

Tube Decoration May Not Be Cryptic for *Diopatra cuprea* (Polychaeta: Onuphidae)

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Abstract. Previous studies have suggested several adaptive functions for the decorated tube caps of *Diopatra cuprea* (Polychaeta: Onuphidae). We experimentally tested the hypothesis that decoration provides crypsis. A series of field experiments quantified predation-related damage done to tube caps that were (1) devoid of decoration, (2) decorated with algae, or (3) decorated with shell fragments. If decoration provides crypsis, then undecorated tube caps should experience more damage than decorated tube caps; this pattern was not observed. Decoration may still reduce predation rates by means other than crypsis, but these results strongly suggest that tube decoration does not interfere with predator recognition of *D. cuprea* tube caps and that crypsis is consequently not important in this system.

Introduction

Polychaete tubes display a range of complexity from simple tubes of mucous-bound particles to tubes with well-developed inner linings and distinct exterior surfaces that incorporate larger materials (Richards, 1978). Onuphid, nereidid, and terebellid species often enhance their tube walls with fragments of shell, algae, and other debris (Hartman, 1968, 1969). Such tubes are called ornamented or decorated (see review in Berke *et al.*, 2006). The function of tube decoration is imperfectly understood, although reduced predation risk or enhanced feeding are frequently suggested (Mangum *et al.*, 1968; Brenchley, 1976; Woodin, 1977). The onuphid genus *Diopatra* includes many decorating species worldwide (Day, 1967; Paxton, 1998), including the western Atlantic *D. cuprea*. The data support three func-

tions for *D. cuprea* tube decoration: (1) feeding (Mangum *et al.*, 1968; Brenchley and Tidball, 1980); (2) reducing sediment scour by disrupting solenoidal eddies (B. Little and M. LaBarbera, University of Chicago, unpubl. data); (3) extending the worm's sensory capacity by transmitting physical disturbances to the inner wall of the tube, which may facilitate prey capture or predator avoidance (Brenchley, 1976). A fourth untested hypothesis is reduced predation through crypsis (Myers, 1972; Brenchley, 1976), in which decoration renders the tube visually or chemically less recognizable as a prey item (*sensu* Endler, 1981; Stowe, 1988).

To test the hypothesis that tube decoration confers crypsis, we manipulated decoration and quantified damage sustained in the field as evidence of predator attacks. We additionally manipulated tube-associated odor cues to ask whether odor influences decoration's cryptic function, if any. If crypsis occurs, then decorated tubes should be attacked less often than undecorated tubes. Attacks on tubes were both common and temporally variable with regard to decoration type; however, decoration did not reduce predator attacks, suggesting that *D. cuprea* decoration does not confer crypsis.

Materials and Methods

Study organism

Diopatra cuprea (Bosc 1802) occurs in sedimentary systems from Cape Cod to Brazil (Mangum *et al.*, 1968; Fauchald, 1977). This large worm builds deep vertical tubes emerging 2–5 cm above the sediment surface in a hook-shaped “tube cap” to which the worm actively attaches debris (Fig. 1, Myers, 1972). The worm extends from the tube to feed, thus exposing itself to lethal and sublethal predation by fast-moving predators. Even when withdrawn, the worm is vulnerable to suction-feeding and digging pred-

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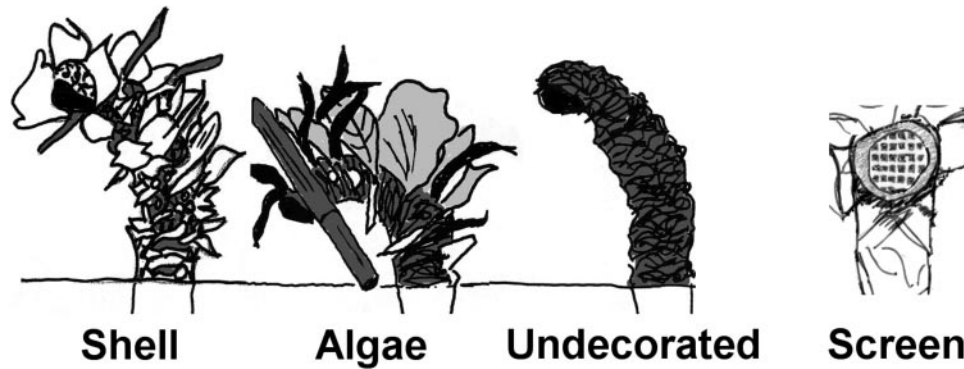


