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A Sponge-Eating Worm from Bermuda: *Branchiosyllis oculata (Polychaeta, Syllidae)**+

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With 8 figures and 3 tables

Key words: *Polychaeta, Porifera,* pigmentation, commensalism, morphology, density.

Abstract. *Branchiosyllis oculata* is a small, errant polychaete that lives only on the surface of sponges: among inshore Bermudian sponges, 9 out of 16 species surveyed were infested. All of these sponges were conspicuously colored, but the bodies and gut contents of associated polychaetes matched the sponge color only for *Tedania ignis* (red), *Cinachyra alloclada* (yellow) and *Spheciospongia othella* (brownish-black). For the remaining 6 sponge species, the polychaete bodies were uncolored and the polychaete gut contents were inconspicuously brown or grey. Uncolored polychaetes with grey gut contents were removed from a dark green *Tethya actinia* and placed on a red *Tedania ignis:* 2 days later, the polychaete gut contents were red, although the tissues were still uncolored. Acetone extractions of *Tedania ignis* and *Cinachyra alloclada* were prepared from sponge tissue and from the gut-free tissue of their respective polychaetes: absorption spectra matched for each sponge/polychaete pair. To test the influence of ingested sponge pigments on polychaete body color, red polychaetes from *Tedania ignis* were induced to autotomize their posterior ends, transplanted to other sponge species and allowed to regenerate new posterior segments for 20 days. At the end of the experiment the original segments were still red, but the regenerated ones were either yellow (for polychaetes transplanted onto *Cinachyra alloclada,* on which resident worms are yellow) or colorless (for polychaetes transplanted onto *Chondrilla nucula* or *Tethya actinia,* on which resident worms are uncolored). The foregoing observations suggest that (1) the polychaetes consume the soft parts of the sponges on which they live and (2) the pigments vary among sponge species: pigments from some sponges are stored in the polychaete body, while pigments from other sponges are not. Additional information on the morphology, distribution and natural history of *Branchiosyllis oculata* is presented and discussed.

Problem

Sponges supply a habitat for many marine invertebrates and fish, undoubtedly providing protection, a continuous flow of water and food in the form of

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plankton, organic detritus and sponge tissue itself. Inventories of the polyphyletic assemblages found within the canals of the larger sponge species have been provided by PEARSE (1932, 1950) for Caribbean sponges, LONG (1968) for 3 species of Oregonian sponges and RÜTZLER (1975) for Tunisian commercial sponges. More recently, WESTINGA & HOETJES (1981) quantitatively found that the assemblage of organisms living within the Caribbean loggerhead sponge *Spheciospongia vesparium* constituted an ecological community.

Little is known about the feeding behavior of sponge-inhabiting (symbiotic or inquilinistic) invertebrates. Among crustaceans, some alpheid shrimps have been reported to consume sponge tissue, and a number of isopods and amphipods parasitize sponges (ARNDT, 1933; RÜTZLER, 1975). The syllid polychaete *Syllis spongicola* occurs in large numbers on some sponges (DAUER, 1974) and has been directly observed grazing on them (FAUCHALD & JUMARS, 1979). However, it is often very difficult to establish a predator/prey or parasite/host relationship for small invertebrates when direct observations of feeding are impossible and if the analysis of the gut contents of field specimens is inconclusive.

Few marine organisms which match the color of their prey/host have been studied to any extent. LEE (1966) and LEE & GILCHRIST (1972) have demonstrated that some isopods deposit within their cuticles carotenoid pigments from ingested plants.

Branchiosyllis oculata is a small (adult length of 4–8 mm) syllid polychaete that inhabits sponges of the Gulf of Mexico, West Indies and Bermuda (UEBELACKER, pers. comm.). *B. oculata* has been found in the canals of the large, Caribbean loggerhead sponge *Spheciospongia vesparium* in sponge-symbiote inventories carried out by PEARSE (1932) and WESTINGA & HOETJES (1981). In a study of the polychaetes associated with 8 common Gulf of Mexico sponges, DAUER (1974) found *B. oculata* solely in and on specimens of *S. vesparium*. Up to now, nothing has been presented concerning the biology and distribution of this polychaete, beyond what can be found in a taxonomic description of the organism (EHLERS, 1887) and the information presented in surveys of the inhabitants of loggerhead sponges.

The purpose of this study was to examine the *B. oculata*/sponge association with special attention to (1) the consumption of sponge by the worm, (2) the derivation of the color of the polychaete from the sponge, (3) the adaptations of the worm for living on sponge surfaces and (4) the distribution and abundance of polychaetes among Bermudian sponges.

Material and Methods

Sixteen species of Bermudian inshore sponges were surveyed in June, 1981 for the presence of *Branchiosyllis oculata* EHLERS (1887). At least 10 whole specimens of each sponge species were collected via SCUBA and snorkel and kept in separate containers for transportation to the Biological Station. The sponges were identified (RÜTZLER, 1983) and examined within 12 hr of collection. Until that time, and during the course of all subsequent experiments, sponges were kept within separate finger bowls in one of three approximately 100 liter aquaria, each continually flushed with filtered seawater.

The surface of each sponge was thoroughly examined under a low-power dissection microscope for the presence of *B. oculata*, then each sponge was dissected and the surface of any existing internal canals was scrutinized. *B. oculata* from various sponges were photographed using a Nikkormat camera, Nikon 50 mm macro lens with attached extension tubes, and two Vivitar strobes. For future reference, voucher specimens of *B. oculata* from the sponge *Tedania ignis* were deposited at the National Museum of Natural History, Washington D. C. (Department of Invertebrate Zoology, Catalog number 71409).

