Oecologia (Berl.) 47, 340–343 (1980)

Oecologia

Reversal of Digestive Interactions Between Pacific Reef Corals: Mediation by Sweeper Tentacles

Gerard M. Wellington
Marine Science Institute and Department of Biological Sciences, University of California, Santa Barbara, Ca 93106, and
Smithsonian Tropical Research Institute APO Miami, Fl 34002, USA

Summary. Aggressive interactions among reef corals involving direct interference through extracoelenteric digestion has previously been considered as a potential mechanism for the maintenance of high species diversity. In this report I show that induced development of sweeper tentacles can reverse initial digestive interactions. In the eastern Pacific these reversals contribute to resource monopolization by fast growing pocilloporid corals. This suggests that other mechanisms must account for the maintenance of local species diversity.

Reef building corals are often space limited. The occurrence of processes involving exploitative competition (overtopping) and interference competition (aggressive interactions and overgrowth) has been amply demonstrated (Connell 1973, 1976, 1978; Glynn et al. 1972, 1976; Lang 1970, 1973; Maragos 1972; Porter 1974). Aggression, through extracoelenteric digestion, has been described as a purely transitive phenomenon with exceptions to predicted outcomes rare (Connell 1976; Lang 1970, 1973). As such, digestive ability has been emphasized as a counterbalance to rapid growth rate thus providing a potential mechanism for the maintenance of coral species diversity (Lang 1973; Porter 1972). Species with a low linear growth rate yet high digestive ability could prevent or forestall exclusion by a weaker yet faster growing species. I show here that induced development of sweeper tentacles can lead to the reversal of initial outcomes for some digestive interactions. These reversals act to decrease diversity and contribute to eventual resource (space) monopolization by fast growing branching corals on reefs in the eastern Pacific.

In corals, a direct interference mechanism "extracoelenteric digestion", involves the ability of an individual colony to extend digestive mesenterial filaments from the gut and kill the opposing tissues of an adjacent species immediate to the zone of contact. This phenomenon occurs mainly between different species, although some limited conspecific involvement has been reported (Dustan 1975). Digestive interactions do not usually result in death of the entire colony of the subordinate species unless it is quite small (< 3 cm colony diameter; Lang 1970).

Based on short term field and laboratory experiments using interspecific pairs of fifty Caribbean species, Lang (1970, 1973) established a dominance hierarchy: in general, species of the suborder Faviina > Fungiina > Astrocoeniina. This ranking suggests that, with few exceptions, the slower growing massive species are aggressively dominant over the faster growing branching corals. Therefore, the contrasting characteristics of digestive rate could provide a mechanism for the coexistence of coral space competitors.

Coral reefs in the eastern Pacific are composed primarily of species belonging to two genera – *Pocillopora* (Astrocoeniina) and *Pavona* (Fungiina) (Glynn et al. 1972; Glynn 1976; Porter 1974). *Pocillopora spp.* predominate in shallow water (0–6 m depth) and *Pavona* spp. in deep water (6–10 m). Preliminary field observations based on the presence of post-interactive scars (contact sites between intergeneric pairs in which a portion of one colony was killed and encrusted with coralline algae), suggested that *Pocillopora* was dominant over *Pavona* (Glynn et al. 1972; Porter 1974). Observational data collected in this study corroborated these previous findings (see Table 1). In contrast, laboratory experiments clearly demonstrated the superiority of *Pavona* with respect to mesenterial digestion. In these experiments the outcome of digestive interactions were evident within 0.5 h to 12 h after tissue contact (Glynn 1974).

