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FREE-LIVING MARINE NEMATODES OF HARD BOTTOM SUBSTRATES IN TRINIDAD AND TOBAGO, WEST INDIES

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ABSTRACT

As part of a larger comparative study, marine nematode hard-bottom assemblages from Trinidad and Tobago were surveyed using artificial substrates. The collectors (nylon pan scourers) were used as a standard substratum for the colonization by marine nematodes inhabiting subtidal hard, rocky bottom substrata. The artificial substrate units (ASUs) were deployed at four sites off the islands of Trinidad and Tobago, the former being the southernmost of the Caribbean chain of islands. The nematode fauna was represented by 5 orders, 25 families, 52 genera, and 70 species. The Chromadoridae were most abundant followed by the Cyatholaimidae. At the family level, the nematode fauna was found to be similar to other temperate and tropical locations including those of a few previously described Caribbean assemblages. Epigrowth feeders were dominant (65.2%) on the substrate followed by non-selective deposit-feeders (13.3%). Free-living marine nematodes of the western and southern Caribbean are not well known, while nematode fauna of hard-bottom substrates are even less known. This survey provides first records of the hard-bottom nematode fauna of Trinidad and Tobago and also adds new evidence for the geographic range of some nematode species.

The coastal and marine environments of the Caribbean islands are generally oases of high production associated with shallow waters, coral reefs, mangrove swamps, estuaries, and coastal lagoons, surrounded by deep oligotrophic seas (Agard and Gobin, 2000). The benthic environments support a high biodiversity of organisms most of which have only been studied to a limited extent (e.g., mostly coral reefs). Meiofaunal, and in particular, marine nematode studies in the Caribbean are rare. Tietjen (1984, 1989) described nematode assemblages of deep environments in Venezuela and Puerto Rico. In the Mexican (western) Caribbean, the composition and distribution of nematodes in Laguna de Buena Vista and in Banco Chincorro were studied by de Jesus-Navarrete (1993a, 2003), and de Jesus-Navarrete and Herrera-Gomez (1999, 2002) described horizontal and vertical nematode distributions in the soft bottom sediments of the Chetumal Bay, Quintana Roo, Mexico. De Jesus-Navarrete (1993b) also examined the distribution and abundance of benthic nematodes from Campeche Sound, in the Gulf of Mexico. There have been even fewer surveys of marine nematodes of the Caribbean islands chain (the West Indies): Lewis and Hollingsworth (1982) compared leaf epifauna (including nematodes) of the seagrass *Thalassia testudinum* Konig, with that of other seagrasses in Barbados; Renaud-Mornant and Gourbault (1981) and Boucher and Gorbault (1990) described nematode distribution, composition, and abundance in soft sediments of Guadeloupe; other nematode taxonomic descriptions exist for Guadeloupe (Decraemer and Gourbault, 1986, 1987; Gourbault and Decraemer, 1986, 1987, 1988; Gourbault and Vincx, 1990), Cuba (Botosoneau, 1970; Andrassy, 1973), and Martinique (Wagenaar Hummerlinck, 1977).

The use of artificial substrates enables sampling of macroinvertebrates in areas where orthodox sampling methods are not effective (e.g., hard bottom surfaces) and counteracts the reduced variability associated with conventional sampling de-

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vices (Cairns, 1982; Rosenberg and Resh, 1982). Another advantage to their use in ecological studies is that artificial substrates can be constructed out of inexpensive materials (Flannagan and Rosenberg, 1982). Many studies have utilized a range of artificial substrates under experimental conditions and compared their colonization process with that of natural substrates (Ghelardi, 1960, 1971; Kensler and Crisp, 1964; Schoener, 1974; Myers and Southgate, 1980; Costello, 1988; Edgar, 1991). These studies suggest that communities on artificial substrates are quite similar to those occurring in the natural environment. In fact, Myers and Southgate (1980) found that communities on "nylon pan scourers" were comparable with those on red algal turfs in the littoral rocky areas of Bantry Bay, Ireland. Nylon pan scourers were selected as the experimental substrate in this study, because of their reported success in a number of earlier ecological studies (e.g., Schoener, 1974; Myers and Southgate, 1980; Costello, 1988).

