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Factors affecting meiofaunal colonization and assemblage structure in marine soft sediments

by

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To my mom,
Colleen Ann Marshall,
for showing me the good life.

ABSTRACT

Meiofauna are an abundant, diverse and important component of the marine biota, however, much of their ecology has been neglected. Despite their high densities, meiofaunal abundance is often patchy. Meiofauna present in high numbers at one site will often be less abundant in seemingly similar adjacent sites. What factors govern this variability? How readily do these animals colonize new patches? How do various biological and environmental factors affect meiofaunal colonization rate and resulting assemblage structure?

The response of meiofauna to changes in abiotic factors, including sediment grain size, depth, exposure and distance from the ocean floor, was quite variable. Often one factor would affect certain taxa and not others. Even slight increases in depth resulted in drastic declines of harpacticoid copepods while nematodes were unaffected. Meiofauna were also fewer in sediments with large interstitial spaces. Some meiofauna were most abundant in sediments placed closer to the ocean floor. Other taxa colonized distant substrata as rapidly as they did substrate located closer to the ocean floor. This suggested differences between taxa in their rates of active dispersal.

The effects of macrofauna on meiofauna have been debated. In particular, how do clams affect the colonization and assemblage structure of meiofauna? Certain characteristics of clams were isolated and evaluated: feeding behaviour, bioturbation rate/depth and metabolic byproducts. Clams that caused the greatest meiofauna declines were shallow burrowing deposit-feeders. Constant disturbance to the upper sediment by these clams was likely responsible for meiofaunal impact. Conversely, suspension-

feeding clams that passed quickly to deeper sediment and remained stationary had little impact on meiofauna.

Finally, a survey of local marine nematodes added nine genera new to Canada and 24 genera new to British Columbia. A review was also compiled that shows nematodes and other meiofauna have been neglected for much of Canada. Although these small and abundant animals are quick to colonize even distant habitats they are quite sensitive to cues from the surrounding biotic and abiotic environment. This sensitivity combined with their ease of collection make meiofauna a valuable asset to any number of ecological investigations.

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CHAPTER 1.

GENERAL INTRODUCTION

Today, several hundred scientists are working to expand our knowledge on meiofauna from alpine lakes to the deep-sea floor, from tropical atolls to Antarctic sea ice. However, wide areas remain terra incognita in the field of meiobenthology.

-Giere, 1993

1.1 ECOLOGY OF MARINE ENVIRONMENTS

About 71% of our planet's surface is covered by oceans, which are subtended by a diverse array of benthic habitats ranging from rocky intertidal to muddy abyssal plains. The exceptionally diverse and often peculiar animals that live on and in the ocean floor have been subjects of human interest for millennia as food, sources of pharmaceuticals, and objects of beauty. From the more recent standpoint of scientific research, rocky-intertidal ecology has probably received the greatest amount of attention, and work by Robert Paine and others has provided information on how environmental and biological interactions structure rocky communities (Paine, 1969). Less frequently investigated has been the ecology of the ocean floor below the low-tide mark. This is primarily due to the logistical difficulties, high costs and effort associated with conducting research at depth.

However, given that approximately 65.5% of the Earth is covered by ocean that is deeper than 130m there is likely still much to learn about the ecology and biodiversity of subtidal marine sediments (Snelgrove, 1999).

1.2 THE MEIOFAUNA

The ocean floor is predominantly covered in soft sediments. These sediments are home to a large number of familiar organisms including a variety of clams, polychaete worms, crustaceans and other macrofauna (larger than 1 mm in size). Far less familiar are the microscopic animals referred to commonly as the "meiofauna". Meiofauna is the cross-phylum term given to small (63-1000 μm, based on the standardized mesh width of sieves) metazoan animals that inhabit interstitial spaces of nearly every type of sediment world-wide (Giere, 1993). The term meiofauna was coined by Mare (1942) and means "smaller-animals" because they were bigger than microfauna but smaller than macrofauna. Some animals including most nematodes and many species of copepods remain meiofauna for their entire lives while other animals such as some polychaetes and crustaceans are only meiofauna in the early stages of development, later growing into macrofauna. These groups are termed permanent and temporary meiofauna, respectively. Twenty-two of the 33 metazoan phyla include at least some meiofaunal representatives (Coull, 1988). The diets of meiofauna are variable between and within taxa. Marine nematodes will most commonly be predators, microvores, ciliate-feeders, deposit-feeders or epigrowth-feeders (Moens & Vincx, 1997) feeding on other meiofauna, algae, bacteria, ciliates or decomposing organic matter. Harpacticoid copepods are mainly detritus-feeders but some will also selectively feed on bacteria, protozoans and diatoms

(Giere, 2009). Meiofauna proliferate in virtually every aquatic environment capable of supporting life, from mosses growing atop mountains to marine sediment of the abyssal plains but are often overlooked due to their small size.

1.3 A HISTORY OF MEIOBENTHOLOGY

Literature pertaining to zoological investigations and detailed taxonomic descriptions of tiny benthic animals began to appear in the mid-19th century. Some of the earliest works were focused on kinorhynchs (Dujardin, 1851) and archiannelids (Giard, 1904). Early in the development of meiobenthology studies were focused on the biology of the individual taxon (Giere, 1993). The first ecological investigations took place much later and were aimed at studying the interactions within these minute communities. Initial advances were slow given the arduous task of sorting the animals from the sediment. As sampling methods improved the meiobenthos of a broader range of habitats were discovered. The exceptional abundance and morphological diversity of the animals inhabiting the interstitial spaces of aquatic sediments world-wide was becoming realized. Remane (1933) first coined the term "Sand-lückenfauna" later termed "interstitial fauna" by Nicholls (1935) and then "meiofauna" by Mare (1942). Remane was the first to recognize that the wide array of taxa inhabiting the interstitial spaces exhibited characteristics suited to interstitial living including small size and vermiform shape. Remane's initial work sparked interest first from other German scientists then from other parts of Europe (Giere, 1993). The first review on the ecology of marine benthos was completed by McIntyre (1969). The field of meiobenthology took longer to reach North America and was precipitated by early studies in the 1950's and 1960's conducted by

visiting European scientists including Wieser and Riedl (Giere, 1993). North America is now one of the centres of meiofauna research with investigations aimed primarily toward ecological studies. Work conducted by Coull (1973, 1985) on the Atlantic coast of the United States studied meiofaunal ecology using sophisticated experimental methods and long-term datasets. This drew the attention of many other North American marine biologists to meiofauna (Giere, 1993). The high abundance and species richness of meiofaunal communities combined with ease of collection appealed to ecologists. Today, scientists world-wide use meiofauna to address pressing ecological issues including ecosystem dynamics, climate change, anthropogenic impacts and habitat recovery (see for example Giere, 2009).

1.4 THE ROLES OF MARINE MEIOFAUNA IN BENTHIC ECOSYSTEMS

Studies of marine community ecology often do not look closely enough to include the benthic meiofauna. Because they are not visible to the naked eye it is easy to overlook meiofauna in favour of more obvious megafauna. However, these tiny benthic organisms play several important roles in the marine ecosystem. One of the first and most influential works describing the importance of meiofauna was by Gerlach (1971). He, and others since (including Giere (2009) and Warwick (1989)), discussed how marine meiofauna in some locations were equally or more important to certain ecological processes than neighbouring macrofauna. First, marine meiofauna often reach exceptional abundances in marine soft sediments ranging from 55 000 to over 100 000 specimens per m^2 (Wieser, 1960; McIntyre, 1969). Second, although the biomass of marine meiofauna is typically far lower than macrofauna (~ 3%), a higher percentage of meiofaunal biomass has been

recorded for brackish water, intertidal beaches and from the deep sea, where the biomass of each can be equal (Gerlach, 1971). Third, meiofauna have much higher respiration rates than macrofauna. Meiofauna consume oxygen at a rate of 200-2000 O_2/h/g versus 200-500 O_2/h/g for small macrofauna and 10-100 O_2/h/g for large macrofauna (Gerlach, 1971). Production and metabolic rates have been calculated from these respiration values. The high respiration rates of meiofauna compared to macrofauna indicate that meiofauna have a metabolic rate about five times larger than that of the macrobenthos. Stated differently, meiofauna will consume five times more energy than macrofauna of the same biomass (Giere, 1993). Thus, benthic productivity tends to be dominated by meiofauna in habitats where meio- and macrofaunal biomass is nearly equal. Generally, however, meiofauna will produce about one quarter of the total energetic budget of an average benthic marine biotype (Giere, 1993). Meiofauna are also exceptionally quick to colonize distant habitats and have a turnover rate much higher than most macrofauna (21 times higher for nematodes; Fenchel, 1978) making them especially useful for impact and recovery studies (McIntyre, 1964).

Furthermore, meiofauna play vital roles in nutrient cycling and pollutant metabolism (Gerlach, 1971; Giere, 1993; Snelgrove, 1999). They are also important as food for organisms at higher trophic levels. For example, harpacticoid copepods are a preferred food for many juvenile fish (Coull, 1990) and young shrimp will feed often voraciously on meiofauna (Nilsson et al, 1993). Despite the many roles meiofauna play in marine benthic ecosystems little experimental research has been conducted which documents specific biotic and abiotic factors that play important roles in structuring meiofaunal assemblages.

1.5 Factors affecting meiofaunal dispersal

A recurring topic in marine meiobenthology is the seemingly paradoxical ubiquity of taxa in completely divergent areas. Meiofauna are generally adapted to success in the interstices of sediment and not for long-distance dispersal. How then, do the same meiofaunal species often bridge oceans and occupy completely disjunct shores (Gerlach, 1977; Westheide, 1987)? More recently, through the use of molecular methods, species previously believed to be cosmopolitan or widespread have revealed complexes of morphologically similar species (Bhadury et al, 2008). However, molecular methods have reinforced the notion of global ubiquity for many other meiofaunal taxa suggesting some level of ongoing transoceanic genetic exchange (Giere, 2009; Westheide et al, 2003). Various dispersal modes have been proposed to account for the often widespread distribution patterns for many meiofauna. These include transportation through the water column (Palmer, 1988; Armonies, 1988), erosion/suspension (Palmer and Gust, 1985), emersion/suspension (Armonies, 1988) and by rafting on algal mats and floating debris (Hicks, 1988). Many of these proposed dispersal methods were likely involved in achieving the level of meiofaunal ubiquity we see today. However, actual experimental investigation of such dispersal modes has rarely been attempted and little is presently known about specific biotic and abiotic factors that most affect rates of dispersal and colonization.

1.6 Factors affecting meiofaunal colonization

Meiofauna are exceptionally quick to colonize new and often distant sediment but less is known about how various biotic and abiotic factors affect the rate and resulting assemblage structures of the new colonies. Depth has been investigated repeatedly for effects on meiofauna. Generally, meiofauna tend to decline in abundance with increasing oceanic depth (see for example Rowe, 1983; Thiel, 1983; Lampitt et al., 1986; Alongi, 1992; Vanhove et al., 2004; Baguley et al., 2006; Grove et al., 2006). However, nearly all studies have had a shallow starting depth of over 100 metres. How is meiofaunal colonization and assemblage structure of azoic sediment affected by a much shallower depth gradient? At what depths do meiofaunal assemblages begin to decline and are certain taxa more adversely affected than others?

Another recurring topic in meiobenthology has been the impact of macrofaunal animals on meiofauna. Ólafsson (2003) reviewed 77 studies that looked at the effects 44 macrofaunal species on the colonization and assemblage structure of various meiofaunal taxa. However, studies were highly variable with regard to the targeted disturbance and only a few attempted to investigate many types of disturbance from a given taxon simultaneously (e.g. burrowing, predation, biogenic structure, overall effects). Given this variation among studies, results were often inconclusive or contradictory. Ólafsson (2003) concluded that the disturbances caused by macrofauna are too variable among species to apply general theories. Instead, the potentially disruptive behaviours must be isolated and investigated individually. Once this is done certain generalizations regarding the effects of specific macrofaunal behaviours might be made.

1.7 THESIS GOALS

The aim of this thesis was to use both experimental and correlative approaches to investigate how specific biological and environmental factors affect meiobenthic assemblages. In Chapters 2 and 3 I examine how abiotic factors including depth, exposure, distance to new substrate and substrate porosity affect meiobenthic dispersal and colonization rates. Chapters 4 and 5 investigate the effects of clam bioturbation, predation and metabolic byproducts on meiobenthic colonization and assemblage structure. Finally, in Chapter 6 a survey of marine nematodes across a variety of intertidal and subtidal habitats in Trevor Channel was conducted. Also included in this chapter is a review of all current published records of Canadian marine nematodes. These investigations represent the first sub-tidal, experimental studies of marine meiofauna on the west coast of Canada.

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CHAPTER 2.

REVISITING THE MEIOFAUNA PARADOX: DISPERSAL AND COLONIZATION OF NEMATODES AND OTHER MEIOFAUNAL ORGANISMS IN LOW AND HIGH ENERGY ENVIRONMENTS[1]

2.1 INTRODUCTION

The marine benthic environment is home to an enormous diversity and abundance of meiofaunal organisms (metazoans passing through a sieve with a mesh of 1 mm and retained on a mesh of ca. 63 µm) (Snelgrove, 1999; Heip et al., 1985). Meiofauna are often the numerically dominant metazoans in marine environments ranging from abyssal plains and trenches (Tselepides & Lampadariou, 2004) to the muddy intertidal (Heip et al., 1985) and are often the first metazoans to colonize newly available sediments (Ullberg & Ólafsson, 2003). Many species are wide-spread or cosmopolitan (Coomans, 2000; Bhadury et al., 2008; Derycke et al., 2008) which is surprising given that benthic meiofaunal organisms typically do not have planktonic larval stages (Giere, 1993; Fenchel & Finlay 2004; Bhadury et al., 2008). Instead they have direct development or brooding of the early stages of young that, when ready, are released into nearby sediment as smaller versions of the adult. Considering these dispersal limitations the global ubiquity of meiofauna has been called a paradox (Giere, 1993). How have these small, benthic organisms with little mobility become cosmopolitan over such large geographic ranges?

Nematodes and post-larval harpacticoid copepods (referred to as harpacticoid copepods from this point forward) are generally the most abundant marine meiofaunal

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animals (Platt & Warwick, 1980; Heip et al., 1985). These two taxa reach their greatest abundances in fine-grained or muddy sediments. Heip et al. (1985) found that although marine nematode density was usually greater in finer sediments, species diversity was generally greater in coarser sediments. A shift in dominance from nematodes to harpacticoid copepods with larger grain size was observed by Coull (1970). Large numbers of harpacticoid nauplii are also encountered typically in sites with adult harpacticoids. Meiofaunal polychaetes, of which there are approximately 250 species, generally rank in the top four most abundant meiofauna (Giere, 1993). Unlike many larger macrofaunal polychaetes that release larvae into the water column (Qian, 1999) the meiofaunal polychaetes do not have planktonic trochophore larvae (Giere, 1993). Small amphipods, although often exceeding the upper meiofaunal size limits, can also be abundant and exhibit adaptations for a meiobenthic existence including small size and vermiform body (Giere, 1993).

Meiofaunal capacity for active dispersal by crawling or swimming is generally low but varies between taxa (Sterrer, 1973; Gerlach, 1977; Savidge & Taghon, 1988; Ólafsson, 2003). Although nematodes have been collected from plankton samples (Hagerman & Rieger, 1981; Sibert, 1981) and marine snow (Shanks & Walters, 1997), they are poor swimmers (Fegley, 1985) and likely become suspended in the water column via external forces (water currents or bioturbation), as is assumed for most meiofaunal taxa (Hagerman & Rieger, 1981; Mott & Harrison, 1983; Fleeger et al., 1984; Fegley, 1985; Armonies, 1988; Palmer, 1988; Bertelsen, 1998; Powers, 1998; Fonseca-Genevois et al., 2006). Many harpacticoid copepods, however, are much better active dispersers than nematodes (Widbom, 1983; Ólafsson & Moore, 1990; 1992) and occasionally enter

the water column under their own power (Alldredge & King, 1980; 1985; Bell et al., 1988; Kurdziel and Bell, 1992; Walters and Bell, 1994; Teasdale et al., 2004). Fonseca-Genevois et al. (2006) found that the colonization of azoic plates suspended above the ocean floor was faster for harpacticoids than for nematodes, which relied more heavily on periodic upwelling events for dispersal. Remarkably, Kurdziel and Bell (1992) found that sea-grasses positioned as high as 20 m away from potential harpacticoid colonists reached background densities after only 2 days. However, with the exception of some harpacticoids, most meiofauna appear capable of only limited active dispersal into the water column and their presence there is rare compared to their high densities in sediment (Sibert, 1981; Ullberg & Ólafsson, 2003).

Once in the water column, meiofaunal organisms may be carried long distances by oceanic currents, which are believed to be of crucial importance to long-range dispersal of benthic meiofauna including juvenile polychaetes (Gerlach, 1977; Hagerman and Rieger, 1981; Palmer & Gust, 1985; Butman, 1987; Derycke et al., 2007). Epibenthic harpacticoids and nematodes are more easily dispersed by currents given their typical position on the surface of sediments (Fleeger et al., 1984) while species residing deeper in the sediment are less likely to become suspended and transported passively. In habitats where currents are not strong enough to suspend meiofaunal animals into the water column, colonization of azoic sediments is much slower and may be limited to the active dispersal capacities of the meiofauna (Alldredge & King, 1980; 1985; Thistle, 1980; Alongi et al., 1983; Chandler & Fleeger, 1983; Sherman et al., 1983; Widbom, 1983; Walters and Bell, 1986; DePatra & Levin, 1989; Ólafsson & Moore, 1990; 1992; Aarnio

& Bonsdorff, 1992; Bonsdorff, 1992; Vriser, 1998) or by the bioturbation of larger animals (Ullberg & Ólafsson, 2003).

Although sediment grain size, water currents and distance to the new habitat have all been found to affect dispersal and colonization of new substrates by meiofauna, these factors have rarely been studied simultaneously to determine which most limits meiofaunal colonization. Our first aim for this study was to examine meiofaunal colonization rates of coarse and fine azoic sediment suspended at increasing distances above the ocean floor in a low energy environment. Given relative rates of active dispersal we predicted that harpacticoid copepods would colonize nearby habitats faster and more abundantly than the slower dispersing nematodes and that colonization of the most distant sediment will be slowest for all meiofaunal taxa. Our second aim was to survey the occurrences of meiofaunal organisms in the water column by simultaneously sampling plankton at 1 m intervals above the ocean floor (from 0.5-6.5 m) in several low and high energy environments.

2.2 MATERIALS AND METHODS

2.2.1 The study site

Field studies were conducted at the Bamfield Marine Sciences Centre on Vancouver Island, British Columbia, Canada (48^{o} 49’ 50 N; 125^{o} 07’ 56 W)(Fig. 2-1). The sediment colonization study was run from 18 October to 28 November 2005 inside a protected inlet at a maximum depth of 12 m. The plankton surveys were conducted from 18-20 July 2006 inside and outside three sheltered inlets at a maximum depth of 8 m.

2.2.2 Part One: Colonization rates of coarse and fine azoic sediment suspended at different heights above the ocean floor in a low energy environment

A PVC grid was constructed and suspended 4 m above the ocean floor (12 m depth, Fig. 2-2b). Eighteen ropes of three different lengths were hung from the grid: six each of 3 m, 2 m and 1 m lengths. Two rectangular cages (8 x 6 x 4 cm) containing either fine gravel (grain size 1-5 mm retained by a 1mm plastic mesh) or coarse gravel (grain size 6-10 mm retained by a 5 mm plastic mesh) were attached to the ends of each rope hanging from the suspended grid (Fig. 2-2a). Sediment was made azoic by rinsing thoroughly with hot fresh water (80^{o} C) and then freezing for 48 hours at -20^{o} C. Samples of each sediment type were subsequently investigated and confirmed to be free of any residual animals. The sediment cages were suspended from above rather than being tied to the ocean floor to eliminate the possibility of meiofauna creeping up the ropes (Gerlach, 1977). Half of the sediment cages were carefully collected in sealed containers by SCUBA divers (3 cages from each rope length) after 21 days and the second half after 42 days. Video footage of the study apparatus and collection procedure are available as electronic supplementary materials from The University of Alberta, the author or online: www.ualberta.ca/~boeckner . The sediment below the study apparatus was primarily mud littered with shell and woody debris and was haphazardly core sampled three times at the end of the study. The cores consisted of 5 cc of sediment and were taken using a 10 cc plastic syringe cylinder (1.5 cm diameter, 8 cm height). Nematodes from these cores were identified and compared to those that colonized the baskets above.

2.2.3 Part Two: Surveying vertical distribution of meiofauna in the water column

Six sites were chosen based on exposure level and associated intensity of water movement: 3 protected sites situated inside sheltered inlets and 3 exposed sites in the unprotected channel (Fig. 2-1). The ocean floor at each of the six sites was typified by fine and silty sediment littered with shell and woody debris. We fabricated a plankton-collecting device (PCD) to simultaneously collect plankton samples from 0.5 m, 1.5 m, 2.5 m, 3.5 m, 4.5 m, 5.5 m and 6.5 m heights above the sea floor (Fig. 2-2c). At each of the six sites the PCD was held vertically in the water column by two divers, one at the bottom and one at the top. Each of the seven plankton samplers attached to the device consisted of a 10 cm diameter PVC cylinder with a 53 µm Nitex® net secured with elastic bands over one end. The other end of each cylinder was kept sealed with a PVC cap during deployment to prevent plankton entering until the PCD was in the correct position in the water column. Once in position at a depth of 10 m the caps were removed from each of the seven plankton samplers and the PCD was pushed through the water column along a pre-laid transect-line for 50 m (maintaining a maximum depth of 10 m). It took approximately 10 minutes at each of the sites for the PCD to travel the entire 50 m. At the end of the transect the two divers re-capped all of the plankton samplers and the entire device was carefully hauled out of the water and into the boat where the Nitex nets were removed, bagged and fixed in 8% formalin.

2.2.4 Processing and analysis of meiofauna

Samples from the sediment colonization study were preserved in 8% formalin. Meiofauna were isolated from sediments first by sieving through a 1 mm mesh and then via LUDOX flotation (See Warwick et al., 1998 for description). Animals were sorted into broad taxonomic/life-history groups under a stereo microscope (25 X). Nematodes were slowly processed to glycerin (Seinhorst, 1959), slide mounted and identified to genus under DIC and phase-contrast lighting using several taxonomic guides (Warwick et al., 1998; Wieser, 1954).

For the colonization study, differences in numbers of the numerically dominant groups of meiofauna (nematodes, post-larval harpacticoid copepods, crustacean nauplii and polychaetes) between sediment and height treatments and over time were investigated using 2 two-way ANOVAs (one for each sediment type, abundance data was log+1 transformed to improve normality) and Tukey's Post Hoc Tests (SPSS 13.0 for Windows). A series of paired t-tests were also conducted to investigate differences in abundances of animals colonizing the coarse and fine grained sediment baskets at the end of each line (SPSS 13.0 for Windows). For the plankton study, abundances of meiofauna between the various water column heights and exposure classes were also analyzed for the plankton collection experiment using ANOVA (SPSS 13.0 for Windows).

2.3 RESULTS

2.3.1 Part One: Colonization rates of coarse and fine azoic sediment suspended at varying heights above the ocean floor in a low energy environment

Nearly 10 000 animals colonized the sediment cages over the duration of the study (Table 2-1). Harpacticoid copepods accounted for 85% of all individuals sorted. Nauplius larvae and nematodes were the second and third most abundant taxa, respectively, followed by polychaetes and turbellarian flatworms. Euphausids, juvenile bivalves and halacarid mites were slowest to colonize and were the least abundant taxa. Although nauplii and some polychaete larvae are typically planktonic and are often found in the water column they are included here as meiofauna given that they colonized the sediment within the cages. Six nematode genera were identified from the background sediment collected below the baskets (Table 2-2).

Harpacticoid copepod abundance declined between weeks 3 and 6 in the fine sediment treatments ($DF:1, F=20.12, P=0.001$) but increased from week 3 to 6 in the coarse sediment treatments ($DF:1, F=13.46, P=0.003$, Fig. 2-3a and b. However, copepod abundance was lower in the coarse grain treatments throughout the study (3 weeks: $DF:8, t=9.219, P<0.0001$; 6 weeks: $DF:8, t=3.94, P=0.004$; Fig. 2-4) and it took more time for copepods to become abundant compared to the fine grain sediment. There was no difference in numbers of copepods colonizing substrate cages at different heights in the water column for the fine sediment treatments ($DF:2, F=2.295, P=0.143$). However, in the coarse sediment treatments copepods were faster to colonize sediment cages lower in the water column than those farther from the ocean floor ($DF:2, F=4.528, P=0.034$). Nauplii showed the opposite trend to adult harpacticoid copepods with regard to colonization time and sediment size (Fig. 2-3c and d). Nauplii abundance in fine sediment was greatest after 6 weeks ($DF:1, F=4.773, P=0.049$), but was greatest after 3 weeks in the coarse sediment ($DF:1, F=34.897, P<0.001$). Overall nauplii abundance was initially

greater in the coarse grained sediment but by the end of the study nauplii were most abundant in fine sediment treatments (3 weeks: DF:8, t=-5.688, P=0.0005; 6 weeks: DF:8, t=2.684, P=0.028; Fig. 2-4). There were no significant differences in nauplii abundance between the different height treatments for both the fine and coarse sediment treatments (DF:2, F=3.459, P=0.065 and DF:2, F=1.721, P=0.220, respectively).

Nematode abundance across height treatments tended to increase over time for both the fine and coarse sediments but was significant only for the fine sediment (DF:1, F=8.607, P=0.013 for fine, DF:1, F=4.224, P=0.062 for coarse)(Fig. 2-3e and f). Overall nematode abundance was greater in the fine sediment treatments versus the coarse sediment treatments although this relationship was only significant after 6 weeks (3 weeks: DF:8, t=1.695, P=0.13; 6 weeks: DF:8, t=3.957, P=0.004; Fig. 2-4). Like the nauplii, there were no significant differences in nematode abundances among the three different height treatments for both the fine and coarse sediment treatments (DF:2, F=0.181, P=0.837 and DF:2, F=1.5, P=0.262, respectively). Nematodes were as quick after three weeks to colonize treatments farther from the ocean floor as they were to colonize those hanging lower in the water column.

Thirty nematode genera colonized the sediment baskets over the six week study (Only 262 of the 426 specimens could be identified due to either poor condition or loss of specimens during processing, Table 2-2). After 3 weeks, the genera represented by 10 or more individuals were *Neochromadora* (N=19), *Oncholaimus* (N=17) and *Paracanthonchus* (N=13); after 6 weeks, the genera with most individuals were *Prochromadorella* (N=33), *Oncholaimus* (N=28), *Paracanthonchus* (N=23), *Hypodontolaimus* (N=18), *Draconema* (N=15), *Anticoma* (N=11) and *Theristus* (N=10).

Members of the chromadorids are epigrowth feeders and comprised 56% and 32 % of the nematode fauna after 3 weeks and 6 weeks respectively (Table 2-2). *Neochromadora* had the greatest abundance after 3 weeks (primarily in fine grained treatments) but was not found again in any of the sediment baskets after six weeks. Conversely, *Prochromadorella* had the greatest abundances of all nematode genera after 6 weeks but was not found in any baskets at 3 weeks. *Oncholaimus* and *Paracanthonchus* were found in relatively large numbers after both 3 and 6 weeks. Only 2 of the 6 nematode genera identified from the background sediment samples were also found colonizing the suspended baskets (Table 2-2).

Amphipod abundance showed no significant relationship with colonization time for either the fine or coarse sediment treatments (DF:1, F=0.025, P=0.877 and DF:1, F=1.665, P=0.221, respectively; Fig. 2-3g and h), nor did it differ between sediment grain sizes (3 weeks: DF:8, t=0.00, P=1.00; 6 weeks: DF:8, t=1.437, P=0.189; Fig. 2-4) or with respect to distance of the substrate from the ocean floor for either the fine or the coarse sediment treatments (DF:2, F=0.259, P=0.776 and DF:2, F=0.094, P=0.911, respectively). Thus, as for the nauplii and nematodes, amphipod colonization appears not to have been hampered by increasing distance from the ocean floor.

Polychaete abundance did not change significantly over time for either the fine or coarse sediment treatments (DF:1, F=0.389, P=0.544 and DF:1, F=1.831, P=0.201, respectively; Fig. 2-3i and j). Overall polychaete abundance was greater in the fine sediment treatments versus the coarse sediment treatments although this relationship was only significant after 6 weeks (3 weeks: DF:8, t=1.302, P=0.229; 6 weeks: DF:8, t=3.368, P=0.010; Fig. 2-4). Polychaetes from the fine sediment were more abundant in the lower-

hanging treatments than in cages suspended higher in the water column (DF:2, F=7.924, P=0.006). This was not found for polychaetes colonizing the coarse sediment treatments (DF:2, F=0.802, P=0.471) which had overall lower abundances compared to the fine sediment regardless height in the water column.

2.3.2 Part Two: Surveying vertical distribution of meiofauna in the water column

Each cylinder of the plankton-collecting device sieved approximately 400 000 cubic centimeters of sea water along the 50 m transect line. Planktonic calanoid copepods and various types of crustacean larvae vastly dominated the taxa collected by the PCD and are not considered further in this study of benthic meiofauna. Harpacticoid copepods (154, approx. 1/2600 cc of seawater), polychaetes (93, approx. 1/4300 cc of seawater) and nematodes (69, approx. 1/5800 cc of seawater) were far less abundant in the plankton samples (Table 2-3). Cladocerans (104, approx. 1/3850 cc of seawater) were also encountered in similar abundances as the meiofauna and are included in the study as a planktonic comparison. Fourteen nematode genera were identified from those collected in the water column (Only 39 of the 69 specimens could be identified due to poor condition, Table 2-4). Over half of them (52%) belong to the Chromadoridae, a family comprised of epigrowth feeders. There did not appear to be a predominance of any particular genus as most were represented by one or two specimens.

Harpacticoid copepods, although present at every height sampled, tended to occur most abundantly in plankton samples collected closest to the ocean floor (Fig. 2-5) although this difference was not significant (DF:6, F=2.280, P=0.060). Nematodes were also present at least once per height sampled (across exposure classes) and abundances

were significantly greater in the samples closer to the ocean floor than those high in the water column (DF:6, F=3.013, P=0.018). Polychaetes were also present at least once per height treatment (across exposure classes) and did not show any relationship between abundance and height in the water column (DF:6, F=1.748, P=0.141). Cladocerans were not found in the samples closest to the ocean floor and instead showed a greater abundance in samples higher in the water column (DF:6, F=2.656, P=0.033) as might be expected for typically planktonic animals. There was no significant difference in abundance of harpacticoid copepods (DF:1, F=2.082, P=0.157), nematodes (DF:1, F=0.247, P=0.622) or cladocerans (DF:1, F=0.182, P=0.672) between the exposed and protected sample sites although nematodes and harpacticoids were generally more abundant lower in the water column of protected versus exposed sites (Fig. 2-5). Polychaetes were more abundant in plankton samples collected from protected sites than from more exposed sites (DF:1, F=14.43, P=0.001).

2.4 Discussion

2.4.1 Part One: Colonization rates of coarse and fine azoic sediment suspended at varying heights above the ocean floor in a low energy environment

Colonization in a protected site: The sediment baskets were quickly colonized by a variety of meiofauna despite the relatively sheltered study location and presumably low rates of suspension of benthic materials by currents. Harpacticoid copepods were found in the greatest abundances followed by nauplii, nematodes, amphipods and polychaetes. Previous work on colonization by meiofauna has also shown that copepods establish

fastest and in the greatest numbers (e.g. Thistle, 1980; Alongi et al., 1983; Chandler & Fleeger, 1983; Aarnio & Bonsdorff, 1992). In their colonization study Fonseca-Genevois et al. (2006) found that copepods quickly established after only one day followed by nematodes, turbellarians, ostracods and other meiofaunal taxa.

Effect of increasing distance from ocean floor: It was surprising to find that nematodes, usually considered poor active dispersers, had attained their greatest abundances in cages farthest from the ocean floor. Even by the end of the study nematodes were as or more abundant in baskets higher up in the water column than in those further down. The nematode genera found most abundantly throughout the study showed no obvious relationship to sediment height but instead were spread evenly across height treatments. There were however many less abundant genera that were absent from either the high or low treatments. Nematodes that were never encountered in the highest sediment treatments were *Acanthonchus, Anticoma*, *Araeolaimus*, *Symplocostoma* and the species *Sabatieria hilarula*. Conversely, nematodes that were never found in the lowest sediment treatments were *Hypodontolaimus*, *Chromadorita*, *Ptycholaimellus*, *Axonolaimus*, *Deontostoma*, *Desmosolex* and *Diplolaimella*. The occurrence of such an array of nematode genera in only the higher treatments is striking and suggests that these nematodes were not arriving via active vertical migration. Furthermore, we found only two genera in common between the baskets and background sediment which supports the notion that nematodes were not arriving solely from below. It is more probable that these colonizers arrived after becoming suspended by some external force. Fonseca-Genevois et al. (Brazil, 2006) also reported that *Acanthonchus, Chromadorina, Oncholaimus*,

Ptycholaimellus and *Viscosia* colonized new habitats suspended above the ocean floor and attributed their arrival to periodic upwelling events. Despite the protected nature of our study site, it was still subjected to regular tidal cycles which may have carried nematodes from exposed environments outside the inlet to the sediment cages. The inlet also experienced high recreational boat traffic throughout the experiment which may also have contributed to nematode passive dispersal. Finally, it is important to recognize that in addition to colonization over time, reproduction by early arriving individuals may have also contributed to increases in abundances over the six week study.

Similarly, abundance of nauplii and small amphipods showed no relationship to distance from the ocean floor. They were also likely transported passively to the sediment baskets via external forces. In contrast, harpacticoid copepods and polychaetes colonized the three height treatments in a manner more indicative of active vertical dispersal from the sediment below. Juvenile polychaetes were found in greatest abundance in the fine sediment treatments closest to the ocean floor. They remained scarce in the high hanging treatments throughout the study. This suggests that juvenile polychaetes likely arrived at the low hanging treatments via short-range active dispersal. Although only significant in the coarse sediment, by the end of the study harpacticoids also tended to be more abundant in the low-hanging treatments. It is likely that many harpacticoid copepods, capable of actively departing the sediment (Alldredge & King, 1980; 1985; Bell et al., 1988; Kurdziel and Bell, 1992; Walters and Bell, 1994; Teasdale et al., 2004), arrived at the baskets under their own power.

Effect of grain size: Sediment size was an important factor affecting meiofaunal colonization and/or establishment. Abundances of copepods, nematodes and juvenile polychaetes were lower in the coarse than the fine sediments throughout the study. Whether these taxa actively chose fine over coarse gravel as demonstrated by Ullberg and Olafsson (2003) or were simply not retained by the larger interstitial spaces of the coarse sediment is uncertain. Veit-Köhler (2005) also found harpacticoid abundances to be greatest in fine-grained sediments, although total organic matter rather than grain size *per se* was considered the limiting factor. However, there is a point at which sediment becomes too fine for copepods as interstitial spaces become too small or clogged with silt. Reports have shown that copepod abundance peaks in sandy sediment (0.5-1.5 mm grain size) but declines sharply as mud/silt content increases (Wigley & McIntyre, 1964; Challis, 1969). The fine sediment cages in our study became lightly fouled with silt and other material over the duration of the study (visual inspection upon collection). This might explain the early and abundant colonization by copepods of the clean, fine-sediment followed by a decline in overall abundance as the interstitial spaces became clogged. Conversely, siltation may have contributed to the increase in nematodes in the fine sediment cages over the duration of the study as nematode abundance tends to be greatest in fine to muddy sediments (Heip et al., 1985). Although nematode density tends to be greater in finer sediments, greater diversities have been recorded in coarse sediments (Heip et al., 1985). We found no such pattern in this study. Instead, seven genera were found only in fine sediment, another seven only in coarse sediment, while the remaining fifteen genera were found in both fine and coarse sediment. Few studies have investigated colonization preferences by polychaete larvae, and those that have

mention little about effects of sediment size. Bhaud (1990) reported that larvae of a terebellid polychaete settled in the presence of sediment fine enough to be manipulated and used in tube building. However we could find no other reports of polychaetes reaching greater abundances in fine versus coarse sediment. Finally, although we studied the effects of distance, time and sediment grain size independently, it is likely that these factors interact in nature to influence meiofaunal colonization of new sediments.

2.4.2 Part Two: Surveying vertical distribution of meiofauna in the water column

Vertical distribution: Harpacticoid copepods, nematodes and juvenile polychaetes, though meiofauna and typical within sediment, were encountered throughout the water column. Harpacticoids were most abundant and present in all samples. Nematodes and juvenile polychaetes were also found at every height sampled but their numbers were far fewer than the harpacticoids. Both nematode and harpacticoid copepod abundance tended to decline the higher the samples were collected in the water column. This was not surprising given that these taxa are almost exclusively benthic. Even though some meiofauna are capable of limited active dispersal, passive suspension via water currents or bioturbation likely caused epifaunal and shallow infaunal meiofauna to arrive in the water column. With the exception of the chromadorid nematodes *Neochromadora* and *Prochromadorella,* which were found in slightly greater abundances, there appeared to be no predominance of particular nematode genera in the water column. These genera and *Oncholaimus sp*. are known to occur in the upper two cm of sediment (see for example Sharma & Webster, 1983) and thus are more likely to be suspended in the water column

by turbulence than nematodes that reside deeper in the sediment. Gobin & Warwick (2006) found chromadorids, cyatholaimids and microlaimids to be most successful in colonizing new substrates. Abundance of juvenile polychaetes, however, did not vary with position of the sampler in the water column. Instead polychaetes were found fairly evenly across all height samples in the protected site. In our basket-colonization study we found juvenile polychaetes abundant only close to the sediment in the protected site. Perhaps polychaetes extend higher into the water column in the summer (plankton study) than in the fall (basket study) which would account for this discrepancy.

Exposed versus protected: It has been frequently suggested that meiofauna depend on external forces to become suspended in the water column and carried to distant habitats (Hagerman & Rieger, 1981; Mott & Harrison, 1983; Fleeger et al., 1984; Fegley, 1985; Armonies, 1988; Palmer, 1988; Bertelsen, 1998; Powers, 1998). One would thus expect to encounter more meiofauna in the water column of high energy environments than of more protected ones. However, we found almost no difference between the abundance of meiofauna collected from the exposed and the protected sites. The one exception was a greater abundance of juvenile polychaetes in the protected sites. Perhaps the levels of exposure were too similar to elicit a difference in suspended meiofauna. The tides may also cause sufficient mixing to disperse meiofauna evenly throughout both exposure classes. Whatever the cause, this study did not find evidence for more abundant suspended meiofauna in higher energy environments.

