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MORPHOLOGICAL, REPRODUCTIVE, AND BEHAVIOURAL ADAPTATIONS OF TWO INTERSTITIAL POLYCHAETES FROM SUBMERGED MANGROVE ROOTS IN A BAHAMIAN LAND-LOCKED MARINE LAKE

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ABSTRACT

Two species of interstitial syllid polychaetes (*Exogone* sp. and *Sphaerosyllis sp.*) were collected from epiphytic communities on submerged red mangrove roots in Osprey Lake, San Salvador Island, Bahamas. The external morphology of both species is described. Both are minute and apparently lack a swimming phase during reproduction. They have relatively smaller appendages and fewer segments than larger syllid species and produce a few, proportionately large eggs that undergo direct development attached to the outside of the body. The adaptive significance of their morphology, reproduction and behavior is discussed.

INTRODUCTION

Several polychaete species were collected from algal covered (principally *Batophora sp.* and *Vaucheria sp.)* red mangrove roots in Osprey Lake, a land-locked marine body of water on San Salvador Island, Bahamas. At least two of these species, *Exogone* sp. and *Sphaerosyllis sp.* (Polychaeta: Syllidae), have features unique to interstitial polychaetes normally associated with sand or mud. The morphological, reproductive and behavioral adaptations to living in this unique environment are discussed below.

MATERIALS AND METHODS

Two *Rhiziophora mangle* prop roots, extensively colonized by *Batophora sp.* and *Vaucheria sp.*, were collected from Osprey Lake, San Salvador Island, Bahamas, on 5/5/96. In the laboratory all polychaetes were removed, relaxed in 5% magnesium sulfate and fixed in a 5% formalin/seawater solution. Later, specimens were transferred to 70% ethanol for long term storage. To date only members of the Family Syllidae have been studied.

Specimens were mounted in Hoyer's solution to clear body tissue so that teeth and setae would be clearly visible (Zottoli and Long, 1997).

Measurements were made under compound or dissecting microscopes with a calibrated grid. Body length was measured from the tip of the prostomium to the end of the pygidium; for twisted specimens, the grid was rotated along the body. Body width was measured across the dorsal surface of the 4th setiger from the tip of the right notopodium to the left.

HABITAT

Inland, saline bodies of water (Godfrey, et al., 1994) are found on most large Bahamian islands. They are often fed by tidal water issuing through cracks and crevices in the carbonate rock beneath the island. They are isolated from the ocean and because of this, species found here might have evolved differently than similar species from coastal locations. Osprey Lake is essentially marine with a salinity of about 35 ppt. The lake is about 1 m deep and the underlying sediment, derived from decaying organic matter, is approximately 0.5 m or less thick. The top layers of sediment are grayish and somewhat flocculent. According to Godfrey, et al. (1994), "Anna Hicks (1993) found 53 species of microorganisms in this living sediment, and suspects there are many more. She estimated that one drop of flocculent-laden water contains 3000 individuals." For comparison, floating detritus collected at Twin Cays, Belize (Faust and Gulledge, 1996) contained dinoflagellates, diatoms, cyanobacteria, ciliates, nematodes, crustacean larvae and copepods.

Even though Osprey Lake receives tidal water each day, one would expect that heavy rainstorms would significantly reduce the salinity from time to time and that strong winds would occasionally stir up bottom sediments, reducing oxygen levels. In addition, water along the edge of the lake could become hypersaline due to evaporation. All three of these conditions could be stressful to inhabitants.

Schools of the sheepshead minnow (*Cyprinodon variegatus*) and mosquito fish (*Gambusia affinis*) were observed swimming above the suspended sediment near the shores edge. Both species are omnivorous and have been known to consume algae and insect larvae.

Clumps of the red mangrove, *Rhizophora mangle*, grow just offshore, around the perimeter of Osprey Lake. Prop roots, characteristic of this species, extend out into the shallow water (Lugo and Snedaker, 1974, and Tomlinson, 1986). They are often colonized by a large number of algal and invertebrate species (Ellison and Farnsworth, 1992; Faust and Gulledge, 1996; and Sutherland, 1980). In Osprey Lake prop roots were covered by colonies of the green algae *Batophora sp.* and *Vaucheria sp.*, but few invertebrates were evident, except for the abundant, minute polychaetes.