Figure 1. *Diopatra cuprea* tube caps, drawn from photographs: “shell” and “algae” both occur naturally; “undecorated” had decoration experimentally removed. Small squares of insect screening were placed in the aperture of each tube before filling with odor-containing agar, as shown. The screen’s dislodgment was used as one indicator of attack by a potential predator (see text). Drawings are representative, but note that curvature varies irrespective of decoration.

ators such as dasytid rays and skates that can heavily damage or excavate the tube (Howard and Doerjes, 1972, and pers. obs.). Other predators include clearnosed skate *Raja eglanteria*, Atlantic croaker *Micropogonias undulatus*, windowpane flounder *Scophthalmus aquosus*, and spot *Leiostomus xanthurus* (Bowman *et al.*, 2000).

Study site

The site is an intertidal 8- × 12-m sand flat at Oyster Landing, a low-energy tidal creek in the North Inlet–Winyah Bay National Estuarine Research Reserve, South Carolina, USA (33°21′03N, 79°11′27W). Individuals of *D. cuprea* at this site decorate with a mixture of shell, algal, and plant fragments (*Ulva*, *Gracilaria*, *Agardhiella*, *Spartina*, tree leaves, pine needles, and pine bark). This site is typical of other *Diopatra* habitats we have visited in the United States and Europe in that decoration materials do not litter the mud flat; rather, the worms “catch” debris as it passes by. The sediment surface is thus generally free of debris, although drift algae occurs sporadically, and *D. cuprea* tube caps are the most conspicuous emergent features. The site experiences virtually no boat or foot traffic. Mainstream flow is slow, reaching top speeds of 34 cm/s only during peak tidal exchange (Finelli *et al.*, 2000). The experiments were performed in summer months when predators on *D. cuprea* are abundant (Grant, 1983; Bowman *et al.*, 2000; Allen and Ogburn-Matthews, 2005).

Rationale for tube damage as predation metric

Predation risk is difficult to quantify for *D. cuprea*. Adult mortality rates are low (Woodin, 1981; Peckol and Baxter, 1986). Sublethal “browsing” predation (*sensu* Woodin, 1982) is common (Myers, 1972, and pers. field obs.), but requires destructive sampling to measure. However, large

predators that eat *D. cuprea* are abundant in this habitat (Bowman *et al.*, 2000; Allen and Ogburn-Matthews, 2005) and commonly cause damage to tube caps such as tearing holes through the tube wall or ripping off portions of the tube (field obs.). Anthropogenic sources of damage are negligible at this site, and the low-energy flow regime is highly unlikely to cause structural damage to the robust, heavy, and slightly flexible tube caps. Tube damage is thus a practical indicator of predation intensity.

Diopatra cuprea repairs damage to tube caps rapidly and completely—large holes intentionally cut in the tube wall are not discernible 24 h later (Berke, unpubl. data). Therefore, to measure damage done to experimental tubes, it was necessary to decouple the tubes from the worms. By manipulating tubes without the worms, we focus on the tube itself as a potential visual cue to predators.