2.5 Conclusion

In less exposed habitats the transport of meiofauna via water currents is likely enhanced by taxa that are able to actively enter the water column. Once in the water column even relatively small currents can transport the animals to distant habitats. However, for how long and over what distance can these benthic organisms remain suspended in the water column? Is there evidence of meiofauna in the water column of the open ocean? How long can meiofauna live suspended and on what do they subsist? Answers to these questions may help further our understanding of how these small benthic animals have reached their current levels of global ubiquity.

Table 2-1. Abundances of fauna that colonized the sediment baskets in fall 2005 (summed across all height and grain treatments).

Taxon	Week 3	Week 6	Total
harpacticoid copepods	4816	3633	8449
nauplius larvae	367	192	559
nematodes	135	291	426
amphipods	146	114	260
polychaetes	69	58	127
turbellarian flatworms	44	59	103
euphausids	4	7	11
juvenile bivalves	0	6	6
halacarid mites	0	3	3

Table 2-2. Abundances of nematode genera that colonized the sediment baskets in fall 2005. A large number of specimens were damaged, lost during processing for slide-mounting, or were otherwise unidentifiable and are not listed here. The abundance of each nematode genus represented in samples of background sediment is given in parentheses following the genus name.

	3 Weeks																		6 Weeks															
	Low (1 m)						Middle (2 m)						High (3 m)						Low (1 m)						Middle (2 m)						High (3 m)			
	Fine			Coarse			Fine			Coarse			Fine			Coarse			Fine			Coarse			Fine			Coarse			Fine			Coarse	
ENOPLEA																																		
Phanodermatidae																																		
Phanoderma												1																						
Anticomidae																																		
Anticooma	1																		1	1		1		2		2	1	3						
Leptosomatidae																																		
Deontostoma																															1			
Thoracostoma																			1				1							1				
Oncholaimidae																																		
Oncholaimus (1)	2			2			1		3	2	1	1	2	1	1	1				1		2		1	2	5		3	2	8	2		1		1
Viscosia (1)						1											2		1			1		1		1	2				1		1		1
Enchelidiidae																																		
Eurystomina																			3					1	1	1					1				2
Symplocostoma						1						1																							
Rhabdomemaniidae																																		
Rhabdodemania																								1										
CHROMADORIDA																																		
Siphonolaimidae																																		
Siphonolaimus (1)																																		
Axonolaimidae																																		
Ascolaimus						1	1	2			1							3																	
Axonolaimus																																		1
Desmoscolecidae																																		
Desmoscolex																															1			
Diplopeltidae																																		

Araeolaimus																			1		1				1											
Draconamatodae																																			
Draconema													1					1		1		2	2		2		1	1	2	1	1	1		
Epsilonematidea																																			
Epsilonema																					1		1							1		1		
Chromadoridae																																			
Acanthonchus	1						2				1																								
Actinonema											1																								
Chromadora (3)																																			
Chromadorina	1												2					2																	
Chromadorita													1	3																					
Dichromadora (1)																																			
Hypodontolaimus																									1			11	6						
Neochromadora	2	1	2				4	2	2			1	3	1					1																
Parapinnanema											1																								
Prochromadorella																			3	6			1	1	4	3		2		4	1	2	1	2	3
Ptycholaimellus													2																						
Cyantholaimidae																																			
Paracanthonchus					1	1	2			2	1		3			1	2		2	1	1			1	1	2			4	8		1			2
Desmodoridae																																			
Metachromadora																									1										
MONHYSTERIDA																																			
Xyalidae																																			
Diplolaimella																													1						
Theristus														3				1	2	1						2			2		2	1			
AREOLAIMIDA																																			
Axonolaimidae																																			
Axonolaimus (1)																																			
Comesomatidae																																			
Sabatieria hilarula	1																																		
Aegialoalaimidae																																			
Aegiolaimus																				2													1		

Table 2-3. Fauna from the plankton samples collected in the summer of 2006 excluding highly abundant normally planktonic animals (e.g. calanoid copepods and crustacean larval stages). Damaged and otherwise unidentifiable nematodes are not listed here.

	Protected	Exposed	Total
harpacticoids	86	68	154
polychaetes	78	15	93
nematodes	45	24	69

Table 2-4. Abundances of nematode genera from the plankton collected in summer of 2006. Heights represent plankton collectors positioned at one m intervals from 0.5-6.5 m above the ocean floor. Exposed locations are denoted with an "E" while protected sites are indicated by "P". Only plankton-samples that yielded nematodes are listed here. See fig. 2-1 for location of study sites. Damaged, missing and otherwise unidentifiable nematodes are not listed here.

Site	Height	E/P	**ENOPLEA**	Actinolaimidae	*Anticoma*	Oxystominidae	*Halailaimus*	Oncholaimidae	*Viscosia*	*Viscosia carnleyensis*	Trefusiidae	*Trefusia*	**CHROMADORIDA**	*Chromadorina*	*Chromadorina laeta*	*Neochromadora*	*Parapinnanema*	*Prochromadorella neapolitana*	*Spilophorella*	Desmodoridae	*Desmodora*	**MONHYSTERIDA**	Xyalidae	*Daptonema*	*Theristus*	**AREOLAMIDA**	Axonolaimidae	*Odontophora*	Comesomatidae	*Sabatieria hilarula*
E3	0.5	E															1		2		1				1					1
E3	1.5	E														1														
E2	2.5	E												1																
E2	4.5	E										1																		
E1	5.5	E															1													
P1	1.5	P												2																
P1	6.5	P														1														
P3	1.5	P							1	1																				
P3	2.5	P		1																										
P3	4.5	P												1																
P3	5.5	P		1																										
P2	0.5	P													1	9		1	2					1				1		1
P2	1.5	P			1		1							2																

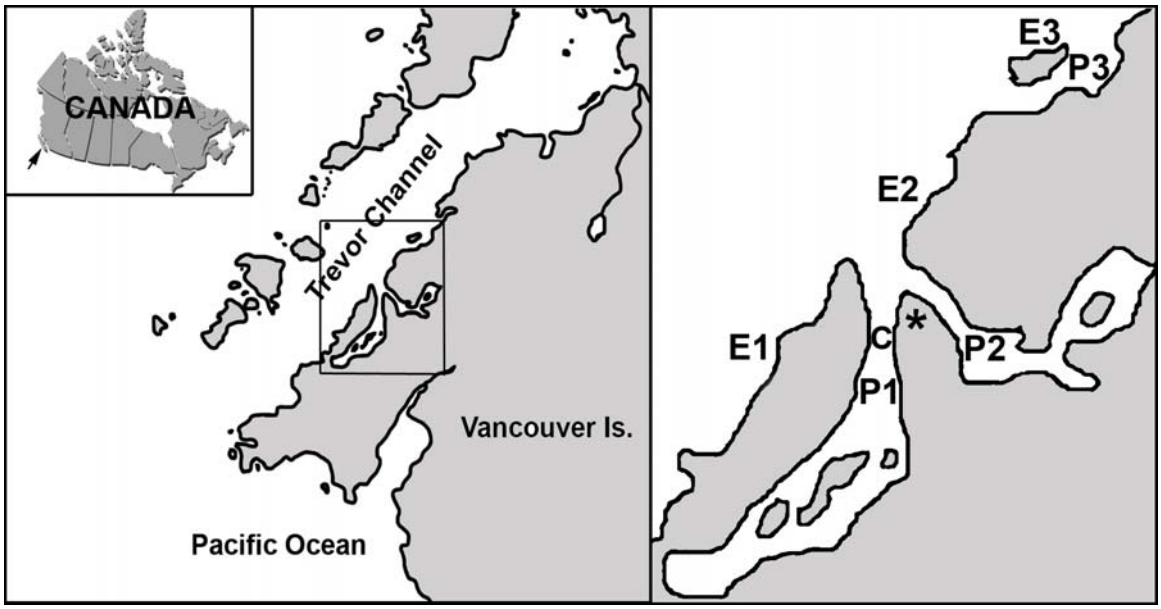

Fig. 2-1. Map showing location of study sites on Vancouver Island, British Columbia, Canada. Exposed plankton collection sites are denoted by "E" and protected sites by "P". Sediment colonization study location denoted by "C". Bamfield Marine Sciences Centre represented by the asterisk (*). Site names: E1, Scott's Bay; E2, Goby Town; E3, Dixon Out; P1, Bamfield Inlet; P2, Grappler Inlet; P3, Dixon In.

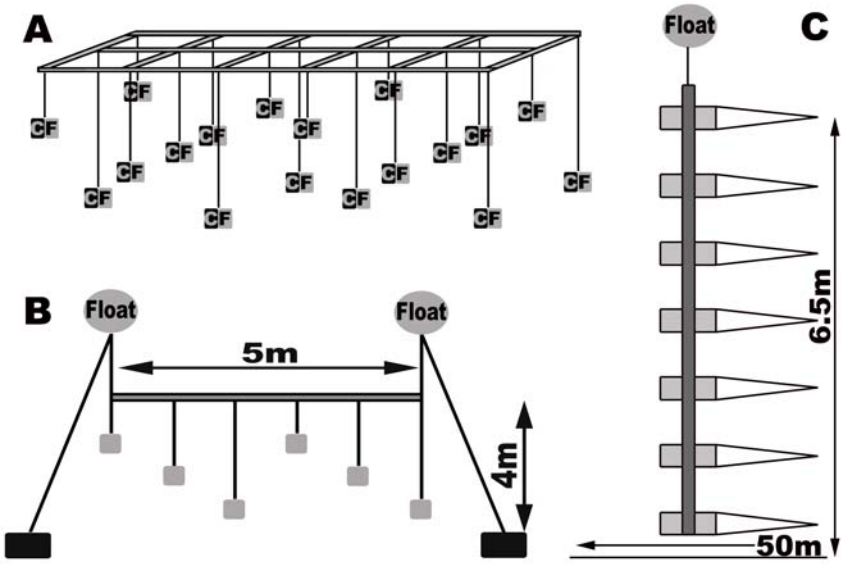

Fig. 2-2. Sediment colonization grid showing A) arrangement of height / grain size treatments (C = coarse grain, F = fine grain) and B) method of suspending the grid above the ocean floor. C) Plankton collection device with seven plankton nets.

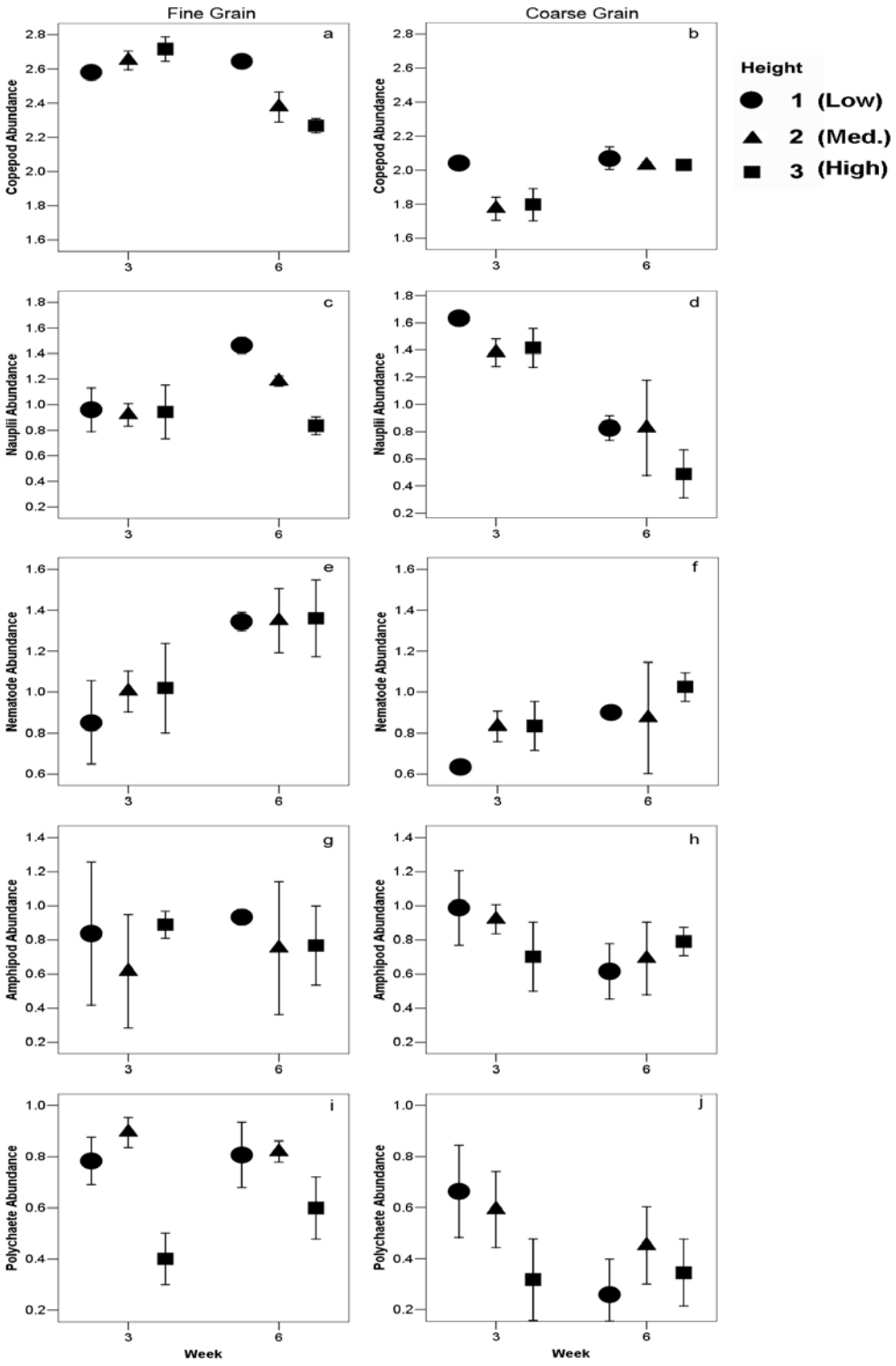

Fig. 2-3. Mean abundances of the five taxa that colonized the sediment baskets in the greatest densities (+/- 1 Standard Error, log+1 transformed) between the two colonization times (3 and 6 weeks), 3 height treatments (N=3) and two sediment grain sizes (fine and coarse).

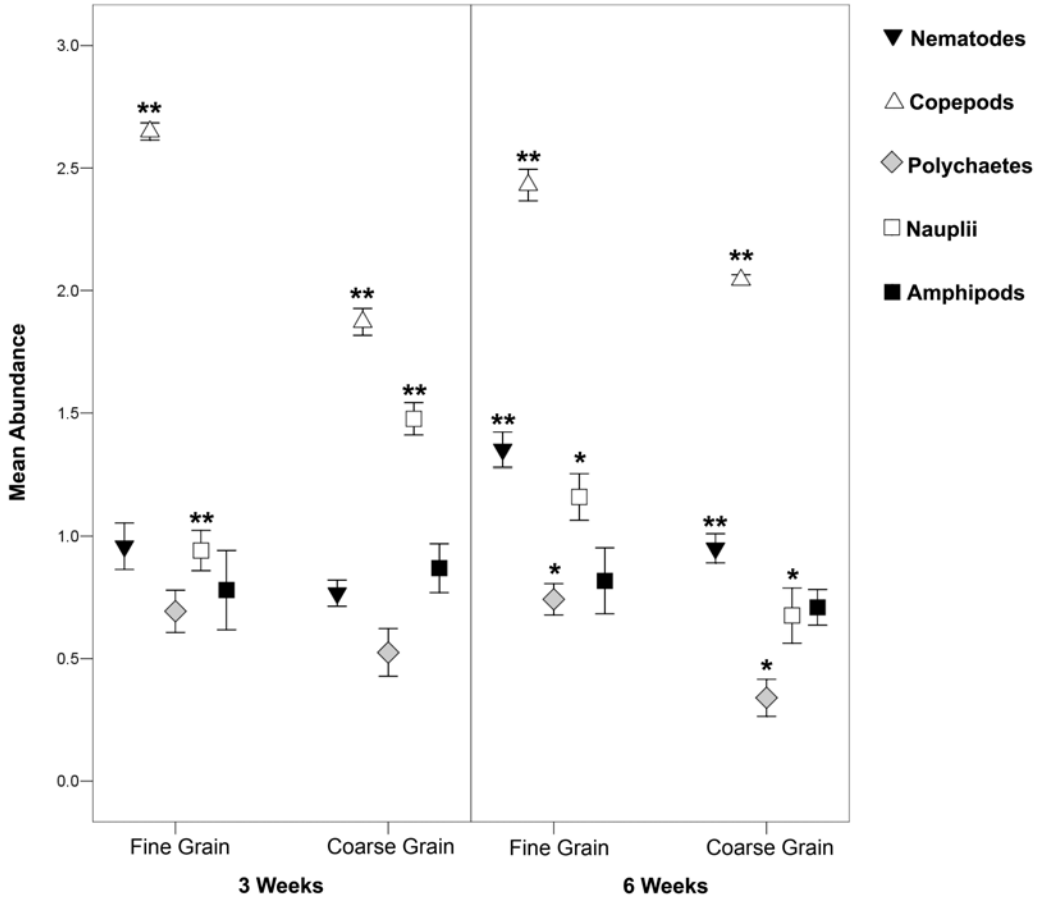

Fig. 2-4. Mean abundances for the five main groups (log +1 transformed, +/- 1 standard error) between the two sediment grain sizes. Paired t-test significance values denoted as: ** $P < 0.01$; * $P < 0.05$.

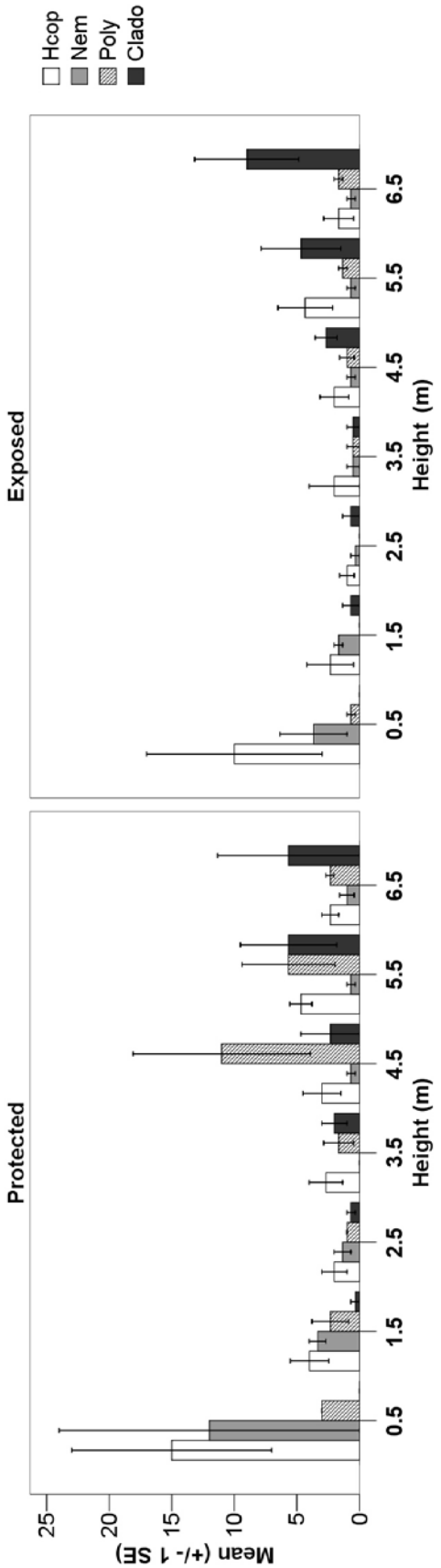

Fig. 2-5. Relative abundances of the four major taxa found in plankton samples between exposed (N=3) and sheltered locations (N=3) and heights in the water column collected at 1 m intervals from 0.5 m to 6.5 m. Hcop: harpacticoid copepods, Nem: nematodes, Poly: polychaetes, Clado: cladocerans.

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CHAPTER 3.

EFFECTS OF A DEPTH GRADIENT ON COLONIZATION OF SEDIMENT BY MARINE INVERTEBRATES IN SHALLOW COASTAL WATERS

3.1 INTRODUCTION

Marine meiofauna are important as food for higher trophic levels and can dominate total annual animal production in deep sea and some shallow benthic systems (Coull, 1988; Giere, 1993). However, environmental disturbances, both natural and anthropogenic, can often greatly reduce the abundance of meiofauna. For example seasonal hypoxia/anoxia of coastal waters (Lu & Wu, 2000), seismic events (Vanhove et al., 2004), pollution (Coull & Chandler, 1992) or bottom trawling (Snelgrove, 1999) can completely de-faunate a habitat leaving it open for re-colonization. How will fauna establish newly available soft sediments and what are the effects of depth (and other associated environmental factors) on the structure of the assemblages?

Many studies have investigated how marine benthic communities are affected by increasing depth. Generally, the abundance of both large and small animals (meio and macrofauna, respectively) decreases with increasing oceanic depth (see for example Rowe, 1983; Thiel, 1983; Lampitt et al., 1986; Alongi, 1992; Vanhove et al., 2004; Baguley et al., 2006; Grove et al., 2006). Supply of detritus used as a source of organic food by many benthic animals decreases with increasing depth, which has been considered a cause of reduced faunal abundance (Thiel, 1978; Pfannkuche, 1993; Danovaro et al., 1995; Gooday et al., 1996; Relexans et al., 1996; Soltwedel, 1997; Fabiano & Danovaro, 1999; Shimanaga & Shirayama, 2000; Gooday, 2002).

However, these studies generally compared communities of organisms across very broad depth gradients with the shallowest samples often taken at more than 100 meters. How are near shore benthic communities affected by increasing depth? Oceanic productivity is highest in shallow coastal waters (Bertness et al., 2001) and meiofauna, with their relatively high metabolic (about five times higher than macrobenthos; Gerlach, 1971) and annual turnover rates coupled with their high abundance play important roles in the total animal production of shallow soft sediments (Gerlach, 1971; Coull, 1988; Giere, 1993). If even small depth changes affect benthic faunal abundance the ecology of coastal habitats may be largely contingent on shoreline topography and floor profile.

Most depth related studies survey samples of established sediment taken directly from the ocean floor. However, as many sediment characteristics (e.g. porosity, oxygen content, heterogeneity of grain sizes, etc) likely vary between sites it may be difficult to attribute ecological patterns to a depth gradient alone. The aim of this study was to investigate how the assemblage structure of fauna that colonize sterile, identical, marine sediments is affected by changes in environmental conditions associated with a shallow depth gradient (6 - 30 m) while controlling sediment structure. If the patterns observed previously in much deeper sites apply in relatively shallow waters then I predict most fauna (including harpacticoid copepods) will decline in abundance along a shallow depth gradient while a few (including nematodes) will remain unchanged. Environmental variables measured and investigated for their effects on colonizing communities included depth, light intensity, temperature, exposure class, background sediment, time allowed for

colonization (2-6 weeks) and quantity of materials accumulating from the overlying water column.

3.2 MATERIALS AND METHODS

3.2.1 The study sites

The field study was conducted between May 20th and July 2nd 2008 at the Bamfield Marine Sciences Centre on Vancouver Island, British Columbia, Canada (48^{o} 49' 50 N; 125^{o} 07' 56 W) (Fig. 3-1). Experimental arrays were deployed at 6 sites chosen for their steeply and consistently sloping ocean floor (~ 30^{o}, Fig. 3-1). Two of the sites were situated within the sheltered Bamfield Inlet while the other arrays were placed in the more exposed Trevor Channel.

Sediment beneath the arrays varied between study sites. The two sites within the sheltered inlet (Bamfield and Tyee) had soft mud and silt bottoms littered with coarse shell and woody debris while sites outside the inlet were typified by fine, sandy substrates. The substrate also varied within each site, with the greatest difference at the shallow 6 m depth which was typified by a boulder/cobble mix (Fig. 3-2a). Substrate became more uniform from 12 to 30 m depths in each site. Video footage was made of an entire dive at each site taking special note of background environment as well as sampling technique and is available at electronic supplementary material from The University of Alberta, the author or online: www.ualberta.ca/~boeckner .

3.2.2 Deployment of the arrays

Colonization dishes were deployed at 5 depths in each of the 6 study sites for a total of 30 dishes. Each experimental container consisted of a square plastic dish (12 cm^2 x 9 cm deep) filled 7/8 full (800 ml) with fine, clean, sterile sand (grain size: > 100 µm, < 500 µm) and was held approximately parallel to the horizon by a PVC stand that compensated for the grade of the ocean floor (Fig. 3-2b). A transect line (0.64 cm yellow polypropylene) was laid along the ocean floor at each site at the beginning of the study and extended from 6 m (near shore) to a depth of 30 m (Fig. 3-1). Immediately prior to being sumberged the experimental sediment dishes were sealed tightly with snap-on lids and transported by SCUBA divers to 5 depths along transect line: 6, 12, 18, 24 and 30 m depths (Fig. 3-2a). Each PVC stand was anchored to the transect line with cable ties. After placement, the lids were removed from each dish taking care not to disturb the surrounding sediment. Each dish was fitted with galvanized steel mesh cages (1 cm mesh diameter) to prevent disturbance by megafauna such as fish, crabs, octopus, seastars, etc. Temperature (^oC) and light intensity (lux) were measured at every dish using a TUSA IQ-700 dive computer and Extech Instruments digital foot candle/lux meter, respectively. Each dish was subsequently sampled after 2, 4 and 6 weeks by SCUBA divers. Samples consisted of a cylindrical 5 cc core. No new sediment was added to replace the cores. The flocculent layer that had accumulated on top of the sediment was included with each core.

In addition to the sediment dishes, each PVC stand was fitted with a second dish that was empty at the beginning of the study (Fig. 3-2b(i)). These dishes were

used to quantify the amount of particulate matter precipitating from the water column (= ‘marine snow’) over 6 weeks. These marine snow dishes were also fitted with steel mesh lids but were not sampled until the time of collection at the end of the study.

After 6 weeks all of the sediment and marine snow dishes were tightly sealed and brought back to the surface. Cores were also taken of background sediment below each dish (one core per dish). Back at the lab, the contents of the sediment dishes were sieved through a 1 mm mesh under fresh flowing sea water and macrofauna that remained on the sieve were enumerated. The contents of the marine snow dishes were drained of water using filter paper (Whatman by Schleicher and Schuell, 125mm Cat No. 1001 125) and a Büchner funnel apparatus then dried at 50 ^{o}C for 48 hours to remove the remaining moisture before being weighed on an AEP precision top-loading balance (Model: AEP-1500G).

3.2.3 Processing and analysis

Meiofauna were preserved in 8% formalin and then separated from the sediment samples via LUDOX floatation (see Warwick et al., 1998 for description) and sorted into broad taxonomic/life-history groups under a stereo microscope (25 X). Macrofauna were also preserved in 8% formalin, identified to broad taxonomic groups and incorporated into the analyses.

Multivariate analyses were conducted to investigate the relationships between depth, light intensity, exposure, temperature and marine snow deposition on assemblage structure of colonizing animals (using SPSS 13.0). Specifically, a non-metric multidimensional scaling analysis was used based on Sorensen (Bray-Curtis)

distance measure. Stress levels of less than 20 were deemed acceptable. Abundances of the dominant meiofaunal taxa within the dishes at the end of the study were also compared to those of the background sediment using paired t-tests.

Various factors resulted in the loss of a few study dishes over the 6 weeks. There were no 6 m samples for the Goby Town site owing to initial difficulties deploying the array. After 4 weeks in the field the 12 m site at Helby and the 6 m site at Bamfield had overturned and did not contribute data for the remainder of the study. Also, no background samples were collected for 6 m or 12 m depths at Goby Town.

3.3 RESULTS

Nearly 3000 meiofaunal and 1200 macrofaunal organisms were processed from the samples collected over the six weeks. The most abundant meiofauna were nematodes, post-larval harpacticoid copepods (referred to as harpacticoid copepods from this point forward), polychaetes, bivalves, nauplii, amphipods and halacarid mites (in order of decreasing abundance, Table 3-1). All other meiofauna taxa were represented by fewer than 10 individuals. Polychaetes, gammarid amphipods, pectinid bivalves and hippolytid shrimp dominated macrofauna abundance (in order of decreasing abundance, Table 3-1).

The environmental variables measured at each site and at every depth were plotted. Light intensity decreased with increasing depth at each site (Fig. 3-3a). The quantity of accumulated marine snow was generally higher in the BMSC and Scott's Bay sites (Fig. 3-3b). Temperature varied by as much as 4 ^{o}C between sites but in ways that were inconsistent with changes in depth or with study site (Fig. 3-3c).

3.3.1 Meiofauna colonization patterns

A non-metric multidimensional scaling (nMDS) analysis was completed for the meiofauna colonization data collected over the six week study. The analysis found a combination of three dimensions that accounted for 88.9 % ($r^2 = 0.889$) of the total variability in the dataset with an acceptable stress value of 14. A majority of the variability of the dataset was explained by only two axes. Axis one and axis two accounted for 38% ($r^2 = 0.381$) and 35% ($r^2 = 0.351$) of the variability, respectively. Axis three contributed less, did not correlate with any environmental variables measured and is not discussed further here ($r^2 = 0.157$).

The nMDS overlays also showed which environmental variables were correlated with the two axes that accounted for the greatest amount of variability in the dataset (Table 3-2). Depth, light intensity and, to a lesser degree, exposure class correlated strongly with axis 1. Because light intensity declined with increasing depth the two were negatively correlated with each other. Thus, axis one ris correlated with a depth/light intensity gradient with shallow sites on the left and deeper sites on the right (Fig. 3-4a, 3-4b). This is also evident from the vector plot of the relationship between the axes and environmental variables (Fig. 3-5). Time (weeks), exposure class (Fig. 3-4c, 3-4d) and, to a lesser degree, quantity of marine snow and temperature were correlated with axis 2. Thus, axis 2 related primarily to colonization time and exposure class with exposed sites on the upper half of the axis and later colonizers and more sheltered sites on the lower half.

The nMDS analysis provided values for how correlated the independent variables (meiofauna) were with each axis (Table 3-3). Meiofauna most closely

associated with the depth/light intensity gradient (axis 1) were polychaetes, bivalves, harpacticoid copepods, amphipods, halacarid mites and nauplii in order of decreasing correlation (Fig. 3-5). The abundance of these taxa tended to decline with increasing depth and decreasing light intensity. The exception was halacarid mites, which were found in greater abundances in the deeper, darker sites. Nematodes, cumaceans and oligochaetes contributed least to the variability of this axis and were generally found in equal abundances across all depths and light intensities. Although only a single calanoid copepod was encountered once throughout the study it was found in one of the shallowest sites and thus correlated with the depth gradient represented by the axis 1. However, the nMDS downplays the importance of less abundant taxa and they contributed less to the variability of the dataset than more abundant taxa.

Meiofauna that shared a relationship to exposure/colonization time (axis 2) were nematodes, halacarid mites, nauplii, bivalves and cumaceans in order of decreasing correlation. Nematodes, halacarid mites and juvenile bivalves each accounted for a large proportion of the variability found along axis 2 and were typically found in greatest abundances at the end of the study and in less exposed sites. Although far less abundant and contributing less to the variability of the axis, cumaceans and chironomids also tended to be found later in the study and in more sheltered sites. Abundance of nauplii was also strongly correlated to the colonization time/exposure gradient of axis 2 except, unlike the other meiofauna, they were found in greatest abundances at the start of the study and in relatively exposed sites (Fig. 3-5). Although only a single rotifer was encountered it was also found at the start of the study and thus correlated with the time gradient represented by the axis 2.

3.3.2 Macrofauna colonization patterns

A second nMDS analysis investigated patterns in macrofaunal colonization in the study dishes after 6 weeks. These animals may have entered the dishes as macrofauna via active dispersal or matured from "temporary meiofauna" that had colonized in earlier weeks. The analysis found a combination of two dimensions that accounted for 84.9 % ($r^2 = 0.849$) of the total variability in the dataset with an acceptable stress value of 15. Axis one and axis two accounted for 49% ($r^2 = 0.489$) and 36% ($r^2 = 0.36$) of the variability in the dataset, respectively.

Sample depth was strongly correlated with axis one (r = 0.745, tau = 0.608; Fig. 3-6). Macrofauna on the left hand side of axis one occurred primarily in shallow sites, those on the right were typically found at depth and those near the centroid were found more evenly across all depths. The taxa that contributed most to the variability of axis one (depth gradient) were gammarid amphipods, polychaetes, caprellid amphipods, brachyurans, mussels (*Mytilus sp.*) and miscellaneous juvenile bivalves (Table 3-3). The abundance of nearly all macrofauna declined with increasing depth. Only hippolytid shrimps were found primarily in deeper sites. Two types of isopod (members of the suborder Flabellifera and *Munna* sp.) and an anomuran crab (*Pagurus* sp.), although encountered seldom throughout the study were only ever found in either the shallowest or deepest sites and thus correlated strongly with the depth gradient represented by the axis 1. However, the nMDS downplays the importance of less abundant taxa and they contributed less to the variability of the dataset than more abundant taxa. All other macrofauna taxa did not correlate strongly with depth. Axis two did not relate to any of the environmental factors measured

throughout the study and accounted for variability in the dataset to which I was unable to assign a causal factor.

3.3.3 Six week assemblages compared to background abundances

A series of paired t-tests compared abundances of meiofauna from background samples with those that had colonized the study dishes after 6 weeks (Table 3-4). Of the 5 most abundant taxa identified during the study (harpacticoids, nematodes, polychaetes, bivalves and halacarid mites) only the abundance of nematodes differed between the study dishes and the background samples. Nematode abundance, even after six weeks, was significantly and consistently lower in the study dishes ($t = -6.403$, $df = 25$, $P<0.00001$, Fig. 3-6a). Harpacticoid copepods, polychaetes, bivalves and mites had colonized the study dishes in abundances similar to the background sediment (Fig. 3-6b, Table 3-5).

3.4 DISCUSSION

3.4.1 Colonization versus depth/light intensity

Ordination results suggest that water depth and the strongly correlated factor of light intensity had the greatest impacts on colonization of sediment dishes by both meiofauna and macrofauna. The abundance of most meio- and macrofauna had a negative relationship with water depth, a trend that has been observed repeatedly worldwide but typically at much greater depths (See for example Rowe, 1983; Thiel, 1983; Lampitt et al., 1986; Alongi, 1992; Vanhove et al., 2004; Baguley et al., 2006; Grove et al., 2006). Polychaetes, bivalves, harpacticoid copepods and amphipods were the meiofauna that quickly declined in abundance with increasing water depth.

While previous depth-related trends have been typically attributed to a decreasing supply of organic matter with increasing depth and distance from land (Thiel, 1978; Pfannkuche, 1993; Danovaro et al., 1995; Gooday et al., 1996; Relexans et al., 1996; Soltwedel, 1997; Fabiano & Danovaro, 1999; Shimanaga & Shirayama, 2000; Gooday, 2002), I noted the same pattern but in relatively shallow water and close to shore. Furthermore, the declining faunal abundance did not correlate with rate of organic matter raining down from the water column above. Not all fauna exhibited this negative relationship with depth. Halacarid mites were more abundant in the deeper sites, while other fauna including nematodes, cumaceans, chironomids, and oligochaetes showed no depth related patterns in abundance. Gutzmann et al. (2004) and Alongi (1992) also noted that not all meiofaunal taxa decrease in abundance with depth. Alongi (1992) found that nematode densities did not change with depth and they were the most abundant taxon at all sites. Gutzmann et al. (2004) also cited nematodes as the most abundant taxon and less affected by a depth gradient than other meiofauna. Similarly, Vanhove et al. (2004) and Flach et al. (1999) found that nematodes dominated every depth sampled and were only marginally affected by a depth gradient. Muthumbi et al. (2004) also found only slight declines in nematode abundance with depth and that abundance was more associated with changes in oxygen concentrations. Given that these studies sampled far broader ranges of depths and still found little/no change in nematode abundance, it is not surprising that the relatively shallow range of depths covered in our study had little effect on nematode abundance. It is striking, however, that the shallow depth gradient was sufficient to

reveal declines in the other abundant taxa including harpacticoid copepods, polychaetes, amphipods and polychaetes.

Macrofaunal abundance was also negatively correlated with depth. Far fewer macrofauna had established within the deep versus the shallow dishes. Flach et al. (1999) reported a linear increase in the ratio between meio- and macrofauna densities with increasing water depth. At the continental shelf meiofauna densities were approximately 50 times higher than macrofauna densities, whereas in the abyss meiofauna densities were more than 1000 times higher suggesting that macrofauna were less suited to deeper zones than meiofauna. Similarly, I found macrofauna were four times more abundant in shallow versus deep sites; a change much greater than was noted for meiofauna which were only twice abundant in shallow sites than deeper sites. The only macrofaunal taxon that occurred primarily in the deeper sites was hippolytid shrimps which often have ranges extending far deeper than those sampled by this study (Jensen 1995).

3.4.2 Colonization over time

Harpacticoids, polychaetes and amphipods showed early and abundant arrival while nematodes, mites and bivalves were slower to colonize. This was likely due to differences in active dispersal abilities between the meiofauna. Active dispersal rates of meiofauna via crawling or swimming is generally low (Gerlach, 1977; Savidge & Taghon, 1988). Many harpacticoid copepods, however, are better active dispersers than nematodes (Widbom, 1983; Ólafsson & Moore, 1990; 1992). Numerous studies have shown that some harpacticoids will occasionally enter the water column under

their own power (Alldredge & King, 1980; 1985; Bell et al., 1988; Kurdziel & Bell, 1992; Walters & Bell, 1994; Teasdale et al., 2004). Similarly, it is not uncommon for benthic polychaetes and amphipods to enter the water column periodically. Thus, harpacticoids, polychaetes and amphipods could have quickly and actively colonized from the background sediment below while nematodes, mites and bivalves depended more on external forces (water currents or bioturbation) to carry them more slowly into the study dishes. This was indeed the case for Fonseca-Genevois et al. (2006) who found that the colonization of azoic plates suspended above the ocean floor was faster for harpacticoids than nematodes which relied more heavily on periodic upwelling events for dispersal. Nauplii were found in greatest abundances initially but declined in number by the end of the study. Perhaps nauplii were among the first meiofauna to establish and had matured into juvenile and adult crustaceans in later sample collections. Why, however, did so few new nauplii colonize subsequent weeks to replace those that had matured? Perhaps competition for food and space, or presence of later-colonizing predators, made the established sediment less suitable for subsequent nauplii colonization. This hypothesis is also supported by the fact that I encountered so few nauplii in the samples taken from the background sediment.

