SYSTEMATICS AND ECOLOGY OF THE POLYCHAETA (ANNELIDA) OF A SEAGRASS BED IN BERMUDA

by

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ABSTRACT

SYSTEMATICS AND ECOLOGY OF THE POLYCHAETEA (ANNELIDA) OF A SEAGRASS BED IN BERMUDA

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A review of the literature showed 267 species of polychaetes have been found in Bermuda. In this study, 4618 individuals from 91 species of polychaetes were collected from four sites, sampled in spring and fall. Three new species were described. Confusion found in the literature about some species assigned to *Branchiosyllis* (Syllidae) required redescription of this genus, and a new genus - *Ungulosyllis* (Syllidae:Polychaeta) - is proposed. Phylogenetic analysis of all Syllinae genera did not resolve *Ungulosyllis* as the immediate sister to the confusing genera.

Statistical analysis of polychaete species and abundance in spring and fall, and across the seabed showed notable differences. The species found, their life histories, and their feeding strategies, suggest that these seagrass beds are different (less stable) than seagrass beds of other subtropical locations. It is suggested that polychaetes may be used as an indicator of the status of the entire macrobenthic community.

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CONTRIBUTION OF P.P.

Chapter 1.

- Developed the concept of assessing the status of the polychaete fauna of Bermuda.
- Performed the literature search, and prepared a list of polychaetes reported from Bermuda over the last 115 years.
- Where possible, collected original description of all species reported from Bermuda.
- Identified all of the polychaetes in 64 sediment samples taken as part of an ecological survey along the North Shore of Bermuda in 1992.
- The study was done based upon the concept that polychaetes might be used to assess the status and health of the entire benthic community of a seagrass bed associated with coral island ecosystems.

Chapter 2.

- Recognized a problem regarding the identification of some syllids.
- Discovered confusion of the syllid genera in the literature.
- Examined original descriptions of the confused genera, and both type material and new material from type locality.
- Revised the genus *Branchiosyllis* and described a new genus *Ungulosyllis*.

Chapter 3.

- Recognized some specimens in the study as previously undescribed (confirmed this by examining type material of similar species from Bermuda deposited by A. E. Verrill at the Yale Peabody Museum of Natural History).
- Described and illustrated three new species of polychaetes.

Chapter 4.

- Reviewed literature on the macrofauna of seagrass bed.
- Prepared the polychaete data for analysis; analyzed data and interpreted results.

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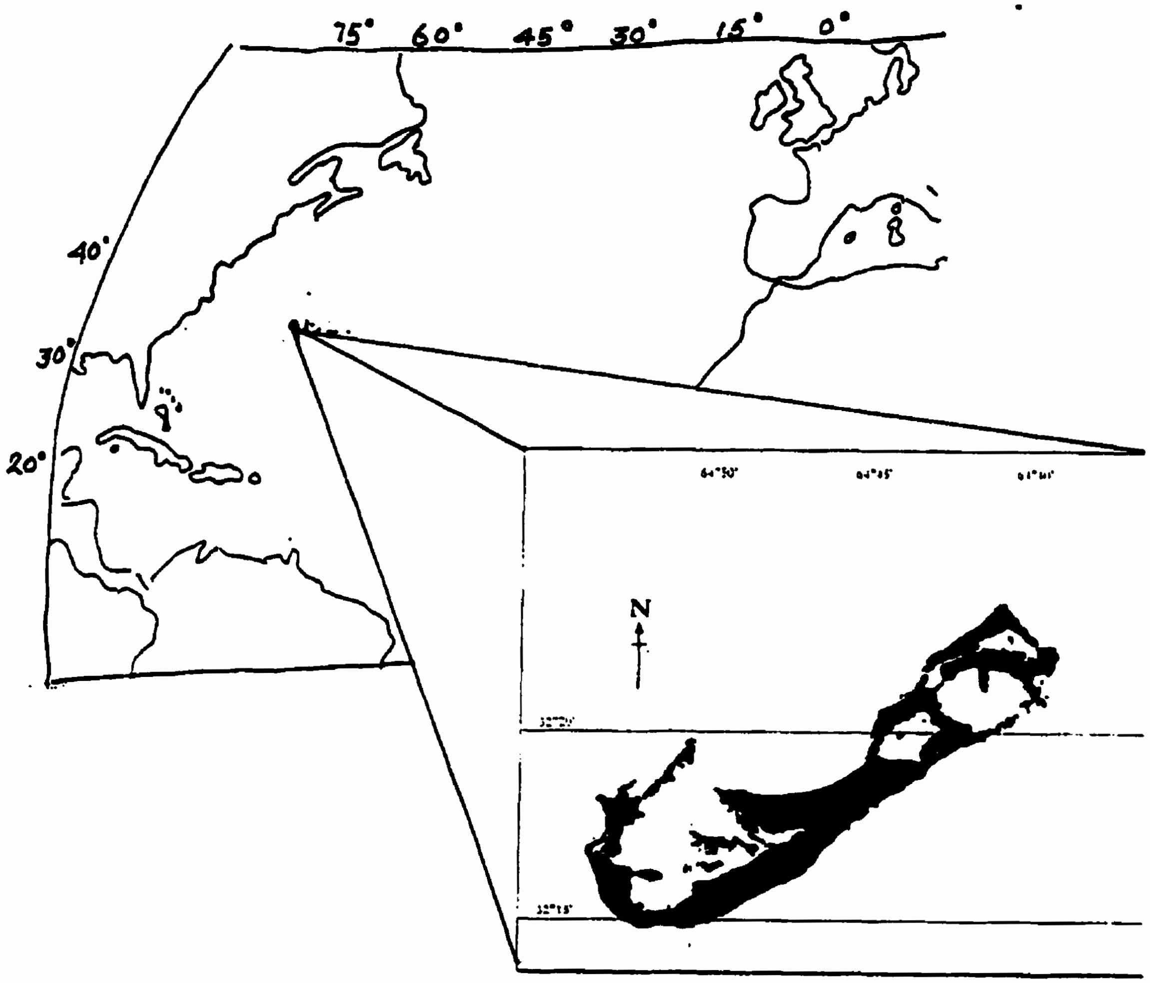
CHAPTER 1

SYSTEMATICS AND ECOLOGY OF POLYCHAETES COLLECTED IN A BERMUDA SEAGRASS BED

INTRODUCTION

The Bermuda Islands lie in the northwest Atlantic Ocean at about 32^0 N and 64^0 W. They are approximately 960km southeast of Cape Hatteras, N.C., 1280km south of Yarmouth, N.S., 1368km northeast of the Bahamas, and 1564km north of Puerto Rico (Fig. 1-1). Unique in the northwest Atlantic (in contrast, the northeast Atlantic has many islands), Bermuda consists of an archipelago of about 120 islands capping a seamount of volcanic origin, rising from depths of about 4000m (Thomas and Logan 1992). The Bermuda pedestal was formed as a result of volcanic activity which began approximately 110 million years ago (MYA). It has had a history of submersion and emergence as sea level rose and fell. A second volcanic eruption about 34 MYA accounted for the most recent emergence (Morris et al. 1977). The archipelago extends over about 22 miles, running primarily east to west and lies along the southern edge of the Bermuda platform. Bermuda itself is considered a coral "pseudoatoll", both because the reef rim is submerged and because the islands stand high above sea level (**Verrill 1902**).

Figure 1-1. Map of the North Atlantic showing the location of Bermuda



The climate of Bermuda is atypically warm for its northerly latitude; coral reefs, beds of tropical and subtropical species of seagrasses (Barnes and Hughes 1999) and mangroves are dominant biostructural components of its ecosystem. Bermuda possesses the northernmost coral reefs and mangroves in the Atlantic Ocean. The marine flora and fauna associated with the islands is thought to represent a northern extension of Caribbean subtropical systems (Sterrer and Schoepfer-Sterrer 1986; Thomas and Logan 1992). Seagrass beds, in contrast, are found in temperate, tropic and subtropic marine environments. Ecosystem interactions at tropical and subtropical latitudes have recently been reviewed (Birkeland 1998; Barnes and Hughes 1999).

Though seagrass beds are thought to have similar ecological characteristics in environments both adjacent to continents and around oceanic islands, the underlying structure of the sedimentary regimes can be different in these two types of locations. For example, sedimentary environments adjacent to continents, or large non-coralline islands, are usually characterized by the input of river-transported sediments often rich in organic matter. Sedimentary environments of islands developed from and dominated by coral reefs are not usually influenced by river-inputs. Their sediments are autochthonous - consisting primarily of well-sorted, biogenically-derived carbonate particles.

Islands are exposed on all sides to water movement, with the consequence that sedimentary ecosystems associated with coral reefs experience considerable natural disturbance through tidal currents and wave action. This higher energy water carries sediments in suspension. Seagrass beds are especially important to these reef ecosystems as they help to modify the sedimentary regime by trapping sediments, and preventing their resuspension. In so doing they protect the coral reef, as sediments in suspension are known to be deleterious to sessile taxa. For example, these organisms risk having their feeding and respiratory structures obstructed by particles in suspension as well as being buried by high sediment loads carried by turbulent water.

Once established, seagrass beds function as nurseries and refugia for a variety of fishes and invertebrates (Orth et al. 1984; Orth 1992). The spatially complex habitats provide protection to smaller organisms from predators known to occur on the nearby coral reefs. The roots offer a variety of habitats and refugia for infaunal organisms below the sediment surface, while the leaves offer the same for epifaunal and small swimming animals above the sediment surface. The plants themselves through the break-up of their leaves provide a rich supply of detritus that enhances the development of the associated flora and fauna.

Polychaetes are an integral part of all of the seagrass subhabitats. They occur in the water between the blades, on the grass blades, and in the sediment among the roots and they are sensitive to the physical characteristics of the habitat (Muniz and Pires 1999). It has been shown that sediment grain-size and stability are the main determinants of the species of polychaetes found in any environment (Gaston 1987). For example, filter feeders, such as serpulids and spirorbids, can be found in high-energy environments such as rocky shores characterized by stable, very large grain size sediments of low organic content. Whereas burrowing deposit feeding species, such as some members of the family Capitellidae, are more abundant in the fine grained sediments of depositional environments with high organic content. There is an abundance of information on environmental preferences and responses of polychaetes, and this group of annelids has been used as an indicator of the health of a number of marine environments (Pocklington and Wells 1992).

The objective of this study is to examine the structure of the polychaete community found in a seagrass bed and use it as an indicator of the ecological structure and stability of the seagrass bed community. In order to do this, I will analyze the abundance, diversity, taxonomy, and ecology of the polychaete fraction of the benthic community and extrapolate from this the condition of the whole benthic community in a seagrass bed in Bermuda. Biological characteristics such as feeding mode and life history will be examined in order to determine the trophic relationships as well as possible pathways followed by these organisms for colonizing the seagrass bed. This project will contribute to a larger study that has as its objective the production of ground truth information for a typical seagrass bed in Bermuda in anticipation of anthropogenic impact (Smith et al.1998). It will also contribute to general hypotheses and theories of seagrass bed dynamics, in particular about the stability of such environments in different climatic regimes.

In order to be able to identify the species of polychaetes collected during the seagrass sampling program, it was necessary to assemble taxonomic information on what species of polychaetes are likely to be found. Since the turn of the last century, only one study undertook to review the diversity and taxonomy of polychaetes found in Bermuda (Jones et al. 1986). This study mentioned only about 25% of the species previously reported from Bermuda's marine environment despite the fact that the island has been a center of marine biological studies for nearly a century.

History of Polychaete Systematic Studies in Bermuda

Bermuda was settled in 1612. Early anecdotal accounts of the natural history of these islands largely ignored marine worms (Lefroy 1981). However, towards the end of the 19th century, taxonomic specialists visited Bermuda and undertook studies of its marine fauna. From these investigations, several seminal papers on the polychaete fauna of Bermuda were produced. For example, Webster (1884) reported on collections made by Brown-Goode, and McIntosh (1885) reported on both shallow - and deepwater collections made by the H.M.S. *Challenger,* during its visit to Bermuda (1873-1876). More importantly, the well-known naturalist, associated with the Peabody Museum of Natural History of Yale University, A.E. Verrill, mounted a number of expeditions to the Bermuda Islands. Papers from his early expeditions formed the foundation of our knowledge of Bermuda's marine fauna in general and of the many sub-tropical marine annelids in particular. Verrill (1900, 1901) described many new polychaete species from the Bermuda material as did Bush (1907, 1910). Augener (1906) mentioned Bermuda polychaetes. Hoagland (1919) investigated marine annelids from Puerto Rico, the Florida Keys, and Bermuda and added new species as well as new records to the fauna of Bermuda. Treadwell, who worked primarily on the marine fauna of the West Indies, also took an interest in the marine annelids of Bermuda. He visited the island several times and described a number of new species from his Bermuda collections (Treadwell 1906, 1911, 1921). He also examined material collected by Beebe of bathysphere fame (Treadwell 1936 and 1941). Berkeley (1936) reported on polychaete species collected in the plankton off Bermuda. Hartman, while investigating the type species of polychaetes held by Yale University's Peabody Museum, took an interest in the specimens deposited by Verrill and reviewed the types of many species from Bermuda (Hartman 1942). Later, Hartman worked on collections of polychaetes from a deepwater transect between Gay Head, Massachusetts and Bermuda (Hartman 1965; Hartman and Fauchald 1971).

There followed a hiatus in interest in the polychaetes of Bermuda for any species but the local bioluminescent fireworm *Odontosyllis enopla* Verrill, 1900. This worm, whose spectacular bioluminescent spawning display occurs with lunar periodicity, has been the subject of several investigations (Galloway and Welch 1911; Huntsman 1948; Markert et al. 1961; Wolken and Florida 1984; Fischer and Fischer 1995). In more recent times, Gardiner (1979) reported on some polychaete species found in Bermuda. Only very occasionally in the past 30 years has a paper describing a new species from Bermuda appeared in the literature, e.g., Westheide (1973), Fauchald (1982), Sterrer and Iliffe (1982), and Eibye-Jacobsen and Kristensen (1994), or a new record is reported (James 1969; Pawlik 1983; Mendez-Ubach 1988).

The most recent comprehensive work on the polychaete fauna of Bermuda is a chapter by Jones et al. (1986) where only 69 of the more than 250 species reported from Bermuda are mentioned. For the present study, using the above literature plus some unpublished accounts, it was found that 35 families of polychaetes including 137 genera and at least 265 species have been reported from Bermuda (Appendix 1). This new assembly of information provides a good starting position for the identification of the polychaetes collected during the Bermuda North Shore seagrass bed study undertaken by the Bermuda Biological Station for Research Inc. (Smith et al. 1998).

Taxonomy

In environmental assessment studies all taxa should be identified to the lowest taxonomic level. Meaningful interpretation of data requires that the data are accurate - that each individual species be correctly identified every time it is encountered. Only that provides a clear idea of the composition and biological functioning of the community. Errors can be introduced if more than one species is lumped in a record, e. g., if the thirteen species of the Family Syllidae were simply lumped into one category such as "Syllid indeterminate". The theoretical reasons for this lie in the basic concept of the species as a distinct evolutionary and ecological unit. With all of the polychaetes identified to species and enumerated, it is possible to examine spatial and temporal variation of the polychaetes associated with seagrass beds and the environmental correlates of this variation.

In instances where the taxonomy of a species is unclear, it becomes necessary to review and revise descriptions of the problematic species. Evidence of such areas of uncertainty occurs when specimens do not correspond completely or at all with published descriptions. Accurate identifications are necessary for zoogeographic comparisons, for community comparisons, and for comparisons of genetic sequencing, to name a few.

In this study, such taxonomic uncertainty was found with regard to the genus *Branchiosyllis*, and a group of species recently synonymized with *Syllis (Typosyllis) exilis* Gravier, 1900 (Hartmann-Schröder 1978 and Licher 2000). For a number of specimens of the families Cirratulidae, Dorvilleidae, and Syllidae there was no existing species description to which they corresponded. Thus, this new examination of Bermuda's polychaete fauna leads to the exploration of the ideas about the extent of the endemism in the marine fauna of Bermuda, an area that has been recently reviewed by Sterrer (1998).

From the mid-1900's until recently, it was the convention to "lump" taxa found across broad geographical areas. This was especially true in the case of marine organisms, where the prevailing idea was that these were "open" species, i.e. not restricted by biogeographic barriers (Myers 1997). Recent studies and techniques, however, reveal a surprising genetic diversity in species thought merely to have a wide distribution (Myers 1997 and references therein e.g. Grassle and Grassle 1974; Poore and Wilson 1993). With the advent of phylogenetic analysis, taxonomists are encouraged to provide far more detailed descriptions of each species and include characteristics not previously employed, i.e. reproductive patterns and/or genetic markers. Using these additional characteristics, previous synonymies of marine taxa have been questioned and indeed reversed (Anger 1984). With this in mind, a closer examination of diagnostic characters in species found in this study, and thought to have a wide distribution was made, especially of those species described from Bermuda by Verrill (1900, 1901).

Ecology

Methods of evaluating the relationship of the organisms to their environment under pristine conditions are best achieved through multivariate methods such as cluster analysis, and ordination techniques such as correspondence analysis. Using these techniques community structure can also be revealed (Gauch 1982).

In this study, multivariate methods are used to make clear any patterns of natural variation in the macrobenthic community between two sampling dates, i.e., spring and fall in one year, and also between locations in the seagrass bed, i.e. the outer edges versus inner sites. Through the use of these methods, the principal environmental factors responsible for the observed patterns may be inferred from among those measured. The factors recorded in this study include the location of the samples in the seagrass bed, the date the samples were taken, and the density of different species of plants found in the seagrass bed.

There are a few methods that are frequently used for the ecological analysis of benthic communities. One such method is the calculation of a diversity index, of which there are several e.g. the Shannon Weaver Diversity Index H' (Shannon and Weaver 1949), and McIntosh's Index (McIntosh 1967). The numeric estimates made by such analyses, i.e., species richness, and the evenness with which the individuals are distributed among the species, are said to reflect the organization of a community. Such analyses are mostly used when impacted conditions are suspected. If the structure of a community is altered such as through anthropological input, the changes are readily recognized through recalculating diversity indices i.e., species' diversity and evenness (Clark and Warwick 1994) and comparing these values with preimpact measurements. In this way, the relative degree of the impact can be assessed. These indices were not generated at this time as the environment was considered pristine.

Biology

Life History and Distribution

Marine invertebrates display a wide range of reproductive and feeding strategies and these characteristics largely determine their abilities as colonizing organisms. Particular life history patterns are strongly represented among successful colonizers of oceanic islands (Scheltema 1990). One life-history attribute that is thought to improve a species' success in colonizing isolated habitats is possession of a pelagic larval stage (Hutchings and Murray 1982; Scheltema 1990). Colonization success of a species also has been related directly to length of larval life (Thorsen 1950, 1961; Bhaud and Cazaux 1987; Dial and Roughgarden 1999). It seems probable that animals with a pelagic stage and/or a long larval life have a better chance of encountering a habitat suitable for settlement at a longer distance from their production than those with a short or no pelagic stage (Paulay 1994). Their survival also would be improved if the larvae were planktotrophic and numerous. Examples of taxa with these larval strategies are found among the Echinodermata (Palumbi 1995), Mollusca (Kohn 1997), and Polychaeta (Bhaud and Cazaux 1987; Scheltema 1990), at least. In contrast, the ability to quickly fill up a habitat once colonized would seem to depend on restriction of larval dispersal, or asexual reproduction, and rapid reproduction.

Feeding Strategies

The feeding strategy of marine invertebrates can reveal much about the environment in which they live (Dauer 1984). For example, filter-feeding taxa are more frequently found in environments of clean, moving water. They can be found cemented or attached to hard substrates (including cobbles found on soft sediments). Some long-lived species among this feeding type may indicate a very stable environment. Burrowing deposit-feeders on the other hand are adapted to soft sediments and are usually found in depositional environments of a grain-size through which they are able to burrow by one of a number of locomotory behaviours. Carnivorous animals are not as restricted and are frequently highly mobile and considered to be more opportunistic than species with other feeding strategies (Grassle and Sanders 1973). Opportunistic animals are usually the first in the progression of animals seen in studies of ecological succession (Rhoads et al. 1978). With this in mind, examination of the predominant feeding strategies of the fauna that are found in the study site can suggest stability and/or general sediment characteristics of the habitat integrated over time, as opposed to when a sample is taken.

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CHAPTER 2

DISCUSSION OF THE *BRANCHIOSYLLIS EXILIS* GROUP AND DESCRIPTION OF A NEW GENUS (SYLLIDAE, ANNELIDA).

ABSTRACT

The syllid fraction of a collection of polychaetes taken from a seagrass bed in Bermuda was examined in detail. Identification of some of the individuals was problematic because they did not fit established generic characteristics. A review of the literature suggested that a group of species originally assigned to the genus *Typosyllis*, but more recently assigned to the genus *Branchiosyllis*, possessed a combination of characters that differed from these, and other genera of the subfamily Syllinae (Syllidae). A new genus – *Ungulosyllis* – is proposed for this group of species. The new genus can be distinguished from *Branchiosyllis* by the absence of branchiae, the form of the cirrophores, the presence of more than one kind of compound setae, and by having a greater number of articles in the cirri. It is distinguished from the genus *Typosyllis* by the absence of simple setae, and by the presence of compound falcigers with claw-like blades on segments posterior to the proventriculus. In a phylogenetic analysis of the genera of Syllinae, the new genus is not resolved as the sister group of either *Typosyllis* or *Branchiosyllis*. In addition, two species of syllid, *Branchiosyllis lamellifera* Verrill, 1900 and *Ungulosyllis annularis* (Verrill, 1900) are redescribed and recalled from synonymy based on type and new material from Bermuda.

INTRODUCTION

In the late 1800's and early 1900's, Bermuda was visited by several expeditions (including the *Challenger* expedition) from which many species of polychaetes were reported. A.E. Verrill, a naturalist at Yale University's Peabody Museum of Natural History (YPMNH) - best known for his contribution to the description of marine fauna of the eastern seaboard of the United States –

made two collecting trips to the islands, once in 1899 and again in 1901. He was a key player in the natural history observations of Bermuda (Verrill 1900; 1901). He reported a rich and varied invertebrate fauna, including 111 species of polychaetes, 55 of them new to science. He deposited much of his collection, along with many types, in the Peabody Museum (YPMNH).

Thirty-one of the 111 species of polychaetes Verrill collected in Bermuda belonged to one family - the Syllidae - a taxonomically difficult group. Of these 31 species, 27 were new, with ten of these assigned to the genus *Syllis* (subfamily Syllinae). Half a century later, Hartman (1942) examined Verrill's collection at YPMNH and suggested that many of his new species were junior synonyms. However, she did not examine fresh material from the type locality.

During an analysis of the polychaete fauna found in association with a seagrass bed along the North Shore of Bermuda, specimens of syllids corresponding to species described by Verrill (1900), but subsequently synonymized by Hartman (1942), were found. The diagnostic characters noted by Verrill (1900) are easily discerned in fresh material, and as a result of examination of this new material, it is proposed that at least two species be re-established.

Also, it became apparent that there was confusion in the literature about the defining characteristics of, and thus which species belonged in, the genus *Branchiosyllis,* (Subfamily Syllinae). Some species of the genus *Typosyllis,* (i.e., *Syllis (Typosyllis) exilis* Gravier, 1900) were recently assigned to *Branchiosyllis* as the *exilis*-group by Licher (2000). This taxonomic revision was made despite the fact that members of this species group do not have branchiae, one of the diagnostic characters of *Branchiosyllis*, and was based simply on the shared presence of compound setae with a claw-like blade. Examination of the literature, as well as examination of type specimens of members of the genera in question, indicated that the genus *Branchiosyllis*, species of the *Branchiosyllis exilis*-group, and the genus *Typosyllis* could all be distinguished from each other. The *Branchiosyllis exilis*-group of species possesses a combination of characters not seen together in the other two genera. In this paper, the genus

Branchiosyllis is redefined, and a new genus, *Ungulosyllis*, is proposed for the group of species recently assigned to *Branchiosyllis exilis*-group.

Subfamily *Syllinae*

The subfamily Syllinae is distinguished from other subfamilies of the Syllidae by having palpi free to base or absent and distinctly articulated dorsal cirri (Fauchald 1977). This subfamily is moderately diverse with about 200 species in 15 genera. Within the Syllinae there are some very speciose genera, particularly, because some authors accord *Typosyllis*, *Ehlersia*, and occasionally *Haplosyllis* only subgeneric status within *Syllis*. However, the consensus of recent opinions is to assign *Haplosyllis* full generic status (see: Fauchald 1977; Uebelacker 1984; San Martin 1992). San Martin (1992) ably reviewed the history of the genus since it was established by Savigny (in Lamarck 1818). He did not recognize formally subgenera in *Syllis sensu lato* though he acknowledges that such ranking would be practical from a taxonomic point of view. The genus *Syllis sensu lato* includes more than 140 species whereas most of the other genera of Syllinae have only a few species, *Branchiosyllis* among them with only five (Fauchald 1977).

Licher (2000) reviewed, revised, and redefined *Typosyllis* Langerhans, 1879, with type species *Syllis (Typosyllis) krohnii* (Ehlers, 1864). He accorded it generic status in the subfamily Syllinae and assigned 80 species to this genus, removing nine, most of which were reassigned to *Branchiosyllis*, as noted above (Licher 2000) (see Table 2-1).

Table 2-1. Taxa of the *Syllis (Typosyllis) exilis* group, transferred to *Branchiosyllis* sensu Licher 2000. (Note the circumtropical distribution of these species.)

SPECIES	LOCATION	REFERENCE
Syllis (Typosyllis) exilis Gravier, 1900	Djibouti (Red Sea)	Gravier 1900
Branchiosyllis exilis (Gravier, 1900)	Maui, Hawaii	Hartmann-Schröder 1978
	Costa Rica	Hartmann-Schröder 1978
	Galapagos	Westheide 1974
	Cuba	San Martin 1992
Trypanosyllis uncinigera, Hartmann-Schröder, 1960 (?syn. *Ungulosyllis exilis*, pers. obs.)	Red Sea	Hartmann-Schröder 1960
Syllis (Typosyllis) annularis Verrill, 1900	Bermuda	Verrill 1900
Syllis (Typosyllis) verruculosa Augener, 1914	W Australia	Augener 1914
	Easter Island	Kohn & Lloyd 1973
	Tortugas	Hartman 1959
Syllis (Typosyllis) fuscosuturata Augener, 1922	Tortugas, Fla.	Augener 1922
	Dry Tortugas	Monro 1933
Typosyllis maculata Imajima, 1966	Japan Sea	Imajima 1966
Syllis (Typosyllis) nigropharyngea Day, 1967	South Africa	Day 1967
Syllis (Typosyllis) plessisi Rullier, 1972	New Caledonia	Rullier 1972
Typosyllis bathyalis Kirkegaard, 1995	Philippines	Kirkegaard 1995

Characters for Distinguishing Genera

Fauchald (1977) used several morphological characters to distinguish genera of the subfamily Syllinae. These included characters such as absence or presence and shape of palps, shape and armature of pharynx, features of the integument, shape of parapodia, presence or absence of nuchal lappets, presence of digitate, dorsal and ventral parapodial lamellae, and shape of the setae. This last character is especially important, as there is a great diversity in setal morphology in the subfamily Syllinae. Setal shapes were the primary characters used by Fauchald (1977) to distinguish three of the four most species-rich genera i.e., *Syllis, Ehlersia,* and *Typosyllis.* Both compound and simple setae are found in these genera, but the shapes of the components of the compound setae (e.g. shafts, joints, and blades) vary considerably and thus are very useful characters for separating them. For example, members of the genus *Syllis* possess compound setae in anterior and posterior segments, but stout Y-shaped setae without blades in mid-body segments. Species of the genus *Typosyllis* possess compound falcigers with short and moderate length, more or less straight, dentate blades, and one or two simple setae. Species of the genus *Ehlersia* possess compound falcigers with moderately long to extremely long, slender, dentate blades, along with one or two simple setae (Fauchald 1977).

The presence and shape of the parapodial lamellae was used by Fauchald (1977) to distinguish the genus *Branchiosyllis* from other genera. This character is not sufficient, as there are representatives of other genera of the Syllinae that have similar digitate, parapodial lamellae e.g., *Dentatisyllis* Perkins, 1981 (Uebelacker 1984; San Martin and Bone 1999) and the new genus. The most useful diagnostic character for separating *Branchiosyllis* from other genera of the Syllinae is the presence of branchiae, as it is the only genus of the subfamily with branchiae.

Characters for distinguishing Species

In addition to the shape of the setae, the relative position of the different types of setae is an important morphological feature for distinguishing species. All setae may be similar in a parapodium or they may vary in number, size, shape and form (e.g., compound or simple), and from dorsal to ventral position. They may vary along the body from anterior to posterior setigers, and they may vary in relation to the acicula. For these reasons, Fauchald (1977) has cautioned that when using setal morphology to discriminate species, all setae along the whole length of the animal must be examined. San Martin (1992) holds a similar view, and recommends that additional characters, such as length and width of body, number of setigers, number and arrangement of eyes, number of articles in dorsal cirri, relative length of pharynx and proventriculus, shape of acicula, and color pattern, also be considered.

Phylogenetic Relationships

Phylogenetic systematics depends upon the comparison of the condition of characters found in one clade with the condition of these same characters found in a taxon or taxa considered to be related, but outside the clade under study. Phylogenetic analysis lead to hypotheses of evolution, such as of the ecological and morphological conditions of species at the origin of the clade and of patterns of change within the clade. These analyses also aid in recognition of taxa, independent lineages, from within lineage variants, by illustrating autapomorphies.

The family Syllidae has been considered a distinct, well-defined clade based on the presence of a proventriculus (Rouse and Fauchald 1995; Rouse and Fauchald 1997). Other distinguishing characteristics are dentate or tapering compound setae, and a first segment that is similar to other body segments, often setigerous and not fused with the peristomium (Rouse and Fauchald 1997, p.118). Syllidae is divided into a number of subfamilies (Fauchald 1977). The taxa studied here are all within the subfamily Syllinae, which is defined by the presence of one or several teeth on the pharynx, articulation of the dorsal, parapodial cirri, and palps that, if present and if fused, are fused only at the base.

Phylogenetic analyses are applied in this study to produce a clear indication of the relationships of the three Syllinae genera recognized here, *Branchiosyllis, Typosyllis*, and a new genus. Sixteen genera of Syllinae (including the new genus) are considered, a number of which are monospecific and are poorly characterized.

METHODS AND MATERIALS

Systematic studies

The literature was reviewed in order to assess all the characteristics of the two described genera in question. Original descriptions of these genera were consulted, and type specimens of some species from the genera were examined, e.g., *Branchiosyllis lamellifera* Verrill, 1900, *Syllis (Typosyllis) annularis* Verrill, 1900, and *Syllis (Typosyllis) exilis* Gravier, 1900, along with fresh and preserved material from the type locality of Verrill's species. The type material and some additional materials are held at YPMNH and, the last species, at Musée National d'histoire Naturel (MNHN). A fresh specimen matching the description of *Branchiosyllis oculata* Ehlers, 1887 was also examined.

Fresh material of species known from Bermuda came from a 1992 sampling program along the North Shore of Bermuda (Smith et al.1998), as well as from hand collections by the author in June 2000. Collections made in June 2000 were from one 20-cm tall, specimen of the fire sponge, *Tedania ignis*. After collection, the sponge was placed in a large dish and allowed to sit overnight at ambient temperature. The following day numerous invertebrates had exited the sponge, including several specimens of the polychaetes under study: eight specimens of *B. lamellifera* and four specimens of species referable to *S. (T.) annularis* Verrill, 1900.

All specimens were examined using a binocular microscope and, in some cases, parapodia were mounted on slides and examined using an Olympus Provis AX70 compound microscope with video image analysis system. Images were captured on video and stored electronically.

Cladistic Analysis

Sixteen gross structural characters were selected and coded (Table 2-2). The characters are those commonly considered in taxonomic studies (see "Characters for distinguishing genera"; and Fauchald 1977). All but two characters were coded as binary (Pleijel 1995; Rouse and Fauchald 1997). The others were coded as multistate, unidirected, characters because of the undesirable effects on the analyses of the presence of inapplicable/missing data. Sixteen genera of Syllinae were included and some "logical" assumptions were made in order to reduce the numbers of missing data for poorly known taxa (Table 2-3). For example, it was assumed that the single species of *Haplosyllides* had only simple setae, based on its name, indicating a superficial similarity to *Syllides*, both having cirri that are not distinctly articulated but with the former being "simple" in respect to setae. The genus *Eusyllis* (Syllidae: Eusyllinae) was used as the outgroup to root the tree and to establish evolutionary transformations of character states.

The program MacClade 3.02 (Maddison and Maddison 1992) was used to create the data matrix (Table 2-3) and to examine character transitions predicted by my analyses. Cladistic analysis was performed with the program PAUP 3.1.1 (Swofford 1993). A number of program options were applied: a Branch and Bound search, both with ACCTRAN, random trees (100 were generated), and bootstrapping (100 bootstrap replicates were made). The set of most parsimonious trees was reduced in size by filtering out unresolved or polytomous trees for which there was a consistent, more resolved tree in the set.

