EFFECTS OF ZONE AND WAVE EXPOSURE ON POPULATION STRUCTURE AND RECRUITMENT OF THE MUSSEL (PERNA PERNA) IN SOUTH AFRICA

THESIS

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requirements for the degree of
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by

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DECLARATION

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

J. Lindsay

J.R. Lindsay

19/05/98

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ABSTRACT

Certain aspects of the population dynamics of the brown mussel, *Perna perna*, were examined at 18 sites along the south coast of South African. Specifically the effects of wave exposure and tidal height were examined in relation to mussel size, biomass and density. A single set of samples was removed from each of the 18 sites, over three spring tide cycles. Sites were classified as exposed or sheltered prior to sampling. Principal component analysis (PCA) (based on mussel length data) and length frequency histograms revealed that there was a general decrease in the modal size of the adult mussel cohort with an increase in tidal height. The effects of exposure on mussel size decreased higher on the shore. On the exposed low shore the maximum size of mussels had a mean length of 102.3mm and was significantly larger (ANOVA, $p<0.0001$) than that for mussels on sheltered shores (86.7mm). The difference between mean maximum lengths of mussels on the mid shore was not so great, exposed sites had a average mean maximum length of 79.9, while on the sheltered shores it was 68.4mm. On the high shore the difference between the average mean maximum lengths at exposed and sheltered sites was only 3.9mm. The fact that the effects of exposure were greatest on the low shore was also borne out in the PCA. In this analysis low shore exposed and sheltered zones separated into two groups with little overlap, mid shore exposed and sheltered zones were positioned next to each other, and exposed and sheltered high shore zones were clumped together. Densities of adult mussels (>15mm) were calculated as real densities from randomly placed quads i.e. not from areas of 100% cover. Density decreased up the shore; low, mid and high shore zones were significantly different from each other (ANOVA, $p<0.0001$; followed by multiple range tests). There was no significant difference between the densities of mussels at exposed and sheltered sites within each zone (ANOVA, $p=0.7155$). Recruit (<15mm) densities increased with an increase in adult mussel densities, and this relationship was significant at all zones and for both degrees of exposure (regression analysis, $p<0.05$ in all cases). The regression between recruits and adults was strongest on the mid and high shore exposed sites. There was a general trend towards stronger regressions and greater predictability with an increase in shore height. The presence of free space within the mussel beds and significant regressions between recruit and adult densities indicates that mussel populations are recruit limited.

Mean biomass decreased with an increase in shore height and was probably related to the decrease in size and density of mussels at higher shore levels. Exposure did not affect the average biomass within each zone.

A fine scale study of the effects of wave exposure, tidal height and substratum type on recruit densities was undertaken at two sites, viz. Diaz Cross and High Rocks. Two shores, one exposed and one sheltered were identified at each of the sites. All shores were classified prior to sampling. Sampling was completed over a 30 day period during peak recruitment, and samples were removed on as many days as sea and tide conditions permitted i.e. daily when possible. The total density of early plantigrades was greater at Diaz Cross than it was at the High Rocks, and this may be related to the local hydrodynamic patterns adjacent to the two sites. Exposure affected the densities of early and late plantigrades on algae on the low shore sites, where greater numbers of recruits were recorded on exposed low shore zones. Densities of plantigrades on the mussel bed and on algae on the mid and high shore were not affected by exposure. Low and mid shore zones usually had greater densities (at 100% cover of substratum) of plantigrades than the high shore zones, this was probably related to lower settlement rates on the high shore as a result of reduced submergence time. Generally greater plantigrade densities were recorded on algal substrata than on the mussel bed. In only one of the 20 comparisons completed was the density of plantigrades greater on mussels than it was on algae. However when the area of the substratum within a zone was taken into account the number of plantigrades in the mussel bed at a zone was often greater than the number on algae within the same zone. In close to half of these comparisons the total numbers of plantigrades were greater on the mussels than on the algae. This was due to the greater area of mussel bed available to recruits. There was no evidence supporting the suggestion of secondary settlement of plantigrades from algae to the mussel bed.

The results of this study demonstrate the importance of wave exposure, tidal height and substratum on certain aspects of the ecology of *Perna perna*. The importance of these factors is demonstrated at both the adult and early recruit stages of this mussel.

GENERAL INTRODUCTION

Perna perna is one of the most common intertidal mussels on the east coast of southern Africa where it forms dense beds on rocky shores in the intertidal region and is an important source of protein to people living in certain areas (Lasiak, 1993; Dye *et al.*, 1994). Although experimental laboratory studies have been undertaken on *Perna perna* (van Erkom Schurink & Griffiths, 1991), a limited amount of work has been published on the influence of physical factors on naturally occurring populations of this mussel (Berry, 1978; Phillips, 1994, Lasiak & Barnard, 1995). *Perna perna* is also a potentially threatened species with mussel beds being over exploited by human collectors in some places and being out competed for space by the invasive mussel, *Mytilus galloprovincialis*, in other areas (Griffiths *et al.*, 1992; Dye *et al.*, 1994). The biology of a species may vary on different shore types (Jones & Demetropoulos, 1968; Raimondi, 1988; Delafontaine & Flemming, 1989; Boulding & Van-Alstyne, 1993; Alvarado & Castilla, 1996), and this should be taken into account prior to the implementation of management strategies

Within the marine intertidal system many factors are responsible for shaping community population structure and dynamics. Degree of wave action has been known to affect the growth (Lindsay, 1998), shape (McLachlan *et al.*, 1995), size (Alvarado & Castilla, 1996), biomass (McQuaid & Branch, 1985), recruitment (Menge, 1991) and density (McLachlan, *et al.*, 1995) of intertidal organisms. Jones & Demetropoulos (1968), consider wave action to be one of the most important physical factors affecting rocky shores. The effects of tidal height on intertidal communities are well documented, and it is generally accepted that increases in tidal height and the resulting physical stress caused by aerial exposure are responsible for decreases in growth rates (Baird, 1966; Griffiths & Buffenstein, 1981; Griffiths & Hockey, 1987; Barnes & Hughes, 1988). Stress caused by increased tidal height normally sets the upper limits of a species' distribution (Suchanek, 1985), while Differences in recruitment rates between the low and high shore distribution of a species are also known to occur (Menge, 1991). Substratum type can affect the density of recruits on a shore (Phillips, 1994), which in turn can affect the population structure of the adult community (Connell, 1985).

It is difficult to isolate a single physical factor responsible for influencing the population dynamics of a species. The interaction of physical factors with each other can give rise to a confusing pattern. In many cases biological factors also affect the population dynamics of intertidal species . Predation and competition can be more important than physical factors in structuring mussel bed communities (Paine, 1974; Barkai & Branch, 1989). Community regulation incorporates the effects of biological and physical factors, physical factors may operate within a framework of biological factors or vice versa (Menge & Sutherland, 1987). Although this study does not incorporate the effects of biological factors on mussel populations, it provides an insight into the influences of wave exposure, tidal height and substratum on adult and juvenile *Perna perna*.

CHAPTER 1

THE EFFECT OF EXPOSURE AND TIDAL HEIGHT ON MUSSEL POPULATION STRUCTURE, SIZE, DENSITY, AND BIOMASS.

INTRODUCTION

Rocky shore community structure is influenced by a host of interacting biological and physical factors (Paine, 1966; Dayton, 1971; McQuaid & Branch, 1985; Connell, 1985; Barnes & Hughes, 1988), two of these factors, degree of wave exposure and tidal elevation have been related to differences in the population and community structure of intertidal organisms (Jones & Demetropoulos, 1968; Griffiths & Buffenstein, 1981; McQuaid & Branch, 1984, 1985; Griffiths & Hockey, 1987; Menge & Farrell, 1989).

Differences in the trophic structure of Cape Peninsula (South Africa) shores are associated with wave exposure, sheltered sites are dominated by grazers, while exposed sites are dominated by filter feeders (McQuaid & Branch, 1985). Total filter feeder biomass is also higher on shores experiencing greater wave action (McQuaid & Branch, 1985). Wave exposure can act directly on mytilid populations by physically removing individuals (Harger & Landenberger, 1971), which can result in more exposed sites being dominated by smaller mussels (Alvarado & Castilla 1996). Patch formation and the resulting decreased mussel densities caused by factors such as wave action or predation result in an increase in mussel growth rates (Petraitis, 1995). Suspension of detritus clouds by increased wave action may enhance the food supply for mussel beds, and result in faster growth rates and larger mussels at exposed sites (Berry 1978). However in contrast to this, Fréchette & Grant (1991) have demonstrated that the resuspension of particulate organic matter had no effect on the growth rates of *Mytilus edulis.* Increased silt loads in the water can decrease the growth rates of certain mussels, while the growth rates of others can show an increase (van Erkom Schurink & Griffiths, 1993). At least four species of mytilids (including *Perna perna*) reveal increases in growth rates with an increase in water circulation (van Erkom Schurink & Griffiths, 1993). Leeb (1995) demonstrated that *Mytilus galloprovincialis* grew faster and achieved greater sizes on a more exposed shore. Large size, high growth rates and low densities of mussels seem to be characteristics of exposed South African shores (Leeb, 1995; Lindsay, 1998).

Tidal height is a factor influencing the growth of intertidal organisms, this is especially true for sedentary species (Barnes & Hughes,1988). Reduced growth rates with increasing shore height are considered to be a function of decreased feeding time (Baird, 1966; Griffiths & Buffenstein, 1981), and this can lead to smaller individuals at these higher levels (Baird, 1966; Griffiths & Buffenstein, 1981; Griffiths & Hockey, 1987; van Erkom Schurink & Griffiths, 1993; Leeb, 1995). Competition and predation are known to limit the lower end of an intertidal species' distribution (Denley & Underwood, 1979; Underwood, 1981), while environmental stress (which increases with increasing tidal height) is thought to be more important in setting the upper limit (Seed, 1969b; Tan, 1975; Tsuchiya, 1983; Suchanek, 1985, Iwasaki, 1994). Mussel densities can also be affected by shore height, *Mytilus edulis* densities in the Exe Estuary (England) were lowest at high shore levels (McGrorty *et al.* 1993).

The brown mussel (*Perna perna)* is the most common intertidal bivalve on the south and east coasts of South Africa (Dye *et al.* 1994). It is very heavily exploited in certain parts of the country, to the point where local stock depletion occurs (Lasiak, 1991a&b; Dye *et al.* 1994). Other parts of the country, where there is strict control of harvesting, have healthier stocks (Dye *et al.* 1994).

There are few published data for the state of mussel stocks and the level of exploitation for the south coast of South Africa (but see Lasiak, 1991a&b; Dye *et al.* 1994). Investigation of the size structure, biomass and density of *Perna perna* stocks in relation to wave exposure and tidal elevation is important as differences in biology on different shores could have implications for future management approaches. As *Perna perna* is potentially threatened by the invasion of the Mediterranean mussel, *Mytilus galloprovincialis* (Griffiths *et al.*, 1992) the results obtained from this study may be of interest by way of comparison in future years.

1 MATERIALS AND METHODS

1.1 Study Area and Sites

The South African south coast is classified as warm-temperate, with the eastern most areas verging on sub-tropical (Brown & Jarman, 1978). Mean monthly sea temperatures vary between 15 and 22°C and are largely influenced by the warm Agulhas Current and localised upwelling (Ross, 1988; Field & Griffiths, 1991). A daily tidal cycle of two high and two low tides occurs. Spring tides alternate with neap tides to form two spring tides and two neap tides every month. The tidal range for spring tides is about 2m, while for neap tides it is only 1m (Stone, 1988; Field & Griffiths, 1991). As a whole the coastline is considered to be exposed in terms of wave action, but areas of relative shelter do exist.

18 sites between Port Elizabeth and Kei Mouth on the south coast of South Africa were selected for an examination of mussel beds on shores of different exposure (Figure 1.1) (Table 1.1). Prior to sampling, sites were classified as either exposed or sheltered. Exposed sites were in areas of higher wave energy, while sheltered sites in areas of lower wave energy. This classification was subjective, and was based on, 1- the aspect of mussel beds to prevailing sea and weather conditions and, 2- the wave development prior to a wave reaching the mussel covered rocks. Exposed sites were normally located on headlands where the mussel beds are subjected to the prevailing westerly winter swells and the easterly summer swells. These sites were also characterised by having visibly heavy wave action, waves would break onto or just before the mussel bed. In contrast to this, the more sheltered sites were usually in bays, where waves break further offshore and roll onto the rocks as white water. Swells are transporters of energy, a swell will lose very little energy as it travels across the ocean (Strahler & Strahler, 1989), but when a swell reaches shallow water the drag of the sea bottom causes the wave to steepen and break. Once broken the wave's energy is dissipated as it approaches the shore. Areas where the waves break further off shore are of a lower wave energy than those that are near the break line. Exposure is a relative term, what is described as sheltered by South African standards may be viewed as exposed in other countries or vice versa. Any comparisons made between these sites and those elsewhere should be viewed with caution.

Table 1.1 All sites sampled, the date on which they were sampled and classification as exposed and sheltered sites.

Date	Sheltered sites	Date	Exposed sites
28/04/95	Hougham Park (HP)	30/04/95	Fish River (FR)
29/04/95	Riet River (RI)	13/05/95	Cannon Rocks (CR)
01/05/95	Mpekweni (MP)	16/05/95	Kayser's Beach (KB)
02/05/95	Mgwalana (MG)	17/05/95	Kidd's Beach (KD)
14/05/95	Rufanes River (RU)	27/05/95	Glen Gariff (GG)
15/05/95	Old Woman's River (OW)	28/05/95	Glen Muir (GM)
18/05/95	Winterstrand (WS)	29/05/95	Cape Henderson (CH)
30/05/95	Black Rock (BS)	30/05/95	Black Rock (BE)
31/05/95	Morgan's Bay (MB)	09/06/95	Kwaai Hoek (KH)

At each site the mussel bed was divided into three vertical zones; low shore mussel beds, mid shore mussel beds and high shore mussel beds. Separation into zones was not physically measured, but biologically based.

Low shore

This zone was characterised by having a high percent of the rock covered by a continuous mussel bed. Upright coralline algae were common on the mussels and rock of the exposed sites, but less prevalent on the sheltered sites.

Mid shore

The mussels in this zone did not form a continuous mussel bed, but occurred in patches. The upright red alga, *Gelidium pristoides,* was commonly found both on and among mussels.

High shore

Small isolated clumps of mussels were associated with *G. pristoides* and the barnacle, *Tetraclita serrata.*

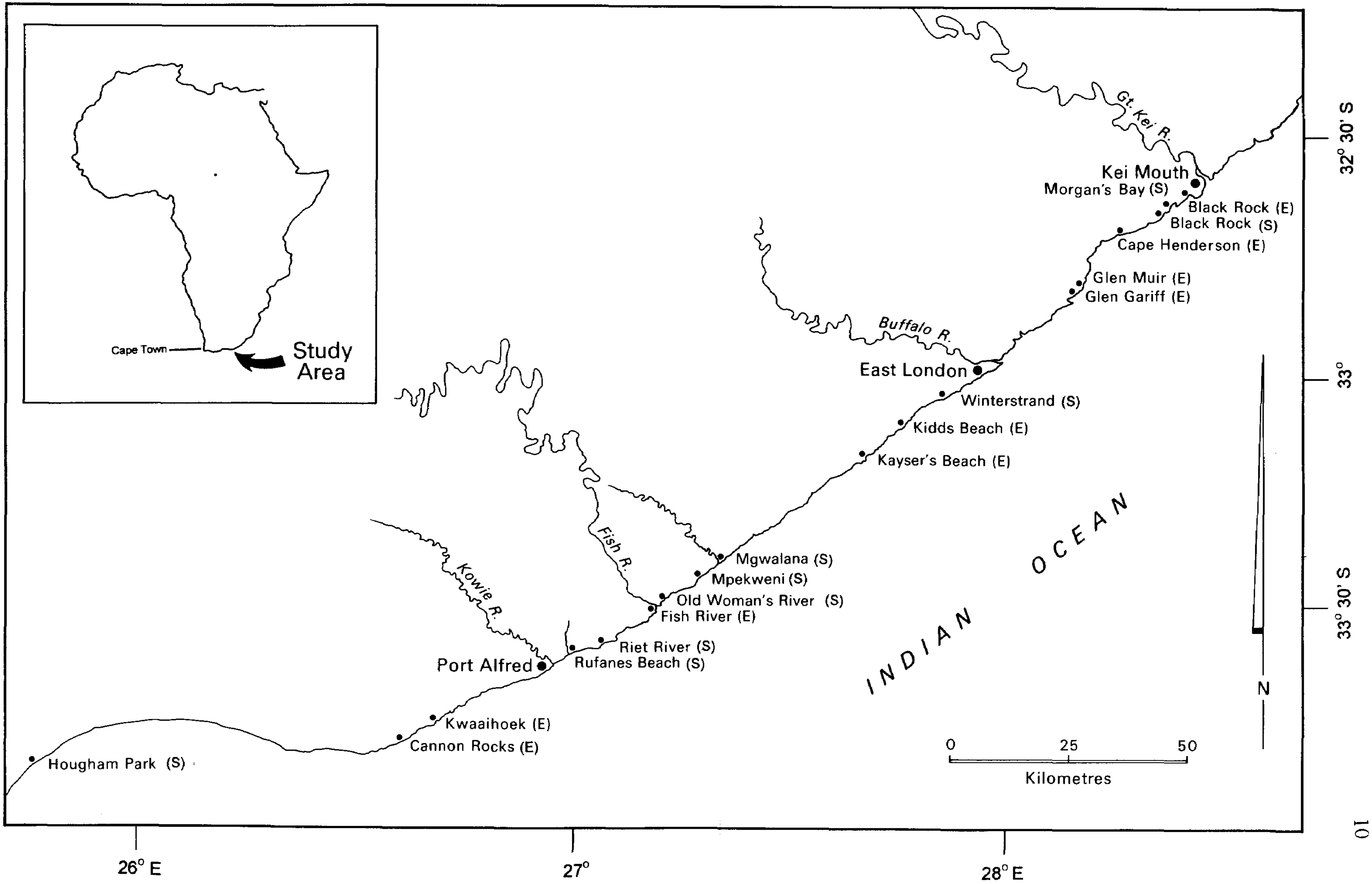


Figure 1.1 Map of study area, showing all exposed (e) and sheltered (s) sites sampled.

1.2 Data Collection

Mussels were collected over a five week period that included two spring tide cycles. Each shore was sampled on a single day. Fifteen 12x12cm quadrats were placed randomly in each zone at each site. All mussels that fell within the quadrat area were collected by scraping the rock with a metal instrument. Mussels from each quadrat were placed in separate bags and brought back to the lab for analysis.

1.3 Data analysis

Unless otherwise stated statistical analyses were completed using Statgraphics (v.7.0) software. Many statistical tests require that data sets conform to certain conditions. Normality of distribution and homogeneity of variances are probably the two most important requirements for many parametric statistics (Zar, 1996). If data did not conform to these requirements, transformations were undertaken to normalise distributions and homogenise variances. Details of transformations, when used, appear in the relevant sections of the Materials and Methods. If transformation brought data nearer to the desired conditions, then transformed data were used in the analysis. If transformations had no effect on the distribution of data or homogeneity of variances, then analyses were carried out on the untransformed data. Zar (1996) stresses that ANOVA is robust even when used with heterogeneous data (as long as samples are similar in number) and with data which deviate from normality. Even considerable deviations from ideal criteria only affect the analysis very slightly. In the event of a significant result using ANOVA, Tukey's multiple range test was used to isolate differences.

All collected mussels were measured and counted. The following aspects of the exposed and sheltered mussel populations were examined: size structure, adult/recruit relationships, maximum lengths, density, biomass and density/biomass relationships.

Size Structure

Maximum lengths of mussels >1mm were measured by hand (vernier callipers to the nearest 0.1mm) and by using the image analyser, PC Image (to the nearest 0.1mm). Frequency histograms (using 5mm size intervals) were generated for each zone at each site.

Image analysis made it possible to measure and count many individual mussels at the same time. A video camera (Panasonic F10 CCD) connected to a personal computer (486) was positioned directly above a light table on which the mussels were placed. Once PC Image had taken a "photograph" of the mussels on the light table it was possible for the software to measure each distinct object (in this case each mussels). Calibration of the program prior to analysis allowed the computer to convert the length of a pixel into a fraction of a millimetre (0.3mm=1 pixel for small mussels and 0.6mm=1 pixel for large mussel). PC Image then converts the number of pixels that each mussel consists of into a meaningful length measurement. To ensure accurate measurements, small mussels (1-15mm) were measured under a different zoom setting to larger mussels (15-80mm). Mussels larger than 80mm were measured by hand.

To test the accuracy of the image analysis a comparison of the two measuring methods was performed by regressing the vernier measurements of mussels against the computer derived values for the same mussels. The r^2 value showed that measurements were close to identical (r^2=0.9996, $p<0.05$, n=63) (Figure 1.2).

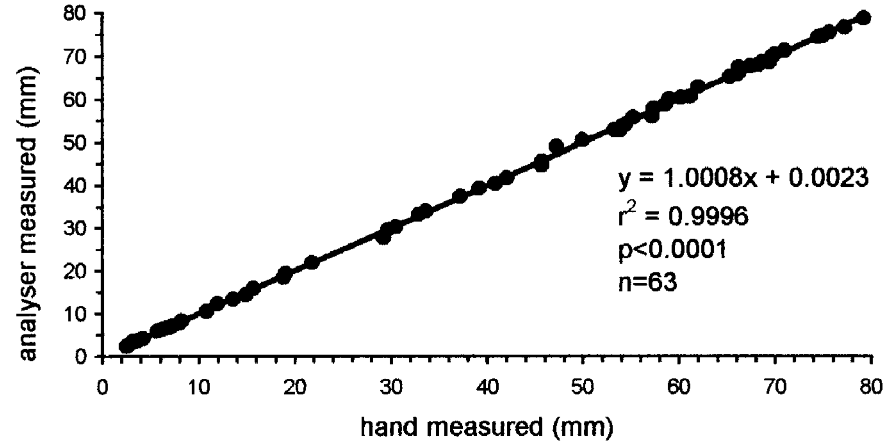


Figure 1.2 Regression of computer measured mussels versus hand measured mussels. Regression analysis was performed on Statgraphics (v.7.0).

Principal component analysis (PCA) was carried out on length frequency data using the standardised frequencies (percentages) of 10mm size classes as data variables. Large numbers of recently settled juveniles at some sites and not at others could mask similarities between sites. For this reason mussels under 15mm were excluded from the PCA. Phillips (1994) and Berry (1978) considered mussels of about this size to be capable of suddenly appearing in large numbers on the intertidal zone.

PCA is an ordination technique that projects a multidimensional set of points onto a graph (Randerson, 1993). Mussels from each site and at each zone were divided into 10mm size classes (starting with 10-20mm and ending with 120-130mm), each of these size classes can be considered to be a variable. Each variable is then assigned a **component weight** according to its importance (frequency) in relation to the other variables. A plot of the position of the **component weights** for each variable in relation to each other can be obtained. A **principal component graph** can now be generated, each point on the PCA chart represents a zone at a site. The position of a point on the PCA chart (in this case a zone at a site) is influenced by the dominant size categories of the mussels in that zone and the **component weight** values assigned to these dominant size classes. For example, if the component weights for the smaller size classes fall to the left of the **component weights chart**, then a zone with many mussels in the smaller size categories will be pulled to the left of the **PCA chart**. By overlaying **the component weights chart** and the **PCA chart**, it is possible to see which **component weights** are influencing the position of a zone on the **PCA chart**. Zones with mussels of a similar size structure are weighted similarly and so group together on the graph.

Two-way ANOVA was performed on the principal component one values from the PCA, zone and exposure were used as factors.

Mean maximum lengths

To examine any differences in maximum size relating to wave exposure and tidal height, the mean maximum lengths of mussels were calculated by taking the average size of the 10 largest mussels in each zone from each site. Pooled average mean maximum sizes were calculated for exposed and sheltered, low, mid and high shore zones. Two-way ANOVA was used to examine the effects of zone (low, mid, high) and exposure (exposed, sheltered) on mean maximum lengths. A multiple range test revealed where significant differences occurred.

For each of the three zones (low, mid, high) a one-way ANOVA was performed on the mean maximum lengths using site as a factor.

Density

An average density of adult mussels (>15mm) per m^2 was calculated for each of the zones at each site. To test possible relationships a two-way ANOVA was run on root transformed data comparing the factors zone and exposure.

As quadrats were placed randomly, densities reflect the density of the mussel bed and not of mussels at 100% cover. It was therefore not possible to obtain any information on the packing densities of *Perna perna*. The densities of juvenile mussels (<15mm) were compared with a two way ANOVA using zone and exposure as factors.

The recruit/adult relationship was investigated at each shore level. Six regression analyses of juvenile density against adult density were performed, one for each of the three zones within the categories of sheltered and exposed, using data pooled from all sites.

Biomass

Sub-samples of mussels (n=25-60) were used to establish the relationship between mussel length and dry mass. Mussels were hand measured and the flesh removed and placed in an oven at 60°C. Mussels were considered dry when no further weight loss was recorded (about two days). Dried mussels were removed and weighed to four decimal places of a gram. Linear regression equations for mussels in each zone at each site were calculated using log/log transformed data (*i.e.* 54 regressions). Estimates of the dry mass of each mussel measured (from the length data) were obtained by applying the mussel lengths to the dry mass/length equation. An estimate of the biomass for each 12x12cm quadrat was calculated, juveniles less than 15mm were excluded from this analysis. Effects of zone and exposure on biomass were examined with a two-way ANOVA.

Biomass/Density Relationship

The relationship between biomass and density was examined for each shore height. No separation was made between exposed and sheltered shores, as neither density nor biomass data showed any significant effect due to exposure. A regression between the density for each quadrat and the estimated biomass for each quadrat was completed separately for low, mid and high shore sites.

1.4 RESULTS

Size Structure

There was a decrease in the size of adult mussels (>15mm) with an increase in shore height. Sheltered shores all showed similar patterns of size distributions and were roughly bimodal, though bimodality was not always pronounced (Figures 1.3a-i). The modal size of the adult cohort was between 35-65mm on the low shore. This bimodal pattern was observed through the different zones. Exceptions to this pattern were the sites at Hougham Park (Figure 1.3i) and Old Woman's River (Figure 1.3f), where the mode of the low shore adult cohort occurred in the size classes 75-79.9mm and 80-84.9mm respectively. The pattern for the exposed low and mid shore sites was similar to those of the sheltered sites (*i.e.* bimodal), however the modal size of the adult cohort for the exposed sites was larger (between 65-80mm for low shore sites) (Figures 1.3j-r) than its equivalent for the sheltered shores. The exceptions to the bimodal pattern observed at the sheltered sites and at the exposed low and mid shore zones were six of the exposed high shore zones, which showed unimodal length distributions (Kwaai Hoek, Figure 1.3q; Black Rock (e), Figure 1.3j; and Kayser's Beach, Figure 1.3o; exhibited bimodal distributions) (Table 1.2).

Table 1.2 Summary of characteristics of length frequency data for low, mid and high shore; exposed and sheltered sites. Adult mode refers to the adult modal cohort (*i.e.* mussels greater than 15mm).

Shore type	Low shore	Mid shore	High shore
Exposed	• Bimodal • Adult mode: 65-80mm	• Bimodal • Adult mode: 25-60mm	• Unimodal • Adult mode: 20-40mm (exceptions, Kwaai Hoek, Black Rock, Kayser's Beach)
Sheltered	• Bimodal • Adult mode: 35-65mm (exceptions, Old Woman's River, Hougham Park)	• Bimodal • Adult mode: 20-60mm	• Bimodal (except Winterstrand) • Adult mode: 20-45mm (except Old Woman's River)

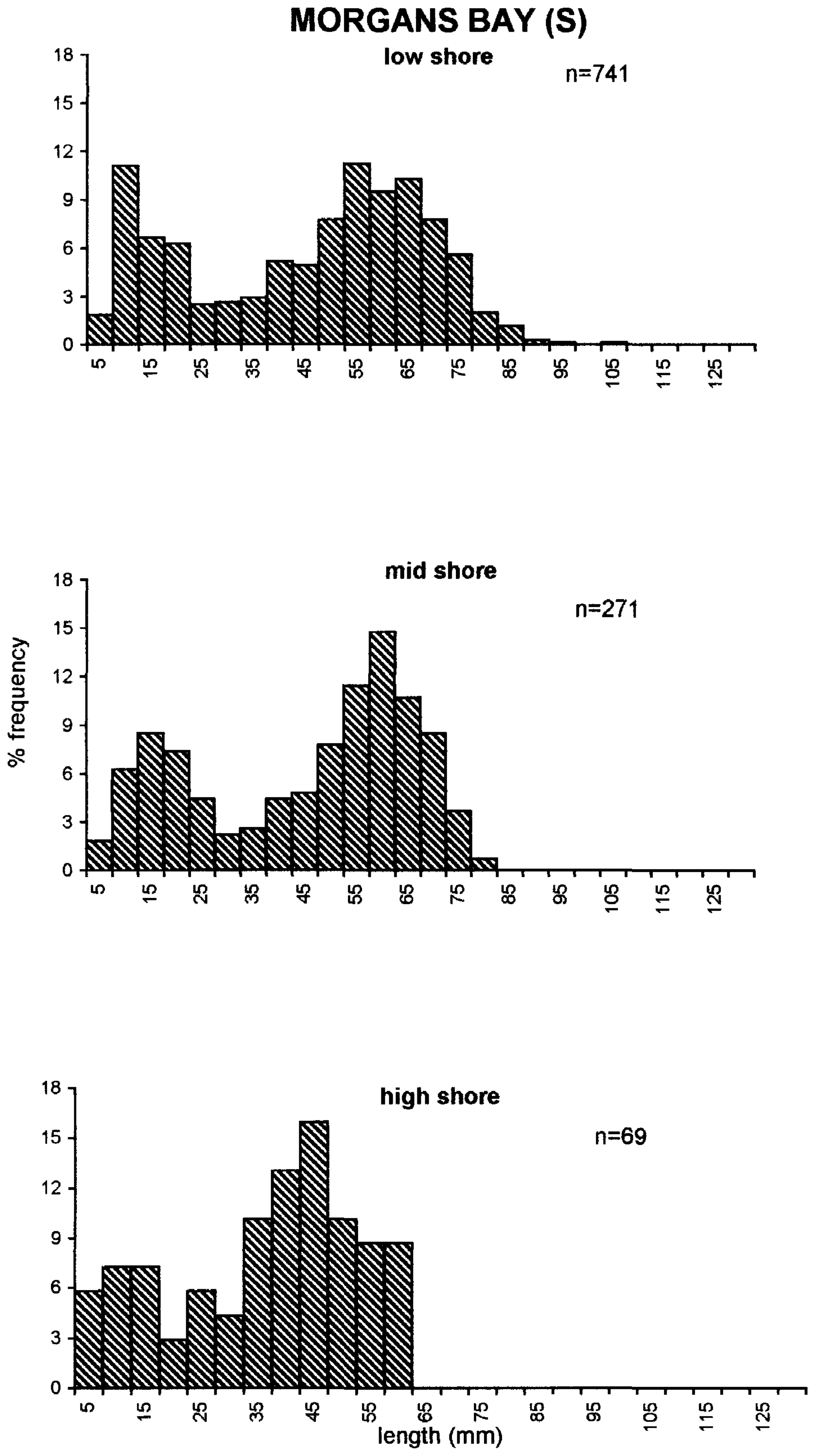


Figure 1.3a

Figure 1.3 Length frequency histograms of mussels on low, mid and high shore zones at sheltered (a-i) and exposed (j-r) shores. E or S after the name of a site represents degree of exposure as exposed or sheltered respectively. The number 5 on the x-axis scale represents the size class 1-4.99mm, the number 15 represents the size class 14-14.99mm etc. In cases of very high frequencies, the number at the top of the column shows the frequency for that size class.

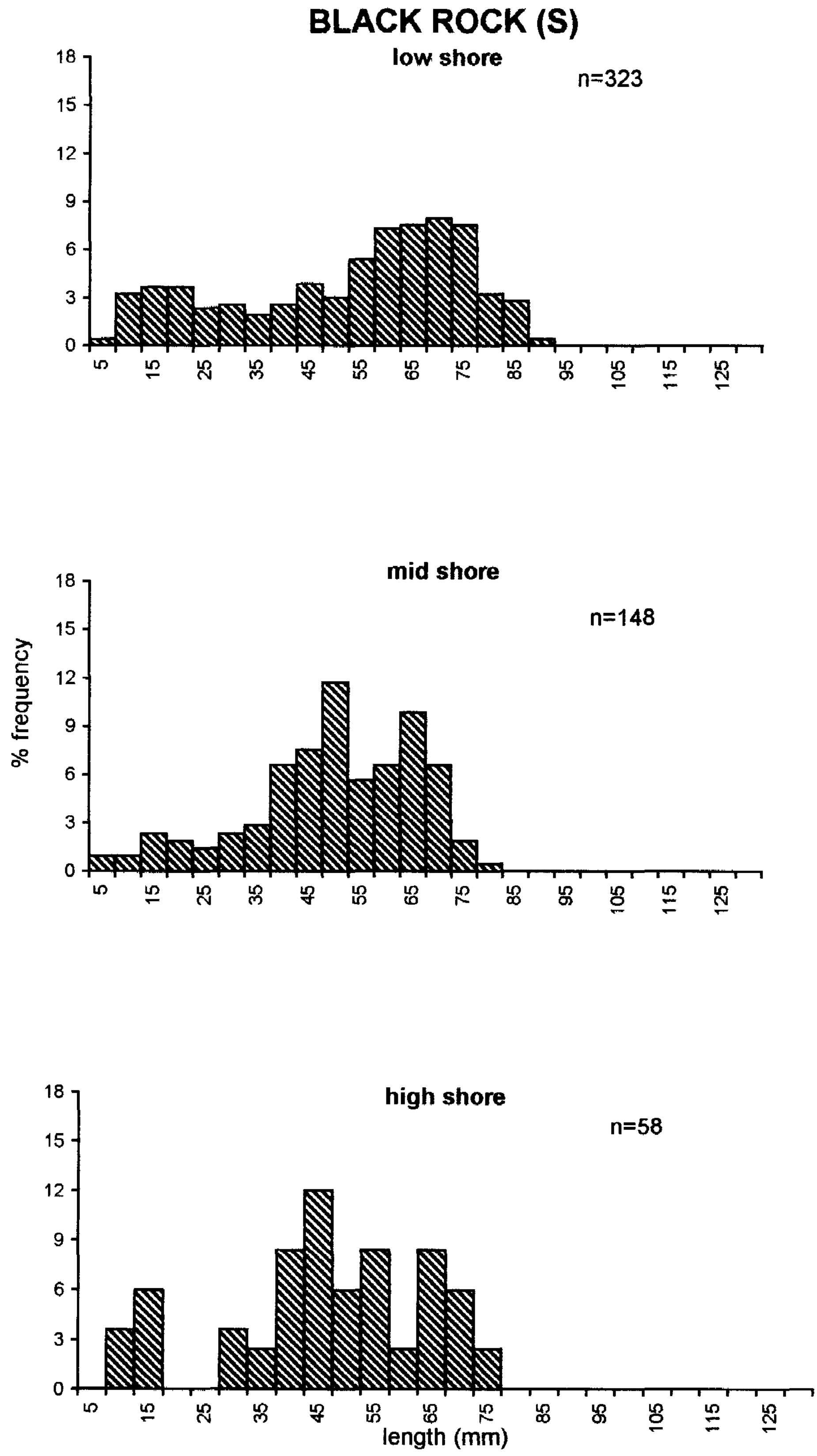

BLACK ROCK (S)
low shore
n=323
mid shore
n=148
high shore
n=58
% frequency
length (mm)
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125

Figure 1.3b

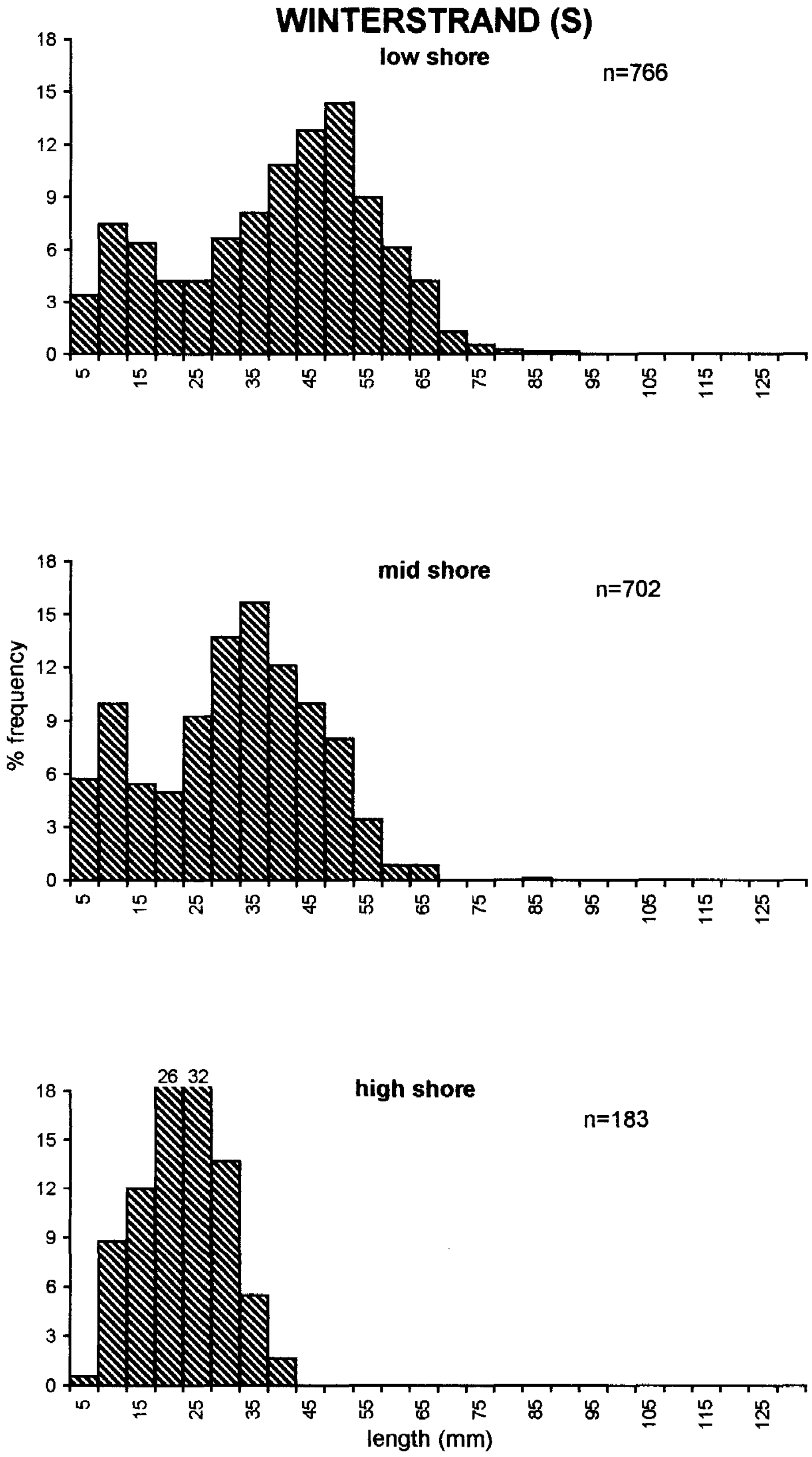

WINTERSTRAND (S)
low shore
n=766
mid shore
n=702
high shore
n=183
26
32
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3c

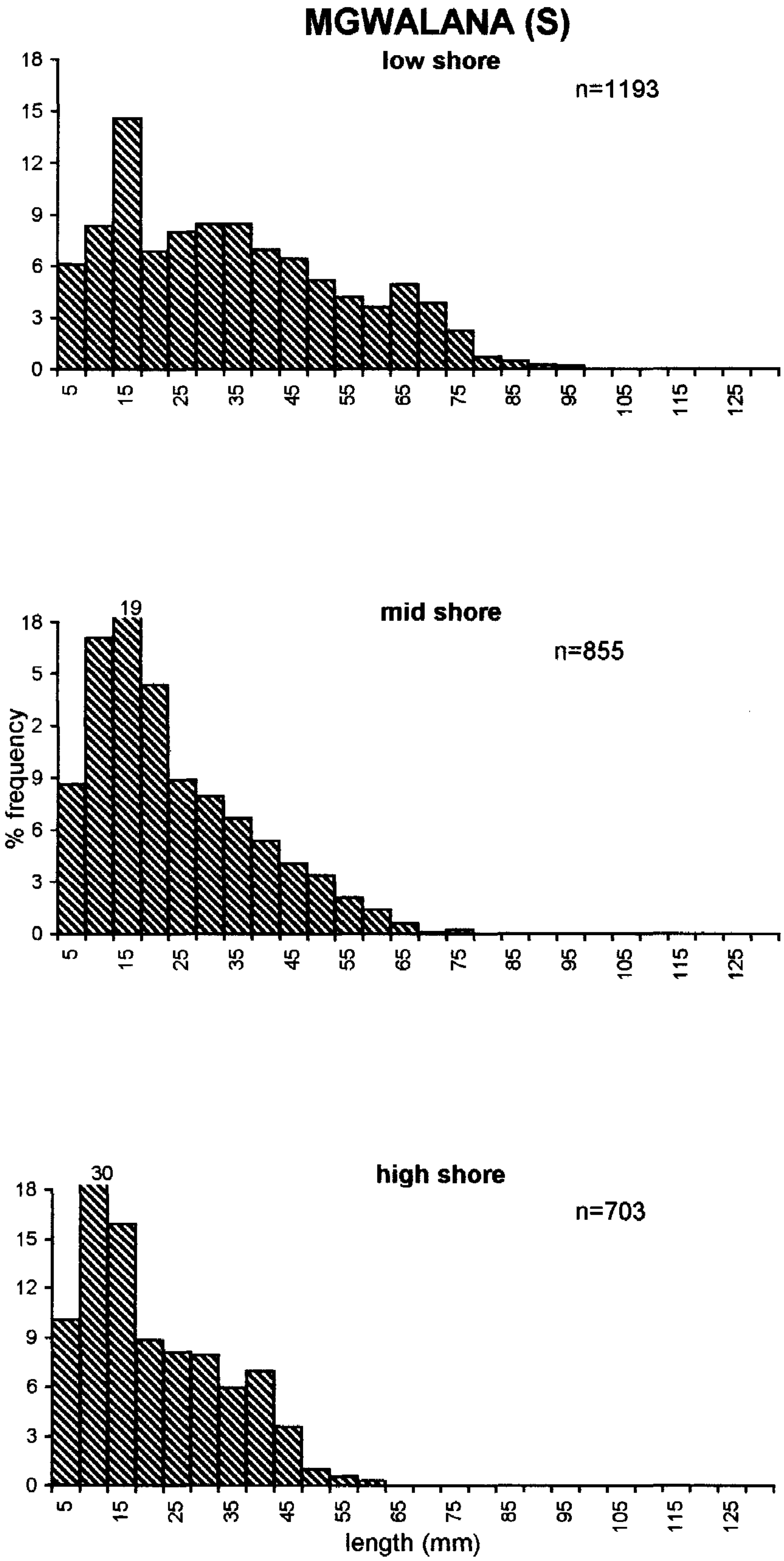

MGWALANA (S)
low shore
n=1193
18
15
12
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
mid shore
19
n=855
18
5
2
9
6
3
0
% frequency
high shore
30
n=703
length (mm)

Figure 1.3d

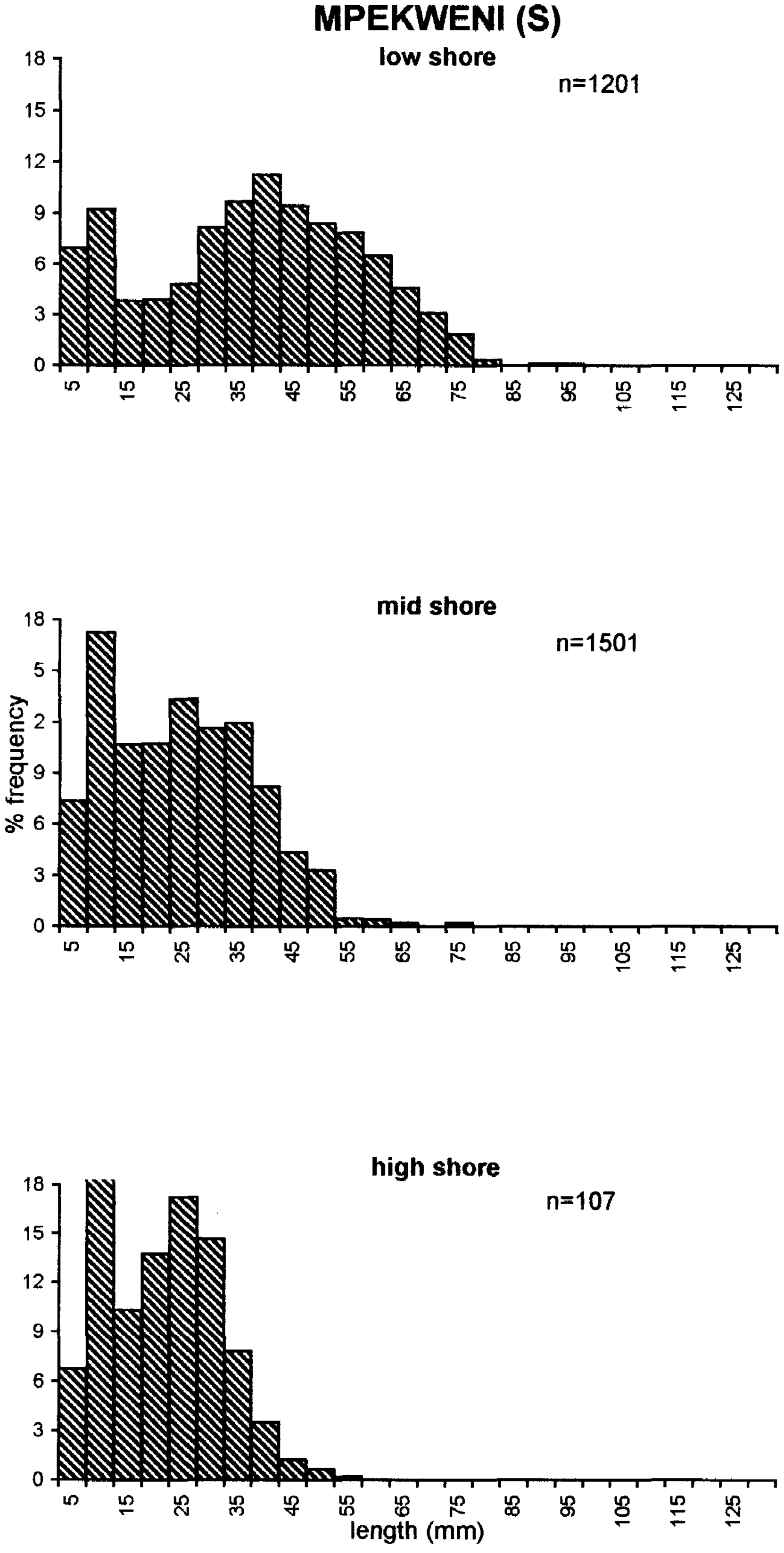

MPEKWENI (S)
low shore
n=1201
18
15
12
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
mid shore
n=1501
% frequency
18
5
2
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
high shore
n=107
18
15
12
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3e

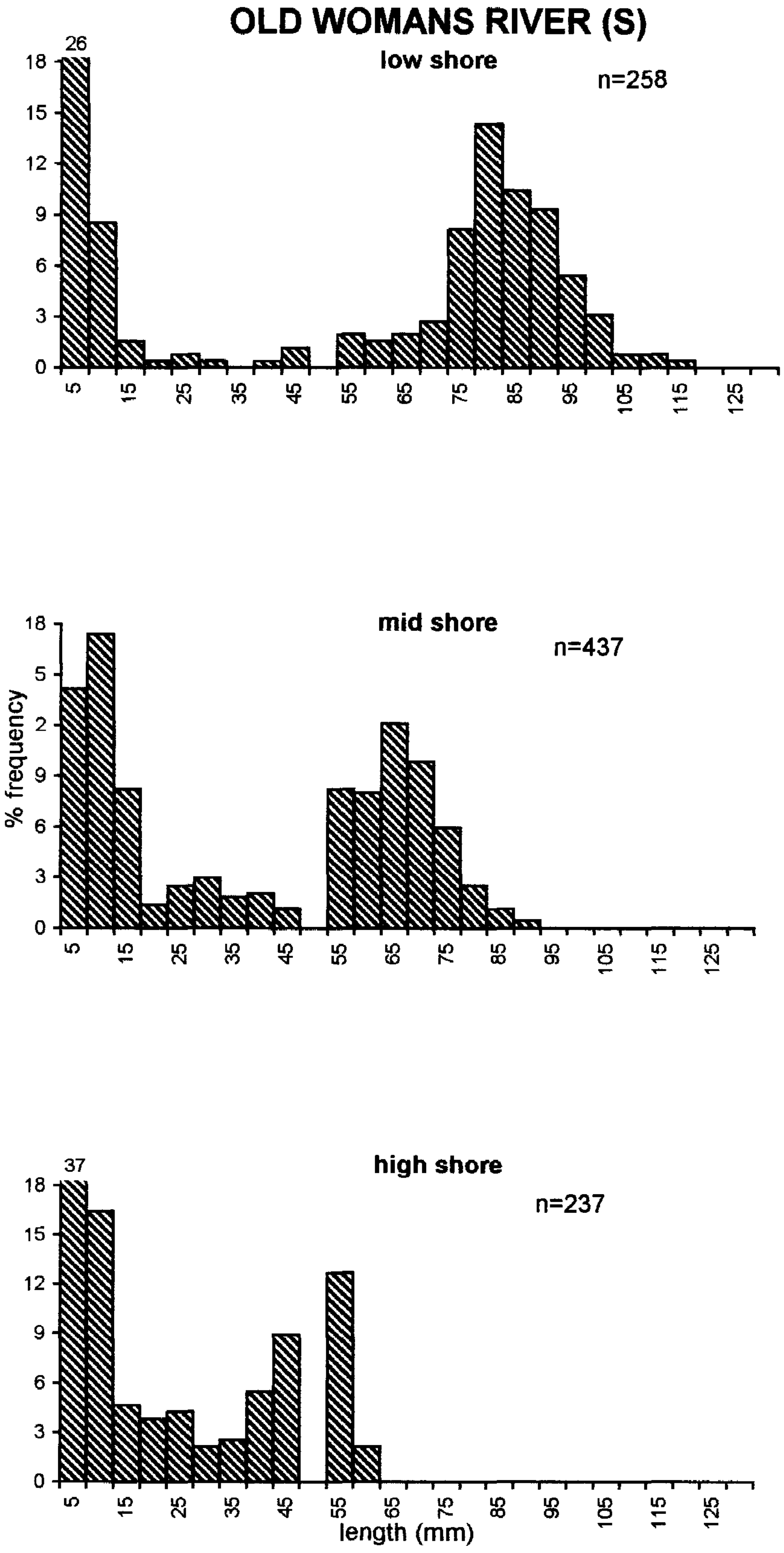

OLD WOMANS RIVER (S)
low shore
n=258
26
18
15
12
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
mid shore
n=437
18
5
2
9
6
3
0
% frequency
high shore
n=237
37
length (mm)

