

**THE CONSEQUENCES OF DIRECT COMPETITION BETWEEN
SCLERACTINIAN REEF CORALS: DEVELOPMENT AND USE OF
SWEEPER TENTACLES**

by

Elizabeth Ann Chornesky, A.B.

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Elizabeth Ann Chornesky, A.B.

DISSERTATION

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

THE UNIVERSITY OF TEXAS AT AUSTIN

August, 1984

THE CONSEQUENCES OF DIRECT COMPETITION BETWEEN SCLERACTINIAN REEF
CORALS: DEVELOPMENT AND USE OF SWEEPER TENTACLES

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ACKNOWLEDGEMENTS

Many people and institutions contributed to the completion of this work. I am grateful to them all.

Judy Lang taught me about corals and also much about being human. I have appreciated her consistent generosity and patience, and benefited greatly from her stimulating intellect and willingness to consider new ideas. My association with Charlie Wahle during the past three years brought new rigor to my thinking and approach, and I will continue to value his critical insight, in addition to his humor and love. Throughout, Larry Gilbert generously provided his support and advice, and showed an unusual willingness to think about a different world. I was propelled into graduate school by William McFarland, who has remained an interested and supportive friend for the duration.

Over the past six years, many other friends provided essential feedback on my work, assistance, and companionship in the field, including: Carlos Brunet, Ivan Gill, Diane Marshall, Joe Neigel, Bruce Nyden, Michael Pearson, Esther Peters, Mike Robblee, Christine Rooney, Tom Schultz, Liz Sides, Cherie Van Zant, Susan Williams, and Carole Wolin. Countless people assisted with my field work; I am especially grateful to Susan Williams who enthusiastically gathered much of the data for Chapter two, and to Raechelle Ramsay and John Gordy who participated in my research at their own expense. Portions of this dissertation were improved by

the comments of: Judy Lang, Charlie Wahle, Carlos Brunet, Eric Pianka, Beryl Simpson, and Jerry Wellington.

The Discovery Bay Marine Laboratory, the West Indies Laboratory, and the Hydrolab (St. Croix) furnished facilities for my field research. Ted Delevoryas, Joanne Rhodes, and the staff of the Division of Biological Sciences gave essential assistance back at the University of Texas.

This work would not have been possible without financial support from the National Science Foundation, the National Oceanographic and Atmospheric Administration, the Houston Underwater Society, the Lerner-Gray Fund of the American Museum of Natural History, Sigma Xi, the Division of Biological Sciences and the Office of Graduate Studies at the University of Texas.

Finally, my parents, George and Mary Chornesky, provided moral and financial support whenever needed. I have taken great joy in opening this one small part of the world to them as I myself explored it.

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CORALS: DEVELOPMENT AND USE OF SWEEPER TENTACLES

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The University of Texas at Austin, 1984

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ABSTRACT

On crowded reefs, unoccupied substrate space is often rare, and many scleractinian corals compete directly for limited living space by damaging neighboring corals.

Under both natural and experimental conditions, the Caribbean coral Agaricia agaricites (L.) develops elongate sweeper tentacles specifically in response to direct competition. Sweeper development occurs approximately thirty days after contact with competitors, regardless of whether or not such contact involves damage to A. agaricites. These specialized tentacles are localized exclusively on tissues surrounding the contact zone, and can damage tissues of opponents within their reach. A range of potential

competitors, including various corals, a gorgonian , and a zooanthid induce sweeper development; the necessary stimulus appears to be recognition of opponent tissues. Sweeper tentacles may regress when stimulation ceases, and in nature they are found only on margins of A. agaricites colonies adjacent to other sessile animals.

In contrast, Montastraea cavernosa (L.) frequently has sweeper tentacles distributed over colonies in patterns which do not correspond to ongoing competitive encounters. Nevertheless, damage by opponents stimulates an increase both in the number of polyps with sweeper tentacles and in the number of sweepers per polyp close to the encounter. Since sweeper tentacles on this species do not necessarily regress, their distribution may reflect at least a temporary historical record of past encounters.

The delayed development and potential regression of sweeper tentacles, coupled with the use of other competitive mechanisms, creates the potential for considerable variation in the outcome of ongoing competitive interactions. Repeated observation of natural encounters between A. agaricites and other corals, showed that the apparent winner can switch repeatedly as competitive interactions progress. Neither opponent ultimately wins these dynamic "stalemates," and consequently such encounters may have little direct effect on the structure of reef communities.

Spatial resources may vary in importance to opposing competitors, as may the costs in fitness incurred during the loss

and/or gain of space. Thus, observable patterns of dominance provide only limited information which, without quantifying the costs and rewards of competing, are insufficient to evaluate accurately the relative effects of direct competition on participants.

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GENERAL INTRODUCTION

Modern tropical reefs support a diverse sessile fauna which is typically dominated by scleractinian corals (e.g., Porter, 1972, 1974; Glynn, 1973; Lang, 1973; Jackson, 1977). These animals create reef structures by depositing a stony skeleton as they grow, and occupy much of the surface area thus produced (Dana, 1872; Goreau, 1959). Morphological variation is common among corals, both within and between species (e.g., Porter, 1974, 1976; Foster, 1979; Jackson, 1979a; see also species descriptions in Wells, 1973). Some grow in tree-like or upright shapes, while the growth of others is restricted more to low-lying or recumbent forms, sometimes encrusting over reef surfaces. For the latter group, which includes members of most common Western Atlantic families, colony size is often limited by the availability of unoccupied substrate space or by the encroachment of neighboring organisms (Fig. 1 and Fig. 2).

Because colonial corals are assumed to have indeterminate growth, an increase in colony size potentially leads to an increase in the total number of reproductive polyps (Connell, 1973; Jackson, 1977). Similarly, with increasing size, the probability of whole colony mortality decreases, as does the severity of injury when it occurs (Connell, 1973; Loya, 1976; Hughes and Jackson, 1980, in press; Woodley et al., 1981; Chornesky, unpub. data). Hence, for many corals both survivorship and fecundity should be positively

Figure 1. Colonies of Agaricia agaricites growing on the exposed skeleton of a colony of Montastraea cavernosa and in close proximity to live tissues of the M. cavernosa.



Figure 2. Colonies of Agaricia agaricites, Madracis decactis, and Porites astreoides growing under crowded conditions.



associated with large size.

It is not surprising then that scleractinian corals have evolved mechanisms to compete directly with neighboring animals for space on which to live and grow (for recent review see: Sheppard, 1982). These include the eversion of digestive filaments (e.g., Lang, 1973; Sheppard, 1979) and the development and use of sweeper tentacles (Richardson et al., 1979; Wellington, 1980; Bak et al., 1982; Chornesky, 1983, Chornesky and Williams, 1983). Other potential competitive mechanisms have been suggested, but their role and generality remain to be demonstrated. These include: the use of sweeper polyps (Sheppard, 1982); immune responses (Hildeman et al., 1975; Potts, 1977; Johnston et al., 1981); and the release of cytotoxins (Johnston et al., 1981) or pheromones (Rinkevich and Loya, 1983). Most of these function by destroying adjacent tissues on neighboring corals, and may thus deter overgrowth and/or clear space as a precursor for lateral growth.

Competition for two dimensional space between corals growing along reef surfaces involves a relatively simple and easily quantified resource. In other sessile communities, analyses of competition are often complicated by the association of space with other resources such as nutrients, water, or light, or with pronounced environmental gradients (e.g., Dayton, 1971; Harper, 1977; Jackson and Winston, 1982; Peterson, 1982). Despite this conceptual simplicity, assessing the effects of competition between reef corals is difficult because their potential longevity (e.g.,

Dana, 1872; Connell, 1973) and slow recruitment (Bak and Engel, 1979; Rylaarsdam, 1983) preclude experimental manipulations of density (sensu Gause, 1934; Connell, 1961, 1975; Pianka, 1975). The effects of competition on the structure of coral communities must therefore be interpreted from observations of processes occurring over a relatively short time interval. The accuracy of this approach clearly rests on an understanding of how such processes operate under natural conditions and over an extended period of time.

This study focuses on the mechanisms and long-term consequences of direct competition for the abundant (Goreau, 1959) Caribbean reef coral Agaricia agaricites (Linnaeus). The variability of this species both in gross morphology and in a suite of other phenotypic traits suggests that it is a complex of two (van Moorsel, 1983) or more (Chornesky, unpublished data) species. For the purposes of this study I chose to examine only A. agaricites f. purpurea and f. carinata (after Wells, 1973) and where appropriate specify which form was used. I did not discriminate among phenotypes within each form. Each of the five formae of A. agaricites (Wells, 1973) is common, and, given its historical attribution as a poor direct competitor (Lang, 1973), the general ubiquity of A. agaricites has been ascribed to frequent sexual reproduction and rapid growth (Bak and Engel, 1979).

Chapter 1 describes the development and use of specialized competitive structures (sweeper tentacles) by A. agaricites both in

nature and under experimental conditions. Chapter 2 demonstrates that sweeper tentacles appear in a similar manner on the reef coral Montastraea cavernosa (Linnaeus), which differs from A. agaricites in many important life history traits. I examine the long-term consequences of direct competitive interactions involving A. agaricites in Chapter 3, and in Chapter 4 explore the theoretical implications of these and other findings for evaluating and measuring the effects of direct competition between sessile animals.

CHAPTER ONE

INDUCED DEVELOPMENT OF SWEEPER TENTACLES ON AGARICIA AGARICITES: A RESPONSE TO DIRECT COMPETITION

ABSTRACT

The scleractinian coral Agaricia agaricites often has elongate sweeper tentacles on colony margins close to other sessile animals. Sweeper tentacles can damage tissues of opponents and are probably used in direct competition for substrate space. Furthermore, contact with tissues or mesenterial filaments of other corals, or with tissues of the gorgonian Erythropodium caribaeorum or the zooanthid Palythoa caribbea can stimulate the development of sweeper tentacles by A. agaricites. Depending on both the particular competitor species involved, and the distance separating it from A. agaricites, events leading to the development of sweeper tentacles may or may not include tissue loss by A. agaricites. On average the development of sweeper tentacles takes thirty days, and is localized exclusively on tissues close to the region in contact with competitors. Sweeper tentacles do not develop in response to artificial stimuli simulating tactile contact or damage such as occur in natural interactions with other corals. Thus, recognition of competitor tissues appears to be a necessary stimulus for sweeper formation.

INTRODUCTION

Sessile colonial animals, particularly scleractinian corals, crowd many tropical reefs where space for growth often becomes limited (e.g., Porter, 1972, 1974; Glynn, 1973; Connell, 1976, 1978; Sheppard, 1979, 1982). Although upright or branching corals may partially escape this problem by growing up and over adjacent animals (Porter, 1974; Connell, 1976; Glynn, 1976; Jackson, 1979; Wellington, 1980), many corals growing along reef surfaces frequently encounter other sessile animals. Thus, competition for substrate space is considered one of the processes structuring coral reef communities and selecting for life history characteristics and other attributes of sessile reef inhabitants (Connell, 1973, 1976; Glynn, 1973; Lang, 1973; Porter, 1974, 1976; Jackson, 1977, 1979; Potts, 1977; Bak and Engel, 1979; Sheppard, 1982).

When stony corals grow close together, they often directly damage one another by using mesenterial filaments or sweeper tentacles (Lang, 1971, 1973; Richardson et al., 1979; Sheppard, 1979; Wellington, 1980; Bak et al., 1982). If corals of different species are placed in direct contact, many can extend their mesenterial filaments within hours and use them to digest away tissues on the opposing coral (Lang, 1971, 1973; Glynn, 1976; Sheppard, 1979). The consequences of such interactions are generally predictable; certain "digestively dominant" species, particularly of the suborder Faviina, are consistently able to use mesenterial filaments to damage others (Lang, 1973; Sheppard,

1979). The additional use of sweeper tentacles in natural interactions by some corals, however, may alter the long term outcomes of these otherwise predictable encounters (Richardson et al., 1979; Wellington, 1980; Bak et al., 1982; Sheppard, 1982). Sweeper tentacles are longer than normal (Lewis and Price, 1975; Bak and Elgershuizen, 1976) and armed with specialized cnidae (den Hartog, 1977; Wellington, 1980). When expanded, these tentacles increase the volume within reach of live coral tissues and may deter other corals from growing too closely (Richardson et al., 1979) or may actively damage competitor tissues (Wellington, 1980; Bak et al., 1982).

All coral polyps have mesenterial filaments. In contrast, the distribution of sweeper tentacles is erratic, and the determinants of their presence are poorly understood. For species which can form sweeper tentacles, neither every colony in a population, nor every polyp on a colony necessarily possesses sweepers. On Montastraea cavernosa, these tentacles, which are present on most colonies, are thought to extend in response to water currents and are most abundant around colony perimeters (Price, 1973 in den Hartog, 1977; den Hartog, 1977; Richardson et al., 1979). On Pocillopora sp. (Wellington, 1980) and Madracis mirabilis (Duchassaing and Michelotti) (Bak et al., 1982) sweepers develop on polyps next to wounds caused by the mesenterial filaments of adjacent corals.

Since the stimulus for sweeper development determines their location on a colony, it will also determine whether or not they are used in competitive interactions. Thus, the consequences of direct encounters involving corals depend not only on the relative effects of mesenterial filaments and sweeper tentacles, but also on the factors which initiate sweeper formation. Many of the responses of other cnidarians to direct competition are thought to be stimulated by contact and recognition of opponent tissues (Theodor, 1970; Ivker, 1972; Francis, 1973; Purcell, 1977; Ottaway, 1978; Brace et al., 1979; Bigger, 1980; Watson and Mariscal, 1983).

This chapter explores the conditions under which sweeper tentacles form on the Caribbean reef coral Agaricia agaricites. This species has short mesenterial filaments which extend only a few mm away from the corallum (Bak et al., 1982), and can use them to digest only a few other species of coral (Lang, 1973). Polyps of A. agaricites are flat and normally have short tentacles (approximately two mm long, Lewis and Price, 1975). In contrast, sweeper tentacles on A. agaricites may be over a cm in length (Bak and Elgershuizen, 1976; personal observations; Fig. 1A). The occurrence of these special tentacles only on portions of colonies of A. agaricites adjacent to other species of sessile animals (personal observations) suggests strongly that they develop specifically in response to direct competitive interactions.

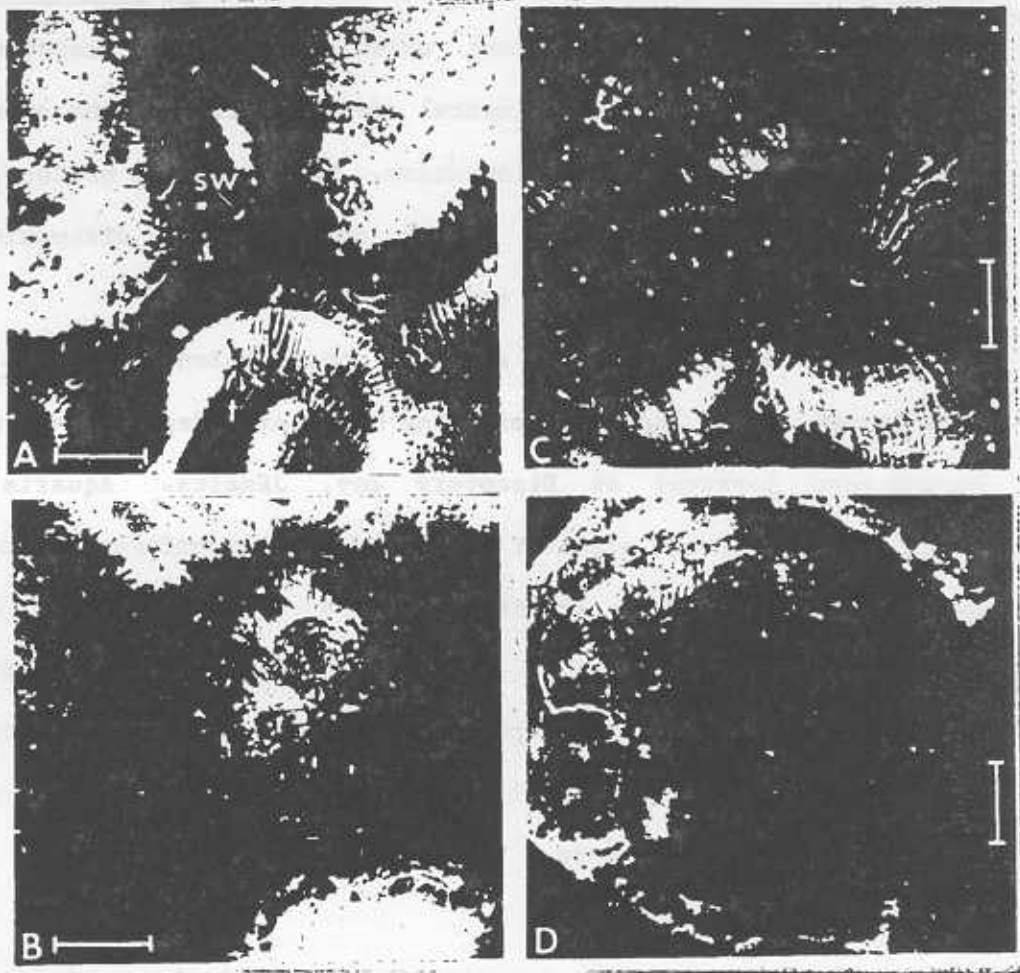
Here I examine the potential function of sweeper tentacles on A. agaricites and the stimulus for their development.

