MACROINVERTEBRATE COMMUNITY RESPONSES TO CLAM AQUACULTURE PRACTICES IN BRITISH COLUMBIA, CANADA

by

Jonathan Arthur Whiteley
B.Sc.(Env.), University of Guelph 2001

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the
Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

Spring 2005

APPROVAL

Name: Jonathan Arthur Whiteley

Degree: Master of Science

Title of Thesis:

Macroinvertebrate community responses to clam aquaculture practices in British Columbia, Canada

Examining Committee:

Chair: Dr. A. Harestad, Professor

Dr. L. Bendell-Young, Professor
Department of Biological Sciences, S.F.U.

Dr. A. Mooers, Assistant Professor
Department of Biological Sciences, S.F.U.

Dr. R. Ydenberg, Professor
Department of Biological Sciences, S.F.U.

Dr. A. deBruyn, Adjunct Professor
School of Resource and Environmental Management, S.F.U.
Public Examiner

Date Approved April 15, 05

SIMON FRASER UNIVERSITY

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ABSTRACT

Despite recent growth of shellfish aquaculture in B.C., Canada, very little is known regarding impacts of common practices. Seeding and netting are frequently employed on clam farms to increase production of *Venerupis philippinarum*. A pilot netting experiment found no observable effect of predation at small scales. A field study compared bivalve communities on clam farms with matched reference sites, using density and biomass data. *V. philippinarum* was the only species found in higher abundance on farm sites, consistent with values expected from clam seeding. Bivalve communities were not significantly different on farm sites, but were more similar on average than reference sites, leading to a loss of regional distinctness. These results are consistent with recent research suggesting that predation and competition may play minor roles in structuring communities in soft-bottom environments. Given the remaining uncertainties, a precautionary approach is recommended in future development of the intertidal for clam aquaculture.

DEDICATION

To my family, whose love and support have encouraged me to challenge myself.

ACKNOWLEDGEMENTS

I am forever grateful to Leah Bendell-Young, for supervising and funding this project, and to all members of my supervisory committee, Ron Ydenberg and Arne Mooers, for asking the hard questions and for their invaluable advice. I wish to thank Judy Higham and Deb Lacroix for help with planning, paperwork and other administrative necessities. I can't thank Molly Kirk enough for her hard work and dedication as a field technician, and Ian McKeachie, Kate Henderson, David Leung, Natalie Martens, Vanessa Sadler, Robyn Davidson, Blake Bartzen, Rian Dickson, and Tyler Lewis, who also sifted through beach sediment and collected samples in adverse weather to collect data for this project. I thank Dan Esler, Rob Butler, Sean Boyd, and Tyler Lewis for collaborating on the Sustainable Shellfish Aquaculture Initiative and for sharing their thoughts, feedback and results with me.

This work would not have been possible without the co-operation of the clam farmers who granted permission to sample on their leases and I am thankful for all their support. I would also like to thank Sarah Dudas, Bamfield folk, Rick Harbo and others who helped with identification of unknown critters. Thanks also to Ramunas Zydelis for introducing me to PRIMER software and multivariate community analysis, and to Colin Bates for helping me understand it. I am also grateful to Ian Bercowitz, of the Statistical consulting service at S.F.U., who answered many questions about repeated measures analysis and other statistical procedures. Many thanks to Joline Widmeyer, Christy Morrissey, Niki Cook, Tracey Brunjes, Carolyn Duckham, Jeff Christie, and all the lab-mates and fellow grad students who listened to my frustrations, successes, advice, and shared theirs with me.

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DEFINITION OF TERMS

Intertidal:	The area of land normally exposed and covered during an average tidal cycle. This is typically defined as extending from the yearly average of the lowest low tide level to the average of the highest high tides among each cycle.
Mid Intertidal:	In this work, "Mid" intertidal refers to beach areas between 2m and 3m above chart datum.
Low Intertidal:	In this work, "Low" Intertidal refers to beach areas between 1m and 2m above chart datum.
Soft-bottom:	Benthic substrate composed primarily of unconsolidated clastic sediment particles, typically deposited by water movement. This includes a range of substrate types, from mud to loose cobble. Appendix A defines substrate types in terms of particle sizes.
Rocky Bottom:	Benthic substrate composed primarily of solid mineral structures, such as cliff faces and bedrock.
Infauna:	Refers to animals that are typically found below the sediment surface, in soft-bottom benthic environments.
Epifauna / Epibenthic:	Refers to animals that are typically found on the surface of benthic environments.

1.0 INTRODUCTION

The role of biodiversity in ecosystems has become a major concern of scientists and the public, in light of increasing numbers of documented species extinctions. If biodiversity is to be maintained, a greater understanding is required of the mechanisms that structure this diversity, and ecologists are particularly interested in the diversity of species and the structure of their associated communities. Ecological factors that are important in structuring diversity at a local scale include predation, competition, migration, physical structures, environmental and habitat complexity, and disturbance. The relative importance of these factors may vary between ecosystems and each can operate individually or in combination to structure local diversity.

The research described in this work is intended to assess in a descriptive manner if and how practices associated with shellfish aquaculture of clams in British-Columbia (B.C.), Canada are associated with changes in species diversity or community structure of intertidal benthic macroinvertebrate communities. The goal is to quantify the potential impacts of an expanding shellfish aquaculture industry over large regional scales in coastal B.C.

Because predator exclusion is an important aspect of clam aquaculture in B.C., this industry offers a unique opportunity to examine the roles of predation and competition in structuring intertidal communities. Results from field studies and a small experiment will be used to explore differences in the community structure of macroinvertebrates associated with common shellfish aquaculture practices, in soft-bottom intertidal habitats.

1.1 Clam Aquaculture in British Columbia, Canada

Bivalves are an important component of many soft-bottom marine communities. Their activities play a major role in cycling nutrients between sediments and the overlying water column (Dame 1996). Filter and deposit-feeding by many bivalves aid in moving nutrients and organic particles from the water column into sediments. Bivalves also excrete metabolic biproducts back up into the water. The burrowing activities of bivalves and other infaunal invertebrates also mobilize nutrients stored in the sediments back up into the water column, a process known as bioturbation (Groffman and Bohlen 1999, Snelgrove 1999). Infaunal bivalves (clams) also serve as an important food source for a variety of marine predators, including crabs (Spencer *et al.* 1992), worms (Bourque *et al.* 2001), fish (de Goeij *et al.* 2001), snails (Peitso *et al.* 1994), birds such as sea ducks (Jamieson *et al.* 2001) and humans.

Clams were harvested traditionally by aboriginal people in British Columbia (B.C.), Canada prior to European settlement, and there has been a clam fishery in B.C. since the late 19th century (Quayle and Bourne 1972). The industry initially consisted of commercial harvesting, predominantly of butter clams (*Saxidomus gigantea*; Deshayes 1839) and native littlenecks (*Protothaca staminea*; Conrad 1837). Japanese littlenecks, or manila clams (*Venerupis philippinarum*; A. Adams & Reeve, 1850) were introduced to B.C. with Japanese oyster seed (*Crassostrea gigas*; Thunberg, 1793), and first recorded in 1936 (Quayle and Bourne 1972). After spreading throughout southern areas of coastal B.C., they have grown in importance to become the single largest component of the clam fishery and clam aquaculture in the region (Harbo 1997).

Other clam species have been introduced to B.C., including a deliberate release of *Mya arenaria*, a commercially valuable species on it's native Atlantic shores that has never achieved a similar popularity in B.C. (Quayle and Bourne 1972). A more recent invasion by the varnish clam, also known as the dark-mahogany or savoury clam (*Nuttallia obscurata*; Reeve, 1857) occurred in the late 1980s to early 1990s (Harbo 1997). *Nuttallia obscurata* is generally thought to have arrived from Japan in ballast water (Gillespie *et al.* 1999). This new arrival has primarily colonized intertidal areas even higher than *Venerupis philippinarum,* which might allow it to avoid competition with other intertidal clam species, or intense predation prevalent in lower intertidal areas.

Aquaculture of clams in B.C. began in an experimental stage in Baynes Sound (see Figure 1) in 1969, but has only been licensed formally since 1991 (Jamieson *et al.* 2001). Access to suitable sites has been identified as a major factor limiting the expansion of shellfish aquaculture (Coopers & Lybrand 1997), and the industry has turned to increasing the intensity of production at existing sites (BCSGA 2004a). *Venerupis philippinarum* is the commercially dominant species in the industry. Production of this species is enhanced on tenures primarily using a combination of two common practices: (1) the addition of hatchery-reared juvenile *Venerupis philippinarum* to intertidal sediments, a process referred to as "seeding", (2) the application of netting over the seeded substrate to protect the juvenile clams from predation (Jamieson *et al.* 2001). Clams are harvested year-round using hand-raking, once they reach a minimum legal size of 38 mm (1.5 inches) approximately 2-4 years after seeding (Jamieson *et al.* 2001).

1.2 Clam Netting

Protective nets used in B.C. include a variety of plastic netting with 1.25 cm apertures, called "car cover" by many farmers, and woven rope netting with apertures up to approximately 3.5 cm. These nets are applied in 1 or 2 layers, then anchored at the corners and along the edges with large rocks, or steel posts, bent into an inverted U-shape and pounded into the sediment. Similar to observations by Spencer *et al.* (1996, 1997), nets used in B.C. frequently attract growth of macroalgae and other "bio-fouling" organisms, which must be removed manually as large amounts can reduce the availability of food particles to the sediment surface (Jamieson *et al.* 2001). In some areas, the amount of labour required to keep nets clear of biofouling is so great that some clam farmers have abandoned the use of nets in intertidal areas (personal communication).

There appears to be no consensus among clam farmers regarding the reasons for applying nets over cultured clam beds. This practice was originally proposed to protect the clams from predators in the water column (Spencer *et al.* 1992). While survival of juvenile *Venerupis philippinarum* is enhanced by netting (Spencer *et al.* 1992), survival of larger individuals of this species appears unaffected by netting (Jamieson *et al.* 2001). Spencer *et al.* (1997) reported a survival rate of only 5% for adults under netted plots, and farmers expect a 40-50% loss of their crop even under nets (BCSGA 2004b).

Some believe that the stabilizing effect on the sediment is more important than protection from predators. Nets tend to increase sedimentation rates in intertidal areas, with a subsequent benefit to bivalves through an increase in the availability of food particles (Spencer *et al.* 1996). Increased sedimentation can also lead to changes in community structure, independent of predator exclusion.

This sampling artefact has been a common confounding factor in many predator-exclusion experiments that use structures such as nets or cages to exclude predators from soft-bottom marine sediments (Gee *et al.* 1985, Reise 1985).

In the UK, netting cover for cultured clam beds was also proposed to prevent the introduced cultured clam species, *Venerupis philippinarum*, from escaping and colonizing local habitats (Spencer *et al.* 1996). In order to achieve this, the netting was buried along all edges, to an unspecified depth. Although the same Japanese species, *V. philippinarum*, is cultured in B.C., netting is not applied in a comparable manner. This species is capable of breeding in southern B.C. coastal waters and was already well established in the wild before clam aquaculture and netting was present in the region. Offspring from cultured clams colonize areas outside shellfish tenures, where they are harvested along with wild set by recreational users with a fishing license, wild harvesters with a commercial license, and poachers, who are the largest unknown and unregulated harvesters.

1.3 Predator Exclusion: Current Theory and Evidence

Whether intentional or not, the presence of netting in soft-bottom intertidal habitats is likely to exclude large, epibenthic predators from access to infaunal prey species. The exclusion of predators is often used as an experimental, though indirect means of manipulating the intensity of competition. The removal of intense predation pressure theoretically allows populations to reach a carrying capacity where resources become limiting, and the effects of competition should be observed. Experimental evidence, however, has shown inconsistent effects of excluding predators from marine benthic environments.

1.3.1 Building on research in Rocky Intertidal Habitats

Caging experiments have demonstrated that predators help to maintain species richness and diversity in rocky bottom communities (Dayton 1971, Gee *et al.* 1985, Paine 1974). When large, mobile predators are excluded with cages, populations of producers and sessile organisms increase to a point where space on the surface on the rocky habitat becomes limiting, and interspecific competition becomes more important in structuring communities. Species that lose out in competition are excluded from these areas, and all available space becomes occupied by a few, dominant species (Dayton 1971).

These observations suggest that predation keeps populations of competitively superior species low enough to create empty patches on rocky substrata, which are available to be colonized by other opportunistic species. Predation is thought to reduce the dominance of otherwise competitively superior species, effectively depressing the strength of interspecific competition (Paine 1974).

Many broad ecological theories about the structuring role of competition in communities have been based on results from experiments in rocky-bottom habitats (Peterson 1992). This may be a result, in part, of the relative ease of conducting experiments in these systems. The challenges of sub-surface, sediment-dwelling organisms that are difficult to capture or observe in their natural setting, along with the complexity of interactions in benthic food webs may have discouraged early experimentation in soft-bottom systems. However, Peterson (1992) argues that organisms in these habitats are less mobile than other (terrestrial) environments, but easily transportable as they are not directly attached to the substrate. These characteristics make this system extremely amenable to "rigorous experimental manipulation", once the challenges of finding and counting such fragile organisms are overcome.

Recent research in soft-bottom benthic systems suggests that space is not as limiting a factor as it is in rocky-bottom habitats, due to the three-dimensional nature of sediments, and the relatively greater mobility of organisms (Peterson 1979b, 1992). This increased habitat complexity may offer more opportunities for competition avoidance, even in the absence of predation. Therefore, competition may not play an important role in structuring benthic marine communities in soft-bottom sedimentary habitats. As a result, the exclusion of predators does not often lead to changes in community structure in soft-bottom substrata, because interspecific competition may not be enhanced in the absence of predators. This contrasts sharply with results from experiments in rocky bottom environments, due to fundamental differences in physical and biotic characteristics between these two ecosystems. Any theory regarding the structuring role of predation in soft-bottom habitats can not be inferred from research conducted in rocky bottom environments, but must be based on direct observations from soft-bottom communities themselves.

1.3.2 Predation in soft-bottom marine benthic communities

Predator exclusion experiments and studies in soft-bottom habitats have found at times strong or weak effects of predation on community structure. Current theory predicts that predation could play an important role in structuring communities if it is intense enough to limit populations below the point at which competition, or some other factor becomes more important and structures communities differently. If predation is not limiting when present, it would be unlikely to affect community structure.

Although experiments often disagree on the mechanisms or role of predation in structuring soft-bottom benthic communities, the evidence strongly suggests that predation is often limiting for many benthic populations in unvegetated sediments (Peterson 1979a, 1982, 1983, Quammen 1984, Reise 1985, Summerson and Peterson 1984). Several experiments have found that when predators are excluded from these systems using various forms of cages and nets, that overall densities within exclosures tend to increase, sometimes double or more that of controls (Reise 1985). Summerson and Peterson (1984) found that the response to predator exclusion varied by physical and trophic position within unvegetated sediment. Suspension feeders benefited the most, followed by predator-scavengers, while surface and sub-surface deposit feeders responded very little, and deep-dwelling deposit feeders responded the least. These differences were explained by relative susceptibility to predation. Deep-dwelling species are naturally well protected from large, mobile predators on the surface. Many deposit feeders are prey, not only to epibenthic predators, but also infaunal predator-scavengers such as polychaete and nemertean worms. These predator-scavengers, in turn, are often the largest of the benthic macroinvertebrates, least costly to consume, and therefore make excellent prey for epibenthic predators. Suspension feeders, who must expose some part of their body to the water column to obtain food, seem to be the most susceptible to predators on the surface and in the water. Posey *et al.* (2002) found similar increases in the density of sedentary and near-surface dwelling fauna when predators where excluded.

Such differential responses to predation might lead to a prediction of changing community structure in exclosure plots, although Summerson and Peterson (1984) also reported no changes in species richness (number of species present), evenness (dominance), or diversity (heterogeneity). Any such differences could be explained by a simple, additive curve of species accumulation with increasing number of individuals sampled. Thus, as abundances of benthic species increased, so too did their chance of being observed in a sample, in a simple additive fashion. The total number of species present likely did not change.

In a study of a predatory moonsnail, *Polinices duplicatus*, Wiltse *et al.* (1980) found a significant negative relationship between predator density and the number of observed species, evenness, diversity, and density of benthic invertebrates. This negative effect of predation was attributed to the high specificity of the predator, which selectively preyed on thin-shelled bivalves and other rare species in the community, having little or no impact on already dominant species. The use of observed species as a metric of richness may not allow a sound conclusion that species were actually excluded by predators, because if densities of rare species are depressed so as to reduce the probability of detection in a sample, they would not be observed, despite being present at extremely low densities. A non-parametric estimator of richness is often preferred over observed richness and might be more appropriate in this situation (Brose *et al.* 2003, Foggo *et al.* 2003, Gray 2002, Hellmann and Fowler 1999, Heltshe and Forrester 1983). Nevertheless, the depression of rare species leading to increased dominance by already dominant species, definitely accounts for lower evenness associated with this predator. This predatory moonsnail was also found to have negative effects associated with its burrowing activities, independent of feeding impacts. Sediment disturbance caused by burrowing and foraging movements within the sediment were also found to decrease densities of certain species (Wiltse 1980). It was concluded that this predator was able to maintain "population densities below the level where strong competition would occur" (Wiltse 1980).

Disturbance by predation, or any number of other environmental sources, may also negatively affect bivalves or other benthic invertebrates. Beal *et al.* (2001) found a slight increase in growth rates of bivalves in predator exclosures in low intertidal areas, but not in mid or high intertidal. It was hypothesized that this increase may have been due to reduced disturbance by predation, which incurs metabolic costs of repositioning oneself within disturbed sediment, or of activities related to predator avoidance (see Beal *et al.* 2001). Thus, even if densities of larger benthic invertebrates are not increased in the absence of predation, total biomass might increase instead as a result of higher growth rates.

Many long-term experiments have found seasonal changes in the effects of epibenthic predators. In most cases, a release from the limitation of epibenthic predation was strongest during late summer, and warmer water temperatures, when larger predators (excluded by 6 mm wire mesh) were most metabolically active (Drake and Arias 1996, Quammen 1984, Reise 1985). At other times of the year, benthic populations may presumably be limited by other sources of mortality (Gee *et al.* 1985) such as metabolic constraints, stress and disturbance, or possibly food.

Impacts of predation can also be size-specific. Bivalves may face predation from different sources at different stages of their life-cycle (Peterson 1982). Planktonic larvae are most susceptible to predation by planktonic predators and suspension filter-feeders, including adults of their own species, until settlement in a benthic habitat, where they may still be prey to deposit-feeders on and within the sediment. Once juveniles are large enough, predators may be able to choose individuals based on energetic payoffs, and predation is expected to be most intense from fish, shorebirds, and small crabs, which often remove the entire shell and body, leaving no evidence of the prey. Larger adult bivalves may reach a "size refuge" and become too large for these predators to handle, although larger individuals may face an increase risk of predation from even larger predators, such as shell-boring gastropods, large crabs (Peterson 1982), and humans.

Impacts of predation on community structure generally depend on which predators have access to a particular community, and how the physical structure of that community mediates the efficiency of the predators. Experimental evidence in unvegetated soft-bottom marine habitats generally supports the hypothesis that predation is often limiting in these environments. It may occur seasonally, or continuously, or affect some components of the community selectively. Nevertheless, large epibenthic predators are able to keep populations of benthic infaunal invertebrates below carrying capacity. When such predators are excluded from soft-bottom intertidal systems, some, if not all portions of the community are expected to increase in density or biomass in the absence of all other limiting factors such as disturbance, competition, food or other resources.

This is particularly relevant in B.C., where exclusion nets that were originally developed in the United Kingdom to exclude crabs (Spencer *et al.* 1992) are now being applied to also exclude scoters, fish and other large predators. The British Columbia Shellfish Growers' Association (BCSGA) asserts that without such predator exclusion, approximately 40% of clams would be lost to predation, in addition to the 40-50% expected losses even under such nets. Relative strengths of predation may be variable within B.C., although fish, crabs, and a variety of shorebirds and diving ducks are abundant in many areas of coastal British-Columbia, often in areas that may coincide with shellfish aquaculture tenures (Jamieson *et al.* 2001). These species are each important epibenthic predators of soft-bottom communities and are potentially excluded by clam netting.

1.3.3 Infaunal Predation & Predator Exclusion Netting

Ambrose (1984) reminds us that not all predators of soft-bottom communities are epibenthic, and that several species of infauna (polychaetes, nemerteans, gastropods) are themselves also predators of other infauna. Infaunal predators are not excluded by nets, cages or other physical structures often used in predator exclusion experiments carried out in soft-bottom systems.

"The exclusion of epibenthic predators affects predatory and non-predatory infauna differently" as a consequence of several possible mechanisms (Ambrose 1984):

1. Preferential predation on predatory infauna by epibenthic predators
2. Preferential predation on predatory infauna and predation by predatory infauna on other infauna
3. Equal predation on predatory and non-predatory infauna with additional predation by predatory infauna on other infaunal species
4. Competition between predatory and non-predatory infauna, with predatory infauna out-competing non-predatory infauna.

Infaunal predators are often larger and energetically less costly in terms of handling time, than most other infaunal invertebrates, and so can be high quality, preferred prey for epibenthic predators. When epibenthic predators are excluded, infaunal predators benefit, and become more important sources of predation for other infaunal invertebrates. Infaunal predators may mediate indirect effects of epibenthic predators on non-predatory infauna. This may explain observations in some experiments of no net change in invertebrate abundance (Gee *et al.* 1985, Vargas 1988), or even a decrease in abundance (Ambrose 1984), when epibenthic predators are excluded.

Infaunal predators have negative effects on other infauna through direct feeding (Ambrose 1984, Commito 1982), but also induce mortality through physical disturbance and alteration of surface sediment caused by these large predators ploughing through the sediment as they move. Such disturbance effects may be difficult to separate from predation effects (Ambrose 1991). Ambrose (1991) notes that "infaunal predators may have their greatest effects on prey population dynamics as a consequence of injuring their prey rather than consuming it". Infauna have also been observed to emigrate from the sediment in response to predators. Experimentally observed reductions in infaunal densities can therefore be a result of emigration rather than mortality.

