

Influence of hydrodynamics on the passive dispersal and initial recruitment of larvae of *Acanthaster planci* (Echinodermata: Asteroidea) on the Great Barrier Reef

K. P. Black¹, P. J. Moran²

¹ Victorian Institute of Marine Sciences, 14 Parliament Place, Melbourne, 3002 Australia

² Australian Institute of Marine Science, PMB 3, Townsville MC, 4810 Australia

ABSTRACT: Numerical hydrodynamic and particle dispersion simulations showed that neutrally buoyant larvae are subject to a complex circulation pattern which induces a spatial variability in their relative numbers. The interaction of tidal, wind and gradient-driven flows with the reef were found to cause some areas within individual reefs to retain higher numbers of larvae than others. These locations were compared with diver observations of the abundance of *Acanthaster planci* (L.) at the beginnings of outbreaks and a clear correspondence was found in all 6 simulated cases. Results suggest that hydrodynamics have a major influence on not only the dispersal of larvae of *A. planci* but also perhaps the location of their initial recruitment. Surveillance of these locations may provide an 'early warning' strategy for monitoring and controlling future outbreaks of this starfish on reefs.

INTRODUCTION

The crown-of-thorns starfish *Acanthaster planci* (L.) forms large aggregations which can lead to the destruction of extensive areas of hard coral. Impacts of this type have been recorded in a number of reef systems throughout the Indo-Pacific region (Moran 1986). Two series of outbreaks have been recorded on the Great Barrier Reef (hereafter GBR) since the early 1960s, the second of which is still underway (Johnson et al. 1988, Moran et al. 1988). The cause of these outbreaks is still unknown (Moran & Bradbury 1989) despite a recent multidisciplinary program of research in Australia (Zann & Moran 1988). The work presented here has formed part of that large research effort (Baker & Moran 1987).

Whilst knowledge of the early life history of *Acanthaster planci* continues to improve (e.g. Zann et al. 1987, Olson & Olson 1989) its dispersal and recruitment are still poorly understood. For example, it is still not known on which part of a reef the larvae normally settle. Such processes are central to understanding the cause(s) of outbreaks (Moran 1986).

Similarly, at the beginning of this study very little was known about residence times or patterns of larval

dispersal at the scale of the reef and its surrounds. There had been no experiments, apart from some short-term localised measurements (Ludington 1981, Andrews et al. 1984), which measured the long-term, reef-scale dispersal characteristics around individual reefs on the GBR. Over the last few years, a numerical modelling investigation was established that utilised measured water velocities to reproduce flow patterns around individual reefs (Black & Gay 1987a). Dispersal characteristics were then examined numerically at the appropriate time scales using the velocities produced by the numerical hydrodynamic model (Black 1988).

In this paper, data on the distribution and abundance of *Acanthaster planci* and associated coral mortality are combined with those from numerical model investigations of larval dispersal. Repetitive observations of the former, at the beginning of outbreaks, provide useful information about the possible location of recruitment sites. However, the significance of this information is limited when considered in isolation. The objective of the present study was to compare these data with those from numerical hydrodynamic and particle dispersion simulations of the same reefs to gain useful insights into the larval dispersal and recruitment of *A. planci*. The results also have application for the management

of coral reefs and the strategies adopted for the control of the starfish.

METHODS

Biological data. Surveys of the distribution and abundance of *Acanthaster planci* were initiated on a number of reefs off Townsville in October 1982. These were conducted using the rapid reconnaissance technique of manta towing, which had been used in some earlier surveys of the starfish (Endean & Stablum 1973). The advantages and disadvantages of manta towing have been discussed by Kenchington & Morton (1976). Despite the fact that the data are subject to various errors and biases, the technique has proved extremely useful as a means of locating major changes in the distribution and abundance of *A. planci* (Fernandes et al. in press).

The technique involves towing an observer (who holds onto a board) behind a small boat at a constant speed (generally about 1.5 knots). The observer generally is towed along the surface and in areas of shallow water (e.g. reef perimeter) where the reef is readily visible. Three variables were recorded during the manta tow surveys: the number of *Acanthaster planci* and the cover of live and dead coral. These variables were integrated over a 2 min period after which time the boat was stopped and the observer recorded a value for each. In the case of live and dead coral cover the values were given as one of 6 categories: 0 = 0%, 1 = 1–10%, 2 = 11–30%, 3 = 31–50%, 4 = 51–75%, 5 = 76–100%. All manta tow surveys were conducted around the perimeter of each reef. The technique is described in more detail by Moran et al. (1989).

Many of the reefs off Townsville had experienced outbreaks of *Acanthaster planci* during the early 1970s and, on a number of these reefs, starfish were beginning to outbreak again during the present surveys. As a consequence, the surveys were repeated on an annual basis, and in some instances as often as 4 times a year (see Moran et al. 1985).