Figure 1. Coral polyps expanded at night. Corals are: A) Agaricia agaricites, B) Madracis decactis, C) Montastraea cavernosa, and D) Montastraea annularis. Arrows indicate sweeper tentacles (sw) and regular tentacles (t), and scale bars equal approximately 5 mm. In (A) compare length of regular and sweeper tentacles on A. agaricites, here shown next to a damaged colony of Madracis decactis. Photographs were taken in situ using a Nikonas camera, one to two framer, extension tube, and strobe.

EXPERIMENTAL PROCEDURES AND RESULTS

This study has two components: (1) determination of the

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GENERAL MATERIALS AND METHODS

This study has two components: i) determination of the potential function of sweeper tentacles on A. agaricites and observation of their development under natural and experimental conditions; and ii) experimental determination of the nature of stimuli which induce sweeper formation. The specific protocol and results for each section follow this general discussion of information pertaining to the entire study.

All collections of animals, observations, and in situ experiments were accomplished using SCUBA at a depth of -10 meters on the west forereef at Discovery Bay, Jamaica. Aquaria with running, unfiltered seawater for laboratory experiments concerning sweeper function were provided by the Discovery Bay Marine Laboratory of the University of the West Indies. Since the sweeper tentacles of A. agaricites expand maximally at night (Chornesky, unpub. data), all behavioral observations were made after sunset between 2000 and 2400 hours. This study took place between March 1981 and September 1982.

Observations and experiments involved A. agaricites and various sessile animals spanning a range of competitive strategies and including four corals, a zooanthid and a gorgonian (Table I). Among the stony corals used, A. agaricites can digest two species (Madracis decactis (Lyman) and Porites astreoides Lesueur) and can be digested by the two other species (Montastraea annularis (Ellis and Solander) and Montastraea cavernosa) (Lang, 1973). Within each

Table I. Characteristics of competitor species used in observations and experiments. Abbreviations for species names are: A.a. = Agaricia agaricites, P.a. = Porites astreoides, M.d. = Madracis decactis, M.a. = Montastraea annularis, M.c. = Montastraea cavernosa, P.c. = Palythoa caribea, E.c. = Erythropodium caribeorum.

TABLE I

ORDER: SPECIES:	Scleractinia				Zooanthidae	Gorgonaceae
	PA	MD	MA	MC	PC	EC
Aa can digest	+	+	-	-	--	--
Can digest Aa	-	-	+	+	--	--
May have sweepers	-	+	-	+	--	--
Other	--	--	--	--	cytotoxins? overgrowth	overgrowth
Length polyps	med	long	short	long	med	long
Length tentacles	short	long	short	long	short	long

pair of digestively dominant or subordinate corals, one can sometimes possess sweeper tentacles (Madracis decactis, personal observations; M. cavernosa, Lewis and Price 1975) while the other does not (P. astreoides and M. annularis) (Table I). The zooanthid Palythoa caribbea Duchassaing and the gorgonian Erythropodium caribaeorum Duchassaing and Michelotti sometimes overgrow A. agaricites (Karlson, 1980). P. caribbea contains secondary chemicals which might be used against competing animals (Cieresko and Karns, 1973).

Unless stated otherwise, all colonies of A. agaricites and Madracis decactis used in these experiments lacked sweeper tentacles prior to treatment. Colonies of A. agaricites used were of the formae A. agaricites f. purpurea or A. agaricites f. carinata as described by Wells (1973).

A. FUNCTION AND DEVELOPMENT OF SWEEPER TENTACLES ON A. AGARICITES

MATERIALS AND METHODS

1) Function

Lewis and Price (1975) originally described the sweeper tentacles of A. agaricites as appendages for feeding. Nevertheless, in hundreds of separate observations I have never seen A. agaricites use sweepers to capture visible particulate food, although specifically searching for this behavior. This failure to observe feeding, combined with my consistent observations that sweeper tentacles on A. agaricites only occur on colony margins close to

other animals, implied that on this species sweeper tentacles might play a role in competitive interactions.

Experiments were conducted in seawater aquaria to determine the potential function of sweeper tentacles on A. agaricites in spatial competition. Colonies of A. agaricites already possessing sweeper tentacles, along with colonies of several competitor species, were collected on the forereef and transferred to the aquaria. The A. agaricites were then observed on several nights after expansion. After determining the location of sweepers on these colonies, during the day colonies of Madracis decactis (n=5), P. astreoides (n=7), and M. annularis (n=8) were placed within "sweeper length" of the A. agaricites. These artificially arranged interactions were then observed on several (3 to 5) nights for the behavior and condition of both corals in each pair. Opponent species used in these experiments were selected because they all seem to maintain normal behavior and health in a running seawater system.

2) Development: Natural Interactions

To determine the frequency with which sweeper tentacles occur on portions of A. agaricites involved in competitive interactions, I labeled a series of natural encounters where colonies of A. agaricites were already within one cm of competitors. These interactions were visited repeatedly at night and scored for the presence or absence of sweeper tentacles on the A. agaricites. Interactions observed were with: P. astreoides (n=28),

Madracis decactis (n=17), M. annularis (n=15), P. caribbea (n=14), and E. caribaeorum (n=9).

To examine, moreover, whether sweeper tentacles develop over time as competitive interactions progress, the labeled encounters between A. agaricites and P. astreoides, Madracis decactis, and M. annularis were subsequently scored for the presence or absence of sweeper tentacles during four observation periods throughout the following ten months.

Within each observation period, labeled interactions were visited on at least three nights to minimize the chance that sweepers were contracted due to incidental activity of other nocturnally active animals or other unpredictable events.

3) Development: Experimentally Induced

The following experiments tested whether sweeper tentacles form specifically as a consequence of contact between A. agaricites and adjacent animals. Encounters among reef corals generally result from gradual growth, and the first contact between neighboring animals may often involve intermittently expanded tentacles and polyps. Such intermittent contact may stimulate a different response from that of close tissue and skeletal contact which presumably occur in natural encounters as the animals grow closer and any interaction proceeds (c.f., Lang, 1973; Potts, 1977; Sheppard, 1979; Wellington, 1980; Johnston et al., 1981; Bak et al., 1982). Two kinds of experiments were conducted in situ in which: 1) animals were placed in very close tissue and skeletal

contact; and 2) animals were fixed a small and consistent distance apart, simulating initial interactions resulting from gradual growth.

Close contact

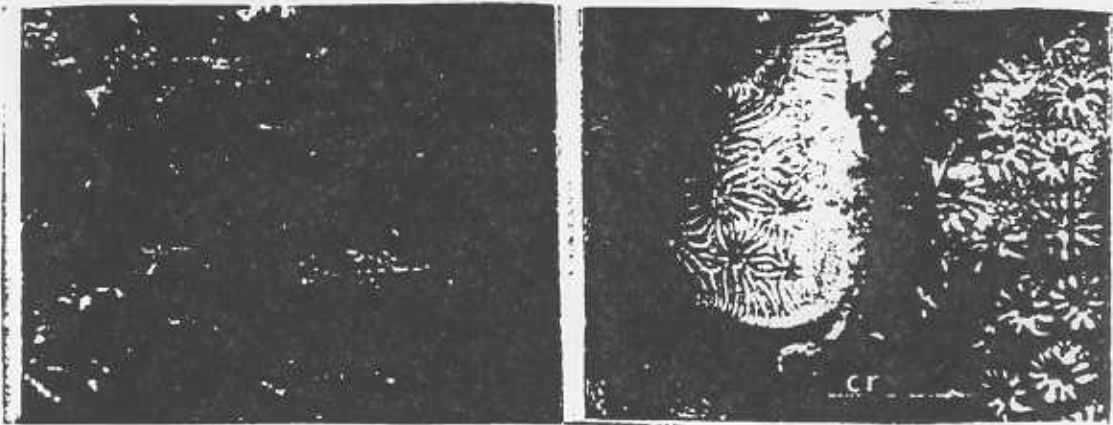
Colonies of A. agaricites were dislodged using a chisel and placed in direct contact with the corals P. astreoides (n=6), Madracis decactis (n=5), and M. annularis (n=11), the zooanthid P. caribbea (n=5), and the encrusting gorgonian E. caribaeorum (n=6). Paired colonies touched even when both polyps and tissues were contracted, ensuring constant contact independent of patterns of tissue and tentacle expansion. Presence of sweeper tentacles on A. agaricites was assessed nocturnally at weekly intervals for a period of up to fifty days.

Controlled distance

To simulate more accurately the initial contact between competitors as it occurs in natural interactions, colonies of A. agaricites were cemented by basal portions of bare skeleton onto cinder blocks (Fig. 2A) or onto stationary asbestos tiles at a small distance from colonies of M. cavernosa (n=10), Madracis decactis (n=18), and M. annularis (n=34). The underwater epoxy-putty used to fix corals in place was never in contact with live coral tissues and appears to be non-toxic (Birkeland, 1976). Specimens of Madracis decactis and M. cavernosa (both of which have long polyps and tentacles; Figs. 1B, 1C, Table 1) were positioned so that

Figure 2. A) Corals cemented onto cinder blocks in controlled distance experiments. B) Photograph taken at night of a small crab (cr) in the crevice formed between colonies of A. agaricites and M. annularis in controlled distance experiments. Scale bar is equal to approximately 5 mm.

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contact occurred only between tentacle tips of these species and tissues of the A. agaricites when corals were fully expanded at night. Approximate distances between contracted corals were 3 mm with Madracis decactis and 2 cm with M. cavernosa. Colonies of A. agaricites next to M. annularis (which has short polyps and tentacles; Fig. 1D, Table I) were positioned so that their polyps were separated by a 1-2 mm gap even when both animals were fully expanded at night (distance between contracted corals of 2-3 mm). In four of these interactions, tissues of A. agaricites and M. annularis were in contact when expanded because colonies slipped into closer proximity before the epoxy-putty hardened. Interactions were observed frequently during the day and a minimum of once a week at night for a period of eighty days.

RESULTS

1) Function

Under laboratory conditions, without exception, tissues of competitor corals placed close to the sweeper tentacles of A. agaricites were damaged. The behavior of sweeper tentacles is similar to that of the catch tentacles of anemones (Purcell, 1977). Extended sweepers brush against and sometimes adhere to opponents, creating patches of sloughing necrotic tissues within their reach. Such lesions are easily distinguished from the regions of clean bare skeleton resulting from digestion by mesenterial filaments.

2) Development: Natural interactions

In natural interactions, sweeper tentacles were initially present on between forty-seven and fifty-seven percent of A. agaricites colonies, depending on the competitor species (Table IIA). In contrast to these initial frequencies, the cumulative frequency of colonies having sweepers sometime during the ten months was between sixty-five and eighty percent. This suggests that proximity to other corals stimulates the development of sweeper tentacles on colonies of A. agaricites and therefore the duration of observations may greatly influence the interpretation of the frequency of sweeper occurrence in natural interactions. If the presence of sweeper tentacles on these corals is compared between successive observations (Table III), it is clear that colonies both lost and gained sweepers over the ten months, sometimes repeatedly. This suggests that sweeper tentacles on A. agaricites may sometimes regress.

3) Development: Experimental Induction

Close contact

Sweeper tentacles developed on A. agaricites in response to close contact with all opponent species (Table IIB). Their development was restricted to tissues within approximately 5 mm of the competitor. The sequence of events varied with opponent species. For example, on colonies next to Madracis decactis and P. astreoides, sweepers developed after the digestive filaments of

Table II. Development of sweeper tentacles on Agaricia agaricites in natural (A) and experimental (B, C) interactions. Abbreviations used in table are: sw = sweeper tentacles, P.a. = Porites astreoides, M.d. = Madracis decactis, M.a. = Montastraea annularis, M.c. = Montastraea cavernosa, P.c. = Palythoa caribbea, E.c. = Erythropodium caribeorum.

TABLE II

COMPETITOR	A. Natural Interactions			B. Direct Contact		C. Controlled Distance	
	N	% Colonies With Sw		N	% Develop Sw	N	% Develop Sw
		initial	cumulative				
PA	28	57	71	6	50	--	--
MD	17	47	65	5	80	--	--
MA	15	47	80	11	64	34	56 (76% of 26 digested)
MC	--	--	--	--	--	10	90
PC	14	56	--	5	40	--	--
EC	9	57	--	6	50	--	--

Table III. Changes in the presence (s) or absence (n) of sweeper tentacles on colonies of Agaricia agaricites in natural competitive encounters. Only 25% of colonies either never had sweeper tentacles (n-n) or always had sweeper tentacles (s-s) throughout the ten month observation period. This suggests that sweeper tentacles frequently develop and regress on colonies of A. agaricites during competitive encounters.

TABLE III

NUMBER OF CHANGES IN THE PRESENCE OF SWEEPER TENTACLES

COMPETITOR	N	0		1		2		3	
		s--s	n--n	s--n	n--s	s--n--s	n--s--n	s--n--s--n	n--s--n--s
PA	29	1	5	8	4	1	7	0	2
MD	17	1	5	6	1	0	4	0	0
MA	15	2	1	4	1	2	4	0	1

A. agaricites damaged tissues of the Madracis and the Porites. In contrast, on colonies adjacent to M. annularis, sweepers developed around wounds caused by digestion of A. agaricites by mesenterial filaments of M. annularis. Thus, direct contact with other animals can stimulate development of sweeper tentacles on A. agaricites, and this response is localized around the zone of contact.

Controlled distance

Although sweeper tentacles also developed on colonies of A. agaricites at a fixed distance from opponents, the sequence of events differed in perhaps important ways from that occurring when corals were in closer contact.

Most colonies of A. agaricites (90%) placed within reach of M. cavernosa tentacle tips developed sweeper tentacles (Table IIC). No M. cavernosa ever digested tissues of A. agaricites, nor did they develop sweeper tentacles in interactions prior to the colonies of A. agaricites (although M. cavernosa may develop sweepers during competitive interactions, Chapter 2 and Chornesky and Williams, 1983).

Fifteen of eighteen colonies (83%) of A. agaricites placed within tentacle reach of Madracis decactis developed sweeper tentacles (Table IIC). There was no evidence that the A. agaricites ever damaged tissues of Madracis decactis with mesenterial filaments. Thirteen of the eighteen colonies of Madracis decactis also developed sweeper tentacles. Interestingly, the three A. agaricites which did not form sweepers during the experiment were

adjacent to colonies of Madracis which had developed sweeper tentacles first and then used them to create extensive wounds on the A. agaricites. Sweepers developed around one of these wounds on A. agaricites at the end of the study. In many of the interactions where sweeper tentacles did develop first on the A. agaricites, nearby tissues of the Madracis decactis were damaged, confirming laboratory predictions of sweeper function (test for association between development of sweeper tentacles by A. agaricites and damage to Madracis decactis tissues: $X^2=8.08$, d.f.=1, $P<.005$).