Infaunal predators certainly have the ability to limit infaunal prey populations and may often be important in determining community structure, but mechanisms, and generality of results, to different predatory species and habitats, has "barely been investigated" (Ambrose 1991). Nevertheless, conclusions from studies of epibenthic predator exclusion may be dramatically different if predatory infauna are not considered separately from other infauna. After all, "predatory infauna are predicted to have their largest effects in habitats where other forms of control (abiotic disturbance and epibenthic predators) are rare or of reduced importance" (Ambrose 1991) such as under clam netting.

1.3.4 Competition in soft-bottom marine benthic communities

In some systems, the primary role of predation in structuring communities is to limit populations below a point where intense competition would result in a different community structure. Epibenthic predators have the ability to limit populations of infaunal macroinvertebrates, predatory and otherwise, below carrying capacity. The question remains whether competition becomes an important structuring force in soft-bottom systems, particularly in the absence of epibenthic predation.

Competition for space has been documented for a few species of large, deep-dwelling bivalves (Peterson and Andre 1980), although such competition has not been observed to result in mortality, only reduced growth. Competition for space can also be avoided by burial at different depths (Peterson and Andre 1980). Certain pairs of species, such as burrowing shrimp and clams, tube worms and shrimp, are able to alternately dominate soft-bottom communities by modifying the sediment to mutually exclude each other (Peterson 1984). Black and Peterson (1988) describe these as cases of "indirect interference operating through environmental alterations", and not true interspecific competition. Based on more recent experiments of density-manipulation, in combination with predator exclusion, it was later concluded that "competition is largely ineffective in structuring communities of benthic infauna in soft substrata" (Black and Peterson 1988).

On the other hand, intraspecific competition may increase in the absence of predation, and food is often proposed as the limiting resource (Gee *et al.* 1985, Peterson 1982, 1983, 1992, Peterson and Beal 1989, Reise 1985, Summerson and Peterson 1984). Density-dependent growth has been observed in several cases, with growth rate and also reproductive output simultaneously decreasing with increasing density, despite large amounts of apparent space available, suggesting food depletion to be responsible (Peterson 1982, Peterson and Beal 1989). In cases of low water velocity and mudflats with small slopes, filter feeders can deplete suspended food in the water at the sediment surface, unless some mixing occurs with the upper water column (Peterson and Black 1991). Food limitation is less likely in steeper habitats, or in cases where physical structures or water velocities generate enough turbulence to allow mixing and prevent intertidal food depletion. Extremely high water velocities can also interfere with suspension feeding, and generate metabolic costs associated with repositioning in shifting sediments, or increased turbidity.

A lack of density-dependent growth in artificially enhanced bivalve densities has also been reported (Peterson and Andre 1980), and Beal *et al.* (2001) observed density-dependent growth only in high-tide plots, where resources and environmental stress were probably most limiting. Therefore, "competition may be sporadic and limited to occasions when and where resources are in short supply" (Beal *et al.* 2001). Most importantly, in every reported case of apparent intraspecific competition, the only evidence was reduced growth, never increased mortality as a result of starvation, or competitive exclusion (Beal *et al.* 2001, Peterson 1992). Competition may serve to segregate populations spatially, leading to small-scale local patchiness, but predation is expected to play a much larger role in limiting populations on a broader scale (Beal *et al.* 2001).

1.4 Measuring differences in non-target species

Although information is plentiful regarding how shellfish aquaculture practices affect the cultured species, with respect to enhancing survival, little is known about how these practices affect non-target species in intertidal areas (Jamieson *et al.* 2001, Spencer *et al.* 1997). Our study focuses on the practices used by clam farmers who seed intertidal areas with juvenile *Venerupis philippinarum*, and cover these seeded areas with nets.

A paired-site design was used to allow the comparison of active clam farms to reference sites that are not directly affected by aquaculture activities. This analytical study is intended to be representative of active tenures from a geographically large area in coastal B.C. Any consistent differences observed are therefore independent of site-specific conditions. In addition, a small netting experiment used paired plots to explore effects of netting alone, at small spatial and temporal scales.

This research addresses the following objectives and questions:

1. Are bivalve species more or less abundant on farm sites, relative to paired reference sites, and is there evidence of competitive exclusion within predator refuges of clam farms?
2. Is bivalve community structure (species richness, evenness, composition) different between paired sites?

3. Is the density of predatory, and non-predatory infauna different between netted and control plots?
4. If large epibenthic predators are excluded by nets, is macroinvertebrate community structure (species richness, evenness, composition) affected by their exclusion?

In particular, we are asking if native species are affected by the practices used in the production and harvesting of a single non-native bivalve species.

2.0 MATERIALS AND METHODS

The research presented here includes two separate studies: A field study on active clam tenures and a small-scale netting experiment. Both aspects of the research occurred in the same study areas, although the sites and design differed between the two approaches.

2.1 Study Area

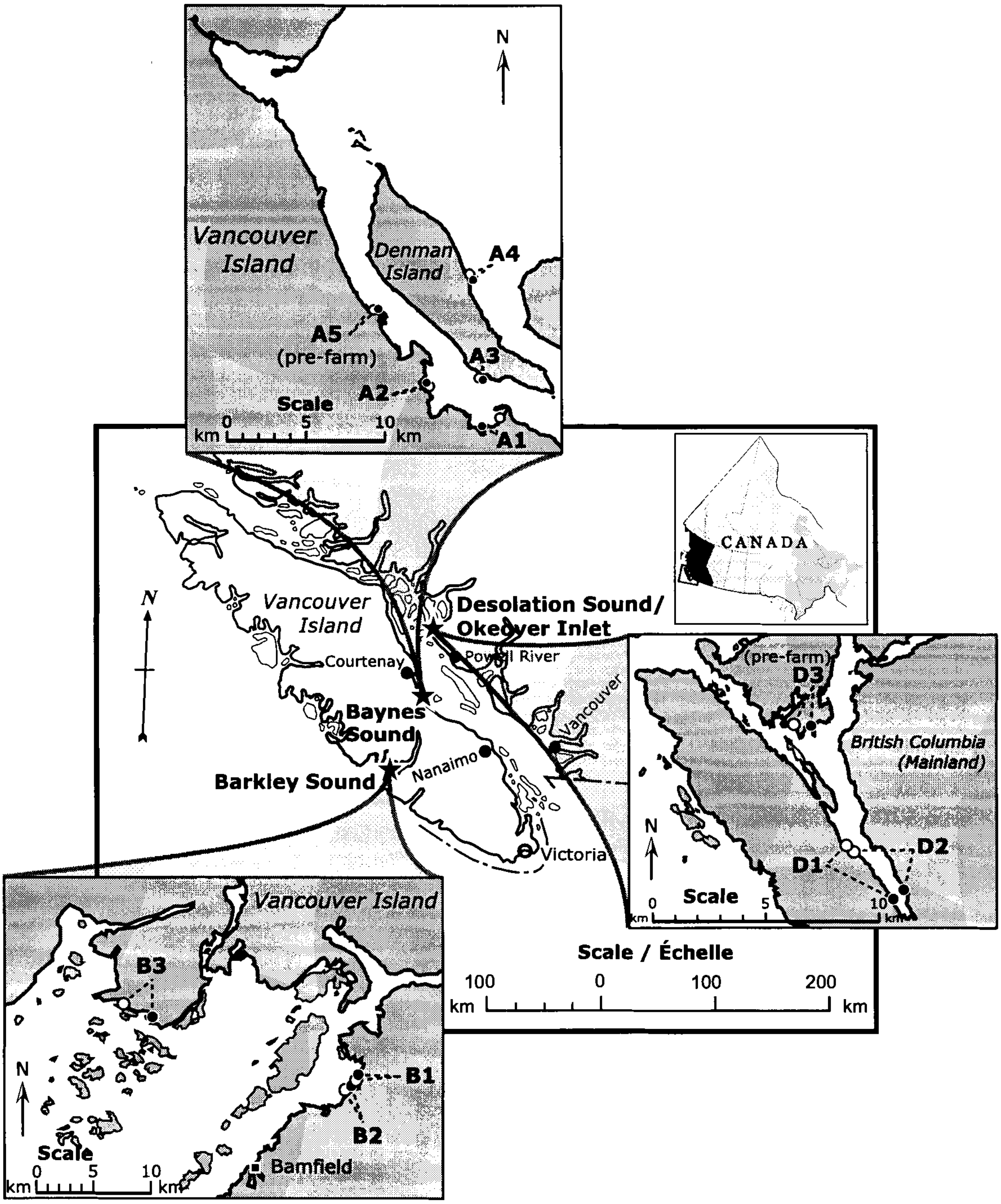
All field sampling occurred at sites in southern coastal British Columbia, Canada, within three distinct regions: Barkley Sound, Baynes Sound, and Desolation Sound (Okeover Inlet) (see Figure 1). All three regions are areas of shellfish aquaculture development, with different overall levels of activity and unique geographical characteristics.

Barkley Sound is situated on the east coast of Vancouver Island, and is the most exposed of the three regions studied. Shellfish aquaculture is less intense in this region compared to others included in this study. Experience with clam aquaculture practices has led many clam farmers to abandon the use of protective netting, as a result of the unmanageable build up of biofouling that seems to be common in this region (personal communication).

Baynes Sound is located within the Straight of Georgia between a portion of the east coast of Vancouver Island and Denman Island. Of the three regions included in the study, aquaculture is most intense in Baynes Sound, with over half of the annual production of cultured clams in B.C. produced in this region. Moreover, Baynes Sound is recognized internationally as an important area for wintering and migrating birds (Jamieson *et al.* 2001).

The third region included in this study was Okeover Inlet, a portion of Desolation Sound, along the west coast of mainland B.C. The Desolation Sound area is a popular destination for kayakers and other recreational users, and includes Desolation Sound Marine Park, established in 1973 by the Province of British Columbia (BC Parks 2003). Soft-bottom habitats suitable for clam aquaculture are not as common here as in the other regions studied, though a few large bays exist, along with small areas found among the many rocky shores of the inlet.

Figure 1. **British Columbia (B.C.) Canada. Location of three study areas highlighted with stars. Within each region, study sites are labelled with circles (open for reference sites, closed for farm sites). Outline map adapted from Natural Resources Canada, with permission (http://atlas.gc.ca).**



2.2 Field study

2.2.1 Study Sites

The principal component of this research is a large-scale field study. Matched pairs of sites were sampled for species counts and environmental data during daytime tides from May to August of 2003. Each pair of sites includes a farm site, which was an active tenure employing the main practices of seeding and netting, and a matched reference site, which was intended to be similar to the farm site in most respects, apart from the lack of past or present aquaculture activity.

Site pairs are referred to with a two-digit label, beginning with a letter, denoting their regional location (A = Baynes Sound, B = Barkley Sound, D = Desolation sound / Okeover Inlet), and a number, applied to sites in no particular order within each region. Within each pair, farm and reference sites may be differentiated by a suffix ("-F" = farm, "-R" = reference), although the same 2-digit label is used to denote the pairwise relationship. The approximate location of each site is shown in Figure 1. Site characteristics and sample sizes are listed in Table 1.

Table 1. **Characteristics of study sites, including sample size (# quadrats sampled). Sites are labelled by region (A = Baynes Sound, B = Barkley Sound, D = Okeover Inlet, Desolation Sound) and a number, to identify each pair. * Indicates sites that were seeded without nets.**

Region	Site	Stratum	Type	Size (m^2)	Age of Farm (years)	Sediment Type	# Quadrats Sampled
Baynes	A1	low	Farm	500	4	sand, silt	12
Sound			Reference	11638		sand, silt	12
		mid	Farm	3650	4	gravel, sand	12
			Reference	8575		sand, silt	12
	A2	low	Farm	1400	2	sand, silt	18
			Reference	1400		sand, silt	18
	A3	mid	Farm	1120	6	gravel, sand	18
*		(seeded)	Reference	995	6	gravel, sand	18
	A4	mid	Farm	7965	4	cobble, gravel	18
			Reference	21750		cobble, gravel	18
	A5	low	Pre-Farm	600	-	sand, silt	12
			Reference	600		sand, silt	12
		mid	Pre-Farm	600	-	sand, silt	12
			Reference	660		sand, silt	12
Barkley	B1	low	Farm	1158	1	gravel, sand	18
Sound			Reference	800		gravel, silt	18
	B2	low	Farm	1190	1	gravel, sand	18
			Reference	501		gravel, sand	18
*	B3	low	Farm (no nets)	1822		gravel, sand	18
			Reference	2035		gravel, sand	18
Desolation	D1	mid	Farm	739	10	gravel, sand	18
Sound			Reference	700		gravel, sand	18
	D2	mid	Farm	449	7	gravel, sand	18
			Reference	342		gravel, sand	18
	D3	low	Pre-Farm	451	-	gravel, sand	12
			Reference	623		gravel, sand	12
		mid	Pre-Farm	449	-	gravel, sand	12
			Reference	198		gravel, sand	12

Reference sites were selected from available nearby sites to match a paired farm site with respect to sediment type (assessed visually, see below), slope, size, wave exposure and approximate salinity. Farm sites were selected based on permission from the owners, and the availability of a suitable reference site. This type of observational sampling also integrates changes in response to aquaculture practices over the entire history of the site, including 1 – 10 years of aquaculture activity, depending on the site (see Table 1). This study did not include the largest clam aquaculture leases currently active in B.C., therefore the results are only reflective of the relatively small-scale aquaculture tenures that were sampled.

A paired design also allows comparisons that account for site differences between pairs, and should therefore help to control spatial variability that has confounded intertidal experiments in the past (see Beal *et al.* 2001, Richards *et al.* 1999, Sewell 1996). By matching reference and farm sites as closely as possible, we hope to control for factors such as sediment type, beach slope, size, wave exposure, and average temperature, which is assumed to be approximately equal within each matched pair. The most important difference between each farm and reference site within pairs is the application of seeding and netting to the farm sites. Because both seeding and netting are present together on farm sites in this study, it is difficult to tease apart the relative contribution of these two practices to any observed differences. This study is primarily concerned with the combined, cumulative effects associated with these two practices used together.

Site B3-farm, and A3-reference were the only sites sampled that did not use protective netting over seeded clam areas. The owner of the B3-farm lease reported that this farm site was rarely visited by scoters, which did appear frequently at the matched reference site chosen for this study. Such a small sample size does not permit a rigorous comparison of the relative effects of seeding and netting between treatment groups. Nevertheless, data from these sites are reported for tentative comparison, and in the event it can be used in conjunction with data collected in the future.

Although harvesting is also a possible source of disturbance that can affect intertidal community structure, nearly all reference sites were also exposed to recreational and commercial wild harvesting, as well as unknown levels of poaching (personal observation). It is therefore assumed in this study that the physical disturbance of digging associated with bivalve harvesting is similar between farm and reference sites.

The only exception to this was one reference site (D2), which was located in an area closed to shellfish aquaculture, within 100m of a public dock. High public traffic may have discouraged any form of harvesting, including poaching, in this area. The absence of anthropogenic bivalve removal at this site makes it anomalous in the context of this study, although it also provides an example of a possible "true baseline" state of an intertidal habitat in the absence of shellfish harvesting.

Two "farm" sites sampled had been selected for future clam aquaculture, although no aquaculture activity had started as of the time of sampling: A5 and D3. These sites were sampled for baseline data with the intention to follow-up and sample again once aquaculture practices such as seeding and netting had been applied to the site. Unfortunately, such practices had not started at either site in time to include follow-up data in this project. Nevertheless, data from these sites is included to address whether sites chosen for shellfish aquaculture were already different from reference sites, independent of aquaculture practices. Such baseline data is also useful if these sites are ever sampled again, to make more direct comparisons.

2.2.2 Sampling methodology

Sampling methods were based on those developed by Gillespie & Kronlund (1999) for intertidal clam sampling, but adapted for sampling a range of clam species. Only the infaunal bivalve data from the field study was included and reported here. All field data and samples were collected between May and August 2003.

Sites were stratified by tide height; areas between 1 and 2 metres above chart datum were classified as "low", and areas above 2 metres were classified as "mid". The highest points sampled in this study were at 2.7 metres above chart datum. Average tides in the Barkley Sound region were much lower than in the other regions, so stratum boundaries were shifted 0.5 m lower, to include intertidal areas where netting is currently used in this region. Areas of netting set the practical boundaries and limits of sampling on the farm beaches. Paired reference beaches were laid out similarly to match the farm site according to size of area and tidal range, within patches of similar sediment type and habitat.

Quadrats were placed randomly within each stratum at each beach (see Table 1 for sample sizes). A stainless steel square frame (0.5 x 0.5 x 0.3 m deep) was inserted into the sediment to isolate the quadrat area to be sampled. Sediment was removed using a shovel, to a depth of 20 cm, and sifted through a 6 mm mesh to remove fine particles. A sub-sample of sediment (0.25 x 0.25 m) within the top-right corner of each quadrat was also passed through a 1 mm mesh sieve, under the 6 mm sieve, to capture smaller individuals. Sediment retained in each sieve was also hand-sifted to locate organisms.

All individuals were identified in the field to the lowest taxonomic level possible, usually species. If a pair of species was difficult to tell apart, for example small *Macoma obliqua* or *M. inquinata*, individuals were assigned to a default species (*M. inquinata*), unless clear diagnostic features identified them as the other species. Field guides were used for initial identification (Harbo 1997, Jensen 1995, Sept 1999), but difficult or unknown specimens were placed in plastic or glass vials and stored in ethanol for later identification using further resources (e.g. Kozloff 1983, Kozloff and Price 1987), or invertebrate experts (e.g. the Bamfield Marine Sciences Centre, in Bamfield, B.C.). At one-third of the quadrats from each site, the blotted wet weight of individual bivalves was recorded to the nearest 0.1 g, before being returned to the sediment.

The position of each quadrat was recorded, relative to a reference point on the beach, as well as tide height and qualitative sediment type. The height of each quadrat above the water was measured using Abney levels and a measuring tape (Giles 1971). Tide predictions from the Canadian Hydrologic Service were used to obtain the height of the water at the time of the height measurement. These two heights were added to obtain an approximate height above chart datum for any point on the beach. A similar method was used to locate stratum boundaries, usually by marking the height of the water at a specified time from tidal predictions to locate pre-defined heights. It was found through experience that the Abney levels were only accurate within a distance of approximately 30m, which is within the range of many commercial laser levels of similar cost, although simply following the water level on an incoming tide and noting the time of submersion was often adequate for determining tidal elevation. The sediment type at each quadrat was assessed qualitatively by recording the two most abundant particle size classes present in the sediment (Wentworth 1922).

2.2.3 Statistical Treatment and Analysis

For the field study, only the infaunal bivalve (clam) data from the sampled communities were included for analysis. For each quadrat, counts of smaller individuals, from the 0.25 x 0.25 m sub-sample, were multiplied by 4 to normalize by area, and added to counts of larger individuals from the 0.5 x 0.5 m quadrat. For each estimate, paired t-tests were used to assess consistent differences between farm and reference sites. Differences within each pair were weighted by the inverse of a pooled estimate of within-site standard error, if available (for differences in mean density, for example, but not indices of diversity). All statistical comparisons and tests were calculated using a pooled estimate of variance across the low and mid strata, allowing for differences between strata, and a significance level of 0.05. Equality of variance between farm and reference sites was also tested, over all tide heights, for each estimate used. Equality of variances is not required for a paired test, but some results indicated definite patterns among paired differences that might be explained by changes in between-site variation within treatments.

Estimates of species richness and diversity indices were calculated using the EstimateS software program (Colwell 1997). There is an ever-growing list of possible estimators to use to compare species richness, but few of them have been well-characterized and there is much disagreement over which estimators are better in which situation, although non-parametric estimators may be more accurate and precise (Brose *et al.* 2003, see Colwell 1997 for formulae and references, Foggo *et al.* 2003, Hellmann and Fowler 1999, Purvis and Hector 2000). While some estimators are better at reducing bias, others have higher precision. For this study, estimating the true number of species (reducing bias) is less important than the ability to discriminate between estimates (high precision). The first-order Jackknife estimator (Jack-1) has been well characterized for a long period throughout the literature (Burnham and Overton 1978, 1979, Heltshe and Forrester 1983, 1985) and consistently found to be a relatively precise estimator, which can also reduce bias at small sample sizes (Brose *et al.* 2003, Foggo *et al.* 2003, Hellmann and Fowler 1999). Newer coverage-based estimators developed by Anne Chao (Chao *et al.* 2000, Chao and Lee 1992, Chao and Yang 1993, Chazdon *et al.* 1998) have shown promise, although the incidence-based version (ICE) seems to perform better than its abundance-based sibling (ACE) (Brose *et al.* 2003, Foggo *et al.* 2003). Other estimators were found in our data to be either less precise than those already mentioned, or theoretically inappropriate.

Both the Jackknife and ICE estimators are incidence-based, which means they extrapolate the number of estimated species based on the incidence of observed species within a collection of repeated samples (quadrats). Such estimators are potentially sensitive to changes in spatial distribution, or patchiness (Brose *et al.* 2003, Foggo *et al.* 2003). A decrease in patchiness may result in a lower estimate of species richness, independent of any actual change in the number of species present at a site. This was the primary reason for also comparing sites using the abundance-coverage estimator (ACE). No single estimator in this case could be argued convincingly to be "the best", so results were compared using all three proposed estimators as a method of assessing how robust they are.

Sites were also compared with respect to community evenness, using Simpson's evenness index, and heterogeneity, calculated using the Shannon-Weiner function (see Krebs 1999). Heterogeneity is a composite measure incorporating richness and community evenness, often termed "diversity". Observed changes in such a composite measure are difficult to interpret, which is why it is important and an increasingly popular practice to separate diversity into measures of richness and evenness. The Shannon-Weiner function is included here primarily to allow comparison with other studies that have used only this univariate index of diversity.

Multivariate comparisons of communities were performed using the PRIMER software. Five of the species sampled were unidentified, and observed only once or twice at individual sites. These species were excluded from the multivariate analysis because they would contribute little information and their unidentified status could complicate the interpretation of results. Measures of species weights and counts were converted to an average biomass and density per square metre, to standardize for different sample sizes. Density and biomass data were analyzed separately. Similarity matrices were calculated using the Bray-Curtis index of similarity (see Legendre and Legendre 1998) on fourth-root transformed data, which was used to draw an MDS plot (non-metric Multi-Dimensional Scaling).

