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# Meiofaunal Colonization of Artificial Substrates.

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# MEIOFAUNAL COLONIZATION OF ARTIFICIAL SUBSTRATES

A Dissertation

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## ABSTRACT

Meiofaunal colonization of artificial substrates was investigated in a shallow estuarine embayment. Meiofauna colonized various artificial substrates rapidly, at a rate of 1000 individuals collector$^{-1}$ day$^{-1}$ regardless of season, suggesting that high abundances of meiofauna commonly exist in the water column. These water-column meiofauna may be important in fish diets and may serve as a dispersing pool that aids recolonization after disturbance events.

Colonization of artificial substrates by transient meiofauna of unknown origin(s) occurred through the water column. To determine the source of meiofauna colonizing artificial substrates, sediment and pier-piling meiofauna were sampled and compared to artificial-substrate colonists. Assemblages of copepods and nematodes were significantly different among the three habitats. Artificial-substrate communities were more similar to pier-piling than sediment communities, and the morphology of most copepods colonizing artificial substrates resembled phytal dwellers. These observations suggest that most colonists primarily originated from microalgae-covered portions of pier pilings. There were also significant but smaller contributions from sediments. Selected pier-piling taxa were very good colonists, suggesting they migrate frequently into the water column and contribute to a rapidly dispersing pool of meiofauna.

Habitat complexity and flow greatly influence meiofaunal colonization of artificial substrates. To investigate the effects of habitat complexity on meiofaunal colonization, the physical structure of plastic bottle brushes was altered by clipping and removing their bristles. Abundances of meiofauna increased with increased habitat

complexity (the ratio of total surface area of bristles to volume of the brush) and surface area. Nematodes responded more to changes in bristle density and copepods and two constituent copepod species responded more to changes in substrate surface area. Flow fields around artificial substrates were observed in a laboratory flume at 5 and 15 cm $s^{-1}$ flow velocities. Flow velocity, transmissivity, and turbulence intensity indicated important relationships between colonization and the structural properties of the substrates. These data suggest that meiofaunal colonization of artificial substrates is a function of water flow and filtration rate through the substrate, and that complexity and substrate shape influence capture rate.

# CHAPTER 1

# GENERAL INTRODUCTION

Relationships between the complexity of a given habitat and the diversity and abundance of organisms have long been an interest of both terrestrial and marine ecologists (MacArthur & MacArthur, 1961; Coull & Wells, 1983; Bell, 1985). Habitat complexity is generally considered to have two components: (1) habitat heterogeneity, or the diversity of different habitat types across a landscape, and (2) habitat structure which is the physical or architectural component of complexity within a habitat type (Sebens, 1991). The physical complexity of a habitat is important because increased complexity provides more surface area for inhabitants or colonists, and structurally complex environments might therefore be expected to maintain higher equilibrium population abundances or experience higher colonization rates. Species diversity is also generally expected to be higher in architecturally complex habitats. Complex environments provide refuge from predators and more available space for colonization and the growth of food resources. In addition, MacArthur and Wilson's Island Biogeography Theory (1967) suggests that equilibrium population sizes should be higher on large islands compared to small islands, resulting in lower species extinctions and higher number of species on large islands (or in habitats with large surface areas). Thus, habitat structure may influence both population abundance and species diversity.

In marine environments, structural complexity varies among habitats. In soft sediments, studies of habitat complexity have mostly focused on the role of biogenic structures such as seagrass beds, animal burrows, fecal mounds, oyster beds and polychaete tube-caps (Rhodes et al., 1978; Heck & Orth, 1980; Bertness & Miller, 1984; Hoffman et al., 1984; Bell, 1985; Beck, 1995). All such structures increase habitat

patchiness and provide inhabitable surface areas for new assemblages. Moreover, such biogenic substrates are fragmented in space, thus acting as habitat islands, and frequently differ in their faunal assemblages compared to surrounding environments (Sutherland, 1971, 1984).

Meiofauna are benthic metazoans that are small enough to pass through a 500μm sieve but large enough to be retained on meshes of 40-65μm (Higgins & Thiel, 1988). Meiofauna live in or on a variety of marine and estuarine substrates including sediments, animal burrows, macrophytes, and variety of surfaces that support macroalgae and microalgal growth. Meiofaunal assemblages associated with fouling, plant communities and various animal structures differ from surrounding sediment assemblages, and are very specific to habitat types (Rutledge & Fleeger, 1993; Walters & Bell, 1984). Meiofauna from sediments typically avoid the water column, display negative phototaxis, and traits, such as adhesive glands, associated with a sedimentary life style (Coull, 1988; Giere et al., 1988). Meiofauna typically lack pelagic larvae, although water-column dispersal of adults and juveniles is common in marine and lotic systems (Palmer, 1992). Meiofauna are especially affected by habitat complexity in phytal habitats (Coull, 1999) where complex architecture not only supports higher species diversity and abundances (Hicks, 1980; Bell, 1983), but also provides refuge from fish predation (Coull & Wells, 1983).

Meiofauna also represent a taxonomically rich group of animals which may serve as an excellent model for biodiversity studies. For example, 22 of the 33 metazoan phyla have at least some meiobenthic taxa. They are also rich in species.

Over 10,000 species of harpacticoid copepods have been described; however, a realistic estimate of the true number of species is about one million (Huys, personal comm.). High abundances of meiofauna can be obtained in small sample sizes, and therefore, small manageable samples can provide detailed information on their community structure and spatial distribution.

Although meiofauna are traditionally considered to be sediment dwelling, large numbers (>3000 individuals $m^{-2}$ $h^{-1}$) of meiofauna, especially harpacticoid copepods, emerge into the water column in shallow estuaries (Walters, 1988). Relatively little is known about the meiofaunal assemblage found in the water column. Some meiofauna enter the water column by active swimming with diurnal periodicity (Walter, 1987, 1988), but the majority from muddy sediment enter by passive processes associated with erosion (Palmer & Gust, 1985; Palmer, 1988; Fleeger et al., 1995). Meiofauna may feed in the water column (Suderman & Thistle, 1998) and some authors speculate that they enter the water column for mate finding (Bell et al., 1988). Nevertheless, this assemblage is likely to be a valuable food source for fish. Dietary studies showed that some meiofauna (especially crustaceans) found in fish guts usually do not occur in sediments, nor are they known to be associated with macroalgae (McCall, 1992; Toepfer & Fleeger, 1995). Also, it is common to find copepod species with body features similar to phytal-dwelling species (e.g., prehensile first legs and mouth parts or dorso-ventrally and laterally flattened body shapes) in sediments but in very low abundances. Such a meiofaunal assemblage appears to be common in Louisiana estuaries where macroalgae is rare (Atilla, personal observation). It is possible that meiofauna present

in the water column also emerge from artificial hard substrates of anthropogenic origin, such as submerged rubble, pier pilings and bulkheads, and, due to their active swimming and dispersion abilities, occur in the water column in high abundances. However, findings regarding this species assemblage is largely speculative because such structures are difficult to sample by traditional coring and towing procedures. Species that are rarely observed are sometimes called cryptic due to their unknown origin.

Meiofauna that frequent the water column settle and colonize a variety of different substrates including sediments, cyanobacterial mats, seagrass culms and attached and floating macroalgae (Hicks, 1980; Hall & Bell, 1988; Bell & Hicks, 1991; Vopel & Arlt, 1995). Additionally, seagrass culms and *Spartina alterniflora* stems support meiofauna associated with epiphytes often in higher densities than surrounding environments (Rutledge & Fleeger, 1993; Hall & Bell, 1988). The value of this dispersal to meiofauna is unknown but is potentially important to opportunistic life styles.

As coastlines develop due to antropogenic demand, construction of artificial hard substrates including pier pilings, bulk heads and pontoons, becomes ever more prominent. In addition, artificial reefs, made out of rubber, concrete and other structures, are frequently built to create more habitable area for natural reef communities (Bonshack, 1990). Such artificial structures provide large vertical relief which support large populations of marine epifauna and microalgae. Epifauna living on these artificial substrates have been examined in a cursory fashion (Connell & Glasby, 1999; Butler & Connolly, 1996), but the meiofauna of these environments have been greatly

understudied because they are highly motile and difficult to sample. Meiofauna may live in high abundances on artificial hard substrates because they live in commensal relationships with epifauna (Gee & Davey, 1986), and free-living forms presumably associate with microalgae that foul such substrates. Artificial hard substrates can be suitable habitats for meiofaunal settlement. Little (1986) reported that high abundances of meiofauna live in association with aufwuchs on tiles. Algal growth and presence of sessile macrofauna such as barnacles on pier pilings and bulkheads provide refuge because of the complex structure of their surface. Abundant food resources such as filamentous algae suggest that these substrates can be surrogate environments for dispersing meiofauna.

Meso-scale ($cm^2$ scale) artificial substrates have been used as mimics of natural habitats such as seagrass blades and marsh grass shoots (Eckman, 1983; Hall & Bell, 1988; Hicks, 1989; Benoit et al., 1998), and are sometimes used in biodiversity and pollution-monitoring studies. Such artificial substrates are usually designed as complex structures providing a large surface area for colonization by small invertebrates within a small volume. In order to quantify the structural complexity of phytal habitats, the ratio of total surface area (e.g., surface area of fronds of a branching algae) and volume of the substrates has been suggested by Harrod & Hall (1962), and has been used by many investigators (Coull & Wells, 1983; Hicks, 1980; Bell, 1985). Estimating surface area to volume ratio of biogenic structures such as micro- and macroalgae can be laborious due to an irregular structure. Artificial substrates, however, have very small within-replicate variability, and their surface area and volume can be estimated easily.

Additionally, artificial substrates can be placed in the marine environment for extended periods of time without change in their physical structure, and their structure can easily be manipulated. Few investigators have examined abundance/diversity and complexity relationships associated with artificial substrates. Such studies are needed to be sure that artificial substrates can serve as adequate mimics of natural structures or be used reliably in monitoring studies.

Water movement plays an important role in marine ecology by acting as a transport medium for organisms and their propagules (Vogel, 1981; Nowell & Jumars, 1984; Denny, 1993). Flow above a critical erosion velocity has been shown to erode meiofauna from sediment into the water column (Palmer & Gust, 1985) and increase the supply of meiofauna and sediment particles in the water column. Hagerman & Reiger (1981) reported that copepods found in water samples taken near a dock consisted of a variety of species possibly originating from relatively distant marsh, seagrass beds, and perhaps nearby pier pilings. Although dispersal distances of meiofaunal individuals are poorly known, distances of tens of meters have been estimated when flows are low, and estimated distances may exceed hundreds of meters at high flows (Palmer, 1988, 1992). Studies have typically assumed that water-column meiofauna have a sediment or phytal origin (Fleeger, 1984; Palmer, 1988; Walter, 1991; Waters & Bell, 1994); however, little is known about other possible sources.

Once emerged, dispersing meiofauna can colonize new habitats rapidly. Many studies have investigated meiofaunal settlement and its interaction with flow (Sun & Fleeger, 1991; Hicks, 1980; Palmer, 1988). Other studies have focused on the substrate-

flow interaction and settlement of macrofaunal larvae on a variety of macro-scale (1 to10 $m^2$) substrates such as boulders, reefs, kelp beds and seagrass beds (Eckman, 1984; Cusson & Bourget, 1997; Harvey & Bourget, 1997). For example, several studies showed that flow characteristics differ above and below large structures such as macroalgal (kelp) or seagrass beds. Flow is characterized by low sheer stress and turbulence below algal bed canopies and high sheer stress and turbulence above canopies (Gambi et al., 1990). This condition has been shown to increase particle settlement (including larvae) below the canopy (Duggins et al., 1990). Meiofauna and macrofaunal larvae are similar in size and sinking characteristics. Although there may be an active component to settlement of some macrofaunal larvae, water-column movements of both are primarily passive (Butman,1987; Palmer et al., 1996). Because of their similarity in size and behavior, meiofauna may serve as an excellent model for larval settlement.

In a flow field where the only heterogeneity is represented by artificial substrates, initial colonization of meiofauna may be affected by three factors: (1) flow velocity and nature of flow, (2) the structure's capture efficiency, and (3) the availability of meiofauna. Large complex structures such as woody debris and artificially created structures have been reported to have higher meiofaunal abundances during high flow in stream beds (Palmer,1996; Lancaster, 2000), presumably because emerged meiofauna are captured with high efficiency and the supply is high. Similar to many branching algae or hydrozoan colonies, meso-scale artificial substrates cause a hydrodynamic drag, and therefore change the nature of flow. Although the effects of hydrodynamics

on larval settlement and habitat selection of invertebrates onto unvegetated bottoms are well investigated (Butman, 1987; Butman, 1989; Grassle et al., 1992; Harvey & Bourget, 1997), much less is known regarding invertebrate colonization of biogenic or non-biogenic meso-scale structures.

Colonization of organisms onto complex structures exposed to sea water may be a function of habitat complexity and its interaction with flow. The settlement of particles onto meso-scale substrates has been studied in the field and in laboratory flumes (Hannan, 1984; Bell, 1985; Harvey et al., 1995, Benoit et al., 1998); however, few studies have examined the relationship between structural complexity, flow fields and particle capture. Anderson & Charters (1982) found that a mass of filamentous benthic algae (~35 cm in length) created downstream turbulence above a critical flow velocity of 14 cm $s^{-1}$. They also reported that filamentous algae suppressed turbulence below this critical flow velocity. Harvey et al (1995) suggested that at slow flow velocities this kind of interaction with flow and structurally complex substrates may cause reduced turbulence intensities and influence capture rates of small particles such as invertebrate larvae. Also, in case of active dispersion, complex habitats can provide better refuge than bare sediment presumably increasing the settlement rate of organisms (Palmer, 1996).

The overall objective of my dissertation was to examine the colonization of meiofauna onto artificial substrates as mimics of meso-scale structurally complex algal habitats such as filamentous drift algae. Because colonization of these substrates occurs through the water column, interactions of flow with substrates and the behavior of

meiofauna may be potentially important. I combined field and laboratory flow studies to investigate net colonization, community structure and the source or origin of meiofauna, as well as interactions between habitat complexity and flow patterns. My focus was primarily to examine colonization over a short time, before recruitment by reproduction could occur. These water-column meiofauna have potential ecological importance because they are likely subject to higher rates of predation than when they are associated with a substratum (McCall & Fleeger,1995), and they represent a rapidly dispersing pool of meiofauna that quickly recolonizes disturbed areas. Further, these studies will enhance our understanding of meiofaunal biodiversity by sampling a greatly understudied portion of the fauna in the Gulf of Mexico.

The second chapter of this dissertation examined meiofaunal colonization onto artificial substrates in an estuarine embayment. As indicated earlier, meiofauna frequenting the water column are difficult to document in detail, mainly due to the lack of adequate sampling methods. The purpose of this study was to (1) describe the colonization dynamics and community structure of cryptic water-column meiofauna with the use of artificial substrates, (2) investigate the dynamics of their colonization and the seasonality of the colonists associated with artificial substrates, and (3) test the collecting abilities of different types of artificial substrates as sampling tools. In order to determine the characteristics of a good artificial substrate, a preliminary study was conducted using three types of artificial substrates: (1) plastic mesh pads (commercially available as pot scrubbers), (2) bottle brushes, and (3) Hester-Dendy plates (tile plates stacked on an eye bolt allowing 1-cm gaps in between). Community structure of

meiofauna colonizing on artificial substrates was analyzed to obtain information on seasonality, colonization rates, and copepod species richness, evenness and diversity. The first chapter has been published in Marine Ecology P.S.Z.N.I, Volume 21, issue 1, pp.1-15 (2000).

In the third chapter of this study, I investigated the possible sources of meiofauna that colonize artificial substrates. I hypothesized that meiofauna dispersing in the water column colonize artificial substrates suspended in the water column and therefore the community structure of meiofauna on artificial substrates should reflect the characteristics of source communities. This study was carried out at the same study site used for the experiments in the first chapter, but with the use of plastic mesh pads. Meiofauna from sediments and pier pilings were synoptically sampled and compared to colonists of suspended artificial substrates. All three communities were compared and analyzed to determine the contribution of the two source communities to artificial substrates. In the meiofaunal assemblage, nematode (to genus) and copepod (to species) community structure were investigated in detail to provide more precise information on the source of the colonists found on artificial substrates. This study provided information on not only the source of the colonists but also the never-before documented pier-piling nematode and copepod assemblage through the use of a suction sampler designed for this purpose.

In the fourth chapter, I investigated the effects of habitat complexity and flow on meiofaunal settlement on artificial substrates. The first two studies in this dissertation strongly indicated that colonization is a function of flow and dispersion. The

hypotheses of this study were that (1) abundance and species diversity of meiofauna colonizing on artificial substrates are affected by habitat complexity and/or surface area, and (2) colonization of meiofauna on artificial substrates is affected by flow around these structurally-complex artificial substrates. In this study, again conducted at the study site used in previous investigations, plastic bottle brushes were manipulated to create six levels of structural complexity and surface area by clipping and removing the bristles of the brushes. Abundances of meiofauna colonizing brushes at each level of complexity and the species diversity of adult copepods were determined. I also documented the flow fields around these substrates in a paddle-wheel flume at flow velocities similar to that of the field and examined the interactions between flow and structural complexity and their relationship to settlement of meiofauna.

# CHAPTER 2

## MEIOFAUNAL COLONIZATION OF ARTIFICIAL SUBSTRATES IN AN ESTUARINE EMBAYMENT*

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**Introduction**

Studies of the meiobenthos have traditionally focused on sedimentary habitats (Hicks & Coull, 1983; Coull,1988), although meiofauna associated with macroalgae have also been examined in some detail (e.g., Hicks, 1980; 1985; Williamson & Creese, 1996). Recent studies have shown that non-traditional habitats may also harbor abundant meiofaunal assemblages. For example, seagrass culms (Hall & Bell, 1988; Bell & Hicks, 1991) and *Spartina alterniflora* stems (Rutledge & Fleeger, 1993) support meiofauna associated with epiphytic algae in densities that can exceed those of surrounding sediments. Vopel & Arlt (1995) reported that in a shallow brackish environment the density of meiofauna living on cyanobacterial mats was five times higher than that in adjacent sediment. Shanks & Walters (1997) found that nematodes reside on marine snow, and that harpacticoid copepod nauplii, juveniles and adults take temporary refuge on marine snow. These habitats generally share certain features; they are structurally complex, rich in organic material, and potentially provide a refuge from predators.

Another non-traditional habitat for meiofauna is the surface of hard substrates. Biofilm and microalgal growth can be luxurious on hard substrates such as bulkheads, piers, pilings and even mollusk shells. Little (1986) showed that in a freshwater environment a diverse group of meiofauna is associated with the aufwuchs of submerged tiles, and marine polychaete tube caps have been shown to be a rich habitat for epibenthic meiofauna (Bell & Coen, 1982). Hard substrates have received little attention partly because they are very difficult to sample. Many hard-substrate

associated fauna are fast swimmers with strong avoidance reactions that reduce sampling efficiency (Atilla personal observation), although this problem may be overcome by using non-traditional techniques such as suction sampling devices (e.g, Taylor et al.,1995). Metazoans that are poorly sampled with cores, nets and grabs (Wells, 1976) are sometimes called cryptic fauna, and hard substrates could be a source of a highly transient meiofaunal assemblage.

Several lines of evidence suggest that a cryptic meiofauna exists in estuaries. Dietary studies often find that fish gut contents contain meiofauna that do not typically occur in the sediments or on macroalgae (McCall, 1992). Toepfer & Fleeger (1995) reported that species in the harpacticoid copepod genera *Harpacticus*, *Paronychocamptus* and *Zausodes* were found in the gut contents of three juvenile fish species, but these species are very rare in sediment samples from the area (Fleeger, 1985). Additionally, many harpacticoid copepod species have morphologies such as prehensile mouth parts and limbs that are typically associated with phytal life styles (Hicks & Coull, 1983; McCall & Fleeger, 1995), but occasionally occur in sediment samples in estuaries (Fleeger, personal observation). Macroalgae are rare in many sub-tropical estuaries and probably cannot account for the presence of these phytal-like forms.

The purpose of this study was to quantify meiofauna that colonize artificial substrates in a Louisiana estuary as a preliminary test of the applicability of artificial substrates for biomonitoring studies. The use of artificial substrates has been promoted as a method to quantify biodiversity (Warwick, personnel comm.), and artificial

substrates have been used in aquatic systems for biomonitoring programs for some time (Cairns et al., 1973; McCormick et al., 1988). Artificial substrates with a complex structure provide refugia from predators for meiofauna and juvenile macrofauna; however, relatively little is known regarding the dynamics of colonization, seasonality or the source pool of colonists associated with artificial substrates. The major taxa of meiofauna and species composition of copepods colonizing three types of artificial substrates were quantified in two seasons.

## Methods

### Study Area

Samples were collected from Grand Isle, Louisiana (29°N, 90°W) in a shallow embayment (< 2 m deep) adjacent to Caminada Pass. Water depth at this site varied with frontal passage and tides, and ranged from 2 - 0.5 m. Artificial substrates were placed near an oyster hatchery where oyster shells, wood bulkheads and pier pilings, and other man-made structures were present.

### Preliminary Study

A preliminary experiment was conducted in February 1997 to compare the utility of three artificial substrates and determine short-term colonization rates. A completely randomized design was implemented with three artificial substrates (mesh and brush collectors and Hester-Dendy plates) and sampled over a 12-day period. Our mesh collectors are commercially available as pot scrubbers and are made out of plastic threads (approximately 74 m in length) woven into pads. Those used in this experiment were approximately 9 cm in diameter and 2 cm thick yielding a geometric volume of

159 $cm^3$. The surface area of the mesh collectors was estimated by measuring the three dimensions of the thread that comprises the mesh collector. Width and height (thickness) of the thread were measured with calipers. To estimate length, all mesh collectors were first weighed. To obtain a relationship between thread weight and length, several replicates of a 1-m long section of the thread were weighed and an average weight was obtained ($\bar{X}$ = 0.08797 g $m^{-1}$). The total weight of the each mesh collector was divided by this value to estimate the total length of the thread comprising the mesh collector. Width, length and height were multiplied to estimate the surface area. Brush collectors are bottle brushes which are approximately 20 cm long, with 2.5 cm-long plastic bristles (0.025 cm in diameter) attached on a long metal axis (with a geometric volume of 392.5 $cm^3$). Bristles on a 2 cm section of a bottle brush were removed, counted and weighed to estimate the total number and weight of bristles on a brush (4400 bristles $brush^{-1}$, 4.6 g $brush^{-1}$). The surface area of the bristles was calculated by considering each bristle as a cylinder. Total surface area of the bristles was estimated by multiplying the average surface area of a bristle ($\bar{X}$ = 0.064 $cm^2$) by the total number of bristles. The volume of the mesh thread and the brush bristles was also measured by water displacement. Hester-Dendy plates (Hester & Dendy, 1962) have little structural complexity compared to mesh and brush collectors. They can be made out of thin plates of various materials stacked on an eye bolt equally distant from each other. In this study we used square ceramic tiles (11 cm x 11 cm), each with a surface area of 121 $cm^2$ and a weight of 7 g. Five tiles attached on an eye bolt were separated by washers (ca 5 mm) from each other and comprised a cube with a geometric

volume of 605 $cm^3$. The volume of Hester-Dendy plates was also measured by water displacement.

