Water flow and coral colony size: Interhabitat comparisons of the octocoral *Alcyonium siderium*

(Anthozoa/body size/growth/size gradients/population structure)

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Communicated by E. O. Wilson, May 16, 1984

ABSTRACT Colonies of the octocoral Alcyonium siderium Verrill form aggregations on subtidal vertical rock walls in the Gulf of Maine. Maximum and mean colony sizes increase dramatically from protected embayments to sites exposed to ocean swells and from the bottom to the top of each vertical wall studied. Water movement along the substratum, generated by surface waves and tides, also increases along both gradients. Although plankton concentrations were similar at all sites during a 2-yr period, increased encounter rates of zooplankton with coral tentacles will result in greater energy intake and. thus, faster growth rates at the more exposed sites with greater flow. Other hypotheses for the proximate cause of the size gradient, such as differential mortality of large colonies or generally higher mortality rates at the protected site, are not consistent with available data.

Coral colonies are long-lived organisms that display highly indeterminate growth (1-3). Environmental variables such as depth, plankton concentration, and light intensity are known to influence coral growth (4, 5). Water movement (current, wave action) also affects the shape of coral colonies (6-8)and probably their growth rate as well (5).

The octocoral Alcyonium siderium grows as globose or lobed colonies on subtidal rock walls (6–18 m depth) in the Gulf of Maine (8–13). Sites within embayments, protected from the prevailing ocean swells, have small finger-like colonies (Fig. 1) [e.g., $11 \pm 4 \text{ mm}$ (SD) contracted width, $17 \pm 6 \text{ mm}$ (SD) height], while sites facing the ocean swells (Shag Rocks) have larger and more globose colonies [e.g., $15 \pm 11 \text{ mm}$ (SD) width, $30 \pm 12 \text{ mm}$ (SD) height]. The largest colonies observed to date are on the ocean-facing side of an offshore rock pinnacle [Halfway Rock, $55 \pm 28 \text{ mm}$ (SD) width, $56 \pm 23 \text{ mm}$ (SD) height]. Alcyonium is a passive suspension feeder, capturing small zooplankton [300 $\pm 250 \mu \text{m}$ (SD)] and detritus particles, but not phytoplankton, with its finely branched (pinnate) tentacles (9).

This study is an attempt to determine the possible causal factors by which colony size increases in habitats with greater water movement. Water movement may directly affect colony growth rate, mortality, or reproduction. Alternatively, the effects of predators, or the availability of food, may differ between these sites, all of which may affect size.

METHODS

Alcyonium Population Characteristics. Study sites were located along the coast of northern Massachusetts (Nahant, 42°25' N: 70°54' W; Halfway Rock, 42°30' N: 70°46' W). At each study site, the rock walls with the greatest vertical extent and the most extensive populations of Alcyonium were chosen for study. Colony sizes were measured by beginning at one of three points on the wall (0.5 m below the top, 0.5 m above the bottom, and at the center of the wall) and working outward radially until 50 colonies of \geq 5 mm diameter had been measured. The height and two diameters (maximum, minimum) of each expanded colony were recorded.

Growth and mortality of *Alcyonium* were determined by mapping colonies from projected photographs of marked quadrats (four 18×28 cm quadrats per site). Colonies were measured (two diameters) during the winter when most were contracted (January-March of 1982 and 1983). The annual size changes of individual colonies were then plotted for 170-200 colonies per site. Regressions of size after 1 yr to initial size could then be compared statistically between sites. Mortality was determined by summing the colonies in each original size class that disappeared over 1 yr.

Water Movement and Zooplankton Concentrations. Water movement at each site was quantified by three methods. (i) A single observer estimated the average height of the largest one-third of waves passing the boat mooring on each site visit. (ii) The vertical displacement of the intertidal barnacle (*Balanus balanoides*) above mean low water was estimated by measuring (sighting on the horizon) the elevation on a pole held at low water and the elevation of the top of the barnacle zone at five points >2 m apart. (iii) Near-substratum flow was measured on several site visits with a microthermistor flow meter held on a tripod with the thermistor bead 1 cm above a large *Alcyonium* colony (M. Patterson, personal communication).

