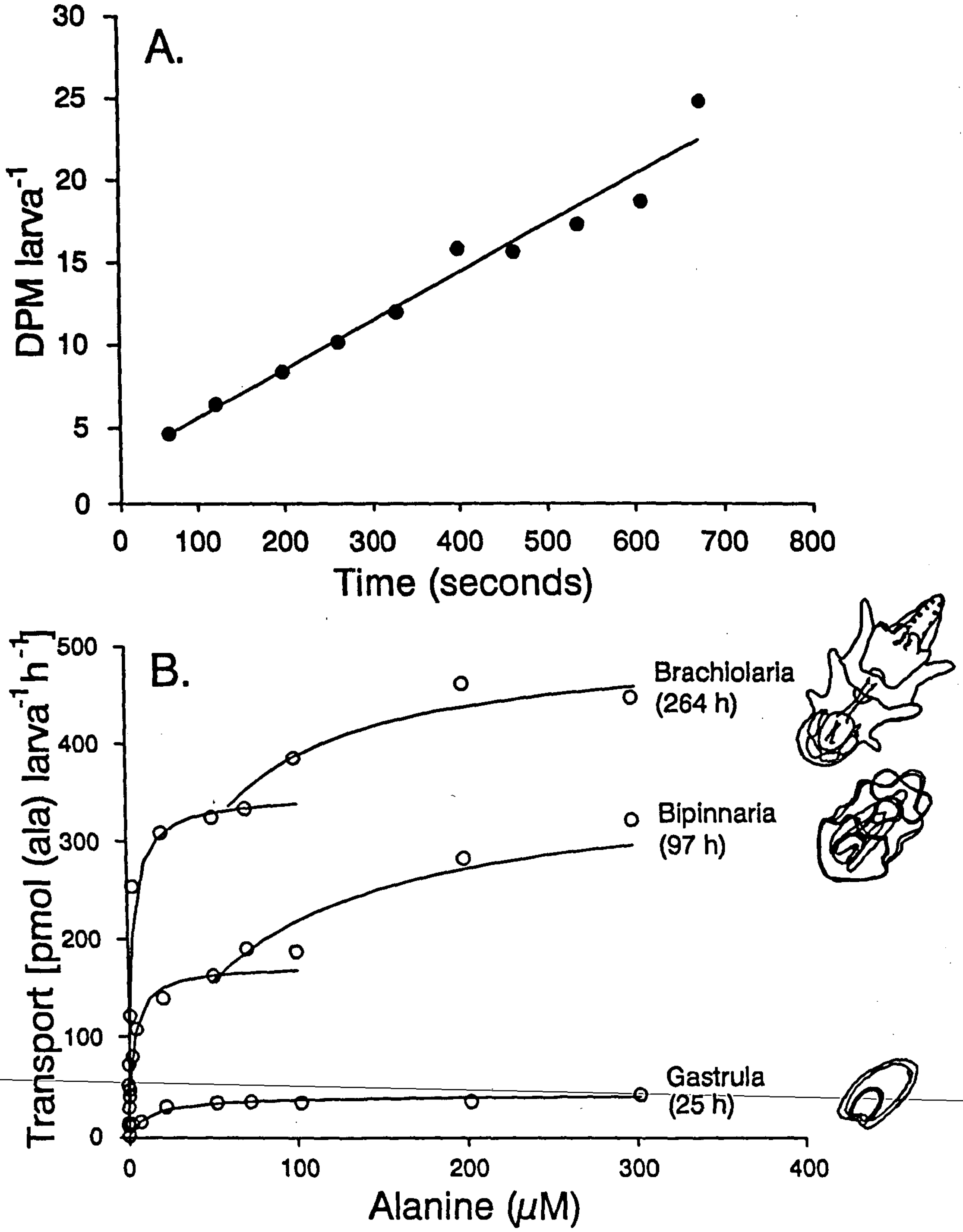

Figure 2: **(A)** Example of data collected during transport kinetics experiments. Shown are data from experimental trial measuring the alanine uptake by gastrula of *Acanthaster planci* at a substrate concentration of 200.9 μM. Shown is line of best fit by least squares regression ($Y = 3.94X + 351.5$, $r^2 = 0.96$). Each sample represents the radioactivity of 134 gastrulas.

(B) The rate of transport of alanine as a function of the concentration of alanine. Lines shown were fitted to data using the Michaelis-Menten equation (parameters K_t and J^{in}_{max} are listed in Table 1) and Eadie-Hofstee plots *(Fig. 3)*. Drawings show representative appearance and approximate relative size of larvae at each stage.

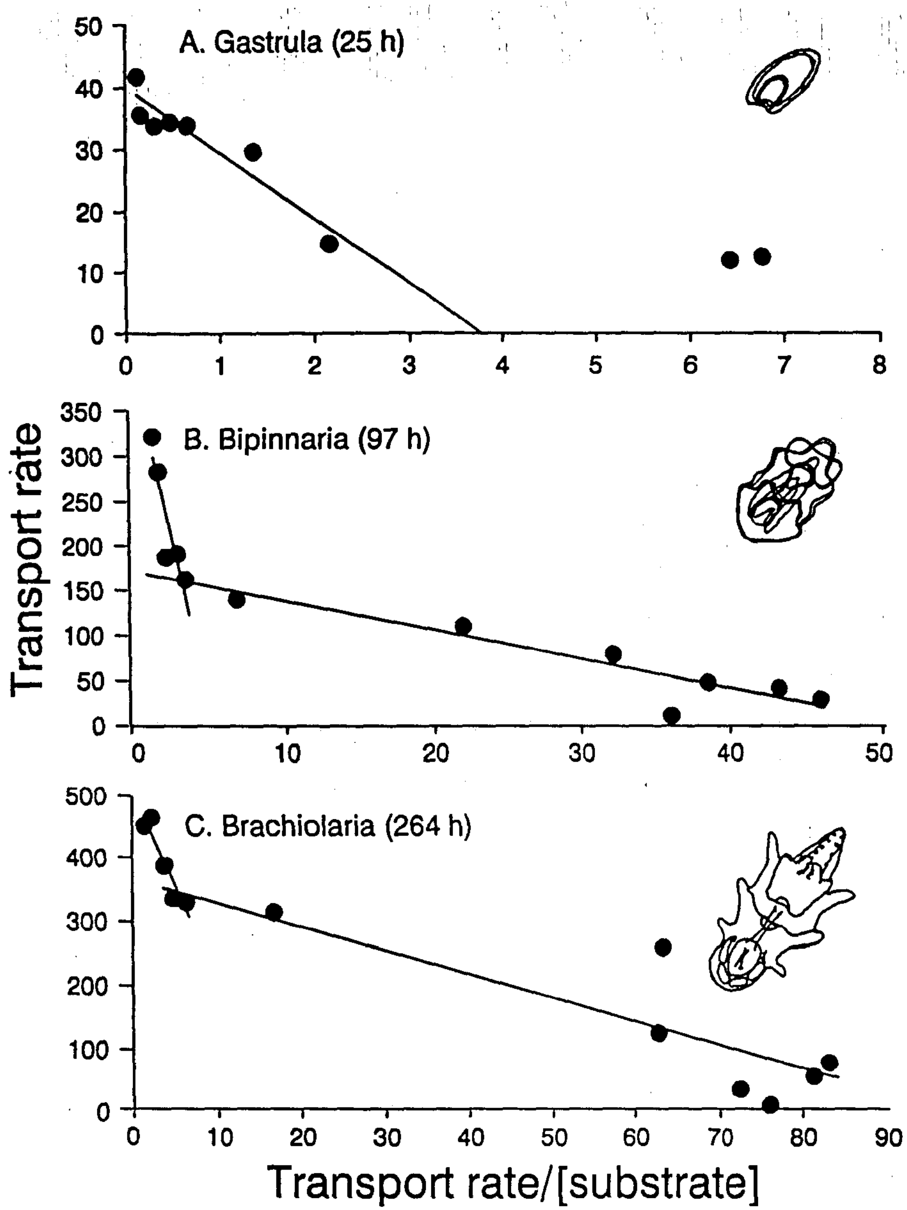

Figure 3: Eadie-Hofstee plots of kinetic data from *Fig. 1* for three larval stages of *Acanthaster planci.* Lines were fitted using linear regression analysis.

(b) Kinetic parameters of glucose transport

Glucose was also transported by larvae of *A. planci.* However, kinetic analysis of this transport system revealed a fairly low affinity system (compared with alanine), which saturated at relatively low transport rates in both early bipinnaria and brachiolaria (*Fig. 4, Table 1*). Eadie-Hofstee analysis did not reveal evidence of biphasic kinetics in early bipinnaria (*Fig. 5*). Data for the transport of glucose into brachiolaria did show some deviation from linearity in the Eadie-Hofstee plot, suggesting the possible appearance of a transport system at concentrations of glucose of more than 200 μM. The few transport assays done at concentrations of more than 200 μM, however, did not allow further analysis of the characteristics of this second transport system. Transport capacity (J^{in}_{max}) of glucose for the larvae of *A. planci* decreased with age, and was lowest in the older, larger brachiolaria (*Fig. 6B*).

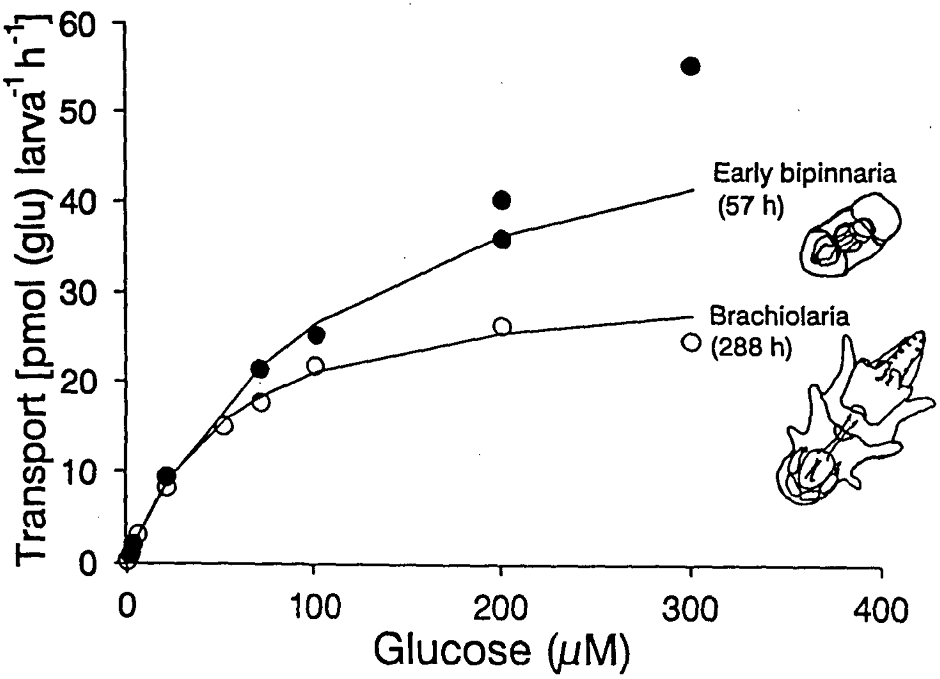

Figure 4: The rate of transport of glucose as a function of the concentration of glucose. Lines shown were fitted to data using the Michaelis-Menten formulation (K_t and J^{in}_{max} are listed in Table 1) and Eadie-Hofstee plots (*Fig. 5*).

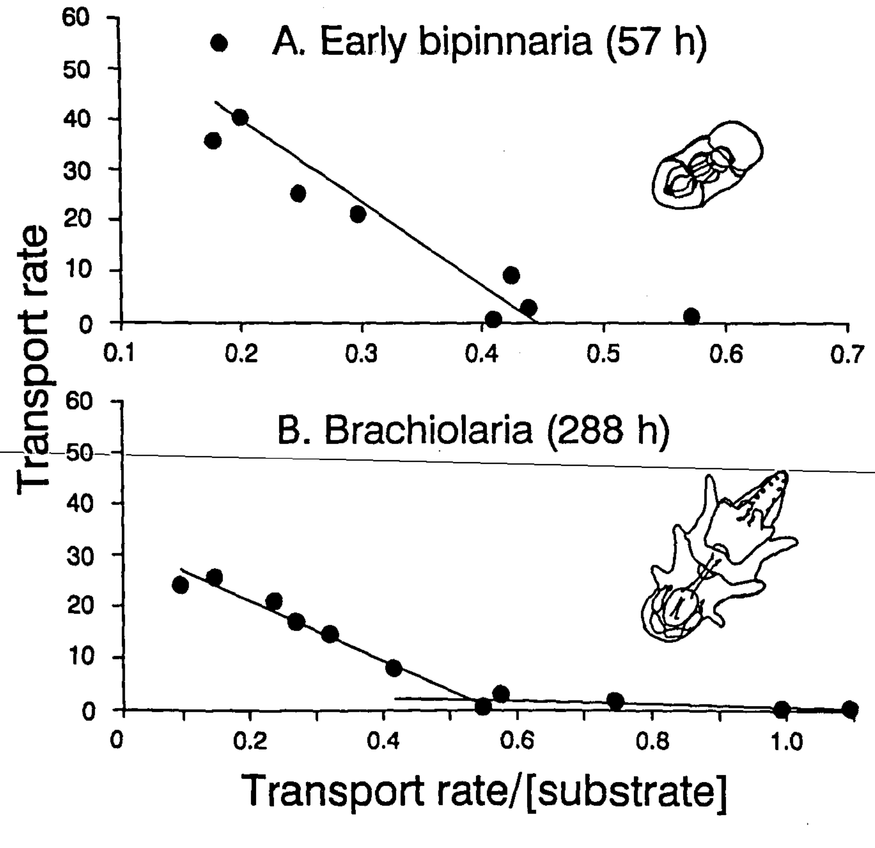

Figure 5: Eadie-Hofstee plots of kinetic data from *Fig. 1* for larval stages of *Acanthaster planci*. Lines were fitted using linear regression analysis. Drawings show representative appearance and approximate relative size of larvae at each stage.

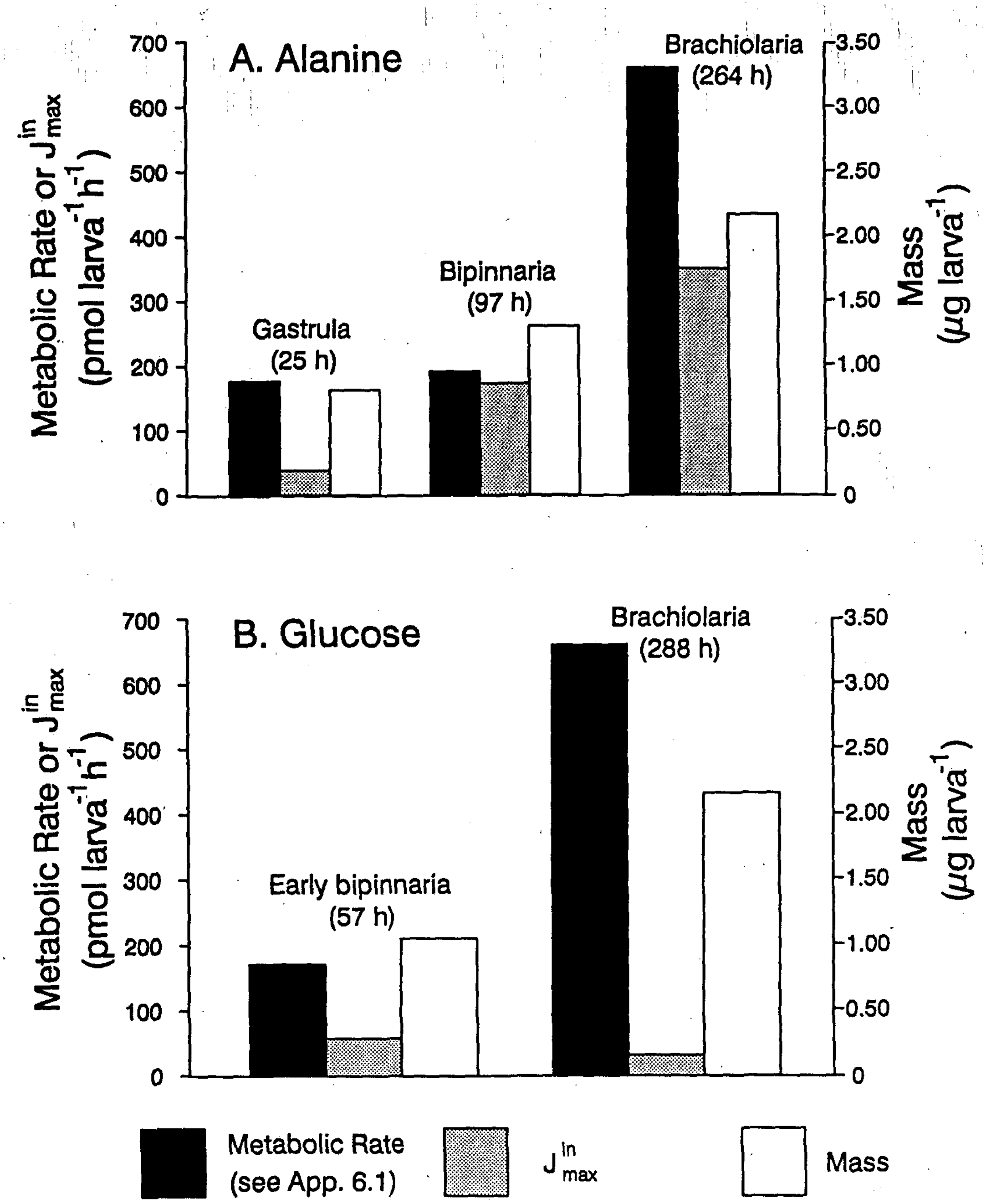

Figure 6: Mean metabolic rate, maximum transport rate (J^{in}_{max}) and mass (as ash-free dry organic mass) for *Acanthaster planci* at various stages of larval development for the substrates A. alanine and B. glucose.

3. *The concentration of dissolved free amino acids in the water column of the central Great Barrier Reef.*

Nine amino acids were detected in seawater collected from the water column (*Table* 2). The availability of dissolved amino acids in the water column is generally low, and in many cases was below the limits of detection. Concentrations in the water column ranged between 0 and 70 nM for most sites across the Great Barrier Reef and Coral Sea (*Fig. 7*). Samples taken close to the substratum had concentrations that were approximately 5 times higher (*Table* 2).

Table 2: Typical amino acid sample. Sample taken from 1 cm height above algal-covered surface on Myrmidon Reef by diver-operated syringe.

	Concentration (nM)
Aspartate	20.9
Glutamate	30.0
Serine	6.6
Histidine	50.9
Glycine	18.4
Alanine	13.3
Tyrosine	7.9

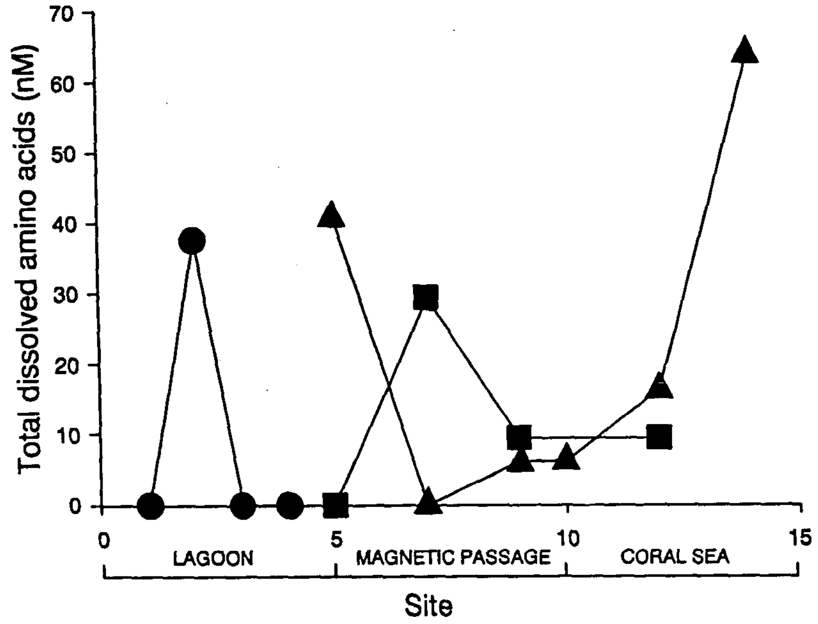

Figure 7: Concentration of total pool of free amino acids from 16 sites across the Great Barrier Reef Lagoon, Magnetic passage and Coral Sea.

4. Comparison of "supply" (from the transport of alanine or glucose) with the energetic "demand" of larvae.

The relationship between the environmental availability of alanine, the metabolic demand for substrate and ontogenetic stage is illustrated in *Fig. 8*. The alanine concentration at which full compensation occurred for substrates consumed during respiration (determined from respirometry) was 1.8 µM and 4.6 µM for bipinnaria (*Fig. 8B*) and brachiolaria (*Fig. 8C*) respectively. Gastrulas did not have the potential to achieve full compensation by the transport of alanine for substrates consumed during respiration (*Fig. 8A*).

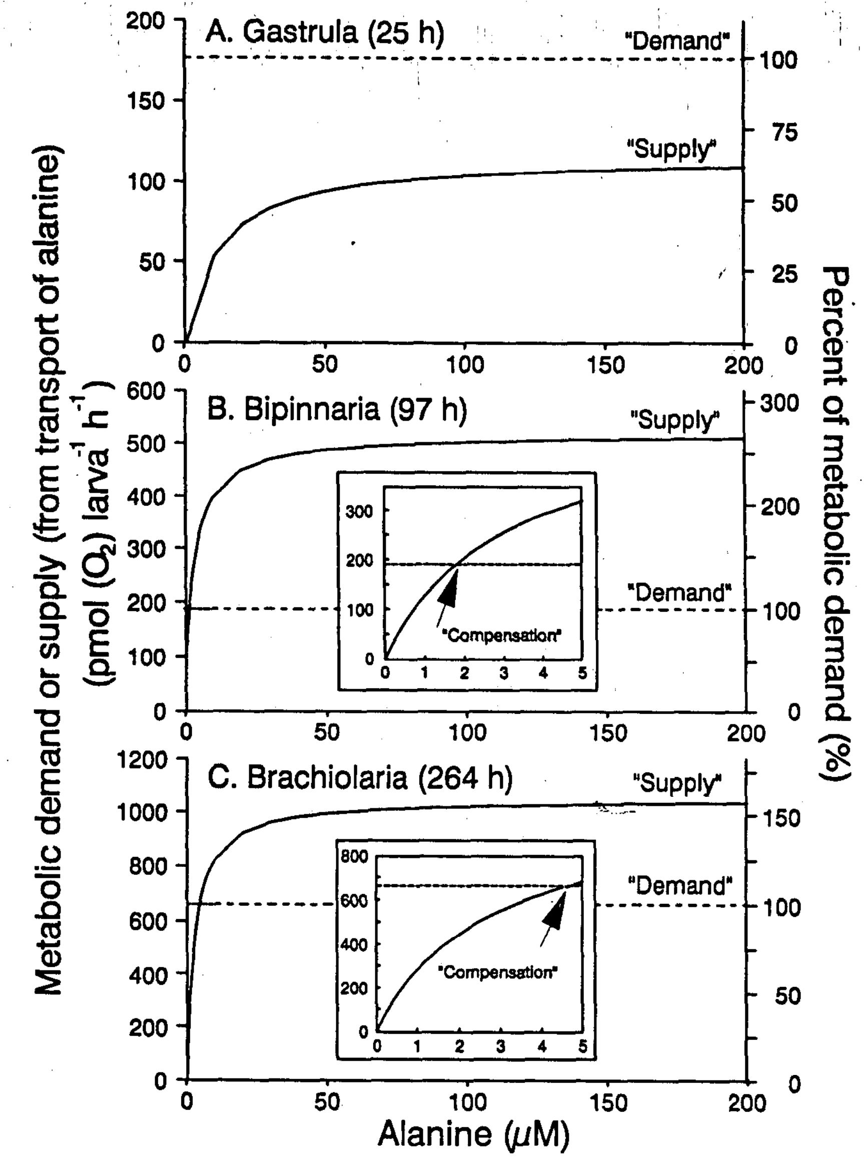

Figure 8: Comparison of metabolic equivalents supplied by transport from activity of high affinity transport system ("supply") to the instantaneous respiratory demand ("demand"). Estimated lines are for different larval stages of *Acanthaster planci* (A., B. and C.) and are a function of the external concentration of alanine. Inserts show detail of relationship at low concentrations of alanine. "Compensation" indicates the substrate concentration at which alanine transport supplies enough energy as metabolic equivalents as pmol $[O_2]$ larva^{-1}h^{-1}) to offset instantaneous respiratory demand of larva. Metabolic equivalents supplied by alanine transport were calculated by multiplying the number of moles of alanine transported (from Michaelis-Menten equations, parameters listed in *Table 1*) by 3 (assuming that the combustion of alanine requires 3 moles of oxygen).

The concentration of glucose required for larval transport processes to compensate for the respiratory consumption of metabolic substrates was 125 μM in the early bipinnaria stage larvae *(Fig. 9A)*. Glucose transport did not have the potential to compensate for the respiratory consumption of metabolic substrates in the older brachiolaria larva *(Fig. 9B)*.

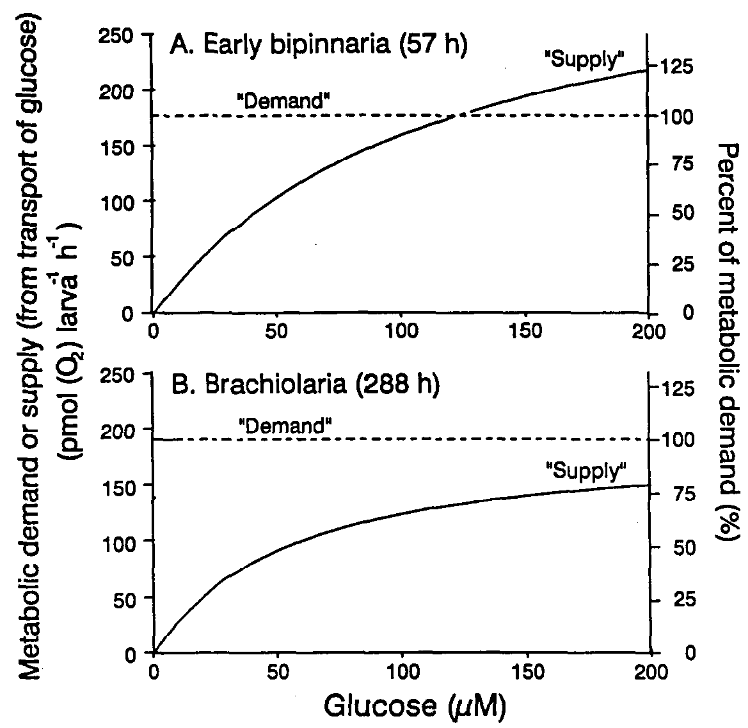

Figure 9: Comparison of metabolic equivalents supplied by transport of glucose ("supply") to the instantaneous respiratory demand ("demand"). Estimates are for different larval stages of *Acanthaster planci* incubated in external concentrations ranging from 0 to 200 μM. Calculations were made as described in the legend to *Fig. 7* with the additional assumption that the combustion of glucose requires 6 moles of oxygen.

The total energy contribution of alanine and glucose transport processes was compared to the total demand for energy during the entire larval development of *A. planci* (*Table* 3). Energy invested into biomass was converted into units of energy using the mean combustion energy for protein, carbohydrate and lipid (Gnaiger 1983). The total amount of oxygen used during development was converted into units of energy using the mean oxy-calorific equivalent for the same three classes of substrate (Gnaiger 1983). The total amount of energy required by *A. planci* for development to proceed was 75.5 mJ individual^{-1} (see *Table* 3 for calculations). Alanine transported over the entire larval life of *A. planci* had the potential of supplying 28.9% and 71.3% at external alanine concentrations of 1 μM and 5 μM respectively. Glucose transport, by comparison, could only supply 0.6% and 2.8% at 1.0 μM and 5.0 μM external glucose respectively.

Table 3: Total mass changes were calculated by subtracting the ash-free dry organic mass (AFDM) of the egg from the AFDM of a competent brachiolaria. Energy associated with the increase in mass was calculated by multiplying the change in mass by the mean energy of combustion of protein, carbohydrate and lipid (Gnaiger 1983, 24 kJ g). The energy liberated from the combustion of metabolic substrates was calculated by integrating oxygen consumption (metabolic rate) as a function of time for the entire course of development. The calculated value was converted into a measure of the energy of metabolic combustion by multiplying the total integrated oxygen consumption by the mean oxy-calorific value for protein, carbohydrate and

oxygen consumption by the mean oxy-calorific value for protein, carbohydrate and lipid (480.3 kJ mol$(O_2)^{-1}$, Gnaiger 1983). The total energy use during development is calculated as the sum of the energy invested into new biomass and the energy released during the consumption of metabolic fuels. The efficiency of assimilation is calculated by dividing the amount of energy invested into new biomass by the total energy used during development. The energy contributed from the uptake of substrate (glucose and alanine) was calculated by (a) integrating the transport rate of substrate (at either 1µM or 5 µM) over the entire course of development, and (b) converting that number into a measure of energy using the ratio 6 O_2:1 glucose or 3 O_2:1 alanine and the oxy-calorific equivalent (480.3 kJ mol^{-1}, Gnaiger 1983).

A: Total energy use during development

(1) *Biomass change:*	1.583 µg $larva^{-1}$	
Energy invested into biomass:		38.0 mJ $larva^{-1}$
(2) *Oxygen consumed:*	78.165 nmol $larva^{-1}$	
Energy consumed:		37.5 mJ $larva^{-1}$
(3) Total energy used:		75.5 mJ $larva^{-1}$

B. Energy contributed from the transport of alanine

1. Oxygen equivalents of total alanine transported (pmol larva^{-1}):

	Age period (h)			
	[0->60]	[61->181]	[182->288]	Total
At 1 µM	319.9	15130.8	30001.2	45451.9
At 5 µM	1599.3	38340.0	72186.0	112125.3

2. Energy equivalents of total alanine transported (mJ ind^{-1}):

	Age period (h)			
	[0->60]	[61->181]	[182->288]	Total (% of 75.5 mJ)
At 1 µM	0.17	7.27	14.41	21.83 (28.9%)
At 5 µM	0.77	18.41	34.67	53.85 (71.3%)

3. Energy equivalents of glucose transported (0 - 288 h)

	Oxygen equivalents (pmol larva^{-1})	Energy equivalents (mJ larva^{-1})	% of 75.5 mJ
At 1 µM	912.9	0.44	0.6
At 5 µM	4322.9	2.08	2.8

Discussion

As a planktotrophic larva, *Acanthaster planci* requires metabolic energy from external food sources in order to complete its embryonic and larval development. How this requirement for metabolic fuel is acquired by the planktonic stages of *A. planci* is not known. Data from both laboratory culture and the field, however, suggest that the availability of conventional food sources (phytoplankton) in the field is at least an order of magnitude below that considered optimal for the successful completion of larval development by *A. planci* (Lucas 1982). Lucas (1982) suggested two other possible food sources for the larvae of *A. planci*, (a) bacteria (see Ayukai, this volume) and (b) dissolved organic matter (DOM). The potential role of DOM as a food source for the larvae of *A. planci* was examined in this study.

Do the larvae of A. planci have the capability of transporting alanine and glucose from seawater?

