

NOTE

Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: predator pressure as a mechanism of coevolution?

L. M. DeVantier, R. E. Reichelt, & R. H. Bradbury

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

ABSTRACT: A novel mutualistic relation has been observed between serpulid worms *Spirobranchus giganteus* and massive coral colonies of *Porites lutea* and *P. lobata* in response to *Acanthaster planci* predation on reefs of the central Great Barrier Reef (GBR), Australia. As feeding aggregations of *A. planci* have caused mass mortality of hard corals in these areas, predator-induced selection may be operating as an ecological mechanism in the development of the interaction from the *S. giganteus* commensalism into a facultative mutualism. For the worms, massive *Porites* colonies provide both protection and an ideal location for suspension feeding (Strathmann et al. 1984, Smith pers. comm.). For the coral colony, the worms provide a refuge for adjacent polyps from predation by *A. planci*. Such protected polyps initiate regeneration, ensuring the survival of the colony. As *Porites lutea* and *P. lobata* have long colonial lives (>500 yr) (Potts et al. 1985) the long term survival of individual colonies is an important factor in their life history strategies and in maintaining the observed broad distribution of size classes of these species (Potts et al. 1985, Cameron & Endean 1985). In relation to continued predation by *A. planci*, this mutualism may be an important buffer acting to preserve reef community structure and accelerate the recovery process.

INTRODUCTION

Coral reef communities are renowned for their ecological complexity. This complexity is exemplified by a high level of coevolution among interacting species. For instance, specific interactions between predator and prey over evolutionary time scales have led to symbiotic relations (Cameron 1983) that can ameliorate the predation effects. An example of this kind of interaction has been described by Glynn (1980) in relation to hard coral predation by the crown-of-thorns starfish *Acanthaster planci*. He has shown that crustaceans living within pocilloporid coral colonies, and feeding on mucus from the coral, can chemically sense approaching *A. planci* and will attack their tube feet and spines, thus protecting the host coral.

Apart from such symbiotic relations, other predator-selected adaptations may also have evolved, while some corals may be pre-adapted to survive predation. For example, prey preference by *Acanthaster planci* is selective both among coral species and individual colonies in relation to palatability, defensive mechanisms and availability (Barnes et al. 1970, Brauer et al. 1970, Collins 1974, 1975a,b, Huxley 1976, Ormond et al. 1976). While massive colonies of *Porites* spp. are less preferred prey (Barnes et al. 1970, Brauer et al. 1970, Pearson 1973), *A. planci* do occasionally prey upon these species (Goreau 1964, Chesher 1969, Barnes et al. 1970, Glynn 1974, Done 1985). Indeed, the large populations of starfish recently aggregated on reefs of the central Great Barrier Reef (GBR) have preyed upon many of these colonies (Cameron & Endean 1985, Done 1985).

A survey of a large number of *Porites* colonies on these reefs and one reef in Pulau Seribu (Indonesia) has demonstrated that such predation is often non-lethal to the colony. It has also indicated that a relation frequently exists between the distribution of certain serpulid worms (*Spirobranchus giganteus*: taxonomic status currently under revision, R. Smith pers. comm.) on these colonies and the remaining living tissue.

While working on *Porites* in the Red Sea, Goreau (1964) noted that many tubicolous worms survived death of the host coral by *Acanthaster planci* predation. He did not record the survival of any adjacent coral polyps. However, in our study area, the only living polyps on *Porites* colonies following predation commonly occur in patches hosting populations of serpulids, or directly below the worms' extended branchial crowns (3 to 5 cm diameter). On a broader geographical scale the phenomenon is likely to be patchy, in relation to intensity of predation, although it has

been observed elsewhere on the Great Barrier Reef (R. Smith pers. comm.).

As a result of such avoidance of *Spirobranchus giganteus*, a refuge is provided for the adjacent polyps and a ring of protected tissue persists after predation. These relict polyps could initiate colony regeneration and ensure survival of the colony.

METHODS AND RESULTS

To examine the significance of these observations, field censuses were carried out at Potter Reef (17° 42' S, 146° 33' E) in the central section of the GBR in April and June 1985. This reef, along with many others in the region, supported large populations of *Acanthaster planci* throughout 1983-84. At the coral population level, significant positive associations between the co-occurrence of the remaining living *Porites lutea* and *P. lobata* colonies and *Spirobranchus giganteus* established prior to the predation event were found (Table 1).

More specifically, the distributions of *Spirobranchus giganteus* and the living tissue on those colonies show strong positive association (Table 2).

Table 1. Visual census data from Potter Reef, GBR (April 1985). Contingency analysis (Kendall & Stuart 1979) of partially versus totally consumed *Porites* colonies shows a strong positive relation between the presence of *Spirobranchus giganteus* and live colonies

State of predation of colony	Number of colonies with or without (w/wo) worms		Total
	w	wo	
Partial	15	5	20
Total	0	11	11

Fisher Exact Test $P < 0.001$

Table 2. Contingency analysis of randomly located, paired, 25 cm × 25 cm quadrats on partially consumed *Porites* colonies. For 5 of the 7 colonies there was a significant positive association between the presence of *Spirobranchus giganteus* and living tissue. a: *S. giganteus* and dead coral; b: no *S. giganteus* and dead coral; c: *S. giganteus* and live coral; d: no *S. giganteus* and live coral; P = Fisher Exact Probability (Kendall & Stuart 1979) or G-Test (Sokal & Rohlf 1969) for Totals