Most of the rocky substrate nematode studies published to date have been conducted on phytal associations: the colonization of seaweeds and algal holdfasts (Wieser, 1953; Moore, 1971; Warwick, 1977; Kito, 1982). Only few studies have utilized artificial substrates to examine meiofauna (i.e., nematodes) on sublittoral rocky substrates. Montagna and Ruber (1980) used plastic mesh litter bags filled with packages of *Spartina alterniflora* Loisel, to census bacteria, nematodes, diatoms, ciliates, and flagellates at marsh sites. Cummings and Ruber (1987) used plastic twine to mimic *S. alterniflora* plants in soft sediment marshes, while De Troch et al. (2005) used plastic seagrass mimics to study colonization by copepods. Two studies recently used artificial collectors suspended in water to compare meiofauna living on microalgal-covered pilings of a wood pier and sediment-dwelling meiofauna with meiofauna trapped onto the suspended artificial collectors (Atilla et al., 2003), and to examine colonization and succession patterns of meiofauna on suspended aluminium plates in upwelling areas (da Fonseca-Genevois et al., 2006). However, Atilla et al. (2003) confirm the existing paucity of data on the abundance, diversity, and colonizing abilities of hard substrate meiofauna. This present study provides the first records (including ecological information) of free-living nematode fauna associated with hard substrates, for the southern Caribbean and Trinidad and Tobago, West Indies.

Materials and Methods

This study was part of a larger global survey using artificial substrate units (ASUs) to examine diversity patterns of a single component of the macrobenthic (polychaete) and meiobenthic (nematode) communities inhabiting hard bottoms at different latitudes (Gobin, 1994; Gobin and Warwick, 2006). The geographic locations in that survey included the southwest coast of England (50°N), the northwestern areas of Trinidad and Tobago (10°N), and Signy Island of the South Orkneys in Antarctica (60°S). The Trinidad and Tobago survey is the focus of the present study. For this survey, five ASUs were deployed at each of five stations (total of 25 ASUs) between January and February 1991. Four stations (D, E, F, G) were located along the chain of tiny islands (known as "Five Islands") off the northwest peninsula of Trinidad and the fifth (H) was located off the northwest coast of Tobago (Fig.1).

Each ASU consisted of four nylon pads (pan-scourers). A stainless steel ring was strung through each pad. The four rings were all attached onto a shackle that was bolted onto a 20 cm long stainless steel piton (Fig. 2). SCUBA divers of the Institute of Marine Affairs (IMA) in Trinidad deployed and retrieved all ASUs. Each ASU was imbedded into a rocky substrate (rock ledge or crevice) at water depths of 12–15 m. The ASUs were collected approximately