SPECIES IDENTIFICATIONS

The quality of any scientific work rests on the presumption that it can be replicated. In the case of studies such as this one, this means that the species being studied must be known to current and future workers. Therefore, sufficient information is included below for both species so that a correct identity can be determined at a later date.

Two species of the Class Polychaeta, Family Syllidae were found on submerged red mangrove prop roots: *Exogone* sp. and *Sphaerosyllis* sp.

There have been over 50 species of *Exogone* described world-wide, 15 of which have been reported from the Caribbean and associated waters (Salazar-Vallejo, 1992). There have been over 28 species of *Sphaerosyllis* described world-wide, 19 of which have been reported from the Caribbean and associated waters (Salazar-Vallejo, 1992).

Thus far we have been unable to comfortably assign a species name to either syllid. In addition to the fact that many of original descriptions don't illustrate or discuss key characters, they sometimes report spurious data. This may be due in part to the following: 1. Diagnostic setae may include artifacts (Riser, 1991, p. 214) making them appear different; 2. Specimens may not have been properly relaxed and fixed, thus changing their appearance; 3. Equipment used to view specimens may not have been adequate; and 4. The investigator(s) may have been inexperienced. For instance, figures 75-78 in the original description of *Exogone breviantennata* by Hartmann-Schröder, 1959, show no decoration on the setae and yet San Martín's illustration (1991, Figure 8) of apparently the same species shows elaborate decoration. Both of the syllids described here are new to the Bahamas regardless of their species designation.

SPECIES DESCRIPTIONS

Exogone sp.

Description. The following description is based on 32 complete specimens ranging in length from 0.34 to 2.7 mm in length and 0.1 to 0.22 mm in width with 6-31 setigers.

Typically, five diagnostic characters are necessary in order to identify a species of *Exogone*. For the species from Osprey Lake, these are as follows (see Figures 1 and 2): (1) Dorsal cirrus present on setiger 2; (2) Three truncate, straight-sided prostomial antennae of nearly equal length, shorter than prostomium, and placed close together in line near posterior margin of prostomium; (3) Two pairs of dark red, lensed eyes, largest, anterior-most pair lateral to both lateral prostomial antennae, smallest pair posterior both to lateral antennae and anterior pair of eyes and slightly medial to latter; (4) Pharynx and proventriculus extending through varying number of segments (maximum of 1 through 3 and 1 through 6, respectively), probably dependent upon fixation (see Riser, 1991); pharyngeal tooth anterior; and (5) Five types of setae (see Figure 3): (a) Simple dorsal seta, one per parapodium, terminates bluntly with about 10 short serrations; (b) Single, heterogomph spiniger with finely drawn-out blade; (c) One to four heterogomph falcigers with blades with coarse serrations and bidentate tips; (d) Ventral simple seta strongly hooked near tip and with terminal short, slender spines; and (e) Single acicula with rounded, slightly concave tip.

Sphaerosyllis sp.

Description. The following description is based on 53 complete specimens ranging in length from 0.41 to 1.1 mm in length and 0.08 to 0.2 mm in width with 10-19 setigers.

Typically, seven diagnostic characters are necessary in order to identify a species of *Sphaerosyllis*. For the species from Osprey Lake, these are as follows (see Figures 4 and 5): (1) Prostomium and peristomium distinct; (2) Three prostomial antennae of nearly equal length, all bulbous basally and tapering towards tip; median originating on posterior margin of prostomium, extending to or slightly beyond tips of palps, laterals originating anterio-lateral to the median and extending just beyond palps; (3) Three pairs of lensed eyes in trapezoidal arrangement with anterior-most pair between lateral antennae; second pair posterior to and in line with lateral antennae; and third, largest pair, posterior to and medial to second pair, at posterior-lateral margins of prostomium; (4) Dorsal cirrus absent on setiger two; (5) Parapodial glands not seen; (6) Pygidium somewhat pentagonal

