POPULATION DYNAMICS AND GROWTH RATES OF THE BROWN MUSSEL (*PERNA PERNA*) ON WAVE EXPOSED AND WAVE SHELTERED SHORES OF SOUTH AFRICA.

Submitted in fulfilment of the requirements for the Degree of

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by

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ABSTRACT

Population dynamics of *Perna perna* in low shore mussel beds were investigated over a 15 month period at six sites along the south coast of South Africa, with particular reference to the effects of wave exposure. The degree of exposure was first quantitatively ascertained using the dissolution of cement blocks to measure average wave force and dynamometers to measure maximum wave force. The mean mass loss of the cement blocks was higher at Diaz Cross and Kwaai Hoek than at Mgwalana, Rufanes and Riet River. No data were available for Fish River. The mean maximum wave force encountered at Diaz Cross, Kwaai Hoek and Fish River was significantly higher ($p<0.05$) than that at Mgwalana, Rufanes and Riet River. These results allowed the former sites to be classified as exposed and the latter as sheltered.

Early recruitment (1-5 mm) occurred throughout the year, but peaked significantly ($p<0.05$) from January 1995 to May 1996 on both shore types. Although mean recruit density (1-15 mm) was significantly higher at the exposed (5 896.m^{-2}) than the sheltered shores (2 986.m^{-2}), some sites did not show this trend. Further investigation revealed that the densities of recruits (1-5 & 6-10 mm) were significantly higher on algae than on mussels ($p<0.05$). Adult densities (>15 mm) were positively correlated with recruit densities (1-5 mm) for both shore types ($p<0.05$).

In turn, adult density (>15 mm) was significantly lower on exposed (mean of 3 348.m^{-2}) than on sheltered shores (mean of 4 796.m^{-2}) ($p<0.05$). Adult mussels on exposed shores had significantly higher mean and maximum lengths than those on sheltered shores ($p<0.05$). Biomass, which is a product of density and length, showed no significant difference between the two shore types ($p>0.05$).

The effect of exposure on growth rate formed the focal point of this study and was determined using three different approaches. The first technique, mark-recapture, involved filing notches on the growing edges of mussels in the field. After 111 days, mussels were removed and the growth measured. The second approach used internal growth bands to measure growth rates, once the periodicity with which these bands were laid down was established. Thirdly, using Shepherd's length composition analysis (SLCA), growth rates were determined from length frequency distributions in 11 samples taken over 15 months. The general conclusion from all three approaches was that growth rate was twice as fast on the exposed shores as on the sheltered shores ($p<0.05$). A mean length (averaged from all three methods) of 47.06 mm was attained within the first year of growth at the exposed shores and 22.07 mm at the sheltered shores. There were however considerable differences among these approaches. The mark-recapture method predicted the lowest growth rates, followed by growth band method and lastly SLCA.

The mean mortality index ($Z.year^{-1}$) for mussels was significantly ($p<0.05$) higher at the exposed shores ($Z=1.81$) than at the sheltered shores ($Z=0.73$). Consequently, the percentage survival rates per annum of mussels of all ages (total), 18 days to 6 months (juveniles) and 12 months to mortality (adults) was lower on the exposed than the sheltered shores. The survival rate of juveniles was as low as 0.71% per annum on the exposed shores and 9.29% per annum on the sheltered shores. The adult survival rate of exposed shore mussels was 11.78% per annum, considerably lower than that of sheltered shore mussels, 48.05%. The turnover rate on exposed shores was faster than on sheltered shores as the mean longevities were 2.6 and 6.7 years respectively. In conclusion, these findings showed that the effects of exposure on recruitment, growth and mortality are important in low shore mussel beds.

DECLARATION

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

Tracy Lynn Lindsay

T. Lindsay

19-05-1998

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I am most grateful to my parents and parents-in-law for encouraging and supporting me through my studies. Finally, many thanks to my colleague, friend and husband, Justin, for his time spent in the field, in discussions, for his encouragement and love of life.

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MUSSEL SPECIES MENTIONED IN THIS THESIS

Common name	Scientific name
Ribbed mussel	*Aulacomya ater*
Black mussel	*Choromytilus meridionalis*
Subtidal mussel	*Modiolus modiolus*
Californian mussel	*Mytilus californianus*
Blue mussel	*Mytilus edulis*
Mediterranean mussel	*Mytilus galloprovincialis*
Brown mussel	*Perna perna*
Peru mussel	*Perumytilus purpuratus*

GENERAL INTRODUCTION

A population is a product of past and present physical and biological interactions acting at global, regional and local scales (Sutherland 1974). It is the integrated effects of the main controlling factors that need to be addressed in an attempt to understand a community (Delafontaine & Flemming 1989). In New England, differences in the relative importance of predation, competition and physical disturbance have led to sites in close proximity to one another displaying different intertidal community structures (Menge 1976, Lubchenco & Menge 1978). In some cases, the influence of one factor may outweigh the effects of others in structuring or eliminating a population. A classical example of predator pressure controlling a population occurs on Malgas Island off the west coast of South Africa, where mussels are scarce due to intense predation by rock-lobsters (Barkai & Branch 1989). In other circumstances, interspecific competition may be more important in influencing population dynamics as is evident off the west coast of South Africa where the exotic Mediterranean mussel, *Mytilus galloprovincialis* has largely replaced the indigenous ribbed mussel, *Aulacomya ater* (Griffiths *et al.* 1992).

Along the South African coast the decreasing gradient of intertidal primary production and nutrient concentration from the west coast to the east coast would be expected to be reflected in the biomass attained by filter feeders (Bustamante *et al.*. 1995). The absence of such a relationship, however, is due to the over-riding effect of wave action on biomass at a local scale (Bustamante *et al.* 1995).

The effects of wave action on individuals and populations are varied and have been documented for several species of filter feeders (Jones & Demetropoulos 1968, Harger 1970, Raubenheimer & Cook 1990, Leeb 1995). The magnitude of wave exposure is responsible for patterns of distribution at fine and broad scales (Menge & Farrell 1989). The absence of the blue mussel, *Mytilus edulis* from exposed Californian sites where the Californian mussel, *Mytilus californianus* is dominant, has been explained by the inability of the former species to attach effectively at high wave exposure (Harger 1968, 1970, Harger & Landenberger 1971). Delafontaine & Flemming (1989) stated that the factor limiting the lower boundary of the barnacle, *Tetraclita serrata* was excessive wave impact during submergence. Wave exposure also had an influence on the distribution of the anemone, *Anthopleura elegantissima* in Washington (Dayton 1971). Gastropods, *Littorina* sp., from wave exposed shores were shown to have thinner shells than those from wave protected shores (Boulding & Van Alstyne 1993). Along the west coast of South Africa the degree of exposure affects the balance between trophic levels by shifting the biomass of certain levels (McQuaid & Branch 1985). The absolute biomass of filter feeders, carnivores and omnivores increased with an increase in wave exposure (McQuaid & Branch 1985). Furthermore, the patterns of energy flow will thus vary between exposed and sheltered shores, as greater energy is imported into the system on exposed shores (McQuaid 1980, McLachlan *et al.* 1981, McQuaid & Branch 1984, 1985).

It is widely accepted that wave exposure affects growth rates of mussels (Jones & Demetropoulos 1968, Harger & Landenberger 1971, Raubenheimer & Cook 1990). However, some authors have shown a decrease in growth rates with increasing exposure (Seed 1968, Jørgensen 1976), and others have shown an increase in growth rates with increasing exposure (Van Erkom Schurink & Griffiths 1993, Leeb 1995). Strong wave action can also prevent predators from controlling populations and thereby influence rates of mussel mortality (Kitching *et al.* 1958, Dayton 1971).

Species may survive in an environment in one of two ways, either "resistance adaptation" whereby an organism is able to tolerate a wide range of environmental variables or "capacity adaptation" whereby rate functions are optimal for "normal" conditions (Gillmor 1982). A population higher up the shore must be able to tolerate fluctuations in environmental conditions and is therefore more likely to be resistance adapted. Low shore organisms are expected to be capacity adapted as their environment is more stable (Gillmor 1982). However, low shore organisms on wave exposed and wave sheltered shores can be expected to show different adaptations. Exposed shores tend to receive more splash and spray which reduces the physical harshness of aerial exposure and may result in capacity adaptation, whereas sheltered shore organisms may need to be resistance adapted due to the harsher conditions of aerial exposure (Underwood 1981, Gillmor 1982).

Species in localities of close proximity can exhibit widely differing responses to disturbance (Dye 1988). Populations of *Mytilus galloprovincialis* on Tatoosh Island (Washington) received greater wave action than those at Shi Shi (Washington) and had faster recovery rates after disturbance (Suchanek 1985).

Due to its cosmopolitan nature, a vast amount of the literature on mussels deals with *Mytilus edulis* (Seed 1969a & 1969b, Theisen 1973, Widdows *et al.*. 1984, Page & Hubbard 1987). In South Africa research has concentrated on the black mussel, *Choromytilus meridionalis* (Griffiths 1981, Griffiths & Buffenstein 1981), *Aulacomya ater* (Griffiths 1977, Griffiths & King 1979a & 1979b) and in more recent years on *Perna perna* (Berry 1978, Crawford & Bower 1983, Lasiak & Dye 1989, Culverwell 1992, Van Erkom Schurink & Griffiths 1993, Phillips 1994, Tomalin 1995). Harvesting by local people has placed considerable pressure on *Perna perna* along the former Transkei coast and raises questions about the sustainability of *Perna perna* elsewhere along the South African coast (Lasiak & Dye 1989, Lasiak 1991). Resource management can only be undertaken with a sound knowledge of the basic processes, namely, recruitment, growth and mortality rates, which regulate the size and structure of a population (Isaac 1990). From preliminary observations it appeared that mussel populations were affected by wave exposure and as a result the effects of exposure formed the basis of this study. As wave exposure can affect every stage of the mussels' life cycle from settlement (Petraitis 1991) to adult mortality (Harger 1970), the effects of exposure on recruitment, growth and mortality were investigated in *Perna perna* populations on the south coast of South Africa.

CHAPTER 1

QUANTIFYING WAVE EXPOSURE ON SHORES

1. INTRODUCTION

It is well recognised that both the distribution and the abundance of intertidal organisms are the results of complex physical and biological interactions (Palumbi 1984, Dalla Via *et. al.* 1987). Of the many physical aspects that shape the intertidal biome, the degree of wave exposure is thought to be one of the most important (Jones & Demetropoulos 1968, Jørgensen 1976, Palumbi 1984, Leeb 1995). Wave exposure can act on a broad scale by influencing the species composition of communities (Ballantine 1961), and on a finer scale by affecting all aspects of a marine organism's life history, such as settlement (Bertness *et al.* 1992), growth (Seed 1968, Jørgensen 1976, Leeb 1995) and mortality (Dayton 1971, Witman & Suchanek 1984).

The most obvious physical effects of wave action on mussels are lift and drag (Denny 1987), although damage by abrasion and pressure has also been suggested as being important in some species (Jones & Demetropoulos 1968, Leeb 1995). Lift is generated by the pressure differential caused by the differences in water velocity flowing above and within the mussel bed, and acts perpendicular to the direction of water flow (Denny 1987). The damaging effect of lift is greater in dense, firmly packed beds than in loosely packed, sparse ones and may result in sheets of mussels being removed (Denny 1987). Indirect measures of lift have been made by measuring the vertical force required to remove a mussel from the substratum (Harger 1970, Price 1980, 1982, Denny 1987, Leeb 1995). The force required to remove mussels from rocks increases as mussel size increases (Leeb 1995), but the proportion of increase varies between species (Harger 1970). Jones & Demetropoulos (1968) suggested that drag represents the greatest hazard to marine organisms not subject to abrasion. Drag, when increased by the presence of macroalgae, is capable of dislodging individual mussels (Dayton 1973), although seldom removes entire mussel patches as lift does (Witman & Suchanek 1984). However, experiments conducted on *Mytilus californianus* on the exposed coast of Tatoosh Island (Washington) have shown that drag alone was not capable of dislodging mussels (Witman & Suchanek 1984, Denny 1987). Besides the effects of drag and lift, wave action also has important influences on mass water flux (overall water motion), turbulence and erosion (Craik 1980, Bell & Denny 1994).

The subjective classification of a coastline as exposed or sheltered is usually undertaken relative to local or regional wave conditions. However, relating local wave exposure to that experienced nationally or internationally is hampered without the quantification of wave action. On a world-wide scale, for example, the South African coastline is generally regarded as a wave exposed coast (Field & Griffiths 1991), although on a regional scale varying degrees of wave exposure are encountered. Along the South African south coast sheltered bays, less exposed open shores and more exposed rocky headlands have been subjectively identified (Phillips 1994). These are useful categories, but without quantification they mean very little internationally. In efforts to make results more comparable, several scientists over the past 30 years have measured wave action using fairly simple and relatively cheap devices (Jones & Demetropoulos 1968, Doty 1971, Harger 1970, Craik 1980, Denny 1983, Palumbi 1984, Bell & Denny 1994, Alvarado & Castilla 1996). These methods rely on one of three basic approaches, the erosion or dissolution of material (Doty 1971), direct measures of mean and/or maximum wave forces (Jones & Demetropoulos 1968) and indirect measures, using the strength of byssal threads (Leeb 1995), prevailing wind conditions (Moore 1935) and the width of white splash (Underwood 1981).

The manner in which wave action is measured depends upon the process being examined. If filter feeding rates, larval settlement or passive dispersal were being studied then mass flux would be important (Bell & Denny 1994). This can be determined by measuring the dissolution rate of elements, for example cement blocks (Doty 1971, Craik 1980). However, additional factors such as turbulence and the erosion potential of suspended particles, can affect the dissolution rate (Craik 1980, Bell & Denny 1994). Furthermore, mortality and disturbance would possibly be better explained by a measure of maximum wave force rather than average water flow (Witman & Suchanek 1984, Denny & Gaines 1990). This highlights the importance of first defining the process under investigation before deciding how to quantify the forces affecting it. In this study the effects of wave exposure on many processes, such as, timing of early recruitment, recruit density, adult density, size, biomass, growth and mortality were under investigation. This necessitated the use of two types of measuring devices; one to measure average velocity and mass water flux, and the other to quantify maximum wave force.

The aims of this chapter were to:

- give a brief description of the study sites,
- subjectively classify the sites into more exposed or less exposed shores, and
- classify the sites using two quantitative measures of wave exposure, and in so doing produce results comparable to world-wide studies.

2. MATERIALS AND METHODS

Localities

The south-east coast consists of long sandy beaches which are interspersed with rocky stretches. Even within these stretches, rocks are intermittent so that mussel beds are encountered on a scale of metres (usually less than 100 m) rather than kilometres. After an investigative trip from Port Elizabeth to Kei Mouth, six sites were chosen that had mussel beds suitable for the investigation and were easily accessible (Figure 1.1). Diaz Cross (Dz) and Kwaai Hoek (Kw) are situated on small headlands and Fish River (Fs) is on a point. From observation these sites seemed to display characteristics of a reflective shore, having high energy waves which were reflected from the rocky mussel platforms or points. Mgwalana (Mg), Rufanes (Ru) and Riet River (Ri) were situated along straight stretches of shore. The waves at these sites seemed to have lower energy, much of which was probably dissipated by offshore sand banks or reefs, and as a result waves rolled rather than crashed onto the mussel bed.

Mussels at Diaz Cross, Kwaai Hoek and Riet River are situated on aeolianite or dune-rock. According to Marker (1988) aeolianite headlands, such as those at Diaz Cross and Kwaai Hoek have deep water offshore which allows big waves to pound the coast. The rocks at Fish River, Mgwalana and Rufanes, although dissimilar in appearance and hardness, are all of sandstone origin. The sampling sites at Rufanes and Fish River were separated from the shore by a gully, but all other sampling sites were directly accessible. All sites were at approximately the same tidal height. As an alternative to a thorough description of each site, photographs have been included (Figure 1.2 a-f).

Measurements of wave exposure at each site were undertaken in the lowest zone of intertidal mussels on the shore. Exposure was quantified by measuring maximum wave force using dynamometers and by comparative mass loss of cement blocks which gave relative measures of average water flux.

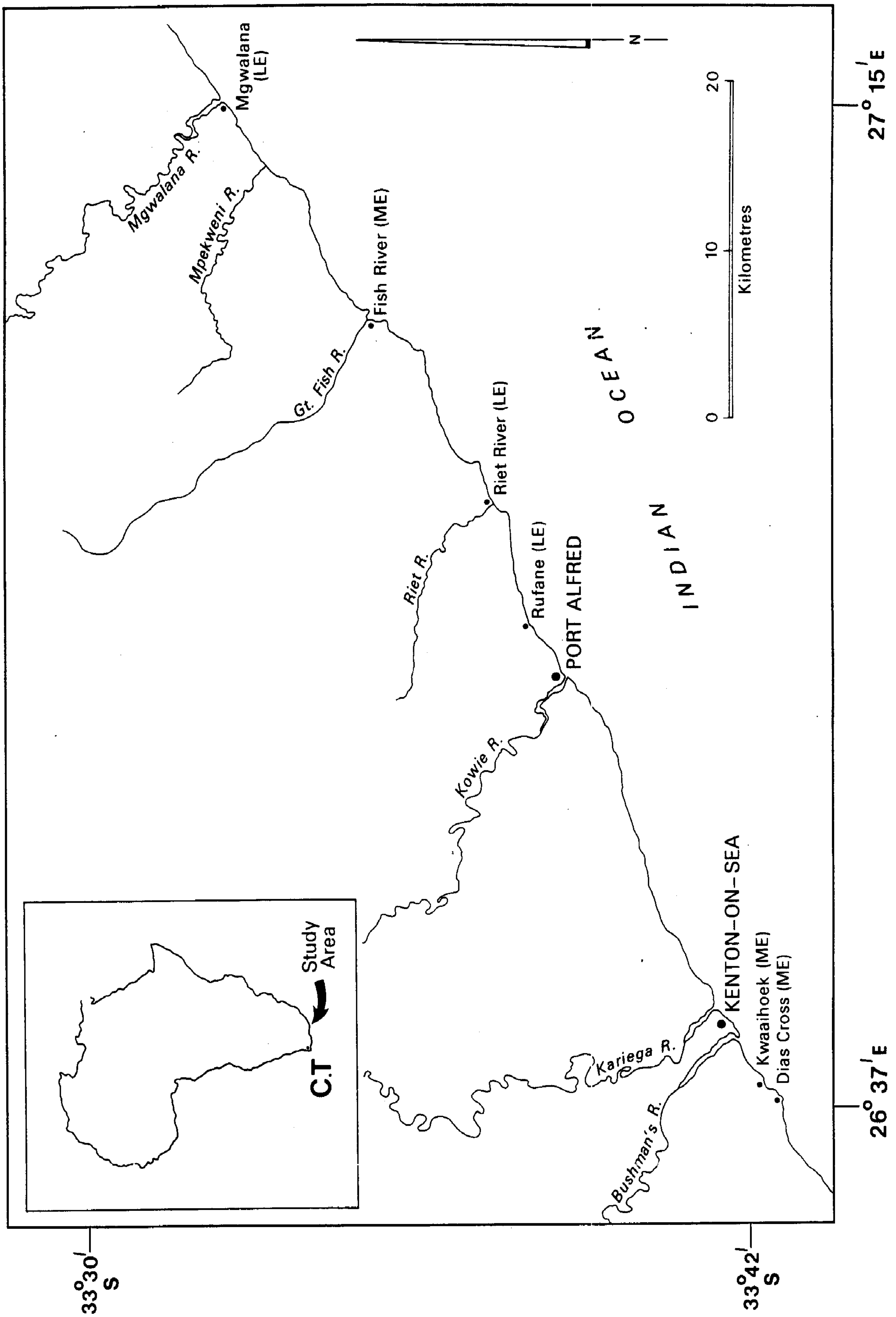

Figure 1.1 The locations of the sample sites along the south-east coast of South Africa. Less exposed sites (LE) are referred to in the text as sheltered sites and more exposed sites (ME) as exposed sites.

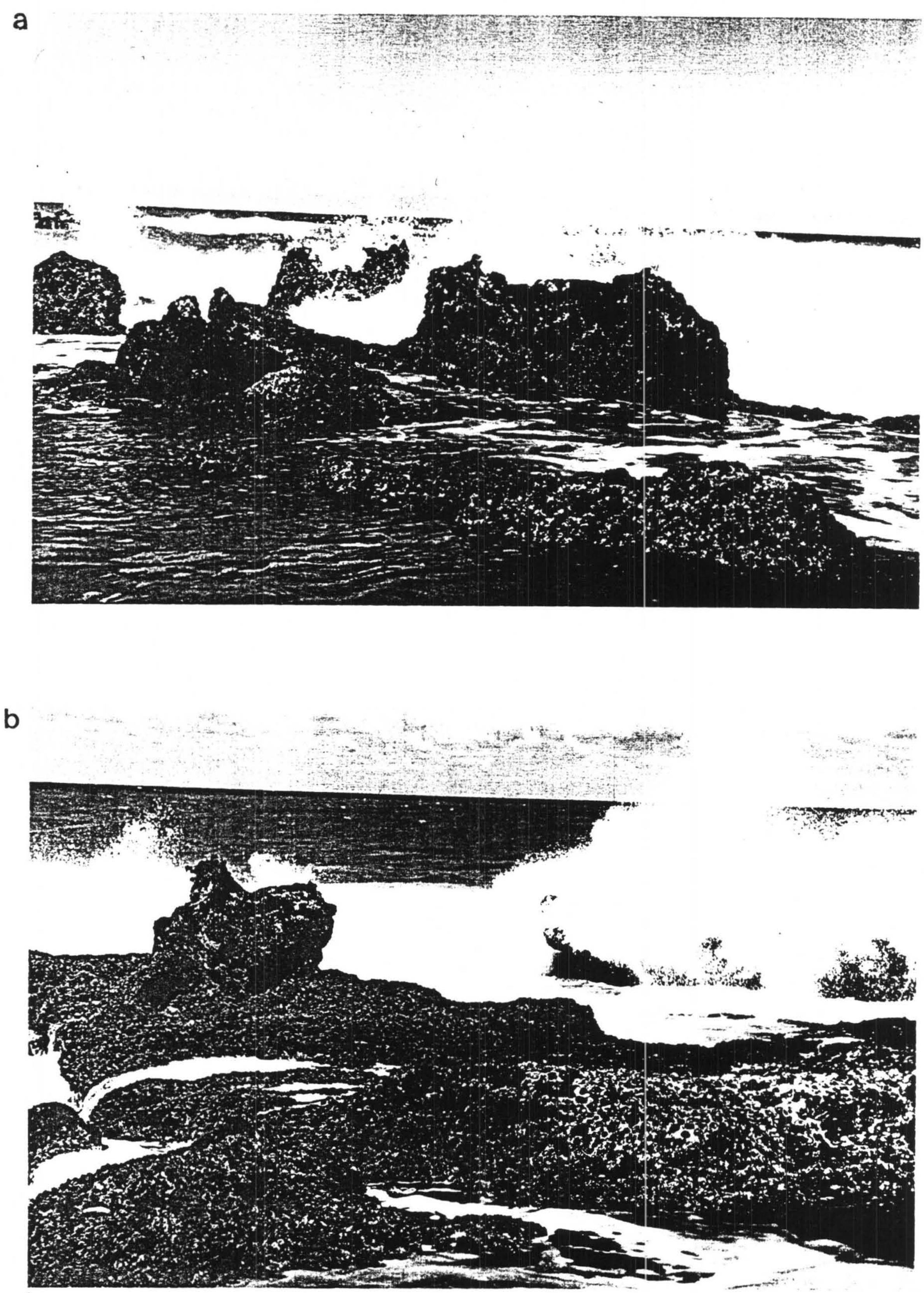

Figure 1.2 a) The mussel bed sampled at Diaz Cross and b) Kwaai Hoek. Note how the waves break close in-shore.

c

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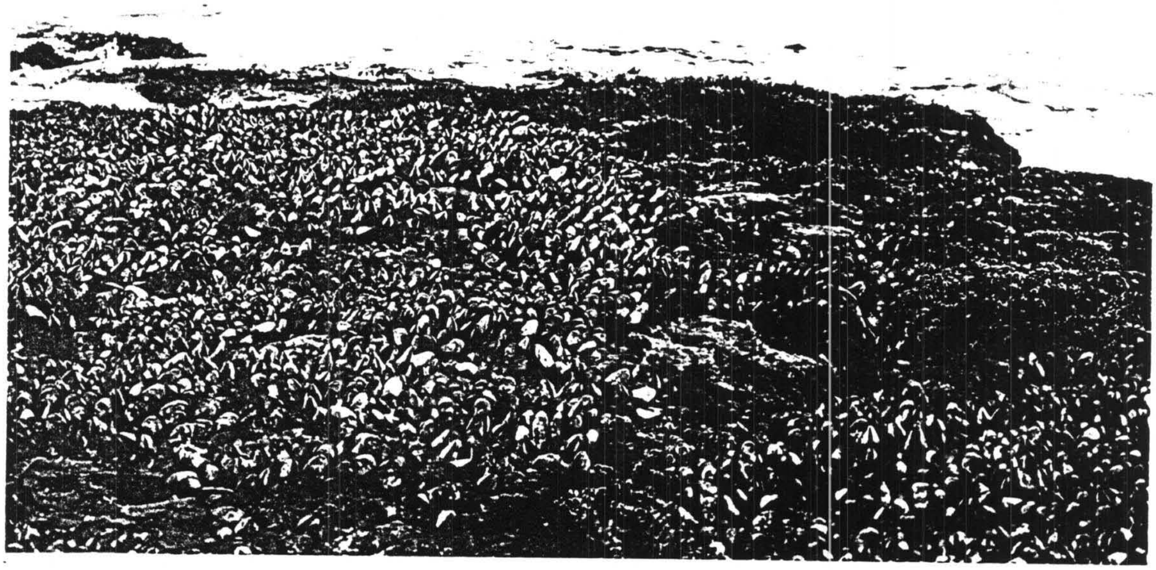

Figure 1.2 cont. c) The mussel beds sampled at Fish River, and d) Mgwalana.

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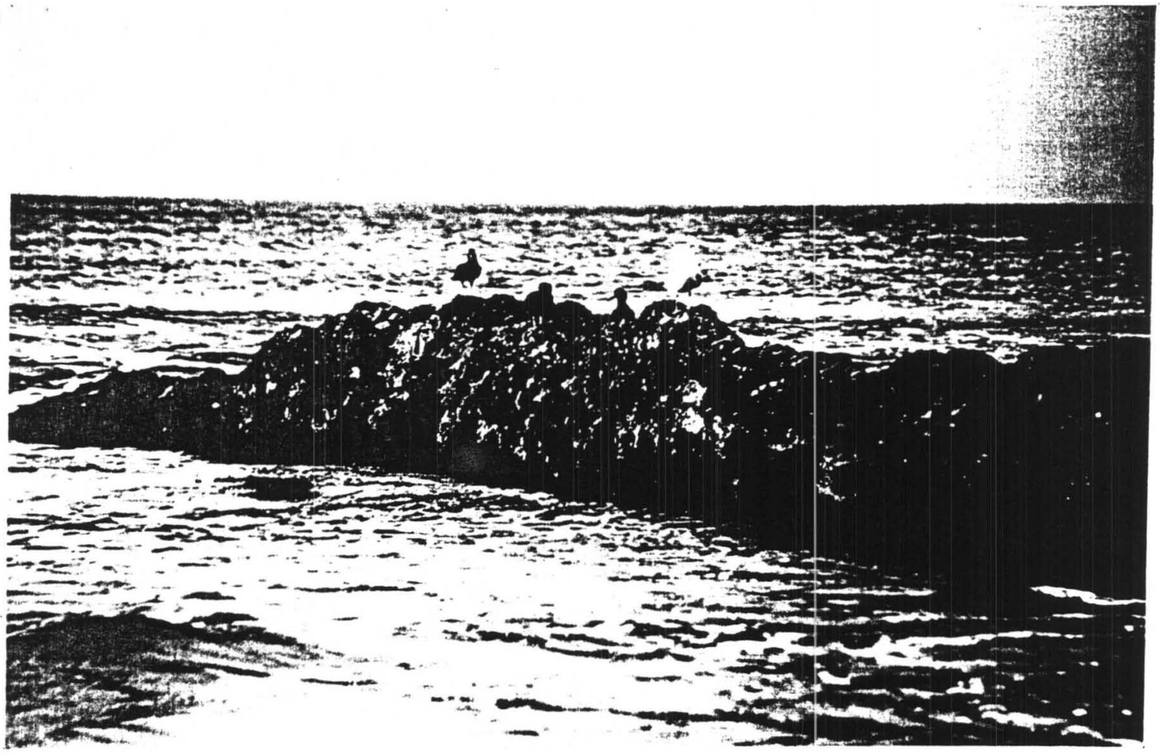

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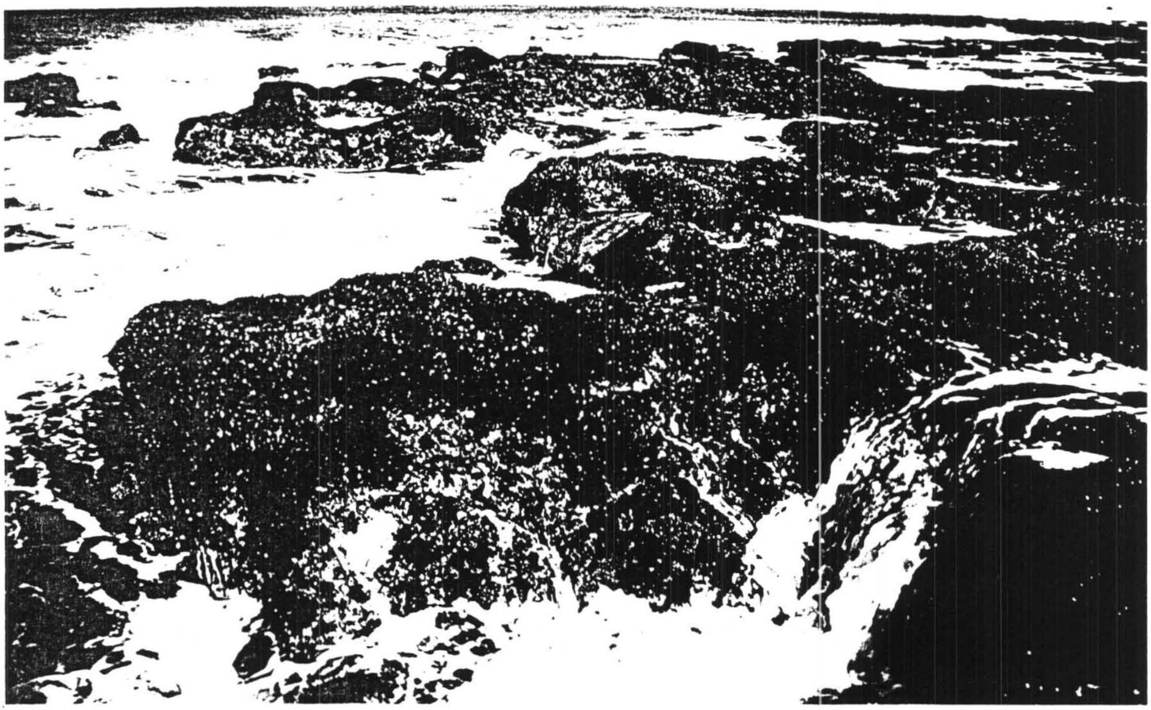


Figure 1.2cont. e) The mussel beds sampled at Rufanes, and f) Riet River.

Dynamometers

The dynamometers used to measure maximum wave force were modelled on those used by Palumbi (1984) although adjustments to the design were made to suit local conditions. Each dynamometer was constructed from a plastic electrical cable tie (200 mm x 4 mm), surgical rubber tube (70 mm x 7 mm) and a plastic bath plug (diameter of 40 mm). The cable tie was cut into two pieces: a) the cable tie head and a tab of 10 mm (referred to as the head) and; b) the remaining 190 mm of the cable tie (referred to as the tail) (Figure 1.3a). The tapered end of the tail was fed through the head as depicted in Figure 1.3a. It was then inserted into a small hole pierced about 10 mm from the end of the surgical tube. The other end of the surgical tube was slipped over the 10 mm long tab and firmly secured with thin wire. A 100 mm length of fishing nylon (22 kg) was tied below the head and fastened to the bath plug that acted as a drogue. A piece of thick wire was inserted into the tapered end, doubled back and looped around a nail-in anchor. The device could be re-primed by gently depressing the restraining tab inside the head. The whole device was ready to be deployed by hammering the nail-in anchor into a drilled hole in the rock (Figure 1.3b).

When a wave washed over the mussel bed the force on the drogue caused the head of the cable tie to move (Figure 1.3c). As the elastic surgical tubing provided resistance, the force of the wave had to exceed this before the head moved. The cable tie worked as a ratchet and the head could therefore not slip back. Due to the elasticity of the surgical tubing, force was not accumulative and a force greater than the strongest wave experienced thus far was required to slide the head further. The elasticity enabled the drogue to return to its original position. (Figure 1.3c).

On the first day during low tide, six dynamometers were placed at each site within the low shore mussel bed used for sampling (*i.e.* 36 dynamometers) (Table 1.1). Each of the six dynamometers was positioned at the same tidal height and with the same aspect. Nearby algae which could snag the drogue were removed. The following day the dynamometers that remained were removed from four of the sites and replaced with six new dynamometers at each of the four sites. Due to rough seas the dynamometers at the remaining two sites, Fish River and Rufanes could not be removed or replaced. On the third day the dynamometers were removed from all six sites and those from Fish River and Rufanes were discarded. As the whole procedure was very time-consuming and required considerable man power an attempt was made to salvage the results rather than repeat the entire experiment. On day 3, six new dynamometers were deployed at Fish River, Rufanes and Riet River (*i.e.* 18 dynamometers), using Riet River as a reference point. The dynamometers remaining at Fish River, Rufanes and Riet River were removed on day 4. For each recovered dynamometer, the force required to move the head was measured in kilograms using a spring scale and presented in Newtons (F= m x a ; a=0 & g=0). To enable these results to be comparable with other studies the force was expressed as $N.m^{-2}$ (as the area of the drogue was $1.26x10^{-3}$ m^2). It is recognised that other factors would cause resistance, but all that was required in this study was a relative measure of wave force.

Cement Blocks

The idea of using dissolution of a block to measure average wave exposure was adopted from Doty (1971). A trial period ensued during which varying proportions of plaster of Paris and 'Rockset' (a quick setting cement) were used to obtain the combination most suited for use in local wave conditions. The blocks were finally made using full strength 'Rockset' which was cast in oblong polyethylene ice-cube trays, each block measuring 50 mm long, 35 mm wide and 40 mm deep. Once set, the blocks were turned out of the mould and glued to asbestos plates (100 mm x 100 mm) with an epoxy cement (Epidermix 372). Prior to this a hole was drilled through the asbestos plate so that it could later be secured to the rock with a nail-in anchor (Figure 1.3d). Once the block was attached, each device (block plus plate) was weighed and labelled. After the experiment each device was dried thoroughly before being reweighed. The percentage mass loss was calculated and used as a relative measure of wave exposure.

Five cement blocks were placed at each site within the low shore mussel bed used for sampling (*i.e.* 30 devices). They were removed from four of the six sites on day two and no replacements were made. Due to rough seas, two of the sites, Fish River and Rufanes were inaccessible and the devices could not be removed. On day three, five new devices were deployed at Fish River, Rufanes and Riet River (*i.e.* 15 devices); Riet River acted as a reference point. These were removed on day 4. This gave a total of 45 blocks used over the experimental period. As the dynamometer and cement block experiments were conducted simultaneously for the three days, conditions applying to the dynamometers also applied to the cement blocks.

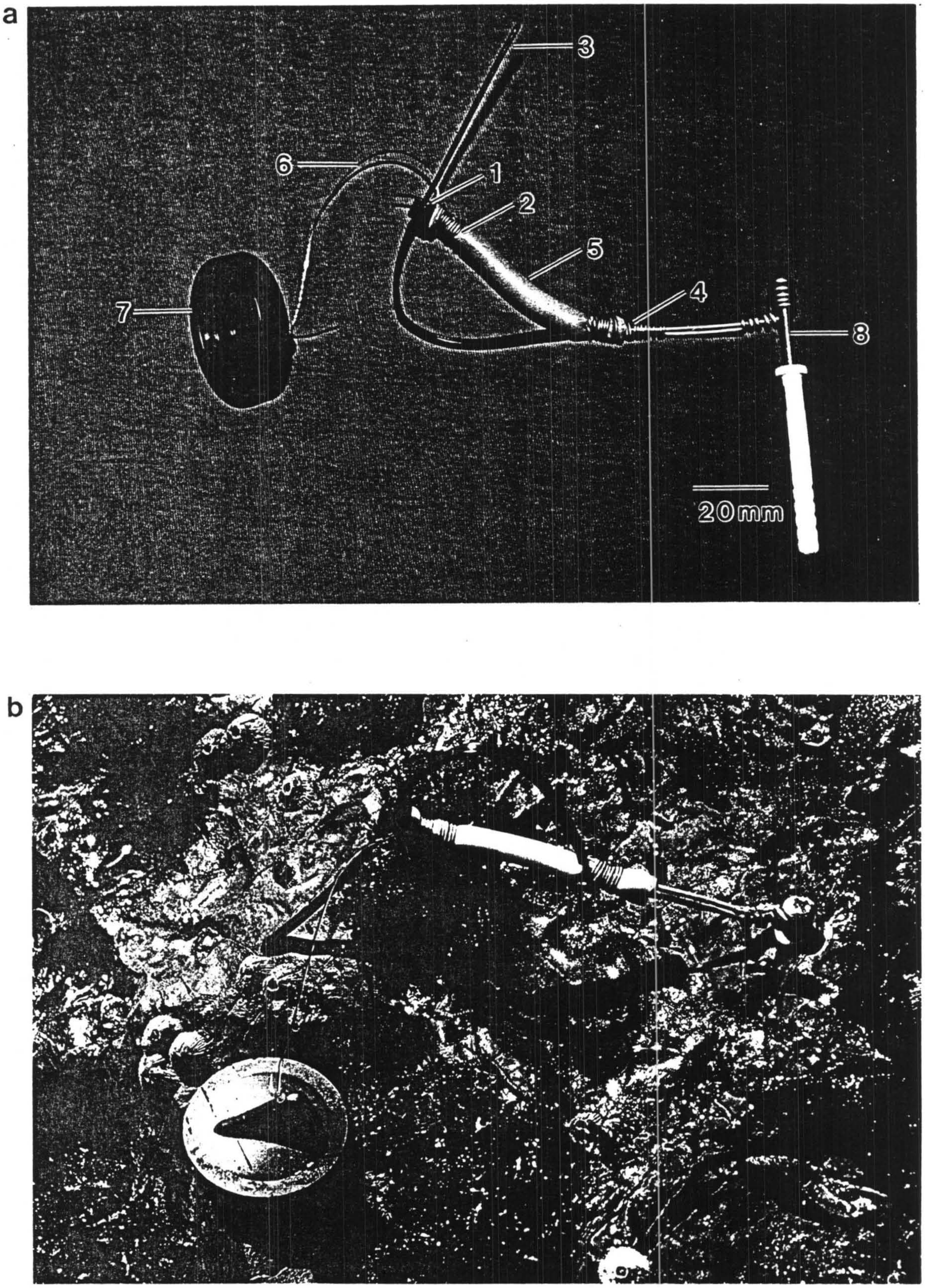


Figure 1.3 a) The dynamometer, 1- head of cable tie, 2- tab, 3- cut end of cable tie (tail), 4- tapered uncut end of cable tie (tail), 5- surgical tube, 6- fishing line, 7- drogue, 8- nail-in anchor. b) The dynamometer in situ.

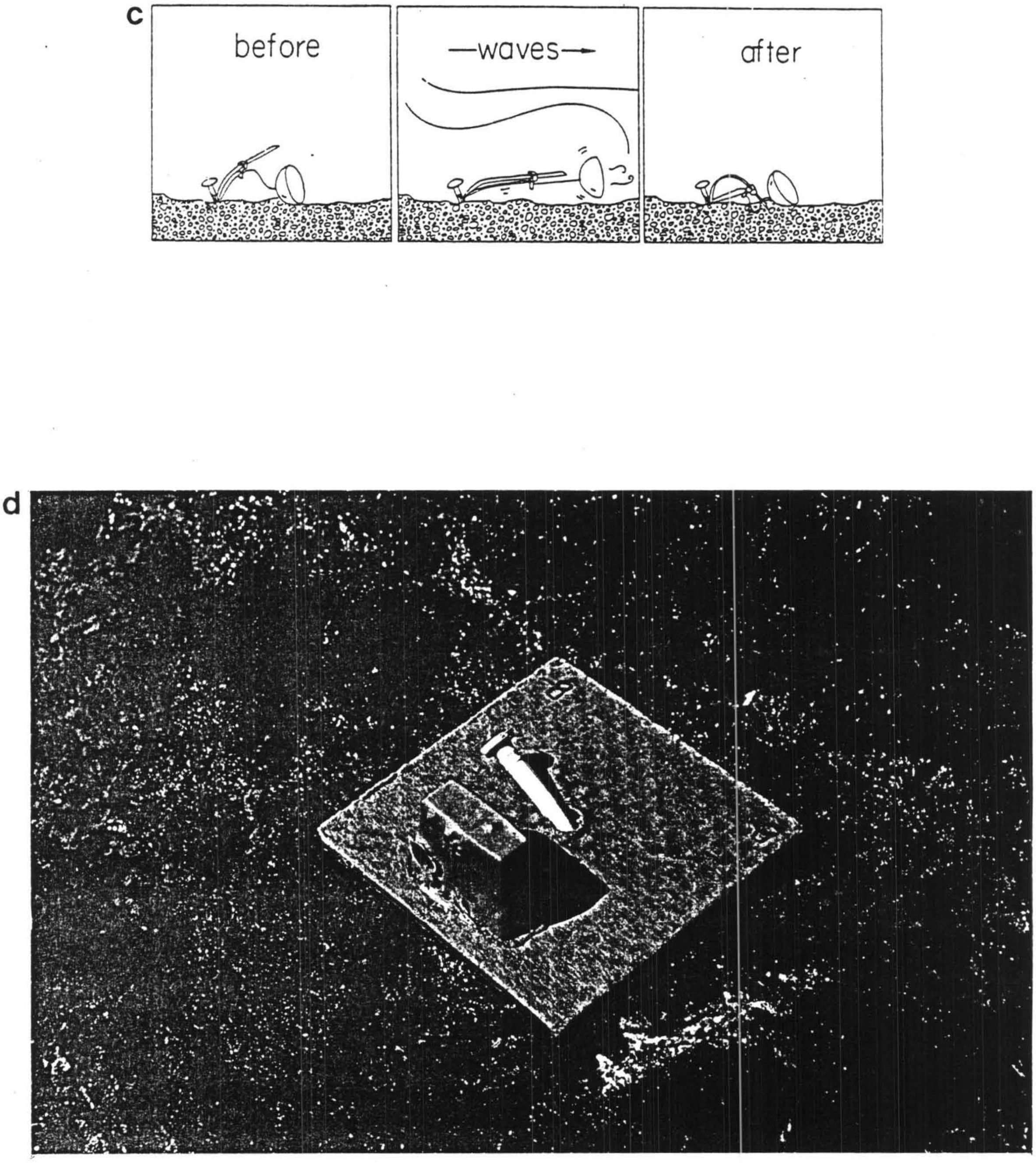


Figure 1.3 c) A representation of in situ views of the dynamometers before, during and after exposure to wave action, reprinted from Palumbi (1984) (p173). d) The cement block on the asbestos plate in situ.

Table 1.1 The number of dynamometers and cement blocks at the sampling sites. Out = placed new dynamometer or cement block and in = recovered dynamometer or cement block from the rocks.

	Day 1	Day 2	Day 3	Day 4
Dynam.	• out 36, 6 at each site	• in 16 from Dz, Kw, Mg & Ri • out 24 at Dz, Kw, Mg & Ri • Fs & Ru inaccessible	• in 13 from Dz, Kw, Mg & Ri • out 16 at Fs, Ru & Ri	• in 10 from Fs, Ru & Ri
Cement blocks	• out 30, 5 at each site	• in 13 from Dz, Kw, Mg & Ri	• out 15 at Fs, Ru & Ri	• in 6 from Ru & Ri. Fs=0

Statistical analyses

Statistical analyses were all performed with Statgraphics version 7.0. Throughout this thesis normality of data was tested using the Kolmogorov-Smirnov test and homogeneity of variance was tested using Bartlett's test. The data from the dynamometer readings were normally distributed and variance was homogeneous ($p>0.05$). As Riet River was the reference point, it first had to be established whether there was any significant difference in the results from the three consecutive days. A students t-test revealed no significant difference between the maximum wave forces recorded for pooled site data (Dz, Kw, Mg & Ri) from day two and pooled site data for day three (Dz, Kw, Mg & Ri) ($p>0.05$). As a result, wave forces recorded at Riet River on day two and three were pooled and tested against forces recorded at Riet River on day four, using a students t-test. There was no significant difference, thus results from all days were combined and a one-way ANOVA was performed to determine whether site had a significant effect on force. Tukey's multiple range analysis was used to identify where the differences lay. For the cement blocks, loss of devices led to insufficient replication within sites, so that the data could not be analysed statistically.

3. RESULTS

Dynamometers

The results showed that Fish River , Kwaai Hoek and Diaz Cross experienced greater wave force than Mgwalana, Rufanes and Riet River (Figure 1.4).

Of the original 66 dynamometers attached to the rocks (this excludes the 12 dynamometers placed at Fish River and Rufanes on day 1) only 39 were recovered. The students t-test showed there to be no significant difference between the wave forces recorded on day two and three (Dz, Kw, Mg & Ri) ($n=29$, $p>0.05$). Similarly, there was no significant difference when pooled data from day two and three for Riet River were compared with data from day four ($n=8$, $p>0.05$ ($p=0.705$)). The results of the one-way ANOVA showed that there was a significant difference in the force recorded between sites ($p<0.05$, Table 1.2). Tukey's multiple range test identified a significantly greater force at Fish River, Diaz Cross and Kwaai Hoek than at Mgwalana, Riet River and Rufanes ($p<0.05$, Table 1.3). Rufanes experienced significantly lower wave forces than all the other sites ($p<0.05$, Table 1.3). Fish River, Diaz Cross, Kwaai Hoek were therefore the most exposed, followed by Mgwalana and Riet River, and Rufanes was the least exposure (Table 1.3).

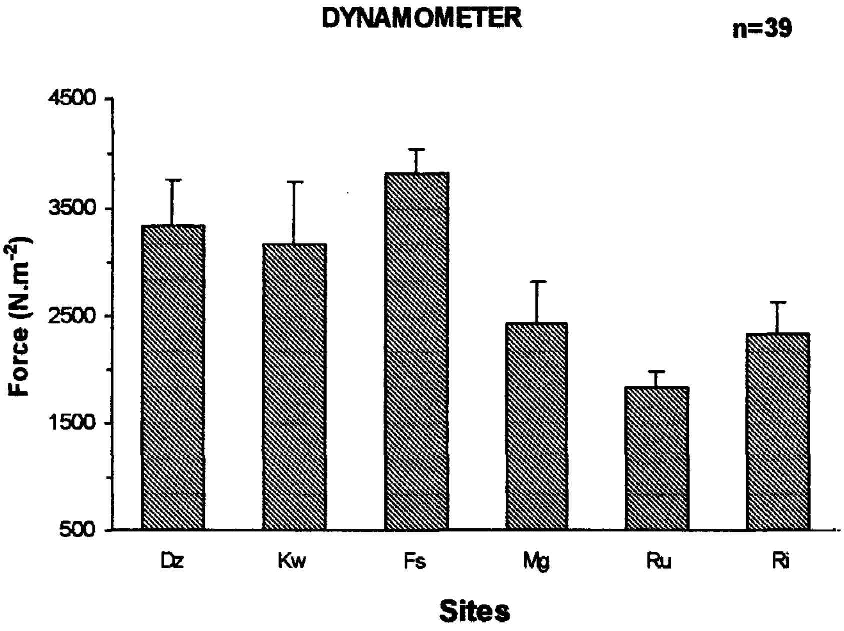


Figure 1.4 Mean of maximum wave forces (+ std. dev.) measured at six sites using dynamometers. Replicates were undertaken on three consecutive days (refer to text for details).

Table 1.2 A one-way ANOVA of the relationship between site and force measurements recorded from dynamometers. Abbreviations are as follows throughout the thesis: df = degrees of freedom, SS = sum of squares, MS = mean square, F = F-ratio and P = probability level.

Source of variation	**df**	**SS**	**MS**	**F**	**P**
Between	5	19.71	3.94	14.98	<0.0001
Within	33	8.68	0.26		

Table 1.3 Tukey's multiple range analysis to determine the significance of the differences in force (N.m^{-2}) at the six sites. Abbreviations for the sites are standard throughout the thesis: Ru = Rufanes, Ri = Riet River, Mg = Mgwalana, Kw = Kwaai Hoek, Dz = Diaz Cross and Fs = Fish River. Common letters indicate no significant difference (p> 0.05) and different letters indicate a significant difference (p<0.05).

Site	**Count**	**Mean force (N.m^{-2})**	**Homogenous groups**
Ru	5	1829.54	a
Ri	8	2336.65	b
Mg	9	2430.56	b
Kw	8	3161.93	c
Dz	7	3329.55	c
Fs	2	3818.18	c

Cement Blocks

The mean percentage mass loss was greatest at Kwaai Hoek followed by Diaz Cross, Rufanes, Mgwalana, and Riet River (Table 1.4 & Figure 1.5). The higher the loss of cement, the greater the average wave force experienced. The loss of entire cement blocks was considerable and of the original 45 blocks only 17 were recovered. No blocks were recovered from Fish River, which could be taken to indicate strong wave action. Diaz Cross and Kwaai Hoek appeared to have greater wave exposure than Mgwalana, Rufanes and Riet River, although due to small sample sizes the results could not be analysed using statistics. The asbestos plates were not ideal as wear in the plate around the nail-in anchor increased the size of the hole, which resulted in plates being ripped off. In other cases, the plates were broken, the blocks came free from the epoxy or the entire apparatus (nails included) was missing. No human interference was suspected.

Table 1.4 The mean percentage mass loss from cement blocks for five sites. Riet River was used as a reference site.

Site	Day	N	Mean % mass loss
Dz	2	3	12.68
Kw	2	4	15.00
Fs	2	0	-
Mg	2	3	11.06
Ru	2	0	-
Ri	2	3	7.54
Fs	4	0	-
Ru	4	2	11.29
Ri	4	2	9.57

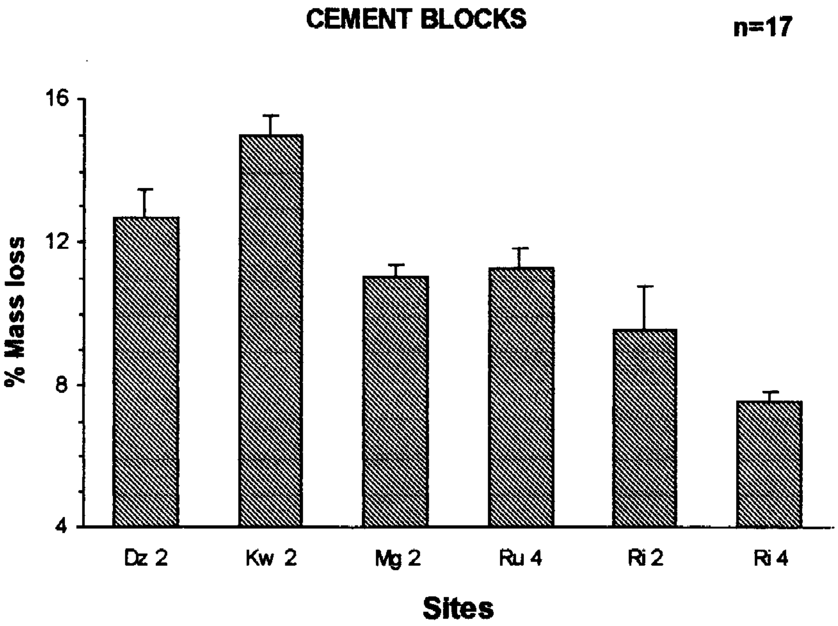


Figure 1.5 The mean percentage mass loss (+std. dev.) of cement blocks at five sites. The higher the percentage mass loss the greater the average wave force. Blocks were recovered from Diaz Cross, Kwaai Hoek, Mgwalana and Riet River on day two and from Rufanes and Riet River on day four (see text for details).

4. DISCUSSION

The complex hydrodynamic forces influencing intertidal organisms are shaped by numerous factors, some of which are tidal height, slope, substratum, depth, currents, local eddies, winds and offshore reefs or sand banks. Two important aspects of wave action, namely maximum wave force and average water motion have profoundly different effects on marine life. The survival of organisms is more likely to be governed by dislodgement due to maximum wave force than by overall water motion (Harger & Landenberger 1971, Denny & Gaines 1990). Drag is usually the most detrimental consequence of maximum wave force, although pressure and abrasion may be important at sites, particularly those with heavy sand loads (Denny & Gaines 1990). Whether the cumulative disturbance and mortality caused by large waves encountered every few days differs from that associated with freak storm waves is uncertain. Using dynamometers Palumbi (1984) showed that the maximum wave force measured over a twenty-four hour period was double that recorded in five minutes and the force recorded over 11 days was 20 % higher than the daily maximum.

Several scientists have designed devices to measure maximum wave force. The earlier dynamometer designed by Jones and Demetropoulos in 1968 made use of a spring scale and a drogue. Although it is costly to replicate and measures force in one direction only, this dynamometer has proved to be comparable in effectiveness to more modern designs. In 1970, Harger used the downward movement of a plate to measure cumulative wave force. The downfall of this design was that the final result could be a product of either many smaller waves or a few large waves. Denny (1983) successfully used a dynamometer (consisting of a replica of the organisms, rubber bands and smoked glass on which a pin scratched marks for wave activity) which recorded both the magnitude and direction of maximum force. Palumbi's dynamometer, which was modified for this study, consisted of a drogue and a cable tie which also measured maximum wave force. Two weaknesses of this design are that it has internal friction and that it is apt to record non-hydrodynamic forces (Bell & Denny 1994). One of the most recent dynamometers used by Bell and Denny (1994) records maximum velocity with the aid of a spring and a drogue.

