Historical patterns and current trends in the broadscale distribution of crown-of-thorns starfish in the northern and central sections of the Great Barrier Reef

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ABSTRACT

The Great Barrier Reef (GBR) is experiencing a third series of crown-of-thorns starfish (COTS) outbreaks. Current trends in the broadscale distribution of COTS appear to follow the pattern of the last two series of outbreaks recorded from 1966 to 1974 and 1979 to 1991. The first outbreaks in this current series were observed in the Cooktown/Lizard Island sector in 1993 and 1994. COTS activity in this sector continued to increase until 1999, but has since declined. COTS outbreaks were subsequently observed in the Cairns sector in 1995, the Innisfail sector in 1997, and the Townsville sector in 1999. Since then, COTS activity in the Cairns, Innisfail and Townsville sectors have continued to increase. The current pattern of outbreaks is consistent with the hypothesis that COTS outbreaks have their genesis in the Cooktown/Lizard Island sector (north of 16°S) and then cascade southward down through the GBR reef mosaic in subsequent years and generations. This pattern of outbreaks is also qualitatively consistent with numerical models of hydrodynamics and larval dispersal that have previously been used to simulate the large-scale population dynamics of COTS. Implications for reefs currently affected and those recovering from previous COTS outbreaks are discussed.

Keywords Crown-of-thorns, Coral, Distribution, Trends, Great Barrier Reef

Introduction

Over the last forty years Acanthaster planci (the crown-of-thorns starfish or COTS) has caused significant coral mortality throughout the tropical Indo-Pacific. Two series of outbreaks on Australia’s Great Barrier Reef (GBR) between 1966-1974 and 1979-1991 (Moran et al. 1992) have posed a considerable threat to reef productivity and reef based industries. More recently a third series of outbreaks has been recorded from the GBR (Sweatman et al. 1998).

Historically the first confirmed COTS outbreak on the GBR was at Green Island in 1962 (Barnes 1966). Between 1966 and 1974 a variety of surveys were conducted at various times and locations to determine the extent of COTS activity on the GBR (Moran 1986). From these surveys it became apparent that outbreaks occurred further south with time (Talbot and Talbot 1971, Pearson 1972, Endean 1974). Kenchington (1977) suggested that primary outbreaks responsible for the observed COTS activity had occurred north of Green Island in the 1950’s. Primary outbreaks produced a cloud of larvae that traveled south with water currents seeding reefs downstream. In turn secondary outbreaks produced more larvae that travel further south and outbreaks appeared to move down the GBR with time. Kenchington (1977) based his hypothesis on size frequency data. Unfortunately there were a number of problems with this model: alternative interpretations of the size frequency data; lack of evidence for primary outbreaks; lack of consistency in the southward trend (i.e. surveys themselves tended to be conducted further south with time); and a lack of information about water circulation in the matrix of reefs comprising the GBR (Moran 1986).

By 1977, the threat of COTS to the GBR was considered to have faded (Kenchington and Pearson 1982). No outbreaks were recorded after 1977 for almost two years (due in part to a lack of major scientific surveys during this period (Moran 1986)). In late 1979 another large population was observed on Green Island (Endean 1982). By the end of 1984, 24 mid-shelf reefs in the Cairns/Innisfail sectors of the GBR had extensive areas of dead coral attributed to COTS predatory activity (Great Barrier Reef Marine Park Authority 1985). By the middle of 1985, the southern and northern limits of this second series of outbreaks were to be found at reefs near Townsville and Lizard Island respectively (Moran 1986). Broadscale surveys of the entire reef system using manta tow were implemented by the Australian Institute of Marine Science (AIMS) in 1985. AIMS surveys addressed methodological differences common in previous surveys (Moran et al. 1988). For the first time the entire expanse of the GBR was sampled systematically in a single year. Reefs have been sampled annually using the manta tow technique along the length of the GBR since this time (Sweatman et al. 2000). AIMS surveys indicated that by 1990-91 the second series of outbreaks had almost run its course (Baker et al. 1992).