Naturally occurring damage

We quantified both damage to the tube wall and damage done to decoration, but we analyze only damage to the tube wall because decoration can be damaged by passing debris and drag forces. To assess the types of damage that occur in nature, 34 tube caps were collected and examined in the laboratory. Of the 24 collected from intact tubes, one was clearly damaged; the hooked portion was missing and the upper 1 cm had collapsed inward so that no opening was visible, indicating that a cutting/biting action had severed it; the lower half and the sub-sediment tube looked normal and clear of sediment, indicating that the tube was inhabited and the damage was recent (Mangum *et al.*, 1968). The remaining 10 tube caps had been found loose on the sediment surface. In this habitat, one commonly finds fresh, loose tube caps that have been severed by predators or by the worm itself prior to rebuilding (pers. obs. and Myers, 1972).

Of the 10 loose tube caps, 7 were clearly damaged, having 3–5-mm circular holes and torn aperture rims. Such damage could only have resulted from animal activities—the aperture is sheltered by facing toward the sediment, and debris in the water column is very unlikely to poke holes through the thick tube wall.

Tube manipulations

Tube caps were severed at the sediment surface, brought to the laboratory, and glued to wooden dowel rods (18-cm \times 0.3–0.6-cm) using a waterproof epoxy (Marine Tex); the dowels permitted later deployment in the field. Tube caps decorated primarily with algae/plant fragments or shell fragments were assigned to the “algae” and “shell” treatments, respectively (Fig. 1). A third “undecorated” treatment was made by cutting all decoration flush with the tube wall. Undecorated tube caps are rare in this habitat, whereas algae- and shell-decorated tube caps are both common (all tube caps have a mixture of algae, plant matter, and shell, but the relative proportions differ). We distinguished between algae and shell because their different material properties might influence their propensity to sustain damage. Each experiment used fresh tubes that had been collected 1–2 days beforehand and kept damp at 4 °C until use.

To manipulate tube-associated odor, the tube caps were filled with 0.5–1.0 ml of 2% agar made in liquid containing the desired cue (more details below). We chose 2% agar because it is very hard and does not visibly dissolve, even when agitated in seawater overnight. Thus, any visually obvious agar loss in the field experiments was attributable to biotic activity. Chemicals in the agar do diffuse, however: 50%–60% of fluorescein dye (1 g/l) diffused from agar plugs (0.8 cm³, $n = 5$) into the surrounding seawater over a 24-h period (estimated by fluorometry).

To further differentiate between agar eaten by small animals and agar eaten by potential predators of the worm itself, squares of insect screening were embedded in the tubes before filling with agar (Fig. 1). We expected that small non-*D. cuprea*-eating organisms, such as amphipods, would eat the agar without removing the screen, whereas potential predators of *D. cuprea* would displace the screen during attacks. These expectations were supported by preliminary experiments placing manipulated tubes inside predator exclusion cages—neither screen loss nor wall damage occurred in the absence of large predators ($n = 30$ total, 5 per treatment of algae, shell, and undecorated tube caps crossed with no-odor and clam-odor treatments inside 0.5-cm hardware cloth cages, 20 cm high and 15 cm in diameter).

Each tube cap was videotaped from all angles before being deployed in the field. The dowel rods were driven 17 cm into the sediment so that the base of the tube cap was just below the sediment surface; to our eyes, manipulated

tube caps were indistinguishable from unmanipulated tube caps. The next day each tube cap was compared to the “before” video and scored for screen loss and damage to the tube wall. These often co-occurred and were therefore combined into a single binary “predator attack” category.

Effects of decoration and a strong feeding cue. To ask whether decoration influences damage rates, two trials were conducted in 2002 (day 1, 20–21 June, $n = 10$ per treatment; day 2, 24–25 June, $n = 15$ per treatment). To ask whether decoration’s effect (if any) changed in the presence of a highly salient feeding cue, the three decoration treatments were crossed with two odor treatments, a no-odor control (agar made in seawater) or clam odor (2% agar dissolved in bottle-strength Doxsee All Natural Clam Juice, Snow’s Food Company, Portland, ME). Decoration might be expected to obscure an odor cue if it alters local flow in a way that disrupts odor plumes, resulting in olfactory crypsis. The clam-odor treatment served the secondary purpose of indicating whether predators were active in the system during these experiments; this metric was necessary given that predators in estuaries are both spatially and temporally variable over tidal cycles (Kneib and Wagner, 1994; Salgado *et al.*, 2004). If predators were present, we expected damage rates to be elevated for clam-odor treatments *versus* no-odor treatments. All manipulated tube caps (60 on day 1, 90 on day 2) were haphazardly arrayed within a 100-m² area on their native sand flat. Each was marked with two wooden stakes placed 50 cm away on either side, and tubes were spaced meters apart from each other.

