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Habitat preferences and species associations of shallow-water marine Tubificidae (Oligochaeta) from the barrier reef ecosystems off Belize, Central America

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Abstract

The marine tubificid oligochaete fauna of Belize is the most diverse that has been described for the Caribbean Sea, with records for over 50% of all known Caribbean species. Tubificids were sampled at 77 stations around the outer barrier of the coral reefs off the Belize mainland. A total of 1,529 individuals representing 52 species were collected. Species distribution patterns were controlled mainly by sediment type and the presence or absence of mangroves. Six species (*Phallodrilus molestus*, *Tubificoides bermudae*, *Inanidrilus leukodermatus*, *Heterodrilus flexuosus*, *Bathydrilus formosus*, *Smithsonidrilus hummelincki*) with diverse life history characteristics were common and had broad habitat preferences being found in various types of heterogeneous sandy sediments. *Heterodrilus flexuosus* was the only common species in these samples known only in Belize. The other five common species range from Belize to Florida or Bermuda. Most other species have narrower habitat preferences and are limited to specific habitats. For example, one group of gutless species was restricted to organically enriched fine to medium sands, a group of Limnodriloidinae occurred only in mud around mangrove cays, and a group of meiofaunal species were restricted to saline groundwater.

Introduction

The total species diversity of marine Tubificidae (Oligochaeta) has surpassed that of the freshwater Tubificidae. Compared to the freshwater species, however, little is known of the ecology and habitat preferences of the marine species. Some work has been done on the autecology of individual tubificid species from temperate areas (Brinkhurst, 1964; Hunter & Aurthur, 1978; Birtwell & Arthur, 1980; Diaz, 1980; Bamber & Spencer, 1984; Erséus & Diaz, 1989) and on temperate marine tubificid assemblages (Cook, 1971; Baker, 1984; Davies, 1985; and Diaz *et al.*, 1987) but little is known of subtropical and tropical assemblages. Taxonomic studies of shallow subtropical and tropical marine tubificid oligochaetes indicate that they are very diverse and abundant (Erséus, 1990 and references therein).

The marine tubificid fauna of the Caribbean region (Bermuda, Florida, Barbados, and Belize) has received the most taxonomic attention with over 100 species described. Belize appears to be the most species rich area of the Caribbean with about 50% of these species (Erséus, 1990). In this paper we have taken the data on the 'Belizean' fauna collected by Erséus (1990) and analyzed them for ecological patterns and habitat preferences.

The belize barrier reef ecosystems

The barrier reef ecosystem off the Belize mainland is the largest continuous reef in the Caribbean Sea. It is 10 to 32 km wide and 250 km long (Rützler & Macintyre, 1982a). Carrie Bow Cay, the center of our collection area, sits on top of the barrier reef proper. The area to the west of Carrie Bow Cay forms a shallow *Thalassia* dominated lagoon, less than 5 m deep (Rützler & Macintyre, 1982a). To the east of Carrie Bow Cay the reef system rapidly grades from reef crest to inner fore reef, 2 to 12 m, to outer fore reef, 12 to 40 m, to outer barrier reef platform over a distance of less than a kilometer (Burke, 1982). Further eastward, about 22 km, is a large platform reef (Glovers Reef) that protects the Carrie Bow Cay area from open ocean waves. This protection is a principle factor that has allowed the development of highly diverse communities in the Carrie Bow Cay area (Burke, 1982).

The tide around Carrie Bow Cay has a mean range of 15 cm and is mixed semidiurnal (Kjerfve *et al.*, 1982). Channels to the north and south of Carrie Bow Cay are the main exchange routes between the reef system and ocean. While tidal currents are weak the almost constant wind-wave action supports the movement of materials on and off the reef. The complex physical structures of the reef system interacting with the water currents and protection from ocean waves have led to an extremely high diversity of habitats. This physical diversity of habitats is further enhanced by the organisms occupying and building the reefs. Details of the physical and biological aspects of the Belize barrier reef ecosystems can be found in (Rützler & Macintyre, 1982b).

Materials and methods

Erséus (1990), with the assistance of others, collected marine tubificid oligochaetes at 85 stations around the outer barrier of the coral reefs off the Belize mainland. While the purpose of these collections was primarily taxonomic, sufficient material was collected to evaluate ecological and habitat relationships. At each station approximately equal amounts of sediment were examined for Tubificidae. Because of taxonomic problems with immature individuals only sexually mature individuals were preserved and identified to species. Qualitative notes were also made on the physical characteristics of the site.

Numerical classification was used to classify species and stations into groups based on species abundance and distribution patterns. The flexible sorting algorithm was used ($\beta = -0.25$) with the quantitative form of the Bray-Curtis similarity coefficient (Boesch, 1977). Both species and station analyses were done on a reduced set of the original data. Species with only one or two collection occurrences were dropped from the analysis. To evaluate the strength of the species and station groups nodal analysis was conducted (Lambert & Williams, 1962). Nodal analysis is a post classification analysis that compares how well species station groups are formed.

Constancy and fidelity statistics (Lambert & Williams, 1962) were used to estimate the strength of the species-station groups. Constancy is a measure of species occurrence and can be expressed as

$$C_{ij} = a_{ij} \cdot 100\% / (n_i n_j),$$

where a_{ij} is the total number of occurrences of species in species group i and site group j, and n_i and n_j are total number of species and stations in the respective groups being compared. Expressed as a percentage, 100% constancy means every species group occurred at least once at every station in the site group being considered. Fifty percent constancy is when any combination of species occurrences is half the total possible number of species × station occurrences.