The color variability of the sponges infested with *B. oculata* provided for a simple and conclusive experiment to determine whether the polychaetes were consuming sponge tissue. Ten uncolored worms from each of the sponges *Chondrilla nucula, Ircinia felix* and *Tethya actinia* (dark green morphs) were placed separately on the surface of small (3 cm in diameter) polychaete-free specimens of the red sponge *T. ignis*. After 48 hrs, the color of the gut contents of the transplanted *B. oculata* was compared with that of control specimens that had been returned to their original sponges. The results were photographed as before. Gut contents were removed by dissection and examined under a compound microscope for the presence of sponge spicules.

B. oculata from two sponges, *T. ignis* and *Cinachyra alloclada,* were noted during the preliminary survey to have body pigmentation identical to the coloration of the sponges they inhabit. Absorption spectra of each of these sponges and their associated polychaetes were prepared as follows: A 10 × 10 × 1 mm section of the clean ectosome of each sponge was carefully removed, dipped into distilled water for 5 seconds to remove salts, spread on filter paper for a few minutes to absorb excess water and then macerated in a test tube containing 2.5 ml of cold acetone. Similarly, 20 specimens of *B. oculata* were removed from each sponge, dipped into distilled water for 5 seconds (at this point, the

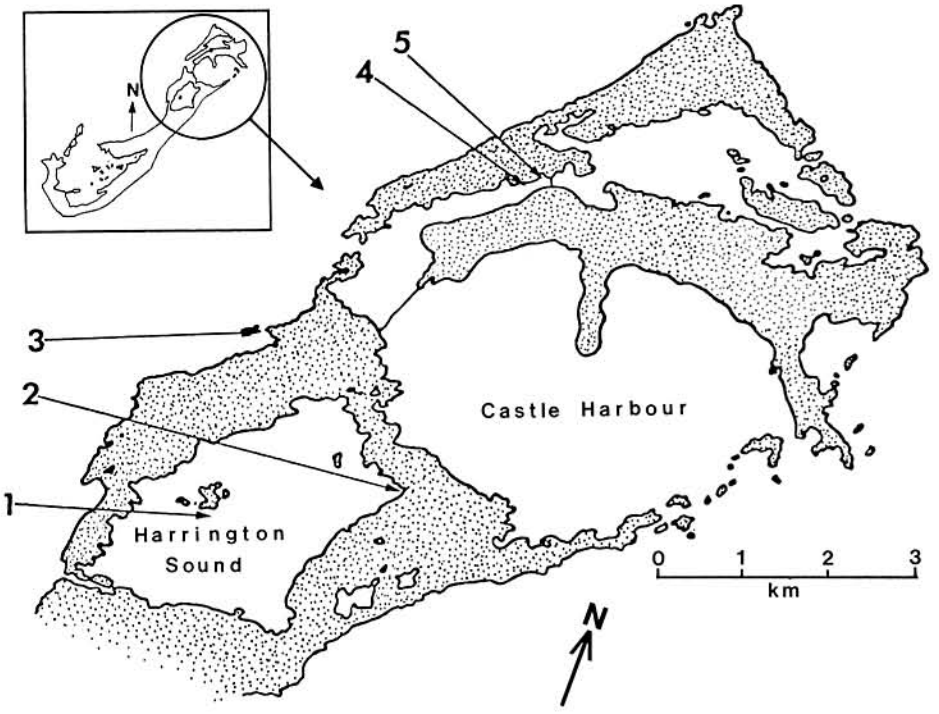

Fig. 1. Northeastern end of the Bermuda Islands (64°42′ W, 32°20′ N). Study sites: 1. Deep water off Trunk Island, Harrington Sound; silty bottom, 4–5 m; 2. Shark's Hole, Harrington Sound; undercuts and exposed boulders, to 4 m; 3. Bailey's Bar; sea grass beds, to 1.5 m; 4. Ferry Reach; boulder pile, to 1 m; 5. Ferry Reach; sea grass beds, to 1 m.

gut contents of the polychaetes were removed, either by forcing the contents out through the anus, or by scraping the contents from the gut after rupture of the body wall on treatment with distilled water), spread on filter paper and macerated in a test tube containing 2.5 ml of cold acetone. The freshly ground tissues were immediately centrifuged for 5 minutes at medium speed, and the clear supernatant was decanted. Absorption curves over the visible spectrum (350–750 nm) were obtained for each sample with a Beckman Model 25 scanning spectrophotometer.

To test the hypothesis that the polychaetes take on the pigments of the sponge tissue they consume, the following experiment was undertaken: Polychaetes from *T. ignis* were induced to autotomize (shed) their most posterior setigers (approximately ⅓ of the total body length) by lightly clamping down on the posterior segments with forceps. Ten of these autotomized worms were placed on each of three specimens of the sponges *C. nucula, C. alloclada* and *T. actinia* (dark green morphs). Ten control polychaetes were similarly induced to autotomize and were returned to their original sponges. After 20 days, transplanted and control polychaetes were removed from the sponges and photographed as before.

External features of *B. oculata* were photographed with a Polaroid camera-compound microscope set-up (model ED-10) and by scanning electron microscopy. In preparation for scanning electron microscopy, whole polychaetes were (1) fixed for 24 h at 26 °C in 10 % Formalin in seawater ($CaCO_3$ saturated), (2) stored in 70 % ethanol in seawater ($CaCO_3$ saturated), (3) dehydrated in an ethanol solvent series, (4) dried in a CO_2-critical point drying apparatus and (5) coated with carbon, then gold, in a Denton vacuum evaporator. Specimens were examined in a Hitachi S-450 scanning electron microscope.

