

TRADEOFFS BETWEEN PREDATOR AVOIDANCE STRATEGIES IN TWO SABELLID FAN WORMS

BRIGETTE A. JONES AND ALLISON M. CITRO

Faculty Editor: David R. Peart

Abstract: Organisms avoid predation in many ways. Sabellid fan worms exhibit four methods for avoiding predation: cryptic habitat, cryptic coloration, unpalatability, and behavioral predator avoidance (escape). We examined the tradeoffs between cryptic habitat and predator avoidance in two species of fan worms (Order Sabellidae), the yellow fan worm, *Notualax occidentalis*, and the split-crown feather duster, *Anamobaea orstedii*. We made four predictions. (P1) We predicted that yellow fan worm individuals in more cryptic habitats would be less sensitive to disturbances because they are more protected from predation. (P2) We predicted that there would be no relationship between fan worm diameter (which should be positively related to growth and survival) and crevice depth, because of a potential tradeoff between exposure to predators in the water column and increased food availability and growth rate in an exposed position. (P3) Between species, we predicted that the split-crown feather dusters would be more sensitive to disturbances than the yellow fan worms because the feather dusters are more exposed and therefore more vulnerable to predation. (P4) Across both species, we predicted that fan worms that retracted at a greater distance from the disturbance would take longer to re-emerge, and that larger fan worms would be more sensitive to disturbance because they would be at higher risk for predation.

Our first prediction about the yellow fan worm was not supported, indicating that the advantages of living in a more cryptic habitat are not associated with response to perceived predation risks. Our remaining three predictions were supported by our results. We feel that *N. occidentalis* and *A. orstedii* are characteristic of the order sabellidae because they span a large portion of the size range of the sabellids and represent two of the largest families in the order. Therefore, our results indicate that sabellid worms as a whole may experience strong tradeoffs between habitat crypticity and behavioral predator avoidance.

Key Words: *Notualax occidentalis*, *Anamobaea orstedii*, Sabellidae, *fan worms*, *polychaetes*, *cryptic habitat*

INTRODUCTION

Sessile organisms have many strategies for minimizing predation, including camouflage and unpalatability. However, behavioral mechanisms for avoiding predation in sessile organisms are not as well understood, because these strategies typically involve significant

movement. Sabellid fan worms are unusual in this respect; though sessile, they are not completely immobile. The bodies of sabellid fan worms remain in protective tubes in the substrate while the fan worm's radioles extend out for feeding and respiration; the crown of radioles retracts inside the tube when the

worm is threatened (Fauchaud 1977, Fauchaud and Jumars 1979).

Sabellid fan worms have four strategies for deterring predation: cryptic habitat, cryptic coloration, unpalatability, and behavioral avoidance (escape), and any combination is possible. The tradeoff between palatability and escape has been demonstrated by Kicklighter and Hay (2007), who found that there is a negative relationship between palatability and sensitivity to disturbance for all of the species they studied.

We examined the relationship between habitat crypticity and escape (measured as crown retraction) in two species of fan worm. One species, the yellow fan worm *Notualax occidentalis* (Sabellidae), has a bright yellow radiole fan that ranges from 1 – 4.5 cm in diameter (Table 2) and is found in crevices of varying sizes in the coral rock of tropical reefs. We predicted that worms in deeper crevices would be less sensitive to disturbance (P1), because they are less vulnerable to predators than those in shallower crevices. However, we predicted that there would be no relationship between fan worm diameter and crevice depth (P2), because although worms in deeper crevices should have higher survivorship, they may receive less food from the water column, and thus have slower growth rates.

We also compared *N. occidentalis* to the split-crown feather duster, *Anamobaea orstedii* (Sabellidae). Split-crown feather duster worms have white and either maroon or brown bands on the fans, which range from 2 – 7 cm in diameter (Table 2). They live directly in the sand and hard pan substrate and are typically found on the edges of depressions in the sea floor. Although they are usually more exposed than the yellow fan worms, their coloring is more cryptic. We predicted that the feather dusters would retract when the potential predator was farther away (P3a) and take longer to re-emerge (P3b) than the yellow fan worms, because the feather dusters are larger (and potentially more valuable prey for fish) and their habitats are less cryptic.

Across both species, we expected that the time until the worm re-emerged would increase with the distance at which it retracted (P4a). We reasoned that worms that are at high risk of predation would retract from fish predators at greater distances, and would also remain retracted longer, to minimize the probability of consumption by a fish that had recently disturbed them. We also predicted that the larger fan worms would be more sensitive to disturbance than the smaller fan worms (P4b), because they would be

more susceptible to predation because of their larger size.

METHODS

Study System: We collected data between 0800 and 1800 on 3 and 4 March, 2007 on Little Cayman Island. We studied *N. occidentalis* in Grape Tree Bay behind the Little Cayman Research Center, and *A. orstedii* in Jackson's Bay Marine Park.