Zooplankton concentrations were measured from samples taken every 2 weeks for 2 yr. Divers towed a 50- μ m mesh plankton net between known points along rock walls (20–30 m apart) at a distance of 10–40 cm from the substratum. Samples were preserved in 4% buffered formalin in seawater. Zooplankton were counted, measured, and identified from subsamples until 100 recognizable items, starting from a random point, were encountered. The volume of the subsample searched (in a Sedgwick–Rafter cell) as a fraction of the total sample volume was used to calculate total zooplankton in the sample. Only zooplankton $\leq 600 \ \mu$ m were included because items $> 600 \ \mu$ m were very rare in the *Alcyonium* diet (9). Net opening size, net porosity, and towed distance length were used to calculate total water volume processed to collect each sample.

RESULTS

Mean colony diameters differed significantly between sites at the tops (analysis of variance, $F_s = 123$, df = 2, 131, P < 0.001), middles ($F_s = 209$, df = 1, 97, P < 0.001), and bottoms ($F_s = 118$, df = 2, 147, P < 0.001) of the three walls, with sizes increasing from inner East Point to the Shag Rocks to Halfway Rock (Fig. 1). Multiple comparison tests (Student-Newman-Keuls test) showed significant differences between Halfway Rock and each of the other sites but not between inner East Point and Shag Rocks. There were significant differences in mean colony diameter between samples from the same wall at the Shag Rocks ($F_s = 3.4$, df = 2, 145, P < 0.05), where the top sample differed signifi-

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FIG. 1. (Upper) Mean and maximum widths (mean of two diameters) of Alcyonium siderium at the top (\bullet), middle (\blacktriangle), and bottom (\odot) of subtidal vertical rock walls (7–10 m depth). Means ± 1 SD of each dimension are given for 40–50 corals. Sites, in order of increasing water movement, are as follows: inner East Point, Shag Rocks, Halfway Rock. Total wall heights were 1.5 m at inner East Point, 2 m at Shag Rocks, and 3 m at Halfway Rock. (Lower) Histograms illustrate the population size structure on the largest wall (Halfway Rock). See text for statistical differences between mean and maximum sizes across sites and within each wall.

cantly from the bottom one, and at Halfway Rock ($F_s = 4.1$, df = 2, 132, P < 0.05), where the top and middle samples differed from the bottom one by the multiple comparisons test, but there were no significant differences between top and bottom at inner East Point.

Maximum colony diameters were determined as the mean of the largest 10% of colonies in each sample. These values also differed significantly between sites at the tops ($F_s =$ 38.2, df = 2, 12, P < 0.001), middles ($F_s = 90.9$, df = 2, 12, P << 0.001), and bottoms ($F_s = 58.6$, df = 2, 12, P < 0.001) of the three walls, with sizes increasing in the same direction as the mean diameters. By this measure, both inner East Point and the Shag Rocks differed from Halfway Rock (multiple comparisons test). At Halfway Rock, there were significant differences between samples from the same wall ($F_s = 14.8$, df = 2, 12, P < 0.01), where the means of top and middle samples were both larger than that of the bottom sample. Differences were not significant for walls at Shag Rocks and inner East Point.

Colony height also increased from inner East Point to the Shag Rocks to Halfway Rock and from the bottom to top of each wall, although most differences were not significant because colonies increase the height to width ratio from the top to the bottom of walls at the Shag Rocks and at Halfway Rock. Colony volume must thus also change across habitats following the same pattern as for mean diameter.