Quantitative data on the distribution of *B. oculata* for eight sponge species were obtained for five study sites in Bermudian inshore waters in late August, 1981 (Fig. 1). Within each study site, sponge samples were divided on the basis of (1) species differences, (2) polychromatic variation within a species (for *T. actinia*) and (3) differences in the topography of the study site. In the last case, the rocky undercuts at Shark's Hole, Harrington Sound, were delimited into four regions (Fig. 2), the terms of which have been borrowed from oceanographic descriptions of continental margins.

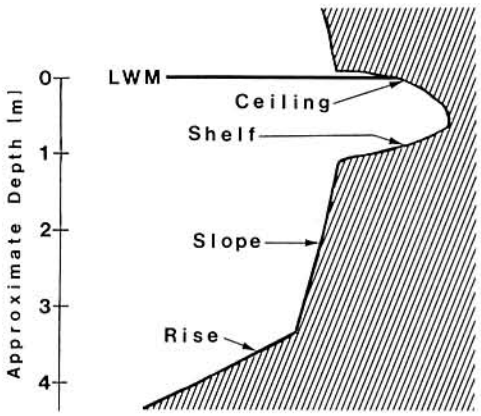

Fig. 2. Diagrammatic profile of a typical undercut at Shark's Hole, Harrington Sound, indicating sponge collection sites. LWM = low water mean.

Specimens of *B. oculata* were removed from the sponge exterior by placing the sponge in a jar approximately twice the size of the sponge, covering the sponge sample with a solution of $MgCl_2$ isotonic with seawater (approximately 6 % $MgCl_2$) and shaking the jar intermittently over a period of 5 minutes. The sponge was then removed and the isotonic solution rinsed repeatedly over the sponge surface and through a 125 micrometer mesh. Worms were counted by examining the mesh under a dissecting microscope. Sponges were dissected before and after $MgCl_2$ treatment in order to examine internal canals for the presence of *B. oculata*. The total area of exposed sponge surface was estimated by summing the area of planes, cones, cylinders and spheres which approximate the sponge exterior.

Results

The results of the survey of Bermudian inshore sponges for the presence of *Branchiosyllis oculata* are shown in Tables 1 a and 1 b.

Specimens of *B. oculata* were found solely on the external surface of the sponges examined, never in the internal canals or tissues. The polychaetes occupied shallow trenches which were created in the sponge surface as the worms moved forward.

Table 1. a: Bermudian sponges infested with the polychaete *Branchiosyllis oculata*. All the species listed belong to the class *Demospongiae*. Note the comparison between the sponge color and the color of associated *B. oculata*. "–" indicates uncolored polychaetes. b: Bermudian sponges free of *B. oculata*. "*" indicates that the species belongs to the class *Calcarea*. The remaining species belong to the class *Demospongiae*.

a Species	Order	Sponge color	*B. oculata* Body color
Aplysilla longispina George & Wilson	*Keratosa*	bright yellow	–
Aplysina fistularis (Pallas)	*Keratosa*	golden	–
Chondrilla nucula (Schmidt)	*Hadromerida*	cream to brown	–
Cinachyra alloclada Uliczka	*Spirophorida*	yellow	yellow
Ircinia felix (Duch. & Mich.)	*Keratosa*	brown	–
Pseudoceratina crassa (Hyatt)	*Keratosa*	greenish-yellow or purple	–
Spheciospongia othella de Laubenfels	*Hadromerida*	brownish-black	brownish-black
Tedania ignis (Duch. & Mich.)	*Poecilosclerida*	red	red
Tethya actinia de Laubenfels	*Hadromerida*	dark green, orange or reddish-brown	–

b Species	Order
Amphimedon viridis Duch. & Mich.	*Haplosclerida*
*Clathrina coriacea** (Montagu)	*Clathrinida*
Dysidea etheria de Laubenfels	*Keratosa*
Leucandra aspera (Schmidt)	*Sycettida*
*Leucetta microraphis** (Haeckel)	*Leucettida*
Niphates erecta Duch. & Mich.	*Hapolosclerida*
Ulosa ruetzleri Wiedenmayer	*Halichondriida*

Fig. 3. a: Left: Control *B. oculata* from *Tethya actinia* (note grey gut contents). Middle: *B. oculata* transplanted from *T. actinia* to *Tedania ignis* and photographed after 48 hours (note red gut contents). Right: Control *B. oculata* from *T. ignis* (note red gut contents; actual length, *T. ignis* control: 6.1 mm).
b: Left: Control *B. oculata* from *Tedania ignis*. Middle: *B. oculata* removed from *T. ignis*, induced to autotomize posterior segments and transplanted to *Tethya actinia* 20 days prior to photography. Right: Control *B. oculata* from *T. actinia* (actual length, *T. actinia* control: 4.9 mm).

The color of the gut contents and body of *B. oculata* from the sponges *Cinachyra alloclada, Spheciospongia othella* and *Tedania ignis* was yellow, brownish-black and red, respectively, each the same color as their sponge host. Worms from the 6 remaining infested sponge species had uncolored bodies (Table 1 a), with gut contents varying in color from brown to grey. Approximately 10 % of the worms sampled from *Ircinia felix* and *Pseudocertina crassa* had dark bands on an otherwise uncolored body.

All uncolored *B. oculata* which had been transferred from the sponges *Chondrilla nucula, Ircinia felix* and *Tethya actinia* to specimens of the red sponge *T. ignis* were observed to have taken on red-colored gut contents 48 hours after transplantation (see Fig. 3 a for *T. actinia* result). Control polychaetes maintained the original color of their gut contents (brown for *C. nucula* and *I. felix*, grey for *T. actinia*). Sponge spicules were not present in the gut contents of the polychaetes.

