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Benefits to general understanding.

Crown-of-thorns starfish, *Acanthaster planci* (L.): Synopsis of recent research

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Introduction

Outbreaks of the crown-of-thorns starfish, *Acanthaster planci* (L.), have been reported on a many reefs within the Indo-Pacific region over the last 30 years (Moran 1986, Birkeland and Lucas 1990). A considerable amount of research has been undertaken in that time mainly in order to determine why these events occurred and whether they may have been induced through some anthropogenic means.

Not surprisingly, the literature which has accumulated on the starfish is extensive and a number of reviews (e.g. Potts 1981, Moran 1986, Endean and Cameron 1990) have been written which have synthesised our understanding of the phenomenon. The most recent and comprehensive of these works has been that produced by Birkeland and Lucas (1990).

A problem with most scientific reviews is that with time they gradually become outdated. Those on the crown-of-thorns starfish are no exception because research conducted recently (i.e. over the last 5-6 years) has generated, and is still generating, a large number of scientific publications (Birkeland and Lucas 1990) covering many different disciplines and aspects of the "crown-of-thorns phenomenon". Consequently, the intention of this paper is to provide a synoptic review of the research which has been conducted recently, particularly that which has taken place in the last few years. In addition the review will highlight new knowledge and identify where significant gains in our understanding of the phenomenon have been achieved. It is not intended to go over "old ground" although reference to earlier works is unavoidable if the recent research is to be put in its proper perspective.

The present paper is not comprehensive in its scope, rather it concentrates on the results of research conducted in four main areas: the distribution and abundance of the starfish, its effects on corals and associated organisms, general biology and ecology of the starfish, and management of the phenomenon. Analysis of publications produced in the last 6 years indicates that the majority of them have addressed topics in these areas (Table 1). Mathematical modelling represents another important field of endeavour which has led to the production of numerous publications. It has not been considered in this paper as an up-to-date synthesis and review of research in this area has been given by Bradbury (1990). Nonetheless, several of the papers in that volume have been referred to in the present work. In general, reference is made largely to seminal publications from which other references can be sourced.

Research programs

By far the majority of new information that has emerged on the crown-of-thorns starfish has come from research programs conducted in either Australia or Japan. The former has been extensive and has given rise to about 70% of all scientific publications in the last 6 years (Table 1). Approximately $10 million has been spent on research by the Australian Government (through a variety of sources) since this program was initiated in early 1986 (Table 2). In essence the program can be divided into two parts; one comprising projects (about 58) funded as a consequence of the recommendations of the Crown of Thorns Starfish Advisory Committee (COTSAC), the other comprising projects (about 30) funded under the auspices of the Crown of Thorns Starfish Research Committee (COTSREC). The former was reviewed by Anderson (1989) who concluded that the research had been defined, reviewed and operated in an efficient and productive manner and that the Great Barrier Reef Marine Park Authority's policy for limited control measures in areas of importance to tourism or science was soundly based. Continuation of the program therefore was recommended for a further 3-5 years under the direction of a new committee (COTSREC). Subsequently, this period of research was reviewed by Johannes (1991) who concluded that it had also been carried out efficiently and productively. In addition, continued funding was recommended for certain aspects of research (e.g. monitoring, development of monoclonal antibodies for larvae) but not others (e.g. geological studies and hydrodynamic modelling), leading to development of a smaller, more integrated group of projects.

In general, the research program conducted in Australia over the last 6 years has involved research in four areas (Lassig and Kelleher 1991):

1. general biology and ecology of the starfish;
2. understanding the causes of starfish outbreaks;
3. development of appropriate control techniques;
4. understanding the extent of activity and effects of the starfish.

Details of the history, structure and achievements of the program are provided by Moran and Johnson (1990, 1991) and Lassig (1991). More recently, Lassig and Kelleher (1991) have reviewed the development of the entire program, its general objectives, and aspects relating to management of the "crown-of-thorns problem".

The program of research in Japan was conducted from 1984 to 1988 mainly on reefs in the Ryukyu Islands. It involved some 30 projects (Ikenouye *et al* 1989) principally grouped into two main areas: biology of starfish, and the preservation of coral reefs. The former included research into the distribution and abundance of starfish, reproduction, larval development and dispersal, and the predators of larvae and juveniles. The latter mainly involved isolation of a starfish attractant for controlling starfish, restoring reefs after outbreaks and historical surveys of past outbreaks. Approximately 11 million yen (ca. $A110,000) was provided per year to support the program. After that time this research effort would appear to have declined substantially. The results of the program have been summarised by Ikenouye *et al* (1988, 1989).

Distribution and abundance of starfish

Outbreaking populations

Surveys of the distribution and abundance of crown-of-thorns starfish have been an important part of the research programs carried out on the Great Barrier Reef (GBR) and reefs of the Ryukyu Islands. Indeed, over the last 30 years they have often been a priority when outbreaks of starfish have been reported on reefs (Moran 1986). Surveys have been conducted annually throughout the GBR since 1985 using the manta tow technique. Those conducted in Japan have been more localised and patchy in their coverage, and have involved both the manta tow and line transect techniques. The most recent of these surveys were conducted on reefs surrounding Iriomote and Hateruma Islands in the southern part of the Ryukyu Islands (Ikenouye *et al* 1988, 1990, Yokochi *et al* 1991). Large aggregations of starfish were recorded around these islands during 1985 and 1986. They were responsible for producing substantial coral mortality in some areas. By 1988, some 2 years after the populations had declined, these areas were showing signs of early recovery.

Annual broadscale surveys of the Great Barrier Reef have provided a good synoptic view of the activity of the starfish. They indicate the extent to which they may effect corals in large archipelagic systems. Recent summaries and analyses of the data (Moran et al 1988, Baker *et al* 1991, Moran *et al* in press) indicate the following:

1. About 28% of all reefs surveyed in the GBR have experienced outbreaks of starfish in the last 12 years.
2. The number of outbreaking populations has declined substantially over the last few years, the proportion of reefs with outbreaks declining from 16% in 1988/89 to around 3% in 1990/91. Only one new outbreak was recorded in 1990/91.
3. The outbreaks have mainly occurred on reefs in the Cairns and Central Sections of the GBR Marine Park (between Lizard Island and the Whitsunday region)(Figure 1).
4. Outbreaks appeared to arise from reefs near latitude 16^{0}S during 1979. Since that time they have moved both to the north and south of that region, the latter being the more dominant of the two. The initial rates of movement of these northern and southern "drifts" were 57 km/yr and 77 km/yr respectively. The former had almost stopped by 1984 while the latter continued to move southwards until about 1991 after which time it had slowed greatly.

Whilst outbreaks of starfish have declined on the GBR in the last few years reports indicate that they have increased in a number of areas around Australia including reefs off Gove Peninsula (C. Christie personal observation), in Torres Strait (R. Watson personal communication), Elizabeth and Middleton Reefs to the north-east of Lord Howe Island (Hutchings 1989) and reefs in the Dampier Archipelago (Johnson and Stoddart 1987)(Figure 1). Small populations of starfish have also been found on Lord Howe island (DeVantier and Deacon 1990) making them the most southerly in the world and raising questions as to their origins.

Within the Indo-Pacific region outbreaks have been reported in recent times on reefs in the Maldives (Anon, 1990), Vanuatu (Zann et al 1990a), Fiji (Zann et al 1990b) the Gulf of Oman (R. Jensen personal communication), Yule Island off Papua New Guinea (J. Prescott personal communication), Malaysia (Rahmann 1988), Moorea Island (Faure 1989) and the Red Sea (Moore 1991)(Figure 1). Low to moderate populations are present in Tonga (Vavau), Fiji (Viti Levu), Western Samoa and the northern Gilbert Islands (L. Zann personal communication). It has been suggested that Fiji may now have chronic levels of crown-of-thorns starfish (Zann et al 1990b). Annual surveys of starfish and corals are to be continued on the GBR in case a new series of outbreaks occurs. This will enable more precise identification of where primary outbreaks first arise.

Survey techniques

In determining the extent of activity of the crown-of-thorns starfish and its effects on corals great reliance has been placed on certain survey methodologies, particularly the manta tow technique and to a lesser extent the line transect technique. While both have been used in coral reefs systems for many years (see Moran and De'ath in press, Mundy 1991) their precision and accuracy have received little attention. As a consequence these two aspects of the techniques have been investigated in recent times.