Figure 1.3f

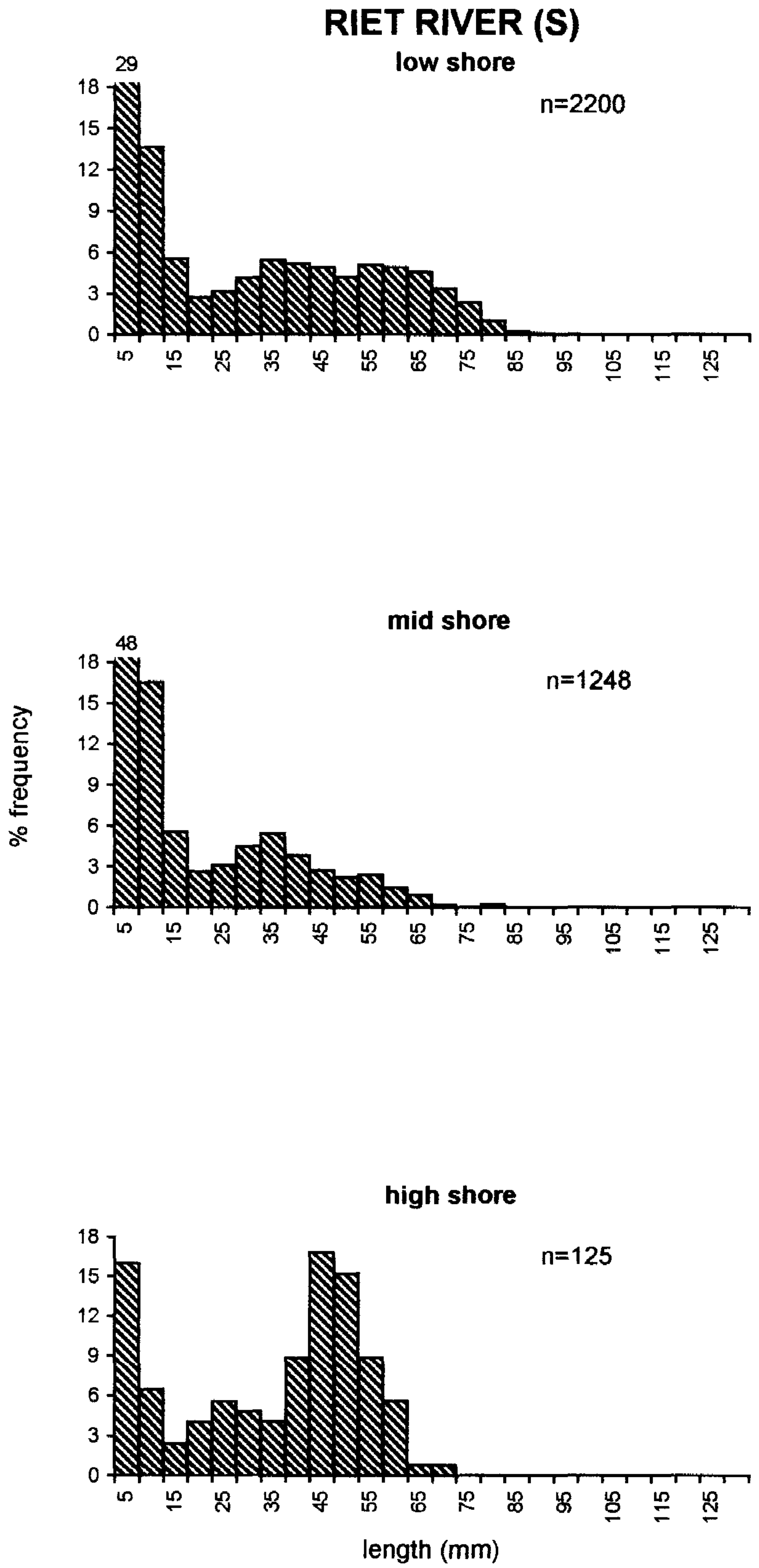

RIET RIVER (S)
low shore
n=2200
29
mid shore
n=1248
48
high shore
n=125
18
15
12
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
% frequency
length (mm)

Figure 1.3g

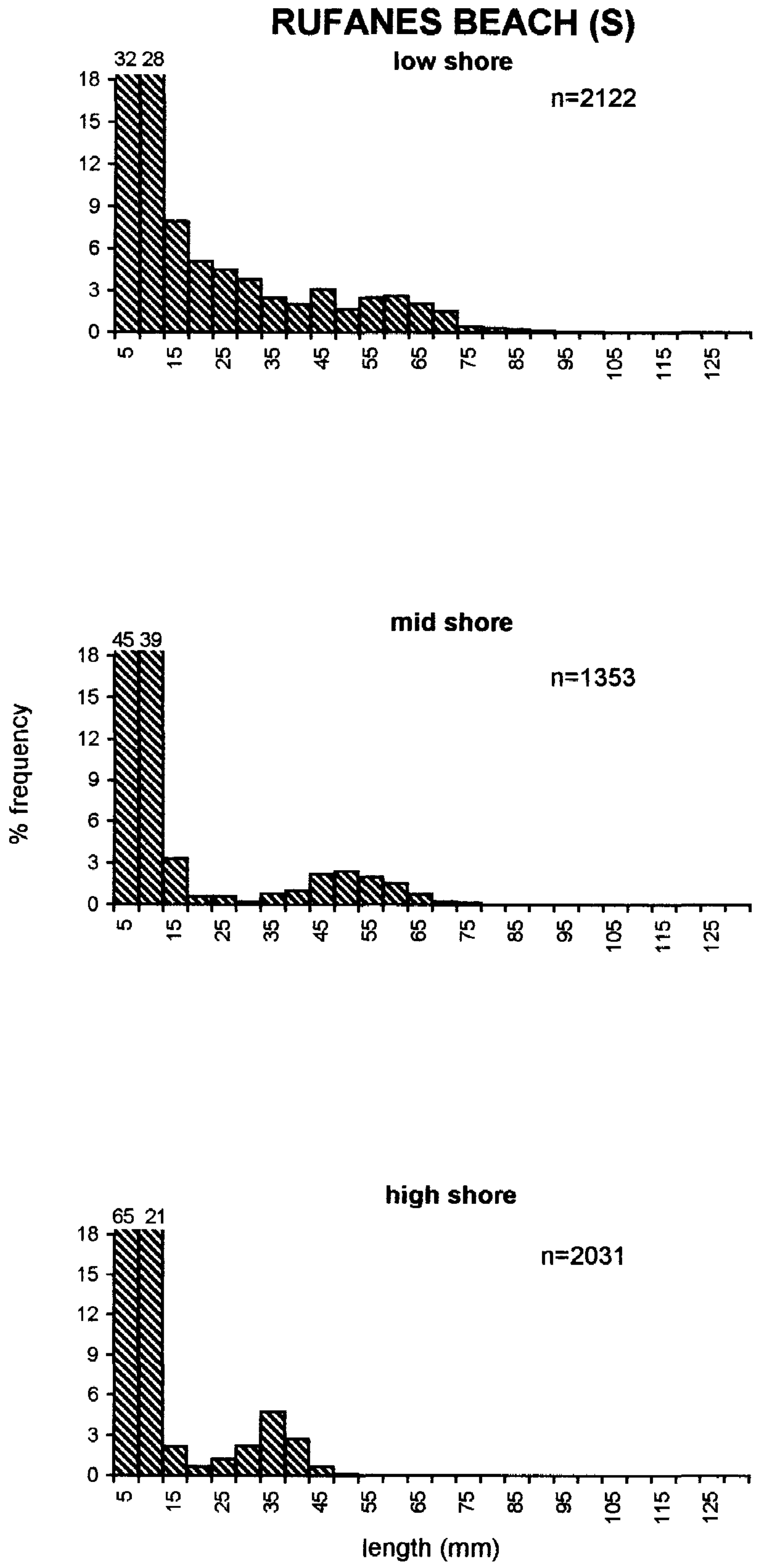

RUFANES BEACH (S)
low shore
n=2122
32 28
mid shore
n=1353
45 39
high shore
n=2031
65 21
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3h

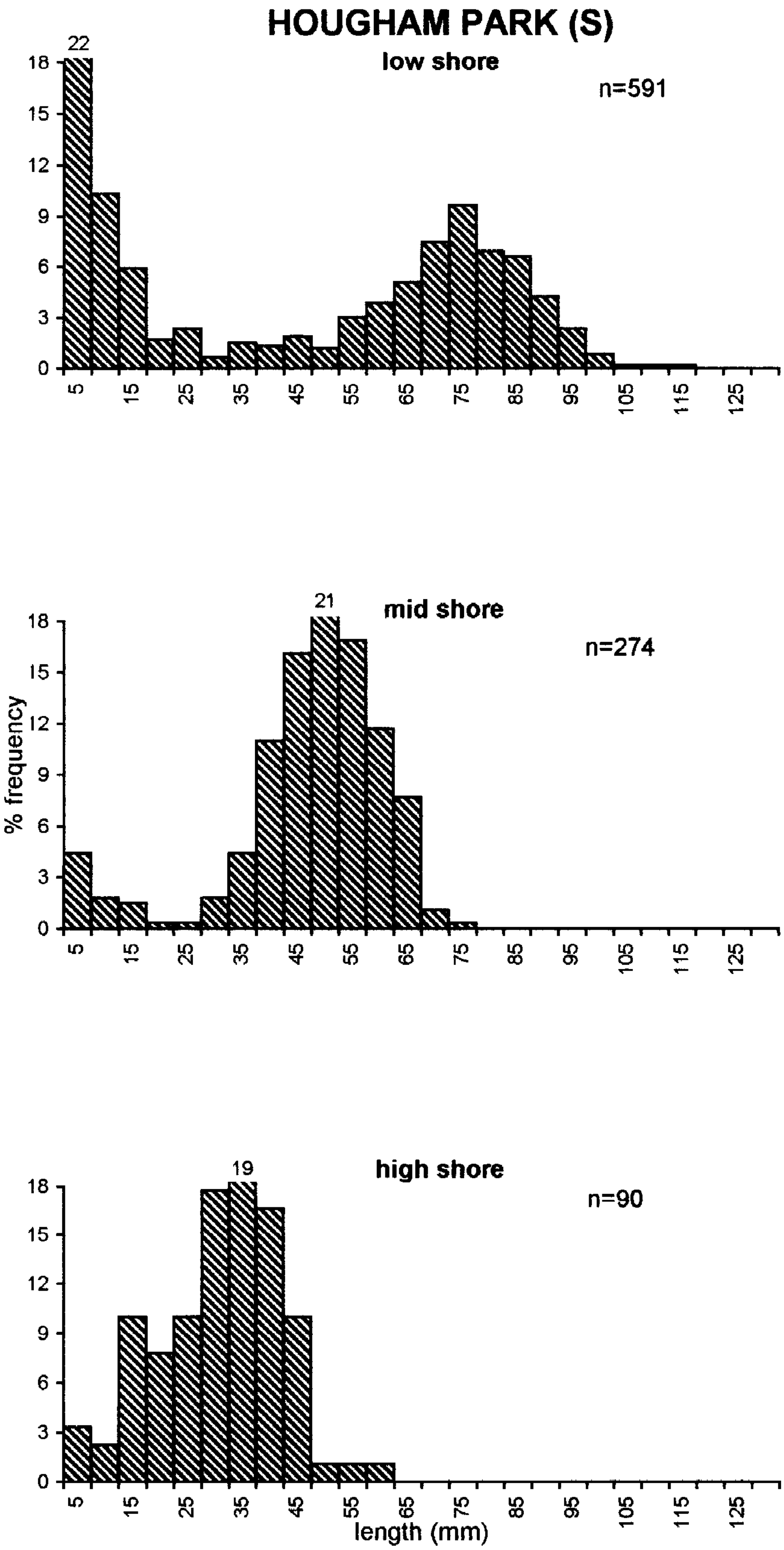

HOUGHAM PARK (S)
low shore
n=591
22
18
15
12
9
6
3
0
5
15
25
35
45
55
65
75
85
95
105
115
125
mid shore
n=274
21
% frequency
high shore
n=90
19
length (mm)

Figure 1.3i

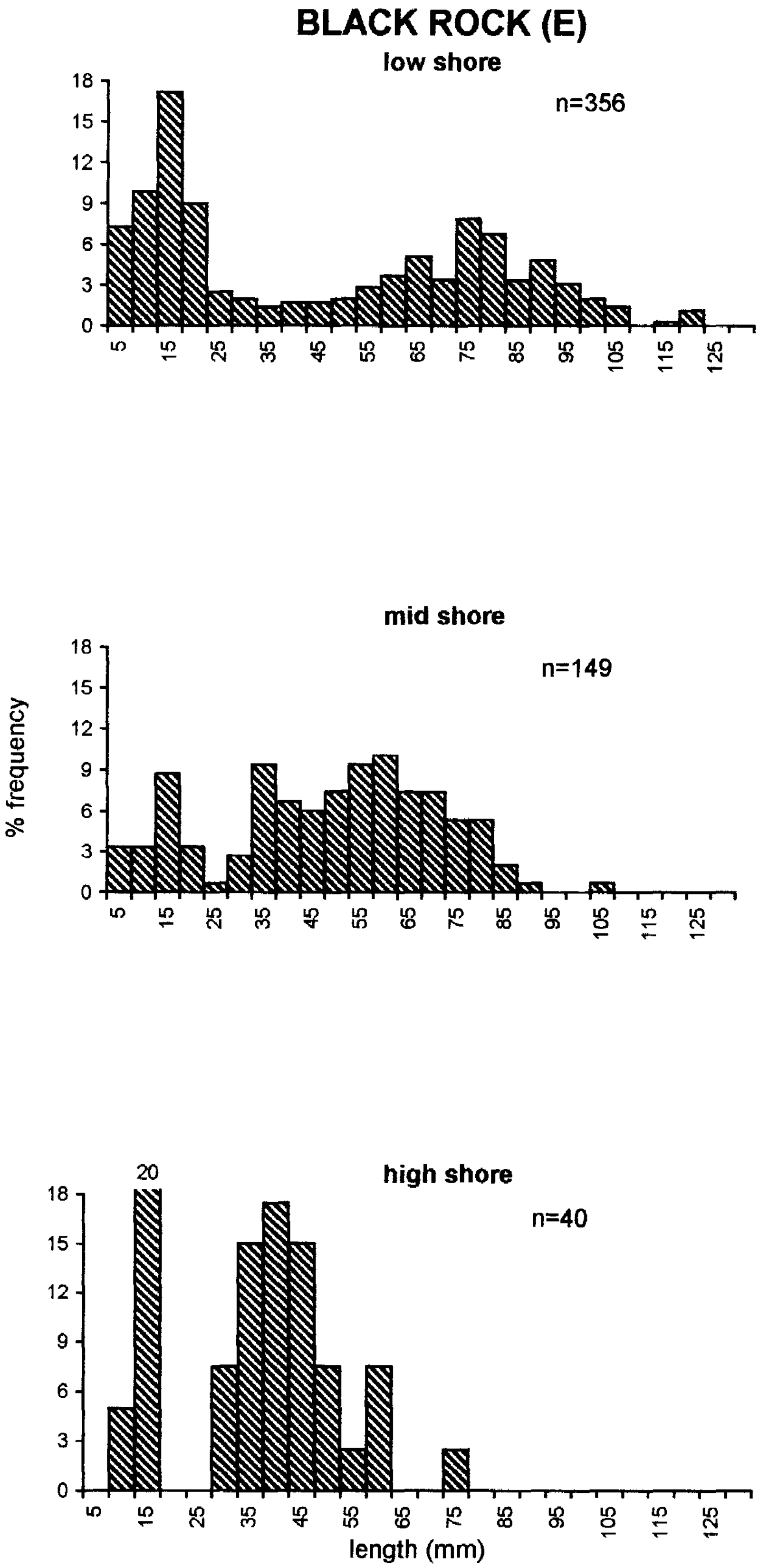

BLACK ROCK (E)
low shore
n=356
mid shore
n=149
high shore
n=40
20
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3j

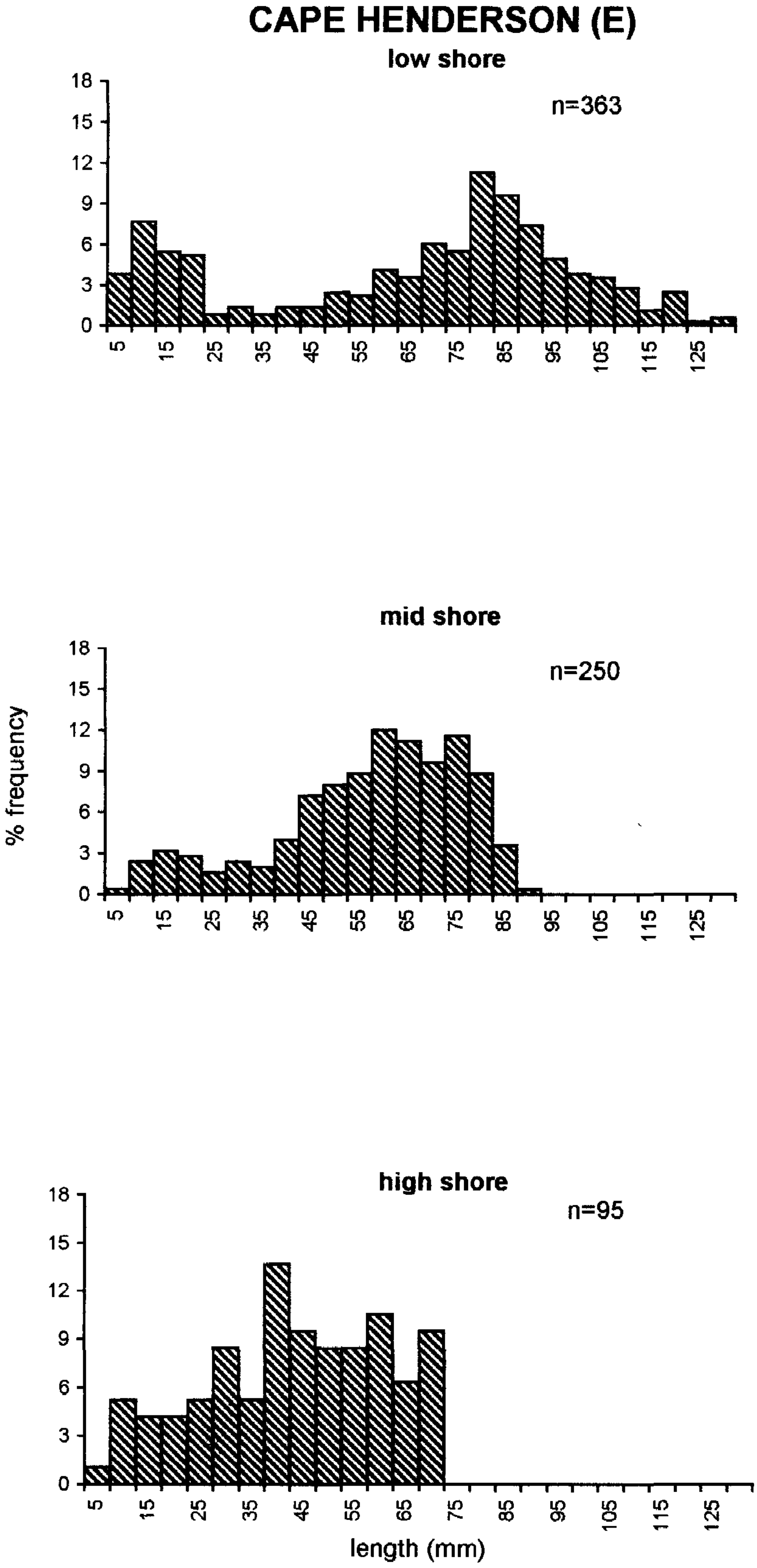

CAPE HENDERSON (E)
low shore
n=363
mid shore
n=250
high shore
n=95
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3k

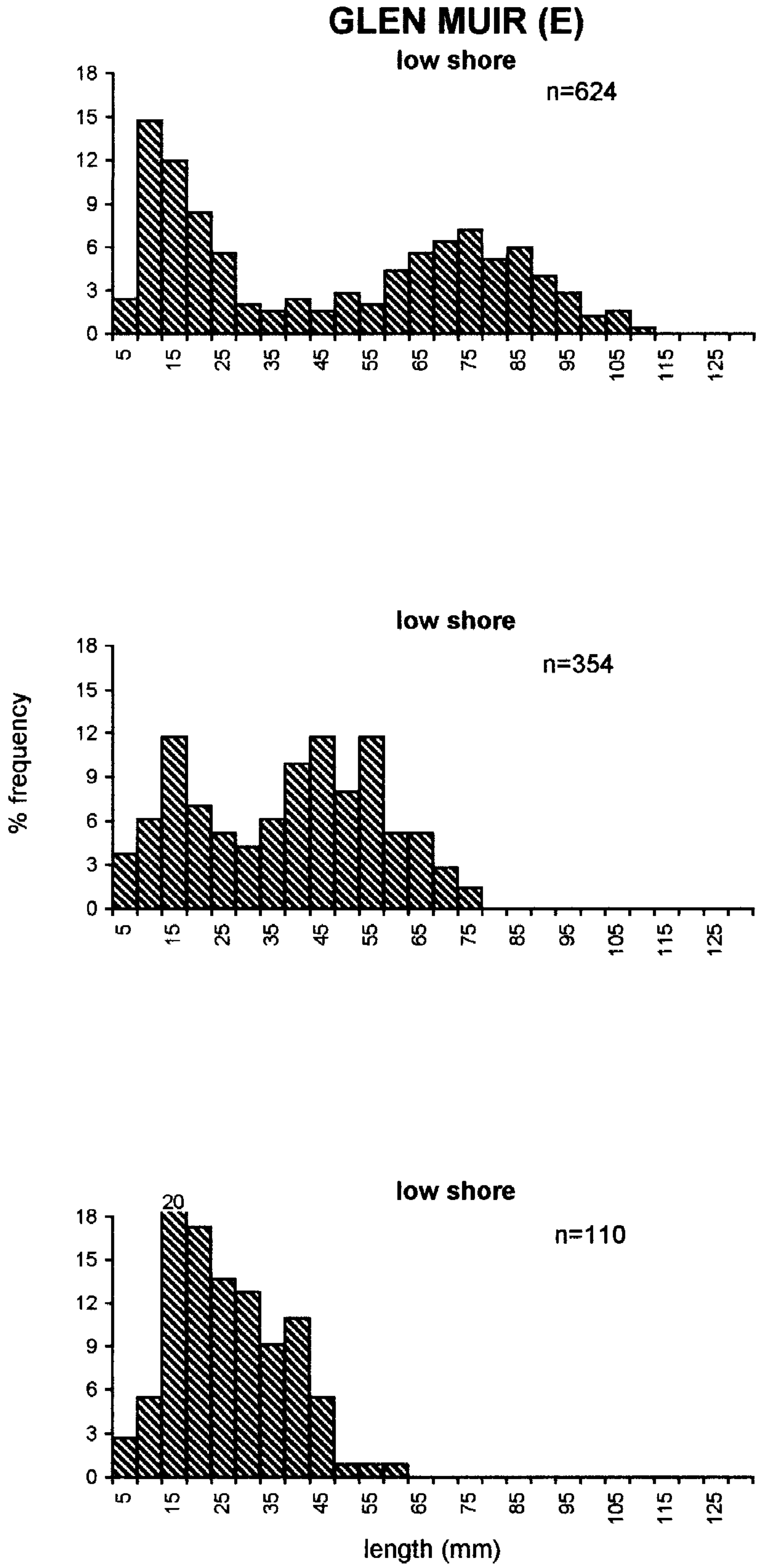

GLEN MUIR (E)
low shore
n=624
low shore
n=354
low shore
n=110
20
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3l

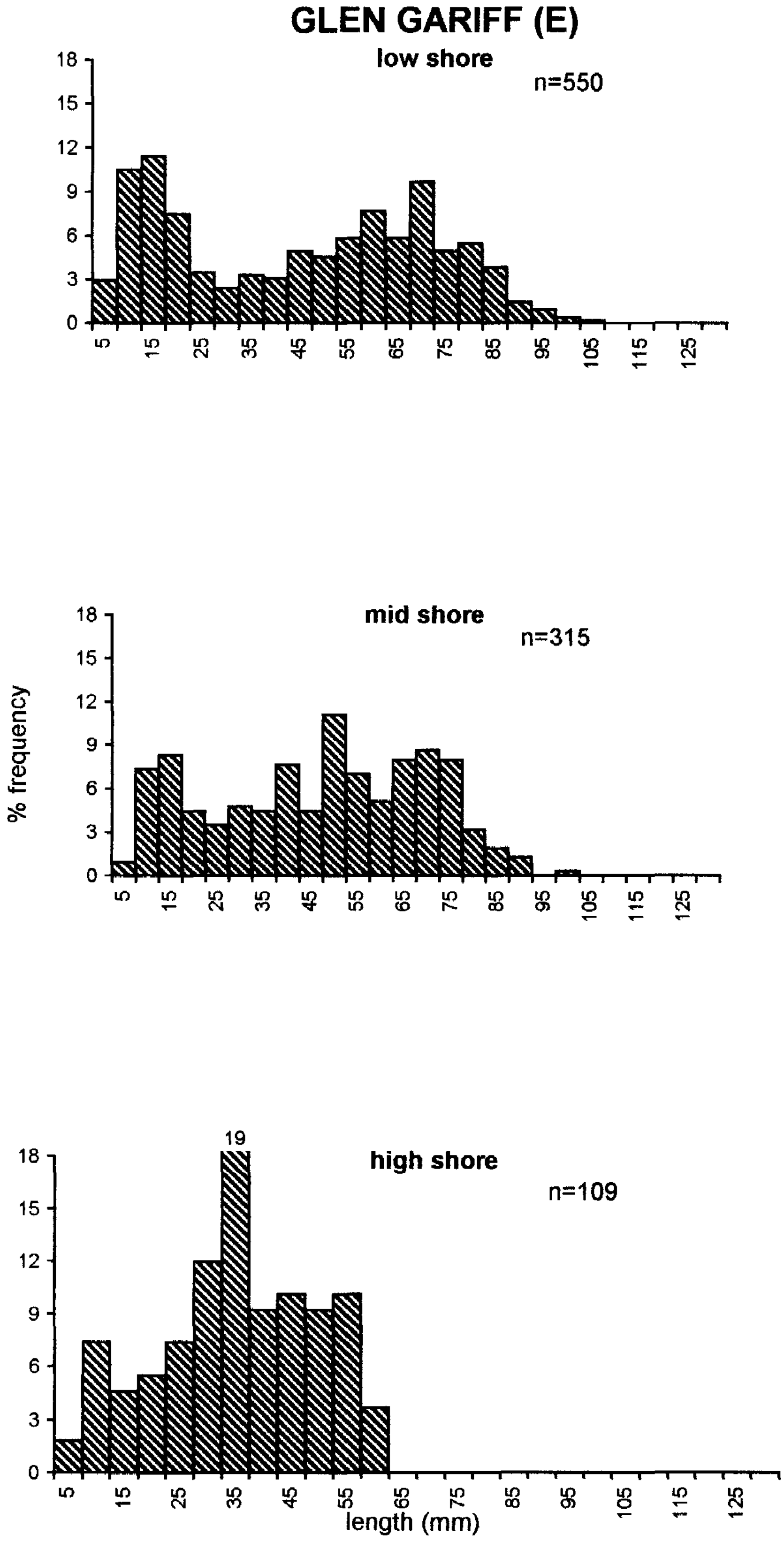
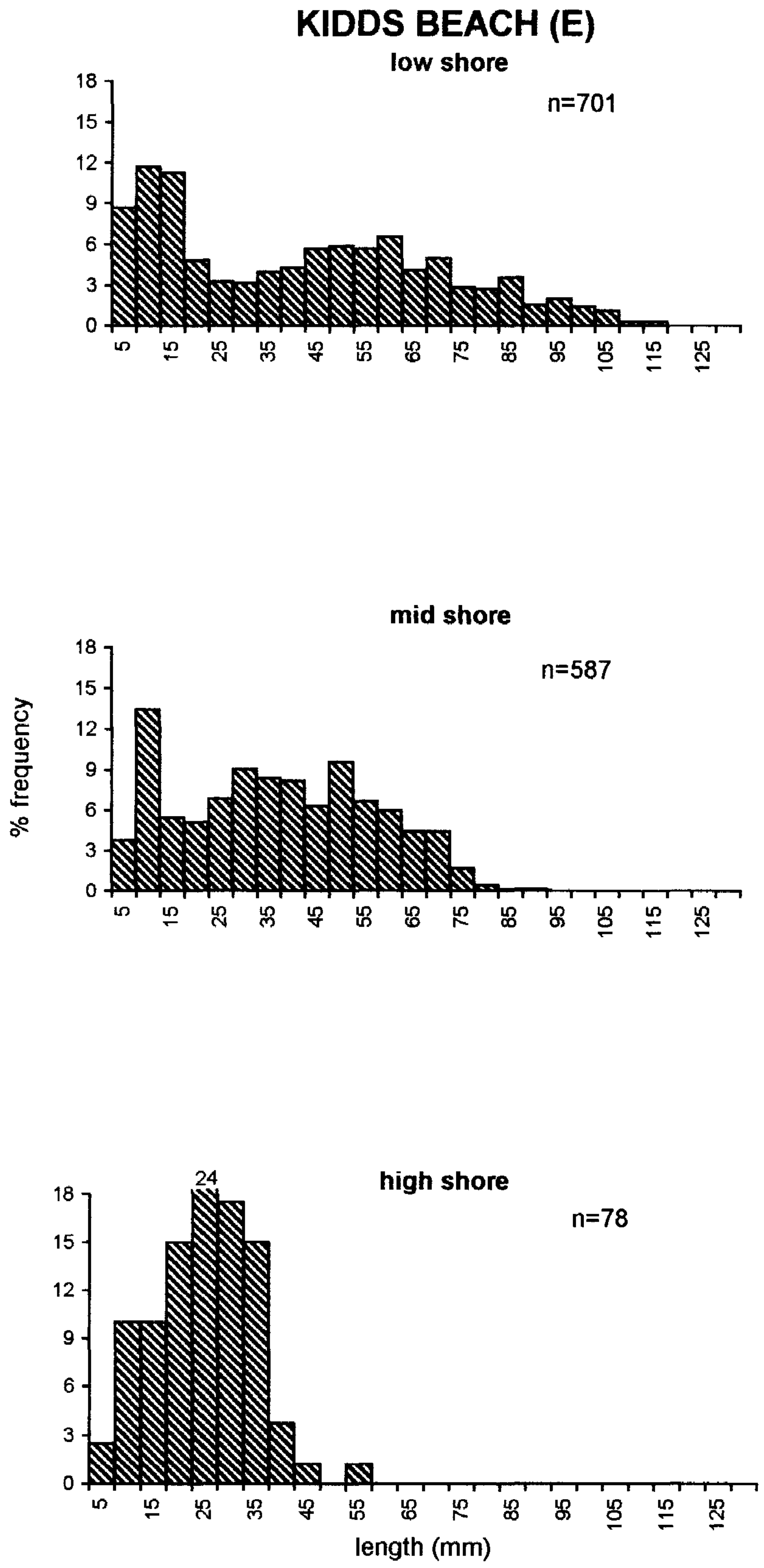

GLEN GARIFF (E)
low shore
n=550
mid shore
n=315
high shore
n=109
19
% frequency
length (mm)
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125

Figure 1.3m



KIDDS BEACH (E)

low shore

mid shore

high shore

Figure 1.3n

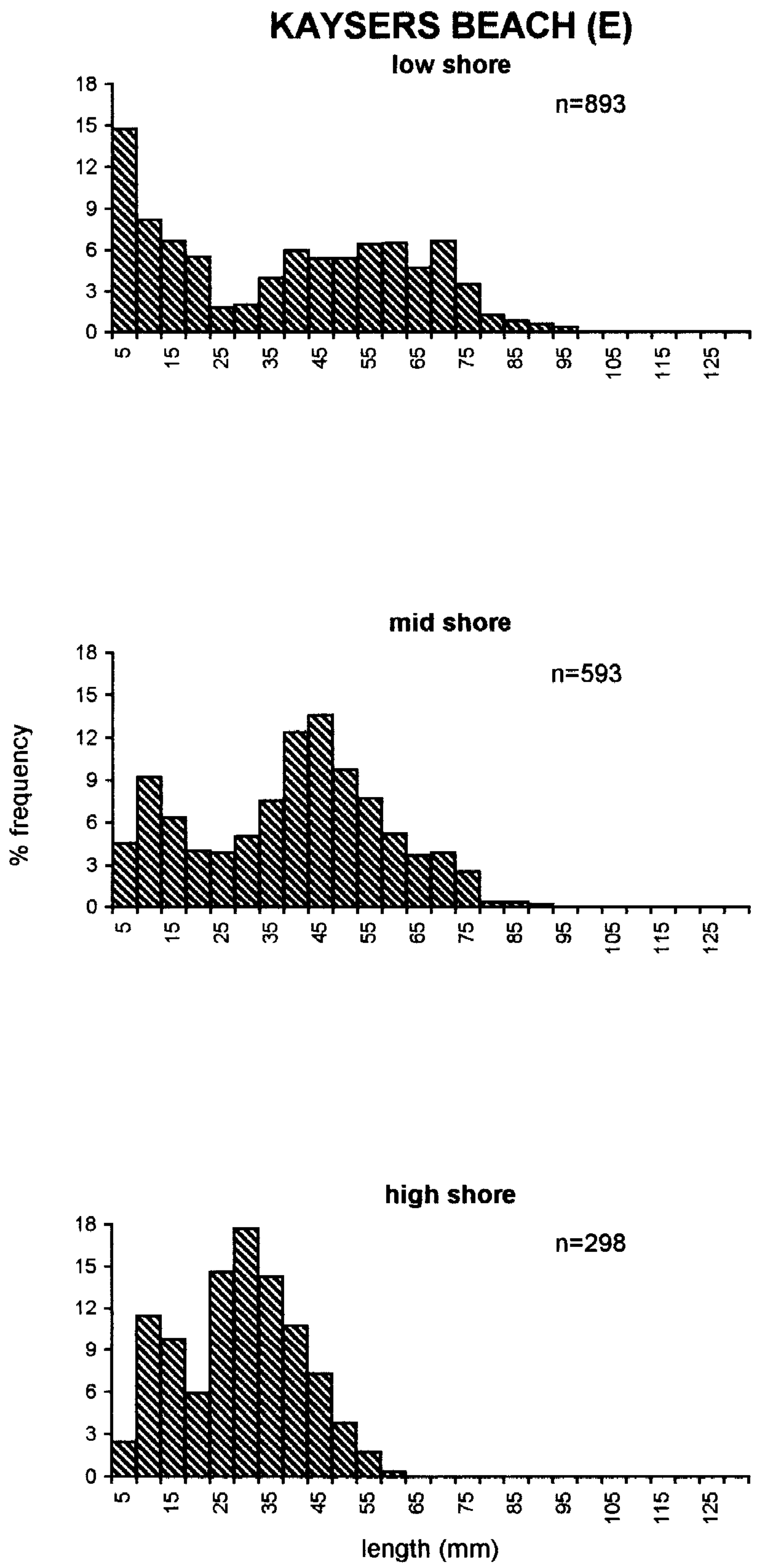

KAYSERS BEACH (E)
low shore
n=893
mid shore
n=593
high shore
n=298
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3o

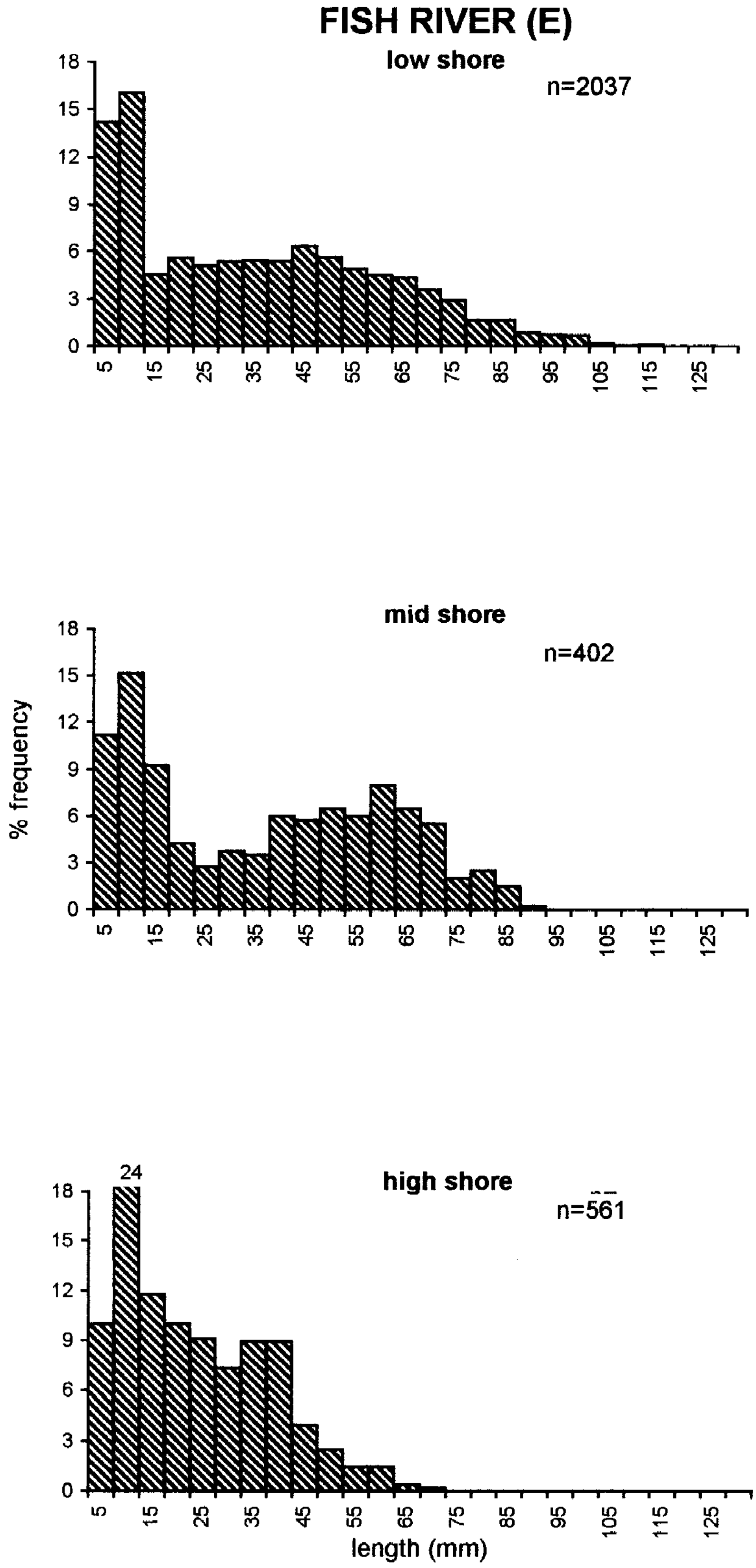

FISH RIVER (E)
low shore
n=2037
mid shore
n=402
high shore
n=561
24
% frequency
length (mm)
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125

Figure 1.3p

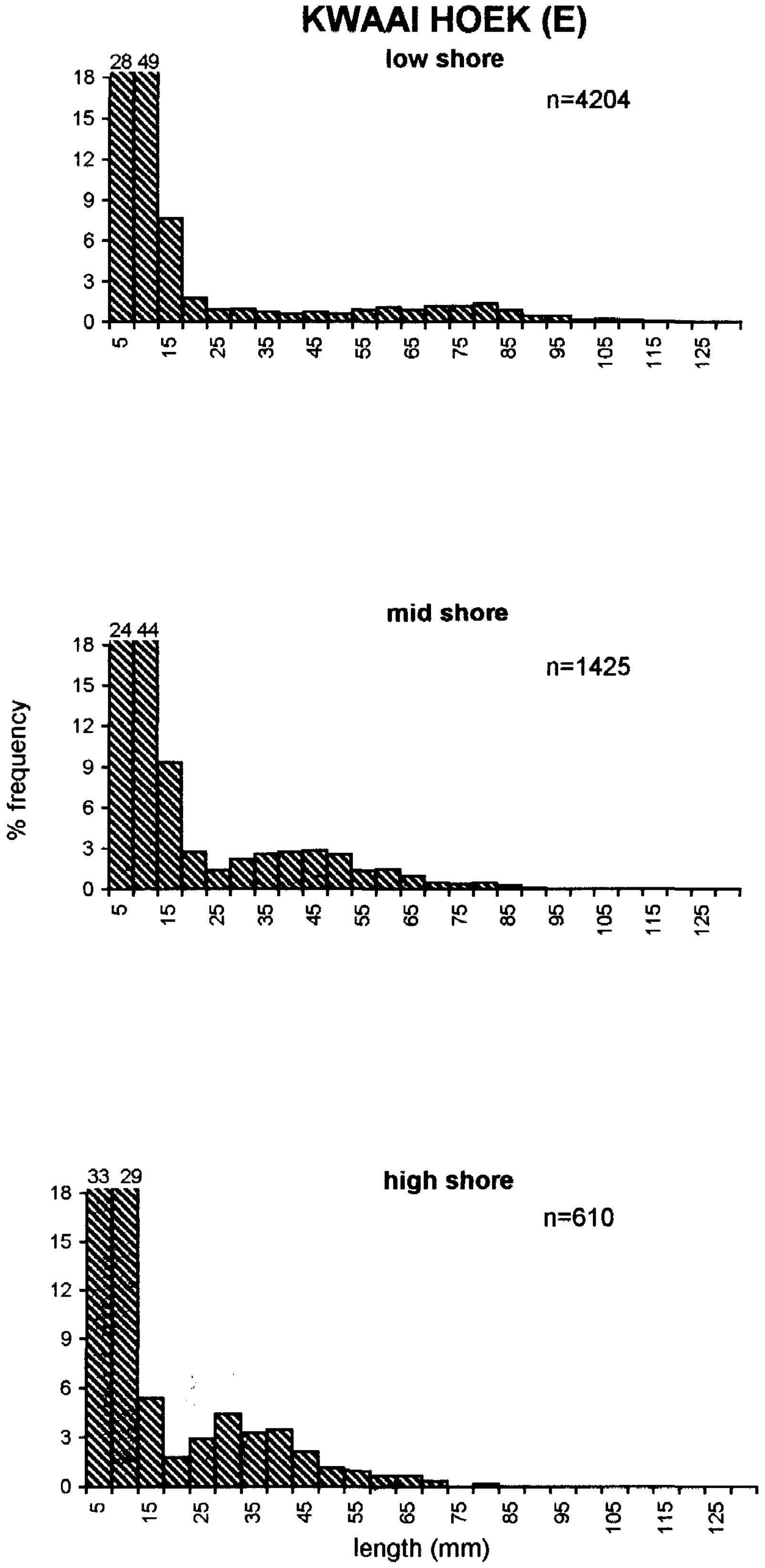

KWAAI HOEK (E)
low shore
n=4204
28 49
mid shore
n=1425
24 44
high shore
n=610
33 29
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3q

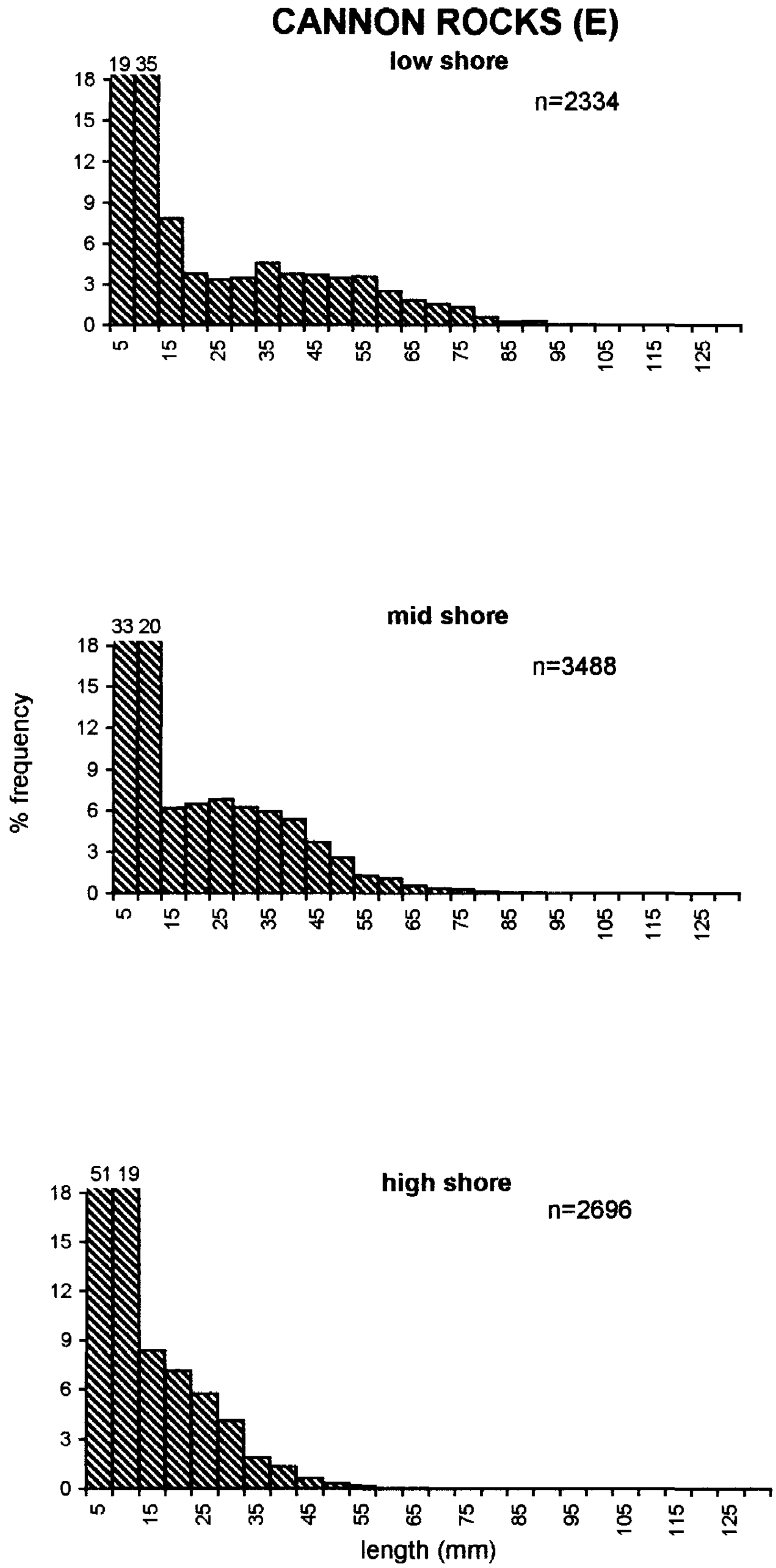

CANNON ROCKS (E)
low shore
n=2334
19 35
mid shore
n=3488
33 20
high shore
n=2696
51 19
% frequency
0
3
6
9
12
15
18
5
15
25
35
45
55
65
75
85
95
105
115
125
length (mm)

Figure 1.3r

The principal component weightings (Figure 1.4) indicate that any point on the right of the PCA graph was placed there due to the presence of larger mussels (>70mm). Conversely any point placed on the left of graph indicated a zone dominated by small mussels (<50mm). Points in between were dominated by medium sized mussels. 76% of the variation in the PCA was attributed to principal component one, which was therefore the most significant in terms of explaining any variation.

PCA summarises the observations of the size frequency histograms in a graphical form and includes the total data set of 18 shores (9 exposed/9 sheltered) and three zones (low, mid and high). The analysis was done by considering the effects of exposure alone (zones pooled, Figure 1.5), zone alone (exposure categories pooled, Figure 1.6) and both exposure and zone (Figure 1.7).

When zones were categorised solely according to exposure (*i.e.* exposed or sheltered) it was clear that some exposed zones were associated with the largest mussels, this pulled these points to the right of the graph. Sheltered zones were interspersed with exposed zones, but despite the overlap, points on the extreme right of the graph were all zones at exposed sites (Figure 1.5). Separation of low, mid and high shore zones was distinct (Figure 1.6). Low shore zones were dominated by large mussels, mid shore zones were dominated by medium sized mussels and low shore zones were dominated by small mussels, reflecting a clear decrease in the mean size of mussels farther up shore. The separation of sheltered and exposed zones became clearer down shore (Figure 1.7). Exposed and sheltered high shore zones grouped together. Larger mussels at exposed mid shore zones pulled these points to the right of the sheltered mid shore zones. Although there was overlap between exposed and sheltered low shore zones, there was a trend towards larger mussels on the exposed low shore. The subjective interpretation of length frequencies was borne out in the quantitative PCA.

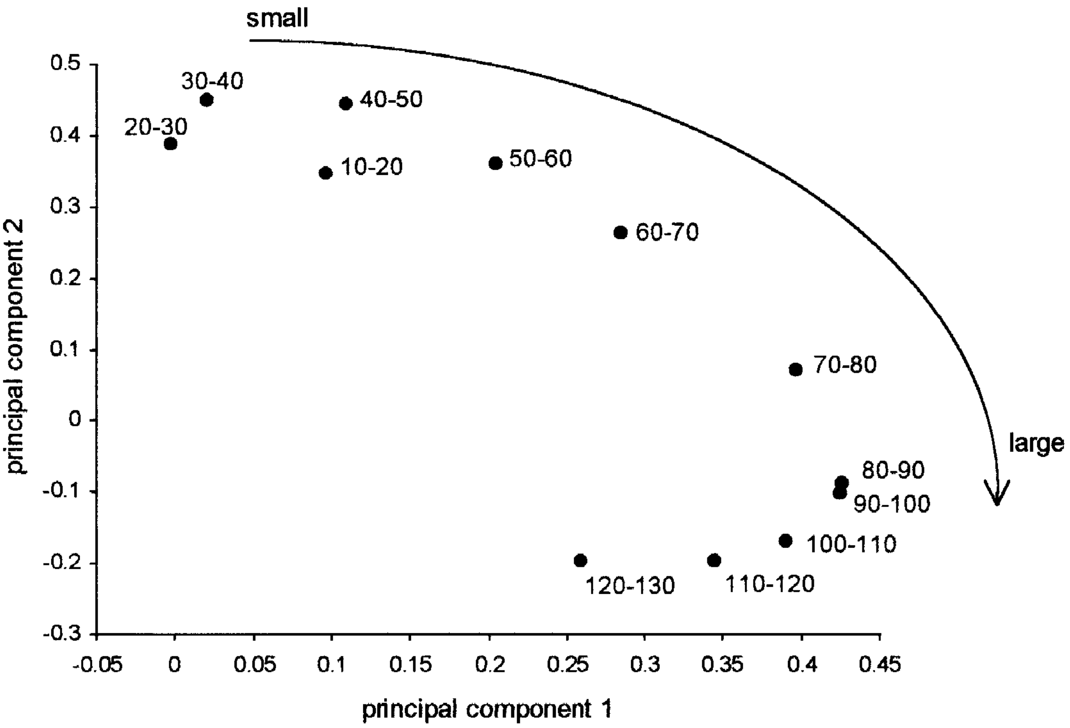


Figure 1.4 Principal component weightings for each of the size classes used in the PCA. Each point represents a size class, given as two figures next to each point. Higher weightings for pc1 apply to zones with larger mussels (>70mm), while lower weightings will affect zones with smaller mussels. The curved arrow shows the change of weightings from left to right, weightings affecting small mussels on the left gradual move through to weightings affecting large mussels on the right.