Fidelity measures the average frequency of occurrence of species in a group relative to the rest of the collection. It estimates the preference or avoidance of species for a particular site group and can be expressed as

$$F_{ij} = (a_{ij} \Sigma_j n_j)/(n_j \Sigma_j a_{ij})$$

using the same terms as constancy. The summation terms go across all site groups ($j = 1,...,J$) for a particular species group (i). When fidelity is equal to 1 the species group (i) has no preference for the site group (j), less than 1 indicates avoidance, and greater than 1 preference. Programs COMPAH and NODAL of the Virginia Institute of Marine Science, College of William and Mary were used for these analyses.

Results

Of the 90 stations collected by Erséus (1990) we used 72. Eight of the stations dropped were collected at different times or with different methods. The other ten stations were dropped because of their low information content, as explained below. The physical descriptions of the retained stations are given in Erséus (1990). The location of each sampling area is in Fig 1.

Faunal composition

A total of 1,529 individuals representing 52 tubificid species in 15 genera were collected (Table 1). About half of the genera (7 of 15) were represented by one or two species, accounting for about 20% of the total species. The four most speciose genera, accounting for about half (27 of 52) of the species, were *Heterodrilus*, *Phallodrilus*, *Olavius*, and *Limnodriloides*. The remaining four genera (*Inanidrilus*, *Bathydrilus*, *Thalassodrilides*, and *Smithsonidrilus*) represented about 30% (16 of 52) of the species.

Of the 52 species in the collection 21 (40%) occurred at only one or two stations and were considered rare. A third of the species (17) occurred at three to six different stations and were considered uncommon. Of the remaining species, 14 occurred at eight or more stations and were common. Three species (*Heterodrilus flexuosus* Erséus, 1990, *Phallodrilus molestus* Erséus, 1988, *Inanidrilus leukodermatus* (Giere, 1979)) were very common, occurring at 30 or more stations. These three species also accounted for 42% of the total individuals collected (Table 1). Their average

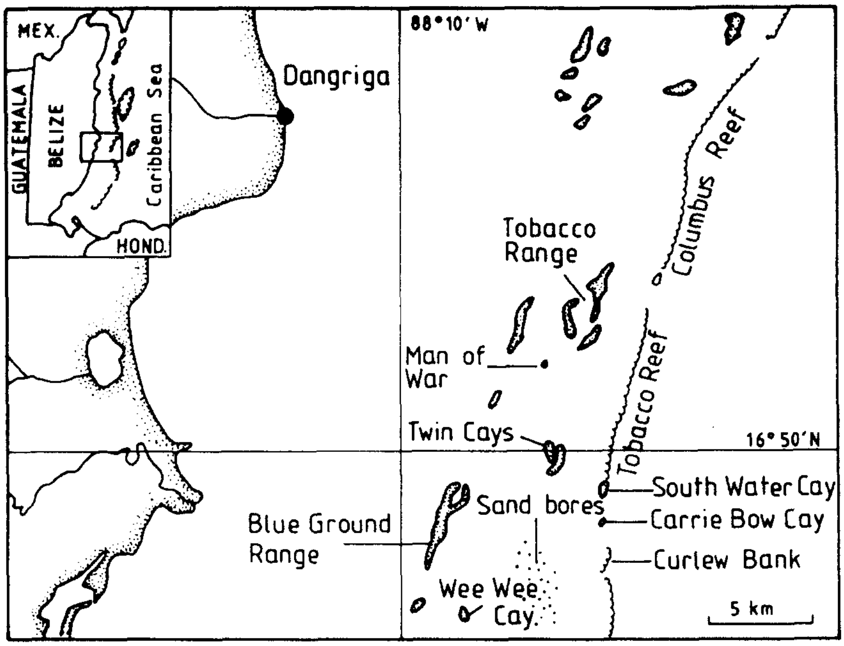

Fig. 1. Location of sampling areas on the barrier reef ecosystems off the coast of Belize.

Table 1. Marine Tubificidae collected at 77 stations located throughout the outer barrier of the coral reef ecosystems off the coast of Belize.

