INVERTEBRATE ENDOFAUNA ASSOCIATED WITH SPONGE AND OCTOCORAL EPIFAUNA AT GRAY'S REEF NATIONAL MARINE SANCTUARY OFF THE COAST OF GEORGIA

A thesis submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

in

MARINE BIOLOGY

by

ANNA KJELLIN GREENE
AUGUST 2008

at

THE GRADUATE SCHOOL OF THE COLLEGE OF CHARLESTON

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ABSTRACT

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A study was conducted to characterize the assemblages of invertebrate endofaunal organisms that live in association with the sessile epifauna inhabiting live-bottom reefs at the Gray's Reef National Marine Sanctuary (GRNMS) off the coast of Georgia. Epifaunal hosts were collected in May 2005 from areas described previously as containing densely colonized, live-bottom habitat. A subset of 24 hosts, consisting of three individuals from each of three sponge species (*Ircinia felix*, *Ptilocaulis walpersi*, and *Axinella polycapella*) and five individuals from each of three octocoral species (*Leptogorgia hebes*, *L. virgulata*, and *Titanideum frauenfeldii*), were selected for analysis in the present study. The 24 hosts examined contained a total of 132,056 solitary and 61 colonial associates, belonging to 115 taxonomic groups. Densities of endofauna were very high as compared to endofaunal densities in other areas. An analysis of similarity indicated that the composition of endofaunal associates between the two host groups were significantly different and a cluster analysis revealed further endofaunal differences among host species and morphological types. It is clear from this study that epifaunal sponges and octocorals at GRNMS provide important habitat for abundant and diverse assemblages of associated endofauna. Also, as these assemblages appear to vary among hosts, it is apparent that a thorough characterization of these endofauna for a specific ecosystem would benefit from the analysis of multiple host species.

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INTRODUCTION

The benthic habitat of the South Atlantic Bight (SAB) is primarily composed of large expanses of sandy bottom (ca 70%; Parker et al., 1983). In some areas, the soft sediment of this continental shelf is broken up by patches of hard bottom in the form of rock outcrops. The total coverage of these hard-bottom areas makes up less than 30% of the South Atlantic Bight benthos. Though spatially limited, the hard-bottom outcrops allow for the settlement and growth of a complex assemblage of organisms referred to locally as "live bottom" (Cummins *et al.*, 1962). This assemblage is generally composed of numerous species of sponges, corals, ascidians, bryozoans, hydroids, and other sessile invertebrate organisms, all of which require the hard substrate as a point of attachment (Cummins *et al.*, 1962; Struhsaker, 1969). The rocky-reef topography with its diverse epifaunal invertebrates in turn attracts numerous species of fishes, larger motile invertebrates (shrimp, crab, lobster), and populations of protected species such as the threatened loggerhead sea turtle (GRNMS(a), 1980). One of the largest near-shore, live-bottom habitats in the SAB is Gray's Reef, located 32 km east of the Georgia coastline, and encompassing 58 km^2 (Hyland et al., 2006).

In order to protect this local live-bottom habitat and encourage research to better understand it, the area was designated a National Marine Sanctuary in 1981 (GRNMS(b), 2006). In keeping with the goals identified at the time of its designation, Gray's Reef

National Marine Sanctuary (GRNMS) has been the study area for numerous research projects ranging in focus from the geology of the reef habitat (Hunt, 1974), to the infauna inhabiting the sandy bottoms surrounding the reefs (Hyland et al., 2006; Cooksey *et al.*, 2004; Rexing, 2006), to the populations of fishes and epifaunal invertebrates that the reefs directly support (Gilligan, 1989; Sedberry *et al*., 1998). Such studies have helped to demonstrate the value of these live-bottom habitats to the ecology of the area, as a reservoir of biodiversity, shelter from predation, and source of food for foraging fishes and invertebrates.

Scientific studies of the epifaunal assemblages comprising the live bottom of Gray's Reef date as early as 1969 when Hunt made some basic observations regarding the biology of the reefs in order to enhance his geological study of the region. Studies which focused solely on the composition of live-bottom epifauna, however, began in earnest with a 1983 study by Wenner *et al*. A sampling site from within sanctuary boundaries was included in their overall characterization of the invertebrate assemblages colonizing the hard-bottom habitats of the SAB. Another ongoing study has focused more specifically on the characterization of the epifauna inhabiting the live-bottom reefs of GRNMS (Gleason *et al.*, 2005). Both studies by Wenner *et al.* and Gleason *et al.*, as well as other studies conducted in the general SAB region (Pearse and Williams, 1951; Wenner *et al.*, 1984), have identified sponges and octocorals to be among the more common invertebrate epifauna comprising these live-bottom habitats. The implications of this observation are important, as such structure-forming organisms are known to serve as hosts to an abundant assemblage of smaller fauna (mostly invertebrates) living on or

within their tissues and internal spaces. Abdo (2007) refers to such associated organisms as "endofauna," which will be used similarly throughout this report.

Once called "living hotels" by Pearse (1932), sponges are a particularly important source of biogenic structure for colonization by other associated endofaunal invertebrates. Associations between sponges and their endofauna have been documented in the northeast Atlantic Ocean (Klitgaard, 1995), the northeast Pacific Ocean (Beaulieu, 2001), the Mediterranean Sea (Ilan *et al*., 1994), the Aegean Sea (Koukouras *et al*., 1985; Voultsiadou-Koukoura *et al*., 1987), the Red Sea (Fishelson, 1962), throughout the western Atlantic Ocean (Wendt *et al*., 1985; Crowe, 2001), the Caribbean (Pearse, 1950; Westinga and Hoetjes, 1981), the Gulf of Mexico (Dauer, 1973), the Great Barrier Reef (Skilleter *et al.*, 2005), and the Antarctic (Schiaparelli *et al.*, 2003). Octocorals are also known to host invertebrate endofaunal assemblages. Such associations have been studied in a number of places, including the Caribbean (Bayer, 1961) and the western Atlantic (DeVictor, 2008; Muzik, 1982), though not as thoroughly or systematically as those involving sponge hosts.

Some common patterns have emerged from these prior studies. Generally the endofauna associated with sponges are dominated by polychaetes, amphipods, decapods, and molluscs, which reside either on the sponge surface as epibionts or within the canal system as endobionts (Pearse, 1932; Wendt *et al.*, 1985; Voultsiadou-Koukoura, 1987; Duarte and Nalesso, 1996; Ribeiro *et al*., 2003). Octocorals lack the extensive canal system of sponges; however, the external surface area of their branches is able to support a variety of small invertebrates such as amphipods, gastropods, and bivalves (Patton, 1972, Wendt *et al*., 1985). While such patterns may be observed at these broad

taxonomic levels, the species composition and relative abundances of the associates often vary greatly in relation to unique characteristics of the specific host environment. Variables such as geographic location, taxonomic group of the epifaunal host (host type), host chemistry, and size and morphology of the host can all potentially affect the composition, diversity, and abundance of the associated invertebrate fauna.

Variations in the endofauna of sponges on a geographic scale have been observed in prior studies by Pearse (1950) and Westinga and Hoetjes (1981). Pearse surveyed the associates of various sponge species and noted differences in the composition and overall density of associates between sponges from Bimini and those from Dry Tortugas. He also specifically noted that the abundance of the associated fauna from the sponge *Spheciospongia vesparia* varied between the two locations. Westinga and Hoetjes compared the associated assemblage observed in their study of *Spheciospongia vesparia* from Curacao and Bonaire with that of Pearse's and found among-site differences in both species composition and relative abundance.

In addition to such geographic variations, the composition, diversity, and abundance of the associated endofauna may also vary between individual hosts collected from the same location. As examples, the influence that host type may have on the associated assemblage has been addressed by Wendt *et al*. (1985) and Fiore (2006) in studies of sponges vs. octocorals, and sponges vs. tunicates, respectively. Both studies observed the diversity and the composition of associated endofauna to vary between the two host taxonomic groups. Such variations have also been observed between two different host species within the same higher taxonomic level. Two separate studies, each comparing two species of sponge, revealed significant differences in both the

abundance and species composition of the associated invertebrate assemblage (Villamizar and Laughlin, 1991; Skilleter *et al.,* 2005). The distinctions observed were attributed to biological differences between the species of sponge. Sponges often differ visibly in the complexity of their morphological structure, which has in turn been linked to variations in the assemblage associated with those sponges (Abdo, 2007; Villamizar and Laughlin, 1991). A second biological variation that may occur between different sponge species is the chemistry of secondary metabolites that many produce. These chemicals and their individual ability to deter predation on the host may thus lead to differences in the composition and abundances of associated fauna inhabiting the host (Skilleter *et al.*, 2005). All of these possible sources of variation among host species, from geographic to biological, may influence the patterns of associated endofauna.

In addition to patterns in composition and abundance, the value of these endofaunal organisms in the general live bottom habitats has also been investigated. Many reef associates are believed to be of trophic importance, as endofaunal organisms have been observed as prey items of fishes and other larger demersal invertebrates (Caine, 1987; Lindquist *et al*., 1994). In reef habitats off the coast of North Carolina, stomach content analyses indicated that black sea bass (*Centropristis striata*) may prefer reef associated organisms as their prey; and though scup (*Stenotomus chrysops*) did appear to feed on the soft sediment infauna, reef associated prey also made up an important portion of their diet (Lindquist *et al*., 1994). Such predator prey relationships may be occurring in the Gray's Reef live bottoms; however, in order to make such connections between the reef predators and the endofauna it is first necessary to know what organisms are present in the local endofaunal assemblages. In Gray's Reef, both

sponges and octocorals have been observed to harbor endofaunal organisms; however, a

detailed characterization of these assemblages has been lacking. Thus, the present study

was conducted to provide the first characterization of the small, endofaunal forms living

in association with sponges and octocorals on the live-bottom habitat of GRNMS.

Results should be useful in helping to address one of the key strategic goals of the

GRNMS Management Plan (GRNMS(b), 2006) aimed at providing thorough

characterizations of its various ecological resources, as well as related requirements under

the National Marine Sanctuaries Act (Title III 16 USC 1431-1445 C-1) to characterize,

protect, and manage such areas.

PURPOSE OF STUDY

The present study is part of a broader project designed to characterize the assemblages of small, invertebrate endofaunal organisms that live in close association with larger sessile epifauna inhabiting live-bottom habitats of GRNMS off the coast of Georgia. While a variety of host species (sponges, octocorals, bryozoans, hydrozoans, tunicates, attached bivalves) were collected as part of the overall supporting field effort, the present study focuses on an examination of the fauna associated with a subset of sponge and octocoral species.

Primary Objective

The primary objective of the present study is to characterize the species composition, abundance, and diversity of the assemblages of small invertebrate organisms living in association with common sponge and octocoral epifauna of GRNMS. This objective is addressed through the examination of invertebrate, endofaunal associates from a total of 24 epifaunal hosts, consisting of three individuals from each of three sponge species (*Ircinia felix*, *Ptilocaulis walpersi*, and *Axinella polycapella*) and five individuals from each of three octocoral species (*Leptogorgia hebes*, *Leptogorgia virgulata*, and *Titanideum frauenfeldii*), collected from five random transects at GRNMS.

Secondary Objective

A second objective is to evaluate patterns of potential variation in these associated assemblages between the two host groups and among host species within a group.

MATERIALS AND METHODS

Study Area

GRNMS is located in inner-shelf waters 32.2 kilometers east of Sapelo Island,

Georgia (Figure 1). The sanctuary boundaries encompass 58 km^2 (GRNMS(a, b), 2006;

Hyland et al., 2006) of which ca. 25% is considered to be live bottom (Kendall et al.,

2005). These live-bottom habitats are created by limestone outcrops that form a

complexity of ledges, caves, and troughs colonized by a diverse assemblage of epifaunal

organisms (Figure 2; Hunt, 1969). Kendall et al. (2005) describe these areas as

consisting of low-relief sparsely colonized hard bottom (SCHB), which cover about 25%

of the sanctuary seafloor, and higher-relief (0.5-2 m) densely colonized hard bottom

(DCHB), which represents < 1% of the sanctuary seafloor.

Field Sampling

Sample Collection

Field sampling took place May 2–11, 2005 from the NOAA ship Nancy Foster.

Five sampling areas were chosen randomly from a larger population of sites within the

sanctuary known to consist of densely colonized, live-bottom habitat (Figure 3, from

Kendall et al., 2005). At each site, scuba divers traversed a 12 m transect through the

live-bottom habitat and captured video clips in order to observe the organisms in their

natural habitat. Four replicate quadrats, each measuring 0.25 m^2, were placed evenly

along the transect in progress. All targeted organisms that fell within each of these

quadrats were collected by the divers. Targeted organisms consisted of sponges,

bryozoans, tunicates, zooantharians (sea fans, sea whips, sea pens, sea pansies),

hydrozoans, and attached bivalves. Collections were limited to organisms < 50 cm high

in order to minimize impacts on the sanctuary ecosystem.

The collections were accomplished by placing a plastic bag of appropriate size

over the organism and gathering the bag at the base. The organism was then detached

from the substrate and the plastic bag sealed. Ideally this method minimized the number

of associated organisms lost from the surface of the host. Once filled, the plastic bags

were placed in a mesh bag numbered for the corresponding replicate quadrat and

transported to the ship for processing. Water depth, temperature, salinity, dissolved

oxygen, and pH were also measured at each site through the use of a CTD.

Shipboard Processing

All seawater inadvertently collected with each host sample was poured out of the

plastic bag and through a 0.5 mm sieve. Anything retained on the sieve was washed into

a labeled storage container and fixed in a 10% buffered-formalin solution. A photograph

of the host was recorded to document the original shape and color of the organism and

was later used to assist in identification of host species. The volume of the host was then

estimated, based on water displacement, after which the host was transferred to a storage

container and fixed in a 10% buffered-formalin solution. The water used in the volume

measurement was also sieved and all organisms retained were saved and preserved with

those from the original collection bag. All hosts and associates were transported back to the laboratory for further processing upon completion of the cruise.

Lab Processing

Upon arrival in the laboratory all samples were transferred from the 10% buffered-formalin solution that was initially used to fix the organisms into a 70% ethanol solution for long-term preservation. This transfer was completed within seven days of collection for all host organisms. The decanted formalin was passed through a 0.5 mm sieve so as not to lose any associated organisms and the hosts were individually rinsed over a 0.5 mm sieve in order to capture any lingering associated surface organisms that may have become dislodged during the rinse. The host organisms and their associates were then stored in separate containers for further processing.

Host Identification and Selection

Each host sample was identified to the lowest practical identification level (LPIL) using the photographs taken in the field, taxonomic keys, and the primary literature. As noted above, the overall field sampling effort was designed to provide enough data (and host species representation) to complete a full-scale characterization of the endofaunal assemblage living in association with the epifauna of GRNMS. However, the time frame of the present study, supporting a graduate master's degree, could not accommodate the processing of all samples collected, especially given the enormous abundance of organisms comprising these endofaunal assemblages. Thus a subset of the total host

collection is used in the present study and the remainder has been archived for possible future analysis to supplement what is reported here.

Porifera and Octocorallia were the dominant members of the epifaunal host collection, thus it was anticipated that they would provide the best representative subset of host species for a characterization of the associated organisms inhabiting the live-bottom habitat at GRNMS. Individual host specimens from each host category and species were selected from as many transects and size ranges as possible in order to maximize the overall representation of samples throughout GRNMS. As a result, a subset of 24 epifaunal hosts, consisting of three individuals from each of three sponge species (*Ircinia felix*, *Ptilocaulis walpersi*, and *Axinella polycapella*) and five individuals from each of three octocoral species (*Leptogorgia hebes*, *Leptogorgia virgulata*, and *Titanideum frauenfeldii*), were selected for analysis in the present study (Table 1).

Sorting and Identification of Associated Individuals

Once host species were selected and identified, sorting and enumeration of associated organisms proceeded. One sample at a time, the host organisms were sectioned into manageable pieces, placed in a Petri dish, and pulled apart in order to remove all associated individuals. These animals were placed into small vials and counted as they were separated into general taxonomic groups. The preservation of all associated organisms was maintained with the addition of 70% ethanol to the vials. Each individual vial was then labeled with the sample ID, the date of sorting, the taxonomic group, and the number of organisms in the vial. A rigorous quality assurance/quality control (QA/QC) procedure was applied in order to maintain a sorting efficiency of 95%.

Accordingly, for every ten host animals dissected, one was randomly selected to be re-dissected and sorted by a second qualified party. A sorting efficiency of less than 95% in the representative sample would require the re-sorting of all samples associated with that representative. However, no QA/QC tests were failed and thus no samples required re-sorting.