During 1978–1980, 393 Alcyonium were collected from the three sites (monthly to bimonthly, three 10×10 cm quadrats

per site). All colonies were relaxed in 7.5% MgCl (1:1 in seawater) then preserved in 7% buffered formalin in seawater. Mean colony biomass (blotted wet weight, square root transform) was 0.29 g, 0.25–0.34 g 95% confidence limits (n =221) at inner East Point, 0.76 g, 0.60–0.93 g 95% confidence limits (n = 121) at Shag Rocks, 6.71 g, 4.34–9.59 g 95% confidence limits (n = 51) at Halfway Rock. These samples are all significantly different from each other (analysis of variance; $F_s = 26.5$; df = 2, 390; P < 0.001, Student–Newman–Keuls multiple comparison test). Biomass thus increases along the same gradient of habitats as does the mean diameter.

Water movement at these sites (6–8 m depth) is primarily bidirectional surge generated by incoming ocean swells and by wind waves (8) with some effect of tidal flow. Observed wave heights during 2 yr of site visits indicate that Halfway Rock experiences almost twice the wave action as at the Shag Rocks site; the protected inner East Point site experiences the least, approximately one-half that at Shag Rocks (Table 1).

Another, and probably more accurate, index of wave action at each site is the vertical extension of the intertidal barnacle zone (Balanus balanoides). Barnacles can survive higher on the shore when there is more wave action and splash. This measure, which biologically integrates longterm wave conditions, also indicates that Halfway Rock has by far the most wave action, and inner East Point has the least (Table 1). Thermistor flow meter recordings taken at the height of the largest colony tops on 16 sampling visits also showed the slowest flow at inner East Point, faster water flow at the Shag Rocks, and the greatest water flow at Halfway Rock (M. Patterson, personal communication). In addition, Halfway Rock is 5 km offshore and tidal currents are much more noticeable there and at the Shag Rocks than at inner East Point (unpublished observations). Water movement also increases substantially from the bottom of vertical rock walls to the top. Patterson (8) measured flow at points along a wall at the inner East Point site during moderately heavy wave action and found mean speeds of 12 cm·s⁻¹ near the bottom to 35 cm \cdot s⁻¹ at the top of the wall.

The general pattern that emerges is that colonies are larger where water movement is the greatest on both geographic (between sites) and microhabitat (within walls) scales. Although there is a clear correlation between greater water movement and large colony size, there are several alternative (but not mutually exclusive) hypotheses that might explain the proximate cause of this pattern. They are as follows: (*i*) growth rates and, thus, final (maximum) colony sizes are greater at the more exposed sites, (*ii*) mortality rates are greater at the more protected sites and, thus, colonies never persist long enough to grow to a large size, and (*iii*) there has been genetic differentiation between populations leading to different controls on growth rate and, thus,

Table 1. Indicators of water movement at the three study sites

Site	Water movement		
	Wave height, m	Exposure, m	Mean flow, cm·s ⁻¹
Inner East		· · · · · · · · · · · · · · · · · · ·	
Point	0.24 ± 0.24 (38)	1.2 ± 0.2 (5)	9.5 ± 4.7 (18)
Shag Rocks	0.45 ± 0.24 (38)	1.7 ± 0.1 (5)	$13.7 \pm 8.6(21)$
Halfway Rock	0.78 ± 0.45 (15)	2.5 ± 0.1 (5)	19.8 ± 10.2 (5)

Wave height is the average of the greatest one-third of waves estimated by a single observer. The exposure index is the vertical extention of the intertidal barnacle (*B. balanoides*) zone. Barnacles live higher on the shore where there is more wave action and splash. Mean flow was calculated from microthermistor readings taken 1 cm above the top of *Alcyonium* colonies in the field (M. Patterson, personal communication). All values are means ± 1 SD. Number of observations is in parentheses. on final colony size at each site.