Table 2-2. Characters, states and coding

1.	palps	0: absent	1: present		
2.	pharynx	0: no tooth	1: one tooth	2: several teeth	
3.	pharynx - trepan	0: absent	1: present		
4.	nuchal lappets	0: absent	1: present		
5.	body shape	0: cylindrical	1: flattened		
6.	parapodia with-digitate lamellae	0: absent	1:present		
7.	simple setae	0: present	1: absent		
8.	dorsum of body	0: papillate	1: smooth		
9.	cirrophore	0: rudimentary	1: pronounced		
10.	cirrophore integument	0: smooth	1: with rugose patch		
11.	dorsal cirri	0: not articulated	1: articulated		
12.	dorsal cirrus	0: many articles	1: few articles		
13.	branchiae	0: absent	1: present		
14.	compound setae	0: none	1: claws	2: claws and straight	3: straight
15.	ventral cirri	0: pointed	1: reduced		
16.	dorsal cirri	0: moniliform	1: some thick or bulbous		

Table 2-3. Matrix for Phylogenetic Analysis of the Genera of Syllinae Using *Eusyllis* As Outgroup

CHARACTERS GENERA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15 (VC)	16 (DC)
Branchiosyllis	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0
Dentatisyllis	1	1	1	0	0	1	0	1	0	0	1	0	0	3	0	0
Ehlersia	1	1	0	0	0	0	0	1	0	0	1	0	0	3	0	0
Geminosyllis	1	1	1	0	0	0	?	1	0	0	1	0	0	0	?	0
Haplosyllides	0	1	0	0	0	?	0	1	0	0	0	0	0	0	1	0
Haplosyllis	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Opisthosyllis	1	1	0	0	0	0	1	1	0	0	1	?	0	3	0	0
Parapterosyllis	1	0	0	1	0	0	1	1	0	0	1	?	0	3	0	0
Parasphaerosyllis	1	1	0	0	0	0	1	1	0	0	1	0	0	3	0	1
Paratyposyllis	1	1	0	0	0	0	1	1	0	0	1	0	0	3	0	0
Pseudosyllides	1	0	0	0	0	0	1	1	?	0	1	0	0	?	0	0
Syllis	1	1	0	0	0	0	0	1	0	0	1	0	0	3	0	0
Trypanosyllis	1	1	1	0	1	0	0	1	0	0	1	0	0	3	0	0
Typosyllis	1	1	0	0	0	0	0	1	0	0	1	0	0	3	0	0
Ungulosyllis	1	1	0	0	0	1	1	1	0	0	1	0	0	2	0	0
Xenosyllis	1	0	0	0	1	0	1	0	1	0	1	1	0	3	1	1
Eusyllis	1	2	0	0	1	0	0	1	0	0	0	0	0	3	0	0

RESULTS

Systematic Section

Descriptions of the three genera *Typosyllis*, *Branchiosyllis*, and *Ungulosyllis* **new genus** are given based on examination of the literature and representatives of a few species of *Typosyllis* and of type and new material of the last two. The diagnosis of *Typosyllis* is included to confirm the distinction of the *Branchiosyllis exilis*-group (Licher 2000) and in order to include new observations on characters that further differentiate these taxonomic groups.

Typosyllis Langerhans, 1879

Type species *Syllis (Typosyllis) krohnii* (Ehlers, 1864)

Diagnosis: General appearance is that of a slender, threadlike syllid with ventral cirri, and articulated dorsal cirri that are highly variable in length and number of articles. Dorsal cirrophores low and without rugose patches. Eversible pharynx has a single acute tooth at the anterior end of the pharynx. Parapodia are rounded and are without branchiae, parapodial lamellae not distinct. Eyes usually arranged in a quadrangle. Setae include compound falcigers with straight to very slightly curved, toothed blades of moderate length (Type 1 setae), as well as one or two simple setae on parapodia of posterior setigers. Type 1 setal blades show a variety of shapes and dentition but are usually narrow, lanceolate, with an incurved tip, they are faintly to strongly bidentate with fine teeth on inner edge (see Figs 2-3c and 2-4 c).

Branchiosyllis Ehlers 1887

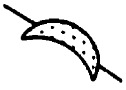
Type species: *Branchiosyllis oculata* Ehlers, 1887

Diagnosis (based on *B. oculata*, after Ehlers, 1887): "*Syllidarum genus pinnis labia conica et branchiam lamellosam gerentibus*".

Syllids with conical-lobed parapodia, bearing branchiae between the dorsal cirrus and the parapodium. It is the only syllid genus possessing branchiae. The prostomium is wider than long and bears two pairs of eyes, almost in a row, with the outer pair crescent shaped and larger than the round, inner pair. The antennae, tentacular cirri, and dorsal cirri have few (4-8) articles (Fig.2-1a, after Ehlers 1887, Tafel 39, Fig. 1). Pharynx extends through six segments and is equipped with one obtuse tooth at the anterior end. The proventriculus extends over four or five segments and has 23 muscle rows. In this genus there is only one setal form - Type 2 setae. Type 2 setae are compound setae with stout shafts and short, smooth, very curved, claw-like blades (Fig. 2-1b, after Ehlers 1887, Tafel 39, Fig. 7) (note that this figure shows four setae, two complete setae alternating with different views of two shafts with blades missing). The cirrophores are stout, and extend out from the body in this genus (Fig. 2-1a, dorsal view, Fig. 2-1c, lateral view, after Ehlers 1887, Tafel 39, Figs 1 and 3, respectively). Each cirrophore is characterized by the presence of a verrucose or rugose patch of integument on the dorsal side and a dense patch of cilia on the ventral side. The parapodia are pointed and have digitate dorsal and ventral lamellae of which the ventral lamellae are slightly longer than the dorsal (Fig. 2-1d after Ehlers 1887, Tafel 39, Fig. 6).

Remarks: When examined side by side, members of this genus are stouter and flatter than members of both *Typosyllis* and the new genus *Ungulosyllis*. These last two genera have cylindrical bodies and are frequently described as threadlike. Four nominal species of *Branchiosyllis* are included: *B. oculata* Ehlers, 1887, *B. lamellifera* Verrill, 1900, *B. diazi* Rioja, 1959, and *B. pacifica* Rioja, 1941. *Branchiosyllis lamellifera* had been synonymized with *B. oculata* by Hartman (1942) and this was accepted by Hartmann-Schröder (1978) but this synonymy is reversed here. Hartmann-Schröder (1978) also reviewed the three other species in this genus (Table 2-4).

Table 2-4. Variation in Characters Seen in the Genus *Branchiosyllis*. (Modified from Hartmann-Schröder 1978). (Note: MID-D.C. = midbody dorsal cirri)

SPECIES	NO. OF SEGS	LENGTH	NO. OF ART. IN MID-D.C.	SHAPE OF BRANCHIA	ACICULA	NO. OF SETAE/ PARAPOD.	NO. OF SEGS. IN PHARYNX
B. diazi	50-125	10-25	18-45		2-3	~ 7	~2
B. oculata	112	21	24		1	5-7	~8
B. pacifica	>47	>5	15-22		1	3-6	~3
B. lamellifera	24	4.5	8-15		1	4	~6

Branchiosyllis oculata Ehlers, 1887

Branchiosyllis oculata Ehlers, 1887: 148-151, figs 1, 3, 6 & 7.

Branchiosyllis oculata -- Hartmann-Schröder, 1978:60

Branchiosyllis oculata -- Uebelacker 1984: 30-107, fig. 30-102 a-d.

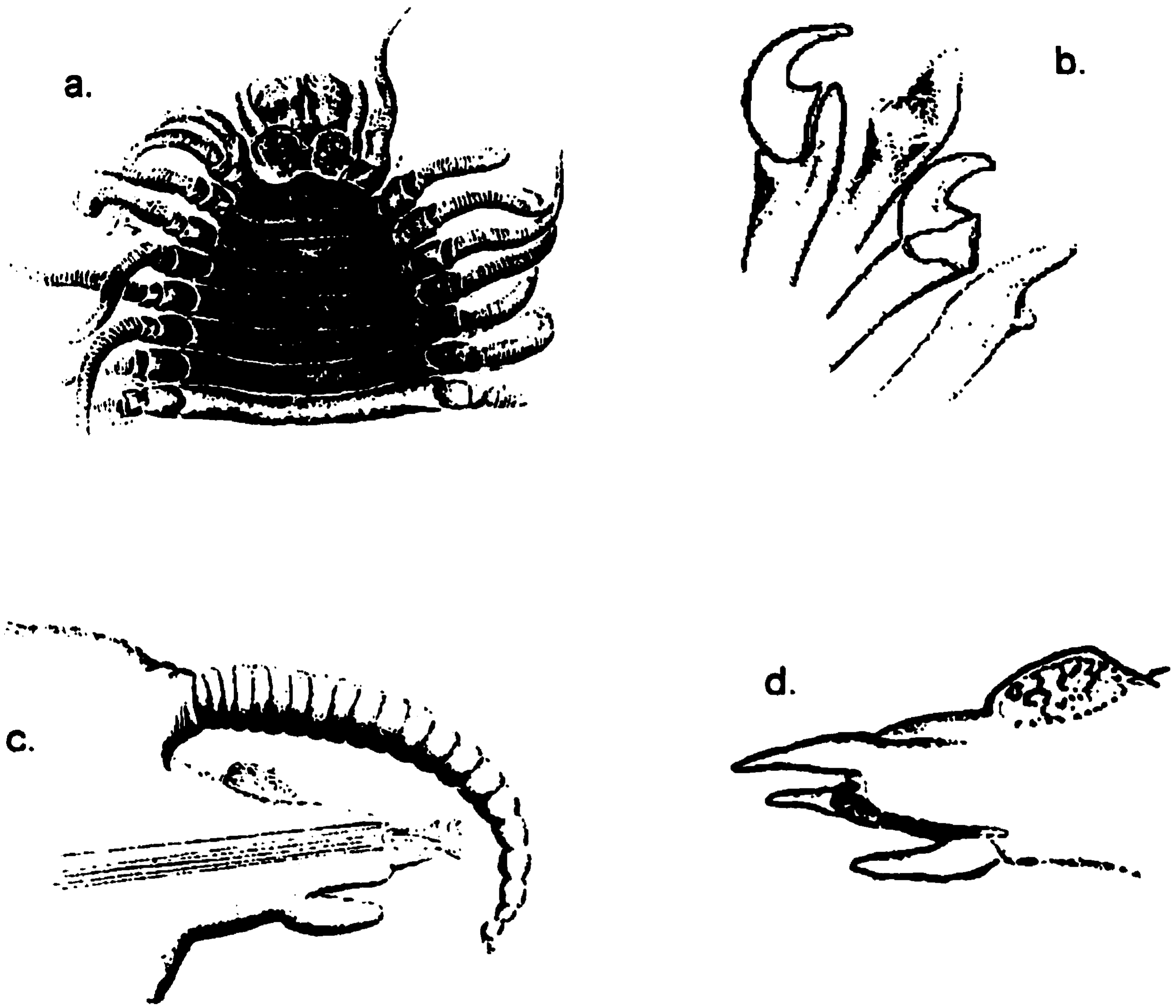
non Branchiosyllis oculata – sensu Hartman 1942:44, figs 62 – 63. [=*Branchiosyllis lamellifera* Verrill, 1900]

non Branchiosyllis oculata – sensu Pawlik 1983: 65, figs 3, 5 – 8. [=*Branchiosyllis lamellifera* Verrill,1900]

Material examined: Preserved specimen from Tynes Bay, North Shore Bermuda, collected 1992 by S.R. Smith.

Description: As for genus, given above. The branchiae are slightly developed, or blister-like and the same color as the rest of the integument (flesh colored).

Figure 2-1. *Branchiosyllis oculata* **Ehlers, 1887. a) prostomium dorsal view, b) parapodium showing branchia and lamellae , c) parapodium with dorsal cirrus and branchia, d) stout compound setae with claw-like blades (from Ehlers 1887 plate 39 figs 1,3,6,7)**



Remarks: The distinguishing character separating this species from others in the genus is the shape and undistinguished coloration of the branchiae (Table 2-4). The type specimen of the genus was not examined, but Ehler's (1887) description (given above) is very detailed.

Branchiosyllis lamellifera Verrill, 1900

Branchiosyllis lamellifera Verrill, 1900: 624-626.

Branchiosyllis oculata Ehlers *sensu* Hartman 1942:44, figs 62, 63.

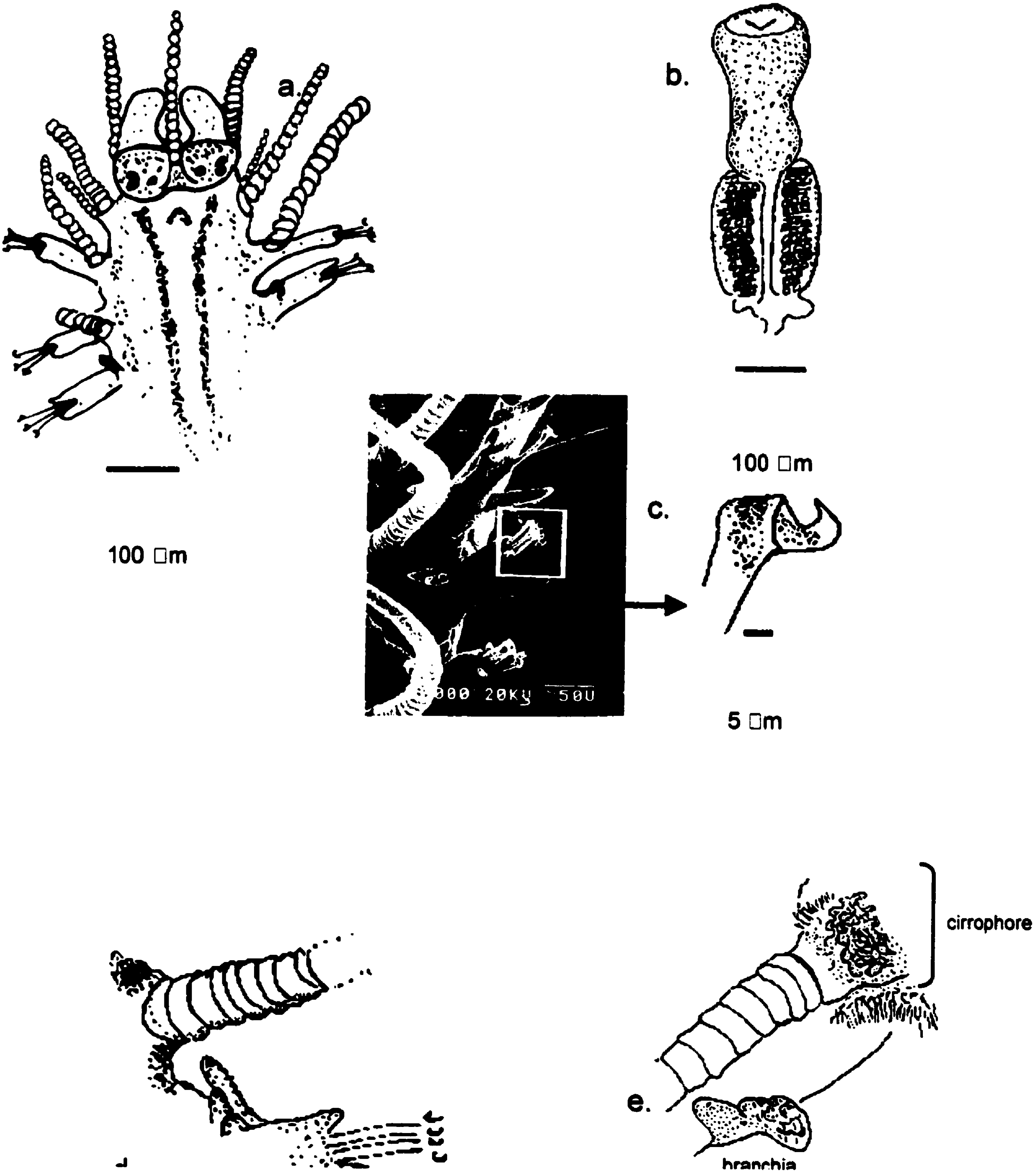
Branchiosyllis oculata Ehlers *sensu* Pawlik 1983:65 figs 3, 5-8.

Material examined: - YPMNH Box O slides 5, 6, and 7. *Branchiosyllis lamellifera* Verrill, 1900 TYPE (labeled "B. lamellosa" on slide # 5, but agrees with the published description of *B. lamellifera*). It is suspected that Verrill simply made an error when writing the name "Branchiosyllis lamellosa" or changed his mind about the name after labeling the slide.

Eight specimens collected from a sponge found in Richardson's Cove, St. George's Bermuda.

Diagnosis: A complete animal 7 mm long has 46 setigers. Color red, i.e., same color as the sponge in which it was found. The prostomium is wider than long with four eyes almost in a line, outer pair larger than inner pair, and with a pair of eyespots at base of lateral antenna (Fig. 2-2a). Median antenna with 10–14 articles, lateral antennae 7-14 articles, dorsal tentacular cirri 14 articles, ventral tentacular cirri 7 articles. Dorsal cirri have 14 – 15 articles and stout cirrophores. Pharynx occupies six segments and has one obtuse tooth on anterior end (Fig. 2-2b). Proventriculus occupies 4 segments and has 18 muscle rows (Fig. 2-2b). Up to four similar setae per parapodium; all setae are Type 2 (Fig. 2-2c). Just below each dorsal cirrus is a raised,

Figure 2-2. *Branchiosyllis lamellifera* Verrill, 1900. a) anterior segments dorsal view, b) pharynx & proventriculus, c) claw-like blades, d) raised lobed branchia, E) cirrophore showing verrucose patch and cilia



three or four lobed branchia (Fig. 2-2d). Prominent cirrophores bear a rugose or verrucose patch on the dorsal side and a patch of cilia on the ventral side (Fig. 2-2e). With digitate dorsal and ventral parapodial lamellae. The articulated anal cirri are long and slender.

Remarks: *Branchiosyllis lamellifera* Verrill, 1900 formerly synonymized with *B. oculata*, and recalled from synonymy in this paper, is typical of this genus. *Branchiosyllis lamellifera* differs from all other species in the genus by having a greater number of articles in the dorsal cirri and, as *B. oculata*, it is distinguished by the shape of the branchiae (Table 2-4; Fig.2- 2d, and compare, for example, with Fig. 2-1 d).

Distribution and Biology: *Branchiosyllis lamellifera* is known only from Bermuda. It is reported as a symbiont of sponges, including of *Tedania ignis*.

Ungulosyllis new genus

Type species: *Syllis (Typosyllis) annularis* Verrill, 1900

Diagnosis: Slender syllids with thread-like cirri. Palps broadly triangular and free to base, and the eversible pharynx has a single tooth at the anterior end of the pharynx. The prostomium bears two pairs of eyes almost in a row, with the crescent-shaped, anterior pair larger than, and lateral to the posterior pair; additional eye spots sometimes visible at base of lateral antennae. Three antennae, of which the median originates between the posterior pair of eyes and, the slightly shorter, lateral antennae originate near the forward edge of prostomium. Two pairs of tentacular cirri, dorsal longer than the ventral. Parapodia have ventral cirri and strongly articulated dorsal cirri; dorsal cirrophores low and without the rugose patches. Parapodia conical with pointed dorsal and ventral lamellae. No branchiae. Aciculae present, compound setae of two principal kinds, slender falcigers with straight blades (Type 1) and much stouter falcigers with strongly curved claw-like blades (Type 2). The Type 1 setae are present from the first setiger. Type 2 setae occur initially only in the lower bundle of setae and only posterior to the proventriculus. The blades of some setae in the upper bundle of transitional setigers may appear reflected in some species. Posteriorly, Type 1 setae are fewer in number, and there are only Type 2 setae in the pre-pygidial setigers. There are no simple setae.

Etymology: The name is derived from the Latin words *ungulo* (claw) referring to the shape of some of the blades of some setae, and from *–syllis,* indicating relationship to the family Syllidae.

Remarks: The following species are assigned to the new genus as they all have two distinctive kinds of falcigers; i. e., falcigers with straight, dentate, blades in anterior setigers and falcigers with smooth, claw-like blades in setigers posterior to the proventriculus, and do not have branchiae: *Syllis (Typosyllis) exilis* Gravier, 1900, *Syllis (Typosyllis) annularis* Verrill, 1900, *Syllis (Typosyllis) verruculosa* Augener, 1914, *Syllis (Typosyllis) fuscosuturata* Augener, 1914, *Typosyllis maculata* Imajima, 1966, *Syllis (Typosyllis) nigropharyngea* Day, 1967, *Syllis (Typosyllis) plessisi* Rullier, 1972 and *Typosyllis bathyalis* Kirkegaard, 1995.

Ungulosyllis exilis (Gravier, 1900) n. comb.

Syllis (Typosyllis) exilis Gravier, 1900: 160-163, Pl. IX, fig. 9; text figs 28-30

Branchiosyllis exilis Gravier -- Hartmann-Schröder (in part) 1978: 57-58, figs 15-20.

Branchiosyllis exilis Gravier -- Licher (in part) 2000: 333.

Branchiosyllis exilis – Westheide 1974: 60, fig. 26.

Material examined: Type specimen: MNHN, Jar 24 A.

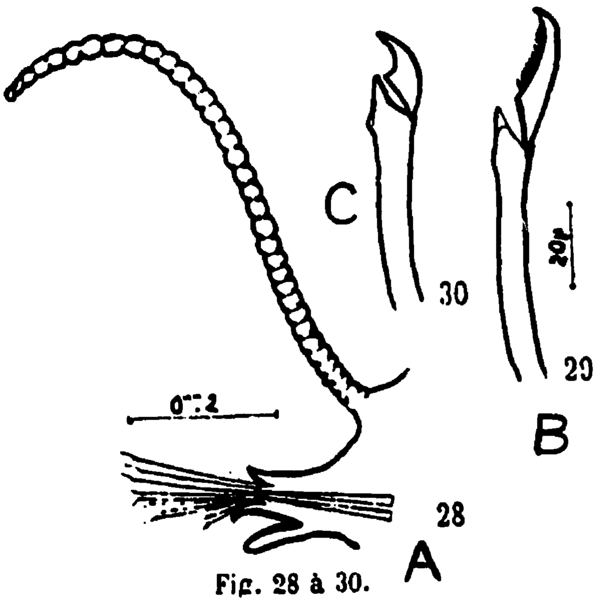
Diagnosis: A slender syllid with 61 setigers, 8 mm in length, segments have bands of pigment (much faded in the type material). Prostomium is wider than long, and the palps, which are longer than the prostomium, are free to base. There are two pairs of eyes and these are almost in a straight line, with the larger, crescent-shaped outer pair slightly anterior to the smaller round, inner pair. There are no eyespots. Only one lateral antenna of 15 articles remained on the specimen. Both pair of tentacular cirri and all but the most posterior dorsal cirri are missing (none seen in the bottom of the vial). The cirrophores are not prominent. Gravier (1900) reported that the dorsal cirri had 35-40 articles. The remaining posterior dorsal cirri are very short (5 articles). The pharynx, which has one acute tooth, occupies seven segments, as does the proventriculus. The latter has 29 rows of muscle cells. The parapodia project from the body and have pointed dorsal and ventral lamellae (Fig. 2-3a). The dorsal lamellae are smaller than the ventral (Gravier 1900: 162 Fig. 28) (Fig. 2-3a). There are no branchiae.

Type 1 setae have a finely denticulated blade that is very slightly bent toward the articulated joint, with one tooth projecting beyond the others (Gravier 1900: 162, Fig. 29) (Fig. 2-3c). The Type 2 – setae have a stout stem that is curved at the blade-facing edge, and a strongly curved blade without serrations (Gravier 1900: 162, Fig. 30) (Fig. 2-3b). Type 2 setae first appear in the most ventral bundle of setae of setigers posterior to the proventriculus (they are similar in appearance to the setae found in the genus *Branchiosyllis*). In the first 12 – 16 setigers, the upper bundles of setae have seven to ten Type 1 falcigers. At setiger 17 (the segment following the end of the proventriculus) there are one or two straight-bladed setae with their blades oriented backwards (reflected setae). By setiger 22 - 24 the shafts of the setae are stout and the blades are claw-like (Type 2). These Type 2 setae are restricted to the lower bundle of setae. By setiger 31, the setae in the upper bundle have also changed; there are fewer setae and the blades of these setae are shorter, broader, and distinctly curved. In the posterior-most segments there are only one or two Type 2 setae. No spots of pigment were seen in the remaining dorsal cirri, and pigment spots were not noted by Gravier (1900).

Remarks: the species named *Typosyllis uncinigera* Hartmann-Schröder, 1960 is probably also a synonym of *U. exilis* (Gravier, 1900). It was collected in the Red Sea.

Distribution and Biology: This species was first found near the port city of Djibouti in the Gulf of Aden. It has also been reported from Hawaii and Costa Rica (Hartmann-Schröder 1978), and the Galapagos (Westheide 1974).

Figure 2-3. ***Ungulosyllis exilis*** **n.comb. (Gravier, 1900) A) parapodium, b) compound seta with straight dentate blade, c) compound seta with Claw-Like blade (a, b, c, from Gravier 1900 Plate 9 figs. 28, 29, 30)**



Ungulosyllis annularis (Verrill, 1900) n. comb.

Syllis (Typosyllis) annularis Verrill, 1900: 608.

Syllis grandigularis Verrill, 1900: 604, **new synonymy**

Typosyllis annularis Verrill --Imajima 1966: 279.

Branchiosyllis exilis (Gravier), (in part) -- Hartmann-Schröder 1978: 57-58, figs 15-20.

Branchiosyllis exilis (Gravier) -- Uebelacker 1984:30-105, fig. 30-100 a-f.

Branchiosyllis exilis (Gravier) sensu San Martin 1992

Branchiosyllis lorena San Martin and Bone, 1999: 320-325, figs 2,3 and 4. **new synonymy.**

Branchiosyllis exilis (Gravier) – Licher 2000: 379.

Material examined: "Syllis annulicirrata", YPMNH (Box M slide 3) TYPE [variant spelling]

Syllis (Typosyllis) annularis Verrill, 1900, YPMNH, Box O slides 16 and 17.

Syllis grandigularis Verrill, 1900 Type YPMNH Box P slide 11.

Numerous specimens of preserved material collected by R. Smith, from the North Shore of Bermuda, October 1992 at Station SW 2- 8 (32^0 18'41"N, 64^0 46'14"W), Bermuda.

Four specimens of fresh material collected by author from a fire sponge found in Richardson's Cove, Bermuda (32^0 18'43"N, 64^0 46'12"W), June 2000.

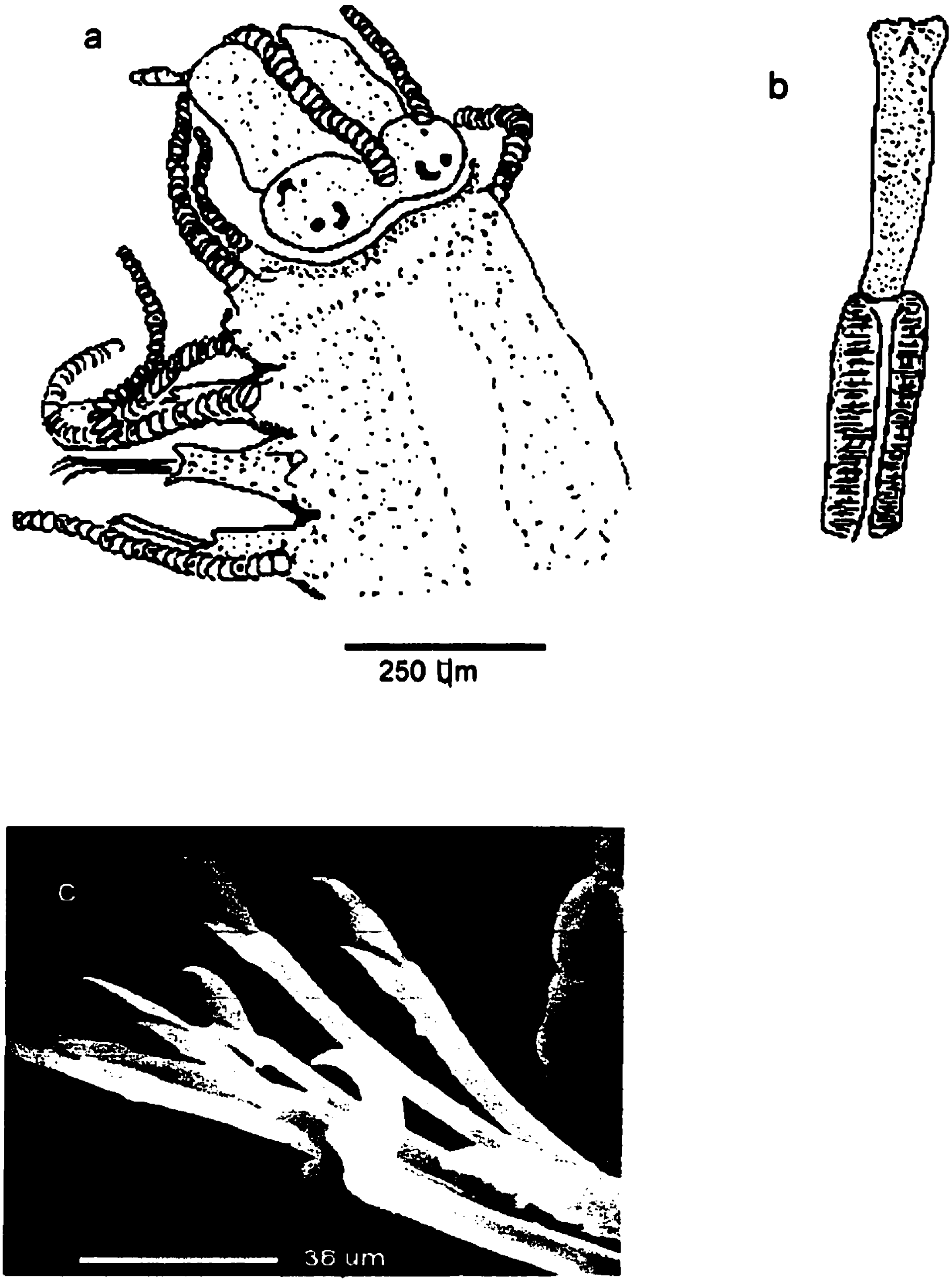
Additional reference material: A specimen from the North Shore seagrass bed of Bermuda has been deposited at the YPMNH.

Description of materials examined: "Syllis annulicirrata" TYPE for *Syllis annularis* Verrill, 1900, single specimen, YPMNH (Box M slide 3): the specimen is dried and very contracted. Verrill (1900) noted that the [Holo]Type was 14.5 mm long for 57 segments, with 14 new caudal segments being regenerated. The following could be observed in this specimen. There are 19 articles in the lateral antennae. The pharynx extends through 9 segments and the proventriculus through 8. Blades of anterior falcigers are straight and dentate. By setiger 21, one or two Type 2 setae could be seen in the lower setal bundle. Though no longer visible on the type specimen, Verrill (1900) noted that every fourth annulus in the dorsal cirri had spots of pigment.

Syllis (Typosyllis) annularis Verrill, 1900, single specimen, YPMNH Box O, 16 and 17: a more detailed description of this species can be given from examination of this specimen, one of the two originally deposited by Verrill. The fragment on slide 16 is the anterior 32 setigers of a small slender animal, 7.5 mm long, with all cirri long and thread-like; the posterior fragment of this animal is on slide 17. Prostomium wider than long, with a pair of palps free to base, two pair of eyes; anterior pair, crescent-shaped, slightly forward and larger than the posterior pair. Minute eyespots at base of palps (Fig. 2-4a). Median antenna has 20 articles and is slightly longer than the two lateral antennae, which have 17 articles. Dorsal tentacular cirri longer than ventral with 23 and 14 articles, respectively. Dorsal cirri of first setiger have 38 – 40 articles, thereafter variable, ranging from 38 to 52. Pharynx occupies 8 segments and has an acutely pointed tooth (Fig. 2-4b). Proventriculus occupies 7 segments; the number of muscle rows could not be discerned. Anterior segments (setigers 1 – 16) have several Type 1 falcigers, with straight, dentate blades (Type 1) (Fig. 2-4c) bearing a sub-distal tooth larger than the end tooth. The claw-like Type 2 setae also seen in (Fig. 2-4c) are not discernable till setiger 30 due to the condition of the specimen.

Syllis grandigularis Verrill, 1900 Type YPMNH Box P slide 11: in this specimen the pharynx is everted. The proventriculus occupies 7 setigers and has 35 rows of muscle cells. The compound setae include straight-bladed falcigers that are difficult to discern but are present in the anterior segments, setae with reflected blades on setiger 17, and setae with claw-like blades (Type 2) in the following setigers. These Type 2 setae are restricted to the ventral bundles of setae and became more numerous posteriorly. In his description, Verrill (1900: 604) noted that every fourth article of the dorsal cirri was strongly pigmented but this is no longer visible

Figure 2-4. ***Ugulosyllis annularis*** **(Vrrill, 1900). a) dorsum, b) pharynx with acute tooth and proventriculus, c) Scanning electron micrograph of parapodium of setiger 22.**



New Specimens from Bermuda: specimens from a North Shore seagrass bed: single specimen had only Type 1 setae in the first 16 setigers, setae with reflected blades are found from setiger 17, the setiger following the end of the proventriculus, thereafter the setae in the lower bundle are Type 2. The number of setae in both upper and lower bundles decreases toward the posterior of the animal. Pigment spots occur on every fourth annulus of the dorsal cirri. One specimen from a red fire sponge (*Tedania ignis*) found in Richardson's Cove, was 6 mm long with 25 segments. The prostomium is as described above (Fig. 2-4a), the pharynx extends through 5 setigers, with one acutely pointed tooth, the proventriculus extends through 5 setigers and has 33 muscle rows (Fig. 2-4b). The median antenna arises from between the posterior most eyes and has up to 30 articles and the lateral antennae are slightly shorter and have 17 - 18 articles. The dorsal tentacular cirri have 23 - 25 articles and the ventral tentacular cirri are slightly shorter. There are 23 - 38 articles in the dorsal cirri of the anterior and posterior segments, whereas the dorsal cirri are longer in mid-body segments, having up to 50 articles. There are pigment spots on every fourth article of these cirri. The cirrophores are not prominent. Type 2 falcigers commence at setiger 11, in the first segment following the end of the proventriculus. For the four specimens from the sponge, the first appearance of Type 2 setae ranged from setiger 11 to 17, corresponding to different total lengths of the pharynx plus proventriculus. Though no specific data were collected, this probably is correlated to the overall length of the animal. Initially, there is one Type 2 seta per parapodium located in the ventral-most position, they gradually increase in number as the number of Type 1 falcigers decreases. There are no simple setae. The anal cirri are short and stubby.