Colony number	Frequencies				Total number of quadrats	P	Colony dimensions		
	a	b	c	d			Circumference (m)	Height (m)	Live cover (%)
1	2	4	8	6	20	0.31	8.1	2.7	60
2	0	5	10	5	20	0.02	5.5	2.0	30
3	1	10	9	0	20	<0.01	4.8	2.9	10
4	1	7	8	2	18	<0.01	5.7	2.1	20
5	0	5	5	0	10	<0.01	17.1	4.1	<10
6	0	5	5	0	10	<0.01	9.0	1.9	<10
7	1	3	8	6	18	0.29	12.2	3.0	10
7	5	39	53	19	116	<0.001			

Thirdly, more than 2 yr after predation, the areas of living polyps beneath the worms' branchial crowns showed evidence of regrowth. During this period, these remnant polyps had grown above the surrounding algal covered skeleton, and asexual budding was occurring in the outermost polyps. Monitoring of these colonies will allow continued assessment of recovery. *Porites* polyps were not protected in all cases.

Field observations indicate that these worms generally retreat into their tubes on initial contact with foreign organisms, reappearing after a short interval to continue feeding. The length of time between retraction and reappearance seems to vary among individual worms in relation to the type of stimulus, its intensity and frequency. Preliminary field experiments indicate that for certain worms, contact by *Acanthaster planci* induces retraction followed by almost immediate reappearance, with the operculum and branchial crowns pushing against the tube feet and arms of the starfish. This caused the predator to move quickly away. However, other worms on the same *Porites* colony did not attempt to expose their branchial crowns during the period of observation, thereby allowing the starfish to remain in position over their tubes.

Whether these different behavioural responses are related to genotypic, or perhaps phenotypic, variations within the *Spirobranchus giganteus* species complex, with only certain types capable of repelling *Acanthaster* (R. Smith pers. comm.), is currently unknown. Further areas of research include ethology, chemistry and genetic studies of the coral-worm-starfish interaction.

DISCUSSION

It seems likely that those worms which attempt to expose their branchial crowns and opercular hooks upon coverage by *Acanthaster planci* sufficiently irri-

tate the predator to induce the starfish to move away. That irritation of the starfish's tube feet or everted stomach discourages feeding is well documented (Barnes et al. 1970, Glynn 1980). However, the level of response by the starfish may be mediated by its nutritional and physiological state, the amount of food available, and the population densities of predator and worm.

The long term consequence is the continued growth of those polyps protected by *Spirobranchus giganteus* and the survival of the colony. The long term survival of the same colonies is an important strategy in the life histories of these corals. Indeed, one colony has been dated at over 600 yr (Potts et al. 1985). Such large, old colonies, comprising perhaps millions of polyps, are potentially highly fecund, producing large numbers of gametes annually (Kojis & Quinn 1981, Harriott 1983). Further, under certain conditions such old corals may produce new daughter colonies by asexual fragmentation (Highsmith 1980), thereby perpetuating the parent genotype (Potts et al. 1985). Cameron & Endean (1985) have proposed that 'complex coral reef communities are based on (such) long lived corals which persist as individual colonies at specific sites for many years'. Certainly, with regard to predation by *Acanthaster planci*, the survival of these colonies by regrowth is important in the recovery process, allowing eventual restocking of decimated areas (Glynn 1976) with planulae, or by fragmentation. Partial predation by *A. planci* may enhance the latter process by isolating patches of living polyps beneath *S. giganteus* and in crevices etc. During regeneration these polyps may form separate colonies which become increasingly subject to dislodgement from the parent colony during storm events.

The continued upward growth of protected polyps and *Spirobranchus giganteus* would ensure the worms remain in advantageous positions for feeding, above the boundary layers of lower strata benthos (Strathmann et al. 1984). In contrast, when host *Porites* colonies die, settlement by fouling species and growth of the surrounding organisms may tend to block the essential water currents or lead to competitive interactions for space. It seems reasonable that worms living in growing *Porites* colonies may be selectively favoured. Indeed, recruiting *S. giganteus* larvae actively select living *Porites* colonies as settlement sites (Smith 1985). Over evolutionary time, mechanisms which assist the survival of the adjacent polyps may have developed. Bryan (1973) noted that spirorbid worms residing on a *Porites lutea* colony in Guam were not encrusted by the sponge *Terpios* sp., possibly due to their mechanical movements. Considering the above, it appears possible that polyp refuges may similarly evolve in this and other overgrowth interactions.

CONCLUSIONS

Boucher et al. (1982) have considered the wider implications of the evolution of mutualism: 'In cases starting as symbiotic commensalisms, the evolution of mutualism may proceed by the commensal's providing some benefit that would be selected for if it increased the host's chances of survival . . . a change in ecological circumstances or the presence of an ecological opportunity could transform the relationship into a mutualism if the commensal happens to render the host better able to survive or take advantage of the situation'.

Whether polyp protection is a specialized response to *Acanthaster planci* predation or other selective pressures over coevolutionary time, or merely an inadvertent by-product of the *Acanthaster-Spirobranchus* interaction, remains to be seen. That the repellent effect may be limited to certain types within the *Spirobranchus* species complex suggests that predation-induced selection may be currently taking place. If large-scale outbreaks of *A. planci* are a relatively recent phenomenon, then it is conceivable that we may be witnessing the initial stages in the coevolutionary development of this mutualism.

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