Alcyonium reproduces by brooding and then releasing crawling larvae, which generally settle within centimeters of an adult colony (10–13). Given such short-range dispersal, there is certainly the potential for genetic differentiation between populations at different sites. However, this last hypothesis is unlikely to be the primary cause of the size gradient on any one wall given that a similar pattern of increasing colony size with greater water movement occurs within each population (bottom to top of walls) as well as between populations (sites). Experimental transplants of Alcyonium between sites have been initiated to determine the extent to which growth is environmentally determined.

The mortality hypothesis was tested by photographing and mapping colonies at the most protected and most exposed sites over the period January 1982 to January 1983. During that period there was much greater mortality at the exposed than at the protected sites (Fig. 2); this is exactly the opposite of the hypothesized result. In addition, large colonies at both sites had the lowest mortality, indicating that mortality alone is not preventing corals at the protected site from attaining large colony size. Alcyonium has few predators; the most important is the nudibranch Coryphella verrucosa, although the sea urchin Strongylocentrotus droebachiensis can kill small colonies (13). Both were present at the two exposed sites: the protected site had only the nudibranch. Coryphella grazes polyps from even the largest colonies. Its densities during fall, winter, and spring of 1981-1983 were $5.6 \text{ m}^{-2} \pm 6.6 \text{ (SD)} (n = 11) \text{ at inner East Point, } 15.9 \text{ m}^{-2} \pm 10^{-2} \text{ m}^{-2} \text{ m}^$ 16.9 (SD) (n = 9) at Shag Rocks and 10.1·m⁻² ± 11.1 (SD) (n= 10) at Halfway Rock. The sudden disappearance of large colonies at Halfway Rock suggests that hydrodynamic drag induced by winter storms may have torn at least some of the colonies off the rock. Total mortality is the sum of that from both physical and biological sources, both of which are greater at the exposed sites.

According to the growth hypothesis, whole colony growth rates should be greater at the exposed site; this was indeed the case. Contracted colonies were measured in photographs 1 yr apart, and their annual growth increments are shown on a Ford-Walford plot (Fig. 3). The regressions of size in the second year to size in the first year had a higher slope (1.09, with 95% confidence limits of 1.01-1.16) at the exposed site than at the protected site (0.71, with 95% confidence limits of 0.59-0.88), although slopes did not differ by analysis of covariance. The elevations of the two lines were significantly different (t = 2.77; P < 0.001), indicating significantly



FIG. 2. Mortality of *Alcyonium* colonies over 1 yr (1982–1983) as a function of mean colony diameter at Halfway Rock (most exposed) and at the inner East Point site (most protected). Numbers above bars are the initial sample sizes of colonies within that size class. Larger colonies have been combined into wider categories because of the fewer number of colonies available.



FIG. 3. Growth rates of Alcyonium colonies (mean of two diameters) at Halfway Rock (most exposed) and at the inner East Point site (most protected). Graphs are Ford-Walford plots where ZG = zero growth line (y = x); least-squares regressions were $y = 1.09 \times +1.12$ exposed, $R^2 = 0.91$; $y = 0.712 \times +2.95$ protected, $R^2 = 0.42$. Note that the axes are drawn to different scales. RP, regression line for corals at the protected site; RE, regression line for corals at the exposed site. Both are drawn on the exposed site plot for comparison.

greater annual growth at any size class. Of great interest is the fact that the regression line at the protected site has a slope significantly <1.0, indicating that colonies at this site were approaching a size asymptote at about 12-mm mean diameter, where the regression line crosses the diagonal (y = x) of the plot. Colonies at Halfway Rock were still growing at all sizes, including the largest, and no such asymptotic size can be predicted. Put another way, colonies at the protected site appear to be reaching an energetically determined size limit where energy intake from prey capture just equals the summed cost of maintenance metabolism and the allocation to reproduction (14, 15). Colonies at the most exposed site still have energy that can be allocated to growth and thus their maximum size must be set by other factors.