Both alanine and glucose are transported into the larvae of *A. planci* at developmental stages ranging from gastrula to brachiolaria. Both transport mechanisms show Michaelis-Menten kinetics (*Fig. 2B* and *Fig. 4*), indicating carrier-mediated transport. The kinetic properties of the alanine and glucose transport are, however, very different. Alanine transport was biphasic, with the involvement of both a high affinity (*Fig. 2B, Table 1*, K_t = 2.71 - 3.11 μM), and low affinity (*Fig. 2B, Table 1*, K_t = 30.2 - 66.0 μM) transport system. Maximal velocities for these two alanine transport systems were substantial (*Fig. 2B, Table 1*, J^{in}_{max} = 38.74 - 506.5 pmol larva^{-1}h^{-1}). The glucose transport system on the other hand, was monophasic and was typified by low affinities for glucose (*Fig. 4, Table 1*, K_t = 55.0-119.0 μM) and low maximal transport rates (*Fig. 4, Table 1*, J^{in}_{max} = 32 - 57 pmol larva^{-1}h^{-1}).

The substrate affinity (K_t) observed for alanine transport in this study matches directly those done by other workers on temperate larvae. Manahan (1983) observed K_t's of 3 - 4 μM for oyster (*Crassostrea gigas*) and mussel (*Mytilus edulis*) larvae for alanine and glycine. Trochophore and veliger larvae of the gastropod, *Haliotus rufescens* had K_t's for alanine of 8.4 and 22.7 μM respectively, while early plutei of the urchin, *Strongylocentrotus purpuratus* had K_t's ranging from 1.0 to 1.9 μM (Manahan *et al.* 1989). It is interesting to note that Manahan *et al.* (1989) also saw similar biphasic kinetics for *S. purpuratus* larvae. Generally, literature values of J^{in}_{max} have been in the range 5.6 (*S. purpuratus*) and 71.1 (*H. rufescens*) pmol larva^{-1}h^{-1} (Manahan 1983, Jaeckle and Manahan 1989b, Manahan *et al.* 1989). There are no cases, however, of J^{in}_{max} values as high as those reported for alanine in this study (> 350 pmol larva^{-1}h^{-1}). The high rates of transport seen in the present study are partially due to the higher incubation temperatures of this study (28°C as opposed to 15 - 20°C of most temperate studies). However, even after allowing for the effects of temperature, the J^{in}_{max} values reported here are high (using a Q_{10} of 2, the highest J^{in}_{max} reported here would still be 175 pmol larva^{-1}h^{-1} at 28°C).

This suggests either of two possible scenarios:

(1) that asteroid larvae have high rates of alanine transport (unexplored so far), or that (2) tropical larvae like those of *A. planci* have specialized in the acquisition of amino acids from seawater to a greater extent than their temperate counterparts.

Given the impoverished nature of tropical oceans with respect to "conventional" particulate foods such as phytoplankton (see discussion in Lucas 1982), the second hypothesis is attractive.

How much energy does A. planci require to complete embryonic and larval development?

The development of *Acanthaster planci* from fertilized egg to competent larva requires 75.5 mJ of energy per individual (*Table 3*). The asteroid *Asterina miniata* develops from a slightly smaller egg (180 µm, Hoegh-Guldberg unpublished, versus 210 µm of *A. planci*, the present study) through a similar set of developmental stages (to a similar sized juvenile) in 40 days. It uses 243 mJ larva^{-1} to complete larval development (Hoegh-Guldberg and Manahan 1991). Although the slightly more massive egg of *A. planci* does translate as greater amount of initial energy, and hence a lower requirement for energy acquisition during development, it does not explain why the cost of development is so much lower in the case of *A. planci*.

What is the potential contribution of the transport of alanine and glucose to the energy requirements of A. planci during development?

The contribution of the transport of alanine and glucose to the metabolic requirements of larval development was calculated for 1.0 and 5.0 µM substrate concentrations. The energy budget calculations are unambiguous, whereas alanine has the potential to supply 28.9% of the energy demands of larval growth and development at environmental concentrations of 1.0 µM, dissolved glucose does not (contribution at 1.0 µM glucose = 0.6%). At alanine concentrations of 5.0 µM, the calculated contribution to the energetic requirements of larval growth and development rises to 71.3% of total metabolic costs. The potential contribution of glucose at concentrations of 5.0 µM remains low at 2.8% of total energy requirements.

Crucial to the analysis of the potential of dissolved amino acids to contribute to the energetic requirements of *A. planci* during larval development is the availability of amino acids in the environment. Two recent reports of the concentrations of amino acids from tropical waters associated with coral reefs have shown that concentrations of amino acids at least range from 0.05 to 1 µM (Ferrier 1991, Schlichter and Liebezeit 1991). Estimates from other oceans suggest that free amino acid concentrations can vary from as little as 30-40 nM (Baltic Sea, Mopper and Lindroth 1982) to as much as 896 µM (sea-ice interface, Antarctica, Welborn and Manahan 1992). In this study, values for the concentration of amino acids mid-water column ranging between 0 and 70 nM, with values taken near the substrate approaching those found by Schlichter and Liebezeit (1991, ca. 1 µM). This brief survey does not encompass aspects of the temporal and spatial variability found by other authors in other oceans (eg. Mopper and Lindroth 1982; Welborn and Manahan 1992).

This survey does, however, suggest that concentrations of amino acids on coral reefs are potentially higher near the substrate, and that they do approach those required by larvae if they are to be of energetic significance.

The results of this study indicate that the larvae of *A. planci* have the potential to supplement their metabolic requirements by transporting amino acids from the water around them. It is important to note two aspects of this conclusion. The first is that around them. It is important to note two aspects of this conclusion. The first is that amino acids represent less than 10% of the total pool of available dissolved organic matter (Williams 1975), and therefore, it is likely that this conclusion is conservative. There are several other, potentially more important, classes of DOM available to larvae (eg. lipids, often released from reef-corals). The relatively large energetic impact of a rather minor proportion of the total DOM pool suggests that the conclusions drawn from the study of amino acids are likely to be conservative rather than over-estimates of the significance of DOM in the diet of *A. planci* larvae. The second aspect is that the levels of amino acids reported here represent the background levels of amino acids available to larvae. How amino acids levels vary during seasonal changes and with circumstances like elevated river-runoff (*cf.* Birkeland 1982) is not known. This study, however, has shown another potential link between changes in water chemistry and the growth and survival of larval *A. planci*.

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In situ rearing of COTS larvae

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Abstract

The in situ larval rearing equipment developed by Olson was modified with a series of in-line filters (100 µm, 1, 0.2 and Activated Charcoal Filter-ACF) to determine what parameters are most important for the nutrition and survival of A. planci larvae. The result of the trial showed that a higher proportion of larvae were ready to settle in 100 µm filtered seawater (100 FSW), while a slightly lower proportion were ready to settle in 1 and 0.2 FSW. The larvae reared in ACF water did not develop beyond early brachiolaria stage. This seemed to suggest that adequate nutrients were available in natural seawater to support larval development. However, assessment of water quality inside the plastic larval chamber revealed that chlorophyll a levels of 100, 1 and 0.2 FSW were significantly higher than natural. This indicates that seawater inside the chambers was possibly more nutritious than natural seawater. The elevated chlorophyll a level may be due to algal fouling on the wall of the chambers and / or filter system. Environmental parameters, as an index of food availability, needs to be assessed when seeking to relate feeding and nutrition in the study of A. planci larvae.

Field measurement of survival rates of juvenile *Acanthaster planci* (L.): techniques and preliminary results *

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Abstract

Techniques are described which enable measurement of mortality rates of post-metamorphic Acanthaster planci *as small as 0.5 mm in the field. Results indicate that mortality rates at this time are significant, viz. 6.49% day^{-1} for 1-month-old starfish (mean size = 1.1 mm) decreasing to 1.24% and 0.45% day^{-1} for 4 (2.7 mm) and 7-month-old (5.5 mm) starfish respectively. Experiments involving exclusion of predators indicated that the major source of mortality was predation by epibenthic fauna. Results also show that in the presence of adequate food supply juvenile* A. planci *move very little. This suggests that survival will be enhanced by settling in areas where predation will be minimal.*

Introduction

Population outbreaks of the crown-of-thorns starfish, *Acanthaster planci* (L.) remain the most important management issue on coral reefs in the Indo-Pacific region (Birkeland and Lucas 1990). In common with most marine invertebrates, a major barrier to understanding the population dynamics of *A. planci* is that very little is known about the juvenile stage of life and the factors that affect survival at this stage. Variability in post-settlement survivorship has been demonstrated for a number of taxa and is dependent on a number of factors including habitat type, settlement density and

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predation (Cameron and Schroeter 1980, Young and Chia 1982,1984, Luckenbach 1984, Keough 1986, Keough and Downes 1982, Rowley 1989,1990, McShane 1991).

Acanthaster planci have a 2 week planktonic period after which larvae settle and metamorphose into 5-armed starfish about 0.5 mm in diameter (Yamaguchi 1974). They live in a complex habitat of dead coral rubble (Yokochi and Ogura 1987) and feed on coralline algae. After about 4-6 months at a size of about 10 mm the starfish change their diet and begin to feed on corals and grow much more rapidly (Yamaguchi 1974). Little is known of the mortality patterns of small *A. planci*, but that they are readily consumed by crabs (Lucas 1973) and under some circumstances field populations may be greatly affected by disease (Zann *et al.* 1987).

It is known that starfish outbreaks on reefs can be initiated by large recruitment events (Zann *et al.* 1987, Doherty and Davidson 1988). Some recruitment rates of *A. planci* have been measured and have been found to vary both on a temporal scale and spatially both between reefs (Doherty and Davidson 1988) and within reefs (Zann *et al.* 1987, Yokochi *et al.* 1988). However just how recruitment rates are related to rates of larval settlement is not known and whether any significant reduction in starfish numbers or some sort of regulatory control acts on starfish populations prior to them reaching a size at which recruitment can be measured with any accuracy (eg. about 20 mm or 8 months, Zann *et al.* 1987) is not known (Keesing and Halford 1992). In order to establish what levels of starfish settlement and/or recruitment on reefs are necessary to precipitate outbreak numbers of adults 3 years later, it is necessary to have an understanding of the mortality rates of small starfish and the factors which influence them.

To determine what factors are important to *A. planci* population dynamics we have developed techniques to work with juvenile *A. planci* as small as 0.5 mm in the field. These techniques enable rates of mortality to be measured under near natural conditions. The purpose of this paper is to describe these techniques and present the results of field deployment of 1, 4, 7 and 16-month-old laboratory reared *A. planci* juveniles.

Materials and Methods

Large numbers of small juvenile *A. planci* were reared in the December-January period of 1989/90 and 1990/91 using techniques similar to that described by Birkeland and Lucas (1990). Full details of the rearing operation are to be described elsewhere. Field deployment experiments were carried out in February 1991 (1 month post-settlement), May 1991 (4 and 16 months) and August 1991 (7-month-old). Starfish were deployed in the field in plastic boxes with tight fitting lids. Three sizes of commercially available plastic boxes were used. Boxes 26 cm x 18 cm x 8 cm deep were used to deploy 1 and 4-month-old starfish. Larger boxes were used to deploy 16-month-old starfish (35 cm x 25 cm x 12 cm) and 7-month-old starfish (57 cm x 32 cm x 9 cm). The lids and sides of the two smaller box types were covered in 0.2-mm mesh (*Fig. 1a*) and 0.5 mm mesh was used to cover all surfaces of the larger boxes (*Fig. 1b*). The lids of the largest of the boxes did not fit as well as those on the smaller boxes and some problems with starfish escape were subsequently encountered (see later). The boxes containing starfish were deployed on the leeward side of Davies Reef (18°50'S, 147°39'E) in about 12 - 15 m depth in an area of dead coral rubble (Fig. 1c).

The basic aim of the experiments was to compare the survival of small starfish living in their natural habitat (among dead coral coated in crustose coralline algae and other organisms, see Yokochi and Ogura 1987) with that of starfish living among a similar substrate which provided a food source and shelter, but in the absence of potential predators or other hazards. For the natural rubble treatment (hereafter TREATMENT), pieces of unconsolidated dead coral rubble complete with algal and motile epifaunal assemblages were collected directly from the seabed at the time of deployment. For the control rubble treatment (hereafter CONTROL), sun-bleached or beach-collected coral rubble was used after conditioning in flow-through-aquaria for several weeks to allow a biological coating of bacteria, diatoms, filamentous and coralline algae to grow on the rubble surface. Benthic diatoms provide an adequate food source for young juvenile starfish (Keesing and Halford, *unpublished*).

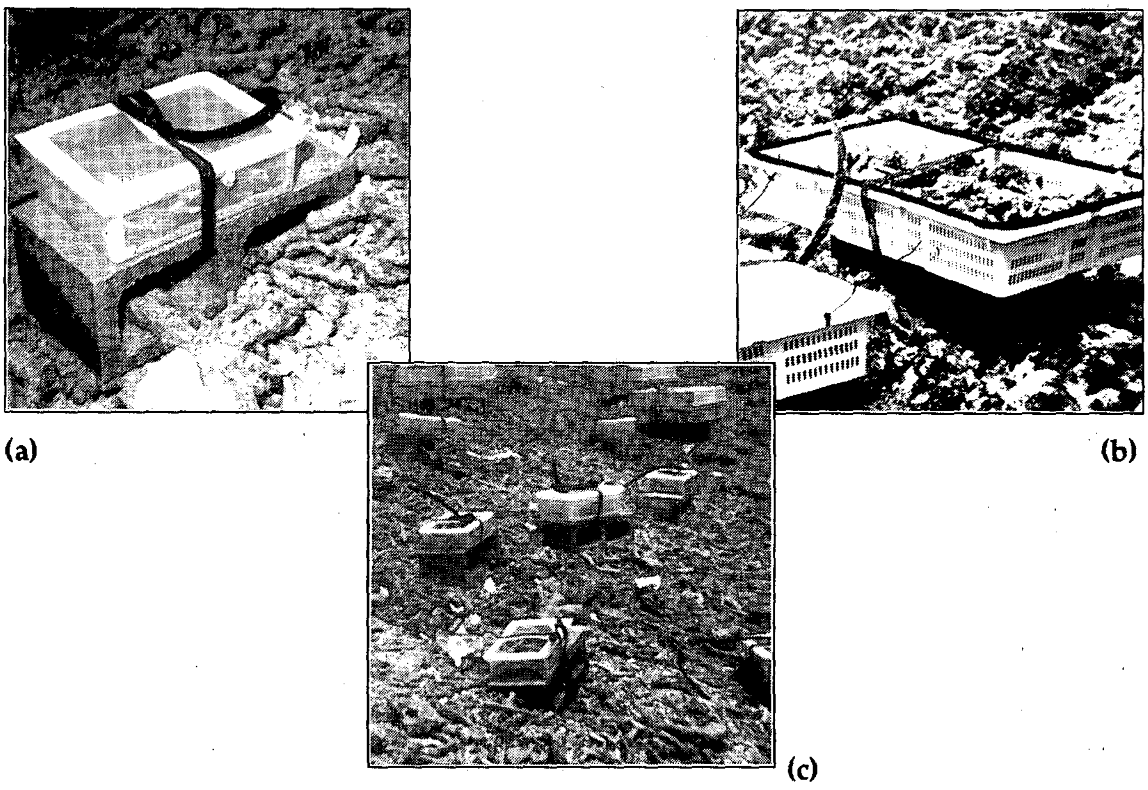

Figure 1: (**a**): Small mesh boxes (26 x 18 x 8 cm) fixed to concrete block. This size box was used to deploy 1 and 4-month-old *A. planci;* (**b**): Large mesh boxes (57 x 32 x 9 cm) used to deploy 7-month-old *A. planci.* Lid removed from right box to show rubble inside; (**c**): Dead coral rubble habitat on Davies Reef where experimental deployments were carried out. Large boxes in background are ESCAPE CONTROLS and the left most box in the foreground is a DOUBLE-MESH type box (see text). The starfish reared in the laboratory and the conditioned rubble were taken to the field in 100-litre tanks aboard a research vessel. They were then transferred to the deployment site in a small inflatable boat. Conditioned rubble was placed into the CONTROL boxes on the surface at the deployment site while rubble from the seabed at the deployment site was collected by divers and placed in the TREATMENT boxes and then brought to the surface. Batches of starfish which had been counted out previously were then washed into the CONTROL and TREATMENT boxes and the lids were fitted. The boxes were then gently lowered into the water to allow any trapped air to escape and taken to the bottom by divers where the boxes were tied to concrete blocks using rubber straps.

Initial densities varied for each experiment depending on the availability of starfish at different ages. For the first experiment, 100 of the 1-month-old starfish were stocked to each of the boxes (equivalent to 2137 m^{-2}), 35 per box at 4 months (748 m^{-2}), 20 per box at 7 months (110 m^{-2}) and 10 per box at 16 months (114 m^{-2}). Starfish sizes could not be measured prior to deployment (but see *Table 1).*

Water exchange in boxes

The mesh on the boxes was cleaned each day or every second day by lightly brushing the mesh to ensure water flow was not occluded by silt. To assess the adequacy of water flow, water samples were syringed from the boxes periodically over the course of one experiment and the dissolved oxygen content was measured using an ICI Dissolved Oxygen Meter. Water samples were also taken from CLOSED boxes (no possible water flow) and boxes within boxes (DOUBLE-MESH, *Fig. 1c*) which had been deployed with natural coral rubble. Fluorocene dye was also injected into some extra boxes to further examine the effect of the caging on water flow.

Escape controls

Ten boxes for each of the CONTROL and TREATMENT type were used for the 1, 4 and 7-month-old starfish whilst five natural rubble TREATMENT boxes only were used for the 16-month-old starfish. Two variations of the boxes were used for deployment of the 1, 7 and 16-month-old *A. planci.* Five replicate OPEN treatment boxes (the same as TREATMENT boxes but without lids) were deployed with 7-month old *A. planci.* These OPEN boxes allow free movement of starfish and predators in and out of the boxes. In order to examine movement rates of the small starfish and their propensity to escape from the OPEN boxes we used small boxes without lids inside larger boxes. These are termed ESCAPE controls and were deployed for the 1, 7 and 16-month-old starfish. Upon recovery of the boxes we counted the number of starfish that had moved out of the smaller inner box into the larger outer box.

Recovery of deployed starfish

After the boxes had been in place for 6, 13, 16 and 13 days for the 1, 4, 7 and 16-month-old starfish respectively, they were collected by divers and brought back to the research vessel where the contents were carefully washed into bottles and the entire contents fixed in buffered 10% formalin in seawater. The fixative also contained Rose-Bengal stain to make subsequent sorting of animals from rubble and debris easier. Prior to fixing, any starfish which could be recovered alive were removed, counted and measured (greatest diameter).

The fixed contents of the boxes were sorted by washing the rubble over 6, 1 and 0.1 mm mesh screens. In this way all rubble was retained in the 6 mm mesh and starfish and other epifauna were retained by the smaller meshes. Following this, each piece of rubble was individually washed over the mesh. All starfish were then recovered from the mesh screens and counted and measured. The other epifauna in the 1 mm screen were also counted and categorised with the aid of a dissecting microscope.

Controls for handling and sorting efficiency

To measure the efficiency of the recovery (sorting) technique, small starfish (N=50 for 1-month-old and N=30 for 4-month-old) were seeded into each of four TREATMENT boxes and the contents were fixed after a few minutes and sorted as for the experimental samples. To ensure that the degree of handling of the starfish during the counting and deployment procedure did not contribute to starfish mortality, handling controls were also carried out. These consisted of 2 or 4 replicate batches of starfish, which had been subject to the same amount of handling as those placed in the boxes were kept in dishes overnight and examined the morning following the deployment of the boxes.

Analysis

The proportions of surviving starfish in the CONTROLS and TREATMENTS were compared using a t-test. Where required an *arcsin* transformation was used to correct variance structure. Mortality rate was determined to be the daily rate of loss in the TREATMENT boxes. Predation rate was determined to be the difference between the mortality rates in the TREATMENT and CONTROL boxes where a significant difference in survival was detected between the two.

Results

Starfish size

The sizes of the different age classes of starfish recovered after each experiment are indicated in *Table 1*. The mean size of starfish remaining in the TREATMENT and CONTROL boxes following recovery was determined to examine for evidence of size-dependent mortality. *Table 1* indicates that for 1 and 4-month-old *A. planci*, on which significant effects of predation were detected, that no differences in starfish size existed at the end of the deployment period (t-test, $p > 0.05$). This indicates no size- selective predation was occurring over the limited size range of starfish present. Seven-month old *A. planci* recovered from the TREATMENT boxes were significantly larger (on average 0.6 mm larger) than in the CONTROLS (t-test, $p = 0.011$). This is most likely the result of faster growth in the boxes containing natural rubble, but may indicate the larger starfish were more likely to escape (see later). Note that the 7 and 16-month-old starfish are stunted compared to what could be expected on average for starfish of that age in a natural population [eg. 21 mm (range 12-28) and 77 mm (range 34-156) respectively (Zann *et al.* 1990)]. The stunting in our laboratory reared animals is due to an absence of coral food but does not appear to affect the health of starfish for up to two years of age (Lucas 1984, Keesing and Halford 1992).

Table 1: Mean size ± 1SD of juvenile *Acanthaster planci* recovered after field experiments. The 1, 4, 7 and 16-month-old starfish were deployed for 6, 13, 16 and 13 days respectively; nd: no data.

Date deployed	*Starfish age (month)*	*Controls mean size (mm)*	*Treatments mean size (mm)*	*Size range (mm)*
Feb 1991	1 month	1.0 ± 0.1	1.1 ± 0.1	0.6 - 1.7
May 1991	4 months	2.8 ± 0.1	2.7 ± 0.2	0.7 - 4.7
Aug 1991	7 months	4.9 ± 0.4	5.5 ± 0.4	1.4 - 6.0
May 1991	16 months	nd	16.2 ± 0.3	9.0 - 23

Handling and sorting efficiency controls

No starfish in the handling controls died. The mean number of 1-month old starfish recovered from the sorting efficiency controls was 45.25 ± 1.71, n = 4, indicating a 9.5% loss. In subsequent analyses, this correction factor was added to the number of starfish recovered from each of the natural rubble TREATMENT boxes. For 4-month-old starfish, all individuals were recovered from the sorting efficiency controls, so no correction factor was necessary.

Survival rates of starfish

1-month-old starfish

After deployment in the field for 6 days (actual time 5.75 days including 5 full night periods), a mean of 62% of starfish were recovered from the TREATMENT boxes and 92% were recovered from the CONTROLS (*Table* 2). This indicates a significant rate of mortality (t-test on transformed data, p = 0.0005) equivalent to about 6.49% day^{-1} in the TREATMENT boxes compared to 1.44% in the CONTROLS. This constitutes a predation rate of 5.05% day^{-1} in the TREATMENT boxes.

Table 2: Contents of CONTROL and TREATMENT boxes 6 days after deployment at Davies Reef. Each box was deployed with 100 juvenile *A. planci* (mean size ca. 1 mm, range 0.7 - 1.6 mm) initially. Unequal sample sizes resulted from 3 of the samples being lost when the barge carrying them accidentally submerged. Units are mean numbers ± 1SD; n: no. of replicates.

Fauna recovered from rubble	*Natural rubble treatment (n = 9)*	*Aquarium rubble control (n = 8)*
small *A. planci*	62.0 ± 16.1	92.0 ± 7.8
Worms		
mostly polychaetes	70.8 ± 32.7	18.0 ± 6.3
turbellarians	0.7 ± 1.3	-
Crustaceans		
crabs	1.1 ± 1.0	-
shrimps	3.2 ± 2.8	-
Galathiads	2.2 ± 1.2	-
isopods	2.7 ± 1.2	3.0 ± 2.7
others (mostly amphipods)	33.0 ± 12.9	2.2 ± 1.4
Molluscs		
gastropods	7.5 ± 7.4	-
bivalves	3.0 ± 1.4	0.5 ± 1.4
chitons	1.1 ± 0.9	-
opistobranchs	0.9 ± 0.6	-
Echinoderms		
echinoids	1.4 ± 1.3	-
ophiuroids	0.7 ± 0.7	0.6 ± 0.7
Fish	0.1 ± 0.3	-

4-month-old starfish

Starfish of this age were deployed for 13 days and after that time a mean of 85% of starfish had survived in the TREATMENT boxes compared with 95% in the CONTROLS (*Table* 3). This 10% difference was significant (t-test, $p = 0.002$) and amounts to a mortality rate of 1.24% day^{-1} in the TREATMENTS and 0.39% in the CONTROLS (predation rate=0.85% day^{1}).

Table 3: Contents of CONTROL and TREATMENT boxes 13 days after deployment at Davies Reef. Each box was deployed with 35 juvenile *A. planci* (mean size ca. 3 mm, range 1.5 - 4.5 mm) initially. Units are mean numbers ± 1SD; n: number of replicates.

Fauna recovered from rubble	*Natural rubble treatment (n = 10)*	*Aquarium rubble control (n = 10)*
small *A. planci*	30.1 ± 2.4	33.4 ± 1.7
Worms		
mostly polychaetes	47.4 ± 13.1	16.1 ± 6.9
turbellarians	0.5 ± 1.1	0.1 ± 0.3
Crustaceans		
crabs	1.8 ± 0.9	-
shrimps	4.2 ± 3.0	0.1 ± 0.3
isopods	6.9 ± 6.5	1.4 ± 1.9
others (mostly amphipods)	19.0 ± 11.6	0.1 ± 0.3
Molluscs		
gastropods	45.5 ± 13.8	-
bivalves	9.2 ± 2.3	
chitons	1.1 ± 0.9	0.1 ± 0.3
Echinoderms		
echinoids	1.0 ± 0.9	-
ophiuroids	0.9 ± 1.3	-
Fish	0.3 ± 0.5	-

7-month-old starfish

After 16 days deployment a mean of 94% of starfish were recovered from the TREATMENT boxes and 88% from the CONTROLS. This difference was not significant (t-test, $p = 0.184$). As all starfish recovered from the CONTROLS appeared healthy and no potential predators were encountered when sorting through the contents of the boxes it was feared that the majority of starfish missing from the CONTROLS had either somehow escaped between the box and the lid in response to lack of food or had not been sorted and counted efficiently (rubble from CONTROLS was not fixed in formalin and sieved prior to sorting). A trial was carried out *a posteriori* in large aquaria to examine whether starfish would escape from the boxes in the absence of food and to measure the sorting efficiency. The trial, carried out over five days, showed that while sorting efficiency was 100%, that 30% of the starfish escaped from the boxes that had no substratum and 5% escaped from the boxes with

CONTROL rubble. Thus we expect that the lower rate of recovery of starfish from the CONTROL boxes in the field experiment was due largely to escape.

The mean percentage of *A. planci* recovered from the OPEN boxes was 93%. There was no significant difference between this and the percentage recovered from the TREATMENT boxes (t-test, $p = 0.816$). These data indicate firstly, that exposing the animals to mobile predators outside the boxes did not contribute significantly to the mortality rate over the period of the deployment. Secondly, they indicate that few starfish escaped from the OPEN boxes and that leaving the lids off the boxes did not contribute significantly to the escape rate. So although escape from the TREATMENT boxes cannot be ruled out we suggest the measured mortality rate of 0.45% day^{-1} is reasonable.

16-month-old starfish

No starfish were lost from the experimental deployment of this age class over 13 days. Longer deployments using larger enclosures will be required to assess whether mortality rates of these larger starfish are high enough in field populations to be detected.

Rubble epifauna

Assessment of the motile epifauna present among the natural rubble indicated that worms, crustaceans and molluscs were common amongst the rubble (*Tables 2/3*). Polychaetes, amphipods and gastropods made up most of the mobile epifauna, although crustaceans such as crabs and shrimps were also found in the samples. It is likely that some of these animals would be predators of the small starfish. Non-mobile epifauna were not quantified but included corals, bryozoa, zoanthids, sponges and oysters.

Escape Controls

Results from the recovery of starfish from the ESCAPE controls (*Table 4*) indicate that starfish move very little initially and become more mobile as they grow. None of the 1-month-old starfish moved from the inner to the outer section of the boxes. The low rates of movement in the larger starfish suggests that in the future these can be deployed in larger OPEN boxes for longer periods which may provide greater information on predation rates.

Table 4: Proportion of juvenile *Acanthaster planci* recovered from ESCAPE control boxes after field experiments. All starfish were initially placed in the inner boxes; 50 starfish per box at age 1 month, 20 at 7 months and 10 at 16 months. Calculation of percentage escaped assumes that starfish unaccounted for died in the inner and outer boxes in proportion to the living ones recovered from those boxes; n: number of replicates.

Deployment date (days)	*Starfish age (months)*	*Inner box* ($X \pm 1SD$)	*Outer box* ($X \pm 1SD$)	*Percent escaped (%)*	*n*
Feb 1991 (6)	1	44.5 ± 0.7	0.0 ± 0.0	0	2
Aug 1991 (16)	7	16.6 ± 1.5	2.0 ± 1.0	11	5
May 1991 (13)	16	7.8 ± 2.2	2.2 ± 2.2	22	5

Water exchange in boxes

Fluctuations in dissolved oxygen content of water in the CLOSED box demonstrate the effects of obstructing water flow to the epibenthic community living on dead coral rubble (*Table 5*). Deprived of any water exchange, oxygen levels in the CLOSED box rose rapidly to more than double that of normal by the second day and then plummeted to only 20% of normal after 3 days. Slight elevation followed by depression of oxygen levels in the DOUBLE-MESH boxes indicates that some significant reduction in water flow was occurring. Oxygen levels in the TREATMENT boxes were unaffected over the four days examined. All visible fluorocene had cleared from the TREATMENT boxes within 10 minutes. Substantial amounts of the dye remained in the DOUBLE-MESH box after 30 minutes but had cleared completely after three hours. These results made us confident that sufficient water exchange was occurring in the TREATMENT boxes and not contributing to survival rates of starfish.

Table 5: Dissolved oxygen content of water (mean ± 1SD) sampled from TREATMENT boxes 0 to 4 days after deployment; n: number of replicates; nd: no data.

Water sampled from		*Dissolved oxygen (mg/l^{-1})*			
	n	*Day 1*	*Day 2*	*Day 3*	*Day 4*
Water column	2	6.5 ± 0.1	nd	6.6 ± 0.0	6.6 ±0.0
Interstitial water	2	6.4 ± 0.1	nd	nd	6.7 ±0.1
Mesh box	2	6.4 ± 0.1	nd	6.6 ± 0.1	6.6 ±0.1
Double mesh box	2	6.3 ± 0.2	nd	6.8 ± 0.5	5.4 ±1.1
Closed box	2	6.5 ± 0.1	14.3 ± 0.1	1.4 ±0.7	nd

Discussion

Mortality rates

Mortality rates for *A. planci* in field populations have been measured at 99.3% between 8 and 23 months of age (1.08% day^{-1}) (Zann *et al.* 1987) and 75% between 22 and 34 months of age (0.39% day^{-1}) (Doherty and Davidson 1988). Mortality rates for younger starfish have not previously been presented and our results confirm an expected age dependent decrease in mortality, based on the assumption that caging was restricting mortality of the larger starfish in the boxes. The high rates of mortality in 1-month-old starfish found in this study also indicate that mortality levels following settlement are very high and thus have the potential to influence the population dynamics of *A. planci.*

All measured rates of mortality for *A. planci* (ie. Zann *et al.* 1987, Doherty and Davidson 1988, this study) have come from populations with very high (ie. outbreak) densities. If mortality rates are density dependent then these rates may be lower than might be expected in low density populations. McCallum *et al.* (1989) have discussed how predators with a *Type II* functional response (*sensu* Holling 1959) could greatly affect population dynamics of *A. planci* at low densities. On the other hand if predators exhibit a *Type III* functional response (Ormond *et al.* 1990) then predation rates at low density will be disproportionately lower than at high density. Now that the techniques described here have been tested it is planned to repeat the experiments described here examining the influence of starfish density on mortality rates. Density dependent mortality in newly settled non-sessile marine invertebrates (abalone) has been demonstrated by McShane (1991). He suggested that intraspecific competition for favourable living sites resulted in higher levels of predation and dislodgment by strong water movement at high densities.

