Effects of small-scale water movement on the settlement and growth rates of the brown mussel *Perna perna*, on the south-east coast of South Africa

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By
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Abstract

The effects of small scale (cm) water movement on the settlement and growth rates of the brown mussel *Perna perna* were investigated on the south-east coast of South Africa (33°28′S, 27°10′E). L-shaped metal baffles attached to the substratum decreased the erosion rates of cement balls and it was concluded that the baffles decreased the water flow rate around cement balls. These L-shaped baffles were then used to decrease water flow rates around mussel patches and pot-scouring pads used as artificial substrata for the settlement of *P.perna* larvae. Anova indicated that settlement rate varied by date and site while decreased water flow rate significantly increased larval settlement ($p<0.05$), only on the site and day that had the overall highest number of settlers.

Mussels in the low zone had significantly higher growth rates than those in the high zone. Decreased water flow rate significantly increased mussel growth rate in the lower zone (Anova, $p<0.05$), while it did not have a significant effect on the mussel in the high zone. Thus water flow manipulation increased growth rates in the zone, which already had high growth rate.

It was concluded that small-scale (cm) water flow patterns have an effect on both *Perna perna* settlement and growth rates, but only under specific conditions. Larval settlement rate was significantly increased by water flow manipulation on the site and day that had the highest number of settlers. Growth rates were significantly increased by decreased water flow rate only in the low zone, where growth rates are the highest. Although water flow was manipulated in both zones its effect in the high zone was insignificant (Anova) compared to other factors affecting growth rates at this tidal level.

Declaration

This dissertation is my own unaided work and is being submitted for the Master of Science in the Zoology and Entomology Department, Grahamstown. It has not been submitted in whole or in part for any degree or examination in any other university.

Tendamudzimu Titus Mathagu

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Chapter 1

General introduction

Bivalves are a very diverse group some of which have high economic or ecological importance (Seed, 1980; Seed *et al*, 2000). Mussels play a significant role in shaping intertidal communities. Mussels form a large proportion of filter feeder standing stocks and consume phytoplankton and detritus from the near shore water column, supplementing energy input into both the inter- and subtidal systems (McQuaid *et al*, 2000).

Mussels serve as food for birds, for example black oystercatchers, which completely rely on the shoreline for survival (Hockey and Underhill, 1983; Andres, 1998), starfish (Seed, 1993; Sommer *et al*, 1999; Saier, 2001), crabs, fish and mammals (Seed, 1993). An analysis of stomach contents and lair middens showed that *Perna perna* was the dominant food organism of the octopus *Octopus vulgaris* Cuvier, inhabiting sublittorial reefs off the east coast of South Africa (Smale and Buchan, 1981). This octopus preys on small mussels by simply pulling them open, while it drills and then opens the larger ones (McQuaid, 1994). By serving as food for both land-based and sea-based organisms, mussels act as a link between marine and terrestrial food webs (McQuaid *et al*, 2000).

Dense mussel beds can drastically modify local environments by providing a complex physical habitat (Jacobi, 1987; Seed, 2000; Lawrie and McQuaid, 2001). Mussel beds also act as bio-stabilizers and modify their environments by reducing tidal currents, wave action and sediment resuspension. The reduction of tidal currents leads to the reduction of sediment resuspension, leading to decreased turbidity and increased sunlight penetration (Widdows and Brinsley, 2002).

In low motion water, with high sediment deposition, gastropods and polychaets are found in the mussel beds. Both byssus threads and bivalve shells provide substrata for sessile and nesting invertebrates. Crustaceans, particularly amphipods are found associated with mussel beds regardless of the water flow rates (Jacobi, 1987).

Dense mussel beds can enhance biodeposition thereby increasing species richness (Jacobi, 1987). On the other hand, if mussels become a dominant species on the shoreline, they can potentially monopolize resources such as space and food for other epibenthic communities, resulting in a reduction in diversity (Seed, 2000).

Twenty-seven mussel species have been recorded on the south coast of southern African (Kilburn and Rippey, 1982). Of these, only four species are abundant in southern Africa namely: *Aulacomya ater, Choromytilus meridionalis*, *Mytilus galloprovincialis* and *Perna perna* (van Erkom Schurink and Griffiths, 1990; 1993). *A. ater*, *C. meridionalis* and *M. galloprovincialis* are mainly found in the cool upwelled waters of the west coast (van Erkom Schurink and Griffiths, 1990). The brown mussel *Perna perna* is more abundant on the warmer south and east coast (van Erkom Schurink and Griffiths, 1990; Grant *et al*, 1992).

Mussels of the genus *Perna* have been the subject of much research because of their economic importance in different parts of the world (Shafee, 1992). For example *Perna perna* contributes 39% of the total standing stock of intertidal mussels in southern Africa (van Erkom Schurink and Griffiths, 1990). *P.perna* is abundant from the Cape of Good Hope to Mozambique, and northwards from Namibia. Lack of strong surf limits *P.perna* distribution north of Mozambique. On the west coast of South Africa, north of the Cape Peninsula it is limited by the cold waters of the Benguela Upwelling System (Grant *et al*, 1992). *P. perna* appears again in small numbers at Lüderitz, Namibia, 1000km from the Cape of Good Hope and becomes more abundant at Walvis Bay and in the tropical waters to the North (Grant *et al*, 1992). *P.perna* is the predominant mussel species in the sub-tropical and warm temperate south and east coastal regions of South Africa (van Erkom Schurink and Griffiths, 1990).

Shellfish harvesting has been a tradition among the coastal inhabitants of southern Africa for centuries (van Erkom Schurink and Griffiths, 1990; Hockey and Bosman, 1986). Although there is an abundance of mussels on the south and west coasts of South Africa, there is minimal exploitation. This is because these areas have low human populations and mussels are not part of their main diet. There are also risks involved in mussel collection, including paralytic shellfish poisoning (van Erkom Schurink and Griffiths, 1990).

In contrast, shellfish harvesting is prevalent among the indigenous people on the east coast of southern Africa. The harvesters collect mainly for food, medicinal use and recreation (Hockey and Bosman, 1986; Hockey *et al*, 1988; Lasiak, 1991a; 1991b; Kyle *et al*, 1997; Tomalin and Kyle, 1998). Harvesting is mainly done by women and children who come down from their settlements during spring low tides, to collect shellfish from the intertidal zone (Hockey and Bosman, 1986; Kyle *et al.*, 1997). In the harvesters' collections *P.perna,* the abalone *Haliotis spadicea,* the turban shell *Turbo sarmaticus* together with various patellid limpets, are the preferred species, with *P.perna* forming 80% of the total collection (Lasiak, 1991a; Fielding *et al*, 1994).

P. perna alone was found to contribute 16% of the annual protein requirements of harvesters and supplements a diet that is mainly based on maize (Siegfried *et al.*, 1985; Hockey and Bosman, 1986). High exploitation pressure in this area led to a reduction in size and density of *P. perna* between 1978 and 1984. The decrease in *P.perna* availability and the increased search effort needed to find mussels resulted in harvesters turning to less preferred longer-lived species. The number of mussels found in the harvesters' collections dropped from 92% in 1978 to 57% in 1984, while the number of limpets in the collections increased from 7% to 37% during same period. The shift to longer lived species can lead to complete destruction of the shores which are the source of much needed food for the local people as the harvesters will indiscriminately collect any organisms they can find on the shores leaving only bare rocks and inedible species (Siegfried *et al.*, 1985).

Perna perna and the limpet *Patella oculus* appear to be the two species that could be susceptible to depletion in the Transkei area (Lasiak, 1991b). Lasiak and Dye (1989) observed a delay in re-establishment of brown mussels on the south-east coast of South Africa. This delay together with low productivity led to the conclusion that it was not only over-exploitation that was a problem in these areas (Lasiak and Dye, 1989), although other factors such as pollution are insignificant in shaping these mussel communities (Watling and Watling, 1979).

Humans are selective tool-using predators. This tool-using skill makes it impossible for any intertidal organisms to escape from shellfish harvesters, resulting in complete predation imbalance (Hockey *et al*, 1988). There are also natural processes like strong wave action and sand scouring during heavy storms, that occasionally cause mass diebacks of intertidal organisms (Lambert and Steinke, 1986).

In most cases, algae replace *P.perna* on shores that have been overexploited. Mussel larvae seem to prefer settling on already existing mussel beds, rather than on other natural and artificial substrata. This means that mussel over-exploitation does not only decrease mussel reproductive output, but also removes the preferred settlement substratum (Dye *et al*, 1997).

Completely cleared shores show a delay of about 2 years before being re-colonized by sessile macro-invertebrates. It takes more than eight years for *P.perna* simply to re-appear on completely cleared shores and it does not become the dominant species on such shores (Lambert and Steinke, 1986; Dye *et al*, 1997).

Different workers have suggested different plans for mussel management. *P.perna* would be managed in a 14-month rotational cycle (Siegfried *et al*, 1985). This could be possible because *P.perna* has high productivity and turnover rates. Although there is over-exploitation, Lasiak (1991b) found no evidence of recruitment failure. More recently Harris *et al* (1998) demonstrated particularly low levels of mussel recruitment in the Transkei, where adult mussel are depleted more than anywhere else on the coast of Namibia and South Africa. *P.perna* along the Transkei, coast reaches a length of 30-40mm by the end of its first year. By the end of their second year the majority could be about 50mm (McQuaid *et al*, 2000). Berry (1978) observed rapid growth, with shell lengths reaching 75mm in the subtidal zone, while shells of mussels in the intertidal zones were between 50-65mm after one year.

Intertidal communities are shaped by both abiotic and biotic factors (Chelazzi and Vannini, 1980; McQuaid and Branch, 1985; Roughgarden *et al*, 1988; Menge and Olson, 1990; Craig, 1994; Dowd, 1997; Chavaund *et al*, 1998). Biotic factors can include recruitment, predation, parasitism (Mouritsen *et al*, 1999) and competition. Calvo-Ugarteburu and McQuaid (1998) showed that trematodes that infect *P.perna* decrease growth rates and castrate reproductive individuals. The effects of these trematodes can give the invasive *M. galloprovincialis* competitive advantage over the indigenous *P.perna*. The competitive advantage gained by *M. galloprovincialis* over *P.perna* can result in the lowering of *P.perna* abundance in affected communities, leading to local extinction of *P.perna* and hence modification of local community structure.

Abiotic factors that influence intertidal community structure include water flow, salinity, temperature and wave exposure (McQuaid and Branch, 1984; McQuaid and Branch 1985). Moving water brings food to suspension feeding intertidal organisms. Water velocity and the degree to which organisms are exposed to wave action influence the amount of food that reaches suspension-feeding sessile organisms. The degree of exposure has often been shown to influence community structures profoundly (Menge and Olson, 1990; Leichter and Witman, 1997).

Topography influences water flow patterns and its interaction with varying local flow conditions leads to the creation of physical gradients (Leichter and Witman, 1997). Small rocks oriented perpendicular to oncoming water current act as small baffles. These baffles have accelerated turbulent flow over their edges and a slow unmixed flow around their bases (Denny, 1988). This small-scale variation in flow regime directly affects food availability by either decreasing or increasing food encounter rates by marine organisms thereby affecting growth rates and community structure (Leichter and Witman, 1997; MacKenzie and Kiørboe, 2000).

Physical gradients, such as salinity and water flow, influence the patterns of abundance, diversity and the complexity of interactions among different levels of organizations (Jacobsen, 1990; Menge and Olson, 1990; Ramón *et al*, 1995). As an example, Kaehler and Williams (1996) showed that on tropical rocky shores with varying degrees of wave exposure in Hong Kong, the abundance of encrusting algae was highest on shores with intermediate exposure and decreased with increasing exposure. On more exposed shores barnacles and bivalves were the dominant species.

Greater understanding of the factors that affect settlement, recruitment, growth and reproduction of mussels at different spatial and temporal scales can help in implementing proper management projects. This understanding can add to the already existing pool of knowledge and hence give rise to well conceived management strategies. Much of the work done on environmental gradients affecting settlement and growth rates of the brown mussel *P.perna* has been at among sites or regional scales (McQuaid *et al*, 2000; McQuaid and Phillips, 2000).

Variations caused by physical gradients occur over different spatial scales, from within a site (local) to amongst regions (global scale) (Menge and Olson, 1990; Arnold *et al*, 1991; De Wolf, 1997; Akester and Martel, 2000). For example among sites (kilometer scale) studies have shown that growth rates of *P.perna* on exposed shores are approximately double those on sheltered shores (McQuaid *et al*, 2000).

The aims of this study were:

- To determine a way in which water movement could manipulated at small scales (cm) *in situ*.

- To manipulate water movement at small scales (cm) around artificial larval settlement substrata in order to determine the effect of small-scale water flow patterns on the settlement rate of *P.perna* larvae.

- To manipulate water movement around *P.perna* patches *in situ* at small scales (cm), in order to determine the effect of small-scale water flow patterns on mussel (*P.perna*) growth rate.

Chapter 2

Small-scale water flow manipulation

1. Introduction

The role played by water movement in structuring marine communities has long been recognised (Walton Smith, 1946; Jones and Demetropolous, 1968; Muus, 1968; Jokiel, 1978; Craik, 1980; Denny, 1983, 87). In 1946, Walton Smith investigated the role of water current on attachment and growth of barnacles that were abundant in Miami. In this work Walton Smith refers to workers from as early as 1924 who made some reference to wave velocity, water current and exposure to wave action as factors possibly affecting marine communities, but without going into further details (Walton Smith, 1946).

Unlike other environmental factors, such as oxygen content, pH and temperature, wave action has been difficult to quantify (Jones and Demetropolous, 1968; Palumbi, 1984; Ayal and Safriel, 1980). A wave comes as turbulent flow characterised by random motion of small water masses (Muus, 1968; Sanford, 1997). This random flow is difficult to quantify using conventional flow meters designed for laminar or uniform flow (Muus, 1968) and the apparatus required for measuring random flow is expensive (Muus, 1968; Ayal and Safriel, 1980).

In spite of this difficulty in quantifying wave action, it was still recognised that an even gradient should occur between vegetation-sheltered lagoons and cliffs exposed to heavy surfs (Muus, 1968). The identification of the importance of hydrodynamic factors prompted many workers to introduce different methods of quantifying wave motion (Walton Smith 1946; Jones and Demetropolous, 1968; Muus, 1968; Craik, 1980; Denny, 1983; Jokiel and Morrissey, 1993; Thompson and Glen, 1994; Sanford, 1997).

Ballantine (1961) divided rocky shores into a series of eight degrees of exposure based on the abundance of species. These rocky shore divisions formed a range from “most sheltered” to “most exposed” areas on the rocky shores. Although this method was useful, it could not be standardised over wide areas (see Jones and Demetropoulos, 1968; Craik, 1980).

In using organisms to classify shores as either exposed or sheltered, small-scale hydrodynamic patterns are not taken into consideration resulting in some organisms being found in areas in which these organisms are not expected. These unexpected organisms settle where they are found because of the action of local scale hydrodynamic (Muus, 1968).

Muus (1968) introduced a method of using spheres made from “plaster of Paris” (calcium sulphate) to measure local wave motion. Dissolution rate of plaster spheres was taken as a measure of wave motion. ‘Clod cards’ were later introduced by Doty (1971) using the same principle that is using dissolution rates of calcium sulphate as a measure of relative water motion.

The use of dissolution rate of spheres or blocks made from ‘plaster of Paris’ was later evaluated more carefully. Temperature and salinity influence calcium sulphate’s dissolution rate. The control plaster spheres or blocks must be in the same water body as the experimental for the results not to be distorted. Spheres are recommended for measuring water motion as they offer the same area and profile in all directions (Jokiel and Morrissey, 1993; Thompson and Glenn, 1994).

In intertidal environments, water flow patterns are influenced by several factors including sessile marine invertebrates, marine plants and physical parameters such as substratum topography (Denny, 1988). On small scales, water movement affects intertidal ecosystems in four interrelated ways: predator-prey interactions, particle aggregation and disaggregation, small-scale patchiness and species related growth inhibition (Sanford, 1997).

Most methods for measuring water motion discussed in this section have only been used to measure natural hydrodynamic conditions. Little work if any has been done on manipulation of water flow *in situ* in intertidal areas. The aim of this study was to manipulate (increase or decrease) turbulence at small-scales using barriers. As a first step, the relative effects of different barriers on water motion were measured.

2. Materials and Methods

2.1. The study site

This study was conducted on the south-eastern coast of South Africa in the area between the Great Fish and Mpekweni rivers next to the “Old Woman’s river” which forms a closed estuary. The Great Fish River Sun’s management controls the access to this site. Unlike many areas on the south east coast of South Africa, mussel harvesting is not frequently observed here. During the study the only collectors of marine resources observed were fishermen and occasionally people collecting seaweed. In other areas on the east coast of South Africa, people have been observed to tamper with experiments on the shore. With controlled access to this part of the coast, the chances of people vandalising experiments were relatively low.

This area consists of sandy beaches interspersed with rocky stretches, as is most of the south-east coast (Lindsay, 1998). The rocky shore at the study site consists of gently sloping platforms made of sandstone rock, with moderate wave exposure. These isolated rocky patches (Plate 2.1) show spatial variation in their mussel communities. Isolated mussel patches are found on the high zone, with continuous mussel beds appearing and becoming denser on the rock edges towards the low zone (Plate 2.2).