The results from the dynamometers used in this study agreed with the earlier subjective classification of sites. Higher dynamometer readings were recorded at Diaz Cross, Kwaai Hoek and Fish River, subjectively termed reflective shores and lower readings were recorded at Mgwalana, Rufanes and Riet River, shores termed dissipative. Wave action has been shown to be highest when waves break directly over dynamometers, a more likely occurrence at reflective than dissipative shores (Jones & Demetropoulos 1968, Palumbi 1984). The dynamometers used in this study were modelled on Palumbi's and the results compared favourably with those of his study. Palumbi classified a site receiving 7100 N.m^2 as very exposed and one with forces of 3600 N.m^2 as exposed. Two further classifications were sheltered and very sheltered. Using this as a guideline, Diaz Cross (3350 N.m^2), Kwaai Hoek (3180 N.m^2) and Fish River (3840 N.m^2) would all be classified as exposed. Accordingly, the remaining three sites, Mgwalana (2450 N.m^2), Rufanes (1840 N.m^2) and Riet River (2350 N.m^2) would be classified as sheltered sites. Palumbi did not include force readings of sheltered sites which could be used for comparison. These classifications are therefore used loosely as the introduction of a finer scale could include more categories and the sites classed as sheltered above could also be classed as less exposed.

Measuring maximum or average wave force quantitatively may not provide as clear a picture of the influences on organisms as was previously hoped. Rather than reflecting maximum wave action, Bell and Denny (1994) have suggested that the presence of typically wave exposed species may be a reflection of mass flow or turbulence. Perhaps then, the use of a biological scale, such as Ballantine's (1961), which rather than measuring flow, turbulence, force etc. uses characteristics of the habitat to show exposure, should not be discarded. Despite this, Ballantine's exposure scale developed for the United Kingdom, still remains extremely subjective and is not easily transferable to other localities. (Palumbi 1984).

There have been fewer attempts to measure water flow than maximum wave force, perhaps because the effects of the latter are often more dramatic or the complexity of the former is daunting. The effects that water flow rate have on the densities of larval invertebrates have been documented by Graham and Sebens (1996). Many studies in the field of hydrodynamics have concentrated on diffusion rather than mass flow, wave force or surge and have used the diffusion of blocks of cement, plaster of Paris or other substances to provide a measure of overall water motion (McConnell & Sigler 1959, Muus 1968, Doty 1971, Craik 1980). Many biological processes such as filter feeding rates, fertilisation, dispersal and settlement might depend on diffusion rates (Doty 1971). The rate of diffusion is also influenced by current velocities, turbulence and scouring by sand (Craik 1980).

It is possible that sand scour was responsible for the higher than expected mass losses at Rufanes and Mgwalana. Of five sites (no blocks were recovered at Fish River) these two sites experienced considerable sand movement throughout the year. Over the fifteen month sampling period (chapter 2) sand was frequently present within the mussel bed in much higher quantities at Rufanes than at the remaining sites. At Mgwalana during the experimental period a gully of approximately one metre deep was totally sanded up (pers. ob.). Despite the trend towards a greater percentage mass loss at Diaz Cross and Kwaai Hoek than Mgwalana, Rufanes and Riet River *i.e.* the same trend as shown by the dynamometers, these results should be viewed with caution due to the possible interplay of the above mentioned factors.

Although the dynamometer readings were subject to fewer extraneous influences than the cement blocks, an ideal ranking of the sites should include experiments repeated under a variety of sea conditions. In addition, matching the incomplete data sets from the dynamometer readings (using Riet River as a reference point) to include Fish River and Rufanes provided less accurate results than would have been achieved had the entire experiment been repeated. Along the south east coast stormy seas occur in winter due to westerly winds from a low pressure system which develops in Cape Town and moves across towards Port Alfred, often being deflected further out to sea before reaching East London, unless it is a strongly developed low pressure cell (pers. ob.). It is under these frontal conditions that much of the heavy wave action along this coast occurs.

The dynamometers did provide a measure sufficiently accurate to warrant classifying Diaz Cross, Kwaai Hoek and Fish River as more exposed, and Mgwalana, Rufanes and Riet River as less exposed shores. Similarly, results from the cement blocks allowed Diaz Cross and Kwaai Hoek to be classified as more exposed shores and Mgwalana, Rufanes and Riet River as less exposed shores. These two classifications are preferable to those used by Palumbi because of the exposed nature of the South African coastline. However, for ease of discussion from hence forth the 'more exposed sites' will be referred to as **exposed sites** and the 'less exposed sites' as **sheltered sites**.

CHAPTER 2

POPULATION DYNAMICS AND THE EFFECTS OF WAVE EXPOSURE ON *PERNA PERNA*

1. INTRODUCTION

Mussels, especially those in exposed habitats, have world-wide success as space-dominators and represent some of the most productive species on earth (Suchanek 1985). In the light of this, mussels deserve attention not only in terms of fisheries management, but also as complex ecological systems that are home to a countless variety of species (Witman 1983, Suchanek 1980, 1985, Lasiak & Field 1995). Population size structure, density and biomass give easily accessible and important baseline information about a population (Seed 1976, Berry 1978). This initial phase of data collection sets the stage for further investigations by identifying the products of biotic and abiotic processes. For example, once the density of individuals at a site has been established, explanations as to the cause and effect of these densities can be studied. To obtain a complete understanding of a population, the processes of settlement/recruitment, growth and mortality and the factors affecting them need to be addressed. Even small environmental differences may produce large effects on growth rates and maximum size (Sebens 1987 in Cerrato & Keith 1992). An important factor responsible for influencing population structure indirectly and/or directly is wave action. Changes in food availability, feeding time (see chapter 3 discussion) and physical removal of mussels (Harger 1970, Harger & Landenberger 1971) are possible direct results of wave action. Indirect effects are frequently more subtle and difficult to isolate from the effects of tidal height, current, temperature, biotic interactions *etc.* (Griffiths 1981, Griffiths & Hockey 1987, Van Erkom Schurink & Griffiths 1990). The indirect influences of wave exposure on growth rates (see chapter 3), settlement and recruitment, mean and maximum lengths, density and biomass of intertidal organisms have been well documented (Jones & Demetropoulos 1968, Harger 1970, Griffiths 1977, Beckley 1979, McQuaid & Branch 1985, Menge 1991, Petraitis 1991, Bertness *et al.* 1992, Leeb 1995, McLachlan *et al.* 1995).

The comparison of mussel populations is confounded by variations over time and space and the degree of interaction which occurs between recruitment, size, growth, density and biomass (Peterson & Beal 1989, Dye *et al.* 1994). The size of individuals is dependent on growth (Baird 1966) and mortality (Seed 1976, Griffiths & Buffenstein 1981); growth is frequently dependent on density (Broom 1982, Fréchette & Bourget 1985a & 1985b, Newell & Shumway 1993) and in turn, density is dependent on mortality, spawning, settlement and recruitment success (Connell 1985). The subsequent survival of recruits may be enhanced by the refuge afforded by adults and can thus depend on adult density (Petersen 1984, Alvarado & Castilla 1996).

Biomass is a reflection of the density, size, and growth rates of mussels (Dickie *et al.* 1984), and all these factors are influenced by other biological and physical processes.

In sedentary organisms, particularly those limited by space and food, density-dependent interactions are likely to be strong (Griffiths & Hockey 1987, Hughes & Griffiths 1988). Spatial dominance is maintained by recruitment, growth and mortality (Petraitis 1995). The same cover can be maintained either by achieving high densities of small mussels where growth rates have been suppressed by crowding, or by lower densities of larger mussels that have been thinned by physical disturbance or predators (Petraitis 1995).

The prediction of recruitment success, mussel size, carrying capacity, and longevity is important for management and for a biological understanding of the system (Grant *et al.* 1993). As these processes are influenced by wave action, it follows that the vulnerability of a population to exploitation may depend on the degree of wave exposure. The objectives of this chapter were to determine the density and substratum "choice" of recruits, the timing of early recruitment, the mean and maximum size of adults, the density of adults and the biomass of the entire population, all with respect to wave exposure.

2. MATERIALS AND METHODS

The main objective of this entire study was to determine growth rates of *Perna perna*, and one of the methods utilised was analysis of length frequency distributions. These data also provide information on population dynamics. Length frequencies were obtained by sampling mussel beds at approximately six weekly intervals at three exposed sites; Diaz Cross, Kwaai Hoek, Fish River and three sheltered sites; Mgwalana, Rufanes and Riet River (refer to chapter 1 for quantification of exposure). All sampling was undertaken randomly from rocks with approximately 100% mussel cover, in low shore mussel beds (the lowest intertidal mussel bed accessible on a spring low tide). For the growth study, a minimum of 200 mussels was required from each site at each sampling interval. To obtain this number, four to five quadrats of 10x10 cm were destructively sampled by removing all mussels and algae from each site per sampling session. However, all the investigations under population dynamics, that is, size structure, timing of early recruitment, recruit densities, mean and maximum lengths, densities and biomass, used data from only four quadrats (chosen randomly where 5 quadrats were collected) per site per sampling session. Sampling was undertaken over a 15 month period from July 1995 to October 1996 and included 11 sampling sessions. These sampling sessions will in future be referred to as **sampling months** even though they were obtained at six weekly intervals. **Shore type** will refer to the exposure of the shore *i.e.* exposed or sheltered. Mussels greater than 1 mm were measured in the laboratory to the nearest 0.1 mm, initially by hand using stainless steel vernier callipers, and later by an image analysing program, PC Image. Lindsay (1998) showed that the PC Image program measured mussels with a high degree of accuracy (0.01 mm) and a regression coefficient of 0.9996 ($n=63$, $p<0.05$) was obtained when hand measured mussels were plotted against those measured by PC Image. All statistical analyses were undertaken on Statgraphics version 7.0, unless otherwise stated. Normality and homogeneity were tested using the Kolmogorov-Smirnov and the Bartlett's test respectively before applying parametric procedures. When significant differences were established from ANOVAs, Tukey's multiple range test was used to identify where the differences occurred.

2.1. POPULATION SIZE STRUCTURE

The length frequency data from 4 quadrats for 11 sampling months (6 sites) were expressed as the mean number of mussels per m^2 for each size class for each site. The modal size structure of each population was examined.

2.2. TIMING OF EARLY RECRUITMENT, SUBSTRATUM UTILISATION AND DENSITY OF RECRUITS

Definition of recruit and adult

Mussels are often separated into juveniles and adults. Adults of *Perna perna* have been classified as >20 mm by Phillips (1994) and >15 mm by Leeb (1995). Juveniles are often further subdivided into settlers and recruits. Mussel settlers are usually defined as less than 1 mm, as this is the size at which they settle out of the plankton (Seed 1976). Recruits have been defined as 0-19 mm by Phillips (1994) and 0-15 mm by Leeb (1995). For the purpose of this study the term recruits will refer to mussels 1-15 mm, although some analyses have been restricted to certain size classes within this division. In these cases, the term recruit is always followed by the size class used, eg. recruit (1-5 mm). Adults are defined as >15 mm in length and have not been defined according to reproductive maturity. Rather, this definition has arisen due to the stabilisation in population numbers that occurred after approximately the 15 mm size class *i.e.* high mortality or emigration occurred up to 15 mm after which numbers declined more gradually (Chapter 4).

This was a subjective finding achieved by examining length frequency graphs of each site throughout the year (Figure 3.11) as well as composite graphs of all months for each site (Figure 2.1).

Timing of early recruitment

Data obtained from length frequency distributions were used to determine the months of peak early recruitment and whether this was site or exposure dependent. Mussels from each quadrat sampled were counted and measured, irrespective of whether they were found on algae or directly on mussels. Where algae were present, they were attached to mussels and not directly to the rock. Densities of mussels 1-5 mm were obtained for each site using the total densities of 4 quadrats per site from each sampling month. This size range was chosen so that the timing of early recruitment could be limited to those mussels which had most recently settled *i.e.* late plantigrades, as true settlers (<1 mm) were not included in this study. At each site the total number of mussels (1-5 mm) counted over the entire sampling period (also using 4 quads) was calculated. Using this information, the number of recruits (1-5 mm) per month were calculated as a percentage of the total number of recruits (1-5 mm), for each site. Figures were converted to percentages as extreme differences in recruit densities occurred, which would have masked comparisons between sites and shore type. After square root transformation, data were normally distributed ($p>0.05$), but not homogeneous ($p<0.05$). Despite this, ANOVAs were used due to their robustness to deviations from homogeneity (Zar 1996). A two-way ANOVA with interactions using site and month as factors was performed to determine when peak early recruitment occurred and how this varied among sites. A second two-way ANOVA with interactions was performed on combined sites to compare how wave exposure and month affected early recruitment.

The effect of exposure, site and substratum on recruit densities

The primary points of interest were:

- does the degree of exposure affect recruit densities,
- does site affect recruit densities, and
- does substratum affect recruit densities.

Ideally a 3-way ANOVA would be undertaken, however this was not possible as algae was absent on two of the shores, namely Riet River and Mgwalana. The analysis was therefore broken down into analysing subsets of the data as follows:

- the percentage cover of algae (Dz, Kw, Fs & Ru)
- the effects of site and substratum on true densities of recruits (1-5 & 6-10 mm)
- the effects of site and substratum on standardised densities of recruits (1-5 & 6-10 mm)
- the effects of site on densities of true recruits (1-5 & 6-10 mm) on algae
- the effects of exposure and site on densities of recruits (1-5 & 6-10 mm) on adult mussels
- the effects of exposure, site and month on densities of recruits (1-15 mm)
- the regression of recruit (1-5 mm) against adult (>15 mm) densities

Algal cover

At Diaz Cross, Kwaai Hoek, Fish River and Rufanes recruits were found on algae (which were attached to mussels) and on mussels. At Mgwalana and Riet River algae were absent and therefore recruits were found only on the mussels. Although the site of attachment of recruits *i.e.* on mussels or on algae was noted, the percentage cover of algae was not recorded during the 15 month sampling period, but was obtained in a once-off survey in February 1996. The section of the mussel bed sampled had approximately 100% mussel cover. Twenty 25x25 cm^2 randomly placed quadrats were sampled quantitatively within the low shore mussel bed at each site and the percentage cover of the dominant algae was recorded. To determine whether the percentage cover of algae differed statistically between sites, a one-way ANOVA was undertaken on data from Diaz Cross, Kwaai Hoek, Fish River and Rufanes *i.e.* those sites where algae were present.

Effects of substratum and site on true densities of recruits (1-5 & 6-10 mm)

Due to the absence of algae at Riet River and Mgwalana, the analyses on the effects of substratum and site on recruit densities were restricted to the remaining four sites, Diaz Cross, Kwaai Hoek, Fish River and Rufanes. For these analyses true recruit densities on algae and mussels were used. Mussel cover was approximately 100%, and although algal cover varied from site to site, recruit densities were not standardised. The abundance of recruits of 1-5 mm and 6-10 mm on algae and on mussels, was determined during the peak early recruitment months, *i.e.* January, February, April and May. Densities were obtained from four quadrats at each site for each of the four months, with the exception of the January sample for Rufanes where only two quadrats were used (information as to whether recruits were found on algae or mussels was absent for 2 quads). Although data from four months were used, the 16 and 14 quadrats respectively were treated as replicates, with no reference to month. Two 2-way ANOVAs with interactions were performed to determine whether substratum or site had a significant effect on recruit densities, firstly on recruits 1-5 mm and secondly on recruits 6-10 mm. Where significant interactions occurred between site and substratum, one-way ANOVAs were undertaken at each site using substratum as a factor.

Effects of site and substratum on standardised densities of recruits (1-5 & 6-10 mm)

The second question that arose was whether substratum had an effect on recruit densities when algal cover was standardised to 100% cover. Analyses were undertaken using data from the same quadrats during the four peak recruitment months at Diaz Cross, Kwaai Hoek, Fish River and Rufanes, as detailed above. A single conversion factor obtained from the percentage algal cover data from February was used for all data (from January, February, April and May) from each site. The data were standardised as follows, for example, if the mean algal cover at a site (in a quadrat) was 50% and 2 recruits were found on the algae (in this quadrat) then the density of recruits per quadrat with 100% algae cover would be 4. This was then converted to no.m^{-2}. As mussels had 100% cover, the densities of recruits from both algae and mussel were now directly comparable. Two 2-way ANOVAs with interactions were undertaken to determine whether substratum and site affected recruit densities, firstly on recruits 1-5 mm and secondly on recruits 6-10 mm. Where significant interactions occurred between site and substratum, one-way ANOVAs were undertaken at each site using substratum as a factor.

Effects of site on densities of true recruits (1-5 & 6-10 mm) on algae

The third question compared true recruit densities on algae at the four sites at which it was present, namely Diaz Cross, Kwaai Hoek, Fish River and Rufanes. Two separate one-way ANOVAs were undertaken, one on 1-5 mm size class and the other on 6-10 mm size class, to determine whether recruit densities on algae differed between the four sites. Analyses were undertaken on quadrats from the four peak recruitment months as detailed in "Effects of substratum and site on true densities of recruits (Dz, Kw, Fs & Ru)".

Effects of exposure and site on densities of recruits (1-5 & 6-10 mm) on adult (>15 mm) mussels

The final question was whether recruit densities on mussels differed between exposures and sites, particularly those where algae were present (Dz, Kw, Fs & Ru) and those where algae were absent (Mg & Ri). The abundance of recruits on mussels, was determined during the peak early recruitment months, *i.e.* January, February, April and May. Densities were obtained from four quadrats at each site for each of the four months, with the exception of the January sample for Rufanes where only two quadrats were used (information as to whether recruits were found on algae or mussels was absent for 2 quads). Recruits found on algae were ignored for these analyses. Using data from all six sites, two one-way ANOVAs were undertaken to test the effect of exposure on recruit densities, one for each size class (1-5 & 6-10 mm). A further two one-way ANOVAs were undertaken to test the effect of site on recruit densities, one for each size class.

Effects of exposure, site and month on densities of recruits (1-15 mm)

Densities of recruits, 1-15 mm were calculated for each of the four quadrats, at each sampling month and at each site using data from length-frequency distributions. All recruits 1-15 mm were counted irrespective of whether they were attached to mussels or algae, to determine whether there was a relationship between exposure, site, month, and recruit density. After a $\log_e(x+1)$ transformation, data were normally distributed and homogeneous in all cases ($p>0.05$).

A two-way ANOVA with interactions was used to determine the effect of exposure and month on recruit densities. A second two-way ANOVA was performed to determine whether site and month affected recruit densities significantly. Where significant differences were noted Tukey's multiple range test was used to identify where the differences lay.

Regression of recruit (1-5 mm) against adult (>15 mm) densities

Linear regression analyses were undertaken of adult densities (independent) against recruit densities (1-15 mm) (dependent) using the least squares method. Data were obtained from 4 quadrats per sampling month for each of the six sites. The total number of recruits (1-5 mm) on algae plus on mussels was utilised. Regressions were undertaken for both shore types (site data pooled) and separately for each site.

2.3 MEAN AND MAXIMUM LENGTHS, ADULT DENSITIES AND TOTAL BIOMASS

Mean lengths

The mean lengths of adults (>15 mm) were calculated from length frequency data. To calculate mean lengths, data analysis was performed on a UNIX computer using the statistical package, BMDP. A Welch Brown-Forsythe's test established that after a $\sqrt{x+1}$ transformation, homogeneity of variance was achieved ($p>0.05$). Normality was assumed due to the large sample size (n=10 547) (Zar 1996). To determine whether exposure and month had any relationship with mean lengths, a two-way ANOVA with interactions was performed on length data. A second two-way ANOVA tested the effect of site and month on mean lengths.

Maximum lengths

The maximum lengths were established by using the ten largest mussels for each sampling month at each site. Data were normal ($p>0.05$), but not homogeneous ($p<0.05$). As the ANOVA is robust to deviations from homogeneity it was still used (Zar 1996).The effect of exposure and month on maximum lengths was compared using a two-way ANOVA. A second two-way ANOVA was then performed on site and month data.

Adult densities

Densities of adults (>15 mm) were obtained from 4 quadrats for each of the 11 sampling months and for each of the six sites, to determine whether a relationship existed between exposure, site, month and density. Densities of adults were calculated separately from recruits in an attempt to remove the influence of early recruitment. Two-way ANOVAs with interactions were utilised on normal and homogeneous data ($p>0.05$) to determine statistically whether exposure, site and month had an effect on adult densities.

A correlation analysis was undertaken to determine whether there was a significant relationship between mean monthly densities of mussels (recruits plus adults) and mean monthly lengths of mussels *i.e.* a mean density and a corresponding mean length was calculated for each month, at each site, n=66. A correlation analysis was undertaken to determine whether there was any relationship between the mean adult densities (>15 mm) at each site and the mean maximum wave force ($N.m^{-2}$) (from chapter 1) recorded at each site.

Biomass

Using mussels collected between February and April 1995, regression equations of length against dry mass were generated for Kwaai Hoek, Fish River, Mgwalana, Rufanes and Riet River by J. Lindsay (1998). These regression equations were used to calculate biomass from the length of each mussel collected during 11 sampling sessions (4 quadrats each time) at each of the six sites. As lengths and length-frequency distributions at Diaz Cross and Kwaai Hoek were similar, the regression equation generated for Kwaai Hoek was used for Diaz Cross as well. Total biomass for each quadrat, at each sampling month and site was calculated. The relationships between exposure, site, month and biomass were determined using two-way ANOVAs with interactions on normal and homogeneous data ($p>0.05$).

Three correlations were undertaken to determine whether biomass could be predicted from length, density or both. Firstly, the mean biomass of mussels (recruits plus adults) at each site was correlated against the mean lengths (recruits plus adults) at each site. Secondly, the mean biomass (recruits plus adults) at each site was correlated against the mean densities (recruits plus adults) at each site. Lastly, the correlation coefficients obtained by correlating the mean length from each sampling month against the mean density from each sampling month at each site ($n=11$ for each site), were correlated against the mean mass at each site ($n=6$).

3. RESULTS

3.1. POPULATION SIZE STRUCTURE

The length frequency data from 4 quadrats for 11 sampling months were summed to give the mean number of mussels per m^2 for each size class for each site (Figure 2.1). The mussel populations at Diaz Cross, Kwaai Hoek, Fish River, Mgwalana and Riet River were bimodal, having distinct juvenile and adult peaks. The population at Rufanes was skewed to the left. However, closer examination of monthly length frequencies (Figure 3.3.1) revealed that the population at Rufanes was usually bimodal, with high densities of small mussels (<20 mm) occurring throughout the year. This trickle recruitment into the population was probably responsible for disguising the adult cohort.

The modal size of the juvenile 'cohorts' were lower at the exposed shores than the sheltered shores, occurring at 5 mm at Diaz Cross, Kwaai Hoek and Fish River and at 10 mm at Mgwalana, Rufanes and Riet River (Figure 2.1). The modal size of the adult 'cohorts' were higher on the exposed shores than the sheltered shore, that is 76-85 mm at Diaz Cross, 61-70 mm at Kwaai Hoek, 51-60 mm at Fish River, 36-40 mm at Mgwalana and 41-55 mm at Riet River.

The maximum length class was higher at the exposed sites (106-110 mm) than at the sheltered sites (86-90 mm). Mean and maximum lengths will be dealt with in section 2.3. Even from this glimpse of *Perna perna's* population structure at several sites some pertinent questions can be raised. Why are the densities of recruits <10 mm so much higher at Diaz Cross, Kwaai Hoek and Rufanes than at the other sites? Why is the apparent difference in juvenile and adult density greater at Diaz Cross and Kwaai Hoek than Rufanes? Despite the lower densities of recruits at Fish River, Mgwalana and Riet River compared to the other sites, the adult densities recorded over the 15 month period are higher than those at Diaz Cross, Kwaai Hoek and Rufanes, why? This thesis in general and this chapter in particular will give more insight into the possible answers to these questions.

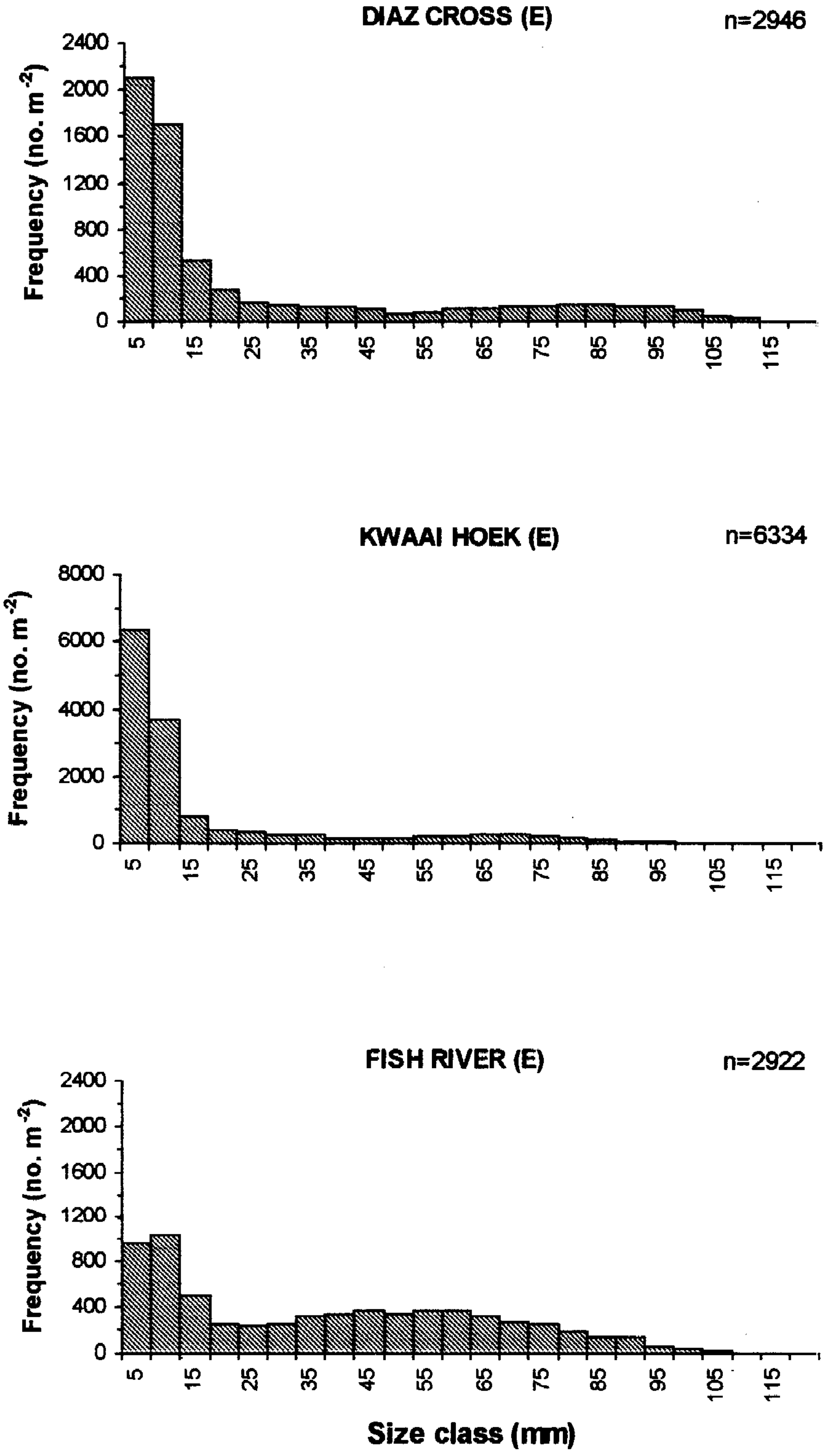


Figure 2.1 Length frequency distributions of mussels over the entire sampling period. Note the different scale at Kwaai Hoek. Upper limit of each size class is presented.

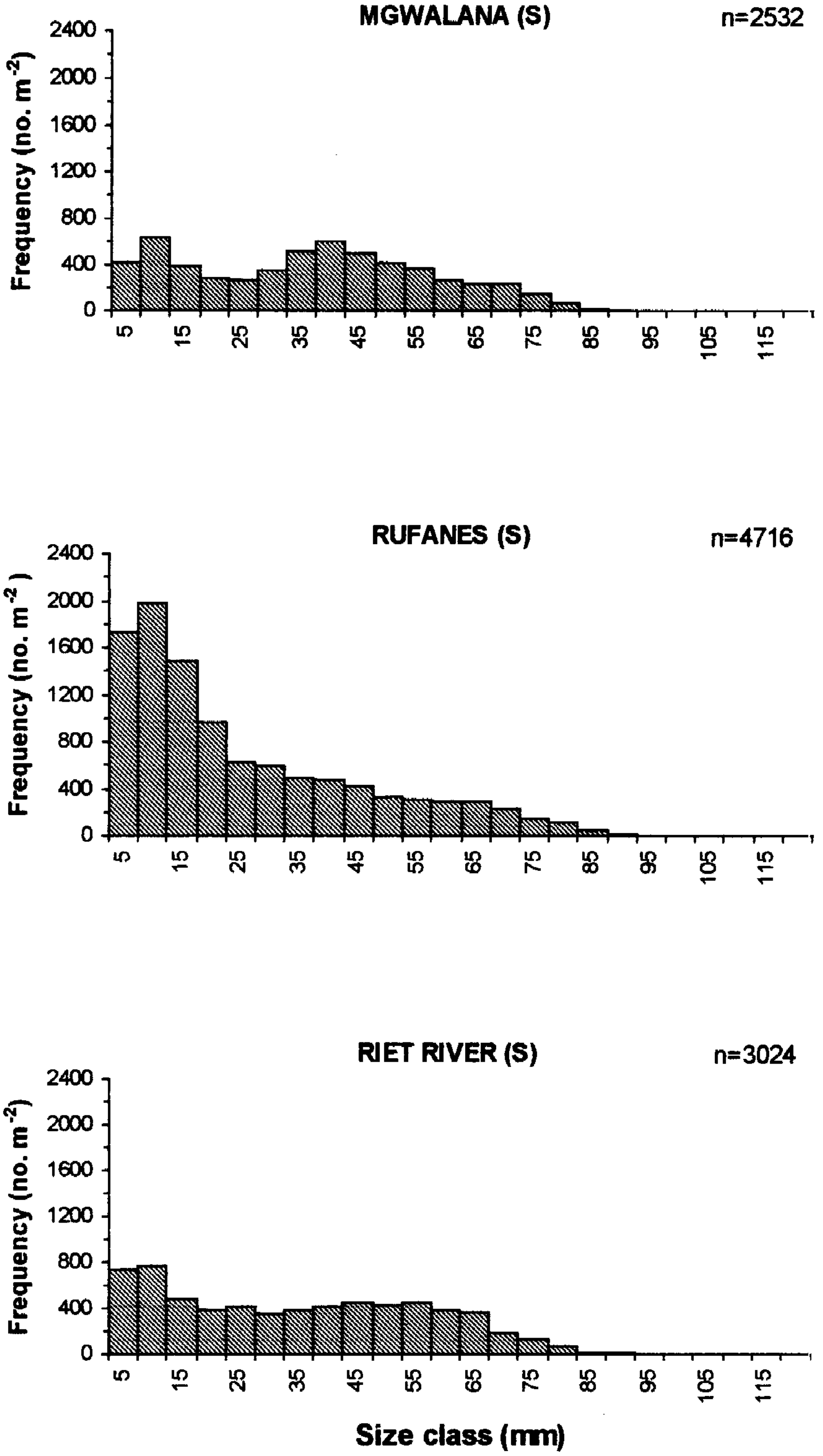


Figure 2.1 cont. Length frequency distributions of mussels for the entire sampling period.

3.2. TIMING OF EARLY RECRUITMENT, DENSITY OF RECRUITS AND SUBSTRATUM UTILISATION

Timing of early recruitment

Peak early recruitment occurred from January 1995 to April 1996 at both the exposed and sheltered shores (Figure 2.2). The results of the two-way ANOVAs showed that although exposure and site had no significant effect on the percentage of recruits (1-5 mm) per month relative to the total number of recruits (1-5 mm) for the 11 months ($p>0.05$, Tables 2.1 & 2.2), month did have a significant effect ($p<0.05$, Tables 2.1 & 2.2). Sites and shore types showed the same pattern of early recruitment over time, as indicated by the non-significant interactions ($p>0.05$, Tables 2.1 & 2.2). Tukey's multiple range test revealed that the percentage of recruits (1-5 mm) per month relative to the total number of recruits (1-5 mm) for the 11 months at each site was significantly higher from January to May 1996, than during the other months ($p<0.05$, Table 2.3). Approximately 64 % of the total percentage of recruits (1-5 mm) occurred during these months, with early recruitment peaking in February, when recruit density was significantly greater than in all other months (Figure 2.2). The remaining 36 % of recruits were evenly distributed throughout the rest of the year, with no more major peaks.

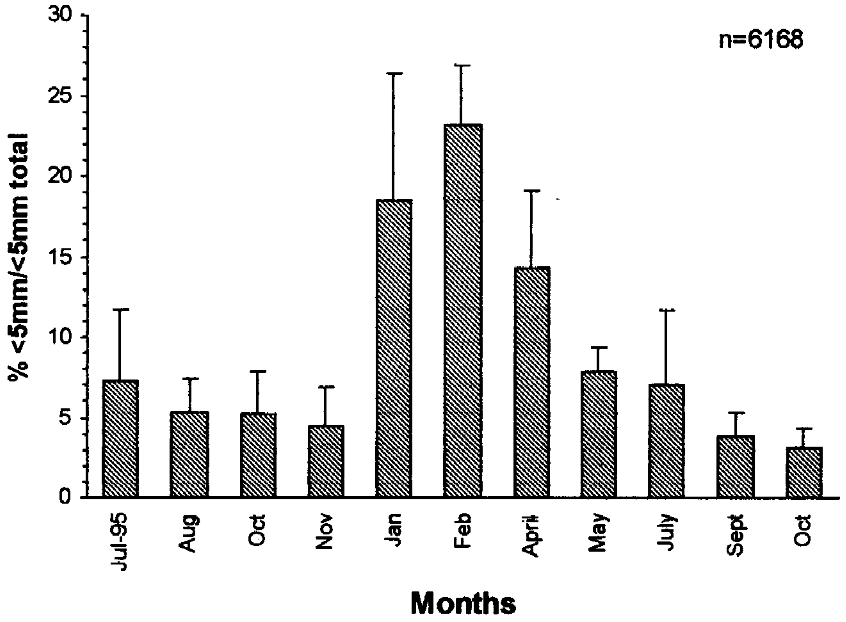


Figure 2.2 The mean number (+std. dev.) of recruits (1-5 mm) represented as a percentage of the total number of recruits (1-5 mm). For each site the number of recruits (1-5 mm) per month were calculated as a percentage of the total number of recruits over the 11 months for that site, and thus mean percentages and standard deviations for each month could be calculated.

Table 2.1 Two-way ANOVA with interactions on the effect of exposure and month on the percentage of recruits (1-5 mm) per month relative to the total number of recruits (1-5 mm) for the sampling period. Percentages of recruits per month were calculated separately for each site. Data were square root transformed for analysis.

Source of variation	df	SS	MS	F	P
Exposure	1	0.03	0.32	0.07	0.7943
Month	10	67.69	6.77	14.62	<0.0001
Interactions	10	3.89	0.39	0.84	0.5899
Residual	242	112.08	0.46		

Table 2.2 Two-way ANOVA with interactions on the effect of site and month on the percentage of recruits (1-5 mm) per month relative to the total number of recruits (1-5 mm) for the entire sampling period. Percentages of recruits per month were calculated separately for each site. Data were square root transformed for analysis.

Source of variation	df	SS	MS	F	P
Site	5	0.32	0.06	0.14	0.9818
Month	10	67.69	6.77	15.16	0.0001
Interactions	50	27.25	0.54	1.22	0.1715
Residual	198	88.44	0.45		

Table 2.3 Tukey's multiple range test on the effect of month on the percentage of recruits (1-5 mm) relative to the total number of recruits (1-5 mm) throughout the 11 sampling months for six sites. Data were square root transformed for analysis.

Month	Count	Mean	Homogeneous groups
October '96	24	0.73	a
September '96	24	0.76	a
November '95	24	0.78	a
October '95	24	0.94	a
August '95	24	1.02	a
July '95	24	1.04	a
July '96	24	1.07	a
May '96	24	1.48	b
April '96	24	1.78	b c
January '96	24	1.91	c
February '96	24	2.30	d

The effect of exposure, site and substratum on recruit densities

Algal cover

The predominant algae at Diaz Cross, Kwaai Hoek and Fish River were upright corallines, while at Rufanes, the foliose red alga *Gelidium pristoides* was most abundant. The percentage cover of algae was significantly different at the individual sites ($p<0.05$, Table 2.4). Diaz Cross had the highest percentage of algal cover (64.12%), followed by Kwaai Hoek (39.70%), Fish River (20.44%) and Rufanes (6.18%)(Table 2.5). No algae were present in the mussel beds at Riet River and Mgwalana.

Effects of site and substratum on true densities of recruits (1-5 & 6-10 mm)

These results were obtained from quadrats of 100% mussel cover and the associated algal cover. Recruit densities (1-5 & 6-10 mm) were considerably higher on algae than on mussels at Diaz Cross and Kwaai Hoek (Figure 2.3a). The results of the two-way ANOVAs confirmed that a significant relationship existed between the density of recruits (1-5 mm & 6-10 mm) and substratum ($p<0.05$, Tables 2.6 & 2.7). However, there were significant interactions for both size classes ($p<0.05$, Tables 2.6 & 2.7). Results of the one-way ANOVAs performed separately on each site and each size class (*i.e.* 1-5 & 6-10 mm), showed that there were no significant differences in recruit densities on algae and mussels at Fish River and Rufanes ($p>0.05$). However, the one-way ANOVAs showed significantly higher recruit densities on coralline algae than on mussels at Diaz Cross and Kwaai Hoek ($p<0.05$).

Effects of site and substratum on standardised densities of recruits (1-5 & 6-10 mm)

There was no significant relationship ($p>0.05$) between the percentage of algal cover and the densities of recruits found on algae *i.e.* Diaz Cross had the highest percentage algal cover, but Kwaai Hoek had the highest recruit density. The densities of recruits for both size classes (1-5 & 6-10 mm) were unequivocally higher on algae than on mussels when densities were standardised to 100% algal cover (Figure 2.3b). This was confirmed by the results of the two-way ANOVAs, which showed substratum and site to have significant effects on recruit densities of both size classes ($p<0.05$, Tables 2.8 & 2.9). The interaction between site and substrate was not significant for 1-5 mm ($p>0.05$, Table 2.8) but was for 6-10 mm ($p<0.05$, Table 2.9).The results of both the separate one-way ANOVAs run on recruit densities (1-5 & 6-10 mm) showed that substratum had a significant effect at Diaz Cross, Kwaai Hoek and Rufanes ($p<0.05$), but not at Fish River ($p>0.05$).

Effects of site on true densities of recruits (1-5 & 6-10 mm) on algae

The true density of 1-5 mm recruits on algae was significantly higher at Kwaai Hoek than at the remaining sites ($p<0.05$, Figure 2.3a, Tables 2.10 & 2.12). In the 6-10 mm size class the density differences between sites were less extreme than in the 1-5 mm size class. There was, however, a significant difference between densities (6-10 mm) on algae at Fish River and Kwaai Hoek ($p<0.05$, Table 2.11 & 2.12).

Effects of exposure and site on densities of recruits (1-5 & 6-10 mm) on adult mussels

The densities of recruits on adult mussels appeared to be fairly constant between sites for both the 1-5 mm and the 6-10 mm size classes (Figure 2.3a). The results of the one-way ANOVAs showed that the densities of recruits (1-5 & 6-10 mm) on mussels were not significantly affected by exposure ($p>0.05$, Tables 2.13 & 2.14). Site, however did affect recruit density on mussels for both size classes ($p<0.05$, Tables 2.15 & 2.16). Tukey's multiple range tests showed that the density at Diaz Cross was significantly lower than that at the other five sites for both size classes ($p<0.05$, Table 2.17). This is despite a high overall density of recruits at Diaz Cross (Figure 2.1) and indicates that the majority of recruits were present on algae at this site (Figure 2.3). Recruit densities (both 1-5 and 6-10 mm) showed greater variability among sites on algae than on mussel (Figure 2.3).

Table 2.4 The effect of site on algal percentage cover. Data were $\sqrt{x+1}$ transformed.

Source of variation	df	SS	MS	F	P
Between	3	321.72	107.24	22.39	<0.0001
Within	76	364.03	4.79		

Table 2.5 Tukey's multiple range test showing differences in algal cover at sites. Data were $\sqrt{x+1}$ transformed.

Site	Exposure	Count	Mean	Homogeneous groups
Ru	S	20	2.68	a
Fs	E	20	4.63	b
Kw	E	20	6.38	c
Dz	E	20	8.07	d

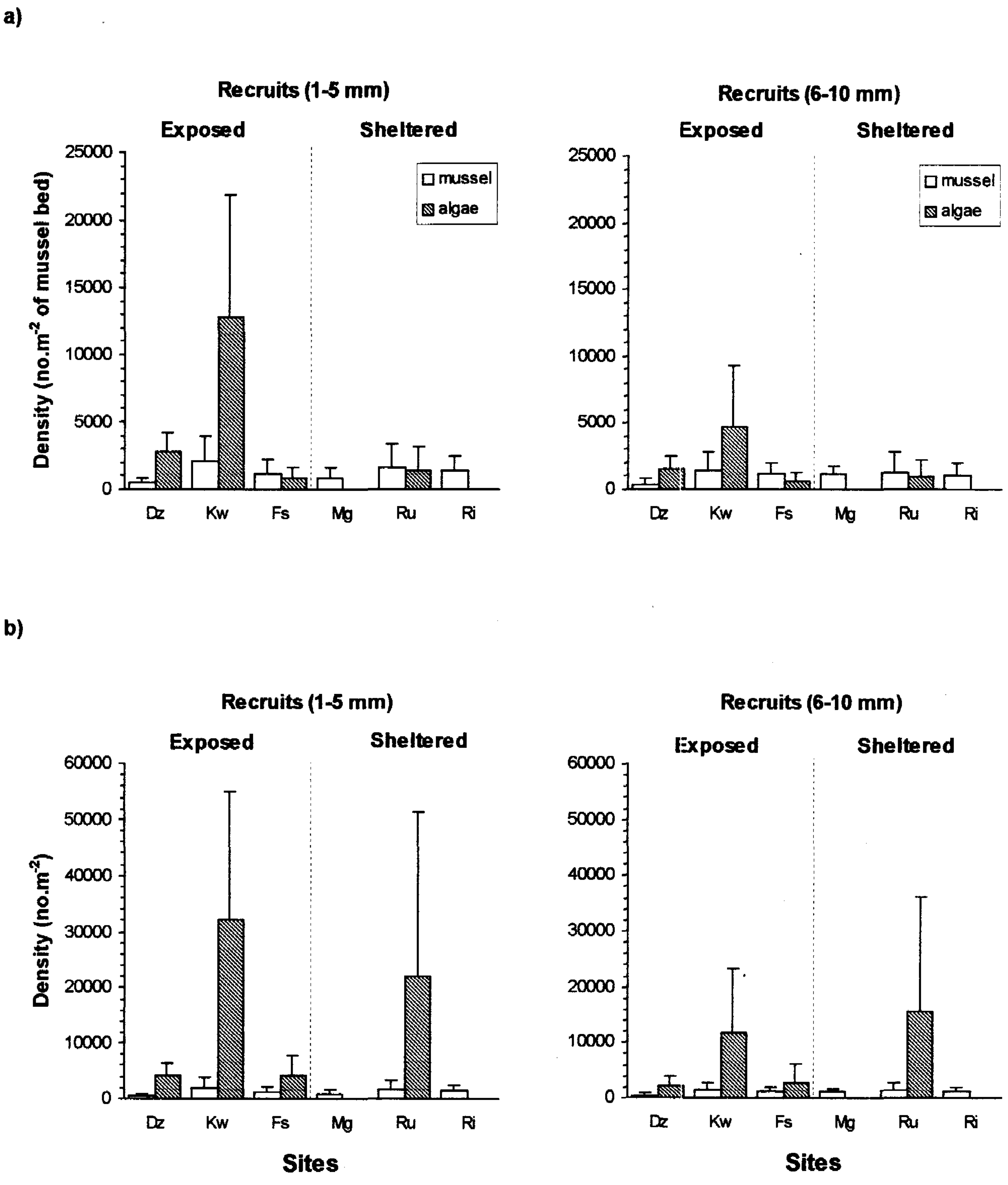


Figure 2.3 Mean recruit (1-5 mm & 6-10 mm) densities (+std. dev.) on algae and mussels over the peak early recruitment months (January, February, April and May). a) (1-5 & 6-10 mm) presents true densities whereas b) presents standardised density data *i.e.* using 100% algal cover. The dominant alga at Rufanes was *Gelidium pristoides* and at Diaz Cross, Kwaai Hoek and Fish River, corallines.

Table 2.6 Two-way ANOVA on the relationship between recruit densities (1-5 mm), substratum and site, using true recruit densities (*i.e.* actually encountered in the field, algal cover has not been standardised). Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	3	10.18	3.39	21.01	<0.0001
Substratum	1	2.81	2.81	17.40	0.0001
Interactions	3	7.64	2.55	15.77	<0.0001
Residual	116	18.74	0.16		

Table 2.7 Two-way ANOVA on the relationship between recruit density (6-10 mm), substratum and site, using true recruit density (*i.e.* actually encountered in the field, algal cover has not been standardised). Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	3	3.03	1.01	4.88	0.0031
Substratum	1	0.84	0.84	4.06	0.0463
Interactions	3	5.94	1.98	9.56	<0.0001
Residual	116	24.01	0.21		

Table 2.8 Two-way ANOVA on the relationship between setter density (1-5 mm), substratum and site, using standardised algal cover. Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	3	3.81	1.27	3.80	0.0122
Substratum	1	12.39	12.39	37.04	<0.0001
Interactions	3	2.49	0.83	2.48	0.0644
Residual	116	38.79	0.33		

Table 2.9 Two-way ANOVA on the relationship between recruit density (6-10 mm), substratum and site, using standardised algal cover. Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	3	8.94	2.98	10.326	<0.0001
Substratum	1	19.53	19.53	67.66	<0.0001
Interactions	3	3.28	1.09	3.79	0.0124
Residual	116	33.49	0.29		

Table 2.10 One-way ANOVA on the relationship between site and true recruit density on algae (1-5 mm). Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Between	3	10.23	3.41	8.21	0.0001
Within	58	24.07	0.42		

Table 2.11 One-way ANOVA on the relationship between site and true recruit density on algae (6-10 mm). Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Between	3	4.01	1.34	2.92	0.0417
Within	58	26.58	0.46		

Table 2.12 Tukey's multiple range test showing true recruit density of 1-5 mm and 6-10 mm on algae at four sites. Data were $\log_{10}(x+1)$ transformed.

Sites	Exposure	n	1-5 mm	6-10mm
Fs	E	16	a	a
Dz	E	16	a	a b
Ru	S	14	a	a b
Kw	E	16	b	b

Table 2.13 One-way ANOVA on the effect of exposure on recruit (1-5 mm) density on adult mussels. Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Between	1	0.04	0.04	0.20	0.6583
Within	92	16.97	0.18		

Table 2.14 One-way ANOVA on the effect of exposure on recruit (6-10 mm) density on adult mussels. Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Between	1	0.55	0.55	2.60	0.1101
Within	92	19.44	0.21		

Table 2.15 One-way ANOVA on the effect of site on recruit (1-5 mm) density on adult mussels. Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Between	5	2.30	0.46	2.76	0.0232
Within	85	14.70	0.17		

Table 2.16 One-way ANOVA on the effect of site on recruit (6-10 mm) densities on adult mussels. Data were $\log_{10}(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Between	5	2.79	0.56	2.85	0.0197
Within	85	17.20	0.20		

Table 2.17 Tukey's multiple range test showing differences in recruit (1-5 & 6-10 mm) density on mussels at the 6 sites. Data were $\log_{10}(x+1)$ transformed.

Site	Exposure	Count	Homogeneous groups (1-5 mm)	Homogeneous groups (6-10 mm)
Dz	E	16	a	a
Ri	S	16	b	b
Kw	E	16	b	b
Ru	S	14	b	b
Fs	E	16	b	b
Mg	S	16	b	b

Effects of exposure, site and month on densities of recruits (1-15 mm)

The mean density of recruits (1-15 mm) over the 11 sampling months (site data pooled) was higher at the exposed shores ($5896.m^{-2}$) than at the sheltered shores ($2986.m^{-2}$) (Figure 2.4). This was confirmed by the ANOVA which showed that exposure and month had significant effects on recruit density ($p<0.05$, Table 2.18). Interactions between the factors exposure and month were not significant ($p>0.05$, Table 2.18), but those between site and month were significant ($p>0.05$, Table 2.19). On the level of site, recruit densities were highest at Kwaai Hoek ($10986.m^{-2}$) (exposed), and Rufanes ($5223.m^{-2}$) (sheltered) (Figure 2.5). Results of the two-way ANOVA showed that site and month had a significant effect on recruit densities ($p<0.05$, Table 2.19). Fish River, an exposed site had densities similar to those at Riet River, a sheltered site, indicating that differences were not simply exposure related (Figure 2.5).

The significant interaction between month and site ($p<0.05$, Table 2.19) indicates differences in timing of recruitment among sites. The significant effect of month shows temporal variations within sites ($p<0.05$, Table 2.19). Diaz Cross showed an additional peak in recruit density in July 1995 and at Fish River the peak extended from January 1996 to June 1996 (Figures 2.6 a & c). Kwaai Hoek had a more defined recruitment peak than all other sites. This peak occurred between January and May and had recruit densities up to six times that of other months (Figure 2.6 b). Recruit density at Mgwalana peaked from January 1996 to May 1996 (Figure 2.6 d). Rufanes showed two recruitment peaks, one narrow peak in

August 1995 and an extended period of high recruit density from August 1995 to June 1996 (Figure 2.6 e). At Riet River, recruit densities were highest in July 1995 and in February, April and May 1996 (Figure 2.6 f)

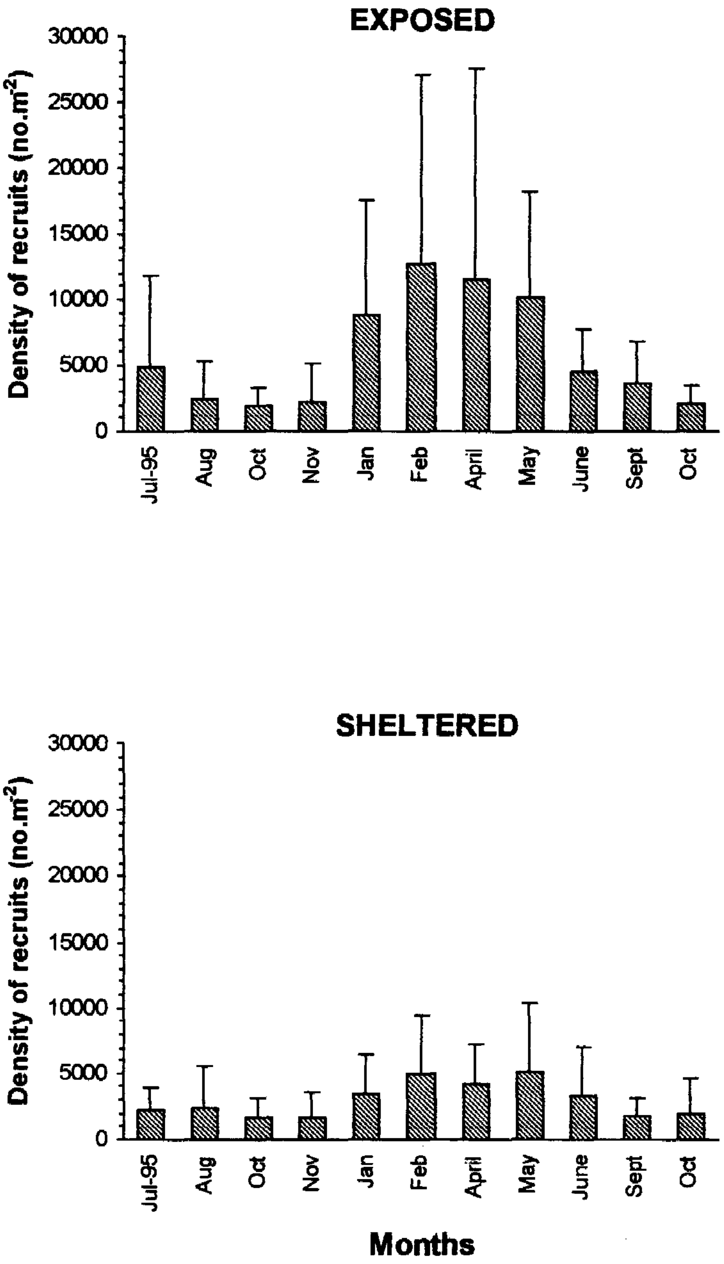


Figure 2.4 Mean recruit (1-15 mm) densities (+std. dev.) for exposed (Diaz Cross, Kwaai Hoek and Fish River) and sheltered shores (Mgwalana, Rufanes and Riet River), for 11 sampling months.

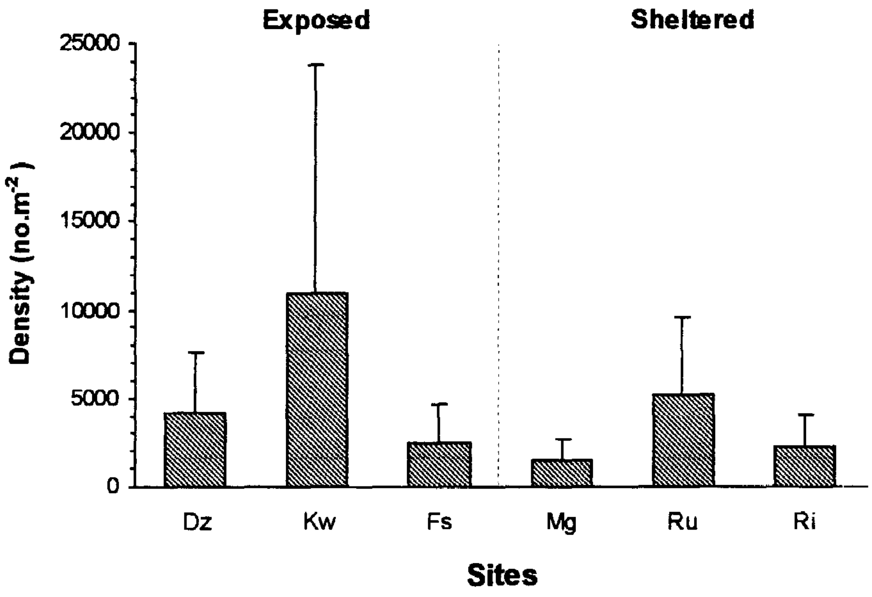


Figure 2.5 Mean recruit (1-15 mm) densities (+std. dev.) for 11 sampling months at six localities.