	Station occurrences	Number of individuals
Subfamily Rhyacodrilina		
Heronidrilus gravidus Erséus, 1990	5	8
Heterodrilus flexuosus Erséus, 1990	37	158
Heterodrilus rarus Erséus, 1990	2	5
Heterodrilus paucifascis Milligan, 1987	9	97
Heterodrilus modestus Erséus, 1990	10	34
Heterodrilus pentcheffi Erséus, 1981	17	48
Heterodrilus quadrithecatus (Erséus, 1981)	1	1
Heterodrilus ersei (Giere, 1979)	3	6
Subfamily Phallodrilinae		
Coralliodrilus rugosus Erséus, 1990	1	1
Phallodrilus compactus Erséus, 1990	5	9
Phallodrilus singularis Erséus, 1990	1	1
Phallodrilus deminutius Erséus, 1979	6	8
Phallodrilus molestus Erséus, 1988	33	199
Phallodrilus vicinus Erséus, 1990	1	1
Phallodrilus nastus Erséus, 1990	1	1
Phallodrilus bipartitus Erséus, 1990	1	4
Aktedrilus longitubularis Finogenova & Shurova, 1980	1	1
Aktedrilus parvithecatus (Erséus, 1978)	2	10
Jamiesoniella athecata Erséus, 1981	1	1
Inanidrilus leukodermatus (Giere, 1979)	30	284
Inanidrilus scalprum Erséus, 198	12	18
Inanidrilus belizensis Erséus, 1984	4	4
Inanidrilus aduncosetis Erséus, 1984	3	6
Inanidrilus reginae Erséus, 1990	1	2
Olavius imperfectus Erséus, 1984	6	40
Olavius tenuissimus (Erséus, 1979)	3	4
Olavius finitimus Erséus, 1990	2	5
Olavius vacuus Erséus, 1990	6	12
Olavius (Olavius) tantulus Erséus, 1984	6	18
Olavius (Olavius) pravus Erséus, 1990	1	3
Olavius (Olavius) longissimus (Giere, 1979)	2	8
Duridrilus tardus Erséus, 1983	13	30
Bathydrilus vetustus Erséus, 1990	1	3
Bathydrilus egenus Erséus, 1990	1	9
Bathydrilus adriaticus (Hrabê, 1971)	3	7
Bathydrilus formosus Erséus, 1986	19	96
Subfamily Limnodriloidinae		
Thalassodrilides gurwitschi (Hrabê, 1971)	5	20
Thalassodrilides bruneti Erséus, 1990	4	60
Thalassodrilides ineri (Righi & Kanner, 1979)	2	6
Tectidrilus bori (Righi & Kanner, 1979)	3	3
Limnodriloides monothecus Cook, 1974	1	2
Limnodriloides anxius Erséus, 1990	2	8
Limnodriloides uniampullatus Erséus, 1982	2	2
Limnodriloides sacculus Erséus, 1990	4	5

Table 1. (Continued)

	Station occurrences	Number of individuals
Limnodriloides barnardi Cook, 1974	8	18
Limnodriloides rubicundus Erséus, 1982	6	35
Smithsonidrilus luteolus (Erséus, 1983)	18	40
Smithsonidrilus appositus Erséus, 1990	15	23
Smithsondrilus hummelincki (Right & Kanner, 1979)	20	65
Smithsondrilus involutus Erséus, 1990	3	7
Subfamily Tubuficinae		
Tubificoides bermudae Råsmark & Erséus, 1986	16	92
Tubificoides parviductus Helgason & Erséus, 1987	1	1

abundance was 4.3, 6.0, and 9.5 individuals/station, respectively. Other species that did not occur as frequently but when they occurred had high average station abundance were *Thalassodrilides bruneti* Erséus, 1990 (15.0 individuals/station), *Heterodrilus paucifascis* Milligan, 1987 (10.8), and *Bathydrilus egenus* Erséus, 1990 (9). Species with the highest individual station abundances were the gutless *I. leukodermatus* with 64 individuals at station 13, *T. bruneti* with 52 individuals at station 61, and *H. paucifascis* with 42 individuals at station 6. It must be noted, however, that the sampling was semi-quantitative.

For 47 species there were sufficient individuals to get an estimate of size (Table 2). The majority of the species were small ranging from 5 to 10 mm in length. Eight species were of a meiofaunal size and belong to genera that are among the smallest for marine Tubificidae (*Aktedrilus*, *Phallodrilus*, *Coralliodrilus*). The exception was the genus *Heterodrilus* which also contains very large species (Table 2). Two of the largest species were gutless, with *Olavius (Olavius) longissimus* (Giere, 1979) reaching a maximum length of 46 mm. The maximum length for *Olavius vacuus* Erséus, 1990 was 20 mm. The other three large species belong to genera that contain a broad size range of species (*Heterodrilus*, *Bathydrilus*, *Thalassodrilides*).

Species distribution patterns

Cluster analysis was done using a reduced data matrix which included only species that occurred at three or more stations. This reduced the data to 31 species and 74 stations. Eight stations were dropped because they only had 'rare' species (< 3 occurrences). If retained, the prevalence of 'rare' species in the collection would tend to weken the cluster analysis and make pattern recognition difficult. After the deletion of rare species two additional stations (20, 34) were dropped from the analysis because they ended up having only a single species. The species analysis at the nine group level (Fig. 2) and the station analysis at the 12 group level (Fig. 3) were interpretable relative to species characteristics and sediment type.

Species groups A and B were the most common species in the collection. The three species (*P. molestus*, *Tubificoides bermudae* Råsmark & Erséus, 1986, *I. leukodermatus*) that composed group A had highest constancy and fidelity with site groups 1 and 2 which were characterized by clean fine-medium sands a meter or less in depth (Figs 4 & 5). A few stations in these site groups were deeper (2, 44) or had finer sediments (2, 26). Species group B (*H. flexuosus*, *Bathydrilus formosus* Erséus, 1986, *Smithsonidrilus hummelincki* Righi & Kanner, 1979) contained the most broadly distributed species. Group B was strongly

Table 2. Size categories and other life history characters of marine tubificids collected on the barrier reef ecosystems off the coast of Belize. Measurements for each species are maximum preserved length in mm and maximum reported collection depth from Erséus (1990). A depth of 0 indicates intertidal or saline groundwater.