Table 1. Field observations of in-situ coral interactions

Species pairs	Observed outcomes		
	Poc. > *Pav.*	*Poc.* < *Pav.*	*Poc.* = *Pav.*
Pocillopora damicornis vs. *Pavona clavus*	62	5	2
Pocillopora damicornis vs. *Pavona gigantea*	58	14	0
Pocillopora robusta vs. *Pavona clavus*	36	1	0
Pocillopora robusta vs. *Pavona gigantea*	47	8	0

Outcomes of coral-coral interactions presented are from random field observations on reefs surrounding Isla Contadora [Archipiélago de las Perlas], República de Panamá. The direction of dominance is indicated as *Pocillopora* (*Poc.*) > dominant over *Pavona* (*Pav.*) or, *Pocillopora* < subordinate to *Pavona*. These were designated as such when one species apparently had caused tissue damage to the other as evidenced by the presence of exposed skeleton and/or an algal encrustation. Equal (=) means that both species have sustained damage and indicates an intermediate reversal stage. These data indicate that branching corals (*Pocillopora spp.*) are dominant over massive species (*Pavona spp.*) under natural conditions

0029-8549/80/0047/0340/$01.00

Table 2. Coral interaction experiment

Treatment		Shallow sites (3 replicates/Treat.)			Deep sites (6 replicates/Treat.)		
	after:	2 days	60 days	270 days	2 days	60 days	150 days
Pocillopora damicornis	Po < Pa	2*	0	0	4^a	0	0
vs.	Po > Pa	0	3	3	0	5^b	5^c
Pavona clavus	% reversals	–	100	100	–	100	100
Pocillopora damicornis	Po < Pa	3	1	1	4^a	2^b	1
vs.	Po > Pa	0	2	2	0	3	5
Pavona gigantea	% reversals	–	67	67	–	60	83
Pocillopora robusta	Po < Pa	3	0	0	4^a	2	2
vs.	Po > Pa	0	3	3	0	4	4
Pavona clavus	% reversals	–	100	100	–	67	67
Pocillopora robusta	Po < Pa	3	2	0	5^b	2	2
vs.	Po > Pa	0	1	3	0	4	4
Pavona gigantea	% reversals	–	33	100	–	67	67
Congeneric pairs and Conspecific pairs			no reaction			no reaction	
Summary of pooled data	Po < Pa	11	3	1	17	6	5
	Po > Pa	0	9	11	0	16	18
	% reversals	–	75	92	–	73	78

These results show changes in direction of dominance between same individual pairs through time. Po means *Pocillopora*, Pa means *Pavona*. Criteria for determining direction of dominance are the same as described in Table 1. *-one replicate with no reaction; a-two replicates with no reaction; b-one replicate with no reaction (for a and b see text for explanation of delayed interaction); c-sponge infection killed *Pocillopora damicornis* in replicate no. 3

To test the hypothesis that the vertical zonation pattern among corals in the eastern Pacific result from differential changes in digestive ability along a depth gradient, I established 3–6 replicates of each possible combination (6) between interspecific pairs of four coral species – *Pocillopora damicornis* Linnaeus, *Pocillopora robusta* Verrill, *Pavona clavus* Dana, and *Pavona gigantea* Verrill in shallow (−1.0 m MLLW) and deep sites (−10.0 m MLLW). These experiments were conducted over a nine month period on the southwestern fringing reef at Isla Contadora (Archipiélago de las Perlas) in the Gulf of Panamá. Shallow water experiments were initiated on 9/XII/78 and those in deep water on 4/IV/79.

The results (Table 2) illustrated that initial outcomes followed the hierarchy previously proposed; *Pavona* extended its mesenterial filaments and killed the opposing tissues of *Pocillopora*. However, in the majority of cases reversals in dominance appeared within 7–60 days. These reversals were associated with the modification of certain feeding tentacles into elongated sweeper tentacles tipped with enlarged acrospheres. Feeding tentacles are 1–2 mm in length while sweeper tentacles reach up to 30 mm in length. Sweeper tentacles were restricted to polyps on branches immediately adjacent to the region of contact between coral colonies (Fig. 1c). Concomitant with these morphological changes, the cnidom showed a marked increase in the nematocyst (principally basitrichous isorhizas; see Mariscal, 1974): spirocyst ratio. Prior to transformation this ratio was 1:4 ($n = 12$ tentacles), after the elongation of sweeper tentacles the ratio shifted to 1:0.2 ($n = 12$ tentacles). These induced changes in tentacle form suggest a switch from food capture to one of defense and/or aggression (den Hartog 1977).