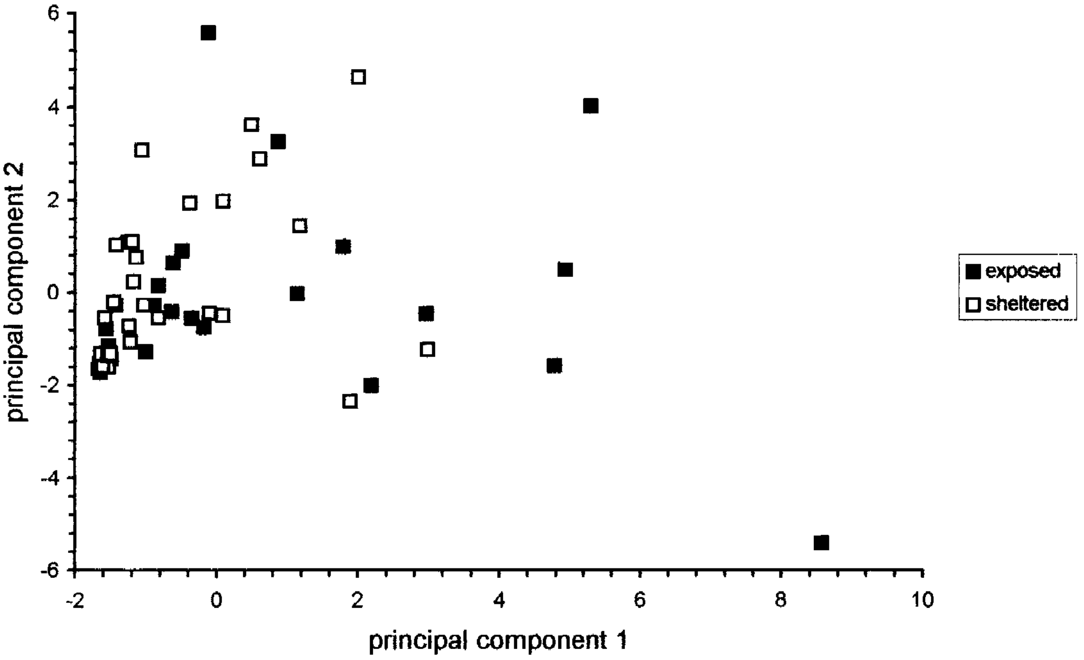


Figure 1.5 Principal component plot of principal component1 vs. principal component 2, points identified by exposure as either exposed or sheltered. Each point represents a zone at a site.

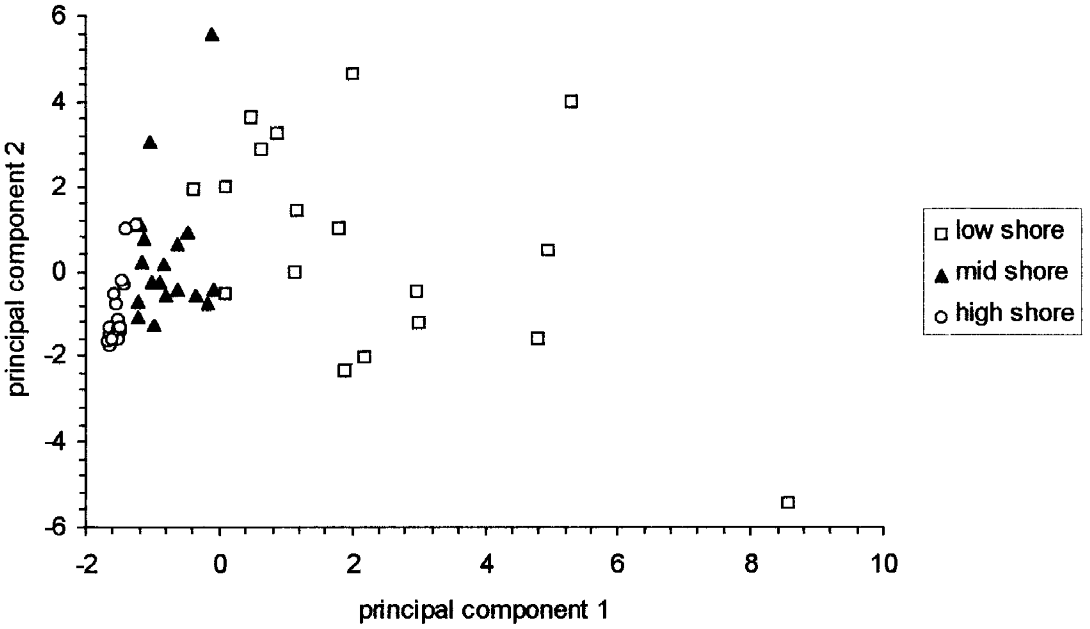


Figure 1.6 Principal component plot of principal component1 vs. principal component 2, points identified by zone as either low, mid or high. Each point represents a zone at a site.

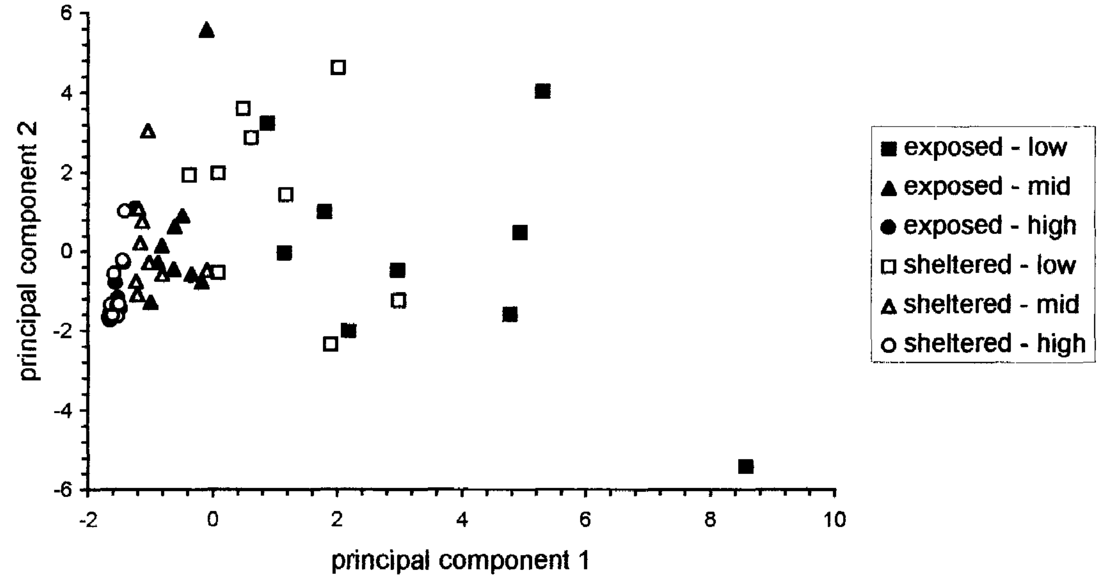


Figure 1.7 Principal component plot of principal component1 vs. principal component 2, points identified by exposure and zone for example low shore sheltered or high shore exposed. Each point represents a zone at a site.

On average the component scores of pc1 for exposed low shore zones were greater than those of the sheltered low shore zones, this difference was significant (Table 1.3; Figure 1.8). The average component values for exposed and sheltered, mid and high shore zones were very similar to each other, but much lower than those of the low shore zones. Mid and high shore zones were not significantly different from each other, but were significantly different from low shore zones. There was a significant interaction between zone and exposure indicating that zones were affected differently by exposure (Table 1.3). Exposure had no effect on mid and high shore adult mussel populations, but did on the low shore (Figure 1.8). The fact that exposed and sheltered zones only separate on the low shore is indicated by the significant interaction term

Table 1.3 Two-way ANOVA table for principal component one scores, using zone and exposure as factors. d.f.=degrees of freedom; SS=sum of squares; MS=mean square; F=F-ratio; p=significance level.

Source of variation	d.f.	SS	MS	F	p
Exposure	1	14.09607	14.096065	10.981	0.0018
Zone	2	149.42567	74.712833	58.202	p<0.0001
Interactions	2	17.677288	8.8386440	6.885	0.0023
Residual	48	61.616931	1.2836861		
Total	53	242.81595			

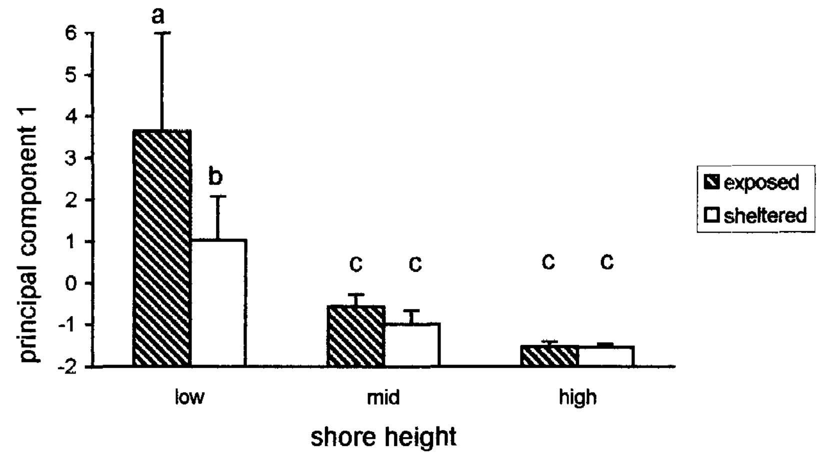


Figure 1.8 The mean scores for principal component one for low, mid and high shore sites, separated according to degree of (+ std). Data were pooled for each degree of exposure and zone. Letters above each column indicate the result of a multiple range test (a is different from b; all c's group together and are different from a and b).

Mean Maximum Lengths

Within each zone, the mean maximum sizes of mussels from the exposed sites were on average larger than those from the sheltered sites. Differences in average mean maximum lengths between the exposed and sheltered sites decreased with an increase in shore height. The largest mussels, were found on the exposed low shore (mean = 102.3mm), and were on average 15.6 mm larger than those found on the sheltered low sites (mean = 86.7mm). Mussels on exposed mid shore zones were on average 11.5mm larger (mean = 79.9mm) than their equivalents on sheltered sites (mean = 68.4mm). A difference of only 3.9mm between exposed (mean = 54mm) and sheltered (mean = 51.1mm) sites was measured on the high shore. Although there was a clear difference between exposed and sheltered sites at low and mid shore sites, there were some outlying sites. On the exposed low shore Cannon Rocks (CR) had a low mean maximum size (87.2mm) that was more like that of the sheltered sites. Two sheltered sites, Old Woman's River (OW) and Hougham Park (HP), had very high mean maximum sizes (100.2mm and 99.4mm). The mid shore site of Kayser's Beach (KB) had a low maximum size (68.7mm) and once again the sheltered site of Old Woman's River (OW) had a high maximum size (Figure 1.9).

In the mid and low shore zones, means for exposed and sheltered shores were all significantly different from each other. High shore zones were not statistically different from each other, but were significantly different from the other zones (Table 1.4; Figure 1.10) Two-way ANOVA revealed that zone and exposure had significant effects on mean maximum size and that there was a significant interaction between exposure and zone (Table 1.4).

It has already been established that there was a trend towards the largest mussels occurring on the low shore, and that at any given zone mussels were larger for exposed shores. One-way ANOVA's (Tables 1.5; 1.6; 1.7) and the resulting multiple range tests carried out separately for each zone using site as a factor confirm this (Tables 1.8; 1.9; 1.10). Remarkably clear separation of exposed and sheltered sites within low (Table 1.8) and mid shore (Table 1.9) zones was observed. High shore zones did not separate clearly into sheltered or exposed categories (Table 1.10).

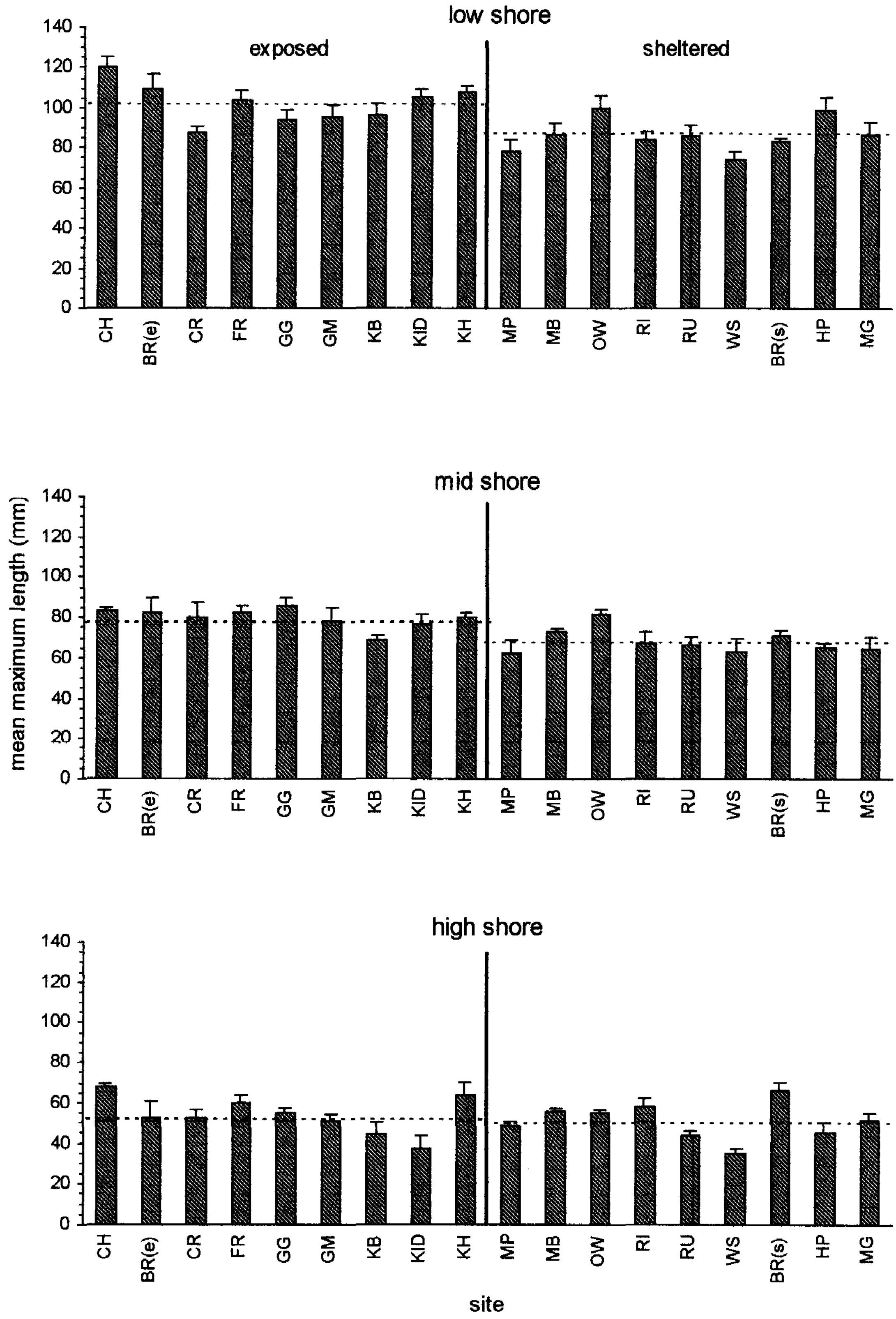


Figure 1.9 Mean maximum lengths (+std) for all exposed and sheltered sites at low, mid and high shore levels. The dotted lines represent average mean maximum size for each category.

Seven of the nine low shore sheltered zones grouped together, however Old Woman's River and Hougham Park grouped with the low shore exposed zones (Table 1.8). On the mid shore there was a trend towards larger mussels on exposed sites, two exceptions to this were the Old Woman's River (sheltered) site grouping with the exposed sites and the Kayser's Beach (exposed) site falling in with the sheltered sites. The pattern revealed here followed more of a gradation, probably representing a gradient of exposure arbitrarily divided into two classes (Table 1.9). The high shore zones, show no pattern in relation to exposure, exposed and sheltered sites were intermingled throughout the multiple range test (Table 1.10).

Table 1.4 Result of two-way ANOVA performed on the mean maximum lengths from all sites, zone and exposure were used as factors.

Source of variation	d.f.	SS	MS	F	p
Zone	2	158667.52	79333.759	952.564	<0.0001
Exposure	1	13595.50	13595.502	163.242	<0.0001
Interactions	2	3794.7019	1897.3509	22.782	<0.0001
Residual	534	44473.896	83.284450		
Total	539	220531.62			

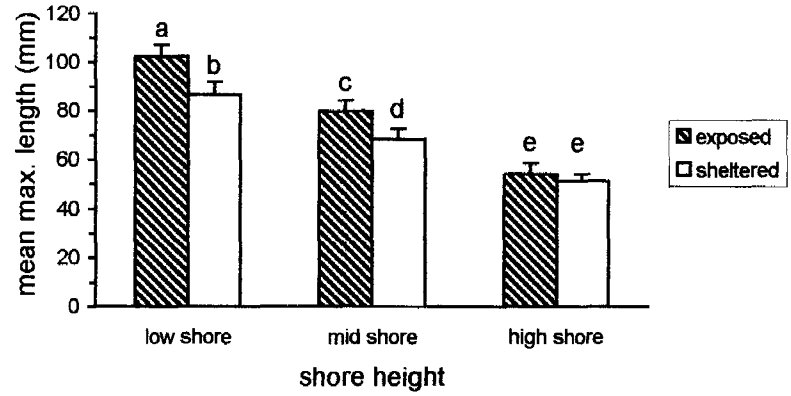


Figure 1.10 Mean maximum length (+std) of mussels at three shore heights and two degrees of exposure. Data were pooled for each degree of exposure and zone. Letters above each column indicate the result of a multiple range test.

Table 1.5 Result of 1-way ANOVA, using site as a factor, on low shore mean maximum lengths.

Source of variation	**d.f.**	**SS**	**MS**	**F**	**p**
Between groups	17	24671.736	1451.2786	49.408	p<0.0001
Within groups	162	4758.436	29.3731		
Total	179	29430.172			

Table 1.6 Result of 1-way ANOVA, using site as a factor, on mid shore mean maximum lengths.

Source of variation	**d.f.**	**SS**	**MS**	**F**	**p**
Between groups	17	39492.627	2323.0957	91.288	p<0.0001
Within groups	162	4122.574	25.4480		
Total	179	43615.202			

Table 1.7 Result of 1-way ANOVA, using site as a factor, on high shore mean maximum lengths.

Source of variation	**d.f.**	**SS**	**MS**	**F**	**p**
Between groups	17	23420.164	1377.6567	82.014	p<0.0001
Within groups	162	2721.246	16.7978		
Total	179	26141.410			

Table 1.8 Multiple range test of mean maximum size for low shore zones.

Site (abbreviation)	Mean max. length (mm)	Homogenous groups	Exposure (S/E)
Winterstrand (WS)	74.6	X	S
Mpekweni (MP)	78.5	X	S
Black Rock (BS)	83.3	X	S
Riet River (RI)	84	X	S
Rufane's Beach (RU)	86.2	X	S
Morgan's Bay (MB)	87	X	S
Mgwalana (MG)	87.1	X	S
Cannon Rocks (CR)	87.2	X	E
Glen Gariff (GG)	94.3	X	E
Glen Muir (GM)	95.5	XX	E
Kayser's Beach (KB)	96.9	XX	E
Hougham Park (HP)	99.4	XX	S
Old Woman's River (OW)	100.2	XX	S
Fish River (FR)	103.7	XX	E
Kidd's Beach (KD)	105.5	XX	E
Kwaai Hoek (KH)	107.7	XX	E
Black Rock (BE)	109.7	X	E
Cape Henderson (CH)	120.4	X	E

Table 1.9 Multiple range test of mean maximum size for mid shore zones.

Site (abbreviation)	Maximum length (mm)	Homogenous groups	Exposure(S/E)
Mpekweni (MP)	62.3	X	S
Winterstrand (WS)	63.3	XX	S
Mgwalana (MG)	64.6	XXX	S
Hougham Park (HP)	65.4	XXX	S
Rufane's Beach (RU)	66.4	XXX	S
Riet River (RI)	66.8	XX	S
Kayser's Beach (KB)	68.7	XX	E
Black Rock (BS)	71.4	XX	S
Morgan's Bay (MB)	73	XX	S
Kidd's Beach (KD)	77.2	XX	E
Glen Muir (GM)	78.3	XX	E
Kwaai Hoek (KH)	80.3	XXX	E
Cannon Rocks (CR)	80.4	XXX	E
Old Woman's River (OW)	81.9	XXX	S
Fish River (FR)	82.5	XXX	E
Black Rock (BE)	82.8	XX	E
Cape Henderson (CH)	83.4	XX	E
Glen Gariff (GG)	85.9	X	E

Table 1.10 Multiple range test of mean maximum size for high shore zones.

Site (abbreviation)	Maximum length (mm)	Homogenous groups	Exposure(S/E)
Winterstrand (WS)	34.9	X	S
Kidd's Beach (KD)	37.3	X	E
Rufane's Beach (RU)	43.8	X	S
Kayser's Beach (KB)	44.8	XX	E
Hougham Park (HP)	45.2	XX	S
Mpekweni (MP)	48.2	XX	S
Glen Muir (GM)	51.1	XX	E
Mgwalana (MG)	51.9	XXX	S
Black Rock (BE)	52.3	XXX	E
Cannon Rocks (CR)	52.4	XXX	E
Old Woman's River (OW)	54.9	XXXX	S
Glen Gariff (GG)	55.4	XXX	E
Morgan's Bay (MB)	55.7	XX	S
Riet River (RI)	58.4	XX	S
Fish River (FR)	60.2	X	E
Kwaai Hoek (KH)	64.2	X	E
Black Rock (BS)	66.7	XX	S
Cape Henderson (CH)	68.1	X	E

Density

Average adult mussel density decreased with an increase in shore height (Figure 1.11). Two-way ANOVA showed that, although exposure did not have a significant effect on density, high, mid and low shore mean adult densities were significantly different from each other (Table 1.11). There was no significant interaction between zone and exposure (Table 1.11). Exceptions to the pattern of decreasing density with an increase in shore height were found at the Old Woman's, Rufanes, Cannon Rock's and Fish River sites, where increases in densities occurred on the mid or high shores.

The average density of juvenile mussels (recruits of <15mm) was extremely variable and was highest at the low shore exposed sites, where juvenile densities were significantly ($p<0.05$) greater on the low shore than on the mid and high shore (Figure 1.12, Table 1.12). Exposure did not significantly affect the density of mussel recruits ($p>0.05$, Table 1.12).

Although there was a significant positive correlation between recruit and adult densities, indicating a trend towards higher recruit numbers with an increase in adult mussel density (Figure 1.13 & 1.14), this should be viewed with caution. r^2 squared values were extremely low (poor predictability) and very high adult densities were often only associated with moderate numbers of juveniles. In other cases (especially exposed low shore) very high juvenile densities were recorded with almost no adults. Considering the sample sizes used for adult/recruit relationships (135 points for each zone within a particular shore type), there were surprisingly few cases where high adult mussel numbers were associated with high juvenile numbers. In exposed mid and high shore zones the adult/recruit relationship was the strongest. As adult mussel densities decreased up shore and the mussels formed discrete clumps separated by bare rock, juveniles seemed to be more concentrated around these mussels. For sheltered shores the relationship between juveniles and adults remained similar throughout the three zones

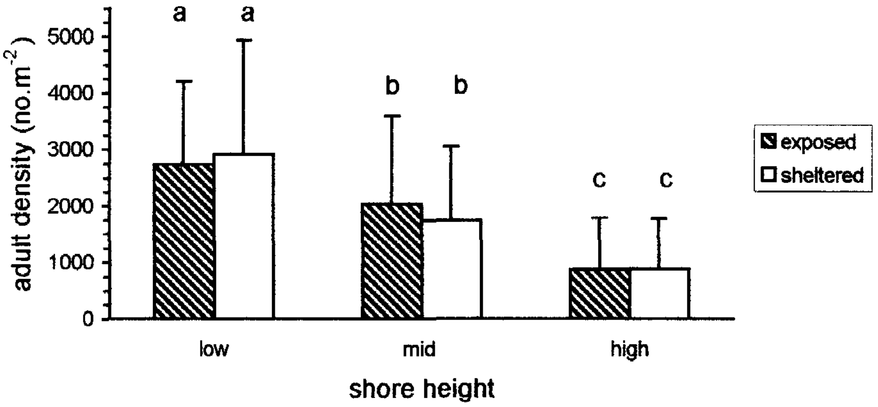


Figure 1.11 Pooled mean adult mussel density (>15mm) for low, mid and high shore exposed and sheltered sites (+std). Letters above columns indicate the result of a multiple range test.

Table 1.11 Results of two-way ANOVA (factors zone and exposure) on adult mussel density. Data for this analysis were transformed √x+1.

Source of variation	d.f.	SS	MS	F	p
Exposure	1	0.7903	0.79029	0.137	0.7155
Zone	2	1183.1755	591.58776	102.461	<0.0001
Interactions	2	3.8894138	1.9447069	0.337	0.7141
Residual	804	4642.1089	5.77737673		
Total	809	5829.9641			

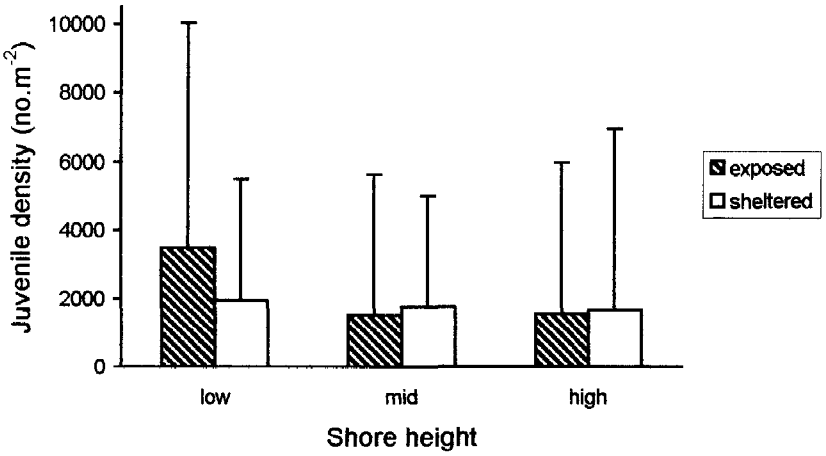


Figure 1.12 Pooled mean juvenile (<15mm) mussel density for low, mid and high shore exposed and sheltered sites (+std).

Table 1.12 Results of two-way ANOVA (factors zone and exposure) on juvenile mussel density. Data for this analysis were transformed √x+1.

Source of variation	**d.f.**	**SS**	**MS**	**F**	**p**
Exposure	1	169.875	169. 875	0.163	0.6911
Zone	2	45834.950	22917.475	21.953	<0.0001
Interactions	2	12835.237	6417.6187	6.148	0.0022
Residual	804	839309.13	1043.9168		
Total	809	898149.19			

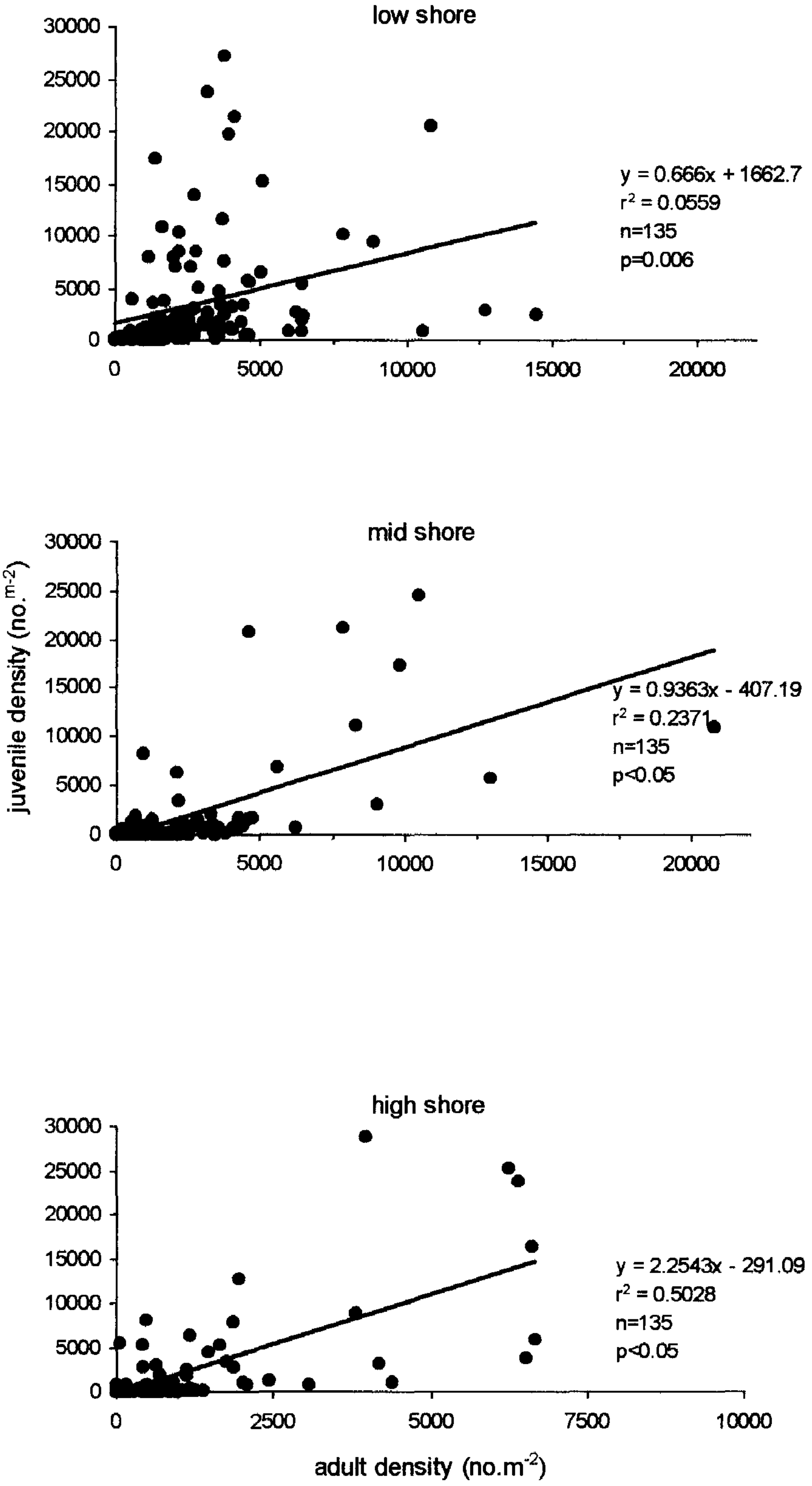


Figure 1.13 Adult/recruit relationships at low, mid and high shore exposed sites.

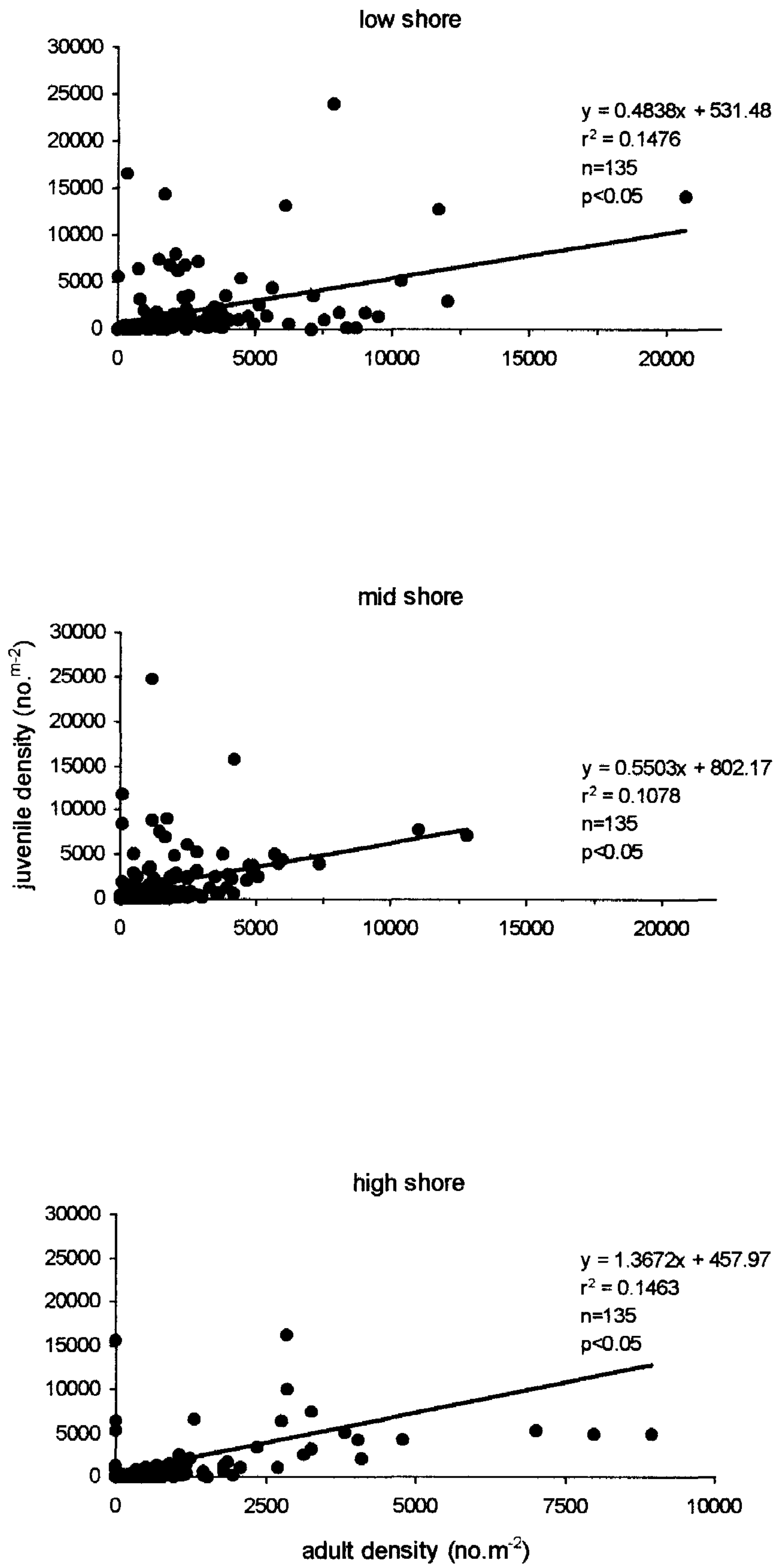


Figure 1.14 Adult/recruit relationships at low, mid and high shore sheltered sites.

Biomass

The intercepts and slopes for the regression equation for each zone (Table 1.13) were inserted into the following equation:

$$y = 10^{((a) + (b \log (x)))} \qquad 1.1$$

where: a = intercept

b = slope

x = independent variable (mussel length mm)

y = dry mass (g).

The average biomass ($.m^{-2}$) for each zone, calculated from the length frequencies and these regressions, decreased with an increase in tidal height. Biomass estimates for sheltered and exposed sites were very similar at each tidal height (Figure 1.15). Two-way ANOVA showed that exposure did not have a significant effect on the biomass of sheltered and exposed sites, but there was a significant difference between the means of high, mid and low shore zones (Table 1.14). There was no significant interaction between zone and exposure (Table 1.14).

All sites except for Rufane's Beach showed this pattern of decreasing biomass with an increase in tidal height.

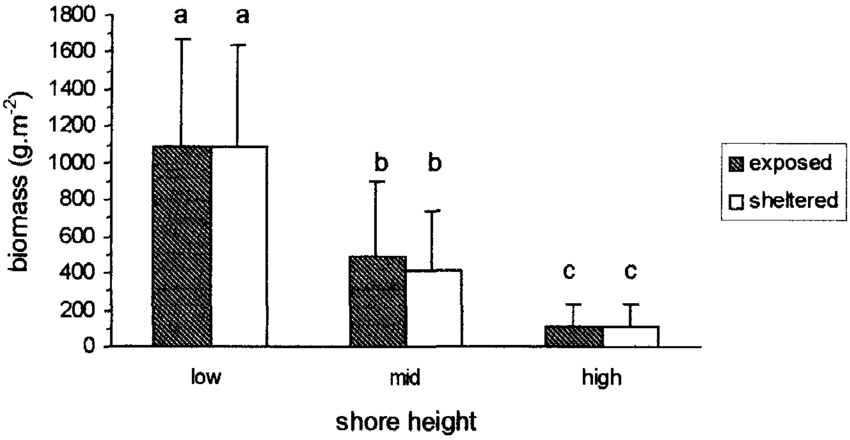


Figure 1.15 Mean biomass (g.m-2 drymass) for exposed and sheltered sites at the three tidal heights. Data were pooled for each exposure in each zone. As before letters indicate the result of a multiple range test.

Table 1.14 Two-way ANOVA performed on the biomass data, zone and exposure were used as factors. Data were transformed $\sqrt{x+1}$.

Source of variation	d.f.	SS	MS	F	p
Zone	2	752.110	376.065	350.065	<0.0001
Exposure	1	0.222	0.222	0.207	0.654
Interactions	2	0.912	0.456	0.424	0.654
Residual	804	863.692	1.074		
Total	809	1616.936			

Table 1.13 Details of regressions used to calculate dry mass, the intercept and slope are given for each zone at each site. Dry mass estimates for mussel length can be calculated from equation 1.1.

Site and exposure	Zone	Intercept (a)	Slope (b)	df	F-ratio	r^2	P
Cape Henderson (CH)	low	-5.39838	2.82926	59	1496.105	0.962	<0.0001
(Exposed)	mid	-5.70923	3.07957	49	769.1461	0.941	<0.0001
	high	-5.83738	3.15771	34	533.8138	0.942	<0.0001
Black Rock (BE)	low	-5.19619	2.75881	58	2866.740	0.981	<0.0001
(Exposed)	mid	-5.28956	2.87684	38	1287.234	0.972	<0.0001
	high	-5.83265	3.17228	25	267.0718	0.918	<0.0001
Cannon Rocks (CR)	low	-5.31479	2.78808	40	789.6157	0.953	<0.0001
(Exposed)	mid	-4.30315	2.1909	41	325.7042	0.891	<0.0001
	high	NO DATA					
Fish River (FR)	low	-4.99522	2.59401	51	2406.754	0.98	<0.0001
(Exposed)	mid	-4.6771	2.45899	46	2118.712	0.979	<0.0001
	high	-4.49453	2.36797	39	795.66	0.954	<0.0001
Glen Gariff (GG)	low	-5.40621	2.71705	44	1127.604	0.963	<0.0001
(Exposed)	mid	-5.12701	2.49591	44	516.2690	0.923	<0.0001
	high	-4.97707	2.47337	29	211.9794	0.883	<0.0001
Glen Muir (GM)	low	-5.45695	2.8805	51	1696.531	0.971	<0.0001
(Exposed)	mid	-5.35902	2.86586	41	1620.602	0.976	<0.0001
	high	-6.26058	3.56404	33	207.1285	0.866	<0.0001
Kayser's Beach (KB)	low	-5.16488	2.72682	55	1275.482	0.959	<0.0001
(Exposed)	mid	-4.87124	2.5108	47	243.8175	0.841	<0.0001
	high	-4.8755	2.57474	44	263.0408	0.860	<0.0001
Kidd's Beach (KD)	low	-4.63265	2.44575	54	377.9039	0.877	<0.0001
(Exposed)	mid	-3.58764	1.80105	50	245.2979	0.834	<0.0001
	high	-4.32419	2.23935	43	124.6346	0.748	<0.0001
Kwaai Hoek (KH)	low	-4.80024	2.43053	52	1069.080	0.955	<0.0001
(Exposed)	mid	-5.23474	2.83262	45	850.0748	0.951	<0.0001
	high	NO DATA					
Mpekweni (MP)	low	-3.92803	2.04418	55	1325.481	0.961	<0.0001
(Sheltered)	mid	-3.40641	1.58127	55	221.3744	0.804	<0.0001
	high	-3.81049	1.88472	47	342.1832	0.882	<0.0001
Morgan's Bay (MB)	low	-5.43594	2.97939	44	2177.345	0.981	<0.0001
(Sheltered)	mid	-5.85364	3.23672	44	772.2392	0.947	<0.0001
	high	-5.64687	3.14754	35	210.3680	0.861	<0.0001
Old Woman's River (OW)	low	-4.45985	2.29818	37	300.6574	0.893	<0.0001
(Sheltered)	mid	-3.71127	1.90794	49	589.0704	0.925	<0.0001
	high	-4.01917	2.00959	49	564.7084	0.922	<0.0001
Riet River (RI)	low	-3.68534	1.85943	49	829.1029	0.945	<0.0001
(Sheltered)	mid	-6.11591	3.35594	34	608.5405	0.947	<0.0001
	high	-5.32172	2.85745	40	1599.517	0.976	<0.0001
Winterstrand (WS)	low	-4.52205	2.41624	39	2113.603	0.982	<0.0001
(Sheltered)	mid	-4.01528	2.10806	35	447.2970	0.929	<0.0001
	high	-4.18791	2.18039	26	243.1528	0.907	<0.0001
Mgwalana (MG)	low	-4.62166	2.41202	44	1090.755	0.961	<0.0001
(Sheltered)	mid	-4.80558	2.53401	41	875.2373	0.942	<0.0001
	high	-3.53535	1.73263	49	291.8864	0.976	<0.0001
Black Rock (BS)	low	-5.11028	2.64029	46	1097.844	0.961	<0.0001
(Sheltered)	mid	-5.22442	2.84034	41	653.0153	0.942	<0.0001
	high	-5.32172	2.85745	40	1599.517	0.976	<0.0001
Hougham Park (HP)	low	-5.19182	2.82058	53	762.8236	0.936	<0.0001
(Sheltered)	mid	-4.63216	2.56161	32	460.3058	0.937	<0.0001
	high	-5.29939	2.9657	31	151.3959	0.835	<0.0001
Rufane's Beach (RU)	low	-3.88195	1.99114	52	509.6820	0.909	<0.0001
(Sheltered)	mid	NO DATA					
	high	-4.23959	2.20046	30	109.2084	0.790	<0.0001

Biomass/Density Relationship

It must be remembered that the density and calculated biomass figures for the following regressions are based on mussel bed densities and not densities at 100% mussel cover. As expected the relationship between adult mussel densities and biomass showed a trend towards higher biomass at higher densities. Low shore sites (Figure 1.16), showed an increase in biomass with an increase in density. At densities of over 4000 mussels per m^2, biomass did not increase, but started to level off. High densities were associated with smaller mussels, but many smaller mussels did not increase the biomass to any great degree.

On the mid shore a similar pattern was seen (Figure 1.16), except that the levelling off of biomass at high densities was not as noticeable.

On the high shore (Figure 1.16), the levelling off of biomass with high densities did not occur. This zone was generally represented by small mussels and low densities, the densities and sizes of mussels that would result in a high biomass were not reached and so the graph did not level off.

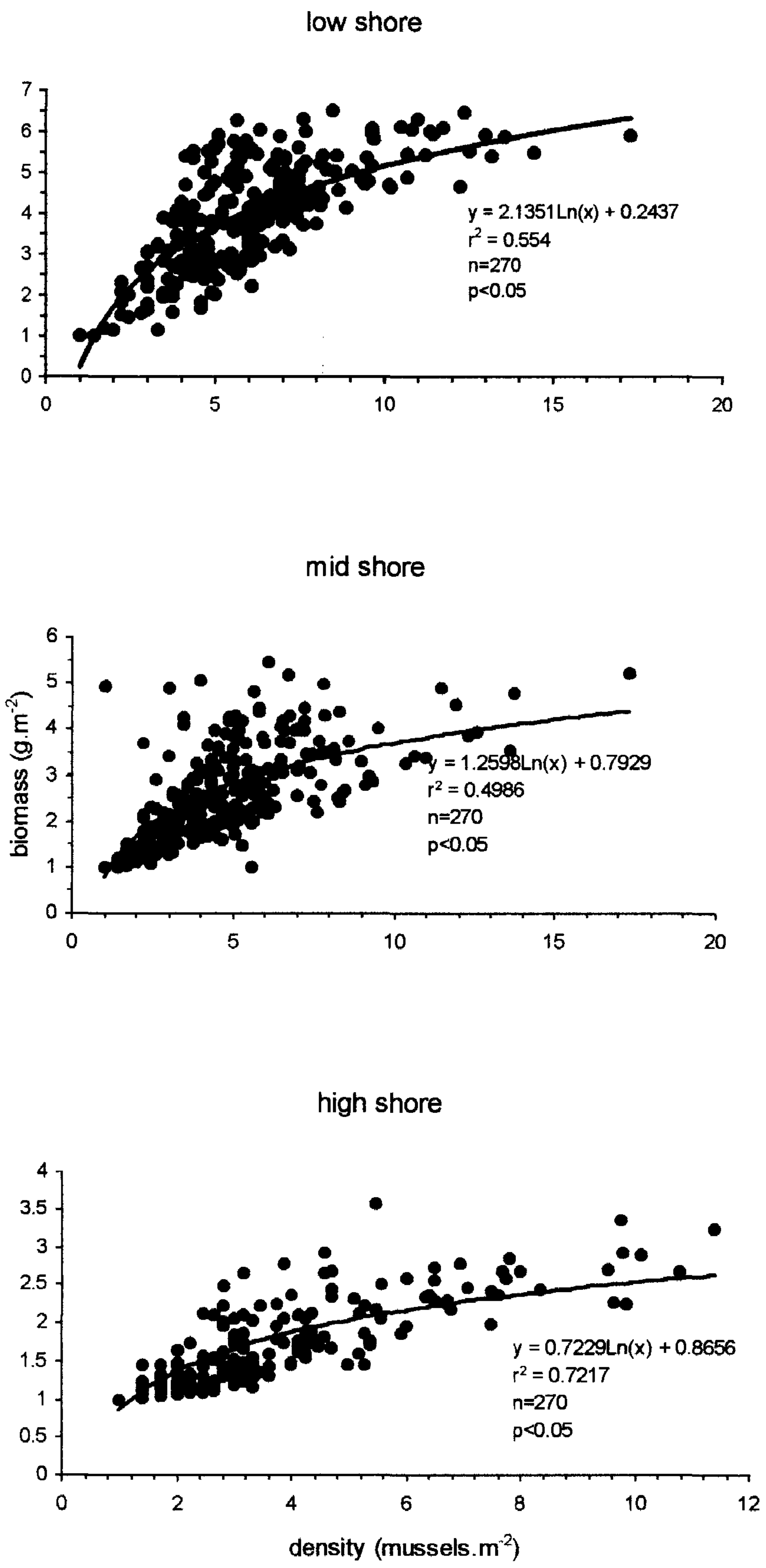


Figure 1.16 Biomass density regressions for low, mid and high zones. Exposed and sheltered shores were combined for this analysis. Axes were transformed √x+1 in order to accommodate zero values.

1.5 DISCUSSION

Certain aspects of the population structure (eg. size, density, biomass) of *Perna perna* on the south coast of South Africa were related to changes in tidal height and the degree of wave exposure on rocky shores. These relationships may be a result of direct or indirect influences of tidal height and exposure.

Mussel Size

In the present study the size of adult mussels decreased at higher shore levels. This has also been noted for *Mytilus galloprovincialis* (Leeb, 1995), *Mytilus edulis* (Seed, 1969a; Seed 1969b), and *Choromytilus meridionalis* (Griffiths, 1981a). Mussels may be smaller higher up the shore as a result of slower growth rates (Seed, 1969a; Seed, 1969b), due to a decrease in the available feeding time (Seed, 1969a; Seed, 1969b; Griffiths & Buffenstein, 1981; van Erkom Schurink & Griffiths, 1993; Leeb, 1995). Increased mortality of larger mussels on the high shore by predation could also give rise to a pattern of small mussels in this area. However Griffiths & Hockey (1987) did not consider predation on mussels to increase with shore height. Van Erkom Schurink & Griffiths (1993) have experimentally shown that growth rates of *Perna perna* were retarded with a decrease in feeding time, and that this probably results in smaller sized mussels on the high shore.

There was a trend toward larger mussels on more exposed sites, however this pattern was not as strong as the one caused by tidal height. With an increase in tidal height the difference in mean maximum size between sheltered and exposed sites decreased from 15.6mm on the low shore to 3.9mm on the high shore, indicating that the possible effect of exposure diminished up the shore. Exposure could act directly or indirectly on mussel beds to produce this pattern. Waves can act directly on rocky shore communities by physically removing individuals or groups of animals (Jones & Demetropoulos, 1968; Harger & Landenberger 1971; Paine & Levin, 1981; Denny, 1987). Alvarado and Castilla (1996), working on *Perumytilus purpuratus* sites in Chile, found that mussels on exposed sites were on average smaller than those on sheltered sites. It was proposed that these larger mussels experienced higher mortality due to mechanical wave removal, Griffiths (1981a) observed a similar phenomenon for *Choromytilus meridionalis*. Contrary to this, a study of *Mytilus galloprovincialis* on an exposed west coast South Africa shore attributed the occurrence of larger mussels on more exposed sites to increased growth rates (Leeb, 1995). Even if the largest *Perna perna* on exposed shores were lost to wave action, the maximum size reached by mussels on the exposed shores were on average larger than those at the sheltered sites (Table 1.4; Figure 1.10).

Heavy predation is able to influence the average size of mussels (Kitching *et al.* 1958; Lambert & Steinke, 1986). *Mytilus edulis*, occurring in sheltered conditions were able to attain larger sizes than their counterparts living on exposed sites. This was due to a greater abundance of predators on exposed shores, the predators selectively choosing larger individuals (Kitching *et al.* 1958). Natural predators of mussels along the South African coastline include kelp gulls (Griffiths & Hockey, 1987), black oyster catchers (Hockey & Underhill, 1984), octopuses (Smale & Buchan, 1981), whelks (*Nucella* spp.) (Griffiths, 1981b), necklace shells (*Natica tecta*) (Griffiths, 1981b) and spiny lobsters (Berry & Smale, 1980). Despite the abundance of species that prey on South African mussels, competition is thought to be the dominant factor controlling mussel beds and not predation (Griffiths & Hockey, 1987). However on some sections of the South African coast harvesting of mussels by human collectors has had devastating effects on *Perna perna* populations (Hockey & Bosman, 1986; Lambert & Steinke, 1986; Lasiak, 1991a&b; Dye *et al.*, 1994). Selective harvesting of mussels, by humans, from either exposed or sheltered sites could result in differences in mussel size between the two shore types. In certain areas entire beds of *Perna perna* have been removed (Lasiak, 1991a), and recovery of these mussel beds is slow to non-existent (Lambert & Steinke, 1986). In spite of this, overall size distributions of mussels at study sites for this project seem to reflect healthy mussel populations. Frequency histograms for mussels were similar to those from marine reserves (where no human mussel collection occurs) both to the north and south of the study area (Crawford & Bower, 1983; Hockey unpublished, in van Erkom Schurink & Griffiths, 1990). Differences between sheltered and exposed shores are probably not due to predation by animals or man.

Sea temperature is an important factor affecting the growth rates of mussels and changes in temperature could give rise to different sized mussels on different shores (Bayne & Worrall, 1980; Sukhotin & Kulakowski, 1992). *Perna perna* is known to show increased growth rates at higher temperatures (van Erkom Schurink & Griffiths, 1993). Higher growth rates for *Perna perna* on the South African east coast (sub-tropical) (Berry 1978) when compared to growth rates on the south coast (warm temperate), have been attributed to differences in sea temperature (van Erkom Schurink & Griffiths, 1990). However, Tomalin (1995) showed such high variation in the growth rates of *Perna perna* in Natal, that the effect of temperature over a larger area was not thought to be important. To counteract the effect of biogeographic change (such as sea temperature) in this study, exposed and sheltered sites were geographically interspersed throughout the study area (Figure 1.1), and therefore the effect of temperature can be ignored.

Initial settlement of planktonic marine organisms and the ensuing recruitment may directly affect the structure of intertidal communities (Connell, 1985; Hunt & Scheibling, 1996). For example, unusually heavy settlement and recruitment of *Perna perna* has resulted in the formation of mussel beds in areas that were previously devoid of the bivalve (Berry, 1978; Tomalin, 1995). The relationship between wave exposure and settlement is dealt with in greater detail in the following chapter.