	Length	Depth	Gutless	Papillae	Brackish	Circumtropical
UP TO ABOUT 4 mm						
Heterodrilus quadrithecatus	3	15				
Coralliodrilus rugosus	3	0				
Phallodrilus vicinus	4	< 1				
Phallodrilus nasutus	2	0				
Phallodrilus compactus	3	2				
Phallodrilus bipartitus	4	0				YES
Aktedrilus longitubularis	2	0				
Aktedrilus parvithecatus	3	0				YES
ABOUT 5–10 mm						
Heterodrilus flexuosus	10	24				
Heterodrilus rarus	8	1				
Heterodrilus modestus	6	9				
Heterodrilus pentcheffi	11	39				
Phallodrilus deminutius	6	14				
Phallodrilus molestus	7	70				YES?
Inanidrilus leukodermatus	11	16	YES			
Inanidrilus scalporum	11	27	YES			
Inanidrilus belizensis	9	24	YES			
Inanidrilus aduncosetis	13	8	YES			
Olavius imperfectus	9	8	YES			
Olavius tenuissimus	10	141	YES			
Olavius finitimus	7	2	YES			
Olavius (Olavius) pravus	7	1	YES			
Olavius (Olavius) tantulus	6	27	YES			
Bathydrilus adriaticus	10	32				YES
Thalassodrilides gurwitschi	8				YES	YES
Thalassodrilides bruneti	5	0				
Limnodriloides monothecus	9	583			YES	YES
Limnodriloides anxius	9	20			YES	
Limnodriloides sacculus	5	1				
Limnodriloides barnardi	6	150				
Smithsonidrilus luteolus	9	24				
Smithsonidrilus appositus	6	3				
Smithsonidrilus involutus	10	1				
ABOUT 10–15 mm						
Heronidrilus gravidus	11					
Heterodrilus paucifascis	12	39				
Duridrilus tardus	16	39		YES		YES?
Bathydrilus vetustus	12	6				
Tectidrilus bori	11	70				YES?
Limnodriloides rubicundus	16	74				YES
Smithsonidrilus hummelincki	14	21				
Tubificoides bermudae	14	15		YES		
MORE THAN 15 mm						
Heterodrilus ersei	25	9				

Table 2. (Continued)

	Length	Depth	Gutless	Papillae	Brackish	Circumtropical
Olavius vacuus	20	58	YES			
Olavius (Olavius) longissimus	46	2	YES			
Bathydrilus formosus	18	20				YES
Bathydrilus egenus	20	2				
Thalassodrilides ineri	25	2				

associated with site group 5 which was primarily coarse sand and rubble, with the exception of two stations that were muddy (32, 35). Both species groups A and B were poorly represented at site groups 9, 10, and 11. Site group 9 was all coarse sand and rubble around Carrie Bow Cay on the outer barrier side. Site group 10 was all fine sand muddy stations around mangrove cays. Site group 11 was also fine grained muddy sediments and included the deepest stations.

Species group C (*Phallodrilus deminutius* Erséus, 1979, *Smithsonidrilus luteolus* (Erséus, 1983a), *Duridrilus tardus* Erséus, 1983b) was primarily associated with site group 8, which was mainly outer barrier coarse sands with secondary heterogeneity consisting of *Halimeda* flakes, rubble, and *Thalassia*. The species in group C did not occur or appeared to avoid, based on fidelity, site groups with muddy fine grained stations, including groups 4, 10, and 12. Species group D was composed of three *Heterodrilus* species (*paucifascis*, *modestus* Erséus, 1990, *ersei* Giere, 1979) that were strongly associated only with site group 9 which was outer barrier coarse sand rubble stations that likely were exposed to higher wave energies. Group D species also did not occur at site groups with muddy stations, including groups 2, 3, 4, 10, and 12. Species group E was five species (*Smithsonidrilus appositus* Erséus, 1990, *Smithsonidrilus involutus* Erséus, 1990, *Heronidrilus gravidus* Erséus, 1990, *Limnodriloides barnardi* Cook, 1974, *Limnodriloides sacculus* Erséus, 1990) that were associated with only site group 6. This site group was unique being composed of outer barrier coarse sand and *Halimeda* flake sediments. There was only one other coarse sand *Halimeda* flake station in the collection not in site group 6, it was station 30 in group 7. There were four other *Halimeda* flake stations with finer grain sediments. Species group E did not occur at site groups 3, 7, or 9 and was only weakly associated with one other site group, 4 (Fig. 5).

With the exception of *Heterodrilus pentcheffi* Erséus, 1981a species group F was exclusively composed of gutless species. The species in this group were highly associated with the shallow cleaner fine to medium sand stations of site group 1. Group F was, to a lesser degree, also associated with site group 11 which was composed of shallow and deep fine to medium sand stations that were intermediate in organic content. Group F did not occur at the muddy mangrove cays site group 10 or at site group 12. If *H. pentcheffi* is excluded from group F, the remaining species, all gutless, also did not occur at site groups 5 and 9, both of which were coarse-rubble station groups.

Species group G was a weak association of *Phallodrilus compactus* Erséus, 1990 and *Bathydrilus adriaticus* (Hrabê, 1971) that had very high fidelity to the more organic finer sand stations of site group 11. This species group did not occur at half the site groups (2, 6, 7, 8, 9, 10). Species group H was also not well-defined but included two gutless species (*Olavius tenuissimus* Erséus, 1979, *Inanidrilus aduncosetis* Erséus, 1984) and *Tectidrilus bori* (Righi & Kanner, 1979) that were moderately associated with the coarser sediment site group 9 and the fine sand-muddy site group 11. Species group H did not occur at site groups 2, 3, 4, 7, and 8.

