

POPULATION BIOLOGY OF MUSSELS
(*Aulacomya maoriana*, *Mytilus galloprovincialis* and
***Perna canaliculus*) FROM ROCKY INTERTIDAL**
SHORES IN WELLINGTON HARBOUR,
NEW ZEALAND.

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Who Made Me?

The land that grew the roots

That grew me

And the sea that fed the fish and birds

That fed me

And the wind that drove the world

And knew me

And blew over all -

(Kerí Hulme, "Stonefish")

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ABSTRACT

This study examines the population ecology and dynamics of three co-existing mussel species (*Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*) in Wellington Harbour, New Zealand. The present study investigates the role of multiple environmental factors and their multiple effects on the intertidal mussel population. Wellington Harbour is a complex system, supporting speciose intertidal invertebrate communities. CTD data loggers recording seawater temperature, turbidity, chlorophyll *a* concentration and salinity at Evans Bay, Seatoun, Matiu-Somes Island and Petone provided the environmental data. The data suggest the existence of distinct zones within Wellington Harbour, with different hydrological regimes present at each zone. Consistently high salinity (35.08 ± 2.9 PSU) and chlorophyll *a* concentration ($9.42 \pm 4.33 \mu\text{g l}^{-1}$) were found at Evans Bay, while these parameters displayed a degree of temporal variation and were significantly lower at Seatoun (31.5 ± 4.17 PSU and $2.15 \pm 2.1 \mu\text{g l}^{-1}$) and Matiu-Somes Island (33.26 ± 0.99 PSU and $1.23 \pm 1.79 \mu\text{g l}^{-1}$). At Petone, a site located near the Hutt river mouth, salinities were reduced (31.59 ± 3.21 PSU) while chlorophyll *a* levels were similar to those at Matiu-Somes Island ($1.64 \pm 1.08 \mu\text{g l}^{-1}$). Mean turbidity values were similar at Seatoun and Evans Bay (11.51 ± 18.53 FTU and 11.89 ± 5.52 FTU, respectively), with mean turbidity slightly reduced at Petone (8.20 ± 11.16 FTU) and elevated at Matiu-Somes Island (15.35 ± 11.12 FTU). Further, CTD data revealed similar seawater temperature at all sites, with mean values oscillating around 13 - 15°C.

The ecology of larval stages was expressed in this study by quantifying the rates at which mussel larvae settled on the experimental substrate. A year-round spawning, as well as temporal and spatial variability in mussel recruitment at four experimental sites was revealed. Evans Bay was the site with consistently higher recruitment rates but not the mean recruit numbers (721 ± 879 larvae), while the highest number of recruits (9851 larvae) was recorded at Petone (1041 ± 2112 larvae). Recruitment rates were lower at Seatoun (729 ± 536 larvae) and Matiu-Somes Island (410 ± 636 larvae). However, only

at Seatoun was this variability clearly linked to the environmental conditions of water turbidity, chlorophyll *a* concentration, and salinity.

The post-larval ecology part of this study concentrates on the condition index and gonad mass, and the degree of infestation with a parasitic pea crab *Pinnotheres novaezelandiae* studied at four sites. Spatial and temporal variation in condition index and gonad mass was revealed in all three species investigated, with both condition index and gonad mass of adult mussels being highest at Matiu-Somes Island (14.59 ± 4.41 and 0.21 ± 0.16 g), followed by Kau Point (13.47 ± 6.99 and 0.17 ± 0.10 g), Seatoun (13.32 ± 7.79 and 0.11 ± 0.10 g) and Evans Bay (11.99 ± 2.78 and 0.14 ± 0.14 g). Condition index was significantly correlated with gonad mass, and was highest in *Aulacomya maoriana* (15.85 ± 9.38), followed by *Perna canaliculus* (12.52 ± 4.39) and *Mytilus galloprovincialis* (11.66 ± 5.91). The condition was generally reduced in mussels infested with the pea crab *Pinnotheres novaezelandiae*, although the overall infestation rate was low (3.28%).

In order to describe the pattern of mussel community development, patches of bare rock were experimentally created in the mid-intertidal zone. Subsequently, predator-exclusion cages were set up in those areas and monitored regularly. The abundance of main groups of intertidal taxa settling on the cleared substrate was expressed in terms of percent cover, and was highest at Evans Bay ($59.57 \pm 80.27\%$), lowest at Kau Point ($13.96 \pm 26.18\%$) and intermediate at Seatoun ($22.56 \pm 41.64\%$). However, the bottom-up factors were visibly linked to the community development at Seatoun. The full cage experimental treatment provided the maximum protection from predation and desiccation, therefore the community recovery was most pronounced under this treatment. *Mytilus galloprovincialis* was revealed as the most competitive mussel species, in some cases able to colonise the entire available substrate and exclude other two mussel species.

Further, seasonality of mussel response to wave action and desiccation was investigated. Mussel species-specific strength of attachment to the rocky substrate was

expressed in kg (effectively the force) required for the mussel to be removed from the rocky substrate at shores facing south and north in Wellington Harbour. The strength of attachment was highest in *Perna canaliculus* ($5.81 \text{ kg} \pm 2.27$), followed by *Aulacomya maoriana* ($3.63 \text{ kg} \pm 1.63$) and *Mytilus galloprovincialis* ($3.44 \text{ kg} \pm 1.70$). Mussel strength of attachment was generally higher at south-facing sites, due to stronger waves generated by southerly winds. In a separate experiment, in which mussels were exposed to air at six different shore levels within the intertidal zone, desiccation tolerance was highest in *Mytilus galloprovincialis* on the south-facing sites ($\text{LD}_{50}=0.62\text{m}$ and 0.87 for north- and south-facing sites, respectively), followed by *Aulacomya maoriana* ($\text{LD}_{50}=0.65$ and 0.75m for north- and south-facing sites, respectively) and *Perna canaliculus* ($\text{LD}_{50}=0.20$ and 0.35m for north- and south-facing sites, respectively). LD_{50} desiccation exposure values were lower in all three species found on the north-facing shores, indicating that mussels on those shores are less tolerant to desiccation-induced stress and therefore died more rapidly.

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CHAPTER ONE:

LINKING INTERTIDAL MUSSEL ECOLOGY AND THE WATER COLUMN

1.1. Factors affecting rocky intertidal assemblages

Filter-feeders, such as mussels, dominate the rocky intertidal zone worldwide. This can be attributed to two factors: access to various food resources and the low energetic cost of food capture (Gili & Coma, 1998; Ricciardi & Bourget, 1999). Filter-feeders have access to numerous food resources, including phytoplankton, detritus, bacteria and dissolved organic matter, that are produced in the three-dimensional pelagic environment and are continually replenished by tidal currents and wave action flowing over the attached invertebrates (Fréchette & Bourget, 1985). By contrast, grazers (e.g. limpets and chitons) utilise algal food that is produced in a relatively limited, two-dimensional space on the rocky surface and less frequently replenished (Bustamante *et al.*, 1995).

The intertidal zone represents a transition between marine and terrestrial environments, and is not therefore uniform in nature. Its vertical extent changes from day to day because of water movements associated with waves, sea spray and the varying height of the tides. Temperate rocky intertidal shores around the world have three distinct horizontal bands, the supra-littoral (the upper intertidal), the eulittoral (the mid-intertidal) and the sub-littoral (the lower intertidal). Each band is distinguished from those adjacent by a combination of morphology and dominant organisms. The vertical extent of rocky intertidal zones varies, depending on the exposure to wave action, the slope of the rocky surface and the tidal range. A gradual slope to the rock will produce broad individual zones, but on a vertical face, under conditions of similar wave and tidal exposure, the individual zones will be narrow. Similarly, as a result of the sea spray, intertidal zones are broader on exposed surfaces than on sheltered surfaces (Nybakken, 2001). Because of the constant water movement resulting from waves, spray and tides, the transition between

terrestrial and marine environments is gradual and creates a habitat in which emersion is stressful to fully marine organisms, while immersion is stressful to fully terrestrial organisms (Barnes & Hughes, 2002). Consequently, the organisms inhabiting the intertidal zone, such as mussels, must be able to cope with both elements in order to survive. For mussels, the distribution within the zone is dictated by how well they can withstand the changing physical and biological factors.

Physical factors

A number of physical factors, often working together, regulate the distribution of mussels in the intertidal zone. These factors include tidal range and exposure to wave action. Recently, latitude has also been suggested as an important factor in the structuring of intertidal mussel communities worldwide (e.g. Ricciardi & Bourget, 1999). Each of these factors is discussed in turn.

The tidal range is perhaps the single most important determinant of the upper distribution of mussels in the intertidal zone (Barnes & Hughes, 2002), as it involves exposure to air temperatures and consequently to desiccation stress and potentially harmful ultraviolet (UV) radiation. Because of fluctuations in tidal height, a very short vertical movement on the shore can result in significant changes in exposure time. Therefore, mussels growing higher on the rocky shore suffer longer emersion and reduced access to food (which in turn reduces feeding time), unlike mussels living lower in the intertidal zone, where the total immersion time, food availability and protection from air temperatures are greater. Longer intervals between the full immersion periods force mussels to utilise greater amounts of stored energy in order to meet their metabolic requirements, which results in reduced mussel growth. Further, mussels exposed to air suffer from desiccation and have to expend more energy in order to repair their tissues damaged by the water loss caused by heat.

Wave exposure has been proposed as another limiting factor for intertidal mussel communities. Ricciardi & Bourget (1999) report that the biomass of filter-feeding

communities, including mussels, is higher on exposed (rather than sheltered) rocky shores. Exposed shores host high-density populations of filter-feeders (mussels, barnacles and ascidians), while sheltered rocky shores are dominated by macroalgae and grazers (e.g. limpets and chitons) (McQuaid & Branch, 1984, 1985). Increased exposure to wave action leads to an increase in food availability and feeding time for mussels and subsequently to their greater abundance and increased growth (Dahlhoff & Menge, 1996). Moreover, under conditions of high wave exposure, other members of intertidal communities such as mobile consumers (carnivores, scavengers and grazers) are limited in their foraging, unless they have access to rock crevices that can act as refugia, which may contribute to mussel dominance of the rocky intertidal (Lubchenco & Menge, 1978; Burrows & Hughes, 1989).

Physical disturbance by intense wave action, scouring ice or floating logs can severely reduce and alter intertidal mussel communities. Propelled by waves, floating logs pound against the community and can dislodge significant numbers of mussels, creating patches of bare substrate among the competitive dominants. This is further intensified by wave action, often removing individual mussels from the edges of a colony. The space that has suddenly become available is quickly recolonised by other recruiting species, which adds to the species diversity. Ice scour can create very harsh conditions, forcing the members of intertidal communities to retreat to rock crevices. Bergeron & Bourget (1986) report typical intertidal zonation inside such crevices, where the upper part is devoid of organisms, the middle part hosts barnacles and fucoid algae, with mussels found in the lower part. Carroll & Higsmith (1996) describe how ice disturbance can alter the balance between mussels and their predators in the upper intertidal zone. As the mussels *Mytilus trossulus* recolonised space from which they had previously been removed by ice, the predatory whelk *Nucella lima* preyed upon the juvenile mussels. While *N. lima* was previously unable to control adult *M. trossulus*, it was suddenly able to control the juveniles and thus the predator-prey balance was changed.

Finally, high exposure to wave action can result in the increased load of sediment brought into the community by waves. Sediments accumulating on rocky substrata cause stress and burial of mussels, resulting in hypoxic conditions and subsequent death. Further, increased sedimentation can lead to scour of the substrate, which has negative effect of larval settlement and recruitment to intertidal communities (Airoidi, 2003).

Latitude is another factor regulating intertidal mussel communities. From a global perspective, temperate intertidal mussel communities (25-60°N and 25-60°S) have a greater biomass (expressed as ash-free dry weight, ASDW) when compared with intertidal communities from tropical (25°N-25°S) and polar (>60°N and >60°S) regions (Ricciardi & Bourget, 1999). The low biomass of intertidal mussel communities in polar latitudes might be a result of unfavourable factors such as freezing temperatures and ice scouring (Bergeron & Bourget, 1986), whereas in tropical regions rocky intertidal communities experience severe desiccation, hypoxic and salinity stress (Lubchenco *et al.*, 1984; Menge *et al.*, 1986). In tropical regions, primary phytoplankton production is continuous and in phase with pelagic herbivore production, and thus the transfer of energy to benthic levels is reduced, whereas in temperate latitudes this primary production is seasonal and generates an enormous amount of phytoplankton. A substantial part of this phytoplankton production in temperate regions subsequently avoids being consumed by zooplankton and is thus more readily available to benthic consumers, in particular mussels (Ricciardi & Bourget, 1999). Mussel biomass in temperate regions is further increased by the substantial input of organic detritus from kelp beds in winter, when phytoplankton production is low (Bustamante & Branch, 1996).

Biological factors

Biological factors (e.g. interspecific competition, intraspecific competition and predation) play a major role in the distribution patterns of mussels in the rocky intertidal zone. Typically, mussels densely populate temperate rocky shores. Because the major resources (such as space and food) available to mussels in the intertidal zone are limited,

competition for those resources among the members of the intertidal communities is inevitable. Mussels can compete for the resources with other species (interspecific competition) or the competition for resources can occur among individuals within the same mussel species (intraspecific competition). Mussels are dominant competitors, they are able to exploit their resources, quickly outcompete other competitors, dominate the available space and ultimately reduce the species diversity on the rocky substrate. According to the species diversity competition hypothesis proposed by Sanders (1968), interspecific competition favours increased specialisation of species and helps to reduce the intensity of the competition, provided that the environment is stable for a sufficient period of time. This situation leads to the inclusion of new species in the intertidal community and thus to an increase in species diversity (Mann, 2000). However, the inclusion of new species in the community can have adverse and unpredictable effects. The accidental introduction of the mussel *Mytilus galloprovincialis* on the west coast of South Africa has almost eliminated the slower-growing indigenous mussel *Aulacomys ater*. The former is now spreading east, where it is likely to become competitive with the native mussel *Perna perna* (Griffiths *et al.*, 1992). The fact that *P. perna* is heavily infested with a trematode *Proctoeces*, while *M. galloprovincialis* is free of this parasite, may give the latter a competitive advantage and eventually lead to displacement of the native *P. perna* from the higher intertidal (Calvo-Ugarteburu & McQuaid, 1998).

Predation is another important factor determining the abundance and distribution of mussels in the intertidal zone. Various studies (e.g. Paine, 1966; Dayton, 1971; Menge & Sutherland, 1976; Menge *et al.*, 1994) show that predators (such as starfish) can maintain the numbers of mussels at low levels, thus preventing the exclusion of algal and other invertebrate species from the habitat. The major mussel predators include starfish, gastropods, crabs (although crabs are limited to the lower intertidal) and birds. Predation by starfish acts in a fashion similar to that of physical disturbance: starfish can create breaks in the mussel cover, thus providing free space for other species to colonise and preventing mussels from taking over the habitat, and eventually providing conditions for species diversity within the community (Menge & Sutherland, 1976). Starfish either open the mussel shell with their arms and tubular feet, then evert their stomach to engulf the

mussel and digest its tissues, or they secrete an anaesthetic that numbs the mussel, causing it to gape.

Gastropods are also significant predators on mussels and choose their prey on the basis of profitability (i.e. the potential energy gain from a food item relative to handling time), which increases with prey size. Seed (1969) reports that gastropods can consume up to two mussels (1-3cm in shell length) per week in summer, at the height of their predatory activity. Gastropods can drill a hole in the mussel shell, rasp the tissues with their radula and then devour them, or inject paralysing toxins with a proboscis through the gape in the mussel shell and then consume their prey.

Typically, three crab genera prey on mussels in the lower intertidal and subtidal zone: *Cancer*, *Carcinus* and *Pachygrapsus*. Crab predation on mussels is seasonal, with reduced intensity in winter, when crabs migrate offshore. Like gastropods, crabs select their prey size, with the upper limit directly related to the size of the crab, and normally choose small mussels (<45 mm) because these are easier to handle, while the energetic cost of handling is also lower (Rovero *et al*, 2000). Crabs crush mussel shells with their claws.

The most important bird group preying on mussels includes oystercatchers *Haematopus* spp. and Eider ducks *Somateria* spp. Oystercatchers prey extensively on mussels and cannot normally survive if their diet is limited to one or two species, and generally rely on three or four species (Gosling, 2003). Similarly, mussels constitute as much as 60% of the dietary requirements of Eider ducks, which can remove significant numbers of individuals from a mussel clump (Gosling, 2003). Birds open mussels by stabbing into gaping mussels, prising open closed ones or by hammering a hole in the dorsal or ventral regions of the shell (Gosscustard *et al.*, 1993; Nehls & Ruth, 1994).

In the course of evolution, however, mussels have developed specific mechanisms designed to protect them from predators. Dolmer (1998) reports that starfish can prey only on the surface of the mussel bed and that smaller mussels find refuge from predators

inside the bed. Moreover, predator-exposed mussels have thicker shells and stronger adductor muscles (Reimer & Tedegren, 1996). Similarly, mussels exposed to heavy predation from crabs develop more robust shells and thicker byssus (Cote, 1995; Leonard *et al.*, 1999). Further, Norberg & Tedengren (1995) report that not all mussels are equally vulnerable to starfish predation. According to the authors, 70% of *Mytilus edulis* in the North Sea were able to escape predation from the starfish *Asterias rubens*, while *M. edulis* from the Baltic Sea were opened within an hour.

Case studies performed by Dayton (1971) and Paine (1966, 1974) can serve as examples demonstrating the subtle interplay between biological factors (such as competition and predation) in the intertidal mussel beds on the Washington coast. Whenever an open space occurred, it was first colonised by rapidly growing algae, which were in turn displaced by the barnacles *Balanus gladula*, *B. cariosus* and *Pollicipes polymerus*, which in turn were eventually smothered by the mussel *Mytilus californianus*. Because no other organism can settle and smother *M. californianus*, these mussels dominate the intertidal shore and grow there in distinct horizontal bands, while being absent in the subtidal zone, where the starfish *Pisaster ochraceus* controls them. This voracious predator is able to consume *M. californianus* in numbers large enough to prevent the mussels from monopolising all the available space; therefore it has been shown as capable of influencing the entire community structure. As such, *P. ochraceus* can be regarded as a keystone species (Paine, 1966).

1.2. Benthic-pelagic coupling

The term “benthic-pelagic coupling” has been used to describe numerous interactions between benthic invertebrate communities and the nearshore water environment, including the physics of the coastal waters, life history of the coastal species, larval supply, settlement and recruitment, and nutrient cycling between bivalve communities and the water column (Dame *et al.*, 1989; Schiel, 2004).

The importance of larval supply

Traditionally, temperate rocky intertidal communities have been viewed as the outcome of physical and biological factors discussed above (Dayton, 1971; Connell, 1972; Paine, 1974; Peterson, 1979). Recently, however, intertidal communities have been shown to depend heavily on the influence of physical oceanography through the transport and dispersal of invertebrate larvae (Shanks, 1995; Harris *et al.*, 1998; Mann, 2000; Swearer *et al.*, 2002). Advective processes in coastal systems leading to significant larval dispersal ultimately affect larval recruitment to intertidal communities. This, in turn, is crucial to the subsequent population dynamics of the intertidal system (Botsford *et al.*, 1994, 1998; Young, 1995; Pineda, 1999).

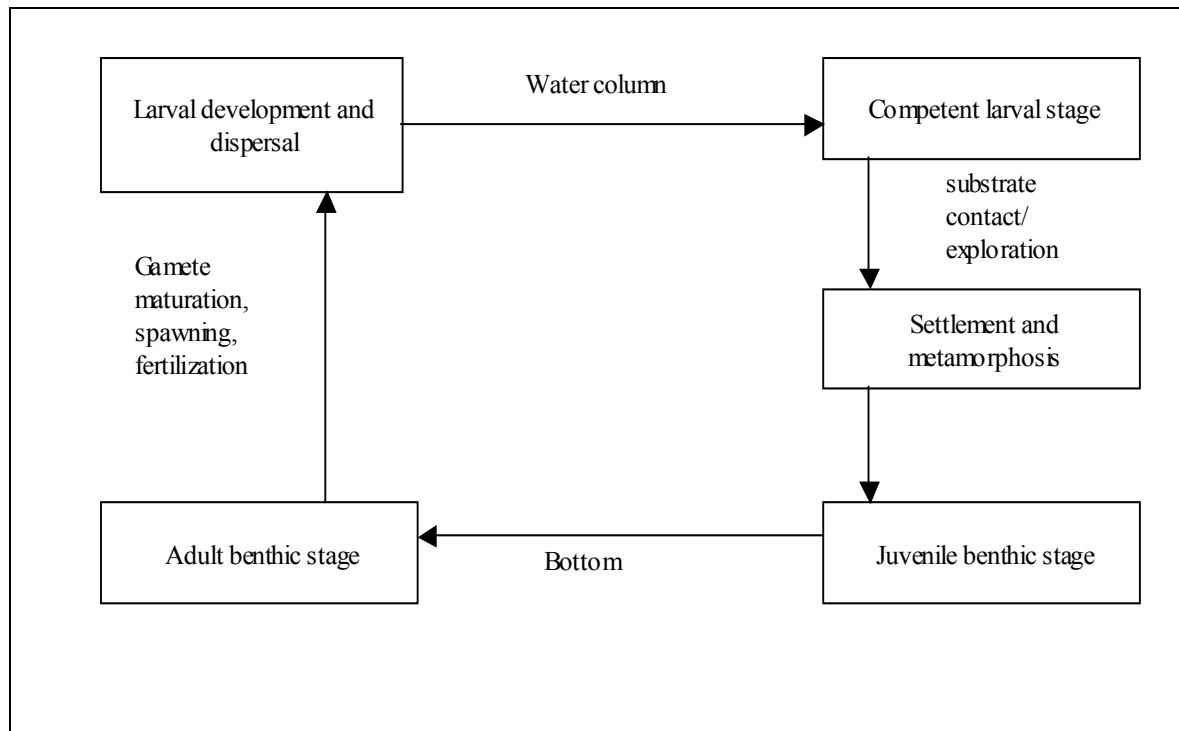


Figure 1.1. A schematic mussel life cycle with a planktonic larval and benthic adult phases (adapted from Eckman, 1996).

Transport of larvae by tidal currents has a profound impact on intertidal communities as the advection creates recruitment variation and determines whether the

larvae complete their development near a favourable habitat. Factors such as larval condition, settlement and subsequent recruitment to the intertidal community have a strong effect on adult density and establish a pattern in such communities (Menge, 2000; Chícharo & Chícharo, 2001), whereas the post-recruitment processes of predation, competition, heat and desiccation modify that pattern (Gaines & Bertness, 1992; Shanks, 1995; Palmer *et al.*, 1996; Phillips, 2002). In mussels, the life cycle includes two different and complex, yet interdependent, phases: a planktonic larva and a benthic, sedentary adult (Fig. 1.1). For larvae, the benthic adult fecundity and fertilisation success, subsequent growth and larval stage duration, larval mortality, behaviour and dispersal by currents, and settlement resulting in metamorphosis are crucial. Morgan (1995) lists numerous factors affecting larval survival, including extreme or variable temperatures and salinities, reduced oxygen levels, pollution, UV and starvation. Moreover, prolonged development in the planktonic phase can also be detrimental to larvae as it increases the probability of predation, advection from adult habitats and reduction of suitable habitats.

Larvae are generally believed to be most sensitive to changes in temperature and salinity, with the greatest mortality occurring from fluctuating temperature at the northern and southern limits of species distribution, in shallow bays and near the beginning of their larval life. Spring rainfalls can often reduce salinity in estuaries and harbours, rapidly creating stressful conditions for larvae. However, larvae can recover from salinity shock more quickly than from temperature shock (Morgan, 1995). Naturally, tolerance to changes in temperature and salinity reflects the prevailing conditions in the intertidal habitats the larvae originated from, so that these two factors can alter larval survival rates only at the margins of the species range.

Starvation has been recognised as a major source of larval mortality. Traditionally, the food abundance in the water column for larvae and adult mussels has been expressed as chlorophyll *a* concentration. It has been suggested, however, that this method is a gross estimate and may not always indicate the true nutritional conditions, since the suitability of phytoplankton and zooplankton varies among bivalve species (Morgan, 1995). Attention has been given to highly unsaturated fatty acids (HUFA)

content in phytoplankton cells as being essential for larval development, success at recruitment and the subsequent development of a community (Olson & Olson, 1989; Caers *et al.*, 2003).

Exchange of nutrients

A two-way exchange of organic matter between the mussels and the overlying water is important for both the benthic and pelagic components of the intertidal system (Zhang, 2000). Understanding the physical, chemical and biological processes governing both the planktonic and the benthic compartments of the intertidal systems is vital to our knowledge of the spatial and temporal distributions, abundances, intertidal population structure and growth rate (Eckman, 1996; Ackerman *et al.*, 2001). From an ecological perspective, the limiting factors of primary production by phytoplankton, influx of nutrients into aquatic ecosystems and both horizontal and vertical transport (i.e. bottom-up processes) and consumption by grazers (i.e. top-down processes) have been of particular interest (Fretwell, 1987; Menge *et al.*, 1997). In the bottom-up processes, the phytoplankton growth can be limited by the lack of nutrients, whereas in the top-down processes pelagic grazing of phytoplankton is the limiting factor (Ackerman *et al.*, 2001). Benthic suspension-feeders such as mussels also contribute to the consumption of phytoplankton by removing it from the water column, thus establishing a link between the pelagic and benthic components. This benthic-pelagic relationship is further limited by water depth, the physical processes responsible for the water column mixing and subsequent re-suspension of organic particles, and biological processes modifying phytoplankton availability to the benthos, such as variation in the quality and quantity of food and in the filtration rate (Fréchette *et al.*, 1989; Fréchette & Grant, 1991; Butman *et al.*, 1994; O’Riordan *et al.*, 1995; Marcus & Boero, 1998; Widdicombe & Austen, 2001).

The importance of organic matter subsidies from subtidal kelp beds to intertidal systems worldwide has been emphasised by numerous researchers (e.g. Duggins *et al.*, 1989; Bustamante *et al.*, 1995; Bustamante & Branch, 1996; Bégin *et al.*, 2004). As highly productive seaweeds, macroalgae provide organic detritus (particulate and dissolved) to

the intertidal communities, which subsequently stimulates the growth of invertebrate grazers, such as limpets, and the filter-feeders, such as mussels and barnacles. Further, macroalgae can impact on the benthic-pelagic coupling in temperate intertidal systems by preventing the diffusion of dissolved inorganic nitrogen (DIN) from the water column to the sediments and by intercepting urea from the sediment to the water column (Tyler *et al.*, 2001).

Mussels are responsible for a significant share of the energy flow from the pelagic to the benthic system, often benefiting from the pelagic primary production in the overlying water column (Graf *et al.*, 1982; Christensen & Kannevorff, 1986; Grall & Chavaud, 2002). Further, mussels stimulate the transfer of seston and nutrients from the water column to the benthos (Porter *et al.*, 1996) and subsequently release the nutrients back into the water column (Raffaelli *et al.*, 2003). When the amount of food filtered by individual mussels exceeds their demand, pseudofaeces are produced. These pseudofaeces include the excess particulate organic matter, which is then deposited outside the mussel and utilised as a food source by other members of the community, such as bacteria which release the nutrients into the water column (Graf, 1992). Moreover, mussels can significantly reduce the phytoplankton biomass in the intertidal system by filtering it from the water column (Officer *et al.*, 1982; Connell, 1985; Olive, 1985; Dame *et al.*, 1989; Frechette *et al.*, 1989; Ogilvie *et al.*, 2000), but they have also been shown to promote primary production by converting particulate nitrogen into dissolved organic nitrogen (DIN), thus making it available for phytoplankton (Asmus & Asmus, 1991). Mussels can also retain essential nutrients in the intertidal system (Kuenzler, 1961; Jordan & Valiela, 1982; Bertness, 1984) and have a stabilising effect on the phytoplankton biomass, reducing high levels in winter (grazing effect) and slightly increasing low levels in summer (Gibbs & Vant, 1997; Ogilvie *et al.*, 2003). In winter, when levels of nitrogen in the water column are high, mussel grazing can reduce the phytoplankton production. In summer, however, mussels can stimulate the phytoplankton biomass by excreting metabolic ammonium, which can be subsequently utilised by phytoplankton (Ogilvie *et al.*, 2003). Thus, the links between mussels and pelagic production in intertidal communities are two-fold: supply and regeneration of nutrients

into the water column and simultaneously reducing the planktonic production by phytoplankton consumption.

1.3. Worldwide research of mussel communities

Until recently, analysis of the distribution of mussels worldwide has been based mostly on shell morphometry, often creating confusion – a result of inaccuracies associated with morphometric techniques that fail to account for the mussel shell response to environmental conditions. With the advent of more advanced techniques, such as nuclear DNA markers and the analysis of mitochondrial DNA (mtDNA), the distribution of some mussel species had to be revised (Koehn, 1991; Gosling, 2003; Gardner, 2004).

Mytilidae is a family dating from the Devonian period and includes important genera such as *Mytilus*, *Perna* and *Aulacomya* (Seed & Richardson, 1990). In the northern hemisphere the genus *Mytilus* is represented by *M. trossulus* in the Pacific, the north-western Atlantic and the Baltic Sea, *M. edulis* in the Atlantic and *M. galloprovincialis* in the Mediterranean and along the Atlantic coast of southern Europe and North Africa (McDonald & Koehn, 1988; McDonald *et al.*, 1991; Gosling, 1992; Comesaña *et al.*, 1998). *M. galloprovincialis* has also been introduced to the Sea of Japan, southern California and Puget Sound (Hilbish *et al.*, 2000). Where the ranges of *M. edulis*, *M. trossulus* and *M. galloprovincialis* overlap, various degrees of hybridisation occur (Gosling, 2003). *Perna viridis* represents the genus *Perna* in the northern hemisphere in the sub-tropical regions of the Arabian Sea, Bay of Bengal, the East China Sea and the South China Sea. *P. viridis* also inhabits tropical latitudes in the Malaysian waters (Gosling, 2003). In the southern hemisphere, shell morphometric analyses and protein markers techniques identified the genus *Mytilus* as *M. edulis* or *M. galloprovincialis* (McDonald *et al.*, 1991). However, recent analyses of mtDNA revealed that the mussels in the southern hemisphere developed from migration events from the northern hemisphere (Gardner, 2004). As a result, the southern hemisphere *M. edulis* and *M. galloprovincialis* are similar but not identical to *M. edulis* and *M. galloprovincialis*

from the northern hemisphere (Hilbish *et al.*, 2000; Gosling, 2003). *M. edulis* can be found along the southern coasts of South America, while *M. galloprovincialis* inhabits waters in southern Australia, Tasmania and New Zealand (Hilbish *et al.*, 2000). *M. galloprovincialis* has recently invaded the western shores of South Africa and Namibia and, as noted earlier, is currently spreading east, threatening three indigenous mussel species: *Choromytilus meridionalis*, *Perna perna* and *Aulacomya ater* (Grant & Cherry, 1985; Branch & Steffani, 2004). The genus *Perna* is represented in the southern hemisphere by *P. perna*, *P. viridis* and *P. canaliculus*. *P. perna* inhabits waters off South America, South Africa and eastern Madagascar Island, *P. viridis* is found in the tropical waters of Indonesia, while *P. canaliculus* is indigenous only to New Zealand (Siddal, 1980; Calvo-Ugarteburu & McQuaid, 1998). Two species from the genus *Aulacomya* are found in the southern hemisphere: *A. ater* and *A. maoriana*. The former inhabits the coast of South Africa and also the Pacific and Atlantic shores of South America, while the latter is indigenous to New Zealand (Gosling, 2003). The distribution of the main commercially important mussel species is presented in Fig. 1.2.

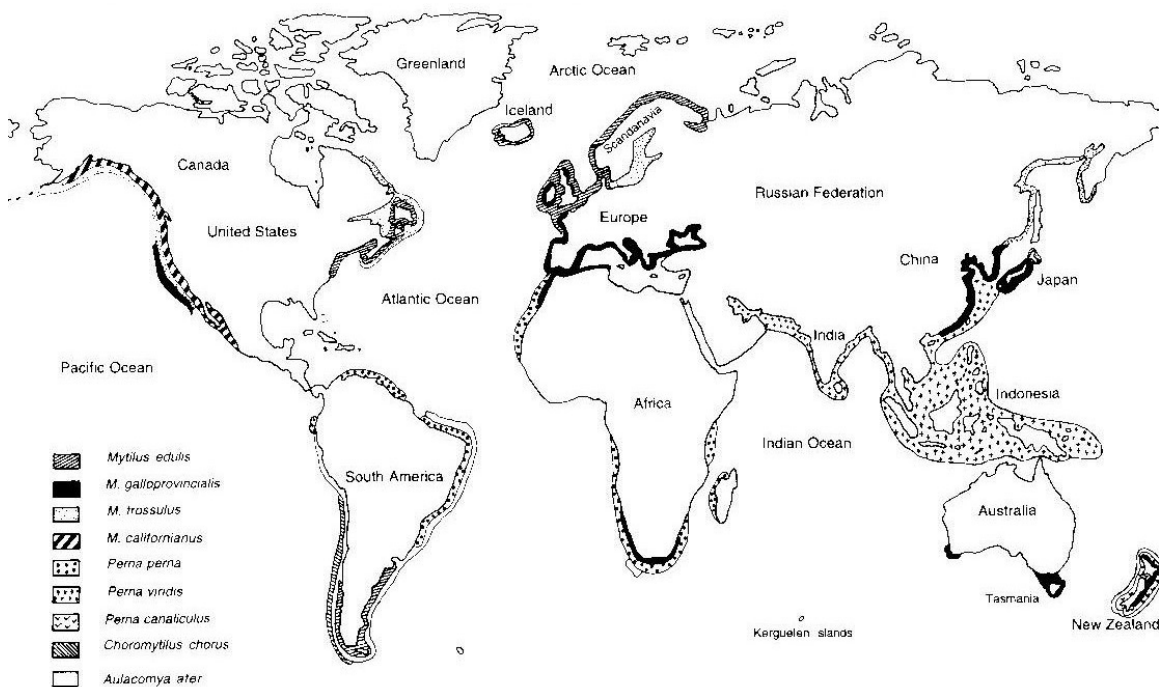


Figure 1.2. Global distribution of the main commercially important mussel species (adapted from Gosling, 2003).

Voluminous literature has been dedicated to various aspects of the ecology of marine mussels in North America, where genus *Mytilus* has been investigated at numerous sites, including New England, Newfoundland, the Bay of Fundy, British Columbia, Québec, California and the Oregon Coast. These studies concentrate mainly on the physiological energetics of the mussels (e.g. Harger, 1970; Thompson, 1984; Emmet *et al.*, 1987; Gardner & Thomas, 1987), the relationship between the mussels and the environmental parameters such as temperature, salinity and food abundance (e.g. Page & Hubbard, 1987; Fréchette *et al.*, 1989; Alunno-Bruscia *et al.*, 2001; Gardner & Thompson, 2001), the relationship between the mussels and other members of the coastal communities, including predators (e.g. starfish and gastropods) and filter-feeders such as barnacles (Paine, 1976; Paine & Levin, 1981; Roughgarden *et al.*, 1988; Menge, 1991; Menge, 1992; Lohse, 1993; Menge *et al.*, 1994; Petraitis *et al.*, 2003), and on the structure of mussel beds (e.g. Commito & Rusignuolo, 2000; Dahlhoff *et al.*, 2002).

Research in South America also relates to various aspects of the biology of single mussel species. For example, Prieto *et al.* (1999) studied the reproduction and growth in *Perna perna* in Venezuela, Chaparro & Winter (1983) and Gray *et al.* (1997) studied the reproduction and growth of *Mytilus edulis chilensis* in Chile and the Falkland Islands, respectively. The interactions between mussels, environmental variables and other invertebrates in the rocky intertidal have been described for the genus *Brachidontes* by Tanaka & Magalhães (2002) and Adami *et al.* (2004) in Brazil and Argentina, respectively. Further, the physiological ecology of a Chilean mytilid *Choromytilus chorus* was investigated by Navarro (1988). Paine *et al.* (1985) and Navarette and Castilla (1990) studied the succession dynamics in mussel beds of *Peromytilus purpuratus* in Chile, while Guíñez & Castilla (1999) developed a self-thinning model for multi-layered intertidal beds of the same mussel species. It is worth noting that some parts of the world, including South America, Africa and Asia, are under-represented because of few comprehensive accounts (Gosling, 2003).

The ecology of the European *Mytilus edulis* has been extensively studied at numerous sites in Germany, Sweden, the Netherlands, England, France, Italy and Spain.

Secondary production, growth and the physiological energetics of this species were described by many workers, for example Thompson & Bayne (1974), Bayne & Worrall (1980), Rosenberg & Loo (1983), Craeymeersch *et al.* (1986), Widdows & Johnson (1988) and Hawkins *et al.* (1996). Relationships between *Mytilus* and salinity, temperature and food availability were investigated by, among others, Livingstone *et al.* (1979), Widdows *et al.* (1979), Widdows (1985), Hawkins *et al.* (1986), Seed & Richardson (1990), Hawkins & Bayne (1991) and McGrorty & Goss-Custard (1993), while the ecological interactions between *M. edulis* and other invertebrates in European waters were investigated by, among others, Buschbaum (2000; 2001), Davenport *et al.* (2002) and Kostylev & Erlandsson (2001). The population dynamics of *Mytilus galloprovincialis* were investigated by Ardizzone *et al.* (1996). On a number of occasions, *Mytilus edulis* is described in conjunction with another European species, *Mytilus galloprovincialis*, for example in relation to fecundity and growth (Gardner & Skibinski, 1990; Camacho *et al.*, 1995).

There are many South African reports dealing with various aspects of the ecology of a single species, such as the influence of wave exposure on *Mytilus galloprovincialis* beds (e.g. Raubenheimer & Cook, 1990; Steffani & Branch, 2003; Hammond & Griffiths, 2004), the ecological energetics of *Aulacomya ater* (e.g. Griffiths & King, 1979) and the population structure in genus *Choromytilus* (e.g. Griffiths, 1980; Griffiths & Hockey, 1987; Clarke & Griffiths, 1990). However, numerous South African researchers have investigated the trophic structure and population dynamics of more than one species within the same community, such as *Choromytilus meridionalis*, *Perna perna*, *Aulacomya ater* and *Mytilus galloprovincialis*, thus describing the interspecific relationships in mussel beds in greater detail (e.g. Bayne *et al.* 1984; Wickens & Griffiths, 1985; van Erkom Schurink & Griffiths, 1990; van Erkom Schurink & Griffiths, 1991, 1992, 1993; Bustamante & Branch, 1996b; Bustamante *et al.*, 1997).

A search of the available scientific literature revealed that in most cases only single mussel species are studied at particular locations. Therefore, records examining relationships among more than one taxa within the same community are scarce. This

thesis, however, investigates the population dynamics of three mussel species co-existing in a speciose environment: *Mytilus galloprovincialis*, *Aulacomya maoriana* and *Perna canaliculus*. Thus, a high-resolution picture of the ecological relationships that occur among different taxa within the same habitat is provided.

1.4. Intertidal mussel communities in Wellington Harbour

In Wellington Harbour (Fig. 1.4) the intertidal zone is rather compressed, with a small tidal range of about 1.5 m. The degree of wave exposure varies between moderately exposed and moderately sheltered rocky reefs, with very exposed reefs found only on the South Coast of Wellington (Northcote, 1998). Such physical zonation influences the distribution and survivorship of various life forms within this region. The upper shore is generally colonised by lichens and gastropods, which are replaced lower down by barnacles, which in turn give way further down to mussels and algae (Morton & Miller, 1968, Morton, 2004). The upper limit of the supra-littoral is influenced by sea spray, so on shores exposed to wave action this band will be wider than on sheltered shores, whereas the lower limit of the supra-littoral is the upper limit for barnacles. The primary producers in this band are the lichens *Verrucaria*, cyanobacteria and microscopic green algae, while seaweeds are scarce. Characteristic herbivores are the Littorinid gastropods *Littorina unifasciata* and *Littorina cincta*. The mid-intertidal zone is the broadest and extends from the upper limit for barnacles to the upper limit for large rockweeds (e.g. *Hormosira banksii*). The barnacles *Chamaesipho brunnea* and *Ch. columna* and *Elminius modestus* are common, replaced lower down by mussels (Fig. 1.3). Herbivores include the limpets *Cellana ornata*, *C. radians* and *C. denticulata*. Coralline algae, for example the common *Corallina officinalis*, also inhabit this part of the intertidal zone. Other common intertidal algal species in Wellington Harbour include *Ulva lactuca*, *Porphyra columbina*, *Codium adhaerens* and *Champia novaezelandiae*. The lowest part of the intertidal zone, the sub-littoral, extends from the low-water mark at spring tide to the upper limit of the large kelps, including *Carpophyllum maschalocarpum*.

Wellington Harbour constitutes a speciose, model system for investigating mussel ecology for a number of reasons. In Wellington Harbour, three species of mussels co-exist: endemic to New Zealand ribbed mussel *Aulacomya maoriana*, the greenshell mussel *Perna canaliculus* and the Mediterranean mussel *Mytilus galloprovincialis*. Such situation creates a rare and unique opportunity to study the dynamics among three co-existing intertidal mussel species. Given the fact that all of these species commonly occur throughout the rocky intertidal zone in the Harbour, gradients of interspecific competition must occur. Such competition can be manifested through a species-specific variability of each ecological parameter, i.e. maintaining higher juvenile recruitment, or higher adult condition by one of the species and therefore its greater ability to contribute to the next generation by producing more offspring, or producing it more frequently during either the reproductive season or throughout the entire year, and eventually outcompeting the remaining species within the community. Further, Wellington Harbour is a subject of significant variation in the water column parameters, with numerous sites lying in close proximity, yet consistently remaining in different hydrology regimes, such as the input of heavy, saline, oceanic waters from Cook Strait in the south and a large input of fresh water from the Hutt River in the north of the Harbour.

Wellington Harbour study system

Located in central New Zealand (41°16' S; 174°51' E), Wellington Harbour (Fig. 1.4) lies on the boundary of the Pacific and Australian tectonic plates, in the middle of a zone of parallel NE-SW trending faults. The bedrock is greywacke, and the landscape of the whole Wellington area can be presented as a series of tilted blocks, uplifted on the western side of the main fault lines (Molloy & Smith, 2002). The Harbour has been described as one of the finest natural harbours in the world and, despite the fact that it has been heavily modified by urban and port development together with land reclamation, some of its areas remain intact (Dix *et al.*, 1990; Northcote, 1998).



Figure 1.3. The mid-intertidal zone in Wellington, uncovered at low tide. Note the shore dominated by the Mediterranean mussel *Mytilus galloprovincialis*, oystercatchers *Haematopus unicolor* and floating kelp *Macrocystis*.

Wellington Harbour is a roughly circular, semi-enclosed embayment with three islands: Matiu-Somes Island, Mokopuna Island (just north of Matiu-Somes Island) and Ward Island. The total area of the Harbour is 85 km² (Wear & Gardner, 2001) with an average depth of 14 metres and the greatest depth of 32 metres just south of Somes Island (Booth, 1975; Wear & Gardner, 2001). The maximum width of the Harbour is 11.1 km and the minimum width is 1.8 km (Heath, 1977). The water volume has been estimated as approximately $1320 \times 10^6 \text{ m}^3$ (McConchie, 2000). The total catchment area of the Harbour is 725 km², with the Hutt River being the main source of fresh water, discharging a minimum of 2.6×10^6 tons to a maximum of 180×10^6 tons of fresh water per day (Maxwell, 1956). Other sources of fresh water input into Wellington Harbour are the small streams of Ngauranga, Korokoro and Kaiwharawhara, but their water input is of

secondary importance. The Hutt River drains the southern Tararua Mountains and heavy rainfall in that area often creates

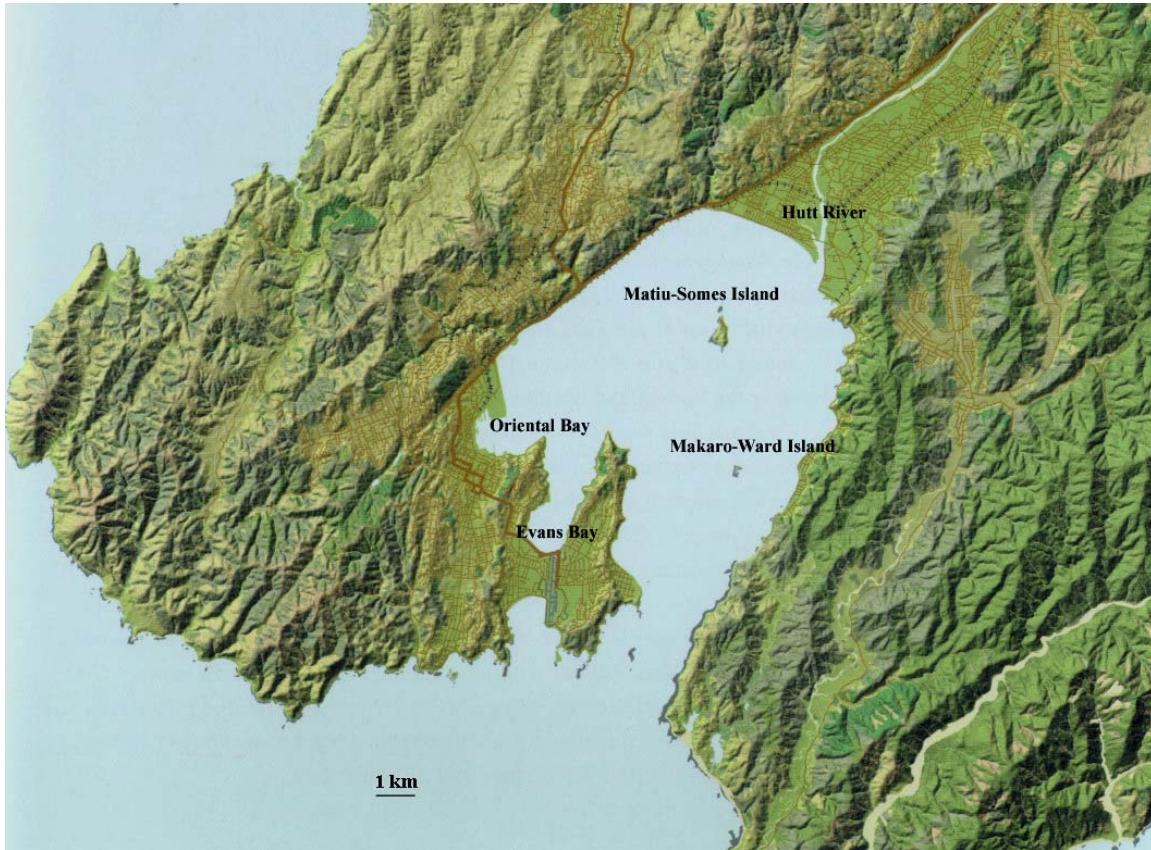


Figure 1.4. Wellington Harbour area (adapted from Molloy & Smith, 2002).

a surplus of water, which is carried downstream with large amounts of suspended sediment and then discharged into the Harbour. This phenomenon creates a large, cool layer of lower salinity that enters the Harbour as a conspicuously brown plume and mixes with its waters to a depth of about 5 m (McConchie, 2000). In northerly winds (accounting for 50–60% of winds in the Wellington region), the plume is pushed along the eastern shores of the Harbour, past eastern Matiu-Somes Island, reaching as far south as Camp Bay. In southerly wind conditions, the plume is often trapped against the northern end of the Harbour (McConchie, 2000; Brodie, 1958). Wellington Harbour experiences semi-diurnal tides with the mean tide approximately 0.75 metres (Maxwell, 1956). Heath (1977) calculates that the total flushing time is approximately 10 days. There is only one entrance to the Harbour, in the south, connecting it with the open ocean

via Cook Strait. As such, the Harbour can be regarded as an area where fresh water from the Hutt River mixes with saline oceanic water. Indeed, the Cook Strait water seeps into the Harbour near the bottom, while the fresh water is confined to the upper 5 m and is often found in much thinner layers. Heath (1977) reports that the salinity of Cook Strait water ranges from 34.5 ‰ to 35 ‰ and Brodie (1958) gives the salinity of the Harbour ranges from 32.8 ‰ to 33.7 ‰. In fact, the saline oceanic water entering Wellington Harbour is a mixture of three major currents, which meet in central New Zealand (Fig. 1.5). Heath (1971) identifies and describes those currents as:

- The subtropical and sub-surface, warm *East Cape Current* flowing towards Cook Strait from the northeast, along the eastern coast of the North Island, but entering the Cook Strait area from the southeast;
- The subtropical and sub-surface, warm and low-nutrient *D'Urville Current* travelling up the west coast of the South Island, but entering Cook Strait from the north because of the influence of the strong, prevailing northerly winds in the area;
- The sub-Antarctic, cool and low-salinity *Southland Current*, originally subtropical and flowing from Australia as the Tasman Current but deflected round the southernmost part of New Zealand and travelling along the eastern coast of the South Island (Westerskov & Probert, 1981). This current interacts with the southward-flowing East Cape Current and the D'Urville Current (Sutton, 2003).

The Tasman Sea waters are effectively excluded from the Cook Strait–Wellington Harbour system by a submarine isthmus, or “land bridge”, approximately 100–200 metres deep stretching as far north as the Taranaki Bight (Westerskov & Probert, 1981; Bowman, 1983). Stevens (1974) describes the land bridge as a land connection between the North and South Islands which has been drowned by the ocean very recently, about 10,000 years ago. The resulting hydrological situation is remarkable: Cook Strait being a highly dynamic system where numerous currents meet and mix, sweeping the ocean floor, and Wellington Harbour being a sheltered and speciose embayment, rich in

nutrients from the river and surrounding land, supporting numerous invertebrate communities.

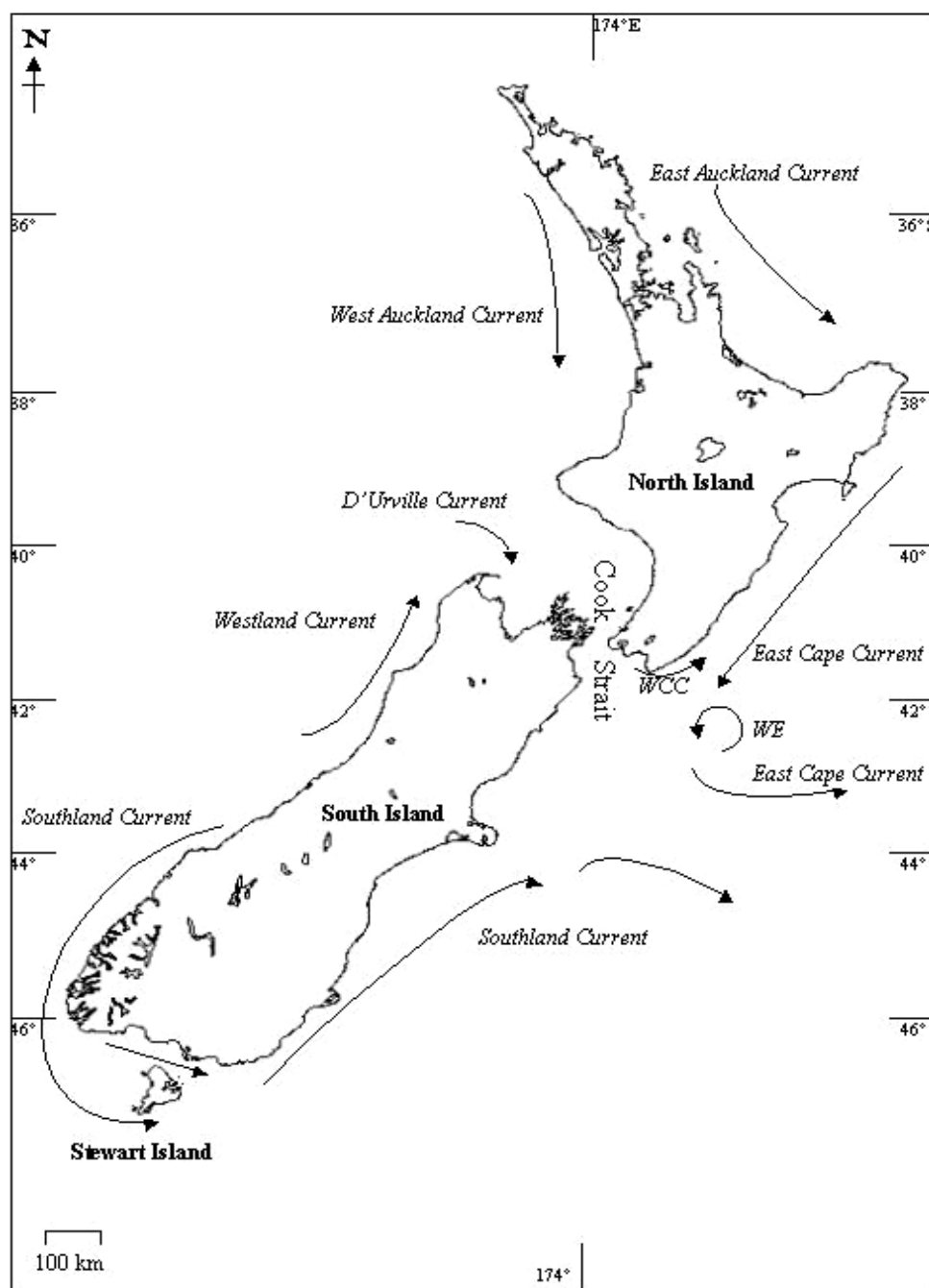


Figure 1.5. Major ocean currents around New Zealand (adapted from Morton & Miller, 1968). WCC=Wairarapa Coastal Current, WE=Wairarapa Eddy.

Like the rest of New Zealand, Wellington Harbour is a dynamic environment that has been subject to dramatic changes. The scale of those changes can perhaps be best understood in terms of the geological history of the Harbour: at the time when the Hutt River was created, about 4 million years ago, the average depth in the Harbour was estimated at between 900 and 1800 metres (Davis, 1982). Since then, the river has been constantly depositing sediments in Wellington Harbour. Also, land erosion has resulted in vast quantities of rocks and boulders being brought down into the harbour basin. Consequently, present-day Wellington Harbour has an average depth of only 14–16 metres.

1.5. Thesis outline

The mechanisms shaping intertidal communities, such as larval settlement and recruitment, combined with the interactions among adult members of the intertidal communities (e.g. competition and predation) have been the subjects of great international interest. This thesis relates Wellington Harbour local findings to global ecological trends reported elsewhere. This thesis describes the structure of mussel communities in Wellington Harbour, the numerous physical and biological factors influencing the structure of such communities, the ecological mechanisms occurring at the level of both the individual mussel and the entire population, and the way these ecological mechanisms help to establish and maintain the communities. The present study contributes to the existing knowledge of intertidal ecology by focusing on both local-scale (within metres) and broad-scale patterns (kilometres), and as such constitutes a combination of multi-site and multi-species scientific studies of important aspects of ecology of rocky intertidal mussel communities in Wellington Harbour. Further, the approach taken in this study follows the idea that animal behaviour is complex and varies according to variation of local-scale cues that cannot be ignored because it establishes and maintains the observed patterns in intertidal communities (Chapman, 2000). The present study presents the results based on a novel set of data obtained from a highly productive, dynamic system supporting speciose algal and invertebrate intertidal communities that are dominated by three co-existing mussel species. Such co-occurrence

of three different and dominant mussel species presented a rare and unique opportunity to study the dynamics of these communities at the level of each mussel species, as well as the level of the entire community.

The larval ecology part of this study concentrates on the rates at which mussel larvae settled on the experimental substrate. The reproductive cycle and the timing of the settlement of larvae are crucial to the subsequent life of adult stages. Upon settlement, the successful larvae metamorphose into juvenile mussels and join the already mature adult mussel colonies, or establish new colonies. Quantifying the settlement density on the substrate helps to create a picture of temporal and spatial variability in mussel recruitment. This, in turn, reflects the environmental conditions that shape the entire mussel population. It is possible that co-existing species of mussels will spawn and produce their planktonic larvae at different times of the year. For example, on the West Coast of the United States, *Mytilus galloprovincialis* spawns between October and February, whereas *Mytilus californianus* dribbles gametes continuously throughout the year (Gosling, 2003). A year-round spawning is a flexible reproductive strategy and a reflection of adaptability to prevailing environmental conditions.

The post-larval ecology part of this study concentrates on various factors affecting the intertidal adult mussel community. These include the general state of mussel fitness, expressed as the condition index and gonad mass, and the degree of infestation with a parasitic pea crab *Pinnotheres novaezelandiae*. As described earlier, mussels free from parasites can gain competitive advantage over infested mussels. This may result in the higher condition index of the healthy mussels and lead to their dominance within the habitat. In the present study, spatial and temporal species-specific variation in condition index, gonad mass and the degree of infestation with the pea crab were investigated and related to the patterns of within-community dominance observed *in situ*.

International data show the stages of recolonisation of the rocky substrate and the recovery of intertidal communities from physical disturbance (reviewed by Schiel, 2004). In order to describe the pattern of succession in mussel communities, from bare rock to

mature community, patches of bare rocky substrate were experimentally created and monitored. Predator-exclusion cages were set up in the intertidal zone. The abundance of gradually settling intertidal organisms was expressed in terms of percent cover, revealing complex interactions among members of the intertidal community and the mechanisms of community regulation according to the experimental cage treatment

Further, seasonality of mussel response to wave action and desiccation was investigated. An experiment was designed, in which mussels were exposed to air at six different shore levels within the intertidal zone. In a separate study, species-specific mussel strength of attachment to the rocky substrate was quantified at shores facing south and north in Wellington Harbour.

In order to obtain environmental data of the water column parameters, electronic Conductivity-Temperature-Depth data loggers (CTDs) were employed in this study and deployed at four localities within Wellington Harbour from December 2001 until November 2003. Environmental data provided by the data loggers assisted in understanding of the subtle and often complex ecological processes that determine patterns of life in the intertidal zone. Moreover, the data obtained by the CTDs helped to link the ecological processes taking place within the intertidal mussel communities and the physical processes occurring in the nearshore water column. The CTDs recorded seawater data of conductivity, temperature, turbidity, chlorophyll *a*, salinity and water pressure.

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CHAPTER TWO: WATER COLUMN CHARACTERISTICS

2.1. Introduction

Ecological studies of marine invertebrates often include examination of the ambient water characteristics. Seawater parameters help us understand differences underlying the distribution of invertebrates and structure of their communities. A study of the water column characteristics is a powerful tool helpful in explaining the spatial and temporal variability of those characteristics. Temperature, salinity, chlorophyll *a* concentration and turbidity are among the most widely studied seawater parameters. Temperature and salinity can be linked to various phases of bivalve lives, including gametogenesis and reproduction, larval settlement and recruitment, together with subsequent growth and condition of adult stages. Seston quality, often expressed as chlorophyll *a* concentration, suggests the concentration of phytoplankton on which filter feeders rely as food. It also points to dietary conditions in which those animals live, as variety of suspended particles present in the water column, such as detritus, bacteria and phytoplankton, differently contribute to the nutrient acquisition by invertebrates (Gosling, 2003). Seston quantity can be referred to as turbidity and typically defined as the amount of suspended sediment particles in water (Mylvaganam & Jakobsen, 2000). Thus, chlorophyll *a* provides the qualitative measure of seston in the water column, while turbidity is a quantitative seston measure. When combined, the two parameters can often provide the information about the amount of particles suspended in the water column, as well as their potential nourishment value to seston-feeding bivalves, although chlorophyll *a* estimates may not always reflect the true nutritional conditions as the suitability of phytoplankton varies among bivalve species (Morgan, 1995).

Understanding the interplay among the physical, chemical and biological processes governing the planktonic and the benthic compartments of the intertidal systems is essential to our knowledge of the distribution and abundances of bivalve taxa (Eckman, 1996; Ackerman *et al.*, 2001). Temperature, salinity and food availability are

significant factors regulating the dynamics of filter-feeder communities. These factors are often further affected by hydrological regimes, such as currents, gyres, flow patterns, and local water residence time that distribute food particles among coastal areas and stimulate life cycles and succession in such communities by altering temperature and salinity regimes (Officer *et al.*, 1982, Menge *et al.*, 1997, Dower & Brodeur, 2004).

Although most marine bivalves can tolerate temperatures ranging from -3°C to $+44^{\circ}\text{C}$, this tolerance is species-specific; and within each species, embryonic and larval stages have a narrower temperature tolerance than the adult stages. Further, temperatures required for spawning are always higher than temperatures required for growth (Vernberg & Vernberg, 1972). Thus, all of these factors set limits to the natural distribution of individual bivalve species. For example, in a coldwater scallop species *Placopecten magellanicus*, Brand (1991) found that the optimum temperature for existence is 10°C and the upper lethal temperature is 24°C . In the northern end of the species range (Newfoundland), the scallop is found in shallow areas where low water temperature in summer prolong the larval development thus reducing recruitment or don't trigger spawning at all, but further south (Cape Hatteras, North Carolina) the species occurs in deeper waters (over 55m), separated from the cooler surface layers by a thermocline. A similar comment can be made about the larval stages of the mussel *Mytilus edulis*, also limited in their distribution to Cape Hatteras. This is achieved by the interplay of the warm Gulf Stream moving north and the cold Labrador Current travelling south, both currents meeting near Cape Hatters and creating a temperature barrier for the distribution of *Mytilus* larvae south of this area (Gosling, 2003).