Five replicates of each type for each collection date were hung from a wooden walkway with 50 lb monofilament line at a mid-depth in the water column to avoid air exposure during low tides. Three replicates of each type were retrieved after 1, 2, 3, 6 and 12 days. Because generation times in meiofauna usually exceed 14 days at temperatures at our study site (6-27 °C) (Hicks & Coull, 1983), we considered that meiofauna found on artificial substrates were a result of colonization rather than recruitment by reproduction.

Summer and Winter Data Collections

The preliminary experiment showed that Hester-Dendey plates collected fewer meiofauna than the brush and mesh collectors, which achieved similar densities. Due to their cost effectiveness and ease of handling, mesh collectors were used for further investigations. Mesh collectors were exposed to colonization in July and December 1997. Four replicates for each collection date were attached to two PVC pipe frames, fastened at both ends to the substrate with 50 lb monofilament line. The frame was placed ca. 5 m from the oyster hatchery walkway with the substrates at mid-depth in the water column. Individual substrates were collected inside plastic containers while under the water to avoid flushing meiofauna from the substrates during collection.

In July 1997, mesh collectors were exposed for colonization for two weeks (14 days). An 8-week colonization period was implemented in December to determine if an equilibrium abundance could be achieved. Substrates were collected after 2 weeks (D1)

(also used for the comparisons between July and December), 4 weeks (D2) and 8 weeks (D3).

Laboratory Analyses

All samples were preserved with 10% formalin stained with Rose Bengal immediately after field collection. Rinsing and sieving of the collectors were done in the laboratory with nested 500 μm and 63 μm sieves. The 63 μm sieve fraction was subsampled using a plankton-wheel subsampler; 1/8 of each sample was examined for enumeration. Major taxa of meiofauna were enumerated and all copepod species were identified to at least a nominal species taxon by using the taxonomic aids of Wells (1976), Huys et al. (1996), and Lang (1965).

Suspended particles that accumulated on the mesh collectors was also quantified to estimate particle capture and retention. Suspended sediment capture is presumably influenced by hydrodynamic regime; flow above critical erosion velocity should increase suspended sediment load in the water and concomitantly increase water movement, and thus capture rate, through artificial substrates. Alternatively, very high flows might remove suspended particles from substrates. After the enumeration of meiofauna, sediment retained on the 63 μm sieve was measured by drying in an oven at 80 °C for 24 h in pre-weighed aluminum dishes. After drying the dishes were cooled in a desiccator and then re-weighed. To help to interpret suspended particle capture data, wind speed for all collection dates was obtained from a NOAA (National Oceanographic and Atmospheric Administration) weather station located on Grand Isle. Wind speed was recorded hourly from which daily averages were calculated.

Multiple analysis of variance (MANOVA) was performed on the relative proportions of abundances to test the null hypotheses of no difference in relative abundance among artificial substrate types and among collection dates in the preliminary experiment (problems with normality prevented comparisons of absolute abundance). A log(x+1) transformation on the relative proportions of the abundances of major taxa successfully normalized these data. The overall MANOVA was significant (Table 2.1) and individual major taxa were tested by two way ANOVA. MANOVA was also used to compare meiofaunal relative abundance in seasonal and long-term collections. The analyses were performed on the relative proportions of total abundances of meiofauna and one way ANOVA was conducted on individual taxa after log(x+1) transformation.

Shannon-Wiener diversity, using natural logarithms, ($H'$) and evenness (Pielou's $J$) were calculated using PRIMER software. Differences between seasons and across long-term sampling dates were tested using one-way ANOVA. One-way analysis of variance (ANOVA) was also performed to test the significant differences among suspended particle accumulation from different seasons and long-term collection dates. Tukey's studentized range test was performed as an *a posteriori* test. Statistical Analysis Software (SAS)(SAS INSTITUTE, 1985) was used to perform all ANOVA and MANOVA procedures.

**Results**

Artificial substrates

The estimated total surface areas of the bristles of the brush and thread of the mesh collectors were 279.3 and1470.0 $cm^2$, respectively. The combined volume (water

displacement) of the bristles of the brush and the thread of the mesh collectors was 5 and 31 ml, respectively. Their surface area was normalized by their average weight (4.7 and 7.0 g) which yielded similar surface to volume ratios of 56.7 and 47.4 $cm^2$ $ml^{-1}$, respectively, suggesting that these two types of artificial substrates have similar structural complexity. Hester-Dendy plates, on the other hand, have a very small surface to volume ratio (1.75 $cm^2$ $ml^{-1}$) primarily due to their heavy weight (883 g) and small normalized surface area (0.7 $cm^2$ $g^{-1}$). Although the geometric volumes of mesh and brush collectors were comparable, mesh collectors had a slightly higher surface area compressed in a smaller geometric volume than brush collectors.

Preliminary Experiment

Large numbers of meiofauna colonized all three types of artificial substrates. Although planktonic copepods were observed, their low abundance (<2 individuals $collector^{-1}$) suggests that colonization was negligible and values are not reported. Colonization began within 1 day of exposure (Fig. 2.1). Nematodes, copepods and copepod nauplii were the most abundant taxa on all substrate types. Polychaetes, amphipods and juvenile grass shrimp and juvenile crabs were also present (reported as others in Figure 2.1) along with sessile organisms (not reported) such as bryozoans and barnacles recruited by larval settlement. For all artificial substrate types, the density of meiofauna increased from 1-3 days but fluctuated between days 3-6. The highest density of meiofauna was observed on day 12 on all collector types (Fig. 2.1). On day 12, the mean abundance of total meiofauna reached 3558 (± 1250.5 standard error, hereafter SE) individuals $collector^{-1}$ (hereafter ind $col^{-1}$) and 4786 ind $col^{-1}$ ( ± 309.4

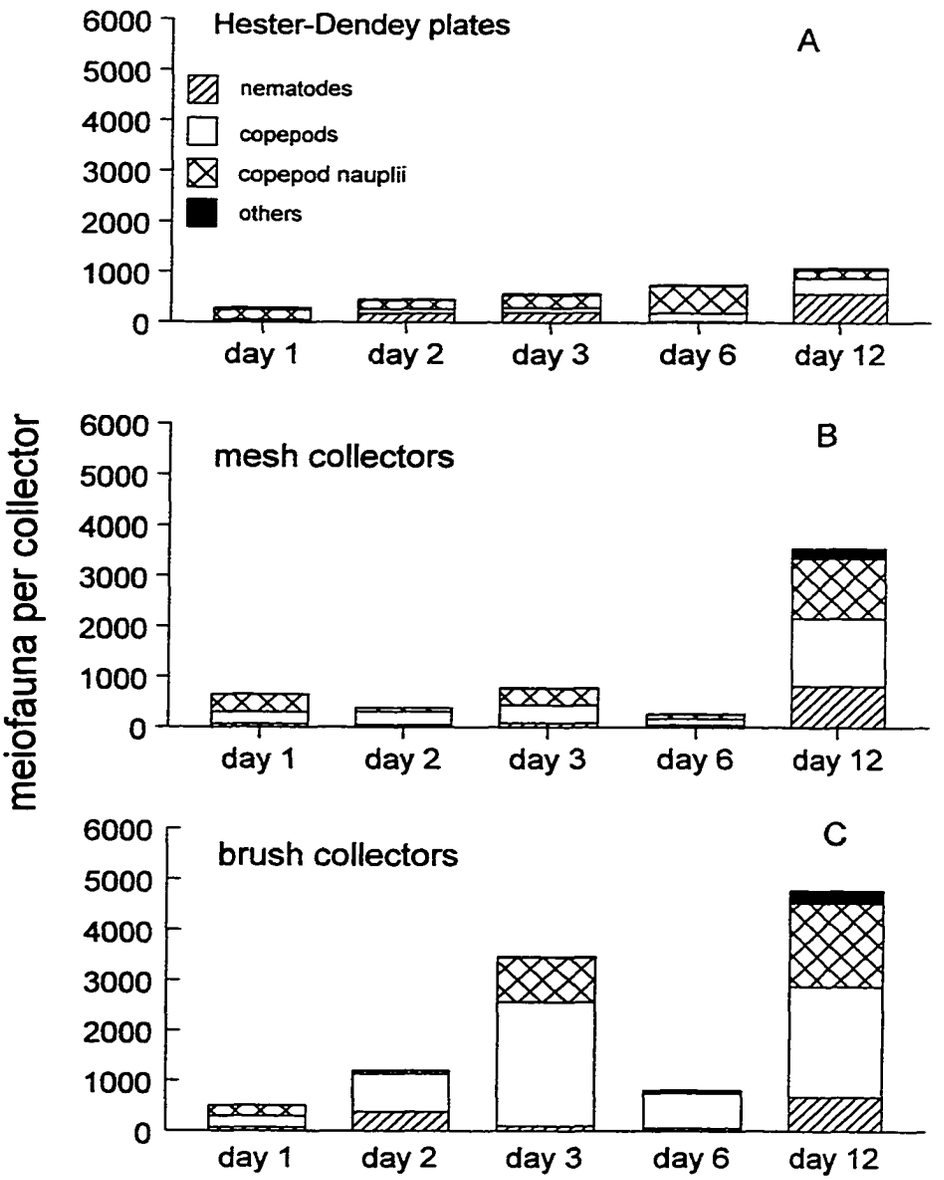


Figure 2.1. Changes in the abundance of four meiofauna taxa found on Hester-Dendy plates(A), mesh (B) and brush (C) collectors during the 12-day preliminary experiment. Values are means of three replicates.

SE), on mesh and brush substrates, respectively, while there was a mean of 1081 individuals ( ± 458.8 SE) Hester-Dendy plate$^{-1}$ (Fig. 2.1). Overall, copepods comprised the most abundant taxon on mesh and brush collectors. Copepods on Hester-Dendy plates were the second most abundant taxon and reached a mean abundance of 308 ind col$^{-1}$ (± 130.6 SE) which was 28% of total meiofauna (Fig. 2.1a). Mean abundance of copepods reached 1340 ind col$^{-1}$ (± 677.2 SE) and 2200 ind col$^{-1}$ (± 196.6 SE) for mesh and brush collectors (37% and 46%, respectively) (Fig. 2.1b, 2.1c). Abundance of nematodes gradually increased through time. On day 12, the density of nematodes was similar among all collectors (Fig. 2.1), and nematodes were the most abundant taxon on Hester-Dendy plates with 53% of the total meiofauna collected (Fig. 2.1).

The relative proportions of the abundance of major taxa were significantly different among collection dates ($p<0.0001$) and substrate type ($p<0.0001$). A significant date by substrate type interaction was also observed. Individual taxa were examined by two-way ANOVA. In all cases, significant effects of date, substrate type and date substrate type interactions on nematodes, copepods, nauplii and other meiofauna were noted. The significant interaction term makes the interpretation of main effects difficult. Nevertheless, the pattern strongly suggests that copepods were very successful early colonists; nematodes reached high abundances but only on later collection dates. *A posteriori* tests among collection dates showed that nematode relative abundance was significantly higher on day 12; copepods were found in their lowest relative abundance on day 12. Copepods were particularly poor colonists on Hester-Dendy plates; the relative proportion of nematodes was significantly highest of

all substrate types on day 12. The proportion of copepods found on Hester-Dendy plates on days 1-6 was significantly lower than that found on mesh and brush collectors.

Summer and Winter Experiments

Meiofauna were highly abundant after two weeks of exposure on mesh collectors in July and December. In July collections, the mean densities of total meiofauna were the highest recorded at 20,160 ind $col^{-1}$ (± 1602 SE), while in December collections (D1), the mean was 966 ind $col^{-1}$ (± 319.6 SE). Nematodes (88% and 38% of July and December meiofauna respectively) and copepods (11% and 36% in July and December respectively) were the two most abundant taxa. Aforementioned December collection results were also reported as the first of three collections in a long-term study. The abundances of meiofauna increased through the 8-week period. Total meiofauna increased to a mean of 4692 ind $col^{-1}$ (± 1356.5 SE) on D2 and 9332 ind $col^{-1}$ (± 849 SE) on D3. No copepod nauplii were encountered in July collections and their abundance showed irregular increases and decreases during three winter collection times. All other taxa (nematodes, copepods and others) gradually increased in abundance from the first (D1) to the third long-term collection date (D3) (Fig. 2.2). Polychaetes, which made up over 95% of the group "others" also gradually increased. There were significant differences between the relative abundances of major taxa after two weeks in July and December (D1) ($p<0.0001$), and among three long term collections in December (D1, D2 and D3) ($p<0.001$) (Table 1). Individual ANOVA tests showed significant differences for all major taxa for July and December and long-term experiments (Table 2.1). The relative proportion of nematodes was significantly greater in July, while

Table 2.1. Summary of multiple analysis of variance on results of summer and winter colonization experiments and long-term winter collections; one way analysis of variance on four meiofaunal taxa; diversity, evenness and dry weight of sediment. Seasonal comparison: July versus D1 (2 weeks); long-term experiment = D1 (2 weeks). D2 (4 weeks), D3 (8 weeks).

| | Seasonal comparison | Long-term experiment |
|---|---|---|
| MANOVA (Wilk's Lambda) | F = 279.34 **P < 0.0001** | F = 30.67 **P < 0.0001** |
| Nematodes | F = 86.44 **P < 0.0001** | F = 77.35 **P < 0.0001** |
| Copepods | F = 125.34 **P < 0.0001** | F = 10.73 **P < 0.0006** |
| Copepod Nauplii | F = 162.63 **P < 0.0001** | F = 90.22 **P < 0.0001** |
| Others | F = 7.34 **P < 0.017** | F = 4.54 **P < 0.02** |
| Diversity (H') | F = 231.35 **P < 0.0001** | F = 121.11 **P < 0.0001** |
| Evenness (J) | F = 59.05 **P < 0.0003** | F = 7.4 **P < 0.0126** |
| Sediment | F = 21.88 **P < 0.0034** | F = 3.59 **P < 0.07** |

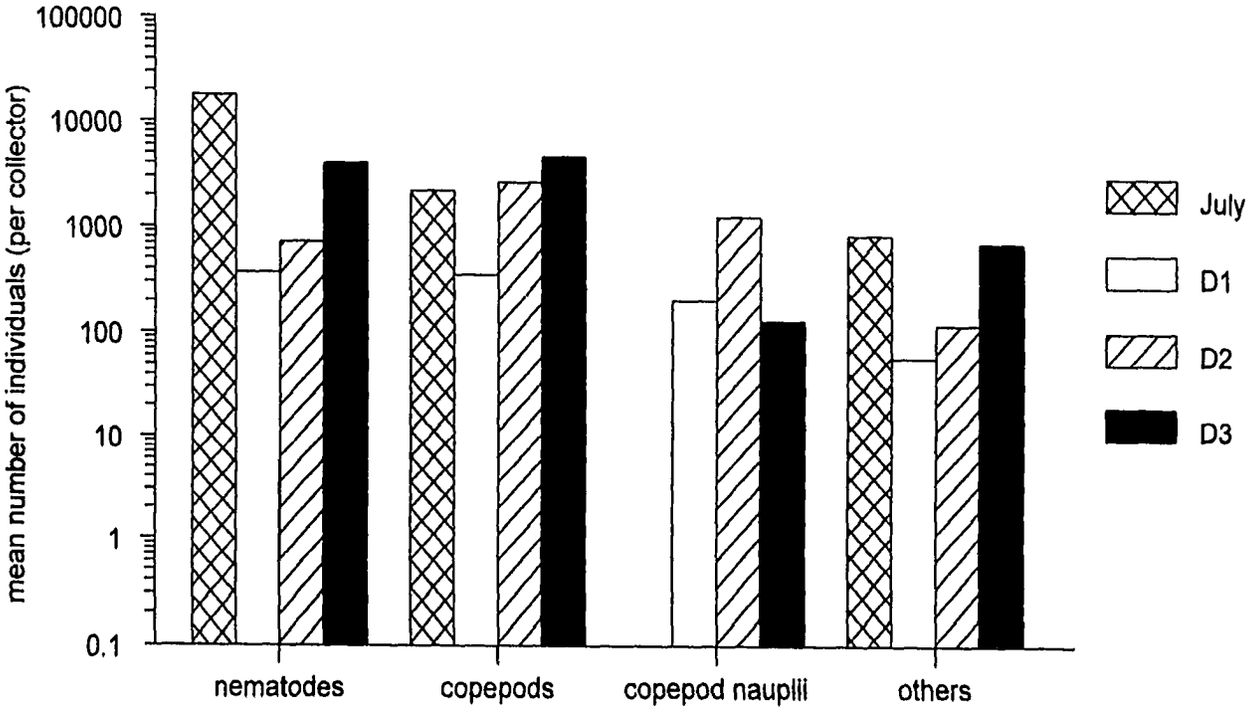


Figure 2.2. Changes in the abundance of four meiofauna taxa colonized on faunal collectors during short-term (July, 2 weeks) and, in December. D1, D2 and D3 represent 2, 4, and 8 weeks of colonization in December and January. Values are means of four replicates.

Table 2.2. Relative proportions [%] of copepod species found during summer and winter collections on mesh collectors. Total number of species is also reported.

| | July 15 '97 | Dec. 16 '97 D1 | Dec. 31 '97 D2 | Jan. 27 '98 D3 |
|---|---|---|---|---|
| | % | % | % | % |
| *Parategastes* sp. | 91.5 | 1.2 | 0.1 | 0.2 |
| *Harpacticus* sp. | 0.2 | 35.6 | 79.4 | 59.9 |
| *Halicyclops coulli* | 3.7 | 0.7 | 0.1 | 1.5 |
| Ectinosomatidae (sp.1) | 0.8 | 15.2 | 4.4 | 29.8 |
| Diosaccidae (sp. B) | 1.5 | 21.3 | 9.6 | 4.6 |
| *Zausodes* sp. | - | 12.8 | 2.7 | 0.8 |
| *Onychocamptus mohammed* | - | 2.4 | 1.3 | 1.5 |
| *Paranychocamptus wilsoni* | - | 5.5 | 2.2 | 1.7 |
| *Pseudostenhelia wellsi* | - | 3.6 | - | - |
| *Microarthridion* cf. *littorale* | - | 1.2 | - | - |
| *Oithona* sp. | - | 0.5 | - | - |
| *Nitocra lacustris* | 2.3 | - | - | - |
| Cyclopoida (sp.W) | - | - | 0.2 | - |
| total | 100 | 100 | 100 | 100 |
| number of species | 6 | 11 | 9 | 8 |

copepods represented the largest proportion of meiofaunal groups in December. The relative proportions of meiofaunal taxa varied significantly in the long term study but specific patterns were difficult to discern as most taxa gradually increased over time.

Copepod species composition qualitatively differed between July and December collections. The most abundant July species were *Parategastes* sp., *Halicyclops coulli* Herbst , *Nitocra lacustris* (Schmakevitsch), and a Diosaccid species (sp. B), while *Harpacticus* sp., *Zausodes* sp., Diosaccid (sp. B), and a species in the family Ectinosomatidae were most abundant in December (Figures 2.3 & 2.4). Other species found on artificial substrates were two species from the family Laophontidae (*Paronycocamptus wilsoni* (Coull) and *Onychocamptus mohamed* (Blanchard & Richard)), *Pseudostenhelia wellsi* Coull & Fleeger, *Microarthridion* cf *littorale*, *Nitocra lacustris* and an unidentified Cyclopoid species (sp. W). In July collections *Parategastes* sp. was the most abundant species with 1994 ind $col^{-1}$ (± 115.7 SE), while the abundance of all other species was less than 100 ind $col^{-1}$ (Fig. 2.3). The abundance of *Harpacticus* sp. increased from D1 to D2 and the highest abundance was observed in D3 (Fig. 2.4). Ectinosomatid abundance also increased in D3 collections. *Harpacticus* sp. and Ectinosomatids were the most abundant species in D3 samples (1183 ind $col^{-1}$ (± 335.6 SE)) (Fig. 2.4).

Copepod species diversity and evenness values for July 0.882 (± 0.05 SE) and 0.51 (± 0.05 SE) H' and J respectively) were significantly lower than December values 1.75 (± 0.05 SE) and 0.86 (± 0.04 SE), H' and J respectively) (Fig. 2.4 and Table 2.1). During the long-term collection period the total number of copepod species varied from

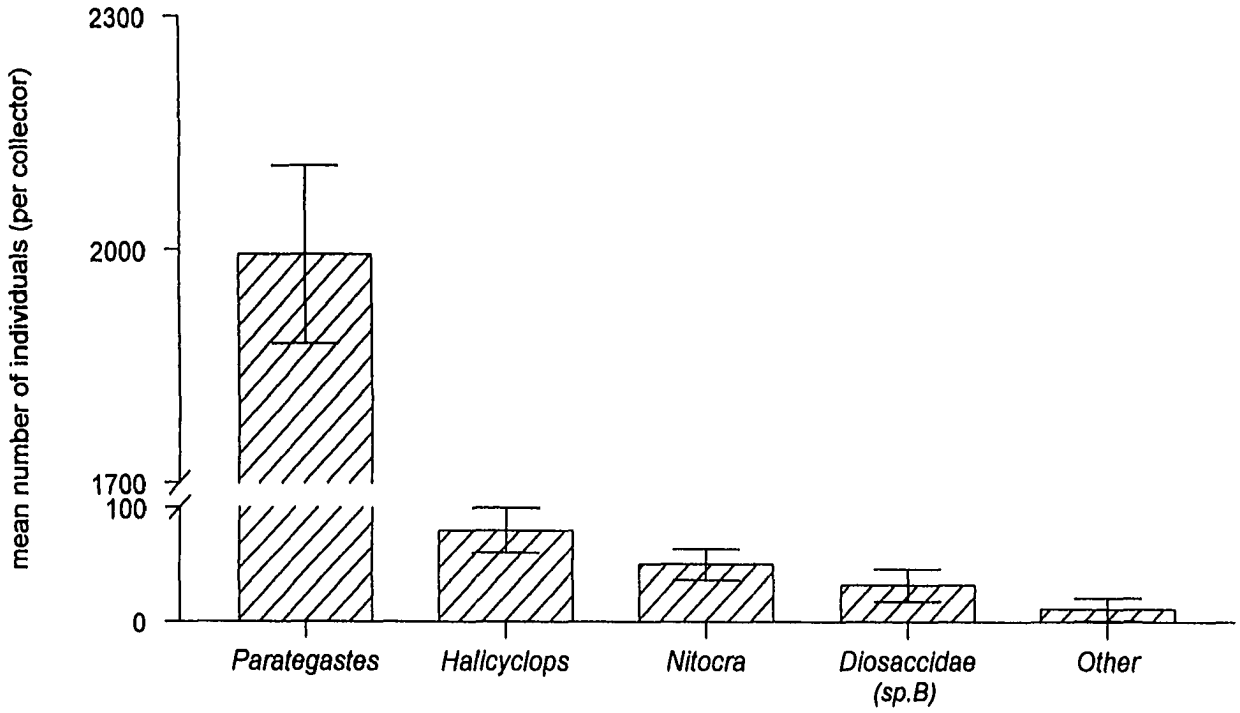


Figure 2.3. Abundances of copepod species found on faunal collectors in July. Values are means of four replicates, upper bars indicate standard error of the mean.