When paired with M. annularis, sweepers developed on over half (56%) of the colonies of A. agaricites placed adjacent to, but out of reach of opponents' polyps and tentacles. Development occurred after the M. annularis digested A. agaricites tissues (test for association between digestion and sweeper development: $X^2=7.99$, d.f.=1, $P<.005$) (Table IIC). Sweeper tentacles which developed in these interactions seemed to function both to damage nearby M. annularis tissues and to prevent further digestion by M. annularis. In forty-three percent of the interactions where sweeper tentacles developed on the A. agaricites, wounds appeared on adjacent colonies of M. annularis which could be attributed to the action of sweeper tentacles. In only a total of five interactions (19%) were colonies of A. agaricites digested a second time by the M. annularis. In four of these cases, sweeper tentacles had not yet developed on the A. agaricites; the one colony redigested despite having developed sweeper tentacles had previously been severely

injured by the predaceous gastropod Coralliophila abbreviata (Lamarck).

The rate at which sweeper tentacles develop on A. agaricites is best reflected in data from experiments with Madracis decactis and M. annularis. Mean development time of sweepers on colonies of A. agaricites adjacent to Madracis decactis was 30.2 days after corals were cemented close together (standard deviation 16 days). For colonies adjacent to M. annularis, the mean development time after digestion by M. annularis was 31.6 days (standard deviation 18.5 days). There is no significant difference between rates of sweeper formation in experiments with Madracis decactis and M. annularis (Mann-Whitney $U=132$, $n_1=18$ $n_2=15$, $P>.1$).

In a few cases, unexpected factors affected sweeper tentacle development. Shortly after corals were cemented in place, seventeen of the thirty-four pairs of A. agaricites and M. annularis were temporarily invaded by small crabs (identified tentatively as Domecia acanthophora f. acanthophora (Desbonne and Schramm), Austin Williams pers. communication). A single crab was usually seen in the crevice formed between adjacent corals (Fig. 2B). In hundreds of observations, during the day and at night, I have never seen these crabs in natural interactions among corals, and I strongly suspect their presence was an experimental artifact. Comparison of interactions with and without resident crabs shows that crabs decreased the likelihood that colonies of A. agaricites already digested by M. annularis would develop sweeper tentacles (test for

association between presence of crabs and inability to develop sweepers: $X^2=3.87$, d.f.=1, $P<.05$). On those colonies which did develop sweepers after crabs appeared, however, the crabs had no significant effect on the amount of time between digestion by M. annularis and the appearance of sweeper tentacles (Mann-Whitney $U=28$, $n_1=6$ $n_2=12$, $P>.1$). Other factors inhibiting sweeper formation after digestion by M. annularis included enlargement of the wound by the predaceous gastropod Coralliophila (1 of the 26 digested) and redigestion by M. annularis resulting in destruction of tissues surrounding the initial wound (3 of the 26). Bak et. al. (1982) note the ability of Domecia and Coralliophila to damage coral tissues close to the site of competitive interactions.

In summary, development of sweeper tentacles can occur prior to close tissue and skeletal contact between adjacent corals. The distance at which the interaction begins is a function of the length of competitor species' polyps, tentacles, and mesenterial filaments, and their readiness to evert mesenterial filaments. In addition, development of sweeper tentacles or repeated use of mesenterial filaments by competitors may delay sweeper formation by A. agaricites. Sweeper development may also be inhibited by activity of epifauna such as crabs and gastropods. After development, the sweeper tentacles of A. agaricites sometimes injure tissues of competitors and may help prevent further damage by the mesenterial filaments of opponents.

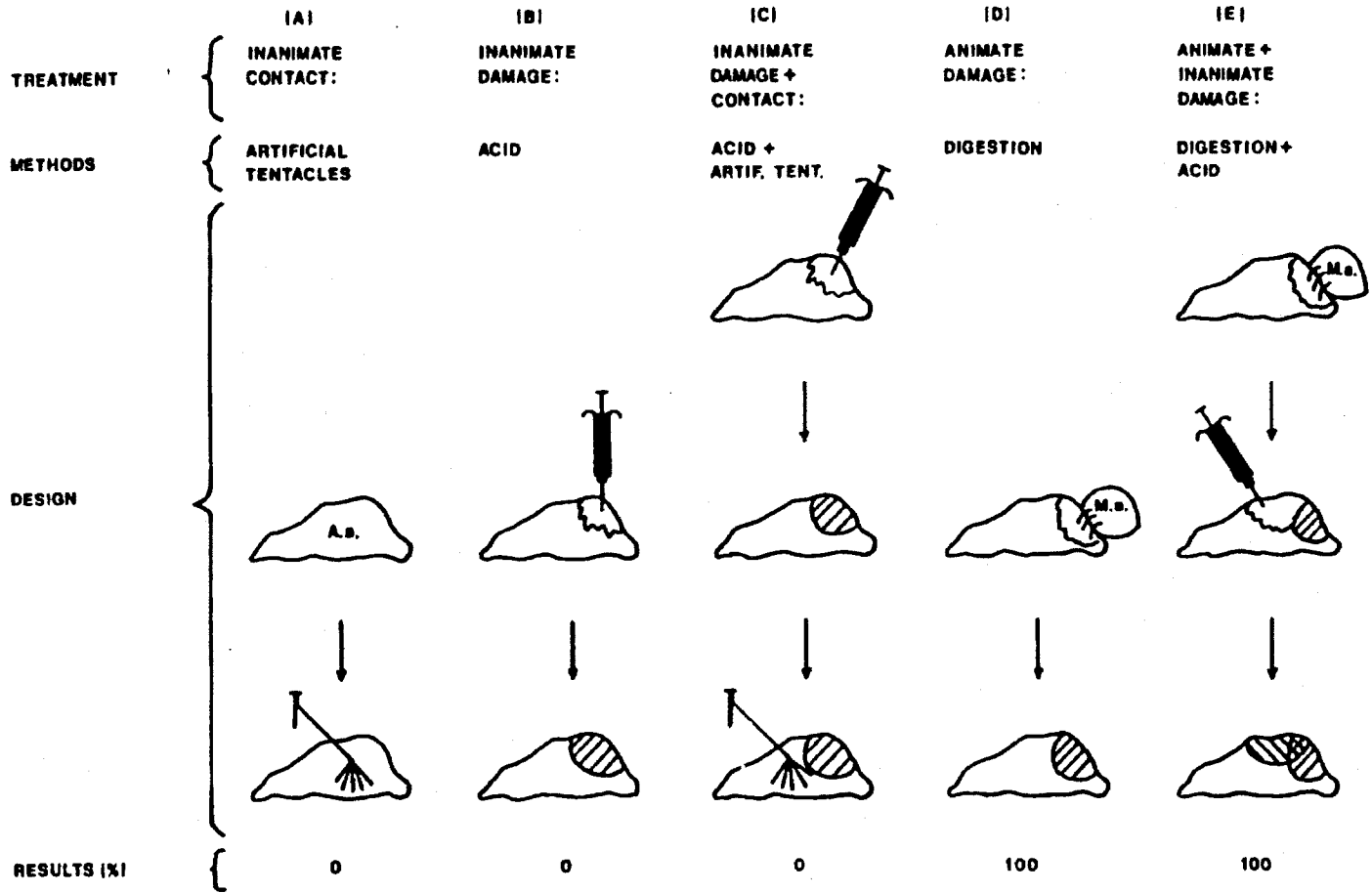
B. STIMULUS FOR SWEEPER TENTACLE DEVELOPMENT

MATERIALS AND METHODS

The preceding experiments demonstrate that contact with various competitors can stimulate development of sweeper tentacles on A. agaricites. Although differing in specific form among competitors, this contact generally involves three components which occur simultaneously: 1) tactile contact; 1) damage, for example by tentacular nematocysts or by the digestive enzymes or nematocysts of mesenterial filaments; or 3) chemical recognition of competitor tissues. The following experiments were designed to separate the role of these factors in stimulating the formation of sweeper tentacles. Corals were exposed to one of the following five stimuli: A) inanimate tactile contact; B) inanimate damage; C) inanimate contact plus damage; D) animate damage; and E) inanimate plus animate damage (see Fig. 3). After application of each treatment in situ, corals were observed for development of sweeper tentacles approximately once a week at night for a minimum of forty days.

To test whether inanimate tactile contact alone can induce sweepers, tufts of artificial tentacles made of nylon monofilament line were nailed above colonies of A. agaricites (n=5; Fig. 3A). Tips of these artificial tentacles swayed slightly in the surge and were constantly in contact with a portion of the A. agaricites.

Figure 3. Experimental determination of stimulus for sweeper tentacle development. Corals were treated with various combinations of artificial tentacles, artificial wounds created with HCl, and wounds caused by mesenterial filaments of M. annularis. Results are presented as percent of colonies which developed sweeper tentacles. In treatment E, sweeper development occurred only around wounds caused by mesenterial filaments of M. annularis.



To determine whether inanimate damage alone can induce sweeper tentacles, portions of live tissues on colonies of A. agaricites were destroyed to mimic digestion by mesenterial filaments (n=5; Fig. 3B). Small amounts of concentrated hydrochloric acid were applied to live tissues using a glass hypodermic syringe. Because the viscosity and specific gravity of concentrated acid is greater than seawater, it remained where applied and killed only a discrete patch of tissues. There was no apparent damage to surrounding tissues. The acid left the skeleton denuded of coral tissues, resembling lesions from digestion by other corals.

To simulate both the damage and tactile components of natural interactions, HCl and artificial tentacles were applied to a series of A. agaricites (n=5; Fig. 3C). Here, artificial tentacles were positioned over live coral tissues next to the wound created with HCl.

When coral tissues are destroyed by mesenterial filaments, damage is accompanied by the potential for chemical recognition of competitors. In this treatment (animate damage), corals were damaged by mesenterial filaments in a way which allows comparison with the inanimate damage treatment described above. Colonies of A. agaricites were allowed to be digested overnight by M. annularis (n=6; Fig. 3D), and the corals were separated the next day and then kept separate for the duration of the experiment.

When a colony of A. agaricites is stimulated by a competitor, development of sweeper tentacles is localized around the affected region. This final treatment was designed to test the extent to which recognition of a competitor affects other tissues within a colony by artificially creating a second inanimate wound on corals already digested by M. annularis. Colonies of A. agaricites were allowed to be digested by M. annularis, after which the corals were separated. One day later, a second wound which overlapped the first wound slightly on one side was artificially created using HCl (n=5; see Fig. 3E). Development of sweepers around the artificial wound would reflect the degree to which surrounding tissues were also affected by digestion of other tissues within the colony. This treatment also controlled for whether the use of concentrated HCl was appropriate to simulate damage in natural interactions, since application of HCl might conceivably disrupt normal physiological processes and thereby inhibit sweeper tentacle formation. This would be apparent if sweepers did not develop next to the M. annularis wound close to where the two wounds overlapped.

RESULTS

Sweeper tentacles did not form on colonies of A. agaricites in response to any of the inanimate treatments—artificial tentacles, HCl lesions, or a combination of the two (Fig. 3A-C). Sweepers did form, however, on all A. agaricites with lesions from M. annularis mesenterial filaments (Fig. 3D). These sweeper

tentacles appeared within eighteen days, were smaller than usual, and regressed within three weeks of development. In nature, I have seen sweeper tentacles regress as the regenerating edges of wounds caused by mesenterial filaments begin to advance (see also Fig. 3). Sweeper tentacles also formed on all colonies of A. agaricites with both M. annularis and HCl lesions (Fig. 3E), but only adjacent to the M. annularis wound. Similarly, these sweepers were smaller than usual and regressed within three weeks. The regression of sweeper tentacles in these experiments suggests that repeated stimulation may be necessary for sustained sweeper development. There was no evidence that HCl inhibited development of sweeper tentacles anywhere near the first wound. There are two alternative explanations for why sweepers developed only adjacent to the M. annularis wound on these colonies: 1) the response to recognition of another animal within A. agaricites colonies may be quite localized, here occurring only adjacent to the M. annularis wound; or 2) if recognition is colony-wide, tactile contact may also be required to stimulate sweeper tentacle development.

DISCUSSION

Cnidarians display a remarkable array of responses to competitors, including: agonistic behavior (Lang, 1971, 1973; Francis, 1973; Bigger, 1976, 1980; Ottaway, 1978; Brace et al., 1979; Sheppard, 1979; Purcell and Kitting, 1981), development and use of elongate tentacles (Purcell, 1977; Wellington, 1980; Bak et

al., 1982; Watson and Mariscal, 1983), directed growth (Ivker, 1972; Potts, 1977; Wahle, 1980) or an "immune response" (Theodor, 1970; Hildeman et al., 1975; Rinkevich and Loya, 1983). Most of these processes operate between animals within taxonomic orders, either intraspecifically (Theodor, 1970; Ivker, 1972; Francis, 1973; Hildeman et al., 1975; Potts, 1977; Purcell, 1977; Ottaway, 1978; Brace et al., 1979; Rinkevich and Loya, 1983; Watson and Mariscal, 1983) or interspecifically (Lang, 1971, 1973; Purcell, 1977; Sheppard, 1979; Bigger, 1980; Wellington, 1980), with a few exceptions (Bigger, 1977; Wahle, 1980; Sammarco et al., 1983). The scleractinian coral Agaricia agaricites develops sweeper tentacles in response to encounters with a range of other animals, including various corals, a gorgonian, and a zooanthid.

Interactions among sessile reef animals usually result from gradual growth. Particularly for a species like A. agaricites, having flat polyps, short tentacles, and short mesenterial filaments, the nature of direct competitive encounters will vary with characteristics of its opponents. The morphology of competitor polyps, tentacles, and mesenterial filaments, as well as their readiness to evert mesenterial filaments, determine how they first contact A. agaricites.

Regardless of the specific mode of contact between A. agaricites and various anthozoan competitors, all such contact stimulates A. agaricites to develop sweeper tentacles. For example, when A. agaricites grows close to corals having long tentacles, the

first contact will be with their tentacle tips. In experiments simulating such encounters, corals which are digestively dominant when in close contact (M. cavernosa and A. agaricites) did not evert mesenterial filaments onto opposing corals (A. agaricites and Madracis decactis, respectively). Contact with only tentacle tips of opponents stimulated development of sweepers on nearby A. agaricites tissues. This differs from controlled distance experiments with M. annularis, a digestively dominant coral having short polyps and tentacles and long mesenterial filaments. Here, the first contact between corals was digestion of A. agaricites, and sweeper tentacles developed around the resulting wounds. The distance between interacting corals did not affect the behavior of M. annularis, as seen by Wellington (1980) for Pavona.

Interestingly, in these experiments the distance separating competitors affected the readiness to evert mesenterial filaments of some corals (ie. M. cavernosa--c. f. this study and Lang, 1973) and not of others (ie. M. annularis--this study). This, combined with evidence from controlled distance experiments that contact was not necessarily required to stimulate eversion of mesenterial filaments by M. annularis, suggests that controls over the use of mesenterial filaments in competition may be quite complex and perhaps involves some form of indirect sensing.

Development of sweeper tentacles on A. agaricites apparently occurs only after recognition of competitor tissues. Tactile contact and damage to tissues may also be involved in initiating

this process, although neither alone nor the two combined is sufficient. In natural interactions however, contact, damage, and recognition are probably inseparable. Corals being digested by mesenterial filaments surely have the potential to recognize competitor tissues. Likewise, those in contact with tentacle tips of adjacent corals may incur small scale damage from the tentacular nematocysts. However, if chemical recognition is sufficient to induce sweeper tentacle formation, the stimulus is probably not a diffusible substance (sensu Bigger, 1976). Colonies of A. agaricites separated by only 1-2 mm from tissues of M. annularis did not develop sweeper tentacles until after digestion by M. annularis.

