in Fig. 1b (17). The close association of provinces with water masses is apparent. We suggest that the northern coastal province is related to marginal waters, the northern shelf province to shelf (coastal) water, the northern outer shelf and slope province to slope water, and the northern slope and rise province to open Atlantic water characterized in the study area by the Western Boundary Undercurrent and the Gulf Stream. South of Cape Hatteras, the shelf province is related to southern shelf (coastal) water and the southern slope province (inner Blake Plateau) to water of the Florida and Antilles currents. The northern slope province is more closely similar to the southern slope province than to the northern shelf province, again indicating close association of provinces with water masses. In southern Florida a tropical province (the Bahaman) makes its first appearance and may be related to a change of the sedimentary environment (18) to a mainly carbonate regime.

A meaningful pattern thus results from the analysis of a large data set based on the work of 102 investigators over 130 years. The outcome presented here should encourage workers to compile and analyze similar data sets on other groups of organisms.

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14 February 1980; revised 25 April 1980

Detection, Pursuit, and Overgrowth of Tropical Gorgonians by Milleporid Hydrocorals: Perseus and Medusa Revisited

Abstract. *Encounters leading to competitive interactions between colonies on coral reefs are to some extent accidents of patterns of recruitment and growth. In contrast, colonies of* Millepora *spp. actively detect nearby arborescent gorgonians and subsequently redirect growth in order to contact and overgrow them. Detection is dependent on water flow over the two colonies.*

Interactions between organisms are common and important ecological phenomena often affecting their fitness, distribution, and abundance. Many very different types of interaction, such as predator-prey, direct competition, parasite-host, and mating involve, and are preceded by, direct contact between organisms. The predictability of such encounters between potentially interacting organisms is an important ecological parameter. A species' ability to influence its interactions by precipitating or avoiding specific encounters will depend largely on its degree of mobility and behavioral complexity. Thus, interactions between many sessile organisms, such as plants and colonial animals, appear to be the result of patterns of recruitment and normal, vegetative growth (1, 2). Here I describe a competitive interaction between adult colonies of two common coral reef taxa in which the initial encounter results from mechanisms more often associated with mobile organisms: detection and pursuit (in the form of directed growth) of arborescent gorgonians by competitively superior (3) milleporid hydrocorals.

Millepora alcicornis (branched) and *M. complanata* (bladelike) normally produce erect, planar colonies oriented perpendicularly to water flow (4, 5). In contrast, colonies of both species pursuing nearby gorgonians redirect growth of varying numbers of specialized branches out of the colony plane, horizontally toward the target gorgonian. These attack branches (6) elongate, bifurcating into handlike structures that eventually contact, abrade, encircle, and encrust branches of the target gorgonian, ultimately overgrowing the entire colony (Fig. 1, a and b).

A survey of this interaction on the shallow (7 m) fore reef of northern Jamaica reveals two characteristic patterns, substantiated by qualitative observations elsewhere in Jamaica and in Belize (C.A.). *Millepora* colonies produced attack branches exclusively toward nearby (within 30 cm) living colonies of many of the common gorgonian species, and never into open water or toward other potential substrata, such as dead gorgonians, live or dead coral, sponges, algae, or other *Millepora*. Attacks by *Millepora* exhibited a highly significant directional component. Of 75 recorded attacks, 95 percent originated from *Millepora* colonies down-current (in the oscillating wave surge) from target gorgonians (7). The observed specificity and directionality of attacks suggest that production of attack branches by *Millepora* is neither a device to randomly search for new substrata, nor a general response to any nearby object; rather it is a specific response to living gorgonians detected by water flow over them and onto *Millepora*.

I tested these hypotheses by experimentally inducing in situ production of attack branches from previously normal, planar, and noninteractive colonies of *M. alcicornis*. To determine whether

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Millepora can distinguish (measured by differential response) between a living gorgonian colony and an inanimate model of similar shape and proportions, I paired ten *M. alcicornis* colonies with living colonies of the common gorgonian, *Plexaura homomalla*, and ten with *P. homomalla*'s internal skeleton, stripped of living tissue. To test whether detection of a potential target (live or dead) is dependent on water flow over it, half the *Millepora* colonies in each treatment were placed down-current from their target, and half cross-current (*8*).