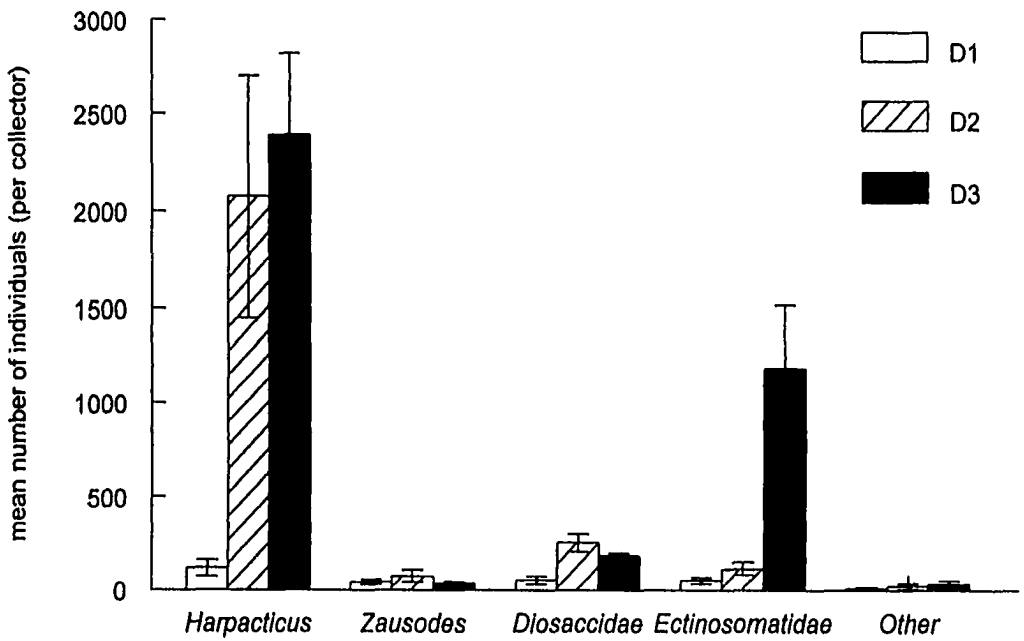


Figure 2.4. The number of copepod species colonized on faunal collectors during long-term (8 weeks) collections from December and January. D1, D2 and D3 is 2, 4, and 8 weeks of colonization, respectively. Values are means of four replicates, upper bars indicate standard error of the mean.

11 (D1) to 8 (D3). In July only 6 copepod species were observed (Table 2.2). Diversity significantly decreased during the long- term study (Fig. 2.5). Evenness and diversity dropped significantly from week two (D1) (1.75 ± 0.05 SE) to week four (D2) (0.811 ± 0.107 SE) due to a dramatic increase in the *Harpacticus* sp. abundance on D2 (2076 ± 625.3 SE)(Fig. 2.4 and Table 2.1). On D3, the total number of species was the lowest (8) for the winter sampling period; however, evenness was higher than D2 (1.5 ± 0.04 SE)(Fig. 2.5). At this sampling date Ectinosomatids increased in abundance causing a more even distribution of species (Fig. 2.4).

Wind Effects and Sedimentation

The amount of suspended particles >63 μm retained on mesh collectors varied among collections; More particles accumulated on collectors in July (0.80 g dry weight $col^{-1}$ (± 0.01 SE) than on D1 (0.27 g dry weight $col^{-1}$ (± 0.1SE), ($p<0.0034$)) (Fig.2.6 and Table 2.1). The mean wind speed was higher for the colonization period in December (D1) (3.4 m $s^{-1}$ ± 0.5SE) than during the colonization period in July (2.4 m $s^{-1}$ ± 0.5SE). During the long-term collection period the amount of retained sediment fluctuated slightly from D1 to D2 (0.27g dry weight $col^{-1}$(± 0.1 SE) and 0.22 g dry weight $col^{-1}$ (± 0.08 SE) respectively) (Fig. 2.6), and there was a large increase from D2 to D3 (to 0.919 g dry weight $col^{-1}$± 0.33 SE) (Fig. 2.6). Mean wind speed was 3.3 m $s^{-1}$ ± 0.3SE, throughout the 8 week colonization period, but the wind speed fluctuated greatly from day to day. There were no significant differences detected in the dry weight of sediment captured during the three winter sampling periods ($p<0.07$) (Table 2.1).

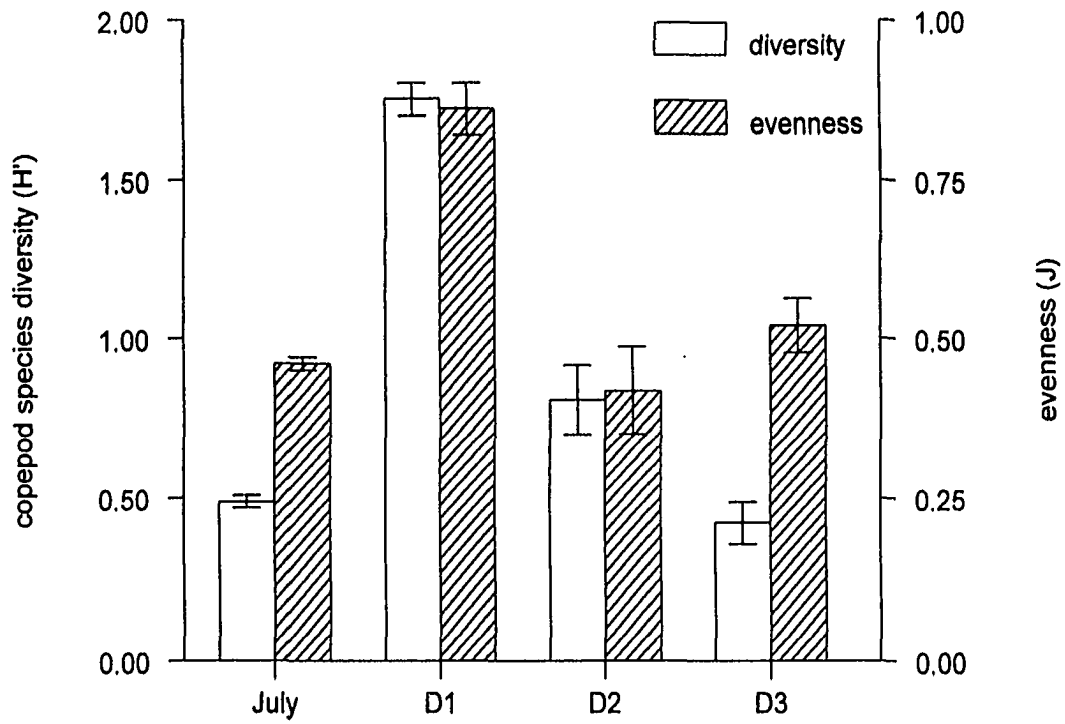


Figure 2.5. Copepod species diversity (H') and evenness (J) values in short-term (July, 2 weeks) and long-term (December through January). D1, D2 and D3 represent2, 4, and 8 weeks of colonization period, respectively. Values are means of four replicates. Upper bars indicate standard error of the mean.

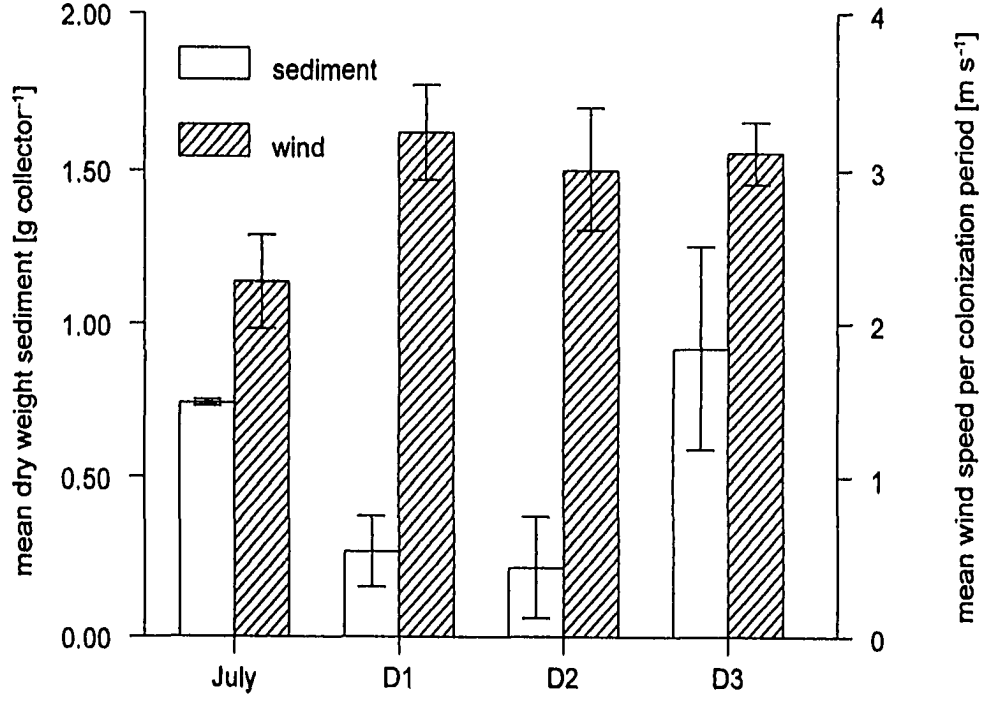


Figure 2.6. Dry weight of suspended sediment collected in faunal collectors and wind speed during short-term (July) and long-term (December through January). D1, D2 and D3 represent 2, 4, and 8 week collections, respectively. Upper bars indicate standard error of the mean.

**Discussion**

Colonization of meiofauna was successful in all seasons and on all artificial substrate types tested; abundances often exceeded 3000 and a maximum of 20,000 individuals collector$^{-1}$ was observed. Our data suggest that cryptic meiofauna colonized brush and mesh collectors equally well but generally at a higher rate than Hester-Dendy plates. Structural complexity probably contributed to the higher meiofaunal abundances on brush and mesh collectors. Hester-Dendy plates are very simple in structure constructed with gaps between tile plates with a combined plate surface area of 605 cm$^2$ and surface to volume ratio of only 1.75 cm$^2$ ml$^{-1}$ normalized by weight. Brush and mesh collectors had similar but much higher surface to volume ratios (56.2 and 47.4 cm$^2$ ml$^{-1}$, respectively, each normalized by weight), and were capable of collecting large amounts of suspended particles. The reduced structural complexity of Hester-Dendy plates may have made them less attractive to meiofaunal colonists or less likely to retain meiofauna after capture.

The most abundant copepod colonists on all artificial substrates examined were *Harpacticus* sp. and *Parategastes* sp., and each composed from 35-91% of the copepods collected (Table 2.3). Both have a phytal morphology (as defined by Bell et. al. (1987)), and both are closely related to species associated with macroalgae and with strong swimming abilities (Hicks, 1985). Foliose macroalgae do not occur in the study area, and filamentous microalgae (*Enteromorpha* sp.) are present on sediment surfaces only from January to March. The highest abundances of all taxa were recorded in July when filamentous microalgae were not present, which suggests that the source of these cryptic

meiofauna was a combination of hard-substrate (e.g., wood pilings, piers, mollusc shells) and sediment habitats. *Parategastes* sp., the predominant July species, is not typically found in sediments, although the rarer species encountered (Ectinosomatids, *Microarthridion littorale* and *Halicyclops coulli*) lack phytal morphology, but are commonly reported from throughout Atlantic and Gulf marsh sediments (Coull, 1977; Coull & Dudley, 1985; Fleeger, 1979; 1985). During long-term collections, filamentous microalgae became abundant in surrounding sediments and were found attached to some artificial substrates. This algae is seasonal in Louisiana marshes and supports a high abundance of *Harpacticus* sp. (Fleeger, personal obs.), which was the most abundant copepod in December and January collections. No studies on hard-substrate meiofauna from pilings and bulkheads in marine systems are known to us, nor are meiofaunal studies of seasonally ephemeral microalgae. The high abundances of meiofauna colonizing artificial substrates from non-sediment sources indicates that cryptic meiofauna are present in the sampling area (moving through the water column, colonizing new habitats, etc.) in very high numbers. Given the increasing presence of pilings and bulkheads in many coastal areas, a meiofaunal assemblage this abundant may well have an ecological importance, energetically and in trophic dynamics, that is unappreciated.

We could not follow individual meiofauna making it difficult to separate immigration from emigration events. Colonization of cryptic meiofauna onto artificial substrates can occur by active or passive means. If colonization is active, meiofauna must behaviorally seek out artificial substrates, and abundance increases occur when

immigration of individuals from their natural habitat to artificial substrates exceeds emigration. If colonization is passive, artificial collectors must act as filters capturing and retaining meiofauna as they encounter the substrate. Harpacticoid copepods are generally good swimmers which facilitates their immigration from their natural habitat to artificial substrates, and our data suggest that they are excellent early colonists onto collectors, as has been shown in azoic sediment (Sun & Fleeger, 1994). Copepod density and diversity variation from date to date was high in short and long-term studies suggesting that copepod emigration and immigration are frequent events. Copepods appear to be active colonists.

Nematodes are generally thought to be poor swimmers, although a few species are known to be active swimmers (Jensen, 1981). Furthermore, nematodes have been shown to be poor colonists in azoic sediment (Chandler & Fleeger, 1983; Sun & Fleeger, 1994). In our study nematode abundance always gradually increased over time, surprisingly surpassing the abundance of copepods, suggesting passive colonization and low or constant rates of emigration. If colonization is passive, immigration rates of nematodes would be affected by both the volume of water filtered through the collector and the density of suspended animals in the water column. As suspended particles (sediment) are accumulated in the artificial substrates, the ability of the artificial substrates to filter water should be reduced, potentially reducing immigration rates over time. Nematodes, however, generally favor high amounts of organic matter and have been shown to be abundant on the retained sediment in the fronds and holdfasts of macroalgae (Hicks, 1985). Related studies on *Sargassum* (Mukai, 1971; Kito, 1975)

have shown that nematodes become more abundant than copepods when structural complexity and suspended sediment load of *Sargassum* is highest. Because nematodes may favor conditions which lead to higher concentrations of organic matter related to sediment load, we performed a linear regression analysis on the amount of sediment >63 μm and the abundance of nematodes in the long-term study. Although the amount of sediment accumulated on the mesh collectors increased over time, the relationship between the amount of sediment and the abundance of nematodes was weakly correlated ($r^2$= 0.284, $p<0.0742$, n=16). Alternatively, nematode increases in the long-term study might have been due to recruitment by reproduction. On the other hand, increasing amounts of sediment very likely limit the habitable space for copepods. However, copepods showed similar density patterns both in short and long-term collections even though the amounts of sediment accumulated on mesh collectors were quite different. It is likely that abundance patterns on artificial substrates are governed by a number of complex factors; supply, water flow, capture efficiency as well as the behavior of individual taxa.

One factor that undoubtedly influences meiofaunal abundance on artificial substrates is water flow. Flows above critical erosion velocity have been shown to erode surface-dwelling meiofauna from sediment into the water column (Palmer & Gust, 1985), increasing the supply of meiofauna and sediment particles as well as the volume of water contacting artificial substrates. If the flow is too high, however, erosion from substrates is likely to occur, decreasing meiofaunal abundance on our collectors. Studies documenting flow around and through such structures are very rare

(see Anderson & Charters, 1982 for an exception) making prediction difficult. In July the average wind speed near the collecting site was 2.4 m $s^{-1}$ and sediment and meiofauna retained on mesh collectors were significantly higher than during December. The higher wind speed (3.4 m $s^{-1}$) in December may have enhanced erosion of sediment and fauna from mesh collectors. Clearly, short-term changes in flow have a great potential to cause rapid variation in meiofauna abundance of artificial substrates and should be taken into account when artificial substrates are used in monitoring programs.

The harpacticoid copepod species assemblage on mesh collectors qualitatively differed in July and December (Table 2.2). In July collections a very low Shannon diversity of 0.5 was observed with a total number of 6 species, while in December collections the Shannon diversity was 1.75 with a total number of 11 species. During the long-term study, diversity decreased from two (1.75) to four (0.81) but increased after eight weeks (0.91). These rapid changes suggest that the species composition of cryptic meiofauna colonized on artificial substrates, especially copepods, is quite dynamic. Artificial substrates have been suggested as a simple way to measure diversity and monitor pollution. Our results indicate that diversity changes with seasons and over short time scales, and suggest that the length of exposure of artificial substrates will greatly influence results.

# CHAPTER 3

# PIER PILING AND SEDIMENT CONTRIBUTIONS TO MEIOFAUNAL COLONIZATION OF ARTIFICIAL SUBSTRATES

**Introduction**

Meiofauna from sediments and seagrass or algal beds have been shown to enter the water column passively via erosion and by active emergence as a function of behavior, hydrodynamic regime, above-ground structure, taxonomic composition, and disturbance (Palmer, 1988). Several studies examined emergence patterns from sediment (Fleeger et al., 1984) and seagrass beds (Bell et al., 1989; Walters, 1991; Kurdizel and Bell, 1992; Walters and Bell, 1994) and generally concluded that meiofauna are frequently widespread and abundant in the water column (Walters and Bell, 1986). Palmer and Gust (1985) suggested that some meiobenthic copepods in the water column could be could be dispersed up to 200 m from the origin. Kurdizel and Bell (1992) showed that emergent phytal copepods are capable of horizontal migration up to 20 m from seagrass beds. This widely dispersing pool of meiofauna promotes rapid colonization (Bell and Sherman, 1980; Chandler and Fleeger, 1983; Sun and Fleeger, 1994). Nevertheless, the origin of meiofauna in the water column is not well documented (see Hagerman and Reiger, 1981).

It is possible that natural and artificial hard substrates contribute meiofauna to this rapidly dispersing pool found in the water column. Hard structures are common in estuaries and are populated by numerous epifauna (Butler and Connolly, 1996; Glasby, 1999). Meiofauna live commensally on epifauna (e.g., Gee and Davey, 1986), and free-living species are undoubtably common but understudied. For example, Little (1986), in one of the few studies of hard-substrate meiofauna, reported over 500 ind. 10 $cm^{-2}$ on tiles colonized by aufwuchs. Hagerman and Reiger (1981) examined meiofauna in

water samples taken near pier pilings and found many phytal-associated meiofauna that could not be accounted for in surrounding sediments, suggesting pier pilings may have contributed colonists. In addition, Atilla and Fleeger (2000) recently documented that meiofauna capably colonize small, physically complex structures suspended near pier pilings. Total meiofaunal abundances increased by about 1000 individuals collector$^{-1}$ day$^{-1}$. Again, the most abundant copepod colonists displayed phytal characteristics not typically associated with surrounding sediment-dwelling copepods. In the absence of seagrasses and macroalgae, Atilla and Fleeger (2000) hypothesized that artificial hard substrates such as submerged wood pilings served as the source of the phytal copepod colonists.

This is the first study that directly sampled meiofauna from artificial hard substrates. We synoptically sampled sediments and artificial hard substrates (pier pilings) and compared these meiofaunal assemblages to colonists of suspended faunal collectors. Copepods and nematodes were identified to the lowest possible taxon to best determine the origin of colonists. Meiofauna colonizing faunal collectors must disperse in the water column and, therefore, their presence on faunal collectors reveals information on the source of meiofauna in the water column.

**Methods**

The study area was a shallow water embayment (<2 m) in Grand Isle, Louisiana (29°W, 90°N) adjacent to Caminada Pass. Sampling was conducted at an oyster hatchery with a variety of submerged hard substrates including large quantities of mollusc shells, wood pilings associated with a pier/walkway over the water, wood

bulkheads, stone and concrete rip-rap and other artificial structures. Sediment at the study area was sandy (6% silt and clay). The experiment was conducted in August when seasonally abundant drift filamentous algae were not present. No foliose macroalgae, seagrass or natural hard substrates were present in the study area. A filamentous green algal cover of about 5 mm thickness to a depth of 10-15 cm was, however, common on submerged pilings and on other hard surfaces in the area.

Synoptic samples were collected at three different locations in a randomized block design to determine the potential source-pool of meiofauna colonizing plastic collectors. Hard substrate (at two locations from pier pilings and at one location from wood planking associated with pier pilings), sediment and faunal-collector samples were examined at each location.

Mesh pads, commercially available as pot scrubbers, were used as faunal collectors. They are made out of a plastic thread woven into a pad approximately 9 cm in diameter and 2 cm thick (with a geometric volume of 159 $cm^3$). Each mesh collector was weighed and labeled before placed in the field for colonization. Surface area was estimated by measuring the three dimensions of the thread. The width and the height of the thread were measured with a caliper to be 0.75 mm in width and 0.14 mm in height. To obtain the total length of the thread, 10 replicates of 1-m long threads were weighed. The total length of the thread in a mesh collector was estimated from this weight-length relationship. Thread length averaged 75 m $collector^{-1}$ and the mean surface area was therefore estimated to be 1470 $cm^2$ $collector^{-1}$, with a surface area to geometric volume ratio of 9.3.