3.4.3 Exposure class, temperature and marine snow

The remaining 3 environmental factors had less of an effect on fauna colonization, although there was a slight trend toward greater faunal abundance in the two more sheltered sites (Fig. 3-5). There was also a slight negative correlation between accumulations of marine snow and exposure class (Fig. 3-5). Amount of

marine snow was highly variable among sites (Fig. 3-3b) but did not correlate strongly with differences in faunal abundance. Previous studies cited reduced organic matter with increasing depth as partially responsible for faunal declines (Thiel, 1978; Pfannkuche, 1993; Danovaro et al., 1995; Gooday et al., 1996; Relexans et al., 1996; Soltwedel, 1997; Fabiano & Danovaro, 1999; Shimanaga & Shirayama, 2000; Gooday, 2002), however, because the deepest sites in our study often received as much or more marine snow than many of the shallower sites it does not seem that a lack of organic matter was the cause of faunal declines with increasing depth. Because meiofauna have been found to inhabit these passively sinking aggregates marine snow may have actually helped deliver continual supply of colonists to the sediment (Shanks & Edmondson, 1990). Temperature varied by as much as 4 ^{o}C across all depths and study sites but was idiosyncratic and did not correlate with patterns in faunal abundance (Fig. 3-3c).

3.5 Conclusion

Our results corroborate the broad array of studies that have been conducted world-wide and over much larger depth scales: abundance of most benthic fauna tends to decline with depth. However, I found that abundances decline over relatively small changes in depth at sites that are all close to shore. I also found that the two taxa generally most abundant in benthic habitats, nematodes and harpacticoid copepods, reacted very differently to changes in depth. Availability of organic matter and distance to land masses, previously implicated in depth related faunal declines, were unlikely responsible for the reduced abundances noted in this study. Thus, a question

remains: what is it about depth that limits the abundance of some taxa and not others? Perhaps decreasing light intensity limits algal production causing declines in algivorous taxa, while fauna that utilize bacteria and other non-photosynthesizing food sources remain unaffected. Further study of the feeding habits of taxa along a depth gradient would be useful to address the validity of such speculation.

Table 3-1. Abundance of meio- and macrofauna colonists that had settled in the sediment dishes after six weeks, summed over all depths and sites. Taxa only found in background samples denoted by (B). Organized by phylum.

	Meiofauna	Macrofauna
Mollusca		
Gastropoda (*Calliostoma sp.*)	---	8
Gastropoda (unidentified taxa)	1	9
Bivalvia (*Mytilus sp.*)	---	4
Bivalvia (Pectinidae)	---	25
Bivalvia (unidentified taxa)	157	5
Annelida		
Polychaeta (unidentified errant taxa)	178	843
Oligochaeta	3	---
Arthropoda		
Anomura (*Pagurus sp.*)	---	1
Amphipoda (*Caprella sp.*)	---	9
Amphipoda (Gammaridae)	---	237
Amphipoda (unidentified taxa)	31	---
Brachyura (unidentified juveniles)	---	8
Caridea (Hippolytidae)	---	21
Caridea (*Pandalus sp.*)	---	1
Chironomidae (larvae)	2	---
Copepoda (Calanoid)	1	---
Copepoda (Harpacticoid)	1145	---
Cumacea	5	2
Halacaridae	26	---
Isopoda (Flabellifera)	---	1
Isopoda (*Munna sp.*)	---	1
Isopoda (unidentified taxa)	3	---
Nauplii	83	---
Pycnogonida (B)	1	---
Tanaidacea (B)	3	---
Nematoda	1334	---
Rotifera	1	---
Echinodermata (Ophiuridae)	---	1
Pisces (Cottidae)	---	4

Table 3-2. Pearson (r) and Kendall (tau) correlations showing the relationship between environmental factors and each of the two main axes of the macrofaunal nMDS analysis. Values closer to +/- 1 indicate strong positive/negative correlations of that variable to the axis. Strong correlations are shown in bold.

	Axis 1		Axis 2	
	r	tau	r	tau
Depth	**0.572**	**0.435**	0.034	0.039
Exposure Class	**0.243**	**0.199**	**0.237**	**0.227**
Light Intensity	**-0.541**	**-0.370**	-0.071	-0.024
Marine Snow	-0.091	-0.051	-0.142	-0.078
Site	0.042	0.063	**0.243**	**0.199**
Temperature	0.005	0.083	-0.109	-0.152
Weeks	-0.061	0.000	**-0.334**	**-0.345**

Table 3-3. Pearson (r) and Kendall (tau) correlations showing the relationship between faunal groups and each of the two main axes of the macrofaunal nMDS analysis. Values closer to +/- 1 indicate strong positive/negative correlations of that variable to the axis. Taxa with values less than +/- 0.1 not reported. Taxa with (*) or (**) were only encountered once or twice throughout the entire study, respectively.

	Axis 1		Axis 2	
	r	tau	r	tau
Meiofauna				
Amphipoda	-0.318	-0.289	---	---
Bivalvia	-0.594	-0.530	-0.291	-0.295
Calanoida*	-0.208	-0.151	---	---
Chironomidae**	---	---	-0.213	-0.190
Cumacea	---	---	-0.117	-0.131
Gastropoda	-0.115	-0.095	---	---
Halacaridae	0.179	0.154	-0.306	-0.303
Harpacticoida	-0.589	-0.479	---	---
Nauplii	-0.129	-0.091	0.384	0.351
Nematoda	---	---	-0.522	-0.483
Polychaeta	-0.786	-0.678	---	---
Rotifera*	---	---	0.118	0.117
Macrofauna				
Bivalvia	-0.479	-0.321	---	---
Brachyura	-0.546	-0.385	---	---
Calliostoma sp.	-0.210	-0.203	---	---
Caprella sp.	-0.611	-0.418	---	---
Flabellifera*	-0.427	-0.272	---	---
Gammaridae	-0.825	-0.680	---	---
Gastropoda	-0.174	-0.241	---	---
Hippolytidae	0.245	0.224	---	---
*Munna sp.**	-0.427	-0.272	---	---
Mytilus sp.	-0.482	-0.332	---	---
*Pagurus sp.**	0.141	0.167	---	---
Pisces	-0.105	-0.050	---	---
Polychaeta	-0.709	-0.520	---	---

Table 3-4. Abundance of individuals within each taxon from samples taken from the colonization dishes and background sediment at the six week period (summed over all depths and sites). Core samples measured 5 cc. Results of the t-Tests that evaluated differences between colonization and background samples for the 5 most abundant meiofaunal taxa are listed on the right. Sorted by background abundance.

	6 Weeks	Background	t-Test
Nematoda	221	1000	DF:25, t=-6.403, P<0.001
Copepoda	326	357	DF:25, t=-1.187, P=0.246
Bivalvia	21	21	DF:25, t= 0.671, P=0.508
Polychaeta	32	21	DF:25, t= 1.732, P=0.096
Halacaridae	14	10	DF:25, t= 0.968, P=0.342
Amphipoda	5	5	---
Tanaidacea	0	3	---
Oligochaeta	0	2	---
Cumacea	0	2	---
Isopoda	1	1	---
Pycnogonidae	0	1	---
Nauplii	6	0	---
Chironomidae	2	0	---

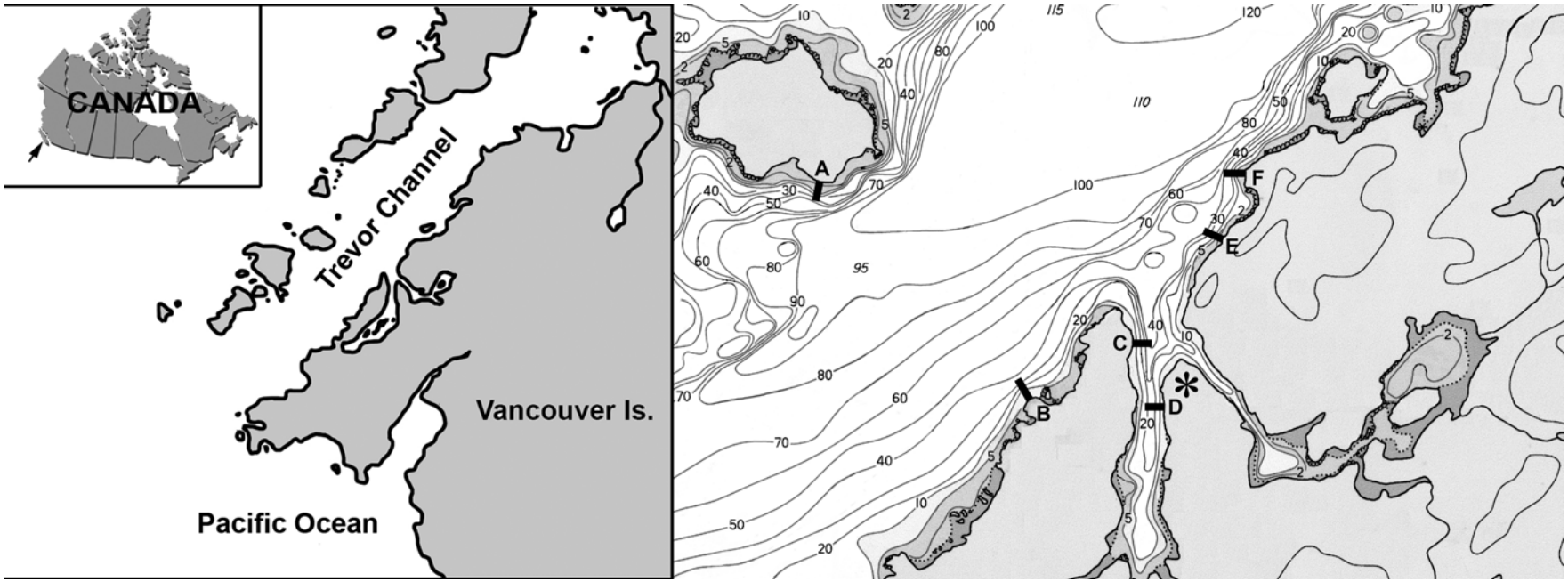

Fig. 3-1. Location of study sites in Trevor Channel, Vancouver Island, British Columbia. A, Helby Island; B, Scott's Bay; C, Tyee; D, BMSC; E, Goby Town; F, Dixon. Depth in meters is indicated by the contour lines. Bamfield Marine Sciences Centre (BMSC) denoted by asterisk (*).

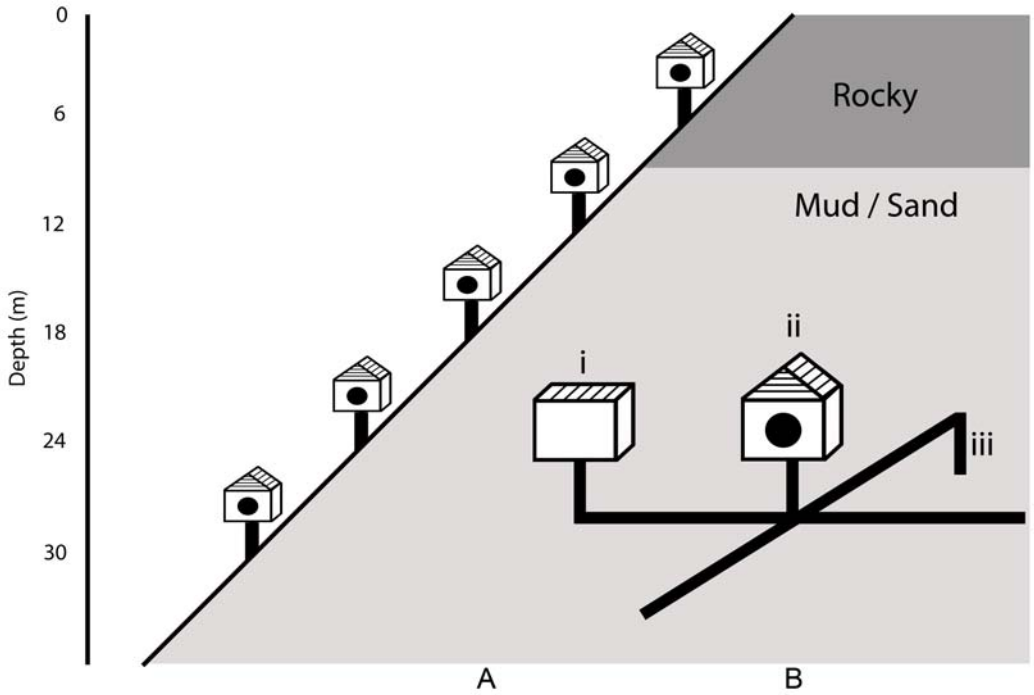

Fig. 3-2. A) Position of colonization dishes along the depth gradient (6-30 m). Stands held the surface of the colonization dishes parallel to the horizon. B) Detail of a single colonization apparatus: i) marine snow collector fitted with metal mesh cover. ii) colonization dish filled with azoic sediment, fitted with a metal mesh cover and a circular vent (one per side) covered with 100 µm plastic mesh. iii) PVC anchor driven into the soft substrate to prevent apparatus from sliding down the sloping ocean floor.

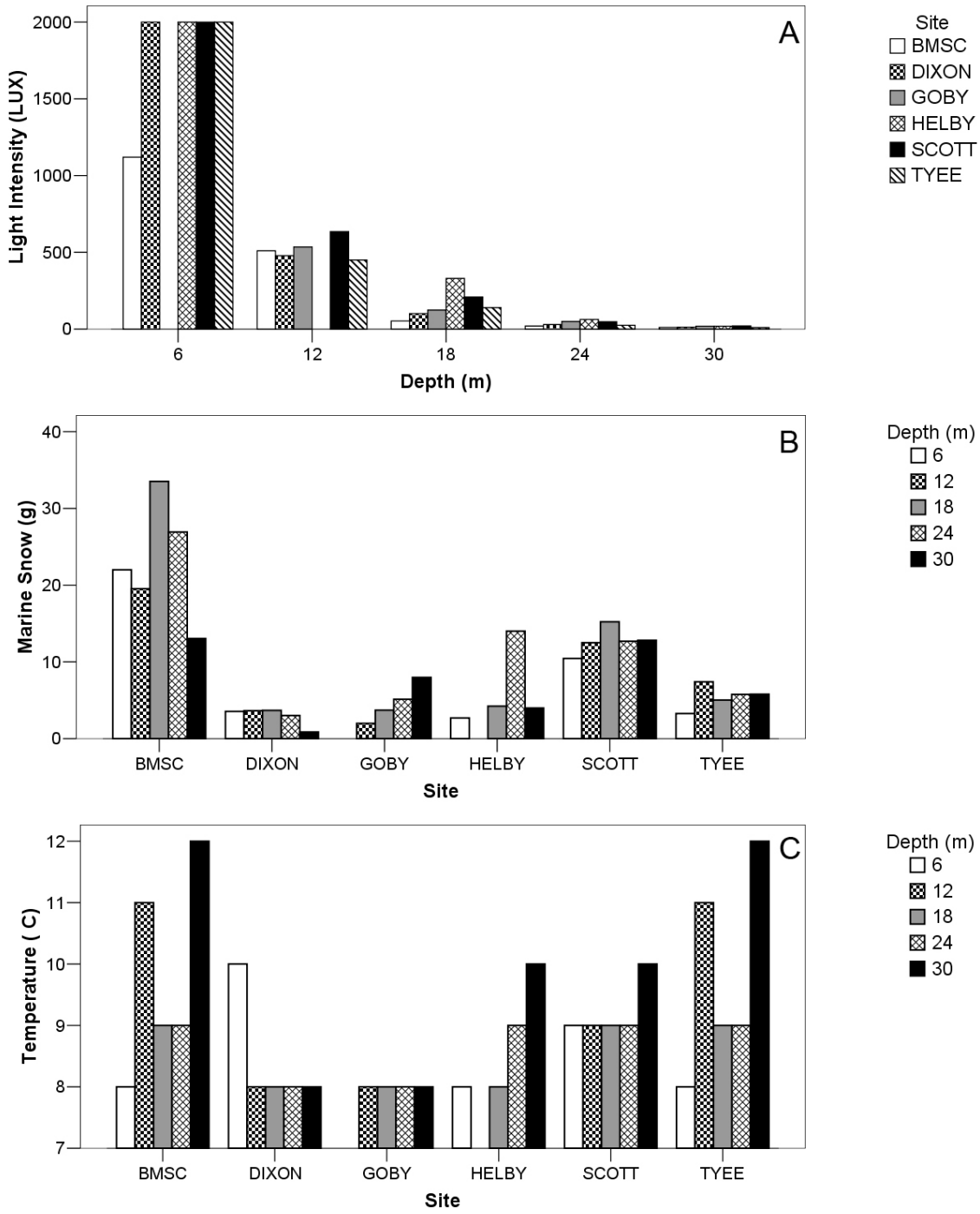

Fig. 3-3. Environmental variables recorded: A) Light intensity recorded at each study site (LUX, measured on May 20th, 2009); B) accumulation of marine snow (g) at each site after 6 weeks (measured at the end of the 6 week study, July 2nd, 2009); C) temperature (^{o}C) at each site recorded during initial study deployment (May 20th, 2009).

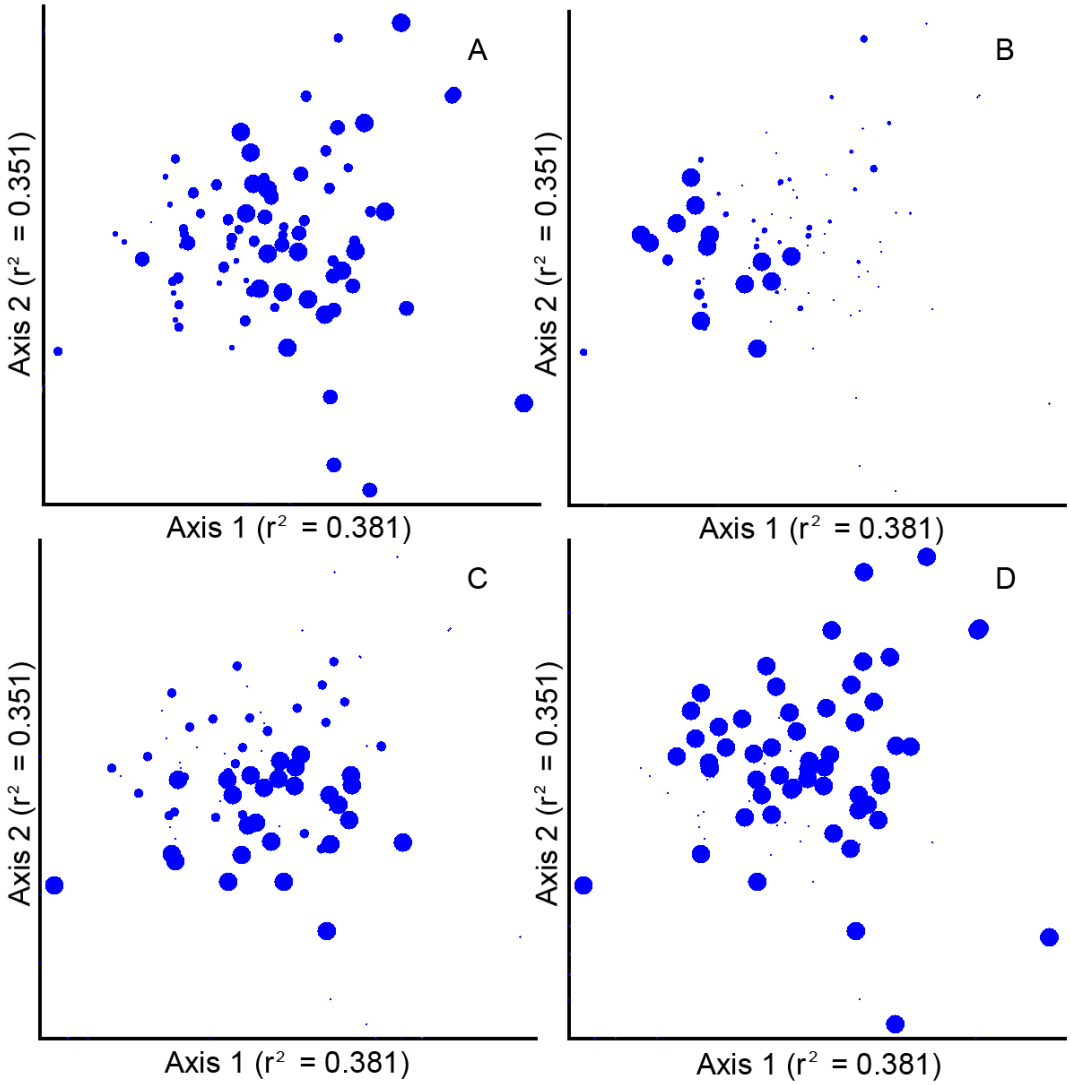

Fig. 3-4. Study samples with relation to the 4 main environmental factors plotted by the nMDS on the two axes that accounted for the greatest amount of variability: A) depth: points increase in size with increasing sample depth; B) light intensity: points increase in size with increasing light intensity; C) time: points increase in size with study duration; D) exposure class: sheltered and exposed sites represented by small and large points, respectively.

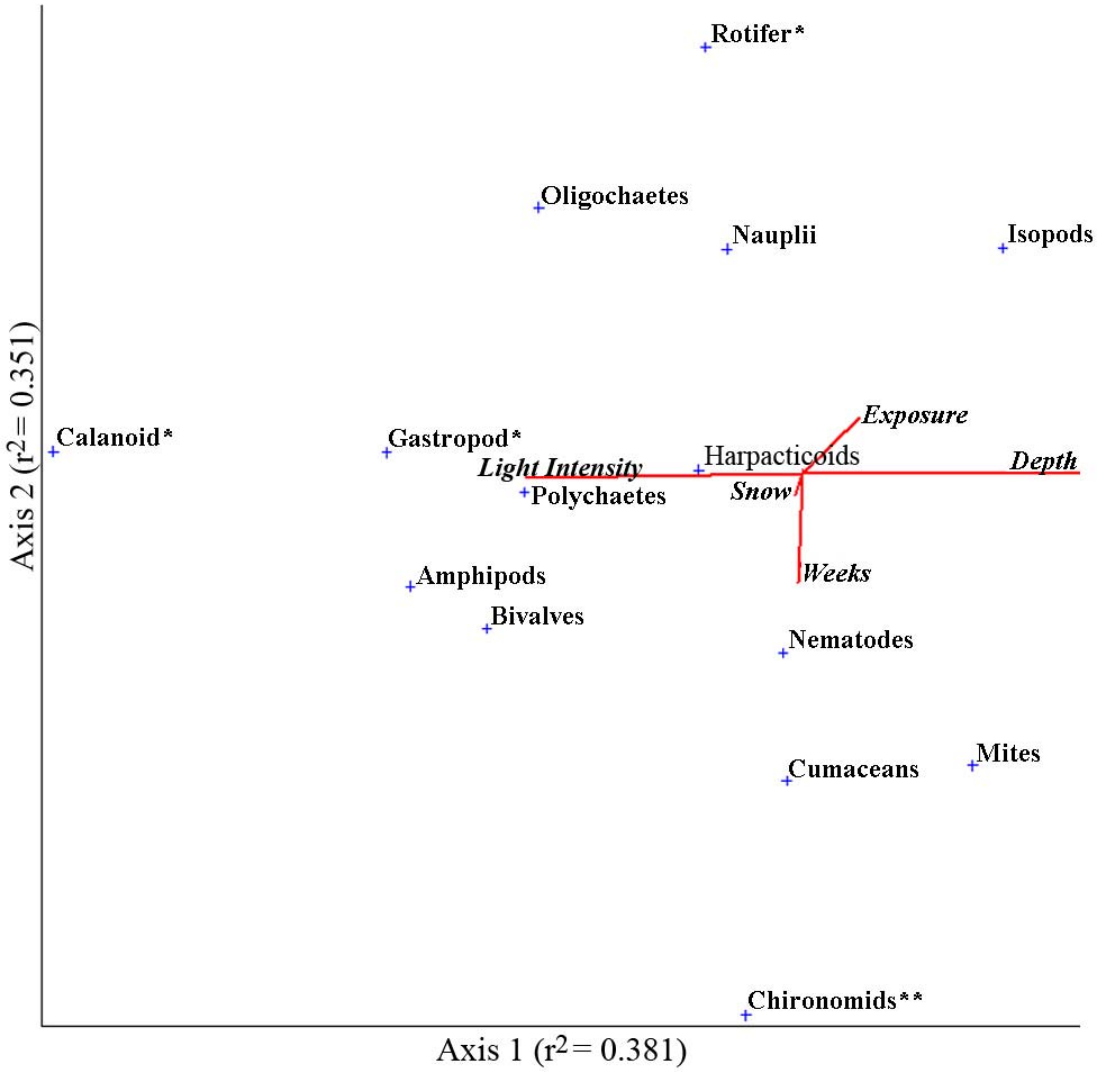

Fig. 3-5. The nMDS graphical output of meiofaunal colonization detailing the relationships of fauna to the two axes responsible for most of the variability in the dataset. Correlation of the environmental factors (labeled in italics) with each axis represented as vector lines extending from the centroid. Taxa only found once or twice are denoted by * and **, respectively.

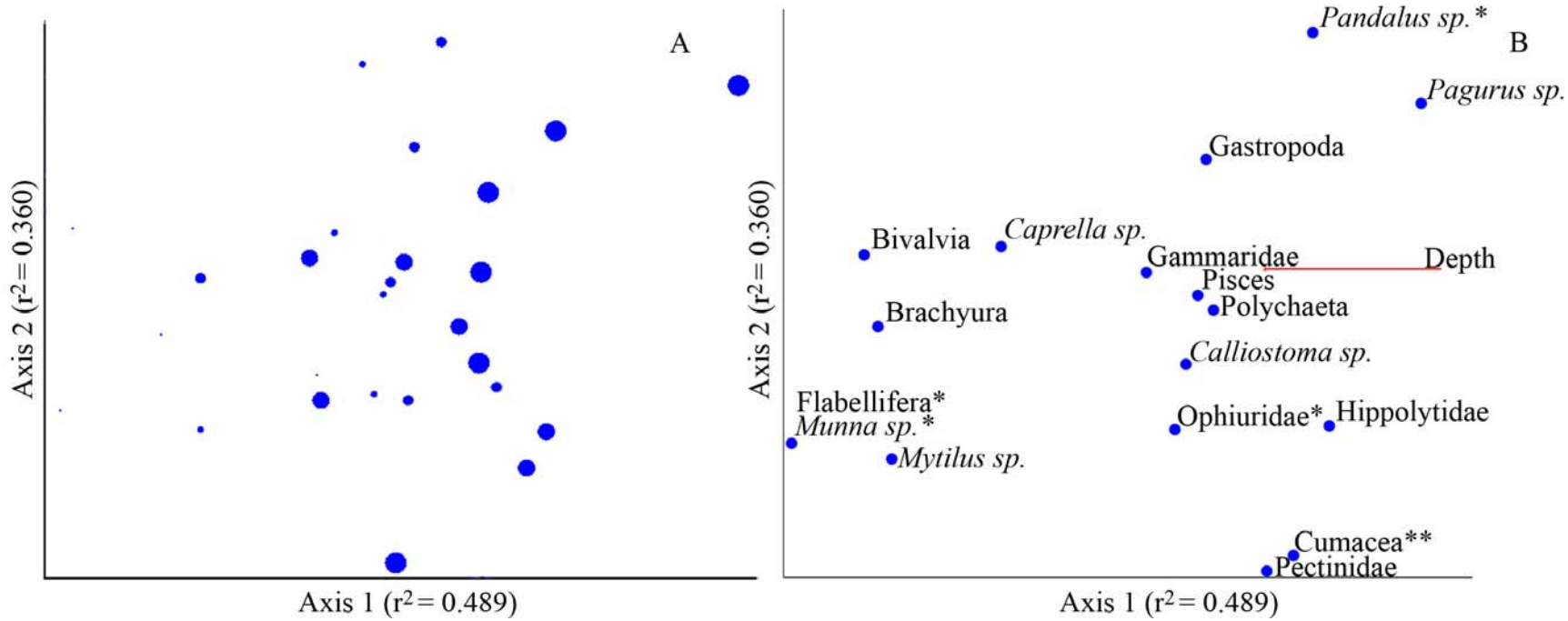

Fig. 3-6. The nMDS graphical output of macrofaunal colonization detailing the relationships of (A) samples (small to large points represent shallow to deep sites, respectively) and (B) taxa to the two axes responsible for most of the variability in the dataset. Correlation of depth with each axis is represented as vector lines extending from the centroid. Taxa only found once or twice are denoted by * and **, respectively.

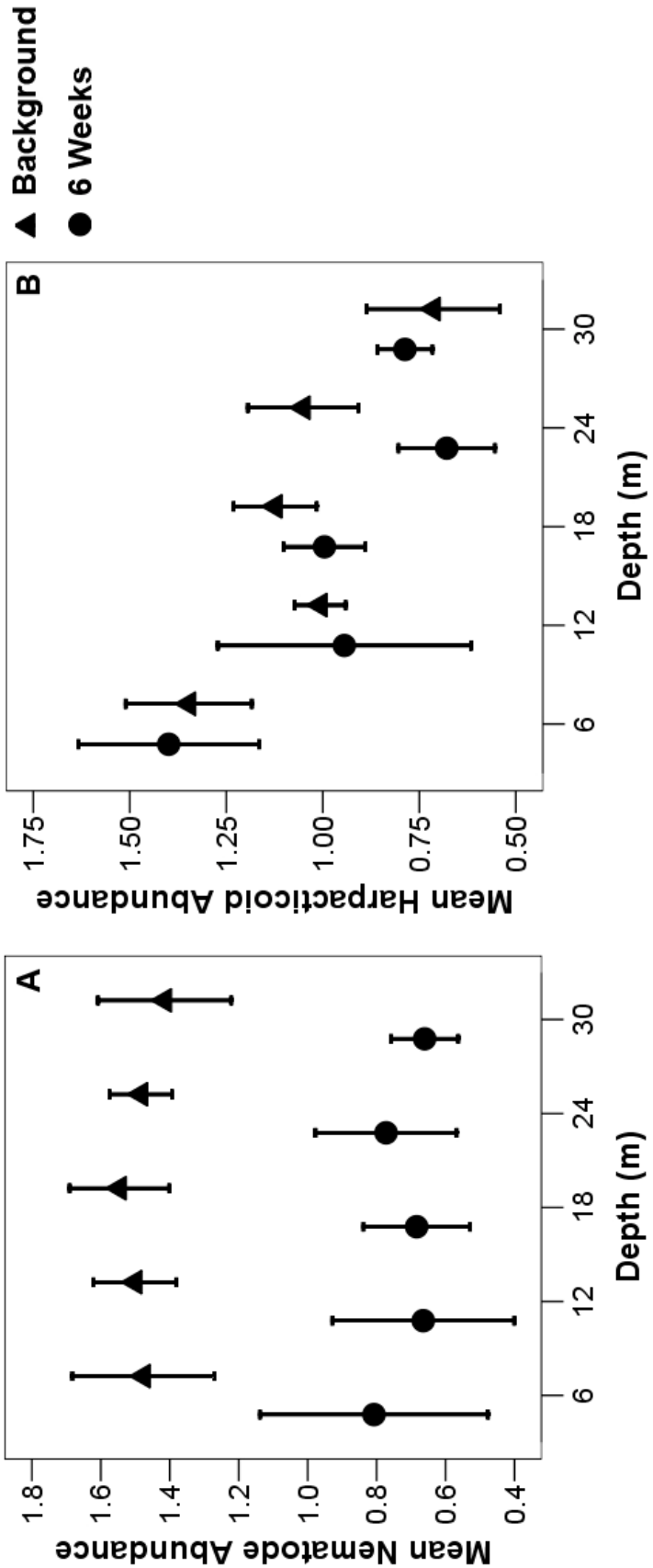

Fig. 3-7. Changes in (A) nematode and (B) harpacticoid abundances across a depth gradient after 6 weeks of colonization time compared to background levels (also sampled at the 6 week collection time, N=6). Values represent individuals per 5 cc sediment core collected from 6 depth transects each with 5 depth treatments: 30 samples total. Error bars represent a standard error of +/- 1.

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CHAPTER 4.

IMPACT OF CLAMS ON MARINE MEIOFAUNAL ASSEMBLAGES IN SOFT SEDIMENT: DIGGING FOR ANSWERS

4.1 INTRODUCTION

Our understanding of ecological relationships among most benthic marine animals is poor despite their high species diversity and abundance and the many roles they are assumed to serve in ecosystem functioning (Coull & Bell, 1979; Snelgrove, 1999). Studies of benthic invertebrate ecology tend to be split into those that focus on large-bodied macrofauna (animals retained on a 1 mm mesh) and those that focus on small-bodied meiofauna (metazoans passing through a sieve with a mesh of 1 mm and retained on a mesh of 40 μm), but rarely do researchers incorporate interactions between these two size classes. Of the studies that have examined effects of macrofauna on meiofauna, the role of predation has been the main focus (reviewed by Ólafsson, 2003). Not only do macrofauna affect meiofauna via predation (Ólafsson, 2003) but less frequently investigated and potentially as important in soft bottomed habitats, is the role of physical substrate disturbance by macrofauna (bioturbation). Bioturbation is generally the most important mechanism for reworking sediments and releasing contaminants in sediments of low energy environments (Lee & Schwartz, 1980; Gschwend et al., 1987; Reible et al., 1991). Ólafsson (2003) points out that many studies of the role of macrofaunal predation on meiofauna (e.g. Scherer & Reise, 1981; Gee et al., 1985) have not taken into account the potential effects of bioturbation. Another potential influence of macrofauna on meiofauna is the chemical

metabolites and faecal products released by the larger organisms. The effects of these metabolic byproducts have never been explicitly examined. Previous studies of macrofaunal and meiofaunal interactions have attempted to discern patterns that can be applied across broad taxonomic groups (i.e. at the levels of phylum or class). However, behavioural and morphological variation within a given macrofaunal taxon creates problems when trying to apply generalizations.

One of the most frequently examined taxa in studies of macro- and meiofaunal interactions is Bivalvia (Mollusca). To date, eight studies have investigated effects of bivalves on meiofauna (Table 4-1). Most of these considered effects of bivalves on major meiofaunal groups at higher taxonomic levels. Bivalves usually dominate the biomass of infaunal communities in sedimentary habitats such as tidal flats (Peterson, 1977; Legendre et al., 1997) and affect the vertical distribution and stability of sediments when burrowing (bioturbation) (Rhoads & Young, 1970; Nowell et al., 1981; Hall, 1994; Reise, 2002). Many bivalves, such as the bent-nose clam (*Macoma nasuta* Conrad), feed using incurrent siphons to suck-up deposits and tiny animals that have accumulated on the surface of the sediment (Quayle, 1960; Jørgensen, 1990). Other bivalves, including the littleneck clam *Protothaca staminea* (Conrad), feed on suspended particles (Shaw, 1986; Kennedy, 1993) and may affect benthic communities by ingesting potential colonists arriving from the water column, but likely have little effect once meiofauna have reached the sediment. Pseudofecal pellets consisting of aggregated indigestible materials and released as byproducts of bivalve feeding can also alter sediment particle composition (Reise, 2002). Furthermore, bivalves can strongly affect surrounding water chemistry via release of

waste products containing ammonium and phosphate (Magni et al., 2000; Magni & Montani, 2006). Only one of the 8 studies investigating bivalve effects on meiofauna (Table 4-1) investigated differences between suspension and deposit feeding bivalves and found that Turbellaria abundance increased at the sediment surface in the presence of deposit feeding clams (Reise, 1983). Bioturbation, predation and byproducts of metabolism likely differ in the magnitude of their effects on meiofauna, and their intensities likely vary between bivalve species (Francois et al., 1999). Because of this variability in bivalve behaviour, the inconclusive and sometimes contradictory results of previous studies are not surprising (Table 4-1).

Although it is easy to understand how macrofaunal predation would cause declines in abundance of some meiofaunal groups, the expected effects of bioturbation are less obvious. Some investigations on other macrofauna have investigated the role of bioturbation on meiofauna (burrowing by shrimp, Bell & Coull, 1978; digging by crabs, Schratzberger & Warwick, 1999; and burrowing by polychaetes, Reise, 1987, Tita et al., 2000), but the effects of bivalve bioturbation have seldom been investigated and the relationships are unclear. As bivalves burrow the sediment is redistributed (Nowell et al., 1981), the oxygen regime changes (Michaud et al., 2005) and nutrient flow increases between the sediment and the water column (Michaud et al., 2006). Nutrients are also redistributed by bioturbation and may become buried in anoxic layers where it is difficult to consume for meiobenthic organisms. Conversely, already buried organic matter can be transported to the surface layers, where it becomes an available food source. Many meiofaunal organisms reach their highest densities in the top-most layers (~2 cm) of the sediment

and many are epifaunal (Coull, 1988). This is especially the case in fine sediments when oxygen and nutrients decline with increasing depth. As bivalves burrow, meiofauna may be displaced to deeper portions of the sediment where they are less adapted for survival. Meiofauna in sandy substrates may also be physically damaged by the abrasive motion of sediment as the bivalve burrows. On the other hand, bivalve burrowing may bring oxygen to previously anoxic regions thus increasing the depth of suitable meiofaunal habitat. Bioturbation rates likely vary between clam species. Deposit feeding clams may impact sediment communities more than suspension feeders by frequently moving to adjacent areas seeking fresh deposits and via disturbances (or ingestion) caused by the movement of the siphons while feeding.

The aims of this study were to 1) determine whether effects of bivalves on meiofaunal colonization was associated with different modes of bivalve feeding, 2) compare effects on meiofauna of high vs low movement of bivalves in the substrate, 3) assess if chemicals associated with bivalve metabolism affect meiofaunal colonization. I used a variety of caged and un-caged suspension and deposit feeding bivalve treatments and no-bivalve controls to address these aims. I hypothesized that bioturbation effects of clams would be greater when un-caged. Also, I predicted that deposit feeding clams would have a greater effect than suspension feeders given that deposit feeders likely disturb more surface dwelling meiofauna. Lastly, if chemicals associated with bivalve metabolism have a negative effect then we predicted that both caged and uncaged bivalves would be associated with lower meiofaunal abundances than in the no-bivalve controls.