The first to revisit the Kenchington southern drift hypothesis were Reichelt et al. (1990). Their results indicated a strong southward drift of COTS activity consistent with the speed and direction of average summer currents on the GBR. They predicted that if outbreaks are coupled to coral recovery patterns then the next period of high COTS activity in the central section of the GBR would be expected in the late 1990’s. However at that time they could not demonstrate the concept of a discrete seed area to initiate the wave. Further analysis by Moran et al. (1992) detected a strong southern drift for both previous series of outbreaks as well as a weak northern drift in the second series of outbreaks and suggested a likely epicenter for outbreaks on the GBR of around 16°S. Extensive modelling of water currents (e.g.

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Dight et al. 1990a, James and Scandol 1992), passive larval transport within the lagoon of the GBR (e.g. Dight et al. 1990b, Scandol and James 1992) and genetic structure of COTS populations (Benzie 1992) provided further support for the hypothesis. However Van der Laan and Hogeweg (1992) did indicate that the observed waves of COTS outbreaks on the GBR did not necessarily imply that there was a seed area in the north.

More recent analysis of the historical data has provided an alternate view. Bradbury and Seymour (1997) suggested that in fact the travelling wave of outbreaks was becoming less distinct with time and changing towards a more system wide pulse as the proportion of reefs available to host outbreaks declined through time. This was interpreted as an indication that community structure was being damaged over time and was perhaps a signal of the long-term decline on the GBR (Seymour and Bradbury 1999).

Recent data obtained from manta tow surveys of the GBR indicate that there has been a marked increase in COTS activity in the Northern (Cairns) and Central sections of the GBR over the last five years (see Miller et al. 1997, Sweatman et al. 1998). A similar pattern has also occurred in the Swain Reefs to the south. Factors affecting outbreaks in the Swain Sector have been largely unexplored. Though Benzie (1992) highlighted the strong genetic linkages between COTS outbreaks in the southern GBR and those further north they are generally considered as a separate issue (Moran et al. 1992, Reichelt et al. 1990). Thus data from this region is not included. This paper presents a preliminary analysis of the AIMs manta tow survey data since 1992 to determine; if the current series of outbreaks confirm to Kenchington's 1977 southern drift hypothesis, how outbreaks affect regional (i.e. sectional) coral cover, and implications for reefs recovering from previous outbreaks to the south of those currently affected.

Methods

A suite of reefs, in 11 cross shelf sectors has been surveyed annually since 1985 using manta tow. Before 1992 reefs were sampled haphazardly with logistical efficiency determining numbers of reefs sampled within each of the sectors. In 1992 manta tow surveys were incorporated into the AIMS long-term monitoring program (LTMP) with a systematic sampling protocol (Sweatman et al. 2000). This paper presents results from four of the eleven cross-shelf sectors in the Northern and Central Sections of the GBR (Cooktown/Lizard Island, Cairns, Innisfail and Townsville)(Fig. 1). Reefs in these sectors had been repeatedly surveyed well before the first outbreaks in the current series were detected. The sampling program includes key and cycle reefs (Table 1). Key reefs are sampled annually, while cycle reefs are surveyed every three years. Small numbers of reefs have been dropped from the survey in some years due to poor weather.

![Fig. 1 Map of the northern and central Great Barrier Reef showing location of reef sectors.](image_url)

**Table 1.** Number of key and cycle reefs in four cross-shelf sectors of the GBR that are targeted by the AIMS LTMP on an annual basis.