Effects of decoration and worm odor. To ask whether decoration influences damage rates when the tube is associated with a polychaete chemical cue, two trials were conducted in 2006 comparing tube caps containing either seawater agar (no-odor control), clam-odor agar, or agar containing *D. cuprea* effluent as the odor cue. Clam odor was included to facilitate comparison to the 2002 data and, again, to indicate whether predators were active during the experiment. The effluent was made by holding four living specimens of *D. cuprea*, without their tubes, in 1 l of continuously aerated seawater for 28.5 h. This is more concentrated than a living worm’s effluent, given that *D. cuprea* completely exchanges its tube-water every 10–15 min (an estimate based on irrigation rates, Mangum *et al.*, 1968). Twenty replicate 1-m² quadrats were marked with stakes in the field, arrayed in five haphazardly placed clusters. Each quadrat received one tube cap of each decoration/odor combination, arranged randomly. Tubes were thus 20–30 cm from their nearest neighbor, and tubes within a single treatment were separated by at least 20 cm but as much as many meters. Unexpectedly brief low tides during this period forced us to deploy the replicates over 2 days, and 2 of the 20 planned replicates were lost (day 1, 11–12 August, $n =$

7 per treatment; day 2, 12–13 August, $n = 11$ per treatment).

Data analysis

The frequency counts of attacked tube caps (those with screen loss, wall damage, or both) were analyzed by weighted least-squares analysis of variance using the SAS Institute's CATMOD procedure with a significance level of $\alpha = 0.05$ (SAS 9.1, 2002–2003 SAS Institute Inc., Cary, NC, Stokes *et al.*, 2000). Contrasts were constructed between parameters of interest if the main effect was significant. Unlike traditional ANOVA, there is no limit to the number of allowable contrasts in the CATMOD procedure (Stokes *et al.*, 2000). For each year, we analyzed a three-way model for the main effects of decoration, odor (control *versus* worm odor) and day, with all possible interactions. The three-way interaction term was nonsignificant in both years and was consequently dropped from both models.

We consulted the University of South Carolina Statistical Consulting Laboratory to ensure that our power analysis was appropriate for the CATMOD test. Using the CATMOD test χ^2 statistics as non-centrality parameters, we used the SAS function PROBCHI to return β , given the test degrees of freedom and the χ^2 critical value for a specified α . We computed power for both $\alpha = 0.05$ and $\alpha = 0.1$.

Results

The types of damage to experimental tube caps were similar to damage found on unmanipulated tube caps in the field. Wall damage ranged from small tears to torn apertures

Table 1

Weighted least-squares ANOVA for 2002

Source	df	χ^2	P	Power	
				$\alpha = 0.05$	$\alpha = 0.10$
decoration	2	6.29	0.04	0.61	0.72
odor	1	23.96	<0.0001	1.00	1.00
day	1	0.55	0.46	0.12	0.19
odor*decoration	2	8.53	0.01	0.75	0.84
odor*day	1	5.15	0.02	0.62	0.73
dec*day	2	6.05	0.05	0.59	0.71
Contrasts					
shell & algae <i>vs.</i> undec	1	0.06	0.81		
algae & undec <i>vs.</i> shell	1	4.73	0.03		
shell & undec <i>vs.</i> algae	1	4.73	0.03		