4.2 MATERIALS AND METHODS

4.2.1 Comparing effects of suspension feeding and deposit feeding bivalves

The first study in this series was conducted in a sheltered inlet adjacent to the Bamfield Marine Sciences Centre on the west-coast of Vancouver Island, Canada (48° 49' N; 125° 07' W). Two species of bivalve, the tellinid *Macoma nasuta* (bent-nosed clam, deposit-feeder) and the venerid *Protothaca staminea* (littleneck clam, suspension feeder), were hand-collected from nearby mudflats at low-tide. Both clam species are typical of sandy/muddy habitats in coastal British Columbia (Rehder, 1981), and are shallow (~10 cm) burrowers (Shaw, 1986) that actively move and bioturbate (Quayle & Bourne, 1972; Peterson, 1982). Both species are common from shallow water to depths of greater than 13 m (Quayle & Bourne, 1972; Rehder, 1981). The bivalves were transported back to the laboratory where they were placed in sea-water tables. To ensure consistency in size, only those that displaced 20-25 ml of water and measured roughly 6 cm L x 4 cm W x 2 cm H were initially considered for use. Once sorted by size, only active bivalves with fully extended feet and siphons were selected.

Each experimental container consisted of a square plastic dish (12 cm^2 x 9 cm deep) filled ¾ full (500 ml) with fine, clean, sterile sand (grain size: > 100 µm, < 500 µm) (Fig. 4-1a). A 5 cm diameter hole was cut into each side of every dish and covered with 50 µm mesh screen to increase permeability to surrounding water. There were four treatments: (1: high bioturbation) four deposit-feeding bivalves per dish (*M. nasuta*) (8 replicates); (2: medium bioturbation) two deposit-feeding bivalves and two suspension-feeding bivalves (*P. staminea*) per dish (4 replicates); (3:low bioturbation) four suspension-feeding bivalves per dish (8 replicates); (4) no bivalves (8 replicates).

More replication was given to the 100% deposit- and suspension-feeding treatments because the primary objective was to distinguish between the two feeding types (Fig. 4-1b). The bivalves were initially added to each dish in a 2 x 2 matrix with the foot oriented down (Fig. 4-1a). Position of each bivalve within the dish was recorded during a two hour observation period. If after two hours any bivalve had remained inactive it was removed and replaced with another. These substitutes were also evaluated for activity after a further 2 hours. The majority of bivalves immediately buried themselves and only three substitutions were made. The bivalves were then allowed to acclimate to their surroundings in a flowing-filtered seawater tank for 24 hours.

The experimental dishes were sealed tightly with lids and carefully carried to the nearby station docks. Divers transported the dishes from the docks to a depth of 12 m where they were secured 20 cm above the ocean floor to a large, anchored PVC grid (Fig 1b). Two additional dishes of azoic sediment were also included but were only sampled at the end of the study (denoted as E in Fig. 4-1b). The abundances of meiofauna in these dishes (E) were compared to the No Bivalve treatments of week eight to determine if weekly sub-sampling had an effect on meiofaunal densities. After placement, the lids were removed from each dish taking care not to disturb the surrounding sediment. Each treatment was then fitted with plastic mesh cages (1 cm mesh diameter) to prevent predation on the bivalves by crabs, octopus and seastars (Fig. 4-1a). With the exception of the E treatment, the sediment within each dish was sub-sampled after one, three, six and eight weeks via SCUBA. Two 5 cc cores were taken at haphazard locations within each dish using a 10 cc plastic syringe cylinder

(1.5 cm diameter, 8 cm height). The two cores were later combined as one 10 cc sample per dish. No new sediment was added to replace that taken each week. Care was taken not to disturb the water surrounding the cages so that the supra-sediment flocculent layer would be included with each core.

4.2.2 Tests with additional bivalve species and effects of metabolic byproducts

In order to test the consistency and our interpretations of findings from the 2005 study, an additional study was carried out in the summer of 2006 that investigated the effects of a broader range of bivalve species and the influence of bivalve metabolism on meiofaunal colonization. This portion of the study was conducted in the same location as the fall 2005 study. Six species of bivalve were hand collected from nearby mudflats at low tide. Two were tellinids with long, separate incurrent siphons used for feeding on deposits: *Macoma nasuta* and *Nuttallia obscurata* Reeve, 1857 (varnish clam, deposit/suspension-feeder). Strictly suspension-feeding bivalves were represented by four species with fused siphons: *Panopea abrupta* Conrad, 1849 (geoduck clam), and three venerid species, *Protothaca staminea*, *Venerupis philippinarum* A. Adams & Reeve, 1850 (manila clam) and *Saxidomus gigantea* Deshayes, 1839 (butter clam). All clam species are typical of sandy/muddy habitats in coastal British Columbia (Rehder, 1981), and are shallow (~10 cm) burrowers (Abbot, 1974; Shaw, 1986). All species are common from shallow water to depths of greater than 13 m (Quayle & Bourne, 1972; Rehder, 1981). The bivalves were transported back to the laboratory where they were placed in sea-water tables. To ensure consistency in size, only those that displaced 20-25 ml

of water and measured roughly 6 cm L x 4 cm W x 2 cm H were initially considered for use. Once sorted by size, only active bivalves with fully extended feet and siphons were selected.

For consistency, the same experimental containers were used as in the fall 2005 study. The only difference was the addition of a "caged bivalve" treatment in which three plastic mesh cages were secured to restrict bivalve movement (Fig. 4-2). There were 8 bivalve treatments, a mechanical disturbance treatment and a no-bivalve/no-stirring control. The bivalve treatments each consisted of: (1) three caged deposit-feeding *M. nasuta;* (2) three caged suspension-feeding *P. staminea*; (3) three un-caged deposit-feeding *M. nasuta*; (4) three un-caged suspension-feeding *P. staminea*; 5) three un-caged suspension-feeding/deposit-feeding *N. obscurata*; 6) three un-caged suspension-feeding *V. phillipinarum*; 7) three un-caged suspension-feeding *P. abrupta* and 8) three un-caged suspension-feeding *S. gigantean* (Fig. 4-3). The mechanical disturbance treatment involved drawing a thin metal rod through the sediment from side to side for thirty seconds disturbing all of the sediment evenly. Each treatment was replicated three times. The bivalves were initially added to each dish with the foot oriented down. Position of each bivalve within the dish was recorded during a two hour observation period. If after two hours any bivalve had remained inactive it was removed and replaced with another. These substitutes were also evaluated for activity after a further 2 hours. The bivalves were then allowed to acclimate to their surroundings in a flowing, filtered seawater tank for 24 hours.

Deployment and sampling procedure was the same as in the fall 2005 study. The experimental grid was visited and each dish sampled at ten times throughout the

study: day 1 (the day after placement of the dishes), day 6, day 18, day 30 and day 42. Samples from the hand-mixed treatment were collected prior to mixing. Video footage detailing the experimental layout and sampling procedure is available as electronic supplementary material from The University of Alberta, the author or online: www.ualberta.ca/~boeckner .

4.2.3 Meiofaunal processing and analysis

Samples were preserved in 8% formalin and then meiofauna were separated from the sediment via LUDOX floatation (See Warwick et al., 1998 for description) and sorted into broad taxonomic/life-history groups under a stereo microscope (25 X). Nematodes collected from the end of the summer 2006 study (day 42) were processed to glycerin (Seinhorst, 1959), slide mounted and identified to genus. Guides by Warwick et al. (1998) and Wieser (1954) were used to identify nematodes.

Differences in abundances of the most common groups of meiofauna (nematodes, post-larval harpacticoid copepods [referred from here on simply as harpacticoids], juvenile polychaetes and nauplii) between treatments and over time were investigated using repeated measures ANOVA (SPSS 13.0 for Windows). Detailed statistical output is available in the Appendices). Although other interesting patterns may have been revealed by identifying all organisms to finer taxonomic levels, the goal of this experiment was to look for patterns at the broad taxonomic levels reported in previous studies (see Table 4-1).

4.3 RESULTS

4.3.1 Comparing effects of suspension-feeding M. nasuta *and deposit-feeding* P. staminea

Over 8000 meiofaunal animals were sorted throughout the study (Table 4-2). Nematodes, post-naupliar stages of harpacticoid copepods and nauplii were by far the most abundant taxa/stages. Less often encountered were (in order of decreasing abundance) polychaetes, ostracods, amphipods, bivalves (other than the experimental animals), oligochaetes, halacarid mites, turbellarian flatworms, cumaceans, tanaids, gastropods and isopods. Nematodes dominated after the first week; however, their numbers gradually declined as the study progressed. Nauplii and harpacticoids were also abundant after only one week. Abundance of nauplii, like nematodes, decreased as the study went on while abundance of harpacticoids tended to climb. Although far less numerous, amphipods, ostracods and polychaetes were represented by more than 20 individuals in the first week and did not appear to increase or decline in abundance over the 8 weeks. Bivalves, isopods, gastropods and tanaids were encountered only late in the study and were represented by very few individuals. The remaining taxa were few in number and did not show any clear patterns in abundance over time. Weekly sub-sampling did not appear to have an effect as there was no difference in abundances of harpacticoids (DF:1, F=0.920, P=0.360), nematodes (DF:1, F=3.341, P=0.098) or nauplii (DF:1, F=1.915, P=0.197) after 8 weeks between the No-bivalve treatments (sampled weekly) and the Controls, E (sampled only at the end of the study).

4.3.1.1 Effects of bivalves on meiofauna abundance

Harpacticoid copepods: The repeated measures ANOVA showed a highly significant interaction ($P<0.001$) between time (week of collection) and bivalve treatment (Appendix 4-1, Fig. 4-4a). After one week the abundance of copepods showed no significant pattern related to bivalve treatment. As the study progressed, harpacticoid abundance climbed until week 6 in both No Bivalve and Only Suspension-feeding treatments, and then plateaued. In contrast, their abundance in Deposit-feeding and 50/50 Deposit-feeding and Suspension-feeding treatments remained at low levels throughout the experiment. At week 8, mean abundance of copepods for No Bivalves was significantly greater than for all other treatments (No Bivalve vs. Suspension-feeding: $P=0.01$; No Bivalve vs. 50/50 Deposit-feeding and Suspension-feeding: $P<0.0001$; No Bivalve vs. Deposit-feeding: $P<0.00001$) (Appendix 4-2). Abundance was also significantly lower in the Deposit-feeding treatments versus the Suspension-feeding treatments ($P=0.001$). The 50/50 treatment yielded copepod abundances intermediate between the entirely Deposit-feeding and entirely Suspension-feeding bivalves in weeks 3, 6 and 8; however, the values were not significantly different from those of the entirely deposit-feeding treatment.

Nematodes and nauplii: Abundances of nematodes and nauplii decreased almost continuously over the eight week period. Repeated measures analysis revealed no significant interaction of time (week of collection) with the various bivalve treatments (Appendix 4-1, Fig. 4-4b and 4-3c). Compared to No Bivalve treatments, abundances of nematodes and nauplii were lower in treatments with entirely deposit-feeding

bivalves (nematodes: $P<0.01$; nauplii: $P<0.01$). However, unlike for copepods, the Deposit-feeding treatment did not have significantly lower abundances of nematodes or nauplii than the Only Suspension-feeding treatment. Although nematodes and nauplii also tended to be less abundant in the Suspension feeding bivalve treatment and the 50/50 bivalve mix, these differences were not significant.

4.3.2 Tests with additional bivalve species and effects of metabolic byproducts

Over 5 400 meiofaunal animals were sorted throughout the summer 2006 study (Table 4-2). The most abundant taxa/stages were harpacticoids, nematodes, polychaetes and nauplii, respectively. Fourteen genera of nematodes were represented in the 136 identified individuals sampled after 42 days (Table 4-3). The genus *Chromadorina* was the most abundant and was present in all of the bivalve species treatments by day 42. Taxa less frequently observed were Calanoida (Copepoda), Amphipoda, Halacaridae, Tanaidacea, Bivalvia, Isopoda, Gastropoda, Euphausiacea and Cumacea (listed in order of decreasing abundance). In contrast to results from the autumn 2005 study, nematodes did not dominate after one week of colonization time. Instead, harpacticoid copepods were the most abundant colonizers early on and remained the most abundant taxon/stage throughout the 42 day study. Abundance of the two most numerous meiofaunal taxa, nematodes and harpacticoids increased throughout the duration of the study. Juvenile polychaetes and nauplii increased in abundance until day 24 where their abundance declined slightly. The remaining taxa were too few in number to present any clear temporal patterns.

4.3.2.1 Bivalve effects on meiofauna: Broadening the range of bivalves

All bivalve species had either no effect or a negative effect on meiofaunal abundance (Fig. 4-5). The species that most negatively affected nematode, harpacticoid and nauplius abundance were *M. nasuta*, *V. philippinarum* and *N. obscurata* in order of decreasing impact. Abundances of the above three meiofaunal groups were significantly lower in treatments with *M. nasuta* and *V. philippinarum* when compared to the no bivalve treatments. Treatments with *N. obscurata* also contained significantly fewer nematodes, (P=0.0308) and harpacticoid copepods, (P=0.0156), but not nauplii (P=0.1968) (Appendix 4-3). The remaining species, *P. abrupta*, *P. staminea* and *S. giganteus* were not associated with any significant declines in meiofaunal abundance. The overall most abundant nematode genus found in this study, *Chromadorina,* also tended to be least abundant in treatments of *M. nasuta*, *V. philippinarum* and *N. obscurata*. Weekly stirring was not associated with a decline in abundance of any of the meiofauna. Polychaetes showed no apparent responses to bivalve presence and activity, but instead increased in abundance in all treatments throughout the study.

4.3.2.2 Effects of caging on impacts of M. nasuta *and* P. staminea *impacts on meiofauna abundance*

<u>Harpacticoid copepods:</u> copepod abundance climbed early in the study until day 30 then began to plateau by day 42 in all treatments except for the un-caged deposit feeding *M. nasuta* in which they remained at low abundances throughout the study

(Appendix 4-5 and 6, Fig. 4-6A). The repeated measures analysis of variance showed the abundance of harpacticoids in the un-caged *M. nasuta* treatment was significantly lower than in the caged *M. nasuta* treatment (P = 0.0013). There was no significant difference in copepod abundance between the caged and un-caged *P. staminea* treatment (P=0.8249). Abundance of copepods in the un-caged *M. nasuta* treatment was significantly lower than in no-bivalve control, caged *M. nasuta* and both caged and un-caged *P. staminea* treatments.

Nematodes: Nematode abundance was highly variable within treatments over the duration of the study and neither increased nor decreased consistently over time (Appendix 4-5 and 4-6, Fig. 4-6B). Compared to the no-bivalve control, abundances of nematodes were lower in the presence of un-caged, deposit feeding *M. nasuta* (P = 0.003). Although not significant (P=0.057), nematode abundance also tended to be lower in un-caged verses caged treatments of *M. nasuta*. There were no significant differences between the no-bivalve treatment, caged/un-caged *P. staminea* treatments and caged *M. nasuta* treatment. Thus impeding bioturbation and predation with caged *M. nasuta* reduced its impact on nematodes as well as on copepods.

Nauplii: Abundance of nauplii increased in all treatments over the 42 days, albeit not consistently (Appendix 4-5 and 4-6, Fig. 4-6C). The rate of increase was lowest for nauplii in the un-caged bivalve treatments. After the first 6 days the lowest abundances were consistently recorded in the un-caged bivalve treatments. The abundance of nauplii in the un-caged *M. nasuta* treatment was significantly lower

than in the caged *M. nasuta* treatment (P=0.004). Similarly, nauplius abundances were consistently lower in the un-caged versus caged *P. staminea* treatments, although not significantly so (P=0.497). There was no significant difference between the abundances of nauplii in the no-bivalve control and the other treatments likely owing to the high degree of variability in nauplius abundance within the controls.

Polychaetes: Abundance of polychaetes gradually increased at the start of the study then rapidly rose from day 18 to day 30 followed by a moderate decline at the end between day 30 and day 42 (Fig. 4-6D). Abundance of polychaetes showed no significant patterns related to the various bivalve and no-bivalve treatments.

4.4 Discussion

4.4.1 Comparing effects of bioturbation and metabolic byproducts

Although only two bivalve species (*Macoma nasuta* and *Protothaca staminea*) were considered in the autumn 2005 study, both had a negative effect on the three groups of numerically dominant meiofauna: nematodes, harpacticoid copepods and nauplii. Furthermore, this decline was not solely caused by the feeding action of the tellinid siphons because abundances were also lower in the Suspension-feeding treatments. Although the decline associated with suspension-feeding bivalves was likely due to bioturbation or byproducts of metabolism, the removal of potential colonizers from the water column by suspension feeding cannot be ruled out. While harpacticoids showed the greatest decline in deposit-feeding bivalve treatments, nematodes and nauplii were equally affected by both the suspension and deposit

feeding bivalves. In the summer of 2006 a further aspect of bivalve impact was considered: the effects of clam metabolic byproducts. Similar to the results of the 2005 study, I found that the presence of un-caged *M. nasuta* was associated with the greatest declines in harpacticoids, nematodes, nauplii and polychaetes (although not significant, for polychaetes). Caging *M. nasuta* reduced the negative effects on meiofauna, which was predicted if bioturbation was instrumental in meiofaunal declines. Release of metabolic byproducts from the bivalves should not have differed greatly between the caged and un-caged treatments, but the rate of bioturbation and probably also feeding would have been hindered for the caged bivalves. The fact that un-caged *M. nasuta* had an effect and caged *M. nasuta* did not implies that bioturbation (impeded by caging) was the factor responsible for meiofaunal declines and not byproducts of bivalve metabolism. The congeneric bivalve *Macoma balthica* has been recorded to increase sediment re-suspension by a factor of four (Widdows et al., 1998). Perhaps *Macoma nasuta* shares this high rate of bioturbation which has a negative effect on meiofauna. Furthermore, the effects of uncaged *M. nasuta* on sediment mixing and deposits were visible at the end of the study by the reduced amounts of surface flocculent when compared to the caged and un-caged suspension feeder treatments (Fig. 4-7).

Meiofaunal abundance was generally the same for both caged and un-caged treatments of *P. staminea*. In fact, in contrast to our observations from autumn 2005, I did not find any significant effect of *P. staminea* on meiofaunal abundance. *Protothaca staminea* had significantly less of a negative effect on meiofauna in 2005 than did *M. nasuta*. Perhaps differences in effect of *P. staminea* between the two

studies were due to seasonal changes. For example, plankton concentrations were higher in the summer 2006 than in autumn 2005 (pers. obs.). Perhaps low plankton concentration causes increased rates of bioturbation by suspension-feeding bivalves as they attempt to locate favourable habitat or stir-up deposits to consume. This is speculation and requires further investigation to assess validity given that Stead and Thompson (2006) found increased bivalve bioturbation rates during periods of high planktonic algal concentrations. Maire et al. (2007) also found a decrease in bivalve bioturbation rate associated with colder water temperatures. However variable conditions may have been between the two years, the deposit-feeding *M. nasuta* produced consistently negative effects on meiofaunal abundance and this effect seemed to be primarily due to high rates of bioturbation via burrowing and feeding siphons. In comparison the suspension-feeding *P. staminea* had less of an effect, likely because of a reduced rate of bioturbation compared to *M. nasuta*.

4.4.2 Towards a generalization for bivalve effects on meiofauna

The four additional bivalve species added in the summer 2006 study were included to determine if there were any general effects of bivalves on meiofaunal colonization and subsequent proliferation. I did find some consistent patterns. There was no detectable effect of any of the six bivalve species on numbers of small polychaetes. Though small compared with other benthic polychaetes, the polychaetes (100 – 500 um) found in this study were generally much larger than the other meiofaunal groups and may have allowed them to escape disturbance from *M. nasuta's* feeding siphons. Bioturbation may have also have had less of an effect on these larger animals, which

may have been able to burrow through the sediment back to a preferred location after being dislodged. The other major meiofaunal taxa (nematodes, harpacticoid copepods and nauplii) were negatively affected by some but not all of the bivalves studied. The bivalves that had the most negative effect on abundance were *M. nasuta*, *V. philippinarum* and *N. obscurata* (in order of decreasing affect, from 2006). With the exception of *P. staminea* in 2005 the other three bivalve species did not significantly affect meiofauna abundance. I initially hypothesized that *M. nasuta* and *N. obscurata* would have a greater total effect than the other bivalves because they disturb the sediment both by burrowing and via long flexible incurrent siphons while feeding on deposits. The other bivalves also bioturbate as they move within the sediment, however, they do not feed upon deposits but instead on particles from the water column with two fused, upright siphons. Thus, these suspension feeders may have been preventing some suspended meiofaunal colonists from reaching the sediment but it is unlikely that they had as great an effect on meiofauna already established. As hypothesized, both *M. nasuta* and *N. obscurata* caused a greater decline in meiofauna than did most of the suspension-feeding species. The exception to our prediction was the suspension-feeding *V. philippinarum*, which was associated with a more severe decline in meiofaunal abundance than was the deposit-feeding *N. obscurata*. It is possible that *V. philippinarum* has an unusually high rate of bioturbation or particularly foul waste products that resulted in a greater decline in meiofauna. Differences in bioturbation rates between bivalve species have been documented previously for two other venerid clams (Francois et al., 1999). Further research comparing the nature of sediment disturbance (e.g. horizontal vs. vertical or initial vs.

continuous burrowing) for the 5 clams studied here would be useful in clarifying relationship between bivalve bioturbation and meiofaunal abundance.

Ólafsson (2003) argued that the effects of macrofauna on meiofauna are too variable among macrofaunal species to make generalizations regarding the effects of any one group. The results of our studies support this argument, as they show that not all bivalves affect meiofauna, and that when there is an effect, its intensity varies among the different groups of meiofauna. All but one of the previously published studies on bivalves and meiofauna found that bivalves had either no effect or a negative effect on meiofaunal abundance (Table 4-1). Surprisingly, the one study that found an increase in meiofaunal abundance (nematodes and turbellarians) used the deposit-feeding bivalve *Macoma balthica* (Reise, 1981); a congener of the species that I found had the strongest negative effect (*M. nasuta*). However, in another study Reise (1983) found that meiofauna at the surface were negatively affected by the presence of *M. balthica*. Ólafsson et al. (1993) also found that *M. balthica* negatively affected copepod abundance. Two other bivalve species have also been implicated in the decline of nematodes: *Atrina zelandica* Gray, 1835 (Warwick et al., 1997) and *Nuculoma tenuis* Montagu, 1808 (Austen et al., 1998). Our results agree with those studies that found a negative effect of bivalves on meiofaunal abundance. However, our results suggest that the largest impacts occur from bivalves with high rates of sediment disturbance. I found no effects of weekly stirring on infaunal abundance suggesting that the clam treatments that resulted in meiofaunal declines were subjected to more frequent and chronic disturbances. Suspension feeding bivalves that procure their nourishment from the water column such as *P. staminea* have less need

to displace the sediments compared with deposit feeders that need to burrow to new regions as deposits are used up. Furthermore, deposit feeders have the additional affect of sediment disturbance from the sweeping motion of incurrent feeding siphons. These additive effects on abundance of meiofauna may explain why previous studies that addressed a single behaviour or only overall effects found conflicting patterns between species. For example, Kennedy (1993), examining the effects of suspension-feeding cockles, failed to find an effect of bivalves on meiofauna while Ólafsson et al. (1993) and Reise (1983), working with deposit-feeding clams, did.

In conclusion, bivalves can have a strong negative effect on meiofaunal colonization and abundance. Large concentrations of highly mobile bivalves likely have the greatest effect. A survey of clams near Bamfield Marine Sciences Centre by Wong et al. 2005 found that field densities can often exceed that at which I stocked our experimental dishes: *N. obscurata* 340/m^2; *S. gigantea*, 320/m^2; *M. nasuta*, 220/m^2; *V. philippinarum*, 112/m^2 and *P. staminea*, 76/m^2 (values indicate maximum densities encountered throughout the survey). Thus, the meiofaunal ecology of an entire site may be strongly tied to the density and make-up of the bivalve community.

4.4.3 Significance of initial meiofaunal colonization

Colonization by various taxa during the fall 2005 study revealed several interesting patterns. Of greatest surprise was the early and abundant colonization by nematodes, which dominated the samples after only one week in the field. This is noteworthy given the common belief that marine nematodes are slow to disperse and usually rely upon entrainment with suspended substrate to spread to new habitats

(Gerlach, 1977; Jensen, 1981; Armonies, 1988; Ólafsson, 2003). Our study site was in a sheltered inlet and it seems unlikely that dispersal of nematodes into the containers was due to deposition of sediments carried by currents. I also took great care not to disturb surrounding sediment during the weekly field collections; however, physical disturbance caused by other animals in the habitat cannot be ruled out. Many large and small fishes, crabs and sea-stars were common in the study area and may have aided the dispersal of nematodes and other meiofauna to the treatment grid. No matter what the mode of dispersal was, it was striking that nematodes were three times more abundant after one week than were the copepods, which are capable of higher rates of active dispersal (Ólafsson & Moore, 1990; 1992). However, far fewer nematodes colonized the sediment after one week in 2006 than in 2005 (ANOVA; $P < 0.0001$) suggesting that the initial abundant appearance of nematodes in 2005 may have been due to a particular disturbance event rather than habitual active dispersal. However, there was no significant difference in copepod abundance between 2005 and 2006 ($P = 0.197$) samples suggesting that whatever caused the initial arrival of nematodes in 2005 did not have the same effect on copepods.

There was a sharp decline in nematode and nauplius abundances as the autumn 2005 study progressed. Although harpacticoids tended to increase in abundance over most of the study, they too declined toward the end. This was not observed in the summer of 2006 where the abundances of dominant meiofauna increased as the study progressed. Perhaps meiofaunal declines in 2005 were due to the onset of cooler water temperatures. Such seasonal fluctuations in meiofaunal

abundance have been noted before and generally maximum abundances occur in the warmer months of the year (Coull, 1988).

Table 4-1. Studies that have investigated bivalve impact on meiofauna in soft sediments (condensed and modified from Ólafsson 2003).

Bivalve Species	Mechanism Studied	Meiofauna Studied*	Effect on Density 0 = no effect (-) = decline (+) = increase	Reference
Atrina zelandica Gray	Overall effects	Nem	- Nem	Warwick et al. 1997
Atrina zelandica Gray	Overall effects	MT, Nem	0 MT, 0 Nem	Austen & Thrush 2001
Abra alba (Wood)	Overall effects	Nem	0 Nem	Austen et al. 1998
Nuculoma tenuis (Montagu)	Overall effects	Nem	- Nem	Austen et al. 1998
Cerastoderma edule (Linnaeus)	Overall effects	Tur	0 Tur	Reise 1983
Cerastoderma edule (Linnaeus)	Overall effects	MT	~ 0	Kennedy 1993
Macoma balthica (Linnaeus)	Biogenic structure	MT	+ Nem, + Tur	Reise 1981
Macoma balthica (Linnaeus)	Overall effects	Tur	- Tur (surface)	Reise 1983
Macoma balthica (Linnaeus)	Overall effects	Tur	+ Tur (deeper)	Reise 1983
Macoma balthica (Linnaeus)	Overall effects	MT, Nem	0 Nem, - Harp	Ólafsson et al. 1993
Macoma balthica (Linnaeus)	Dead tissue	MT, Nem	0 Nem, - Harp	Ólafsson 1992
Scrobicularia plana (Da Costa)	Overall effects	MT	~ 0	Kennedy 1993

[a] Nem = Nematoda, MT = Major Taxa (all types of meiofauna consolidated into one group), Tur = Turbellaria

Table 4-2. Total abundance of each meiofaunal taxon that colonized the experimental sediment over time. Values reflect number of individuals found within the 10 cc sediment samples collected from each dish and summed across all treatments for the fall 2005 and summer 2006 studies. Listed in order of decreasing abundance.

	Days after deployment (Fall 2005)					Days after deployment (Summer 2006)					
	6	18	36	48	Total	0	6	18	30	42	Total
Nematods	1237	1026	788	749	3800	120	165	183	219	361	1048
Harpacticoids	361	603	1141	888	2993	16	332	540	1005	1195	3088
Nauplii	363	246	171	48	828	0	46	94	168	130	438
Polychaets	59	62	97	38	256	0	17	41	409	278	745
Ostracods	33	55	2	65	155	0	0	0	0	0	0
Amphipods	28	26	15	19	88	0	1	4	3	4	12
Bivalves[a]	0	3	6	9	18	0	5	0	1	1	7
Oligochaets	4	12	0	0	16	0	0	0	0	0	0
Acarines	5	5	3	1	14	0	6	1	0	2	9
Turbellarians	1	8	0	2	11	0	0	0	0	0	0
Cumaceans	2	1	1	3	7	0	0	0	0	1	1
Tanaids	0	0	1	2	3	0	2	1	1	3	7
Gastropods	0	0	0	1	1	0	1	0	0	0	1
Isopods	0	0	1	0	1	0	1	1	3	0	5
Calanoids	0	0	0	0	0	0	65	2	0	7	74
Shrimp	0	0	0	0	0	0	1	0	0	0	1
Total	2093	2047	2226	1825	8191	136	642	867	1809	1982	5436

[a] excluding experimentally added bivalves

Table 4-3. Total number of nematode genera encountered in sediment samples over the entire 42 day study for each of the eight treatments (Summer 2006).

	M. nastuta	***N. obscurata***	***V. philippinarum***	***P. staminea***	***P. abrupta***	***S. gigantea***	**Stir**	**None**
Chromadorina sp.	4	5	3	8	28	9	17	11
Daptonema sp.		1			3	4	3	1
Desmodora sp.		1		1				1
Marylynnia sp.					1			2
Mononchus sp.							2	
Neochromadora sp.				1	1			
Oxystomina sp.							2	
Paralinhomoeus sp.					1		2	
Parascolaimus sp.					2			
Phanoderma sp.				6				
Spilophorella sp.		1			2			1
Theristus sp.	1	1			4		2	
Viscosia sp.						1	2	1
Damaged	6	1		2	5	5	6	4
Total	**11**	**10**	**3**	**18**	**47**	**19**	**36**	**21**

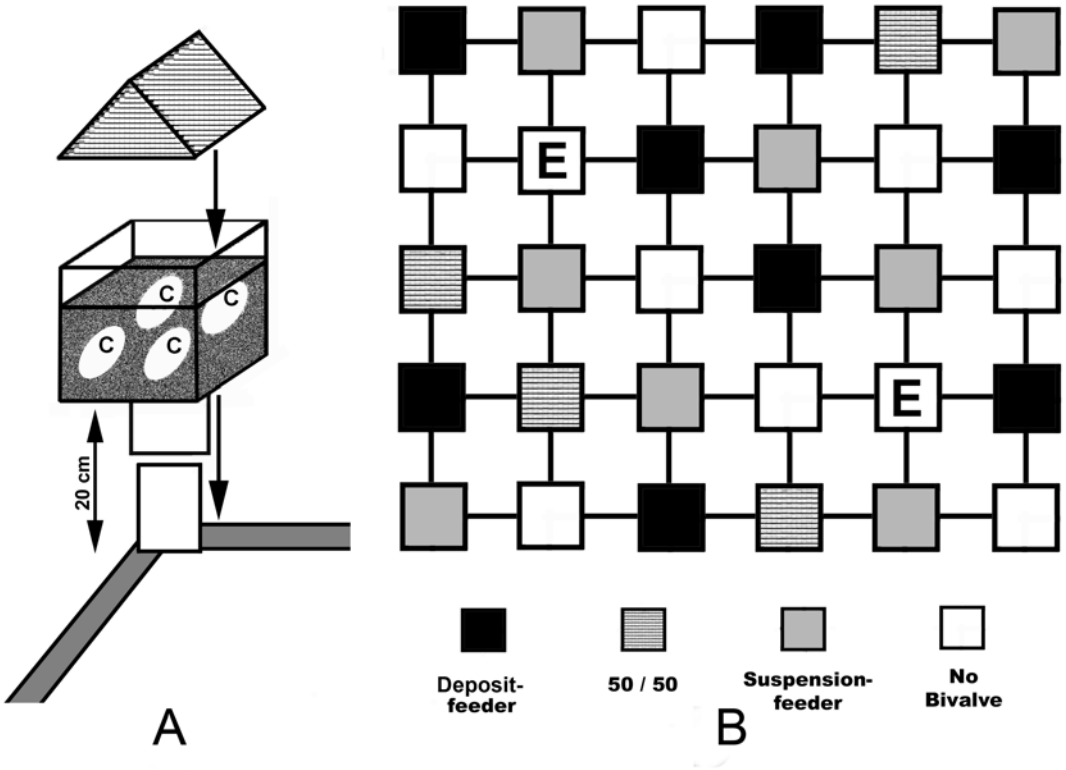

Fig. 4-1. A) Detail of a single treatment dish (Autumn 2005), c = clam. Triangular mesh covering prevented disturbance of the sediment within each dish. Arrows indicate how the component parts were assembled under water. B) The entire study grid showing replication of each treatment and position of controls (E). Each clam treatment contained either four *M. nasuta* (deposit-feeder), four *P. staminea* (suspension-feeder) or two of each (50/50).

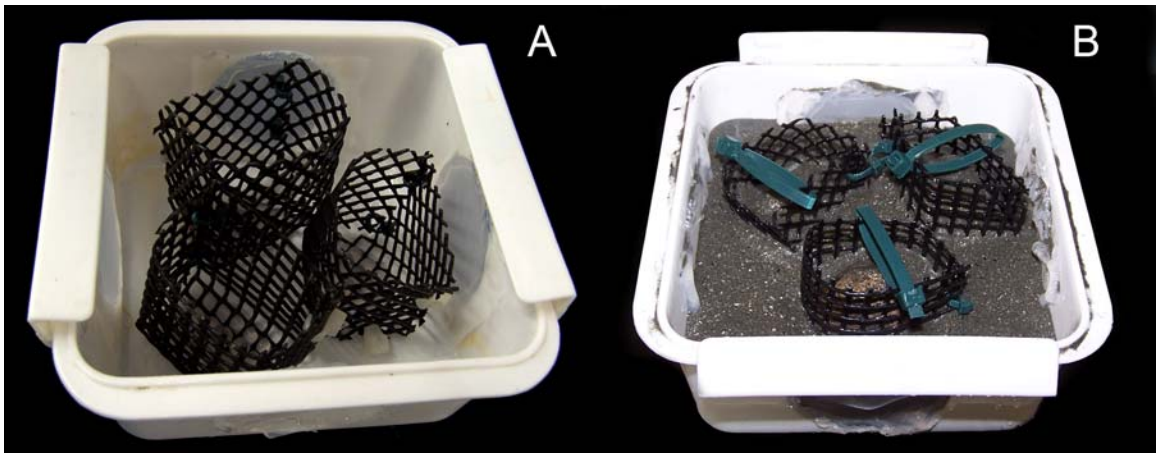

Fig. 4-2. Method used to restrict bivalve bioturbation and test for chemical effects. A) empty dish showing individual cages B) clams and sediment added. A cable placed across the top of each cage prevented the escape of clams.

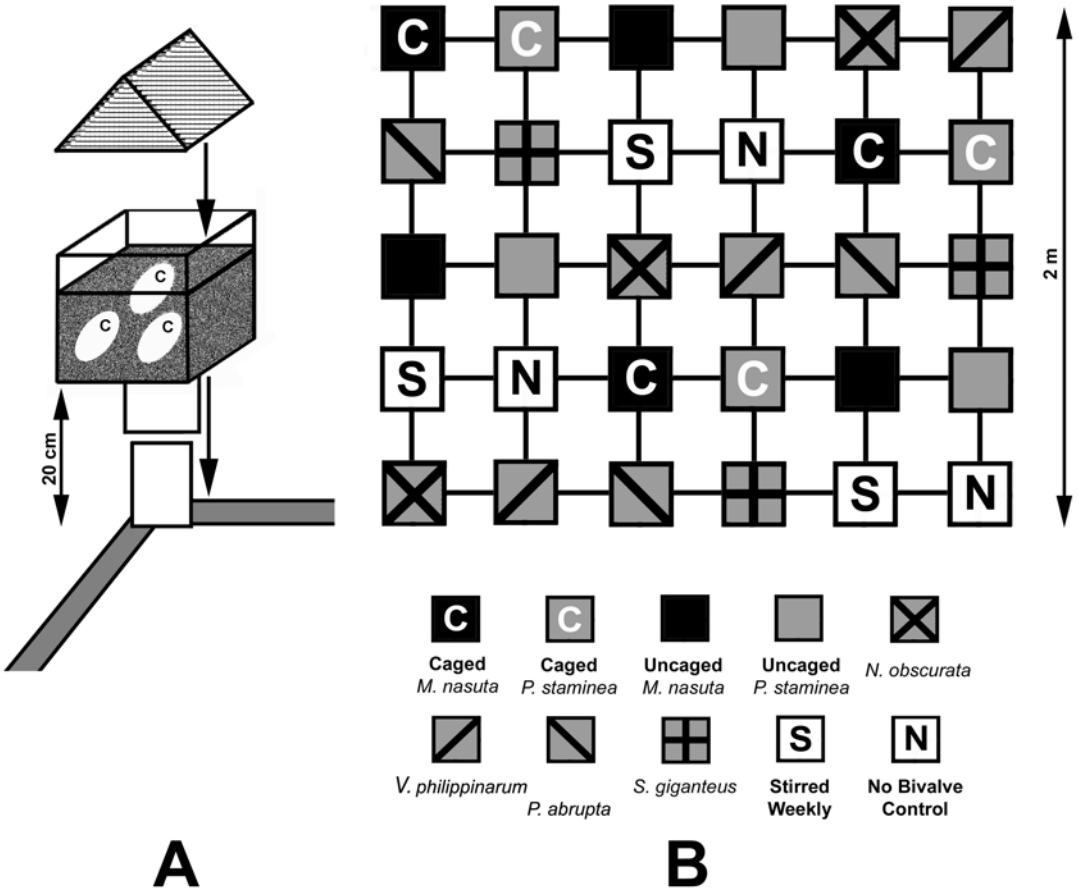

Fig. 4-3. A) Detail of a single treatment dish (Summer 2006), c = clam. Triangular mesh covering prevented disturbance of the sediment within each dish. Arrows indicate how the component parts were assembled under water. B) the entire study grid showing positions of each treatment and no-bivalve controls.