All associated organisms were identified to the lowest practical identification level (LPIL), i.e. to family level (or lower if possible), using taxonomic keys, primary literature, and, as necessary, consultation with experts. As they were identified, the organisms were counted into small vials that corresponded to the taxonomic identifications. Taxonomic consultation was sought for any problematic taxa. In addition, for each LPIL identified, a voucher specimen was set aside for further QA/QC purposes. This step in the QA/QC process consisted of having at least 10% of the voucher specimens re-identified by a second party with expertise in the particular taxonomic group being validated. Any specimens found to differ from their original identification would have required all other individuals previously identified to that family to be reconsidered. Fortunately, all voucher specimens were found to be correctly identified so no further corrective measures were necessary.

Data Analysis

All associated organisms from the 24 sponge and octocoral hosts were identified and enumerated; however, colonial and unidentifiable larval members were only marked as present or absent and not included in the present data analysis. All statistical analyses were performed using the R Project for Statistical Computing (R Development Core

Team, 2008) with the exception of the Similarity Percentages (SIMPER) analysis, which was performed in the PRIMER software package (Clarke and Gorley 2001).

Abundance, density, percent total, and frequency of occurrence were calculated as response variables for each associated taxonomic group regardless of host, as well as for the dominant taxonomic groups associated with each of the two distinct host groups and each of the six host species. In addition to these variables, the number of species (s), the Shannon index of diversity (H' using base-2 logarithms) (Shannon and Weaver, 1949), evenness (J') (Pielou, 1975), and the Margalef measure of species richness (SR) (Margalef, 1958) were also calculated for the endofaunal assemblages on each of the 24 host individuals. Student t-Tests were used to compare the above response variables between the two host groups of sponges and octocorals and one-way analysis of variance (ANOVA) was employed to compare these same response variables among the three species of each host group. The Kruskal-Wallis non-parametric test was used in place of the one-way ANOVA if the assumptions of the ANOVA were not met before and after appropriate data transformations. In the case of significant ANOVA results, Tukey's Honestly Significant Difference test was used as a post-hoc comparison to determine which of the three host species within a host group was significantly different.

Possible differences in the composition of associated endofauna were examined among the hosts both quantitatively and graphically. Both types of analyses were based on a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) calculated from double-square-root transformed abundance data standardized to the volume of the host organism (individuals per cm^3 of host tissue). Due to varying levels of identification of the associated organisms, all taxonomic groups were rolled to the level of family for the

construction of this matrix. Normal (Q mode) hierarchical cluster analysis (using group-average sorting as the agglomeration method), in combination with non-metric multidimensional scaling, were performed to display patterns in the assemblages associated with the various host organisms. A Similarity Percentages (SIMPER) analysis was also performed on double-square-root transformed, family-level density data to investigate which endofauna contributed most to the separation of cluster groups. An analysis of similarity (ANOSIM) was performed to compare statistically the composition of the associated endofauna between the two host groups and an additional SIMPER analysis was run (using untransformed density data) to illustrate which endofaunal families were varying between the two host groups.

In addition to the normal (Q-mode) cluster analysis, an inverse (R-mode) cluster analysis also was performed on the data to look for patterns in the groupings of associated fauna based on host samples as attributes. Like the normal cluster analysis, the inverse analysis was based on a Bray-Curtis dissimilarity matrix and had all taxonomic groups rolled to the level of family. However, in this analysis the number of families included was reduced to those that made up greater than 1% of the associated assemblage of any one host organism (Field *et al*. 1982), and the dissimilarity matrix was calculated from untransformed, standardized abundances. Each family within a host organism was standardized to the total for that family across all host organisms (Field *et al*. 1982).

RESULTS

Host Epifauna

The overall sampling effort for this project generated numerous epifaunal hosts, but as noted above only three species of octocoral and three species of sponge were selected for the present analysis. These hosts were the octocorals *Leptogorgia hebes* (Figure 7)*, Leptogorgia virgulata* (Figure 8), and *Titanideum frauenfeldii* (Figure 9) and the sponges *Ircinia felix* (Figure 4)*, Ptilocaulis walpersi* (Figure 5)*,* and *Axinella polycapella* (Figure 6). Each of the octocoral species included five replicate individuals, while each of the sponge species included three individuals. The individual replicates of each host species were of varying volumes and, as desired, represented different locations throughout the sanctuary's live bottom habitats (Table 1).

Abundance and Diversity of Associated Fauna

Dissection of the 24 sponge and octocoral host organisms yielded a total of 132,056 solitary endofauna (Table 2) and 61 occurrences of colonial endofauna (Table 3) representing 115 taxonomic groups (100 solitary, 15 colonial). All subsequent calculations of diversity, evenness, number of taxa, and species richness were based only on the solitary associates. The diversity of the overall assemblage associated with the sponges and octocorals of GRNMS was calculated to be 2.18 with an evenness of 0.47

and a species richness of 8.4. Of the individual associates, 75,305 were observed

inhabiting sponge hosts, while the remaining 56,751 originated from octocoral hosts.

This difference in abundance between the two host groups was not significant (Table 5),

however, it was notable that when normalized for the volume of tissue sampled for each

host group, the octocoral hosts had a higher abundance of associates per cm^3 of tissue

than did the sponge hosts (Figure 10). Because there was substantial variation in the

volume of the host specimens, the remaining analyses of abundance all consider the

abundance of associates per cm^3 of host tissue. The slight differences in the abundance

of the associated populations between the two host groups were observed to a greater

degree at the level of the host species within each group. Within the sponge hosts, the

associated fauna of both *P. walpersi* and *I. felix* showed higher mean abundances than *A.*

polycapella, but only the fauna of *P. walpersi* were significantly higher (Figure 11). The

endofauna associated with the octocoral hosts showed a similar trend with two of the

hosts having a higher abundance of associates than the other. In this case, however, both

L. hebes and *L. virgulata* had a significantly more abundant endofaunal assemblage than

T. frauenfeldii (Figure 11).

In addition to abundance, differences in number of species, species richness,

diversity, and evenness were also calculated and statistically compared between host

groups and between host species within each host group (Tables 4 and 5). Neither the

diversity nor the evenness of the endofaunal assemblage was observed to be significantly

different within or between host groups, as there was a great deal of variation of these

two measurements between individuals of many of the host species (Figure 12). The

mean diversity calculated for endofauna associated with the sponge hosts was 1.41 but

ranged from a low of 0.28 to a high of 2.16. There was a great deal of variation in the diversity of those endofauna associated with the *I. felix* sponge hosts and this was also true, to a lesser extent, of those associated with the *A. polycapella* sponge hosts. Individuals of the sponge *P. walpersi*, in contrast, hosted an endofaunal assemblage with a more consistent diversity. The variation observed in the evenness of the sponge associates mirrored that of the diversity. The octocorals had a similar result to the sponge hosts in that there was a great deal of variation in the diversity of the associated endofauna across host individuals. The mean diversity value was calculated as 1.25 but ranged from 0.27 to 2.20. The diversity of assemblages associated with *L. virgulata* and T. *frauenfeldii* varied greatly, but like *P. walpersi* of the sponge hosts, the diversity of the endofauna associated with *L. hebes* remained comparatively stable. Again, as observed for the sponge hosts, the evenness of the endofauna varied similarly to diversity.

Unlike diversity and evenness, there were significant differences detected in the measurements of number of taxa and species richness. Though not observed at the level of host groups, such differences were detected among the various species within each host group (Table 5). The endofauna associated with *I. felix* and *P. walpersi* were both determined to have a greater number of associated taxa and greater species richness than *A. polycapella*, however only the difference between *I. felix* and *A. polycapella* was significant (Figure 13). Within the octocoral hosts, the endofauna associated with *L. hebes* was significantly greater in both number of taxa and species richness than that of *T. frauenfeldii*. The endofauna associated with *L. virgulata* was also higher in number of taxa and species richness than *T. frauenfeldii*, though not significantly (Figure 14).

Composition of Endofaunal Assemblages

Overall Associated Assemblage

Of the many taxa inhabiting the reef epifauna, amphipods and polychaetes were by far the most abundant, representing 96% of the total endofauna, followed by gastropods, anthozoans, barnacles, and nematodes (Table 6). These six taxonomic groups account for more than 99% of the total associated assemblage. While the amphipods were the most abundant group present in the endofauna (59%), the polychaete *Haplosyllis spongicola* was the single most abundant species. This polychaete represented 36% of the total abundance of all associates, though present on only 11 of the hosts. The remaining individuals representing at least 1% of the total endofauna were all amphipods (Table 7). The most abundant of these amphipods were juveniles of the family Caprellidae, representing 20% of the total assemblage and inhabiting all 24 of the host organisms. The genus *Ericthonius* was the second-most abundant amphipod taxon, which was observed in all but one of the host organisms and represented 17% of the total assemblage. *Caprella equilibra* contributed 13% of the total endofauna and like the juveniles of the same family, were present on all of the host epifauna. The final two amphipods with an abundance of greater than 1% were *Microjassa* and *Photis* which were observed on 13 and 19 hosts respectively.

Sponge Hosts

The six major taxonomic groups previously mentioned as contributing to 99% of the total endofaunal assemblage were not uniformly distributed throughout the epifaunal host organisms (Figure 15). While amphipods were observed to be the most abundant

group overall, this observation did not extend to the host sponges. Of the endofauna associated with these epifauna, the polychaetes were the most abundant group. Contributing heavily to this inconsistency were individuals of the polychaete *H. spongicola*. This single polychaete made up 63% of the endofauna associated with sponge hosts, were present on all of the host sponges collected, and were observed to be the most abundant associates on the sponge hosts as a group (Table 8). Because *H. spongicola* was overwhelmingly abundant, its numbers were removed and the total faunal percentages were re-calculated for the remaining associates to allow a better understanding of the contributions of some of these less numerous, yet still dominant, members (Table 8).

The amphipod *Ericthonius* was second in dominance to *H. spongicola* and made up 19% of the endofauna associated with the sponge hosts, though it was observed in low abundance in two specimens of *A. polycapella* and was absent in the third. In addition to *H. spongicola*, the only other associates to be present on all of the individual host sponges were juveniles of the family Caprellidae and individuals of *Caprella equilibra*, which contributed to 5% and 3% of the associated assemblage respectively. Other organisms that contributed to at least 1% of the sponge endofauna were less consistent in their occurrence on host species. Members of the gastropod family Vitrinellidae and *Actiniaria* sp. A (with the exception of one individual) were observed only in samples of the sponge *I. felix*. The Amphipod *Gammaropsis* was slightly more prevalent, appearing as a dominant associate of both *P. walpersi* and *A.polycapella*, though not *I. felix*. *Microjassa* was another amphipod observed in abundance on the sponge host *P. walpersi* and was absent from all other host sponges with the single exception of one individual on

one specimen of *I. felix*. The amphipod *Photis* was a dominant in both *I. felix* and *P. walpersi,* but was rarely observed (with the exception of one individual) in the assemblage associated with *A. polycapella*.

Octocoral Hosts

As was observed for both host groups combined, amphipods clearly dominated the endofauna associated with octocorals (Figure 15). This dominance was largely due to the presence of the family Caprellidae. Thirty-nine percent of the endofauna associated with the octocoral hosts were dominated by juveniles of this family, which were present on every octocoral host specimen collected (Table 9). The dominance of juvenile Caprellidae was closely followed by adults of *Caprella equilibra* which were also present on all octocoral hosts and contributed 26% of the total endofauna associated with these octocorals. These two groups of amphipods were the top-two dominants on all three octocoral host species. Just as *H. spongicola* overwhelmed the endofauna associated with the sponge hosts, so did the juvenile caprellids with respect to octocoral hosts. Thus, similar to the analysis of sponges with and without *H. spongicola*, the octocoral data were analyzed for dominance with and without the presence of juvenile Caprellidae to better understand the remaining endofaunal assemblage (Table 9).

A third amphipod, *Ericthonius*, made up 12% of the total octocoral endofauna, and like the Caprellidae, was observed associated with all 15 of the octocoral hosts. The remaining six associated groups that contributed to at least 1% of these endofauna were more intermittent in their distribution among the octocoral host species. *Microjassa* was the third most abundant associate of the octocoral hosts, contributing 14% of the total

assemblage; however, this dominance was mainly due to its abundance on the *L .hebes*

hosts, as it was far less common on *L. virgulata* and *T. frauenfeldii*. The only barnacle

found among the octocoral hosts was *Conopea galeata* and while it was a dominant

species in the context of the overall endofauna associated with octocorals, like

Microjassa it was not particularly abundant on specimens of either *L. virgulata* or *T.

frauenfeldii*. The amphipod family Stenothoidae was another associate that was more

abundant on *L. hebes* than the other octocoral hosts, on which it contributed to less than

1% of the total abundance associated with these two species. The final three associated

organisms that contributed to at least 1% of the total octocoral endofauna were the

amphipods *Photis* and *Gammaropsis* and the Nemata, all of which were dominant only in

the host species *L. virgulata*.

Similarity of Endofaunal Assemblages

Normal Analysis

The normal cluster analysis indicated that the endofauna associated with each of

the host sponge species were relatively distinct, as the three specimens of each species of

sponge clustered among themselves (Figure 16). When the endofauna of these cluster

groups were compared in a SIMPER analysis, much of the dissimilarity between the two

sponge hosts *I. felix* and *P. walpersi* resulted from the greater amphipod abundances on

P. walpersi, particularly with respect to the families Caprellidae and Ischyroceridae

(specifically *Microjassa*) (Table 10a). Also influential were two families of molluscs,

Vitrinellidae and Hiatellidae, both of which were present only on *I. felix* and which

contributed to 2.9% and 5.7% of the dissimilarity respectively. Despite their distinctions,

specimens of *P. walpersi* and *I. felix* shared a number of common associates that were missing from the endofauna of *A. polycapella*. The absence of the family Ischyroceridae (specifically *Ericthonius*) from the endofauna of *A. polycapella* had the greatest influence on the dissimilarity between *A. polycapella* and the other two sponge hosts (Table 10b). Two other amphipod families were also important; both Isaeidae (specifically *Photis*) and Ampithoidae were absent from the endofauna of *A. polycapella* and each contributed 4% and 3.25% respectively to the dissimilarity between *A. polycapella* and specimens of *I. felix* and *P. walpersi*. Amphipods were not alone in distinguishing the endofauna of *I. felix* and *P. walpersi* from that of *A. polycapella*. The polychaete family Terebellidae and the tanaid family Leptocheliidae also contributed to this dissimilarity, as they were both absent from hosts of *A. polycapella*. In addition to these differences, *A. polycapella* hosts also contained no colonial endofauna, which was in stark contrast to both *P. walpersi* and *I. felix*.

The substantial differences in the endofaunal assemblages that were observed between host specimens of *P. walpersi* and *I. felix* and specimens of *A. polycapella* illustrated that the endofauna associated with *P. walpersi* (Group 1) and *I. felix* (Group 2) were more similar to one another than to those associated with *A. polycapella* (Group 6). Interestingly, instead of grouping with the other sponge hosts, *A. polycapella* clustered more closely with one of the octocoral host species, *T. frauenfeldii* (Group 5). The similarity of these two groups may be due to the consistently lower numbers of taxa and abundances of endofauna that were observed as compared to the various other sponge and octocoral host species.

The distinction between the endofauna associated with the three octocoral species was not as clear as that of the sponge hosts. All five specimens of the octocoral *L. hebes* (Group 3) clustered together, as well as the five specimens of *T. frauenfeldii* (Group 5). The endofauna associated with these two species groups varied greatly, as *L. hebes* hosted assemblages that were far more abundant and had a greater number of taxa present than those of *T. frauenfeldii* even for the most dominant associates (Table 9, Table 4). However, unlike the distinct clusters for *L. hebes* and *T. frauenfeldii*, two of the *L. virgulata* hosts clustered together (Group 4) while three were incorporated into the *L. hebes* and *T. frauenfeldii* clusters. These three cluster groupings of *L. virgulata* were compared in a SIMPER analysis to determine which endofauna were contributing to the dissimilarities between the host specimens. Much of the dissimilarity (~25%) between the *L. virgulata* specimens which clustered with *L. hebes* (Group 3) and the two that clustered individually (Group 4) could be attributed to a difference in abundances of the amphipod families Ischyroceridae, Isaeidae, Melitidae, and Caprellidae (Table 11a). Also of importance in this dissimilarity was the occurrence of the families Pteriidae and Styelidae. These winged oysters and solitary ascidians were present in cluster Group 3, though they did not appear on any of the other octocoral hosts. Thirteen percent of the dissimilarity between the specimen of *L. virgulata* that clustered with *T. frauenfeldii* (Group 5) and those that clustered individually (Group 4) was due to the absence of associated individuals of *Conopea galeata* (family Archaeobalanidae) (Table 11b). This barnacle was associated with all other *Leptogorgia* hosts, but with none of the *T. frauenfeldii* hosts (Table 2).

