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Speculations on the Distribution and Function of Color Morphs in Fanworms at Discovery Bay, Jamaica.

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Abstract

In a study at Discovery Bay, the distribution of color morphs of Sabellid and Serpulid fanworms was examined within an area less than two meters deep on various substrates, and between areas at 40 feet and 80 feet on coral only. The common, shallow _Sabella_ spp. was tested for palatability to fish and to nocturnal predators on a limited basis. The _Sabella_s were found to be clumped, most commonly near coral and coral rubble. When fanworms were found on corals in the shallow zone, they were more often on vertical than on horizontal surfaces. Greater color pattern richness and diversity were found at 80 feet than at 40 feet. A variety of fish and local nocturnal predators seem to find the _Sabella_, the crown in particular, to be unpalatable. Speculations were made as to the factors influencing the development of the multiplicity of colors in the tentacular crowns of these polychaetes.

Introduction

The polychaetes known as "fanworms" or "feather duster worms" commonly found in the lagoon and reef areas at Discovery Bay are members of two different families. Those in the family serpulidae secrete a calcareous tube from which their ciliated radioles protrude as they collect detritus from and exchange gases with the surrounding water. The radioles may be withdrawn into this tube and the tube plugged with a modified radiole called the operculum. The showy "Christmas-tree worms" are included in this family, their radioles being whorled so that they appear to be in several tiers.

The family Sabellidae, on the other hand, builds a flexible tube of sand grains and mucus. The crown of radioles may be drawn into this tube as in the serpulids, but there is no operculum. Instead, the end of the tube pinches shut in many cases as the sabellid retreats into the far end of its refuge.

During explorations of various habitats in and around Discovery Bay, it was noted that a variety of crown colors is exhibited within both of these families, and it was speculated that the distribution of colors might be correlated with depth or substrate type. Since resources are not considered limiting in polychaete populations (Barnes, 1977), other factors were considered as potential influences. Physical factors such as temperature fluctuations, salinity, sedimentation rates, turbulence, and currents might all contribute to the pattern of species found at a particular site. These factors may have local effects, such as where a freshwater spring enters the lagoon or on the reef crest where turbulence is particularly high, creating a microhabitat suitable for or inadequate for a particular species or color morph of fanworm. However, in general, the salinity doesn't vary much in the Discovery Bay area; its range is 34 to 36‰ according to Jackson (1972). Similarly, there is only a small temperature range of from 26° to 30° C in the Bay area (Reiswig, 1971).

One physical factor that has been shown to have a strong effect on invertebrates is the amount of ultra-violet radiation incident on the body tissues. In a study by Jokiel (1980) it was shown that natural UV radiation could kill unprotected sponges, tunicates, and bryozoans which usually live underneath rubble. Details of substrate type, slope, and exposure all affect the amount of incident light on a microhabitat scale (Brakel, 1979); and UV light is known to decrease with depth (4.4% per meter of depth in fresh water) (Jerlov, 1970).

In addition, there is some evidence that certain Sabellids may have adaptations that help them to withstand UV radiation. Porphyrins are compounds which act as photosensitizing mutagens in the bodies of invertebrates such as worms, causing damage in the presence of light and oxygen. It has been found that the crowns of three species of sabellids

(*Sabella penicillus*, *Myxicola infundibulum*, and *Megalomma vesiculosum*), when exposed to light when feeding during the daytime, contain no free porphyrin (Segal, 1970). This suggests that at least some Sabellids have adaptations enabling them to exist in areas with significant amounts of UV radiation.

Biological factors may also influence the distribution of species and colors in the fanworms. Inter or intra-specific competition may influence the survival of ~~of~~ individuals in high density areas. Woodin and Jackson (1979) cite several examples of competition between tube-building polychaetes, though fanworms are not mentioned specifically. Benchley (1978) notes that mortality rates of juvenile tube builders (again, does this include fanworms?) are greater in sediments dominated by organisms that destabilize sediments.

Differential predation might also be a biological factor influencing which species or colors are capable of surviving on a certain substrate or at a certain depth where a particular set of predators exists. One might expect that an organism as visible (at least to the human eye) as a fanworm would be attractive to a hungry predator. The current view in the literature is that, while desensitization to mechanical, photo, and baro stimuli may occur, fanworms withdraw into their tubes to avoid (fish?) predation. However, during our preliminary studies, it was noted that fanworms would often not respond to the close passage of a fish. This led us to speculate that the worms may be unpalatable to fish.