A. planci have been observed in the laboratory to have strong preferences to settle on particular substrates, perhaps induced by some chemical cue provided by bacteria (Johnson *et al.* 1991). Just how important these settling preferences are in determining post-settlement survival rates is not known. However juvenile starfish in our experiments moved very little suggesting that settlement in areas where predators are few would enhance survival rates. This type of behaviour is known to enhance survival in echinoids (Highsmith 1982) and ascidians (Young 1989). However preferential settlement in areas of favourable food supply would also enhance survival as suitable food availability is known to greatly affect growth rates (Lucas 1984, Keesing and Halford 1992).

The only other published information on mortality rates of newly settled echinoderms in the field is that of Rowley (1990) who recorded change in density of newly settled sea urchins in two habitats and found that mortality over the first 40 days or so was 5.59% day^{-1} in kelp beds and 3.10% day^{-1} outside kelp beds. Such habitat differences may also be important for survival rates of *A. planci.* Yokochi *et al.* (1988) recorded recruitment rates of 0.82 m^{-2} on the slope and 0.06 m^{-2} on the reef flat of the same reef. Zann *et al.* (1987) also found within reef differences in recruitment rates. It is not known whether these differences result from differential levels of settlement or post-settlement mortality or a combination of both. Black and Moran (1991) have demonstrated how small scale hydrodynamics may influence settlement density of *A. planci* within reefs. To determine whether the most significant influences on *A. planci* population dynamics take place pre- or post-settlement, studies which seek to isolate settlement rates from recruitment rates will be vital.

Techniques

Whilst other studies have monitored the survival rates of newly settled marine invertebrates (eg. Rowley 1990, Luckenbach 1984) and carried out laboratory experiments on survival rates of reared juveniles (eg. Highsmith 1982), ours is the first study to our knowledge undertaking field deployment of large numbers of juveniles reared in the laboratory. This approach has been necessary because, despite large numbers of outbreaks of adults, juveniles are rarely encountered in the field (Johnson 1992) and certainly not in numbers required for manipulative ecological experimentation.

This study has demonstrated that the techniques outlined allow measurement of mortality rates of small non-sessile benthic animals in the field allowing for partitioning the effects of predator and non-predator induced mortality. The low rates of movement detected for the starfish suggests that in the future they can be deployed in OPEN boxes for long periods will provide greater information on predation rates and overcome the problem of artificially excluding the larger mobile predators such as fish which occurs in the boxes with lids.

Because our experiments excluded these large mobile predators, the extent to which our measured rates of mortality are typical of nature is not known. With both predator and prey caged, interactions between the starfish and larger more mobile prey are not adequately measured. This means that at present our measured rates of mortality are likely to be underestimates, particularly at ages > than 1 month.

Schiel and Welden (1987) found that laboratory reared abalone had less well developed predator avoidance behaviour than wild caught abalone and were thus significantly more vulnerable to predation. It is not known how our laboratory reared *A. planci* compare with wild animals although they exhibit the same diel pattern of remaining cryptic during the day and emerging at night to feed as has been recorded for large juvenile starfish in the field (Keesing 1990).

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An experimental investigation of the ability of adult crown-of-thorns starfish to survive physical damage.

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Abstract

On three occasions, adult Acanthaster planci were collected from a high density population and subjected to various levels of physical damage including bi- and tri-section. They were then held in cages for approximately 15 days to monitor survival. Results were variable: in one instance, where even bisection did not affect survival over the experimental period. On the other occasions damaged individuals showed poorer survival. Starving the animals for six weeks prior to the experiment did not reduce survival compared with that of newly collected individuals. Varying the density of animals in cages found lower survival at lower densities implying that the transmission of pathogens was not artificially high in cages. Given the variable results of this and other studies, and the frequency of damaged but healed or regenerating starfish in natural populations, predation is only conclusively lethal if the whole starfish is removed.

Introduction

Attention has been focussed on potential predators of the crown-of-thorns starfish, *Acanthaster planci,* because several authors have suggested that human impacts on populations of predators have increased the frequency of outbreaks (Endean 1976, Endean and Cameron 1990, Ormond *et al.* 1990). An adult *A. planci* represents a large prey item for all but the largest fishes and gastropods and it is well documented that *A. planci* of all sizes frequently have damaged and regenerating arms (refs. in Moran

1986, McCallum *et al.* 1989, Yokochi and Ogura 1987, Zann *et al.* 1987), which suggests that a proportion of predatory encounters are not fatal. Observations of predation are rare, but there are instances both of one fish killing a starfish (Ormond and Campbell 1974, Randall *et al.* 1978, *Marine Biologic* 1991) and of a fish's guts containing only part of a starfish (Birdsey 1988).

It is also of interest to know the extent of damage that is likely to be fatal to starfish for the purposes of control. Physical cutting of starfish seems to have been avoided as a control method for fear that the animals will regenerate damaged parts and survive and even multiply (Birkeland and 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, requiring equipment of varying sophistication, careful handling and involving risks to other reef organisms as well as the operators themselves. In this study we set out to investigate the extent of damage that would be fatal to adult starfish.

Materials and Methods

All fieldwork was carried out at Davies Reef (18^{o} 50'S, 147^{o} 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 three experiments: winter 1991, summer 1991 and winter 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 hours before processing.

The winter 1991 experiment 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. The treatment groups were: controls, two-, four-, eight-arms cut off and bisected starfish. Controls were collected and transferred to the holding tank, then lifted out of the tank placed on a flat surface, and then placed in another tank for transportation to the experimental cage. 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 at the point where the arm joined the oral disc with a diving knife. A final group was treated similarly except that starfish were cut in half across the oral disc and one half was discarded. *Figure 1* shows the frequency of arm damage in starfish in outbreak populations from two reefs in the central area of the Great Barrier Reef in the late 1980s. While 63% of individuals had damage to one or more arms, most had lost parts of one or two arms only and individuals with damage to more than six arms were very rare. Assuming that more extensive damage is fatal, the experimental treatments range from non-lethal to lethal.

The 20 members of each treatment group were then placed in a pen of 12 mm square mesh 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. 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.

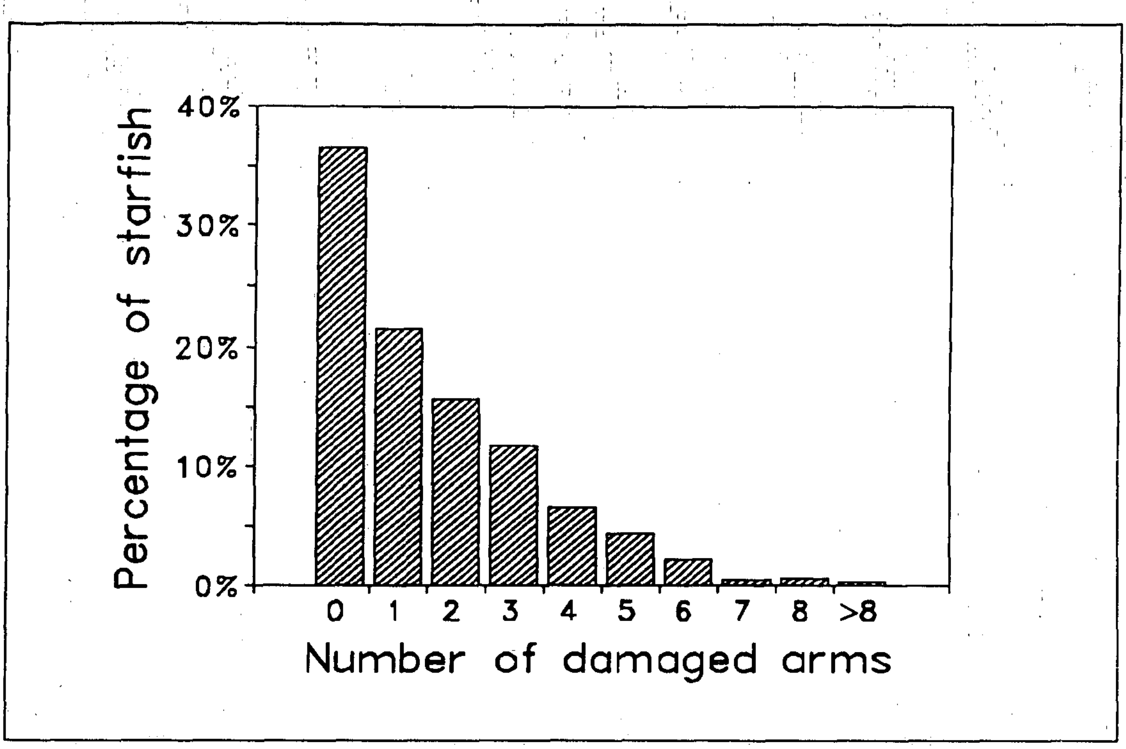

Figure 1: Proportion of 638 *A. planci* from natural populations with damaged arms. Samples from outbreaks at Keeper and Helix Reefs 1985-87 (Kettle, *unpublished*).

In the first experiment (winter 1991), very few starfish died in the two week period following damage. There have been elevated densities of starfish at Davies Reef for some years, but the population does not appear to have formed local concentrations that decimate all the coral and lead to malnutrition. For this reason, we decided to include animals that were less healthy due to starvation in future experiments to simulate a situation where high densities of starfish eat the coral to extinction. Kettle (1991) 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. He found that about half the total decline occurred in six weeks. In mid-October 1991, six weeks prior to the summer 1991 experiment, 108 starfish were collected and kept in cages without any live coral. Ninety-seven animals survived after six weeks.

The summer 1991 experiment was set up 6 - 14 December. There were two other differences to the winter 1991 experiment beside the inclusion of a starvation treatment. The damage treatments were also changed by omission of the loss of two arms and addition of a treatment where two thirds of the 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. The design of cages was also different: rather than having a single pen, we used rectangular cages 3.5 x 1.5 x 0.45 m made of the same 12 mm square mesh. Each cage was divided into two compartments so that the starved and unstarved animals were kept separated but 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 all put into one cage and later omitted from analyses. To compensate, twenty-five more unstarved starfish were placed in the other cage on 14 December. Cages were checked on 21 December (7 - 15 days) and the experiment finished 3 January 1992 (20 - 27 days).

The winter 1992 experiment was set up 25 - 29 May and was similar to the preceeding experiment and involved the same damage levels for newly collected starfish. Once again, animals that were cut in half were combined with those that had two thirds of their arms removed for analysis. One hundred and twelve *A. planci* were collected six weeks before, but all except 30 died during the period of starvation, and five of those had obvious necrosis.

The remaining 25 starved animals were put in one cage and allocated to only two treatments: undamaged controls and loss of eight adjacent arms. 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. All cages were made of heavier mesh to resist puffer fish. Each cage consisted of a single compartment measuring 1.2 x 2.0 x 0.4 m. The experiment finished 12 June (14 - 17 days).

In all experiments, the counts of survivors after approximately 15 days were used. At the end of each experiment, the starfish were inspected individually before release to determine which treatment group they belonged to. This was not always obvious because the body wall may contract to seal wounds causing the animal to assume contorted shapes. Also, necrotic tissue may also form along the edge of wounds so it may become hard, for example, to distinguish animals cut in half from those that lost eight arms. In the experiment in summer 1991, the animals were censused at 7 - 15 days by looking at them through the cage, though they were handled and inspected individually at the end of the experiment. For analysis we used counts from the 7 - 15 day census but adjusted them where these contradicted the final census.

Results

Effects of damage

When freshly collected and apparently healthy animals are considered, the effects of increasing arm loss varied among the experiments (*Fig. 2a - 2c*, significant interaction in *Table 1*). Because of this the experiments will be considered separately. In the experiment in May 1991, there was no significant difference in survival among the groups of damaged animals (*Fig. 2a*). This was true whether the five levels of damage were considered separately (logistic regression, slope not significantly different from zero, $x^2 1 = 0.0$) or all damaged starfish were grouped together and compared with the undamaged control group ($x^2 1 = 0.06$). By contrast in the experiment in December 1991, survival tended to decrease with increasing arm damage for unstarved *A. planci*

(*Fig.* 2*b*, logistic regression, slope greater than zero, $x^{2}1 = 18.88$, $p < 0.001$). In the experiment in May - June 1992, survival was less among damaged individuals than among controls, but it did not decrease linearly with increasing extent of the damage (*Fig. 2c, Table* 2).

Table 1: Effect of damage on survival of freshly collected *A. planci*. Analysis of deviance table for May 1991 (-2 arms omitted), December 1991 and May 1992 (- $^{1}/_{2}$ and - $^{2}/_{3}$ combined). I = intercept, D = damage, E = experiment.

Model	Deviance	df	Difference	δdf	component	p
I+E	103.5	10	$d_{I+D+E} - d_{I+E}$ = 53.31	1	D	0.000
I+D	115.0	10	$d_{I+D+E} - d_{I+D}$ = 64.81	1	E	0.000
I+D+E	53.90	9	$d_{I+D+E+DxE} - d_{I+D+E}$ = 46.19	6	DxE	0.000
I+D+E+DxE	7.71	3				0.052

Table 2: Effect of damage on survival of freshly collected *A. planci*. Analysis of deviance tables for experiment in May 1992 (- $^{1}/_{2}$ and - $^{2}/_{3}$ combined).
I = intercept, D = damage.

Model	Deviance	df	Difference	δdf	component	p
Linear scale of increasing damage.						
I	50.60	3	$d_{I+D} - d_{I}$ = 43.66	1	D	0.000
I+D	6.94	2				0.031
Controls vs all damaged animals combined.						
I	50.60	3	$d_{I+D} - d_{I}$ = 47.50	1	D	0.000
I+D	3.10	2				0.212

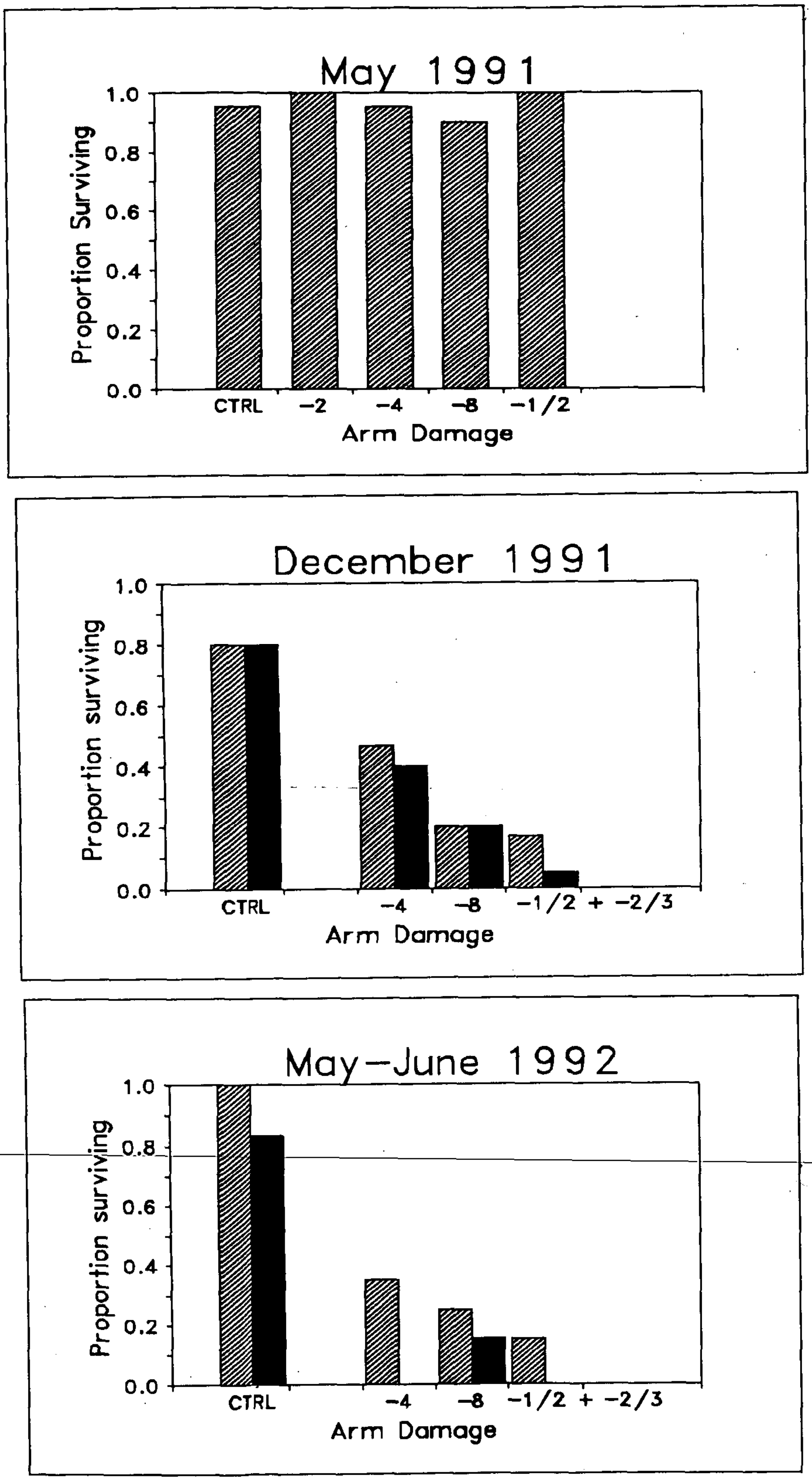

Figure 2: Proportions of *A. planci* subject to different levels of arm damage surviving in the three experiments. Hatched bars represent newly collected animals, filled bars represent starved animals.

Effect of starvation and damage

The low survival of starfish over the six week starvation period prior to the experiment in May 1992 meant that the effect of starvation could only be examined at two levels of damage (controls and -8 arms). Considering these levels of damage in the December 1991 and May 1992 experiments, there was no evidence that starvation had a significant effect (*Table* 3). The intensity of the effect of damage differed between experiments (*Table* 3), but in each experiment damaged starved starfish showed poorer survival than starved control animals (*Fig.* 2*b*, 2*c*).

Table 3: Effect of starvation on survival of damaged *A. planci*. Analysis of deviance table for experiments in December 1991 and May 1992. Data from two damage treatments (Control and -8 arms) subjected to logistic regression.
I = intercept, D = damage, E = experiment and S = starvation.

Model	Deviance	df	Difference	δdf	component	p
I+E	65.33	6	$d_{I+D+E} - d_{I+E}$ = 55.84	1	D	0.000
I+D	20.37	6	$d_{I+D+E} - d_{I+D}$ = 10.88	1	E	0.001
I+D+E	9.49	5	$d_{I+D+E+DxE} - d_{I+D+E}$ = 3.87	1	DxE	0.049
I+D+E+DxE	5.62	4	$d_{I+D+E+S+DxE} -$ $d_{I+D+E+DxE}$ = 1.75	1	S	ns
I+D+E+S+DxE	3.87	3	$d_{I+D+E+S+DxE+SxE} -$ $d_{I+D+E+S+DxE}$ = 0.99	1	SxE	ns
I+D+E+S+DxE +SxE	2.88	2	$d_{I+D+E+S+DxE+DxS+SxE} -$ $d_{I+D+E+S+DxE+SxE}$ = 1.86	1	DxS	ns
I+D+E+S+Dx+ DxS+SxE	1.02	1				

Table 4: Effect of starvation on survival of damaged *A. planci*. Analysis of deviance table for December 1991 with 4 levels of damage (- $^1/_2$ and - $^2/_3$ combined) subject to logistic regression. I = intercept, D = damage, S = starvation.

Model	Deviance	df	Difference	δdf	component	p
I+D	47.99	6	$d_{I+D+S} - d_{I+S}$ = 44.35	1	D	0.000
I+S	4.54	6	$d_{I+D+S} - d_{I+D}$ = 0.90	1	S	ns
I+D+S	3.64	5	$d_{I+D+S+DxS} - d_{I+D+S}$ = 0.30	1	DxS	ns
I+D+S+DxS	3.34	4				ns

There is no statistical evidence that starvation affected survival in the December 1991 experiment when freshly collected and starved animals were subjected to four levels of damage (*Fig. 2b*; *Table 4*) or in May 1992 (*Fig. 2c*, logistic regression,$x^{2}1 = 2.41$, $p > 0.1$).

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 (*Fig. 3, Table 5*) but the difference was a matter of degree rather than a qualitative difference. More importantly, survival was lower at the low density (*Fig. 3*). There was no evidence that the experimental density increased mortality by favouring pathogens.

Table 5: Effect of density on survival of damaged *A. planci*. Analysis of deviance table for May 1992. I = intercept, D = damage, LD = low density.

Model	Deviance	df	Difference	δdf	component	p
I+LD	41.03	2	$d_{I+D+LD} - d_{I+LD}$ $= 31.50$	2	D	0.000
I+D	9.53	2	$d_{I+D+LD} - d_{I+D}$ $= 4.20$	1	LD	0.040
I+D+LD	5.33	1	$d_{I+D+LD+DxLD} - d_{I+D+LD}$ $= 5.33$	1	DxLD	0.021

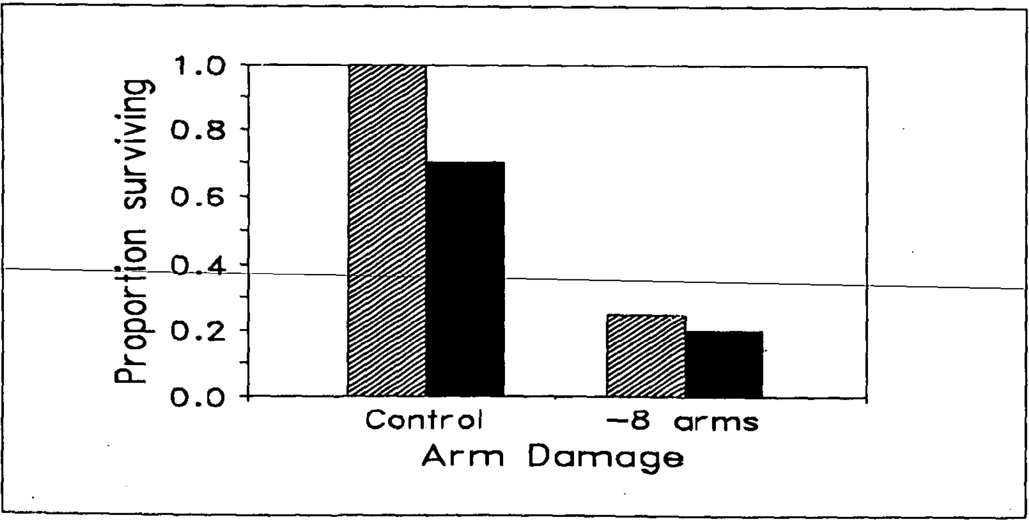

Figure 3: Comparison of survivorship of *A. planci* held at experimental density (hatched bars) and a lower density (filled bars), May - June 1992.

DISCUSSION

The aim of this project was to determine the degree of arm damage that is fatal to adult crown-of-thorns starfish. The results of the three 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 two experiments. There are two obvious sources of variation among experiments: seasonal changes in reproductive condition and progressive ageing of the main cohort of the population.

There was a decrease in survival of control starfish in the December 1991 experiment. Controls serve to show the effect of handling on the experimental animals. The experimental procedure meant that handling was a considerable source of stress, since the animals were lifted out of the water during collection and during experimental processing; at either instance the coelomic membrane could rupture. The experiment coincided with the main spawning period for 1991 at Davies Reef (R Babcock, *pers. comm.*). The bulk of the current population reached maturity in summer 1988-89 which would make them 6+ years old at the time of the experiment. We suggest that the low survivorship even among control animals in December 1991 was due to the experimentally induced stresses being added to the physiological stresses of gonad production. This would mean that adult *A. planci* are most susceptible to damage at the time when they have maximally developed gonads and so would presumably be most energetically rewarding as prey. The differences in survival rate over the two periods of starvation prior to the experiments in December 1991 (about 90%) and May-June 1992 (<25%) suggests that there may be a general ageing of the population. Prior to the last experiment, the starfish were held in four cages each containing 28 animals. The poor survival was general: all the starfish in one cage were dead after six weeks and no cage contained more than ten intact starfish.

However the differences among experiments came about, the finding of the experiment in May 1991, 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 in diameter) 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 and Lucas 1990). Predation is only certainly lethal if the whole starfish is taken, though this may be achieved by several predators acting together.

Our 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 50m 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 366 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 and Lucas 1990). In summary, the extent of physical damage that *A. planci* can survive seems very variable and, though size may be important, there are clearly other unknown factors involved.

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Are crown-of-thorns starfish populations chaotic?

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Abstract

A model of the interaction between coral and starfish is presented. The model is based on time-delayed differential equations, and addresses the question of whether crown-of-thorns starfish populations display chaotic dynamics. The preliminary conclusion is that they do not appear to do so: for most reasonable parameter combinations the model approaches a stable equilibrium, and even sustained cycles occur only for a narrow range of parameter values. It therefore appears that the apparent unpredictability in starfish population dynamics is generated mostly by stochastic variation, rather than by intrinsic properties of the interaction. This conclusion must, however, be qualified until further work is completed.

Introduction

The suggestion that the population dynamics of the crown-of-thorns starfish may be chaotic has been made a number of times (eg. Bradbury *et al.* 1985, McCallum 1992a). The life history of the starfish has features that contain the "seeds of chaos": a very high reproductive potential per generation, coupled with over-exploitation of a slowly recovering resource (coral).

Apart from the theoretical interest in demonstrating that the population dynamics of the starfish are chaotic, there are issues of practical importance. If the underlying dynamics of the coral-starfish interaction are chaotic, then very small changes in the amount of interchange of larvae between reefs may result in very large differences in population behaviour (McCallum 1992a, b). Conversely, if the underlying dynamics of the interaction are not chaotic, and the observed variation in starfish numbers is caused purely by stochastic factors, then small changes in the rate of larval interchange will make only small changes in the resulting behaviour of the system. If a system is governed by deterministic chaos, long term prediction of its behaviour is impossible because of the sensitivity to initial conditions which is one of the hallmarks of chaos. However, since the underlying processes are deterministic, short term predictions of the behaviour of the system may be possible (Sugihara and May 1990).

Detection of deterministic chaos in any natural population is difficult. There are two possible approaches. First, an extended time series of population data may be interpreted, and either an attractor reconstructed (Takens 1981, Schaffer 1985) or a form of non-linear forecasting used (Sugihara and May 1990). Analysis of time series is unlikely to be successful with *Acanthaster*, because of the short run of available data (covering less than 30 years and two outbreaks for the Great Barrier Reef; Reichelt 1990). A second approach is to develop a model appropriate to the system, and demonstrate that, with appropriate parameter values, the model behaviour is chaotic. This was the approach used by Hassell, Lawton and May (1975) in their (largely unsuccessful) search for chaos in single-species insect systems, and is the approach taken in this paper.

A Simple Model

Rationale

The model which follows attempts to represent the following features of the starfish-coral interaction:

(a) Starfish have four distinct life history stages: pelagic eggs and larvae (approximately 30 days from spawning to settlement); algal feeding juveniles (approximately 6 months duration post settlement), coral feeding pre-reproductive juveniles (from 6 months to approximately 2 years post settlement); and reproductive adults, with an indefinite life span, but a life expectancy of approximately 2 years post maturity (provided coral is available). Larvae and algal feeding juveniles are assumed to have density-independent death rates, and hence are not explicitly included in the model, although the time delay caused by transition through these stages is included. For simplicity, and so that a stage-structured approach (Gurney, Nisbett and Lawton 1983) can be used, all pre-reproductive coral feeders are considered to be identical, as are all starfish of reproductive age. Two basic variables thus describe the starfish population: $A(t)$ the number of coral feeding juveniles at time t; and $N(t)$, the number of reproductive adults.

(b) Coral communities on the Barrier Reef have very high species diversity, and one of the main concerns about the crown-of-thorns is that it may have irreversible and fundamental effects on this diversity (Done 1990, Endean *et al.* 1989). Nevertheless, corals of the genus *Acropora* are the preferred prey of *Acanthaster*, the dominant taxon in terms of cover and amongst the most rapidly-recovering corals following crown-of-thorns attack. Coral is therefore included in this model as a single variable, $C(t)$, representing the coral cover per hectare, with parameters appropriate to *Acropora*.

Coral dynamics are represented by a simple logistic equation with carrying capacity K and intrinsic growth rate r. This simple representation assumes that coral recovery occurs through vegetative growth from colony remnants, rather than requiring settlement from off the reef.

(c) Starfish eat coral at a constant *per capita* rate, unless coral cover is very low, in which case the consumption rate will be restricted by the ability of starfish to locate coral. Although there is little evidence on the functional response of starfish to corals, a type II response seems reasonable, given the above argument. As obligate corallivores, there is little possibility that starfish will be able to switch to alternative prey at low coral densities, and thus generate a type III functional response. As reproductive age-starfish $N(t)$ are much larger than immature starfish $A(t)$, I assume that only mature starfish have a noticeable effect on coral cover. Coral cover, however, has an effect on the death rate of both age classes of starfish, and also on the development rate of immature starfish.

There is no doubt that recruitment is highly stochastic in the crown-of-thorns, and that starfish populations on the scale of single reefs (of a size from 0.5 to 20 km) are open, and subject to substantial larval inflow and outflow. The objective of this paper, however, is to examine the possibility that the observed extreme temporal variability in crown of thorns populations may be at least in part a function of intrinsic population processes, rather than purely a result of environmental variation. Initially, stochastic effects are therefore not included.

Model Structure

The model is constructed as a variant of the basic stage-structured approach of Gurney, Nisbett and Lawton (1983), in which the length of one or more stages is allowed to be a dynamic variable (Nisbett and Gurney 1983).

The following equations describe the system:

Stages

Coral feeding juveniles $A(t)$
Duration of period τ_A depends on coral cover, as does mortality $\delta_A(t)$. As juveniles are much smaller than adults, their impact on coral cover is negligible. Algal feeding juveniles must pass through an algal feeding stage of fixed duration τ_j, during which they have a constant mortality rate of δ_j.

Adults *N(t)*

Indefinite lifespan, though mortality $\delta_N(t)$ is dependent on coral cover, as is fecundity $\lambda(t)$. Starfish eat coral according to a type II functional response.

Coral *C(t)*

Grows according to a simple logistic, with intrinsic growth rate r and carrying capacity K. It is significantly consumed only by adults, following a type II functional response, represented as

$$\text{consumption}=\frac{C(t)\eta}{C(t)+q} \tag{1}$$

where η is the coral consumption rate at high coral densities, and q describes the coral cover at which searching limitations become important.