Remarks: The main diagnostic character for the species is the pigment on the cirri, i.e., every fourth annulus has a distinct pigment spot. This is in contrast to *Ungulosyllis exilis* (Gravier, 1900) that has bands of pigment across the dorsum. There was little variation among the specimens examined. Although the exact setiger in which Type 2 setae began was somewhat variable. In fresh material this was always the first setiger posterior to the proventriculus, from setiger 11 to

17. In some of the older, preserved, material these setae were first seen in more posterior setigers but this is almost certainly due to the condition of the material – setae have been lost or broken or the specimens are badly distorted and contracted.

Both *Syllis (Typosyllis) annularis* Verrill, 1900 and *Syllis grandigularis* Verrill, 1900 were described in the same publication, but the description of *S. (T.). annularis* was far more detailed and the holotype as well as a second, originally described, specimen were available, therefore this name was chosen for the species represented by all this material.

A thorough search for any specimen labeled the type of *S. (T.) annularis* was unfruitful. Verrill (1900) noted that only two specimens of this species were ever found, and there were only two similar-looking specimens in his collection. All of the Bermuda material collected by Verrill was deposited at the YPMNH and kept together, so it is not likely that any material was lost. He did label a single specimen "*Syllis annulicirrata*", YPMNH Box M slide # 3 TYPE", however, this name was not mentioned in print (Verrill 1900, 1901). I suspect that Verrill had considered a variety of names but had not decided on a name for the new species until he published, and chose *annularis* as the specific name. Even though there is a specimen of that name in the YPMNH collection, it was not designated as a type. The condition of the specimen labeled "*Syllis annulicirrata*" is too poor to discern any details.

The description and figures given for *Branchiosyllis lorena* San Martin and Bone, 1999 are indistinguishable from those given by Verrill (1900) for *Syllis (Typosyllis) annularis* (see synonymy). San Martin and Bone (1999) say that *B. lorena* has branchiae, however, examination of their figures makes it clear these are digitate parapodial lamellae and not branchiae, as seen in species of *Branchiosyllis*.

Distribution and Biology: *Ungulosyllis annularis* is reported from Bermuda, Cuba (San Martin 1992), Venezuela (San Martin and Bone 1999), and the northern Gulf of Mexico (Uebelacker 1984)

Results of phylogenetic analyses

Eight equally parsimonious trees were obtained using Branch and Bound search option (Fig. 2-5). These eight were obtained by filtering the set of 24 shortest trees, to remove all less-resolved trees and retaining only the fully compatible, more-resolved trees. Most parsimonious trees had a length of 27 steps, Consistency Index 0.704, Retention Index 0.667, Homoplasy Index 0.296, and Rescaled Consistency Index 0.469. Consensus trees, 50% Majority Rule, Strict, and Adams, varied from similar resolutions to those seen in each of the eight trees to highly unresolved, with polytomies at deep, internal nodes (Fig. 2-6 a,b,c). None of the random trees generated from the data seta had a length less than 31 steps and the average length was 36.7 steps, much longer than the shortest trees found. Bootstrapping showed that subsamples of the character data set could only strongly support the sister relationship of *Branchiosyllis* and *Xenosyllis*. However, this was not consider a particularly surprising or elucidating result as all the morphological characters were chosen for their significance to resolving the ingroup and, as anticipated, eliminating some of them reduced the overall resolution of the analyses. It does point out, however, a probable weakness of the data set and analyses, a relatively small number of characters.

The topologies of the eight trees could be grouped into three categories (Fig. 2-5), based on the position of *Ungulosyllis*. *Ungulosyllis* was always associated with five genera: *Opisthosyllis*, *Parapterosyllis*, *Pseudosyllides*, *Parasphaerosyllis*, and *Paratyposyllis*. In one of the eight trees, Type 1 topology, the *Ungulosyllis*-group was the sister to a clade of six genera including *Ehlersia*, *Typosyllis*, *Syllis* and the lineage of *Haplosyllis*, *Haplosylllides*, and *Geminosyllis* (Fig. 2-5a). This clade of six genera was only resolved in one other of the eight trees (Fig.2- 5b), Type 2 topology. The other six trees formed an unresolved polytomy at the basal node of the *Ungulosyllis*-group and *Branchiosyllis* + *Xenosyllis* pair (Fig. 2-5c), Type 3 topology. In seven of the eight most resolved, shortest trees, Type 2 and 3 topologies (Fig. 2-5b, c), the *Ungulosyllis*-group was in a clade with the terminal sister pair *Branchiosyllis* + *Xenosyllis*. In individual trees of the general topology summarized as Type 3, one or two (*Parapterosyllis* + *Pseudosyllides*) of the group of six genera was resolved from the polytomy as the sister to *Branchiosyllis* + *Xenosyllis*. The 50% majority-rule consensus tree (Fig. 2-6a) has the same general topology as Type 3 trees.

DISCUSSION

Systematics

Species that had been attributed to *Syllis (Typosyllis) exilis* group (Gravier, 1900), including Bermuda species described by Verrill (1900), were assigned, in error, to the genus *Branchiosyllis* by both Hartmann-Schröder (1978) and Licher (2000). The latter author recognized that this group of species could be distinguished from the genus *Typosyllis* and established a category "*Branchiosyllis exilis* group". The main diagnostic characters used for distinguishing the different species in this group are color pattern and pigmentation of the dorsal cirri.

Species of the genus *Branchiosyllis* and the group of species that were referred to the *Branchiosyllis exilis* group (now *Ungulosyllis)* bear a superficial resemblance. For example, eye position, shape of palps, prostomium, parapodia, and falcigers with short claw-like blades, a readily observed characteristic, are similar in both genera. Representatives of both genera appear in Bermuda, but comparative studies show that there are several characters that clearly distinguish *Ungulosyllis* from *Branchiosyllis sensu stricto*. In particular, *Branchiosyllis* has branchiae, and prominent cirrophores, as well as unique features on the cirrophores such as a verrucose or rugose patch of integument on the dorsal surface and dense patches of cilia on the ventral surface. In *Branchiosyllis*, there are few (2 - 4) setae per parapodium and the setae are all of one type – stout compound falcigers with sharply-curved, smooth, claw-like blades. Finally, the overall shape of the body is dorso-ventrally compressed in species of *Branchiosyllis*.

Species of *Ungulosyllis*, instead, have two types of compound setae, both those with smooth, claw-like blades and those with longer, dentate blades. They have no branchiae, nor modifications of the epidermis of the cirrophores, and they have a more slender, cylindrical body shape.

Relationships of *Ungulosyllis*

Ungulosyllis new genus is separated from *Branchiosyllis* and *Xenosyllis* by having both claw-shaped and straight bladed compound setae. This is regarded here as an apomorphic, feature. It distinguishes the species of *Ungulosyllis* from all those genera from which it is not clearly resolved by other unique characters, for as far as we know, they do not have claw-like setae. It remains problematic, nonetheless, as *Branchiosyllis* has only claws and its apparent sister genus, *Xenosyllis* has only dentate, compound setae and this implies non-homology or loss of the claws in some taxa (Figs 5a, 6a). *Branchiosyllis* is separated from both *Ungulosyllis* and *Xenosyllis* by possessing branchiae, in a variety of forms, and cirrophores with both ciliated and rugose patches. Hartmann-Schröder (1978) did recognize characteristics of the species of the new genus *Ungulosyllis* that indicated a close relationship to *Branchiosyllis* and other authors followed this opinion. Here, however, it is shown that you can separate these species into two taxa, with distinct histories. Underlying their separation also are a number of characteristics which could indicate distinct ecologies, in particular the body-shape of *Branchiosyllis* (and its sister genus *Xenosyllis*) and its development of specialized respiratory and structures on the cirrophores which are thought to be sensory. Unlike any other taxa, the species of *Ungulosyllis* have both claws and elongate compound setae, which similarly may be related to their specific ecological characters.

The monophyly of neither *Ungulosyllis* nor *Branchiosyllis* was tested in the phylogenetic analysis, but all species now included in these genera do have the defining, distinguishing characteristics. Only some of the species of these two genera and all species of *Xenosyllis* are inadequately described and this makes species-level phylogenies very difficult at this time. Unfortunately, this also is true for a number of the other currently recognized genera of Syllinae, including many that form a polytomy with *Ungulosyllis* in our analyses. This, without doubt, contributes to their relationships being poorly resolved in our analyses. It seems to be certain, however, that all the taxa mentioned here are without simple setae, which does differentiate them from the other general of Syllinae (Fig. 2-5c).

Typosyllis, with which the species of *Ungulosyllis* have also been confounded, appears to have quite distinct relationships from both *Branchiosyllis* and *Ungulosyllis* among the genera of Syllinae. It belongs to the part of the Syllinae that have simple setae (Fig. 2-5c), apparently a plesiomorphic trait.

Figure 2-5. Results of the phylogenetic analysis: a) Type 1 topology; b) Type 2 topology; c) Type 3 topology.

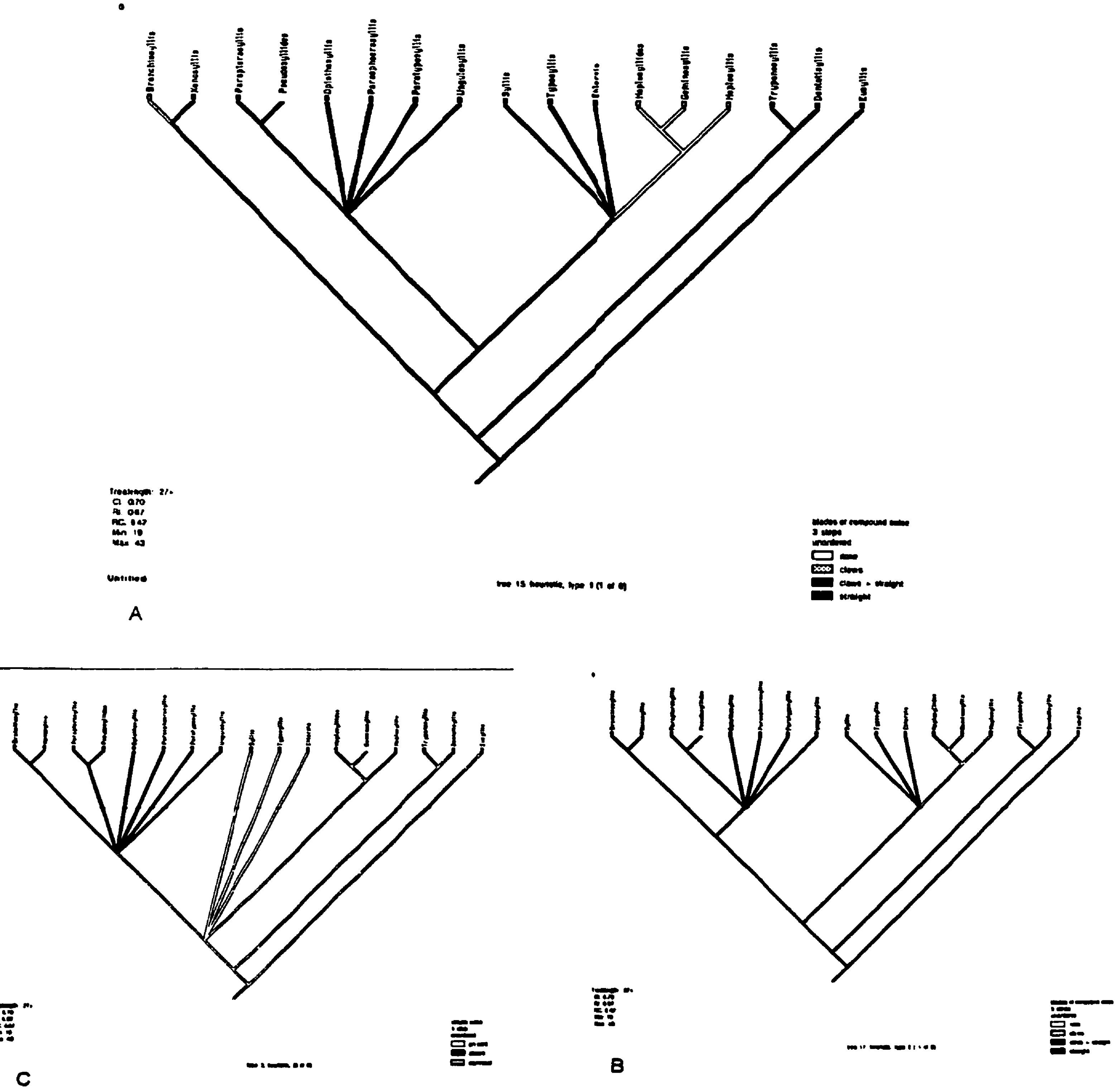
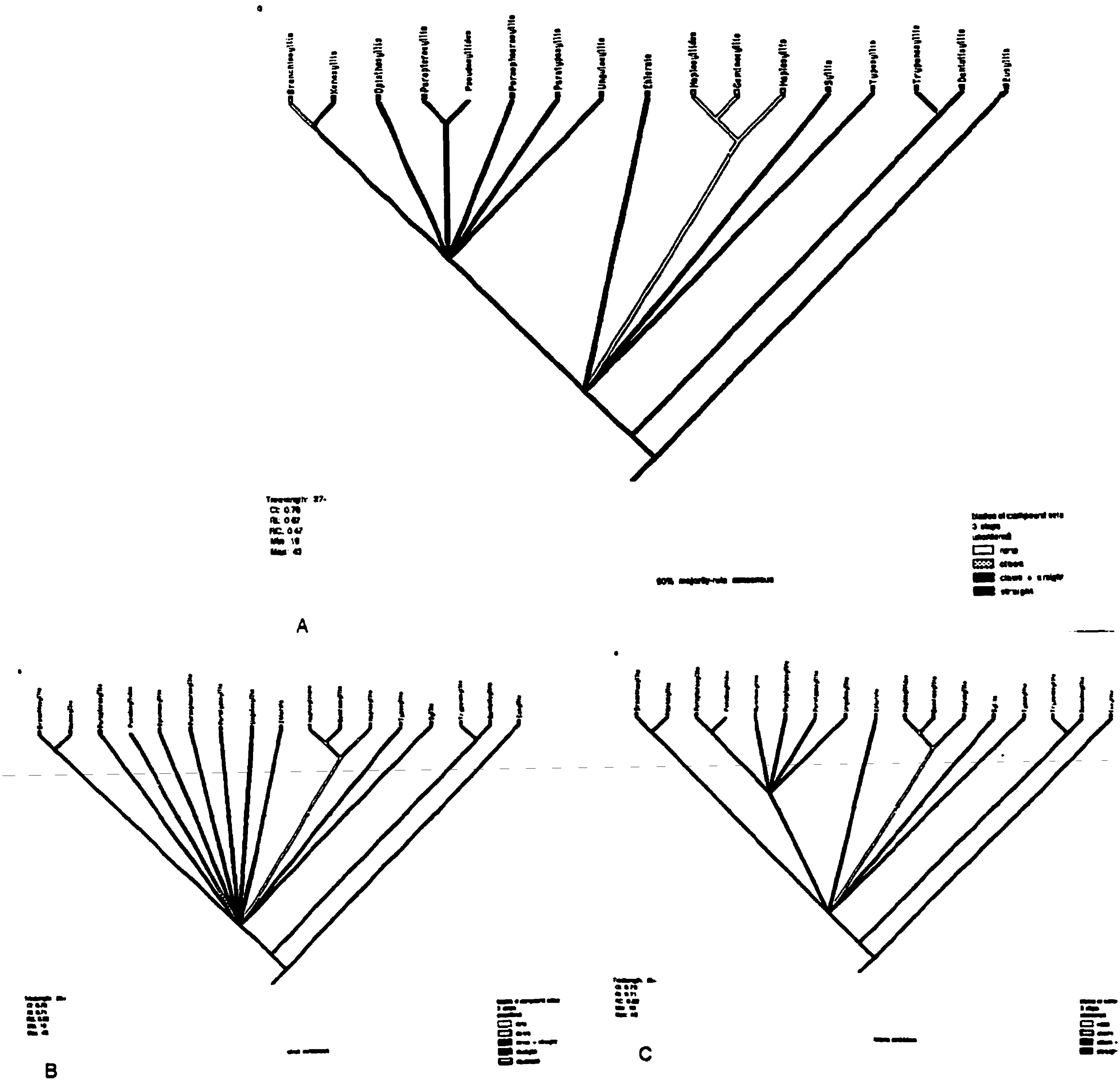


Figure 2-6. A) 50 % Majority rule consensus of 8 trees,B) Strict Consensus, C) Adams consensus



Setal forms and polychaete relationships

One character that is consistently used in systematic studies, at many hierarchical levels, is setal form. There are a wide variety of setal types within the Polychaeta, ranging from simple spines to highly complex, articulated and dentate forms. Rouse and Fauchald (1997) considered 124 different characters in their phylogenetic study of Polychaeta (plus a few other classes and phyla); of these, 20 were related to setae. Setal features have been used many times as unifying characters of polychaete clades (Fitzhugh 1989, Fitzhugh and Wolfe 1990, Licher and Westheide 1994). However, setal morphology alone is not sufficient to separate all taxa at all levels, for example, in the family Capitellidae it is not just the form of hooded hooks but also where they occur on the body that distinguish the genera *Mediomastus*, *Heteromastus*, and *Notomastus* (Warren et al. 1994).

Rouse and Fauchald (1995) indicate that the plesiomorphic form of seta for the polychaetes is still uncertain. However, other authors have asserted that the simplest, spine-like form is the plesiomorphic state (Rosenfeldt 1982, cited in ten Hove 1984; Glasby 1993). Nielsen and Holthe (1985), Knight-Jones and Fordy (1979), and ten Hove (1984) based hypotheses of evolution within the Terebellidae, Sabellidae, and Serpulidae, respectively, on patterns of increasing setal structural and functional complexity. Other authors (Licher and Westheide 1994) have suggested that some simpler forms of setae, in some taxa, are apomorphic. Given the diversity and complexity of the polychaetes and their occupation of a multiplicity of niches, it is most likely that both complex and simple setae represent derived forms, in different lineages.

In the family Syllidae the shapes of the components of compound setae, blades, joints, and stems, have been used to characterize both genera and species. In the present analyses, not all this variability was explored, however, the absence of compound setae does distinguish a clade of three genera (Fig. 2-5c), and the complete absence of simple setae distinguishes a clade of eight genera from the other seven genera in Syllinae (Fig. 2-5c). The transition pattern in Syllinae is one of having both simple and compound setae, to losing either the compound setae or losing the simple setae. It appears that both these losses were derivative from having both setal types. Thus, a simple assumption of either "increasing" or "decreasing" complexity in setal forms and complements in the evolution of this group would be incomplete. This does not mean, however, that the underlying genetics or sequence of events leading to the setal complements we observe do not become more complex as the lineages evolve.

These analyses also indicate more than one modification in the shape of the blade of compound setae from a plesiomorphic straight, dentate, form to a stout, curved blade, with a smooth inner edge (Figs 5b, 6a). This derived form is similarly recognized in both *Branchiosyllis* and *Ungulosyllis,* but they do not appear to be most closely related to each other among all the genera of Syllinae.

Another modification in the blade of compound setae in the Syllinae, that has received some previous attention, is found in *Syllis*. This genus has both normal compound and slender simple setae, but in mid-body segments of some species there are stout, simple (?pseudocomposite) setae, with y-shaped tips. These are a unique form in *Syllis* and are thought to have evolved from compound setae due either to fusion of a short blade with the shaft of the seta (Fauvel 1923; Perkins 1980), or by the loss of the blade element (San Martin 1992). Clearly there are many forms of highly modified setae within the Syllinae, and no one "trend" can explain the many changes in setal form that have occurred within the subfamily.

Function of the claw-like blades

Species of both *Branchiosyllis* and *Ungulosyllis* are found living within the water system of marine demosponges. Pawlik (1983) described how the hooked blades of these specialized setae in *Branchiosyllis lamellifera* Verrill, 1900, acted both to firmly anchor the animal in the sponge as well as to produce shallow excavations in the sponge tissue. Woodin and Merz (1987) and Merz and Woodin (1991) suggested that hooked uncini found in the families Maldanidae and Terebellidae act as anchors which prevent tube-dwelling organisms from being drawn out by suctorial, piscine, predators attacking the open ends of the worm tubes. Similarly the claws of the syllids may be important in preventing the worms from being washed out of the sponge by the feeding currents of the sponge itself. Other syllid species found in sponges such as *Haplosyllis* have simple setae, but both these and the aciculae can be strongly modified in posterior setigers, where they become enlarged and strongly hooked (Uebelacker 1984; pers. obs. of *Haplosyllis spongicola*), and may serve a similar anchoring function. Life within a sponge does, therefore, seem a strong force for adaptive development of anchoring-type setae.

CONCLUSIONS

It is here suggested that species similar or related to *Syllis (Typosyllis) exilis* Gravier, 1900 should not be assigned to the genus *Branchiosyllis* but should be assigned to a new genus – *Ungulosyllis* which is in the same lineage of Syllinae as the sister taxa *Branchiosyllis* and *Xenosyllis*. This clade is distinguished by the absence of simple setae. Both *Branchiosyllis* and *Ungulosyllis* are distinguished by the presence of claw-like compound setae.

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CHAPTER 3

THREE NEW SPECIES OF POLYCHAETA (ANNELIDA) FROM BERMUDA

ABSTRACT

Three new species of Polychaeta (Annelida) are described from a seagrass bed in Bermuda: one species of *Caulleriella* (Family Cirratulidae), one species of *Schistomeringos* (Family Dorvilleidae), and one species of *Exogone* (Subfamily Exogoninae, Family Syllidae). The new cirratulid has a novel arrangement of bifid hooks in both neuro- and notopodia, the new dorvilleid has a single furcate seta, with subequal tynes, in each parapodium, and the new syllid has a novel arrangement of the simple setae. The specimens of all the new species were collected at depths of 8 – 9 metres, in the grassbed rhizosphere. The new species from the seagrass collections, in combination with other still-unidentified species from the seagrass bed, indicate thatthe polychaete diversity of Bermuda is relatively high, is incompletely known, and is significant to the overall diversity and complexity of Bermudian seagrass beds.

INTRODUCTION

In the course of a study to determine spatial and temporal variation of the polychaete fraction of flora and fauna of a subtropical seagrass bed in Bermuda it was found that the taxonomy of this group of organisms was not as well documented for Bermuda as expected. The most recently published review (Jones et al. 1986) of polychaetes in Bermuda provided the names and short descriptions of only 69 species of polychaetes, plus short descriptions of another ten assigned only to genus. This necessitated a comprehensive review of the literature on polychaetes reported from Bermuda which resulted in a list of more than 265 species in 137 genera and 35 families (Appendix 1), and this excludes four families of "archiannelids". In addition, a large number of specimens found in samples from the seagrass bed study could not be assigned to any known species from Bermuda or elsewhere. Descriptions of new species are presented for one very abundant species, one moderately abundant species, and one rare species, all collected from *Syringodium filiforme* seagrass and algal beds along the shores of Tynes Bay, on the north shore of Bermuda.

METHODS AND MATERIALS

Study Site

The study site was located in Tyne's Bay on the north shore of Bermuda (Fig. 3-1). This shore faces a wide, deep, lagoon enclosed by a coral rim reef lying approximately 7 km away at the edge of the shallow Bermuda platform. Tynes Bay has extensive mixed seagrass and algal beds at depths up to 9 metres. The beds extend from shallow nearshore areas, less than 100 m from shore in about 1 – 3 m of water, to their maximum depths (9 m) 350 to 400 m offshore. They run parallel to the shore for many kilometers. The nearshore seagrass beds are dominated by *Thalassia testudinum*, turtle grass. The deeper offshore beds are

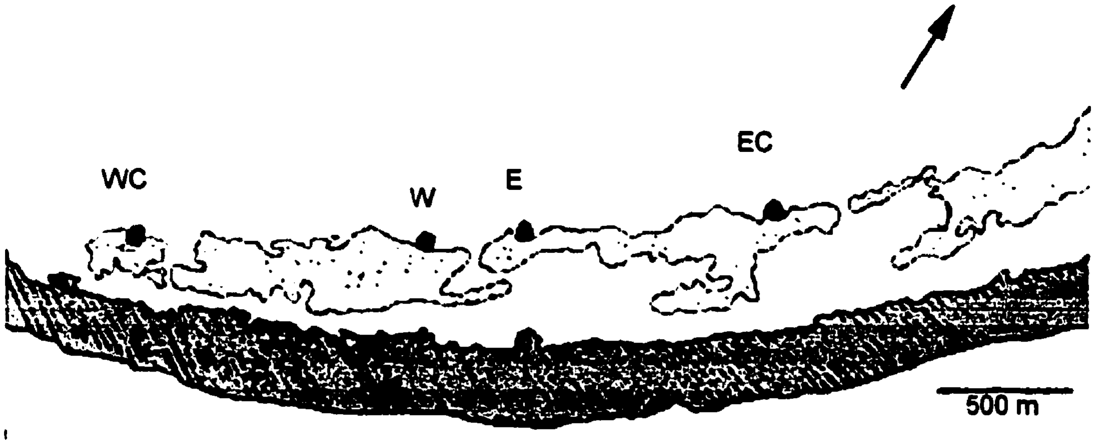

Figure 3-1. Map of Tynes Bay showing sampling sites in the seagrass bed

dominated by *Syringodium filiforme*, manatee grass, but there are some fairly abundant species of calcareous green algae (Chlorophyta), including *Penicillus capitatus*, *Halimeda incrassata* and *H. monile*. Beyond the seagrass beds, small patches of coral reef are found out to the south, shipping channel (approximately 1.5 km offshore).

The infauna of four stations (Fig 3-1) in the *S. filiforme* bed were studied in varying detail from 1991 to 1993 (Smith et al. 1998) as part of a pre-impact study for a heated, seawater, effluent. Two stations, approximately 400 m apart, were located near the middle of a continuous seagrass bed extending across the bay: East ([E] 32^0 18' 78"N, 64^0 45' 97"W); and West ([W] 32^0 18' 41"N, 64^0 46' 14"W). Two stations were located towards the edges of the seagrass bed, one 1 km to the east of E (East Contour [EC] 32^0 19' 01"N, 64^0 45' 25"W), and one 1 km to the west of W (West Contour [WC] 32° 18' 30"N, 64° 46' 54"W). All four stations were approximately 300 m from the shore, in water between 8-9 m deep (Fig. 3-1), and about 20 m inshore of the seaward edge of the grass bed. The samples used in this study were taken at the four sites in April/May, 1992 and September/October, 1992. Bucket cores were taken at two locations, each sampling location about 4 to 5 m^2, at each site. Cores were taken about 20 m apart at each sampling location. Four bucket cores, using a 0.053 m^2 bucket corer (diameter 26 cm, sampling depth about 25 cm), were taken at each of the two locations for each station. Thus, 64 core samples were collected and studied, 32 from each sampling date. The sediments from within the bucket cores for 1992, were airlifted and held in 500 μm mesh sample bags. The whole core samples were fixed with 5% formalin and stained with Rose Bengal prior to sorting. Samples taken in April/May are abbreviated in the text as WE, WW, WEC, and WWC, and those taken in September/October as SE, SW, SEC, and SWC.

Polychaete specimens were examined using a binocular microscope at low (10X) through high (40X) powers of magnification. Slide mounts, in water, of excised parapodia were examined on an Olympus Provis AX70 compound microscope with video image analysis system. Images were captured on video and stored electronically.

For comparative purposes, I examined all Bermudian polychaetes assigned by Verrill to the genus *Stauronereis* (Verrill 1900). These are deposited in the Yale Peabody Museum of Natural History (YPMNH), Yale University, New Haven, Conn. Included are the type specimens of *S. melanops*, Box O, slide 20, and of *S. polydonta*, Box O, slide 21. There were also slides labeled "type" *S. megalops*, Box O, slide 22, but this is probably just a variant spelling *for S. melanops*, as Verrill (1900) did not describe a species with this name. Additional specimens of *Stauronereis melanops* Verrill, 1900, from Box O, slide #s 17, 18 and 19, and one specimen labeled as *Stauronereis erythrops* were also examined. *Stauronereis polydonta* is now assigned to *Schistomeringos* (Jumars 1974), *S. erythrops* has been synonymized with *S. melanops* and assigned to the genus *Dorvillea* (Jumars 1974).

Type and other reference material of new species have been deposited at the Nova Scotia Museum of Natural History (NSMNH); Bermuda Biological Station for Research, Inc, BERP laboratory (BBSR); Bermuda Aquarium, Museum and Zoo (BAMZ), and the Yale Peabody Museum of Natural History (YPMNH).

The names that appear in this thesis are not valid until published in the primary literature and should not be cited.

Family Cirratulidae Ryckholdt, 1851

Genus *Caulleriella* Chamberlin, 1919

Type species: *Cirratulus bioculatus* Keferstein, 1862

Diagnosis after Blake (1996):

Prostomium elongate; peristomium long or short, dorsal tentacles may begin anterior to setiger 1. The bidentate spines consist of a main fang surmounted by a smaller apical tooth. The genus is distinguished from other bi-tentaculate cirratulids by the presence of distally bifid or trifid spines (crochet-like hooks) in addition to capillary setae.

The genus is easily recognized and well-defined (Wolf 1984). To date, 16 species and one subspecies have been assigned to this genus (see below). Species are distinguished based on the presence and distribution of the specialized, bifid or trifid setae, location of dorsal tentacles, color patterns of the body, and by presence or absence and shape of eyes.

Caulleriella cabbsiorum n.sp.

Caulleriella sp.-- Smith et al., 1998: 181, 186, 192.

Caulleriella sp. – Pocklington 2001, Chapter 4, herein.

Material examined: About 70 specimens from the Tynes Bay seagrass bed, Collected at stations W, WC, E, and EC in Sept./Oct., and at WC, E, and EC in April/May (see Fig. 3-1).

Holotype: Whole specimen, fixed in 5% formalin, preserved in 70% ethanol. Catalogue number XXXX. Tynes Bay seagrass bed, Bermuda (32° 18' 30"N, 64° 46' 54"W), sample TB-92-S-WC2, Sept., 1992, collected by R. S. Smith of BBSR.

Paratype: One whole specimen, fixed and preserved as holotype. Deposition location to be determined. Tynes Bay seagrass bed, Bermuda sample TB-92-S-WC2 (32° 18' 30"N, 64° 46' 54"W), Sept., 1992, collected by R. S. Smith.

Description: The holotype specimen is 7.0 mm long and 0.8 mm wide and has 84 segments, it has neither eyespots nor color pattern. The tapered prostomium, peristomium and first asetigerous segment give a bluntly conical appearance to the anterior end of the animal (Fig. 3-2a). Two dorsal tentacular cirri (grooved tentacles) emerge from the posterior margin of the setiger 3, each with a small lobe at the base (Fig. 3-2a). Branchial filaments begin on setiger 4 and their base is lateral to the line of the dorsal tentacular cirri; the first branchial filament is twice as long as the following ones. Branchial filaments are sporadic on the body, but continue to setiger 80. The anterior segments are much broader than long, and are compressed; after about setiger 30 the segments lengthen out a little, but are still much wider than long. The posterior setigers are slightly wider than the middle segments and more compressed dorso-ventrally.

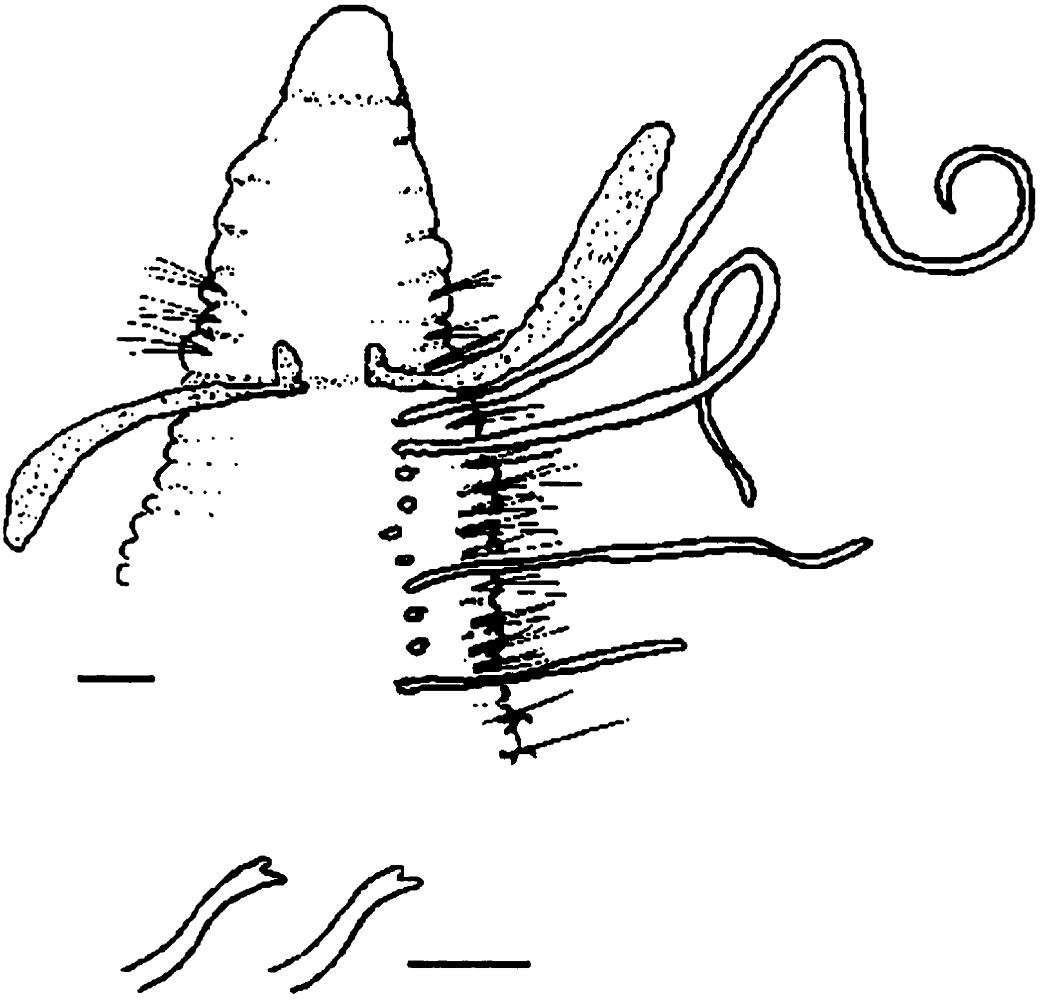

Figure 3-2. ***Caulleriella cabbsiorum*** **n.sp. a) dorsal view, anterior end showing tentacular cirri, b) bidentate sigmoid hooks.**

The pygidium is only a small pointed papilla. Noto- and neurochaetal bundles are widely separated. Anterior neuropodia have up to eight capillary setae. All hooks are sigmoid and bidentate with an apical tooth about half as long as the main fang (Fig. 3-2b). Neuropodial hooks begin at setiger 10. At the appearance of the first neuropodial hook, the neuropodia have one hook (H) and several capillary setae (C). The number of hooks gradually increases and the number of capillary setae decreases so that in the posterior neuropodia there are three or four hooks and only one capillary seta. Neurosetal arrangement from dorsal to ventral is CHCHH in the anterior segments and HHCH in the posterior segments. Notopodial hooks begin at setiger 15 or 16, with one or two hooks and two or three capillaries in setigers 15 to 20, and two or three hooks and one or two capillaries in the midbody segments. In the posterior-most notopodia there are three or four hooks and only one capillary seta, as in the neuropodia.