Salinity and temperature are key factors setting limits to the natural distribution of species at geographical and local scales. Mussels are generally considered as euryhaline bivalves (i.e. able to tolerate a wide range of salinities), and consequently present in many estuaries and bays where local salinities can significantly fluctuate from the average open ocean salinity of 35 PSU. Bayne (1976) reports that *Mytilus edulis* can survive in salinities as low as 4 PSU and as high as 40 PSU. Sivalingham (1977) makes a

similar comment about *Perna viridis*, whose normal salinity range is 27 – 33 PSU. The author reports that the experimental LD₅₀ salinity for this species was as high as 80 PSU.

Until the last decade, measurements of the physical, chemical and biological properties of seawater used to be costly, time- and labour-consuming. Measurement procedures often were limited by factors including transport, collection techniques, site availability and weather. Traditional field measurements often failed to alert in time to events such as bacterial contamination of shellfish, harmful algal blooms or oxygen depletion. Also, the data quality might have been compromised because of extended holding times before analysis or use of non-standardised methodologies (Pettinger, 1971; Teillet *et al.*, 2002; Glasgow *et al.*, 2004). The emergence of CTD sensors has enabled marine scientists to obtain rapid, high-quality bio-hydrological data (Mills & Tett, 1990; Kalashnikov *et al.*, 1998). Optical sensors, such as the ones employed in this study, are able to provide rapid and high-resolution *in situ* measurements of chlorophyll concentration and turbidity, based on the fact that since the chlorophyll and phaeopigment in phytoplankton are fluorescent, chlorophylls can be detected (Yentsch & Yentsch, 1984; Smith *et al.*, 1981).

Study system

In general, available literature on Wellington Harbour hydrology and water column characteristics is scarce and fragmented. Although previous investigations in this area did include examination of the seawater parameters (e.g. Booth, 1975; Gardner & Kathiravetpillai, 1997; Helson & Gardner, 2004), the water column data collected in the present study were obtained by means of fully automated, electronic data loggers. The present study is therefore the first multi-site, detailed and inter-annual sampling series of the water column characteristics performed in Wellington Harbour. The configuration and hydrological conditions in Wellington Harbour affect its tidal currents and their speed, total flushing time of the Harbour (estimated as about 10 days) and the amount of nutrients entering the Harbour at different locations (Maxwell, 1956; Brodie, 1958;

Heath, 1974). These factors, in turn, affect the water parameters and ultimately invertebrate communities within the Harbour.

2.2. Materials and Methods

Four Richard Brancker Research Ltd XR 420 CTDs (Fig. 2.1) were used in this study, all deployed at a depth of 2 –3 m using SCUBA. Each CTD was equipped with a Seapoint chlorophyll fluorometer for *in situ* measurements of chlorophyll *a* and Seapoint turbidity meter for measuring turbidity by detecting light scattered by suspended particles in the water column. All sensors were factory calibrated: temperature sensors were calibrated to an accuracy of $\pm 0.002^{\circ}\text{C}$, over the range -5 to $+35^{\circ}\text{C}$, conductivity sensors were calibrated to an accuracy of ± 0.03 milliSiemens (mS cm^{-1}) over the range 1 to 70 mS cm^{-1} , depth sensors were calibrated to an accuracy of $\pm 0.05\%$ of the full scale with the full scale range 10 to 4000 m. Salinity was a derived parameter, i.e. calculated by the software from conductivity, temperature and pressure data. Turbidity sensors were factory calibrated to an accuracy of $\pm 2\%$ of the full scale, with the range 0 to 125 Formazin Turbidity Units (FTU). Chlorophyll *a* fluorometer sensor was calibrated, with the minimum detectable level of $0 \mu\text{g l}^{-1}$ and maximum detectable level of $15 \mu\text{g l}^{-1}$.



Figure 2.1 Data loggers used in the present study.

First two data loggers were deployed in December 2001 and the next two were acquired and deployed in August 2002. All loggers were set to record the following environmental data: temperature ($^{\circ}\text{C}$), salinity measured in Practical Salinity Units (PSU), pressure (deciBars), depth (m), turbidity measured in Formazin Turbidity Units (FTU), conductivity measured in miliSiemens per centimetre (mS cm^{-1}) and chlorophyll *a* concentration ($\mu\text{g l}^{-1}$). These water column characteristics were recorded every hour for ten seconds and then automatically averaged. The CTDs were retrieved after approximately a month of recording and the data from each logger were downloaded onto a computer and subsequently analysed. The four CTDs were deployed at the following sites (Fig. 2.2): Petone wharf, Evans Bay (at Miramar wharf), Matiu-Somes Island (at northern wharf), and at the Front Lead light in the shipping channel (this CTD, hereafter referred to as Seatoun, was moved to a nearby Falcon Shoal light in April 2003 due to renovation works at the Front Lead light). Such multi-site deployment of the loggers was dictated by the interest in collecting data from a variety of environmental conditions present in various parts of Wellington Harbour. Because of adverse weather conditions and sporadic gear failure, it was not always possible to collect data for the entire period of this study. Also, Front Lead and Matiu-Somes Island loggers had already been collecting data for nine months before the Evans Bay and Petone loggers were first used. For these reasons the final data set is incomplete and fragmented. Nevertheless, it is the most comprehensive data set of its kind collected for Wellington Harbour. Four water column parameters were analysed: temperature, salinity, chlorophyll *a* concentration and turbidity.

Data analysis

Two sets of data were selected and analysed. One set represented data obtained at all four sites between August 2002 and September 2003 (data were not obtained in July 2003), and the second set represented data obtained at Seatoun and Matiu-Somes Island between March 2002 and September 2003 (data were not obtained in July 2002 and July 2003). Within each data set, differences among sites and months for each parameter were analysed. Further, the influence of the parameters on aspects of intertidal mussel ecology

are analysed in conjunction with the biological data collected in this study and discussed in the following chapters.

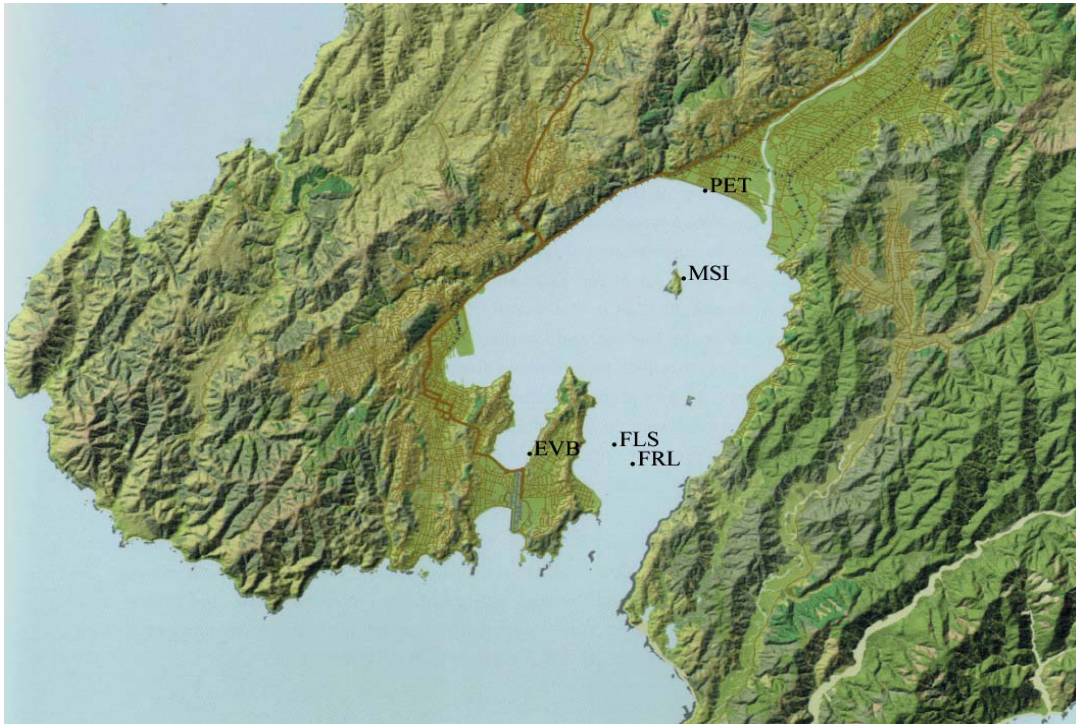


Figure 2.2. Map of Wellington Harbour with the sites of data loggers deployment (adapted from Molloy & Smith, 2002). PET – Petone, MSI – Matiu-Somes Island, FLS – Falcon Shoal, FRL – Front Lead, EVB – Evans Bay.

Plots of the auto-correlation function for each variable confirmed no correlation if a lag of 48 hours was used (Hurlbert, 1984; Venables & Ripley, 2002). Subsequently, to reduce the size of data sets, but to maintain its integrity, data points were allocated to separate bins of 48-hour duration. Comparison of the raw (non-binned) and the binned data sets indicated that the temporal trends of both were similar and that the binned data set was representative of the raw data set. All subsequent analyses were carried out on the binned data set. CTD data were \log_{10} -transformed in order to meet the requirements of distribution normality and homogeneity of variances. Subsequently, a repeated-measures ANOVA was performed on each data set to investigate the spatial and temporal differences in each water column parameter. ANOVA procedure was employed despite the fact that data showed some non-normality (even after transformation), as these procedures are sufficiently robust against even gross deviations from normality and

variance homogeneity, and in situations when the number of data points is large ($n > 100$), as was the case in this study (Zar, 1984; Quinn & Keough, 2002).

A non-parametric correlation coefficient *Gamma* (γ) was employed to investigate correlations between the water column variables, in particular between turbidity and concentration of chlorophyll *a*. The *Gamma* statistic is preferable to Spearman's *R* or Kendall's *Tau* (*T*), in particular when data set includes many tied observations, as was the case in this experiment between chlorophyll *a* concentration and turbidity. *Gamma* expresses the probability of agreement between the rank-ordered variables being tested (Liebetrau, 1983, Stanisiz, 1998; Zielinski, 1999; Gardner et al., 2004).

Finally, the Principal Component Analysis (PCA) was used as a multivariate exploratory technique. PCA was chosen as a tool to summarise and examine site-specific and time-dependent relationships among variables. In PCA, separate points representing each variable in each data set can present a summary of the overall variation. Similarly, separate points representing each variable can further show the overall variation at each site. PCA was employed here for raw data for all four variables, and is subsequently presented in the form of site-specific scatterplots. PCA analysis was performed on residuals of raw data, as this technique has been shown to best reveal gross features of the data, where the known data structure had been removed (Venables & Ripley, 2002). All statistical analyses were performed using Statistica software version 6.0 (StatSoft Inc. 2001, USA).

2.3. Results

Two separate data sets were independently analyzed: Seatoun, Matiu-Somes Island, Evans Bay and Petone data recorded between August 2002 and September 2003, and Seatoun with Matiu-Somes Island data collected between March 2002 and September 2003. Tables 2.1 and 2.2 give descriptive statistics for each data set.

Table 2.1. Descriptive statistics. All sites, August 2002 – September 2003.

Parameter/Site	N	Mean	Min.	Max.	SD
Temp. (°C)					
Evans Bay	147	13.498	10.175	18.766	2.223
Matiu-Somes Island	148	13.815	10.303	18.135	2.483
Seatoun	167	13.909	10.548	17.886	2.250
Petone	158	13.402	10.003	18.557	2.254
Salinity (PSU)					
Evans Bay	147	34.894	29.128	36.273	1.649
Matiu-Somes Island	148	33.371	29.002	34.697	0.959
Seatoun	167	29.798	15.663	34.879	5.384
Petone	158	31.786	20.623	34.936	2.722
Chl. a ($\mu\text{g l}^{-1}$)					
Evans Bay	147	8.885	0.177	14.245	4.354
Matiu-Somes Island	148	1.174	0.062	10.874	1.655
Seatoun	167	2.603	0.077	22.615	2.977
Petone	158	1.91	0.073	8.126	1.031
Turb. (FTU)					
Evans Bay	147	10.489	0.208	27.360	4.749
Matiu-Somes Island	148	16.531	1.163	103.831	11.240
Seatoun	167	8.024	0.403	43.187	9.841
Petone	158	7.244	0.346	72.521	8.182

Table 2.2. Descriptive statistics. Matiu-Somes Island and Seatoun, March 2002 – September 2003.

Parameter	N	Mean	Min.	Max.	SD
Temp. (°C)					
Matiu-Somes Island	184	13.968	10.302	18.135	2.343
Seatoun	199	14.211	10.707	33.459	2.591
Salinity (PSU)					
Matiu-Somes Island	184	33.275	29.002	34.699	0.942
Seatoun	199	30.496	15.663	34.878	5.027
Chl. a ($\mu\text{g l}^{-1}$)					
Matiu-Somes Island	184	1.213	0.062	10.874	1.770
Seatoun	199	2.298	0.077	33.459	3.027
Turb. (FTU)					
Matiu-Somes Island	184	14.632	1.163	103.831	11.008
Seatoun	199	17.521	0.403	118.074	27.273

All sites, August 2002 – September 2003.

Seasonal and spatial patterns were evident in data collected at all sites between August 2002 and September 2003 (Table 2.1). Temperature displayed typical seasonal fluctuation (Fig. 2.3). Maximum mean monthly temperature (17.84°C) was recorded at Evans Bay in January 2003. The minimum mean monthly temperature (10.69°C) was recorded at Matiu-Somes Island in August 2002. In January 2003 average monthly

temperature at Petone was noticeably reduced (12.84°C). Simultaneously, average monthly salinity was also reduced at this site in January 2003 (27.09 PSU) (Fig. 2.4), which suggests that reduced temperature and salinity were a result of heavy rainfall and subsequent formation of a cold and freshwater plume that enters the Harbour from the Hutt River.

Salinity displayed significant variation (Fig. 2.4), with the highest mean monthly salinity recorded in April 2003 at Evans Bay (36.15 PSU) and the minimum monthly salinity (21.67 PSU) at Seatoun in March 2003. Significant decreases in salinity were recorded between December 2002 and February 2003 at Matiu-Somes Island, Petone and Evans Bay (values as low as 32–28 PSU). Salinity readings were also reduced at Seatoun between March and April 2003 (21.74 PSU).

Chlorophyll *a* concentration varied significantly around the Harbour and the data suggest a division of Wellington Harbour into several areas, each with different prevalent regime (Fig. 2.5). Maximum mean monthly chlorophyll *a* concentration ($14.14\ \mu\text{g l}^{-1}$) was recorded at Evans Bay in April 2003; the minimum mean monthly chlorophyll *a* concentration ($0.27\ \mu\text{g l}^{-1}$) was recorded at Matiu-Somes Island in December 2002. The northern part (represented here by Petone and Matiu-Somes Island) had consistently low chlorophyll concentration ($0\text{--}2\ \mu\text{g l}^{-1}$), and this trend displayed a slight variation at the end of the recording period. At Seatoun, chlorophyll *a* concentration was greatly variable, originally elevated (up to $8.41\ \mu\text{g l}^{-1}$ in November 2002), and later reduced to $2\text{--}3\ \mu\text{g l}^{-1}$ per month. The inner zone of the Harbour, represented here by Evans Bay, had significantly higher chlorophyll *a* concentration compared to the other sites. Average chlorophyll concentration at Evans Bay was $9.98\ \mu\text{g l}^{-1}$.

Turbidity was highly variable at all sites throughout the study period and no clear pattern was found (Fig. 2.6). The highest mean monthly value was recorded in September 2003 at Matiu-Somes Island and Seatoun (34.02 and 32.28 FTU, respectively). The lowest mean monthly turbidity ($0.70\ \text{FTU}$) was recorded at Petone in December 2002.

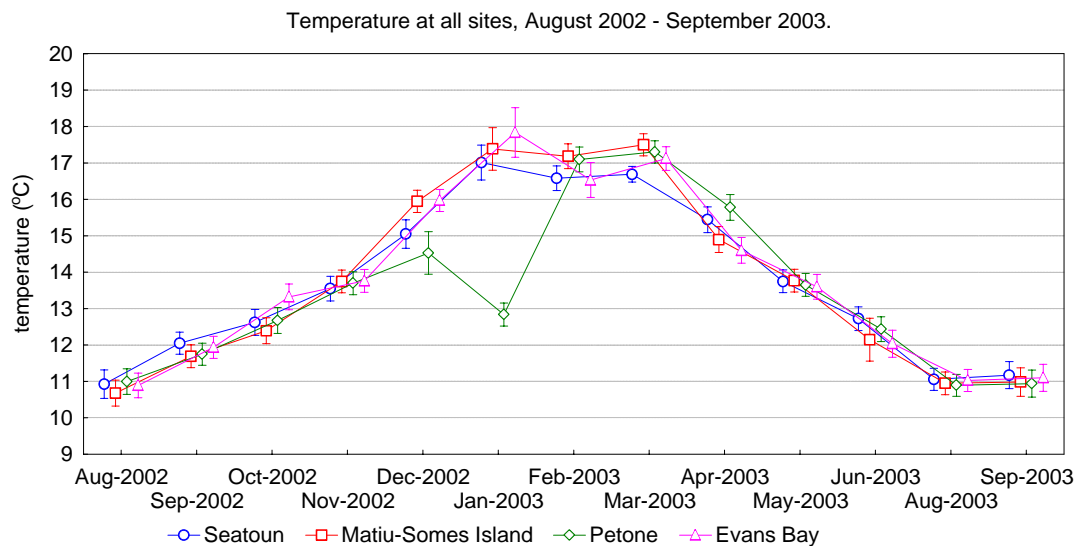


Figure 2.3. Temperature at all sites, August 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

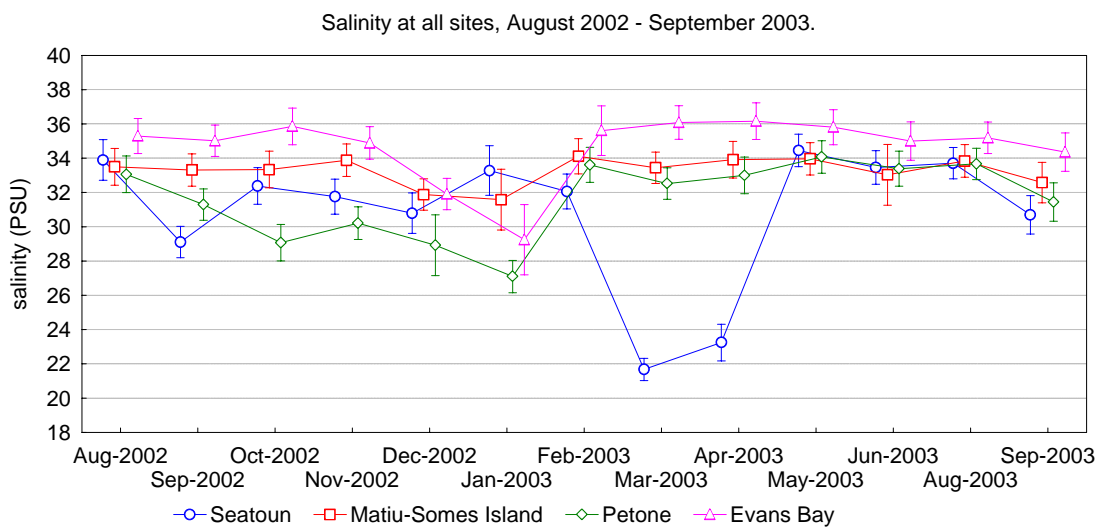


Figure 2.4. Salinity at all sites, August 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

Repeated-measures ANOVA revealed significant spatial and temporal variability of the water column parameters in this data set (Table 2.3). Among sites, Evans Bay stands out as the warmest site, where the water is also most saline and most chlorophyll-rich (Table 2.5). The overall model for each variable in this data set was accepted (Table 2.4).

Table 2.3. MANOVA, all sites, August 2002 – September 2003.

Effect	λ -value	Effect df	Error df	F	<i>p</i> -value
Site	0.203	12	1495.141	102.975	<0.001
Month	0.024	48	2178.478	73.598	<0.001
Site*Month	0.069	144	2252.933	14.887	<0.001

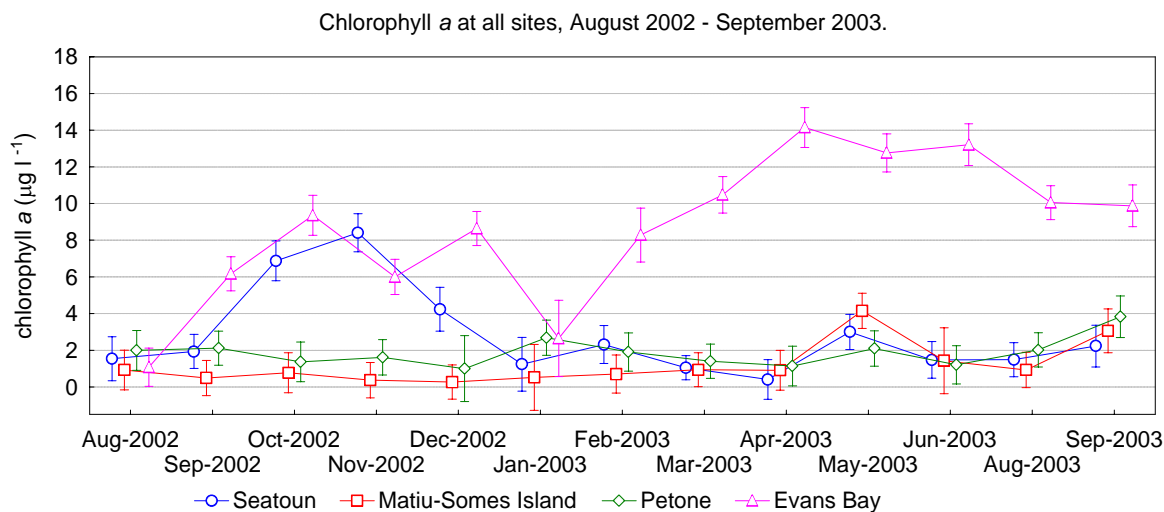
Figure 2.5. Chlorophyll *a* at all sites, August 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

Table 2.4. MANOVA, overall model. All sites, August 2002 – September 2003.

Variable	R	R ²	SS Model	df Model	MS Model	F	<i>p</i> -value
Temperature	0.970	0.942	3.048	51	0.060	180.414	<0.001
Salinity	0.877	0.769	1.716	51	0.034	37.141	<0.001
Chlorophyll <i>a</i>	0.874	0.764	127.072	51	2.492	36.087	<0.001
Turbidity	0.849	0.720	95.939	51	1.881	28.678	<0.001

Table 2.5. Differences among sites in each water parameter.

Variable	Differences among sites	<i>p</i> -value
Temperature (°C)	Evans Bay=Matiu-Somes Island=Seatoun>Petone	<0.001
Turbidity (FTU)	Matiu-Somes Island>Evans Bay>Seatoun=Petone	<0.001
Chlorophyll <i>a</i> (µg l ⁻¹)	Evans Bay>Seatoun=Petone>Matiu-Somes Island	<0.001
Salinity (PSU)	Evans Bay>Matiu-Somes Island>Petone>Seatoun	<0.001

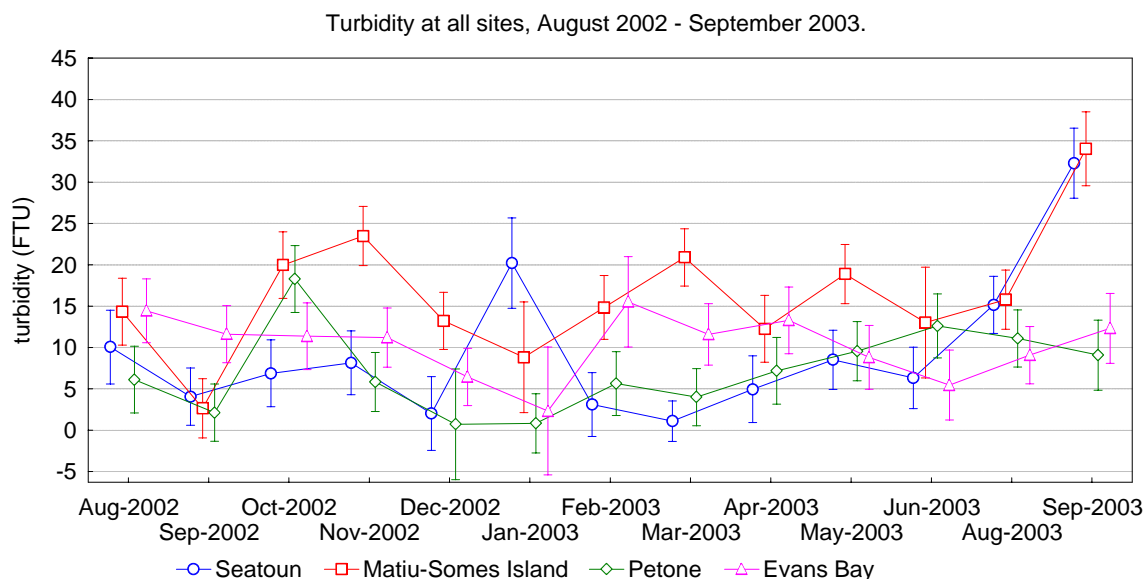


Figure 2.6. Turbidity at all sites, August 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

Gamma (γ), the non-parametric correlation coefficient, revealed a number of correlations among the water column characteristics from this data set (Tables 2.6-2.9). Turbidity and chlorophyll *a* concentration were significantly correlated at Seatoun, but not at Evans Bay, Matiu-Somes Island and Petone.

Table 2.6. *Gamma* values for water parameters at Evans Bay.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.56$	$p=0.04$	$p=0.03$
Turbidity	$\gamma=-0.033$	-	$p=0.39$	$p<0.001^*$
Chlorophyll <i>a</i>	$\gamma=0.112$	$\gamma=-0.048$	-	$p=0.001^*$
Salinity	$\gamma=0.123$	$\gamma=0.258$	$\gamma=0.177$	-

* Significant after Bonferroni correction for multiple testing.

Table 2.7. *Gamma* values for water parameters at Seatoun.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p < 0.001^*$	$p=0.11$	$p < 0.001^*$
Turbidity	$\gamma=-0.314$	-	$p=0.043$	$p < 0.001^*$
Chlorophyll <i>a</i>	$\gamma=-0.083$	$\gamma=0.106$	-	$p < 0.001^*$
Salinity	$\gamma=-0.311$	$\gamma=0.379$	$\gamma=0.172$	-

* Significant after Bonferroni correction for multiple testing.

Table 2.8. *Gamma* values for water parameters at Matiu-Somes Island.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.75$	$p=0.027$	$p=0.76$
Turbidity	$\gamma=0.018$	-	$p=0.039$	$p=0.28$
Chlorophyll <i>a</i>	$\gamma=-0.122$	$\gamma=0.114$	-	$p=0.33$
Salinity	$\gamma=0.017$	$\gamma=0.060$	$\gamma=0.054$	-

Table 2.9. *Gamma* values for water parameters at Petone.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.005$	$p=0.003^*$	$p=0.379$
Turbidity	$\gamma=-0.151$	-	$p=0.036$	$p<0.001^*$
Chlorophyll <i>a</i>	$\gamma=-0.161$	$\gamma=-0.112$	-	$p=0.088$
Salinity	$\gamma=0.047$	$\gamma=0.341$	$\gamma=-0.091$	-

* Significant after Bonferroni correction for multiple testing.

In the Principal Component Analysis (PCA), PC1 and PC2 explained 53.56% of the total variation in this data set (Fig. 2.7). At Seatoun, 61.88% of the variation in the data set was explained, and 54.98% at Evans Bay (Fig. 2.8). The procedure also explained 65.01% variation in this data set at Petone and 64.03% at Matiu-Somes Island (Fig. 2.9). At most sites, the PCA procedure displayed turbidity and chlorophyll *a* concentration as points near each other, which revealed a degree of similarity between these variables.

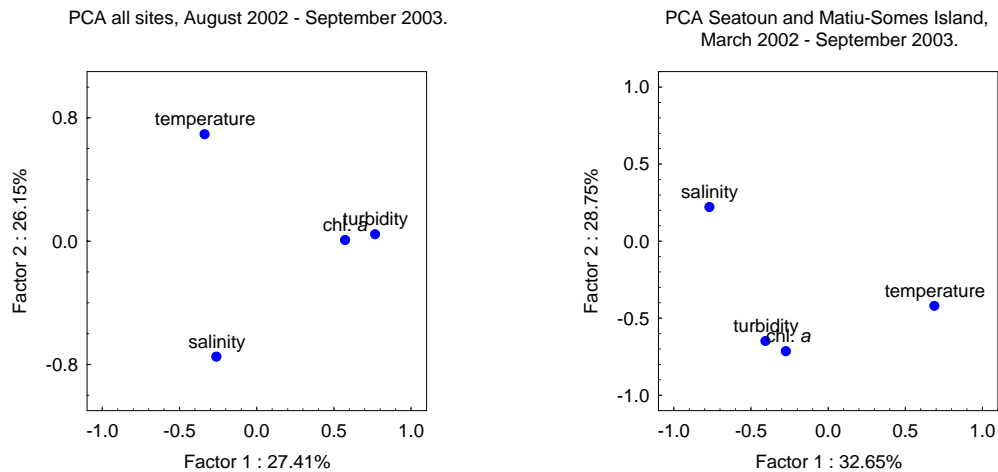


Figure 2.7. PCA global results for both data sets.

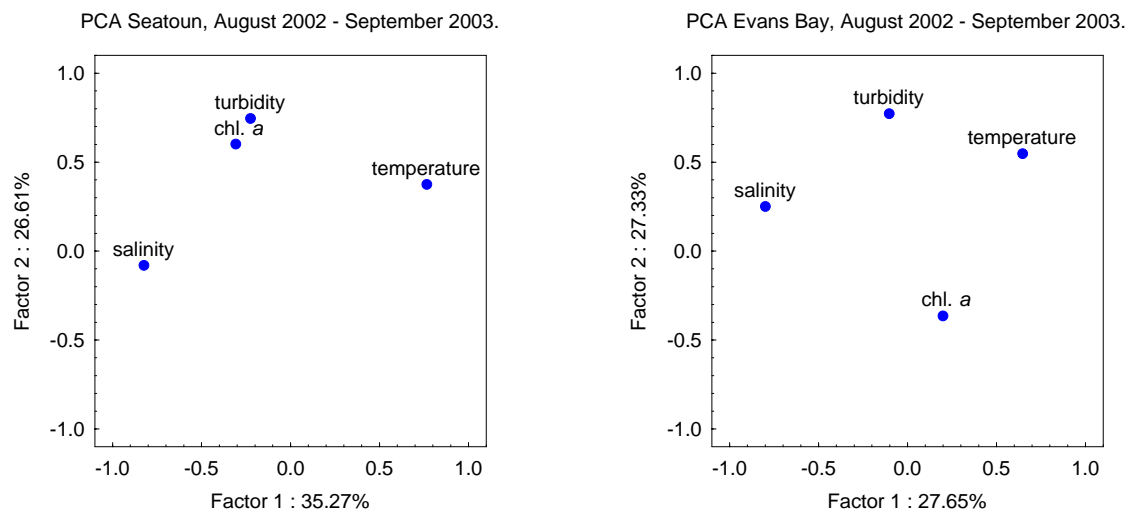


Figure 2.8. PCA results at Seatoun and Evans Bay, August 2002 – September 2003.

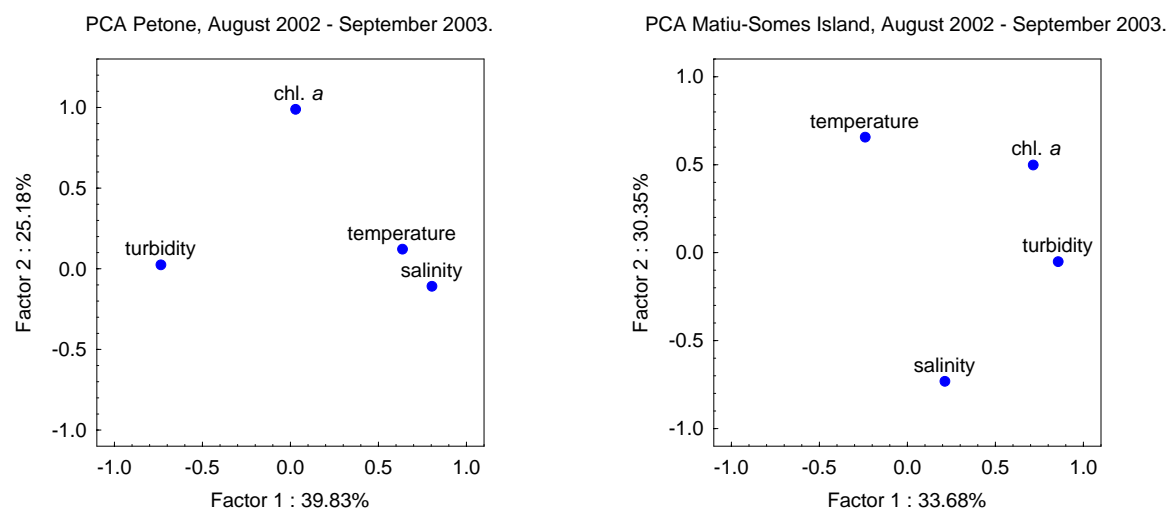


Figure 2.9. PCA results at Petone and Matiu-Somes Island, August 2002 – September 2003.

Seatoun and Matiu-Somes Island, March 2002 – September 2003.

Spatial and temporal variability in data were evident (Table 2.2). Throughout the recording period, temperature displayed seasonal fluctuations, with the highest mean monthly temperature (17.50°C) recorded at Matiu-Somes Island in March 2003. The

minimum mean monthly temperature (10.68°C) was also recorded at Matiu-Somes Island in August 2002 (Fig. 2.10).

Chlorophyll *a* concentration was variable, as the CTD at Seatoun recorded higher concentration throughout most of the recording period. The highest mean monthly chlorophyll concentration ($8.41 \mu\text{g l}^{-1}$) was recorded at Seatoun in November 2002, whereas the minimum mean monthly chlorophyll *a* concentration ($0.01 \mu\text{g l}^{-1}$) was recorded at Matiu-Somes Island in May 2002 (Fig. 2.11).

Although the maximum mean monthly salinity (34.45 PSU in May 2003) was recorded at Seatoun, salinity at this site was generally reduced for almost entire sampling period (recorded range between 34 and 31 PSU). The lowest mean monthly salinity at Seatoun was 21.67 PSU in March 2003. At Matiu-Somes Island salinity was less variable and it ranged between 32 and 34 PSU. Maximum monthly salinity at Matiu-Somes Island was 34.11 PSU in February 2003 and minimum monthly salinity was 31.58 PSU in January 2003 (Fig. 2.12).

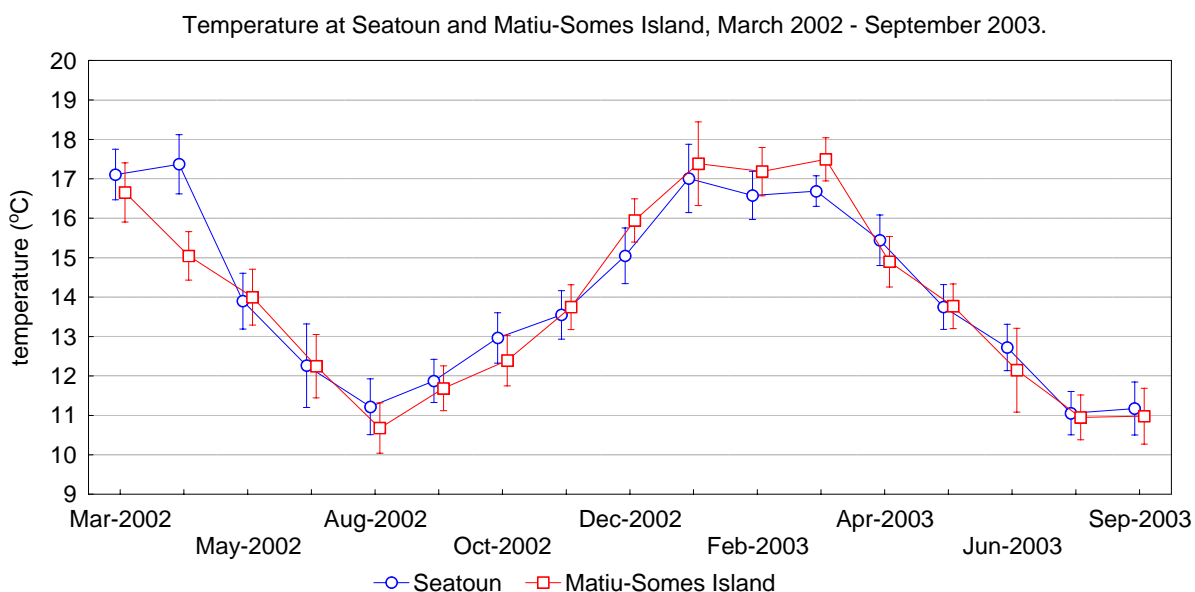


Figure 2.10. Temperature at Seatoun and Matiu-Somes Island, March 2002 – September 2003. Points represent mean monthly values \pm %95 confidence interval.

Turbidity oscillated around 20 FTU for most of the sampling period (Fig. 2.13), indicating that suspended particles were always present in the water column at both sites. Originally, however, turbidity was significantly higher at Seatoun (March – May 2002) and the maximum mean monthly turbidity was recorded at Seatoun in April 2002 (97.14 FTU). Maximum monthly turbidity at Matiu-Somes Island was 34.0 FTU in September 2003. Minimum mean monthly salinity (1.09 FTU) was recorded at Seatoun in March 2003.

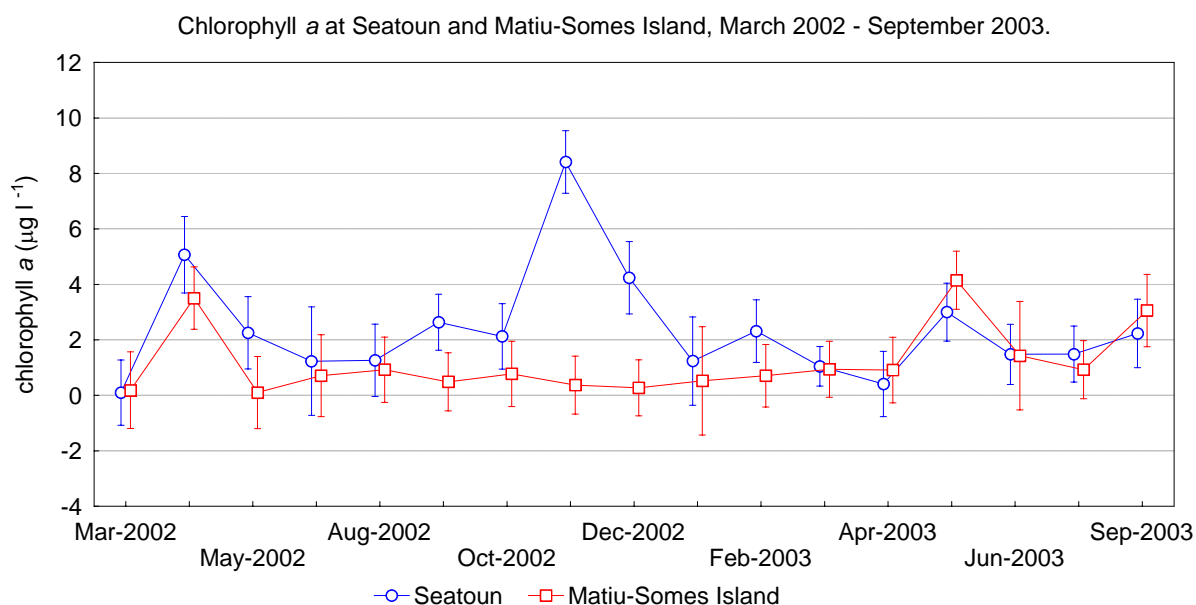


Figure 2.11. Chlorophyll *a* at Seatoun and Matiu-Somes Island, March 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

Repeated-measures ANOVA revealed significant spatial and temporal variability of the water column parameters in this data set (Table 2.10). Seatoun was shown as a site with marginally warmer and significantly more chlorophyll *a* - rich water, whereas water at Matiu-Somes had significantly higher salinity and turbidity (Table 2.12). The overall model for each variable at both sites was accepted (Table 2.11).

Table 2.10. MANOVA, Seatoun and Matiu-Somes Island, March 2002 – September 2003.

Effect	λ -value	Effect df	Error df	F	p-value
Site	0.537	4	346.000	74.608	<0.001
Month	0.01	64	1356.805	46.792	<0.001
Site*Month	0.075	64	1356.805	19.845	<0.001

Table 2.11. MANOVA, overall model for each variable. Seatoun and Matiu-Somes Island, March 2002 – September 2003.

Variable	R	R ²	SS Model	df Model	MS Model	F	p-value
Temperature	0.948	0.900	1.853	33	0.056	94.688	<0.001
Turbidity	0.888	0.788	88.993	33	2.697	39.239	<0.001
Salinity	0.885	0.782	1.291	33	0.039	38.038	<0.001
Chlorophyll <i>a</i>	0.859	0.738	74.357	33	2.253	29.79	<0.001

Table 2.12. Differences in water parameters between Seatoun and Matiu-Somes Island.

Variable	Differences among sites	p-value
Temperature (°C)	Seatoun=Matiu-Somes Island	<0.001
Turbidity (FTU)	Matiu-Somes Island>Seatoun	<0.001
Chlorophyll <i>a</i> (µg l ⁻¹)	Seatoun>Matiu-Somes Island	<0.001
Salinity (PSU)	Matiu-Somes Island>Seatoun	<0.001

Gamma (γ) revealed significant correlation among the water column characteristics recorded at both sites. Turbidity and chlorophyll *a* were not significantly correlated at Seatoun (Table 2.13), but they were correlated at Matiu-Somes Island (Tables 2.14).

Table 2.13. *Gamma* values for water parameters at Seatoun.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.009$	$p=0.001^*$	$p<0.001^*$
Turbidity	$\gamma=-0.125$	-	$p=0.31$	$p<0.001^*$
Chlorophyll <i>a</i>	$\gamma=-0.155$	$\gamma=-0.048$	-	$p=0.08$
Salinity	$\gamma=-0.238$	$\gamma=0.315$	$\gamma=0.084$	-

* Significant after Bonferroni correction for multiple testing.

Table 2.14. *Gamma* values for water parameters at Matiu-Somes Island.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.81$	$p=0.051$	$p=0.28$
Turbidity	$\gamma=0.012$	-	$p=0.008$	$p<0.001^*$
Chlorophyll <i>a</i>	$\gamma=-0.097$	$\gamma=0.130$	-	$p=0.21$
Salinity	$\gamma=-0.053$	$\gamma=0.167$	$\gamma=0.062$	-

* Significant after Bonferroni correction for multiple testing.

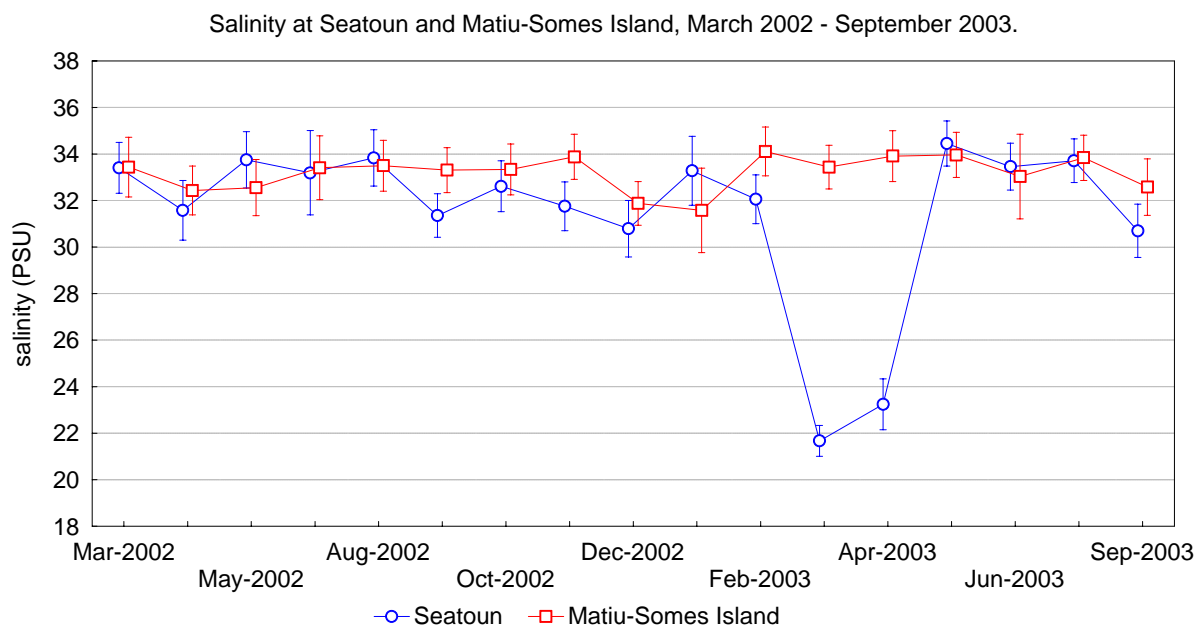


Figure 2.12. Salinity at Seatoun and Matiu-Somes Island, March 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

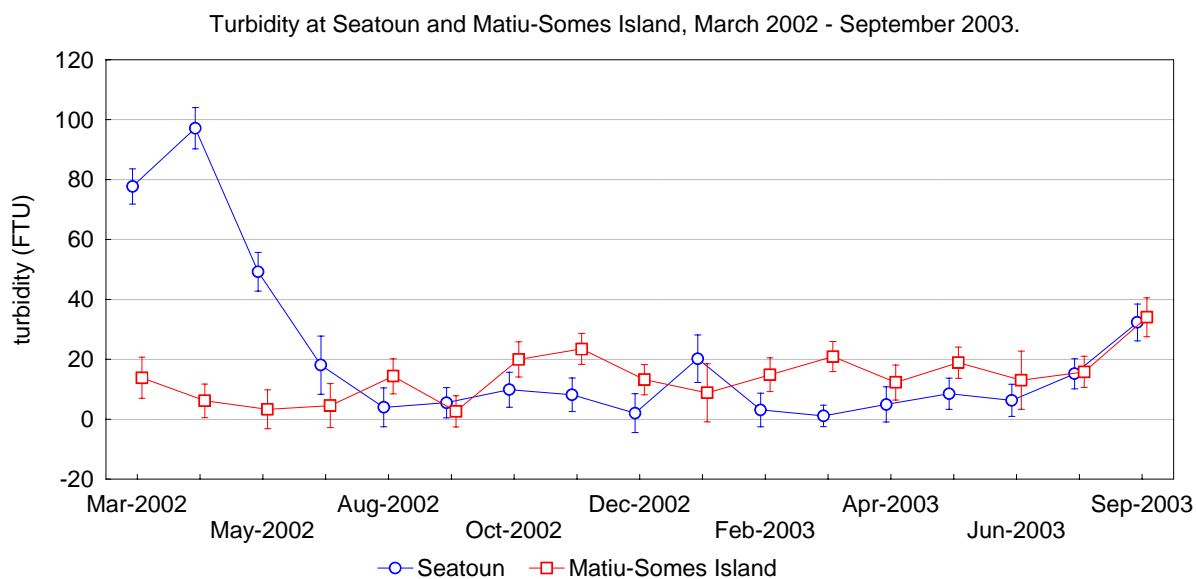


Figure 2.13. Turbidity at Seatoun and Matiu-Somes Island, March 2002 – September 2003. Points represent mean monthly values \pm 95% confidence interval.

Employed as an exploratory technique here, PCA explained 61.40% of the total variation in this data set (Fig. 2.7). When performed again for each site separately, PCA explained 61.92% of the variation among the environmental variables at Seatoun and 62.29% at Matiu-Somes Island (Fig. 2.14). As in the previous data set, PCA displayed concentration of chlorophyll *a* and turbidity as points lying close to each other, which suggests a degree of similarity between these two variables.

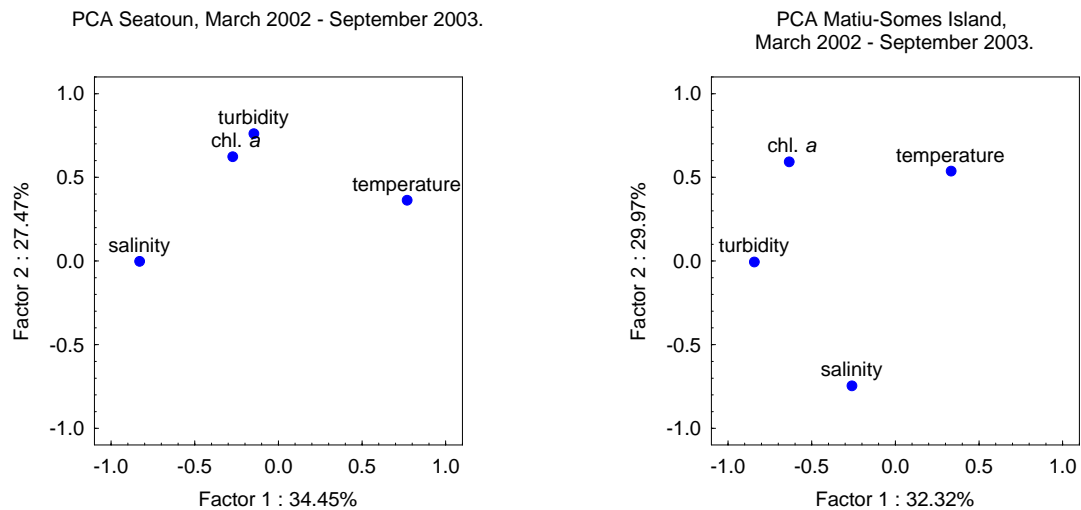


Figure 2.14. PCA results at Seatoun and Matiu-Somes Island, March 2002 – September 2003.

2.4. Discussion

Significant spatial and temporal differences among the seawater variables were detected in the course of this study. Data obtained in the present study are at odds with the traditional view that Wellington Harbour is a homogenous and well-mixed body of water. Instead, the data suggest that distinct aquatic zones are present in Wellington Harbour. Thus, in the inner Harbour, represented here by Evans Bay, water has consistently high salinity and is rich in chlorophyll *a*. Inner areas of Wellington Harbour probably receive significant volumes of terrigenous nutrients, further stimulating the local phytoplankton production. However, further research is needed to clarify the role of the land-derived nutrients in chlorophyll *a* production. In the northern areas of the Harbour, such as Petone, heavily influenced by the Hutt River discharge of fresh water,

salinities are frequently reduced and sometimes high-turbidity loads of organic matter can be detected. Such riverine inputs often form a distinct plume travelling south, and altering the hydrological regimes within the Harbour. It also appears that in central Harbour zone, represented here by Matiu-Somes Island, salinity, chlorophyll *a* and turbidity regimes can be highly variable. The Hutt River plume, most often travelling south along the Eastbourne coast, heavily affects these central parts of the Harbour. However, salinity, chlorophyll *a* and turbidity were variable at Seatoun. A CTD deployed there also detected elevated concentrations of chlorophyll *a*, as well as reduced salinity, although the readings were not as consistent as at Evans Bay, which suggests more variable chlorophyll *a* and salinity regime in the Harbour areas surrounding Seatoun. Variable salinity at Seatoun most likely originated not only from a freshwater runoff after storm events, but also from the cool and freshwater plume that frequently enters the Harbour from the Hutt River and can travel along the Eastbourne coast, as far south as the Harbour entrance.

The data analysis showed that temperature, salinity and chlorophyll *a* readings were higher at Evans Bay than any other site during the study period (Tables 2.5 and 2.12). This is perhaps explained by the location of the bay, which is a shallow body of water, largely surrounded by north-south oriented land masses of the Miramar Peninsula in the east, Kilbirnie and Rongotai flats in the south and the Hataitai and Roseneath hills in the west. Such a configuration facilitates nutrients input from the land, as well as input from the numerous storm water drains that feed into Evans Bay. Although the scale of the direct input of chlorophyll *a* into the Harbour remains unclear, it is likely that elevated concentrations of nutrients enter the Harbour from the land through the stormwater drains. Such terrigenous input of nutrients stimulates the chlorophyll *a* production in the Harbour, which in turn was detected by the data loggers (Hickman *et al.*, 1991; Gibbs *et al.*, 1992; Wieters *et al.*, 2003).

Further, there is evidence that the circulation rate in the Harbour is not steady at all locations. Heath (1977) reports that the flow rate is at its fastest near the entrance channel ($0.45\text{--}0.5\text{ m s}^{-1}$) and then it slows down substantially in the main Harbour (0.03

m s^{-1}), before it slows down even further, to 0.015 m s^{-1} in Lambton Harbour. One can therefore expect that the flushing time of Evans Bay be longer compared to the central parts of Wellington Harbour. As a result of such reduced water circulation rate in inner Harbour areas, longer periods of time are required for the water of to be replaced in Evans Bay. This increased water residence period further contributes to the fact that Evans Bay waters are chlorophyll *a*-rich, because with longer residence time, the waters can become more saturated with nutrients entering the Bay through numerous storm water drains, thus stimulating local chlorophyll *a* production.

Water temperature data obtained in this study are very similar to seasonal temperature cycle reported by Helson *et al.* (2004) who recorded 17.6°C in summer and 11.8°C in winter, and Booth (1975) (17.2°C in summer and 11.2°C in winter). In the present study, mean winter and summer values oscillated around $17\text{--}18^{\circ}\text{C}$ in summer and $10\text{--}11^{\circ}\text{C}$ in winter (Figs. 2.3 and 2.10). Maxwell (1956) reported difference in temperature between western (Oriental Bay) and eastern Wellington Harbour (York Bay). Western Harbour waters were warmer (14°C) than eastern Harbour waters ($12.5\text{--}13.5^{\circ}\text{C}$). Such a change in temperature was accompanied by reduced salinities, from 33.5‰ – 35‰ in Oriental Bay to 31.0‰ – 32.0‰ in York Bay. These two phenomena were attributed to the fresh water plume entering the Harbour from the Hutt River and flowing south along the Eastbourne coastline.

Large volumes of organic matter enter the Harbour in the north as a high-turbidity plume originating from the Hutt River. It is estimated (McConchie, 2000) that the Hutt River drains an area of 555.5 km^2 and discharges into the Harbour on average 25.6 m^3 of fresh water every second. Other freshwater inputs within the Harbour include Waiwhetu ($0.27 \text{ m}^3 \text{ s}^{-1}$) and Korokoro streams ($0.25 \text{ m}^3 \text{ s}^{-1}$). In the prevailing north-westerly wind conditions in Wellington, the Hutt River plume is often pushed against the eastern shores of the Harbour (Brodie, 1958; McConchie, 2000). As this brackish plume travels south towards the Harbour entrance, it passes the north-eastern shores of Matiu-Somes Island. A CTD deployed there detected conditions of high turbidity and reduced salinity. Helson *et al.* (2004) found greatly reduced salinity at Eastbourne between spring and autumn,

with the lowest salinity reading obtained 28.0‰, which strongly points at the Hutt River plume. Booth (1975) also found that northern part of Wellington Harbour is prone to lowered salinities resulting from freshwater riverine inflow.

Turbidity has been classified as an ecologically important parameter (Mylvaganam & Jakobsen, 2000) and can be regarded as a good indicator of the presence of various suspended particles in the ecosystem. The particle list includes clay, silt, plankton or organic and inorganic compounds. High turbidity, when combined with sedimentation, can be related to a decrease in primary production (Henley *et al.*, 2000), which can lead to decreases in available food, reproduction or recruitment. Although no apparent seasonal turbidity trend was detected in the present study at any site, elevated turbidity recorded at Seatoun and Matiu-Somes Island between September 2003 and a short-lived turbidity peak in April - May 2002 at Seatoun might be related to increased rainfall. In autumn 2002 and spring 2003 turbidity appeared as closely related to chlorophyll *a* levels (Tables 2.6–2.9 and 2.13–2.14), and the PCA results confirmed this (Figs. 2.9 and 2.14). The significant turbidity-chlorophyll correlations means that the particles suspended in the water column most likely were phytoplankton cells. This also means that the conditions of high food concentration were favourable for filter-feeders, such as mussels. However, it is possible that at the same site reduced chlorophyll levels accompany elevated turbidity, as was the case at Matiu-Somes Island in both data sets (Table 2.7-2.9, 2.14). Gardner *et al.* (2004) recorded low chlorophyll levels together with high turbidity, and explain this by suggesting that an oceanographic regime, such as greater current strength, could be responsible for such phenomena.

From the perspective of intertidal mussel communities, the presence of distinct zones within Wellington Harbour implies variability in the environmental regimes, which have impact on mussel ecology. Analysis of the temperature data suggested that mussel communities in Wellington Harbour are never limited by this parameter, so temperature-induced massive mussel mortalities rarely, if ever, occur. Thus, the water temperature regime in the Harbour is well within the tolerance range of mussels.

Variation of salinity or chlorophyll *a*, however, can affect mussel communities through reduced adult condition. Variable salinity and chlorophyll regimes could also affect larval recruitment rates to such communities, thus slowing down substrate recolonisation processes or the ability of the community to recover from occasional disturbance. Reduced salinity creates environmental osmotic stress for recruiting mussel larvae that, in order to survive, need to expend considerably more energy to cover the metabolic costs of osmoregulation. In bivalve larvae, these costs can only be covered through intensified food intake and subsequent energy release. In a low-seson regime, such as the one discovered at Matiu-Somes Island, this is difficult to achieve. As a result, one would expect reduced recruitment and survival of mussel larvae at such sites. Occasional pulses or consistently high seston concentration, as recorded in the present study for example at Seatoun and Evans Bay, respectively, can be a signal for the intertidal mussel communities that the environmental conditions are favourable for reproduction. Thus, it could be possible to find high larval recruitment at sites with elevated chlorophyll, although temperature is the major signal for spawning. Mussels, however, are opportunistic spawners, which means that water temperature is not a prerequisite, and other environmental stimuli, such as elevated seston concentration, can trigger spawning in mussels. Consequently, sites with elevated seston, and steady salinity would be characterised by elevated recruitment and community development.

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CHAPTER THREE:
CONDITION INDEX, GONAD MASS, PEA CRABS,
AND RECRUITMENT OF BIVALVE LARVAE

3.1. Introduction

Condition, volume of gonad tissue, and the current reproductive stage of bivalves are closely related. Intense reproductive activity often results in reduced gonad volume and therefore in reduced condition. This, in turn, heavily depends on the resources currently available to fuel the tissue growth of the animals. These ecological traits are all shaped by the parameters of the aquatic environment, such as temperature, salinity and the concentration of food. Thus, at the height of the reproductive season and spawning activity, when the gonad reaches its minimum volume, a negative relationship exists between mussel condition and the concentration of recruiting larvae in the water column.

This chapter investigates the interplay among several ecological traits of mussels, such as gonad mass, adult condition and environmental parameters affecting these traits in three mussel species in Wellington Harbour: *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*. Simultaneously, the effects of the pea crab *Pinnotheres novaezelandiae* on condition of their host mussels are investigated. Finally, the concentration of bivalve larvae in the water column is related to gonad mass and condition of these mussel species.

Mussel condition

Condition of mussels is typically expressed through condition index (hereafter referred to as CI), which has been widely applied in aquaculture as a useful indicator of bivalve growth and health (Smaal & van Stralen, 1990; Camacho *et al.*, 1995). The index allows marine scientists and aquaculturists to follow seasonal changes of nutrient reserves of the animals and thus evaluate the commercial quality of bivalves (Crosby & Gale, 1990; Hickman & Illingworth, 1980). CI is typically presented as the meat content

of the shellfish relative to total size of the animal. The meat content fluctuates according to environmental conditions, and as mussels undergo seasonal cycle of growth, glycogen is accumulated as the main energy source. As a result, the meat yield (i.e. tissue volume) will gradually improve and the condition of the animal will increase. During the reproduction phase however, mussels heavily utilise their reserves in order to meet the energetic requirements of gametogenesis and spawning. As a result, spawning leads to a decrease in flesh weight and lower CI. Thus, the volume of tissues will increase or decrease, reflecting conditions to which mussels are subjected. This would be particularly true about self-seeding communities, where the offspring production happens directly at a cost of adult condition. However, in many other communities, condition of adult mussels may not necessarily be directly reduced as a result of spawning, as larvae can be advected into a community from elsewhere (Palmer *et al.*, 1996).