Auxiliary variables: *P(t)* and $\tau_A(t)$

The stage-structured formulation with variable time lags requires two variables in addition to the life history stages themselves for each stage with an explicit delay: one for the time lag, and a second for the proportion of individuals that survive through the stage. $P(t)$ is the proportion of individuals surviving through $A(t)$ at time t and $\tau_A(t)$ is the time these individuals have spent as subadults. Thus, the basic equations are:

$$\frac{dA}{dt}=R_A(t)-\frac{g(t)}{g(t-\tau_A(t))}R_A\left(t-\tau_A(t)\right)P(t)-\delta_A(t)A(t) \tag{2}$$

$$\frac{dN(t)}{dt}=\frac{g(t)}{g(t-\tau_A(t))}R_A\left(t-\tau_A(t)\right)P(t)-\delta_N(t)N(t) \tag{3}$$

$$\frac{dC(t)}{dt}=rC(t)\left(1-\frac{C(t)}{K}\right)-\frac{N(t)C(t)\eta}{C(t)+q} \tag{4}$$

$$\frac{dP(t)}{dt}=P(t)\left[\frac{g(t)\delta_A\left(t-\tau_A(t)\right)}{g\left(t-\tau_A(t)\right)}-\delta_A(t)\right] \tag{5}$$

$$\frac{d\tau_A(t)}{dt}=1-\frac{g(t)}{g\left(t-\tau_A(t)\right)} \tag{6}$$

$$g(t)=\frac{bC(t)}{q+C(t)} \tag{7}$$

Here, $g(t)$ is the growth rate of subadults at time t. The scaling parameter b is arbitrary. The death rate of subadults, as a function of coral cover, is given by:

$$\delta_A(t)=\frac{\mu_{A1}q+\mu_{A2}C(t)}{q+C(t)} \tag{8}$$

and the death rate of adult starfish is:

$$\delta_N(t)=\frac{\mu_{N1}q+\mu_{N2}C(t)}{q+C(t)} \tag{9}$$

The reproductive rate of starfish is similarly a function of their coral consumption rate. At high coral cover, it is assumed to reach a maximum of Λ, but is assumed to decrease with coral cover following the type II functional response. Hence, the per capita rate of larval production $\lambda(t)$ is given by:

$$\lambda(t)=\frac{C(t)\Lambda}{q+C(t)} \tag{10}$$

As starfish are thought to spawn annually, a pulsed recruitment function $R_A(t)$ is used, in which starfish reproduce only in the first two months of the year.

If $T\left(t-\tau_j\right)<60$,

$$R_A(t)=\lambda\left(t-\tau_j\right)N\left(t-\tau_j\right)\exp\left(-\tau_j\delta_j\right) \tag{11}$$

otherwise, $R_A(t)=0$.

Here,

$$T(t)=t-\text{Int}\left(t/365\right)\times 365 \tag{12}$$

The model structure is shown schematically in *Figure 1*.

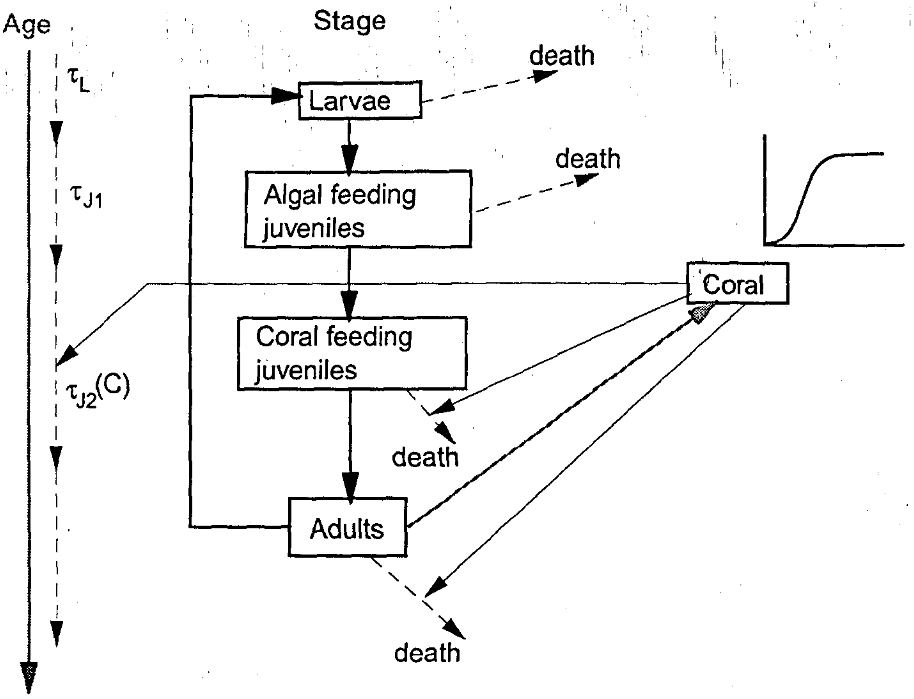

Figure 1: Structure of the model: Compartments within the model are represented as boxes. Heavy black arrows represent transitions between life history stages of the starfish, and the heavy grey arrow represents removal of coral biomass by starfish. Time delays are represented on the time line to the left of the figure, and light arrows represent effects of coral cover on various parameters.

Model Parameters

Parameter values used in these initial simulations are given in *Table 1*. These were derived from a variety of sources, principally Moran (1986), and will require extensive sensitivity testing. Time units for all parameters are days. Population density or other spatial units are in square metres.

Table 1: Parameter values used for initial simulations.

Parameter	meaning	value
τ_j	time in algal feeding stage	180
δ_j	death rate of algal feeders	0.02
μ_{A1}	death rate of juvenile coral feeders without food	0.05
μ_{A2}	death rate of juvenile coral feeders with excess food	0.002
μ_{N1}	death rate of adults without food	0.02
μ_{N2}	death rate of adults with excess food	0.002
b	arbitrary scaling parameter for growth	1
K	maximum coral cover	5,000
η	maximum rate of coral consumption by adults	0.164
r	rate of coral recovery	0.00082
Λ	maximum annual starfish fecundity (recruits/adult)	100,000
$\tau_A(0)$	Time delay in subadult stage with excess coral	547

Model Results

A complex model such as this requires extensive sensitivity analysis and exploration with a full range of parameter combinations. In this preliminary investigation, however, I have focussed attention on one particularly important parameter, q, which describes the way the coral consumption rate of the adult starfish (and hence their mortality) depends on coral cover. Biologically, this parameter will be a function both of the behaviour of the starfish and the physical patchiness of the coral resource. *Figure 2* shows the functional response of the starfish (equation 1) for various values of q. The main point to be gained from this figure is that q=400, q=350 and q=330 would be essentially indistinguishable in practice, and in each, the predation rate of starfish is not markedly reduced until coral cover drops to about 20%. In contrast, when q=800, the predation rate does not asymptote until coral cover is close to the carrying capacity of 5000 m^2. Runs of the model for each of the values of q in *Figure* 2 are shown in *Figures* 3-6. When q=800 (*Figure* 3), the system settles quite rapidly to an equilibrium with coral cover slightly depressed and a "chronic" starfish population of less than 10 ha^{-1}. (Note that the short-period oscillations in both starfish and coral are a function of the pulsed annual recruitment, and are not related to predator-prey cycling.)

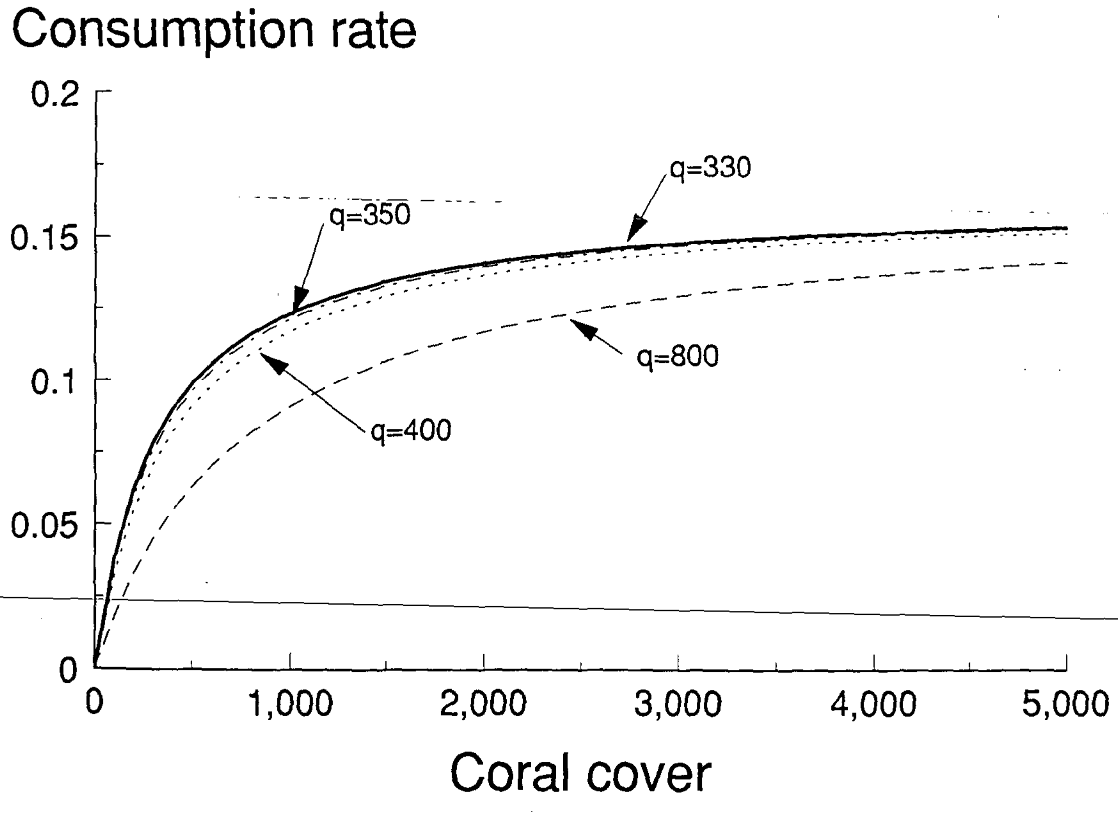

Figure 2: Representative starfish functional responses.

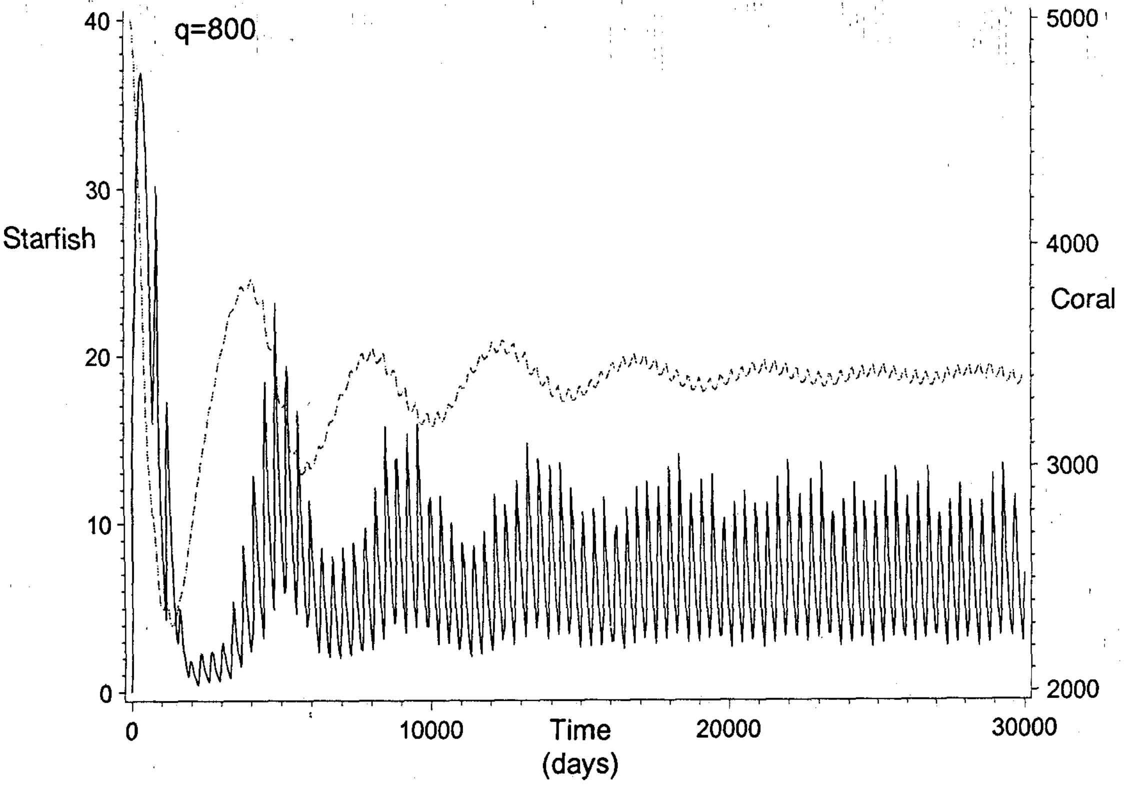

Figure 3: Adult starfish numbers and coral cover with $q=800$. Adult starfish numbers (ha^{-1}) are shown as a solid line, scaled on the axis to the left of the figure. Coral cover (m^2ha^{-1}) is shown as a dashed line, scaled on the axis to the right.

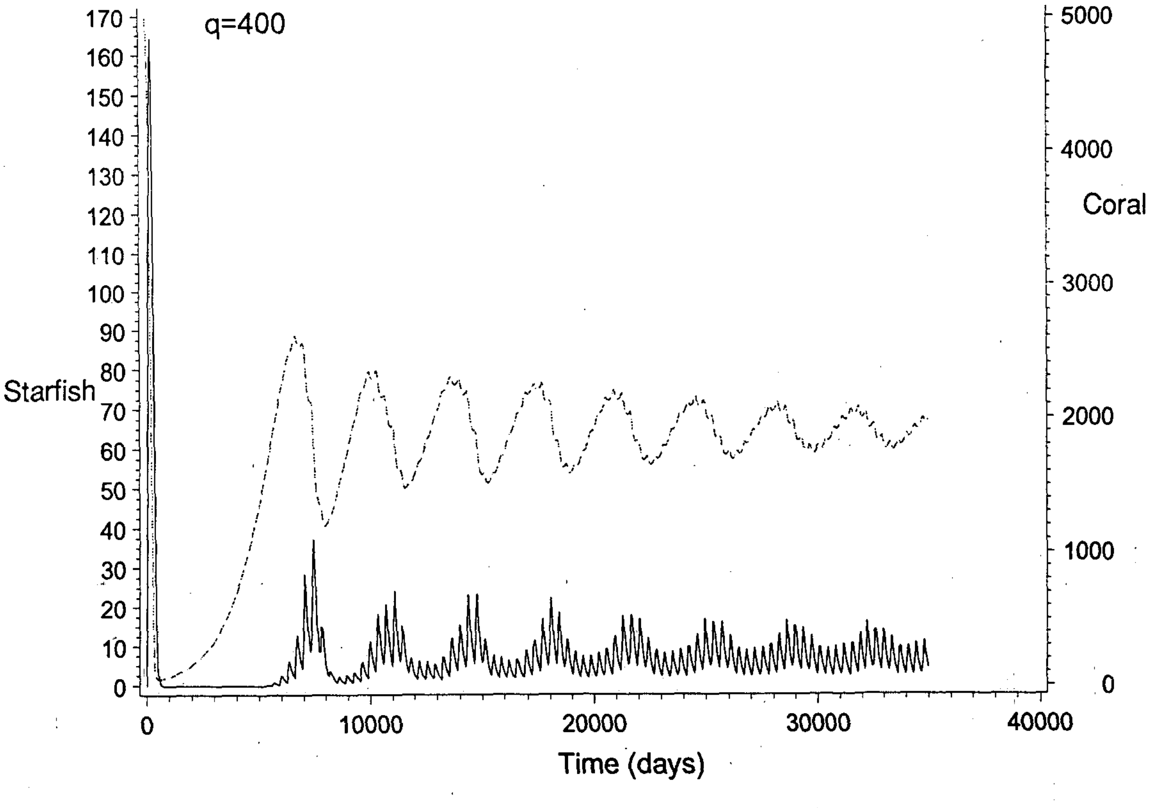

Figure 4: Adult starfish numbers and coral cover with $q=400$. Details as in *Figure* 3.

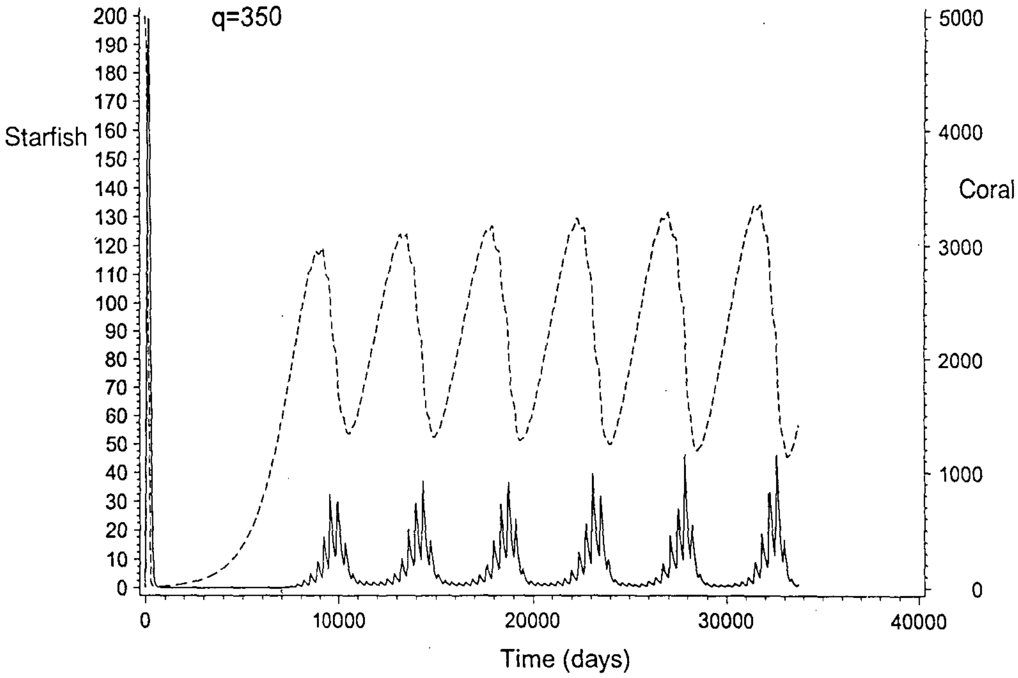

Figure 5: Adult starfish numbers and coral cover with q**=350.** Details as in *Figure 3.*

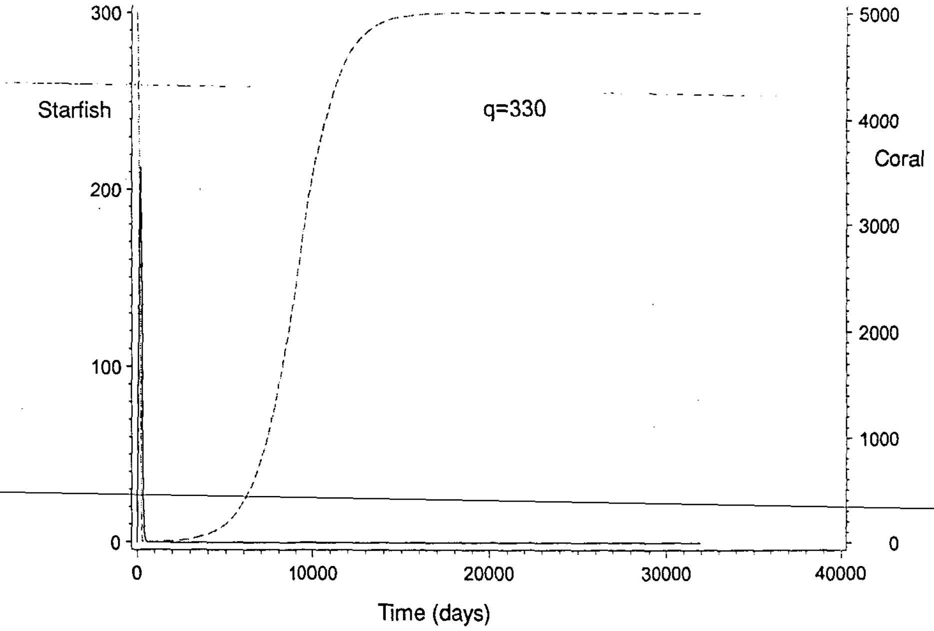

Figure 6: Adult starfish numbers and coral cover with q**=330.** Details as in *Figure 3.*

At q=400 (*Figure 4*), starfish feeding efficiency is maintained at lower coral cover, and as might be expected, this results in both lower coral cover, and a less stable coral-starfish interaction. Nevertheless, the system appears to be settling toward an equilibrium. A slight decrease in q to 350 produces a very different result: the cycles do not damp out at all: a stable limit cycle with coral cover varying between approximately 1000 and 3500 m^{-2} occurs (*Figure 5*). Decreasing q to 330 (*Figure 6*) appears to result in a single starfish outbreak which depresses coral cover to such a level that there is no successful starfish recruitment in the next generation at all.

Discussion

The results reported here are very preliminary investigations of a model which is likely to have extremely complex behaviour. A full analysis with far more runs together with stability analysis is now in progress. These preliminary results are nevertheless interesting. They suggest that *Acanthaster* population dynamics are not of the type that can be expected readily to generate deterministic chaos. This means that the apparent unpredictability in *Acanthaster* dynamics probably is not a result of deterministic processes: it is rather a function of environmental stochasticity. A further somewhat surprising result is that persistent cycles are apparent for a narrow range of parameter values only. For most values of q, the cycles damp to a constant "chronic" starfish population fairly rapidly. Thus "qualitatively stable cycles" (Bradbury *et al.* 1985) are unlikely to be generated purely by a deterministic coral-starfish interaction. As the approach to equilibrium is oscillatory, however, random variations may maintain cyclical behaviour indefinitely. The conclusion that *Acanthaster* populations do not exhibit chaotic behaviour must, at this stage, be qualified extensively. Although a wider range of parameter combinations has been explored informally than is reported on here, a systematic survey of the entire plausible parameter space has not yet been completed. It may be that an extensive region of chaos exists which has yet to be found. One problem of particular concern is the behaviour for small values of q. As reported above, the starfish go extinct if q is too small. This can be prevented by setting a "floor" on coral cover (corresponding to some sort of refuge from predation) but the level at which this floor should be set is hard to determine. As the size of such a floor can determine whether chaos occurs in much simpler models (McCallum 1992a), addition of a floor to this model may considerably complicate the results. A second possibility is that there may be a "chaotic repellor" existing somewhere in the system. Very few mathematical models have been published which combine, as this model does, the inherent cyclicity of exploiter-victim interactions together with extrinsic seasonal cyclical forcing. One of the few such models was developed by Rand and Wilson (1991), and is based on seasonally-forced measles and chickenpox epidemics. The model was found to have an equilibrium annual cycle, but the approach to this cycle was such that it took a very long time to reach it, and the transitory behaviour was chaotic in nature, around a "chaotic repellor". This meant that relatively small amounts of stochastic variation were sufficient to maintain very unpredictable behaviour in the long term. In other words, the deterministic structure of the model was acting as an "amplifier" of the random variation. This crown-of-thorns model may well behave in a similar manner. It has similarities in structure to Rand and Wilson's model, and it appears that whether the cycles and stable points shown in *Figures 3-6* are reached depends quite sensitively on the starting conditions. The difficulty with confirming this possibility is that it is hard to distinguish numerical difficulties with the integration procedure from complex behaviour caused by the underlying model. Work is continuing on this problem. If the existence of chaotic repellors is confirmed, the practical implication will be that the amount of unpredictability or variation in adult crown-of-thorns numbers is very much greater than that expected on the basis of variable larval survival alone. In these initial investigations, I have focussed attention on the parameter q. This single parameter encompasses several features of the coral-starfish interaction. Whilst it represents the searching efficiency of the starfish, describing the way in which the feeding rate varies as a function of coral density, it is in fact a function of the spatial configuration of the coral as much as it is a feature of the feeding behaviour of the starfish. On a reef where coral is present in a large, contiguous area, the rate of coral consumption by starfish will not decline markedly until the coral is greatly depleted: starfish move across the coral in a "feeding front" (McCallum *et al.* 1989) and can maintain maximal feeding rates until there is no longer live coral in front of the advancing starfish. Conversely, on reefs or reef systems where coral cover is very patchy, relatively small amounts of coral depletion will result in particular patches being depleted, causing the starfish to traverse areas with no coral in order to continue feeding, thus depressing the feeding rate. This raises an obvious and important question: on what scale and where is this model intended to be applicable? As the model implicitly assumes a stock-recruitment relationship, the starfish population must be defined at a level and in a region in which most recruitment is internal. Spatial structure within this population is then expressed through the parameter q. At present, it is unclear what physical scale this requirement corresponds to. The model is most useful in seeking to explain the origin of "primary outbreaks" in the area around 16ºS (Johnson 1992) rather than the "secondary outbreaks" which appear to move southward down the reef in response to primary outbreaks. Whilst hydrodynamic models (James, Dight and Bode 1990) convincingly demonstrate that larvae may be dispersed over substantial distances, even in the northern part of the GBR, they cannot predict the proportion of larvae that are transported between reefs. It may be that most larvae are captured in the boundary layer and never leave their home reef.

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Are the hydrodynamics guilty of causing or stimulating outbreaks of crown-of-thorns starfish on the Great Barrier Reef ?

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Abstract

Are there causal links between the outbreaks of starfish and the GBR hydrodynamics? The evidence suggests that hydrodynamics are certainly implicated and may play a significant role in determining the evolution of outbreaks. Secondary outbreaks appear to be a consequence of larval recruitment from other sources. An initial outbreak seeds nearby reefs causing subsequent outbreaks some 2 - 4 years later. The excursion of the dispersing larvae is determined by (i) the current strength during the pelagic phase, (ii) the interaction of the continental shelf coastal currents with the reef-scale circulation, and (iii) the location along and across the shelf of the source of larvae. A 25-year time series of predicted currents in the central GBR confirms that the observed distribution and migration of outbreaks may be simply a response to inter-reef larval exchange, carried by a reversing low frequency current from a reef saturated with spawning adults. However, cyclical behaviour in the outbreaks may yet prove to be related to other ocean-scale factors, eg. longshore oscillations in the point of attachment of the East Australian current. Even, El Nino events may play a role. The cause of initial outbreaks appears far more complex. Do the adult numbers simply build up until a threshold in fertilised larval numbers is exceeded and an outbreak results? Do hydrodynamics interact with reef morphology to create zones of relatively high recruitment on and around reefs, as suggested by Black and Moran (1991) ? Such zones may also maintain low level populations of adults until a drop in the coastal current strength during the spawning season causes many larvae to be retained, and local recruitment increases dramatically. Several successive years of low currents may be needed to create an "outbreak". Small-scale tests over distances of metres have clearly shown that the larvae are passive, ie. their swimming speeds and buoyancies are negated by the action of random vertical turbulence in natural currents. Measured negative buoyancies are

unlikely to bring larvae to the sea bed. They may, however, help them to attach once they get close.

This paper takes a broad view of cause and effect at a number of physical scales. Much of what we have learned implicates the hydrodynamics. This is hardly surprising as passive larvae undoubtedly find themselves at the whim of the currents.

Introduction

Through the use of numerical techniques which are typically applied to engineering and environmental assessments (Healy *et al.* 1987, Colman and Black 1988, Keough and Black 1992) in conjunction with field data analyses (Gay *et al.* 1991, Burrage *et al.* 1991), some of the problems relating to Great Barrier Reef (GBR) hydrodynamics have been unravelled, at least in the vertically-homogeneous case (Black and Gay 1987, Deleersnijder *et al.* 1992, Dight *et al.* 1990, a). Consequently, some of the mysteries surrounding dispersal of passive larvae have been dispelled. This has enabled several studies of crown-of-thorns starfish (COTS) to seek links between the physical oceanographic characteristics of the GBR and the outbreaks of COTS (Dight *et al.* 1990b, Black and Moran 1991, James and Scandol 1992).

The development of better models and a better knowledge of the processes has resulted in a constant improvement in the techniques being applied. For example, boundary conditions applied by Dight *et al.* (1990, a) were partially schematic in that variations in the East Australian Current were not considered. Moreover, their models did not fully represent or account for the circulation around the individual reefs (Dight and Black 1991). Similarly, the small-scale models of Black (1992b) did not initially attempt to simulate particular years during the outbreaks, although actual currents were modelled (Gay *et al.* 1991, Black *et al.* 1990). Both groups, however, established a basis for a broader understanding of GBR dispersal.

More recently, grid size refinements and new methods to predict the currents during the outbreak years have greatly enhanced our ability to examine particular events at a regional scale (see below). More field data from micro to regional scales have been collected (Benzie *et al.*, *in prep.*, Moran *et al.* 1992) so that the dispersal at small scales and the results at large scales can be jointly assessed. These efforts make it possible to examine the "*Acanthaster* phenomenon" (Moran 1986) in a hydrodynamic context.

Secondary Outbreaks

We choose to distinguish between "primary" and "secondary" outbreaks. Secondary outbreaks result from an infestation originally derived from a primary source. The primary source represents the initial location or region where the outbreak starts. There may be no primary source, as such, as low-level populations of starfish may exist throughout the GBR at all times.

Dight *et al.* (1990a, b) were the first to use numerical techniques on a regional scale to model COTS larval dispersal during the pelagic period of 14 - 28 days. With "coarse" grid models (9 km cells) of the Central and Cairns Sections of the GBR, they demonstrated the potential for large excursions exceeding 10's of kilometres during the pelagic period. Their results appear to qualitatively match progressive excursions constructed from current meter measurements in the central GBR (Williams *et al.* 1984).

Most importantly, the measurements and the simulations indicate a net southward drift in the regions of the reefs and offshore (Williams *et al.* 1984, Andrews 1983, Burrage *et al.* 1991), although reversals do occur.

The observation of a net southward current coincides with an observed tendency for southward drift in COTS outbreaks (Reichelt *et al.* 1990, Moran *et al.* 1992). Indeed, recent detailed surveys of starfish numbers have identified a clear southerly trend in the movement of outbreaks over successive years (Moran *et al.* 1992) and confirmed the less definitive patterns in the earlier data sets (Reichelt *et al.* 1990). Thus, the trends in outbreak progression and the currents may be linked (James and Scandol 1992).

However, current reversals occur during the spawning period and a much more convincing case would be established if actual currents could be deterministically correlated with observations of starfish movements during particular years. Ultimately, confirmation would be obtained by simulating the actual cases numerically. These matters are being treated presently by Black and co-workers (Black, Burrage, Moran and De'ath).

As current measurements were not available in sufficient detail to establish the above correlations, the group's attention was directed towards oceanographic predictive techniques to provide more accurate empirical and numerical models.

Burrage, Black and Ness (*submitted*) utilised earlier results of Burrage *et al.* (1991) to predict currents in the central GBR over the 25 year period during the known modern history of the starfish outbreaks. Using the sea level differences between Townsville (in the central GBR) and Noumea (in the western Pacific) to estimate currents, the procedure utilised the observed geostrophic balance between cross-shelf sea gradient and currents on the shelf. The results were confirmed using data from circulation experiments (Burrage *et al.* 1991, Gay *et al.* 1991). The method provided a useful technique to formulate boundary conditions for more comprehensive numerical simulations of the hydrodynamics and dispersal during the outbreaks.