The manta tow technique has been used in the past for detecting major changes in coral reef systems. It has a number of advantages and disadvantages associated with its use (Moran and De'ath in press). Fernandes et al (1990) found that manta tow observers on average counted only 23% of the total number of starfish recorded during SCUBA surveys of the same areas. The variability associated with this could be explained by a number of variables including starfish behaviour (i.e. proportion cryptic) and the complexity of the reef topography. Further investigations indicated that the precision of the technique could be improved by conducting the surveys in a more standardised manner (e.g. taking into account the effects of sun and water visibility) and by limiting the search width to 9m (Fernandes 1990). The latter however, has proved to be difficult to implement.

More recently, Moran and De'ath (in press) demonstrated that there was a strong statistical relationship between the counts of starfish derived from manta tows and those derived from SCUBA surveys. Consequently, they concluded that the former could be calibrated to predict the latter. Apart from being cost effective, Moran and De'ath (in press) found that if the unit of interest was relatively large (e.g. an individual reef of 50-60 tows) then the manta tow technique provided a reasonably accurate and precise way of detecting relative changes (up to 20% in an outbreaking population) in the distribution and abundance of crown-of-thorns starfish. Research by Fernandes (1991) also showed that the technique generally was suitable for recording broad changes in coral cover. As yet it is not known whether the technique is suitable for recording the distribution and abundance of other sedentary organisms. Clearly, further research is needed in this area.

Despite being relatively cost effective, the manta tow technique still requires considerable resources if it is to be conducted over large spatial scales. This has prompted research into the feasibility of using alternative techniques such as satellite imagery and low level infra-red aerial photography, for detecting the presence of outbreaks on reefs. Investigations by Reichelt and Bainbridge (1988) suggested that imagery from present satellites (e.g. Landsat MSS, SPOT) was largely unsuitable for detecting changes in coral cover on reefs. On the other hand, Hopley and Catt (1988) found that such changes could be detected using low level infra-red aerial photography but only in reef flat environments. Consequently, it is unlikely that these technologies will replace broadscale surveys in the foreseeable future although they still have potential to augment that which is being done at present. For this to occur however, considerable research is needed to overcome many of the practical problems associated with their use.

The line transect technique has been used mainly to estimate changes in the cover of organisms or groups of organisms. Recent investigations by Mundy (1991) have indicated that it is suitable for "detecting small to moderate changes" in the the cover of abundant species and lifeforms. A minimum of 6 randomly positioned transects of 20 m length is required however, in order to achieve this. Significant variation in the accuracy of the technique was found to be due to differences in the way observers classified various species, lifeforms and coral morphologies. In contrast, individual observers generally were found to be reliable in recording information using the line transect technique.

Effects of outbreaks

Coral mortality and recovery

It is well documented that outbreaks of crown-of-thorns starfish can have dramatic effects on the abundance of corals (Birkeland and Lucas, 1990). Recent broadscale surveys conducted on the GBR have provided information on how extensive these effects can be within large heterogeneous reef systems. Moran et al (1988) reported that approximately 57% of reefs with outbreaks had moderate to high coral mortality (>50%) over at least a third of their perimeters. In addition only 10% of reefs had high coral mortality (>50% mortality) over most of their perimeters. Overall, it was found that outbreaks produced an 11% (3.4 fold) increase in the levels of dead coral cover on reefs (Moran et al 1991). Clearly, these results indicate that outbreaks of crown-of-thorns starfish do not affect all reefs to the same extent and that a relatively small percentage of the total number of reefs surveyed within the GBR have suffered "serious" damage in the past 12 years. These effects however, may well be compounded through time where outbreaks occur at intervals which do not allow for complete recovery of coral community structure. Further research is needed in order to understand the long term consequences of repeated outbreaks of short duration.

The mortality of corals at smaller spatial scales has also received attention in recent years. Faure (1989) reported that greater than 80% of corals were killed as a result of the activites of crown-of-thorns starfish at Moorea Island (French Polynesia). Similar estimates have been derived for other areas in the Indo-Pacific region. Both Colgan (1987) and Done et al (1988) reported that extremely low levels of coral cover (ca. 1-5%) remained after outbreaks on reefs in Micronesia and the GBR respectively. In general, the size frequency distribution of coral communities is also affected by the starfish. Done et al (1988) found that the average size of corals after an outbreak at John Brewer Reef was about 5 cm. Most of these were small remnant colonies which were present in densities up to $60m^{-2}$.

Previous research into the effects of outbreaks on corals has concentrated on the more abundant faster growing corals particularly *Acropora*, *Montipora* and *Pocillopora*. This is partly because these types of corals are known to be the preferred prey of the starfish (see Moran 1986). In the last few years however, more attention has been given to understanding the effects of outbreaks on slower growing massive corals which are regarded as being important components of reef systems - the equivalent of the red cedars of rainforests. Detailed surveys of permanent plots by Cameron et al (1991a) revealed that reefs affected by outbreaks had only 1/3 the number of massive coral colonies as those that had not been affected by outbreaks. In addition, greater than 50% of colonies surviving on the former exhibited damage to at least a 1/3 of their surface.

Clearly, these results indicate that massive corals can be severely affected by crown-of-thorns starfish even though they may not be a preferred source of food. Recent field studies have also indicated that certain massive corals may be more preferred by starfish than others. Cameron et al (1991a) found that corals of the family Poritidae were dominant on reefs which had experienced recent outbreaks while those of the family Faviidae were dominant on reefs that had not been affected by outbreaks. Endean et al (1988) had argued previously that members of the former were more resistant to predation by starfish than most other massive corals. Cameron et al (1991b) also suggested that *Diploastrea heliopora* was relatively immune to these effects on the basis of field data (i.e. density, colony size and extent of damage).

Survival of small parts of individual massive corals (even during severe outbreaks) may arise as a result of the activity of inquiline species. DeVantier et al (1986) and DeVantier and Endean (1988) suggested on the basis of field and laboratory data that the serpulid, *Spirobranchus giganteus*, and the scallop, *Pedum spondyloideum*, may not only protect some massive corals from complete mortality but also aid in maintaining their community structure and recovery. Glynn and Colgan (1988) found that certain territorial damselfishes were also able to defend massive as well as branching forms of coral from predation by crown-of-thorns starfish. Like DeVantier and Endean (1988) they suggested that this might be an important mechanism for maintaining coral diversity and aiding recovery.

Whilst the mortality of corals may be partially or fully prevented by the presence of coral associates it can be enhanced indirectly through the effects of other disturbances. For example, Glynn (1990) observed starfish feeding on corals that had previously been protected from predation by thickets of *Pocillopora* (which generally repel the starfish due to the presence of nematocysts and crustacean guards). Predation of these protected corals (which proceeded at least 6 years) came about because much of the *Pocillopora* was killed as a result of widespread coral bleaching which occurred during a prolonged El-Nino event. Large scale mortality of corals through bleaching also led to starfish feeding on non-preferred corals (e.g. *Porites lobata*) in other localities.

Previous research has shown that recovery of reefs may take from 12-15 years (see Moran 1986). Such estimates are largely based on measures that relate to coral cover and to a lesser extent species richness. At a broad level, recovery of coral communities in areas previously affected by outbreaks has been observed in recent times. Surveys conducted over the past 3 years on the GBR have indicated coral recovery on reefs (e.g. Green Island off Cairns) affected by outbreaks about 12 years ago. The extent of recovery has been patchy both within and between different reefs (Moran et al 1991). On the basis of the results so far, it would seem that recovery of some reefs on the GBR will take much longer than the 12-15 year period proposed by some. The reason for this is not clear although it might have to do with the availability of recruits in the system and the relatively small interval between outbreak episodes (approximately 15 years).

Recruitment of corals to reefs after outbreaks is an important part of the recovery process. Initial predictions by Done (1985) that small remnant corals would play a significant role in recovery on John Brewer Reef proved incorrect. Indeed, Done et al (1988) found that most of these remnants (apart from the larger ones on massive corals) contributed little to recovery on that reef, either declining in number or showing little growth. Overall, recovery was being initiated through the influx of new recruits belonging mainly to faster growing genera such as *Acropora*. Reefs which have been seriously affected by outbreaks of starfish may have to rely on coral recruits coming from nearby reefs (Fisk and Harriott 1991). If large numbers of reefs in a region (e.g. reefs off Townsville between 1985-1989) suffer extensive coral mortality then recovery may well depend on coral recruits travelling some tens to hundreds of kilometers from reefs upstream.