The results shown in Table 1 confirm both hypotheses. *Millepora* respond only to living gorgonians (Table 1); inanimate models are not detected (χ^2 test of independence, with down-current pairs; $P < .001$). Detection of living gorgonians is significantly related to orientation of the *Millepora*-target pair relative to current direction (χ^2 test of independence; $P < .05$), with *Millepora* colonies down-current from living targets responding more often than those cross-current. Among responding *Millepora* colonies, the initial change in growth direction was evident after 1.5 months and was followed by elongation and bifurcation of attack branches up to 3 cm horizontally toward target gorgonians (Fig. 1, c to f).

The observation that *Millepora* attacks only gorgonians, combined with its

Table 1. Induction of attack branches in *M. alcicornis* (ratio of colonies responding/colonies in treatment).

Orientation	Target	
	Live	Dead
Down-current	5/6	0/4
Cross-current	1/5	0/5

demonstrated ability to distinguish between living and dead colonies, strongly suggests that *Millepora* colonies detect and respond to some product or products of biological processes unique to living gorgonaceans (*9*). Detection of other organisms by chemoreception is common among many marine taxa and is involved in feeding, reproductive, and social interactions (*10*). Caribbean gorgonians contain a variety of unique compounds (*11*), and there is evidence that *P. homomalla* secretes compounds detectable by other organisms (*12*). Lack of response by experimental *Millepora* colonies to intermittent contact with dead gorgonian targets and observations of attacks by colonies physically separated from their living gorgonian targets argue against mechanical stimulation by swaying gorgonian branches as the primary mechanism of detection. Perhaps chemoreception and mechanical stimulation act sequentially; the former initiating production of attack branches, the latter influencing morphological changes in approaching attack branches.

This competitive interaction between sessile marine animals is analogous to detection and location of host trees by some tropical climbing vines that grow toward the darkness of their trunks (*13*). In contrast to these obligate climbers, *Millepora* is a facultative encrusting genus, able to independently construct a carbonate corallum (*4*). Nevertheless, *Millepora* colonies undergo radical changes in growth form and direction in order to encounter and encrust nearby gorgonians. In doing so, a *Millepora* colony can predictably expand over preexisting erect substrata of similar orientation, with relatively less expenditure of skeletal materials than production of an independent, nonencrusting corallum (*14*). Asexual reproduction of physically separate but genetically identical *Millepora* colonies may increase the probability of genotype survivorship (*15*), and it creates the potential for unlimited increase in colony size (and presumably fecundity). Random searching or directed growth induced by any nearby object could result in contact with unsuitable substrata or with potentially superior competitors such as some sponges (*15a*). Among colonial animals for which limited contact can lead to complete overgrowth, perhaps the apparent specificity of this response reflects the importance