Plate 2.1: This study was conducted on the south-eastern coast of South Africa in the area between the Great Fish and Mpekweni river next to the "Old Woman's river" which forms a closed estuary. The Great Fish River Sun's management controls the access to this site.

Plate 2.2: The brown mussel *Perna perna* forms the main mussel cover on this part of the south-eastern coast of South Africa with *Mytilus galloprovincialis* in low numbers among *P.perna* and *Choromytilus meridionalis* at a few sites, on the lower zone. The mussel cover is interspersed with the reef forming polychaete *Gunnarea capensis* and the barnacle *Tertraclita serrata.*

2.2. Manipulation and measurement of water movement

Calcium sulphate as used by (Doty, 1971) and Muus (1968) has a high dissolution rate. Blocks or spheres made of “plaster of Paris” can be used to measure water motion only over a period of one to two hours. Cement balls and blocks made from Rockset® (Kaehler, 1999), could be left in the shore for up to 72 hours.

Rockset® was suitable for this study because the relative water motion needed to be measured over a period of about 24 hours. Exposing cement balls to wave action for this period gives a realistic indication of the average effect of water movement.

2.2.1.Experiment 1: Metal rods cement blocks

Six cement blocks with the dimensions 10cm X 3cm X 2cm (length x breadth x height) were made from a paste made from Rockset® and water. A wooden plate formed a base for each cement block. Each plate had a hole drilled on either end for attachment to the rocks on the shore. Blocks were air dried for about twelve hours after which the wooden frames were removed. They were oven dried at 40°C for four days before being taken to the shore.

Water movement around cement blocks was manipulated using metal rods of 0.7 or 1cm diameter cut into 12cm lengths. Cement blocks were attached to a flat rocky shore in randomly selected positions. Three rods of the same size (1cm diameter) were sunk into the rock 5cm apart in front (seawards) of two randomly chosen blocks leaving approximately 10cm of the rod protruding from the rock (Plate 2.3). The same was done with smaller (0.7cm-diameter) rods. Two cement blocks were left without any metal rods and they served as control. This arrangement was left on the shore for three days. The cement blocks were collected, air-dried for 12 hours and again oven dried for four days. They were visually compared in order to determine if the rods had any effect on erosion of the cement blocks.

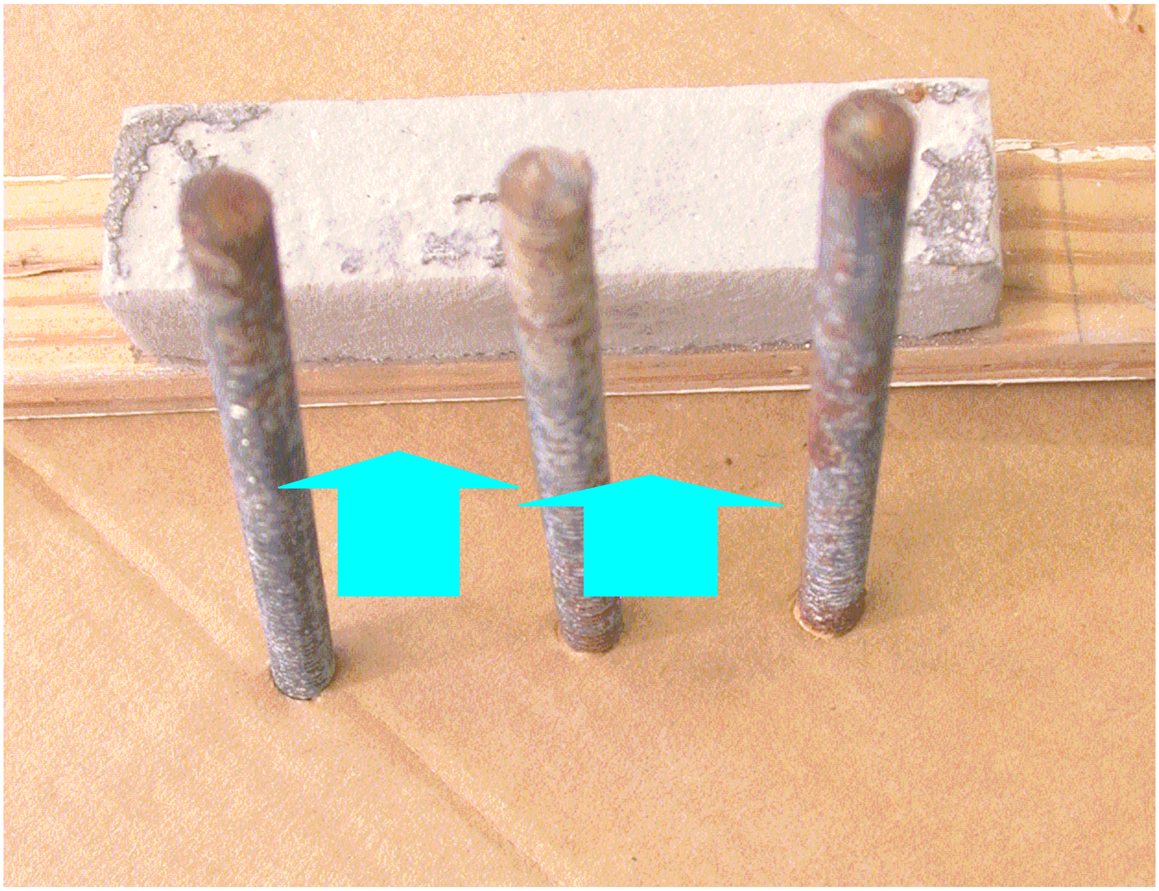

Plate 2.3: Three metal rods were sunk into the rock 5cm apart on the seaward side of the cement block. The arrows show the direction of the water flow.

2.2.2.Experiment 2: Metal rods and cement balls

Cement blocks were deemed not reliable in quantifying the effects of wave motion on intertidal organisms. This led to the next trial using cement balls, a method adapted from Muus (1968). Different methods to manipulate water movement were also tried with the aim of altering turbulence.

Fifty table tennis balls were cut in half. They were then closed to their original shape with masking tape holding the halves together. A hole with a diameter of 1cm was made on one side of each ball. Through this hole a screw of 7cm was inserted headfirst halfway into the ball leaving 5cm of the screw outside. The part of the screw left outside the ball was for the attachment of the cement ball to the rocky shore.

A paste of fast-setting cement and water was gently poured into each ball leaving the screws in the centre. The cement was left overnight to set, the following morning the mould was removed leaving, smooth, well-rounded balls attached to a screw. These balls were dried at room temperature for three days and then oven dried to constant weight at 40°C for three days. The balls were labelled and weighed individually before being taken to the shore. This mass was recorded as the initial mass.

All these balls were screwed onto the shore using a hole drilled onto the shore and fitted with a wall plug making sure that each ball touched the rock surface. Water movement around cement balls was manipulated using metal rods of 0.7cm or 1cm diameter cut into 12cm lengths. These metal rods were sunken 2cm deep into holes drilled into the rock and 5cm seawards from each ball.

Different ball and rod combinations were made giving 5 treatments overall:

- 2 (1cm-diameter) rods were positioned seawards of each ball
- 2 (0.7cm-diameter) rods were positioned seawards of each ball
- 1 (1cm-diameter) rods was sunk positioned of each ball
- 1 (0.7cm-diameter) rods was positioned seawards of each of ball
- Control without any metal rods

Each treatment was allocated to 10 randomly selected balls. After two days the cement balls were carefully unscrewed from the shore, labelled and collected. They were dried at room temperature and then oven dried at 40°C for three days. They were then weighed and the mass was recorded as the final mass. Percentage mass loss was calculated. A one-way Anova (model I, fixed effects) was conducted using Statistica 6.0 software to determine if treatment had a significant effect on the dissolution rates of cement balls. This experiment was repeated three more times.

2.2.3. Experiment 3: Metal rods, fences and L-shaped metal baffles

To find a reliable method of manipulating water movement, forty cement balls were made and dried to constant weight at 40°C. Their initial mass was measured and recorded before they were attached to the shore. Water movement around the cement balls was manipulated in several way providing four treatments overall. Treatments were assigned randomly to the balls; n was 10 for each treatment.

The treatments were:

- Five holes drilled around each ball equidistant from each other forming a ring of rods 1cm in diameter, 5cm away from the ball.
- Ten L-shaped baffles were made from an aluminium sheet. Each of the baffles was 8cm high and each side was 15cm high. These dimensions were chosen such that the baffles were higher than the largest mussels on the shore, while the side length would accommodate the biggest patch to be used in experiments. The sides were bent at right angles giving 5cm wide flanges for attachment to the shore. On these surfaces holes were drilled. Ten balls were randomly attached to the rocks and the baffles attached 2cm from the balls with the right angles facing seawards (Plate 2.4).
- Two right-angled baffles were joined to form a complete square fence. Ten of these fences were made and attached to the shore. Each one of these formed a fence surrounding a single cement ball.
- The remaining ten balls were not manipulated and served as controls.

After two days the cement balls were carefully unscrewed from the shore, labelled and collected. They were dried at room temperature and then oven dried at 40°C for three days. They were weighed and the mass was recorded as the final mass. To find the total mass lost by each cement ball, the final mass was subtracted from the initial mass and this mass lost was converted to percentage mass loss. A 1-way ANOVA (model I, fixed effects) was carried out to determine the effect of treatment on the dissolution rate of the cement balls, after testing the data for homogeneity of variances and normal distribution. This experiment was repeated four times.

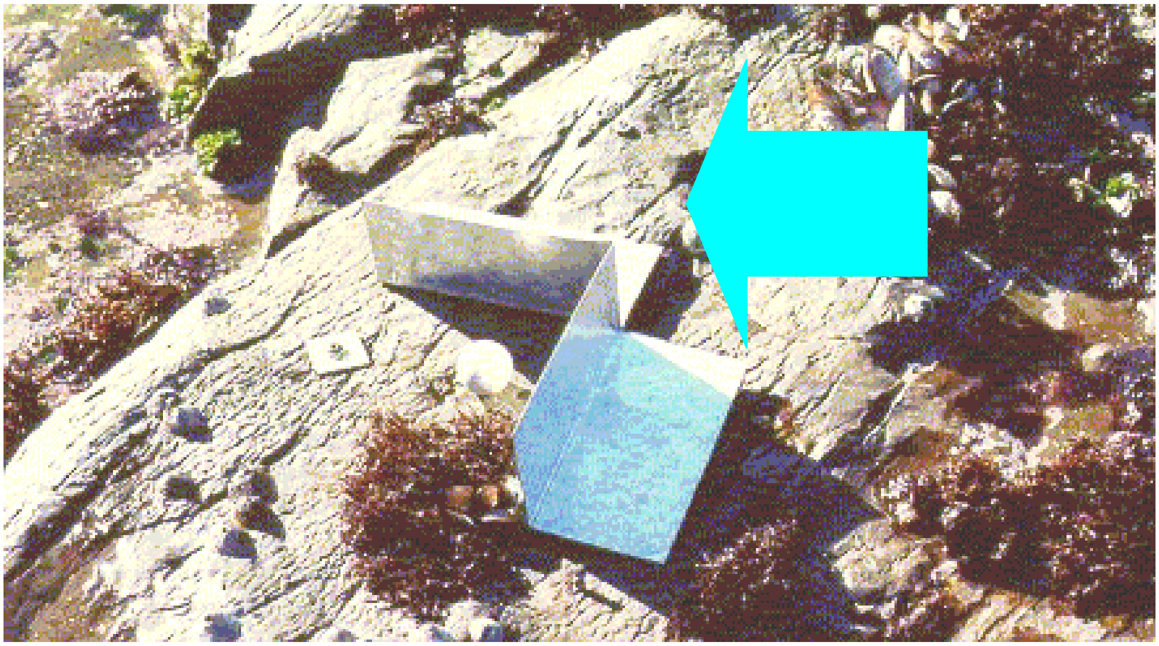

Plate 2.4: Metal baffles were screwed onto the substratum 5cm away from the cement balls using expanding screws. The arrow shows the predominant wave direction.

3. Results

3.1. Experiment 1: Metal rods cement blocks

The results showed that rods influenced the flow around the blocks. Cement blocks with rods (Plate 2.5A), were more eroded than the ones without the rods (Plate 2.5B), but this was difficult to quantify. In addition, the rectangular shape of the blocks made it impossible for similar water flow patterns to be experienced all around the block. The visual results from this experiment showed that metal rods sunk around a cement block increased the rate of erosion on the surface of a cement block.

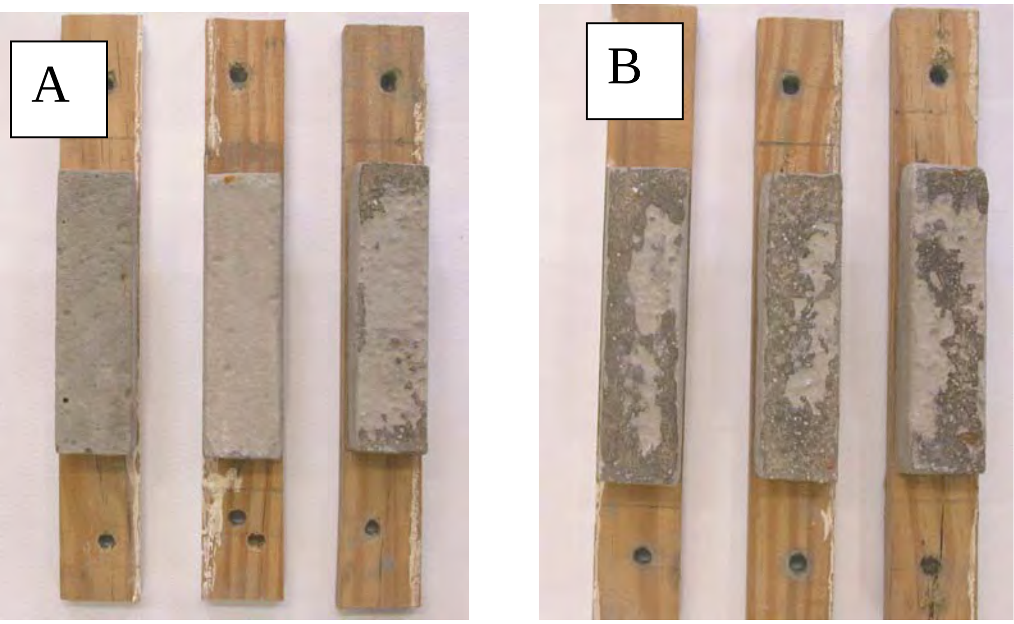

Plate 2.5: Surface layers of cement blocks were dark in colour and when eroded, revealed paler deeper layers. Blocks in A show more erosion than those in B. The blocks in B served as controls and did not have any metal rods.

3.2. Experiment 2: Metal rods and cement balls

The first experiment showed that metal rods increased the dissolution rates of cement balls at $p<0.05$ (Table 2.1). However, when this experiment was repeated, treatment did not have a significant effect on the dissolution rate of the cement balls at $p>0.05$ (Table 2.2). It was concluded that the results obtained from this experiment were not reliable. The effects of metal rods observed in this experiment might have been influenced differently by other factors for example the magnitude of the waves and water current speeds during the 72hours that the balls were left in the shore.

3.3. Experiment 3: Metal rods, fences and L-shaped metal baffles

One-way ANOVA showed that treatment had a significant effect on the dissolution rate of cement balls at $p<0.05$. For typical results obtained after four repetitions, see Tables 2.3A and 2.3B. Tukey's test (Tables 2.4A and 2.4B) showed that the dissolution rate of cement balls with L-shaped baffles was the lowest and was significantly different from cement balls with metal rods and complete fences (Figure 2.1 a and B). It was concluded that L-shaped metal baffles decreased water flow rate around the cement balls thereby decreasing the dissolution rate of cement balls.