Mathematical models have been used to make predictions about the recovery of massive corals whose replacement times may be as great as several centuries. Done (1987) showed that the *Porites* populations on John Brewer Reef could be sustained if outbreaks occurred at 15 year intervals but only if the survivorship of juvenile and adult corals was high. This and more recent work (Done 1988) demonstrated that recovery may be highly variable and dependent on not only survivorship of corals but also the initial structure of the population, the extent and intensity of the outbreak, the interval between outbreaks, and rates of colony growth, and recruitment. Despite a lack of field data on certain key parameters the models were able to demonstrate that all large *Porites* colonies (>60 cm dia.) would be lost from the coral community if coral mortality between outbreaks was high, rates of recruitment were generally low, the outbreaks occurred at 10-30 year intervals, and they were of an intensity similar to those recorded in recent times on the GBR. Even assuming that no further outbreaks occurred the models predicted that it would take most populations of *Porites* at least 50 years to recover. Consequently, if Cameron et al (1991a,b) are right in suggesting that corals such as *Porites* spp. and *Diploastrea* spp. are less susceptible to predation by crown-of-thorns starfish then recovery times for other massive corals may be considerably longer than those predicted by Done (1987, 1988).

Given that the recovery of massive corals may take tens of years to decades it has been argued that the population structure of these corals provides strong evidence regarding the history of outbreaks on reefs (Done et al (1988). Reefs that have had a frequent history of outbreaks would comprise coral communities dominated by faster growing species and benthic algae. On the basis of this argument Cameron et al (1991a) have proposed that prior to the 1960s outbreaks of crown-of-thorns starfish had not affected the GBR over the last centruy or more. This conclusion needs to be treated with caution however, since the evidence for this came from field studies conducted on a relatively small number (12) of reefs and the effects of outbreaks are known to be highly variable. At this stage it would appear that the evidence is insufficient to draw conclusions about the occurrence of severe outbreaks over longer time intervals (Done et al 1988). Our knowledge of the recovery of coral communities, and in particular massive corals, needs to be extended through the collection of more detailed information on poopulation dynamics (e.g. rates of recuitment, colony growth and mortality). Using comunnity structures to hindcast the outbreak history of reefs needs further research involving detailed studies of massive corals before, during and after outbreaks. Broadscale surveys of massive corals on reefs with known outbreak history should be undertaken to expand upon work conducted by Cameron et al (1991a) thereby providing a broader framework of information upon which conclusions can be made about the previous oucrrences of outbreaks, their intensity and frequency of occurrence.

Effects on other organisms

Outbreaks of crown-of-thorns starfish are capable of producing dramatic shifts in the biological structure and organisation of reefs. Bradbury and Mundy (1989) showed that substantial changes in benthic biomass had taken place on the GBR in response to recent outbreaks of the starfish. A major part of the system had changed from being one where reefs were largely dominated by corals to one where they were dominated by algae.

They postulated that shifts in dominance to lifeforms with differing metabolic activites could lead to fundamental changes in community metabolism. Larkum (1988) has been the only one to directly address this question. He showed (based on experiments with individual coral colonies) that colonies encrusted with algae fixed nitrogen at over 3 times the rate of nearby living coral colonies. In situations where outbreaks have produced large areas of algal covered corals Larkum (1988) suggested that this could lead to enhanced levels of organic nitrogen and greater primary and secondary production. Further research into this topic is necessary in order to determine whether large scale disturbances such as outbreaks lead to greater productivity and reef growth. This information is essential if we are to understand the long term consequences of these outbreaks on the ecology, evolution and geomorphology of coral reefs.

Outbreaks have also been studied in terms of their effects on fish communities. Much of the information available is contradictory. Research by Williams (1986) showed that outbreaks did not lead to fundmental changes in the abundance and community structure of coral reef fishes. In contrast, Sano et al (1987) found a substantial decrease in the number and density of fishes from all trophic groups (i.e. herbivores, omnivores and benthic animal feeders) for at least several years after an outbreak of crown-of-thorns starfish. The most noticeable decline in abundance was recorded for coral feeding fishes. A decline in these types of fishes was also recorded by Wass (1987) along with an increase in some surgeonfishes and damselfishes which fed on benthic algae. Additional studies by Williams (1988) detected a decline in the abundance of two species that fed on coral and another two that were dependent on live coral for recuitment. It has been postulated that recovery of the former may be slower than the latter (Moran and Johnson 1989) since it will depend on the regrowth of sustainable amounts of coral.

Variations observed in the response of fish communities to large outbreaks suggest that their population levels are determined by a variety of factors including the availability of food and recruitment success. It is possible that the fish communities are responding to the disturbance in more subtle ways which involve changes in biomass, growth rates, and size/class structures. These aspects are now under investigation in Australia (Moran and Johnson 1991).

General biology and ecology

Reproduction

Recent reproductive studies of *A. planci* have taken a variety of approaches in attempting to determine how aspects of this starfish's population dynamics affect reproductive output. Such determinations are important in providing accurate data for numerical models of crown-of-thorns populations. One factor of critical importance to the reproductive success *A. planci*, and other marine invertebrates with external fertilisation, is reproductive synchrony. Previous work on *A. planci* has demonstrated that chemical signals are released before or during spawning which act as a stimulus to trigger spawning in other starfish (Beach *et al.* 1975, Lucas 1984). Based on this evidence, and numerous anecdotal reports of aggregation at the time of spawning, (Owens 1971, Cheney 1974), Okaji (1991), studied the gametogenic cycle of starfish in aggregated and dispersed populations at various sites around the island of Okinawa. He found that populations of aggregated starfish spawned several weeks earlier than did starfish in dispersed populations. This difference was attributed to the influence of the chemical spawning stimulus, which would be more effective in the aggregated populations. This work provides important corroborative evidence for the importance of chemical signals in crown-of-thorns reproductions. Attempts should be made to repeat such a study, using several (replicated) dispersed and aggregated populations. Our understanding of these processes would also benefit from a more detailed knowledge of the chemical nature of the signal compound. This would make possible monitoring of levels throughout the spawning season as well as direct behavioural experiments.

The influence of physical variables in the timing of reproduction has become better known over recent years as a result of numerous observations of natural spawning behaviour (Birkeland and Lucas 1990, Babcock and Mundy 1992). It is still not possible to demonstrate any lunar pattern of spawning periodicity, though spawning has almost invariably been reported during periods of falling tides or at low tide (Babcock and Mundy 1992). Until recently almost all observations of crown-of-thorns spawning had been made during the afternoon, but it appears that spawning at night may be more common than previously assumed. Five of the last seven observations of spawning on Davies Reef (1990-92) have been made at night, coinciding with increased frequency of nocturnal observations there (Babcock and Mundy unpublished observations). Intensive studies at this reef have made possible observation of repeated spawnings of starfish populations. These observations directly support the assumptions of repeated spawnings based on apparent partial spawnings of individuals (Birkeland and Lucas 1990). There have been further advances in understanding of the timing of spawning with regard to seasonality. Studies in Okinawa (Okaji 1991) and on the GBR (Babcock and Mundy 1992a, b) indicate that although spawning may take place over a period of several months, the bulk of gametes are probably shed over a much shorter timespan, during a small number of intense spawning events. These events appear to be more likely around the beginning of the reported spawning period. Comparable data are still lacking from low latitude reefs where, if spawning is spread over the entire year, reproductive success may be influenced more heavily by factors such as aggregation, rather than spawning synchrony.

The effects of synchrony and aggregation on reproductive success in *A. planci* have recently been determined by Babcock and Mundy (1992), using a submersible plankton sampling device which has allowed measurement of fertilization rates for spawning female starfish *in situ*. At distances greater than 30m downstream from a single spawning male fertilization was over 50% of that measured when spawning females and males were directly adjacent. There was still measurable fertilization, greater than 20%, at 64m downstream. These values are around two orders of magnitude greater than those for other marine invertebrates for which comparable data are available (eg Pennington 1985), probably due to the large volume of gametes which can be released by *A. planci*. Synchrony of spawning starfish has also been shown to have measurable effects on fertility, with 83% fertilization measured for eggs sampled during the peak of a large spawning event, and only 23% for eggs released at the end of the same event, less than one hour later (Babcock 1992). These data provide an empirical basis for larval inputs to numerical population models, and allow research to focus on the dynamics of the next stage of the life cycle.