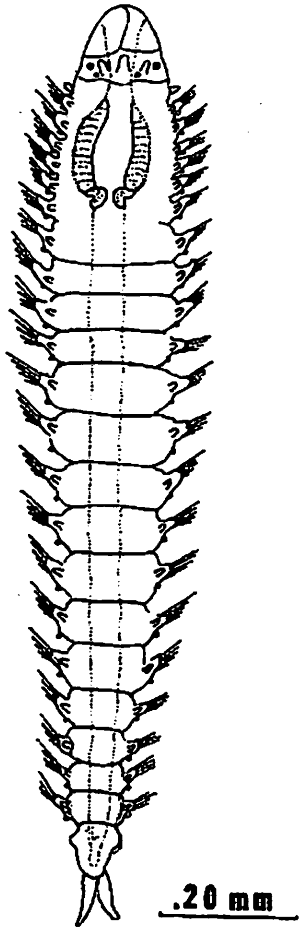


Figure 1. *Exogone sp.* **Entire 21-setiger worm. Dorsal view. Length = 1.5 mm, maximum width = 0.2 mm.**

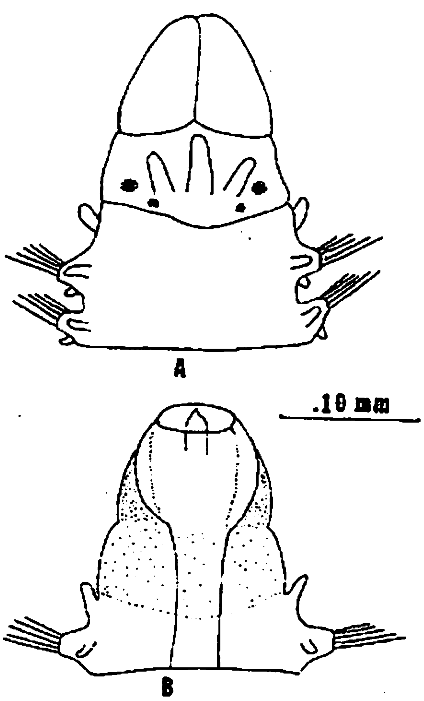


Figure 2. *Exogone* **sp. A. Anterior end of 25-setiger worm. Dorsal view. Length = 2.0 mm, maximum width = 0.2 mm. B. Anterior end of 21-setiger worm. Ventral view. Length = 2.0 mm, maximum width = 0.2 mm.**

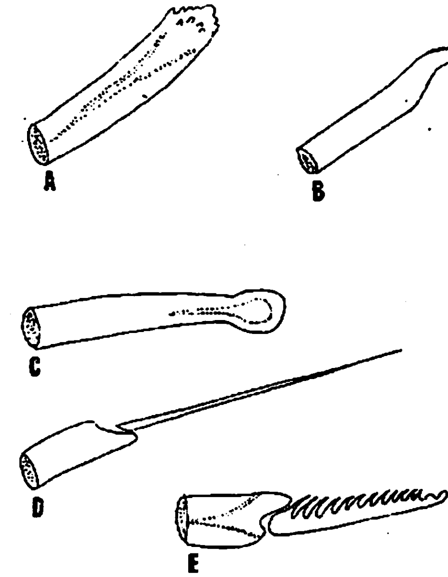


Figure 3. *Exogone* **sp. Setal types. A. Dorsal simple seta, basal width = 36 µm. B. Ventral simple seta, basal width = 30 µm. C. Acicula, basal width = 60 µm. D. Heterogomph spiniger, blade = 14 µm in length. E. Heterogomph falciger, blade length = 6 µm.**