Table 2.18 Two-way ANOVA on the effect of exposure and month on recruit densities (1-15 mm). Data were $\log_e(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Exposure	1	14.56	14.56	13.87	0.0002
Month	10	76.74	7.67	7.31	<0.0001
Interactions	10	7.55	0.75	0.72	0.7061
Residual	242	254.02	1.05		

Table 2.19 Two-way ANOVA showing the effect of site and month on recruit densities (1-15 mm). Data were $\log_e(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	5	75.52	15.10	20.75	<0.0001
Month	10	76.74	7.67	10.54	<0.0001
Interactions	50	56.49	1.13	1.55	0.0184
Residual	198	144.11	0.73		

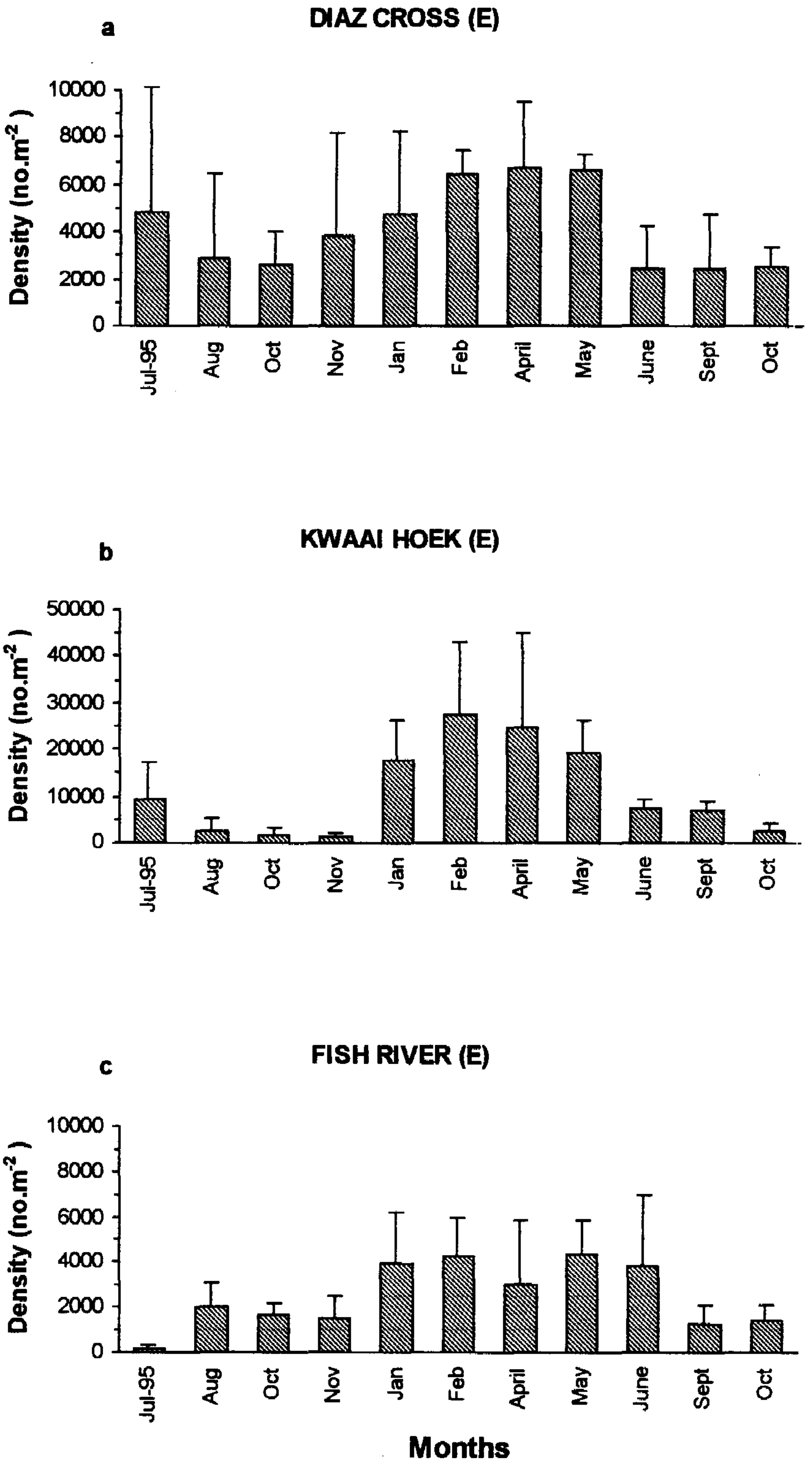


Figure 2.6 a-c Mean recruit (1-15 mm) density (+std. dev.) over 11 sampling months at Diaz Cross, Kwaai Hoek and Fish River (exposed).

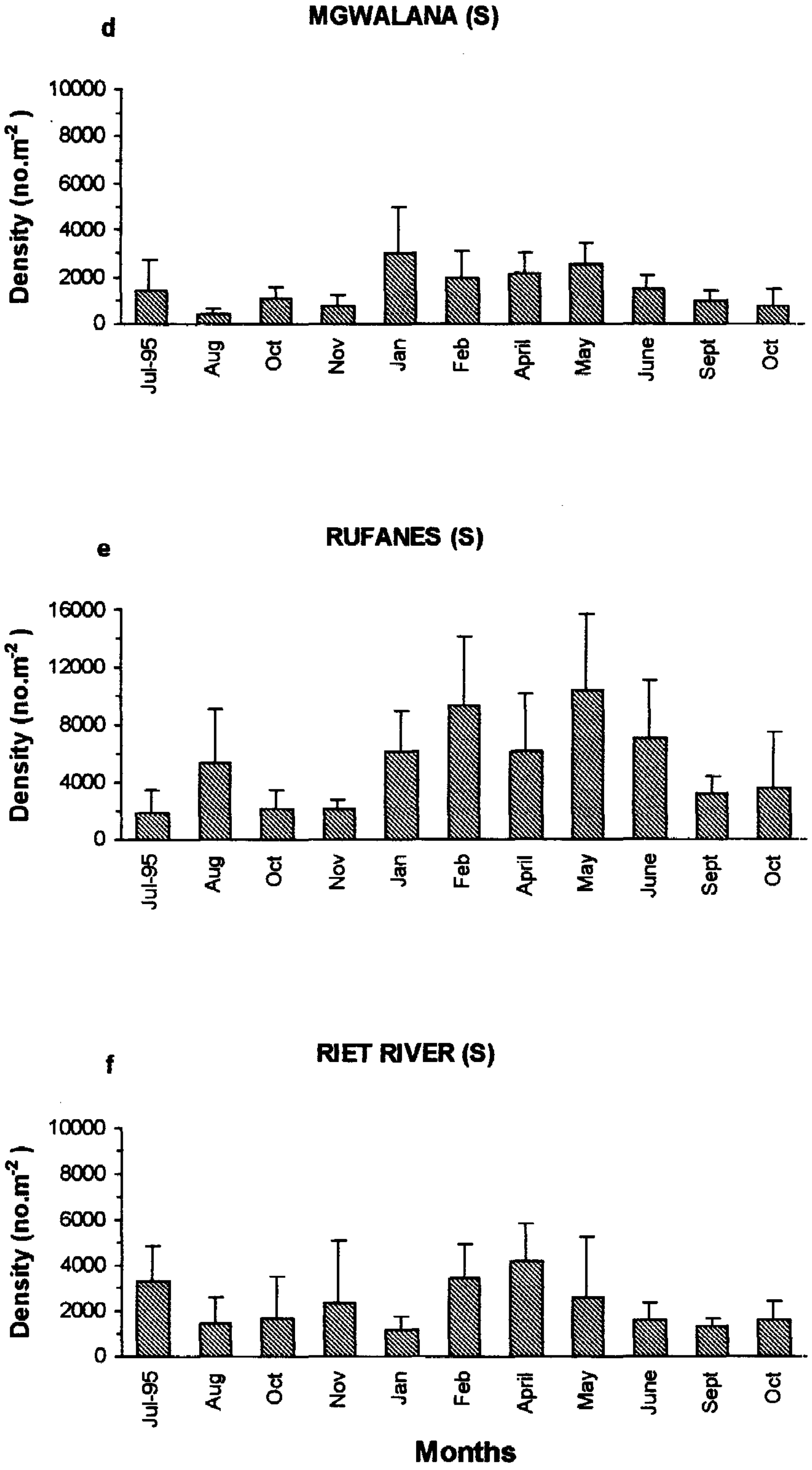


Figure 2.6 d-f Mean recruit (1-15 mm) density (+std. dev.) over 11 sampling months at Mgwalana, Rufanes and Riet River (sheltered).

Regression of recruit (1-5 mm) against adult (>15 mm) densities

On sheltered and exposed shores increases in adult densities were associated with increases in recruit densities (Figure 2.7). Although significant ($p<0.05$), the relationship for both shore types was weak, as indicated by the low r^2 values, and data from sheltered shores showed a slightly stronger relationship than exposed shore data (r^2 = 4.98% & 5.95%). The spread of the data showed higher recruit density, but lower adult density at the exposed shores. The sheltered shores showed the opposite pattern, with lower recruit densities and higher adult densities occurring (Figure 2.7). Examination of the regressions from each site revealed that the overall pattern shown by the exposed shores was highly skewed by data from Kwaai Hoek (Figure 2.8a). The r^2 values for the regressions of adult against juvenile density for each site revealed that only three sites, Kwaai Hoek, Fish River and Riet River, had significant r^2 values ($p<0.05$, Table 2.20). Therefore, even at the level of site, the differences between the regressions did not show any pattern with regards to exposure. Kwaai Hoek had the steepest slope (greater than y=x) due to the lower adult density and higher recruit density.

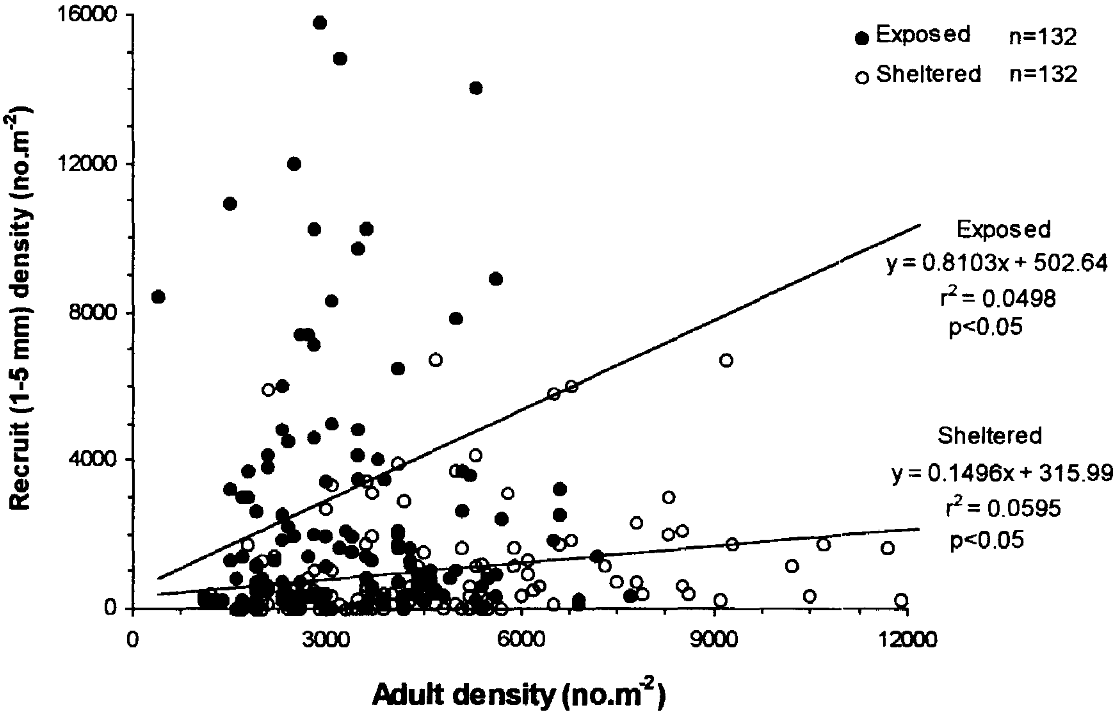


Figure 2.7 Linear regression of adult densities (>15 mm) against recruit (1-5 mm) densities for sheltered and exposed shores. 4 outlying data points have been excluded from the graph, but not the regression calculations.

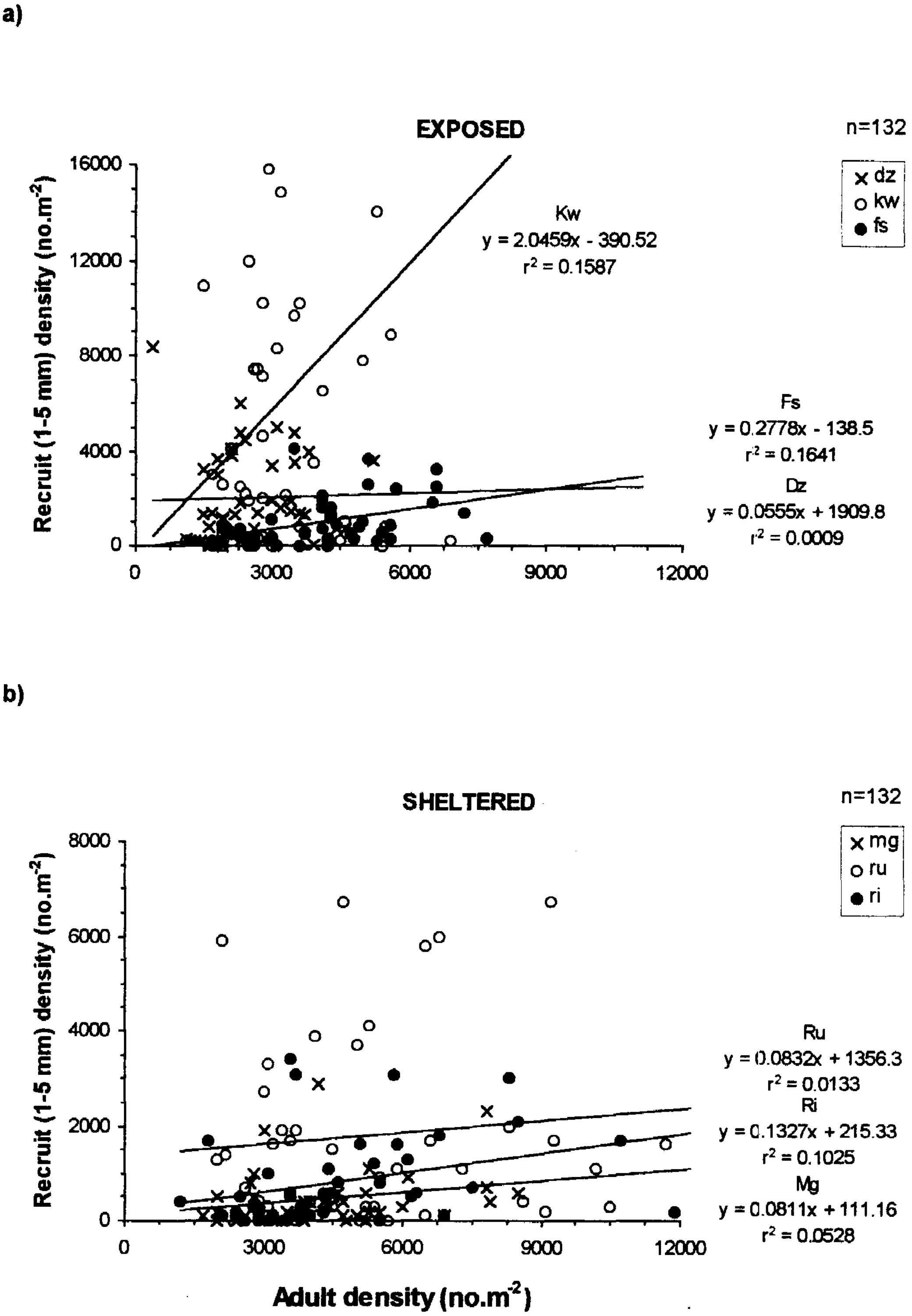


Figure 2.8 Linear regression of adult (>15 mm) density against recruit (1-5 mm) density for a) the exposed sites and b) sheltered sites.

Table 2.20 r^2 and P values for the linear regression of adult density (>15 mm) against recruit density (1-5 mm) for each site.

Site	Exposure	n	r^2 (%)	P
Dz	E	44	0.09	0.8500
Kw	E	44	15.87	0.0070
Fs	E	44	16.41	0.0063
Mg	S	44	5.28	0.1335
Ru	S	44	1.33	0.4558
Ri	S	44	10.25	0.0342

3.3 MEAN AND MAXIMUM LENGTHS, ADULT DENSITY AND TOTAL BIOMASS

Mean adult lengths (>15 mm)

Mean adult lengths were higher on the exposed shores (52.94 mm) than on the sheltered shores (41.59 mm) (Figure 2.9). The highest mean lengths were recorded at Diaz Cross (58.41 mm), followed by Fish River (51.08 mm), Kwaai Hoek (49.32 mm), Mgwalana (43.58 mm), Riet River (42.26 mm) and Rufanes (38.92 mm) (Figure 2.9). These findings were confirmed by the results from the two-way ANOVAs which revealed that a significant relationship existed between exposure and mean length ($p<0.05$, Table 2.21) and site and mean length ($p<0.05$, Table 2.22). Although month had a significant effect on mean lengths, no general trend was apparent among sites, as indicated by the significant interaction ($p<0.05$, Table 2.22).

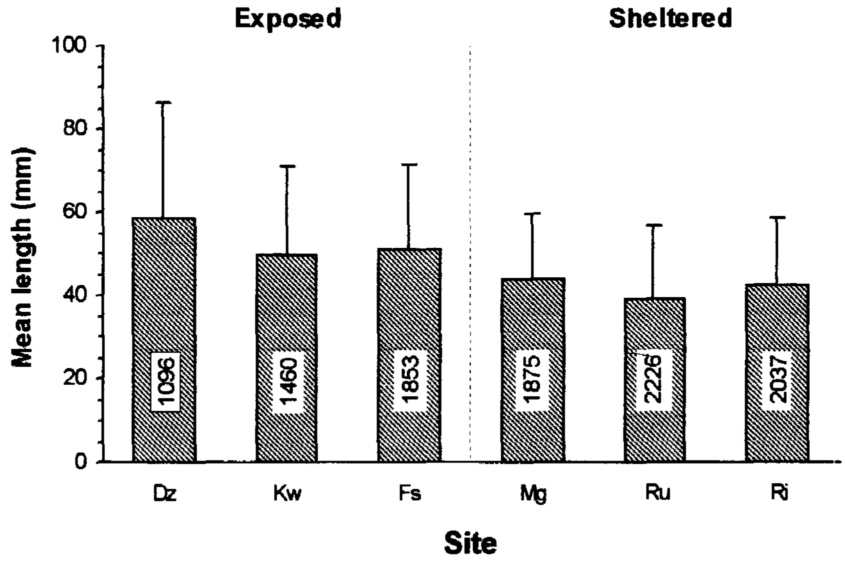


Figure 2.9 The mean adult (>15 mm) lengths (+std. dev.) obtained from 11 sampling months, for six sites. Sample sizes for each site are presented in a text box.

Table 2.21 The relationship between exposure, month and mean adult lengths (>15 mm) as shown by the results of a two-way ANOVA with interactions. Data were √x+1 transformed.

Source of variation	df	SS	MS	F	P
Exposure	1	1293.05	1293.05	610.86	<0.0001
Month	10	225.21	22.52	10.64	<0.0001
Interaction	10	67.42	6.74	3.18	0.0004
Residual		22264.21	2.12		

Table 2.22 The relationship between site, month and mean adult lengths (>15 mm) as shown by the results of a two-way ANOVA with interactions. Data were √x+1 transformed.

Source of variation	df	SS	MS	F	P
Site	5	1682.83	336.67	218.15	<0.0001
Month	10	168.89	16.89	10.95	<0.0001
Interaction	50	941.20	18.82	12.20	<0.0001
Residual		17066.35	1.54		

Maximum Lengths

Mean maximum lengths were higher at the exposed shores (93.62 mm) than at the sheltered shores (75.48 mm) (Figure 2.10). This was confirmed by the results from the two-way ANOVA which showed that a significant relationship existed between exposure, month and maximum lengths ($p<0.05$,Table 2.23). Maximum lengths were highest at Diaz Cross (101.18 mm), followed by Fish River (92.72 mm), Kwaai Hoek (86.97 mm), Rufanes (76.34 mm), Mgwalana (75.36 mm) and Riet River (74.73 mm). The second two-way ANOVA showed a significant difference in the maximum lengths between sites and months (Table 2.24). There was a significant interaction between exposure and month and site and month ($p<0.05$, Tables 2.23 & 2.24).

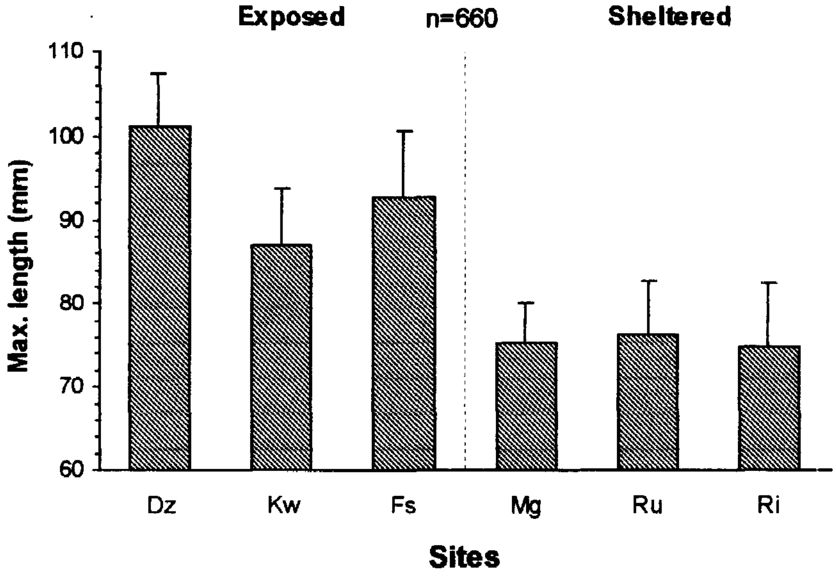


Figure 2.10 Mean maximum lengths (+std. dev.) from the 10 largest mussels each sampling month for each site.

Table 2.23 Two-way ANOVA showing the relationship between exposure, month and maximum length.

Source of variation	df	SS	MS	F	P
Exposure	1	54336.06	54336.06	949.52	<0.0001
Months	10	3189.91	318.99	5.57	<0.0001
Interaction	10	1432.45	143.25	2.50	0.0059
Residual	638	36509.52	57.22		

Table 2.24 Two-way ANOVA showing the relationship between site, month and maximum length.

Source of variation	df	SS	MS	F	P
Site	5	65728.46	13145.69	512.24	<0.0001
Month	10	3189.91	318.99	12.43	<0.0001
Interaction	50	11305.55	226.11	8.81	<0.0001
Residual	594	15244.02	25.66		

Adult densities

Mean adult (>15 mm) densities of mussels were higher (4796.m^{-2}) on the sheltered shores than the exposed shores (3348.m^{-2}) (Figure 2.11). However, at the level of site, densities were highest at Rufanes and Riet River (5495 & 4630.m^{-2}), intermediate at Mgwalana and Fish River (4264 & 4148.m^{-2}) and lowest at Kwaai Hoek and Diaz Cross (3409 & 2486.m^{-2}) (Figure 2.11). These findings were confirmed by the results from the ANOVAs. A significant relationship existed between exposure and density ($p<0.05$, Table

2.25) and between site and density ($p<0.05$, Table 2.26). Densities at Diaz Cross and Kwaai Hoek were significantly lower than those at the remaining sites ($p<0.05$, Table 2.27). There was no significant difference between adult densities at Fish River (exposed site), Mgwalana and Riet River (sheltered sites) ($p>0.05$, Table 2.27). Month did not have a significant effect on adult densities, nor were there significant interactions ($p>0.05$, Tables 2.25 & 2.26).

The correlation of mean monthly densities (recruits + adults) against mean monthly lengths (recruit + adult) for the six sites pooled gave a significant correlation coefficient of -0.81, indicating that as densities increased so lengths decreased, although this relationship was not linear ($p<0.05$, Figure 2.12). Adult densities were not significantly correlated with wave force when data from all 6 sites were used ($r^2 = -0.71$, $p>0.05$, Figure 2.13). However, when data from Fish River were excluded a significant ($p<0.05$) correlation of -0.98 was found. As the mean wave force at Fish River was calculated from only two readings (Chapter 1), it is highly likely that the mean was an inaccurate measure of wave force. From the correlation results, as well as various trends throughout this thesis, it appeared that, although obviously still an exposed site, the wave force at Fish River was over-estimated.

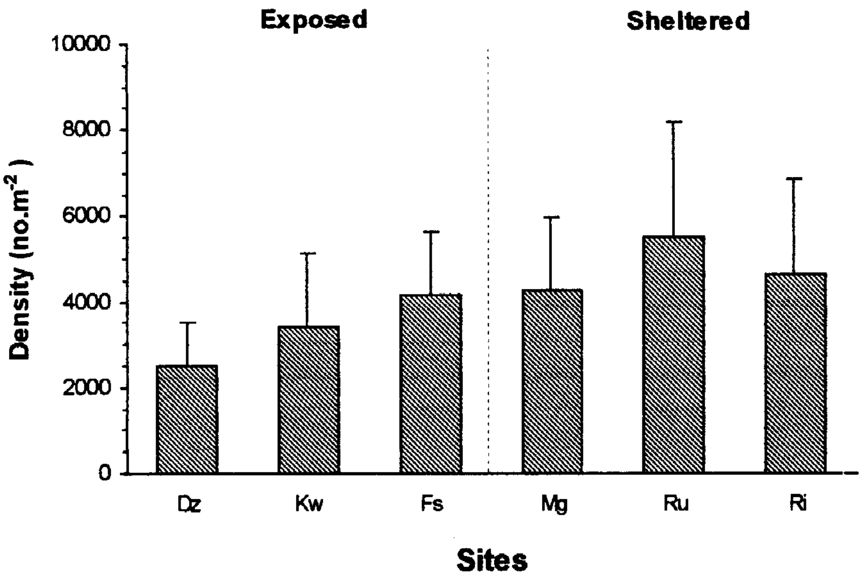


Figure 2.11 Mean adult (>15mm) densities (+std. dev.) over 11 sampling months and at six sites.

Table 2.25 Two-way ANOVA showing the relationship between exposure, month and adult density. Data were $\log_e(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Exposure	1	8.11	8.11	39.71	<0.0001
Month	10	2.15	0.21	1.05	0.4006
Interactions	10	2.57	0.26	1.26	0.2558
Residual	242	49.41	0.20		

Table 2.26 Two-way ANOVA showing the relationship between site, month and adult density. Data were $\log_e(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	5	15.05	3.01	17.42	<0.0001
Month	10	2.15	0.21	1.24	0.2656
Interactions	50	10.83	0.22	1.25	0.1415
Residual	198	34.21	0.17		

Table 2.27 Tukey's multiple range test showing the differences in adult density (> 15 mm) between sites. Data were $\log_e(x+1)$ transformed.

Site	Exposure	Mean no.m^{-2}	Count	Homogeneous groups
Diaz Cross	E	3.17	44	a
Kwaai Hoek	E	3.47	44	b
Fish River	E	3.68	44	c
Mgwalana	S	3.70	44	c
Riet River	S	3.75	44	c d
Rufanes	S	3.91	44	d

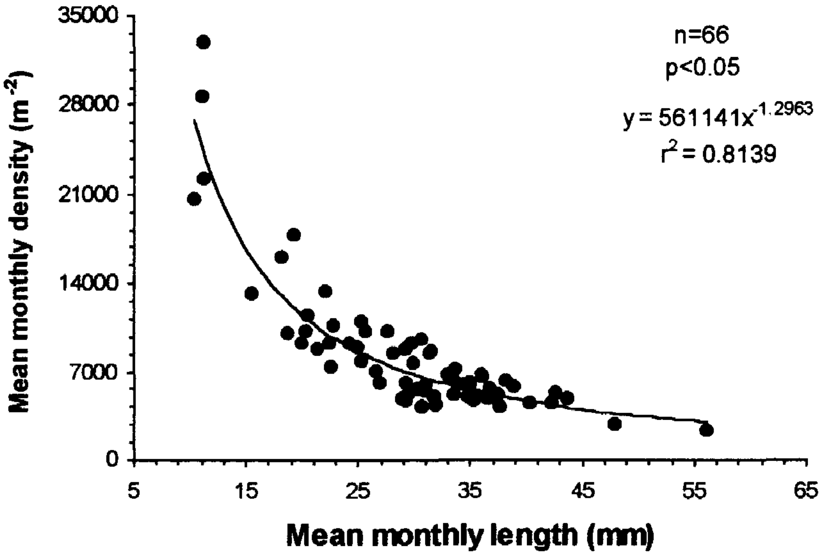


Figure 2.12 Correlation of mean monthly densities of mussels (recruits + adults) against mean monthly lengths (recruits + adults) for the six sites (*i.e.* 11x6 = 66 = n).

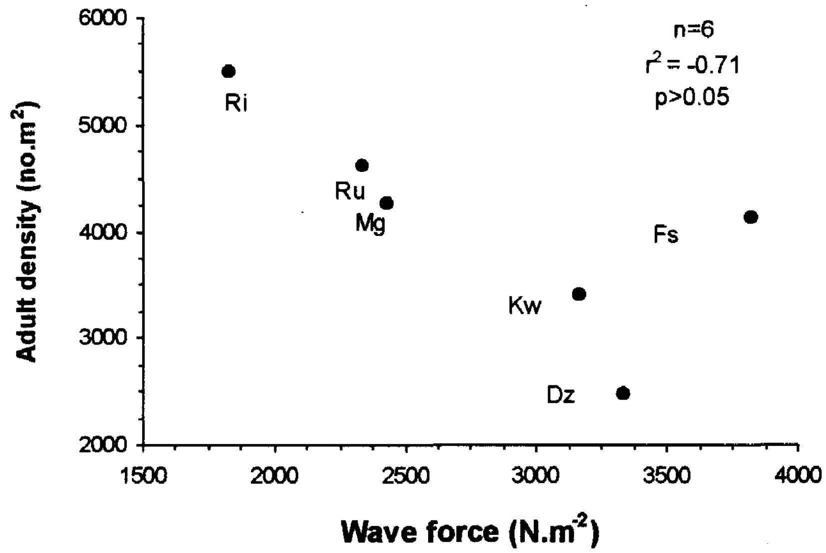


Figure 2.13 Correlation of mean maximum wave force (N.m-2) (Chapter 1) at each site against mean adult density (>15 mm) at each site.

Biomass

Biomass differed considerably between sites and no obvious relationship between exposure and biomass was evident (Figure 2.14). Density and size compensated for each other to produce similar biomass at both shore types. The results of the two-way ANOVA confirmed that no significant relationship existed between exposure and biomass ($p > 0.05$, Table 2.28), however site did have a significant effect on biomass ($p < 0.05$, Table 2.29). Month had a significant effect on biomass ($p < 0.05$, Tables 2.28 & 2.29) but had no interaction with exposure or site ($p > 0.05$, Tables 2.28 &2.29). As biomass was extrapolated from length data, mass changes are not an indication of gondal mass fluctuations. There were no significant correlations ($p > 0.05$) between mean mass and mean lengths (Figure 2.15), mean mass and mean densities (Figure 2.16) and mean mass against the length:density correlation coefficients (Figure 2.17).

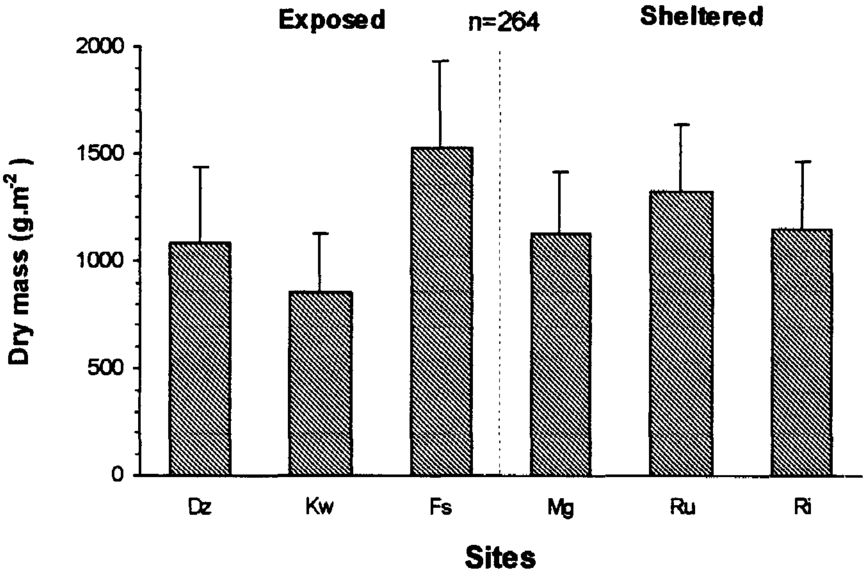


Figure 2.14 Mean biomass (g.m^{-2}) (+std. dev.) for 11 sampling months at six sites.

Table 2.28 Two-way ANOVA on the relationship between exposure, month and biomass. Data were log$_e$(x+1) transformed.

Source of variation	df	SS	MS	F	P
Exposure	1	0.08	0.08	1.01	0.3160
Month	10	1.73	0.17	2.13	0.0233
Interactions	10	1.48	0.15	1.82	0.0575
Residual	242	19.70	0.08		

Table 2.29 Two-way ANOVA on the relationship between site, month and biomass. Data were $\log_e(x+1)$ transformed.

Source of variation	df	SS	MS	F	P
Site	5	5.46	1.09	18.56	<0.0001
Month	10	1.73	0.17	2.94	0.0018
Interactions	50	4.15	0.08	1.41	0.0520
Residual	198	11.65	0.06		

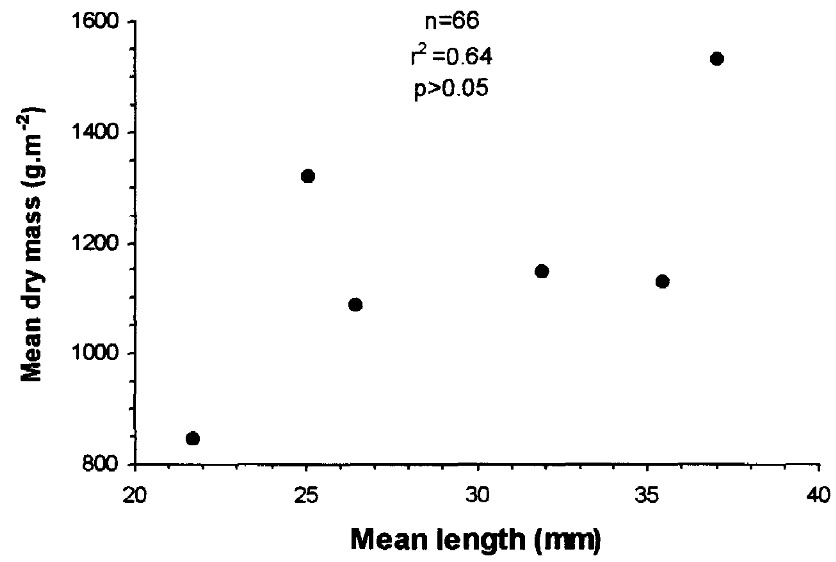


Figure 2.15 Correlation of mean dry mass at each site against mean length at each site. Data from the entire sampling period and both adults plus recruits were used.

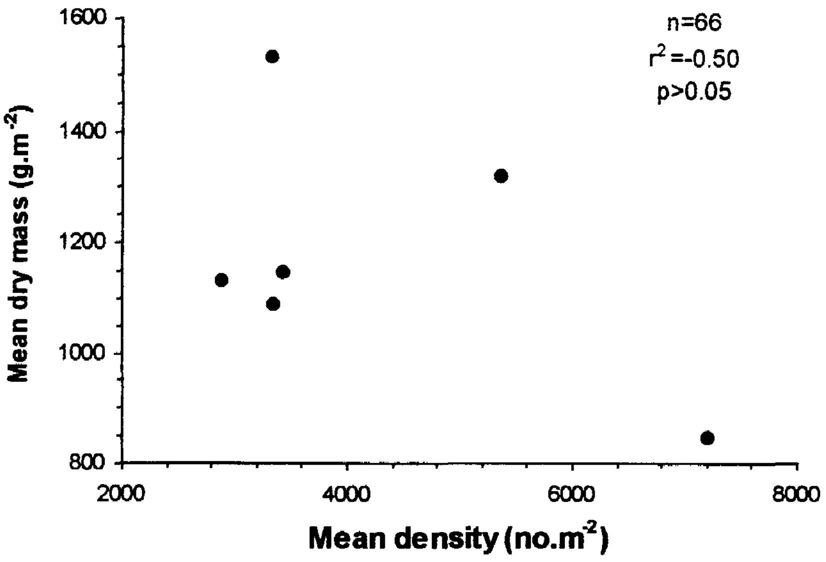


Figure 2.16 Correlation of mean dry mass at each site against mean density at each site. Data from the entire sampling period and both adults plus recruits were used.

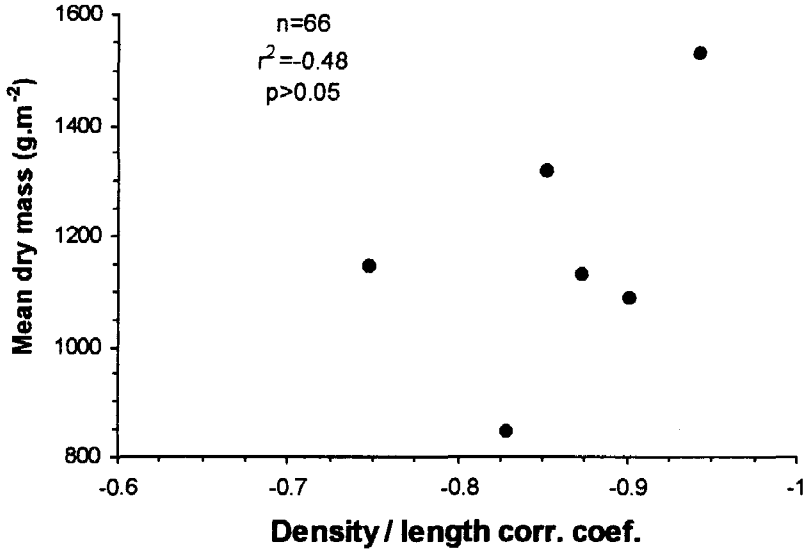


Figure 2.17 Correlation of the mean dry mass at each site against the correlation coefficients obtained from previously correlating density against length. Both adult and recruit mussels were used in all cases.

4. DISCUSSION

The size-frequency distribution of a population is a product of settlement and recruitment, growth and mortality (Seed & Brown 1978). These processes are largely unpredictable, and vary both spatially and temporally (Yamaguchi 1975, Griffiths 1981). Possible reasons for a bimodal population structure, as was observed at all six sites (Figure 2.1), have been outlined by Alvarado and Castilla (1996). These include juvenile mortality (also Seed & Brown 1978), the year-round presence of juveniles, slower growth rates in the adult mode which results in class overlap, a decrease in mortality as size increases, a critical size after which mortality increases dramatically (physical removal by predators or waves) (see Petraitis 1990, Alvarado & Castilla 1996). The smaller adult mode (48 mm) at sheltered shores than at exposed shores (73 mm) (Figure 2.1) was most likely a result of decreased growth rate (see chapter 3) but could in theory be due to size-dependent mortality. Although informative, size-frequency distributions present an inconclusive picture of population dynamics (Yamaguchi 1975).

Settlement and recruitment

From the vast amount of literature on spawning, settlement and recruitment it is apparent that these processes are dynamic both in time and space (Dare 1976, Caffey 1985, Lasiak 1986, King *et al.* 1989, Roegner & Mann 1995, Hunt & Scheibling 1996). The erratic and somewhat patchy occurrence of mussel beds is better recognised against this background of variability. The spawning cycle can perhaps be regarded as the first of a series of events leading to the establishment of a mature mussel bed. Mussels of the same species may spawn at different times of the year due, in part, to differences in local conditions. *Perna perna* along the south Cape coast (South Africa) has a spawning peak from May to October (winter to spring) (Phillips 1994, Ndzipa pers. com.), whereas in the former Transkei (South Africa), the spawning period was more prolonged, extending from February to September (summer to spring) (Lasiak 1986). The black mussel, *Choromytilus meridionalis* and the ribbed mussel, *Aulacomya ater* in the south western Cape showed both synchronous and asynchronous spawning from August to February (spring to summer) (Griffiths 1977). Preliminary findings on *Perna perna* (Ndzipa pers. comm.) indicate the gonadal output occurs slightly earlier in mussels on exposed shores than on sheltered shores. Spawning intensity is also affected by wave action, and for *Perna perna* has been documented as being more intense in bays than on the open coast (Phillips 1994). An increase in mussel size is associated with an increase in gamete production (Griffiths & King 1979b on *Aulacomya ater* and Sprung 1983 on *Mytilus edulis*). Therefore the presence of larger mussels on the exposed shores (Figures 2.9 & 2.10) may result in higher gonad production than on the sheltered shores. This phenomenon has been noted with reference to shore height, as higher shore individuals are smaller and have lower gamete production (Griffiths & Buffenstein 1981 on *Choromytilus meridionalis* and Seed 1976 on *Mytilus edulis*). Although an increase in the density of reproductive adults would also increase gonadal output, the proportional influence of large mussels is more dramatic, for example, a *Choromytilus meridionalis* of 100 mm releases two to three times the weight of gametes that a 50 mm mussel does (Griffiths 1977).

The second phase at which wave action is important is that of larval dispersal. The hydrodynamics on the coast may confine larvae locally by eddies or transport them off-shore (Grant *et al.* 1992). If larvae reach mainstream currents, for example the Agulhas current, they could be passively transported for hundreds of kilometres (Wildish and Kristmanson 1993). Young larvae are planktonic and once in suspension they rapidly produce mucous threads which may prolong drifting (Lane *et al.* 1985). They are also capable of delaying metamorphosis for several weeks until a suitable substratum has been reached (Bayne 1965). If in this present study spawning occurred in October (this was the latest spawning peak noted on the south Cape coast by Phillips 1994) then the interval between spawning and early recruitment (1-5 mm) in January (Figure 2.2), would have been approximately two months. Settlement would have occurred sometime prior to early recruitment. When larval drift, larval metamorphosis, settlement and recruit growth are accounted for, this time interval between the two processes is reasonable, indicating that a spawning peak probably did occur in October and possibly continued for a month or two (considering that the early recruitment peak occurred from January to April). Lasiak and Barnard (1995) recorded high densities of early (<500μm) plantigrades of *Perna perna* on mussel clumps from June to September (winter) and high densities of late (>0.5 to 3.5 mm) plantigrades on mussel clumps from June to October. This could indicate that the time interval between the early and late plantigrade stage is less than one month. In contrast, the time interval between peak densities in early and late plantigrades on algae was 2-3 months (Lasiak and Barnard 1995). Spawning is not necessarily followed by settlement as indicated for *Mytilus edulis* in Britain where settlement can be absent after the major spring spawning (Dare 1976).

Larvae are brought into contact with various substrata by a combination of hydrodynamic processes (water flux, turbulence, drag, flushing time) interacting with local physical factors (height, depth, substratum, slope) (Hunt & Scheibling 1996). Whether the final selection of a substratum is active or passive remains a point of much debate. It seems likely that active substratum selection is possible in less turbulent conditions when larvae are closer to the bottom (Bourget *et al.* 1994, Wildish & Kristmanson 1993) and may even be trapped in the viscous sublayer (Jonsson *et al.* 1991). Larvae have been reported to be capable of crawling along the substratum and thereby may actively choose a settlement substratum (Harger 1968, Caceres-Martinez *et al.* 1994). Recruitment (1-5 mm) occurred at low numbers throughout the year, but was highest from January to April (summer/autumn), peaking in February (Figure 2.2). In a study on *Perna perna* on St. Croix Island (Algoa bay, South Africa) high numbers of recruits (1-3 mm) were noted from February to April (corresponding to the finding in this study) and in September/October (Beckley 1979). The summer/autumn secondary settlement peak was also documented for *Perna perna* in Tsitsikamma (South Africa) (Crawford & Bower 1983), whereas along the Transkei coast (South Africa), late plantigrades (>0.5 to 3.5 mm) reached peak abundance in winter on mussels and in spring/early summer on algae (Lasiak & Barnard 1995).

The densities of recruits, 1-5 and 6-10 mm (from January to May) were significantly higher on algae than mussels (Tables 2.6 to 2.9). This was the case for both true densities and those obtained from 100% algal cover. This finding is in agreement with that of Petersen (1984) who suggested that higher numbers of *Mytilus californianus* plantigrades in Oregon were found on algae as it acted as a net, filtering out and trapping settlers. In contrast, in the former Transkei, substratum had no effect on the densities of early *Perna perna* plantigrades, but the number of late plantigrades (>0.5 to 3.5 mm) were higher on mussels than on algae (Lasiak & Barnard 1995). A number of bivalve species settle on algae, for example *Mytilus edulis* on filamentous algae (Bayne 1964, Seed 1969a, Seed 1976, Suchanek 1978, Petersen 1984, Eyster & Pechenik 1987), *Choromytilus meridionalis* on *Polysiphonia incompta* and *Gracilaria* (Griffiths 1976, du Plessis 1977), *Perna perna* on *Gelidium pristoides* and corallines (Berry 1978, Beckley 1979, Lasiak & Barnard 1995, Phillips 1994) and *Mytilus californianus* on corallines (Petersen 1984). Recruits were present on the mussel bed at all sites (Figure 2.3). Due to the absence of algae on the mussel beds studied at Riet River and Mgwalana, the presence of recruits was likely a result of direct settlement. Direct settlement onto adult mussel beds has been noted for *Mytilus edulis* (McGrath *et al.* 1988), *Choromytilus meridionalis* (Griffiths 1981), *Mytilus galloprovincialis* (Caceres-Martinez *et al.* 1994) and *Perna perna* (Phillips 1994, Lasiak & Barnard 1995). Exposure did not significantly affect the density of recruits on mussels (Figure

2.13 & 2.14), although there were significant differences in the densities on algae (Tables 2.10 & 2.11). These results indicated that despite high numbers of recruits (1-10 mm) on algae, they do not appear to be recruiting into the population and affecting the densities of recruits (1-10 mm) in the mussel bed.

The theme of primary and secondary settlement was originally described by Bayne (1964). He documented *Mytilus edulis* plantigrades, 250 to 350 μm, on algae and the subsequent recruitment of plantigrades, 1.0 to 1.5 mm, into the mussel bed. The presence of *Perna perna* settlers on upright corallines and their subsequent migration to adult mussel beds at 0.6 to 7 mm (Phillips 1994) gives evidence in favour of primary and secondary settlement. It therefore appears that if secondary settlement occurred it would be most prevalent in recruits $\leqslant$ 7mm. In this study, the abundance of juveniles >7mm on algae (particularly on corallines), adds more circumstantial evidence to refute secondary settlement in *Perna perna* . In addition, Petersen (1984) observed that *Mytilus californianus* settlers and plantigrades on algae (found on adult mussels) did not increase or decrease recruitment into the mussel bed. Lasiak and Barnard (1995) noted that the recruitment pattern of *Perna perna* also did not conform to primary and secondary settlement. Unlike the spat of *Choromytilus meridionalis* that move from the adult shell to the substratum (Griffiths 1981), recruits of *Perna perna* do not, and adult mortality will result in recruit mortality, both of settlers/recruits on the algae and on the byssal threads (Berry 1978). Connell (1985) reported the density of barnacle recruits to be a direct reflection of settler density.

Densities of recruits, 1-15 mm for the 11 months, were significantly higher on the exposed than the sheltered shores (Table 2.18 & 2.19). However, considering the high recruit (1-5 & 6-10 mm) density on algae (Figure 2.3), it seems likely that the presence of algae as well as exposure caused the differences in recruit (1-15 mm) densities. This was deduced by the fact that recruit (1-15 mm) densities at Rufanes (sheltered & had algae) were more similar to those at the exposed sites (had algae) than the other sheltered sites (no algae). The effect of algae may mask the effects of exposure and should not be ignored. Higher settlement on exposed than sheltered shores has been noted for the acorn barnacle *Semibalanus balanoides* (Menge 1991, Bertness *et al.* 1992). Recruitment density (1-15 mm) for *Mytilus galloprovincialis* was also twice as high on exposed shores than sheltered shores (Leeb 1995). Water movement has been shown to enhance settlement onto algae (Eyster & Pechenik 1987). In contrast, mean settlement intensity was higher in Algoa bay (sheltered) than the open coast (more exposed) (Phillips 1994). Petraitis (1991) did not find consistent differences between the numbers of *Mytilus edulis* recruits and exposure in Maine, but in general recruitment was higher on wave exposed shores, suggesting that some other factor was influencing recruitment as well.

Total density (on algae + on mussel) of recruits (1-15 mm) was site dependent (Table 2.11), mean densities were six times higher at Kwaai Hoek than at Mgwalana. High standard deviations in juvenile densities at Kwaai Hoek probably resulted from patchy distribution. Petersen (1984) also noted high standard deviations which increased as sample size increased. An increase in adult density was associated with an increase in juvenile density, which agrees with Leeb's (1995) finding on *Mytilus galloprovincialis*. This is understandable as adults provide suitable settlement areas for juveniles in the form of byssal threads and crevices in which settlers can seek refuge (Alvarado & Castilla 1996).

Although the regression between adult and recruit (1-5 mm) densities were significant for both shore types, the predictability of recruit densities from adult densities was low (Figure 2.7 & Table 2.20). Harris (pers. comm.) found significant correlations between adult and recruit (1-10 mm) densities for mussels in general in South Africa, obtaining a correlation coefficient (r=0.437) considerably higher than those obtained for the exposed (0.231) and sheltered shore mussels (0.244) in the present study.

In general settlement is very variable (Suchanek 1978, Griffiths 1981, King *et al.* 1989), difficult to explain (Seed 1969a) and related to a variety of biological and physical factors (Dare 1976, Dye 1995, Hunt & Scheibling 1996, Young *et al.* 1996).

Mean and maximum lengths

The mean maximum length attained by *Perna perna* was higher at the exposed sites than at the sheltered sites (Figure 2.9, Table 2.21), a finding also noted for the Mediterranean mussel, *Mytilus galloprovincialis* in the low shore at Camps Bay and Groenrivier (Cape Town, South Africa) (Leeb 1995). However, Hager (1970) recorded a decrease in maximum length with an increase in exposure for the blue mussel, *Mytilus edulis*. Mussels on exposed shores had higher mean lengths than those on sheltered shores (Figure 2.10 Table 2.23). This has also been documented for *Mytilus edulis* (Jones & Demetropoulos 1968, Seed 1969b). Several studies have shown that larger mussels occur on more sheltered sites (Harger 1970, Petraitis 1991, Alvarado & Castilla 1996). Theoretically, the critical size at which mussels are removed by wave action should be lower on wave exposed than wave sheltered shores (Harger 1970). However, it seems reasonable to assume that this is dependent on not only the degree of wave exposure but also the frequency, time period and dominant force (drag or lift) that the mussels are subjected to. Mussels living under certain conditions may be physically adapted to survive there, for example *Mytilus galloprovincialis* from the low shore were more firmly attached than on the high shore and similarly mussels from the exposed high shore were more firmly attached than those from the sheltered high shore (Leeb 1995).

The force required to remove mussels from rocks increases as mussel size increases, but this relationship varies between species (Harger 1970, Leeb 1995). Harger (1970) presents evidence that suggests that a higher number of stronger byssal threads are produced in *Mytilus galloprovincialis* when exposed to greater wave action. Hepburn *et al.* (1979) showed that *Perna perna* had stronger byssal threads under conditions of greater wave exposure. Harger (1970), Price (1980, 1982) and Leeb (1995) determined the strength of attachment by measuring the vertical force required to remove a mussel. This vertical force is a measure of the amount of lift that the mussels can withstand and acts perpendicular to the direction of water flow (Denny 1987). As lift is generated by the pressure difference caused by water velocity above and within the mussel bed, the damaging effects of lift are more prevalent in dense, firmly packed beds than loosely packed, sparse ones (Denny 1987). By virtue of their greater size, mussels at the exposed shores would experience greater drag (see Sousa 1985). In addition, the presence of macroalgae, particularly at Diaz Cross and Kwaai Hoek, would increase drag (Witman & Suchanek 1984).

Mean and maximum mussel lengths are frequently dependent on growth rates or vice versa (Seed 1969b, Jørgensen 1976, chapter 3). The availability of food may be the main factor determining the growth rate and the maximum size a species or individual can attain (Jørgensen 1976, Kautsky 1982, see Chapter 3 discussion). Size is not necessarily indicative of growth, for example, shell length of the bivalve, *Geukensia demissa* did not decrease upshore although the growth rate did (Franz 1993). Size may also be determined by predator selection (Seed & Brown 1978), man in particular favours larger mussels (Hockey & Brosman 1986). As the largest mussels are also the most fecund, too much harvesting pressure could be detrimental to the supply of recruits in the long term (Branch 1975, Berry 1978, Dye *et al.* 1994).

Packing Density

Density in this study referred to the number of mussels in an area of approximately 100% mussel cover *i.e.* packing density. Adult (>15 mm) densities were significantly higher on the exposed shores than the sheltered shores (Table 2.25). However, this pattern was not as distinct at the level of site, where lowest densities (2486-3409.m^{-2}) were shown for two exposed sites, intermediate densities (4148-4264.m^{-2}) for one exposed and one sheltered site and highest densities for two sheltered sites (4630-5495.m^{-2}) (Figure 2.11). A significant negative correlation was obtained between wave force and adult densities when data from Fish River was excluded (Figure 2.13). This is in opposition to the findings of several authors who have documented higher densities at exposed sites (Jones & Demetropoulos 1968, Beckley 1979, Crawford & Bower 1983, Leeb 1995). The densities recorded for *Perna perna* were high (2486-5495.m^{-2}) in comparison to those reported for *Choromytilus meridionalis* (1025.m^{-2}) (Griffiths 1977). Although mean densities of *Perna perna* along the Tsitsikamma coast varied considerably between localities (480-19860.m^{-2}), being higher at more exposed sites, the overall mean density for the coast was 3819.m^{-2} (Crawford & Bower 1983).

Densities are related to the mean and maximum size of mussels present, as higher numbers of small mussels can be packed into a given area than large ones (Griffiths 1981). The clam, *Spisula soldissima* showed density dependent size from five years of age, whereupon length decreased as density increased (Cerrato & Keith 1992). There was also a negative correlation between growth rate and density (Chapter 3). This has also been documented for other species, such as *Mercenaria mercenaria* (Peterson & Beal 1989). In the ribbed mussel, *Geukensia demissa* occurring at high densities, individuals in the centre of a mussel clump have been shown to grow slower than those at lower densities at the edge (Bertness & Grosholz 1985). Crowding may decrease the scope for growth due to seston depletion or food competition (Kautsky 1982, Newell & Shumway 1993). Predators, including man are also responsible for a decrease in densities (Seed 1969b, Hockey & Bosman 1986) (see Chapter 4). For many species the supply of recruits is independent of local adult populations, particularly where propagules disperse widely (Roughgarden *et al.* 1985 in Menge & Sutherland 1987). In species with localised dispersal, adult densities are dependent on recruit density (Roughgarden *et al.* 1985 in Menge & Sutherland 1987). Connell (1985) noted that adult density was positively correlated with recruit density when recruitment was light but was uncorrelated when it was heavy.