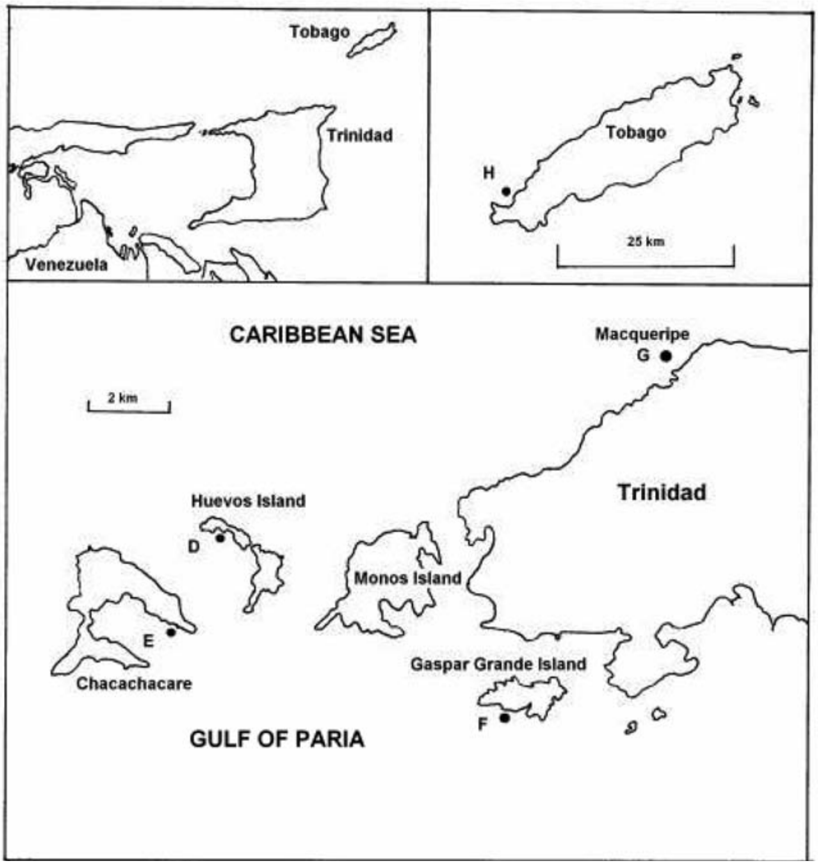

Figure 1. Sampling stations D, E, F, and G located in the northwestern chain of islands off Trinidad and H, off the west coast of Tobago in the West Indies (10°N).

5 mo after deployment, a period previously established as optimal for maximal colonization onto the substrates (Gobin, 1994).

In the laboratory, each pad was separated (and retained as a replicate) by removing the central metallic clasp. The entire pad (mesh) was unraveled and the contents were thoroughly washed (with freshwater) into a container. Fauna attached to the mesh were also collected and the entire content of each container was then carefully washed over two sieves: one with mesh size of 125 μm (to retain the macrofauna) and one with mesh size of 63 μm (to retain the meiofauna). Meiofauna were again washed to remove all formalin and the meiofaunal organisms were separated from any sediment that had accumulated in the ASU by flotation with Ludox TM, following the methods of Platt and Warwick (1983). Subsequently, the samples were washed, re-sieved, and dehydrated (at 45 °C) in a 10% glycerol solution overnight. From each station, five replicate samples were used in the analyses. The dehydrated samples were wholemounted onto slides and examined. All nematodes were counted and identified to genus, or species level where possible. The nematode taxonomic keys by Platt and Warwick (1983, 1988) were used for identifications (up to genus level) with on-site (Plymouth Marine Laboratory, United Kingdom) verifications by one of the key authors (R. M. Warwick.). The lack of nematode taxonomic literature for the Caribbean and the potential for new species made identification to a known species level almost impossible. Putative species were assigned to these organisms, as well as families or genera, once recognized. The nematode slide collection will be catalogued and deposited in the National Biodiversity Centre (at the University of the West Indies, St. Augustine Campus, Trinidad and Tobago).

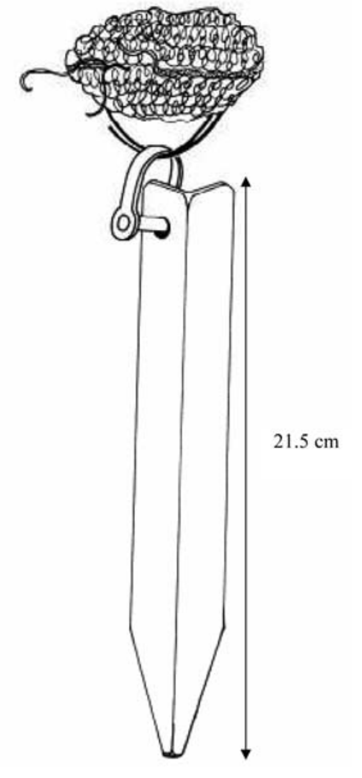

Figure 2. Components of the artificial substrate unit (ASU) used for sampling nematodes.