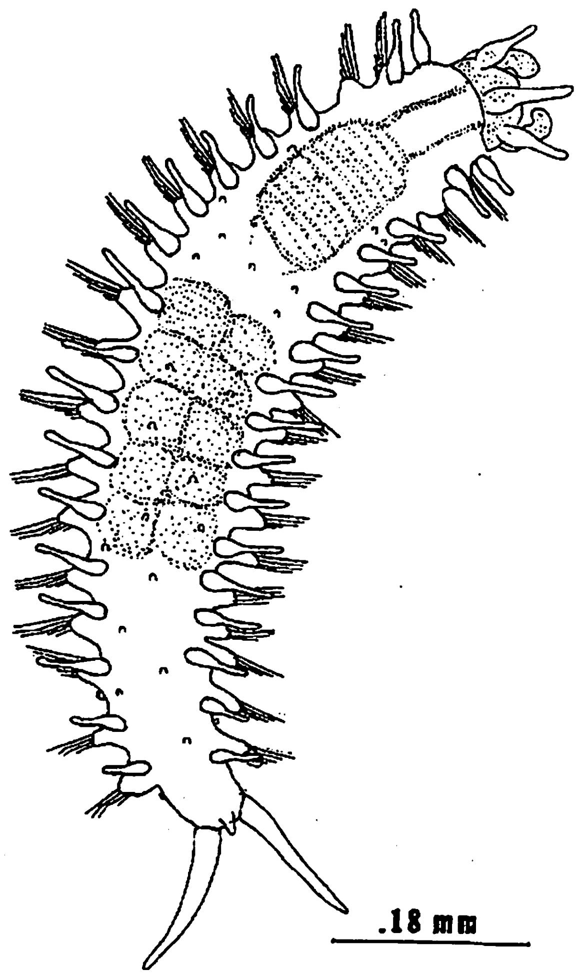
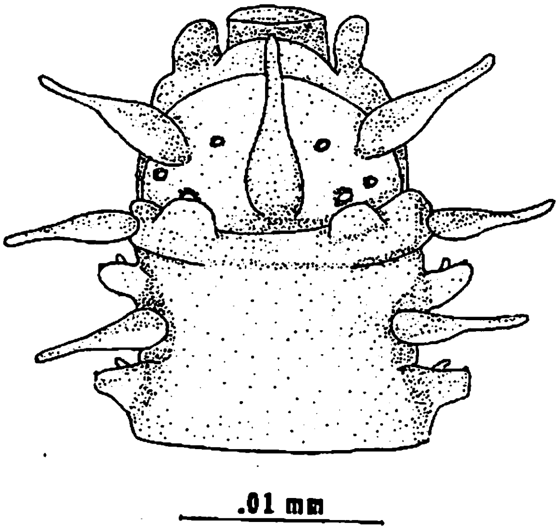


Figure 4. *Sphaerosyllis sp.* **Entire 17-setiger worm. Dorsal view. Length = 1.1 mm, maximum width = 18 mm.**

Figure 5. *Sphaerosyllis sp.* Anterior end of 15-setiger worm. Dorsal view. Length = 0.75 mm, maximum width = 0.17 mm.



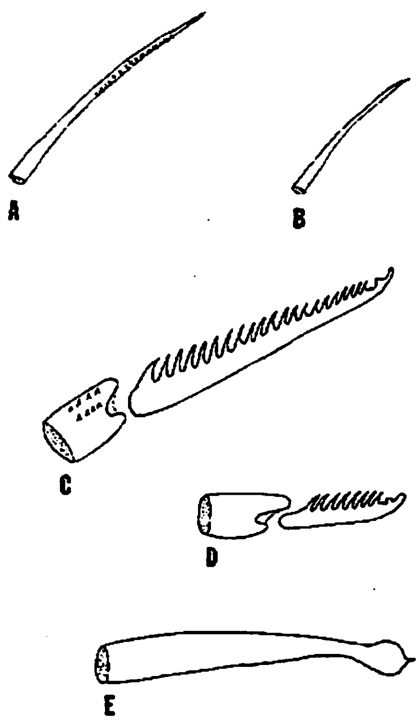


Figure 6. *Sphaerosyllis sp.* Setal types. A. Dorsal simple seta, basal width = 30 µm. B. Ventral simple seta, basal width = 20 µm. C. Heterogomph falciger, blade length = 30 µm. D. Heterogomph falciger, blade length = 12 µm. E. Acicula, basal width = 40 µm.