Sweeper tentacles develop only within a zone of approximately 5 mm surrounding tissues stimulated by another animal. For example, on colonies with wounds resulting from both digestion by M. annularis and HCl, sweepers formed only around the wound inflicted by M. annularis. Moreover, disturbance by crabs or predaceous gastropods to tissues immediately surrounding stimulated regions prevented a few A. agaricites from developing sweeper tentacles at wounds caused by M. annularis. Development of sweeper tentacles on A. agaricites was also inhibited or delayed by the formation of sweeper tentacles on opposing colonies of Madracis decactis or by redigestion by M. annularis. These various disturbances all damaged the small region of "responsive" tissues where sweepers would have formed, and thereby prevented their

development. This suggests that recognition of competitors stimulates a localized and not a colony-wide response within colonies of A. agaricites.

In contrast to mesenterial filaments, sweeper tentacles are not generally present on A. agaricites, but develop specifically as a response to competitive encounters with other sessile animals. These sweepers have the potential to damage tissues of competitors and may affect the long term outcome of competitive interactions (Chapter 3). The exact sequence of events leading to formation of sweeper tentacles depends upon characteristics of the opponent species and the distance at which encounters occur. These two factors will therefore determine the extent of damage to A. agaricites before it develops sweeper tentacles. Understanding the dynamics of such complex processes may be important for interpretation of the mechanism and consequences of natural and experimental encounters among many reef corals.

CHAPTER TWO

THE DISTRIBUTION OF SWEEPER TENTACLES ON MONTASTRAEA CAVERNOSA

ABSTRACT

In direct competition among reef corals for limited substrate space, some species utilize elongate tentacles with specialized cnidae, or sweeper tentacles, to damage opponents. On several species described thus far, these tentacles are not generally present, but develop as competitive interactions progress. Colonies of the Caribbean reef coral Montastraea cavernosa frequently have sweeper tentacles distributed over colony surfaces in patterns which do not necessarily correspond to ongoing competitive encounters. Nevertheless, when injured by the congeneric species M. annularis, colonies of M. cavernosa increase both the number of polyps with sweeper tentacles and the number of sweeper tentacles per polyp expanded on colony regions close to the encounter.

INTRODUCTION

Reef corals are known to use a variety of mechanisms to compete for limited substrate space in crowded reef environments. Two of the best described are the use of mesenterial filaments (Lang, 1971, 1973; Sheppard, 1979) and of "sweeper tentacles" (Richardson et al., 1979; Wellington, 1980; Bak et al., 1982; Chapter 1 and Chornesky, 1983) by some corals to damage the tissues of neighboring corals.

Mesenterial filaments are invariably present in all coral polyps (Wells, 1956). When corals of different species are placed into direct contact, these digestive filaments are deployed rapidly and extracoelenteric digestion of opponent tissues may take place within hours (Lang, 1971, 1973). Unlike mesenterial filaments, sweeper tentacles (elongate tentacles with specialized cnidae) are found only on certain species of coral (see: Lewis and Price, 1975; Bak and Elgershuizen, 1976). Moreover, within these species, sweepers may not be present on all colonies, and when present, may be erratically distributed over the colony surface. On some corals, sweeper tentacles develop specifically after damage by mesenterial filaments (Wellington, 1980; Bak et al., 1982; Chapter 1 and Chornesky, 1983) or after contact and recognition (Chapter 1 and Chornesky, 1983) of other corals. In natural interactions, this delayed development, and thus the ability to utilize sweepers against a neighbor, occurs about 30 days after the interaction has begun (Wellington, 1980; Bak et al., 1982; Chapter 1 and

Chornesky, 1983). However, on at least one species of coral, sweeper tentacles are routinely present, and are therefore "ready" to participate in competitive interactions with neighboring corals which grow too close.

Sweeper tentacles are commonly seen on colonies of the Caribbean coral Montastraea cavernosa. Descriptive patterns of the location of sweeper tentacles on this coral variously include: concentration around colony perimeters (den Hartog, 1977; Richardson et al., 1979); maximal expansion in response to water currents (Price, 1973, in den Hartog 1977); or a less predictable pattern of distribution over colony surfaces (Lang unpub. data). Perhaps in part because they are usually present, sweepers on M. cavernosa have been described as feeding appendages (Lewis and Price, 1975), defensive structures to deter close growth of adjacent competitors (Richardson et al., 1979), and "polyfunctional" structures which might serve both functions (Lang, 1979).

Here I present data on the behavior and development of sweeper tentacles on M. cavernosa in artificial competitive interactions with the congeneric species M. annularis.

MATERIALS AND METHODS

These experiments were conducted at a depth of, 18 meters in Salt River Canyon, on the north coast of St. Croix Island. They were initiated during a saturation dive in the NOAA NULS II Underwater Habitat in March of 1982. Paired colonies of

M. annularis and M. cavernosa (n = 8) were cemented to cinder blocks using underwater epoxy-putty (see Chapter 1 and Chornesky, 1983 for methods). Corals were arranged so that a gap of about 1 cm remained between the colonies of M. annularis and of M. cavernosa when their polyps and tissues were contracted during the day.

My initial intent was to examine whether introduction of other corals close to colonies of M. cavernosa would affect the expansion patterns of its sweepers. Thus, prior to introducing colonies of M. annularis, locations of existing sweeper tentacles were carefully mapped. The first night after corals were cemented into place, all colonies of M. annularis digested nearby expanded polyps of M. cavernosa in contact with their tissues. Subsequently, polyps of the digested M. cavernosa remained contracted in the area surrounding the resulting wounds. This unpredicted behavioral response made it impossible to observe the behavior of their sweeper tentacles during the remainder of the saturation dive.

Nevertheless, this manipulation did provide an opportunity to follow the longer-term consequences of such interactions for colonies of M. cavernosa on which the location of sweeper tentacles was already well documented. These interactions were subsequently observed on six nights over the following two months by S. L. Williams. During each observation, positions of sweepers on the colonies of M. cavernosa were carefully mapped and the behavior and condition of both corals recorded. For data analysis, each colony of M. cavernosa was divided into regions adjacent to and not

adjacent to the M. annularis. Boundaries of these regions were designated arbitrarily on maps resulting from the first set of observations, and then held constant for all subsequent observations. Data were analyzed by contrasting changes in the number of polyps with sweeper tentacles on adjacent and non-adjacent regions of colonies. Adjacent regions were consistently smaller than non-adjacent regions on the same colony (about a third of the size); therefore, a comparison of the two yields a conservative estimate of the density of polyps with sweeper tentacles on adjacent regions.

RESULTS

Figure 1 compares the number of polyps with sweeper tentacles on tissues adjacent to (plain bars) and not adjacent to (striped bars) M. annularis. The median and a quarter of the range are plotted since these data were clearly non-normal and sample sizes were small ($n=7$ to 8). There is a significant correlation between the number of polyps with sweeper tentacles on adjacent tissues and time after initiation of the experiment (Spearman rank correlation $\rho = .333$, $P < .05$). The correlation for non-adjacent tissues is not statistically significant ($\rho = -.133$, $P > .05$). The ratio of the number of polyps with sweepers on adjacent to that on non-adjacent tissues is plotted in figure 2 and demonstrates that the relative proportion on adjacent regions increased during the observation period. Figure 3 shows the median cumulative changes

Figure 1. Changes on M. cavernosa in the number of polyps with sweeper tentacles on adjacent (plain bars) and non-adjacent (striped bars) tissues one day before (-1) and up to 60 days after damage by M. annularis. The median and a quartile range are plotted since these data were non-normal.

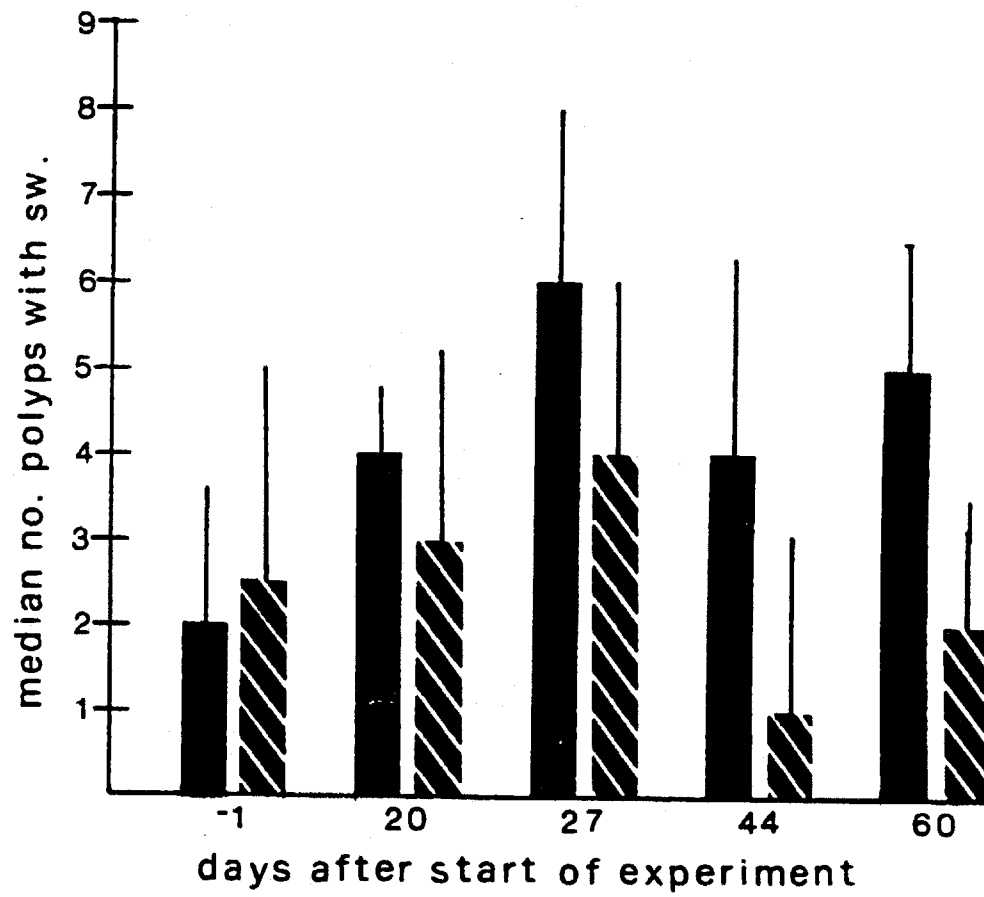
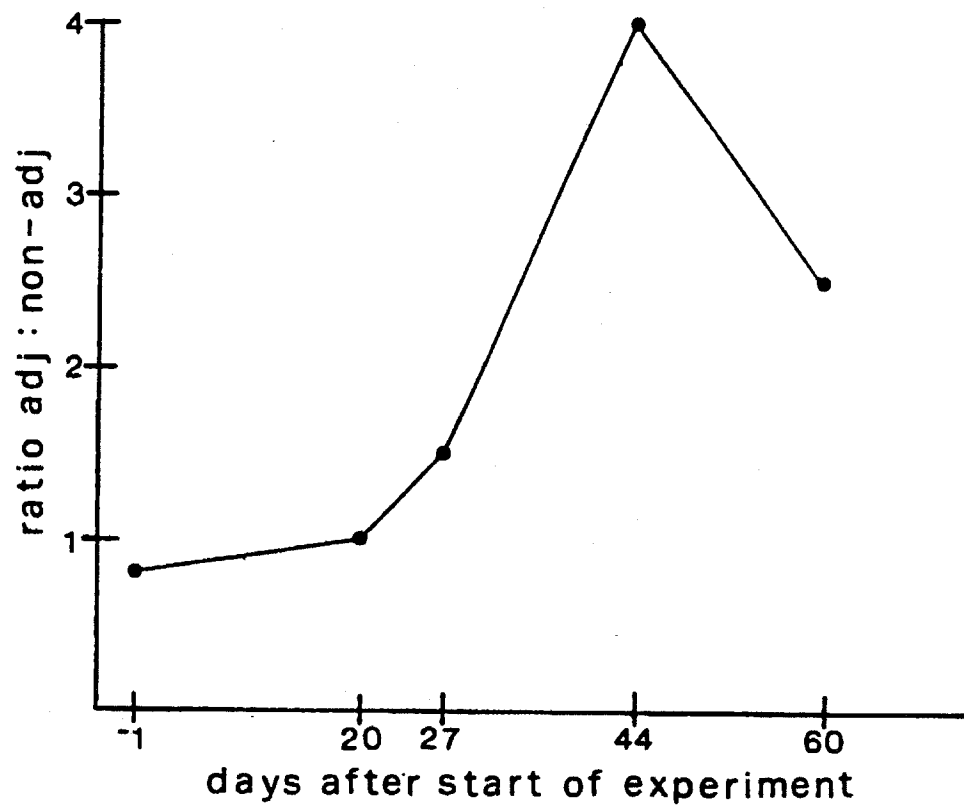


Figure 2. Change in the relative proportion of polyps with sweeper tentacles on adjacent and non-adjacent tissues. The ratio of (the number on adjacent) : (the number on non-adjacent) is plotted against the time after damage by M. annularis.



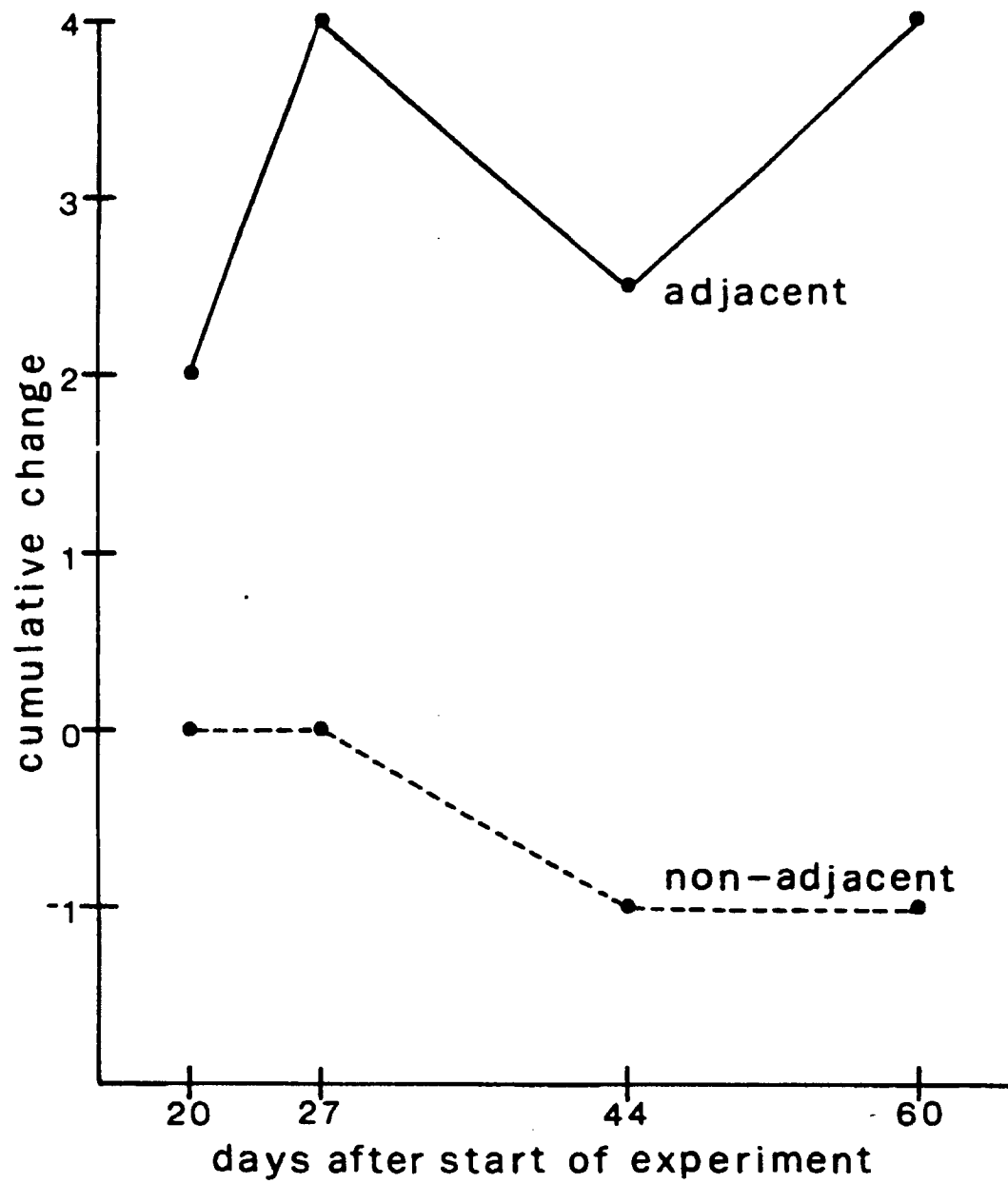
(sum of changes to that date) in the number of polyps with sweepers on adjacent and non-adjacent regions at various times after initiation of the experiment. These data suggest a cumulative decrease in the number of sweepers on tissues not adjacent to colonies of M. annularis. This was clearly true for at least two colonies of M. cavernosa on which sweeper tentacles on non-adjacent tissues disappeared after the experiments were begun (4 and 6 weeks, respectively).