Thus, our studies were directed in three main areas. First, we looked at the distribution of color morphs within a depth, that is all less than 2 m, hypothesizing that there would be some type of substrate specificity at this depth. Next we compared the color morphs found at 40 feet and 80 feet, hypothesizing that amount of pigment or relative abundance of colors would change with depth, perhaps due to physical or biotic factors. Third, we hypothesized that fan worms are unpalatable to fish, and set out to test this for a subset of the local fish fauna.

reading this handwriting is tough!

Materials and Methods

The following experiments were carried out from February 26 - March 5, 1983 at Discovery Bay Marine Laboratory, Jamaica, West Indies.

To determine whether substrate specificity could be shown for the different fanworm color pattern "operational taxonomic units" ("... generic subdivisions within the family are nevertheless debatable." (Fauchald, 1976) or at least very difficult to distinguish (Dale Ward and Thistle Anderson, personal observation)), a survey was taken on the West Back Reef ~~area~~ lagoon area of Discovery Bay. All of the survey was taken in depths from 1 to 2 meters. ~~in a fixed~~ We hoped that this within depth survey would control for biotic factors (such as coral community composition) and abiotic factors (light intensity, turbulence) ~~to~~ which would be difficult to take into account otherwise.

Two sampling methods were utilized. The first consisted of standing at an arbitrary spot of the back reef flats and randomly throwing a one meter^2 quadrat out. It was timed for two minutes after it settled on the bottom to give the worms time to re-emerge. We then swam over to the quadrat, counted the exposed fanworms and classified the terrain type within as either sand, sand/rubble or sand/rubble/grass.

We decided to abandon this method on the third day of censusing due to time limitations. The quadrat method sampled such a small area at one time that a very large number of samples would have to be made before a true(?) picture of fanworm distribution would emerge especially if the fanworms were as clumped as they looked qualitatively.

Our second censusing method was to attach a 20 m string to an object on the bottom and swim out to one of the four compass points with it. From 2-3 minutes were allowed for worm reemergence, then ~~the~~ an area 2 m wide was examined for the length of the string for fanworms, giving an area of 40 m²/transect. If worms were found, their immediate surroundings were classified as to sand, sand/rubble, or sand/rubble/grass. The process was then repeated for the other points of the compass.

A problem with this method of censusing was that a large part of each belt transect would include open sand habitat unsuitable for fanworms. Since we wanted to look at the occurrence of clumping within suitable habitats (since including unsuitable habitat would obviously result in a clumping of the population in the suitable), a mean/variance test for random distribution was made.

An attempt was made to quantify the substrate selection of fanworms living on the rubble itself rather than in the sediment. This was done by ~~swim~~ snorkelling back and forth the West Beach Reef area looking for exposed worm crowns, noting their color, whether the substrate they were on was vertical or horizontal and whether the substrate was living or dead coral. The patchiness of worm distribution (and coral "island" patchiness) made a transect type of survey unfeasible. A G-Test was made on the data to determine whether fanworms tended to occur on the vertical or the horizontal components of the coral. It was necessary to lump the live coral and the rubble data in order to get a reasonably large sample size.

inc. sentence

The attempt was made to see whether it was possible to determine changes in the color pattern of fanworms with increasing depth. Dives were made to 40 feet and 80 feet using SCUBA equipment. It was only possible to do a 15 minute survey at each depth due to meterological conditions and other circumstances beyond our control (such as transportation difficulties).

Censusing was carried out by having the diver swim along at a certain depth, noting the occurrences and relative abundances of different fanworm colors/patterns. We were just looking to see whether these changed, recognizing that we would be unlikely to find a definite mechanism explaining these color changes, and therefore did not look at other variables such as coral community composition. The data thus collected were analyzed by calculating H' and the color pattern richness for each site.

The third major thrust of our investigation involved testing the fanworms for palability to fish predators. Because of difficulties experienced procuring a sufficient quantity of fanworms for testing, it was decided to restrict our experiment to just one type of Sabellid fanworm, tentatively identified as _Sabella melanostigma_. Tests were carried out in the Mangrove Cove slightly to the west of the boat docks to avoid the rough weather in the bay.