Absorption spectra of acetone extractions of *T. ignis* and associated specimens of *B. oculata* (Fig. 4 a) have similar curves and broad absorption peaks at approximately 475 nm. Spectra of acetone extractions of *C. alloclada* and associated *B. oculata* (Fig. 4 b) also display similar peaks, with a central maximum at approximately 450 nm and shoulders on either side at approximately 420 and 460 nm.

Transplanted, autotomized specimens of *B. oculata* originally from the red sponge *T. ignis* regenerated posterior setigers with pigmentation identical to that of *B. oculata* normally found on the surrogate sponges. There was no detectable change in the red color of the anterior setigers of the transplanted polychaetes during the course of the experiment. Red polychaetes transferred to

Table 2. Quantitative data on *B. oculata* distribution for 8 sponge species from Bermudian inshore waters. 1 = off Trunk Island, Harrington Sound; 2 = Shark's Hole, Harrington Sound; 3 = Bailey's Bay, sea grass beds; 4 = Ferry Reach, boulder pile; 5 = Ferry Reach, sea grass beds (also refer to Figs. 1 and 2). For *Tethya actinia:* OR = orange morphs; RB = reddish-brown morphs; DG = dark green morphs. Standard deviation of the average density is provided.

Species	Locality	N	Ave. Sponge Area (cm^2)	Ave. number of Worms	Ave. Density ($worms/cm^2$)
Aplysina fistularis	3: to 1.5 m	5	209.8	34.0	0.16 ± 0.04
Chondrilla nucula	2: shelf to 1.5 m	10	16.9	10.3	0.69 ± 0.40
	4: to 1 m	5	16.4	9.4	0.62 ± 0.28
	TOTAL	15	16.7	10.0	0.67 ± 0.36
Cinachyra alloclada	2: shelf to 1.5 m	14	25.7	16.8	0.67 ± 0.52
	2: slope & rise 2–4 m	6	35.2	12.8	0.43 ± 0.20
	TOTAL	20	28.6	15.6	0.59 ± 0.46
Ircinia felix	2: exposed to 3 m	6	47.1	0.5	0.01 ± 0.02
	4: to 1 m	5	48.8	5.2	0.09 ± 0.06
	TOTAL	11	47.9	2.6	0.05 ± 0.06
Pseudoceratina crassa	2: exposed to 3 m	11	44.7	10.7	0.36 ± 0.31
Spheciospongia othella	5: to 1 m	9	38.1	4.1	0.12 ± 0.07
Tedania ignis	1: 4–5 m	2	85.7	100.0	1.16 ± 0.14
	2: ceiling to 0.5 m	5	39.5	6.6	0.16 ± 0.06
	2: shelf to 1.5 m	3	35.0	32.0	0.91 ± 0.03
	2: exposed to 3 m	8	59.4	13.8	0.28 ± 0.23
	3: to 1 m	10	62.6	24.5	0.37 ± 0.21
	5: to 1 m	11	42.5	19.1	0.63 ± 0.53
	TOTAL	39	52.4	22.9	0.48 ± 0.41
Tethya actinia	2: shelf, OR to 1.5 m	4	15.2	0.8	0.04 ± 0.05
	2: shelf, RB to 1.5 m	4	23.2	4.5	0.18 ± 0.16
	2: shelf, DG to 1.5 m	15	23.2	4.1	0.16 ± 0.11
	4: to 1 m, DG	5	17.0	7.0	0.59 ± 0.62
	TOTAL	28	20.9	4.2	0.22 ± 0.31

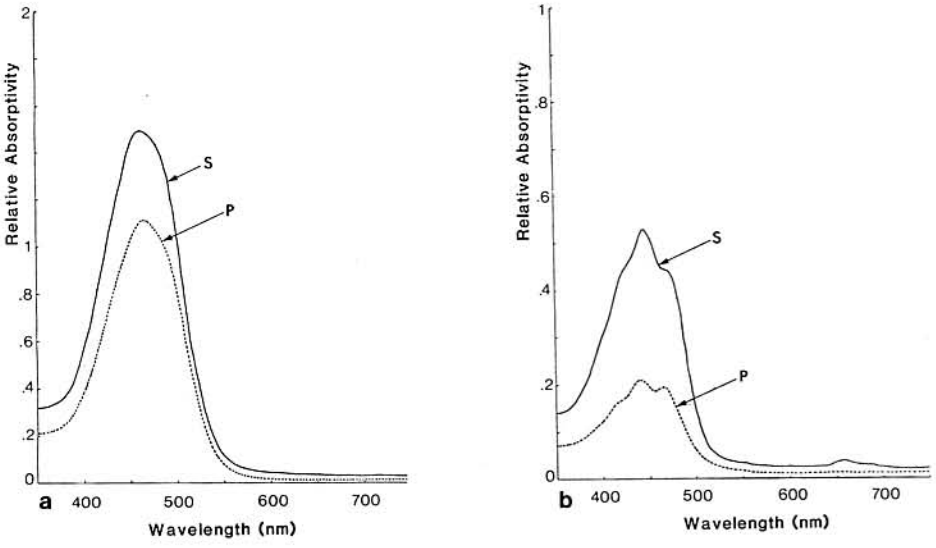

Fig. 4. a: Absorption spectra of acetone extractions of (S) the ectosome of the red sponge *Tedania ignis* and (P) whole, gut-free specimens of *B. oculata* from the surface of *T. ignis*. Absorption maximum at approximately 475 nm. b: Absorption spectra of acetone extractions of (S) the ectosome of the yellow sponge *Cinachyra alloclada* and (P) whole, gut-free specimens of *B. oculata* from the surface of *C. alloclada*. Absorption maximum at approximately 450 nm.

the yellow sponge *C. alloclada* took on yellow pigmentation in regenerated setigers and became bicolored, while the worms placed on *C. nucula* and *T. actinia* regenerated uncolored setigers (see Fig. 3 b for *T. actinia* result).