Etymology: The proposed species name – *cabbsiorum* - is derived from the acronym CABBS of the Canadian Associates of the Bermuda Biological Station, who provided funding towards this research and who have been long time supporters of education and research programs at BBSR. CABBS is treated here as a masculine proper name for a group of individuals, thus it is in the genitive, masculine plural.

Distribution and Biology: Known only from Bermuda. Found in the rhizosphere throughout an extensive *Syringodium filiforme* bed seagrass bed on the north shore of Bermuda. *Caulleriella cabbsiorum* was not considered to be very abundant in any one sample studied at this time, although overall it was one of the 15 most abundant species found in the Tynes Bay seagrass bed in 1992. It was ubiquitous in the bed in Sept/Oct but not in April/May, however, it was slightly more abundant in April/May (Pocklington, herein, Chapter 4).

Remarks: Literature searches indicate there are 16 species and one subspecies previously assigned to *Caulleriella*, and this has been confirmed by Mary Petersen (pers. comm.). These taxa are: *C. acicula* Day, 1961, *C. alata* (Southern, 1914), *C. alata maculata* (Annenkova, 1934), *C. apicula* Blake, 1996, *C. bioculata* (Keferstein, 1862), *C. chilensis* Carrasco, 1978, *C. cristata* Blake, 1996, *C. fragilis* (Leidy, 1855), *C. glabra* Gallardo, 1968, *C. hamata* (Hartman, 1948), *C. lajolla* Blake, 1996, *C. magnaoculata* Hartmann-Schröder, 1962, *C. pacifica* Berkeley, 1929, *C. parva* Gillandt, 1979, *C. tricapillata* Hutchings and Rainer, 1979, *C. viridis* (Langerhans, 1880), and *C. zetlandica* (McIntosh, 1911).

The new species differs from all others in *Caulleriella* in that the bidentate hooks are curved and are not alate, and they begin in the neuropodia of setiger 10 and notopodia of setiger 15-16. Also, the dorsal tentacles are located on the posterior edge of the third setiger and have small lobes at their base (Fig. 3-2a), which seems to be unique within the genus. The new species is eyeless.

In his recent key to the species of *Caulleriella* found in the Santa Barbara region of California, Blake (1996) provided two alternatives for the first position of the neuropodial hooks. They either occurred from setiger 1 or did not begin until setigers 20 to 30. He did not describe any unique features of the tentacular cirri such as the basal lobe, seen in the new species. *Caulleriella magnaoculata* Hartmann-Schröder, 1962, described from Chimbote, Peru, does have bidentate hooks beginning in the neuropodia of setiger 10, as in the new species, but bidentate notopodial hooks do not begin until setiger 37. In addition, Hartmann-Schröder's species has large eyes and the tentacular cirri begin at setiger 1. Among all the cirratulid species from the western North Atlantic (see review by Blake 1991) and from the Gulf of Mexico (Wolf 1984), there are no others that are similar to the new species.

Jones et al. (1986), in their review of the polychaetes of Bermuda noted one species of the genus *Caulleriella* but they did not assign it to a known species. Their species is different from *C. cabbsiorum* as it has 2 dark red eyes near the posterolateral margin of the prostomium, the tentacular cirri are on setiger 1, and the bidentate hooks occur in all neuropodia. There are bidentate notopodial hooks, but they begin at setiger 25 (Jones et al. 1986, p. 249; Mary Petersen pers. comm.). In contrast, C. *cabbsiorum* is eyeless, the neuropodial bidentate hooks commence at setiger 10, and notopodial bidentate hooks commence at setiger 15-16. *Caulleriella* sp. (Jones et al. 1986) is reported to be from *Thalassia* seagrass beds or in bare sand.

Family Dorvilleidae Chamberlin, 1919

Genus *Schistomeringos* Jumars, 1974

Type species *Nereis rudolphi* delle Chiaje, 1828

Diagnosis after Jumars (1974):

Prostomium with one pair of multi-articulate antennae and one pair of biarticulate palps, antennae and palps subequal. Prostomium slightly compressed dorsoventrally. Notopodia reduced, with aciculae and some setae, represented as a dorsal biarticulate cirrus, and containing an aciculum. Setae include capillary, furcate, and compound heterogomph setae. Jaws usually visible through the integument and comprised of two series of jaw pieces, mandibles and paired maxillae. Maxillae with basal plates of upper series fused.

To date, there are 16 species in *Schistomeringos*: *S. annulata* (Moore, 1906), *S. filiforma* Hutchings and Murray, 1984, *S. furcata* (Hartman, 1953), *S. japonica* (Annenkova, 1937), *S. longicornis* (Ehlers, 1901), *S. loveni* (Kinberg, 1864), *S. mediofurca* Jumars, 1974, *S. mossambica* (Hartmann-Schröder, 1974), *S. neglecta* (Fauvel, 1923), *S. pacifica* (Westheide, 1977), *S. paraloveni* Hartmann-Schröder, 1985, *S. pectinata* Perkins, 1979, *S. polydonta* (Verrill, 1900), *S. rudolphi* (delle Chiaje, 1828), *S. sphairatolobos* Glasby, 1984, and *S. subaequalis* Oug, 1978.

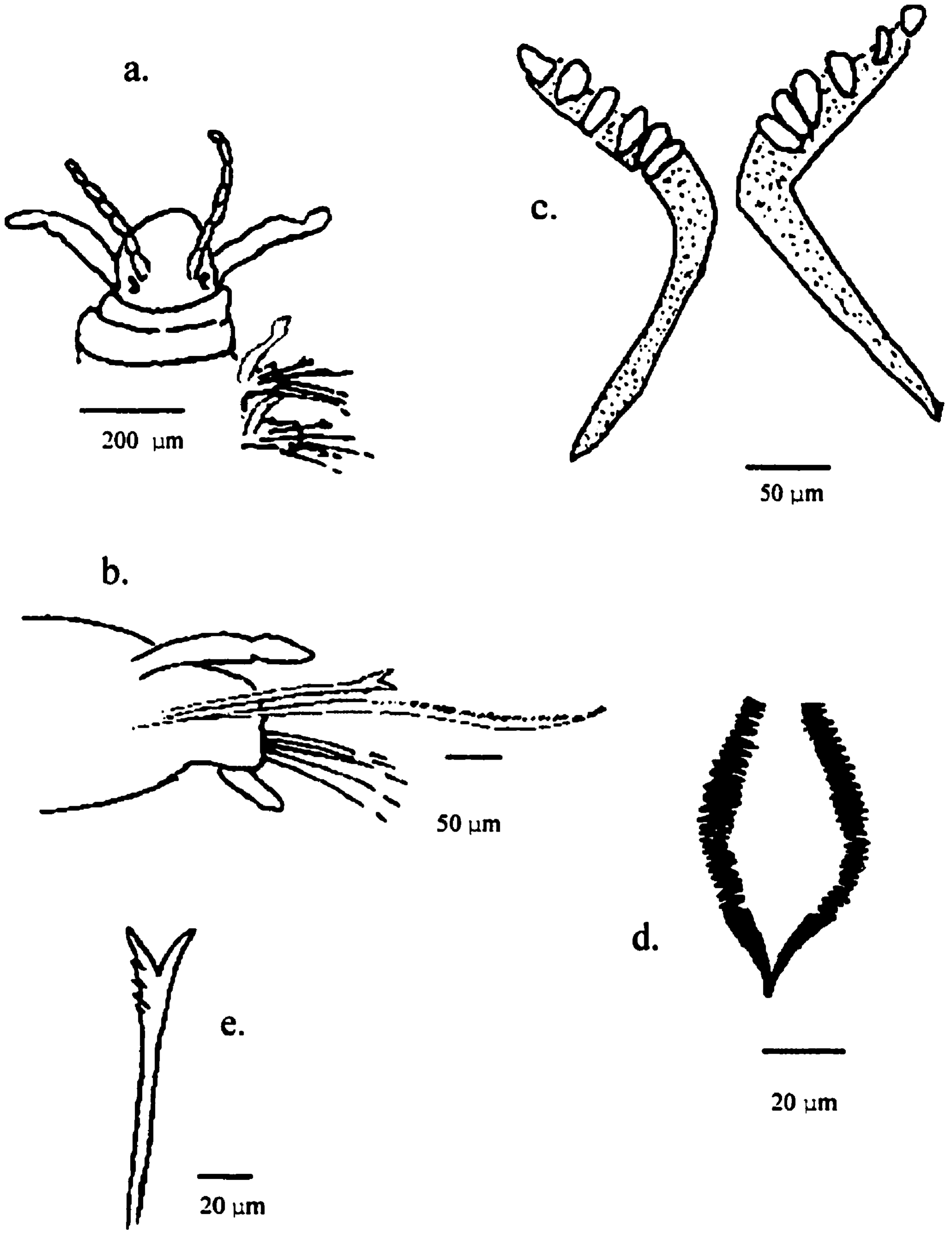

Figure 3-3. ***Schistomeringos rogeri*** **n.sp. a). dorsal view of head and anterior setigers, b). parapodium, c). mandibles, d). maxillae, and e) furcate seta**

Schistomeringos rogeri n.sp.

Dorvillea sp. -- Smith et al 1998:181, 186, 192.

Schistomeringos sp. – Pocklington 2001, Chapter 4, herein.

Material examined: Numerous specimens of more than 800 individuals, from Tynes Bay seagrass bed (Fig. 3-1). Specimens were found in all samples, at all stations, E, EC, W, and WC (see Fig. 3-1), in both April/May (W) and Sept./Oct. (S) of 1992.

Holotype: Whole specimen, fixed in 5% formalin, preserved in 70% ethanol. Catalogue number XXXX. Tynes Bay seagrass bed, North Shore of Bermuda TB-92-S-WC 8 (32° 18' 30"N, 64° 46' 54"W), Sept., 1992, collected by R. S. Smith.

Paratype: One whole specimen, fixed and preserved as holotype. Tynes Bay seagrass bed, North Shore of Bermuda, 92-TB-S-W-1, (32° 18' 41"N, 64° 46' 14"W), Sept. 1992, collected by R. S. Smith. Specimen to be deposited at YPMNH, New Haven, Conn.

Description: Based on a specimen from station TB-92-WW. This specimen is complete and in good condition. Length of animal is 8 mm with 47 segments. There is a conspicuous pair of crescent eyes at the base of the antennae (Fig. 3-3a). The biarticulate palps are about the same length as antennae but are somewhat stouter, with cylindrical basal joints and short terminal joints. The antennae have 6 - 10 articles. Anterior setigers compressed, first two segments apodous and asetous. Biarticulate dorsal cirri from setiger 1, as long as parapodial lobe on first one or two setigers, thereafter, cirri are slightly longer than parapodia. Both dorsal and ventral cirri of segment three are shorter than parapodial lobe. Jaws visible through integument. Mandibles flared and denticled (Fig 3-3b), maxillae consist of a pair of jaws each comprised of two rows of 18 to 21, minute, curved, pointed teeth (Fig. 3-3d). Each parapodium has five or six heterogomph falcigers equipped with minute, bidentate-tipped blades (Fig. 3-3c). From setiger 1, there is one supra-acicular, furcate seta per parapodium. These furcate setae have three rows of fine hairs on the outer edge of the shaft (Fig. 3-3e) and subequal tynes. The furcate setae are usually accompanied by one or two finely denticulate capillary, companion setae. Pygidium equipped with four anal cirri, dorsal pair longer than ventral.

Etymology: The species is named "*rogeri*" for my husband Roger in appreciation of his support and encouragement of my polychaete research.

Distribution and Biology: *Schistomeringos rogeri* n. sp. was the most abundant species in the seagrass bed in April/May samples and the third most abundant in Sept./Oct. samples of 1992. In April/May the abundance of this species was even across the bed, whereas, in Sept./Oct. there was an increase in abundance across the bed from east to west. However, the number of individuals at each of the stations in Sept./Oct., except the westernmost, was much lower than in the April/May samples (Chapter 4, herein). At the westernmost station in Sept./Oct., the numbers were about double the April/May numbers. This trend could suggest either active movement or transport across the seagrass bed from east to west, under the influence of prevailing currents, different death rates in various parts of the bed, or different recruitment rates in different parts of the bed at different times of the year.

Remarks: The presence of a single furcate seta, with subequal tynes on all setigers and beginning at setiger 1, and the dentition form, one pair of maxillae with about 18 – 22 teeth and a pair of mandibles with five or six small plates on their distal ends (Fig. 3-3 c), set the new species apart from its congeners.

The form of the furcate setae in *S. rogeri* n. sp. differs from that of all others in the genus except *S. filiforma* and *S. pectinata*. These three species have furcate setae with short tynes. However, the combination of the number and distribution of furcate setae with short, sub-equal tynes distinguishes *S. rogeri*, whereas, in *S. pectinata*, the tynes of the furcate setae are distinctly unequal. In *S. pectinata* the dorsal cirri are generally longer than the parapodia and begin in setiger 2; whereas, in *S. rogeri* the dorsal cirri are slightly longer than the parapodia in anterior setigers and slightly shorter in posterior setigers, and they begin on setiger 1. In *S. filiforma* the dorsal cirri are approximately the same length as the parapodia and also begin at setiger 2.

Type and other specimens of members of the family Dorvilleidae, collected by A.E. Verrill in Bermuda and deposited at YPMNH, were examined and were found to differ from the new species. These included: *Dorvillea melanops* (Verrill, 1900), with synonym *Stauronereis erythrops* Verrill, 1900 (also described from Bermuda), and *Schistomeringos polydonta* (Verrill, 1900). *Dorvillea melanops* (including specimens labeled "*Stauronereis megalops*" and *Stauronereis erythrops*) does not have furcate setae. No new examples of these two species were collected in this study.

The only other species of *Schistomeringos* reported from Bermuda, *S. polydonta*, has furcate setae with distinctly unequal tynes, described as "unequally bifid" by Treadwell (1921, p. 121, text-figure 437) and has a dentition pattern distinct from *S. rogeri*; with numerous sharp teeth, about 35-40 per row of the maxillae. The new species also differs from *S. polydonta*, as redescribed by Treadwell (1921, p. 121, Text-Figure 436), as it has no simple spines. Hartman, (1965) reported *Schistomeringos rudolphi* and *S. R. anoculata* from deep water near Bermuda
The furcate setae of these two species have very unequal tynes.

In his work on Bermuda annelids, Verrill (1900) proposed the generic name *Stauronereis* for a group of dorvilleid species, including some closely related to *S. rogeri* n. sp., and some others species not considered to be as closely related. *Stauronereis* was specifically proposed as a replacement name for *Staurocephalus* Grube, 1855, a name preoccupied by a genus of crustaceans (Verrill 1900). The type of the genus erected by Grube (1855) was *Staurocephalus rubrovitattus* (delle Chiaje, 1928). However, Verrill (1900) stated that the type of *Stauronereis* was *Staurocephalus rudolphi* (delle Chiaje, 1828) as emended by Ehlers. McIntosh (1910) considered the morphological characters of *S. rubrovittatus*, suggested new synonymies, and resolved its troubled nomenclature by removing it along with the other species of *Stauronereis* to the genus *Dorvillea*. It is now *D. rubrovittata*.

As later published by Jumars (1974), *Stauronereis* is rendered an unavailable name, according to the articles of ICZN (2000), by the actions of Verrill (1900). Thus, he proposed the new name *Schistomeringos* for a genus-group, with the type as *Nereis rudolphi* delle Chiaje, 1828, and that did not include *S. rubrovittatus* (delle Chiaje, 1828). This action by Jumars (1974) was based on something that also was recognized by Verrill (1900). Among the species included in *Staurocephalus* by 1900, there were two distinct groups. Verrill (1900) recognized these as a group with long articulated antennae, including *S. rudolphi* (a "...European species", Verrill 1900: 648), and a group including *S. rubrovittatus* with "much shorter articulated antennae" (Verrill 1900:648). As later recognized formally by Jumars (1974), species of the former group can also be distinguished by the presence of furcate setae on at least some setigers.

Verrill (1900) did not report either of *S. rudolphi* or *S. rubrovittatus* from Bermuda, but three new species, *Stauronereis melanops, Stauronereis erythrops*, and *Stauronereis polydonta*. The first two Verrill (1900) thought might be male and female forms of one species and had some characters more like *S. rudolphi* than *S. rubrovitattus*. They are now synonymized with *Dorvillea melanops* (Verrill, 1900). The description of the last was very short and incomplete, but later emended by Treadwell (1921).

Jumars (1974) erected the new genus *Schistomeringos* for all the species with furcate setae that were, at that time, included in *Dorvillea*. These species were: *Schistomeringos rudolphi* (delle Chiaje, 1828), *S. polydonta* (Verrill, 1900), *S. incerta* (Schmarda, 1861), *S. caeca* (Webster and Benedict, 1884), *S. longicornis* (Ehlers, 1901), *S. annulata* (Moore, 1906), *S. neglecta* (Fauvel, 1923), *S. japonica* (Annekova, 1937). *S. furcata* (Hartman, 1953) along with a new species *S. mediofurca* Jumars, 1974. More recently *S. caeca* (Webster and Benedict, 1884) has been placed in *Parougia* (Wolf 1986).

Family Syllidae Grube, 1850 - Subfamily Exogoninae Grube, 1850

Genus ***Exogone* Oersted, 1845**

Type species: Exogone naidina Oersted, 1845

Diagnosis, from Oersted (1845):

Small forms, usually less than 8 mm, palps fused for at least half their length. Prostomium with three antennae, inconspicuous nuchal organs, one pair of tentacular cirri, and pharynx armed with a single tooth. Tentacular, dorsal, and ventral cirri are ovoid. Dorsal cirri may be absent from setiger 2.

There are 41 species known for this genus.

Exogone somersensis n. sp.

Material examined: Two specimens, from the Tynes Bay seagrass bed, Bermuda, station W (see Fig. 3-1), April/May. From one sample.

Holotype: Whole specimen, fixed in 5% formalin, preserved in 70% ethanol. Catalogue number XXXX. Tynes Bay seagrass bed, North Shore of Bermuda Station TB –92-W-WC-7 (32° 18' 30"N, 64° 46' 54"W), May 1992, collected by R. S. Smith.

Paratype: One whole specimen, fixed and preserved as holotype. Deposition location to be determined. Tynes Bay seagrass bed, North Shore of Bermuda Station TB –92-W-WC-7 (32° 18' 30"N, 64° 46' 54"W), May 1992, collected by R. S. Smith.

Description of the holotype: Whole, fixed specimen 3.0 mm in length with 34 setigers. Palps fused dorsally, prostomium rounded to globular. Two pairs of eyes, one conspicuous pair close to posterior margin of prostomium, and an additional small pair (eyespots) medial to these and towards the anterior edge of the prostomium. Three minute, subequal antennae arranged in a row on posterior edge of prostomium (Fig. 3-4a), their bases partly covered by the anterior edge of the tentacular segment. Tentacular cirri minute and papilliform, dorsal cirri papilliform, missing from setiger 2; ventral cirri with rounded lobes, extending slightly past parapodium. Pharynx extending through four setigers, (contracted in the holotype); proventriculus also extending through four setigers,

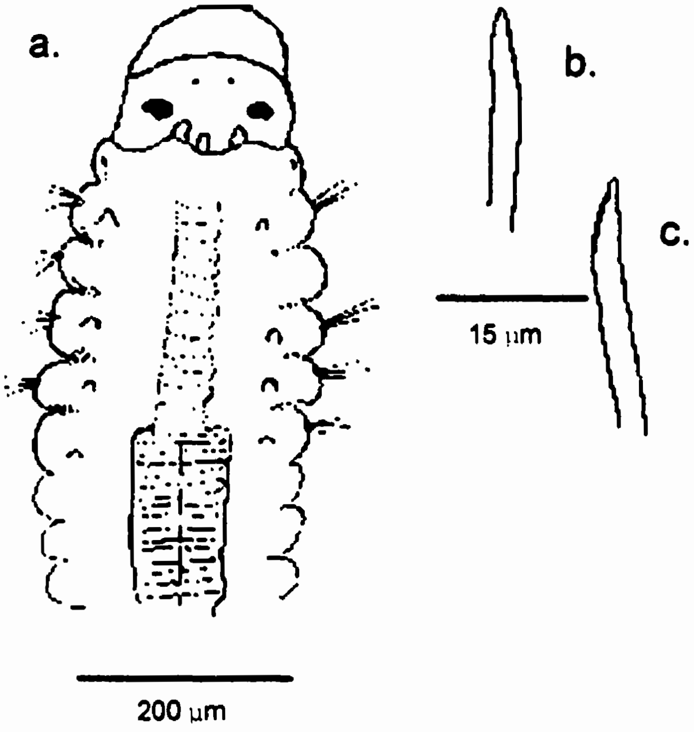

Figure 3-4. *Exogone somersensis* n. s. a) dorsal view of anterior end, b & c) simple setae

with 13 to 16 rows of muscle cells, the anterior three or four less well-defined than those following. Anal cirri short, directed laterally. Setae both compound and simple; compound falcigers with both short and long, toothed, blades in anterior setigers, only short-bladed falcigers in posterior four setigers; simple setae pointed with a finely toothed distal edge (Fig. 3-4b, c), simple setae begin at setiger 13 – 14. Aciculae stout with bluntly rounded tips.

Etymology: The proposed specific name – *somersensis* - refers to Somers Isles, the original name for Bermuda the type locality of this species.

Distribution and Biology: The new species is presently considered rare as only two specimens were found, both in the same core sample. The number of specimens identified so far is too small to support any ideas about seasonal or spatial patterns.

Remarks: There are only three other species of *Exogone* that have minute antennae originating at the extreme posterior margin of the prostomium, *E. microtentaculata* Westheide, 1974, *E. atlantica* Perkins, 1980, and *E. breviantennata* Pascual, Nuñez and San Martin, 1996. The bases of the antennae, in all these species, appear to be partly covered by the tentacular segment. Of these, the new species is most like *E. atlantica*, but differs from it in having the simple setae begin at setiger 13-14, not on setiger 1, as in *E. atlantica*. The new species differs from *E. breviantennata* in the shape as well as distribution of the simple setae. *Exogone somersensis* n. sp. differs from *E. microtentaculata*, from the Galapagos Islands, in several ways. (1) The general shape of the anterior end is different, as the palps are relatively long and tapered in the Galapagos species, whereas they are short and rounded in the new species. (2) The new species does not have S-shaped setae in the posterior segments, as described and figured by Westheide (1974, Abb. 56 K). (3) The blades of the compound setae have fewer teeth in the Bermuda species. (4) The anal cirri in the Galapagos species are long and slender, whereas the anal cirri of the Bermuda species are short.

Altogether, there are about 36 species of syllid now recognized from Bermuda including four species of *Exogone*, *E. dispar* (Webster, 1879), *E. gemmifera* (Pagenstecher ,1862), *E. hebes* (Webster and Benedict, 1884) and *E. verrugera* (Claparede, 1868). They differ most obviously from the new species in the shape of the palps, and position of the antennae. In *E. dispar*, the lateral antennae are located anterior to the eyes, and the median antenna is long. In *E. hebes* the median antenna is also long and fusiform, while the lateral antennae are small and originate at the same level as the eyes. In *E. gemmifera* all antennae are short, but do not originate at the posterior margin of the prostomium and the eyes are posterior to the antennae. In *E. verrugera* the short, unequal antennae are also more anterior on the prostomium, anterior to both the eyes and the eyespots. Both *E. dispar* and *E. verrugera* are reported from *Thalassia* seagrass beds according to Jones et al. (1986).

CONCLUSIONS

In the years since the first systematic explorations of the marine fauna of Bermuda (Verrill 1900, 1901), there have been many changes to taxonomic and systematic practices and theory, as well as additions to the list of species reported from Bermuda (Jones et al., 1986; Appendix 1). Here, three new species are reported from a single seagrass bed. It is likely that these species are more widespread in Bermuda, and possibly will be found in distant locations, although presently they are considered endemic.

It is also likely that there are more new species to be discovered in this and other seagrass beds as well as in the bare sediments of the Bermuda platform. Some of the polychaetes that remain unidentified from the seagrass study are species of *Aonides*, *Ehlersia*, *Eunice*, *Lumbrineris*, *Typosyllis* and *Scolelepis* (Pocklington 2001, Chapter 4, herein). From other studies (Jones et al. 1986) and personal investigations, there are known to be additional unidentified species of *Naiades*, *Mastobranchus*, *Dorvillea*, *Caulleriella*, *Dodecaceria*, *Parasclerochielus*, *Polydora*, *Aricidea*, *Magelona*, *Cossura*, and others. At least a few of these unidentified taxa may be new species and some may even be endemics.

Faunal studies, such as the present one, contribute to very broad areas of contemporary interest and concern such as biological complexity, biodiversity, zoogeography, and phylogenetics. They also lead us to question whether any marine areas can be considered well-known (Sterrer 1998) as far as the many ecologically important and abundant, but very small taxa are concerned. These data also provide direct data to ecological perspectives of polychaetes in subtropical seagrass beds.

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CHAPTER 4

THE POLYCHAETE FAUNA OF A BERMUDA SEAGRASS BED: TEMPORAL AND SPATIAL DISTRIBUTION AND RELATIONSHIP TO TROPHIC STRUCTURE AND LIFE-HISTORY

ABSTRACT

In a study of infaunal macrofauna of a seagrass bed along the North Shore of Bermuda (a coral reef island in the north-west Atlantic), dominated by the manatee grass, *Syringodium filiforme*, the most diverse and abundant taxon was the Class Polychaeta (Phylum Annelida). Polychaetes were found in all samples, over two sampling periods (April/May and September/October). Presence and abundance data from these samples were subjected to several statistical treatments to determine temporal and spatial variation. These analyses indicated that there was a different pattern in species occurrence and abundance between the two sampling periods. They also showed that there was a spatial pattern. The analysis suggested that there was a spatial heterogeneity in September/October that was not evident in April/May.

Each species was assigned to a "feeding strategy" or guild, and the different trophic groups were examined for their numerical importance. Carnivores were the most abundant trophic group at both times; deposit feeders were less abundant. This is in contrast to findings for seagrass beds in similar, fine-grained sediments from shallow water subtropical and tropical ecosystems of continental based ecosystems. Changes in abundance, spatial heterogeneity, and trophic

structure suggest that seagrass beds in Bermuda provide a less stable physical environment for benthic invertebrates than has been hypothesized in general for seagrass beds.

INTRODUCTION

Seagrass beds are prominent bio-structural components of shallow tropical and sub-tropical waters. They are found in association with both continental and island marine ecosystems. Seagrass beds are found on, and are surrounded by unconsolidated sediments. On coral islands, like Bermuda, the sedimentary environment is primarily carbonate - derived from calcareous foraminiferans, mollusks, echinoderms, annelids, cnidarians, and calcareous green algae. These sediments are highly mobile; and undergo considerable disturbance from regular tidal movement and wave action, to extreme disturbance during hurricanes (Morris et al. 1977; VanTussenbroek 1994).

Seagrass beds are especially important in areas adjacent to coral reefs as they stabilize this highly mobile sedimentary regime. The grass beds modify the hydrodynamics of the overlying water. The blades of the plants reduce the rate of water flow at and above the sediment surface, thereby increasing the deposition of fine and light suspended particles, e.g. silt and clay-sized particles (Ginsburg and Lowenstam 1958) and particles rich in organic carbon (Scoffin 1970). Through this "baffle effect" (Ginsburg and Lowenstam 1958), they improve the environment for reef-building corals, which are adversely affected by high sediment loads (Hubbard 1987; 1997) and they modify sediment characteristics to enhance the development of a diverse infaunal community (Orth et al 1984). Seagrasses are also known to enhance the settlement of the larvae of some invertebrates (Ekman 1983; Butman 1987; Grassle and Butman 1989), and this may depend on the same reduction of water flow rates over and through the grass bed.

The root/rhizome systems of seagrasses are important in terms of sediment stability and infaunal diversity (Orth et al 1984). This system can extend from millimeters to tens of centimeters below the sediment-water interface, and physically holds the sediments in place (Orth 1977). Such extensive systems provide complex and varied habitats for infaunal organisms (Orth 1971; 1977;

1992; Orth et al 1984; Stoner 1980). Besides reducing the likelihood of organisms being washed away, they also act as a barrier to large burrowing predators such as sea stars, crabs, sea cucumbers and fish (Orth et al.1984). In an examination of the macrofauna microhabitats within a seagrass meadow in north Florida, Lewis and Stoner (1983) determined that at least 67% of the individuals and 80% of the macrofaunal species collected were found in direct association with sediments held by the plants. It is here that most polychaetes associated with seagrass are found.

The seagrass blades also contribute to the development of a diverse and unique habitat. They offer substrate to some epifaunal species, and refuge to species living in the water column, such as young fish and squid (Stoner 1980). The blades are fragile and friable and provide food in the form of a constant supply of macroscopic debris and amorphous detrital organic material (Miyajuma et al. 1998). This detritus nourishes herbivorous and bacteriophagous taxa, which in turn recycle nutrients, making them available to the plants and thus encouraging expansion and growth of the vegetation comprising the seagrass bed.

Through the investigation of the different feeding guilds and associations encountered in seagrass beds, the complex food webs of seagrass beds are gradually being elucidated (Hatcher 1997; Ogden 1997). Such trophic relationships have underlined the nursery and refuge functions of seagrass beds for a wide variety of fishes and invertebrates (Butman 1987; Grassle and Butman 1989; Orth et al. 1996). Seagrass beds are also important feeding sites for nocturnal, foraging fish and mobile invertebrates from nearby reefs (Ogden 1997).

The importance of seagrass beds to the health of nearby reefs and to marine biodiversity, in general, cannot be overstated. Along with the positive aspects of the presence of seagrass beds, die off of seagrass beds can have serious consequences. Seagrass bed die off has been linked to increased loads of suspended particles and increased nutrient levels, at least in the short term, and this can be followed by extensive blooms of algae that overgrow sessile organisms (Ogden 1997), and/or phytoplankton blooms that cause lower light transmission. Loss of seagrass habitat also results in increased predation on a variety of invertebrates including commercially important species such as crabs, shrimp, and mollusks (Orth et al. 1984, 1996).

Seagrass beds are traditionally considered to be stable environments in a fairly dynamic ecosystem. However, they are not immune to disturbance. It has recently been reported that they can lose a significant amount of their biomass during severe storms and hurricanes (Posey et al. 1996, Barnes and Hughes 1999), when blade debris or even whole clumps of plants can be transported widely. They can also be subject to disturbance in the form of bioturbation by both resident infauna and mobile organisms such as rays and bottom feeding fish. These organisms have been shown to fully disturb the seagrass rhizosphere (Townsend and Fonseca 1998) producing spatial heterogeneity within seagrass beds. These characteristics would indicate instead, that the seagrass beds are relatively unstable in comparison, for example, with habitats found in other depositional environments, e. g., those found in deeper water, and that they can provide a diversity of small sub-habitats rather than a single, large, uniform habitat. These complexities increase the difficulty in predicting or modeling the effects of both recurrent and stochastic events on the structure, diversity and longevity of seagrass bed communities.

Marine macro-infaunal organisms are very responsive to the physical and biological environment. Physical characteristics such as grain size and organic carbon content of the substrate are major controlling factors to macrofaunal distribution (Boesch et al. 1976; Estes and Peterson 2000), as are factors such as water temperature and current speed (Mann and Lazier 1991), and tidal change (Young and Young 1978). Both predictable as well as episodic events, such as hurricanes, also influence community composition and population dynamics of continental based ecosystems (Posey et al. 1996). Biological factors have all been shown to influence faunal presence and abundance. These include food availability (Wildish 1977; Dauer 1984), inter- and intra-species interactions (Woodin 1974), prey/predator interactions (Young and Young 1978), reproductive timing and larval settlement (Grassle and Grassle 1974; Butman 1987; Grassle and

Butman 1989), pre- and post settlement processes (Olafson et al. 1994), and substrate availability (Shull 1997)

In temperate and boreal systems, some of these factors are known to undergo extreme seasonality. For example, increased temperature, light, and nutrient levels result in plankton blooms that deliver pulses of food to the benthos in spring and autumn (Hargrave 1980). The seasonal changes in some of these factors are less obvious in tropical and subtropical systems. As a result, the role of seasonal changes in the dynamics of community structure and diversity and their effects are not well-documented for tropical and subtropical regions.