Initially, we removed some whole worms from their tubes and ~~through~~ threw them out to groups of fish, including needlefish (_Strongylura notata_ ?), Dusky Damselfish (_Eupomacentrus dorsopunicans_), blue head wrasses (_Thalassoma bifasciatum_) and Sergeant Majors (_Abudefduf saxatilis_), as well as Bermuda Chubs (_Kyphosus sectatrix_). This was primarily to determine the feasibility of carrying a palatability study out.

Our next experiment consisted of cutting the bodies of several _Sabella_ into portions of approximately 1cm, leaving the tentacles together as a discrete unit. These were fed to an aggregation of fish and the fishes' reactions ~~was~~ were noted. A "1" was scored if a fish ate the piece, a "2" if the fish ingested but then spat the piece out, and a "3" if the fish darted towards the fragment as if to eat it, but turned away at the last moment (within ~10cm of the fragment). *Echinometra* sea urchin gut pieces of approximately equivalent size were used as controls.

The third part of this experiment consisted of removing the tentacular crown from a *Sabella* and attaching it to a piece of cardboard which was to serve as an artificial substrate. Due to difficulties in attaching the crown to the cardboard in a manner which would hold the crown on (we finally ended up using staples), only three worm crowns were prepared in this manner. We did not have a control (try stapling sea urchin guts to cardboard sometime).

The cardboard was then carried to the cove, placed in about 6-7' water, weighted down with sediment and a diving weight and left until the next morning (~4:00PM - ~8-9:00AM). The idea of this portion of the experiment was to tell us whether a) some nocturnal predator was preying upon worms, or b) the fish were responding to our presence or the unnatural presentation of the fragment (falling through the water) in their behavior.

Results: The results of the shallow water within depth survey may be seen in tables 1+2. Table one includes a Mean/Variance ratio test for clumping. The fanworms were found to be distributed in clumps ($.01 > p > .001$) rather than randomly or evenly dispersed. Table 2 includes the data gathered from the on-coral within depth survey, an attempt to see if the worm color OTU's partitioned the substrate according to their OTU. We were unable to determine this with our categories of "vertical" and horizontal", although we did find that fanworms on coral rubble tend to be found on vertical or overhanging portions of the rubble (G-test, $.05 > p > .02$). The vertical/horizontal distinction does not supply a sufficiently fine resolution to determine habitat partitioning. We did observe, however, that a.) the bright yellow fanworms tended to occur in pockmarks or overhangs on the rubble, in more protected areas; b.) Christmas tree worms, especially the small ones (1/2-1 cm diameter) tended to occur on the open exposed portions of ~~coral~~ rubble, even living coral; and c.) The clumping observed in Christmas tree worms seemed to be more intense than in the Sabellids. ~~studied~~

Table 1
Results of Shallow-Water 1 m^2 Quadrat Survey

Substrate:	Sand	Rubble/Grass/Sand	Rubble/Sand
	0	3	0
~~Framed~~	0	2	3
Quadrats	0	2	0
= # *Sabella*	0	0	2
per m^2	0	0	1
↓	(discontinued)	1	1
		1	6
	0	1	13
	density = 0 worms/m^2	0	
		0	1.86 worms/m^2
		0	
		1	
		0	
		2	
		13	
		0.93 worms/m^2	

↓ Rubble/grass/sand and rubble/sand lumped

Variance/Mean $= \frac{1}{n\bar{x}}\left[\sum_{j=1}^{n}(x_j-\bar{x})^2\right]$; $\bar{x} = (\sum x_j)/n$

$$= \frac{.86}{14}\left[2(3-\overset{1.19}{\cancel{.86}})^2 + \overset{4}{\cancel{3}}(2-\overset{1.19}{\cancel{.86}})^2 + 5(1-1.19)^2 + 9(-1.19)^2 + 6(6-1.19)^2\right] = 1.81$$

$$= \frac{V}{M} > 1, \text{ therefore clumped.}$$

$$x^2 = \left[\frac{9(0-1.19)^2}{1.19} + \frac{5(1-1.19)^2}{1.19} + \frac{4(2-1.19)^2}{1.19} + \frac{2(3-1.19)^2}{1.19} + \frac{(6-1.19)^2}{1.19}\right] = 38.02$$

= 20 degrees freedom

Therefore, significantly clumped (.01 > p > .001)