Each mesh collector was randomly assigned to one of three PVC frames. Six replicate mesh collectors were attached to each frame with a 50-lb monofilament line fastened to both ends of the substrates. The frames were placed in the water at mid-depth and anchored to the bottom at three separate locations approximately 0.5 to 7 m from the walkway. The distance between frames was approximately 20-25 m. After 1 week, individual collectors were sampled by placing them inside plastic containers while under water to avoid flushing meiofauna from substrates during collection. On the day faunal collectors were deployed, pier-piling and sediment samples were collected in close proximity to each PVC frame. Pier-piling samples were taken first followed by sediment cores.

The pier-piling meiofaunal assemblage was sampled by using an underwater suction sampler modified from Taylor et al. (1995). An electric bilge pump running on a 12-volt motorcycle battery attached to the body of the device allowed us to aspirate meiofauna from the surface of wood pilings at about 10 cm below the surface of the water. To standardize pier-piling samples, a 100 $cm^2$ flexible frame with 2 cm wide edges was placed over pier pilings near each PVC frame holding mesh collectors and meiofauna aspirated for 1 min for each replicate; six replicates were collected per location. Water flowing from the nozzle to the body passed through a 63-μm mesh bag attached to the end of the nozzle. One mesh bag per replicate was used and mesh bags were preserved with 10% formalin immediately after collection. The suction generated was strong enough to remove a few dead barnacle shells and some small clumps of filamentous algae.

Six replicate sediment cores (5-cm inner diameter, 19.6 $cm^2$) were taken 0.5-1 m from each PVC frame. The upper 2 cm were extruded and fixed with 10% formalin stained with Rose Bengal.

Laboratory Analyses

Meiofauna from collectors was extracted by sieving through nested 500 μm and 63 μm mesh size sieves. The 63 μm sieve fraction was subsampled using a plankton wheel subsampler; 1/8 of each sample was enumerated. Meiofauna from the sediment was extracted by elutriation and a 1/8 subsample from a plankton wheel was enumerated. Pier-piling meiofauna was retained over a 63 μm mesh during the sample collection, and examined without subsampling.

Major taxa were enumerated and all copepod species were identified to a nominal species taxon by using taxonomic aids of Wells (1976), Huys et al., (1996) and Lang (1965). Nematodes were dehydrated with anhydrous glycerine and mounted on slides for identification under a high-power objective (Riemann, 1988). Nematodes were identified to genus. Most nematode genera were represented by a single species but a few genera (e.g., *Daptonema*) likely had more than one species. Copepod species were also assigned to body-shape groups described by Coull (1977), because body shape reveals information regarding habitat type. Based on observations of the first leg morphology of our specimens (Bell et al., 1987), copepods with strongly prehensile first legs or fusiform-prehensile body shape and compressed body forms were considered phytal species. Cylindrical, fusiform, depressed, fusiform-non prehensile and specimens lacking a prehensile first leg, were classified as sediment dwellers. Although

these body shape classes were proposed for harpacticoid copepods, we assigned a cyclopoid copepod species (*Halicyclops coulli*) and a poecilostomatoid species to the most appropriate body shape class (fusiform depressed).

Abundances from all substrates were standardized to individuals 100 $cm^{-2}$. Analysis of variance was used to test for differences in the total number of meiofauna among the three sampling locations (treated as randomized blocks) as well as among substrates. Bray-Curtis similarity, one-way analyses of similarity (ANOSIM), multi-dimensional scaling (MDS) analyses and diversity indices (Shannon-Wiener *H'* diversity, Pielou's *J* evenness, and number of species for richness) were performed on copepod and nematode species composition data (standardized by individuals per 100 $cm^2$) by using PRIMER (Plymouth Routine In Multivariate Ecological Research) to compare community structure among three different substrates.

**Results**

Mesh-collector total meiofauna averaged 7000 ind. $col^{-1}$ after one week of colonization. However, due to the very large collector surface area (1470 $cm^2$ $collector^{-1}$) abundances standardized to 100 $cm^2$ were much lower than pier-piling or sediment collections. Total meiofauna averaged 113 ind. 100 $cm^{-2}$ (± 19.9 SE) on collectors, 5222 ind. 100 $cm^{-2}$ (± 1074.4 SE) in sediment, and 1234 ind. 100 $cm^{-2}$ (± 251 SE) on pier pilings (Fig. 3.1). Abundances of total meiofauna in the three locations sampled were, however, very similar (Fig.3.1). Randomized block ANOVA showed that there were no significant differences in total meiofauna among the three locations ($p<0.749$), but total meiofauna differed significantly among substrates ($p<0.0099$). Tukey's studentized test

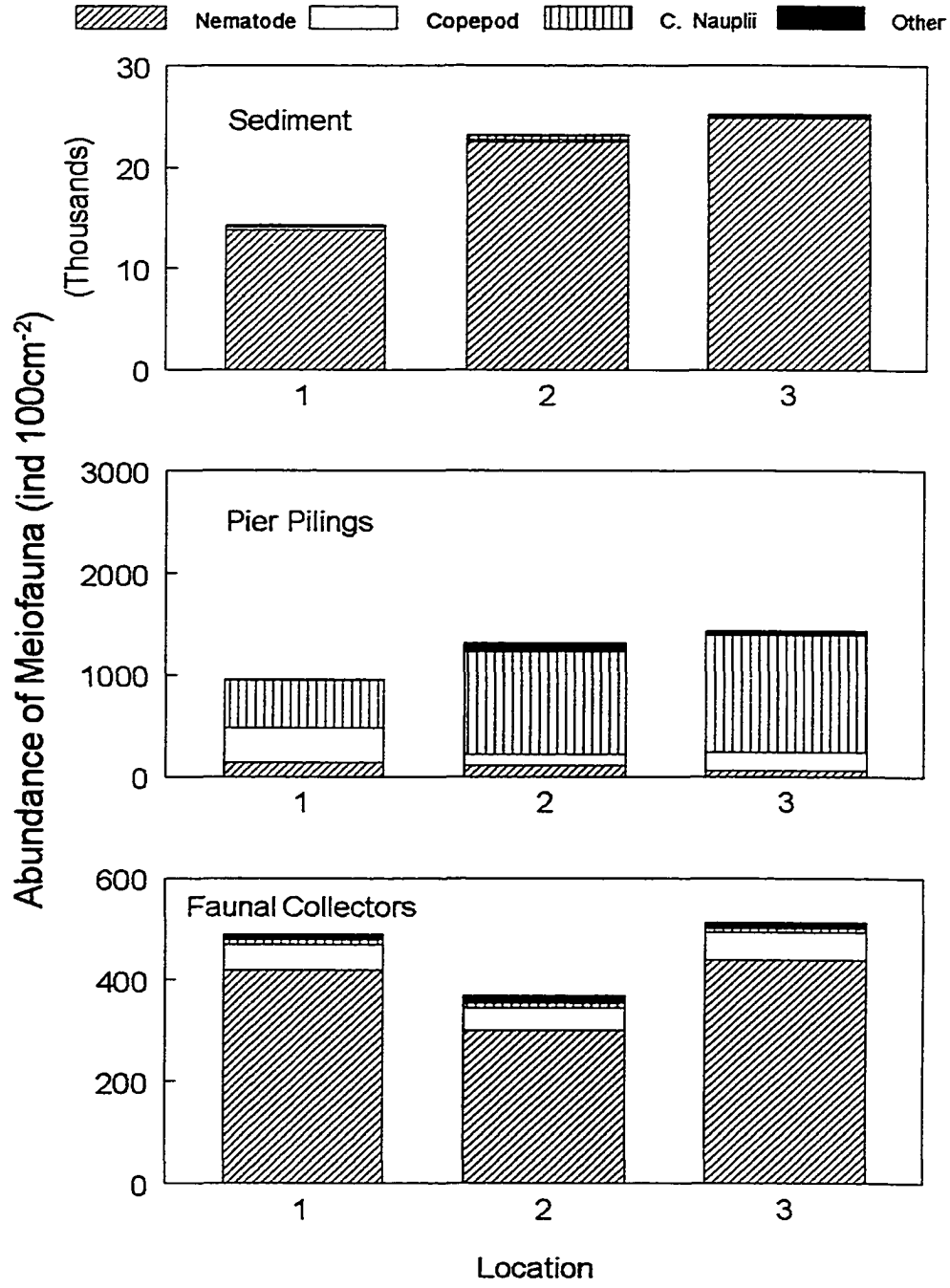


Figure 3.1. Mean abundance of meiofauna taxa on pier pilings, faunal collectors and sediment at three locations. Note different scale for faunal collectors. The values are means of four replicates.

Table 3.1. Relative proportions (%) of copepod and nematode taxa found on hard substrate, artificial substrate and sediment. Taxa reported represent over 1% in any of the substrates. Total number of taxa is also reported. * shows copepods with phytal morphology. **See textfor definitions of successful and unsuccessful colonists.

| | Hard substrates % | Faunal collectors % | Sediment % | Body shape |
|---|---|---|---|---|
| **Copepoda** | | | | |
| **Harpacticoida** | | | | |
| *Coullana* sp. | - | - | 7.0 | Fusiform non-prehensile |
| Ectinosomidae 1 | 0.1 | 11.6 | 15.5 | Fusiform |
| Ectinosomidae 2 | - | 0.9 | - | Fusiform |
| *Enhydrosoma* | - | - | 2.8 | Cylindirical |
| *Harpacticus* sp. | 44.3 | 4.4 | - | Fusiform prehensile* |
| Laophontidae | 0.7 | 1.1 | 5.6 | Fusiform prehensile* |
| *Nitocra lacustris* | 0.5 | 5.2 | - | Cylindirical |
| *Parategastes* sp. * | 45.2 | 53.7 | - | Compressed* |
| *Stenhelia* sp. ** | - | - | 26.8 | Fusiform compressed |
| *Robertsonia* sp. | 4.6 | - | - | Fusiform prehensile* |
| Diosaccidae * | 2.6 | 7.6 | - | Fusiform prehensile* |
| *Zausodes* sp. ** | - | - | 11.3 | Depressed |
| **Cyclopoida** | | | | |
| *Halicyclops coulli* | 0.2 | 15.5 | 31.0 | Fusiform depressed |
| **Poecilostomatoida** | 1.8 | - | - | Fusiform depressed |
| Number of species | 9 | 8 | 7.0 | |
| **Nematoda** | | | | |
| *Anoplostoma* | 5.2 | 1.2 | - | |
| *Chromadorina* ** | 17.5 | 3.2 | 0.1 | |
| *Daptonema* * | 10.9 | 34.1 | 17.2 | |
| *Eleuterolaimus* | - | 1.2 | - | |
| *Halalaimus* | - | - | 3.8 | |
| *Metachromadora* | 1.3 | - | 3.6 | |
| *Microlaimus* | 0.3 | - | 2.4 | |
| *Odontanticoma* | - | 0.3 | 8.7 | |
| *Odontophora* | 0.1 | 0.3 | 6.4 | |
| *Oncholaimus* ** | 24.7 | 11.9 | 0.1 | |
| *Paracanthonchus* | 1.9 | 1.4 | 0.2 | |
| *Paralinhomoeus* | 0.3 | - | 9.5 | |
| *Pomponema* | 0.1 | - | 1.3 | |
| *Prochromadorella* * | 30.5 | 40.3 | 1.9 | |
| *Ptycholaimellus* | - | - | 7.5 | |
| *Sabatieria* ** | 0.2 | 0.3 | 10.2 | |
| *Spirinia* | 2.0 | 0.6 | 8.9 | |
| *Terschellingia* | - | - | 6.4 | |
| *Theristus* | - | 1.4 | - | |
| *Viscosia* | 0.5 | 1.4 | 3.1 | |
| Number of genera | 20 | 18 | 31 | |

* Successful colonists

** Unsuccessful colonists

results showed that abundances of collector meiofauna were significantly lower than sediment or pier-piling meiofauna. Because location did not influence total meiofaunal abundance, locations were pooled for community-structure analyses.

The relative abundances of major meiofaunal taxa differed among substrate types. Sediment and collector samples were both dominated by nematodes (97% in sediment and 84% in collectors). Copepod and copepod nauplii, respectively, made up 3.4% of sediment meiofauna and 14% of the collector meiofauna. On the pier pilings, nematodes represented 8.2%, while copepods and copepod nauplii made up to 88% of the total meiofauna.

Fifty four lower taxa were identified from the three substrates; 14 copepod species and 40 nematode genera. A total of 9, 8, and 7 copepod species were observed on pier pilings, artificial substrates, and in sediments, respectively (Table 3.1). Although the number of species was similar among all substrate types, species composition differed. Species that comprised >10% of the total in each substrate types were selected for detailed comparisons (Table 3.1). *Halicyclops coulli*, a cyclopoid copepod, an unidentified species in family Ectinosomatidae, *Stenhelia* sp. and *Zausodes* sp. were the most abundant harpacticoid copepod species in sediment samples together comprising 85% of the total (Fig. 3.2). *Harpacticus* sp. and *Parategastes* sp. were the most abundant copepod species on pier pilings representing over 90% of the total copepods (Fig.3.2). On faunal collectors, *Halicyclops coulli*, an unidentified species in family Ectinosomatidae and *Parategastes* sp. comprised 81% of the total (Fig. 3.2). Neither *Harpacticus* sp. nor *Parategastes* sp. were observed in sediment samples. On

the other hand, abundant copepod species from sediments *(Halicyclops coulli)* and pier pilings (*Parategastes* sp.), both colonized artificial substrates.

Copepod body shapes also differed among substrates. Faunal-collector and pier-piling copepods were predominantly phytal (67% and 97%, respectively). Sediment-dwelling copepods represented 33% of the total copepod abundance on faunal collectors and 3% on pier pilings (Table 3.1). About 94% of copepods found in sediment samples displayed a sediment-dwelling copepod body form; < 6% displayed phytal morphology.

The total number of nematode genera identified were 31, 24 and 18 from sediments, pier pilings and collectors, respectively (Table 3.1). Genera that comprised >10% of the total nematodes on each substrate type were examined in detail. Species in the genera *Paralinhomoeus*, *Sabatieria* and *Daptonema* were the most abundant nematodes in sediment (Fig. 3.3) and together they made up 37% of total nematode abundance. *Prochromadorella*, *Oncholaimus*, *Daptonema* and *Chromadorina* were the most abundant nematode genera found on pier pilings, comprising 84% of the total. On artificial substrates, *Prochromadorella*, *Oncholaimus* and *Daptonema* were the three most abundant genera comprising 86% of the total (Fig. 3.3); *Prochromadorella* alone comprised 73% of the total nematodes. Of the 43 nematode genera, 11 were exclusively sediment dwellers, 6 were found only in faunal collectors and 5 were found only in pier-piling collections. Eighteen genera were represented in pier-piling and sediment collections and 12 genera were shared between sediment and faunal collectors. Only 10 genera were observed on all three substrates, of which *Prochromdorella* was most abundant.

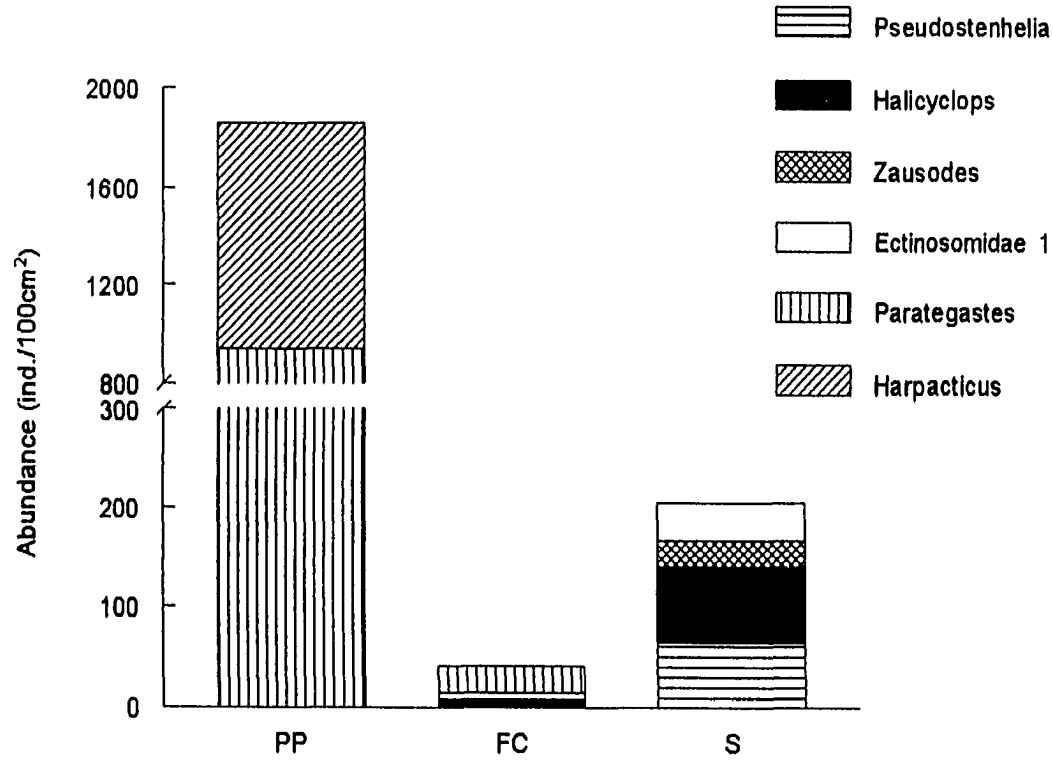


Figure 3.2. Mean abundance of copepods in sediment (S), pier pilings (PP) and faunal collectors (FC). Copepod species presented in the figure represent >10% of total copepod assemblage. Values are means of 12 replicates.

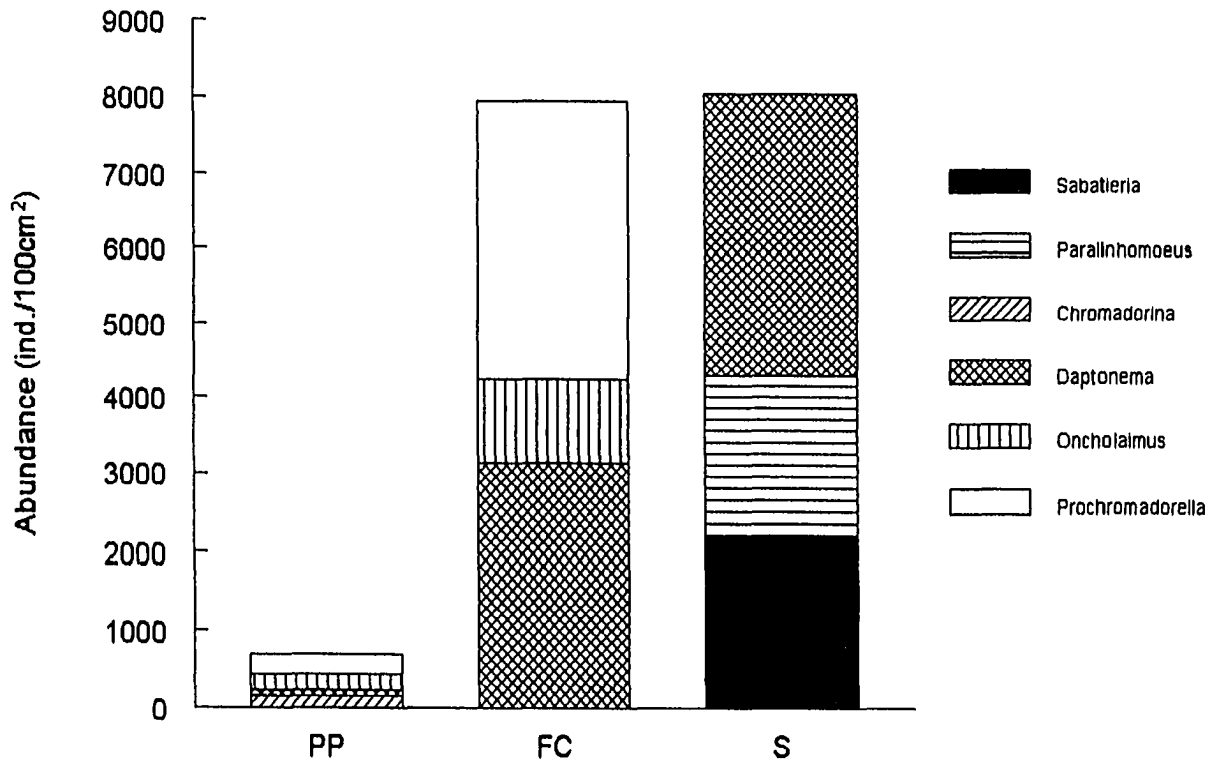


Figure 3.3. Mean abundance of nematodes in sediment (S), pier pilings (PP) and faunal collectors (FC). Nematode genera presented in this figure represent >10% of total nematode assemblage. Values are means of 12 replicates for pier pilings and sediment and 17 replicates for faunal collectors.

Differing degrees of colonization success among nematodes and copepods were observed. By using a criterion of higher relative abundance of a nematode or copepod taxon on faunal collectors than either source pool (sediments and pier pilings), we categorized taxa as "successful"or "unsuccessful" colonizers. Among nematodes, *Daptonema* and *Prochromadorella* were highly successful colonizers (Table 3.1) and were found on pier pilings, sediment and faunal collectors. *Daptonema* was particularly successful and comprised 15% of the total meiofauna on faunal collectors. Three nematode genera (*Chromadorina*, *Oncholaimus* and *Sabatieria* ) and the copepod *Harpacticus* sp. were found in lower relative proportions on collectors than their respective sources suggesting these were unsuccessful colonizers. Among copepod taxa, an unidentified species in the family Diosaccidae and *Parategastes* sp. were found in higher relative proportions on collectors than either source. *Parategastes* sp. was most abundant on pier pilings and a highly successful colonizer based on absolute abundance (>350 ind. $col^{-1}$). No sediment-dwelling copepod species were successful colonizers. Two sediment species, *Stenhelia* sp. and *Zausodes* sp., were absent from collectors.

Non-metric multidimensional scaling ordination analysis was performed on nematode genera and copepod species, separately and combined. Analysis of copepod species yielded three well-defined clusters (stress = 0.10) (Fig. 3.4a). Collector and pier-piling samples formed two tight clusters. Sediment samples, however, formed a rather scattered cluster indicating high variability among replicates. Nematode MDS showed that only sediment samples formed a well defined cluster (stress = 0.09) (Fig.