<table>
<thead>
<tr>
<th>Reef sector</th>
<th>Key</th>
<th>Cycle</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooktown/ Lizard Is</td>
<td>9</td>
<td>30(10/year)</td>
<td>19</td>
</tr>
<tr>
<td>Cairns</td>
<td>11</td>
<td>21(7/year)</td>
<td>18</td>
</tr>
<tr>
<td>Innisfail</td>
<td>2</td>
<td>12(4/year)</td>
<td>6</td>
</tr>
<tr>
<td>Townsville</td>
<td>10</td>
<td>6(2/year)</td>
<td>12</td>
</tr>
</tbody>
</table>

At each survey reef a snorkeler is towed behind a small boat at 3-5 km/h by holding on to a manta board. The boat driver tows the observer parallel to the reef crest and close enough for the observer to see as much of the reef slope as possible. Two boats tow observers in opposite directions from a designated starting point, around the reef perimeter, until they meet. As the observers proceed along the reef edge they visually scan the benthos. At two-minute intervals the driver stops the boat and the observers record the data from the previous tow on waterproof paper attached to the manta board. Data consists of COTS counts and estimates of live coral, dead coral and soft coral. This process continues until the entire reef perimeter is surveyed (Bass and Miller 1996).

To define survey reefs with respect to COTS activity AIMS classify reefs according to their outbreak status. Definitions of outbreaks are strongly related to the type of survey technique used to count COTS (Moran 1986). In principle Active Outbreaks occur when starfish densities reach levels where loss of coral tissue through starfish
feeding is estimated to be faster than the growth of the coral. Historically coral cover, the number of COTS per reef and the average number of COTS per tow have been used to make the assessment (Fernandes 1991, Moran and De’ath 1992). For AIMS broadscale survey the definition of an Outbreaking COTS population has evolved over the time. Initially, reefs with active outbreaks were those where >40 COTS were recorded over the whole reef and >30% of coral was dead. Examination of manta tow data from reefs of all categories found that 90% of reefs with active outbreaks by these criteria supported >1500 COTS km² (Moran and De’ath 1992). This is approximately 0.22 COTS per two-minute tow. This figure has been used to denote the minimum criteria for Outbreaking status.

For each survey, reef-wide percent cover of live coral was calculated by adding the mid-point of the range of each recorded cover category and dividing them by the number of tows for that reef. Similarly mean counts of COTS (COTS/tow) were also calculated for each reef. Linear models were used to fit simple (quadratic) curves to the sequence of observations of mean coral cover (reef-wide coral cover) and mean numbers of COTS per tow from each reef for the previous six years (after Sweatman et al. 2000). The fitted values from these curves for individual reefs were then used to estimate the overall six-year trend and the current (last survey year) trend for each sector.

Sector trends were obtained in the following fashion:

1. For each reef the following quadratic model was fit:
   \[ y_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + \epsilon_i \]
   Where \( y_i \) represents the average coral cover or the transformed COTS count \((\text{mean COTS count} + 1)\) on a given reef for year \( i \), \( \beta_0 \) represents the average response at year \( Z \), \( \beta \) represents the slope at year \( Z \), \( \beta_2 \) represents the curvature of the trend, \( x_i = \text{survey number} - Z \), and \( \epsilon_i \) represents the error.

2. For each reef, the response for each year (including the years where some observations are missing) was estimated using the model presented in (1).

3. For each sector, the estimate of the average response was obtained by averaging the predicted response for each reef for each year (Table 2). Comparisons between relative densities of COTS through time and between sectors are explored graphically. In this case the average number of COTS recorded from each sector in each year are compared since 1990 (Fig. 2). To examine the relationship between new outbreaks and latitude the first recorded outbreak on reefs surveyed since 1990 were compared through time. The distribution of outbreaks for the period 1993 to 2000 was modelled by regressing the decimal latitude of first recorded outbreaks (N=42) with month of survey. The linear model was found to provide the best fit (Fig. 3).

**Results**

Outbreaks were first detected in the Cooktown/Lizard Island sector in 1993. COTS densities increased up until 1997, peaking at 0.45 COTS/tow before a decline in 2000. While there was no average trend in coral cover, the recent decline in COTS has been mirrored by increasing reef-wide live coral cover (Table 2).