A series of underwater searches also were conducted on some reefs to obtain more detailed estimates of starfish abundance. During these surveys a team of 3 divers swam over a defined section of the reef perimeter. They swam ca 2 to 3 m apart and covered a total search width of about 12 m. The depth at which each diver swam varied according to the slope of the reef. Whilst swimming, each diver kept a record of the number of *Acanthaster planci* sighted. Each starfish was marked (by slashing it with a knife) once it had been recorded to avoid the same individual being counted by another diver. Areas of coral in the vicinity of feeding scars (patches of dead, white coral) were

searched intensively on reefs where few starfish were evident. The location of the start and finish of each swim were accurately recorded on an aerial photograph of the reef at the completion of each survey.

A total of 22 outbreking reefs were surveyed off Townsville using one or both techniques described above. Overall, the data from 8 of these reefs (Bowden, Davies, Dip, Faraday, Glow, Helix, John Brewer, and Wheeler) were sufficient to indicate where large populations of starfish were first located. The positions of these reefs and extent of the various surveys undertaken on each are given in Figs. 1 & 2, and details of the surveys are in Table 1.

It should be stressed that the biological data were not chosen to fit the results of the simulations, as both projects were carried out independently of each other. The former were conducted from October 1982 to October 1987 while the latter were conducted from January 1987 to May 1989.

Hydrodynamic models. Hydrodynamic modelling of 6 reefs (Bowden, Davies, Glow, Helix, John Brewer and Wheeler) was undertaken with the 2- and 3-dimensional numerical model 2DD (Black 1989) which has the necessary features for simulation of coral reef circulation, including wetting and drying of inter-tidal zones, non-linear terms and a choice of boundary procedures. The model was designed to be portable and had been applied to estuarine, ocean and continental shelf environments (Black & Gay 1987b, McShane et al. 1988, Black et al. 1989). For the grids employed in this study, which had 4 open boundaries, it was necessary to apply analytical solutions for coastal influences outside the grid and the non-linear interactions of the current components which occur on the GBR continental shelf (Black & Gay 1987a, Black & Gay in press a). Dispersal modelling was undertaken with the fully Lagrangian 2- and 3-dimensional particle model 3AD (Black 1988). Lagrangian residuals (i.e. the distance moved by a particle over a known time interval and starting from a known location) were used in preference to Eulerian residuals (i.e. the average current over a time interval at a point in space) as they account for spatial variations in currents and thus are the better indicator of larval transport over a tidal cycle. The model corrected for flow curvature to second-order and eliminated the numerical dispersion characteristics of Eulerian finite difference schemes (Black & Gay in press b).

The hydrodynamic model was calibrated using the measurements of Pickard (1986) from Davies Reef, and then verified against drogue measurements on John Brewer Reef (Black & Gay 1987a). Bed friction was established using wave measurements from a Hawaiian coral reef (Lee & Black 1978) and from direct measurements of the sea bed boundary layer on the