Mussel beds at Fish River were multi-layered which explains the higher densities relative to Kwaai Hoek and Diaz Cross. In theory, if small mussels occur in a patch and mortality is low, the growth needs to go somewhere. Outward expansion occurs to a degree, but not enough for the rapidly growing mussels and as a result multi-layering occurs (Petraitis 1995). Multi-layering could also be a result of an event in the history of the system, for example the occurrence of factors which promoted higher settlement, recruitment or better post- settlement/recruitment survival (Sutherland 1974, Clarke & Warwick 1994 in Leeb 1995). This could become self perpetuating as multi-layering allows greater retention and survival of juveniles (Alvarado & Castilla 1996).

Biomass

There was no obvious relationship between exposure and biomass (Figure 2.14 & Table 2.28), although indirectly due to its influence on densities and mean lengths, wave exposure would have an affect. Density and length must affect biomass, but the relationship between these variables was not obvious (Figure 2.15 to 2.17). Off the Cape of Good Hope, filter-feeders carnivores and omnivores all had significantly higher biomass under exposed conditions (McQuaid & Branch 1985). Dickie *et al.* (1984) have reported "geno-adaptation" *i.e.* genetic adaptation, which is the ability for *Mytilus edulis* which have been transplanted from tough conditions to more favourable ones to obtain higher growth rates, survival rates and therefore biomass than mussels originating from favourable conditions. Biomass is therefore a product of the environment, the mussels' genes, size, density and growth rate (gonadal and somatic) (Dickie *et al.* 1984). An increase in water movement and seston supply has been shown to increase feeding, growth rate and ultimately the biomass of the clam, *Modiolus modiolus* (Wildish & Kristmanson 1993). The average biomass for *Perna perna* in this study was 1177g.m $^{-2}$, considerably higher than the 790g.m^{-2} reported for *Choromytilus meridionalis* (Griffiths 1977). As previously mentioned densities for *Choromytilus meridionalis* were also lower than for *Perna perna*, which would directly affect biomass. Biomass within restricted areas is higher than areas where exploitation occurs (Crawford & Bower 1983).

In conclusion, exposure has a true effect on the population dynamics of *Perna perna*. The influence of wave action on recruitment, size and density has resulted in quite distinct populations on exposed and sheltered shores. The populations may even be structured by different processes. Findings from chapters 1, 2 and 4 serve to support the suggestion and provide more justification for the division of mussel populations on exposed and sheltered shores.

SUMMARY

- Peak early recruitment occurred from January to April at both exposed and sheltered shores.
-

Sites	Exposure	Algae	Recruit density (1-15 mm.m^{-2})	% Recruits (1-10 mm) on mussels using true densities	% Recruits (1-10mm) on algae using true densities
Diaz Cross	E	Coralline	4 209.09	16.73	83.27
Kwaai Hoek	E	Coralline	10 986.36	16.52	83.48
Fish River	E	Coralline	2 493.18	61.67	38.33
Mgwalana	S	-	1 490.91	100.00	0
Rufanes	S	Gelidium	5 222.73	56.21	43.79
Riet River	S	-	2 243.18	100.00	0

- During peak early recruitment months, there were significantly more recruits (1-5 & 6-10 mm) on algae than on the mussel bed.
- During peak early recruitment months, there was no significant difference in recruit density (1-5 & 6-10 mm) on adult mussels between sites.
- The density of recruits, 1-15 mm (on algae + mussel) was significantly higher on exposed shores, but this pattern was not evident at the level of site.
- There were significant adult-recruit regressions for both shore types, but r^2 values were very low.
- Mean adult lengths were higher on the exposed shores.
- Mean maximum lengths were higher on the exposed shores.
- Mean adult density was higher on the sheltered shores.
- Adult density decreased with an increase in wave force (Fish River excluded).
- There was no significant difference in biomass between shore types.

CHAPTER 3

USING THREE APPROACHES TO DETERMINE GROWTH RATES OF *PERNA PERNA* ON WAVE EXPOSED AND WAVE SHELTERED SHORES

1. INTRODUCTION

Growth rate studies are essential when attempting to understand the complexities of a population, whether it be purely for biological reasons or from a management point of view. These growth studies contribute to the estimates of production, biomass, recruitment and mortality of a population (Isaac 1990).

Intertidal organisms are renowned for their plasticity, particularly in growth, which enables them to adapt to a wide range of environmental factors (Seed 1976, Von Erkom Schurink & Griffiths 1993). For example, the mussel *Mytilus edulis* on the coast of Washington had fast growth which enabled it to act as an opportunistic species by rapidly colonising an area and reaching reproductive size (Suchanek 1978). Alternative growth patterns were observed in the clam, *Spisula solidissima* which had slower growth rates and a shorter lifespan inshore than offshore (Cerrato & Keith 1992). The flexibility of growth rates enables some populations to rapidly grow beyond a size selected by most predators (Griffiths & Hockey 1987). Rapid growth can also enable an organism to compete more successfully for a limited resource (Seed & Brown 1978). In some cases a trade-off exists and energy is channelled into reproduction rather than into somatic growth (Seed & Brown 1978). Despite this plasticity, environmental factors can constrain growth rate, for example, old non-growing *Mytilus edulis* transplanted from unfavourable to favourable conditions, quickly resumed growth (Seed 1968). Rates of growth are influenced by genetic and environmental factors, including wave action (Jones & Demetropoulos 1968, Harger & Landenberger 1971, Raubenheimer & Cook 1990, Leeb 1995), currents (van Erkom Schurink & Griffiths 1993), tidal height (Griffiths 1981, Takada 1995), emergence time (Griffiths & Buffenstein 1981), temperature (Thiesen 1973, Ceccherelli & Rossie 1984, Pechenik *et al.* 1990), food quality and quantity (Griffiths 1980a & 1980b, Tsuchiya 1980, Newell & Shumway 1993) and packing density (Cerrato & Keith 1992). Biological influences by parasites (Lasiak 1993, Calvo-Ugarteburu & McQuaid in press) and predators (Menge 1976) also affect growth rates directly and indirectly respectively. Although it is difficult to isolate the effect of one particular factor in a naturally occurring mussel population (Kautsky 1982), several authors have documented the effects of wave action on growth rates (Jones & Demetropoulos 1968, Jørgensen 1976, Raubenheimer & Cook 1990). Evidence has shown that the effects are not uniform, as an increase in wave exposure may lead to increased (Van Erkom Schurink & Griffiths 1993, Leeb 1995) or decreased growth rates (Seed 1968, Jørgensen 1976). The effects of wave action on the growth rate of *Perna perna* along the South African south Cape coast therefore warrant further investigation.

The growth rate of a population in a fishery can be estimated by the mark-recapture method (Peterson *et al.* 1983, Dickie *et al.* 1984, Mallet *et al* 1987a); growth band analysis from otoliths, bones or shells (Yamaguchi 1975, Sukhotin & Kulakowski 1992); analysing length-frequency data (Pauly & David 1981) and following a cohort after a heavy spatfall on a natural substratum (Griffiths & King 1979b, Griffiths 1981) or on artificial settling ropes (Kautsky 1982). At the outset there is often uncertainty as to the suitability of the method chosen for the species under investigation, and it is therefore advantageous to use more than one method. This has a two-fold benefit: if one of the methods prove unsatisfactory, results can be obtained from the other and if both methods are suitable, the results from two independent studies can be compared.

The use of several methods to determine the growth rate of a population is not a novel idea. Munday and Keegan (1992) compared growth rates of an echinoderm, *Amphiura chiajei* which were obtained from growth bands and length frequency distributions (Bhattacharya's approach, 1967). Defeo *et al.* (1992a & 1992b) used growth bands and length frequency distributions (Bhattacharya's approach and ELEFAN) to compare the growth rates of the yellow clam, *Mesodesma mactroides*. However, the majority of studies still rely on the use of only one method, which if inappropriate for the species concerned could be entirely unsuccessful. A study by Kautsky (1982) on the blue mussel, *Mytilus edulis* would have revealed little on growth rates if only length frequency distributions were utilised, as this method proved unsuitable. In this case, growth bands and measurements of caged mussels were also used and growth rates could be determined.

Mark-recapture (Takada 1995), growth band analysis (Richardson 1989, Anwar *et al.* 1990) and length frequency distributions (Seed 1969b, Bayne & Worrall 1980, Tomalin 1995) are the most widely and successfully employed methods.

Using these three methods independently, the growth rate of *Perna perna* in its natural environment along the South African south coast was determined. The mark-recapture (A), growth band (B) and length frequency distribution (C) analyses were used to obtain growth data for populations at 6 sites. The effect of wave exposure was incorporated by having 3 exposed and 3 sheltered sites. Where possible growth at length was established before growth curves of age at length were constructed as selection by mussel collectors, fecundity, predation and growth are often better correlated with size than with age (Seed 1968, Jørgensen 1976, Kaufmann 1981).

2. MATERIALS AND METHODS

Using quantitative measures of exposure, Diaz Cross, Kwaai Hoek and Fish River were classified as exposed shores and Mgwalana, Rufanes and Riet River as sheltered shores (Chapter 1). As discussed in chapter 1 the sites were all sampled in the low shore mussel zone. At each site, sampling for all three methods was undertaken in a ± 20m stretch of mussel bed, with approximately the same aspect, tidal height and local conditions. **Throughout this chapter the term "site" will refer to the individual sites *i.e.* Diaz Cross etc. and the term "shore type" will refer to the exposed or sheltered shores *i.e.* pooled site data, where available.**

Statistical analyses were all performed with Statgraphics version 7.0. Differences and relationships between shore exposure and the growth rate of *Perna perna* were investigated by using ANCOVA's, ANOVA's, t-tests and regression analysis. Where significant differences were found Tukey's multiple range test was used to identify the differences. Throughout this chapter normality of data was examined using Kolmogorov-Smirnov's test and homogeneity of variance was established using Bartlett's test.

A. MARK-RECAPTURE METHOD

Marking procedures

The mark-recapture technique may be used in different ways, but basically involves obtaining an initial measurement at marking and a final measurement at recapture. Growth estimates were made by comparing growth increments of marked mussels. Mussels were marked *in situ* at each of the six localities by filing a small v-shaped notch (1mm) (Figure 3.1-1) in the growing edge of the shell to produce a growth check (Figure 3.1-3) (Ekaratne & Crisp 1982). Growth left the filed v-shaped notch clearly visible (Figure 3.1-1), and allowed the growth that had subsequently taken place to be measured. Only mussels >25 mm were marked as smaller individuals were frequently tucked between larger mussels making them difficult to file. At each site all mussels (>25 mm) in three 25x25 cm quadrats were marked. The following number of mussels were marked on the 28/29 December 1995: Diaz Cross-247, Kwaai Hoek-264, Fish River-228, Mgwalana-300, Rufanes-245 and Riet River-330. The quadrat corners were marked with nail-in anchors and cable ties. The quadrats were large enough to contain sufficient mussels for marking and to enable the author to relocate the marked mussels after a few months. They were also small enough to cause minimal damage when the mussels were removed. After an interval of 111 days, the remaining mussels were removed and returned to the laboratory. For each mussel the initial length (from the apex to the v-check) and the final length (from the apex to the growing edge) were measured (Figure 3.1). Measurements were taken with vernier callipers to the nearest 0.1 mm. The sex of each mussel was determined by examination of the gonad colour, as males are white and females are orange (Lasiak 1986).

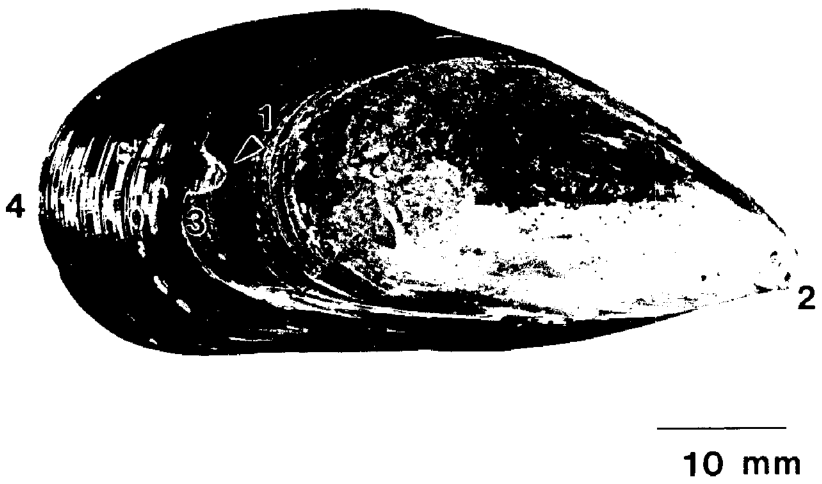


Figure 3.1 (1) The v-shaped notch, (2) the apex, (3) the growth check caused by interruption of growth when the notch was filed, and (4) growing edge.

Analysis of growth rates

After $\log_{10}(n+1)$ transformations were performed on all growth and initial length data (the covariate), normality and homogeneity were achieved ($p>0.05$).

The effect of sex on growth rate

The growth rates of males and females at each site were calculated separately to establish whether sex affected growth rates. This was statistically analysed by performing a two-way ANCOVA with interactions on growth data, using initial length as a covariate and site and sex as factors.

Site and initial length

As marked mussels were removed randomly from naturally occurring populations they reflected the population size structure. To establish whether there was any significant difference in the initial lengths of marked mussels at each site, a one-way ANOVA was performed. This assumes that the initial and final length distribution were equal and that no differential loss of a particular size class occurred.

Growth rate, exposure and site

Growth rates were examined at the broader scale of exposure and the finer scale of site. Using initial length as a covariate, two separate one-way ANCOVA's were performed to determine whether there was a relationship between growth rates and exposure, and growth rates and site.

Linear regressions of initial length versus growth

Initial length was plotted against growth over 111 days for each site using log transformed data. F-tests were used to compare differences in slope as these slopes gave an indication of the rate at which growth decreased as size (or age) increased. The F-tests used the pooled residual sum of squares (total of all the residual sum of squares calculated from six separate ANOVA's) and the common residual sum of squares (obtained from an ANOVA run on a multiple regression which encompassed the data from all six sites in one calculation). Significance was checked at both the one and two-tailed levels (Zar 1996).

Growth parameters and Von Bertalanffy growth curves

The Gulland-Holt plot (Equation 3.1) which takes the time interval between marking and recapture into account, was used to generate the parameters, growth coefficient (K) and L-infinity (L_∞), required for input into the Von Bertalanffy growth equation (see Sparre & Venema 1993). L-infinity is defined as the theoretical maximum length at which growth rate is zero. The Ford Walford plot was not used as it required a time interval of a year and did not have a time coefficient in its equation. The Gulland-Holt plot (available in the program FiSAT, an FAO stock assessment tool (Gayanilo *et al.* 1994) was used on the growth increment data for each site.

$\triangle L/\triangle t = a+bL_{(mean)}$ **Equation 3.1**

where $\triangle L = L_{recapture} - L_{marked}$

$\triangle t = t_r - t_m$ and

$L_{(mean)} = (L_r+L_m)/2$

therefore $L_\infty=-a/b$ and $K= -b\ t_{(no.\ days)}$

The L_∞ and K values were used to generate phi prime (Φ') values, which gave an index of overall growth performance (Pauly and Munro 1984, Tomalin 1995). These were calculated for each site using the following equation:

$\Phi' = \log K + 2 + \log L_\infty$ **Equation 3.2**

These values allow quick comparisons of growth between sites or stocks without the need of graphs and/or involved equations. T-tests were performed on Φ', L_∞ and K data to ascertain whether there was a relationship between exposure and each of the growth parameters. Normal distribution could not be tested due to the small sample size (n=3) (Zar 1996).

To estimate maximum lengths, life span and growth rates at different ages, length data were converted to age data using the Von Bertalanffy growth equation (Equation 3.3). The Von Bertalanffy growth curve was chosen as it is known to describe the growth of 'larger' mussels (the size range which was being studied) better than the Gompertz curve which is more suited to describing the growth of juveniles (Theisen 1973). The Von Bertalanffy curve was subsequently used on the growth band and cohort data, so as to make results comparable.

$Lt = L_\infty[1-e^{-K(t-t_0)}]$ **Equation 3.3**

Biologically t_0 is meaningless as growth begins at time of hatching. For the purposes of this study t_0 was considered to be zero as the growth rate of mussels smaller than 25 mm was not being considered. The parameters K and L_∞, from the Gulland-Holt plot, were inserted into the Von Bertalanffy growth equation and growth curves for each site were constructed. Lengths at one year of age at the different sites were compared.

B. GROWTH BAND ANALYSIS METHOD

Growth band periodicity

This technique generally relies on the periodicity of growth bands (annual, tidal or daily) to calculate growth and may use external or inner growth bands. The frequency with which the inner growth bands were laid down was determined by counting the bands in marked mussels (chapter 3.2 A). As the marked mussels were in the field for a known period of 111 days, all that remained was to count the number of bands laid down from the file check mark to the growing edge, in that time. The ratio of the number of bands to days gave an indication of the periodicity of bands.

Bivalve band validation was carried out following procedures of Pentilla *et. al.* (1988) and Richardson (1989). Marked mussels (30-90 mm) were used from Kwaai Hoek (exposed) and Mgwalana (sheltered). The mussels were immersed for an hour in 3.5% Sodium Hypochlorite (full strength household bleach) to remove organic debris. Shells were rinsed in water to remove bleach and embedded in casting resin. For uniformity only the left valves were used. Shells were sectioned longitudinally along the anterior-posterior axis using a diamond saw (Figure 3.2).

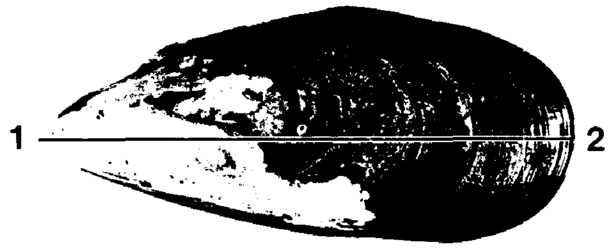


Figure 3.2 The shells were sectioned longitudinally along the (1) anterior (2) posterior axis.

An industrial rotating sander with different grades of sanding discs was used to smooth the cut surface before polishing to a blemish-free surface with 'Brasso' household metal polish. Once the optimum etching time had been determined by trial and error, shell surfaces were etched by immersion in 0.01M

Hydrochloric acid for 40 minutes (see Richardson *et. al.* 1979). Acetate peels, as used by Richardson (1989) and Nakaoka & Matsui (1994), were used to produces replicas of the shells growth bands. Strips of acetate peel were immersed in ethyl acetate for 20-25 seconds before applying to the cut surface. Once dry, the acetate peel with the growth band impression was peeled off and sandwiched between two glass slides. Mussels ranging from 34 to 82 mm were utilised and 10 acceptable slides (*i.e.* 10 mussels within this size range for each site) were obtained from Kwaai Hoek and Mgwalana mussels. The growth bands were later counted under a phase contrast light microscope. For each shell, growth bands were counted from the growth check (caused by marking the shell) to the growing edge.

Exposure (site) and growth band formation

To determine the relationship between exposure (site) and band formation, a one-way ANOVA was performed on the growth band count data. These data were normal ($p>0.05$) and homogeneous ($p>0.05$). The mean number of bands laid down at each site over the 111 days was recorded.

Growth measured using growth bands

Once it was established that internal growth bands were laid down tidally (twice a day), the age and growth of **unmarked** mussels could be determined. No annual, winter/summer or spring/neap tide bands were observed. The initial objective was to establish the length at age directly by counting the number of bands in the entire shell. Due to compression of bands, indistinct bands and shell erosion, growth bands could not be counted over the entirety of the shell. As a result, measurements of growth over the last 30 day period *i.e.* 60 bands, were used to establish growth rates and calculate age at length. The distance between successive tidally induced bands has been shown to represent the actual linear increase in shell length (Richardson *et al.* 1990).

A total of 54 **unmarked** mussels were collected in March 1997 from the same six sites (Diaz, Kwaai Hoek, Fish River, Mgwalana, Rufanes and Riet River) used previously. 3 Mussels in each size class 20-25 mm, 40-45 mm and 70-75 mm, from each site, were embedded in resin as described earlier. In lieu of counting bands through the light microscope, a video camera was used to transmit the slide image to a personal computer. The band print images were then saved as tif files in Program X Image 4 and printed from Aldus Photostyler 2.0. After enlarging the laser printed images on a photostat machine, growth was measured to the nearest 0.01 mm. The initial lengths were obtained by subtracting the growth increments *i.e.* over 30 days, from the lengths which were originally measured.

Failure in the acetate stage (62% failure rate) resulted in many indistinct slides, making it necessary to pool the acceptable results from the three exposed sites (Diaz Cross, Kwaai Hoek and Fish River) and also to pool those from the three sheltered sites (Mgwalana, Rufanes and Riet River). This meant that only difference in exposure (shore type) and not site could be ascertained.

Analysis of growth rates

Initial length, exposure and growth rates

To determine whether there was a relationship between exposure and growth rate, an ANCOVA was performed on the normal and homogeneous growth rate data ($p>0.05$) using initial length as a covariate. The data from the exposed and sheltered sites were graphically presented in a plot of initial length against growth in millimetres over the 30 day (60 bands) period.

Comparison of the linear regression slopes

The slopes, which gave an indication of the rate at which growth decreased as length (or age) increased, were compared using a t-test for the comparison of slopes of two lines. However, before this could be undertaken both the growth and initial length data were logged (base 10) to linearise the regression equation.

Growth parameters and Von Bertalanffy growth curves

Statistical analysis of the effect of exposure on the growth parameters could not be undertaken as there was no replication. In lieu of this, results were tabulated for comparison. Pauly's growth performance index - Φ' (Longhurst & Pauly 1987) (Equation 3.2) which gives an indication of overall growth performance, was also calculated and compared for both shore types. Data were converted to age at length by fitting the Von Bertalanffy growth curve (Equation 3.3). L_∞ and K were obtained from the Gulland-Holt plot. The resultant Von Bertalanffy growth curves allowed visual comparison of the slopes and of the lengths attained at a year between exposed and sheltered shores.

C. LENGTH FREQUENCY DISTRIBUTION METHODS

Length frequencies were obtained by sampling mussel beds at approximately six weekly intervals at three exposed sites, Diaz Cross, Kwaai Hoek, Fish River and three sheltered sites, Mgwalana, Rufanes and Riet River (refer to chapter 1 for quantification of exposure). A minimum of 200 mussels was required from each site at each sampling interval. To obtain this number, four to five quadrats of 10x10 cm were destructively sampled at each site per sampling session. The quadrats were taken randomly in areas of approximately 100% mussel cover within the lower mussel zone. Sampling was undertaken over a 15 month period from July 1995 to October 1996 and encompassed 11 sampling sessions. All mussels ≥1 mm were measured in the laboratory, initially by hand using stainless steel vernier callipers and later with the aid of an image analysing program, PC Image. Lindsay (1998) showed that the PC Image program measured mussels with a high degree of accuracy and a regression coefficient of 0.9996 ($p<0.05$) (size range 2-80 mm; $n=63$) was obtained when hand measured mussels were plotted against those measured by PC Image.

Length frequency distributions were analysed in two ways; by **modal progression analysis** (MPGA) and by direct length frequency methods. Modal progression analysis was undertaken using Bhattacharya's and NORMSEPs (Gayanilo *et al.* 1994) approach . These approaches assign mean lengths to cohorts in a time series which can then be linked up to form growth curves. The direct length frequency methods used to analyse distributions were **Electronic Length Frequency Analysis** (ELEFAN 1) and **Shepherd's Length Composition Analysis** (SLCA, Shepherd 1987). MPGA, ELEFAN 1 and SLCA were all undertaken using the suite of programs presented in FiSAT (Fisheries Stock Assessment Tools) version 1.10 (Gayanilo *et al.* 1994).

MODAL PROGRESSION ANALYSIS METHOD

For modal progression analysis to succeed it was necessary to separate mixtures of normal frequency distributions into their constituent parts. This was attempted with the use of Bhattacharya's method which identified the mode of each cohort, after which NORMSEP, which is a more powerful tool (Gayanilo *et al.* 1994), was used to refine the modes. Despite trials with various size classes, cohorts in this study were not discreet or clearly defined and the composite curves fitted to the data by NORMSEP were significantly different from the observed distribution (Chi-squared test, $p<0.05$). The degrees of freedom were often <10, which according to Gayanilo *et al.* (1994) could lead to unreliable results. MPGA could therefore not be utilised in estimating growth parameters for *Perna perna* in this study.

ELECTRONIC LENGTH FREQUENCY ANALYSIS (ELEFAN) METHOD

Both ELEFAN and SLCA are used to identify the growth curve that best fits a set of length-frequency data arranged sequentially in time. The data are reconstructed to generate "peaks" and "troughs" (representing high and low frequencies). The curves, which are generated from various combinations of L_∞ and K, are scored (goodness of fit index) by the number of peaks and troughs through which they pass, allowing the most probable curve to be fitted to the data (Pauly & David 1981). ELEFAN takes seasonality of growth into account and therefore in addition to estimating L_∞, K , the starting length (SL) and the starting sample (SS), the amplitude (C) and the winter point (WP) (the rate at which growth changes from season to season), had to be estimated. The estimation process, while easy for populations with distinct seasonal cohorts, becomes very time consuming and a matter of trial and error for populations with less defined cohorts.

SHEPHERD'S LENGTH COMPOSITION ANALYSIS (SLCA) METHOD

Growth parameters and Von Bertalanffy growth curves

Shepherd's length composition analysis was performed on length frequency data using 3 mm size classes. Shepherd's length composition analysis is analogous to the more commonly used ELEFAN with the difference being that it does not allow for seasonal differences in growth and therefore only requires L_∞ and K as inputs. Shepherd's length composition analysis offered two routines, scan of K values and response surface analysis, which were used co-operatively, for estimating the best L_∞ and K combinations for each data set. The scan of K values plots goodness of fit values (Rn) for a range of K values (0.10 to 10) on a log scale. The response surface analysis outputs an 11 by 11 matrix (of L_∞ & K) showing Rn values and highlights the best 10 values, enabling selection of the "best" combination of growth parameters (Gayanilo *et al.* 1994). As Shepherd's length composition analysis works best when L_∞ has been estimated using another method (Gayanilo *et al* 1994), the Powell-Wetherall plot and the 10 largest mussels over the sampling period at each site were used to estimate L_∞. For each Powell-Wetherall plot, pooled length-frequency data from each site were utilised (Equation 3.4) (Wetherall 1986).

$L_{mean} - L' = a + bL'$ **Equation 3.4**

where L' is the cut-off point,

L_{mean} is the mean length of all animals larger than L',

and a and b are parameters of the linear regression.

Initially, to prevent exclusion of 'optimum' values slightly out of the range of the L_∞'s estimated above, a wider margin of L_∞ values was used. The K-scan option enabled the identification of the optimum K value/s for particular values of L_∞. The K and L_∞ values thus obtained, were used as minimum and maximum inputs for the response surface routine. The different combinations of K and L_∞ were scored and several of the highest scoring pairs were used to produce growth curves over the length frequency time series data. Growth curves were fitted using a graphical output in ELEFAN, and those curves which were obviously unreasonable were excluded (Tomalin 1995). The combination of L_∞ and K with the highest score, obtained after exclusion of "obviously unreasonable" results, was inserted into the Von Bertalanffy equation for each site. As in chapter 3.2A, the differences in growth rates of mussels between sites and exposures were compared using Φ' (Equation 3.2), L_∞ and K.

When studying growth rates it is customary to compare the resultant curves and/or phi prime values, both of which describe L_∞ and K (Almatar 1993, Tomalin 1995). However, it was also of interest to know how K and more particularly L_∞ compared at the different sites. The relationship between exposure and Φ', L_∞ and K was compared using three t-tests. Due to the small sample size (n=3) normality could not be tested for. As there was no replication within sites, Φ', L_∞ and K were tabulated to determine whether site had an effect on growth parameters.

Von Bertalanffy growth curves of length at age for each site were constructed and compared. The length attained at one year of age at the six sites was tabulated for comparison. The approximate age at L_∞ was also calculated.

D. WAVE FORCE, DENSITY AND GROWTH RATES.

The mean maximum wave forces ($N.m^{-2}$) recorded for exposed and sheltered shores (chapter 1) were correlated with the phi prime values (Φ') for each shore type determined by the mark-recapture method and SLCA. A correlation of wave force and phi prime values for individual sites was also undertaken. Mean densities of adults >15 mm (chapter 2) at each shore type (rather than sites) were correlated against mean phi prime values obtained from each of the three methods (site data pooled). The mean densities obtained at each site were correlated with phi prime values from each site (mark-recapture & SLCA). The correlations were performed using the computer package, Statgraphics version 7.0. Data were all normally distributed ($p>0.05$).

3. RESULTS

A. MARK-RECAPTURE METHOD

After 111 days the remaining mussels were removed; Diaz Cross - 97, Kwaai Hoek - 116, Fish River - 92, Mgwalana - 171, Rufanes - 113 and Riet River - 134. Mortality of marked mussels, caused by shell damage during marking, fishing and natural causes, resulted in a mean survival rate of 41.09% at the exposed shores and 47.91% at the sheltered shores. Initially, renewed growth in many of the mussels occurred on the interior surface of the damaged edge, prior to an increase in length.

The effect of sex on growth rates

The overall growth rate of males and females was the same, as shown by the results of the two-way ANCOVA ($p>0.05$, Table 3.1). At Mgwalana there was a small significant difference ($0.04>p<0.05$) between the growth rate of males and females, as indicated by the results of the one-way ANOVA. This resulted in the significant interaction between factors (Table 3.1). As sex did not have a significant effect on the growth rates for the remaining sites, all further analyses were undertaken on combined male and female data.

Table 3.1 Two-way ANCOVA on the effect of sex and site on growth rate. Growth & initial length were $\log_{10}$ transformed.

Source of variation	df	SS	MS	F	P
Initial length (covariant)	1	24.90	24.90	632.30	<0.0001
Site (factor)	1	40.77	8.15	207.01	<0.0001
Sex (factor)	5	0.01	0.01	0.34	0.5656
Interaction of factors	5	0.64	0.13	3.25	0.0065
Residual	710	27.96	0.04		

The relationship between site and the initial length of marked mussels

The size range of the marked mussels (>25 mm) reflected lengths occurring naturally in the population (see mean lengths - Chapter 2). The mean lengths of marked mussels were highest at Diaz Cross and lowest at Riet River (Table 3.3). A one-way ANOVA showed that there was a significant difference ($p<0.05$) between the initial lengths at the different sites (Table 3.2). The mean lengths at the exposed sites ranked above the sheltered sites, with an overlap at Rufanes and Fish River, as shown by Tukey's multiple range test (Table 3.3).

Table 3.2 One-way ANOVA on the effect of site on the initial lengths of mussels.

Source of variation	df	SS	MS	F	P
Among	5	2.19	0.44	45.59	<0.0001
Within	717	6.88	0.01		

Table 3.3 Tukey's multiple range analysis on initial length at site. Analysis was performed on $\log_{10}$ transformed data.

Site	Exposure	N	Initial length (mm)	Homogenous groups
Ri	S	134	44.09	a
Mg	S	171	48.08	b
Ru	S	113	48.62	b c
Fs	E	92	52.34	c
Kw	E	116	56.41	d
Dz	E	97	67.06	e

The relationship between exposure, site, initial length and growth rates

The mean growth rate of mussels on the exposed shores (4.90 mm.111 days^{-1}) was higher than that on the sheltered shores (1.72 mm.111 days^{-1}). Mussels grew faster at Diaz Cross, Kwaai Hoek and Fish River (exposed) than Rufanes, Mgwalana and Riet River (sheltered) (Figure 3.3). Smaller mussels had higher growth rates than larger ones (Figure 3.3). These findings were confirmed by the results of the one-way ANCOVA's which revealed that exposure, site and initial length had significant effects on growth rates of *Perna perna* ($p<0.05$, Tables 3.4 & 3.5). Results from Tukey's multiple range test showed that, although there were significant differences in growth rates among all sites ($p<0.05$, Table 3.6), the sheltered sites ranked well below the exposed sites.

The mean growth rates (Table 3.6) were not directly comparable among sites due to the differences in the initial lengths of marked mussels. As it has been shown that small mussels grow faster than large ones (Figure 3.4), the mean growth rates of mussels at Diaz Cross and Kwaai Hoek (where mussels had higher mean initial lengths than at the other sites) were lower than they would have been had mussels of the same size (44.09 to 48.62 mm) as those at the sheltered sites been used. Therefore, the difference in growth rates between exposed and sheltered shores was even greater than calculated.

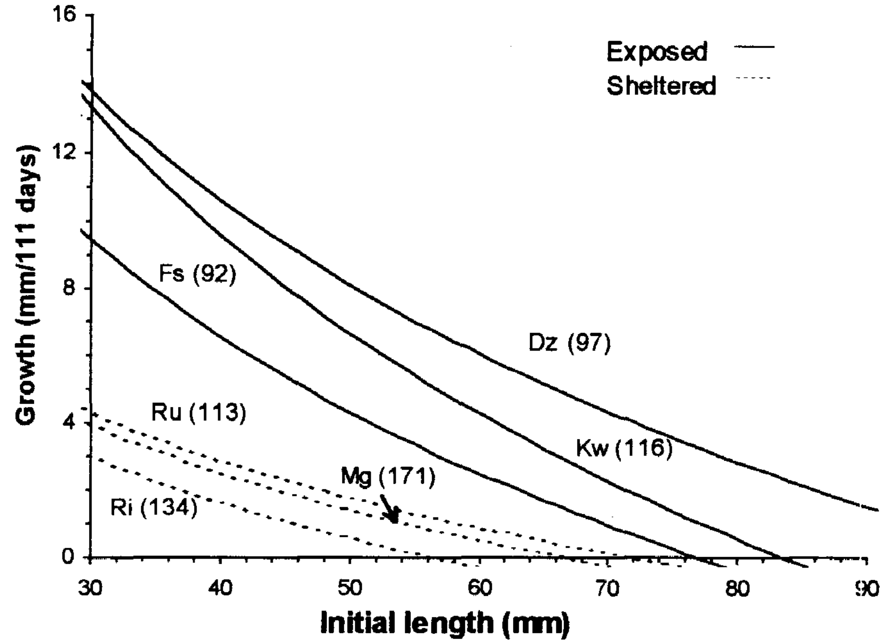


Figure 3.3 Growth of marked mussels using untransformed data. Only the regression lines of initial length versus growth in millimetres for 111 days. are shown, data points have been excluded for simplicity, but are presented in Figure 3.4 (a-f).

Table 3.4 One-way ANCOVA on the relationship between exposure, initial length and growth rates. Data were $\log_{10}$ transformed.

Source of variation	df	SS	MS	F	P
Exposure	1	35.74	35.74	748.66	<0.0001
Covariate: Initial	1	20.63	20.63	432.15	<0.0001
Residual	720	34.37	0.05		

Table 3.5 One-way ANCOVA on the relationship between site, initial length and growth rate. Data were $\log_{10}$ transformed.

Source of variation	df	SS	MS	F	P
Site	5	41.45	8.29	207.13	<0.0000
Covariate: Initial	1	25.06	25.06	626.16	<0.0001
Residual	716	28.66	0.04		

Table 3.6 Tukey's multiple range analysis for the mean growth of all mussels at each site using $\log_{10}$ transformed growth data. The mean growth rate is expressed (untransformed) in mm.111 days^{-1}.

Site	Exposure	N	Mean growth rate (mm.111 days^{-1})	Homogeneous groups
Ri	S	134	1.32	a
Mg	S	171	1.79	b
Ru	S	113	2.05	c
Fs	E	92	4.16	d
Kw	E	116	5.45	e
Dz	E	97	5.09	f

Linear regressions of initial length versus growth

Growth rate and initial length were significantly correlated at each site, with smaller mussels growing faster than larger ones ($p<0.05$ in all cases, Figure 3.4 & Table 3.7). The rate at which growth decreased as length (age) increased was the same at all sites as the slopes were equal ($p>0.05$, 1 & 2-tailed level, Table 3.7). A considerable variation in growth occurred amongst individuals, even within a site, as indicated by the low r^2 values (Figure 3.4 & Table 3.7).

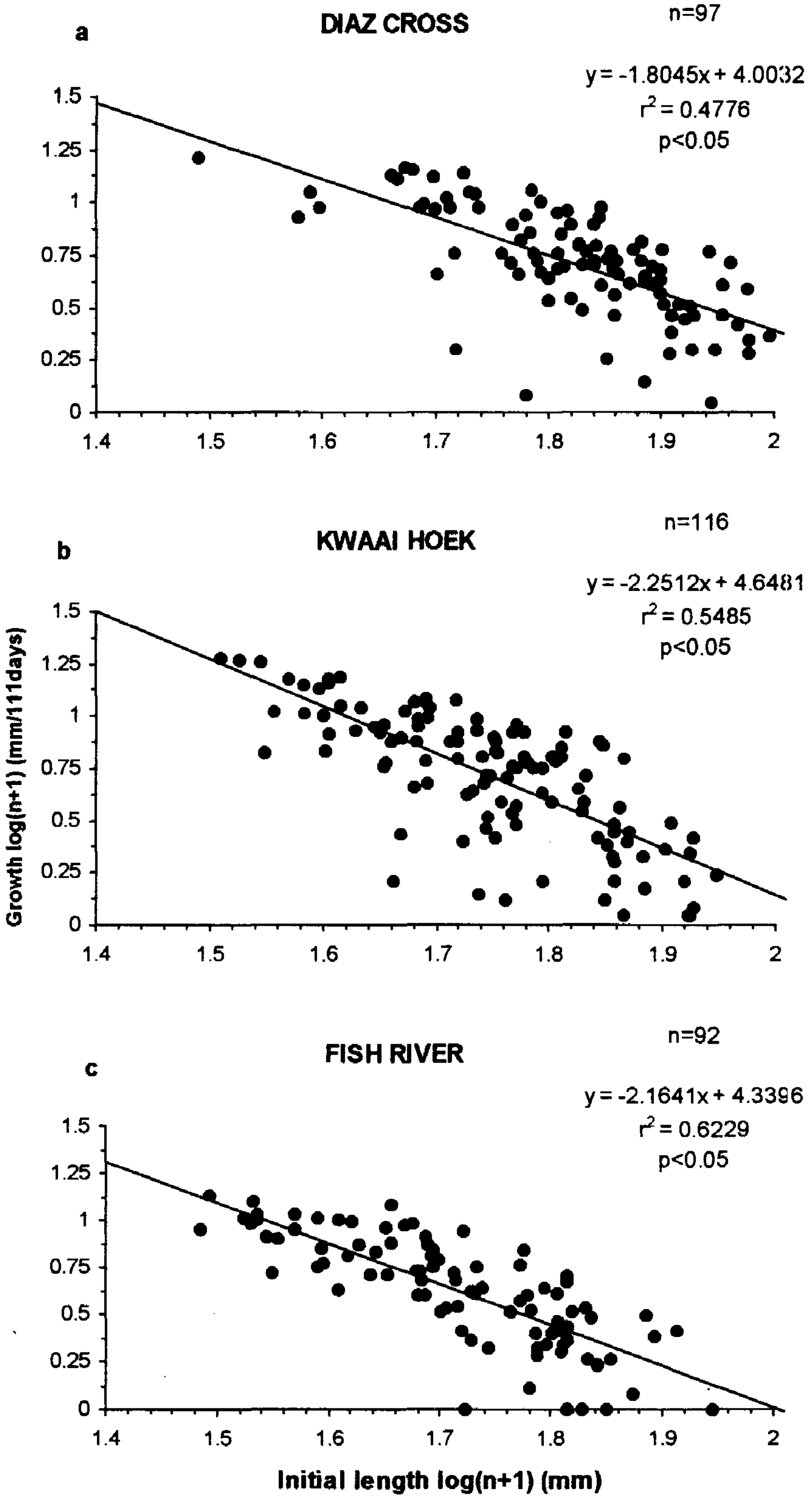


Figure 3.4 Linear regressions of initial length ($\log_{10}(n+1)$) against growth rate ($\log_{10}(n+1)$) for marked mussels at (a-c) three exposed sites.

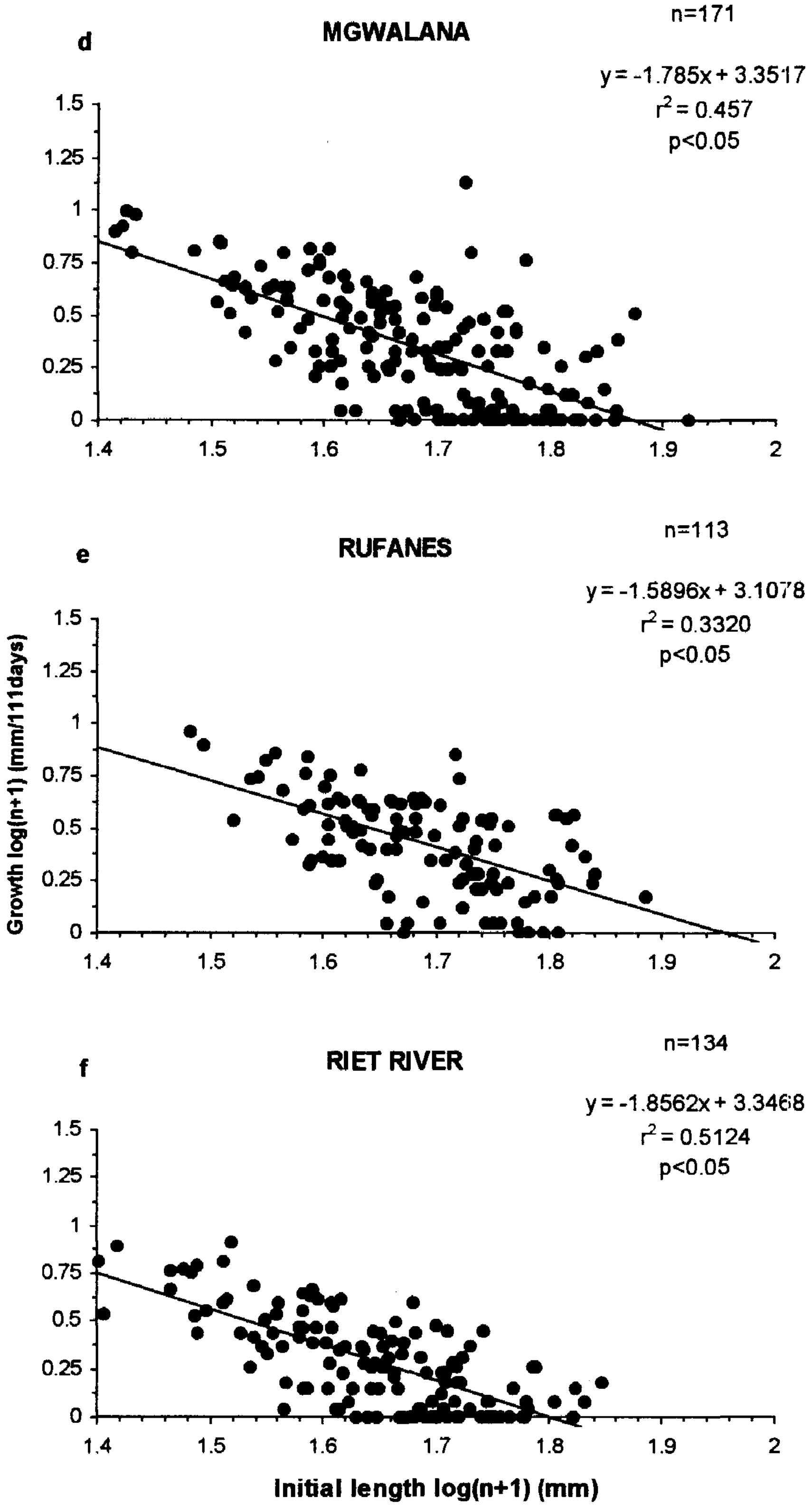


Figure 3.4 cont. Linear regressions of initial length ($\log_{10}(n+1)$) against growth rate ($\log_{10}(n+1)$) for marked mussels at (d-f) three sheltered sites.

Table 3.7 Results of the individual ANOVA's run on each site and the common ANOVA which gave the residual sums of squares required to calculate the F-value used to compare slopes.

Site	Source	df	SS	MS	F	P	r^2
Dz	Model	1	3.03	3.03	86.86	<0.0001	47.76
	Residual	95	3.31	0.03			
Kw	Model	1	5.98	5.98	138.50	<0.0001	54.85
	Residual	114	4.92	0.04			
Fs	Model	1	4.67	4.67	148.64	<0.0001	62.29
	Residual	90	2.83	0.03			
Mg	Model	1	5.90	5.90	142.24	<0.0001	45.70
	Residual	169	7.01	0.04			
Ru	Model	1	1.97	1.97	55.16	<0.0001	33.20
	Residual	111	3.96	0.04			
Ri	Model	1	3.95	3.95	138.71	<0.0001	51.24
	Residual	132	3.76	0.03			
Common	Model	7	223.84	31.98	876.64	<0.0001	0.90
	Residual	716	26.12	0.04			

Growth parameters and growth curves

Exposure, site and growth parameters

The Gulland-Holt plots which were used to generate growth parameters are presented (Figure 3.5). Mean estimates of all three growth parameters were higher on the exposed shores than on the sheltered shores (Table 3.8). At the level of site, the growth parameters were higher at the three exposed sites than the three sheltered sites (Table 3.9). Mussels from Kwaai Hoek had the highest growth performance (Φ' = 3.76) and those from Riet River the lowest (Φ' = 3.04). The variation in Φ' values within the exposed sites was similar to that within the sheltered sites. Mussels at each of the exposed sites reached their maximum theoretical lengths (L_∞) faster than those from sheltered sites, as indicated by the higher K. However, the results of the t-tests undertaken on growth parameter data revealed that, although there was a significant relationship between exposure and K and Φ' values ($p<0.05$), there was no significant relationship between exposure and L_∞ ($p>0.05$) (Table 3.10). This was suprising, but was possibly an effect of the small sample size (n=3).

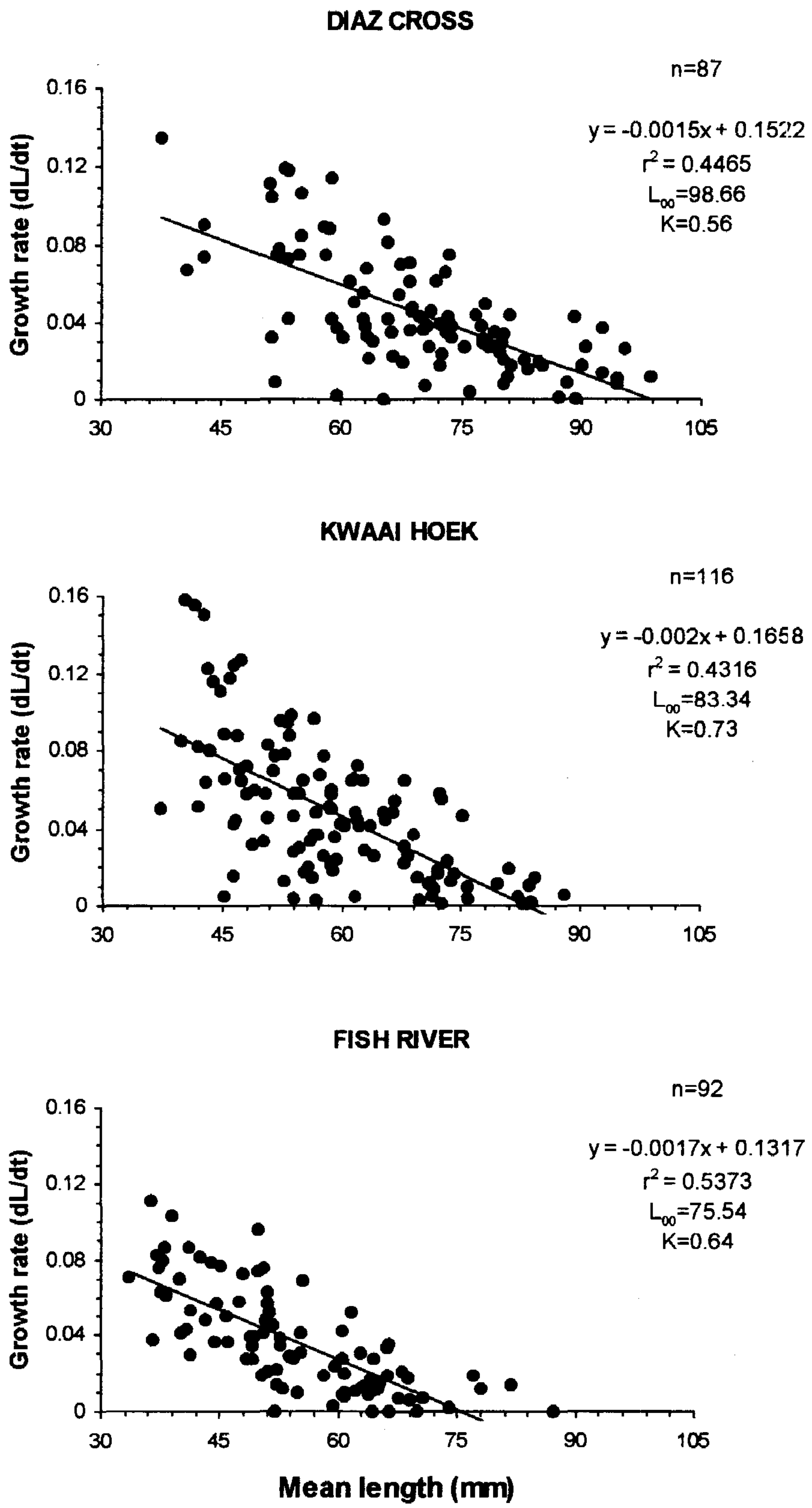


Figure 3.5 The Gulland-Holt plots of growth rate against mean length for the exposed shores. The growth parameters were obtained according to Equation 3.1.

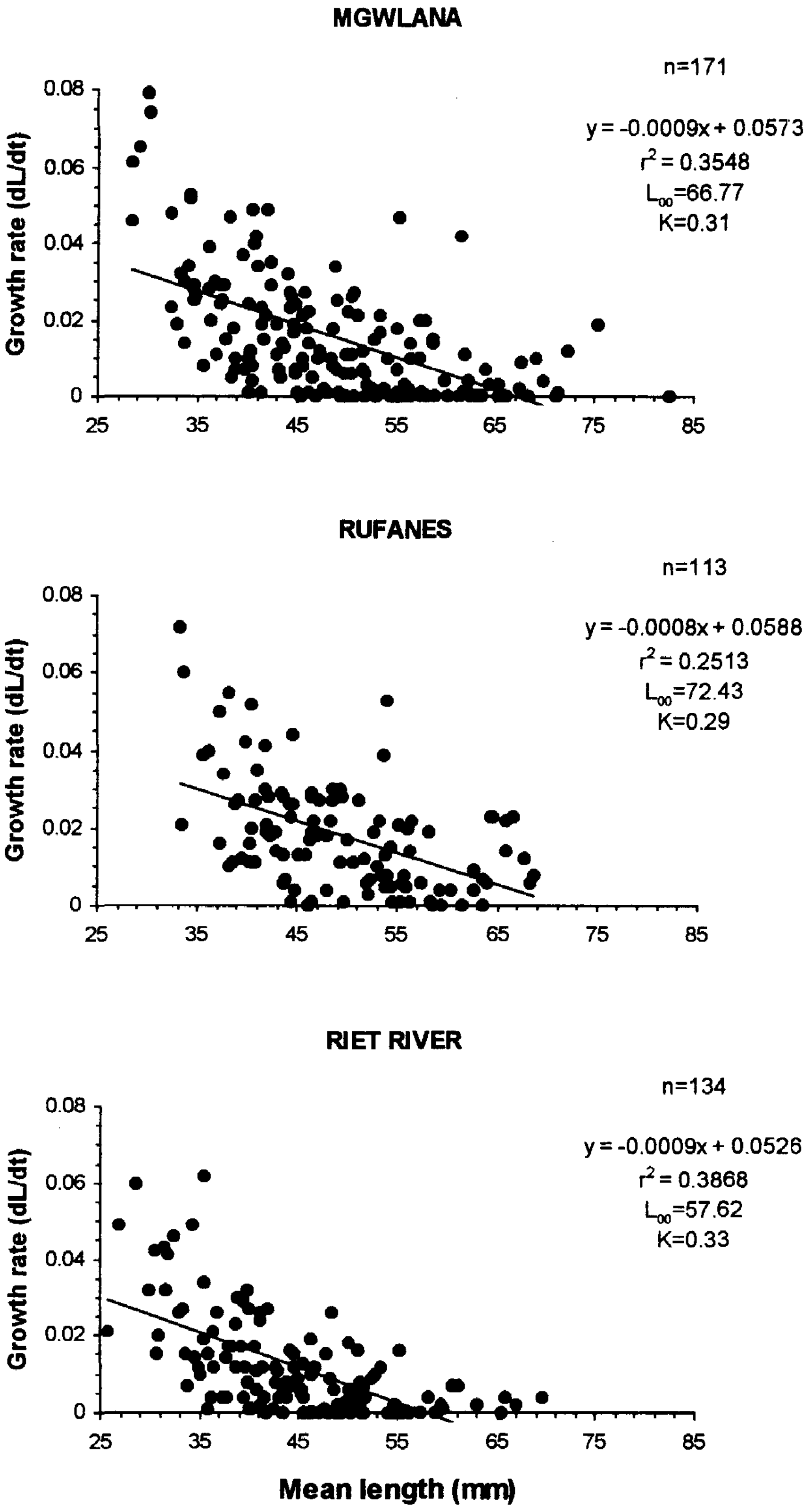


Figure 3.5 cont. The Gulland-Holt plots of growth rate against mean length for the sheltered shores. The growth parameters were obtained according to Equation 3.1.

Table 3.8 Mean values of Φ', L_∞ and K at exposed and sheltered shores (site data pooled).

Exposure	Mean Φ'	Mean L_∞	Mean K
Sheltered	3.14	65.58	0.31
Exposed	3.70	85.85	0.64

Table 3.9 Growth parameters obtained from the Gulland-Holt (GH) plot.

Sites	Φ'	L_∞	K
Dz	3.74	98.66	0.56
Kw	3.76	83.34	0.73
Fs	3.56	75.54	0.64
Mg	3.14	66.70	0.31
Ru	3.23	72.43	0.29
Ri	3.04	57.62	0.33

Table 3.10 Three t-tests comparing growth parameters Φ', L_∞ and K for exposed and sheltered shores.