Species group I was the most unique of all the species groups. It was composed of three Lim-

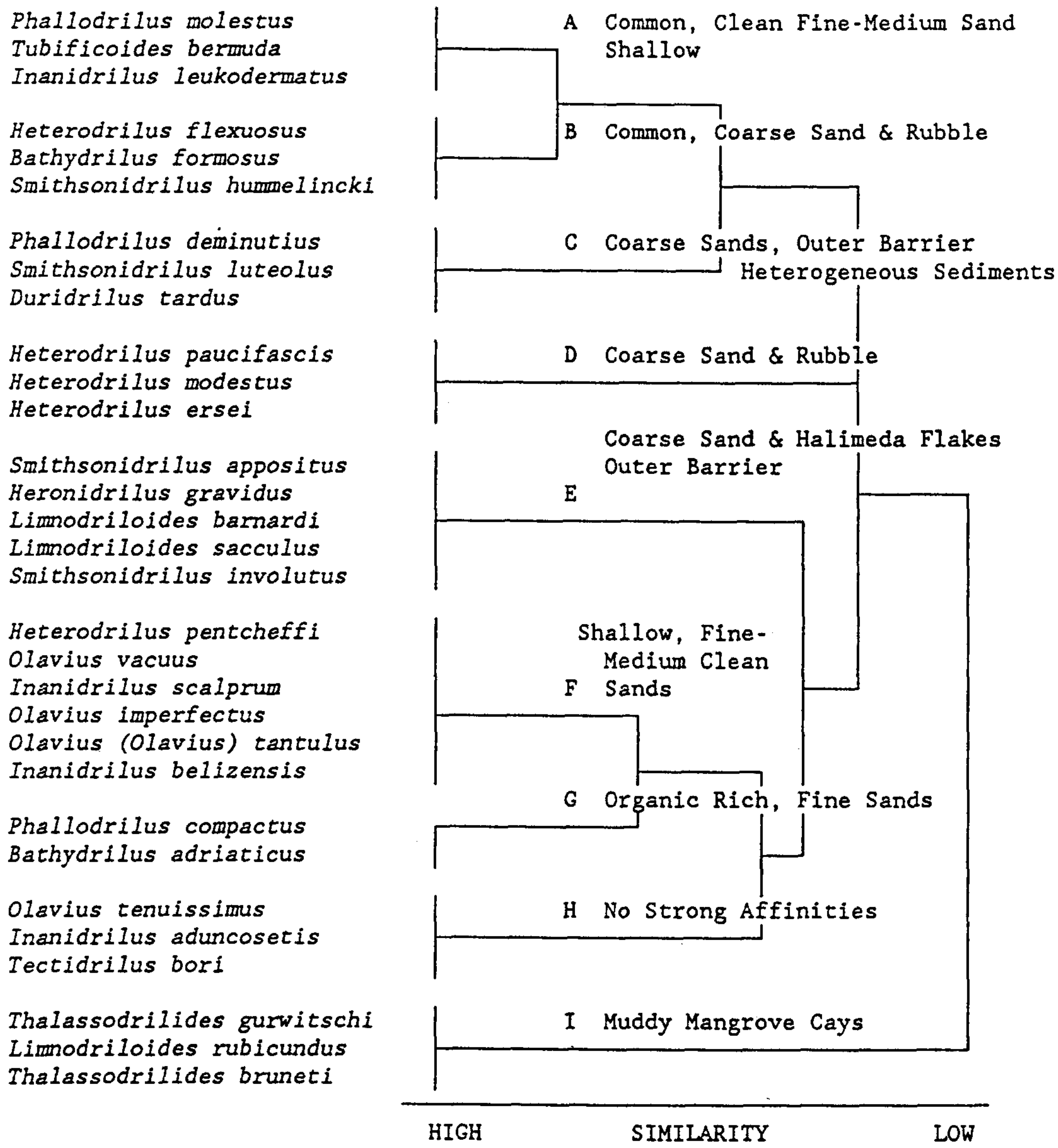

Fig. 2. Species groups defined from cluster analysis of Belize marine tubificid oligochaetes. See text for analysis detail and group characteristics.

nodriloidinae species (*Thalassodrilides gurwitschi* (Hrabê, 1971), *T. bruneti*, *Limnodriloides rubicundus* Erséus, 1982) that had very high constancy and fidelity to the muddy mangrove cays site group 10. Outside site group 10, the only other occurrences of *T. bruneti* (sandy station 43) and *L. rubicundus* (muddy station 52) were at site group 12, which was a mix of outer barrier and mangrove stations.