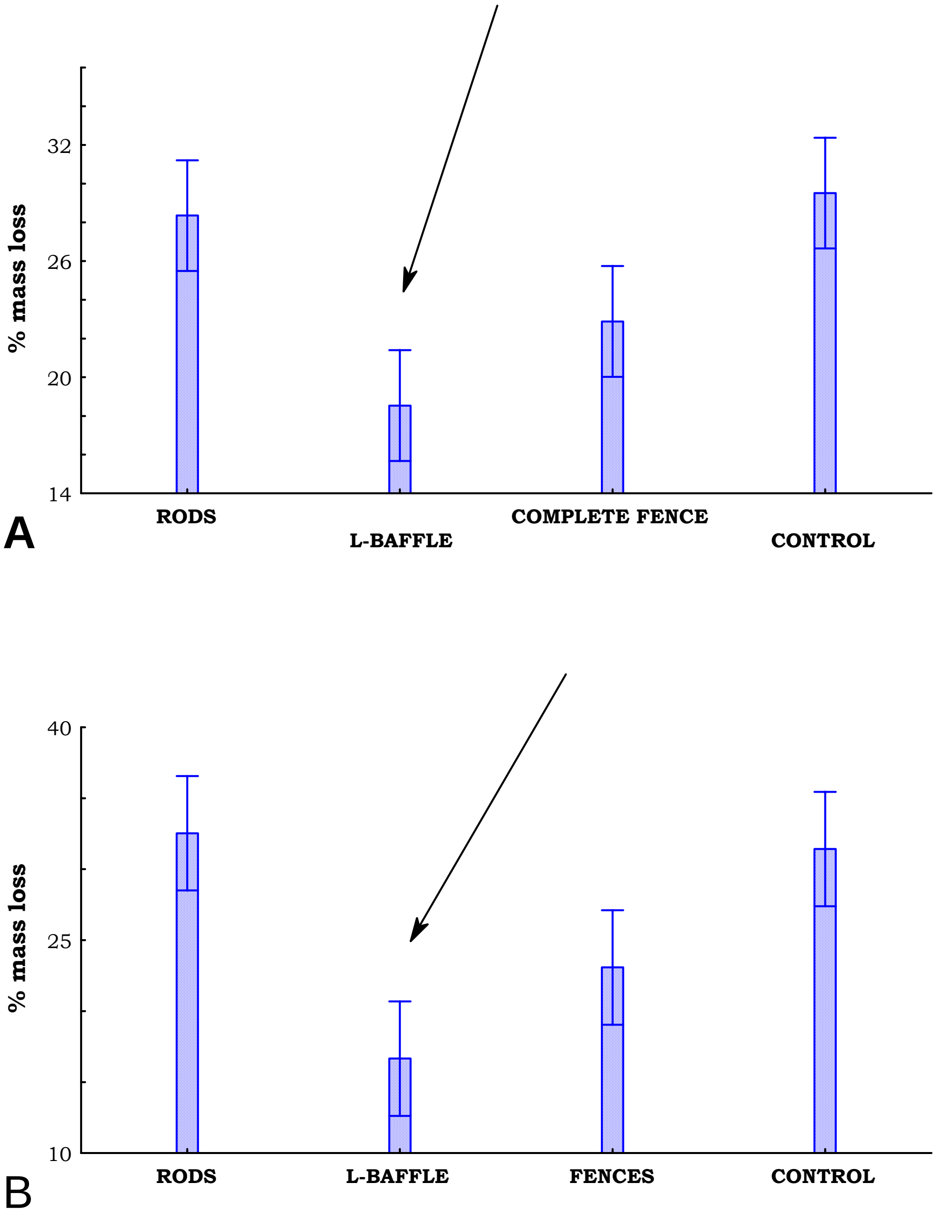

Figure 2.1 (A and B): The relationship between different kinds of baffles and the dissolution rates of cement balls. Data are means ±SD (n=10). The lower the percentage mass loss, the lower the water flow rate. Note the L-shaped metal baffles pointed indicated by an arrow. These are the typical results obtained after four repetitions of this experiment.

Statistical results

Table 2.1: Experiment 2. One-way Anova on the relationship between treatment and percentage mass loss. Treatment had a significant effect on the dissolution rate of cement balls.

Effect	**df**	**M.S.**	**F**	**p**
Treatment	4	19.77	5.154	0.003

Table 2.2: Experiment 2 repeat. One-way Anova on the relationship between treatment and percentage mass loss. Treatment did not have a significant effect on the dissolution rate of cement balls.

Effect	**df**	**M.S.**	**F**	**p**
Treatment	4	22.45	0.328	0.857

Table 2.3A: Experiment 3. One-way Anova showing the relationship between treatment and percentage mass loss when different kinds of baffles were used. Treatment had a significant effect on the dissolution rate of cement balls.

Effect	**df**	**M.S.**	**F**	**p**
Treatment	3	129.7	14.23	<0.001

Table 2.3B: Experiment 3 repeat. One way Anova showing the relationship between treatment and percentage mass loss when different kinds of baffles were used. Treatment had a significant effect on the dissolution rate of cement balls. The results are typical of all four trials.

Effect	**df**	**M.S.**	**F**	**p**
Treatment	3	279.6	15.48	<0.001

Table 2.4 A: Experiment 3. The results of Tukey's test showing the effect each treatment had on the dissolution rates of cement ball, with L-shaped baffles having a significant effect.

TREATMENT	**{1}**	**{2}**	**{3}**	**{4}**
1 Rods		-	-	-
2 L-shaped baffle	0.000665		-	-
3 Complete fences	0.049693	0.145184		-
4 Control	0.927583	0.000331	0.014970	

Table: 2.4B: The results of Tukey's test showing the effect each treatment had on the dissolution rates of cement ball, with L-shaped baffles having a significant effect. The results are typical results obtained of all four trials.

TREATMENT	{1}	{2}	{3}	{4}
1 Rods		-	-	-
2 L-shaped baffle	0.000288		-	-
3 Complete fences	0.013820	0.119568		-
4 Control	0.97554	0.000425	0.031392	

4. Discussion

It is generally agreed that water movement is among the most important factors that shape intertidal communities (Walton Smith, 1946; Muus, 1968; Thompson and Glenn, 1994; Leichter and Witman, 1997). The effect of water movement on intertidal communities is experienced at different scales. The effect of large-scale wave exposure on *P.perna* has been quantified at large scales (kilometres) (Lindsay, 1999). It is also important to quantify the effect of water movement at local scales on the shore, but unlike with other factors such as water temperature, water movement is difficult to quantify at centimetre scales (Jones and Demotropoulos, 1968; Muus; 1968; Craik, 1980).

Most affordable apparatus available are designed for the measurement of laminar flow. Natural flows consist of random motion of small water masses, which cannot be easily measured except by expensive electric recorders that are not readily available (Muus, 1968).

Most of the methods used in the laboratory for water flow manipulation may not work in the field. In the laboratory, the amount of force created by water flow can be controlled. Several workers have designed different apparatus for measuring relative wave motion in the field. Unfortunately most of these apparatus can only be used for specific studies. Craik (1980) introduced the use of cement blocks to measure relative scouring. Although this method worked well, it could only be used in widely spaced areas.

Dynamometers used by Jones and Demetropoulos (1968) could only measure the action of specific waves, not giving the average effect of individual waves combined over a specified period. “Plaster of Paris” used by Muus (1968) and Doty (1971) has a high dissolution rate in water and can only be left on the shore for up to an hour or so. Measuring wave action over a longer period (at least 24hours) gives a better indication of the average wave action experienced by intertidal organisms. In order to quantify wave action over a long period the apparatus must be designed to be able to withstand different wave forces, and they must be able to record the average effect of the different waves they experience. Most experiments conducted on the effect of wave action on *P.perna* communities have been observational (Lindsay, 1998; 1999). This study required the manipulation of water movement *in situ* and its quantification.

Protruding structures affect water movement, including its ability to erode, the rate of fluid transport and the production of turbulence (Eckman, 1983; Denny, 1988). This idea was used when water movement was manipulated and quantified.

After several trials Rockset® was found to be able to withstand exposure to the intertidal zone for more than 72 hours. Cement blocks adapted from Craik (1980) and rods used in this experiment showed that rods increase the rate of erosion rates of the cement blocks (Plate 2.5). It was concluded that metal rods increased turbulence around the cement rods. Cement blocks without rods were almost not eroded and the erosion on the blocks with metal rods was not uniform. These results were not easy to quantify and hence they were only visualized. A method that could show potential average wave action around a mussel patch or an artificial substratum was required.

Thompson and Glenn (1994) suggest the use of spheres to quantify relative wave action. This is because spherical shapes project the same surface area in all directions. Cement balls with metal rods around them showed that upright metal rods significantly increased the dissolution rates of cement balls (Table 2.1). After four repetitions of this experiment different results were obtained; in some experiments treatment had no significant effect on the dissolution rates of cement balls (Table 2.2). Large wave forces could have masked the effect of metal rods at small scales.

Different baffles and metal rods were used. L-shaped metal baffles significantly decreased the dissolution rates of cement balls, in each repetition of the experiment (Tables 2.4A and B). These L-shaped metal baffles were then used in the settlement and growth rate experiment.

L-shaped baffles allowed water to flow freely without the potential of forming artificial pools around mussel patches and artificial settlement substrata. These baffles were considered favourable because unlike complete fences, they did not encourage artificial sedimentation.

Chapter 3

Effects of small-scale water movement on larval settlement

1. Introduction

The majority of intertidal organisms have complex life cycles that involve sessile adults producing larvae that inhabit pelagic environments (Yoshioka, 1982; Gaines and Roughgarden, 1985; Olson and Oslon 1985; Roughgarden *et al*, 1985; Knowlton and Keller, 1986; Shanks, 1986; Strathmann, 1990; Fogarty *et al,* 1991; Menge, 1991; Commito *et al* 1995; Pineda, 2000; Dobretsov and Miron, 2001; van der Meer, 2002). Adult sessile marine organisms can only be dispersed if they are attached to floating objects such as floats and rafts. In most sessile intertidal organisms the dispersal of adults is infrequent compared to larval dispersal (Gerrodette, 1981; Willis and Oliver, 1990).

Pelagic larvae are dispersed over a wide range of distances. These distances can range from only a few centimetres or metres to thousands of kilometres across oceans (Shanks, 1983; Hannan, 1984; Gaines and Roughgarden, 1985; Scheltema, 1986; Heath, 1987; Levin, 1987; Davis and Butler, 1989; Sammarco and Andrews, 1989; Willis and Oliver, 1990; Gaines and Bertness, 1993; Hovel and Morgan 1997; Verdier-Bonnet *et al*, 1997).

Larval transport from the release site is facilitated by a combination of currents or horizontal advection and random eddy-like wave motions on different spatial and temporal scales. (Knowlton and Keller, 1986; Hill, 1990; Possingham and Roughgardern, 1990; Hill, 1991).

Pelagic larvae are considered planktonic because they are microscopic and the distances they can travel against water currents are small compared to those they travel in the direction of the currents (Black, 1993; Bourget and Harvey, 1998; Pearce *et al*, 1998; McQuaid and Phillips, 2000). This implies that these larvae must devise means to stay close to a suitable substratum if they are to complete their life cycles (Dobretsov and Miron, 2001).

Although some marine larvae settle in the close proximity to their parents (Knowlton and Keller, 1986), their ability to disperse and the probability of colonising a given habitat are important in determining the distribution and abundance of sessile marine organisms (Roegner, 1991). Colonising new islands and patches increases species persistence even when local extinctions are inevitable. Larval dispersal also allows exchange of genetic material among populations that are otherwise geographically separated (Muus, 1968; Crisp, 1976, Gerrodette, 1981; Levin, 1983; Crisp, 1984; Sammarco and Andrews, 1989; Possingham and Roughgarden, 1990; Willis and Oliver, 1990; Hinckely *et al*, 1991; Graham and Sebens, 1996).

The pelagic larvae of intertidal organisms must return shorewards to complete their life cycle (Beukema and Vlas, 1989; Hill, 1991; Pineda, 2000). Some larvae are known to be able to delay metamorphosis until a suitable substratum is found. However, the longer the larvae stay in the water column, the higher the chances of mortality become. There must be a balance between the time spent looking for a suitable settlement site and increasing mortality in the water column (Graham and Sebens, 1996).

Planktonic larvae detect a substratum, test it and if favourable they attach permanently. The process of detecting a suitable substratum and permanent attachment to it is called settlement and the rate at which planktonic larvae establish permanent contact with the substratum is called the settlement rate (Pineda, 1991). Settlement is a sporadic process and is difficult to quantify (Rittschoff *et al*, 1984). On the other hand recruitment is the density of settlers that survive over a certain arbitrary period decided upon by a researcher (Roegner, 1991; Minchinton and Scheibling, 1993a).

There are many factors that influence larval settlement, including the number of larvae reaching a settlement site, larval behaviour and local hydrodynamic conditions. These factors act only at small scales compared to major currents that act on scales up to thousands of kilometres (Wethey, 1984; Gaines and Roughgarden, 1985; Roberts *et al*, 1991; Graham and Sebens, 1996; Pineda and Caswell, 1997). For instance local adult stocks may not contribute to the number of settlers available but can influence larval settlement behaviour thereby increasing the number of settlers at a given site (Kendall *et al*, 1985; Hughes, 1990; Hovel and Morgan, 1997; van der Meer *et al*, 2001).

Although larvae appear to behave passively, it has been shown that at small-scales they can control their positions in the water column and also during settlement (Bourget and Harvey, 1998; McQuaid and Phillips; 2000). Active larval settlement choices are important because once larvae settle they lose their ability to be dispersed. If larvae settle on unfavourable substrata such errors can decrease their survival rates. On unfavourable substrata predation, desiccation and dislodgement due to strong wave action can increase settler mortality rates. Some of these causes of mortality can be avoided if pelagic larvae can actively choose substrata that can offer a high survival rate, during settlement (Bourget and Harvey, 1998).

The aim of this study was to manipulate water movement patterns *in situ,* and to determine the effects of small-scale (cm) water flow rates on the settlement rates of larvae of the brown mussel *Perna perna*.

2. Materials and Methods

Three rocky shore stretches of approximately 100m separated by sandy beaches were chosen. A distance of approximately 500m separated the sites A, B and C respectively. Mussel larvae seem to prefer settling on already existing mussel beds, rather than on other natural and artificial substrata (Dye *et al*, 1997). The three sites chosen had established mussel patches. Both the topography and tidal height of the three sites were the same.

At each site 10 right-angled (L-shaped) metal baffles 8cm high with sides 15cm long, were attached in random positions to the rock among established mussel patches. A hole was drilled inside the area protected by each baffle and fitted with a wall plug for the attachment of a nylon pot-scouring pad (Figure 3.1). These pot-scouring pads had a diameter and a height of approximately 10.5 and 2.5cm respectively. Among these mussel patches another 10 spots were chosen. A hole was drilled and fitted with a wall plug to be used for the attachment of a pot-scouring pad, these pads acted as control.

Artificial substrata offer a constant surface area. They are also easy to place and remove, allowing settlement to be monitored over a specified period, and have been used in different larval settlement studies (King *et al*, 1990; Todd and Keough, 1994; Devakie and Ali, 2002; Alfaro and Jeffs, 2003). During low tide, scouring pads were attached to the shore with 5cm screws were screwed down into the wall plug in the rock.

Plastic washers (3x3cm) were used to hold the pads against the substratum.

Scouring pads were attached 5cm away from the sides of the baffles (Plate 3.1). Both the experimental (low water flow rate) and control (high flow rate) pads were left for 24 hours on the shore. They were then carefully collected, placed in plastic sandwich bags and replaced with new pads. This was done for three consecutive days.

In the laboratory, the pads and the sandwich bags that contained them were carefully rinsed in about 250ml of fresh water. This water was filtered through a glass microfibre filter, 47mm Ø (GF/C) (Whatman®). The content of the filter paper was observed under a dissecting microscope and the number of *Perna perna* settlers (less than 300µm) (Plate 3.2) counted and recorded. These larvae were collected with fine forceps and preserved in 40% ethyl alcohol in labelled Eppendorff tubes.

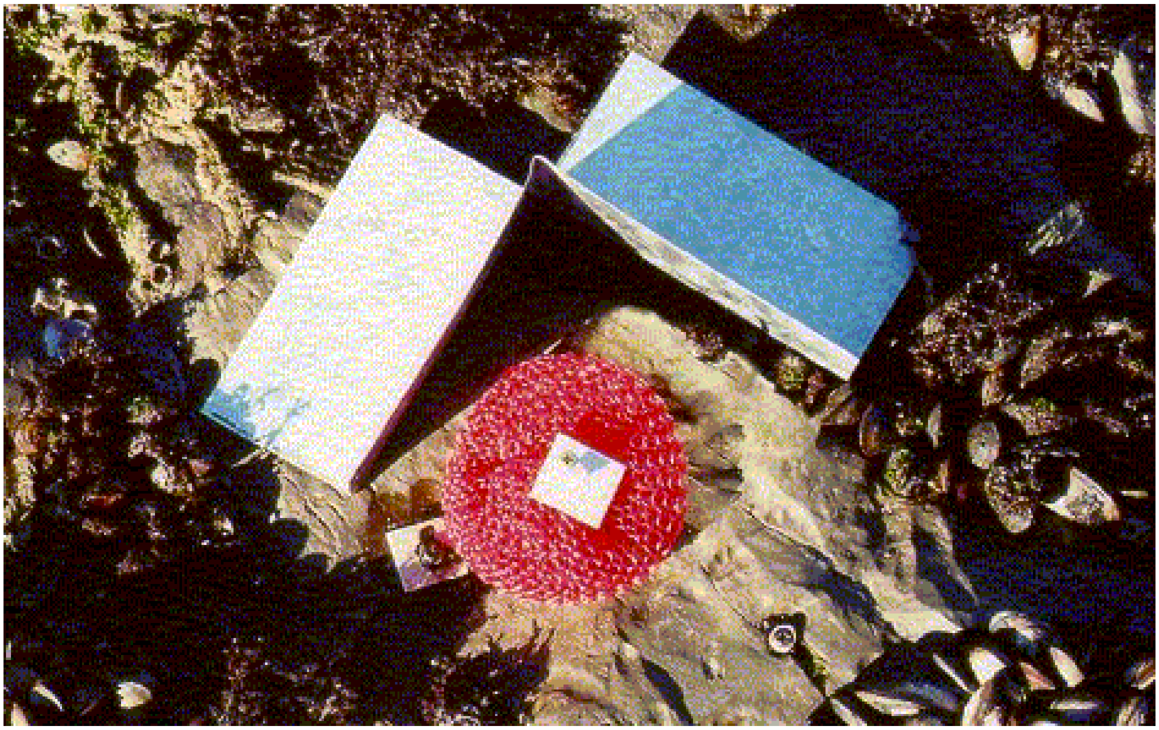

Plate 3.1: Nylon pot scouring pads were used for the collection of *Perna perna* larvae. Half of the pads had L-shaped metal baffles attached around them as shown. The pads were individually numbered with aluminium tags attached to the substratum.