Larval development

Behaviour, nutrition and mortality of larval *Acanthaster* remain problematical areas in our knowledge of this species. As noted by Birkeland and Lucas (1990), crown-of-thorns larvae have proved an elusive component of the plankton, a fact which has contributed significantly to our lack of knowledge in this area. It is possible that with our improved understanding of reproductive timing this work may become possible. Until these studies occur, we must rely on laboratory and other studies in this field area for advances in our knowledge. Lucas (1982) suggested that *Acanthaster* larvae might utilize DOM or bacteria as sources of nutrition in addition to the phytoplankton which he provided. Subsequent *in situ* culturing of larvae at Lizard island on the GBR (Olson 1987) showed that despite chlorophyll levels which would have been considered inadequate on the basis of Lucas' data, larvae survived and settled at high rates without artificially enhanced diets. In addition to its important implications for the potential role of plankton blooms in causing crown-of-thorns outbreaks, this work further implicated food sources other than phytoplankton, such as bacteria and DOM, as important components in the diet of larval starfish. Two different approaches have been used to determine the nature and importance of these dietary inputs.

The first of these is a modification of the Olson apparatus in which successively finer particles are filtered out of the seawater, finishing off with a filtration step to remove DOM. Preliminary work (Okaji, unpublished data) has indicated that even in the absence of phytoplankton (>1μm), significant numbers of larvae can reach bipinnaria and late bipinnaria, and that some can even settle. Development and settlement rates for these larvae are low relative to larvae with access to phytoplankton. These larvae are presumably feeding on particles in the bacterial size range, and possibly DOM, since their development is more rapid than that of larvae denied food from these sources. A more direct approach to determining the diet of *A. planci* larvae has been used by other researchers. This has involved incubating larvae in cultures of planktonic food organisms (phytoplankton and picoplankton) as well as DOM (Ayukai and Hoegh-Gouldberg, unpublished). These studies have shown by direct observation that picoplankton such as photosynthetic bacteria are taken up by the larvae, as are a variety of dissolved organic compounds. The identification of these food sources will provide a basis for a rigorous assessment of the role of nutrient limitation in the initiation and propagation of starfish outbreaks. While none of these sources of nutrition seem to be limiting on the GBR under most conditions (Olson 1987), this may not be the case in other areas of the Indo-Pacific such as Micronesia or Oceania, where islands and reefs can be quite isolated and surrounded by truly oligotrophic waters in which nutrient enrichment from terrestrial sources may play a vital role (Birkeland 1982).

Experiments on the nutrition of larvae can give us valuable insights about relative rates of mortality for larvae, but we still do not have an empirical basis for making estimates of mortality during the planktonic phase. A variety of benthic predators on eggs and larvae have been identified (Ormond and Campbell 1971, Pearson and Endean 1969, Birkeland and Lucas 1990), but larvae and eggs spend only a short period of time on reefs during which such encounters may occur. More accurate estimates for this parameter should be an urgent priority. Other aspects of larval biology, especially larval behaviour, also require further study. Ontogenetic changes in larval density, floating/sinking rates, larval photo/geotaxis and swimming rates can now be incorporated into three-dimensional numerical models of larval dispersal, in which they have the potential to markedly affect predicted rates of dispersal (Black). As yet we have little qualitative information and almost no quantitative information to use in such models.

Larval dispersal

Over the past five years we have seen an increasing level of refinement in the numerical hydrodynamic models being used to predict (or hindcast) the dispersal of larval *A. planci* in the central GBR. These refinements have come in three areas. Techniques have extended to groups of reefs (Black in press), a scale intermediate to previous studies of single reef circulation (Black *et al.* 1990, Wolanski and King 1990) and inter-reef (Dight *et al.*) dispersal studies. This is an important intermediate step in linking models at the two scales for a more realistic synoptic picture. Models using three-dimensional techniques have also been introduced (Black *et al.* 1991), representing an important step forward in the field of modelling dispersal around reefs. Comparison of the predictions of two- and three-dimensional models have indicated relatively small differences between the two approaches (Black *et al.* 1991), but this has been based on neutral density particles. Results from a variety of research have demonstrated both photopositive (Lucas 1982) and geonegative larval behaviour (Olson 1985), as well as ontogenetic changes in larval density (Olson pers. comm.), which may make measurable differences to larval transport, at least under certain conditions. Now that numerical models operating in three dimensions exist it should be an important priority to obtain such information. Finally, further steps have been made in correlating the predictions of models and observations of the distribution and abundance of crown-of-thorns and other reef organisms. Simulations of particle retention around several reefs in the central GBR have shown a generally good agreement between areas of predicted high larval retention and portions of the same reefs first affected by *Acanthaster* (Black and Moran 1991). This type of agreement between dispersal models and the appearance of starfish outbreaks is similar to that demonstrated for inter-reef dispersal (Dight *et al.* 1990). Unfortunately in both instances models must rely on the appearance of adult starfish for corroboration. The degree of confidence in the predictions of the models is consequently reduced due to the time lag between the larval settlement and the appearance of adults, during which time factors other than larval dispersal would have had a chance to markedly affect starfish distributions.

There is a high degree of expectation that numerical models such as these will increase our ability to understand the maintenance of starfish populations and predict the progress of outbreaks, yet without further rigorous quantitative tests of their predictive ability they will not realize this potential. The reason for this is clear if we compare the premises of the majority of within-reef scale modelling and that of the between-reef dispersal studies. The reef scale studies have largely presented the case that, in most circumstances, sufficient particles are retained around a reef so that most of the recruitment will be the result of self-seeding (Black 1988, Black *et al.* 1990, Sammarco and Andrews 1989). Yet at the same time we are confronted with waves of secondary, larvally propagated outbreaks travelling down the Queensland coast from one affected reef to another (Moran *et al.* in press), with a corresponding set of models (Dight *et al.* 1988, 1990) describing this process. Which one of these scenarios is correct? It is most unlikely that both are correct, and that the important question is not to discriminate between them but to quantify the proportions of larvae moving around reefs and from one reef to another at appropriate scales. This is not a simple task (*vis.* Oliver *et al.* in press) and can only be satisfactorily achieved by field studies which set out with the deliberate goal of testing the predictions of the models. It is disappointing to see that such a verification has not yet been achieved, and may have to await the next set of outbreaks, whenever that may be. It would also be useful to see these methods applied to oceanic reef systems affected by *A. planci* (e.g. Lobel and Robinson 1986), where the question of self-seeding, combined with nutrient enrichment in island wakes (Heywood *et al.* 1990), may be much more critical in the *Acanthaster* phenomenon (Birkeland 1982).

Larval settlement

Settlement behaviour, during the final phase of larval life, may also influence the distribution of starfish around reefs. Larvae of *Acanthaster* show a marked preference for settlement on particular coralline algae (*Lithothamnion pseudsorum*), mediated by the presence of bacteria on the surface of the algae (Johnson *et al.* 1991). This alga appears to be a rich food source for juvenile starfish before they switch to a coral diet, although they do also feed on other types of algae. Settlement onto a rich food source such as *Lithothamnion* could significantly improve the growth and survival of juvenile starfish but it is not yet known whether this alga is preferred to other algae as a food source. Johnson *et al.* (1991) have proposed that settlement induction by particular algae, especially *Lithothamnion*, may influence the distribution of *Acanthaster* in the early stages of outbreaks. They cite the presence of beds of this alga in deep water and the fact that most outbreaks on the GBR have been first seen in deep water as evidence supporting this possibility.

Behaviour of juveniles and adults

Recent studies of behaviour of the crown-of-thorns starfish have centered on understanding what influences variability in the activities of individual starfish and populations of starfish. Starfish size and time of day have been found to strongly influence daily activity patterns (Keesing 1990). Juvenile *A. planci* (<20cm) are highly cryptic during the day and emerge at night to feed. As starfish grow they adhere less closely to this pattern and very large starfish (=>40cm) are rarely cryptic and feed day and night. The nature of these observations supports the hypothesis that small starfish are subject to a high degree of pressure from predators which decreases as starfish grow, gradually achieving a refuge in size.

New information on the movement rates of *A. planci* show variation in movement of individual starfish depends on starfish size, food availability and population density. Keesing and Lucas (in press) monitored individual movement rates in adult starfish measuring a mean rate of 2.8 m.d^{-1}). Starfish in areas of high food availability (coral cover) moved far less than those in areas of depauperate coral cover. Starfish were also found to be highly mobile at high population density but low food availability. These types of conditions are those that exist at the end of outbreaks and explain how starfish can quickly disperse from a reef and disappear following outbreaks.

Until recently, measurements of feeding rate of individual starfish in field populations was lacking. Keesing and Lucas (in press) followed tagged starfish several days in different seasons and measured an average of 238 cm^2 of coral or 0.8 colonies killed .d^{-1}. Seasonal and size-dependent factors were found to greatly influence rates of feeding. Starfish fed twice as often in summer, killing twice as much coral, as in winter and small starfish consumed much less coral than larger starfish.