The shell weight is relatively constant compared to flesh weight (Bayne, 1973), therefore any variation in tissue weight will alter the tissue weight to shell weight ratio, which consequently will increase or decrease throughout the year. This principle lies at the basics of various experimental methods for assessing bivalve condition, as specified by Davenport & Chen (1987) and Crosby & Gale (1990). The authors give a thorough review of various methods for calculating condition indices for mussels. They also note that freezing is a desirable and convenient handling method, which is flexible and makes the measurements less rushed. Freezing of the samples makes estimation of the total volume accurate and reduces the variance of the parameter measured. However, freezing can render the tissues too soft and macerated, which may create difficulty when trying to separate different body parts of the animal (McKinnon, 2002).

Mussels are not the only bivalve group in which condition has been investigated. Oysters, scallops, cockles and clams may too experience variation in condition, depending on environmental parameters. Westley (1959) was the first man to discuss the methods of calculating condition index, and calculated condition for two oyster species, *Crassostrea gigas* and *Ostrea luida* in Washington State. Haven (1960), who looked at seasonality of condition index of *Crassostrea virginica* in New York State, concluded

that the differences in levels of condition index were associated with the bottom characteristics and changes in water salinity. Cyclicity in condition index and glycogen content in Jamaican mangrove oysters *Crassostrea rhizophorae* were studied by Littlewood & Gordon (1988), who noted that condition was not reflected in glycogen content but was related to periods of post-spawning towards the end of each rainy season. Marsden & Pilkington (1995) investigated spatial and temporal variations in condition of New Zealand cockles *Austrovenus stutchburyi*. In that study, mean condition index fluctuated seasonally and it increased with higher salinity and higher chlorophyll *a* levels, depending on the site (marine or more estuarine). Hawkins and Rowell (1987) found that the presence of the sediment in the gut of the soft-shell clam *Mya arenaria* influenced the meat yield and subsequently the condition index. Rheault & Rice (1996) and Shriver *et al.* (2002) studied the bay scallop *Argopecten irradians*, whose growth rates and condition were linearly correlated with the average chlorophyll ration consumed.

Mussel gonad mass

When food concentration is high, mussels store the nutrients as glycogen, mainly in their adductor muscle and the gonad. Throughout most of the year gonad activity is minimal. With the onset of gametogenesis however, the energy reserves can be utilised in order to meet the requirements of the reproductive cycle. With glycogen levels being gradually reduced, the volume of gonad mass (hereafter referred to as GM) also decreases, thus leading to a decrease in the overall mussel condition. Thus, on a seasonal basis, CI increases during the period of energy storage and gametogenesis, and declines during spawning activity of mussels (Gosling, 2003). Further, the volume of gonad tissue is also of interest when the animal is under nutritional stress, because the gonad tissue can be reabsorbed and used to supplement an inadequate diet, thus further affecting mussel CI (Emmet *et al.*, 1987).

Bivalve recruitment

Intertidal communities are typically influenced by physical variables (including aspect of the shore, water temperature and salinity, and wave exposure) and biological variables (including food supply, predation and competition) (Connell, 1972; Paine, 1974; Barnes & Hughes, 2002). More recently however, larval supply to these communities, and subsequent larval settlement and recruitment, have been studied as additional factors affecting those intertidal communities (Connell, 1985a, b; Menge, 1991; Petraitis, 1991; McQuaid & Phillips, 2000). Settlement, defined as the process during which the larva descends from the plankton to the sea bottom and attaches itself to the suitable substrate with the byssus, is difficult to measure in the field and is usually inferred from recruitment data (Gosling, 2003). Recruitment has been defined as the process of successful colonisation after a specified amount of time (days or even weeks) during which some post-settlement larval mortality will have occurred (Seed & Suchanek, 1992). The process of larval settlement to a community often depends on near-shore hydrology affecting the transport of the larvae to the settlement sites, weather conditions prior to settlement, larval abnormalities, lack of adequate settlement substrate and larval mortality through predation (Farrell *et al.*, 1991; Roughgarden *et al.* 1991; Ebert *et al.*, 1994; Wing *et al.*, 1995; Navarette *et al.*, 2002; Gosling, 2003).

Larval settlement is a complex process. Bayne (1964) described the primary and secondary settlement of *Mytilus edulis* larvae in North Wales. His observations revealed that young plantigrades originally could first attach themselves to filamentous algae (primary settlement) and subsequently detach from them. A migratory phase would follow (secondary settlement) when plantigrades re-entered the water column and were transported by currents to sites of secondary attachment. This pattern was repeated several times until the final place of settlement. Pascual & Zampatti (1995) observed similar behaviour in the larvae of the oyster *Ostrea puelchana*: “The pediveliger larva actively explores the substratum, crawling back and forth on its foot over each particle of surface, stopping on certain substrata for variable periods of time, occasionally resuming swimming, and crawling further again, until final cementing”. However, *Mytilus* larvae

have been reported to settle directly from the water column onto adult mussel beds in Ireland (McGrath *et al.*, 1988), Spain (Cáceres-Martinez *et al.*, 1993) and Sweden (Kautsky, 1982). A similar phenomenon has been described for the greenshell mussel *Perna canaliculus* in New Zealand (Buchanan & Babcock, 1997) and the brown mussel *Perna perna* in South Africa (Lasiak & Barnard, 1995). Direct measurement of settlement in nature is difficult and usually settlement data are inferred from recruitment data, measured by counting the spat on natural substrates (such as filamentous algae) or artificial substrates. While the type of cultch (the substrate for settling larvae) used most often in hatcheries is mollusk shells, for experimental purposes various types of artificial substrates have been widely used. These include: plastic plates, asbestos, concrete, mortar, wood, glass, polystyrene, rope and domestic scour pads (e.g. Cranfield, 1970; Henschel *et al.*, 1990; McGrath *et al.*, 1994; Knuckey, 1995; Dobretsov & Miron, 2001; Phillips & Gaines, 2002). Unlike natural substrates, artificial materials have a relatively constant surface and texture, which makes quantifying the recruitment over fixed time periods easier (Gosling, 2003).

Dynamics in intertidal mussel communities

In investigating rocky intertidal communities, populations of mussels can be generally studied in terms of constant processes of gain and loss of individuals (Fig. 3.1), where loss to the population results from numerous factors, including human exploitation of mussels, vertebrate (e.g. fish or avian) and invertebrate (e.g. whelk, starfish or crab) predation, inter- and intraspecific competition among mussels, and effects of physical factors impacting mussel communities, such as wave action and desiccation. The population gain component is essential for developing the full picture of the dynamics in intertidal communities of mussels, with the new individuals gained predominantly through larval settlement and recruitment and, to an extent, through the immigration of mussel non-larval stages, for example from neighbouring communities. Because this component provides vital knowledge of how the communities are fuelled and replenished with new individuals, it needs to be investigated so that a link between larval and adult stages can be created.

Both of the components discussed above are affected by the environmental parameters, of which temperature, salinity, chlorophyll *a* concentration and turbidity are among the most widely studied. Temperature and salinity can be linked to various phases of bivalve lives, including gametogenesis and reproduction, larval settlement and recruitment, and subsequent growth and condition. Seston quality, often expressed as chlorophyll *a* concentration, expresses the concentration of phytoplankton on which filter feeders rely as food. It also points to dietary conditions in which those animals live, because a variety of suspended particles present in the water column, such as detritus, bacteria and phytoplankton, differently contribute to the nutrient acquisition by invertebrates (Gosling, 2003).

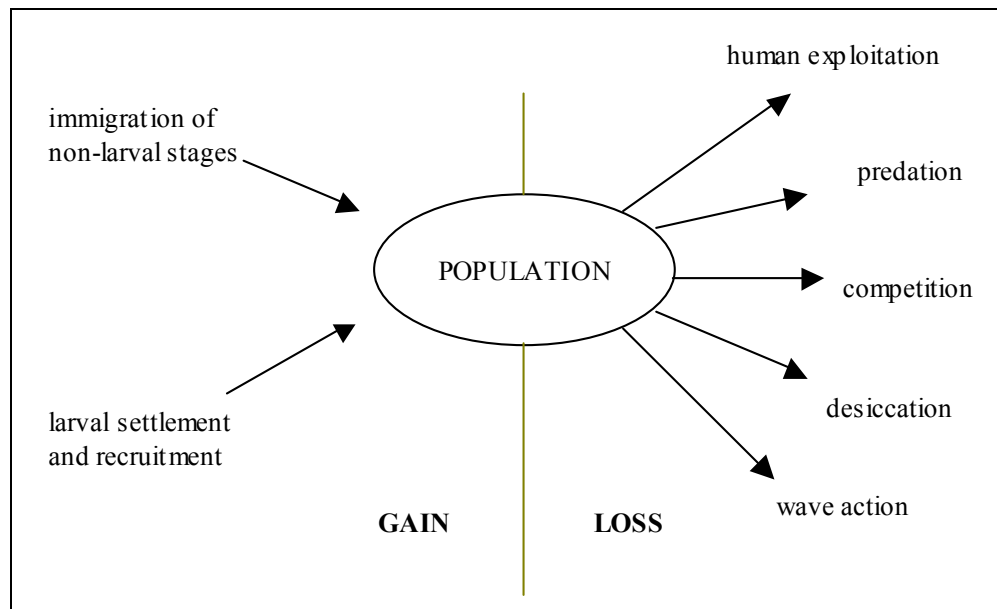


Figure 3. 1. Schematic representation of the dynamics in rocky intertidal mussel communities.

Seston quantity can be referred to as turbidity, and typically it is defined as the amount of suspended sediment particles in water (Mylvaganam & Jakobsen, 2000). Thus, chlorophyll *a* provides the qualitative measure of seston in the water column, while turbidity is a quantitative seston measure. When combined, the two parameters can provide the information about the amount of particles suspended in the water column, as

well as their potential nourishment value to seston-feeding bivalves. Therefore, from the ecological perspective, a study of seawater parameters is a powerful tool, helpful in understanding the differences underlying structure of rocky intertidal communities, the distribution and the dynamics among their members.

The present study attempts to quantify the recruitment of mussel larvae on an artificial substrate at several experimental sites inside Wellington Harbour, and to evaluate the influence of the environmental factors affecting such recruitment. Further, to link information from larval settlement and recruitment study with subsequent adult stages of mussel lifecycle, condition index, gonad mass and pea crab infestation were investigated in adult stages. In order to achieve this, a sampling programme was designed to take account of spatial and temporal variability in larval abundance and adult condition.

3.2. Materials and Methods

Water column characteristics

In order to obtain environmental parameters data, four Richard Brancker Research Ltd XR-420 loggers were used in this study. Because it was desirable to obtain the water column data from a maximum variety of environmental regimes within Wellington Harbour, as well as for practicality reasons (the loggers could only be safely deployed on underwater pilings), four experimental sites were selected for deployment of the CTDs: The Front Lead light (this logger, hereafter referred to as Seatoun logger, was moved to a nearby Falcon Shoal light in April 2003 due to renovation works at the Front Lead), Evans Bay (at Miramar wharf), Matiu-Somes Island (the northern wharf) and at Petone wharf. The Front Lead and Falcon Shoal logger will be hereafter referred to as the Seatoun logger, due to its proximity to Seatoun (Fig. 3.3). It was ascertained that the data loggers were as close to the experimental sites as possible, so that the water column characteristics provided by the loggers would be a fair reflection of the conditions at the experimental sites. The loggers were set to record water column data of temperature [$^{\circ}\text{C}$],

salinity measured in Practical Salinity Units [PSU], chlorophyll *a* [$\mu\text{g l}^{-1}$] and turbidity measured in Formazin Turbidity Units [FTU]. Each logger took a mean reading of the environmental variables over 10-second period every hour. Environmental data were obtained at the experimental sites between April 2002 and November 2003. Data from each data logger were downloaded onto a computer and subsequently analysed. Due to a lack of wharf pilings at Kau Point, no CTD was deployed there.

Data analysis

Two CTD data sets were created and analysed. The first CTD data set contained data relevant to the Condition Index experiment, obtained between August 2002 and May 2003. The second CTD data set contained data relevant to the Larval Settlement and Recruitment experiment, obtained between August 2002 and September 2003 (the analysis and results of this data set are discussed in chapter 2, data set a). In order to investigate the spatial and temporal differences in each water column parameter, a repeated-measures ANOVA was performed on each data set. In the analysis, the four parameters were specified as dependent variables, while site and month were specified as crossed factors. As described in previous chapter, *Gamma* (γ), a non-parametric correlation coefficient, was employed to investigate the correlation between water parameters at each site.

Condition Index

Twenty mussels of each species (*P. canaliculus*, *A. maoriana* and *M. galloprovincialis*) were collected from the low tide mark each month from June 2001 until May 2003 at each of four sites: Seatoun, Kau Point, rocks north of Matiu-Somes Island, and Evans Bay (Fig. 3.2). Hickman & Illingworth (1980) and Marsden & Weatherhead (1999) report that collecting mussels from different tidal heights can influence the value of CI of *P. canaliculus*, therefore care was taken to collect all mussels from the low intertidal zone. The animals were taken to the Island Bay Marine Laboratory (IBML) and dissected. Gonad tissue was excised from the somatic tissue and then those tissues were dried separately at 60°C for 24 – 48 hours (depending on the size

of the mussel) and weighed again. All weight measurements were made using an Ainsworth ACA 100 KS balance to an accuracy of 0.0001g. The shell length of each mussel was recorded using standard Vernier callipers to an accuracy of 1.0 mm. The CI was calculated according to Hickman and Illingworth (1980):

$$CI = DFW \times 100 / (WWW - WSW)$$

Where DFW = dry flesh weight (added dry gonad weight and somatic tissue weight)

WWW = whole wet weight of the animal

WSW = wet shell weight

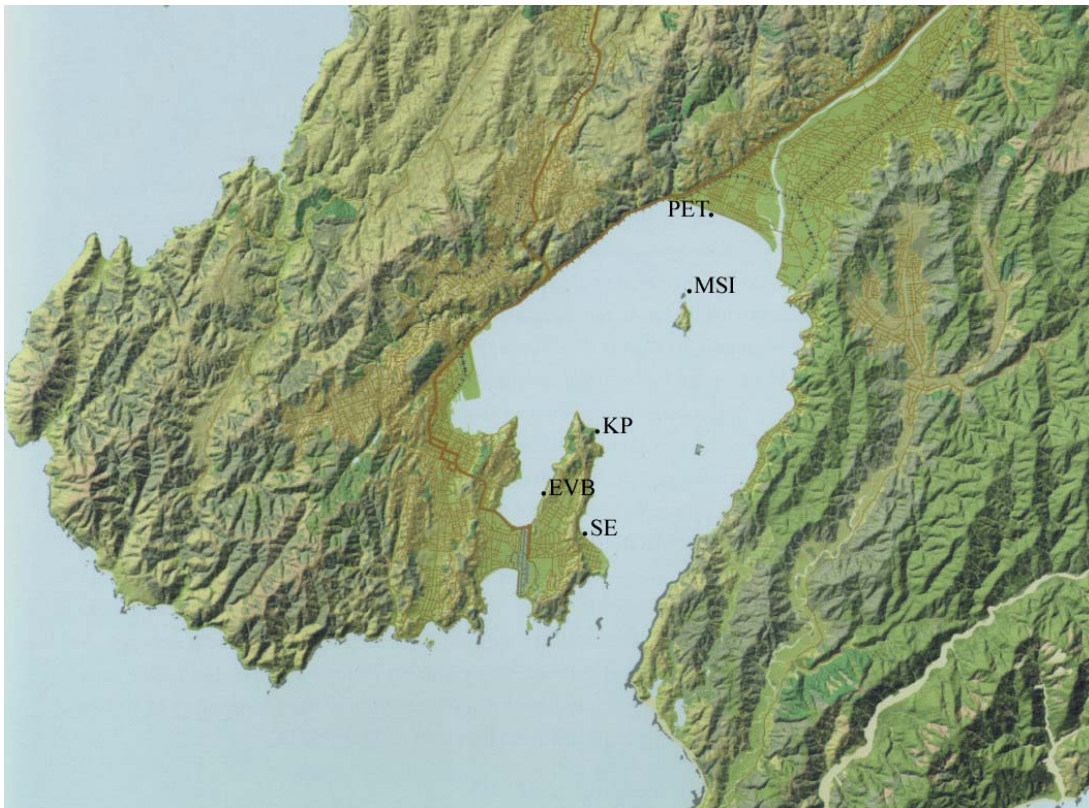


Figure 3. 2. Map of Wellington Harbour (adapted from Molloy & Smith, 2002). Condition Index experiment was conducted at MSI – Matiu-Somes Island, SE – Seatoun, EVB – Evans Bay and KP – Kau Point. Bivalve larval settlement experiment was conducted at MSI – Matiu-Somes Island, SE – Seatoun, EVB – Evans Bay and PET– Petone.

Data analysis

CI data were \log_{10} -transformed in order to meet the requirements of normality of distribution and homogeneity of variances. Analysis of Covariance (ANCOVA) was performed on \log_{10} -transformed data to test for differences in CI throughout all months in all species and at all sites. CI data were specified as a dependent variable, while gonad mass and shell length data were specified as covariates, and site, month and species were specified as crossed factors. In order to investigate spatial and temporal variation of species-specific CI, a series of post-hoc Honest Significant Difference (Tukey HSD) tests was performed. Subsequently, Pearson coefficient was employed to investigate species-specific correlation between CI and shell length (hereafter referred to as SL), CI and GM, and CI and water column characteristics. In order to avoid spurious correlations possibly driven by site and month effects in this analysis, residuals of CI, GM and SL were used instead of the raw data.

Gonad mass

GM data were collected for each dissected mussel, and subsequently analysed. Gonad tissues of the animals were processed in the same manner as the somatic tissues (see section 3.2.1 above).

Data analysis

GM data were \log_{10} -transformed in order to meet the requirements of normality of distribution and homogeneity of variances. ANCOVA was performed on \log_{10} -transformed GM data to investigate the differences in gonad mass throughout all months in all species at all sites. In the analysis, GM was specified as a dependent variable, CI and SL data were specified as covariates, and site, month and species specified as crossed factors. In order to investigate spatial and temporal variation of species-specific GM, a series of post-hoc Honest Significant Difference (Tukey HSD) tests was performed.

Subsequently, Pearson correlation coefficient was employed to investigate the relationship between GM of each species and the water column parameters.

Pea crab infestation

During the experiment, the presence of the pea crab *Pinnotheres novaezelandiae* in each mussel was recorded. The carapace width was measured to an accuracy of 1.0 mm and the pea crabs were weighed to an accuracy of 0.0001 g.

Data analysis

A series of ANOVA tests was employed to test for species-specific differences in CI of infested and healthy mussels. All analyses were performed on transformed CI data.

Bivalve settlement and recruitment

Experimental settlement pads were constructed of nylon shade cloth previously folded five times to form a square 200 x 200 mm (0.04 m²). Nylon shade cloth has been reported as a good artificial substrate, attracting mussel spat (Manning, 1985; Helson & Gardner, 2004). An assemblage of three pads tied together with cable ties formed a set. Each set was then tied to a rope, which was then tied around a wharf pile in the intertidal zone. It was decided later to move the sets below chart datum after a number of pads had been lost due to rough weather. Also, catches of mussel spat in subtidal sites have been reported as more reliable because they are less dependent on weather conditions (Hayden, 1994a, b). One set of pads was deployed at each four sites (Fig. 3.2): Petone wharf, Matiu-Somes Island northern wharf, Evans Bay (Burnham wharf) and Seatoun wharf. The pads were replaced monthly. The experiment was conducted from April 2002 to December 2003. Pads were not conditioned in seawater, as this process has been shown to be unnecessary for artificial substrates (McGrath *et al.*, 1994). Upon retrieval, pads were left for 24 hours in a solution of fresh water and 2% formalin. Subsequently, mussel larvae were removed from each pad with a moderate flow of fresh water, which was then

filtered through a 125 μm sieve. The larvae retained on the sieve were transferred into jars and labelled. The contents of each jar were then treated with a 1% solution of formalin and stained with Rose Bengal. Rose Bengal helped to distinguish between mussel spat (stained red) and inorganic material (unstained). Before counting the larvae, each sample was homogenised by inverting the jar and swirling the contents. Five sub-samples of 5 ml each were then taken from each jar, to enable the larvae to be counted under a microscope at 10 times magnification. Finally, the total number of mussel larvae was extrapolated from the five sub-samples. Veliger-stage larvae were distinguished from other molluscs using criteria given by Redfearn (1982), Hayden (1994a, b), Redfearn *et al.* (1986), Booth (1977, 1983) and Tortell (1980). Due to the high density of larvae settling in numerous samples and the difficulty in distinguishing separate taxa (Chanley & Andrews, 1971; Booth, 1977), no attempt was made to classify larvae into separate species.

Data analysis

Bivalve larval settlement data were \log_{10} -transformed and subsequently tested for distribution normality and homogeneity of variance. A factorial ANOVA was performed to test for differences in the number of settling larvae among sites and months. Subsequently, Multiple Regression was employed to investigate the relationship between larval data and the CTD data. \log_{10} -transformed larval density data were specified as a dependent variable, while \log_{10} -transformed water column data (i.e. temperature, salinity, turbidity and chlorophyll *a*) were specified as independent variables.

Monthly rainfall data (collected at Shandon Golf Club near the Hutt River and in Wellington City near Regional Council Centre) were provided by Greater Wellington, Environmental Division.

3.3. Results

Condition Index, Gonad Mass And Pea Crab Infestation

Water column characteristics (August 2002-May 2003)

Temperature data displayed a typical seasonal cycle, similar at all sites (Table 3.1, Fig. 3.3). Maximum mean monthly temperature was recorded at Evans Bay in January 2003 (17.8 °C), while the lowest temperature was recorded at Matiu-Somes Island at August 2002 (10.7 °C).

Table 3.1. Descriptive statistics of the water column parameters (August 2002-May 2003).

Parameter	Site	N	Mean	Min.	Max.	SD
Temp. [°C]	Setoun	30	14.366	10.925	17.011	2.040
	Evans Bay	30	14.556	10.890	17.836	2.196
	M-S Island	30	14.518	10.679	17.497	2.380
Salinity [PSU]	Seatoun	30	30.264	21.672	34.453	4.249
	Evans Bay	30	34.586	29.244	36.154	2.166
	M-S Island	30	33.291	31.577	34.112	0.842
Chl. <i>a</i> [$\mu\text{g l}^{-1}$]	Seatoun	30	3.101	0.408	8.412	2.555
	Evans Bay	30	7.955	1.079	14.141	3.975
	M-S Island	30	1.006	0.271	4.150	1.091
Turb. [FTU]	Seatoun	30	6.901	1.088	20.209	5.335
	Evans Bay	30	10.655	2.320	15.520	3.779
	M-S Island	30	14.932	2.644	23.478	6.004

M-S Island = Matiu-Somes Island

Turbidity data did not show any clear pattern (Table 3.1, Fig. 3.4). Turbidity varied significantly at all sites, with the maximum mean monthly value recorded at Matiu-Somes Island in November 2002 (23.5 FTU), at Seatoun in January 2003 (20.21 FTU), and at Evans Bay was recorded in February 2003 (15.52 FTU). The lowest mean monthly turbidity value was recorded at Seatoun in March 2003 (1.03 FTU), followed by Evans Bay in January 2003 (2.32 FTU) and Matiu-Somes Island in September 2002 (2.64 FTU).

Concentration of chlorophyll *a* was shown as the highest at Evans Bay for most of the experiment, with similar levels only initially recorded at Seatoun, while the

chlorophyll *a* concentration was systematically lowest at Matiu-Somes Island (Table 3.1, Fig. 3.5). The highest mean monthly chlorophyll *a* concentration was recorded at Evans Bay in April 2003 ($14.1 \mu\text{g l}^{-1}$), while the lowest value was obtained at Matiu-Somes Island in December 2002 ($0.3 \mu\text{g l}^{-1}$).

A trend of gradual increase in salinity was detected, in which sites lying towards the inner areas of Wellington Harbour, such as Evans Bay and Matiu-Somes Island were surrounded by more saline water, while outer areas of Wellington Harbour, such as Seatoun, had greatly reduced salinity (Table 3.1, Fig. 3.6). The highest mean monthly salinity was obtained at Evans Bay in April 2003 (36.2 PSU), while the lowest value was recorded at Seatoun in March 2003 (21.7 PSU).

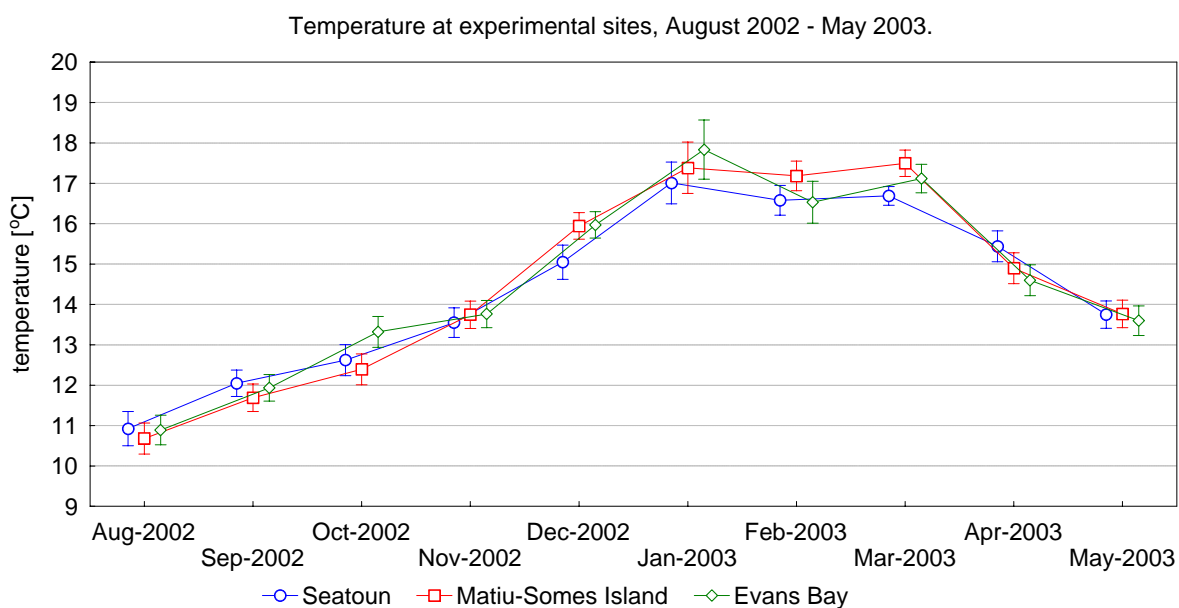


Figure 3. 3. Temperature at all sites, August 2002 – May 2003. Points represent mean monthly values \pm 95% confidence interval.

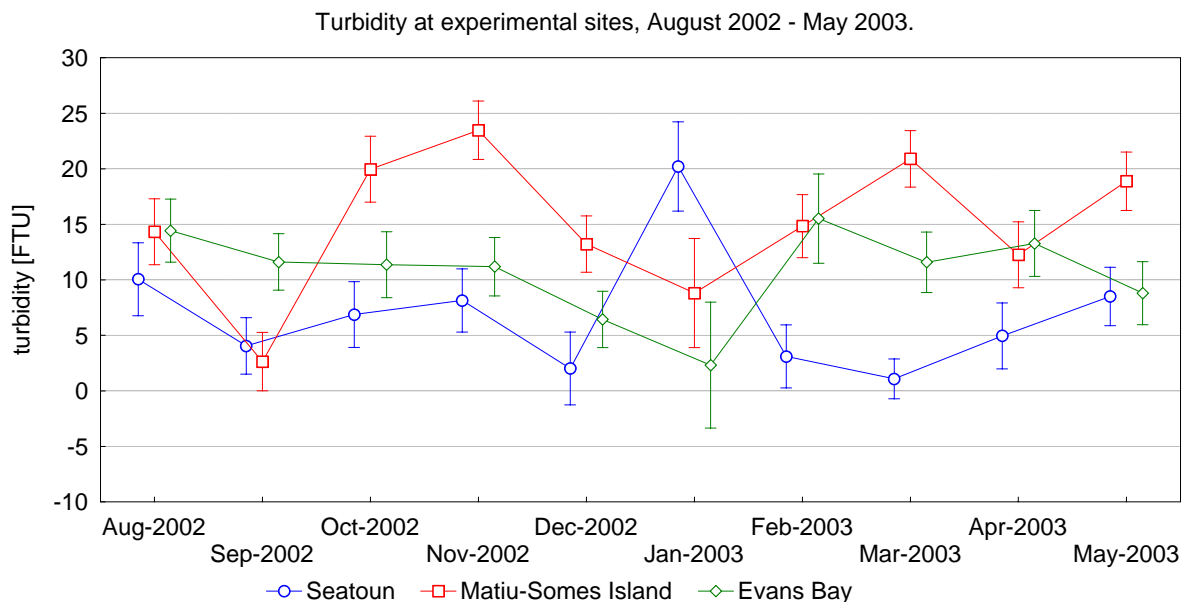


Figure 3. 4. Turbidity at all sites, August 2002 – May 2003. Points represent mean monthly values \pm 95% confidence interval.

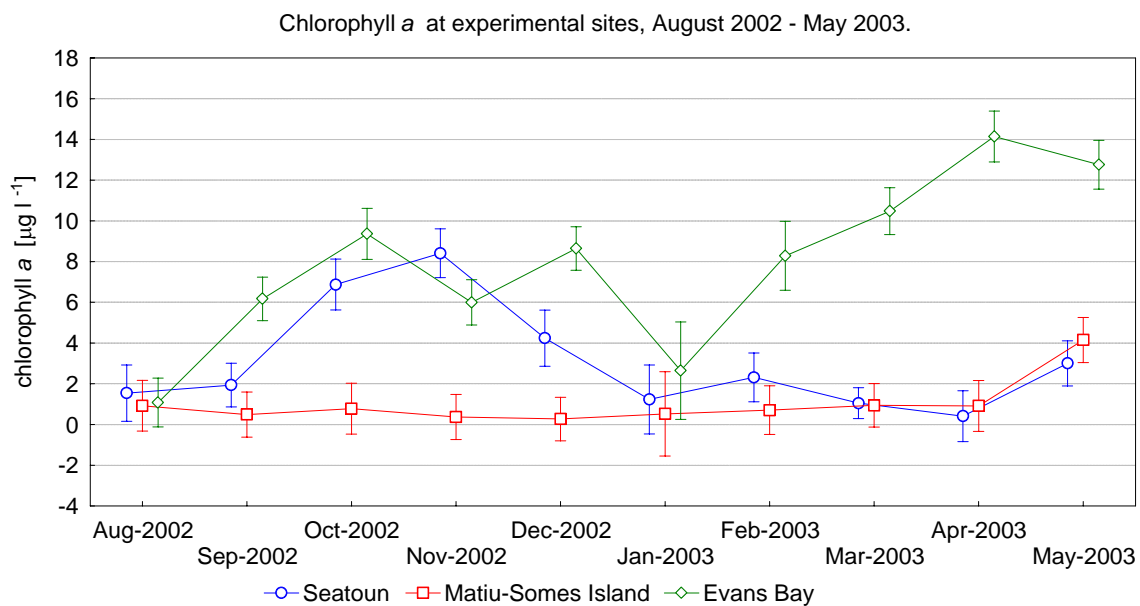


Figure 3. 5. Chlorophyll *a* at all sites, August 2002 – May 2003. Points represent mean monthly values \pm 95% confidence interval.

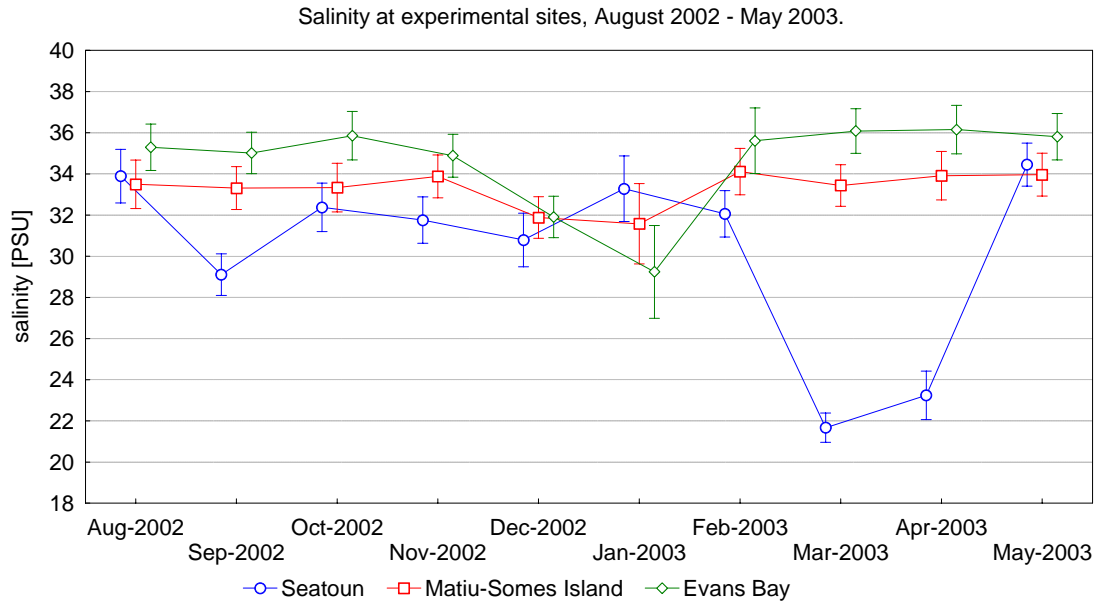


Figure 3. 6. Salinity at all sites, August 2002 – May 2003. Points represent mean monthly values \pm 95% confidence interval.

As shown by *Gamma* correlation coefficient, at Seatoun turbidity was significantly correlated to salinity (Table 3.2), at Evans Bay turbidity was correlated to temperature and salinity, and chlorophyll *a* was correlated to salinity (Table 3.3), and at Matiu-Somes Island salinity was correlated to turbidity and chlorophyll *a* (Table 3.4).

Table 3.2. *Gamma* values for water parameters at Seatoun.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.121$	$p=0.58$	$p=0.121$
Turbidity	$\gamma=-0.200$	-	$p=0.836$	$p<0.001^*$
Chlorophyll <i>a</i>	$\gamma=-0.244$	$\gamma=-0.002$	-	$p=0.058$
Salinity	$\gamma=-0.200$	$\gamma=0.556$	$\gamma=0.244$	-

* Significant after Bonferroni correction for multiple testing.

Table 3.3. *Gamma* values for water parameters at Evans Bay.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.025$	$p=0.389$	$p=0.389$
Turbidity	$\gamma=-0.289$	-	$p=0.605$	$p<0.001^*$
Chlorophyll <i>a</i>	$\gamma=0.111$	$\gamma=0.067$	-	$p<0.001^*$
Salinity	$\gamma=0.111$	$\gamma=0.467$	$\gamma=0.60$	-

* Significant after Bonferroni correction for multiple testing.

Table 3.4. *Gamma* values for water parameters at Matiu-Somes Island.

Variable	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Temperature	-	$p=0.863$	$p=0.863$	$p=0.863$
Turbidity	$\gamma=0.022$	-	$p=0.058$	$p=0.025$
Chlorophyll <i>a</i>	$\gamma=-0.022$	$\gamma=0.244$	-	$p=0.010$
Salinity	$\gamma=0.022$	$\gamma=0.289$	$\gamma=0.333$	-

Repeated measures ANOVA revealed significant differences in all water column characteristics among all sites and months, as well as a significant site*month interaction, which indicated that all water column parameters varied differentially according to site and month (Table 3.5). The overall model was accepted (Table 3.6).

Table 3.5. MANOVA model for differences in water characteristic.

Effect	λ -value	F	Effect df	Error df	<i>p</i> -value
Site	0.182	110.8	8	658.000	<0.001
Month	0.028	54.7	36	1234.653	<0.001
Site*Month	0.116	13.1	72	1296.071	<0.001

Table 3.6. MANOVA - the overall model.

Parameter	R^2	SS	df	MS	F	<i>p</i> -value
Temperature	0.926	1.520	29	0.052	143.108	<0.001
Turbidity	0.737	60.140	29	2.074	32.035	<0.001
Chlorophyll <i>a</i>	0.780	101.634	29	3.505	40.486	<0.001
Salinity	0.795	1.496	29	0.052	44.290	<0.001

Condition Index

ANCOVA ($R^2=0.707$, $F=45.696$, $df=289$, $p<0.001$) revealed significant differences in CI for all species, among all sites and months (Table 3.7). All interaction terms were significant, including two-way interactions month*site, site*species and month*species, and a three-way interaction month*site*species, which indicated that CI varied significantly according to site, month and mussel species. Shell length (SL) and GM were also found to be significant.

Table 3.7. General ANCOVA for differences in CI among all mussel species, sites and months.

Effect	SS	df	MS	F	p-value
GM	11.206	1	11.206	1221.523	<0.001
SL	2.364	1	2.364	257.738	<0.001
Month	18.312	23	0.796	86.787	<0.001
Site	1.352	3	0.451	49.125	<0.001
Species	10.059	2	5.029	548.234	<0.001
Month*Site	12.780	69	0.185	20.190	<0.001
Month*Species	6.608	46	0.144	15.659	<0.001
Site*Species	1.360	6	0.227	24.715	<0.001
Month*Site*Species	10.429	138	0.076	8.238	<0.001

The Least Significant Difference post-hoc Tukey test revealed that *Aulacomya maoriana* had the highest condition, followed by *Perna canaliculus* and *Mytilus galloprovincialis*. This pattern was observed at all sites except for Evans Bay, where *Perna canaliculus* had the highest condition, followed by *Aulacomya maoriana* and *Mytilus galloprovincialis* (Fig. 3.7).

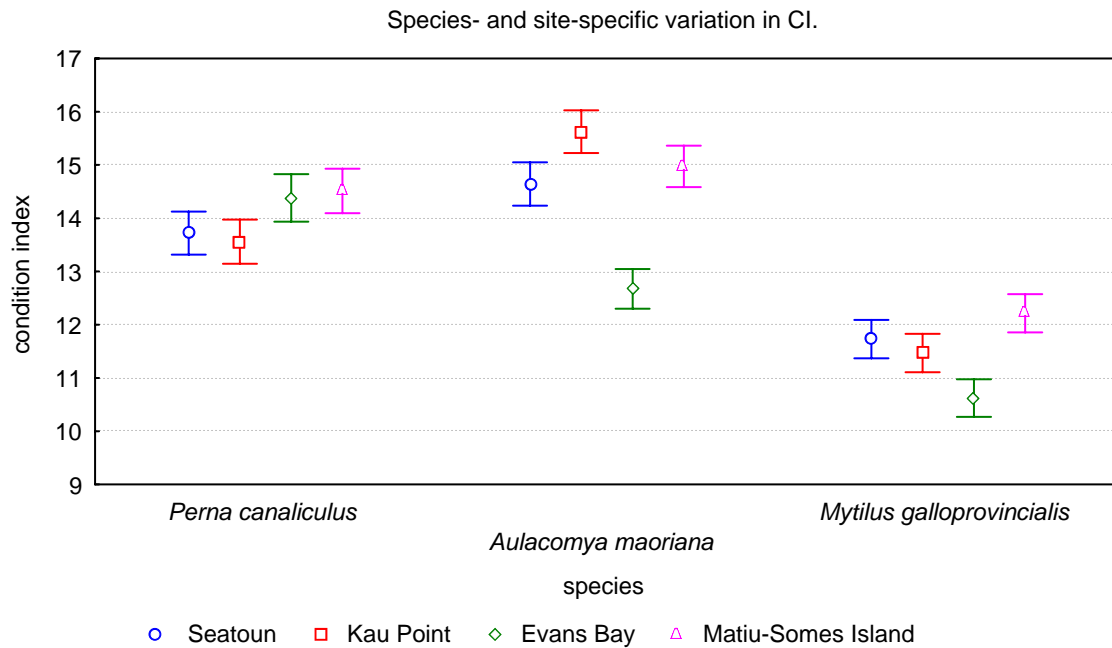


Figure 3.7. CI in all three mussel species at all four sites. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Aulacomya maoriana

CI of the ribbed mussel displayed significant spatial and temporal variation (Fig. 3.8), generally with lower CI in cooler seasons and higher CI in warmer seasons. On average, CI was within the range 10-20, although the highest monthly average was recorded in November 2002 at Seatoun (55.8), Kau Point (51.14) and Matiu-Somes Island (29.56). The highest monthly average CI at Evans Bay was recorded in May 2002 (18.52). The lowest monthly average value of CI at Seatoun was recorded in August 2002 (8.07), at Matiu-Somes Island in October 2001 (9.71), Evans Bay in December 2002 (7.54) and at Kau Point in August 2002 (9.59).

Pearson correlation coefficient revealed a significant relationship between CI and SL at all sites, and a significant CI-GM correlation at all sites except for Kau Point (Table 3.8).

Table 3.8. *Aulacomya maoriana*, CI vs. SL and CI vs. GM correlation.

Site	CI vs. SL		CI vs. GM	
	R	<i>p</i> -value	R	<i>p</i> -value
Seatoun	-0.314	<0.001*	0.148	0.002*
Kau Point	-0.515	<0.001*	0.059	0.26
Evans Bay	-0.443	0.647	0.11	0.024
Matiu-Somes Is.	-0.15	0.003*	0.42	<0.001*

* Significant after Bonferroni correction for multiple testing.

Further, Pearson coefficient showed a significant correlation of CI to temperature, turbidity and salinity at Evans Bay, but none of these parameters was correlated to CI at Matiu-Somes Island. At Seatoun, CI was significantly correlated only to salinity (Table 3.9).

Table 3.9. *Aulacomya maoriana*, CI vs. CTD correlation (August 2002-May 2003).

Site	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Seatoun	R=0.096 <i>p</i> =0.088	R=0.056 <i>p</i> =0.318	R=0.132 <i>p</i> =0.018	R=0.191 <i>p</i> =0.001*
Evans Bay	R=-0.257 <i>p</i> =0.001*	R=0.292 <i>p</i> =0.001*	R=-0.027 <i>p</i> =0.718	R=0.221 <i>p</i> =0.003*
Matiu-Somes Island	R=-0.025 <i>p</i> =0.755	R=-0.03 <i>p</i> =0.706	R=0.102 <i>p</i> =0.198	R=0.001 <i>p</i> =0.902

* Significant after Bonferroni correction for multiple testing.

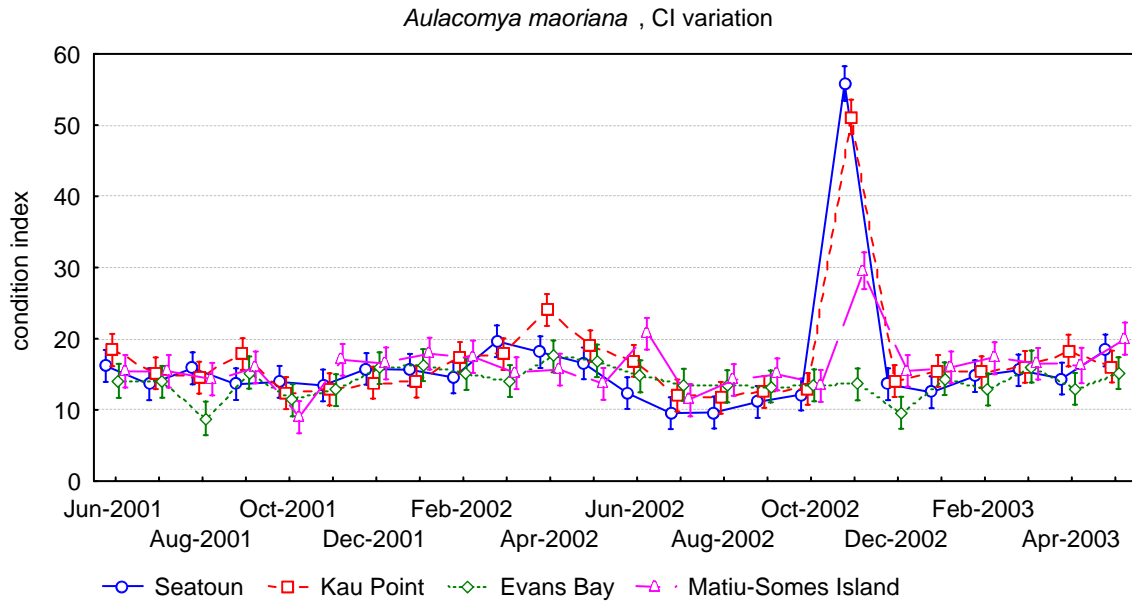


Figure 3. 8. *Aulacomya maoriana*, general variation of CI. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Mytilus galloprovincialis

CI of the blue mussel was generally within the range 5-15 (Fig. 3.9). However, the maximum mean monthly CI values recorded at Seatoun and Kau Point, well above that range, were recorded in November 2002 (35.42 and 26.67, respectively). The minimum mean monthly CI value at Seatoun was recorded in June 2002 (7.76) and at Kau Point in July 2002 (5.66). At Evans Bay the maximum mean monthly CI was recorded in June 2002 (13.94) and the minimum value in December 2002 (7.87), while at Matiu-Somes Island the maximum and minimum mean monthly CI values were recorded in August 2002 (15.20) and May 2002 (8.12), respectively.

Pearson correlation revealed a significant CI-GM and CI-SL correlation at all sites (Table 3.10). CI was also significantly correlated with temperature and chlorophyll *a* only at Seatoun and Evans Bay (Table 3.11).

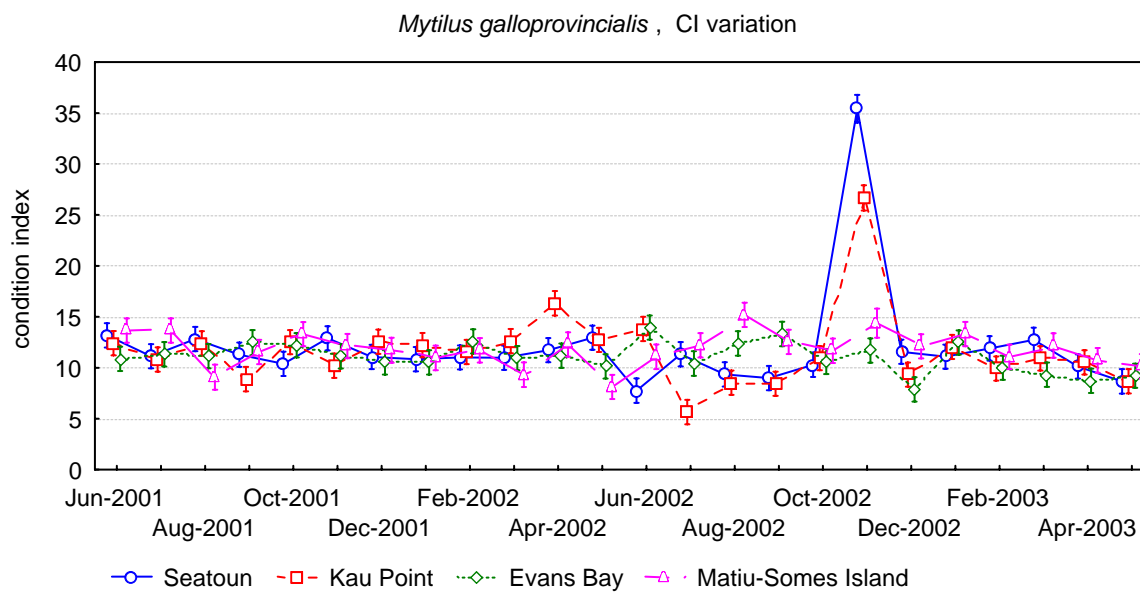


Figure 3. 9. *Mytilus galloprovincialis*, general variation of CI. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Table 3. 10. *Mytilus galloprovincialis*, CI vs. SL and CI vs. GM correlation.

Site	CI vs. SL		CI vs. GM	
	R	p-value	R	p-value
Seatoun	0.204	<0.001*	0.493	<0.001*
Kau Point	-0.348	<0.001*	0.134	0.006*
Evans Bay	0.57	<0.001*	0.7	<0.001*
Matiu-Somes Is.	0.57	0.001*	0.665	<0.001*

* Significant after Bonferroni correction for multiple testing.

Table 3.11. *Mytilus galloprovincialis*, CI vs. CTD correlation (August 2002-May 2003).

Site	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Seatoun	R=0.201	R=0.022	R=0.307	R=-0.082
	p<0.001*	p=0.693	p<0.001*	p=0.148
Evans Bay	R=-0.211	R=0.036	R=-0.428	R=-0.149
	p=0.004*	p=0.627	p<0.001*	p=0.044
Matiu-Somes Island	R=-0.019	R=0.093	R=0.03	R=0.059
	p=0.806	p=0.217	p=0.693	p=0.437

* Significant after Bonferroni correction for multiple testing.

Perna canaliculus

Although the general CI range for the greenshell mussel was 10-15 (Fig. 3.10), the maximum mean monthly values peaked in November 2002 at Seatoun (20.05), Kau Point (23.04) and Matiu-Somes Island (20.03). The maximum mean monthly CI at Evans Bay was recorded in May 2002 (19.05). The minimum mean monthly CI values at each site were: 8.59 at Seatoun (December 2001), 7.49 at Kau Point (May 2002), 6.73 at Matiu-Somes Island (October 2001) and 8.30 at Evans Bay (October 2001). Pearson coefficient revealed a significant CI-SL correlation at Kau Point and Matiu-Somes Island, and a significant CI-GM correlation at all sites (Table 3.12).

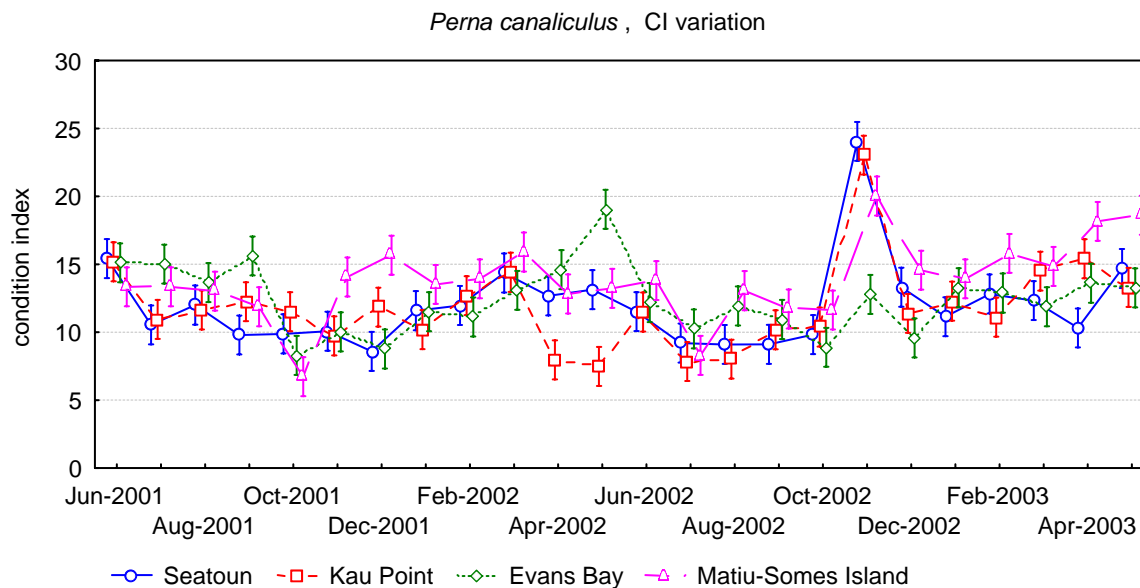


Figure 3. 10. *Perna canaliculus*, general variation of CI. Points represent mean monthly values (N=20) with 0.95 confidence interval error bars.

Table 3.12. *Perna canaliculus*, CI vs. SL and CI vs. GM correlation.

Site	CI vs. SL		CI vs. GM	
	R	p-value	R	p-value
Seatoun	-0.043	0.37	0.3	<0.001*
Kau Point	-0.478	<0.001*	0.213	<0.001*
Evans Bay	0.084	0.074	0.427	<0.01*
Matiu-Somes Is.	0.281	<0.001*	0.54	<0.01*

* Significant after Bonferroni correction for multiple testing.

As shown by the Pearson coefficient, CI was correlated to salinity and chlorophyll *a* only at Seatoun, while at Evans Bay CI was correlated only to chlorophyll *a* (Table 3.13).

Table 3.13. *Perna canaliculus*, CI vs. CTD correlation (August 2002-May 2003).

Site	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Seatoun	R=-0.084 <i>p</i> =0.132	R=0.114 <i>p</i> =0.043	R=0.379 <i>p</i> <0.001*	R=0.27 <i>p</i> <0.001*
Evans Bay	R=-0.139 <i>p</i> =0.056	R=0.021 <i>p</i> =0.774	R=-0.289 <i>p</i> <0.001*	R=-0.092 <i>p</i> =0.206
Matiu-Somes Island	R=-0.056 <i>p</i> =0.438	R=0.174 <i>p</i> =0.015	R=0.111 <i>p</i> =0.123	R=0.157 <i>p</i> =0.029

* Significant after Bonferroni correction for multiple testing.

Gonad Mass

ANCOVA ($R^2=0.670$, $F=38.442$, $df=289$, $p<0.001$) revealed significant differences in GM among species, sites and months, with all interaction terms significant, indicating that GM varied according to site, month and species (Table 3.14). SL and CI were significant covariates.

Table 3.14. General ANCOVA for differences in GM among all mussel species, sites and months.

Effect	SS	df	MS	F	<i>p</i> -value
CI	142.352	1	142.352	1221.523	<0.001
SL	194.346	1	194.346	1667.682	<0.001
Month	67.692	23	2.943	25.255	<0.001
Site	34.666	3	11.555	99.155	<0.001
Species	101.470	2	50.735	435.356	<0.001
Month*Site	85.842	69	1.244	10.675	<0.001
Month*Species	30.735	46	0.668	5.733	<0.001
Site*Species	13.614	6	2.269	19.470	<0.001
Month*Site*Species	74.430	138	0.539	4.628	<0.001

The Least Significant Difference post-hoc Tukey test revealed that generally *Aulacomya maoriana* had the highest gonad mass, followed by *Mytilus galloprovincialis* and *Perna canaliculus*. However, at Kau Point and Matiu-Somes Island there was no difference in GM between *Aulacomya maoriana* and *Mytilus galloprovincialis* (Fig. 3.11).

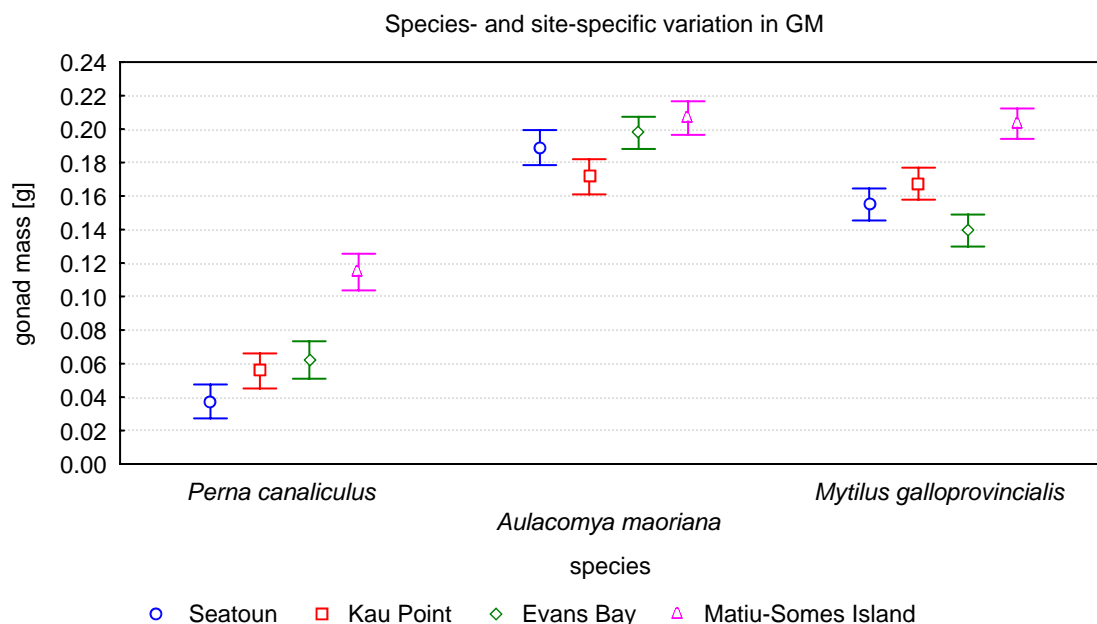


Figure 3.11. GM in all three mussel species at all four sites. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Aulacomya maoriana

GM of the ribbed mussel reflected variation in CI, and generally was elevated at all sites in winter 2001, winter 2002 and spring 2002 (Fig. 3.12). The highest mean monthly GM values at Seatoun, Kau Point and Evans Bay were recorded in November 2002 (0.53g, 0.56g and 0.77g, respectively), while the maximum GM at Evans Bay was recorded in June 2001 (0.45g). Minimum mean monthly GM values obtained at each site were: 0.02g at Seatoun (August 2002), 0.02g at Kau Point (November 2001 and July 2002), 0.03g at Matiu-Somes Island (July 2002) and 0.03g at Evans Bay (November 2001).

Pearson coefficient revealed a significant correlation between GM and chlorophyll *a* at Seatoun and Evans Bay, and between GM and salinity at Seatoun and Matiu-Somes Island (Table 3.15). When employed to explore a GM-SL correlation,

Pearson coefficient was significant for data obtained at Kau Point and Matiu-Somes Island (Table 3.18).

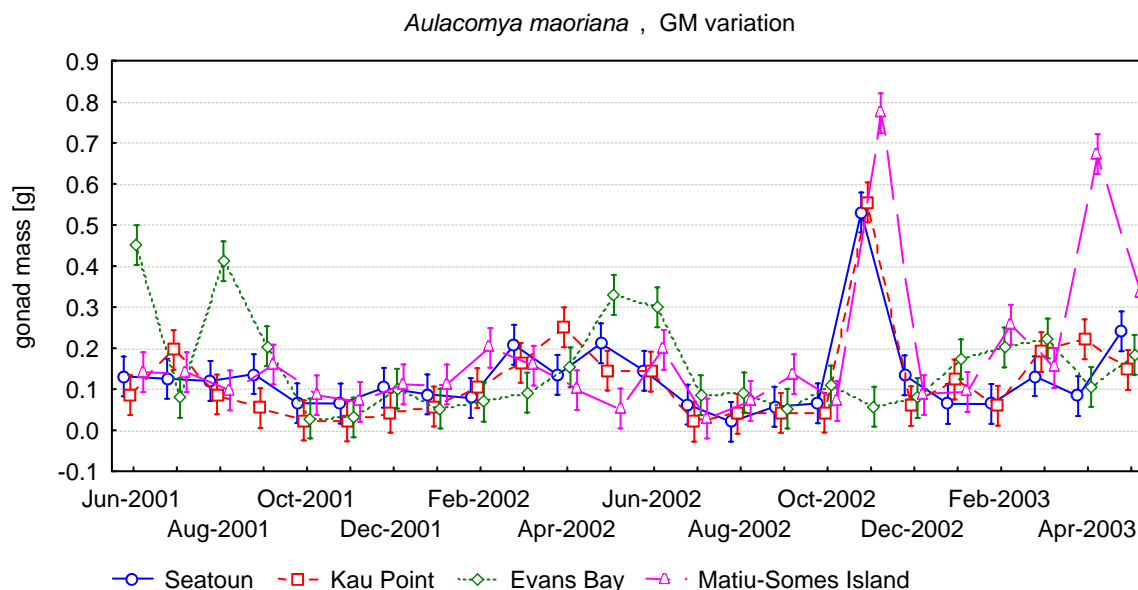


Figure 3. 12. *Aulacomya maoriana*, general variation of GM. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Table 3.15. *Aulacomya maoriana*, GM vs. CTD correlation (August 2002-May 2003).

Site	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Seatoun	R=-0.045	R=0.040	R=0.288	R=0.284
	p=0.424	p=0.476	p<0.001*	p<0.001*
Evans Bay	R=0.19	R=-0.078	R=-0.205	R=-0.112
	p=0.011	p=0.299	p=0.006*	p=0.135
Matiu-Somes Island	R=-0.011	R=-0.082	R=0.148	R=0.225
	p=0.886	p=0.303	p=0.061	p=0.004*

* Significant after Bonferroni correction for multiple testing.

Mytilus galloprovincialis

For the blue mussel, general variation in GM reflected the variation of CI, and was marked with a steady increase until June 2002 and subsequent decrease, followed by another increase in November 2002 (Fig. 3.13). Maximum mean monthly GM values at Seatoun (0.52g), Kau Point (0.34g) and Matiu-Somes Island (0.70g) were recorded in

November 2002, while the maximum GM at Evans Bay (0.27g) was recorded in September 2001. Minimum mean monthly GM values at each site were: 0.02g at Seatoun (December 2001 and August 2002), 0.02g at Kau Point (October and November 2001), 0.03g at Matiu-Somes Island (July 2002) and 0.01g at Evans Bay (January 2002).