Rare species

Among the rare species (1 or 2 station occurrences) there were four gutless species, all of which occurred at stations with heterogeneous sediments. *Inanidrilus reginae* Erséus, 1990 occurred in a muddy *Thalassia* bed (station 49) giving it an affinity with the gutless species of species group H. *Olavius (Olavius) pravus* Erséus, 1990, *O.*

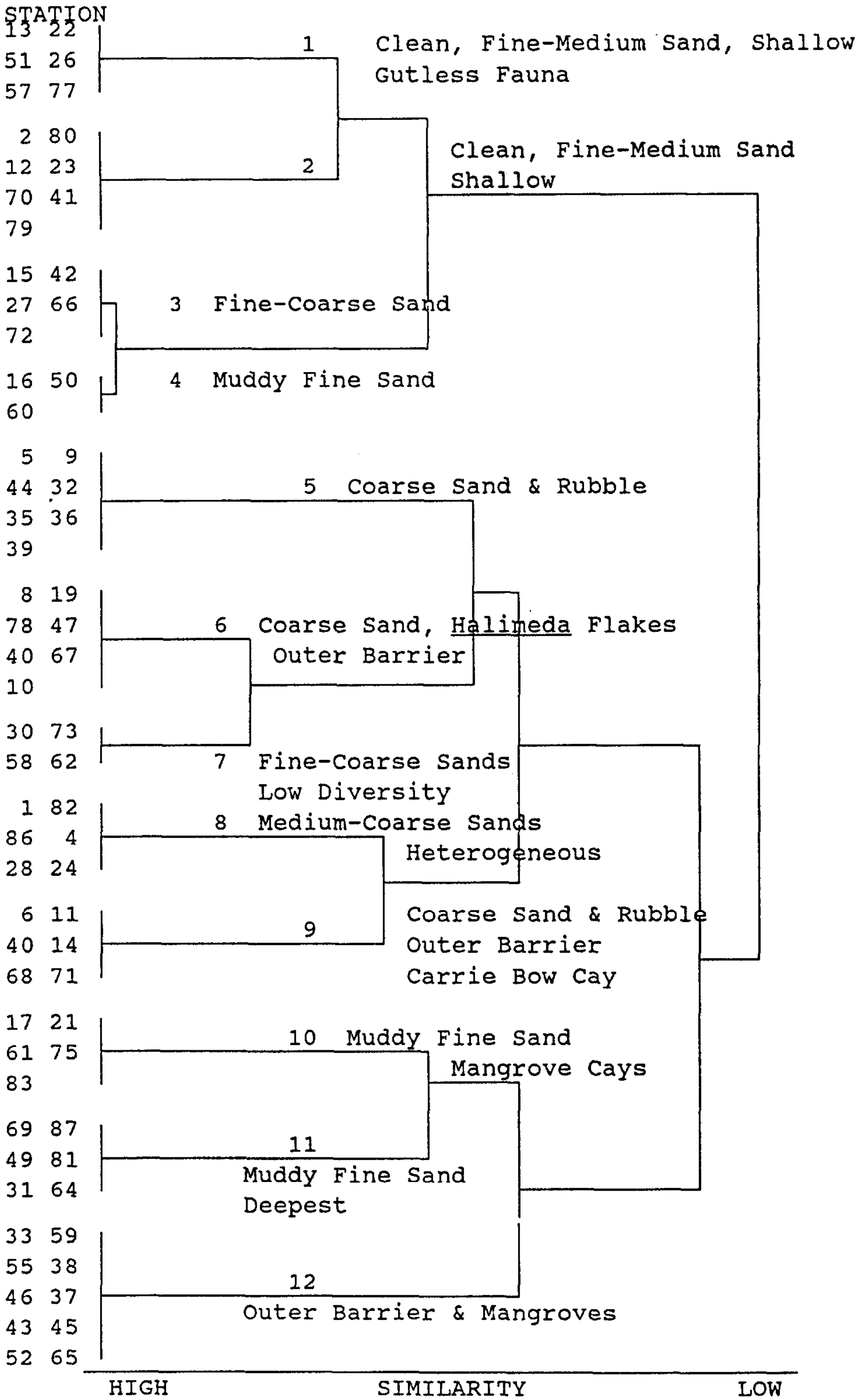

Fig. 3. Site groups defined from cluster analysis of Belize marine tubificid oligochaetes. See text for detail of analysis and group characteristics.