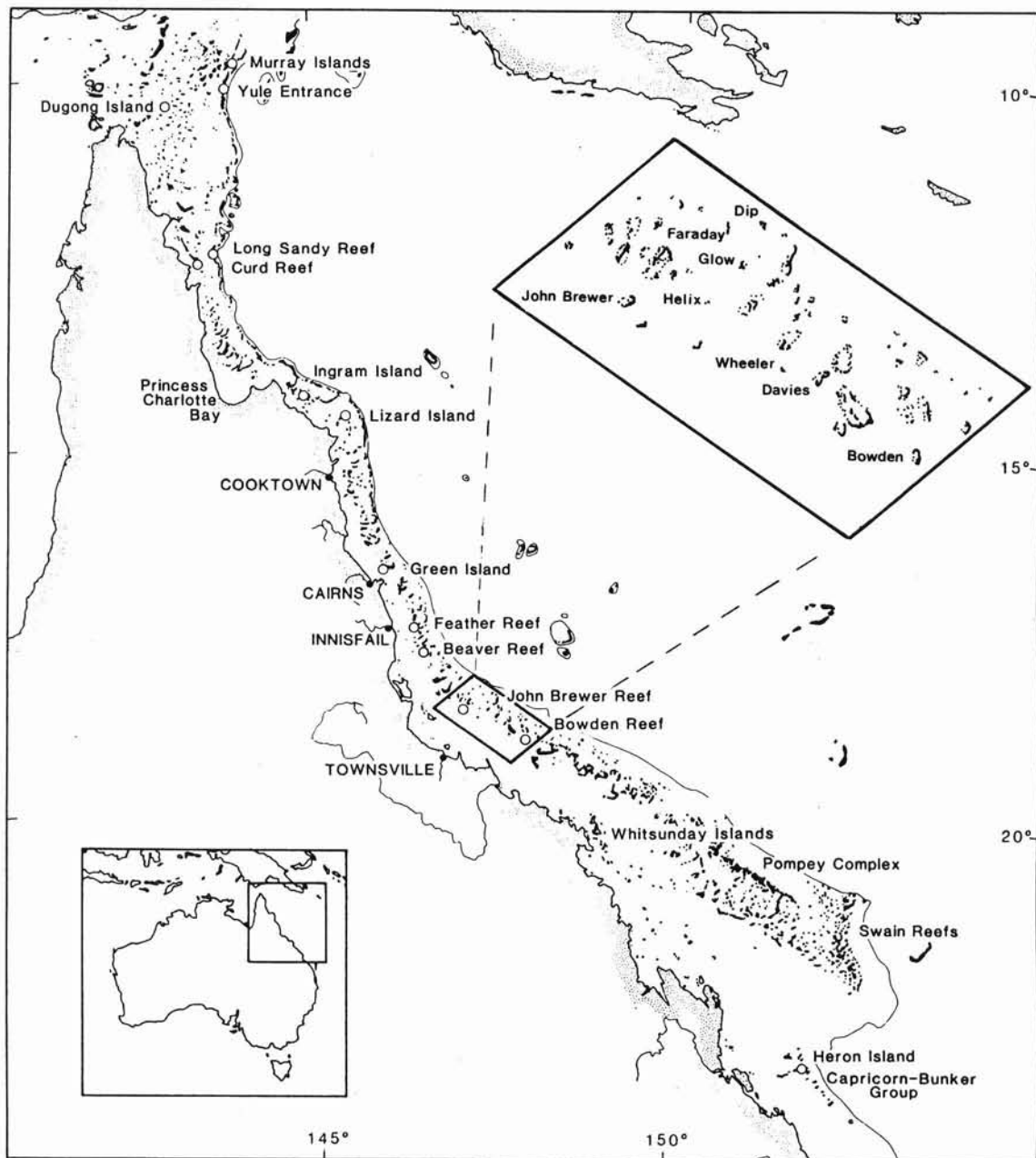


Fig. 1. Location of reefs in the central Great Barrier Reef

GBR. Further confirmation of the model was obtained by simulating Rattray Island (Black & Gay 1987b, Black 1989) where detailed flow measurements had been made (Wolanski et al. 1984).

Advection in the particle model was determined by the predicted flow patterns, and therefore was calibrated at the hydrodynamic model stage. All particles were treated as being neutrally buoyant, very much like the gametes and larvae of *Acanthaster planci*. Specific gravity measurements by Olson (pers. comm.) and field observations made by the authors indicate

that they are close to neutral buoyancy. Dispersion associated with turbulent current oscillations and vertical shear was modelled as a random walk, with separate lateral and longitudinal horizontal diffusion coefficients. Because of the complex flow patterns on a coral reef, advective dispersion caused by horizontal velocity gradients dominated, and the general conclusions presented here were found to be unaffected by the choice of the horizontal diffusion coefficients. High diffusion caused gradients in integrated particle retention rates to be spatially smoothed.