Early studies on feeding of *A. planci* demonstrated they exhibit a general preference for Acropora in Indo-Pacific reefs where this genus is dominant (eg. Pearson and Endean 1969, Ormond *et al.* 1976) and recent studies have confirmed this pattern (Glynn and Colgan 1988, Keesing 1990). In addition the importance of food availability in influencing preferences has been demonstrated (Keesing 1990). Common genera which are preferred are *Acropora, Seriatopora* and *Stylophora* whilst common general not preferred are *Porites, Favites, Goniastrea, Cyphastrea* and *Pocillopora.* Feeding preferences depend strongly on relative abundances of alternative prey. In situations where food is abundant *A. planci* show a very strong preference for *Stylophora* and *Acropora*. A wider diet is accepted when food is scarce. Under laboratory conditions and given equal availability of prey types *A. planci* show a sequential pattern of preference of acroporids over pocilloporids over faviids over poritids and this pattern is correlated directly with relative feeding efficiencies. On the basis of these field and laboratory studies, Keesing (1990) hypothesised that the benefits of exploiting a prey which was common and could be fed upon with a high degree of efficiency best explained observed patterns of feeding preferences and behaviour in *A. planci* .

Physiology of starfish

Kettle and Lucas (1987) recorded a number of important physiological attributes of *A. planci* and discussed their importance. As the starfish grow they partition energy heavily toward gonad production and away from the body wall and pyloric caecae. This explains the abrupt slowing of growth after reaching adulthood (Lucas 1984) and the importance of possessing venomous spines to protect a weakened somatic growth as they age. This strategy appears to allow *A. planci* to more efficiently exploit its food resource by allowing greater agility than slower growing more heavily armoured species such as *Culcita novaeguineae* which also preys on coral (Birkeland 1989).

Kettle and Lucas (1987) also measured respiration rates of *A. planci* over a large size range and found oxygen consumption varied uniformly with weight. The significance of this is that because the mass of metabolizing tissue in *A. planci* increases at a rate which outstrips its capacity to feed, at some point growth will cease and starfish condition may deteriorate. Lucas (1984) suggested senility would develop under these conditions and Kettle (1990) proposed that post-spawning morbidity may result and explain the sudden disappearance of starfish following outbreaks.

The development of a novel technique to age adult *A. planci* (Stump and Lucas 1990, Stump in press) means significant progress in demographic studies of *A. planci* may now be possible. These studies and that of Zann *et al.* 1990 have provided the first field estimate of longevity of *A. planci*. This was first suggested to be 5-8 years by Lucas (1984) on the basis of the life span of laboratory reared animals. Zann *et al.* (1990) followed a cohort of *A. planci* to virtual extinction after 7 - 8 years in Fiji, concurring with Lucas' earlier estimate. On the basis of numbers of spine bands, Stump (in press) has suggested that very large individuals in low density populations in the southern part of the Great BBarrier Reef may live as long as 12 years. Stump suggested that longevity may be a function of starfish density as previous studies of high density populations suggested a strategy of shortened life span and increased reproductive output (Kettle 1990). The unusually long life span (12y) determined by Stump (in press) may also be explained by the lower temperatures in this area. Keesing (1990) suggested that large *A. planci* would have difficulty consuming sufficient food to meet their metabolic demands at summer temperatures in the northern Great Barrier Reef. Q_{10} values for O_2 consumption versus temperatures increase from 2-4 over the 25 - 30°C temperature range (Birkeland and Lucas 1990).

General ecology

Recent advances in understanding the ecology of *A. planci* have been in the areas of habitat discovery, recruitment and mortality rates of juveniles. Zann *et al.* (1987) and

Yokochi and Ogura (1987) have provided the first field data on the habitat of very small *A. planci*. Yokochi and Ogura (1987) found *A. planci* as small as 0.55 in diameter. These and larger juveniles were found feeding on coralline algae covered dead coral rubble on the reef slope and at the base of the slope between 5 and 15 m depth. The habitat occupied by juveniles in Fiji was more varied and included fissures in coralline pavement on the reef crest and amongst the dead bases of living *Acropora* colonies. None were found in intertidal areas (Zann *et al.* 1987). The first data on growth rates of juvenile *A. planci* in the field have also come from Zann *et al.* (1987, 1990) who remarked particularly on the variability within and between cohorts.

Studies in Fiji, Japan and Australia have provided information on natural rates of *A. planci* recruitment and temporal and spatial variability. Zann *et al.* (1990) monitored recruitment of 0+ and 1+ year classes of *A. planci* on Suva Reef in Fiji recording recruitment which varied 2000 fold (0.01 - 20.6 m^{-2}, as well as zero values) indicating the massive variation in recruitment which can occur. Doherty and Davidson (1988) found recruitment levels varied both temporally and spatially (between reefs) on the Great Barrier Reef and Yokochi *et al.* (1988) recorded within reef variability in recruitment of 0+ starfish in a single year, with recruitment rates on the reef slope being an order of magnitude higher than on the reef flat. To what extent observed variability in measured recruitment levels reflect differential larval settlement rates and/or differential rates of post-settlement survival is not known.

Experimental studies have been undertaken to measure mortality rates of small juvenile *A. planci* in the field. Keesing and Halford (in press) recorded rates of mortality as high as 5%.d^{-1} in 1 month old starfish attributing most of this predation. Mortality rates were found to decrease quickly with size, dropping to about 1%.d^{-1} at 4 months.

Whilst the above study has confirmed small starfish are subject to high rates of predation, most interest has focussed on the effects of larger predators on juvenile and sub-adult *A. planci*. Previously the giant triton, *Charonia tritonis* (Endean 1974), puffer fish (Tetraodontidae) and trigger fishes (Balistidae) Ormond and Campbell (1974) had been touted as potentially the most important predators of crown-of-thorns starfish. Recent surveys by Birdsey (1988) and Marine Bio Logic (1991) confirm the triton as the most important predator of post juvenile *A. planci* but also found the hump headed maori wrasse, Cheilinus undulatus, the sweetlip and spangled emperors *Lethrinus miniata* and *L. nebulosus* to be important predators of *A. planci*.

It is not known however if these predators of adult *A. planci* are important as agents of population regulation. Recent modelling studies (McCallum 1988; Ormond *et al.* 1990) have demonstrated that hypothetical but realistic rates of predation by generalist fish predators are capable of regulating populations of sub-adult *A. planci* below certain levels. Other studies (McCallum 1990, McCallum *et al.* (1990) point to the importance of relative densities of *A. planci* and putative predators and the nature of the foraging behaviour of these predators. There is negligible information available about these areas.

Other sources of mortality of *A. planci* include disease. A catastrophic mortality of juvenile *A. planci* in Fiji which killed 99% of an entire cohort was thought to result from an epizootic sporozoon infection (Zann *et al.* 1987, 1990).

Management

In recent times research has focussed more on issues of direct relevance to management. The research program in Australia involved a number of projects which have addressed specific management issues. Overall, management-related research has been carried out in four main areas:

1. Understanding the causes of outbreaks and in particular the possible influence of human activities on the frequency and/or intensity of occurrence of outbreaks.
2. Identifying methods for more efficiently and effectively controlling outbreaks.
3. Understanding the socio-economic consequences of outbreaks.
4. Accumulating evidence of previous outbreaks through use of geological and historical surveys.

Outbreak causes and anthropogenic effects

Controlling outbreaks

Socio-economic impacts

Previous outbreaks

Summary

A large amount of research has been conducted in recent years, particularly in Australia and Japan, which has led to a substantial increase in understanding the crown-of-thorns starfish phenomenon. Yet despite this, it is still not known why outbreaking populations of the starfish have occurred. In recent years there has been a clear trend away from simple explanations of the phenomenon as it has been recognised that no one factor may be responsible for causeing outbreaks (Moran and Bradbury 1989). In the past outbreaks have been explained largely either in terms of natural or man-induced factors. Information derived in recent times suggests however, that more parsimonious explanations may involve both types of factors. For example, it is conceivable that outbreaks of crown-of-thorns starfish are natural events, having occurred in the geological past (as suggested by some recent research), but that their intensity and frequency of occurrence has been increased through anthropogenic effects. Recent research has indicated that the starfish's reproductive characteristics may predispose it to occurring in large numbers from time to time. These populations also may have originated through anthropogenic effects (e.g. terrestrial run-off) since many outbreaks in the Indo-Pacific region would appear to have arisen close to human settlements (e.g. Maldives, Vanuatu).