	N	t-statistic	Significance
Φ'	3	6.5849	0.0028
L_∞	3	2.5157	0.0660
K	3	6.6082	0.0027

Growth curves

Von Bertalanffy growth curves showed that growth rates at the exposed sites were faster than those at the sheltered sites (Figure 3.6). At one year of age, the lengths reached at the exposed sites were more than twice those at the sheltered sites (Table 3.11). At two years of age the mussels from the sheltered sites had almost doubled in length whereas those from the exposed sites had increased their lengths by about 50%. At two years of age, exposed shore mussels were double the length of sheltered shore ones (Table 3.11). Mussels of equivalent lengths will therefore be older at the sheltered sites than at the exposed sites. When the Von Bertalanffy growth curves were extended until **approximations** of L_∞ were reached, mussels could in theory be reaching ages of 8-9 years on exposed shores and 14-18 years on sheltered shores. Regardless of what these exact ages are, mussels reaching L_∞ on sheltered shores are almost twice the age of those reaching L_∞ on exposed shores.

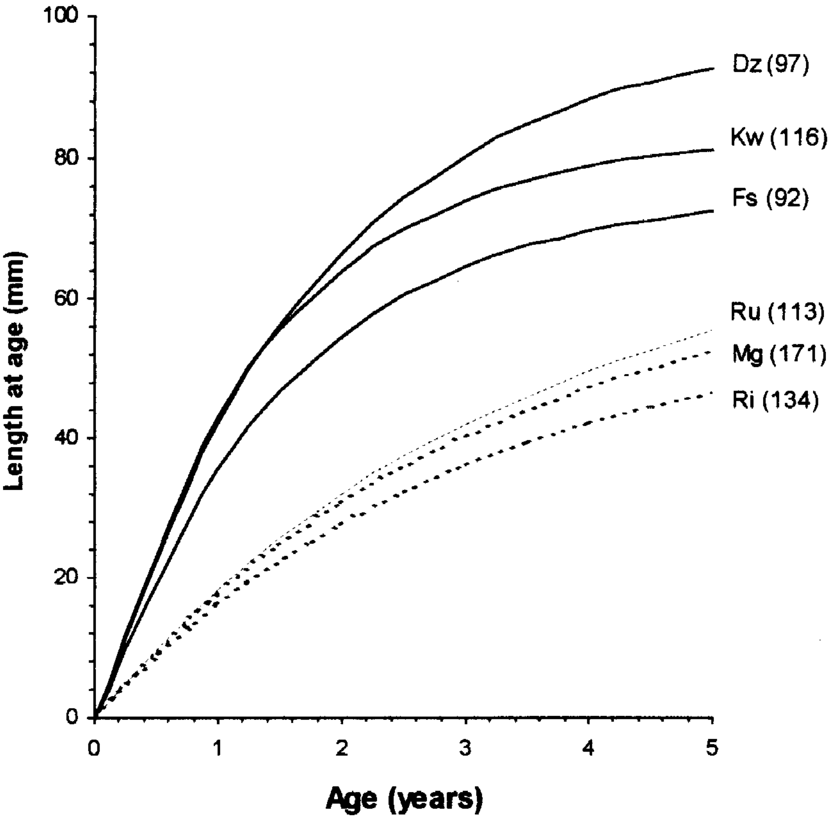


Figure 3.6 Von Bertalanffy growth curves at six sites using L_∞ and K values generated from length increment data. Estimates of L_∞ and K were obtained from the Gulland-Holt plot. N values are given in brackets.

Table 3.11 Mean lengths at one and two years at six sites, values calculated from Von Bertalanffy's equation using marked mussels.

Site	Exposure	Length (mm) at 1 year	Length (mm) at 2 years
Diaz Cross	E	42.30	66.47
Kwaai Hoek	E	43.18	63.99
Fish River	E	35.71	54.54
Mgwalana	S	17.80	30.85
Rufanes	S	18.23	31.88
Riet River	S	16.20	27.84

B. GROWTH BAND ANALYSIS

Growth band periodicity

Growth checks made by the filed notch were clearly visible in the acetate peel replicas of the shells (Figure 3.6). Many acetate peels had indistinct bands due to the compression of growth bands (particularly larger shells), erosion, air bubbles and unknown factors. The mean number of bands recorded at Mgwalana over the 111 days was 209.70 (±25.56) and at Kwaai Hoek 207.60 (±21.36). This gave similar frequencies of 1.87 and 1.89 bands per day, presumably reflecting a tidal pattern. The accuracy of these estimations were determined by dividing the observed mean number of bands (208.65) by the expected number of bands (*i.e.* 2 low tides per day = 222 tides), which gave a coefficient of estimation of 0.94 or 94%. The results of a one-way ANOVA confirmed that there was no significant difference in the number of bands laid down at Mgwalana and Kwaai Hoek (p<0.05, Table 3.12).

Table 3.12 One-way ANOVA on the effect of wave exposure on the periodicity of growth bands.

Source of variation	df	SS	MS	F	P
Among	1	22.05	22.05	0.040	0.8463
Within	18	9986.50	554.81		

Growth measured using growth bands

As growth bands were laid down at every low tide they were used to measure the growth of **unmarked** shells. The number of growth bands were counted from Laser printed images (Figure 3.7).

Figure 3.6 The check mark made by the filed notch on an acetate peel replica of a shell.

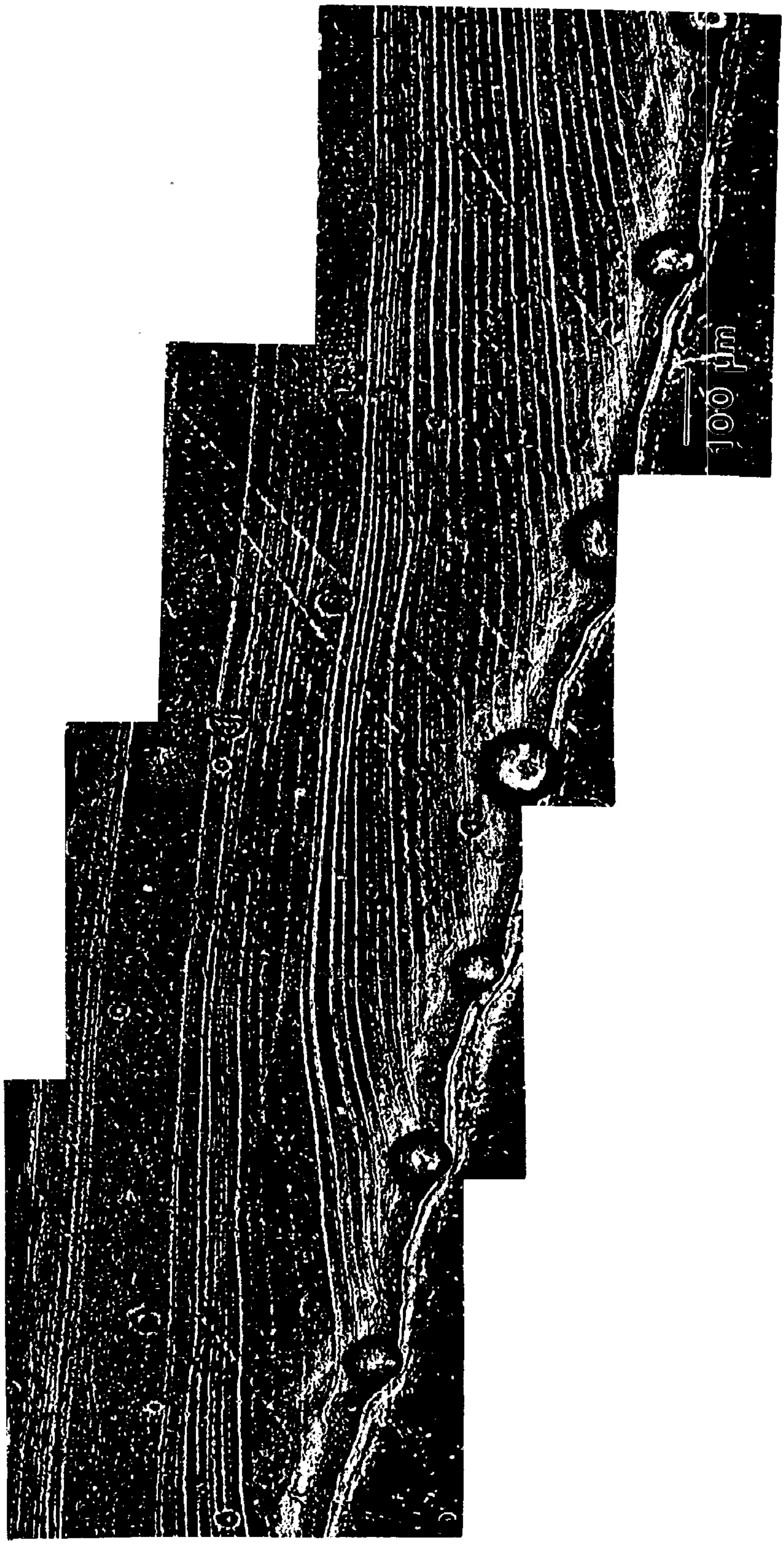


Figure 3.7 Laser print of growth bands from an unmarked mussel

Exposure, initial length and growth rates

The mean growth rate for the combined length classes was higher at the exposed shores (2.42 mm/mnth) than at the sheltered shores (1.32 mm/mnth). The growth rate of smaller mussels was greater than larger mussels (Figure 3.8). The results of the ANCOVA confirmed these findings as both initial length and exposure had a significant effect on mussel growth rate ($p<0.05$, Table 3.13).

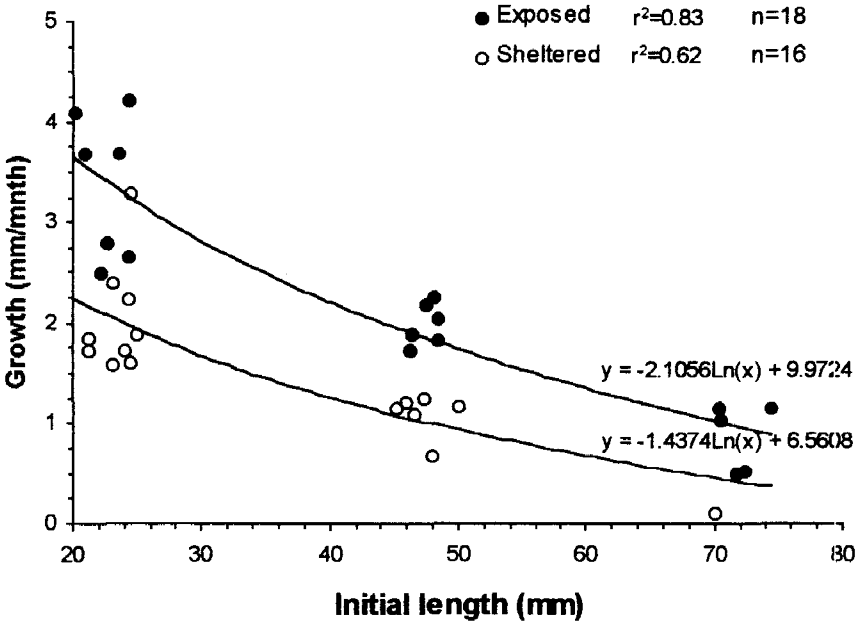


Figure 3.8 The growth rate over 60 bands (30 day period) at the exposed and sheltered shores (site data pooled).

Table 3.13 ANCOVA on the relationship between exposure, initial length and growth rates.

Source of variation	df	SS	MS	F	P
Covariate: initial	1	23.74	23.74	107.92	<0.0001
Exposure	1	9.61	9.61	43.67	<0.0001
Residual	31	6.82	0.22		

Comparison of the linear regression slopes

The decrease in growth as mussels increased in size (or age) occurred at the same rate on exposed and sheltered sites. There was no significant difference between the slopes for the exposed and sheltered sites ($p>0.05$) (calculated $t_{(2), 30} = 1.035$ and from t-table, $t_{0.2 (2), 30} = 1.310$). Due to this equal rate and the lower growth rate at sheltered sites, the maximum length reached should also be lower than at exposed sites as indicated in Figure 3.9.

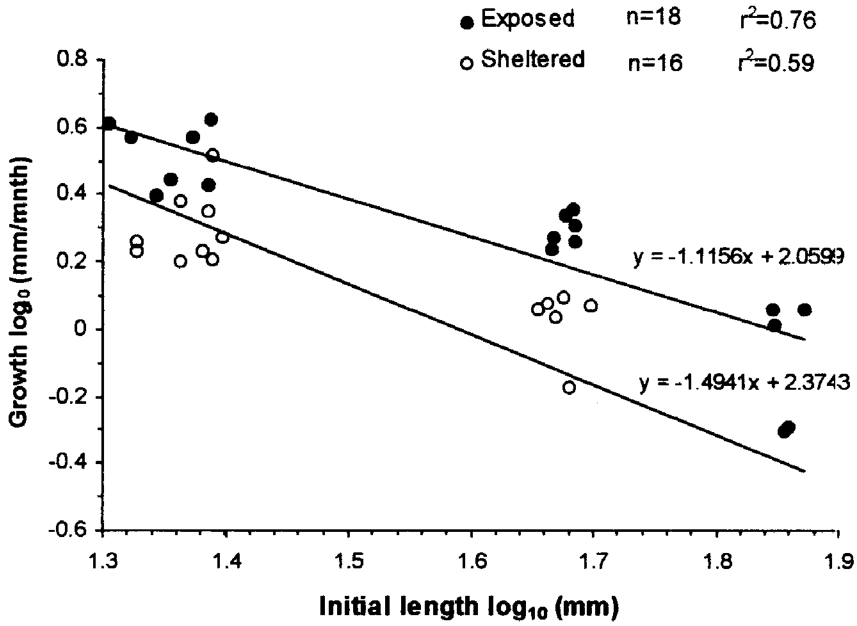


Figure 3.9 A comparison of the regression slopes from growth data ($\log_{10}$) against initial length ($\log_{10}$) from the exposed and sheltered shores.

Growth parameters and growth curves

All three growth parameters, Φ', L_∞ and K, obtained from the Gulland-Holt plot were higher at the exposed shores than at the sheltered shores (Table 3.14). The higher Φ' values showed that mussels had an overall higher growth performance on exposed shores than sheltered shores. Due to a high failure rate in the acetate stage, sample sizes were inadequate and results from the sites were pooled (into exposed or sheltered shore).

The exposed shore mussels showed faster growth rates than those from sheltered shores and lengths of 41.62 mm and 27.40 mm respectively, were attained in a year (Figure 3.10 & Table 3.15). There was a greater difference between the lengths of mussels from exposed and sheltered shores at one year than two years of age (Table 3.15). Mussels of equal length taken from shores of different exposures would therefore be older at the sheltered shores (Figure 3.10). L_∞ was reached sooner at exposed sites than at sheltered sites as shown by the steeper slope and higher K value (Figure 3.10). Mussels at the exposed shores took 8 years to reach lengths of 87.5 mm and those at sheltered shores theoretically took approximately 12 years to reach lengths of 76.5 mm.

Table 3.14 The relationship between exposure and Φ', L_∞ and K calculated from growth bands

Exposure	**Φ'**	**L_∞**	**K**
Exposed	3.70	88.05	0.64
Sheltered	3.42	76.98	0.44

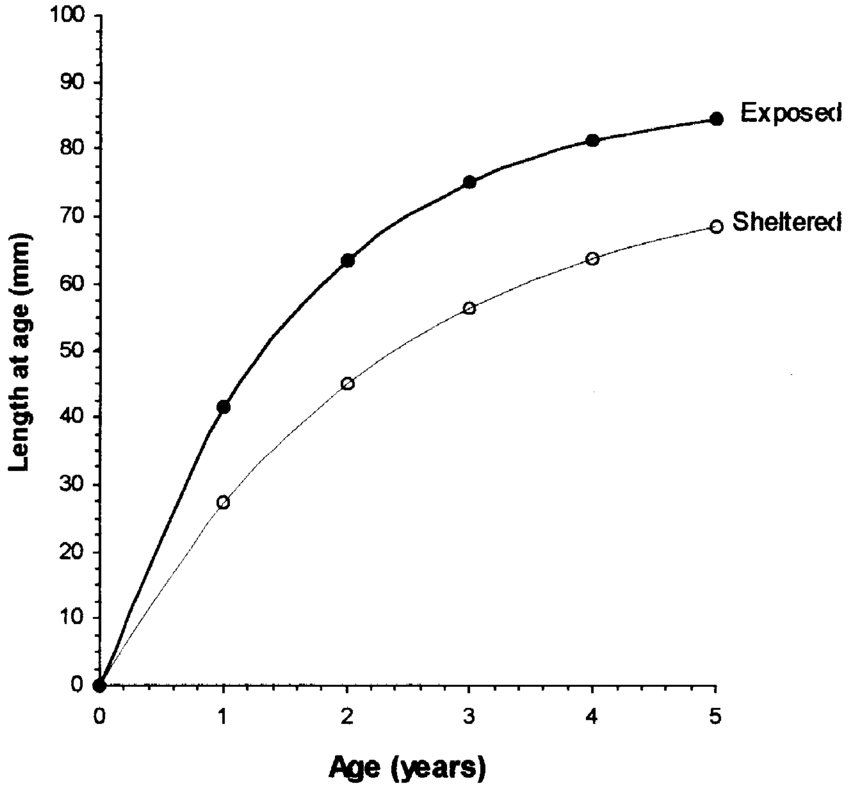


Figure 3.10 The Von Bertalanffy growth curve at the exposed and sheltered shores (sites pooled), established from the growth measured over 60 growth bands (± 30 days). Growth parameters generated from the Gulland-Holt plot were used.

Table 3.15 Mean lengths at one and two years at exposed and sheltered shores, values calculated from Von Bertalanffy's equation using growth band analysis.

Exposure	**Length (mm) at 1 year**	**Length (mm) at 2 years**
E	41.62	63.57
S	27.40	45.05

C. LENGTH FREQUENCY DISTRIBUTIONS

MODAL PROGRESSION ANALYSIS - the results could not be analysed by this technique (see materials & methods).

ELECTRONIC LENGTH FREQUENCY ANALYSIS (ELEFAN)

The results from the ELEFAN procedure have not been extensively expanded upon as the analysis was not suitable for all sites (Table 3.16). The estimate of no growth over winter at Mgwalana was inaccurate (1=no growth). A comparison of the average estimates of K obtained from the mark-recapture and growth band method showed that the value of K appears to have been overestimated for both Mgwalana and Riet River.

Table 3.16 The growth parameters generated from the ELEFAN procedure. C = amplitude, WP = winter point, SS = starting sample, SL = starting length and Rn = goodness of fit score. Estimates in bold were considered inaccurate when compared to general estimates obtained from the mark-recapture and growth band method.

Sites	L_∞	K	C	WP	SS	SL	Rn
Ru	99	0.48	0.3	0.8	4	1.5	0.120
Dz	135	0.77	0.6	0.4	5	1.5	0.117
Kw	121	0.73	0.7	0.8	4	1.5	0.130
Fs	117	0.66	0.8	0.6	4	2.5	0.123
Mg	114	0.70	**1.0**	**1.0**	5	4.5	0.150
Ri	120	**1.45**	0.6	0.3	5	3.0	0.118

SHEPHERD'S LENGTH COMPOSITION ANALYSIS (SLCA)

Exposure, site and growth parameters

The overall growth performance index (Φ'), L-infinity (L_∞) and the growth coefficient (K) were all significantly higher at the exposed shores (pooled) than at the sheltered shores (pooled) as shown by the results of t-tests ($p<0.05$ in all cases, Table 3.17). The Φ', L_∞ and K values were highest at Diaz Cross, Kwaai Hoek and Fish River. Of all the sites, growth parameters from Rufanes, Riet River and Mgwalana always ranked in the lowest three readings (Table 3.18). There was never any overlap in the ranking of growth parameters from the exposed and sheltered sites.

Table 3.17 Results of t-tests comparing growth parameters at exposed and sheltered sites.

	N	t-statistic	Significance
Φ'	3	6.4181	0.0030
L_∞	3	3.5694	0.0230
K	3	8.6489	0.0010

Table 3.18 Estimates of Φ', L_∞ and K from Shepherds length composition analysis (SLCA) at each site.

Site	Exposure	Φ'	L_∞	K
Dz	E	4.08	129.80	0.71
Kw	E	3.98	114.90	0.73
Fs	E	3.89	108.32	0.66
Mg	S	3.26	86.06	0.27
Ru	S	3.51	91.90	0.39
Ri	S	3.42	97.86	0.27

Von Bertalanffy growth curves

Although cohorts were not easily identifiable there was one cohort at all sites which could be traced from recruitment in November 1995/January 1996 through to August/September 1996 (marked as an arrow in Figure 3.11).

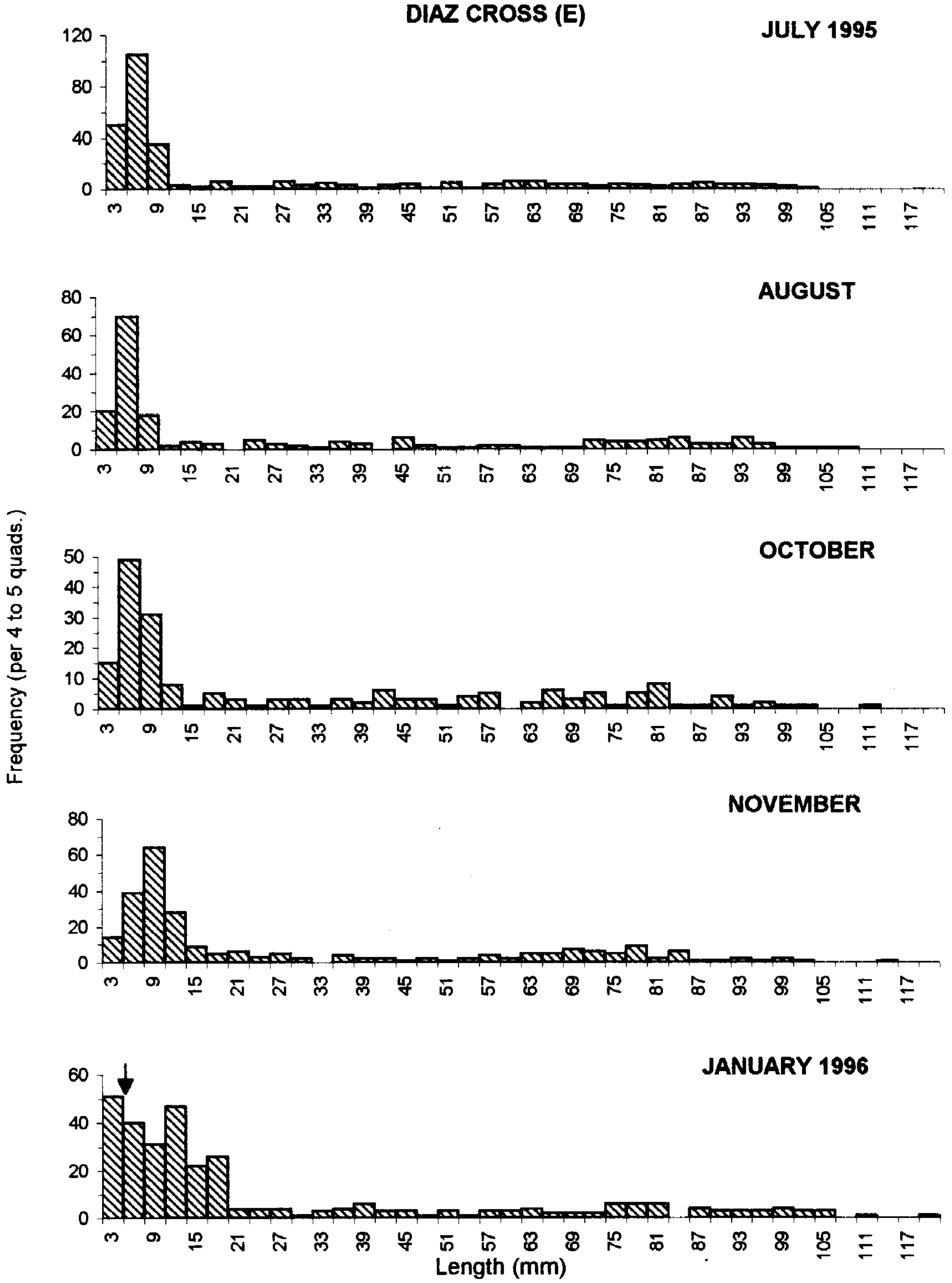


Figure 3.11 The best Von Bertalanffy growth curves which were generated by SLCA using length frequency distributions for 11 sampling months. The arrows indicate the cohorts that were followed. The upper size (mm) limits are presented. a) Diaz Cross

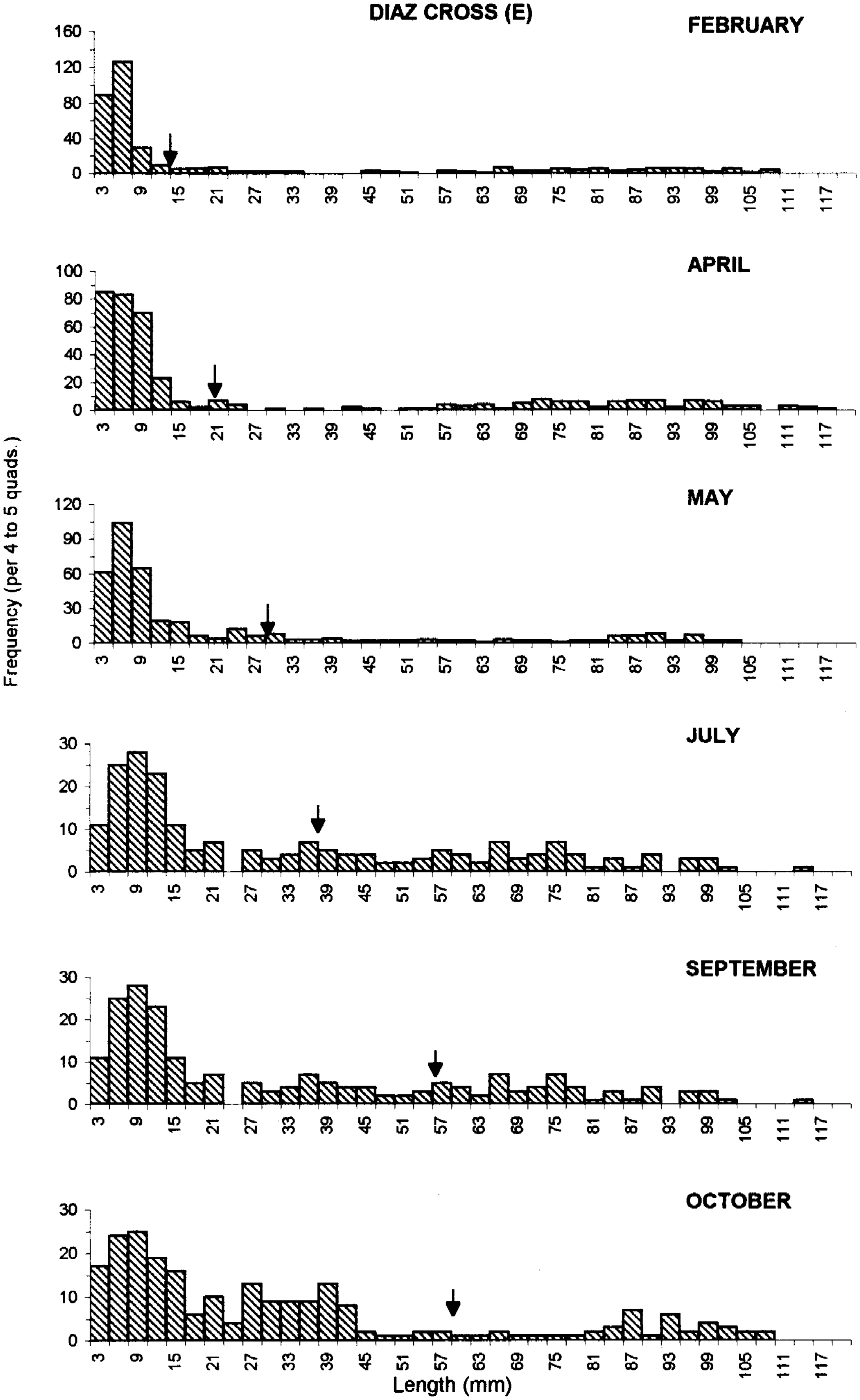


Figure 3.11 a) cont.

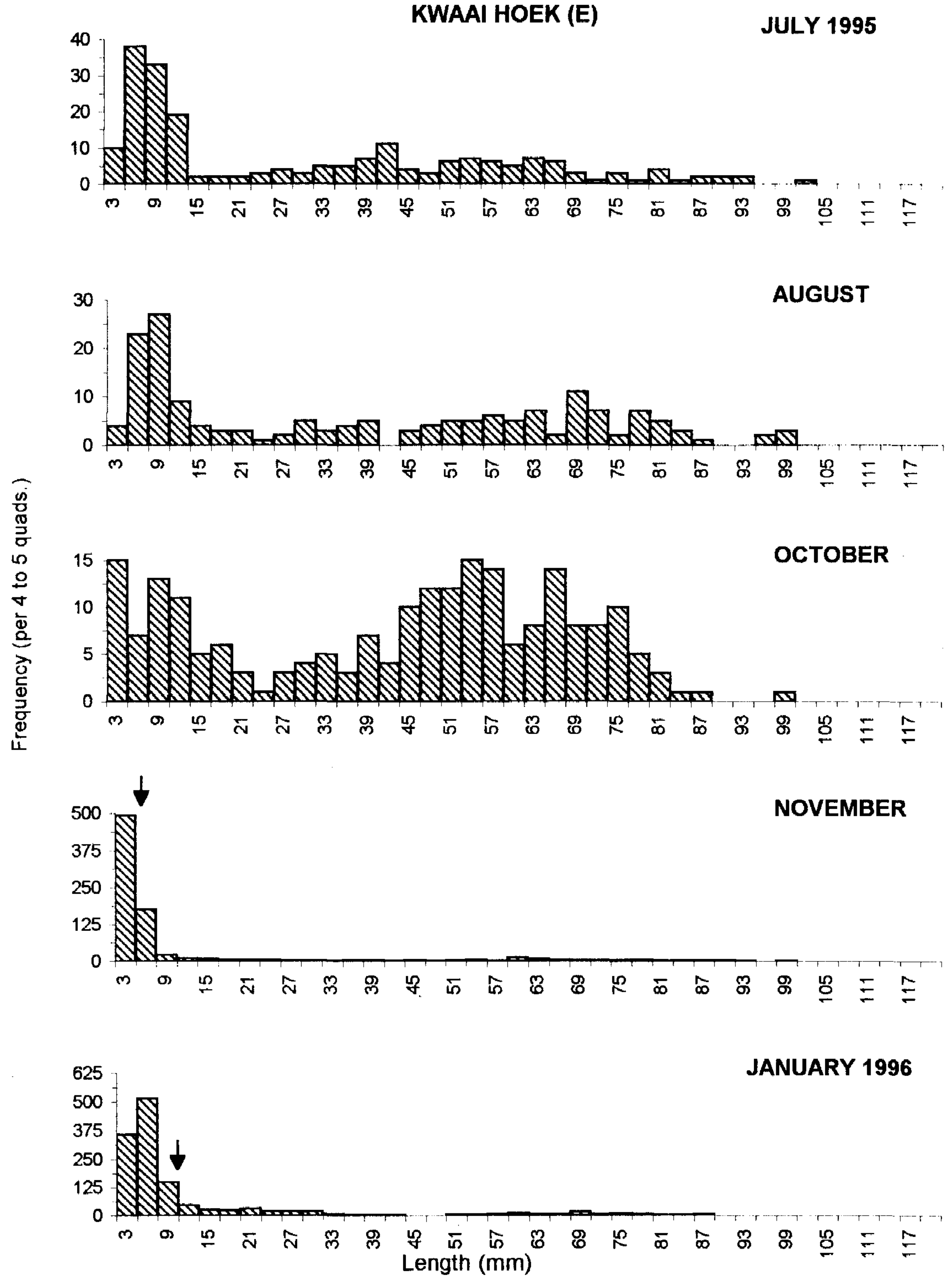
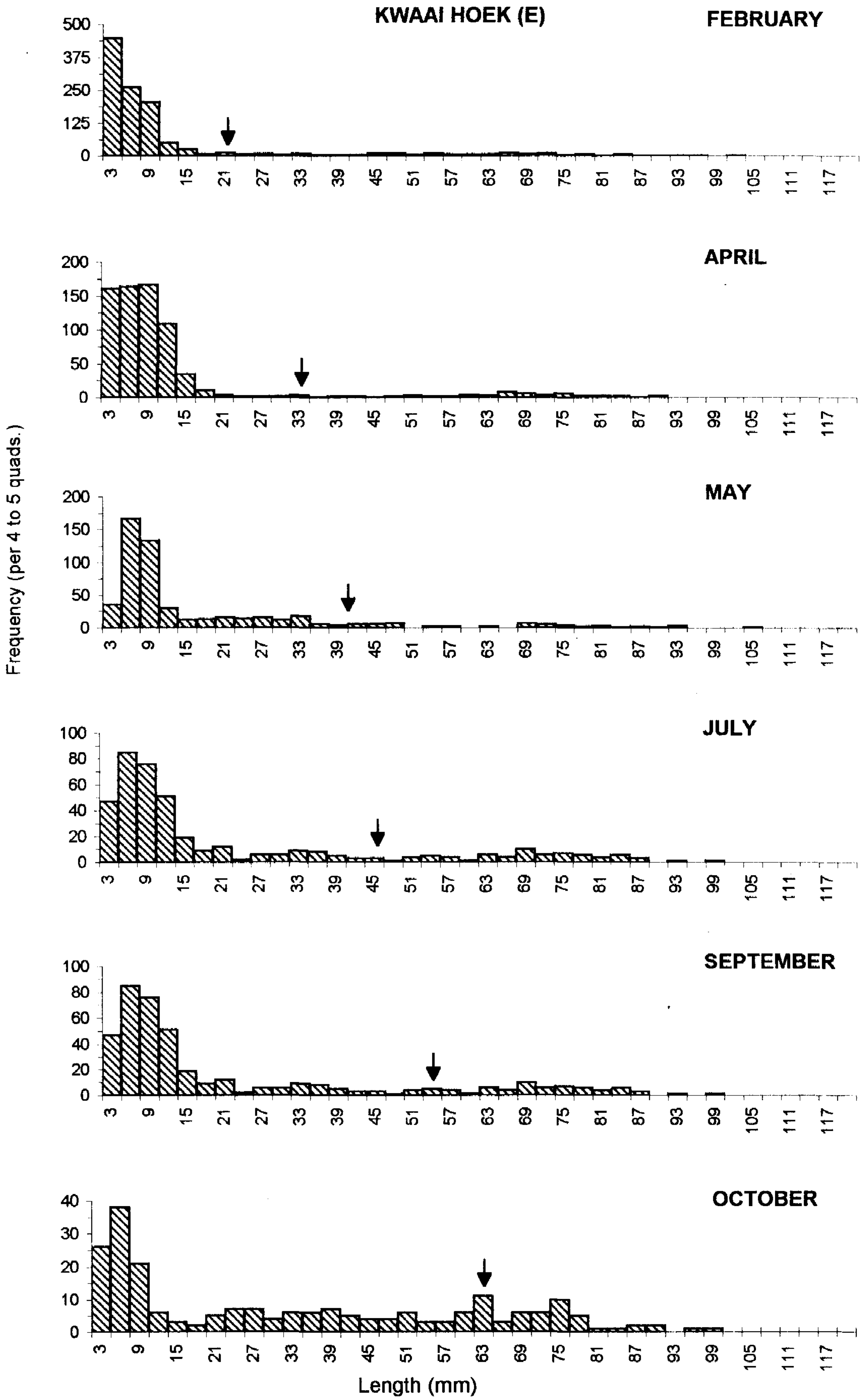


Figure 3.11 b) Kwaai Hoek



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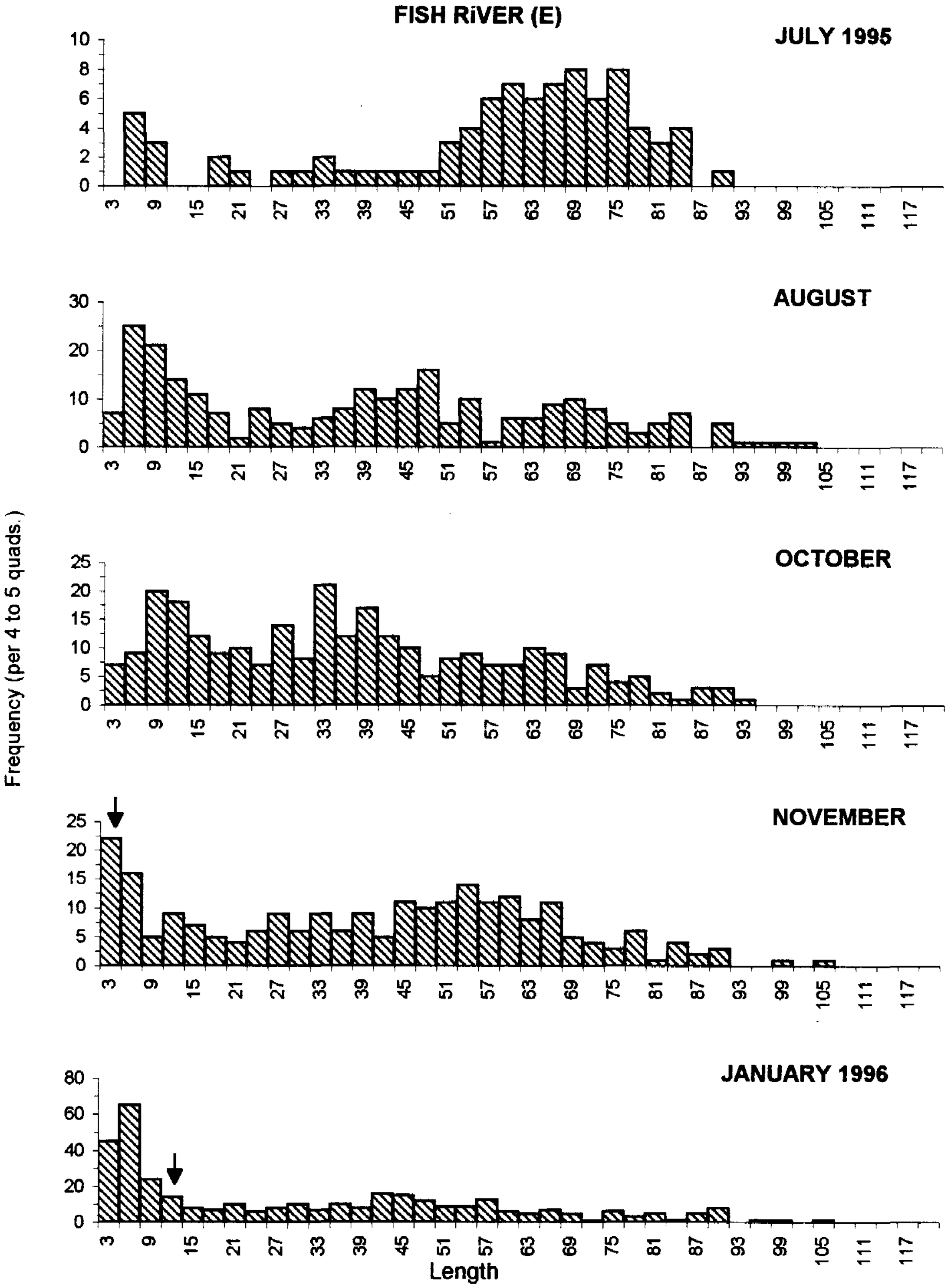


Figure 3.11 c) Fish River

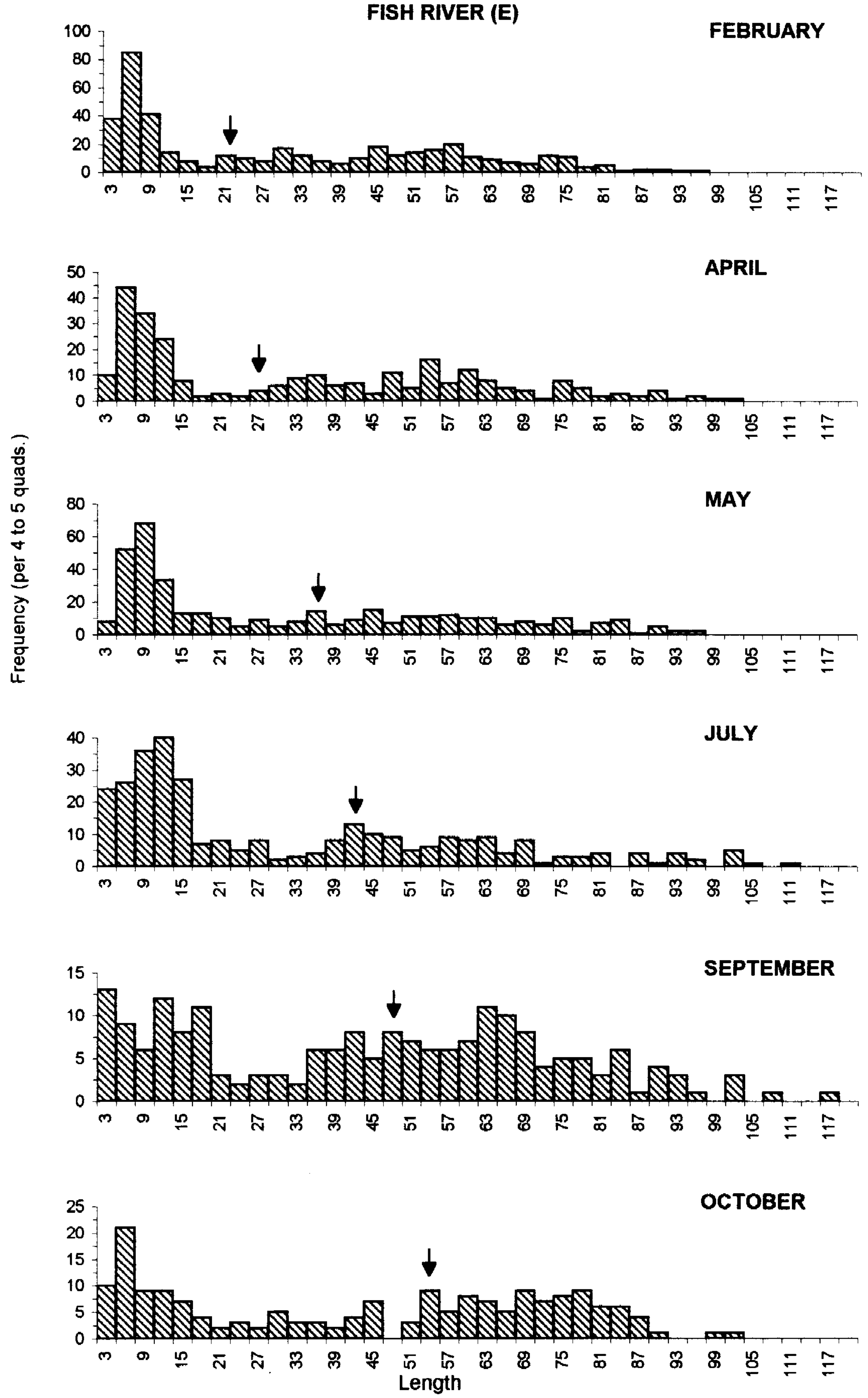


Figure 3.11 c) cont.

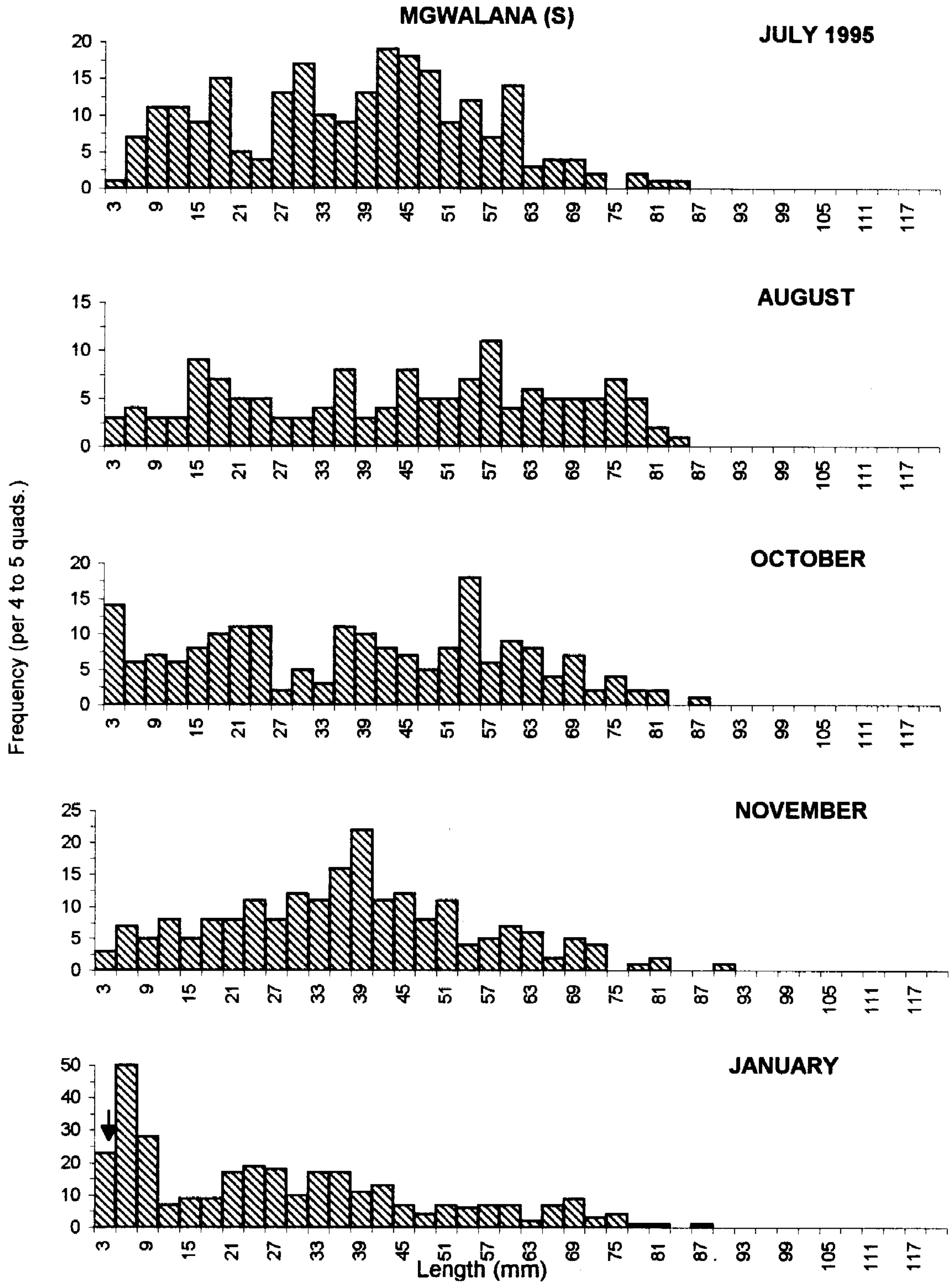


Figure 3.11 d) Mgwalana

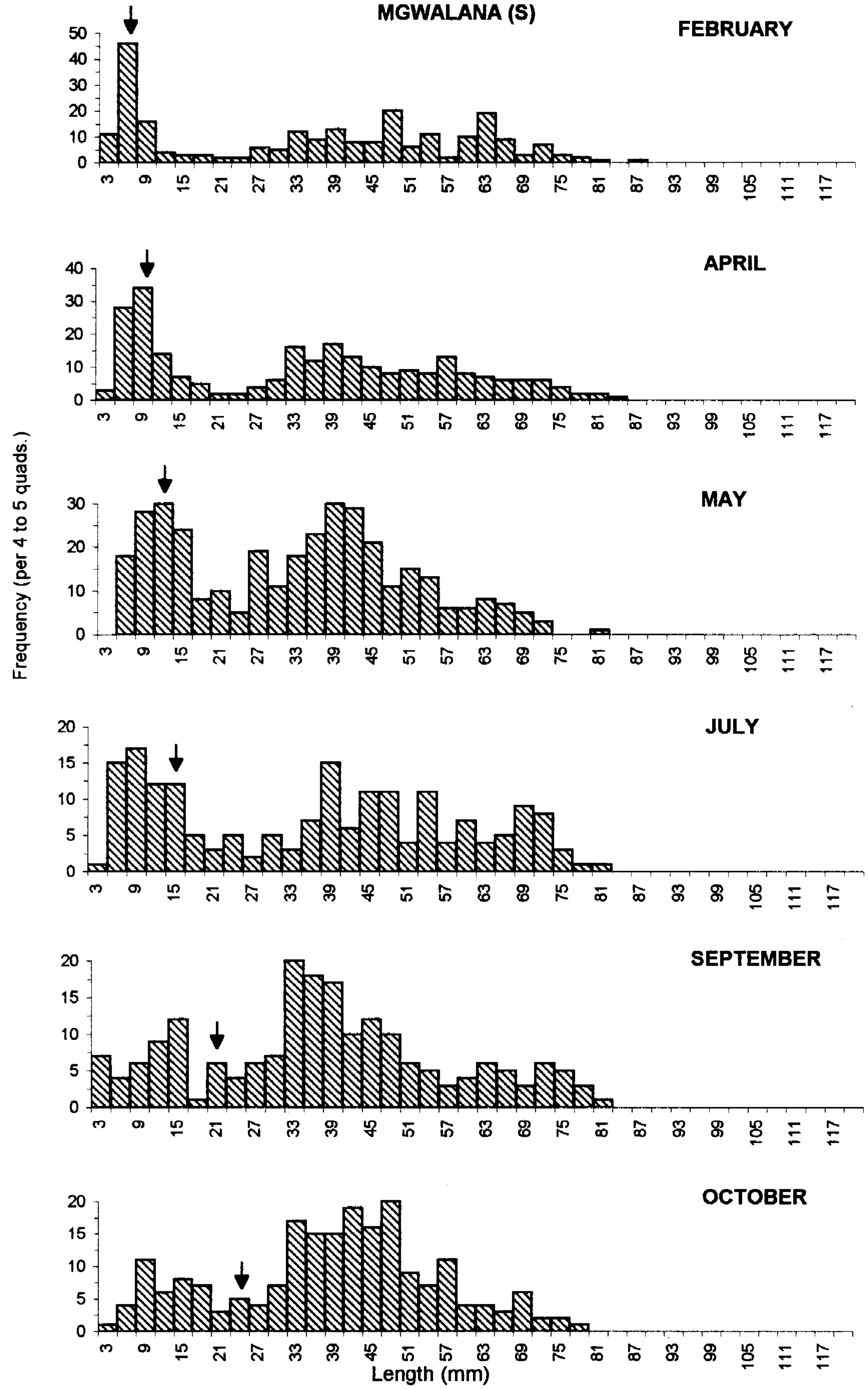


Figure 3.11 d) cont.