MDS and ANOSIM

      The results of the non-metric multidimensional scaling repeated those of the normal cluster analysis (Figure 17). The individual specimens of each of the three species of sponge grouped together, with the host species *I. felix* and *P. walpersi* falling closer to each other than to the individuals of *A. polycapella*. The octocorals split into three groups, one containing all of the specimens of *L. hebes* and two specimens of *L. virgulata*, one containing all of the specimens of *T. frauenfeldii* and one specimen of *L. virgulata*, and one containing the final two specimens of *L. virgulata*.

      Both the cluster analysis and the MDS plot indicated that fauna associated with the sponge *A. polycapella* and the octocoral *T. frauenfeldii* were more similar to each other than to the other host species. The same was observed for the sponges *I. felix* and *P. walpersi* and for the two *Leptogorgia* octocorals. However, an analysis of similarity (ANOSIM) revealed that there was a significant difference (p-value < 0.001, R = 0.5604) in the assemblage composition between the overall octocoral and sponge host groups. Thus, with some exceptions, there appear to be distinct differences in the associated fauna of sponges vs. octocorals. A SIMPER analysis revealed that 42% of this difference was due to the family Caprellidae, i.e. amphipods that were far more abundant on the octocoral hosts. Also, the polychaete family Syllidae was more abundant on the sponge hosts and contributed 29% of the difference between the two host groups (Table 12).

Inverse Analysis

      The inverse cluster analysis (performed on family-level data) resulted in five groups of associated fauna (Figure 18). The first two groups (Groups A and B) were

families that were common on specimens of the sponge *I. felix*, though Group A families were also common on host specimens of the sponge *P. walpersi* and octocoral *L. hebes*. A third faunal group (Group C) was composed of only two families, both of which were common to all of the octocoral hosts. Group D consisted of families that were the most abundant on the two species of *Leptogorgia,* though also common on the other host species. The remaining faunal cluster group (Group E) was composed of families that were not specific to any one host species or type, but were observed in associated assemblages across all of the host specimens.

Environmental Variables

Little variation was observed in the measurements of depth, salinity, temperature, pH, and dissolved oxygen among the five transect sites (Table 13). Thus, while serving as a record of environmental conditions for the study, these variables were not considered as possible controlling factors contributing to observed among-sample variations in the assemblages of epifaunal associates.

DISCUSSION

Endofaunal Diversity and Abundance

The complex structures provided by epifaunal invertebrates such as sponges and octocorals are known to harbor assemblages of smaller endofaunal metazoans (mostly invertebrates). The present study sought to characterize such endofaunal assemblages living in association with common sponge and octocoral species of the live-bottom habitats of GRNMS. To address this goal, five individuals from each of three octocoral species and three individuals from each of three sponge species were selected as representative host specimens from a larger collection of epifauna, obtained from DCHB areas of the sanctuary in May 2005.

Associated endofauna were not only present in all 24 of the host specimens, but these assemblages also appeared to be highly abundant and diverse as evidenced by densities and family-level richness values that are substantially larger than those typically reported in similar studies. There were a total of 115 identifiable taxa observed in the endofaunal assemblages of GRNMS; however, comparisons of taxonomic richness between the present study and others were made at the family and higher level of identification as the present study only identified the more common endofauna to the species level. A total of 101 families or higher-level taxa were encountered in the present study. Other studies incorporating a similar number of host organisms have reported

between 50 and 70 associated endofaunal families (Voultsiadou-Koukoura et al., 1987; Ribeiro et al., 2003; Duarte and Nalesso, 1996; Fiore, 2006). Of these prior studies, only Fiore (2006) considered the endofauna associated with more than one epifaunal host type by surveying both sponges and tunicates. From this latter survey, Fiore observed a richness of 70 associated families, which was the highest reported among the previously mentioned publications. In the present study, 71 and 81 families were identified from octocoral and sponge hosts, respectively. While each of these assemblages had a family-level richness nearer to those of previous publications dealing with a single host group, the two together revealed the presence of a much richer assemblage of associated fauna overall.

In addition to the presence of a large number of taxonomic families, the abundances of these associated endofauna were unexpectedly high as well. A total of 132,056 endofaunal specimens (solitary forms) were encountered among the 24 sponge and octocoral hosts. Because the abundances of these fauna are thought to vary with the amount of host tissue available for colonization (Westinga and Hoetjes, 1981; Villamizar and Laughlin, 1991; Duarte and Nalesso, 1996) it is useful to report abundances as densities based on the volume of the hosts from which the associates were collected. Thus, normalizing the associated endofauna of each host to the corresponding host volume yielded an average density of 27 individuals per cm^3 of host tissue. This density is still far higher than what has been observed in other related studies, which include values ranging from a low of 0.05 individuals per cm^3 (Koukouras *et al*., 1985) to a high of 3.42 individuals per cm^3 of host tissue (Peattie and Hoare, 1981). The average density of invertebrate endofauna in the present study was similarly high for both the host

sponges and octocorals. Endofaunal densities averaged 22.7 individuals per cm^3 for sponges and 29.6 individuals per cm^3 for octocorals. The high densities and diversity of endofaunal assemblages found in the present study of living resources at GRNMS is a particularly important take-home message from a sanctuary-management perspective.

The densities of these endofaunal assemblages also appear to be higher in comparison to other components of the benthos at GRNMS. For example, infaunal densities at GRNMS appear to be much lower on a per-volume basis, ranging in one sanctuary wide study from an estimated 0.004 to 0.503 individuals per cm^3 of sediment (based on mean densities of 423 to 50,258 per m^2, as reported in Hyland *et al.*, 2006, and assuming an average sediment sampling depth of 10 cm). In addition, Rexing (2006) looked at infaunal assemblages in close proximity to live-bottom reefs at GRNMS and found densities ranging from an average of 0.104 to 0.130 individuals per cm^3. Wendt *et al.* (1985) discussed such a pattern of heightened abundances of endofauna vs. infauna and attributed it to the possible benefits that the endofauna may be deriving from their association with the host organism. Such benefits may include protection from environmental stressors (Frith 1976) or predation (Klitgaard 1995), access to a food source (Patton 1972), or simply a substrate to inhabit (Westinga and Hoetjes, 1981). Regarding the latter point, many invertebrate host species provide a more structurally complex habitat than the surrounding soft-bottom sediments. Any of these benefits could potentially compel organisms to associate with host epifauna at densities higher than observed for the surrounding infauna.

Sponge Hosts

The endofaunal assemblages inhabiting sponge hosts in the present study were dominated by polychaetes and amphipods. Amphipod crustaceans made up 31.7% of the associated endofauna and of these organisms, the genus *Ericthonius* was the most abundant. The presence of *Ericthonius* as a dominant associate of sponges is consistent with other previous studies. For example, Wendt *et al.* (1985) and Costello and Meyers (1987) both found this species to be a dominant inhabitant of sponges, though neither study converted their abundance values into density estimates for comparative purposes. Ribeiro et al. (2003) also observed *Ericthonius* as a dominant associate of sponges from southeast Brazil at a density of 0.063 individuals per cm^3. In contrast to this study and consistent with the higher abundance noted for the overall endofaunal assemblage, in the present study a total of 14,675 individuals of *Ericthonius* were recorded at an average density of 5.59 individuals per cm^3 of sponge tissue. Also dominant were amphipods of the family Caprellidae. With respect to endofauna living on sponge hosts, this family reached its highest abundance on the sponge *P.walpersi* and maintained densities averaging 2.24 individuals per cm^3 of sponge tissue for juveniles, and 1.70 individuals per cm^3 of sponge tissue for adults of *Caprella equilibra*. Ribeiro *et al.* (2003) observed members of this family, including gravid females, at a lower density of 0.005 individuals per cm^3 of sponge tissue. However, Peattie and Hoare (1981) found the closely related species *Caprella linearis* to be a common inhabitant of sponges with an average density of 2.02 individuals per cm^3 of sponge tissue.

In addition to *Ericthonius* and the family Caprellidae, other amphipods that were commonly observed on sponge hosts (i.e., at high densities and/or high frequencies of

occurrence among host samples) were *Microjassa spp.*, *Gammaropsis spp.*, *Photis spp.*,

and the families Podoceridae, Stenothoidae, and Ampithoidae. Each of these groups of

amphipods have been observed previously as common, if not dominant, members of the

endofauna associated with sponges (Peattie and Hoare, 1981; Ribeiro *et al*., 2003;

Koukouras *et al.*, 1985). One family of amphipods that was expected to occur at higher

abundances than were observed was the Leucothoidae. This family has been observed in

prior studies to be among the most dominant associates of sponges (Westinga and

Hoetjes, 1981; Wendt *et al*., 1985; Koukouras *et al*., 1985; Ribeiro *et al.*, 2003) and

though documented here as a dominant of *I. felix*, the family made up only 0.19% of the

total endofauna associated with sponges.

While amphipods made up 31.7% of the endofauna associated with sponge hosts,

the polychaetes were the most abundant group, contributing to 64.5% of the total sponge

associates. There were a total of 16 families of polychaetes associated with the sponge

hosts; however, one species – *Haplosyllis spongicola* – accounted for 98.6% of the total

polychaete abundance on sponges. Though rarely present in the second host type

(octocorals), its high numbers in sponges resulted in it being the most abundant

endofaunal member overall regardless of host type. *Haplosyllis spongicola* is a parasitic

polychaete of the family Syllidae that has been observed inhabiting various species of

sponge (Magnino *et al*., 1999; Dauer, 1973; Lopez *et al*., 2001; Klitgaard, 1995) from

locations as widespread as the western Atlantic (Fiore, 2006; Wendt *et al.*, 1985), the

Indian Ocean (Magnino and Gaino, 1998; Magnino *et al.,* 1999), and the Mediterranean

Sea (Lopez *et al.,* 2001). This polychaete generally lives in large aggregations,

particularly when observed in tropical settings (Lopez *et al*., 2001) and individuals may

reside in either the canals or the internal tissue of the sponge. Although believed to

consume host tissue, and in spite of substantial densities, the parasitic aggregations of *H.*

spongicola have been observed to have little to no impact on the growth rate or

reproductive abilities of the host sponges (Neves and Omena, 2003; Tsurumi and

Reiswig, 1997). Even in sponges under nutritional stress, the hosts remained able to

support this parasite at considerably high densities (Maldonado and Young, 1998).

In the present study, individuals of the polychaete *H. spongicola* were observed in

all of the sponge species collected, though the highest densities were recorded from

specimens of *Ircinia felix* (up to 32.42 per cm^3). The larger populations of *H. spongicola*

present in *I. felix* may be due, in part, to the morphological structure of this sponge

species. Neves and Omena (2003) observed that lobate sponges, such as *I. felix*, often

support denser populations of *Haplosyllis* than other sponges, possibly due to high

growth rates that can accommodate the parasitic activity. Maldonado and Young (1998)

similarly reported densities of *H. spongicola* in samples of *I. felix* as high as 20 to 50

individuals per cm^3 of host tissue.

While the aggregations of *H. spongicola* may not have a deleterious effect on the

host organism, it has been proposed that they may have an impact on the rest of the

associated assemblage. High densities of *H. spongicola* in host sponges, for example,

have been linked to a reduction in the overall diversity of the associated polychaete

endofauna (Neves and Omena, 2003). In the present study, the largest variation in

densities of *H. spongicola* were displayed in samples of *I. felix* (0.02, 14.9, and 32.4

individuals per cm^3 among the three individual specimens) and this pattern was inversely

related to H' diversity indices calculated for the overall endofaunal assemblages associated with these same specimens (i.e., 2.16, 1.77, and 0.28 respectively).

Octocoral Hosts

Octocoral hosts were consistently dominated by amphipod crustaceans, which comprised 96.3% of the associated endofaunal assemblage. This finding is supported from the literature by the only other quantitative study of octocoral associates (Wendt *et al.*, 1985). The most abundant amphipod species inhabiting octocorals in the present study was *Caprella equilibra*, which also was observed as a dominant by Wendt *et al* (1985), though at lower abundances. The abundances given in the Wendt *et al.* study were not reported on a per-volume density basis; however, as it was the only other quantitative study regarding the endofauna associated with octocorals, a tentative comparison will be made here. Accordingly, Wendt *et al.* observed only 119 individuals of *C. equilibra* among nine host specimens. In contrast, 14,793 individuals of *C. equilibra*, in addition to 22,470 juveniles of the parent Caprellidae family, were observed among the 15 octocoral hosts examined in the present study.

The Caprellidae are a family of amphipods specifically adapted for an epibiotic existence of clinging to the surfaces of various biotic structures including algae, hydroids, sponges, and octocorals (Sconfietti and Luparia, 1995; Guerra-Garcia, 2001). Many species of Caprellidae have been documented to breed year round and juveniles of *C. equilibra* have been observed on various substrates throughout the year (Sconfietti and Luparia, 1995; Bynum, 1978). While this would indicate that previous studies of host octocorals should have reported an abundance of juvenile caprellids similar to that of the

present study, the breeding activity of *C. equilibra* has been observed to fluctuate with peaks in the spring months. The samples for the present study were collected in early May while those for Wendt *et al.* were collected in the summer and fall, which may explain part of the observed abundance variations between the two studies. However, there was still a far greater abundance of adult *C. equilibra* observed in the present survey. The presence of Caprellid amphipods on octocorals, similar to the presence of the polychaete *H. spongicola* and gammarid amphipod *Ericthonius* on sponges, contributed largely to the unusually high abundances observed among the various sponge and octocoral host species overall.

Other associates of octocorals were observed at relatively high abundances as well. For example, two other dominant amphipods were *Microjassa* and *Ericthonius*, totaling 8,039 and 7,274 individuals respectively. In comparison, Wendt et al. (1985) noted these two genera as being dominant inhabitants of octocorals in other south Atlantic Bight locations, though at abundances of only 241 individuals of *Microjassa* and 160 individuals of *Ericthonius*. In addition to amphipods, other invertebrates reported as being common associates of octocorals are the barnacle *Conopea galeata*, the bivalve family Pteriidae, and the gastropod families Tritoniidae and Ovulidae (Patton, 1972; DeVictor, 2008). As was the case in the present study, *C. galeata* (the sea whip barnacle) may be difficult to observe, as it becomes overgrown by the host's tissue. Nevertheless, it was abundant on host specimens of both *L. hebes* and *L. virgulata*. Snails of the family Ovulidae were present only on *L. hebes*, whereas winged oysters of the family Pteriidae were present on both *L. hebes* and *L. virgulata*. Members of the nudibranch family

Tritoniidae were observed on all octocoral host species and morphologically resembled the polyps of these octocorals.

Endofaunal Patterns in Relation to Host Type and Species

Host Type (Sponge vs. Octocoral) Variations

There were distinct differences between the endofaunal assemblages inhabiting the two host groups. Foremost, the octocorals were largely dominated by caprellid amphipods, while the sponges were dominated by the parasitic polychaete *H. spongicola*. This difference is probably related to morphological distinctions between the two host groups, with the latter sponge hosts offering a greater degree of biogenic structure for infestation of the surfaces, tissue, and inner spaces. There were also differences in the presence and overall relative abundances of remaining endofaunal species. The overall endofauna associated with both the sponge and octocoral hosts contained 115 taxonomic groups that were identified to the lowest practical identification level. Sponge hosts maintained an assemblage of 95 taxonomic groups with 36 of those groups being unique to the sponges. Octocoral hosts were inhabited by 79 taxonomic groups with 20 unique to the octocoral hosts. Thus there were only 59 of the total 115 endofaunal taxa that were common to both host groups. This difference was confirmed through an analysis of similarity which revealed a significant difference in the overall composition of endofauna between the two host groups. As was proposed for the dominant endofaunal members, morphological differences between the sponge and octocoral hosts may also account for such variations in the structure and composition of the overall endofaunal assemblage. The more complex biotic structure of sponges may make them a more accommodating

host for a variety of small invertebrates in addition to the dominant polychaetes, particularly in comparison to octocorals on which the only readily available space for colonization is the surface. The octocoral surface, however, may be an ideal habitat for such animals as amphipods to cling onto and gain access to food in the surrounding water column.

Prior studies of endofaunal patterns among varying host types have been limited but show some similarities with the results observed here. For example, Wendt *et al.* (1985) found octocoral hosts to have endofaunal assemblages more similar to one another than to those inhabiting sponge hosts, though in this case the octocoral associates were more diverse than the sponge associates. A study by Fiore (2006), which looked at multiple sponge species and one species of tunicate, also found that the endofauna associated with the tunicates were more similar to one another than to the sponge hosts; however, there were fewer tunicate hosts than sponges so the comparison was far from conclusive.