Plate 3.2: *Perna perna* larvae less than 300μm (not to scale) were taken to be settlers. These larvae are the ones that were used to compare the effects of different flow patterns on the settlement rates.

Statistical analysis

A 3-way mixed model Anova was conducted on larval abundance using the software package Statistica 6.0. Treatment was treated as a fixed factor with date and site treated as random factors. Data were tested for homogeneity and normality using Levin's test. No transformation of data was required.

3. Results

The number of settling larvae was low with an average of only five settlers.pad^{-1}.day^{-1} on two days of collection. A 3-way Anova indicated that date, site and treatment all had significant effects on larval settlement rates ($p<0.05$ Table 3.1). There was also a significant interaction among all factors ($p<0.001$). This means that treatment only had a significant effect on certain days and at certain sites. Treatment only had a significant effect when the larval abundance was high (Figure 3.1). The effect of treatment is observed on Day 1 (Figure 3.1) at Site A (Figure 3.2), where the settler abundance was increased by decreased water flow rate (Table 3.2). Treatment did not have a significant effect on settlement rates on Day 2 (Figure 3.3) or Day 3 (Figure 3.4) (Tables 3.3 and 3.4). Treatment, site and their interaction did not have significant effects on settlement rates on the third day of collection. This was the day that had the lowest number of settlers.

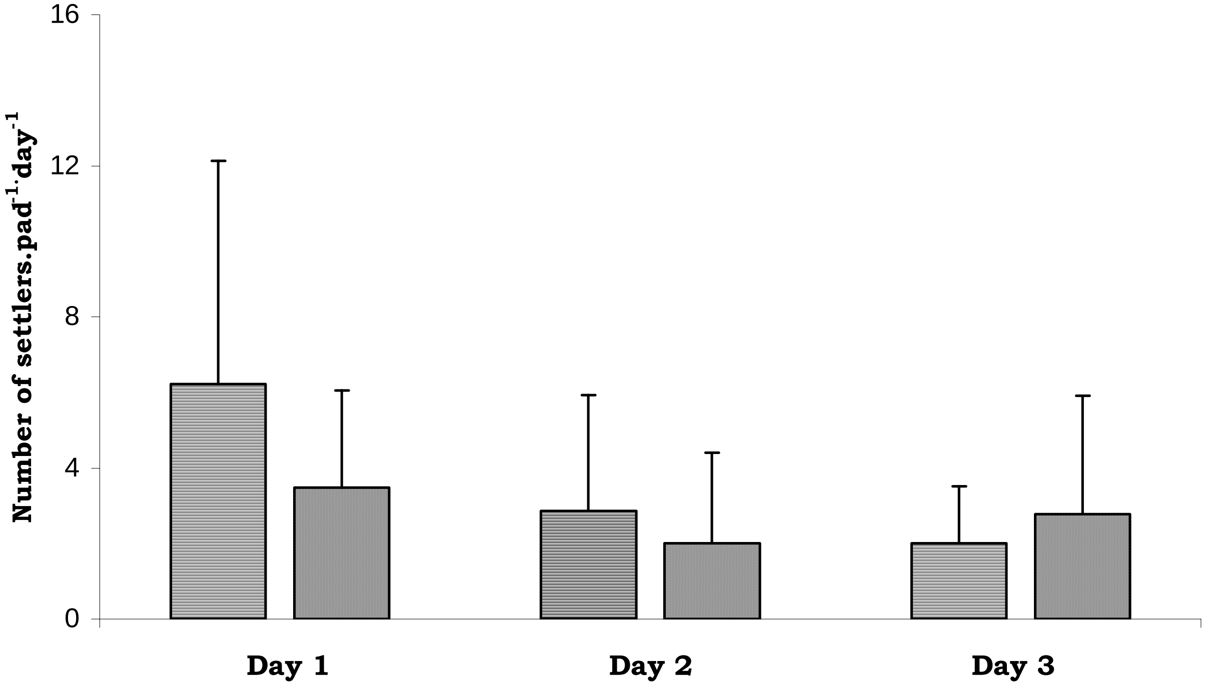

Figure 3.1: Mean settlement rates (number of mussels.pad^{-1}.day^{-1}) on different days of larval collection on both control and experimental pads. The experimental pads had their water flow rate decreased while the flow around the control pads was not manipulated. Horizontal shading and fine hatching represent experimental and control patches respectively.

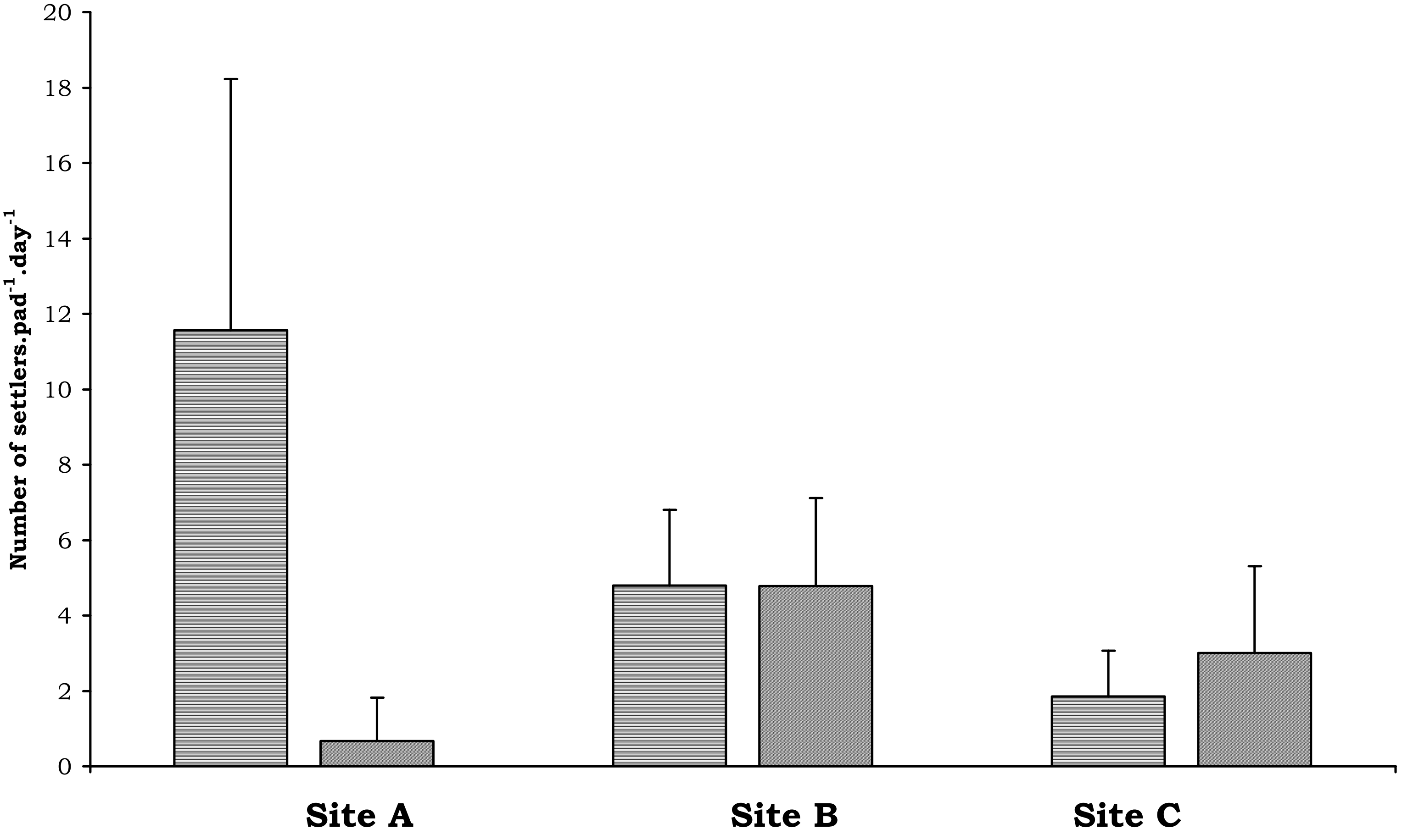

Figure 3.2: Mean settlement rates (number of mussel.pad^{-1}.day^{-1}) at the three sites A, B and C on the first day of larval collection on pads on both experimental and control pads. Water flow rate around the experimental patches was decreased. Horizontal shading and fine hatchings represent experiment and control respectively.

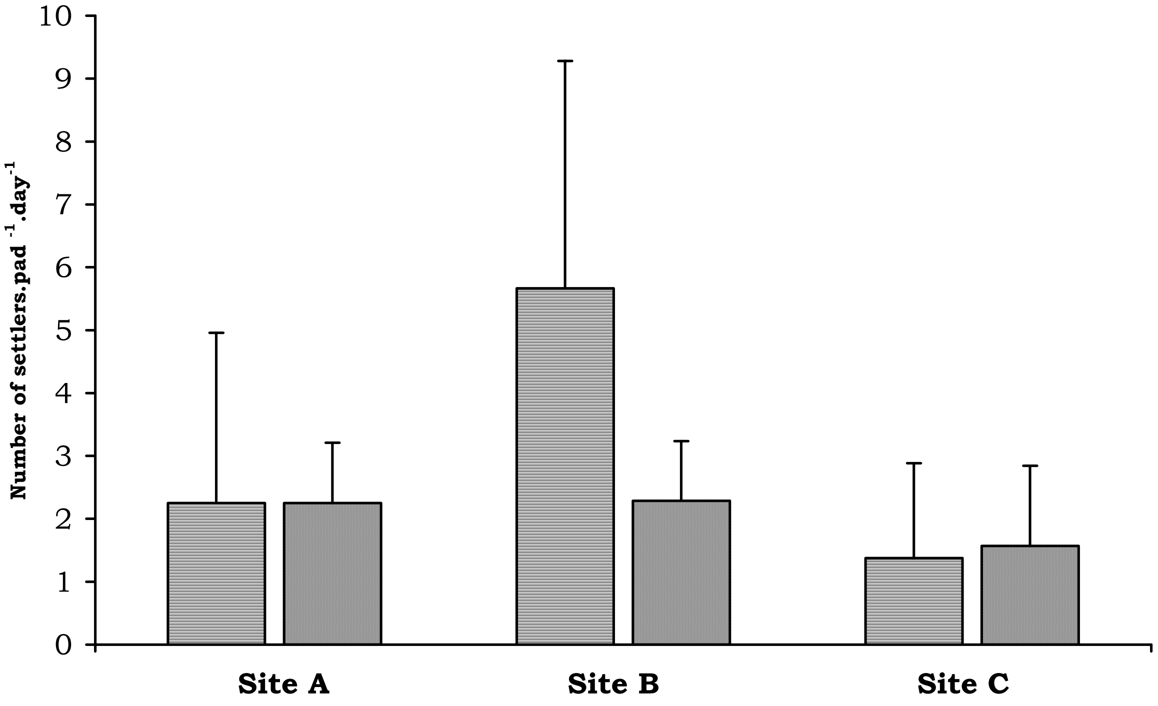

Figure 3.3: Mean settlement rates (number of mussels.pad^{-1}.day^{-1}) at the three sites A, B and C on the second day of larval collection on pads on both experimental and control pads. Water flow rate around the experimental patches was decreased. Horizontal shading and fine hatchings represent experimental and control pads respectively.

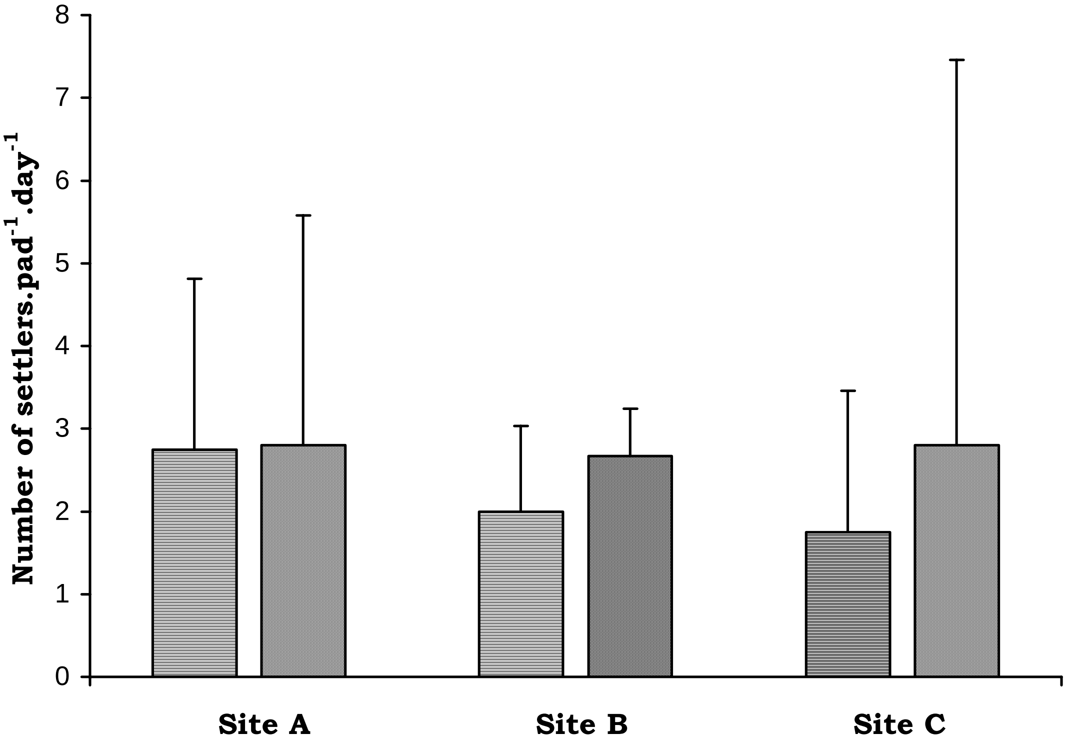

Figure 3.4: Mean settlement rates (number of mussels.pad^{-1}.day^{-1}) at the three sites A, B and C on the third day of larval collection on pads on both experimental and control pads. Water flow rate around the experimental patches was decreased. Horizontal shading and fine hatchings represent experiment and control respectively.

Statistical results

Table 3.1: A 3-way ANOVA on the relationship between date, site, treatment and the settlement of *Perna perna* larvae.

	d.f.	**M.S.**	**F**	**P**
Date	2	41.6888	5.53	0.005462
Site	2	29.3753	3.90	0.023874
Treatment	1	34.4858	4.58	0.035176
Date/ Site	4	13.0933	1.74	0.148818
Date/ Treatment	2	29.2224	3.88	0.024323
Site/ Treatment	2	38.3341	5.10	0.008123
Date/ Site/ Treatment	4	42.1964	5.60	0.000464
Error	87	7.5321		

Table 3.2: A 2-way ANOVA on the relationship between site, treatment and settlement rate on the first day of larval collection.

	d.f.	**M.S.**	**F**	**P**
Site	2	39.6452	3.49	0.042581
Treatment	1	89.2150	7.85	0.008548
Site/Treatment	2	06.7295	9.39	0.000617
Error	32	11.3623		

Table 3.3: A 2-way ANOVA on the relationship between site, treatment and settlement rate on second day of larval collection.

	d.f.	**M.S.**	**F**	**P**
Site	2	22.2709	5.17	0.010996
Treatment	1	10.6483	2.47	0.125331
Site/Treatment	2	13.1466	3.05	0.060542
Error	34	4.3118		

Table 3.4: A 2-way ANOVA on the relationship between site, treatment and settlement rate on the third day of larval collection.

	d.f.	**M.S.**	**F**	**P**
Site	2	0.9098	0.13	0.877349
Treatment	1	3.1500	0.46	0.506917
Site/Treatment	2	0.6952	0.10	0.904713
Error	21	6.9095		

4. Discussion

Larval settlement varied according to time (day of collection) and space (site). Site A had the highest mean settlement rate on the first day of larval collection (Figure 3.2). This was the day and site on which treatment (decreased water flow rate) had a significant effect on the larval settlement rate (Table 3.2). In a study conducted by Gaines *et al* (1985), settlement rates varied by order of two magnitudes among their three sites. Settlement rate on each site was proportional to the larval abundance in the water column perpendicular to each individual site. Settlement shows both spatial and temporal variability and hence it is important in shaping intertidal communities (Wethey, 1984; Menge and Olson; 1990; Hurlbut, 1991; Harris *et al*, 1999; Jenkins *et al*, 2000, Alfaro and Jeffs, 2003).