Photographs and micrographs of morphological characteristics of *B. oculata* are presented in Figures 5–8. The setae are all composite falcigers, each possessing a hinged, extensible hook on the end of the shaft (compare Figs. 6 b and 7 b). The dorsal cirri are composed of 31 to 47 articles. The base of each dorsal cirrus is surrounded ventrally by a heavily ciliated band and dorsally by a verrucose region with short, well-spaced cilia (Fig. 8). Large (> 7 mm) *B. oculata* bear modified posterior setigers with long simple setae.

A summary of the data on the distribution of *B. oculata* is presented for 8 sponge species at 5 study sites in Table 2.

To test the significance of single variable comparisons (same species of sponge, different locality; same locality, different species, *etc.*), the non-parametric MANN-WHITNEY U-test for two samples was employed (SOKAL & ROHLF, 1969), with a Null Hypothesis that there is no difference in the mean polychaete density between the two sponge samples chosen. The Null Hypothesis is rejected if the U-statistic gives a P-value that is less than 0.20 (tests which satisfy lower alpha-levels are indicated as such). The results of these comparisons are presented in Table 3.

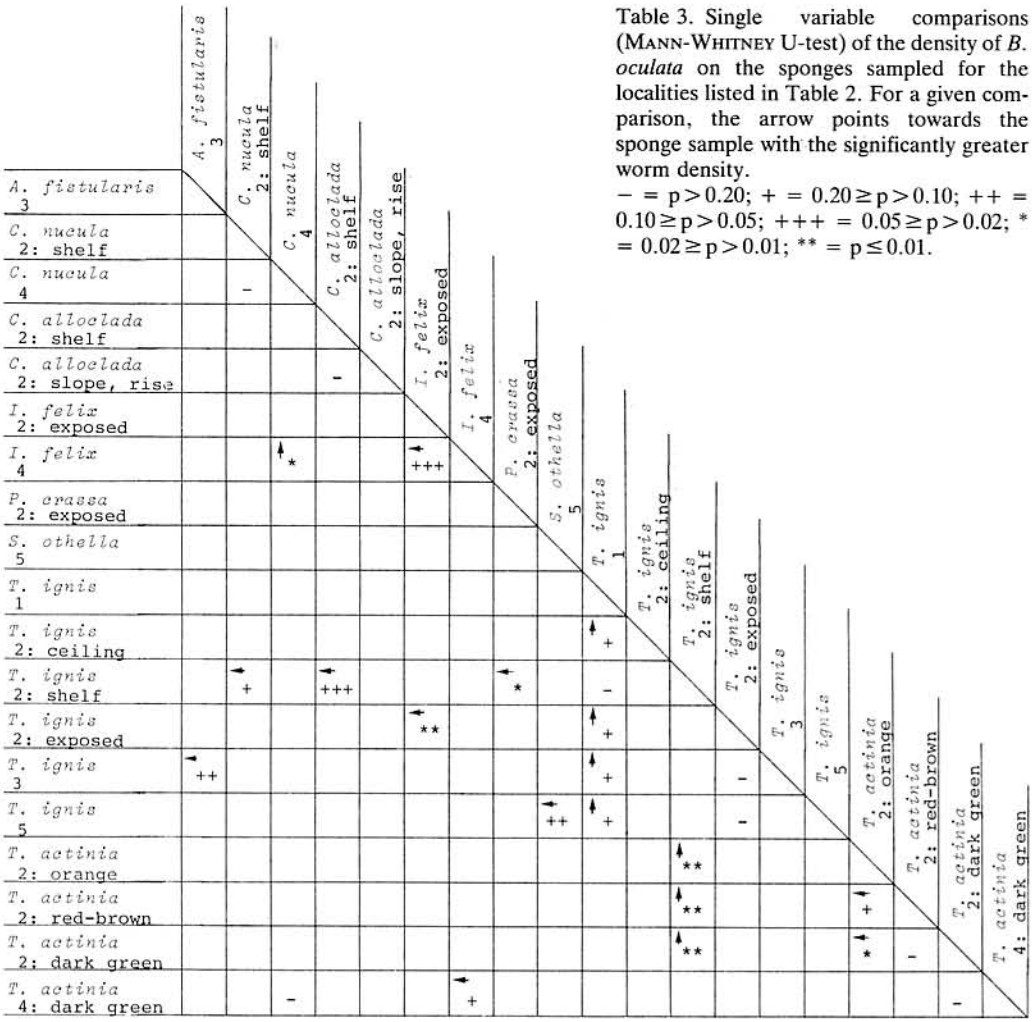

Table 3. Single variable comparisons (MANN-WHITNEY U-test) of the density of *B. oculata* on the sponges sampled for the localities listed in Table 2. For a given comparison, the arrow points towards the sponge sample with the significantly greater worm density.
$-$ = $p > 0.20$; + = $0.20 \geq p > 0.10$; ++ = $0.10 \geq p > 0.05$; +++ = $0.05 \geq p > 0.02$; * = $0.02 \geq p > 0.01$; ** = $p \leq 0.01$.