These events followed a predictable sequence. Within 2 days after initial contact, *Pavona* extended its mesenterial filaments and destroyed tissues of *Pocillopora*, exposing a portion of the skeleton (Fig. 1a). The *Pavona* mesenterial filaments were then retracted and algae quickly invaded and became established on the dead areas of *Pocillopora*. From one to two months later, as tissue regenerated over the dead skeletal portions, sweeper tentacles developed on the peripheral branches of *Pocillopora*. The extended sweeper tentacles moved passively in the surge and frequently made contact with the adjacent *Pavona* colony. These contacts resulted in the necrosis and sloughing of the *Pavona* tissues. The exposed skeleton was then rapidly invaded by filamentous algae and later an encrustation of coralline algae (Fig. 1b). Once the coralline algae became established it acted as a buffer zone between the two corals. The sweeper tentacles of *Pocillopora* then retracted and reverted to their pre-encounter size and feeding function. This sequence was repeated at a later date if subsequent growth by either coral species resulted in renewed tissue contact. Eventually, however, *Pavona* was usually overtopped by *Pocillopora* due to the more rapid linear growth rate of the latter [~5 cm vs. 1.5 to 2.0 cm/yr for *Pavona* (Maguire and Porter 1977; Glynn and Stewart 1973; Wellington unpubl. data)]. In this sequence it is unclear why *Pavona* does not retaliate by extending its mesenterial filaments in response to sweeper tentacle attack; unless, perhaps, these tentacles are more powerful than the mesenterial filaments of *Pavona*.

Time to digestive reversal appeared to be directly related to the degree of initial damage sustained by *Pocillopora* from the mesenterial filaments of *Pavona*. In some cases, extensive tissue sloughing (up to 4 cm) distal to the contract point may have resulted from secondary bacterial infections of the injured *Pocillopora* tissues. Recovery and reversal under these conditions proceed quite slowly, requiring at least several months and account for some of the non-reversals evident after the 150–270 day observation periods in Table 2. In the experiments at the shallow site all replicates were placed in direct skeletal contact. However, 12 of the 24 replicates (3 of 6 replicates/treatment) at the deep site were placed 1–2 mm apart (polyp contact only). In these replicates