Table 2
Within Depth Horizontal/Vertical Specificity
(Live and Dead Coral)

worm color OTU	horizontal f	horizontal $\hat{f}$	vertical f	vertical $\hat{f}$	total f
yellow	2	4.7	16	13.29	18
orange & tan	0	.52	2	1.48	2
black and white	0	1.05	4	2.95	4
black and white & tan	9	3.14	3	8.86	12
orange	0	.26	1	.74	1
Christmas Tree	5	4.97	14	11.81	19
brown & white Sabella	1	2.35	8	6.65	9
	17		48		65

$$G = 2\left[\sum^{a} f_i \ln f_i - \sum^{a} f_i \ln \hat{f}_i\right]$$

$$= 2[(1.386 + 19.775 + 8.047 + 44.36 + 1.386 + 5.545 + 3.296 + 36.947 + 16.636) - (3.10 + 10.30 + 8.02 + .85 + 41.39 + .78 + 4.33 + 6.54 + 34.56 - .30 + 15.16)]$$

$$= 12.65 \text{ with 6 degrees freedom}$$

Null hypothesis (Worms occur independently of vertical or horizontal aspects of coral faces) rejected,

$.05 > p > .02$

(assumes vertical and horizontal substrate occurrences are approximately equivalent)

We were unable to utilize the data collected on the belt transects due to the inclusion of habitat unsuitable for tube building polychaetes (open, loose sand). This produced fanworm densities almost an order of magnitude lower than those attained with the quadrat method. We are also suspicious of the numbers attained with the belt transects because of the high possibility that the wave action on the days this survey was made moved the string back and forth over the substrate, scaring the fanworms.

We concluded that the fanworm density in open sandy areas is almost zero by swimming over such areas and visually searching for them. We found very few. Density was highest in areas of rubble and sand (1.86 worms/m^2) and intermediate in rubble, grass, sand areas (0.93 worms/m^2). This would seem to indicate that the worms tend to be associated with rubble areas (their tubes often extend under the rubble, for protection or erosion prevention?), and that perhaps they are competing for space with Thalassia ([illegible] the last statement might be a little bit far out...)

Other factors, such as particulate organic matter availability, may also have something to do with this distribution.

Our survey at depth (40' vs 80'), while brief, does provide some interesting data. The two different depths have almost entirely different fanworm color patterns associated with them. (Table 3). Diversity (H') of color patterns ~~a~~ was approximately 33% greater at 80 feet than at 40 feet. While it is impossible to draw conclusions from these data without larger sample sizes and/or replicate sites, they are interesting.

Just as an aside, a Christmas Tree worm was noted at 80 feet on a _Monastrea annularis_ coral. Miguel Damen (78) stated in an earlier study that _Spirobranchus_ tends to occur with _M. annularis_ at depths up to about 65'. He notes that _M. annularis_ exhibits a bimodal distribution with depth, a node occurring about 65', and that _Spirobranchus_ could appear on the other side of the node with _M. annularis_. While the finding of one worm at 80 feet is hardly conclusive, it is suggestive that perhaps there is something to what he says.

We were unable to do surveys on the open sand at depth due

point unclear

Table 3
Survey at Depth on Corals

40' #	40' freq.	fanworm OTU	80' #	80' freq.
13	.72	Br. & Yellow serpulid	2	.11
1	.06	red/brown/white " "	0	0
3	.17	red/brown Xmas Tree	0	0
1	.06	cream & black Xmas Tree	0	0
0	0	purple/red Xmas tree	1	.06
0	0	cream & brown serpulid	2	.11
0	0	cream & white sabellid	3	.17
0	0	orange & cream " "	1	.06
0	0	yellow-white ?	2	.11
0	0	white ?	7	.39
18	1.01		18	1.01

$$H'_{40'} = \frac{\Sigma p_i \ln p_i}{H_{max}} = \frac{-.24-.17-.30-.17}{4(.25 \ln .25)} = \frac{-.88}{-1.39} = \underline{\underline{0.63}}$$

$$H'_{80'} = \frac{-.24-.17-.24-.30-.17-.24-.37}{7(.14 \ln .14)} = \frac{-1.73}{-1.93} = \underline{\underline{0.90}}$$

Depth	OTU "Species" richness	H'
40'	4	0.63
80'	7	0.90

to logistical problems, but did note qualitatively that dense clumps of white fanworms occur in the open sand at 40' and 80'. Their ability to colonize loose sandy areas may be due to reduced turbulence at depth, i.e. decreased exposing of their tube to sediment removal.