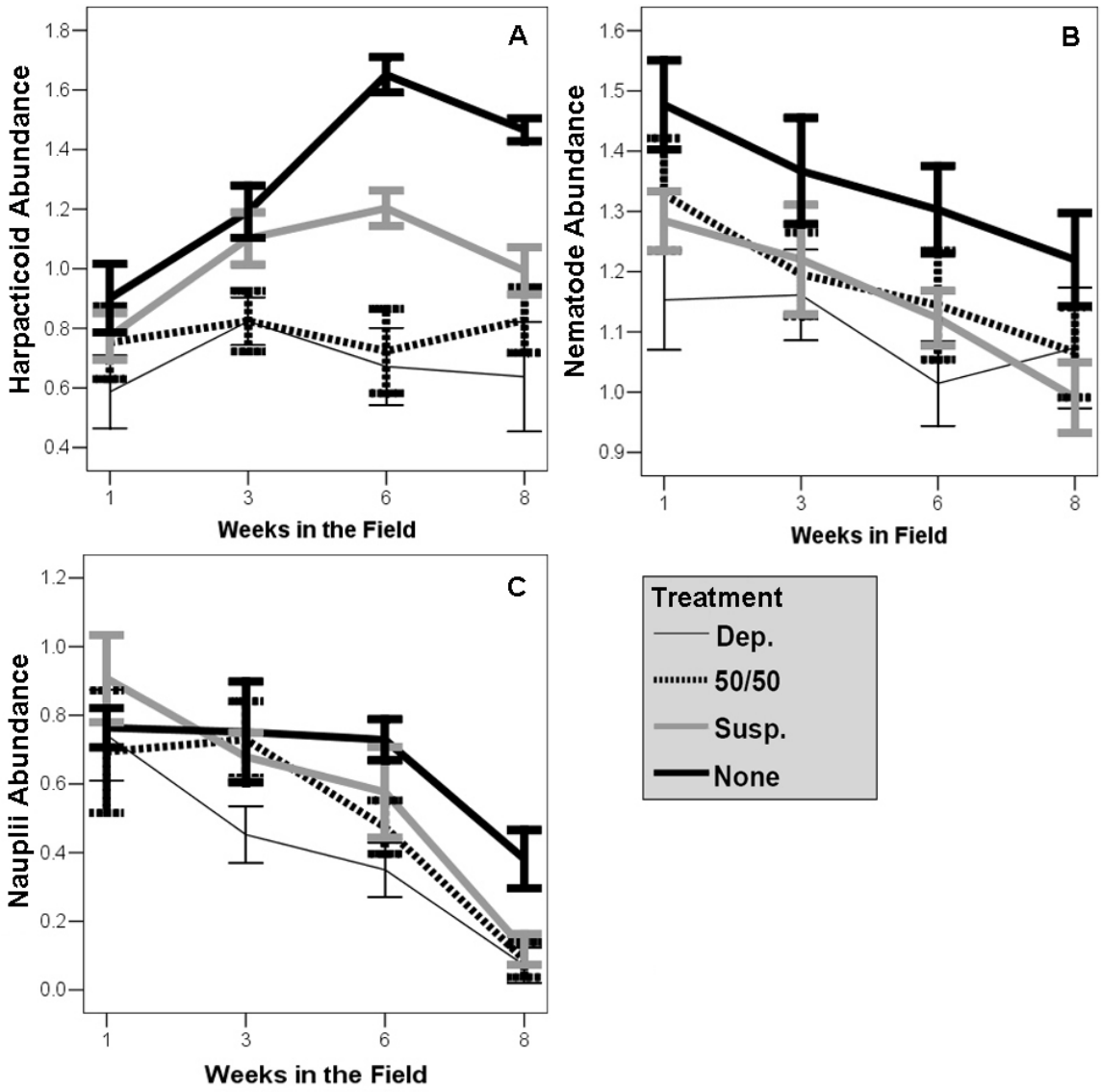

Fig. 4-4. Mean abundance of A) copepods, B) nematodes and C) nauplii from 10 cc of sediment taken from each treatment (eight replicates) at 4 separate times (weeks 1, 3, 6 and 8). Data has been log10+1 transformed, error bars represent +/- 1 SE. Dep.: only deposit-feeding bivalves; 50/50: half deposit-feeding and half suspension-feeding bivalves; Susp.: suspension-feeding bivalves; None: no bivalves.

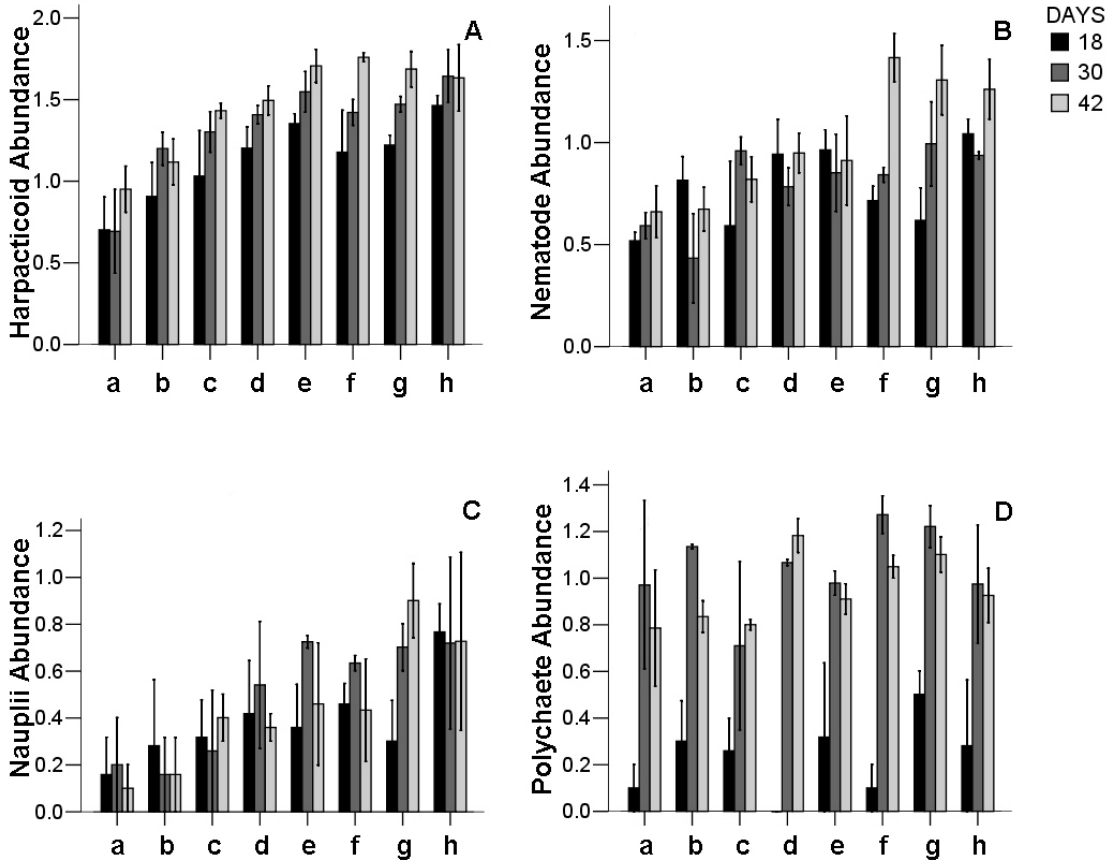

Fig. 4-5. Towards a generalization for bivalve effects on meiofauna (Summer 2006). Mean abundance of A) harpacticoids, B) nematodes, C) nauplii and D) polychaetes associated with each bivalve species over the 42 day study (individuals per 10 cc sediment sample per dish, replicated three times per treatment) Data was log10+1 transformed, error bars represent +/- 1 SE. Treatments: a) *M. nasuta*, b) *V. philippinarum*, c) *N. obscurata*, d) *S. gigantea*, e) *P. staminea*, f) *P. abrupta*, g) stirred-weekly, h) no-bivalve control.

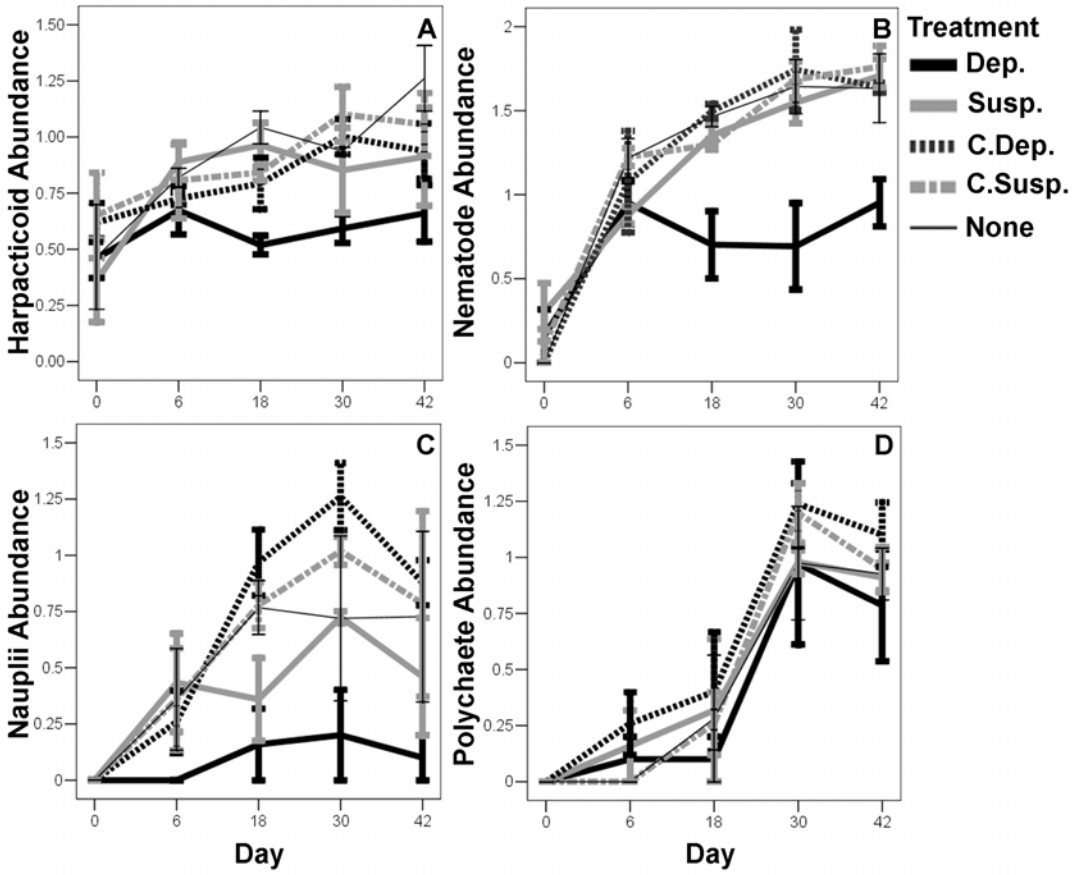

Fig. 4-6. Mean abundance of A) harpacticoids, B) nematodes, C) nauplii and D) polychaetes for each treatment throughout the 42 day study (Individuals per 10 cc sediment sample per dish, replicated three times per treatment). Data was log10+1 transformed, error bars represent +/- 1 SE. Treatments: Dep.- uncaged deposit-feeding bivalves (*M. nasuta*), Susp.- uncaged suspension-feeding bivalves (*P. staminea*), C.Dep.- caged deposit-feeding bivalves, C.Susp.- caged suspension-feeding bivalves, None- no bivalve control.

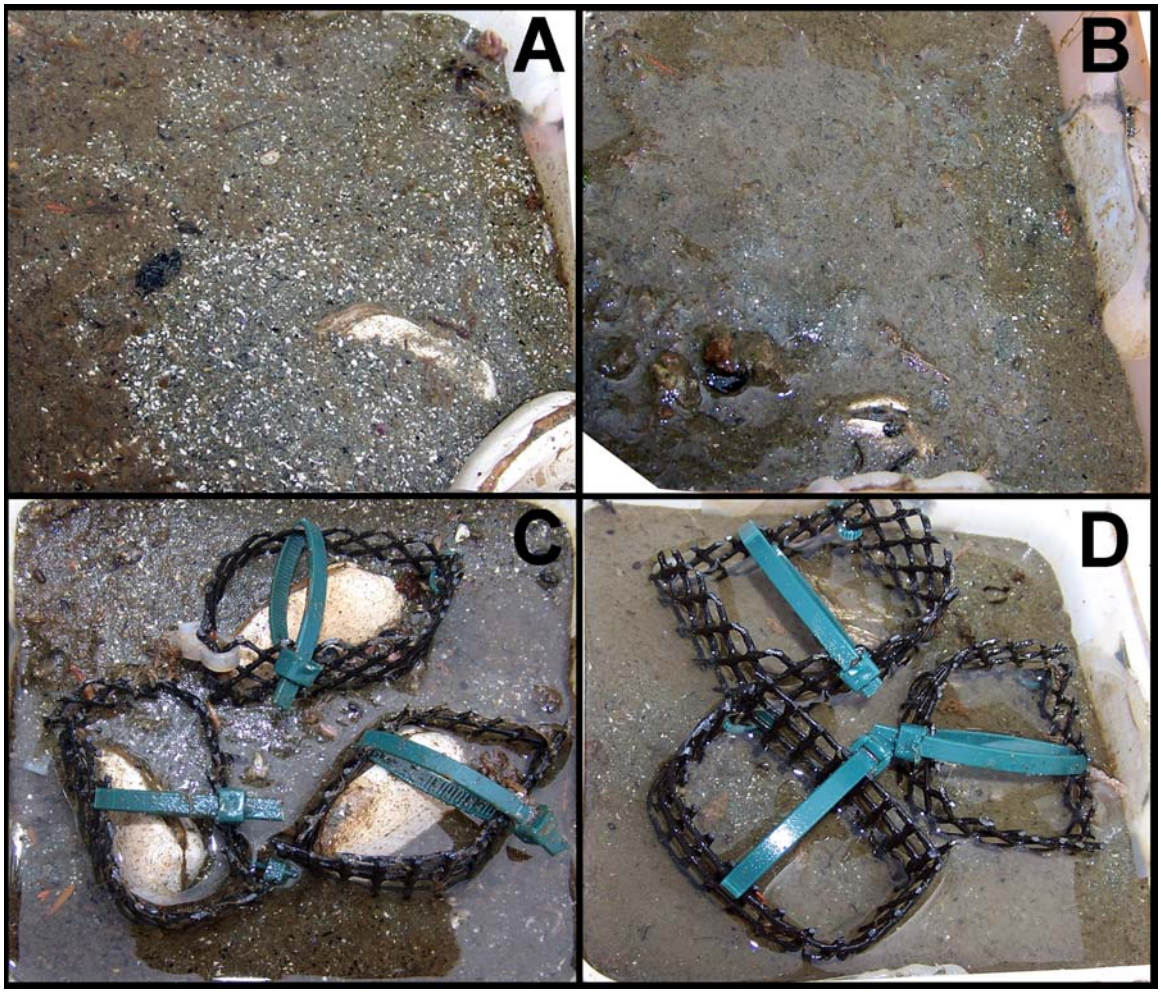

Fig. 4-7. Photos showing the variability of flocculent accumulation between treatments after 42 days. A) deposit-feeder, B) suspension-feeder, C) caged deposit-feeder and D) caged suspension-feeder.

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CHAPTER 5.

QUANTITATIVE MEASUREMENTS OF BIOTURBATION BY DEPOSIT- AND SUSPENSION-FEEDING CLAMS

5.1 INTRODUCTION

Bivalve molluscs are an abundant and diverse component of the marine biota. Hard-substrate bivalves such as mussels and oysters rely on currents to suspend materials that they filter from the water. Soft-substrate bivalves including some clams may either filter from the water column (suspension-feeders) or, particularly in low energy environments, draw deposits from the surface of surrounding sediment into the mantle cavity with long and flexible incurrent siphon (deposit-feeders). Some clams including *Nuttallia obscurata* either deposit- or suspension-feed depending on which is more profitable at the time (Gillespie et al, 1999). Deposit-feeding clams live predominantly in finer sediments while suspension-feeders are common in coarser sediments (Rhoads and Young, 1970). Suspension- and deposit-feeding clams may occupy separate habitats because the burrowing and sediment suspension of the deposit-feeders can hamper suspension-feeding (Rhoads & Young, 1970; Dame, 1996).

Bivalves often dominate the biomass of infaunal communities in sedimentary habitats and impact the sediment environment in many ways (Peterson, 1977; Legendre et al., 1997). Burrowing by clams affects the vertical distribution and lowers the stability of sediments (Rhoads & Young, 1970; Nowell et al., 1981; Hall, 1994; Reise, 2002). Pseudofecal pellets consisting of aggregated indigestible materials and released as byproducts of bivalve feeding may: alter sediment particle composition (Reise, 2002),

clog the feeding structures of neighbouring suspension-feeders, or render substratum unsuitable for colonization by larvae (Rhoads & Young, 1970). Clams can strongly affect surrounding sediment chemistry via release of waste products containing ammonium and phosphate (Magni et al., 2000; Magni & Montani, 2006). Deposit-feeding bivalves in particular intensively rework and alter sediment characteristics (Rhoads & Young, 1970; Gingras et al., 2008) which may have important consequences to neighbouring fauna. Many small and abundant taxa residing close to the sediment surface (including nematodes and copepods) can be negatively affected by the burrowing of deposit-feeding bivalves (see for example Quayle, 1960; Jørgensen, 1990; Ólafsson, 2003). Suspension-feeding clams may affect benthic communities by ingesting potential colonists arriving from the water column (Shaw, 1986; Kennedy, 1993).

Given all the ways bivalve bioturbation can impact the ecology of soft-sediment systems, very little is actually known about the rate and pattern of bioturbation among species. Which species burrow the fastest/slowest or disturb the greatest/least amount of sediment as they move? Do certain clams burrow more deeply or shallowly than others? Is there a measurable difference in bioturbation rate between deposit- and suspension-feeding clams? I documented variation in bioturbation effects among 5 species of clam (2 deposit-feeders and 3 suspension-feeders) and discuss the role each may play in their respective habitats. I predicted that surface deposit-feeders would burrow more shallowly, chronically disturbing the sediment as they search for food than suspension-feeders, which would initially burrow to deeper regions then remain relatively stationary feeding from the water column via extended siphons.

5.2 Materials and methods

5.2.1 Specimen collection and selection

Five species of clam were collected from intertidal, soft-sediment sites near Bamfield Marine Sciences Centre, British Columbia and taken to the lab where they were allowed to acclimate to local water conditions for 48 hours. Two deposit-feeding species (*Macoma nasuta* Conrad, 1837 and *Nuttallia obscurata* Reeve, 1857) and three suspension-feeders (*Venerupis philippinarum* A.Adams & Reeve, 1850, *Protothaca staminea* Conrad, 1837 and *Panopea abrupta* Conrad, 1849) were collected (Fig. 5-1). Bivalves of similar size (and small enough to maneuver freely between the walls of the aquaria, maximum thickness of 2 cm) were initially selected for use in the study, and then observed for 24-hours. Only those that extended a foot and siphons were included in the study.

5.2.2 Experimental aquaria

Thirty-six thin, Plexiglas aquaria were assembled; 6 for each of the 5 clam species and 6 for the no-clam controls. Each tank was 2.5 cm wide, 15 cm long and 12 cm high. Aquaria needed to be thin to allow adequate x-ray transmission (technique adapted from Gingras et al., 2007). Alternating layers of silica and magnetite sand were added to the aquaria (Fig. 5-2). Each band of silica sand measured 1.5 cm thick and each band of magnetite 0.2 cm thick. Sterilized silica sand was purchased while magnetite was harvested from dry sand at a nearby beach (Brady's Beach) using a strong magnet. There were 6 bands of silica and five bands of magnetite in each aquarium giving a total depth of 10 cm. Magnetite sand completely blocked out x-rays while silica sand did not.

Bivalve bioturbation was measured based on the degree to which the bands of sand changed over time.

5.2.3 X-ray procedure

Each of the 36 aquaria had its own source of filtered sea-water (drawn from an overhead reservoir) with a flow rate of 22 L/hour (Fig. 5-2) and allowed to rinse for 48 hours prior to the start of the experiment. With the exception of the six no-clam controls, each aquarium was stocked with three conspecific clams. Bivalves were initially added to the aquaria by orienting the animal foot down and pressing gently until buried about half way (Fig. 5-3a). Initial x-rays were taken immediately after the bivalves were added (Time 0). Further x-rays were taken for each tank after 6, 12, 18, 24, 48, 72, 96 and 120 hours. The opening of each aquaria was plugged with a tightly fitting rectangular sponge (to prevent movement of substrate during x-ray) and placed horizontally under a LIXI PS500 OS X-ray system and images were recording using LIXI image processing software (Huntley, IL, USA). Technical specifications for X-ray were 35 kV tube voltage, 155 uA tube current with a 5 cm focal window. Due to the limited field of view (5 x 5 cm), 8 x-ray images needed to be taken of each aquarium (4 across top half and 4 across bottom half) at each time-step and arranged together using Adobe Photoshop CS3 into a single image (Figs. 5-3b and 5-4). A guide composed of a metal grid was snapped onto each tank before x-raying to ensure that photos were always taken of the same region. These images were then arranged into short animations that showed how each species disturbed the sediment as it burrowed and are available as electronic supplementary materials through the University of Alberta, the author or online:

www.ualberta.ca/~boeckner. X-ray photograph collages assembled after 0, 12, 24 and 120 hours can be found in Appendix 5-1.

5.2.4 Measuring disturbance

To evaluate differences in bioturbation between the bivalve species, the degree of sediment disturbance in each aquarium was quantified. The portion of undisturbed (pure white) silica sand in each x-ray photo was traced using the "freehand selections" tool of the Image-J 1.38x graphic application: http://rsbweb.nih.gov/ij (Fig. 5-3d). The area of silica sand in each photo was then calculated in square centimetres. The areas for the upper four and lower four x-ray photos of each aquarium were averaged to determine shallow and deep bioturbation rates, respectively (lower mean area of silica sand = greater amount of bioturbation). This was done for each aquarium at 0, 12, 24 and 120 hours. Repeated measures ANOVAs were conducted to determine differences in bioturbation rates and depths between the bivalve species over time (N=6 per clam species, with the exception of aquaria that became damaged during the experiment, see results). Two separate repeated measures ANOVAs were run, one for each the shallow and deep portions of the aquaria using the SPSS 13.0 statistics package.

5.3 RESULTS

Aquaria containing bivalves showed significant declines in area of non-bioturbated silica sand while the control tanks remained virtually unchanged over the 5 day study (Fig. 5-5). Clam species differed in their levels of sediment disturbance, time taken to disturb the sediment and depth of disturbance. These differences did not seem to

be strictly due to bivalve feeding types. A repeated measures analysis was conducted to determine which species of bivalve had significant impacts on both the shallow (0 – 5 cm) and deep (5 – 10 cm) sand profiles and if the level of disturbance was consistent for the duration of the study. Fig. 5-5 shows the degree to which each clam species affected both shallow and deep silica layers. Four aquaria were damaged in early stages of the experiment and so could not be used: *V. philippinarum* (replicate 1), *P. staminea* (replicate 6), *P. abrupta* (replicates 5 and 6).

5.3.1 Shallow region

All assumptions for the repeated measures analysis were met including non-equality of covariance matrices and tests for sphericity. The amount of silica disturbed *within* each clam treatment changed significantly over time ($DF=15$; $F=3.262$; $P<0.001$). Therefore the amount of undisturbed silica sand in the shallow regions of the aquaria underwent substantial changes over the 120 hour study. The amounts of undisturbed silica also differed significantly *among* the various bivalve treatments (and control) ($DF=5$; $F=13.06$; $P<0.001$). The partial ETA squared for the effects of treatment was 0.740 which indicated that species identity explained a large proportion of the variation in area of undisturbed silica sand. A Post Hoc test (Tukey's) was conducted to identify treatments that were significantly different from one another (homogeneous subsets). The control had significantly less disturbed silica than all the bivalve treatments (significance of $P<0.0005$ for contrasts between each of the 5 clam species and the control). However, no bivalves differed significantly in their disturbance of the upper sand levels. In other words, all of the clams investigated showed equal capacity for shallow bioturbation.

5.3.2 Deep region

The assumption that the variance-covariance matrix of the dependent variable should be spherical in form was not met for bioturbation in the deep region of the experimental aquaria, so a Greenhouse-Geisser adjustment was made and I used the more conservative values from this adjustment (resulting in some non-integer degrees of freedom). The amount of silica disturbed *within* each treatment changed significantly over time (DF=9.946; F=2.249; P=0.031), so the amount of undisturbed silica sand in the deep regions of the aquaria varied over the 120 hour study. The amounts of undisturbed silica also differed significantly among treatments (DF=5; F=1.108; P=0.046). The partial ETA squared for the effects of treatment was 0.370 which indicated that this factor explained a moderate proportion of the variation in area of undisturbed silica sand. A Tukey's Post Hoc test showed that the suspension-feeding clam, *P. abrupta* disturbed the greatest amount of silica in the deeper regions and was most different from the control (P=0.108) and from *M. nasuta* (P=0.037), which did not have an effect on deep layers. Although not significantly different from the control, *P. staminea* (a suspension-feeder) was beginning to have an effect on undisturbed silica in the deep layers toward the end of the study (Fig. 5-5).

5.3.3 Bioturbation animations

Animations were made of the x-ray images to provide a visual impression of how each clam species moved through the sediment over the five day study. These animations were created using the software package Easy GIF Animator 4.0 and are available as online supplementary material available from The University of Alberta, the author or

online: www.ualberta.ca/~boeckner. Time lapse X-ray photographs taken after 0, 12, 24 and 120 hours are found in Appendix 5-1. The animations show those species that tended to remain in the shallow portions of the sediment versus those that quickly moved to deeper regions. Generally, *P. staminea* and *P. abrupta* (suspension-feeders) tended be found mainly in deeper sediment by the end of the 5 days. Conversely, *M. nasuta*, *N. obscurata* (deposit-feeders) and *V. philippinarum* (suspension-feeder) generally remained in shallower regions of the aquaria.

5.4 Discussion

Bioturbation effects differed considerably among five clam species studied. *Macoma nasuta*, *Nuttallia obscurata* and *Venerupis philippinarum* were the shallowest burrowers and remained primarily in the upper five cm of the sediment. Conversely, the two suspension-feeding clams, *Protothaca staminea* and *Panopea abrupta* burrowed quickly to deeper sediment. Both deposit-feeding clams were clearly shallow burrowers. Perhaps there is an advantage for deposit-feeding in shallow sediments. Deposit-feeding clams consume large amounts of materials in a short period of time and sediment ingestion rates as high as 10-20x the clam's body weight/hr have been reported for *Yoldia limulata* (Lopez & Levinton, 1987). Although not nearly as high as *Y. limulata* the daily feeding rate for *M. nasuta* is still 1-2 times its body weight (Lopez & Levinton, 1987). As the sediment surface is cleaned of nutrients clams will need to move to adjacent regions to feed. *Macoma nasuta* and *N. obscurata* feed primarily on deposits that accumulate at the sediment-water interface and would likely benefit by residing closer to the sediment surface where they can more easily move to new areas to feed. Suspension-feeding clams

are less likely to migrate after they have settled because their nutritional needs are met via circulating water above, which would suggest why two of the suspension-feeding clams in this study were typically deeper burrowers. The exception was the suspension-feeder *V. philippinarum* which is remarkably similar in form to *P. staminea* (Fig. 5-1) but remained in the shallow sediment throughout the experiment. Gillespie et al. (2001) also described *V. philippinarum* as being found close to the surface of the sediment. Although these two clams are morphologically similar and feed on suspended material, they seem to exhibit distinct burrowing depth preferences. Perhaps siphon lengths are shorter for these two species, which would account for why they didn't burrow as deeply.

The five clams were also varied considerably in the amounts of sediment they disturbed. Although all five species significantly mixed the shallow sediment, *M. nasuta* disturbed the smallest amount. I had originally predicted that this species would greatly disturb shallow sediment layers. However, throughout the study *M. nasuta* remained very close to the surface of the sediment, often just barely buried. Although *N. obscurata* and *V. philippinarum* mixed the shallow sediment more than *M. nasuta* none of the three had any effect on deeper sediment regions. The remaining clams, *P. abrupta* and *P. staminea*, also initially disturbed upper sediment layers but as the study progressed individuals of these two species moved to deeper sediments. *Panopea abrupta* had little effect on the shallow sediment after the initial twelve hours. *Protothaca staminea* reached deeper sediment more slowly likely owing to its spherical shape (Fig. 5-1). The juvenile geoduck clams (*P. abrupta*) had the greatest impact on deeper sediment. This was expected given that adults of this species are exceptionally deep burrowers residing generally one metre below the surface of the sediment (Kozloff, 2000).

My initial prediction was that deposit-feeding clams would have a greater and more prolonged effect on shallow sediment than suspension-feeding clams. In a similar study the deposit-feeding clam *Dosinia discus* was found to burrow further and displace far greater amounts of sediment (7-10 cm^3 of sand per hour) than the suspension-feeding bivalves *Labiosa lineate* and *Solen viridis* (~0.5 cm^3 of sand per hour) (Gingras et al., 2008). However, our results show very little difference in actual disturbance to the shallow sediment between suspension- and deposit-feeders. Perhaps if the study had been allowed to continue for a longer period I would have observed a chronic disturbance of the shallow sediment by the deposit-feeders and a more benign effect of suspension-feeders.

The shallow and prolonged bioturbation of deposit-feeding clams such as *M. nasuta* and *N. obscurata* is likely to have ramifications to neighbouring organisms that might be sensitive to these disturbances. For example, *M. balthica*, a congener of *M. nasuta*, has been implicated repeatedly in declines of various other organisms. Ólafsson et al (2005) found that *M. balthica* prevented formation of algal mats and resulted in lower abundances of meiofauna. Reise (1983) even found that *M. balthica* prevented the establishment of macrofaunal, tube-dwelling polychaetes. Conversely, because suspension-feeders had a more benign effect on sediment mixing after the initial stages of burrowing and feed on materials suspended in the water column it is less likely that these clams have as great an effect on neighbouring fauna residing in the sediment. For example, Kennedy (1993) did not find any effect of suspension-feeding cockles on nearby fauna. Thus actively bioturbating, deposit-feeding clams may have more of a negative impact on neighbouring organisms than suspension-feeders. If true, this could

have pronounced ecological implications. Deposit- and suspension-feeding clams have often shown “reciprocal spatial distributions” (Dame, 1996) and therefore the ecology of seemingly similar coastal habitats may be drastically different based on the behaviours of the resident clam species.

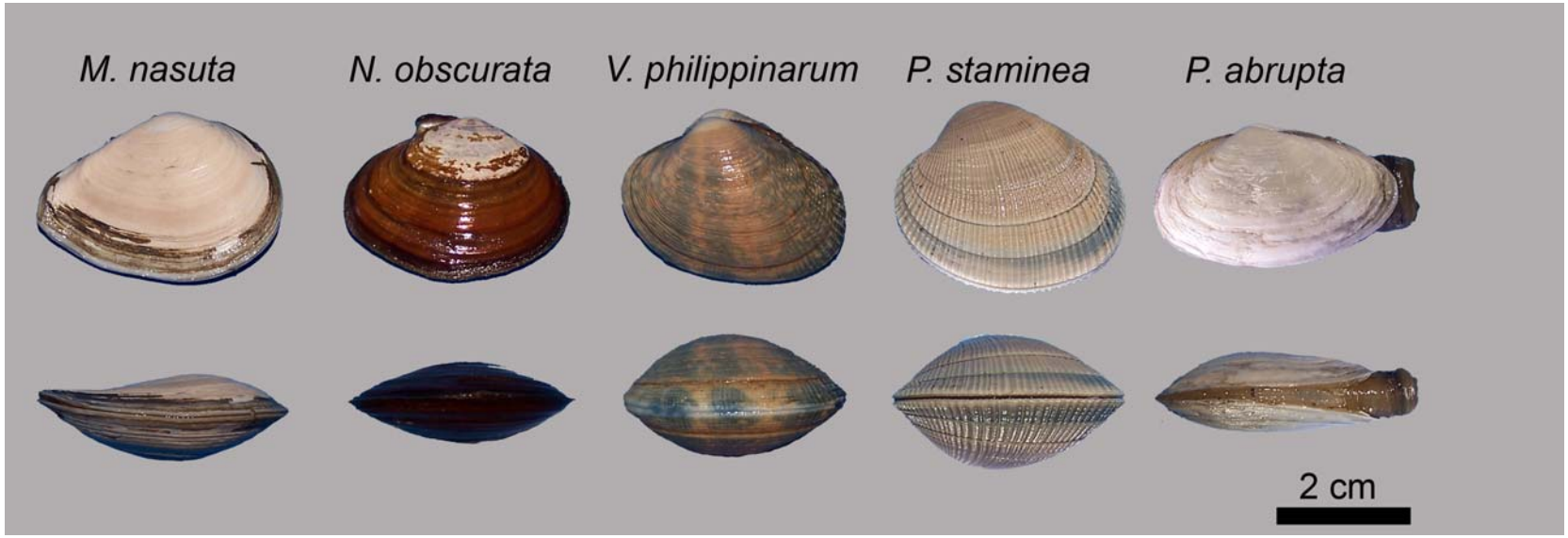

Fig. 5-1. Lateral and dorsal views of the five clam species used in this study: *Macoma nasuta* (Bent-nose clam), *Nuttallia obscurata* (Varnish clam), *Venerupis philippinarum* (Manila clam), *Protothaca staminea* (Littleneck clam), *Panopea abrupta* (Geoduck).

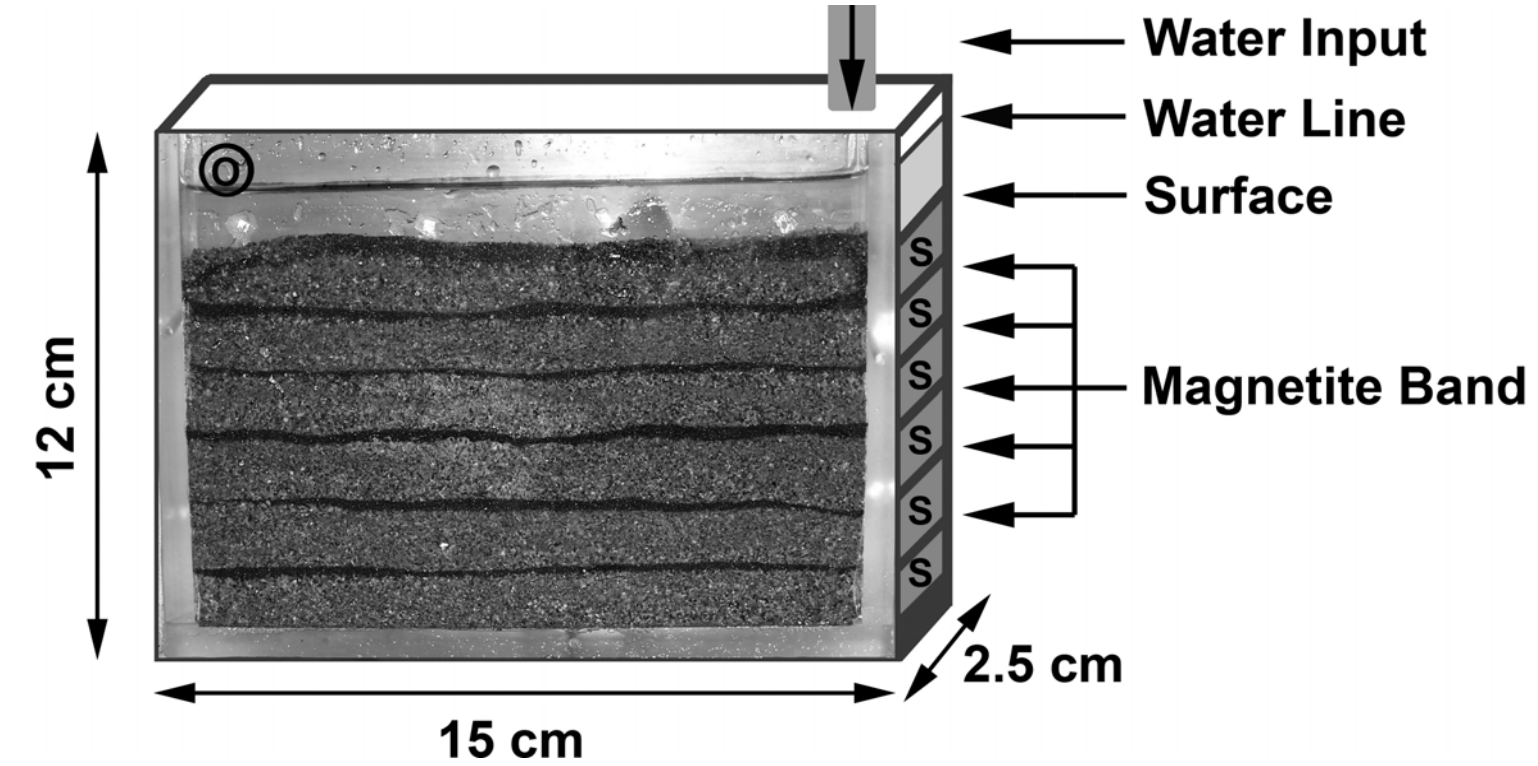

Fig. 5-2. Photo-diagram of a single aquarium filled with alternating layers of magnetite and silica (S) sand before clams were introduced. “O” indicates the overflow drain.