Perna perna on exposed South African shores have been shown to grow almost twice as fast as those on sheltered shores (Lindsay, 1998). It seems likely that this increased growth rate results in mussels reaching greater sizes on exposed shores. For the scope of this project it is only possible to postulate as to the cause of this difference. Food supply is one of the most important factors affecting mussel growth (Kautsky, 1982). Although there are few data on biogeographic variation in primary production for South Africa, there is a gradient of both inshore phytoplankton production (Brown ,1992) and intertidal benthic microalgal production around the coast of southern Africa (Bustamante, *et al.* 1995). Highest values of both occur on the west coast of South Africa and the lowest values in Natal on the east coast. Average biomass values of filter feeder biomass (mainly *Perna perna*) were related to this gradient, but local wave action (affecting water turn over) and nearshore productivity were considered more important in maintaining a constant food supply (Bustamante *et al.*, 1995). Transplantation experiments involving *Mytilus edulis* have revealed that local conditions are important in influencing growth rates (Dickie *et al.*, 1984). Mussels at exposed sites possibly receive a more constant food supply than those at sheltered sites. There would be a faster turnover of food in the water and local depletion due to filter feeding is less likely to occur. Greater wave action is also likely to keep larger particles in suspension.

High growth rates of *Perna perna* occurring in Natal were attributed to increased food quantity by the resuspension of detritus clouds (Berry, 1978). Although *Perna perna* digests phytoplankton and microzooplankton more efficiently than detritus (Simon, 1997), mussels can respond both physiologically (e.g. gut clearance rates, pseudofaeces production, respiration, absorption) (Widdows *et al*, 1984; Barnes, 1993) and morphologically (e.g. morphology of digestive tubules, size of gills and labial palps) to changes in their food environment (Bayne, 1993). Frequent re-suspension of detrital matter at exposed sites could allow mussels at these sites to utilise a food source not always available to mussels at more sheltered sites. Mussels at exposed sites may respond physiologically or morphologically (or both) to make better use of detritus as an abundant food supply.

Density

Adult mussel density showed no relationship with exposure, but decreased with an increase in shore height. Densities in this study were partly a reflection of mussel cover and not packing density as quadrats were placed randomly in the mussel zone and not just in areas of 100% cover. Increased physiological stress associated with tidal height elevation often sets the upper limits of a species distribution (Suchanek, 1978; Griffiths & Buffenstein, 1981; Tsuchiya, 1983), and this can lead to a decrease in mussel cover (Leeb, 1995). Lindsay (1998) working on *Perna perna* revealed that the packing densities of adult mussels were greater on sheltered shores, while Underwood (1981) revealed that greater densities of sessile animals occurred at sheltered sites.

Juvenile *Perna perna* densities were significantly affected by tidal height, but not by exposure (Table 1.12; Figure 1.12). Densities on the low shore were on average higher than those on the mid and high shore, however there was a considerable amount of variation in juvenile densities at all shore levels. *Perna perna* shows extremely variable settlement and recruitment (Phillips, 1994) and a once-off sample (such as this study) would only reveal this variability. Matters are further complicated by the fact that densities, for this study, partially reflect mussel cover and not just packing density. Chapter 2 deals with this topic in greater detail.

There were significant trends towards higher juvenile numbers with an increase in adult densities at both exposures and all shore levels. This relationship was strongest for mid and high shore exposed zones, reflecting higher predictability of recruit numbers with an increase in shore height. On the mid and high shore zones the mussels occurred in clumps and did not form continuous beds, recruits were associated with these clumps and this explains the strong relationship between recruits and adults. The increasing predictability of recruits from adult densities from the low to the high shore was not as strong for the sheltered zones as it was for the exposed zones, but was significant in all cases. The relationship between adult and juvenile densities of sessile space occupiers is predictable at low levels of recruitment, but at high levels of recruitment mortality becomes density-dependant and uncouples this relationship (Connell, 1985). Low recruitment occurring on the mid and high shore results in density independent mortality giving rise to a stronger correlation between adults and recruits. On the low shore, higher recruitment means that recruit mortality is more density dependent and a weaker correlation between adults and recruits exists. However free space existing within the mussel beds (at all tidal heights) means that more recruits could be accommodated and that populations are recruit limited. Very high settlement and the increased recruitment could be beneficial to mussel beds. Based on these results management strategies should aim to maximise recruit input. No-take zones interspersed with harvesting areas could provide a continued supply of recruits. Recruits are dependant on adults and the stripping of large numbers of adults in harvesting areas could result in recruitment failure. Harvesting of mussels should be by the removal of individuals within clumps and not by removal of the whole clump.

Biomass

Mussel size usually decreased up shore and this combined with lower densities resulted in reduced biomass estimates at higher tidal levels. McQuaid & Branch (1985) showed a decrease in the biomass of all filter feeders associated with sheltered shores. Increases in mussel biomass were correlated with increases in density and no trend between exposed and sheltered sites were observed. It is possible that the degrees of exposure that McQuaid & Branch (1985) were working on were much more extreme than those of this study, or that other filter feeders (e.g. barnacles, sea-squirts) were responsible for these trends.

A trend that often emerged in this study was that with an increase in shore height the differences between sheltered and exposed zones were reduced often to the point where they were not significant. An explanation for this is that high shore populations are possibly limited by more extreme physical conditions at both the juvenile (e.g. decreased recruit density - this study) and adult (Lindsay, 1998) levels. This study revealed that recruit densities were lower on the high shore than on the low shore. Lindsay (1998) found that *Perna perna* occurring under conditions of increased environmental stress grew more slower and reached smaller sizes than those living in a less stressful habitat. High shore populations may be strongly influenced by physical conditions, which mask the effects of exposure. Low shore environments are physically less stressful than those on the high shore and may allow exposure to play an important role in structuring the community.

A major short coming of this study lies in the fact that wave exposure was not quantified. Although biologists agree that wave action is very important in rocky shore intertidal communities, there is dispute as to the best method of measuring wave force (Jones & Demetropoulos, 1968; Harger, 1970; Doty, 1971; Craik, 1980; Palumbi, 1984; Denny, 1983; Bell & Denny, 1994). Direct measurements of exposure require the deployment of some device that can measure wave force. Most devices fall into one of two categories: those that measure maximum wave force (e.g. Jones & Demetropoulos, 1968; Harger, 1970; Bell & Denny, 1994) and those that measure average wave action (Doty, 1971; Craik, 1980). Ballantine (1961) proposed an exposure scale based on the fauna and flora of different shorelines. Biological criteria for a particular shoreline allow it to be classified on a scale ranging from sheltered to exposed. Indirect measures of exposure can also combine the direction and speed of prevailing winds and the aspect of a particular site to these conditions (Moore, 1935). Due to the distance between study sites and the fact that devices need to be deployed over the same time period it was not possible to measure exposure directly. No exposure scales based on biological aspects of the shoreline were available for the south coast of South Africa at the time that this study was undertaken. As the study area for this project does not consist of sheltered inlets protected by large headlands, it would be very difficult to utilise some type of exposure index based on prevailing wind and wave direction.

Although there are many problems with the subjective classification of shores, favourable results regarding animal size, indicate that there was a difference between what were classified as exposed and sheltered shores. Sites in this study, have been classed as either exposed or sheltered (prior to sampling), this is only a categorisation that makes classifying each shore easier. In reality shores are subject to a continuum of exposures from very sheltered to very exposed. The division between exposed and sheltered shores is only relative to conditions experienced along the South African south coast and is not comparable to other shores.

In recent years concern has been expressed regarding the potential spread of *Mytilus galloprovincialis* along the south coast of southern Africa (Griffiths *et al.*, 1992, Phillips, 1994). The spread of this mussel along the west coast of southern Africa has resulted in it out-competing and displacing the indigenous ribbed mussel, *Aulacomya ater* (Griffiths *et al.*, 1992). *Mytilus galloprovincialis* is capable of out competing *Perna perna*, it grows faster, is not affected by parasites and is able to colonise areas that have been denuded of mussels (van Erkom Schurink & Griffiths, 1993; Calvo-Ugarteburu & McQuaid, 1998). Phillips (1994) and Griffiths *et al.* (1992) recorded this mussel as far north as East London. Only one *Mytilus galloprovincialis* was recorded during this survey and that was in the former Ciskei, at Mpekweni. However a year after sampling for this project was undertaken a number of small invasive mussels were noted at the Old Woman's River site, where previously none had been recorded. As yet *Mytilus galloprovincialis* has not formed extensive mussel beds on the southern South African coast, north of Hougham Park.

CHAPTER 2

THE EFFECT OF EXPOSURE , TIDAL HEIGHT AND SUBSTRATUM ON RECRUITMENT PATTERNS OF JUVENILE MUSSELS.

INTRODUCTION

Free swimming pelagic larvae form a critical stage in the life cycle of many marine sedentary invertebrates (Barnes, 1987). The subsequent settlement of these larvae onto more permanent substrata, followed by their growth and mortality, can affect the parent populations (Roughgarden *et al.* 1988; Roegner & Mann, 1995). In the case of hard substrata, settlement refers to the attachment of larvae (in some cases metamorphosed and in others not) onto the substratum. Recruitment follows settlement when the juvenile survives for a certain period after settling (Connell, 1985). Many studies have focused on the effects of physical and biological factors on sedentary marine adult populations (Introduction, Chapter one), and it is only more recently that biologists have begun to establish the importance of variations in the initial settlement of larvae (Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985; Raimondi, 1988; Minchinton & Scheibling, 1993; Hunt & Scheibling, 1996). Initial settlement can be important in structuring adult communities. Physical and/or biological factors usually affect this settlement and so provide the mechanism involved in shaping communities (Connell, 1985). However in some species initial settlement and early recruitment do not influence the structure of adult communities (Luckenbach, 1984; Delafontaine & Flemming, 1989), this is especially true at high recruitment densities, when the link between recruits and adults is severed because of density dependant mortality (Connell, 1985).

Prior to settlement, fluctuations in diatom blooms can cause larval failure due to decreases in nutrient levels (Barnes, 1956). Once settlement size has been reached, hydrodynamic processes can be very important in regulating the supply of larvae reaching potential settling sites (Kendall *et al.* 1982; Roughgarden *et al.* 1988; Armonies & Hellwig-Armonies, 1992; Fuentes & Molares, 1994). Upwelling conditions during peak settlement season of *Balanus glandula* can prevent larvae from reaching potential settling sites and this results in low settlement rates. Larval *Balanus glandula* cannot delay settlement and if no suitable substrata are reached the larvae will die (Roughgarden *et al.* 1988). In contrast to this the larvae of some mytilids can postpone settlement until a suitable substratum is reached (Pechenik *et al.* 1990; Mokady *et al.* 1991; Widdows, 1991).

Certain cues are significant in initiating the settlement of larvae. Larval barnacles are known to avoid settling on substrata previously occupied by mobile predators (Johnson & Strathmann, 1989), whereas some species are attracted to sites occupied by con-specifics (Rittschof *et al.*, 1984; Bushek, 1988). Some barnacles prefer to settle on certain rock types and in free space (Raimondi, 1988; Minchinton & Scheibling, 1993). The barnacle *Tesseropora rosea* settles in sunny areas exposed to wave action while *Tetraclita purpurascens* prefers to settle in shady areas (Denley & Underwood, 1979). The presence of crevices, old shells, shaded areas, con-specifics and low water motion all enhance the settlement of the oyster, *Crassostrea virginica* (Bushek, 1988; Michener & Kenny, 1991). Hydroid settlement is influenced by surface chemistry while that of bryozoans is affected by light intensity (Roberts *et al.* 1991; Widdows, 1991).

Mussel larvae favour filamentous and other algae as settling sites, however unlike the juveniles of many sedentary invertebrates, mytilid larvae once settled can spend an extended period on the substratum without permanently attaching to it (Bayne, 1964; Berry, 1978; Petersen, 1964 a&b; Cáceres-Martinez *et al.*, 1993, 1994; Phillips, 1994; Lasiak & Barnard, 1995; Thorarinsdottir, 1996). Bayne (1964) quantitatively recorded primary settlement of *Mytilus edulis* on filamentous algae, this was followed by secondary settlement, which occurred when primary settlers left the filamentous algae to settle into the mussel bed. Other research has confirmed Bayne's observations (McGrath & King, 1991), but in most instances studies have revealed that although secondary settlement (*i.e.* settlement from algae into the mussel bed) occurs, there was also primary settlement of larvae directly into the mussel bed (Berry, 1978; Petersen a&b, 1984b; McGrath *et al.*, 1988; King *et.al.*, 1990; McGrath & King, 1991; Cáceres-Martinez *et al.*, 1993, 1994; Phillips, 1994; Lasiak & Barnard, 1995; Thorarinsdottir, 1996). Primarily settled mussels are able to leave a substratum and re-enter the plankton by secreting byssus 'drifting threads' which are different from byssus attachment threads (Sigurdsson *et al.* 1976; Lane *et al.* 1985, Yankson, 1986; Beukema & de Vlas, 1989). Drag forces act on the thread and keep the mussel suspended in the water column, *Mytilus edulis* post-larvae of up to 2.5mm (Lane *et al.* 1985) and *Macoma balthica* of up to 10mm (Beukema & de Vlas, 1989) have been recorded drifting in this way. *Perna perna* of less than 10mm are regarded as highly motile and capable of relocating (Berry, 1978), while those less than 20mm are still able to move about on the substratum (Phillips, 1994).

Studies of the settlement of *Perna perna* have produced contradictory results, Phillips (1994) found settlement on algae to be significantly greater than on other substrata, while Lasiak & Barnard (1995) found no significant difference between the numbers of settlers on mussels and on algae. Both these studies concluded that although secondary settlement from algae to mussel beds occurred there was also primary settlement into the mussel bed. Settlement intensity of *Perna perna* is generally lower than that for most mytilids (Phillips, 1994; Lasiak & Barnard, 1995), but under favourable conditions very high settlement can occur, resulting in the establishment of new mussel beds (Berry, 1978).

Wave exposure (either directly or indirectly) does have an effect on growth rates of adult *Perna perna*, with populations on more exposed sites having lower densities (Lindsay, 1998) and reaching larger sizes than those on more sheltered shores (chapter 1). Whether differences in the initial settlement of larvae are responsible for these differences is not known. Previous studies have suggested that degree of wave exposure is not important in affecting the intensity of initial larval settlement (Petraitis, 1991; Phillips, 1994). Laboratory experiments have revealed that mussel larvae tend to settle when there is an increase in the degree of water agitation, but whether the differences between exposed and sheltered sites would be great enough to influence settlement rates is not known (Eyster & Pechenik, 1987). Rocks nearer the sea and seaward facing receive greater numbers of settling *Mytilus edulis* (Fuentes & Molares, 1994) and this suggests that exposed sites may receive larger numbers of larvae than would sheltered sites. Differences in mussel populations with increasing shore height have been associated with differences in the post settlement mortality of recruits rather than with differences in the initial settlement of larvae (Leeb, 1995) the only in-depth studies of the early recruitment of *Perna perna* undertaken in southern Africa have been those of Phillips (1994) and Lasiak & Barnard (1995). Both these studies were undertaken on coarse temporal scales not taking into account the daily changes in early recruit numbers. This studies aims to look at effects of wave exposure, shore height and substratum type on the early recruitment of *Perna perna* on a fine temporal scale. No studies have been completed on the daily settlement rates of mussels in the intertidal zone, and therefore this work is unique in its field.

2 MATERIALS AND METHODS

2.1 Study sites

The density, distribution and size of *Perna perna* recruits were quantified at 2 exposed and 2 sheltered shores near Kenton-on-Sea (south cape coast, South Africa) (Figure 2.1). East of Kenton-on-Sea the High Rocks area consisted of one exposed and one sheltered site, Diaz Cross to the west also had one exposed and one sheltered site. Sites were subjectively classified as exposed or sheltered prior to sampling, as in chapter one. Sheltered sites were more sheltered than those sampled previously, but exposed sites were of similar exposure to those described in the first chapter. Diaz Cross and High Rocks were only 7km apart, at each site exposed and sheltered shores were not more than 150m apart (Figure 2.1). Both the sites consisted of flat aeolianite (dune rock) platforms. At these sites the most likely settlement substrata were the mussel beds, the red foliose algae *Gelidium pristoides* and red coralline algae (*Corallina* spp.). Recently settled mussels have been observed on all of these substrata (Berry, 1978; Beckley, 1979; Phillips, 1994; Lasiak & Barnard, 1995).

For the remainder of this chapter the term site refers to either Diaz Cross or High Rocks, while the term shore refers to the locality plus the degree of exposure. Shores sampled were therefore Diaz Cross exposed (DE), Diaz Cross sheltered (DS), High Rocks exposed (HE) and High Rocks sheltered (HE).

2.2 Sampling Periodicity

Daily sampling from the 20/04/1996 to the 21/05/1996 was undertaken. By alternating sites it was possible to sample one exposed and one sheltered site each day. This sampling regime was subject to tide and sea conditions being favourable.

2.3 Sampling Procedure

The settlement of larvae at different tidal heights (low, mid and high shore) and on different substrata, was examined by removing three 10x10 cm quadrats with 100% cover of each substrata within each tidal height. The substrata sampled at each tidal height and at each exposure were recorded in Table 2.1. High shore sites do not refer to the highest zone on the shore, but rather to the high shore mussel beds and the same applies to mid and low shore sites. Sheltered low shore sites were the only exception to this, in this area mussels were so scarce that it was not possible to sample them. Low shore sheltered shores were defined equivalent to the low shore exposed shores due to the presence of coralline algae at both and to the similar shore height observed at both (Table 2.2). This may seem to contradict the results obtained in chapter 1, however as already explained, the sheltered sites for this part of the study were more sheltered than those described in chapter 1 and differences between them were possible.

Table 2.1 Substrata sampled at low, mid and high shore, exposed and sheltered sites.

Shore height	Exposed	Sheltered
low	mussel & coralline	coralline
mid	mussel & *Gelidium*	mussel & *Gelidium*
high	mussel & *Gelidium*	mussel & *Gelidium*

The entire area of the substratum within a quadrat was removed and the rock scraped bare. Each sample was placed in a bag and taken to the laboratory. Individual samples were placed in a 12% commercial bleach solution (Sodium Hypochlorite) for 5-10 minutes. Sodium Hypochlorite causes recently settled mussels to release their hold on the substratum (Davies, 1974). Agitation of the container holding the bleach and substratum ensured that no settlers remained on/in the substratum. The substratum and solution was then poured through a series of sieves (0.5mm and 0.3mm), ending in a sieve with a diameter of 149 micrometers. The substratum left in the top sieve was thoroughly rinsed with water to ensure that no larvae remained on it. Mussels less than 15mm were washed into filter paper funnels and frozen. Later all mussels were counted using a dissecting microscope fitted with a micrometer. All mussels were measured (to the nearest 0.083 of a millimetre), except in cases of many individuals, when a representative sub-sample was used.

To determine the availability of potential settling sites for larvae, the percentage cover of each of the substrata to be sampled was estimated by placing six random 50x50 cm quadrats in each height at all four sites (Table 2.2). The large quadrat was sub-divided into 100cm^2 quads with string to aid cover estimates.

Table 2.2 The percentage cover (± std) of each of the possible settling substrata on each shore and at all tidal heights. E and S represent exposed and sheltered sites respectively. An * indicates the absence of a substratum at that particular zone.

Shore		**Tidal height**	**% Coralline (± std)**	**% Mussel (± std)**	**% *Gelidium* (± std)**
Diaz Cross	E	low	68.6 (18.6)	61.1 (17.4)	*
		mid	*	15.4 (7.5)	20.1 (8.9)
		high	*	17.1 (5.4)	14.0 (2.0)
Diaz Cross	S	low	94.6 (6.9)	1.0 (1.3)	*
		mid	*	16.6 (5.7)	1.9 (1.5)
		high	*	18.6 (6.6)	17.4 (6.8)
High Rocks	E	low	56.4 (16.1)	61.3 (19.6)	*
		mid	*	20.7 (4.4)	8.1 (3.5)
		high	*	16.3 (5.1)	6.7 (2.8)
High Rock	S	low	84.0 (12.0)	1.3 (0.6)	*
		mid	*	30.9 (10.1)	14.6 (19.0)
		high	*	5.3 (1.7)	6.5 (1.8)

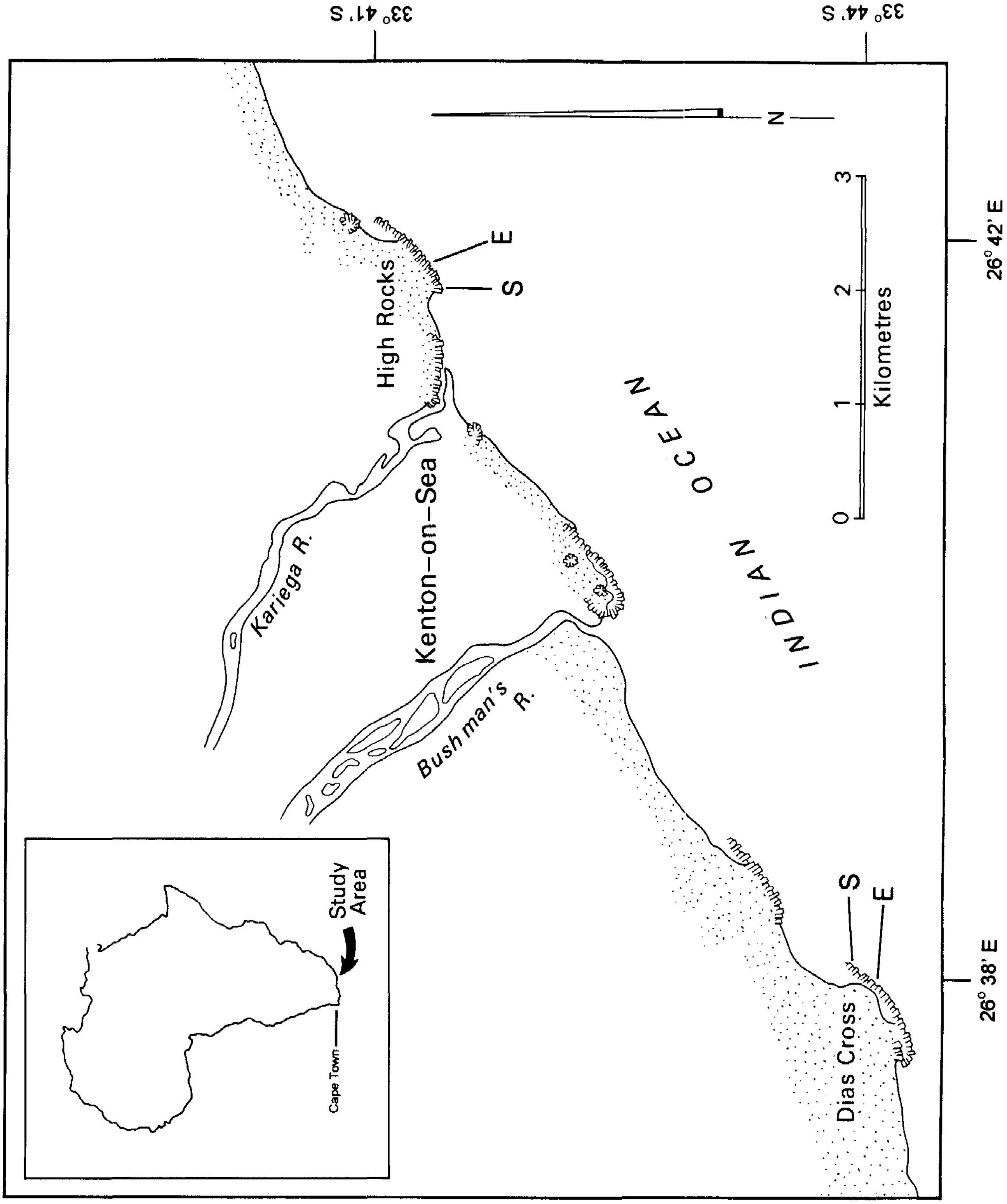


Figure 2.1 Map of study area, showing Diaz Cross and High Rocks, exposed (e) and sheltered (s) shores.

2.4 Data Analysis

Statistical analyses were carried out using Statgraphics (v.7.0) software. Normality of distribution and homogeneity of variances are probably the two most important requirements for most parametric statistics (Zar, 1996). Statistical analyses for this chapter were carried out on untransformed data unless transformations improved the suitability of the data set in terms of the requirements for the intended tests. Details of transformations are given in the sections where they were used. Zar (1996) stresses that ANOVA is robust even when used with heterogeneous data (as long as samples are similar in number) and with data which deviate from normality. Even considerable deviations from ideal criteria only affect the analysis very slightly. When required Tukey's multiple range tests were used in conjunction with analysis of variance. All statistical procedures were undertaken at a confidence level of 95%.

For most of the statistical analyses the recruits were divided into two size classes and the data for each size class was treated as a separate data set. Early recruits <1mm in length were termed early plantigrades, recruits 1-4.99mm were termed late plantigrades. There is a certain amount of confusion surrounding the size which constitutes an early or late plantigrade for *Perna perna* (Berry, 1978; Phillips, 1994; Lasiak & Barnard, 1995). For this study the sizes suggested by Phillips (1994) for early plantigrades were used, and for late plantigrades a compromise between the size used by Lasiak & Barnard (1995) (0.5-3.5mm) and that used by Berry (1978) (1-9mm) was decided on.

Size Structure

Size frequencies for each day sampled were generated from the length data. Due to the fine scale measurements (an accuracy of 0.083 mm) and the fact that measurements ranged from 0.250mm to 15mm it was necessary to have size class intervals of increasing breadth along the x-axis (Table 2.3). These size class intervals were only used for the presentation of graphs and not for data analyses.

Table 2.3 Lengths and the corresponding size class intervals into which they were grouped for presentation.

Length (mm)	Size class interval (mm)
0.25-3.99	0.1
4.00-9.99	0.5
10.00-14.99	1

Synchrony of recruitment

The total density of early and late plantigrades at each exposure, all tidal heights and both sites were calculated for each day sampled. Patterns in the number of recruits sampled on each day were examined, with reference to sites, substrata and tidal heights. Observations were divided into two broad categories, 1- the synchrony of plantigrade densities on a particular substratum at each tidal height, 2 - the synchrony of plantigrade densities between substrata at a particular tidal height. This was carried out for the Diaz Cross and High Rocks data independently and was completed separately for early and late plantigrades.

Density

The analyses for mussel densities were divided into two parts: densities of early plantigrades and densities of late plantigrades. As the statistical analyses for early and late plantigrade densities were identical the procedures used are only described once, but can be applied to both. Ideally the analysis for this section would involve one 4-way ANOVA, however due to absence of one substratum (*i.e.* mussel bed) at the sheltered low shore sites the analysis had to be divided into sections. The analyses of the density data were divided into four sections, a-d.

a- Effects of shore, exposure and zone on recruit densities on algae

The densities of settlers on algae were examined with a 3-way ANOVA using as factors, shore (D,H), exposure (sheltered, exposed) and zone (low, mid, high). For this analysis, coralline alga and *Gelidium* were not distinguished from each other and were treated as algae. The analyses were carried out on log transformed data (log x+1). For early plantigrades the log transformation normalised the data ($p>0.05$), however only for exposure ($p>0.05$) was homogeneity of variances achieved. Data for site and zone did not achieve homogeneity of variances even after transformation ($p<0.05$). Transformed data for late plantigrades failed the test for a normal distribution ($p<0.05$). Homogeneity of variances was also not achieved for factors site, zone and exposure data ($p<0.05$ in all cases).

b- Effects of shore, zone and substratum on recruit densities under exposed conditions

To examine differences in recruit densities at the two exposed sites, a three-way ANOVA was carried out using shore (DE, HE), zone (low, mid, high) and substratum (mussel, algae) as factors. The analyses (for recruits <1mm and for recruits 1-4.99mm) were carried out on log transformed data (log x+1), even though the requirements for normality and homogeneity of variances were not always achieved. Data for the early plantigrades was normalised by the log transformation ($p>0.05$). However factors site, zone and substratum did not achieve homogeneity of variances even after transformation ($p<0.01$ in all cases). Data for the late plantigrades were normalised by log transformation ($p>0.05$). After transformation factors site and zone, for late plantigrade data, did not achieve homogeneity of variances ($p<0.0001$ in both cases), however homogeneity was achieved by the data for the substratum factor ($p>0.05$). This analysis could not be repeated for the sheltered shores because low shore mussels were missing.

c- Effects of shore, exposure, zone and substratum on the mid and high shore

The effects of shore (D, H), exposure (E,S), zone (mid, high) and substratum (mussel, algae) on recruit densities on the mid and high shore were examined using a 4-way ANOVA. The analyses (for recruits <1mm and for recruits 1-4.99mm) were carried out on log transformed data (log x+1), even though normality and homogeneity of variances were not always achieved. For the early plantigrade data, transformation normalised the data ($p>0.05$), however homogeneity of variances was only achieved for the factor exposure ($p>0.05$). Variances for the site, zone and substratum data were not homogeneous ($p<0.02$ in all cases). A normal distribution was achieved, through transformation, for the late plantigrade data ($p>0.05$). After transformation homogeneity of variances was achieved for the exposure and substratum data ($p>0.05$ in both cases), but not for the site and zone data ($p<0.05$ in both).

d- Comparison of settler densities on mussels and on algae

A comparison of the densities of recruits on algae and on mussel substrata at each zone and for each exposure were completed using one-way ANOVA's. For each exposed shore three 1-way ANOVA's were completed, one comparison for each tidal height. Due to the absence of mussel substratum on the low shore sheltered zones, two 1-way ANOVA's were carried out on mid and high shore sheltered zones. As these analyses were repeated for recruits <1mm and recruits 1-4.99mm a total of 20 ANOVA's were carried out. In most of these analyses data conformed to the requirements of normality and homogeneity and the data were not transformed and all analyses were carried out on untransformed data. Data were normally distributed for all 10 of the analyses undertaken for the early plantigrades, without transforming the data. Six of the 10 data sets for early plantigrades achieved homogeneity of variances, without transformation. For the late plantigrades all 10 data sets had normal distributions, and variances for five of the 10 possible data sets were homogeneous.

The above analyses apply to areas of 100% cover of algae or mussel bed. It was also desirable to estimate the densities of recruits not only in areas with 100% cover of a particular substratum, but also on a "typical" square metre of shore, which included a mixture of substrata. Using the percentage cover of potential settling sites (Table 2.2) an estimate of the density of settlers per metre square of shore could be calculated for each zone at each shore. The formula (Equation 2.1) used to calculate this, takes into account the number of settlers on a particular substratum as well as the percentage cover of that substratum in the zone. Using these adjusted densities, comparisons of pooled settler densities on algae and mussel substrata could be compared for each zone at each shore by using one-way ANOVA's. Untransformed data sets were used for these analyses, as data in most cases conformed to the requirements for ANOVA tests. For early plantigrades nine of the 10 data sets had normal distributions ($p>0.05$ in nine cases) and homogeneity of variances was present in four of the 10 cases. For the late plantigrades, all 10 data sets were normally distributed ($p>0.05$ in all cases), and homogeneity of variances was achieved in four of the 10 analyses.

Equation 2.1

$N = a \times d$

Where:

N = Number of recruits on substratum.m^{-2} of shore,

a = area of substratum.m^{-2} of shore, expressed as a fraction of 1 (i.e. 50% cover = 0.5),

d = recruit density.m^{-2} on substratum at 100% cover

2.5 RESULTS

Size

Even though there were many length frequency histograms for mussels sampled at both sites and on different days (Figures 2.2-2.5) they have been included as extremely clear patterns exist. A summary of the size structure of recruits on each substratum is also included (Table 2.4).

Low shore, exposed, coralline

Most noticeable was the strong presence of a cohort in the larger size classes between six and 15mm. At High Rocks peaks in these size classes exceeded most of the peaks in the smaller size classes, which represented direct settlement. These peaks in the larger size classes were not as pronounced at Diaz Cross, but were still strongly apparent. The fact that only six days were sampled on the low shore make it difficult to follow any single cohort through time.

Low shore, sheltered, coralline

Few settlers over 2mm were recorded. Settler densities were very low except on the 21/04 at High Rocks, where fairly large numbers of settlers appeared in the smaller size classes.

Low shore, exposed, mussel

Recruitment into the mussel bed ensured that there were recruits (late plantigrades) in the larger size classes of the frequency histograms. At High Rocks there was a fairly continuous series of peaks throughout the size range of the frequency histogram, while at Diaz Cross there was a gap in the middle size classes. This probably reflected differences in settlement at the two sites prior to this study being undertaken. It could also indicate differences in mortality, but this is not the simplest or most likely explanation.

Mid shore, exposed, *Gelidium*

This substratum showed a similar pattern to that observed for the sheltered shores, with few mussels in the larger size categories. However histograms from both Diaz Cross and High Rocks showed a standing peak of settlers in the 0.99-1.09mm size class. At Diaz Cross there were large numbers of recruits in the smaller size classes on the 22 and 24 of April.

Mid shore, sheltered, *Gelidium*

Few mussels above 2.5mm were recorded on this substratum, and in most cases at least half of the mussels were under 1mm in length. At Diaz Cross the 0.99-1.09mm size class showed a peak on most days sampled, and there was no progression of this size class over time. Both sites showed few settlers in the smallest size classes.

Mid shore, exposed, mussel

The frequency histograms for High Rocks reveal a pattern close to that observed at the sheltered mussel site, with a spread of settlers throughout the size range, and in many cases bimodal histograms. At Diaz Cross the frequency histograms for the exposed and sheltered mid shore mussel beds were similar to each other with fewer mussels in the larger size classes and not such an even spread of mussels throughout the size range.

Mid shore, sheltered, mussel

High Rocks showed a fairly even spread of mussels in all size classes with few distinct peaks of settlement or early recruitment. The Diaz Cross site did not have as many mussels in the larger size classes and had well defined peaks falling between 0.99-1.29mm.

High shore, exposed, *Gelidium*

In most cases there were few individuals above 3.00mm, this was not as strongly evident at High Rocks as it was at Diaz Cross. Many of the graphs peaked between 0.89 and 1.09mm. There were early settlers in the smaller size classes less than 0.60mm.

Mid shore, sheltered, mussel

High Rocks showed a fairly even spread of mussels in all size classes with few distinct peaks of settlement or early recruitment. The Diaz Cross site did not have as many mussels in the larger size classes and had well defined peaks falling between 0.99-1.29mm.

High shore, exposed, mussel

A fair number of mussels occurred in the larger size categories. Peaks in the smaller sizes once again fell between 0.90 and 1.09mm. Very few settlers occurred in the very smallest size classes.

High shore, sheltered, mussel

Low numbers of mussels occurred in size classes over 3mm, this was especially apparent at the High Rocks site. Early settlers in the smallest size classes were also scarce.

Exposed

High Rocks - low shore - coralline algae

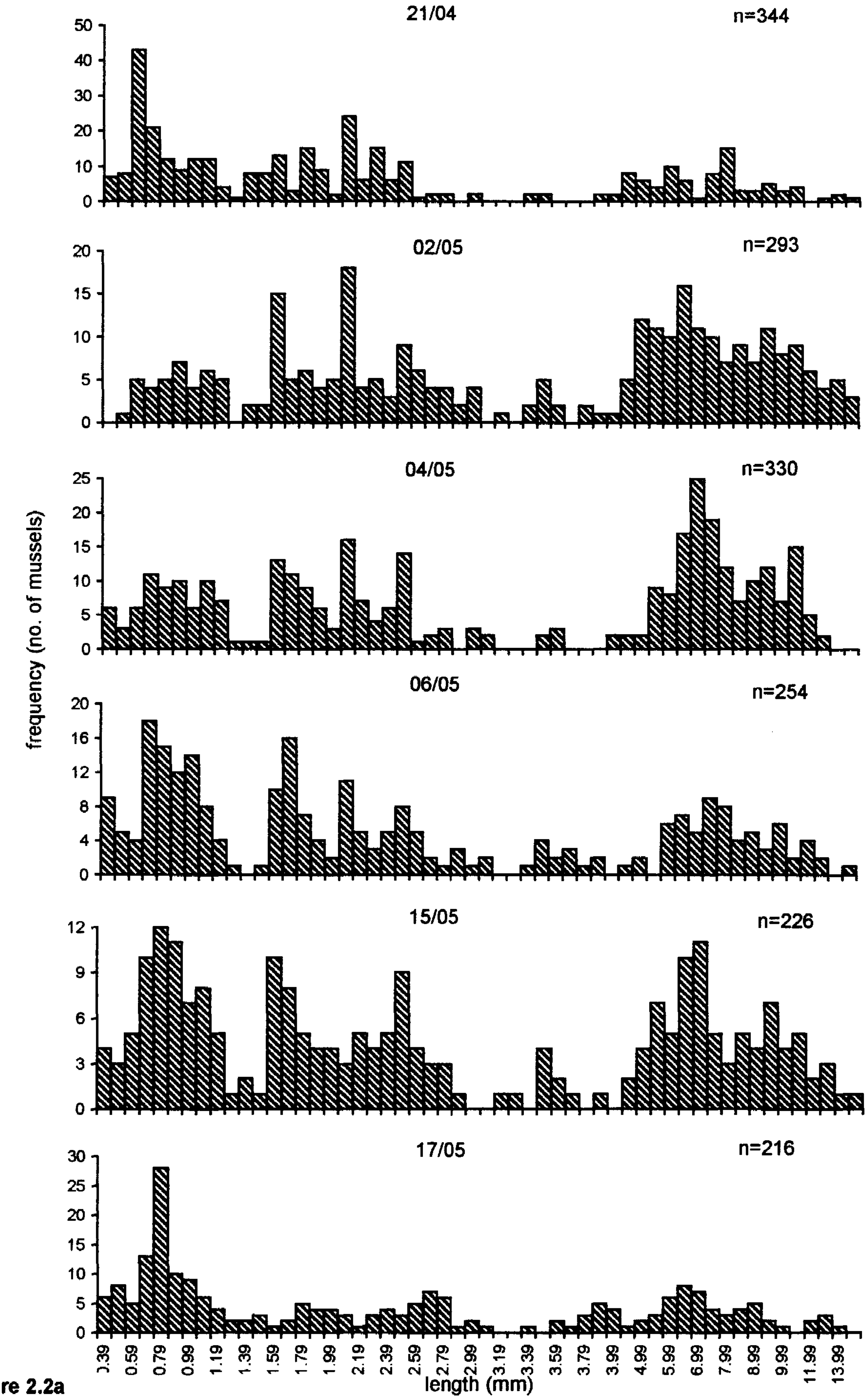


Figure 2.2a

Figure 2.2 Length (mm) frequency distributions of mussel plantigrades collected from the High Rocks exposed shore, at low, mid and high shore levels, and on algae and mussel substrata. Histograms for each day sampled on a substratum at a particular z one have been included, as well as the dates on which shores were sampled.The figure at the base of each column represents the upper limit of a size class.