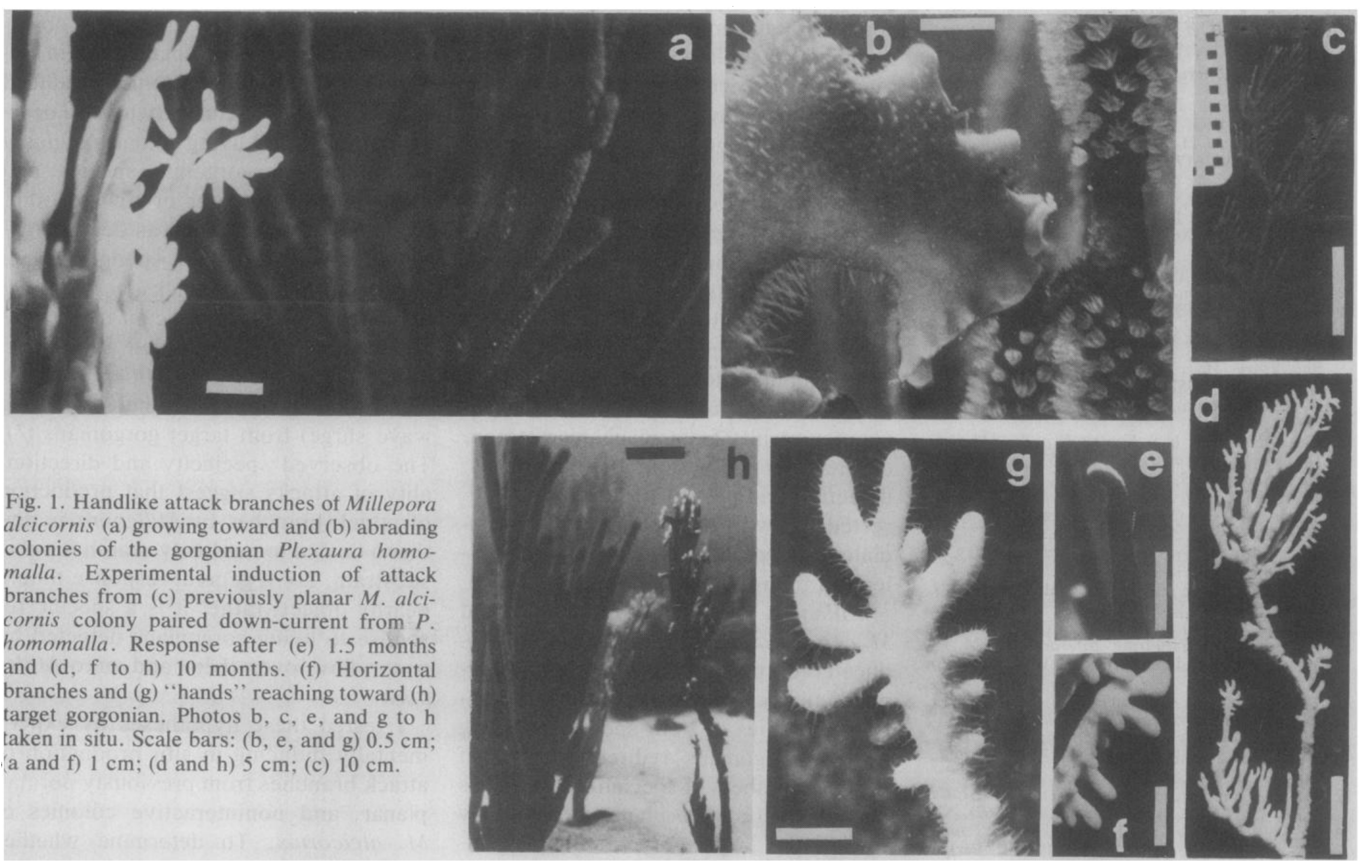

Fig. 1. Handlike attack branches of *Millepora alcicornis* (a) growing toward and (b) abrading colonies of the gorgonian *Plexaura homomalla*. Experimental induction of attack branches from (c) previously planar *M. alcicornis* colony paired down-current from *P. homomalla*. Response after (e) 1.5 months and (d, f to h) 10 months. (f) Horizontal branches and (g) "hands" reaching toward (h) target gorgonian. Photos b, c, e, and g to h taken in situ. Scale bars: (b, e, and g) 0.5 cm; (a and f) 1 cm; (d and h) 5 cm; (c) 10 cm.

of avoiding the wrong competitive encounters as much as precipitating the right ones.

Competitive interactions between colonies on a coral reef often occur over relatively short distances at zones of contact (*16*). Thus, whether two colonies will meet and interact will depend largely on patterns of recruitment and normal, asexual growth. The erect and planar growth form of *Millepora* and many gorgonians makes sustained contact and interaction relatively unlikely. *Millepora*'s ability to actively detect and pursue a predictably inferior competitor from some distance has some interesting implications for the mechanics of interactions on coral reefs. In effect, this interaction begins not when contact is made (and observed) but when the target gorgonian is detected. This means that, as an interactive unit, the effective boundaries of a potential target gorgonian extend beyond its physical margins to the distance over which it can be detected. Since detection is dependent on directional water flow, the initial settlement patterns of potentially interacting colonies will profoundly affect future events.