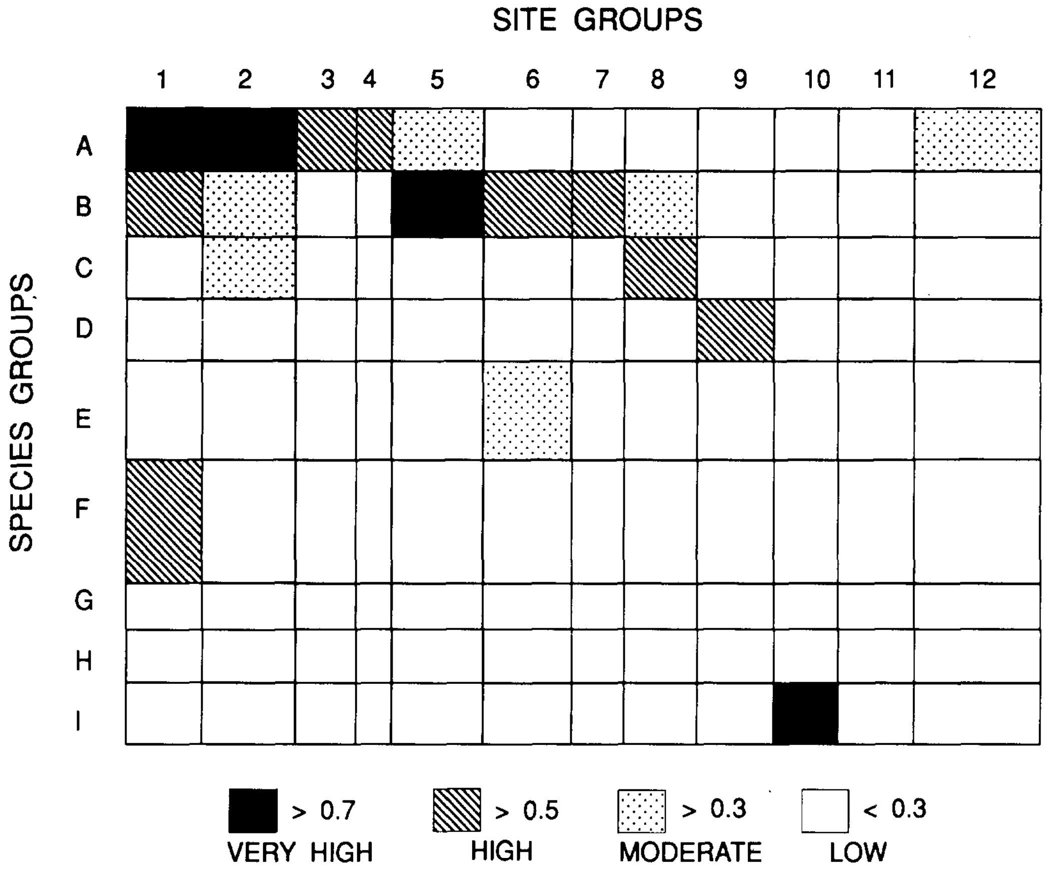

Fig. 4. Nodal consistency in a two-way table of species and site groups as described in Figs 2 & 3.

(O.) longissimus and *Olavius finitimus* Erséus, 1990 were all found in coarse sediments (stations 22, 31, 57, 68, 71) giving them affinity to species group F.

Seven rare species were found in muddy sediments giving them an affinity with species group I and site group 10. *Thalassodrilides ineri* (Righi & Kanner, 1979) occurred in muddy *Thalassia* and mangrove areas (stations 17 and 83), as did *Limnodriloides monothecus* Cook, 1974 (49). The other five muddy sediment species were *Limnodriloides anxius* Erséus, 1990 (52, 61), *Limnodriloides uniampullatus* Erséus, 1982 (61, 75), *Heterodrilus quadrithecatus* (Erséus, 1982a) (50), *Heterodrilus rarus* Erséus, 1990 (22, 25), and *Phallodrilus singularis* Erséus, 1990 (2). The small meiofaunal *Aktedrilus parvithecatus* (Erséus, 1978) (7, 20), *Aktedrilus longitubularis* Finogenova & Shurova, 1980 (54), *Jamiesoniella athecata* Erséus, 1981b (54), *Phallodrilus nasutus* Erséus, 1990 (18), *Phallodrilus bipartitus* Erséus, 1990 (7), and *Coralliodrilus rugosus* Erséus, 1990 (18) occurred in a range of sediments from organic rich mud to medium-coarse sands, but only at or near the high tide line in saline groundwater. None of these five species were found subtidally. The remaining four single-station occurring species were all found in medium to coarse sands and included *Phallodrilus vicinus* Erséus, 1990 (11), *Bathydrilus vetustus* Erséus, 1990 (36), *B. egenus* (9), and *Tubificoides parviductus* Helgason & Erséus, 1978 (82).

Discussion

For the Caribbean, the marine Tubificidae fauna of Belize is the most diverse known with records for over 50% of all Caribbean species. This in-