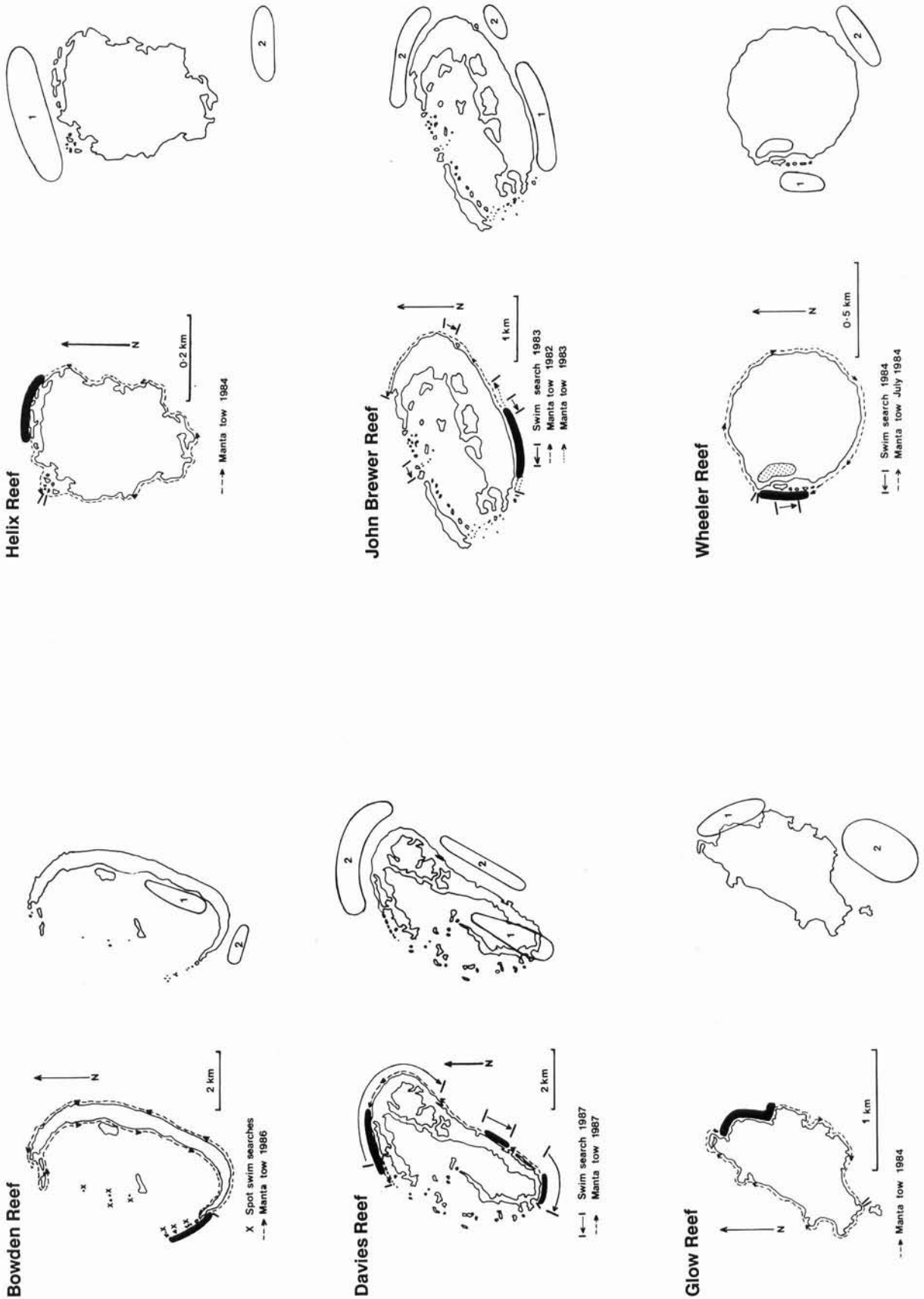


Fig. 2. *Acanthaster planci*. Observed locations of adults at the beginnings of outbreaks on 6 reefs (dark areas) compared with integrated larval numbers from the numerical model. Primary and secondary zones (marked as 1 and 2 respectively) are shown for the latter. Internal (self-seeding) releases were simulated in all cases except for Helix Reef

Table 1. *Acanthaster planci*. Distribution and abundance during the initial stages of outbreaks on 8 reefs. Extent: total extent of survey; No.: number of starfish and (in brackets) number of consecutive tows over which starfish were recorded; FS: number of feeding scars (i.e. patches of recently dead coral): C (common), P (present), A (absent)

Reef	Type	Survey Date	Extent	No.	<i>A. planci</i>		Depth	Description
					Location	FS		
Bowden	Swim search	Oct 1986	7 sites (10 min.)	300	SW leeward	C	3–10 m	Large numbers of starfish and feeding scars recorded on several patch reefs along SW leeward margin during October 1986. Dead coral cover high (30–50 %) in deeper water (> 12 m) at these sites. Numerous patches of white coral identified also in deep water (> 20 m) along S flank during manta tow survey. No other signs of starfish activity observed during that period over rest of reef. Large aggregation of starfish present on S flank during 1987. No other starfish reported
	Manta tow	Oct 1986	Perimeter (94 tows)	0	S flank	C	> 20 m	
	Manta tow	Oct 1987	Perimeter (91 tows)	114 (10)	S flank	C	> 10 m	
Davies	Swim search	Jan 1987	Perimeter (7.5 km)	122	NW flank	C	> 6 m	Numerous starfish recorded along NW flank during underwater searches conducted in January 1987. Smaller aggregation of starfish also observed along S flank. No other individuals sighted except for small, isolated group on SE windward slope. Generally, cover of live coral high (30–50 %) apart from areas where starfish recorded. Numerous feeding scars present along NW flank and S flank. Old dead coral (algal covered) present in large amounts at base of reef (> 15 m) along NW flank. Only a few feeding scars noted near starfish on SE windward margin. Increase in this population observed in a subsequent manta tow survey. Starfish aggregations also recorded in the other 2 areas but not over rest of reef
				24	S flank	C	> 6 m	
				3	SE windward	P	> 12 m	
	Manta tow	Oct 1987	Perimeter (55 tows)	9	NW flank	C	3–6 m	
				10	S flank	C	3–6 m	
Dip	Manta tow	Mar 1984	Perimeter (100 m)	15	SE windward	C	> 6 m	
Dip	Manta tow	Mar 1984	Perimeter	0	N flank	C	> 15 m	Large number of feeding scars observed along N flank during manta tow surveys conducted in March 1984. All scars located in deep water (> 15 m). No other signs of starfish activity around perimeter of reef. Swim searches undertaken along N flank revealed 100's of starfish and large amounts of recently dead coral
	Swim search	Mar 1984	N flank (100 m)	> 100	N flank	C	> 15 m	
Faraday	Manta tow	Mar 1984	Perimeter (46 tows)	9 (2)	N flank	C	> 10 m	Numerous feeding scars recorded in deep water along N flank during March 1984. Small number of starfish also noted in this area. Very few starfish (3) observed along rest of reef where coral cover was moderate to high (20–50 %)
Glow	Manta tow	Mar 1984	Perimeter (35 tows)	148 (7)	NE windward	C	> 12 m	Large numbers of starfish and feeding scars observed in deep water (12–15 m). Most concentrated along NE windward slope. A few starfish (about 19 in 5 tows) noted in adjacent areas. No starfish activity reported along leeward side of reef and live coral cover was moderate (10–30 %)