In my study, the polychaete component of the macrobenthic community of the North Shore seagrass bed was examined for natural occurring spatial and temporal variation using a variety of multivariate statistical methods. Clarke and Warwick (1994; 1995) presented a variety of statistical methods for evaluating marine communities. Some of their suggested methods were selected for the statistical analysis of the data, e.g., Cluster Analysis, Correspondence Analysis, and Canonical Correspondence Analysis. I focussed on the polychaetes found in the seagrass bed because of their wide variety of feeding modes, their sensitivity to changes in the quality and characteristics of the habitat (Pearson and Rosenberg 1978; Reish 1979; Riddle 1988; Pocklington and Wells 1992), and their numerical abundance. Of the macrofauna found during this study, the polychaetes (Annelida) were numerically dominant over the other phyla, as they represented 32% of the total number of individuals collected. Polychaetes also had consistently higher average number of species per sample (17) than any other phylum (Smith et al. 1998).

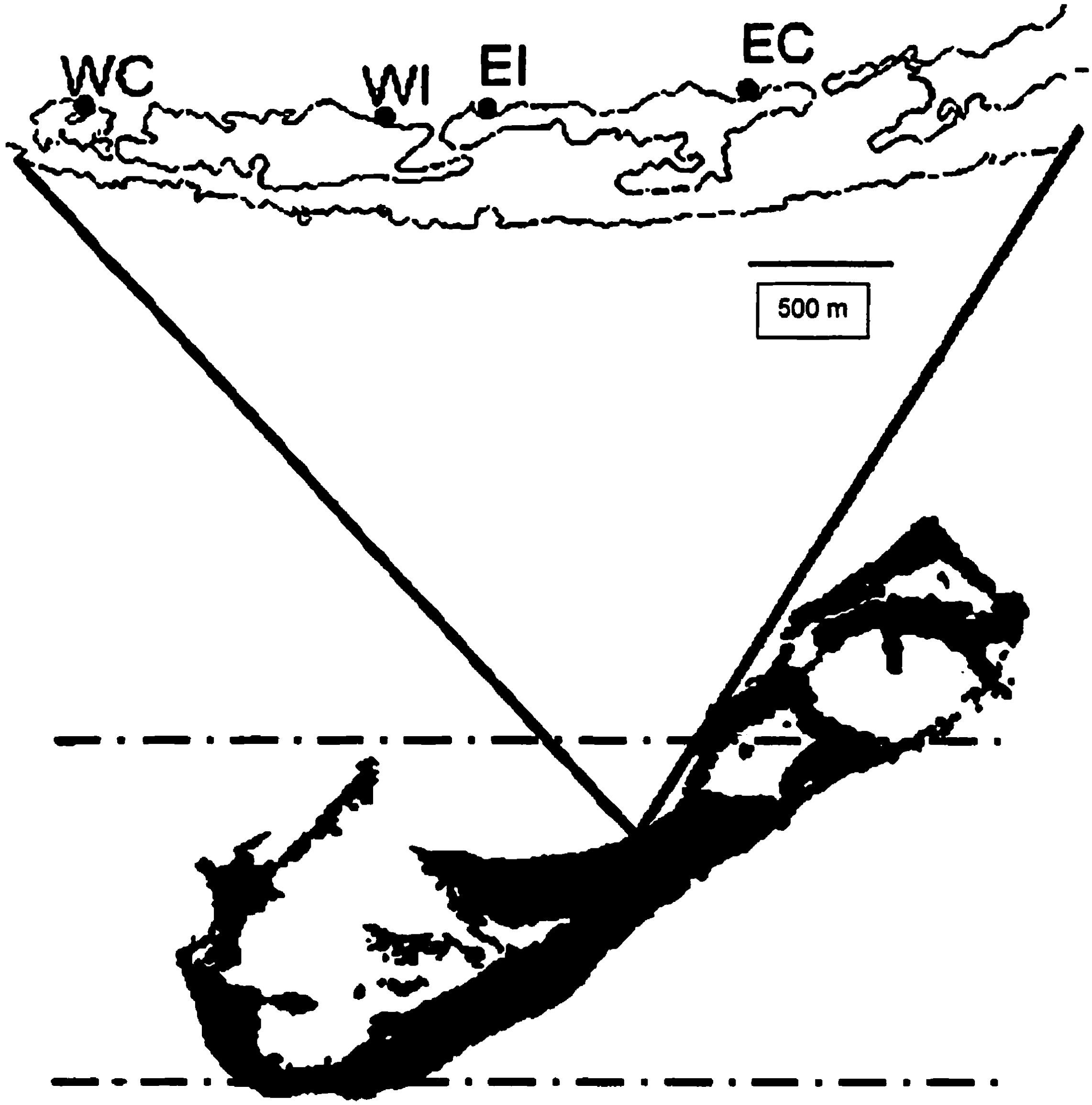
The predominant feeding mode and/or the distribution of feeding modes of the macrobenthic population is an important indicator of the structure of a marine ecosystem. It can indicate for example, the physical properties (e.g. grain size or current velocity) of an ecosystem (Stoner 1980; Pinedo et al. 1997). Life-history traits including reproductive strategies found of the community are also important as this feature can provide important information about the stability of the environment, as disturbance influences community composition and population dynamics (Posey et al. 1996). For example, communities experiencing frequent disturbance are often dominated by species able to quickly colonize an area, and/or deep burrowing taxa that can be found below the disturbed layer and are tolerant of sediment movement. Polychaetes cover the range of life-history strategies found among marine invertebrates as well, they include a wide range of animal/sediment interactions. Life-history strategies range between two extremes. There are species that display highly variable population size with variable and unpredictable mortality; they have some common features such as small size, short life cycle, rapid reproduction and development, and respond rapidly to resources (either food or habitat) availability. On the other end of the continuum are species with a more constant and predictable population size and mortality, they can be larger, with fewer offspring for which they provide some care, and, often live longer. Animals of this strategy are thought to be characteristic of stable environments (Ricklefs 1990). There are a variety of combinations and degree of these strategies seen in different species that influence community dynamics and these too are influenced by such characteristics as dispersal ability (Gaines and Bertness 1993).

This study of the species composition, abundance, spatial and temporal variation, trophic structure, and life-history patterns of polychaetes of the North Shore seagrass bed can be used as an indication of normal variation and structure of a healthy seagrass infaunal community. Such basic information and understanding is necessary to assess increasing anthropogenic influences. Concerns that are of particular interest to the North Shore include increasing ground water derived nutrient inputs and increased amounts of suspended sediments generated in adjacent navigation channels (Smith et al. 1998).

METHODS AND MATERIALS

Study Site:

Figure 4-1. Map of Bermuda with a blow up showing the location of sampling sites on the North Shore



The seagrass beds are distributed along the North Shore of Bermuda (Fig. 4-1) and face the off shore reefs approximately 7 km away; there is an unbroken fetch across the north shore lagoon into the bay for winds blowing from the west-northwest. The bottom is covered by a mixed seagrass and algal bed running both parallel to the shore, and to approximately 300 m off shore. There are small patches of coral reef beyond the bed out as far as the south shipping channel (1.5km offshore), with larger patches of reef beyond. The sediment in this area has a mean size of 0.2mm (range: 0.1 to 1 0mm) (Knap et al. 1991). The seagrass bed is dominated by *Syringodium filiforme*, but also includes the calcareous chlorophytes - *Halimeda incrassata* and *Penicillus capitatus*.

Four stations were selected in the seagrass bed and sampled in both April/May and September/October of 1992 (Smith et al. 1998). Two stations, E and W, approximately 400 m apart, were located more or less in the middle of the seagrass bed (inner stations): E (32^0 18' 78"N, 64^0 45' 97"W); W (32^0 18' 41"N, 64^0 46' 14"W). Two stations, EC and WC, located towards the outer edges of the sea grass bed: one 1km to the east of the east inner site E: (32^0 19' 01"N, 64^0 45 '25"W), and one 1km to the west of the west inner site W (32^0 18' 30"N, 64^0 46' 54"W). All sites were approximately 300 m from the shore in water between 3-9 m deep. The April/May sites were WE, WW, WEC, and WWC and the September/October sites were SE, SW, SEC, SWC. Eight samples, (in two groups of four, 20 meters apart), were taken at each site, on each occasion, using bucket cores (diameter of 26cm, and depth of about 25cm). This size of corer has been found to collect a suitable representation of infaunal organisms (Lewis and Stoner 1981, 1983). The benthic samples were preserved in 5% buffered formalin, then washed on a 0.5 mm mesh sieve in order to recover the greatest number of macro-invertebrates (Reish 1959; Lewis and Stoner 1981). A total of 64 samples were examined for this study.

Environmental Variables

Environmental variables recorded at the site include water temperature, percent of seabed covered by *Syringodium filiforme*; number of plants/m^2 of the calcareous algae *Halimeda* *incrassata* and *Penicillus capitatus* (Tables 4-1and 4-2). These data were extracted from Smith et al. (1998). The estimated percent coverage of the sediment by the seagrass *Syringodium filiforme* was approximately 45% (range 30 to 60) in April/May and it decreased to approximately 33% (range 22 to 50) in September/October. The average number of individuals of the calcareous green alga –*Penicillus capitatus* also decreased from 22.5/m^2 in spring, (range 12.0 to 35.0 ind./m^2) to 11.0/m^2 in fall (range 5 to 17 ind./ m^2). (Table 4-2). In contrast, the number of individuals of the calcareous alga, *Halimeda incrassata* increased from 2.5 individuals /m^2 in spring (range: 0 to 6.0 individuals /m^2) to a mean of 7.5 individuals/m^2 in fall (range: 2.5 to 12.0 individuals/m^2) (Table 4-2).

Water temperature at the sample site was 21 – 22 ^{0}C in spring and 22 – 24 ^{0} C in fall.

Community Structure

In this study, only the polychaete fraction of the macro-benthos was analyzed and all specimens were identified to species where possible. Number of individuals per species was recorded for each sample at each time (Appendix 2). Those taxa that could not be identified to species were coded as Species A, B. etc, and in some cases were described as new (Chapter 3). The number of families and species per station per sampling period (Table 4-3) and percent dominance at both the species and family level were calculated (Table 4-4), and examined seasonally and spatially.

Statistics

Those species with less than a total of 10 individuals, and/or occurring at fewer than four replicates were removed from the data set. This was done because similarities between rare species have little meaning (Clarke and Warwick 1994 Chap. 2, p. 2-6), and if these values are left in the matrix they can confuse the pattern. The abundance data were $\log_{10}$ (x +1) transformed before classification in order to make the frequency distribution more symmetrical (Sokal and Rolf 1981 p. 382). The transformed data were subjected to various analyses with different objectives. Cluster Analysis using the Bray-Curtis similarity co-efficient (Bray and Curtis 1957) was used to determine the similarity of replicates for sites and dates. Correspondence Analysis and Canonical Correspondence Analysis (CCA) were used to make a direct interpretation of possible relationships among species, stations and environmental variables. CANOCO version 3.12, (ter Braak 1991; 1995) was used for both Correspondence Analysis and Canonical Correspondence Analysis. These analyses were performed on 38 species from 64 samples. Correspondence Analysis uses reciprocal weighted averaging to find an inherent structure within a data set, while in Canonical (or constrained) Correspondence Analysis, the ordination axes are forced to represent a relationship between species and the environmental data.

Ecology

In order to understand food web relationships (trophic structure) of the polychaete fraction of the benthic community, the species were assigned to major feeding guilds e.g. carnivores, herbivores, omnivores, deposit feeders, and filter feeders using Fauchald and Jumars (1979). Percent dominance by abundance per feeding guild per sampling period was determined. Whatever information on reproduction for each species found in the study was available in the literature (Schröder and Hermans 1975; Strathmann 1987; Giangrande 1997), was also assembled and the results were examined for seasonal and temporal patterns.

Table 4-1. *Estimated Percent Coverage by *Syringodium filiforme* Per Station

SEASON	STATION	% COVER	SEASON	STATION	% COVERAGE
APRIL/MAY	WW	~30	SEPT/OCT	SW	~22
	WWC	~30		SWC	~22
	WE	~60		SE	~40
	WEC	~60		SEC	~50
		AVG = 45%			AVERAGE = 33 %

Table 4-2. *Density of *Penicillus capitatus* and *Halimeda incrassata* Plants Per Station

SEASON	STATION	AVERAGE NO. OF INDIVIDUALS/m^{2}*	
		P. capitatus	*H. incrassata*
APRIL/MAY	WW	22.0	0
	WWC	12.0	1.0
	WE	35.0	6.0
	WEC	20.0	3.0
		AVERAGE = 22.5	AVERAGE = 2.5
SEPT/OCT	SW	10.0	2.5
	SWC	17.0	12.0
	SE	12.0	5.0
	SEC	5.0	12.0
		AVERAGE = 11.0	AVERAGE = 7.5

**Data extracted from Figures 1.9 a & b (Smith et al.1998)*

RESULTS

Abundance and Species Richness

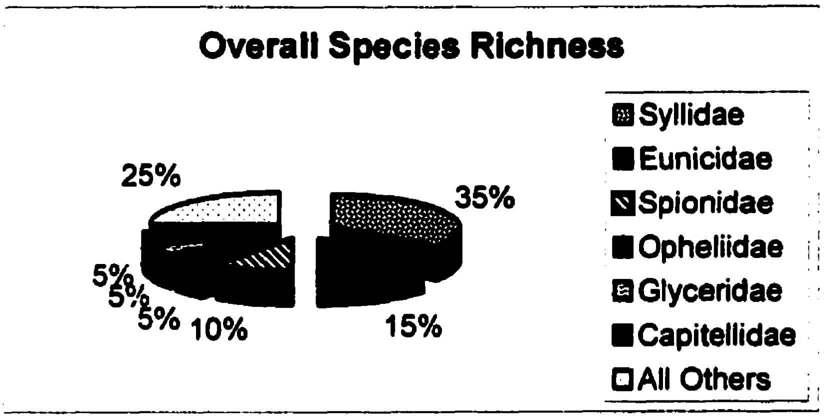
In all, 4618 identifiable individual polychaetes distributed among 51 species and 18 families were distinguished (Appendix 2 and 3); 2094 individuals were collected in spring and 2524 in fall.

Table 4-3. Individuals/0.053m ^{2}, Species and Families Per Station Per Season

SEASON	STN.	MEAN NO OF IND./0.05m ^{2}	SPECIES RICH/STN	FAM./ STN.	NO. SYLLID SPECIES/ STN.
APRIL/MAY	W	59.25	34	17.00	7.00
	WC	56.50	35	16.00	8.00
	E	76.125	31	17.00	8.00
	EC	69.875	32	18.00	8.00
Species Total 47 in Spring		X = 65.44	X = 33.50	X= 17.00	X = 7.75
SEPT/OCT	W	73.375	33	18	8.00
	WC	95.625	33	17	7.00
	E	66.5	31	18	6.00
	EC	78	28	15	6.00
Species Total 44 in Fall		X = 78.375	X = 31	X = 17.20	X = 6.25

Of the 51 species, 47 were collected in the spring with an average of 33.50 per station, and 44 were collected in the fall with an average of 31.25 per station and. Overall, 35% of the species belonged to one family the Syllidae. The next most species rich families were, in descending order: Eunicidae, Spionidae, Opheliidae, and Glyceridae. The remaining families were represented by one species each (Fig. 4-2).

Figure 4-2. Overall species richness per family



The family Syllidae was also the most numerically abundant family, as six of the ten most numerically abundant species were syllids. There were 1681 individuals of this family that accounted for 36.4% (33.8% in spring and 38.5% in fall) of the total number of polychaetes collected. Other families with large numbers of individuals were Dorvilleidae, Eunicidae, Amphinomidae, Opheliidae, Spionidae, and Lumbrineridae (Fig. 4-3). These seven families accounted for approximately 90% of all individuals collected during the study. Those remaining were distributed among the other eleven families, the Cirratulidae, Hesionidae, Nereidae, Terebellidae, Glyceridae, Capitellidae, Sabellidae, Pectinariidae, Arabellidae, Serpulidae, and Sigalionidae

Figure 4-3. Overall numerical abundance per family

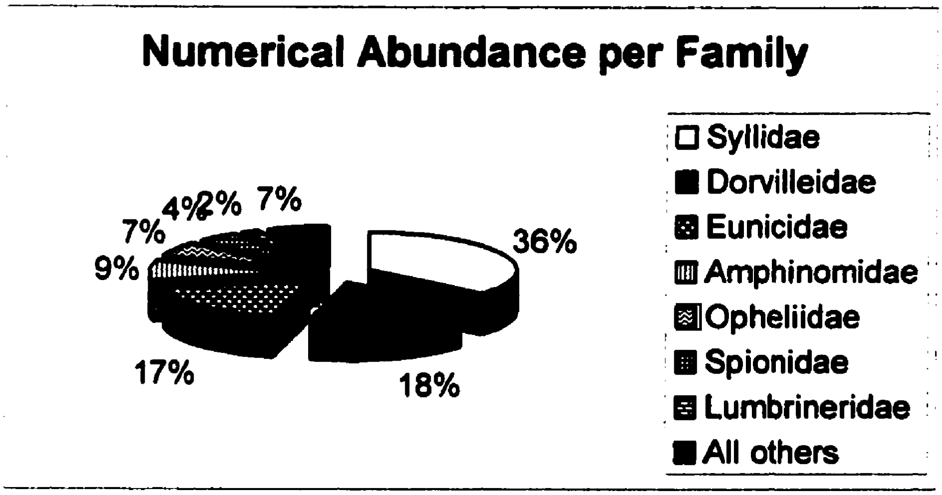
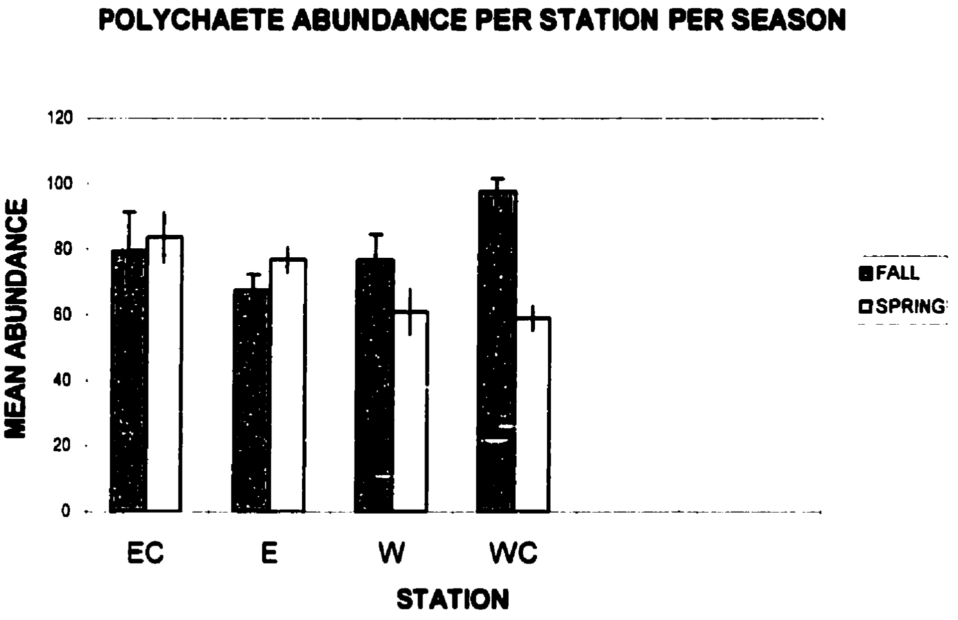


Figure 4-4. Mean abundance of polychaetes per station per season *

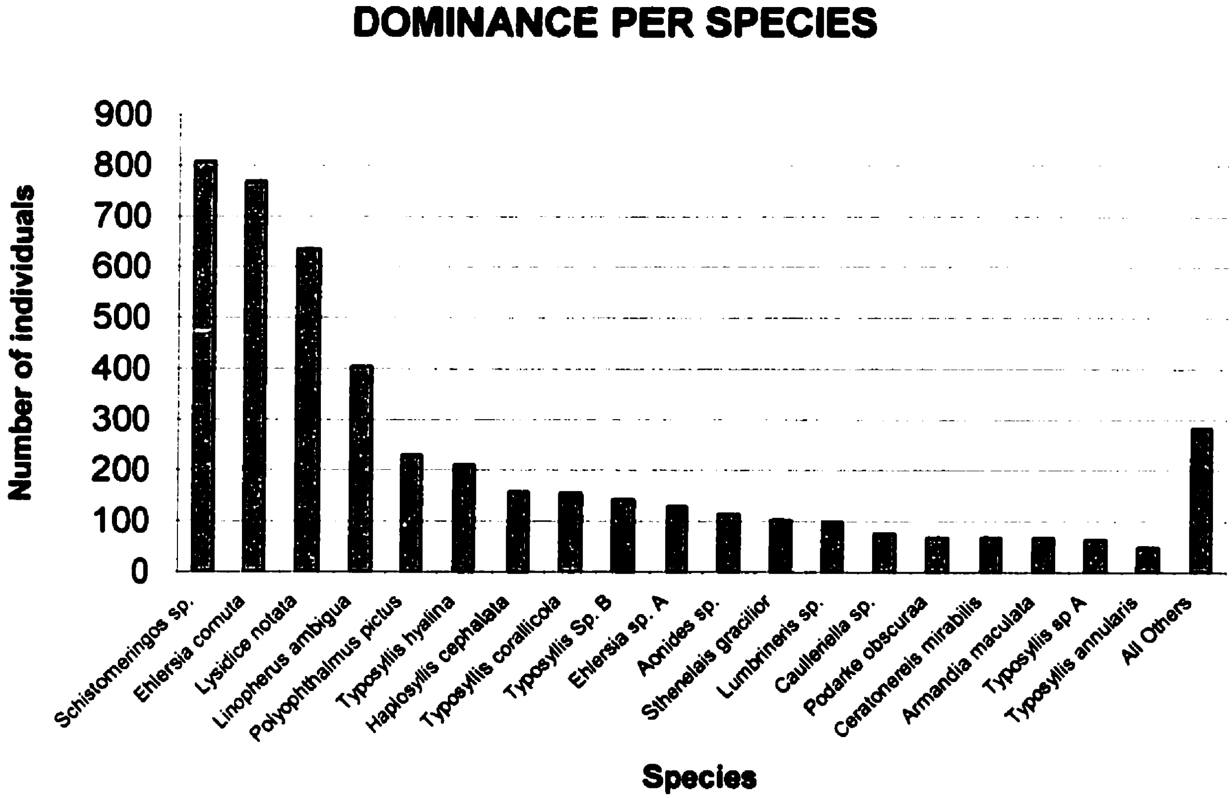


*(To calculate number of individuals per square m, we can multiply number of individuals per grab by 188.6 or individuals per station by 23.6).

Figure 4-4 shows more clearly the relative mean abundance of animals (bars indicate Standard Error) at the different sites in each season. For example, on the eastern side of the seagrass bed there were slightly more animals in spring than in fall, whereas on the western side of the seagrass bed there were more animals in fall than in spring.

Though at the level of family, the Syllidae had the most individuals, at the level of species, the single most numerically abundant species was a representative of the family Dorvilleidae, *Schistomeringos* sp. a previously undescribed species (see Chapter 3). This species represented 17% of the total number of individuals collected and was found to be slightly more abundant in spring than fall. Other abundant species included the syllid *Ehlersia cornuta*, the eunicid *Lysidice notata*, the amphinomid *Linopherus ambigua*, and the opheliid *Polyophthalmus pictus*, representing 16%, 13%, 8% and 4.7% respectively, of the total number of individuals (Figure 4-3). These species were more abundant in fall.

Figure 4-5. Overall species dominance by total abundance in all samples



Temporal variation

The species richness was greater in the spring than in the fall but not substantially so (47 vs. 44). Four species, *Clymenella* sp. A, *Pectinaria regalis*, *Synsyllis longigularis*, and *Typosyllis* sp. B were found scattered throughout the seagrass bed in fall but not in spring, and seven species, *Eunice vitatta*, *Eusyllis longosetosis*, *Exogone* sp. A, *Poecilchaetous bermudensis*, *Prionospio cristata*, *Typosyllis* sp. A., and an unidentified maldanid, were found in spring but not in fall. The average number of families in spring and fall was approximately the same (Table 4-3). The average number of species per station was 33.5 in spring (range 31-35) and 31.2 in fall (range 28-

33) (Table 4-3). The number of species did not change at the inner stations between spring and fall but did at the edge stations. Overall, the eastern edge had the fewest number of families, but four more species in spring than fall (increase of 14.3%) and 2 more at the western edge an increase of 6%. The number of species between spring and fall in the inner stations did not vary.

There were approximately 23% more individuals in the fall than in the spring (2524 vs. 2094). About half of the species were represented by a higher abundance of individuals in the spring and half with higher abundance in the fall. With the exception of *Schistomeringos* sp., the six most numerous species were more abundant in fall (Fig.4- 6).

Spatial variation

The eastern edge of the seagrass bed had fewer species but higher abundance than the western edge in spring. The inner sites were intermediate, i.e., there was a gradation in the number of species decreasing from east to west. In fall, numerical abundance increased from east to west (Fig. 4-4). In fall, *Lysidice notata, Ehlersia cornuta* and *Linopherus ambigua* were the dominants on the eastern edge and *Ehlersia cornuta* and *Schistomeringos* on the western edge. *Ehlersia cornuta, Lysidice notata and Schistomeringos* sp. were co-dominants on the eastern edge in spring and only *Schistomeringos* sp. and *Lysidice notata* were the most numerically abundant species on the western edge.

The numbers of *Polyophthalmus pictus*, a sub-surface, deposit-feeding polychaete did not vary much between stations or seasons. Other numerically important species such as *Ehlersia* sp. and *Syllis (Typosyllis)* sp. B and a few slightly larger species such as, *Eunice gagzoi*, *Arabella iricolor*, and *Dasybranchus lumbricoides*, were more abundant on the eastern edge of the seagrass bed.

Figure 4-6. Species dominance by season

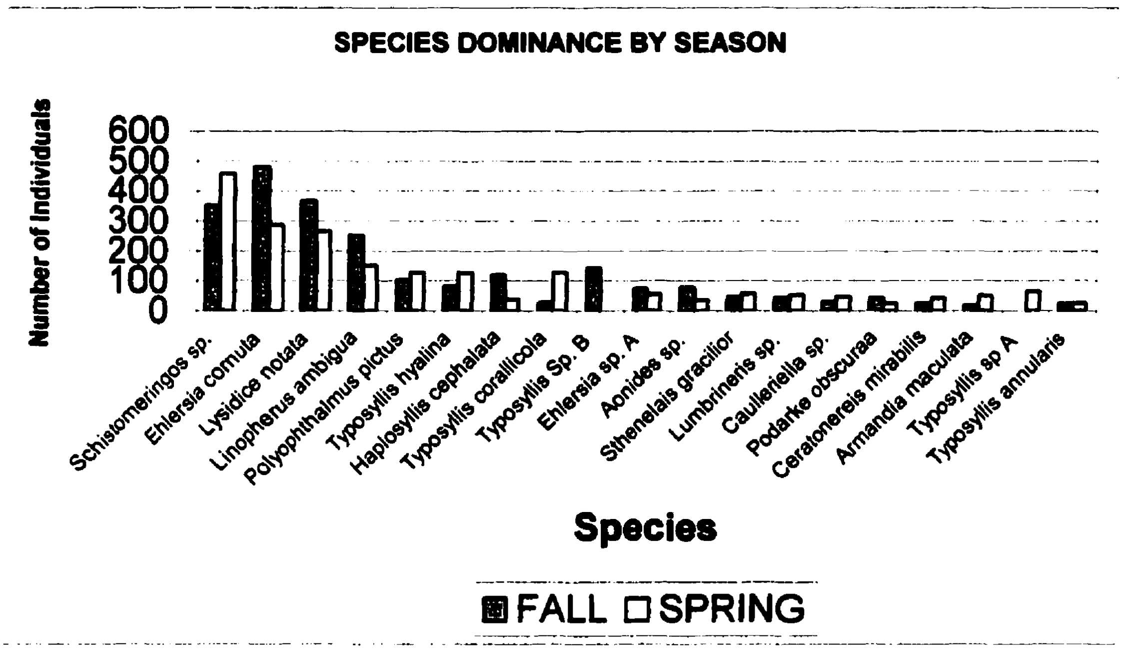


Figure. 4-7. Dominant species per station a = spring, b = fall

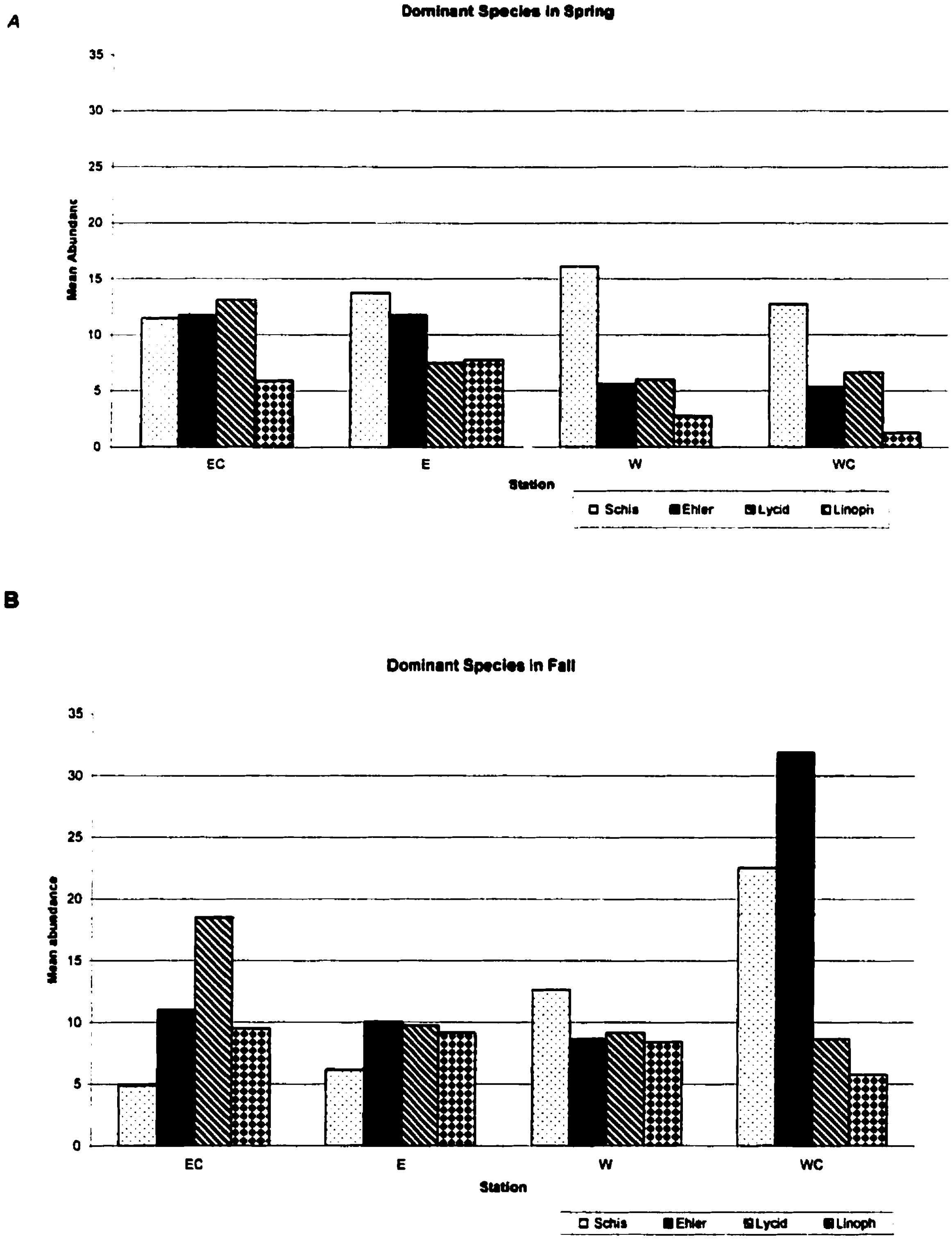


TABLE 4-4. Abundance of Dominant Species per Station per Season (upper number is average number of individuals per grab, lower number is the percentage of the total number of polychaetes collected at the station this species represents).