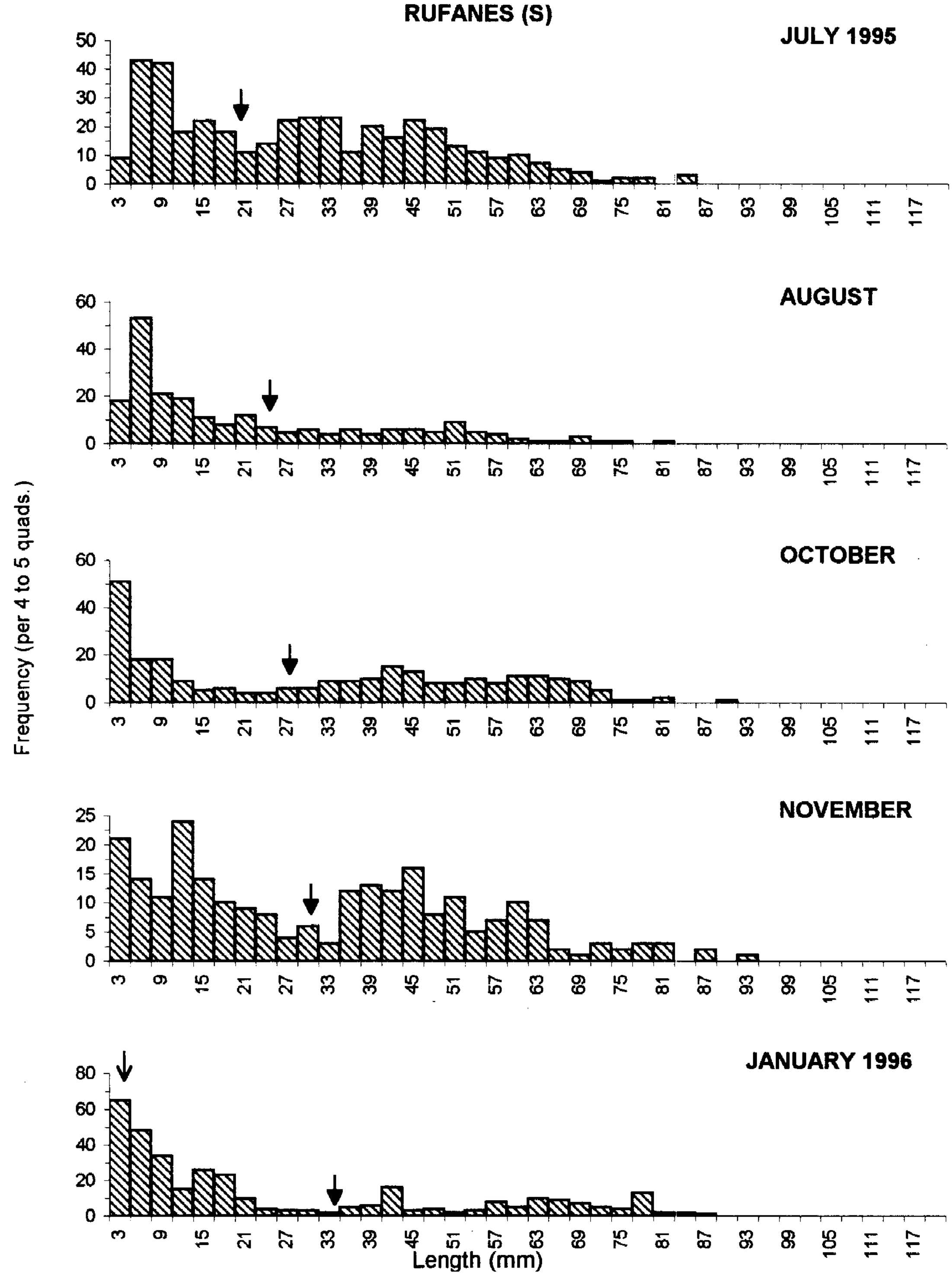


Figure 3.11 e) Rufanes

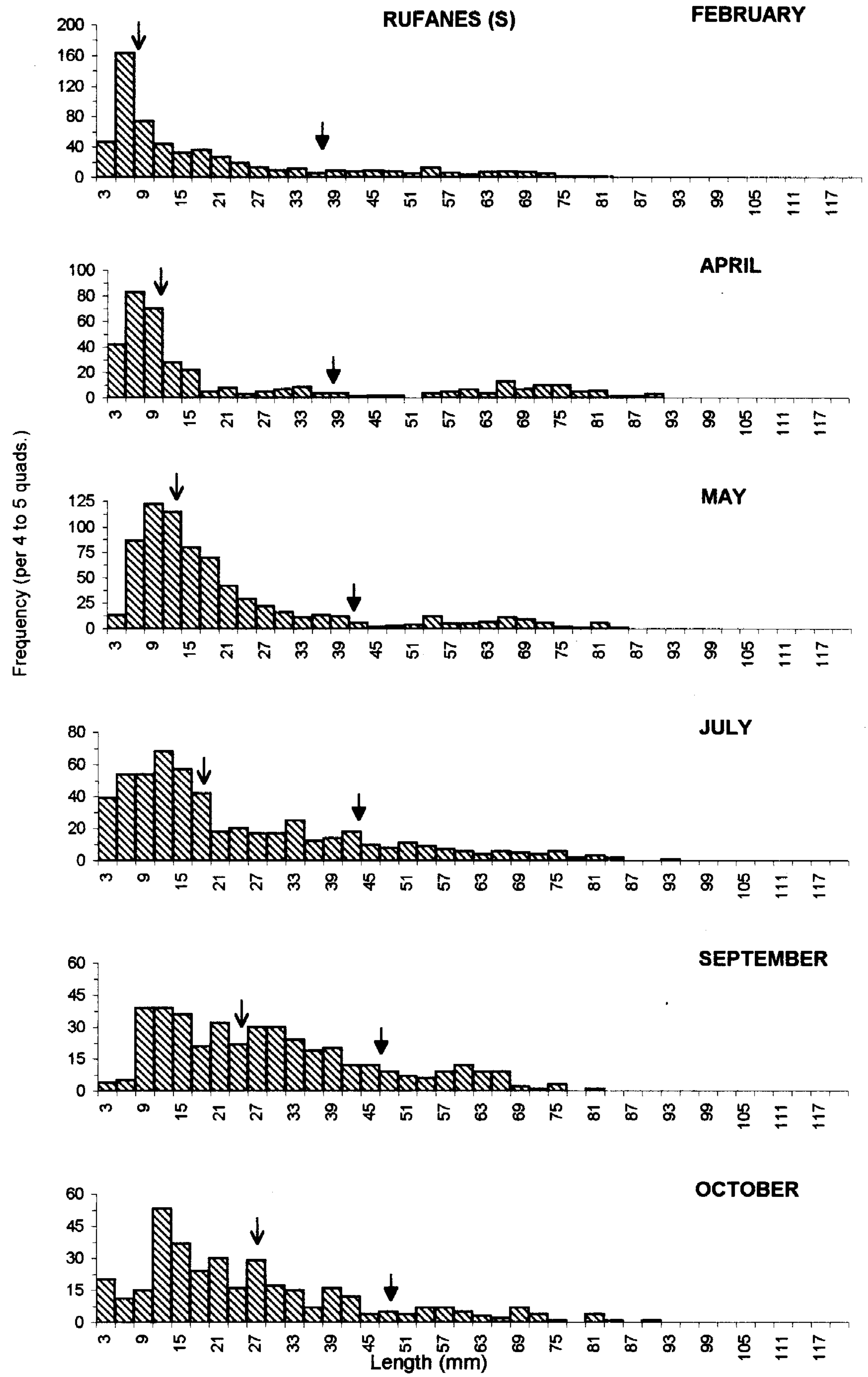


Figure 3.11 e) cont.

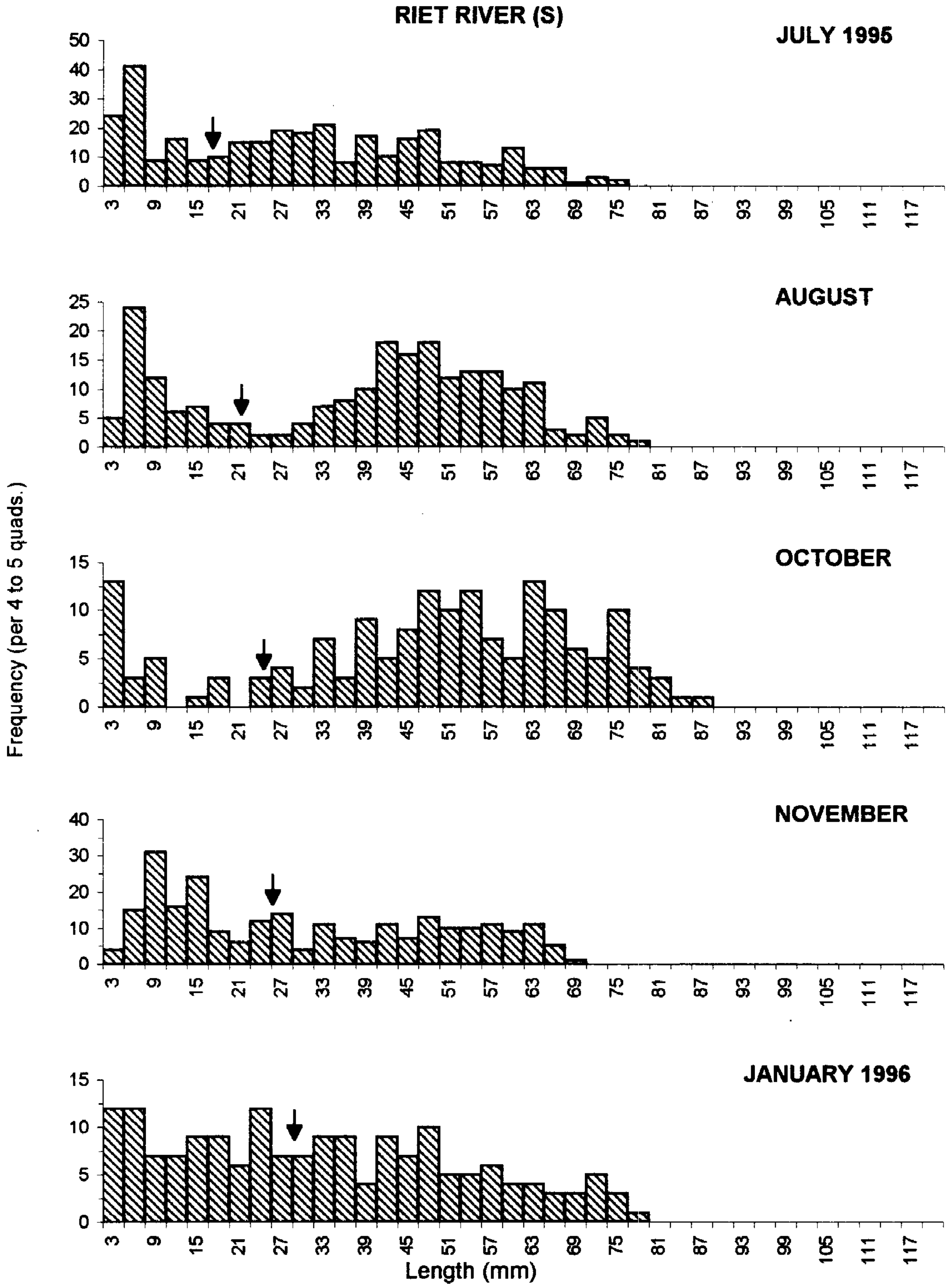


Figure 3.11 f) Riet River

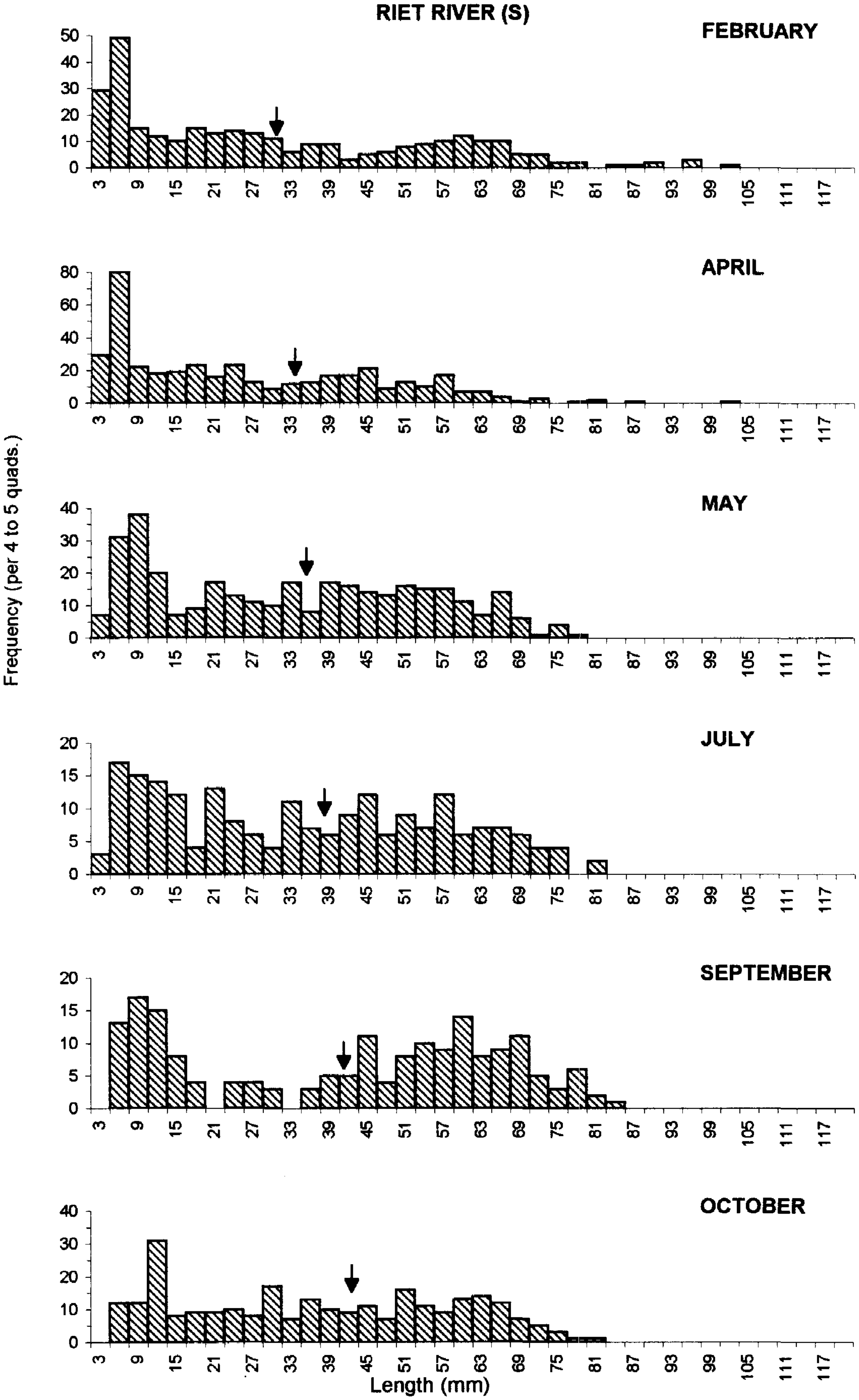


Figure 3.11 f) cont.

The growth parameters obtained from Shepherd's method were used to construct length at age Von Bertalanffy growth curves (Figure 3.12). A comparison of the mean length at one year of age at each site showed that the lengths at the exposed sites (mean of 59.16 mm) were higher than those at the sheltered sites (mean of 24.4 mm) (Table 3.19). Mussels of equal length are therefore older at sheltered shores than exposed shores. Younger mussels grew faster than older ones at both shores (Figure 3.12). By extending the ages represented in the Von Bertalanffy growth curves approximate ages at L_∞ lengths were calculated. Mussels at the sheltered sites took longer to reach L_∞ (12-15 years) than those at the exposed sites (8-9 years). This was also shown by the more gradual slope and lower K values at the sheltered shores.

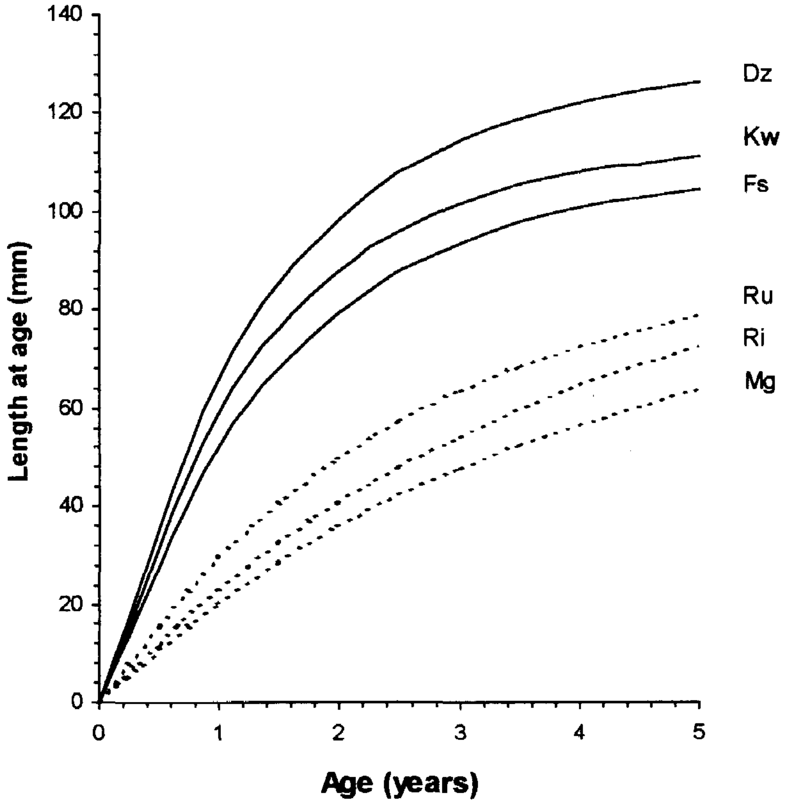


Figure 3.12 Von Bertalanffy growth curves at six sites using SLCA to obtain growth parameters.

Table 3.19 Mean length at one and two years at six sites, values calculated from Von Bertalanffy's equation.

Site	Exposure	Length (mm) at 1 year	Length (mm) at 2 years
Diaz Cross	E	65.99	98.43
Kwaai Hoek	E	59.16	87.67
Fish River	E	52.34	79.38
Mgwalana	S	20.36	35.91
Rufanes	S	29.68	49.77
Riet River	S	23.16	40.83

COMPARISON OF RESULTS OBTAINED FROM MARK-RECAPTURE, GROWTH BAND AND LENGTH FREQUENCY DISTRIBUTIONS

Comparing growth rates obtained from mark-recapture and growth band methods.

Data from the mark-recapture method were converted to growth in a 30 day period, to be comparable with growth band data. Homogeneity of variance was achieved by a √ (x+ 0.375) transformation of the data ($p>0.05$, Zar 1996). Despite deviations from normality ($p<0.05$), to which the ANOVA is robust (Zar 1996), ANOVA's were used in preference to less powerful non-parametric statistics. Growth rates of mussels were higher at the exposed shores than the sheltered shores for both methods (Figure 3.13 & Table 3.20). The growth band method resulted in higher growth rate estimates than the mark-recapture method for both the exposed and the sheltered shores (Table 3.20). The ANCOVAs confirmed that initial length, exposure and method had statistically significant effects ($p<0.05$, Table 3.21).

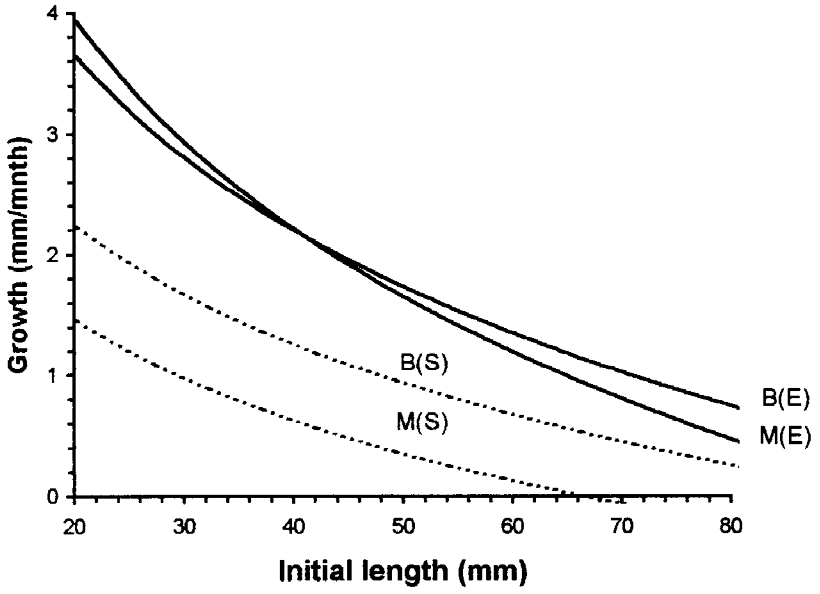


Figure 3.13. Growth rates from mark-recapture and growth band analysis for 30 days. M = mark-recapture method and B = growth band analysis at (S) sheltered shores (dashed lines) and (E) exposed shores (solid lines).

Table 3.20 Mean growth rate at exposed and sheltered shores using the mark-recapture and growth band method to obtain growth rates.

Method	Exposure	N	Mean growth rate mm. mnth^{-1}
mark-recapture	Sheltered	418	0.82
growth band	Sheltered	16	1.09
Mark-recapture	Exposed	305	1.36
Growth band	Exposed	18	1.44

Table 3.21 The ANCOVA on the relationship between initial length, exposure and methods and growth rates. The methods being compared are the mark-recapture and the growth band method. Data were $\sqrt{(x+0.375)}$ transformed.

Source	df	SS	MS	F	P
Covariate: initial length	1	27.86	27.86	536.22	<0.0001
Exposure (factor)	1	6.29	6.29	121.14	<0.0001
Method (factor)	1	0.88	0.88	16.91	<0.0001
Interaction: factors	1	0.29	0.29	5.63	0.0179
Residual	752	39.07	0.05		

Comparing growth parameters and growth curves obtained by mark-recapture, growth band and length frequency methods.

Exposure, method and growth parameters

The mean Φ', L_∞ and K values were higher on the exposed shores than the sheltered shores (methods pooled) (Table 3.22). This was the case irrespective of the method used (Table 3.23). T-tests confirmed that the growth parameters were significantly higher on exposed shores than sheltered shores ($p<0.05$, Table 3.24). The effect of method on the determination of each growth parameter could not be statistical analysed due to small sample sizes (n=2, *i.e.* exposed & sheltered) (Zar 1996). Growth parameters for mussels on exposed, but not sheltered shores, were highest when estimated by Shepherd's length composition analysis (Table 3.23). Growth parameters estimated by the mark-recapture method were lowest at both the exposed and sheltered shores (Table 3.23).

Table 3.22 The mean values of the growth parameters, at exposed and sheltered shores (methods pooled).

Exposure	Φ'	L_∞	K
Exposed	3.79	97.11	0.66
Sheltered	3.32	78.18	0.35

Table 3.23 A comparison of the L_∞, K and Φ' values generated at the exposed and sheltered shores using the mark-recapture (M), growth band analysis (B) and Shepherds length composition analysis (SLCA). Means are presented for mark-recapture and Shepherd's method as replication in sites was undertaken.

Method	Exposure	L_∞	K	Φ'
M	E	85.85	0.64	3.69
B	E	88.05	0.64	3.70
SLCA	E	117.44	0.70	3.98
M	S	65.61	0.31	3.14
B	S	76.98	0.44	3.42
SLCA	S	91.94	0.31	3.40

Table 3.24 Three t-tests on growth parameters meaned from results of all three methods, testing the effect of exposure.

	N	T-statistic	Significance
Φ'	3	5.6812	<0.0001
L_∞	3	2.3574	0.0362
K	3	10.0541	<0.0001

Exposure, method and growth curves

The growth curves showed mussels to have faster growth rates on the exposed shores than on sheltered shores, irrespective of the method used to procure them (Figure 3.14). The growth curve obtained for mussels on exposed shores using the SLCA method showed higher growth rates than growth rates obtained from the other methods. The growth curves for the mark-recapture and growth band method at the exposed shore were very similar, with growth rate dropping noticeably from approximately three years of age. The growth curves for SLCA and the growth band method at the sheltered shore initially followed a similar line but diverged slightly after four years of age. Curves for the mark-recapture method were much lower than the other two for the sheltered shores. Although there was considerable variation in the lengths at one year obtained using the different methods, lengths at exposed shores were always higher than at the sheltered shores (Table 3.25). There was greater variation in the estimated mean lengths at one year of age for the exposed shores (40.40 to 59.16) than for the sheltered shores (17.41 to 27.40). SLCA yielded the highest length at both exposures and similarly the mark-recapture method always produced the lowest estimates. Mussels took 8-9 years to reach an approximation of L_∞ on the exposed shores and 12-18 years on the sheltered shores.

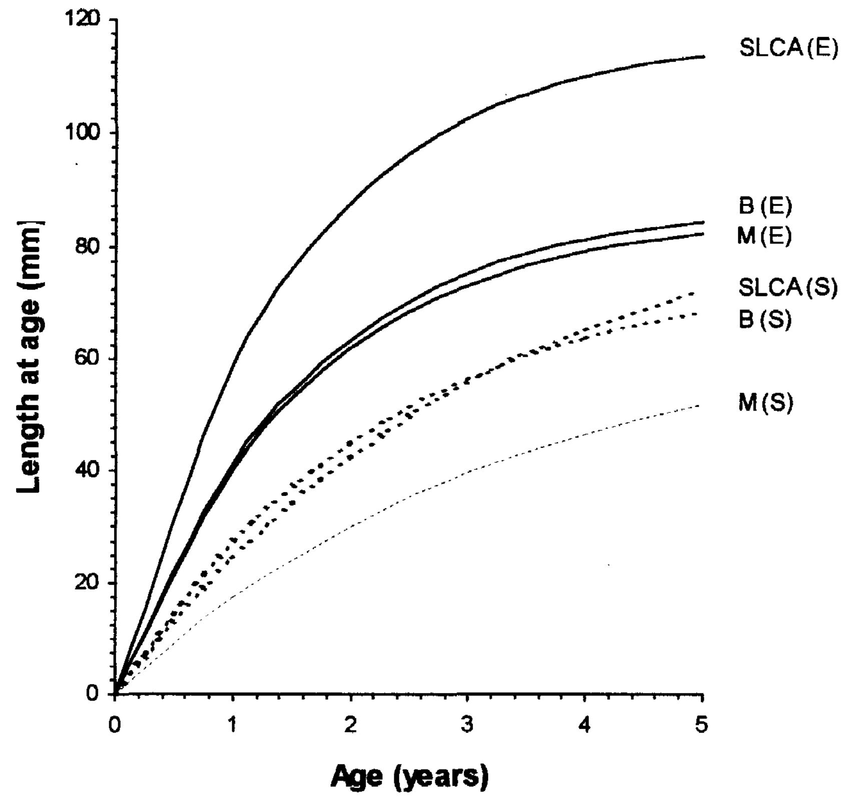


Figure 3.14 A comparison of the Von Bertalanffy growth curves generated from growth rates obtained by the mark-recapture (M), growth band (B) and SLCA. (E) = exposed shore and (S) = sheltered shore.

Table 3.25 A comparison of lengths at one year of age on exposed and sheltered shores obtained using three different methods.

Exposure	Method	N	Mean length at a year (mm)
E	Mark-recapture	3	40.40
E	Band	1	41.62
E	SLCA	3	59.16
S	Mark-recapture	3	17.41
S	Band	1	24.40
S	SLCA	3	27.40

Site, method (mark-recapture and SLCA) growth parameters and growth curves

The overall ranking of L_∞, K and Φ' by both methods showed the exposed sites within the top three ranks and the sheltered sites in the bottom three ranks, without any overlap (Table 3.26) . At the **exposed** sites the L_∞ values generated from SLCA were higher than those from the mark-recapture method but sites still ranked in the same order; Diaz Cross always had the highest L_∞ followed by Kwaai Hoek and Fish River. Due to no within site replication statistical analysis could not be performed. In a comparison of the exposed sites, both methods ranked Diaz Cross mussels as having the fastest growth rates followed by Kwaai Hoek and Fish River. In a similar comparison of the sheltered sites, it was apparent that there was less variation in the growth rate of mussels amongst sheltered sites than exposed sites. Although both methods ranked the mussels from Rufanes as the fastest growers from the sheltered sites, there was no agreement in the ranking of the remaining two sites. SLCA gave consistently higher readings than the mark-recapture method or vice versa.

The length at one year of age for both methods was considerably higher at the three exposed sites than at the three sheltered sites (Table 3.27). Although the lengths varied according to the method used there was less variation in lengths at the sheltered sites (16.20 - 29.68 mm) than at the exposed sites (35.71 - 65.99 mm). Diaz Cross was ranked by both mark-recapture and SLCA method as having mussels of the greatest length at one year, followed by Kwaai Hoek and Fish River. At maximum lengths mussels would be older on sheltered sites than on the exposed sites (this was observed by extending the growth curves till L_∞ was reached) (Figure 3.15). As K , the growth coefficient, gives the rate at which L_∞ is reached, a lower K value (*i.e.* flatter slope) would indicate that L_∞ is reached at a slower rate at sheltered sites (Figure 3.15).

Table 3.26 A comparison of the growth parameters generated from mark-recapture and Shepherds length composition analysis (SLCA).

Site	Exposure	Marked L_∞	SLCA L_∞	Marked K	SLCA K	Marked Φ'	SLCA Φ'
Dz	E	98.66	129.80	0.56	0.71	3.74	4.08
Kw	E	83.34	114.19	0.73	0.73	3.76	3.98
Fs	E	75.54	108.32	0.64	0.66	3.56	3.89
Mg	S	66.77	86.06	0.31	0.27	3.14	3.26
Ru	S	72.43	91.90	0.29	0.39	3.23	3.51
Ri	S	57.62	97.86	0.33	0.27	3.04	3.42

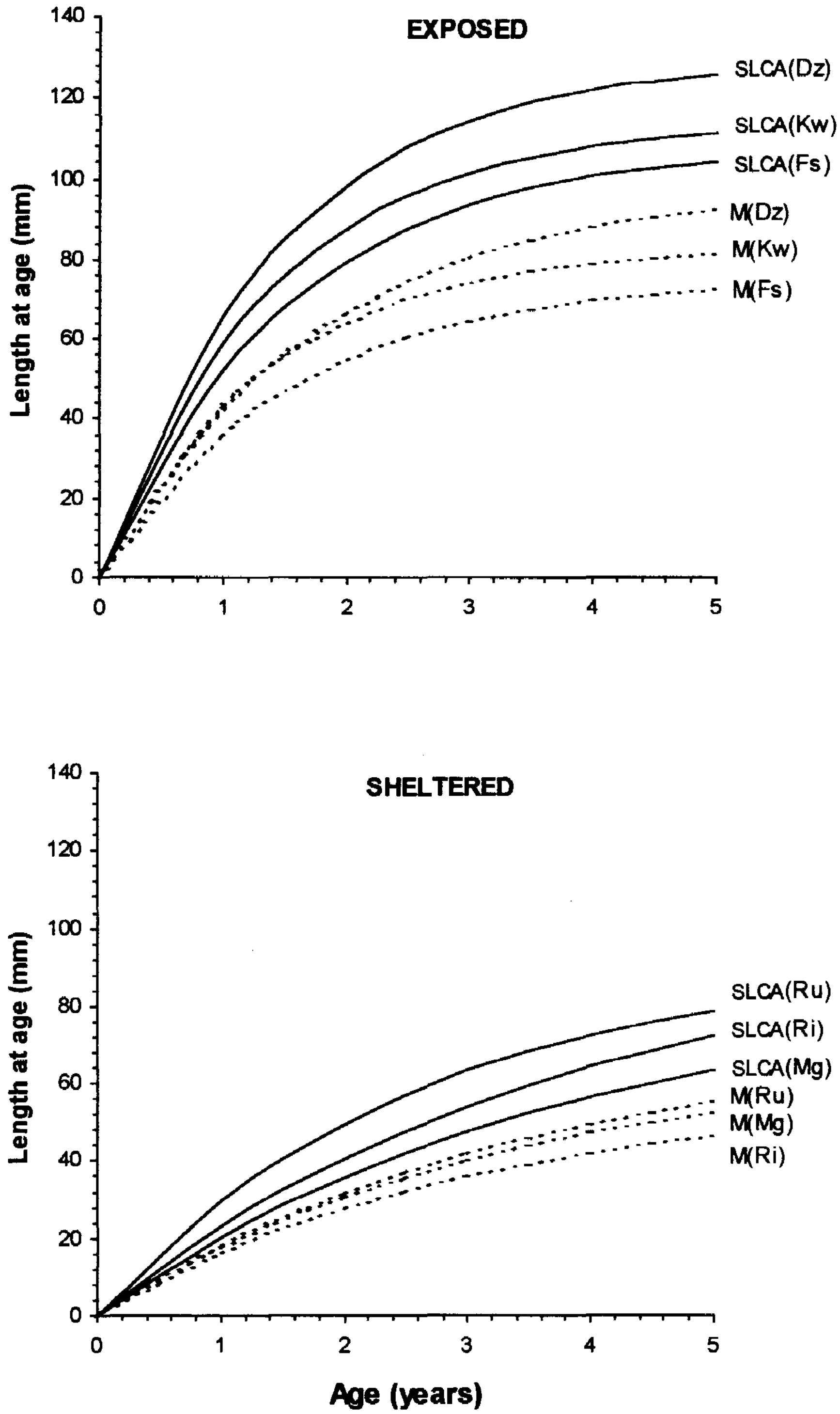


Figure 3.15 A comparison of the Von Bertalanffy growth curves generated using the mark-recapture (M) and SLCA method at the exposed and sheltered sites.

Table 3.27 The lengths (mm) of mussels at six sites at one year of age (from Von Bertalanffy equation) generated by two methods namely, mark-recapture and cohort analysis.

Site	Exposure	Mark-recapture	SLCA
Dz	E	42.30	65.99
Kw	E	43.18	59.16
Fs	E	35.71	52.34
Mg	S	17.80	20.36
Ri	S	16.20	29.68
Ru	S	18.23	23.16

D. The relationship between wave force, density and growth rates

The three sheltered sites at which lower wave forces were recorded correlated with lower overall growth performance (phi prime values) and the three exposed sites where greater wave forces were recorded had higher growth performance (Figure 3.16). The correlation of wave force against phi prime values at individual sites (methods pooled) was significant ($p<0.05$) and showed a positive correlation coefficient of 0.71. The correlation of mean wave force (at both shore types) against mean phi prime values (mean values for each shore type from all three methods *i.e.* $n=6$) resulted in a significant ($p<0.05$) correlation coefficient of 0.87 (Figure 3.17).

An overall pattern of higher growth performance in mussel beds of lower density and lower growth performance in mussel beds of higher density was found (Figure 3.18). The correlation of density against phi prime values (from 2 methods) at individual sites was significant ($p<0.05$) and showed a correlation coefficient of -0.68. At the level of exposure (sites pooled), which used phi prime values from all three methods, a significant ($p<0.05$) negative correlation coefficient of -0.87 was found. Although Mgwalana and Fish River experienced extremely different wave action and had mussels with very different phi prime values, both sites supported mussel beds of similar packing density (Figure 3.16 & 3.18). This could imply that the correlation between density and phi prime is simply a correlation and that the real effect on phi prime is caused by wave action. This implies that growth is a response to the degree of wave action and not density, although density generally decreases on exposed shores.

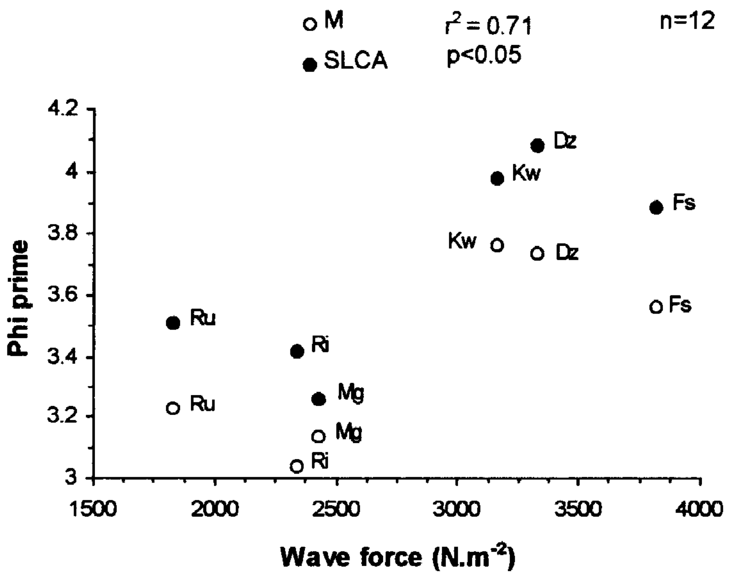


Figure 3.16 Relationship between wave force (N.m^{-2}) measured by the dynamometers at each site and overall growth performance index (phi prime value) using results of each site from the mark-recapture and SLCA.

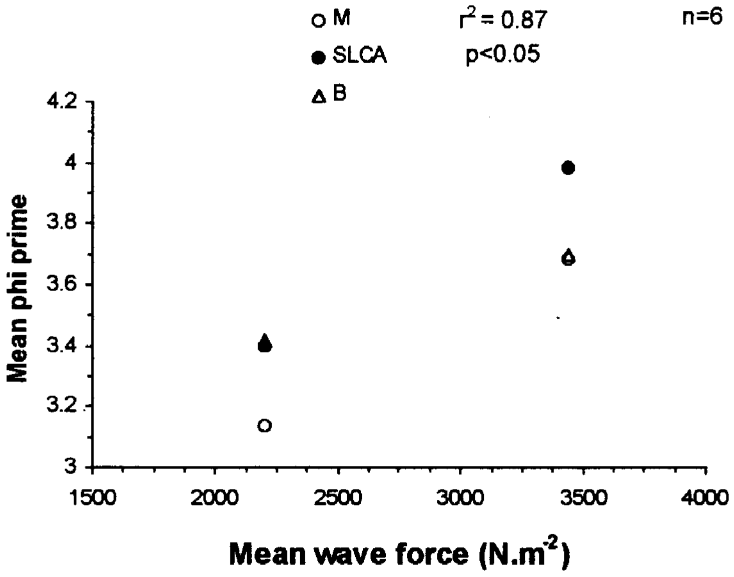


Figure 3.17 Relationship between mean wave force (N.m-2) measured by the dynamometers at both shore types and overall growth performance index (phi prime) using results of each shore type from the mark-recapture, SLCA and growth band method.

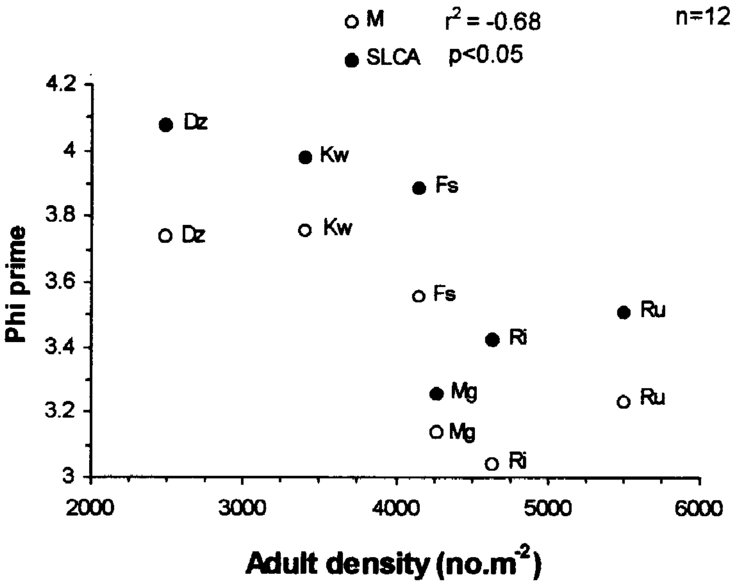


Figure 3.18 The correlation of mean density and phi prime values obtained at each of the six sites for the mark-recapture and cohort method.

4. DISCUSSION

Discussion of results obtained using different methods

Mark-recapture

Amongst the various techniques available for producing growth checks, such as immersion in acetasolamide, cold treatment and 'overfeeding' in the laboratory, the file mark method ranked as one of the best in a study undertaken by Ekaratne & Crisp (1982). One of the disadvantages in using the file check is that it could cause damage to the shell margin and possibly to the shell secreting mantle epithelium (Richardson 1989). Of the 55% mortality observed in the marked mussels, some was due to excessive damage caused when marking the shells. Another problem with this method was that in a few cases after filing, growth was not continuous with the structure of the old shell but continued toward the inside of the shell, a factor which would result in an underestimation of growth rate. Future growth studies would benefit by investigating the use of tetracycline as a shell marker, as it is incorporated into the mussel during filtration, does not damage the shell, and produces a distinctive mark which is visible for several months (Dey & Bolton 1978).

Growth band analysis

The considerably more tedious growth band method (pers. ob., Richardson *et. al.* 1979) has seen widespread use in ageing studies of bivalves (Lutz 1976 , Peterson *et. al.* 1983, Ropes & Jearld 1987). Whereas validation of the periodicity of growth bands is essential and has been well documented (see review on validation by Beamish & McFarlane 1983), many studies do not seem to have progressed past this to a stage where findings are used to construct age and growth curves. As in this study no broader patterns such as annual rings (Ropes & Jearld 1987, Cerrato & Keith 1992), summer/winter checks (Thiesen 1973) or spring tidal bands (Richardson 1989, Anwar *et. al.* 1990) were observed, micro bands which were shown to be of tidal origin were used for comparing growth rates. Until fairly recently banding in intertidal bivalves was assumed to be of daily origin (Pannella & MacClintock 1968). A considerable amount of research has now shown that banding usually occurs twice daily, corresponding to low tide (emmersion period) (Richardson *et. al.* 1979, Ekaratne & Crisp 1982, Richardson 1988). In this study, the bands which were laid down twice daily were also assumed to be of low tide origin. Clark (1968) suggested the maximum band count as the most representative validation, as lower counts could indicate that bands had been missed out. Stress bands which are laid down under unfavourable conditions could however result in counts higher than the number of tides experienced (Seed 1969b, Ekaratne & Crisp 1982). Underestimation of bands, as observed in this study, may have been due to no or slow growth (Richardson *et.al.* 1979). Even spawning has been observed to interrupt the daily increments in the clam, *Mercenaria mercenaris* (Pannella & MacClintock 1968). The mean number of bands per tide were frequently under or overestimated by other authors. A comparison of the mean number of observed growth lines divided by the expected number of growth lines obtained by various authors revealed values of 0.97 for a study on *Cerastoderme edule* (Richardson *et. al.* 1979), 0.89-0.96 for *Spisula subtruncata* (Richardson 1988) and 0.94 for *Perna perna* in this study.

Although not as susceptible to erosion or dissolution as surface bands (Lutz 1976, Anwar *et. al.* 1990) micro growth bands were observed to be more distinct in younger shells than in older shells where bands had become compressed. Banding was also clearer along the outer edge than the inner (also noted by Ekaratne & Crisp 1982), toward the growing tip and at certain sites eg. Mgwalana and Riet River. According to Richardson (1988 & 1989) the clarity of bands depended upon the preparation and the strength of the band. Within intertidal mussels, he noted clear bands in some shells and not in others. As a general pattern however, the more exposed a site to aerial exposure the stronger the banding (Richardson 1989). This could perhaps explain the more distinct bands at Mgwalana and Riet River, both of which are sheltered sites and as a result of less wave action and splash, are more exposed to the air than the exposed sites. The phenomenon of decreased emmersion time due to an increase in splash caused by greater exposure to wave action has been documented by Underwood (1981).

Length frequency distributions

Many techniques are available for obtaining growth parameters from length frequency distributions. Of these techniques, modal progression analysis (Bhattacharya and NORMSEP) and direct length frequency techniques, such as Electronic Length Frequency Analysis (ELEFAN) and Shepherd's Length Composition Analysis (SLCA) have found success for a wide range of species. Examples of this success are evident in a number of growth studies, for example, Shafee (1992) used NORMSEP for mussels, Tomalin (1995) used ELEFAN & SLCA for *Perna perna* and Cretchley (1997) used NORMSEP for prawns. Prior to the 1980's the probability paper methods of Harding (1949) and Cassie (1954) were the most commonly used techniques for analysing length frequency data (Robson 1986). Several studies from this time period did not even make use of probability paper but traced cohorts by eye and then made educated 'guesses' when assigning ages to various cohorts (Berry 1978, Crawford & Bower 1983). All analyses are not equally suitable and modal progression analysis proved unsatisfactory for determining growth parameters for *Perna perna* along the south coast of South Africa in this study. Similarly, modal progression analysis was unsuitable for determining the growth rate of the ribbed mussel *Aulacomya ater* (Griffiths & King 1979b) and *Perna perna* on the Transkei coast (Lasiak & Dye 1989) as merging of cohorts occurred.

The lack of discreet, easily discernible cohorts is troublesome for all three length frequency analyses, but particularly for modal progression analysis. In the words of Gulland (1987, p337) "Under favorable circumstances, with good sampling and clear modes that progress from sample to sample in a consistent manner, all methods work well. With poor data and poor differentiation between modes few work well." Some of the factors that are frequently responsible for unclear modes will now be examined. Narrow discrete cohorts did not occur because of the prolonged settlement period of small mussels (0-5 mm) observed in this study, which although highest from January to April (chapter 2), extended through most of the year. A similar pattern of prolonged settlement was recorded in *Perna perna* by Philips (1994) at Diaz Cross and Kwaai Hoek, sites which were common to both studies. In a study by Kautsky (1982) length frequency distribution techniques were futile as peaks in juvenile blue mussels *Mytilus edulis* (0-2 mm) were present throughout the year and the cohorts failed to carry through. As most length frequency analyses assume regular spawning, settlement and recruitment, the occurrence of sporadic spawning or settlement, particularly more than once per annum, can prove difficult. Three spawning events per annum were reported in the ribbed mussel *Aulacomya ater* by Griffiths and King (1979b). Philips (1994) also documented peaks of newly settled *Perna perna* (0-9mm) more than once annually, in October/November, April/May and sometimes July (at certain sites). Several studies have highlighted the variability in spawning and settlement, as well as the presence of chance events which lead to exceptionally good or poor recruitment (Berry 1978, Griffiths 1981, Harris pers. com.). Differential growth rate of a cohort due to individual variability (discussed earlier), even from very seasonal spawning, can result in merging of cohorts from different year classes (Munday & Keegan 1992). Cohort overlapping commonly occurs in older slower growing individuals (Pauly & Caddy 1985). These factors could affect the clarity and hinder the interpretation of cohorts and length frequency distributions.

As growth for the mark-recapture and growth band method was measured over the summer period and then extrapolated for the entire year, it is likely that growth was either under or overestimated due to seasonal differences in growth. To enable growth parameters from all three methods to be compared, length frequency distributions were analysed by SLCA, which does not take seasonality into account. In addition data were only available for 15 months and did not show clear cohorts, making seasonal interpretation difficult, if not impossible. Tomalin (1995) when studying growth rates of *Perna perna* in KwaZulu-Natal did not take season into account at one site, Umdoni, as samples were taken for only 12 months. Isaac (1990) observed that despite this limitation of SLCA the existence of a seasonal growth oscillation did not greatly influence the estimates of L_∞ and K. Berry (1978) remarked that *Perna perna* showed no distinct seasonal fluctuation in growth along the Natal coast. In a later study on the brown mussel at four sites along the KwaZulu-Natal coast, one population showed a high degree of growth retardation, two showed slower growth rates and the fourth showed no effect during the winter period (Tomalin 1995). Defeo *et al.* (1992a) noted that growth curves constructed from annual growth bands could not account for seasonality, but with the use of ELEFAN a sinusoidal growth curve due to a seasonal effect could be observed.

One of the drawbacks of the current versions of ELEFAN and Shepherd's method is that no variance around the mean is calculated. Tomalin (1995) solved this by dividing his monthly data set (in total 24 sampling periods) into three groups of eight quarterly samples and calculating growth parameters for each group. Unfortunately, due to the shorter sampling period of 15 months (11 sampling periods) this method of obtaining variation was inappropriate for the current study as it would result in many groups with too few samples.

It has become common-place to compare values of L-infinity (L_∞), phi prime (Φ') and length at a year between sites and methods (Tomalin 1995). If the limitations of comparing these growth parameters are recognised, the comparisons would benefit rather than hinder the study. The parameters of the Von Bertalanffy equation are affected by the representation of large mussels (Yamaguchi 1975). For the present study low numbers of large brown mussels possibly led to an underestimation of L_∞ in the mark-recapture and growth band method (Table 3.25). Takada (1995) showed that L_{max} estimates for the gastropod *Monodonta labio* from his mark-recapture method were lower than estimates from cohort analysis used in other studies. As these studies were undertaken at two different sites in Japan, this difference could have been attributed to site or method. The small sample size for the growth band analysis could have caused a bias in the growth parameters, particularly as *Perna perna* has considerable variation in individual growth rates. As length frequency distributions were taken at six weekly intervals over a 15 month period the population was adequately sampled and large mussels were well represented for SLCA. The L_∞ values from the mark-recapture and growth band method were always lower than those estimated from SLCA (Table 3.4.5 & 3.4.7). This could be due to an overestimation of the theoretical maximum length using Shepherd's length composition analysis. The same estimates of size (>40 mm) at one year for the mussels on the exposed shores was obtained by the mark-recapture and growth band techniques. However, the estimates for mussels on the sheltered shores were much lower using the mark-recapture than the growth band method.

The L_∞ estimates obtained using ELEFAN were slightly higher than those from SLCA. Studies on the brown mussel *Perna perna* (Tomalin 1995) and the yellow clam *Mesodesma mactroides* (Defeo *et al.* 1992a) reported lower estimates of L_∞ by ELEFAN than SLCA. In a comprehensive review on length-based methods for studying populations, particularly of fish, Isaac (1990) concluded that the ELEFAN method was more suitable for fast-growing short-lived organisms and the SLCA for slow-growing long-lived organisms. In Isaac's investigation both these analyses had a tendency to overestimate L_∞ and underestimate K. When individual variability of growth parameters was high, ELEFAN was more accurate at predicting L_∞ than SLCA, but SLCA was more accurate for predictions of K (Isaac 1990). However, when long recruitment periods occurred, estimates of L_∞ by SLCA and Power-Wetherall were more accurate than estimates from ELEFAN (Isaac 1990). SLCA is particularly suited to data that includes small lengths (*i.e.* in preference to fishing catches of larger fish curtailed by mesh size) as older modes tend to overlap (Shepherd 1987). As *Perna perna* showed high individual variability, long recruitment periods and included smaller sizes, the use of Power-Wetherall to estimate L_∞ and SLCA to estimate K probably gave the most reliable results.

The SLCA program (in the FiSAT version 1.10 package) used in this study was reported by Pauly and Arreguín-Sánchez (1995) to have limitations that often resulted in overestimation of K. However, this did not always seem to occur as estimates of K from SLCA were higher than estimates from the mark-recapture method at three sites, equal at one site and lower at the remaining two sites. The K values obtained for the exposed sites (this study) using ELEFAN and SLCA were also quite comparable (Table 3.16 & 3.19). This contrasts with Tomalin's findings where ELEFAN gave lower K estimates than SLCA (Tomalin 1995).

Phi prime values from SLCA were, with the exception of the estimate from the growth band method at the sheltered shore, higher than estimates from the other two methods. As phi prime is a function of L_∞ and K , and SLCA's estimates of L_∞ were always higher than those from the mark-recapture and growth band method, this was to be expected. The growth parameters obtained for the yellow clam *Mesodesma mactroides* from ELEFAN were slightly (though not significantly) higher than those obtained from growth bands (Defeo *et al.* 1992a). The periodicity in the formation of the main rings in this clam was in agreement with results obtained using modal progression analysis (Bhattacharya's method) (Defeo *et al.* 1992a).

Munday & Keegan (1992) concluded that results from growth bands compared favourably to those from modal progression analysis (Bhattacharya's approach). Despite their conclusion, merging of juvenile cohorts and slow growth in adults actually obscured some year classes and it was doubtful whether ages could have been assigned to cohorts independently of the growth band results. Due to the paucity of studies that have used more than one method to determine growth rates, it was difficult to ascertain whether certain methods had a tendency to over/underestimate growth parameters. Even independent research on the same species but using different methods is seldom comparable because of site or stock specific variation.

Despite the few inconsistencies in the growth parameters derived from the different methods, all three methods showed faster growth, higher Φ', L_∞ and K values at the exposed shores than at the sheltered shores. Within the exposed sites there was even agreement between mark-recapture and SLCA in the ranking of sites according to growth parameters.

General results and possible factors causing them

Despite variations in growth rates obtained using three different methods, the overall results showed higher growth rates, at exposed shores than sheltered shores and, in smaller, younger mussels than larger, older mussels. Considerable variation in growth rates between individuals of the same size at a site occurred, a finding which has been observed by Seed (1968) and Griffiths (1981). In this study variation in growth rates between individuals was not attributed to the sex of the individual. References to sexual differences in growth rates in mussels could not be found, either because sex does not have an effect on growth or because this effect was not considered. Conch shells are one of the few shellfish for which the effect of sex on growth has been recorded and here females grew faster than males (Reed 1993). Gage (1992) assigned the variation in growth rates of individual urchins under the same conditions to genetic differences. Although faster growth rate has been observed in more heterozygous mussels, this accounts for <16% of individual variation in growth rate (Koehn & Gaffney 1984, Hawkins *et. al.* 1986). The genetic homogeneity of *Perna perna* over 1700 km of the Southern African coast would suggest that genetics is not an important consideration for growth in *Perna perna* (Grant *et al.* 1992). However, small-scale heterogeneity may occur due to chance events which are common in invertebrates with pelagic larvae (Johnson & Black 1984). Mallet *et al.* (1987a) showed that although both stock and site were important for shell growth in the blue mussel *Mytilus edulis*, site accounted for most of the variation in tissue growth. Gage (1992) cautioned that this variation should not be ignored when assessing differences in population size or age structure thought to be related to environmental variations.

A higher mean growth rate (1.32 mm.mnth^{-1}) was observed for mussels at the exposed shores than at the sheltered shores (0.46 mm.mnth^{-1}). Using modal progression analysis (MULTIFAN) Leeb (1995) found average growth for the Mediterranean mussel *Mytilus galloprovincialis* to be higher (though not statistically) at the exposed low shore (0.82 mm.mnth^{-1}) than at the sheltered low shore (0.61 mm.mnth^{-1}).

There was a positive correlation between wave force measured by dynamometers (chapter 1) and the overall growth performance (Φ'). Raubenheimer & Cook (1990) suggested that in areas of strong wave action the increased calcium ions caused by abrasion of calcium-rich organisms could increase growth rates. These calcium ions are necessary for the shell growth of marine invertebrates (Wilbur & Jodrey 1952). On heavily exposed shores, growth was more likely to result in an increase in shell thickness than length (Seed 1968, Raubenheimer & Cook 1990). A probable result of increased wave action is increased water flow over the gills, a factor which has been shown to increase growth rates in mussels (van Erkom Schurink & Griffiths 1993). An increase in wave exposure has also been shown to have negative effects on growth rates in *Mytilus edulis* (Jørgensen 1976).

Wave action and tidal currents maintain detritus, faeces and plankton in suspension and could make more food available in areas of greater wave action (Griffiths 1980a & 1980b, Bayne 1993). Wave action also assists in breaking up macroalgae which can be digested by *Perna perna* (Simon 1997). The individual growth in bivalve populations may be phytoplankton-limited due to their tremendous filtration capacity (Fréchette & Bourget 1985a & 1985b, Bricelj *et. al.* 1984). In such instances the benefits of homogenisation and resuspension of the seston due to rough seas becomes apparent (Fréchette & Grant 1991). Differential digestion rates of various carbohydrates by *Perna perna* suggest that this species relies more on plankton than detritus (Simon 1997). On ORI reef, near Durban in Natal (South Africa), *Perna perna* fed predominantly on detrital material from macroalgae, perhaps due to its abundance (Berry & Schleyer 1983). The components of the seston that are utilised by bivalves depends primarily on what the species can digest and the quantities available (Asmus & Asmus 1993). The black mussel *Choromytilus meridionalis* utilises small quantities of phytoplankton as well as macroalgae (Griffiths 1980a), whereas the sea scallop *Placopecten magellanicus* digests phytoplankton, macroalgae, detritus and resuspended sediments (Grant & Cranford 1991). Changes in suspended food may occur seasonally, tidally or randomly (Fielding & Davis 1989) and due to their plasticity mussels can adapt morphologically and physiologically. Some adaptations, for instance altering the size of gills may take months, whereas others, like changing the clearance râte take a matter of minutes (Bayne 1993). The absorption efficiency and ultimately the amount of energy available for growth are dependent on the proportion of inorganic matter to organic matter in the ingested food (Bayne & Worrall 1980). Even when there is a large amount of organic material in the water column, ingestion and absorption rates can be limited by particle size, concentration and quality, water flow and assimilation efficiency (Newell *et al* 1989, Asmus & Asmus 1993, Fréchette *et al.* 1993, Grant *et al.* 1993).

Possible adverse effects of exposure to air on growth rates (Seed 1968, van Erkom Schurink & Griffiths 1993) could have been moderated at the exposed sites in this study due to an increase in splash (Underwood 1981). Increased wave action effectively results in an elevation of the littoral (Jones &

Demetropoulos 1968). Splash and greater wave action, which increase immersion time, would effectively increase the time available for feeding. Food supply appears to be the single most important factor in determining growth rate (Seed 1969b). If food is limited, the number of individuals competing for this resource will determine the food supply which in turn will affect the growth rate, and ultimately the size structure of the population.

In this study there was a negative correlation between the phi prime values (index of overall growth performance) and the density of adults (>15 mm). This may indicate one of the following scenarios; the increase in the densities of mussels resulted in a decrease in growth (Kautsky 1982, Peterson & Beal 1989, Defeo *et al.* 1992b, van Erkom Schurink & Griffiths 1993); the effect of decreased growth resulted in smaller mussels which could reach higher packing densities (Seed 1968, Griffiths 1981) or both density and growth reacted independently to other influences, for example, wave action, food availability and recruitment (Jones & Demetropoulos 1968, Berry 1978, Griffiths 1980a, van Erkom Schurink & Griffiths 1993, Phillips 1994). The results supported the last scenario as despite huge differences in wave force and Φ' values at Mgwalana and Fish River, densities were similar (Figure 3.16 & 3.18). This implied that although densities were greater on exposed shores, growth was a response to wave action and was independent of density. Kautsky (1982) noted that, due to competition for food and space, large blue mussels *Mytilus edulis* suppressed the growth of small mussels. Predation could maintain a population at lower densities, creating more space for growth (Menge 1976). Higher packing densities occurred on sheltered than exposed shores (chapter 2). Underwood (1981), noted greater densities of sessile organisms at the sheltered than at the exposed shore type. For further discussion on factors affecting density refer to chapter 2.