Table 1 (continued)

Reef	Type	Survey Date	Extent	No.	<i>A. planci</i>			Description
					Location	FS	Depth	
Helix	Manta tow	May 1984	Perimeter (24 tows)	65 (3)	N flank	C	> 10 m	Large aggregation of starfish identified along N flank during manta tow survey conducted in May 1984. Most starfish and dead coral in deeper water (> 10 m) at base of reef. Very few starfish (5) observed outside this area. Several feeding scars noted along S windward slope in deep water (> 15 m)
John Brewer	Swim search	May 1983	S windward	30	SE windward	C	> 15 m	A number of feeding scars observed in deep water (> 15 m) along S windward slope during October 1982. Starfish common in this area by May 1983, although not recorded during surveys along other sections of the reef perimeter. Increasing amounts of recently dead coral and large numbers of starfish present in shallower waters of S windward slope by Aug 1983. No starfish observed during survey swims along NE windward slope. (See Moran et al. 1985)
	Swim search	May 1983	E windward	0	NE windward	A		
	Swim search	May 1983	NW leeward (200 m)	0	NW leeward	A		
	Manta tow	Oct 1982	Perimeter (41 tows)	3 (2)	S windward	C	> 15 m	
	Manta tow	Aug 1983	S perimeter (15 tows)	> 100 (3)	S windward	C	> 8 m	
Wheeler	Swim search	Jul 1984	10 min.	100	W flank	C	6–12 m	Numerous starfish and feeding scars recorded adjacent to cay in deeper water (> 6 m) during July 1984. Increase in the abundance of starfish and dead corals recorded in this area by August 1985. Very few starfish (3) observed over remaining perimeter. Cover of live coral high (30–50 %) in these areas
	Manta tow	Jul 1984	Perimeter (20 tows)	19 (2)	W flank	C	6–12 m	
	Manta tow	Aug 1985	Perimeter (32 tows)	32 (3)	W flank	C	6–12 m	

For the 6 coral reefs presented here, spring and neap tides, trade and northerly winds and varying coastal current strengths were modelled. However, this paper is primarily concerned with 'average' summer conditions. The other conditions provide indications of the influence of variability in the weather patterns as discussed below. Current meter deployments by Andrews (1983) and Church et al. (1985) provided the mean amplitude and orientations of low-frequency currents and tidal ellipses respectively in the central GBR (Fig. 1). A standing tidal wave crosses the shelf nearly perpendicular to the coast and to an approximately coast-parallel, gradient-driven current (Andrews 1983, Church et al. 1985), although the steady current has a cross-isobath component at the offshore reefs. Complete details of boundary conditions at all reefs are provided by Black & Gay (1987a).

To summarise the dispersal modelling, an integrated larval abundance was defined which specified the relative probability of larval occurrence. After each model time step, a cell-by-cell counter was incremented to record the particle's presence. Summation in time and

normalisation by the total number of occurrences over the full model run provided an indication of the locations which were frequently visited or where particles spent most time. Mostly, the modelling simulated the dispersal of larvae of *Acanthaster planci* over 10 d, which is the minimum time that they may spend in the water column prior to settlement (Olson 1987).

During the modelling no attempt was made to impose a larval mortality rate onto the solution, although this could have been included if adequate biological data were available. The results are species independent and are equally as relevant to the passage of pollutants such as sewage (Black et al. in press). As such they demonstrate the hydrodynamic influences in isolation.

Flow patterns. The complex dynamics around coral reefs (Black & Gay 1987a,b, Black 1988) are typified (Fig. 3) by large variations over short time and space scales. One of the most important features is the phase eddy which develops during the later stages of each half tidal cycle in response to the variation in velocity phase between the free stream and the lee of the reef.

