EFFECTS OF AMBIENT CURRENT, LIGHT, AND PREDATION ON THE MORPHOLOGY AND BEHAVIOR OF THE SERPULID POLYCHAETE, SPIROBRANCHUS GIGANTEUS

Hannah M. Fouts and Peter S. Woodson

ABSTRACT (HMF)

Morphological and behavioral characteristics in Spirobranchus giganteus were observed at 6, 12, 18 and 24m depths on the west fore reef of Discovery Bay, Jamaica. Several predictions were made based on the hypothesis that environmental factors and community interactions would exert different selective pressures at different depths. No individuals were found at 24m. Height/tube diameter ratios remained constant throughout the shallower depths. Re-emergence time was rapid in shallow waters where current may have habituated individuals to agitation. In addition, large worms exposed themselves later at 12m, presumably due to greater predation risks caused by higher visibility. There is a high variation in color patterns at all depths which may be a mechanism for predator avoidance (reduced search image). Preferences in location and orientation on a coral head in different current regimes may be important in maximizing the filtering process of the tentacles.

Key Words: Spirobranchus giganteus, color morphs, predator avoidance, suspension feeding

INTRODUCTION (PSW)

The serpulid polychaete, Spirobranchus giganteus, is a common inhabitant of the coral reefs of the Caribbean where they can be seen extending colorful tentacles from coral heads into the water column. S. giganteus is an obligate associate of live coral. It does not bore into the coral as some sponges do, instead it builds its tube on the living surface of the coral. Coral then grows over the tube (Hunte et al., 1990). Larvae have been found to prefer a certain species of coral for settlement, in particular Diploria strigosa, Agaricia agaricites, Millepora complanata, Montastrea annularis, Madracis spp., and Porites asteroides. S. giganteus is estimated to live as long as 20 years (Hunte et al., 1990).

S. giganteus feeds on plankton by circulating water through the radioles of its two tentacles. Strathman et al. (1984) found that S. giganteus is different from all other current-generating suspension feeders in that it refilters water. The compact spiral design of the tentacles results in the upper whorls filtering water that has previously been filtered by lower whorls. Filtering water twice is inefficient; therefore they concluded that ambient currents of as little as 3 cm/s are crucial in preventing this refiltering by moving water horizontally across the radioles. They go on to suggest that the amount of ambient current may have an effect on the size of the tentacles that is required to capture sufficient prey, and that S. giganteus evolved this compact tentacle form in order to decrease predation by fish.

It is generally believed that the number of potential predators of S. giganteus decreases with depth (John J. Gilbert, personal communication). We hypothesized that 1) ambient currents will influence worm morphology, and 2) predation pressure will shape both worm behavior and morphology. From these hypotheses, we made two predictions: 1) the tentacle to body size ratio will be greater at depth due to decreased ambient current and decreased risk of predation, and 2) tentacles will re-emerge sooner at greater depth due to the decreased predation risk.

In this study, we also attempted to determine if there were any patterns of significance in the different color morphs. Fleischmann (1989) found that between 3 and 9m, 50% of the light was attenuated from tropical marine waters. We therefore, predicted that color morphs would either be more bland (browns and oranges instead of pinks and blues) or more heterogeneous at greater depths due to the decrease in importance of color from the lack of light.

As a final point of interest, we looked at tube position on the coral. We predicted that the tube opening would be oriented into the prevailing ambient current and that the tubes would be located on the tops of the coral promontory as opposed to the side or near the base.

METHODS (HMF)

Observations were made in the vicinity of LTS mooring on the west fore reef of Discovery Bay, Jamaica. Two dives were completed at each study depth of 6, 12 and 18 meters. Qualitative observations were recorded at the deeper depths of 21m (Rio Bueno and 24m (LTS deep mooring). In all, 103 worms were observed per 12.7 SCUBA hours.

When an individual was located, the following information was recorded: radiole color pattern, coral substrate (species) and color shading, location on coral head (top, side or bottom), orientation (compass heading of calcareous tube opening), and tentacle height.

A disturbance was created with a brush of the hand and re-emergence time was measured from the moment of retreat to the time at which all radioles were re-extended. Tube diameter was then measured only after time trials as the caliper/tube contact was believed to alter worm behavior.

Difference between depths were statistically compared with ANOVA followed by Scheffe's pairwise comparison test if a significant effect was found. T-tests were used to analyse small versus large worms (heights less than or greater than the mean, respectively) within each depth. A Chi-square test was used to analyse location and orientation.