Individual Host Species Variations

While the two host types (sponges vs. octocorals) in the present study were observed to support different assemblages of associated endofauna, the cluster analysis revealed additional variations among host species within the host groups and other similarities that were independent of host type. With a few exceptions, each of the three sponge species and each of the three octocoral species formed separate host cluster groups consisting of individual samples of the same species (Figure 16). Exceptions were the intermixing of samples of the octocoral *L. virgulata* with samples of the other

two octocoral species, *L. hebes* and *T. frauenfeldii*. However, while such patterns were apparent for the individual host species, there were additional cluster groupings that were more likely related to morphological similarities of the hosts or other environmental factors. For example, the endofauna inhabiting the sponges *I. felix* and *P. walpersi* appeared to be more similar to those associated with the octocorals *L. hebes* and *L. virgulata* than to those associated with the sponge *Axinella polycapella*. The inverse cluster analysis confirmed this result with endofaunal Cluster Group A containing those associates which were common to hosts *I. felix*, *P. walpersi*, and *L. hebes*. Moreover, samples of the sponge *A. polycapella* and the octocoral *T. frauenfeldii* clustered more closely together than with other corresponding sponge or octocoral species and were inhabited by similarly sparse endofaunal assemblages.

Thus the groupings in the cluster analyses reveal both similarities and dissimilarities in the composition and relative abundances of endofauna among the various host species. Such variability could be a reflection of a number of factors including variations in habitat depth (Pearse, 1932), geographic location (Duarte and Nalesso, 1996), biochemical metabolites produced by the hosts (Skilleter *et al*., 2005), or host morphology and corresponding structural complexity (Abdo, 2007; Frith, 1976; Villamizar and Laughlin, 1991). With respect to the present study, neither the depth nor the geographic location of hosts should have had a major influence on endofaunal variability, as all host specimens originated from similar depths in the same general reef area. As each of these host animals were collected from a similar physical environment, differences in their associated endofauna are most likely a reflection of biological (e.g., biochemical or morphological) characteristics of the host animals.

Many epifaunal host animals, including both sponges and octocorals, are known to produce secondary metabolites that act as feeding deterrents to reef fish (Pennings *et al.*, 1994; Waddell and Pawlik, 2000; Hill *et al.,* 2005; Harvell *et al.*, 1988; Van Alstyne and Paul, 1992; Harvell *et al.*, 1993; Pawlik *et al.*, 1987). The ability of a host to minimize predation would be of benefit to endofauna by providing a more stable and suitable host environment. Skilleter *et al.* proposed that significant differences observed in the composition of assemblages associated with two species of sponge were a product of differing secondary metabolites produced by those sponges (2005). However, as many species related to the epifaunal hosts sampled in the present study are known to possess chemical defenses (Pawlik *et al.*, 1995; Pawlik *et al.*, 2002), the differences observed here in both the abundance and composition of the associated endofauna are probably not a product of such defenses. All three of the sponge hosts examined in the present study have been assessed previously for their ability to deter predation. Chemicals produced by both *I. felix* and multiple species of *Axinella* are known to deter predation, while those of *P. walpersi* have not been observed as strong deterrents. Yet both *P. walpersi* and *I. felix* were observed in the present study to have a much more abundant and taxonomically rich endofaunal assemblage than *A. polycapella*. Though certainly not impossible, it seems unlikely that such similar biochemical activity present in two host species from the same area would create a favorable environment in one case and not the other.

Of the possible controlling factors that are discussed here, differences in host morphology seem to be the most probable explanation for the observed variations in endofauna among the different host species and types. As previously mentioned, there were morphological differences in the basic structure of the two host groups and among

individual host species. The three sponge species, for example, are morphologically

different, with *I. felix* being lobate in shape with a rough, conulose surface (Figure 4); *P.*

walpersi being upright and branching with a rough surface (Figure 5); and *A. polycapella*

being slightly upright with a few, short branches but having a smooth surface and tough

axial core (Figure 6). With its upright branches, *P. walpersi* had an associated

endofaunal assemblage that was richer in amphipods than either of the other sponge

species. These branches may have increased the available surface area for amphipods to

inhabit and at the same time, by extending up into the water column, granted them access

to a food source that neither of the other sponge species could have provided. This was

especially true for caprellid amphipods, which cling to the branches of *P. walpersi* as

they do on octocorals. Though specimens of *A. polycapella* displayed a small degree of

branching, these sponges were observed to have a very smooth surface. This smooth,

less complex surface may be important in explaining the distinct assemblage associated

with *A. polycapella,* as it has previously been suggested that sponges with a less complex

external surface harbor less abundant and diverse endofaunal assemblages (Villamizar

and Laughlin, 1991). As both abundance and number of taxa were significantly lower in

the endofauna associated with *A. polycapella*, this likely resulted in its clustering

independently of the other two.

Host morphology also may account for the observed patterns in the endofauna

associated with the various octocoral species. The two species of *Leptogorgia*, *L. hebes*

and *L. virgulata*, were not drastically different in their structure (Figures 7 and 8). They

were both upright and branching with a hard axial core. Though *L. hebes*

characteristically had far more small branches, possibly contributing to a slightly more

abundant endofaunal assemblage, there were no statistically significant differences in various endofaunal response variables between these two host species. As such, samples of these two octocoral species grouped closely together in the cluster analysis. The third octocoral, *T. frauenfeldii*, was the most distinct of the three in that it was structurally very simple, consisting of a single, smooth, upright branch (Figure 9). With its low structural complexity, similar to that of the sponge *A. polycapella*, this species harbored a much less abundant and diverse endofaunal assemblage in comparison to the other octocorals. Hence, samples of *T. frauenfeldii* clustered more closely with those of *A. polycapella* than with other octocorals.

It is clear from this study that such dominant species of epifaunal sponges and octocorals at GRNMS provide important habitat for thriving assemblages of associated endofauna. Also, regardless of the exact processes that are the most influential in driving their composition, abundance, and diversity, an important observation from this study is that these assemblages appear to vary significantly among the different host species and host types. Many studies have focused previously on describing the associates of a single host or host type. However, if a goal is to provide a thorough characterization of these assemblages for a particular coastal ecosystem, then it would be necessary to incorporate more than one host type, particularly in live-bottom habitats where a diverse assemblage of epifaunal hosts may be present.

CONCLUSIONS

The present study was the first attempt to conduct a quantitative characterization
of the assemblages of endofaunal metazoans (mostly small invertebrates) living in
association with the larger sessile epifauna, such as sponges and corals, that inhabit the
live-bottom habitats of GRNMS. While believed to be of trophic importance to fishes
and other larger invertebrates feeding on the reefs, a detailed characterization of these
assemblages within the sanctuary waters has been lacking. To address this goal,
epifaunal hosts were collected in May 2005 from a series of four quadrats along each of
five transects which were randomly chosen from areas described previously as containing
densely colonized, live-bottom habitat. Due to time constraints, a subset of 24 epifaunal
hosts, consisting of three individuals from each of three sponge species (*Ircinia felix*,
Ptilocaulis walpersi, and *Axinella polycapella*) and five individuals from each of three
octocoral species (*Leptogorgia hebes*, *Leptogorgia virgulata*, and *Titanideum
frauenfeldii*), were selected for analysis in the present study. It is clear from this study
that these common epifaunal host species at GRNMS provide important habitat for highly
abundant and diverse assemblages of associated endofauna. These assemblages were
dominated by numerous polychaetes and amphipods, specifically the polychaete
Haplosyllis spongicola and the amphipod family Caprellidae (including *Caprella
equilibra* and unidentified juvenile caprellids). However, these two dominants, in

addition to other endofaunal taxa, were not equally distributed among the various epifaunal hosts. As a result, it was observed that the host species were inhabited by different endofaunal assemblages, possibly due to morphological variations among the host animals. Such variation illustrates the importance of each of these epifauna as they host unique assemblages of endofaunal organisms and emphasizes the need to continue this study (e.g., with the analysis of remaining collected material) in order to fully characterize the assemblages of endofaunal invertebrates that may be associated with the many different species and forms of epifauna that inhabit the live-bottom habitats of GRNMS.

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FIGURES

Figure 1. Location of Gray's Reef National Marine Sanctuary (GRNMS) with respect to the Southeastern United States.

Virginia

North Carolina

Cape
Hatteras

Cape
Fear

South Carolina

Georgia

Gray's Reef
National Marine Sanctuary

Florida

Cape
Canaveral

Lake Okeechobee

N

0   100   200   Miles
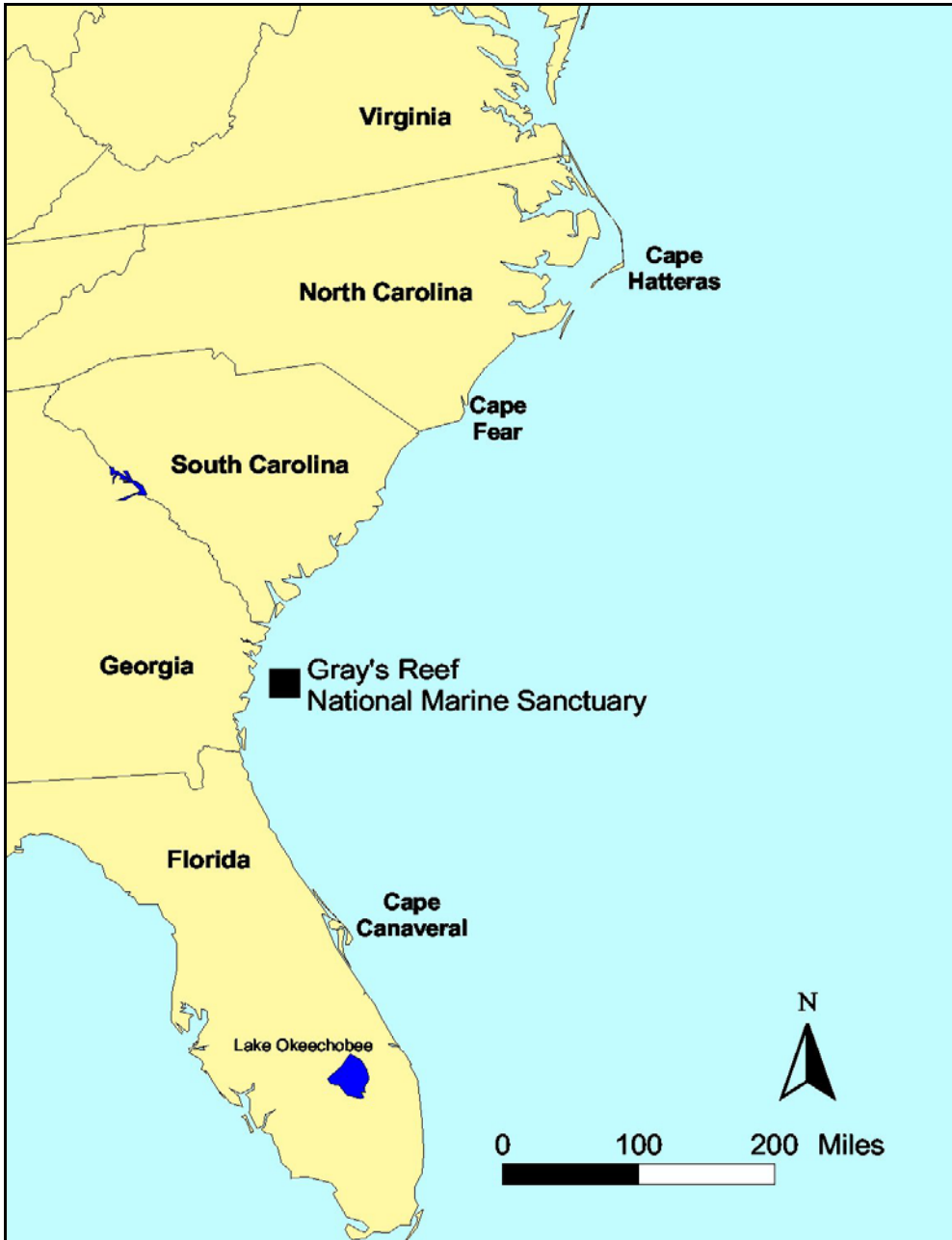
Figure 2. Illustration of the benthic topography of the live bottom habitat of GRNMS displaying the ridges and troughs created by the limestone outcrops (Hunt, 1969).

SLOPE

FLAT TOP RIDGE

SCARP

FLAT BOTTOM
TROUGH

LEDGE

SLOPE
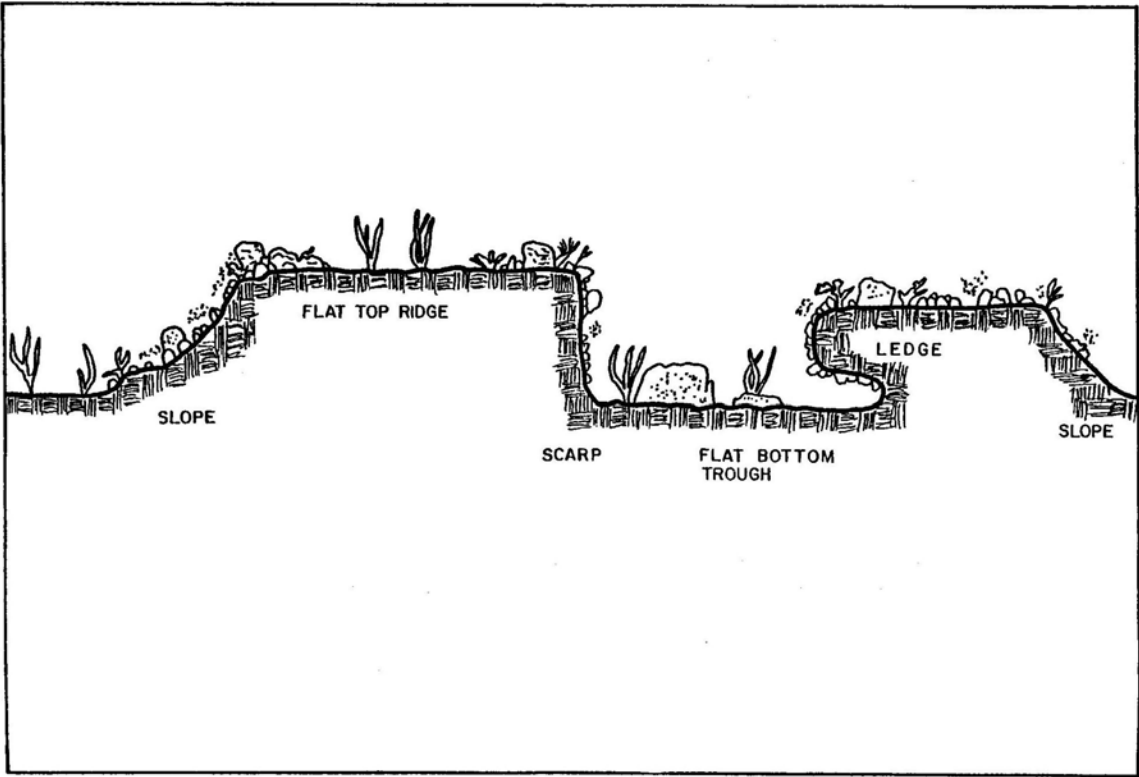
Figure 3. Map of benthic habitats within GRNMS and the location of transects used as sampling sites in the present study. Site "G" (as labeled on this map) was re-named site "E" throughout this document.

The habitat map was modified from Kendall *et al*. (2005) and the layover of sample sites was produced by Len Balthis (NOAA, CCEHBR, Charleston, SC).