Field Methods: We haphazardly selected 67 yellow fan worms (*N. occidentalis*) on 3 March and 69 split-crown feather dusters (*A. orstedii*) on 4 March. As one measure of sensitivity to disturbance we simulated an approaching fish predator by swimming at the fan worm while waving a ruler in front, until the crown retracted. We recorded the distance from the edge of the ruler to the fan worm at the time of retraction. When it was necessary to touch the fan worm to induce retraction, a distance of 0 cm was recorded. Our second measure of sensitivity to disturbance was the time between retraction and the complete re-emergence of the crown. We measured the diameter of yellow fan worm crowns and width of split-crown feather duster crowns to the nearest 0.5 cm. For the yellow fan worms, the length and width of the crevice opening was measured, as well as the depth to the fan worm in the crevice.

Statistical Analyses: We used a total of three MANOVAs within and combining species to test the effect of diameter as the independent variable on the two dependent variables, re-emergence time and response distance. We used pair-wise correlations within species and combining species to analyze the relationships between crevice size, depth, response distance, response time, and crown diameter. We tested the differences in re-emergence time, response distance, and diameter between the two species with three t-tests assuming unequal variances.

RESULTS

Within N. occidentalis: A MANOVA of the effect of diameter on re-emergence time and response distance was marginally significant ($F_{2,64} = 2.60$, $P = 0.082$). The strongest correlation for the yellow fan worm was between worm diameter and response distance (Table 1). There were no other significant correlations between depth inside crevice, response distance, re-emergence time, and diameter for *N. occidentalis* (Table 1).

Table 1. Correlation coefficients and associated p-values for each pair of variables for the yellow fan worm *Notualax occidentalis*. “Distance” refers to the distance between the edge of the ruler (simulated fish disturbance) and the fan worm crown at the time of retraction. “Diameter” is the approximated diameter of the extended fan worm crown. “Time” refers to the total time from full retraction until the fan worm was fully re-extended. “Depth” is the depth to the fan worm inside a crevice. n = 67 worms.

Variable Pair	r	P
Distance (cm) by Diameter (cm)	-0.2309	0.0602
Distance (cm) by Time (s)	0.1088	0.3806
Time (s) by Diameter (cm)	0.1216	0.3271
Diameter (cm) by Depth (cm)	-0.0487	0.6958

Within A. orstedii: A MANOVA of the effect of crown diameter on re-emergence time and response distance was not significant ($F_{2,66} = 0.012$, $P = 0.67$). For the 69 feather duster worms, response distance and re-emergence time were correlated ($r = 0.52$, $P < 0.0001$). Crown diameter was not correlated with either distance ($r = 0.11$, $P = 0.39$) or re-emergence time ($r = 0.031$, $P = 0.80$).

Between species: The split-crown feather dusters had a significantly greater re-emergence time ($t_{75.87} = 7.59$, $P < 0.0001$) and response distance ($t_{98.99} = 8.93$, $P < 0.0001$) than the yellow fan worm. The split-crown feather dusters were also 47% larger than the yellow fan worms ($t_{123.50} = 7.57$, $P < 0.0001$; Table 2).

Table 2. Means and ranges of the diameter, response distance, and re-emergence time for the yellow fan worm *Notualax occidentalis* (n=67) and the split-crown feather duster *Anamobaea orstedii* (n=69). “Diameter” is the approximated diameter of the extended fan worm crown. “Distance” refers to the distance between the edge of the ruler (simulated fish disturbance) and the fan worm crown at the time of retraction. “Time” refers to the total time from full retraction until the fan worm was fully re-extended.

	<i>N. occidentalis</i>			<i>A. orstedii</i>		
	Mean ± 1 SE	Min	Max	Mean ± 1 SE	Min	Max
Diameter (cm)	2.58 ± 0.093	2	7	3.79 ± 0.13	1	4.5
Distance (cm)	1.42 ± 0.26	0	10	9.94 ± 1.1	1	40
Time (sec)	22.70 ± 2.65	3	114	76.32 ± 5.39	15	225

Combined species: Combining both species (N = 136 worms), strengthened the correlation between re-emergence time and response distance ($r = 0.64$, $P < 0.0001$; Fig. 1). A MANOVA of the effect of worm diameter on re-emergence time and response distance was highly significant ($F_{2,133} = 0.18$, $P < 0.0001$;

Fig. 1). With both species, diameter was also positively correlated with both re-emergence time ($r = 0.37$, $P < 0.0001$) and response distance ($r = 0.33$, $P < 0.0001$; Fig. 2).