**Table 2** Modelling results for COTS and reef-wide live coral cover in four sectors of the GBR. The average slope indicates average change over the last six years. The current slope is the change due to surveys in the year 2000 compared to the six year average. Significant result’s (P<0.05) are marked with an asterisk.

<table>
<thead>
<tr>
<th>Sector</th>
<th>Type</th>
<th>Average slope</th>
<th>P-value</th>
<th>Current slope</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooktown/Lizard Island</td>
<td>COTS</td>
<td>-0.033</td>
<td>0.784</td>
<td>-1.026</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td></td>
<td>Coral</td>
<td>-0.045</td>
<td>0.266</td>
<td>0.230</td>
<td>0.003*</td>
</tr>
<tr>
<td>Cairns</td>
<td>COTS</td>
<td>0.311</td>
<td>0.018*</td>
<td>0.697</td>
<td>0.005*</td>
</tr>
<tr>
<td></td>
<td>Coral</td>
<td>0.022</td>
<td>0.611</td>
<td>0.0256</td>
<td>0.750</td>
</tr>
<tr>
<td>Innisfail</td>
<td>COTS</td>
<td>0.720</td>
<td>0.002*</td>
<td>1.041</td>
<td>0.003*</td>
</tr>
<tr>
<td></td>
<td>Coral</td>
<td>-0.238</td>
<td>0.002*</td>
<td>-0.697</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>Townsville</td>
<td>COTS</td>
<td>0.365</td>
<td>0.040*</td>
<td>0.929</td>
<td>0.003*</td>
</tr>
<tr>
<td></td>
<td>Coral</td>
<td>-0.104</td>
<td>0.086</td>
<td>-0.490</td>
<td>&lt;0.001*</td>
</tr>
</tbody>
</table>

**Fig. 2** Chart showing the average number of COTS counted per reef through time (years) in four sectors of the Great Barrier Reef.

In the Cairns sector COTS populations have shown a significant trend of increase since 1994. Surveys in 2000 indicate a continued increase to a level of 0.37 COTS/tow (Fig. 2). Coral cover remained generally unchanged.

For the Innisfail sector the first Outbreaks were recorded in 1997. There has been a significant increase in
COTS activity since this time (Table 2). The large number of COTS recorded in 2000 (currently 3.07 COTS/tow) drives the six year trend. High number of COTS in recent years has lead to a significant decrease in reef-wide coral cover in both the long-term (six year trend) and short term (2000).

The first outbreaks were recorded in the Townsville sector in 1999. The large number of COTS seen in 2000 (currently 3.49 COTS/tow) drives the six year trend (Table 2). COTS continue to increase and there has been a corresponding decrease in live coral cover.

The modelling results are reflected in Fig. 2. Prior to the current series of outbreaks residual COTS populations were present in the Townsville sector. These subsequently declined. COTS built up over a number of years in the Cooktown/Lizard Island sector followed by the Cairns sector. In the Innisfail and Townsville sectors the build up was sudden with COTS numbers increasing sharply in 2000. Average COTS counts for both these sectors (in 2000) are nearly an order of magnitude larger than in either the Cairns or Cooktown/Lizard Island sectors.

The travelling wave of new outbreaks is seen clearly in Fig. 3. Results indicate a significant linear trend (P<0.001) of outbreaks moving progressively southward with time. The southern drift originated in the Cooktown/Lizard Island sector at 14.7° S. Outbreaks moved southward at a relatively constant rate averaging 43 km year⁻¹. The rate of southern drift though initially slower than that recorded during the previous two outbreaks still compares favourably overall (Table 3). There is little indication of a northern drift with only one COTS outbreak recorded on reefs in the Princess Charlotte Bay sector immediately to the north of the Cooktown/Lizard Island sector between 1993 and 2000.

![Fig. 3 Scatter plot of latitude of reefs where outbreaks were first detected compared to time during the period 1992 to 2000. Solid line indicate the fitted regression line](image)

**Table 3** Estimated speed of southerly movement (degrees of latitude year⁻¹) of the centre of outbreaks for the periods 1966-74, 1979-91 and the current series of outbreaks (since 1994).