3.4b). Nematodes in pier-piling and collector samples displayed a scattered pattern with very little overlap suggesting more similar nematode generic composition between these two substrates. The most well separated and compact clusters were formed when nematode and copepod taxa were combined (stress = 0.07) (Fig. 3.4c). Pier-piling and collector clusters were closer to each other than to sediments suggesting greater similarities among replicates. Sediment clusters were completely separated from collectors and pier pilings. ANOSIM results on nematode genera, copepod species and all taxa combined showed that the difference between the clusters was significant for pier pilings, faunal collectors, and sediments (Table 4.3). The highest affinity for both nematodes and copepods was between pier-piling and faunal-collector samples (Bray Curtis similarities were 40.2% for nematodes and 41% for copepods). Similarities between faunal collectors and sediment was low (20.6% for nematodes and 26.2% for copepods). Although a better ordination was obtained by combining nematode and copepod taxa (stress = 0.07) in comparison to separate analysis of each group (stress = 0.10 and 0.09 for copepod and nematodes, respectively), the goodness of fit was not significantly different between individual and combined taxa. However, low stress values for copepods, nematodes and both taxa combined indicated that ordinations did not likely lead to misinterpretations.

Copepod species richness (6.75 ± 0.25 SE) and diversity (1.39 ± 0.07 SE) were highest in faunal-collector samples (Table 3.2). Species richness on pier pilings and sediments were significantly different ($p<0.0001$, Table 3.2). Species diversity of faunal-collector colonists was significantly higher than pier-piling or sediment

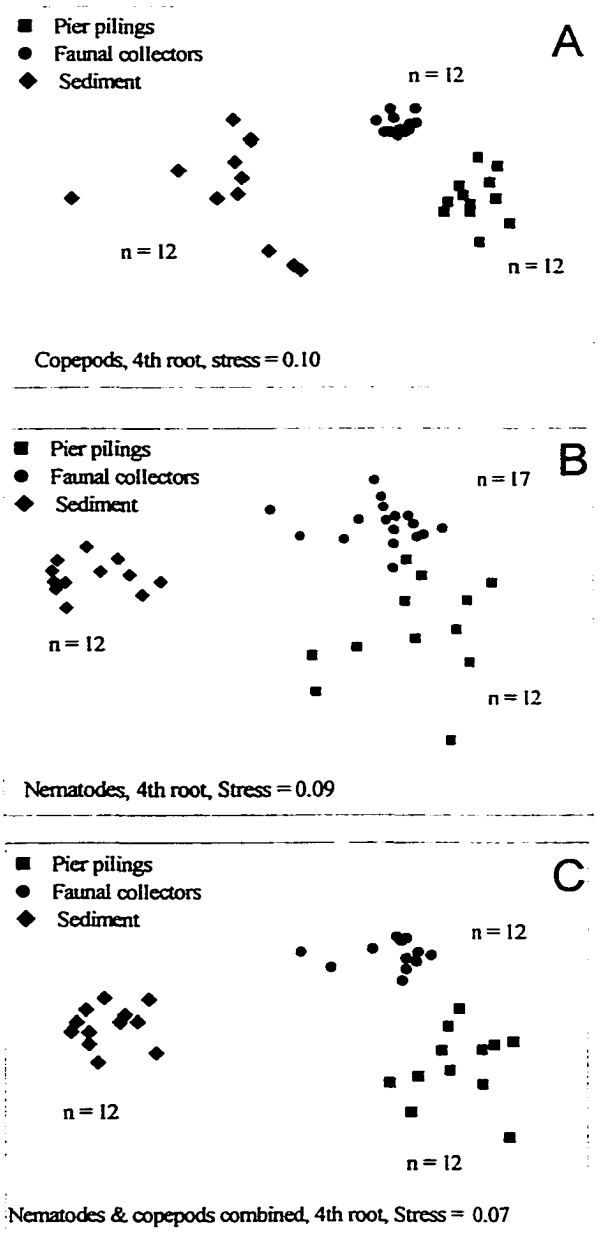


Figure 3.4. Two dimensional configurations of samples from multidimensional scaling ordination (MDS) of double square root transformed data for copepods (A), nematodes (B) and both groups combined (C). ●faunal collector, ▲ sediment, ■ pier pilings.

assemblages ($p<0.005$). Evenness was highest in sediment samples (0.82 ± 0.1 SE) and lowest in pier-piling samples (0.58 ± 0.05 SE) and differed significantly among substrates ($p<0.0129$). Nematode genus richness (14.08 ± 0.29 SE), diversity (2.32 ± 0.07 SE) and evenness (0.88 ± 0.02 SE) were highest in sediment samples (Table 3.2). Richness and diversity of nematode genera were significantly different among all three substrate types ($p<0.0001$); evenness values did not differ significantly ($p<0.4399$).

**Discussion**

Hundreds of quantitative studies have been conducted on meiofauna inhabiting sediments (Hicks and Coull, 1983; Coull, 1988; Coull and Chandler, 1992; Coull, 1999), but studies of hard-substrate associated meiofauna are extremely rare. Excluding phytal habitats, we know of quantitative studies only on epiphyte-covered macrophytes (Hall and Bell, 1988; Rutledge and Fleeger, 1993; Walters et al., 1996), animal biogenic structures (Bell and Coen, 1982; Bell, 1985; Thistle et al., 1993) and aufwuchs on suspended tiles (Little, 1986). Our suction samples from the surface of pier pilings revealed a surprisingly dense (1200 ind.100 $cm^{-2}$) meiofaunal assemblage with abundance, standardized to unit surface area, similar to that in the surrounding sediments. However, pier-piling and sediment assemblages were taxonomically distinct. Nematodes comprised 98% of the total meiofauna from sediment samples while pier-piling samples were dominated by copepods (17%) and copepod nauplii (71%). Moreover, MDS and ANOSIM clearly separated pier-piling and sediment copepod and nematode assemblages at lower taxonomic designations. *Harpacticus* sp. and *Parategastes* sp. comprised nearly 90% of the total copepods on pier pilings, and

Table 3.2. Comparison of mean richness (number of species), evenness (Pielou's $J$) and diversity (Shannon-Wiener $H'$) of copepods and nematodes on faunal collectors (FC),pier pilings (PP) and sediment (S). Results are Tukey's studentized range results. Alpha=0.05. Mean values joined by a common line are not significantly different.

| | | | | |
|---|---|---|---|---|
| **Copepoda** | | | | |
| Richness | FC | PP | S | F = 37.68 |
| | 6.75 | 6.16 | 2.91 | p < 0.0001 |
| Diversity (H') | FC | PP | S | F = 9.69 |
| | 1.39 | 0.97 | 0.89 | p < 0.005 |
| Evenness (J) | S | FC | PP | F = 4.97 |
| | 0.82 | 0.73 | 0.58 | p < 0.0129 |
| **Nematoda** | | | | |
| Richness | S | FC | PP | F = 62.26 |
| | 14.08 | 7.83 | 5.16 | p < 0.0001 |
| Diversity (H') | S | PP | FC | F = 35.43 |
| | 2.32 | 1.65 | 1.3 | p < 0.0001 |
| Evenness (J) | S | PP | FC | F = 0.84 |
| | 0.88 | 0.83 | 0.82 | p < 0.4399 |

Table 3.3. Results of analysis of similarity (ANOSIM) and Bray-Curtis similarity percentages between pier pilings, faunal collectors and sediment. for nematodes, copepods and nematodes and copeods combined.

| | **Anosim** | | |
|---|---|---|---|
| | Nematodes | Copepods | All genera |
| Pier pilings vs. faunal collectors | $p < 0.0005$ | $p < 0.0005$ | $p < 0.0005$ |
| Pier pilings vs. Sediment | $p < 0.0005$ | $p < 0.0005$ | $p < 0.0005$ |
| Faunal collectors vs. Sediment | $p < 0.0005$ | $p < 0.0005$ | $p < 0.0005$ |
| | **Bray-Curtis Similarity** | | |
| Pier pilings vs. faunal collectors | 40.16 | 41 | 40.63 |
| Pier pilings vs. Sediment | 15.29 | 4.95 | 13.09 |
| Faunal collectors vs. Sediment | 20.55 | 26.16 | 21.6 |

are strongly phytal in morphology based on criteria developed by Hicks (1985) and Bell et al. (1987). In fact, > 97% of the copepod species associated with pier pilings were classified as phytal, and phytal copepods were rare in sediment samples. *Prochromadorella*, *Chromadorina* and *Oncholaimus* were the three most abundant nematode genera on pier pilings, and each has been reported from various phytal habitats (Moore, 1977; Warwick, 1977; Trotter and Webster, 1983; Coull et al., 1983). A filamentous algal cover about 5 mm in thickness that extended to a water depth of 20 cm on pier pilings likely accommodated these phytal nematodes and copepods.

Meiofauna rapidly colonized faunal collectors. The abundance of collector meiofauna averaged 113 ind. 100 $cm^{-2}$, but net colonization averaged about 1000 ind. $col^{-1}$ $d^{-1}$. Our community analysis suggests that nematodes and copepods from pier-pilings and sediments both successfully colonized collectors; however, contributions from pier pilings to collectors clearly exceeded that from the sediments. Bray-Curtis similarities were highest between pier pilings and collectors (over 40% for both nematodes and copepods) and lowest between sediment and collector assemblages (similarities ranged from 20 - 26% for both copepods and nematodes). *Daptonema* was the most abundant nematode genus in faunal collectors and pier-piling collections, and comprised 34% of all nematodes on faunal collectors. *Parategastes* sp., which was the most abundant copepod on pier pilings, constituted over 50% of the collector copepod assemblage and 6% of the total collector meiofauna. Our copepod data suggest that about 67% of the collector fauna was phytal (originating from pier pilings), with the remaining 33% from sediments. Given the widely dispersing capabilities of phytal

meiofauna (Palmer and Gust, 1985; Kurdizel and Bell, 1992), it is likely that nematodes and copepods either swam (Jensen, 1981) or were eroded from the algal cover on the pier pilings and recruited through the water column to faunal collectors.

Oyster shells, algal-covered rocks and other non-wooden artificial substrates were common at the sampling site but were not sampled. Although there were no foliose macroalgae or seagrasses in the area, it is possible that we overestimated the contribution of pier pilings to faunal collectors if such unsampled hard substrates have a high abundance of dispersing phytal meiofauna. Furthermore, pier pilings may serve as habitats similar to natural hard substrates (e.g., oyster reefs) accommodating similar assemblages to natural hard-substrate assemblages. Faunal collectors were placed close to pier pilings (0.5 - 7 m) by design and other non-sampled substrates in the area (e.g., oyster shells, submerged concrete structures) were several meters more distant. Colonization rate decreases with increasing distance from a source pool (MacArthur and Wilson, 1967), suggesting that pier pilings contributed the highest numbers of colonists to faunal collectors. The theory of island biogeography also predicts that area affects colonization rate, and visual observation of the study site (data not presented) suggested most of the total surface area of hard substrates was composed of wood pilings and associated bulkheads rather than other types of artificial substrates. Furthermore, the number of shared taxa between pier pilings and faunal collectors were high (out of 55 lower taxa, 18 were shared), and only 6 taxa that recruited to faunal collectors could not be accounted for from sediment or pier pilings.

Copepods and nematodes inhabiting pier pilings and sediments showed differing degrees of colonization success, but pier-piling meiofauna generally colonized faunal collectors more successfully than sediment-dwellers (77% of pier-piling but 24% of sediment-dwelling copepod species colonized faunal collectors). Species-specific responses to flow and differences in active migration/swimming abilities are known to occur among sediment-dwelling and phytal meiofauna (Palmer, 1984; Waters and Bell, 1994; Thistle, 1995), and these differences may lead to variation in entry into the water column. Many sediment dwellers avoid emergence (Palmer et al., 1992; Thistle, 1995) including members of the tube-building genus *Stenhelia* (Fleeger et al., 1984; Williams-Howze and Fleeger, 1987), suggesting reduced susceptibility to erosion. Unfortunately, little is known of the behavior of the most successful colonists, including the nematode genera *Daptonema* (15% of total faunal-collector meiofauna) and *Prochromadorella*, and the phytal copepod *Parategastes* sp., which represented over 50% of all copepods on faunal collectors. However, since *Daptonema* was present on all three substrate types it is at least possible, if not likely, that more than one species represented this genus. *Harpacticus* sp. was the most abundant copepod or nematode that did not recruit from pier pilings to faunal collectors. We observed *Harpacticus* sp. on faunal collectors in our previous study (Atilla and Fleeger, 2000), but only when seasonally abundant algae became entangled on collectors, further suggesting *Harpacticus* sp. does not venture away from algae.

Several studies have reported that copepods are more rapid sediment colonizers than nematodes (Chandler and Fleeger, 1983; Armonies, 1988), but nematode

abundances on faunal collectors in our study exceeded that of copepods. Assuming both have equal rates of emergence, taxon-specific differences in capture and retention on our artificial substrates might explain the differences in abundance. Our earlier study suggested that faunal collectors probably passively filter nematodes from the water column (Atilla and Fleeger, 2000). Nematode abundances increased gradually over time suggesting they are captured and retained at high rates, while variation in copepod abundances was high over short periods of time suggesting frequent emigration events (Atilla and Fleeger, 2000). Nematodes may be retained at high rates on faunal collectors because of the nature of the mesh structure; perhaps the spaces between the thread and large surface area favor retention in the interior of the collector for nematodes. Species-diversity analysis showed that nematode diversity was highest in sediment samples, and lowest in faunal collectors suggesting only a few species from either environment are good dispersers. Copepod species diversity was highest on faunal collectors, and lowest in sediment samples compared to faunal collectors, suggesting that copepods from both pier pilings and sediment contributed to the higher diversity.

Palmer (1988) modeled meiofaunal emergence into the water column from sediment and phytal habitats. Her models were based on patterns of active and passive emergence and data on water-column abundance but did not consider meiofauna from undersampled sources such as hard substrates. Our data suggest that hard-substrate meiofauna may be present in the water column at high abundances, and contribute more than sediments to colonization of substrates through the water column. A wide variety of artificial substrates (pontoons, piers, walkways, artificial reefs, etc.) with surfaces that

can be colonized by microalgae are very common in shallow water (Duedall and Champ, 1991; Conell and Glasby, 1999), and provide a considerable amount of habitable space (e.g., an oil platform has an approximate surface area of > 300 $m^2$). Such habitats may contribute substantially to emergent meiofauna but the phytal appearance of hard-substrate meiofauna may lead researchers to assume a seagrass or macroalgal origin. In order to evaluate the potential importance of hard substrates, future research should determine if faunal emergence is active or passive and include extensive sampling of hard-substrate meiofauna to survey their abundance. The suction sampler used in our study proved to be effective, easy to use, inexpensive, and appears to be an excellent device to collect meiofauna from hard substrates. We encourage its use in future studies. The small, inexpensive faunal collectors also used here may serve as convenient water-column meiofauna collectors.

This study presents compelling evidence that an understudied pier-piling meiofauna represents a unique community, and that algal-covered hard substrates potentially play an important role in meiofaunal community dynamics. The origin of artificial substrate meiofauna community is unclear but likely comes from naturally occurring hard substrates such as oyster reefs. Artificial structures are undoubtably becoming more abundant as coastline development takes place and provide extended habitable space for meiofauna. Emergent meiofauna from hard substrates appear to be abundant and may have under appreciated roles in community dynamics and food chains in many marine environments.

# CHAPTER 4

# AN EXPERIMENTAL INVESTIGATION OF THE EFFECT OF HABITAT COMPLEXITY ON THE ABUNDANCE AND SPECIES DIVERSITY OF MEIOFAUNA

**Introduction**

Complex macro-scale (1 - 10 $m^2$ and greater) biogenic and non-biogenic structures such as coral reefs, artificial reefs, seagrass beds, oyster reefs and arrays of macrofaunal tubes and burrows often support communities of marine benthic invertebrates that are higher in abundance and species diversity than surrounding habitats (Heck, 1977; Rhodes, 1978; Heck, 1980; Hicks, 1980, 1982; Bonschak, 1990). Due to their structural complexity, these habitats provide large inhabitable surface areas, abundant food resources and predator refuge. These features also have the potential to influence larval and adult recruitment patterns by interaction with flow regime, and behavioral preferences of individual taxa may also favor areas of complex structure (Boesch and Turner, 1984; Bell and Coen, 1982; Beck, 1995; Eckman, 1995; Gage, 1996; Rooker et al., 1998). Unfortunately, there is no consensus on how complex structures come to harbor more abundant and diverse communities, and the importance of various factors (e.g., predator refuge, structural complexity, etc.) may differ from habitat to habitat.

Meso-scale habitats ($cm^2$ scale) such as branching and filamentous drift and floating algae as well as branching benthic algal masses and hydrozoan colonies, are also common in the marine environment, but have received much less attention. These structures create important complex habitats in the water column, and they harbor large numbers of small invertebrates; abundances may surpass invertebrate densities in surrounding habitats, and may even exceed that reported in seagrass communities (Mukai, 1981; Hicks, 1985; Norkko et al., 2000). Such structures also support groups

of invertebrates for critical parts of their life history. For example, Ingolfsson and Olafsson (1997) reported that naupliiar and ovigerous stages of the pelagic harpacticoid copepod *Parathalestris croni* live only on the brown algae *Ascophyllum nodosum*. Also, fish gut contents often contain invertebrates that do not typically occur in sediments (McCall, 1992; Toepfer and Fleeger 1995; Fleeger, 1985), and in the absence of natural hard substrates suggests that ephemeral substrates such as filamentous algae or hydrozoan colonies may provide other habitats for invertebrates.

Unfortunately, there is very limited information on the interaction between meso-scale substrates with their physical environment. The settlement of particles onto meso-scale substrates has been studied in the field and in laboratory flumes (Hannan, 1984; Bell, 1985; Harvey et al., 1995; Benoit et al., 1998), however, few studies have examined the relationship between complexity, flow fields and particle capture. Anderson and Charters (1982) showed that flow patterns through an attached filamentous algal mass ca 35 cm in length created downstream turbulence above a critical flow velocity. They also reported that filamentous algae suppresses turbulence below this critical flow velocity. Similarly, Harvey et al. (1995) indicated that in slow-flow velocities, meso-scale filamentous structures may reduce turbulence intensity and influence capture rate of small passive inert particles as mimics of marine larvae.

Meso-scale artificial substrates such as plastic mesh pads and bottle brushes have been shown to be rapidly colonized by meiofauna (metazoans <1 mm length) at high rates, and they may serve as good model habitats for drift and floating filamentous algae (Atilla and Fleeger, 2000). Meiofauna colonize these structures from the water

column, and the abundance of meiofauna colonizing these artificial substrates over short time intervals (before colonists can reproduce) must be a complex function of capture of meiofauna in the water and retention of meiofauna after initial capture. The physical properties (size, surface area, arrangement and density of the repetitious elements; i.e., bristles of bottle brushes) of these substrates suggest that substrates of different shapes and arrangement of elements may have unique capture efficiencies. Meiofauna, with sizes and swimming abilities similar to invertebrate larvae (Hannan, 1984; Palmer, 1988; Butman, 1989) have been shown to act like passive particles at flow velocities above critical erosion velocity (Fleeger et al., 1995), and it is likely that most meiofauna cannot avoid capture in turbulent flows associated with the substrates in tidally driven marine systems. Thus, the capture rate of meiofauna by an artificial substrate must be dependent on the availability of meiofauna in the water column and rate of water passage through the substrate. Therefore, the architectural complexity of a substrate and its surrounding flow regime undoubtably interact, and the results must influence the patterns of meiofaunal colonization onto artificial substrates. Post-settlement behavior (associated with faunal body shape, behavior, and swimming abilities) may also influence meiofaunal abundance and different taxonomic groups may be retained at different rates onto meso-scale substrates at different rates. Atilla and Fleeger (2000) showed that two major taxa of meiofauna, nematodes and copepods, colonized artificial substrates differently. They reported that over long colonization periods copepod abundance and composition changed rapidly possibly due to their active emigration abilities; however, steadily increasing abundance of nematodes suggested continuous recruitment and low emigration rates.

Here, I report on a study that extends research on artificial structures as experimental tools for investigating ecological processes and colonization of meiofauna. For this study, bottle brush-type collectors (after Atilla and Fleeger, 2000) were used because they gather large numbers of meiofauna and because they are easy to manipulate to create different levels of architectural complexity. Colonization patterns of meiofauna on these collectors were examined on brushes with varying habitat complexity. Because flow may differ around structures of different architectural complexity, flow fields around modified structurally complex substrates were examined in a laboratory flume. Specific goals were (1) to determine effects of habitat complexity and surface area on species diversity and abundance associated with meiofaunal colonization of artificial substrates, and (2) to investigate interactions between artificial substrates and water flow as a factor potentially influencing meiofaunal colonization.

**Methods**

Complexity Experiment

The study area was a shallow water embayment (< 2 m) on a protected beach on Grand Isle, Louisiana (29°W 90°N) adjacent to Caminada Pass. Sampling was conducted at an oyster hatchery with a variety of submerged hard substrates including large quantities of mollusc shells, wood pilings associated with a pier-piling walkway over the water, bulkheads and miscellaneous concrete structures.

The experiment was conducted in October 1999. Plastic bottle brushes were used as artificial substrates. Bottle brushes were 20 cm long with approximately 4000, 3-cm long bristles. The density and length of bristles on brushes were manipulated.

Bristles were clipped to reduce the length by half to create short- (1.5 cm) and long-bristle (3.0 cm) brushes. Bristle density was manipulated by removing 0%, 20% or 80% of the bristles from both long- and short-bristled brushes in a pattern to obtain a regular distribution of bristles along the axis of the brush for each removal level. Unmanipulated brushes were composed of 40 whirls of bristles around its axis. Each whirl of bristles contain approximately 100 bristles. One in five of the whirls was systematically removed in the 20% removal treatment. For the 80% removal treatment 3 out of 4 whirls and the second whirl from top and the bottom of the brush were removed to keep the length of the bristled part of the brush the same as the 20 and 0% removal treatments. In order to avoid the loss of bristles from the brush axis, non-toxic silicon sealant was used to secure the remaining bristles to the brush axis. In each whirl, bristles emerge from a central point and the distance between two adjacent bristles increases from their bases to their tips. The distance between two adjacent bristles was also measured on short- and long-bristled brushes. Ten nearest-neighbor pairs of bristles were selected randomly and the distance between their tips was measured with a caliper. This distance was 2.06 mm at the tips of the bristles on short-bristled brushes and 4.5 mm on the long-bristled brushes.