Pearson coefficient revealed significant correlation between GM and temperature and chlorophyll *a* at all sites, and between GM and salinity at Seatoun and Evans Bay (Table 3.16). GM was significantly correlated to SL at Kau Point, Evans Bay and Matiu-Somes Island (Table 3.18).

Table 3.16. *Mytilus galloprovincialis*, GM vs. CTD correlation (August 2002-May 2003).

Site	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Seatoun	$R=-0.16$ $p=0.005^*$	$R=0.043$ $p=0.444$	$R=0.326$ $p<0.001^*$	$R=0.18$ $p=0.001^*$
Evans Bay	$R=-0.201$ $p=0.007^*$	$R=0.21$ $p=0.781$	$R=-0.515$ $p<0.001^*$	$R=-0.203$ $p=0.006^*$
Matiu-Somes Island	$R=0.214$ $p<0.004^*$	$R=0.085$ $p=0.263$	$R=0.21$ $p=0.005^*$	$R=0.103$ $p=0.174$

* Significant after Bonferroni correction for multiple testing.

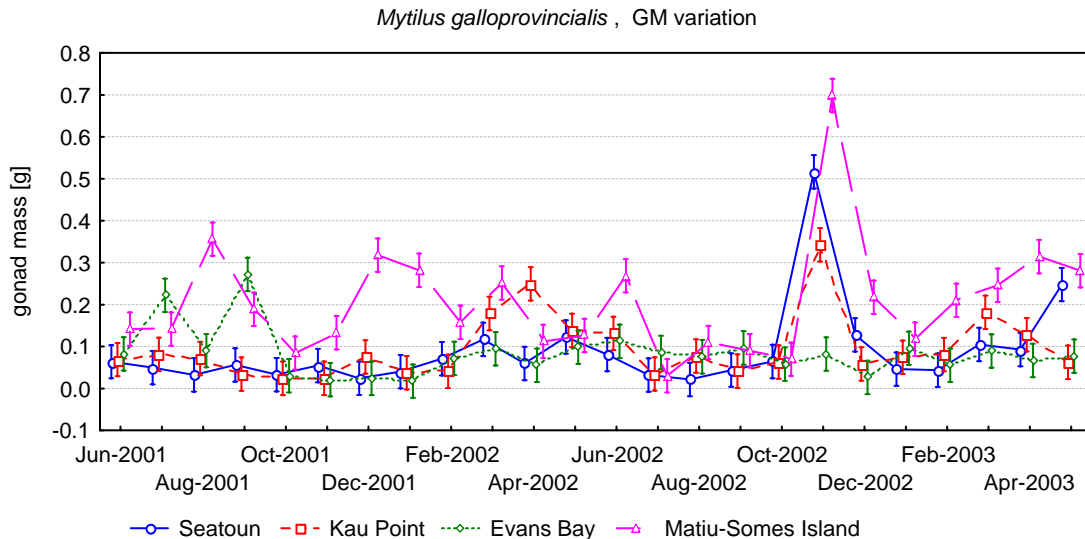


Figure 3. 13. *Mytilus galloprovincialis*, general variation of GM. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Perna canaliculus

GM of the greenshell mussel displayed spatial and temporal variation (Fig. 3.14). The maximum mean monthly GM value at Seatoun was recorded in November 2002 (0.58g), at Kau Point in November 2002 (0.58g), at Matiu-Somes Island in November 2002 (0.69g) and at Evans Bay in June 2001 (0.68g). The minimum mean monthly GM values were: 0.02g at Seatoun (December 2001), 0.03g at Kau Point (November 2001), 0.04g at Matiu-Somes Island (July 2002) and 0.02g at Evans Bay (December 2001). Pearson coefficient revealed significant correlation between GM and temperature, chlorophyll *a* and salinity at Seatoun, GM, salinity and turbidity at Evans Bay, and between GM and all four water column parameters at Matiu-Somes Island (Table 3.17). Table 3.18 shows the correlation between GM and SL for all species at all sites.

Table 3.17. *Perna canaliculus*, GM vs. CTD correlation (August 2002-May 2003).

Site	Temperature	Turbidity	Chlorophyll <i>a</i>	Salinity
Seatoun	R=-0.276 <i>p</i> =0.001*	R=0.159 <i>p</i> =0.005*	R=0.338 <i>p</i> <0.001*	R=0.272 <i>p</i> <0.001*
Evans Bay	R=0.041 <i>p</i> =0.571	R=-0.111 <i>p</i> =0.127	R=-0.073 <i>p</i> =0.315	R=-0.136 <i>p</i> =0.062
Matiu-Somes Island	R=0.113 <i>p</i> =0.118	R=0.203 <i>P</i> =0.005*	R=0.402 <i>p</i> <0.001*	R=0.234 <i>p</i> <0.001*

* Significant after Bonferroni correction for multiple testing.

Table 3.18. Correlation between GM and SL in all species.

Site	<i>A. maoriana</i>	<i>M. galloprovincialis</i>	<i>P. canaliculus</i>
Seatoun	R=0.464 <i>p</i> <0.001*	R=0.36 <i>p</i> <0.001*	R=0.465 <i>p</i> <0.001*
Kau Point	R=0.259 <i>p</i> <0.001*	R=0.522 <i>p</i> <0.001*	R=0.58 <i>p</i> <0.001*
Evans Bay	R=0.539 <i>p</i> <0.001*	R=0.465 <i>P</i> <0.001*	R=0.623 <i>p</i> <0.001*
Matiu-Somes Island	R=0.51 <i>p</i> <0.001*	R=0.404 <i>p</i> <0.001*	R=0.613 <i>p</i> <0.001*

* Significant after Bonferroni correction for multiple testing.

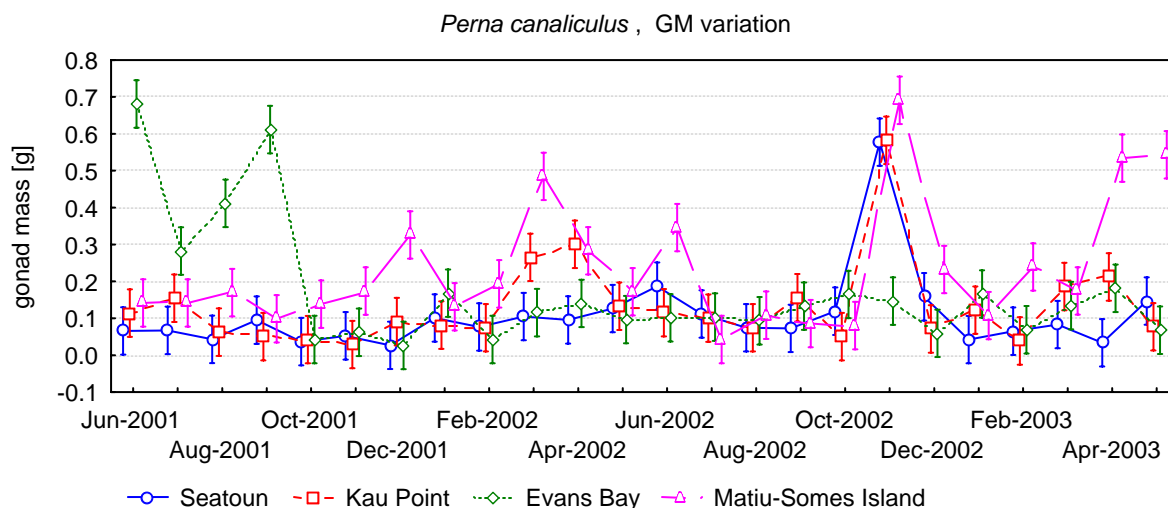


Figure 3.14. *Perna canaliculus*, general variation of GM. Points represent mean monthly values (N=20) with 95% confidence interval error bars.

Table 3.19. Site- and species-specific differences in the water column parameters, CI, GM and SL.

Parameter	Differences among sites/species	p-value
Temperature	Evans Bay > Matiu-Somes Island > Seatoun	<0.001
Turbidity	Matiu-Somes Island > Evans Bay > Seatoun	<0.001
Chlorophyll a	Evans Bay > Seatoun > Matiu-Somes Island	<0.001
Salinity	Evans Bay > Matiu-Somes Island > Seatoun	<0.001
CI	Matiu-Somes Island >> Kau Point = Seatoun > Evans Bay	<0.001
GM	Matiu-Somes Island >> Kau Point = Seatoun = Evans Bay	<0.001
SL	Evans Bay > Matiu-Somes Island >> Kau Point > Seatoun	<0.001
CI	<i>A. maoriana</i> > <i>P. canaliculus</i> > <i>M. galloprovincialis</i>	<0.001
GM	<i>A. maoriana</i> > <i>P. canaliculus</i> > <i>M. galloprovincialis</i>	<0.001
SL	<i>P. canaliculus</i> > <i>M. galloprovincialis</i> > <i>A. maoriana</i>	<0.001

Monthly rainfall data (collected at Shandon Golf Club near the Hutt River and in Wellington City near Regional Council Centre) were provided by Greater Wellington, Environmental Division (Fig. 3.15). Missing data were replaced with their interpolated means (Underwood, 1997). The data displayed generally similar rainfall at both sites (Wellington site mean 66.9 ± 42.08 mm, the Hutt River site mean 83.98 ± 54.56 mm).

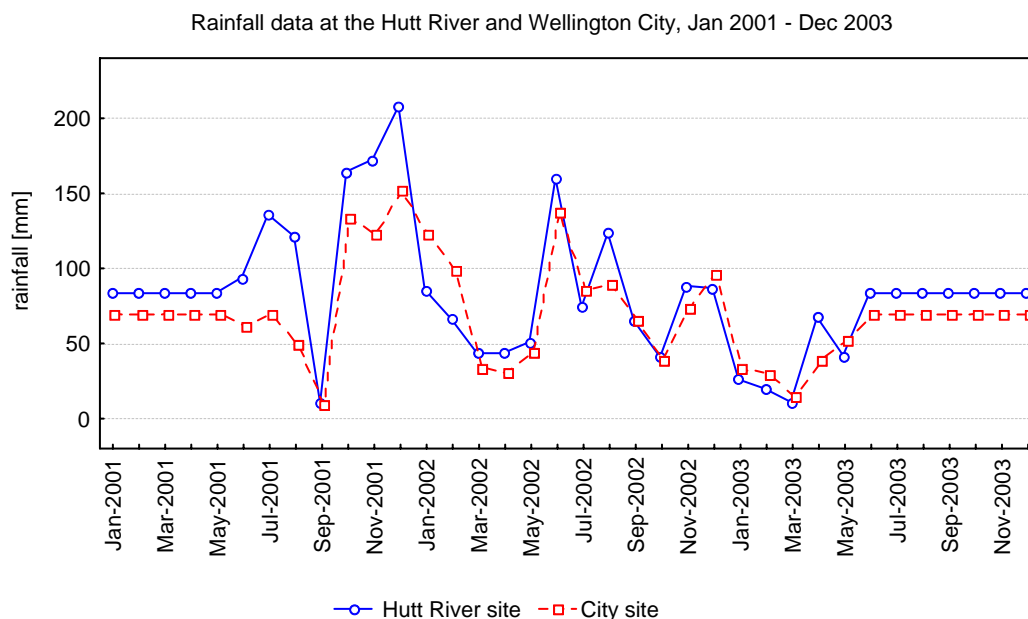


Figure 3.15. Rainfall data in Wellington area (January 2001 – December 2003)

Pea crab infestation

Presence of the pea crab *Pinnotheres novaezelandiae* was noted in all species examined throughout the present study. In total, 189 pea crabs were found in 5760 mussels. No multiple infestations were recorded. The overall infestation rate therefore is 3.28%.

Aulacomya maoriana

26 pea crabs infestations were found in this species (Table 3.20). ANOVA ($R^2=0.011$, $F=22.133$, $df=1$, $p<0.001$) revealed significant differences in condition of healthy and infested mussels (Table 3.23, Fig. 3.16). The overall infestation rate of this species is 1.35%.

Table 3.20. *Aulacomya maoriana* - pea crab infestation.

	Seatoun	Kau Point	Evans Bay	Matiu-Somes Is.
N	2	1	19	4
Mean wt. [g]	0.313	0.579	0.355	0.319
Min.	0.255	-	0.006	0.033
Max.	0.371	-	0.832	0.529
SD	0.082	-	0.222	0.212
Mean carapace width [mm]	6.5	11	6.789	6.25
Min.	5	-	4	3
Max.	8	-	11	10
SD	2.121	-	2.043	2.872

Mytilus galloprovincialis

89 blue mussels were infested with pea crabs (Table 3.21). ANOVA ($R^2=0.01$, $F=19.385$, $df=1$, $p<0.001$) revealed significant differences in condition of healthy and infested mussels (Table 3.23, Fig. 3.16). The overall infestation rate of this species is 4.64%.

Table 3.21. *Mytilus galloprovincialis* - pea crab infestation.

	Seatoun	Kau Point	Evans Bay	Matiu-Somes Is.
N	6	8	68	7
Mean wt. [g]	0.311	0.444	0.434	0.622
Min.	0.201	0.099	0.066	0.116
Max.	0.428	1.111	1.497	1.428
SD	0.11	0.34	0.325	0.45
Mean carapace width [mm]	6.167	6.375	6.985	7.714
Min.	4	3	3	4
Max.	8	12	14	15
SD	1.472	2.774	2.69	4.231

Perna canaliculus

74 green mussels were infested with pea crabs (Table 3.22). ANOVA ($R^2=0.002$, $F=4.742$, $df=1$, $p<0.001$) revealed significant differences in condition of healthy and infested mussels (Table 3.23, Fig. 3.16). The overall infestation rate of this species is 3.85%.

Table 3.22. *Perna canaliculus* - pea crab infestation.

	Seatoun	Kau Point	Evans Bay	Matiu-Somes Is.
N	6	13	39	16
Mean wt. [g]	0.554	0.95	0.53	0.879
Min.	0.087	0.363	0.122	0.314
Max.	1.385	1.638	1.75	1.677
SD	0.49	0.399	0.342	0.355
Mean carapace width [mm]	8.5	11	8.205	10.563
Min.	4	7	4	5
Max.	14	15	17	15
SD	3.782	2.799	2.949	3.265

Table 3.23. Comparison of mean CI of infested and healthy mussels.

	Infested mussels			Healthy mussels			p-value
	Mean CI	SD	N	Mean CI	SD	N	
<i>A. maoriana</i>	11.253	6.373	26	15.914	9.404	1894	<0.001
<i>M. galloprovincialis</i>	9.401	3.12	89	11.772	5.989	1831	<0.001
<i>P. canaliculus</i>	11.431	2.915	74	12.561	4.434	1846	0.029

Larval Settlement And Recruitment

Water column characteristics – Larval settlement and recruitment (August 2002-September 2003)

Results of the analysis of this data set are described in previous chapter.

Larval densities at recruitment

Mussel larvae were always present in the water column and were settling on the experimental substrate throughout the entire period of this study (Fig. 3.17). At Seatoun, two recruitment peaks were recorded: In August 2002 (with the average of 755 larvae per pad) and in June 2003 (2367 larvae). At Evans Bay three peaks of larval recruitment were recorded: In August 2002 (2249 larvae), February 2003 (2022 larvae) and in May 2003 (2931 larvae). Similarly, three peaks of larval recruitment were recorded at Petone: August 2002 (1671 larvae), March 2003 (1891 larvae) and in May 2003 (9851 larvae). At

Matiu-Somes Island, two peaks of larval recruitment were recorded: in August 2002 (532 larvae) and May 2003 (2688 larvae).

Factorial ANOVA ($R^2=0.965$, $F=56.406$, $df=83$, $p<0.001$) revealed significant differences in larval densities among all experimental sites and months, as well as a significant site*month interaction, indicating that larval settlement and recruitment varied according to location and time (Table 3.24). Multiple Regression (Table 3.25) revealed significant correlation between larval densities and the water column parameters at all experimental sites. However, the overall regression model was not accepted at Petone. At Seatoun, larval density was significantly correlated with turbidity, chlorophyll *a* and salinity. At Petone, larval density was not correlated with any variable. At Evans Bay, larval density was significantly correlated with temperature, turbidity and salinity. At Matiu-Somes Island, the larval density was significantly correlated only with chlorophyll *a*.

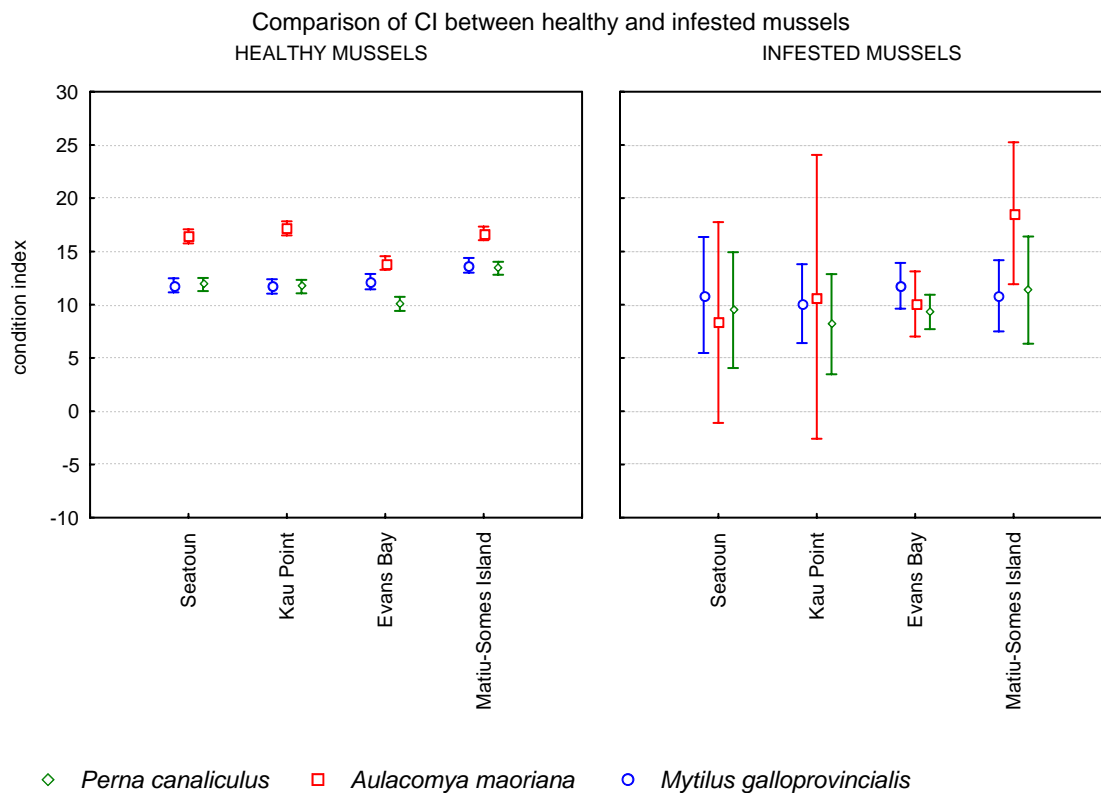


Figure 3. 16. CI of infested and healthy mussels. Points represent mean, species-specific CI values with 95% confidence interval error bars.

Table 3.24. Factorial ANOVA for differences in larval density among sites and months

Effect	SS	df	MS	F	p-value
Month	922.96	20	46.15	155.04	<0.001
Site	115.70	3	38.57	129.57	<0.001
Month*Site	147.79	60	2.46	8.28	<0.001

Table 3.25. Site-specific correlation between CTD and larval settlement data (St. err.=standard error).

Site/Parameter	β	St. err. β	t-value	p-value
Seatoun ($R^2=0.397$, $F(4,43)=7.068$, $p<0.001$)				
Temperature	-0.099	0.132	-0.746	0.459
Turbidity	-0.439	0.159	-2.768	0.008*
Chlorophyll a	-0.421	0.150	-2.814	0.007*
Salinity	0.888	0.188	4.712	<0.001*
Petone ($R^2=0.174$, $F(4,40)=2.109$, $p=0.097$)				
Temperature	-0.019	0.189	-0.102	0.920
Turbidity	-0.501	0.211	-2.378	0.022
Chlorophyll a	0.238	0.194	1.224	0.228
Salinity	0.354	0.215	1.648	0.107
Evans Bay ($R^2=0.414$, $F(4,37)=6.528$, $p<0.001$)				
Temperature	-0.355	0.141	-2.518	0.016
Turbidity	-0.503	0.193	-2.605	0.013
Chlorophyll a	0.017	0.159	0.104	0.918
Salinity	0.706	0.223	3.165	0.003*
Matiu-Somes Is. ($R^2=0.267$, $F(4,46)=4.186$, $p=0.006$)				
Temperature	-0.055	0.134	-0.413	0.681
Turbidity	0.151	0.142	1.062	0.294
Chlorophyll a	0.293	0.138	2.124	0.039*
Salinity	0.242	0.139	1.740	0.089

* Significant after Bonferroni correction for multiple testing.

Table 3.26. Site-specific differences in the water column parameters and larval settlement.

Parameter	Differences among sites	p-value
Temperature	Evans Bay > Matiu-Somes Island > Seatoun > Petone	<0.001
Turbidity	Matiu-Somes Island > Seatoun > Evans Bay > Petone	<0.001
Chlorophyll a	Evans Bay > Seatoun > Petone > Matiu-Somes Island	<0.001
Salinity	Evans Bay > Matiu-Somes Island > Petone > Seatoun	<0.001
Larval settlement	Evans Bay > Petone > Matiu-Somes Island > Seatoun	<0.001

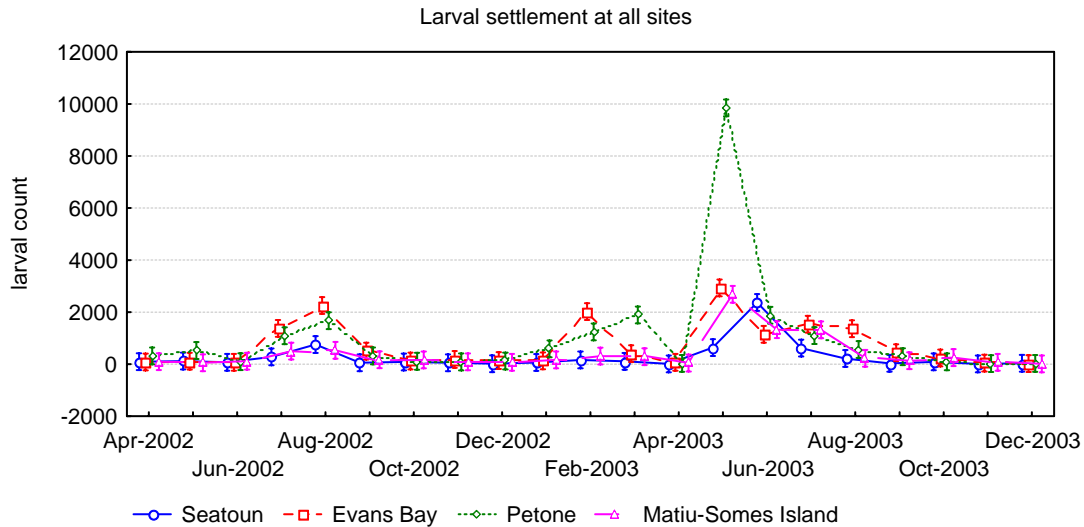


Figure 3.17. Larval densities at settlement – comparison among sites.

3.4. Discussion

Condition index and gonad mass

Condition in bivalves is shaped by numerous factors, including food quality and quantity, water parameters, such as temperature and salinity, bivalve population density, pollution, height on the shore and emersion time, genotypic characteristics or presence of parasites. Often there are marked cross-correlations among those variables, which prevents the clear identification of a single environmental factor determining mussel condition (e.g. Chaparro & Winter, 1983; Lucas & Beninger, 1985; Hawkins & Bayne, 1991; Koehn, 1991; Marsden & Pilkington, 1995; Rheault & Rice, 1996). Results from the present study clearly show that mussel condition varied according to the location and was linked to the environmental parameters in Wellington Harbour. Both condition index and mussel gonad mass were highest at Matiu-Somes Island, followed by Kau point, Seatoun and Evans Bay (Table 3.19), and both of these mussel characteristics were clearly linked to the water column parameters at all of the experimental sites. The effects of fluctuating nutrient runoff after rain, particularly noticeable in this experiment in spring 2002, were manifested through the elevated condition and gonad mass in

November 2002, which presumably resulted from one of the Hutt River high-turbidity plumes carrying high volumes of organic particles (see rainfall data Fig. 3.15). This frequently occurring riverine input can alter hydrological conditions in Wellington Harbour (McConchie *et al.*, 2000), and so affect the ecology of its inhabitants. General range of condition index varied in all three species investigated in the present study and reflected species-specific gonad mass, with both condition index and gonad mass being highest in *Aulacomya maoriana*, followed by *Perna canaliculus* and *Mytilus galloprovincialis* (Table 3.19). Mussel condition and gonad mass also varied temporally, with all species displaying higher condition and gonad mass in cooler seasons and decrease in warmer seasons (Figs. 3.8-3.10 and 3.12-3.14). This most likely was a result of a seasonal cycle occurring in the mussel gonad. In this cycle, gametogenesis takes place in winter and spawning activity subsequently occurs in spring-summer, which points at the influence of temperature on gonad cycle. Indeed, the gonad activity in all three species was clearly affected by the environmental parameters (mainly chlorophyll *a* and salinity), with most of them significantly correlated with gonad mass at all sites (Tables 3.15-3.17). In mussels, condition index depends on the gonad mass, and as the gonad mass increases in warmer seasons, so does condition index. In the present study, all mussel species displayed a trend of gonad restoration between summer and autumn 2002 (December 2001- April 2002) (Figs. 3.12-3.14), which was subsequently followed by massive spawning activity detected at all sites in winter 2002 (Fig. 3.17). A similar pattern was reported for green mussels *P. canaliculus* (Buchanan, 2001) and the blue mussels *M. galloprovincialis* (Villalba, 1995; Helson & Gardner, 2004). Gonad mass data available from this study confirm those findings and also that fact that the ribbed mussel in Wellington Harbour *A. maoriana* follows a similar pattern. Zandee *et al.* (1980) and Gabbott & Peck (1991) examined biochemistry of the mantle in *Mytilus edulis* in relation to gametogenesis. The authors observed controlled autophagy in the connective tissue as a way of mobilising energy stores for gamete formation. In winter, as glycogen stores start to decrease, the energy gained from this process is used for development of eggs and the synthesis of lipids in eggs. Simultaneously, the levels of protein and lipids are increasing and will remain high until the time of spawning and massive shedding of eggs containing large reserves of protein and lipids. By summer, high levels of glycogen and

protein are re-built but lipid concentrations are still low and recovering slowly, as glycogen is deposited in the mantle tissue.

The quality and quantity of seston in coastal waters have been shown to vary in space and season. Phytoplankton from the water column is believed to be the principal energy source for bivalves, whereas the degree to which detritus is exploited depends largely on sorting mechanisms of the gill (retention efficiency of the particles) (Gosling, 2003). Bivalve physiological status has been documented to be clearly dependent on the ambient food levels (e.g. Navarro *et al.* 1991; Stuart, 1982; Fréchette & Grant, 1991). In the present study, spatial variability of mussel condition was revealed, in which mussels from inner areas of Wellington Harbour (represented here by Evans Bay and Matiu-Somes Island) had significantly higher condition than mussels from the outer areas, such as Kau point and Seatoun. A similar regional variation was reported by Hickman *et al.* (1991) who detected a pattern of condition in the greenshell mussel *Perna canaliculus* along the main channel of Pelorus – Kenepuru Sound in New Zealand. In that study, mussel condition was consistent with chlorophyll *a* levels decreasing from inner to the outer Sound. The authors did not find a strong correlation between condition and chlorophyll *a*, however, but the results pointed to available food (measured as particulate carbon, PC) as the primary factor controlling mussel condition. Smaal & Stralen (1990) reported similar findings for mussels sampled at inward and seaward parts of an estuary. The condition index of *Mytilus edulis* from that study was higher in western part of the Scheldt estuary (the Netherlands) compared to its central area. Chlorophyll *a* concentration and primary production were also higher in the western part. However, there was no significant correlation between mussel condition and chlorophyll *a* concentration, but there was a highly significant correlation between condition and primary production. The authors conclude that in years with lower primary production mussels suffered lower condition. They also suggested that the lack of a direct link between condition and chlorophyll *a* may be explained by higher turnover of phytoplankton by suspension feeders (including the mussels), particularly in seasons of high primary production (spring-summer), which would make the detection of chlorophyll more difficult. A seasonal pattern for condition of the mussel *Mytilus edulis*

and chlorophyll *a* was also evident in a study performed by Rosenberg & Loo (1983) who concluded that food quality is a limiting factor for the mussel *Mytilus edulis*. As seston concentration decreased during winter, the resulting poor quantity of food available to mussels was reflected in lowered mussel energy content and ultimately in lower condition.

Pea crab infestations

In bivalves, pea crabs live inside the mantle cavity, often placed on the gills, where they collect food particles previously filtered by their host (McLay, 1988). The nature of the relationship between the crabs and their bivalve hosts has been so far unresolved, with some authors (e.g. Bierbaum & Ferson, 1986; Stevens, 1992) reporting adverse effects of pea crabs on bivalve condition, while other workers (Goodbody, 1960; Haven, 1960; Pearce, 1962; Hsueh, 2003) consider the relationship to be commensal or even symbiotic. Results from the present study suggest a parasitic relationship, because condition index was significantly reduced in infested mussels, compared to healthy mussels (Table, 3.23, Fig. 3.16), indicating that the pea crabs caused damage to their hosts. However, given a high variability in condition of infested mussels demonstrated here by the size of error bars (Fig. 3.16), it would appear that some individuals had actually higher condition when infested with the pea crab. Damage done to a bivalve host can include slower growth (Bierbaum & Ferson, 1986), erosion of gill tissue and fibrous growth on the mantle (Jones, 1977), lower meat weight and effectively lower condition index (Tablado & Gappa, 1995), and reduced gonad area and effectively reduced reproductive capability (O'Beirn & Walker, 1999). Although the pea crab *Pinnotheres novaezelandiae* was found in all three species, the overall infestation rate was low (3.28 %). Therefore, from the perspective of the entire Wellington Harbour mussel population, the effects of the pea crab are negligible.

Larval settlement and recruitment

The numbers of mussels recruiting onto the experimental substrate in this study exhibited significant spatial and temporal variability. These results are consistent with similar variability in settlement and recruitment reported by other researchers for a number of mussel species, including *Mytilus edulis* in England (Dare, 1976), Ireland (Snodden & Roberts, 1997) and the USA (Petratis, 1991), *Mytilus galloprovincialis* in Italy (Ceccherelli & Rossi, 1984), New Zealand (Helson & Gardner, 2004) and Spain (Cáceres-Martínez *et al.*, 1993; Molares & Fuentes, 1995), *Perna perna* in South Africa (Lasiak & Barnard, 1995), and *Perna viridis* in India (Rajagopal *et al.*, 1998a, b). In the present study, recruitment of mussel larvae occurred throughout the year, consistent with the data presented by other New Zealand researchers (e.g. *M. galloprovincialis* in Helson & Gardner, 2004; *M. galloprovincialis* and *P. canaliculus* in Meredyth-Young & Jenkins, 1978; *P. canaliculus* in Buchanan & Babcock, 1997 and Alfaro *et al.*, 2001). This phenomenon in New Zealand waters has been described as the result of continuous spawning (“trickle spawning”) by Booth (1983), who also reported the presence of *Mytilus edulis aoteanus* (now *Mytilus galloprovincialis*) and *Perna canaliculus* larvae in the water column in Wellington Harbour throughout the entire year.

In the present study, three peaks of mussel larvae density were recorded at all sites in the same periods in August 2002, February 2003 and June 2003, resulting from spawning events in winter 2002, summer 2002/2003 and autumn 2003, respectively. Such prolonged reproductive activity and spawning periods clearly give mussels ecological advantage over other community members, thus ensuring that more offspring will be produced, potentially securing the mussel dominance in the communities. While in Wellington Harbour mussels are clearly able to spawn on more than one occasion a year, in many other temperate environments only single major peaks of larval recruitment have been described as a common phenomenon in mussel reproductive ecology. In European waters, for example in the Ria de Vigo (NW Spain), Cáceres-Martínez *et al.* (1993) found that *Mytilus galloprovincialis* underwent one major spawning event in spring. Similarly, Chipperfield (1953) and Dare (1976) recorded high larval abundances in British waters in

May-June. Mussel populations can, however, produce larvae continually throughout the entire year. Cáceres-Martínez & Figueras (1998) found mussel larvae in the Ria de Vigo on every sampling occasion and reported two major peaks of larval abundance in March-April and May-June in two consecutive years of their study. Harris *et al.* (1998) reported similar temporal variation along the coast of South Africa, where mussel larvae were recruiting predominantly in June-July, December-January and March-April. In New Zealand, Helson & Gardner (2004) reported recruitment of mussel larvae on every sampling occasion in Wellington Harbour with the highest recruitment densities in winter. Results from the present study are also consistent with those reported by Alfaro *et al.* (2001), who reported a similar spawning season for mussels (June-December) and the continuing appearance of mussel spat outside the season (i.e. trickle spawning) in Ninety Mile Beach, northern New Zealand. At Taylor's Mistake near Christchurch, New Zealand, Kennedy (1977) reported intensive spawning in *Mytilus edulis aoteanus* and *Aulacomya maoriana* as water temperatures were rising from 8°C to 19°C and gonad condition declined. The author also reports that *Perna canaliculus* spawns at the same time as *Mytilus edulis aoteanus* and *Aulacomya maoriana*, from late August to early February.

Typically, water temperature, salinity and food abundance (often expressed as water turbidity and chlorophyll concentration in the water column) are identified as key factors to the mussel reproductive cycle (e.g., Carriker, 1961; Bayne, 1965; Hrs-Brenko, 1978; Hines, 1979; Pechenik *et al.*, 1990; Starr *et al.*, 1990; Rajagopal *et al.*, 1998b). These parameters are often synergistic in their effects on ecology of marine invertebrate communities. For example, food availability can interact with temperature and influence the energy budget of mussels, their spawning ability and ultimately larval success, because upon the utilisation of protein, lipid and glycogen reserves in the planktotrophic eggs, the developing planktotrophic larva depends on plankton for food. Thus, conditions of insufficient food quality or quantity combined with stressful temperatures that increase metabolism and the subsequent demand for resources needed to cover the metabolic costs will result in less viable larvae or malnourished adults with reduced condition and reproductive output, as opposed to non-stressed individuals (Calabrese, 1969; Bayne,

1973; Kingston, 1974; Widdows, 1978a, b; Newell *et al.*, 1982, Sprung, 1984, 1985; Pechenik *et al.*, 1990; Ardizzone *et al.*, 1996). In invertebrates, phytoplankton bloom-induced spawning serves as a good example of the interplay between temperature and food abundance in an aquatic environment. Starr *et al.* (1990) suggest that the close timing between phytoplankton bloom and the release of planktonic larvae gives the invertebrates the advantage of securing the food supply to the larvae and ensuring that larval mortality due to zooplankton predation may be minimal (during phytoplankton bloom many species are spawning simultaneously, increasing the volume of larvae in the water column and thus reducing the probability of predation-related mortality of larvae).

In the present study, larval settlement was correlated with salinity at Evans Bay, chlorophyll *a* concentration at Matiu-Somes Island, and by synergistically acting turbidity, chlorophyll *a* and salinity at Seatoun (Table 3.25). These results are at odds, given the synergistic effects of salinity and bottom-up factors (i.e. turbidity and chlorophyll *a*) on larval settlement at Seatoun and the fact that some of the highest peaks in larval settlement were recorded at Evans Bay and Petone. At the time of the peak settlement at Seatoun (June 2003), turbidity was reduced, but elevated salinity and chlorophyll remaining after a secondary peak of chlorophyll concentration that took place a month earlier might have triggered spawning in mussels at this site. The synergistic effects of salinity and temperature affecting larval settlement have been also documented by Hrs-Brenko (1978), who reported the optimal salinity range for larval development in *Mytilus galloprovincialis* in the Adriatic Sea as being between 30 and 35‰. The salinity range supporting larval development and metamorphosis was shown to depend heavily on varying temperature, with the best larval development occurring in moderate temperatures. In Portugal, Chícharo & Chícharo (2001) reported a significant seasonal interplay between larval and post-larval abundances and environmental parameters in a coastal lagoon. Their study revealed a correlation among temperature, chlorophyll *a* levels and salinity. The correlation between the concentration of *Ruditapes decussatus* larvae and temperature was also found to be a major factor affecting larval abundance. Further, salinity and levels of chlorophyll *a* proved important, although the authors did not consider salinity as a factor limiting larval abundance because salinity values in the

lagoon were close to typical open sea salinity, with a very small freshwater input. Chlorophyll *a* was also excluded as a limiting factor because of the productive nature of the lagoon, with abundant chlorophyll and suspended and dissolved organic matter.

Because in the present study mussel larvae were settling on the artificial substrate in Wellington Harbour throughout the entire sampling period (Fig. 3.17), it is clear that the temperatures in the Harbour (8-20°C) are unlikely to limit gametogenesis and spawning. It is possible, however, that recruiting larvae were advected into Wellington Harbour from elsewhere, thus contributing to the numbers of larvae recorded. Judging from the conspicuous peaks of larval abundances at certain times of the year, the temperature range in the Harbour that stimulates gametogenesis would appear in late autumn (April-May), when the water temperature drops to 11-12°C and gamete maturation takes place, and last until spring (September-October) at water temperatures reaching 14-15°C. Such a trend was recorded at all experimental sites, in addition to the middle peak of larval abundance recorded in February 2003, when environmental conditions in the Harbour were conducive to spawning and larvae development. The link between temperature and larval success is created by chlorophyll concentration, because temperature is needed by plankton for photosynthesis. Therefore higher temperature stimulates photosynthetic activity of phytoplankton cells and results in greater concentration of chlorophyll. This, in turn, stimulates spawning and aids with the subsequent larval settlement. Similar results were reported from India, where Manoj & Appukuttan (2003) found a direct relationship between temperature and larval development in *Perna viridis*. The larval growth and settlement rates in that study increased with an increase in temperature. The authors suggested that at lower temperatures the lack of growth in larvae could be caused by their inability to activate the enzymatic system necessary for food digestion, whereas at high temperatures larval mortality can result from the destruction of algal cells and the subsequent bacterial build-up in the hatchery rearing system. An inverse relationship between water temperature and the duration of the larval phase was reported by Pascual & Zampatti (1995), who found that an increase in temperature stimulated larval development and settlement at a smaller size in *Ostrea puelchana*. When the temperature increased from 19-20°C to 23-25°C, the

planktonic lifespan became shorter (from 20-22 days to 17 days) and the pediveligers were smaller at the time of settlement (310 and 284 μm , respectively). In the field, the authors reported a positive relationship between phytoplankton bloom and invertebrate spawning activity, when the increased algal concentration stimulated gamete release.

A clear gradient detected in the abundance of settling mussel larvae towards the inner reaches of Wellington Harbour, was accompanied by a similar gradient of condition index and gonad mass in adult mussels. In the present study, condition index of the blue mussel *M. galloprovincialis*, greenshell mussel *P. canaliculus* and ribbed mussel *A. maoriana* improved towards the inner areas of the Harbour. In particular, condition index was highest in *A. maoriana*. Also, the environmental variables (most noticeably chlorophyll *a* concentration and salinity) were clearly significant for the gonad mass. Further, the gonad development directly affected the adult condition and (at least partially) contributed to the larval densities detected on the artificial collectors. Significant correlation of the numbers of larvae settling on the artificial substrate and condition of adults signified the synergistic effect of the environmental parameters (Bayne, 1973; Widdows, 1973). Generally, the water column parameters, such as temperature, salinity and chlorophyll *a* (particularly decreased between January and May 2003) were lower at Seatoun, compared with other sites (Fig. 3.3-3.6), which might be the reason for the consistently lowest rate of settlement at this southernmost site, as well as the reduced adult condition (Table 3.26). Inside the Harbour, however, some of the highest recruit densities were recorded at Evans Bay, where the temperature, salinity and chlorophyll *a* concentration were consistently higher than at other sites, and further towards the northern parts of the Harbour, where the highest adult condition was found (Matiu-Somes Island) and the highest larval abundance (Petone).

Heath (1977) reported that the flow rate decreases inside the Harbour from 0.46-0.50 m s^{-1} in the entrance channel to 0.03 m s^{-1} in the main part, and to less than 0.015 m s^{-1} in Lambton Harbour. Further, there is evidence (Vernier-Bonnet *et al.*, 1997; Todd *et al.*, 1998; McQuaid & Phillips, 2000) that under the most common wind conditions larvae in the water column would show little exchange with bays further than 2 km away.

It is possible, therefore, that what appears to be a high settlement rate of mussel larvae in Evans Bay could be simply a result of their retention by slow currents and the prevailing north-westerly winds in that bay. However, further detailed study of the hydrology of Wellington Harbour is needed to verify that hypothesis.

Mussel larvae have a planktonic duration of 2–4 weeks (Seed & Suchanek, 1992; Jeffs *et al.*, 1999; McQuaid & Phillips, 2000) and therefore many of them may not have sufficient time to fully develop in Wellington Harbour, which has an estimated total flushing time of only 10 days (Heath, 1971). As a result, those larvae will be carried outside the Harbour into Cook Strait well before they are competent to settle at harbour sites (Helson & Gardner, 2004). Further, since mussels are almost entirely absent from the Wellington South Coast (Gardner, 2000) and mussel populations on the nearby Kapiti Coast are poorly developed, Wellington Harbour appears to be the only major source of mussel larvae in this region. As yet, the source of the larvae transported from outside into the Harbour and subsequently settle there is unknown. Larvae originating from regions outside Wellington might be brought here by three separate currents (described in chapter one) originating in subtropical and sub-Antarctic waters, which experience mixing in north-western Cook Strait (Gilmour, 1960; Bowman, 1983a, b). However, the presence of a large and well-developed mussel population inside the Harbour and the striking absence of similar communities immediately outside the Harbour make the Harbour community an isolated one. This state could be intensified by the hydrological conditions in Cook Strait, where the strong flow possibly carries the larvae away from the Harbour. Because the flow in Cook Strait is turbulent and fluctuates rapidly in both speed and direction, with the subsurface flow velocities of roughly similar magnitude to the surface velocities, estimated at 18 cm sec^{-1} (Gilmour, 1960; Heath, 1969; Heath, 1971; Bowman *et al.*, 1983a), it is possible that the Wellington Harbour mussel community is even further separated from other larvae-supplying communities, and could therefore be a self-seeding population. Since larval dispersal direction and ranges can be estimated from hydrographic and genetic markers data (McQuaid & Phillips, 2000), up-to-date research investigating the hydrology of Wellington Harbour and the rate of water exchange

between it and Cook Strait needs to be undertaken. Currently, the lack of such data makes it difficult to speculate about the self-seeding nature of Wellington Harbour.

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CHAPTER FOUR: INTERTIDAL MUSSEL COMMUNITY DEVELOPMENT

4.1. Introduction

Intertidal systems are dynamic environments, constantly subjecting their inhabitants to varying conditions of temperature, humidity and salinity, as well as physical disturbance from storms and wave action (Creese & Kingsford, 1998; Madarasz, 2003). While varying levels of temperature, salinity and nutrients reaching intertidal communities can result from hydrodynamic regimes, the dynamics of intertidal populations are also closely linked to biological processes (e.g. predation, settlement or competition for resources). These biological processes, in turn, can depend on the harshness of the environment, which will eventually lead to spatial and temporal variability within such populations and communities (Underwood & Chapman, 2000; Thompson *et al.*, 2002). The importance of oceanographic processes in structuring intertidal and shallow subtidal communities has become clearer, in particular within the recent decades, through the fact that such processes may drive constant among-site differences in community composition (Roughgarden *et al.*, 1988; Menge, 1992; Witman *et al.*, 1993; Roughgarden *et al.*, 1994; Menge *et al.*, 1997a, b; Connolly & Roughgarden, 1998). Thus, coastal areas characterized by gyres, eddies, upwelling events or advective currents may be able to retain high concentrations of phytoplankton and zooplankton, which are transported onshore and utilized heavily by filter feeders, thereby contributing greatly to the biomass of those invertebrate communities. By fuelling the growth of filter feeder communities, high phytoplankton abundance is also believed to contribute to the reduced abundance of macrophytes, which are less competitive than filter feeders. Subsequently, as filter feeders dominate a coastal area, predators are attracted to them in greater numbers, which leads to higher predation rates, eventually keeping the invertebrate growth in check. Thus, pelagic and benthic systems are coupled in the following way: gyres/eddies → higher concentration of phytoplankton → higher settlement and growth of invertebrates → higher predation rate (Menge *et al.*, 1999).

Community regulation

Traditionally, the composition of mussel communities is believed to be a product of the biotic interactions among various community members, and between the community and the resources it acquires from its environment (Metaxas & Scheibling, 1996). Typically, two groups of factors are held responsible for regulating such communities: Bottom-up and top-down factors.

Bottom-up factors are related to levels of nutrients, plant-derived detritus and primary production (of phytoplankton or macrophytes) that affect higher trophic levels within a community. Increased levels of nutrients can “cascade up” food webs and affect higher trophic levels, thus leading to higher abundance of herbivores and predators in an aquatic community (Hall *et al.*, 1970; Hunter & Price, 1992). Mussel recruitment can also be considered as a bottom-up factor, since it can significantly affect the future development of the community. However, because other distinct processes, of which we may not have sufficient knowledge, may be linked to larval settlement (e.g. larval nutrition or larval transport), at present larval recruitment should be considered separately from nutrients and primary productivity as bottom-up factors affecting marine communities (Menge *et al.*, 1999). To establish how bottom-up processes influence an aquatic community a study would have to be designed in which levels of nutrients would be manipulated and community response recorded (Neill & Peacock, 1980). However, marine systems are too open for such manipulations to be feasible, therefore alternative studies are needed, in which nutrient levels and a subsequent community response are simultaneously recorded. Accordingly, it is believed that an increase in nutrients would stimulate larval growth rate, abundance and survival, possibly leading to a similar increase in growth, abundance and survival of the community, eventually giving way to top-down processes (Menge, 1992; Forde & Raimondi, 2004).

Top-down processes (also known as “trophic cascades”) refer to effects of higher trophic levels on lower trophic levels within a mussel community, such as effects of predation or grazing (Hairston *et al.*, 1960; Menge, 1992). As such, top-down factors

affect abundance, distribution and diversity of invertebrates and/or algae controlled by predators and/or grazers (Paine, 1966; 1974; 1980, Dayton, 1971; Menge *et al.*, 1986). Controlled manipulations, such as caging experiments where predators are excluded from a community, are the most direct ways of examining top-down effects (Menge, 1992). The response of mussel community to predator manipulation can be thoroughly estimated, provided the study was of sufficient duration to allow the mussels to colonise the substrate, but in short-term studies the results can be misleading, because they may not have allowed for the fact that mussels can colonise the substrate sporadically or with delay (Menge, 1997). For example, in an experiment involving starfish removal from a mussel bed on the Pacific coast of Washington, Paine (1966) observed a mussel dominance of the substrate after 2 years. Similarly, Menge *et al.* (1986) reported little change in prey community structure in Panama after a year of predator exclusion, but a great shift in substrate colonization from algal stage, through barnacle domination to oyster domination in experimental plots after 3 years. In both cases, if the studies had been terminated too soon the results would have been incomplete or misleading.

Natural mussel communities are multi-factorial, with bottom-up and top-down factors dynamically linked and affecting communities at the same time, hardly ever acting in isolation. It is now believed that bottom-up factors shape the future structure of a community, determining the number of trophic levels, which in turn will be important for the community structure and the influence of top-down effects. As such, higher concentrations of nutrients stimulate consumer biomass and support more trophic levels, eventually leading to increased consumer pressure on lower trophic levels (Menge, 1992). Studies stressing the significance of bottom-up effects (e.g. Duggins *et al.*, 1989; Bosman & Hockey, 1986, Wootton, 1991) and top-down effects on prey communities (e.g. Fairweather, 1985; Dungan, 1986), where variation in the top-down effects was attributable to environmental stress resulting from wave action or desiccation, serve as good examples demonstrating the importance of these factors for aquatic communities.

The role of physical disturbance

In rocky intertidal assemblages mussels often monopolize the substrate by creating dense beds or mats. While such beds offer shelter from drag and acceleration of water currents to other members of bed-associated fauna (Hunt & Scheibling, 2002), such mussel beds can be often dislodged from the substrate by waves or pounding logs (Denny, 1987; Herlyn & Millat, 2000) or the shearing forces of waves (Harger & Landenberger, 1971), thus leaving large areas of the substrate empty and available for recolonisation (Denny, 1987). Patches of bare substrate can also be created by substrate movement (Osman, 1977). Wave exposure has been regarded as an important indicator of community structure, because it affects the pathways of mussel succession, activity of mobile predators and effectively trophic relations within the mussel community (Menge & Sutherland, 1976, 1987). One single important effect wave exposure has on mussel communities is the way it regulates their ability to attach and stay attached, thus affecting community composition and the distribution of its members. When one mussel is detached from the bed, hydrodynamic forces of drag and lift can often remove several individuals, thus exposing large areas of the substrate to potentially new colonizers (Schiel, 2004).

The role of biological interactions

With the removal of competitively dominant mussels by physical or biological disturbance, previously competitively inferior species that had been unable to establish themselves and persist in a community, can now colonise rocky substrate. As this succession takes place, major biological factors come into play: Competition among species for resources (such as space and nutrition), predation and grazing.

Competition

Competition, one of the ecological processes structuring communities (Paine, 1971, Chase *et al.*, 2002) can potentially alter intertidal communities in three ways: by

one species preventing other species from settling from the water column onto the substrate (pre-emptive competition), by one community inhabitant directly eliminating another one, for example by killing it (interference competition), or when several species need the same space to feed but the amount of food to support them is insufficient (exploitative competition) (Underwood, 2000). Examples of these types of competition on rocky intertidal shores include preventing barnacles from settling by algal fronds sweeping the rocky surfaces (Connell, 1961a, b), fast-growing barnacles gradually eliminating slower-growing algae (Dayton, 1971), or mussels smothering other community members by settling directly onto them (Paine, 1974; Menge, 1976).

Predation

Abundance of predators has traditionally been regarded as crucial in the development of marine communities (Paine, 1974; Menge & Sutherland, 1976, 1987). While competition occurs most often among groups of organisms sharing resources within the same trophic level (e.g. mussels and barnacles competing for space and food), predation links different trophic levels, where predators and prey share different resources (e.g. mussels and whelks) (Connell, 1975). In intertidal systems, predation can alter the pathways of succession, in particular when mussel are involved, as predators can reduce the number of individuals competing for the same resources and thus reduce the competition itself. As a result, competitively inferior organisms are able to co-exist with the competitively dominant mussels within the assemblage (Paine, 1971).

Physical and biological factors are often found interplaying, thus shaping the vertical distribution of algae and animals in intertidal communities. Physical factors may influence patterns of distribution and abundance of intertidal populations directly (by limiting growth of the members of the communities) or indirectly (by mediating the activity of predators) (Benedetti-Cecchi *et al.*, 2000).

The importance of the water column parameters

Temperature, salinity, chlorophyll *a* concentration and turbidity are among the most widely studied seawater parameters. Temperature and salinity can be linked to various phases of bivalve lives, including gametogenesis and reproduction, larval settlement and recruitment, together with subsequent growth and condition. Seston quality, often expressed as chlorophyll *a* concentration, suggests the concentration of phytoplankton on which filter feeders rely as food. It also points to dietary conditions in which those animals live, because a variety of suspended particles present in the water column, such as detritus, bacteria and phytoplankton, differently contribute to the nutrient acquisition by invertebrates (Gosling, 2003). On the other hand, seston quantity can be referred to as turbidity and is typically defined as the amount of suspended sediment particles in the water column (Mylvaganam & Jakobsen, 2000). Thus, chlorophyll *a* provides the quantitative measure of seston in the water column, while turbidity is a qualitative seston measure. When combined, the two parameters can provide information about the amount of particles suspended in the water column, as well as their potential nutritional value to seston-feeding organisms, such as bivalves. Therefore, from the ecological perspective, a study of seawater parameters is a powerful tool, helping us understand differences underlying structure of rocky intertidal communities, the distribution of their members and the intra-community dynamics among those members.

Most published experimental studies investigating rocky intertidal assemblage structure concentrate on dynamics of communities dominated by one or two mytilid species. A large part of this work has been done on North American intertidal shores (e.g., Menge, 1976, 1992; Bertness & Grosholz, 1985; Wootton, 1993; Lively *et al.*, 1993; Menge *et al.*, 1994; Berlow & Navarette, 1997; Connolly & Roughgarden, 1998) and, to a lesser degree, in European systems (e.g., Ardizzone *et al.*, 1996; Buschbaum, 2000). Similar reports of rocky intertidal communities from New Zealand include studies by Poore (1968) and Menge *et al.* (1999, 2003). Investigations of community dynamics with two mytilids species within a rocky intertidal system include reports by Henschel *et al.* (1990) from South Africa, Bertness and Leonard (1997) from North America, and

Paine (1971) and Boyle *et al.* (2001) from New Zealand. While investigations of the dynamics among three or more co-existing mussel taxa and the structure of such communities are interesting, few studies are available in which such studies have been conducted (for example, Bustamante & Branch, 1996). Following the community development in multi-species mussel assemblages uncovers the often-complex ecological mechanisms, thus allowing us to create detailed models of the intertidal system community structure.

This chapter presents results of a long-term examination (24 months) and focuses on the dynamics of rocky intertidal communities in a complex system dominated by three sympatric mussel species: two species endemic to New Zealand: the ribbed mussel *Aulacomya maoriana* and the greenshell mussel *Perna canaliculus*, and the blue mussel originating from the Mediterranean, *Mytilus galloprovincialis*. The work presented here is unique in that it differs from other published reports from systems dominated by most often one, occasionally two mussel species. The present study was conducted in a speciose environment supporting three co-existing mussel species, where succession within intertidal communities consequently includes numerous algal and invertebrate taxa that colonise the substrate and subsequently are excluded by dominant competitors. Naturally, the mechanisms of succession and competition in such a system are expected to be more complex, especially where there are numerous dominant species involved. Long-term examination of such a complex, multi-site and multi-species environment allows us to gain enhanced knowledge of the often subtle and difficult to detect stages of succession and resource partitioning in intertidal systems. Further, given a complex hydrology of Wellington Harbour and its effect on the water column parameters, a study of the mechanisms of succession and competition are of special interest as they can shed more light on the dynamics of the intertidal zone communities supporting numerous dominant species. While previous work described intertidal, mussel-dominated community continuation, this study concentrates on the multi-species mussel community recovery following the mimicked physical disturbance, and establishes a link between the rate of such recovery and food abundance in an intertidal system.

In the present study, a series of experiments was performed in Wellington Harbour in order to quantify the successional pathways and structure of intertidal communities typically dominated by three sympatrically occurring mytilids. Complete clearing of substrate combined with a set up of experimental cages was chosen as a method of mimicked disturbance (Connell, 1961b; Dayton, 1971). This approach gave the advantage of simultaneous comparison of disturbance at three experimental sites (Fig. 4.1) and elimination of possible effects from survivors (Foster *et al.*, 2003). In particular, estimates were calculated for the following guilds of intertidal community invertebrate members: algae, barnacles, mussels, grazers (such as limpets) and predators (such as whelks). Proportion of bare, unutilized substrate was also included in this study. Further, the interplay between succession mechanism in rocky intertidal communities and the water column characteristics in Wellington Harbour was also investigated.

4.2. Materials and Methods

Water column data

In order to obtain environmental data two Richard Brancker Research Ltd XR-420 loggers were used. Data were obtained at Evans Bay and Seatoun between August 2002 and September 2003 (Fig. 4.1), and subsequently processed and analyzed as described in chapter two.

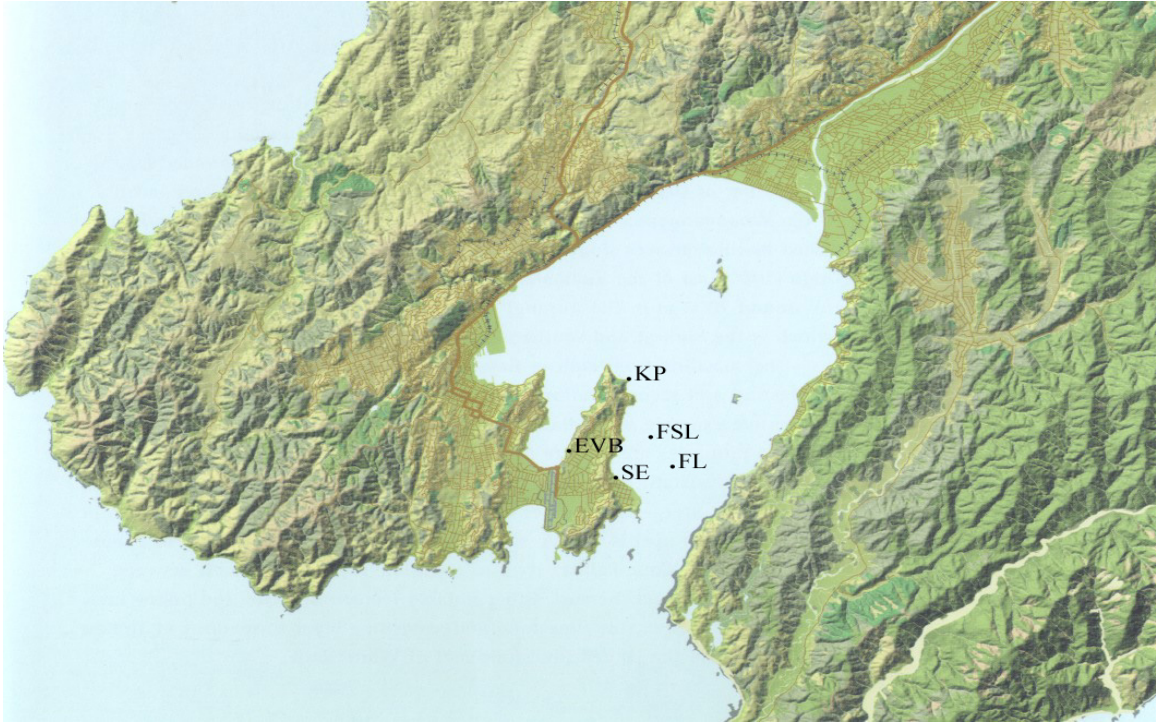


Figure 4.1. Location of experimental sites in Wellington Harbour (adapted from Molloy & Smith, 2002). Caging experiments were conducted at: EVB – Evans Bay, SE – Seatoun and KP – Kau Point. The water column data were collected at: EVB – Evans Bay, FL – Front Lead light and FSL – Falcon Shoal light.

Caging experiment

To quantify the rate of intertidal community recovery, development and the subsequent recolonisation of the rocky substrate by algal and invertebrate taxa, a factorial-designed, caging experiment was conducted between November 2001 and October 2003 (month, site and cage treatment as fixed factors). Because it was desirable to obtain information about the rate of community recovery according to localized hydrological and wave exposure regimes from as many sites as possible, but the number of locations suitable for this experiment was limited, the following experimental rocky intertidal sites were selected: Seatoun, Kau Point and Evans Bay (Fig. 4.1). At each of these sites the exposure to prevailing winds and resulting wave action is different. In Wellington, there is a strong dominance of northerly (~60%) and southerly (~30%) winds. Although southerlies are less frequent and less gusty, they are about twice as strong as northerlies, most likely a result of the great wind acceleration on the Kaikoura

coast (McConchie, 2000). For this reason, southerly-generated oceanic swells and waves carry more energy than northerly-generated waves and therefore intertidal communities at south-facing sites within Wellington Harbour receive a large amount of wave pounding, which can affect the processes of development and dynamics within such communities (Dayton, 1971; Underwood *et al.*, 1983; Bustamante *et al.*, 1997). Evans Bay is protected from destructive southerly swells and significantly protected from northerly-generated surge, thus it is the most sheltered site in this experiment. Seatoun receives some of the energy carried by southerly swells and is also exposed to northerly winds, although not as much as Kau Point, which receives the full strength of both southerly and northerly winds and therefore is the most exposed site in this study. Thus, in terms of exposure to wave action, these sites can be ranked as follows: Kau Point > Seatoun > Evans Bay.