To test the correlation between outbreak movement and currents, a simple advection model was developed using the predicted currents to specify the dispersal ranges during spawning (Black, Moran, De'ath and Burrage, *in prep.*). Successive outbreak years since 1966 were examined. The predicted larval excursions were compared with the observed movement of starfish outbreaks. Comparisons of the predictions with the observed dispersal ranges showed a high degree of correlation and, while two of the years were anomalous, the preliminary results almost unambiguously confirmed that secondary starfish outbreaks could indeed be caused by larvae coming from infested reefs "upstream". Small-scale numerical models confirmed that the circulation patterns around individual reefs would allow this to occur. The bulk of the flow goes around the downstream reefs, but the tidal currents cause some of the passing material to be trapped (Black 1992a).

Primary Outbreaks

Studies of small-scale circulation and dispersal around individual reefs and reef groups, and of inter-reef dispersal at small-scales has indicated a complex hydrodynamic environment acting to retain material around individual reefs for times which can be of the same order as the COTS pelagic period (Black *et al.* 1991). By directing attention towards correlations between COTS outbreaks and hydrodynamic processes, while simultaneously establishing a basis for our present understanding of reef and reef group-scale dispersal of COTS larvae, correlations between outbreaks on individual reefs and passive dispersal patterns were obtained (eg. Black and Moran 1991). Are there possible links between these factors and primary outbreaks of COTS? A number of hydrodynamic processes could be responsible.

Recent work by Moran *et al.* (1992) suggests that the primary outbreaks occurred in the Cairns Section around 16°S during the two documented infestations in the 60's, 70's and 80's. If we assume this region is the initial source, we must identify processes which distinguish the area from other parts of the GBR; all regions evidently contain some low-level background populations of COTS at all times. While asking what hydrodynamic processes may cause the outbreaks, we must equally consider why outbreaks don't occur elsewhere in the GBR. Indeed, the region may be a larval "sink" where larvae from outside are more likely to settle. Alternatively, the region may simply retain larvae better than other locations.

A number of possible hydrodynamic explanations or hypotheses are considered:

(i) Regional variations in low frequency currents along the length of the GBR cause some areas to retain more larvae than others.

The modelling of Dight *et al.* (1990b) indicated slower currents and therefore smaller larval excursions in the Cairns Section of the GBR than in the Central Section. As the primary outbreaks are thought to initiate in the Cairns Section (Moran *et al.* 1992), the slower currents may be correlated with the establishment of outbreaks. Indeed, small-scale modelling shows that local retention around reefs or within reef groups is critically dependent on current strength (Black *et al.* 1989). In slower currents, larvae could be retained in greater numbers at an individual reef scale, as well as at a regional scale.

However, very little current meter data is available in the Cairns Section to confirm these findings. Recently, Steven and Black (1992) obtained current measurements in deep water near Green Island, but a full analysis of this data is pending. Prior measurements made close to Green Island (Wolanski and Bennett 1983) offered some information about regional circulation.

Further north, useful measurements away from the reefs have been made by Frith *et al.* (1986) in the region of Lizard Island, but these measurements are north of the "primary" source and have not been used to confirm the findings of Dight *et al.* (1990a).

(ii) Slow currents over successive years cause a build up in locally retained larvae (from regional to individual reef scales).

The 25-year time series shows inter-annual variability which was correlated with El Nino Southern Oscillation events (ENSO) (Burrage, Black and Ness, *submitted*; Burrage, Black and Steinberg, *in prep.*). The time series is characterised by periods of several years of net northerly or weak currents during the spawning period. These are interspersed with a succession of years when pronounced southerly flows predominated (Black, Moran, De'ath and Burrage, *in prep.*).

The number of spawning larvae retained around the natal reef is a strong function of the low frequency current strength and variations in retained numbers occur in response to the variability in flow patterns (Black *et al.* 1990). As such, a succession of years during which the currents were slow could cause a build up in local numbers to reach outbreak proportions. This could occur at a reef scale or a regional scale. In particular, in a region which already experiences relatively small currents on the average, slow currents during a succession of years could provide sufficient impetus to initiate an outbreak.

(iii) Net northerly currents during the pelagic dispersal period cause larval numbers to increase.

Periods of northerly current may cause greater retention of larvae within the GBR matrix or within the primary outbreak region. No evidence to support this possibility is presented here, although the inter-annual cycles in the 25-year time series are being examined to see if the current reversals play a significant role.

(iv) The pumping action of the flood-tidal jets between the ribbon reefs brings nutrient rich water onto the shelf.

The jets between the reef gaps have a very significant influence on the shelf circulation. In particular, they bring nutrients from deep offshore waters onto the shelf (Wolanski *et al.* 1988, Young *et al.* 1992) and the momentum of the jet carries the nutrients several kilometres shorewards. Young, Black and Heron (1992) have supplemented the measurements of Frith *et al.* (1986) with their own data (current meters, surface radar, satellite images) to develop a numerical model of the region at a fine (400 m grid) scale. The model shows wide variability in "nutrient" concentration shorewards of the reefs, as a function of reef gap width, gap orientation and spacing between gaps. In general, bands of high concentration occur several kilometres shoreward of the reefs. Wolanski *et al.* (1988) had previously demonstrated a likely correlation between currents (bringing nutrients from the ocean) and the presence and shoreward location of *Halimeda*-banks in the region.

Starfish larvae from "distant" sources may be carried into the GBR lagoon by the jets. Alternatively, the nutrients may enhance starfish fecundity, recruitment success or growth causing the region to be more suited to starfish recruitment and development.

(v) Other possible factors.

Babcock and Mundy (*unpublished*) noted that development and fertilisation of starfish were significantly higher in inshore water than in water from the offshore reefs. The reasons for the higher development and fertilisation rates are not known. This result highlights the need to examine various factors that differentiate the nearshore and offshore zones and the longshore variability.

A number of physical factors, unrelated to dispersal, need to be included in this discussion. These are:

- salinity variations (in response to rainfall variations);
- temperature changes (the starfish are particularly sensitive to excess temperatures, Babcock and Mundy 1992);
- pollutants, nutrient run-off from land sources and turbidity.

Some of these factors are now being examined and the groundwork has been established for more detailed assessments in all of the above categories (eg. Burrage, Black and Steinberg, *in prep.*, Black, *unpublished*).

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Some perspectives on the *Acanthaster* phenomenon.

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Abstract

Although outbreaks of Acanthaster planci have occurred in many, widely separated coral reefs of the Indo-Pacific over the past 30 years, research on the phenomenon and its causes has almost exclusively centred on the Great Barrier Reef. However, because of the GBR's physical, ecological and oceanographic complexity, the low level and subtle nature of anthropogenic effects, and the low number of outbreak events (ie. two), correlative studies on possible causes have not been possible.

This study takes a wider view of the phenomenon by examining the recent history of A. planci in other parts of the Indo-Pacific, particularly in the geographically isolated groups in the South Pacific. Outbreak episodes in isolated groups are more likely to be independent, primary events. The groups investigated are smaller in size, less complex oceanographically, and anthropogenic effects are more extreme, ranging from minimal to very severe. The number of 'independent' outbreak events examined also provides some statistical 'pseudo-replication' for correlative studies.

Outbreak histories were reconstructed from oral histories, published and unpublished reports, and dedicated studies in Fiji, Western Samoa, Vanuatu, Cook Islands, Kiribati, Tuvalu, and from published and unpublished reports in Tokelau, New Caledonia, French Polynesia, Niue, Solomon Islands, in Papua New Guinea in the South Pacific, and in Johnson Island, Hawaii, the Marianas, Carollines and Japan in the Northern Pacific. The timing of the onset of outbreak episodes was established where possible, and recruitment times were estimated (by backdating these 2 years). Annual recruitment of juveniles was directly monitored in the Suva Reef in Fiji since 1977. The outbreak histories in the main study groups and subgroups were related to their characteristics (geomorphology (low / high islands), geography, and extent of anthropogenic impacts (eg. coastal populations, development, fisheries, agriculture, run-off, and pollution).

Life history characteristics of *Acanthaster planci* (L.) populations, potential clues to causes of outbreaks.

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Abstract

The dynamic processes which lead to the formation of primary outbreak populations of Acanthaster planci (L.) are not well understood. This is partly due to a lack of information on the characteristics of their life history in populations. A novel method of age determination using pigment band counts in aboral spines has offered potential insights into A. planci population biology, under the assumption that the results of validation are widely applicable.

Variable expression of morphology and physiology in response to the environment is widespread amongst echinoderm species. In A. planci growth, longevity and reproductive effort appear to be determined by the interaction between available coral resources and population density. Maximum determined age in populations ranged up to 8+ years for Davies Reef, Central GBR, 9+ years for Hook Island, Whitsunday Group, and 12+ years for Lady Musgrave Island, Southern GBR. Therefore, potential longevity in A. planci may be considerably greater than previously estimated from outbreak population studies. Life history characteristics probably vary according to the population density experienced prior to maturity. Although there is inherent ambiguity in resolving the causes of this strategy from field studies, it appears to be achieved by phenotype plasticity, a strategy for maximising reproductive fitness in variable reef environments.

A qualitative model of population dynamics is presented to explain how a primary outbreak may be initiated. In particular hydrodynamic conditions, low density populations may seed intermediate populations with consistent age structure, through successive small-scale

recruitment over several years. Further successful recruitment increases population density to a point where the switch between low density and outbreak phenotypic states is triggered in the developing recruits. These starfish approach maturity preconditioned for the first mass spawning event (which may also include older adults) and subsequently produce the first secondary outbreak downstream.

Phenotypic expression of life history characteristics in A. planci which promote reproductive success in high density populations suggests that outbreaks have probably occurred in the past over a long time scale. However, it is possible that increased outbreaking activity in the Indo-Pacific region may be an indication of recent environmental stress on those reefs.

Introduction

Population studies on *Acanthaster planci* (L.) have not, so far, revealed conclusive information on the circumstances which lead to the occurrence of outbreaks. The lack of consensus on causes of outbreaks is demonstrated by the wide spectrum of hypotheses found in the literature, from physical controls of outbreaks to those stressing biological control by endogenous or trophic factors (see Moran 1986, Birkeland and Lucas 1990). Indeed the fact that no one hypothesis can account fully for their occurrence suggests that a number of processes may be involved (Moran 1986). Birkeland and Lucas (1990) concluded that attention had been focussed on ecological processes at the expense of species-specific phenomena and suggested that the characteristics of natural life history are essential to take into account when analysing the *A. planci* phenomenon.

Field studies on *A. planci* have encountered a number of significant impediments to the collection of data regarding life history characteristics. The lack of information on recruitment of *A. planci* has greatly hindered investigation of the cause(s) of outbreaks (Zann *et al.* 1990). Slow progress in the description of population dynamics has also been due to the limited success of the techniques used in field investigations (ie. reliable marking methods for age and growth studies). Kettle and Lucas (1987), while considering the effect of body size on *A. planci* physiology, recognised that population studies were limited by the inability to determine the age of individual starfish. Field data on growth, longevity and mortality are essential to achieving a basic understanding of the dynamics of *A. planci* populations (Moran 1986).

Parslow (1990) also found there were insufficient data for modelling the development of outbreaks because so little is known of the factors affecting starfish population growth at low population densities. Primary outbreaks are abrupt population increases of at least two orders of magnitude in a time and place that do not allow the outbreak to be explained as having arisen from previous outbreaks (Birkeland and Lucas 1990). By contrast, it is generally accepted that secondary outbreaks (which develop in relation to previous outbreaks ie. downcurrent) arise due to the characteristic formation of feeding and subsequent spawning aggregations. The pattern of secondary outbreaks on the GBR has been shown to develop by annual southerly migration (Kenchington 1977, Reichelt *et al.* 1990). A parsimonious interpretation of this temporal pattern in populations is by a sequential advection of massive larval clouds between reefs followed by settlement, a juvenile phase of 3 years and a short adult lifespan of approximately 1-2 years. This pattern has contributed to the maintenance of a panmictic population over the GBR. Thus *A. planci* is a "fugitive" in its larval stage by virtue of current advection; and in its adult stage, from predator pressure (Moore 1990).

Growth rates and final sizes of marine invertebrates are often constrained by environmental conditions rather than by genetics ie. they are plastic, ontogenetic responses to local conditions (Sebens 1987). Lawrence (1987) stated that although it is generally assumed that an increase in population density will decrease the food availability and subsequent size in echinoderms, it was not always the case. He reported that all combinations of density and size of individuals occurred within *Echinometra mathaei* populations, suggesting multiple control of alternate states. This suggests that variation in expression of the phenotype may not be simply due to the available food resource levels, other potential factors include conspecific stimulus (Lucas 1984) (ie. aggregating behaviour) and age. Lawrence (1987) suggested that reported giant specimens in a number of echinoderm species indicates that asymptotic size and the growth constant *K* (used in the von Bertalanffy equation - see growth section) may be restricted within populations. *A. planci* is particularly well suited to respond to environmental conditions being a relatively soft bodied asteroid. It exhibits a wide size range in populations, and it can also shrink when conditions become adverse (Stump, *in preparation*).

Population Dynamics

Reichelt (1990) used a simple graphical model to illustrate historical records on the movement of adult populations in two periods over the last 25 years caused by advective transport of larvae. Both episodes appeared to be initiated in the Northern Section and outbreaks generally disappeared soon after a rapid decline in live coral cover on affected reefs. Despite inadequate data a number of studies have attempted to produce realistic population models to explain the occurrence of outbreaks. Models developed by Antonelli and Kazarinoff (1984), Bradbury *et al.* (1985), and Antonelli *et al.* (1990) have identified:(*a*) stable limit cycles (from the starfish-coral interaction) at the scale of individual reefs and; (*b*) larval transport and survival, as important processes involved in the development of outbreaks.

A. planci occurs in both endemic and epidemic populations where varying ecological characteristics (ie. live coral cover and population density) may well influence population behaviour and dynamics. Cameron and Endean (1981) stated that outbreaks do not occur under natural conditions because the life history of *A. planci* is compatible with the view that the species is normally a rare and specialised carnivore and not a *r*-strategist prone to outbreaks. Moore (1990) proposed a life history strategy which alternates according to habitat, affecting reproductive activity by shifting their position along the *r*-*K* continuum, a common feature of outbreaking organisms, such as locusts. As far as is known, *A. planci* does not have such flexible adaptations as locusts, however, knowledge of *A. planci*'s ecology may still be at the stage equivalent to that of locusts before the discovery of phases (Moore 1990). Therefore, in order to assess possible causes of outbreaks the biological characteristics of both high and low density populations must be clearly understood.

Age and Growth

Valid age-determination is essential for characterisation of growth in the field and has only been achieved outside the laboratory for juvenile populations in studies by Zann *et al.* (1987, 1990) and Habe *et al.* (1989) where populations were dominated by a single cohort. The rapid growth rate which occurs during the juvenile phase enabled year classes to be readily identified from size-frequency distributions. Zann *et al.* (1990) concluded that where sample sizes are adequate, the mean or modal size classes are good indicators of age for the first 2 years, and a fair indicator for the third year of local populations.

Despite finding determinate body growth in *A. planci* in both laboratory studies (Yamaguchi 1974, Lucas 1984) and in the field (Branham *et al.* 1971, Stump, *in preparation*) multiple size-frequency modes suggest age classes remain a characteristic of many adult populations. Therefore, the mode of growth in the laboratory, where food limitation effects probably occur during the second year, may differ from growth in field populations. The resolution of this apparent inconsistency and a description of growth in a broad range of population densities is crucial to the advancement of studies in population dynamics and life-history theory of *A. planci.*

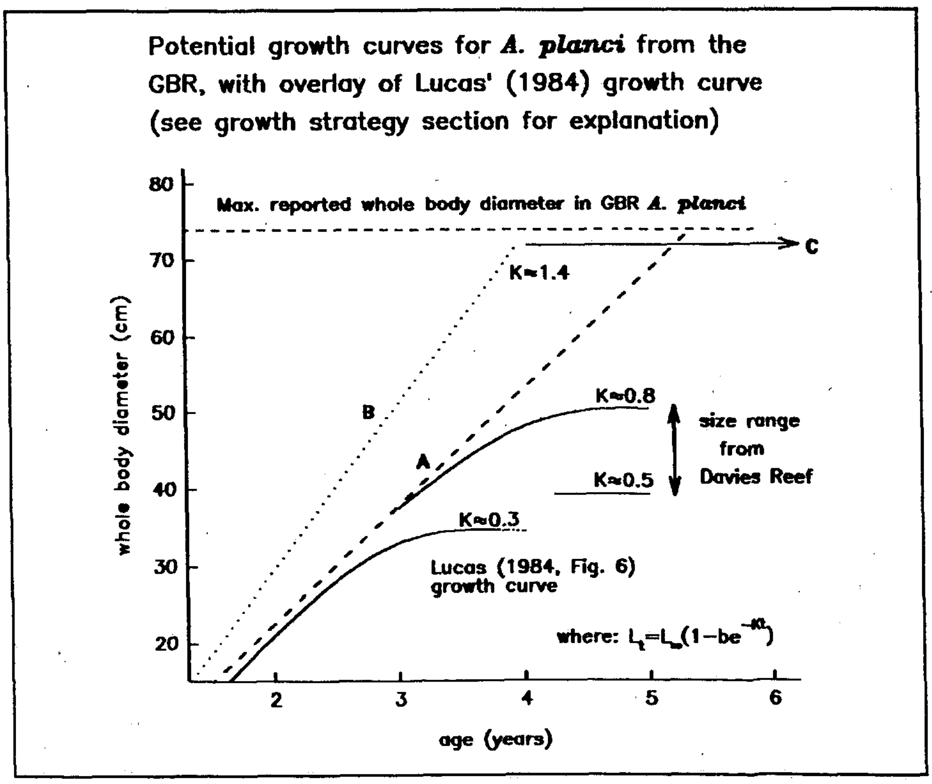
Stump and Lucas (1990) proposed a novel method of determining age in adult *A. planci* using pigment band counts on aboral spine ossicles. They combined several techniques for individual identification using tetracycline, arm amputation and morphological characteristics to develop a reliable system of marking for subsequent-recapture studies. Following a 38 months study on Davies Reef, Central GBR, Stump (*in preparation*) obtained 13 recaptures with release periods of more than 12 months to determine the validity of the method. Validation of the method was obtained in all but 1 recapture where equivocal band growth was recorded and may have been due to its poor state of health, and perhaps senility. The banding occurs perpendicular to the long axis of aboral spine ossicles. Dark coloured bands appear on new spine growth at the spine ossicle base in adult *A. planci* during winter and light bands in the warmer months, although the exact timing of the development of the bands appears to be variable amongst individuals. Juvenile *A. planci* do not develop a clear banding pattern during the development of the spine apex due to the rapid increase in spine dimensions during this phase.

The causes of spine pigment banding are not known. Analyses of spine samples from equatorial (Guam, Kiribati), high tropical (Lady Musgrave Island, GBR) and sub-tropical latitudes (Lord Howe Island, NSW) demonstrated that the development of pigment banding in *A. planci* is widespread and therefore may not be directly temperature dependent (Stump, *in preparation*). This supports the idea that banding may be caused by an endogenous factor which may in turn be stimulated by exogenous influences. Two cyclic phenomena which have been previously described for *A. planci* appear to coincide with the development of pigment banding; these are annual gametogenesis (Lucas 1984) and the seasonal changes in rate of feeding (Keesing 1990). However, coincidence in the timing of potential factors does not necessarily imply a causal relationship.

Plasticity in Growth, Reproduction and Longevity

Using the pigment band ageing method a determinate growth pattern was found in individuals from the Davies Reef outbreak population with a range of maximum body diameter of approximately 35 to 50 cm. Maximum body size was reached soon after maturity at 3+ years, with a seasonal fluctuation in size (2-3 cm) due to gametogenesis, then spawning, and declined slowly after 4+ years. *A. planci* from very low-density populations have been recorded in excess of 70 cm (ie. Kenchington, *pers. comm., in:* Lucas 1984) and are approximately 50% larger than the largest individuals which had developed under outbreak conditions (ie. the Davies Reef population). Large starfish must be either significantly older, having developed under a different mode of growth, or are very fast-growing in order to achieve their asymptotic size at the same age as smaller starfish.

If, for the purpose of argument, we assume that the pigment band ageing method is widely applicable then growth curves can be constructed for individuals from a wide range of population densities (*Figure 1*). Growth trajectories were compared using the von Bertalanffy growth equation in the form; $L_t = L\ be^{-Kt})$ where; L_t = whole body diameter (cm) at age t, L = asymptotic whole body diameter (cm), b = correction factor for size at recruitment, K = growth constant (yr^{-1}). Age determination results showed that asymptotic size was achieved by maturity (3+ years) and estimated *K* was 0.8 yr^{-1} (dashed line **A**). For *A. planci* to attain the maximum reported whole body diameter >70 cm at maturity (3+ years) ie. with a similar mode of growth to Davies Reef starfish, then a growth constant of approximately 1.4 yr^{-1} (dotted line B) would be required.



Potential growth curves for *A. planci* from the GBR, with overlay of Lucas' (1984) growth curve (see growth strategy section for explanation)

Figure 1:

Organisms have fixed resources of time, energy and nutrients at their disposal and are therefore often involved in trade offs between allocation to somatic maintenance, growth and reproduction (Partridge 1987). Ebert (1985) found there was a tradeoff between rapid growth and long life in sea urchins, such that a doubling of lifespan resulted in a halving of K. If this applies to very large *A. planci* then they would not reach asymptotic size at age 3+ years but several years later with $K < 0.8$ yr^{-1}. A growth constant $K >> 0.8$ yr^{-1} is unlikely unless the energetic constraints of reproduction (ie. age and size at maturity) are changed or feeding efficiency is significantly increased.

The mode of feeding in *A. planci* is similar to that of grazing herbivores and there are no apparent morphological or behavioural differences between average and very large individuals which might improve feeding efficiency. It is more likely that in low density populations reproductive effort is lower and therefore allows growth to continue past maturity. Therefore (dotted line) **B** is likely to shift to a maximum gradient of (dashed line) **A**, but more likely to be lower (C) (*Fig. l*) due to the tradeoff suggested by Ebert (1985). Delayed maturity is not known for this species. and there appears to be a lack of stimulus to feed in lower densities, without aggregations, or with age. Lucas (1984) found the influence of intrinsic appetite affected growth and this factor changed in nature and intensity during the life cycle. Longevity estimates of *A. planci* were obtained for several populations: Lady Musgrave Island, 12+ years (68 cm; n=l); Davies Reef, pre-outbreak group, 8+ years (35-50 cm; n=27); Hook Island, pre-outbreak group 9+ years (50-56 cm; n=2). Therefore very large starfish in low density populations are likely to be at least 5+ years when they reach asymptotic size with a growth rate K of < 0.8 yr^{-1}.

A. planci in higher density populations, partitioning increasingly heavily towards reproduction and consuming food resources rapidly, are likely to be restricted in their maximum size by food limitations (Kettle and Lucas 1987). Calow (1978) described a negative relationship between food ration and reproductive effort as reproductive recklessness. Recklessness will only be selected when progeny have an equal or better chance of surviving through harsh nutritive conditions than parents (Calow 1978). This situation clearly describes the "fugitive" character of outbreak populations in temporary habitats (see Moore 1990). This strategy would appear to preclude the existence of persistent low density populations without frequent recruitment episodes. However, Zann *et al.* (1990) found annual recruitment of *A. planci* over a 13-year period to be very patchy in time and space on Suva Reef, Fiji.

Stump and Lucas (1991) found a negative relationship between fecundity (adjusted for mean whole body diameter) and age over several adult age-classes from pre- and post-outbreak cohorts. They used spine ossicle length to infer age which was later confirmed using pigment band counts on spines (Stump, *in preparation*). Therefore fecundity was maximised at maturity and older starfish which had developed prior to the outbreak group appeared to devote less energy to reproduction through lowered fecundity. A tradeoff between longevity and reproduction may explain why *A. planci* produce short lived outbreaks and yet can also develop persistent low density populations.

Alternative Life History Characteristics

In a large part, life-cycles are moulded by the way resources derived from food are allocated between various metabolic demands because the allocation of resources is fundamental for the form and function of organisms (Calow 1984). Lawrence (1990) described the life-cycle characteristics of *A. planci* in terms of the influence of stress and disturbance, a competitive strategy includes long life, low reproductive effort but high fecundity and a rapid growth rate. However, Kettle (1990) ascribed a ruderal strategy to *A. planci* in high density populations which are food limited and have a very high reproductive effort resulting in a shortened lifespan. Stump *(in preparation)* found *A. planci* may live to 12+ years and can attain sizes of well over 50 cm in low density populations. Clearly there are very distinct phenotypes developed between low and high density populations.

It is important to distinguish whether the effect of food availability or population density influence the reproductive strategy in *A. planci.* Variation in reproductive performance in lower vertebrates and invertebrates could thus indicate either variation in reproductive effort or variation in food resource levels with constant reproductive effort (Nichols *et al.* 1976). In the GBR population studies we have not been able to distinguish between the effects of food resource levels and population density. In the high density outbreaks on the GBR both factors have probably influenced populations at approximately the same time.

A recent study in Guam by Stump (*in preparation*) found considerable numbers of *A. planci* from three different bays had developed in habitats with low coral cover, therefore effectively separating the effects of high density from food limitation. Poor coral assemblages have been reported on reefs around Guam for at least the past 10 years (Lucas, *pers. comm.*). Individuals appeared to be maintained apart by the low coral cover (no aggregations were observed although *A. planci* were common) and were probably food limited as evidenced by their small body size and feeding scars commonly observed on *Porites spp.* (generally not a preferred species). While there was evidence of some partially spawned individuals most demonstrated lower fecundity but higher somatic weights than those predicted from GBR populations. This would appear to indicate a more conservative life history strategy which promotes longevity. Thus, population density appears to be more important than food resource levels in determining the life history characteristics in *A. planci.*

Variation in life history characteristics which are well suited to particular environments suggests that distinct phenotypes are developed in either low or high density populations. Marcus (1983) reported that phenotypic variability is widespread amongst echinoderm species as a significant form of adaptation to environmental factors. Therefore the life history characteristics of *A. planci* are probably determined by extrinsic factors, including population density, prior to maturity. Further study on the physiology of starfish in low density populations is required to complement the studies of Kettle and Lucas (1987) and Kettle (1990) and so determine the variability in reproductive effort in those populations. It should be noted that there is some inherent ambiguity in the conclusions drawn from several field studies where variable responses to the environment are compared between populations which have developed under different sets of conditions.

Bradbury *et al.* (1985) speculated that the observed behaviour of the *Acanthaster* phenomenon can be explained in terms of the life history parameters of the prey and predator. Antonelli *et al.* (1990) concluded that, apart from the life-history characteristics, the only feature capable of suppressing limit cycles in *A. planci* populations is increased predator pressure on the starfish. It was first suggested by Moore (1990) that *A. planci* persists on reefs by being adapted to life in a range of reef habitats through alternate life-histories, a common feature of outbreaking organisms. The interpretation of data by Stump (*in preparation*) supports this idea of variable characteristics which allow populations to persist and succeed under varying habitat conditions.

Adaptive life history tactics may affect longevity by conferring fitness in *A. planci* on the GBR to (*a*) mature at a smaller size and maximise first reproduction in high density populations with limited resources, or (*b*) mature at a large size and maximise the potential for reproductive success in low density populations via iteroparity, or (*c*) increase body size considerably, by devoting more energy for growth with age in very low density populations through large investment in somatic tissues and postponing reproduction. Moran (1992) stated that in order to maintain the ability to develop alternative life history characteristics, the developmental cues in the juvenile environment must be matched with the environment in which phenotype is selected (ie. they must be reproductively successful). In *A. planci* this may be achieved when high density recruitment results in food limitation soon after maturity where semelparous reproducers are more successful, while juveniles in low density populations do not receive the degree of stimulus from conspecifics and reproductive effort is lower at maturity promoting iteroparity and longevity. Further low density population studies and laboratory rearing experiments under controlled conditions are needed to verify these findings.

An Hypothesis for Primary Outbreaks

Two major characteristics of starfish populations on open water reefs - high hydrodynamic flushing rates and very low endemic starfish population densities - argue against their role as initiators of primary outbreaks (Moore 1990). Since 1962 the two recorded outbreak episodes on the GBR may have developed from the same region. The notion of a discrete seed area is plausible but not testable with available data (Reichelt *et al.* 1990). Moore (1990) reasoned that despite the fact that high fecundity in *A. planci* may justify an argument for sparse populations precipitating outbreaks and cited Birkeland (1982), that many other coral reef invertebrates also are highly fecund but few outbreak, and therefore the argument should be treated with reservation. There is no evidence of randomly occurring outbreaks on the GBR despite the presence of widespread low density populations in reef communities. Therefore, with all available information, it appears unlikely that outbreak populations can be propagated directly from low density populations.

The results of Stump (*in preparation*) are used to develop a qualitative model to demonstrate how a primary outbreak may be initiated. The characteristics of age-structure and longevity are used to show how a low density population develops and, given certain environmental conditions, may give rise to a population increasing in size with well- defined age structure. Survival rates between the larval phase and first adult spawning were obtained from the estimated size of secondary outbreaks observed in the Central Section during the 1980's. In general, outbreaks on average sized reefs were estimated to consist of 10^4-10^5 starfish (see Kettle 1990, Stump, *in preparation*). The difference between potential larval production of outbreak populations and downstream outbreak population size was therefore used to estimate survival rates ($2x10^{12}$ larvae produced in a single mass spawning; with a population sex ratio of 1:1, mean diameter 40 cm, each with $4x10^7$ oocytes and 100% fertilisation). This simple calculation showed approximately $2.5x10^{-9}$ to $2.5x10^{-8}$ survival. Other effects may influence these estimates but were not included for simplicity.

Poor survival rates of early life stages emphasise the remote possibility of an outbreak emanating directly from a low density population. Therefore, low density populations are more likely to reproduce with limited success over time and, in region of random connectivity between reefs (ie. northern region of the GBR (James *et al.* 1990)), may seed larger persistent populations with consistent, wide ranges in age classes. The persistence of adults in these populations for approximately 4 - 6 years increases the chances of successful reproduction and, under certain environmental conditions, increases the potential for continuing annual recruitment amongst reefs. Given these circumstances, at some point, further recruitment will trigger the outbreak phenotypic state in the juvenile population. When this occurs population density amongst recruits is high enough to produce the first mass spawning event. The release of pheromones to coordinate spawning would affect all age classes present in the population and further increase the number of larvae produced. Advection and subsequent settlement of this first mass larval cloud gives rise to the first secondary outbreak in the region.

Conclusions

The results of this study suggest that the processes which lead to the occurrence of outbreaks are due to a combination of the life history characteristics and favourable environmental conditions, including particular current patterns as suggested by James *et al.* (1990). Further, this also suggests that there has been a natural history of outbreaking events through time on the GBR because *A. planci* appears to be predisposed to developing outbreaks. However, the important question as to whether the frequency of outbreaks is increasing in recent times compared with that of the past still needs to be addressed. The findings of Zann *et al.* (1990) suggested that outbreaks had increased in frequency and abundance in the Suva area (Fiji) over the past 50 years. Recent recognition of the apparent world-wide decline in coral reefs from stress caused by impacts from human populations is a primary cause for concern (Wilkinson, *in press*). The occurrence of repeated outbreaks of *A. planci* in parts of the Indo-Pacific may well be an indicator of environmental stress on reefs and a significant contributor to their decline.