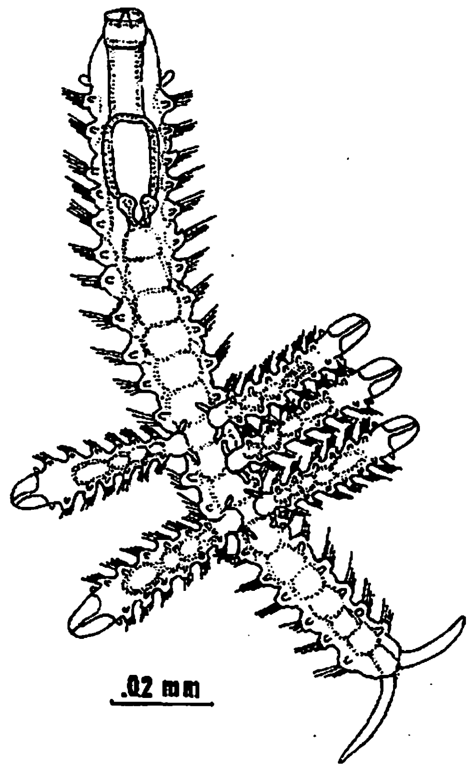


Figure 7. *Exogone.* Entire 21-setiger worm with attached larvae, Ventral view. Length = 1.4 mm, maximum width = 0.2 mm.

with two slender, lateral anal cirri, 0.11 to 0.13 mm long; and single, terminal mid-dorsal cirrus, about .014 mm long; and (7) There are four types of setae (see Figure 6): (a) Slender dorsal seta with two rows of minute serrations. (b) Three to seven distally bidentate compound falcigers with unevenly walled sockets; 8 to 30 coarse teeth on blades and some with small number of serrations on upper shaft, blades ranging in length from 8-42 μm with increases in length from dorsal to ventral setae and with longest blades in mid-body setigers; (c) Acicula expanded subdistally with a pointed tip; and (d) Smooth, slender ventral seta.

ADAPTATIONS

Morphology. When comparing these two species with their open ocean relatives, most of which are found in fine sands, they are much smaller and have fewer segments. For instance, two Caribbean syllids *Exogone atlantica* and *E. lourei*, have respective sizes of 6.9 mm and 8 mm in length and a width of 0.2 mm, with 46 and 52 setigers (Uebelacker and Johnson, 1984). The Bahamian interstitial species, by contrast, are maximally 2.7 x 0.22 mm (*Exogone* sp.) and 1.1 mm x 0.2 mm (*Sphaerosyllis sp.*). Additionally, they have relatively smaller appendages (antennae, parapodia, and dorsal, ventral and pygidial cirri) compared to overall body size than do larger species in the same family.

The combination of small body size and appendages would allow them to move freely through the small spaces between algal filaments. Presumably, fewer segments means fewer cells and therefore less energy consumed. In addition, small size may provide easy access to food and make it difficult for potential predators such as mosquito fish and sheepshead minnow to find them. Small size may also be an evolutionary response to low nutrient levels. Reduction in size would allow a larger population to be maintained in an area with a fixed level of nutrients.

Reproduction. Sexually mature adults of both species from Osprey Lake show no obvious morphological adaptations associated with reproduction. This is in contrast to most syllids, which develop additional setae, modified for swimming, and enlarged sense organs (Potts,1913; Garwood, 1991). This suggests that the Osprey Lake species lack a swimming phase prior to fertilization.

Both species produce a few, proportionately large, lecithotrophic eggs (1-8 in *Exogone* and 2-10 in *Sphaerosyllis*) which are attached to the outside of the female where they undergo direct development. Refer to Figure 8 (after Raff, 1996, p. 222) for a summary of costs and benefits associated with direct and planktonic development. There are no apparent segmental rings of propulsive cilia. These characters suggest that they lack a free-swimming larva, a feature shared with most other interstitial polychaetes (Garwood, 1991). In Osprey Lake, a free-swimming larva would most likely be subject to heavy predation by fishes and arthropods, possibly resulting in a lower survival rate. Retention of larvae by the female, on the other hand, ensures a higher survival rate because it provides protection against predation and environmental stresses. This would be especially important in these two species because of the small number of eggs produced.

No evidence of asexual reproduction was found in either of the two species. This is not surprising since asexual reproduction is relatively rare amongst polychaetes. Asexual reproduction presumably has the advantage of allowing a population to maintain a highly fit genotype, and as long as environmental conditions don't drastically change, the species will flourish. If, however the environment deteriorates, the species may not be able to cope and be driven to extinction. In asexually producing organisms, any mutation that occurs in the genome would be retained and passed on to the next generation unchanged since there is essentially no rearrangement of genetic material. Harmful mutations therefore would tend to accumulate over time especially in organisms with a high mutation rate. This would most likely negatively effect population size and ultimate survival.