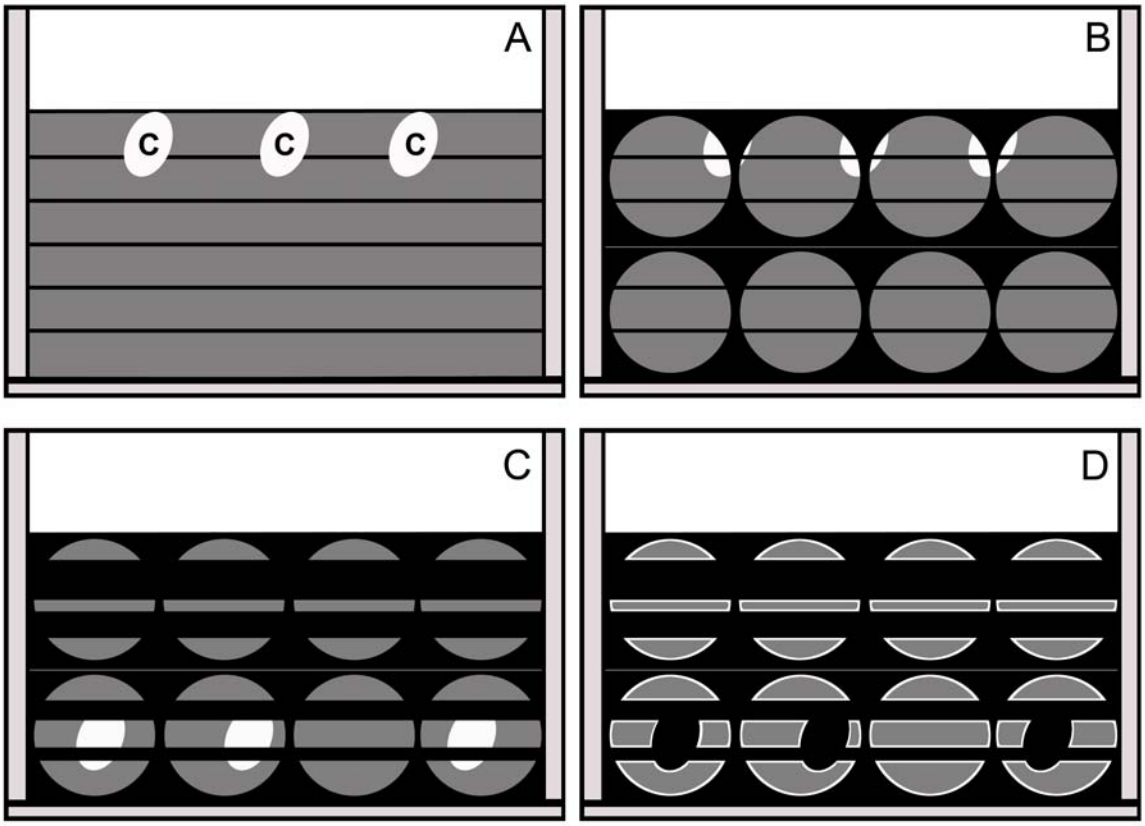

Fig. 5-3. A) A single aquarium at the start of the study after addition of clams (c); horizontal lines represent thin layers of magnetite. B) How eight portions of the aquarium (circles) were x-rayed and arranged to represent a single image of an entire aquarium. C) Illustrating the spread of the magnetite sand (thick horizontal lines) as the bivalve burrows to deeper regions over time. D) The portion of silica sand measured with Image-J (outlined in white).

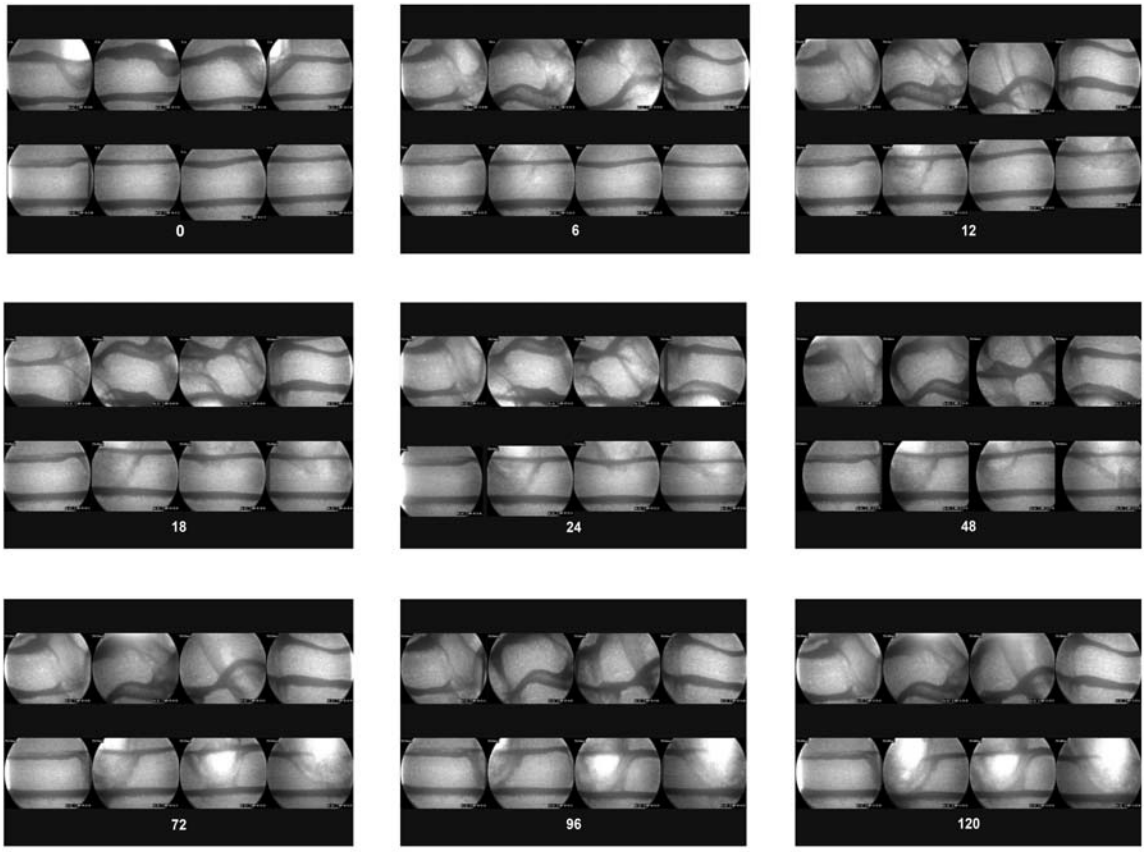

Fig. 5-4. A sample of the images captured at 9 times (0, 6, 12, 18, 24, 48, 72, 96 and 120 hours as marked beneath each collage) throughout the study prior to animation formatting. These photos are from the first replicate of *Panopea abrupta*. The images in time 48 were off centre due to improper initial calibration of the x-ray camera.

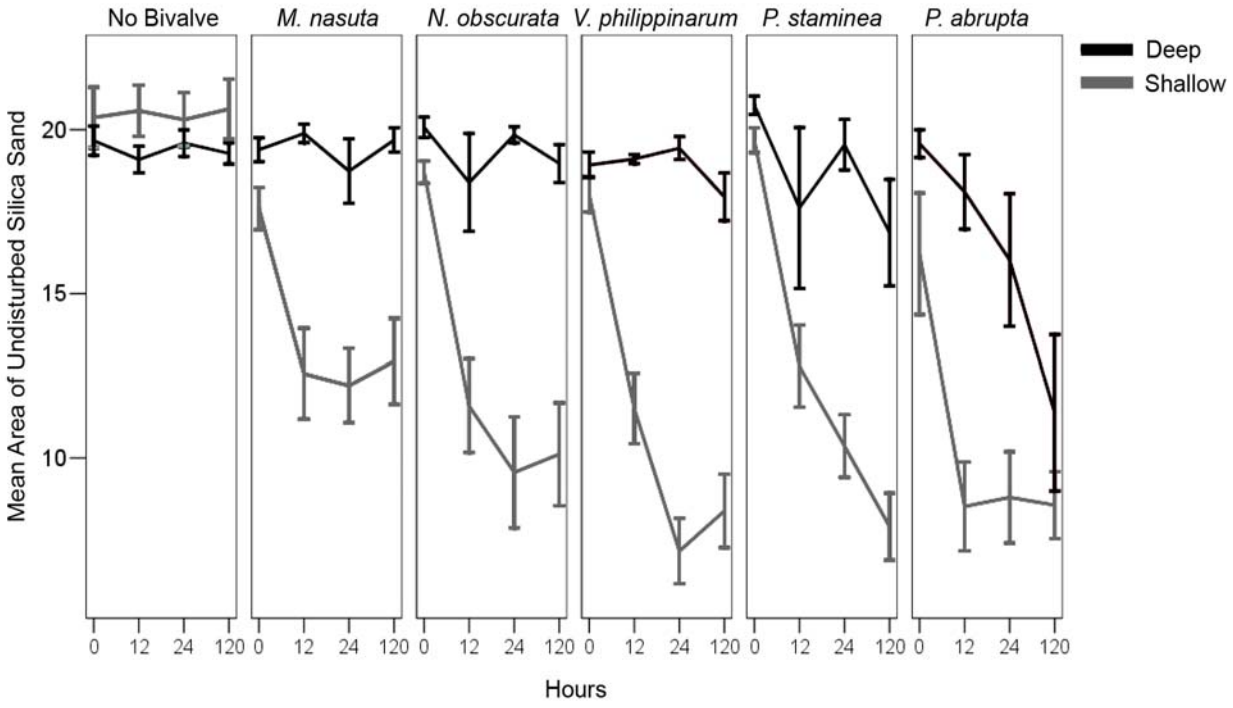

Fig. 5-5. The mean area of undisturbed silica sand (CM2, +/- 1 standard error) in shallow (grey bars) and deep (black bars) regions of the aquaria for each of the five bivalves (N=6) and the no-bivalve control (N=3) over the 120 hour study.

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CHAPTER 6.

THE MARINE NEMATODES OF CANADA: A REVIEW INCLUDING TWENTY-THREE GENERA NEW FOR BRITISH COLUMBIA

6.1 INTRODUCTION

Nematodes represent one of the most abundant and species-rich taxa on Earth and inhabit an astonishing array of terrestrial and aquatic environments (Giere, 1993). In marine habitats the greatest density of nematodes typically occurs in fine sediments (Heip et al., 1985). Exceptional abundances reaching as high as 100 million individuals/m^2 in shallow, productive marine sediments (Lambshead & Boucher, 2003) combined with high metabolic rates make nematodes of considerable ecological importance (Giere, 1993). However, difficulties inherent with identifying these tiny animals have resulted in relatively few detailed investigations (Giere, 1993). Over four thousand species of marine nematodes have been identified (Warwick et al., 1998), but given that relatively little of the ocean has been sampled for nematodes, it is very likely that this number represents only a small proportion of the actual total. It has even been suggested that nematodes are a hyperdiverse group with species richness > 1 million (Lambshead & Boucher, 2003). However, this was based on extrapolations from values of local species diversity and until further investigations are made using larger datasets it will be difficult to assess the validity of such projected species richness (Lambshead & Boucher, 2003).

Canada is bordered by three oceans, the Pacific, Arctic and Atlantic, and possesses a tremendous amount of coastline. These characteristics combine to provide

a prime opportunity to study nematode species diversity and geographic ranges. Is there continuity of species along all three coasts or are they highly variable? Given that Canada lies on both sides of the Arctic Circle is there evidence to suggest a latitudinal distribution pattern for any species? Despite this opportunity relatively few Canadian studies have investigated marine nematodes making it currently impossible to address such questions. The aims of this study were to 1) compile a review of published nematode genus/species records for Canada, 2) add new records from various habitats in Trevor Channel, British Columbia and 3) report interesting patterns of distribution.

6.2 MATERIALS AND METHODS

6.2.1 Review of marine nematodes of Canada

A literature search was conducted for published records of marine nematodes from Canadian waters. ISI Web of Science[SM] and ISI Zoological Record[SM] were the two online databases used to compile the reports (1864-present). Words used to query the records were: 'nematode', 'marine' and 'Canada'. Also, a checklist of marine nematodes for Washington and British Columbia compiled in 1983 (Austin, 1983) was included which contained records for coastal Washington State, the coastline of which is contiguous with that of southern British Columbia.

6.2.2 Survey of marine nematodes of Trevor Channel

Free-living marine nematodes were collected between the years 2004-2007 from a variety of habitats and substrates located near the Bamfield Marine Sciences

Centre on Vancouver Island (48°49'50'' N; 125°07'56'' W, Fig. 6-1). Sediment samples were haphazardly collected from a variety of habitats (see below).

Nematodes from samples of *Fucus gardneri* (Linnaeus) Silva (Autumn 2003): Grab-samples of the macro algae *Fucus gardneri* were collected from Grappler Inlet (Fig. 6-1L1) and rinsed vigorously with filtered sea water through a 1 mm and 50 μm mesh. Nematodes retained by the 50 μm sieve were identified and included in this survey.

Robber's Passage (Autumn 2004): The nematodes identified from Robber's Passage (Fig. 6-1E) were those that colonized plastic artificial substrate mounted on cement bricks (8 x 15 x 6 cm). The bricks were placed on the muddy ocean floor just below the low-tide line and allowed to colonize for 30 days before counting the meiofauna that established. Due to the overwhelmingly large number of nematodes that colonized the artificial substrates only a small sub-sample was identified and included within this survey.

Nematodes found within some spirorbid polychaetes tubes (Autumn 2004): Twelve nematodes were found by Dr. T. McDonald in the tubes of living spirorbid polychaetes collected off rocks in Grappler Inlet (Fig. 6-1L2) and were donated to this survey.

Subtidal colonization of gravel suspended in the water column (Autumn 2005): A further subtidal study in Bamfield Inlet (Fig. 6-1J3) investigated the effect of distance from substrate on meiofaunal colonization. Thirty-six mesh cages containing two size classes of gravel (fine [1-5 mm] and coarse [6-10mm]) were suspended at varying heights above the ocean floor and allowed to colonize for up to six weeks. The nematodes that had colonized the gravel were identified and are included here. For more information on this study see Boeckner et al, 2009 and chapter 2 of this thesis.

Muddy subtidal (Summer 2006): Four sediment cores (approx 10 cc each) were collected from the muddy ocean floor at a depth of 12 metres in Bamfield Inlet (Fig. 6-1J2) using a 10 cc plastic syringe cylinder (1.5 cm diameter, 8 cm length).

Nematodes from the water column (Summer 2006): A study to document presence of nematodes in the plankton at various heights above the ocean floor was conducted in Trevor Channel (Fig. 6-1K). Nematodes collected from plankton samples using 50 μm mesh nets were identified and are included in this survey. For more information on this study see Boeckner et al, 2009 and chapter 2 of this thesis.

Subtidal colonization of sand (Summer 2006): A subtidal (12 m depth) study took place in Bamfield Inlet (Fig. 6-1J1) that investigated the influence of clams on colonization of meiofauna in fine, azoic sand. The nematodes that had colonized after 42 days were identified and are included here. For more information on this study see chapter 4 of this thesis.

Sandy and muddy beaches (Autumn 2007): Dodger Channel (Fig. 6-1A), Wizard Islet (Fig. 6-1C), Ross Islets (Fig. 6-1D), First Beach (Fig. 6-1F), Bluestone (Fig. 6-1G), Brady's Beach (Fig. 6-1H) and Eagle Bay (Fig. 6-1I) are wave-swept beaches consisting of fine silica sand. The beaches at Voss Point (Fig. 6-1B) and Dixon Island (Fig. 6-1M) consisted of a mixture of mud and gravel. Cores (approx 10 cc each) were collected from the low intertidal zone of each beach using a 10 cc plastic syringe cylinder (1.5 cm diameter, 8 cm length).

6.2.3 Processing nematode samples

Nematodes were isolated from coarse sediments first by sieving through a 1 mm mesh and then via LUDOX flotation (See Warwick et al. 1998 for details of this method). Nematodes were slowly processed to glycerin (Seinhorst, 1959), slide mounted and identified to genus (species where possible) under DIC and phase-contrast lighting using several taxonomic guides (Warwick et al., 1998; Wieser, 1954).

6.3 RESULTS

6.3.1 Review of Canadian marine nematodes

Our literature survey returned 16 studies (including the checklist by Austin, 1983) of Canadian marine nematodes that were published between the years 1968 and 2002 (Table 6-1). Although there were a number of additional studies regarding the ecology of marine nematodes, only those that attempted identification to at least genus level are included in this review. Eight of these studies were conducted on the

west coast, 4 from the St. Lawrence Seaway within the province of Quebec, 3 on the east coast and 2 from the Arctic. A total of 327 records of Canadian nematode genera/species were compiled in all (including records from the present study, Table 6-1). Based on our literature and field surveys, 194 marine nematode species have now been recorded for Canada.

6.3.2 *Marine nematodes of Trevor Channel*

Fifty three genera and four species of nematode were identified from over 600 specimens collected from habitats surrounding Trevor Channel. One of the four nematodes identified to species was a new record for British Columbia: *Sabatieria hilarula* de Man. Twenty four genera were new records for British Columbia and 9 were new records for Canada (Table 6-1). The genera new to Canadian marine records are *Trileptium* Cobb, *Deontostoma* Filipjev, *Rhabdodemania* Balvis and Daubney, *Mononchus* Bastian, *Actinonema* Cobb, *Vasostoma* Wieser, *Longicyantholaimus* Micoletzky, *Echinodesmodora* Blome and *Thoracostoma* Marion.

The gravel substrate in Bamfield Inlet (J3) yielded the highest number of genera for a single site, with 30 genera identified from 262 specimens. Second highest was the muddy substrate of Robbers Passage (E), with 20 genera identified from 55 individuals. The plankton tows (K) and Bamfield Inlet (J1) mud had the next highest number of genera with 18 and 12, respectively. All other sites yielded fewer than 10 genera and had overall low nematode abundances. The most abundant genera found throughout the survey were *Chromadorina* Filipjev (97 individuals) and *Oncholaimus*

Dujardin, 1844 (77). The genera found in the greatest number of sites surveyed were *Theristus* Bastin (9 sites) and *Viscosia* de Man (7 sites). These two genera were also recorded from the plankton samples (K).

6.4 Discussion

Our literature review revealed that surveys of marine nematodes of Canada are few or lacking entirely for many areas. The parts of Canada that have had the greatest amount of focused attention are southern British Columbia and parts of the St. Lawrence Seaway in Quebec. Although Canada's marine nematode records would benefit from any new surveys, areas especially in need of investigation include the Arctic, northern British Columbia and much of the east coast of Canada including Labrador, New Brunswick and Nova Scotia. Surveys that include collection from a variety of habitats and sediment types are particularly valuable given that nematode taxa often vary between substrate types (Giere, 1993).

In the Trevor Channel survey, I took care to collect samples from a wide array of habitats and sediment types in effort to collect a broad range of nematodes. Gravel and mud substrates in sheltered inlets tended to yield the greatest number of genera as well as the highest abundances. Conversely, samples taken from sandy beaches had relatively low abundances and generic diversity likely due to harsher conditions and a low food supply in the clean, wave-swept substrates (Giere, 1993). The two most abundant genera found in this survey, *Chromadorina* and *Oncholaimus*, have both been reported previously from numerous locations across Canada. The same holds for the two genera found in the greatest number of sites surveyed, *Theristus* and *Viscosia*.

Interestingly, these two genera were also recorded from the plankton samples (K) suggesting that transport via oceanic currents may be responsible for the widespread nature of these and many other nematode genera (see Boeckner et al (2009) and chapter 2 of this thesis).

Most of the 53 genera identified in the Trevor Channel study have been reported previously for many parts Canada and appear to have widespread distributions: *Enoplus* Dujardin, *Enoplolaimus* de Man, *Halalaimus* de Man, *Oxystomina* Filipjev, *Oncholaimus, Viscosia, Chromadora* Bastian, *Chromadorina, Chromadorita* Filipjev, *Hypodontolaimus* de Man, *Prochromadorella* Micoletzky, *Paracanthonchus* Micoletzky, *Halichoanolaimus* de Man, *Desmodora* de Man, *Microlaimus* de Man, *Desmoscolex* Claparede, *Daptonema* Cobb, *Theristus* Bastian, *Axonolaimus* de Man, *Odontophora* Butschli and *Araeolaimus* de Man (Table 6-1). A number of genera (24) were first records for British Columbia including nine that were also new records for all of Canada (Table 6-1). Although individuals within the genera *Enoplolaimus*, *Hypodontolaimus*, made their first British Columbia appearances within this study, they have been previously reported for the west coast of North America in Washington, USA. Canadian records for the species *Prochromadorella neapolitana* de Man and *Viscosia carnleyensis* Ditlevsen and the genera *Acanthonchus* Cobb and *Parascolaimus* Wieser found in this study are restricted to the west coast (Table 6-1).

Three of the genera new for Canada are listed in Austen's (1983) checklist for Washington making their appearance in British Columbia less surprising: *Trileptium, Rhabdodemania, Actinonema*. However, some genera new for Canada are absent

from the Washington checklist making them more noteworthy: *Deontostoma, Mononchus, Vasostoma*, *Longicyantholaimus*, *Echinodesmodora* and *Thoracostoma*. Finally, *Sabatieria hilarula* is a new record for British Columbia. This species has been documented previously in Canada from the Gulf of St. Lawrence (Brunel et al 1998).

Although this review and accompanying survey will help clarify our knowledge of Canada's marine nematodes a vast amount of coastline has yet to be surveyed. I have shown that a small number of surveys on a very limited portion of coast can result in the addition many genera not previously recorded. Future surveys conducted in more northern reaches of Canadian coastline and in the Arctic are particularly desirable given their rarity in the literature. With each additional survey we come closer to appreciating the diversity of these tiny animals and gain information on range and dispersal capabilities vital to understanding their ecology and evolution.

Table 6-1. Marine nematode genera/species from Canada including new records from Trevor Channel, British Columbia (also included are some records from Washington, USA). Names in bold and followed by one or two asterisks (*) indicate new marine nematode records for British Columbia and Canada, respectively. Locations (see Fig. 6-1) and abundances of nematodes identified from the present study are listed in the right column. **Key to study abbreviations:** Austin 1983 (A); Boeckner et al *present study* (B); Brunel et al 1998 (BBL); Grainger et al 1985 (GML); Hopper 1968 (H); Nelson et al 1971 (NWB); Nelson et al 1972 (NHW); Reynolds & Finney-Crawley 1998 (RF); Riemann & Sime-Ngando 1997 (RS); Sharma & Vinx 1982 (SV); Sharma & Webster 1983 (SW); Tita et al 1999 (TVD); Tita et al 2001 (TDVGL); Tita et al 2002 (TDVC); Trotter & Webster 1983 (TW); Sudhaus & Nimrich 1989 (SN); Yeow et al 1999 (YFLK). **Key to study regions:** Arctic, A; British Columbia, BC; Newfoundland, NL; Prince Edward Island, PEI; St. Lawrence, SL; Washington, W.

Taxa	Location (Author)	Current Study Location (Abundance)
Enoplidae		
Enoplus Dujardin, 1845	SL(TVD), SL(TDVC), NL(YFLK), BC(NWB), SL(BBL),	C(2), E(17)
Enoplus anisospiculus Nelson, 1972	BC(NHW)	
Enoplus communis Bastian, 1865	SL(BBL)	
Enoplus intermis Bastian, 1865	W(A)	
Enoplus paralittoralis Wieser, 1953	W(A)	
Enoplus velatus Wieser, 1959	W(A)	
Thoracostomopsidae		
Enoploides harpax Wieser, 1959	W(A)	
Enoplolaimus* de Man, 1893	SL(TVD), SL(TDVC), NL(YFLK), SL(BBL), BC(BSP)	C(2)
Enoplolaimus lenunculus Wieser, 1959	W(A)	
Enoplolaimus paralittoralis Wieser, 1959	W(A)	
Epacanthion Wieser, 1954	SL(TDVC)	
Epacanthion multipapillatum (Wieser, 1959)	W(A)	
Mesacanthion Filipjev, 1927	BC(SW)	
Mesacanthion arcuatilis Wieser, 1959	W(A)	
Mesacanthion cricetoides Wieser, 1959	W(A)	
Mesacanthion pali Wieser, 1959	W(A)	
Mesacanthion pannosum Wieser, 1959	W(A)	
Mesacanthoides sinuosus Wieser, 1959	W(A)	
Oxyonchus Filipjev, 1927	BC(SW)	
Oxyonchus culcitatus Wieser, 1959	W(A)	
Trileptium* Cobb, 1933	BC(BSP)	E(1)
Trileptium iacobinum Wieser, 1959	W(A)	
Anoplostomatidae		
Anoplostoma Buetschli, 1874	BC(SW), SL(BBL), BC(BSP)	E(2)
Anoplostoma blanchardi de Man, 1888	SL(TVD), SL(TDVC)	
Anoplostoma viviparum (Butschli, 1974)	W(A)	
Chaetonema Filipjev, 1927	SL(TVD), SL(TDVC)	
Phanodermatidae		
Crenopharynx Filipjev, 1934	NL(RF)	
Phanoderma* Bastian, 1865	NL(RF), BC(BSP)	J1(6), J3(1)
Phanodermopsis Ditlevsen, 1926	SL(BBL)	

Anticomidae	BC(BSP)	K(2)
Anticoma Bastian, 1865	NL(RF), NL(YFLK), BC(BSP)	A(2), E(2), J3(12), K(1)
Anticoma acuminate (Eberth, 1863)	BC(TW), NL(RF), W(A)	
Anticoma pellucida Bastian, 1865	BC(SW)	
Ironidae		
Trissonchulus benepapillosus (Schulz, 1935)	W(A)	
Leptosomatidae		
Deontostoma** Filipjev, 1925	BC(BSP)	J3(1)
Leptosomatum elongatum Bastian, 1865	NL(RF)	
Platycoma Cobb, 1894	NL(YFLK)	
Oxystominidae		
Halalaimus de Man, 1888	BC(SW), SL(TDVC), SL(TDVGL), NL(YFLK), SL(BBL),	D(3), E(1), K(1)
Halalaimus gracilis de Man, 1888	NL(RF)	
Oxystomina Filipjev, 1921	BC(SW), SL(TVD), SL(TDVC), NL(RF), SL(TDVGL), BC(NWB), BC(BSP)	J1(2)
Oncholaimidae		
Adoncholaimus fuscus (Bastian, 1865)	SL(TVD), SL(TDVC)	
Metoncholaimus Filipjev, 1918	SL(BBL)	
Metoncholaimus uvifer Wieser, 1959	W(A)	
Oncholaimus Dujardin, 1844	SL(TVD), SL(TDVC), NL(RF), NL(YFLK), BC(BSP)	C(1), E(1), G(5), J2(1), J3(45), L1(24)
Oncholaimus apostematus Wieser, 1959	W(A)	
Oncholaimus attenuatus Dujardin, 1845	NL(RF)	
Oncholaimus brachycercus de Man 1888	W(A)	
Oncholaimus campylocercoides de Coninck and *Stekhoven, 1933*	W(A)	
Oncholaimus dujardini de Man, 1876	BC(TW)	
Oncholaimus martini Wieser, 1959	W(A)	
Oncholaimus oxyuris Ditlevsen, 1911	NL(RF)	
Oncholaimus skawensis Ditlevsen, 1921	BC(SW), BC(NWB), BC(A)	
Oncholaimus vesicarius (Wieser, 1959)	BC(SW), BC(NWB), BC(A)	
Pareurystomina pugetensis Wieser, 1959	W(A)	
Pontonema simile (Southern, 1914)	NL(RF)	
Pontonema vulgare (Bastian, 1865)	NL(RF)	
Viscosia de Man, 1891	SL(TVD), SL(TDVC), NL(RF), NL(YFLK), SL(BBL), BC(BSP)	A(4), E(3), J1(4), J2(1), J3(45), K(1), L2(2)
Viscosia carnleyensis (Ditlevsen, 1921)	BC(SW), BC(BSP)	K(1)
Viscosia glabra (Bastian, 1865)	NL(RF)	

Viscosia tumidula Wieser, 1959	BC(SW)	
Enchelidiidae		
Belbolla Andrassy, 1973	BC(SW), BC(BSP)	E(1)
Belbolla tenuidens (Cobb, 1920)	SL(BBL)	
Calyptronema Marion, 1870	SL(BBL)	
Calyptronema maxweberi (de Man, 1922)	W(A)	
Calyptronema pachyderma Wieser, 1959	W(A)	
Eurystomina Filipjev, 1921	BC(SW), NL(RF), BC(BSP)	J3(9), L1(1)
Eurystomina repanda Wieser, 1959	W(A)	
Polygastrophora de Man, 1922	SL(TVD), SL(TDVC)	
Symplocostoma Bastian, 1865	BC(SW), SL(TDVC), BC(BSP)	J3(2)
Tripyloididae		
Bathylaimus Cobb, 1894	SL(TVD), SL(TDVC), NL(RF), NL(YFLK), SL(BBL)	
Bathylaimus australis Cobb, 1894	W(A)	
Bathylaimus bicoronatus Wieser, 1959	W(A)	
Bathylaimus capacosus Hopper, 1962	PEI(H), SL(BBL)	
Bathylaimus hamatus Hopper, 1968	PEI(H), SL(BBL)	
Bathylaimus parafilicaudatus Allgen, 1935	PEI(H), SL(BBL)	
Bathylaimus tarsioides Wieser, 1959	W(A)	
Paratripyloides Schuurmans and Stekhoven, 1950	BC(SW)	
Triploides gracilis (Ditlevsen, 1918)	BC(SW), SL(BBL), W(A)	
Triploides imitans Wieser, 1959	W(A)	
Tripyloides de Man, 1886	SL(TVD), SL(TDVC), NL(YFLK), SL(BBL)	
Rhabdodemaniidae		
Rhabdodemania** Balylis and Daubney, 1926	BC(BSP)	J3(1)
Rhabdodemania illgi Wieser, 1959	W(A)	
Trefusiidae		
Cytolaimium Cobb, 1920	BC(SW), SL(BBL)	
Halanonchus Cobb, 1920	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL)	
Rhabdocoma Cobb, 1920	BC(SW)	
Trefusia* de Man, 1893	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL), BC(BSP)	K(1)
Lauratonematidae		
Lauratonema mentulatum Wieser, 1959	W(A)	
Lauratonema pugiunculus Wieser, 1959	BC(SW), W(A)	
Mononchidae		
Mononchus** Bastian, 1865	BC(BSP)	K(2)

Chromadoridae	BC(BSP)	L2(2)
Atrochromadora Wieser, 1959	SL(TDVGL), SL(BBL)	
Atrochromadora obscura Wieser, 1959	W(A)	
Chromadora Bastian, 1865	SL(TVD), SL(TDVC), NL(YFLK), SL(BBL), BC(BSP)	E(3), J2(3), L2(2)
Chromadora axi Gerlach, 1951	SL(BBL)	
Chromadora macrolaima de Man, 1998	SL(TVD), SL(TDVC)	
Chromadora (nudicapitata) bipapillata Micoletzky, 1922	BC(TW), SL(BBL)	
Chromadora undecimpapillata Filipjev, 1918	W(A)	
Chromadorella edmondsoni Wieser, 1959	W(A)	
Chromadorella galeata Wieser, 1959	W(A)	
Chromadorina Filipjev, 1918	SL(BBL), BC(BSP)	E(1), J1(85), J3(5), K(6)
Chromadorina germanica (Butschli, 1874)	BC(SW), NL(RF), BC(NWB), BC(A), W(A)	K(1)
Chromadorina laeta (de Man, 1876)	BC(TW), BC(BSP)	
Chromadorita* Filipjev, 1922	SL(TVD), SL(TDVC), NL(RF), SL(BBL), BC(BSP)	J3(4)
Chromadorita tenuis (G. Schneider, 1906)	PEI(H), NL(RF), SL(BBL)	
Denticulella Cobb, 1933	BC(SW)	
Dichromadora* Kreis, 1929	SL(TVD), SL(TDVC), SL(BBL), BC(BSP)	A(2), B(1), D(1), E(4), J2(1)
Dichromadora hyalocheile de Coninck and Stekhoven, 1933	SL(TVD), SL(TDVC)	
Euchromadora de Man, 1886	BC(SW), NL(RF), NL(YFLK)	
Euchromadora vulgaris (Bastian, 1865)	NL(RF)	
Graphonema clivosa Wieser, 1959	W(A)	
Graphonema flaccida Wieser, 1959	W(A)	
Hypodontolaimus* de Man, 1886	NL(RF), NL(YFLK), SL(BBL), BC(BSP)	J3(18)
Hypodontolaimus balticus (G. Schneider, 1906)	SL(TVD), SL(TDVC), SL(BBL)	
Hypodontolaimus inaequalis (Bastian, 1865)	SL(TVD), SL(TDVC), W(A)	
Hypodontolaimus reverses Hopper, 1968	PEI(H), SL(BBL)	
Hypodontolaimus schuurmansstekoveni Gerlach, 1951	SL(TVD), SL(TDVC)	
Innocuonema Inglis, 1969	SL(TVD), SL(TDVC), SL(BBL)	
Innocuonema clivosum (Wieser, 1959)	BC(SW)	
Karkinochromadora Blome, 1982	SL(TVD), SL(TDVC)	
Neochromadora Micoletzky, 1924	SL(TVD), SL(TDVC), BC(BSP)	B(10), I(1), J1(2), J3(19), K(11)
Neochromadora appiana Wieser, 1959	BC(SW), W(A)	
Neochromadora bicoronata (Wieser, 1959)	W(A)	
Neochromadora poecilosoma (de Man, 1893)	SL(TVD), SL(TDVC), W(A)	
Neochromadora pugilator Wieser, 1959	W(A)	
Parapinnanema* Inglis, 1969	NL(YFLK), BC(BSP)	J3(1), K(2), L1(1)

Prochromadora* Filipjev, 1922	NL(RF), BC(BSP)	E(1)
Prochromadorella Micoletzky, 1924	NL(RF), SL(BBL), BC(BSP)	B(1), E(1), J3(33)
Prochromadorella ditevseni de Man, 1922	NL(RF)	
Prochromadorella neapolitana de Man, 1876	BC(TW), BC(BSP)	K(1)
Prochromadorella triangularis Wieser, 1959	W(A)	
Ptycholaimellus* Cobb, 1920	BC(BSP)	J3(2)
Ptycholaimellus ponticus (Filipjev, 1922)	SL(TVD), SL(TDVC)	
Spilophorella Filipjev, 1917	SL(TVD), SL(TDVC), BC(BSP)	J1(4), K(4)
Spilophorella paradoxa de Man, 1888	BC(SW), W(A)	
Steineridora adriatica (Daday, 1901)	NL(RF)	
Steineridora loricata (Steiner, 1916)	SL(BBL)	
Cyatholaimidae		
Biarmifer gibber Wieser, 1959	W(A)	
Phyllolaimus dentatus Wieser, 1959	W(A)	
Propomponema websteri (Sharma and Vincx, 1982)	BC(SV), BC(SW)	
Actinolaimidae		
Actinonema* Cobb, 1920	BC(BSP)	J3(1)
Actinonema longicaudata Steiner	W(A)	
Comesomatidae		
Dorylaimopsis Ditlevsen, 1918	SL(TDVGL), SL(BBL)	
Metacomesoma Wieser, 1954	SL(BBL)	
Pierrickia Vitiello, 1970	SL(BBL)	
Sabatieria Rouville, 1903	SL(TDVGL), NL(YFLK), SL(BBL)	
Sabatieria americana Timm, 1952	W(A), BC(SW)	
Sabatieria ancudiana Wieser, 1954	BC(SW)	
Sabatieria clavicauda G. Schneider, 1906	W(A)	
Sabatieria (cupida) celtica Southern, 1914	W(A)	
Sabatieria hilarula* de Man, 1922	BC(BSP), SL(BBL)	J3(1), K(2)
Sabatieria jubata (Cobb, 1898)	W(A)	
Sabatieria longispinosa Lorenze, 1972	SL(TVD), SL(TDVC)	
Sabatieria ornata (Ditlevsen, 1918)	SL(TVD), SL(TDVC)	
Sabatieria pulchra (G. Schneider, 1906)	BC(SW)	
Sabatieria punctata G. Schneider, 1906	SL(TVD), SL(TDVC)	
Vasostoma* Wieser, 1954	BC(BSP)	M(1)
Ethmolaimidae		
Nannolaimus Cobb, 1920	SL(TDVGL), SL(BBL)	
Neotonchus Cobb, 1933	BC(SW)	

Cyantholaimidae	BC(BSP)	L2(1)
Acanthonchus Cobb, 1920	BC(SW), BC(BSP)	J3(4)
Acanthonchus duplicatus Wieser, 1959	W(A)	
Acanthonchus rostratus Wieser, 1959	W(A)	
Cyatholaimus Bastian, 1865	BC(SW), SL(BBL)	
Longicyantholaimus** Micoletzky, 1924	BC(BSP)	I(1)
Marylynnia Hopper, 1977	BC(BSP)	J1(3)
Marylynnia hopperi Sharma and Vincx, 1982	BC (SV),	
Minolaimus Vitiello, 1970	SL(TDVGL), SL(BBL)	
Nannolaimoides effilatus (Boucher, 1976)	SL(TVD), SL(TDVC), SL(BBL)	
Paracanthonchus Micoletzky, 1922	SL(TVD), SL(TDVC), BC(TW), SL(TDVGL), NL(YFLK), BC(NWB), BC(BSP)	E(4), I(1), J3(36)
Paracanthonchus caecus (Bastian, 1865)	BC(SW), SL(TVD), SL(TDVC), NL(RF)	
Paracanthonchus mutates Wieser, 1959	W(A)	
Paracanthonchus quinquepapillatus Wieser, 1959	W(A)	
Paracanthonchus serratus Wieser, 1959	W(A)	
Paracyantholaimus vancouverensis Sharma and Vinx, 1981	BC(SV), BC(SW), W(A)	
Paracyatholaimus pugettensis Wieser and Hopper, 1967	BC(SV), BC(SW), W(A)	
Paralongicyatholaimus Stekhoven, 1942	SL(TDVGL), SL(BBL)	
Pomponema sedecima Platt, 1973	SL(TVD), SL(TDVC)	
Pomponema segregate Wieser, 1959	W(A)	
Pomponema websteri *Authority pending*	BC(SV)	
Selachnematidae		
Choanolaimus de Man, 1880	NL(RF)	
Choniolaimus macrodentatus (Wieser, 1959)	W(A)	
Gammanema Cobb, 1920	SL(TVD), SL(TDVC)	
Gammanema (ferox)rapax (Ssaweljev, 1912)	W(A)	
Gammanema smithi Murphy, 1964	W(A)	
Halichoanolaimus de Man, 1886	BC(SW), BC(BSP)	A(1)
Halichoanolaimus robustus (Bastian, 1865)	SL(TVD), SL(TDVC), NL(RF)	
Latronema serata Wieser, 1959	W(A)	
Richtersia Steiner, 1916	NL(YFLK)	
Richtersia inaequalis Riemann, 1966	SL(TDVC)	
Desmodoridae		
Chromaspirina spinulosa Wieser, 1959	W(A)	
Desmodora* de Man, 1889	SL(TVD), SL(TDVC), BC(BSP)	J1(3), K(1), M(2)