SPECIES	SEC	SE	SW	SWC	FALL. TOT (2524)	WEC	WE	WW	WWC	SPR. TOT (2094).
Fam. Dorvilleidae	4.9	6.13	12.63	22	365	11.5	13.75	16.13	12.75	433
Schistomeringos sp.	6.13	9.07	16.48	22.52		16.17	18.03	40.06	22.32	
Fam. Syllidae	11	10	8.63	31.88	492	11.75	11.75	5.62	5.38	276
Ehlersia cornuta	13.84	14.82	11.26	32.65		19.52	15.41	13.98	9.41	
Fam. Eunicidae	18.5	9.75	9.13	8.63	368	13.13	7.5	6	6.63	266
Lysidice notata	23.27	14.44	11.9	8.83		18.45	9.84	14.91	11.60	
Fam. Amphinomidae	9.5	9.13	8.38	5.75	262	5.88	7.75	2.75	1.25	141
Linopheros ambigua	11.95	13.52	10.93	5.90		8.26	10.17	6.83	2.19	
Fam. Opheliidae	3.25	0.88	3.75	5	103	3.13	5.63	3.5	3.75	128
Polyophthalmus pictus	3.93	1.30	4.5	5.12		4.39	7.38	8.70	6.57	

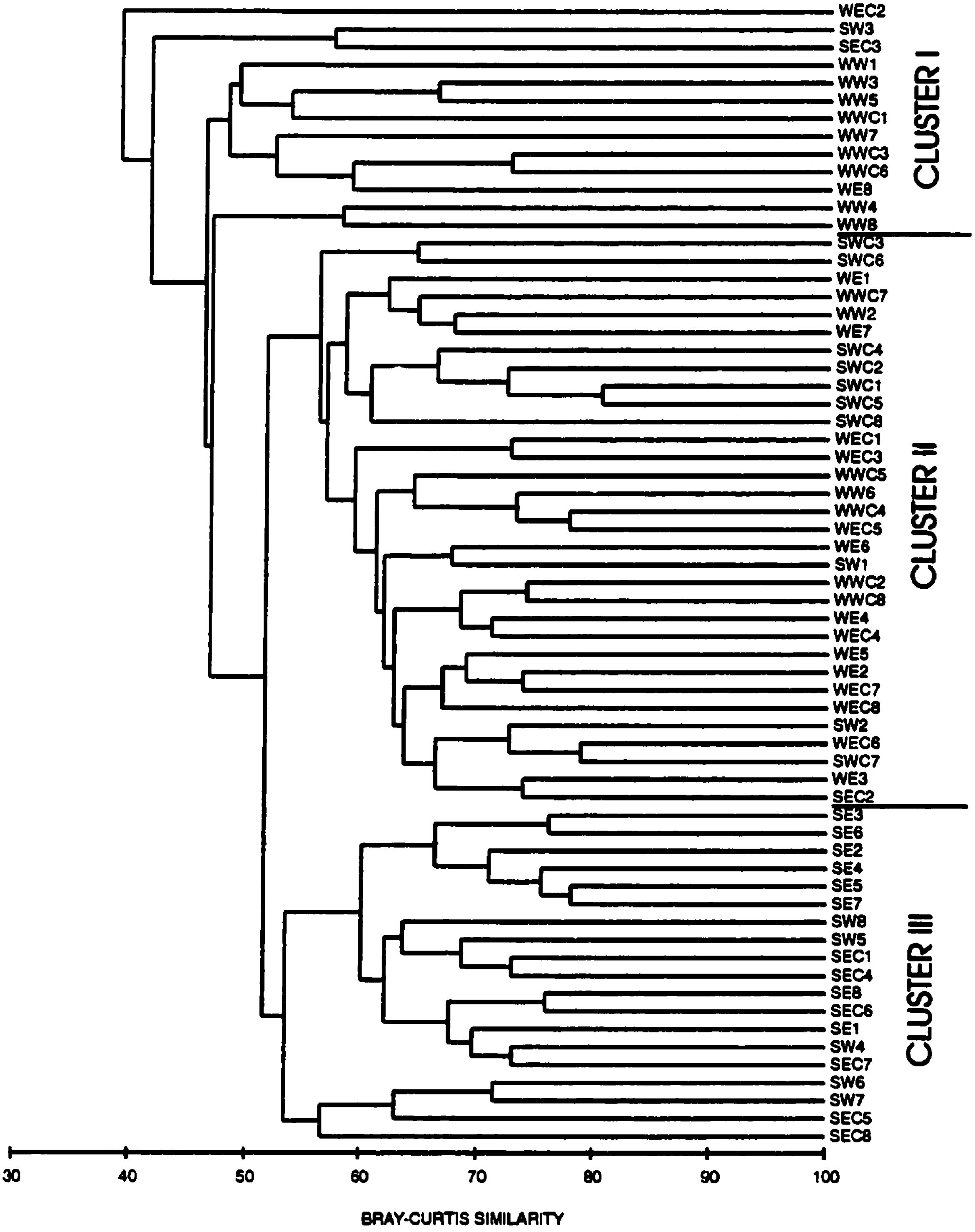
Cluster Analysis

The dendrogram produced in the Cluster Analysis (Fig. 4-8) has three main clusters with a few pairs, and lone outliers. The components of Cluster I are not united at a high similarity level. These are primarily individual grabs (replicates) from April/May samples at the west stations (WWC, WW) with one or two from stations WE, WEC, SW and SE. They are characterized by having lower numbers of individuals than other stations, and by having S*histomeringos* sp. as the numerically dominant species. This is in contrast to Sept/Oct. when *Ehlersia cornuta, Lysidice notata*, and *Linopheros ambigua*, were more abundant at these sites. (Table 4-4).

Cluster II includes the rest of the April/May samples from the stations WE, WEC, WW, and WWC, it also includes six of the samples taken at the western contour (SWC) of the grass bed in September/October, two samples from SW, and one from SEC. This cluster is divided into two sub-clusters that, in large part, separate the SWC samples from the spring samples. Six of these SWC samples are more similar to the spring stations than to other fall samples. Station SWC has high numbers of *Schistomeringos* sp. such as are found at all stations in the spring and this might account for the association of this group of samples with spring samples.

Cluster III includes only samples taken in Sept/Oct. It has four sub-clusters. One subcluster contains 6 of the 8 samples from the inner site on the east side (SE samples), these show a greater than 60 % similarity, one subcluster with 4 replicates from SEC. The rest of the samples from SEC and SW are intermingled in the other subclusters.

Figure 4-8. Cluster analysis based on species and abundance using Bray curtis Similarity Coefficient.



Correspondence Analysis and Canonical Correspondence Analysis

Season (Sept/Oct and April/May), NEAR and FAR (the edges of the seagrass bed), EAST I and WEST I (inner sites of the seagrass bed), (H) number of *Halimeda incrassata* plants, (P) number of *Penicillus capitatus* plants, (S) percent cover by *Syringodium filiforme*, and (T) temperature (i.e., all variables) were included as environmental factors in both the Correspondence Analysis and the Canonical Correspondence Analysis (Figs 4-9 & 4-10). No variables were selected over and above any others (all variables selected). The numbers in the lower plots of Figs 4-9 and 4 -10, correspond to the species in Table 4-5. From the patterns generated in the CA, and CCA and shown in the upper plots of Figs 4-9 and 4-10 respectively, the following observations were made.

In both cases, the first ordination axis (X-axis) accounted for the greatest amount of variance explained by the analysis (eiganvalues of 0.128 in both cases or 12.8% in CA; 12.8% in CCA). The samples taken in Sept./Oct. had high positive scores on this axis and the April/May samples have modest negative scores. The second ordination axis (Y- axis) accounted for the next amount of variance (eiganvalues of 0.062 and 0.060 or 6.2% and 6.0% respectively). The samples taken at the edges of the seagrass bed, NEAR and FAR, have moderate to high positive scores on this axis while the inner sites of the seagrass bed, EAST I and WEST I, have negative scores on this axis.

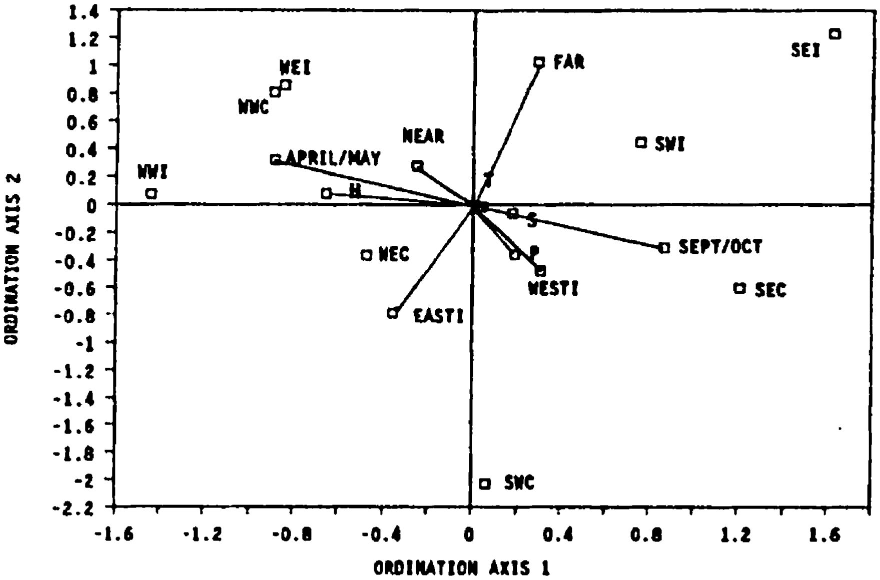
Factors such as (T) temperature, (S) percent coverage by *Syringodium filiforme*, and (P) number of *Pennicillus capitatus* plants show a very slight positive correlation with Axis 1, and very slight negative correlation with the second ordination axis. The number of *Halimeda incrassata* plants (H) shows a negative correlation with the first ordination axis and a very slight positive correlation with the second ordination axis. With regard to the percent cover by *Syringodium filiforme*, this corresponds positively (albeit weakly) to the locations WEC (60%) and SEC (50%). The difference in percent coverage between the two seasons is small (only 12%), therefore the *Syringodium filiforme* vector (S) is small, it has low positive scores on Axis 1 and low negative score on Axis 2. The score for the number of *Pennicilus capitatus* plants (P) is similar to the score for *Syringodium* *filiforme* with regard to the first axis, but is slightly more negative in Axis 2. There is a slight correspondence of P with location. For example, there were more *Pennicilus capitatus* plants at the inner sites than the edge sites in April/May (22 and 35, *vs.* 12 and 20 plants/m^2 in fall). This was observed on only the eastern side of the seagrass bed at the Sept./Oct. sampling period. On the western side, in Sept./Oct the number of *Penicillus capitatus* plants was higher at the edge (17 plants/ m ^{2}) than at the inner site (10 plants/m^2).

In Correspondence Analysis, the centroids for the species: *Typosyllis sp. B* (32*)*, *Pectinaria regalis* (19), *Eunice rubrivitatta* (9), *Haplosyllis cephalata* (30), *Eunice* sp. (7), *Podarke obscura* (14) and *Ehlersia cornuta* (35) have positive scores for Axis 1 and negative scores for Axis two, (similar to Sept./Oct. and inner sites). *Typosyllis sp. B* (32*)*, *Pectinaria regalis* (19) for example, show the highest scores on Axis 1 and were closer to Sept./Oct. as they were not found in April/May. The centroids for *Branchiosyllis lamellifera* (29), *Arabella iricolor* (2), *Dasybranchus lumbricoides* (4), *Aonides sp.* (25), *Ehlersia* sp. (36), and *Sthenelais gracilior* (22) have positive scores for both Axis 1 similar to Sept./Oct., and Axis 2, similar to edges of seagrass bed. Centroids for *Scolelepis* sp. A. (26), *Spirorbis formosus* (21), *Glycera oxycephala* (13), *Aonides mayaguezensis* (24), *Typosyllis corallicola (*34), *Glycera abranchiata* (12), and Sabellidae (20) have negative scores on the first ordination axis and positive scores on the second ordination axis, similar to April/May and the western edge of the seagrass bed. Lastly, Syllidae (27), *Notomastus latericeus* (3), *Typosyllis* sp. A (28), *Ungulosyllis annularis* (31), *Loimia medusa* (38), *Armaqndia maculata (*17), *Polyophthalmus pictus* (18), *Nematonereis hebes* (11) and *Terebellides stroemi* (37) have negative scores on both the first and second ordination axes similar to April/May and the eastern edge. The centroids for *Typosyllis* sp. A (28) and *Eunice rubrivitatta* (9) score similar to SWC

The numerically most abundant species were found, for the most part, to be widespread throughout the seagrass bed and present at both sampling times. The centroids of these species, e.g., *Schistomeringos* sp. (6), *Linopheros ambigua* (1), *Lysidice notata* (10), *Ehlersia cornuta* (35), *Nematonereis hebes* (11), and *Caulleriella* sp. (5) are found close to the origin of the two axes with only slight emphasis in one direction or another indicating that they are slightly more abundant at one site or season than another.

In the Canonical Correspondence Analysis, the sites WWC, WEI, WWI, April/May, the number of *Halimeda* plants, and NEAR show correspondence with abundance and distribution of *Schistomeringos, sp.* (6) *Armandia maculata* (17), *Lumbrineris sp.* (15), *Typosyllis corallicola* (34), *Notomastus latericeus* (3), *Spirorbis formosus* (21), and Syllidae (27). The centroids of these species have scores similar to these sites and environmental variables. *Aonides mayaguezensis* (24), on the other hand, corresponds only weakly with these sites and environmental variables. The abundance and distribution of *Branchiosyllis lamellifera* (29), *Ehlersia* sp. (36), and *Aonides sp.* (25) corresponds with FAR (the outer edges of the seagrass bed), whereas those of *Typosyllis* sp. B (32) and *Sthenelais gracilior* (22) correspond with SWI. *Ehlersia cornuta* (35), *Haplosyllis cephalata* (30), *Podarke obscura* (14), and *Nematonereis hebes* (11) correspond with each other and percent coverage of *Syringodium*, and weakly with numbers of *Penicillus* plants. These 11 species score positively along with Sept./Oct. on the first ordination axis. Stations WEI, WEC, WWI, and WWC are more similar to each other in species and abundance in April/May than SEI, SWI and SEC in Sept./ Oct. As shown in the cluster analysis, SWC is different from the other stations sampled in Sept../Oct. The centroids for the following species were found closer to the inner site on the west sides and the fall sampling period, Sept./Oct.: *Ehlersia cornuta* (35), *Haplosyllis cephalata* (30), *Podarke obscura* (14), *Pectinaria regalis* (19), *Eunice rubrivitatta* (9), while *Loimia medusa* (38), *Ungulosyllis annularis* (31), *Typosyllis hyalina* (33), *Nematonereis hebes* (11), and *Polyophthalmus pictus* (18) scored closer to the inner site on the eastern side and the spring sampling period, i.e., negative on both the first and second ordination axes.

Figure 4-9. Correspondence Analysis (CA)


TYNES BAY POLYCHAETES, CA
Stations and Environmental Variables

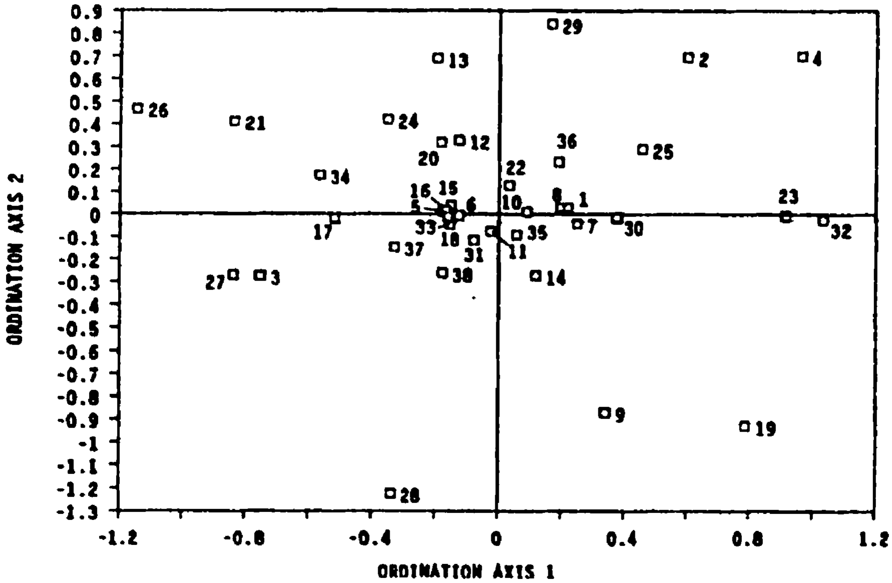
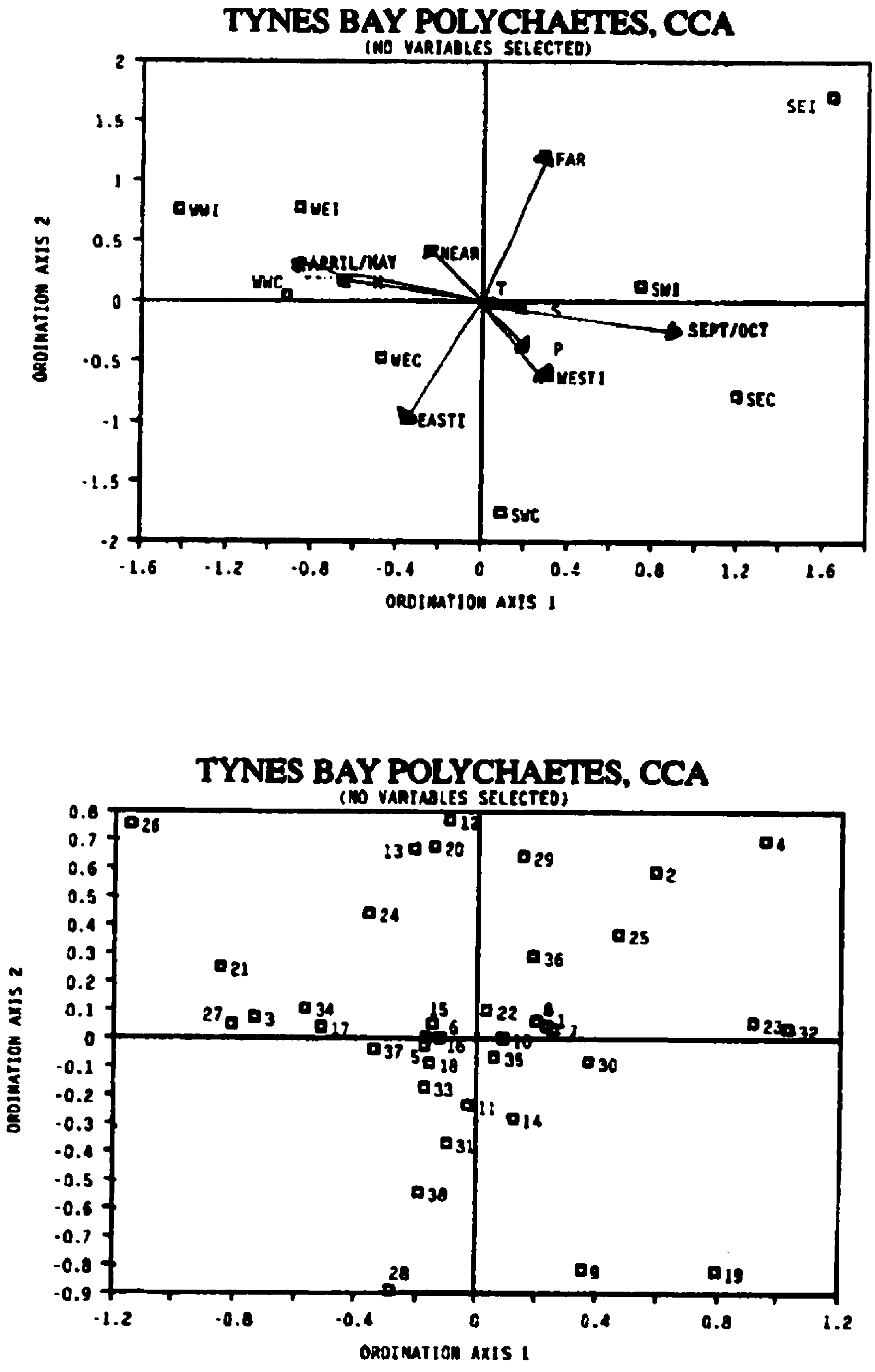

TYNES BAY POLYCHAETES, CA
Species

Figure 4-10. Canonical Correspondence Analysis (CCA)



Feeding Guilds

Table 4-5. Feeding Guilds of Polychaetes of North Shore Seagrass Bed

(Burrowing deposit feeder = BDF; Surface deposit feeder = SDF)

Species No.	SPECIES	FEEDING GUILD	Species No.	SPECIES	FEEDING GUILD
1	*Linopherus ambigua*	Carnivore	21	*Spirorbis formosus*	Filter Feeder
2	*Arabella iricolor*	Carnivore	22	*Sthenelais gracilior*	Carnivore
3	*Notomastus latericeus*	BDF	23	*Spionidae*	SDF
4	*Dasybranchus lumbricoides*	BDF	24	*Aonides mayaguezensis*	SDF
5	*Caulleriella sp.*	BDF	25	*Aonides sp. A.*	SDF
6	*Schistomeringos sp. A*	Carnivore	26	*Scolelepis sp. A*	SDF
7	*Eunice sp.*	Carnivore	27	*Syllidae*	Omnivore
8	*Eunice gagzoi*	Carnivore	28	*Typosyllis sp. A.*	Carnivore
9	*Eunice rubrivitatta*	Carnivore	29	*Branchiosyllis lamellifera*	Carnivore
10	*Lysidice notata*	Omnivore	30	*Haplosyllis cephalata*	Carnivore
11	*Nematonereis hebes*	Omnivore	31	*Typosyllis annularis*	Carnivore
12	*Glycera abranchiata*	Carnivore	33	*Typosyllis hyalina*	Carnivore
13	*Glycera oxycephala*	Carnivore	34	*Typosyllis corallicola*	Carnivore
14	*Podarke obscura*	Carnivore	32	*Typosyllis sp. B*	Carnivore
15	*Lumbrineris sp.*	Carnivore	35	*Ehlersia cornuta*	Carnivore
16	*Ceratonereis mirabilis*	Carnivore	36	*Ehlersia sp.*	Carnivore
17	*Armandia maculata*	BDF	37	*Terebellides stroemi*	SDF
18	*Polyophthalmus pictus*	BDF	38	*Loimia medusa*	SDF
19	*Pectinaria regalis*	BDF			
20	*Sabellidae*	Filter Feeder			

Thirty-eight species were assigned to feeding guilds (primary feeding modes) based on their individual feeding strategies (Table 4-5). Just over half (53.8%) of the species found in the seagrass bed study were jawed mobile carnivores (Fig. 4-11). Deposit feeders, both burrowing deposit feeders (BDF) and surface deposit feeders (SDF) accounted for the next most species-rich group (30%), and filter feeders and omnivores accounted for the least species-rich groups at 7.5% each (Fig. 4-11), no facultative herbivores were identified in the species found.

When the distribution of the feeding modes on a per season basis is examined (Fig. 4-12), it can be seen that there is a slight difference in the relative abundance of the different trophic groups between seasons. For example, carnivores were more abundant in the fall and burrowing deposit feeders were more abundant in spring, whereas the abundance of surface deposit feeders and filter feeders do not show between season variation. Spatially, microphagous carnivores such as *Schistomeringos* sp. A. and *Ehlersia cornuta* are most abundant at station WC in fall, while burrowing deposit feeders such as *Polyophthalmus pictus*, *Armandia maculata, Caulleriella* sp., *Dasybranchus lumbricoides* and *Notomastus latericeus* as a group were more abundant at stations W and WE in fall.

Reproductive Patterns

Twenty-two species could be categorized by reproductive pattern (Table 4-6). All but six (a tube brooder and five species that undergo direct development) have some known characteristics of their reproductive pattern that suggest free living larvae, or this reproductive mode is known definitely. This latter reproductive mode (i.e. those with pelagic larvae) is usually a characteristic of species with good dispersal capability, i.e. they are free spawners or they are epitokous, they may reproduce frequently, may produce large numbers of young, and are usually short lived.

Figure 4-11. Percent dominance by feeding guild

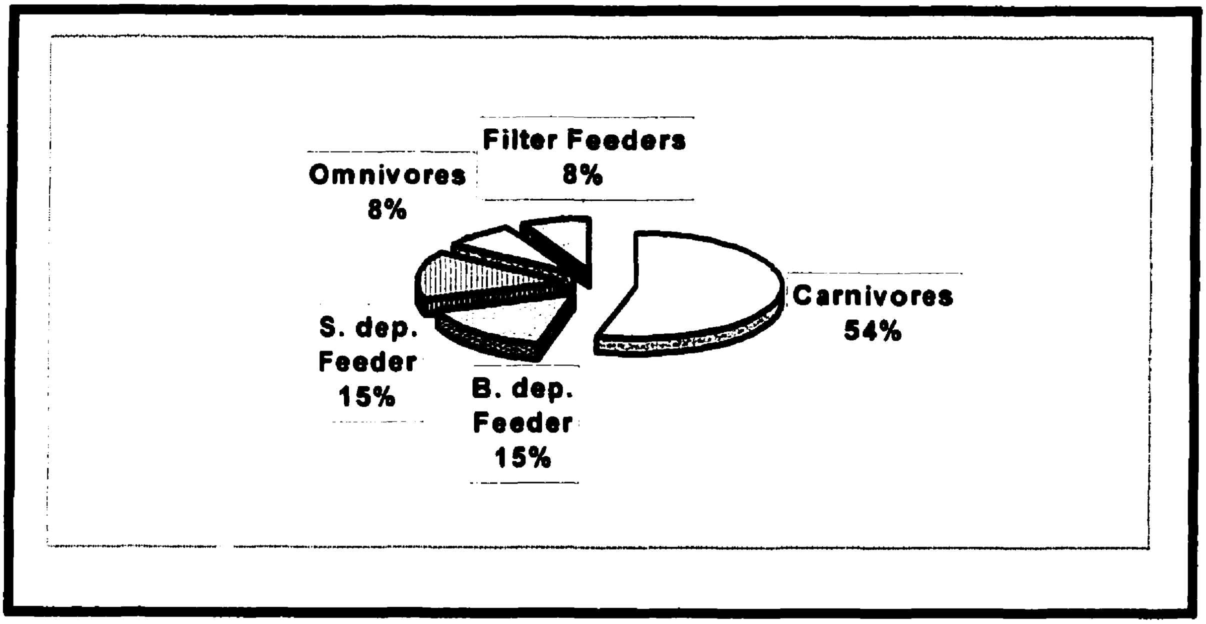


Figure 4-12. Relative abundance of feeding guilds per season. **Fall = Sept/Oct; Spring = April/May; CARN = carnivore, Omn = omnivore, BDF = deep deposit feeder, SDF = surface deposit feeder, FF = filter feeder.**

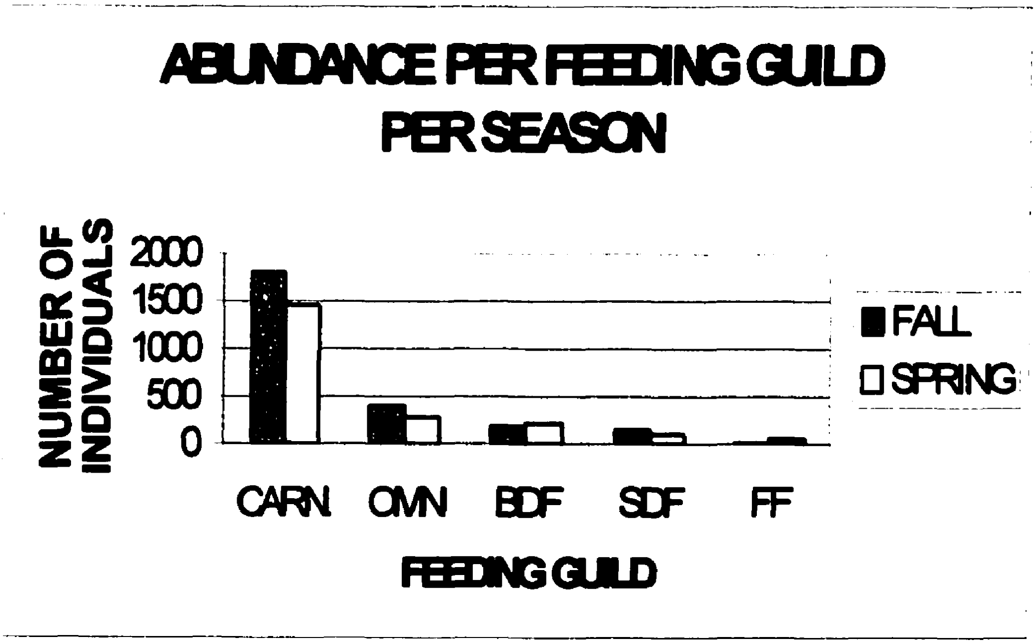


Table 4-6. Reproductive Mode and Life-History Strategy of Polychaetes from the North Shore Seagrass Bed (blank cell means no information was found)

Species #	SPECIES	REPRODUCTIVE MODE	Species #	SPECIES	REPRODUCTIVE MODE
1	Linopherus ambigua		21	Spirorbis formosus	Brooding in tubes
2	Arabella iricolor		22	Sthenelais gracilior	Free spawning Planktonic ?
3	Notomastus latericeus	Free spawning lecithotrophic	23	Spionidae	Brooding and free spawning
4	Dasybranchus lumbricoides	Lecithotrophic development ?	24	Aonides mayaguezensis	Pelagic development
5	Caulleriella sp.	Direct dev	25	Aonides sp. A.	Planktonic larvae?
6	Schistomeringos sp.	Pelagic larvae	26	Scolelepis sp. A	F.S. and planktonic
7	Eunice sp.		27	Fam. Syllidae	Variety
8	Eunice gagzoi		28	Typosyllis sp. A.	Epitoky with pelagic larvae
9	Eunice rubrivitatta		29	Branchiosyllis lamellifera	Small eggs
10	Lysidice notata	Planktonic	30	Haplosyllis cephalata	
11	Nematonereis hebes	Planktonic larvae?	31	Typosyllis annularis	Epitoky
12	Glycera abranchiata	Planktonic larvae	33	Typosyllis hyalina	Epitoky
13	Glycera oxycephala	Planktonic larvae	34	Typosyllis corallicola	Epitoky
14	Podarke obscura	Free spawning planktonic	32	Typosyllis sp. B	Epitoky
15	Lumbrineris sp.	Brood/dir. dev.	35	Ehlersia cornuta	
16	Ceratonereis mirabilis	Brood/dir. dev	36	Ehlersia sp.	
17	Armandia maculata	Free spawning , planktonic	37	Terebellides stroemi	Eggs in gel, direct dev
18	Polyophthalmus pictus		38	Loimia medusa	Planktonic larvae
19	Pectinaria regalis	Planktonic larvae			
20	Sabellidae				

DISCUSSION

Abundance and Species Richness

Dominant Species

Four species of polychaetes, by their numerical abundance, are considered to be the dominant species in the North Shore seagrass bed. These include the dorvilleid *Schistomeringos* sp. which was most abundant in April/May, the syllid *Ehlersia cornuta*, the eunicid *Lycidice notata*, and the amphinomid *Linopherus ambigua* which were more abundant in Sept/Oct. Other numerically abundant species include the opheliid *Polyophthalmus pictus* and the syllids, *Typosyllis hyalina, Haplosyllis cephalata* and *Typosyllis corallicola.* These findings are consistent with macrofaunal components described for seagrass beds in tropical/subtropical environments, where members of the family Syllidae have been reported to be among the most abundant macrofaunal species for reef and seagrass-associated sediments (Kohn and Lloyd 1973; Stoner 1980; Riddle 1988; Pascual et al. 1996; Cinar and Ergen 1998). Members of the family Eunicidae are also common and abundant in tropical/subtropical environments, e.g., the Caribbean (Treadwell 1921). Syllids have also been reported to be important in other benthic communities such as coastal lagoons in Italy (Cognetti 1957 in Sordino et al. 1989), in the Tyrrhenian Sea (Somaschini and Gavina 1994), and the upper reaches of temperate estuaries on the east coast of the United States (Orth et al. 1984). Sordino et al. (1989) re-examined an Italian coastal lagoon that had been studied 30 years earlier and noted that, "... due to pollution ...", the species composition of the lagoons changed over that interval, and syllids no longer dominated the benthic community, suggesting a sensitivity of this polychaete group to pollution. The high diversity of syllids in this study suggests that the environment is healthy.

Species Richness per Family

In addition to being numerically abundant, the family Syllidae was also represented by the greatest number of species (13) in this study (four of which were among the dominant species) and this family was likely to be responsible for many of the patterns seen in this study. The Eunicidae, another species-rich family, was represented by only four species and only one was moderately abundant. With respect to the Syllidae, there was a greater change in abundance of *Ehlersia cornuta* (the second most abundant species in this study) between spring and fall on the western edge of the seagrass bed, than on the eastern edge. Similarly, there was a large change in abundance of *Schistomeringos* sp. between spring and fall on the western edge of the seagrass bed and only a moderate change between spring and fall on the eastern edge. *Lysidice notata*, on the other hand was more abundant on the east side of the seagrass bed at both sampling times. *Haplosyllis cephalata* was one of the numerically abundant species at the west inner site in spring but occurred in very low numbers at this station in the fall.

Other Abundant Species

Though the Syllidae was the most abundant family, the single, most numerically abundant species encountered in this study was a representative of the family Dorvilleidae - *Schistomeringos* sp. This species was the most abundant species found in the study in the spring, when it was the most abundant species at all stations except the east inner station. Numbers of this species decreased significantly on the eastern side in September/October at all stations except WC, where it remained very abundant. A congener, *Shistomeringos rudolphi*, is known as an opportunistic fouling organism with juvenile stages appearing in the fouling community in the months of June, July and August. Their larvae spend up to a week in the plankton, but can take several months or more to mature (Richards 1967). If the Bermuda species, *Schistomeringos* sp. exhibits a similar developmental pattern, this might account for the dominance of this species at station WC, the western edge, in fall. This suggests that the abundance seen at this time might represents successful settlement and growth of summer's reproduction and recruitment to the western edge. The spring samples were taken in April/May and this species was abundant and evenly distributed over the seagrass bed at this time. There was little information in the literature on the reproductive modes of the other dominant species such as the amphinomid, *Linopherus ambigua*, and the eunicid, *Lysidice notata*. However, at the family level, planktonic larvae have been reported for representatives of both Amphinomidae and Eunicidae. Both *Linopherus ambigua* and *Lysidice notata* were more abundant in the fall than the spring indicating summer reproduction, and both had consistently higher numbers on the eastern edge of the seagrass bed than on the western edge.