Growth rate of mussels (<30 mm) has been shown to be negatively affected by some species of parasites, for example the trematode, *Proctoeces* which infects *Perna perna* (Calvo-Ugarteburu & McQuaid in press). Two of the methods in this investigation did not examine mussels <25 mm and therefore the presence of *Proctoeces* was not considered.

All three methods showed both smaller and younger mussels to have faster growth rates than larger and older ones, a result frequently encountered in other studies (Griffiths & King 1979a, Kautsky 1982, Kennish *et al.* 1994, Sukhotin & Maximovich 1994). A relatively slower flow rate occurs in larger mussels, which results in decreased food uptake and may determine the maximum size a species or individual attains (Jørgensen 1976). The assimilation efficiency of mussels has been shown to be only slightly dependent (Widdows 1978) or independent of size (Griffiths & King 1979a).

The variation in individual growth rates can result in mussels from the same age class falling into different length classes (Griffiths 1981). When age at length or length at age information is obtained from the Von Bertalanffy growth curve the individual variability should be borne in mind. The growth curve should be used as a guideline for ascertaining the most probable age class to which a length belongs or vice versa (Kaufmann 1981). According to Sainsbury (1980) this is particularly important when an age-length relationship is derived from growth increment data rather than age data. This, in addition to the fact that each Von Bertalanffy curve is relevant to the limit of length data from which it was constructed, possibly prompted Thiesen (1973) to state that extrapolations should not be made and estimated parameters should not be used to compare populations.

Despite Thiesen's warning studies have compared growth rates of populations using growth parameter estimates (Leeb 1995, Tomalin 1995). Growth coefficient values (K) were higher on exposed shores than sheltered shores a finding in agreement with that of Leeb (1995) who found slightly higher K values for the Mediterranean mussel *Mytilus galloprovincialis* on the exposed low shore than on the sheltered low shore. However, this is where the similarities ended. Φ' values for *Mytilus galloprovincialis* (not given by Leeb, but calculated using her L_∞ and K values) were lower at the exposed shore than at the sheltered shore. Maximum lengths obtained from the length frequency distributions were higher at the exposed shore than at the sheltered shore for both the current study (chapter 2) and that of Leeb (1995). Jones and Demetropoulos (1968) found that the average length of blue mussels *Mytilus edulis* increased as exposure increased. As predation on mussels has been shown to decrease with an increase in wave exposure, the maximum size attained by mussels on sheltered shores may be constrained or regulated by predators (Menge 1976). In striking contrast to these findings, some authors have noted that maximum sizes were negatively correlated with wave action (Jørgensen 1976). On exposed shores larger individuals may be dislodged by wave action and never attain their potential maximum length (Griffiths 1981).

The growth rates of *Perna perna* obtained in this study are compared with those of other studies (Table 3.30). The lengths attained at one year of age at the three sheltered sites, Mgwalana, Rufanes and Riet River were considerably lower than those attained in all the other studies. These lengths were the most comparable to those obtained in a study at Dwesa (Lasiak & Dye 1989). Mussels from Diaz Cross, Kwaai Hoek and Fish River attained lengths at a year of age that were quite similar to those recorded in previous studies (Table 3.30).

In comparison to *Perna perna's* high growth rate (Table 3.30), the black mussel *Choromytilus meridionalis* reached an average of only 20 mm in a year in False Bay (Griffiths 1981). When four different species were grown under submerged culture conditions at Algoa Bay the average lengths attained in a year were as follows; *Mytilus galloprovincialis* - 70 mm, *Perna perna* - 60 mm, *Choromytilus meridionalis* - 55 mm and *Aulacomya ater* - 35 mm (van Erkom Shurink & Griffiths 1993). *Perna perna* favours warmer waters and higher growth rates occur in the warmer Algoa Bay than cooler Saldanha Bay. In contrast, the black mussel *Choromytilus meridionalis* and the ribbed mussel *Aulacomya ater* had higher growth rates in Saldanha Bay than Algoa Bay (van Erkom Schurink & Griffiths 1993). Although temperature does affect the growth rate of *Perna perna*, it's effect within naturally occurring populations is perhaps not as exaggerated as suggested by van Erkom Schurink and Griffiths (1993), as growth rate tends to fluctuate considerably even at a local level (Table 3.30). A general growth curve for mussels (*Perna perna* and *Choromytilus meridionalis*) along the South African south coast showed that a one year old mussel attained a length of approximately 32 mm (Phillips 1994). An important outcome that emerged from all these studies was that growth rates differed considerably even on a local scale and were strongly influenced by local conditions (Seed 1969b, Arnold *et al.* 1991).

Mussels on sheltered shores took twice as long as those on exposed shores to reach L_∞. Increased life expectancy where growth was slower, has also been reported in the blue mussel *Mytilus edulis* (Jørgensen 1976).

Table 3.30 A comparison of growth rates for *Perna perna* obtained in this and other studies in South Africa. All studies used wild populations, with the exception of van Erkom Schurink & Griffiths (1993) who used mussels from suspended culture. This table was modified from Tomalin (1995).

Author	**Location**	**Length at 1 year (mm)**	**Method**
Van Erkom Schurink & Griffiths (1993)*	Port Elizabeth	60	Increments
	Saldanha Bay	45-60	Increments
Crawford & Bower (1983)	Storms River	40	Eye
Lasiak & Dye (1989)	Dwesa	30-40	Eye
Berry (1978)	Peace Cottage	65	?
	Pennington	50	?
Culverwell (1992)	South Ledges	52	Cohort separation
	Cape Vidal	46	Cohort separation
	Black Rock	51	Cohort separation
	Island Rock	49	Cohort separation
Tomalin (1995)	Peace Cottage	57.5	ELEFAN I
	West Street Peer	57.7	ELEFAN I
	Umdoni	46.1	ELEFAN I
	Pennington	52.1	ELEFAN I
This study	Diaz Cross	42.3 & 65.9	Mark-recapture & SLCA
	Kwaai Hoek	43.2 & 59.2	Mark-recapture & SLCA
	Fish River	35.7 & 52.3	Mark-recapture & SLCA
	Mgwalana	17.8 & 20.4	Mark-recapture & SLCA
	Rufanes	16.2 & 29.7	Mark-recapture & SLCA
	Riet River	18.2 & 23.2	Mark-recapture & SLCA
	Dz, Kw, Fs (pooled)	41.62	Growth band
	Mg, Ru, Ri (pooled)	24.4	Growth band

* This study was undertaken on subtidal cultured mussels.

SUMMARY

- Growth rates were faster for mussels at the exposed than the sheltered shores.
- Growth estimates varied between methods.
- The highest estimates of length at one year were made using the SLCA method, followed by growth band analysis, and the lowest estimates were from the mark-recapture method.
- Mussels on exposed shores reached L_∞ faster than on sheltered shores.
- Longevity of mussels was higher on sheltered shores than on exposed shores.
- Wave force had a significant positive correlation with Φ'.
- Adult density had a significant negative correlation with Φ', but this was simply a correlation.

CHAPTER 4

MORTALITY RATES OF *PERNA PERNA* ON WAVE EXPOSED AND WAVE SHELTERED SHORES

1. INTRODUCTION

It has been suggested that mortality is at least as important as growth in the overall dynamics of mussel production (Dickie *et al.* 1984). Greater emphasis, however, is usually placed on growth rates than mortality rates as precise estimates of mortality are difficult to obtain. As a result, mortality is assumed to be consistent, irrespective of size, age, and fishing pressure. This could have serious ramifications as the utilisation of a resource, particularly when size-selective, would change the size and age structure of breeding stocks and affect the biomass yield (Dickie *et al.* 1984). This occurs when humans select larger mussels (Crawford & Bower 1983, Lasiak & Dye 1989). Mortality has also been shown to vary with size, for example, in the Danish Wadden Sea mortality of *Mytilus edulis* decreases as size increases (Theisen 1968 in Theisen 1973) and if ignored age dependent variation could lead to gross miscalculations of mortality.

Mortality is regulated by biotic and abiotic factors, including predation, disturbance, competition, settlement and recruitment (Dayton 1971, Berry 1978, Griffiths & Seiderer 1980, Griffiths & Hockey 1987). Growth rate and recruitment success will affect these interactions by altering the population size structure. The most important factors that can limit the survival of settlers and recruits are suitable environmental conditions, adequate food, ingestion by filter feeders, predation, grazing by herbivores and suitable settling substrata (Seed 1969b, Bayne 1976, Andre *et al.* 1993, Branch & Moreno 1994). The extent to which mortality influences a population is highly variable and depends on the interaction of the above-mentioned factors. At times the influence of a particular factor may prevail over the influence of all others. On Malgas Island, off the west coast of South Africa, for example, intense predation by rock lobsters prevents *Choromytilus meridionalis* from establishing itself despite suitable physical environmental conditions (Barkai & Branch 1989). Regulation by predators has been well documented (Lubchenco & Menge 1978, Barkai & Branch 1989), but is not always the dominant cause of mortality. Storms and wave impact have been shown to result in extensive mortality, particularly in dense mussel beds (Harger 1970, Harger & Landenberger 1971). Some populations are capable of withstanding considerable mortality pressure by having fast growth rates and high recruitment, for example, *Mytilus edulis*, where a 60% mortality rate had no effect on the percentage of mussel cover (Petraitis 1991).

The ability to maintain spatial dominance is the main reason that mussel beds persist. Intraspecific competition, although a cause of mortality, is less important in terms of overall bed survival than interspecific competition (Griffiths 1981, Bertness & Grosholz 1985). Along the Western Cape, the Mediterranean mussel, *Mytilus galloprovincialis* has dominated beds of the ribbed mussel, *Aulacomya ater*, by having faster growth and lower mortality rates and it seems also capable of out competing the brown mussel *Perna perna* (Griffiths *et al.* 1992, Van Erkom Schurink & Griffiths 1993, Phillips 1994).

Mortality can be determined firstly by counting the number of dead organisms, an unsuitable technique in the intertidal, as wave action rapidly removes dead shells; secondly by using length frequency data, which becomes difficult as older cohorts merge and thirdly by marking mussels (Seed 1969b, Krebs 1989). The last two techniques were used to determine mortality in *Perna perna* in this study.

2. MATERIALS AND METHODS

Mussels sampled for growth analysis over the entire fifteen month period were used to determine annual total mortality rates (Z). The rate of decrease of relative abundance with age is a reflection of the annual rate of mortality (Munro 1984). A Von Bertalanffy growth curve of length at age was constructed from growth at length data (see chapter 3). Overall size distributions at Diaz Cross, Kwaai Hoek, Fish River, Mgwalana, Rufanes and Riet River were used to generate catch curves for each site (see Pauly 1990). This was undertaken using FiSAT version 1.10 (Fisheries Stock Assessment Tools) (Gayanilo *et al.* 1994) and required the input of L_∞ and K. These growth parameters were obtained from analyses performed on length frequency data (Chapter 3). An estimate of mortality (Z) was obtained from the gradient of the catch curve after excluding the first size class, as it appeared to be under sampled (see Pauly 1990, Pauly *et al.* 1995) (Equation 4.1).

$\mathrm{Log}_e (N_i/\Delta t_i) = a + bt_i$ **Equation 4.1**

N = number of organisms in length class i

t = age corresponding to mid-length of each length class

Δt = the time needed to grow through the length class

b = slope = -Z

a = estimated through regression analysis

Mortality of the entire size range *i.e.* total mortality, mortality of juveniles (0.6 month to 6 months) and mortality of adults (12 months to mortality) was calculated for mussels at each site. Three t-tests were undertaken to determine whether exposure had an effect on total, juvenile and adult mortalities. Total mortality (Z) = natural mortality (M) + fishing mortality (C). Using total mortality, the percentage survival rate per annum was calculated for each site (Equation 4.2). The percentage survival rates from 18 days to 6 months and from 12 months to mortality were also calculated for each site. Estimates of longevity were obtained for each site (Equation 4.3). Although mussel collecting does occur at some of the sites under investigation, it is still very light (pers. obs.) and an estimate of longevity was obtained by letting total mortality (Z) equal natural mortality (M). Lifespan is the age at which 99% of the cohort has died (Alagaraja 1984 in Siegel 1991).

$$\text{survival rate (\%)} = e^{-Z} \times 100 \qquad \textbf{Equation 4.2}$$

$$Tm = -\ln(0.01)/M_{\%} \qquad \textbf{Equation 4.3}$$

where Tm = longevity and M = natural mortality.

To determine whether a relationship existed between wave force and mortality, a linear correlation was undertaken using force data from the dynamometers (chapter 1) and total annual mortality rates. A regression was undertaken to establish whether the juvenile survival rate (0.6 to 6 mnths) was dependent on adult density (>15 mm). A correlation of the juvenile survival rate (%) at each site against the mean algal cover (%) at each site was undertaken to determine whether a relationship existed between algal cover and the survival rate. A linear correlation was also undertaken between the overall growth index (phi prime - Φ') (from Chapter 3) at each site and total mortality (Z) at each site.

Attempts to determine survival by marking mussels were unsuccessful. Some mortality, which cannot assumed to be equal on exposed and sheltered shores, occurred when file-marking mussels. A variety of paints, dyes and waxes were used to mark mussels at all sites. However, most substances required either a dry surface on which to adhere to or needed several minutes drying time, conditions which could not easily be met, particularly on the exposed low shore. Whole dead mussels found in the six weekly samples were examined for holes to determine whether any predation from whelks occurred. Shells are rapidly washed away, presumably at varying rates at the different sites, preventing any further comparisons from being made.

3. RESULTS

The overall length frequencies for the entire sampling period showed that the high juvenile densities at Diaz Cross and Kwaai Hoek were not reflected in the adult densities at these two sites, indicating mortality of recruits rather than secondary settlement onto mussels was occurring. Adult densities at Rufanes were high ($5495.m^{-2}$, chapter 2), possibly as a result of high recruitment and/or low mortality. Figure 4.1 illustrates the overall size distributions and Figure 4.2 shows the corresponding abundance ($\ln (N_t / t_2 - t_1)$) at age. The catch curves fitted better at Fish River, Rufanes, Mgwalana and Riet River (mean $r^2 = 94.5$ %) than Diaz Cross and Kwaai Hoek (mean $r^2 = 85.0$ %) (Table 4.1) (Figure 4.2).

Total, juvenile (0.6 to 6 months) and adult (12 months +) mortality rates were significantly higher at the exposed shores than at the sheltered shores (Figure 4.3, $p<0.05$, Table 4.2). Kwaai Hoek had the highest total and adult mortality rates and Mgwalana had the lowest total, juvenile and adult mortality rates (Figure 4.3 & Table 4.1). The greatest differences in mortality rates between the exposed and sheltered sites occurred in the juveniles (Figure 4.3). The sites ranked in the same order for the total, juvenile and adult mortality, with the exception of juvenile mortality at Diaz Cross or Kwaai Hoek which ranked higher or lower respectively (Figure 4.3). Juvenile mortality was 2-3 times higher than adult mortality at all sites, but the difference was particularly high at Diaz Cross, Kwaai Hoek and Fish River. A considerably lower mean total survival rate (16.99 % p.a.) was obtained at the exposed shores than at the sheltered shores (49.94 % p.a.) (Table 4.3).

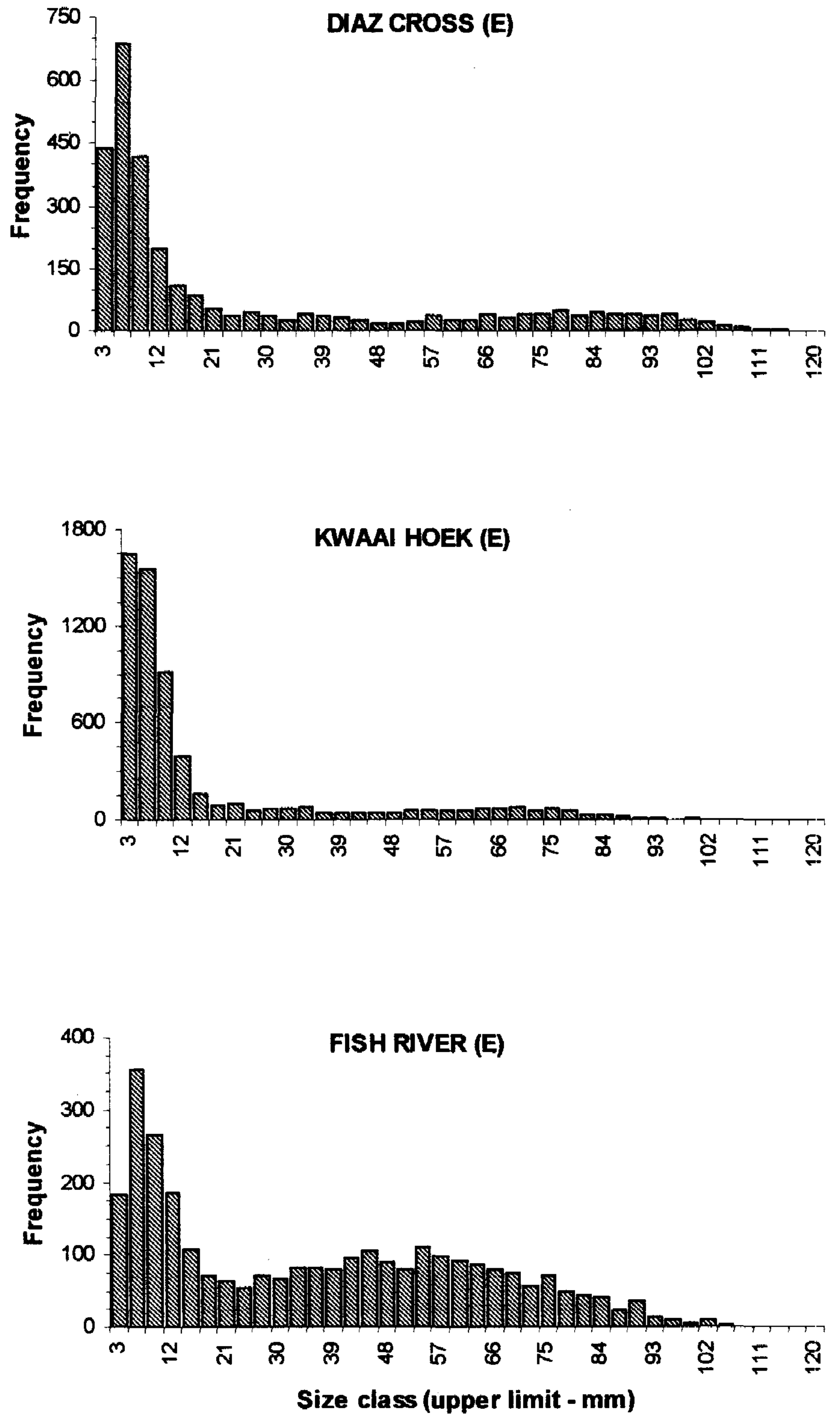


Figure 4.1 Total length frequency distributions for the entire 15 month sampling period at each site.

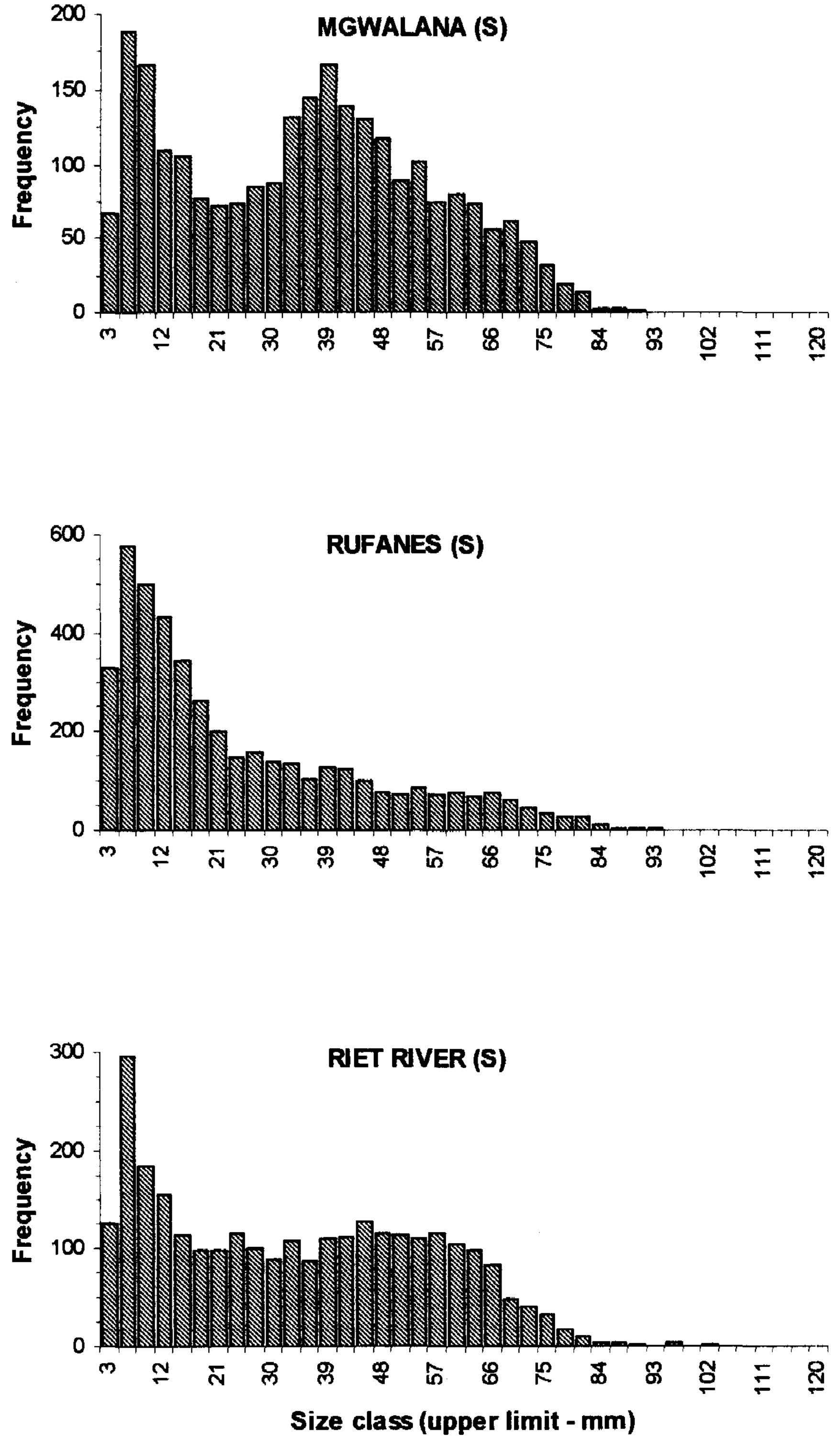


Figure 4.1 cont.

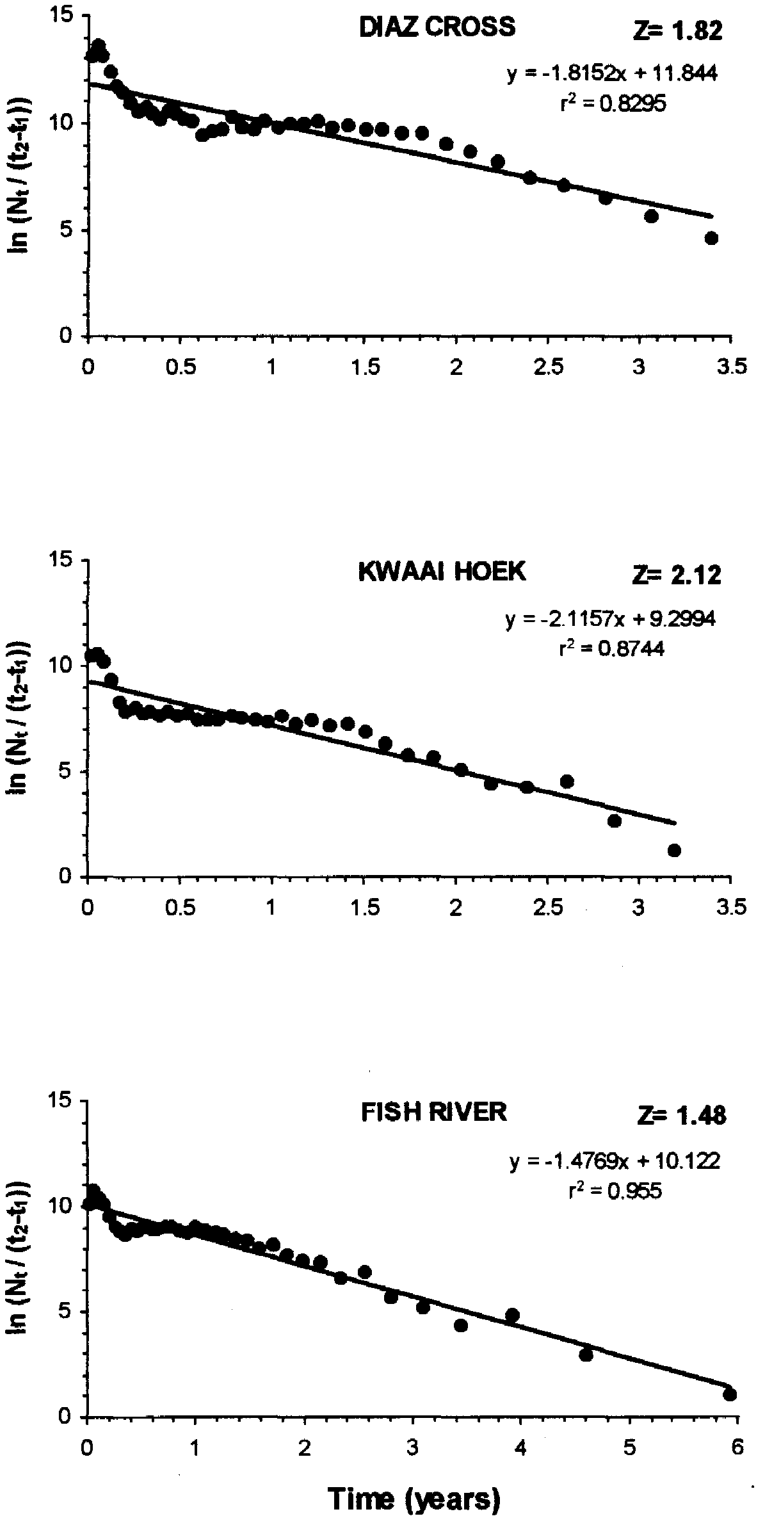


Figure 4.2 Catch curves for each site generated from length frequency data for the entire 15 month sampling period. L_∞ and K were obtained from Shepherd's Length Composition Analysis (chapter 3).

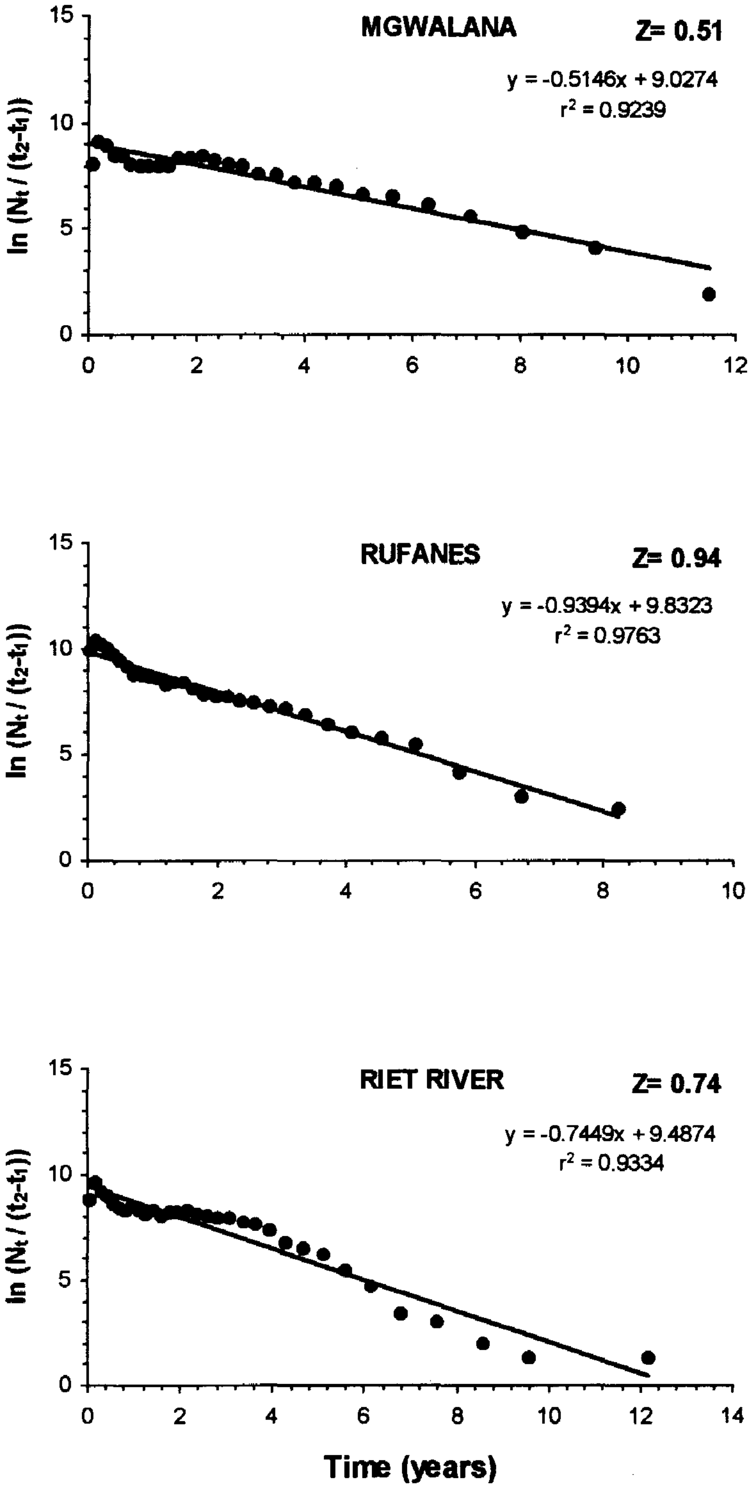


Figure 4.2 cont.

Table 4.1 Annual total mortality (all age classes), juvenile mortality (0.6 to 6 months) and adult mortality rates (12 months +), calculated from total length frequency data obtained over 15 months. The correlation coefficient for each respective catch curve for each site is included (Equation 4.1).

Site	Total mortality (Z) per year	r^2	Juvenile mortality (Z) per year	r^2	Adult mortality (Z) per year	r^2
Dz	1.82	0.91	6.39	0.87	2.31	0.97
Kw	2.12	0.94	6.15	0.83	2.72	0.98
Fs	1.48	0.98	4.04	0.85	1.67	0.99
Mg	0.51	0.96	2.14	0.97	0.55	0.97
Ru	0.94	0.94	2.52	1.00	0.89	0.99
Ri	0.74	0.97	2.52	0.99	0.79	0.97

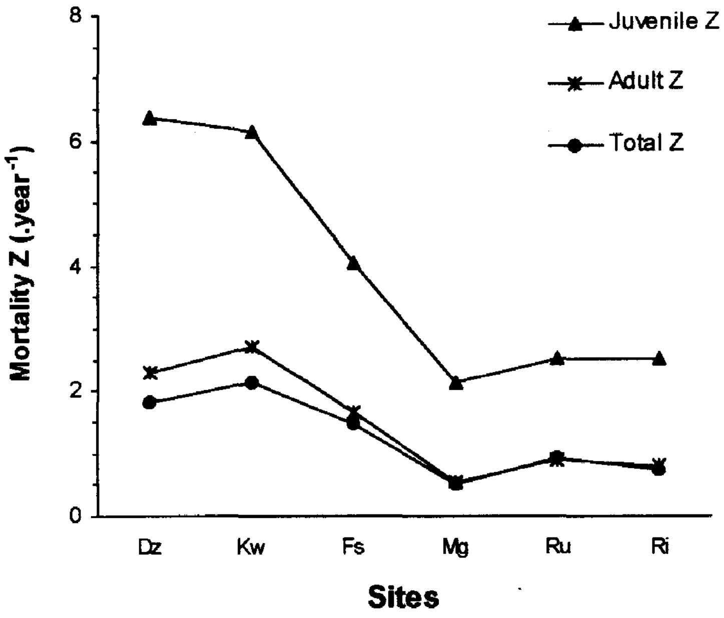


Figure 4.3 Juvenile (0.6 to 6 months), adult (12 months to death) and total (all age classes) mortality rates calculated from length frequency data for the entire 15 months, using L_∞ and K values generated from Shepherd's Length Composition Analysis (SLCA - chapter 3).

Table 4.2 Three t-tests comparing juvenile, adult and total annual mortality rates at exposed and sheltered shores.

	N	t-statistic	Significance
Juvenile Z	3	4.1379	0.0144
Adult Z	3	4.6309	0.0098
Total Z	3	4.8338	0.0084

Table 4.3 Annual survival and mortality rates of the total population (all age classes). Survival and mortality rates from 18 days to 6 months and from 12 months to mortality.

Sites	Survival (%) Total	Mortality (%) Total	Survival (%) Juvenile	Mortality (%) Juvenile	Survival (%) Adult	Mortality (%) Adult
Dz	16.20	83.80	0.17	99.83	9.93	90.07
Kw	12.00	88.00	0.21	99.79	6.59	93.41
Fs	22.76	77.24	1.76	98.24	18.82	81.18
Mg	60.05	39.95	11.77	88.23	57.69	42.31
Ru	39.06	60.94	8.05	91.95	41.07	58.93
Ri	47.71	52.29	8.05	91.95	45.38	56.62

Mean longevity was higher on the sheltered shores (6.7 years) than the exposed shores (2.6 years) (Table 4.4). Mussels at Diaz Cross and Kwaai Hoek had the shortest lifespan (± 2 years), followed by Fish River (± 3 years), Rufanes (± 5 years), Riet River (± 6 years) and Mgwalana (± 9 years). These values are approximate as individual mussels often have different growth and mortality rates from the mean for the population and total mortality, not natural mortality was utilised.

Table 4.4 Longevity calculated at six sites using Equation 4.3. Note that the natural mortality (M) inserted into the equation has been replaced with total mortality (Z) (Z= natural mortality + fishing mortality) as collecting pressure at these sites was low.

Sites	Exposure	Longevity (years)
Dz	E	2.53
Kw	E	2.17
Fs	E	3.11
Mg	S	9.03
Ru	S	4.90
Ri	S	6.22

No significant correlation existed between total mortality (Z) and wave force (N) ($p>0.05$, Figure 4.4). The regression of juvenile survival rate (%) against adult density showed a significant exponential regression (r^2 = 74.37%, $p<0.05$, Figure 4.5). The was a significant negative correlation (r^2 = -0.92, $p<0.05$) between the percentage cover of algae and juvenile survival rate (Figure 4.6). There was a significant linear relationship between the estimates of the growth index (Φ') and corresponding estimates of total mortality (Z) ($p<0.05$, r^2 = 0.92) (Figure 4.7).

Of 96 whole dead mussel shells ranging in size from 5 to 87 mm, drilled holes were found in 26 % (*i.e.* 25) of them. Data were sparse and fewer dead shells were found at Diaz Cross and Kwaai Hoek than the other sites (presumably due to removal by wave action) making any further comparisons unreliable.

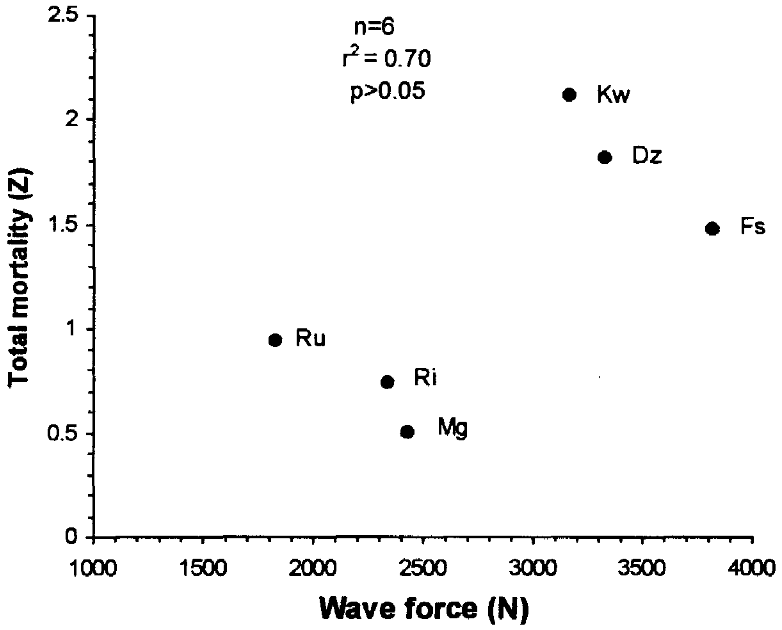


Figure 4.4 Correlation of total mortality (all age classes) against wave force (N).

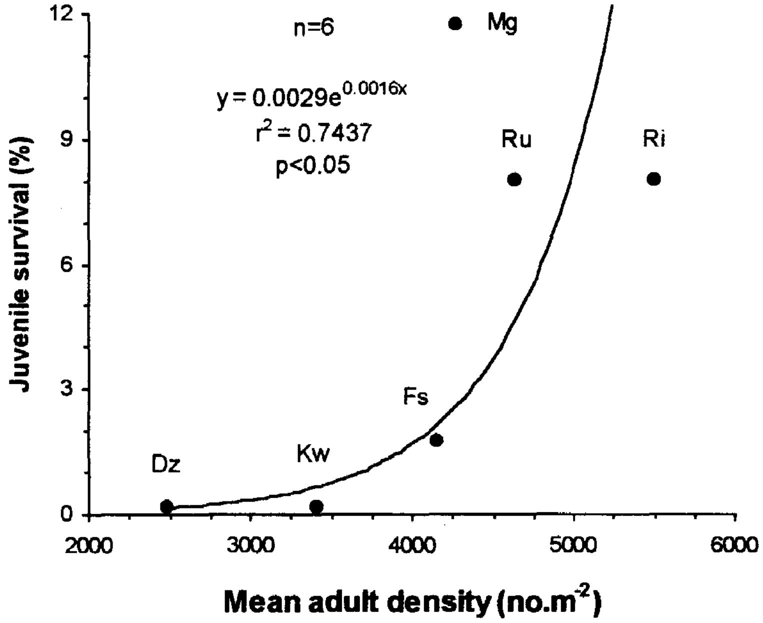


Figure 4.5 An exponential regression of the mean adult density (for 11 sampling months) at each site against the juvenile survival rate (%) at each site.

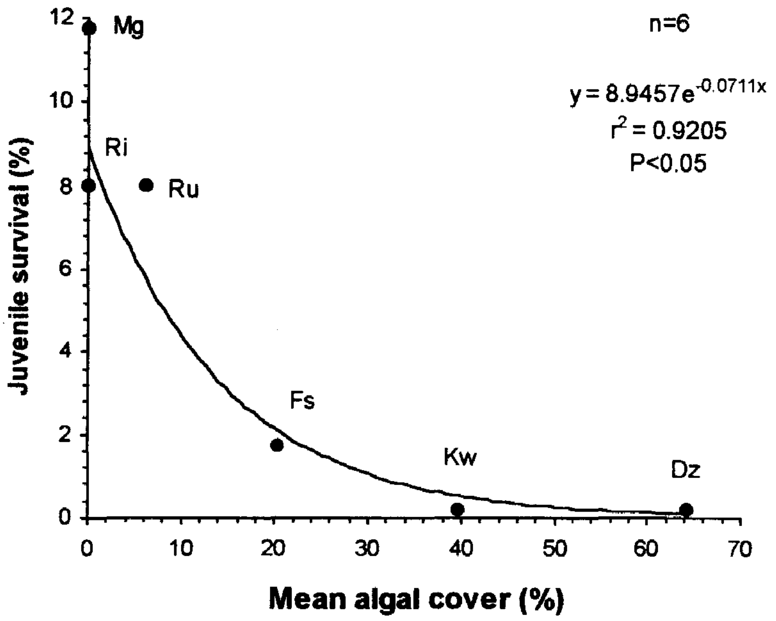


Figure 4.6 Correlation of the mean algal cover (%) on 1m^2 of mussel bed against juvenile survival rate (%) at each site.

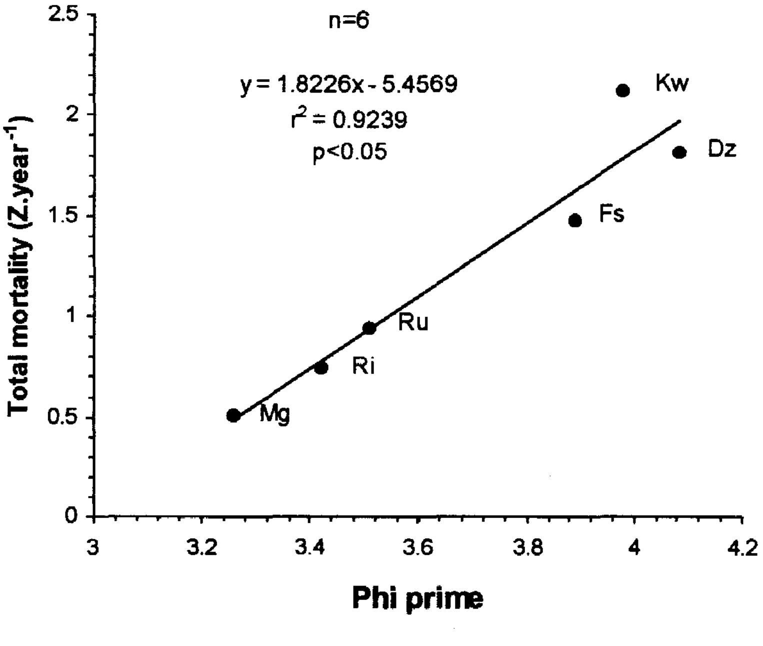


Figure 4.7 Linear correlation between total mortality (all age classes) and the growth index, phi prime from Shepherd's Length Composition Analysis (SLCA - chapter 3).

4. DISCUSSION

The most widely used technique to calculate mortality is to use catch curves. These may be constructed from age data (*i.e.* directly from bands or rings) or from length-converted catch curves, which may or may not take seasonality of growth into account. Length-converted catch curves that ignore seasonality, as in this study, have been shown to overestimate total mortality (Z) (Pauly *et. al.* 1995), particularly in short-lived animals with strong seasonal growth (Pauly 1990). Total mortality estimates are dependent on the accuracy of the method used to obtain L_∞ and K. In this study, estimates of Z ranged from 0.51 to 2.12, and compared favourably to the estimates (0.42 to 3.70) obtained for *Perna perna* on the KwaZulu-Natal coast (South Africa) (Tomalin 1995). A factor which improved the accuracy of estimates of total mortality was that size-dependent selection did not occur during sampling (*i.e.* all mussels ⩾ 1mm were included) (see Isaac 1990).

Total (juvenile + adult), juvenile and adult mortalities were significantly higher on the exposed than the sheltered shores (Figure 4.3 & Table 4.2). Despite this distinct separation, there was no significant correlation between mortality and wave force. When sites with extremely different wave action were examined, for example Diaz Cross and Mgwalana, the trend of higher mortality at higher wave exposures was more obvious.

Juvenile mortality can be important in influencing mussel population abundance (Gosselin & Qian 1997). Mortality between 18 days and 6 months of age was high, with a mean mortality rate of 98.29% at the exposed sites and 90.71% at the sheltered sites (Table 4.2). In a review of juvenile mortality in benthic marine invertebrates, the pooled survivorship data of 32 species showed an exponential decrease in the total percentage of survivors from the first days until by four months virtually all cohorts were reduced to < 20% of their initial numbers (Gosselin & Qian 1997). Mortality of juvenile marine invertebrates may exceed 98.6% (Bayne 1976, Thorson 1966 in Gosselin & Qian 1997). After the first year, the mean annual mortality of *Mytilus edulis* in Morecambe Bay (Wales) was 96.6% (Dare 1976). In the present study on *Perna perna*, juvenile mortality rates would have been even higher had settlers <1 mm been included, as juvenile mortalities have been shown to exceed 30% on the first day (Gosselin & Qian 1997).

Petersen (1984) suggested that the holes and crevices in both algae and the mussel bed protect juveniles from wave action to some extent. This implies that wave action can be detrimental to juveniles, and may be the reason for higher juvenile mortality on the wave exposed shores. Higher juvenile survival rate was also evident at sites with higher adult densities, possibly due to increased refuge (Figure 4.5). Once juveniles are amongst byssal threads, mortality can still occur as the small mussels are unable to successfully compete with the adults (Seed 1969b). The low juvenile mortality rate at Fish River compared to the other two exposed sites (Figure 4.3), could be a result of increased protection of recruits due to the multi-layering of mussels noted at this site (see Alvarado & Castilla 1996). The strong negative correlation between algal cover and juvenile survival rate (Figure 4.6), indicated that algae may have a detrimental effect on recruit survival. Algal cover and exposure are confounded (*i.e.* algal cover varies with exposure) and their effects cannot be separated in this study. Mortality could not be calculated separately for juveniles on the mussel bed and on algae, making it impossible to establish whether the recruits on these substrata had differing mortality rates. As the species of algae at Rufanes (*Gelidium*) differed from that found at the three exposed sites (coralline), it was difficult to ascertain whether the higher juvenile survival rate at Rufanes was a reflection of decreased wave exposure, substratum or some other factor. *Gelidium* has a very different structure from foliose coralline algae (Branch *et al.* 1994) and this combined with decreased wave impact may have increased chances of recruit survival. Theisen (1973) has proposed that spat settling on algae may loosen as they grow. This provides support for the theory that recruits on algae grow until they are swept off by wave action (see Chapter 2).

Very high settlement/recruitment is uncommon for *Perna perna* in South Africa (Berry 1978), but when it does occur the adult mussel beds can be negatively affected. Mass settlement of juveniles can choke underlying mussels causing them to loosen and be removed by wave action as recorded for *Mytilus edulis* in Filey bay by Seed (1969b).

Mean adult mortality (12 mnths to mortality) was higher for exposed shore mussels (88.22%.) than sheltered shore mussels (52.62%) (Figure 4.3 & Table 4.2). Griffiths (1981) suggested that groups of larger *Choromytilus meridionalis* individuals may be dislodged by wave action. Drag, according to Jones and Demetropoulos (1968) probably represents one of the greatest hazards to life on shore. Fouling by algae may increase the drag and therefore increase the chance of mussels being removed by wave action (Dayton 1973, Witman & Suchanek 1984). As the maximum mussel lengths at the exposed sites were significantly higher than at the sheltered sites (Figure 2.10), dislodgement by wave action may be responsible for the higher adult mortality rate at the exposed sites, particularly at Diaz Cross and Kwaai

Hoek, where mussels had a high cover of foliose coralline algae. According to Griffiths (1981) density may then be expected to decline with increasing shell length, as was indeed the case in this study (Figure 2.12).

The mean total (juvenile + adult) mortality rate of mussels was higher on the exposed shore (83.01% p.a.) than the sheltered shore (51.06% p.a.) (Figure 4.3 & Table 4.2). Phillips (1994), by following the density of a cohort over time, showed that for *Perna perna* higher up the shore on the east Cape coast, only 17-29% of the cohort survived to maturity (*i.e.* 71-83% mortality). An annual mortality rate of 74% was calculated for *Perna picta* on the Moroccan coast (Shafee 1992). Considerably higher annual mortality rates (95-100%) than those in the present study have been observed for *Mytilus edulis* at Morecambe Bay (Wales), where few mussels survive to their third year (Dare 1976). In contrast, mortality rates of cultured *Mytilus edulis* in Scottish sea lochs were as low as 6 to 7% a year (Stirling & Okumus 1994).

On both shore types, juvenile mortality was higher than adult mortality (Figure 4.3, Table 4.1). This has also been noted for *Mytilus edulis* cultured in the White sea, where maximum mortality occurred during the first year of settlement (Sukhotin & Kulakowski 1992). This decrease in mortality rate as size increases is known as Lee's phenomenon (Lee 1912, in Theisen 1973). Although the mortality rate can dramatically increase in older mussels (Ceccherelli & Rossi 1984, Mallet *et.al.* 1987b), this was not evident in *Perna perna* in this study.

The significant positive correlation between the estimate of mortality and the growth index (Figure 4.7) has also been noted for *Perna perna* in KwaZulu-Natal (Tomalin 1995). This relationship may be real or an artefact of the estimation method (Tomalin 1995). Mortality rates proportional to growth rates were documented for *Choromytilus meridionalis* occurring off the south west coast of South Africa (Griffiths & Hockey 1987). This pattern is not reflected among species. A study by Van Erkom Schurink and Griffiths (1993) showed that *Mytilus galloprovincialis* had both the highest growth and survival rates, followed by *Perna perna*, *Choromytilus meridionalis* and *Aulacomya ater*.

Growth may offset the effects of mortality, as small mussels (*Mytilus edulis*) can double their length in a year, which is sufficient to withstand 60% mortality per year without an increase in free space (Petraitis 1995). This appears to be the pattern in this study, where mussels with higher mortality rates had faster growth rates and maintained 100% cover despite differences in size and density (Chapters 2 & 3). As both growth and mortality are size-specific, a point will be reached at which growth no longer offsets mortality (Petraitis 1995).

Where brown mussels form part of subsistence utilisation, for example along the former Transkei coast, South Africa, collection pressure is considerably higher than in other areas (Lasiak 1991). Lasiak (1991) has shown that, for subsistence use, harvesting is indiscriminate and mussels are only sorted after removal from the rocks. In contrast, mortality caused by casual collecting is usually size selective as larger mussels are favoured (Siegfried *et. al.* 1985, Hockey & Bosman 1986). Removing individual mussels as opposed to clearing patches is less damaging, because natural mortality caused by intra-specific competition for space is high anyway as mussels undergo "self-thinning" (Griffiths & Hockey 1987, Hughes & Griffiths 1988). The disadvantage of size selection, is that the larger mussels are also the most fecund (Berry 1978, Dye *et al.* 1994). Spatial competition particularly due to fast growth leads to loss of mussels (Seed 1969b). Hummocking of mussels may occur as a result of space limitation and mussels in the middle of the clump become detached and torn away by wave action (Seed 1969b, Harger & Landenberger 1971, Seed 1976, Griffiths 1981, Paine & Levin 1981). In some regions of the world the removal of a clump of mussels sets in motion a ripple process whereby surrounding mussels are removed as a mat. This results in high mortality and patch formation (Dayton 1971). In dense beds where mussels are attached to each other rather than the substratum, mortality from storms is high (Harger & Landenberger 1971). As mussel beds along the south coast of South Africa are rarely dense and multi-layered, mortality at this scale is unlikely to occur (pers. obs.). Intraspecific competition can also result in overcrowding and a resultant decrease in food availability and growth (Bertness & Grosholz 1985, Kautsky 1982).

Mortality by predation can markedly influence the population structure. Predation pressure early in life may determine whether energy is channelled into somatic growth, as occurs in juvenile horse mussels, *Modiolus modiolus* (Seed & Brown 1978), or into reproduction, as occurs in the cockle, *Cerastoderma edule* (Seed & Brown 1978). In New Zealand, once *Perna canaliculus* has reached a size large enough to escape consumption by the sea star, they may persist for 30 years (Paine *et. al.* 1985). In *Mytilus edulis* and *Mytilus californianus* the combination of sheltered conditions and the absence of predation resulted in mussels reaching lengths of 150 and 300 mm respectively (Harger 1970). Low shore populations of marked *Mytilus edulis* had particularly heavy mortality due to predation and rarely reached 3 years of age. However, on the higher shore, mussels reached 17-20 years of age (Seed 1969b). In this study 26% of the dead *Perna*

perna shells, found on exposed and sheltered shores had been drilled by whelks, which possibly led to their death or a decrease in condition resulting in an inability to remain firmly attached to the substratum. Whelks *Nucella cingulatai* have been shown to cause a greater number of fatalities in small (mean of 44 mm) than in large mussels (mean of 60.5 mm) (Griffiths & Blaine 1994). If no vital organs are damaged in the attacks, mussels are able to repair the nacreous material (Griffiths & Blaine 1994). Drilling whelks, *Thais lapillus* are important predators of *Mytilus edulis* and are most abundant on the low shore (Seed 1969b, Edwards *et. al.* 1982, Seed 1993). Low shores exposed to heavy wave action, in contrast, have fewer predators and as a result predators seldom constrain mussel size on these shores (Lubchenco & Menge 1978, Seed 1993). In theory this would mean that the higher mortality rates noted at the exposed shores (Figure 4.3) were not a result of increased predation.

Most studies on mussel mortality in South Africa have been undertaken on *Choromytilus meridionalis* and *Aulacomya ater* on the west coast (Pollock 1979, Griffiths & Seiderer 1980, Griffiths 1981). Potential predators identified for mussels include, rock lobsters (*Jasus lalandii*), gastropods (*Natica tecta & Nucella cingulata*), kelp gulls (*Larus dominicanusl*) oystercatchers (*Haematopus moquini*), musselcrackers (*Sparadon durbanensis*) (Griffiths 1981, Meire 1993) and the octopus, *Octopus vulgaris* (Smale & Buchan 1981, McQuaid 1994). The blue-green alga, *Mastigocoleus sp.* which burrows into and weakens shells has been recorded in *Perna perna*, *Choromytilus meridionalis* and *Mytilus galloprovincialis* (Webb & Korrûbel 1994). Once weakened by borers, shells are more susceptible to wave action and predation (Baxter 1984). Along the south coast of South Africa, mussels higher up the shore tended to show more damage by borers than low shore mussels (Kaehler pers. comm., pers. obs.). Boring sponges *Cliona celata* and polychaetes, *Polydora sp.* have been found to cause minor damage on abalone, *Haliotis tuberculata* and potentially may damage mussels (Clavier 1992).

Mortality may occur by silting or recruit smothering, both factors which would also prevent feeding (Seed 1976, Daly & Mathieson 1977, Suchanek 1985, Van Erkom Schurink & Griffiths 1993). Sand deposition did not readily occur on exposed shores in this study. Sand movement was only noted at two of the sheltered sites, namely, Rufanes and Mgwalana. *Perna perna* appears able to tolerate sand inundation for at least a month without mortality occurring (Harris pers. com.). However, mass mortality due to sand burial has been observed and may in fact limit the distribution of mussels in sheltered areas prone to sand inundation (Marshall & McQuaid 1993, pers. obs.).