Analysis of Similarity (ANOSIM) was also performed on the same similarity matrices, using the PRIMER software. This procedure is a multivariate non-parametric test of differences between groups defined *a priori*, analogous to analysis of variance (ANOVA). The test uses an R-statistic calculated as follows (Clarke 1993):

$$R = \frac{\bar{r}_B - \bar{r}_W}{n(n-1)/4} \tag{1}$$

Where:

$\bar{r}_B$ = Mean rank similarity between groups

$\bar{r}_W$ = Mean rank similarity within groups

n = total number of samples under consideration.

Values of this R-statistic range from –1 to +1, with larger positive values indicating higher rank similarities within groups than between groups. Negative values imply the converse. The test calculates an R-statistic for the existing data, and compares that to a distribution of R-statistics calculated from the random permutations of the site identities (Clarke 1993, Clarke and Green 1988). A maximum of 999 permutations were randomly used from a set of all possible permutations in any test. The result is a probability of observing a relative dissimilarity between groups as large as that in the data, assuming the null hypothesis that the communities were assigned to groups randomly. The null hypothesis can also be stated as 'no group differences' (Clarke and Green 1988).

We tested for differences among types (farm or reference) and tide height strata (low or mid-intertidal) in a two-factor crossed analysis. This method tests for differences in each factor, averaged over all levels of the second factor (Clarke 1993). Tests for differences between regions were performed as a 2-way crossed analysis with type (farm or reference), if sites did not significantly differ by any other factor. Differences by region and tide height are somewhat confounded, as some regions did not include sites in all tide height strata, so some combinations of region and stratum do not exist. In the absence of significant differences for any other factor, regional differences would indicate that community structure is more strongly determined by local factors that vary by region (salinity, water currents, temperature, etc.), as opposed to the broader factors of tide height and farming practices.

Sites that were sampled under pre-farming conditions (A5 and D3) were included in these analyses as additional reference sites. The two sites sampled that had been seeded but not netted (A3 reference and B3 farm) were excluded, because only two sites did not allow for a statistically rigorous comparison of this treatment with others. We focused instead on the combined practices of seeding and netting (farm sites), as compared to reference sites where these activities were absent.

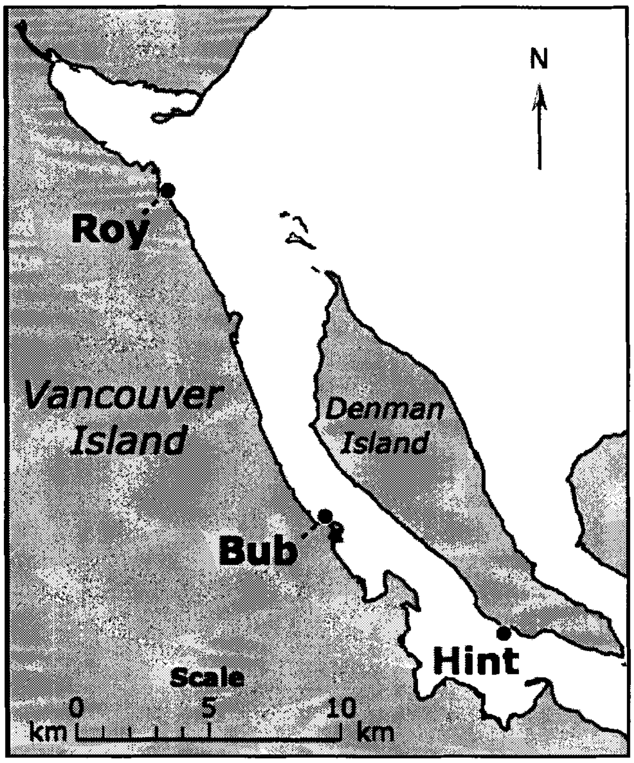
2.3 Netting Experiment

A small, pilot experiment was conducted to examine any possible short-term effects of predator exclusion, using nets typically used in industry. The short duration of the experiment (see below) did not allow for possible changes in community structure as a result of recruitment or competitive differences between treatments, but the goal was to observe whether or not prey depletion in control plots also occurred under netted plots.

2.3.1 Study Sites and Treatment Structure

Three study sites were chosen within Baynes Sound (see Figure 2), labelled using an abbreviation of a name of the location. At each site, the netting treatment was applied randomly to one plot within each pair, with the other left uncovered. Each plot pair consisted of two square plots, 5 x 5 m in area, separated by 2m to reduce edge effects between treatments. Each plot was arranged beside its pair, parallel to the water's edge. At each site, one pair of plots was set at 3.0 m above chart datum (labelled "A" stratum) and a second pair at 2.5m ("B" stratum). This design resulted in three (3) replicate treatment and control pairs at each site and tide height combination.

Figure 2. Location of Sites used in Netting Experiment, within Baynes Sound, B.C.



A commercial-type net was used for the netting treatment, constructed of medium-weight plastic with apertures of 1.25 cm ("car cover"). The netting was cut into 5 x 5 m squares and secured with rebar posts, bent into an inverted "U" shape and pounded into the sediment. Control plots were outlined with yellow plastic rope secured with long plastic pegs inserted into the sediment. We also contacted local groups who were known to frequently dig clams, or who owned shellfish tenures, and asked them not to dig within either control, or netted plots. No evidence was ever observed of digging for clams within any plots during the course of the experiment, except for the digging associated with faunal sampling (see below).

2.3.2 Sampling methodology

Sampling protocols for the netting experiment are similar in most ways to the field study (see above), except as follows. Quadrats used were the same size (50 x 50 cm x 30cm deep), and five quadrats were sampled randomly within each plot, accounting for approximately 5% of the total surface area of each plot. It was determined that the amount of time required to sieve down to 1 mm was too costly compared to the small amount of information gained (see Appendix B). Therefore, sediment within each quadrat was sieved through only a 6 mm wire mesh sieve.

Each plot was sampled at three separate times during the course of the experiment. The first was during October, 2003 (time = 0), as a baseline state prior to the addition of the netting treatment. Plots were sampled a second time during May of 2004 (time = 1), and again near the end of August, 2004 (time = 2). Each sampling period lasted about 10 days.

2.3.3 Statistical Treatment and Analysis

The netting experiment carried out over a period of 10 months was designed as a small-scale pilot experiment, with the goal of measuring depletion by predators over a winter, and the following summer season. If the nets prevented predation from large epibenthic predators such as scoters, crabs, or fish, it is predicted that areas of beach under randomly-assigned netted plots would show less reduction in prey faunal densities than nearby areas without netting. In the context of the paired plots used in this experiment (see above), the difference in faunal density within pairs (net – control) is expected to be larger (more positive) after a season, than it was during the baseline, initial sampling period.

Because the experiment was designed with treatment grouped into pairs, a difference was calculated for each paired plot (net value – control value) for each variable of interest, and these differences were used in a repeated measures analysis (Sokal and Rohlf 1981) to examine significant linear changes through time, accounting for possible differences between tide height strata. JMP software was used to perform the repeated measures analysis.

The first sampling period (t=0) collected data before any netting treatment was applied, therefore the average difference for this time period is not a result of any experimental treatment effects. The average difference between plots may not be zero for the baseline sampling period, by chance, but the repeated measures analysis examines how this average difference changes once the netting treatment is applied to one plot within each pair.

Species counts at each quadrat were converted to density values (individuals$\cdot$m^{-2}) by multiplying counts by four (4) to scale the area of the quadrat (0.25 m^2) to 1.0 m^2. Sample sizes were equal among all plots, but this conversion allows values to be compared with other research presented herein, and other published data. Mean densities for each plot (net or control), over five quadrats, were computed at each sampling period, and used to analyze changes in faunal density associated with netting similar to that used in commercial clam aquaculture in B.C.

Faunal densities were grouped by simple ecological roles:

- Epifauna
- Predatory Infauna
- Non-predatory Infauna (Including Infaunal Bivalves)
- Venerupis philippinarum

The last group includes only the commercial species, *V. philippinarum*, which was analyzed separately to allow a comparison with data from other sources, including the field study presented in this work. This species is also very abundant and often the dominant species within bivalve communities, and even non-predatory infauna at some sites. Therefore, some groups (infaunal bivalves, non-predatory infauna, total infauna) were re-analyzed with *V. philippinarum* excluded.

Species richness, evenness, and diversity were calculated in an identical manner as for the field study data (see above), and examined using repeated measures analysis of the differences between net and control plots, as described above.

Multivariate analysis of communities was carried out using the same software and general methods as for field study data (see above), although the analysis was changed to match the treatment structure of the experiment. A matrix was constructed with counts of each species pooled across five quadrats, for each plot and sampling period. A similarity matrix was then calculated for each plot, at each sampling period, using the Bray-Curtis index of similarity, based on fourth-root transformed data. This similarity matrix was used to construct MDS plots, and perform Analysis of Similarity (ANOSIM).

ANOSIM was performed to test hypotheses concerning differences among levels of various factors. At each sampling period, a two-way ANOSIM was used to test for differences between treatment levels (net, control plots), crossed with tide height stratum. No difference was predicted for t=0 (baseline), since no netting had been applied, but a difference was predicted for either t=1, or t=2, or both. A second approach was used to test temporal changes, in a way that would be analogous to the repeated measures analysis for a single variable described above. A one-way ANOSIM was used to test differences between time periods (each pair), within each treatment level (net and control). If none of these tests showed any significant changes, other factors were examined to explore which ones could explain the majority of the structure in the MDS plots (see Results, below).

3.0 RESULTS

Results are presented separately for each community studied: Infaunal bivalve component of the field study, and netting experiment (whole community).

3.1 Field Study – Infaunal Bivalve Community

3.1.1 Pre-Farm Sites

A summary of bivalve data from pre-farm sites and paired reference sites is presented in Table 2. In terms of bivalve density, the farm and reference sites within the D3 pair appear no different. The A5 pre-farm site in the low stratum, however, has a higher mean density of *Venerupis philippinarum*, lower density of other bivalves, but similar total bivalve density as the paired reference site. The biomass of V. philippinarum, however, is no different between the pre-farm and reference site at A5, but the D3 pre-farm site appears to have lower biomass of this species than the paired reference site.

There is also a remarkable lack of consistency between these site pairs with respect to differences in species richness, diversity and evenness (see Table 24). In some cases, values are higher on the pre-farm site, others are very similar, or even lower.

This data demonstrates that some farmed sites may differ inherently from reference sites, particularly in the case of species of commercial interest. Some sites selected for clam farming, on the other hand, may be very similar to other sites in terms of pre-existing biotic conditions.

Table 2. Bivalve density, biomass, and community indices for pre-farm sites.

Variable	Site, Stratum Treatment	A5 low	A5 mid	D3 low	D3 mid
Density (individuals·m^{-2})	mean ±95% confidence interval width				
Venerupis philippinarum	Pre-Farm	114.7 ±22.8	141.3 ±33.1	40.7 ±33.0	104.7 ±50.4
	Reference	49.7 ±18.1	119.0 ±45.5	15.3 ±14.0	61.0 ±22.9
Other Bivalves	Pre-Farm	93.0 ±30.5	53.7 ±20.1	155.3 ±46.1	99.7 ±36.7
	Reference	283.7 ±57.4	185.7 ±56.7	98.0 ±39.5	77.0 ±52.0
Total Bivalves	Pre-Farm	207.7 ±38.6	195 ±44.4	196 ±57.6	204.3 ±78.3
	Reference	333.3 ±54.0	304.7 ±57.3	113.3 ±46.6	138 ±66.9
Biomass (g·m^{-2})	mean ±95% confidence interval width				
Venerupis philippinarum	Pre-Farm	141.0 ±78.0	573.0 ±421.8	1.5 ±3.1	78.1 ±181.0
	Reference	94.0 ±125.3	394.2 ±263.5	145 ±461.5	1554.0 ±1302.3
Other Bivalves	Pre-Farm	127.0 ±72.8	224.5 ±311.6	340.6 ±563.1	961.6 ±1124.0
	Reference	1058 ±1787.3	315.5 ±322.7	1443.2 ±874.4	1222.5 ±2231.8
Total Bivalves	Pre-Farm	268.0 ±63.9	797.5 ±709.9	342.1 ±562.3	1039.7 ±1077.6
	Reference	1152.0 ±1818.6	709.7 ±359.3	1588.2 ±1160.9	2776.5 ±3318.9
Univariate Community Indices					
# Observed spp.	Pre-Farm	10	10	14	7
	Reference	11	12	10	7
ACE	Pre-Farm	11.6	10.4	17.2	7.9
	Reference	11.0	15.8	13.1	7.6
ICE	Pre-Farm	11.7	11.1	15.9	8.8
	Reference	11.9	16.0	12.7	7.7
Jack1	Pre-Farm	11.8	11.8	16.8	8.8
	Reference	12.8	15.7	12.8	7.9
Shannon-Weiner	Pre-Farm	1.27	0.94	1.66	1.13
	Reference	1.39	1.39	1.01	0.93
Simpson's Evenness	Pre-Farm	0.265	0.180	0.245	0.369
	Reference	0.277	0.261	0.189	0.316

3.1.2 Density and Biomass

Average density of infaunal bivalves (clams) is presented for each site in Figure 3. Average biomass of clams is presented in Figure 4. The D2 reference site appears to be a possible outlier, particularly with respect to biomass data, with values much higher than any other site sampled in this study. This reference site was within an area closed to shellfish harvesting, which could account for the abnormally high abundance, or it could be the result of enhanced nutrient inputs from unknown sources. Regardless of the cause, this site was highly influential in the analysis of biomass values and was excluded as an outlier.

Paired t-tests (see Table 3) reveal that total clam density was higher on farm sites in the low stratum, but not the mid. *Venerupis philippinarum* was present in higher density and biomass on farm sites in the low, but not the mid stratum. In fact, the average difference in density of *V. philippinarum* is approximately the same as the observed difference in total clam density in the low stratum. Total clam density and biomass, excluding *V. philippinarum* was not significantly different between farm and reference sites. The observed higher total clam density in the low is attributable to the higher density of *V. philippinarum*, with no significant contribution from other bivalve species.

Figure 3. **Mean clam density (individuals·m^{-2}) at field study sites. Shaded bars indicate densities of *Venerupis philippinarum*, open bars layered behind indicate total clam density. Circles indicate density of all clams, excluding *V. philippinarum* (shaded = farm site, open = reference site). Error bars represent 95% confidence intervals about each mean.**

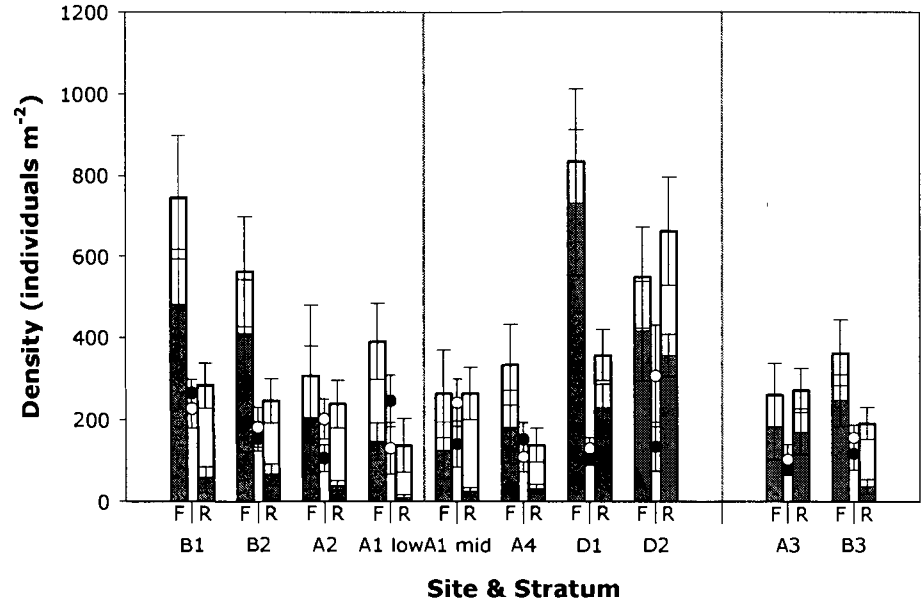


Figure 4. **Mean clam biomass (g·m^{-2}) at field study sites. See Figure 3 caption for explanation of symbols.**

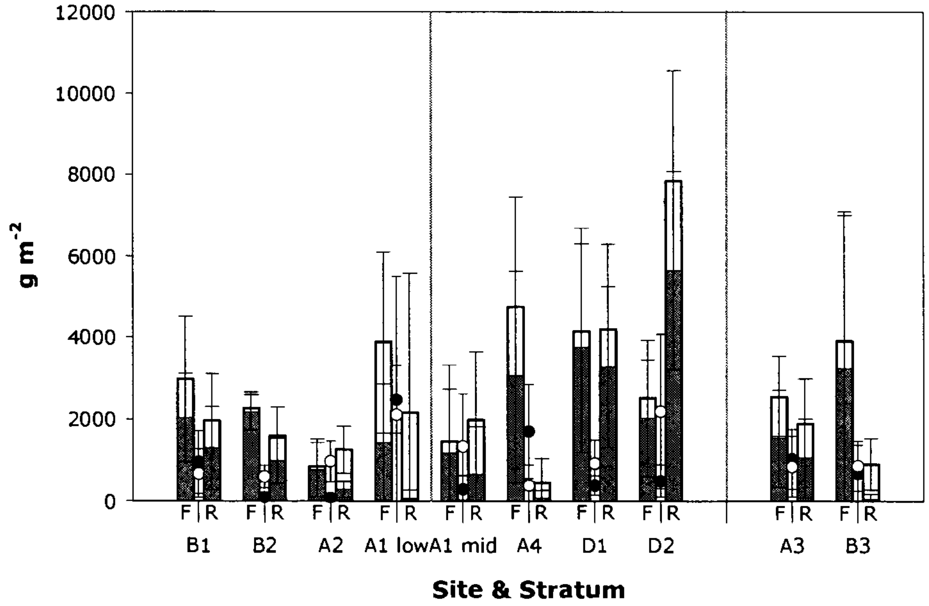


Table 3. Results of weighted paired analyses of bivalve abundance, including Mean Difference (Farm-Reference) ±95% confidence interval width (with degrees of freedom), for each estimate. Mean differences significantly different from zero (2-tailed) are highlighted in bold, with *. [d] Site D2, in the mid stratum, was highly influential in tests using biomass data and a potential outlier, so was omitted from the calculation.

	Low Stratum		**Mid Stratum**		
Test	**Mean Difference (F-R) ± 95% CI**	**p-value**	**Mean Difference (F-R) ± 95% CI**	**p-value**	**Unequal Variance (F-test)**
Density (individuals·m^{-2}) (df = 6)					(df=7)
Total clams	**279.6 ±241.6**	**0.030***	131.8 ±237.7	0.224	0.527
Venerupis philippinarum	**227.0 ±176.4**	**0.020***	162.8 ±185.7	0.076	0.197
Other clams (V. philippinarum excluded)	-2.1 ±100.5	0.960	-34.1 ±97.0	0.422	0.891
Biomass (g·m^{-2}) (df = 5[d])					(df=6[d])
Total clams	444 ±1698.0	0.531	1089.7 ±2812.0	0.365	0.294
Venerupis philippinarum	**872.9 ±792.9**	**0.037***	1201.3 ±1449.5	0.086	0.727
Other clams (*V. philippinarum* excluded)	-452.3 ±852.1	0.231	-226.1 ±1228.4	0.656	0.203

Although the biomass of other clams (excluding *V. philippinarum*) was, on average, lower at farm sites, the low sample sizes and between-site variability created noise larger than this signal. It seems unlikely that that there is no change in abundance of other bivalves, if total clam abundance does not change (density in the mid, biomass in both strata), and the commercial species is more abundant on farm sites. In the presence of greater density and biomass of *V. philippinarum* on farm sites, either total bivalve abundance must increase by a corresponding amount, or the abundance of other species must decline, or some combination of both.

It is not surprising to observe a significant difference in the abundance of *V. philippinarum*, given that this species is added as juvenile seed clams to the farm sites. What is surprising is that both density and biomass of this commercial species, and all clam species combined, was not significantly different between sites in the mid stratum.

3.1.3 Univariate Community Indices

The number of observed and estimates bivalve species, as well as community evenness and diversity are presented for each site in Table 4. 27 bivalve species were observed in total on all sites, including five unique and unidentified species that were excluded from the multivariate analysis below. Tests of paired differences and equality of variances show no significant difference in the number of bivalve species, evenness or diversity between farm and reference sites (see Table 5). The three estimators of species richness showed close agreement, indicating that these results are robust.