Temporal and Spatial Patterns

Temporal

Abundance of macro-faunal polychaetes of the North Shore seagrass bed showed temporal variation and spatial variation. As seen in the cluster analysis (Fig. 4-8), there was a difference between spring and fall samples. Also, the replicates from each fall station clustered more closely to each other indicating a spatial distinction that was not apparent in the spring. In spring, the distribution of species throughout the seagrass bed was in general more homogenous. This observation was supported by the results of Correspondence Analysis and Canonical Correspondence Analysis (Figs 4-9 & 4-10). These techniques are used to find a multidimensional representation of dependancies between species and the samples in which they are found.

This suggests that there is patchiness in the seagrass bed, i.e., it is not entirely homogenous, and the pattern is more distinct in the fall than in the spring. The variables responsible for the patterns showed a little more clearly in the CA and CCA (Figs 4-9 and 4-10).

The number of *Halimeda incrassata* plants was lower in the spring than fall and percent coverage by *Syringodium filiforme* and the number of *Penicillus capitatus* plants were both lower in the fall than in spring. No clear relationship between abundance of plants and polychaete abundance was seen. But CA and CCA indicated that there was some correspondence between the latter two plants and a few polychaete species, e.g. *Sthenelais gracilior*, *Eunice gagzoi*, *Eunice sp.*, *Haplosyllis cephalata* and three of the dominants, *Ehlersia cornuta*, *Lysidice notata*, and *Linopherus ambigua*. There did not appear to be a strong pattern in the spatial distribution of the different plants, apart from the suggestion that presence of *Halimeda incrassata* was negatively correlated with presence of the other two plants (Figs 4-9 and 4-10). CCA shows a weak correspondence of *Penicillus capitatus* to the WI and SEC. As there was only a weak relationship between the numbers of individuals and macrophyte abundance, this factor could not be used to explain the distribution patterns observed in the polychaete distribution. As only the seagrass bed was sampled, no comparison between vegetated and unvegetated seabed could be made. Other studies have shown that the number of individuals is higher in vegetated versus unvegetated sediments (Orth 1972; Stoner 1980; Lewis and Stoner 1983).

Burrowers such as *Lumbrineris* sp., *Armandia maculata* and *Notomastus latericeus* were among the species thought to contribute to the temporal pattern seen. These three species corresponded with spring and the higher number of *Halimeda* plants. Other species, e.g., *Dasybranchus lumbricoides* and *Arabella iricolor* and the surface deposit feeder *Aonides* sp. showed a strong correspondence with the edge sites and the fall. SWC varies from other fall stations likely because of the high abundance of *Schistomeringos* sp. and, perhaps, *Eunice rubrocincta*. Also, the density of *Pennicilus capitatus* plants on the western edge in the fall varies from the other stations sampled at that time (Sept/Oct), as does the density of *Halimeda* plants.

For the most part the centroids around which the species clustered were similar in both Correspondence Analysis and Canonical Correspondence Analysis (lower plots in both Fig. 4-9 and Fig. 4-10). This suggests that the additional steps taken to calculate the CCA do not provide a great deal more insight into the species and sample and thus environmental relationships.

There could be many explanations for the observed species and their abundance between spring and fall, i.e. predation, mortality, variable recruitment, or changes in the hydrodynamic regime.

Temporal variation of the macrobenthos for this sub-tropical seagrass bed is not unexpected and it may relate partly to reproductive patterns of the dominant species. There are species of polychaetes, e.g the Palolo worm *Eunice palolo*, and the Bermuda fire worm *Odontosyllis enopla* known from the tropics and sub tropics that reproduce on a lunar cycle all year long but have spectacular reproductive displays that peak in spring and summer months (Huntsman 1948). There is not enough detailed information about reproductive periodicity of other polychaete species known from Bermuda to make further evaluations. Seasonality of overall polychaete density, with maximum numbers in the spring (April – May) and minimum numbers in fall (October-November), has been reported from other tropical/sub-tropical locations, e.g. Florida (Stoner 1980), and this has been related to productivity. This is in contrast to the observations in this study where higher numbers were seen in the fall.

Increases in primary productivity as a result of plankton blooms are not as substantial at lower as at higher latitudes, though changes in primary productivity do occur. In Bermuda, productivity is higher in summer months (Dr. S. R. Smith, marine ecologist and research scientist at BBSR, pers. comm.) than in the spring, and this might account for the observed successful summer reproduction and subsequent recruitment of several species. In addition, duration of planktonic phases and growth rates of juveniles can affect the times at which recruitment subsequent to reproduction could be detected (see sieve size in this study for example).

Disturbance is a physical factor that may come into play in the temporal variation of polychaete abundance observed in this study. Waves and currents are able to alter the sedimentary environment and it has been reported that they can even remove some species from unconsolidated sedimentary environments (Brey 1991; Hall 1994). Waves (caused by winds) and currents are seasonally variable in Bermuda, in particular the direction of strong winds changes seasonally and this is likely a major factor in physical disturbance at any given shallow water location. In Bermuda, hurricane season is from June to November (Elsner and Kara 1999; and D. Malmquest in the office of the Risk Prediction Initiative [RPI] at BBSR pers. comm.), but northwest gales during the winter months are frequent on the North Shore (Dr. S. R. Smith, marine ecologist and research scientist at BBSR, pers. comm.).

In the tropics and subtropics, high winds (hurricanes for example) can be very severe and extreme physical disturbance of unconsolidated, shallow sediments can occur over a very brief interval (Posey et al. 1996). Roughgarden et al. (1985) and Dial and Roughgarden (1999) reported a direct relationship between removal of adult organisms and disturbance, as well as a direct relationship between recruitment and available space. Such conditions may account for the spatial variation observed between the edges and the middle of the seagrass bed. If some species are removed by predation, mortality or by removal by wave action or currents, then other species could readily colonize the newly available habitats. *Schistomeringos* sp., a species that may have larvae available at all times, may be such a species. This might account for uniformly high numbers of this species observed in the April/May sampling period especially on the western edge of the seagrass bed. The prevailing wind and current pattern is from the west-southwest.

In both the tropics and higher latitudes, there are annual patterns to storm severity and wind directions. This may be the explanation for the observation that the fauna is more homogenous throughout the seagrass bed at times of maximum disturbance i.e. over the winter and into early spring, and more patchy in September/October before the worst of the winter storms.

Spatial

It was found that spatial distribution of the species and their abundance was more defined in Sept/Oct. In cluster analysis, the replicates of SEC, SE and SWC taken during the Sept./Oct sampling period, showed strong within station similarity whereas the same level of within station similarity was not seen in samples taken during April/May (see Fig. 4 -8 for example). Though the spring stations as a group were distinguished from most fall stations (Fig. 4-8). At station EC there were three equally abundant species in the spring, *Schistomeringos* sp. *Ehlersia cornuta* and *Lysidice notata*. This station was dominated by a high number of *Lycidice notata* in the fall. At station WC abundance of all species except *Schistomertingos* sp. were low in the spring. In the fall, however, this station was dominated by two species - *Ehlersia cornuta* and *Schistomeringos* sp. This suggests that there is a seasonal difference between these two stations (edges of the seagrass bed). In fact, during the period of the study, this fall station (SWC) had the highest abundance of these two species. Species abundance found at the inner stations were similar to each other in the fall (but were quite different from the edge stations) suggesting a uniformity of the inner parts of the seagrass bed. In the spring the number of *Schistomeringos* was high throughout the seagrass bed whereas the numbers of the other species were lower and more evenly distributed across the bed but with a slight gradient from the east edge to the western edge.

Community Trophic Structure

Feeding strategies

Carnivores

It was found that most of the animals collected throughout the seagrass bed (Table 4-5) and at both seasons belong to the feeding guild of mobile carnivores (Fig. 4-12). This group includes large, highly mobile, aggressive carnivores such as members of the families Glyceridae, Eunicidae, Nereidae, Arabellidae (Fauchald and Jumars 1979), as well as numerous tiny (3-15 mm long) representatives of the families Syllidae and Dorvilleidae. Some members of the Syllidae and Dorvilleidae are considered to be microphagous carnivores (Uebelacker 1984, Cinar and Ergen 1998) as they feed on other small organisms such as hydroids that are common amongst the roots and rhizomes of seagrass beds (Coull 1988; Calder 1988) while others eat larger prey. This finding is in contrast to observations by Stoner (1980) and Young and Young (1977) who in a comparable study found burrowing deposit feeding species of polychaetes to be the dominant feeding guild in seagrass beds comprised primarily of *Halodule wrightii*. It is also in contrast to the faunal dominants normally found in soft sediments, i.e. burrowing deposit feeders (Pearson and Rosenberg 1978).

Some species such as *Branchiosyllis oculata*, *Branchiosyllis lamellifera* and *Haplosyllis spongicola* also found in this seagrass study are also known to live and feed on sponges (Fauchald and Jumars 1978; Pawlik 1982, 1983; Pascual et al 1996). The species *Ungulosyllis annularis* formerly known as *Syllis (Typosyllis) annularis* may also be added to this list as it was found, along with *B. lamellifera* and *Haplosyllis cephalata* in association with sponges.

The presence of an abundance of small mobile carnivores has been linked to environments subject to frequent disturbance (Rees et al.1977), and coarse sediments (Gaston 1987). It could be that the patterns observed in this study are related to factors such as grain-size which, unfortunately, was not measured.

Deposit feeders

After the carnivores, the next most abundant feeding strategy (at the species level) was that of deposit feeding. Overall, there were more deposit feeders in the spring than in fall. There were two types of deposit feeders, burrowing deposit feeders and surface deposit feeders. Deposit feeders that corresponded with spring and the west side of the seagrass bed were the burrowing deposit feeders *Lumbrineris* sp., *Armandia maculata*, *Notomastus latericeus*, *Caulleriella* sp. and the surface deposit feeders *Loimia medusa*, *Aonides mayaguezensis* and *Scolelepis* sp. The deposit feeders that corresponded with fall and the eastside of the seagrass bed, were the burrowing deposit feeder *Dasybranchus lumbricoides*, and the surface deposit feeder *Aonides* sp., and other spionids. The distribution and abundance of these animals probably accounts for the separation of the eastern and western sides of the seagrass bed in the fall in the analysis (Figs 4-9 and 4-10 a and b).

Surface deposit feeders are not very mobile. These include members of the families Spionidae, that tend to be tube-builders living attached to firm substrates, and Terebellidae that can be found vertically oriented within the sediment. Among these, the species extending to the deeper layers of the sediment such as the terebellids can resist being dislodged better than smaller or un-anchored species, and perhaps can better tolerate the periodic movement of sediment. In this study spionids were more abundant in the fall and terebellids were more abundant in the spring.

Filter Feeders

The feeding strategy least represented in this study is filter feeding. Serpulids and sabellids are the most familiar filter feeders among the polychaetes. These families are well represented in Bermuda, but not in this study. Filter feeders are usually sessile and are frequently found attached to firm substrates (hard surfaces) in moderately clean water; highly turbid waters can damage or obstruct their filter feeding structures (Sanders 1958). They capture microplankton and other small particles directly from the water. Though serpulids such as *Spirorbis* spp. can be found attached to seagrass blades, they are not usually encountered within the sediments. As much as anything, the absence of suitable substrate probably accounts for the absence of animals of this feeding strategy. But, periodic turbulence may also account for their low abundance.

Feeding Types and Microhabitat

Stoner (1980) reported that species composition and trophic structure of organisms found in a seagrass bed were related to microhabitat pattern and diversity. We can infer the character of sediment grain-size in general areas of the seagrass bed from the species (and their feeding strategies) found together at a site. Burrowing deposit feeders have been found to be more abundant in fine-grained stable sediments but mobile carnivores are not so restricted. In fall, though mobile carnivores are the prevalent feeding mode, burrowing deposit feeders occur on the east edge, suggesting there could be lighter, more organic sediments as a result of slower currents and reduced wave-generated disturbance. In contrast, the abundance of carnivorous species at the western edge suggests that the sediment here might be of a coarser grain and thus imply higher energy.

Life-History

Means of understanding the variability of a benthic community can be through an understanding of the life-history of the organisms encountered. At the family level, the Syllidae are extremely plastic in their reproductive modes (Schröder and Hermans 1975, Wilson 1991; Giangrande 1997). Brooding, both externally and internally by pelagic females (recently reviewed by Garwood 1991), is not unusual and representatives of many syllid species have been collected in the plankton with eggs and/or larvae attached to their bodies. Epitoky is also known in this family and periodic pelagic stages may contribute to the success of these species in colonizing distant locations. Also, epitoky such as is seen in the Syllidae could be a reproductive strategy compensating for small size and for living in dense clusters (Gaingrande 1997). But, as Gaines and Bertness (1993) point out, range of propagule dispersal is a continuum. The characteristics shown by the Syllidae may have been influential in the initial colonization of Bermuda, but now account for the maintenance of the populations on the island. For, once a population is established, the factors determining distribution of propagules over short distances relate to the density of reproductive adults, timing and output of reproduction and distance propagules have to travel (Gaines and Bertness 1993; Roughgarden et al. 1988). It is also related to oceanographic characteristics of the locality, and species with planktonic stages, that can be locally retained within the lagoon, might account for the numerical success of the dominant families found in this study.

Giangrande (1997), in her review of reproduction in the Polychaeta noted that egg abundance per female largely depends upon adult size and egg size. She concluded that small species such as syllids produce fewer, large eggs, and that egg production was related to ecological factors such as population size and food availability. As most of the polychaetes found in this study were small (<15mm), it might be that seasonal variation in the numbers of individuals of these dominant species is a function of seasonal availability of food.

Seasonal Distribution

In September/October, the numerically most abundant species were *Linopherus ambigua, Lysidice notata, Ehlersia cornuta*, and *Haplosyllis cephalata*. This suggests a summer reproduction for these species. The genus *Linopherus* is in the family Amphinomidae, representatives of this family have been reported to be pelagic when reproductive (Schröder and

Hermans 1975), and their larvae can spend a long time in the plankton (Richards 1967). *Schistomeringos* sp., though very abundant at one station in the fall was uniformly abundant over the whole seagrass bed in the spring. Reproduction in this species includes a planktonic phase and a long development phase and might account for their success in occupying available habitat created by winter storms *sensu* Roughgarden et al. (1985) and Dial and Roughgarden (1999).

As shown in Table 4-6, little reproductive information is available for the Bermuda seagrass species such as *Lysidice notata, Polyophthalmus pictus*, and *Linopherus ambigua*. However, it is postulated that most of the species collected during this study a of a reproductive strategy with the potential for dispersal e.g., Eusyllinae (Syllidae) and Dorvilleidae. A predominance of individuals with such characteristics could indicate a community not in equilibrium, but in this case it indicates a method of colonization. The presence of a preponderance of species with pelagic larvae in this study may illustrate either ongoing recruitment from afar, or a retention of larvae by means of oceanographic conditions. For, as San Martin (1984) has pointed out, great distances of open water are a barrier to syllid dispersal, so the source of recruitment of syllids and perhaps the dorvilleid species found in this study most likely could be from the local population.

Opportunists

The most abundant macrobenthic polychaetes found in this seagrass bed are considered to be opportunists (Odum 1969; Schröder and Hermans 1975), i.e. they are small, short-lived species (Table 4-6) that are able to rapidly reproduce and thus colonize disturbed environments. Disturbed areas are also sites where, in some cases, mobile predators are favored (Rees et al. 1977; Ekman 1983). The word "disturbed" is used in the sense of physical disturbance whereby the seagrass bed can be broken up or fragmented periodically by storms, hurricanes, or shifting sand. Because of the characteristics of the macrobenthic polychaetes, the seagrass bed along the North Shore is not considered here as a stable environment in equilibrium *sensu* Orth (1977), but rather as an environment of variable stability, subject to periodic physical disturbance and characterized by small species able to maintain populations.

Only a few species displaying the other end of the life-history continuum were found in this study. This suggests that the seagrass bed on the North Shore of Bermuda is not a community in equilibrium and perhaps is either still evolving or is subject to greater disturbance than previously thought

Spatial Patterns

No spatial patterns related to life-history were observed, as, for the most part, the species collected in this study were considered to be largely opportunistic species with planktonic larvae.

CONCLUSIONS

Significance of the Polychaete Fauna Found in the Grass Beds

The major conclusion to be drawn from this study is that the seagrass beds on the north shore of Bermuda are healthy. The high species richness found in this study is typical for tropical and subtropical seagrass environments (Alongi 1998), and the dominant species are not those that normally tolerate polluted conditions (Pocklington and Wells 1992).

Secondarily, seasonal variation is seen in abundance of the individual species, and this might reflect seasonal recruitment. Though the suite of species changes slightly at the sampling sites between the two seasons, there is a more-noticeable change in the numbers of individuals. The high numbers of individuals of some species in the fall suggests summer reproduction and fall recruitment for those species. High numbers of other species could suggest winter reproduction with a spring recruitment; it could also indicate that these species are more or less always available to occupy habitat left empty by other species through mortality, predation or through physical removal by seasonal storms. In fall, peak numbers of some species were found on the edges of the seagrass bed, whereas in the spring there was not a large distinction between the edges and middle of the bed.

Thirdly, the fauna collected during this study is comprised of small species, many of which are thought to have pelagic larvae and many of which are carnivorous. These characteristics suggest a less stable environment than previously thought for a seagrass bed. The predominant reproductive strategy found during this study is that of species with dispersal potential. This observation might indicate how Bermuda was initially colonized, i.e., by species having a pelagic phase and it might further indicate that the fauna of the island is in early stages of community development.

Examination of life-histories and feeding modes of the species suggests that the small species found in this study are generally opportunistic. Though these species are found throughout the seagrass bed, the fluctuations of their numbers indicate that the outer edges of the seagrass bed are more variable and appear to be subject to greater "disturbance" during the winter stormy period.

Previous studies in other locations have reported that high wave action during the hurricane season alters, and even destroys, the physical integrity of a sea grass bed (Van Tussenbroek 1994; Cortes and Risk 1985). Cacchione et al. (1987) have also shown that the heterogeneity of grain–size is altered in favor of greater uniformity in fall and winter by increased turbulence generated by higher wave action. Such appears to be the case along the North Shore in fall.

This study is a further example of how the polychaete community may represent the whole macrobenthic community. Their appearance and disappearance as dominants in response to pollution is well documented (Pearson and Rosenberg 1978), while here it is shown that they might be indicators of the stability of an environment. Their appearance and disappearance in response to seasonal natural events in the tropical/subtropical environment makes them excellent candidates for inclusion in both actual evaluations of the health and status of a benthic community as well as in theoretical models

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CHAPTER 5

THE SIGNIFICANCE OF THE POLYCHAETE FAUNA OF A SEAGRASS BED IN BERMUDA

GENERAL CONCLUSIONS

In this study, one element of the macrobenthic organisms, the polychaetous annelids, collected on two sampling dates (one in September/October, at the end of the hurricane season, and one in April/May, just before hurricane season but after the winter storms) from a number of selected locations in a seagrass bed in Bermuda was examined. This was done in order to assess natural variation of the polychaetes of a benthic community in space and time and relate this to biological and ecological factors.

Taxonomic Part

Before the data could be subjected to statistical analysis to determine ecological relationships, it was necessary to identify all of the species collected in the study. As the polychaetes of Bermuda are poorly known, this entailed a literature search of the polychaetes reported from this remote, sub-tropical island in the past. As a result, it was found that 267 species from 137 genera had been reported from this island, and the first complete review of the polychaetes of Bermuda was produced (Chapter 1 and Appendix 1). Besides the list of species, the literature review of Caribbean and North Atlantic sub-tropical polychaetes provides a good working tool for future research on this group of animals in seagrass beds.

As some specimens could not be assigned to a described species, and others did not seem to conform unequivocally to described taxa, further taxonomic analysis was required to clarify these problems. These detailed studies resulted in the description of three new species: one in the genus *Caulleriella* (Family Cirratulidae), one in the genus *Schistomeringos* (Family Dorvilleidae), and one in the genus *Exogone* (Subfamily Exogoninae, Family Syllidae) (Chapter 3). Also during this study, it was also found that there was confusion in the literature about the genus *Branchiosyllis* (Subfamily Syllinae, Family Syllidae) (Pawlik 1983) and a group of species formerly placed in the genus, (or subgenus), *Typosyllis*, but recently assigned to *Branchiosyllis exilis*-group by Licher (2000). By going back to the original description of the genera and by examining types as well as freshly-collected material, it was possible to re-define the genus *Branchiosyllis*, and, using phylogenetic analysis, clearly distinguish from it the *Branchiosyllis exilis* group. Based on this study, a new genus - *Ungulosyllis* - is proposed for species recently assigned by Licher (2000) to the *Branchiosyllis exilis* group. *Ungulosyllis annularis* (Verrill, 1900) - originally named *Syllis (Typosyllis) annularis* Verrill, 1900 but synonymized with *Syllis (Typosyllis) exilis* Gravier, 1900 by a variety of authors - is re-established as a valid species, redescribed, and designated as the type species of the new genus (Chapter 2).

The recognition of a new genus, and the description of three new species in three different genera contribute to the idea that Bermuda may have a larger endemic fauna than the 3% of the known fauna recently proposed (Sterrer 1998). Verrill (1900; 1901) first suggested that there is a large endemic fauna in Bermuda when he distinguished many Bermuda polychaete species from North American and Caribbean species. Such a conclusion has been drawn for other Bermuda taxa e.g., Mollusca (P. Barnes pers. comm.), anomuran crustaceans (Provenzano 1960), and Crustaceans (Lazo-Wasem pers. comm), as well as other taxa, previously thought to have wide distributions e.g., the reef building coral *Montastraea annularis* (Knowlton 1993).

Importance of taxonomy

Carlton (1993) went so far as to suggest that the major crisis in marine biodiversity at the end of the 20th century was the "extinction" of taxonomists and biogeographers of the marine realm. With this thought in mind, the importance of accurate taxonomy can not be emphasized enough. Accurate taxonomy is the first step in recognizing the degree of endemism in Bermuda. Accurate taxonomy is a prerequisite for studies of global biodiversity. It has been suggested that coral reefs and their associated ecosystems will be found to have as great a diversity as rain forests (Reaka Kudla 1997), therefore, knowledge of the fauna associated with coral reefs is extremely important (Done et al. 1996). In addition, accurate identifications are necessary for statistical analyses as the results of such analyses can be misleading, and erroneous conclusions can be drawn from results produced from imperfect data generated when for example, several species are included under one name.

Ecological Part

The primary ecological objective of the seagrass study was to assess the ecological status of the seagrass bed. Secondarily, it was to discover what the patterns of polychaete species and abundance were, and thirdly, to suggest the factors responsible for the observed patterns. To achieve these objectives, the species list generated in this study was examined for "indicator species". [High abundance of individuals of species known to tolerate pollution or disturbance can suggest the status of the health of the marine environment.] The species richness of the study site was examined based on the assumption that high species richness and diversity suggests a healthier environment than low species richness and diversity. To examine spatial and temporal patterns, the presence and abundance data were subjected to a variety of multivariate analyses. These analyses were used to determine correspondence of species and their abundance with parameters such as time of year, location in the bed, degree of coverage by the seagrass *Syringodium filiforme*, and density of marine algae such as *Halimeda incrassata* or *Penicillus capitatus*. The feeding mode and the reproductive mode of the polychaetes found in this study were examined in order to aid in the interpretation of the patterns of distribution and abundance of the species collected.

It was found that there was a relatively high species richness at all stations at both times of the year and this suggests a healthy marine environment. It was also found that the family Syllidae was represented by the most individuals, followed closely by the family Dorvilleidae. These observations are in keeping with observations in other tropical/subtropical seagrass bed environments where members of the family Syllidae have been found to be highly abundant.

It was found in the multivariate analyses that correlations were strongest between species presence and abundance and time of year; moderate with location in the seagrass bed; weak between some of the species and the vegetation. There was not, for example, the strong relationship between density of plants and abundance of organisms seen in other studies (e.g. Lewis and Stoner 1983). The patterns found suggested a summer recruitment of most of the dominant species, as numbers of many of these species were much higher in Sept./Oct than in the spring. The data also suggested that along with mortality and predation, higher energy environments seen during the winter (winter storms) either removes or redistributes the small (0.5-1.5mm long) organisms from the sediments of the seagrass bed.

Seasonality in macrobenthic invertebrates is best known for northern latitudes where large changes in water temperature and light levels along with dramatic changes in primary productivity occur. There is a growing body of evidence showing seasonality in environments with less variable parameters such as tropical and subtropical environments (Hatcher 1997). The cues for these changes are still being elucidated (Bhaud and Cazaux 1987). The hydrodynamic environment is more turbulent in winter and has been known to change grain size in other sand habitats at other locations (Grant 1983). For this reason, high wave action and turbulence generated by winter storms and/or hurricanes are thought to have created a more homogenous sedimentary environment throughout the seagrass bed. Various results of this could be that the turbulent hydrodynamic regime: 1) changed the organic carbon content as well as grain size of the sediments, 2) removed small organisms and /or redistributed them over a wider area, 3) transported in mature larvae of opportunistic species to occupy empty niches created by the wave action.

The sizes of the numerically important species are important in this study, as most of the species accounting for the largest proportion of individuals collected in this study are very small (0.5 – 1.5mm). The changes in their distribution might have occurred either by choice (as the sediments become less stable, the species relocate elsewhere), or by their inability to resist the physical redistribution under the turbulent conditions with the result that the animals were "washed-out" of the habitat. A third option - recruitment - is also thought to play a part in the observed changes as has been shown by Hutchings and Murray (1993) in coral island of the Great Barrier Reef. For example, it is thought that instances where numerical abundance of some species increased in fall, e.g., *Schistomeringos* sp. represented either an example of settlement of mature larvae into newly-available niches, or an example of small animals of a certain size being redistributed by this highly turbulent water.

Diversity of the species composition and abundance has been examined for many shallow water ecosystems in different zoogeographic zones. It has been found that there is considerable temporal and spatial variation in the species composition of communities found in shallow water habitats, and a number of explanations have been put forth to explain the generation and maintenance of species diversity. Characteristics of the substrate e.g., rocky or soft substrates are major controlling factors (Estes and Patterson 2000). Factors such as grain size and organic carbon content of the sediment (Sanders 1958; Rhoads and Young (1970), temperature of water and speed of currents (Mann and Lazier 1991), tidal change (Young and Young 1977), diurnal periodicity (Mileikovsky 1970) and physical disturbance (Hall 1994), all influence macrofaunal presence and abundance. Biological factors, such as food availability (Sanders 1958), inter- and intra-species interactions (Woodin 1974), prey/predator interactions (Young and Young 1978), density of plants (Lewis and Stoner 1983), larval availability and settlement (Butman 1987; Grassle and Butman 1989) have been shown to be important in generating and maintaining species diversity. These factors along with cues for larval recruitment e.g., chemical and geophysical cues (Pawlik 1992), pre- and post settlement processes (Olafson et al. 1994), reproductive timing and substrate availability (Shull 1997) have also been shown to influence faunal presence and abundance. More recently, Dial and Roughgarden (1999) have postulated an intermediate disturbance theory that explains patterns in species presence and abundance in terms of a response to a certain amount of disturbance.

Variation in the benthic community is therefore the result of very complex interactions between species and their physical and biological environment. Some of these interactions such as temperature, light levels, and food availability govern intrinsic characteristics of the animals such as mode of reproduction and reproductive timing, as well as other physiological characteristics. Other interactions, such as activity of predators, alteration of the grain size of the sediment through changes in the hydrodynamic level, or changes to the organic carbon levels through anthropogenic causes, resulting in a variation in the benthic community are extrinsic. The term 'biocomplexity' has been coined for this broader concept (Colwell 1998). It recognizes and acknowledges the diversity of factors involved in determining the biodiversity of a marine benthic community as well as the feed back from diversity to complexity. Colwell (2000) has also suggested that it is not enough to inventory the species of the world's ecosystems, but it is necessary to explore and discover physical, biological, and social interactions within them. This idea has been considered by Snelgrove and Butman (1994), who, in a recent review of animal-sediment relationships concluded "... no single variable, and no simple paradigm explains the spatial and temporal variation of a macro-invertebrate community found in association with the sea bed."

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APPENDIX 1

THE POLYCHAETESOF BERMUDA

FAMILY	SPECIES
ALCIOPIDAE	*Alciopa reynaudii* Audoin & Milne Edwards, 1833
	Naiades sp.
	Torrea candida (Delle Chiaje, 1828)
	Vanadis formosa Claparede, 1870
	Vanadis fuscapunctata Treadwell ,1906
	Vanadis longissima (Levinsen, 1885)
AMPHARETIDAE	*Amage inhamata* Hoagland, 1919
	Muggoides cinctus Hartman, 1964
AMPHINOMIDAE	*Amphinome rostrata* (Pallas, 1776)
	Eurythoe complanata (Pallas, 1776)
	Eurythoe macrotricha Baird, 1868
	Eurythoe pacifica Kinberg, 1857
	Hermodice carunculata (Pallas, 1766)
	Hipponoa gaudichaudi Audoin & Milne Edwards, 1830
	Linopherus ambigua Monro, 1933
	Notopygos megalops McIntosh, 1885
ARABELLIDAE	*Arabella iricolor* (Montagu, 1804)
	=*Arabella maculosa* Verrill, 1900
	Arabella multidentata (Ehlers, 1887)
	Arabella mutans (Chamberlin, 1919)
	Arabella opalina Verrill, 1874
ARENICOLIDAE	*Arenicola cristata* Stimpson, 1884
CAPITELLIDAE	*Capitella capitata* (Fabricius, 1780)
	Dasybranchus lumbricoides Grube, 1878
	Dasybranchus lunulatus Ehlers, 1887
	Eunotomastus grubei McIntosh, 1885
	Mastobranchus sp.
	Notomastus latericeus Sars, 1851

	Notomastus teres Hartman, 1965
CHAETOPTERIDAE	*Mesochaetopterus minutus* Potts, 1914
	Spiochaetopterus costarum oculatus Webster, 1879
CHRYSOPETALIDAE	*Bhawania goodei* Webster, 1884
	Paleonotus elegans (Bush in Verrill, 1900)
	=*Chrysopetalum elegans* Bush in Verrill, 1900
	Palmyra elongata Grube, 1856
CIRRATULIDAE	*Caulleriella n. sp* Pocklington, 2000 in prep.
	Caulleriella sp B
	Cirratulis websteri Verrill Verrill, 1900
	Cirratulus assimilis McIntosh, 1885
	Cirratulus grandis Verrill, 1900
	Cirratulus tenuis Webster, 1884
	Cirriformia capillaris (Verrill, 1900)
	=*Cirratulus capillaris* Verrill, 1900
	Cirriformia multicirratus Treadwell, 1936
	Cirriformia punctata (Grube, 1858)
	Cirriformia pygidia (Treadwell, 1936)
	Cirriformia websteri (Verrill, 1900)
	=*Cirratulus (Audouinia) websteri* Verrill, 1900
DORVILLEIDAE	*Dorvillea (Dorvillea) largidentis* Wolf, 1986
	Dorvillea melanops Verrill, 1900
	=*Stauronereis melanops* Verrill, 1900
	=*Stauronereis erythrops* Verrill, 1900
	Dorvillea sociabilis Webster, 1879
	Dorvillea sp. A
	Neotenotrocha sterreri Eibye-Jacobsen & Kristensen, 1994
	Schistomeringos polydonta (Verrill, 1900)
	= *Stauronereis polydonta Verrill, 1900*
	Schistomeringos rudolphi (delle Chiaje, 1828)
	Schistomeringos rudolphi anoculata (Hartman, 1965)
	= *Dorvillea rudolphi anoculata* Hartman 1965
	Schistomeringos new species Pocklington, 2000 in prep
EULEPITHIDAE	*Pareulepis wyvillei* (McIntosh, 1885)
EUNICIDAE	*Eunice afra* Peters, 1854
	Eunice binominata Quatrefage, 1866
	=*Leodice binominata* Quatrefage, 1866
	Eunice cariboea Grube, 1856
	Eunice cirrobranchiata McIntosh, 1885

= *Eunice denticulata* Webster 1884
Eunice concinna (Verrill, 1900)
  =*L. concinna* Verrill, 1900
Eunice culebra (Treadwell, 1921)
  = *L. culebra* Treadwell,1921
Eunice filamentosa Grube, 1856
  =*L. denticulata* Webster, 1884
Eunice gagzoi Augener, 1922
Eunice goodseri (McIntosh, 1885)
  = *Marphysa goodseri* McIntosh, 1885
Eunice longicirrata Webster, 1884
  =*L. elegans* Verrill, 1900
  = *L. longicirrata* Webster, 1884
  =*L. margaritacea* Verrill, 1900
Eunice longisetis Webster, 1884
  =*Leodice longisetis* (Webster, 1884)
  = *L. longisetis* (Webster, 1884)
Eunice mutilata Webster, 1884
  =*Eunice barvicensis* McIntosh, 1885
  =*L. mutilata* Webster, 1884
Eunice rubra Grube, 1856
Eunice rubrivitatta (Treadwell, 1921)
  = *L. rubrivitatta* Treadwell,1921
Eunice schemacephala Schmarda, 1861
Eunice tenuicirrata (Verrill, 1900)
  = *L. tenuicirrata* Verrill,1900
Eunice unifrons (Verrill, 1900)
  = *L. unifrons* Verrill, 1900
Eunice violacea Grube, 1856
Eunice violaceomaculata Ehlers, 1887
  =*L. violaceomaculata* Ehlers, 1887
Eunice vitatta delle Chiaje, 1828
  =*L. stigmatura* Verrill, 1900
  =*L. unifrons* Verrill, 1900
  = *L. unifrons Verrill, 1900*
Heteromarphysa tenuis Verrill, 1900
Lycidice notata Ehlers, 1887
Lysidice bilobata Verrill, 1900
Lysidice ninetta Audoin and Milne Edwards, 1834
Marphysa acicularum Webster, 1884