Mussels at the exposed sites had lower lifespans than those at the sheltered sites, but they were of a larger mean size because of higher growth rates (see chapter 2 & 3). Longevity may decrease with an increase in growth rate as mussels attain their size limit faster (Seed 1969b, Bayne 1976). *Mytilus edulis* higher up the shore can live to 17-20 years, whereas low shore (sheltered) predators prevent long-lived populations (Seed 1969b). Faster growing *Mytilus edulis* (35 mm at one year) are frequently short-lived (3 years) (Dare 1976) whereas those with slower growth rates may reach 15-20 years (Seed 1969b). Berry (1978) also suggests that under unfavourable conditions with slow growth, longevity of *Perna perna* may be longer than three years.

Due to variability in individual growth and mortality rates, marking mussels would probably give a more accurate measure of mortality than length-converted catch curves. Over-exploitation is a real problem in parts of South Africa and utilisation is likely to increase along the south coast.

In conclusion, higher total, juvenile and adult mortalities were observed at the exposed shores than at the sheltered shores. At the exposed shores this could have been a result of increased physical removal of juveniles and adults by wave action and/or increased juvenile mortality due to lower adult densities (less protection). Furthermore, the presence of algae, which is affected by wave action, may decrease juvenile survival rate. Wave exposure therefore has an important effect on the mortality rate of *Perna perna*.

SUMMARY

- Mortality rates were significantly higher for total, juvenile and adult mussels on the exposed than the sheltere shores.
- There was no significant correlation between total mortality (Z) and wave force (N).
- There was a significant exponential regression for juvenile survival rate against adult density.
- There was a significant linear relationship between the estimates of the growth index (Φ') and total mortality (Z).
- The lifespan for mussels on the exposed shores was shorter (2 to 3 years) than for those on the sheltered shore (5 to 9 years).

CHAPTER 5

GENERAL DISCUSSION AND SYNTHESIS

GENERAL DISCUSSION AND SYNTHESIS

Space is a potentially limiting resource (Dayton 1971), central to the survival of mussels specifically, and sessile organisms in general. Unlike some mussel species, eg. *Mytilus californianus* (Dayton 1971), *Perna perna* is not a competitive dominant and when removed may be replaced by coralline algae which could dominate for several years (Lambert & Steinke 1986). The way in which space is utilised by mussels is determined by the balance between recruitment, size, density, growth and mortality (Petraitis 1995). It is usually assumed that high recruitment and low mortality enable individuals of a single species to occupy large areas (Dayton 1971, Paine 1976), however as will later be established these are not the only ways. As mussel beds form part of the larger intertidal community in which energy pathways are the lifeblood, biomass becomes important both as a source (prey) and sink (filter feeder). Within the individual, energy may be channelled into either reproductive or somatic growth (Seed & Brown 1978).

Connell (1985) noted that certain sites showed consistent ranking in recruitment over time and ascribed this to the interaction of local physical conditions at a site, such as, currents, wave action, substratum and tidal height. If applied to this study, the higher adult densities at Rufanes may be explained by local conditions regularly resulting in high recruitment and higher juvenile and adult survival rates. However, even where settlement and recruitment have shown predictable annual trends, occasional massive settlements have occurred (Berry 1978, Suchanek 1978).

Early recruitment occurred at the exposed and sheltered sites throughout the year, peaking significantly from January to May (Table 5.1). There was no apparent relationship between the percentage cover of algae and the density of recruits. When algal cover was standardised to 100% cover, it was revealed that recruit density was significantly higher on algae than on mussels (Table 5.1). Recruit density (1-15 mm) at the exposed shores, which had greater algal cover, was significantly higher than at the sheltered shores (Table 5.1). However, high juvenile mortality appeared to override the advantages of high recruit density, particularly on the exposed shores. Mean survival rate of juvenile mussels (from 0.6 to 6 months) was higher at the sheltered shores (9.29%) than the exposed shores (0.71%). Due to this high mortality rate, the density of juveniles entering into the adult population was actually less on the exposed than the sheltered shores, despite the initial higher density of recruits in the former. The number of juveniles adding to spatial occupation therefore seems to be more dependent on juvenile mortality than on initial recruit density (Figure 5.1).

Early juvenile mortality has been shown to influence population abundance in a number of marine invertebrates (Gosselin & Qian 1997).

The different environmental conditions under which the populations on the exposed and sheltered shores exist means that energy is partitioned in different ways (McQuaid & Branch 1985). Mussels on the sheltered shores put less energy into growth than those at the exposed shores, and therefore had slower growth rates. Whether there was a trade-off between growth and reproduction as has been noted in the cockle, *Cerastoderma edule* (Seed & Brown 1978). More likely, the lower growth rate was a result of less food availability, decreased feeding times or greater aerial exposure (Jørgensen 1976), and a reflection of an induced condition rather than partitioning of energy. The high growth rates on the exposed shores enable individuals to procure space rapidly. Within the first year of growth, mussels on the exposed shores attained lengths twice those obtained on the sheltered shores. Despite the higher adult mortality rate at the exposed sites in the present study, approximately 100% spatial cover was maintained by faster growth and larger individuals (Table 5.1, Figure 5.1). An increase in growth rates also resulted in an increase in biomass (Figure 5.1). Similarly, *Mytilus edulis* has been known to use growth to offset the effects of mortality (Petraitis 1995).

Growth was negatively correlated with density ($p<0.05$), a finding previously noted for *Choromytilus meridionalis* (Hughes & Griffiths 1988) and for the clam, *Mercenaria mercenaria* (Peterson & Beal 1989). Adult density was significantly higher at the sheltered sites than the exposed sites (Table 5.1 & Figure 5.1). The covariation of body size and density is important for maintaining spatial dominance by sessile invertebrates (Petraitis 1995). The same space occupancy can be achieved by having higher packing densities and smaller individuals, as was found at the sheltered shore; or lower packing density and larger individuals, as occurred on the exposed shore (Table 5.1 & Figure 5.1). In terms of biomass, a trade-off between density and size occurs (Figure 5.1). Larger mussels are in turn associated with higher gonadal output which may/may not have a feedback effect depending on whether larval dispersal is local or further afield (Figure 5.1) (Branch 1975, Berry 1978).

Mortality causes loss of biomass and freeing of space. Space created by mortality may be filled by mussels leaning over and lateral movement of surrounding mussels, growth of smaller individuals, or settlement (Connell & Slatyer 1977, Suchanek 1978, Paine & Levin 1981, Tokeshi & Romero 1995). If the latter is the case, juvenile survival and growth rate will determine how rapidly the space is filled. Available space may be utilised by other organisms eg. limpets and chitons which, through continual grazing, keep patches free of sessile organisms (Dayton 1971, Suchanek 1978). The removal of individual mussels or small rather than large patches, resulted in faster recovery rate of the mussel bed (pers. obs.), a finding which has been widely documented (Paine & Levin 1981, Sousa 1984 in Sousa 1985, Lambert & Steinke 1986). Griffiths & Hockey (1987) have suggested that, as natural mortality caused by intraspecific competition for space is high, predatory losses (or limited exploitation by humans) would simply reduce the intensity of competition. Over-exploitation leads to a decrease in the adult reproductive stock and a decline in suitable habitats for settlement and subsequent refuge for recruits (Branch 1975, Bertness *et. al.* 1991, Miron *et. al.* 1995) . A multitude of other factors contribute to the rate of mussel bed recovery: the type of disturbance, size of disturbed patch, disturbance season, height on shore, thickness of mussel bed and larval recruitment (Suchanek 1978, Paine & Levin 1981, Sousa 1985, Tokeshi & Romero 1995). Intervals between successive disturbances have been shown to be longer at less exposed sites (Paine & Levin 1981). Exposed sites have been shown to exhibit faster recovery after disturbance than sheltered sites (Suchanek 1985). The stable points of exposed and sheltered mussel communities may differ in their resistance and response to perturbations (Connell & Slatyer 1977) . As a result, the same disturbance may, for example, drive one population to extinction whereas the other may find an alternative stable state (Sutherland 1974).

Due to greater longevity, the slower turnover rate on sheltered shores probably means that space availability occurs less frequently than on exposed shores where longevity is shorter (Table 5.1). A faster turnover rate of individuals within a productive mussel bed where growth is rapid and critical size is reached quickly, has been predicted by Petraitis (1995). The slower growth rate coupled with high longevity and low mortality of sheltered mussels produced populations which exhibit characteristics typical of a K population. In contrast, mussels on the exposed shores had higher growth rate, lower longevity and higher mortality, resembling an r population. These characteristics are perhaps better termed "induced r and K" life histories as they are a product of physical and biological conditions of the environment (see Widdows *et. al.* 1984). The important influence of site has been clearly shown by the increased growth rates achieved by *Mytilus edulis* when transplanted from less to more favourable habitats (Seed 1968, Mallet *et. al.* 1987a).

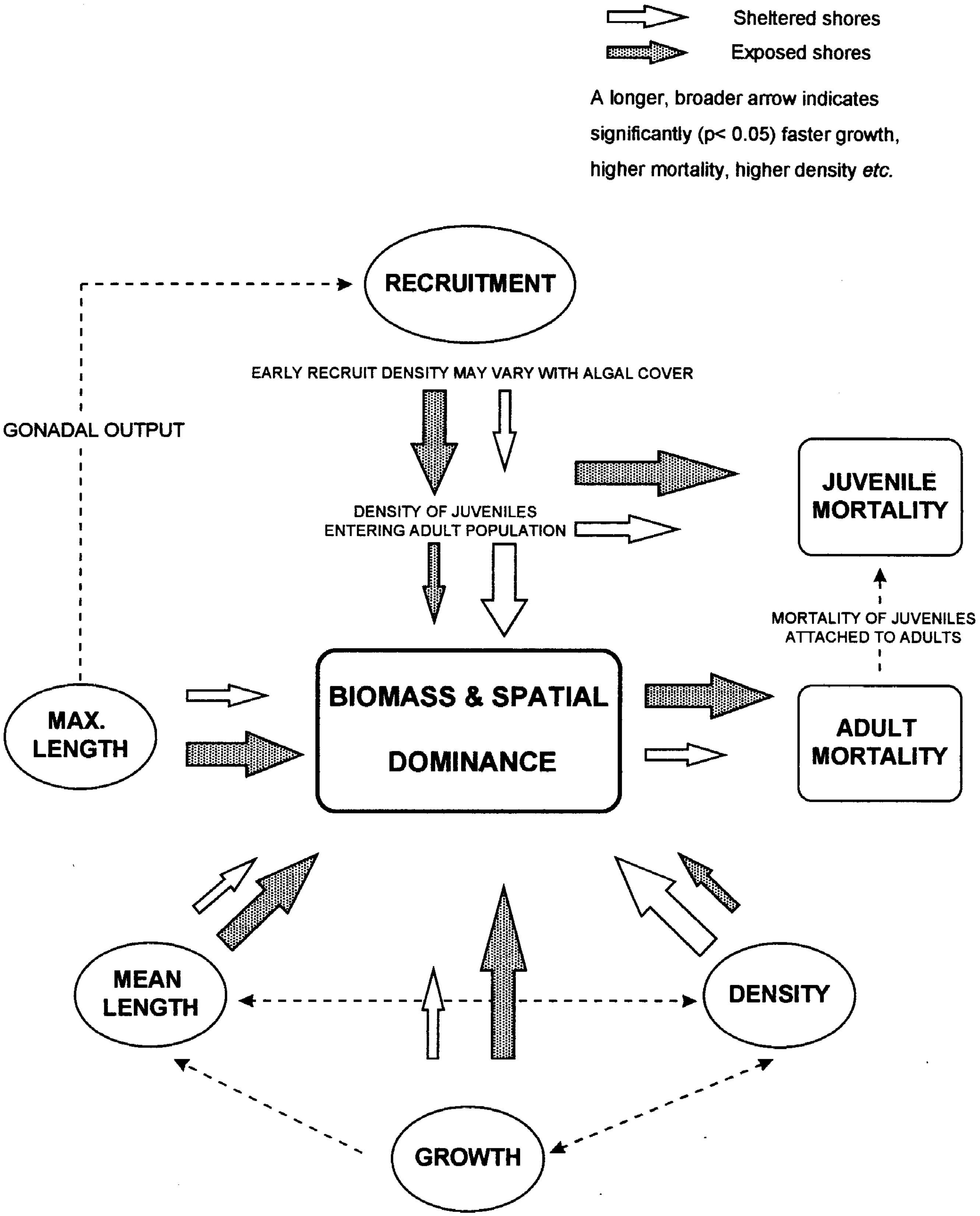
Taking lengths (mean and maximum), density, growth rates and mortality into account, the six sites selected for this study have clearly separated into two broad categories, namely Diaz Cross, Kwaai Hoek and Fish River; and Mgwalana, Rufanes and Riet River. This separation was likely a direct or indirect reflection of wave exposure. It is acknowledged that this alone is not sufficient evidence to prove that the characteristics noted were a result of wave exposure, as another factor may produce the same effects. In conclusion, wave action may affect mussels indirectly or directly in every stage of the life-cycle, from larval distribution, settlement intensity, post-settlement mortality, recruitment, growth, densities, biomass, mean and maximum lengths to adult mortality, recovery after disturbance and longevity. The effects of wave exposure can shape a population and thereby indirectly influence the entire community of grazers, algae, invertebrates and predators.

Table 5.1 Synthesis of results for the exposed and sheltered shores. nsa = not statistically analysed.

FACTORS	EXPOSED		SHELTERED		P
Recruitment timing (1-5 mm)	Same	January-April	Same	January-April	$p>0.05$
Recruit density (1-15 mm)	Higher	5896.m^{-2}	Lower	2986.m^{-2}	$p<0.05$
Juvenile mortality	Higher	99.29%	Lower	90.71%	nsa
Adult density (>15 mm)	Lower	3348.m^{-2}	Higher	4796.m^{-2}	$p<0.05$
Adult mean length	Higher	52.94 mm	Lower	41.59 mm	$p<0.05$
Adult maximum length	Higher	93.62 mm	Lower	75.48 mm	$p<0.05$
Biomass	Similar	1156 g.m^{-2}	Similar	1199 g.m^{-2}	$p>0.05$
Growth rate -mark recapture	Faster	40.40 mm at 1 year	Slower	14.41 mm at 1 year	$p<0.05$
-bands	Faster	41.62 mm at 1 year	Slower	24.40 mm at 1 year	$p<0.05$
-SLCA	Faster	59.16 mm at 1 year	Slower	27.40 mm at 1 year	$p<0.05$
Adult mortality	Higher	88.22%	Lower	51.95%	$p<0.05$
Total mortality	Higher	83.01%	Lower	51.06%	$p<0.05$
Longevity	Shorter	2.6 years	Longer	6.7 years	nsa

Explanation of the diagrammatic synthesis (Figure 5.1)

In a mussel bed, space is a limiting resource without which mussels cannot survive. Various aspects of population dynamics serve to increase and decrease the biomass that is present in this space. Beginning at the top of Figure 5.1, recruitment is higher on exposed than sheltered shores, possibly due to wave exposure and an interaction with algae. However, juvenile mortality on the exposed shores is considerably higher than on the sheltered shores, resulting in fewer juveniles being available to enter the adult population. These surviving juveniles will increase space usage and biomass. Working in a clock-wise direction, adult mortality results in a loss of biomass from the system and at the same time space becomes available. Density increases biomass and takes up space, while interacting with size and growth. Growth, which is higher on the exposed shores, increases biomass and increases space occupancy (*i.e.* decreases free space), and interacts with size and density. The size of a mussel will determine how much space occupancy will be increased. Finally, the maximum sized mussels will also lead to an increase in biomass and spatial dominance, as well as being more fecund. Mortality rates may also be influenced by the size and density of the mussels.



A longer, broader arrow indicates significantly ($p < 0.05$) faster growth, higher mortality, higher density *etc.*

Figure 5.1 Synthesis of results showing the interaction of various factors and how they ultimately affect space and biomass.

REFERENCES

Almatar,S (1993): A comparison of length-related and age-related growth parameters of Newaiby *Otolithes ruber* in Kuwait waters. *NAGA ICLARM Q.* 16, 32-34.

Alvarado,JL; Castilla,JC (1996): Tridimensional matrices of mussels *Perumytilus purpuratus* on intertidal platforms with varying wave forces in central Chile. *Mar. Ecol. Prog. Ser.* 133, 135-141.

Andre,C; Jonsson,PR; Lindegarth,M (1993): Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. *Mar. Ecol. Prog. Ser.* 97:183-192.

Anwar,NA; Richardson,CA; Seed,R (1990): Age determination, growth rate and population structure of the horse mussel *Modiolus modiolus*. *J. Mar. Biol. Ass. U.K.* 70, 441-457.

Arnold,WS; Marelli,DC; Bert,TM; Jones,DS; Quitmyer,IR (1991): Habitat-specific growth of hard clams *Mercenaria mercenaria* (L.) from the Indian River, Florida. *J. Exp. Mar. Biol. Ecol.* 147, 245-265.

Asmus,H; Asmus,RM (1993): Phytoplankton-mussel bed interactions in intertidal ecosystems. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. Series G. Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 58-84.

Baird,RH (1966): Factors affecting the growth and conditions of mussels (*Mytilus edulis*). *Fishery Invest. Ser. II.* 25, 1-33.

Ballantine,WJ (1961): A biologically-defined exposure scale for the comparative description of rocky shores. *Fld. Stud.* I, 1-19.

Barkai,A; Branch,GM (1989): Growth and mortality of the mussels *Choromytilus meridionalis*

(Krauss) and *Aulocomya ater* (Molina) as indicators of biotic conditions. *J. Moll. Stud.* 55, 329-342.

Baxter,JM (1984): The incidence of *Polydora ciliata* and *Cliona celata* boring the shell of *Patella vulgata* in Orkney. *J. Mar. Biol. Ass. U.K.* 64, 728-729.

Bayne,BL (1964): Primary and secondary settlement in *Mytilus edulis* (L.) (Mollusca). J. *Anim. Ecol.* 33, 513-523.

Bayne,BL (1965): Growth and delay of metamorphosis of the larvae of *Mytilus edulis* (L.). *Ophelia* 2, 1-47.

Bayne,BL (1976): Aspects of reproduction in bivalve molluscs. In: Estuarine processes Vol. 1. Use, stresses and adaptation to the estuary. (Ed: Wiley) Academic Press Inc., New York, 432-448.

Bayne,BL (1993): Feeding physiology of bivalves: time-dependence and compensation for changes in food availability. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. Series G. Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 1-24.

Bayne,BL; Worrall,CM (1980): Growth and production of mussels *Mytilus edulis* from two populations. *Mar. Ecol. Prog. Ser.* 3, 317-328.

Beamish,RJ; McFarlane,GA (1983): The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112, 735-743.

Beckley,LE (1979): Primary settlement of *Perna perna* (L.) on littoral seaweeds on St Croix Island. *S. Afr. J. Zool.* 14, 171.

Bell,EC;Denny, MW: (1994): Quantifying "wave exposure" : a simple device for recording maximum velocity and results of its use at several field sites. *J. Exp. Mar. Biol. Ecol.* 181, 9-29.

Berry,PF (1978): Reproduction, growth and production in the mussel, *Perna perna* (Linnaeus), on the east coast of South Africa. *Investl. Rep. Oceanogr. Res. Inst.* 48, 1-28.

Berry,PF; Schleyer,MH (1983): The brown mussel *Perna perna* on the Natal coast, South Africa: utilisation of available energy budget. *Mar. Ecol. Prog. Ser.* 13, 201-210.

Bertness,MD; Gaines,SD; Bermudez,D; Sanford,E (1991): Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.* 75, 91-100.

Bertness,MD; Gaines,SD; Stephens,SG; Yund,PO (1992): Components of recruitment in populations of the acorn barnacle, *Semibalanus balanoides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 156, 199-215.

Bertness,MD; Grosholz,E (1985): Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 67, 192-197.

Bhattacharya,CG (1967): A simple method of resolution of a distribution into Gaussian components. *Biometrics* 23, 115-130.

Boulding,EG; Van Alstyne,KL (1993): Mechanisms of differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. *J. Exp. Mar. Biol. Ecol.* 169, 139-166.

Bourget,E; De Guise,J; Daigle,G (1994): Scales of substratum heterogeneity, structural complexity, and the early establishment of a marine epibenthic community. *J. Exp. Mar. Biol. Ecol.* 181, 31-51.

Branch,GM (1975): Mechanisms reducing intraspecific competition in *Patella* spp: migration, differentiation and territorial behaviour. *J. Anim. Ecol.* 44, 575-600.

Branch,GM; Griffiths,CL; Branch,ML; Beckley,LE (Eds.) (1994): Two oceans, a guide to the marine life of Southern Africa. National Book Printers, Goodwood, South Africa. 360pp.

Branch,GM; Moreno,CA (1994): Intertidal and subtidal grazers. In: Ecological Studies - Rocky shores: exploitation in Chile and South Africa. (Ed: Siegried,WR) Springer-Verlag, Berlin, 76-100.

Bricelj,VM; Epp,J; Malouf,RE (1984): Intraspecific variation in reproductive and somatic growth cycles of bay scallops *Argopecten irradians*. *Mar. Ecol. Prog. Ser.* 36, 123-137.

Broom,MJ (1982): Analysis of the growth of *Anadara granosa* (Bivalvia:Arcidae) in natural, artificially seeded and experimental populations. *Mar. Ecol. Prog. Ser.* 9, 69-70.

Bustamante,RH; Branch,GM; Eekhout,S; Robertson,B; Zoutendyk,P; Schleyer,M; Dye,A; Hanekom,N; Keats,D; Jurd,M; McQuaid,C (1995): Gradients of intertidal primary productivity around the coast of South Africa, and their relationships with consumer biomass. *Oecologia* 102, 189-201.

Caceres-Martinez,J; Robledo,JAF; Figueras,A (1994): Settlement and post-larvae behaviour of *Mytilus galloprovincialis*: field and laboratory experiments. *Mar. Ecol. Prog. Ser.* 112, 107-117.

Caffey,HM (1985): Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol. Monogr.* 55, 313-332.

Calvo Ugarteburu, MG; McQuaid CD: Parasitism and invasive species: effects of digenetic trematodes on mussels. *Mar. Ecol. Prog. Ser.* (in press).

Cassie,SE (1954): Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Mar. Freshwat. Res.* 5, 513-522.

Ceccherelli,VU; Rossi,R (1984): Settlement, growth and production of the mussel *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* 16, 173-184.

Cerrato,RM; DL,Keith (1992): Age structure, growth and morphometric variations in the Atlantic surf clam, *Spisula solidissima*, from estuarine and inshore waters. *Mar. Biol.* 114, 581-593.

Clark,G (1968): Mollusc shell: daily growth lines. *Science* 161, 800-802.

Clavier,J (1992): Infestation of *Haliotis tuberculata* shells by *Cliona celata* and *Polydora species*. *S. Aust. Dept. Fish. Res. Paper* 24, 16-20.

Connell,JH (1985): The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* 93, 11-45.

Connell,JH; Slatyer,RO (1977): Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111, 1119-1144.

Craik,GJS (1980): Simple method for measuring the relative scouring of intertidal areas. *Mar. Biol.* 59, 257-260.

Crawford,RJM; Bower,DF (1983): Aspects of growth, recruitment and conservation of the brown mussel *Perna perna* along the Tsitsikamma coast. *Koedoe* 26, 123-133.

Cretchley,R (1997) Exploitation of the bait organism *Upogebia africana* (Crustacea: Anomura) in the Knysna estuary. M.Sc. Thesis, Rhodes University. 133pp.

Culverwell,J (1992): Effects of exploitation on the structure of populations of brown mussels (*L*) in Zululand, South Africa. M.Sc. Thesis, University of Newcastle-upon-Tyne. 86pp.

Dalla Via,GJ; Tappeiner,U; Bitterlich,G (1987): Shore-level related morphological and physiological variations in the mussel *Mytilus galloprovincialis* (Lamarck, 1819) (Mollusca Bivalvia). *Monitore Zoo. Ita.* 21, 293-305.

Daly,MA; Mathieson,AC (1977): The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Mar. Biol.* 43, 45-55.

Dare,PJ (1976): Settlement, growth and production of the mussel, *Mytilus edulis* in Morecombe Bay, England. *Fishery Invest. Ser.* II 28, 1-25.

Dayton,PK (1971): Competition, disturbance and community organization: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351-389.

Dayton,PK (1973): Dispersion, dispersal and persistence of the annual intertidal alga, *Postelsia palmaeformis*. *Ecol.* 54, 433-438.

Defeo,O; Arreguin-Sanchez,F; Sanchez,J (1992a): Growth study of the yellow clam *Mesodesma mactroides* :a comparative analysis of length-based methods. *Scientia Mar. Barcelona* 56, 53-59.

Defeo,O; Oritz,E; Castilla,JC (1992b): Growth, mortality and recruitment of the yellow clam *Mesodesma mactroides* on Uruguayan beaches. *Mar. Biol.* 114, 429-437.

Delafontaine,MT; Flemming,BW (1989): Effects of larval settlement, topography and wave action on the establishment of the intertidal barnacle *Tetraclita serrata* Darwin. In: Reproduction, genetics and distributions of marine organisms. 23rd European Biology Symposium ed. (Eds: Ryland,JS; Tyler,PA) Olsen and Olsen, Fredensborg, Denmark, 363-371.

Denny,MW (1983): A simple device for recording the maximum force exerted on intertidal organisms. *Limnol. Oceanogr.* 28, 1269-1274.

Denny,MW (1987): Lift as a mechanism of patch initiation in mussel beds. *J. Exp. Mar. Biol. Ecol.* 113, 231-245.

Denny,MW; Gaines,SD (1990): On the prediction of maximal intertidal wave forces. *Limnol. Oceanogr.* 35, 1-15.

Dey,DD; Bolton,ET (1978): Tetracycline as a bivalve shell marker. *Proc. Nat. Shel. Ass.* 68, 77.

Dickie,LM; Boudreau,PR; Freeman,KR (1984): Influences of stock site on growth and mortality in the blue mussel (*Mytilus edulis*). *Can. J. Fish. Aquat. Sci.* 41, 134-140.

Doty,MS (1971): Measurement of water movement in reference to benthic algal growth. *Bot. Mar.* 14, 32-35.

Du Plessis,AJ (1977): Larval development, settlement and growth of the black mussel *Choromytilus meridionalis* in the Saldanha Bay region. *Trans. Roy. Soc. S. Afr.* 42, 303-316.

Dye,AH (1988): Rocky shore surveillance on the Transkei coast: temporal and spatial variability in the balanoid zone at Dwesa. *S. Afr. J. Mar. Sci.* 7, 87-99.

Dye,AH (1995): The effects of excluding limpets from the lower balanoid zone of rocky shores in Transkei, South Africa. *S. Afr. J. Mar. Sci.* 15, 9-15.

Dye,AH; Schleyer,MH; Lambert,G; Lasiak,TA (1994): Intertidal and subtidal filter-feeders in Southern Africa. In: Ecological Studies - Rocky shores: exploitation in Chile and South Africa. (Ed: Siegfried,WR) Springer-Verlag, Berlin, 57-73.

Edwards,DC; Conover,DO; Sutter,F (1982): Mobile predators and the structure of marine intertidal communities. *Ecol.* 63, 1175-1180.

Ekaratne,SUK; Crisp,DJ (1982): Tidal micro-growth bands in intertidal gastropod shells, with an evaluation of band-dating techniques. *Proc. R. Soc. Lond. B.* 214, 305-323.

Eyster,LS; Pechenik,JA (1987): Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water agitation. *J. Exp. Mar. Biol. Ecol.* 114, 99-110.

Field,JG; Griffiths,CL (1991): Littoral and sublittoral ecosystems of southern Africa. In: Ecosystems of the world. (Eds: Mathieson,AC; Nienhus,PH) Elsevier, Amsterdam, 323-346.

Fielding,PJ; Davis,CL (1989): Carbon and nitrogen resources available to kelp bed filter feeders in an upwelling environment. *Mar. Ecol. Prog. Ser.* 55, 181-189.

Franz,DR (1993): Allometry of shell and body weight in relation to shore level in the intertidal bivalve *Geukensia demissa* (Bivalvia:Mytilidae). *J. Exp. Mar. Biol. Ecol.* 174, 193-207.

Fréchette,M; Bourget,E (1985a): Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. *Can. J. Fish. Aquat. Sci.* 42, 1158-1165.

Fréchette,M; Bourget,E (1985b): Food-limited growth of *Mytilus edulis* in relation to the benthic boundary layer. *Can. J. Fish. Aquat. Sci.* 42, 1166-1170.

Fréchette,M; Grant,J (1991): An in situ estimation of the effect of wind-driven resuspension on the growth of the mussel *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 148, 201-213.

Fréchette,M; Lefaivre,D; Butman,CA (1993): Bivalve feeding and the benthic boundary layer. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. Series G ed. Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 325-369.

Gage,JD (1992): Natural growth bands and growth variability in the sea urchin *Echinus esculentus*: results from tetracycline tagging. *Mar. Biol.* 114, 607-616.

Gayanilo,FC Jr; Sparre,P; Pauly,D (1994): The FAO-ICLARM stock assessment tools (FiSAT) user's guide. *FAO Comp. Info. S.* 6, 186pp.

Gillmor,RB (1982): Assessment of intertidal growth and capacity adaptations in suspension-feeding bivalves. *Mar. Biol.* 68, 277-286.

Gosselin,LA; Qian,PY (1997): Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 146, 265-282.

Graham,KR; Sebens,KP (1996): The distribution of marine invertebrate larvae near vertical surfaces in the rocky subtidal zone. *Ecol.* 77, 933-949.

Grant,J; Cranford,PJ (1991): Carbon and nitrogen scope for growth as a function of diet in the sea scallop *Placopecten magellanicus*. *J. Mar. Biol. Ass. U.K.* 71, 437-450.

Grant,J; Dowd,M; Thompson,K; Emerson,C; Hatcher,A (1993): Perspectives on field studies and related biological models of bivalve growth and carrying capacity. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. Series G ed. Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 579.

Grant,WS; Schneider,AC; Leslie,RW; Cherry,MI (1992): Population genetics of the brown mussel *Perna perna* in southern Africa. *J. Exp. Mar. Biol. Ecol.* 165, 45-58.

Griffiths,CL; Blaine,MJ (1994): Non-fatal cropping of large mussels by drilling whelks, *Nucella cingulata* (Linneaus 1771). *J. Moll. Stud.* 60, 346-348.

Griffiths,CL; Hockey,PAR (1987): A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. *S. Afr. J. Mar. Sci.* 5, 547-556.

Griffiths,CL; Hockey,PAR; Van Erkom Schurink,C; Le Roux,PJ (1992): Marine invasive aliens on South

African shores: implications for community structure and trophic functioning. *S. Afr. J. Mar. Sci.* 12, 713-722.

Griffiths,CL; King,JA (1979a): Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. *Mar. Biol.* 51, 141-149.

Griffiths,CL; King,JA (1979b): Energy expended on growth and gonad output in the ribbed mussel *Aulacomya ater*. *Mar. Biol.* 53, 217-222.

Griffiths,CL; Seiderer,JL (1980): Rock-lobsters and mussels - limitations and preferences in a predator-prey interaction. *J. Exp. Mar. Biol. Ecol.* 44, 95-109.

Griffiths,RJ (1976): Reproduction, growth and larval development of *Choromytilus meridionalis* (Kr.) First Interdisciplinary Conference on Marine and Freshwater Research in southern Africa, University of Port Elizabeth, 5-10 July 1976.

Griffiths,RJ (1977): Reproductive cycles in littoral populations of *Choromytilus meridionalis* (Kr.) and *Aulacomya ater* (Molina) with a quantitative assessment of gamete production in the former. *J. Exp. Mar. Biol. Ecol.* 30, 53-71.

Griffiths,RJ (1980a): Filtration, respiration and assimilation in the black mussel *Choromytilus meridionalis*. *Mar. Ecol. Prog. Ser.* 3, 63-70.

Griffiths,RJ (1980b): Natural food availability and assimilation in the bivalve *Choromytilus meridionalis*. *Mar. Ecol. Prog. Ser.* 3, 151-156.

Griffiths,RJ (1981): Population dynamics and growth of the bivalve *Choromytilus meridionalis* (Kr.) at different tidal levels. *Estuarine Coastal Shelf Sci.* 12, 101-118.

Griffiths,RJ; Buffenstein,R (1981): Aerial exposure and energy input in the bivalve *Choromytilus meridionalis*(Kr.). *J. Exp. Mar. Biol. Ecol.* 52, 219-229.

Gulland,JA (1987): Length-based methods in fisheries research: theory to application. 335-342. In: Length-based methods in fisheries research. (Eds: Pauly,D; Morgan,GR) (ICLARM Conference Proceedings, 13.), Manila, Philippines, Kuwait, 486pp.

Harding,JP (1949): The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Ass. U.K.* 28, 141-153.

Harger,JRE (1968): The role of behavioural traits in influencing the distribution of two species of sea mussel, *Mytilus californianus* and *Mytilus edulis*. *The Veliger* 11, 45-49.

Harger,JRE (1970): The effect of wave impact on some aspects of the biology of sea mussels. *The Veliger* 12, 401-414.

Harger,JRE; Landenberger,DE (1971): The effect of storms as a density dependent mortality factor on populations of sea mussels. *The Veliger* 14, 195-201.

Hawkins,AJS; Bayne,BL; Day,AJ (1986): Protein turnover, physiological energetics and heterozygosity in the blue mussel, *Mytilus edulis* : the basis of variable age-specific growth. *Proc. R. Soc. Lond.' B.* 229, 161-176.

Hepburn,HR; Sinclair,GS; Davidoff,MR; Moss,EA; Chandler,HD; Ripley,S (1979). Byssus threads and their tenacity. *S.Afr. J. Sci.* 75, 187-189.

Hockey,PAR; Bosman,AL (1986): Man as an intertidal predator in Transkei: *disturbance, community convergence and management of a natural food resource. Oikos 46, 3-14.*

Hughes,RN; Griffiths,CL (1988): Self-thinning in barnacles and mussels: the geometry of packing. *Am. Nat.* 132, 484-491.

Hunt,HL; Scheibling,RE (1996): Physical and biological factors influencing mussel (*Mytilus trossulus, Mytilus edulis*) settlement on a wave-exposed rocky shore. *Mar. Ecol. Prog. Ser.* 142, 135-145.

Isaac,VJ (1990): The accuracy of some length-based methods for fish population studies. *ICLARM Tech. Rep.* 27, 1-81.

Johnson,HS; Black,R (1984): The Wahlund effect and the geographical scale of variation in the intertidal limpet *Siphonaria sp. Mar. Biol.* 79, 295-302.

Jones,WE; Demetropoulos,A (1968): Exposure to wave action: measurements of an important ecological parameter on rocky shores on Anglesey. *J. Exp. Mar. Biol. Ecol.* 2, 46-63.

Jonsson,PR; Andre,C; Lindegarth,M (1991): Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: evidence for near-bottom confinement. *Mar. Ecol. Prog. Ser.* 79, 67-76.

Jòrgensen,CB (1976): Growth efficiencies and factors controlling size in some mytilid bivalves, especially *Mytilus edulis* L.: Review and interpretation. *Ophelia* 15, 175-192.

Kaufmann,KW (1981): Fitting and using growth curves. *Oecologia* 49, 293-299.

Kautsky,N (1982): Growth and size structure in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68, 117-133.

Kennish,MJ; Lutz,RA; Dobarro,JA; Fritz,LW (1994): *In situ* growth rates of the ocean quahog, *Arctica islandica* (Linnaeus, 1767), in the middle Atlantic Bight. J. Shelfsh. Res. 13, 473-478.

King,PA; McGrath,D; Gosling,EM (1989): Reproduction and settlement of *Mytilus edulis* on an exposed rocky shore in Galway Bay, west coast of Ireland. *J. Mar. Biol. Ass. U.K.* 69, 355-365.

Kitching,JA; Sloane,JF; Ebling,FJ (1958): The ecology of Lough Ine VIII. Mussels and their predators. *J. Anim. Ecol.* 27, 331-341.

Koehn,RK; Gaffney,PM (1984): Genetic heterozygosity and growth rate in *Mytilus edulis*. *Mar. Biol.* 82, 1-7.

Krebs,CJ (1989): Survival rates. In: Ecological Methodology. First ed. (Eds: Wilson,CM; Pisano,S) Harper Collins Publishers, New York, 654pp.

Lambert,G,T.D. Steinke (1986): Effects of destroying juxtaposed mussel-dominated and coralline algal communities at Umdoni Park, Natal Coast. South Africa. *S. Afr. J. Mar. Sci.* 4, 203-217.

Lane,DJW; Beaumont,AR; Hunter,JR (1985): Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. *Mar. Biol.* 84, 301-308.

Lasiak,T (1986): The reproductive cycles of the intertidal bivalves *Crassostrea cucullata* (Born, 1778) and *Perna perna* (Linnaeus, 1758) from the Transkei coast, Southern Africa. *The Veliger* 29, 226-230.

Lasiak,T (1991): The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal people of Transkei, Southern Africa. *Biol. Conserv.* 56, 245-264.

Lasiak,T; Dye,A (1989): The ecology of the brown mussel *Perna perna* in Transkei, Southern Africa: Implications for the management of a traditional food resource. *Biol. Conserv.* 47, 245-257.

Lasiak,TA (1993): Bicephalid trematode infections in the brown mussel *Perna perna* (Bivalvia: Mytilidae). *J.Mar.Sci.* 13, 127-134.

Lasiak,TA; Barnard,TCE (1995): Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary/secondary settlement hypothesis. *Mar. Ecol. Prog. Ser.* 120, 147-153.

Lasiak,TA; Field,JG (1995): Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. *J. Exp. Mar. Biol. Ecol.* 185, 33-53.

Leeb,A (1995): Patterns of recruitment, growth and mortality of the mussel *Mytilus galloprovincialis* in relation to wave exposure and tidal elevation. M.Sc. Thesis, University of Cape Town, 102pp.

Lindsay, JR (1998): Population structure and recruitment of the brown mussel (*Perna perna*) in relation to wave exposure, tidal height and substratum. M.Sc. Thesis, Rhodes University, 171pp.

Longhurst, AR; Pauly, D (1987): *Ecology of Tropical Oceans.* San Diego. Academic Press, 407pp.

Lubchenco,J; Menge,BA (1978): Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 34, 1-16.

Lutz,RA (1976): Annual growth patterns in the inner shell layer of *Mytilus edulis* L. *J. Mar. Biol. Ass. U.K.* 56, 723-731.

Mallet,AL; Carver,CEA; Coffen,SS; Freeman,KR (1987a): Winter growth of the blue mussel *Mytilus edulis* L.: importance of stock and site. *J. Exp. Mar. Biol. Ecol.* 108, 217-228.

Mallet,AL; Carver,CEA; Coffen,SS; Freeman,KR (1987b): Mortality variations in natural populations of the blue mussel, *Mytilus edulis. Can. J. Fish. Aquat. Sci.* 44, 1589-1594.

Marker,ME (1988): Geology and geomorphology. In: A field guide to the eastern Cape coast. (Eds: Lubke,R; Gess,F; Bruton,M) Grahamstown centre of the wildlife society of Southern Africa, Grahamstown, 9-18.

Marshall, DJ; McQuaid,CD (1993): Differential, physiological and behavioural responses of the intertidal mussels, *Choromytilus meridionalis* (Kr.) and *Perna perna* (L.), to exposure to hypoxia and air: a basis for spatial separation. *J. Exp. Mar. Biol. Ecol.* 171, 225-237.

McConnell,WJ; Sigler,WF (1959): Chlorophyll and productivity in a mountain river. *Limnol. Oceanogr.* 4, 335-351.

McGrath,D; King,PA; Gosling,EM (1988): Evidence for the direct settlement of *Mytilus edulis* larvae on adult mussel beds. *Mar. Ecol. Prog. Ser.* 47, 103-106.

McLachlan,A; Jaramillo,E; Defeo,O; Dugan,J; de Ruyck,A; Coetzee,P (1995): Adaptations of bivalves to different beach types. *J. Exp. Mar. Biol. Ecol.* 187, 147-160.

McLachlan,A; Lombard,HW; Louwrens,S (1981): Trophic structure and biomass distribution on two East Cape rocky shores. *S. Afr. J. Zool.* 16, 85-88.

McQuaid (1994): Feeding behaviour and selection of bivalve prey by *Octopus vulgaris* Cuvier. *J. Exp. Mar. Biol. Ecol.* 177, 187-202.

McQuaid,CD (1980): Spatial and temporal variations in rocky intertidal communities. Ph.D. Dissertation, University of Cape Town.

McQuaid,CD; Branch,GM (1984): The influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Mar. Ecol. Prog. Ser.* 19, 145-151.

McQuaid,CD; Branch,GM (1985): Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Mar. Ecol. Prog. Ser.* 22, 153-161.

Meire,PM (1993): The impact of bird predation on marine and estuarine bivalve populations: a selective review of patterns and underlying causes. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. Series G ed. Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 213-243.

Menge,BA (1976): Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46, 355-393.

Menge,BA (1991): Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *J. Exp. Mar. Biol. Ecol.* 146, 69-100.

Menge,BA; Farrell,TM (1989): Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Adv. Ecol. Res.* 19, 189-262.

Menge,BA; Sutherland,JP (1987): Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130, 730-757.

Miron,G; Boudreau,B; Bourget,E (1995): Use of larval supply in benthic ecology: testing correlations between larval supply and larval settlement. *Mar. Ecol. Prog. Ser.* 124, 301-305.

Moore,HB (1935): The biology of *Balanus balanoides*. IV. Relation to environmental factors. *J. Mar. Biol. Ass. U.K.* 20, 279-307.

Munday,BW; Keegan,BF (1992): Population dynamics of *Amphiura chiajei* (Echinodermata: Ophiuroidea) in Killary Harbour, on the west coast of Ireland. *Mar. Biol.* 114, 595-605.

Munro,JL (1984): Estimation of natural mortality rates from selectivity and catch length-frequency data. *Fishbyte* 2, 11-14.

Muus,BJ (1968): A field method for measuring "exposure" by means of plaster balls. A preliminary account. *Sarsia* 34, 61-68.

Nakaoka,M; Matsui,S (1994): Annual variation in the growth rate of *Yolia notabilis* (Bivalvia: Nuculanidae) in Otsuchi Bay, northeastern Japan, analysed shell microgrowth patterns. *Mar. Biol.* 119, 397-404.

Newell,CR; Shumway,SE (1993): Grazing of natural particulates by bivalve molluscs: a spatial and temporal perspective. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. NATO ASI Series ed. Vol. G 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg.

Newell,CR; Shumway,SE; Cussi,TL; Selvin,R (1989): The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. *J. Shelfsh. Res.* 8, 187-196.

Page,HM; Hubbard,DM (1987): Temporal and spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. *J. Exp. Mar. Biol. Ecol.* 111, 159-179.

Paine,RT (1976): Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecol.* 57, 858-873.

Paine,RT; Castilla,JC; Cancino,J (1985): Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand and Washington State. *Am. Nat.* 125, 679-691.

Paine,RT; Levin,SA (1981): Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51, 145-178.

Palumbi,SR (1984): Measuring intertidal wave force. *J. Exp. Mar. Biol. Ecol.* 81, 171-179.

Pannella,G; MacClintock,C (1968): Biological and environmental rhythms reflected in molluscan shell growth. *J. Palaen.* 42, 64-80.

Pauly,D (1990): Length-converted catch curves and the seasonal growth of fishes. *Fishbyte* 8, 33-38.

Pauly,D; Arreguin-Sanchez,F (1995): Improving Shepherd's length composition analysis (SLCA) method for growth parameter estimations. *NAGA ICLARM Q.* 18, 31-33.

Pauly,D; Caddy,JF (1985): A modification of Bhattacharya's method for the analysis of mixtures of normal distributions. *FAO Fisheries Circular* 781, 1-10.

Pauly,D; David,N (1981): Elefan 1, a BASIC program for the objective extraction of growth parameters from length-frequency data. *Meeresforsch* 28, 205-211.

Pauly,D; Moreau,J; Abad,N (1995): Comparison of age-structured and length-converted catch curves of brown trout *Salmo trutta* in two French rivers. *Fish. Res.* 22, 197-204.

Pauly,D; Munro,J (1984): ICLARM's activities in tropical stock assessment: 1979-1984, and beyond. *ICLARM Newsletter* 7, 7-9.

Pechenik,JA; Eyster,LS; Widdows,J; Bayne,BL (1990): The influence of food concentration and temperature on growth and morphological differentiation of blue mussel *Mytilus edulis* L. larvae. *J. Exp. Mar. Biol. Ecol.* 136, 47-64.

Pentilla,J; Jearld,A; Clark,S (1988): Age determination methods for Northwest Atlantic species. *NOAA Tech. Rep.* 72, 3-135.

Petersen,JH (1984): Establishment of mussel beds: attachment behaviour and distribution of recently settled mussels (*Mytilus californianus*). *The Veliger* 27, 7-13.

Peterson,CH; Beal,BF (1989): Bivalve growth and higher order interactions: importance of density, site and time. *Ecol.* 70, 1390-1404.

Peterson,CH; Duncan,PB; Summerson,HC; Safrit,GW (1983): A mark-recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. *Fish. Bull.* 81, 765-779.

Petraitis,PS (1990): Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. *Oecologia* 83, 405-413.

Petraitis,PS (1991): Recruitment of the mussel *Mytilus edulis* L. on sheltered and exposed shores in Maine, USA. *J. Exp. Mar. Biol. Ecol.* 147, 65-80.

Petraitis,PS (1995): The role of growth in maintaining spatial dominance by mussels *Mytilus edulis*. *Ecol.* 76, 1337-1346.

Phillips,TE (1994): Dispersal, settlement and recruitment: their influence on the population dynamics of intertidal mussels. Ph.D. Dissertation, Rhodes University, Grahamstown.

Pollock,DE (1979): Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape west coast of Africa. *Mar. Biol.* 52, 347-356.

Price,HA (1980): Seasonal variation in the strength of byssal attachment of the common mussel *Mytilus edulis* L. *J. Mar. Biol. Ass. U.K.* 60, 1035-1037.

Price,HA (1982): An analysis of factors in determining seasonal variation in the byssal attachment strength of *Mytilus edulis*. *J. Mar. Biol. Ass. U.K.* 62, 147-155.

Raubenheimer,D; Cook,P (1990): Effects of exposure to wave action on allocation of resources to shell and meat growth by the subtidal mussel, *Mytilus galloprovincialis*. *J. Shelfsh. Res.* 9, 87-93.

Reed,SE (1993): Size difference between sexes (including masculinized females) in *Strombus pugilis* (Mesogastropoda: Strombidae). *J. Shelfsh. Res.* 12, 77-79.

Richardson,CA (1988): Tidally produced growth bands in the subtidal bivalve *Spisula subtruncata* (Da Costa). *J. Moll. Stud.* 54, 71-82.

Richardson,CA (1989): An analysis of the microgrowth bands in the shell of the common mussel *Mytilus edulis*. *J. Mar. Biol. Ass. U.K.* 69, 477-491.

Richardson,CA; Crisp,DJ; Runham,NW (1979): Tidally deposited growth bands in the shell of the common cockle, *Cerastoderma edule* (L.). *Malacologia* 18, 277-290.

Richardson,CA; Seed,R; Naylor,E (1990): Use of internal growth bands for measuring individual and population growth rates in *Mytilus edulis* from offshore production platforms. *Mar. Ecol. Prog. Ser.* 66, 259-265.

Robson,G (1986): Aspects of the biology of a new species of South African *Patella* (Mollusca: Gastropoda: Patellidae). M.Sc. Thesis, University of Natal (Pietermaritsburg).

Roegner,GC; Mann,R (1995): Early recruitment and growth of the American oyster *Crassostrea virginica* (Bivalvia: Ostreidae) with respect to tidal zonation and season. *Mar. Ecol. Prog. Ser.* 117, 91-101.

Ropes,JW; Jearld,A (1987): Age determination of ocean bivalves. (Series Eds: Summerfelt,RC; Hall,GE.) The Iowa State university press, Iowa.

Sainsbury,KJ (1980): Effect of individual variability on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* 37, 241-247.

Seed,R (1968): Factors influencing shell shape in the mussel *Mytilus edulis*. *J. Mar. Biol. Ass. U.K.* 48, 561-584.

Seed,R (1969a): The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores I. breeding and settlement. *Oecologia* 3, 277-316.

Seed,R (1969b): The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores II. Growth and mortality. *Oecologia* 3, 317-350.

Seed,R (1976): Ecology. In: Marine mussels: their ecology and physiology. (Ed: Bayne,BL) Cambridge University Press, Cambridge, 13-65.

Seed,R (1993): Invertebrate predators and their role in structuring coastal and estuarine populations of filter feeding bivalves. In: Bivalve filter feeders in estuarine and coastal ecosystems processes. Series G Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 579.

Seed,R; Brown,RA (1978): Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *J. Anim. Ecol.* 47, 283-292.

Shafee.MS (1992): Production estimate of a mussel population *Perna picta* (Born) on the Atlantic coast of Morocco. *J. Exp. Mar. Biol. Ecol.* 163, 183-197.

Shepherd,JG (1987): A weakly parametric method for estimating growth parameters from length composition data. Chap. 113-119. In: Length-based methods in fisheries research. (Eds: Pauly,D; Morgan,GR) (ICLARM Conference Proceedings, 13.), Manila, Philippines, Kuwait, 486 pp.

Siegel,V (1991): Estimation of krill (*Euphausia superba*) mortality and production rate in the Antarctic Peninsula region. (Scientific committee for the conservation of Antarctic marine living resources - Selected scientific papers). Tasmania, Australia.

Siegfried,WR; Hockey,PAR; Crowe,AA (1985): Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Environ. Conserv.* 12, 303-307.

Simon,CA (1997): Extracellular digestion in two intertidal mussels and the role played in their gut bacteria. M.Sc. Thesis, Rhodes University. 121 pp.

Smale,MJ; Buchan,PR (1981): Biology of *Octopus vulgaris* off the east coast of South Africa]. *Mar. Biol.* 65, 1-12.

Sousa,WP (1985): Disturbance and patch dynamics on rocky intertidal shores. In: The ecology of natural disturbance and patch formation. (Eds: Pickett,STA; White,PS) Academic Press, New York, 101-124.

Sparre,P; Venema,SC (1993): Introduction to tropical fish stock assessment. Part I manual. *FAO. Fish. Tech. Pap. Rev.* 1, 376.

Sprung,M (1983): Reproduction and fecundity of the mussel *Mytilus edulis* at Helgoland (North Sea). *HELOA* 36, 243-255.

Stirling,HP; Okumus,I (1994): Growth, mortality and shell morphology of cultivated mussel (*Mytilus edulis*) stocks cross-planted between two Scottish sea lochs. *Mar. Biol.* 119, 115-123.

Suchanek,TH (1978): The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* 31, 105-120.

Suchanek,TH (1980): Diversity in natural and artificial mussel bed communities of *Mytilus californianus. Am. Zoo.* 20, 807.

Suchanek,TH (1985): Mussels and their role in structuring rocky shore communities. In: The ecology of rocky coasts. (Eds: Moore,PG; Seed,R) Hodder and Stoughton, London, 70-96.

Sukhotin,AA; Kulakowski,EE (1992): Growth and population dynamics in mussels (*Mytilus edulis*) L. cultured in the White Sea. *Aquaculture* 101, 59-73.

Sukhotin,AA; Maximovich,NV (1994): Variability of growth rate in *Mytilus edulis* L. from the Chupa Inlet (the White Sea). *J. Exp. Mar. Biol. Ecol.* 176, 15-26.

Sutherland,JP (1974): Multiple stable points in natural communities. *Am. Nat.* 108, 859-1144.

Takada,Y (1995): Variation of growth rate with tidal level in the gastropod *Monodonta labio* on a boulder shore. *Mar. Ecol. Prog. Ser.* 117, 103-110.

Theisen,BF (1973): The growth of *Mytilus edulis* L. (Bivalvia) from Disko and Thule District, Greenland. *Ophelia* 12, 59-77.

Tokeshi,M; Romero,L (1995): Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Mar. Ecol. Prog. Ser.* 119, 167-176.

Tomalin,BJ (1995): Growth and mortality rates of brown mussels *Perna perna* (Linnaeus) in Kwazulu-Natal: a comparison between sites and methods using non-parametric length-based analysis. *S. Afr. J. Mar. Sci.* 16, 241-254.

Tsuchiya,M (1980): Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. *J. Exp. Mar. Biol. Ecol.* 47, 203-222.

Underwood,AJ (1981): Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *J. Exp. Mar. Biol. Ecol.* 51, 57-85.

van Erkom Schurink,C; Griffiths,CL (1990): Marine mussels of Southern Africa-their distribution patterns, standing stocks, exploitation and culture. *J. Shelfsh. Res.* 9, 75-85.

van Erkom Schurink,C; Griffiths,CL (1993): Factors affecting relative rates of growth in four South African mussel species. *Aquaculture* 109, 257-273.

Webb,SC; Korrûbel,JL (1994): Shell weakening in marine mytilids attributable to blue-green alga *Mastigocoleus sp* (Nostochopsidaceae). *J. Shelfsh. Res.* 13, 11-17.

Wetherall,JA (1986): A new method for estimating growth and mortality parameters from length-frequency data. *Fishbyte* 4, 12-14.

Widdows,J (1978): Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J. Mar. Biol. Ass. U.K.* 58, 109-124.

Widdows,J; Salkeld,PN; Cleary,JJ; Lowe,DM; Evans,SV; Thompson,PE (1984): Relative importance of environmental factors in determining physiological differences between two populations of mussels (*Mytilus edulis*). *Mar. Ecol. Prog. Ser.* 17, 33-47.

Wilbur,KM; Jodrey,LH (1952): Studies on shell formation. Measurement of the rate of shell formation using CA45. *Biol. Bull. Mar. Biol. Lab.* 103, 269-276.

Wildish,DJ; Kristmanson,DD (1993): Hydrodynamic control of bivalve filter feeders: a conceptual view. In: Bivalve filter feeders in estuarine and coastal ecosystem processes. Series G ed. Vol. 33. (Ed: Dame,RF) Springer-Verlag, Berlin Heidelberg, 299-324.

Witman,J (1983): The importance of competition, physical disturbance and mutualism in maintaining the depth zonation of kelp and mussels. *Am. Zoo.* 23, 1001.

Witman,J; Suchanek,T (1984): Mussels in flow: drag and dislodgement by epizoans. *Mar. Ecol. Prog. Ser.* 16, 255-268.

Yamaguchi,M (1975): Estimating growth parameters from growth rate data, problems with marine sedentary invertebrates. *Oecologia* 20, 321-332.

Young,EF; Bigg,GR; Grant,A (1996): A statistical study of environmental influences on bivalve recruitment in the Wash, England. *Mar. Ecol. Prog. Ser.* 143, 121-129.

Zar,JH (Ed.) (1996): Biostatistical analysis. Prentice-Hall Inc., New Jersey. 718 pp.