Necrotic wounds appeared on most colonies of M. annularis close to the colonies of M. cavernosa. Most (5 of 6) wounds formed in intervals between observations, during which time the number of M. cavernosa polyps with sweeper tentacles also increased. Sweeper tentacles of M. cavernosa were often observed touching live M. annularis tissues close to necrotic regions.

DISCUSSION

M. cavernosa apparently can increase the number of polyps with expanded sweeper tentacles close to the site of competitive encounters with other corals. Although these data specifically reported the number of polyps having sweeper tentacles, additional observations by S.L. Williams (pers. comm.) suggest that the number of sweeper tentacles per polyp and the size of acrospheres on existing sweeper tentacles may also increase close to the site of such encounters.

Figure 3. Median cumulative change in the number of polyps with sweeper tentacles on adjacent (unbroken line) and non-adjacent (dashed line) tissues. Each point is the sum of changes up to that day. There was a cumulative increase on adjacent tissues and a cumulative decrease on non-adjacent tissues.



Moreover, these data suggest that either the number of polyps with sweeper tentacles or expansion of sweeper tentacles on portions of colonies not involved in competitive interactions may decrease as the number of expanded sweepers close to the interaction increases. If so, this might reflect a "cost" incurred by the production and/or expansion of additional sweeper tentacles close to the site of competitive encounters.

Although caution should be exercised in ascribing causes for wounds in coral-coral interactions (Bak et al., 1982; Chapter 1 and Chornesky, 1983), it appears that the sweeper tentacles of M. cavernosa were capable of damaging tissues of M. annularis within their reach. Whether the course of natural interactions is similar to these experiments is less clear (i.e. digestion of M. cavernosa by M. annularis: development of sweeper tentacles by M. cavernosa: damage to M. annularis by M. cavernosa sweepers). For example, when colonies grow gradually into contact, M. cavernosa may be able to develop sweeper tentacles prior to digestion by M. annularis. Similarly, at a greater distance than the, 1 cm gap in these experiments, M. cavernosa sweeper tentacles might efficiently deter close growth and/or digestion by M. annularis (sensu Richardson et al., 1979; see Chapter 1 and Chornesky, 1983 for how natural and experimental interactions sometimes may differ).

On other corals for which the development of sweeper tentacles during direct competition has been documented, sweepers are not generally present, but appear in response to the encounter

and may later regress (Wellington, 1980; Chapter 1 and Chornesky, 1983). Since colonies of M. cavernosa normally possess sweeper tentacles distributed in seemingly disordered patterns over colony surfaces, it is particularly interesting that interactions with other corals seem to affect sweeper distribution within colonies—increasing in density on adjacent tissues and perhaps decreasing on tissues away from the zone of the interaction. Since sweeper tentacles on M. cavernosa apparently do not regress after an interaction ceases and may remain on a colony for an extended period of time, the distribution of sweeper tentacles over a colony may reflect at least a short-term historical record of past competitive encounters.

CHAPTER THREE

REPEATED REVERSALS AND STALEMATES IN COMPETITION BETWEEN REEF CORALS

ABSTRACT

Repeated observation of direct competitive encounters between Agaricia agaricites and two other reef corals revealed that the apparent winner of individual interactions can switch repeatedly over time. Such interactions may have no ultimate resolution, and in contrast to previously described cases of competition between sessile animals, may have little direct or obvious effect on the structure of reef communities.

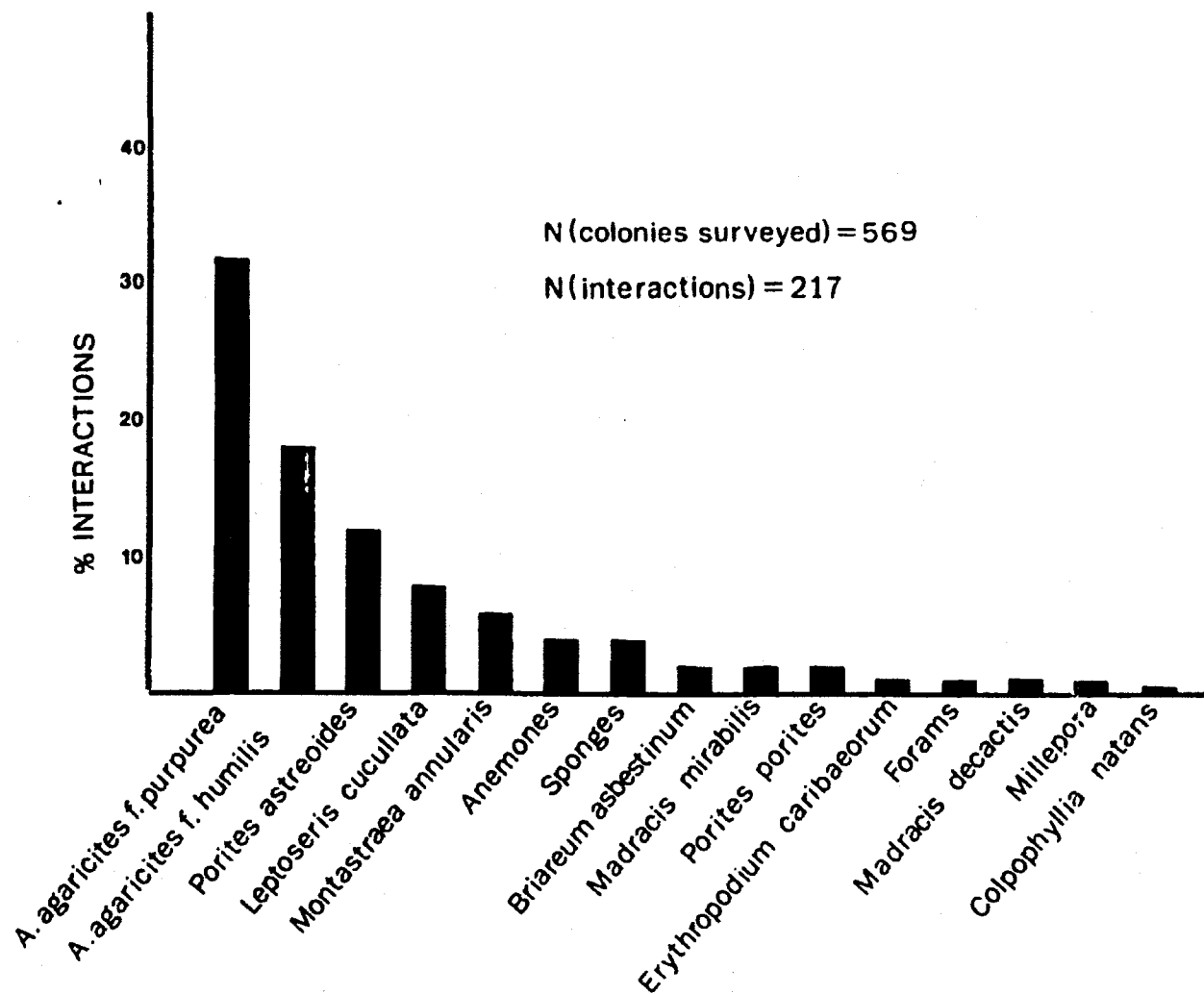
INTRODUCTION

In communities of sessile marine organisms, direct competition for limited space is common (e.g., Connell, 1961, 1976; Dayton, 1971; Lang, 1973; Stebbings, 1973; Osman, 1977; Buss and Jackson, 1979). The patterns and effects of competition in these communities are often evaluated by ranking species according to their relative ability to damage and/or overgrow neighboring organisms (Lang, 1973; Connell, 1976; Osman, 1977; Buss and Jackson, 1979; Sheppard, 1979; Rubin, 1982; Russ, 1982; Quinn, 1982; Karlson and Shenk, 1983). Whether such rankings follow a linear hierarchy in which few species dominate (Lang, 1973; Connell, 1976; Sheppard, 1979; Quinn, 1982; Russ, 1982) or a network in which none dominates (Buss and Jackson, 1979; Jackson, 1979; Buss, 1980; Rubin, 1982; Russ, 1982; Karlson and Shenk, 1983), all assume that any given interaction between individuals of different species will yield some unambiguous result. Here, I describe interactions between three abundant (Goreau, 1959) Jamaican reef corals which seem to violate this assumption, and do not conform to existing models for direct competition between sessile animals. These interactions have no clear long-term winner. Instead, individual encounters are characterized by repeated reversals leading to little net change in the relative positions of competitors, and no determinate outcome (or winner) at either the individual or population level.

Encounters with adjacent animals often limit the size of corals growing along reef surfaces (e.g., Glynn, 1973; Lang, 1973; Porter, 1974; Sheppard, 1979, 1982). When crowded, these animals may compete directly for substrate resources by damaging neighboring colonies using mesenterial (digestive) filaments (Lang, 1973; Sheppard, 1979) or sweeper tentacles (Wellington, 1980; Bak et al., 1982; Chapter 1 and Chornesky, 1983). Mesenterial filaments and sweeper tentacles may function over very different time intervals (days versus weeks after contact with competitors) (see Chapters 1 and 2 for discussion). In addition, coral species vary in their propensity to use mesenterial filaments and in their ability to develop sweeper tentacles. Thus, there is the potential for sequential deployment of different competitive mechanisms by competing corals, resulting in considerable variation over time in the outcome of ongoing encounters.

To examine how this affects the process and consequences of competitive interactions, I repeatedly observed natural encounters between Agaricia agaricites forma purpurea (Wells, 1973) and two other corals, Porites astreoides and Montastraea annularis. Colonies of M. annularis were of the subcolumnar form described by Dustan (1975). Direct competition between these species is common (Fig. 1), and involves mutual damage. M. annularis can digest A. agaricites (Lang, 1973). Although originally described as digestively subordinate to A. agaricites (Lang, 1973), in natural and experimental encounters, I have seen P. astreoides extend polyps

Figure 1. Frequency of natural encounters between A. agaricites f. purpurea and other sessile animals at 15 m on the west forereef of Discovery Bay. Intraspecific encounters with the same or a different (f. humilis) forma were the most frequent. P. astreoides, Leptoseris (= Helioseris) cucullata, and M. annularis were the three other species most frequently encountered.



between colonies and damage A. agaricites, presumably using mesenterial filaments. In contrast, A. agaricites can develop and use sweeper tentacles against both M. annularis and P. astreoides (Chapter 1 and Chornesky, 1983).

MATERIALS AND METHODS

Naturally occurring interactions at a depth of 13 m on the west forereef at Discovery Bay, Jamaica were labeled and then photographed using a one-to-two close-up framer in Oct. 1981, Aug. 1982, and June 1983. The same regions were photographed each time by in situ comparison of previous prints of the interaction. The following variables were compared between successive observations: i) the position of the edge of each competitor; ii) the location of the midpoint between the two corals; and iii) the size of the gap separating the corals. Edge position provides information about losses and gains by each coral. Midpoint location incorporates changes in edges of both corals and is the best indicator of the coral gaining more space or "winner," and gap size reveals the overall dynamics of the interaction. These measures were used since often both corals in an interaction were damaged and/or regrew; thus, unlike many previous studies, the animal remaining undamaged at any given time did not necessarily win.

On printed photographs of each interaction, I identified at least two distinctive polyps on the A. agaricites on a plane parallel to the competing edge, and drew a reference line between

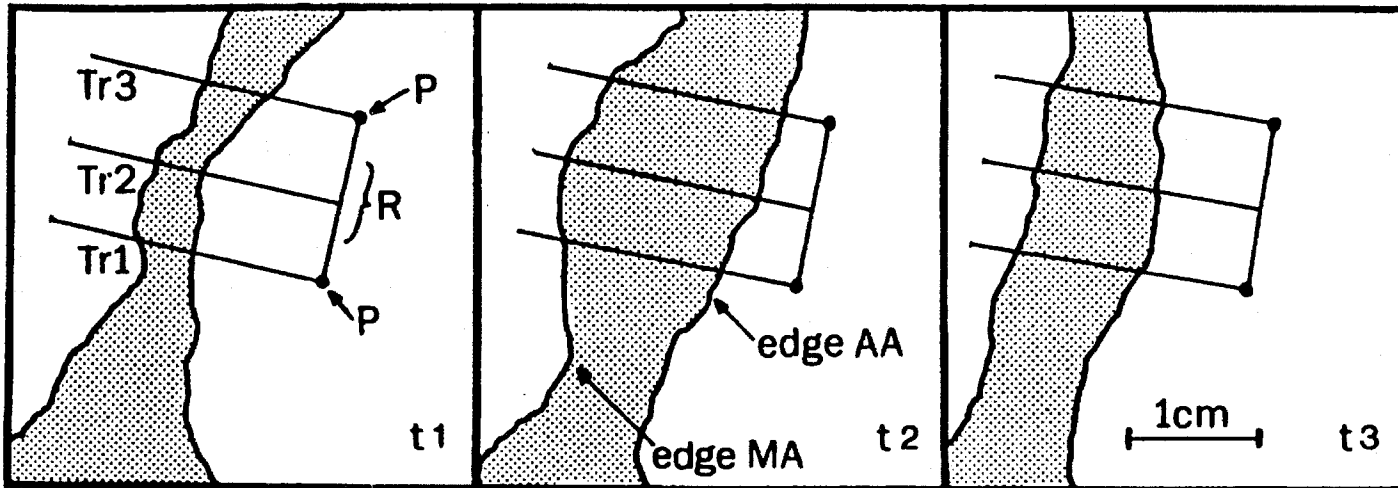
them (Fig. 2). Three equidistant transect lines were drawn perpendicular to this reference line and used to measure distances to the edges of live tissues of A. agaricites and its competitor. I discarded cases where: unique polyps could not be identified; new polyps budded over colony surfaces indicating potential shifts in the location of unique polyps during colony growth; the photographic angle varied among pictures; or the interaction was at all three dimensional.

For each variable (edges, midpoint, gap), I calculated the net and gross change over the 20 month period. The net change is the difference between the beginning and the end of the study, and can be either positive or negative. The gross change, or cumulative losses and gains during the study, was calculated by summing the absolute value of differences between successive photographs. Comparison of the gross change to the absolute value of the net change provides an estimate of the magnitude of temporary modifications of coral edges which were not reflected in final colony positions.