Table 4. **Number of observed and estimated clam species, values of diversity and evenness indices at each site.**

	Site:	B1	B2	A2	A1		A4	D1	D2	B3	A3
	Stratum:	low	low	low	low	mid	mid	mid	mid	low	mid
Index	Trt										
Observed # spp.	F	9	7	9	13	10	6	9	10	10	11
	R	8	7	12	12	13	12	10	9	14	11
ACE	F	11.6	7.0	9.0	14.7	13.0	6.0	9.0	11.7	10.7	13.2
	R	8.6	7.5	19.8	12.5	13.5	12.3	11.9	9.0	14.0	15.1
ICE	F	10.6	7.0	9.0	14.4	11.4	6.0	9.3	11.2	10.5	13.3
	R	8.6	8.0	19.4	13.3	14.4	13.6	13.3	9.8	14.9	15.2
Jackknife 1	F	10.9	7.0	9.0	14.8	11.8	6.0	9.9	11.9	10.9	13.8
	R	8.9	7.9	15.8	13.8	14.8	14.8	12.8	9.9	15.9	14.8
Shannon-Weiner	F	0.99	0.82	1.07	1.78	1.45	0.9	0.54	0.93	1.15	0.92
	R	1.17	1.48	1.60	1.59	1.61	1.51	0.86	1.12	1.75	1.05
Simpson's Evenness	F	0.23	0.25	0.23	0.36	0.33	0.36	0.14	0.17	0.20	0.17
	R	0.31	0.51	0.35	0.29	0.28	0.25	0.20	0.27	0.26	0.19

Table 5. **Results of paired analysis and tests for equality of variances (F- test) for estimates of species richness, evenness and diversity, between farm and reference sites. Significant differences ($\alpha = 0.05$) are highlighted in bold with *.**

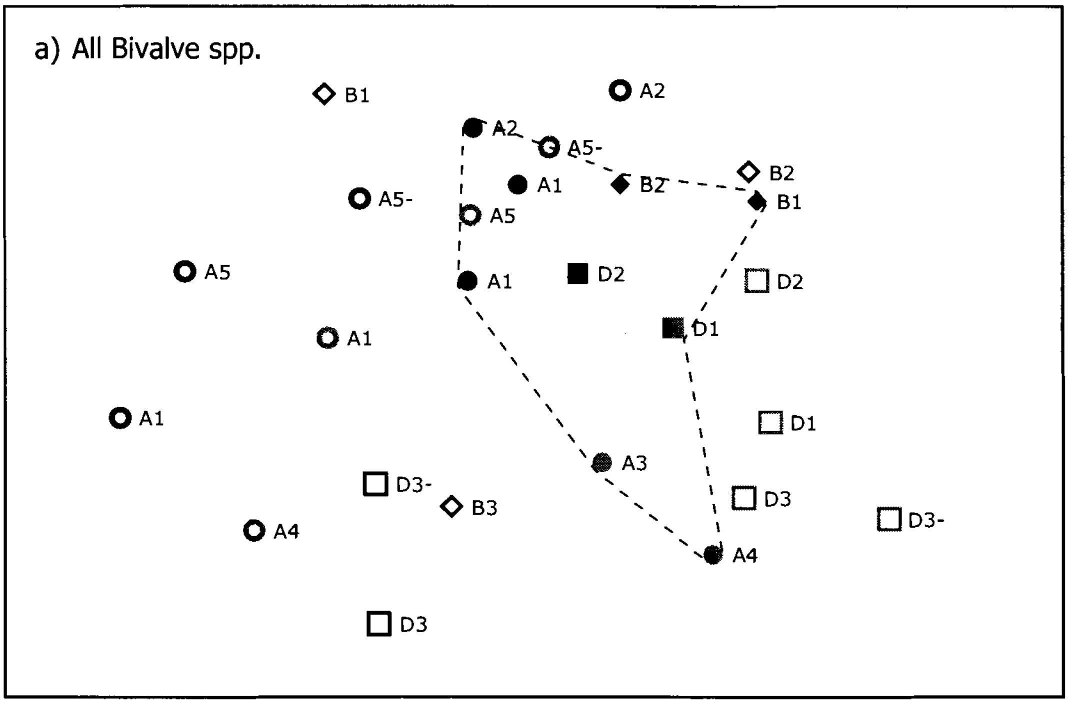
	low	(df=6)	mid	(df=6)	(df=7)
Index	**Mean Difference (F-R) ± 95% CI**	**p-value**	**Mean Difference (F-R) ± 95% CI**	**p-value**	**Unequal Variance (F-Test)**
ACE	-1.5 ±6.4	0.582	-1.8 ±6.4	0.529	0.5236
ICE	-2.1 ±5.9	0.421	-3.3 ±5.9	0.218	0.3981
Jackknife 1	-1.2 ±5.1	0.595	-3.2 ±5.1	0.180	0.8749
Shannon-Weiner	-0.30 ±0.37	0.103	-0.32 ±0.37	0.082	0.4197
Simpson's Evenness	-0.79 ±1.31	0.192	-0.67 ±1.31	0.257	0.7877

3.1.4 Multivariate Analysis

MDS ordinations of sites are displayed in Figure 5 (Density data) and Figure 6 (Biomass data). The relatively high stresses in Figure 5 indicate that individual relationships are poorly represented, but the overall ordination is acceptable. Higher stresses in Figure 6 indicate a higher risk of misleading interpretations, but is still within an acceptable range (Clarke 1993). When *Venerupis philippinarum* was excluded from the analyses, the overall ordination changed little for density data, apart from a small rotation evident in the MDS plot, which is meaningless in this non-metric context. *V. philippinarum* appears far more influential with regards to biomass data, where its absence reduces the overall similarity among farm sites.

ANOSIM tests (see Table 6) found no significant differences in rank similarities between farm and reference sites, in any crossed analysis. No significant differences were found for any factor considered (tide height, region, treatment) with respect to biomass data. In terms of density, significant differences between regions were apparent, regardless of the inclusion of *V. philippinarum* in the analysis. More detailed tests reveal that these regional differences are only significant within reference sites, but not within farm sites (see Table 6).

Figure 5 **(a & b). MDS Plot of average density (individuals·m^{-2}) of clam species (a, stress = 0.18) and results of the same analysis, with *Venerupis philippinarum* excluded (b, stress = 0.19). Sites are identified by region (◆ = Barkley sound, ● = Baynes Sound, ■ = Desolation Sound), stratum (black = low, grey = mid), and type (open = reference, closed = farm). Site labels ending in a dash (D3-, A5-) indicate "pre-farming" sites. Active farm sites have also been outlined in a dashed line within the reduced ordination space.**


a) All Bivalve spp.

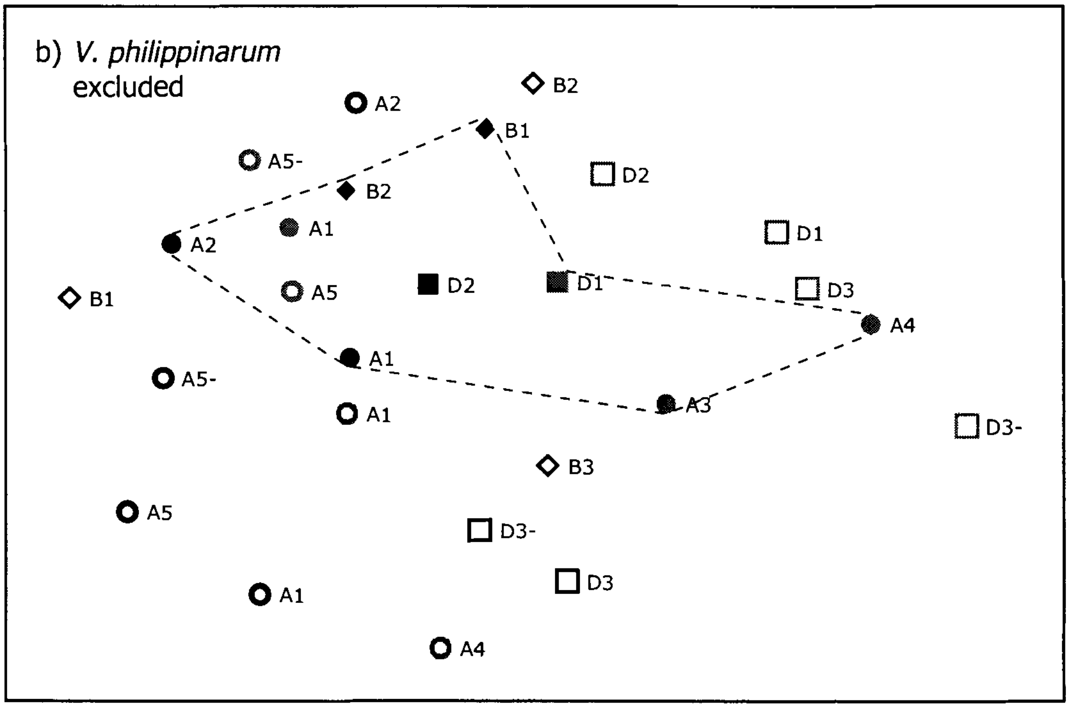

b) *V. philippinarum* excluded

Figure 6 (a & b). MDS Plot of average biomass ($g \cdot m^{-2}$) of clam species (a, stress = 0.22) and the results of the same analysis, with *Venerupis philippinarum* excluded (b, stress = 0.23). See Figure 5 caption for labels and legend.

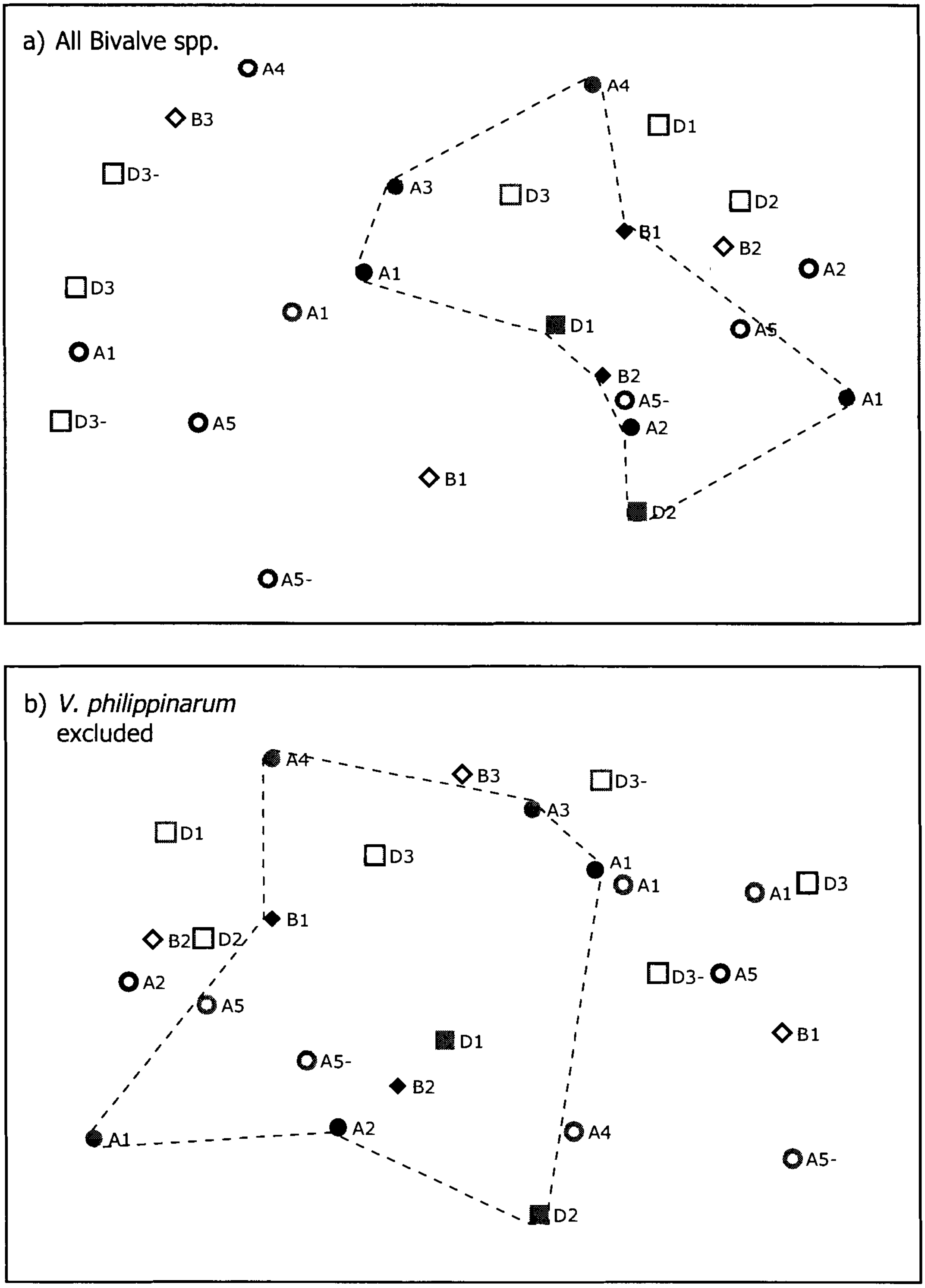


Table 6. **ANOSIM results for bivalve community. Factors in 2-way crossed analyses are listed with the crossed factor identified in brackets. Statistically significant results are highlighted in bold with an asterisk *.**

Species included	Factor (X crossed with)	R-statistic	p-value
Density			
All	Farming Practices (X Stratum)	-0.123	0.939
	Stratum (X Farming Practices)	0.057	0.229
	Farming Practices (X Region)	-0.071	0.697
	Region (X Farming Practices)	**0.301**	**0.002***
	▸ Region – Farm only	0.16	0.222
	▸ **Region – Reference only**	**0.341**	**0.005***
Not *Venerupis philippinarum*	Farming Practices (X Stratum)	-0.213	0.998
	Stratum (X Farming Practices)	0.033	0.289
	Farming Practices (X Region)	-0.149	0.903
	Region (X Farming Practices)	**0.312**	**0.004***
	▸ Region – Farm only	0.049	0.405
	▸ **Region – Reference only**	**0.385**	**0.004***
Biomass			
All	Farming Practices (X Stratum)	-0.037	0.628
	Stratum (X Farming Practices)	0.054	0.227
	Farming Practices (X Region)	0.009	0.420
	Region (X Farming Practices)	-0.061	0.730
Not *Venerupis philippinarum*	Farming Practices (X Stratum)	-0.042	0.643
	Stratum (X Farming Practices)	0.047	0.232
	Farming Practices (X Region)	0.009	0.433
	Region (X Farming Practices)	-0.061	0.723

Comparing the ANOSIM results to the MDS ordination, it appears that farm sites may be more similar as a group than reference sites, to the point where regional differences between communities that are apparent within reference sites, become less evident among the more similar farm sites. Although no differences in community similarity were observed between farm and reference sites, the average pairwise similarity between farm sites is higher than between reference sites, in every case but biomass data excluding *V. philippinarum* (see Figure 7). Excluding *V. philippinarum* from the data also reduces mean similarity within all groups.

Figure 7. Mean pairwise Bray-Curtis Similarity (of fourth-root transformed data) within groups. Values for farm sites are on the left of each pair, shaded in grey. White bars represent values for reference sites. Error bars show 95% confidence intervals about each mean.

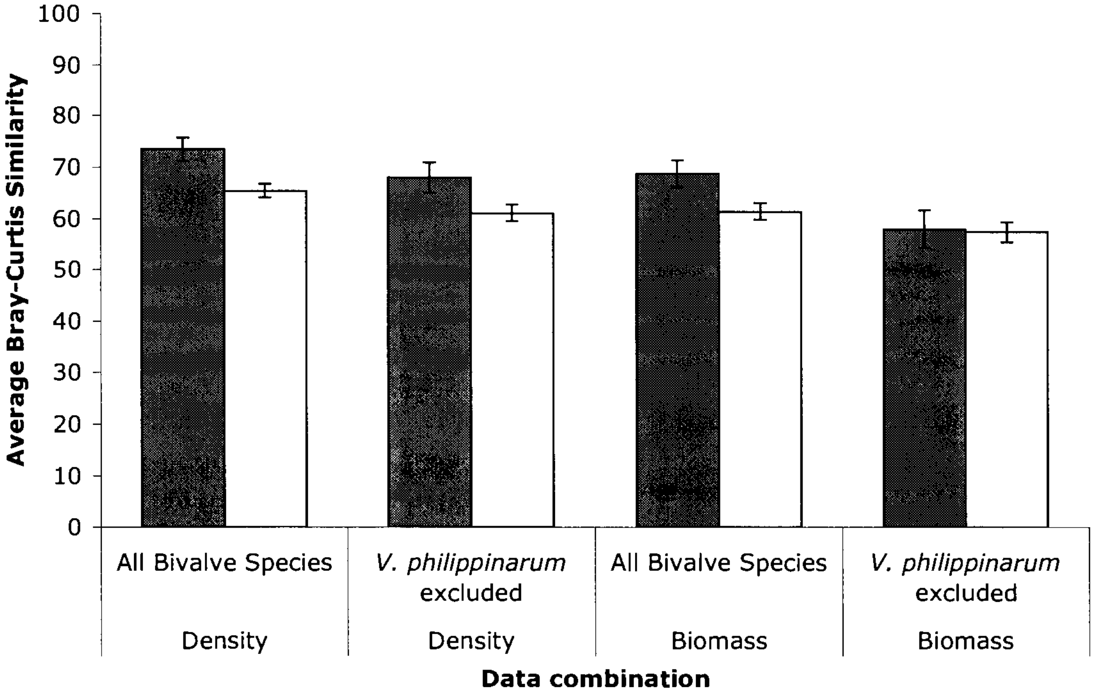


Table 7 shows the contribution of bivalve species to the overall similarity among both farm and reference sites. The ratio of mean similarity to the standard deviation of similarities within each group is a measure of how consistently each species contributes to the overall similarity within that group (Clarke 1993). A higher ratio indicates that a species is present at high densities (leading to higher mean similarity) and is consistently at high densities within the group (leading to a low standard deviation of similarities). For species contributing most to the similarity among farm sites, they also contribute more consistently (see Table 7), which may account for the higher overall similarity of farm sites.

Table 7. **Consistency of species' contributions to the similarities within farm and reference sites, by density. Species are listed in the order of their contribution to the average similarity within the group.**

Farm		Reference	
Species	**Avg. Sim. / SD(Sim.)**	**Species**	**Avg. Sim. / SD(Sim.)**
Average Similarity	73.5%		65.4%
Venerupis philippinarum	**6.62**	*Venerupis philippinarum*	3.93
Protothaca staminea	**3.83**	*Protothaca staminea*	2.52
Macoma balthica	**2.53**	*Cryptomya californica*	2.68
Cryptomya californica	**4.75**	*Macoma balthica*	1.99
Macoma inquinata	1.66	*Mya arenaria*	**2.10**
Macoma nasuta	**1.53**	*Macoma inquinata*	**2.26**
Mya arenaria	1.66	*Macoma nasuta*	1.12
		Nuttallia obscurata	**0.77**

Table 8 lists species in order of their contribution to the dissimilarity between farm and reference sites by density data. There is no hypothesis test as to whether or not densities of each species may differ between groups, but it is apparent that no species is absent in one group or another, but vary slightly by abundance between the two groups. Not surprisingly, the commercially seeded species *Venerupis philippinarum* accounts for the largest single component of the dissimilarity between farms and reference sites. Deposit feeders such as *Macoma nasuta, Nuttallia obscurata* and *Cryptomya californica* seem to have slightly lower densities on farm sites. Densities of smaller filter feeders such as *Macoma balthica* and *M. inquinata* are higher on farm sites. Other species vary by tide height and may have slightly higher densities on reference sites in the mid, but higher farm densities in the low intertidal.

Table 8. Species responsible for 90% of the dissimilarity between farm and reference sites, listed in order of importance of their contribution to the average Bray-Curtis dissimilarity. Density values listed are untransformed average density (individuals·m^{-2}) in each group.

	Mean Density	
Species	**Farm**	**Reference**
Mid		
Macoma nasuta	14.07	**19.04**
Venerupis philippinarum	**326.8**	132.87
Macoma balthica	**20.84**	14.18
Nuttallia obscurata	4.13	**33.69**
Protothaca staminea	**59.96**	50.04
Cryptomya californica	14.33	**24.29**
Macoma inquinata	**4.91**	2.71
Saxidomus gigantea	0.36	**0.61**
Rhamphidonta retifera	**0.44**	0.40
Mya arenaria	1.58	**2.17**
Pseudopythina rugifera	0.18	**0.29**
Macoma obliqua	0.11	**0.26**
Parvalucina tenuisculpta	0	**0.31**
Low		
Venerupis philippinarum	**310.28**	46.73
Macoma balthica	**91.69**	45.73
Macoma nasuta	17.75	**25.25**
Nuttallia obscurata	2.33	**8.40**
Macoma inquinata	**14.47**	2.85
Cryptomya californica	26.53	**33.2**
Mya arenaria	**12.31**	8.40
Saxidomus gigantea	0.72	**2.70**
Protothaca staminea	24.03	**38.37**
Parvalucina tenuisculpta	0	**0.64**
Clinocardium nuttallii	0.06	**0.60**
Macoma obliqua	**0.61**	0.21
Pseudopythina rugifera	**0.31**	0.06

Table 9 lists species in order of their contribution to the dissimilarity between farm and reference sites by biomass data. Once again, *Venerupis philippinarum* is responsible for most of the dissimilarity. Otherwise, the order of species in Table 9 is generally the opposite of Table 8. Larger species contribute more to differences in biomass, but are so numerically uncommon that they contribute very little in terms of density. The opposite is true for smaller, more abundant species. Not only are species such as *V. philippinarum, P. staminea* and *M. inquinata* present in higher densities on farm sites, their biomass is also higher. Although *M. balthica* was less dense on farm sites, the total biomass is higher, suggesting a possible change in body size demographics for this species on farm sites. The reverse pattern is observed for *Mya arenaria*, which may be smaller on farm sites.

Table 9. Species responsible for 90% of the dissimilarity between farm and reference, listed in order of importance of their contribution to the average Bray-Curtis dissimilarity. Biomass values listed are untransformed average biomass ($g \cdot m^{-2}$) in each group.

	Mean Biomass	
Species	**Farm**	**Reference**
Mid		
Venerupis philippinarum	**2301.36**	1533.26
Mya arenaria	18.55	**89.68**
Nuttallia obscurata	35.32	**218.88**
Macoma nasuta	**55.11**	18.34
Protothaca staminea	**618.96**	536.53
Saxidomus gigantea	23.92	**60.38**
Macoma inquinata	**15.00**	3.00
Macoma balthica	**8.71**	1.64
Low		
Venerupis philippinarum	**1591.90**	339.36
Saxidomus gigantea	**120.69**	109.45
Mya arenaria	156.68	**206.03**
Protothaca staminea	**537.85**	431.93
Nuttallia obscurata	17.23	**96.76**
Macoma nasuta	21.40	**41.98**
Macoma inquinata	**23.96**	4.94
Macoma balthica	**7.47**	4.36
Cryptomya californica	7.42	**9.39**
Clinocardium nuttallii	**5.90**	3.42

3.2 Netting Experiment

3.2.1 Density

Faunal densities appear to vary little through time, and no decrease was observed, even within control plots where depletion was expected due to predation (see Figure 8). Repeated measures analysis of paired differences found that the addition of the netting treatment after the baseline sampling period had no effect on the difference in densities between netted and paired control plots (see Table 10). There was also no significant interaction between time and stratum on the paired differences in density for any faunal grouping considered.