The most recent research has led to better understanding in several major areas:

1. Biology and ecology.
    - Reproduction and larval dispersal.
    - Nutrition of larvae.
    - Feeding preference and behaviour of starfish.
    - Movement of starfish.
    - Survival and mortality of starfish, especially juveniles.
    - Population genetics.
    - Settlement cues for larvae.

2. Distribution and abundance of starfish.
    - Densities of starfish in outbreaking and non-outbreaking populations.
    - Propogation of outbreaks through large archipelagic systems (e.g. GBR, Ryukyu Islands).
    - Survey techniques.

3. Effects of outbreaks

   Broadscale effects in large reefal systems (e.g. GBR).

   Mortality of massive corals.

   Recovery of coral communities after outbreaks, especially massive corals.

   Changes in fish communities and their recovery.

   Importance of inquilistic species.

4. Causes

   Influence of hydrodynamics in the dispersal of larvae and the propogation of outbreaks.

   Possible effects of predators, particularly on pre-reproductive starfish.

   Occurrence of outbreaks in the geologic past.

   Occurrence of outbreaks within the last 100 years.

5. Management

   Techniques for controlling outbreaks (biological controls).

   Socio-economic effects of outbreaks.

   Identification of possible anthropogenic links to outbreaks.

One weakness of past research has been its tendency to address issues at a local or regional level. Apart from Birkeland (1982) there has been few attempts recently to try and synthesise patterns at a world-level. The possiblity of establishing common patterns and perhaps establishing a common mechanism(s) would appear possible given that outbreaks have occurred on a number of reefs within that region at about the same time and there is now a growing body of information on the starfish and related environemntal and socio-econimic factors. There is realisation that the distribution and abundance of certain organisms are correlated with the occurrence of large regional processes such as ENSO events (Glynn, 1991). Studies should be attempted with repect to COTS. Whilst such studies may not led to definitive answers they may point to important menchanisms which can be investiagted in conjunction with those factros (e,.g. fishing, runoff events) which may occur over much smaller scales. Clearly, this will require further investigation.

Unanswered questions

1. Can the location of primary outbreaks be clearly identified?

2. What are the major predators of the crown-of-thorns starfish? What effects can they, and do they have, on the distribution and abundance of adult starfish? On what part of the starfish's life cycle do they have greatest effect? Has their abundance either increased or decreased in the last 50 years? Has man had some part to play in such changes?

3. How far do larvae disperse in large reefal systems? Where do they settle on reefs? What are normal rates of settlement? What density of settlement is needed to produce an outbreak? Can techniques be developed to monitor larval dispersal and settlement?

4. How well do current hydrodynamic models mimic the actual dispersal of larvae over varying spatial scales? Can this be tested?

5. How important are pheromones and other chemical cues in promoting aggregation of starfish and synchronisation in spawning?

6. What effects do outbreaks have on reef systems, particularly metaboism, calcification and growth?

7. Can techniques be developed to determine key population parameters such as mortality, age, growth, immigration and emigration?

8. Processes responsible for fossilizing skeletal remains. Better dating techniques.

9. Before, during and after studies of corals, particularly massives.

10. Quantify effects of outbreaks over braod scale. Place in eprspective previous research.

11. Emphasis on control methods: aggregation technique, mass controls, biological controls.

12. Settlemtn and recruitment. Larval dispersal. Rate of loss of larvae in field.

13. Where do larvae settle?

14. Mathematical modelling: predation

15. World-wide view

16.

Need to plan in event of further outbreaks. to avoid lengthy delays in research and controls. In Aurtalia plans being made for contingency funding (Lassig et al. in press).

References

Anon (1988) COT Newsletter. Maldives Ministry of Fisheries and Agriculture. Marine Research Section. Volume 1, 8p

Anderson DT (1989) A report to the Minister for the Arts, Sport, The Environment, Tourism and Territories, Senator the Honourable Graham Richardson. Canberra. February 1989. 57p

Babcock RC, Mundy CN (in press a) Reproductive biology, spawning and field fertilization rates of *Acanthaster planci*. Aust J Mar Freshwat Res 42:

Babcock RC, Mundy CN (in press b) Seasonal changes in fertility and fecundity in *Acanthaster planci*. Proc 7th Int Coral Reef Symp

Baker VJ, Bass DK, Christie CA, Miller IR, Miller-Smith BA, Thompson AA (1991) Broadscale surveys of crown-of-thorns starfish on the Great Barrier Reef: 1990-1991. Australian Institute of Marine Science, Townsville 170p

Beach DH, Hanscomb NA, Ormond RFG. (1975) Spawning pheromone in crown-of-thorns starfish. Nature 254:135-136

Benzie JAH, Stoddart JA (1992) Genetic structure of outbreaking and non-outbreaking crown-of-thorns starfish (*Acanthaster planci*) populations on the Great Barrier Reef. Mar Biol 112:119-130

Birdsey R (1988) Large reef fishes as potential predators of *Acanthaster planci*. Unpublished report to the Great Barrier Reef Marine Park Authority, Townsville, Australia, 19p

Birkeland CE (1982) Terrestrial runoff as a cause of outbreaks of Acanthaster planci (Echinodermata: Asteroidea). Mar Biol 69:175-185

Birkeland C (1987) Partial correlations of island size, human population size and *Acanthaster planci* abundance. Bull Mar Sci 41:633

Birkeland C (1989) Influence of echinoderms on coral reef communities. In: Jangoux M, Lawrence JM (eds) Echinoderm studies. AA Balkema, Rotterdam (V/3, pp 1-79)

Birkeland CE, Lucas JS (1990) *Acanthaster planci*: major management problem of coral reefs. CRC:Boca Raton, 257p

Black KP (1988) The relationships of reef hyrodynamicsto variations in numbers of planktonic larvae on and around coral reefs. Proc 6th Coral Reef Symp 2:125-130

Black KP (in press) Proceedings of Boden Conference - BIGRID paper

Black KP, Gay SL and Andrews JC (1990) Residence times of neutrally-buoyant matter such as larvae, sewerage of nutrients on coral reefs. Coral Reefs 9:105-114

Black KP, Moran PJ (1991) Influence of hydrodynamics on the passive dispersal and initial recruitment of larvae of Acanthaster planci (Echinodermata: Asteroidea) on the Great Barrier Reef. Mar Ecol Prog Ser 69:55-65

Black KP, Moran PJ, Hammond LS (1991) Numerical models show coral reefs can be self seeding. Mar Ecol Prog Ser 74:1-11

Bradbury RH (1990) *Acanthaster* and the coral reef: a theoretical perspective. Springer Verlag, Berlin 338p

Bradbury RH, Mundy CN (1989) Large scale shifts in biomass of the Great Barrier Reef ecosystem. In: Sherman K, Alexander L (eds) Biomass and geography of large marine ecosystems. Westview, Boulder (pp 143-167)

Cameron AM, Endean R, DeVantier L (1991a) Predation on massive corals: are devastating population outbreaks of *Acanthaster planci* novel events? Mar Ecol Prog Ser 75:251-258

Cameron AM, Endean R, DeVantier L (1991b) The effects of *Acanthaster planci* predation on populations of two species of massive corals. Hydrobiologia 216/217:257-262

Cheney DP (1974) Spawning and aggregation of *Acanthaster planci* in Micronesia. Proc 2nd Int Coral Reef Symp. 1:591-594

Colgan MW (1987) Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. Ecology 68:1592-1605

DeSilva MWRN (1988) Status of *Acanthaster planci* infestations and attempts to control them in peninsular Malaysia. Abstracts, 6th Int Coral Reef Symp 23.

DeVantier LM, Reichelt RE, Bradbury RH (1986) Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: predator pressure as a mechanism of coevolution? Mar Ecol Prog Ser 32:307-310

DeVantier LM, Endean R (1988) The scallop *Pedum spondyloideum* mitigates the effects of *Acanthaster planci* predation on the host coral *Porites*: host defence facilitated by exaptation? Mar Ecol Prog Ser 47: 293-301

DeVantier LM, Deacon G (1990) Distribution of *Acanthaster planci* at Lord Howe Island, the southern-most Indo-Pacific reef. Coral Reefs 9:145-148

Dight IJ, Bode L, James MK (1988) Models of larval dispersal in the Central Great Barrier Reef: patterns of connectivity and their implications for species distributions. Proc 6th Coral Reef Symp 3:217-224

Dight IJ, Bode L, James MK (1990) Modelling the larval dispersal of Acanthaster planci II. Patterns of reef connectivity. Coral Reefs 9:125-134

Doherty PJ, Davidson J (1988) Monitoring the distribution and abundance of juvenile *Acanthaster planci* in the central Great Barrier Reef. Proc 6th Int Coral Reef Symp 2:131-136

Done TJ (1987) Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: evidence of population resilence? Coral Reefs 6:75-90

Done TJ (1988) Simulation of recovery of pre-disturbance size structure in populations of *Porites* spp. damaged by crown-of-thorns starfish *Acanthaster planci*.