Discussion

Results of the experiments involving the color change in gut contents of transplanted *Branchiosyllis oculata* clearly demonstrate that the polychaete feeds on sponge tissue. Unlike organisms that were shown to be sponge feeders by a simple examination of the gut contents for sponge spicules (reef fishes; RANDALL & HARTMAN, 1968), *B. oculata* appears to be small enough to avoid spicules when consuming sponge tissue, as none were found in gut examinations. The color change of the gut contents of transplanted polychaetes provided a simple and conclusive means of identifying a sponge-eating organism.

Comparisons of the absorption spectra of pigmented specimens of *B. oculata* and their host sponges provides evidence that the polychaetes are incorporating sponge pigments into their body tissues. This is further supported by regeneration experiments involving transplanted, autotomized polychaetes. Although the analysis necessary to confirm identification was not undertaken, the absorption spectrum and solvent solubility of the red pigment indicates that it could be astaxanthin (D. L. Fox, personal communication; November, 1982).

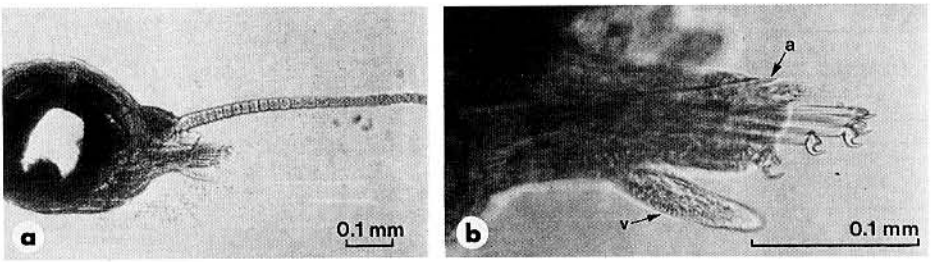

Fig. 5. a: Cross-section through the proventricular region of *B. oculata* showing the long dorsal cirrus. b: Close-up of the parapodium in Fig. 5 a. Notice the hooked, falcigerous setae. a = distal tip of aciculum; v = ventral cirrus.

Polychaetes that have the same color as the sponges they inhabit may have a distinct anti-predatory advantage. Uncolored *B. oculata* are much easier to see on the sponges they occupy, and exposed worms were readily eaten when offered to small damselfishes *(Abudefduf saxatilis)* in a laboratory aquarium. Differences in the chemistry of the sponge pigments are presumably responsible for uncolored *B. oculata* from 6 of the 9 sponge species sampled. Further chemical analyses could be undertaken to determine the nature of the pigments involved. Interestingly, DAUER (1974) reported that the sponge-inhabiting polychaete *Syllis spongicola* occurred in three different color forms, pale (= uncolored), brown and a pale morph with an orange pharynx, depending to a limited extent on the species of sponge inhabited by the polychaete. Perhaps a relationship between sponge and polychaete coloration similar to that of *B. oculata* could be shown for *S. spongicola.*

B. oculata appear to be well adapted to living on the surface of sponges. The hinged setae of the worm are structurally complex and presumably keep the polychaete firmly attached to the sponge. As with most errant polychaetes, the setae of *B. oculata* can be extended out of or withdrawn into the parapodium depending on the muscular contractions along the body wall. Therefore, as *B. oculata* advances on the sponge surfaces, the polychaete extends and implants the claw-like hooks of the setae into the sponge tissue, then partially withdraws the setae, causing the implanted, hinged claws to extend and firmly hook into the tissue. The polychaete can release itself from the sponge surface, as it does when agitated, by moving backwards; apparently the angle at which the parapodia move, combined with the withdrawal of the setae into the parapodium, effectively reverses the attachment process. In addition to providing a firm anchor, the setae excavate shallow trenches in the sponge ectosome in

which the worms are usually found (consumption of the sponge is also likely to help produce the trenches). I have also observed entrenched polychaetes on *Tedania ignis* using their setae to pull the surrounding sponge tissue over themselves, leaving only their dorsal cirri exposed.

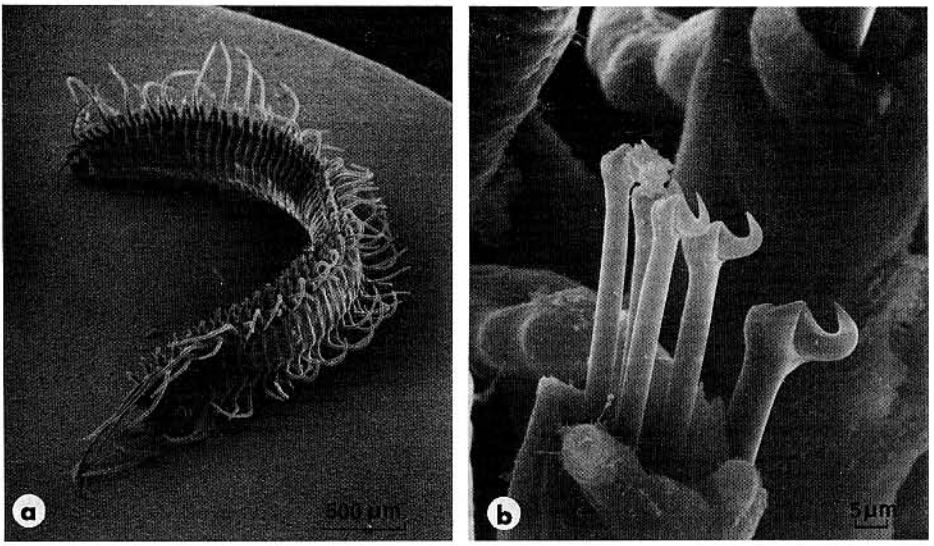

Fig. 6. a: Scanning electron micrograph of *Branchiosyllis oculata*. Posterior-dorsal in the foreground, anterior-ventral in the background. This specimen is missing posterior setigers. b: Falciger-ous setae of *B. oculata*. The claw-like hooks are retracted (compare with Fig. 7 b).