Weighted least-squares analysis of variance and contrasts (SAS proc CATMOD). The response variable was the occurrence or absence of a likely predator attack, defined as a lost screen and/or damage to the tube wall. Algae, shell, and undecorated (undec) tube-cap treatments were crossed with seawater and clam-juice odor. The CATMOD procedure can test unlimited numbers of contrasts (Stokes *et al.*, 2000). Power values are given for alpha values of 0.05 and 0.10.

and severe mangling. This is consistent with ripping or biting attacks by fish or crabs. One tube cap in the algae/no-odor category (2002 day 2) disappeared and was supplanted by a shallow 20-cm-wide feeding pit, indicating ray or skate predation.

Effects of decoration and a strong feeding cue (2002)

If decoration reduces the likelihood that predators will recognize and attack a tube, then undecorated tubes should experience more attacks than decorated tubes. This was not observed in 2002 (Table 1, Fig. 2). Although the “decoration” main effect was significant ($P = 0.04$, Table 1), this was driven by significantly higher damage rates on shell and algae tube caps (both contrasts $P = 0.03$, Table 1), as is visually obvious from Figure 2. This pattern is not consistent with the crypsis hypothesis, nor was it consistent across days or repeated in 2006. Overall damage rates were similar across both days but were distributed differently among treatments, leading to an insignificant “day” main effect ($P = 0.46$, Table 1) but significant temporal interactions with both odor ($P = 0.02$) and decoration treatments ($P = 0.05$, Table 1).

Power analyses indicate that these results have adequate power to differentiate significant main effects (Table 1) and certainly to detect trends in support of crypsis; no such trends were seen.

Effects of decoration and worm odor (2006)

As in 2002, undecorated tube caps were not damaged more often than other treatments. Again, the “decoration” main effect was significant ($P = 0.02$, Table 2), but this was driven by patterns not consistent with crypsis. Shell tube caps were damaged significantly more often in the no-odor and clam-odor treatments on day 1 (contrast $P = 0.02$, Table 2, Fig. 2). On day 1, clam-odor treatments again experienced significantly more damage than no-odor and worm-odor treatments (contrast $P < 0.0001$, Table 2); worm-odor and no-odor treatments were not different. Damage rates were very low overall on day 2, driving a highly significant “day” main effect ($P < 0.0001$, Table 2) as well as significant interaction terms (Table 2).

As in 2002, power analyses indicate that these results have adequate power to differentiate significant main effects (Table 2) and certainly to detect trends in support of crypsis; no such trends were seen.

Discussion

Decorating phenotypes are widespread among the animal phyla and are frequently assumed to provide crypsis. Data supporting this hypothesis exist for many insect larvae including caddisflies, lacewings, tortoise beetles, and assassin bugs, as well as sea urchins and decorator crabs (re-