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SESSION 2

THE CONSEQUENCES OF OUTBREAKS

Juvenile Starfish

Chair: Dr Leon Zann (GBRMPA)

CotSim: Scientific visualisation and gaming-simulation for the *Acanthaster* phenomenon

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Abstract

CotSim is a new type of population model for Acanthaster planci on the Great Barrier Reef (GBR). This multi-reef model simulates the population dynamics of Acanthaster on 270 reefs in the central GBR and integrates recent oceanographic modelling studies of the area. It has been designed to facilitate experimentation by non-modellers. Users can change initial conditions or any of the parameters for the underlying model, as well as editing (eg. controlling) starfish populations while the model is running. The model uses the standard graphical user interface, Microsoft Windows 3.x. Populations on reefs are viewed using simple point and click operations, and the history of Acanthaster / coral dynamics is easily accessed. Latitude versus time plots of Acanthaster populations on the GBR can also be constructed. Acanthaster dynamics are represented by a density-dependent size structured matrix model. Coral dynamics are represented by logistic equations. Spawning and fertilisation are stochastic processes quantified by user-defined parameters. The spatial structure of larval dispersal is determined by extensive oceanographic studies of the GBR. The motivation for this research was to experiment with new methods of presenting models to the scientific community. Surveys have been designed and distributed in an attempt to gather responses.

Introduction

The *Acanthaster* phenomenon (Moran 1986, Birkeland and Lucas 1990) is a potentially recurrent management problem on the Great Barrier Reef (GBR). The two documented outbreaks of the starfish have affected substantial portions of the central GBR and there is still scientific ambivalence about whether the cause(s) of outbreaks are natural or anthropogenic. *Acanthaster* therefore remains one of the most contentious issues of GBR management (Lassig and Kelleher 1991). The significance and complexity of the *Acanthaster* phenomenon has generated a surge of public interest. The Great Barrier Reef Marine Park Authority continues to encourage this interest and understanding by presenting accessible research summaries to the public in both written/illustrated (Zann and Eager 1987, Engelhardt and Lassig 1992) and video formats (GBRMPA and AIMS 1992). This use of alternative communication media is what originally motivated this paper. Scientists working with *Acanthaster* also need to experiment with new ways of presenting information and ideas amongst themselves. Pragmatic considerations were also incorporated into this research. Increasing scientific specialisation continues to restrict accessibility of information between fields. Researchers become isolated by syntax, literature, interests and time constraints. The modelling approach (Bradbury 1990) is not immune to these symptoms. Models have to compete for the restricted attention available in the scientific and management communities (Jones 1992, Cruickshank 1992).

This paper introduces the concepts for more effective communication of the structure and results of large scale *Acanthaster* models. I will outline the background, objectives, definition and evaluation methodologies for an interactive large scale population model of *Acanthaster* on the GBR, referred to as *CotSim* (Scandol 1992).

Background

Two related bodies of thought provide the methodological basis for *CotSim:* scientific visualisation and gaming-simulation. Scientific visualisation is concerned with improving the information flow between a researcher and a computer model. Modelling is an integral, but often unrecognised, process in scientific discovery and decision making. The iterative loop of model definition, model testing/observation and then model redefinition is a basic procedure in science (Nielson 1991). However, when models are realised with computers, the rate determining step is often the ease with which a researcher can extract meaningful information from a model. Utilisation of modern computer facilities with graphical output generates images that communicate large amounts of visual information to the researcher on demand. The ability of the user to interact with the images (for example rotate them), helps to improve the communication flow between data and researcher.

In summary, scientific visualisation allows the researcher to access and display large amounts of information. Huge tables of printed results are no longer an acceptable form of output for modellers or their sponsors. Unfortunately the glamorous images of Thalmann (1990) ignore the important parallel results that less computer-resource-hungry applications can offer. The limited consistency, availability and familiarity of more powerful computers were seen as critical impediments to effective implementation of *CotSim* on these systems.

Gaming-simulation is a more abstract area, with principles not bound in computer application. Greenblat (1988) discusses the application of gaming-simulation techniques to a variety of social scenarios. However, the themes are relevant to any complex problem. The central idea is to develop an interactive system which enables users to obtain an overall perspective and to initiate their own responses. Players are integrated into the actual realisation, their decisions determining the course of events. Application of gaming-simulation to computers is a logical application of these ideas. The contrasting roles of *Monte Carlo* simulation and gaming simulation have been addressed by Gray and Borovits (1986).

CotSim extracts methodologies from both these fields to define an interactive model of the large scale population dynamics for *Acanthaster* on the GBR. It was inspired by *SharkSim* of Sluczanowski (1991). This model for the South Australian Department of Fisheries has allowed effective communication between managers, scientists and the end users of the marine resources.

Objectives

CotSim has three objectives:

1. To present a non-literature-based interactive large scale population model of *Acanthaster* on the GBR to management personnel, research scientists and other individuals interested in the phenomenon.

Simulation models are dynamic. This critical aspect is lost, along with much impact, when presenting results in the scientific literature. A conventionally published model is necessarily limited in its domain. To follow conventions for probability estimation and sensitivity testing, simulations models must be very focussed. Although the importance of this formalism is not questioned, one must query what information or inspiration is sacrificed in order to satisfy statistical rigour. If new ideas are realised, then a more stringent analysis can always be performed with a carefully defined experiment. *CotSim* presents a complementary approach that may benefit research and management of the *Acanthaster* phenomenon simply by being orthogonal to other modelling approaches. Scientific visualisation and gaming-simulation are integrated into *CotSim*. Techniques have been developed to rapidly extract and graphically display large amounts of information about the status and history of *Acanthaster* populations on reefs or integrated over the GBR. The outcome of a realisation of *CotSim* is determined by the user-defined initial conditions, model definition and control efforts. These features interact with the natural stochastic processes affecting starfish populations.

2. To collect information from surveys on:

- usage rates of *CotSim*;
- suggested modifications to the *CotSim* model;
- decision making using models with limited replication.

Surveys have been prepared (*Appendix A*) to attempt to obtain this information. *CotSim* has been installed at a number of test sites (*Appendix B*). The data will be collected from late August to December 1992. The results will be collated and published in Scandol (*in preparation*).

3. To provide a new communication medium for the larval dispersal studies of Dight *et al.*(1990a, b).

CotSim may enable a more developed appreciation of the somewhat abstract and easily misunderstood concepts involved in the Dight *et al.* (1990a, b) project. Improved understanding and acceptance of the models in management agencies may then result (Law and Kelton 1991). Models such as *CotSim* provide a focus for discussion (Walters 1986).

Definition and Implementation

CotSim is a multi-reef population model of *Acanthaster* for the central GBR. The basic structure is from Scandol and James (1992), but much more biological detail has been included. Each of the 270 reefs modelled has a size-classified state vector of starfish densities in starfish/hectare. Post larval development on the reef is defined by a density-dependent matrix model (Caswell 1989). Coral cover is estimated by using a logistic response (Reichelt *et al.* 1990). One or two coral types can be modelled, each with different growth rates, equilibrium densities and *Acanthaster* feeding preferences. The fertilisation model is based upon a density dependent log normal distribution. Spawning is a stochastic or deterministic process depending upon the user's choice. Inter-reef larval transport is defined by using the larval transport models of Dight *et al.* (1990a, b). These simulated dispersal events are used by selecting data from an appropriate source reef and year. Details of the use and design of *CotSim* are provided in Scandol (1992). *Appendix B* of that documentation gives a complete technical specification of the model.

The final form of *CotSim* represents a compromise between functionality and development cost. Many features were excluded simply for reasons of technical difficulty in their implementation, or the excessive computer resources required for their execution.

CotSim was written for the popular Windows 3.x (Microsoft 1992) platform for IBM compatible computers using Visual Basic 1.0 (Microsoft 1991). The benefit of using an industry standard interface such as this is that users are already familiar with the screen controls such as buttons and text boxes, and therefore the "learning curve" is not steep (Foley *et al.* 1990). *CotSim* requires the minimum of a 80286-based processor to run. However because of the extensive numerical calculations that are performed each time step, a 80386DX processor and 80387 co-processor (or faster) are recommended.

Although Visual Basic provided a simple development environment, speed and functionality were sacrificed. Using C++ and Windows development libraries would alleviate these limitations, but would have trebled development time. At the time of writing, many additions to Visual Basic are being published that would have ameliorated many these problems.

Results and Application

During testing *CotSim* has generated a huge variety of replicates. Many of these give confidence that the system is capable of reproducing the gross features of observed large scale *Acanthaster* populations for the GBR. These features include: (*1*) the southerly movement of populations via larval dispersal, (*2*) the suggested 10 - 20 year interval between outbreaks.

Figure 1 is a plot of outbreak latitude versus time for a typical *CotSim* replicate. The previous points are illustrated.

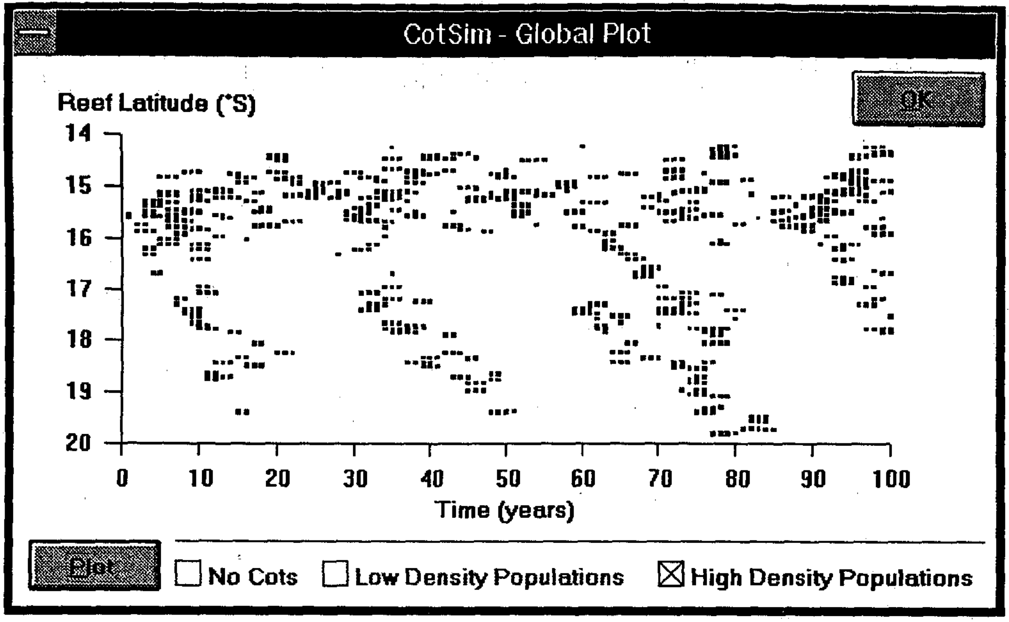

Figure 1: A typical *CotSim* global plot: latitude of reefs with outbreaks vs time. There are no explicit rules for the usage of *CotSim*. The system was not designed for formal experimentation, but exploration of ideas. The following list is a subset of the types of investigation that could be completed with *CotSim*.

- How much variation exists in five different replicates of the system (using the same parameters)?
- What difference in a replicate occurs if started with medium rather than high density populations?
- What initial model definitions give the best qualitative agreement with the field observations? How robust is this answer?
- Does the location of a reef affect the recruitment patterns of *Acanthaster*?
- What is the effect of self-seeding of reefs?
- How difficult would it be to control an outbreak?

CotSim will not answer these questions, merely allow users to explore the ideas. Sample problems for *CotSim* users are suggested in the survey (*Appendix A*).

Discussion

Models have great potential for the construction and explanation of ideas. To realise that potential, we must explore new methods of definition, interpretation and implementation. *CotSim* has introduced concepts from scientific visualisation and gaming-simulation to the *Acanthaster* debate. By monitoring response it is hoped that the role of these techniques can be assessed accurately enough so that integration into future modelling programs can be facilitated. Response will be measured with simple survey techniques. The results of this study will be the first measure of attitude to *Acanthaster* modelling that has been undertaken.

The *CotSim* model won't generate results that are "statistically significant", but may, as a consequence of its design, give some users a better understanding of complex concepts (such as inter-year recruitment variation). Modelling studies can have quite different applications. Some models may provide "intuitive" information, others "statistically significant" information. Both of these may be required for the effective integration of modelling into management strategies.

The potential role of gaming-simulation in *Acanthaster* management is unexplored. These techniques are ideal for dealing with decision systems where parties may have conflicting or contradictory points of view (Gray & Borovits 1986). The management of the *Acanthaster* phenomenon involves physical and biological scientists, industries with large vested interests, media representatives, and an interested general public. Management personnel must deal with these parties by guiding research and justifying their actions (including inaction) to this varied audience. Workshops could be designed to enable such players to simulate their reactions to a third outbreak, and how those actions might effect the outbreak scenario. These sorts of management games may be capable of producing important results. For example, the tourist industry representatives may realise that extensive lobbying for starfish controls may simply create unnecessary concern about the outbreak. Tourism receipts may be adversely affected by this publicity and the control efforts may be worthless and expensive because outbreaks were discovered too late. Simulations of this type could also be used to test the effectiveness of contingency plans (Lassig *et al., in press*).

In management, decisions are inevitable. If experimentation is not possible, deductive inferences are made about the possible outcomes of decisions, using underlying assumptions. If these underlying assumptions are presented clearly, they will be discussed and evaluated critically. Modelling in this general sense is unavoidable, so we should do so openly (Walters 1986). The *CotSim* project attempts to meet this criterion.

Acknowledgements

I would like to thank the APRA Scheme and the ARC for financial assistance to this project. The following people provided encouragement for *CotSim:* I Dight, M James, R Jones, P Sluczanowski and M Tomlinson. P Bikaunieks provided assistance with *CotSim* development.

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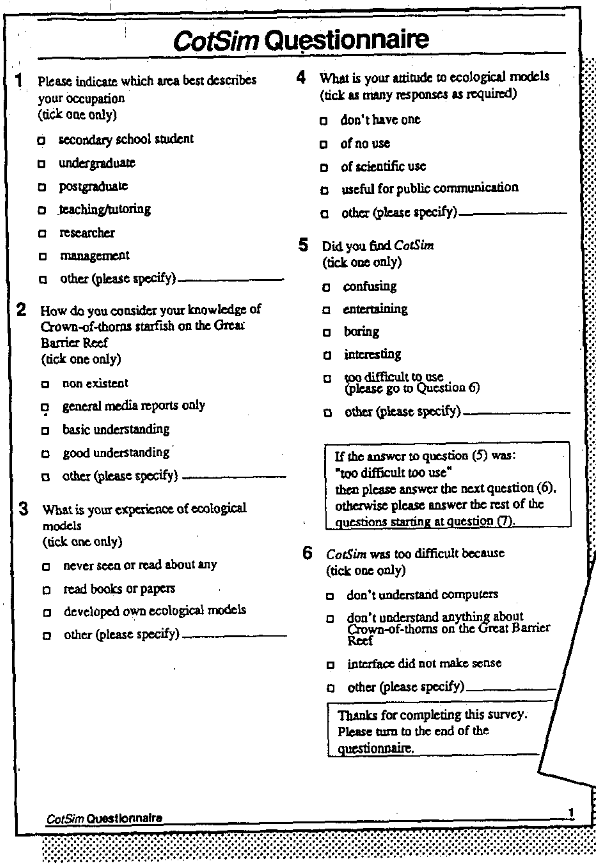
Appendix A: *CotSim* User Survey



CotSim Questionnaire

1 Please indicate which area best describes your occupation
(tick one only)

- ☐ secondary school student
- ☐ undergraduate
- ☐ postgraduate
- ☐ teaching/tutoring
- ☐ researcher
- ☐ management
- ☐ other (please specify) ________

2 How do you consider your knowledge of Crown-of-thorns starfish on the Great Barrier Reef
(tick one only)

- ☐ non existent
- ☐ general media reports only
- ☐ basic understanding
- ☐ good understanding
- ☐ other (please specify) ________

3 What is your experience of ecological models
(tick one only)

- ☐ never seen or read about any
- ☐ read books or papers
- ☐ developed own ecological models
- ☐ other (please specify) ________

4 What is your attitude to ecological models
(tick as many responses as required)

- ☐ don't have one
- ☐ of no use
- ☐ of scientific use
- ☐ useful for public communication
- ☐ other (please specify) ________

5 Did you find *CotSim*
(tick one only)

- ☐ confusing
- ☐ entertaining
- ☐ boring
- ☐ interesting
- ☐ too difficult to use (please go to Question 6)
- ☐ other (please specify) ________

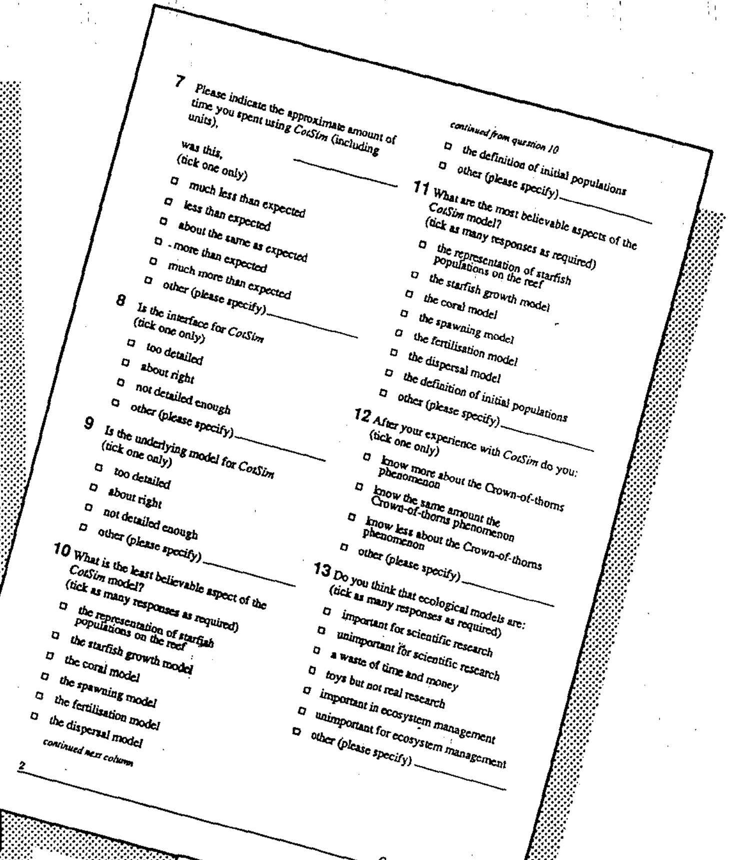
If the answer to question (5) was:
"too difficult too use"
then please answer the next question (6), otherwise please answer the rest of the questions starting at question (7).

6 *CotSim* was too difficult because
(tick one only)

- ☐ don't understand computers
- ☐ don't understand anything about Crown-of-thorns on the Great Barrier Reef
- ☐ interface did not make sense
- ☐ other (please specify) ________

Thanks for completing this survey. Please turn to the end of the questionnaire.

CotSim Questionnaire 1



7 Please indicate the approximate amount of time you spent using *CotSim* (including units), ________

was this,
(tick one only)

- ☐ much less than expected
- ☐ less than expected
- ☐ about the same as expected
- ☐ more than expected
- ☐ much more than expected
- ☐ other (please specify) ________

8 Is the interface for *CotSim*
(tick one only)

- ☐ too detailed
- ☐ about right
- ☐ not detailed enough
- ☐ other (please specify) ________

9 Is the underlying model for *CotSim*
(tick one only)

- ☐ too detailed
- ☐ about right
- ☐ not detailed enough
- ☐ other (please specify) ________

10 What is the least believable aspect of the *CotSim* model?
(tick as many responses as required)

- ☐ the representation of starfish populations on the reef
- ☐ the starfish growth model
- ☐ the coral model
- ☐ the spawning model
- ☐ the fertilisation model
- ☐ the dispersal model

continued next column

continued from question 10

- ☐ the definition of initial populations
- ☐ other (please specify) ________

11 What are the most believable aspects of the *CotSim* model?
(tick as many responses as required)

- ☐ the representation of starfish populations on the reef
- ☐ the starfish growth model
- ☐ the coral model
- ☐ the spawning model
- ☐ the fertilisation model
- ☐ the dispersal model
- ☐ the definition of initial populations
- ☐ other (please specify) ________

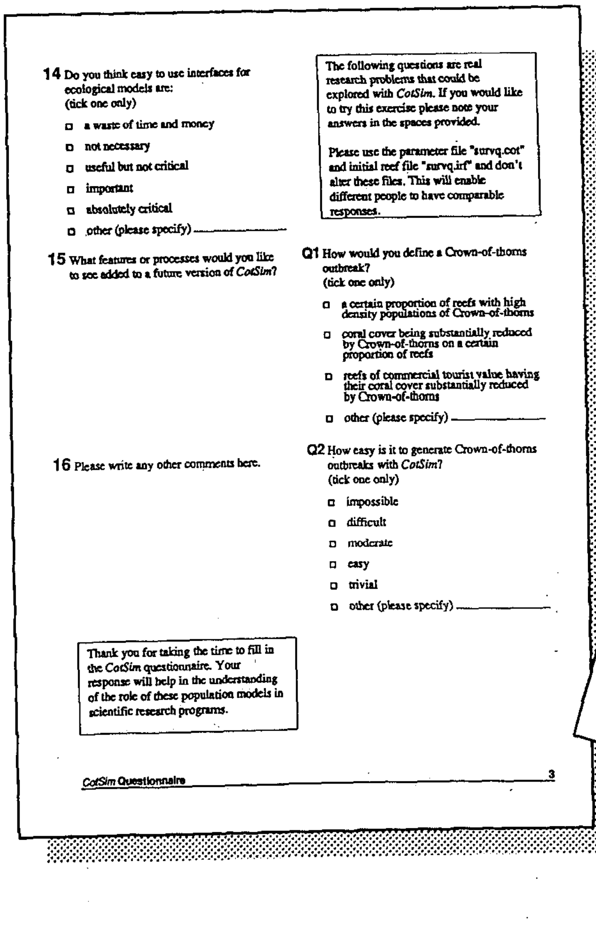
12 After your experience with *CotSim* do you:
(tick one only)

- ☐ know more about the Crown-of-thorns phenomenon
- ☐ know the same amount the Crown-of-thorns phenomenon
- ☐ know less about the Crown-of-thorns phenomenon
- ☐ other (please specify) ________

13 Do you think that ecological models are:
(tick as many responses as required)

- ☐ important for scientific research
- ☐ unimportant for scientific research
- ☐ a waste of time and money
- ☐ toys but not real research
- ☐ important in ecosystem management
- ☐ unimportant for ecosystem management
- ☐ other (please specify) ________

2 *CotSim* Questionnaire



14 Do you think easy to use interfaces for ecological models are:
(tick one only)

- ☐ a waste of time and money
- ☐ not necessary
- ☐ useful but not critical
- ☐ important
- ☐ absolutely critical
- ☐ other (please specify) ________

15 What features or processes would you like to see added to a future version of *CotSim*?

16 Please write any other comments here.

Thank you for taking the time to fill in the *CotSim* questionnaire. Your response will help in the understanding of the role of these population models in scientific research programs.

The following questions are real research problems that could be explored with *CotSim*. If you would like to try this exercise please note your answers in the spaces provided.

Please use the parameter file "survq.cot" and initial reef file "survq.irf" and don't alter these files. This will enable different people to have comparable responses.

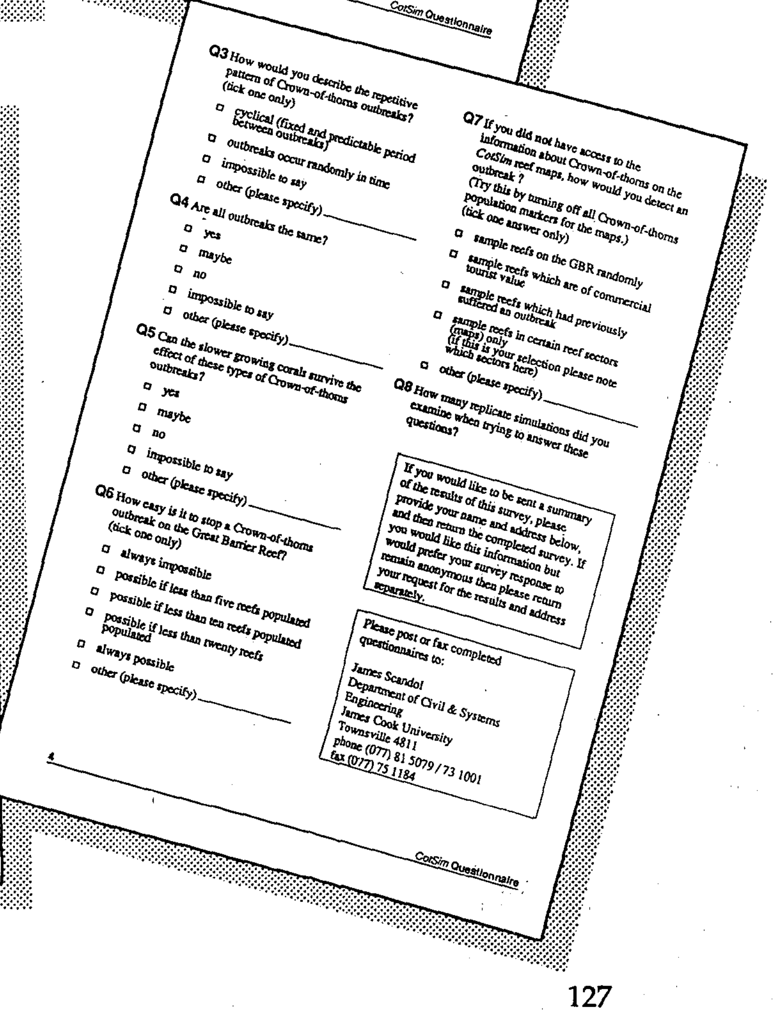
Q1 How would you define a Crown-of-thorns outbreak?
(tick one only)

- ☐ a certain proportion of reefs with high density populations of Crown-of-thorns
- ☐ coral cover being substantially reduced by Crown-of-thorns on a certain proportion of reefs
- ☐ reefs of commercial tourist value having their coral cover substantially reduced by Crown-of-thorns
- ☐ other (please specify) ________

Q2 How easy is it to generate Crown-of-thorns outbreaks with *CotSim*?
(tick one only)

- ☐ impossible
- ☐ difficult
- ☐ moderate
- ☐ easy
- ☐ trivial
- ☐ other (please specify) ________

CotSim Questionnaire 3



Q3 How would you describe the repetitive pattern of Crown-of-thorns outbreaks?
(tick one only)

- ☐ cyclical (fixed and predictable period between outbreaks)
- ☐ outbreaks occur randomly in time
- ☐ impossible to say
- ☐ other (please specify) ________

Q4 Are all outbreaks the same?

- ☐ yes
- ☐ maybe
- ☐ no
- ☐ impossible to say
- ☐ other (please specify) ________

Q5 Can the slower growing corals survive the effect of these types of Crown-of-thorns outbreaks?

- ☐ yes
- ☐ maybe
- ☐ no
- ☐ impossible to say
- ☐ other (please specify) ________

Q6 How easy is it to stop a Crown-of-thorns outbreak on the Great Barrier Reef?
(tick one only)

- ☐ always impossible
- ☐ possible if less than five reefs populated
- ☐ possible if less than ten reefs populated
- ☐ possible if less than twenty reefs populated
- ☐ always possible
- ☐ other (please specify) ________

Q7 If you did not have access to the information about Crown-of-thorns on the *CotSim* reef maps, how would you detect an outbreak ?
(Try this by turning off all Crown-of-thorns population markers for the maps.)
(tick one answer only)

- ☐ sample reefs on the GBR randomly
- ☐ sample reefs which are of commercial tourist value
- ☐ sample reefs which had previously suffered an outbreak
- ☐ sample reefs in certain reef sectors (maps) only (if this is your selection please note which sectors here)
- ☐ other (please specify) ________

Q8 How many replicate simulations did you examine when trying to answer these questions?

If you would like to be sent a summary of the results of this survey, please provide your name and address below, and then return the completed survey. If you would like this information but would prefer your survey response to remain anonymous then please return your request for the results and address separately.

Please post or fax completed questionnaires to:

James Scandol
Department of Civil & Systems Engineering
James Cook University
Townsville 4811
phone (077) 81 5079 / 73 1001
fax (077) 75 1184

4 *CotSim* Questionnaire

Appendix B: List of test sites for *CotSim*

Institution	Expected Number of Respondents
Department of Zoology James Cook University	10
Department of Marine Biology James Cook University	10
Great Barrier Reef Marine Park Authority	5
Australian Institute of Marine Science	10
Department of Civil & Systems Engineering James Cook University	5
Department of Zoology University of Queensland	5
UOG Marine Laboratory University of Guam	5
South Australian Department of Fisheries	3
School of Biological Sciences The University of Sydney	5
School of Resource Science and Management The University of New England	3

Consequences of outbreaks: relationships between spatial scales of outbreaks and temporal scales of recovery.

Craig Johnson and Ann Preece
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Brisbane QLD 4072

Abstract

Spatial models indicate that recovery of coral cover after damage events depends on large-scale system level properties as well as biological ones. Monte Carlo studies showed that the relationship between recovery rate and spatial extent of damage depends on the effective connectivity of the system, which affects availability of larvae for recruitment, and relative magnitudes of larval retention (self-seeding), coral longevity and survivorship of recent pre-damage recruits. Recovery rates (1) may be highly dependent or largely independent of the spatial scale of damage depending on values of these parameters, and (2) may vary with the intensity of damage per reef. At high reef densities coral recovery rates are sensitive to survival of recent pre-damage recruits if coral longevity is short (30 years), but the degree of self-seeding is relatively unimportant. In contrast, if the density of reefs is low, and there is no self-seeding, coral does not recover at all but either stabilises at reduced coral cover or declines, depending on its average longevity. If reef density is low and there is some larval retention (13% cover over 7 days), then recovery depends largely on survival of pre-damage recruits and coral longevity is less important.

NB: This paper will be published in the Proceedings of the Seventh International Coral Reef Symposium (June 1992), Guam, U.S.A.

Long term response of herbivorous fish to crown-of-thorns starfish outbreaks.

Tony Hart
Australian Institute of Marine Science,
PMB No. 3, Townsville MC QLD 4810

Abstract

This project involves a comparative study of three crown-of-thorns impacted (Grub, Yankee, Dip) and three non-impacted (Centipede, Coil, Bowl) reefs in the Townsville section of the GBR. The specific objectives are to compare: 1. substrate characteristics; 2. density, biomass, and size-structure of selected herbivorous fish species; 3. growth rates; 4. body condition; 5. feeding ecology; 6. size at age, and 7. age at maturity of two species, between impacted and non-impacted reefs. The two species are Scarus frenatus (Pisces: Scaridae), and Acanthurus nigrofuscus (Pisces: Acanthuridae). Significant differences for both mean live coral cover (14% and 50% at impacted and non-impacted reefs respectively) and mean turf algal cover (52% and 18% at impacted and non-impacted reefs respectively) were found during June 1991 and January 1992. However, no significant differences were found for densities, biomass, feeding rates or body condition. This is largely due to very distinct between -reef and cross-shelf patterns for all variates which are confounding the impacted/non-impacted comparison. The study concludes that examining densities of these herbivorous fish is of limited value when trying to detect effects of crown-of-thorns perturbations to the reef substrate. This conclusion is supported by the conflicting results cited in the literature to date. Research will now focus on establishing growth rates, size at age, age at maturity, feeding ecology, and changes in body condition over time, in an attempt to detect a variate which will be more useful in detecting effects of COTS outbreaks.

Effects of *Acanthaster* predation on bioerosion: design and preliminary results.