Dive Sites
● A
● B
● C
● D
● G

Gray's Reef Benthic Habitats
■ Densely colonized
■ Sparsely colonized
■ Flat sand
■ Rippled sand

N
W E
S

1   0   1   2   3   4   5 Kilometers
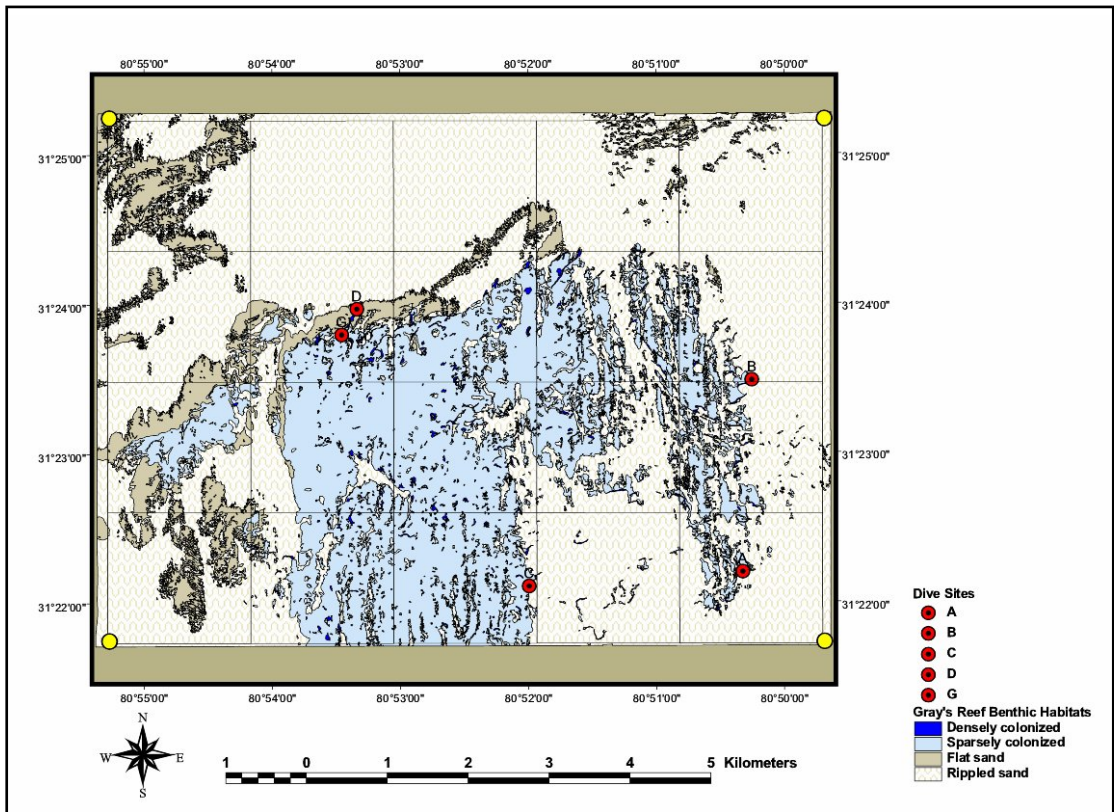
Figure 4. Photograph of *Ircinia felix* specimen GR05 E1 EPI 02.

Figure 5. Photograph of *Ptilocaulis walpersi* specimen GR05 D2 EPI 02.

Figure 6. Photograph of *Axinella polycapella* specimen GR05 C3 EPI 05.

Figure 7. Photograph of *Leptogorgia hebes* specimen GR05 B4 EPI 03.

Figure 8. Photograph of *Leptogorgia virgulata* specimen GR05 E2 EPI 04.

Figure 9. Photograph of *Titanideum frauenfeldii* specimen GR05 C3 EPI 01.

Figure 10. Comparison of the mean abundance **(a)** and the mean density (per cm^3) **(b)** of taxa associated with sponges versus octocorals.
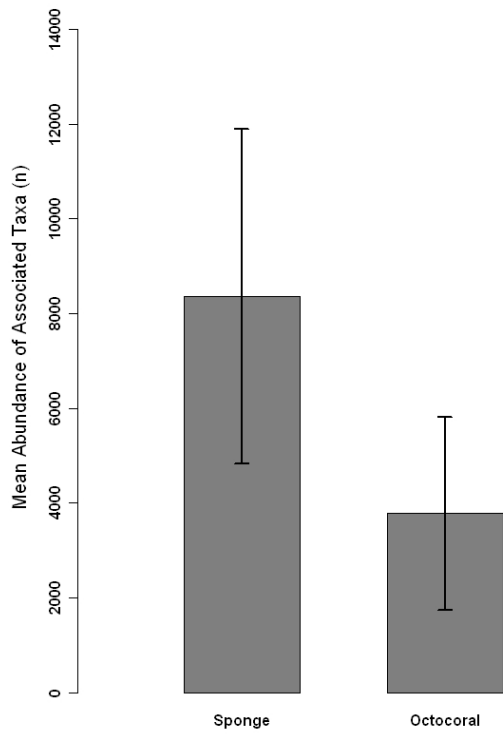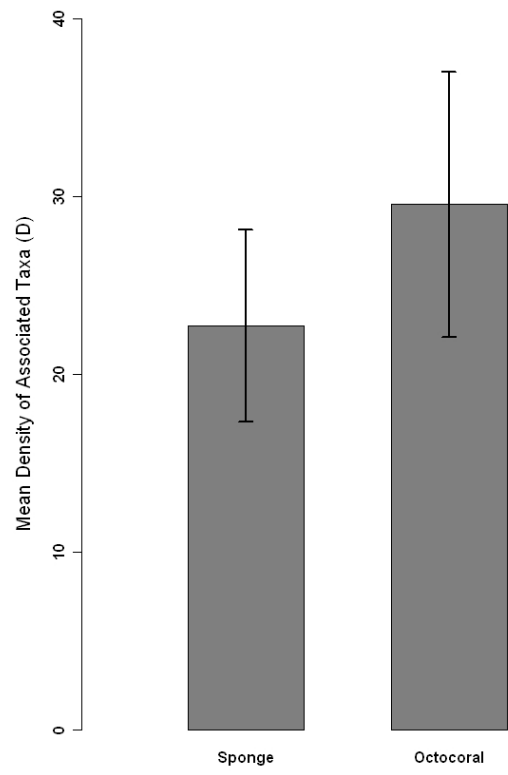
(a)   **(b)**

Figure 11. Comparison of the mean abundance of associated organisms (normalized to host volume) among the various species of host sponge **(a)** and octocoral **(b)**. Means connected by bars are not significantly different at alpha = 0.05.
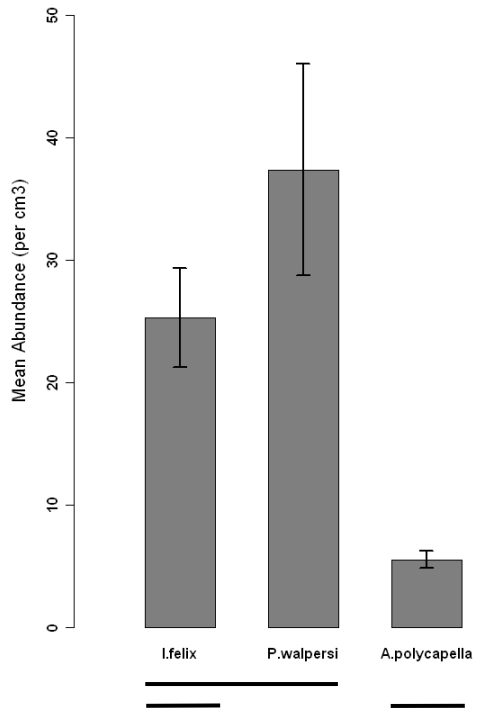
(a)
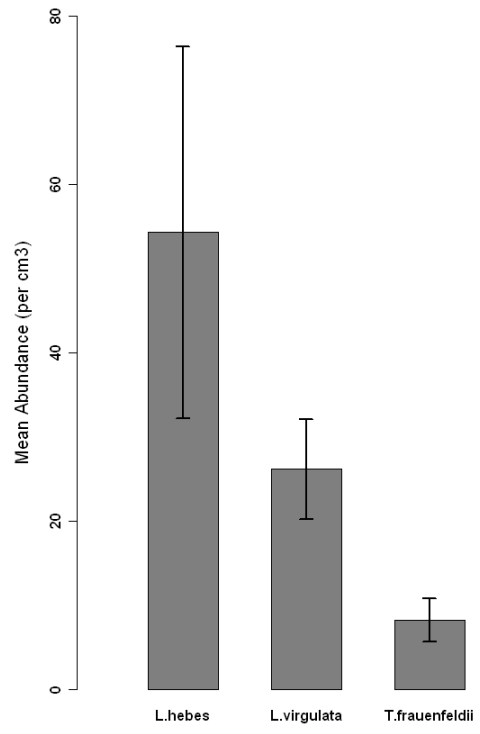
(b)

Figure 12. Diversity (H') and Evenness (J') of all host specimens.
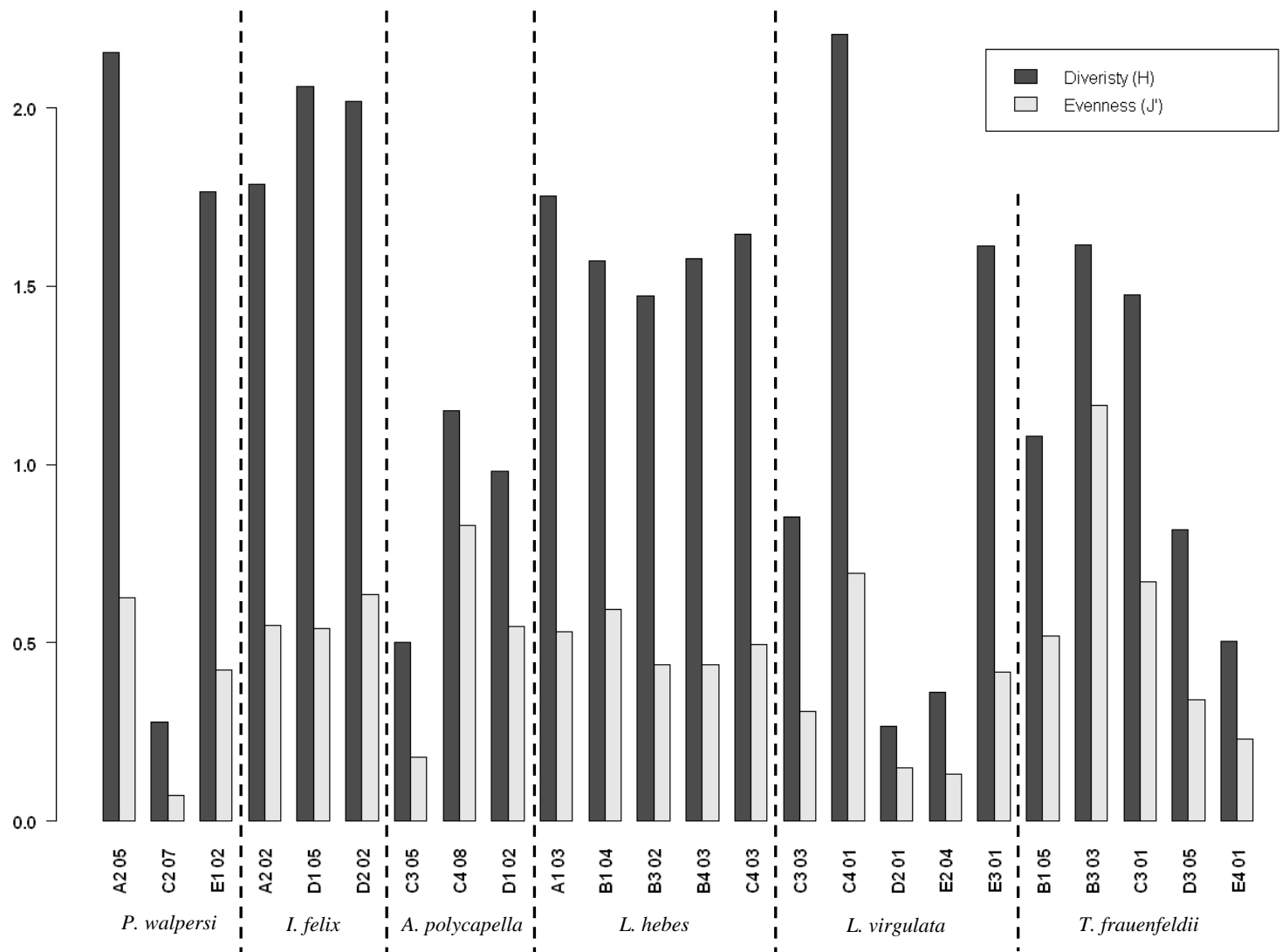
Figure 13. Comparison of the mean number of associated taxa **(a)** and mean species richness **(b)** among the various species of host sponge. Means connected by bars are not significantly different at alpha = 0.05.
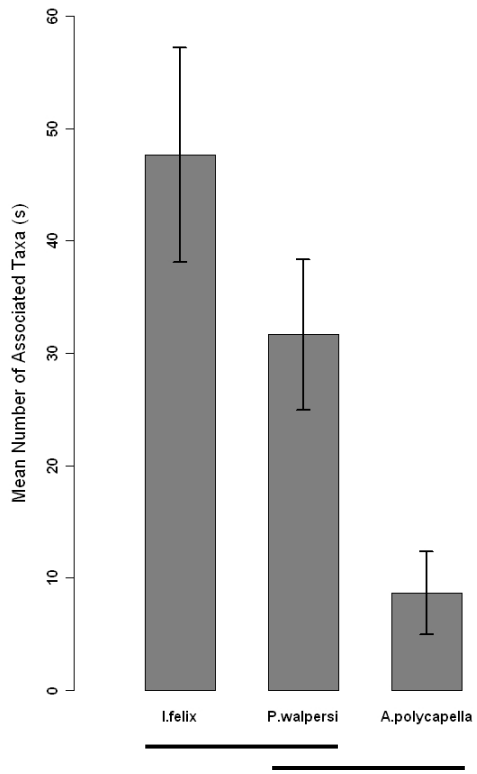
(a)
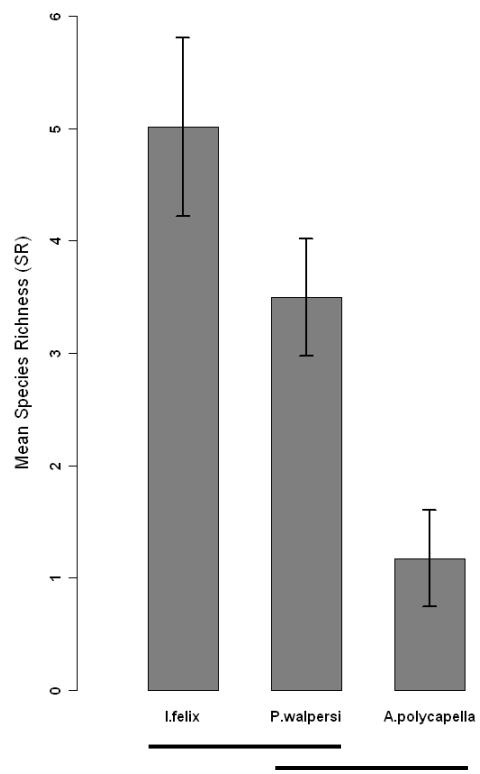
(b)

Figure 14. Comparison of the mean number of associated taxa **(a)** and mean species richness **(b)** among the various species of host octocoral. Means connected by bars are not significantly different at alpha = 0.05.
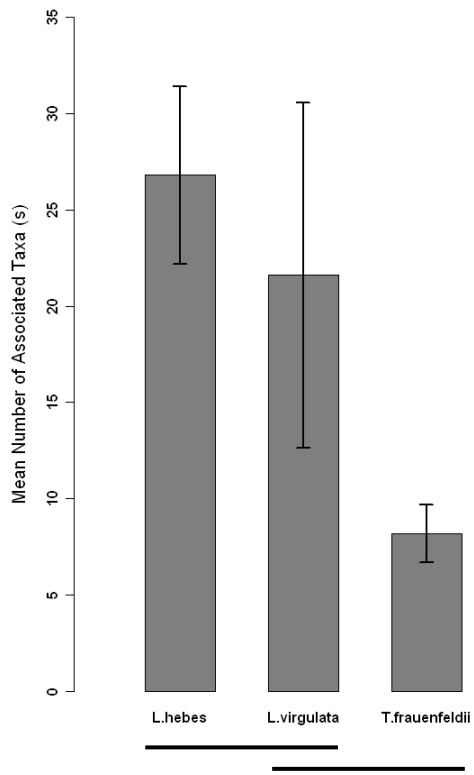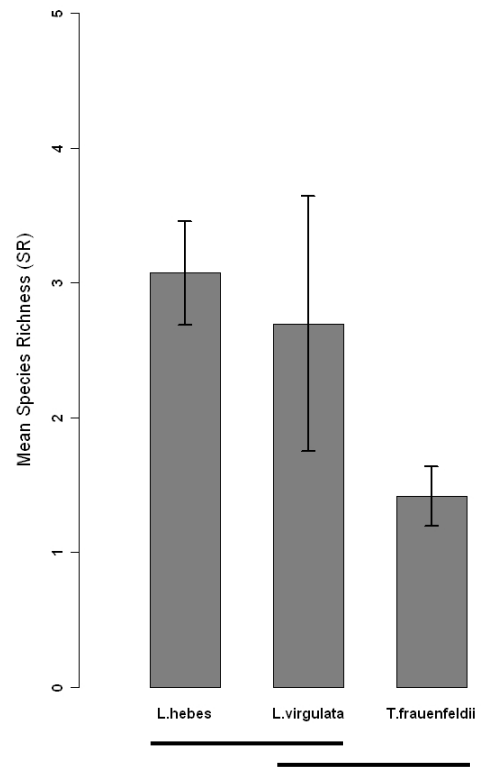
(a)
(b)