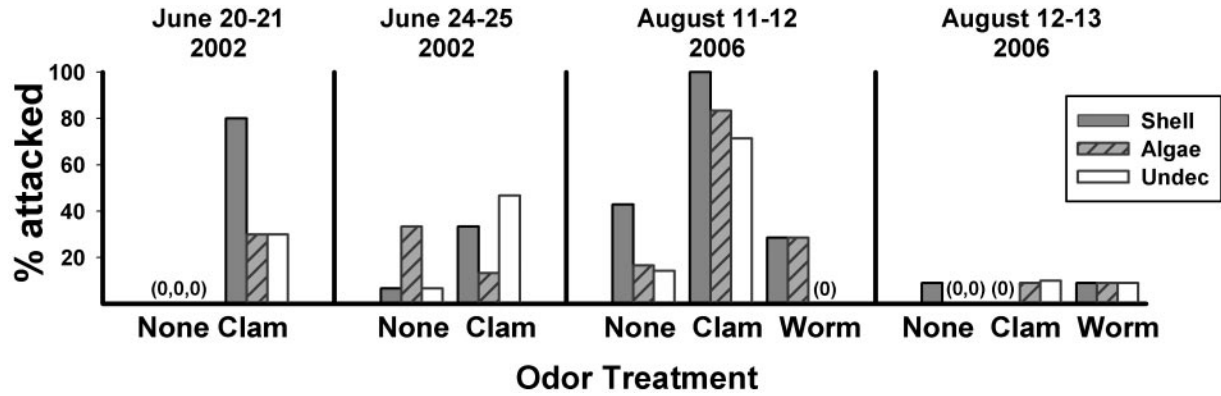


Figure 2. Percent of *Diopatra cuprea* tube caps showing evidence of predator attack. Predator attack was scored if the tube cap lost its screen and/or suffered damage to the tube wall (see text). The three decoration treatments, “shell,” “algae,” and “undecorated,” were the same for all experiments. Odor treatments were seawater agar (“plain”), clam juice agar (“clam”) and agar containing *Diopatra cuprea* effluent (“worm”). Numbers of replicates per treatment were as follows: June 20–21 2002: $n = 10$, June 24–25 2002: $n = 15$, August 11–12 2006: $n = 7$, and August 12–13 2006: $n = 11$.

viewed in Berke *et al.*, 2006). The decoration of *Diopatra cuprea* has been shown to enhance feeding (Mangum *et al.*, 1968) and extend the worm’s sensory range (Brenchley, 1976). The crypsis hypothesis has remained untested, despite being in the literature for decades (Myers, 1972; Brenchley, 1976).

If tube cap decoration confers crypsis, then removing decoration should increase the likelihood that the tube will be attacked. This pattern was not observed (Fig. 2). Damage consistent with potential predator attacks occurred in 12% of tube caps containing seawater or *D. cuprea* effluent and

in 42% of tube caps containing clam odor (averaged across years and treatments), but undecorated tube caps were never at highest risk. Given that *D. cuprea* adult survivorship can approach 100% (Peckol and Baxter, 1986), the 12% attack rates for seawater and worm-odor tube caps are probably realistic.

In principle, crypsis can be difficult to identify if attack rates are low. In this sense, the clam-odor treatments can be seen as experimentally elevating attack rates for the purpose of evaluating the crypsis hypothesis under more predation-intense conditions. Even in this extreme case, undecorated tube caps were not at higher risk than decorated tube caps (Fig. 2). The fact that significant “decoration” main effects and contrasts were detected in both years indicates that our experimental design was powerful enough to detect crypsis if such an effect were present. If anything, the pattern in 2006 was in the opposite direction, with undecorated tube caps at significantly lower risk than shell and algae tube caps (contrast $P = 0.02$, Table 2, Fig. 2). Shell and algae tube caps were each at highest risk on different days in different years, but these patterns were temporally isolated and contradicted each other, giving them little ecological relevance. Such patterns probably reflect variable predator composition and the different material properties of shell and algae-decorated tubes. Most tubes in this habitat have a mixture of algae/plant matter and shell debris; we distinguished between them because we thought that their different material properties would contribute to patterning of variance, as was indeed the case. Fully understanding how different types of decoration function, however, was not a goal of this study.

D. cuprea effluent did not affect damage rates, suggesting that worm odor is not a strong feeding cue for predators in this system. We suggest that this outcome is expected, given

Table 2

Weighted least-squares ANOVA for 2006

Source	df	χ^2	P	Power	
				$\alpha = 0.05$	$\alpha = 0.10$
decoration	2	7.91	0.02	0.71	0.81
odor	2	37.73	<0.0001	1.00	1.00
day	1	78.16	<0.0001	1.00	1.00
odor*decoration	4	2.84	0.59	0.23	0.34
odor*day	2	45.32	<0.0001	1.00	1.00
dec*day	2	8.60	0.01	0.75	0.84
Contrasts					
shell & algae vs. undec	1	5.66	0.02		
undec vs. shell	1	7.90	0.01		
algae & undec vs. shell	1	5.53	0.02		
plain vs. clam	1	25.91	<0.0001		
worm vs. clam	1	30.65	<0.0001		
plain & worm vs. clam	1	37.45	<0.0001		