In order to quantify architectural complexity, surface area to volume ratio of each brush treatment was estimated. The surface area of a bristle was calculated by measuring its diameter (0.025 cm) and length (h = 3 or 1.5 cm), assuming that each bristle is a cylinder, and the total bristle surface area of a brush was estimated by multiplying this figure by the estimated number of bristles per treatment. The total

bristle surface area of the long-bristled control brush and short-bristled control brush were 340 $cm^2$ and 160 $cm^2$, respectively. Long-bristled brushes contained 288 $cm^2$ surface area at 20% removal and 72 $cm^2$ surface area at 80% removal; short-bristled brushes contained 128 $cm^2$ surface area at 20% removal and 32 $cm^2$ surface area at 80% removal. Volume of the brushes were estimated by estimating their geometric volume assuming the shape of a cylinder. Geometric volume of the short-bristled control brush treatment was 141 $cm^3$ compared to 565 $cm^3$ in the long-bristle control brush type. An index of complexity was calculated as the ratio of total bristle surface area to brush geometric volume. The complexity index was the lowest for long-bristled 20% removal (0.1 $cm^2\ cm^{-3}$) and highest for short-bristled control (1.1 $cm^2\ cm^{-3}$) treatments (see Figure 4.1). Short-bristled brushes provided more complexity but less total surface area than long-bristled brushes at each removal level.

Three replicates of each brush type were made available for colonization. Brushes were attached to a PVC pipe frame with monofilament line and placed equally distant from the surface and the bottom of the water column. After 10 days of colonization, substrates were collected with a container while they were still under water to avoid rinsing meiofauna from the substrates. Samples were preserved immediately after collection with 10% formalin stained with Rose Bengal. Meiofauna from each brush was extracted by washing the entire contents of a brush through nested 500 μm and 63 μm mesh size sieves. Major taxa were enumerated and all copepod species were identified to a nominal species taxon by using taxonomic aids of Wells (1976), Huys *et al.*, (1996) and Lang (1965).

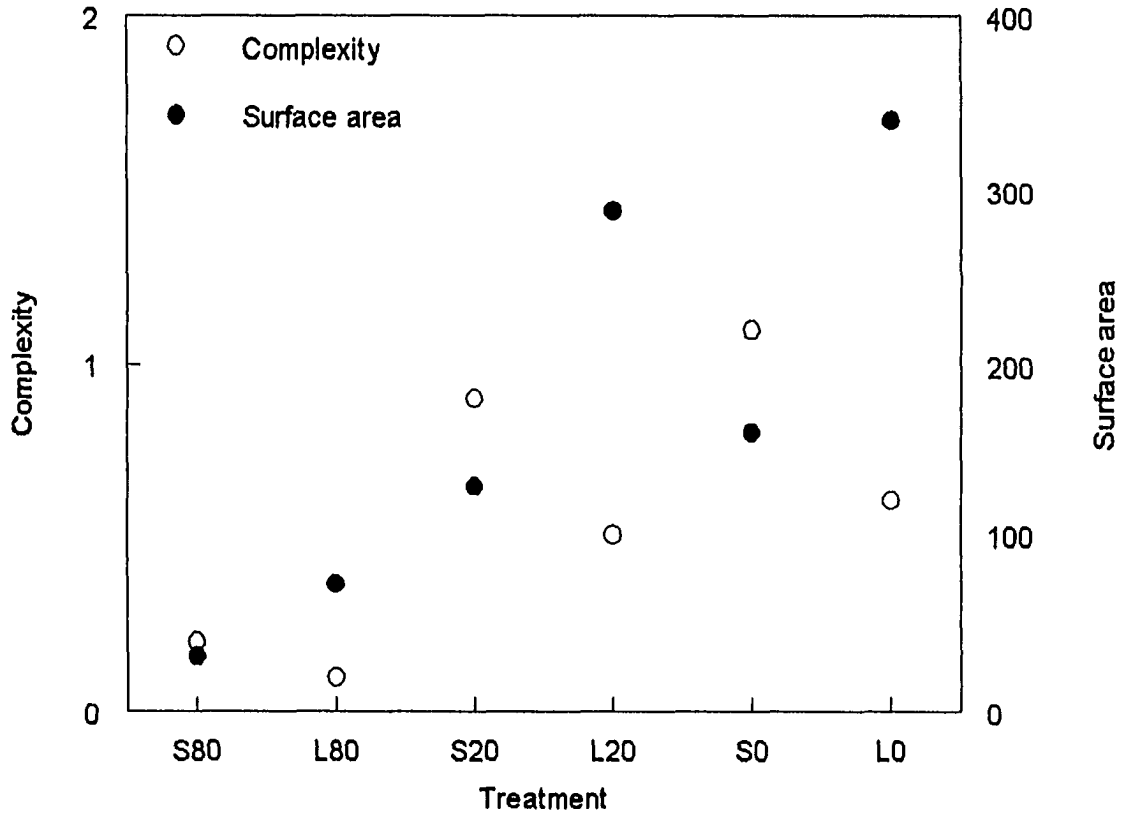


Figure 4.1. Complexity (total bristle area/brush volume ratio) and the total bristle surface area of the brushes at each treatment combination. S and L are represent short- and long- bristled brushes, respectively. 0, 20 and 80 are the percent bristle removal treatment for each brush type.

Two-way analysis of variance (ANOVA) was performed to test the null hypothesis of no effect of complexity or bristle length on meiofaunal abundance and diversity. Shannon-Wiener diversity, using natural logarithms, ($H'$) and evenness (Pielou's $J$) were calculated on adult copepod species abundances using PRIMER software. Differences in abundances between substrate types and treatments were tested using two-way ANOVA. Tukey's studentized range test was performed as an *a posteriori* test. Statistical Analysis Software (SAS) (Sas Institute, 1985) was used to perform all ANOVA procedures.

To help interpret the meiofaunal capture data, wind speeds during the course of the experiment was obtained from a NOAA (National Oceanographic and Atmospheric Administration) weather station located on Grand Isle, Louisiana. Wind speed was recorded hourly from which daily averages were calculated.

Flow Experiments

Flow experiments were conducted to determine the flow field and changes in the flow velocity and turbulence intensity around artificial substrates. These experiments were conducted at the Louisiana Universities Marine Consortium (LUMCON), DeFelice Marine Center in Cocodrie, Louisiana.

The LUMCON flume is a paddle-wheel type made of an acrylic channel 731.5 cm long on one side and 81.3 cm wide and 61 cm deep. Water depth was 30 cm. Brushes of each complexity level were placed individually in a horizontal position, in the flume 4.6 m away from the upstream end in the center of the water column (center of the substrates was 15 cm away from the bottom and the surface of the water) and held

normal to the flow. All substrate types were attached to a ring stand that was positioned on top of the acrylic channel of the paddle-wheel flume. Substrates were connected to the ring stand with a clamp. Flow visualizations were determined at two velocities; 5 and 15 cm $s^{-1}$. Fluorescein dye was used for flow visualizations. Fluorescein powder (0.5 g) was dissolved in 1 L of distilled water a day before the experiments. A fine stream of fluorescein dye (1.5 mm in diameter) was introduced into the flume 10 cm upstream from the substrate. The nozzle from which the fluorescein dye released was 4.5 m away from the upstream end of the flume. The flow fields going into, out of and around the artificial substrates was videotaped with a camcorder.

Current speeds were quantified by a thermistor micro-anemometer with a sensor bead of 0.13 mm in diameter. The probe was calibrated in the flume each day before and after the day's measurements were made. Calibration was performed by moving the probe at varying speeds through a still water bath while recording the probe's output along with its speed, measured with a linear velocity transducer (Transducer Systems, Inc., model P/N 89001-2D). The probe speeds and voltages were transformed according to a modified version of King's Law (Bearman, 1971), after which their relationship was fit via simple linear regression ($R^2$ always exceeded 0.98). Thereafter, this linear regression equation was used to predict ambient current speeds from the anemometer's voltage output. When the ambient water temperature differed from the water temperature during calibration, the anemometer's voltage output was corrected according to Bearman (1971). If calibration equations were available for both the beginning and the end of the day, a single regression line was fitted to the pooled data

for the entire day. The difference in predicted current speed for a given voltage output between these beginning and ending calibration curves averaged ~10%.

Current velocities and turbulence intensity, as the variation in the current velocity, were measured at four points upstream and downstream from the substrate (7, 5, 3, 1 cm) and three points from the upper edge of the brushes (3, 2, 1 cm). The probe's distance from the substrates at upstream, downstream and upper ends was determined with the aid of a stiff extension of the probe support. Fractional transmissivity (in per cent) of the artificial substrates was calculated by dividing flow velocity at 1 cm downstream from the substrates with different treatment combinations by ambient flow velocities of 5 and 15 cm $s^{-1}$. These calculations were obtained to estimate how much of the water passed among the bristles of the brush.

**Results**

Complexity Experiments

Overall, meiofaunal colonists on bottle brushes were dominated by nematodes (73% of the total meiofauna) while copepods were second in abundance and represented 16% of the total meiofauna. Copepod nauplii, polychaetes, gammarid and caprellid amphipods also recruited during the 10-day colonization period. Also, a thick cover of a branching hydrozoan colony was found on the brushes. Total meiofaunal abundance ranged between 2500-7000 individuals per collector (hereafter ind $col^{-1}$) among short- and long-bristled brushes across all complexity levels. These results are generally similar to my previous studies in which meiofaunal colonization rates averaged about 500-1000 ind. $col^{-1}$ $day^{-1}$ (Atilla and Fleeger, 2000; Chapter 3). Nematode and copepod

data were analyzed separately here due to differences in their colonization patterns. Previous work (Atilla and Fleeger, 2000) indicated that nematodes colonized substrates passively and increased steadily in abundance through time, while copepods fluctuated in abundance through time suggesting copepods are more active colonists with better swimming and emigration capabilities (Atilla and Fleeger, 2000).

The abundance of nematodes was significantly affected by bristle removal treatment ($p<0.0001$) (Table 4.1, Fig. 4.2), while bristle length did not influence nematode abundance significantly ($p<0.9459$). A significant interaction term between bristle length and removal treatments was observed ($p<0.014$). *A posteriori* results showed that the only significant differences in nematode abundances were for long-bristled brushes between 80% and 20% removal treatments (2149 ind $col^{-1}$ [± 157.9 SE] and 3827 ind $col^{-1}$ [± 389.4 SE], respectively) and for short-bristled brushes with 20% removal and control treatments (2761 ind $col^{-1}$ [± 400.9 SE] and 4802 ind $col^{-1}$ [± 300.6 SE], respectively) (Table 4.1). Average nematode abundance ranged from 2033 ind $col^{-1}$ (± 254.3 SE) to 4802 ind $col^{-1}$ (± 300.6 SE) on short-bristled 80% removal and short-bristled control brushes, respectively. Nematode abundances were higher in long-bristled brushes with 80% and 20% removal treatments than short-bristled brushes at the same removal treatments, however, in control brushes (0% bristle removal), nematode abundance was higher in short-bristled brushes than in long-bristled brushes. This difference is likely the cause of the significant interaction term. When the effects of total bristle surface area and complexity are compared without regarding bristle length (Fig. 4.2), nematode abundance generally increased with increasing complexity. Highest abundance was found at an intermediate surface area.

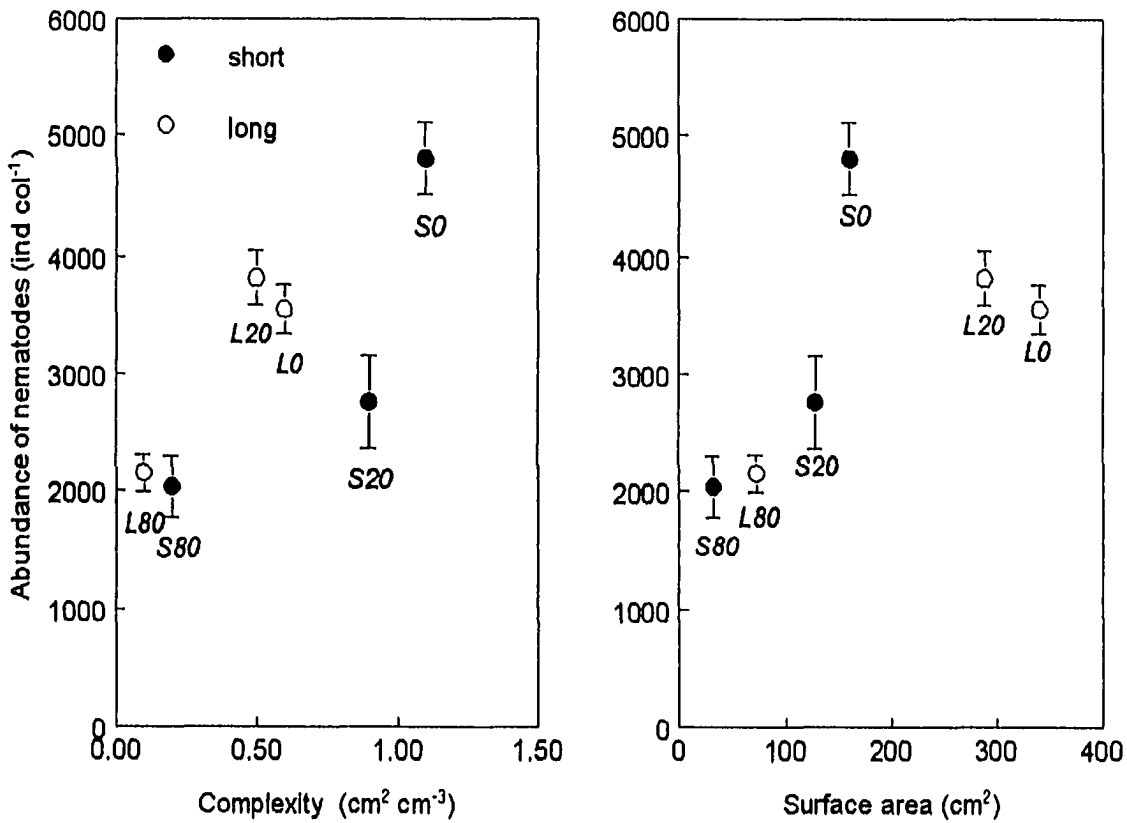


Figure 4.2. Abundance of nematodes on brush collectors at different levels of bristle removal. Complexity is the total bristle area/brush volume ratio for each collector type. Labels next to symbols indicate bristle length (*S*, short; *L*, long) and percent bristle removal. Values are means of three replicates. Upper and lower bars indicate standard error.

Table 4.1. Summary of two-way ANOVA and Tukey's test results of meiofaunal taxa on short and long bristled and 0, 20 and 80% bristle removal brushes. Significance level set at alpha = 0.05. Means for Tukey's test results are reported from highest value to lowest. Treatments with different letters indicate significant differences. S = short-, L = long-bristled brushes.

| | | Bristle Length | Bristle Removal | Interaction |
|---|---|---|---|---|
| Nematodes | F | 0 | 20.24 | 6.16 |
| | p | 0.9459 | 0.0001 | 0.0144 |
| | Tukey | ns | * | |
| Copepods | F | 7.97 | 89.79 | 1.45 |
| | p | 0.154 | 0.0001 | 0.2737 |
| | Tukey | $L^a$ $S^b$ | $0^a$ $20^b$ $80^c$ | |
| *Poecilostomatoida* | F | 7.25 | 60.10 | 1.37 |
| | p | 0.0196 | 0.0001 | 0.2909 |
| | Tukey | $L^a$ $S^b$ | $0^a$ $20^b$ $80^c$ | |
| *Pseudamphiascopsis sp.* | F | 2.14 | 14.38 | 0.74 |
| | p | 0.1692 | 0.0007 | 0.499 |
| | Tukey | ns | $0^a$ $20^a$ $80^b$ | |
| Diversity | F | 0.15 | 10.98 | 0.27 |
| | p | 0.7037 | 0.0019 | 0.7712 |
| | Tukey | ns | $0^a20^a80^b$ | |
| Evenness | F | 1.21 | 0.77 | 1.99 |
| | p | 0.2921 | 0.4856 | 0.1794 |
| | Tukey | ns | ns | |
| Richness | F | 0 | 11.37 | 0.37 |
| | p | 1.0000 | 0.0017 | 0.6951 |
| | Tukey | ns | $0^a20^{ab}80^b$ | |

* See text for comparisons within bristle removal treatments.

Bristle length and removal both affected copepod abundance ($p<0.015$ and $p<0.0001$, respectively); however, the interaction between length and removal was not significant (Table 4.1). Tukey's studentized test results indicated that bristle removal on short- and long-bristled brushes significantly affected copepod abundances such that copepod abundance increased with decreasing bristle removal (Table 4.1). Total copepod abundance on long-bristled brushes was significantly higher than on short-bristled brushes. Mean total copepod abundances ranged between 274 ind $col^{-1}$ (± 52.1 SE) in short-bristled 80% removal brushes and 1127 ind $col^{-1}$ (± 43.8 SE) in short-bristled control brushes (Fig. 4.3). Unlike nematodes, copepods responded to bristle surface area rather than bristle density. Copepod abundance generally increased with increasing total bristle surface area (Fig. 4.3) however, highest copepod abundance was found at intermediate complexity levels.

A total of 11 adult copepod species colonized brushes. The copepod assemblage was represented by Harpacticoida and Poecilostomatoida. One unknown species from Poecilostomatoida was the most abundant copepod species in the assemblage. The harpacticoid species assemblage consisted of *Schizopera knabeni*, *Pseudamphiascopsis* sp., *Robertsonia* sp., *Harpacticus* sp., *Parategastes* sp., *Onycocamptus* sp., *Paronycocamptus huntsmani*, *Nitocra lacustris*, *Zausodes* sp. and a species of the family Ectinosomatidae. Most copepodites were of the poecilostomatoid species.

Poecilostomatoid abundance ranged between 194 ind $col^{-1}$ (± 55.78 SE) and 979 ind $col^{-1}$ (± 92.08 SE) on short-bristled 80% removal treatments and long-bristled controls, respectively (Fig. 4.4) and comprised over 80% of the total copepod

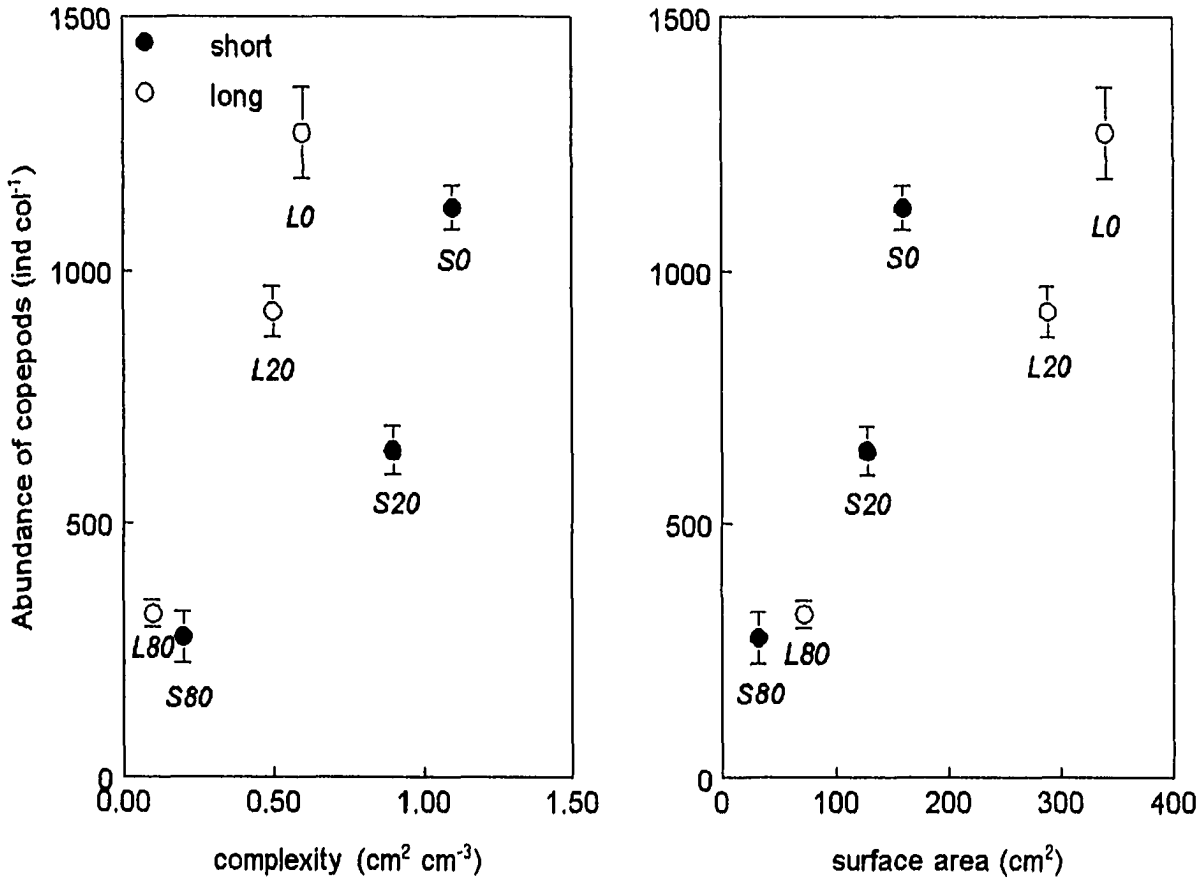


Figure 4.3. Abundance of copepods on brush collectors with different levels of bristle removal. Complexity is the total bristle area/brush volume ratio for each collector type. Labels next to symbols indicate bristle length (*S*, short; *L*, long) and percent bristle removal. Values are means of three replicates. Upper and lower bars indicate standard error.