RESULTS (PSW)

We found no significant difference in the ratio of tentacle height to tube diameter between the three different depths ($F = 0.81$, $df = 2$, $p = 0.448$). There were also no significant differences in mean height or mean tube diameter between the different depths ($F = 1.37$, $df = 2$, $p = 0.259$ and $F = 0.28$, $df = 2$, $p = 0.756$, respectively). Time to re-emergence following disturbance was significantly different between depths ($F = 10.05$, $df = 2$, $p = 0.000$). S. giganteus re-emerged over 2 times more rapidly at the 6 and 12m depths than at 18m (Scheffe, $p = 0.000$ and $p = 0.001$, respectively, Figure 1)

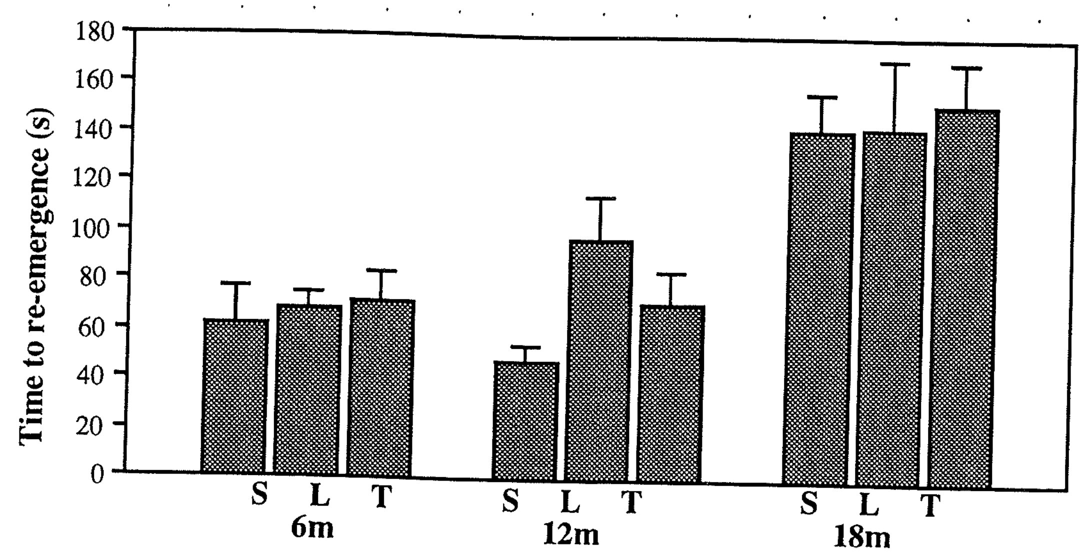

Figure 1. Re-emergence times following disturbance for small (S), large (L) and total (T) S. giganteus at each depth.

By separating the worms into small and large categories by height within each depth, we found that at 12m, small worms emerged nearly twice as rapidly as large worms ($t = 2.78$, $df = 23$, $p < 0.02$; Figure 1). There were no differences in re-emergence times between small and large worms at the 6 and 18m depths ($t = 0.43$, $df = 35$, $p > 0.5$ and $t = 0.0288$, $df = 14$, $p > 0.9$, respectively; Figure 1).

S. giganteus displayed remarkable variance in coloration at all depths with no obvious change to more bland colors with increasing depth (Table 1).

S. giganteus tubes were oriented into the prevailing current at 12m, but not at 6 or 18m (6m: $X^2 = 0.42$, $df = 1$, $p > 0.1$; 12m: $X^2 = 15.04$, $df = 1$, $p < 0.001$; 18m: $X^2 = 0.22$, $df = 1$, $p > 0.1$).

Table 1. Catalog of color morphs and number of individuals observed at 6, 12, and 18m.

Color Morph	6	12	18
Maroon w/ yellow or white tips	10	19	7
Yellow, white, orange, and tan (varied)	12	19	6
Solid orange, tan, or maroon	8	0	1
Maroon with dark egde	4	5	1
All white	1	1	1
Yellow and blue	1	0	0
White and pink	1	0	1
Red with white or yellow	1	2	0