	Marphysa regalis Verrill, 1900
	Marphysa sanguinea (Montagu, 1807)
	Nematonereis unicornis Schmarda, 1861
	= *Nematonereis hebes* Verrill, 1900
	Nicidion kinbergi Webster, 1884
	Paramyphysa longula Verrill, 1900
	=*Paramyphysa obtusa* Verrill, 1900
GLYCERIDAE	*Glycera abranchiata* Treadwell, 1901
	Glycera epipolasis (Chamberlin, 1919)
	= *Telake epipolasis Chamberlin,1919*
	Glycera mimica Hartman, 1965
	Glycera oxycephala Ehlers, 1887
GONIADIDAE	*Progoniada regularis* Hartman, 1965
HESIONIDAE	*Fallacia protochona* (Schmarda, 1861)
	= *Hesione proctochona* Schmarda, 1861
	Hesiocaeca bermudensis Hartman, 1965
	Hesione picta O.F. Muller, 1858
	Microphthalmus arenarius Westheide, 1973
	Microphthalmus bermudensis Westheide, 1973
	Neotenotrocha sterrei Eibye-Jacobsen & Kristensen, 1994
	Podarke obscura Verrill, 1873
LOPADORHYNCHIDAE	*Lopadorhynchus nationalis* Reibisch, 1895
	Lopadorhyncus nans Chamberlin, 1919
	Lopadoryhchus uncinatus Fauvel, 1916
LUMBRINERIDAE	*Lumbrineris coccinea* (Renier, 1804)
	= *Lumbrineris floridana* Ehlers, 1887
	Lumbrineris crassicephala Hartman, 1965
	Lumbrineris impatiens Claparede, 1868
	Lumbrineris inflata Moore, 1911
	Lumbrineris latreilli Audoin & Milne Edwards, 1834
	Lumbrineris nasuta Verrill, 1900
LYSARETIDAE	*Oenone diphyllidia Schmarda, 1861*
	= *Lumbrineris cingulata* Treadwell, 1917
	Oenone fulgida (Savigny, 1818)
MALDANIDAE	*Axiothella somersi* Verrill, 1900
	Clymenura cirrata (Ehlers, 1887)
	Euclymene coronata Verrill, 1900
	Lumbriclymene filifera (Verrill, 1900)
NEPHTYIDAE	*Nephtys paradoxa* Malm, 1874
NEREIDAE	*Ceratonereis mirabilis* Kinberg, 1866

	= *Nereis mirabilis* (Kinberg, 1866)
	Namalycastis profundus Hartman, 1965
	Nereis agassiz Ehlers, 1868
	Nereis antillensis McIntosh, 1885
	Nereis articulata Ehlers, 1887
	Nereis bardii Webster, 1884
	Nereis gracilis Webster, 1884
	Nereis melanocephala McIntosh, 1885
	Nereis nubalis Treadwell, 1941
	Nereis riisei Grube, 1857
	Perinereis andersonni Kinberg, 1866
	Platynereis dumerelli Audouin & Milne-Edwards, 1833
NERILLIDAE	*Mesonerilla prospera* Sterrer and Iliffe, 1982
ONUPHIDAE	*Mooreonuphis jonesi* Fauchald, 1982
	Onuphis quadricuspis Sars, 1872
	Paronuphis bermudensis Hartman, 1965
OPHELIIDAE	*Armandia bermudiensis* (Treadwell, 1936)
	Armandia maculata (Webster, 1884)
	Ophelia profunda Hartman, 1965
	Ophelina cylindricaudatus Hansen, 1878
	Polyophthalmus incertus Treadwell, 1936
	Polyophthalmus pictus (Dujardin, 1839)
	Tachytrapane jeffreysii McIntosh, 1879
ORBINIIDAE	*Haploscoloplos fragilis* (Verrill, 1873)
	Naineris laevigata (Grube, 1856)
	Naineris setosa (Verrill, 1900)
	= *Aricia setosa* Verrill, 1900
	Orbinia platycephalata (McIntosh, 1885)
	= *Aricia platycephala* McIntosh, 1885
OWENIIDAE	*Myriochele heeri* Malmgren, 1867
PARAONIDAE	*Aricidea catherinae* Laubier, 1967
	Paradoneis abranchiata Hartman, 19650
PECTINARIIDAE	*Pectinaria gouldi* (Verrill, 1873)
	Pectinaria regalis Verrill, 1901
PHOLOIDIDAE	*Pholoides bermudensis* (Hartman and Fauchald, 1974)
PHYLLODOCIDAE	*Eulalia megalops* Verrill, 1900
	Eulalia viridis (Linneus, 1767)
	Genetyllis bermudae (Verrill, 1900)
	Mystides gracilis Treadwell, 1941

	Nereiphylla fragilis (Webster, 1879)
	Phyllodoce oculata Ehlers, 1887
POECILOCHAETIDAE	*Poecilochaetus bermudensis* Hartman, 1965
	Poecilochaetus serpens Allen, 1904
POLYNOIDAE	*Acanthicolepis longicirrata* Treadwell, 1941
	Dreischia atlantica Treadwell, 1936
	Eunoe purpurea Treadwell, 1936
	Halosydna leucohyba (Schmarda, 1861)
	= *Polynoe pustulata* (Verrill, 1900)
	Lepidonotus pilosus Treadwell, 1941
SABELLARIDAE	*Lygdamis indicus* Kinberg, 1867
SABELLIDAE	*Branchiomma lobiferum* Ehlers, 1887
	= *Megalomma lobiferum (*Ehlers,1887)
	Branchiomma nigromaculata(Baird, 1865)
	Dasychone bairdi McIntosh, 1885
	Dasychone conspersa Treadwell, 1941
	Jasmineira bermudiensis Hartman, 1965
	Hypsicomus elegans (Webster, 1884)
	= *Protulides elegans* Webster, 1884
	Sabella melanostigma Schmarda, 1861
SCALIBREGMATIDAE	*Parasclerocheilus sp.*
SERPULIDAE	*Eupomatus elegantulus* Bush, 1910
	Filograna implexa Berkeley, 1828
	Hydroides bispinosa Bush, 1910
	Hydroides dianthus Verrill, 1874
	Hydroides elegans (Webster, 1884)
	Hydroides lunulifera (Claparede, 1868)
	= *Eucarphus serratus* Bush in Verrill, 1910
	Hydroides parvus (Treadwell, 1901)
	Hydroides uncinatus (Ehlers, 1887)
	= *Eupomastus uncinatus* Verrill, 1900
	Placostegus assimilis McIntosh, 1885
	Pomatoceros triqueter Linneus, 1767
	Protula longisetis Schmarda, 1861
	Serpula sombrericia McIntosh, 1885
	Spirobranchus glandulata (Treadwell, 1936)
	Spirobranchus occidentalis McIntosh, 1885
	Spirobranchus tricornis Treadwell, 1941
	Spirorbis foraminosus Busch, 1904
SIGALIONIDAE	*Leanira minor* Hartman, 1965

	Pelogenia kinbergi (Hansen, 1882)
	= *Eupholoe nuda Treadwell 1936*
	Psammolyce globula Hartman, 1965
	Sthenelais articulata Verrill, 1900
	Sthenelais setosa Bush in Verrill, 1900
	Sthenelais gracilior McIntosh, 1885
SPIONIDAE	*Aonides mayaguezensis* Foster, 1969
	Aonides sp.
	Polydora sp. A
	Polydora sp. B
	Prionospio cirrifera Wiren, 1883
	Prionospio cristata Foster, 1971
	Scolelepis squamata (O.F. Muller, 1806)
	Spio pettiboneae Foster, 1971
SYLLIDAE	*Ancistrosyllis albini* Langerhans, 1881
	Ancistrosyllis bermudiensis Treadwell, 1941
	Autolytus (P) pseudosimplex (Verrill, 1900)
	= *Autolytus (Procerea) simplex* Verrill, 1900
	Autolytus (P.) rubropunctatus (Grube, 1860)
	Autolytus bidens Treadwell, 1941
	Branchiosyllis lamillifera Verrill, 1900
	Branchiosyllis oculata Ehlers, 1887
	Brania nitidula (Verrill, 1900)
	Brania rugulosa (Verrill, 1900)
	= *Grubea rugulosa* Verrill, 1900
	Ehlersia cornuta (Rathke, 1843)
	Ehlersia sp.
	Eusyllis (Synsyllis) longigularis Verrill, 1900
	= *Eusyllis (Synsyllis) veridula* Verrill, 1900
	Eusyllis longisetosa (Verrill, 1900)
	= *Demosyllis longisetosa* Verrill, 1900
	Exogone n.sp. Pocklington, 2000 in prep
	Exogone dispar (Webster, 1879)
	Exogone gemmifera Pagenstecher, 1862
	Exogone hebes (Webster and Benedict, 1884)
	Exogone verugera (Claparede, 1868)
	Grubeosyllis nitidula (Verrill, 1900)
	Haplosyllis cephalata Verrill, 1900
	Haplosyllis gala Treadwell, 1941
	Haplosyllis palpata Verrill, 1900

Haplosyllis spongicola (Grube, 1855)
= *Hemisyllis dispar* Verrill, 1900
Odontosyllis brachydonta Verrill, 1900
Odontosyllis enopla Verrill, 1900
Opisthosyllis nuchalis Verrill, 1900
Syllis (Ehlersia) nitida Verrill, 1900
= *Syllis (Typosyllis) catenula* Verrill, 1900
Syllis (Typosyllis) diplomorpha Verrill, 1900
Syllis exigua Verrill, 1900
Syllis gracilis Grube, 1855
Trypanosyllis fertilis Verrill, 1900
= *Trypanosyllis attenuata* Verrill, 1900
= *Typanosyllis [sic] fertilis* Verrill, 1900
Trypanosyllis tenella Verrill, 1900
Typosyllis annularis (Verrill, 1900)
= *Syllis (Typosyllis) annularis Verrill, 1900*
= *Syllis grandigularis* Verrill, 1900
Typosyllis cincinnata (Verrill, 1900)
= *Syllis (Typosyllis) cincinnata* Verrill, 1900
Typosyllis corallicola (Verrill, 1900)
= *Syllis (Typosyllis) corallicola* Verrill, 1900
Typosyllis hyalina Grube, 1850

TEREBELLIDAE
Enoplobranchus sanguineus Verrill, 1899
Eupolymnia crassicornis (Schmarda, 1861)
Eupolymnia magnifica (Webster, 1884)
Euthelepis tenuis (Verrill, 1900)
= *Protothelepis tenuis* Verrill, 1900
Loimia bermudensis Verrill,1900
Loimia medusa (Savigny, 1818)
Loimia viridis Moore, 1903
Neoamphitrite bermudensis Verrill, 1900
Nicolea corallicola Verrill, 1900
Nicolea modesta Verrill, 1900
Pista sombreiana McIntosh, 1885
Polycirrus corallicola Verrill, 1900
Polycirrus pennulifera Verrill, 1900
Polycirrus purpureus McIntosh, 1885
= *Polycirrus luminosus* Verrill, 1900
Polymniella aurantiaca (Verrill, 1900)
= *Eupolymnia (Polymniella) aurantiaca* Verrill, 1900

	Pseudeurythoe ambigua (Monro, 1933)
	Streblosoma polybranchia Verrill, 1900
	Terebella crassicornis McIntosh, 1885
	Terebella magnifica Webster, 1884
	Thelepus setosus (Quatrefage, 1865)
TOMOPTERIDAE	*Tomopteris helgolandica* Greef, 1879
	Tomopteris longisetis Treadwell, 1936
TRICHOBRANCHIDAE	*Terebellides stroemi* Sars, 1835
TYPHOSCOLICIDAE	*Travisiopsis atlantica* Treadwell, 1936

APPENDIX 2

APPENDIX 2
species having <10 individuals at < 4stations removed
these species are in bold

APRIL/MAY

SITE: WEST IMPACT
(WOLFGANG)

	WW1	WW2	WW3	WW4	WW5	WW6	WW7	WW8
AMPHINOMIDAE(Linopherus ambigua)	2	4	5	1	1	5	3	1
ARABELLIDAE(Arabella iricolor)								
CAPITELLIDAE (Notomastus latericeus)			5		1			
CAPITELLIDAE(Dasybranchus lumbricoides)								
CIRRATULIDAE(Caulleriella sp.)				3		3		
DORVILLEIDAE(Schistomeringos sp.)	3	32	14	40	4	12	4	20
EUNICIDAE(Eunice sp.)						5		
EUNICIDAE(Eunice gagzoi)						1		
EUNICIDAE(Eunice rubrivittata)						1		
EUNICE (Eunice vitatta)			1					
EUNICIDAE(Lysidice notata)	5	13	8	3	11	3	3	2
EUNICIDAE(Nematoneries hebes)						1		
GLYCERIDAE(Glycera abranchiata)		1		3				1
GLYCERIDAE(Glycera oxycephala)		1		1				
HESIONIDAE(Podarke obscura)	1		2		1		1	
LUMBRINERIDAE(Lumbrineris sp.)	1	2	1	4		1	2	3
NEREIDAE(Ceratonereis mirabilis)		1		2		3	1	2
OPHELIIDAE(Armandia maculata)	2	3	6	2	3	2	2	
OPHELIIDAE(Polyophthalmus pictus)		21			3	1	3	
PECTINARIIDAE (Pectinaria regalis)								
POECILOCHAETIDAE (Poecilochaetus bermudensis)					1			
SABELLIDAE				3				
SERPULIDAE(Spirorbis formosus)							6	
SIGALIONIDAE(Sthenelais gracilior)			2		2		1	1
SPIONIDAE								
SPIONIDAE(Aonides mayaguezensis)	1	1	1		4			
SPIONIDAE(Aonides sp.)			1					
SPIONIDAE(Scolelepis sp.)				1			1	
SYLLIDAE unidentified	5	8		4		3		
SYLLIDAE (Typosyllis sp. 1)				3				3
SYLLIDAE (Branchiosyllis lamellifera)								

SYLLIDAE(Haplosyllis cephalata)						1	2	
SYLLIDAE (Typosyllis annularis)								
SYLLIDAE (Typosyllis sp. 2)								
SYLLIDAE(Typosyllis hyalina)			1			4	3	5
SYLLIDAE (Typosyllis corallicola)	3	4	6	21		2		
SYLLIDAE (Ehlersia cornuta)		7	4	12	1	16		5
SYLLIDAE(Ehlersia sp.A.)			7		10			2
TEREBELLIDAE						2		
TEREBELLIDAE(Loimia medusa)								

SITE: WEST CONTROL (STUART)

	WWC1	WWC2	WWC3	WWC4	WWC5	WWC6	WWC7	WW8
AMPHINOMIDAE(Linopherus ambigua)			3	4	2		1	
ARABELLIDAE(Arabella iricolor)								
CAPITELLIDAE (Notomastus latericeus)								
CAPITELLIDAE(Dasybranchus lumbricoides)							1	
CIRRATULIDAE(Caulleriella sp.)		2	2	2	6	2	1	1
DORVILLEIDAE(Schistomeringos sp.)	5	18	8	7	4	24	25	21
EUNICIDAE(Eunice sp.)	3							
EUNICIDAE(Eunice gagzoi)			1	1	1	1		1
EUNICIDAE(Eunice rubrivittata)								
EUNICIDAE(Lysidice notata)	11	5	6	8	1	6	8	8
EUNICIDAE(Nematoneries hebes)			1	1	4	1		
GLYCERIDAE(Glycera abranchiata)								1
GLYCERIDAE(Glycera oxycephala)								2
GLYCERIDAE(Glycera sp.)							1	
HESIONIDAE(Podarke obscura)	1					1	1	
LUMBRINERIDAE(Lumbrineris sp.)		5		1	3		3	
NEREIDAE				2	1			
NEREIDAE(Ceratonereis mirabilis)		2		2	1	1		2
OPHELIIDAE(Armandia maculata)			1	1	1	2		
OPHELIIDAE(Polyophthalmus pictus)		6	4	1	3	4	2	10
PECTINARIIDAE (Pectinaria regalis)								
SABELLIDAE								
SERPULIDAE(Spirorbis formosus)		5	1			1	1	4
SIGALIONIDAE(Sthenelais gracilior)	1	1	3	1	3	2		1
SPIONIDAE								1

SPIONIDAE(Aonides mayaguezensis)		1			1	2	1	3
SPIONIDAE(Aonides sp.)								1
SPIONIDAE (Prionospio cristata)		1						
SPIONIDAE(Scolelepis sp.)								
SYLLIDAE unidentified							1	
SYLLIDAE (Typosyllis sp. 1)								
SYLLIDAE (Branchiosyllis lamellifera)						4		
SYLLIDAE(Haplosyllis cephalata)	1					1		1
SYLLIDAE (Typosyllis annularis)	2		4	3		4		
SYLLIDAE (Typosyllis sp. 2)								
SYLLIDAE(Typosyllis hyalina)	4	11		3		3	2	7
SYLLIDAE (Typosyllis corallicola)	11	9	5	4	2	3		1
SYLLIDAE (Ehlersia cornuta)	1	5		7	8	1	11	10
SYLLIDAE(Ehlersia sp.A.)	3				1			
SYLLIDAE (Exogone sp.)							1	
TEREBELLIDAE								
TEREBELLIDAE(Loimia medusa)				2	1	3	2	2

SITE: EAST IMPACT
(ELLEN)

	WE1	WE2	WE3	WE4	WE5	WE6	WE7	WE8
AMPHINOMIDAE(Linopherus ambigua)	6	4	6	16	8	11	11	
ARABELLIDAE(Arabella iricolor)	1							
CAPITELLIDAE (Notomastus latericeus)	1		1					
CAPITELLIDAE(Dasybranchus lumbricoides)								
CIRRATULIDAE(Caulleriella sp.)		1	1	5	4			
DORVILLEIDAE(Schistomeringos sp.)	20	15	11	6	16	14	17	11
EUNICIDAE(Eunice sp.)								
EUNICIDAE(Eunice gagzoi)		2		1		2		
EUNICIDAE(Eunice rubrivittata)								
EUNICIDAE(Lysidice notata)	4	9	11	9	5	11	8	3
EUNICIDAE(Nematoneries hebes)		1			4			
GLYCERIDAE(Glycera abranchiata)								
GLYCERIDAE(Glycera oxycephala)	1	1				1		
HESIONIDAE(Podarke obscura)		1			2		1	1
LUMBRINERIDAE(Lumbrineris sp.)	2	1	3		2	2	4	1
NEREIDAE(Ceratonereis mirabilis)	2		2	2		3	3	1

OPHELIIDAE(Armandia maculata)	1	6	1			3		6
OPHELIIDAE(Polyophthalmus pictus)	2	1	10	11	3		1	17
PECTINARIIDAE (Pectinaria regalis)								
POECILOCHAETIDAE (Poecilochaetus bermudensis)		1						
SABELLIDAE								1
SERPULIDAE(Spirorbis formosus)	2	3	1	1	2		2	1
SIGALIONIDAE(Sthenelais gracilior)	2	3	1	1	2	1	1	
SPIONIDAE								3
SPIONIDAE(Aonides mayaguezensis)	8	4	1			1	1	4
SPIONIDAE(Aonides sp.)			3	1		10		
SPIONIDAE(Scolelepis sp.)					2			
SYLLIDAE unidentified							7	
SYLLID (Typosyllis sp. 1)								
SYLLIDAE (Branchiosyllis lamellifera)								
SYLLIDAE (Eusyllis longisetosa)						1		
SYLLIDAE(Haplosyllis cephalata)	1	9						
SYLLIDAE (Typosyllis annularis)	3							4
SYLLIDAE (Typosyllis sp. 2)								
SYLLIDAE(Typosyllis hyalina)		8	4	6	9	6		
SYLLIDAE (Typosyllis corallicola)		11	1	4	1	1	1	2
SYLLIDAE (Ehlersia cornuta)	9	24	29	4	17	3	8	
SYLLIDAE(Ehlersia sp.A.)	1		4			1	8	
TEREBELLIDAE			1		1			
TEREBELLIDAE(Loimia medusa)		1						

SITE: EAST CONTROL (NORMAN)

	WEC1	WEC2	WEC3	WEC4	WEC5	WEC6	WEC7	WEC8
AMPHINOMIDAE(Linopherus ambigua)	15		5	4	2	4	4	13
ARABELLIDAE(Arabella iricolor)								
CAPITELLIDAE (Notomastus latericeus)	1							
CAPITELLIDAE(Dasybranchus lumbricoides)								
CHRYSOPETALIDAE (Bhawania goodei)						1		
CIRRATULIDAE(Caulleriella sp.)				1	2	4	5	1
DORVILLEIDAE(Schistomeringos sp.)	7	1	12	15	11	8	21	17
EUNICIDAE(Eunice sp.)								
EUNICIDAE(Eunice gagzoi)		1	2	4	2		1	

EUNICIDAE(Eunice rubrivittata)				1	2	2		1
EUNICIDAE(Lysidice notata)	18	10	17	7	12	14	13	14
EUNICIDAE(Nematoneries hebes)					1	2		
GLYCERIDAE(Glycera abranchiata)		1						
GLYCERIDAE(Glycera oxycephala)								
HESIONIDAE(Podarke obscura)		2		1		3	5	1
LUMBRINERIDAE(Lumbrineris sp.)	1		2	2	1	1	1	3
MALDANIDAE							1	
NEREIDAE(Ceratonereis mirabilis)	3		4	1	1	3		
OPHELIIDAE(Armandia maculata)			1	1	2	3	1	
OPHELIIDAE(Polyophthalmus pictus)	8	1	2	9		3	1	1
PECTINARIIDAE (Pectinaria regalis)								
SABELLIDAE	2		2					
SERPULIDAE(Spirorbis formosus)	1		1				6	1
SIGALIONIDAE(Sthenelais gracilior)	7	6	6	2	1	2	1	2
SPIONIDAE								
SPIONIDAE(Aonides mayaguezensis)		1	2					
SPIONIDAE(Aonides sp.)	2	4	3	5		1		
SPIONIDAE(Scolelepis sp.)								
SYLLIDAE unidentified				3	1			
SYLLID (Typosyllis sp. 1)		7	5					
SYLLIDAE (Branchiosyllis lamellifera)								1
SYLLIDAE(Haplosyllis cephalata)	6					4		12
SYLLIDAE (Typosyllis annularis)						3		2
SYLLIDAE (Typosyllis sp. 2)								
SYLLIDAE(Typosyllis hyalina)			3	15	2	4	16	13
SYLLIDAE (Typosyllis corallicola)	6		6	5	3	5	11	
SYLLIDAE (Ehlersia cornuta)	2	1	7	11	5	19	42	7
SYLLIDAE(Ehlersia sp.A.)					1	4	12	1
TEREBELLIDAE					1			
TEREBELLIDAE(Loimia medusa)		1	1	1		2		2
APPENDIX 3 SEPTEMBER/OCTOBER								

SITE: WEST IMPACT
(WOLFGANG)

	SW1	SW2	SW3	SW4	SW5	SW6	SW7	SW8
AMPHINOMIDAE(Linopherus ambigua)	3	1	11	2	36	4	3	7
ARABELLIDAE(Arabella iricolor)						1	1	

CAPITELLIDAE (Notomastus latericeus)								
CAPITELLIDAE(Dasybranchus lumbricoides)				1				
CHRYSOPETALIDAE (Bhawania goodei)					1			
CIRRATULIDAE(Caulleriella sp.)		1		2		1		
DORVILLEIDAE(Schistomeringos sp.)	42	14	8	12	9	1	5	10
EUNICIDAE(Eunice sp.)		2	1					2
EUNICIDAE(Eunice gagzoi)	1		1	1				
EUNICIDAE(Eunice rubrivittata)								
EUNICIDAE(Lysidice notata)	7	13	13	9	4	4	8	15
EUNICIDAE(Nematoneries hebes)	5	3			10	2	1	
GLYCERIDAE(Glycera abranchiata)								
GLYCERIDAE(Glycera oxycephala)	1				1			
GLYCERIDAE(Glycera sp.)								1
HESIONIDAE(Podarke obscura)	1	3		1	4	1		2
LUMBRINERIDAE(Lumbrineris sp.)	6	1	4		2	1	1	2
NEREIDAE(Ceratonereis mirabilis)	1	2						1
OPHELIIDAE(Armandia maculata)	2	2				1	1	1
OPHELIIDAE(Polyophthalmus pictus)		6	7	1	7	3	2	4
PECTINARIIDAE (Pectinaria regalis)								
SABELLIDAE								
SERPULIDAE(Spirorbis formosus)	1							
SIGALIONIDAE(Sthenelais gracilior)	1	6		1	2	1	2	4
SPIONIDAE	2	1		1	2	1		4
SPIONIDAE(Aonides mayaguezensis)					2			
SPIONIDAE(Aonides sp.)	2	3		1	4	1	1	5
SPIONIDAE(Scolelepis sp.)								
SYLLIDAE unidentified								
SYLLID (Typosyllis sp. 1)								
SYLLIDAE (Branchiosyllis lamellifera)								
SYLLIDAE(Haplosyllis cephalata)				23	31			4
SYLLIDAE (Typosyllis annularis)		4						3
SYLLIDAE (Typosyllis sp. 2)			2	5	8		5	12
SYLLIDAE(Typosyllis hyalina)	16				6	2	6	
SYLLIDAE (Typosyllis corallicola)		20						
SYLLIDAE (Ehlersia cornuta)	20	8	1	16	18	2	4	
SYLLIDAE(Ehlersia sp.A.)			1	4	2		1	3
SYLLIDAE (Exogone sp.)				1				
SYLLIDAE (Synsyllis longigularis)				3				
TEREBELLIDAE								
TEREBELLIDAE(Loimia medusa)						1		

SITE: WEST CONTROL (STUART)

	SWC1	SWC2	SWC3	SWC4	SWC5	SWC6	SWC7	SWC8
AMPHINOMIDAE(Linopherus ambigua)	8	21	1	4	2		5	5
ARABELLIDAE(Arabella iricolor)								
CAPITELLIDAE (Notomastus latericeus)			1		1			
CAPITELLIDAE(Dasybranchus lumbricoides)								
CIRRATULIDAE(Caulleriella sp.)	1	1	3		1	2	3	2
DORVILLEIDAE(Schistomeringos sp.)	25	24	26	18	22	27	10	24
EUNICIDAE(Eunice sp.)	1	1	1	1			1	
EUNICIDAE(Eunice gagzoi)	1	2	1	2	1			
EUNICIDAE(Eunice rubrivittata)			3		2	2	1	
EUNICIDAE(Lysidice notata)	9	3	9	8	8	9	14	9
EUNICIDAE(Nematoneries hebes)			1		2		4	4
GLYCERIDAE(Glycera abranchiata)			1					
GLYCERIDAE(Glycera oxycephala)								
HESIONIDAE(Podarke obscura)	3	3		2	2	1	3	
LUMBRINERIDAE(Lumbrineris sp.)	3	3	2		2	1	3	2
MALDANIDAE (Clymenella somersi)					1			
NEREIDAE					1			
NEREIDAE(Ceratonereis mirabilis)		1			2		2	2
OPHELIIDAE(Armandia maculata)	1		1	1	1	2	1	1
OPHELIIDAE(Polyophthalmus pictus)	1	10	6	2	2	12	6	1
PECTINARIIDAE (Pectinaria regalis)			1				1	
PHYLLODOCIDAE (Nereiphylla fragilis)	1							
SABELLIDAE								
SERPULIDAE(Spirorbis formosus)								
SIGALIONIDAE(Sthenelais gracilior)	2				1	2	3	
SPIONIDAE			4	2		1		
SPIONIDAE(Aonides mayaguezensis)	1			2				
SPIONIDAE(Aonides sp.)	2				2	1	1	
SPIONIDAE(Scolelepis sp.)								
SYLLIDAE unidentified	3	1			4			
SYLLID (Typosyllis sp. 1)	11	5		10	20			
SYLLIDAE (Branchiosyllis lamellifera)								
SYLLIDAE(Haplosyllis cephalata)				7				3
SYLLIDAE (Typosyllis annularis)			6			2	1	
SYLLIDAE (Typosyllis sp. 2)						6		10

SYLLIDAE(Typosyllis hyalina)			1				9	
SYLLIDAE (Typosyllis corallicola)			6					
SYLLIDAE (Ehlersia cornuta)	21	11	29	72	54	9	18	41
SYLLIDAE(Ehlersia sp.A.)				1				
TEREBELLIDAE				1				
TEREBELLIDAE(Loimia medusa)	2				1		2	

SITE: EAST IMPACT
(ELLEN)

	SE1	SE2	SE3	SE4	SE5	SE6	SE7	SE8
AMPHINOMIDAE(Linopherus ambigua)		2	10	19	14	17	4	7
ARABELLIDAE(Arabella iricolor)							1	
CAPITELLIDAE (Notomastus latericeus)								
CAPITELLIDAE(Dasybranchus lumbricoides)		1			1			
CIRRATULIDAE(Caulleriella sp.)	2		1	2	1		1	
DORVILLEIDAE(Schistomeringos sp.)	2	3	9	12	4	8	8	3
EUNICIDAE(Eunice sp.)		3			1		1	
EUNICIDAE(Eunice gagzoi)	2	3		2	1		1	2
EUNICIDAE(Eunice rubrivittata)			1					
EUNICIDAE(Lysidice notata)	8	12	6	10	11	6	13	12
EUNICIDAE(Nematoneries hebes)						1		
GLYCERIDAE(Glycera abranchiata)			1	1			1	1
GLYCERIDAE(Glycera oxycephala)							1	1
HESIONIDAE(Podarke obscura)				2	1			
LUMBRINERIDAE(Lumbrineris sp.)		1	1	1	1	3	1	
NEREIDAE(Ceratonereis mirabilis)				1	1		2	1
OPHELIIDAE(Armandia maculata)								
OPHELIIDAE(Polyophthalmus pictus)	3		1					3
PECTINARIIDAE (Pectinaria regalis)				1				
PHYLLODOCIDAE (Nereiphylla fragilis)				2				
SABELLIDAE						2		1
SERPULIDAE(Spirorbis formosus)								
SIGALIONIDAE(Sthenelais gracilior)	1	2		1	2	2	5	1
SPIONIDAE	1		1	1		4	2	4
SPIONIDAE(Aonides mayaguezensis)	1				2		4	
SPIONIDAE(Aonides sp.)		5	5	8	17	5	5	2
SPIONIDAE(Scolelepis sp.)								
SYLLIDAE unidentified								

SYLLID (Typosyllis sp. 1)								
SYLLIDAE (Branchiosyllis lamellifera)				3				
SYLLIDAE(Haplosyllis cephalata)	5							8
SYLLIDAE (Typosyllis annularis)								
SYLLIDAE (Typosyllis sp. 2)	9	9	1	13	3	1	7	9
SYLLIDAE(Typosyllis hyalina)								
SYLLIDAE (Typosyllis corallicola)	1							
SYLLIDAE (Ehlersia cornuta)	8	9	6	14	9	11	19	4
SYLLIDAE(Ehlersia sp.A.)		1	2	4	5	2	5	8
TEREBELLIDAE								
TEREBELLIDAE(Loimia medusa)								

SITE: EAST CONTROL (NORMAN)

	SEC1	SEC2	SEC3	SEC4	SEC5	SEC6	SEC7	SEC8
AMPHINOMIDAE(Linopherus ambigua)	28	8	1	18	4	6	9	2
ARABELLIDAE(Arabella iricolor)								
CAPITELLIDAE (Notomastus latericeus)					1			
CAPITELLIDAE(Dasybranchus lumbricoides)	1							
CIRRATULIDAE(Caulleriella sp.)	2			1			2	
DORVILLEIDAE(Schistomeringos sp.)	9	7		11	2	3	7	
EUNICIDAE(Eunice sp.)				3		1		
EUNICIDAE(Eunice gagzoi)			1	1		2	1	
EUNICIDAE(Eunice rubrivittata)	1	3			1	3		2
EUNICIDAE(Lysidice notata)	55	16	11	23	9	12	12	10
EUNICIDAE(Nematoneries hebes)								
GLYCERIDAE(Glycera abranchiata)								
GLYCERIDAE(Glycera oxycephala)								
GLYCERIDAE(Glycera sp.)				1				
HESIONIDAE(Podarke obscura)	1	2		5	2	2	1	
LUMBRINERIDAE(Lumbrineris sp.)		1		1	1		1	
NEREIDAE(Ceratonereis mirabilis)		3		5		1		
OPHELIIDAE(Armandia maculata)		1		1				
OPHELIIDAE(Polyophthalmus pictus)	3	5		2	1	5	7	2
PECTINARIIDAE (Pectinaria regalis)					1	1		
SABELLIDAE								
SERPULIDAE(Spirorbis formosus)								
SIGALIONIDAE(Sthenelais gracilior)				1	2	2	1	1
SPIONIDAE	1	4						1

SPIONIDAE(Aonides mayaguezensis)									
SPIONIDAE(Aonides sp.)	2	2		2	2				
SPIONIDAE(Scolelepis sp.)									
SYLLIDAE unidentified									
SYLLID (Typosyllis sp. 1)									
SYLLIDAE (Branchiosyllis lamellifera)									
SYLLIDAE(Haplosyllis cephalata)				8		21	8	1
SYLLIDAE (Typosyllis annularis)							7		
SYLLIDAE (Typosyllis sp. 2)	9		1	9	7	8	5	3
SYLLIDAE(Typosyllis hyalina)	13	15		14					
SYLLIDAE (Typosyllis corallicola)									
SYLLIDAE (Ehlersia cornuta)	13	36	1	17	3	8	8	2
SYLLIDAE(Ehlersia sp.A.)	12	9	1	2		10			
TEREBELLIDAE		2							
TEREBELLIDAE(Loimia medusa)	1		1	1		1		1