Weighted least squares analysis of variance and contrasts (SAS proc CATMOD); details given in note to Table 1. Algae, shell, and undecorated (undec) tube-cap treatments were crossed with seawater, clam-juice odor, or *Diopatra cuprea* odor.

that *D. cuprea* is very good at escaping predation. The worm can rapidly withdraw to 30 cm or more below the sediment surface; successful predators are those that can attack quickly when the worm is exposed or those that can excavate the tube. In either case, visual cues are likely to be more reliable than chemical cues, especially since *D. cuprea* can control its odor plume by ceasing irrigation, which is part of its rapid withdrawal response (pers. obs.).

Although the crypsis hypothesis was not supported, *D. cuprea* tubes undoubtedly do play a role in reducing mortality risk. Decoration may help the worm behaviorally avoid predation by transmitting vibration, providing early warning of predator attacks (Brenchley, 1976). The tube's hooked shape may reduce sedimentation inside the tube, make it difficult for suction-feeding predators to extract the worm, or hide the worm's activities near the tube aperture from view. Decoration often projects beyond the aperture in an awning-like fashion, which could further hide the worm itself from view. It is important to note, however, that some decorating *Diopatra* species do not have hooked tube caps (i.e., *D. neapolitana*, pers. obs.; and *D. obliqua*, Paxton, 1998), and in these cases decoration does not typically obscure the aperture. In principle, it remains possible that decoration confers crypsis to a small degree not detectable in this experiment. While such small effects could be important over evolutionary time, it seems more likely that *D. cuprea* decoration is selectively maintained by forces other than crypsis, given that other functions related to feeding and predator avoidance have been demonstrated (Mangum *et al.*, 1968; Brenchley, 1976; Brenchley and Tidball, 1980).

Our field survey of naturally occurring damage (see Materials and Methods, *Naturally occurring damage*), together with the experimental data, suggest that *D. cuprea* tubes experience frequent damage due to predators. The sources of damage, and their real relation to lethal and sublethal predation risk, warrant further investigation. Worms with damaged tubes may well sustain injuries that, although nonlethal, have significant fitness consequences. Individuals with recently regenerated anteriors are common in this habitat. Anterior regeneration takes several weeks, during which tube maintenance and feeding are impeded or impossible (pers. obs.). One would expect this period of reduced feeding and somatic rebuilding to influence gonad quality or quantity; therefore even nonlethal predation is expected to be evolutionarily significant. Given the number of damaged tubes found in the field and the worms' capacity for rapid tube repair, repair could be a primary activity for *D. cuprea*. The energetic expenditure of tube repair could significantly affect *D. cuprea*'s energy budget (see Berke *et al.*, 2006), in which case factors influencing repair rates, such as temperature (Myers, 1972) and the presence of some pollutants (Fielman, 2000), may have important implications for *D. cuprea* community dynamics.