To describe the nematode diversity, the Shannon-Wiener index *H’* (Shannon and Weaver, 1965), Pielou’s evenness index *J’*, and Margalef’s species richness *d* were calculated for each station. A one-way non-parametric analyses of variance (ANOVA) test (Kruskal-Wallis) was performed on the pooled set of samples to determine if there were significant differences in diversity.

Results

A very diverse community of macrofaunal and meiofaunal organisms colonized the ASUs, including polychaetes, amphipods, copepods, isopods, asteroids, decapods, gastropods, ascideans, bivalves, as well as some other groups (Gobin, 1994). From the meiofaunal component, 6502 nematodes were counted and identified that belonged to five orders, 25 families, and 52 genera, and comprised 70 species (Table 1).

Taxonomic observations suggest that more than 90% of the nematodes were new species, including one (1) new genus, desmodorid A (Table 1). The family Chromadoridae was highly successful in colonization having the highest representation by both species (17) and individuals (2245). However, the most abundant species was *Cyatholaimus* sp. 1 (of the family Cyatholaimidae), contributing to approximately 18% of the total number of individuals present. Five families: Chromadoridae, Cyatholaimidae, Draconematidae, Oncholaimidae, and Oxystominidae comprised approximately 75 % of the total abundance. All species listed are new and first records for Trinidad and Tobago.

Table 1. Nematode (phylum Nematoda) families and species list for Trinidad and Tobago including total numbers of individuals collected. Family totals are in bold.

Family	Species	No. of individuals
Axonolaimidae	*Southerniella* sp. 1	11
		11
Anticomatidae	*Anticoma* sp. 1	120
		120
Ceranomatidae	*Pselionema* sp. 1	1
		1
Chromadoridae	*Chromadora* sp. 1	10
	Chromadora sp. 2	12
	Chromadorita sp. 1	37
	chromadorid sp. 1	2
	chromadorid sp. 2	616
	Graphonema sp. 1	44
	Hypodontolaimus sp. 1	103
	Neochromadora sp. 1	20
	Neochromadora sp. 2	2
	Prochromadorella sp. 1	895
	Prochromadorella sp. 2	198
	Ptycholaimellus sp. 1	15
	Spilophorella sp. 1	222
	Spiliphera sp.1	2
	Spilophorella sp. 2	67
		2,245
Comesomatidae	*Comesoma* sp.1	2
	Sabatieria sp. 1	2
		4
Cyatholaimidae	*Cyatholaimus* sp. 1	1,161
	Metacyatholaimus sp. 1	7
	Metacyatholaimus sp. 2	1
	Paracanthonchus sp. 1	93
	Paracanthonchus sp. 2	35
		1,297
Desmodoridae	*Desmodora* sp.1	18
	Desmodora sp. 2	14
	Desmodora sp. 3	70
	desmodorid (Genus A)	85
		187
Desmoscolecidae	*Desmoscolex* sp. 1	37
		37
Diplopeltidae	*Diplopeltis* sp. 1	138
		138
Draconematidae	*Draconema* sp. 1	350
	Draconema sp. 2	118
	Paradraconema sp. 1	14
		482
Enoplidae	*Enoplus* sp. 1	1
		1

Table 1. Continued.

