Orientation, Polyp Distribution, and Coenenchyme Regeneration in *Gorgonia ventalina*

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Abstract:

The sea fan Gorgonia ventalina commonly grows on coral reefs throughout the Caribbean. It incurs wave damage by uprooting and abrasion, and tissue loss by such predators as Cyphoma gibbosum. Avoidance of injury and rapid regeneration rates can minimize the susceptibility of G. ventalina to overgrowth by invasive macroorganisms. This study found fans at 50 ft depth were more closely oriented perpendicularly to the prevailing surge than fans at 30 ft, where surge direction is more variable. This may be an adaptation to minimize torsional stress on the fan. Small fans were no less likely than large fans to orient perpendicularly to the prevailing surge. Coenenchyme regeneration occurred slightly more rapidly in central than peripheral parts of the fan. G. ventalina contained more polyps centrally than peripherally, but there was no difference in polyp numbers on sides of the fan facing and away from the surge. Thus, zooplankton capture may be a negligible energy resource relative to zooxanthellae photosynthesis.

Introduction:

The fore reefs of the Caribbean sustain a biota composing organisms tolerant to different light intensities and levels of turbulence. Species propagate from the well-lit shallow waters to the darker, less turbulent ocean depths. Gorgonians are common in both areas. They are believed to derive energy from zooxanthellae photosynthesis as well as small prey capture by polyps (Kinzie, 1970). The broad fans seem well-adapted to receive light and to capture zooplankton, but they are also susceptible to uprooting and abrasion by waves (Barnes, 1968). Predators such as Cyphoma gibbosum (the Flamingo Tongue snail) can remove polyps and coenenchyma, decreasing the potential to utilize light for photosynthesis or the ability to capture microorganisms (Harvell, 1987). Removal of feeding or reproductive polyps may decrease organism fitness (Wahle, 1985). Furthermore, both abrasion and predation can expose the axial rod skeleton beneath the protective coenenchyma, increasing susceptibility to overgrowth by invasive microorganisms (Grigg, 1972; Wahle, 1985). Clearly, the ability to avoid damage or to regenerate rapidly and minimize the probability of overgrowth could improve organism viability and fitness.

Complete avoidance of wave stress is unlikely, particularly where gorgonians grow in well-lit, exposed reef areas (Kinzie, 1973). However, different fan orientations relative to wave direction can alter the stress and potential for damage on the fan. Orientation perpendicular to the current can lessen flutting that might result in stalk damage, skeleton exposure, and increased probability of mortality due to incrustation (Grigg, 1972). If one direction of current or surge prevails, fans might minimize tissue injury by orienting perpendicularly to that surge. Shallow waters tend to be more turbulent and surge multidirectionally,

while surges in deeper, calmer waters occur in more consistent directions (Gregg, 1972). I hypothesized that fans in deeper waters would align more closely to perpendicular with the prevailing surge than fans in shallow water, where no one surge direction was dominant. If increased surface area exposes fans to more surge force, one might expect large fans to orient at 90° to the surge more than small fans.

In addition to minimizing torque, orientation perpendicular to surges may be an adaptation to maximize contact between polyp feeding surfaces and organic matter suspended in the current (Gregg, 1972). Food intake could be increased further with more polyps on the side of the fan facing the current. I hypothesized that the side up-current would contain more polyps than the down-current side.

There may be other polyp differences within fans. Research showed that branch tip injuries regenerate more slowly than primary branch injuries (Wahle, 1983). I hypothesized that coenenchyme would regenerate more quickly in central portions of G. ventalina than in the periphery. This difference may decrease fan fitness.

Methods:

The fore reef at Discovery Bay, Jamaica, supports many gorgonians. I examined G. ventalina from 30m west to 30m east of the LTS mooring line from February 26 to March 6, 1988. Initially, I had hoped to compare fan orientations at 60ft vs 20ft depths, but the paucity of G. ventalina at both depths prevented it. Therefore, I designated my shallow site at 30ft and my deep site at 50ft. I measured three 2m×10m transects at each depth to approximate relative abundance. I randomly placed each transect after swimming from the mooring line to the

appropriate depth, maximum width and height were measured on each fan.