At each of these sites, sixteen 200 x 200 mm plots were randomly selected in the mid-intertidal zone. While it was desirable to select plots that would be within equal distance from each other, the rock configuration did not always allow for this, therefore some plots had to be placed closer together so that all plots would still remain within the mid-intertidal zone. The plots were completely cleaned of all epibionts with a wire brush, so that any subsequent substrate colonization would start from zero where no pre-clearance (i.e. “already present” colonization) bias would be present. Subsequently, three experimental treatments were applied at each site with each treatment replicated four times. Each treatment consisted of an open cage (Fig. 4.2), a full cage (Fig. 4.3), and a “no roof” cage (Fig. 4.4). A boundary was cleared around the plots to prevent movement of adjacent individuals into the cages. Cage-free frames (Fig. 4.5) were nailed into the rocky substrate and were used as controls (also replicated four times) (Menge, 1976, Honkoop *et al.*, 2003). Cages were constructed from plastic baskets (20 x 20 mm, 90 mm high, mesh size 3 mm). Each cage was attached to a plastic frame (250 x 250 mm, 50 mm wide), which was secured into the rock with stainless nails. The cages were then secured onto the plastic frames with brass nuts and bolts (Ø 5 mm, 35 mm in length) and the whole assemblage was then sealed at the bottom with a mixture of mortar and a quick-setting agent Sika-4a, to prevent movement of species under the frame into or out of the experimental plots.

The open cage treatment (Fig. 4.2) allowed predators into the experimental plots. When compared with the control frame and the full cage treatment (Fig. 4.5 and 4.3), the open cage treatment allowed for examination of the effects of (mostly invertebrate) predation on taxa colonizing the previously cleared substrate. This treatment, when compared with the “no roof” treatment (Fig. 4.4), also allowed for testing of desiccation effects by affecting the humidity under the cage, thus altering the desiccation conditions within the experimental plots. The key points of interest behind such a selection of the experimental treatments were:

1. How quickly each of the three mussel species (*A. maoriana*, *M. galloprovincialis* and *P. canaliculus*) recruited onto the substrate, depending on the caging treatment,
2. What other algal and invertebrate taxa would recruit onto the experimental substrate, depending on the treatment,
3. How long each of the communities would require to fully recover from the mimicked disturbance (i.e. substrate clearance).



Figure 4.2. Open cage exposed at low tide.



Figure 4.3. Full cages exposed at low tide.



Figure 4.4. "No roof" cage exposed at low tide.



Figure 4.5. Control frame exposed at low tide.

While caging experiments aiming to estimate the effects of predation on intertidal mussel community, such as the present study, can introduce artifacts to the experimental treatment, they nevertheless provide an estimation of predation, in particular when the predator behaviour and ecological dynamics are concerned (Alfaro & Carpetner, 1999). From the experimental design point of view, the potential artifacts of such enclosure experiments need to be recognized when the interventions required are grossly invasive and obvious, as was the case in the present study (Peterson & Black, 1994). According to the current epistemological practice, if the intervention is applied identically across all experimental treatments and controls so that only the experimental treatment itself varies, then any artifactual effect introduced by caging would also be held constant. Thus, the comparison between and among the experimental treatments and controls would be unaffected by these artifacts. Further, to evaluate the direction and magnitude of biases introduced by caging, controls need to be included in the experimental design. Results from the controls can then be used to estimate the direction and magnitude of the artifact caused by caging and to estimate the conditions under which the experiment was conducted (Kennelly, 1983; Peterson & Black, 1994).

Percent cover estimates

For the period of 24 months, from November 2001 until October 2003, at monthly intervals (except June and July 2002), cages were removed from the base frame and each plot was photographed with a SONY digital camera (model DSC-S75, picture resolution 2048 x 1536 pixels). Digital pictures were subsequently downloaded onto a portable computer and calibrated using SigmaScan Pro (version 4.0, Jandel Scientific). From each picture, percent cover of bare rock and organisms settling on it were estimated by hand-tracing of individual patches of fauna and flora. While the exact measurements of the numbers and sizes of the photographed taxa can provide a good indication of the colonisation and evolution of the population examined over time, percent cover was a preferred method of recolonisation measurement over length/growth measurements, as the latter method could not be reliably estimated from the digital images as a result of the photographed taxa often growing on the substrate at a wrong angle towards the camera to allow for thorough length/growth measurements. Species identifications were obtained by reference to appropriate literature (e.g. Leslie, 1968; Morton & Miller, 1968; Miller & Batt, 1973; Gunson, 1983; Bradstock, 1985; Hawkins & Jones, 1992; Adams, 1994 and 1997; Morton, 2004) or were provided by individual authorities from photographs or specimens.

Data analysis

Raw invertebrate and algal percent cover data were tested for normality of residuals, normality of distribution and homogeneity of variance, and subsequently arcsine square root-transformed. In order to investigate the spatial and temporal variation in percent cover of each species, a MANOVA was employed. Despite the fact that not all transformed data strictly followed normal distribution, this method was chosen because it has been described as being fairly robust against deviations from normality of distribution (Quinn & Keough, 2002). Further, the choice of MANOVA when dealing with non-normally distributed variables can be justified when the data contains a high number ($n > 100$) of observations (Zar, 1984). For this analysis, all algal and invertebrate species, as

well as bare substrate, were specified as dependent variables, with site, month and treatment specified as crossed factors. Subsequently, a similar repeated-measures ANOVA technique was repeated for all functional and the most commonly observed groups of recruiting organisms (i.e. algae, barnacles, mussels, whelks and limpets), including bare substrate. Next, a similar MANOVA technique was performed separately for each site in order to detect differences in percent cover of the functional groups and the recolonising species among months and treatments. Further, a correlation analysis was performed on the CTD data and percent cover data of the functional groups obtained from Evans Bay and Seatoun. Correlation analysis was not performed on Kau Point percent cover data because no CTD was deployed at that site.

Finally, a multiple regression technique was employed. In the analysis, percent cover of each mussel species (*Mytilus galloprovincialis*, *Aulacomya maoriana* and *Perna canaliculus*) was specified as a dependent variable, with barnacles, algal, whelk, and limpet species, as well as bare substrate, specified as independent variables. This analysis was performed for each site. Results of this analysis are presented in Pareto charts by displaying the absolute *t*-values and showing respective significance levels of each independent variable previously specified in the analysis. All statistical analyses were performed using Statistica software version 6.0 (StatSoft Inc., USA, 2001).

4.3. Results

Water column properties

Results of the analysis of the environmental data at set Seatoun and Evans Bay are described in chapter two.

Caging experiment - percent cover estimates

25 intertidal species within 7 phyla and 10 classes were identified and subsequently analyzed in this experiment (Table 4.1). The three barnacle species

Chamaesipho columna, *Ch. brunnea* and *Elminius modestus* were grouped together because the image resolution was often not sufficient to distinguish among the species.

Table 4.1. Algal and invertebrate species for which percent cover data were obtained.

Phylum	Class	Species	Common name
<i>Phycophyta</i>	<i>Chlorophyceae</i>	<i>Ulva lactuca</i>	Sea lettuce
		<i>Enteromorpha</i> sp.	Green alga
	<i>Rhodophyceae</i>	<i>Corallina officinalis</i>	Coralline turf
		Non-geniculate coralline sp.	Coralline paint
		<i>Porphyra</i> sp.	Red alga
		<i>Polysiphonia rudis</i>	Red alga
	<i>Phaeophyceae</i>	<i>Cystophora retroflexa</i>	Brown alga
<i>Cnidaria</i>	<i>Anthozoa</i>	<i>Actinia albocincta</i>	Orange-and-white anemone
		<i>Corynactus haddoni</i>	Haddon's anemone
		<i>Watersipora subtorquata</i>	Bryozoan
<i>Ectoprocta</i>	<i>Gymnolaemata</i>	<i>Pomatoceros cariniferus</i>	Tube worm
<i>Annelida</i>	<i>Polychaeta</i>	<i>Haustorium haustorium</i>	Dark rock shell
<i>Mollusca</i>	<i>Gastropoda</i>	<i>Buccinum</i> sp.	Lined whelk
		<i>Lepsiella scobina</i>	Oyster borer
		<i>Cellana radians</i>	Radiate limpet
		<i>Cellana denticulata</i>	Denticulate limpet
		<i>Cellana ornata</i>	Ornate limpet
	<i>Bivalvia</i>	<i>Mytilus galloprovincialis</i>	Blue mussel
		<i>Aulacomya maoriana</i>	Ribbed mussel
		<i>Perna canaliculus</i>	Greenshell mussel
		<i>Chamaesipho columna</i>	Columnar barnacle
		<i>Chamaesipho brunnea</i>	Brown barnacle
<i>Arthropoda</i>	<i>Crustacea</i>	<i>Elminius modestus</i>	Modest barnacle
		<i>Petrolisthes elongatus</i>	Porcelain crab
<i>Echinodermata</i>	<i>Asteroidea</i>	<i>Patiriella regularis</i>	Cushion star

A repeated-measures ANOVA was employed to test for differences in percent cover of bare substrate, barnacles, and individual algal, mussel, whelk and limpet species recolonising the substrate. The analysis revealed significant differences among sites, months and treatments (Table 4.2). All terms were statistically significant, indicating that percent cover of the recolonising species differed among sites as a function of treatment (i.e. full cage, “no roof” cage, open cage and control) and time.

Table 4.2. Results of MANOVA for differences in percent cover of bare substrate, algal and invertebrate species among sites, treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Site	0.209	36	1550.00	51.067	<0.01
Month	0.207	378	10685.07	3.435	<0.01
Treatment	0.375	54	2310.01	16.625	<0.01
Site x Month	0.103	756	12932.49	2.511	<0.01
Site x Treatment	0.285	108	4448.75	10.074	<0.01
Month x Treatment	0.155	1134	13530.44	1.351	<0.01
Site x Month x Treatment	0.039	2268	13935.36	1.219	<0.01

The overall model was not accepted for one algal species (*Porphyra* sp.) and two invertebrate species, the greenshell mussel *P. canaliculus* and the predatory gastropod *H. haustorium* (Table 4.3).

Table 4.3. Overall model fit of MANOVA for individual species of algae, barnacles, mussels, whelks, limpets and bare substrate (N-g = non-geniculate coralline species).

Species	R	R ²	SS model	df model	F	p-value
Bare substrate	0.829	0.687	123.231	263	6.608	<0.001
Barnacles	0.822	0.676	65.382	263	6.285	<0.001
<i>C. officinalis</i>	0.784	0.614	13.441	263	4.798	<0.001
<i>Enteromorpha</i> sp.	0.752	0.565	25.030	263	3.917	<0.001
<i>C. retroflexa</i>	0.667	0.445	1.699	263	2.413	<0.001
N-g coralline sp.	0.667	0.444	11.634	263	2.409	<0.001
<i>M. galloprovincialis</i>	0.680	0.462	21.204	263	2.585	<0.001
<i>U. lactuca</i>	0.638	0.407	7.739	263	2.064	<0.001
<i>L. scobina</i>	0.628	0.395	0.086	263	1.966	<0.001
<i>Buccinulum</i> sp.	0.587	0.344	0.294	263	1.580	<0.001
<i>C. ornata</i>	0.585	0.343	0.722	263	1.569	<0.001
<i>C. radians</i>	0.583	0.340	0.189	263	1.550	<0.001
<i>A. maoriana</i>	0.579	0.335	0.855	263	1.516	<0.001
<i>P. rudis</i>	0.550	0.302	2.150	263	1.304	0.003
<i>C. denticulata</i>	0.542	0.293	0.203	263	1.250	0.011
<i>H. haustorium</i>	0.524	0.275	0.053	263	1.141	0.089
<i>Porphyra</i> sp.	0.511	0.261	0.846	263	1.062	0.267
<i>P. canaliculus</i>	0.473	0.224	0.209	263	0.867	0.916

A MANOVA was employed to test for differences in percent cover of functional groups of recruiting organisms (such as algae, barnacles, mussels, limpets and whelks) and bare substrate. In the analysis, site, treatment and month were specified as crossed factors (Table 4.4). The three two-way interaction terms were all statistically significant ($p < 0.01$). There was a significant interaction term between all factors (site*treatment*month), indicating that the mean number of organisms recolonising the

experimental plots differed among sites as a function of treatment and time. The overall model for each group of organisms was accepted (Table 4.5).

Table 4.4. MANOVA for differences in percent cover of groups of algae, invertebrates and bare substrate among sites, treatments and months.

Effect	Value	Effect df	Error df	F	p-value
Site	0.360820	12	1718.0	95.173	<0.01
Month	0.110570	138	5016.590	16.681	<0.01
Treatment	0.646860	18	2430.104	22.480	<0.01
Site x Month	0.239585	276	5125.453	5.035	<0.01
Site x Treatment	0.631977	36	3774.894	11.551	<0.01
Month x Treatment	0.517081	414	5146.540	1.449	<0.01
Site x Month x Treatment	0.375485	828	5159.450	1.106	0.0263

Table 4.5. Overall model fit of MANOVA for groups of algae, invertebrates and bare substrate.

Group	R	R ²	SS model	df model	F	p-value
Bare substrate	0.883	0.780	182.396	287	10.703	<0.01
Barnacles	0.829	0.687	69.736	287	6.629	<0.01
Mussels	0.703	0.494	25.428	287	2.948	<0.01
Algae	0.689	0.474	39.578	287	2.718	<0.01
Whelks	0.659	0.434	1.208	287	2.312	<0.01
Limpets	0.608	0.371	0.321	287	1.774	<0.01

Seatoun: Relationship among species of colonizers and bare substrate

A MANOVA was performed on arcsine square root-transformed data to test for differences in percent cover of functional algal and invertebrate groups, including bare substrate. The analysis revealed statistically significant differences in percent cover among months and treatments (Table 4.6). The two-way interaction was also significant, indicating that percent cover of each group under each treatment was a function of time ($p < 0.001$). The overall model for each group of organisms was accepted (Table 4.7).

Table 4.6. Seatoun: Results of MANOVA for differences in percent cover of bare substrate and functional groups of algae and invertebrates among treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Month	0.084	126	1509.499	6.391	<0.001
Treatment	0.435	18	733.048	13.939	<0.001
Month x Treatment	0.148	378	1557.173	1.549	<0.001

Table 4.7. Seatoun: Overall model fit of MANOVA for groups of algae, invertebrates and bare substrate.

Group	R	R ²	SS model	df model	F	p-value
Bare substrate	0.809	0.655	26.875	87	5.758	<0.001
Mussels	0.707	0.500	2.978	87	3.030	<0.001
Algae	0.694	0.482	11.250	87	2.827	<0.001
Whelks	0.627	0.393	0.646	87	1.968	<0.001
Barnacles	0.592	0.350	5.954	87	1.637	0.002
Limpets	0.583	0.340	0.220	87	1.566	<0.001

The analysis was repeated to test for differences in percent cover of bare substrate, as well as individual algal, mussel, whelk and limpet species and barnacles that were gradually recolonising the substrate, thus marking the community recovery (Table 4.8). The analysis revealed statistically significant differences in percent cover of individual species among months and treatments. The two-way interaction was significant, indicating that percent cover of each group under each treatment was a function of time ($p < 0.01$).

Table 4.8. Seatoun: Results of MANOVA for differences in percent cover of bare substrate, algal and invertebrate species among treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Month	0.019	357	3342.616	3.260	<0.01
Treatment	0.249	51	739.142	8.630	<0.01
Month x Treatment	0.008	1071	4170.565	1.323	<0.01

The overall model was not accepted for the alga *Porphyra* sp., the greenshell mussel *Perna canaliculus*, two whelk species, *Lepsiella scobina* and *Haustrum haustorium*, and two limpet species, *Cellana denticulata* and *Cellana radians* (Table 4.9).

Table 4.9. Seatoun: overall model fit of MANOVA for individual species of algae, barnacles, mussels, whelks, limpets and bare substrate (N-g = non-geniculate coralline species).

Species	R	R ²	SS model	df model	F	p-value
Bare substrate	0.798	0.637	28.076	87	5.336	<0.001
<i>C. officinalis</i>	0.762	0.580	10.548	87	4.190	<0.001
<i>M. galloprovincialis</i>	0.714	0.510	3.053	87	3.153	<0.001
<i>C. retroflexa</i>	0.655	0.430	1.597	87	2.285	<0.001
N-g coralline sp.	0.643	0.413	4.183	87	2.138	<0.001
Barnacles	0.624	0.389	7.357	87	1.933	<0.001
<i>P. rudis</i>	0.614	0.377	1.298	87	1.839	<0.001
<i>C. ornata</i>	0.573	0.328	0.385	87	1.484	0.009
<i>U. lactuca</i>	0.572	0.327	1.000	87	1.474	0.010
<i>A. maoriana</i>	0.568	0.322	0.178	87	1.444	0.014

Species	R	R ²	SS model	df model	F	p-value
<i>Buccinulum</i> sp.	0.567	0.322	0.219	87	1.441	0.015
<i>C. denticulata</i>	0.547	0.299	0.142	87	1.294	0.063
<i>H. haustorium</i>	0.538	0.290	0.034	87	1.237	0.103
<i>Porphyra</i> sp.	0.521	0.271	0.542	87	1.130	0.231
<i>C. radians</i>	0.521	0.271	0.072	87	1.129	0.234
<i>P. canaliculus</i>	0.494	0.244	0.010	87	0.980	0.535
<i>L. scobina</i>	0.492	0.242	0.014	87	0.971	0.556

Seatoun: Effects of caging treatments

Seatoun: Control plots

Control plots at Seatoun were very quickly dominated by algae, which reached its highest mean monthly cover of 25.92% in May 2002 and remained at about 20 % until November 2002 (Fig. 4.6). However, after that algal cover declined to about 10%. The lowest algal cover in control plots was recorded in August 2003 (4.80%). Barnacle cover was slow to increase, eventually reaching 10% in December 2002, which was also when algal cover started to diminish in the experimental plots. From that point, barnacles outcompeted algae, reaching their peak monthly cover of 29.43% in April 2003, after which they started to decline. Percent cover of mussels in control plots remained very low (well below 10%) throughout the entire experiment, and the highest mussel cover of 5.11% was recorded in August 2002. Cover of bare substrate systematically decreased until November 2002, when it reached 41.07%. Subsequently, it increased to 75.86% in December 2002 and remained at a level 60-80% until the end of the experiment.

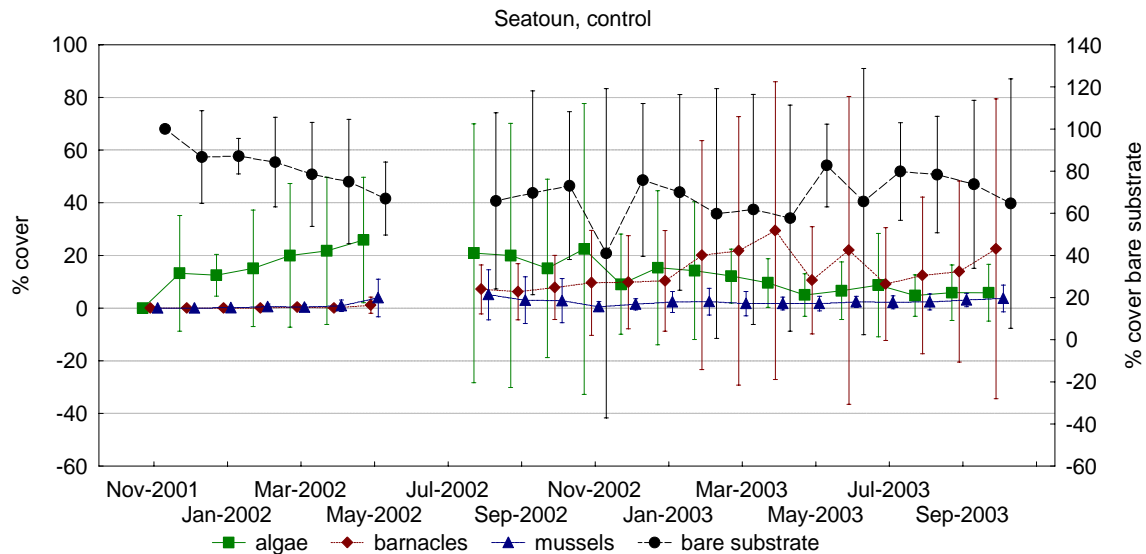


Figure 4. 6. Seatoun, control plots: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Seatoun: “No roof” treatment

Algae quickly colonised the “no roof” plots (Fig. 4.7), reaching their peak monthly cover in May 2002 (19.59%), which lasted until August 2002 (19.28%). Subsequently, algal cover declined to less than 10% for the rest of the sampling period, with the lowest value of 1.55% recorded in October 2003. Mean monthly cover of barnacles was very low until September 2002, when it rose to 18.81% and, after a brief fluctuation, remained at about 20% until January 2003. During that period, barnacle cover peaked at 22.15% in November 2002. Between February and June 2003 barnacle cover, as well as algal and mussel cover, declined, which was accompanied by an increase in bare substrate cover. After that, barnacle cover stabilized at about 15%. Percent cover of mussels remained well below 10% throughout the entire experiment, and the highest mussel cover of 4.66% was recorded in November 2002. Percent cover of bare substrate reached its lowest value in September 2002 and subsequently was increasing until March 2003 (89.99%) and started to decline again, reaching 74.77% in October 2003.

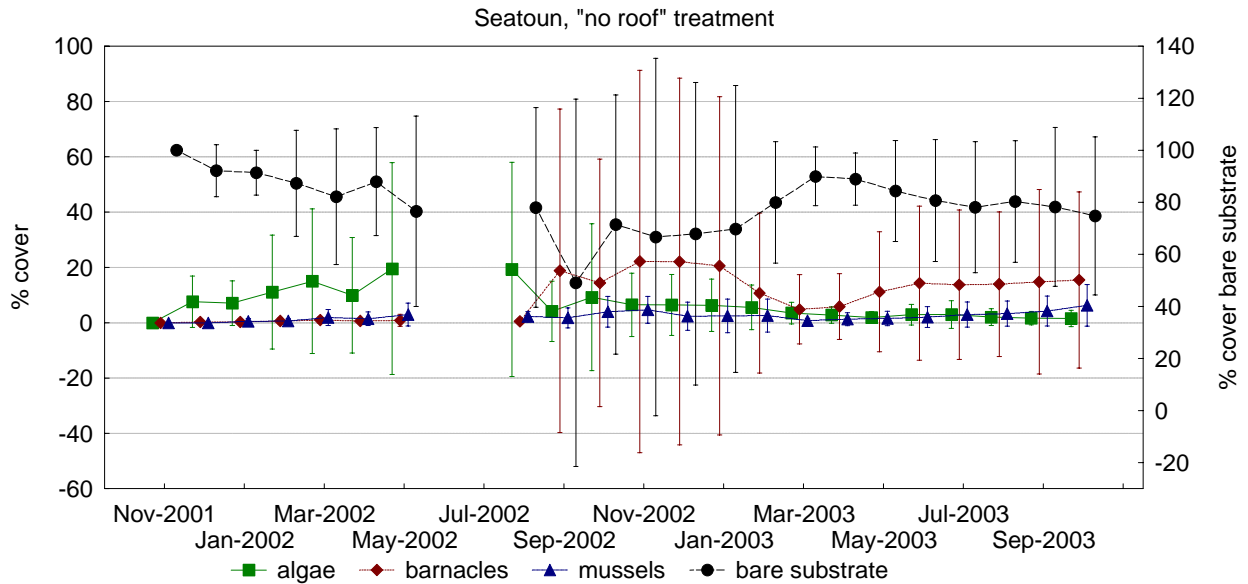


Figure 4. 7. Seatoun, “no roof” treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Seatoun: Open cage treatment

Algal cover in the open cage plots was systematically increasing throughout the experiment (Fig. 4.8). Algae reached 65.55% in June 2003 and, after a brief decline to 14.63% in August 2003, peaked at 68.69% in October 2003. Mean monthly cover of barnacles was very low (less than 10%) throughout the entire experiment, and it reached a maximum of 6.54% in February 2002. For most of the sampling period, mussel cover was less than 10% and it reached greater values on only two occasions: in January 2003 (11.86%) and in May 2003 (11.38%). Bare substrate cover declined to 23.54% in May 2002 and subsequently increased to 88.13% in September 2002. After that, bare substrate cover was generally declining and it reached the minimum value of 9.69% in August 2003.

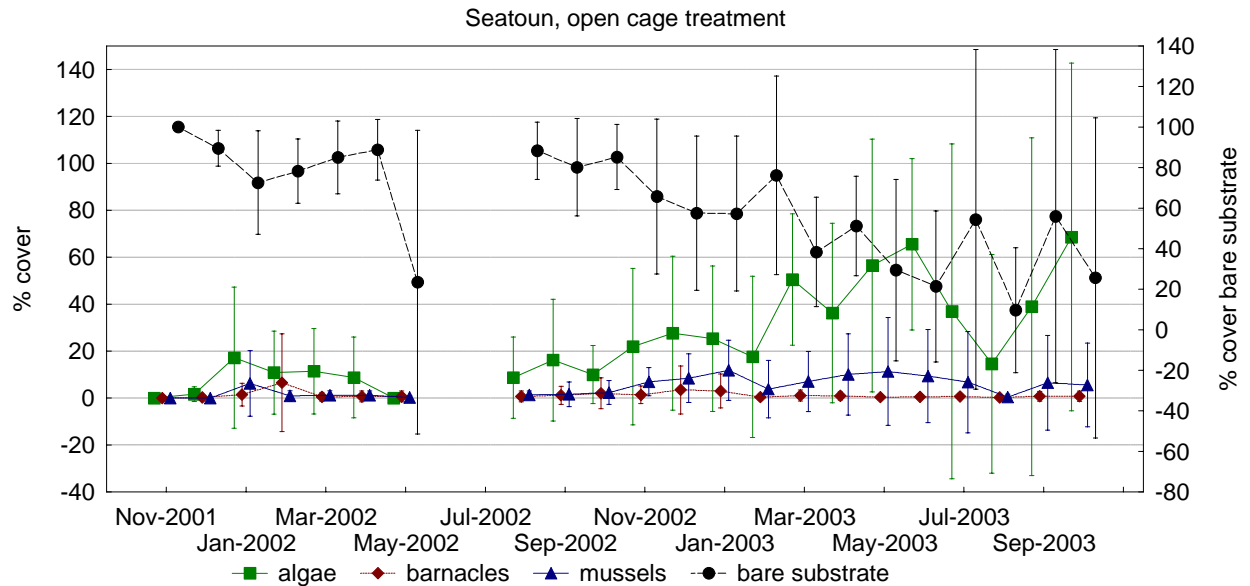


Figure 4. 8. Seatoun, open cage treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Seatoun: Full cage treatment

Algal cover in full cage plots was slow to increase (Fig. 4.9) and it reached the maximum value (7.58%) in February 2003. After that, algal cover remained at about 10% until the end of the experiment. Barnacle cover, after an initial slow increase, peaked at 17.17% in October 2002. Subsequently, it experienced a brief decline to 7.74% in December 2002 and increased again to 16.23% in February 2003, stabilizing at about 20% for the rest of the sampling period. Mussel cover increased, but was less than 10% for most of the experiment. However, mussel cover peaked at the end of the sampling period in September 2003 (at 12.92%) and October 2003 (12.24%). Bare substrate cover was slow to decrease until August 2002 (96.60%). After that, bare substrate cover declined to 78.88% in October 2002 and, after a brief increase to 82.76% in December 2002, it continued to decline until the end of the experiment, when it was 66.72%.

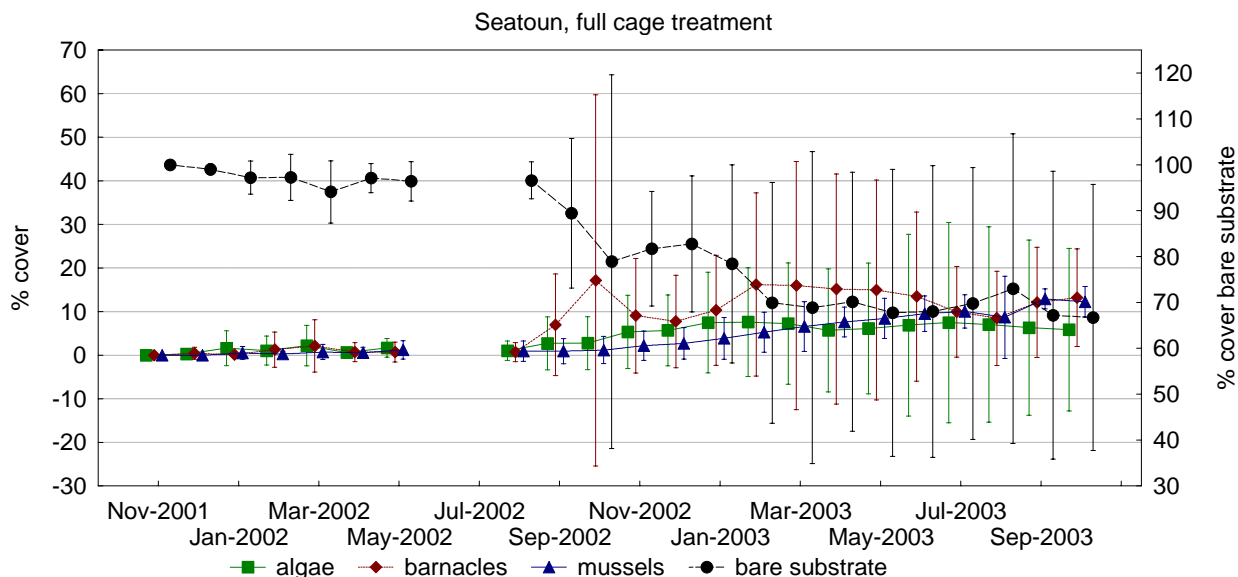


Figure 4. 9. Seatoun, full cage treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Seatoun: CTD-Percent cover correlation

A Product-Moment correlation analysis performed for CTD data and percent cover data of functional groups taken from control plots (i.e. bare substrate, algae, barnacles, mussels, whelks and limpets) revealed that percent cover of both barnacles and whelks was significantly correlated to chlorophyll *a* concentration and salinity. Further, the analysis revealed a statistically significant correlation between limpets and turbidity (Table 4.10).

Table 4.10. Seatoun: Product-Moment correlation analysis for CTD and functional groups percent cover data.

Variable	Algae	Barnacles	Mussels	Whelks	Limpets	Bare substrate
Temperature	R=-0.231 p=0.003*	R=-0.312 p<0.001*	R=-0.294 p<0.001*	R=0.119 p=0.125	R=-0.294 P<0.001*	R=-0.248 p=.001*
Turbidity	R=0.328 p<0.001*	R=0.266 p<0.001*	R=0.453 p<0.001*	R=0.149 p=0.054	R=-0.134 P=0.085	R=0.335 p<0.001*
Chlorophyll <i>a</i>	R=0.103 p=0.186	R=0.423 P<0.001*	R=0.149 p=0.055	R=-0.014 p=0.854	R=0.348 p<0.001*	R=0.362 P<0.001*
Salinity	R=0.333 p<0.001*	R=0.406 p<0.001*	R=0.324 p<0.001*	R=-0.035 p=0.655	R=0.100 p=0.198	R=0.446 p<0.001*

* Significant after Bonferroni correction for multiple testing.

Seatoun: Multiple Regression analysis

Aulacomya maoriana

Multiple Regression analysis revealed a statistically significant ($R^2=0.136$, $F=3.299$, $df=16$, $p<0.001$) interaction between percent cover of the ribbed mussel and the percent cover of the mussel *Mytilus galloprovincialis*, an alga *Polysiphonia rudis*, and a limpet *Cellana denticulata*. (Table 4.11). The Pareto chart in Fig. 4.10 presents the absolute t -values and the significance of these independent variables in relation to *A. maoriana*.

Table 4.11. *Aulacomya maoriana*, Seatoun: Results of the Multiple Regression between the ribbed mussel and other members of the community (N-g. coral. sp.=non-geniculate coralline species).

Variable	SS	df	MS	F	t -value	p -value
<i>M. galloprov.</i>	0.022	1	0.022	15.543	3.942	<0.001
<i>P. rudis</i>	0.016	1	0.016	11.234	3.352	0.001
<i>C. denticulata</i>	0.006	1	0.006	4.254	2.062	0.040
<i>L. scobina</i>	0.005	1	0.005	3.365	1.834	0.067
<i>C. officinalis</i>	0.004	1	0.004	2.908	-1.705	0.089
<i>C. ornata</i>	0.002	1	0.002	1.410	1.187	0.236
<i>Porphyra</i> sp.	0.001	1	0.001	0.970	0.985	0.325
<i>U. lactuca</i>	0.001	1	0.001	0.937	0.968	0.334
<i>C. retroflexa</i>	0.001	1	0.001	0.875	0.935	0.350
N-g. coral. sp.	0.001	1	0.001	0.356	0.597	0.551
<i>H. haustorium</i>	0.001	1	0.001	0.600	-0.775	0.439
Bare substrate	0.001	1	0.001	0.532	-0.729	0.466
<i>C. radiata</i>	0.001	1	0.001	0.469	-0.685	0.494
Barnacles	0.001	1	0.001	0.364	0.603	0.547
<i>P. canaliculus</i>	0.000	1	0.000	0.324	0.569	0.570
<i>Buccinum</i> sp.	0.000	1	0.000	0.089	0.299	0.765

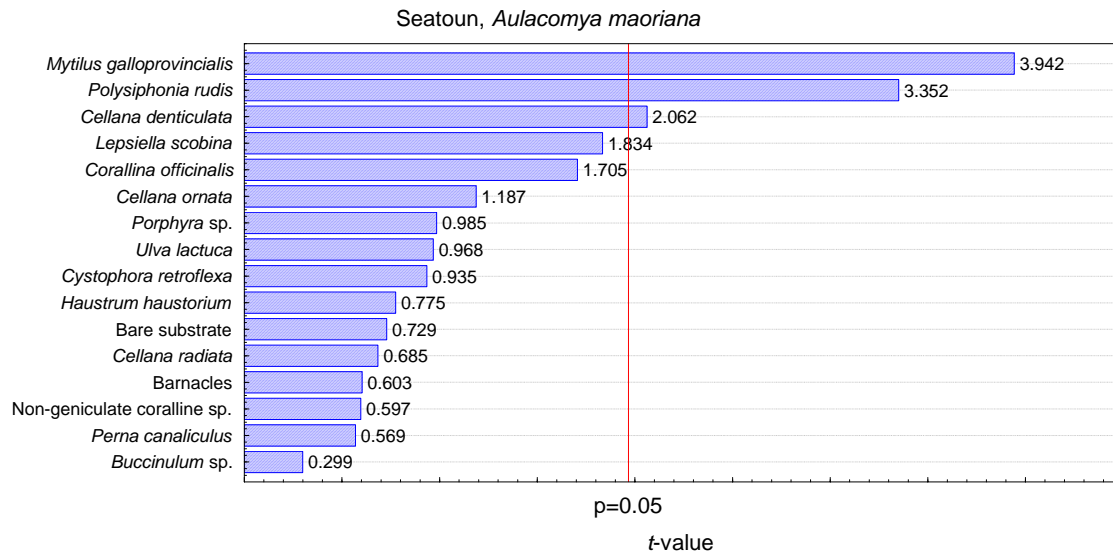


Figure 4.10. Pareto chart for *A. maoriana* at Seatoun.

Mytilus galloprovincialis

Multiple Regression analysis ($R^2=0.279$, $F=8.097$, $df=16$, $p<0.001$) indicated that blue mussel percent cover at Seatoun (Table 4.12) was significantly correlated with percent cover of an alga *Corallina officinalis*, barnacles, a mussel *A. maoriana*, a whelk *Buccinum* sp. and the ornate limpet *Cellana ornata*. The Pareto chart in Fig. 4.11 presents the absolute t -values and the significance of these independent variables in relation to *M. galloprovincialis*.

Table 4.12. *Mytilus galloprovincialis*, Seatoun: Results of the Multiple Regression between the blue mussel and other members of the community (N-g. coral. sp.=non-geniculate coralline species).

Variable	SS	df	MS	F	t-value	p-value
<i>C. officinalis</i>	0.591	1	0.591	45.844	6.770	<0.001
Barnacles	0.335	1	0.335	25.994	5.098	<0.001
<i>A. maoriana</i>	0.200	1	0.200	15.543	3.942	<0.001
<i>Buccinum</i> sp.	0.066	1	0.066	5.127	2.264	0.024
<i>C. ornata</i>	0.052	1	0.052	3.998	-1.999	0.046
<i>C. radians</i>	0.037	1	0.037	2.843	1.686	0.093
N-g. coral. sp.	0.026	1	0.026	2.020	1.421	0.156
Bare substrate	0.012	1	0.012	0.911	0.954	0.340
<i>C. denticulata</i>	0.010	1	0.010	0.772	-0.878	0.380
<i>C. retroflexa</i>	0.008	1	0.008	0.631	0.794	0.428
<i>L. scobina</i>	0.004	1	0.004	0.282	-0.530	0.596
<i>P. rudis</i>	0.004	1	0.004	0.281	-0.530	0.596

Variable	SS	df	MS	F	<i>t</i> -value	<i>p</i> -value
<i>P. canaliculus</i>	0.003	1	0.003	0.270	-0.519	0.604
<i>H. haustorium</i>	0.003	1	0.003	0.230	-0.479	0.632
<i>Porphyra</i> sp.	0.003	1	0.003	0.200	0.447	0.655
<i>U. lactuca</i>	0.000	1	0.000	0.002	0.041	0.967

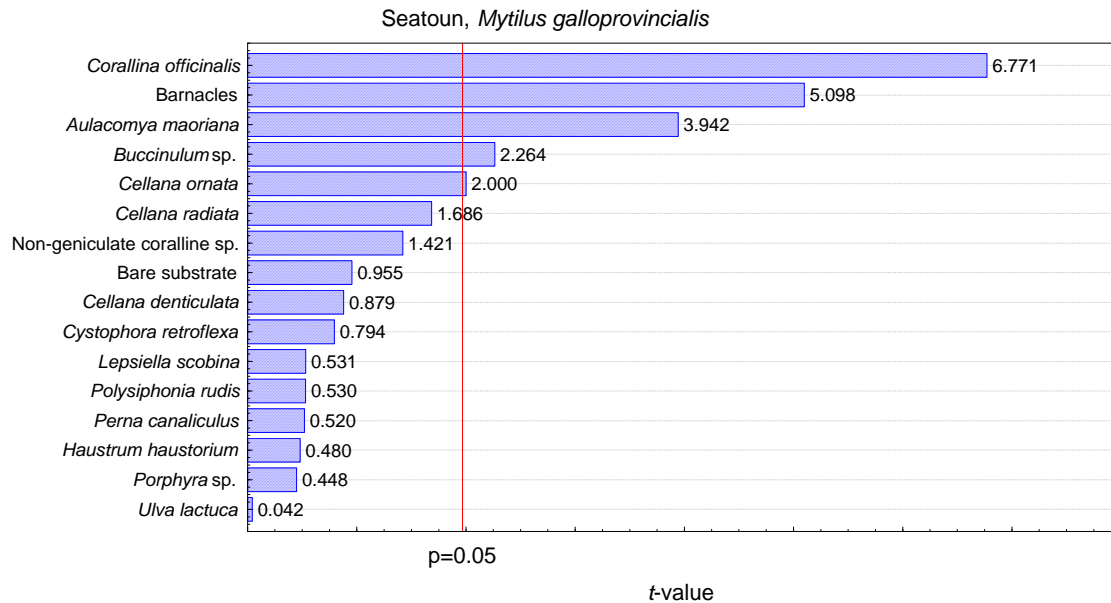


Figure 4.11. Pareto chart for *M. galloprovincialis* at Seatoun.

Perna canaliculus

Multiple Regression analysis revealed a statistically significant ($R^2=0.088$, $F=2.011$, $df=16$, $p=0.012$) interaction between the percent cover of the greenshell mussel and the percent cover of the alga *Cystophora retroflexa* (Table 4.13). The Pareto chart in Fig. 4.12 presents the absolute *t*-value and the significance of this species in relation to *P. canaliculus*.

Table 4.13. *Perna canaliculus*, Seatoun: Results of the Multiple Regression between the greenshell mussel and other members of the community (N-g. coral. sp.=non-geniculate coralline species).

Variable	SS	df	MS	F	<i>t</i> -value	<i>p</i> -value
<i>C. retroflexa</i>	0.002	1	0.002	20.911	4.573	<0.001
<i>Porphyra</i> sp.	0.000	1	0.000	2.051	1.432	0.153
<i>Buccinulum</i> sp.	0.000	1	0.000	1.998	-1.414	0.158
N-g. coral. sp.	0.000	1	0.000	1.894	1.376	0.170

Variable	SS	df	MS	F	<i>t</i> -value	<i>p</i> -value
<i>P. rudis</i>	0.000	1	0.000	0.794	-0.891	0.373
<i>A. maoriana</i>	0.000	1	0.000	0.324	0.569	0.570
<i>C. officinalis</i>	0.000	1	0.000	0.303	0.550	0.583
<i>C. ornata</i>	0.000	1	0.000	0.291	0.539	0.590
<i>M. galloprov.</i>	0.000	1	0.000	0.270	-0.520	0.604
<i>C. denticulata</i>	0.000	1	0.000	0.204	-0.452	0.651
Bare substrate	0.000	1	0.000	0.049	0.220	0.826
<i>L. scobina</i>	0.000	1	0.000	0.042	-0.205	0.838
<i>H. haustorium</i>	0.000	1	0.000	0.026	-0.161	0.872
<i>C. radiata</i>	0.000	1	0.000	0.017	-0.128	0.898
<i>U. lactuca</i>	0.000	1	0.000	0.001	0.031	0.975
Barnacles	0.000	1	0.000	0.000	0.013	0.990

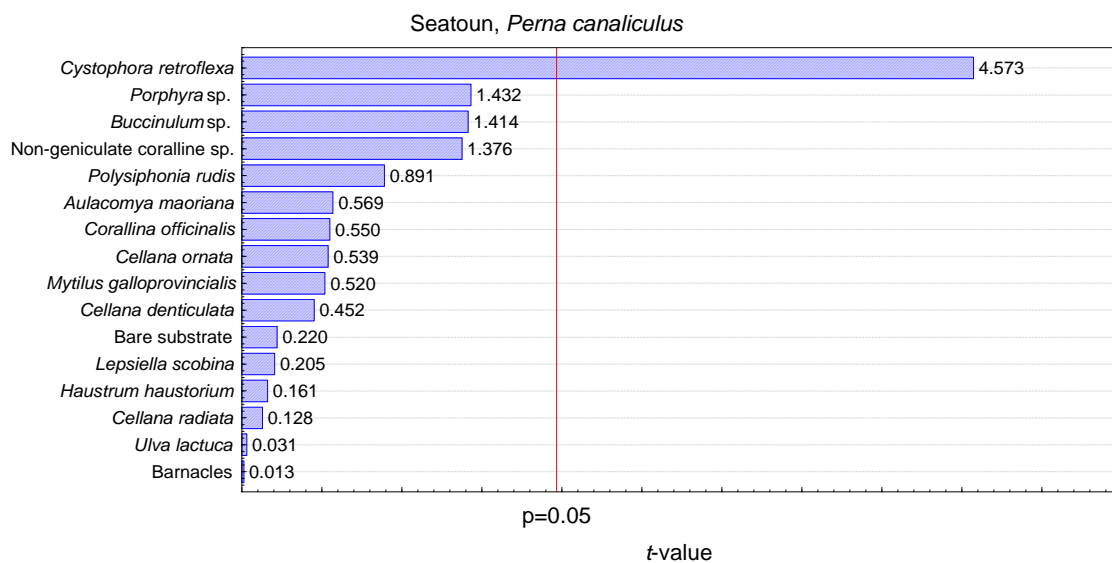


Figure 4.12. Pareto chart for *P. canaliculus* at Seatoun.

Kau Point: Relationship among species of colonizers and bare substrate

A MANOVA was performed on arcsine square root-transformed data to test for differences in percent cover of functional algal and invertebrate groups, including bare substrate. The analysis revealed statistically significant differences in percent cover among months and treatments (Table 4.14). The two-way interaction was also significant, indicating that percent cover of each group under each treatment was a function of time ($p=0.005$).

Table 4.14. Kau Point: Results of MANOVA for differences in percent cover of bare substrate and functional groups of algae and invertebrates among treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Month	0.097	126	1509.499	5.945	<0.01
Treatment	0.288	18	733.048	22.501	<0.01
Month x Treatment	0.211	378	1557.173	1.226	0.005

The overall model for each group of organisms was accepted (Table 4.15)

Table 4.15. Kau Point: Overall model fit of MANOVA for groups of algae, invertebrates and bare substrate.

Group	R	R ²	SS model	df model	F	p-value
Mussels	0.860	0.739	7.205	87	8.606	<0.001
Bare substrate	0.771	0.595	19.452	87	4.458	<0.001
Barnacles	0.742	0.550	0.808	87	3.706	<0.001
Limpets	0.641	0.411	0.402	87	2.113	<0.001
Whelks	0.618	0.382	0.073	87	1.873	<0.001
Algae	0.558	0.312	4.083	87	1.375	0.029

The analysis was subsequently repeated to test for differences in percent cover of bare substrate, as well as individual algal, barnacle, mussel, whelk and limpet species (Table 4.16). The analysis revealed statistically significant differences in percent cover of individual species among months and treatments. The two-way interaction was also significant, indicating that percent cover of each group under each treatment was a function of time ($p < 0.001$).

Table 4.16. Kau Point: Results of MANOVA for differences in percent cover of bare substrate, algal and invertebrate species among treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Month	0.047	357	3342.616	2.437	<0.001
Treatment	0.107	51	739.142	16.248	<0.001
Month x Treatment	0.010	1071	4170.565	1.249	<0.001

The overall model was not accepted for the non-geniculate coralline species, three algal species: *Ulva lactuca*, *Porphyra* sp. and *Polysiphonia rudis*, the greenshell mussel *Perna canaliculus*, the whelk species *Haustrum haustorium*, and the limpet species *Cellana denticulata* (Table 4.17).

Table 4.17. Kau Point: overall model fit of MANOVA for individual species of algae, barnacles, mussels, whelks, limpets and bare substrate (n-g = non-geniculate coralline species).

Species	R	R ²	SS model	df model	F	p-value
<i>M. galloprovincialis</i>	0.784	0.615	5.744	87	4.843	<0.001
Bare substrate	0.782	0.611	23.405	87	4.776	<0.001
Barnacles	0.733	0.537	0.820	87	3.515	<0.001
<i>Enteromorpha</i> sp.	0.721	0.520	0.874	87	3.288	<0.001
<i>L. scobina</i>	0.655	0.430	0.067	87	2.286	<0.001
<i>A. maoriana</i>	0.644	0.414	0.465	87	2.145	<0.001
<i>C. radians</i>	0.624	0.390	0.111	87	1.937	<0.001
<i>Buccinum</i> sp.	0.566	0.320	0.047	87	1.427	0.017
<i>C. ornata</i>	0.555	0.308	0.266	87	1.349	0.038
N-g coralline sp.	0.538	0.290	3.510	87	1.238	0.102
<i>C. denticulata</i>	0.497	0.247	0.052	87	0.997	0.496
<i>H. haustorium</i>	0.494	0.244	0.018	87	0.980	0.534
<i>U. lactuca</i>	0.471	0.222	0.772	87	0.866	0.782
<i>P. canaliculus</i>	0.464	0.215	0.070	87	0.831	0.844
<i>Porphyra</i> sp.	0.458	0.210	0.203	87	0.806	0.881
<i>P. rudis</i>	0.439	0.193	0.675	87	0.725	0.960

Kau Point: Effects of caging treatments

Kau Point: Control plots

After an increase to 18.31% in December 2001, algal percent cover stabilized at around 20% until April 2002 (Fig. 4.13) and subsequently declined. Algal cover was at its lowest in August 2002 (3.64%) but after that it increased and peaked at 22.94% in October 2003. Barnacle cover remained very low throughout the entire experiment (<5%), peaking at 4.33% in August 2003. Mussel cover was also low (<5%), and peaked in June 2003 at 3.94%. Bare substrate cover declined to 77.55% in January 2002 but recovered to 94.41% in August 2002. Subsequently, bare substrate cover systematically declined to the minimum observed value of 68.35% in October 2003.

Kau Point: “No roof” treatment

Algal cover increased and peaked at 10.98% in September 2002 (Fig. 4.14). Subsequently it declined to 2.47% in May 2003 and then rose again until October 2003, when it reached 10.96%. Barnacle cover was low for the entire study, peaking at 2.26% in September 2003. Mussel cover increased for the entire experiment, peaking at 23.68% in September 2003. The steady increase of mussel cover and initial increase of algal cover was reflected in a steady decline of bare substrate cover. Bare substrate cover was reduced to 82.15% in October 2002 and, after stabilizing at about 80-90% between October 2002 and June 2003, it declined further to 64.06% in October 2003.

Kau Point: Open cage treatment

For the first year of the experiment algal cover fluctuated over short periods of time (Fig. 4.15), peaking in December 2001 at 11.94%, May 2002 at 12.16% and in November 2002 at 10.11%. Subsequently, algal cover declined to less than 2% by December 2002 and it remained at this level until the end of the experiment. Barnacle cover was low for the entire experiment, peaking at 1.01% in November 2002. Mussel cover increased steadily until November 2002, when it peaked at 11.95%. Subsequently, mussel cover declined to less than 5%, reaching a second peak value of 3.26% in September 2003. Bare substrate cover declined until November 2002 to its minimum value of 69.60%. After a brief increase to 94.69% in January 2003 it stabilized at ~70% until the end of the experiment.

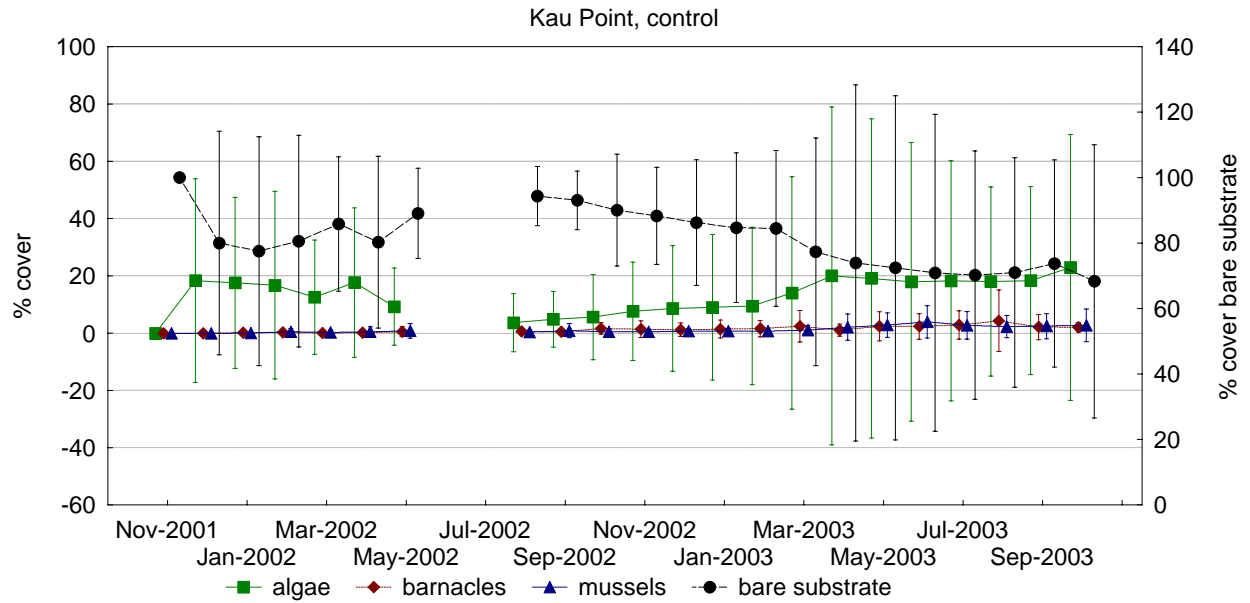


Figure 4. 13. Kau Point, control plots: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

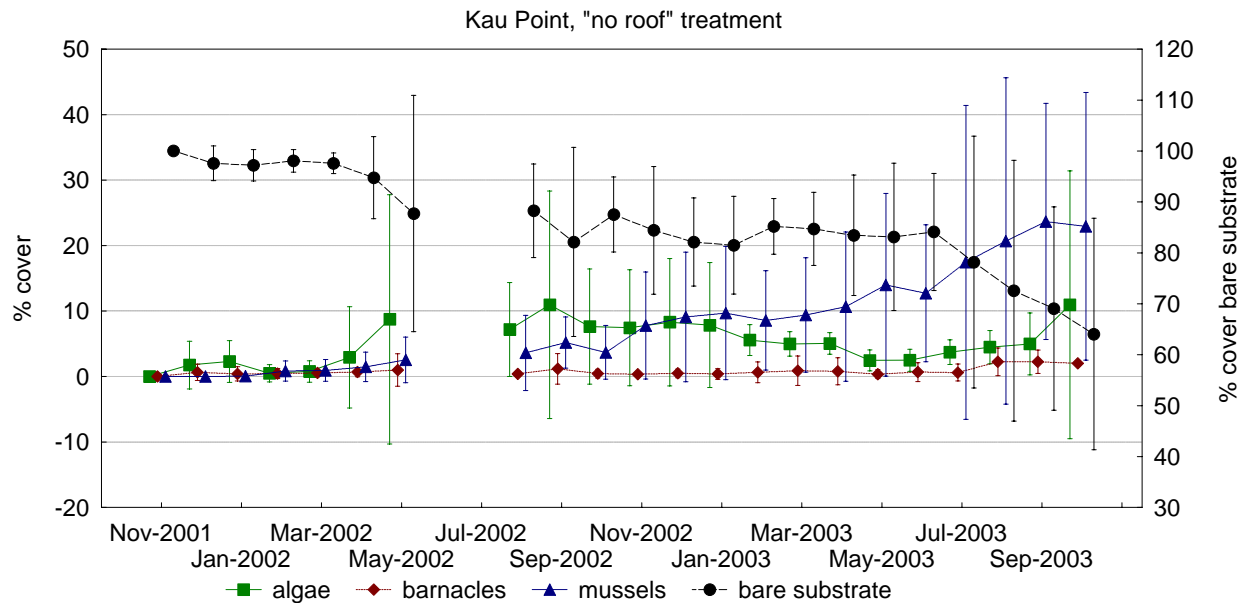


Figure 4. 14. Kau Point, "no roof" treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Kau Point: Full cage treatment

Under full cage treatment, algal cover increased steadily, reaching a maximum of 17.63% in July 2003, after which it declined to 13% for the rest of the experiment (Fig. 4.16). Barnacle cover remained low for the entire experiment and reached 2.62% in December 2002 and 2.36% in May 2003. Mussel cover increased steadily, reaching 15.56% in November 2002 and, after a brief decline to 11.73 in December 2002, it peaked at 19.34% in September 2003. Bare substrate cover gradually declined to 61.26% in October 2002. Subsequently, it increased to 79.79% in December 2002 and then declined to the minimum of 58.16% in July 2003. It remained at ~60% for the rest of the sampling period.

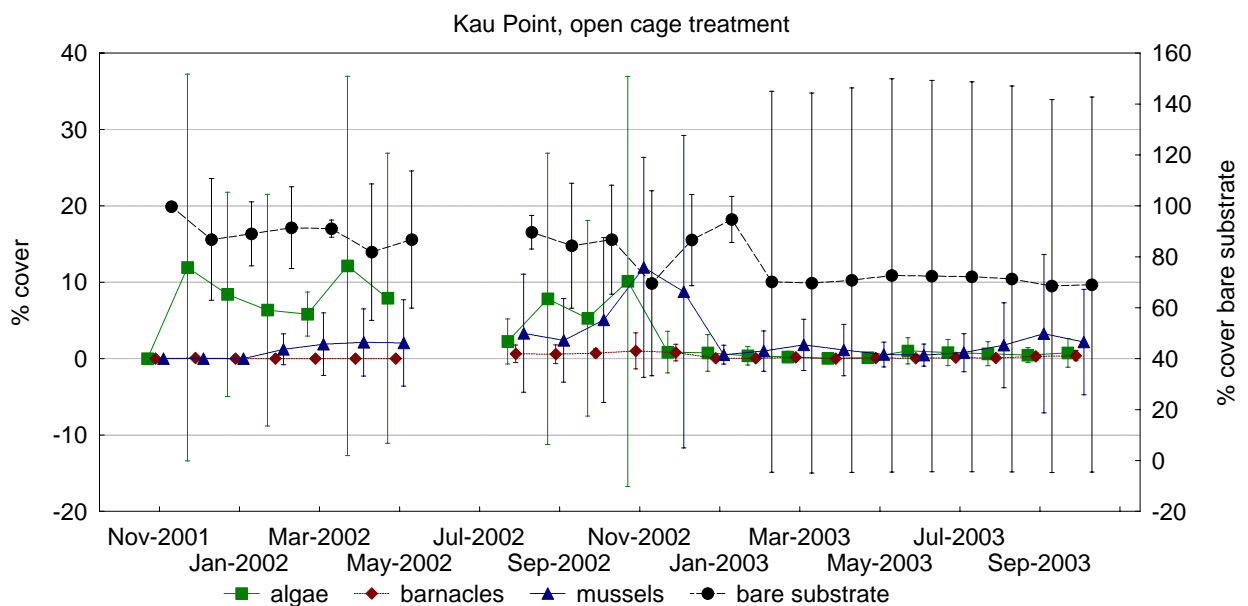


Figure 4. 15. Kau Point, open cage treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

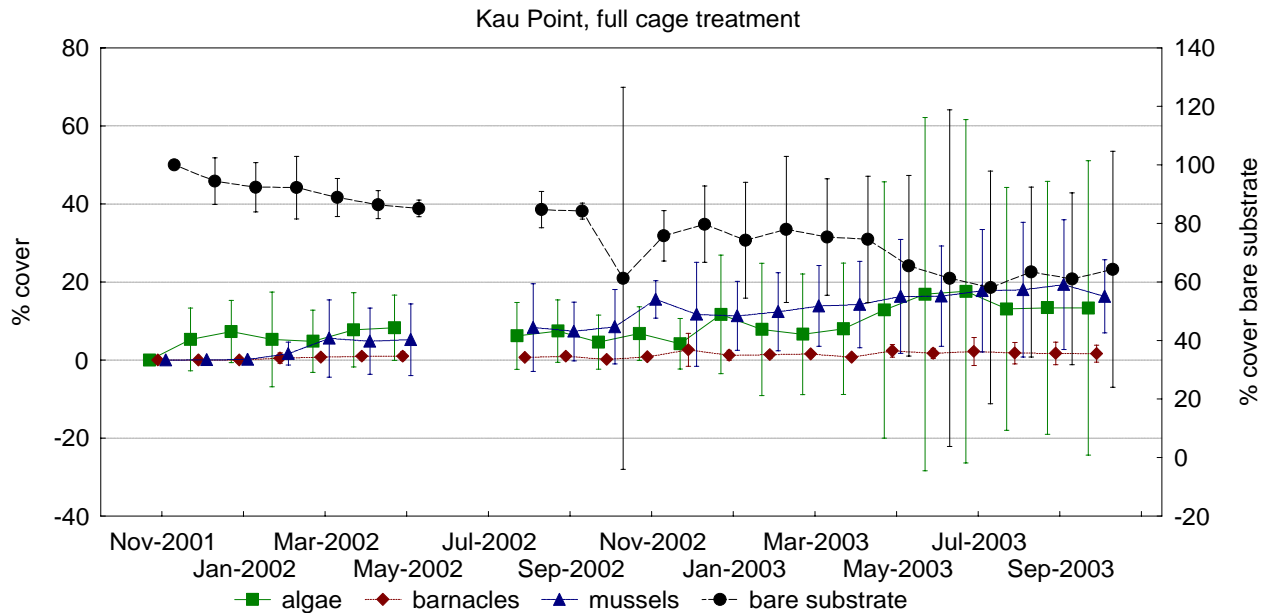


Figure 4. 16. Kau Point, full cage treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Kau point: Multiple Regression analysis

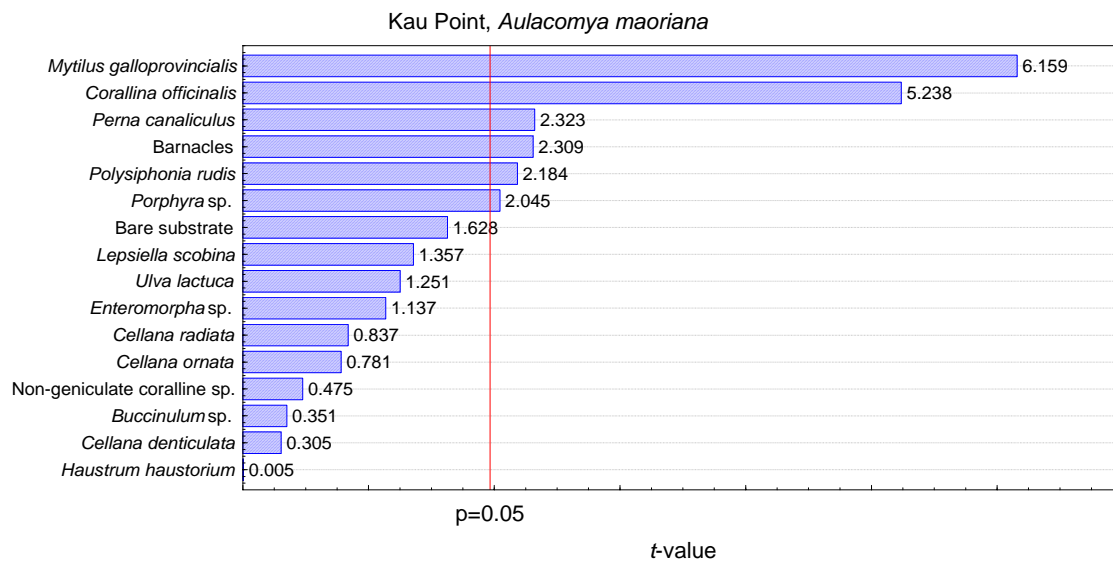
Aulacomya maoriana

Multiple Regression revealed a significant ($R^2=0.238$, $F=6.554$, $df=16$, $p<0.001$) correlation between the percent cover of the blue mussel and the percent cover of three algal species: *Porphyra* sp., *C. officinalis* and *P. rudis*; barnacles, and two mussel species: *M. galloprovincialis* and *P. canaliculus* (Table 4.18). The Pareto chart in Fig. 4.17 presents the absolute t -values and the significance of these independent variables in relation to *A. maoriana*.