Figure 8. **Mean Density (Inividuals·m^{-2}) of fauna at each plot for time 0, 1 and 2. Values for netted plots are shown in black circles connected by a black line. Control means are plotted in open circles connected by a grey line. Error bars represent individual 95% confidence intervals for treatment means of plot values.**

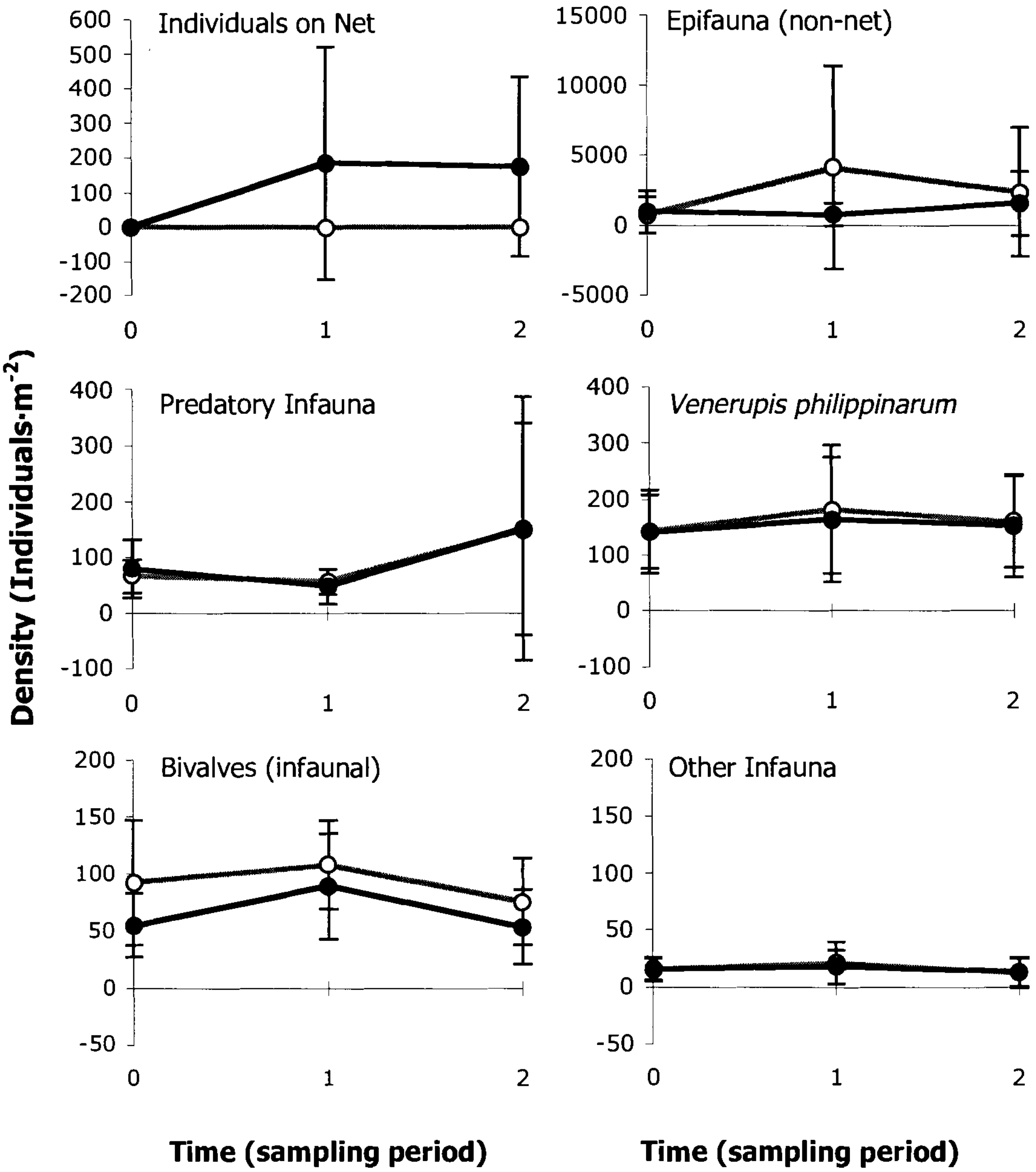


Table 10. Results of repeated measures analysis for paired group densities (individuals·m^{-2}, Net – Control plot). Significant p-values (α=0.05) are highlighted in bold with an asterisk *.

Group	Time	Time X Stratum
Total Density	0.536	0.582
▶ Epifauna (incl. bivalves)	0.540	0.574
▶ Infauna	0.839	0.882
▶ Predatory Infauna	0.092	0.856
▶ Non-Predatory Infauna	0.857	0.729
▶ Bivalves (infaunal)	0.938	0.769
▶ *Venerupis philippinarum*	0.717	0.855
▶ Other Infauna	0.719	0.971
V. philippinarum excluded:		
▶ Infauna	0.948	0.910
▶ Non-Predatory Infauna	0.770	0.714
▶ Bivalves (infaunal)	0.744	0.677

3.2.2 Univariate Community Indices

Table 11 lists observed and estimated species richness, evenness and diversity indices for each plot and time period sampled as part of the netting experiment. Neither time, nor time by stratum interaction were significant for any measure of species richness, evenness or diversity (see Table 12). The addition of netting following the baseline sampling period therefore had no effect on the difference between netted and control plots, for any univariate index of community structure.

Table 11. **Observed, estimated species richness, diversity and evenness for all netting experiment plots.**

			# Observed spp.		ACE		ICE		Jack 1		Shannon-Weiner		Simpson's Evenness	
Stratum	Site	Time	Control	Net	Control	Net	Control	Net	Control	Net	Control	Net	Control	Net
A	Bub	0	16	20	26.1	32.5	21.6	30.2	20.8	27.2	1.97	1.93	0.343	0.248
		1	16	18	17.1	24.3	18.7	23.1	19.2	22.8	2.16	2.15	0.459	0.398
		2	17	18	18.3	24.8	18.7	21.7	19.4	22.0	2.12	1.90	0.408	0.253
	Hint	0	21	28	25.0	34.9	24.1	37.0	25.0	36.0	1.06	1.38	0.081	0.091
		1	19	19	21.4	24.2	22.2	22.4	23.0	23.0	0.75	1.01	0.076	0.089
		2	20	21	24.1	23.5	23.0	22.3	24.0	23.4	1.21	1.12	0.104	0.089
	Roy	0	16	16	17.6	19.7	17.5	19.5	18.4	20.0	1.94	0.98	0.287	0.100
		1	15	14	15.5	14.0	15.4	14.0	15.8	14.0	1.95	1.11	0.344	0.127
		2	17	18	19.0	21.1	19.2	20.3	20.2	21.2	2.01	1.49	0.327	0.153
B	Bub	0	18	16	20.7	17.7	20.5	17.7	21.2	18.4	2.00	2.02	0.277	0.339
		1	26	26	36.6	29.7	33.6	30.9	33.2	31.6	2.36	2.16	0.300	0.238
		2	22	19	22.9	22.9	23.5	23.3	24.4	23.8	1.85	2.05	0.174	0.305
	Hint	0	20	20	24.1	22.3	23.9	23.4	24.8	24.0	1.63	1.53	0.144	0.142
		1	18	22	19.4	37.0	19.4	26.1	20.4	26.8	0.23	1.32	0.060	0.100
		2	25	25	26.0	26.4	26.2	36.2	27.4	33.8	0.87	1.54	0.059	0.115
	Roy	0	17	20	18.2	27.0	17.9	30.8	18.6	27.2	1.92	1.92	0.264	0.252
		1	22	23	31.0	28.4	29.1	28.6	28.4	28.6	1.88	2.08	0.180	0.232
		2	14	17	17.2	23.2	16.6	21.9	17.2	21.8	1.31	1.46	0.187	0.170

Table 12. **Results of repeated measures analysis of paired differences (Net – Control plot) for estimated species richness, evenness and diversity. Significant p-values ($\alpha=0.05$) are highlighted in bold with an asterisk *.**

Index	Time	Time X Stratum
ACE	0.844	0.678
ICE	0.234	0.193
Jackknife 1	0.574	0.380
Shannon	0.682	0.596
Simpson's Evenness	0.855	0.210

3.2.3 Multivariate Analysis

MDS plots for each sampling period show no clear segregation of treatments at any time, although plots from the same site do appear closer together, at all time periods (see Figure 9). Two-way crossed ANOSIM tests for difference between treatment levels and tide height stratum found no significant differences at any time period (see Table 13). Small sample sizes only permitted 100 randomizations for each of these tests.

When plots from all time periods are shown together on a single MDS plot, the lack of separation between netted and control plots becomes more evident (see Figure 10). ANOSIM tests of differences between time periods, for net and control groups separately, show no significant temporal differences whatsoever (see Table 14). Sites are more strongly grouped overall by stratum, or by site (see Table 15). Therefore, changes in community structure through time, with the addition of netting for a period of 10 months, are insignificant relative to differences between tide heights, or sampling sites.

Figure 9. MDS ordinations of plots at each sampling time (t = 0, 1, 2). Plots are identified by location (■ = Hint, ● = Bub, ◆ = Roy), stratum (grey = A, black = B), and treatment (closed = netted, open = control). Stress values are 0.05 (t=0), 0.06 (t=1), 0.04 (t=2).

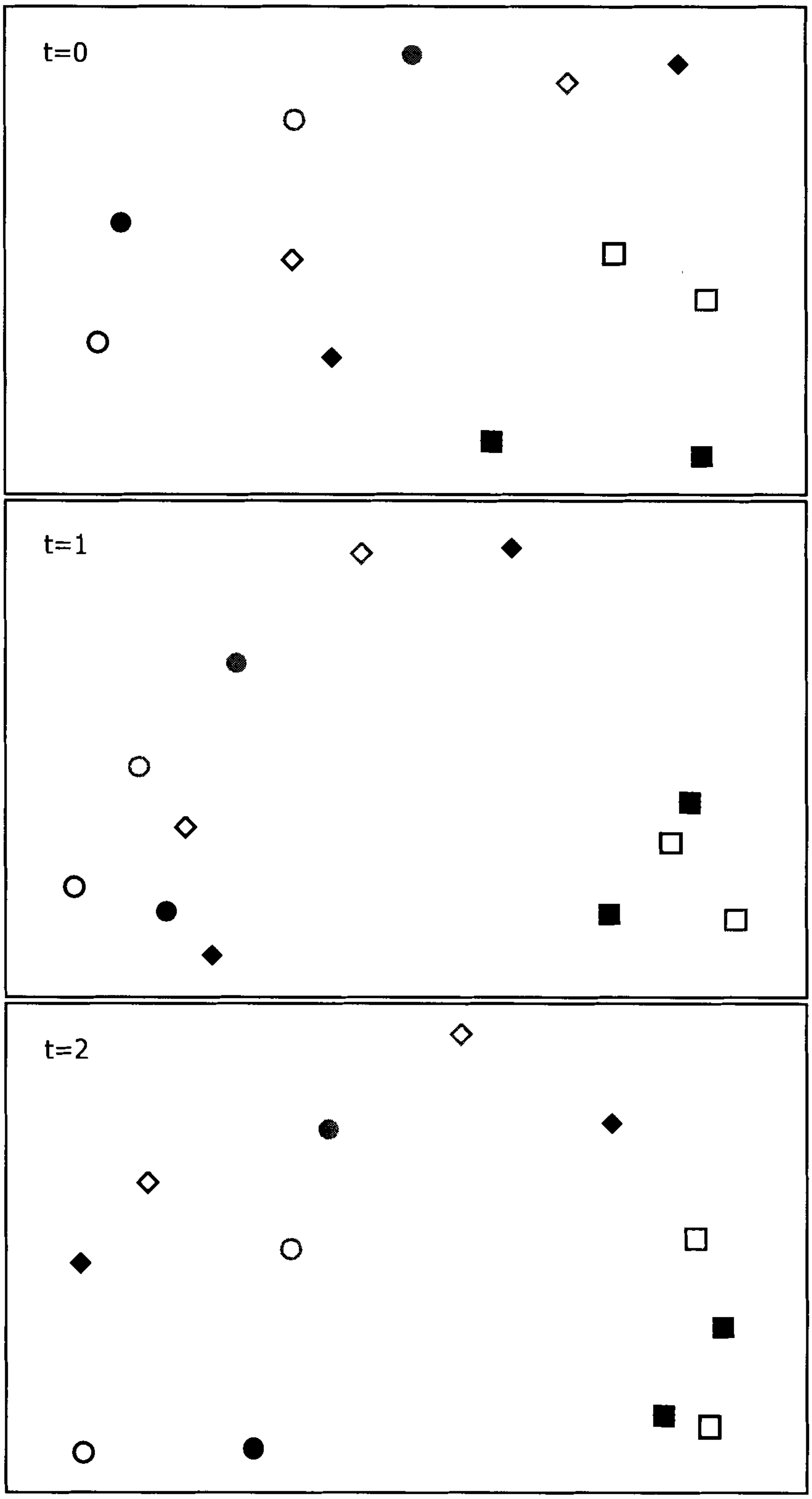


Table 13. **ANOSIM results of factor comparisons at each sampling time. Small sample sizes only permitted 100 randomizations for each test.**

Time:	0		1		2	
Factor (X crossed with)	**R-statistic**	**p-value**	**R-statistic**	**p-value**	**R-statistic**	**p-value**
Treatment (X Stratum)	-0.333	0.95	-0.167	0.77	-0.389	0.98
Stratum (X Treatment)	0.074	0.28	0.037	0.40	0.037	0.34

Figure 10. **Combined MDS ordination of all plots and sampling times. See Figure 9 caption for explanation of symbols. Samples from the same plot are joined by lines, and labelled by sampling time (0,1,2). Stress = 0.12**

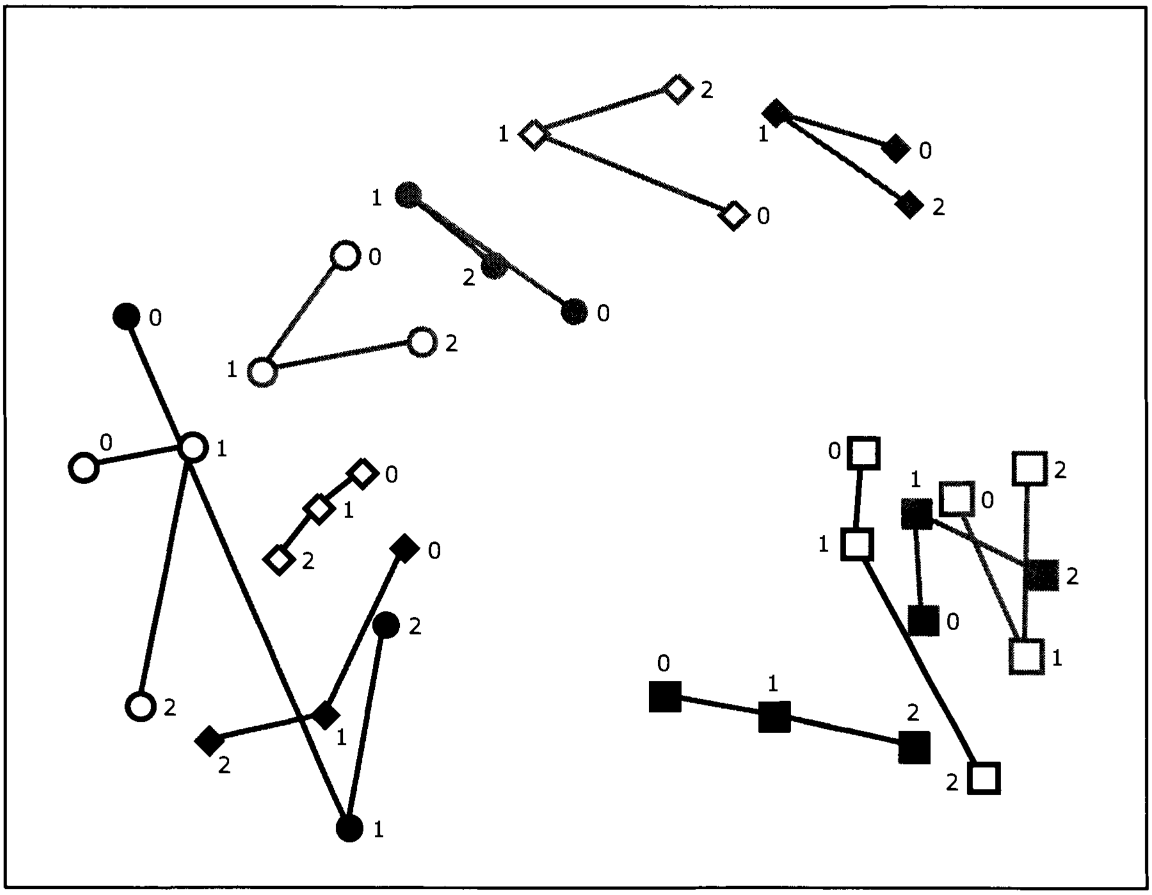


Table 14. ANOSIM results of comparisons between sampling times, within treatments.

	Net		Control	
Time Contrasts	R-statistic	p-value	R-statistic	p-value
0, 1	-0.117	0.797	-0.081	0.697
1, 2	-0.043	0.548	-0.102	0.751
0, 2	-0.080	0.690	-0.033	0.530

Table 15. ANOSIM results of factor comparisons across all sampling times. Significant differences (α=0.05) are highlighted in bold with an asterisk *.

Factor (X crossed with)	R-statistic	p-value
Treatment (X Time)	-0.151	0.998
Time (X Treatment)	-0.077	0.883
Stratum	**0.261**	**0.003***
Site	**0.618**	**0.001***
▸ **Bub, Hint**	**0.954**	**0.001***
▸ **Bub, Roy**	**0.191**	**0.010***
▸ **Hint, Roy**	**0.634**	**0.001***

4.0 DISCUSSION

Farm and reference sites differed very little in terms of most univariate community indices (species richness, evenness, diversity), although multivariate analyses showed subtle changes in variability. A small-scale netting experiment found no general effects of netting, across a range of distinct sites. These results highlight the difficulties of conducting research in intertidal soft-bottom communities, where variability and relevant processes depend greatly on the scale of measurement. Despite these challenges, analysis of species count data can give useful information regarding possible impacts of shellfish aquaculture practices, and lead to recommendations for maintaining the ecological sustainability of this important industry.

Results of the field study provide insights into effects of two common shellfish aquaculture practices operating together. The nature of the study does not allow the separation of effects of netting and seeding practices common to shellfish aquaculture. Nevertheless, these practices are used with the intention of altering the ecology of these communities. Nets are used on clam tenures with the intention of reducing predator pressure on commercial species, and possibly other non-target species as an unintended result. The addition of clam seed is intended to increase the productivity of the commercial species, which can directly change the population dynamics of this species and possibly change the strength and form of competition in intertidal communities. Therefore, the results of this study must be considered within the context of predation and competition and their role in structuring these communities.

The netting experiment was designed to assess the strength of predation across different seasons, rather than directly addressing the effects of netting on long-term community structure. The results of this experiment demonstrate that short-term changes in community structure are unlikely to be affected by netting, and that the temporal changes at a single site are much smaller than differences between sites.

4.1 Netting and Predator Exclusion

Previous research in intertidal soft-bottom habitats suggests that large, mobile epibenthic predators are often effective at limiting populations of intertidal macroinvertebrates, including clams. If netting used in clam aquaculture reliably excludes such predators, then population densities are expected to be higher in areas of netting, relative to unnetted reference sites, all other factors being equal. The results presented in this work are not consistent with such a prediction, indicating a lack of understanding of community dynamics in this system, or invalid assumptions, or both.

Total bivalve density was found to be significantly higher in farm sites, compared to unnetted and unseeded reference sites in the large scale field study. This difference can be attributed entirely to the significantly higher densities of the commercial *Venerupis philippinarum* on farm sites. The fact that this was the only species to show significantly higher densities suggests that most, if not all, clam species were not affected by the presence of netting on the farm sites. This raises the question of what the effects are of intertidal netting on clam farms.

4.1.1 Why only *Venerupis philippinarum*?

There are many possible explanations for why *V. philippinarum* was the only species present in higher densities on farm sites. Clam aquaculture practices may act to maintain a biophysical environment that truly only favours this commercial species. While this might be the intent of aquaculture practices, it seems unlikely that no other species would benefit incidentally.

Intertidal netting used in clam aquaculture may only prevent predation on *V. philippinarum*, and allow other species to be regulated by the same forces acting on the reference sites in this study. This could only be the case if *V. philippinarum* were a preferred prey of a predator that was excluded by the nets.

The simplest explanation is that *V. philippinarum* is the only species added as seed to the farm sites. The British Columbia Shellfish Grower's Association (BCSGA) recommends adding *Venerupis philippinarum* seed at a density of 200 to 400 individuals per square metre, with an expected loss of 40-50% under nets, before reaching harvest (BCSGA 2004b). This should account for a total addition of 100-200 adult individuals of commercial size per square metre. The sites used in this study are at various stages of harvest and seeding, but the average increase in density is consistent with that expected due to seeding. On the other hand, adult *V. philippinarum* are harvested after they are sexually mature, allowing them to spawn for at least one season. The number of individuals on farm sites resulting from natural spawning is unknown, which adds uncertainty to the relative contribution of seeding to the observed differences.

Although *V. philippinarum* was the only bivalve species to show higher densities and biomass on farm sites, total bivalve biomass did not increase significantly. The abundance of other bivalves, excluding *V. philippinarum*, was lower at farm sites on average, though not significantly different. The actual difference may have been smaller than could be detected, due to large variation in the data. Nevertheless, it stands to reason that if *V. philippinarum* is increasing in abundance, yet total biomass is not significantly different, then other species may be less abundant on sites exposed to common aquaculture practices. This suggests that farm sites are dominated more by the commercial species than paired reference sites, which is also supported by abundance data at individual sites.

4.1.2 No Observed Effects of Predator Exclusion

The short-term netting experiment found no effect of netting on densities, or community composition, over a 10-month period. However, the lack of a decrease in densities in control plots also suggests that predation was not affecting densities, and therefore there was no signal due to predation in the data. Even when taking into account possible effects of infaunal predators, no general pattern is apparent.