Done TJ, Osborne K, Navin KF (1988) Recovery of corals post-*Acanthaster*: progress and prospects. Proc 6th Int Coral Reef Symp 2:137-143

Endean R (1974) *Acanthaster planci* on the Great Barrier Reef. Proc 2nd Int Coral Reef Symp 1:563-576

Endean R, Cameron AM (1990) *Acanthaster planci* population outbreaks. In: Dubinsky Z (ed) Coral Reefs. Elsevier Science Publishers, Amsterdam (Ecosystems of the world; 25, pp 419-437)

Endean R, Cameron AM, DeVantier LM (1988) *Acanthaster planci* predation on massive corals: the myth of rapid recovery of devastated reefs. Proc 6th Int Coral Reef Symp 2:143-148

Fernandes L (1990) Effect of the distribution and density of benthic target organisms on manta tow estimates of their abundance. Coral Reefs 9:161-165

Fernandes L (1991) Development of a more robust method for determining the status of individual reefs with respect to outbreaks of crown-of-thorns starfish (*Acanthaster planci*). Report to the Great Barrier Reef Marine Park Authority, Townsville, 47p

Fernandes L, Marsh H, Moran P, Sinclair D (1990) Bias in manta tow surveys of *Acanthaster planci*. Coral Reefs 9:155-160

Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. Mar Biol 107:485-490

Fisk DA, Harriott VJ, Pearson RG (1988) The history and status of crown-of-thorns starfish and corals at Green Island Reef, Great Barrier Reef. Proc 6th Int Coral Reef Symp 2:149-155

Glynn PW (1990b) Coral mortality and disturbance to coral reefs in the tropical Eastern Pacific. In: Glynn PW (ed) Global ecological consequences of the 1982-83 El Nino - Southern Oscillation. Elsevier Science Publishers. Amsterdam (Elsevier Oceanography Series; 52, pp 55-117)

Glynn PW, Colgan MW (1988) Defense of corals and enhancement of coral diversity by territorial damselfishes. Proc 6th Int Coral Reef Symp 2:157-163

Heywood KJ, Barton ED, Simpson JH (1990) The effects of flow disturbance by an oceanic island. J Mar Res 48:55-73

Hopley D, Catt P (1988) Use of infra-red photography for monitoring effects of *Acanthaster planci* outbreaks. Abstracts, 6th Int Coral Reef Symp, 47

Hutchings P (1989) Voyage to Elizabeth and Middleton Reefs. Aust Nat Hist 22:485-488

Ikenouye O *et al.* (1988) Factors affecting the population dynamics of marine organisms and their management in marine ecosystems. Nature Conservation Bureau, Environment Agency, Marine Parks, Tokyo

Ikenouye O *et al* (1989) Abstract of the report for final meeting of the Committee of studies on population dynamics of marine organisms and its management. Nature

Conservation Bureau, Environment Agency, Marine Parks, Tokyo, 59p

Johannes RE (1991) A review of the crown-of-thorns starfish research program 1989-1991. A report to the Great Barrier Reef Marine Park Authority, Townsville, 15p

Johnson DB, Stoddart JA (1988) Report on surveys of the distribution, abundance and impact of *Acanthaster planci* on reefs within the Dampier Archipelago (Western Australia), April 1987. Australian Institute of Marine Science, Townsville, 15p

Johnson CR, Sutton DC, Olson RR, Giddins R (1991) Settlement of crown-of-thorns starfish: role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. Mar Ecol Prog Ser 71:143-162

Keesing JK (1990) Feeding biology of the crown-of-thorns starfish, *Acanthaster planci* (Linnaeus). PhD thesis, James Cook University of North Queensland, 197p

Keesing JK, Lucas JS (in press) Field measurement of feeding and movement rates of the crown-of-thorns starfish *Acanthaster planci* (L.). J Exp Mar Biol Ecol

Keesing JK, Halford AR (in press) Field measurement of survival rates of juvenile *Acanthaster planci* (L.): techniques and preliminary results. Mar Ecol Prog Ser

Kettle BT, Lucas JS (1987) Biometric relationships between organ indices, fecundity, oxygen consumption and body size in *Acanthaster planci* (L.) (Echinodermata: Asteroidea). Bull Mar Sci 41:541-551

Kettle BT (1990) Variations in biometric and physiological parameters of *Acanthaster planci* (L.) (Echinodermata; Asteroidea) during the course of a high density outbreak. PhD thesis, James Cook University of North Queensland

Larkum AWD (1988) High rates of nitrogen fixation on coral skeletons after predation by the crown of thorns starfish *Acanthaster planci*. Mar Biol 97:503-506

Lassig BR (1991) Final report on the results of COTSAC management related research: December 1985 to June 1989. Great Barrier Reef Marine Park Authority, Townsville, 49p

Lassig BR, Kelleher G (1992) Crown-of-thorns starfish on the Great Barrier Reef. In: Environmental research in Australia Case studies. Australian Government Publishing Service, Canberra (Australian Science and Technology Council, pp 39-62)

Lobel PS, Robinson AR (1986) Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. Deep Sea Res 33:483-500

Lucas JS (1982) Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid Acanthaster planci (L) J Exp Mar Biol Ecol 65:173-194

Lucas JS (1984) Growth and maturation of *Acanthaster planci* (L.)(Asteroidea) and hybrids in the laboratory including observations on the effects of diet. J Exp Mar Biol Ecol 79:129-147

Marine Bio Logic (1991) Survey of marine scientists and other experts for anecdotal observations of crown-of-thorns predation. Unpublished report to the Great Barrier Reef Marine Park Authority, Townsville, Australia. 49p

McCallum HI (1987) Predator regulation of *Acanthaster planci*. J Theor Biol 127:207-220

McCallum HI (1988) Effects of predation on organisms with pelagic larval stages: models of metapopulations. Proc 6th Int Coral Reef Symp 2:101106

McCallum HI (1990) Effects of predation on *Acanthaster*: age structured metapopulation models. In: Bradbury RH (ed) *Acanthaster* and the coral reef: A theoretical perspective. Springer Verlag, Berlin (Lecture Notes in Biomathematics No 88, pp 208-219)

McCallum HI, Endean R, Cameron AM (1989) Sublethal damage to *Acanthaster planci* as an index of predation pressure. Mar Ecol Prog Ser 56:29-36

Moore R (1990) Persistent and transient populations of the crown-of-thorns starfish, *Acanthaster planci*. In: Bradbury RH (ed) *Acanthaster* and the coral reef: a theoretical perspective. Springer Verlag, Berlin (Lecture notes in biomathematics; 88, pp 236-277)

Moran PJ (1986) The *Acanthaster* phenomenon. Ocean Mar Biol Ann Rev 24:379-480

Moran PJ, Bradbury RH, Reichelt RE (1988) Distribution of recent outbreaks of crown-of-thorns starfish (*Acanthaster planci*) along the Great Barrier Reef: 1985-86. Coral Reefs 7:125-137

Moran PJ, De'ath G (in press a) Suitability of the manta tow technique Afor estimating relative and absolute abundance of crown-of-thorns starfish (*Acanthaster planci* L.) and corals. Aust J Mar Freshwat Res.