This study shows that small-scale water flow patterns have a significant effect on larval settlement rate only, but under specific conditions. The results obtained in this experiment are likely to have been influenced by the overall low larval settlement rates observed during the period of the study. On the days with lowest number of settlers, scouring pads had a mean of five settlers. If for instance a single larva was missed in any of these pads about 20% of the settlers was lost. This loss would have had more impact on the data and its analysis than when the number of settlers was higher.

It was difficult to get peak larval settlement during the duration of this study. Some workers have reported seasonal larval abundance, but larval settlement depend on several factors including the length of the spawning period, food availability, wave action and water temperature

(Bayne, 1976; Pedrotti and Faux, 1992; Pearce *et al*, 1998; Lasiak, 1991b). Like most natural populations, mussel populations can be regarded as a series of interconnected subpopulations. These subpopulations occupy more or less discrete patches. Their sizes are influenced by dispersal and variations in local conditions (Davies and Butler, 1989). At the same time mussel populations are open systems, with local fecundity not being a major determinant of the final population size (Wethey, 1984; Bence and Nisbet, 1989; Hughes, 1990; Caley *et al*, 1996). Larvae produced by one population may be carried or dispersed over thousands of kilometres by currents, with the larvae behaving like passive particles (Shanks, 1983, Gaines and Roughgarden, 1985; Hovel and Morgan, 1997).

Pads that had their water flow decreased, had the highest number of settlers on the first day of mussel collection on site A (Figure 3.1). These pads also had a large number of gastropods, detritus and sand grains. Although Butman and Grassle (1988) have shown that marine larvae can make active settlement choices, in this study high settlement rate appears to have occurred mainly with mussel larvae behaving passively (Hannan, 1984). The suggestion of passive settlement is supported by the large amount of sand found on the pads with decreased water flow rate. Although not tested, most larvae were found on pads that had a large amount of sand.

At large scales larvae may be considered to behave passively, but at small scales (1mm) active larval choices cannot be ignored (Petersen, 1984; Pawlik *et al*, 1991; Bourget and Harvey, 1998). Eckman (1979,1982) has shown that organisms are affected by water flow patterns that change over distances of a few millimetres to centimetres. This suggests that the high settlement rate observed on the pads with decreased water flow might be a result of both passive larval movement (like sand grains) and active settlement mechanisms. However settlement cannot be attributed to one factor. It is a function of the larval availability in the area, larval behaviour and physical processes that bring the larvae into contact with the substratum and the availability of suitable substrata (Rittschoff *et al*, 1984; Roegner, 1991; Minchinton and Scheibling, 1993b).Much of the work done on the effect of exposure on *P.perna* settlement rates has been at large scales (kilometre). These studies have shown high larval settlement rates on exposed shores at kilometre scales (Lindsay, 1998). This study has shown that at small scales, larval settlement is higher with less water movement. This may mean than large-scale exposure is required for the transportation of larvae to the substratum. Hawkins and Hartnoll (1982) have shown a good correlation between recruitment rates and onshore winds in the case of the barnacle *Semibalanus balanoides*. It might be that *P.perna* larvae require low local flow rates for settlement. Some larvae of marine organisms prefer settling on topographically exposed sites while others prefer settling in pits and crevices (Walters and Wethey, 1996).

This study does not show if *P.perna* larvae actively choose where to settle. Several workers have shown that some marine larvae make active choices when settling (Smith, 1946; Crisp, 1955; Butman and Grassle, 1988; Denley and Underwood, 1979; Hudon and Bourget, 1981; Eckman *et al*, 1990; Holm; 1990; Mullineaux and Butman, 1991; Mullineaux and Garland, 1993; Bourget, 1998). These studies give different results in still flows and realistic defined flows in the laboratory. The results also showed variation among different species and hence their findings are not readily applicable on other species such as *P.perna*. This means that for a thorough understanding of factors affecting *P.perna* larval availability and settlement, more laboratory and field studies need to be conducted.

Chapter 4

The effects of small-scale water movement on growth rates

1.Introduction

Bivalves form the second largest class within the phylum Mollusca and have an accretionary exoskeleton. In this skeleton, the total sequence of growth throughout their ontogeny is recorded (Seed, 1969; Seed, 1980; Cerrato *et al* 1991; Richardson, 1996; Richardson *et al,* 1999; Cerrato, 2000). The records formed in the exoskeleton allow analysis of the effects of environmental changes on shell morphology and growth (Clark II, 1968; Evans, 1972; Seed, 1980; Richardson, 1989; Jones and Quitmyer, 1996; Richardson, 1996; Cerrato, 2000; Millstein and O'Clair, 2001).

Shell growth and morphology are affected by environmental parameters such as: temperature (Sato, 1997; Pechenik *et al* 1990; Richardson, 2001; Richardson *et al* 2001), food availability (Jones and Demetropoulos, 1968; Seed, 1980; Alunno-Bruscia *et al*, 2000; Camacho *et al*, 2000 Richardson *et al* 2001), and most importantly salinity and wave exposure (Hobday, 1995; Jones and Quitmyer, 1996; Brey and Mackensen, 1999; Boulding *et al.*, 1999; Akester and Martel, 2000; Blanchard and Feder, 2000; Cerrato, 2000; McQuaid *et al*, 2000; Richardson, 2001).

Akester and Martel (2000) showed that shell shape and shell thickness in the mussel *Mytilus trossulus* from habitats with differing degrees of wave exposure contrasted markedly. Mussels transferred from wave-exposed to wave-sheltered environments change their shell secretion patterns to match those mussels in the wave-sheltered environments (Seed, 1968; Raubenheimer and Cook, 1990).

Shell growth is an important component of bivalve fitness because shells offer protection against a range of predators (Arnold *et al*, 1996).

Blundon and Kennedy (1982) showed that the mechanical force required to crush a shell is proportionally related to shell size, and hence the more the shell increases in size the more protection it offers against potential predation. Therefore the fitness of fast growing individuals within a population may be greater than that of slower growing ones (Seed and Brown, 1978; Arnold *et al*, 1996).

The variation of growth rates among individuals within a population affects their survival and reproduction rates, thereby affecting the dynamics of the whole population (Hastie *et al*, 2000). Growth rate of individuals is assessed in two principal ways: by relating the size of the whole organism to age, and by measuring growth rate of one part of an organism as a measure of the growth of the whole organism (Seed, 1980; Millstein and O'Clair, 2001). A shell is one of the most prominent molluscan features and has been used to determine effects of different biological and physical factors on mussel growth (Seed, 1980).

Shell growth-increment pattern analysis is a reliable technique for measuring growth rates and for age determination in bivalve molluscs (Seed, 1980; Kautsky, 1982; Hilbish, 1986; Richardson *et al*, 1990; Arnold *et al*, 1991; Craig, 1994; Kesler and Downing, 1997; Chavaund *et al*, 1998; Gasper *et al*, 1999; Richardson *et al*, 1999; Cerrato, 2000; Millstein and O'Clair, 2001).

Variation in shell size and morphology due do degree of wave exposure; can be observed on both macro and regional (kilometres) scales and on micro-geographic or within site (metres) scales (De Wolf, 1997). Arnold *et al* (1991) conducted a microgeographic study on the shell growth rates of *Mercenaria mercenaria*. They concluded that in comparing shell growth rates among different populations of *M. mercenaria* over wide geographic ranges, some consideration must given to shell growth variation within each site.

Akester and Martel (2000) observed that shell morphology of both adult and juvenile *Mytilus trossulus* collected from wave exposed and sheltered sites showed striking differences. These differences were observed even when the separation between sites was only a few hundred metres. Much of the work done to date on the effects of exposure on *P.perna* growth rate has been done at large scales between sites separated by hundreds of metres and kilometres (Harger, 1979; Lindsay, 1998; 1999; García-Esquivel *et al*, 2000; McQuaid *et al*, 2000).

The aim of this study was to manipulate the environment of *Perna perna in situ* and to establish the effects of small-scale (cm) water movement on the growth rates of mussels, using the fluorochrome calcein as an *in situ* growth marker (Kaehler, 1999; Kaehler and McQuaid 1998; 1999; Moran, 2000). Calcein is a non-toxic fluorescent label that is incorporated into growing calcium carbonate structures (Pirker and Schiel, 1993; Rowley and Mckinnon, 1995; Kaehler and McQuaid, 1998; Moran, 2000).

Using calcein as a marker allows the same individual to be marked more than once, as calcein marking is not immediately destructive, thus the growth rate of an individual can be observed over a long period under different environmental conditions. Unlike other methods used in mussel growth studies for example using acetate peels (Lindsay, 1998), calcein marking is not labour intensive and measurements can be taken from either of the bivalve shells. This allows the repetition of measurement.

Calcein marking involves injection of calcein solution into the mantle of a mussel (Kaehler and McQuaid, 1998), resulting in the reduction of time a researcher spends on each individual mussel. This minimizes disturbance and stress experienced by individual mussels when other marking methods are used. Mussels respond to external stresses by forming growth checks or rings (Clark II, 1968; Peck *et al*, 1996). These rings can be confused with those caused by ordinary environmental factors (Peck *et al,* 1996).

2. Materials and methods

A site with a flat, gently sloping substratum with a large number of isolated mussel patches was chosen. The experiment was conducted in two zones, the low and high mussel zones that were about 5m apart horizontally. The main difference between the high and low zone was the period each zone was exposed to air during low tide.

In each zone 20 small mussel patches, each with a maximum number of about 60 mussels, were randomly chosen. All these mussel patches were on a relatively flat rock. The flat rock was chosen to allow the attachment of metal baffles and to prevent confounding effects due to irregular rock topography. Numbers (1-40) were punched onto small (3x3cm), square aluminium plates. These plates were screwed to the rock to mark each of the 40 mussel patches at the site.

A 2*l* calcein-seawater solution with the concentration 400mg.l^{-1} (Sigma, Chem. Abstracts ID No. 1461-15-0) (Kaehler, 1998; Kaehler and McQuaid, 1998) was prepared in a clean 5*l* plastic container. This solution was stored in a dark cupboard to prevent any reactions that could be influenced by sunlight.

It was considered important to inject all mussels within a zone in one day. A day with a low spring tide was chosen. On the shore, 2*l* seawater was added to the calcein solution to decrease the concentration to 200mg.l^{-1}. *P.perna* shell valves gape slightly when the shell is damp. The solution was injected into each mussel *in situ* by gently inserting a syringe between the gaping shell valves into the mantle cavity. Mussels that had their valves tightly closed made it difficult for the needle to penetrate and were sprinkled with seawater. Seawater induced light gaping that allowed the needle to pass through. It was difficult to measure the amount of calcein solution injected into each mussel and so mussels were injected till the mantle cavity overflowed (Kaehler, 1999; Kaehler and McQuaid, 1998). The injection of mussels on the high zone was completed and these mussels were left for 31 days. After this period, ten calcein-injected mussel patches were randomly chosen. L-shaped metal baffles 8cm high with sides of 15cm were attached around each of these ten chosen patches to decrease water flow rate. These baffles were screwed to the rock with the apex pointing seawards. All mussels in 20 patches, i.e. including the ones without baffles were then re-injected with 200mg.l^{-1} calcein solution. These mussels were left for a further 55 days before they were collected.

The low zone was always submerged during the days chosen for injection. To determine if calcein could be incorporated into the mussel shell when the mussels were injected under water; ten mussels were injected while submerged. These injected mussels were removed and transported in seawater in a 500ml plastic jar to a seawater tank.

The mussels were removed from the tank after three days. These mussels had all the soft tissue scraped from the shells. These empty shells were then washed with freshwater, dried, embedded in polyester resin, sagitally sectioned and observed under a fluorescence microscope. All ten mussels had a calcein mark within their shells. It was decided to inject the low zone even when it was awash. All mussels in each of the 20 patches were injected and left for 51 days. L-shape baffles were attached around ten randomly chosen patches as above. All twenty patches were injected with the 200mg.l^{-1} calcein solution for the second time and left for a further 28 days.

Mussels from each patch were collected and put in separate, labelled plastic bags before freezing. Each labelled bag of mussels was taken and allowed to thaw. All the soft tissue was scraped out of each mussel leaving only the empty shell valves. The clean valves were allowed to dry at room temperature. Each pair of valves was marked with numbers written with a black permanent marker (Artline® 700). The left valve from each mussel was used for measurements. These mussel shells were embedded in Polyester resin, using plastic cutlery trays as moulds. They were embedded to prevent them from chipping during cutting. The shells were carefully sectioned sagitally, from the umbo to the tip of the growing edge (Plate 4.1), using a revolving diamond coated blade (Kaehler, 1999; Kaehler and McQuaid 1998).

The total length (L_T), from the umbo to the tip of the growing edge (Plate 4.1) was measured to the nearest 0.02mm with vernier callipers. An Olympus fluorescence microscope exciting at 460 to 490nm (U-MWIB Cube) (Kaehler and McQuaid, 1998; Kaehler, 1999) was used to detect growth lines, visible where calcein had been incorporated into the shell (Plate 4.2). This allowed for the measurement of growth:

- between the two calcein lines (i.e. growth before treatment was applied) this is g_o on Plate 4.2.
- from the second calcein line to the growing tip (i.e. growth after treatment was applied) this g_f on Plate 4.2.

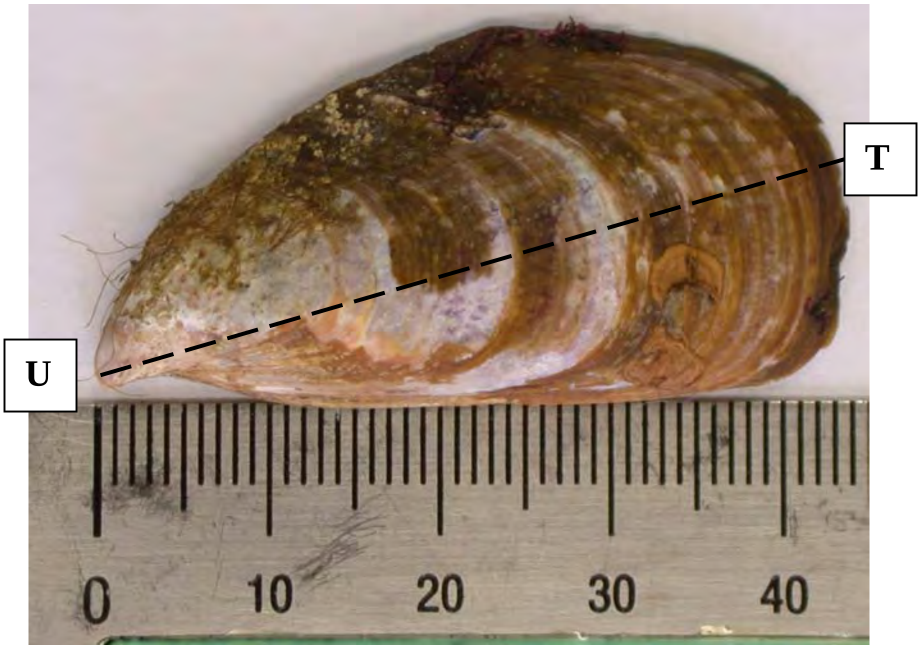

Plate 4.1: Mussel shells were embedded in resin and sagitally sectioned from the tip of the growing edge (T) to the umbo (U), as shown by the dotted line.

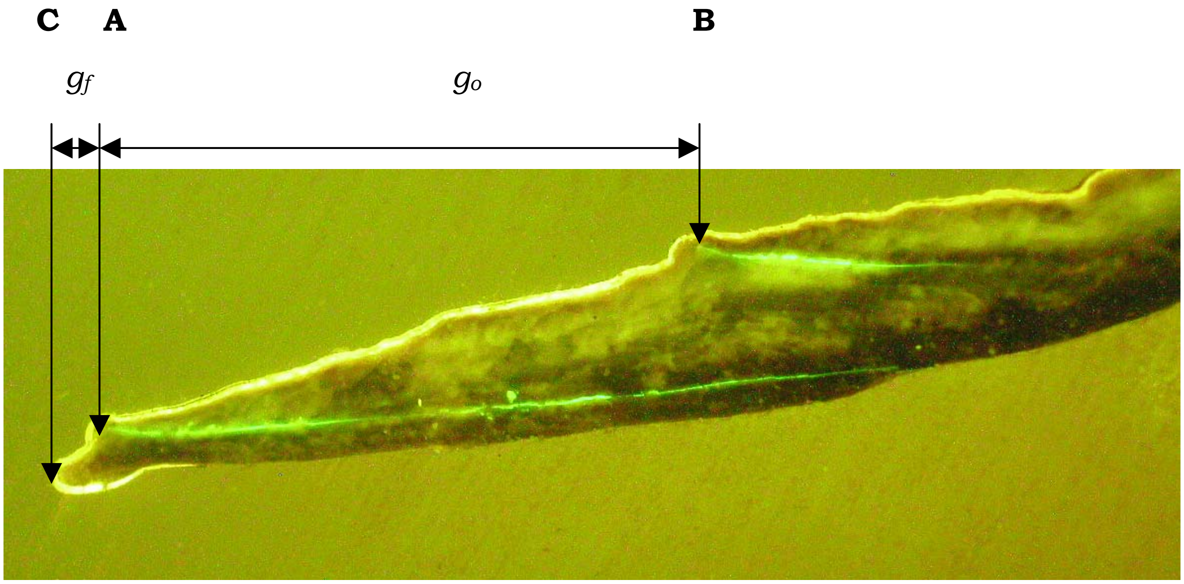

Plate 4.2: Sagittal section of a shell (*not to scale*) showing calcein marks (A and B) that glowed when observed under a fluorescence microscope. C is the growing tip; with g_o the initial growth (growth after the first calcein injection) and g_f the final growth (growth after the second calcein injection).