<table>
<thead>
<tr>
<th>Period</th>
<th>Speed (year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial</td>
<td>Final</td>
</tr>
<tr>
<td>1966-1974</td>
<td>0.440 (1966)</td>
</tr>
<tr>
<td>1979-1991</td>
<td>0.686 (1979)</td>
</tr>
<tr>
<td>1994-</td>
<td>0.390 (1994)</td>
</tr>
</tbody>
</table>

**Discussion**

Sampling by AIMS has provided the first long-term record of the broadscale distribution of COTS on the GBR. At the end of the second series of outbreaks in 1991, surveys continued with a clearly defined methodology and sampling design. Critically, sampling continued in the seed area at 16º S. As a result, surveys were able to map changes in COTS density prior to and during, the third recorded series of outbreaks. For the first time direct comparisons with previous outbreak history can be made.

Results from surveys indicate the current pattern of movement in location of COTS outbreaks in the Northern (Cairns) and Central sections of the GBR is broadly similar to those recorded previously. This is not surprising. Regional scale models based on the hydrodynamics and dispersal of passive COTS larvae (Dight et al. 1990a, Dight et al. 1990b, James and Scandol 1992, Black et al. 1995) show a mechanism for the net southerly movement and recruitment of COTS larvae in prevailing currents. The fact that Reichelt et al. (1990) predicted the current outbreaks on the central section of the GBR and Bradbury and Seymour (1997) entitled their paper “Waiting for COTS” clearly indicates that the current series is not unexpected.

The density of COTS in the central section of the GBR (Innisfail and Townsville sectors) is increasing. This has caused a decline in coral cover. A large mature female COTS can produce up to 60 million eggs per year (Kettle and Lucas 1987). High fecundity combined with the net southerly and onshore larval dispersal patterns found in the central section of the GBR (Dight et al. 1990a, 1990b) makes it inevitable that reefs downstream will soon experience elevated COTS populations. Past history (Moran et al. 1992) and models of larval dispersal (James and Scandol 1992) would suggest that outbreaks are likely together with 95% confidence intervals.
to extend into the Cape Upstart and Whitsunday sectors in coming years. The majority of reefs in these sectors that will be affected are most likely to be mid-shelf reefs with some inconsistencies in the southward drift (i.e. some reefs may experience large populations before outbreaks are observed on reefs further to the north). Many reefs in these sectors are still in a state of recovery from previous outbreaks (Sweatman et al. 2000).

The outbreaks in the northern section (Cooktown/Lizard Island and Cairns sectors) of the GBR present a somewhat different picture. COTS numbers have declined in the Cooktown/Lizard Island sector where no new outbreaks have been recorded since 1998. The lack of significant change in average reef-wide coral cover over the period of outbreaks (1994-1998) is due to the decline in coral cover on affected reefs being counteracted by increases in coral cover on unaffected reefs. New Active Outbreaks were still occurring in the Cairns sector in 2000 where COTS numbers continue to rise. In neither case has the density of COTS approached those currently on reefs in the Innisfail and Townsville sectors. The relatively low densities recorded from the Northern section are apparently sufficient to initiate outbreaks downstream.

The first outbreaks in the current series appeared at 14.7ºS in an area that marked the limit of the northern drift during the second series of outbreaks. Continued sampling of reefs in this area clearly identified outbreaks that may be progenitors of later outbreaks further to the south. However they are not necessarily themselves the “primary” outbreaks for the current series. Just what constitutes a primary outbreak remains open to question (Johnson 1992). While AIMS surveys did detect outbreaks at the beginning of the current series, given the relatively small proportion of reefs sampled (approximately 10%), the possibility remains that other earlier outbreaks may have been missed. Engelhardt et al. (1997) detected increases in COTS numbers on reefs near to and south of Lizard Island in 1994 and 1995 and an increase in recruitment throughout the region 14-16ºS. They considered increases in COTS numbers to have developed over a number of years through several recruitment events. Studies of the genetic structure of these populations (Benzie and Wakeford 1997) indicated that COTS on several reefs in the region act as one mixed population. The genetics were consistent with a small number of reefs contributing to the production of a pool of recruits that build up over time until they contribute significantly to colonisation of reefs downstream and give rise to outbreaks on the central GBR. It was also likely that the same source population has been responsible for the two previous series of outbreaks.