Exposed

High Rocks - low shore - mussel bed

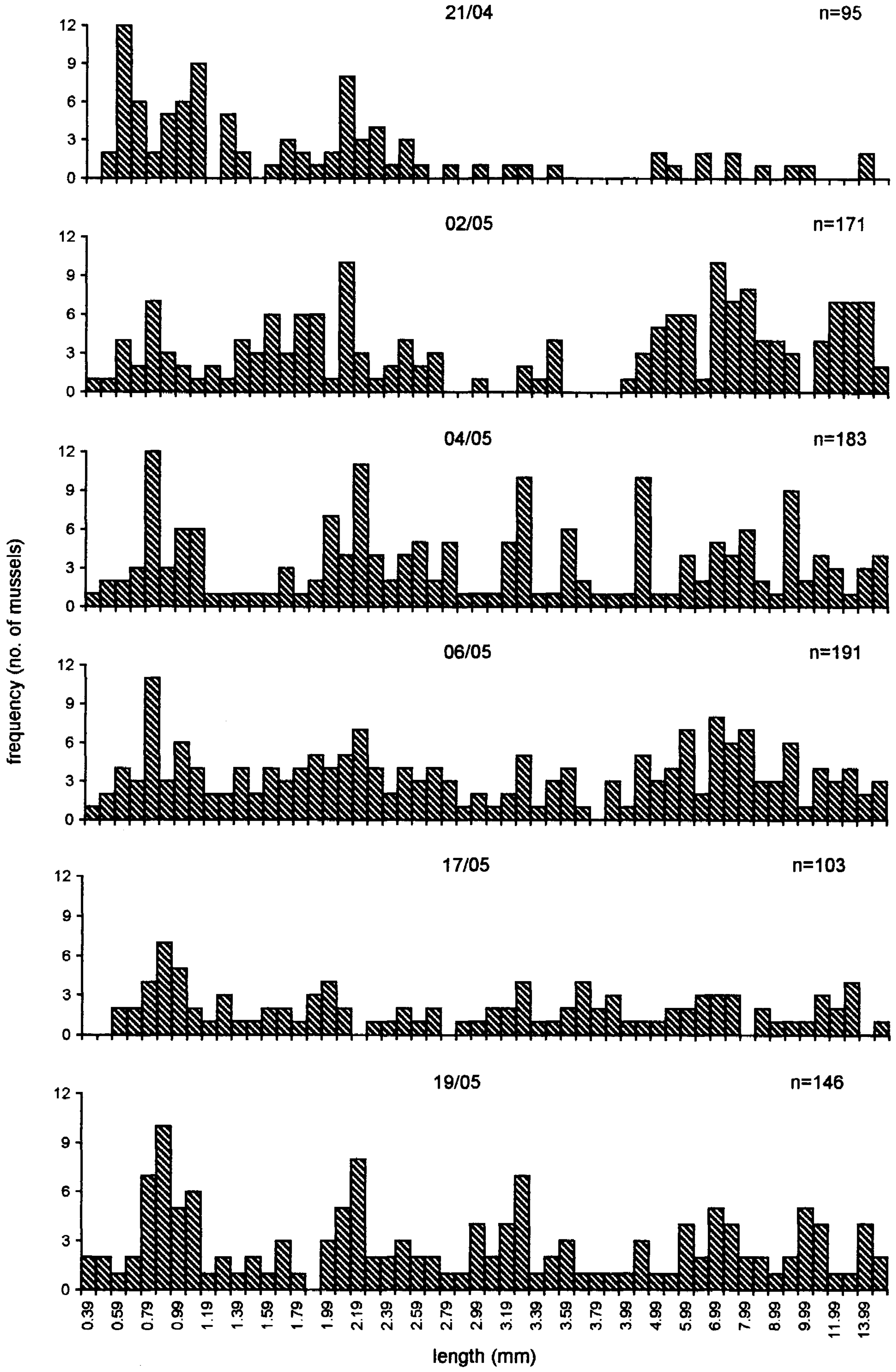


Figure 2.2b

Exposed High Rocks - mid shore - Gelidium

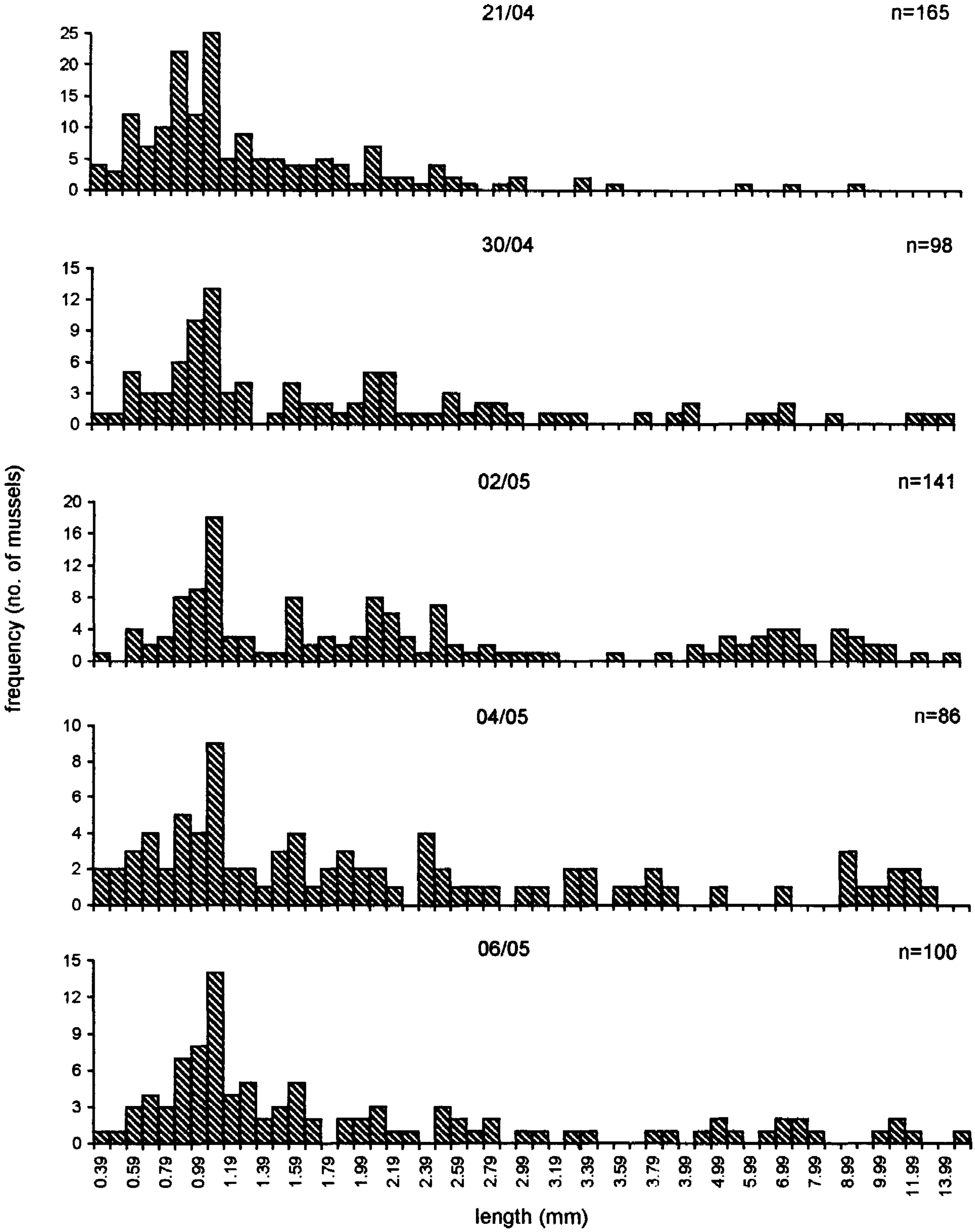


Figure 2.2c

Exposed **High Rocks - mid shore - Gelidium**

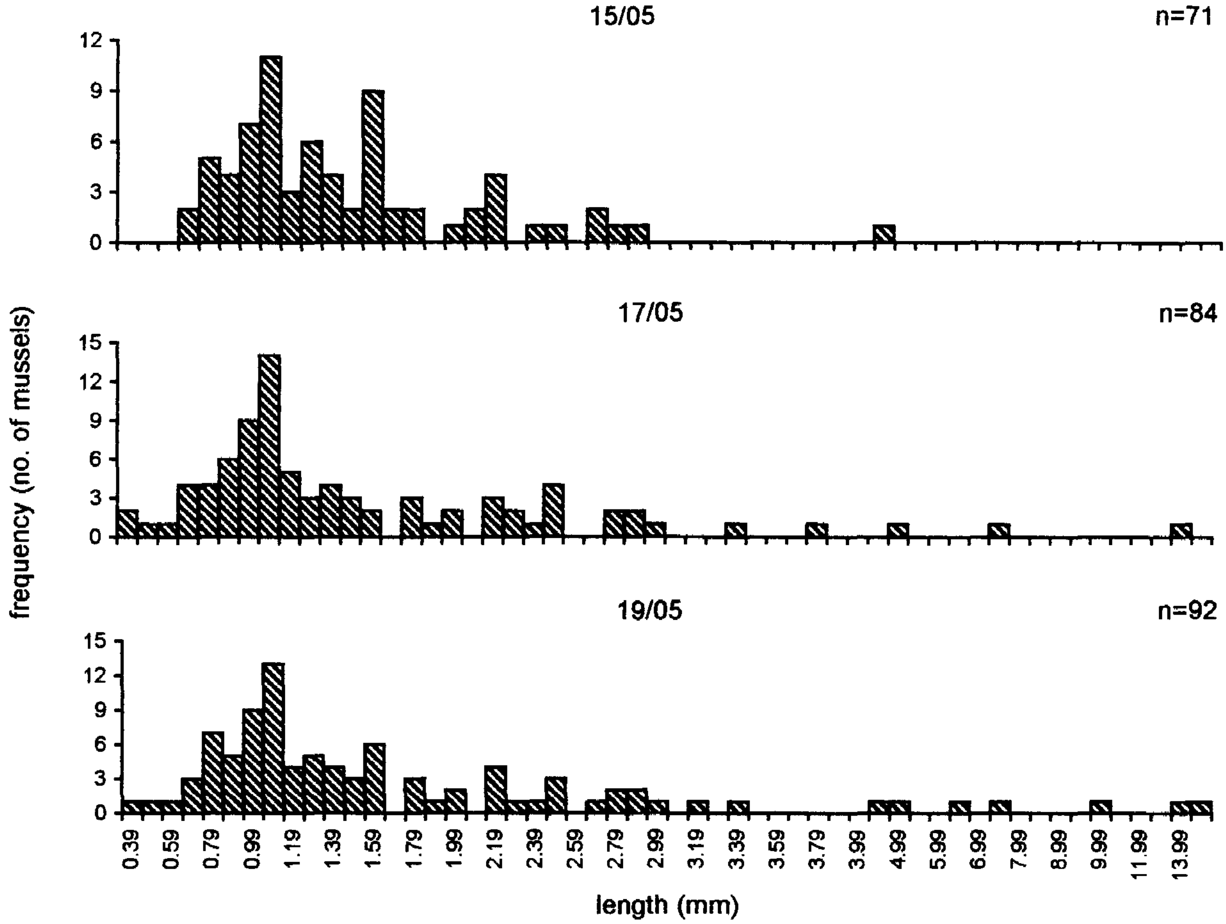


Figure 2.2c Continued

Exposed High Rocks - mid shore - mussel bed

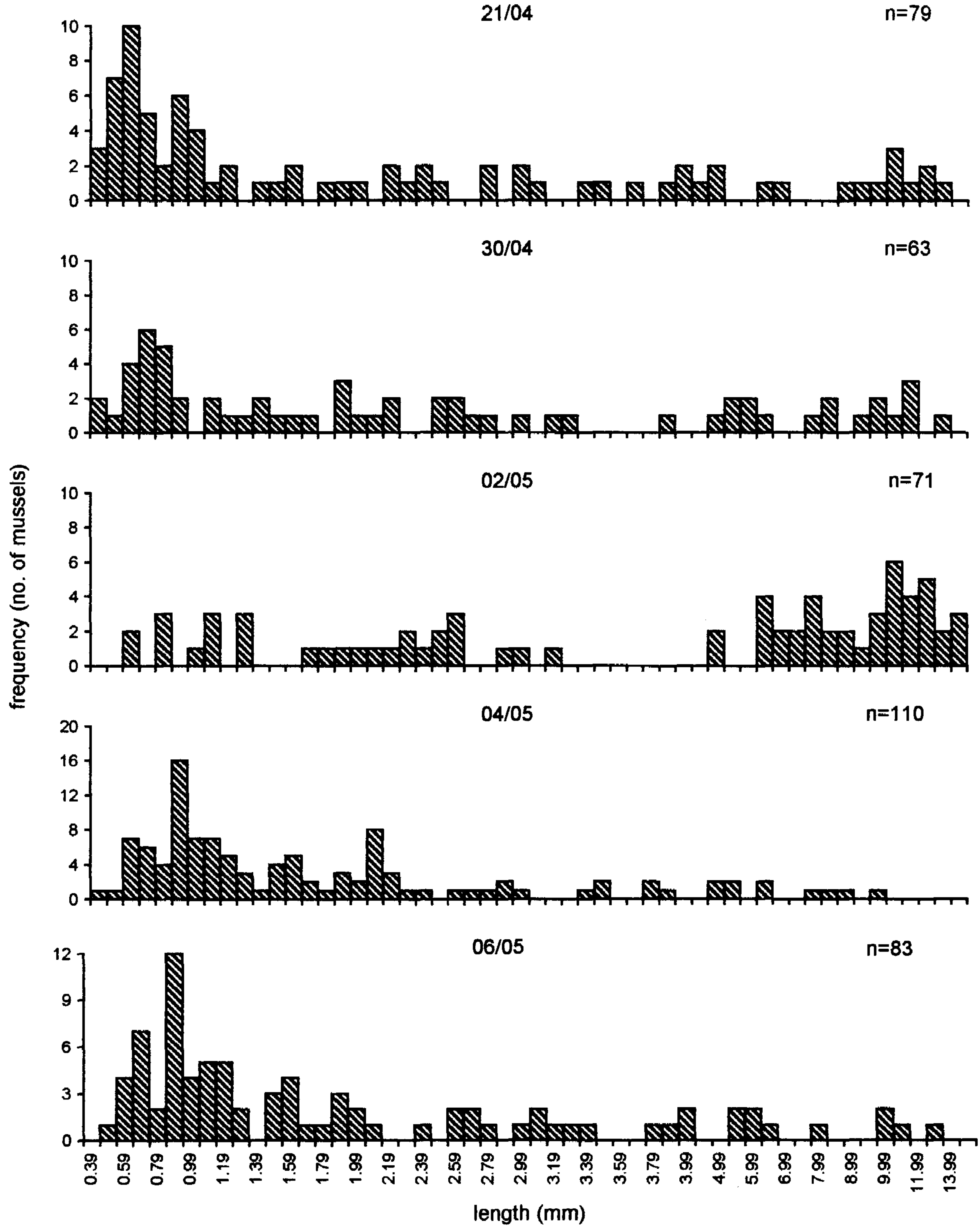


Figure 2.2d

Exposed **High Rocks - mid shore - mussel bed**

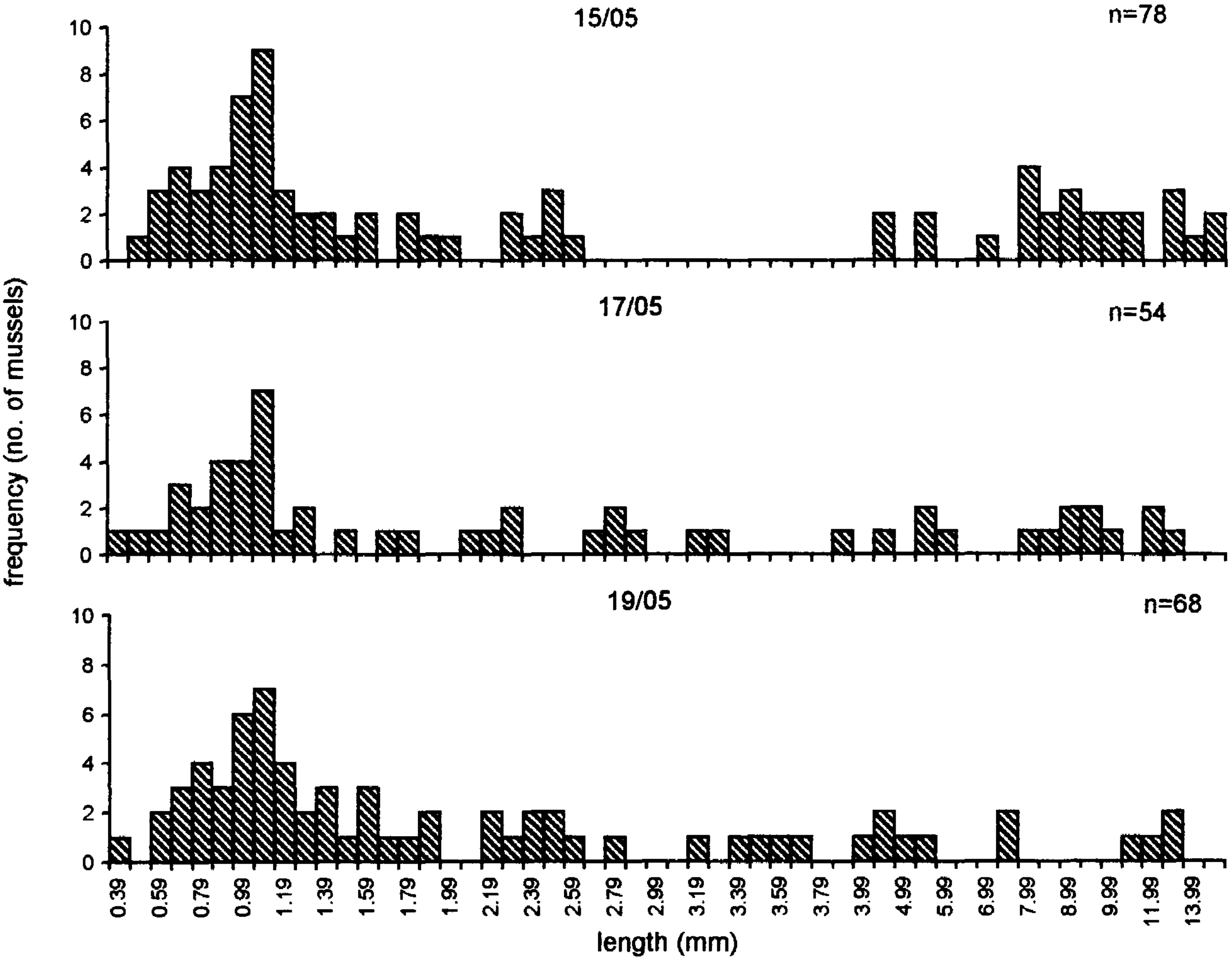


Figure 2.2d Continued

Exposed

High Rocks - high shore - Gelidium

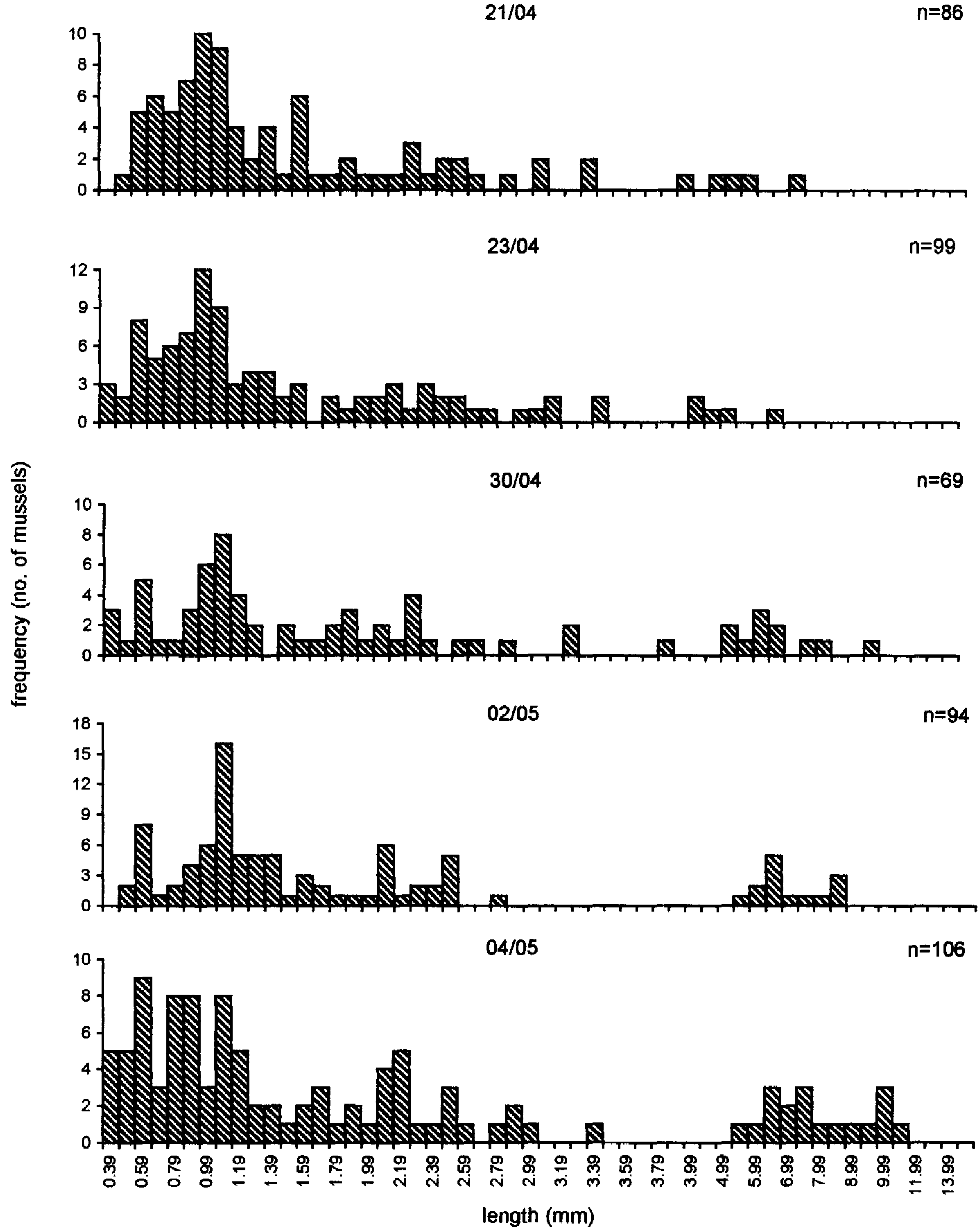


Figure 2.2e

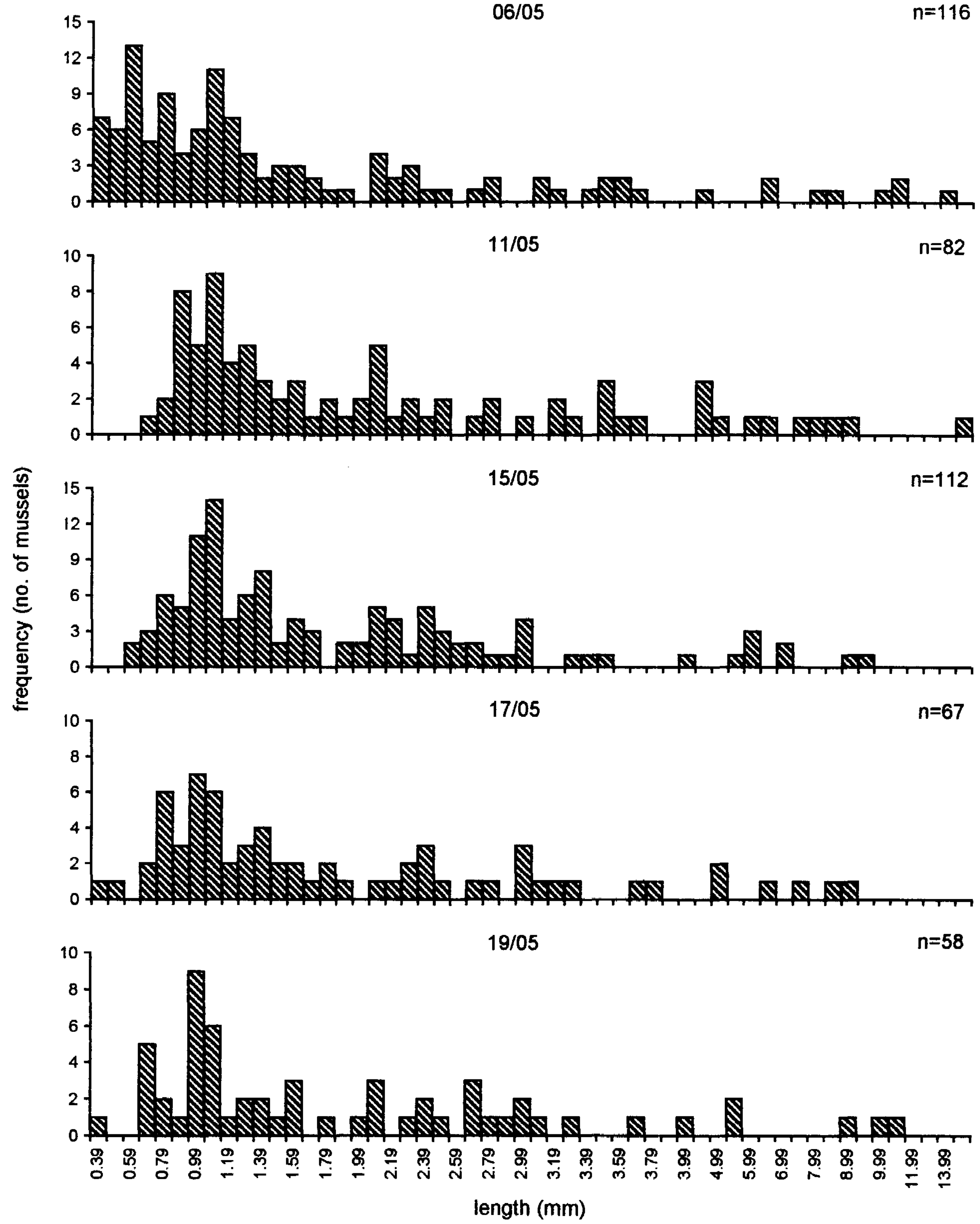


Figure 2.2e Continued

High Rocks - high shore - mussel bed

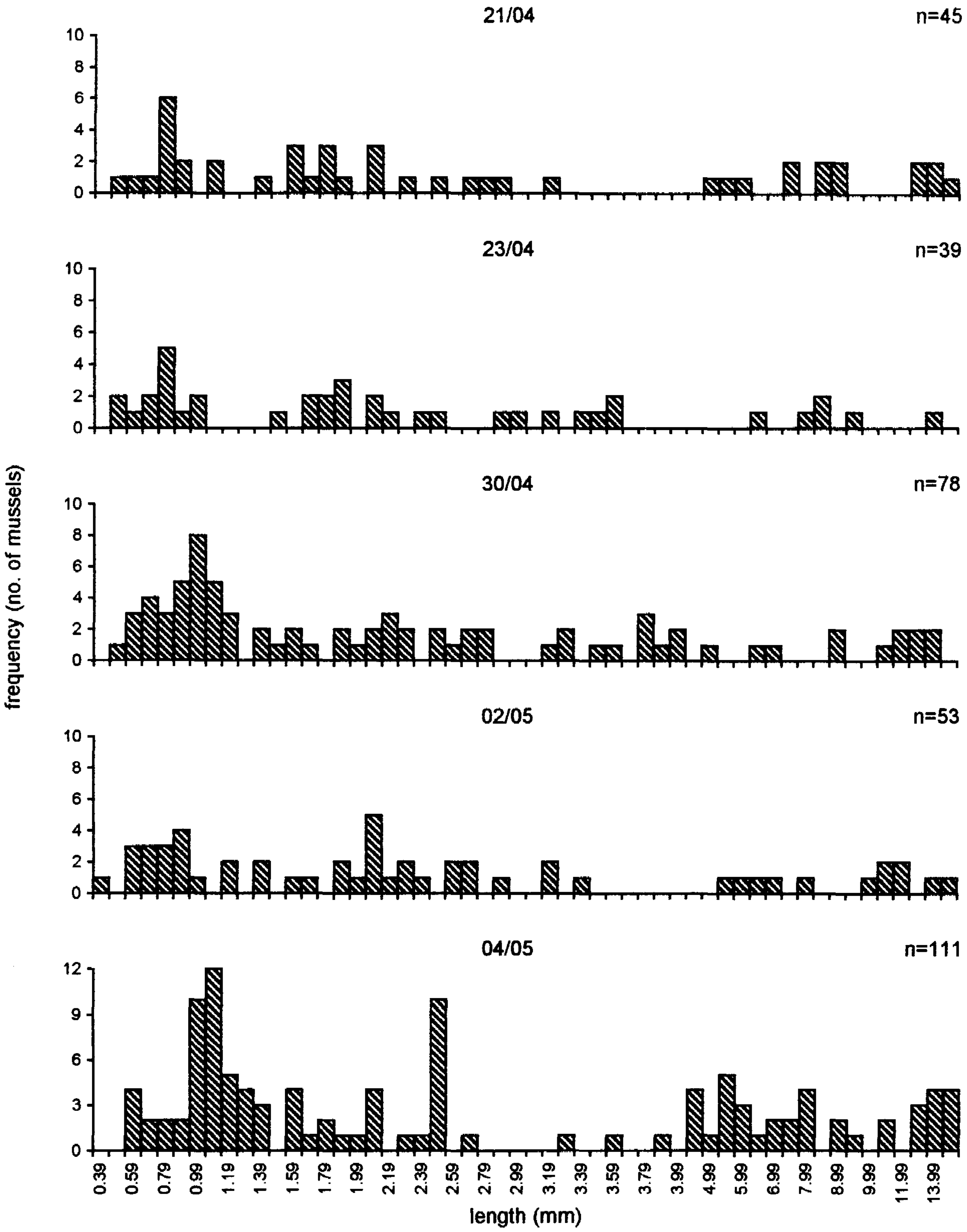
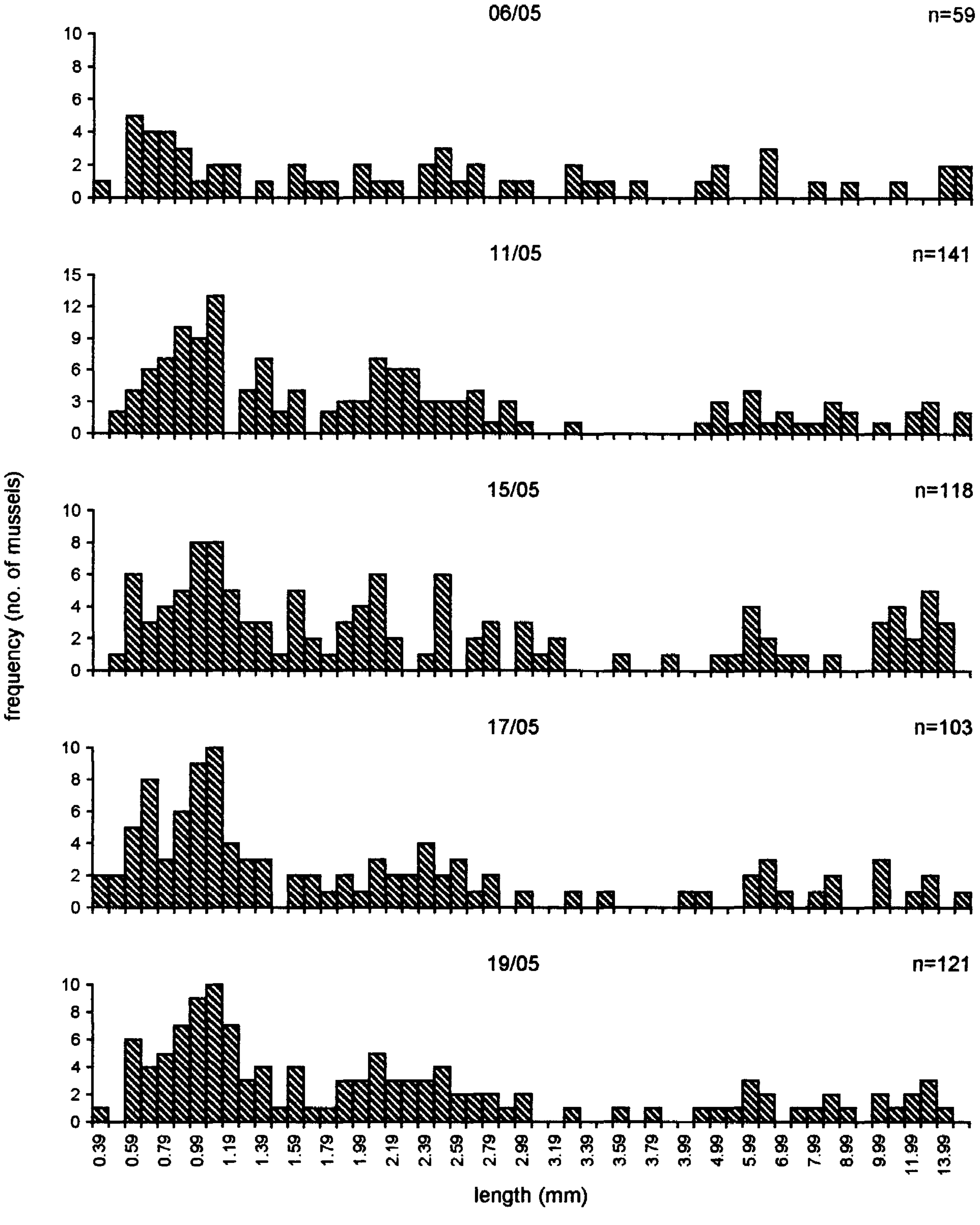


Figure 2.2f



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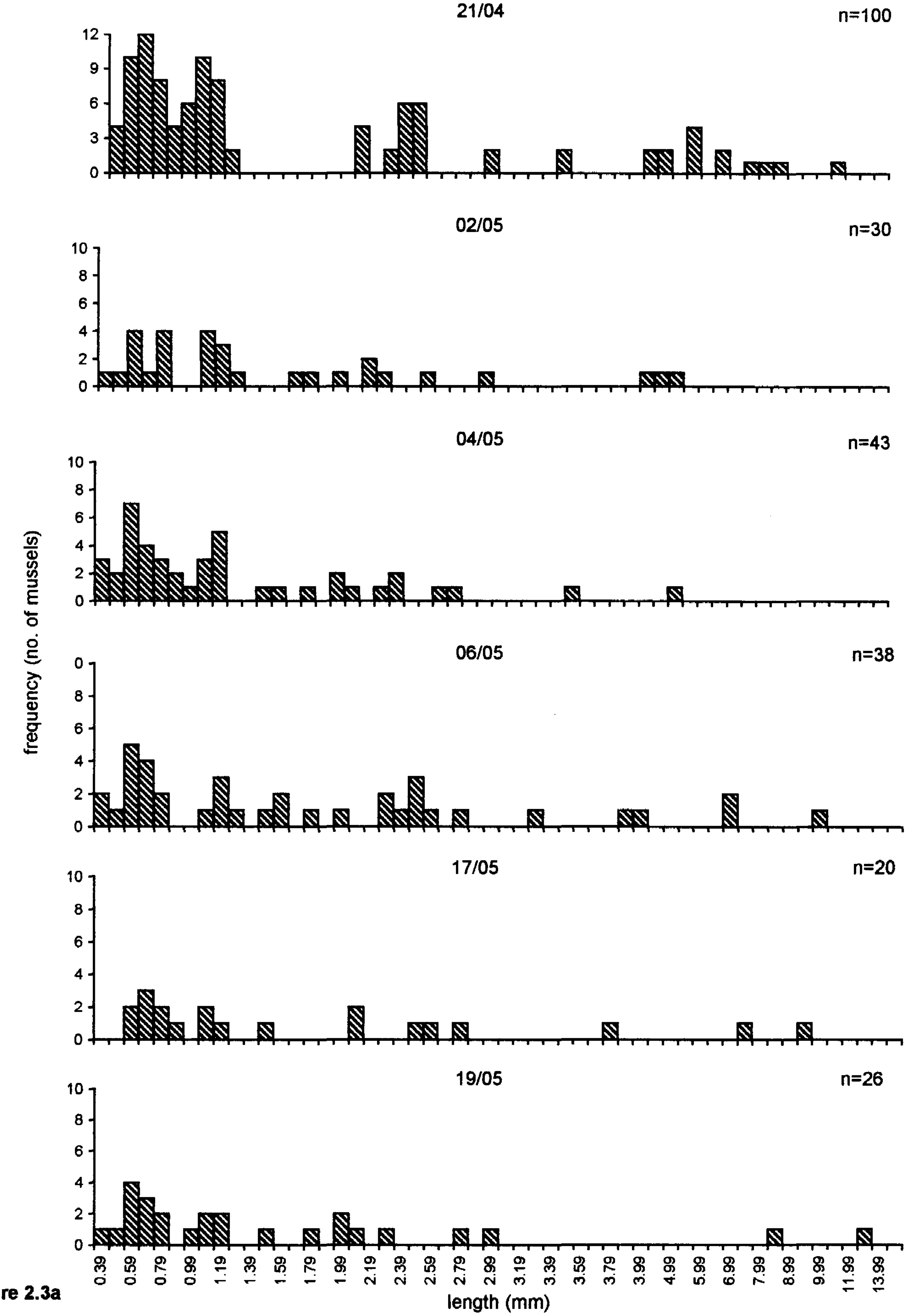


Figure 2.3a

Figure 2.3 Length (mm) frequency distributions of mussel plantigrades collected from the High Rocks sheltered shore, at low, mid and high shore levels, and on algae and mussel substrata. Histograms for each day sampled on a substratum at a particular z one have been included, as well as the dates on which shores were sampled. The figure at the base of each column represents the upper limit of a size class.