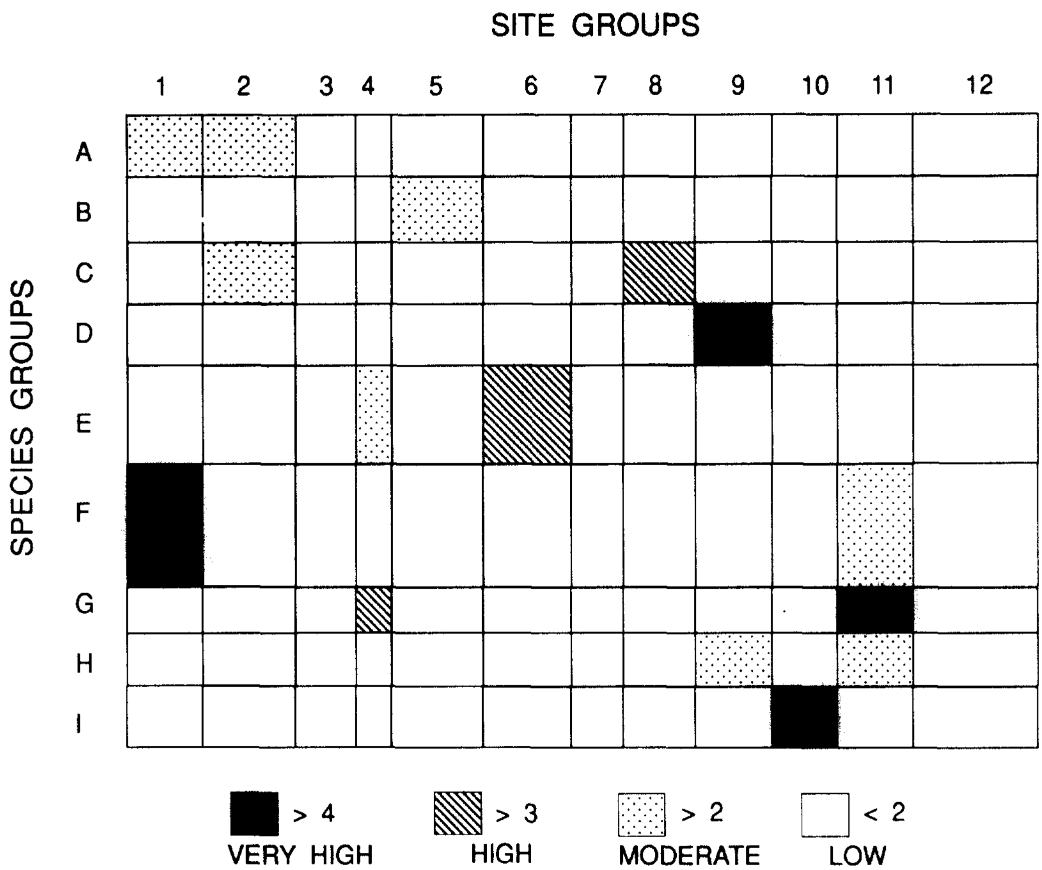

Fig. 5. Nodal fidelity in a two-way table of species and site groups as described in Figs 2 & 3.

cludes the 52 species reported on here plus seven others found by Erséus (1990), that occurred at other stations, compared to a total Caribbean fauna of about 100 species. For other areas of the Caribbean that have been sampled with comparable intensity, Florida is second to Belize with approximately 40% of the species, Bermuda third with 35% and Barbados fourth with about 20%.

The spatial distribution of Belizean marine tubificid species appears to be typical of other benthic fauna with species occurrence and abundance following a negative binomial or Poisson distribution. About 40% of the species were considered rare being represented by a few individuals and occurring at only one or two stations (Table 1). The three most common species (*H. flexuosus*, *P. molestus*, *I. leukodermatus*) occurred at about 60% of the stations and were about 40% of all individuals collected. The habitat preferences of these three abundant species were varied. *Phallodrilus molestus* and *I. leukodermatus* preferred shallow fine-medium clean sands and *H. flexuosus* coarse sand and rubble habitats. *Inanidrilus leukodermatus* is a gutless species that inhabits the aerobic-anaerobic sediment interface (Giere *et al.*, 1982).

The high species diversity and lack of dominance by a single species in the Belize tubificid fauna may be due to a combination of habitat stability through time and habitat heterogeneity. The occurrence of several species per genera also points to a degree of microheterogeneity or niche specialization within or between habitat types (Cohen, 1978). Five genera had five to seven species occurrences (*Heterodrilus*, *Phallodrilus*, *Inanidrilus*, *Olavius*, *Limnodriloides*). *Phallodrilus*, however, is currently being split into a number of smaller genera (Erséus, 1992).

While there were common species that had broad spatial distributions (*P. molestus*, *T. bermudae*, *I. leukodermatus*, *H. flexuosus*, *B. formosus*, *S. hummelincki*, species groups A and B) none of them occurred in all habitat types. Their broad distribution was more a reflection of the predominance of sandy substrates around the cays. These species, however, did show habitat selectivity being completely absent from mud and mangrove associated sites. The highest degree of habitat specificity was shown by the three Limnodriloidinae species (*T. gurwitschi*, *T. bruneti*, *L. rubicundus*, group I) that occurred exclusively in mud and mangrove sites, except for a single occurrence of *T. bruneti* at a sandy station.

The gutless species that were not rare were divided into two groups by their habitat preferences. The majority of them (*O. vacuus*, *Olavius imperfectus* Erséus, 1984, *O. (O.) longissimus*, *Inanidrilus scalprum* Erséus, 1984, *Inanidrilus belizensis* Erséus, 1984) occurred in shallow fine to medium clean sands and did not occur in coarse-rubble sediments. The second group (*O. tenuissimus* and *I. aduncosetis*, species group H) were associated primarily with coarse *Halimeda* sands and rubble sediments and did not occur in other types of sediment. The habitat preferences of the most common gutless species, *I. leukodermatus*, included all the habitats in which the other gutless species occurred with highest affinity for fine to medium clean sands.

The meiofaunal species (*A. parvithecatus*, *A. longitubularis*, *J. athecata*, *P. nasutus*, *P. bipartitus*, *C. rugosus*) consistently occurred at or near the high tide line in saline groundwater. These habitats are particularly favored by meiofaunal oligochaetes from all geographic areas.

The high degree of habitat preference exhibited by the Belizean marine tubificid fauna is not unusual for the Tubificidae. Diaz *et al.* (1987) found a similar high degree of microhabitat partitioning among the Tubificidae of the middle Atlantic Bight. The tubificids in Cape Cod Bay were also very sediment-type specific (Cook, 1971). Slight changes in the sediments in both these areas resulted in changes to the tubificid fauna. The one species that occurred in Cape Cod, the Middle Atlantic Bight, and Belize, *L. monothecus*, was consistently found in fine sands. *Olavius tenuissimus* and *H. pentcheffi* found both in the Middle Atlantic Bight and Belize occupied similar medium to coarse grained habitats. While there are no other Caribbean or tropical studies for comparison the taxonomic literature (summarized by Erséus, 1990) indicates that a high degree of microhabitat partitioning is typical for marine Tubificidae.

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