Barbara M Musso
Department of Marine Biology,
James Cook University of North Queensland,
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Abstract

The downstream effects of COTS outbreaks on non-coral organisms have rarely been investigated. The present work is concerned with the effects of outbreaks on the process of biological degradation of the reef framework. On reefs that have experienced severe outbreaks, the overall reworking of calcium carbonate by biological agents is expected to be greater than on reefs with high live coral cover. To establish whether the rates of bioerosion per unit area of substrate are enhanced on a reef following an outbreak, and what are the causes and effects of degradation of the standing coral skeletons left behind by COTS predation, two research programs have been undertaken. An experimental program consists of simulating COTS predation by killing coral colonies in situ in restricted areas on the reef crest. Three species of Acropora , usually highly preyed upon by Acanthaster, have been used. To date, results show that Acropora hyacinthus undergoes rapid skeletal degradation by external destructive agents, while skeletons of A. gemmifera and A. cuneata remain for longer periods exposed to the action of excavating organisms. The second research program consists of sampling dead substrates occurring on large Porites bommies, on both COT-affected and unaffected reefs. The year of death of these substrates can be estimated, and rates of bioerosion relative to periods of over 30 years could be calculated. Preliminary results show that the method is a powerful tool for establishing both large scale and disturbance-induced variations in the process of internal bioerosion.

Introduction

Since the "*Acanthaster* phenomenon" (Moran 1986) started in the early 1960's, a massive bulk of literature has accumulated on the starfish and on various aspects of the outbreak events. However, studies on the consequences of heavy outbreaks on the reef components other than corals are scarce. In an annotated bibliography of the publications up to 1988 (Moran 1988) relative to the crown-of-thorns starfish (COTS), only 16 out of approximately 470 titles, were in some way concerned with the effects of outbreaks on non-coral organisms. Most of the research induced by the *Acanthaster* debate has focussed on the biology of COTS, in the attempt to shed some light on the origins and causes of the outbreaks. In contrast to the small number of specific studies, many authors have pointed out the importance of investigating the responses of the reef system to the massive coral mortality resulting from a large outbreak (Potts 1981, Bradbury *et al.* 1985, Bradbury and Mundy 1990, Moran 1986). Some downstream effects of outbreaks have been investigated, notably those on algae (Price 1972, 1975, Belk and Belk 1975, Bradbury and Mundy 1990), soft corals (Pearson 1981, Bradbury and Mundy 1990) and fish communities (Sano *et al.* 1984, 1987, Williams 1986).

The consequences of large outbreaks on bioeroding organisms have never been investigated. A number of authors have recognised the potential of the process of bioerosion to be altered following an outbreak (Price 1975, Hutchings 1986, Glynn 1988, Scoffin 1992). This is based on the fact that bioerosion acts primarily on dead coral substrates, and that these substrates predominate on the reef surface following COTS outbreaks. Fabricius and Fabricius (1992) report a high correlation between sedimentation rates and abundance of COTS skeletal elements in subsurface sediment cores from two reefs on the Great Barrier Reef. Although they are unable to relate the relative abundances of skeletal elements in the sediment to absolute population sizes (ie. outbreak population sizes), they discuss the increased susceptibility to erosion (and consequently to sedimentation rates) of a reef surface that has experienced high rates of predation by *Acanthaster.* The present study specifically addresses the effects of extensive coral mortality due to COTS feeding activity on bioerosion. The potential mechanism by which large outbreaks may potentially affect bioerosive processes on a reef is twofold. Firstly, a rapid, dramatic increase in dead coral cover which would result in a linear increase of bioeroded substrate. This increase could be estimated from information on the rates of degradation of newly dead coral skeletons standing on the reef surface. Information of this nature is not available at present. Previous studies which pioneered research on bioerosion on the Great Barrier Reef, have used artificial or transplanted substrates. Their purpose was to quantify the contribution of factors such as surface area, seasonality in recruitment of borers and duration of exposure to the observed rate of erosion (Hutchings and Bamber 1985, Davies and Hutchings 1983, Kiene 1985). Although much information has been gathered on the pattern of succession of boring organisms, nothing is known on how different dead coral skeletons are degraded on the reef surface. The second mechanism through which an outbreak could affect the overall process of bioerosion consists of possible changes in the population dynamics of the organisms responsible for the erosion of the reef framework (ie. boring infauna and vertebrate and invertebrate grazers), which may result in a non-linear increase of the rates of destruction.

The two mechanisms mentioned above are investigated here in two different studies. The first experiment simulates an *Acanthaster* feeding episode on reef crest habitats. It is aimed at estimating rates and nature of degradation in the skeleton of corals that are usually heavily preyed upon by COTS. The relative importance of external and internal bioeroders, and the temporal and spatial variability at a reef scale is estimated in the different coral species. This experimental approach has the advantage of controlling for factors such as time of death and type of substrate, which are responsible for most of the noise usually confounding studies on bioerosion.

The second study is one of the long term rates of bioerosion (over 4 to 33 years) on affected and unaffected reefs. It is designed to estimate possible changes in both rates of bioerosion and community composition of bioeroding invertebrates following *A.*

planci outbreaks. A new method of estimating rates of bioerosion using datable dead coral substrates has been employed to obtain long-term rates.

Methods

Simulation of Acanthaster predation

This experiment commenced at Lizard Island in February 1991 and will run up to February 1993. Coral colonies belonging to 3 species of *Acropora* (*A. hyacinthus*, *A. gemmifera* and *A. cuneata*) have been killed *in situ* on the reef crest. A total of 180 coral colonies have been killed and tagged. Their skeletons will be collected at the end of the experiment and analysed for the extent of internal bioerosion. A total of 90 living colonies (30 of each species) have been tagged and are monitored along with the killed ones.

The colonies are monitored every 3 months with photographic techniques in order to detect and quantify the changes in size due to external degradation. The method is similar to the one used by numerous researchers to study community dynamics of corals by estimating their changes in size and interactions through time. Colonies are photographed from above and the resulting images are digitised which provides an estimate of the planimetric, or projected, surface area of the colony. An estimate of the precision of the technique for parallax error was made by taking replicated photos of the same colonies from angles judged as perpendicular by the photographer. This gave an estimate of the technique bias of about 5% of the area. Presently 5 censuses have been completed (February, May, July and November 1991, February and August 1992) and the data from the first 4 censuses processed and analysed (Musso, *in review*).

The experiment follows a three-way, mixed model, nested ANOVA. In 2 locations (SE winds exposed reef crest / NW winds exposed reef crest), 3 sites per location have been set up. In each site colonies belonging to 3 species have been killed and mapped. The replication for each species is 10 colonies. At the same sites the same number of living colonies have been mapped and are monitored as controls. Due to a lack of independence among observations, data relative to external degradation were analysed with a Repeated Measures Multivariate ANOVA.

In order to convert the changes in surface area observed in *A. hyacinthus* into changes in calcium carbonate weight, 20 recently dead colonies were photographed underwater before and after removing the margins of the plate. The fragments removed were dried and weighed. The planimetric surface areas and dry weight of the margins of recently dead plates of *A. hyacinthus* were significantly correlated. A conversion factor of surface area to weight was estimated as the regression coefficient of a Model II Regression (b = 0.01365, C.L. 0.0123 and 0.015; Bartlett's three groups method for Model II Regression, see *Fig. 1*).

Living colonies belonging to the same species as the experimental ones have been collected and processed to obtain an estimate of the extent of internal bioerosion prior death (Musso, *in review*). The colonies are sectioned in 5 mm thick slices with a rock saw. Each slice is photocopied and the boreholes on the sectioned surfaces are digitised using an image analyser. This provides an accurate estimate of the volume of skeleton removed from the colony. For each slice and colony the relative contribution to bioerosion of different boring taxa has been recorded. Data on extent and species composition of internal bioeroders communities in the three species have been collected and analysed (Musso, (a) *in preparation*).

COTS outbreaks and long-term rates of bioerosion

The sampling of dead substrates on reefs with known history of past outbreaks has been carried out on Green Island (Musso, (b) *in preparation*) and John Brewer Reef (both experienced outbreaks in the 60's and 80's), and Centipede Reef (no evidence of outbreak since 1973; a large population of COTS was reported in 1971 but coral cover remained high). The second unaffected reef included in the design is the reef surrounding Low Isles. Sampling at this reef is scheduled for late January 1993. The reefs were chosen after consultation of the data collected by the A.I.M.S. survey teams.

The sampling is carried out on the dead surfaces occurring on big *Porites* bommies and resulting from partial mortality events (Anonymous 1985). These surfaces are sampled by drilling shallow cores (5 cm diameter by about 8 cm depth) with a pneumatic-drill, driven by a compressor running on the support vessel. One long core (2.5 cm diameter by 25 cm height) is also taken from each sampled surface for determining the year of death. The shallow cores are sectioned and the sections digitised to estimate the total volume removed by the major taxa of borers. The long cores are sectioned longitudinally and placed under UV light to analyse the fluorescent bands in the skeleton. These bands result from skeletal incorporation of run-off humic acids during particularly wet seasons and they allow the dating of the dead surface (Isdale 1984). A year of death is therefore estimated for each substrate sampled. A rate of bioerosion is calculated for each substrate as the volume of calcium carbonate removed divided the number of years since death.

The design includes 4 reefs (2 affected and 2 non-affected) and 2 sites per reef. Although the effect of COTS status on internal bioerosion in each reef could be confounded with other factors, especially shelf position, the levels of such factor are interspersed within the levels of the main treatment. At each site 4 *Porites* bommies with 2 or 3 different aged dead substrates each, have been sampled. For each substrate, 6 replicate cores are taken. The data obtained are analysed by regression analysis and ANCOVA following angular transformation.

Results

Simulation of Acanthaster predation

This paper summarises the major results in order to discuss them in relation to the effects of COTS outbreaks on the degradation of the reef surface. The detailed, preliminary results of this ongoing study may be found in Musso (*in review*).

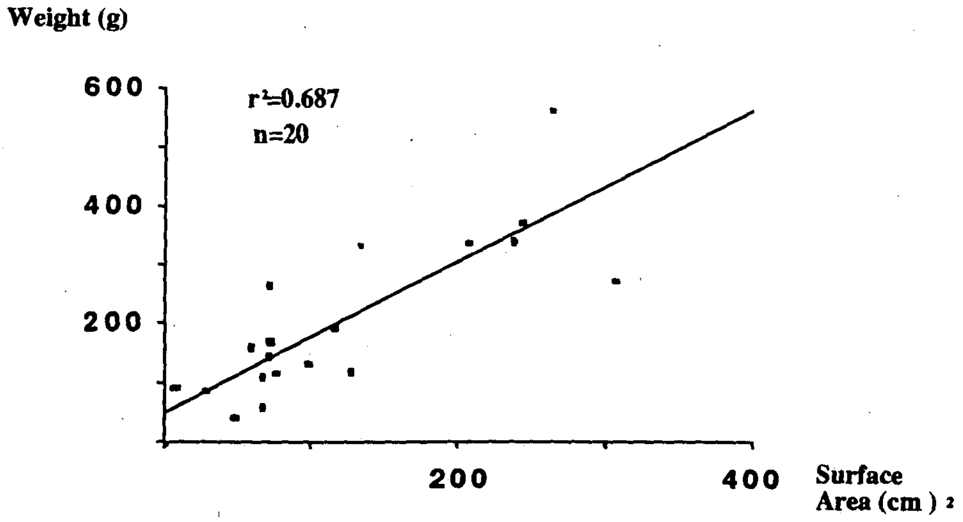
The 3 species of *Acropora* used in the experiment differ greatly in the rates of erosion. High rates of external degradation occurred only in dead colonies of *Acropora hyacinthus* (*Table 1*). The other 2 species showed no changes or changes too small to be detected with the technique employed. There was a significant effect of time, with early, rapid degradation levelling off after three and six months since death in *Acropora hyacinthus* (*Fig.* 2). No significant interactions between time and location, or time and sites were found for *Acropora hyacinthus*. Univariate analyses performed on the data collected after 11 and 34 weeks and relative to *Acropora hyacinthus* showed a significant location effect, with the area removed being higher in the most exposed, S.E. sites (*Fig.* 2).

Table 1: Percent surface area removed from the experimental colonies after 9 months since death. Mean values are shown with standard errors and sample size in parenthesis (from Musso, *in review*).

	S.E. SITES			N.E. SITES		
	1	2	3	1	2	3
Acropora hyacinthus	49.34 ± 6.92	54.72 ± 8.08	57.24 ± 2.47	37.69 ± 4.02	48.51 ± 5.95	27.12 ± 8.43
sample size	(8)	(6)	(10)	(8)	(7)	(4)
Acropora gemmifera	17.28 ± 7.91	6.93 ± 3.08	4.38 ± 2.14	-0.21 ± 3.63	5.96 ± 3.21	3.64 ± 2.96
sample size	(8)	(8)	(10)	(8)	(9)	(10)
Acropora cuneata	-0.25 ± 1.75	-3.40 ± 2.48	2.13 ± 2.04	-2.25 ± 4.00	-1.17 ± 1.59	4.38 ± 1.47
sample size	(5)	(4)	(4)	(8)	(8)	(8)

Table 2: Percent of volume removed by internal bioeroders in living coral colonies. Data were pooled within location. Means are shown with SE.

	S.E. Sites	N.E. Sites
Acropora cuneata	5.99 ± 1.01	7.01 ± 1.71
Acropora hyacinthus	1.10 ± 0.31	1.22 ± 0.38
Acropora gemmifera	3.47 ± 0.92	1.25 ± 0.25



W=(0.013 ±0.001)SA

Figure 1: Conversion factor used for transforming surface areas in dry weight estimates for *A. hyacinthus* plates (from Musso, *in review*).

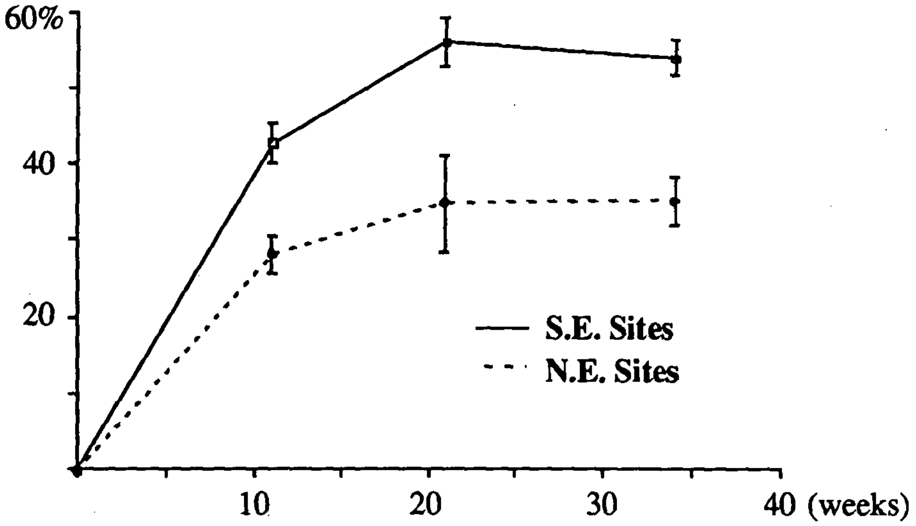


Figure 2: Percent of the initial planimetric area of *A. hyacinthus* plates removed plotted against time, for the two locations. Points are means and error bars are SE (from Musso, *in review*).

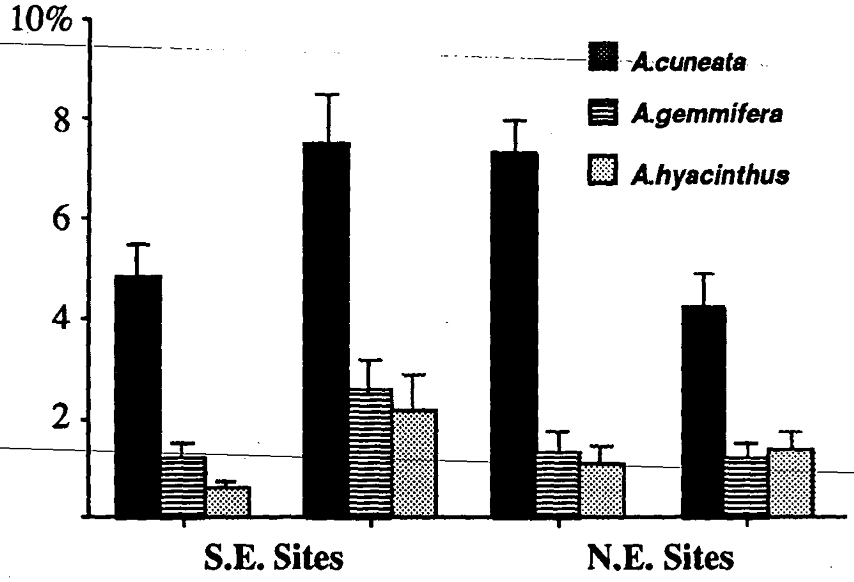


Figure 3: Estimate of the percent volume of skeleton removed by internal bioeroders in the three coral species prior to death (from Musso, *in review*).

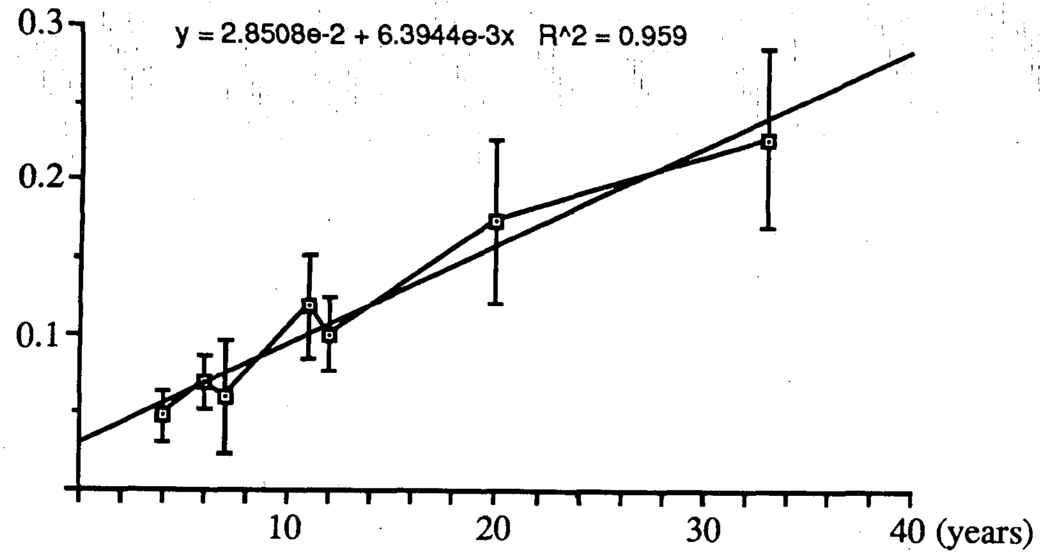


Figure 4: Common regression line of proportion of volume removed (data expressed as *arcsin* of square root of the raw data) from dead *Porites* substrates. Substrates and sites pooled after analysis.

The loss of calcium carbonate from each plate colony after 9 months since death was estimated to be 327.3 g (confidence limits: 296.6 g and 361.6 g) and 226.7 g (confidence limits: 205.5g and 250.5 g) respectively at the more exposed and less exposed locations.

The estimate of the percent volume removed by borers in the three species before death was significantly greater in *A. cuneata* than both *A. hyacinthus* and *A. gemmifera* (*Fig. 3, Table* 2). Preliminary analysis of the taxonomic composition indicates that bioeroding communities in *A. cuneata* differ from the other two species (Musso, (a) *in preparation*).

COTS outbreaks and long-term rates of bioerosion

Data were obtained and analysed from the sampling at Green Island (Musso, (b) *in preparation*). The method of dating dead *Porites* by using skeletal fluorescent bands proved feasible for substrates which died less than 33 years ago. In the case of older substrates, the fluorescent bands were less identifiable. Only data from reliably dated substrates were included in the analysis.

At Green Island a rate of internal bioerosion was obtained for each of eight *Porites* bommies. Each bommie was sampled at two differently aged dead layers (corresponding generally to the time of the two major COTS outbreaks). For each bommie a rate was obtained using regression analysis. A test for homogeneity of slopes showed that the rates of bioerosion were not significantly different among bommies within each site. Finally, an Analysis of Covariance showed no significant difference among the two sites. Power of the test to detect differences among sites was very high (1-b = >0.94). Such results allowed for the estimation of a common regression coefficient, ie. rate of internal bioerosion.

Discussion

The results of the experimental study (simulation of COTS feeding episode) are discussed firstly in relation to previous analogous work on the Great Barrier Reef and secondly to their implications in the context of outbreak events. Also, the results from the pilot study at Green Island on the long term rates of bioerosion are discussed, and possible paths of propagation of the outbreak effects to the bioeroding component of the reef system are presented.

After nine months of monitoring of the colonies killed by simulating *Acanthaster* predation, the results suggest that in plate coral colonies of *A. hyacinthus* very rapid skeletal degradation occurs soon after death. The agents responsible for skeletal degradation act differentially on the skeletons of different coral species. There does not appear to be any relation between the estimated extent of internal bioerosion at the time of death and the rates of the subsequent external degradation. It is likely that both physical degradation and biological erosion by grazing activity (mainly parrotfishes) are responsible for the high size reduction in the skeletons of *A. hyacinthus*. Sammarco *et al.* (1986) conducted a similar experiment with transplanted colonies of a foliaceous coral (*Pachyseris speciosa*). They implemented treatments with and without cages, which allowed them to conclude that the large skeletal degradation observed was mainly due to grazing activity by parrotfish. In the present study the spatial pattern observed in relation to site exposure suggests that physical erosion by wave action is also important. A pilot study for an experiment implementing wide-mesh cages for exclusion of excavator parrotfish is currently underway. The relative importance of these two agents (grazers vs. wave action) is relevant to the carbonate budget of the reef crest, as the two have different by-products, thereby recycling calcium carbonate in different compartments of the reef (Davies 1983).

The preliminary results of this study suggest that after an outbreak of *Acanthaster planci* occurs on the reef crest, the plate colonies that have been preyed upon are likely to disappear quickly. These corals represent the most preferred prey for *A. planci.* (De'ath and Moran, *in press* Faure 1988) and even under non severe outbreak conditions are likely to undergo extensive mortality, especially medium size colonies like the ones considered in this experiment. Larger colonies might be affected only by partial mortality during non severe outbreaks, thus escaping death. A study by Musso and Nelson is currently under way to investigate the effects of simulated scars on plates of *Acropora hyacinthus.*

Following an outbreak, the high rates of degradation in plate corals will result in the reworking of a large amount of calcium carbonate and in a reduction in the rugosity of the reef surface. In contrast, no immediate skeletal degradation appears to occur in the other two species under investigation. This suggests that the process of degradation of the reef surface, and the quantity of calcium carbonate reworked following an outbreak, will depend on the relative abundance of different coral species and on the species composition of the community affected by COTS predation. Thus, it might be possible to make minimum estimates of the effect of an outbreak on the erosion of a coral community, given data on the relative abundance and mortality of different species.

The topographical changes of the reef surface resulting from the quick disappearance of tabulate corals may affect the coral community structure and, in post-outbreak situations, the patterns of coral settlement on the recovering reef. The role of the plate corals in structuring the composition and in increasing diversity of the understorey community has been investigated by some authors with sometimes different results (Sheppard 1981, Stimson 1985). According to Stimson (*op. cit.*) the understorey community has lower density and lower diversity than open substrate. Recently Fisk and Harriott (1992) have reported much lower rates of recruitment under tabulate corals compared to more exposed substrates. However, especially in those habitats that are dominated by *Acropora* plates, ie. the upper slope, structural complexity and tri-dimensionality of the reef surface must rapidly decrease with massive coral mortality. Some effects on the recovering community have to be expected and should be further investigated.

So far I have discussed what I regard as the "immediate" effects of an outbreak on bioerosion: that is to say the linear increase in bioerosion resulting from the increase in "bioerodable" substrate. Another possible effect that is likely to manifest itself over a larger temporal scale is the one resulting from changes in the population dynamics of dead coral indwelling organisms, after living coral cover gets drastically reduced. These changes could affect different stages of the life history of these organisms. For example, if more substrate is available for settlement after COT outbreaks, the population sizes could increase after few reproductive seasons; the reproductive output could consequently increase and so recruitment, at least for those organisms for which the reef is self-seeding. Processes like pre- and post-settlement mortalities could be altered by altered predation pressures. Because boring communities are diverse, different changes in different species could also result in alteration of the community composition. Examples of changes of specific bioeroding organisms to disturbance have been documented (Rose and Risk 1985, Scott 1990).

The study I started at Green Island is aimed at detecting changes that may occur, after large COTS outbreaks, in the long term rates of bioerosion and in the composition of boring communities. Studies investigating bioerosion have generally pointed out the high levels of variability which characterises the process. Sammarco and Risk (1991) reported that up to the 56% of the variance in the extent of bioerosion in *Porites* heads was due to variability among heads and a further 20% to variability within heads. Factors such as duration of exposure (Davies and Hutching 1983, Kiene 1985) as well as type of substrate (Highsmith 1981) are responsible for most of the noise usually confounding studies on bioerosion. Therefore, a fundamental difficulty in determining extent and rates of bioerosion is that an accurate estimate of the time of death of the substrates to be sampled is necessary. This difficulty has usually been circumvented by implementing experimental substrates, for which the time of exposure to bioeroders is known. This implies that the temporal scale over which the rates of bioerosion are calculated is limited by the duration and resources of the study.

This study uses naturally occurring *Porites* substrates for which the time of death can be accurately estimated. The pilot study shows that substrates as old as 33 years can be reliably dated. This length of time spans a period which includes the two major outbreaks reported for the Great Barrier Reef. The analysis of the data from the pilot study at Green Island indicates that when only one type of substrate is analysed for internal bioerosion, and the variability due to the duration of exposure of the substrate to borers can be accounted for, then the variation of the rates of bioerosion within that substrate is low, and consequently power of the tests for detecting treatment effects is likely to be high. The method represents a powerful tool for isolating large spatial scale variability in the process of bioerosion, and variability due to disturbance events like *A. planci* outbreaks. This is the first study of long term rates of bioerosion with the potential of investigating such questions.

Acknowledgements

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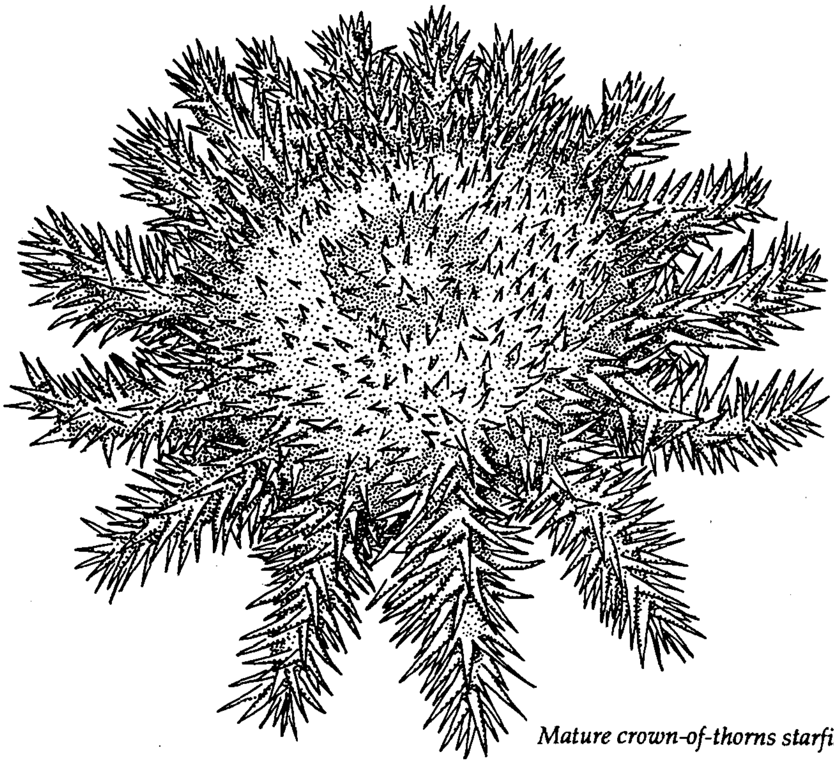
SESSION 3

MANAGEMENT OPTIONS AND THE FUTURE OF THE COTS PROGRAM



Mature crown-of-thorns starfish

Chair: Mr Simon Woodley (GBRMPA)

The history of crown-of-thorns starfish controls on the Great Barrier Reef and an assessment of future needs for controls

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Abstract

The Authority is planning for the next series of outbreaks of crown-of-thorns starfish by developing a Contingency Plan. Part of the Plan is devoted to the feasibility and desirability of primary controls aimed at preventing the southwards spread of outbreaks. This paper reviews the history of the Authority's policy on controls, the results of past and present controls and reasons for their success or failure. The arguments likely to be raised for widespread controls in the event of another outbreak (including the causes of outbreaks, recovery since the last outbreak, usage of reefs) will be discussed. The feasibility of such controls will be examined in terms of costs, possible effectiveness, side effects and alternatives.

Background

Providing for the protection, wise use, understanding and enjoyment of the Great Barrier Reef in perpetuity through the care and development of the Great Barrier Reef Marine Park is the goal of the Great Barrier Reef Marine Park Authority (GBRMPA). Achievement of this goal necessitates the management of problems and their effects. Included in this is the management of the crown-of-thorns starfish phenomenon, which in two outbreak episodes on the Great Barrier Reef has caused considerable damage to coral communities. The current policy of GBRMPA's regarding crown-of-thorns starfish and their control is that, unless it can be proven that outbreaks are either caused or exacerbated by human activity, controls should be limited to small-scale tactical measures in areas important to tourism and science. This policy has evolved from many government enquires and the recommendations of researchers.

The second series of outbreaks of crown-of-thorns starfish on the Great Barrier Reef is coming to an end. However, it is possible that outbreaks will occur in the future. To prepare for this the Great Barrier Reef Marine Park Authority has developed a Contingency Plan to be consulted and activated at the start of the next outbreak episode (Lassig *et al., in press*). The Contingency Plan involves options for monitoring, research and controls. There are likely to be calls for widespread controls of the starfish at the start of the next outbreak, as occurred in both previous outbreaks. Already arguments have been presented for the early eradication of starfish to prevent the coral mortality associated with the southward-progressing waves of secondary outbreaks. Research in the next few years may also suggest a link between human activities and outbreaks. It is therefore timely to re-examine widespread controls, in terms of their desirability, usefulness and effectiveness. In this paper I present a history of the controls issue, a discussion of the likely calls for widespread or primary controls, and an examination of the costs, effectiveness and possible side effects of such measures.

A History of Thoughts about Controls on the Great Barrier Reef

The first recorded outbreak of crown-of-thorns starfish on the Great Barrier Reef was seen on Green Island reef in 1962. High coral mortality and a lack of knowledge about the long term consequences for the Reef led to the popular media and some scientists demanding widespread eradication of the starfish. The impossibility of such measures was recognised early in the history of the crown-of-thorns phenomenon. In the earliest official report on crown-of-thorns starfish in 1965, state fisheries biologist NM Haysom advised that controls would only be practical in very restricted areas. Haysom also recommended control techniques other than "hand harvesting" be investigated and a program of research of the starfish be instigated. The recommended research included distribution and abundance, reproduction, feeding ecology and means of controls.