DISCUSSION

Within species: N. occidentalis:

Contrary to our first prediction, yellow fan worms were not differentially sensitive to disturbance based on their level of habitat crypticity as measured by depth within substrate crevices. This suggests that having a more cryptic habitat may directly decrease predation risk, rather than causing a change in the behavioral response to perceived predation risks. We found no relationship between worm diameter and habitat crypticity, supporting our second prediction that there would be a tradeoff between protection from predation and growth rate. *Between species:* The larger, less cryptically located, split crown feather duster *A. orstedii* was more sensitive to disturbance, supporting our predictions that there should be a positive relationship between size and sensitivity, and a negative relationship between habitat crypticity and sensitivity.

Both species combined: Our measures of sensitivity to disturbance, re-emergence time and response distance were strongly correlated, suggesting that both may be useful measures of sensitivity. Larger fan worms were also more sensitive to disturbance across species, supporting our prediction and suggesting that they may indeed be favored food resources for fish. The more cryptic yellow fan worm

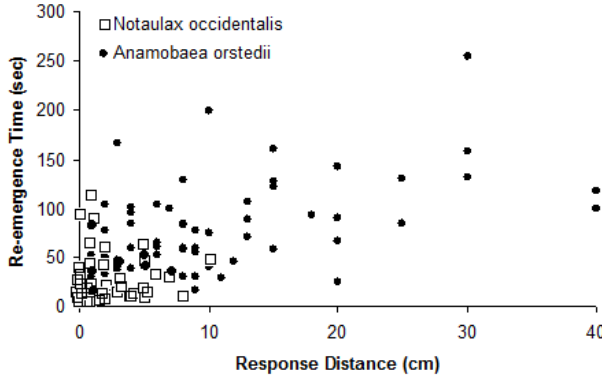


Figure 1. Relationship between two measures of sensitivity to disturbance: time until re-emergence after disturbance and distance between the crown and disturbance at retraction ($r = 0.64$, $P < 0.0001$) for two representative sabellid species: the yellow fan worm *Notaulax occidentalis* ($n=67$) and the split-crown feather duster *Anamobaea orstedii* ($n=69$). “Re-emergence Time” refers to the total time from full retraction until the fan worm was fully re-extended. “Response Distance” refers to the distance between the edge of the ruler (simulated fish disturbance) and the fan worm crown at the time of retraction.

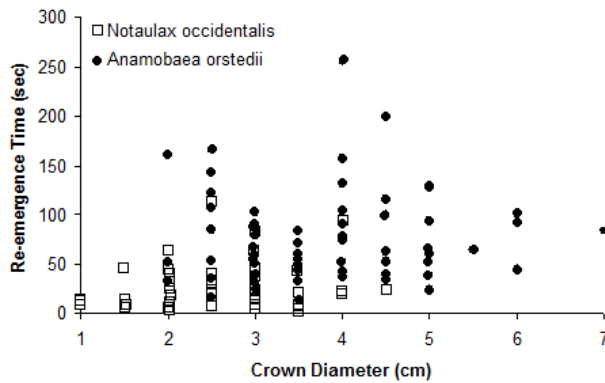


Figure 2. Relationship between crown diameter of the yellow fan worm *Notaulax occidentalis* ($n=67$) and the split-crown feather duster *Anamobaea orstedii* ($n=69$) and re-emergence time ($r = 0.37$, $P < 0.0001$). “Diameter” is the approximated diameter of the extended fan worm crown. “Re-emergence Time” refers to the total time from full retraction until the fan worm was fully re-extended.

N. occidentalis was less sensitive than *A. orstedii*; this negative relationship suggests that there is a tradeoff between cryptic habitat and behavioral predator avoidance strategies.

N. occidentalis and *A. orstedii* span a large portion of the known size range of sabellids (the species overlap in size) and are present in habitats of varied crypticity. We suggest that the positive relationship between sensitivity to disturbance and crown diameter that we observed may apply more generally in the order Sabellidae.

Our findings are consistent with the existence of tradeoffs between escape and habitat crypticity, in addition to the known tradeoffs between escape and deterrence.

Alternatively, this relationship could result from larger fan worms detecting predators sooner, rather than being more vulnerable to predation. Both could result in a greater response distance. Furthermore, the alternative hypothesis that retraction would have greater energetic costs for larger worms would show a negative relationship between fan worm diameter and sensitivity, generating a trend opposite to our results.

Though it has been demonstrated that fan worms have structural and chemical defenses to decrease the palatability of their

radioles (Kicklighter and Hay 2007), we were unable to address the interaction of palatability and crypticity in our study species. The split-crown feather duster has chemically defended radioles (Kicklighter and Hay 2007), but the palatability of the yellow fan worm is unknown. Physical and behavioral methods of decreasing predation appear to be combined by sabellid fan worms to create an effective defense.

LITERATURE CITED

- Fauchald, K. 1977. The Polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Ser* 28: 1-190.
- Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193-284.
- Kicklighter, C. E., and M. E. Hay. 2007. To avoid or deter: interactions among defensive and escape strategies in sabellid worms. *Oecologia* 151: 161-173.