The difference in growth rates and maximum sizes can be the result of at least four factors or combinations of these: (i) greater plankton concentrations in the water at the more exposed sites, (ii) higher encounter rates of zooplankton with coral polyps because of greater water movement, (iii) lower metabolic rates of corals in conditions of greater water movement, or (iv) less energy devoted to reproduction at sites where corals are largest. Plankton samples collected for 2 yr at the three sites (Fig. 4) showed no significant differences in concentration at the sites for the entire year; neither did samples during the 6 warmest months when plankton was most abundant. There was a small but significant difference between the Halfway Rock samples and the inner East Point samples only during the cold months when plankton were least abundant (analysis of variance, $F_s = 3.9$, df = 2, 41, P < 0.05). In general, absolute numbers of zooplankton per unit water volume at the exposed and protected sites were very similar but, because of greater water movement at the exposed sites, the actual encounter rates of zooplankton with coral polyp tentacles are likely to be much higher there. It is this difference in average flow speed that is the most likely proximate cause of the observed colony size gradients.

There is no reason to suppose that metabolic costs are greater at the protected site. Mean and maximum temperatures are nearly identical at the three sites (monthly minimum/maximum thermometer recordings; 1978–1983). Colonies contract during periods of slack water and probably experience lower metabolic rate when contracted (16–18), but slack water periods are more common at the protected site. However, they also contract during very high flow (8), which is likely to be more common at the more exposed sites. The total duration of closure at each site is unknown. Decreased oxygen concentrations are not likely at any of the three sites, considering the well-mixed water and abundant benthic algal growth nearby. Therefore, lowered respiratory rates under low ambient oxygen tension is not likely to be an important factor decreasing energy demands.



FIG. 4. Zooplankton (50–600 μ m) concentrations in seawater from Halfway Rock (HR) (n = 19) (most exposed), Shag Rocks (SR) (n = 41) (moderately exposed), and inner East Point (EP) (n = 42) (least exposed) sites. Samples were collected twice monthly at the latter two sites and monthly at Halfway Rock. Nets were towed by scuba divers, just off the substratum, between fixed points; organisms were counted and identified under a light microscope ($\times 100 \times 400$) in measured aliquots of the sample. Analysis of variance and Student-Newman-Keuls multiple comparisons tests showed no significant differences between sites (all data) or between sites during the warm months. The Halfway Rock sample was significantly different from only the inner East Point site during the cold months (F_s = 3.9, df = 2, 41, P < 0.05).

Alcyonium colonies do not reproduce asexually by whole colony fission or fragmentation. There is one annual reproductive period; larvae are brooded internally from June to August (13) and then released. The amount of energy devoted to sexual reproduction and planula larva formation could potentially differ between sites and could affect the colony growth rate. However, we have observed planulae being brooded by the majority of large colonies at all three sites, and differences in reproduction effort are likely to be small.

DISCUSSION

There is a strong correlation between large Alcyonium colony size and amount of water movement in the octocoral's habitat. Water movement alone offers a possible, although not the only, explanation for the observed size gradients. Currents move zooplankton past the colonies and, thus, the actual prey availability experienced by the corals is a function of current speed and efficiency of prey capture. Of course there will be periods when currents are too strong to allow efficient feeding and colonies may even contract (8) and not feed. There are also periods when water movement is negligible. At such times it may be more costly for the colony to remain expanded, capturing few zooplankton and metabolizing rapidly, than to contract and capture none (16, 17). Habitats where flow is most often between this maximum and minimum offer the greatest potential for prey capture per unit time.

Size Optima. The apparent approach to an asymptotic colony size at the protected site may be a result of colony morphology. Finger-like or globose colonies have feeding surfaces (polyp tentacles) whose total suface area increases approximately isometrically with total colony mass (e.g., as a 0.67 power of weight), while metabolic cost increases more rapidly (as a 0.88 power of weight) (18). Given this scaling difference, there must be a colony size where energy intake just equals metabolic cost, and also a size where the difference between the intake and cost curves is the greatest (14, 15). It is this latter size that should correspond to the asymptotic size, because it allows the greatest allocation of energy to reproduction and, thus, the greatest fitness under local habitat conditions (14, 15). Colonies at the most exposed site are not reaching a size asymptote, probably because of their higher mortality rates. Also, the lobed morphology of large colonies may allow feeding surface to increase at a power of weight greater than that for isometric growth.