Desmodora communis (Butschli, 1874)	NL(RF)	
Desmodora sanguinea Southern, 1914	NL(RF)	
Echinodesmodora** Blome, 1982	BC(BSP)	E(7)
Metachromadora* Filipjev, 1918	SL(TVD), SL(TDVC), SL(BBL), BC(BSP)	E(1), J3(1)
Metachromadora remanei Gerlach, 1951	SL(TVD), SL(TDVC)	
Molgolaimus Ditlevsen, 1921	SL (TDVGL), SL(BBL)	
Onyx rugata Wieser, 1959	W(A)	
Paradesmodora Stekhoven, 1950	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL)	
Spirinia Gerlach, 1963	SL(TVD), SL(TDVC)	
Spirinia laevis (Bastian, 1865)	W(A)	
Epsilonematidae		
Epsilonema* Steiner, 1927	NL(RF), BC(BSP)	J3(4), M(1)
Draconematidae		
Draconema* Cobb, 1913	NL(RF), BC(BSP)	E(1), J3(16)
Notochaetosoma Irwin-Smith, 1918	NL(RF)	
Microlaimidae	BC(BSP)	A(2)
Aponema Jensen, 1978	SL(TVD), SL(TDVC)	
Bolbolaimus Cobb, 1920	SL(TVD), SL(TDVC)	
Microlaimus de Man, 1880	SL(TVD), SL(TDVC), NL(YFLK), SL(BBL), BC(BSP)	M(3)
Microlaimus cochleatus Wieser, 1959	W(A)	
Microlaimus dentatus Allgen, 1935	BC(SW), W(A)	
Microlaimus dixiei Wieser, 1959	W(A)	
Microlaimus taxianus Authority pending	BC(SW)	
Aponchiidae		
Aponchium Cobb, 1920	BC(SW)	
Monoposthiidae		
Monoposthia de Man, 1889	NL(RF), NL(YFLK)	
Monoposthia costata (Bastian, 1865)	BC(SW), SL(BBL), SL(TVD), SL(TDVC), W(A)	
Monoposthia mirabilis Schulz, 1932	NL(RF)	
Nudora Cobb, 1920	SL(BBL)	
Cyartonematidae		
Paraterschellingia Kreis In Stekhoven, 1924	BC(SW)	
Monhystéridae		
Cryonema tenue Tchesunov, 1995	A(RS)	
Monhystera Bastian, 1865	SL(TVD), SL(TDVC), NL(RF), SL(TDVGL), NL(YFLK),	

Monhystera disjuncta Bastian, 1865	BC(TW), W(A)	
Monhystera refringens Schuurmans and Stekhoven,	BC(SW), BC(TW), W(A)	
Leptolaimidae		
Antomicron Cobb, 1920	SL(TVD), SL(TDVC), SL(BBL)	
Camacolaimus de Man, 1889	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL)	
Camacolaimus tardus de Man, 1889	SL(TVD), SL(TDVC)	
Halaphanolaimus Southern, 1914	SL(TDVGL), SL(BBL)	
Leptolaimoides Vitiello, 1971	SL(BBL)	
Leptolaimus de Man, 1876	BC(SW), NL(YFLK), SL(BBL)	
Leptolaimus elegans (Stekhoven and de Cornick, 1933)	SL(BBL), SL(TVD), SL(TDVC)	
Leptolaimus papilliger de Man, 1876	SL(TVD), SL(TDVC)	
Stephanolaimus Ditlevsen, 1914	SL(TVD), SL(TDVC), SL(BBL), W(A)	
Thoracostoma** Marion, 1870	BC(BSP)	J3(3)
Aegialoalaimidae		
Aegialoalaimus* de Man, 1907	SL(TVD), SL(TDVC), BC(BSP)	J3(3)
Cyartonema Cobb, 1920	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL)	
Diplopeltoides Gerlach, 1962	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL)	
Southernia Allgen, 1929	SL(TVD), SL(TDVC)	
Ceramonematidae		
Ceramonema carinatum Wieser, 1959	W(A)	
Paramicrolaimidae		
Paramicrolaimus spirulifer Wieser, 1959	W(A)	
Desmoscolecidea		
Desmoscolex* Claparede, 1863	NL(RF), SL(TDVGL), SL(BBL), BC(BSP)	J3(1)
Desmoscolex falcatus Lorenzen, 1972	SL(TDVC)	
Tricoma Cobb, 1893	SL(BBL)	
Monhysteridae		
Diplolaimella Allgen, 1929	BC(SW), SL(TVD), SL(TDVC), SL(BBL), BC(BSP)	J3(1)
Geomonhystera disjuncta (Bastian, 1865)	SL(BBL)	
Xyalidae	SL(TVD), SL(TDVC)	
Amphimonhysterella Timm, 1961	SL(TVD), SL(TDVC), SL(BBL)	
Cobbia de Man, 1907	SL(TDVGL), SL(BBL)	
Cobbia truncate Wieser, 1959	W(A)	
Cobbia urinator Wieser, 1959	BC(SW), W(A)	
Daptonema Cobb, 1920	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL), BC(BSP)	A(2), B(1), E(1), I(2), J1(12), K(1)

Daptonema (Cylindrotheristus) ecphygmaticus (Wieser, 1959)	W(A)	
Daptonema (Cylindrotheristus) resimus (Wieser, 1959)	BC(SW), W(A)	
Daptonema (Cylindrotheristus) trecuspidatus Wieser, 1959	W(A)	
Daptonema (Mesotheristus) circumscriptus Wieser, 1959	BC(SW)	
Daptonema albigensis (Riemann, 1966)	SL(BBL)	
Daptonema tenuispiculum (Ditlevsen, 1918)	SL(TVD), SL(TDVC), SL(BBL)	
Elzalia Gerlach, 1957	SL(TVD), SL(TDVC), SL(TDVGL), SL(BBL)	
Gnomoxyala Lorenzen, 1977	SL(TVD), SL(TDVC)	
Linhystera Juario, 1974	NL(YFLK), SL(BBL)	
Paramonhystera Steiner, 1916	BC(SW), SL(TVD), SL(TDVC), SL(BBL)	
Paramonhystera elliptica Filipjev, 1918	W(A)	
Paramonhystera mutilus Authority pending	BC(SW)	
Pseudosteineria anticipans (Wieser, 1956)	W(A)	
Rhynchonema Cobb, 1920	BC(SW)	
Rhynchonema cinctum Cobb, 1920	W(A)	
Scaptrella Cobb, 1917	SL(BBL)	
Steineria Micoletzky, 1922	SL(BBL)	
Steineria gerlachi Wieser, 1959	BC(SW), W(A)	
Steineria phimifera Wieser, 1959	W(A)	
Theristus Bastian, 1865	A(GML), PEI(H), SL(TVD), SL(TDVC), NL(RF), NL(YFLK), SL(BBL), BC(BSP)	A(2), B(3), C(1), E(2), H(2), J1(8), J3(14), K(1), M(1)
Theristus acer Skuse, 1888	NL(RF), SL(BBL), W(A)	
Theristus melnikovi chesunov, 1986	A(RS)	
Theristus procerus Gerlach, 1951	SL(TVD), SL(TDVC)	
Theristus sinuosis Wieser, 1959	W(A)	
Theristus uncinatus Wieser, 1959	W(A)	
Theristus wimmeri Wieser, 1959	W(A)	
Therisus modicus Wieser, 1959	BC(SW), W(A)	
Valvaelaimus Lorenzen, 1977	SL(BBL)	
Sphaerolaimidae		
Doliolaimus Lorenzen, 1966	SL(TVD), SL(TDVC), SL(BBL)	
Metasphaerolaimus Gourbault and Boucher, 1981	SL(BBL)	
Parasphaerolaimus Ditlevsen, 1918	SL(BBL)	
Sphaerolaimus Bastin, 1865	BC(SW), SL(TVD), SL(TDVC), SL(TDVGL), NL(YFLK),	
Sphaerolamus penicillus Gerlach, 1956	W(A)	

Siphonolaimidae		
Siphonolaimus de Man, 1893	BC(SW), SL(TVD), SL(TDVC), BC(BSP)	J2(1)
Solenolaimus Cobb, 1894	BC(SW)	
Linhomoeidae		
Desmolaimus de Man, 1880	SL(TVD), SL(TDVC), NL(YFLK)	
Desmolaimus fennicus G. Schneider, 1926	W(A)	
Desmolaimus zeelandicus de Man, 1880	BC(SW)	
Didelta Cobb, 1920	BC(SW)	
Eleutherolaimus Filipjev, 1922	SL(TVD), SL(TDVC), NL(YFLK)	
Eleutherolaimus obtusicaudatus Allgen, 1947	W(A)	
Eleutherolaimus stenosoma (de Man, 1907)	BC(SW), W(A)	
Filipjevinema doliolum Wieser, 1959	W(A)	
Linhomoeus Bastian, 1865	BC(SW), SL(TVD), SL(TDVC)	
Linhomoeus undulates Wieser, 1959	BC(SW)	
Metalinhomoeus de Man, 1907	SL(TDVGL), NL(YFLK), SL(BBL)	
Metalinhomoeus setosus Chitwood, 1951	BC(SW), W(A)	
Paralinhomoeus de Man, 1907	SL(TVD), SL(TDVC), SL(BBL), BC(BSP)	J1(3)
Paralinhomoeus buculentus (Wieser, 1956)	BC(SW), W(A)	
Terschellingia de Man, 1888	SL(TDVGL), NL(YFLK), SL(BBL)	
Terschellingia longicaudata de Man, 1907	BC(SW)	
Axonolaimidae	BC(BSP)	G(9)
Ascolaimus* Ditlevsen, 1919	SL(TVD), SL(TDVC), BC(BSP)	J3(8)
Axonolaimus de Man, 1889	SL(TVD), SL(TDVC), NL(YFLK), SL(BBL), BC(BSP)	F(8), G(17), H(1), J3(1)
Axonolaimus interrogativius Wieser, 1959	W(A)	
Axonolaimus spinosus (Butschli, 1874)	BC(SW)	
Odontophora Butschli, 1874	SL(TVD), SL(TDVC), NL(YFLK), BC(BSP)	B(1), J2(1), K(1)
Odontophora lituifera Wieser, 1959	W(A)	
Odontophora mercurialis Wieser, 1959	W(A)	
Odontophora peritricha Wieser, 1956	BC(SW), W(A)	
Parascolaimus Wieser, 1959	BC(SW), BC(BSP)	J1(2)
Parascolaimus tau Wieser, 1959	W(A)	
Parascolaimus ungulatus Wieser, 1959	W(A)	
Synodontium monhystera Gerlach, 1953	PEI(H), SL(BBL)	
Diplopeltidae		
Araeolaimus de Man, 1888	NL(RF), SL(BBL), BC(BSP)	L2(5)
Araeolaimus boomerangifer Wieser, 1959	W(A), BC(SW)	

Araeolaimus botulus Wieser, 1959	W(A)	
Araeolaimus elegans de Man, 1888	BC(SW), BC(TW)	
Campylaimus Cobb, 1920	SL(TDVGL), SL(BBL)	
Diplopeltis Cobb in Stiles and Hassal, 1905	NL(RF)	
Diplopeltula Gerlach, 1950	SL(BBL)	
Southerniella Allgen, 1932	SL(TDVGL), SL(BBL)	
Rhabditidae		
Pellioditis marina (Bastian, 1865)	SL(BBL)	
Prodontorhabditis wirthi Timm, 1961	BC(SN)	
Rhabditis littorea Sudhaus & Nimrich, 1989	BC(SN)	
Rhabditis marina Vaisanen, 1984	BC(SW), BC(SN)	
Rhabditis stasileonovi Belogurov, 1977	BC(SN)	

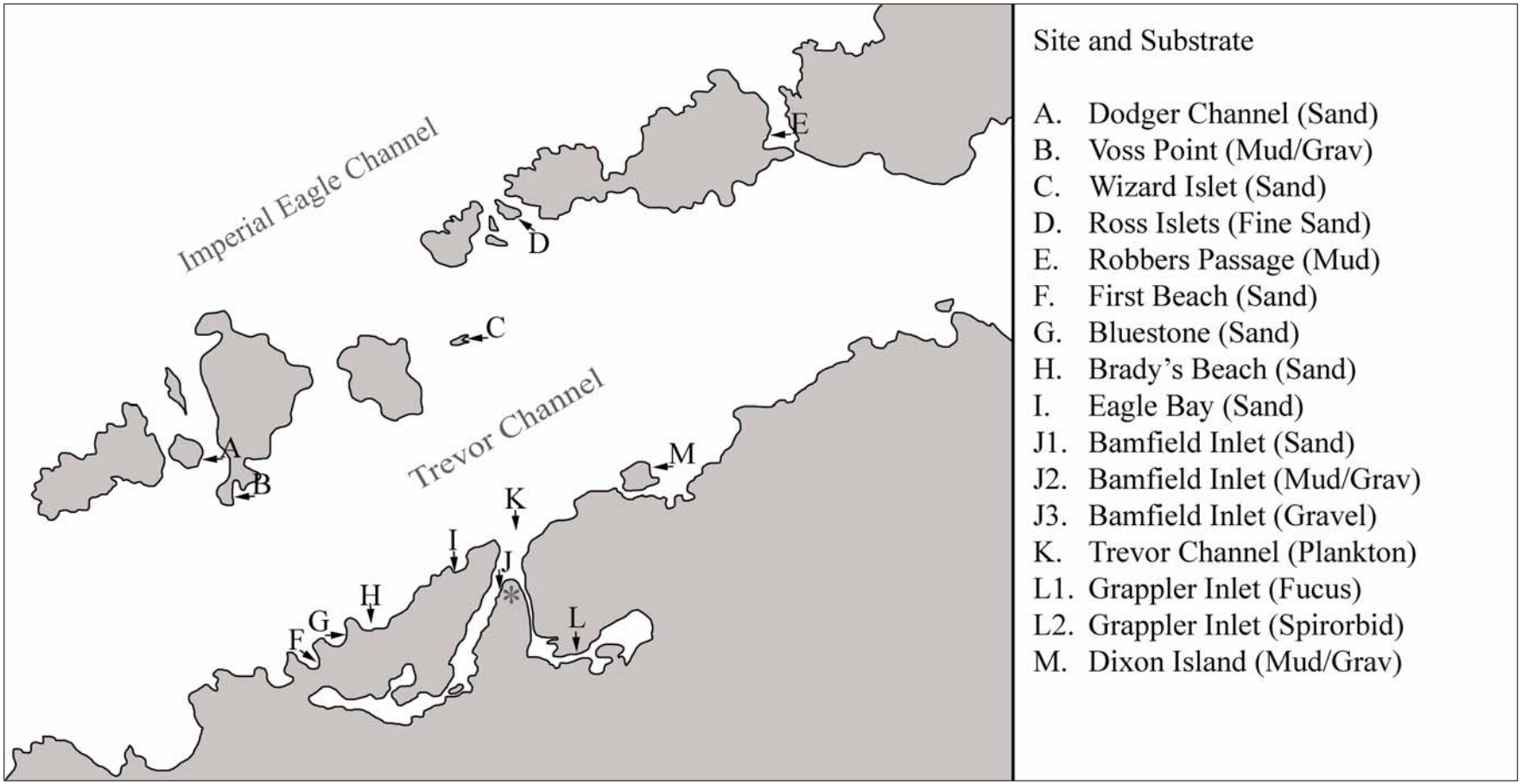

Fig. 6-1. Map showing location of study sites on Vancouver Island, British Columbia, Canada. Bamfield Marine Sciences Centre represented by the asterisk (*).

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CHAPTER 7.

SUMMARY AND CONCLUSIONS

The research in this thesis aimed to address three main objectives relating to meiofaunal ecology. First, it explored the puzzling phenomenon of the "meiofaunal paradox", whereby small and presumably entirely benthic animals exhibit rapid colonization of distant habitats. Second, it investigated how the presence of macrofaunal animals affects the colonization of new sediments by meiofauna. Specifically examined were the effects of clams, which can often reach very high densities in sedimentary habitats. Finally, it provided many new records and a review of the relatively scant literature on marine nematodes of Canada to present what is currently known about species ranges along the western, eastern and northern coastlines.

7.1 Abiotic factors affecting meiofaunal dispersal and assemblage structure

Marine meiofauna are extremely abundant in sediments worldwide from coastal waters to the abyssal plains and play important roles in ecosystem functioning (Snelgrove, 1999). Despite their importance, a combination of factors has resulted in a patchy and incomplete understanding of marine meiofaunal ecology. Some of these factors include their small size, overwhelming abundances, difficulty separating the animals from the sediment and the limited number of meiofaunal specialists. Surprisingly little information exists about how environmental and biological factors

affect colonization and assemblage structure within interstitial communities. More is understood about the recruitment of macrofauna and alga. In general, colonization and succession of benthic habitats will be governed by the characteristics of the patch to be colonized, referred to as *patch dynamics* (Sousa, 2001). Patch type, size and shape, surface characteristics, location and time of creation will all affect colonists to various degrees. For example, aquatic taxa with direct development will not colonize distant patches as quickly as taxa that have planktonic propagules.

In Chapters two and three of this thesis I examined a range of abiotic factors for their effects on meiofaunal colonization and assemblage patterns in new sediment. Specifically I investigated how meiofaunal colonization was affected by sediment grain size, depth, exposure to wave action and distance from the ocean floor. Many of these factors had strong negative effects on colonization while others had less of an effect. For example, even slight increases in depth resulted in drastic declines of harpacticoid copepods while nematodes were unaffected. Meiofauna were also typically less abundant in sediments with large interstitial spaces. Meiofauna were overall most abundant in samples of plankton taken closer to the ocean floor, but the two levels of exposure that I investigated may not have been dissimilar enough to evoke any differences in meiofauna collected from the water column . Many meiofaunal taxa, including nematodes, colonized distant experimental substrata as rapidly as they did substrate located closer to the ocean floor. Others, including harpacticoid copepods, colonized substrata closer to the ocean floor far more quickly and abundantly. This suggested differences between taxa in their rates of active dispersal. However, regardless of the depth, sediment granularity, exposure or

distance from ocean floor, meiofauna in one form or another were surprisingly quick to colonize within every experiment, often reaching background densities in less than a month.

The global ubiquity of small benthic animals that have minimal capability for active dispersal has intrigued meiofaunal ecologists for decades (Giere, 1993; Fenchel & Finlay, 2004). Although recent molecular studies have shown that some cosmopolitan species are actually complexes of many morphologically similar species (Bhadury et al., 2008; Giere, 2009) other meiofauna have maintained their high level of ubiquity even after molecular scrutiny (Giere, 2009; Westheide et al, 2003). How is it possible for these tiny benthic animals to exhibit such broad oceanic ranges and be among the first to colonize new distant habitats? It has now been identified within this thesis and other works that oceanic currents provide the means for meiofauna to passively disperse long distances. This may seem a parsimonious explanation but upon closer inspection several new questions arise. How long and effectively can meiofaunal animals, which are seemingly designed for life in the interstices, survive in the water column? I collected a number of live nematodes in the water column as far off the bottom as 6.5 m. What is the ultimate fate of these suspended nematodes? What proportion actually leaves the water column to return to the sediment? How many starve to death while in suspension, or fall prey to other animals? Although suspension and transportation of meiofauna over short distances to new habitats might be possible it seems unlikely that a majority of suspended meiofauna would survive long enough to reach distant habitats. A more likely explanation is that meiofauna colonizing the most distant habitats and exhibiting the most widespread distributions

travel passively as hitchhikers on drifting materials such as kelp, wood, coconuts or more recently from sediments transported in the ballast tanks of large transport vessels (Ullberg, 2004).

7.2 Effects of clams on meiofaunal colonization and assemblage structure

The impacts of macrofaunal animals on meiofauna have been explored repeatedly, and have often reported contradictory results (Ólafsson, 2003). This is likely due to biological and behavioural differences between macrofaunal species. In my initial investigations (Chapter 4) of how meiofauna are impacted by clams I first determined that meiofauna abundances were negatively affected by some species of bivalves and not others. Throughout the studies I observed that bivalve effects were greatest on nematodes and harpacticoid copepods, an observation also made by Ólafsson (2003). The three clams that had the greatest effects on meiofaunal abundance were *Macoma nasuta, Nuttallia obscurata* and *Venerupis philippinarum*. Two of these clams are deposit-feeders (*M. nasuta* and *N. obscurata*) that affect the sediment via burrowing and movement of the siphons. Suspension-feeding clams tended to be more benign to meiofauna with the exception of *V. philippinarum* which was associated with the second greatest meiofaunal declines (Fig. 4-5). This suggested that differences in burrowing rates and depths between the various clam species may have been responsible for the meiofaunal declines. However, at this point I lacked any quantitative measurements to show such differences in burrowing behaviours.

I then conducted a laboratory experiment to quantify burrowing rates of five species of deposit- and suspension-feeding clams (Chapter 5). This allowed me to test the hypothesis that differences in burrowing behaviours between clam species was the primary factor impacting meiofauna. The three clams previously found to have the greatest impacts on meiofauna, *M. nasuta, N. obscurata* and *V. philippinarum,* continuously disturbed shallow sediment. The two more benign clams (*Protothaca staminea* and *Panopea abrupta*) burrowed quickly to deeper sediment where they remained less active throughout the experiment. Meiofauna tend to be abundant in the upper most layers of the sediment and decline in numbers with increasing depth (Coull 1988). The continuous shallow burrowers (*M. nasuta, N. obscurata* and *V. philippinarum*) presumably displace meiofauna from ideal positions at the surface to deeper less favourable regions where oxygen and food might be harder to attain.

Interestingly, *V. philippinarum* and *P. staminea*, two suspension-feeders of very similar shape and size had very different effects on meiofauna. Why did one of these seemingly similar species remain shallow and the other not? Does *P. staminea* perhaps have longer siphons or a more dexterous foot that would allow it to reside in deeper sediment than *V. philippinarum*? If more time had been allowed to elapse would these two species eventually arrive at similar burial depths?

Overall, bivalves were highly variable in their level of impact on meiofaunal animals. This variability seemed to result from species-specific combinations of burrowing and feeding. Shallow burrowing deposit-feeders had the greatest impacts on meiofauna given their higher displacement and feeding rates. The patterns observed throughout these studies were made using experimental habitats with

artificially constrained dimensions. Now that we have documented these patterns it is necessary to see how readily the effects of clams on meiofauna might be detected in natural, established habitats. Is there a measurable difference in meiofaunal abundance and community structure between similar habitats dominated by either deposit or suspension feeding clams? It would also be worthwhile to observe bivalve burrowing behaviours between species over a longer period of time to distinguish those that eventually remain more stationary from those that continually burrow. Finally, although I concluded (based on comparisons between caged- and un-caged treatments) that chemicals released by bivalves did not have an effect on meiofauna I did not test effects of such chemicals in the absence of clams. A further study that would isolate and directly test the effects of bivalve biogenic chemicals on the colonization of meiofauna would be useful in making final conclusions.

7.3 The state of Canadian marine nematology and concluding remarks

The survey of Trevor Channel revealed nine nematode genera new to Canada and 24 new to British Columbia. However, in compiling the review of Canadian marine nematodes it became clear that only a small portion of Canada's coasts have been adequately sampled. It was difficult to draw many conclusions regarding the distribution patterns of many Canadian records because so few investigations have been made. What may appear at first glance as a species with a limited Canadian distribution may simply reflect lack of adequate sampling. Future surveys conducted in more northern reaches of Canadian coastline and in the Arctic would be particularly valuable given their rarity in the literature.

In conclusion, determining abiotic and biotic factors that affect the colonization of meiofauna in marine habitats is often difficult. Gaining accurate measurements of these tiny and abundant animals in their interstitial homes requires much patience and expertise. However, there are also many benefits of working with meiofauna. Their small size, vast abundance and quick colonization rates make them prime candidates for assessing environmental impact and recovery. Often small cores will capture meiofaunal diversity and abundance where much larger samples would be required to adequately represent the macrofauna. Throughout this thesis I have shown that both biotic and abiotic factors can produce measurable effects in meiofaunal colonization and assemblage structure. As meiofauna sampling and processing techniques continue to improve, the allure of using meiofauna to address ecological questions should intensify. Perhaps the stigma of obscurity will eventually be shed from these fascinating animals and their importance as a diverse and abundant component of the marine biota will be justifiably recognized.

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Appendix 4-1. Comparing the effects of suspension-feeding *M. nasuta* and deposit-feeding *P. staminea* (Autumn 2005). Repeated measures tests of within treatment and between treatment differences across the four sampling periods (Greenhouse-Geisser test). Values less than 0.05 are shown in bold.

	DF	F	Sig.
a) Within-subjects effects			
Copepods (Log10 +1)			
Week	2.325	9.524	**0.0002**
Week * Treatment	6.975	5.119	**0.0002**
Error (time)	46.5		
Nematodes (Log10 +1)			
Week	2.539	7.510	**0.001**
Week * Treatment	7.616	0.491	0.850
Error (week)	58.39		
Nauplii (Log10+1)			
Week	2.709	26.618	**<0.0001**
Week * Treatment	8.126	0.989	0.452
Error (Week)	62.3		
b) Between-subjects effects			
Copepods (Log10 +1)			
Intercept	1	850.266	**<0.0001**
Treatment	3	24.465	**<0.0001**
Error	20		
Nematodes (Log10+1)			
Intercept	1	1848.35	**<0.0001**
Treatment	3	4.439	**0.013**
Error	23		
Nauplii (Log10+1)			
Intercept	1	377.493	**<0.0001**
Treatment	3	4.818	**0.01**
Error	23		

Appendix 4-2. Comparing the effects of suspension-feeding *M. nasuta* and deposit-feeding *P. staminea* (Autumn 2005). Tukey's post-hoc tests for differences in copepod, nematode and nauplius abundances (Log10+1 transformed) between treatments: Treatment 1: Deposit-feeding Bivalves; treatment 2: 50/50 Deposit-feeding/Suspension-feeding Bivalves; treatment 3: Suspension-feeding Bivalves; treatment 4: No Bivalves. Values less than 0.05 are shown in bold.

Comparisons		Copepods	Nematodes	Nauplii
Treatment	Treatment	Sig.	Sig.	Sig.
1	2	0.269	0.763	0.6903
1	3	**0.001**	0.882	0.1154
1	4	**<0.00001**	**0.010**	**0.0061**
2	3	0.086	0.985	0.8236
2	4	**<0.0001**	0.271	0.2510
3	4	**0.01**	0.067	0.6229

Appendix 4-3. Towards a generalization for bivalve effects on meiofauna (Summer 2006): repeated measures tests of within treatment and between treatment differences across the four sampling periods (Greenhouse-Geisser test, treatment = 5 bivalve species).

	DF	F	Sig.
a) Within-subjects effects			
Copepods (Log10 +1)			
Time	2.008	17.113	<0.00001
Time * Treatment	14.057	0.911	0.579
Error (time)	48		
Nematodes (Log10 +1)			
Time	2.715	4.330	0.011
Time * Treatment	19.007	1.482	0.141
Error (time)	43.4444		
Nauplius Larvae (Log10+1)			
Time	2.663	1.450	0.244
Time * Treatment	18.643	0.580	0.898
Error (time)	42.612		
b) Between-subjects effects			
Copepods (Log10 +1)			
Intercept	1	2953.181	<0.00001
Treatment	7	11.959	0.00002
Error	16		
Nematodes (Log10+1)			
Intercept	1	2236.191	<0.00001
Treatment	7	7.280	0.0005
Error	16		
Nauplius Larvae (Log10+1)			
Intercept	1	220.712	<0.00001
Treatment	7	5.476	0.002
Error	16		

Appendix 4-4. Towards a generalization for bivalve effects on meiofauna (Summer 2006): Tukey's post-hoc tests for differences in copepod, nematode and nauplius larvae abundances (Log10+1 transformed) between treatments: 1) *M. nasuta*, 2) *S. gigantea*, 3) *P. abrupta*, 4) *P. staminea*, 5) *V. philippinarum*, 6) No-bivalve control, 7) Stirred weekly and 8) *N. obscurata*. Values less than 0.05 are shown in bold.

Comparisons		Copepods	Nematodes	Nauplius Larvae
		Sig.	Sig.	Sig.
1	2	**0.0020**	0.0668	0.0928
1	3	**0.0007**	**0.0054**	0.2747
1	4	**0.0004**	**0.0138**	**0.0456**
1	5	0.4057	0.8499	0.9915
1	6	**<0.0001**	**0.007**	**0.0032**
1	7	**0.0004**	**0.0089**	**0.0116**
1	8	0.07	0.5194	0.3992
2	3	0.999	0.8846	0.9972
2	4	0.9809	0.9886	0.9999
2	5	0.1261	0.5588	0.3322
2	6	0.3938	0.3057	0.6516
2	7	0.9803	0.9577	0.9482
2	8	0.5934	0.8779	0.9791
3	4	1.00	0.9996	0.9601
3	5	**0.0458**	0.0779	0.6977
3	6	0.7139	0.9494	0.2967
3	7	0.999	1.0	0.6566
3	8	0.2963	0.2162	1.0
4	5	**0.0235**	0.1782	0.1844
4	6	0.8842	0.761	0.8558
4	7	1.00	1.0	0.9954
4	8	0.1719	0.4274	0.8825
5	6	**0.0019**	**0.0097**	**0.0147**
5	7	**0.0233**	0.1215	0.0526
5	8	0.9497	0.9984	0.8379
6	7	0.8862	0.8695	0.9969
6	8	**0.0156**	**0.0308**	0.1968
7	8	0.1705	0.3150	0.4991

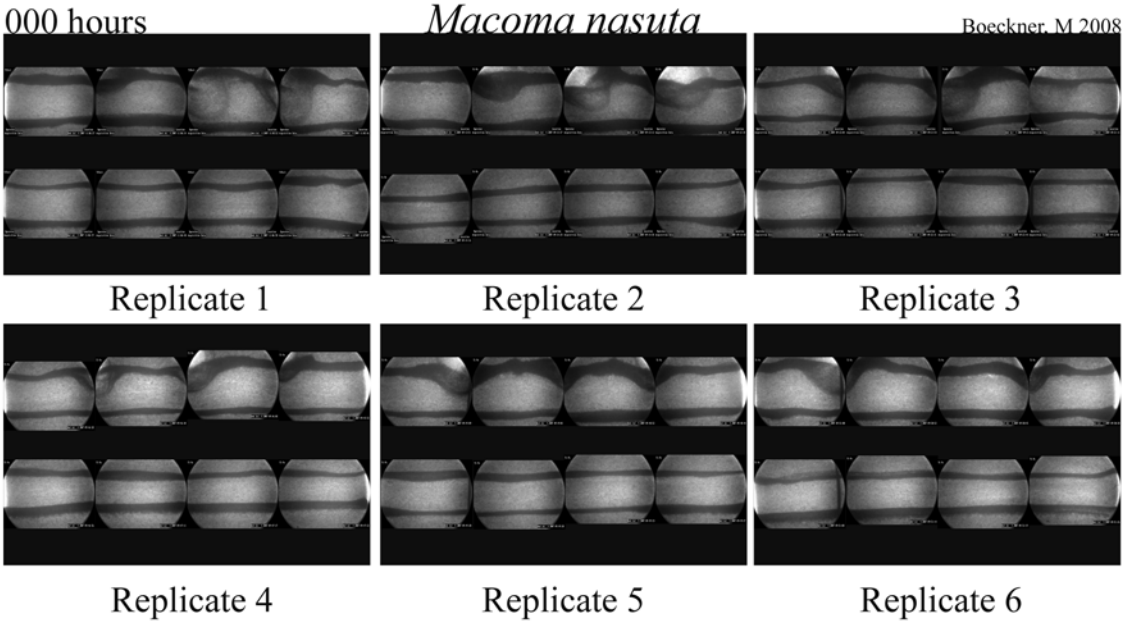
Appendix 4-5. Effects of caging on bivalve impact on meiofauna (Summer 2006): repeated measures tests of within treatment and between treatment differences across the four sampling periods (Greenhouse-Geisser test). Values less than 0.05 are shown in bold.

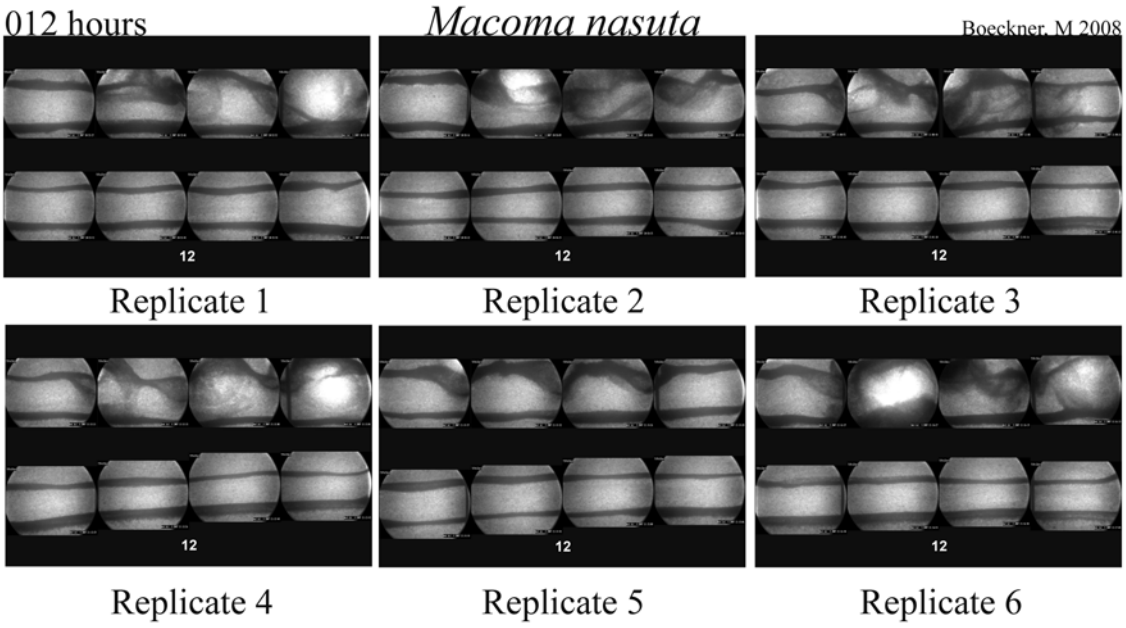
	DF	F	Sig.
a) Within-subjects effects			
Copepods (Log10 +1)			
Time	2.188	70.767	**0.001**
Time * Treatment	8.472	1.539	0.20
Error (time)	21.180		
Nematodes (Log10 +1)			
Time	2.222	2.372	0.112
Time * Treatment	8.888	0.928	0.520
Error (time)	22.219		
Nauplius Larvae (Log10+1)			
Time	2.175	4.884	**0.016**
Time * Treatment	8.701	0.584	0.791
Error (time)	21.752		
b) Between-subjects effects			
Copepods (Log10 +1)			
Intercept	1	1353.313	**<0.00001**
Treatment	4	12.72	**0.001**
Error	10		
Nematodes (Log10+1)			
Intercept	1	1218.042	**<0.00001**
Treatment	4	7.719	**0.004**
Error	10		
Nauplius Larvae (Log10+1)			
Intercept	1	152.203	**<0.00001**
Treatment	4	7.579	**0.004**
Error	10		

Appendix 4-6. Effects on caging on bivalve impact on meiofauna (Summer 2006): Tukey's post-hoc tests for differences in copepod, nematode and nauplius larvae abundances (Log10+1 transformed) between treatments: 1) *M. nasuta*, deposit-feeder (caged); 2) *P. staminea*, suspension-feeder (caged); 3) No Bivalve Control; 4) *M. nasuta*, deposit-feeder (un-caged) and 5) *P. staminea*, suspension-feeder (un-caged). Values less than 0.05 are shown in bold.

Comparisons		**Copepods**	**Nematodes**	**Nauplii**
		Sig.	Sig.	Sig.
1	2	1.0	0.799	0.944
1	3	1.0	0.369	0.660
1	4	**0.0013**	0.057	**0.004**
1	5	0.84	0.985	0.195
2	3	1.0	0.922	0.966
2	4	**0.0012**	**0.010**	**0.011**
2	5	0.8249	0.971	0.497
3	4	**0.0013**	**0.003**	0.092
3	5	0.8363	0.635	0.092
4	5	**0.0053**	**0.026**	0.528

Appendix 5-1. Time-lapse x-ray photograph collages showing how sediment was affected by the 5 clam species (and no clam controls) at 0, 12, 24 and 120 hour intervals.