Figure 15. The relative contribution of major taxonomic groups to the associated endofauna as a whole, as well as to the associated assemblages of sponge and octocoral hosts separately, both with **(a)** and without **(b)** the dominant Polychaetes and Amphipods.
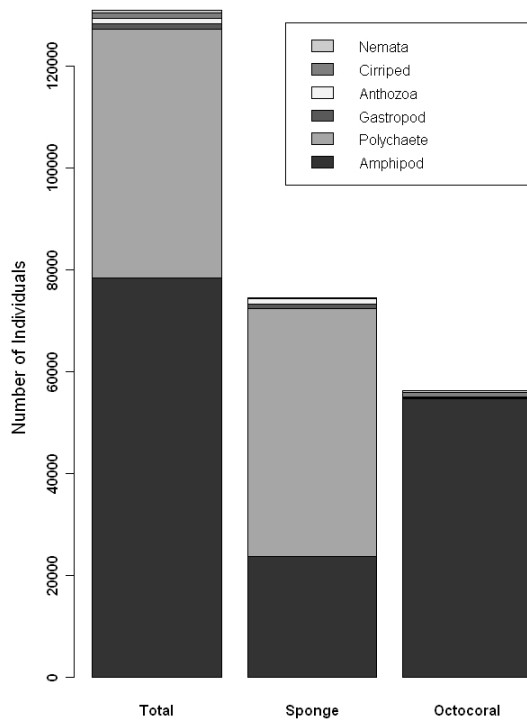
(a)
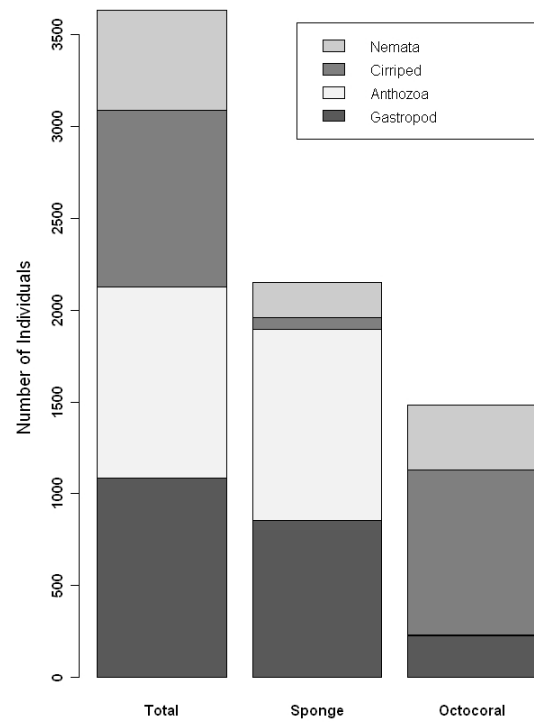
(b)

Figure 16. Cluster analysis dendrogram of host specimens based on a Bray-Curtis dissimilarity matrix. Resulting cluster groups are labeled 1 through 6.
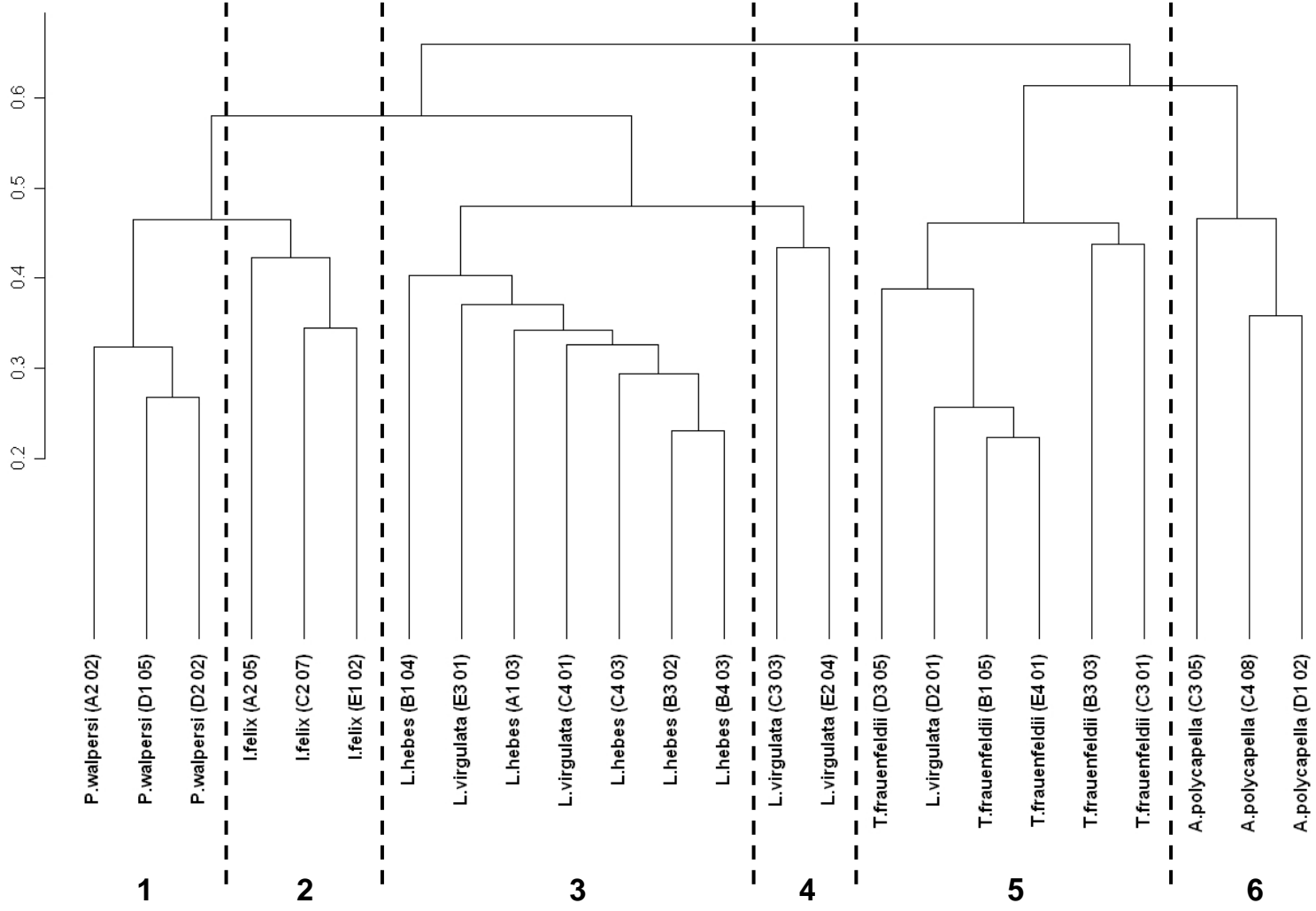
Figure 17. Non-metric MDS ordination of host specimens based on a Bray-Curtis dissimilarity matrix. Resulting groups are indicated by circles.
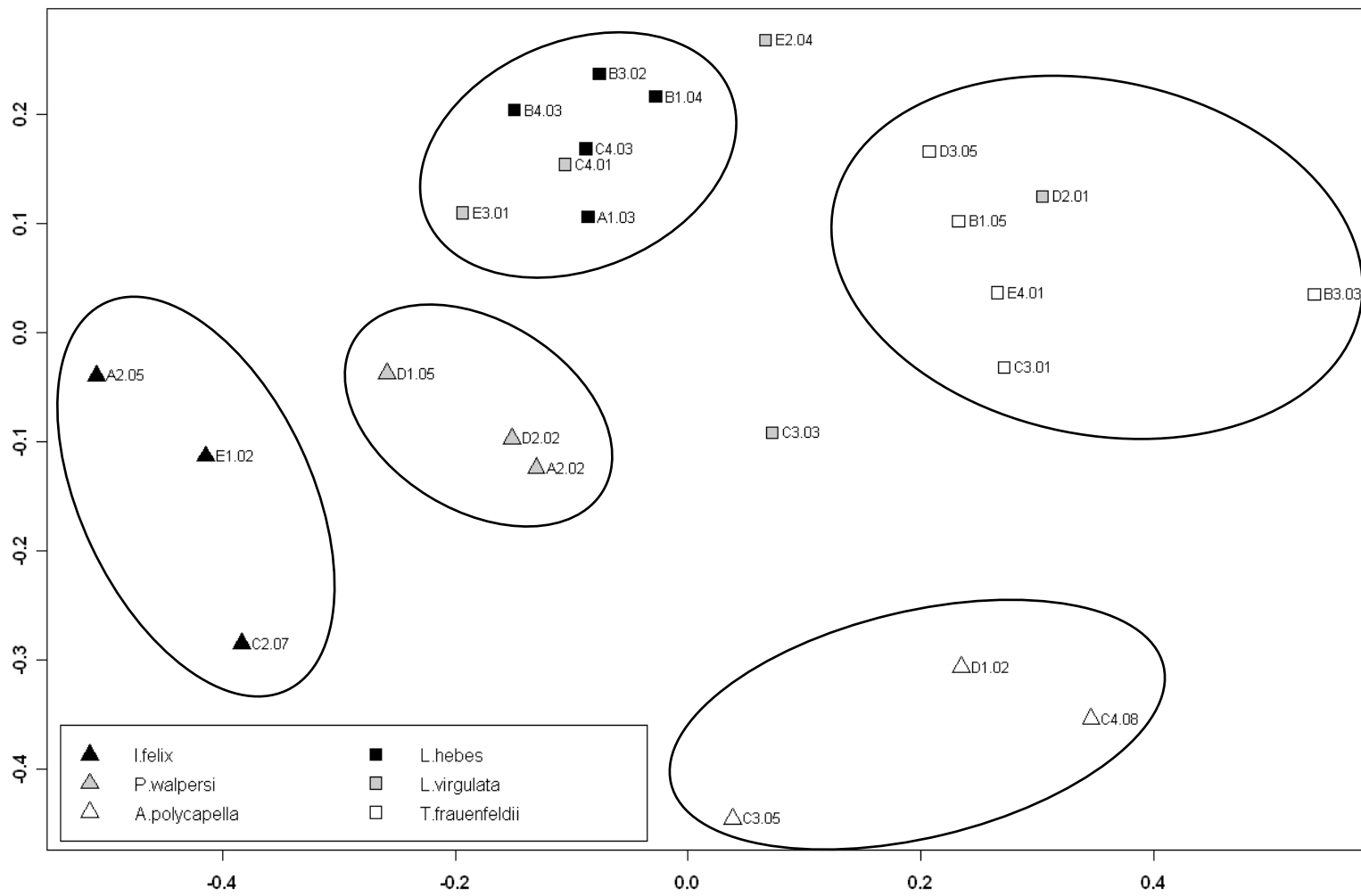
Figure 18. Inverse cluster analysis dendrogram of associated families based on Bray-Curtis dissimilarity matrix. Resulting cluster groups are labeled A through E.
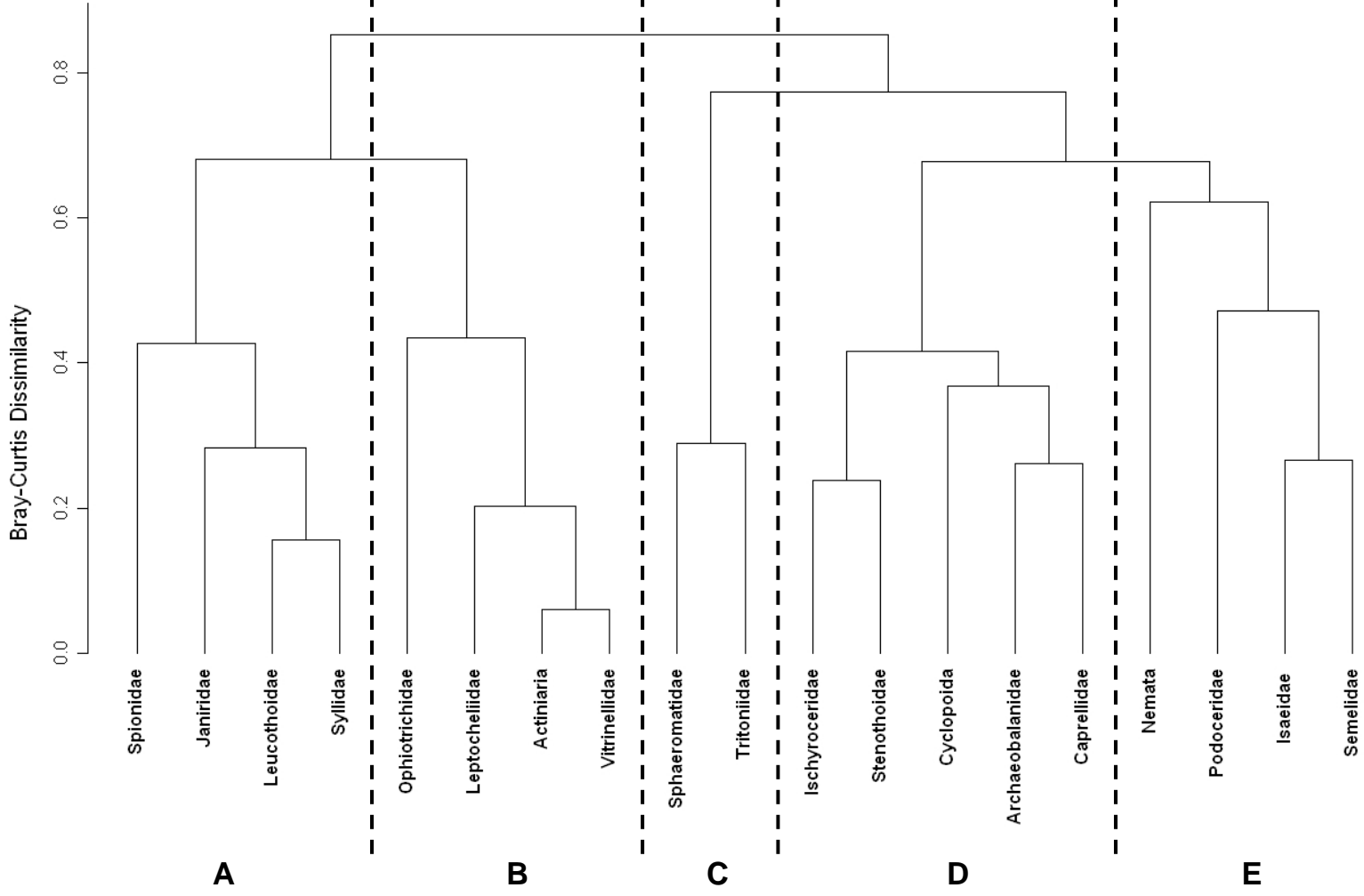
TABLES

Table 1. Distribution of host specimens by host group and host species across sample transects. The sample codes depict a combination of transect location (1st character), quadrat location (2nd character), and host number (3rd and 4th characters). The volume of each host specimen is indicated in parentheses.

Transect		Sponges			Octocorals		
		Ircinia felix	*Ptilocaulis walpersi*	*Axinella polycapella*	*Leptogorgia hebes*	*Leptogorgia virgulata*	*Titanideum frauenfeldii*
	A	A2 05 (100 cm^3)	A2 02 (80 cm^3)		A1 03 (100 cm^3)		
	B				B1 04 (20 cm^3) B3 02 (145 cm^3) B4 03 (260 cm^3)		B1 05 (40 cm^3) B3 03 (12 cm^3)
	C	C2 07 (910 cm^3)		C3 05 (400 cm^3) C4 08 (11 cm^3)	C4 03 (60 cm^3)	C3 03 (10 cm^3) C4 01 (100 cm^3)	C3 01 (14 cm^3)
	D		D1 05 (360 cm^3) D2 02 (140 cm^3)	D1 02 (100 cm^3)		D2 01 (40 cm^3)	D3 05 (20 cm^3)
	E	E1 02 (670 cm^3)				E2 04 (60 cm^3) E3 01 (240 cm^3)	E4 01 (60 cm^3)

Table 2. All host specimens and counts of their individual associated organisms.