Family	Species	No. of individuals
Eurystominidae	*Eurystomina* sp. 1	12
		12
Symplocostomatidae	*Symplocostoma* sp. 1	58
		58
Epsilonematidae	*Epsilonema* sp. 1	117
	Epsilonema sp. 2	69
		186
Ethmolaimidae	*Gomphionchus* sp. 1	42
		42
Rhabdolaimidae	*Syringolaimus* sp. 1	266
		266
Leptolaimidae	*Camacolaimus* sp.1	1
	Leptolaimus sp. 1	18
	Onchium sp. 1	182
		201
Leptosomatidae	*Leptosomatum* sp. 1	3
		3
Linhomoeidae	*Eleutherolaimus* sp. 1	19
	Linhomoeus sp. 1	57
	linhomoeid sp. 1	60
	Metalinhomoeus sp. 1	1
		137
Microlaimidae	*Calomicrolaimus* sp. 1	21
	Microlaimus sp. 1	74
	Molgolaimus sp. 1	14
		109
Oncholaimidae	*Oncholaimus* sp. 1	27
	Oncholaimus sp. 2	222
	Viscosia sp.1	166
		415
Oxystominidae	*Halalaimus* sp. 1	119
	Halalaimus sp. 2	99
	Nemanema sp. 1	63
	Oxystomina sp. 1	62
	Paroxystomina sp. 1	56
		399
Phanodermatidae	phanodermatid sp. 1	7
	phanodermatid sp. 2	2
		9
Choanolaimidae	*Halichoanolaimus* sp. 1	14
		14
Siphonolaimidae	*Siphonolaimus* sp. 1	1
		1
Monohysteridae	*Daptonema* sp. 1	30
	Daptonema sp. 2	35
	Gnomoxyala sp. 1	1
	Paramonohystera sp. 1	1
	Rhynchonema sp. 1	1
	Steineria sp. 1	59
		127
	Total nematodes:	**6,502**

Nematode abundances were not significantly different among stations (one-way ANOVA: P = 0.08) while total numbers of species tended to be significantly higher at station E compared to stations D, F, and H (Tukey: $q_{calc} > q_{critic}$ 10.605; Fig. 3). Species diversity (*H´*) was also significantly higher at E that at D and H (Kruskal Wallis ANOVA: P = 0.04; $q_{calc} > q_{critic}$ 0.5533). Species richness (d) and evenness (J) did not differ significantly among the five stations (Kruskal-Wallis non-parametric ANOVA: P = 0.12 and P = 0.06, respectively).

As there were many putative species identifications, nematode family data were used to group families into trophic guilds following Wieser (1953). Based on Wieser's classification (1953), the epigrazers were dominant (65.2%), followed by the non-selective deposit feeders (13.3%), omnivore/predator group (13.5%), and the selective deposit feeders (8.1%). Combining the two deposit-feeding groups, however, increased their contribution to 21.4%.

Discussion

The hard substrate subtidal nematode fauna of Trinidad and Tobago consists of similar families and genera as in other geographic areas such as New Zealand and the southwest coast of England (Gobin and Warwick, 2006). The Trinidad and Tobago rocky substrate nematode fauna also shows general similarity (in terms of composition) to previously described Caribbean faunal assemblages, although from varying environments: (a) calcareous (Mexico), (b) soft sediments (Guadeloupe), (c) deep waters (Venezuelan Basin), and (d) seagrass epifauna (Barbados). For example, there were 17 families common to Trinidad and Tobago (this survey) and Mexico (Banco Chinchorro) fauna as reported by de Jesus-Navarrete (2003), while the 10 listed families (of 30 recorded in total) from Guadeloupe (Boucher and Gourbault, 1990) were also common in Trinidad and Tobago. Twelve of the 20 dominant genera of the Venezuelan Basin (Tietjen, 1984) were common to Trinidad and Tobago while the 16 nematode species listed by Lewis and Hollingsworth (1982) belonged to nematode families found in Trinidad and Tobago. The observed varying family co-dominance of Chromadoridae and Cyatholaimidae (this study); Desmodoridae and Comesomatidae in Mexico (de Jesus-Navarrete, 2003); and Desmodoridae and Xyalidae in Guadeloupe (Boucher and Gourbault, 1990), however, suggest that these differences may be due mainly to the different substrates sampled.