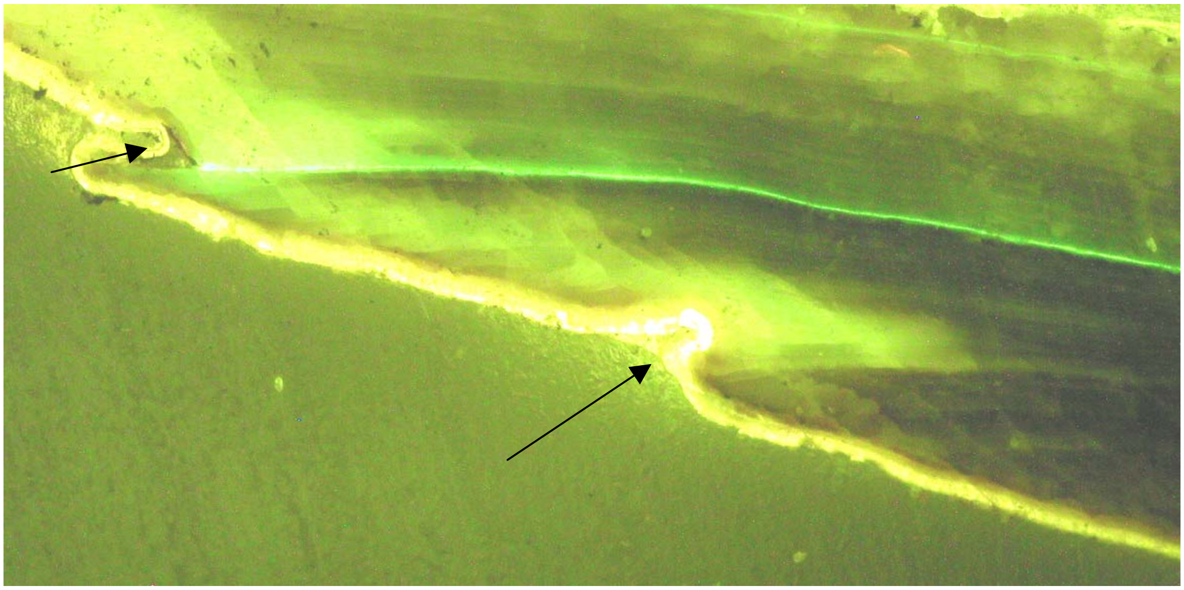

Plate 4.3: Shell (*not to scale*) showing two growth checks. These shells were eliminated from the analysis of growth rates.

Statistical Analysis

A 1-way analysis of co-variance was conducted with growth rate being the dependant variable, initial length as the co-variate and treatment as the fixed factor. For growth before treatment was applied (g_o), the initial length was from the umbo to the first calcein mark. For growth after treatment was applied (g_f), initial length was from the umbo to the second calcein mark. Treatment consisted of mussel patches with manipulated water flow and those mussel patches whose water flow patterns were not manipulated. This analysis was conducted separately for the low and high and low zones as the two sets of measurement covered different dates.

3. Results

The process of injecting calcein caused visible growth checks in some individuals, resulting in inaccurate estimates of growth (Plate 4.3). All mussels that had growth checks were excluded from the final data analysis. The exclusion of mussels with growth checks, combined with the narrow size range, obscured the relationship between initial length and growth rates within each patch (see below). It also resulted in a small number of marked mussels within each patch, making the determination of possible inter-patch variation impossible. The initial intention of introducing “patch” as a second factor in the analysis was abandoned. Data from different patches that had the same treatment in each zone were combined.

Before treatment was administered, initial length as a co-variate had a significant effect on the growth rates at (Tables 4.1 and 4.2) in both the low and high zones (Figures 3.4 and 3.5). This result indicated that growth rates depend on the initial length, as expected. However there was no significant difference between experimental and control patches before treatment was administered.

After treatment was administered, the co-variate initial length had a significant effect only on the low zone (Table 4.3). Likewise treatment had a significant effect only on the low zone (Table 4.3) as shown in figure 4.4. In the low zone mussels in experimental patches had significantly higher growth rates than those in control patches (Figures 4.3 and 4.4). Both treatment and initial length did not have significant effect on the grow rates of the mussels in the high zone after treatment was applied.

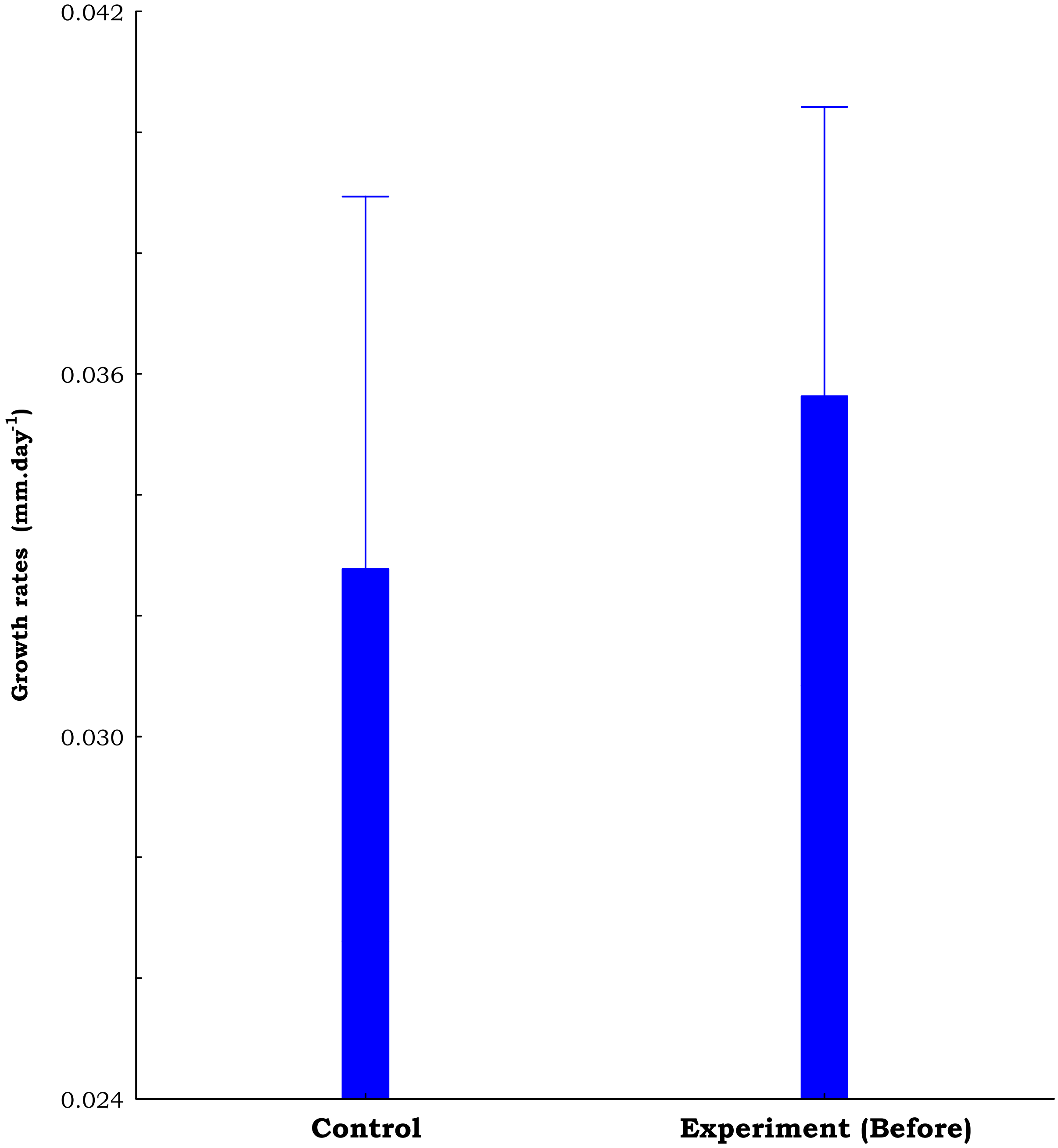

Figure 4.1: Mean growth rates (mm.day^{-1}) and their standard deviations, on control and experimental patches on the high zone before treatment was administered (n=99).

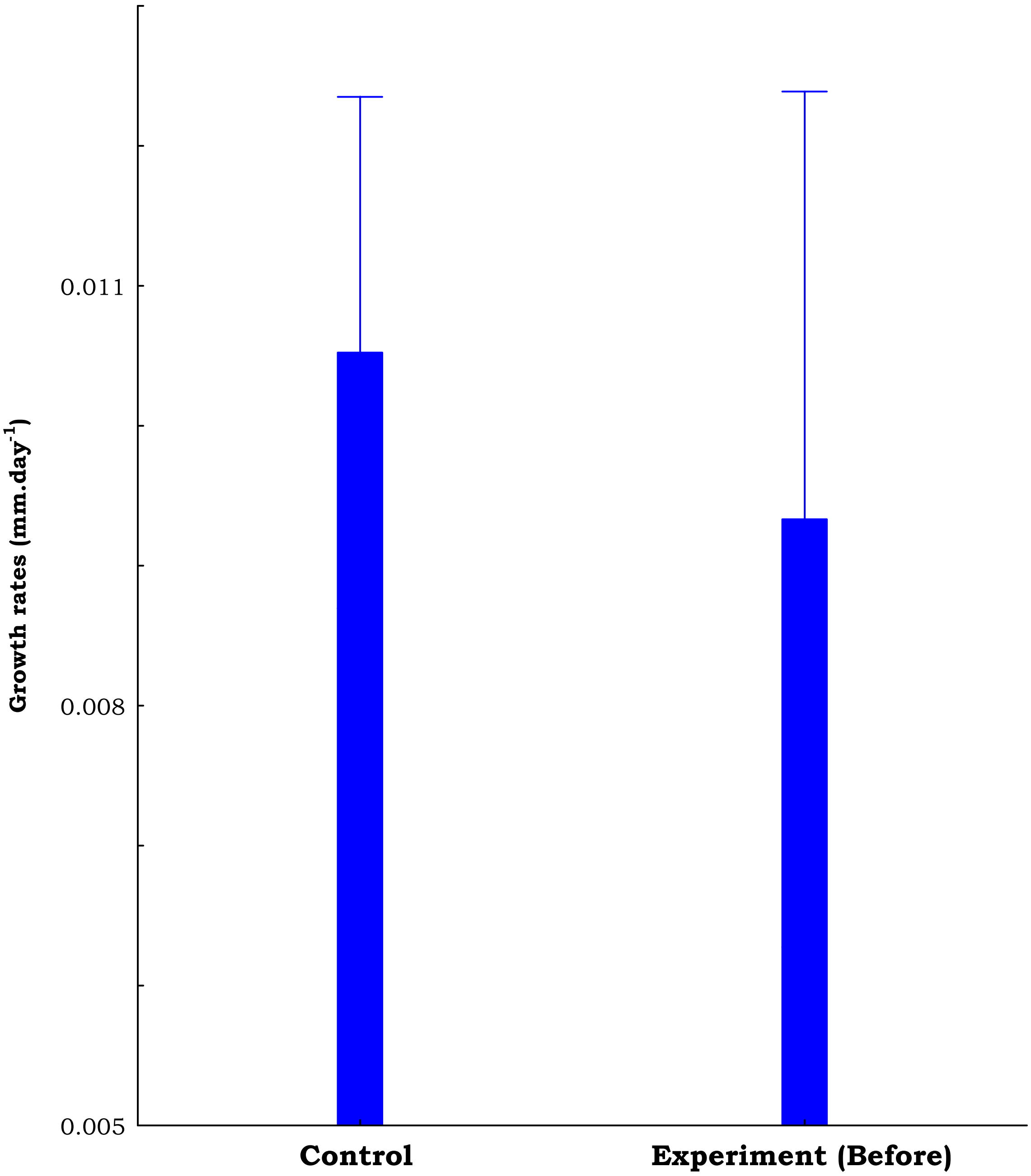

Figure 4.2: Mean growth rates (mm.day^{-1}) and their standard deviations, on control and experimental patches in the low zone before treatment was administered (n= 64).

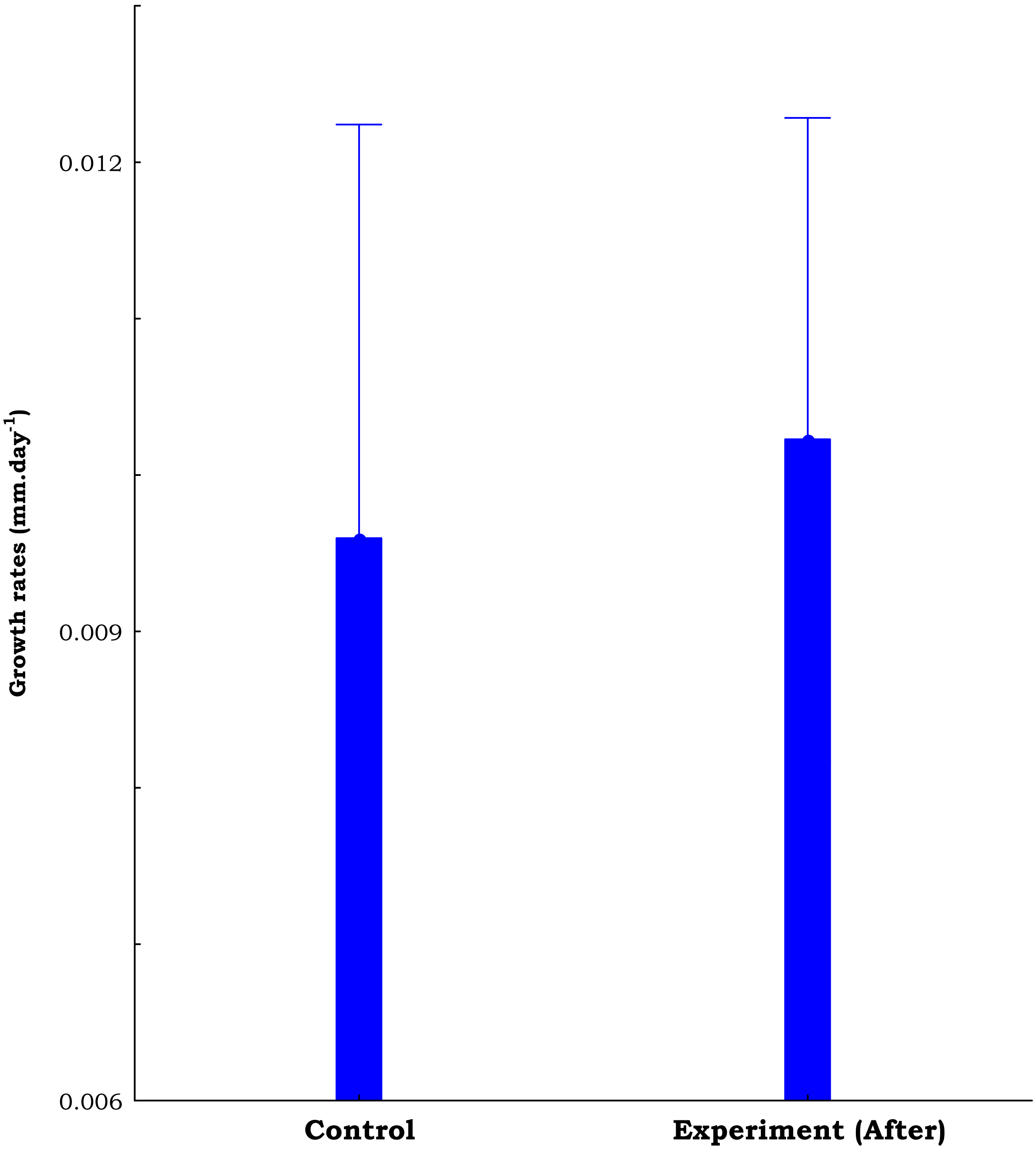

Figure 4.3: Mean growth rates (mm.day^{-1}) and their standard deviations, on control and experimental patches in the high zone after treatment was administered (n= 99).