Sheltered

High Rocks - mid shore - Gelidium

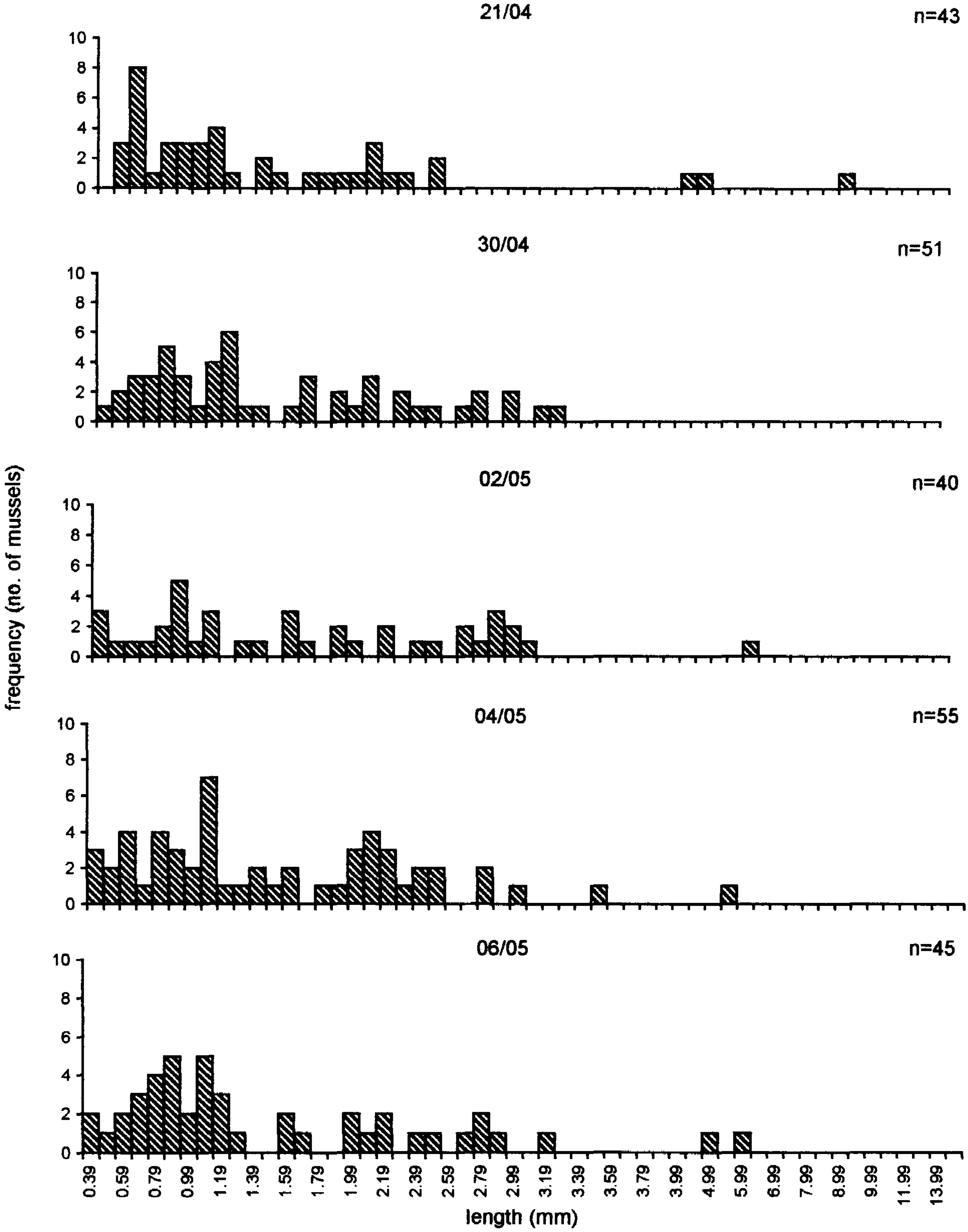


Figure 2.3b

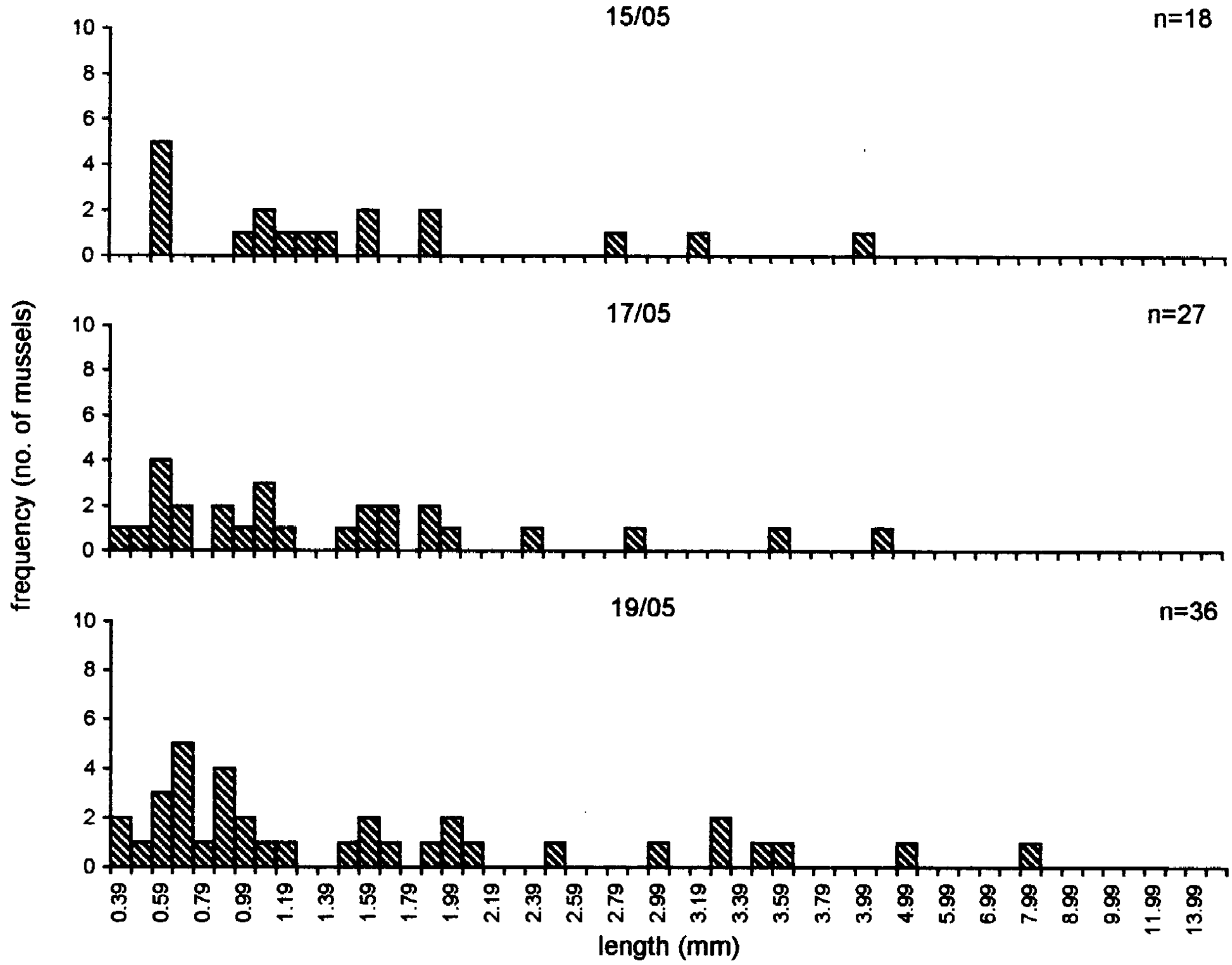


Figure 2.3b Continued

Sheltered **High Rocks - mid shore - mussel bed**

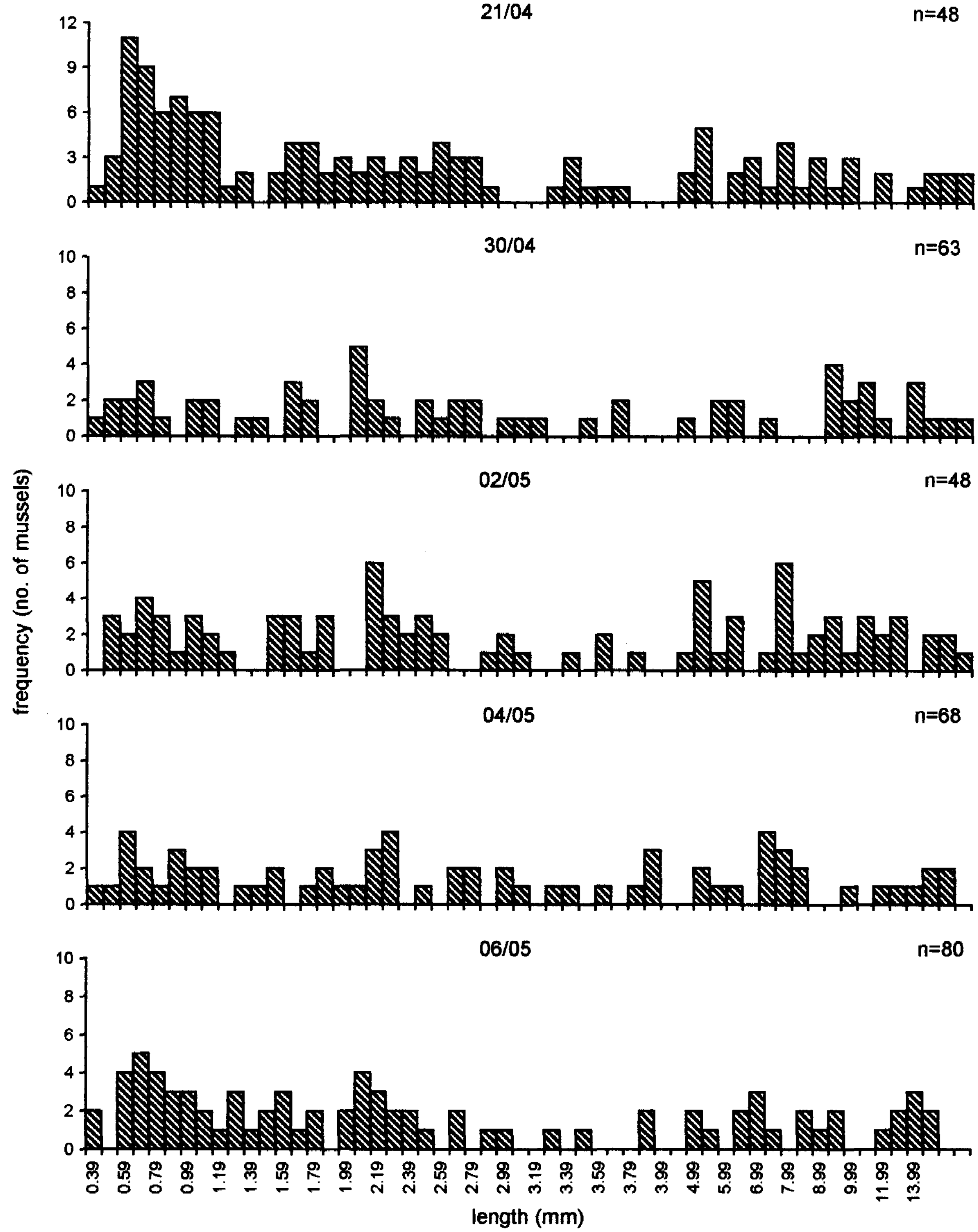


Figure 2.3c

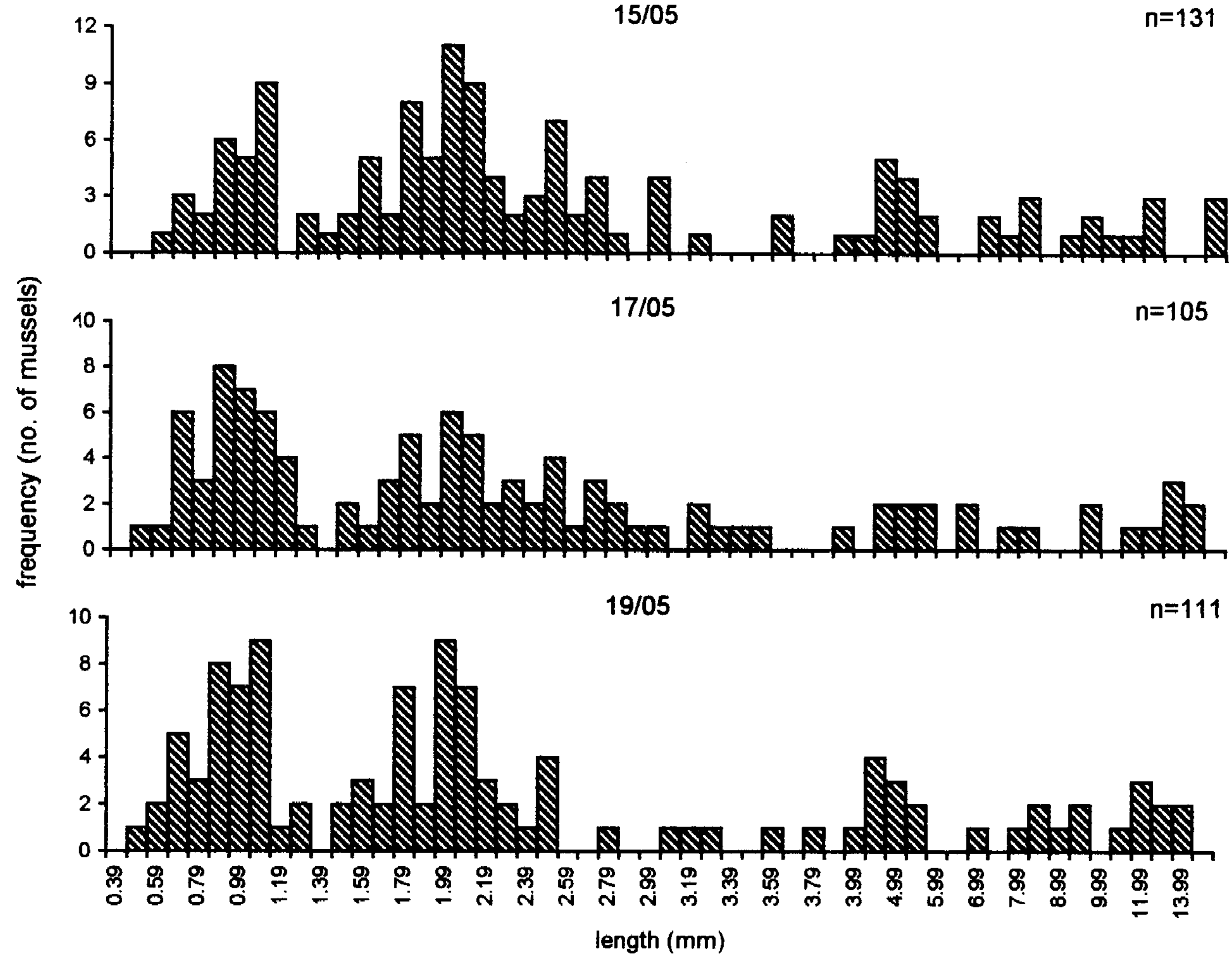


Figure 2.3c Continued

High Rocks - high shore - Gelidium

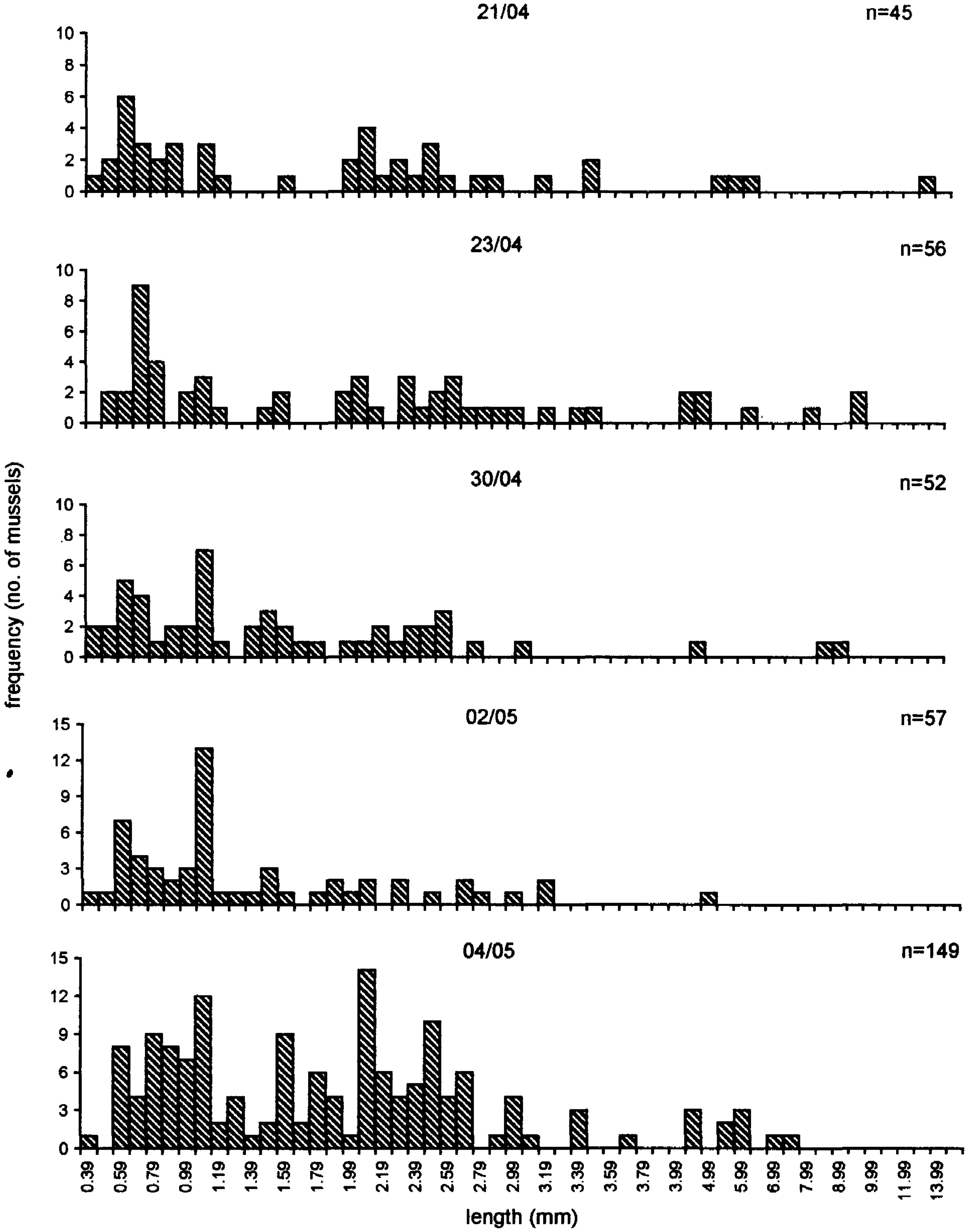


Figure 2.3d

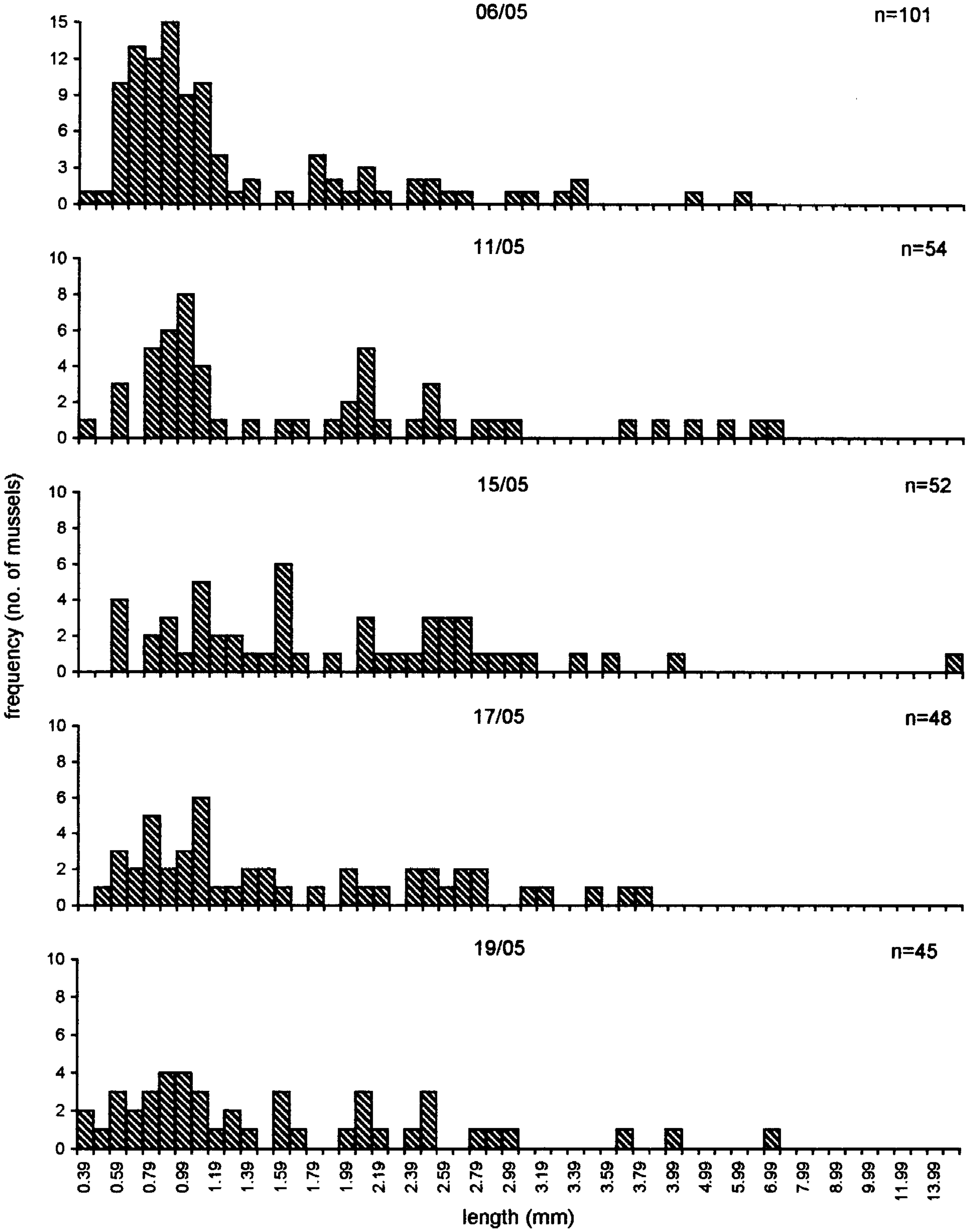


Figure 2.3d Continued

High Rocks - high shore - mussel bed

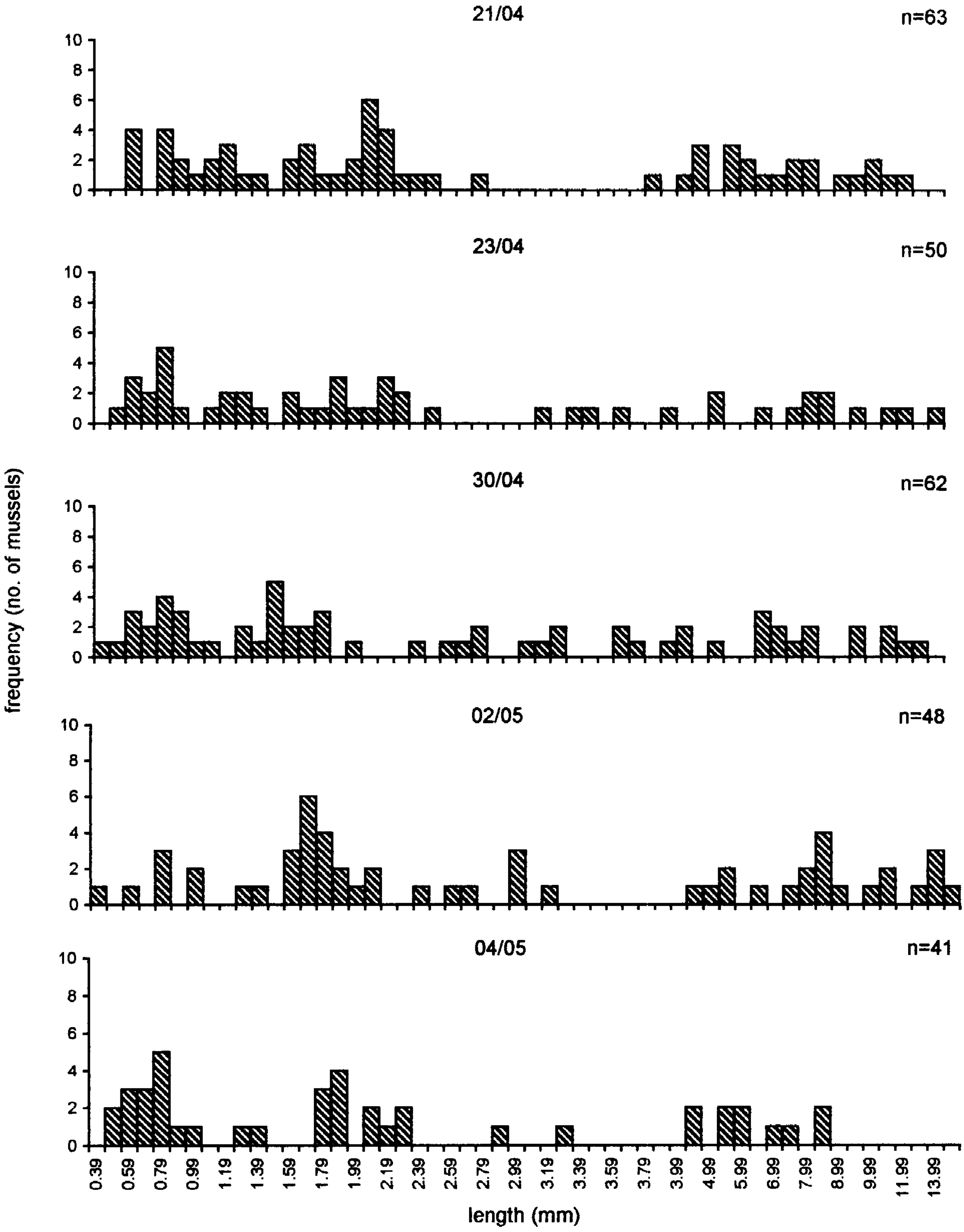


Figure 2.3e

High Rocks - high shore - mussel bed

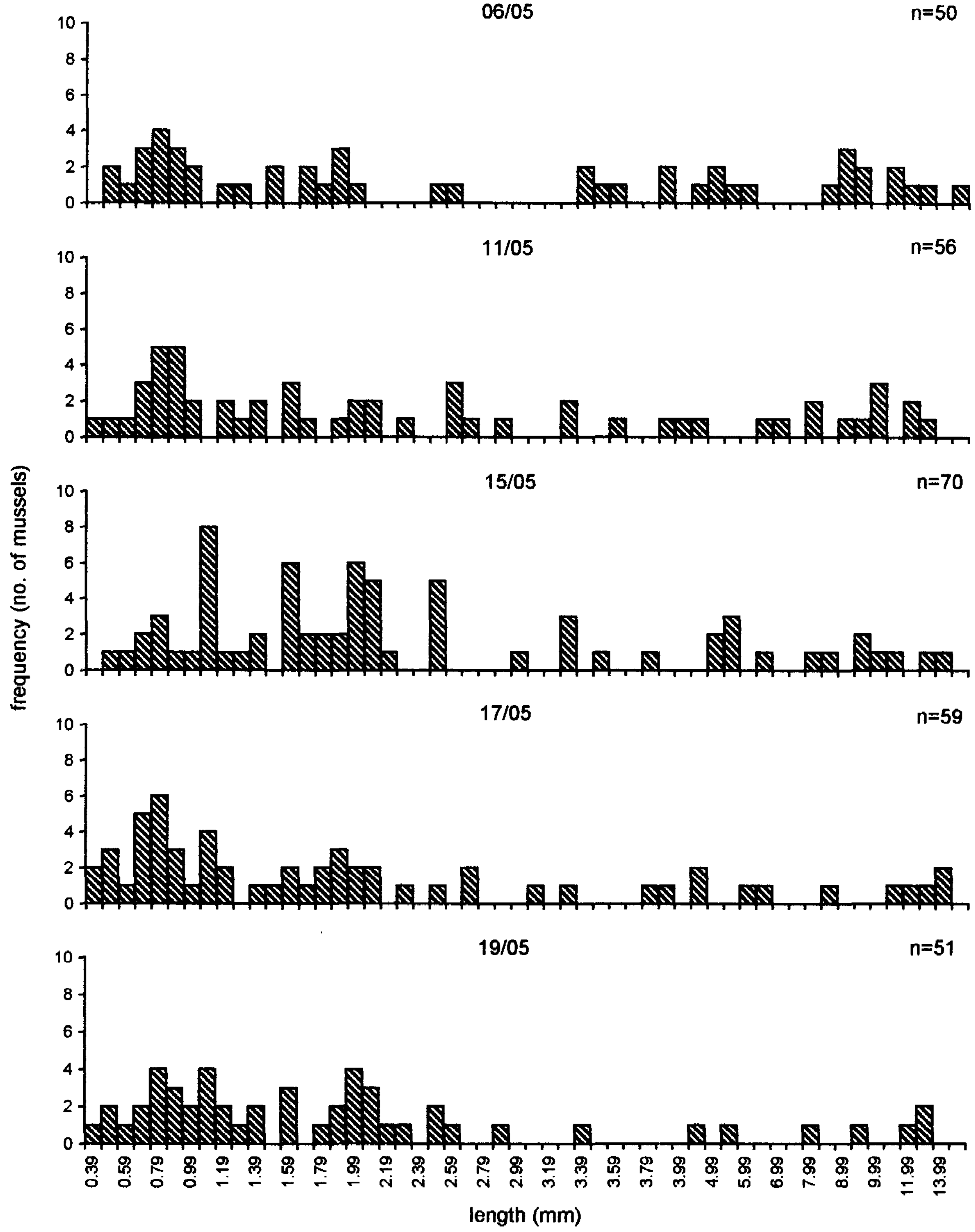


Figure 2.3e Continued

Exposed

Diaz Cross - low shore - Coralline

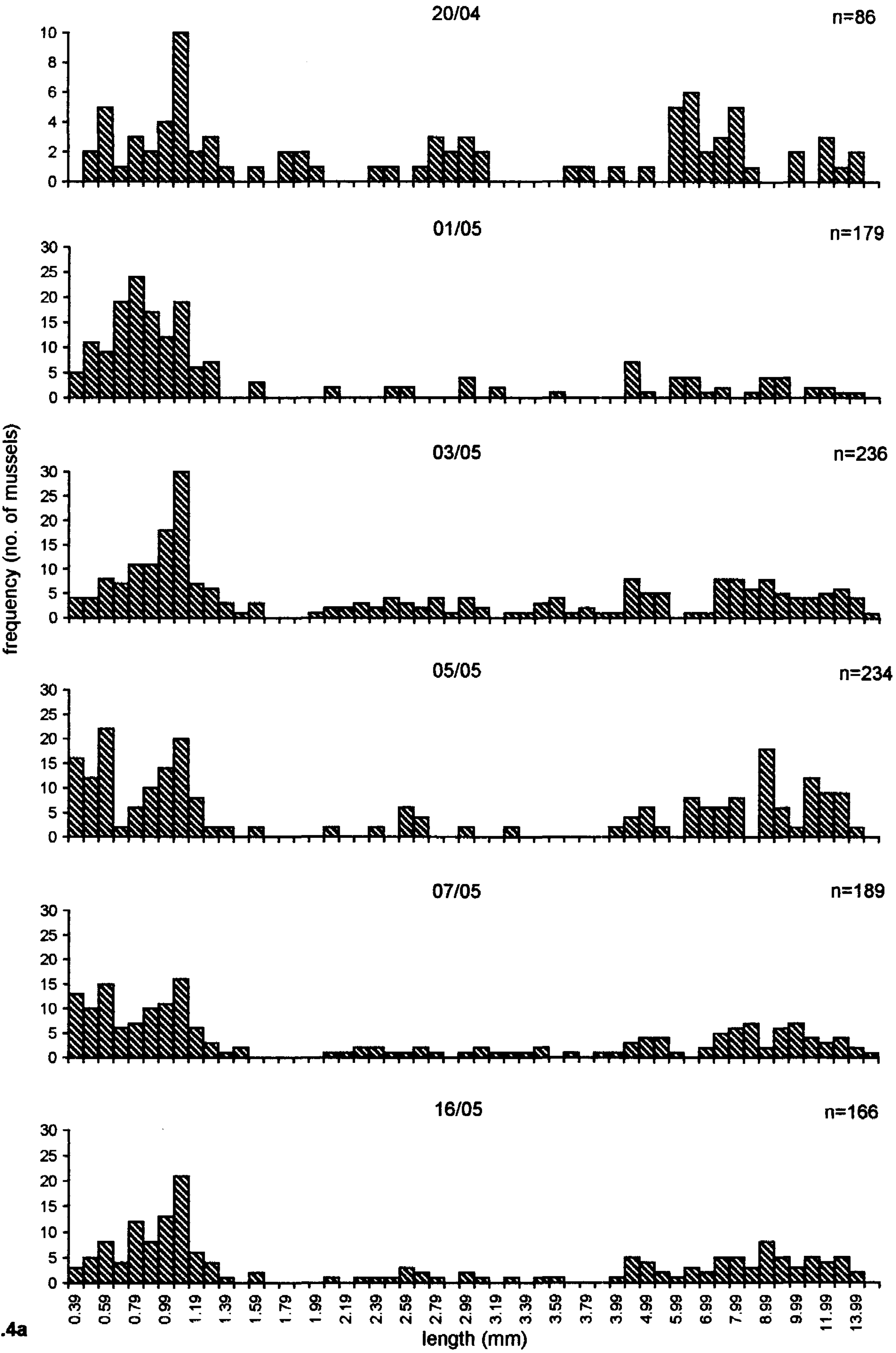


Figure 2.4a

Figure 2.4 Length (mm) frequency distributions of mussel plantigrades collected from Diaz Cross exposed shore, at low, mid and high shore levels, and on algae and mussel substrata. Histograms for each day sampled on a substratum at a particular z one have been included, as well as the dates on which shores were sampled.The figure at the base of each column represents the upper limit of the size class.

Exposed Diaz Cross - low shore - mussel bed

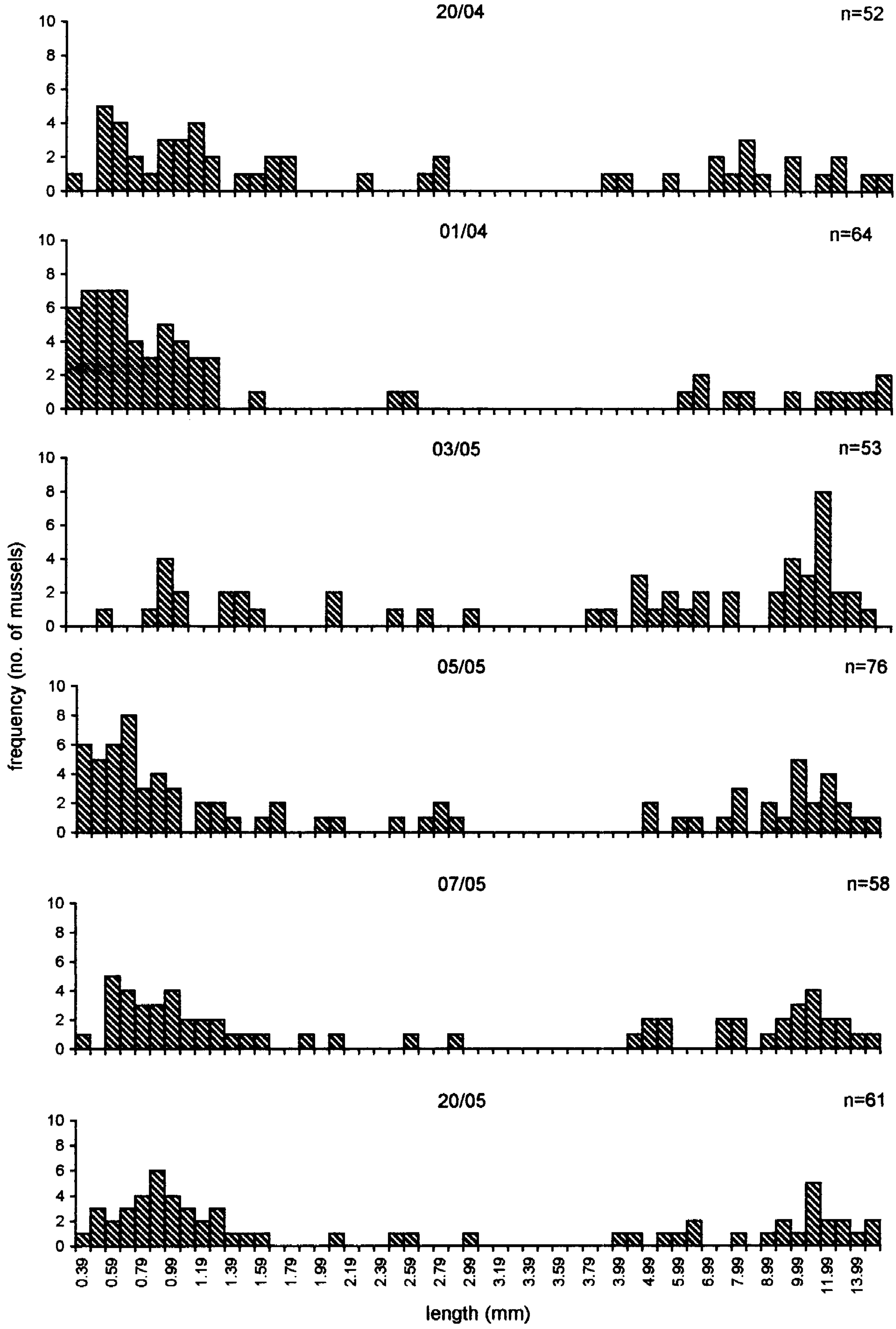


Figure 2.4b

Diaz Cross - mid shore - Gelidium

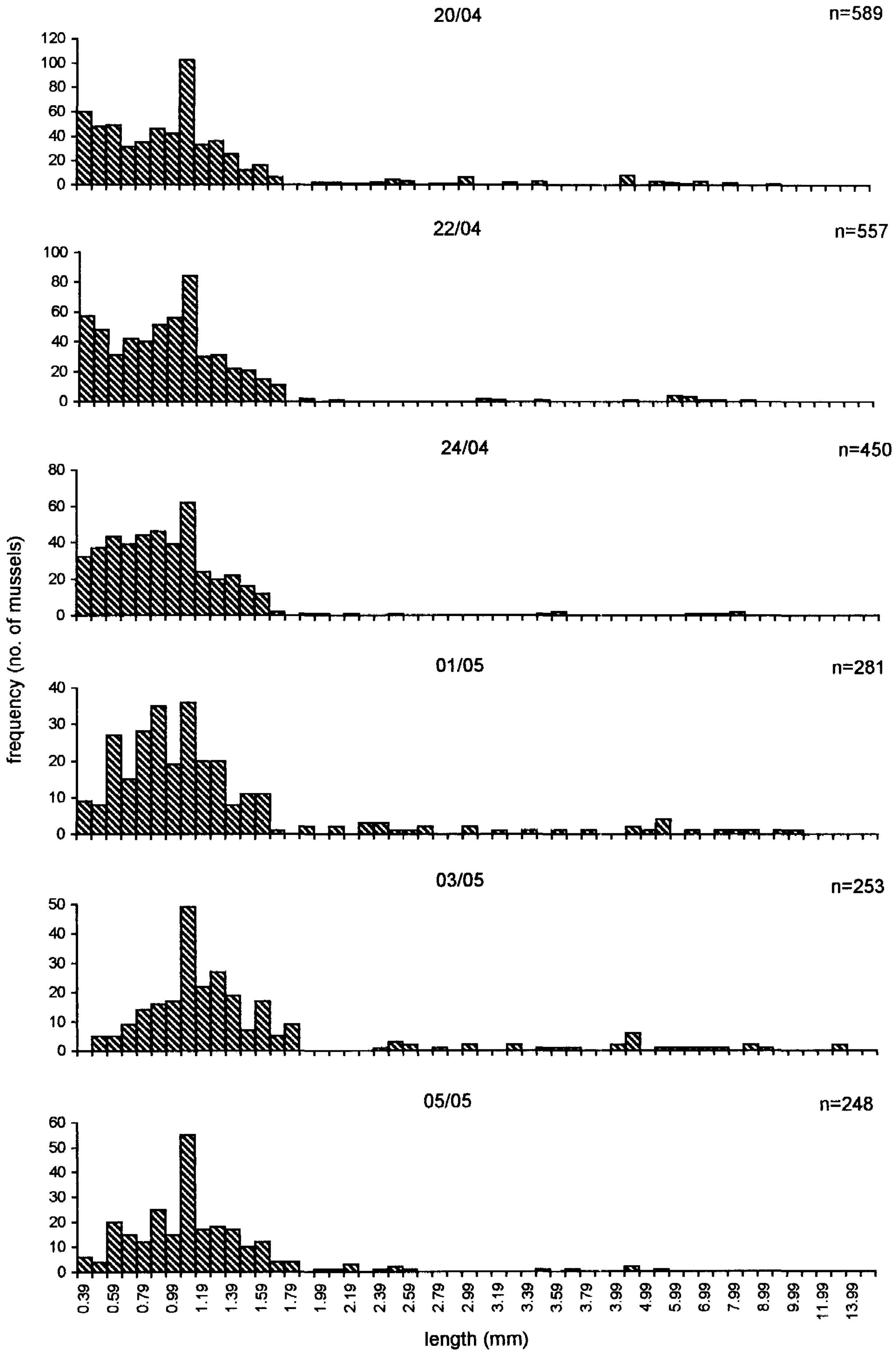


Figure 2.4c

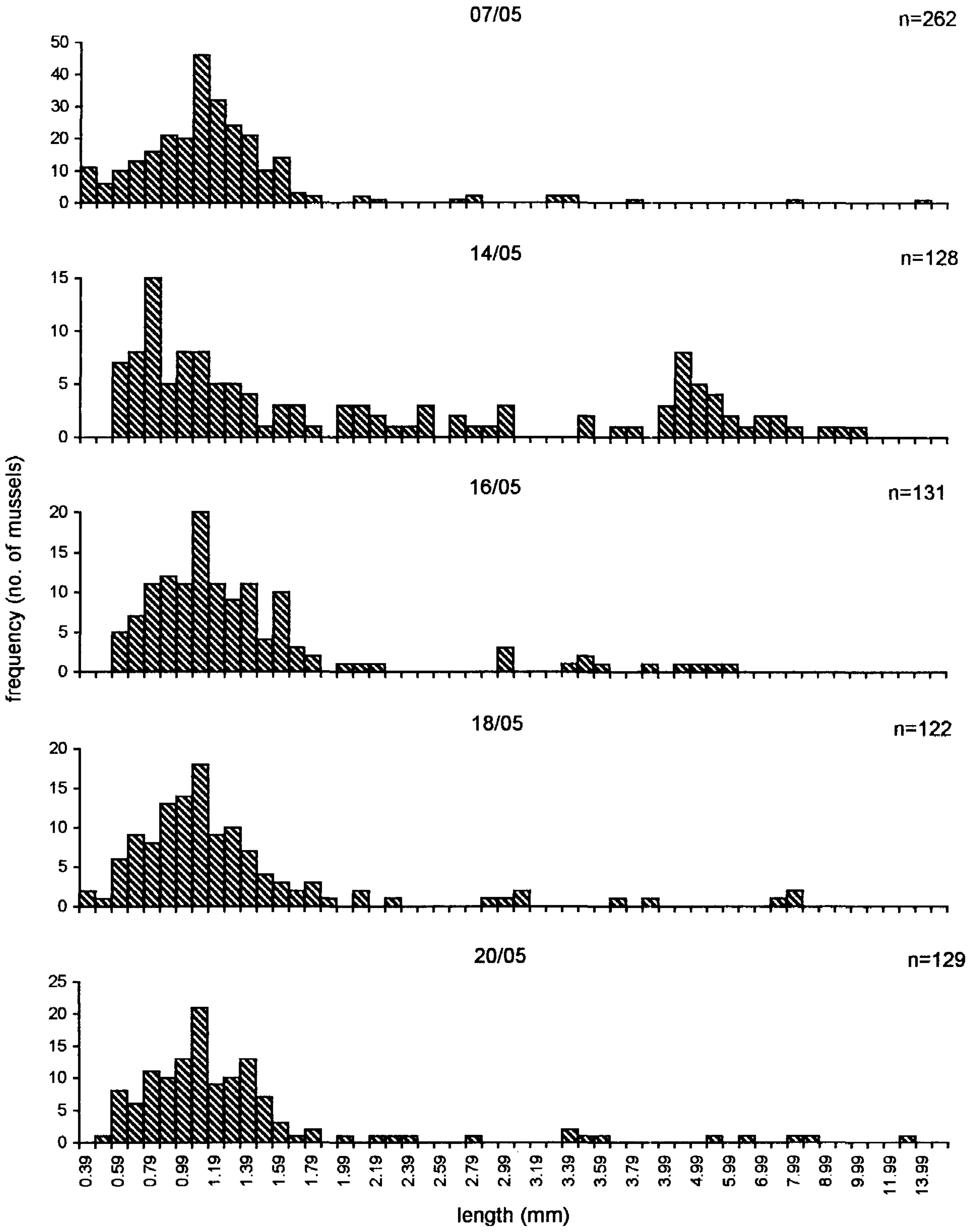
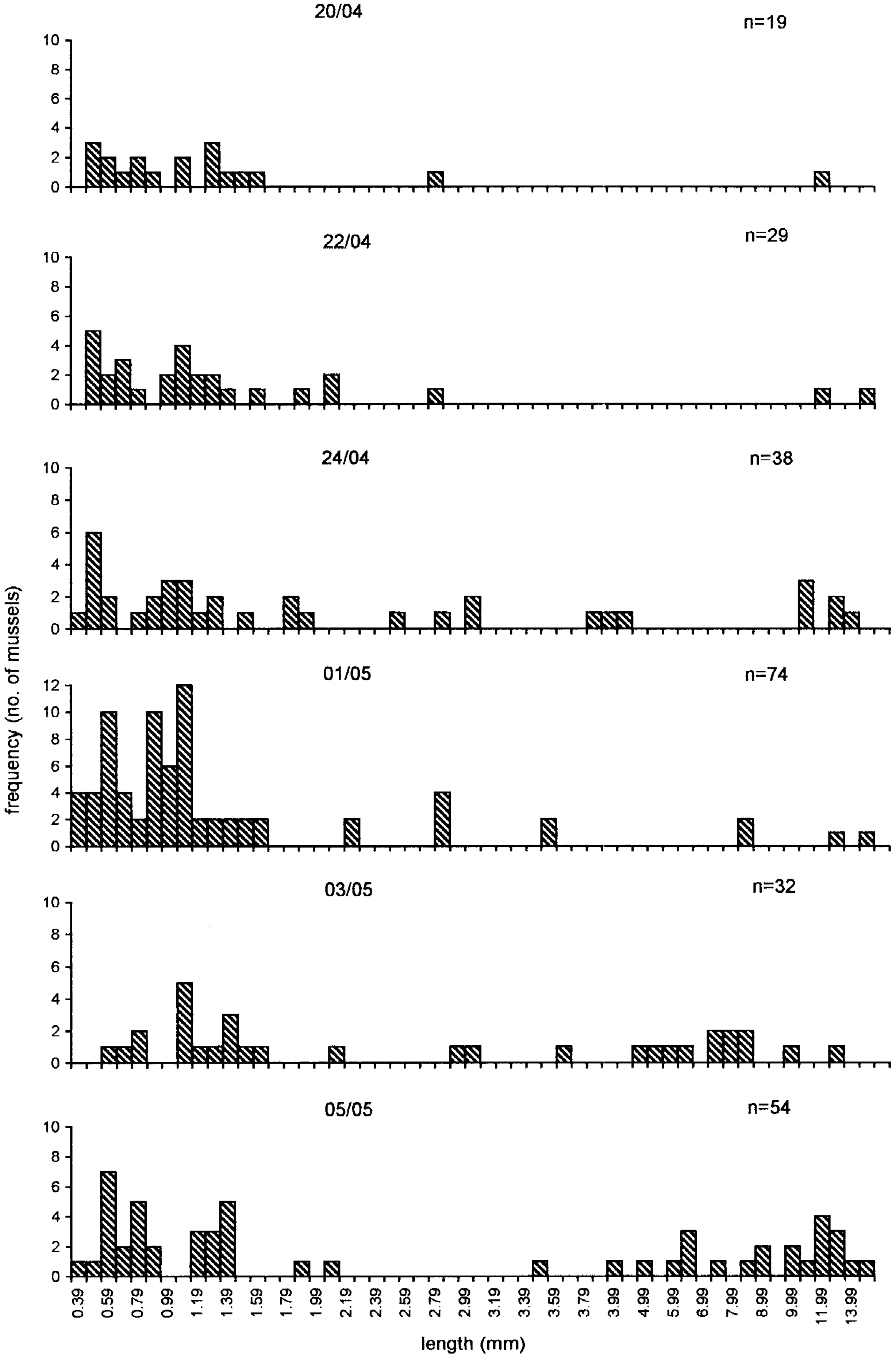


Figure 2.4c Continued

Exposed

Diaz Cross - mid shore - mussel


20/04 n=19

22/04 n=29

24/04 n=38

01/05 n=74

03/05 n=32

05/05 n=54

Figure 2.4d

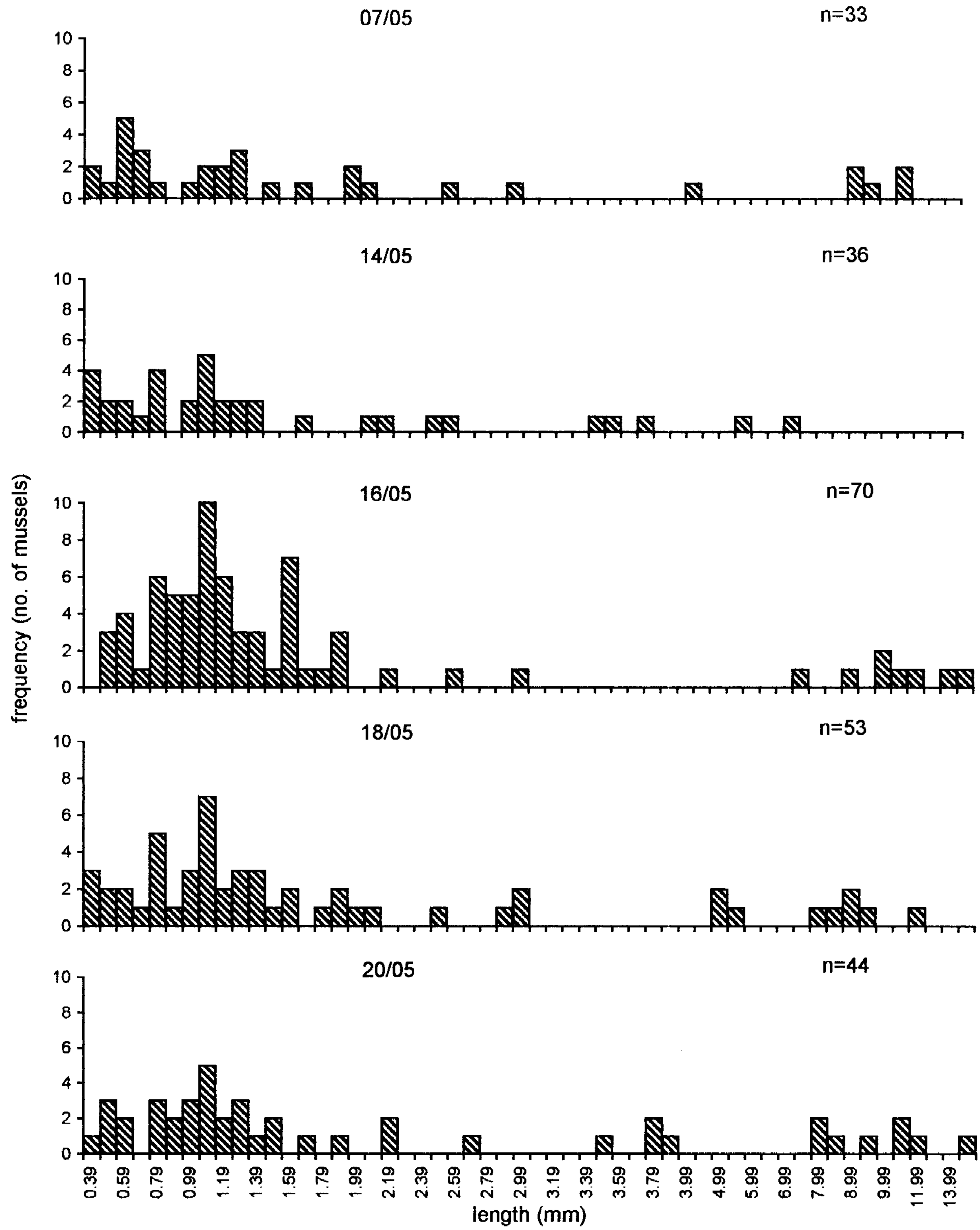


Figure 2.4d Continued

Exposed Diaz Cross - high shore - Gelidium

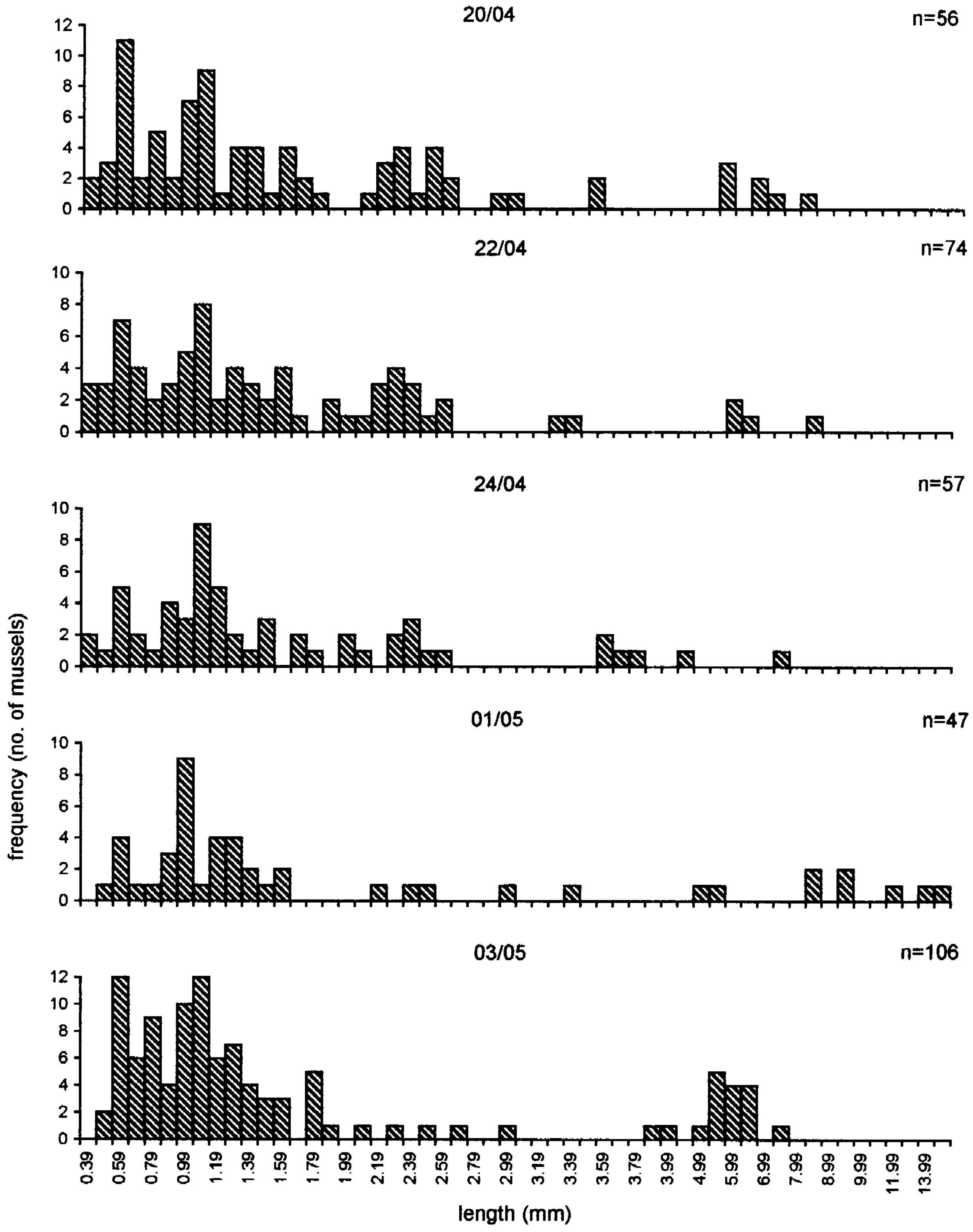


Figure 2.4e

Exposed **Diaz Cross - high shore - Gelidium**

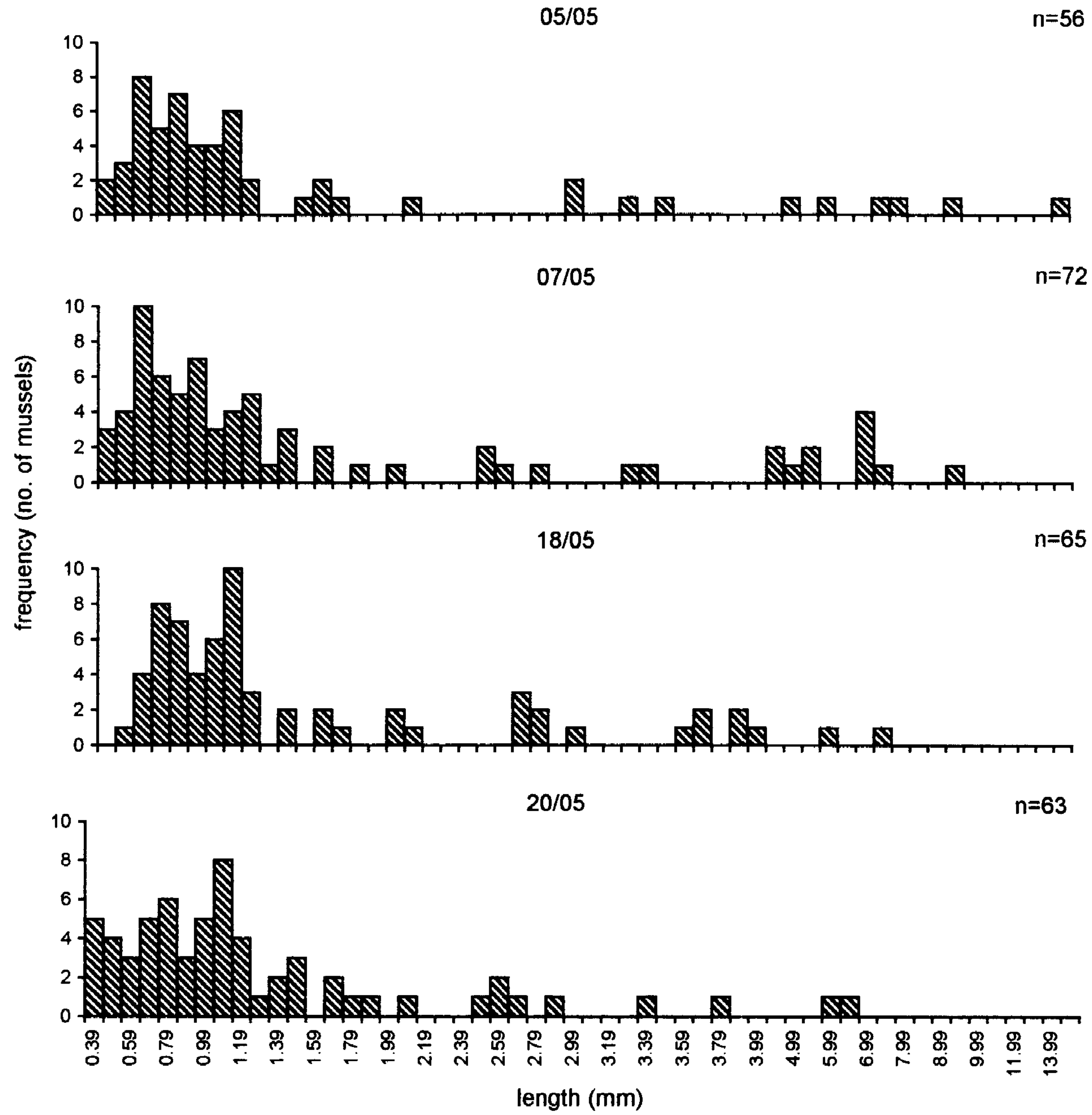


Figure 2.4e Continued

Diaz Cross - high shore - mussel

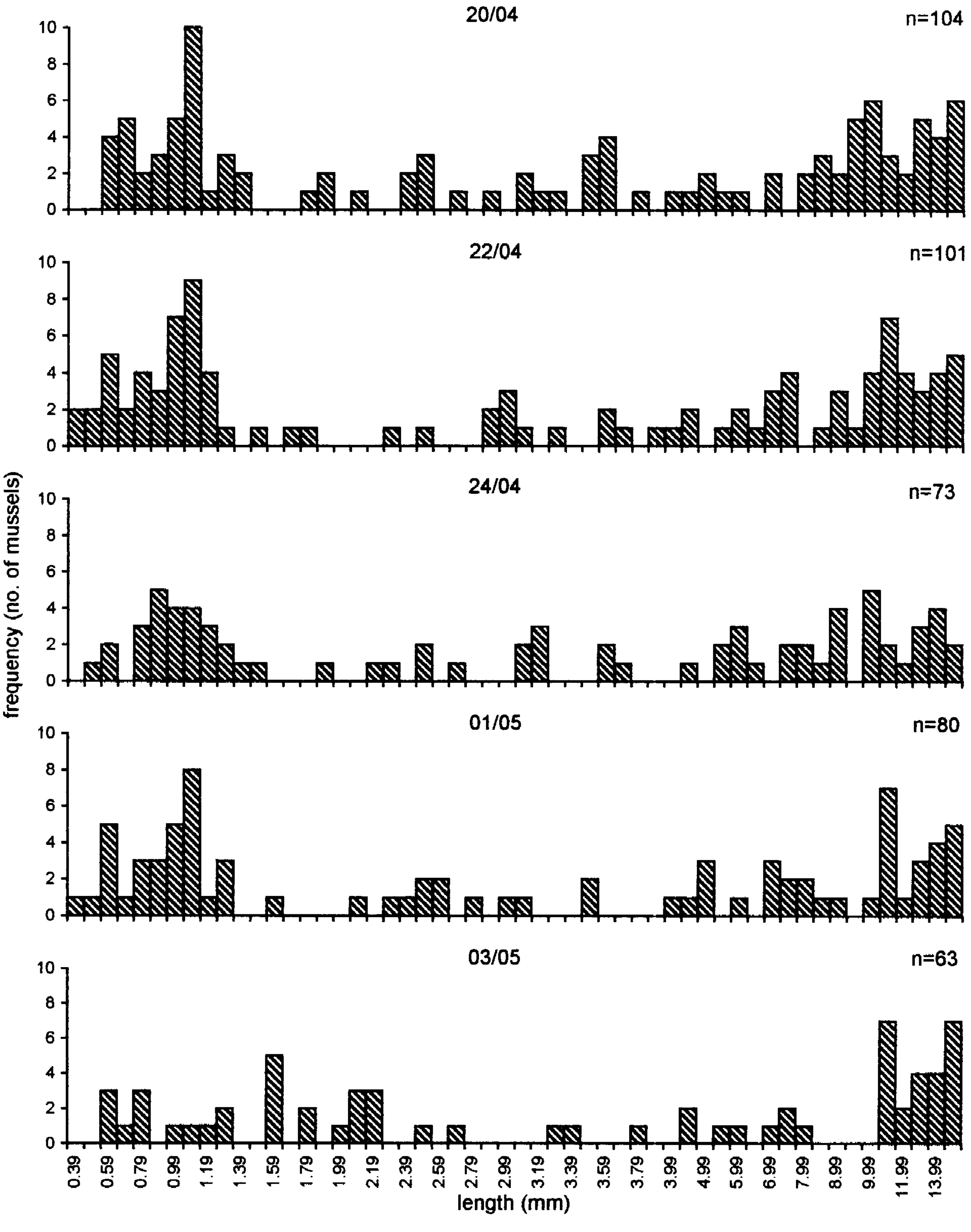


Figure 2.4f

Exposed **Diaz Cross - high shore - mussel**

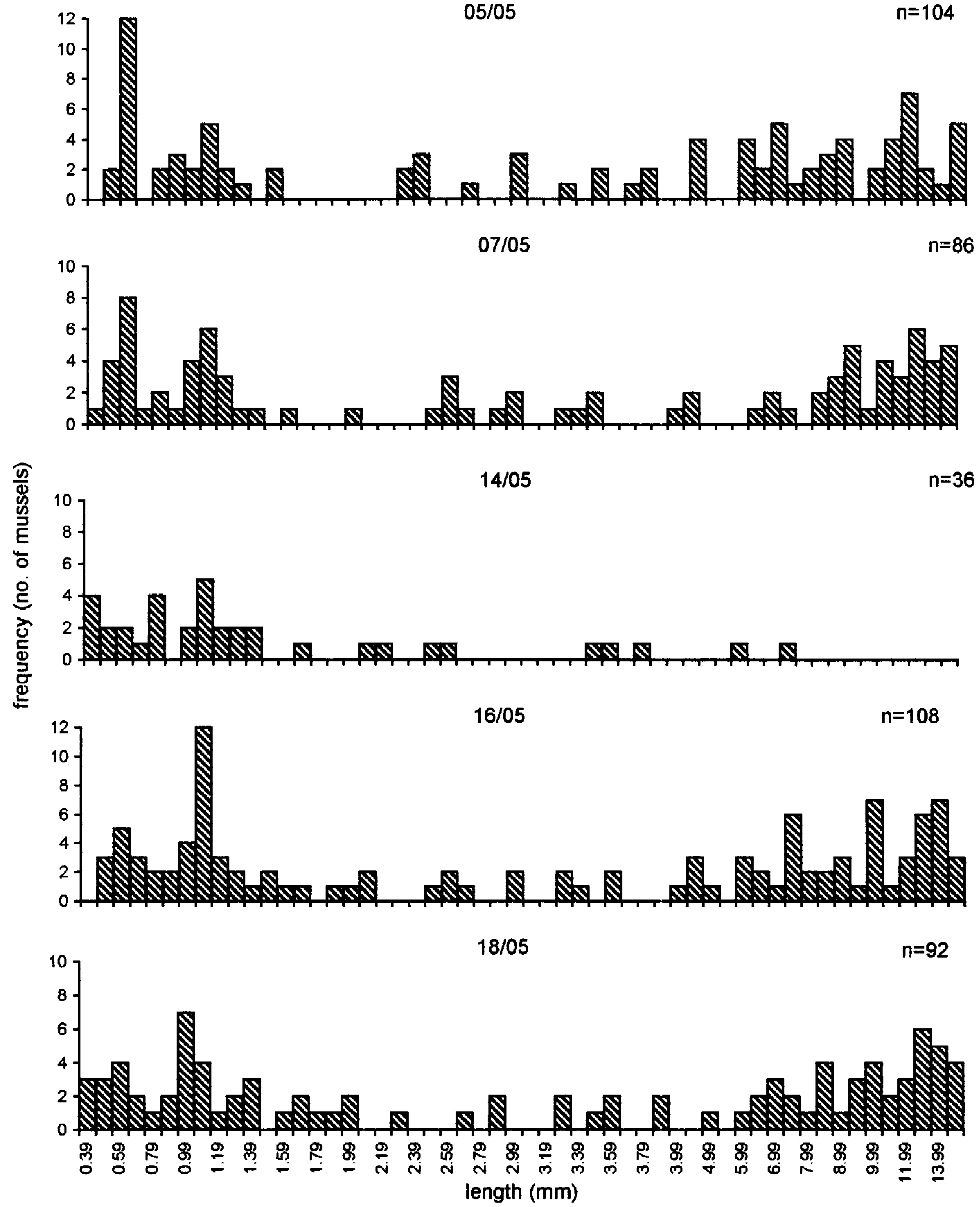


Figure 2.4f Continued

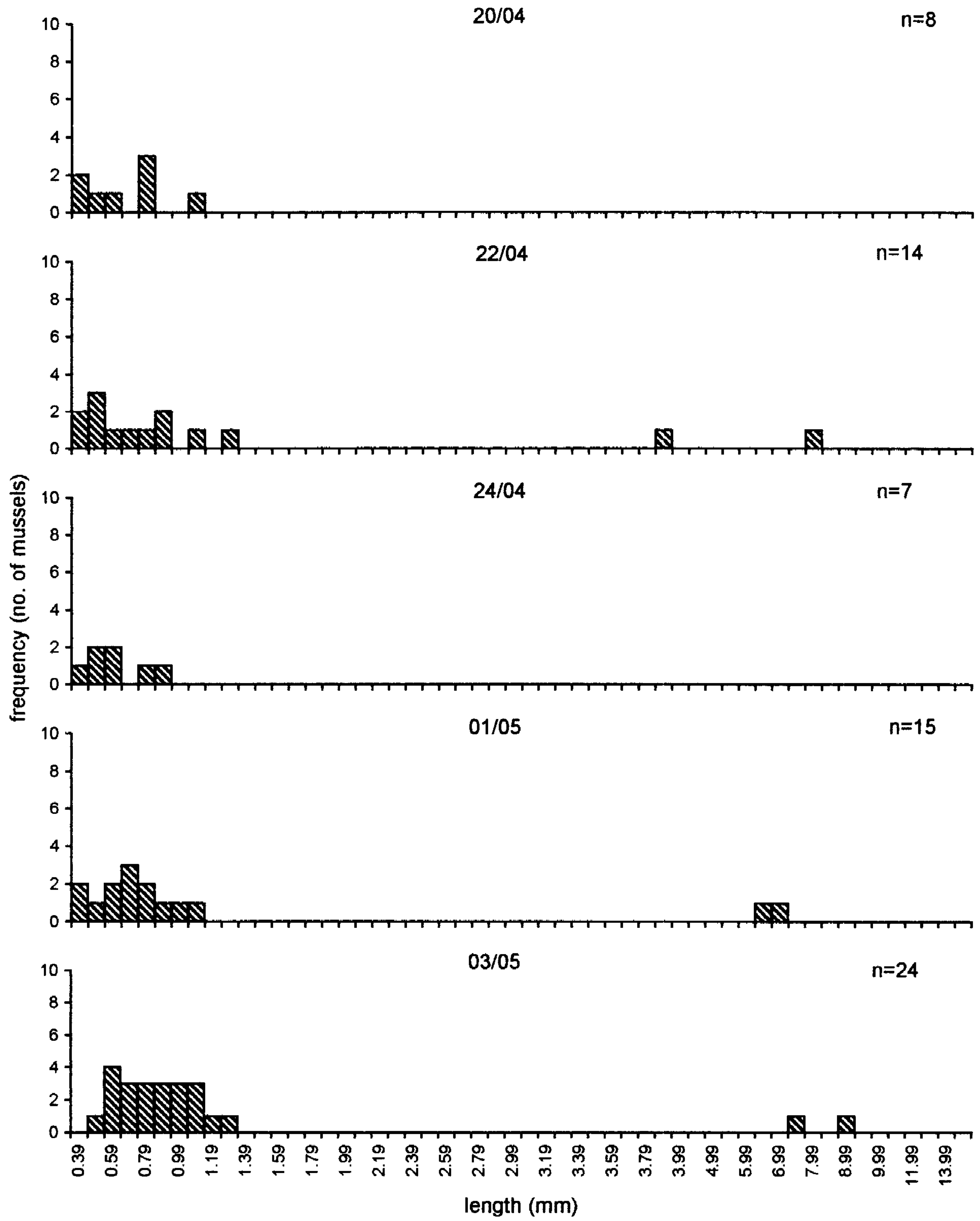


Figure 2.5a

Figure 2.5 Length (mm) frequency distributions of mussel plantigrades collected from Diaz Cross sheltered shore, at low, mid and high shore levels, and on algae and mussel substrata. Histograms for each day sampled on a substratum at a particular z one have been included, as well as the dates on which shores were sampled.The figure at the base of each column represents the upper limit of a size class.