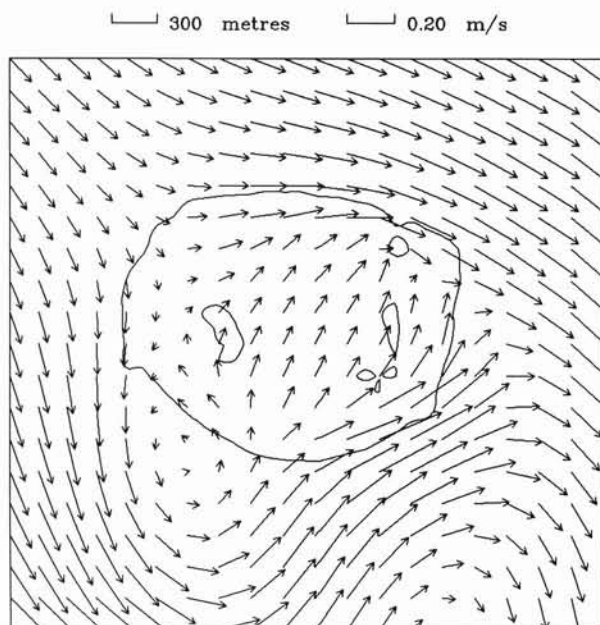


Fig. 3. Wheeler Reef circulation in a phase eddy at high tide. Arrow tails are scaled to represent flow speeds

An example at Wheeler Reef is shown in Fig. 3. A second type of eddy on the GBR, described as 'interactive' (Black & Gay 1987b), results from interaction of the steady and tidal currents. The eddy develops during the half tidal cycle when the directions of the co-aligned components of the tidal and faster steady currents are in opposition. At this time, the flow changes sign only in the lee of the reef and an eddy develops. A third eddy develops in steady-state conditions and can be described as a topographically-induced steady state eddy. This last feature, while being relevant to the mechanisms that assist the formation of phase eddies, is mostly not relevant to the central GBR where tidal, low-frequency and wind-driven currents interact to produce a dynamic, non-steady hydrodynamic environment.

Larval trapping. Black (1988) predicted numerically that passive larval numbers on and around coral reefs should vary widely. The patterns are governed by several factors, which fall into 2 major categories of dynamic and static retention. In the first case, larval retention is high in regions where the velocity orbits are approximately closed over one tidal cycle. For example, relatively high retention rates of larvae can occur in locations around the reef even where tidal currents are large (and the orbital excursion is correspondingly large) if the particles are returned close to their initial point of release after one tidal cycle. Also, high retention rates will occur in model cells which have the most links with other cells. Cells are linked by the initial and final positions of a particle after one tidal

cycle has elapsed. The number of links to any cell specifies the relative retention rates.

Accordingly, both the Eulerian and Lagrangian residual vectors on and around a coral reef are complex and vary with the tidal and current conditions, reef size and eddy formation. It is difficult to identify the locations of low flushing without the particle model simulations which can unify and treat these factors simultaneously. In the dynamic GBR environment, zones of high residence are often not simply associated with static areas of low current speed.

RESULTS

Overview

The integrated larval numbers for the 6 reefs for which simulations were carried out are shown in Fig. 2. Primary peaks are the locations where maximum numbers of neutrally buoyant larvae were predicted to occur. Secondary peaks are locations where the numbers are 40 to 80 % of the maximum. These peaks are compared with the locations where moderate to large numbers of adult *Acanthaster planci* were first sighted at the beginnings of outbreaks on these reefs. A clear correspondence is evident, with the exception of one case, where the habitat was unsuitable.

The majority of starfish were observed in deeper water (i.e. >10 m). In addition, the pattern of coral destruction in these areas indicated that the starfish were moving from deep to shallow water up the slope of the reef. Surveys of another 6 reefs (Dip, Faraday, Hopkinson, Keeper, Lodestone and Yankee Reefs), where outbreaks of the starfish were just beginning, also demonstrated this pattern.

Bowden Reef

Integrated larval numbers were highest at the southern end of the reef and in the southeast of the lagoon. In the latter case, the substrate is mainly sand (pers. obs.) and it is unlikely that settlement would be high in that area (see below). The peak to the south is to be compared with first observations of starfish on several patch reefs along the southwestern leeward margin of the reef. Large aggregations of starfish were reported along the southern end of the reef within several months.

Davies Reef

The southern flank was found to have highest integrated larval numbers whilst secondary peaks in

abundance occurred along the northwestern flank and southeastern windward margin. Starfish were initially recorded in moderate numbers in the northwest location along with a smaller number in the south. A small population of starfish, which appeared to be spatially isolated from the other two, was identified subsequently along the southeastern windward slope. Thus, there is a correspondence with the locations of the primary and secondary peaks at Davies Reef, although the population on the southeastern windward slope was observed 9 mo after the other two.

Glow Reef

The modelling identified a region of high integrated larval numbers along the northeastern windward margin. It was in this area that the main concentration of starfish was first reported in 1984. Smaller numbers of starfish were observed just to the south which may coincide with the secondary peak predicted by the model.