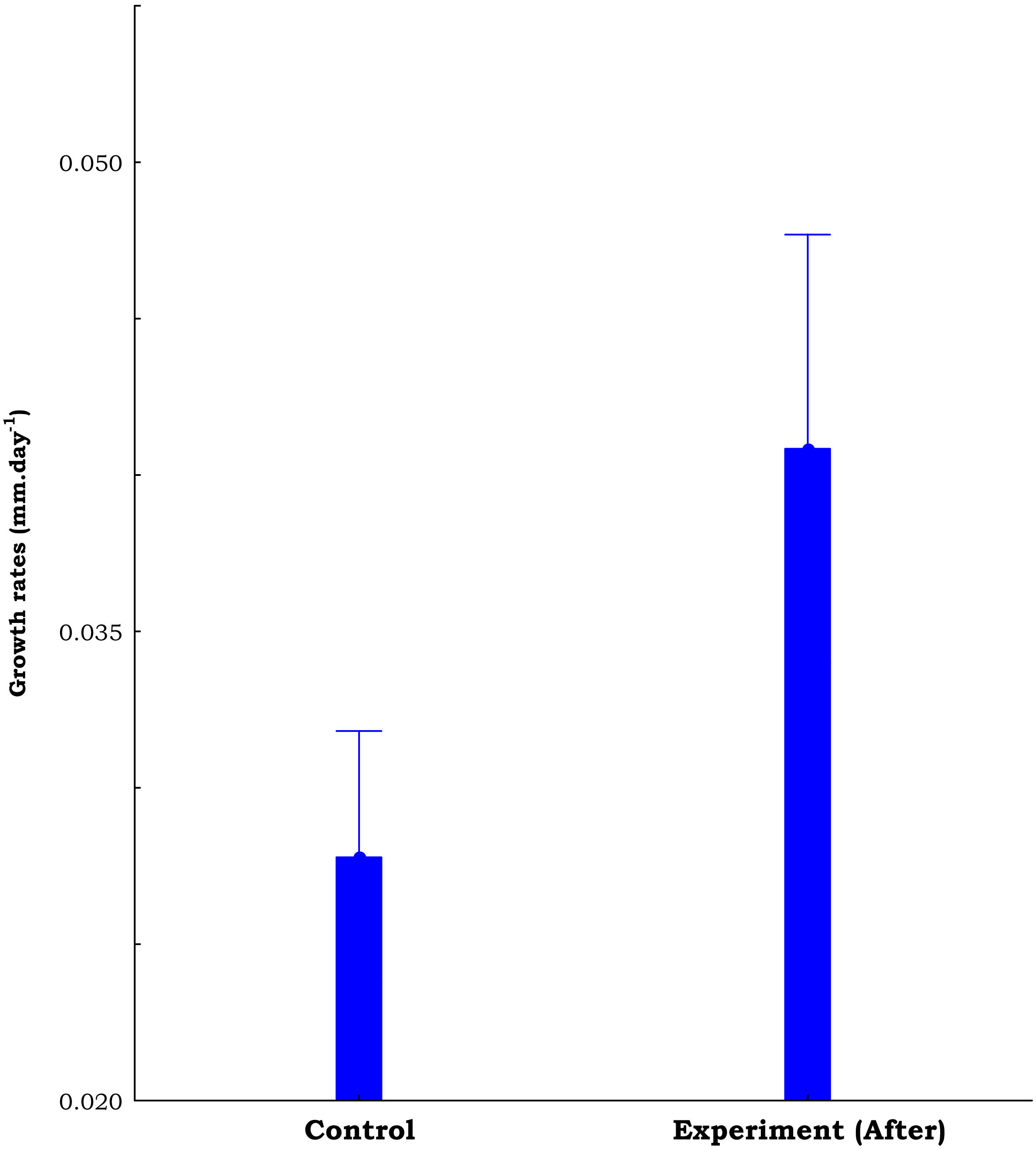

Figure 4.4: Mean growth rates (mm.day^{-1}) and their standard deviations, on control and experimental patches in the low zone after treatment was administered (n= 64).

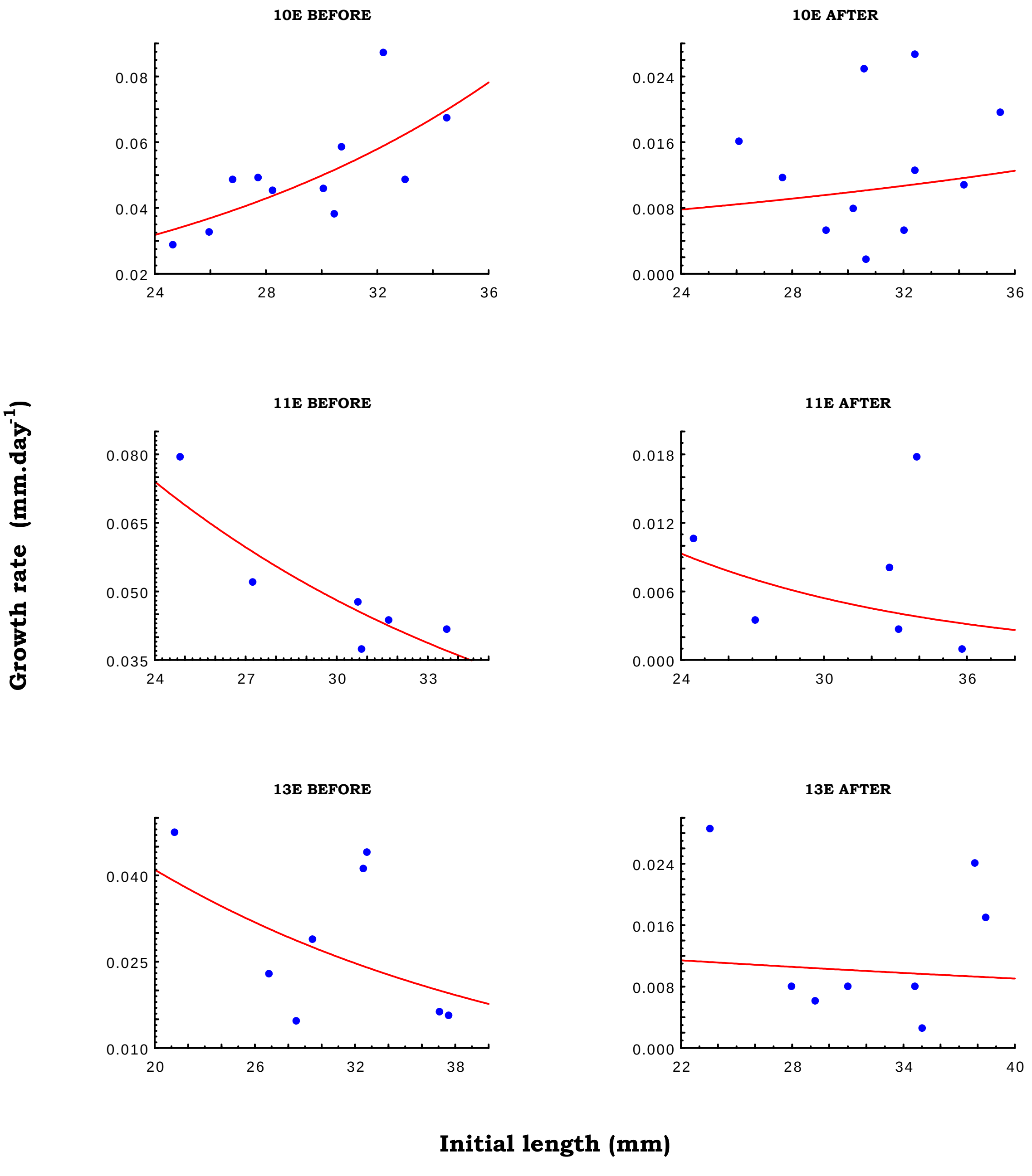

Figure 4.5: Relationship between initial length and growth rates on the high zone. **E** on each title show experimental patches, **C** control and the numbers 10, 13, 16 etc, indicate patch number. **BEFORE** and **AFTER** indicate before and after treatment was administered respectively. Small sample sizes and narrow size ranges resulted in weak or spurious relationships in some cases.

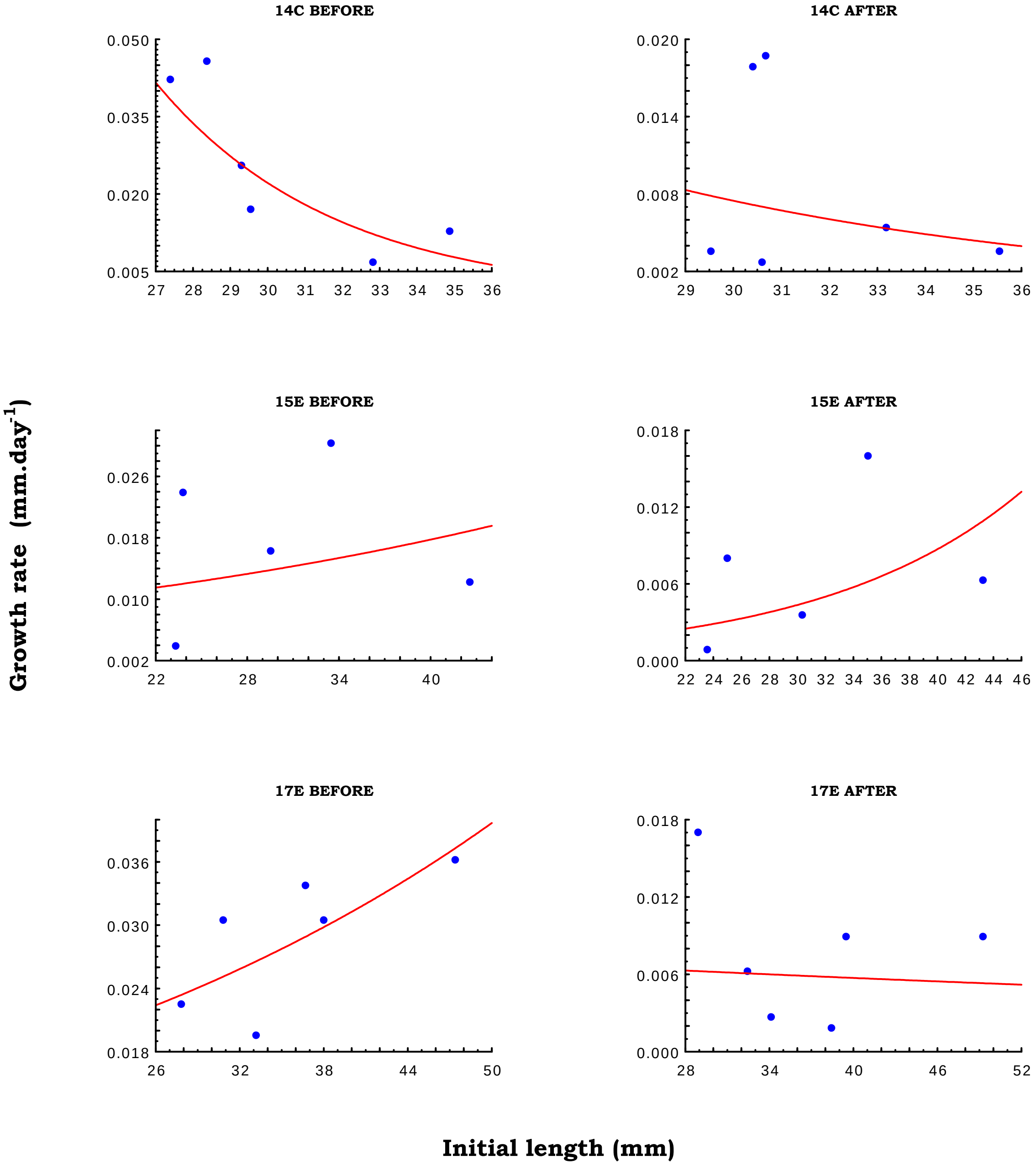

Figure 4.5 Continued:

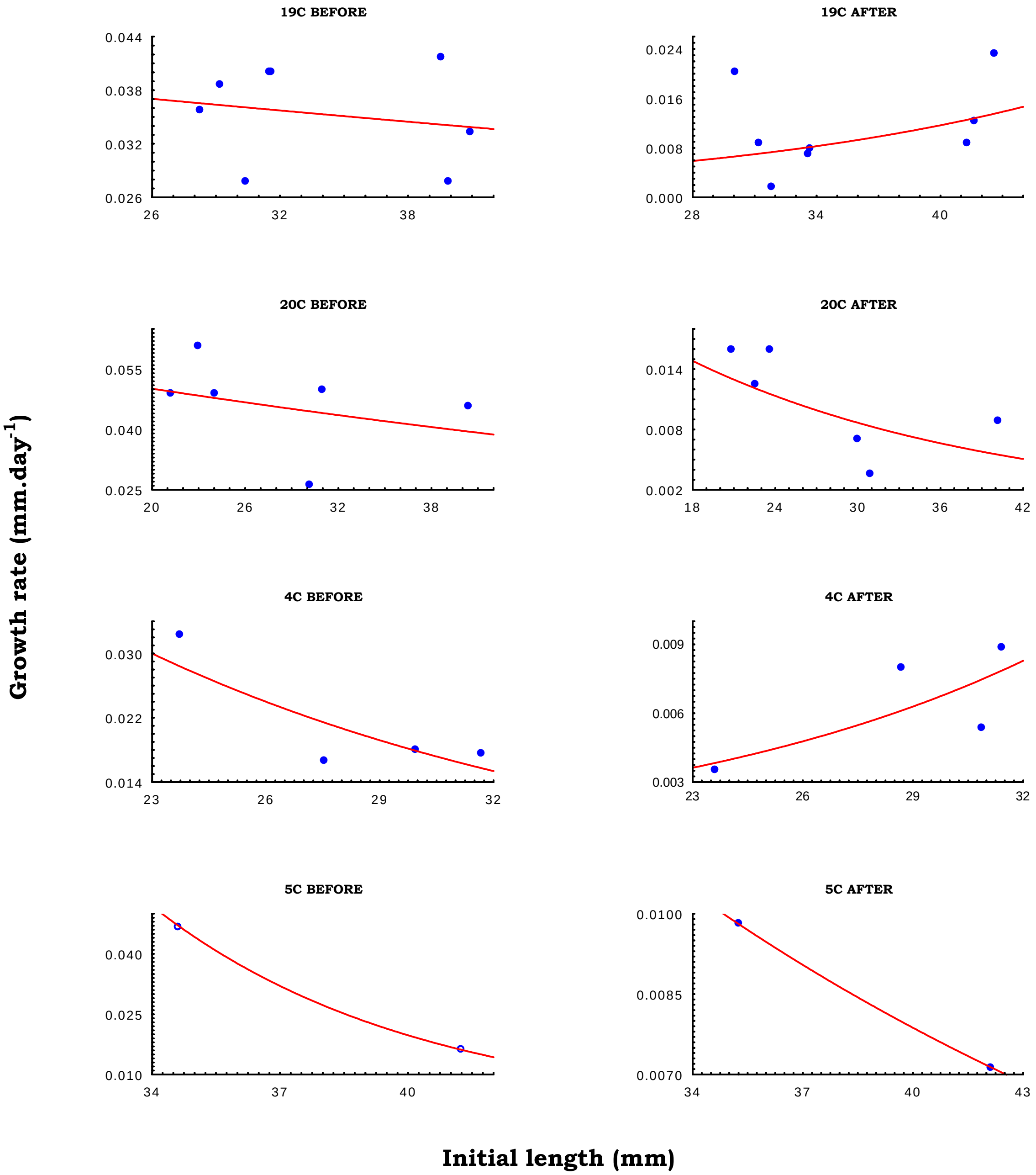

Figure 4.5 Continued:

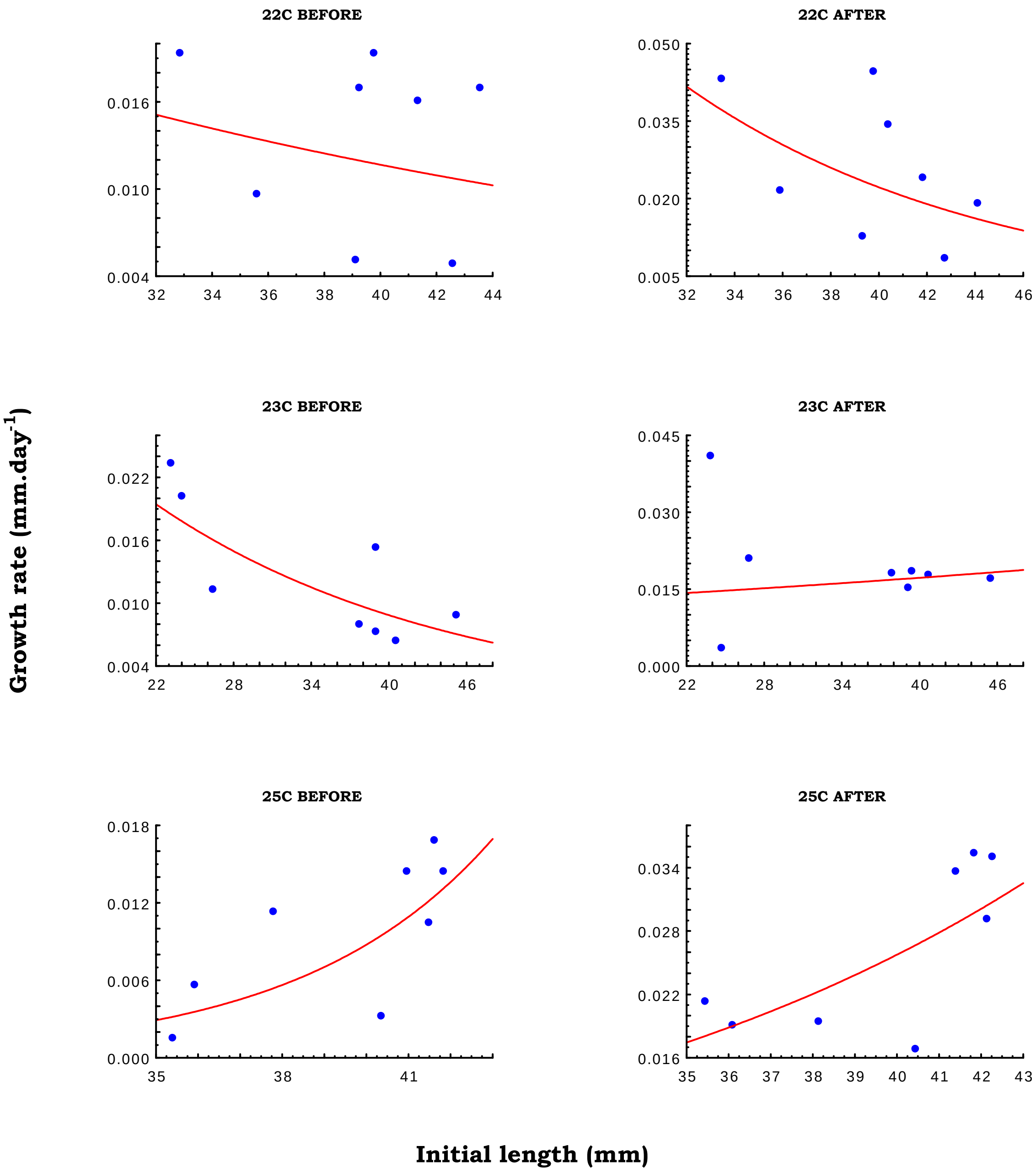

Figure 4.6: Relationship between initial length and growth rates. The title on each graph represents patch number, **E** experimental patches, **C control** patches on the low zone. **BEFORE** and **AFTER** indicate before and after treatment was administered respectively.