Our palatability study results (Table 4) show fairly conclusively that Sabella melanostigma is unpalatable to fish. In no instance did we observe a fish swallowing either the worm's crown or the worm itself when the crown was attached. Fish would mouth the worm if it had the crown, but not eat it. In no instance did we see a fish try to eat the crown portion of the worm alone, but they would eat sections of the body. This leads us to believe that the worm's crown is unpalatable while its body's palatability is debatable. The fish which ate the body sections often did so only after spitting it out several times. This could have been due to the awkwardness of the chunk, although it was not overly large (~1cm long), and not necessarily its unpalatability. It would be arguable that the fish didn't recognize the tentacles

Table 4
Palatability Study Results

A. Preliminary observations - 2 worms removed from their tubes and thrown to fish. The worms were re-used.

1.) French grunt (Haemulon flavolineatum) ~~mouthed and spat~~ Came within 10cm of worm and turned away.
2) Redfin needlefish - mouthed & spat out
3.) dusky damselfish " "
4.) Bermuda chub - " "
5.) Sergeant major - " "
6.) Bluehead wrasse - " "
7.) Many damselfish & wrasses approached worm closely as it sank, but they turned away without ingesting it.
8.) Bartholomea annulata in lab tanks ate two whole worms, worms rejected by Condylactis gigantea in same tank.

B. Palatability of Sabella body parts vs. Urchin guts. Different segments used each time.

I. Echinometra guts (1 = ate; 2 = ingested & spat; 3 = observed closely)

Trial	Fish(es)	Behavior	
1	Bluehead	1, 1	fragmented as they sank.
2	Bluehead	1, 1, 1	
3	Dusky Damselfish	1, 1, 1	
4	Sergeant Major	1, 1, 1	

100% of trials ended in piece being eaten.

Table 4
cont'd

II Sabella body sections

Trial	Fishes	Behavior	Sergeant major
1	Damsels & Sergeant major	2,2,2,2, 2,2,3,2,2, (Damsels)	1
2	Sergeant major	2,3,2,1	
3	Needlefish	2	
4		3,3,3,3,2,2,2,1	
5	Damselfish & Sergeant	3,3, 2,2	
6	Major - if eaten,	3,1	
7	usually by Sergeant	3	
8	Major	3,2,2,1	

.62 of trials, particle eaten

III Worm Crown

Trial	Fish + behavior
1	Bluehead (3), Striped parrot (3)
2	Bluehead (3,3,3); Super ♂ bluehead (3)
3	Bluehead (3) Striped parrot (3), Chubs (3,3,3)
4	~~Sbp~~ Dusky damsel (3), juv. bluehead (3)
5	Sergeant Major (3,3,3,3) juv bluehead (3), chub (3)
~~6~~	Ocean surgeon (3,3,3), Bluestriped (?)
~~7~~	grunt (3)
6	Needlefish (3)
7	Sergeant Major (3,3)

0% of trials tentacles eaten

C. Artificial "worm heads" - all three still there next morning.

as food were it not for our initial observations of fish refusing to eat the worm if the tentacles were still attached. Also, we have observed fish mouthing things which looked even less like food (to us, anyway).

Our experiment of putting the worm crowns out over a long period of time suggests that perhaps the crowns are unpalatable under natural conditions and that perhaps nocturnal predators are not a great problem for the fanworms (in the small Mangrove Cove), but requires a.) a larger sample size; b.) a longer term experiment; and c.) some form of control, such as a piece of fish stuck onto the board beside the worm.

To summarize our results, we found that:

1.) Clumping tends to occur in _Sabella mellanostigma_.
2.) _Sabella mellanostigma_ are most abundant in environments containing coral and/or coral rubble, at least at the shallow depth studied.
3.) Fireworms which live on the coral or rubble itself seem to prefer (via habitat selection or differential mortality) vertical surfaces over horizontal surfaces.

4.) Greater color pattern richness and diversity were found at ~~the~~ 80' than at 40'.

5.) Some fish predators find fanworm crowns unpalatable.

6.) No nocturnal predators ate the fanworm crowns placed in the relatively sheltered mangrove cove.