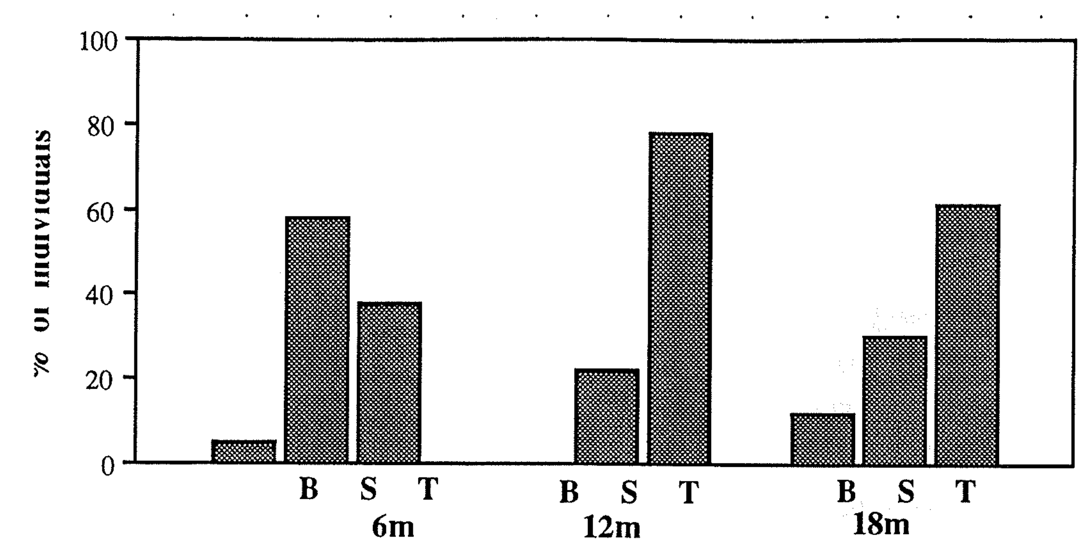

Figure 2. Percent of S. giganteus individuals located near base (B), on the side (S), and on the top (T) of coral heads.

S. giganteus showed a preference in position on the coral head and this preference changed with depth. At 6m, worms were found 37% of the time on the top of the coral head, 58% on the side or in a valley, and 5% near the base ($X^2 = 16.08$, $df = 2$, $p < 0.001$; Figure 2). At 12m, worms were found 78% of the time on the top, 22% on the side, and never near the base ($X^2 = 22.72$, $df = 2$, $p < 0.001$; Figure 2). At 18m, worms were found 61% of the time on top, 30% on the side, and 11% near the base ($X^2 = 6.98$, $df = 2$, $p < 0.05$; Figure 2).

DISCUSSION (HMF)

Although our initial predictions were not supported, our results suggest that there are different selective pressures on worm morphology and behavior at different depths. The uniformity in height and tube diameter suggest that conditions selecting for these traits exist across all three depths. J.B.C. Jackson (1979) indicates that tree form is one of the six adaptive growth strategies of sessile organisms. The constant height to diameter ratio may be the optimal morphological strategy for maintaining tentacle capacity while reducing vertical exposure to predation.

Because S. giganteus did not re-emerge faster in deeper waters as predicted, predation in shallow waters may not be a driving force (supported by intense off-shore fishing). Shallow individuals appeared to be less sensitive and a greater level of disturbance was needed to cause a retreating response (pers. observ.). Perhaps these individuals become habituated to disturbance as current and surge are great in shallow waters. This may explain shallow individuals' shorter re-emergence time as well.

At 12m, larger individuals re-emerged later, presumably because they are more conspicuous and therefore are at greater risk to predation. It has been reported that age is directly correlated to size (Hunte, 1990). Hence, it appears that older worms have either learned to be more cautious, or that individuals quick to re-emerge were differentially eliminated via predation.

Because a wide array of color patterns was observed across all depths, light alternation and its effect on color perception does not appear to be a force selecting color morphology. Predators may not be visually cued or individuals may benefit from variation in color and pattern by straying from a common visual search image. In this case, uniqueness would increase an individual's chance of survival. It appears that worms are palatable or else a convergence upon an aposomatic color pattern would have been observed (John J. Gilbert, pers. comm.). Crypticity may also play a role, although our methods were unable to provide evidence for this.

Worm location and orientation on coral heads change with depth presumably in response to currents. In shallow waters, the majority of S. giganteus seek refuge from waves and surge by positioning themselves on the sides of promontories. At depths greater than 6m, the filtering process may be limited by low ambient current. By locating themselves on top of coral heads, current flow is maximized, filtering efficiency is enhanced, and the chance of refiltering is reduced.

Because this investigation shows that environmental factors and predation risk exert selective pressures on S. giganteus, further studies could possibly pinpoint the mechanisms behind these forces. Specific time trials between cryptic and non-cryptic individuals or comparative studies between sites with varying predation pressure would both delve deeper into the questions behind color patterns and overall morphology and behaviors of the worms.

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