The basic ecological difference between mobile and sessile organisms is the ability to actively change locations and thereby influence specific encounters and interactions. For *Millepora*, and perhaps other sessile marine taxa which use directed growth rather than motion; this apparently fundamental difference is more one of method and time scale than one of effect.

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7. Seventy-five interactions were examined in an area of approximately 200 m^2 at Gorgo City, 3 miles west of Discovery Bay, Jamaica. Surge axis is north–south. Frequency of positions of attacking *Millepora* relative to target gorgonians (north, 40; south, 31; east, 1; west, 3) were significantly different as judged by the χ^2 goodness-of-fit test. Down-current attacks did not differ significantly between north and south.
8. *Millepora*-target pairs were clamped facing the current on parallel P.V.C. pipes separated by 15 cm; pairs were separated by 60 cm. The experiment ran for 10 months between 1 October 1977 and 1 August 1978 at the site in (*7*). Horizontal growth in *Millepora* colonies constituted a positive response. Loss and replacement of some *Millepora* colonies created unequal final sample sizes; all were paired longer than the minimum response time (1.5 months).
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30 January 1980; revised 5 May 1980

Endocytotic Sucrose Uptake in *Amoeba proteus* Induced with the Calcium Ionophore A23187

Abstract. *The calcium ionophore A2187 brings about an influx of calcium and uptake of sucrose by endocytosis in* Amoeba proteus. *The amount of endocytotic sucrose uptake elicited by the ionophore depends upon the external calcium ion concentration. Calcium ion movements may serve to couple the surface phase of endocytosis with cytoplasmic uptake of the endocytotic inducer.*

Endocytosis is a basic cellular process by which extracellular solute is taken up by cell surface membrane infolding and vesiculation. Uptake of solute in this manner, distinct from carrier-mediated transport processes, is a physiological mechanism responsible for the uptake of large, normally impermeant, solute molecules. There is increasing evidence that Ca^{2+} plays an important role in endocytosis, as it apparently does in exocytosis (*1*). In *Amoeba proteus*, a model system used to investigate endocytosis (pinocytosis), maximum endocytotic activity requires an optimal concentration of Ca^{2+} in the external medium, on the order of $10^{-4}M$. In addition, the inducer of endocytosis in the amoeba displaces a dose-dependent amount of calcium from the cell surface (*2*). In this study with amoebas, addition of the calcium ionophore A23187 to the external medium resulted in an influx of Ca^{2+} and the endocytotic uptake of sucrose from the external medium—further evidence that Ca^{2+} plays a pivotal role in the mechanism of endocytosis.

In *Amoeba proteus*, endocytosis is normally brought about by a variety of positively charged solute molecules that bind to the surface of the cell (*3*). This is followed by cessation of locomotion, the development of numerous surface projections, and the invagination of channels leading from the tips of these projections into the cytoplasm. Finally, the bases of the channels are pinched off into vesicles containing surface membrane with adsorbed inducer and a portion of the bulk medium (*4*). How the initial interaction of the endocytotic inducer with the surface is coupled with its eventual uptake by endocytosis is not known, but it has been established that the onset of endocytosis in the amoeba is accompanied by physiological and structural changes in the cell membrane. These include an increase in membrane conductance and a reversible increase in the thickness of the membrane lipid lamella (*5*). Associated with these changes in the cell membrane is a possible movement of the calcium ion, which may serve to couple the surface phase of endocytosis with subsequent cytoplasmic events (*1*). This possibility was investigated by use of the calcium ionophore A23187 (*6*).

This ionophore is an antibiotic that acts as a carrier for Ca^{2+}. Structurally, A23187 is a relatively complex carboxylate compound with a molecular weight of 523. The ionophore forms a complex with Ca^{2+} only in its deprotonated anionic form, with two A23187 anions taking up a pseudocyclic conformation around one calcium ion. In this configuration the

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