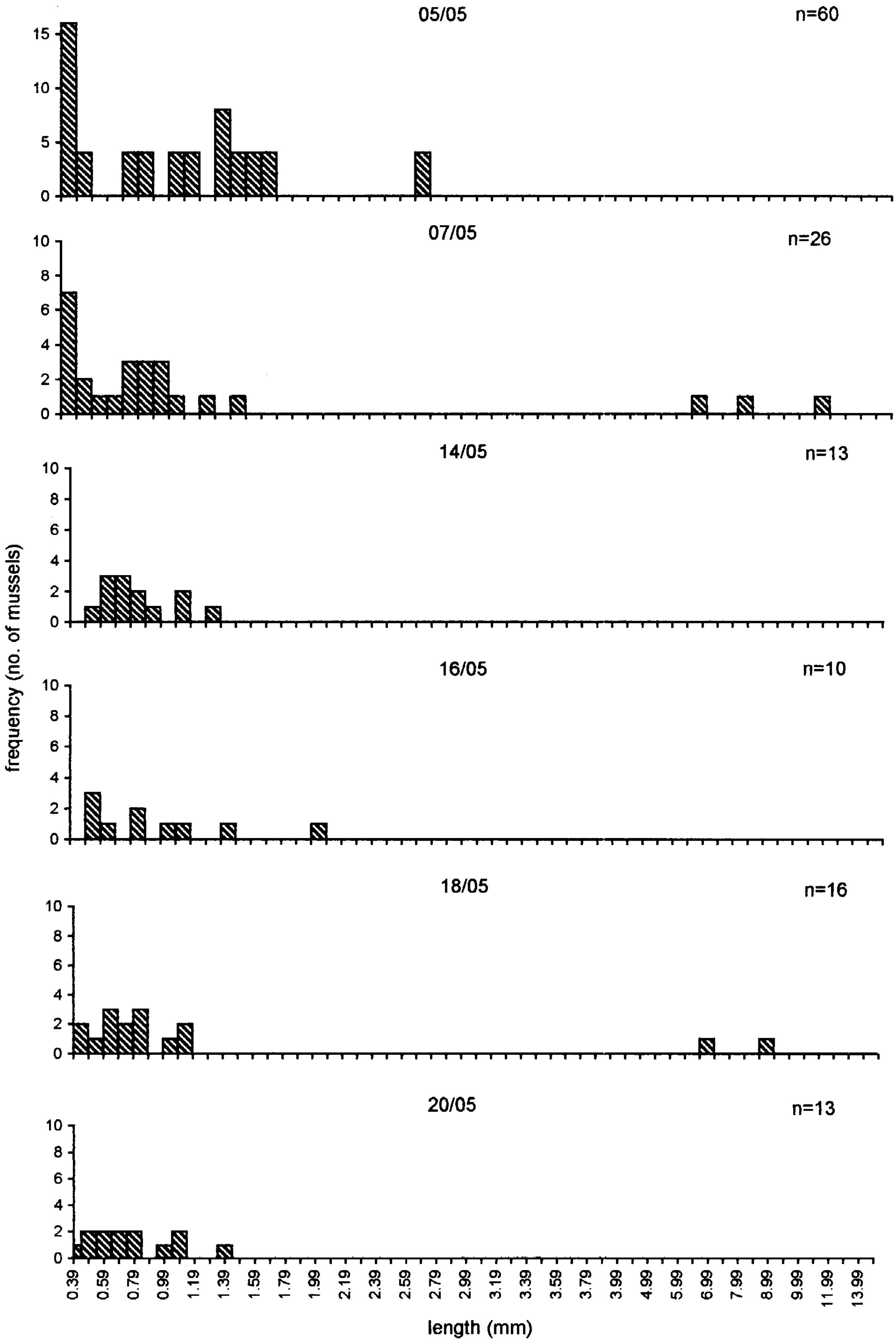


Figure 2.5a Continued

Diaz Cross - mid shore - Gelidium

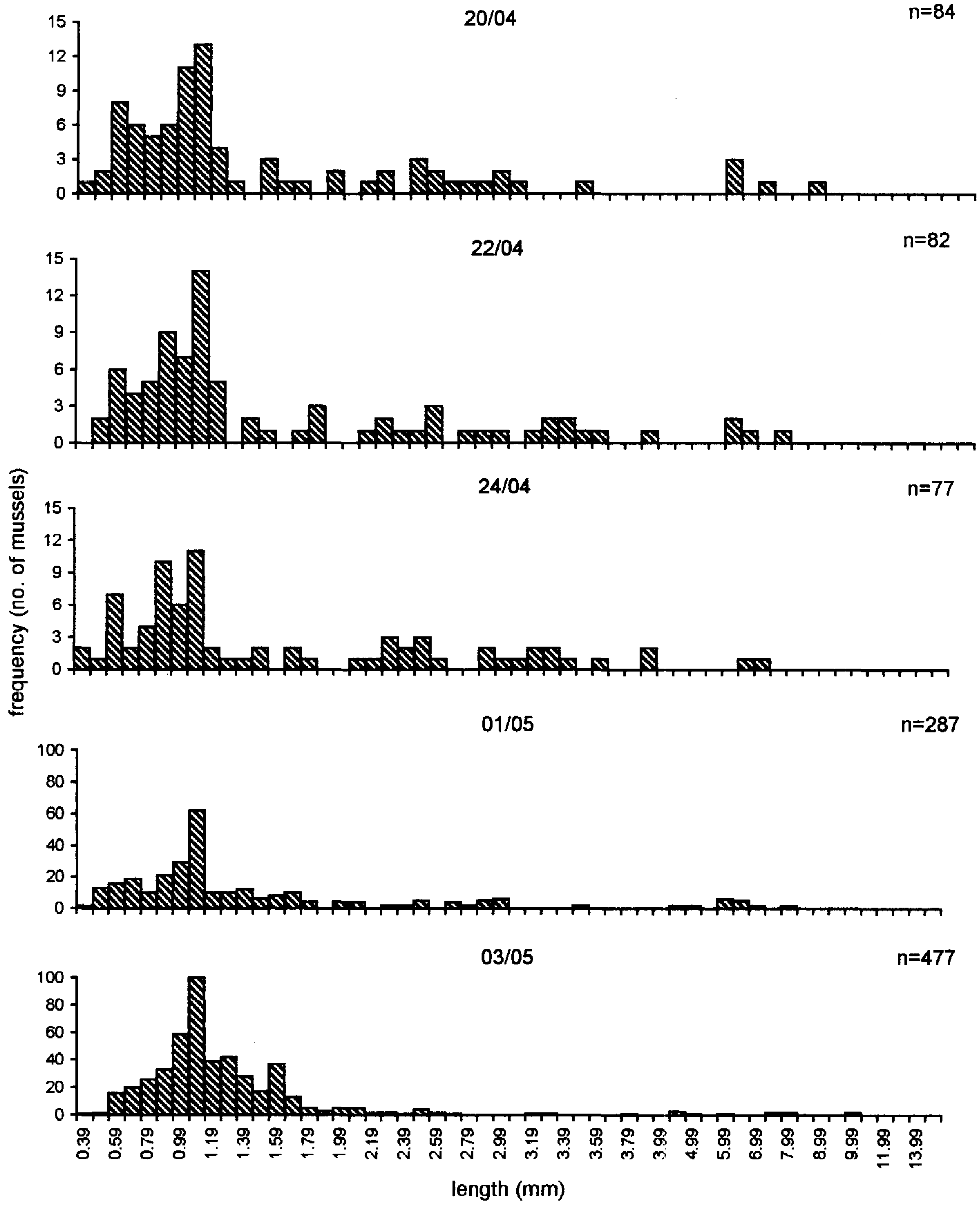


Figure 2.5b

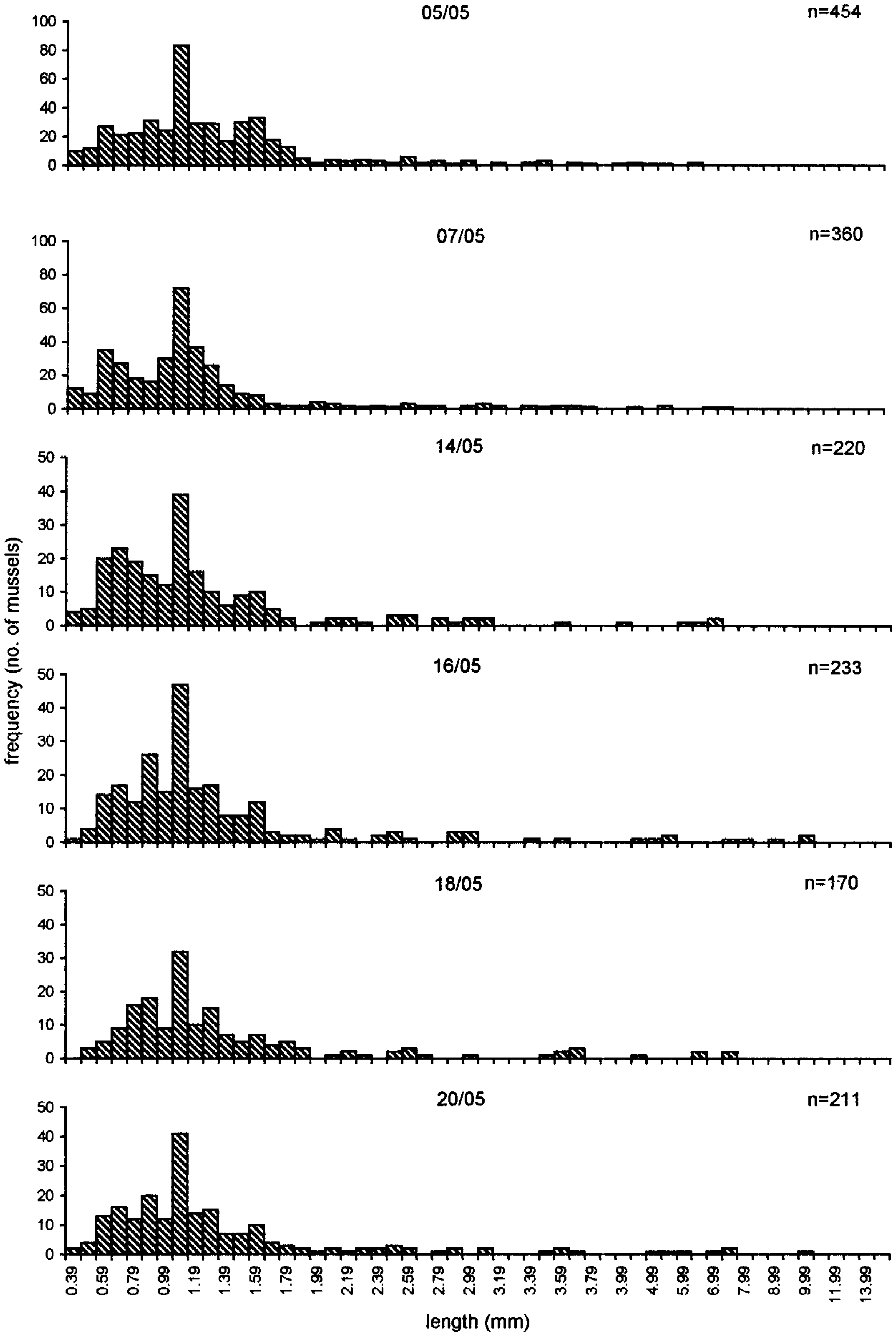


Figure 2.5b Continued

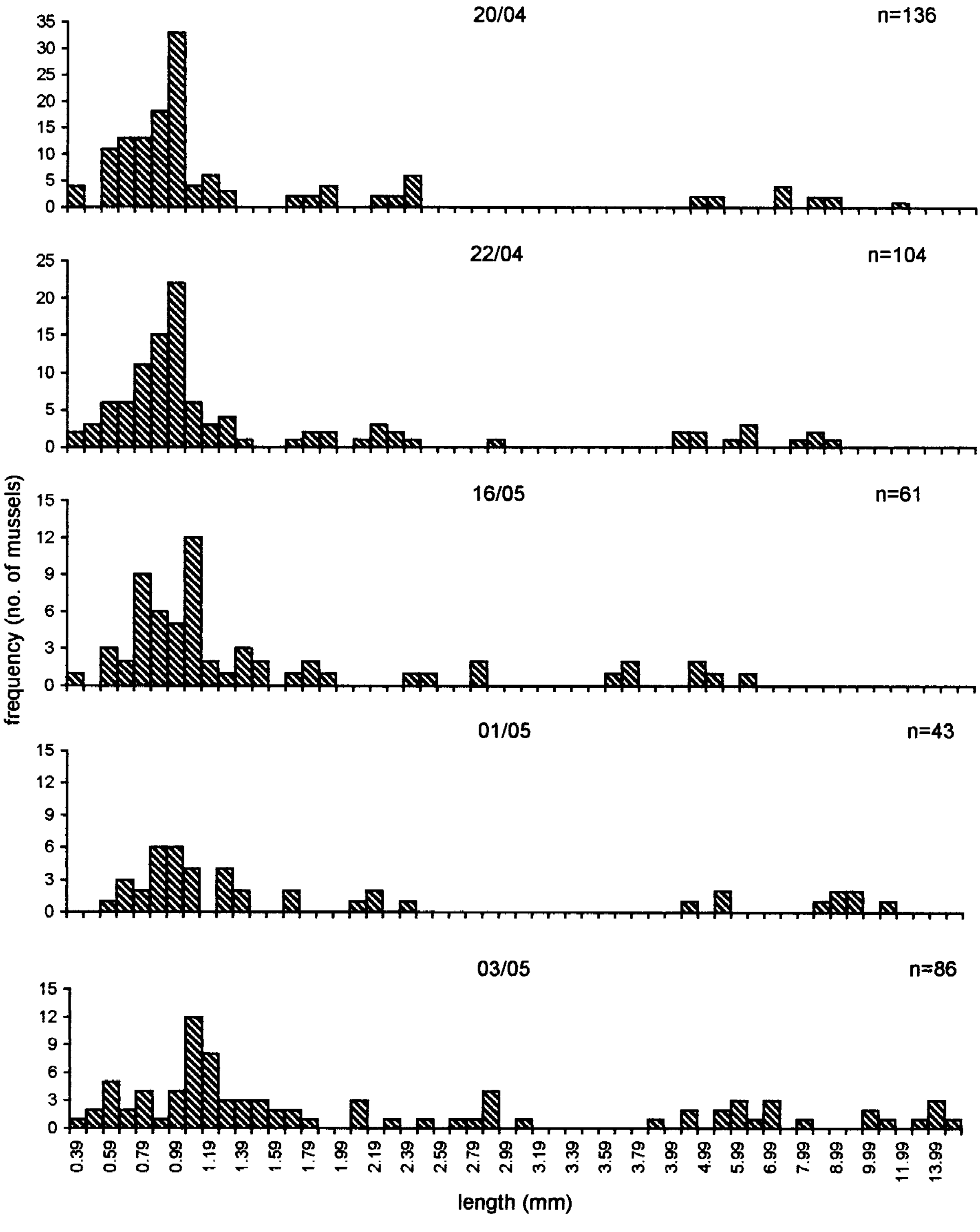

20/04
n=136
35
30
25
20
15
10
5
0
22/04
n=104
25
20
15
10
5
0
16/05
n=61
15
12
9
6
3
0
01/05
n=43
15
12
9
6
3
0
03/05
n=86
15
12
9
6
3
0
frequency (no. of mussels)
0.39
0.59
0.79
0.99
1.19
1.39
1.59
1.79
1.99
2.19
2.39
2.59
2.79
2.99
3.19
3.39
3.59
3.79
3.99
4.99
5.99
6.99
7.99
8.99
9.99
11.99
13.99
length (mm)

Figure 2.5c

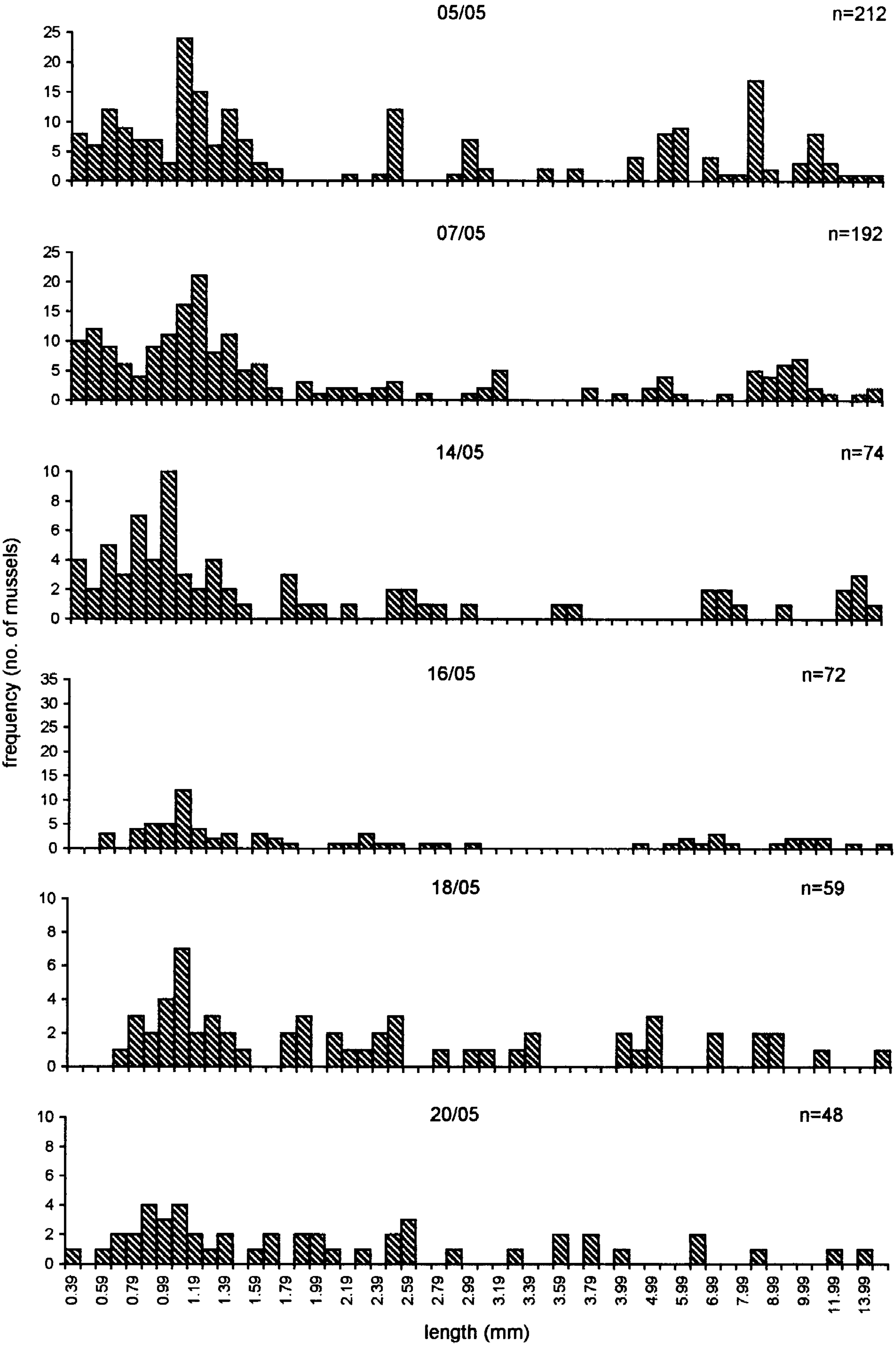


Figure 2.5c Continued

Diaz Cross - high shore - Gelidium

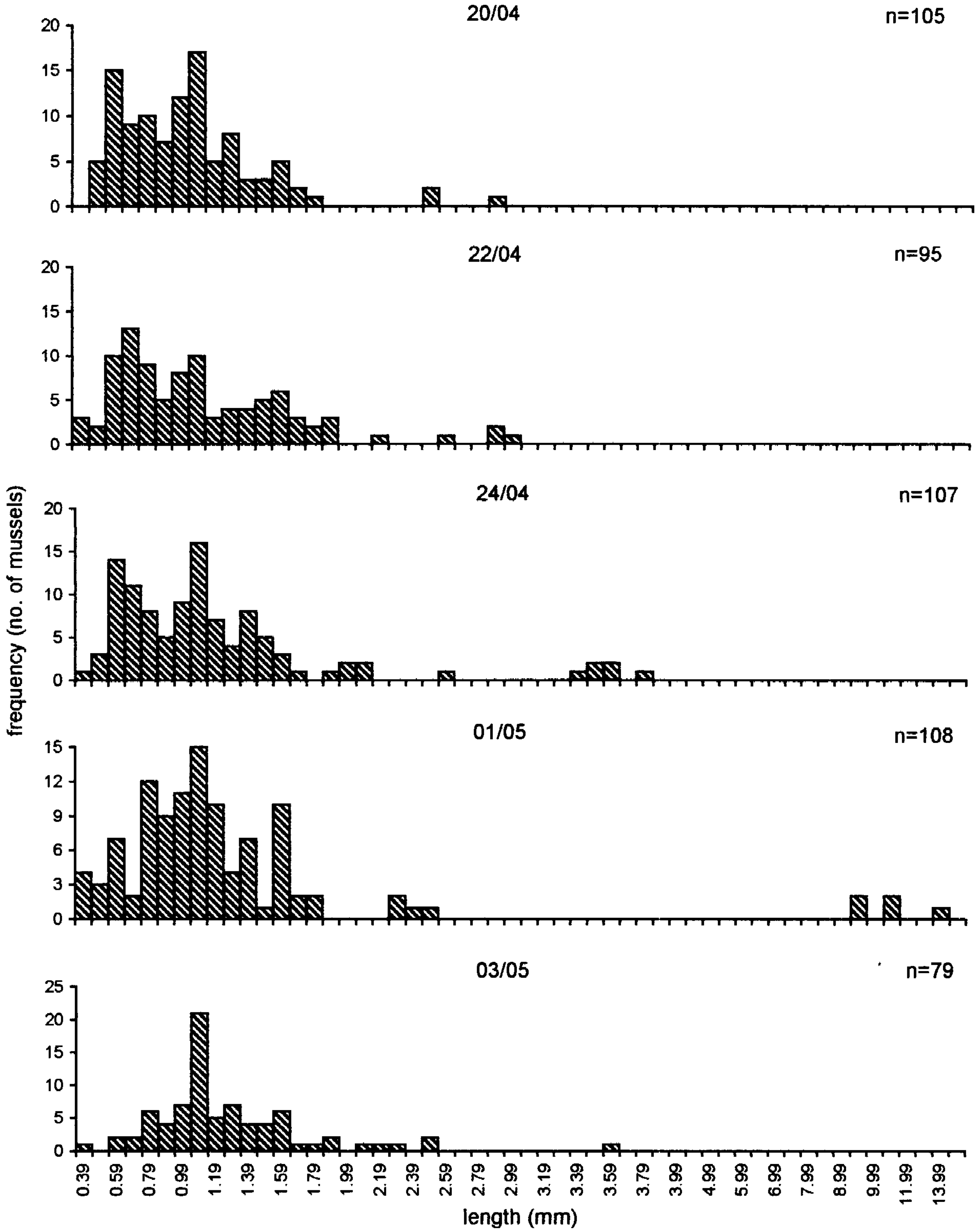


Figure 2.5d

Sheltered **Diaz Cross - high shore - Gelidium**

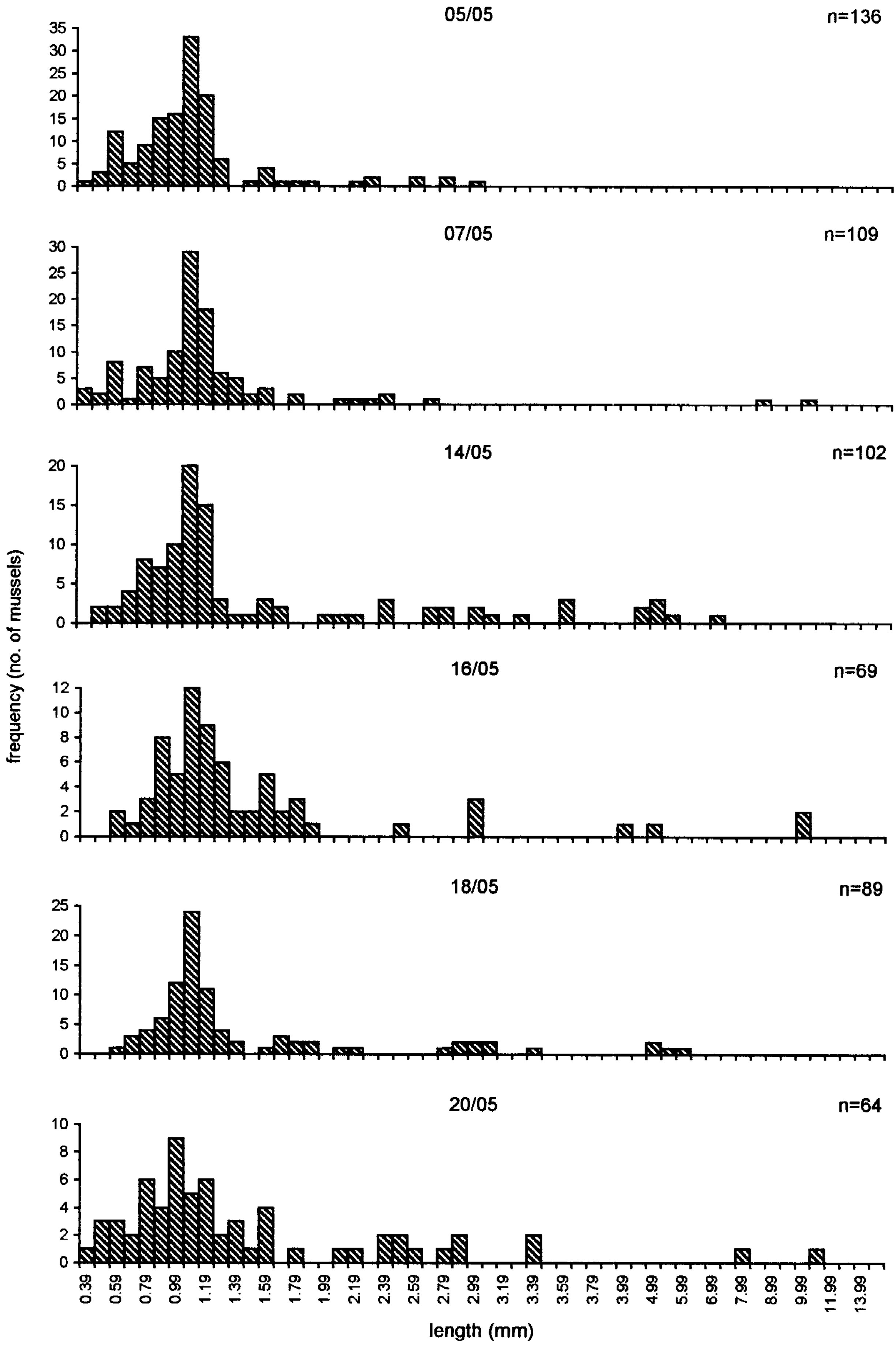


Figure 2.5d Continued

Sheltered **Diaz Cross - high shore - mussel bed**

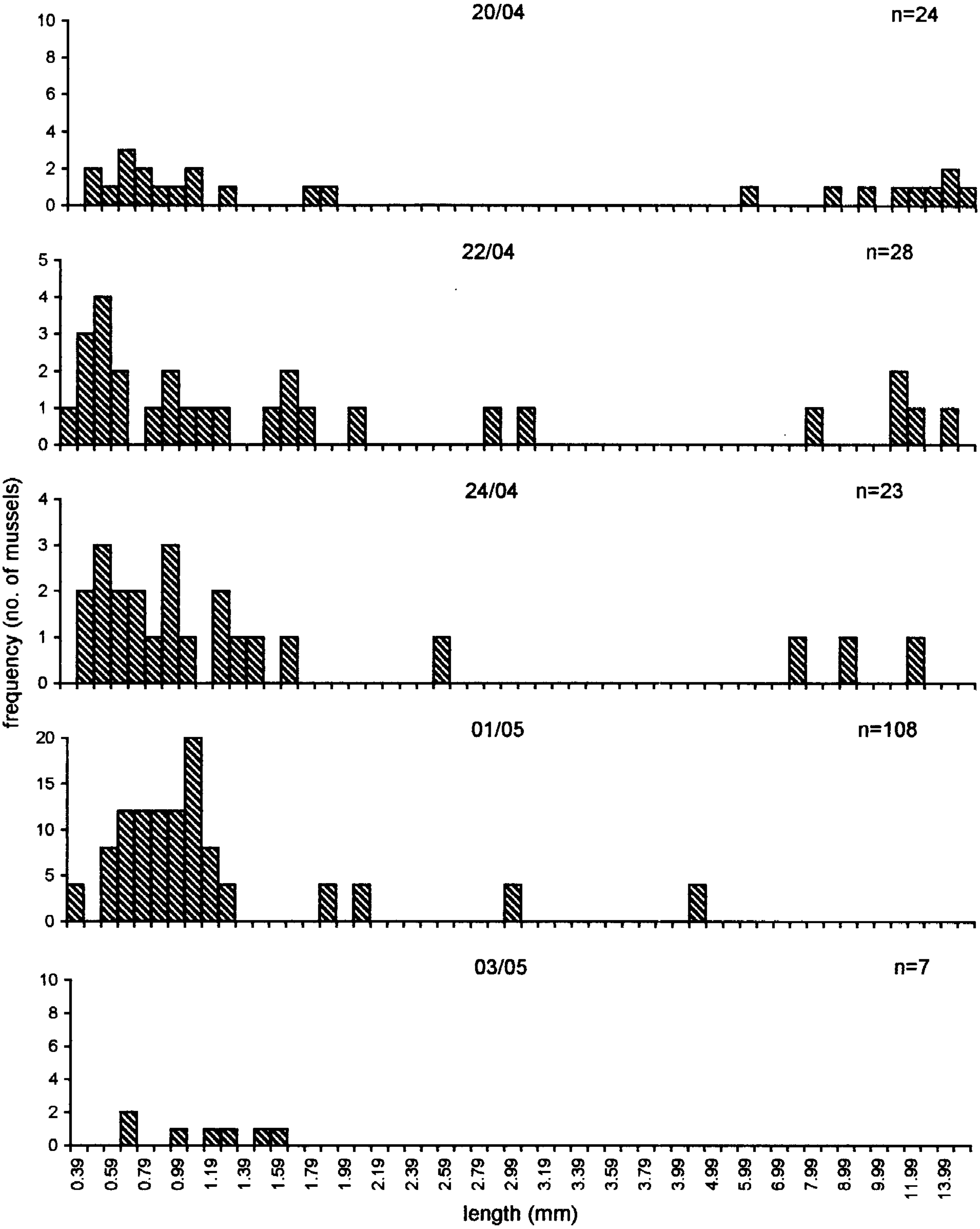


Figure 2.5e

Sheltered **Diaz Cross - high shore - mussel bed**

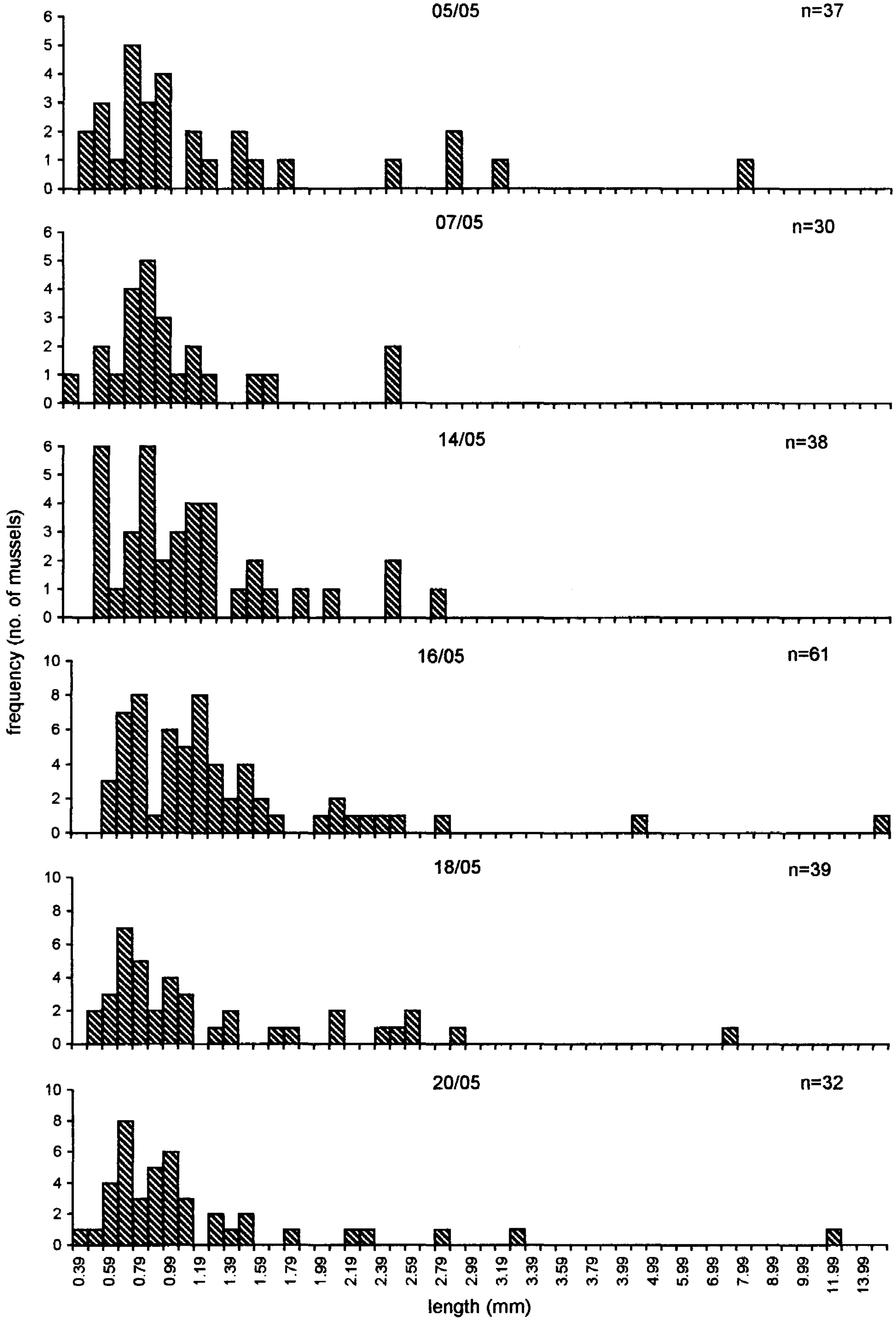


Figure 2.5e Continued

Table 2.4 Summary of the length frequency patterns of recruits at each zone, on each substratum and at exposed and sheltered sites.

Zone & substratum	Exposed	Sheltered
low shore coralline	• bimodal • recruits occurring in all size ranges	• recruits >2mm scarce
low shore mussel	• recruits in all size ranges	• N/A
mid shore *Gelidium*	• recruit nos. peak 0.99-1.09mm • some recruits >2mm, most <2mm	• some recruits >2.5mm
mid shore mussel	• recruits in all size ranges • bimodal length distributions	• recruits in all size ranges • bimodal length distributions
high shore *Gelidium*	• recruits above 3mm scarce • early recruits <0.6mm present	• some recruits <0.60mm and low numbers in the large size classes
high shore mussel	• recruits in all size classes present, but <0.60mm scarce	• most recruits <0.60 >3mm, recruits scarce above 3mm

Synchrony of recruitment

Diaz Cross and High Rocks were out of synchrony with each other. The densities of early and late plantigrades recruits at each exposure, all tidal heights and both sites (Figures 2.6-2.9) revealed that certain patterns existed between shores zones and substrata. Although the analysis for the densities of late plantigrades falls into the following section, there was one obvious pattern involving the densities that can be observed from this analysis on the low shore zones. The densities of plantigrades on exposed algae (low shore) were almost always higher than the densities on exposed mussel (low shore), which in turn were greater than the densities on sheltered algae (low shore).

Synchrony of plantigrade densities on each day on a particular substratum at different zones

Early plantigrades (Recruits <1mm) (Table 2.5) (Figures 2.6; 2.7)

At High Rocks the densities of early plantigrades on each substratum followed similar patterns in time in the low and mid shore zones, on the high shore this pattern broke down. At Diaz Cross there was synchrony on the exposed algae substrata between the low and high shore zones, but not on the mid shore. Diaz Cross exposed mussel substrata also showed a degree of synchrony throughout the zones, while the densities of early plantigrades on sheltered algae were only synchronised at the low and mid shore zones. At both High Rocks and Diaz Cross the densities of early plantigrades on the sheltered mussel beds (mid and high shore only) did not show any clear pattern.

Late plantigrades (recruits 1-4.99mm) (Table 2.6) (Figures 2.8; 2.9)

At High Rocks the densities of plantigrades on exposed algae and exposed mussel at the low and mid shore zones showed similar patterns, as before this pattern broke down on the high shore. Plantigrade densities on sheltered algae showed no pattern, while changes in densities on sheltered mussel at mid and high shore zones were synchronous.

Table 2.5 Summary of the synchrony of early plantigrade (<1mm) densities at each substratum at low, mid and high shore zones. This table is a summary of the daily density data.

Site, substratum and exposure		Comment
High Rocks:	exposed algae	• synchronous at low and mid, not high shore • decrease in density from 21/04-02/05 • high shore peaks from 30/04-06/05
	exposed mussels	• synchronous at low and mid shores, peaking on 04/05 • high shore peaking later on, 11/05
	sheltered algae	• on the low and mid shores the lowest points were synchronous • high shore had highest peak on 06/05, higher than the peaks on other substrata
	sheltered mussels	• no synchrony between mid and high shore zones
Diaz Cross:	exposed algae	• no synchrony between low and mid shores • low and high shores show a similar pattern with the low shore having a peak on 01/05 and the high shore peaking on 03/05
	exposed mussels	• certain degree of synchrony with all zones having a low point on 03/05
	sheltered algae	• synchrony on the low and mid shore, not evident on the high shore
	sheltered mussels	• no synchrony

Figure 2.6 Summary of the synchrony of late plantigrade (1-4.99mm) densities at each substratum at low, mid and high shore zones. This table is a summary of the daily density data.

Site, substratum and exposure	Comment
High Rocks: exposed algae	• low and mid shores show a similar downward trend from 21/04 • high shore not synchronous
exposed mussels	• low and mid shores synchronous, peaking on 04/05 • high shore shows no pattern
sheltered algae	• no synchrony between sheltered algae at each zone
sheltered mussels	• mid and high shore were synchronous with peaks on 15/05
Diaz Cross: exposed algae	• low and high shore show synchrony with plantigrades peaking on 03/05
exposed mussels	• little change over time at low, mid and high shores, difficult to comment on synchrony
sheltered algae	• low, mid and high shores all had peaks around 05/05
sheltered mussels	• no synchrony between mid and high shores

Synchrony of plantigrade densities between substrata at a particular tidal height

Early plantigrades (recruits <1mm) (Table 2.5) (Figures 2.6; 2.7)

The densities of plantigrades on the different substrata at High Rocks low shore zone all followed a very similar pattern. At High Rocks on the mid shore the densities on exposed and sheltered mussel beds and on sheltered algae were synchronous while those on exposed algae followed a different pattern. On the high shore zone at High Rocks, plantigrade densities on exposed and sheltered algae were very synchronous, densities on exposed and sheltered mussel beds were not.

Early plantigrades on exposed algae and mussel at the low shore zone at Diaz Cross follow a similar pattern, while sheltered algae did not. Plantigrade densities at the mid shore zones showed synchrony on exposed algae and sheltered mussel bed, but not on sheltered algae and exposed mussel bed. Patterns at high shore Diaz Cross were opposite to those on the mid shore with densities on sheltered algae and sheltered mussel bed showing synchrony after the 20/05, and densities on exposed algae and mussel showing no pattern.

Late plantigrades (recruits 1-4.99mm) (Table 2.6) (Figures 2.8; 2.9)

Late plantigrade densities at low shore sites at High Rocks showed synchrony on exposed and sheltered algae, but not on exposed mussel bed. The pattern on the mid shore was the same, except with the introduction of another substratum, sheltered mussel bed, which like the densities on the exposed mussel bed was out of synchrony with exposed and sheltered algae. No patterns were observed on the high shore. At Diaz Cross the densities of plantigrades did not follow any pattern of synchrony.

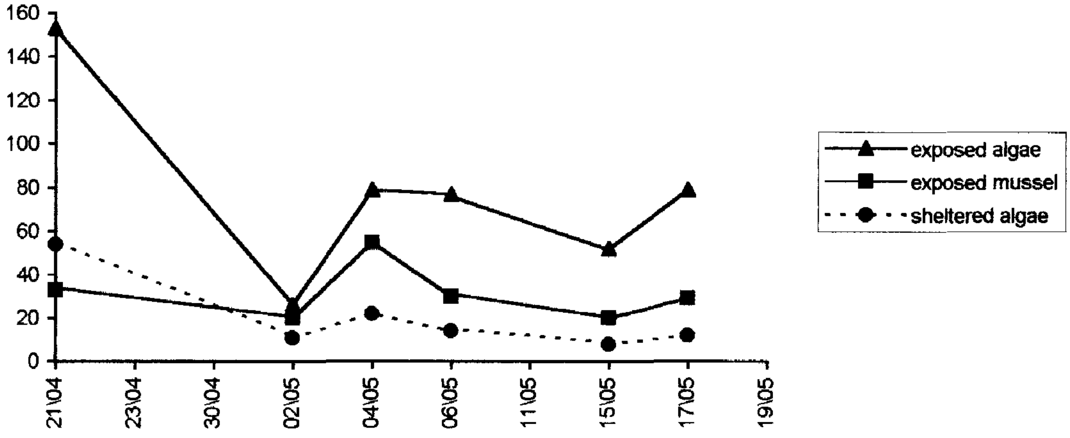
Table 2.5 Summary of synchrony of early plantigrade (<1mm) densities on each substratum within each zone. Data from daily recruitment densities were used for this summary.

Site and zone	Comment
High Rocks: low shore	• same pattern on all substrata • low points on 02/05
mid shore	• synchrony between exposed mussel, and sheltered mussel and algae • with low points on 02/05
high shore	• exposed and sheltered algae show synchrony • both peak on 06/05
Diaz Cross: low shore	• exposed algae and mussel synchronous • peaks on 01/05 and 05/05
mid shore	• similar pattern for exposed algae and sheltered mussel
high shore	• sheltered algae and mussel were synchronous from 01/05-20/05

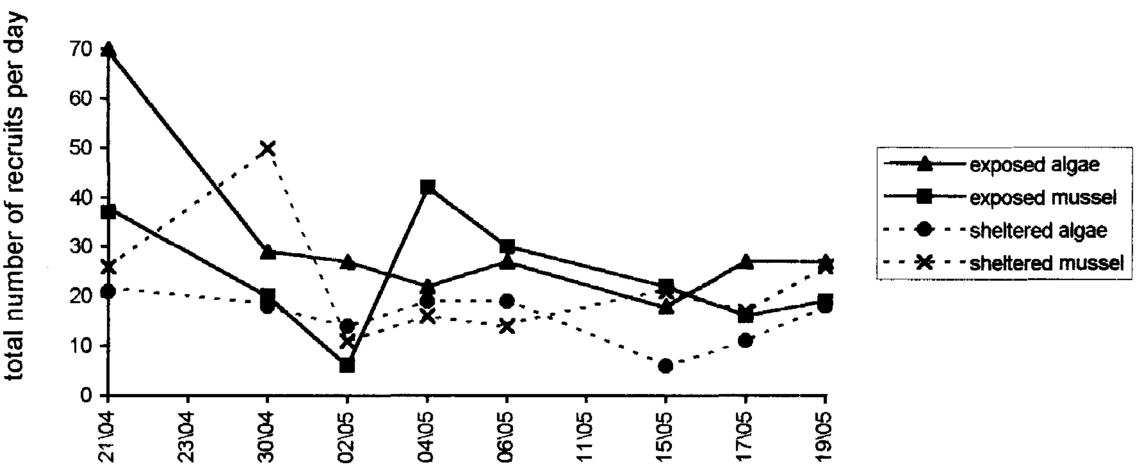
Table 2.6 Summary of synchrony of late plantigrade (1-4.99mm) densities on each substratum within each zone. Data from daily recruitment densities were used for this summary.

Site and zone	Comment
High Rocks: low shore	• exposed and sheltered algae synchronous • exposed mussel did not follow pattern
mid shore	• exposed and sheltered algae followed similar pattern • sheltered and exposed mussel not synchronous
high shore	• no patterns
Diaz Cross: low shore	• no synchrony
mid shore	• one day difference between synchrony on sheltered algae and mussel
high shore	• no pattern

low shore



mid shore



high shore

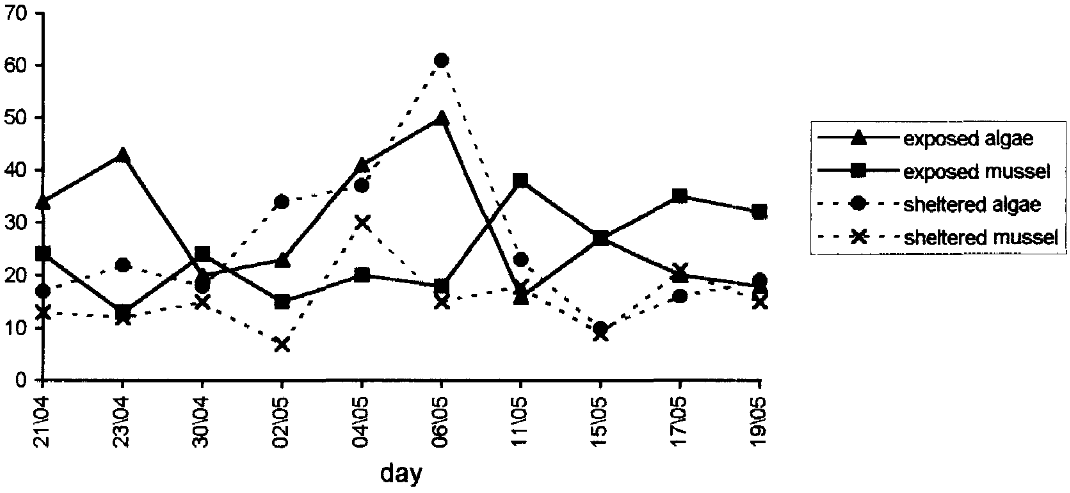


Figure 2.6 Numbers of early plantigrades (<1mm) on each day sampled, on exposed and sheltered shores at low, mid and high zones and on all substrata at the High Rocks. Each point represents the total number of plantigrades for that day.

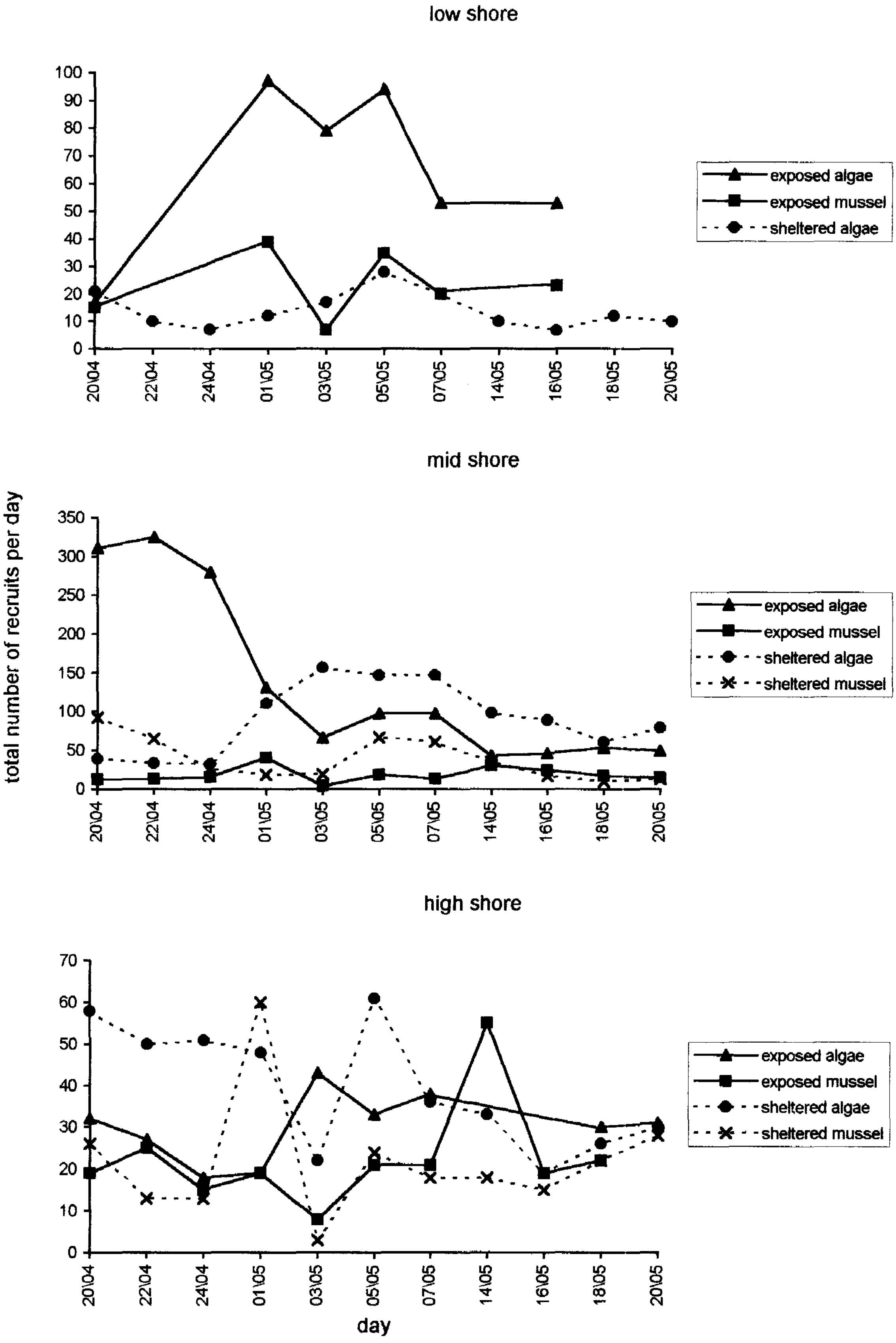


Figure 2.7 Numbers of early plantigrades (<1mm) on each day sampled, on exposed and sheltered shores at low, mid and high zones and on all substrata at Diaz Cross. Each point represents the total number of plantigrades for that day.

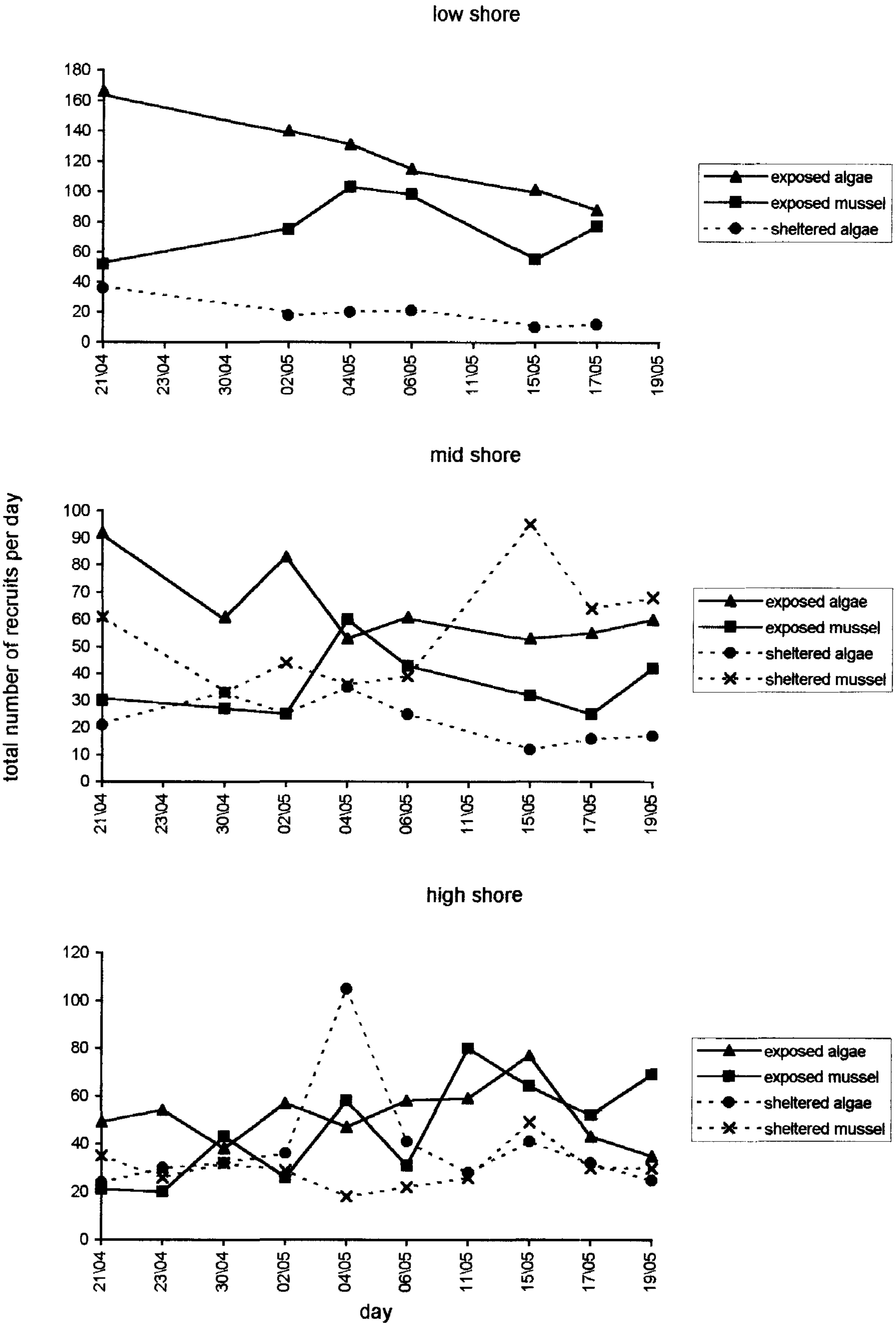


Figure 2.8 Numbers of late plantigrades (1-5mm) on each day sampled, on exposed and sheltered shores at low, mid and high zones and on all substrata at the High Rocks. Each point represents the total number of plantigrades for that day.

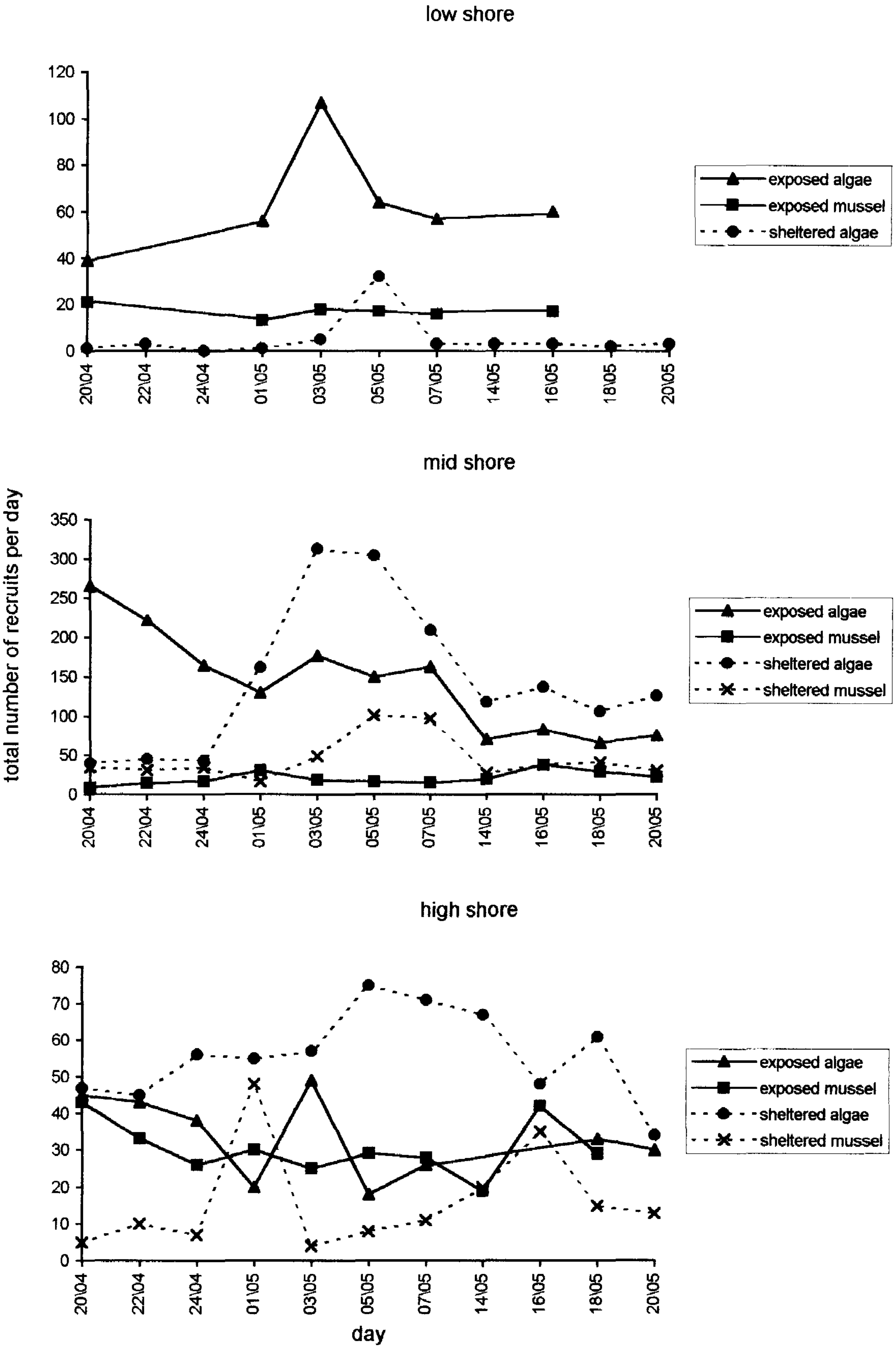


Figure 2.9 Numbers of late plantigrades (1-5mm) on each day sampled, on exposed and sheltered shores at low, mid and high zones and on all substrata at Diaz Cross. Each point represents the total number of plantigrades for that day.