Table 4.18. *Aulacomya maoriana*, Kau Point: Results of the Multiple Regression between the ribbed mussel and other members of the community (N-g. coral. sp.=non-geniculate coralline species).

Variable	SS	df	MS	F	t -value	p -value
<i>M. galloprovincialis</i>	0.097	1	0.097	37.927	6.159	<0.001
<i>C. officinalis</i>	0.070	1	0.070	27.437	5.238	<0.001
<i>P. canaliculus</i>	0.014	1	0.014	5.394	-2.323	0.021
Barnacles	0.014	1	0.014	5.331	-2.309	0.022

Variable	SS	df	MS	F	<i>t</i> -value	<i>p</i> -value
<i>P. rudis</i>	0.012	1	0.012	4.769	-2.184	0.030
<i>Porphyra</i> sp.	0.011	1	0.011	4.184	-2.045	0.042
Bare substrate	0.007	1	0.007	2.650	1.628	0.104
<i>L. scobina</i>	0.005	1	0.005	1.842	1.357	0.176
<i>U. lactuca</i>	0.004	1	0.004	1.565	-1.251	0.212
<i>Enteromorpha</i> sp.	0.003	1	0.003	1.292	1.137	0.256
<i>C. denticulata</i>	0.002	1	0.002	0.701	-0.837	0.403
<i>C. ornata</i>	0.002	1	0.002	0.609	0.781	0.436
N-g. coral. sp.	0.001	1	0.001	0.226	-0.475	0.635
<i>Buccinulum</i> sp.	0.000	1	0.000	0.123	-0.351	0.726
<i>C. radiata</i>	0.000	1	0.000	0.093	0.305	0.761
<i>H. haustorium</i>	0.000	1	0.000	0.000	-0.005	1.000

Figure 4. 17. Pareto chart for *A. maoriana* at Kau Point.*Mytilus galloprovincialis*

Multiple regression analysis revealed significant ($R^2=0.411$, $F=14.624$, $df=16$, $p<0.001$) correlation between the percent cover of the blue mussel and the percent cover of barnacles, the non-geniculate coralline species, a mussel *Aulacomya maoriana*, a whelk *Lepsiella scobina* and a limpet *Cellana ornata* (Table 4.19). The Pareto chart in Fig. 4.18 presents the absolute *t*-values and the significance of these independent variables in relation to *M. galloprovincialis*.

Table 4.19. *Mytilus galloprovincialis*, Kau Point: Results of the Multiple Regression between the blue mussel and other members of the community (N-g. coral. sp.=non-geniculate coralline species).

Variable	SS	df	MS	F	t-value	p-value
Barnacles	1.650	1	1.650	100.514	10.026	<0.001
<i>A. maoriana</i>	0.623	1	0.623	37.927	6.159	<0.001
<i>C. ornata</i>	0.570	1	0.570	34.690	-5.890	<0.001
N-g coral. sp.	0.274	1	0.274	16.708	4.088	<0.001
<i>L. scobina</i>	0.089	1	0.089	5.406	-2.325	0.021
<i>Porphyra</i> sp.	0.052	1	0.052	3.180	1.783	0.075
<i>C. officinalis</i>	0.046	1	0.046	2.811	1.677	0.095
<i>C. denticulata</i>	0.045	1	0.045	2.769	-1.664	0.097
<i>C. radiata</i>	0.045	1	0.045	2.736	-1.654	0.099
<i>P. canaliculus</i>	0.015	1	0.015	0.912	-0.955	0.340
Bare substrate	0.010	1	0.010	0.638	-0.799	0.425
<i>P. rudis</i>	0.007	1	0.007	0.443	-0.666	0.506
<i>Buccinum</i> sp.	0.004	1	0.004	0.224	-0.474	0.636
<i>U. lactuca</i>	0.003	1	0.003	0.159	0.399	0.690
<i>H. haustorium</i>	0.002	1	0.002	0.144	-0.380	0.704
<i>Enteromorpha</i> sp.	0.000	1	0.000	0.000	-0.009	0.993

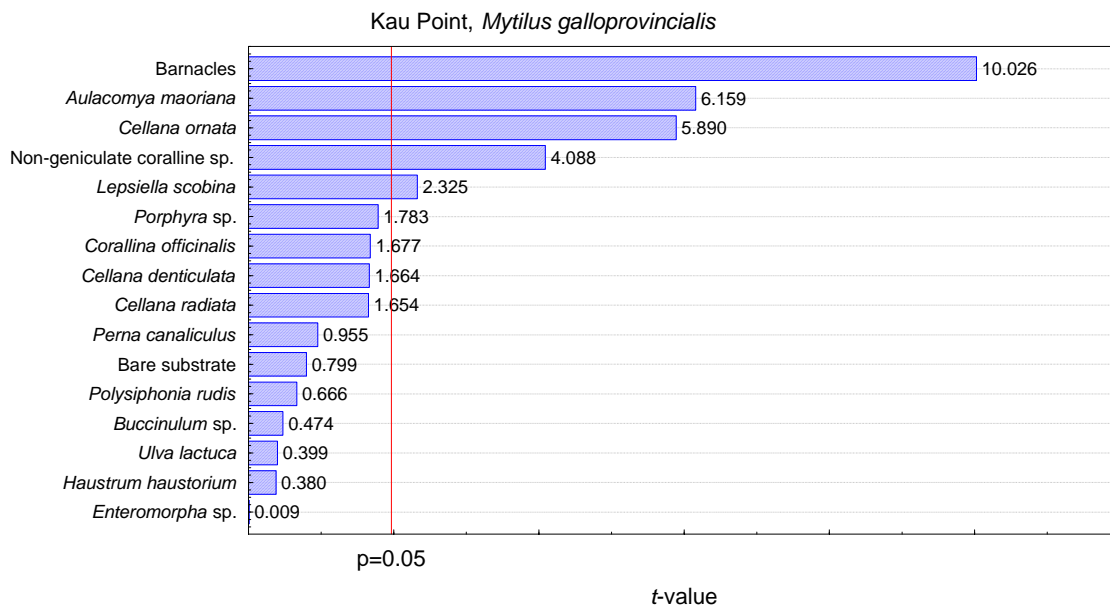


Figure 4. 18. Pareto chart for *M. galloprovincialis* at Kau Point.

Perna canaliculus

Despite a significant relationship between the percent cover of the greenshell mussel and the percent cover of the ribbed mussel *A. maoriana* and an alga *C. officinalis* (Table 4.20), the Multiple Regression analysis model was not statistically significant ($R^2=0.072$, $F=1.634$, $df=16$, $p=0.059$). The Pareto chart in Fig. 4.19 presents the absolute t -values and the significance of these two independent variables in relation to *P. canaliculus*.

Table 4.20. *Perna canaliculus*, Kau Point: Results of the Multiple Regression between the greenshell mussel and other members of the community (N-g. coral. sp.=non-geniculate coralline species).

Variable	SS	df	MS	F	t -value	p -value
<i>C. officinalis</i>	0.006	1	0.006	6.612	2.571	0.011
<i>A. maoriana</i>	0.005	1	0.005	5.394	-2.323	0.021
<i>Porphyra</i> sp.	0.002	1	0.002	2.684	-1.638	0.102
N-g. coral. sp.	0.002	1	0.002	1.868	1.367	0.173
<i>C. denticulata</i>	0.002	1	0.002	1.717	-1.310	0.191
<i>C. ornata</i>	0.001	1	0.001	1.167	-1.080	0.281
<i>Buccinulum</i> sp.	0.001	1	0.001	1.028	-1.014	0.311
<i>M. galloprovincialis</i>	0.001	1	0.001	0.912	-0.955	0.340
<i>U. lactuca</i>	0.001	1	0.001	0.789	-0.888	0.375
Bare substrate	0.001	1	0.001	0.716	0.846	0.398
<i>C. radiata</i>	0.001	1	0.001	0.670	-0.819	0.414
Barnacles	0.000	1	0.000	0.305	0.552	0.581
<i>Enteromorpha</i> sp.	0.000	1	0.000	0.096	-0.311	0.756
<i>H. haustorium</i>	0.000	1	0.000	0.170	-0.412	0.681
<i>P. rudis</i>	0.000	1	0.000	0.149	0.386	0.700
<i>L. scobina</i>	0.000	1	0.000	0.111	-0.334	0.739

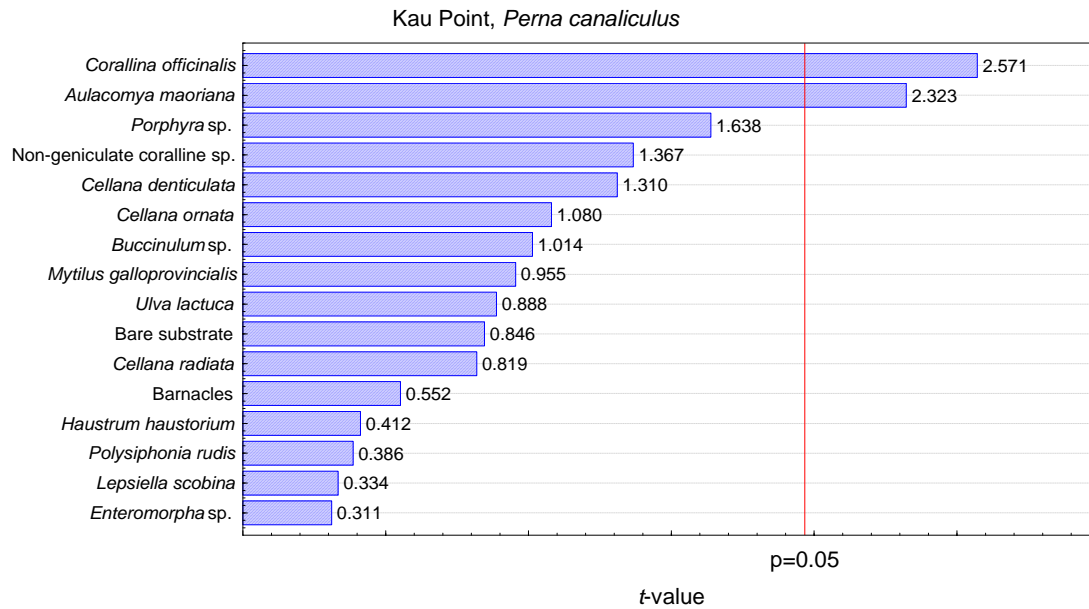


Figure 4. 19. Pareto chart for *P. canaliculus* at Kau Point.

Evans Bay: Relationship among species of colonizers and bare substrate

A MANOVA was performed on arcsine square root-transformed data to test for differences in percent cover of functional algal and invertebrate groups, including bare substrate. The analysis revealed statistically significant differences in percent cover among months and treatments (Table 4.21). The two-way interaction was not significant, indicating that percent cover of each group under each treatment was not a function of time ($p=0.213$).

Table 4.21. Evans Bay: Results of MANOVA for differences in percent cover of bare substrate and functional groups of algae and invertebrates among treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Month	0.142	84	1033.375	7.870	<0.001
Treatment	0.670	12	690.833	9.405	<0.001
Month x Treatment	0.397	252	1045.342	1.079	0.213

The overall model for each group of organisms was accepted (Table 4.22).

Table 4.22. Evans Bay: Overall model fit of MANOVA for groups of algae, invertebrates and bare substrate.

Group	R	R ²	SS model	df model	F	p-value
Bare substrate	0.774	0.599	35.737	87	4.538	<0.001
Barnacles	0.770	0.592	29.005	87	4.407	<0.001
Algae	0.661	0.437	17.642	87	2.354	<0.001
Mussels	0.601	0.362	11.580	87	1.719	0.001

The analysis was subsequently repeated to test for differences in percent cover of bare substrate, barnacles, as well as individual algal and mussel species (Table 4.23). The analysis revealed statistically significant differences in percent cover of individual species among months and treatments. The two-way interaction was also significant, indicating that percent cover of each group under each treatment was a function of time ($p < 0.001$).

Table 4.23. Evans Bay: Results of MANOVA for differences in percent cover of bare substrate, algal and invertebrate species among treatments and months.

Effect	λ -value	Effect df	Error df	F	p-value
Month	0.092	189	2146.515	3.776	<0.001
Treatment	0.426	27	748.294	9.402	<0.001
Month x Treatment	0.088	567	2307.306	1.274	<0.001

The overall model was not accepted for two algal species: *Porphyra* sp. and *Corallina officinalis*, and two mussel species: The greenshell mussel *Perna canaliculus* and the ribbed mussel *Aulacomya maoriana* (Table 4.24).

Table 4.24. Evans Bay: overall model fit of MANOVA for individual species of algae, barnacles, mussels, whelks, limpets and bare substrate (n-g = non-geniculate coralline species).

Species	R	R ²	SS model	df model	F	p-value
Bare substrate	0.774	0.599	37.788	87	4.528	<0.001
Barnacles	0.771	0.594	27.875	87	4.434	<0.001
<i>U. lactuca</i>	0.685	0.469	5.759	87	2.675	<0.001
<i>Enteromorpha</i> sp.	0.655	0.428	13.816	87	2.274	<0.001
<i>M. galloprovincialis</i>	0.621	0.385	11.390	87	1.902	<0.001
<i>C. officinalis</i>	0.498	0.248	0.004	87	1.000	0.488
<i>Porphyra</i> sp.	0.492	0.242	0.056	87	0.969	0.559
<i>P. canaliculus</i>	0.458	0.210	0.116	87	0.804	0.883
<i>A. maoriana</i>	0.433	0.187	0.154	87	0.699	0.975

Evans Bay: Effects of caging treatments

Evans Bay: Control plots

Algae quickly colonised the experimental plots and dominated the substrate until May 2002, when they were outcompeted by barnacles (Fig. 4.20). Algal cover peaked at 33.95% in September 2002 and remained at a similar level until January 2003. Subsequently, algal cover gradually declined to 7.97% in October 2003. Barnacle cover increased and peaked twice, at 78.39% in November 2002 and at 76.27% in February 2003. Subsequently, barnacle cover declined to 46.04% in June 2003 and then increased again, until it reached 60.56% at the end of the experiment. Mussel cover increased for the entire experiment, and peaked at 39.50% in October 2003. Bare substrate cover declined rapidly to 46.55% in February 2002 and, after a brief increase to 69.70% in April 2002, it continued to decline to about 10-20% for the rest of the sampling period, reaching 9.92% in October 2003.

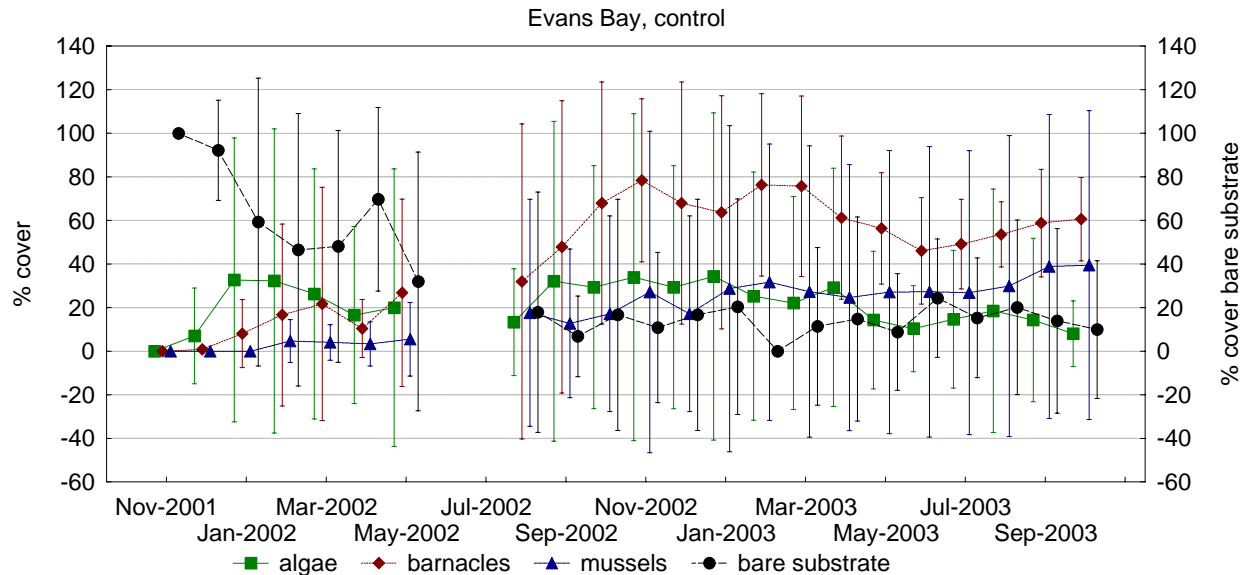


Figure 4. 20. Evans Bay, control plots: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Evans Bay: “No roof” treatment

Algal cover peaked at 63.93% in March 2002, after which it gradually declined to 1.57% in October 2003 (Fig. 4.21). On the other hand, barnacles were slow to recolonise the substrate, reaching their maximum cover of 52.36% in January 2003. Subsequently, barnacle cover declined and by the end of the experiment it was 27.96%. Mussel cover increased and reached the maximum value of 27.14% in October 2003. Bare substrate cover, after a rapid initial decline to 7.21% in May 2002, increased briefly to 48.73% in August 2002. Bare substrate cover declined again to 18.58% in January 2003 and subsequently increased to 42.92% in May 2003, before it reached 24.84% at the end of the experiment.

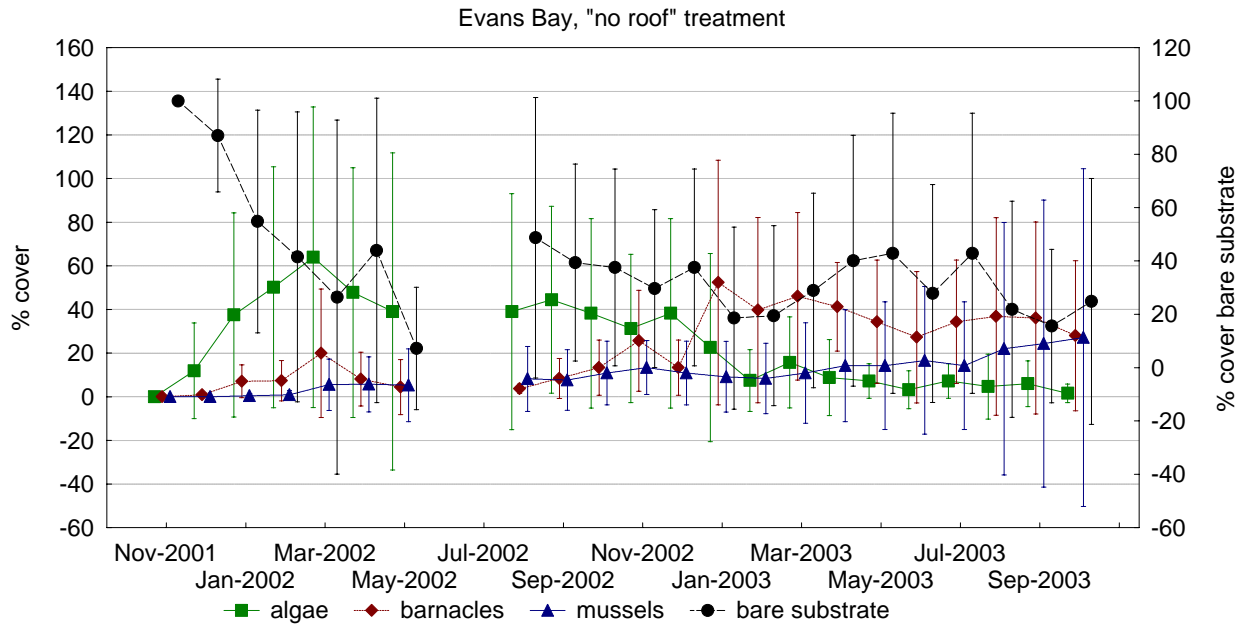


Figure 4. 21. Evans Bay, “no roof” treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Evans Bay: Open cage treatment

Algal cover generally exhibited an increasing trend, although it declined rapidly on a number of occasions (Fig. 4.22). Eventually, algal cover reached a maximum of 69.27% in August 2003. Barnacle cover fluctuated over short periods of time and it peaked twice: in November 2002 (48.13%) and February 2003 (52.91%) after which it declined to 26.90% in October 2003. Mussel cover remained low for the entire experiment, reaching 6.60% in November 2002 and a maximum of 7.09% in August 2003. Bare substrate cover displayed a general decline, with the minimum of 8.89% in March 2003, after which it recovered briefly to 59.48% in June 2003 and decreased again to 24.75% in October 2003.

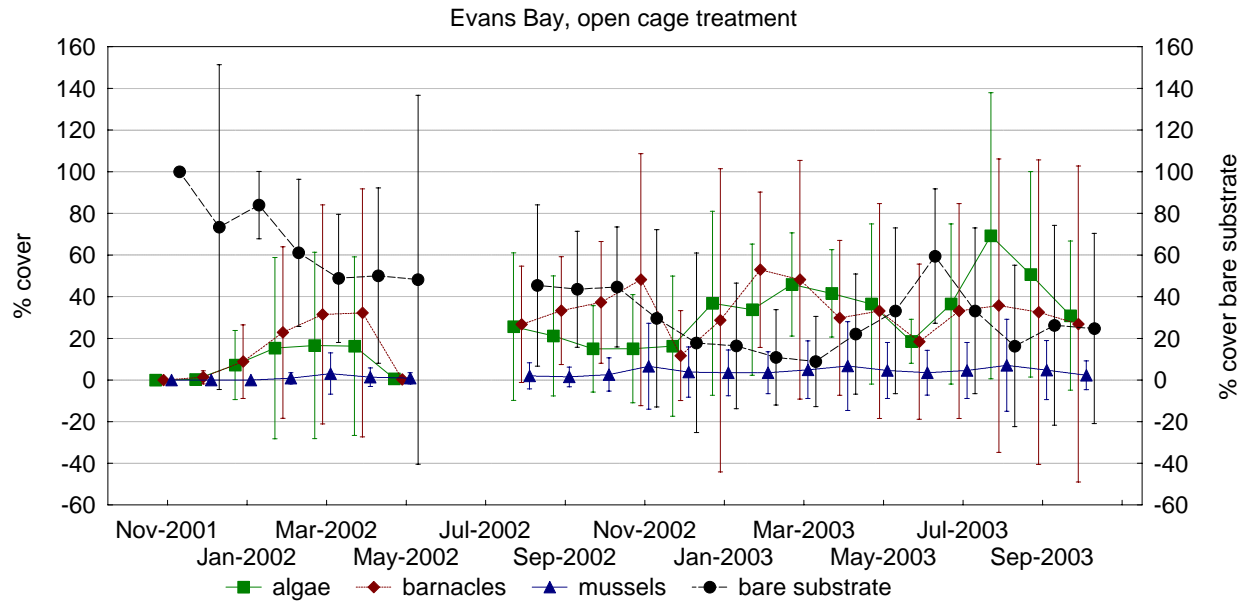


Figure 4. 22. Evans Bay, open cage treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Evans Bay: Full cage treatment

After an initial and rapid increase to 47.59% in January 2002, algal cover declined to less than 10% until a slight increase to 8.74% in May 2003 and 8.76% in July 2003 (Fig. 4.23). Algal cover declined further to 3.81% in October 2003. Barnacle cover exhibited significant variation over short periods of time. It increased to 57.03% in March 2002, peaking at 65.17% in January 2003, before declining to 20.24% in April 2003. It then increased again to 57.56% in August 2003, before it declined again to 36.96% in October 2003. Mussel cover exhibited a slow and steady increase, peaking at 60.17% in October 2003. Bare substrate cover decreased rapidly to 18.38% in May 2002, before it stabilized at about 20% until March 2003. Subsequently, it declined to 1.24% in April 2003 and, after achieving a value of 23.98% in June 2003, it eventually reached 6.77% in October 2003.

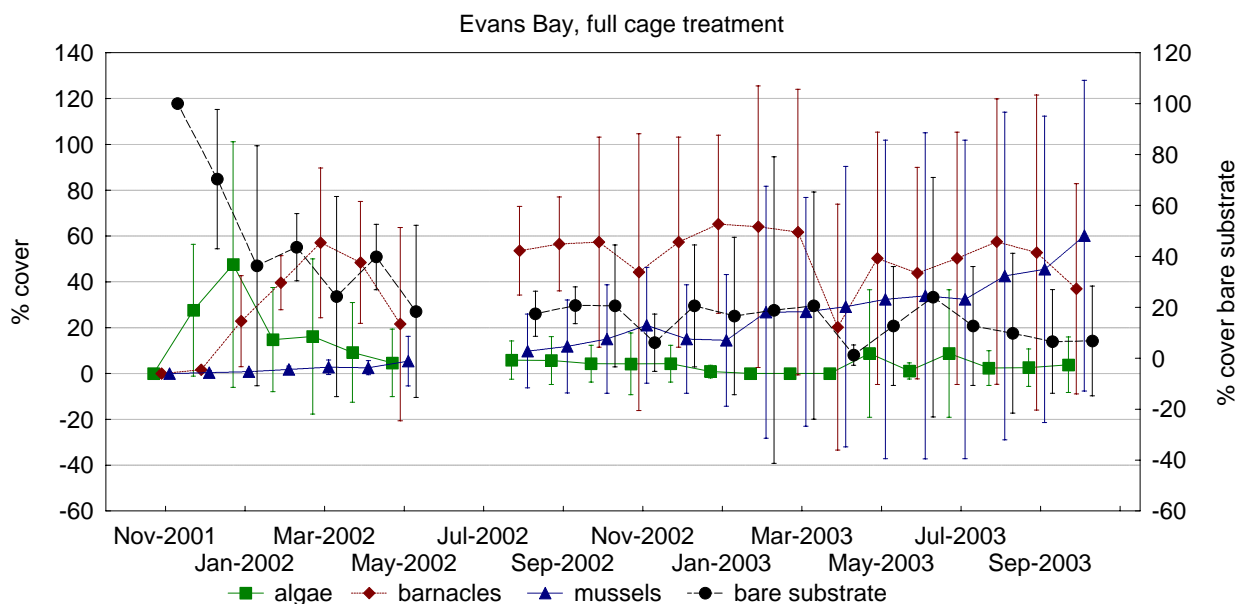


Figure 4. 23. Evans Bay, full cage treatment: Percent cover data for algae, barnacles, mussels and bare substrate. Points represent mean monthly values with 95% confidence interval error bars. Note different y-axis scales.

Evans Bay: CTD-Percent cover correlation

A Product-Moment correlation analysis performed for CTD data and percent cover data of the functional groups (i.e. bare substrate, algae, barnacles and mussels) revealed a significant correlation between temperature and the percent cover of algae, mussels and bare substrate, between turbidity and the percent cover of algae, as well as between the chlorophyll *a* and percent cover of algae (Table 4.25).

Table 4.25. Evans Bay: Product-Moment correlation analysis for CTD and functional groups percent cover data.

Variable	Algae	Barnacles	Mussels	Bare substrate
Temperature	$R=0.415$ $p<0.001^*$	$R=-0.159$ $p=0.054$	$R=-0.236$ $p=0.004^*$	$R=0.052$ $p<0.001^*$
Turbidity	$R=-0.259$ $p=0.002^*$	$R=-0.037$ $p=0.657$	$R=0.052$ $p=0.531$	$R=-0.101$ $p=0.223$
Chlorophyll <i>a</i>	$R=0.223$ $p=0.007^*$	$R=0.055$ $p=0.505$	$R=-0.073$ $p=0.379$	$R=0.125$ $p=0.131$
Salinity	$R=-0.055$ $p=0.508$	$R=0.098$ $p=0.235$	$R=-0.103$ $p=0.213$	$R=-0.141$ $p=0.087$

* Significant after Bonferroni correction for multiple testing.

Evans Bay: Multiple Regression analysis

Aulacomya maoriana

Multiple Regression analysis revealed a significant ($R^2=0.623$, $F=81.316$, $df=7$, $p<0.001$) relationship between the greenshell mussel and the alga *Enteromorpha* sp. and two mussel species: *A. maoriana* and *P. canaliculus* (Table. 4.26). The Pareto chart in Fig. 4.24 presents the absolute t -values and the significance of these independent variables in relation to *A. maoriana*.

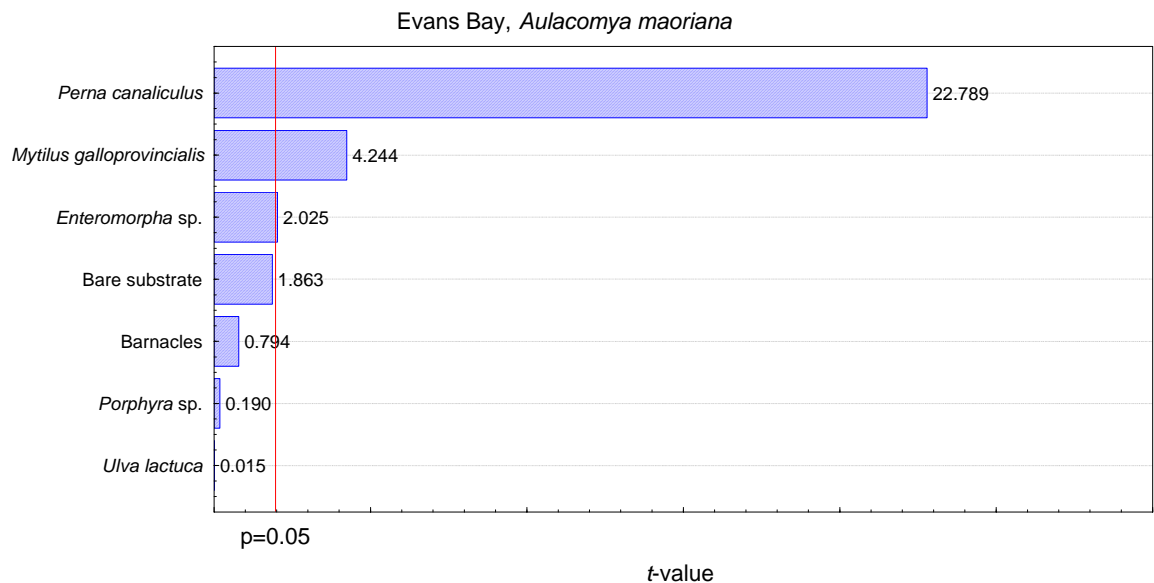


Figure 4. 24. Pareto chart for *A. maoriana* at Evans Bay.

Table 4.26. *Aulacomya maoriana*, Evans Bay: Results of the Multiple Regression between the ribbed mussel and other members of the community.

Variable	SS	df	MS	F	<i>t</i> -value	<i>p</i> -value
<i>P. canaliculus</i>	0.467	1	0.467	519.336	22.789	<0.001
<i>M. galloprovincialis</i>	0.016	1	0.016	18.013	4.244	<0.001
<i>Enteromorpha</i> sp.	0.004	1	0.004	4.102	2.025	0.044
Bare substrate	0.003	1	0.003	3.470	1.863	0.063
Barnacles	0.001	1	0.001	0.631	-0.794	0.428
<i>Porphyra</i> sp.	0.000	1	0.000	0.036	-0.190	0.849
<i>U. lactuca</i>	0.000	1	0.000	0.000	-0.015	0.988

Mytilus galloprovincialis

Multiple Regression revealed a significant ($R^2=0.299$, $F=20.929$, $df=7$, $p<0.001$) interaction between the percent cover of the blue mussel and the percent cover of the alga *Enteromorpha* sp.; two mussel species: *A. maoriana* and *P. canaliculus*; barnacles and bare substrate (Table 4.27). The Pareto chart in Fig. 4.25 presents the absolute t -values and the significance of these independent variables in relation to *M. galloprovincialis*.

Table 4.27. *Mytilus galloprovincialis*, Evans Bay: Results of the Multiple Regression between the blue mussel and other members of the community.

Variable	SS	df	MS	F	t -value	p -value
Bare substrate	3.659	1	3.659	60.716	-7.792	<0.001
<i>Enteromorpha</i> sp.	1.731	1	1.731	28.725	-5.360	<0.001
<i>A. maoriana</i>	1.086	1	1.086	18.013	4.244	<0.001
Barnacles	0.942	1	0.942	15.634	3.954	<0.001
<i>P. canaliculus</i>	0.250	1	0.250	4.141	-2.035	0.043
<i>Porphyra</i> sp.	0.113	1	0.113	1.870	-1.367	0.172
<i>U. lactuca</i>	0.020	1	0.020	0.330	-0.574	0.566

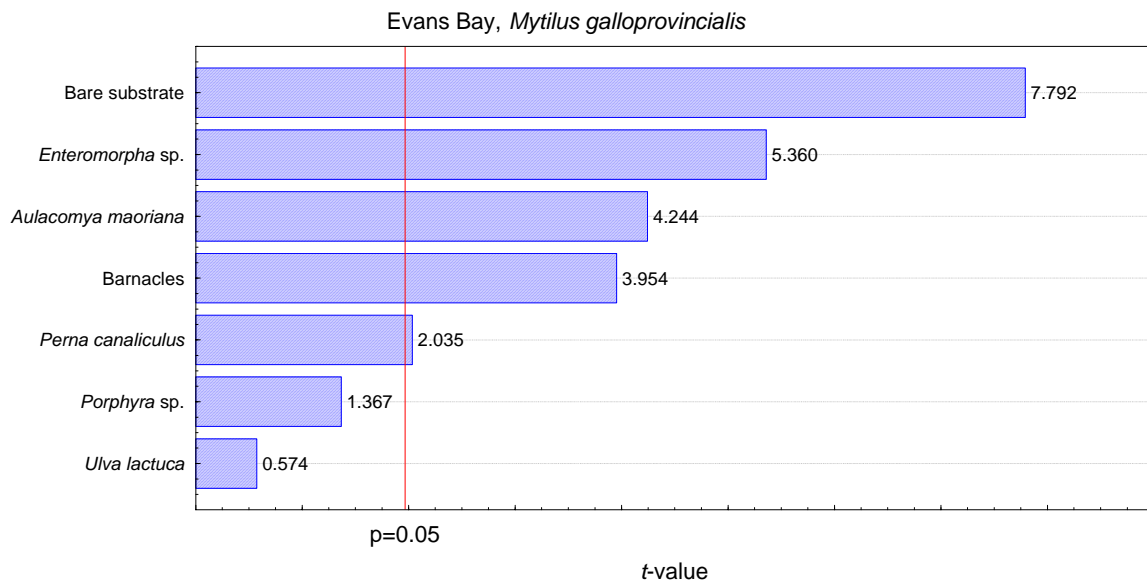


Figure 4. 25. Pareto chart for *M. galloprovincialis* at Evans Bay.

Perna canaliculus

Multiple Regression analysis revealed a significant ($R^2=0.607$, $F=76.079$, $df=7$, $p<0.001$) correlation between the greenshell mussel and two other mussel species, *A. maoriana* and *M. galloprovincialis* (Table 4.28). The Pareto chart in Fig. 4.26 presents the absolute t -values of these independent variables in relation to *P. canaliculus*.

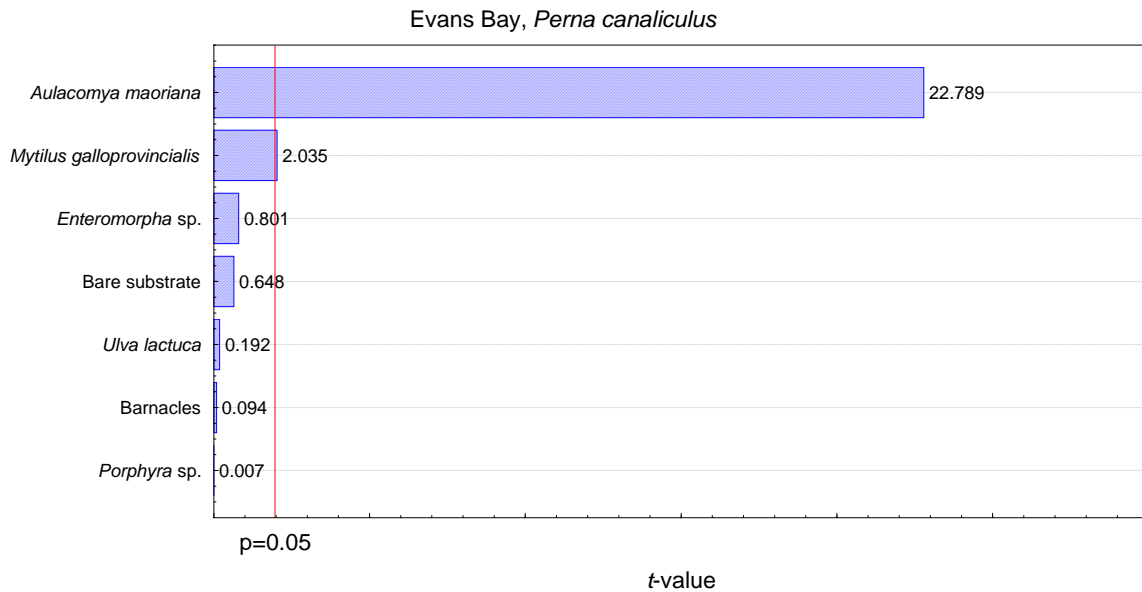


Figure 4. 26. Pareto chart for *P. canaliculus* at Evans Bay.

Table 4.28. *Perna canaliculus*, Evans Bay: Results of the Multiple Regression between the ribbed mussel and other members of the community.

Variable	SS	df	MS	F	t-value	p-value
<i>A. maoriana</i>	0.329	1	0.329	519.336	22.789	<0.001
<i>M. galloprovincialis</i>	0.003	1	0.003	4.141	-2.035	0.043
<i>Enteromorpha</i> sp.	0.000	1	0.000	0.641	-0.801	0.424
Bare substrate	0.000	1	0.000	0.419	-0.648	0.518
<i>U. lactuca</i>	0.000	1	0.000	0.037	0.192	0.848
Barnacles	0.000	1	0.000	0.009	0.094	0.925
<i>Porphyra</i> sp.	0.000	1	0.000	0.000	0.007	1.000

4.4 Discussion

Bottom-up effects

Water column data obtained in this experiment show spatial and temporal variability of water parameters between Seatoun and Evans Bay in Wellington Harbour. Simultaneously, as indicated by Figs. 4.6, 4.13 and 4.20, the rate of the intertidal community recovery was most pronounced at Evans Bay, intermediate rate was observed at Kau Point, and the slowest rate at Seatoun. Although Evans Bay appeared as the area of Wellington Harbour with significantly more saline, chlorophyll-rich, turbid and warmer water (Figures 2.3-2.6 in chapter 2), these bottom-up factors were clearly linked to the community development at Seatoun (Table 4.10). Temperature was negatively correlated to all significant groups of colonizers, but turbidity was positively correlated to algal, barnacle and mussel abundance, as well as bare substrate cover. Chlorophyll *a* concentration was positively correlated to barnacle, limpet and bare substrate cover at that site. Similarly, salinity was positively correlated to algal, barnacle, mussel and bare substrate cover. At Evans Bay however, the bottom-up effects were most important for algae, as this group was significantly correlated with temperature and chlorophyll *a*, but negatively with turbidity (Table 4.25). Also, temperature at this site was negatively correlated with mussel cover and positively with bare substrate cover. These results establish a link between the development of intertidal communities and the water column parameters regulating the dynamics in such communities within Wellington Harbour. Greater inputs of organic particles at Seatoun, expressed jointly as turbidity and chlorophyll *a* levels, as well as increase in salinity, was clearly vital to greater algal, barnacle and mussel cover. This suggests that these bottom-up factors fuelled the community dynamics at Seatoun and the competition for space and exclusion taking place among these three invertebrate guilds. However, as shown by Figures 4.6-4.9, the amount of free space at the end of the experiment at Seatoun was still significant, and these results are somewhat at odds with the widely accepted theoretical assumption that competition occurs only when the resource (i.e. space) is in limited supply (Nybakken, 2001). While it is possible that such contradiction resulted from some experimental bias, such as a non-additive cage effect (e.g. Peterson & Black, 1994, Chapman, 2000), a role

of other, habitat-related factors cannot be ignored. This result possibly was a combination of community dynamics (including competition for space that occur at Seatoun), and adverse environmental conditions (i.e. physical disturbance). At Seatoun, the intertidal communities are constantly exposed to high-energy southerly swells moving large volumes of shingle and suspended sediments that subsequently scour the rocks (pers. obs.), thus presumably slowing down the competition and the overall succession rate in the local community. At Evans Bay, recruitment of algae and their subsequent substrate colonisation were clearly stimulated by temperature and chlorophyll, but negatively affected by turbidity (Table 4.25). This confirmed the results of the water column parameters analysis (see chapter 2), in which Evans Bay was marked as the warmest and most chlorophyll-rich site. While temperature stimulated the settlement and recruitment of algal propagules, the recolonisation of the substrate by algae was simultaneously inhibited by turbidity (i.e. water cloudiness), which means that the algal recruits were not receiving enough light necessary for the photosynthetic activity. However, the fact that other links between the water column parameters and percent cover of intertidal community members were not detected at Evans Bay makes the estimation of the bottom-up factors at this site difficult. Given the fact that the water circulation in the inner Harbour is much slower than in the outer Harbour (Heath, 1977), one can expect that organic particles present in Evans Bay might be retained there for longer periods of time. Also, without a major, natural freshwater outlet, seawater in Evans Bay can maintain its high salinity, whereas Seatoun can occasionally experience significant salinity dips. Further, local hydrology and the influence of the high turbidity, freshwater plume coming out of the Hutt River cannot be ignored. The plume enters Evans Bay very infrequently but often travels as far south as Seatoun, carrying high volumes of organic particles that can be potentially utilized by members of intertidal communities.

Results from the present study reflect the importance of coastal productivity, combined with bottom-up factors, such as salinity and temperature in regulation of invertebrate communities in the intertidal zone reported elsewhere. Sanford & Menge (2001) point at the importance of nearshore primary productivity and its influence on the dynamics of intertidal communities in Oregon, USA. The authors hypothesize that

bottom-up factors, including phytoplankton abundance, are important in the regulation of intertidal communities, in particular during the upwelling relaxation. In that study, barnacles (*Balanus glandula* and *Chthamalus dalii*) attained larger sizes at a site with consistently higher chlorophyll *a* concentration, but the authors noted that high growth rates continued even after chlorophyll concentration had decreased. Simultaneously, zooplankton concentration and water temperature were elevated, thus leading the authors to the conclusion that the increased barnacle growth might be related to combined effects of several additional bottom-up factors, such as zooplankton abundance and temperature. The mechanism behind the increased invertebrate growth following increase in temperature most likely results from the increase in filtering activity, food intake and subsequent assimilation (e.g. Sanford *et al.*, 1994). Further, inhabitants of rocky intertidal communities, such as barnacles (Young & Gotelli, 1988; Anderson, 1994) and mussels (Davenport *et al.*, 2000; Zeldis *et al.*, 2004) have been described as capable of capturing a variety of foods, including crustacean and bivalve larvae suspended in the water column.

As signaled before, local hydrology can be of a significant importance to the intertidal communities. High-turbidity, riverine plume originating from the Hutt River can potentially provide high concentrations of nutrients to such communities, thus stimulating their growth. Local hydrology and availability of nutrients were also described as crucial bottom-up factors in a study of invertebrate growth and substrate colonization performed by Menge *et al.* (2003). The authors used a comparative-experimental approach similar to the one employed in the present study, where local-scale experimentation was replicated at multiple sites spanning larger scale on the west and east coast of the South Island, New Zealand. Examination of the structure of intertidal communities suggested that particular hydrological conditions, such as upwelling, followed by intense water mixing that brought nutrients to the water surface, and subsequent elevated concentration of nutrients stimulated invertebrate growth. At sites with high nutrient subsidies mussel and barnacle abundance were greatest, following equally high recruitment.

Top-down effects

Bottom-up inputs are often strongly associated with top-down effects, thus rocky intertidal communities are effectively regulated by both factors. In the present study, the top-down effects were limited, and only manifested through the chlorophyll *a*-stimulated cover of barnacles and herbivores (i.e. limpets) at Seatoun (Table 4.10). Such relationship potentially resulted in competition for space between the two groups, as the cover of both barnacles and limpets was clearly increasing with chlorophyll levels. Similar top-down effects of herbivores on the intertidal community regulation were described in the South Island, New Zealand, by Menge *et al.* (1999). In that system, high nutrient levels on the west coast stimulated activity of grazers such as *C. radians* and *C. ornata*, which in turn had impact on algal cover. In the present study, whelks were commonly observed at Seatoun, although their percent cover was not significantly correlated to prey cover (Table 4.10). Another group of predators potentially foraging is crabs. Crabs have been reported as able to feed both in the intertidal and subtidal zone, by migrating from the subtidal into intertidal areas at high tide (Hunter & Naylor, 1993). Because crabs are mostly active in spring and summer (Aagaard *et al.*, 1995), and given the fact that the experiment was commenced in austral spring, it is possible that crabs had some effect on the invertebrate recruitment onto the experimental substrate in the present study. However, no evidence of crab predation on shells of recruiting mussels was seen (i.e. chipped shells). It is also possible that the size of the open cages would prevent crabs from accessing the prey. Sea stars are uncommon in the intertidal zone in Wellington Harbour, and have been reported as mainly limited to the subtidal zone (Beadman *et al.*, 2003; Menge *et al.*, 2003). During the entire experiment only one sea star *Stichaster australis* was seen at Seatoun. It is also possible that birds, such as sea gulls and oystercatchers common in Wellington area, preyed intertidally on invertebrates recruiting onto the experimental substrate (Seed, 1969), although the height of the open and “no roof” cages (90 mm) probably made the access to prey difficult, thus discouraging the avian predators.

Algae, barnacles and mussels: patterns of intertidal succession and competition

Availability of clear substrate often leads to colonization by opportunistic species (for example, filamentous green and red algae), characterized by short life span, short development to reach maturity, high death rates and the ability to reproduce more than once per year. Often, these species are soon replaced by other, more competitive, dominant and slower-growing species, such as mussels or algae, which eventually colonise the entire available space (Luckens, 1976). Timing of the space clearance following the disturbance is vital, because the first species that will colonise the available surface are the species whose propagules are ready to settle. The very concept of succession assumes that there is a quantitative difference between initial and climax stages of the community, where the changes in the number and kind of colonizing species are detectable (Poore, 1968).

In the present study, substrate was cleared in November (austral spring), giving way for recolonisation mostly to short-lived algae, such as *Enteromorpha* sp. or *Ulva* sp. The patterns of succession and the intertidal community recovery varied among sites and were fastest at Evans Bay, where first signs of recruitment of pioneering algae appeared as soon as three months after the substrate clearance. Unlike at Seatoun and Kau Point, the succession at Evans Bay visibly proceeded from algae, later outcompeted by barnacles that eventually were smothered by mussels that dominated the substrate. When excluded from the substrate by mussels, barnacles were gregariously settling on mussel shells instead. At Seatoun and Kau Point however, as pointed out before, the substrate recolonisation was much slower and most of the remaining substrate was still bare at the end of the experiment. While at Evans Bay some plots experienced 100% recovery to the pre-clearance levels with mussels totally occupying the substrate, none of the plots at Seatoun and Kau Point had such high recovery rate even after 24 months of the experiment. These results can be attributed to numerous factors, including localized hydrology (exposure to destructive, high-energy swells at Seatoun and Kau Point but not at Evans Bay; slower water exchange with the rest of the Harbour and longer water retention at Evans Bay) directly associated with bottom-up effects (i.e. local hydrology

conditions of Evans Bay resulting in higher temperature, salinity and chlorophyll levels), which in turn significantly affected community recovery and succession.

During this experiment, competition was observed at Evans Bay between the ephemeral algae, such as *Enteromorpha* sp. and *Ulva lactuca*, and later arriving barnacles, which subsequently outcompeted those algal species. Hawkins (1981) examined the relationship between barnacles and algae in the absence of grazers on intertidal shores in England and proposed a successional mechanism in which barnacle shells served as a refuge for diatoms and green alga *Ulothrix*, presence of which seemed to facilitate the establishment of later successional algae, such as *Fucus*. Foster *et al.* (2003) reported that ephemeral algae, such as *Enteromorpha* spp., *Ulva* spp., *Porphyra* spp. and *Urospora* spp. colonised the substrate and could grow rapidly. Subsequently, sessile consumers arrived, such as barnacle species *Balanus glandula* and *Chthamalus* spp., grazing gastropods *Littorina* sp. and limpets *Tegula funebris* (although they did not manage to outcompete the algal pioneers). At Evans Bay however, they did (and to a lesser extent at Seatoun and Kau Point), as the succession from algal stage, through barnacles to mussels was clearly noticeable at that site and it followed a pattern similar to the one reported by Menge (1976) and Lubchenco & Menge (1978). These authors concluded that the mussel *M. edulis* could overgrow several species of macroalgae and smother barnacles, eventually claiming the entire available space. A very similar successional mechanism has been revealed in Wellington Harbour, where algal species give way to barnacles, which are in turn outcompeted by mussels. Simultaneously, mussel shells are utilized by settling barnacles as the secondary substrate available for secondary barnacle settlement.

Barnacle walls, filamentous algae or already established mussel clumps have been described as mediators of mussel recruitment, without which mussel larvae seem to be unable to successfully recruit and colonise the cleared substrate in the intertidal zone (Navarrette & Castilla, 1990). In this process, mussel larvae depend on barnacles as facilitators, although, as signaled before, during the succession in the intertidal zone mussels are capable of taking over the entire free surface, excluding barnacles that they

had previously needed for successful recruitment. This phenomenon, known as the competitive exclusion principle, depends on the size and the number of clear substrate patches in the barnacle bed. More space for mussel recruitment will be available if barnacle beds are disrupted in several small patches, than if only few larger patches are present (Navarrette & Castilla, 1990; Lohse, 1993). Competitive exclusion was detected in the present study, in particular at Evans Bay, where barnacle cover was systematically diminishing due to severe competition for space from mussels. At some point, however, barnacle percent cover started to increase due to barnacles settling on mussel shells, using them as a secondary substrate. This process can serve as an example of the successive facilitation and exclusion theory (Buschbaum, 2001), simultaneously taking place in the rocky intertidal zone. During their secondary settlement, barnacles in Evans Bay preferred certain areas of mussel shells, such as siphonal apertures of living mussels, whereas fragments of shells or shells of dead mussels were avoided (Buschbaum, 2001). In such process, barnacle larvae exploit physical and chemical cues, such as surface contours, water currents carrying food near the siphonal apertures, or biofilms developing on the mussel shells (Crisp & Barnes, 1954; Crisp & Meadows, 1963). The transition from barnacles to mussels observed at Evans Bay could also depend on the presence of algal canopy, because algae can create conditions of increased moisture and shelter from the sun and, to an extent, from predatory whelks.

The effect of treatment on mussel cover

Caging experiments in which invertebrate communities are protected from predators demonstrate that predation has predictable, long-term consequences on developing mussel communities (Osman & Whitlatch, 2004). Freed from predation, such communities are no longer regulated in their species diversity and are soon dominated by the most competitive member. Mussels have been shown in this process as capable of excluding other species, such as algae and barnacles, from the primary space (e.g. Paine, 1966, 1974; Harger, 1972, Menge *et al.*, 1986) and simultaneously providing for those species secondary substratum on their shells (Paine, 1976; Menge *et al.*, 1986). In the present study, mussels were shown as able to increase their cover inside the experimental

plots when protected from their predators by the full cage treatment. This tendency to dominate available substrate and exclude other community members was particularly swift and pronounced at Evans Bay (Fig. 4.23), although percent cover at Seatoun and Kau Point also significantly increased under conditions of full protection from predators (Figs. 4.9 and 4.16, respectively). However, mussels exposed to (mainly invertebrate) predation under the open cage treatment did not manage to dominate the experimental plots and exclude other community members (see Figs. 4.8 for Seatoun, 4.15 for Kau Point and 4.22 for Evans Bay), which points at predation as a factor structuring species diversity in the intertidal communities. These results confirm outcomes reported by other researchers at other locations. In a similar experiment, Menge (1976) tested for competition between barnacles and mussels in New England. The author used full cage treatment to prevent a whelk *Thais lapillus* from accessing its prey *Semibalanus balanoides* and *Mytilus edulis*. Sideless cages (i.e. open cage treatment) were used to control for shading effects of cages and marked, undisturbed areas were used as controls. Menge reported a mechanism of competition very similar to the one found in the present study at Evans Bay, namely that the interspecific competition between barnacles and mussels was discernible only when both guilds were freed from predator pressure, under full cage treatment, and *M. edulis* would eventually outcompete *B. balanoides* for space. A facilitation-exclusion mechanism between barnacles and mussels was thus revealed, because in conditions when whelks were present, mussels were controlled and barnacles could persist, thus facilitating mussel recruitment into the community. The author concluded that predation is the dominant biological interaction that structures communities. Navarrete (1996) studied the impact of predation by whelks *Nucella canaliculata* and *Nucella emarginata* on a mid-intertidal successional mussel community in Oregon, USA. In that study, persistent exclusion of whelks using full cage treatment lead to changes in mussel abundance, community composition and species diversity. Further, a significant increase in the cover of mussels *Mytilus trossulus* was found, while *Mytilus californianus* experienced a slower and smaller increase in abundance. Results from the present study reflect this, as *Mytilus galloprovincialis* in Wellington Harbour can clearly outcompete other mid-intertidal community members, including the two sympatric mussel species *Aulacomya maoriana* and *Perna canaliculus*. Navarrete (1996)

evaluated artifacts introduced by cages, such as shading, by setting up open cages that provided shading and simultaneously allowing whelks and other invertebrates in and out of the experimental plots. In addition, open cages like these stop bird predation. However, the author did not find a significant difference in mussel abundance between open cages and marked controls, which suggests that desiccation exerts less pressure on mussels than predation.

At wave-exposed sites, the energy and nutrient transfer onto the shore can be greater than at protected sites, and can thus stimulate intertidal community development, competition and predation (Menge, 1976). This theoretical assumption appears to be at odds with the results from the present study, where the intertidal community at more exposed sites (Seatoun and Kau Point) developed less successfully and more slowly than the intertidal community at the most sheltered site (Evans Bay), where the succession from bare substrate to the mussel-dominated substrate was fastest. It is possible therefore those communities that are less disrupted and simultaneously can experience high nutrient inputs (i.e. concentrations of chlorophyll), such as Evans Bay in this study, can develop better. On the other hand, site-specific comparisons presented in Pareto charts and the results of Multiple Regression suggest that the dynamics between mussels and other intertidal community members were most intense at the most exposed site (Kau Point), where all three mussel species (*A. maoriana*, *M. galloprovincialis* and *P. canaliculus*) were interacting with as many as 13 other intertidal algal and invertebrate species (Tables 4.18-4.20; Figs. 4.17- 4.19), which would support Menge's (1976) claim that the community dynamics decreases with decreasing exposure to wave shock. However, the intensity and scale of the dynamics between each mussel species and other community members were also intense at Evans Bay, the most sheltered site, where mussels interacted with 11 other intertidal species (Tables 4.26-4.28; Figs. 4.24-4.26). *M. galloprovincialis* and *A. maoriana* were revealed as the two mussel species that experienced most of the interaction with other community members from all guilds at all sites, while percent cover of *P. canaliculus* remained relatively uncorrelated with other community members.

Results obtained in the present study partially confirm the findings of similar experiments at other locations (e.g. Harger 1972; Paine, 1974, 1976; Menge, 1976; Menge *et al.*, 1986; Buschbaum, 2001; Foster *et al.*, 2003; Menge *et al.*, 2003). In this experiment, type of cage treatment had a significant effect on the recovery rate of mussel communities at all experimental sites. For the three mussel species investigated here, overall recolonisation rate of available substrate was markedly higher under conditions of protection from predators and desiccation (the full cage treatment), or under conditions of protection from predators, but not from desiccation (the “roof missing” treatment), which suggests that protection from predators gave mussel recruits greater chance to establish themselves on the substrate than just protection from desiccation. In addition to this, the open cage treatment, correcting for the effects of shading (Navarrete, 1996), had an effect for all three species in most cases. There are exceptions to this, however. For example, there was little difference in percent cover of mussels between the control and the “no roof” treatment at Seatoun (Figs. 4.6 and 4.7) and Evans Bay (Figs. 4.20 and 4.21).

Summary

Present results confirm the findings of similar experiments conducted elsewhere in that mussels are dominant members of intertidal communities, able to outcompete other community members, including other mussel species. However, these findings significantly add to our knowledge of dynamics in intertidal communities dominated by mussels since most of such predator exclusion, substrate recolonisation experiments have involved one or two mussel species, whereas the present study describes three mussel taxa. Further, by investigating succession and competition within a dynamic and speciose environment such as Wellington Harbour, the present study sheds more light onto the often complex nature of these ecological mechanisms. Finally, the present study extensively examined temporal and spatial community recovery, linking the findings to the environmental factors, such as the water column parameters and hydrology regimes.

M. galloprovincialis, commonly found throughout the entire intertidal zone in Wellington Harbour, was the most successful and competitive species, recruiting onto the

cleared substrate at the highest rate, thus colonizing the plots in the most efficient way. The blue mussel took the greatest advantage of the conditions of protection from predators and desiccation, hence the highest percent cover recorded in full cage treatment.

A. maoriana, also common in the intertidal zone, was the second most efficient colonizing mussel species. A number of ribbed mussel recruits were found in open cage plots, where normally they would be expected to be consumed by predators. One possible explanation for this phenomenon could be that those recruits, although readily available to predators, might not have been of sufficient food value (i.e. expected energy unit gained per handling time), therefore a whelk would have to expend more energy than it would gain from consuming those mussels.

P. canaliculus, limited in its distribution mainly to the low-intertidal zone (although some green mussel individuals were recorded in the mid-intertidal), recruited very poorly onto the experimental plots, most likely being the result of the inability of recruits of this species to cope with desiccation at the tidal height of cage deployment. Therefore, drawing any meaningful conclusions related to the effects of experimental treatments for this species is difficult.

The mid-intertidal zone in Wellington Harbour studied in this experiment was revealed as a complex, multi-species system, with complex community responses following the substrate clearance. No simple description for this system can be offered. After 24 months of the experiment, Evans Bay was shown as the site where the community recovery was fastest, while at Seatoun the recovery rate was slowest. Although the percent cover results for each experimental treatment are not clear-cut, the percent cover of mussels at Evans Bay was highest, although uncorrelated to the bottom-up factors, while at Seatoun the bottom-up factors were most pronounced but the mussel percent cover was lowest, which suggests that the impact of physical disturbance processes significantly slows down the community recovery at that site.

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CHAPTER FIVE:

MUSSEL STRENGTH OF ATTACHMENT AND TOLERANCE TO DESICCATION

5.1. Introduction

From the perspective of rocky intertidal communities, wave exposure has been regarded as an important factor, structuring community successional pathways, activity of mobile predators and trophic relations among taxa within such communities. In aquatic environments, waves are associated with rapid water accelerations, sometimes reaching 400 m s^{-2} . Mussels subjected to wave action and high water velocities experience two types of forces: drag and lift. Drag forces push the animals downstream, acting on their sides that are exposed to the flow, while lift forces (also acting on the exposed sides) tend to pull them across the flow, away from the substrate. Consequently, the extent to which these forces are effective depends on the size and shape of the animals (Denny, 1993, 1995). Filter feeders, such as mussels and barnacles, and sessile predators, such as sea anemones, benefit from wave action since water movement can enhance their food supply. However, high exposure to waves often results in a wave-induced stress, potentially limiting growth, survival and feeding activity of intertidal marine biota (Menge & Sutherland, 1976, 1978; Palumbi, 1984; Carrington Bell & Denny, 1994; Hammond & Griffiths, 2004). Typically, in an intertidal system, larger individuals are able to produce more offspring and thus contribute to the next generation, while smaller mussels produce fewer offspring. In a wave-swept environment, however, these relationships are inverted and now larger individuals are at risk of being removed from the community by hydrodynamic forces of drag and lift, while smaller and more streamlined ones experience less drag and lift, and are therefore more likely to survive and continue to reproduce. Thus, in a wave-exposed, rocky intertidal system, hydrodynamic forces control marine organisms and set a balance between their survival and reproductive output (Fig. 5.1). Through the course of evolution these organisms have adapted to their environment in such a way that larger individuals, despite their higher resistance to the water flow and the risk of being dislodged by wave-associated forces,

are able to increase their resistance to hydrodynamic elements with the increase in size. Nevertheless, with double increase in size, larger mussels now are forced to cope with eightfold increases in accelerational forces growing faster than the organisms' strength, thus making the organisms even more likely to be dislodged from the colony (Denny, 1995).