Associate	Associate Phyla	Sponges									Octocorals															Total
		I. felix			*P. walpersi*			*A.polycapella*			*L. hebes*					*L. virgulata*					*T. frauenfeldii*					
		A2 05	C2 07	E1 02	A2 02	D1 05	D2 02	C3 05	C4 08	D1 02	A1 03	B1 04	B3 02	B4 03	C4 03	C3 03	C4 01	D2 01	E2 04	E3 01	B1 05	B3 03	C3 01	D3 05	E4 01	
Haplosyllis	Annelida	2	29505	9962	790	3267	2436	1515	25	438	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	47942
Family Caprellidae (juveniles)	Arthropoda	2	17	37	582	2400	662	15	8	60	601	346	2768	13592	1024	127	346	222	841	1845	167	8	44	114	425	26253
Ericthonius	Arthropoda	1140	255	2554	88	9658	958	3	0	1	530	114	961	3494	257	2	705	10	3	1155	25	4	2	3	9	21931
Caprella equilibra	Arthropoda	2	15	31	179	1435	641	59	33	128	488	245	1820	5535	861	106	391	312	1484	3072	158	2	16	94	209	17316
Microjassa	Arthropoda	0	0	1	2	549	354	0	0	0	36	166	438	7157	114	2	0	0	0	26	64	0	0	0	36	8945
Photis	Arthropoda	20	1	178	7	681	62	0	0	1	21	5	5	49	95	3	91	1	0	487	2	0	0	1	1	1711
Class Actiniaria A	Cnidaria	401	1	636	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1040
Gammaropsis	Arthropoda	0	9	46	9	338	42	1	0	3	36	2	7	23	46	0	135	3	0	220	2	0	0	1	0	923
Conopea galeata	Arthropoda	0	0	0	0	0	0	0	0	0	35	29	112	536	76	4	22	0	50	28	0	0	8	0	1	901
Family Vitrinellidae	Mollusca	265	13	531	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	811
Family Stenothoidae	Arthropoda	0	1	2	6	175	18	1	0	0	11	3	26	362	12	0	16	0	1	63	1	0	0	1	0	699
Phylum Nemata	Nemata	17	31	89	32	20	1	1	0	0	0	0	0	18	9	2	221	0	4	96	0	0	0	0	0	541
Family Spionidae	Annelida	10	103	39	1	14	0	0	0	0	0	2	83	15	5	0	2	0	0	2	0	0	1	3	0	280
Family Janiridae	Arthropoda	33	117	67	9	15	2	1	0	0	6	1	0	0	2	0	0	0	0	1	0	0	0	1	0	255
Order Cyclopoida	Arthropoda	0	0	5	0	0	0	1	0	0	0	0	25	70	4	2	17	3	42	38	0	0	0	0	0	207
Famliy Terebellidae	Annelida	6	17	21	12	67	26	0	0	1	3	1	1	6	4	0	2	0	1	3	0	0	0	0	0	170
Family Tritoniidae	Mollusca	0	0	0	0	0	0	0	0	0	1	0	92	19	32	0	2	1	1	1	1	1	5	12	2	170
Family Leptocheliidae	Arthropoda	66	17	73	6	3	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	169
Family Podoceridae	Arthropoda	0	2	36	17	47	12	2	0	0	25	0	0	0	5	0	0	0	1	1	1	0	2	0	1	152
Family Leucothoidae	Arthropoda	2	90	25	1	1	1	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	142
Cerapus	Arthropoda	0	0	0	0	0	0	0	0	0	0	0	18	114	1	0	0	0	0	1	0	0	0	0	0	134
Family Serpulidae	Annelida	0	0	124	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	125
Caprella penantis	Arthropoda	0	0	0	15	0	0	0	0	0	0	1	0	43	0	0	1	0	0	27	0	0	0	0	0	87
Phylum Nemertea	Nemertea	7	3	35	0	20	1	0	0	0	1	3	1	2	1	0	2	0	2	3	0	0	0	0	0	81
Family Ampithoidae	Arthropoda	5	2	25	9	15	8	0	0	0	9	0	1	1	4	0	0	0	0	1	0	0	0	0	0	80
Family Melitidae	Arthropoda	3	7	3	0	2	0	0	0	0	10	0	2	4	0	0	6	0	0	34	0	0	0	0	0	71
Exogone	Annelida	7	22	13	4	9	0	0	0	0	0	0	1	0	1	6	1	0	0	3	0	0	0	0	0	67
Syllis	Annelida	10	32	14	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	63
Family Balanidae	Arthropoda	0	1	4	0	32	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	55
Brania	Annelida	6	0	16	2	16	3	0	0	0	3	0	2	2	3	0	2	0	0	0	0	0	0	0	0	55
Family Semelidae	Mollusca	0	0	7	0	20	1	0	1	0	2	0	0	6	4	0	0	0	0	9	0	3	1	0	1	55
Deutella incerta	Arthropoda	0	1	1	6	2	2	1	0	0	20	0	1	9	0	6	1	0	0	4	0	0	0	0	0	54
Family Columbellidae	Mollusca	0	13	4	1	2	0	0	0	0	5	0	6	12	0	0	0	0	0	2	0	0	0	0	0	45
Family Pteriidae	Mollusca	0	0	0	0	0	0	0	0	0	4	0	5	20	2	0	4	0	0	2	0	0	0	0	0	37
Paracerceis	Arthropoda	0	0	0	3	0	0	0	0	0	2	0	13	2	10	0	1	0	1	0	0	0	0	3	0	35
Family Hiatellidae	Mollusca	13	5	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34
Order Siphonostomatoida	Arthropoda	16	4	6	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31
Order Harpacticoida	Arthropoda	3	2	9	0	5	2	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	28
Proceraea	Annelida	0	0	4	0	3	0	0	0	0	2	0	0	13	0	1	1	0	1	3	0	0	0	0	0	28
Family Dorvilleidae	Annelida	0	0	0	0	0	0	0	0	0	0	2	3	2	1	1	0	0	2	15	0	0	0	0	0	26
Family Ophiotrichidae	Echinodermata	4	2	9	0	4	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	25
Family Ovulidae	Mollusca	0	0	0	0	0	0	0	0	0	2	0	7	8	5	0	0	0	0	0	0	0	0	0	0	22
Family Sabellidae	Annelida	2	4	7	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	16
Family Parapseudidae	Arthropoda	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
Family Paguridae	Arthropoda	0	0	5	0	1	1	0	0	0	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	14
Styela	Chordata	0	0	3	0	1	0	0	0	0	0	0	1	2	0	0	1	0	0	5	0	0	0	0	0	13
Family Veneridae	Mollusca	0	1	6	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	12
Family Caecidae	Mollusca	0	5	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Family Colomastigidae	Arthropoda	0	1	2	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Family Phyllodocidae	Annelida	0	1	1	0	5	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	9
Molgula	Chordata	2	0	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	9
Family Alpheidae	Arthropoda	2	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8

Table 2 (continued). Continuation of all host specimens and counts of their individual associated organisms.

Associate	Associate Phyla	Sponges									Octocorals															Total
		I. felix			*P. walpersi*			*A.polycapella*			*L. hebes*					*L. virgulata*					*T. frauenfeldii*					
		A2 05	C2 07	E1 02	A2 02	D1 05	D2 02	C3 05	C4 08	D1 02	A1 03	B1 04	B3 02	B4 03	C4 03	C3 03	C4 01	D2 01	E2 04	E3 01	B1 05	B3 03	C3 01	D3 05	E4 01	
Family Eulimidae	Mollusca	3	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Family Archaeobalanidae	Arthropoda	0	0	4	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Family Nereididae	Annelida	0	4	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	7
Family Amphilochidae	Arthropoda	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Family Porcellanidae	Arthropoda	1	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Autolytus	Annelida	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Family Lumbrineridae	Annelida	0	3	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Family Oenonidae	Annelida	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Family Trochidae	Mollusca	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	5
Neopontonides	Arthropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	0	4
Family Phoxichilidiidae	Arthropoda	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	4
Family Maldanidae	Annelida	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4
Family Scalibregmatidae	Annelida	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Family Stiligeridae	Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	4
Family Aoridae	Arthropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3
Family Apseudidae	Arthropoda	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
Family Majidae	Arthropoda	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Branchiosyllis	Annelida	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Family Capitellidae	Annelida	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	3
Family Calyptraeidae	Mollusca	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Family Mytilidae	Mollusca	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3
Family Pyramidellidae	Mollusca	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Class Turbellaria A	Platyhelminthes	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3
Class Turbellaria C	Platyhelminthes	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Family Synopiidae	Arthropoda	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	5
Family Geryonidae	Arthropoda	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Family Lysianassidae	Arthropoda	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Family Xanthidae	Arthropoda	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Trypanosyllis	Annelida	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Family Cirratulidae	Annelida	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2
Family Eunicidae	Annelida	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Family Hesionidae	Annelida	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Family Chamidae	Mollusca	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Family Turritellidae	Mollusca	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Family Aspidosiphonidae	Sipuncula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Family Corophiidae	Arthropoda	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Halacaridae	Arthropoda	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Melphidippidae	Arthropoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Pinnotheridae	Arthropoda	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Order Decapoda	Arthropoda	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Class Ostracoda	Arthropoda	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Family Oweniidae	Annelida	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Sabellariidae	Annelida	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Arbaciidae	Echinodermata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Cucumariidae	Echinodermata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Gorgonocephalidae	Echinodermata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Family Cerithiopsidae	Mollusca	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Family Naticidae	Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Class Turbellaria B	Platyhelminthes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Total		2057	30331	14711	1787	18832	5255	1631	68	633	1859	921	6404	31140	2585	267	1973	552	2436	7173	421	18	81	235	686	132056

Table 3. All host specimens and presence/absence data for colonial associates.

Associate	Associate Phyla	Sponges									Octocorals														
		I. felix			*P. walpersi*			*A.polycapella*			*L. hebes*					*L. virgulata*					*T. frauenfeldii*				
		A2 05	C2 07	E1 02	A2 02	D1 05	D2 02	C3 05	C4 08	D1 02	A1 03	B1 04	B3 02	B4 03	C4 03	C3 03	C4 01	D2 01	E2 04	E3 01	B1 05	B3 03	C3 01	D3 05	E4 01
Order Cheilostomata	Ectoprocta	x	x	x	0	x	0	0	0	0	x	x	x	x	x	x	x	0	0	x	0	x	0	x	0
Family Campanulariidae	Cnidaria	0	x	x	x	x	x	0	0	0	0	x	0	x	x	0	x	0	0	x	x	x	0	0	0
Family Clavulariidae	Cnidaria	0	x	x	0	x	0	0	0	0	0	x	x	0	0	0	0	0	0	x	0	0	0	0	0
Order Cyclostomata	Ectoprocta	x	x	x	x	x	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0
Order Ctenostomata	Ectoprocta	x	x	x	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phylum Porifera A	Porifera	x	x	x	0	x	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0
Family Epizoanthidae	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	x	0	0	0	0	0	0	0	0
Family Sertulariidae	Cnidaria	0	0	0	0	0	0	0	0	0	x	0	0	x	0	0	0	x	0	0	0	0	0	0	0
Diplosoma	Chordata	x	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Family Plumulariidae	Cnidaria	0	0	0	0	x	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0
Archidistoma	Chordata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0
Botryllus	Chordata	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Didemnum	Chordata	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Family Eudendriidae	Cnidaria	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Family Haleciidae	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0
Suborder Epicaridea (larvae)	Arthropoda	0	x	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Order Decapoda (larvae)	Arthropoda	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Class Bivalvia (<< 0.5 mm)	Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0	0	0	0	0	0
Egg Cases	Miscellaneous	0	0	0	0	0	0	0	0	0	x	x	x	x	0	0	0	0	0	x	0	0	0	0	x

Table 4. Response variables for host specimens including, volume (in cm^3), abundance (n), abundance per cm^3 (D), number of taxa (s), species richness (SR), diversity (H'), and evenness (J').

	Host Type	Host Species	Volume	n	D	s	SR	H'	J'
A2 05	Sponge	*I. felix*	100	2057	20.57	31	3.93	2.16	0.63
C2 07	Sponge	*I. felix*	910	30331	33.33	48	4.55	0.28	0.07
E1 02	Sponge	*I. felix*	670	14711	21.96	64	6.56	1.77	0.42
A2 02	Sponge	*P. walpersi*	80	1787	22.34	26	3.34	1.79	0.55
D1 05	Sponge	*P. walpersi*	360	18832	52.31	45	4.47	2.06	0.54
D2 02	Sponge	*P. walpersi*	140	5255	37.54	24	2.68	2.02	0.64
C3 05	Sponge	*A. polycapella*	400	1631	4.08	16	2.03	0.50	0.18
C4 08	Sponge	*A. polycapella*	11	68	6.18	4	0.71	1.15	0.83
D1 02	Sponge	*A. polycapella*	100	633	6.33	6	0.78	0.98	0.55
A1 03	Octocoral	*L. hebes*	100	1859	18.59	27	3.45	1.75	0.53
B1 04	Octocoral	*L. hebes*	20	921	46.05	14	1.90	1.57	0.59
B3 02	Octocoral	*L. hebes*	145	6403	44.16	29	3.19	1.47	0.44
B4 03	Octocoral	*L. hebes*	260	31140	119.77	36	3.38	1.58	0.44
C4 03	Octocoral	*L. hebes*	60	2585	43.08	28	3.44	1.65	0.49
C3 03	Octocoral	*L. virgulata*	10	267	26.70	16	2.68	0.85	0.31
C4 01	Octocoral	*L. virgulata*	100	1973	19.73	24	3.03	2.20	0.69
D2 01	Octocoral	*L. virgulata*	40	552	13.80	6	0.79	0.27	0.15
E2 04	Octocoral	*L. virgulata*	60	2436	40.60	15	1.80	0.36	0.13
E3 01	Octocoral	*L. virgulata*	240	7173	29.89	47	5.18	1.61	0.42
B1 05	Octocoral	*T. frauenfeldii*	40	421	10.53	8	1.16	1.08	0.52
B3 03	Octocoral	*T. frauenfeldii*	12	18	1.50	4	1.04	1.62	1.17
C3 01	Octocoral	*T. frauenfeldii*	14	81	5.79	9	1.82	1.48	0.67
D3 05	Octocoral	*T. frauenfeldii*	20	235	11.75	11	1.83	0.82	0.34
E4 01	Octocoral	*T. frauenfeldii*	60	686	11.43	9	1.22	0.50	0.23

Table 5. Results of statistical analyses between host response variables including abundance (n), abundance per cm^3 (D), number of taxa (s), species richness (SR), diversity (H'), and evenness (J'). Where indicated, data were log transformed (******), or the Kruskal-Wallis test was utilized (*****).

Between Sponge Species		Assemblage Structure Variables					
		n	D	s	SR	H'	J'
	p-value	0.0699 **	0.0179	0.0219	0.0113	0.1775	0.6235
	Significance	NS	S	S	S	NS	NS
	Specifics		Pw > Ap : 0.0154	If > Ap : 0.0185	If > Ap : 0.0096		

Between Octocoral Species		Assemblage Structure Variables					
		n	D	s	SR	H'	J'
	p-value	0.0092 **	0.0022 **	0.0117 **	0.0541 **	0.2808 *	0.2808 *
	Significance	S	S	S	NS	NS	NS
	Specifics	Lh > Tf : 0.0079	Lh > Tf : 0.0019 Lv > Tf : 0.0241	Lh > Tf : 0.0102	Lh > Tf : 0.0468		

Between Host Groups		Assemblage Structure Variables					
		n	D	s	SR	H'	J'
	p-value	0.2381	0.5260	0.1265	0.2019	0.5584	0.8922
	Significance	NS	NS	NS	NS	NS	NS
	Specifics						

Table 6. Major taxonomic groups contributing to the associated assemblage, their abundance and percent contribution.

Associate Taxon	Abundance	Percent of Total
Amphipod	78523	59.462
Polychaete	48830	36.977
Gastropod	1088	0.824
Anthozoa	1040	0.788
Cirriped	963	0.729
Nemata	541	0.410
Isopod	290	0.220
Copepod	266	0.201
Tanaid	187	0.142
Bivalve	141	0.107
Nemertea	81	0.061
Decapod	41	0.031
Ophiuroid	26	0.020
Ascidian	22	0.017
Turbellaria	7	0.005
Pycnogonid	4	0.003
Sipuncula	2	0.002
Arachnid	1	0.001
Echinoid	1	0.001
Holothuroid	1	0.001
Ostracod	1	0.001
Ectoprocta	+	+
Hydrozoa	+	+
Porifera	+	+

Table 7. All independent associated organisms, their respective taxonomic group, abundance, percent contribution to the total, frequency of occurrence out of all 24 host specimens, and abundance per cm^3 of host tissue.

