

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

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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 1×10^{-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 3×10^3 ml⁻¹ sperm and 3×10^2 ml⁻¹ eggs, levels which were 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.

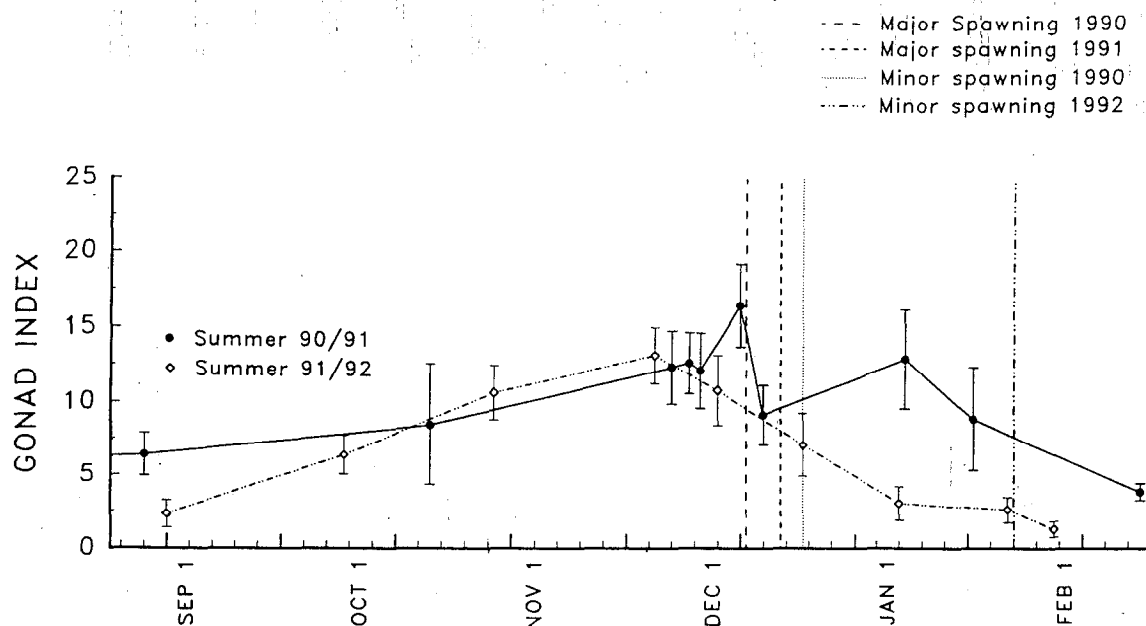


Figure 1: Gonad indices for *Acanthaster planci* population at Davies Reef, 1990-1992. Data are for females and males combined, presented as means and 95% confidence intervals. Vertical lines indicate dates on which spawning was observed at Davies Reef.

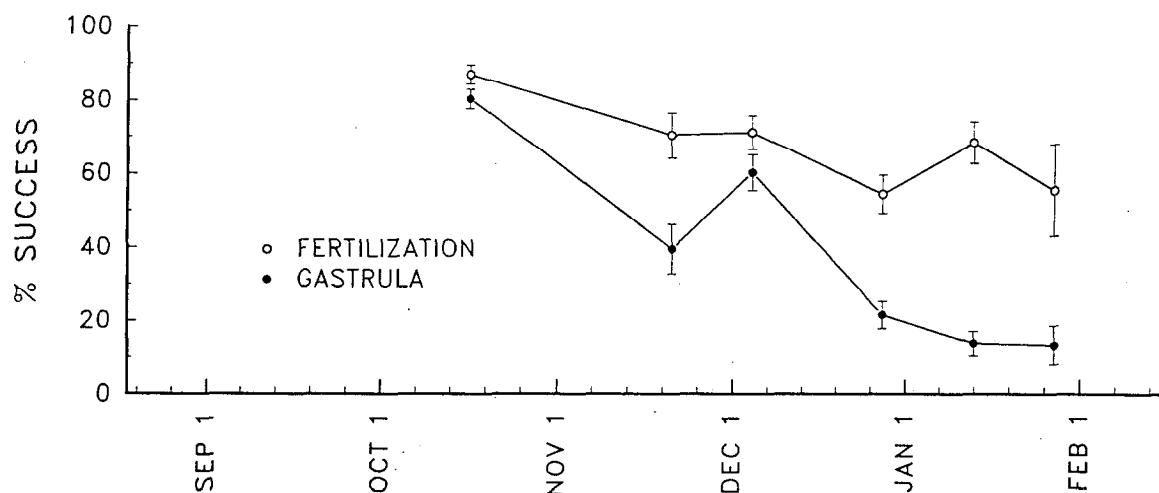


Figure 2: Fertilisation rate and developmental success of *Acanthaster planci* eggs *in vitro*. Data for fertilisation trials are presented as means and 95% confidence intervals. Fertilisation trials marked by asterisks were conducted at Davies Reef. Significance of downward trends in the data over the 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, $p < 0.01$).

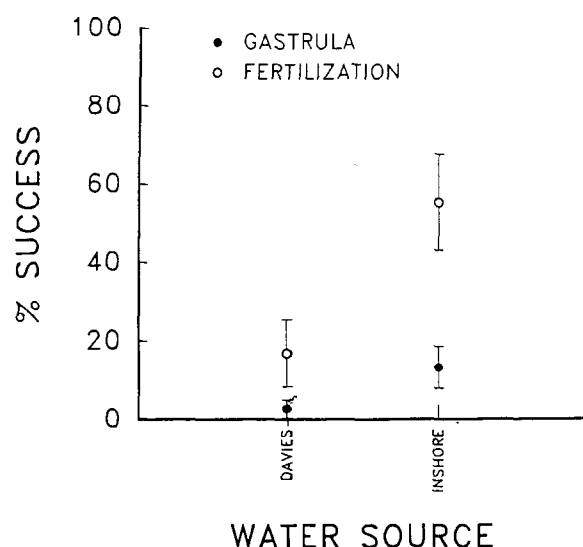


Figure 3: Fertilisation trial comparing seawater from Davies Reef and AIMS seawater system. Means and 95% confidence intervals. Trial conducted 27 January 1992. Differences between water from the two sources were highly significant (T-test; fertilisation $T = -5.24$, $DF = 58$, $p < .0001$, development 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 $<26^{\circ}\text{C}$, 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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