Helix Reef

When larvae were released externally, upstream of the reef, the model identified 2 regions of relatively high larval retention. A dominant peak occurred along the northeastern margin whilst a secondary peak was found along the southern windward slope. Large numbers of starfish were observed in deeper water along the northern margin of the reef in 1984 and while a similar population of starfish was not observed on the southern windward slope, numerous feeding scars were recorded in deep water (i.e. > 15 m) only in this region. When the model simulated an internal or 'self-seeding' release, as for all other reefs, a region of relatively high larval abundance was identified on the southwestern side of the reef. Clearly, this peak did not coincide with the location where the starfish outbreak was first recorded. It should be mentioned here that the peaks generated by the model do not reflect the initial location of the starfish larvae but are a consequence of the interaction of hydrodynamics and bathymetry, at a reef scale.

John Brewer Reef

Integrated larval numbers were highest along the southeastern windward margin with secondary peaks in the north and northwest. The location of the dominant peak coincides with the location where starfish were first sighted on this reef just prior to a large outbreak. The broad changes in the distribution and

abundance of the starfish population on this reef during the first 2 yr of the outbreak have been described by Moran et al. (1985).

Wheeler Reef

The modelling identified a major peak in integrated larval numbers along the western margin of the reef, adjacent to the coral cay. A gradual increase in starfish numbers was recorded in this region between 1983 and 1985, in conjunction with a decline in live coral cover and an increase in the amount of dead coral. A large population of starfish was reported over much of the reef perimeter by 1986.

DISCUSSION

In the present study the results from hydrodynamic and particle dispersal simulations were compared with detailed biological information about the distribution and abundance of *Acanthaster planci* for 6 reefs of the GBR. Overall, a close correspondence was found between regions of highest larval retention and the locations where large numbers of adult starfish were first observed at the beginnings of outbreaks. This finding suggests that hydrodynamics have a major influence on the larval dispersal of *A. planci* and also perhaps the location of its initial recruitment. These results can be applied equally to other species whose larvae behave in a manner similar to those of *A. planci*.

Complete correspondence between regions of high integrated larval numbers and those where adult starfish were first sighted was not obtained in all cases. This is to be expected as the surveys could not be conducted at exactly the same stage of each outbreak. As a consequence, the outbreaks on Bowden and Glow Reefs were at a more advanced stage by the time surveys were conducted than those on the other reefs. The starfish populations on these reefs, therefore, had more time to disperse over the reef away from their point of initial recruitment before the surveys were conducted. Despite this, a general correspondence between the biological and hydrodynamic results was obtained for both reefs.

There was only one instance of a complete lack of correlation between primary areas of high larval numbers and the locations where adult *Acanthaster planci* were first sighted. The southeastern end of the lagoon of Bowden Reef was predicted to have high integrated larval numbers although no starfish were observed in this region of the reef. This result is not surprising as the substrate in this area is composed mainly of sand. Previous studies (Yamaguchi 1973) have indicated that

the larvae of *A. planci* prefer to settle on hard substrata, particularly coralline algae, which becomes a source of food during the early life of the juvenile starfish (Zann et al. 1987).

Not all secondary peaks in integrated larval numbers coincided with regions where starfish were first sighted. For example, no starfish were observed in the 2 secondary areas on John Brewer Reef whilst only feeding scars were sighted in deeper water in the secondary area identified for Helix Reef. This lack of consistency may be due to inadequacies in the survey methods. Whilst manta towing is a useful way of identifying major changes in populations it may not have been appropriate for detecting the starfish populations associated with some of these secondary peaks. Alternatively, the levels of recruitment generated in these secondary areas may be insufficient to sustain a viable population through to the adult outbreak stage. Progression to this stage may be the result of a threshold effect, below which the population does not survive or does not continue to increase in abundance. This is perhaps why *Acanthaster planci* were observed consistently in primary areas whereas they weren't always sighted in secondary areas on the same reefs.

While the results of the hydrodynamic simulations correspond with the biological data they do not indicate whether the larvae are from a local or external source. The patterns of larval retention for all other reefs, except Helix, were based on simulations where the larvae were released internally. On larger reefs (e.g. John Brewer) where particles are retained in the vicinity of the reef for periods of days (Black et al. in press), particles entering the reef system are effectively transported throughout the reef and its surrounds. The modelling in the present study indicated that in these instances the dispersal patterns were always similar regardless of whether the larvae were released from within or outside the reef. However, particles spend a much shorter time around reefs which are very small (e.g. Helix Reef). Regions of initial recruitment may then be spatially biased by the location of initial impact on the reef from an external source rather than being indicative of the effect of local reef-scale hydrodynamics only.