Associate	Associate Taxon	Total Abundance	Percent of Total	Frequency of Occurrence	Density (per cm^3)
Haplosyllis spongicola	Polychaete	47942	36.304	11	12.1311
Family Caprellidae (juveniles)	Amphipod	26253	19.880	24	6.6430
Ericthonius	Amphipod	21931	16.607	23	5.5493
Caprella equilibra	Amphipod	17316	13.113	24	4.3816
Microjassa	Amphipod	8945	6.774	13	2.2634
Photis	Amphipod	1711	1.296	19	0.4329
Class Actiniaria A	Anthozoa	1040	0.788	5	0.2632
Gammaropsis	Amphipod	923	0.699	17	0.2336
Conopea galeata	Cirriped	901	0.682	11	0.2280
Family Vitrinellidae	Gastropod	811	0.614	5	0.2052
Family Stenothoidae	Amphipod	699	0.529	16	0.1769
Phylum Nemata	Nemata	541	0.410	13	0.1369
Family Spionidae	Polychaete	280	0.212	13	0.0709
Family Janiridae	Isopod	255	0.193	12	0.0645
Order Cyclopoida	Copepod	207	0.157	10	0.0524
Family Terebellidae	Polychaete	170	0.129	14	0.0430
Family Tritoniidae	Gastropod	170	0.129	13	0.0430
Family Leptocheliidae	Tanaid	169	0.128	7	0.0428
Family Podoceridae	Amphipod	152	0.115	13	0.0385
Family Leucothoidae	Amphipod	142	0.108	8	0.0359
Cerapus	Amphipod	134	0.101	4	0.0339
Family Serpulidae	Polychaete	125	0.095	2	0.0316
Caprella penantis	Amphipod	87	0.066	5	0.0220
Phylum Nemertea	Nemertea	81	0.061	13	0.0205
Family Ampithoidae	Amphipod	80	0.061	11	0.0202
Family Melitidae	Amphipod	71	0.053	9	0.0177
Exogone	Polychaete	67	0.051	10	0.0170
Syllis	Polychaete	63	0.048	7	0.0159
Family Balanidae	Cirriped	55	0.042	4	0.0139
Brania	Polychaete	55	0.042	10	0.0139
Family Semelidae	Bivalve	55	0.042	11	0.0139
Deutella incerta	Amphipod	54	0.041	12	0.0137
Family Columbellidae	Gastropod	45	0.034	8	0.0114
Family Pteriidae	Bivalve	37	0.028	6	0.0094
Paracerceis	Isopod	35	0.027	8	0.0089
Family Hiatellidae	Bivalve	34	0.026	3	0.0086
Order Siphonostomatoida	Copepod	31	0.023	6	0.0078
Order Harpacticoida	Copepod	28	0.021	6	0.0071
Proceraea	Polychaete	28	0.021	8	0.0071
Family Dorvilleidae	Polychaete	26	0.020	7	0.0066
Family Ophiothricidae	Ophiuroid	25	0.019	10	0.0063
Family Ovulidae	Gastropod	22	0.017	4	0.0056
Family Sabellidae	Polychaete	16	0.012	6	0.0040
Family Parapseudidae	Tanaid	15	0.011	1	0.0038
Family Paguridae	Decapod	14	0.011	5	0.0035
Styela	Ascidian	13	0.010	6	0.0033
Family Veneridae	Bivalve	12	0.009	6	0.0030
Family Caecidae	Gastropod	11	0.008	3	0.0028
Family Colomastigidae	Amphipod	9	0.007	3	0.0023
Family Phyllodocidae	Polychaete	9	0.007	5	0.0023
Molgula	Ascidian	9	0.007	5	0.0023
Family Alpheidae	Decapod	8	0.006	3	0.0020
Family Eulimidae	Gastropod	8	0.006	3	0.0020
Family Archaeobalanidae	Cirriped	7	0.005	3	0.0018
Family Nereididae	Polychaete	7	0.005	4	0.0018
Family Amphilochidae	Amphipod	4	0.005	3	0.0015
Family Porcellanidae	Decapod	6	0.005	3	0.0015
Autolytus	Polychaete	6	0.005	2	0.0015
Family Lumbrineridae	Polychaete	6	0.005	3	0.0015
Family Oenonidae	Polychaete	6	0.005	2	0.0015
Family Trochidae	Gastropod	5	0.004	4	0.0013
Neopontonides	Decapod	4	0.003	3	0.0010
Family Phoxichilidiidae	Pycnogonid	4	0.003	3	0.0010
Family Maldanidae	Polychaete	4	0.003	2	0.0010

Table 7 (continued). Continuation of all independent associated organisms, their respective taxonomic group, abundance, percent contribution to the total, frequency of occurrence out of all 24 host specimens, and abundance per milliliter of host tissue.

Associate	Associate Taxon	Abundance	Percent of Total	Frequency of Occurrence	Density (per cm³)
Family Scalibregmatidae	Polychaete	4	0.003	2	0.0010
Family Stiligeridae	Gastropod	4	0.003	1	0.0010
Family Aoridae	Amphipod	3	0.002	1	0.0008
Family Apseudidae	Tanaid	3	0.002	3	0.0008
Family Majidae	Decapod	3	0.002	3	0.0008
Branchiosyllis	Polychaete	3	0.002	1	0.0008
Family Capitellidae	Polychaete	3	0.002	3	0.0008
Family Calyptraeidae	Gastropod	3	0.002	3	0.0008
Family Mytilidae	Bivalve	3	0.002	2	0.0008
Family Pyramidellidae	Gastropod	3	0.002	3	0.0008
Class Turbellaria A	Turbellaria	3	0.002	3	0.0008
Class Turbellaria C	Turbellaria	3	0.002	1	0.0008
Family Synopiidae	Amphipod	5	0.002	3	0.0005
Family Geryonidae	Decapod	2	0.002	2	0.0005
Family Lysianassidae	Amphipod	2	0.002	2	0.0005
Family Xanthidae	Decapod	2	0.002	1	0.0005
Trypanosyllis	Polychaete	2	0.002	1	0.0005
Family Cirratulidae	Polychaete	2	0.002	2	0.0005
Family Eunicidae	Polychaete	2	0.002	2	0.0005
Family Hesionidae	Polychaete	2	0.002	1	0.0005
Family Chamidae	Gastropod	2	0.002	2	0.0005
Family Turritellidae	Gastropod	2	0.002	1	0.0005
Family Aspidosiphonidae	Sipuncula	2	0.002	2	0.0005
Family Corophiidae	Amphipod	1	0.001	1	0.0003
Family Halacaridae	Arachnid	1	0.001	1	0.0003
Family Melphidippidae	Amphipod	1	0.001	1	0.0003
Family Pinnotheridae	Decapod	1	0.001	1	0.0003
Order Decapoda	Decapod	1	0.001	1	0.0003
Class Ostracoda	Ostracod	1	0.001	1	0.0003
Family Oweniidae	Polychaete	1	0.001	1	0.0003
Family Sabellariidae	Polychaete	1	0.001	1	0.0003
Family Arbaciidae	Echinoid	1	0.001	1	0.0003
Family Cucumariidae	Holothuroid	1	0.001	1	0.0003
Family Gorgonocephalidae	Ophiuroid	1	0.001	1	0.0003
Family Cerithiopsidae	Gastropod	1	0.001	1	0.0003
Family Naticidae	Gastropod	1	0.001	1	0.0003
Class Turbellaria B	Turbellaria	1	0.001	1	0.0003
Order Cheilostomata	Ectoprocta	+		14	
Family Campanulariidae	Hydrozoa	+		12	
Family Clavulariidae	Anthozoa	+		6	
Order Cyclostomata	Ectoprocta	+		6	
Order Ctenostomata	Ectoprocta	+		4	
Phylum Porifera A	Porifera	+		5	
Family Epizoanthidae	Anthozoa	+		2	
Family Sertulariidae	Hydrozoa	+		3	
Diplosoma	Ascidian	+		2	
Family Plumulariidae	Hydrozoa	+		2	
Archidistoma	Ascidian	+		1	
Botryllus	Ascidian	+		1	
Didemnum	Ascidian	+		1	
Family Eudendriidae	Hydrozoa	+		1	
Family Haleciidae	Hydrozoa	+		1	
Total		132056			

Table 8. Endofaunal taxa making up greater than 1% of the total endofaunal assemblage associated with all sponges and each of the three sponge species. Numbers in parentheses are calculations of the percent contribution of that taxon to the total endofauna with individuals of *Haplosyllis* removed from the total abundance.

Note: Endofaunal taxa representing less than 1% of total endofaunal abundance (on sponges) are included in this table if their contributions are greater than 1% when *Haplosyllis* counts were removed from the calculations.

Host	Associate	Total Abundance	Percent of Total	Frequency	Average Density (per cm^3)
All Sponges	*Haplosyllis spongicola*	47940	63.66 (--)	9	10.46
	Ericthonius	14657	19.46 (53.56)	8	5.59
n = 9	Caprellidae (juveniles)	3783	5.02 (13.82)	9	2.24
	Caprella equilibra	2523	3.35 (9.22)	9	1.70
	Actiniaria A	1039	1.38 (3.80)	4	0.55
	Photis	950	1.26 (3.47)	7	0.32
	Microjassa	906	1.20 (3.31)	4	0.45
	Vitrinellidae	809	1.07 (2.96)	3	0.38
	Gammaropsis	448	0.59 (1.64)	7	0.16
I.felix	*Haplosyllis spongicola*	39469	83.73 (--)	3	15.77
	Ericthonius	3949	8.38 (51.49)	3	5.16
n = 3	Actiniaria A	1038	2.20 (13.54)	3	1.65
	Vitrinellidae	809	1.72 (10.55)	3	1.15
	Janiridae	217	0.46 (2.83)	3	0.19
	Photis	199	0.42 (2.59)	3	0.16
	Leptocheliidae	156	0.33 (2.03)	3	0.26
	Spionidae	152	0.32 (1.98)	3	0.09
	Nemata	137	0.29 (1.79)	3	0.11
	Serpulidae	124	0.26 (1.62)	1	0.06
	Leucothoidae	117	0.25 (1.53)	3	0.05
P.walpersi	*Ericthonius*	10704	41.35	3	11.59
	Haplosyllis spongicola	6493	25.08	3	12.12
n = 3	Caprellidae (juveniles)	3644	14.08	3	6.22
	Caprella equilibra	2255	8.71	3	3.60
	Microjassa	905	3.50	3	1.36
	Photis	750	2.90	3	0.81
	Gammaropsis	389	1.50	3	0.45
A.polycapella	*Haplosyllis spongicola*	1978	84.82 (--)	3	3.48
	Caprella equilibra	220	9.43 (62.15)	3	1.48
n = 3	Caprellidae (juveniles)	83	3.56 (23.45)	3	0.45
	Leucothoidae	21	0.90 (5.93)	1	0.02
	Colomastigidae	6	0.26 (1.69)	1	0.01
	Ericthonius	4	0.17 (1.13)	2	0.01
	Gammaropsis	4	0.17 (1.13)	2	0.01

Table 9. Endofaunal taxa making up greater than 1% of the total endofaunal assemblage associated with all octocorals and each of the three octocoral species. Numbers in parentheses are calculations of the percent contribution of that taxon to the total endofauna with juvenile individuals of Family Caprellidae removed from the total abundance.

Note: Endofaunal taxa representing less than 1% of total endofaunal abundance (on octocorals) are included in this table if their contributions are greater than 1% when counts of juveniles of the family Caprellidae were removed from the calculations.

Host	Associate	Total Abundance	Percent of Total	Frequency	Average Density (per cm^3)
All Octocorals	Caprellidae (juveniles)	22470	39.59 (--)	15	11.73
	Caprella equilibra	14793	26.07 (43.15)	15	9.24
n = 15	*Microjassa*	8039	14.17 (23.45)	9	2.91
	Ericthonius	7274	12.82 (21.22)	15	3.27
	Conopea galeata	901	1.59 (2.63)	11	0.54
	Photis	761	1.34 (2.22)	12	0.38
	Stenothoidae	496	0.87 (1.45)	10	0.17
	Gammaropsis	475	0.84 (1.39)	10	0.25
	Nemata	350	0.62 (1.02)	6	0.21
L.hebes	Caprellidae (juveniles)	18331	42.70 (--)	5	22.35
	Caprella equilibra	8949	20.84 (36.38)	5	13.06
n = 5	*Microjassa*	7911	18.43 (32.16)	5	8.22
	Ericthonius	5356	12.48 (21.77)	5	7.07
	Conopea galeata	788	1.84 (3.20)	5	1.18
	Stenothoidae	414	0.96 (1.68)	5	0.41
L.virgulata	*Caprella equilibra*	5365	43.20	5	11.97
	Caprellidae (juveniles)	3381	27.22	5	8.68
n = 5	*Ericthonius*	1875	15.10	5	2.47
	Photis	582	4.69	4	0.65
	Gammaropsis	358	2.88	3	0.47
	Nemata	323	2.60	4	0.58
T.frauenfeldii	Caprellidae (juveniles)	758	52.42 (--)	5	4.15
	Caprella equilibra	479	33.13 (69.62)	5	2.69
n = 5	*Microjassa*	100	6.92 (14.53)	2	0.44
	Ericthonius	43	2.97 (6.25)	5	0.28
	Tritoniidae	21	1.45 (3.05)	5	0.22
	Conopea galeata	9	0.62 (1.31)	2	0.12

Table 10. Results of the Similarity Percentages (SIMPER) analysis including those endofauna that contributed to a cumulative 50% of the dissimilarity between **(a)** *I. felix* versus *P. walpersi* **(b)** *I. felix* and *P. walpersi* versus *A. polycapella*

(a) *I. felix* versus *P. walpersi*		
Endofauna Family	**Endofauna Taxon**	**Contribution to Dissimilarity (%)**
Caprellidae	Amphipod	8.87
Vitrinellidae	Gastropod	5.73
Actiniaria	Anthozoa	5.34
Ischyroceridae	Amphipod	4.44
Syllidae	Polychaete	4.30
Stenothoidae	Amphipod	3.46
Hiatellidae	Bivalve	2.87
Isaeidae	Amphipod	2.70
Podoceridae	Amphipod	2.66
Balanidae	Cirriped	2.24
Spionidae	Polychaete	2.05
Alpheidae	Decapod	1.98
Leptocheliidae	Tanaid	1.88
Ophiothricidae	Ophiuroid	1.78

(b) *I. felix* and *P. walpersi* versus *A. polycapella*		
Endofauna Family	**Endofauna Taxon**	**Contribution to Dissimilarity (%)**
Ischyroceridae	Amphipod	9.32
Caprellidae	Amphipod	4.76
Syllidae	Polychaete	4.65
Isaeidae	Amphipod	4.03
Terebellidae	Polychaete	3.98
Leptocheliidae	Tanaid	3.56
Janiridae	Isopod	3.48
Nemata	Nematode	3.43
Ampithoidae	Amphipod	3.25
Actiniaria	Anthozoa	3.04
Spionidae	Polychaete	2.82
Vitrinellidae	Gastropod	2.81
Podoceridae	Amphipod	2.47

Table 11. Results of the Similarity Percentages (SIMPER) analysis including those endofauna that contributed to a cumulative 50% of the dissimilarity between **(a)** *L. virgulata* in cluster group 4 (solo) versus *L. virgulata* in cluster group 3 (clustered with *L. hebes*) **(b)** *L. virgulata* in cluster group 4 (solo) versus *L. virgulata* in cluster group 5 (clustered with *T. frauenfeldii*)

(a) Solo *L. virgulata* versus *L. virgulata* clustered with *L. hebes*		
Endofaunal Family	**Endofauna Taxon**	**Contribution to Dissimilarity (%)**
Ischyroceridae	Amphipod	8.32
Isaeidae	Amphipod	8.01
Melitidae	Amphipod	4.86
Caprellidae	Amphipod	4.38
Stenothoidae	Amphipod	4.31
Nemata	Nematode	3.95
Pteriidae	Bivalve	3.4
Styelidae	Ascidian	3.06
Spionidae	Polychaete	3.05
Dorvilleidae	Polychaete	2.7
Sabellidae	Polychaete	2.56
Molgulidae	Ascidian	2.46

(b) Solo *L. virgulata* versus *L. virgulata* clustered with *T. frauenfeldii*		
Endofaunal Family	**Endofauna Taxon**	**Contribution to Dissimilarity (%)**
Archaeobalanidae	Cirriped	13.02
Syllidae	Polychaete	9.28
Nemata	Nematode	8.67
Dorvilleidae	Polychaete	7.29
Caprellidae	Amphipod	6.63
Isaeidae	Amphipod	5.6

Table 12. Results of the Similarity Percentages (SIMPER) analysis including those endofauna that contributed to a cumulative 50% of the dissimilarity between Sponge hosts versus Octocoral hosts.

Sponges versus Octocorals		
Endofauna Family	**Endofauna Taxon**	**Contribution to Dissimilarity (%)**
Caprellidae	Amphipod	42.04
Syllidae	Polychaete	29.05
Ischyroceridae	Amphipod	18.19
Isaeidae	Amphipod	2.08

Table 13. Environmental data for each sample station.

Station	Date	depth (m)	depth (f)	salinity	temp (°C)	ph	DO (mg/l)	Latitude	Longitude
GR05 A	5/3/2005	19.68	64.56	33.628	18.97	8.192	7.587	31.40171	-80.86677
GR05 B	5/4/2005	18.27	59.93	34.108	18.89	8.192	7.576	31.36731	-80.84272
GR05 C	5/5/2005	17.71	58.10	33.640	19.06	8.192	7.573	31.37785	-80.88545
GR05 D	5/8/2005	19.01	62.38	33.521	19.06	8.192	7.578	31.38298	-80.86696
GR05 E	5/7/2005	20.40	66.92	33.705	18.79	8.174	7.608	31.39600	-80.85203