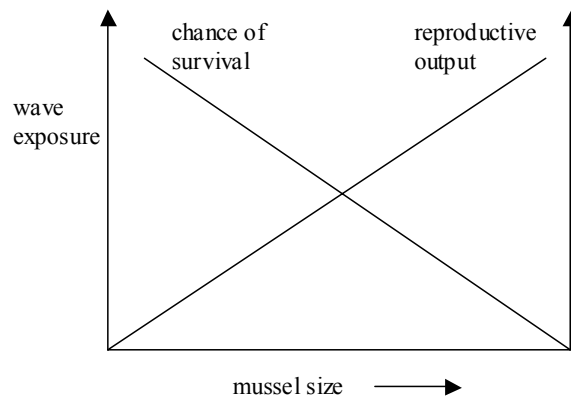


Figure 5. 1. Schematic representation of the competing factors in a wave-swept rocky environment (adapted from Denny, 1995).

Desiccation is another physical factor imposing physiological constraints on growth and survival of members of rocky intertidal communities. As soon as marine organisms are exposed to air, they lose water by evaporation. In order to survive in the intertidal zone, the members of intertidal communities have evolved mechanisms preventing serious water loss and heat shock, such as reducing heat gain from the environment and increasing heat loss from the body (Benedetti-Cecchi *et al.*, 2000). Relatively large body size can help reduce heat gain, as large body size also reduces surface area relative to volume and thus less area for gaining heat. However, in some intertidal organisms (such as mussels, barnacles and limpets), the ability to cool themselves by evaporating water and simultaneously avoiding desiccation has been found (Nybakken, 2001). This can be done by trapping an amount of water inside the animal's mantle cavity, while keeping the shell valves tightly closed (mussels, barnacles), or remaining in close contact within a scar of the substrate and sealing the gap between the scar and the animal's shell with a fold of the mantle (limpets) (Davis, 1969). Typically,

mussels living higher on the shore experience more severe desiccation stress than mussels lower on the shore, therefore they are less likely to survive (Fig. 5.2).

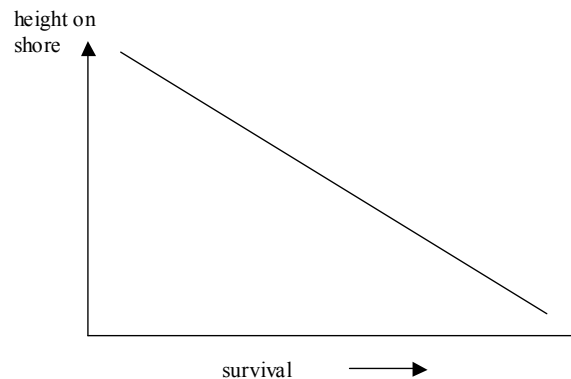


Figure 5. 2. Schematic representation of factors involved in survival of mussels exposed to desiccation.

Synergistic interactions of several factors, such as desiccation and wave exposure, are usually involved in shaping the intertidal invertebrate distribution patterns. While desiccation regulates the community structure in the upper intertidal ranges and can alter the pathways of succession due to the fact that some organisms unable to tolerate heat indefinitely and are forced to give way to other, more resilient ones (for example mussels), wave action has the strongest effect on biomass and size structure of invertebrate communities at low- and mid-intertidal levels, (Bustamante *et al.*, 1997; McQuaid *et al.*, 2000).

This chapter investigates the role two important physical factors play in intertidal community regulation: wave action and desiccation. Both of these factors affect mussel distribution within the zone (see chapter 1), and thus can affect the species diversity and community composition (Barnes & Hughes, 2002). Wave action (or log pounding) can remove individuals, move high loads of sediments or suppress growth, so that mussel populations living under significant wave action consist of smaller individuals (McQuaid *et al.*, 2000). As described in the previous chapter, wave action can lead to formation of a new patch of clear substrate that suddenly becomes available for recolonisation (Petraitis, 1995). Mussels' ability to cope with aerial exposure and desiccation also decides about population- and community-level interactions (Helmuth, 1999), often resulting in higher parts of the intertidal zone inhabited by smaller individuals (Griffiths, 1981). Thus,

thermal stress has been considered to be among the most important abiotic factors of mussel distribution, setting up their vertical limits (Denny & Paine, 1998). The present chapter investigates how strength of attachment to the rocky substrate in three sympatric mussel species is affected by wave action at sites facing north and south in Wellington Harbour. In a separate experiment, individuals from the same three mussel species were exposed to aerial temperatures and desiccation stress at various height levels within the intertidal zone in Wellington Harbour. In both experiments, mussel response to the stressful agents both at north- and south-facing sites was investigated.

Study system

As a body of water with highly variable exposure to winds, and wave action as a result of this, Wellington Harbour constitutes a model system for studying strength of attachment of intertidal mussels. In Wellington, there is a strong dominance of northerly and southerly winds, with roughly twice as many northerlies as there are southerlies. Typically, northerly winds are very gusty, while the velocity of southerlies is more constant due to the uninterrupted passage of the southerly winds over water. Although southerlies are less frequent and less gusty, they are about twice as strong as northerlies, most likely a result of the great wind acceleration on the Kaikoura coast (McConchie, 2000). For this reason, southerly-generated oceanic swells and waves carry more energy than northerly-generated waves and therefore intertidal mussel communities at south-facing sites within Wellington Harbour receive high amount of wave pounding, which can affect the processes of development and dynamics within such communities (Dayton, 1971; Underwood *et al.*, 1983; Bustamante *et al.*, 1997).

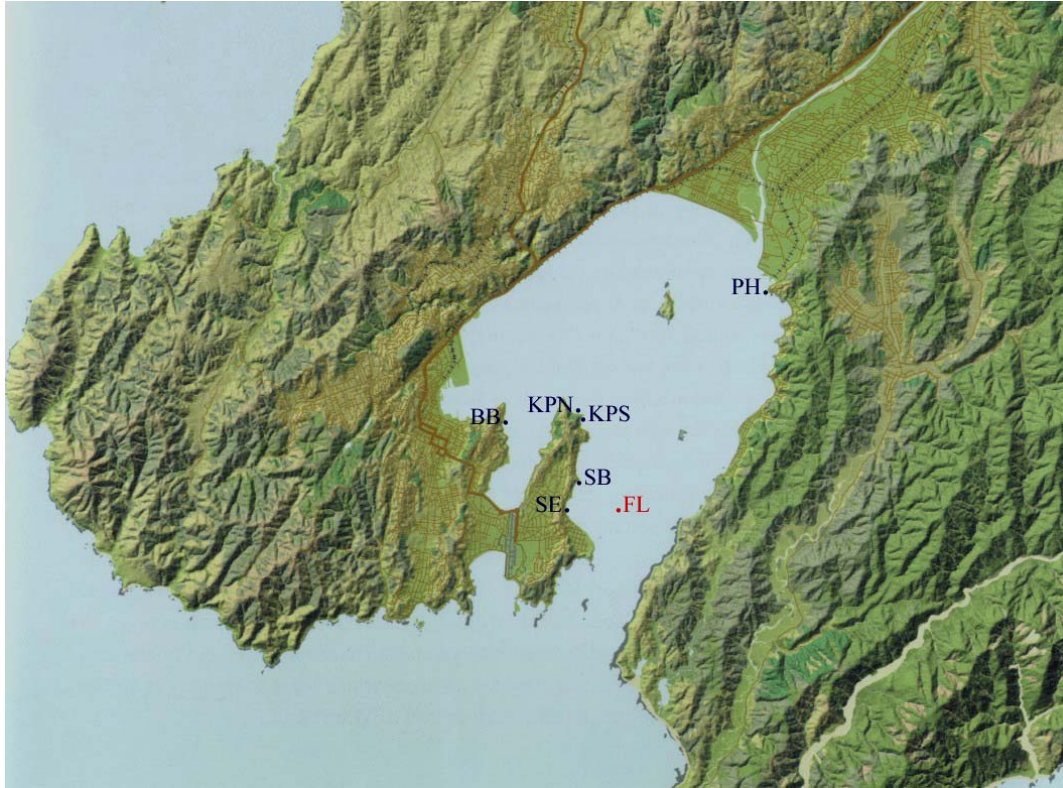


Figure 5.3. Location of experimental sites in Wellington Harbour (adapted from Molloy & Smith, 2002). Strength of mussel attachment experiments (blue) were conducted at: BB – Balaena Bay, SE – Seatoun, KPN – Kau Point north, PH – Point Howard, SB – Scorching Bay and KPS – Kau Point south. Desiccation experiment (red) was conducted at FL – Front Lead light.

5.2. Materials and Methods

Effects of wave exposure on mussel strength of attachment

In order to investigate the influence of wave exposure on mussel survival, a series of measurements of the mussel strength of attachment (SoA) to the rocky surface was conducted. Since quantifying wave exposure at sites was logistically impractical, they were subjectively classified as north- or south-facing prior to sampling. Classification was based on the aspect of mussel beds to the prevailing sea conditions (McQuaid *et al.*, 2000). No mean wave height data were collected. Three south-facing sites (Scorching Bay, Kau Point South and Point Howard) and three north-facing sites (Seatoun, Kau Point North and Balaena Bay) were selected (Fig. 5.3). Measurements of SoA were conducted using a spring balance (e.g. Gardner & Skibinski, 1991; Willis & Skibinski,

1992) and a set of laboratory stand jaws, tightened around each individual mussel and pulled perpendicular to rock with the spring balance (Fig 5.4). In order to avoid experimental bias associated with the SoA measurements, only mussels growing on flat rocky surface were examined in this experiment (mussels growing in cracks and crevices were excluded). The number of byssal threads was not recorded. The stainless steel spring balance (Rapala VMC Corp, MN, USA; model ProGuide 50lb.) was equipped with a marker slide that remained at the maximum reading after the mussel had been removed from the rock. The spring balance was factory-calibrated to the accuracy of 200 g. The measurements of SoA were expressed in kg (effectively the force) required for the mussels to be removed from the substrate.

On each sampling occasion, 30 mussels of each species (*Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*) were selected at each site and detached from the rock with the equipment described above. Subsequently, shell length (SL) of each individual was recorded. All measurements were conducted in the low intertidal zone. The measurements of SoA were repeated seasonally, between austral winter (June 2002) and austral spring (October 2003). Because the seasonality of SoA and the aspect effect were of interest, data were obtained for the following austral seasons: winter 2002 (June 2002), spring 2002 (September 2002), summer 2002 (December 2002), autumn 2003 (April 2003), winter 2003 (July 2003) and spring 2003 (October 2003).

Data analysis

Data were tested for normality of distribution and homogeneity of variances. Subsequently, since the distribution normality requirements were not met, SL data were log₁₀-transformed and SoA data were square root-transformed. In order to investigate spatial (site), temporal (seasonal), species- and aspect-specific (south-facing vs. north-facing sites) differences in SoA of all three mussel species, two separate ANCOVA techniques were employed. In the first analysis, transformed SoA data were specified as a dependent variable, while all sites, all seasons and all three mussel species were specified as independent factors, while transformed SL data were specified as a covariate. In order

to investigate spatial and temporal variation of species-specific SoA, a series of post-hoc Honest Significant Difference (Tukey HSD) tests was performed. Subsequently, the second ANCOVA was performed. In the analysis, transformed SoA data were specified as dependent variable, while season, species and the sites aspect (north- and south-facing) data were specified as crossed factors. As with the first ANCOVA, a series of post-hoc Honest Significant Difference (Tukey HSD) tests was performed in order to investigate spatial and temporal variation of species-specific SoA. Pearson coefficient was employed to investigate species-specific correlation between SoA and shell length. In order to avoid spurious correlations possibly driven by site and season effects in this analysis, residuals of SoA and SL were used instead of the raw data.

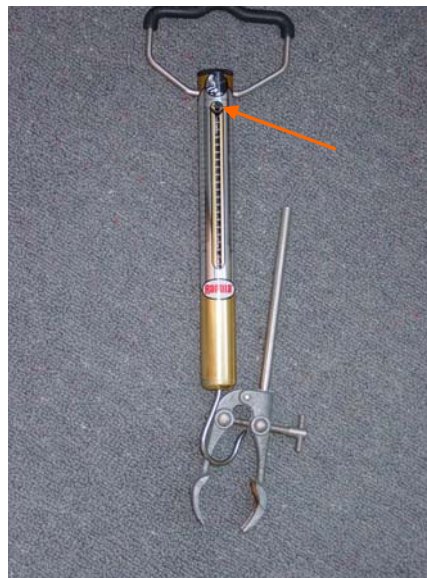


Figure 5.4. Spring balance and stand jaws used to measure the strength of mussel attachment in this study. The arrow indicates the marker slide.

Effects of desiccation on mussel survival

The effect of desiccation on the survival of mussels in the intertidal zone exposed to varying desiccation levels was investigated. An experiment was conducted in which groups of mussels were placed at different tidal levels around a piling structure (i.e. Front Lead light) in the main shipping channel in Wellington Harbour (Fig. 5.3). On each

sampling occasion, a group of 60 mussels (20 mussels per species) were taken from the intertidal zone on the piling structure at Front Lead light and placed in each of 6 nets that were subsequently tied at different tidal heights within the intertidal zone around a pile at Front Lead light (Fig. 5.5). Each net was assigned to five experimental levels (hereafter referred to as treatments): 0.3m, 0.6m, 0.9m, 1.2m and 1.5m above the chart datum. An additional net with the same number of mussels from the same three species was placed below chart datum, therefore acting as a control net. Chart datum can be defined as reference depth of water at the lowest astronomical spring tide to which all depths and drying heights on a chart are related. Chart datum is not a horizontal surface, but may be considered as such over a limited local area (www.epa.qld.gov.au/environmental_management, www.poal.co.nz/glossary). Thus, each net contained 20 green mussels, 20 blue mussels and 20 ribbed mussels. Such arrangement of experimental nets was repeated on the north- and south-facing piles at Front Lead, as the mussel survival was expected to vary according to different levels of solar radiation on the north- and south-exposed sides. The experimental nets were left for one month. Upon each visit to Front Lead, each net was opened and survival of each mussel was checked by pressing the shell valves or inserting wire inside the mantle cavity. If a gaping mussel did not close its valves in response to pressing, it was counted as dead. Similarly, a lack of reaction to insertion of a wire inside the mussel's mantle cavity also qualified it as dead. Thus, for the purposes of statistical analysis mussels were assigned to two groups: those who survived (Y) and those who did not (N). Desiccation tolerance data were obtained for the following austral seasons: summer 2002 (January 2002), autumn 2002 (April 2002), winter 2002 (August 2002), spring 2002 (November 2002), summer 2002 (January 2003) and autumn 2002 (April 2003).

Quantitative solar radiation data for Wellington Harbour were provided by Greater Wellington, Environmental Division. The data were collected only at one site in Wellington region – Waterloo in Lower Hutt. The data present the global solar radiation in the region, and as such do not reflect the north- and south-related distinction.

Data analysis

Mussel SL data were collected from the nets deployed on north- and south-facing sides of Front Lead, hereafter referred to as “facing north” and “facing south” sites. The SL data were tested for normality of distribution and homogeneity of variances. Since the normality requirements were not met, the data were \log_{10} -transformed. Subsequently, the Logistic Regression analysis was performed on mussel survival data, where Y in the data set denoting an alive mussel was given value 1 in the analysis, while N in the data set denoting a dead mussel was given value 0 in the analysis. Thus, a binary data set was created for the analysis. Logistic Regression employed here investigated the relationship between the response variable (1 vs. 0) and the following independent variables: site, season, tidal height and species treated as categorical factors and \log_{10} -transformed SL data as a covariate. Logistic Regression is useful for situations in which the presence or absence of a characteristic depends on a set of factors. It is similar to a linear regression but is more appropriate to a data set with binomial data, as was the case in this study. The analysis introduces a so-called Wald statistic and a p-value for that statistic. The Wald statistic is a test of significance of the regression coefficient based on maximum likelihood estimates. Subsequently, the Product-Moment correlation coefficient was employed to estimate the correlation between the shell length of each species and the residuals, thus revealing the probability of survival of each mussel according to its shell length after allowing for site, season and treatment effects. Finally, LD₅₀, lethal dose of exposure to desiccation at which half of individuals died, was estimated for each species at all treatment heights on north- and south-facing shores.



Figure 5.5. Front Lead: a view of the north-facing side.

5.3. Results

Effects of wave exposure on mussel attachment

First ANCOVA ($R^2=0.483$, $F=26.789$, $df=108$, $p<0.001$) revealed significant differences in SoA among sites, seasons and mussel species (Table 5.1, Fig. 5.6). All interaction terms were significant, indicating that SoA varies differentially according to location within the Harbour, the season and the mussel species.

Table 5.1. ANCOVA results for differences in SOA among sites, species and seasons, with shell length (SL) as a covariate.

Effect	SS	df	MS	F	<i>p</i> -value
SL	39.1077	1	39.10765	260.637	<0.001
Season	51.5394	5	10.30788	68.698	<0.001
Site	29.8344	5	5.96688	39.767	<0.001
Species	49.3317	2	24.66586	164.388	<0.001
Season*Site	59.5335	25	2.38134	15.871	<0.001
Season*Species	14.2808	10	1.42808	9.517	<0.001
Site*Species	14.0704	10	1.40704	9.377	<0.001
Season*Site*Species	21.8965	50	0.43793	2.918	<0.001

Second ANCOVA ($R^2=0.402$, $F=59.201$, $df=36$, $p<0.01$) revealed significant differences in mussel SoA among all seasons, all sites and between sites facing north and south. Also, all interaction terms were significant (i.e. season*species, season*aspect, species*aspect and season*species*aspect) (Table 5.2). Significant differences in SoA

revealed according to site aspect, with generally greater SoA in all three species on south-facing shores. *P. canaliculus* was shown as the species with the highest SoA, followed by *A. maoriana* and *M. galloprovincialis*. This pattern was present in all seasons for which measurements were recorded.

Table 5.2. ANCOVA results for differences in SOA among species, seasons and site aspect, with shell length (SL) as a covariate.

Effect	SS	df	MS	F	<i>p</i> -value
SL	39.284	1	39.284	231.650	<0.001
Season	52.203	5	10.441	61.566	<0.001
Species	54.778	2	27.389	161.506	<0.001
Site aspect	12.562	1	12.562	74.074	<0.001
Season*Species	12.831	10	1.283	7.566	<0.001
Season*Aspect	33.062	5	6.612	38.991	<0.001
Species*Aspect	2.932	2	1.466	8.644	<0.001
Season*Species*Aspect	4.256	10	0.426	2.510	0.005

Aulacomya maoriana

While the mean seasonal SoA across all sites was 3.63 ± 1.63 kg, spatial and temporal variability of SoA was evident (Table 5.3, Fig. 5.6). The lowest mean seasonal SoA of *A. maoriana* was recorded at Scorching Bay in winter 2003 (2.16 kg), while the highest mean seasonal SOA value was recorded at Kau Point south in spring 2003 (5.84 kg). The mean seasonal SL across all sites was 43.26 ± 6.03 mm. The highest mean seasonal SL was recorded at Balaena Bay in summer 2003 (53.5 ± 6.59 mm), while the lowest mean seasonal SL was recorded at Point Howard in winter 2002 (35.97 ± 6.99 mm). Post-hoc LSD Tukey test indicated that SoA of the ribbed mussel was generally higher at south-facing sites ($F=14.326$, $p<0.001$) (Fig. 5.7), although the mean SL of this species was greater at north-facing sites ($F=32.29$, $p<0.001$) (Fig. 5.8). Pearson coefficient revealed positive SL-SoA correlation ($R=0.225$, $p<0.001$), indicating that SoA of this species increases with the increasing size of mussels.

Table 5.3. *Aulacomya maoriana*: Descriptive statistics of SoA at all sites and seasons (mean \pm SD).
 BB=Balaena Bay, KPN=Kau Point north, KPS=Kau Point south, PH=Point Howard, SB=Scorching Bay,
 SE=Seatoun

Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD	Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD
Winter 2002	BB	30	3.593	1.357	42.300	5.559	Autumn 2003	BB	30	3.760	1.966	42.933	5.278
	KPN	30	3.520	1.374	41.700	4.865		KPN	30	4.833	1.929	44.367	6.800
	KPS	30	4.893	1.365	44.567	5.482		KPS	30	4.087	1.838	43.933	5.496
	PH	30	2.620	1.011	35.967	6.995		PH	30	2.927	1.479	40.900	6.578
	SB	30	2.773	1.025	38.967	4.056		SB	30	3.280	1.592	41.100	5.095
	SE	30	3.987	1.337	43.133	4.167		SE	30	3.587	2.406	44.433	4.091
Spring 2002	BB	30	4.200	1.390	43.300	5.784	Winter 2003	BB	30	3.593	1.357	42.300	5.559
	KPN	30	4.063	1.452	45.000	3.184		KPN	30	3.520	1.374	41.700	4.865
	KPS	30	5.067	1.693	43.633	3.961		KPS	30	2.953	1.468	36.967	3.586
	PH	30	4.040	0.983	42.567	5.544		PH	30	4.740	1.638	42.567	4.216
	SB	30	4.273	1.274	39.633	5.957		SB	30	2.157	1.085	42.133	4.644
	SE	30	4.393	0.980	43.433	3.540		SE	30	3.487	2.155	42.967	2.810
Summer 2003	BB	30	3.200	1.022	53.500	6.590	Spring 2003	BB	30	2.247	0.660	38.167	4.990
	KPN	30	2.550	1.078	47.533	5.184		KPN	30	3.467	1.132	49.367	4.575
	KPS	30	3.717	1.343	44.167	3.905		KPS	30	5.840	1.827	44.967	3.978
	PH	30	2.767	1.244	40.533	5.865		PH	30	4.433	1.029	41.633	3.737
	SB	30	2.650	0.832	51.067	4.975		SB	30	4.093	1.461	47.433	3.739
	SE	30	2.967	0.982	44.767	5.131		SE	30	2.387	0.880	43.667	5.750

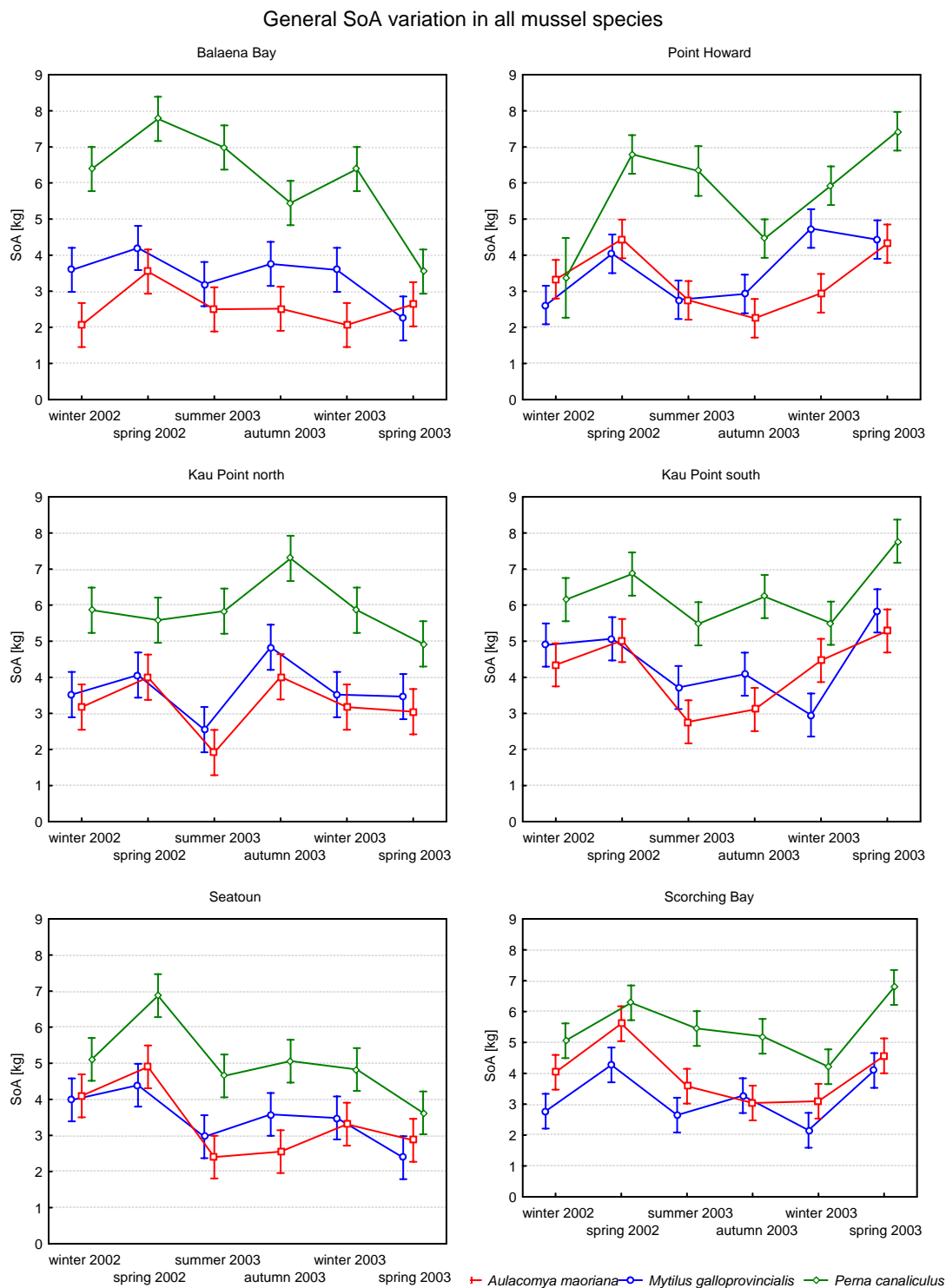


Figure 5. 6. Seasonal, site- and species-specific variation in SoA. Points represent mean seasonal values (N=30) with 0.95 confidence interval error bars. North-facing sites are on the left of the figure; south-facing sites are on the right.

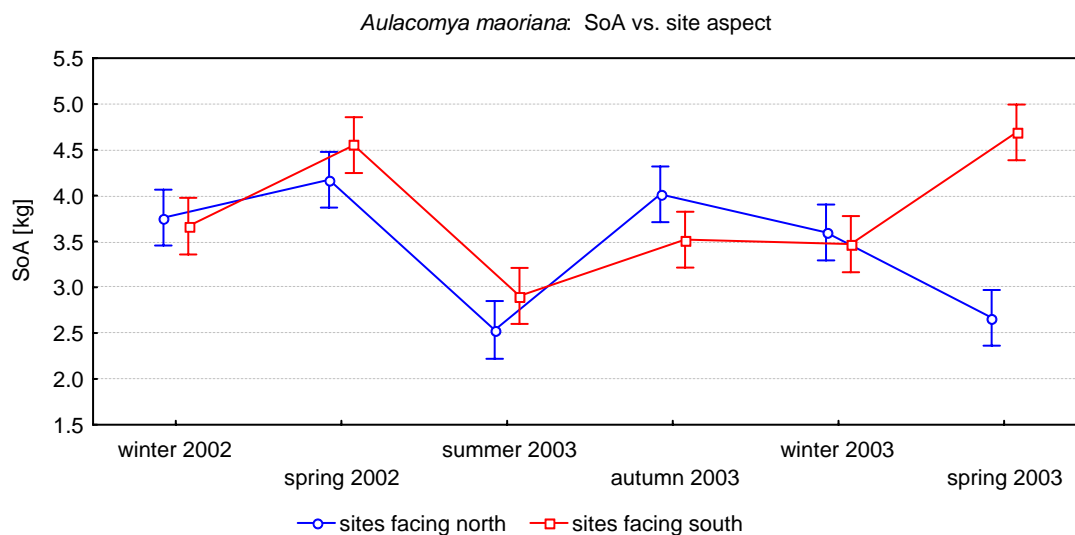


Figure 5.7. *Aulacomya maoriana* SoA at sites facing north and south. Points represent mean values with 0.95 confidence interval error bars.

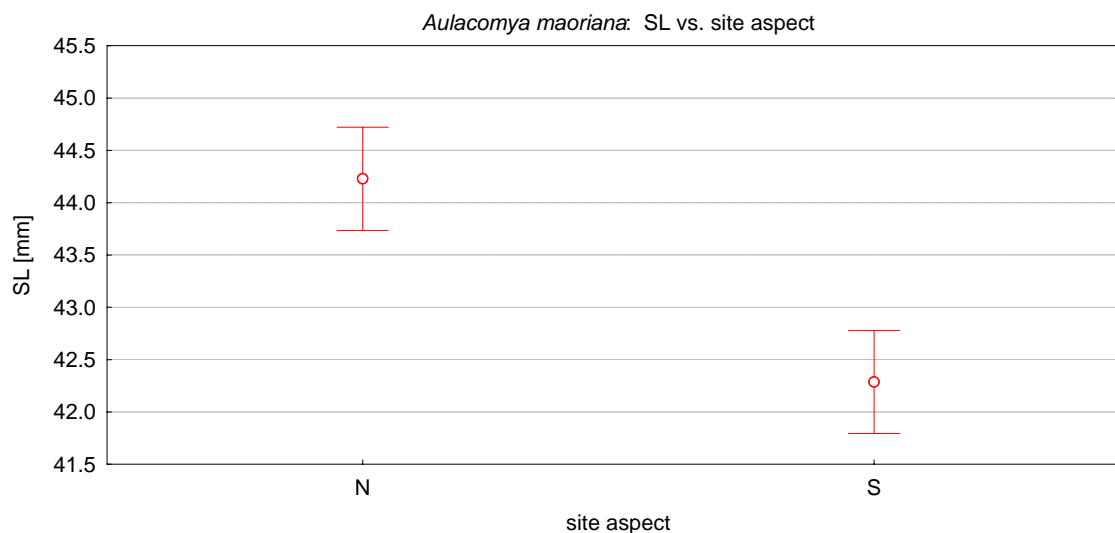


Figure 5. 8. *Aulacomya maoriana*: mean SL according to site aspect (N=facing north, S=facing south). Points represent mean values with 0.95 confidence interval error bars.

Mytilus galloprovincialis

While the mean seasonal SoA across all sites was 3.44 ± 1.69 kg, spatial and temporal variability of SoA was evident (Table 5.4, Fig. 5.6). The lowest mean seasonal SoA of *M. galloprovincialis* was recorded at Kau Point north in summer 2003 (1.92

± 1.07 kg), while the highest mean seasonal SoA value was recorded at Scorching Bay in spring 2002 (5.61 ± 1.58 kg). The mean seasonal SL across all sites was 51.06 ± 7.32 mm. The highest SL of the blue mussel was recorded at Scorching Bay in spring 2003 (59.1 ± 6.7 mm), while the lowest SL was recorded at Point Howard in spring 2002 (44.3 ± 4.69 mm). Post-hoc LSD Tukey test indicated that SoA of the blue mussel was greater at the south-facing sites ($F=72.602$, $p<0.001$, respectively) (Fig. 5.9), although there was no significant difference in the mean SL according to the site aspect ($F=2.26$, $p=0.133$) (Fig. 5.10). Pearson coefficient revealed a positive and significant correlation between SoA and SL ($R=0.331$, $p<0.01$), suggesting that SoA increased with the increasing size of mussels.

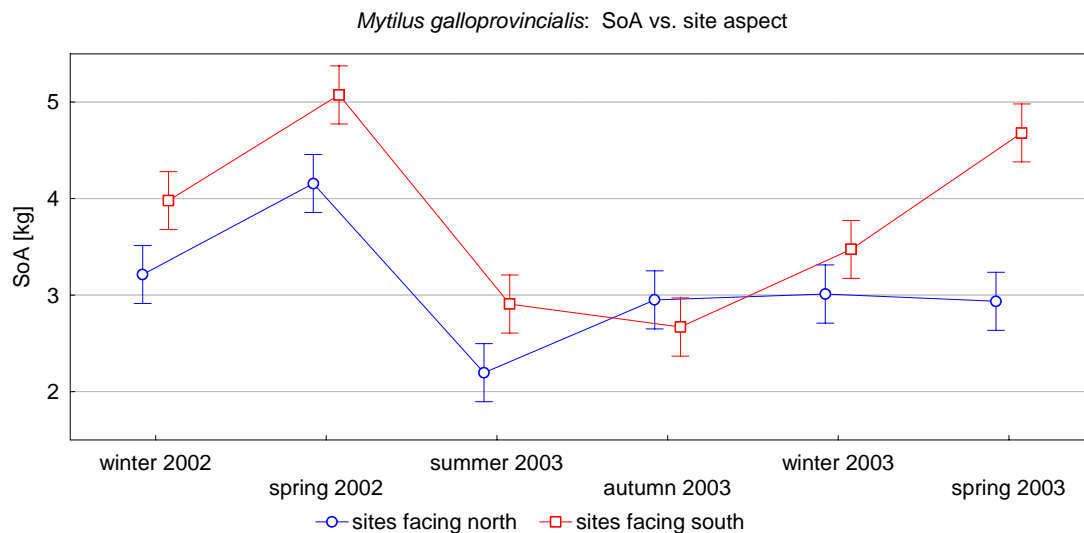


Figure 5.9. *Mytilus galloprovincialis*: SoA at sites facing north and south. Points represent mean values with 0.95 confidence interval error bars.

Table 5.4. *Mytilus galloprovincialis*: Descriptive statistics of SoA at all sites and seasons (mean \pm SD). BB=Balaena Bay, KPN=Kau Point north, KPS=Kau Point south, PH=Point Howard, SB=Scorching Bay, SE=Seatoun

Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD	Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD
Winter 2002	BB	30	2.067	1.234	49.967	7.261	Autumn 2003	BB	30	2.517	1.661	58.400	8.058
	KPN	30	3.173	1.707	47.400	7.881		KPN	30	4.013	2.546	45.233	5.361
	KPS	30	4.347	1.676	47.100	4.326		KPS	30	3.107	1.274	53.300	5.207
	PH	30	3.333	1.181	47.167	4.542		PH	30	2.253	1.362	49.800	5.616
	SB	30	4.033	1.448	54.867	4.848		SB	30	3.040	1.222	56.967	5.499
	SE	30	4.100	1.286	50.433	7.960		SE	30	2.553	0.996	53.633	3.615
Spring 2002	BB	30	3.547	1.509	52.633	7.088	Winter 2003	BB	30	2.067	1.234	49.967	7.261
	KPN	30	4.000	1.475	49.667	6.402		KPN	30	3.173	1.707	47.400	7.881

Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD	Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD
Summer 2003	KPS	30	5.020	1.370	51.267	7.080	Spring 2003	KPS	30	4.467	1.720	48.667	6.535
	PH	30	4.450	1.323	44.300	4.699		PH	30	2.947	1.579	50.467	4.232
	SB	30	5.607	1.584	54.967	5.714		SB	30	3.100	1.584	55.633	4.937
	SE	30	4.900	1.452	50.433	4.847		SE	30	3.313	1.855	47.200	6.122
	BB	30	2.500	1.880	52.667	9.679		BB	30	2.640	1.165	45.233	7.074
	KPN	30	1.917	1.075	52.933	6.491		KPN	30	3.047	1.035	55.200	8.700
	KPS	30	2.767	0.971	51.367	4.319		KPS	30	5.287	0.964	50.200	6.206
	PH	30	2.750	1.230	49.800	5.898		PH	30	4.320	0.895	46.200	4.895
	SB	30	3.583	1.532	58.733	6.812		SB	30	4.567	1.145	59.100	6.666
	SE	30	2.400	0.621	51.600	5.411		SE	30	2.867	1.334	48.167	7.106

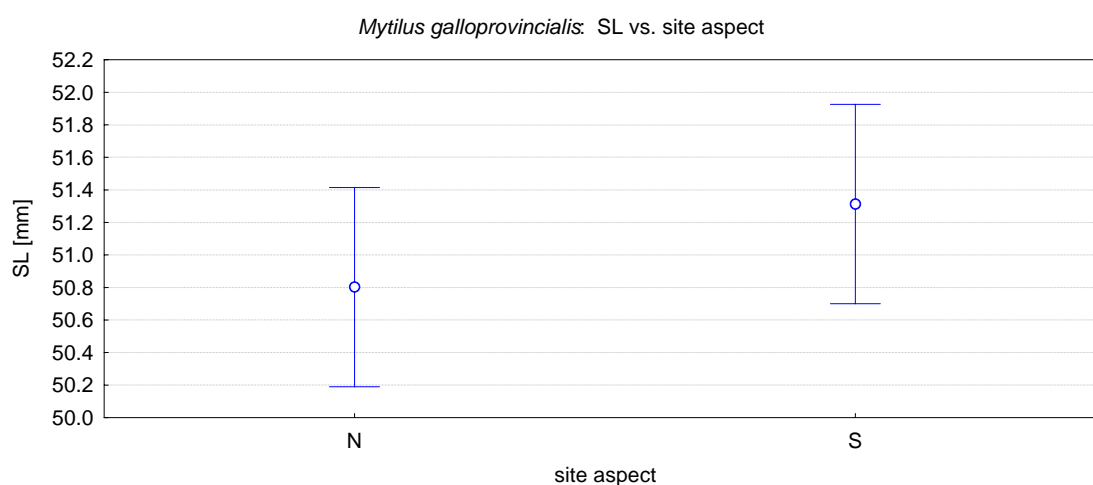


Figure 5. 10. *Mytilus galloprovincialis*: mean shell length according to site aspect (N=facing north, S=facing south). Points represent mean values with 0.95 confidence interval error bars.

Perna canaliculus

While the mean seasonal SoA across all sites was 5.80 ± 2.27 kg, spatial and temporal variability of SoA was evident (Table 5.5, Fig. 5.6). The lowest mean seasonal SoA of *P. canaliculus* was recorded at Point Howard north in winter 2002 (3.37 ± 1.09 kg), while the highest mean seasonal SoA value was recorded at Balaena Bay in spring 2002 (7.77 ± 2.49 kg). The mean seasonal SL across all sites was 68.18 ± 13.47 mm. The highest SL of the green mussel was recorded at Scorching Bay in spring 2003 (80.70 ± 8.46 mm), while the lowest SL was recorded at Point Howard in spring 2002 ($59.86 \pm$

16.98 mm). While SoA of the green mussel for most of the experiment was greater at the north-facing sites (Fig. 5.11), post-hoc LSD Tukey test indicated that the overall SoA was greater at the south-facing sites ($F=8.348$, $p=0.004$) – a result most likely driven by a large difference in SoA of this species in spring 2003. The mean SL was greater at north-facing sites ($F=6.24$, $p=0.013$) (Fig. 5.12). Pearson coefficient revealed a positive and significant correlation between SoA and SL ($R=0.344$, $p<0.01$), indicating that SoA increased with the increasing size of mussels.

Table 5.5. *Perna canaliculus*: Descriptive statistics of SoA at all sites and seasons (mean \pm SD).

BB=Balaena Bay, KPN=Kau Point north, KPS=Kau Point south, PH=Point Howard, SB=Scorching Bay, SE=Seatoun

Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD	Season	Site	N	SoA [kg] Mean	SoA [kg] SD	SL [mm] Mean	SL [mm] SD
Winter 2002	BB	30	6.387	2.064	74.767	17.027	Autumn 2003	BB	30	5.447	2.451	73.300	13.641
	KPN	30	5.860	1.984	64.700	11.998		KPN	30	7.293	2.900	63.000	10.309
	KPS	30	6.153	1.924	59.867	12.586		KPS	30	6.237	2.528	64.500	13.235
	PH	30	3.371	1.092	59.857	16.985		PH	30	4.460	1.574	61.300	10.134
	SB	30	5.057	1.465	69.700	8.591		SB	30	5.200	1.903	68.767	8.361
	SE	30	5.110	1.955	63.200	12.524		SE	30	5.060	2.067	63.733	8.702
Spring 2002	BB	30	7.777	2.488	68.033	12.483	Winter 2003	BB	30	6.387	2.064	74.767	17.027
	KPN	30	5.583	1.445	71.800	16.984		KPN	30	5.860	1.984	64.700	11.998
	KPS	30	6.860	1.941	64.400	16.368		KPS	30	5.500	1.833	61.333	9.034
	PH	30	6.793	2.083	65.900	12.466		PH	30	5.927	2.330	70.367	11.758
	SB	30	6.283	2.146	64.833	9.560		SB	30	4.213	1.686	65.267	10.161
	SE	30	6.873	1.680	69.900	10.293		SE	30	4.827	2.809	71.467	12.381
Summer 2003	BB	30	6.983	2.321	77.167	16.303	Spring 2003	BB	30	3.547	1.510	68.633	20.765
	KPN	30	5.833	2.253	72.733	10.599		KPN	30	4.927	1.688	68.533	17.079
	KPS	30	5.483	1.500	70.567	11.773		KPS	30	7.773	1.990	70.033	11.494
	PH	30	6.333	1.863	64.222	9.564		PH	30	7.433	1.841	69.967	14.092
	SB	30	5.450	2.014	80.700	8.457		SB	30	6.780	2.377	72.967	11.361
	SE	30	4.650	1.762	61.433	8.427		SE	30	3.627	1.443	70.067	14.453

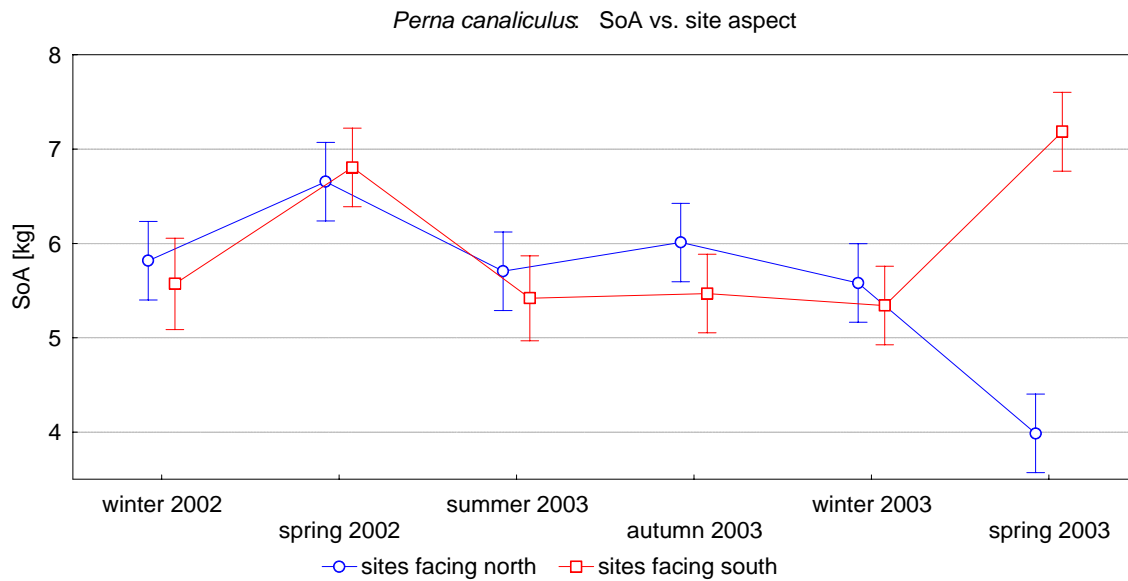


Figure 5.11. *Perna canaliculus*: SoA at sites facing north and south. Points represent mean values with 0.95 confidence interval error bars.

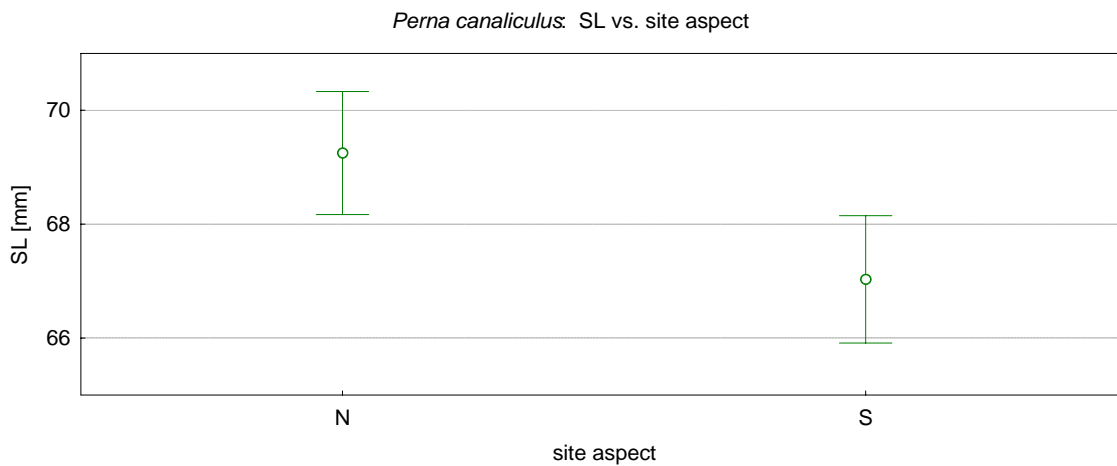


Figure 5. 12. *Perna canaliculus*: mean shell length according to site aspect (N=facing north, S=facing south). Points represent mean values with 0.95 confidence interval error bars.

Effects of desiccation on mussel survival

Logistic Regression (Table 5.6) pointed at all the factors as highly significant in determining the survival of mussels in this experiment. The analysis revealed that the green mussel *P. canaliculus* is the species most vulnerable to, and therefore least able to cope with desiccation and therefore with the lowest probability of survival (25%), the

blue mussel *M. galloprovincialis* as the most desiccation-tolerant of all the species investigated and therefore with the highest probability of survival (50%), and the ribbed mussel *A. maoriana* as a species more robust than *P. canaliculus* but less than *M. galloprovincialis*, with survival probability between 45 and 50%. The probability of survival for all species was higher on the south-facing side at Front Lead than on the north-facing side (Fig. 5.13). Judging by the site aspect, both *Aulacomya maoriana* and *Mytilus galloprovincialis* could greatly increase the chances of their survival at higher levels if they were facing south, while such site aspect made very little difference for *Perna canaliculus* of which very few individuals survived above certain tidal height, regardless of whether they were facing south or north (Fig. 5.14). As judged by the Wald statistic values, tidal height was the most significant factor affecting mussel survival, followed by SL and species (1029.279, 309.76 and 95.501, respectively). On a seasonal basis, the species-specific probability of survival (Figures 5.15, 5.17 and 5.19) was greater for cooler seasons and lower in warmer seasons, reflecting the greater amount of solar radiation (and presumably desiccation stress associated with it) in summer and lower in winter.

Table 5.6. Logistic Regression – general analysis.

Factor	df	Wald statistic	p-value
Tidal height	5	1029.279	<0.001
SL (covariate)	1	309.760	<0.001
Species	2	95.501	<0.001
Season	5	59.417	<0.001
Site	1	56.466	<0.001

Aulacomya maoriana

Logistic Regression revealed that site, season and tidal height are significant factors, and that shell length is a significant covariate for survival of this species (Table 5.7). The probability of survival increased significantly with decreasing tidal height. When emerged, the ribbed mussel survived better on the south-facing side than on the north-facing side, at any treatment height (Fig. 5.15). LD₅₀ was higher on the south-facing side (0.75 m), and lower on the north-facing side (0.65 m).

The seasonal probability of survival was also consistently higher if mussels were located on the south-facing side at Front Lead, except for autumn 2003, when data collected from north-facing side indicated greater survival there. The lowest probability of survival was recorded in summer 2003 and on the south-facing side it was 30%, while on the north-facing side it was 13% (Fig. 5.16).

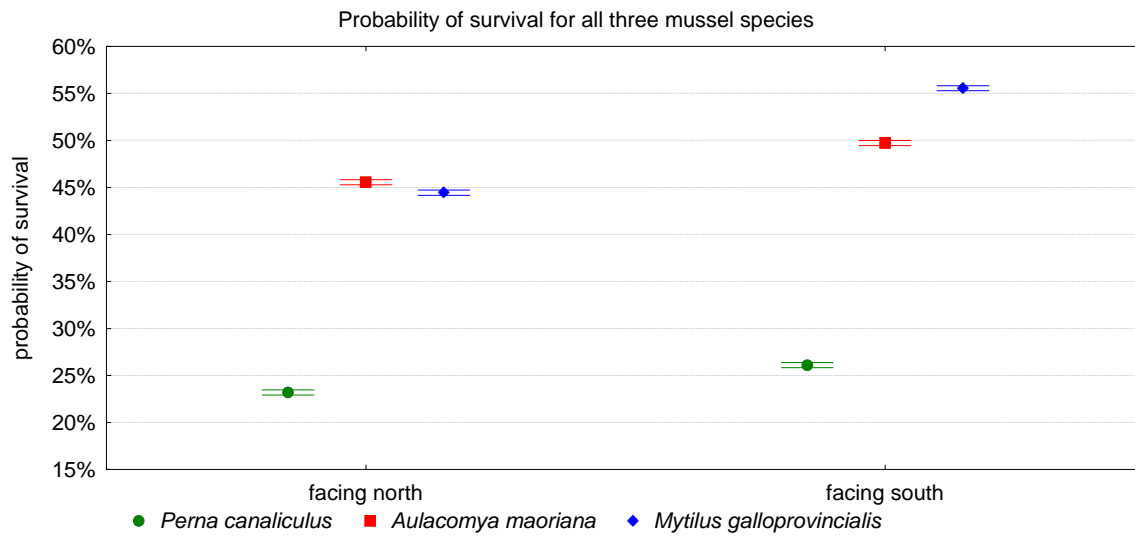


Figure 5. 13. Probability of survival for all three species on north- and south-facing side at Front Lead. Points represent mean values with 0.95 confidence interval error bars.

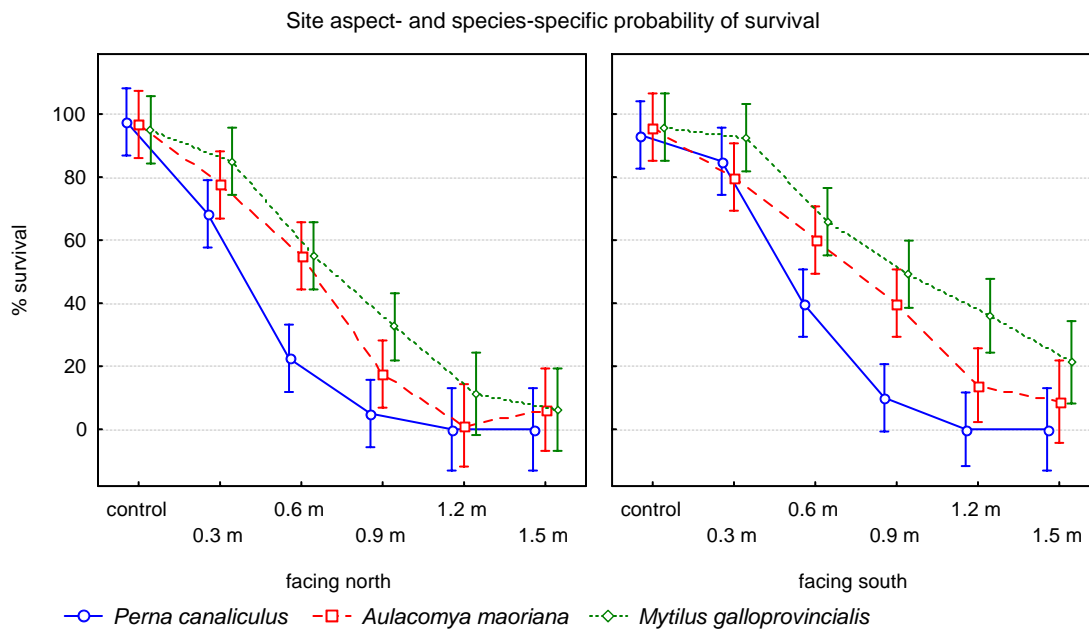


Figure 5.14. Site aspect- and species-specific probability of survival. Points represent mean values with 0.95 confidence interval error bars.

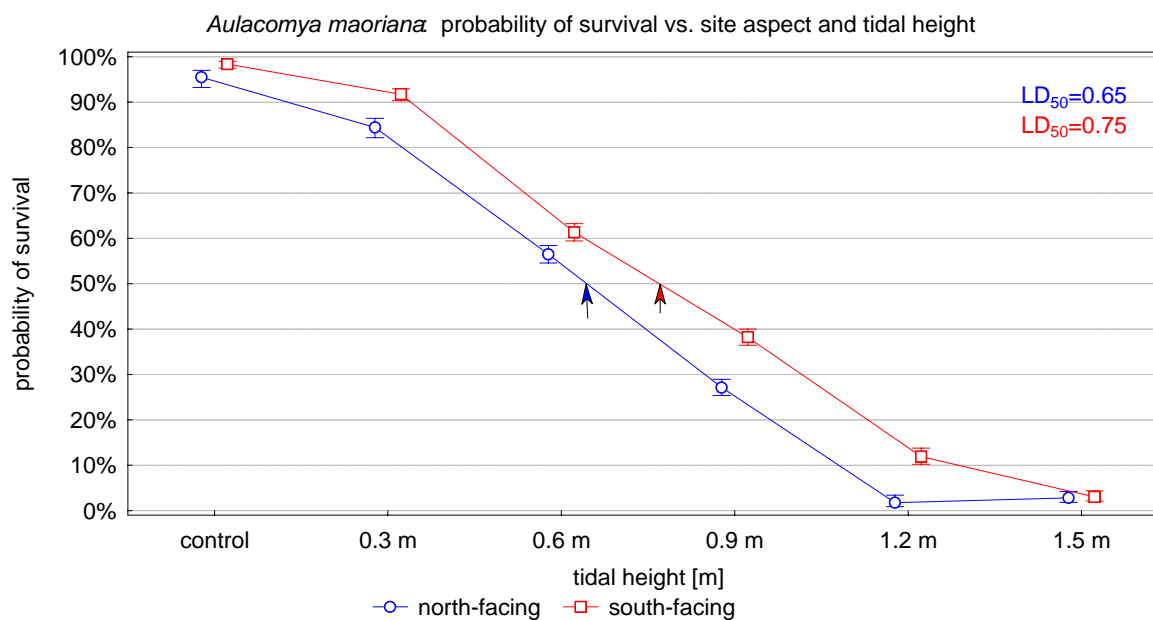


Figure 5. 15. *Aulacomya maoriana*: probability of survival vs. site aspect and tidal height. Points represent mean values with 0.95 confidence interval error bars.

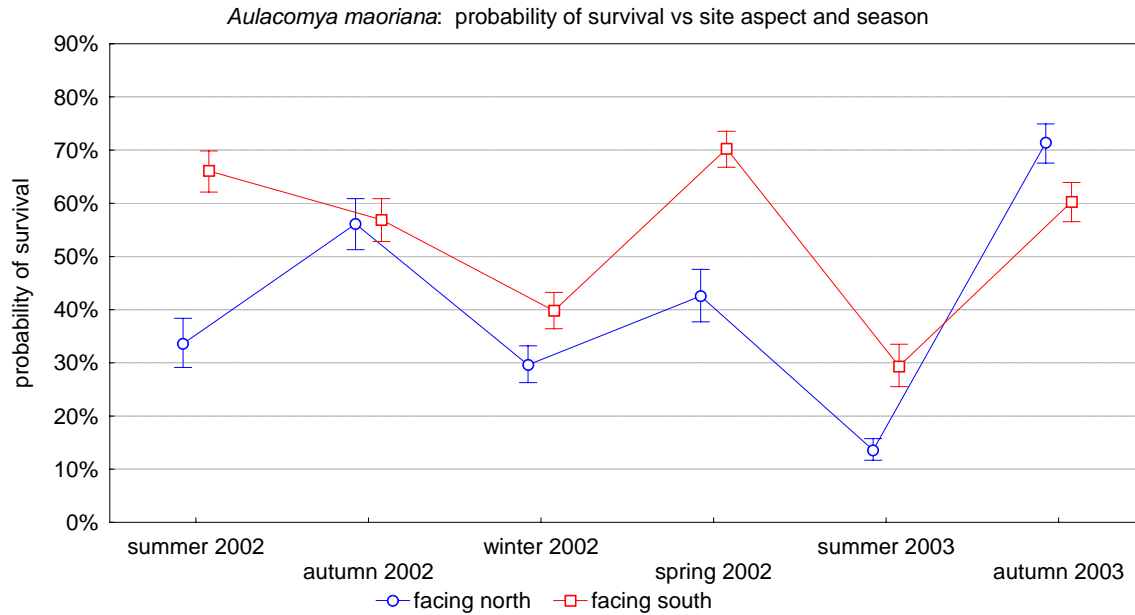


Figure 5.16. *Aulacomya maoriana*: probability of survival vs. site aspect and season. Points represent mean values with 0.95 confidence interval error bars.

The Product-Moment correlation analysis revealed a significant, negative correlation between shell length and the probability of survival ($R=-0.310$, $p<0.01$, $t=-12.359$, $N=1440$).

Table 5.7. *Aulacomya maoriana*: Logistic regression results

Factor	df	Wald statistic	p-value
Tidal height	5	395.4624	<0.001
SL (covariate)	1	108.1855	<0.001
Season	5	51.5553	<0.001
Site (north or south)	1	10.7583	<0.01

Mytilus galloprovincialis

Logistic Regression revealed site, season and tidal height as significant factors, as well as shell length as a significant covariate for this species (Table 5.8)

The probability of survival for *M. galloprovincialis* significantly increased with decreasing tidal height. When exposed to desiccation, the blue mussel survived better on the south-facing side than on north-facing side, at all treatment heights (Fig. 5.17). LD_{50} was higher on the south-facing side (0.87 m) and lower on the north-facing side (0.62 m).

Table 5.8 *Mytilus galloprovincialis*: Logistic regression results

Factor	df	Wald statistic	<i>p</i> -value
Tidal height	5	369.9058	<0.001
SL (covariate)	1	123.1161	<0.001
Season	5	48.9130	<0.001
Site (north or south)	1	38.9549	<0.001

The probability of survival for any given season was also significantly greater if mussels were deployed in nets facing south. The lowest probability of survival for the blue mussel was recorded in summer 2003, when only 35% of mussels facing north survived, compared with 45% of mussels facing south in the same season (Fig. 5.18). The Product-Moment correlation analysis revealed a significant, negative correlation between the shell length and the probability of survival ($R=-0.313$, $p<0.01$, $t=-12.517$, $N=1440$).

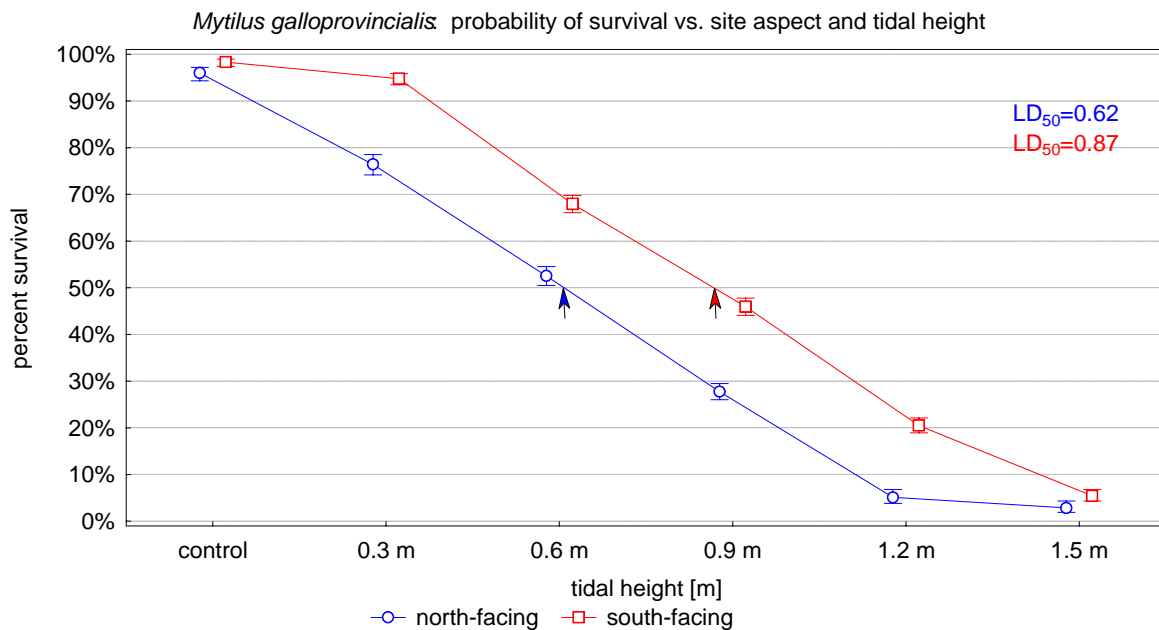


Figure 5. 17. *Mytilus galloprovincialis*: probability of survival vs. site aspect and tidal height. Points represent mean values with 0.95 confidence interval error bars.