It remains unclear why total bivalve densities, excluding *V. philippinarum*, appear to be unaffected by netting in the field study. The fact that total densities are similar between farm and reference sites suggests a few possible explanations. If netting excludes epibenthic predators, then predation may not be limiting at these sites, and that other factors are preventing densities from increasing in its absence. Even if netting provides a predator refuge, then space, food availability, nutrients, or other unknown factors may prevent populations from increasing above the current carrying capacity.

There is little evidence that space is a limiting resource in soft-bottom sediments (Black and Peterson 1988, Peterson 1982, 1992), except perhaps for large, deep-dwelling bivalves (Peterson and Andre 1980), which would have been poorly represented in the sampling methods used in the present studies. There is evidence, however, that food may be limiting in long, flat intertidal areas, where a low rate of vertical mixing in the water column can allow filter-feeding bivalves to deplete food particles at the sediment-water interface (Beal *et al.* 2001, Peterson 1992, Peterson and Black 1991). Experiments that have observed possible food limitation in intertidal bivalves often infer such a limitation from density-dependent growth. Density-dependent mortality has only been attributed to food limitation in combination with environmental stress, but may also be a result of predator responses.

Current research does not support the hypothesis that food limits population sizes, but it can be a significant factor if it interacts with an additional source of mortality, such as environmental stress, disturbance, or predation. Bivalve densities, excluding the seeded *V. philippinarum*, ranged between approximately 100 to 300 individuals m^{-2} at nearly all sites sampled, suggesting a common upper limit to bivalve density. The notable exception to this pattern is the D2 reference site, located near a public dock and within an area closed to shellfish harvesting. The conditions at this site seem to support high densities and biomass of all bivalve species, including *V. philippinarum*. The abundance of bivalves at this site is greater than any other reference site, and exceeded only by two farm sites, B1 and D1, which also have high densities of seeded *V. philippinarum*.

There may also be a balance between the two forces of predator exclusion, and other undocumented farming practices that favour a commercial species over others. If the nets act as a predator refuge, yet other farming practices prevent populations of other bivalves from increasing, with the exception of commercially favoured ones, that might explain the observed patterns in bivalve density between farmed and reference sites. More information about impacts of individual farming practices would help to separate and explain the processes underlying these observations.

Many of the above-mentioned explanations and mechanisms affecting total bivalve density are unlikely to affect all bivalve species in the same way. The limitation of suspended food particles is not likely to limit the growth of deposit-feeders, and selective predators may only limit populations of some bivalve species and not others. Nevertheless, no consistent difference was observed in bivalve biomass, densities or community composition, suggesting that farm sites and reference sites are not fundamentally different in terms of resource limitation. Despite similar densities, bivalve communities are subject to different pressures on farm and references sites, particularly in the case of farming practices and harvesting rates. There remains the question of how predation on the bivalve community differs as a result of these farming practices.

4.1.3 Which Predators?

An alternate explanation for the results of this study is that the nets, as used in B.C., do not effectively exclude epibenthic predators. Predators in the water column may be able to get under the nets when they are submerged by the tides, because some nets float and the edges are rarely buried, or secured to the ground only at large intervals relative to the size of the predators. In the course of our sampling, we occasionally found fish or crabs trapped under nets after the tide had receded. In addition, many predators of benthic infauna are themselves inhabitants of the sediment (Ambrose 1984), and cannot be excluded by surface netting. Infaunal predators tend to be smaller and are generally thought to have a relatively minor, though constant effect on population sizes of prey in soft-bottom sediments (Reise 1985). Infaunal predators may even benefit from the exclusion of epibenthic predators, leading to a shift in predator pressure on the benthic community (Gee *et al.* 1985).

The aperture sizes of nets used in B.C. also would not exclude numerous juvenile and small predators that can have seasonal effects on intertidal populations. If present at appropriate times of the year, these small predators can affect bivalve populations by removing juveniles before they can achieve a large enough size to be unmanageable by small predators (Reise 1985). The only predator reliably excluded may be large diving ducks, which are thought to be a major predator of clams (Jamieson *et al.* 2001), and possibly poachers, whose impacts are unknown.

4.1.4 Where have all the clams gone?

While evidence supports the hypothesis that scoters may be responsible for the majority of clam disappearance at some sites (Lewis, unpublished data), very little is still known about how scoter predation is affected by nets, or the fate of bivalves that disappear from under protective netting. The BCSGA (2004b) expects that as many as 40 – 50% of seeded *Venerupis philippinarum* clams are lost from under nets at a typical clam farm before reaching harvest. Nevertheless, it is unknown whether these clams are consumed by predators, let alone which predators, or if these clams simply migrate out from under the nets to other areas.

Several clam farmers have described seeing clams crawl along the beach surface, under nets, as well as trails left by clams moving within a site. Small juvenile bivalves and gastropods are also able to spin mucous threads that allow them to be pulled by water currents and wave action. This kind of postmetamorphic drifting has been hypothesized to be an effective and important mechanism of dispersal in some species, particularly those lacking a highly mobile planktonic larval stage (Martel and Chia 1991). The ability of *Venerupis philippinarum* to migrate in this manner is poorly understood, although juveniles of the species have been observed to have moved following periods of strong currents and wave action at some sites (Ydenberg, personal communication). A better understanding of the vertical and horizontal dispersal abilities of juvenile and adult *V. philippinarum* would allow more accurate explanations of changes in populations sizes and densities, and bears more detailed study.

The largest unknown factor affecting clam loss or mortality at all sites is the illegal poaching of bivalves for commercial sale. Unprotected sites are more susceptible to poaching, particularly during nighttime low tides in the winter, or remote areas that are infrequently monitored, where poachers are less likely to be observed.

4.1.5 Zonation

Biological interactions, such as predation and competition can play an important role in determining the spatial distribution of intertidal benthic macrofauna. The upper distribution of species is often limited by tolerance to environmental extremes, such as desiccation with receding tide, larger variations in temperature and salinity over short periods of time also associated with tidal water movements, and also changes in sediment type that may occur over a tidal gradient (Dame 1996). Lower intertidal limits of species, on the other hand, appear to be the result of biological interactions including predation and possibly competition (Paine 1974, Peterson 1992, Posey 1986).

Competition between *Venerupis philippinarum* and *Nuttallia obscurata* was thought to account for the difference in distributions: *N. obscurata* is more commonly found higher in the intertidal than *V. philippinarum.* In the sites sampled in the field study, however, *N. obscurata* was found even in low intertidal areas, although at densities slightly lower on farm sites than reference sites. Although the thinner shells of *N. obscurata* might make them more appealing as a prey item, the lower biomass per clam compared to *V. philippinarum* may render them energetically less favourable. *N. obscurata* also has several adaptations which allow them to survive deeper in the sediment than *V. philippinarum* (Gillespie *et al.* 1999), thus avoiding predation and variable environmental conditions at the surface.

There is a trade-off associated with living in intertidal areas. Greater desiccation time in high intertidal areas not only reduces feeding time, but the large fluctuations in environmental conditions can also be physiologically stressful to benthic infauna. This stress can lead to even higher metabolic costs and a non-linear decrease in growth and productivity (Beal *et al.* 2001). Although environmental conditions are less stressful, and food more plentiful in lower intertidal areas, infauna must also face more intense predation. Both epifaunal and infaunal predators are more abundant lower in the intertidal (Ambrose 1991, Beal *et al.* 2001, Peitso *et al.* 1994), which may explain why residents of these areas tend to be species with adaptations to avoid predators, or to increase handling time to the point of being energetically prohibitive (Kabat 1990, Peterson 1982, Seitz *et al.* 2001). Species found higher in the intertidal may be better adapted to surviving the stresses of exposure than predation.

Size-specific predation, in combination with a predation gradient can also generate size gradients in benthic infauna, such as bivalves, with prey size increasing or decreasing with distance from the low tide mark (Ambrose 1991, Peitso *et al.* 1994). In the absence of predation, otherwise competitively dominant species can also expand their distributions lower into the intertidal, where they benefit from better growing conditions within a predator refuge (Paine 1974, Posey 1986). Given the generally weak interspecific competition observed in soft-bottom systems, such changes in distribution are not expected to cause dramatic changes in other species, although dominance, and overall biomass of a community may change in a simple additive manner. The increased complexity of trophic structures in low intertidal areas means that predation probably plays a much more important role in structuring communities in this zone.

Tidal elevation was found to be a significant factor explaining changes in community structure in the netting experiment, though not in the field study. The low contrast between "low" and "mid" intertidal strata in the study may have blurred the differences somewhat. Nevertheless, the difference in *V. philippinarum* density between farm and reference sites was most significant in the low stratum. Any predator-exclusion abilities of netting may be more pronounced in the lower intertidal, where predation is also more intense.

4.2 Physical Changes of Predator Exclusion Structures

Many researchers (Kaiser *et al.* 1996, Peterson and Beal 1989, Spencer *et al.* 1998) have suggested that nets, cages and other physical structures, used to exclude predators in many studies, induce other changes, such as increased sedimentation and food availability, that are independent of predator exclusion and thus constitute an experimental artefact. Conclusions from such studies should be considered in this light, and artefacts controlled for if at all possible.

In the case of netting used by clam farmers, Spencer *et al.* (1997) found that changes in benthic community structure most likely occurred because of changes in the physical characteristics of sediment, rather than the exclusion of predators. Clam netting was shown to increase sedimentation rates, leading to a concomitant increase in the abundance of deposit feeding fauna (Kaiser *et al.* 1996, Spencer *et al.* 1997). Increased sedimentation is often attributed to physical structures used to exclude predators from soft-bottom marine sediments, and can thus be confounded with the desired exclusion of predators (Gee *et al.* 1985). This artefact of experimental manipulation does not seem to be as much of a problem for experiments in rocky substrata.

Predator-exclusion structures can baffle waves, moderate disturbance (Gee *et al.* 1985, Peterson 1984, Reise 1985, Spencer *et al.* 1997), and also act as attachment structures for macroalgae, which can further reduce water velocities and increase the deposition of organic particles to the sediment surface. In the aquaculture industry, these and associated organisms are referred to as "bio-fouling" and are removed regularly to allow water circulation through the nets, and prevent potentially adverse chemical conditions that may occur beneath decomposing carpets of macroalgae.

Physical effects of clam netting were not analyzed in the present study. Possible differences between farm and reference sites were controlled for, but if clam aquaculture practices altered the physical conditions of farm sites from their pre-farm state, this study would not have been able to observe such an effect. Thus, if farming practices altered the physical characteristics of the site, such changes would have occurred prior to sampling, and the reference sites matched to the current state, not the baseline pre-farm state of a farm site. This might account for the overall similarity between farm and reference sites observed in the study, since community structure is heavily influenced by the physical properties of a site, including sediment particle size, exposure, currents, or nutrient availability.

4.3 Change and Variability

Intertidal macroinvertebrate communities are recognized as being highly variable communities in both space and time (Beal *et al.* 2001). This variability has posed a challenge to researchers, making it difficult to detect changes amidst high levels of variation.

Results from the small-scale netting experiment found no difference between treatment groups with respect to macrofaunal densities or community composition. Examination of the data reveals that differences between sites, which were the replicates in this experiment, were greater than differences between treatments, or even tide height strata. MDS plots show that although some degree of a serial shift in community structure through time was observed at each site, differences between time periods remained smaller than average differences between plots. It is possible that differences in the biophysical environment between replicates were large enough to mask any effect of the netting treatment in the multivariate context.

Further such experiments might yield more precise results by better controlling for environmental variables such as sediment particle sizes, tidal submersion, and other factors known to affect the species composition of intertidal communities. Many other experiments that have demonstrated effects of predator exclusion have succeeded in this regard, even when using plots smaller than those in the present study, by replicating within a single site, rather than across possibly different environmental conditions. The physical environment may determine the relative importance of predation and competition in structuring communities. Consistent effects of these biological interactions may not have been observed in our results because of large variations in environmental conditions, and therefore in the strength of predation or competition, or both. Experiments at larger geographical scales are more informative with regards to general impacts (Beal *et al.* 2001, Emmerson *et al.* 2001, Peterson 1992), but individual sites may respond independently, and this must be taken into account.

In the large scale field study of bivalve communities presented here, there was no significant difference between farm and reference sites with respect to univariate community indices, community composition, or macrofaunal densities, excluding *Venerupis philippinarum*. Nevertheless, multivariate community analysis revealed an apparent change in among-site variability in community composition between treatment groups. Farm sites are slightly more similar to each other, on average, than reference sites. This explains why the regional separation evident among reference sites is not as noticeable among farm sites.

These results suggest that although farming practices do not consistently alter community structure to a point that is outside the range observable among reference sites, the farm sites do appear more similar to each other than is the case with unfarmed sites. It is unknown if farm sites have changed from their original pre-farm states, to their current state, which is not noticeably different from existing reference sites. Unfortunately, the baseline data required to make such an assessment is largely absent for many sites where shellfish aquaculture is currently active.

The results of this study suggest that the two common practices of seeding and netting are not associated with large, negative changes in bivalve community structure at a site suitable for aquaculture. The loss of 'regional distinctness' among farm sites appears to be primarily a result of increased consistency in densities of common species at farm sites. Sites selected and approved for clam farming may also represent a sub-set of possible community types, which are common to all regions included in the study. If this were the case, then communities on pre-farm sites would be expected to be most similar to existing farm sites than other reference sites. Although small sample sizes do not permit a statistical test of this hypothesis, a cursory examination of the MDS plots suggests this may not always be the case.

Sites may be affected to varying degrees by farming practices, but it is not known what factors would mitigate such impacts. Depauperate areas, or those exposed to intense predation or disturbance may benefit from the stabilizing effects of netting. On the other hand, regionally representative, unique areas or biodiversity "hotspots" may experience a loss in the abundance of some species and a decrease in diversity as the moderating effects of aquaculture practices lead to an increase in similarity with other farm sites that are dominated by commercial species.

If clam tenures become increasingly dominated by a single commercially valuable species, what are the implications for ecosystem processes, such as nutrient cycling, performed by bivalves? It has been argued that if many species contribute to carry out activities such as filter-feeding, deposit-feeding, burrowing, and nutrient cycling, this can reduce variability in functional processes, as different species operate optimally under different environmental conditions (Emmerson *et al.* 2001, McCann 2000, Yachi and Loreau 1999). In some cases, species-rich communities have been observed to out-perform the best monocultures in total productivity (Tilman *et al.* 2001). On the other hand, a single species may be all that is necessary in some situations to carry out a particular ecosystem function (Worm and Duffy 2003). Species-rich assemblages may simply have a greater chance of including a single, highly active species that results in an overall high level of ecosystem function (Loreau 2000).

The conditions created by clam farming, which are intended to favour the production of commercial species, may create common pressures that drive separate communities toward higher levels of similarity. The homogenizing force of clam farming at large scales appears to be more significant than potential impacts at individual sites. The ability of common farming practices to alter habitat heterogeneity at smaller scales was not documented in the present study, but is deserving of further research. Nevertheless, the increased similarity among farm sites suggests that impacts of clam farming may be more relevant to larger scale processes.

4.4 Scale of changes

In both the netting experiment and field study presented here, no consistent differences were attributable to the treatments applied, yet there was evidence of other factors operating at different scales than that of the experimental units. In the netting experiment, large-scale site and tide differences overshadowed possible treatment differences, or even serial changes through time. This might explain why no effect of predator exclusion was observed in this experiment, in contrast to many other small-scale predator-exclusion experiments.

Many published experiments using nets or cages to exclude predators used plots in the range of 0.25 m^2 to 10 m^2 (Beal *et al.* 2001, Drake and Arias 1996, Reise 1985, Seitz *et al.* 2001, Spencer *et al.* 1996, 1997, 1998, Summerson and Peterson 1984, Vargas 1988, Wiltse 1980), which is at least as small as those used in the experiment presented here. Many of these studies did find at least small effects of predator exclusion, including changes in density (Beal *et al.* 2001, Drake and Arias 1996, Reise 1985, Summerson and Peterson 1984), species richness (Spencer *et al.* 1997, Wiltse 1980), or community composition (Spencer *et al.* 1996, Vargas 1988). Two important differences between our netting experiment and the others might explain the disagreement in results. First, this experiment included a much shorter time scale than most, which did not allow for recruitment, or other multi-generational effects to be observed. Second, most other experiments replicated plots within a single site, or a relatively small geographic area, whereas the plots in the present experiment were spread out over a much larger area. The latter difference would account for the significant site differences, which are likely the result of differences in sediment particle size, exposure, presence of large predator populations, and other factors that significantly affect community structure.

The fact that macroinvertebrate densities did not decrease on control plots suggests that even if predators were excluded by the experimental netting, that the difference in predation rates between treatments may have been insignificant. The size of the netting plots may have been too small to capture effects of predators, if they forage at larger scales. Any differences in density observed may be the result of migration in and out of the plots, or random variation associated with different sampling points within plots. Future studies of the effects of anti-predator netting might yield more informative results by better controlling for confounding factors such as tidal elevation, sediment type, predation intensity and also by including a broader temporal scale by conducting such an experiment over several years.

Some of these considerations are accommodated by the large-scale field study. Active clam farms show integrated changes over the entire length of the tenure. While the spatial difference between a farm and reference site is sometimes a poor surrogate for time, the costs in time and resources of such a study make it more efficient than an experiment at the same scale. Results of this field study show no noticeable differences between farm and reference sites as a whole, but do indicate regional differences among reference sites, which are noticeably smaller among farm sites. Once again, effects at different spatial scales are evident in the data.

This is consistent with a growing body of theory regarding processes affecting marine benthic ecology. Direct, exploitative competition may be relatively unimportant in structuring marine soft-bottom communities (Black and Peterson 1988, Peterson 1992). Habitat heterogeneity, caused by biotic or abiotic processes, may act at the smallest scales, creating random patchiness and variability within a community (Peterson 1984, Posey 1986, Seitz *et al.* 2001, Summerson and Peterson 1984). Predation, as a top-down process, may be most important and evident at intermediate scales, but nutrient dynamics and other bottom-up limitations may dominate at larger scales (Posey *et al.* 2002). Regional differences in the field study, and site differences in the netting experiment are likely the result of differences in either bottom-up or top-down effects. The challenge remains in determining which factor is most relevant, and the absolute size of each scale. In either case, predation does not appear to be a limiting factor at any scale included in the research presented here.

The results of the field study indicate that farming practices, including seeding and netting, may only affect communities at spatial scales larger than even the largest single tenure included in the study. If clam farming is a homogenizing force at large scales, then the most important impact of clam aquaculture would be as a result of smaller, cumulative impacts of several tenures within a given geographical area. For example, if a species is not self-sustaining on sites used for clam aquaculture, but maintained only by the constant influx of larvae from other sites, then large-scale farming may have the potential to affect meta-populations that are relatively unaffected by smaller areas of aquaculture.

There remains a large level of uncertainty regarding impacts of individual practices, or indeed the mechanisms underlying many of the results presented here. Nevertheless, there are clear implications for the management of coastal biological resources in British Columbia, Canada. Given the potential for unknown, large-scale cumulative impacts and the possibility for site-specific responses to farming practices, I would recommend that regulatory efforts focus on baseline data-collection, monitoring and site-selection at the regional scale.

Specific areas of high biodiversity, or uncommon habitats that support endemic species and communities, may be the most susceptible to negative changes resulting from aquaculture activities. Such areas should be identified and protected, in light of the uncertainty surrounding impacts of aquaculture practices. The shellfish aquaculture industry has supported a provincially-enforced standard code of practices to limit impacts at individual sites (BCSGA 2003), but only the government agencies responsible for site approvals are in a position to adequately monitor and control how aquaculture is distributed within regions. The results presented here suggest that this is the scale at which impacts are most likely.

Cumulative impacts resulting from a homogenizing force of clam farming could be most likely if sites are clustered closer together, leading to greater effects to large-scale processes. A precautionary approach therefore suggests spreading out aquaculture sites, rather than clustering several adjacent sites within a single geographic area.

5.0 SUMMARY AND CONCLUSIONS

Shellfish aquaculture has the potential to grow into an economically important industry in British Columbia, Canada. Nevertheless, very little is known about the potential impacts to the environment or biotic resources, particularly to non-target species, which share the same habitat and resources as commercially important species. Research presented here has focused on the common clam farming practices of seeding the intertidal with juvenile *Venerupis philippinarum*, and covering these areas with protective netting.

The intent of the nets is often to exclude large, epibenthic predators, which are believed to significantly deplete populations of commercially important bivalve species, such as *V. philippinarum*. Recent studies of predator exclusion in marine soft-bottom habitats have suggested that predation does not play a major role in structuring communities, but it can limit prey population sizes.

Competition has also been infrequently considered an important determinant of community structure in this environment, although it may lead to patchiness within a community. Intraspecific competition appears to be stronger in soft-bottom communities, primarily affecting growth rates of individuals, and being more common in the presence of stressful abiotic conditions. Nutrient dynamics and food availability have been found to be important at large regional scales, but only occasionally seem to lead to significant intraspecific competition at local scales. The most common factor affecting community structure in marine soft-bottom habitats appears to be abiotic environmental conditions such as sediment size, temperature, and desiccation determined by tidal elevation. Factors such as competition and predation may only affect the tidal elevation or spatial distribution of some populations, while being otherwise largely insignificant to community structure at the local scale.

The results of both a small-scale netting experiment, and a large-scale field study of clam tenures is consistent with these hypotheses. Very few predicted results of predator exclusion were observed under netted areas, either in terms of density, biomass, or community composition. This suggests that either predation is not limiting at the sites sampled, or that the nets do not effectively alter predator pressure. Most variation in the data could be explained by tidal elevation, or even more importantly, by large-scale differences between sites or regions, likely caused by differences in environmental conditions. This also agrees with other studies of the effects of aquaculture netting, which found changes in community structure attributable primarily to increased sedimentation caused by the physical structure of the netting, rather than any effect of predator exclusion.

There were few consistent differences in bivalve communities between active clam tenures using seeding and netting, and paired reference sites. Although there were few site-level differences, there was an increase in overall similarity among farm sites, leading to a decrease in regional distinctness otherwise evident among reference sites. The implications of increased similarity between sites are of greatest concern to large-scale processes. If clam farming sites become increasingly dominated by commercial species, there are also implications for ecosystem functions, such as nutrient cycling.