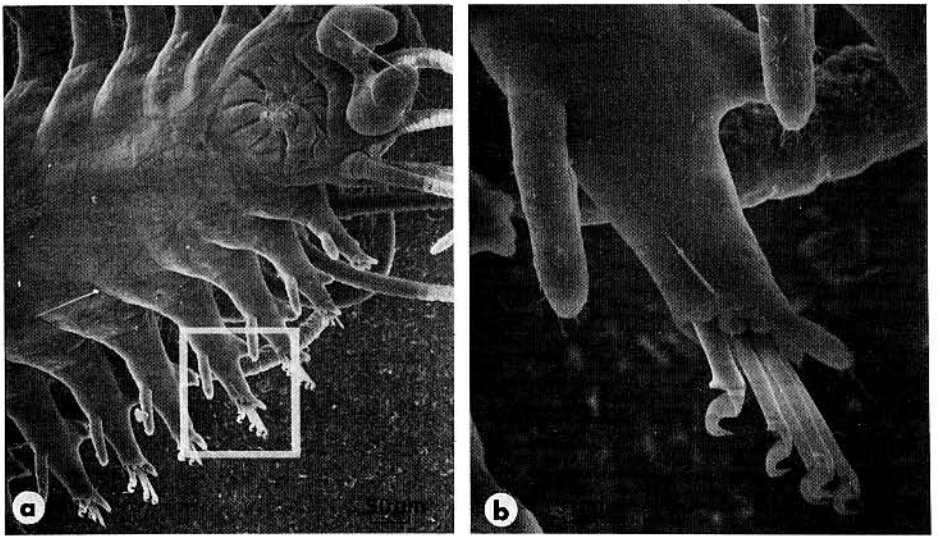

Fig. 7. a: Scanning electron micrograph of *B. oculata*, anterior-ventral region. b: Close-up of the indicated area in Fig. 7 a. The claw-like hooks on the setae are in the extended position (compare with Fig. 6 b).

The articulated dorsal cirri (Fig. 7 a) of Bermudian specimens of *B. oculata* are quite long, considerably longer than the cirri found on specimens described by UEBELACKER (1982) and EHLERS (1887) from the Gulf of Mexico and Florida coasts (8–27 articles versus 31–47 articles). The dorsal cirri appear to have an important mechanosensory function. When the polychaete is embedded in a trench in the sponge ectosome, the long cirri extending outward onto the sponge surface serve to warn the worm of the approach of another organism. Touching the cirri of an entrenched polychaete with a dissection instrument produces a writhing backward motion – to dislodge setae – followed by rapid forward advancement out of the trench and across the sponge surface. The ciliated bands located at the base of each cirrus create a constant water current around the organism, similar to that found for other errant polychaetes (BARNES, 1980), and are undoubtedly involved in providing adequate circulation for respiration. The verrucose region may be responsible for the production of a thin, mucoid coating often found on the dorsal surface of the polychaete.

The modified posterior setigers of large *B. oculata* were identified as a sexual stolon with projecting natatory (swimming) setae (J. M. UEBELACKER, personal communication; July, 1981). The worms were never observed swimming, although one stolon-bearing polychaete was observed shedding eggs from openings in the dorsal surface of mid-body setigers after the specimen was agitated with dissecting forceps. Additional collections would have to be made throughout the year to gain a better understanding of reproduction and sexual morphogenesis in this polychaete.

Quantitative data on polychaete density for 8 sponge species reveal marked variability, reflecting differences in the colonization and/or maintenance of worm populations on host sponges. Of the sponges inhabited by *B. oculata* (Table 1 a), all possess a smooth, fleshy ectosome, all are in the class *Demospongiae* and seven out of nine belong to the orders *Keratosa* or *Hadromerida*. Noninfested sponges (Table 1 b) of the class *Calcarea* bear dense stands of carbonate spicules, while non-infested demosponges bear a highly porous, nonfleshy exterior. It appears as though the sponge surface may play an important role in which sponges are colonized and inhabited by *B. oculata*.

During the course of the polychaete transplant experiments, I observed that *B. oculata* removed from host sponges had little capacity to relocate their original host or to locate a new sponge (polychaetes and sponges were placed on filter paper in finger bowls). Presumably, sponge selection and colonization is carried out solely during larval development, possibly by swimming and crawling larvae, as in the case of the polychaete *Spirorbis borealis,* which preferentially settles out on the alga *Fucus serratus* (WILLIAMS, 1964). Moreover, because *B. oculata* from the various sponges are all morphologically identical and will survive and continue to grow when experimentally transplanted to a surrogate sponge, it appears unlikely that there is any specificity among recruitable larvae for particular sponge species.