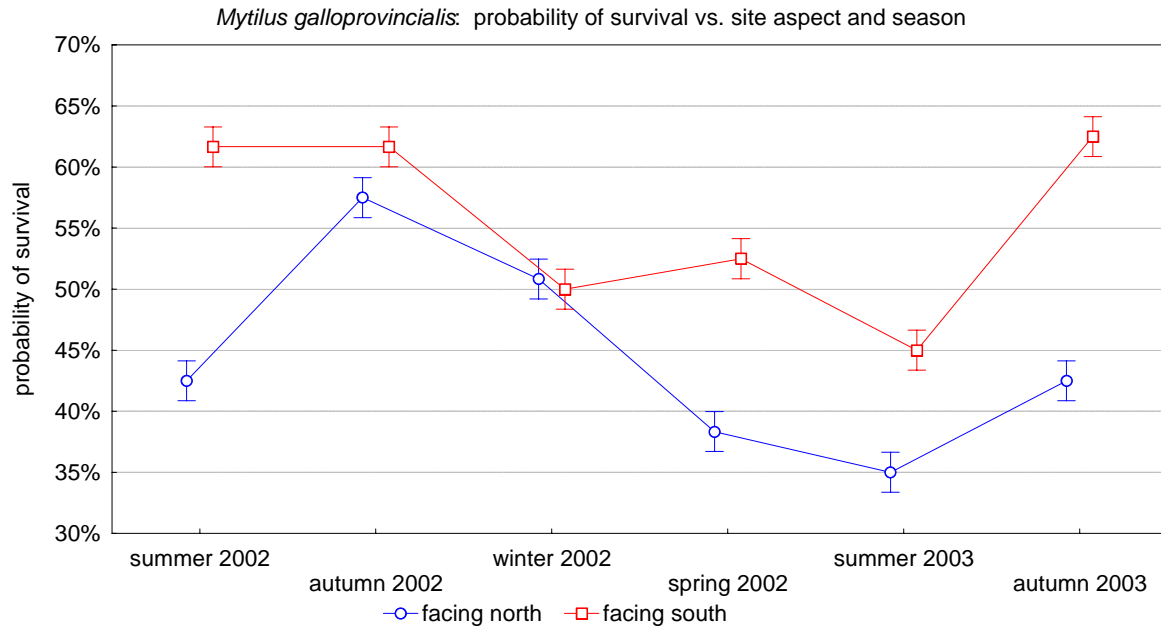


Figure 5. 18. *Mytilus galloprovincialis*: probability of survival vs. site aspect and season. Points represent mean values with 0.95 confidence interval error bars.

Perna canaliculus

Logistic Regression revealed site, tidal height and season as significant factors, as well as shell length as a significant covariate (Table 5.9). The survival of *P. canaliculus* was greatest on south-facing side than on north-facing (Fig. 5.19). However, for this species the survival probability declined more rapidly than in the previous two species, to about 40% at the first tidal height treatment (0.3 m). LD₅₀ was higher on the south-facing side (0.35 m) and lower on the north-facing side (0.20 m). When investigated on a seasonal basis, the probability of survival was lower on the south-facing side on two occasions, in autumn and winter 2002 (Fig. 5.20). Despite this, the highest probability of survival throughout the sampling period was still obtained for mussels facing south (33% in spring 2002), as opposed to mussel placed in nets facing north, where the highest survival probability was 32% (recorded in winter 2002). The Product-Moment correlation analysis revealed a significant, negative correlation between the shell length and the probability of survival ($R=-0.299$, $p<0.01$, $t=-11.902$, $N=1440$).

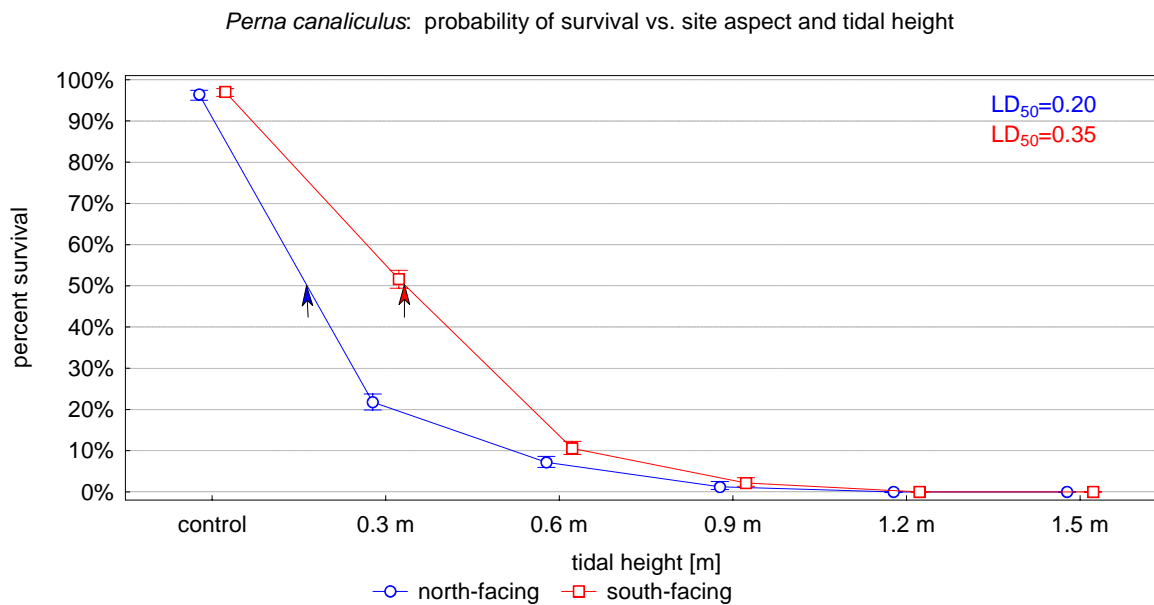


Figure 5. 19. *Perna canaliculus*: probability of survival vs. site aspect and tidal height. Points represent mean values with 0.95 confidence interval error bars.

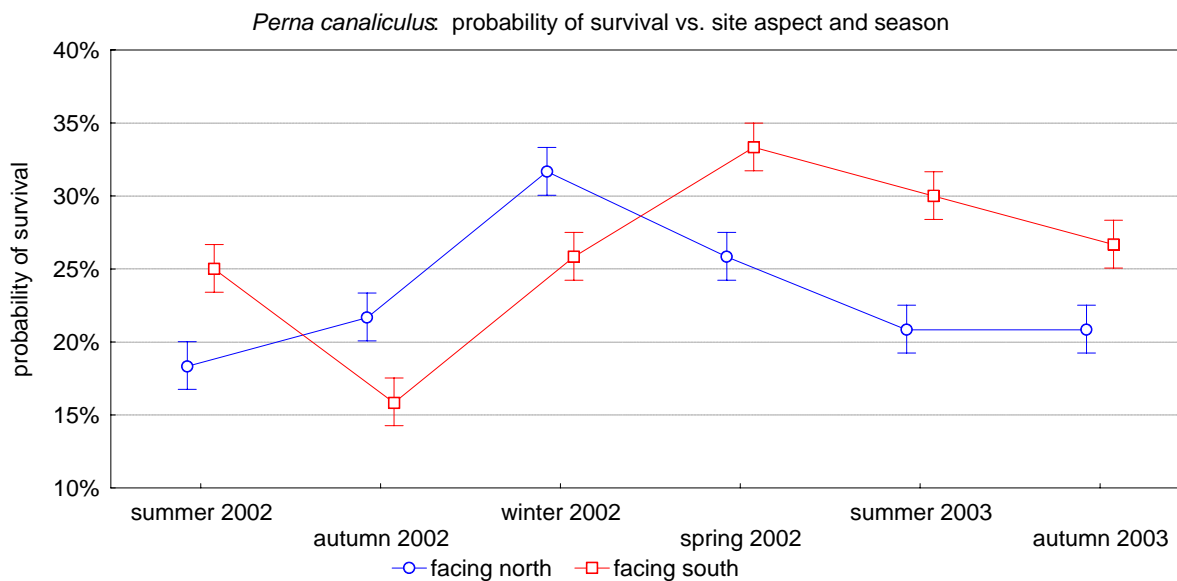


Figure 5. 20. *Perna canaliculus*: probability of survival vs. site aspect and season. Points represent mean values with 0.95 confidence interval error bars.

Table 5.9. *Perna canaliculus*: Logistic regression results

Factor	df	Wald statistic	<i>p</i> -value
Tidal height	5	208.3630	<0.0001
SL (covariate)	1	88.7493	<0.0001
Season	5	20.8406	<0.0001
Site (north or south)	1	15.3008	<0.001

Solar radiation data provided by Greater Wellington, Environment Division displayed a seasonal trend, in which Wellington Harbour receives more solar radiation in summer than in winter (Fig. 5.20).

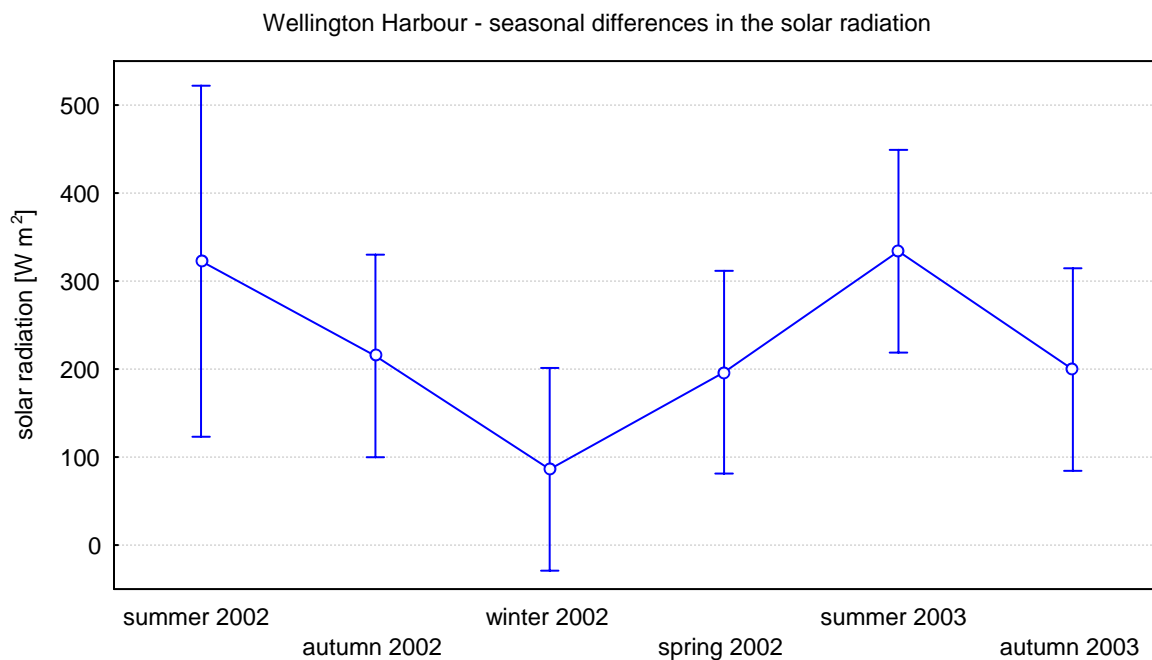


Figure 5.21. Seasonal differences in solar radiation for Wellington Harbour. Points represent mean values with 0.95 confidence interval error bars.

5.4. Discussion

Effects of wave forces and desiccation are the two physical factors generally held most responsible for generating horizontal and vertical zonation of mussels, thus structuring rocky intertidal shores (Dayton, 1971; Price, 1982; Underwood *et al.*, 1983, Bustamante *et al.*, 1997). Results from the two experiments described in this chapter

show that the three mussel species from Wellington Harbour can respond and adapt to varying environmental conditions of wave action and desiccation stress.

Wave exposure

Mussel SoA investigated in the present study varied mostly according to mussel size and species. Larger mussels had greater SoA, with *P. canaliculus* having consistently highest SoA and *A. maoriana* lowest SoA, with *M. galloprovincialis* having intermediate SoA values (Fig. 5.6). Seasonal and spatial variation was also pronounced, with SoA increasing in winter-spring seasons (most likely a result of greater frequency of storms and stronger waves in winter, forcing mussels to increase their attachment) and being generally higher at south-exposed sites. Differences in SoA detected in the present study among the three mussel species in Wellington Harbour can be regarded as a proof of interspecific competition, because individuals of the species with better attachment to the substrate can withstand greater wave pressures and associated water velocities, thus surviving in the colony and contributing more to the next generation. Similar species-specific variation in SoA was reported by Gardner & Skibinski (1991), who compared SoA of two mytilid species in SW England. The authors reported that *M. galloprovincialis* had higher SoA than *M. edulis*, and concluded that physical factors can act selectively on mussels, depending on their size.

Results from the present study partly reflect findings reported in other studies regarding the relationship between shell size, strength of attachment and degree of exposure to wave action. In all three mussel species investigated here, shell length was significantly and positively correlated with the strength of attachment, and greater strength of attachment was found on south-facing shores (Figs. 5.7, 5.9 and 5.11). This suggests that mussels growing on south-exposed shores experienced greater forces of hydrodynamic drag and lift, therefore required greater strength of attachment to the substrate, otherwise they were at risk of dislodgement by waves.

In Wellington, although prevailing winds are the northerlies that blow for roughly twice as much time as southerlies, southerly winds are stronger, and generate more

powerful waves (McConchie *et al.*, 2000). Thus, the wave exposure is greater on south-facing sites and the results of the analyses of mussel strength of attachment support this. In *A. maoriana* examined in the present study, SoA was statistically higher at south-facing sites, but upon the inspection of Fig. 5.7 it becomes clear that the site aspect-specific differences were not large. *M. galloprovincialis* also had higher SoA on south-facing shores (Fig. 5.9), while SoA of *P. canaliculus* was significantly greater at north-facing sites (Fig. 5.11). The relationship between mussel SL and the site aspect followed this pattern in *M. galloprovincialis*, i.e. mussels with greater SoA were larger and they were predominantly found at south-facing sites (Fig. 5.10). However, this pattern appeared to be uncoupled in *A. maoriana*, where SoA was greater on south-exposed shores but larger mussels were found on north-exposed shores (Fig. 5.8). In *P. canaliculus* (Fig. 5.12) greater SoA was found on north-exposed shores and so SL of this species was greater at sites facing north, which is clearly at odds with the fact that in Wellington Harbour mussels are more exposed to waves on south-facing shores. A possible explanation of this contradiction comes from Hammond & Griffiths (2004), who point out that under high wave exposure mussel size can be reduced and growth can be slower, due to reduced food intake in conditions of heavy wave action, when shell remains closed for long periods of time. Harger (1970) and Raubenheimer & Cook (1990) also agree that mussel size is influenced by wave exposure, but argue that at sites with greater wave action hydrodynamic forces of drag and lift control mussel shell length. As a result, at such sites mussels can have reduced size due to greater energy resources being allocated to byssus production and remaining attached to the substrate. Similar result has been reported by Alvarado & Castilla (1996) from Chile where larger mussels *Perumytilus purpuratus* were found at sites of decreasing exposure to waves. In that study, the differences in shell size apparently resulted from varying wave exposures, while temporal differences were due to changes in the number of recruits entering the population. This would confirm the initial assumption that in Wellington Harbour a variable wave exposure is present, associated with both northerly and southerly winds.

Further, the relationship between shell size and wave exposure can be confounded by juvenile recruitment altering the mean shell size at both north- and south-facing sites.

For mussels, the influence of wave action on their ecology starts as early as the larval stage. While having little control over nature of habitat on which they establish themselves, mussel larvae can respond and adapt to changing degrees of wave action. Larvae with thick shells, settling in a sheltered habitat would be disadvantaged, as they would expend unnecessarily more energy on the shell production providing them with protection from strong waves, while larvae with thin shells would not be protected well enough to withstand destructive forces of waves at exposed sites (Raubenheimer & Cook, 1990).

During conditions of strong wave action, mussels cease to feed and grow, and the mantle edge is slightly withdrawn into the shell, thus delaying the accretionary growth at the shell margin. However, areas of strong wave action and water flow can be rich in dissolved calcium coming from calcium-rich marine debris, which stimulates shell growth, unlike sheltered areas, where the reduced concentration of dissolved calcium will result in smaller shells (Seed, 1969; Raubenheimer & Cook 1990). On the other hand, Bustamante & Branch (1996) and Freitas *et al.* (1999) support the “greater wave exposure = greater body size” hypothesis and argue that strong wave action can potentially enhance the quantity and turnover of food particles for filter-feeders, providing the bivalves living in wave-exposed locations with the benefit of more nourishment and energy to stay attached to their substrate, unlike bivalves from sheltered sites). However, the authors predict that wave exposure cannot benefit mussels indefinitely, as at some stage the animals will start to expend considerably more energy to remain attached to the surface if wave action becomes extremely strong, leading to reduced energetic input into somatic and gonadal growth. This polynomial relationship between mussel size and wave exposure has been described for *M. galloprovincialis* in South Africa (Hammond & Griffiths, 2004), where the invasive mussel experienced the highest percent cover, mean length, biomass and mussel bed depth at intermediate wave exposure conditions. In conditions of shelter from waves and in extreme wave exposure the above ecological parameters declined, suggesting reduced bivalve growth under extreme wave exposure, where the animals apparently were channeling more resources to the byssus production in order to stay attached to the substrate. In sheltered areas, the

food supply was reduced, resulting in smaller mussels, while in extremely exposed sites mussels would partly close the valves of their shells to reduce the effects of too strong wave pounding, which also lead to reduced food intake and eventually to smaller mussels. However, Hammond & Griffiths (2004) note that reduced size of mussels found at extremely exposed sites might result from larger mussels being dislodged by strong waves, thus altering the size distribution at those sites.

Desiccation

Tidal cycles have profound consequences for the distribution, abundance and interactions among intertidal organisms, of which many are sessile and sedentary, and therefore unable to change their position on the rocky substrate in relation to the tidal level (Denny & Paine, 1998). From the ecological perspective, the emersion time is of particular importance, as intertidal invertebrates are exposed to stressful aerial temperatures and breaks in feeding, and the duration of such periods directly influences the level of stressful conditions the animals have to withstand. A relationship between the height on the shore and subsequent survival of intertidal community members, with greater mortality of invertebrate and algal species observed higher on the shore points directly at the effects of desiccation (Menconi *et al.*, 1999; Helmuth, 2002). With longer breaks in feeding activity, sessile invertebrates, such as mussels, can suffer slower growth and reduced size. Further, mussels that are present higher on shore experience less thermal relief from water spray generated by waves lower on the shore, and thus suffer thermal damage to their tissues (McQuaid *et al.*, 2000).

The survivorship of the three mussel species investigated here depended significantly on the shell size of the animals, treatment (i.e. shore level), season, and site aspect (facing north or south) (Table 5.5). In all three species, an inverse relationship was found between shell length of mussels and their survival, which indicates that smaller mussels were able to cope with desiccation. The reason for this most likely lies in the fact that larger mussels have to utilize more energy to meet the demand of metabolic costs of the heat protection mechanisms and anaerobic respiration. Also, in larger mussels, the

concentration of anaerobic end-products is greater, further adding to the stress the animal experiences. A similar inverse relationship between rates of desiccation and size of surviving mussels was also reported by Kennedy (1976). In that study, the success in colonizing higher intertidal ranges and air-exposed intertidal habitats was related to the ability of small mussels to tolerate desiccation, especially in hot, windy weather. However, the author notes that small mussels are susceptible to desiccation and can often be found in a mussel clump buffered by larger individuals. It is possible, therefore, that small mussels are able to cope with desiccation at higher shore levels (as this study has shown), but only in the presence of buffering larger individuals. However, the reason why larger mussels did not cope with desiccation stress in the present study remains unclear and requires further investigation.

In all species examined in this study, mussels survived better on the south-facing side at Front Lead and the LD₅₀ values demonstrate that (Figs. 5.15, 5.17 and 5.19). *P. canaliculus* has been shown as the most vulnerable species, with very few mussels able to cope with exposure to air. *M. galloprovincialis* and *A. maoriana* displayed better ability to withstand desiccation stress, with *M. galloprovincialis* LD₅₀ values slightly higher than those of *A. maoriana*. This confirms the distribution patterns of these mussel species observed *in situ*, where *P. canaliculus* typically is limited to the lower intertidal range, while *A. maoriana* individuals can often be seen inside *M. galloprovincialis* clumps at higher shore levels, where they benefit from the conditions of higher moisture and are buffered by *M. galloprovincialis* individuals from desiccation stress.

Mussels have been described as ectotherms, i.e. organisms for which body temperature is determined by external conditions, and during aerial exposure it is driven by numerous climatic factors, such as visible solar radiation, infrared radiation, wind speed, cloud cover and air and ground temperatures (Helmuth, 1999, 2002). During aerial exposure, the body temperature in mussels increases to the point when intracellular proteins are damaged, putting the animal at risk of heat shock and potential death. However, if given time, mussels can adapt to these conditions (Viarengo *et al.*, 1995). Heat stress proteins (hsp) play an important role in thermal acclimation in mussels. The

main function of hsp is to prevent the accumulation of heat-denatured intracellular proteins during the thermal stress and, to a degree, reversing the thermal damage by stabilizing and re-folding already thermally denatured proteins (Gosling, 2003). Trapping a small amount of water inside the closed shell is another adaptive mechanism that helps mussels to cool down and withstand aerial exposure. However, this leads to a severely reduced oxygen uptake (down to as low as 4-17% of the aquatic rate) and a build-up of oxygen debt, which, if prolonged, can also put the mussel's survival at risk. Subsequently, anaerobic end-products, such as alanine, succinate and propionate, can accumulate in mussel tissues, (Widdows *et al.*, 1979). These processes of maintaining the protein pool and temporal cooling with the trapped amount of water inside closed valves come with a metabolic cost. From an ecological perspective, this cost directly affects the mussel physiology, and determines whether particular species of mussels can survive and reproduce in a particular habitat. Thus, this metabolic cost acts as a powerful force in mussel habitat selection (Hofmann & Somero, 1995; Helmuth & Hofmann, 2001).

Often, the survivorship of intertidal mussels fluctuates seasonally, depending on the aerial temperatures, and it increases in colder months, presumably due to increased proportion of cloudy days when the amount of direct sunlight is reduced, and greater spray coming from wave action, generated by more frequent storms. Season was also a significant factor affecting the probability of mussel survival in this study. All three species survived better in cooler seasons, most probably a result of higher storm frequency, greater spray and cloud cover reducing direct solar radiation. Both *A. maoriana* and *M. galloprovincialis* survived in greater numbers in autumn 2002 and autumn 2003 (Figures 5.16, 5.18), while *P. canaliculus* experienced greater survival in winter and spring 2002 (Fig. 5.20). A similar seasonality of desiccation effects and subsequent mussel survivorship at different shore levels has been reported for *M. trossulus* (Hofmann & Somero, 1995), *M. edulis* (Tsuchiya, 1983) and *P. canaliculus* (Marsden & Weatherhead, 1998).

In the southern hemisphere, intertidal communities experience more solar radiation throughout the year on the north-facing shores, while on the south-facing shores

solar radiation is less intense. As a result, desiccation-induced stress is more severe in invertebrate communities facing north, while these communities that are south-exposed exist in less stressful conditions. The conditions of heat exposure and water loss are closely related to warmer seasons, when the amount of direct solar radiation is greater. Therefore, one would expect mussels growing on the north-exposed shores to suffer more from heat exposure and water loss and die sooner than their conspecifics on the south-facing shores. This effect is more pronounced in summer than in winter when the cloud cover is greater and the amount of direct solar radiation is reduced. Results obtained in the present study appear to follow this pattern, as mussels placed on the southern site of Front Lead coped with desiccation better than mussels placed on the north-facing side, and subsequently survived in greater numbers. Moreover, the examination of season-specific mussel survival (Figs. 5.16, 5.18 and 5.20) in the light of the seasonal solar radiation in Wellington Harbour (Fig. 5.20) confirms the importance of the solar radiation received by intertidal communities and its role in structuring mussel survival.

In summary, intertidal mussel communities examined in this chapter were shown as greatly dependent on the interplay of wave action and aerial exposure (i.e. desiccation stress). These factors have been described as two crucial agents determining the community structure, species presence, abundance and distribution (Young, 1983; Eckman & Duggins, 1993; Carrington & Denny, 1994; Schiel, 2004). Results from the present study also point at wave action and desiccation as selective forces regulating the mussel communities. Wave-induced stress can significantly influence mussel strength of attachment, thus altering biological activities and influence composition of rocky intertidal communities (Palumbi, 1984; Hammond & Griffiths, 2004). Structure and zonation of mussel populations also depends on shore height and associated emersion stress. From the ecological perspective, mussels were shown as able to compete for space on the rocky substrate through better ability of some species to withstand exposure to waves and air and thus exclude other, less tolerant species (for example *M. galloprovincialis* vs. *P. canaliculus*). Mussel sizes can decrease at higher shore levels due to temperature extremes and desiccation, and associated high metabolic costs of

persisting at such heights, while the effects of wave exposure are visible lower on the shore and disappear at higher levels. This interplay of physical factors indicates that effects of desiccation override the effects of wave exposure towards the top of the intertidal zone and thus are vital in creating zones of invertebrates in rocky intertidal communities (McQuaid *et al.*, 2000).

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CHAPTER SIX: ROCKY INTERTIDAL COMMUNITY ORGANIZATION

6.1. Community organization model

Marine ecology is the scientific study of marine organisms under the influence of processes that determine their distribution and abundance, the transfer of energy and matter between the organisms and their environment, and the interactions of those organisms among themselves (Lawton, 1994). From this perspective, rocky intertidal communities have long been of widespread interest to ecologists and have often served as model systems for the development of community theory (Connell, 1961; Luckens, 1970; Griffiths & Hockey, 1987; Tokeshi & Romero, 1995). The structure and development of rocky intertidal communities, including Wellington Harbour mussel communities, can be described in terms of combined biotic and abiotic effects. In the present study, both the biotic effects of predation, grazing, inter- and intraspecific competition, and the abiotic effects of desiccation and wave exposure, such as unpredictable weather conditions or floating logs creating patches of bare substrate, were shown as important for the development of the intertidal communities.

A gradient of environmental factors present in Wellington Harbour (see chapter 2) is a result of the general north-south orientation of the Harbour. This gradient impacts intertidal mussel communities (i.e. the prevailing wind direction is from the northwest, and the amount of direct solar illumination is greater on the north-facing shores, which implies greater exposure to desiccation on the north-facing shores, whereas the degree of wave exposure is greater on the south-facing shores). Mussel populations can respond to these forces. This was seen, for example, in the spatial variability of mussel strength of attachment to the rocky substrate, which was generally greater on the south-facing sites because of greater forces of hydrodynamic drag and lift associated with greater wave action that mussels at those sites have to withstand. Although no physiological responses of mussels to desiccation were investigated in this study, it is possible that individuals exposed to severe desiccation had a greater concentration of the heat-shock protein (hsp)

in their tissues, thus increasing the energetic costs associated with the hsp synthesis and ultimately the probability of mortality (Somero, 2002).

During the course of this study, water column parameters were revealed as significant bottom-up factors, important for biochemical cycles of mussel condition, gonad mass and spawning in adults, as well as settlement and recruitment of larval mussel stages. Mussels from the inner areas of the Harbour have greater condition index, gonad mass and were generally larger. A link exists between mussel condition and their strength of attachment, as these two characteristics displayed similar seasonal variation. This was particularly noticeable in spring 2002 and 2003, when increased strength of mussel attachment accompanied a simultaneous decrease in condition. This can be a plastic response of mussels to environmental cues, associated with higher frequency of stormy weather in winter, which stimulated byssus production, or a sign of the energetic trade-off between costs associated with gametogenesis in mussels and their strength of attachment. In the latter case, the balance associated with the allocation of energetic resources to mussel tissues is upset, as more resources are allocated to survival of the animals on the substrate (i.e. byssus production). However, Carrington (2002) suggests that the seasonal shift in allocation of energy in mussels takes place regardless of the environmental factors and benefits gametogenesis rather than the strength of attachment.

The caging experiment conducted in the intertidal zone demonstrated that the time needed for the communities to return to their original state and to recover from physical disturbance varies significantly. Communities near the Harbour entrance (i.e. at Seatoun) require significantly more time to recover, whereas communities inside the Harbour (i.e. at Evans Bay) recover faster. Simultaneously, intraspecific competition and competitive exclusion among algae, barnacles and mussels were most prominent at Evans Bay, which further suggests that the conditions for development of the intertidal communities are better in the inner areas of Wellington Harbour.

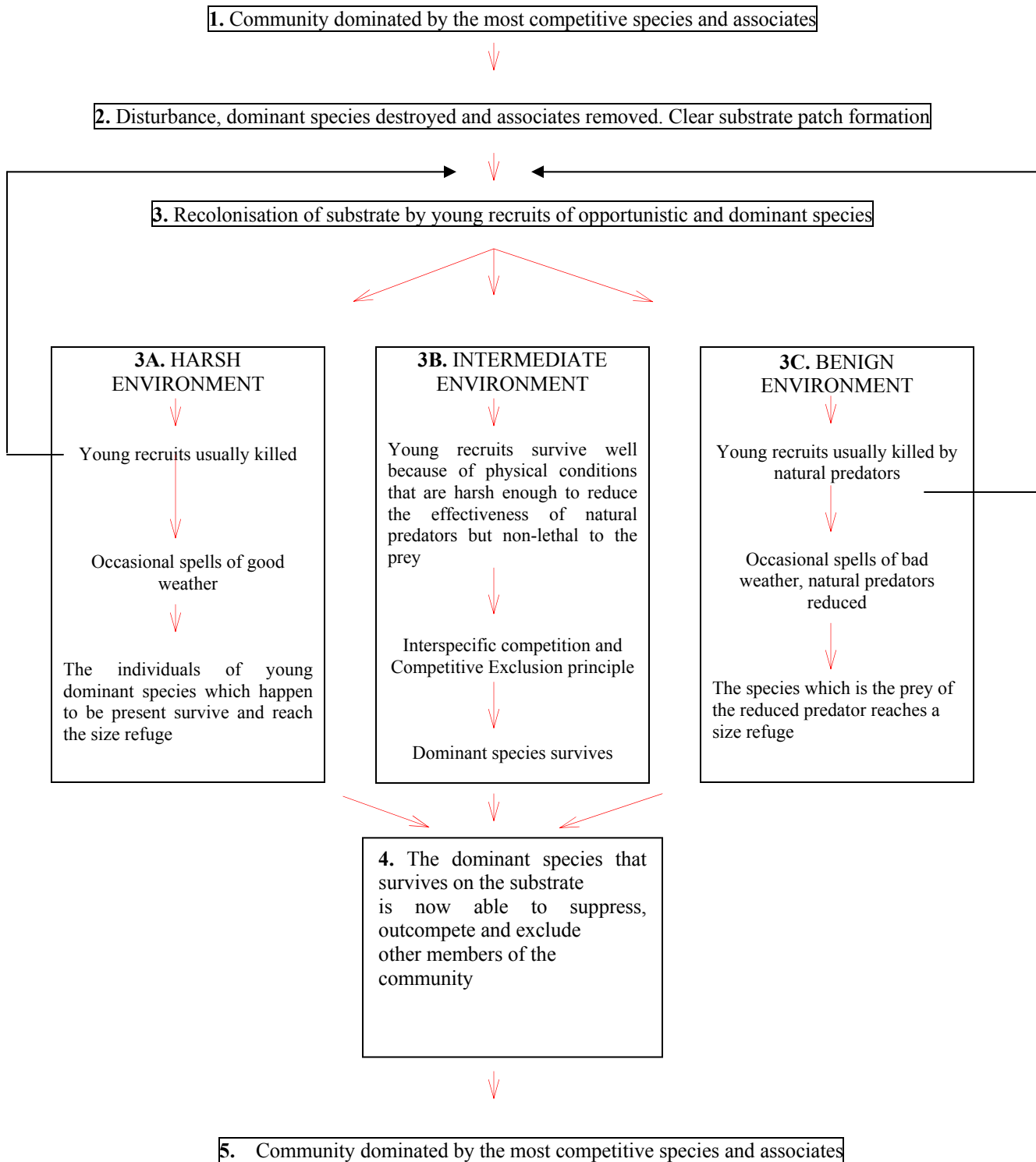


Fig. 6.1. A community development model with mechanisms showing the competitive dominance exclusion (adapted from Connell, 1975).

Following Connell (1975), a community development model, in which a community is gradually taken over by a competitively dominant species following substrate clearance, can be therefore proposed for Wellington Harbour rocky intertidal system. Mussel communities investigated in the present study are clearly dominated by the blue mussel *Mytilus galloprovincialis*, the most resilient and competitive species, displaying a plastic response to the variability of the environmental parameters. In the model, gradients of physical conditions are the factors of primary importance for community development. The present study demonstrates that environmental regimes in Wellington Harbour are significant factors for mussel communities, and that they vary from relatively sheltered and benign to exposed. These include a hydrological regime, wave exposure regime and desiccation regime.

In harsh conditions, for example in the upper intertidal ranges exposed to severe desiccation, or in areas with strong wave action or abrasion, many recruits cannot survive or become established. As a result, large proportions of the previously cleared substrate are continuously colonised and vacated. Firm establishment of a recruiting species is possible only after a spell of favourable weather. Thus, the resulting populations are dominated by only the most resilient and competitive species, often unchecked by its natural predators, also unable to withstand the harshness of the environment (Menge, 1976; Menge & Sutherland, 1987) (steps 3 – 3A, Fig. 6.1). In the present study, Seatoun and Kau Point were the two sites with harsh environmental conditions; in particular in terms of abrasion and the exposure to wave action, unlike Evans Bay, where the local intertidal communities are sheltered from destructive, high-energy southerly swells. Consequently, mussel communities at all those sites respond differently, according to those environmental regimes: while the available substrate was quickly utilized at Evans Bay, large proportions of the cleared substrate was still unoccupied at Seatoun and Kau Point after 24 months of the experiment. *Mytilus galloprovincialis* was shown as the mussel species most able to establish itself and cope with the adverse conditions, while other mussel species, *Aulacomya maoriana* and *Perna canaliculus*, were not common.

When the environmental conditions are benign, competition among colonizing species is reduced due to the influence of predators, now more effective in controlling their prey and preventing the young dominants from growing to invulnerable size. Unless the environmental conditions and the degree of harshness are suddenly altered by an unpredictable situation, such as a short spell of bad weather, or an attack of natural enemies or parasites, this prey-predator balance becomes altered and allows the dominant species to escape competition, grow to invulnerable size and exclude other species from the community. Effectively, the community returns to its original state, where it is colonised by the dominant species and associated species living in its shelter, such as highly diverse mussel bed sub-communities consisting of structurally complex matrix of numerous plant and invertebrate species, layers of accumulated sediment, and mussel shells (Suchanek, 1992) (steps 3 – 3C, Fig. 6.1). Evans Bay was the only site investigated in this study with relatively benign conditions (see above). Although no predators were documented in the digital photographs taken regularly at this site, whelk activity was often noticed at Evans Bay on other occasions. However, the most common mussel species colonizing substrate at Evans Bay, *Mytilus galloprovincialis*, did not appear vulnerable to whelk predation. The fact that this species, followed mainly by *Aulacomya maoriana*, was the quickest to utilize the cleared substrate most likely was once again a result of its competitiveness and adaptability. At the sites with adverse environmental conditions (Seatoun and Kau Point) the blue mussel was the most common coloniser because it was the only species that could withstand those conditions, while at the benign site (Evans Bay) the blue mussel was the most common coloniser because it was also the quickest coloniser, outcompeting the other two species in the substrate utilization.

In intermediate environmental conditions, the mortality of recruits is lower and their natural enemies are less effective, which gives the young recruits a chance to persist and escape being consumed. As a result, these young individuals are able to reach high population densities and start competing with one another for space (Menge & Olson, 1990). This process of interspecific competition will eventually result in one dominant species occupying the whole available substrate. Thus, the community returns to the original state in which it is dominated by one species and its associates (steps 3 – 3B, Fig.

6.1). None of the sites investigated in the present study would fit the “intermediate environmental conditions” description from Connell’s model because in Wellington Harbour such a site would need to be sheltered from the northerly and southerly exposure (which is not the case). Nevertheless, the fact that all rocky intertidal communities in Wellington Harbour are dominated by just one species, the blue mussel *Mytilus galloprovincialis*, strongly suggests that the model is valid in this system. Further, as shown in this study, the blue mussel becomes the dominant species through constant competition with other community members and through their exclusion. Such state seems to be further fuelled by the water column parameters (see chapter 2), shown to be consistently elevated at Evans Bay but somewhat reduced and highly variable at Seatoun.

Shore aspect needs to be incorporated in the community development model, because it is important for the substrate recolonisation and often determines which species will succeed in claiming the available area. Predators are often unable to cope with desiccation and are more abundant in the lower intertidal zone. Some of them, such as starfish, are large and can consume significant quantities of invertebrate prey competing for space with algae (Menge, 1972). Thus, algae are favoured in the low intertidal range, as their competitors and enemies are reduced. This is consistent with the universal scheme of intertidal shores proposed by Stephenson & Stephenson (1949), where plants, rather than invertebrates, dominate the sublittoral fringe. On the other hand, large predators are less common at higher shore levels and are often replaced there by muricid and naticid snails preying heavily on sedentary and sessile prey, such as mussels. Grazing mollusks, such as limpets, are less controlled by whelks, so they are less likely to be reduced to the levels found lower on the shore. This situation results in the mid-intertidal rocky communities that consist of mixed groups of invertebrate and algal species occupying the substrate.

Similarly, oceanographic conditions and mechanisms responsible for delivering the propagules have impact on the composition of rocky intertidal communities (Henschel *et al.*, 1990). The supply of propagules is a crucial limiting factor, which depends on exposure to waves and the variable ability of intertidal organisms to tolerate

wave action, along with the current physiological state of the community members. Therefore, if a population fluctuation is to be successfully forecast, models of community organization, such as the one described above, need to take into account the pelagic larval environment (Roberts, 1997; Guichard *et al.*, 2003).

Direct vs. indirect effects in intertidal community organization

Direct effects among species typically include two species (often two competing species) and involve an interaction in which the activity of one species will cause a change in the other species. Theoretically, this interaction would occur even if the interacting species were kept in isolation (Wootton, 2002). As the rocky intertidal communities change over space and time, in particular following severe disturbance, direct and indirect effects among recruiting species can be studied (Van Tamelen, 1987). In rocky intertidal systems, such as Wellington Harbour, succession often proceeds from small-bodied organisms to large-bodied ones. These display an early peak in diversity, which is then followed by a gradual decline in species number as more space within the community is claimed by the competitively dominant species, such as mussels. However, the dynamics of the early and mid-successional stages can be complex and variable, and many interactions between early and later-arriving sessile species can potentially alter the dynamics of later species (Berlow, 1997). In the present study, a number of direct effects were shown, including competitive exclusion of algae from bare substrate by barnacles, exclusion of barnacles by mussels, and mutual effects of percent cover among the three mussel species (as revealed by Multiple Regression in chapter four). Reduced condition in adult mussels as a consequence of being infested with pea crabs can also be treated as a direct effect of pea crabs on mussels.

Indirect effects among species, however, are usually more difficult to detect and often are discovered when experiments produce unexpected results, which indicates that longer experiments are required before indirect effects can be seen (Sih *et al.*, 1985; Menge, 1997). The interplay between two species can sometimes have an additional, indirect, effect on some other member of a community. Although indirect effects can

complicate interpretation of experimental outcomes, they are important from a management and conservation perspective, as the effects of species loss or environmental disturbance are difficult to predict, and therefore the implementation of management strategies can be problematic for ecological theory of community structure (Connell, 1983; Wootton, 1992, 2002; Underwood, 1999). In the present study, an indirect effect of mussel settlement facilitation among barnacles suppressing algae was detected. Through competitive exclusion of algae, barnacles thermally buffered mussel recruits and simultaneously provided them with the secondary substrate within the barnacle matrix.

The role of facilitation in the intertidal community organization

Direct and indirect effects in rocky intertidal community organization are closely linked with positive and negative effects among the community members. During the succession phase in rocky intertidal communities, three general ecological mechanisms can be identified (Connell & Slatyer, 1977): interspecific facilitation, inhibition and tolerance. Traditionally, facilitative interactions among species have been neglected, as ecological theory has emphasized the competitive and consumer processes instead, despite mounting evidence that positive interactions in aquatic ecosystems are widespread (Stone & Weisburd, 1992; Berlow, 1997; Bertness & Leonard, 1997; Callaway & Walker, 1997; Forde & Raimondi, 2004). Facilitation occurs when a species that already is residing in the developing community enhances the establishment of a new species, for example the facilitative effect of barnacles on mussel settlement found in Evans Bay (chapter four). Living in high-density clumps offers certain advantages, such as co-operative defence against natural enemies, where mussels inside clumps are protected from predation and desiccation, as well as being thermally buffered by surrounding individuals. This facilitative mechanism was observed in mixed-species mussel clumps of *M. galloprovincialis* and *A. maoriana* in Wellington Harbour in the present study (see chapter three). Similarly, juvenile algae or sessile invertebrates living in high-density assemblages in intertidal communities are also sheltered from predators, competitors and physical stress, such as wave exposure, through screening by adult conspecifics – a phenomenon also noticed in the present study. It therefore becomes clear

that groups of individuals are better able to tolerate stressful desiccation than solitary individuals, and so the vertical range of a species is established by the groups of organisms present at a given shore level, not by a single individual (Denny *et al.*, 1985; Bertness, 1989). Inhibition occurs when an established species depresses the recruitment of a newcomer, for example interaction between limpets and barnacles, and mussels and barnacles competing for space in the present study. Interspecific tolerance occurs when the establishment of a newly arriving species does not affect the species already resident in a community (Jernakoff, 1983; Van Tamelen, 1987).

In general, where environmental conditions are benign, competition and exclusion among algal and invertebrate guilds occur. However, when conditions become harsh and stressful, facilitation can take over. One possible explanation for this phenomenon is that in a benign, low intertidal habitat a single individual has greater chances of survival on its own and does not need to be facilitated, whereas it becomes very vulnerable in the harsh conditions of the upper intertidal zone. Therefore, a group of individuals might better withstand physiological stresses than a solitary organism through buffering one another. Thus, one could expect to find positive interspecific interactions in the harsh environmental conditions higher in the intertidal zone (Bertness & Leonard, 1997; Stachowicz, 2001). Stephens & Bertness (1991) report that in the benign conditions of the low intertidal zone and on hard substrate, mussels outcompete barnacles for space, but at the same time can facilitate barnacle survival by buffering them from disturbance and desiccation. Buschbaum (2000) reports that mussel shells can act as a secondary substratum for settling barnacle recruits. Similarly, mussel recruits have been known to require a facilitator already present on the substrate, such as a filamentous alga, barnacles or adult conspecifics, before they can successfully settle (Navarrete & Castilla, 1990).

According to current ecological theory, each species within an ecosystem occupies a fundamental niche, which can be described as the range of environmental conditions within which the species can persist, as long as negative interspecific interactions (i.e. competition, predation and parasitism) are absent (Nybakken, 2001).

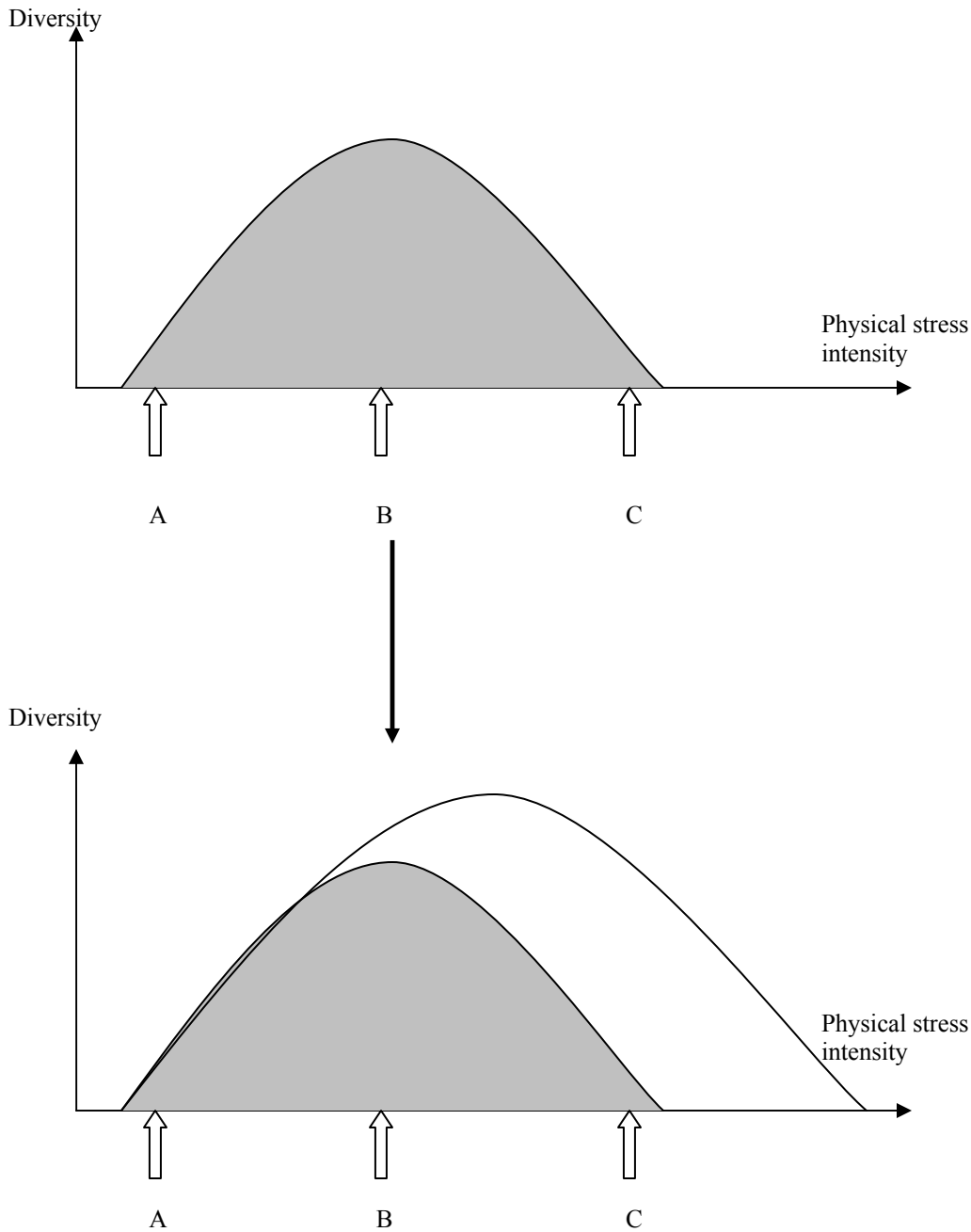


Fig. 6.2. Graphic representation of the incorporation of facilitation theory into community regulation theory. In the gray areas: community species diversity reaches a maximum under conditions of intermediate physical disturbance, mortality and stress from predation (**B**). Diversity decreases at low stress and disturbance due to a competitive dominant excluding other species from a community (**A**). the decrease of diversity in high-disturbance conditions results from the fact that only few species are able to withstand highly stressful conditions (**C**). When present, facilitation effects extend and heighten the community diversity curve (white area) through habitat amelioration in intermediate and high disturbance conditions (adapted from Hacker & Gaines, 1997).

Within this fundamental niche, a realized niche exists, within which the species can survive and utilize resources. There are, however, certain practical limitations on this. The realized niche is the restricted functional space that is actually available for the species after exclusion from the substrate by competitors and enemies. Taking into account the facilitation and habitat amelioration effects, it has to be understood that the realized niche becomes greater than the spatial range predicted by the fundamental niche, as the environmental conditions in which the facilitated species now exists are more benign than before facilitation occurred (Bruno *et al.*, 2003). Further, from the perspective of community diversity, positive interactions increase species diversity by facilitating species that normally would be unable to persist in that community, particularly where the community is exposed to high physical disturbance, stress or predation. Facilitative effects appear to be strongest under conditions of intermediate and high disturbance, as the species diversity in a community can be extended in such conditions (Hacker & Gaines, 1997). Thus, not only does facilitation increase the number of species in a community that are able to survive adverse conditions, but it also positively affects species co-existence through the reduction of competitive exclusion (Fig. 6.2).

Mussels as ecosystem engineers

Ecosystem engineering is common in mussel communities (Table 6.1). Despite the fact that not all effects of engineers are positive for the rest of community members, in general it enhances species diversity (Jones *et al.*, 1997). As ecosystem engineers, mussels physically alter, maintain and create habitat for other species (Jones *et al.*, 1994; Iwasaki, 1995; Seed, 1996). However, not all species can be regarded as ecosystem engineers. Lawton (1994) suggests that a species can become an ecosystem engineer if it has large *per capita* effects on the surrounding environment, lives in high density over large areas for long periods of time, and affects resource utilisation. Through their ability to dominate intertidal communities and exclude other community members, mussels establish high-density colonies that can spread over large parts of the rocky substrate, forming vertically continuous layers (Gosling, 2003). Such mussel communities are also

particularly important with regard to benthic-pelagic coupling because mussels are the major intertidal suspension feeders which link pelagic water column production (seston = particulate food) and benthic production (i.e. intertidal animal biomass).

Perhaps the best example of the ecosystem engineering activity of mussels is their ability to invade new habitats. For example, genera such as *Mytilus* and *Perna* have been described as being highly invasive. Originating from the Mediterranean, *M. galloprovincialis* is gradually taking over the intertidal shores in South Africa (Grant & Cherry, 1995; Branch & Steffani, 2004). Accidentally introduced, the Mediterranean mussel is now present in wild mussel populations along the west coast of South Africa and southern Namibia. This species has found a wide realized niche in which it displays high productivity and fast growth, with the presence of a planktotrophic larva, allowing it to colonise new habitats quickly.

Table 6.1. Examples of mussel marine ecosystem engineering activity (adapted from Jones *et al.*, 1994).

Organism	Habitat	Activity	Impact	Reference
Ribbed mussels <i>Geukensia demissa</i>	Rhode Island <i>Spartina</i> salt marsh	Secrete byssal threads and form dense mussel beds	Stabilize substrate, bind and protect sediment from erosion and disturbance	Bertness 1984
Mussels <i>Mytilus</i> <i>californianus</i>	Rocky intertidal shores in Pacific Northwest of North America	Form dense mussel beds and trap sediment	Stimulate development of rich infauna and provide secondary substrate	Suchanek, 1992
Mussels <i>Musculista</i> <i>senhousia</i>	Intertidal shores of the Mediterranean, Australasia and the Pacific North American coasts	Invade new habitats and form thick mussel mats	Alter infaunal diversity, inhibit the spread of seagrass <i>Zostera marina</i>	Crooks & Khim, 1999
Mussels <i>Brachidontes</i> <i>rodriguezii</i>	Temperate rocky intertidal shores of Argentina	Form dense mussel beds and trap sediment	Stimulate development of rich infauna and provide secondary substrate	Adami <i>et</i> <i>al.</i> , 2004
Mussels <i>Mytilus</i> <i>galloprovincialis</i> , <i>Aulacomya maoriana</i> and <i>Perna canaliculus</i>	Wellington Harbour rocky intertidal communities	Colonise new substrate, secrete byssal threads and form dense mussel beds	Exclude other community members, create secondary substrate and shelter associates from wave action, desiccation and predation	Present study

In addition, *M. galloprovincialis* in South Africa is relatively free from local predators, free from native parasites, and resilient to local ones. However, in New Zealand *M. galloprovincialis* is not regarded as an invader but is thought to be native (Hilbish *et al.*, 2000; Gardner, 2004). The brown mussel *Perna perna* has been successfully colonizing shores in the Gulf of Mexico, after it was introduced by international shipping, probably from Venezuela (Hicks & Tunnell, 1993; Hicks *et al.*, 2001). Under the environmental conditions prevailing in the Gulf of Mexico, this species also exhibits a high growth rate, reproductive effort and recruitment, with values similar to those recorded for endemic populations of this species. Living in dense aggregations, these mussels eventually dominate entire communities, a phenomenon reversible by a short term only through unpredictable and significant disturbance.

6.2. Open vs. closed intertidal populations

The development cycle in many marine animals includes a pelagic larval stage, which can be exported and dispersed by water currents away from the natal community. From this perspective, intertidal communities are often believed to be interconnected and able to produce a common larval “pool”, from which each community can potentially derive its recruits and to which it can contribute its own larvae (Warner & Cowen, 2002). In this state of community openness, recruitment is not linked to local production of larvae, and local community dynamics depend entirely on recruitment and post-recruitment mortality (Caley *et al.*, 1996). However, certain physical and biological factors can determine whether a community is an open or a closed one. Effects associated with water flow (e.g. flow variability, coastal complexity and site isolation), certain biological characteristics of adults (e.g. fecundity, spatial and temporal patterns of spawning, and patterns of larval release) and larval behaviour (e.g. pelagic larval duration, swimming ability and degree of advancement when hatching) can all result in retention or return to parental populations, thus further contributing to self-recruitment of communities (Sponaugle *et al.*, 2002; Largier, 2003).

Physical factors

Coastal complexity often interacts with the water flow and generates turbulent patterns of circulation, such as eddies, fronts and convergences (Wolanski & Hamner, 1988). At small spatial scales (1 to 10 km), the topography- and tidally-induced water circulation around prominent coastal features, such as reefs or headlands, has been found to enhance larval retention directly by increasing the water residence time of local larvae (Black *et al.*, 1991). This is particularly true for larvae with short pelagic periods (i.e. less than several days). For larvae with longer pelagic periods, however, this feature is likely to be less important because small-scale circulation patterns, such as eddies, often stop as soon as the tidal flow reverses (Black & Gay, 1987). At mesoscales (10 to 100 km), the effects of coastal complexity on larval retention become clearer, as numerous headlands and embayments can alter water circulation and create large eddies in the lee of the headlands, thus stimulating larval retention (Wing *et al.*, 1995, 1998). At larger spatial scales, currents can flow along coastlines uninterrupted, resulting in high potential for greater larval dispersal. Major currents meet only at a headland or cape, thus generating gyres and large eddies. In this situation, entire populations of aquatic organisms, and as a result their larvae, can be closed, thus possibly leading to self-seeding (Sponaugle *et al.* 2002). The more isolated a site, the more likely the chance that its population is maintained through self-recruitment, as it is unlikely that an isolated population would be supported by a distant source of larvae. For contiguous sites, some exchange of larvae would usually occur, resulting in increased recruitment subsidies and possibly no change in the locally derived numbers of larvae (Cowen *et al.*, 2000). Self-recruitment at such sites may be between 30 and 60% (Swearer *et al.*, 1999). However, the external sources of larvae and the processes of the larval input are very difficult to identify, and relevant studies are scarce, therefore at present we cannot generalize any further.

Biological factors

For a number of populations of the same species, adult fecundity can influence local self-recruitment, in particular when individual fecundity varies. Thus, larger

individuals will be able to contribute more offspring, which may return to the parental population. Offspring dispersal depends on temporal patterns of larval release by adults and physical conditions at the time the larvae enter the environment (Sponaugle *et al.*, 2002). Where there are greater numbers of offspring, zooplanktrophic predators can be swamped, which further contributes to the survival of marine larvae (Morgan, 1990). Pelagic larval duration, or the time a larva spends in the water column, is inversely related to the probability of that larva returning to its natal population (Sponaugle *et al.*, 2002). For example, larvae of mussels with a pelagic duration range between 2 and 4 weeks (Helson & Gardner, 2004) can be advected from the parental sites and exchanged with other populations. However, larvae with longer pelagic periods have the ability to respond actively to favourable and temporally variable environmental cues, which can greatly increase the chances of larval return to natal populations. Active larval behaviour also includes vertical positioning, horizontal swimming and sensory capabilities. In most coastal environments, the water flow is vertically stratified, which means that the benthic boundary layer moves more slowly than the layers above it (Sponaugle *et al.*, 2002). Invertebrate larvae may be able to exploit this phenomenon and remain in the local population by staying within the benthic boundary layer (Butman, 1987). Moreover, vertical migration of larvae may help to deliver them to suitable settlement habitats. Further, certain oceanographic mechanisms, such as eddies and gyres, can increase both concentrations of the chemical compounds (such as nutrients, proteins, manitol from algae, tannins from terrestrial plants, monosaccharides, amino acids and fatty acids) and environmental stimuli (such as salinity and temperature) to which larvae may become sensitive. Increased concentration of such stimuli makes them more easily detected by the larvae, and this would further increase the likelihood of local larval retention (Kingsford & Gray, 1996; Kingsford *et al.*, 2002). Unique local combinations of salinity and temperature in both horizontal and vertical planes are characteristic of riverine plumes, such as that frequently present in Wellington Harbour from the Hutt River (Mann & Lazier, 1996). For marine larvae, such steep gradients of salinity, turbidity and temperature in local freshwater runoffs, often combined with information on current direction and water source, could provide a powerful cue, possibly further attracting the larvae to the parental population (Barnett & Jahn, 1987). However, current knowledge of

how environmental cues stimulate larval concentration is fairly limited and mainly speculative, and more work remains to be done on this subject.

6.3. Wellington Harbour rocky intertidal mussel assemblages

In Wellington Harbour, mussel communities display diverse ecological traits, commonly stimulated by the physical characteristics of the water environment. As far the vertical distribution of the three intertidal mussel species is concerned, the present study shows that the greenshell mussel *P. canaliculus* cannot prosper in areas above the low-intertidal. This species is unable to withstand the harsher environmental conditions of the mid- and high-intertidal region, of which desiccation is probably the critical factor in determining the vertical distribution of this species on the rocky intertidal shore. *M. galloprovincialis* and *A. maoriana* are often found in mixed clumps, especially in the mid-intertidal. This is probably a result of the higher desiccation tolerance of both species. However, the fact that, of all three species, only *M. galloprovincialis* is found in the higher ranges of the intertidal zone suggests that this species is the most resilient. It also appears that *A. maoriana* additionally benefits from the shading and protection from heat provided by *M. galloprovincialis*, as it was frequently seen surrounded by individuals of *M. galloprovincialis*, where thermal buffering and moisture content are higher. However, the ability to colonise the higher intertidal ranges comes with a price. For *M. galloprovincialis* that is physiological in nature, as this species does not attain certain physiological indexes as high as the other two species. The condition index of *M. galloprovincialis* was considerably lower compared with the condition of *P. canaliculus* and *A. maoriana*, which had very similar values. In the case of *P. canaliculus*, the high condition index was most likely a direct result of living in the low-intertidal zone associated with higher food availability and feeding rates, as this species is immersed and therefore feeding for considerably longer periods of time. For *A. maoriana*, the benefit of being thermally buffered and therefore less exposed to *in situ* desiccation, as well as a possible small energetic costs associated with maintenance of a smaller body size, are probably important factors contributing to higher condition in this species.

The spatial and temporal variability in mussel condition detected in this study was accompanied by a similar variability in the numbers of larvae recruiting to experimental substrata. There was an inverse relationship between the condition of adult mussels and the concentration of recruits, as the increasing number of mussel larvae in the water column was reflected by a general decline in mussel condition. This phenomenon can be explained in terms of mussel physiology, stimulated by water temperature. As the water temperature gradually increases at the end of winter and in spring, more energy is allocated to gamete formation and gamete release. This means that fewer energetic resources are available for maintenance of somatic tissues. As a result, bodily stores of glycogen are depleted. This effectively becomes a stressful situation, leading to a decrease in the volume and weight of somatic tissues (Marsden & Weatherhead, 1999). The pattern of high larval concentration and low body condition is clearly reversed later in the seasonal cycle, when increasing condition values mark the end of the reproductive season. This is also the time when the glycogen resources of mussels are restored and body tissues are rebuilt, thus leading to increase in tissue weight.

Results obtained in this study, where warmer, more saline waters and higher chlorophyll *a* concentration systematically affect certain Harbour areas, suggest that the Harbour is not as homogeneous as previously thought. Further, the conspicuous and frequent plume, rich in organic particles entering the Harbour from the Hutt River significantly alters the environmental regimes as it travels south. Thus, it appears that the environmental parameters are of primary importance in intertidal communities, because they establish a framework on which species composition and diversity is created and perpetually maintained (McQuaid & Branch, 1984; Gosling, 2003; Rupp & Parsons, 2004).

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