RESULTS

Results showed no consistent pattern of advance of one coral at the expense of the other. Rather, in most pairs, both corals sequentially lost and gained tissues along their borders as they were injured by opponents and regrew (Fig. 2). Similarly, the midpoint between competing corals oscillated back and forth through

Figure 2. Example of a competitive encounter between A. agaricites (AA) and M. annularis (MA) photographed during Oct. 1981 (t1), Aug. 1982 (t2), and June 1983 (t3). Drawings are to scale from enlarged negatives. P=unique polyps on A. agaricites, R=reference line, and Tr1-3=perpendicular transect lines. In this interaction both opponents lost tissues, and then regenerated along damaged margins.



time, and gaps between corals became sequentially greater and smaller as corals were damaged and grew back into proximity. For each variable (edges, midpoint, gap), the gross change was consistently and significantly greater than the absolute value of the net change over the 20 month interval (Table Ia), indicating frequent, transient shifts along competing edges.

"Reversal" (sensu Wellington, 1980) can be used to describe interactions where the initial winning competitor is subsequently and predictably beaten when its opponent uses a different competitive mechanism. I often observed (Table Ib) temporal reversals in the direction of movement of coral edges and of the midpoint between interacting corals. It is unlikely that these reversals were due to seasonality as suggested by Cope (1982), as synchronic interactions reversed in both directions. However, my observations differ from previously described reversals in two important ways: i) within a single interaction, two or more reversals were not uncommon; and ii) reversals often occurred in each direction (Table Ib). Because of these frequent and sometimes repeated reversals, in any given interaction there was either no winner (38%), or the interactions proceeded very slowly (on average the midpoint moved only 2.5 mm/yr.). It is important to note that despite the twenty month duration of these observations, they reflect only partial histories of interactions which probably have had and will continue to include many more reversals.

Table I. Changes in interactions between A. agaricites (AA) and P. astreoides (PA) or M. annularis (MA) over 20 months. In (a), significance levels (SIG) are for one-tailed paired t test comparison between the absolute value of net (|NET|) versus gross changes (GROSS). (b) shows the % of interactions with any or ≥ 2 reversals and whether the reversal was from a loss to a gain (-/+) or from gain to loss (+/-). (c) shows mean of actual net changes (NET) for all interactions and % of those changing with a net gain (+) or net loss (-). Direction of net change for midpoint reported relative to A. agaricites colony. |NET| , GROSS, and NET presented in mm/20 mo. and as the mean \pm s.d. Qualitative differences between interactions with M. annularis and P. astreoides are presumably due to differences in their specific competitive strategies and in their energetic investment into lateral growth.

TABLE I

VARIABLE	N	(a)			(b)				(c)		
		NET (mm)	GROSS (mm)	SIG	REVERSALS		DIRECTION %		NET (mm)	DIRECTION %	
					% ANY	% ≥ 2	-/+	+/-		+	-
AA VERSUS PA											
AA edge	15	4.1±2.4	6.4±2.7	***	67	20	64	36	.53±4.8	64	36
PA edge	15	5.5±3.8	8.5±3.0	***	73	20	67	33	-2.4±6.4	42	58
Midpoint	15	4.6±2.9	6.6±2.5	***	67	20	56	44	1.5±5.4	58	42
Gap	15	3.3±1.8	7.8±2.9	***	--	--	--	--	--	--	--
AA VERSUS MA											
AA edge	12	3.6±3.0	11.4±6.1	***	92	83	46	54	-1.7±4.5	43	57
MA edge	10	4.8±2.9	7.3±3.0	**	60	10	36	64	-2.0±5.5	33	67
Midpoint	11	3.7±2.7	7.2±2.8	***	82	45	42	58	.8±4.7	57	43
Gap	11	4.3±4.2	14.0±7.2	***	--	--	--	--	--	--	--

Although competition involves encounters between distinct individuals (here colonies), its effects are often evaluated for the population as a whole (e.g., Osman, 1977; Buss and Jackson, 1979; Kay and Keough, 1981; Russ, 1982). At this level, the advance of one species at the expense of another was negligible. In the 62% of interactions where a net change in the midpoint had occurred, encounters between each species pair were approximately evenly divided in the numbers of net wins and losses for each species (Table Ic). Moreover, the means of actual net changes for the midpoint and edges were less than 2.5 mm over a twenty month period (Table Ic). This is equivalent to an average change of ≤ 1 polyp along edges of colonies consisting of hundreds of polyps. That this distance is significantly less than potential rates of lateral growth in the absence of direct competition (Chornesky unpublished data), suggests strongly that these competitive interactions, while causing minimal tissue loss to participants, exact a significant cost in reduced growth (Table II).

DISCUSSION

The patterns of competition reported here are inconsistent with any of the existing models for direct competitive interactions among sessile animals. None predicts more than one reversal in an interaction, let alone reversals occurring in both directions. Rather, these models assume there is a determinate outcome to any given interaction (Fig. 3a-c). Some describe the winner as

Table II. Comparison of potential rates of lateral growth (calcification) to observed changes along competing edges (= net change in Table I). All values adjusted to mm per year, and presented as the mean \pm standard deviation. Significance levels are for Mann-Whitney comparison. Potential growth was measured as lateral skeletal and tissue expansion by colonies stained with alizarin red S, and which were not in competition with other corals. Values are not presented for M. annularis because colonies of the form used rarely grow substantially along their borders.

TABLE II

	SPECIES			
	AA	n	PA	n
Potential Growth	13.4±2.8	12	7.9±5.1	11
Net change adjacent to MA	-1.7±4.5	12	--	--
Significance level	***			
Net change adjacent to PA	.53±4.8	15	2.4±6.4	15
Significance level	***		*	

predictable at the species level: whenever individuals of species A and B come into contact, species A will always win. This may occur either directly (Fig. 3a) (Lang, 1973; Sheppard, 1979; Quinn, 1982), or involve a unidirectional reversal of the initial outcome (Fig. 3b) (Wellington, 1980; Kay and Keough, 1981; Bak et al., 1982). Others suggest that interactions may be variable at the species level, yet determinate at the level of the individual interaction, with perhaps the ratio in the community of wins to losses for each species being predictable (Fig. 3c) (Buss and Jackson, 1979; Buss, 1980; Kay and Keough, 1981; Rubin, 1982; Russ, 1982; Karlson and Shenk, 1983). In this case, individuals of both A and B sometimes win when these two species come into contact and the winner is determined by such factors as environment, relative size, or encounter angle (Jackson, 1979; Buss, 1980; Rubin, 1982). In addition, several studies mention "standoffs" where encounters lead to a cessation of growth, but no damage to either opponent (e. g. Connell, 1976; Buss and Jackson, 1979; Rubin, 1982; Russ, 1982; Ayling, 1983). These static encounters are generally assumed to be unimportant in determining the consequences of competition (but see Kay and Keough, 1981).

In contrast, the results of this study suggest a model of direct interactions where the apparent winner of any given encounter switches repeatedly through time, and there is no determinate outcome (Fig. 3d). These competitive "stalemates" (defined as dynamic interactions having no resolution) are most likely to occur

Figure 3. Models of interactions between sessile animals. Existing models (a-c) predict a determinate outcome to individual competitive interactions. In a and b, species A wins all competitive interactions with species B. In c, A wins with some probability p , and B wins with some probability q , in interactions between A and B. In contrast to models a, b, and c, the model proposed here, d, does not predict a determinate outcome, since repeated reversals can prevent any clear resolution to interactions. In the Figure, arrows point away from the winning competitor, and subscripts indicate whether all interactions involving these species proceed similarly (Ax vs. Bx) or whether individual interactions may vary (A1 vs. B1, A2 vs. B2).

MODEL	DETERMINATE OUTCOME			NO DETERMINATE OUTCOME COMPETITIVE STALEMATE	
	a) Species Level no reversals	b) Species Level single reversal	c) Individual Level no reversals	d) Individual Level repeated reversals	
time ↓	$A_x \rightarrow B_x$	$A_x \leftarrow B_x$	$A_1 \rightarrow B_1$ $A_2 \leftarrow B_2$	$A_1 \rightarrow B_1$	$A_2 \leftarrow B_2$
	$A_x \rightarrow B_x$	$A_x \rightarrow B_x$	$A_1 \rightarrow B_1$ $A_2 \leftarrow B_2$	$A_1 \leftarrow B_1$	$A_2 \rightarrow B_2$
	$A_x \rightarrow B_x$	$A_x \rightarrow B_x$	$A_1 \rightarrow B_1$ $A_2 \leftarrow B_2$	$A_1 \rightarrow B_1$	$A_2 \leftarrow B_2$
	$A_x \rightarrow B_x$	$A_x \rightarrow B_x$	$A_1 \rightarrow B$ $A_2 \leftarrow B_2$	$A_1 \leftarrow B_1$	$A_2 \rightarrow B_2$
ONE TIME SURVEY OF COMMUNITY	A winning all interactions	A winning, common B winning, rare	A winning, $p=x$ B winning, $q=1-x$	A winning, common B winning, common	
SINGLE INTERACTION OVER TIME	no reversals	single reversal one direction	no reversals	frequent reversals both directions	
LONG-TERM OUTCOME	A always wins	A always wins	A wins, $p=x$ B wins, $q=1-x$	no winner ???	

in competition between colonial organisms, where the loss of tissues along competing borders may not compromise colony survival, and where regeneration or growth along injured edges may be followed by a renewed ability to compete actively. Observations by Ruetzler (1970) and by Jackson (1979b) suggest the potential for stalemates between other colonial animals, including sponges and bryozoans. The consequences of this kind of interaction are best evaluated by the magnitude of successive losses and gains of tissues and space and their effects on the fitness of competitors, rather than by an unambiguous designation of the winner or competitive dominant. Note that stalemates would be indistinguishable from standoffs if observed at a distance or over a long time interval, although their effects on competing animals may be quite different (see Chapter 4).

The differing interpretations presented in figure 3 may in part be due to how competitive mechanisms are observed and evaluated. Evidence supporting existing models is generally from experimental and single or short term observations (Osman, 1977; Buss and Jackson, 1979; Jackson, 1979; Sheppard, 1979; Cope, 1982; Bak et al., 1982; Quinn, 1982; Rubin, 1982; Russ, 1982; Karlson and Shenk, 1983) with only a few including repeated observations (Connell, 1961, 1976; Lang, 1973; Wellington, 1980; Kay and Keough, 1981; Porter et al., 1981; Ayling, 1983) or attempting to discern overgrowth by dissecting competing margins (Buss, 1980; Russ, 1982). The outcome of experimental and natural interactions sometimes differ substantially (Cope, 1982; Chapter 1

and Chornesky, 1983), and observations of short duration can be misleading (Kay and Keough, 1981). For example, a one-time survey of interactions in a community would be insufficient to distinguish which of models b through d were occurring (Fig. 3). Likewise, instantaneous observation of stalemates (any single row in Fig. 3d) could lead to an incorrect interpretation of the ultimate outcome.

Interpretation of how competition proceeds, however, can profoundly influence its perceived effect on the community. Competitive stalemates, although very dynamic, have no clear winner, and thus may have little obvious or direct effect on community structure.

CHAPTER FOUR

ON EVALUATING THE CONSEQUENCES OF DIRECT COMPETITION BETWEEN SESSILE ANIMALS

Introduction

Most studies of benthic colonial invertebrates analyze direct competition from the perspective of community dynamics (e.g., Connell, 1976; Osman, 1977; Jackson and Buss, 1979; Kay and Keough, 1981; Karlson and Schenk, 1983). Competitive ability is generally evaluated as the capability to damage and/or overgrow opponents (e.g., Lang, 1973; Buss and Jackson, 1975; Osman, 1977; Sheppard, 1979; Kay and Keough, 1981). Species are then ranked by relative competitive ability into ordering schemes such as hierarchies and networks that describe the overall effects of direct competition on community structure (e.g., Connell, 1976; Osman, 1977; Jackson and Buss, 1979; Kay and Keough, 1981).

The above approach artificially separates the consequences of direct interference competition on the occupation of space by adults from its potential effects on the life history traits of participating animals. For example, direct competition may affect the fecundity, survivorship, and growth of competitors, all of which are important in determining distribution and abundance. The influence of competition on these life history features may therefore have an important, albeit indirect, influence on community structure.

In this chapter I present an analysis of the costs of direct competition in terms of survivorship and fecundity, and discuss how these costs may vary both within and between species. Although I focus on, and use examples from, communities of scleractinian reef corals, many of the ideas presented are equally applicable to other colonial and clonal invertebrates, and perhaps to many plants.

The costs of competing

Colonial corals are composed of iterated polyps, most of which are potentially reproductive. Changes in the number of polyps in a colony may affect fecundity in three ways. First, if the proportion of reproductive polyps remains constant as corals grow, colony fecundity will increase with size. Second, fecundity per polyp may also be greater in large colonies (Rinkevich and Loya, 1981; Chornesky and Peters, in prep.), and, third, the onset and continuation of sexual maturity may actually be controlled by colony size (Connell, 1973; Wahle, 1983, and in review). Therefore, for many corals colony fecundity should be positively correlated with size.

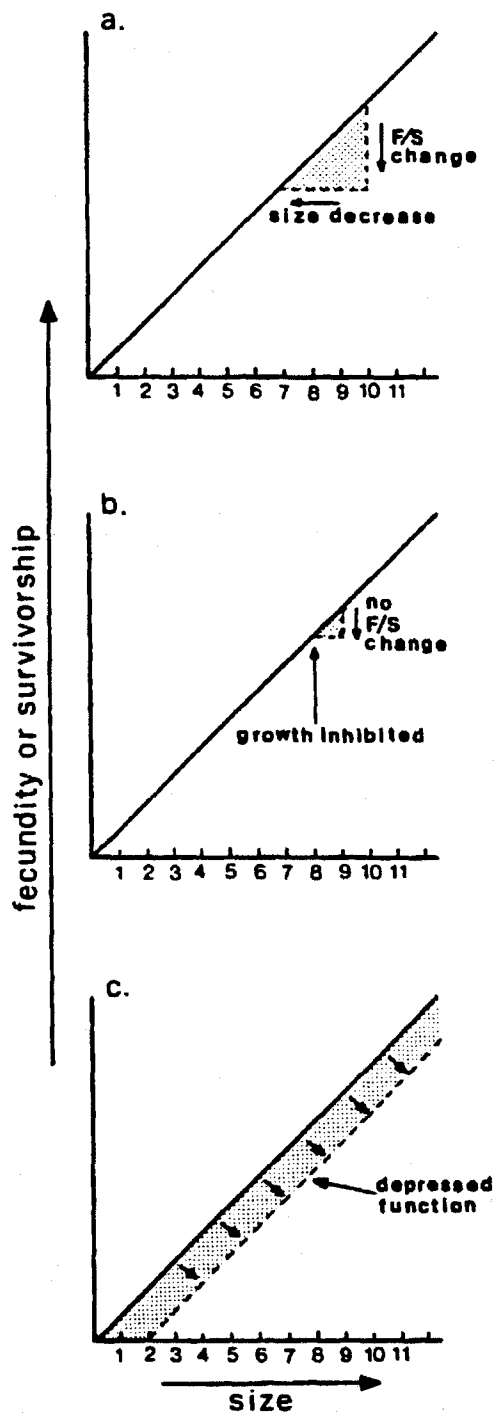
The probability of injury is also related to size (Connell, 1973; Loya, 1976; Hughes and Jackson, 1980; Woodley et al., 1981). Small corals are less likely to be injured, but when injury occurs it is severe and can lead to colony death. Conversely, large colonies have a high probability of sustaining injuries, but such injury is usually minimal, and decreases in severity with increasing colony size (under routine conditions--Hughes and Jackson, 1980;

under hurricane conditions--Woodley et al., 1981; Chornesky, unpublished data). Since fecundity and survivorship are both positively related to size, processes such as direct competition which either inhibit growth or reduce colony size should result in decreased fitness.