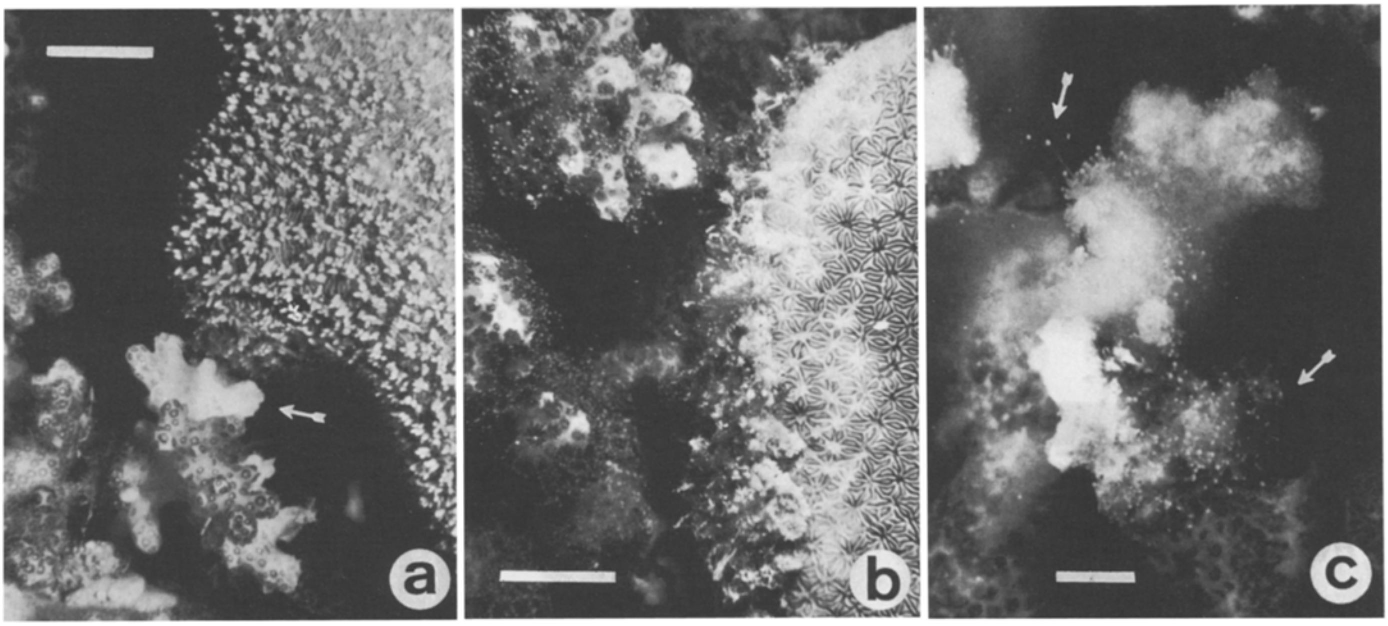

Fig. 1. Experimental corals show result of initial digestive interaction (**a**) between *Pocillopora damicornis (left)* and *Pavona gigantea (right)* after 24 h. Arrow indicates contact zone where *Pocillopora* tissues have begun to slough exposing white skeleton. Reversal of an interaction (**b**) after 60 days; *Pavona* colony opposite *Pocillopora* is encrusted with algae and recent tissue damage appears as whitened patches on surface of corallum. (**c**) close-up of semi-retracted sweeper tentacles are indicated by arrows. Scale bars in (**a**) to (**c**) represent 10,10 and 5 mm respectively

extracoelenteric digestion did not occur until 7–8 days after contact. Skeletal separation apparently postponed time to interaction.

Sweeper tentacle development has been described for several coral species and was originally considered to be a structural adaptation for food capture (Price 1973; Lewis and Price 1975). It has been pointed out, however, that resultant changes in the cnidom of sweeper tentacles resembled those found in the catch tentacles, acrorhagi and marginal tentacles of the Actiniaria (den Hartog 1977). These analogous organs are known, or at least suspected, to be used in both aggressive and defensive interaction (Purcell 1977; Williams 1975; Francis 1973).

The first field evidence that sweeper tentacles function as defensive organs has recently been reported by Richardson et al. (1979). Their observations suggest that the sweeper tentacles of the coral *Montastrea cavernosa* act to fend off encroachment by *Montastrea annularis* – a faster growing, digestively superior species. Richardson et al. suggest that this defensive response contributes to the maintenance of living space for *M. cavernosa*. The reversal mechanism described in this paper, however, ultimately facilitates the competitive dominance of rapid growing branching species (*Pocillopora spp.*) over the slow growing massive corals (*Pavona spp.*). That this is possibly a widespread phenomenon is further suggested by the recent work of Sheppard (1979) in the Indian Ocean. Based on static observations of naturally occurring interactions (similar to those presented in Table 1) he suggests that the ability of a coral to cause tissue damage to another is not associated with particular taxonomic groups or corallum morphology but is often correlated with species abundance within a given depth zone. Sheppard's conclusions corroborate, at least in part, the findings of this report and do not support the linear dominance model of extracoelenteric digestion proposed for the Caribbean. If sweeper tentacles defense is a common mechanism employed by rapidly growing corals, then initial digestive interactions merely delay ultimately sucessful dominance interactions and cannot account for the persistence of slow growing species in coral communities. Rather, mechanisms such as intermediate disturbance or compensatory mortality are probably of greater importance to the maintenance of local coral diversity of reefs (Connell 1978).