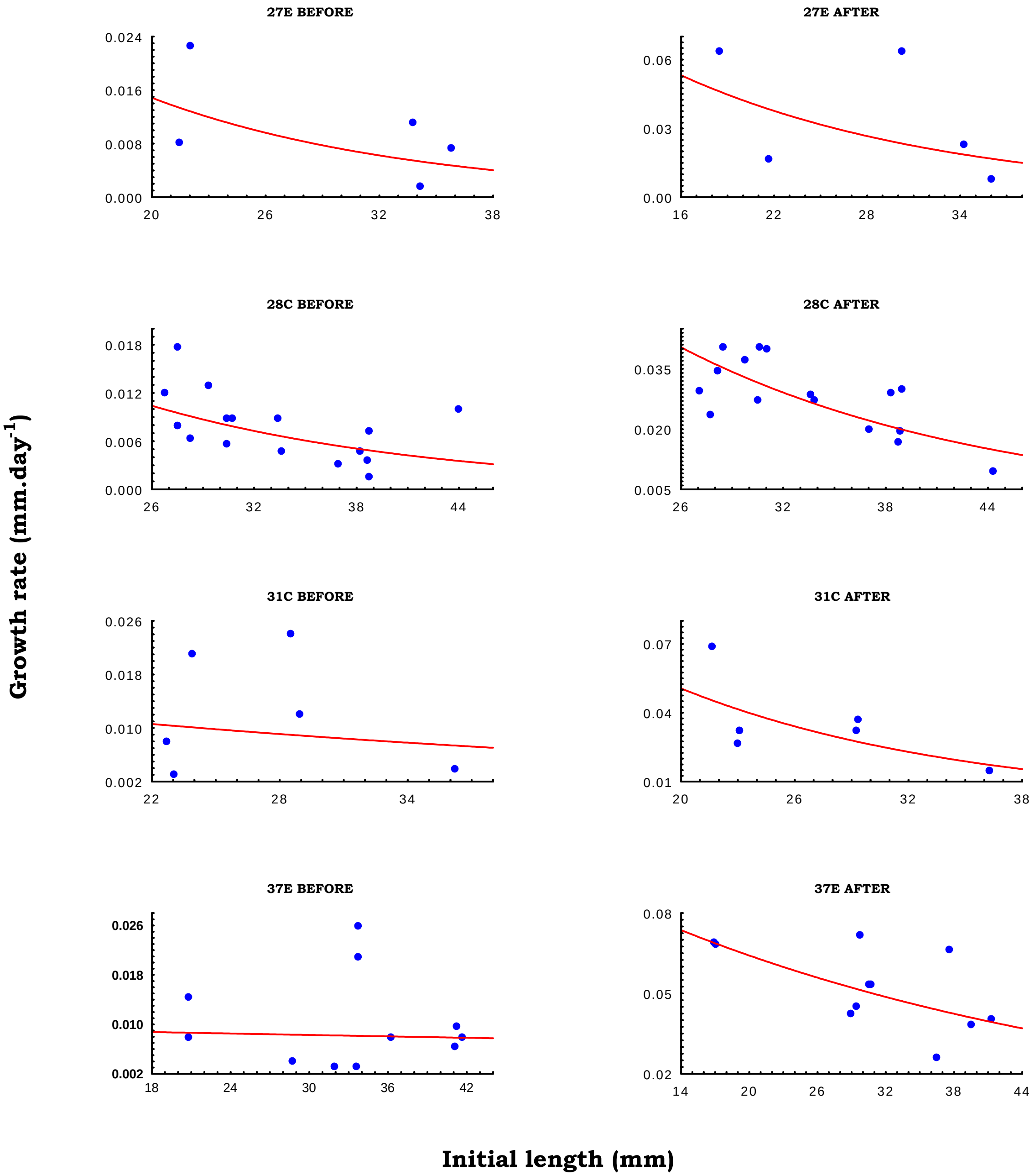

Figure 4.6 Continued:

Statistical results

Table 4.1: ANCOVA comparing patches before treatment was introduced in the low zone. These patches were divided into two groups *i.e.* those that were later manipulated and the control patches, with initial length as a co-variate. IL represents initial length.

	d.f.	**M.S.**	**F**	**P**
Co-variate (IL)	1	0.000170	4.36	0.0410
Treatment	1	0.000017	0.44	0.5081
Error	61	0.000039		

Table 4.2: ANCOVA comparing patches before treatment is introduced in the high zone. These patches were divided into two groups *i.e.* those that were later manipulated and the control patches, with initial length as a co-variate. IL represents initial length.

	d.f.	**M.S.**	**F**	**P**
Co-variate (IL)	1	0.001373	5.57	0.021230
Treatment	1	0.000132	0.53	0.467647
Error	66	0.000246		

Table 4.3: ANCOVA on the relationship between treatment and growth rates, with initial length as a co-variate in the low shore after treatment was administered. IL represents initial length.

	d.f.	**M.S.**	**F**	**P**
Co-variate (IL)	1	0.003144	16.79	0.000125
Treatment	1	0.001959	10.46	0.001967
Error	61	0.000187		

Table 4.4: ANCOVA on the relationship between treatment and growth rates, with initial length as a co-variate in the high shore after treatment was administered. IL represents initial length.

	d.f.	**M.S.**	**F**	**P**
Co-variate (IL)	1	0.000002	0.05	0.818739
Treatment	1	0.000006	0.14	0.707969
Error	66	0.000045		

4. Discussion

This study showed that small-scale flow patterns have a significant effect on mussel growth rates only under specific conditions. In this study the main difference between the high and low zones was the period that each zone was exposed to air and hence both temperature variation and submergence or feeding time. The low zone was submerged for a longer period during each tidal cycle. Although it could not be tested statistically, mussels on the high shore had higher growth rates than those on the lower zone before treatment was administered. However, the low and high zones were not injected with calcein at the same time, hence temporal variation could explain this unexpected result.

On the higher zone initial length did not have a significant effect on the growth rate (Table 4.4). This result is difficult to explain because initial lengths of mussels are normally strongly linked their growth rates (Seed, 1969). Initial shell size is an important parameter in mussel shell-growth analysis studies. Larger mussels grow more slowly in terms of shell length, than smaller mussels (Seed, 1969; Barnes and Hughes, 1982).

There are two possible explanations for these variations in mussels' growth rates: they could be because larger mussels have lower metabolic rates or because larger mussels put most of their energy into mass accumulation rather than increasing in length. However, Seed (1969), suggests that decreased metabolic rate in bigger mussels is not the primary cause of low rates of shell length increase. Larger, non-growing mussels that were moved to conditions considered favourable started growing again.

Mussel growth rate on the high zone was several times lower than in the low zone after treatment was administered. However the low growth rate on the high zone should not have masked the effects of initial length on growth rate. The most probable explanation of this observation is the narrow size range of the mussel shells used in this experiment (Figures 4.5 and 4.6).

Most of the mussels collected within the 5-10mm-size range did not have any calcein marks. This could be due to the fact that small mussels died when the syringe needle penetrated too deep into the tissues during injection and hence the mussels within 5-10mm size range collected were not injected at all. Smaller (<10mm) shells were difficult to handle during drying, embedding and sectioning.

The absence of smaller mussels in the samples, led to the narrowing of the mussel size range used in this study. The narrow size range made it difficult to determine the effect of the initial length on growth rate of mussels within individual patches. It was also impossible to show how much variation there was among patches subjected to the same treatment.

Mussels on the low shore grow faster than the ones on the high shore that have a longer period of aerial exposure. This suggests that mussels on low shore have more extended feeding periods than the ones on the high shore and are subjected to less growth retarding stresses (Seed, 1969; Barnes and Hughes, 1982, Harris *et al*, 1998). Mussels on high intertidal zones can also lower their somatic growth rates in order to increase their reproductive output (Franz, 1997).

Although treatment was administered on both the low and high zone it did not have any significant effect on the growth rates of mussels on the high zone (Table 4.4). The effect of exposure on *P.perna* growth rates decreases with an increase in shore height (McQuaid *et al*, 2000). Apart from decreased food availability (Alunno-Bruscia *et al*, 2000); mussels on higher shores experience greater desiccation and other stresses such as decreased oxygen availability, caused by emersion. These stresses may also mask the effect of exposure on mussel growth rates on the higher shore (Barnes and Hughes, 1982; McQuaid *et al*, 2000).

According to Calvo-Ugarteburu and McQuaid (1998), when mussels are exposed to air they may close their valves and switch to anaerobic metabolism. This mechanism reduces the risks of desiccation, but leads to inefficient use of energy resources resulting in reduced growth rates.

In studying population dynamics, it is important to remember that different factors interact in shaping intertidal communities. This study gives evidence of variations caused by tidal height and small-scale water movement, on the growth rates of the brown mussel *Perna perna*. At small scales (cm) exposure to water motion lowers *P.perna* growth rates, while at larger scales exposure to water movement (wave action) increases growth rate. Organisms experience their environments at small scales, in mussels this is at cm scales. It is recommended that future studies on mussel growth rates be conducted at centimetre scales, as this will show how environmental factors directly affect individuals within a population.

Chapter 5

Synthesis

Synthesis

Environmental gradients shape intertidal communities at different spatial and temporal scales (Bailey, 1981; Hobday, 1995; Tomalin, 1995; Cigarría, 1999; Zacharias *et al*, 1999). Much work has been done on the effects of large scale of exposure on communities of different mussel species including the brown mussel *P.perna* (Alexander and Roughgarden, 1996, Harris *et al*, 1998; Lindsay 1998; 1999; McQuaid *et al*, 2000). Relative wave exposure of interdial organisms has also been quantified at meters and kilometer scales (Muus, 1968, Jokiel and Morrissey, 1993; Lindsay, 1998).

Quantifying relative wave exposure at small scales (cm) is been difficult, as it requires sophisticated electronic equipment (Muus, 1968). Cement balls made from Rockset® offered some insight on the relative effect of small-scale water movement on intertidal organisms (Kaehler, 1999). Most of the work done on the effects of wave exposure (water movement) has been observational (Eckman, 1979).

Intertidal organisms not only experience effects of water motion, they also modify water flow patterns at small scales (Eckman, 1983; Denny, 1988; Friedland and Denny, 1995; Widdows and Brinsley, 2002). Water flow patterns at small scales are hence influenced by both local topography and the organisms found in those local environments (Vogel, 1981; Denny, 1998). L-shaped metal baffles altered local topography at small scales, thereby decreasing water flow at centimeter scales and influencing *P.perna* settlement and growth rates.

Large-scale (kilometers) wave exposure increases settlement rate of the brown mussel *P.perna* (Beckley, 1979; Lindsay, 1998). However at small scales, low exposure to wave action increases larval settlement rates.

Settlement rates are not only determined by hydrodynamic conditions of the suitable substratum but by the interaction of different physical, biological and chemical factors (Fogarty *et al*, 1991). Mussel larvae can be transported by wave action over thousand of kilometers by different large-scale oceanographic conditions such as the direction of water currents (Dobretsov and Miron, 2001; McQuaid and Philips, 2001; Van der Meer *et al,* 2002).

This larval transportation over a wide range of distances determines the availability of larvae in the water column perpendicular to the suitable substrata (Kendall and Bedford, 1987; Bertness *et al*, 1992; McQuaid and Phillips, 2000). Large-scale exposure to wave action is important in bringing mussel larvae into contact with suitable substrata (Pineda, 1991; 2000).

Since the active movement of mussel larvae relative to large-scale water current is small, at these scales larvae behave like passive particles (Possingham and Roughgarden, 1990). Active larval behaviour only becomes important at small scales (centimeters to meters), when larvae have to find a substrate and settle (Hunt and Scheibling, 1996). After reaching a substratum mussel larvae test its suitability and then permanently attach to this substratum if they find it to be suitable (Crisp, 1974; 1984; Rittshoff *et al*, 1984; Lane *et al*, 1985; Pineda and Caswell, 1997).

If exposure to wave action is high when larvae are settling, these larvae can easily get washed away. *P.perna* larvae showed that, although large-scale exposure increases settlement rates, at small scales (cm) sheltered substrata have high settlement rates.

At large scales, exposure to wave action increases the growth rates of the brown mussel *P.perna* (Lindsay, 1999). Water brings the required nutrient and oxygen to intertidal organisms (Leichter and Witman, 1997). Low food availability leads to decreased shell length growth, wet weight and ash free dry weight (Barkati and Choundry; 1988).

The literature suggests that the bigger the water mass intertidal organisms come into contact with, the higher the amount of food particles they can potentially get (Leichter and Witman, 1997). However this study indicates that, if water comes at high velocities, intertidal organisms may not be able to use the resources available in that water mass (MacKenzie and Kiørboe, 2000). This water may pass over them at speeds that do not give enough time to filter through the water mass (Rothschild and Osborn, 1988; Patterson, 1991). *P.perna* mussels that were sheltered at centimetre scales showed increased growth rates compared to exposed individuals on the low zone. This suggests increased food availability in habitats that are sheltered in small scales.

Mussels that are on the high shore are subjected to extended periods of aerial exposure. These individual experience different stresses, including lowered feeding time, desiccation stress and decreased oxygen availability. When intertidal mussels are deprived of oxygen they turn to anaerobic respiration and lower their growth rates (Barkati and Choudhry, 1988; Calvo-Ugarteburu and McQuaid, 1998; Marsden and Weatherhead, 1998; Mouritsen *et al*, 1999; Abades *et al*, 2000).

Lowered water flow rates on the high shore did not have a significant effect on mussel growth rates. Mussel on the high zone had a higher growth rate compared to those on the low zone. This variation in growth rate might not be expected as mussels on the low zone are well supplied with nutrient and experience low desiccation stresses. The high growth rates observed on the high zone before treatment was administered might have been a result of seasonal variation in growth rates. Initial growth rates for the low and high zones were measured at different times of the year. Growth rates vary in both spatial (sites) and temporal (time or seasonal) scales (Garton and Johnson, 2000).

Mussels on the low zone had higher growth rate after treatment was administered compared to those on the high zone. Decreased water flow rate significantly increased mussel growth rates only on the low zone. It is possible that the effects of other stresses to which mussels on the high zone are exposed masked the effects of lowered water flow rates (McQuaid, *et al,* 2000)

In order to understand population dynamics of intertidal organisms, it is important to understand the effects of water movement at different spatial and temporal scales (Todd and Keough, 1994; Menge *et al*, 2002). In this study, cement balls gave an indication of average wave action experienced by intertidal organisms at small scales. L-shaped metal baffles decreased water flow rates at small spatial scales. The methods used in water flow manipulation and quantification can still be improved and used in other studies.

Although calcein has been used in *P.perna* growth studies (Kaehler and McQuaid, 1998), it has never been used in a study of this magnitude. Most (about 40%) of the mussels marked for the growth rate studies did not show any calcein marks (also Bownes, pers. comm.). The use of calcein on the growth rates of *P.perna* must be re-evaluated. It also recommended that other less invasive shell marking methods on *P.perna* be tested.

Several studies have been done on active larval choice by intertidal organisms during settlement (Crisp, 1955; Cranfield, 1973; Doyle, 1975; Raimondi, 1988; Mullineaux and Butman, 1991; Levin, 1990; Jonsson *et al*, 1991; Bourget and Harvey, 1998). Little is known on whether *P.perna* actively seek the substrata on which they settle.

This lack of knowledge calls for intensive laboratory and field studies on a host of factors that influence *P. perna* larval settlement at both spatial and temporal scales. This is the direction future research should follow in order to understand the population dynamics of *P.perna,* which is important in both ecological and economic terms.

Chapter 6

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