The macro- and meiofauna inhabiting the ASUs were in some respects similar to that of kelp holdfasts (Gobin, 1994). Ott (1967) described the algal structure as controlling the degree of shelter as well as the accumulation of sediment. Similarly, the ASU consists of a network system of mesh creating a number of holes and crevices. Wieser (1953) described the clear correlation between the physiognomy of the associated nematode fauna and the substrate type. His Chilean nematode samples (from sublittoral kelp holdfasts) also showed a comparatively similar dominance (as in ASUs) by epigrowth feeders. The presence and expected dominance of epigrazers on such substrates is probably due to the presence of microflora, as has been described previously (Zobell, 1939; Maki et al., 1988; Edgar, 1991), bacteria, and other small organisms (Moens and Vincx, 1997; da Fonseca-Genevois et al., 2006).

Trapped particles in the ASU meshes provided the food supply for the next largest group, the deposit-feeding nematodes (non-selective and selective deposit-feeders combined). Selective deposit feeders are more specific in their choice of food while

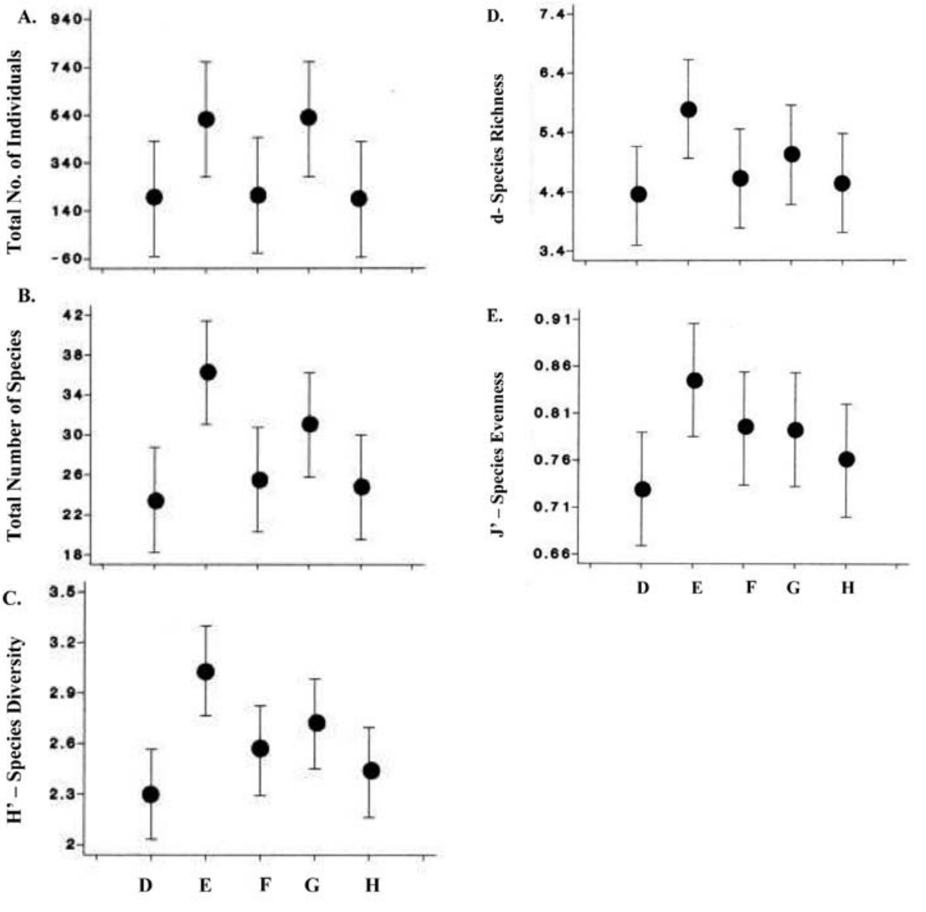

Figure 3. Mean plots (with 95% confidence intervals) of nematode abundance, numbers of species, species richness (*d*), species diversity (*H'*) and evenness (*J'*) of nematodes for stations D, E, F, G, and H.