Acknowledgements. This research was supported by a Smithsonian Predoctoral Fellowship from the Smithsonian Tropical Research Institute and the Marine Science Institute, University of California, Santa Barbara. I thank A. Hooten, R. Rowley and M. Stouder for their able assistance in the field and L. Buss, P. Glynn, C. Hand, J. Lang, A. Sih, R. Trench, R. Warner and particularly A. Kuris for their valuable comments and suggestions on the manuscript.

References

Connell JH (1973) Population ecology of reef-building corals. In: OA Jones and R Endean (eds), Biology and Geology of coral reefs, Vol. 2. Academic Press, New York-London, p 205–245

Connell JH (1976) Competitive interactions and the species diversity of corals. In: GO Mackie (ed), Coelenterate Ecology and Behavior. Plenum: New York, p 51–58

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science, 199:1302–1310

den Hartog JC (1977) The marginal tentacles of *Rhodactis sanctithomae* (Corallimorpharia) and the sweeper tentacles of *Montastrea cavernosa* (Scleractinia) their cnidom and possible function. *In:* Proc Third Int Coral Reef Sym, Univ of Miami, Florida, p 463–469

Dustan P (1975) Genecological differentiation in the reef-building coral *Montastrea annularis*. PhD Thesis, State University of New York, Stonybrook

Francis L (1973) Clone specific segregation in the sea anemone *Anthopleura elegantissima*. Biol Bull 144:64–72

Glynn PW (1974) Rolling stones among the Scleractinia: mobile corallith communities in the Gulf of Panama. In: Proc Second Int Coral Reef Sym, Vol 2. Gt Barrier Reef Comm, Brisbane, Australia, p 183–198

Glynn PW (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol Monogr 46:431–456

Glynn PW, Stewart RH, McCosker JE (1972) Pacific coral reefs in Panama: structure, distribution and predators. Geol Rdsch, 61:483–519

Glynn PW, Steward RH (1973) Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol Oceanogr, 18:367–379

Lang JC (1970) Inter-specific aggression within the Scleractinian reef corals. PhD Thesis, Yale University New Haven

Lang JC (1973) Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. Bull Mar Sci 23:260–279

Lewis JR, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. J Zool (London) 176:527–545

Maguire LA, Porter JW (1977) A spatial model of growth and competition strategies in coral communities. Ecol Modelling 3:249–271

Maragos JE (1972) A study of the ecology of Hawaiian reef coral. PhD Thesis, University of Hawaii Honolulu

Mariscal RN (1974) Nematocysts. In: L Muscatine and HM Lenoff (eds), Coelenterate Biology. Academic Press: New York-London, p 129–178

Porter JW (1972) Patterns of species diversity in Caribbean reef corals. Ecology 53:744–748

Porter JW (1974) Community structure of coral reefs on opposite sides of the Isthmus of Panama. Science 186:543–545

Price WS (1973) Aspects of feeding behavior of West Indian reef corals. M Sc Thesis McGill University Montreal

Purcell JE (1977) Aggressive function and induced development of catch tentacles in the sea anemone, *Metridium senile* (Coelenterata, Actiniaria). Biol Bull 153:335–368

Richardson CA, Dustan P, Lang JC (1979) Maintenance of living space by sweeper tentacles of *Montastrea cavernosa,* a Caribbean reef coral. Mar Biol 55:181–186

Sheppart CRC (1979) Interspecific aggression between reef corals with reference to their distribution. Mar Ecol Prog Ser 1:237–247

Williams RB (1975) Catch-tentacles in sea anemones: occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. J Nat Hist 9:241–248

Received July 7, 1980