An overall hierarchy in the preference of *B. oculata* for infested sponges is reflected in the density determinations, with a range of a relatively high density of polychaetes on samples of *Tedania ignis, Chondrilla nucula* and *Cinachyra alloclada,* and a relatively low density on samples of *Ircinia felix* and *Sphecio-*

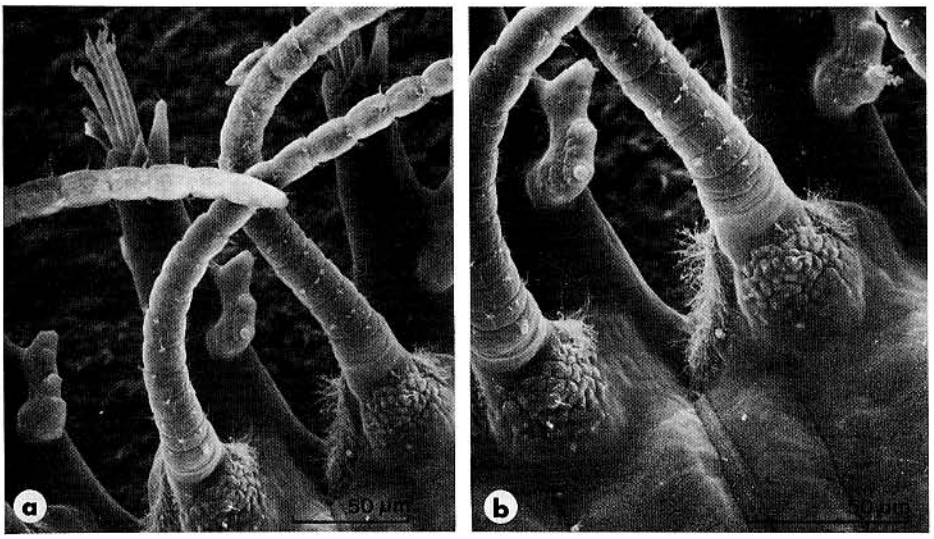

Fig. 8. a: Scanning electron micrograph of the parapodia of the midbody setigers of *B. oculata* (dorsal view). Anterior towards upper right. b: Close-up of the base of the dorsal cirri in Fig. 8 a. Note the heavily ciliated regions lateral to the base of the cirri and the verrucose region dorsally adjacent to the base of the cirri.

spongia othella. This gradation in preference is believed to be the result of one or a combination of two factors:

(1) Differential Recruitment – Polychaete larvae colonize one sponge species more readily than another, as a result of differences in the ability of larvae to find sponge hosts. This may reflect simple differences in the density or accessibility of suitable sponge species (common sponges are encountered more often and colonized to a greater degree) or variations in the chemistry of inhabitable sponges with a corresponding variation in their colonization by chemosensitive larvae (some sponges may give off "odors" which are easier for larvae to detect and follow).

(2) Differential Mortality – Polychaetes are afforded better protection from predators on some sponges than on others, by virtue of a body color that matches the sponge background color, noxious spicules or chemicals found on the sponge surface (possibly passed on to the polychaete) or the inaccessibility of the sponge to potential predators.

Although *T. ignis* had the highest density of *B. oculata* when compared to other sponge species collected from the same site, I observed no physical evidence (deep grooves, exposed endosome, *etc.*) on any of the sponge samples to suggest that the high density of sponge-feeding polychaetes was having a negative effect on sponge growth. Interestingly, DAUER's (1974) study of polychaete sponge associates on the west coast of Florida included two samples of *T. ignis,* neither of which were inhabited by *B. oculata*.

In comparing *B. oculata* density on *T. ignis* at different study locations, the highest values were found for sponges in calm, dark regions (Shark's Hole, shelf region and off Trunk Island), intermediate values for exposed regions (Ferry

Reach, sea-grass beds; Bailey's Bay; Shark's Hole, exposed) and very low values for *T. ignis* collected from the ceiling region in Shark's Hole undercuts. Once again, the variation in density could result from differences in sponge colonization by larval polychaetes, in this case possibly involving differential reactions to light intensity, water motion or the orientation of the substrate, similar to the variation in larval site selection reported in sabellariid polychaetes (ECKELBARGER, 1978) and for some tunicates (BERRILL, 1975). Additional research on *B. oculata* larval settlement would be appropriate.

The marked intraspecific differences in the density of *B. oculata* on the polychromatic sponge *Tethya actinia* are similarly intriguing. It is probable that whatever controls pigmentation in this sponge species – symbiotic algae, genetic variability *etc.* – also has a direct effect on *B. oculata* larval recruitment and/or adult survival.

The results of this study indicate that *B. oculata* is a sponge parasite. The term "parasite" is sometimes used with certain hesitation, because the boundary between parasitism and predation is often unclear. Parasitism as defined by SCHMIDT & ROBERTS (1981) is "symbiosis in which the symbiont benefits from the association, whereas the host is harmed in some way." In this case, the polychaete lives and feeds on the sponge surface (an obvious harm to the sponge), apparently restricted to a single host throughout its adult life. *B. oculata* is morphologically adapted for dwelling on sponge surfaces and, in some cases, even takes on the coloration of its host. Moreover, the polychaete exists on some sponges at surprisingly high densities with no apparent effect on the host.

Summary

Branchiosyllis oculata was found on the surface of 9 out of 16 species of inshore Bermudian sponges. Worms from 3 of the 9 sponges were of the same color as the sponges they inhabit. Within 48 hours, the gut contents of uncolored *B. oculata* that had been transplanted onto a red sponge were observed to take on the red color. Absorption spectra of acetone extractions of the sponges *Tedania ignis* and *Cinachyra alloclada* and specimens of *B. oculata* associated with each sponge revealed similar curves and absorptions peaks for each sponge/polychaete pair. Transplanted, autotomized worms originally from *T. ignis* regenerated posterior setigers in the color of polychaetes found on the surrogate sponge while maintaining the red pigmentation of their original setigers. The density of *B. oculata* on infested sponges was quite variable, with average values for sponge species ranging from 0.05–0.67 polychaetes per cm^2 of exposed sponge surface.

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