non-selective deposit feeders ingest a variety of material of variable size (Moens and Vincx, 1997). This variety may range from individual bacteria to larger inorganic particles with attached bacteria. The oceanography of the southern Lesser Antilles is strongly influenced by the outflow of two of the world's largest river systems, the Amazon and the Orinoco (Agard and Gobin, 2000). Due to the movement of the Guyana current and its eddies around Trinidad and Tobago, estuarine conditions (salinities as low as 16 in the wet season) prevail because of the outflows of these two rivers. The increased amount of suspended particles (including silt and detritus) in the water, combined with high primary productivity in the shallow Gulf of Paria (Agard and Gobin, 2000) probably contribute to these nutrients and food resources. Such resources were likely trapped on the ASUs and thus available to the deposit feeding nematodes. In this respect, the conditions in ASUs were suitable for the development of a significant deposit feeding community since the silt in these waters may have been less "transient" as is more typical of coastal waters.

The greater number of species and species diversity at station E is difficult to explain. While the offshore islands are proximal to both the more oceanic Caribbean

Sea and the more coastal Gulf of Paria, likely enhancing species diversity, station E was the only offshore station with high values. It is possible that local hydrographic conditions (Agard and Gobin, 2000) may have resulted in local concentrations of marine organisms, but without more spatial replication it is impossible to say.

Meiofaunal ecological studies provide valuable information for benthic community research. Changes in spatial and temporal distributions of organisms may be due to natural occurrences, physical perturbation or pollution effects (or a combination of these). The effects of these influences are often reflected in the abundance and species composition of the benthic fauna including meiofaunal nematodes. In fact, Coull and Palmer (1984) suggest that in almost any disturbed area there is an immediate increase in the abundance and diversity of the meiofauna. Nematodes are also important constituents of trophic webs since they are a valuable food source for larger organisms such as fish, hydroids, polychaetes, turbellarians, and tardigrades (McIntyre, 1969; Tietjen et al., 1970). Meiobenthos are selectively consumed by juvenile spot (*Leiostomus xanthurus* Lacépède, 1802) (Feller and Coull, 1995) and juvenile flounder (*Platichthys flesus* Linnaeus, 1758) (Aarnio, 2000).

Comparisons to nearby sediment fauna are not possible as concurrent collections were not part of the original goal (Gobin, 1994). Previous hard-substrate studies of Atilla and Fleeger (2000), and Danovaro and Fraschetti (2002) on meiofauna, and that of da Fonseca-Genevois et al. (2006) on nematodes, indicate that these communities differ radically from those in neighboring sediments. Atilla et al. (2003) found that meiofauna (nematodes and copepods) colonizing artificial collectors (small mesh pads similar to the ASUs) were more similar to that of pier-pilings than that of nearby sediment assemblages. Together with Atilla et al. (2003), the present study confirms the importance of artificial substrates in facilitating ecological experiments in coastal and marine areas. With increasing urbanization and associated encroachment onto coastal areas by artificial engineered substrates, their role in the marine environment and in the ecology of organisms may become even more important.

Nematodes are usually by far the dominant fauna in marine sediments (Heip et al., 1985) and according to Lambshead (2004) only about 4000 species have been identified out of an estimate of between 100,000 and 1 million species worldwide. The paucity of relevant taxonomic information and nematode distribution data for the nations of Mexico, Panama, Colombia, Venezuela, Costa Rica, Cuba, Jamaica, Puerto Rico, and Bermuda has been highlighted recently in the various country-specific reviews of Caribbean and subtropical marine biodiversity (Miloslavich and Klein, 2005). Of the 136 nematodes reported from the Venezuelan Basin (Tietjen, 1984), only two were recognized as described species. Similarly, Boucher and Gourbault (1990) suggested that of the 156 species identified in the Guadeloupe survey, most were new. Approximately 70% of nematode species from Banco Chinchorro were also new to science (De Jesus Navarrete, 2003). The present study has provided the first species list of free living marine nematodes for Trinidad and Tobago and the southern Caribbean. In addition to re-emphasizing the associated taxonomic problems, results of this study confirm the presence of many as yet undescribed species in the area. Further taxonomic studies are critical in order to continue building on our regional biodiversity data.

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