Sexual reproduction and growth presumably draw on the limited energetic and material resources of the individual (for review see: Stearns, 1976). If additional demands are made on these resources, the proportion available for reproduction and growth should decrease. For corals, the development and use of sweeper tentacles may represent an energetically or materially expensive process. This is suggested by the regression of sweeper tentacles by Agaricia agaricites (Chapter 1 and Chornesky, 1983) and Pocillopora (Wellington, 1980) after immediate competition ceases. Similar costs may be incurred by replacement of nematocysts depleted during competition from mesenterial filaments or sweeper tentacles. Regardless of their effect on the outcome of competition, the cost of using various competitive structures may represent a drain on resources available for growth and reproduction.

Direct competition may affect participants in three ways then: i) by reducing colony size; ii) by inhibiting future growth; and iii) by reducing colony resources through the use of competitive mechanisms. Each of these affects fecundity or survivorship somewhat differently. For example, assume that fecundity and/or survivorship is a simple linear function of size (Fig. 1). If a

Figure 1. Potential loss in fecundity and/or survivorship resulting from direct competition. In a, b and c, the solid diagonal line represents the relationship of either fecundity or survivorship to colony size. In a, colony size decreases during competition from 10 to 7, and fecundity/survivorship (F/S) shows a corresponding decrease. In b, competition leads to an inhibition of colony growth. The potential incremental growth in colony size from 8 to 9 during the subsequent year does not occur, and thus F/S does not increase as would occur if the colony grew. In c, total colony resources for reproduction or maintenance of somatic tissues is decreased through expenditure on the use of competitive structures. This causes an overall depression of the F/S function.



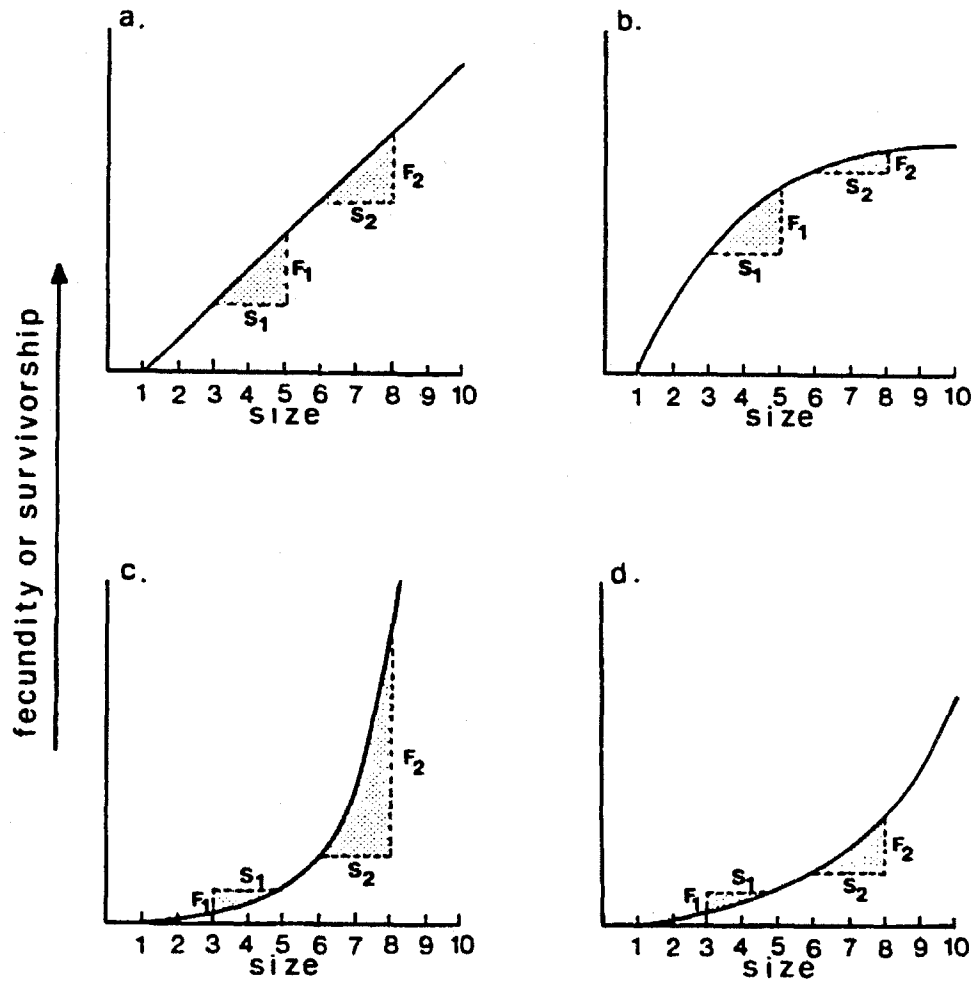
colony decreases in size, it will simultaneously decrease in fecundity or potential survivorship (Fig. 1a). If the growth of a colony is inhibited, it will be prevented from increasing in size and attaining higher survivorship and/or fecundity (Fig. 1b). Finally, if a coral uses specialized structures during competition, the total resources available for sexual reproduction or for the maintenance of somatic tissues will be reduced. The net result will be a depression of the fecundity/survivorship function without a concurrent reduction in size. In the discussion below I use "gain" or "loss" to indicate such changes in fecundity and/or survivorship.

Variation in cost among conspecifics differing in size

The inhibition of growth or equal reduction in size may differentially affect colonies of different sizes. Consider the four hypothetical fecundity/survivorship (F/S) curves in Figure 2.

In Figure 2a, F/S is a linear function of colony size. This might characterize species where the proportion of reproductive polyps remains constant with increasing size, or where the probability of colony death is directly related to colony size. For corals with such linear functions, any given reduction in size will yield an equal absolute loss for colonies of all sizes, although the proportional loss by small colonies will be greater (Fig. 2a). In Figure 2b, F/S increases and then asymptote at some size. Survivorship curves will have this shape if the probability of death for each polyp in a colony is independent and equal, a condition which is most likely to hold for encrusting or plate-shaped corals.

Figure 2. For four hypothetical F/S curves, comparison of the losses in fecundity and/or survivorship (F) for small (1) and large (2) colonies due to an equal reduction in size (S). See text for details.



For species having asymptotic functions, small colonies would experience greater absolute and proportional losses than large colonies after an equal reduction in size. In Figures 2c and 2d survivorship and fecundity are depicted as concave increasing functions of size; in 2c the curve is geometric and has a constant rate of increase whereas in Figure 2d the rate of increase increases with size. Fecundity would assume a function of either shape if the proportion of reproductive polyps and/or the number of gametes produced per polyp increases with increasing size. In real animals, this would be expected to eventually assume a linear form after a maximum proportion of reproductive polyps or fecundity per polyp had been reached. For these concave increasing functions, equal reductions in size would result in greater absolute and equal (Fig. 2c) or greater (Fig. 2d) proportional losses for larger colonies.

A short-term inhibition of growth would differentially affect small and large colonies in the same manner as an equal decrease in size (assuming that large and small colonies potentially grow at the same rate). However, for any given species, the cumulative (lifetime) effects of a permanent inhibition of growth would (Fig. 2a-d) cause greater losses for small than for large colonies.

The use of specialized competitive structures would depress F/S functions uniformly for all size classes (Fig. 1c). The proportionate loss for small colonies would, however, be greater

than that for large colonies.

Variation within species due to different opponents

For any given coral, losing to one competitor may entail greater damage than losing to another. For example, coral species vary in the length of their mesenterial filaments, and individuals of species having long mesenterial filaments produce a larger wound. Hence, individuals of the same species and size competing with different species can suffer quantitatively different losses (Fig. 3).

Variation between species

Available data suggest that coral species vary in the shape of their survivorship and fecundity curves (Connell, 1973; Kojis and Quinn, 1981, 1982; Bothwell, 1982; Harriot, 1982; Fadlallah, 1983; Rylaarsdam, 1983; van Moorsel, 1983; Hughes and Jackson, in press). Competitive interactions resulting in tissue losses of equal area would lead to different costs in fitness for individuals of different species (compare losses of large colonies only in Fig. 2a-2d). Perhaps more importantly, the gains of a winning competitor may not equal the losses of the loser (Fig. 4, compare a and b). The direction and magnitude of this disparity will be determined by the specific fecundity and survivorship curves of each competitor. Thus, the importance of equal amounts of space may vary between individuals of different species. This is suggested by the variation among species in their investment into direct competition

Figure 3. Comparison of losses in F/S (F1, F2) due to unequal reduction in size for same-sized colonies with identical F/S functions.

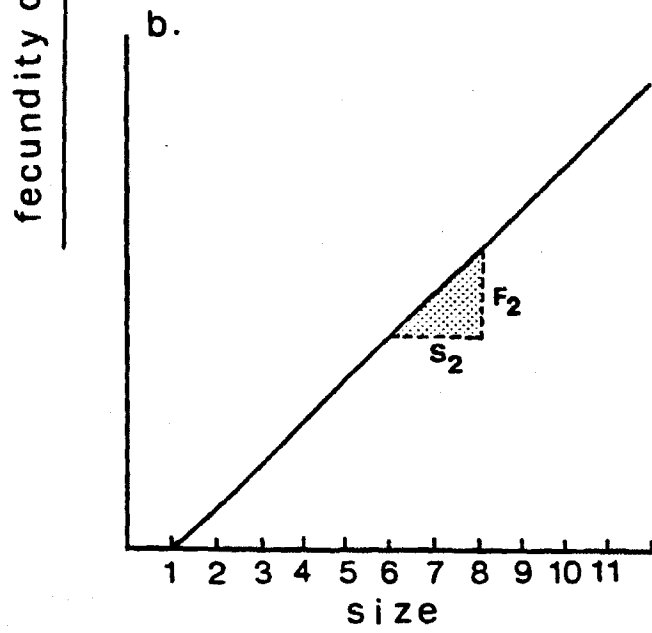
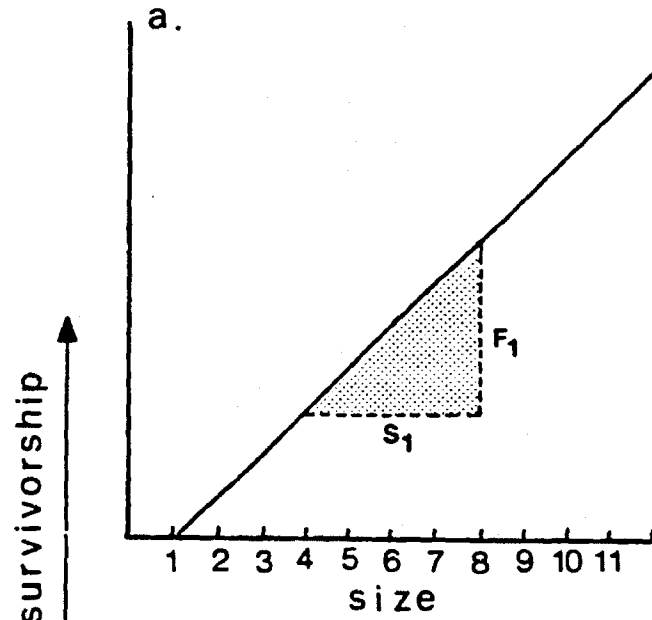
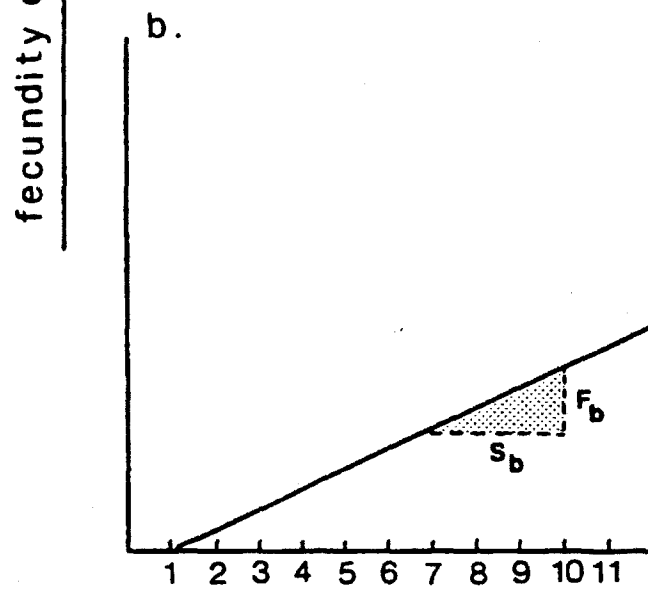
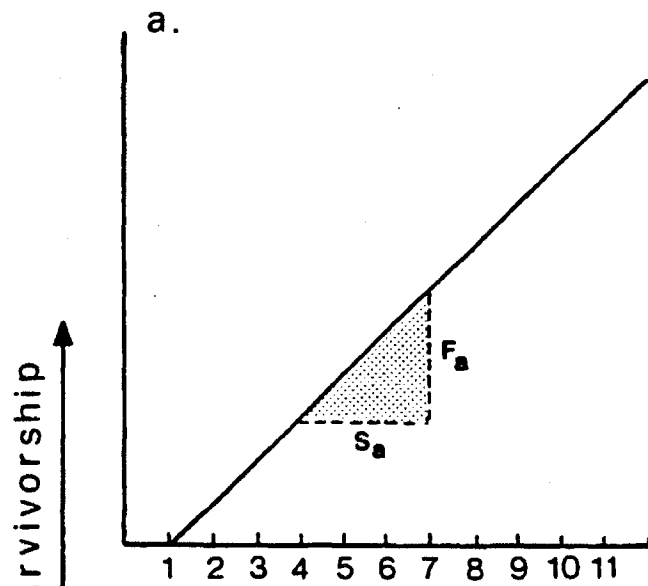


Figure 4. Comparison of the losses of the losing competitor (a) to the gains of the winning competitor (b) when fecundity/survivorship curves differ. Losses in F/S (F_a) of the loser due to a size reduction of 3 units (S_a) are greater than the gains (F_b) of the winner accrued from a size increase of 3 units (S_b).



(e.g., Lang, 1973; Sheppard, 1979, 1982; Chornesky, 1983), and by differences between species in rates of sweeper tentacle regression (c.f. chapters 1 and 2).

When competition has no clear winner

As shown in Chapter 3, direct competition between reef corals can result in stalemates where there is no clear winner. Both opponents repeatedly gain and lose tissues along their borders, and deploy various competitive structures. When stalemates occur, the direct effects of competition on community structure may be minimal. In contrast, effects on the fitness of competitors may be considerable, resulting from (i) a cessation of lateral growth, and (ii) the repeated energetic demands of using competitive structures and regenerating along damaged borders (Fig. 1c). Even though these interactions may have no apparent winner, competitors can suffer different losses depending on their specific F/S curves.

Measuring the effects of direct competition

Studies of reef corals (Lang, 1973; Connell, 1976; Sheppard, 1979; Wellington, 1980; Cope, 1982; Bak et al., 1982) and of other colonial invertebrates (Jackson and Buss, 1979; Russ, 1980; Rubin, 1980; Kay and Keough, 1982; Quinn, 1982; Ayling, 1983) usually evaluate the effects of direct competition by its obvious effects on community structure. Animals which remain undamaged or overgrow others in competitive encounters are unambiguously designated "winners," and those damaged or overgrown

are designated "losers." This is equivalent to assigning very unequal alpha coefficients ("assymetrical" as described by Connell, 1983) based only on observed interactions of adults. In this perspective, apparent "standoffs" where neither opponent gains or loses space have often been assumed to be unimportant (but see Kay and Keough, 1981).

If the above costs in fecundity and survivorship to competitors are incorporated, it becomes apparent that the outcome of direct competitive encounters may not be obvious or related in a clear way to observable patterns of damage and overgrowth. Winning is quantitative, not a qualitative "all or none" process. Ranking species by relative competitive ability will be complex and will require knowledge not only of the mechanisms and process of competition, but also of life histories and the relative importance of substrate space to competing species.

SUMMARY CONCLUSION

Sessile organisms growing on marine hard substrata are often crowded, and may overgrow one another as they increase in size. Hence competition for space is often assumed to be a conspicuous and important process structuring these communities.