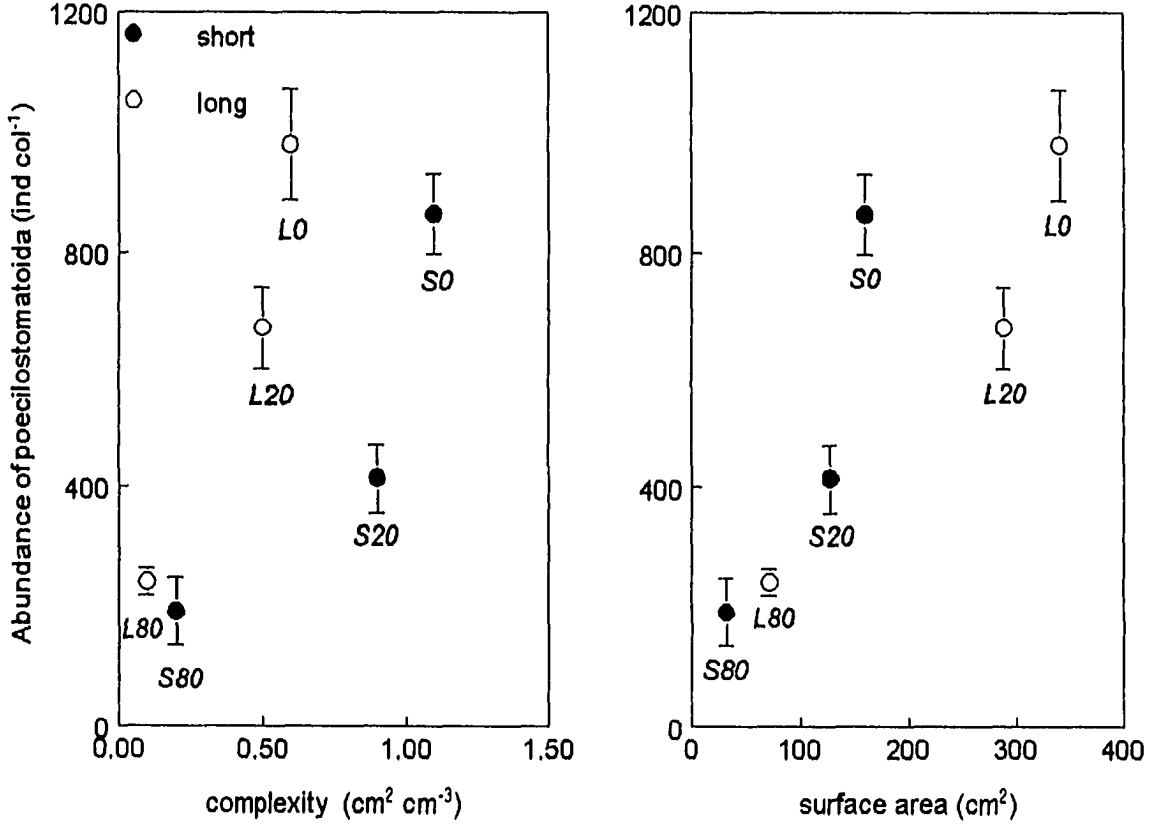


Figure 4.4. Abundance of Poecilostomatoida on brush collectors at different levels of bristle removal. Complexity is the total bristle area/ brush volume ratio for each collector type. Labels next to symbols indicate bristle length (*S*, short; *L*, long) and percent bristle removal. Values are means of three replicates. Upper and lower bars indicate standard error.

assemblage. Bristle length and removal significantly influenced Poecilostomatoid abundance ($p<0.01$ for length and $p<0.0001$ for density) (Table 4.1), and abundance was higher on long-bristled than short-bristled brushes and increased with decreasing removal. The interaction between bristle length and complexity was not significant. Poecilostomatoida abundance increased with increasing surface area (Fig. 4.4) with highest abundance on intermediate complexity levels.

*Pseudamphiascopsis* sp., as the second most abundant copepod, represented 6% of the total copepod assemblage. The abundance of *Pseudamphiascopsis* sp. averaged similar values in both short- (45.33 ± 10.18 SE) and long-bristled brushes (45 ± 1.73 SE) ($p<0.17$). *Pseudamphiascopsis* sp. abundance ranged between 15 ind $col^{-1}$ (± 6.75 SE) and 77 ind $col^{-1}$ (± 13.31 SE) in short-bristled 80% removal and long-bristled control brushes (Fig. 4.5). Bristle removal significantly influenced *Pseudamphiascopsis* sp. abundance ($p<0.0007$) (Table 4.1). No significant interaction term between bristle length and removal observed. Tukey's studentized range test results showed significant differences in *Pseudamphiascopsis* sp. abundance between 80% removal and 20% removal brushes. *Pseudamphiascopsis* sp. abundance was not significantly different between 0% and 20% removal. Similar to overall copepod and Poecilostomatoids, *Pseudamphisascopsis* sp. abundance increased with increasing surface area with highest abundances on brushes with intermediate complexity levels.

Adult copepod species diversity ($H'$) averaged 1.99 (± 0.012 SE) and 1.97 (± 0.08 SE) on short- and long-bristled brushes respectively (Fig. 4.6a). Species diversity was significantly influenced by bristle removal ($p<0.0019$) (Table 4.1) but not bristle

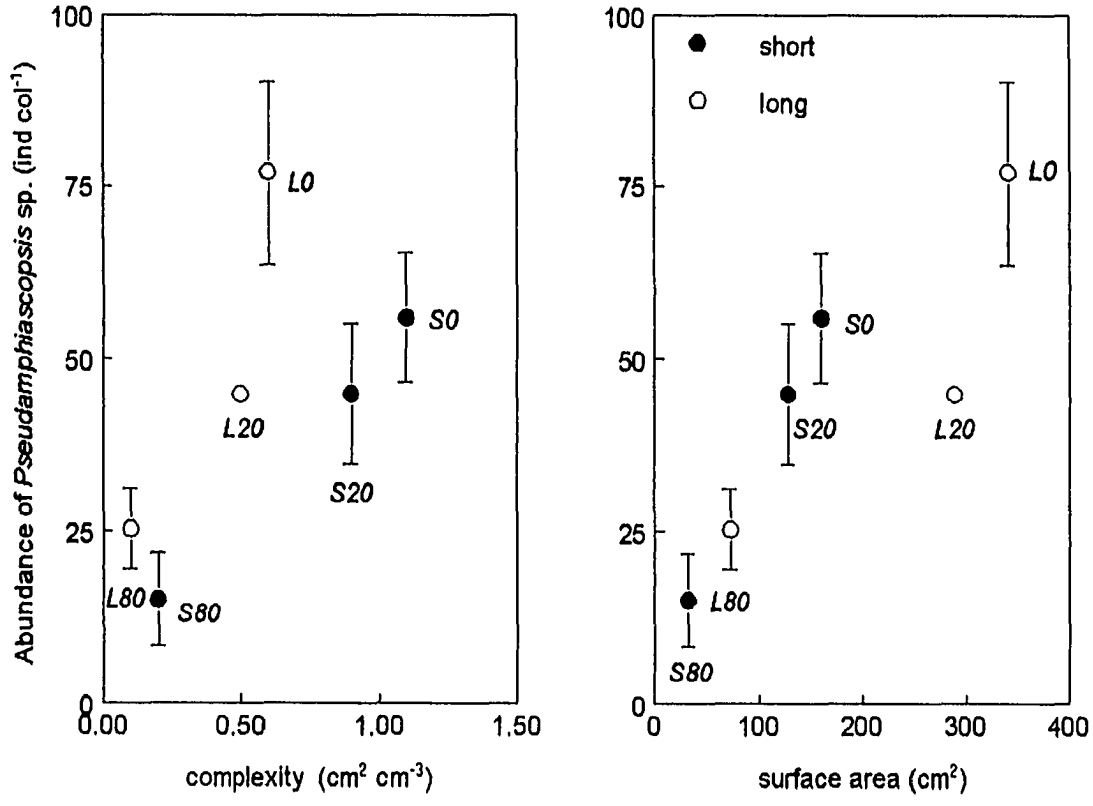


Figure 4.5. Abundance of *Psuedamphiascopsis* sp. on brush collectors with different levels of bristle removal. Complexity is the total bristle area/ brush volume ratio for each collector type. Labels next to symbols indicate bristle length (*S*, short; *L*, long) and percent bristle removal. Values are means of three replicates. Upper and lower bars indicate standard error.

length ($p<0.7037$). Species diversity was similar on 0% and 20% removal bristles, and both were significantly higher than 80% removal brushes. Mean number of adult species ranged between 8 (± 0.578 SE; short-bristled 80% removal) and 11 (± 0 SE; long-bristled control)(Fig. 4.6b). Number of species was significantly influenced by bristle removal level only ($p<0.0017$) (Table 1). Species richness was significantly higher on 0% removal brushes than 80% removal brushes. Average copepod evenness was 0.9 (± 0.01 SE) on short-bristled brushes and 0.89 (± 0.01 SE) on long-bristled brushes (Fig. 4.6c). Neither bristle length ($p<0.2921$) nor bristle removal treatment ($p<0.4856$) affected copepod species evenness (Table 4.1). Species diversity and richness generally increased with increased complexity; highest diversity was observed at intermediate surface area.

Wind speed averaged 2.7 ± 0.3 m $s^{-1}$ during the 10-day course of the experiment ranging between 1.4 to 3.8 m $s^{-1}$. During the first two days of the experiment wind speed was slightly below 4 $ms^{-1}$ and the remaining 8 days it fluctuated between 1.5 to below 3 m $s^{-1}$.

Laboratory Flume Experiments

At 5 cm $s^{-1}$ the fluorescein dye stream dispersed as soon as it encountered any of the brush collectors. The dye stream formed a cone-like structure approximately 2 cm upstream from the long-bristled brushes and 1 cm upstream from the short-bristled brushes at each bristle removal level. In both short- and long-bristled control brushes, most of the dye stream skimmed around the brushes. Dye-stream dispersion around all removal levels of both short- and long-bristled brushes was similar. In control brushes

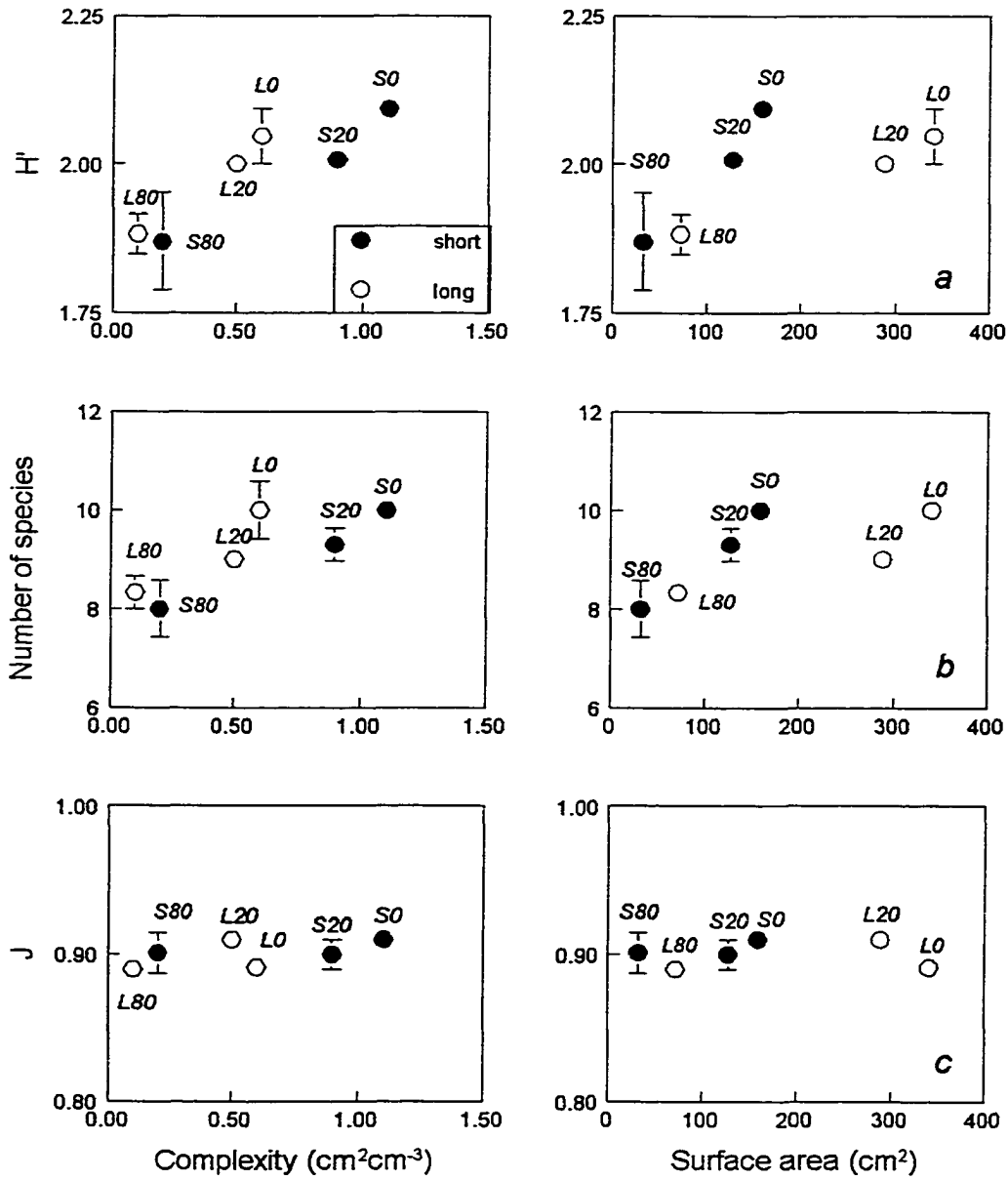


Figure 4.6. Copepod diversity (a), evenness (b) and richness (c) on short- and long-bristled brushes with differing levels of bristle removal. Labels next to symbols indicate different treatments and percent bristle removal. Values are means of three replicates. Upper and lower bars indicate standard error.

the dye stream went through the brushes only occasionally and the downstream pattern of dye was pulse-like. At 20% bristle removal treatments on both short- and long-bristled brushes flow patterns were similar to control brushes as the dye stream skimmed around the brushes with minor disruption. At 80% bristle removal of both short- and long-bristled brushes dye stream was a little disturbed, and dye flowed through the brushes with little disruption.

No differences in the dispersion pattern of the dye stream was observed between long- and short-bristled brushes at 15 cm $s^{-1}$. At this flow velocity, the dye stream became disorganized before it reached the substrate and was completely dispersed upon encounter with the brushes at control and 20% bristle removal levels. Sometimes the dispersion in the downstream end of the brush occurred in pulses mainly due to the disorganized behavior of the dye stream on the upstream end of the brushes. Dispersion was also observed in 80% removal short- and long-bristled brushes but at downstream from the brushes it was more organized with recognizable streaks.

Flow velocities on the upper edge of all treatments varied only slightly from the ambient flow speed (data not shown). A notable decrease in velocity was recorded 3 cm downstream from all brushes (Fig. 4.7). Velocity decreased 3 cm downstream with decreasing bristle removal in both long- and short-bristled brushes at 5 and 15 cm $s^{-1}$. At 3 cm downstream, flow velocities showed a higher percent decline at 5 cm $s^{-1}$ flow velocity than 15 cm $s^{-1}$ flow velocity. Flow velocities decreased by 94% at 3 cm downstream from the long-bristle control and 82% at 3 cm downstream from the short-bristle 80% removal at 5 cm $s^{-1}$ flow velocities. At 15 cm $s^{-1}$, the percent decline in flow

velocity at 3 cm downstream ranged between 68% (long-bristle control) to 18% (short-bristled 80% removal). In long-bristled brushes, flow velocity at 3 cm downstream was the highest for 20% removal brush and lowest for control brushes.

Transmissivity of the substrates was calculated in both 5 and 15 cm $s^{-1}$ flow velocities (Figs. 4.7, 4.8) . At 5 cm $s^{-1}$ transmissivity ranged from 3-50% and was different for long- and short-bristled brushes. Surprisingly, transmissivity increased with decreased bristle removal and increased surface area on long-bristled brushes. Transmissivity also decreased with decreased bristle removal and increased surface area on short-bristled brushes; however, the difference in transmissivity among bristle removal levels was very small. Short-bristled control brushes had the lowest transmissivity of all substrate types. Transmissivity was higher at 15 cm $s^{-1}$, than 5 cm $s^{-1}$, ranging between 37 to 94%. Transmissivity of short-bristled brushes decreased dramatically with decreasing bristle removal level (37 - 94%) while transmissivity was nearly the same in all long-bristled brushes (45 - 53%).

Turbulence intensity at 3 cm downstream was measured at both 5 and 15 cm $s^{-1}$ flow velocities (Fig. 4.7). Turbulence intensity decreased with decreasing bristle removal for both short- and long-bristled brushes in both slow and fast flows (Fig. 4.7). At 5 cm $s^{-1}$, turbulence intensity around short-bristled brushes, however, showed a much steeper decrease with decreasing bristle removal than long-bristled brushes. Turbulence intensity measured at 3 cm downstream from the brushes at 15 cm $s^{-1}$ did not decrease notably. At the same removal levels, turbulence intensity was always greater for short-bristled brushes than long-bristled brushes except at 0 removal at 5 cm $s^{-1}$ where

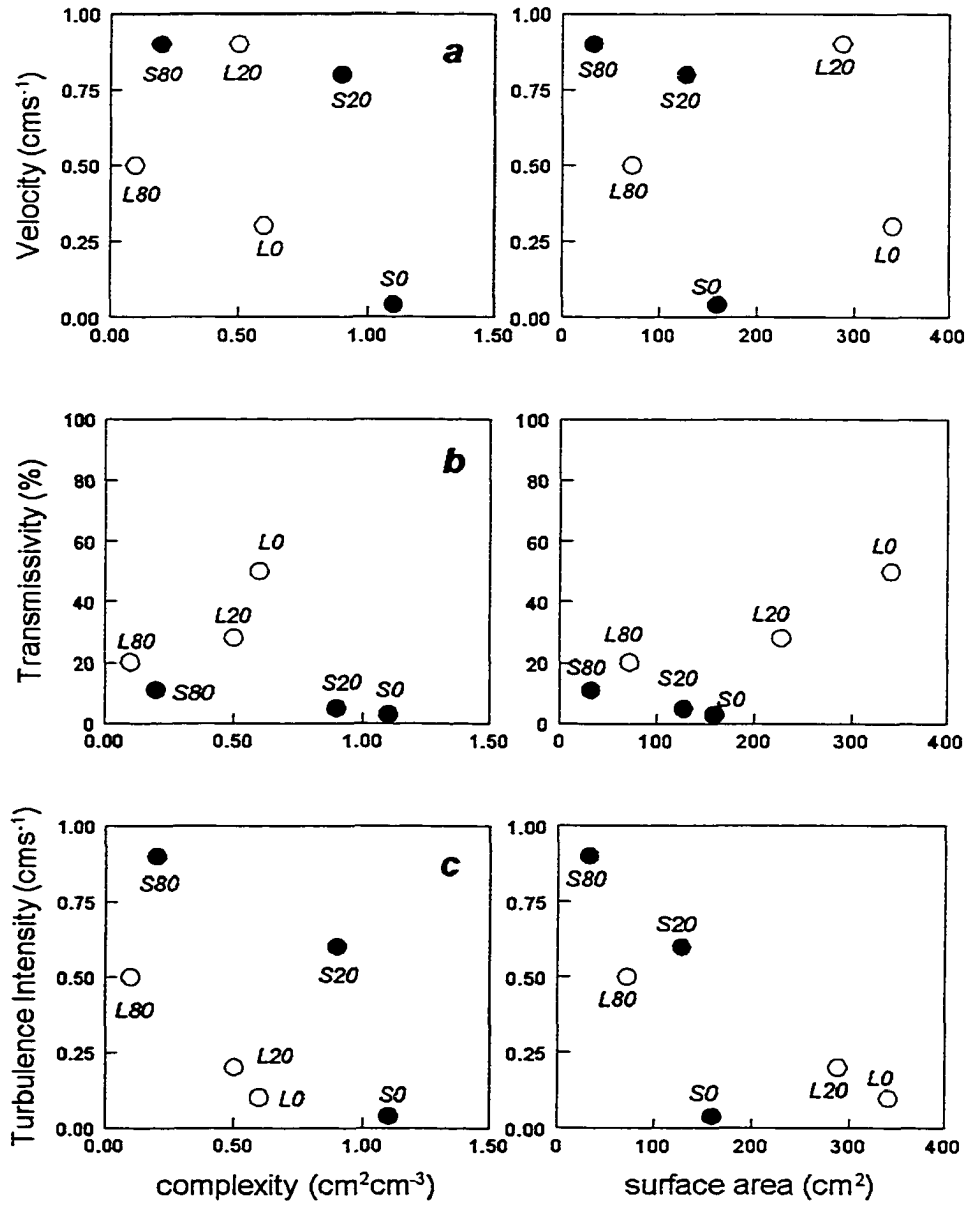


Figure 4.7. Flow velocity, turbulence intensity at 3 cm downstream from the substrates and % transmissivity of the substrates at different bristle removal treatments at 5 cm $s^{-1}$. Complexity is the total bristle surface area/volume ratio for each collector type. Labels next to symbols indicate different treatments and percent bristle removal.