In sexually reproducing animals, genetic material is recombined during meiosis creating new arrangements in the gametes. Then when the gametes are combined, new genotypes can be formed which are different from those of the parents that created them. Thus sexual reproduction maximizes the fitness of a species by providing new genotypes on which natural selection can operate. However, in a changing environment, the genotype that best suits a species today might not be suitable for its survival tomorrow. The process of natural selection will single out the genome best suited to propagate the species under a specific set of environmental conditions. Unfortunately, because of gene recombination and other processes, a highly fit genotype most likely will be lost over time. Through the same processes, harmful mutations will also tend to be weeded out.

Is there any way to take advantage of the benefits of sexual reproduction, but yet retain a highly fit genotype over time? Shields (1982) suggested that inbreeding in small populations of animals with low fecundity would do just that. He said that "Inbreeding (random mating in a small, or nonrandom mating in any size, population) may reduce or eliminate the costs of sex while maintaining an advantage of asexuality, if the faithful transmission of successful parental genomes to progeny is favored in particular environments. Relative to outbreeding, inbreeding will reduce the cost of meiosis owing to the increased

Figure 8 . A Summary of Costs and Benefits for Planktonic versus Direct Developing Larvae Modified from Raff (1996)

FEATURE	DIRECT DEVELOPMENT	PLANKTONIC DEVELOPMENT
Parent's Reproductive Effort	Low	High
Egg Size	Large**	Small
Number of Eggs Produced	Small	Large
Success per Embryo	High Probability	Low Probability
Larval Dispersibility	Low	High
Settling	Predictable	Unpredictable-High Mortality
Distribution	Limited Range	Wide Range
Success in Extreme Environments	High Probability	Low Probability
Adult Body Size	Small Adults Possible	Large to Moderate

** The eggs of both syllids discussed here are proportionately large when compared to body size

relatedness of mates. It will also amoeliorate recombinational load by facilitating greater fidelity (though not perfection) in the transmission of successful and coadapted allele combinations at interacting loci. Relative to asexuality (apomixis or ameiotic parthogenesis) , inbreeding is less likely to suffer a mutation accumulating "ratchet", and thus inbred progeny are likely to suffer lower mutational loads than similar asexual families." *Exogone* sp. and *Sphaerosyllis sp.* seem to fit the bill. They live in a small, isolated environment and both produce a few, large eggs (compared to their overall size). We hypothesize that both species are highly inbred and because of this are able to maintain a highly fit genotype over time. It would be interesting to determine the degree of genetic similarity in both species to test Shield's hypothesis. This hypothesis may also apply to the small, viviparous, self fertilizing echinoderm (Echinodermata: Ophiuroidea) *Amphipholis squamata* (Hendler, et al., 1995) that we found (5/5/96) in Oyster Pond on San Salvador Island, Bahamas.

Some syllid species, including those studied here, carry eggs and larvae attached to the dorsal or ventral body surface (Figure 7), a feature that does not appear to have much adaptive value. Surely , an animal so burdened would have trouble moving around, making it more vulnerable to predators.

A possible answer to this dilemma is provided by Skelly (1997). He exposed both anesthetized and control amphibian tadpoles to a natural predator (dragonfly larvae). Active tadpoles were less than half as active in the presence of predators. Tadpoles therefore were aware of the presence of predators and reduced movement accordingly which in turn increased their chance of survival. Osprey Lake syllid species with attached eggs or larvae moved very slowly in comparison to those of similar size lacking these attachments. Perhaps reduced movement here as in tadpoles, makes animals less visible to predators and therefore enhances their chance of survival. This could be tested experimentally using exclusion cages.

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We were alerted to the interesting polychaete fauna of Osprey Lake by William Lindsay. Our collecting efforts were greatly aided by Daniel Suchy and his staff, who were generous with reprints and maps. We are particularly grateful to Fred Hotchkiss for his identification and information about the life style of the ophiuroid *Amphipholis squamata*, to Marian Pettibone for reviewing the manuscript, and to Fitchburg State College for its continued support.

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