For reef corals, most experimental and observational studies have tended to support this view by demonstrating that, generally, when corals come together one is damaged and susceptible to overgrowth by its undamaged opponent. The persistence of diverse scleractinian faunas despite presumably intense competition has been ascribed to the mediation of alternative processes such as predation or disturbance (Glynn, 1976; Connell, 1978; Porter et al., 1981; Bak et al., 1982) or to the balancing effects of other characteristics of competitively inferior species, such as frequent reproduction or rapid growth (e.g. Lang, 1973; Porter, 1973; Sheppard, 1982).

At least for some species, however, the unambiguous pattern of damage and overgrowth in direct competition does not hold. The delayed development and use of sweeper tentacles (Chapters 1 and 2) can lead to dynamic stalemates where neither opponent overgrows the other (Chapter 3), but both probably suffer losses (energetic or material) from repeated wounding and deployment of competitive structures (Chapter 4). When stalemates occur, competition is unlikely to result directly in the exclusion of species. The costs

in fitness incurred by competing animals (Chapter 4), however, may indirectly affect patterns of distribution by differentially reducing recruitment and survivorship. Such indirect effects will be subtle and slow, and are perhaps often offset by other events such as hurricanes and storms (Connell, 1978; Woodley et al., 1981).

Nevertheless, that some corals are able to develop and use specialized sweeper tentacles suggests that direct competition is a potent selective force on coral reefs. Thus, while competition may not generate community structure, it has probably been important in the evolution of species' adaptive strategies which, in turn, will ultimately define their distributions.

LITERATURE CITED

- Ayling, A.L. 1983. Factors affecting the spatial distributions of thinly encrusting sponges from temperate waters. Oecologia 60: 412-418.
- Bak, R.P.M. , and B.W. Elgershuizen. 1976. Patterns of oil-sediment rejection in corals. Mar. Biol. 37: 105-113.
- Bak, R.P.M., and M.S. Engel. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol. 54: 341- 352.
- Bak, R.P.M., R.M. Termaat and R. Dekker. 1982. Complexity of coral interactions: influence of time, location of interaction and epifauna. Mar. Biol. 69: 215-222.
- Bothwell, A.M. 1982. Fragmentation, a means of asexual reproduction and dispersal in the coral genus Acropora (Scleractinia: Astrocoeniida: Acroporidae)—a preliminary report. Proc. Fourth Int. Coral Reef Symp. 2: 137-144.
- Buss, L.W. 1980. Competitive intransitivity and size-frequency distributions of interacting populations. Proc. Natl. Acad. Sci. 77: 5355-5359.
- Buss, L.W. and J.B.C. Jackson. 1979. Competitive networks: non-transitive competitive relationships in cryptic coral reef environments. Am. Nat. 223-234.

- Bigger, C.H. 1976. The acrorhagial response in Anthopleura krebsi: intraspecific and interspecific recognition. Pp. 127-136 in G.O. Mackie, Ed., Coelenterate Ecology and Behavior. Plenum Press, New York.
- Bigger, C.H. 1980. Interspecific and intraspecific acrorhagial aggressive behavior among sea anemones: a recognition of self and not-self. Biol. Bull. 159:
- Birkeland, C. 1976. An experimental method of studying corals during early stages of growth. Micronesica 12: 319-322.
- Brace, R.C., J. Pavey and D.L.J. Quicke. 1979. Intraspecific aggression in the color morphs of the anemone Actinia equina: the convention governing dominance ranking. Animal Behav. 27: 553-561.
- Chornesky, E.A. 1983. Induced development of sweeper tentacles on the reef coral Agaricia agaricites: a response to direct competition. Biol. Bull. 165: 569-581.
- Chornesky, E.A. and S.L. Williams. 1983. Distribution of sweeper tentacles on Montastraea cavernosa. Pp. 61-68, in M.L. Reaka (ed.), The Ecology of Deep and Shallow Reefs. Symp. Ser. on Undersea Research, Natl. Office of Undersea Research, NOAA, Rockville, Md.

- Ciereszko, L.S. and K.B. Karns. 1973. Comparative biochemistry of coral reef coelenterates. Pp. 183-203 in O.A. Jones and R. Endean, Eds., Biology and Geology of Coral Reefs, vol. II. Academic Press, New York.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Cthamalus stellatus. Ecology 42: 710-723.
- Connell, J.H. 1973. Population ecology of reef-building corals. Pp. 205-245, in O.A. Jones and R. Endean (eds.), Biology and Geology of Coral Reefs, vol. II. Academic Press, New York.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp. 460-490, in M.L. Cody and J.M. Diamond (eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge.
- Connell, J.H. 1976. Competitive interactions and the species diversity of corals. Pp. 51-68 in G.O. Mackie, Ed., Coelenterate Ecology and Behavior. Plenum Press, New York.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122: 661-696.

- Cope, M. 1982. Interspecific coral interactions in Hong Kong. Proc. Fourth Int. Coral Reef Symp. 2: 357-362.
- Dana, J.D. 1872. Corals and Coral Islands. Dodd, Mead, and Co., New York.
- Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.
- den Hartog, J.C. 1977. The marginal tentacles of Rhodactis sanctithomae (Corallimorpharia) and the sweeper tentacles of Montastrea cavernosa (Scleractinia); their cnidom and possible function. Pp. 463-469 in D.L. Taylor, Ed., Proc. Third Int. Coral Reef Symp. Univ. of Miami Press, Coral Gables.
- Dustan, P. 1975. Genecological differentiation in the reef-building coral Montastrea annularis. Ph.D. thesis, State University of New York at Stony Brook, N.Y.
- Fadlallah, Y.H. 1983. Sexual reproduction development and larval biology in scleractinian corals. Coral Reefs 2: 129-150.
- Foster, A.B. 1979. Phenotypic plasticity in the reef corals Montastraea annularis (Ellis and Solander) and Siderastrea siderea (Ellis and Solander). Jour. Exp. Mar. Biol. Ecol. 39: 25-54.

- Cope, M. 1982. Interspecific coral interactions in Hong Kong. Proc. Fourth Int. Coral Reef Symp. 2: 357-362.
- Dana, J.D. 1872. Corals and Coral Islands. Dodd, Mead, and Co., New York.
- Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.
- den Hartog, J.C. 1977. The marginal tentacles of Rhodactis sanctithomae (Corallimorpharia) and the sweeper tentacles of Montastrea cavernosa (Scleractinia); their cnidom and possible function. Pp. 463-469 in D.L. Taylor, Ed., Proc. Third Int. Coral Reef Symp. Univ. of Miami Press, Coral Gables.
- Dustan, P. 1975. Genecological differentiation in the reef-building coral Montastrea annularis. Ph.D. thesis, State University of New York at Stony Brook, N.Y.
- Fadlallah, Y.H. 1983. Sexual reproduction development and larval biology in scleractinian corals. Coral Reefs 2: 129-150.
- Foster, A.B. 1979. Phenotypic plasticity in the reef corals Montastraea annularis (Ellis and Solander) and Siderastrea siderea (Ellis and Solander). Jour. Exp. Mar. Biol. Ecol. 39: 25-54.

- Francis, L. 1973. Interspecific aggression and its effects on the distribution of Anthopleura elegantissima and some related sea anemones. Biol. Bull. 144: 73-92.
- Gause, G.F. 1934. The Struggle for Existence. William and Wilkins, Baltimore, Md.
- Glynn, P.W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. Pp. 271-324 in O.A. Jones and R. Endean, Eds., Biology and Geology of Coral Reefs, vol. II. Academic Press, New York.
- Glynn, P.W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol. Monographs 46: 431-456.
- Goreau, T.F. 1959. The ecology of Jamaican reefs. I. species composition and zonation. Ecology 40: 67-90.
- Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.
- Hildemann, W.H., D.S. Linthicum and D.C. Vann. 1975. Transplantation and immunoincompatibility reactions among reef-building corals. Immunogenetics 2: 269-284.
- Hughes, T.P. and J.B.C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. Science 209: 713-715.
- Hughes, T.P. and J.B.C. Jackson. In press. Population dynamics and life histories of foliaceous corals. Ecol. Monogr.

- Ivker, F.B. 1972. A hierarchy of histo-incompatibility in Hydractinia echinata. Biol. Bull. 143: 162-174.
- Jackson, J.B.C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Amer. Nat. 111: 743-767.
- Jackson, J.B.C. 1979a. Morphological strategies of sessile animals. Pp. 499-555 in G. Larwood and B.R. Rosen, Eds., Biology and Systematic of Colonial Organisms. Academic Press, New York.
- Jackson, J.B.C. 1979b. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. Jour. Anim. Ecol. 48: 805-823.
- Jackson, J.B.C. and J.E. Winston. 1982. Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. Jour. Exp. Mar. Biol. Ecol. 57: 135-147.
- Johnston, I.S., P.L. Jokiel, C.H. Bigger, and W.H. Hildemann. 1981. The influence of temperature on the kinetics of allograft reactions in a tropical sponge and a reef coral. Biol. Bull. 160: 280-291.
- Karlson, R.H. 1980. Alternative competitive strategies in a periodically disturbed habitat. Bull. Mar. Sci. 30: 894-900.

- Karlson, R.H. and M.A. Shenk. 1983. Epifaunal abundance, association, and overgrowth patterns on large hermit crab shells. J. Exp. Mar. Biol. Ecol. 70: 55-64.
- Kay, A.M. and M.J. Keough. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve Pinna bicolor at Edithburgh, South Australia. Oecologia 48: 123-130.
- Kojis B.L. and N.J. Quinn. 1981. Aspects of sexual reproduction and larval development in the shallow water hermatypic coral Goniastrea australensis (Edwards and Haime, 1857). Bull. Mar. Sci. 31: 558-573.
- Kojis B.L. and N.J. Quinn. 1982. Reproductive strategies in four species of Porites (Scleractinia). Proc. Fourth Int. Coral Reef Symp. 2: 143-151.
- Lang, J.C. 1971. Interspecific aggression by scleractinian corals I. the rediscovery of Scolymia cubensis (Milne Edwards and Haime). Bull. Mar. Sci. 21: 952-959.
- Lang, J.C. 1973. Interspecific aggression by scleractinian corals II. why the race is not always to the swift. Bull. Mar. Sci. 23: 260-279.
- Lang, J.C. 1979. Are the sweeper tentacles of Montastraea cavernosa polyfunctional organs? Proc. Assn. Mar. Biol. Lab.

- Lewis, J.B. and W.S. Price. 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. J. Zool. Lond. 176: 527-544.
- Loya, Y. 1976. The Red Sea coral Stylophora pistillata is an r strategist. Nature 259: 478-480.
- Osman, R.W. 1977. The establishment and development of a marine epifaunal community. Ecol. Monogr. 47: 37-63.
- Ottaway, J.R. 1978. Population ecology of the intertidal anemone Actinia tenebrosa I. pedal locomotion and intraspecific aggression. J. Mar. Freshwater Res. 29: 787-802.
- Peterson, C.H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, Protothaca staminea and Chione undatella. Ecol. Monogr. 52: 437-475.
- Pianka, E.R. 1975. Competition and niche theory. Pp. 114-141, in R.M. May (ed.), Theoretical Ecology, Principles and Applications. W.B. Saunders, Co., Philadelphia, Pa.
- Porter, J.W. 1972. Patterns of species diversity in Caribbean reef corals. Ecology 53: 744-748.
- Porter, J.W. 1974. Community structure of coral reefs on opposite sides of the isthmus of Panama. Science 186: 543-545.
- Porter, J.W. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. Amer. Nat. 110: 731-742.

- Porter, J.W., J.D. Woodley, G.D. Smith, J.E. Neigel, J.F. Battey, and D.G. Dallemeyer. 1981. Competition and catastrophe: population trends in Jamaican reef corals. Nature 294: 249-250.
- Potts, D.C. 1977. Growth interactions among morphological variants of the coral Acropora palifera. Pp. 79-88 in G.O. Mackie, Ed., Coelenterate Ecology and Behavior. Plenum Press, New York.
- Purcell, J.E. 1977. Aggressive function and induced development of catch tentacles in the sea anemone Metridium senile (Coelenterata, Actiniaria). Biol. Bull. 153: 355-368.
- Purcell, J.E. and C.L. Kitting. 1982. Intraspecific aggression and population distribution of the sea anemone Metridium senile. Biol. Bull. 162: 345-359.
- Quinn, J.F. 1982. Competitive hierarchies in marine benthic communities. Oecologia 54: 129-135.
- Richardson, C.A., P. Dustan and J.C. Lang. 1979. Maintenance of living space by sweeper tentacles of Montastrea cavernosa. Mar. Biol. 55: 181-186.
- Rinkevich, B. and Y. Loya. 1979. The reproduction of the Red Sea coral Stylophora pistillata. I. Gonads and planulae. Mar. Ecol. Prog. Ser. 1: 133-144.

- Rinkevich, B. and Y. Loya. 1983. Intraspecific competitive networks in the Red Sea Coral Stylophora pistallata. Coral Reefs 1: 161-172.
- Rubin, J.A. 1982. The degree of intransitivity and its measurement in an assemblage of encrusting cheilostome bryozoa. Jour. Exp. Mar. Biol. Ecol. 60: 119-127.
- Russ, G.R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. Oecologia 53: 12-19.
- Ruetzler, K. 1970. Spatial competition among Porifera: solution by epizoism. Oecologia 5: 85-95.
- Rylaarsdam, K.W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. Mar. Ecol. Prog. Ser. 13: 249-260.
- Sammarco, P.W., J.C. Coll, S. La Barre, and B. Willis. 1983. Competitive strategies of soft corals (coelenterata: octocorallia): allelopathic effects on selected scleractinian corals. Coral Reefs 1: 173-178.
- Sheppard, C.R.C. 1979. Interspecific aggression between reef corals with reference to their distribution. Mar. Ecol. Prog. Ser. 1: 237-247.
- Sheppard, C.R.C. 1982. Coral populations on reef slopes and their major controls. Mar. Ecol. Prog. Series 7: 83-115.
- Stearns, S.C. 1976. Life history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

- Stebbing, A.R.D. 1973. Competition for space between the epiphytes of Fucus serratus L. J. Mar. Biol. Assn. U.K. 53: 247-261.
- Theodor, J.L. 1970. Distinction between "self" and "not-self" in lower invertebrates. Nature 227: 690-692.
- van Moorsel, G.W.N.M. 1983. Reproductive strategies of two closely related stony corals (Agaricia, Scleractinia). Mar. Ecol. Prog. Ser. 13: 273-283.
- Wahle, C.M. 1980. Detection, pursuit and overgrowth of tropical gorgonians by Milleporid hydrocorals: Perseus and Medusa revisited. Science 209: 689-691.
- Wahle, C.M. 1983. The roles of age, size and injury in sexual reproduction among Jamaican gorgonians. Amer. Zool. 23: 961.
- Watson, G.M. and R.N. Mariscal. 1983. The development of a sea anemone tentacle specialized for aggression: morphogenesis and regression of the catch tentacle of Haliplanella luciae (cnidaria, anthozoa). Biol. Bull. 164: 506-517.
- Wellington, G.M. 1980. Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47: 340-343.
- Wells, J.W. 1956. Scleractinia. Pp. 328-444, in R.C. Moore (ed.), Treatise on Invertebrate Paleontology. Geol. Soc. of America and Univ. of Kansas Press. Lawrence, Kansas.

Wells, J.W. 1973. New and old scleractinian corals from Jamaica.

Bull. Mar. Sci. 23: 16-58.

Woodley, J.D., E.A. Chornesky, P.A. Clifford, J.B.C. Jackson,

L.S. Kaufman, N. Knowlton, J.C. Lang, M.P. Pearson, J.W.

Porter, M.C. Rooney, K.W. Rylaarsdam, V.J. Tunnicliffe,

C.M. Wahle, J.L. Wulff, A.S.G. Curtis, M.D. Dallemeyer,

B.P. Jupp, M.A.R. Koehl, J. Neigel, and E.M. Sides.

1981. Hurricane Allen's impact on Jamaican coral reefs.

Science 214: 749-755.

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