Discussion: The occurrence of clumping in shallow water populations of Sabella mellamosteyiona may be explained by one of two routes. The first of these assumes that planktonic Sabella larva settle out onto the substrate more or less at random, and that the observed adult distribution is the result of differential mortality. The fact that Sabella was found to generally be associated with rubble in the sand could be because those larva which settled on just plain sand were preyed upon or buried beneath sediment, or experienced any of a number of alternate horrible fates. This view holds that there is just a certain amount of rubble to go around, so naturally fanworms will be found clumped at these sites. While this view may be in part correct, we are not entirely satisfied with it. It appears to us that the number of rubble/sand sites without worms is so great that the chance of occurrence of more than one or two worms at a given site ~~are~~ is small. It is also true that we may not be noticing some ~~[illegible]~~ factor critical to fanworm survival which is missing from these sites. That may be true, but we found clumping occurring within the sand/rubble substrate type.

A possibility which we feel is more likely is based upon a statement by Barnes (1980) that many fanworms are capable of asexual reproduction by budding. Budding would produce groupings of fanworms such as those observed as well as provide a possible explanation for the numerous color varieties observed in fanworms, ~~to~~ which will be returned to later in the paper.

Another possibility is that larvae may tend to settle out of the plankton in response to some sort of cue produced by the adult fanworms. This is certainly feasible, and presents an alternate explanation of the clumping.

Another of our results indicated that fanworm color patterns were more diverse at 80' than at 40'. If these results are valid (more sampling needs to be done, preferably at other depths as well), then they could be explained by the removal of some factor restricting the possible color patterns of the worms. This could be some predator which is restricted to shallow depths, or an abiotic factor such as reduced turbidity which somehow influences worm color. It is conceivable that UV light may play a role, in that we noted an increase of pale, low-pigmented worms at both of the deep sites. If the coloration serves as a form of sunscreen, then a lack of such pigments would be less deleterious to the worms at the deep sites than in shallow water where there is more risk of UV damage.

On the subject of UV screening, laboratory observations revealed that the pigmentation in our _Sabella_ specimens appeared to be on the underside of the radioles, where it would be least effective against direct solar radiation. We did not note this in any of the other OTU's we managed to collect.

Finally, we consider our observation that fanworm crowns (_Sabella melanostigma_ crowns at least) seem to be distasteful to some fish predators. If the worms are unpalatable, one is led to ask what the adaptive significance is of being able to withdraw into the tube when light or pressure stimuli are sufficiently applied. There are three points to consider here: 1) They don't always withdraw - we have observed fish swimming quite near to the worms with no discernable reaction on the part of the worm. 2) Even if they are unpalatable, perhaps the times when they do withdraw may be explained by the worm's seeking to minimize damage that might be done to it by a naive predator (ie one that had not yet learned that the worm is unpalatable). 3) The worms could withdraw to avoid what they perceive to be a natural predator. Margates, eagle rays, stingrays, and swimming crabs are all thought to feed in part on benthic polychaetes (Böhlke and Chaplin, 1968); perhaps fanworms are included.

Another question arises concerning the existence of aposematism in fanworms. First of all, are they as contrastingly colored as they seem at first glance? It is true that a human observer is capable of easily detecting a number of the color morphs; but in censusing the <u>Sabella</u> in particular, we found that careful observation was necessary in order to locate all of the worms present in even a small quadrat. In addition, in a reef ecosystem where there is an abundance of brightly colored, palatable organisms, bright coloration might not be an effective way to advertise distastefulness (the palatability of the showy Christmas tree worms, for example, remains to be tested).

good

If, however, the fanworm's colors are seen as aposematic, then how can the diversity of color patterns (even, apparently, within a species) be explained? Fanworm color patterns could be expected to be forced by predation towards some "norm" which all fanworms might approach in a Müllerian mimicry complex. While not necessarily appearing absolutely identical, they might be expected to converge upon a similar color pattern.

On the other hand, aposematism does not necessitate the development of a color pattern as a warning. Perhaps "morphological aposematism" has occurred, where predators have learned to avoid the distinctive fanworm shape. Alternatively, the fan may contain or exude a noxious clump could thus be viewed as an island, subject to a founder effect depending on the color pattern of the individual which founded the group, but a founder effect intensified by the equivalent of self-fertilization produced by asexual reproduction.

It should be emphasized that the above model for explaining the large number of color pattern morphs in fanworms is highly speculative. A possible test of the model would be to examine clumps of fanworms, hypothesizing that there would be a lower degree of intra-clump color pattern variability than inter-clump variability.

A good, well-integrated study on several aspects of fanworm Biology.
P. 27 Missing!
Good analysis of data and discussion.

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