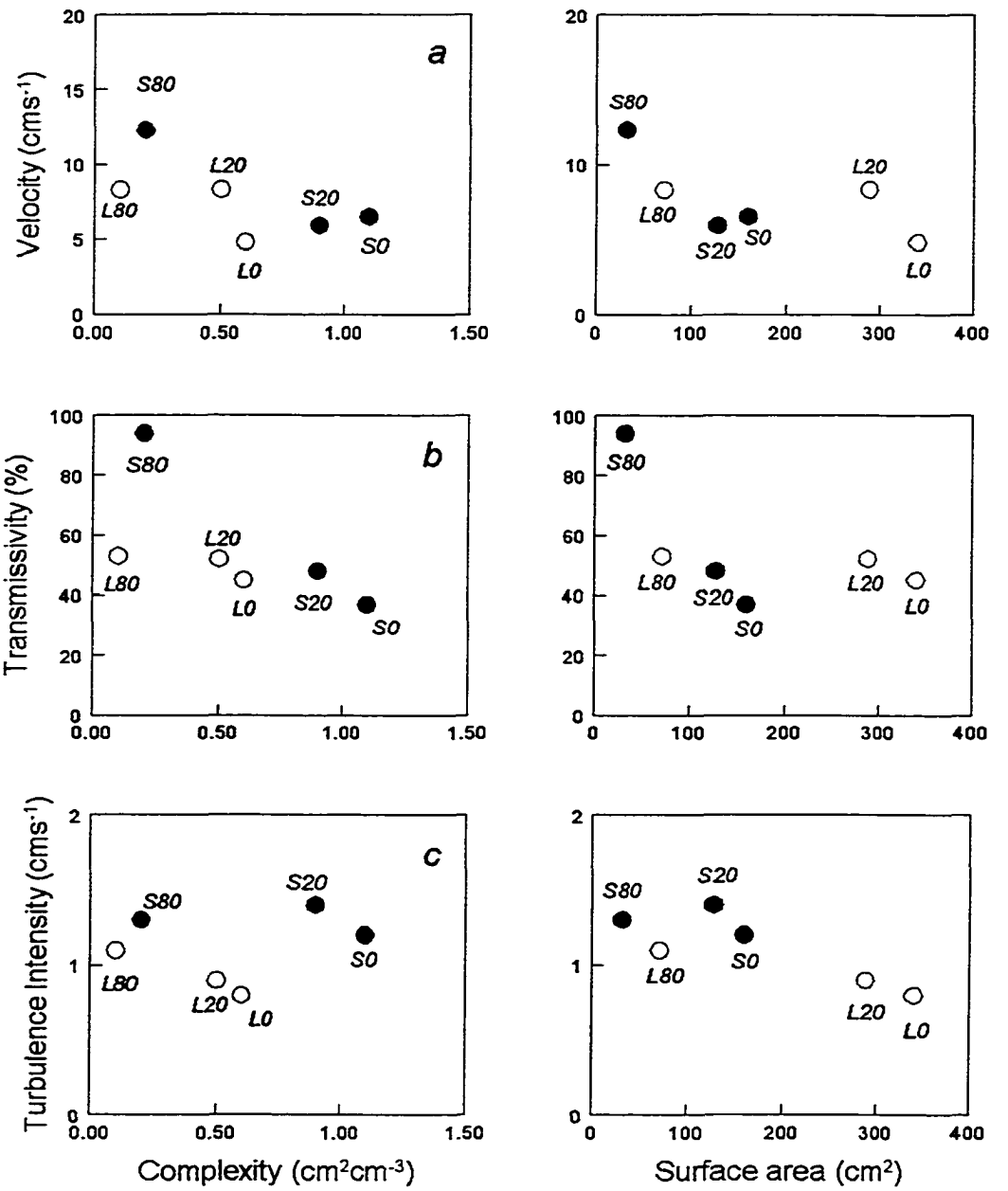


Figure 4.8. Flow velocity, turbulence intensity at 3 cm downstream from the substrates and % transmissivity of the substrates at different bristle removal treatments at 15 cm $s^{-1}$. Complexity is the total bristle surface area/volume ratio for each collector type. Labels next to symbols indicate different treatments and percent bristle removal.

turbulence intensities were essentially equal. Overall, the lowest turbulence intensity was observed with short-bristled 0% removal (control) brushes (highest complexity level obtained) at 5 cm $s^{-1}$ flow velocities.

Flow velocities at 3 cm down stream from the substrates, transmissivity and turbulence intensity responded to surface area and complexity in very similar ways.

**Discussion**

I measured the abundance and species diversity of meiofauna colonizing artificial substrates through the water column in a shallow estuarine embayment. Generation times of most meiofaunal taxa range between 15-21 days (Coull and Chandler, 1992) at the ambient temperatures at the study site, and are too long to allow reproduction to contribute to the observed recruitment of adults through the 10-day colonization period. Further, planktonic copepods were captured in very low abundances, suggesting that zooplankton avoid the artificial substrates. Meiofauna are less capable swimmers than zooplankton, and several studies have shown that they act like passive particles at the flow rates likely experienced at the study site (Butman, 1989; Palmer, 1990; Fleeger et al., 1995), suggesting nematodes and copepods are unlikely to be able to avoid capture on artificial substrates. Meiofauna that are captured may, however, actively swim away during slack tides or be passively eroded from artificial substrates during high flow events. Thus, the final meiofaunal abundance is a complex function of capture and retention. Complexity and total surface area of the artificial substrates may play a role in both capture and retention rates and meiofaunal abundance differed among brush treatments.

In this study, two brush types (long- and short-bristled brushes) were created by manipulation of bristle length. Within each brush type, the removal of bristles predictably altered brush complexity (a measure of bristle density defined as the ratio of total bristle surface area to the geometric volume of the brush) and total bristle surface area of the brushes (Fig.1). Brush complexity and total surface area both increased with decreasing bristle removal level. Long-bristled brushes always had a higher total surface area, but lower complexity at the same bristle removal level compared to short-bristled brushes (Figs. 4.1-4.5). Between the two brush types (long- and short-bristled brushes), the 80% removal treatment had very similar complexity and total surface areas. However, at 20% and 0% removals, short- and long-bristled brushes were quite different in their complexity and surface area. For example, the long-bristled 0% removal brush (L0) was the brush type with the highest surface area, but the short-bristled 0% removal brush (S0) was the brush type with highest complexity. It is possible that flow fields respond more to changes in bristle density (associated with bristle removal treatment levels) than to changes in total surface area. Therefore, capture efficiency of the two brush types is likely to be different due to unique interactions with flow. Furthermore, meiofaunal recruitment may also be influenced by surface area and complexity relationships as they influence retention rates associated with the brushes.

A clear effect of bristle removal on meiofaunal abundance and diversity was observed in this experimental system. Abundances of the meiofaunal major taxa and the diversity of adult copepod species generally increased with increasing bristle density

within each bristle-length treatment. Abundances of copepods and their two principal constituent species increased significantly with decreasing bristle removal regardless of the bristle length (Table 4.1). ANOVA conducted on nematode abundances revealed an interaction between brush type and bristle removal level, although Tukey results showed that where significant differences occurred, more nematodes were collected on brushes with higher complexity or surface area.

Previous research on flow around bristle-like structures has focused on small-scale structures such as insect appendages and bivalve filter-feeding structures (Rubenstein and Koehl,1977; Cheer and Koehl, 1987a, b), and has shown that a filter having many fibers per unit area represents more sites for collecting particles but has a lower flux of particle-laden fluid through it than does a less dense filter (Cheer and Koehl, 1987a, b). These small structures have very small Reynolds numbers (<1) and the environment around them is viscous. However, water moving through the brushes used in my experiments is not highly viscous. The Reynolds numbers associated with bristles will differ greatly depending on their position relative to the direction of the flow. Reynolds numbers of bristles in a 5 cm $s^{-1}$ flow range between 12.5 for both short and long bristles when normal to the flow and, 750 and 1500 for short and long bristles, respectively, when they are in the direction of the flow (0° to the flow direction) ($Re = ud/v$, where $u$, $d$ and $v$ are respectively equal to flow speed, longest measure of the bristle in the flow direction and sea water kinematic viscosity, $v = 0.01$). On the other hand, my dye-stream studies and flow measurements around the brushes suggest that brushes did not create turbulence (see Anderson and Charters, 1982). Thus, it is likely

that flow interacts strongly with the structural elements (bristles) of the brushes. Within a brush type, turbulence intensity (variability of the flow velocity of a laminar flow) decreased with increasing complexity and total surface area, especially in the 5 cm $s^{-1}$ flow. Under these turbulent conditions, dampening of the flow caused water flowing through the bristles of the brush to slow, likely enhancing capture of meiofauna. This probably explains why increased abundance of meiofauna generally occurred with decreasing bristle removal within each brush type.

There were, however, strong effects of bristle length on meiofaunal abundance and these effects were taxon specific. Both brush total surface area and complexity varied among brush treatments and may have influenced colonization in different ways. Total copepods and two copepod species reached their highest abundances in the long-bristled control brush (L0) treatment (Fig 4.3). Copepod abundances increased with increasing surface area across brush types; however, the highest copepod abundance was found at an intermediate complexity level. Nematodes, on the other hand, had their highest abundance on the short-bristled 0% removal brush (S0) treatment (the highest complexity), and a general trend of increased abundance with increasing complexity (Fig 4.2) suggests that nematode colonization responded more to brush complexity than to total surface area.

Long and short bristles differed in their spatial arrangement on the brushes. The distance between the tips of two adjacent long bristles is approximately twice as long as the distance between the tips of short bristles (4.5 and 2.06 mm for long and short-bristled brushes, respectively). Further, distance between nearest neighbor bristles

increases towards the tips. It has been shown that distinct flow regimes occur behind a pair of cylinders in a fashion that depends on both Reynolds number and cylinder spacing (Bearman and Wadcock, 1973; Perry *et al.*, 1983; Lam and Cheung, 1988). When the space between two cylinders is wider than their diameter, two lines of vortices form downstream from the cylinder. When the cylinders are nearly touching, only one line of vortices forms (Bearman and Wadcock, 1973). This behavior of flow is likely to reduce water contact with the lee sides of closely spaced cylinders. In this case, attachment sites for particles in the water is reduced by half because the vortices occur on the lee side of only one bristle instead of two. Long bristles probably provide larger area for attachment than short bristles because long bristles are not as closely spaced as short bristles near their tips. Additionally, groups of (10-30) bristles of long-bristled brushes, when submerged, became clumped (Atilla, pers. observation). This condition probably influenced transmissivity downstream from the long-bristled brushes due to the decreased obstruction of the flow. Transmissivity increased with decreasing bristle removal in long-bristled brushes. Although this clumping of the bristles on long-bristled brushes is likely to reduce the available surface area for copepods to colonize, the higher flux of water through the bristles was possibly compensated by an increasing particle (meiofaunal) encounter with bristles. The inverse situation, decreasing transmissivity with increasing complexity, observed downstream from the short-bristled brushes suggested an increased skimming flow regime. Because short bristles were in close contact, single lines of vortices probably formed around many neighboring bristles limiting water contact with their lee sides and thereby reducing the attachment sites for particles and their capture efficiency.

The final abundances of nematodes and copepods may also have been related to retention rate. Complex meso-scale structures such as filamentous drift or floating algae and artificial substrates capture sediment and other organic matter which may provide an extra food source for some colonists (Atilla and Fleeger, 2000). Once captured, nematodes associated with floating algae such as *Sargassum* are reported to benefit from organic matter from particulate accumulation between the branches (Mukai, 1971; Kito, 1975), and remain on the algae. Furthermore, nematodes are poor swimmers and they move in a thrusting motion when they are not in the sediment. Therefore, once settled, they may be entrapped between the bristles, causing increased retention with increasing bristle density. Copepods, however, are active swimmers with abundances which typically exceed that of nematodes in the water column (Walters, 1988; Bell et al., 1989). Unlike nematodes, copepods do not likely benefit or rely on food available in the brush and, they may require food sources not available in the brush. For example, many copepods use benthic microalgae as their primary food source and a commensal Poecilostomatoid copepod found in high abundances, requires a host probably not associated with brushes (see below). Thus, after being captured, copepods may be more prone to swim away during slack tides, reducing residence times on the brushes. If copepods are passively collected from the flow, their colonization on artificial substrates is therefore more likely to be a function of surface area available for particle attachment than bristle density.

Flow velocities during the 10-day colonization period in the field were not measured. Average monthly water levels on the Louisiana coast vary seasonally by

approximately 25 cm (Bauman, 1987) and astronomical tidal ranges of the Northern Gulf coast average by 32 cm (Bauman, 1990). In shallow estuaries of Louisiana the flow is usually tidal driven and unidirectional for several hours with flow velocities ranging between 0-15 cm $s^{-1}$ (Fleeger et al., 1984). Many researchers who investigate flow-animal interactions work on shallow sandy bottom environments with tidally driven flow because of the predictable behavior of the flow in the field and the ability to create similar conditions in a flume in laboratory (Nowell and Jumars, 1984, 1987; Weissberg and Zimmerfaust, 1993). Records of wind speed taken near the study site suggest that there was no storm event during my experiment which may have caused high surface flow velocities, thus flow velocities in the field were likely to be similar to the flow velocities of 5-15 cm $s^{-1}$ used in the flume study.

Among the copepods colonized on brushes, a species of Poecilostomatoida was surprisingly the most abundant copepod. Previous work at the study site reported the existence of this species on artificial substrates and pier pilings (misidentified as a cyclopoid in Atilla and Fleeger, 2000) but it never reached the high abundances that occurred during the course of this study. The order Poecilostomatoida is largely composed of parasitic and commensal forms associated with a variety of benthic animals such as polychaetes, sea anemones and other larger crustaceans for at least part of their life history (Kim, 2000). Four families within this group are also known to be planktonic, visual predators or associated with mucoid aggregates and abandoned larvacean houses (Huys and Boxshall, 1991). The members of this group are not typically considered to be the members of the meiofauna and are rarely found in

sediment (Fleeger, personal comm.). The species from our collection is most likely to be associated with or benefitting from the branching hydrozoan colony found on the brushes or with barnacles or other animals on the pier pilings. Specimens have been sent to Dr. J. S. Ho at University of California, Long Beach for positive identification. Their existence on artificial substrates (Atilla and Fleeger, 2000; Chapter 3) suggests that they are capable of frequenting the water column. The remainder of copepod species, with the exception of *Nitocra lacustris* and Ectinosomatidae, which are likely to be benthic, have phytal morphologies with prehensile first legs or dorso-ventrally or laterally flattened body shape. The second most abundant harpacticoid copepod (*Pseudamphisacopsis* sp.) colonized on brushes has a fusiform prehensile body shape with strongly prehensile first legs, a morphological character associated with algae.

Many studies have shown that the number of species in a community increases with increased area of a habitat (MacArthur and Wilson, 1967; Diamond, 1973), and species area relationships are well known in the ecological literature (Hanski and Gyllenberg, 1997). Several studies conducted with algal-dwelling meiofauna have shown that as habitat complexity increases, abundance and species diversity increases (Hicks, 1980; Coull and Wells, 1983; Bell, 1985; Hall and Bell, 1988). In my study, adult copepod diversity expressed as the number of species and the Shannon diversity index (H') were significantly lower in 80% removal brushes than other treatments, and there was no influence of bristle length on diversity. During the 10-day colonization period, total number of copepod species averaged 8 on 80% removal brushes. Over 33% more copepods were collected in 0 and 20% removal brushes which also yielded a

higher number of species (9 in 20% removal, 10 in 0% removal brushes). Six of the 11 copepod species were present in all brushes, while 2 rare species (*Zausodes* sp. and *Robertsonia*) only occurred on brushes with the largest surface areas (*Zausodes* sp. only on 0% removal and *Robertsonia* sp. on 20% and 0% removal brushes) where the highest copepod abundances were observed. Further, evenness did not differ among brush treatments suggesting diversity responded to species richness. Rare species were more common on brushes with low bristle removal, that collected more copepods. The MacArthur-Wilson theory (1967) suggests that in an equilibrium community the number of species remains constant through time as a result of a balance between species immigration and extinction. Atilla and Fleeger (2000) showed that species composition changed over short periods of time on artificial substrates without reaching an equilibrium over a 2-month colonization period. It is unlikely that the number of copepod species colonizing brushes in this experiment reached equilibrium as predicted by MacArthur and Wilson's island biogeography theory.

The plastic bottle brushes used in this experiment appear to be excellent mimics of meso-scale attached filamentous structures such as branching algae and hydrozoan colonies. Meiofauna associated with natural or artificial non-traditional substrates such as submerged rocks, pier pilings are not well known. However, some of the individuals of this community have been shown to be an important part of the diet of fishes (McCall, 1992; Toepfer and Fleeger, 1995). These meso-scale substrates also serve as temporary habitats for meiofauna contributing to their dispersal. Meso-scale artificial substrates can be used as sampling tools to investigate this understudied yet potentially

important community. This study shows a clear interaction between colonization, habitat structure and flow; however, more information on variation in capture efficiency of passive particles with complexity of the substrates and measurement of emigration rate of the meiofaunal individuals from artificial substrates is necessary in order to fully understand the dynamics of colonization of meiofauna on structurally complex substrates.

# CHAPTER 5

# SUMMARY AND CONCLUSIONS

The majority of investigations on meiofaunal ecology have focused on sediment, macroalgal and seagrass habitats (Coull, 1999). Although the existence of a meiofaunal assemblage in the water column has been reported from studies using water samples and from fish dietary studies, its origin and ecological role has received relatively little attention. Meiofauna living on hard substrates have also been understudied. Knowledge on the ecology of these meiofaunal assemblages has been limited mainly due to the sampling difficulties. My dissertation has shown that an abundant, understudied meiofaunal community exists in estuaries that is highly capable of dispersal and colonizing artificial substrates. Several of the harpacticoid copepod species found in my study have previously been reported in meiofaunal studies from Louisiana (Fleeger, 1985) but three copepod species are reported here for the first time (Poecilostomatoid species, *Parategastes* sp., and *Pseudamphiascopsis* sp.) from the Gulf of Mexico. Also, the nematode assemblage of sediments and pier pilings was documented in detail, and many nematode genera were reported for the first time. Thus the use of artificial substrates has increased our knowledge of copepod and nematode assemblages.

In the first chapter, the results suggested that the length of time for colonization and the properties of the artificial substrate types should be carefully considered for studies using artificial substrates for pollution or diversity monitoring purposes. Collectors that are inexpensive, easy to manipulate, light in weight and have high structural complexity are recommended. Mesh collectors attained high meiofaunal net abundance (up to 20,000 ind $col^{-1}$) in two-week exposures. The probable sources of

meiofauna at my collecting site include seasonally abundant filamentous microalgae, hard substrates and sediment. The dynamics of colonization is a result of a complex interaction of emigration and immigration rates, and many other factors (such as flow and supply) will influence the abundance and diversity of meiofauna collected. Behavior is also likely to be important; copepods appear to have many immigration and emigration events causing high variation among collections, while nematodes appear to be slow colonists with lower or more constant emigration rates. Data suggest that diversity of artificial substrate meiofauna changes significantly with season and time of deployment, presumably as seasonal changes in the source faunal communities occur.

In chapter 3, submerged pier pilings were sampled for the first time revealing a taxonomically distinct and abundant (1200 ind 10 $cm^{-2}$) meiofaunal assemblage with anatomical similarities with phytal communities. Sediment and pier-piling assemblages were distinctly different faunastically. The colonizing assemblage on artificial substrates was found to have characteristics of both sediment and pier-piling meiofauna; however, the contribution of pier pilings to this assemblage exceeded that from the sediments. The presence of only certain nematode and copepod species suggests that individual taxa differ in their dispersing abilities. Sediment meiofauna found on artificial substrates are likely to be eroded from the sediment surface by flow. Pier pilings provide large habitable surface areas for meiofauna and also greatly contribute to the dispersing pool of meiofauna. However, not all submerged artificial or natural hard substrates, such as rubble or oyster reefs, were sampled and therefore the contribution of pier-piling meiofauna to artificial substrate colonization may have been overestimated.

Meiofaunal colonization of artificial substrates is strongly influenced by the structural complexity of the habitat and the interaction of flow with the physical structure of the habitat. My field investigations on abundance and diversity of meiofauna colonizing artificial substrates suggested that both abundance and adult copepod species diversity increased with decreasing bristle density and surface area. However, different taxa responded to different physical qualities of the habitats. While nematodes responded to bristle density, copepods responded to surface area suggesting taxon-specific behavior influences colonization. Adult copepod species diversity and number of species increased with both increasing surface area and bristle density. Colonization of artificial substrates occurred through the water column where hydrodynamic forces played an important role on meiofaunal dispersion and settlement. Laboratory fume studies performed at flow velocities similar to that of field showed that substrates with differing structural complexity levels interacted with flow differently. Flow velocities and turbulence intensities generally decreased with increasing bristle density. Bristle density also influenced transmissivity of the substrates. It is very difficult to describe the flow patterns within a brush and among its bristles; however, my data suggest that colonization is a function of capture and retention of meiofauna which were influenced by the configuration of the bristles of the brush and their interaction with flow as well as meiofaunal behavior.

This study shows that artificial substrates collect large numbers of water column meiofauna. Those meiofauna include free living forms eroded from hard substrates and sediments and a surprisingly high abundance of a commensal species

(Poecilostomatoida) probably associated with fouling epifauna. While plankton nets are not efficient in shallow waters and pump samples can be used only for short periods of time, artificial substrates sample water-column meiofauna over long time periods. This integration means that artificial substrates may provide a more representative collection of the taxa in the water column and enhance our ability to detect changes in the community over long and short periods of time. Copepod abundance is reported to exceed nematode abundance by over 10x in the water column (Walters, 1988). However, due to the differences in the emigration and immigration capabilities of nematodes and copepods, nematode abundances exceeded copepod abundances by 3x on artificial substrates in my study. Thus, artificial substrates appear to introduce bias and do not directly represent occurrences of meiofaunal assemblages in the water column. In addition, my suction sampling device proved to be a very useful sampling tool for hard substrates and could become the basis for extensive surveys of this understudied habitat. Artificial substrates have been promoted as simple, easy to use samplers that can be useful in biomonitoring studies and to detect differences in biodiversity. They clearly sample a unique portion of meiofaunal community in estuarine settings. If used with caution and appropriate experimental design (e.g., duration of deployment) they should be considered as another tool to better understand the complex faunal relationships and biodiversity in aquatic environments.

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# APPENDIX: LETTER OF PERMISSION

LOUISIANA STATE UNIVERSITY
AND AGRICULTURAL AND MECHANICAL COLLEGE
Department of Biological Sciences

September 13, 2000
Axel Ader
Blackwell Wissenshafts-Verlag
Kurfurstendamm 57
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Dear Mr. Ader,
I am writing to obtain copyright release to include my article entitled "Meiofaunal colonization of artificial substrates in an estuarine embayment", which was published by Marine Ecology P.S.Z.N.I. (Vol. 21(1) 69-83. 2000), in my Ph.D. dissertation. I need your written permission to present this article to Louisiana State University Graduate School. Thank you, in advance, for your time and consideration.

Sincerely,
Nazan Atilla

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Permission granted subject to
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Date: 25.09.00 Signature: A. Frantzke

# VITA

Nazan Atilla was born February 9, 1970, in Istanbul, Turkey. She graduated from Istanbul University in 1991 completing a bachelor of science degree in biology. As a sponsored student by the Turkish Ministry of Education, she came to the United States of America in 1992 to pursue a master's degree. She received her master of science degree in oceanography and coastal sciences at Louisiana State University in 1995. Immediately after completion of her master's degree, she joined the doctoral program at the Department of Zoology and Physiology. Presently, she is a candidate for the degree of Doctor of Philosophy at Department of Biological Sciences, which will be awarded spring 2001.

# DOCTORAL EXAMINATION AND DISSERTATION REPORT

**Candidate:** Nazan Atilla

**Major Field:** Zoology

**Title of Dissertation:** Meiofaunal Colonization of Artificial Substrates

**Approved:**

Major Professor and Chairman

Dean of the Graduate School

**EXAMINING COMMITTEE:**

**Date of Examination:**

November 6, 2000