The results also suggest that sites may respond differently to farming practices, with some benefiting from increased structural heterogeneity, and others losing endemic or rare species to the possible homogenizing effects of aquaculture. This leads to the recommendation that the process of locating and approving sites for clam aquaculture should consider sites in a regional context, in addition to local site criteria. A precautionary approach suggests preventing clam aquaculture sites from being too clustered, thereby limiting possible unforeseen cumulative impacts.

APPENDIX A:
SEDIMENT CLASSIFICATION

(After Wentworth 1922)

Size (mm)		**Wentworth Size Class**		**Descriptive Size Class (for this project)**
[Solid Rock] 4096				Rock shelf
256		Boulder	*Gravel*	Rocky
64		Cobble		Cobble
4		Pebble		Gravel
2	.00	Granule		
1	.00	Very Coarse	*Sand*	Sand
1/2	.5	Coarse		
1/4	.25	Medium		
1/8	.125	Fine		
1/16	.0625	Very Fine		
1/32	.031	Coarse	*Silt*	Silt
1/64	.0156	Medium		
1/128	.0078	Fine		
1/256	.0039	Very Fine		
	.00006	Clay		Clay

APPENDIX B: EFFECT OF SIEVE MESH SIZE

After the first major field season in this project during the summer of 2003, the field sampling methods were re-examined in order to increase the speed and efficiency of data collection. The major limitation in collecting data for this project was time.

Coastal British Columbia, Canada typically has one suitable tidal cycle with the lowest low of the day, allowing 6 – 10 hours exposure for areas below 2 m above chart datum, which is the upper limit of the "low" strata used in this research. In addition, the summer field season only allows a limited number of days with tides low enough to allow such sampling, usually 10 days of every 2 week period. Because tidal cycles themselves oscillate over this time, the lowest tides, and longest sampling days, are in the middle of this 10 day period, while the first and last are the shortest sampling days.

As a consequence of these time constraints, there are a maximal number of quadrats that can be sampled in the season, and the only way to increase this number is to reduce the amount of time required for each quadrat. Although sample sizes seemed to be adequate at each site, no new sites were expected to be included in subsequent sampling efforts, and so to increase power it was deemed that increasing sampling effort at existing sites would increase precision at each site, and hopefully reduce unexplained variation. The sampling procedure described in the Methods section of this work (see above) was intended to capture as much information as possible, but a desire to reduce the time per sample led to a re-examination of the benefits, in terms of information content, of the smaller sieve. Experience in the field indicated that material from a smaller (0.25 x 0.25 m) quadrat sifted through a 1 mm sieve required as much time to process as material in the larger quadrat (0.5 x 0.5 m), sifted through a 6 mm mesh sieve. Time data is not available for each sieve size, but this generality is based on personal experience, and the fact that the 1 mm mesh sieve allows very little sediment to pass through, leaving a large proportion to sift through by hand to locate and count macrofauna, even after pre-sieving with a 6 mm mesh.

Methods & Analysis

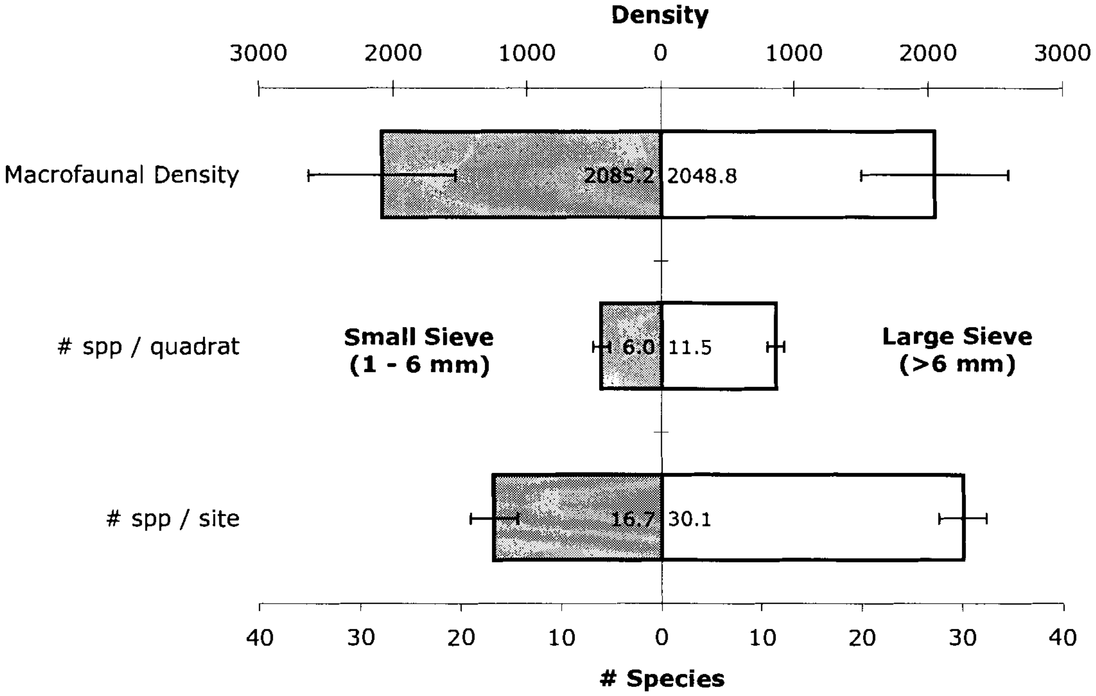
Results presented here include data from 28 sites sampled (14 pairs) in mid and low intertidal areas, from 3 regions in B.C.: Barkley Sound, Baynes Sound, and Okeover Inlet in Desolation Sound. Most sites were sampled with 18 quadrats, although some included only 12 quadrats (see Methods, above for details on sample sizes and site characteristics). All observed macrofaunal species were included in the analysis of the effect of mesh size on results.

It is important to note in the results that counts from the small sieve include only those individuals retained by a 1 mm mesh, and not those retained by the 6 mm mesh. Counts from the large sieve include all individuals retained by a 6 mm mesh, including those from within the subsample that was also sieved through a 1 mm mesh afterward. Because the small quadrat (0.25 m x 0.25 m) was used to sample sediment for the smaller sieve, counts (# individuals) are normalized to the same area as the large quadrat, usually by converting both to individuals$\cdot$m^{-2}. Occasionally, some abundant surface individuals were recorded only in the small quadrat, to help speed up data collection, and some counts may have been accidentally recorded in the incorrect list by field assistants, but this is assumed to be negligible. If anything, it would mean that the number of individuals and species in the small sieve reported here are slightly overestimated.

Mean densities per site were calculated using all quadrat samples at each site. The number of species observed was noted for pooled quadrats at each site, and as a mean per quadrat at each site. Means of each of these values over all sites were plotted on graphs, although to calculate statistical significance, the difference between large and small sieve values at each site were analyzed as a paired t-test.

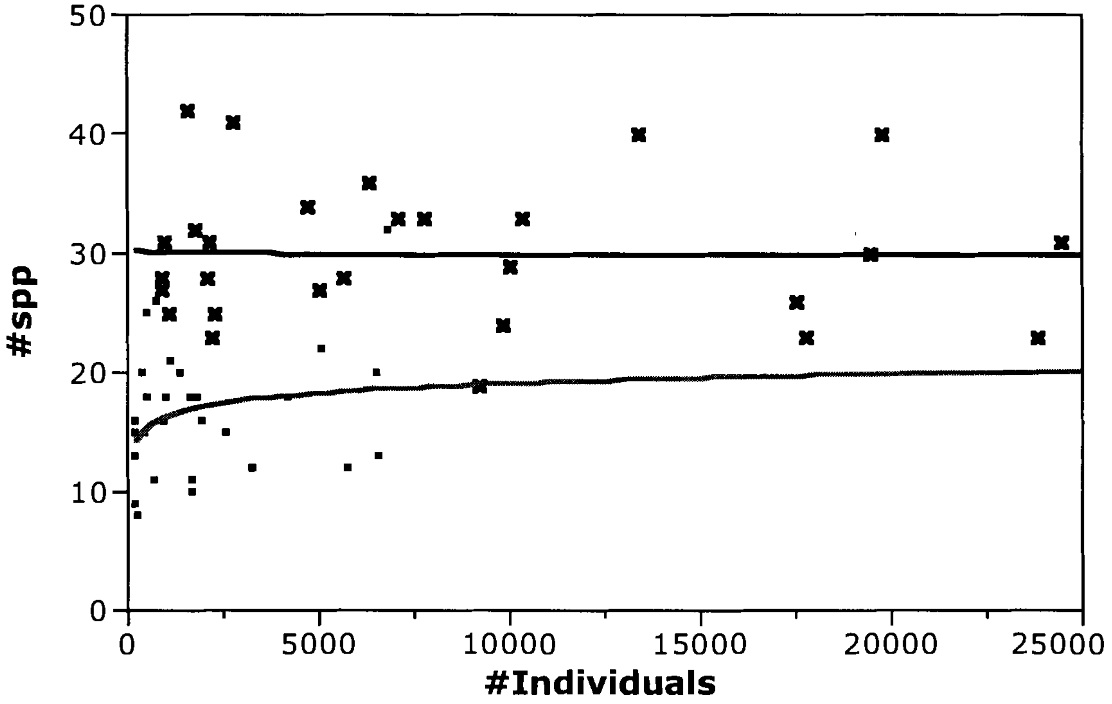
Results and Discussion

Figure 11. Macrofaunal density (individuals·m^{-2}), species richness per sample (quadrat) and per site for large and small sieve samples. Results from the small sieve (1 mm mesh) are plotted on the left side, in grey, with results from the large sieve (6 mm mesh) on the right, in white. Values represent means across all sites with 95% confidence intervals (error bars).



Macrofaunal density and observed number of species are compared between sieve sizes in Figure 11. The density of macrofaunal individuals was no different between sieve sizes, correcting for differences in the area sampled (mean difference Large – small = –9.1 ±56.1 individuals·m^{-2}). However, significantly fewer species were observed in the smaller sieve at each quadrat and site. On average, 13.4 (±2.0) fewer species were observed in the small sieve at each site, and 5.5 (±0.7) fewer species in each quadrat.

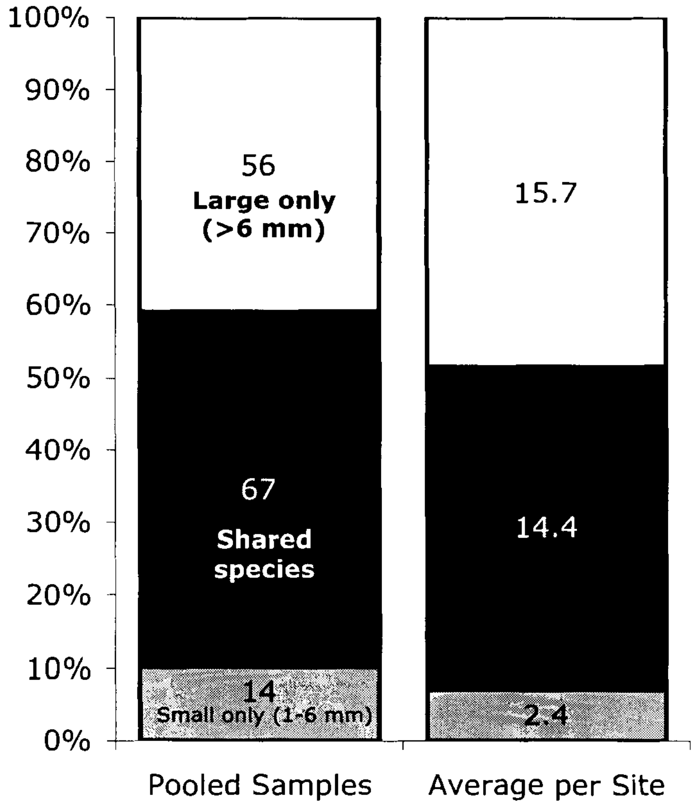
Figure 12. Number of species observed at a site as a function of the number of individuals in the pooled sample. Values from the large sieve (6 mm mesh) are plotted as X's and values from the small sieve (1 mm mesh) as dots. The lines are logistic regressions of #spp on ln(#individuals): large in black, small in grey.



Given that the same density of individuals only included half the number of species, it appears that the small sieve revealed fewer species for the same sampling effort. The densities are normalized for area, but the number of observed species is not. Therefore, observed species were plotted against actual observed number of individuals, pooled at each site, for large and small sieves (see Figure 12). Despite the variation between sites, it is apparent that over the range of similar number of individuals counted (sampling effort), the smaller sieve yields approximately 10 fewer species than the equivalent sampling effort in the large sieve.

Although it is clear that fewer species are observed in the small sieve, this does not indicate the significance of this information. If 16 species at each site were only found within the small sieve, this might represent a significant loss of information. However, only 2.4 species on average were unique to the small sieve, representing fewer than 10 percent of species observed at a site (see Figure 13). Within the entire pooled dataset, 14 of the 137 species observed were exclusively found within the small sieve. Of the remaining species, approximately half overall, and the same proportion at each site, were found in both the large and small sieves.

Figure 13. Shared species between large and small sieves in pooled sample (over all sites) and averaged per site. Number of species shown as values in each bar.



Densities of these shared species are compared in Figure 14. Species falling above the line on the graph are denser in the large sieve, while those below are higher in density in the small sieve. Of the 67 species found in both the large and small sieves within the overall dataset, 37 were more abundant in the large than the small sieve, representing 55.2% of these species. Densities and names of species more abundant in the small sieve are listed in Table 16.

Figure 14. Number of individuals per species in the large versus small sieves (67 shared species only). Values are averaged over all sites, converted to #individuals·m^{-2}, and plotted on a log-log scale to scatter points and include the large range of values.

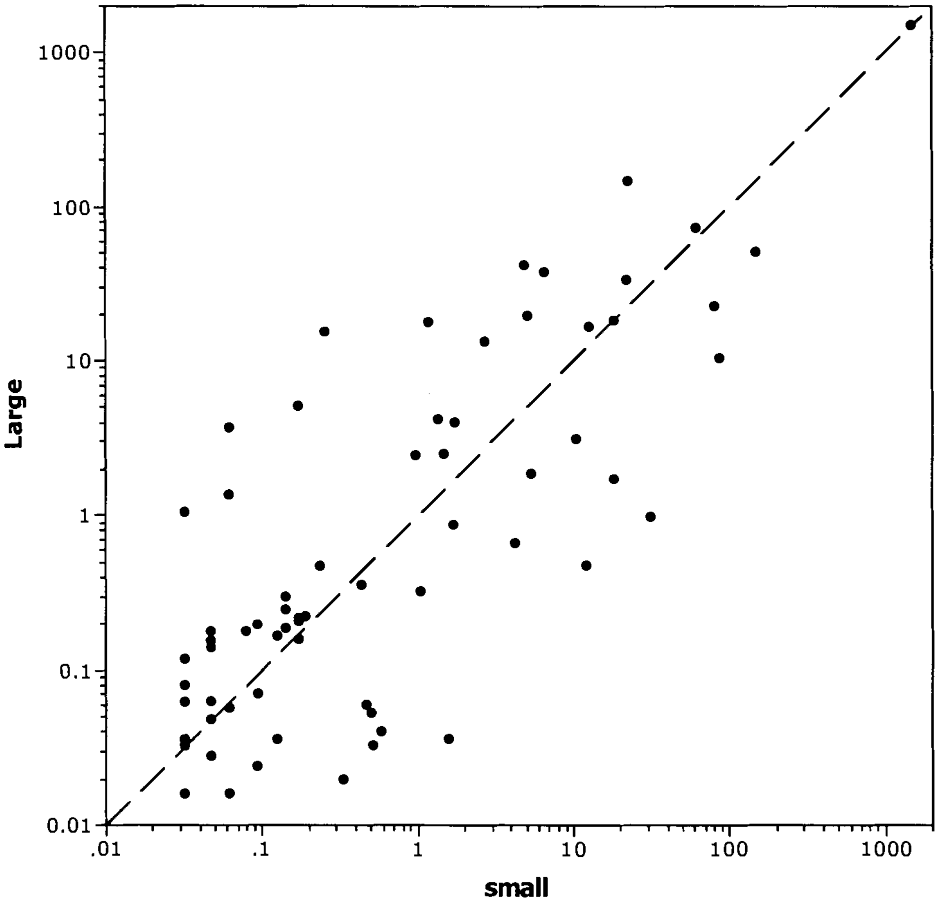


Table 16. Densities of species more abundant in small sieve (1 mm mesh) than the large.

Species	Mean Density in Large sieve (individuals·m^{-2})	Mean Density in small sieve /quadrat (individuals·m^{-2})
Alia carinata	0.020	0.333
Betaeus harrimani	0.357	0.444
Bittium eschrichtii	0.052	0.508
Haminoea vesicula	0.321	1.048
Hemigrapsus nudus	0.659	4.302
Hemigrapsus oregonensis	50.254	152.222
Heptocarpus sitchensis	0.060	0.476
Kaburakia exelsa	0.071	0.095
Littorina scutulata	10.258	88.889
Littorina sitkana	3.083	10.603
Macoma balthica	18.000	18.413
Nucella emarginata	0.008	0.032
Pagurus granosimanus	0.861	1.714
Pagurus hirsutiusculus	1.714	18.397
Pugettia producta	0.028	0.048
Scleroplax granulata	1.853	5.492
Spirorbis sp.	0.992	31.619
Tectura persona	22.552	82.016
Tectura scutum	0.159	0.175
Tonicella sp.	0.016	0.032
Unidentified Amphipoda sp.	0.468	12.175
Unidentified Idoteidae sp.	0.040	0.587
Unidentified Nematoda sp.	0.036	1.587
Unidentified Nematoda sp. (2)	0.036	0.127
Unidentified Polychaetae sp.	0.024	0.095
Unidentified Polynoidae sp.	0.016	0.063
Unidentified sand tube worm	0.056	0.063
Unidentified tube worm	0.032	0.524

Species observed exclusively in small sieve:

Balanus balanoides
Caridae sp.
Chthamalus dalli
Nutricola tantilla
Tellina modesta
Unidentified Annelida sp.
Unidentified Bivalve spp.
Unidentified clam sp.
Unidentified Nematoda sp. (3)
Unidentified Nematoda sp. (yellow)
Unidentified worm sp.
Unidentified worm (b)
Unidentified worm (c)
Unidentified worm (s)

Conclusion

If about half of all observed species are common to both sieves, and half of those shared species are more abundant in the large sieve, then the large sieve includes a significant sample of over three-quarters of the species sampled. By using only a 6 mm mesh and not a 1 mm mesh sieve, fewer than 10% of the species would not be counted, and only 25% of those observed would be under-represented. Considering the equal time required and the lower information content, the small sieve appears to be much less efficient than the larger one, at least in terms of information gain per unit sampling effort and time. I propose that the increased precision achievable with more samples at each site using only the large sieve can be more useful than more detailed information with fewer samples, using a 1 mm mesh sieve.

APPENDIX C:
DATA MATRIXES

Included here are the raw data matrices used in the multivariate community analyses. Replicates (sites) are listed as rows and species as columns. Table 17 shows average density per square metre (# individuals·m^{-2}) for infaunal bivalves species in the field study. Table 18 shows biomass data for the same species, in total g·m^{-2}. Because biomass data was collected at only one of every three quadrats sampled for count data, not all species in the density data are represented in the biomass data. Sites in both these matrices are labelled as follows: The first letter indicates the region (A = Baynes, B = Barkley, D = Desolation), this is followed by a sequential number to identify each site within the region, a lower-case letter indicates the tide height stratum of the site (l = low, m = mid), and the final digit indicates the treatment group of the site (1 = farm, 0 = reference). For example, A1l1 is a site in Baynes Sound (A1), in the low stratum, and is a farm site.

Table 19 presents pooled count data from the small-scale netting experiment, where each value is a total of counts in each plot. Because sample sizes were equal across all plots, there was no need to correct for differences in sampling intensity. These values may be converted to mean density by dividing by the number of quadrats per plot (5) and scaling up to 1 m^2 (x4): multiply each value by 0.8 ($^4/_5$). Plots in the netting experiment are labelled with an abbreviated location name (Bub, Hin, Roy), followed by a dash, then the tide stratum identifier (A or B), treatment (1 = net, 0 = control), and another dash separates the sampling period of the sample (0, 1, 2). For example, Bub-A0-0 is site Bub, stratum 'A' control plot at time 0 (baseline data).

Species that were omitted from the multivariate analysis are included here, but their names are highlighted in bold.

Table 17. Density data matrix (mean # individuals·m^{-2}) for field study (Bivalve community).