Scandol and James (1992) highlighted the importance of the pattern of water currents in the Cairns and Cooktown/Lizard Island sectors to the recruitment of COTS onto reefs in this area. The lack of consistent directionality in water circulation in the northern section of the GBR and the diffuse nature of COTS recruitment would suggest that primary outbreaks might not necessarily occur discretely on a particular reef within the region. This may explain why the northern drift observed by Moran et al. (1992) and modelled by Dight (1990b)was not observed during the current series. It is quite possible for the observed southern moving wave of outbreaks to be initiated further south than 16ºS (Van Der Laan and Hogeweg 1992). Though modeling does indicate that if primary outbreaks do occur to the south of Cairns in the region 17.5ºS to 19.5ºS, they are unlikely to initiate secondary outbreaks (James and Scandol 1992).

Overall the similarities between outbreak episodes are striking. The current series is consistent with the southern drift hypothesis, with a seed area behind the Ribbon Reefs (14ºS to 16ºS). The events leading to initiation of outbreaks remain enigmatic, and the effect to the long-term health of the GBR of repeated COTS outbreaks even more so. Seymour and Bradbury (1999) argue repeated outbreaks can result in a degradation of reef community structure because of the shortening recovery time between successive outbreaks (a view put forward previously by Cameron and Endean (1985), Done et al. (1988), Endean et al. (1988), Hatcher (1997)). Lourey et al. (2000) raised the possibility that in terms of coral cover not all affected reefs on the GBR will recover from sustained outbreaks. Bradbury and Seymour (1997) suggested the dynamics of outbreaks changing from a wave to a systemic spread. However on a regional level (northern and central sections) the results presented here would tend not to support this view.

In the Townsville and Innisfail sectors the large numbers of COTS and the resulting reduction in coral cover suggests that the capacity to sustain repeated outbreaks will strongly depend on the length of time it takes for coral to recover. Repeated outbreaks would be unlikely to occur on these reefs over a short time frame simply due to lack of coral food for COTS. In contrast, for reefs in the northern section the possibility exist for repeated outbreaks within the overall outbreak cycle, made possible by the relatively low densities of COTS having a lesser impact on coral cover and allowing COTS populations to persist in the region. COTS have been observed in the Cooktown/Lizard Island sector in every year of survey by AIMS. This combined with non-directional water currents provides the possibility for outbreaks to develop over a number of years through a series of recruitment events. In fact as discussed previously this is the mechanism that probably led to the initiation of the current series of outbreaks. Indeed Moran and Death (1992) noted three reefs in northern section that, during the second series of outbreaks, experienced outbreaks 3-4 years after the other reefs in the region. Given the current frequency of outbreaks, combined with a predicted increase in the size and frequency of outbreaks the GBR (such as cyclones and coral bleaching) through climate change (Harmelin-Vivien 1994, Hoegh-Guldberg 1999), COTS remain a threat to the long-term health of the GBR.

Acknowledgements I would like to thank the members of the AIMS field team, particularly, Debbie Bass, Alistair Cheal, Ben Fitzpatrick, Rachelle Ninio, Kate Osborne,
Cathy Page and Angus Thompson for collecting the data. Thanks should also go to Greg Coleman for managing the data. I would also like to thank Hugh Sweatman for comments on the manuscript and Dan Ryan and Steve Delean for statistical advice. This is contribution number 1056 from AIMS.

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