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Literature Cited

- Allen, D. M., and V. Ogburn-Matthews. 2005. Sharks, rays and bony fishes: a list of species known from North Inlet Estuary, Hobcaw Barony, SC. Belle W. Baruch Institute, University of South Carolina, Data Archives. [Online]. Available: <http://links.baruch.sc.edu/Data/SpeciesLists/Fishes.html>. [2007, November 6].
- Berke, S. K., M. Miller, and S. A. Woodin. 2006. Modelling the energy-mortality tradeoffs of invertebrate decorating behaviour. *Ecol. Ecol. Res.* **8**: 1409–1425.
- Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of Northwest Atlantic fishes and two common species of squid. *NOAA Tech. Memo.* NMFS-NE-155, Northeast Fisheries Science Center, U.S. Dept. of Commerce.
- Brenchley, G. A. 1976. Predator detection and avoidance: ornamentation of tube-caps of *Diopatra* spp. (Polychaeta: Onuphidae). *Mar. Biol.* **38**: 179–188.
- Brenchley, G. A., and J. G. Tidball. 1980. Tube-cap orientations of *Diopatra cuprea* (Bosc)(Polychaeta): the compromise between physiology and foraging. *Mar. Behav. Physiol.* **7**: 1–13.
- Day, J. H. 1967. *A Monograph on the Polychaeta of Southern Africa. Part 1: Errantia*. British Museum (Natural History), London.
- Endler, J. A. 1981. An overview of the relationships between mimicry and crypsis. *Biol. J. Linn. Soc.* **16**: 25–31.
- Fauchald, K. 1977. Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithson. Contrib. Zool.* **221**: 1–81.
- Fielman, K. 2000. Biogenic halogenated organic compounds and their dehalogenation as determinants of marine benthic community structure. PhD dissertation, University of South Carolina, Columbia.
- Finelli, C. M., N. D. Pentcheff, R. K. Zimmer, and D. S. Wethey. 2000. Physical constraints on ecological processes: a field test of odor-mediated foraging. *Ecology* **81**: 784–797.
- Grant, J. 1983. The relative magnitude of biological and physical sediment reworking in an intertidal community. *J. Mar. Res.* **41**: 673–689.
- Hartman, O. 1968. Atlas of the Errantiate Polychaetous Annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
- Hartman, O. 1969. *Atlas of the Sedentary Polychaetous Annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
- Howard, J. D., and J. Doerjes. 1972. Animal-sediment relationships in two beach-related tidal flats; Sapelo Island Georgia. *J. Sediment. Petrol.* **42**: 608–623.
- Kneib, R. T., and S. L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Mar. Ecol. Prog. Ser.* **106**: 227–238.
- Mangum, C. P., S. L. Santos, and W. R. Rhodes, Jr. 1968. Distribution

- and feeding in the onuphid polychaete, *Diopatra cuprea* (Bosc). *Mar. Biol.* **2**: 33–40.
- Myers, A. C. 1972.** Tube-worm-sediment relationships of *Diopatra cuprea* (Polychaeta: Onuphidae). *Mar. Biol.* **17**: 350–356.
- Paxton, H. 1998.** The *Diopatra chiliensis* confusion—redescription of *D. chiliensis* (Polychaeta, Onuphidae) and implicated species. *Zool. Scr.* **27**: 31–48.
- Peckol, P., and D. Baxter. 1986.** Population dynamics of the onuphid polychaete *Diopatra cuprea* (Bosc) along a tidal exposure gradient. *Estuar. Coast. Shelf Sci.* **22**: 371–377.
- Richards, K. S. 1978.** Epidermis and cuticle. Pp. 33–61 in *Physiology of Annelids*, P. J. Mill, ed. Academic Press, London.
- Salgado, J. P., H. N. Cabral, M. J. Costa, and L. Deegan. 2004.** Nekton use of salt marsh creeks in the Upper Tejo estuary; comparisons among habitats using canonical correspondence analysis. *Estuaries* **27**: 818–825.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2000.** *Categorical Data Analysis Using the SAS System*. SAS Institute, Cary, NC.
- Stowe, M. 1988.** Chemical mimicry. Pp. 513–580 in *Chemical Mediation of Coevolution*, K. Spencer, ed. Academic Press, San Diego, CA.
- Woodin, S. A. 1977.** Algal “gardening” behavior by nereid polychaetes: effects on soft-bottom community structure. *Mar. Biol.* **44**: 39–42.
- Woodin, S. A. 1981.** Disturbance and community structure in a shallow water sand flat. *Ecology* **62**: 1052–1056.
- Woodin, S. A. 1982.** Browsing: important in marine sedimentary environments? Spionid polychaete examples. *J. Exp. Mar. Biol. Ecol.* **60**: 35–45.