Site	*Axinopsida serricata*	*Clinocardium nuttallii*	*Cryptomya californica*	*Diplodonta impolita*	*Macoma balthica*	*Macoma expansa*	*Macoma inquinata*	*Macoma nasuta*	*Macoma obliqua*	*Macoma* sp.	*Mya arenaria*	*Nutricola tantilla*	*Nuttallia obscurata*	*Parvalucina tenuisculpta*
A1l1			19.0		61.0		39.7	60.3	0.7	1.3	3.		8.7	
A1l0		0.7	1.0		5.0		9.3	58.0		3.7	1.7			0.7
A1m1			23.7		58.0		3.7	41.7	0.3		.3		6.7	
A1m0		0.3	4.7		54.0		10.	116.7	1.7		4.		3.3	0.7
A2l1			63.6		8.7		13.8	6.7	1.8		1.1			
A2l0			41.6		86.7		0.2	2.0	1.6	0.2	4.2		55.1	
A4m1			1.8		3.8		7.8						2.2	
A4m0			0.9		1.3		7.1	8.7			1.8	11.6		1.8
B1l1		0.2	8.2		181.3			1.6			40.7		0.7	
B1l0			0.7		164.2		1.8	40.4			16.9			
B2l1			15.3		115.8		4.4	2.4			4.4			
B2l0			25.1		103.8		0.2				30.0		7.3	
D1m1			13.1		14.4		1.1	1.6			4.0		7.8	
D1m0	0.2		0.4		1.8		0.9	0.2	0.4		0.4		15.6	
D2m1			30.9		27.8		2.2	26.7	0.2		0.9		0.2	
D2m0			12.7		24.7		0.7	0.4			5.8		227.3	
Sites with varying treatment combinations (seeded without nets - omitted):														
A3m1			2.2	0.4	0.2		9.8	0.4			2.7		3.8	
A3m0			12.9		1.1		2.7		0.2		0.2	0.9	6.7	
B3l1			6.2		22.4	1.1	12.9	0.2			5.6		45.1	
B3l0		0.4	7.8		6.2	7.1	4.4	1.1			19.1		11.8	1.1
Pre-Farm Sites (all included as reference sites):														
A5l1		1.7	52.3		11.3		1.3	20.3			0.3			
A5l0		2.0	160.3		6.0		1.7	93.0		2.7	3.0			1.3
A5m1			32.3		11.0		1.7	3.3		1.3	1.3		1.3	
A5m0		0.3	120.3		20.3		0.7	23.0			1.7		13.7	
D3l1			6.0		18.3		5.3	12.0	0.3		0.3		1.3	2.3
D3l0		0.7	4.0		10.0		1.3	0.3						0.3
D3m1			20.0								0.3		7.3	
D3m0			3.0		0.3		0.7				2.0		1.0	

Site	*Protothaca staminea*	*Pseudopythina rugifera*	*Rhamphidonta retifera*	*Saxidomus gigantea*	*Tellina carpenteri*	*Tellina modesta*	*Tresus capax*	*Venerupis philippinarum*	**Class Bivalvia**	**[Class Bivalvia] 1**	**[Class Bivalvia] 2**	**[Class Bivalvia] 3**	***Clinocardium* sp.**
A1l1	47.7	0.3		2.7				146.0				0.3	
A1l0	42.0			6.3	0.3			7.3					
A1m1	4.7	0.7						123.3					
A1m0	42.3	1.3		1.7				22.3					
A2l1	7.1	0.9						204.2					
A2l0	8.9	0.2	0.2					36.4					
A4m1	136.0							181.6					
A4m0	70.9			2.2				29.6	0.9				0.2
B1l1	31.1			0.2				481.3					
B1l0	2.0			0.2				56.9					
B2l1	10.2							409.6					
B2l0	14.7							64.7					
D1m1	61.1		0.4					731.6					
D1m0	108.9							228.4					
D2m1	42.2		1.8					415.6					
D2m0	33.6		0.9					356.7					
Sites with varying treatment combinations (seeded without nets - omitted):													
A3m1	55.8	0.2		1.8				182.0					
A3m0	72.4	0.2		3.8				169.6					
B3l1	20.2			2.0				246.9					
B3l0	88.4			5.8				34.9		1.8	0.4		
Pre-Farm Sites (all included as reference sites):													
A5l1	4.7	0.3		0.7				114.7					
A5l0	9.0			4.7				49.7					
A5m1	1.0	0.3						141.3					
A5m0	4.3	0.7	0.3	0.3				119.0					
D3l1	95.3		5.0	6.0		2.7	0.3	40.7					
D3l0	80.3		0.3	0.7				15.3					
D3m1	69.3		2.0	0.7				104.7					
D3m0	70.0							61.0					

Table 18. Biomass data matrix (mean g·m^{-2}) for field study (Bivalve community).

Site	*Macoma expansa*	*Macoma obliqua*	*Macoma* sp.	*Nutricola tantilla*	*Parvalucina tenuisculpta*	*Rhamphidonta retifera*	*Clinocardium nuttallii*	*Cryptomya californica*
B1l1							23.61	2.41
B1l0								
B2l1								3.75
B2l0								5.47
A2l1		1.81						18.58
A2l0		0.23	0.21					14.66
A1l1			2.27					4.93
A1l0					0.46		21.82	
A1m1								6.11
A1m0					0.30		56.70	0.90
A4m1								0.88
A4m0				0.09				0.45
D1m1								7.13
D1m0								
D2m1						0.20		1.00
D2m0								3.47
Sites with varying treatment combinations (seeded without nets - omitted):								
A3m1								.89
A3m0								3.43
B3l1	1.21							1.31
B3l0	0.35			0.01	0.13			0.41
Pre-Farm Sites (all included as reference sites):								
A5l1								14.00
A5l0							2.00	49.00
A5m1								16.00
A5m0						0.19	0.45	34.82
D3l1					0.10			0.60
D3l0							7.00	0.40
D3m1								2.40
D3m0								1.50

Site	*Macoma balthica*	*Macoma inquinata*	*Macoma nasuta*	*Mya arenaria*	*Nuttallia obscurata*	*Protothaca staminea*	*Saxidomus gigantea*	*Venerupis philippinarum*
B1I1	12.35		1.09	434.17	26.73	447.29		2028.29
B1I0	26.21	2.34	77.38	523.51		24.23	17.63	1292.36
B2I1	9.85	4.85	1.79	16.03		63.48		2167.28
B2I0	1.99			282.90	160.01	150.49		980.61
A2I1	0.65	3.03	0.87	23.61		31.05		762.76
A2I0	5.78		0.78	140.55	678.43	123.97		291.67
A1I1	7.02	87.94	81.87	152.91	42.17	1609.57	482.74	1409.27
A1I0	3.82	4.70	88.65	313.27		1194.44	481.48	67.56
A1m1	31.70		118.20		96.13	40.79		1159.48
A1m0	6.58	9.48	130.34	81.61	45.00	794.78	196.02	665.02
A4m1	10.52	34.75			55.99	1595.71		3045.47
A4m0		12.53	4.15	0.15		370.59		79.79
D1m1	1.27	0.73	12.67	15.33		351.33		3745.33
D1m0			2.67	12.00	117.33	786.00		3274.00
D2m1	0.07		144.67			348.00		2027.33
D2m0	3.67		6.67	155.33	1554.67	469.33		5648.00
Sites with varying treatment combinations (seeded without nets - omitted):								
A3m1		39.53		77.40	24.47	758.97	119.59	1529.17
A3m0	0.22				207.21	599.63	27.65	1051.07
B3I1	2.53	5.49	0.99	38.71	459.54	123.35	48.27	3227.30
B3I0		0.08		45.01	32.36	732.22	50.90	40.56
Pre-Farm Sites (all included as reference sites):								
A5I1			18.00			58.00	37.00	141.00
A5I0		1.00	167.00	478.00		224.00	137.00	94.00
A5m1	1.50	1.00		159.00		47.00		573.00
A5m0	1.40		2.91	182.38	33.81	59.52		394.18
D3I1	0.90	23.00	20.00	71.00		107.00	118.00	1.50
D3I0	0.50	13.30	6.00			1273.00	143.00	145.00
D3m1				11.00	0.20	661.00	287.00	78.10
D3m0		1.00		116.00		1104.00		1554.00

Table 19. Data matrix (pooled counts over 5 quadrats) for netting experiment.

Site	*Amphissa columbiana*	*Arctonoe vittata*	*Axiothella rubrocincta*	*Balanus glandula*	*Balcis micans*	*Batillaria cumingi*	*Betaeus harrimani*	*Chthamalus dalli*	*Clevelandia ios*	*Clinocardium nuttallii*	*Crassostrea gigas*
Bub-A0-0				39		65					1
Bub-A1-0				111		52					1
Bub-B0-0						5			1	5	
Bub-B1-0						5			1	1	
Hin-A0-0	1			3425		141		104			
Hin-A1-0	6			2871		151		12			
Hin-B0-0				859	3	7					
Hin-B1-0				858		7	2				
Roy-A0-0				383		41		1			
Roy-A1-0				1683		43		17	1		
Roy-B0-0				9		46	1				
Roy-B1-0				2		74	1		1		
Bub-A0-1						106	5		1		
Bub-A1-1				10		72	2		1		
Bub-B0-1			1	1		70			1		
Bub-B1-1						203	4		1		
Hin-A0-1				8582		63					
Hin-A1-1				1976		59					
Hin-B0-1				20705		6					
Hin-B1-1		1		1708		3	1				
Roy-A0-1				213		32					
Roy-A1-1				1127		29					
Roy-B0-1				32		33	2		1		
Roy-B1-1		1				90					
Bub-A0-2				85		104					3
Bub-A1-2				15		174	1				1
Bub-B0-2			3			3	4				
Bub-B1-2				45		86					
Hin-A0-2				2634		115		93			1
Hin-A1-2				5278		144		176			
Hin-B0-2				11692		36		184			
Hin-B1-2				1854		40		12			1
Roy-A0-2				239		53					
Roy-A1-2				1013		150		155			
Roy-B0-2				3		45	1				
Roy-B1-2						106	2				

Site	*Cryptomya californica*	*Glycera sp.*	*Gnorimosphaeroma sp.*	*Hemigrapsus nudus*	*Hemigrapsus oregonensis*	*Heptocarpus sp.*	*Idotea wosnesenskii*	*Lepidogobius lepidus*	*Lirabuccinum dirum*	*Littorina scutulata*	*Littorina sitkana*
Bub-A0-0	36	57			2				1		
Bub-A1-0	15	60			15				1	1	
Bub-B0-0	127	33									
Bub-B1-0	60	18									
Hin-A0-0	2	34		2	96		1		2	224	37
Hin-A1-0	1	50	1	6	108					168	15
Hin-B0-0	12	82		1	26					39	118
Hin-B1-0	11	146			21	1				15	4
Roy-A0-0	32	49			9					55	27
Roy-A1-0	1	57			17					81	48
Roy-B0-0	82	66			14						
Roy-B1-0	87	49		3	19						1
Bub-A0-1	26	37		1	16						
Bub-A1-1	30	67		5	53						
Bub-B0-1	73	38			15						
Bub-B1-1	131	23		9	37						
Hin-A0-1		26		3	68					868	151
Hin-A1-1	2	10		1	68					126	22
Hin-B0-1	14	57			38					108	23
Hin-B1-1	17	89		1	57					67	28
Roy-A0-1	23	56			24						2
Roy-A1-1	3	37		6	105					20	4
Roy-B0-1	138	36		2	17						
Roy-B1-1	124	41		4	38		1				
Bub-A0-2	15	32			8						2
Bub-A1-2	28	58			23						1
Bub-B0-2	64	13			9			3			
Bub-B1-2	105	10			26						
Hin-A0-2		9			29					542	51
Hin-A1-2	1	19			61					1020	83
Hin-B0-2	15	73			62					610	105
Hin-B1-2	3	40			48					671	49
Roy-A0-2	15	27			13					125	4
Roy-A1-2	2	17			19					254	12
Roy-B0-2	68	22			13						
Roy-B1-2	63	7			166			1			

Site	*Macoma balthica*	*Macoma inquinata*	*Macoma nasuta*	*Macoma obliqua*	*Modiolus rectus*	*Mya arenaria*	*Mytilus trossulus*	*Nassa mendicus*	*Neotrypaea californiensis*	*Nephtys sp.*	*Neanthes brandti*
Bub-A0-0	5		25			1					2
Bub-A1-0	6						1				1
Bub-B0-0	3	7	31			3				1	
Bub-B1-0	6	3	23			4			2		3
Hin-A0-0							9				1
Hin-A1-0	1	4	1	2			12		1		2
Hin-B0-0						1	1				
Hin-B1-0			2								3
Roy-A0-0	144					3	1				
Roy-A1-0	67					1	3				
Roy-B0-0	5	1	14				3			4	7
Roy-B1-0	2		11								3
Bub-A0-1	87		53					3			3
Bub-A1-1	93					1		2			1
Bub-B0-1	7	8	29	1		3			6	1	
Bub-B1-1	3	2	28					2	5		1
Hin-A0-1			1				12				
Hin-A1-1						1	9	1			
Hin-B0-1	1						3				2
Hin-B1-1							1				9
Roy-A0-1	127	26			2						
Roy-A1-1	50	26									
Roy-B0-1	7	1	20						2	1	2
Roy-B1-1	3	3	10		1	1				3	5
Bub-A0-2	9	2	80					5			3
Bub-A1-2	16	3						3			2
Bub-B0-2		7	23			5		2	1	2	1
Bub-B1-2	3		24			2					
Hin-A0-2							5	2			1
Hin-A1-2							10	2			1
Hin-B0-2							3	2		1	1
Hin-B1-2		2						1	3		2
Roy-A0-2	26	105				4				1	
Roy-A1-2		38			1	1					1
Roy-B0-2		1	16		1						4
Roy-B1-2		1	10		1					1	6

Site	*Nereis vexillosa*	*Nucella emarginata*	*Nuttallia obscurata*	*Pagurus granosimanus*	*Pagurus hirsutiusculus*	*Protothaca staminea*	*Pseudopythina rugifera*	*Pugettia producta*	*Rhamphidonta retifera*	*Saxidomus gigantea*	*Scleroplax granulata*
Bub-A0-0				1							1
Bub-A1-0			3		1		1		1		3
Bub-B0-0	1			1		8				5	2
Bub-B1-0						2					1
Hin-A0-0			15		2	49					
Hin-A1-0	1		3			17					
Hin-B0-0			7	1		39			3		
Hin-B1-0	1				1	62					6
Roy-A0-0			27								
Roy-A1-0			14								
Roy-B0-0						3					2
Roy-B1-0	1				1	1					2
Bub-A0-1	2										2
Bub-A1-1			2					1			2
Bub-B0-1	5		1		2		1			6	3
Bub-B1-1	1		4	10	113	6			1	2	3
Hin-A0-1	1		21	3	5	44					
Hin-A1-1	2				1	14					
Hin-B0-1			10			74					1
Hin-B1-1	1			19	44	90					4
Roy-A0-1	4		8								1
Roy-A1-1			13			3					
Roy-B0-1	8				1				1	1	3
Roy-B1-1	6				53	4	4				1
Bub-A0-2					1						1
Bub-A1-2	1		5								
Bub-B0-2	11					6				5	2
Bub-B1-2	7		1	7	11	5				1	1
Hin-A0-2	1	17	7			12					
Hin-A1-2		12	2		2	26					
Hin-B0-2	4	93	14	4	135	63					2
Hin-B1-2		18		3	112	44					1
Roy-A0-2	1	7	8								
Roy-A1-2		9	13								
Roy-B0-2	4										
Roy-B1-2	5						1				2

Site	*Semibalanus cariosus*	*Spirorbis* sp.	*Tectura persona*	*Tectura scutum*	*Tellina carpenteri*	*Upogebia pugettensis*	*Venerupis philippinarum*	Order Amphipoda	Phylum Nemertea	Phylum Phoronida	[Unidentified sand encrusted tube worm]
Bub-A0-0						16	130		9		
Bub-A1-0			4			20	147		6		
Bub-B0-0						24	71		18		
Bub-B1-0						22	74		14		
Hin-A0-0			46			3	276		23		
Hin-A1-0		1177	77	1		3	259	4	35		
Hin-B0-0			66			21	195	9	30		
Hin-B1-0		29	16			18	288		61		
Roy-A0-0						10	144	4	23		
Roy-A1-0							88	7	9		
Roy-B0-0						25	249		72		
Roy-B1-0						23	206	1	95		
Bub-A0-1						24	103		72		
Bub-A1-1						18	98		22		
Bub-B0-1					1	35	106		34	1	3
Bub-B1-1			1			25	144		5		3
Hin-A0-1			148			1	356	18	2		
Hin-A1-1			72			2	222	9	2		
Hin-B0-1			59			8	381	3	18		
Hin-B1-1			14			13	438	1	21		
Roy-A0-1						4	106		8		
Roy-A1-1							81		13		
Roy-B0-1						34	310		42		
Roy-B1-1						31	249	1	30		
Bub-A0-2						10	102		82		
Bub-A1-2			1			8	102		15		
Bub-B0-2						24	122		251		3
Bub-B1-2						15	179		186		1
Hin-A0-2			99	2		1	274		8		
Hin-A1-2			232	78		4	184	28	16		
Hin-B0-2			666	110		6	289	46	12		
Hin-B1-2	4		67	14		5	388	11	25		
Roy-A0-2						1	114		6		
Roy-A1-2						2	80	5	6		
Roy-B0-2						9	306		587		
Roy-B1-2						29	214		740		

APPENDIX D:
SPECIES LISTS

Field Study (Infaunal Bivalves)

ID Code*	Scientific Name	Common Name	Notes
clam1	[Class Bivalvia]1	unknown Clam sp.	Tiny, flat with shiny shell
clam2	[Class Bivalvia]2	unknown Clam sp.	Shiny, transparent shells
clam3	[Class Bivalvia]3	unknown Clam sp.	glossy, approx. 5 mm long
uclam	Class Bivalvia	unknown Clam spp.	
clisp	*Clinocardium* sp.	unknown cockle sp.	most likely *C. nuttallii*
axise	*Axinopsida serricata*	northern axinopsid	
clinu	*Clinocardium nuttallii*	Nuttall's cockle	
crcal	*Cryptomya californica*	california softshell	
diimp	*Diplodonta impolita*	rough diplodon	
macba	*Macoma balthica*	baltic macoma	
macex	*Macoma expansa*	expanded macoma	
macin	*Macoma inquinata*	pointed macoma	
macna	*Macoma nasuta*	bent-nose macoma	
macob	*Macoma obliqua*	oblique macoma	
macsp	*Macoma* sp.	unknown macoma clam	
myare	*Mya arenaria*	softshell clam	
nutan	*Nutricola tantilla*	purple dwarf-venus	
Nutob	*Nuttallia obscurata*	Varnish clam	
paten	*Parvalucina tenuisculpta*	fine-lined lucine	
PROst	*Protothaca staminea*	Pacific littleneck	
psrug	*Pseudopythina rugifera*	wrinkled montacutid	commensal clam on shrimp
rhret	*Rhamphidonta retifera*	netted kellyclam	provincially endangered
Sagig	*Saxidomus gigantea*	butter clam	
tecar	*Tellina carpenteri*	carpenter's tellin	
temod	*Tellina modesta*	plain tellin	
treca	*Tresus capax*	fat gaper	
VEPHI	*Venerupis philippinarum*	manila clam	

Netting Experiment (Macrofauna)

ID Code*	Scientific Name	Common Name & Notes	Habitat
tubes	[sand encrusted tube worm]	unidentified sand-encrusted tube worm	Other Infauna
amcol	*Amphissa columbiana*	wrinkled dove snail	Epifauna
arvit	*Arctonoe vittata*	commensal scaleworm	Epifauna
axrub	*Axiothella rubrocincta*	bamboo worm	Other Infauna
bagla	*Balanus glandula*	acorn barnacles	Epifauna
bamic	*Balcis micans*	shining balcis	Epifauna
bacum	*Batillaria cumingi*	mudflat snails	Epifauna
behar	*Betaeus harrimani*	northern hooded shrimp	Epifauna
chdal	*Chthamalus dalli*	little brown barnacle	Epifauna
clios	*Clevelandia ios*	little goby	Predatory Infauna
clinu	*Clinocardium nuttallii*	Nuttall's cockle	Bivalve (infauna)
CRAGI	*Crassostrea gigas*	pacific oyster	Bivalve (epifauna)
crcal	*Cryptomya californica*	california softshell	Bivalve (infauna)
glysp	*Glycera sp.*	blood worms	Predatory Infauna
gnori	*Gnorimosphaeroma* sp.	"pill bug"	Epifauna
henud	*Hemigrapsus nudus*	purple shore crab	Epifauna
heore	*Hemigrapsus oregonensis*	hairy shore crab	Epifauna
hepsp	*Heptocarpus* sp.	'broken-backed' shrimps	Epifauna
idowo	*Idotea wosnesenskii*	kelp isopod	Epifauna
leple	*Lepidogobius lepidus*	bay goby	Predatory Infauna
lidir	*Lirabuccinum dirum*	dire whelk	Epifauna
liscu	*Littorina scutulata*	checkered periwinkle	Epifauna
lisit	*Littorina sitkana*	sitka periwinkle	Epifauna
macba	*Macoma balthica*	baltic macoma	Bivalve (infauna)
macin	*Macoma inquinata*	pointed macoma	Bivalve (infauna)
macna	*Macoma nasuta*	bent-nose macoma	Bivalve (infauna)
macob	*Macoma obliqua*	oblique macoma	Bivalve (infauna)
morec	*Modiolus rectus*	straight horsemussel	Bivalve (epifauna)
myare	*Mya arenaria*	softshell clam	Bivalve (infauna)
mytro	*Mytilus trossulus*	edible (blue) Mussel	Bivalve (epifauna)
namen	*Nassa mendicus*	western lean nassa	Epifauna
necal	*Neotrypaea californiensis*	bay ghost shrimp	Other Infauna

ID Code*	Scientific Name	Common Name & Notes	Habitat
nepsp	*Nephtys* sp.	sand worm	Predatory Infauna
nebra	*Neanthes brandti*	large nereid worm	Other Infauna
nevex	*Nereis vexillosa*	clam worm	Other Infauna
nuema	*Nucella emarginata*	striped dogwinkle	Epifauna
Nutob	*Nuttallia obscurata*	varnish / dark-mahogany / Savory clam	Bivalve (infauna)
oramp	Order Amphipoda	Amphipods, beach hoppers, etc.	Epifauna
pagra	*Pagurus granosimanus*	granular hermit crab	Epifauna
pahir	*Pagurus hirsutiusculus*	hairy hermit crab	Epifauna
phnem	Phylum Nemertea	nemertean worms, nemertineans	Predatory Infauna
phpho	Phylum phoronida	horseshoe fanworms (encased burrows)	Other Infauna
PROst	*Protothaca staminea*	pacific littleneck	Bivalve (infauna)
psrug	*Pseudopythina rugifera*	wrinkled montacutid	Bivalve (infauna)
pupro	*Pugettia producta*	northern kelp crab	Epifauna
rhret	*Rhamphidonta retifera*	netted kellyclam	Bivalve (infauna)
Sagig	*Saxidomus gigantea*	butter clam	Bivalve (infauna)
scgra	*Scleroplax granulata*	burrow pea crab	Other Infauna
secar	*Semibalanus cariosus*	thatched barnacle	Epifauna
spisp	*Spirorbis* sp.	spiral tube worm	Epifauna
teper	*Tectura persona*	mask limpet	Epifauna
tescu	*Tectura scutum*	plate limpet	Epifauna
tecar	*Tellina carpenteri*	carpenter's tellin	Bivalve (infauna)
uppug	*Upogebia pugettensis*	blue mud shrimp	Other Infauna
VEPHI	*Venerupis philippinarum*	manila clam	Bivalve (infauna)

*Species ID Codes were used to simplify data recording in the field and to track species names in the computer database. A unique code was generated for each species encountered, as required.

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