Orientation was assessed relative to the prevailing surge. I determined surge direction by dropping a lightweight plastic disc above the fan and observing direction of movement. I measured fan orientation in degrees different from perpendicular to the surge. Two measurements each for surge and fan orientation were taken for 15 fans at each depth.

To compare polyp numbers, I counted the polyps along a 1cm line in the central portion of the fan, 1cm from a central branch. I counted 2 central positions on each side (facing and away from current) on ten fans at each depth. In addition, I counted polyps for 2 central and 2 peripheral locations on each fan. "Central" was designated as 1cm from a central branch, while "peripheral" polyps were within 2cm of the fan's edge. I measured ten fans at each depth.

I tried to simulate the injuries inflicted by C. gibbosum to compare regeneration times between central and peripheral parts of the fan. No clear differences in regeneration rates over depth have been found (Wahle, 1983), so I selected 10 fans at 40ft depth. I removed the polyps and light purple coenenchyme with a scalpel, exposing the dark purple skeleton in 1cm × 2cm areas. I made 1 central and 1 peripheral injury on each fan. I checked fans daily and deemed regeneration complete when the internal axis became covered completely with gorgonian tissue (Wahle, 1983).

T-tests were used to compare: deviation from 90° to the prevailing surge in 30ft vs 50ft fans; time of regeneration for central vs. peripheral injuries; and polyp numbers centrally and peripherally in 30ft vs 50ft fans. Small ($\leq 1100 cm^2$) and large ($> 1100 cm^2$) fans were compared in orientation relative to the prevailing surge with a G-test. Paired t-tests compared the numbers of central vs. peripheral polyps and up-current vs. down-current polyps.

Results:

Deep fans were significantly more closely oriented perpendicularly to the prevailing surge than shallow fans ($p < 0.001$, $t = 7.30$, 28 df, Table 1). Small and large fans showed no significant difference in orientation relative to prevailing surge ($p > 0.1$, $G_{adjusted} = 2.03$, 1 df). There was a trend of more fans/area at 50 ft than at 30 ft (Table 2). Fan sizes towards and away from the prevailing surge showed no significant difference in polyp numbers ($p > 0.1$; paired t-test $t = 0.35$, 19 df, Table 3). Fans at 50 ft and 30 ft contained similar numbers of central polyps ($p > 0.1$, $t = 0.87$, 38 df, Table 4a) and similar numbers of peripheral polyps ($p > 0.1$, $t = 1.65$, 38 df, Table 4a). There were significantly more polyps centrally than peripherally ($p < 0.001$, paired t-test $t = 9.07$, 19 df, Table 4b). The data show a trend of regeneration occurring more quickly centrally than peripherally ($0.05 < p < 0.1$, $t = 1.82$, 18 df, Table 5).

TABLE 1:

Fan Orientation:	30 ft	50 ft
Average Difference from Perpendicular to Surge >	29.6 ± 13.2°	3.5 ± 4.1°

TABLE 2:

Transects Average Fan Densities >	30 ft	50 ft
	0.05 fan/m²	0.23 fan/m²

TABLE 3:

	Facing Current	Down Current
Average Polyp Number >	21.8 ± 4.4 polyps/1 cm	21.4 ± 2.7 polyps/1 cm

TABLE 4a:

	Central		Peripheral	
	30 ft	50 ft	30 ft	50 ft
Average Polyp Number >	22.4 ± 3.8 polyp/1 cm	21.1 ± 5.2 polyp/1 cm	14.9 ± 3.6 polyp/1 cm	13.1 ± 3.5 polyp/1 cm

TABLE 4b:

	Central	Peripheral
Average Polyp Number >	21.7 ± 2.6 polyps/cm	14.0 ± 3.3 polyps/cm

TABLE 5:

	Central	Peripheral
Average Time of Coenenchyme Regeneration >	4.9 ± 0.8 days	5.6 ± 0.8 days

Discussion:

This study suggests fan orientation does not occur randomly in G. ventalina. Surge direction varied more at 30ft than at 50ft, thus a particular orientation would be of ~~less~~ benefit to a fan a 30ft than at 50ft in minimizing torque by orientation perpendicular to a single prevailing surge direction. If hydrodynamic forces press the fan from several directions, it is impossible to minimize stress with a specific orientation. The greater tendency of 50ft fans to orient perpendicularly with the prevailing surge can be viewed two ways: first, a relatively consistent surge could twist the fan during growth, permanently orienting the fan perpendicular to that surge (Graig, 1973). Secondly, this orientation may minimize the stress on the fan by that surge, and thus the overall stress if that surge prevails. ~~Less~~ consistent positioning ~~[illegible]~~ occurs in shallow water fans. This might be tested further by determining if deep fans tend to be oriented similarly, while fans in shallow water would be positioned more randomly because disparate force directions neither promote any one orientation nor alleviate torque.

Exposure of more surface area to a surge might increase tissue damage, thus I predicted large fans to orient more perpendicularly to prevailing surges than small fans. No such difference was observed. One possible explanation is that fans establish themselves randomly and orient perpendicularly as they grow. In this instance, older fans would grow closer to 90° to the surge. As with trees, larger sizes may not necessarily correspond with increased age. If one could assess colony age, further research could examine if deep fans are more perpendicularly oriented to the surge with time. An additional factor in orientation can be explained by period of motion. A large fan requires a longer time to complete its oscillation with the incoming and receding surge. Before a large

fan completes this motion, the surge may ~~start and~~ subside. This relatively rapid force change could abbreviate the arc of motion of the fan, making it comparable to that of a small fan. This possibility would require further research.

Perpendicular orientation to the current may increase polyp ability to extract suspended food particles, but the occurrence of such orientation in organisms dependent on zooxanthellae suggests such positioning may not be simply a feeding adaptation (Grigg, 1972). More likely, perpendicular orientation results only from hydrodynamic forces and does not augment zooplankton capture. Because G. ventalina contained equal polyp numbers on both sides, this study demonstrates no adaptations to maximize prey capture. Zooxanthellae may provide most, or all, of the energy necessary for sea fans. This idea is supported by the inability of gorgonians to survive in the dark. Unlike corals, gorgonians do not expel degenerating zooxanthellae in the dark, which may indicate a closer relationship (Kinzie, 1970). The predominance of sea fans at the reef/sand channel interface is suggestive. Sand reflects twice as much light as coral substrates, indicating sea fans may prosper on comparable substrates where the light is more intense (Kinzie, 1970). Gorgonians that rely solely on zooxanthellae photosynthesis for energy needs would gain no trophic benefits from perpendicular orientation or more polyps on the upcurrent side. This condition would explain the similarity in polyp numbers on both fan sides, as well as limiting the causes of perpendicular orientation to hydrodynamic forces, not trophic adaptations.

The apparent consistency of polyp distribution on both fan sides is notably absent when comparing central and peripheral polyps. Central polyps may be more numerous because the inner fan comprises the earliest growth. This could be tested by

counting polyps along a distance gradient from the inner fan to its edges to determine if polyp numbers increase accordingly. Peripheral polyp growth might be impeded further by increased abrasion. It is this difference in polyp numbers that may attribute to the trend of peripheral injuries regenerating more slowly than central lesions. With fewer polyps present to contribute to synthesis of new coenenchyme, regeneration would occur more slowly along the fan's edges. If the number of polyps increases at a given point as the colony ages, the regeneration rate at that point should also increase. Additional research could test this.

It is interesting to note that most injuries occur in this area of somewhat slower regeneration rates, on the periphery (Wahle, 1983). Pawlik, et.al., suggested that "some gorgonian secondary compounds may play a role in preventing fouling by autotrophic microorganisms" (Pawlik, et.al., 1987). These compounds may play some role in tissue regeneration. This could be investigated by comparing secondary compound concentrations in central vs. peripheral portions of the colony to determine if a difference might contribute to disparate regeneration rates. Finally, a larger sample size might show significant differences. Further research could address any of the ideas generated by this study. More specifically, research could test if gorgonian distribution is limited in shallow waters by turbulence and in lower waters, by insufficient light, with zooplankton densities unimportant in determining sea fan abundance.

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