As continental-shelf, low-frequency currents are primarily directed along the isobaths (Andrews 1983) there is variability in current strength and often there are 180° changes in flow direction (those of an intermediate nature are less common). Varying current strengths, which alter the reef flushing rate (Black et al. in press) should result in changes to the rates of recruitment and the likelihood of an outbreak. The correspondence identified in this paper occurred when currents were directed to the south and of moderate to low strength. Thus, one could speculate that outbreaks may occur, at least in part, in direct response to the

occurrence of these types of hydrodynamic conditions at settlement time.

There was a consistent pattern in the locations where starfish were first sighted at the beginnings of outbreaks. These coincided particularly with the north and northeastern margins of the reef perimeter. The biological data for both Faraday and Dip reefs (for which hydrodynamic and dispersal simulations were not available) also produced this same general trend. The simulations of Glow reef showed that this region of high relative larval retention was associated with local hydrodynamics and was not necessarily the point of first contact of larvae coming from upstream. As this is likely to be true in other cases, it cannot be assumed that the regions on the northern sides of reefs are associated with a southerly current bringing larvae from the north (Dight et al. 1988).

Another consistent feature noted during the surveys was that most starfish were first observed in deeper water at the base of the reef slopes (i.e. > 15 m). This pattern was reported during the first series of outbreaks on the GBR (e.g. Endean & Stablum 1973) and was used as evidence to suggest that the starfish had walked from a nearby reef (Endean 1969, Talbot & Talbot 1971). However, since large numbers of *Acanthaster planci* have not been reported between reefs (despite searching) or caught in bottom trawls this is considered unlikely. Given this we suggest that the occurrence of large numbers of adult starfish in deeper water at the beginnings of outbreaks is indicative of starfish having recruited mainly to these regions, at the bases of reefs (i.e. between 15 and 50 m). These areas are likely to contain a diverse range of suitable settlement substrates including an abundance of algal food. Recently, Fisk et al. (1988) suggested that outbreaks of crown-of-thorns starfish appeared to originate from deeper shoal areas on the eastern side of Green Island. These areas were noted to comprise rubble banks and interstitial coralline algae.

The hypothesis of deep water recruitment is founded also on several other pieces of evidence. Firstly, the dispersal simulations indicate that the regions of highest larval retention are to be found somewhat off the reef perimeter in areas of deeper water. Secondly, coral mortality during the initial stages of an outbreak occurs first in deeper areas. This has been reported by several authors (e.g. Endean 1969, Endean & Stablum 1973) and was noted by Moran et al. (1985) during a recent outbreak on John Brewer Reef. Given this pattern it would seem highly unlikely that most larvae recruit to shallow water (i.e. reef flat or crest) and then move to deeper water without leaving evidence (feeding scars) of such movement. Thirdly, there is circumstantial evidence to suggest that the larvae of *Acanthaster planci* become negatively buoyant during the latter stages of

their development. Olson (1985) reported that the larvae tended to sink to the bottom of in situ culture chambers once they had reached the late brachiolaria stage.

The approach adopted in the present study has yielded several important findings that have implications for the dispersal and recruitment of *Acanthaster planci* and species with similar larvae. It should be emphasised here that the results of this study do not suggest that recruitment is limited to only those areas or parts of the reef where starfish were first observed. Indeed the model results indicate that recruitment of larvae may occur over much of the reef, although it is likely to be highest in certain key regions. Nonetheless it is important to note that the initial stages of outbreaks did not occur in areas where larvae were not predicted to occur.

Of course, a necessary prerequisite for successful recruitment is the availability of suitable settlement substrates and ultimately an abundant food resource. As discussed previously recruitment of larvae will not take place if one or other of these factors is missing. Furthermore, just because areas of high larval retention are identified in the simulations it does not necessarily mean that outbreaks of *Acanthaster planci* will arise solely, if at all, in these areas. It is clear that there are a range of other potentially important biological (e.g. predation, competition) and physical factors (natural disturbances such as waves and light) which are likely to affect the distribution and abundance of the starfish.

Nonetheless, in the presence of some or all of these factors a close correspondence has arisen between areas of high larval retention and locations where *Acanthaster planci* were first observed at the beginnings of outbreaks. This suggests to us that hydrodynamics has, at the very least, an important role to play in recruitment processes, particularly the dispersal and settlement of larvae within individual reefs. Further research on other physical and biological processes also may help to provide a better understanding of their relative importance in controlling the population dynamics of *A. planci*.

The identification of areas where larvae of *Acanthaster planci* are likely to accumulate on reefs has important implications for management. Monitoring of these areas in the future, particularly on reefs which have suffered outbreaks on the last 2 occasions, may provide an early warning system for control by identifying large populations of very small starfish. Information of this type is essential if future control programs are to be successful (Moran 1986). From a biological point of view identification of large numbers of juvenile starfish would enable important biological and ecological data to be collected. Such data could provide a significant advance in our understanding of the recruitment of the

starfish and allow important manipulative research to be undertaken to investigate the effects of such processes as predation.

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