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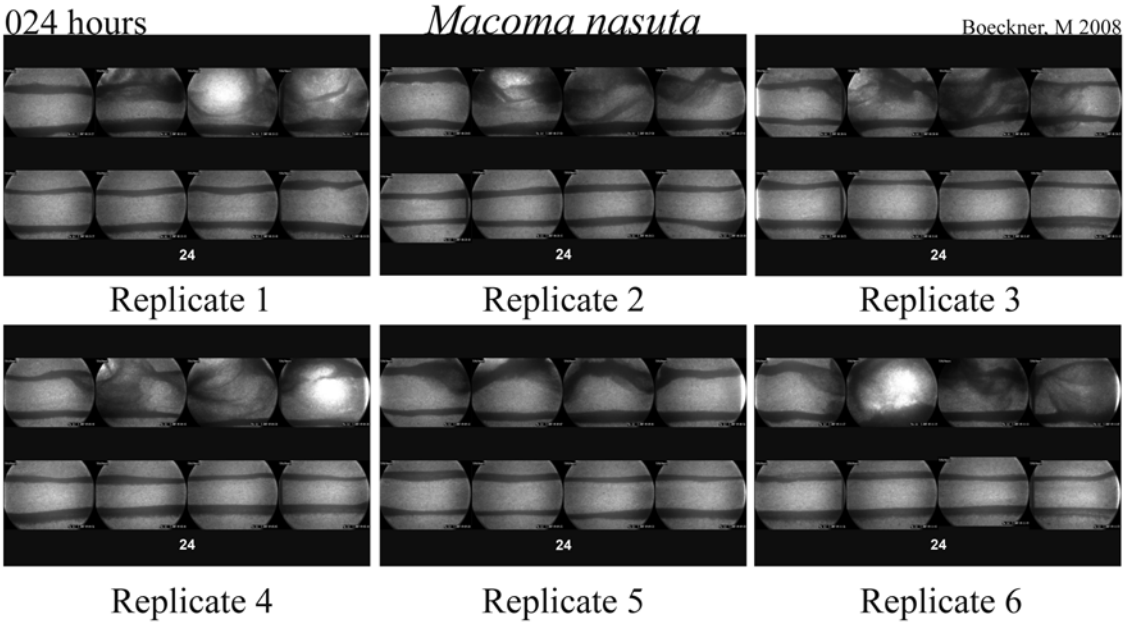

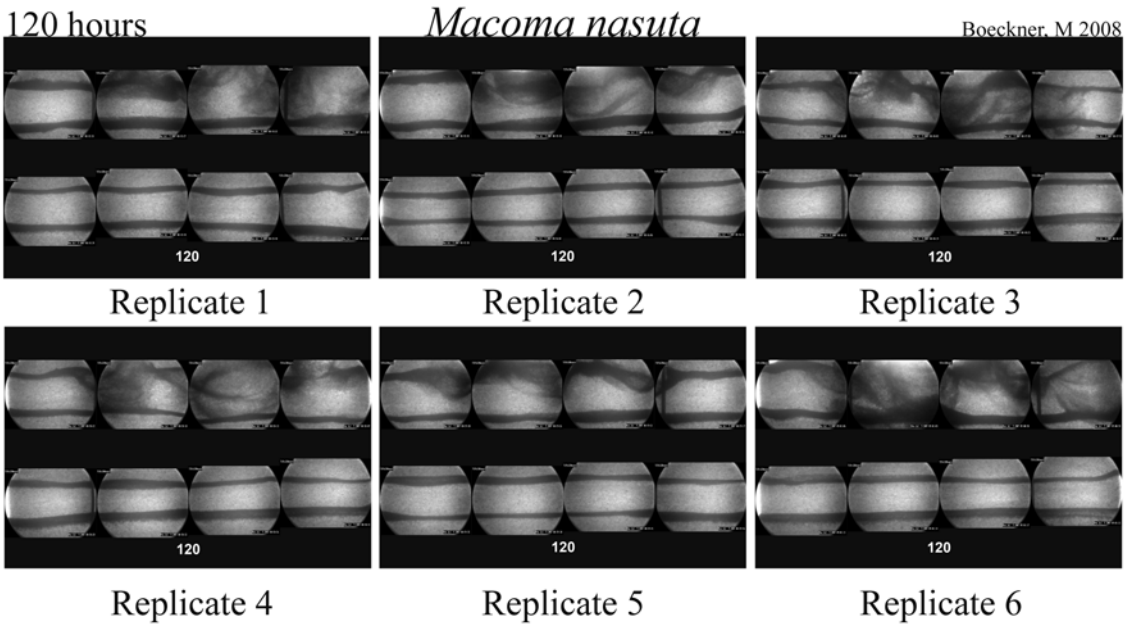

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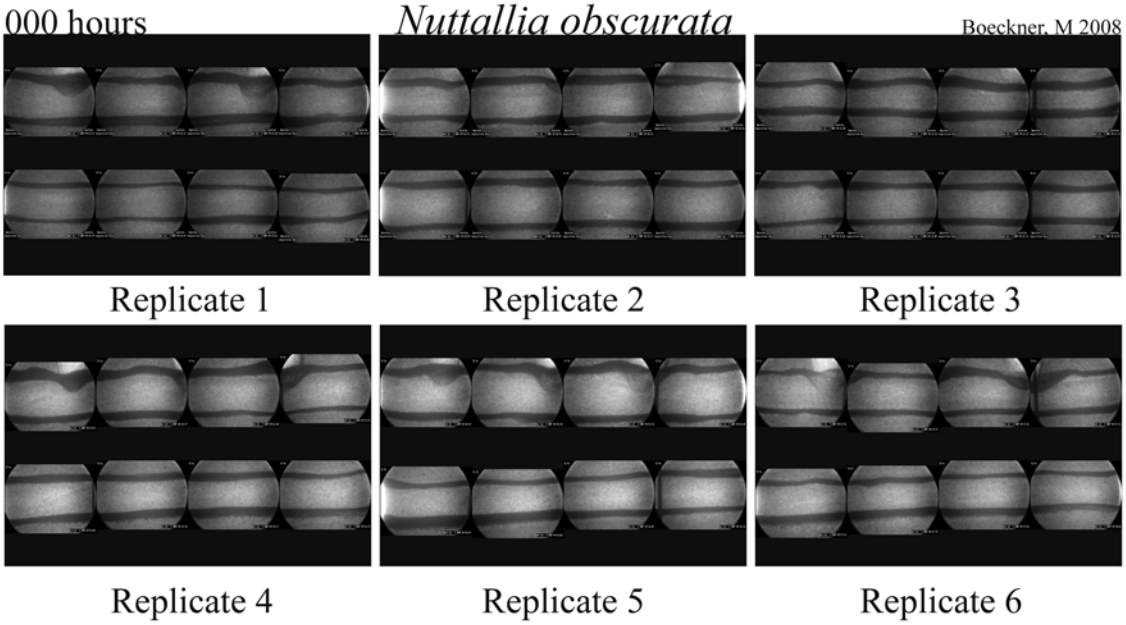

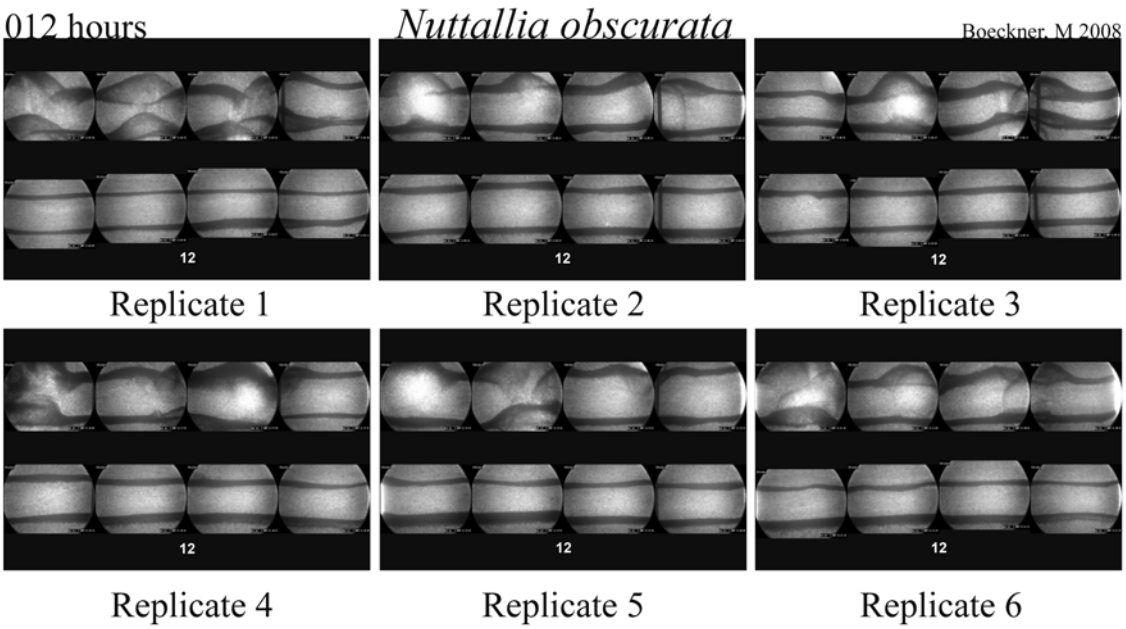

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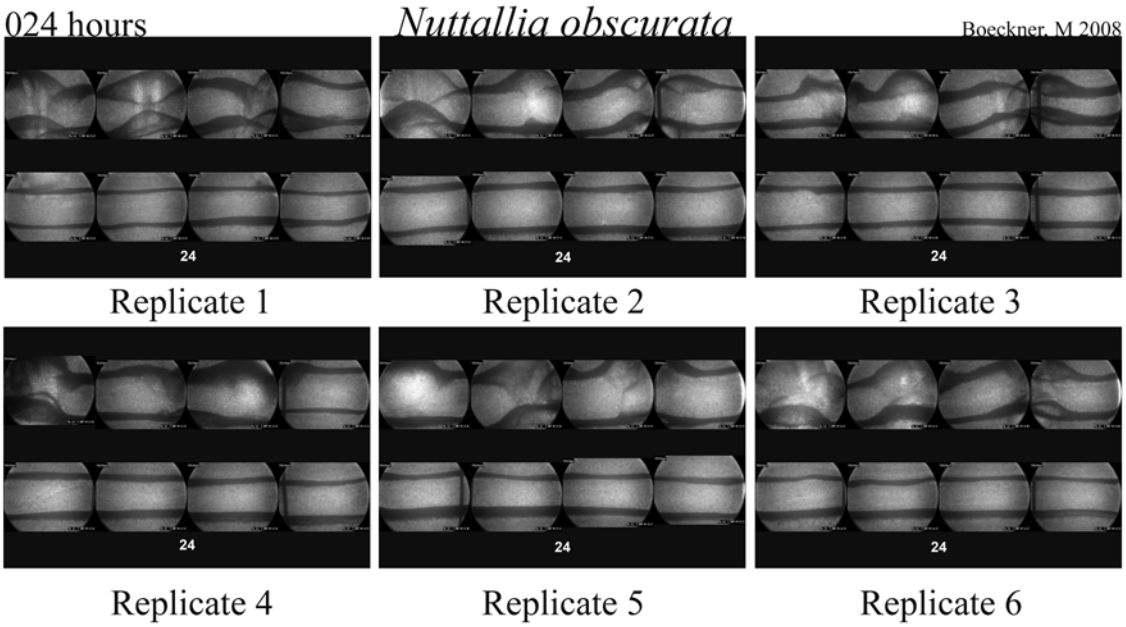
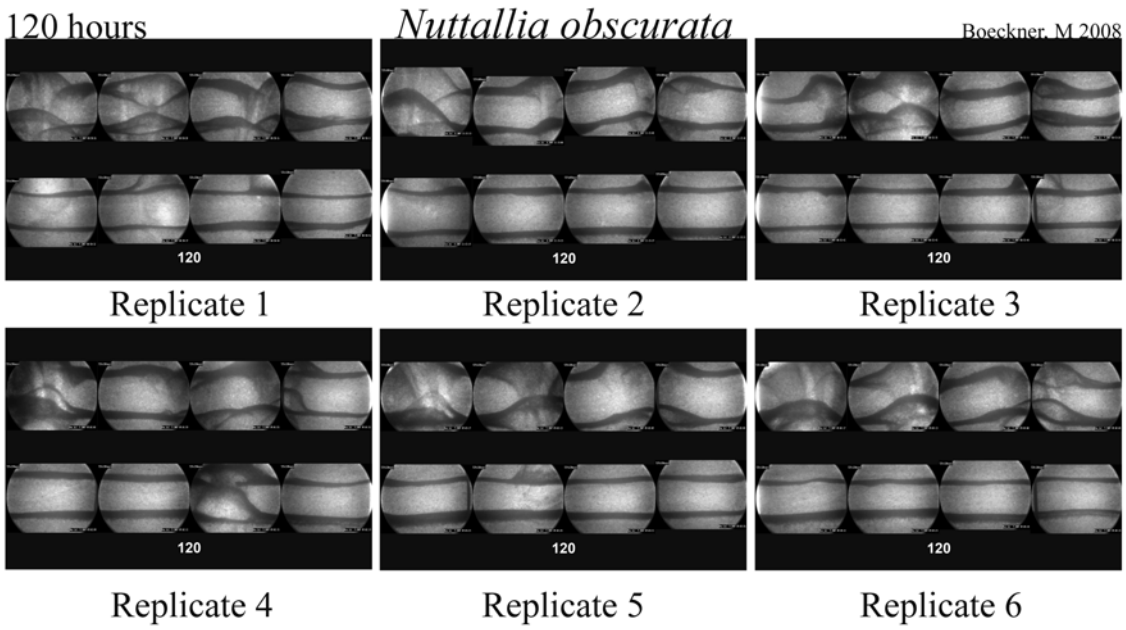
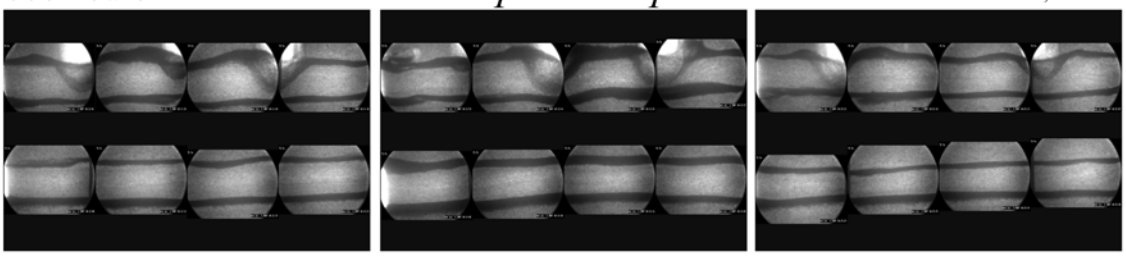




Appendix 5-1 cont'd.

000 hours *Panopea abrupta* Boeckner, M 2008



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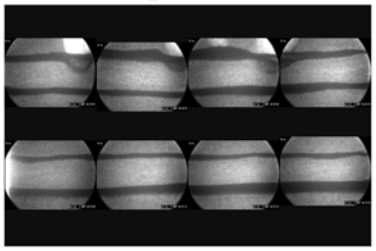

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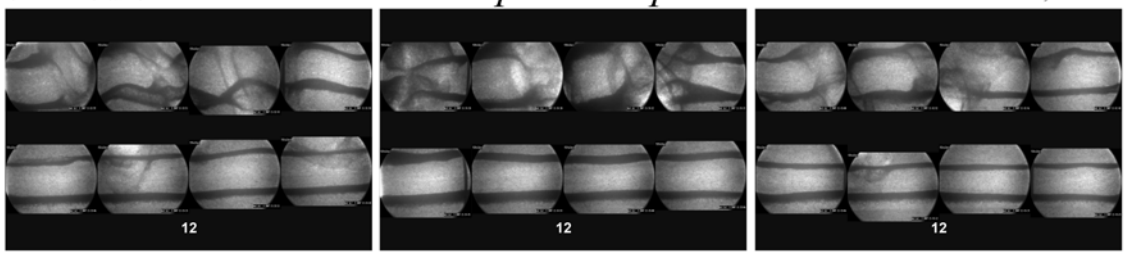

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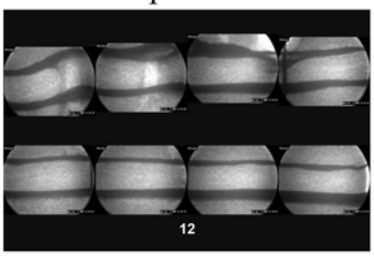

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Appendix 5-1 cont'd.

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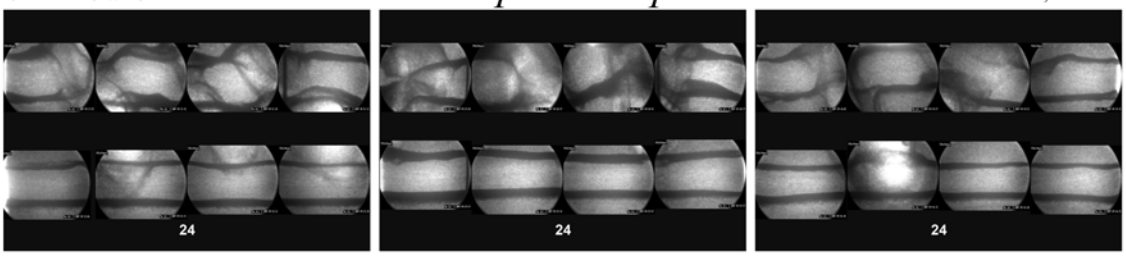

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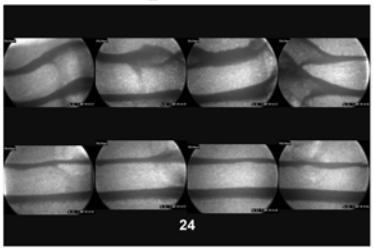

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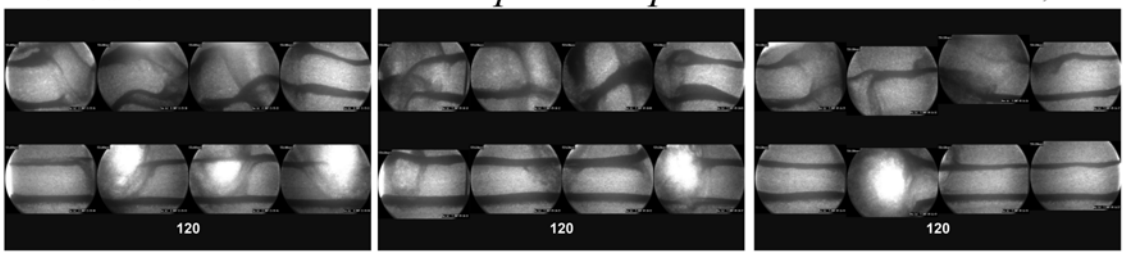

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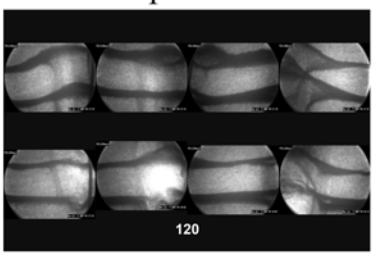

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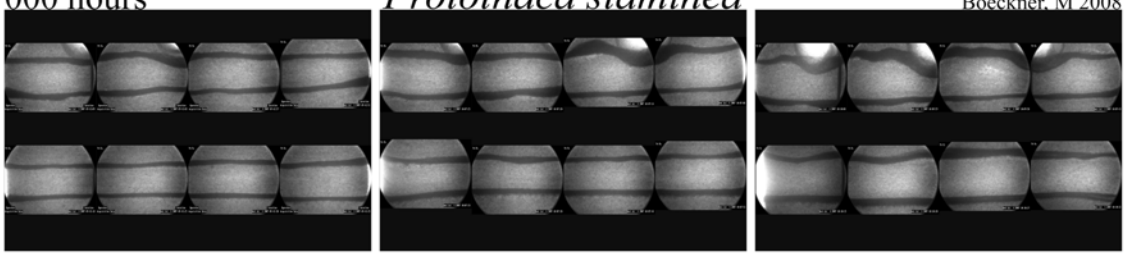
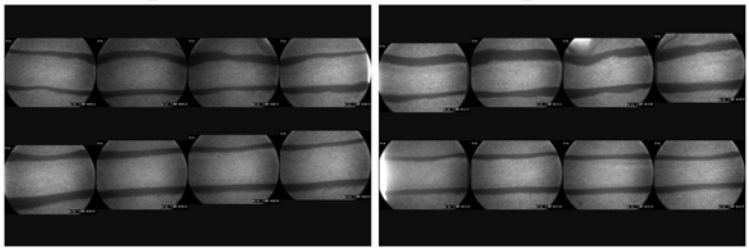
Appendix 5-1 cont'd.

000 hours *Protothaca staminea* Boeckner, M 2008

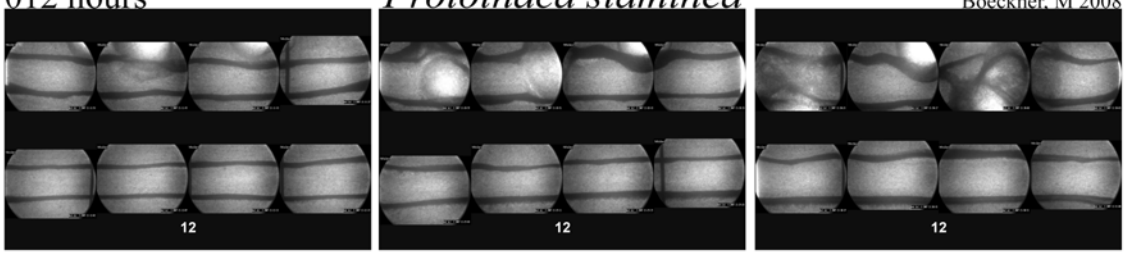


Replicate 1 Replicate 2 Replicate 3



Replicate 4 Replicate 5 Replicate 6

012 hours *Protothaca staminea* Boeckner, M 2008



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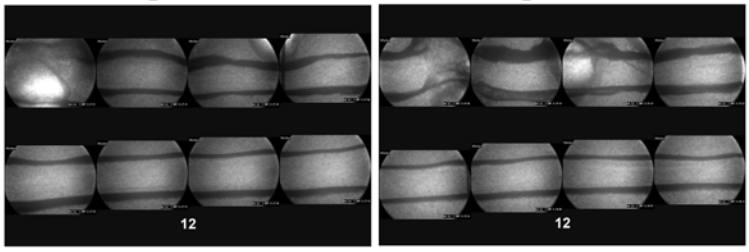
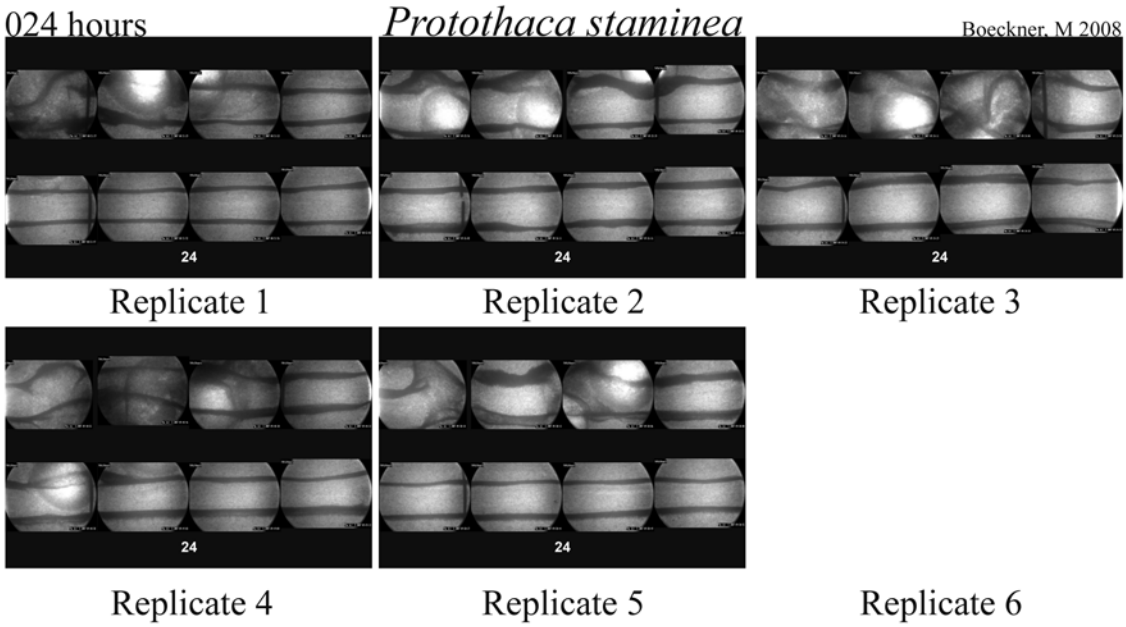
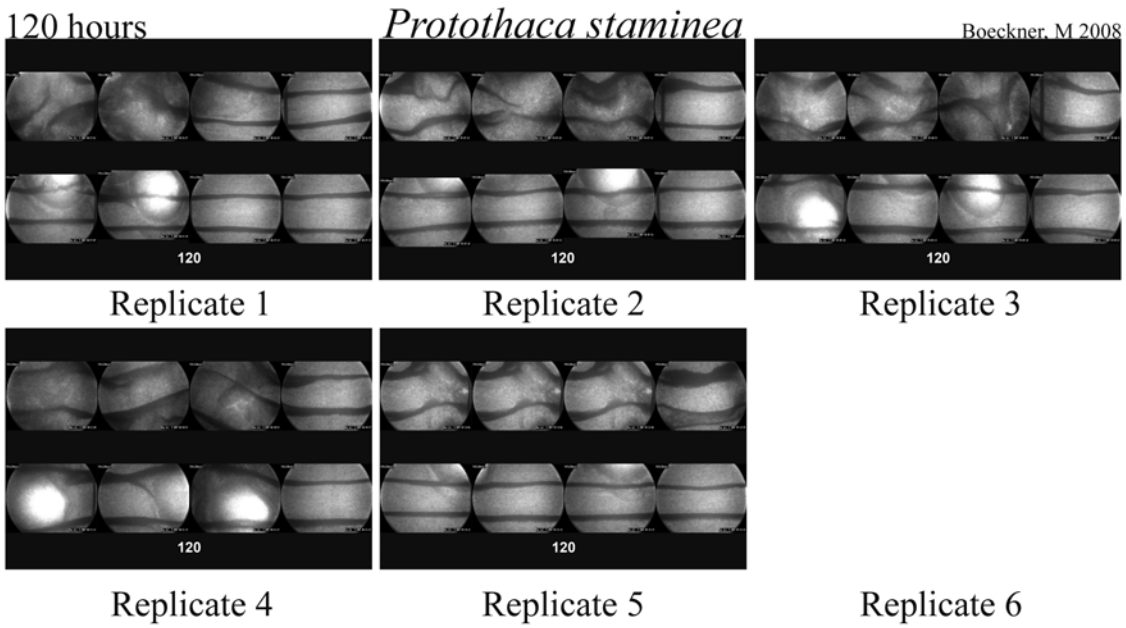


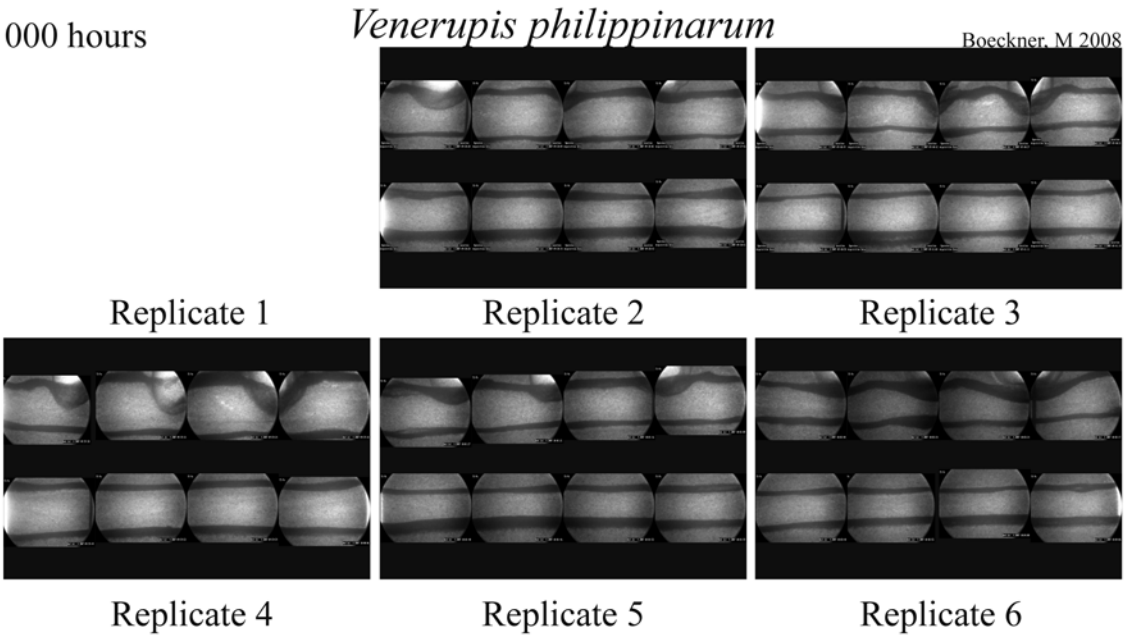
Replicate 4 Replicate 5 Replicate 6

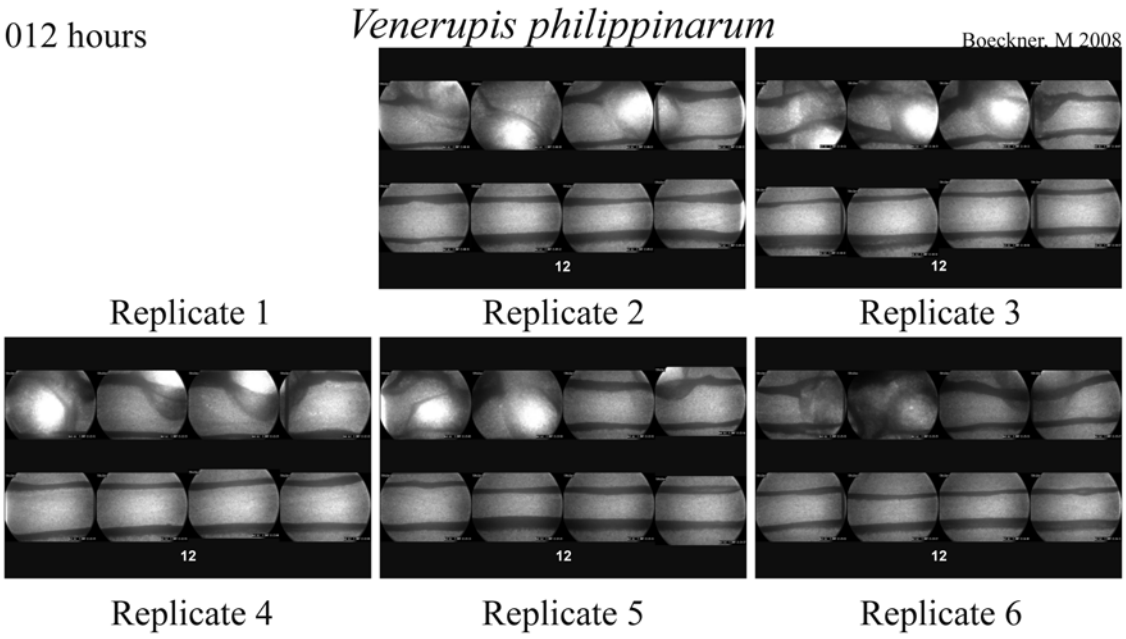
Appendix 5-1 cont'd.





Appendix 5-1 cont'd.



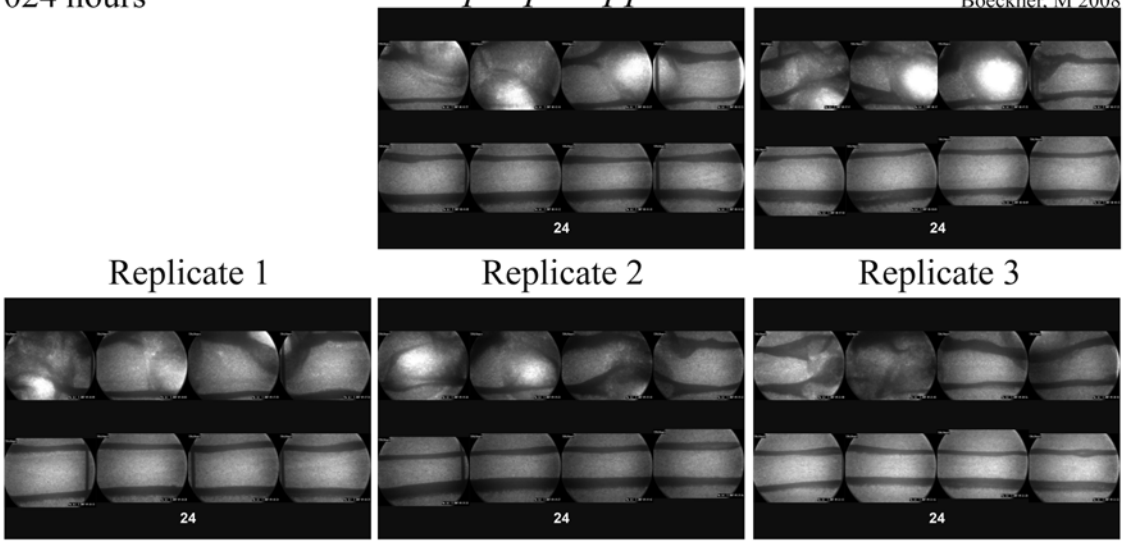


Appendix 5-1 cont'd.

024 hours

Venerupis philippinarum

Boeckner, M 2008



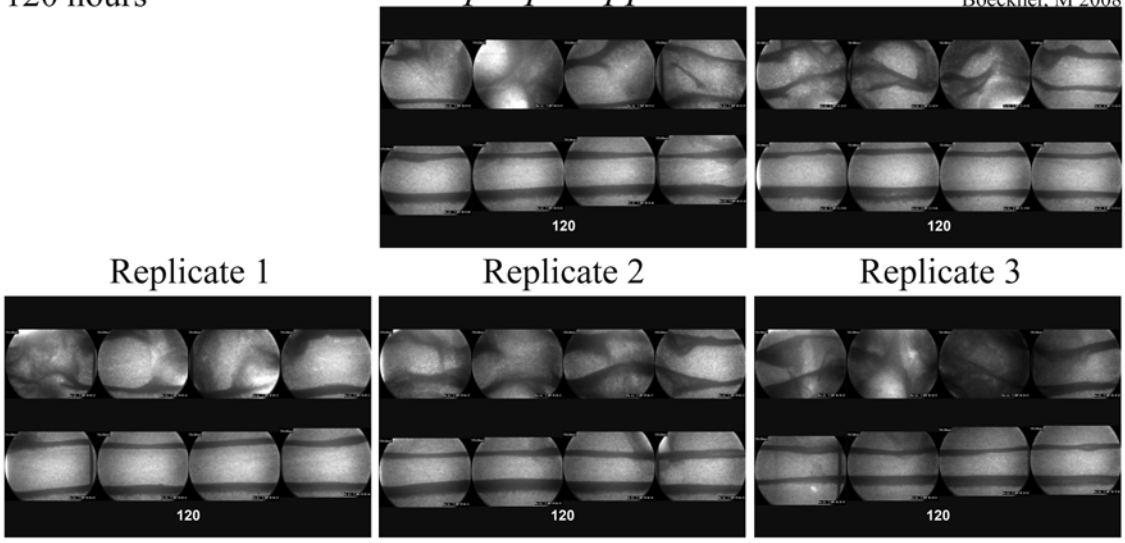
Replicate 1 Replicate 2 Replicate 3

Replicate 4 Replicate 5 Replicate 6

120 hours

Venerupis philippinarum

Boeckner, M 2008

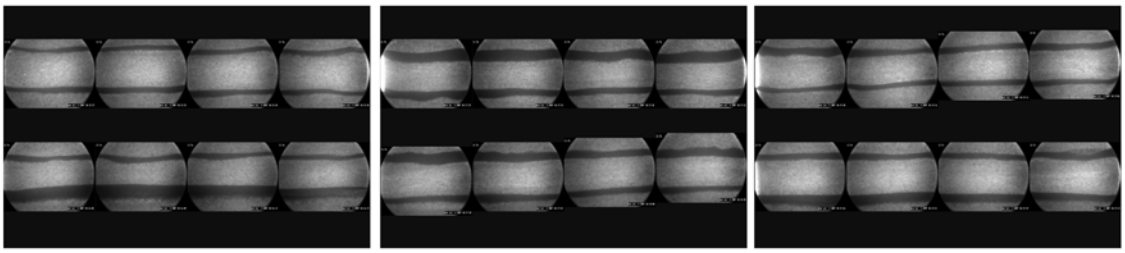


Replicate 1 Replicate 2 Replicate 3

Replicate 4 Replicate 5 Replicate 6

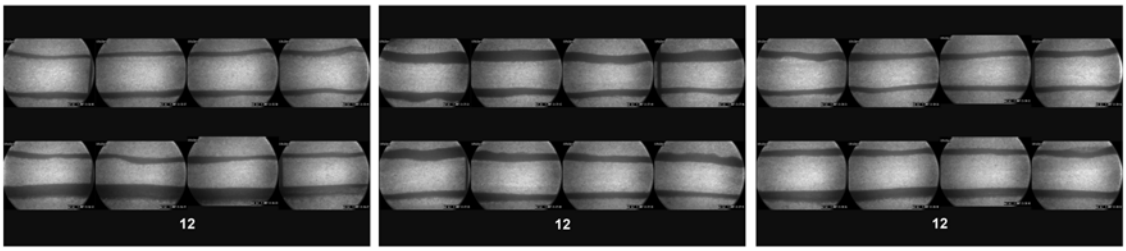
Appendix 5-1 cont'd.

00 hours No-clam Controls



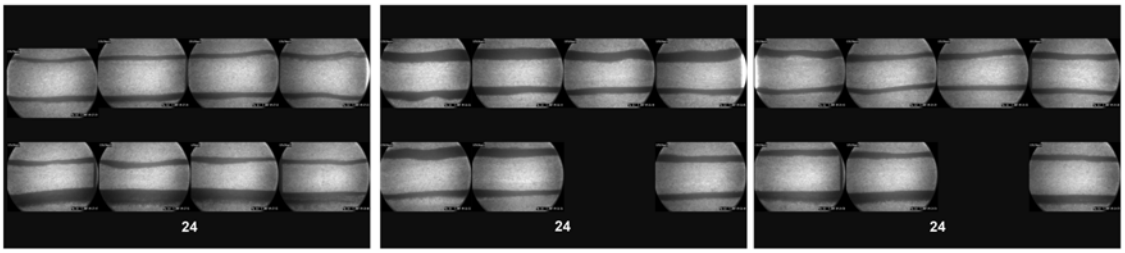
Replicate 1 Replicate 2 Replicate 3

12 hours No-clam Controls



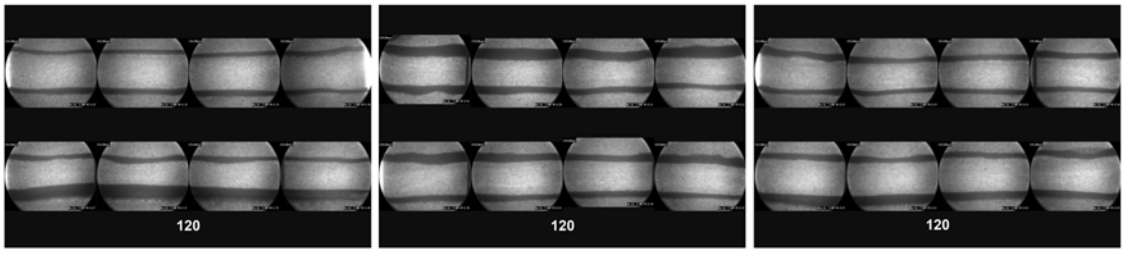
Replicate 1 Replicate 2 Replicate 3

24 hours No-clam Controls Boeckner, M 2008



Replicate 1 Replicate 2 Replicate 3

120 hours No-clam Controls Boeckner, M 2008



Replicate 1 Replicate 2 Replicate 3