In the first report of these investigations Endean (1969) recommended widespread controls by hand harvesting and the use of one of the starfish's predators, the giant triton shell (*Charonia tritonis*), as a control agent. In particular, Endean (1969) recommended breeding and release of large numbers of tritons. In a report of the other main areas of research Pearson and Endean (1969) provided data on the feeding ecology of the giant triton shell suggesting that each triton consumed less than one crown-of-thorns starfish per week. To this day there is little extra information available on the feeding ecology of the giant triton, although popular scientific consensus is that control by tritons is not feasible.

Controlling outbreaks in small areas, such as around tourist sites, has been seen as desirable in all government reviews of the crown-of-thorns starfish phenomenon. The issue of more widespread controls has been an evolving one. In the early years of the phenomenon arguments against widespread controls were utilitarian ie widespread controls were desirable but impractical. A joint conference of Commonwealth and Queensland government officers in 1969 concluded that controls were desirable but should not be undertaken until the methods were evaluated. Research into the giant triton was also recommended. A 1970 report of a committee established by the Australian Academy of Sciences concluded that controls should be confined to small areas around established tourist sites, because practical methods were unavailable to undertake widespread or long-term controls (Walsh *et al.* 1971).

A shift in thinking about widespread controls occurred in 1971. A Committee of Queensland and Commonwealth experts was established in 1970 in response to conflicting expert opinions of the phenomenon. The Committee considered evidence from many experts and also from a growing body of research. The 1971 report of the Committee concluded that the starfish did not threaten the entire Great Barrier Reef, that coral recovery was occurring, and that damage was restricted to reefs between Cairns and Townsville. Importantly, the Committee concluded that the starfish outbreaks may be a natural part of the destructive processes of coral reefs. Eradication of starfish on reefs of "social or commercial importance" was regarded as feasible; however, widespread controls were "unwarranted" (Walsh *et al.* 1971). The scale and success of control programs undertaken during the first outbreak episode has been reviewed by Zann and Weaver (1988).

In 1976 the Great Barrier Reef Marine Park Authority was established and as the government agency responsible for managing the GBR Marine Park, issues related to crown-of-thorns starfish were also its responsibility. GBRMPA's policy on controlling crown-of-thorns starfish appears to have grown from the recommendations of the 1971 Walsh report.

The second episode of outbreaks on the GBR was first reported around Green Island reef in 1979. A number of expert committees were convened by GBRMPA to advise it on the crown-of-thorns starfish problem. The Crown of Thorns Committee (1980) recommended research directions but not controls (Lassig 1991). The 1985 report of the Crown-of-Thorns Starfish Advisory Committee (COTSAC) supported the GBRMPA controls policy and also recommended a program of research into controls. Between 1985/86 and 1989/90 six research projects were funded for a total of $193,210 and covered the costs and effectiveness of copper sulphate injections as controls, underwater fencing to protect small areas of reefs, and the diseases of crown-of-thorns starfish. Results of these programs were summarised by Lassig (1991) and Zann and Weaver (1988). COTSAC also reviewed the available evidence on the results of macro-scale control operations and concluded they were of "limited value in controlling major populations".

GBRMPA's management of the crown-of-thorns phenomenon was again reviewed in 1989 (Anderson 1989) following adverse publicity in the media. The controls policy of GBRMPA was supported and research into biological controls recommended. After serious consideration of the use of biological controls, including costs and risks, the new advisory body to GBRMPA on crown-of-thorns starfish, the Crown-of-Thorns Starfish Research Committee (COTSREC), advised against funding for biological controls research.

A condition of the Federal government funded COTSREC research program was for a mid-term independent review. The report (Johannes 1991) made no mention of controls but recommended a Contingency Plan to be initiated at the start of the next series of crown-of-thorns starfish outbreaks. An important component of the Contingency Plan (described in detail by Lassig *et al., in press*) is an assessment of the possible needs, and options, for controls at the start of the next outbreak episode.

In summary, discussion to date on the desirability of widespread controls has focussed on the impracticalities and costs, the unresolved issue of whether outbreaks are natural or human-influenced, and the damage caused by outbreaks. There is general agreement about the desirability of limited controls around small, important areas. In the next outbreak episode these discussions may be more focussed on the long-term consequences of further outbreaks and the threat to the amenity value of the Reef.

Preparing for the next Outbreak Episode

There were considerable public calls for large-scale controls of COTS at the start of both outbreak episodes on the GBR (Raymond 1986), even in the absence of evidence for human influences in outbreaks. It is anticipated that these calls will be repeated at the start of the next outbreak episode. It is therefore an opportune time for GBRMPA, as a management agency, to begin to prepare for another controls debate by reviewing the scope of controls that may be called for.

The term "primary controls" will be used here to describe controls designed to eradicate COTS on primary outbreak reefs. The aim would be to prevent the southward progression of secondary outbreaks along the GBR.

Calls for Controls

GBRMPA's current policy on controls indicates that larger scales of controls would be considered if evidence suggests that outbreaks are influenced by human activities. At present, no such evidence is available.

During the current outbreak an estimated 17% ± 4% of reefs have been affected, about one-fifth of these (ie. about 3-4% of all reefs) seriously. Given this scale of damage, major ecosystem-wide effects seem unlikely. However, geographic regions, in particular the central section of the GBR, suffered more intense damage (about three-quarters of all surveyed reefs affected) and reefs in this area may not recover fully from another outbreak should one occur in the next 15-20 years.

There have been recent calls for primary controls (Lucas 1990). Lucas (1990) argues that another outbreak in the next few years may fundamentally alter the composition of reefs from highly diverse coral communities to communities dominated by faster growing species. In the past two outbreaks on the GBR many massive corals on affected reefs were eaten (Endean *et al.* 1988; Done and DeVantier 1990). Time for these corals to be replaced, it is predicted, may vary from 9 to more than 100 years (Done 1988). Lucas (1990) has called for primary controls, if the next outbreak occurs within a few years, to prevent further degradation of the reefs.

Calls for primary controls could also come from the tourist industry. The GBR is Australia's most popular tourist destination and generates about A$ 1 b per annum (WS Cummings Economic Research Services 1991). The most popular part of the GBR is the reefs and islands offshore from Cairns on the far northern coast of Queensland. Coincidentally, this is also near to the hypothesised primary outbreak area for COTS on the GBR (Dight *et al.* 1990). Coral reefs are an important commercial resource and their value is expected to grow rapidly. In 1984/85 there were 934,000 visits made to the reefs and islands near Cairns; it is predicted that by 1997/98 this will have risen to 2,608,000 and by 2002/03 it could be 3,310,000 (Thomas 1992). In 1989/90 the value of tourism in the Cairns area was $500 m (WS Cummings Economic Research Services 1991).

If coral reefs were affected by another outbreak of COTS there would be no alternative sites for tourist operators. Suitable sites for either moored pontoons or roving boats are limited, owing to needs for good coral cover, low currents, and a safe anchorage. All suitable sites in the Cairns region are currently utilised. There could be considerable lobbying for primary controls at the start of the next outbreak, by the tourist industry around Cairns and also further south on the GBR, to prevent any damage to reefs.

In conclusion, even without evidence for human influence in COTS outbreaks, it is expected that there will be public demands for primary controls at the start of the next outbreak episode on the GBR. If human influence is proven there needs to be an assessment of the possibility of success of primary controls using current control technology.

The Option of Primary Controls

The aim of primary controls would be to eradicate all COTS in a primary outbreak to prevent the southward progression of secondary outbreaks. This would rely on the primary outbreak being detected as early as possible. COTS become more visible to observers, and reproductively mature, at around two years of age; however fecundity is low until they reach age three years (Birkeland and Lucas 1990). Primary controls would have to be done in that interval between ages two and three. COTS are currently eradicated manually by divers injecting a concentrated solution of copper sulphate. The feasibility of primary controls can be examined in terms of costs, the likelihood of success, possible side effects, and alternatives to current control technology.

Costs

Estimated costs of eradicating all COTS on a reef would vary with such factors as the size of the primary outbreak, the injection rate, distance of the primary outbreak reef from shore-based facilities and the number of reefs with primary outbreaks. Costs have been estimated for primary outbreaks of several sizes: 2 m, 1 m, 0.5 m, 100,000 and 50,000 starfish. The maximum injection rate is around 130 starfish per hour (Birkeland and Lucas 1990) for large outbreaks; for smaller outbreaks the injection rate varies from 10 to 80 per hr (Zann and Weaver 1988; Johnson *et al.* 1990). The cost model assumes that as starfish numbers decline the injection rate also declines because of the additional time spent searching for starfish. The model also assumes the following: time spent diving of 4 hours per day (which takes into account time lost due to poor conditions); a salary of A$ 150 per day per person; a minimum diving team of three (two divers and one boat person); ship charter costs of A$1200 per day; supervisors' salaries; dive equipment costs and services; chemicals; and follow-up surveys of reefs.

Predicted costs for controlling primary outbreaks of each size are:

2m COTS	A$ 3.51m
1m COTS	A$ 1.57m
0.5m COTS	A$ 1.37m
100,000 COTS	A$ 0.50m
50,000 COTS	A$ 0.47m

The high cost of hiring staff to undertake control programs could be offset by the use of volunteer divers. There are a number of problems with using volunteers, including numbers available and their effectiveness. This would be difficult to guarantee, and even more difficult if a large number of reefs had to be controlled. The supply of volunteers would also be subject to the weather, time of year, number of paid jobs available in a nearby centre, the incentive of the individuals, and their success rate in the field (interest would likely to be high when COTS are abundant but decline substantially when there are few).

The number of volunteers would have to be greater than the salaried divers because of the need to continually train personnel in locating and injecting COTS, and the associated longer time to search and find COTS. In a series of control programs in the Whitsundays between 1988 and 1990 the injection rates for experienced local divers were 30.4 ± 10.06 per hr (Mean ± SE) compared with 2.3 ± 0.74 per hr for inexperienced volunteers. The costs of using volunteers for other reefs with different sized outbreaks would be around 40% of those if personnel were paid for the control action, but the costs are still substantial.

There is no information on the possible size of a primary outbreak on the GBR, nor on the number of reefs that might simultaneously experience primary outbreaks. It is therefore difficult to predict total costs. It is feasible that the waves of secondary outbreaks could be generated by a primary outbreak on a single reef. Primary controls would probably need to be done several times on each reef in order to locate cryptic starfish and to kill those recruiting to the adult population. The above costs may therefore represent annual costs, rather than one-off costs. Owing to the high fecundity and fertilisation success of COTS, the prevention of secondary outbreak would depend on the eradication of all COTS from a primary outbreak. If an aggregation of even a few starfish were missed, the control operation would possibly fail.

Likelihood of Success

The effectiveness of past control programs have been reviewed by Zann and Weaver (1988), Birkeland and Lucas (1990), and Johnson *et al.* (1990). Results from these reviews show that controls were successful when there was adequate warning of an approaching outbreak; the COTS were aggregated in small accessible areas; the population was small; there was a rapid response; there were sufficient, dedicated personnel for the job and the controls were repeated. Controls failed when there were too many COTS for the resources available; when there was migration of COTS into the cleared area; and when COTS were difficult to detect owing to reef topography, crypticity and weather.

The most critical factor appears to be early detection of outbreaks. Small primary outbreaks could feasibly be eradicated, however, they would need to be detected at an early stage before they spawn and produce the larger secondary outbreaks. Then, widespread controls would be impossible: none of the above success factors, and all of the above failure factors, would be applicable at this stage.

Possible Side Effects

Eradicating large numbers of COTS with copper sulphate injections risks copper contamination of other organisms. The background level of dissolved copper in GBR waters is around 0.11-0.24 g/L seawater (Denton and Burdon-Jones 1986). About 1 kg of copper sulphate is required to kill 1000 COTS. Outbreaks of the sizes modelled above would add, respectively, 0.40, 0.21, 0.10, 0.02, and 0.01 g dissolved copper / L seawater / day (modelled on the volume of water above the reef at Green Island) to background levels over 6 months.

Zann and Weaver (1988) reported elevated levels of copper in a tridacnid clam and an alga after controls were attempted on a relatively small outbreak (8019 COTS) at Holbourne Island.

In conclusion, there is the possibility of contamination of other reef organisms, and possibly of the divers administering the copper sulphate, if current control measures are used to eradicate large outbreaks.

Alternatives to Copper Sulphate Injections

No alternatives currently exist for eradicating large numbers of COTS. Underwater fences have been successfully trialed (Birkeland and Lucas 1990), but they are only capable of protecting small areas of reef eg. around tourist sites.

Conclusions

The history of the crown-of-thorns starfish phenomenon on the Great Barrier Reef suggests the issue of controls will be raised again at the start of the next outbreak episode. In the absence of any evidence to the contrary current policy allows for limited controls. Other measures may need to be considered if research indicates a link between human activities and outbreaks or if evidence suggests long-term damage to the GBR. The type of evidence indicative of human involvement in the generation of primary outbreaks and/or the prolongation of secondary outbreaks needs to be clarified and agreed to by managers and the scientific community. There is also a need to decide upon the most appropriate management actions available to control large populations of starfish before it becomes necessary to undertake such actions. This is important because of the long time needed to organise operations and the high fecundity of the starfish. One option could be primary controls on a primary outbreaking reef(s) to prevent the southward progression of outbreaks. With current control technology eradication of all starfish on a primary outbreak reef will be uncertain and therefore not guaranteed of preventing secondary outbreaks. Primary outbreaks need to be detected as early as possible to allow for all management options to be considered and any intervention to be instigated quickly.

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A management approach to the COTS question

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Abstract

Scientists and managers often view issues from different perspectives. Scientists as a group have traditionally wished to learn more about an issue for the sake of learning, for the sake of testing a hypothesis, for the sake of furthering their careers or for a combination of these reasons. While managers are also curiosity driven, they are usually required to focus their curiosity on those aspects of matters which are vital to the solution of management problems. From the manager's perspective, the fundamental question to be answered about the COTS phenomenon is whether or not it has been grossly affected by human activity. On the basis of the answer to that question, the manager will determine his response, particularly whether or not to interfere in the "natural" system or to refrain from interference. The logic of this position is discussed.

The Authority's policy on controlling COTS is not to interfere on a large scale unless it can be shown that outbreaks are caused or exacerbated by human activity. However local controls are initiated to protect sites of particular value to tourism or science. Every scientific review of this matter has supported our policy.

Many people adopt one of two fundamentally different explanations for why crown-of-thorns populations suddenly increase dramatically. One is that the phenomenon is entirely "natural". That is, it is not affected by human activity. The other is that it is entirely human-induced.

Of course, bearing in mind the pervasive effect that human activity is having on the world's biosphere, it is quite likely that the truth is a mixture of these two views, that is, that crown-of-thorns infestations are affected to some degree by human activity. We don't, however, know whether this is so, and if it is, whether human activity is contributing to the intensity, frequency or extent of the phenomenon positively or negatively.

The Authority recognises that long-term protection of the Reef ecosystem is the primary reason for the existence of the Authority and for everything that we do. Therefore we approach the crown-of-thorns issue from the perspective of risk.

We know that the animal is a natural inhabitant of the Reef and that it has been around for millenia. We know, therefore, that the Reef as we know and cherish it has developed in the presence of the starfish. That is not to say that there have always been recurrent population explosions, but there may have been.
The primary question is: should we undertake widespread and massive destruction of crown-of-thorns starfish whenever there is a primary outbreak?

What are the risks and benefits of non-interference? Clearly, an immediate benefit is the saving of an enormous amount of money. Experience has shown that it costs up to $35 per starfish to kill large numbers of them using the best methods identified so far - copper sulphate injections (Johnson *et al.* 1990). Since there can be millions of starfish on a single reef, the people of Australia stand to save much more than the annual budget of the Authority by not embarking on massive starfish killing programs.

What are the risks? At the start of both recent starfish infestations we were told that, if the starfish numbers were not controlled, the entire GBR ecosystem would be at risk, with the possibility of a major phase-shift from a coral-dominated community to something else, with massive erosion of the existing reef structure and the adjacent mainland. In fact, thorough surveys have shown that in the last major wave of infestations starting in 1979 and evidently petering out now, only 17 ± 4% of all the 2900 or so reefs of the GBR were affected visibly by infestations and only about one third of these (ie. 6% of all of the GBR reefs) were seriously affected. It is hard to believe that permanent damage to the Reef ecosystem could be caused by an event of only this magnitude.

The conclusions from this last experience therefore are that very significant economic benefits accrued from the "non-interference" policy and that the risks from applying that policy were small.

What about the risks and benefits of applying a policy of massive starfish destruction programs? The benefits have to be conjectural because we cannot be sure that very large populations could be controlled. However I suppose we could assume that the number of reefs seriously affected by the starfish could have been reduced from the 6% that were so affected. But it's not so easy to argue that this is a benefit. Many people have conjectured that crown-of-thorns infestations might be beneficial to reefs in ways similar to the effect of bushfires on some Australian native forests. So perhaps there would have been no benefits.

There would have been great costs, however. Even if only Green Island Reef had been subject to starfish destruction action, the costs would have been many millions of dollars. Further, there is the possibility that our massive interference in what might be a natural element of the Great Barrier Reef system could have major unforeseen ecological effects. I would count such effects as costs because we value the Reef for what it is naturally, not for what human interference might make it. Further still, it is at least conceivable that such an action focussing on Green Island might have shortened the time for the next outbreak or have created a chronic elevated crown-of-thorns population state as has occurred in the Ryukyu Islands (Birkeland and Lucas 1990).

The conclusion is that the risks from adopting a policy of massive destruction of crown-of-thorns starfish are very significant and that the only potential benefits may turn out to be costs in the long run.

In contrast, no long-term risks to the whole GBR are identified in not interfering massively with infestations, unless they are much more extensive and intensive than the two that have been observed. In such a case, the Authority would definitely reconsider its policy. If, for instance, it appeared that 30% of all the reefs of the system were to be seriously affected, then I would be asking the Government for the resources to attempt population control.

This explains why the Authority has maintained the policy of not undertaking massive starfish killing programs. However, I should explain why we do encourage or cooperate in protecting small reef areas that are important for tourism or research. Again, the reasoning is based on benefits and costs. We can in such cases identify very clearly the economic benefits of protecting such reef areas. The costs are limited to the costs of killing comparatively few starfish. There is no risk that this small amount of human interference could have a significant unforeseen effect on the whole Reef ecosystem. So the benefits clearly outweigh the costs, both those that are identifiable and those that can be classified only in risk terms.

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The need for a crown-of-thorns starfish contingency plan

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Abstract

Delays in the provision of funding for research and the initiation of research during both crown-of-thorns starfish outbreak episodes on the Great Barrier Reef resulted in lost opportunities to study primary outbreaks, truncated research program duration, and minimal opportunities for cost-effective research. If control of the outbreaks had been considered a desirable option, the delays would have meant that such action would have been too late to have any chance of successfully preventing the southward progression of outbreaks. A Contingency Plan to secure funds and outline appropriate actions in the event of another outbreak would facilitate a timely and effective response.

The First Outbreak Episode: 1962 - 1975

The first outbreak of crown-of-thorns starfish on the Great Barrier Reef (GBR) was reported at Green Island in 1962. However the extent of the problem was not recognised and brought to the attention of responsible authorities until late 1965 when fisheries biologists from the Queensland Department of Primary Industries (QDPI) were sent to investigate the situation. Surveys of Green Island and neighbouring reefs indicated that large populations of starfish were causing considerable coral mortality. The QDPI staff recommended to the Queensland Government that a research program to investigate the extent, effect and cause of the outbreaks be initiated.

The recommendation was accepted and a two-year study of the problem commenced in 1966. The program involved two field personnel under the supervision of Dr RE

Endean of the University of Queensland. The total budget for the program was $26,400 over two years. Reflecting a lack of appreciation of the scope of the problem and the feasibility of studying it, aims of the investigation were incredibly ambitious given the resources provided:

1. To assess the extent of infestation by *A. planci* of the Great Barrier Reef.
2. To assess the extent of the damage caused by the starfish to living corals on infested reefs.
3. To obtain relevant information about the general biology of the starfish including information on its feeding behaviour, reproduction, habitat preferences, growth rate, predators etc.
4. To determine the cause of the apparent plague of *A. planci* on certain reefs of the Great Barrier Reef.
5. To obtain information which could provide a factual basis for predicting the future course of the *A. planci* plague if it is not controlled.
6. To find a practical means of controlling populations of the starfish on reefs of the Great Barrier Reef.

The report of the study was submitted to the Queensland Government in June 1968 but not published until a year later. It concluded that the starfish represented a serious threat to the Great Barrier Reef (Endean 1969). The Queensland Government continued to support some monitoring of the situation but no further research or attempted control action was supported, contrary to recommendations of the report.

Concern over the findings of the study and liberal interpretation of the study's results elevated the issue to a high media profile. Criticism of the Government's inaction over the problem was a common theme in the media through the early 1970s. The solution from the public's perspective, fuelled by media coverage, was simple - eradicate the pest.

Official responses to the criticism and calls for controlling the starfish involved the establishment of committees to review available information and advise on the seriousness of the threat to the Great Barrier Reef. Reviews were undertaken by the Australian Academy of Science (Walsh *et al.* 1970) and a joint Federal and Queensland Governments Committee of Inquiry (Walsh *et al.* 1971). Both committees concluded that the starfish did not constitute a threat to the GBR as a whole, but both committees highlighted the need for further research.

In 1972 the Commonwealth and Queensland Governments acted on these recommendations, establishing an advisory committee to recommend priority research. Funding was provided for three years with $90,000 in the first year, increasing by $20,000 annually. By 1975 starfish numbers had declined significantly with a commensurate abatement in public outcry. The advisory committee was disbanded on its own recommendation and special crown-of-thorns starfish research funding stopped. The only remaining large populations of starfish were in the Swain Reefs area - too remote for cost-effective research, too far south and remote to constitute a further threat to the GBR.

Significant funds for targeted crown-of-thorns starfish research were thus first made available some 10 years after the outbreak was first detected at Green Island. The cyclic pattern of starfish outbreaks had allowed only three years of concerted research into the problem. Because of the paucity of knowledge of the GBR at that time, the lack of available scientific expertise and proven practical field techniques (particularly for surveying large areas of reef), liberal scrutiny of proposed research and non-specific guidelines for research support, a high proportion of the program's funds were spent on projects not directly focused on crown-of-thorns starfish. Six of the 15 projects funded were only marginally related to crown-of-thorns starfish, covering such diverse topics as identification of zooplankton assemblages, coral taxonomy, reef fish ecology and coral skeleton microstructure (Walsh *et al.* 1975). Advances in understanding of the crown-of-thorns starfish phenomenon were limited.

The Second Outbreak Episode: 1979- 1992

Large numbers of *A. planci* were again reported from Green Island reef in 1979. The biological pattern of southward moving outbreaks was repeated and the socio-political history relived. In the interim between outbreak episodes the GBRMPA had been established and the crown-of-thorns starfish was now the Authority's concern. Review committees were convened in 1980 and again in 1984. The two committee meetings in 1980 recommended four major research directions before disbanding:

- GBR-wide surveys of crown-of-thorns starfish and coral damage;
- Starfish population dynamics;
- Reef sediment analysis for evidence of outbreaks over geological time; and
- Documentation of past human activity on the GBR.

Research in some of these areas was funded by the GBRMPA in the early 1980s, but because of funding constraints, commitments to zoning plans and lack of resources, a comprehensive program of research was not able to be instigated (Kenchington 1987). The GBRMPA established a database and a public questionnaire program to determine the distribution of starfish outbreaks.

In 1984 the Advisory Committee considered available information from research conducted up to that time and noted that the current level of research activity was unlikely to lead to a short-term (3-5 years) resolution to the questions raised by *A. planci* outbreaks on the GBR. To deal with this deficiency, the Committee identified a number of research initiatives which it believed should be implemented immediately (COTSAC 1985). These included:

1. risk analysis to contribute to assessment of the need for controls;
2. monitoring the effectiveness of existing control techniques;
3. feasibility of developing more efficient control techniques such as biological control by predators of pathogens;
4. review of monitoring techniques for crown-of-thorns starfish and corals;
5. surveys of selected reefs;

6. oral history of human use and of experience of the Great Barrier Reef;
7. surface and soft sediment cores to evaluate evidence of prior outbreaks;
8. analysis of existing field data and modelling studies (leading to the identification of priority research);
9. high priority research;
10. testing of hypotheses regarding human factors that may trigger or exacerbate outbreaks;
11. use of geological techniques of climate reconstruction to identify past periods when climatic conditions resembled those prevailing during recent outbreaks;
12. and economic and social consequences of outbreaks.

The Committee recommended the research program be coordinated by the GBRMPA and supported by funding of approximately $3 million over 5 years. In July 1985 the Commonwealth Government indicated the GBRMPA would receive $971,000 for the first year of the program. A Record of Understanding between the GBRMPA and AIMS in which it was agreed that the GBRMPA would coordinate all management-related research projects while the AIMS would be responsible for the "mainly ecological" projects (Zann and Moran 1988). The research program was advertised in the Australian Press, calling for proposals and expressions of interest for relevant research. Following receipt and review of proposals, the program was approved in February 1986. To advise on a program of research and regularly review progress of the program, the GBRMPA established the Crown of Thorns Starfish Advisory Review Committee (COTSARC). Funds of around $1 million were provided annually until 1988/89 but at no stage were funds committed beyond a one-year period.

In a parallel initiative the Australian Institute of Marine Science (AIMS) was provided with over $1 million through the Commonwealth Community Employment Program, primarily to conduct a GBR-wide survey to determine the distribution and abundance of starfish and its effects on the Reef. This field program was commenced in March 1985.

All of the processes associated with the establishment of a research program (reviews of current knowledge, acquisition of funding, advertising for research, establishment of advisory committees, reviewing proposals etc) led to a delay of 6-7 years after the outbreak was first detected at Green Island. The time lags associated with research program initiation during both outbreak episodes are depicted in *Figure 1*.

At the time the GBRMPA research program commenced most of the reefs carrying outbreaks were located off Townsville (Bass *et al.* 1988). Active outbreaks were some 500 km to the south of the area now suspected of being the origin of primary outbreaks (Dight *et al.* 1990). There was no opportunity to study primary outbreaks.

The number of outbreaking populations increased from 1985/86 to a peak in 1988/89 (16% of reefs affected) and has declined to the present (Moran *et al.* 1991). Researchers thus had a 3-4 year window of opportunity to study active outbreaks conveniently located off Townsville, the location of AIMS and James Cook University.

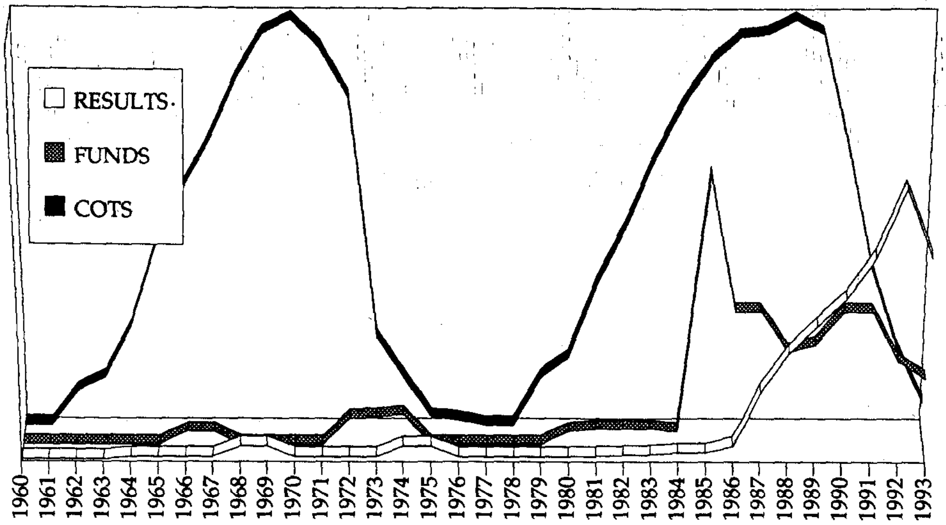

Figure 1: Graphical representation of the time lags between crown-of-thorns starfish abundance (COTS), the provision of funds for research (FUNDS) and the availability of results from the research (RESULTS) during the two outbreak episodes on the Great Barrier Reef. Outbreaks were initially detected at Green Island in 1962 and 1979. Major research funding became available in 1972 and 1985. Y-axis calibrations are approximately consistent for each individual line but different between lines.

The COTSAC program was superseded in 1989/90 following a review requested by the then Minister for the Arts, Sport, the Environment, Tourism and Territories, Senator Graham Richardson (the Portfolio Minister responsible for GBRMPA). Following recommendations of the review, the new program (the COTSREC program, named after the new advisory committee - the Crown-of-thorns Starfish Research Committee) was guaranteed funding of around $1 million per annum for three years, subject to a review before entering into the third year. Critical research that could have been conducted with these funds could not be undertaken because of the unavailability of conveniently located outbreaks. Projects requiring young juvenile starfish (e.g. predation studies) necessitated the development of a rearing program for the production of experimental specimens. Thus, although the funds were put to good use, research would have been much more productive had the support been available considerably earlier in the outbreak episode.

Contingency Plan Recommendation

The review of the COTSREC research program following its second year was conducted by Dr RE Johannes. In reviewing the crown-of-thorns starfish research program Johannes noted that three things were necessary to ensure early detection of the next COTS outbreak and an effective response to it - continued reef-wide monitoring, maintenance of a core research program and the development of a contingency plan (Johannes 1991). He noted that the establishment of a contingency plan would assure the quickest and most effective response to the detection of a future outbreak.

Johannes indicated that the plan should identify:

1. Priority research projects to be activated or expanded in the event of another outbreak.

2. Mechanisms for quickly recruiting and deploying the necessary personnel.
3. Means of making funding available immediately in the event of an outbreak.

Johannes' recommendation was supported by the Crown-of-thorns Starfish Research Committee and accepted by the GBRMPA in late 1991.

The Plan

An outline of the Contingency Plan is provided by Lassig *et al.* (*in press*). The Plan comprises a set of standardised procedures to be followed if outbreaks of COTS occur on the GBR in the future. The plan is intended to enable rapid initiation of actions that are appropriate to the nature and extent of the perceived problem as well as the prevailing political, social and scientific environments. Development of the plan has identified a number of issues in need of resolution if the plan is to be effective. The early detection of outbreaks is paramount.

Discussion

Delays in the provision of funding for research and the initiation of research during both crown-of-thorns starfish outbreak episodes on the GBR resulted in lost opportunities to study primary outbreaks, truncated research program duration, and minimal opportunities for cost-effective research. If control of the outbreaks had been considered a desirable option, the delays would have meant that such action would have been too late to have any chance of successfully preventing the southward progression of outbreaks (see Gladstone 1992).

Cyclicity of funding and research is not unique to the crown-of-thorns starfish phenomenon. After the locust threat receded in Africa in the 1960s control organisations lost their operational edge, research funding was scaled down, expertise was lost and equipment was not maintained (Walsh 1986). When the threat reappeared in the 1980s infrastructure was inadequate and control measures that had been effective during the 1940s and 1950s were regarded as being unsafe and alternatives to toxic pesticides had not been tested for effectiveness and safety.

During previous outbreak episodes a lack of available information on the nature, extent and consequences of the phenomenon contributed to the delays. Research conducted through the GBRMPA program has significantly contributed to our knowledge of the phenomenon but there remain major gaps in our understanding of the causes of outbreaks and long-term ecological consequences. Advances in knowledge mean that further research can be much more focused than in the past, however there is a danger of research being abandoned in the absence of "threatening" outbreaks on the GBR over the next few years.

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