Size Gradients and Water Movement. It is interesting to note that most studies of marine invertebrate size gradients in relation to water movement show the opposite trend, a size decrease with greater water movement (19–21). For example, Ebert (22) found smaller sea urchin sizes and slower annual growth rates in sites with greater wave action. In such cases, water movement probably interferes with feeding activity and with locomotion, thus decreasing energy intake and possibly increasing physiological and repair costs as well. Birkeland (21) showed that large gorgonian sea fans suffer heavy wave-induced mortality during storms and, thus, mean size in populations decreased with wave exposure of the habitat.

A second class of organisms, those that benefit from increased water movement, includes passive suspension feeders (15) or active suspension feeders utilizing induced flow (23). These forms may well show a positive correlation between size and flow (as does *Alcyonium*), up to the point where flow is either too rapid for feeding, or where hydrodynamic drag is so strong that larger organisms frequently become detached from the substratum. Paine (24) found the largest mussels at his most exposed location, and also the largest samples of the seastars that prey on those mussels.

Prey capture by passive suspension feeders may increase linearly with water flow at low flow rates (Fig. 5). As flow



FIG. 5. Hypothetical prey capture or energy intake and metabolic cost curves for Alcyonium (E = energy in arbitrary units) as functions of water flow speed. OF, optimum flow where intake minus cost is at a maximum. H1-H3 represent habitats of increasing mean flow (H1, inner East Point; H2, Shag Rocks; H3, Halfway Rock). CO, points at which whole colony contraction occurs. Habitats where flow is such that C > I on average would be unable to support Alcvonium.

increases, the speed becomes too rapid for the predators to capture prey efficiently (e.g., 20-50 cm·s⁻¹; M. Patterson, personal communication) and, although prey capture may still increase with flow, it will do so less rapidly. In very high flow, prey capture may actually decrease and, at some point, a coral such as Alcyonium will contract if flow is too rapid (8). Prey capture would be very low in habitats where the corals spend most of their time contracted. In habitats of very high flow, it may be biomechanically impossible for such animals to retain their expanded shape and to capture prey from the rapidly moving water (25, 26).

Metabolic cost will probably be at its lowest when flow is very low, especially if colonies remain contracted (Fig. 5), because contraction of most anthozoans decreases metabolic cost by about one-third (18). As mean flow increases, colonies can spend more time expanded and metabolic cost will increase. There may be a slight increase in such costs with greater flow, either because the animals have to expend energy to retain their posture in higher flow, or because higher flow prevents oxygen depletion in the boundary layer of water surrounding the polyps. When flow is very high, colonies contract and metabolic cost again drops. The flow rate that maximizes the difference between intake and cost curves represents the energetic optimum (Fig. 5). Corals in habitats where the mean flow is near this optimum should have the greatest growth rates and, potentially, the largest colony sizes, although very high mortality rates could prevent them from attaining such large sizes. Mortality resulting from extreme water movement (e.g., storm waves) may in fact set the upper limit on the size of certain intertidal animals (27).

The three habitats in this study may be arranged as shown in Fig. 5, increasing in mean flow and thus in energy available for growth and reproduction of the corals. However, the habitat with the greatest mean flow is still probably at or below the optimum rather than above it, because growth rates are highest there, as is maximum colony size. Shick et al. (28) describe a size pattern for the sea anemone Metridium where size decreases with greater flow rate in an intertidal channel that has very rapid flow. This pattern could result if some of the habitats studied lie to the right of the optimum point (Fig. 5). A field analysis of growth and mortality can sort out such patterns and can determine the exact role of water flow as it affects the population structure of sessile marine invertebrates.

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