Moran PJ, De'ath G (in press b) Estimates of the abundance of the crown-of-thorns starfish (*Acanthaster planci*) in outbreaking and non-outbreaking populations on reefs within the Great Barrier Reef. Mar Biol

Moran PJ, Johnson DB (1990) Final report on the results of COTSAC ecological research: December 1985 - June 1989. Australian Institute of Marine Science, Townsville, 40p

Moran PJ, Johnson DB (1991) Report on the progress of COTSREC ecological research: July 1989 - February 1991. Australian Institute of Marine Science, Townsville, 32p

Moran PJ, De'ath G, Baker VJ, Bass DK, Christie CA, Johnson DB, Miller IR, Miller-Smith BA, Mundy CN, Thompson AA (1991) Broadscale surveys of crown-of-thorns starfish and corals along the Great Barrier Reef: 1982-1990. Australian Institute of Marine Science, Townsville, 36p

Mundy CN (1990) A critical evaluation of the line intercept transect methodology for surveying sessile coral reef benthos. MSc thesis, Department of Marine Biology, James Cook University, Townsville, 127p

Nishida M, Lucas JS (1988) Genetic differences between geographic populations of the crown-of-thorns starfish throughout the Pacific region. Mar Biol 98:359-368

Okaji K (1991) Delayed spawning activity in individuals of *Acanthaster planci* in Okinawa. In: Yanagisawa *et al.* (eds) Biology of echinodermata. Balkema, Rotterdam, pp 291-295

Oliver JK, King BA, Willis BL, Babcock RC Wolanski E (in press) Dispersal of coral larvae from a lagoonal reef: II. comparisons between model predictions and observed concentrations. Coastal Shelf Res

Olson RR (1985) In situ culturing of the larvae of the crown-of-thorns starfish *Acanthaster planci*. Mar Ecol Prog Ser 25:207-210

Olson RR (1987) In situ culturing as a test of the larval starvation hypothesis for the crown-of-thorns, *Acanthaster planci*. Limnol Oceanogr 32:895-904

Ormond RFG, Campbell AC (1971) Observations on *Acanthaster planci* and other coral reef echinoderms in the Sudanese Red Sea. Symp Zool Soc Lond 28:433-454

Ormond RFG, Campbell AC (1974) Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. Proc 2nd Int Coral Reef Symp 1:595-619

Ormond RFG, Hanscomb NJ, Beach DH (1976) Food selection in the crown-of-thorns starfish, *Acanthaster planci*. Mar Behav Physiol 4:93-105

Ormond RFG, Bradbury RH, Bainbridge S, Fabricius K, Keesing J, DeVantier LM, Medlay P, Steven A (1990) Test of a model of regulation of crown-of-thorns starfish by fish predators. In: Bradbury RH (ed) *Acanthaster* and the coral reef: A theoretical perspective. Springer Verlag, Berlin (Lecture Notes in Biomathematics No 88, pp 189-207)

Owens D. (1971) *Acanthaster planci* starfish in Fiji: survey of incidence and biological studies. Fiji Agric J 33:15-23

Pearson RG, Endean R (1969) A preliminary study of the coral predator *Acanthaster planci* (L.)(Asteroidea) on the Great Barrier Reef. Qld Dept of Harbour and Marine, Fish Notes 3:27-55

Pennington JT (1985) The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Biol Bull 169:417-430

Reichelt RE, Bainbridge SJ (1988) Shallow water mapping of coral reef habitats: a case study from the Great Barrier Reef. 16th Congress of the International Society for Photogrammetry and Remote Sensing 27(B10): 375-383.

Reichelt RE, Bradbury RH, Moran PJ (1990a) Distribution of *A. planci* outbreaks on the Great Barrier Reef between 1966 and 1989. Coral Reefs 9:97-104

Reichelt RE, Bradbury RH, Moran PJ (1990b) The crown-of-thorns starfish, *Acanthaster planci*, on the Great Barrier Reef. Mathl Comput Modelling 13:45-60

Sammarco PW, Andrews JC (1989) The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. Limnol Oceanogr 34:898-914

Stump RJW (in press) Age and growth of *Acanthaster planci* (L.) on the Great Barrier Reef, Australia. Proc 7th Int Coral Reef Symp.

Stump RJW, Lucas JS (1990) Linear growth in spines from *Acanthaster planci* (L) involving growth lines and periodic pigment bands. Coral Reefs 9:149-154

Wass RC (1987) Influence of *Acanthaster*-induced coral kills on fish communities at Fagatele Bay and at Cape Larsen. NOAA Technical Memorandum, Marine and Estuarine Management Division 3:193-209

Williams DMcB (1986) Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short term effects of *Acanthaster planci* infestation. Mar Ecol Prog Ser 28:157-164

Williams DMcB (1988) Reef fishes: natural variability, replenishment and dispersal. In: Australian Institute of Marine Science annual report 1987-88. Australian Institute of Marine Science, Townsville, 9-14

Wolanski E, Burrage DB, King BA (1989) Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier Reef, following mass coral spawning. Continental Shelf Res 9:479-496

Yokochi H, Ogura M (1987) Spawning period and discovery of juvenile *Acanthaster planci* (L.)(Echinodermata: Asteroidea) at Northwestern Iriomote-Jima, Ryukyu Islands. Bull Mar Sci 41:611-616

Yokochi H, Ueno S, Ogura M, Nagai A, Habe T (1988) Recruitment, diet and growth of juvenile *Acanthaster planci* on reefs in a recovery phase. Abstr. 6th Int Coral Reef Symp 110.

Yokochi H, Ueno S, Ogura M, Nagai A, Habe T (1991) Spatial-temporal changes of the distribution and abundance of *Acanthaster planci* (L.) and corals at northwestern Iriomote-jima, Ryukyu Islands: 1983-1988. J Sch Marine Sci and Tech 32:231-242

Zann L, Brodie J, Berryman C, Nakasima M (1987) Recruitment, ecology, growth and behaviour of juvenile *Acanthaster planci* (L.)(Echinodermata: Asteroidea). Bull Mar Sci 41:561-575

Zann LP, Ayling AM, Done TJ (1990a) Crown-of-thorns starfish. In: Done TJ, Navin KF (eds) Vanuatu marine resources: report of a biological survey. Australian International Development Assistance Bureau, Vanuatu, pp 103-113

Zann L, Brodie J, Vuki V (1990b) History and dynamics of the crown-of-thorns starfish *Acanthaster planci* (L.) in the Suva area, Fiji. Coral Reefs 9:135-144

Table 1. Number and type of scientific papers and technical reports published annually since 1986 - taken from Moran *et al* (1991) and Birkeland and Lucas (1990). The documents have been categorised according to whether they originated from research conducted in Australia or elsewhere. The figures given for 1991 and 1992 are incomplete (*) at the present time.

Category	1986	1987	1988	1989	1990	1991	1992	Aust	Other	Total
Review	3	1	1	3	2	0	0	7	3	10
Distribution	9	17	8	9	5	4	2	36	18	54
Biology	6	12	5	3	3	5	2	18	18	36
Ecology	1	4	4	0	4	0	6	16	3	19
Effects	6	4	9	2	3	2	1	19	8	27
Models	4	4	10	5	31	2	3	39	20	59
Methods	1	5	6	1	5	3	2	22	1	23
Management	5	15	14	4	4	3	5	46	4	50
Biochemical	3	7	6	4	2	1	0	16	7	23
Other	2	0	6	2	1	3	0	5	9	14
TOTAL	40	69	69	33	60	23*	21*	224	91	315

Table 2. Funds (in $Australian) allocated to research on the crown-of-thorns starfish in Australia since 1985/86. Taken from Moran and Johnson (1991), and Lassig and Kelleher (1992).

Source	Funds ($A 000s)							
	1985/86	1986/86	1987/88	1988/89	1989/90	1990/91	1991/92	Total
GBRMPA[a]	1100	805	820	673	750	1000	1000	6148
AIMS[b]	259	497	534	526	171	290	561	2838
Other[c]	1139	131	-	-	-	-	13	1283
TOTAL	2498	1433	1354	1199	921	1290	1574	10269

[a] Great Barrier Reef Marine Park Authority - includes funds allocated to the COTSAC (Crown of Thorns Starfish Advisory Committee) and COTSREC (Crown of Thorns Starfish Research Committee) Programs as well as those provided by Research and Monitoring Section.

[b] Australian Institute of Marine Science - funds allocated in the form of resources (ships, equipment) and personnel.

[c] Includes $1 million for Commonwealth Community Employment Program to survey the Great Barrier Reef, funds provided through Marine Sciences and Technologies Grants (MSTG), Australian Research Council (ARC) Grants and the Department of Industry, Technology and Commerce (DITAC). NB: These figures may not be

complete.

CAPTIONS TO FIGURES

Figure 1. Distribution of outbreaks of crown-of-thorns starfish in the Indo-Pacific region over the last 5 years. The numbers refer to the following locations: (1) Great Barrier Reef (1991; Moran et al 1991), (2) Torres Strait (1987; R. Watson, pers obs), (3) Gove Peninsula (1991, C. Christie, pers obs), (4) Yule Island (1989; J. Prescott, pers obs), (5) Dampier Archipelago (1987; Johnson and Stoddart 1987), (6) Elizabeth and Middleton Reefs (1987; Hutchings 1989), (7) Vanuatu (1988; Zann et al 1990), (8) Maldives (1989; Anon, 1990), (9) Gulf of Oman (1990; R. Jensen, pers obs), (10) Red Sea (Port Sudan)(1987; Moore 1990), (11) Malaysia (1987; Rahmann 1988), (12) Fiji (1987; Zann et al 1990), and (13) Moorea Island (1987; Faure 1989)