Density

In the following analyses (sections a-c), numbers in brackets following the name of a site, degree of exposure, zone or any combination of the three, represent the number of recruits in that category for the analysis averaged over the entire sampling period.

a- Effects of shore, exposure and zone on recruit densities on algae

Early plantigrades (recruits <1mm) (Table 2.7)

Early plantigrade densities on algae were higher at Diaz Cross (20.9) than at High Rocks (11.1) and densities at exposed sites (20.5) were higher than those at sheltered sites (11.4), both these differences were statistically significant ($p<0.0001$). However the interaction between site and exposure was not significant ($p=0.2406$) and this indicates that exposure affected early plantigrade densities on algae in similar ways at both sites.

The densities of early plantigrades on mid shore zones (22.7) were higher than those at low (14.8) and high shore zones (10.4), a significant ($p=0.0024$) result for zone was obtained in the ANOVA, The interaction between site and zone was significant ($p<0.0001$) indicating that zone affected average density at the two sites in different ways. (Figure 2.10)

Effects of exposure were significant ($p<0.0001$). Both the exposed shores had higher numbers (HE-15.3, DE-25.8) of early plantigrade densities than their corresponding sheltered shores (HS-6.8, DS-15.9). The interaction between exposure and site was not significant ($p=0.2406$). This result indicates the importance of exposure on early plantigrade densities occurring on algae.

At each zone the difference between average plantigrade density on exposed and sheltered shores decreased with increasing shore height, to the point where on the high shore the difference between the two was only 1 mussel (Figure 2.11) (significant interaction between exposure and zone, $p<0.0001$). Once again exposure had a large effect on the densities of plantigrades on algae.

The interaction between site, zone and exposure was not significant (p=0.6188)

Table 2.7 Three-way ANOVA table showing differences in densities of early plantigrades (0-1mm) on algae; using site, zone and exposure as factors. The data were pooled for day (3 samples for each) and the average calculated. The averages for each of the days sampled were used as replicates. Data were log transformed.

Source of variation	d.f.	SS	MS	F	p
A : site	1	1.2511409	1.2511409	23.889	p<0.0001
B : zone	2	0.6747183	0.3373592	6.441	0.0024
C : exposure	1	1.9148807	1.9148807	36.562	p<0.0001
Interactions					
AB	2	2.3386785	1.1693393	22.327	p<0.0001
AC	1	0.0730340	0.0730340	1.394	0.2406
BC	2	1.7233260	0.8616630	16.452	p<0.0001
ABC	2	0.0505371	0.0252686	0.482	0.6188
Residual	95	4.9755172	0.523739		
Total	106	13.916316			

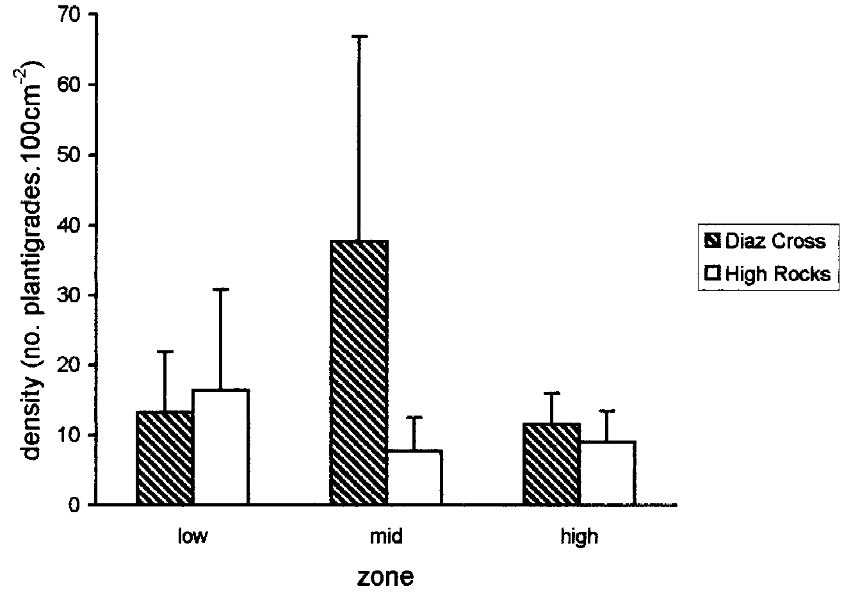


Figure 2.10 Mean density (+ std. dev.) of early plantigrades (<1mm) on algae at Diaz Cross and High Rocks at low, mid and high zones. Means were calculated from all quads pooled.

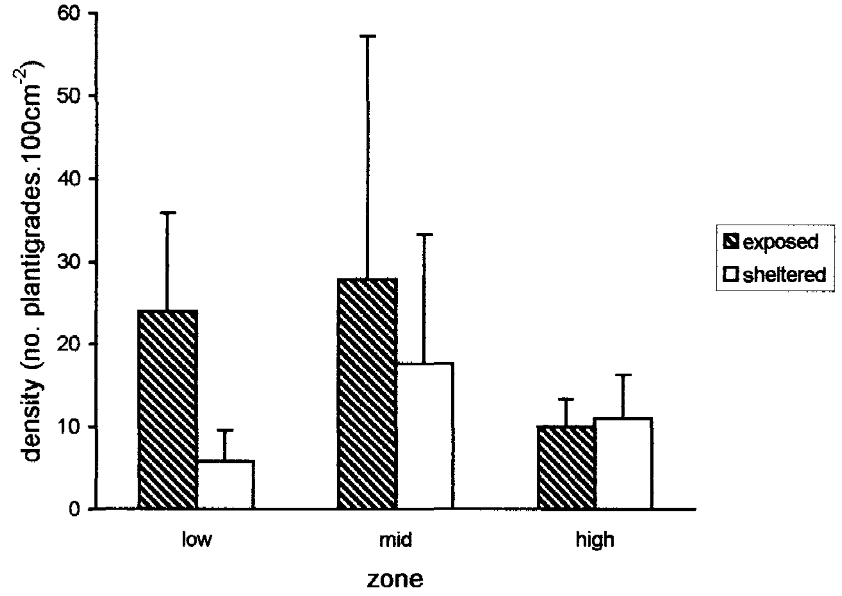


Figure 2.11 Mean density (+std. dev.) of early plantigrades (<1mm) on algae at exposed and sheltered sites at low, mid and high zones. Means were calculated from all quads pooled.

Late plantigrades (recruits 1-4.99mm) (Table 2.8)

Late plantigrade densities at High Rocks (17.9) on algae were on average lower than those on algae at Diaz Cross (24.9), however this difference was not significant ($p=0.7553$).

Densities on low (17.7) and high (15.1) shore zones were much lower than those on the mid shore (31.3) ($p<0.0001$). More than 60% of total recruitment on algae occurred on the exposed shore (26.7) and densities here were significantly greater ($p<0.0001$) than that on sheltered sites (16).

The interaction between zone and site was significant ($p<0.0001$), due to the high numbers of late plantigrades on the mid shore at Diaz Cross (Figure 2.10). This explains the high number of plantigrades recorded on the mid shore.

As with the early plantigrades the average number of late plantigrades on algae were greater at exposed shores at both sites (interaction not significant $p=0.2535$). The Diaz Cross exposed site (26.6) had greater numbers of plantigrades than the sheltered site (23). The difference between the number of late plantigrades at the High Rocks exposed site (26.7) and the High Rocks sheltered site (9.1) was much greater.

On the low shore the difference between the numbers of late plantigrades on exposed (27.1) and sheltered sites (4.1) was great. However this difference was not so marked on the mid and high shore sites and the interaction between zone and exposure was significant (p=0.0001).

Table 2.8 Three-way ANOVA table showing differences in densities of late plantigrades (1-4.99mm) on algae; using site, zone and exposure as factors. The data were pooled for each day and an average taken. The average for each of the days sampled were used as replicates. Data were log transformed.

Source of variation	d.f.	SS	MS	F	p
A : site	1	0.0048051	0.0048051	0.100	0.7553
B : zone	2	3.0070606	1.5035303	31.444	<0.0001
C : exposure	1	4.7225426	4.7225426	98.763	<0.0001
Interactions					
AB	2	4.5147560	2.2573780	47.209	<0.0001
AC	1	0.0631096	0.0631096	1.320	0.2535
BC	2	5.2709821	2.6354910	55.116	<0.0001
ABC	2	1.0488814	0.5244407	10.968	0.0001
Residual	95	4.5426030	0.0478169		
Total	106	28.097132			

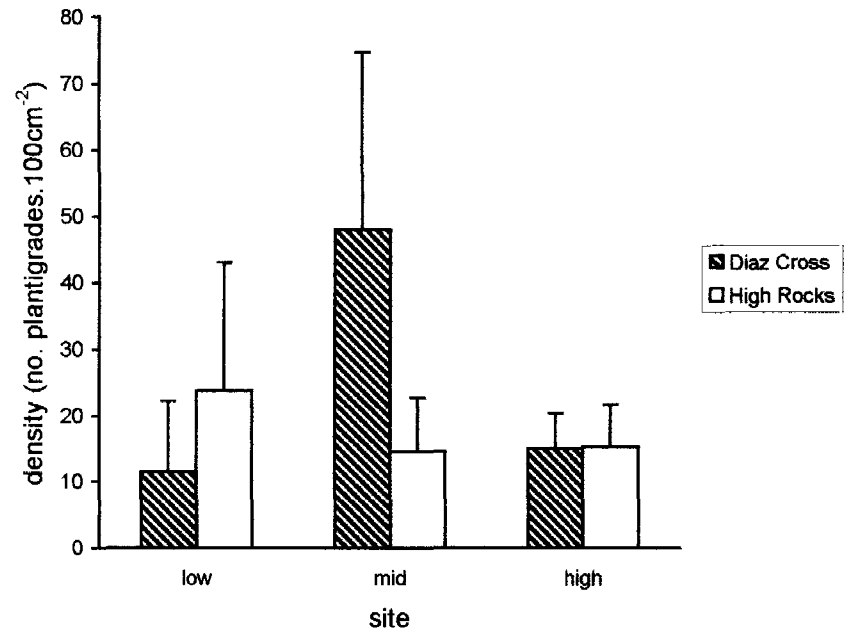


Figure 2.10 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) on algae at Diaz Cross and High Rocks at low, mid and high zones. Means were calculated from all quads pooled.

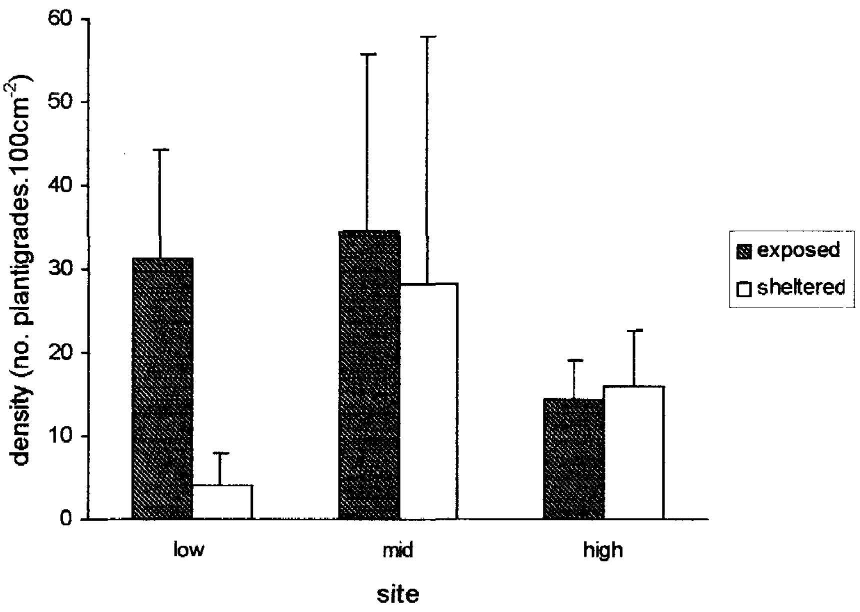


Figure 2.11 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) on algae at exposed and sheltered sites at low, mid and high zones. Means were calculated from all quads pooled.

b- Effects of shore, zone and substratum on recruit densities under exposed conditions

Early plantigrades (recruits<1mm) (Table 2.9)

Densities of early plantigrades at High Rocks (12.1) were lower than those at Diaz Cross (16.4), however this difference was not significant (p=0.5894). Low (16.5) and mid shore (17.4) zones showed similar densities, and were much higher than those on the high shore (8.9), the ANOVA showed a significant difference for zone.

Densities of early plantigrades were significantly higher on algae (20.5) than on the mussel substratum (8.0).

The general trend of decreasing early plantigrade densities from the low shore to the high shore recorded at High Rocks exposed sites, was not noted at Diaz Cross exposed sites (Figure 2.12), consequently the interaction between zone and site was significant (p=0.0156).

For each site (exposed sites only), higher numbers of early plantigrades were recorded on algae than on the mussel bed (Figure 2.13), however the interaction between site and substratum was significant (p=0.0034), indicating a stronger effect of substratum at Diaz Cross than At High Rocks.

Densities of early plantigrades at exposed sites were much higher on algae than they were on the mussel bed in the low and mid shore zones, however on the high shore the difference in densities between the two was minimal (Figure 2.14). This inconsistency between densities on algae and on mussels at each zone led to a significant interaction between zone and substratum (p=0.0027).

Table 2.9 Three-way ANOVA table showing differences in densities of early plantigrades (0-1mm) at exposed sites; using site, zone and substratum as factors. The data were pooled for each day and an average taken. The average for each of the days sampled were used as replicates. Data were log transformed.

Source of variation	d.f.	SS	MS	F	p
A : site	1	0.161807	0.0161807	0.303	0.5894
B : zone	2	0.5992550	0.2996275	5.605	0.0051
C : substratum	1	2.6122307	2.6122307	48.868	<0.0001
Interactions					
AB	2	0.4662953	0.2331477	4.362	0.0156
AC	1	0.4856811	0.4856811	9.086	0.0034
BC	2	0.6749442	0.3374721	6.313	0.0027
ABC	2	0.5004965	0.3374721	4.681	<0.0001
Residual	89	4.7574961	0.534550		
Total	100	10.744356			

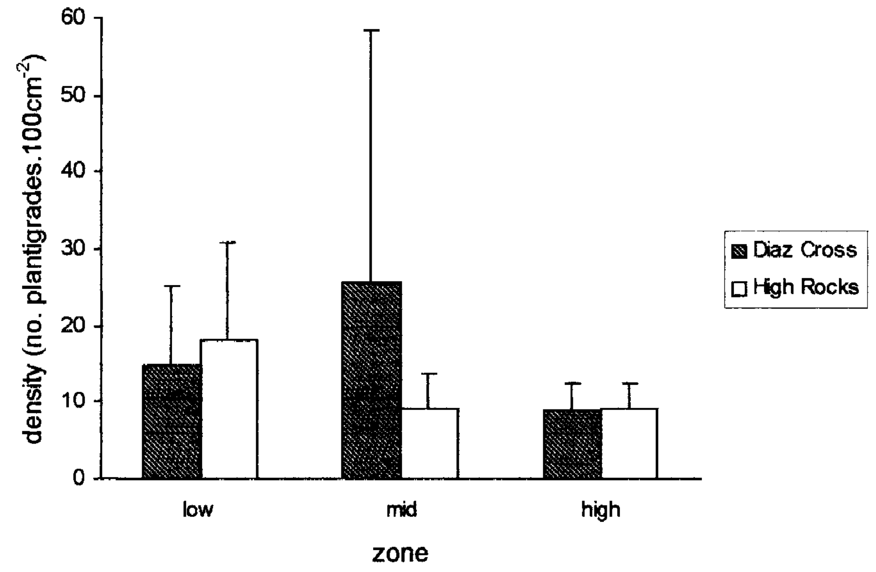


Figure 2.12 Mean density (+ std. dev.) of early plantigrades (<1mm) on low, mid and high shore levels at Diaz Cross and High Rocks exposed shores only. Means were calculated from all quads pooled.

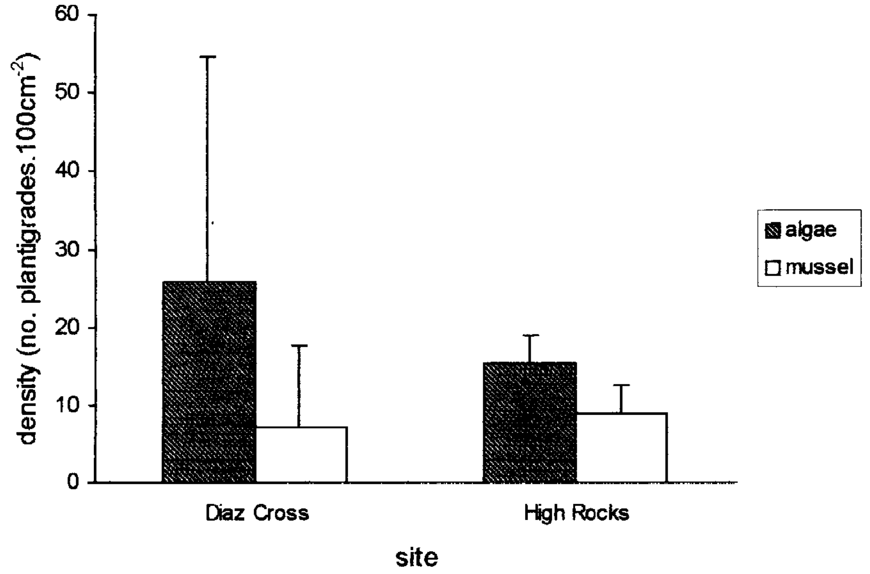


Figure 2.13 Mean density (+ std. dev.) of early plantigrades (<1mm) on algae and mussel substrata at Diaz Cross and High Rocks exposed shores only. Means were calculated from all quads pooled.

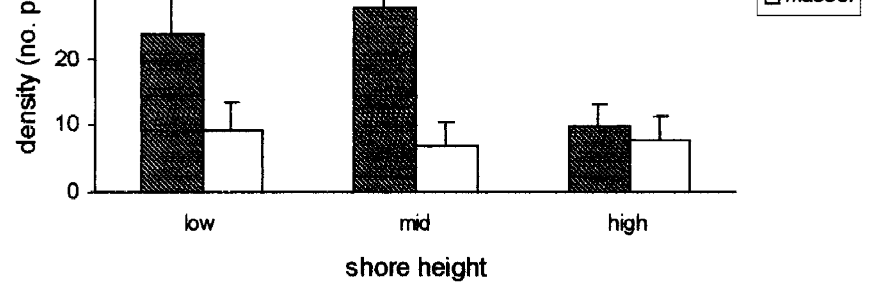


Figure 2.14 Mean density (+ std. dev.) of early plantigrades (<1mm) on algae and mussel substrata on low, mid and high shore zones at exposed shores only. Means were calculated from all quads pooled.

Late plantigrades (recruits 1-4.99mm) (Table 2.10)

On the exposed shores the densities of late plantigrades were greater at High Rocks (22.1) than at Diaz Cross (17.1), this difference was significant ($p<0.0001$). This was in contrast to the result obtained for the equivalent analysis for the early plantigrades. Zone showed a significant difference, once again low (23.4) and mid (21.9) shore zones displayed a greater number of late plantigrades than recorded for the high (13.5) shore zone ($p=0.0001$). Late plantigrade numbers on algae (26.7) were significantly ($p<0.0001$) higher than those on mussel bed (12.6).

The interaction between site and zone was significant ($p<0.0001$). Not conforming to the overall pattern (i.e. decrease in density up shore), the average late plantigrade density at Diaz Cross, low shore (13.5) was lower than that recorded on the mid shore (27.2) at the same site. In contrast to this at High Rocks, the low shore (33.4) recruit density was greater than that on the mid shore (16.7) (Figure 2.15).

The interaction between site and substratum produced a result similar to that for the early plantigrades and although the interaction was significant ($p<0.0001$) a greater density of late plantigrades were found on algae, for the respective sites (Figure 2.16).

When zone and substratum were considered the number of late plantigrades on algae was greater than the number on mussel substratum. As with the early plantigrades, this difference between the number of plantigrades on algae and mussel diminished with increased height up the shore (Figure 2.17). The interaction between zone and substratum was significant ($p<0.0001$).

Table 2.10 Three-way ANOVA table showing differences in densities of late plantigrades (1-4.99mm) at exposed sites; using site, zone and substratum as factors. The data were pooled for each day and an average taken. The average for each of the days sampled were used as replicates. Data were log transformed.

Source of variation	d.f.	SS	MS	F	p
A : site	1	1.0040323	1.0040323	44.370	<0.0001
B : zone	2	0.4570957	0.2285479	10.100	0.0001
C : substratum	1	2.6071450	2.6071450	115.215	<0.0001
Interactions					
AB	2	0.9102454	0.4551227	20.113	<0.0001
AC	1	0.4769520	0.4769520	21.077	<0.0001
BC	2	1.1831635	0.5915817	26.143	<0.0001
ABC	2	0.4496181	0.2248090	9.935	0.0001
Residual	89	2.0139422	0.0226286		
Total	100	9.2641573			

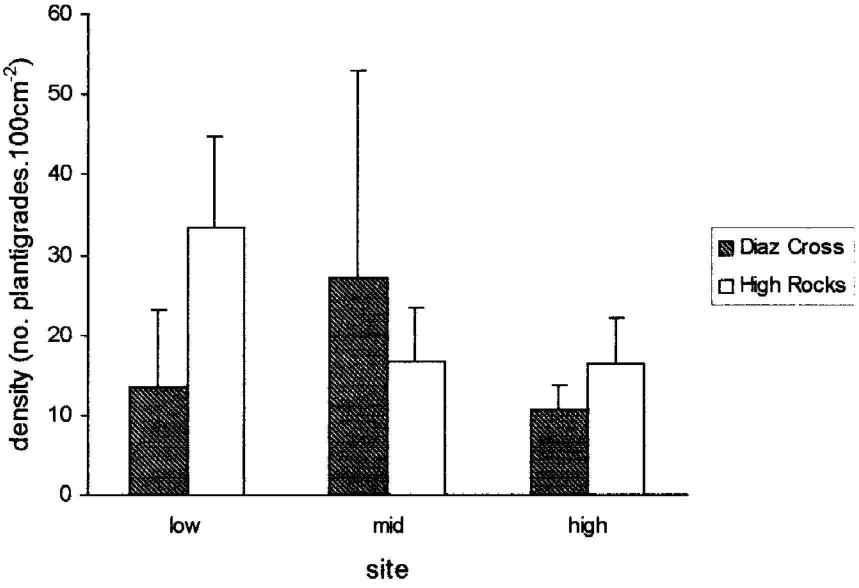


Figure 2.15 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) on low, mid and high shore levels at Diaz Cross and High Rocks exposed shores only. Means were calculated from all quads pooled.

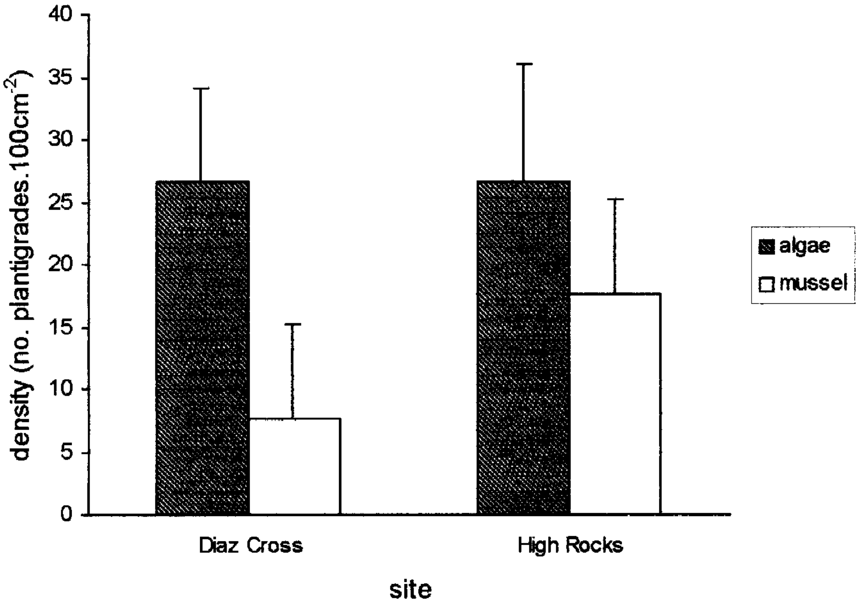


Figure 2.16 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) on algae and mussel substrata at Diaz Cross and High Rocks exposed shores only. Densities for each day were pooled and from these data, means were calculated.

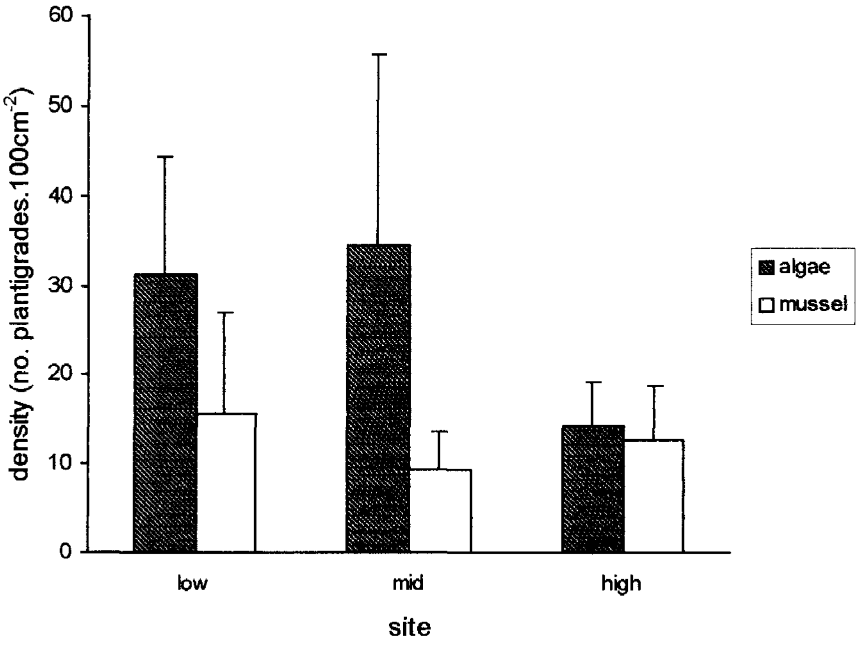


Figure 2.17 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) on algae and mussel substrata on low, mid and high shore zones at exposed shores only. Means were calculated from all quads pooled.

c- Effects of shore, exposure, zone and substratum on the mid and high shore

Early plantigrades (recruits <1mm) (Table 2.11)

On the mid and high shore zones, the densities of early plantigrades were much higher at Diaz Cross (16.5) than they were at High Rocks (7.8). This difference was significant ($p<0.0001$).

Exposure did not significantly effect the densities of early plantigrades on the mid and high shore ($p=0.3052$). The interaction between site and exposure was not significant ($p=0.7915$).

The average density of early plantigrades was much higher on the mid shore (15.7) than it was on the high shore (8.7) ($p=0.0003$). However this pattern was not consistent at both sites and was swayed by the very high numbers of plantigrades found on the mid shore at Diaz Cross (23.6), consequently the interaction between site and zone was significant ($p=0.0002$) (Figure 2.18).

The low average density of early plantigrades recorded at High Rocks on the mid shore and high shore, was also evident on the individual substrata, with the average density on High Rocks algae (8.5) being only slightly higher than that on High Rocks mussel bed (7.2). The mean density of plantigrades on algae (24.7) at Diaz Cross was again high, while on the mussel bed (8.4) it was low. This resulted in a significant interaction between site and substratum (p=0.0001) (Figure 2.19).

Densities on the mid shore exposed (17.4) and sheltered (13.9) shores were higher than densities on the high shore exposed (8.9) and high shore sheltered (8.5) shores, the interaction between exposure and zone was not significant (p=0.4015), indicating the same effect of zone under both exposure regimes.

Substratum had a significant effect on densities of early plantigrades on the mid and high shore, however exposure did not and the interaction between substratum and exposure was not significant (p=0.1520) i.e. densities on mussels were less than those on algae at both levels of exposure. On the other interaction between substratum and zone was significant (p=0.0045, indicating that plantigrade densities were affected differently, by substratum at different zones (Figure 2.20) i.e. the effect of substratum was stronger on the mid shore than on the high shore.

Table 2.11 Four-way ANOVA table showing differences in densities of early plantigrades (<1mm) on mid and high shore zones; using site, exposure, zone and substratum as factors. The data were pooled for each day and an average taken. The average for each of the days sampled were used as replicates in the Anova. Data were log transformed.

Source of variation	d.f.	SS	MS	F	p
A : site	1	2914.2256	2914.2256	21.601	<0.0001
B : exposure	1	142.8946	142.8946	1.059	0.3052
C : zone	1	1879.0197	1879.0197	13.928	0.0003
D : substratum	1	2951.8405	2951.8405	21.880	<0.0001
Interactions					
AB	1	9.7286	9.7286	0.072	0.7915
AC	1	1958.4260	1958.4260	14.516	0.0002
AD	1	2177.6120	2177.6120	16.141	0.0001
BC	1	99.3149	99.3149	0.736	0.4015
BD	1	279.8064	279.8064	2.074	0.1520
CD	1	1124.6408	1124.6408	8.336	0.0045
ABC	1	63.1326	63.1326	0.468	0.5023
ABD	1	156.3991	156.3991	1.159	0.2835
ACD	1	1697.5733	1697.5733	12.583	0.0005
BCD	1	613.5047	613.5047	4.547	0.0347
ABCD	1	217.4537	217.4537	1.612	0.2063
Residual	141	19022.379	134.91049		
Total	156	37141.803			

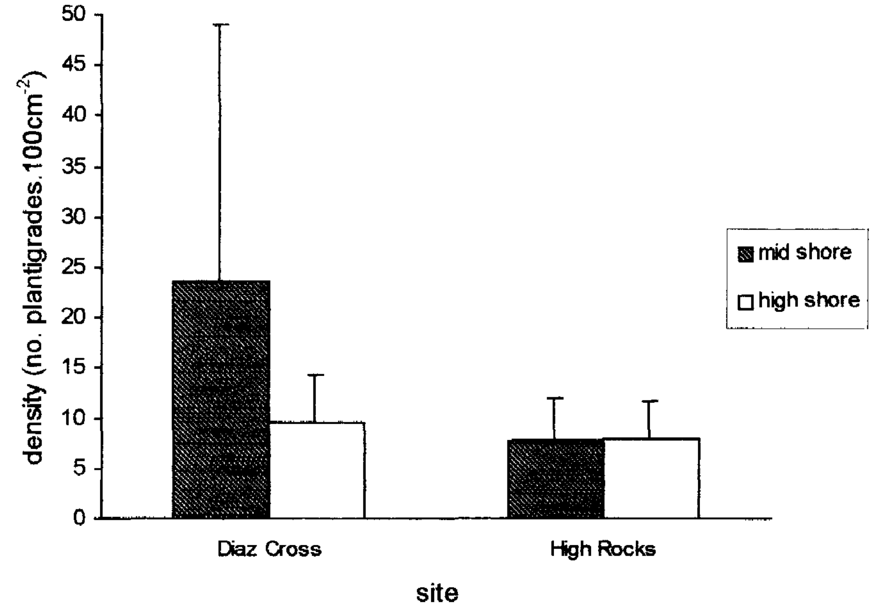


Figure 2.18 Mean density (+ std. dev.) of early plantigrades (<1mm) at Diaz Cross and High Rocks on mid and high shore zones only. Means were calculated from all quads pooled.

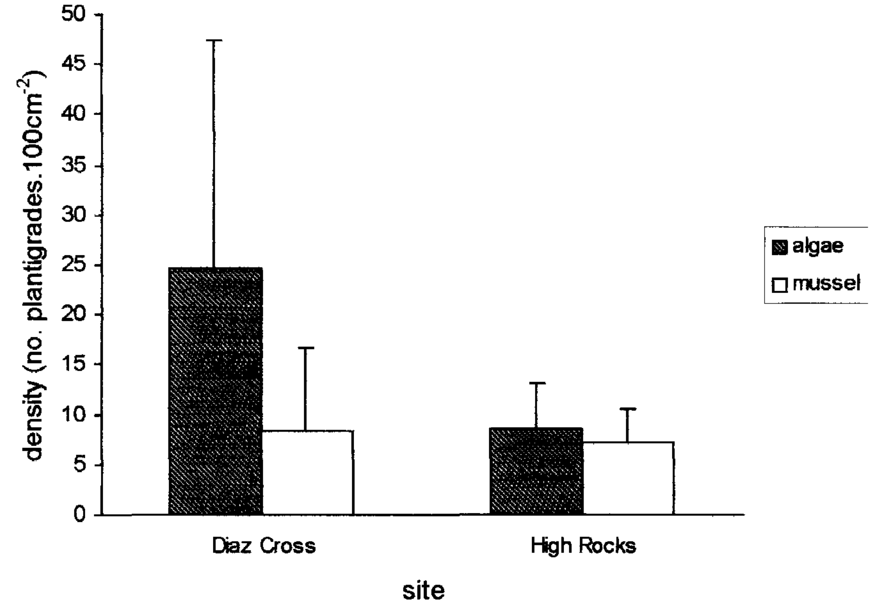


Figure 2.19 Mean density (+ std. dev.) of early plantigrades (<1mm) at Diaz Cross and High Rocks on algae and mussel substrata (mid and high shore zones only). Means were calculated from all quads pooled.

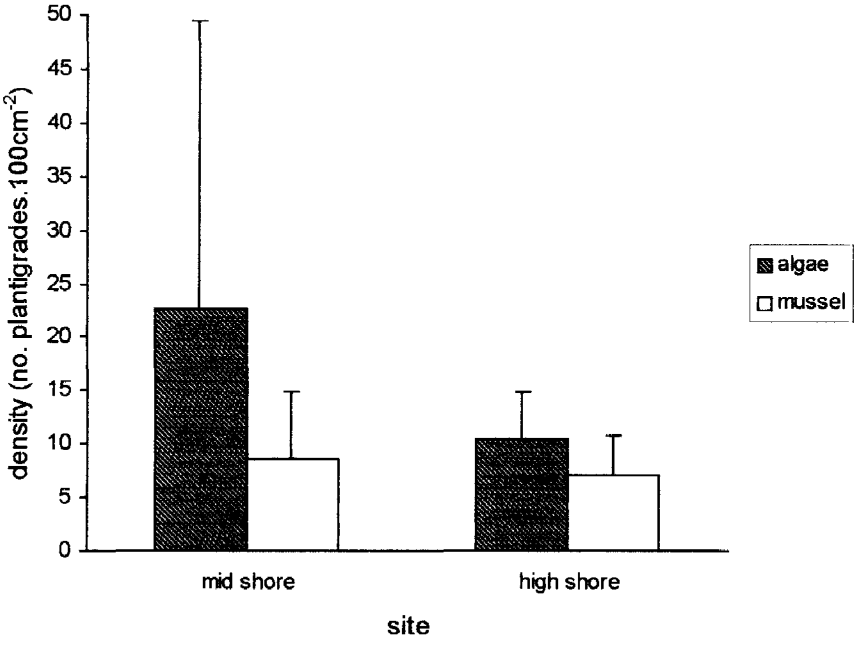


Figure 2.20 Mean density (+ std. dev.) of early plantigrades (<1mm) at mid and high shore zones on algae and mussel substrata. Means were calculated from all quads pooled.

Late plantigrades (recruits 1-4.99mm) (Table 2.12)

The difference between the average density of late plantigrades at Diaz Cross (20.4) and High Rocks (14.4) (on mid and high shore zones only) was not significant ($p=0.5947$). The average density of late plantigrades at exposed sites (17.7) showed no significant difference from that at sheltered sites (17.1) ($p=0.0591$).

On the mid and high shore zones , 64% of the late plantigrades were found on the mid shore (22.2), and only 36% on the high shore (12.6), this difference was significant ($p<0.0001$). The trend of greater numbers of recruits occurring on algal substrata (23.2), than on the mussel bed (11.6) was continued by the late plantigrades on the mid and high shores ($p<0.0001$). However this difference was greatest at Diaz Cross where the difference between the average number of plantigrades on algae (31.5) and that on mussel bed (9.4) was 22.1, the difference at High Rocks was only 1.1 plantigrades (Figure 2.21). Consequently the interaction between site and substratum was significant ($p<0.0001$).

If exposure had an effect on the density of late plantigrades, its effect at Diaz Cross was different to its effect at High Rocks (site/exposure interaction p=0.0048). The average density of late plantigrades at the Diaz Cross exposed shore (18.9) was lower than that for the Diaz Cross sheltered shore (21.9), whereas at High Rocks the density at the exposed site (16.5) was higher than that for the sheltered site (12.3) (Figure 2.22)

The interaction between site and zone (mid and high shore only) was significant (p<0.0001). At Diaz Cross the difference in average late plantigrade density at mid (29.5) and high (11.3) shore zones was much greater than the difference in average density between the same zones at High Rocks (mid=14.9; high=13.9) (Figure 2.23).

The density of plantigrades at exposed (21.9) and sheltered (22.4) mid shore zones were similar, as were those on the high shore (13.5 and 11.8 respectively). The interaction between zone and exposure was not significant (p=0.0694).

Substratum was more important in affecting plantigrade density than exposure. On the algal substrata the average number of plantigrades was 24.4 and 22 on exposed and sheltered shores respectively, while on the mussel bed it was 11.1 and 12.2 on exposed and sheltered shores respectively. Substratum and exposure did not interact significantly (p=0.1370).

At the respective zones (mid and high) the average density of plantigrades was always higher on the algal substrata (31.3 and 15.1) than it was on the mussel bed (13 and 10.2) (zone/substratum interaction p=0.1935).

Table 2.12 Four-way ANOVA table showing differences in densities of late plantigrades (1-4.99mm) on mid and high shore zones; using site, exposure, zone and substratum as factors. The data were pooled for each day and an average taken. The average for each of the days sampled were used as replicates in the Anova. Data were log transformed.

Source of variation	d.f.	SS	MS	F	p
A : site	1	0.110208	0.110208	0.293	0.5947
B : exposure	1	0.1360134	0.1360134	3.620	0.0591
C : zone	1	1.0406924	1.0406924	27.699	<0.0001
D : substratum	1	2.5455007	2.5455007	67.752	<0.0001
Interactions					
AB	1	0.3078697	0.3078697	8.194	0.0048
AC	1	0.8825464	0.8825464	23.490	<0.0001
AD	1	2.2011986	2.2011986	58.588	<0.0001
BC	1	0.1257485	0.1257485	3.347	0.0694
BD	1	0.0840388	0.0840388	2.237	0.1370
CD	1	0.0641229	0.0641229	1.707	0.1935
ABC	1	0.0952971	0.0952971	2.536	0.1135
ABD	1	0.4958197	0.4958197	13.197	0.0004
ACD	1	0.4782203	0.4782203	12.728	0.0005
BCD	1	1.6263172	1.6263172	43.287	<0.0001
ABCD	1	0.0635067	0.0635067	1.690	0.1957
Residual	141	5.2974922	0.037509		
Total	156	16.413860			

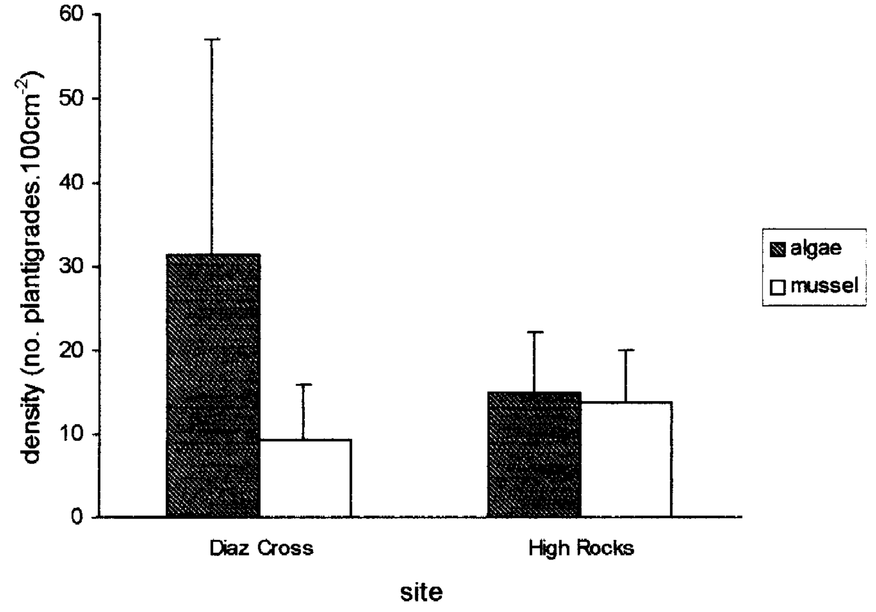


Figure 2.21 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) at Diaz Cross and High Rocks on algae and mussel substrata. Means were calculated from mid and high shore zones only. Means were calculated from all quads pooled.

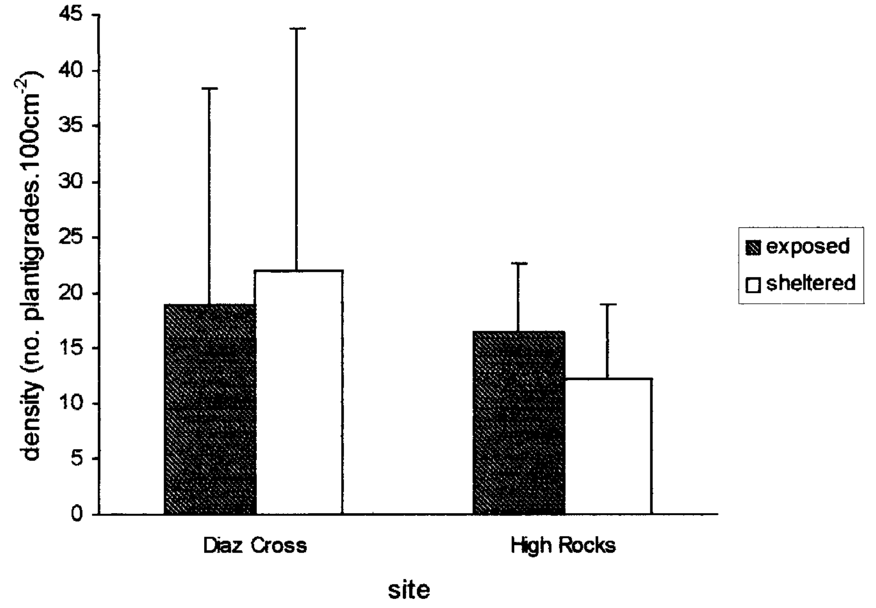


Figure 2.22 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) at Diaz Cross and High Rocks at exposed and sheltered sites. Means are from mid and high shore zones only. Means were calculated from all quads pooled.

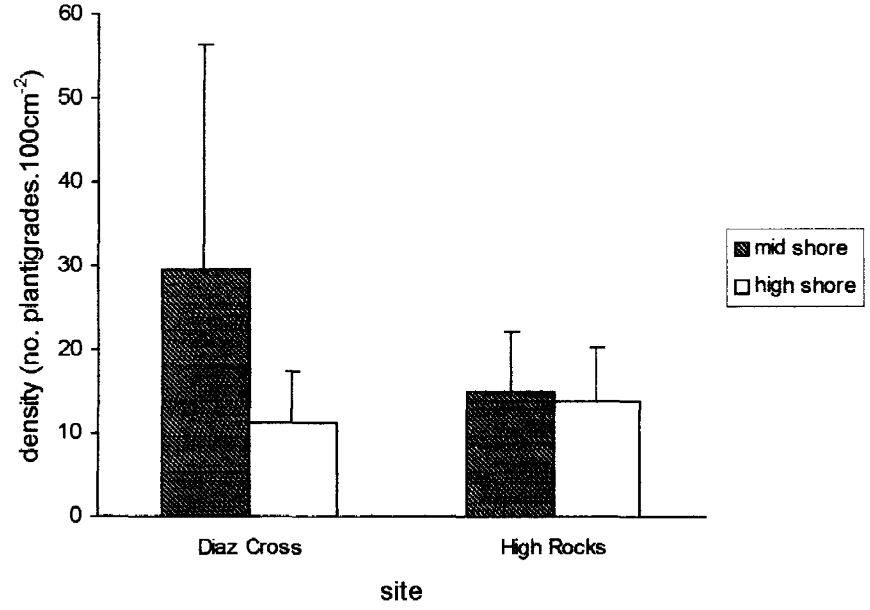


Figure 2.23 Mean density (+ std. dev.) of late plantigrades (1-4.99mm) at Diaz Cross and High Rocks on mid and high shore zones. Means were calculated from all quads pooled.

Summary of analyses a-c (Table 2.13)

The densities of early plantigrades were always higher at Diaz Cross than they were at High Rocks, while with the late plantigrades there was no difference (except on algae). In general more recruits (early and late plantigrades) occurred on the low and mid zones than on the high shore zone. Exposure influenced the number of recruits (both early and late plantigrades) on algae, and this resulted in more recruits occurring on exposed algae than on sheltered algal substrata. The were more recruits (both early and late plantigrades) on algae than there were on the mussel bed.

Table 2.13 Summary of results obtained from ANOVA's in analyses a-c. Comparisons were based on the density of recruits under different tests. Results for both early (<1mm) and late (1-4.99mm) plantigrades have been included. DC = Diaz Cross; HR = High Rocks; N/A = not applicable.

Factor	**Analysis A** **algae**	**Analysis B** **exposed conditions**	**Analysis C** **mid and high zones**
<1mm			
site	• DC > HR	• DC > HR	• DC > HR
zone	• mid > low and high	• Low and mid > high	• mid > high
substratum	• N/A	• algae > mussel	• algae > mussel
exposure	• exposed > sheltered	• N/A	• no effect
1-4.99mm			
site	• DC > HR	• no effect	• no effect
zone	• mid > low and high	• low and mid > high	• mid > high
substratum	• N/A	• algae > mussel	• algae > mussel
exposure	• exposed > sheltered	• N/A	• no effect

d- Effect of substratum at each exposure, zone and site

Comparison of plantigrade densities on algae and mussels at 100% cover of substratum

Early plantigrades (recruits <1mm) (Tables 2.14, 2.15)

Comparisons of the average number of early plantigrades on algae compared to those on mussels at each exposure, at each zone and at each site revealed that of the 10 comparisons carried out, nine had higher numbers of recruits on algae. All but three of these nine comparisons were significant ($p<0.05$). At High Rocks sheltered, mid shore zone the average density of plantigrades on mussels was higher than that on algae, however this difference was not significant ($p>0.05$).

Late plantigrades (recruits 1-4.99mm) (Tables 2.16, 2.17)

Similar results obtained for the early plantigrades were observed for the late plantigrades. Densities on algae were higher than those on mussel bed in nine of the 10 comparisons. Of the nine comparisons where algae had greater densities, six were significant ($p<0.05$). Once again at High Rocks the density of plantigrades on the mussel bed at the sheltered mid shore zone was greater than that on algae, this difference was significant ($p<0.05$).

Table 2.14 Comparison of the mean number of early plantigrades (<1mm) on mussel and algal substrata at each tidal level and for each shore at Diaz Cross. Means were calculated at 100% cover on $100cm^{-2}$ of substratum. The average number of mussels recorded on each day were used to calculate a grand mean. * indicates a significant difference at a tidal height, while n.s. indicates a non-significant result ($p>0.05$). Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	7.7 (4.0)	21.8 (10.2)	*	algae ↑
Mid	6.1 (3.3)	45.4 (37.5)	*	algae ↑
High	7.5 (4.1)	10.0 (2.7)	n.s.	algae ↑
Sheltered				
Mid	12.8 (9.3)	30.1 (15.50	*	algae ↑
High	7.3 (4.8)	13.2 (4.9)	*	algae ↑

Table 2.15 Comparison of the mean number of early plantigrades (<1mm) on mussel and algal substrata at each tidal level and for each shore at High Rocks. Means were calculated at 100% cover on $100cm^{-2}$ of substratum. The average number of mussels recorded on each day were used to calculate a grand mean. * indicates a significant difference at a tidal height, while n.s. indicates a non-significant result ($p>0.05$). Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	10.4 (4.3)	25.9 (14.1)	*	algae ↑
Mid	8.0 (3.9)	10.3 (5.4)	n.s.	algae ↑
High	8.2 (2.8)	9.7 (4.0)	n.s.	algae ↑
Sheltered				
Mid	7.5 (4.1)	5.3 (1.7)	n.s.	mussel ↑
High	5.2 (2.2)	8.6 (4.9)	*	algae ↑

Table 2.16 Comparison of the mean number of late plantigrades (1-4.99mm) on mussel and algal substrata at each tidal level and for each shore at Diaz Cross. Means were calculated at 100% cover on $100cm^{-2}$ of substratum. The average number of mussels recorded on each day were used to calculate a grand mean. * indicates a significant difference at a tidal height, while n.s. indicates a non-significant result ($p>0.05$). Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	5.7 (0.9)	21.3 (7.6)	*	algae ↑
Mid	6.9 (2.8)	47.5 (21.9)	*	algae ↑
High	10.1 (2.5)	11.2 (3.7)	n.s.	algae ↑
Sheltered				
Mid	48.6 (32)	15.2 (9.2)	*	algae ↑
High	18.7 (4.1)	5.3 (4.6)	*	algae ↑

Table 2.17 Comparison of the mean number of late plantigrades (1-4.99mm) on mussel and algal substrata at each tidal level and for each shore at High Rocks. Means were calculated at 100% cover on $100cm^{-2}$ of substratum. The average number of mussels recorded on each day were used to calculate a grand mean. * indicates a significant difference at a tidal height, while n.s. indicates a non-significant result ($p>0.05$). Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	25.6 (7)	41.2 (9.4)	*	algae ↑
Mid	11.8 (4.1)	21.6 (4.9)	*	algae ↑
High	15.5 (7.1)	17.2 (4.1)	n.s.	algae ↑
Sheltered				
Mid	18.3 (7)	7.7 (2.7)	*	mussel ↑
High	9.9 (2.8)	13.1 (7.9)	n.s.	algae ↑

Comparison of settler densities per m^2 of shore (taking into account cover of substrata)

Within each zone the percentage cover of mussels was greater than the percentage cover of algae (see Table 2.3.2). The number of plantigrades on algae, at 100% cover of substratum, was generally higher than the number on the mussel bed. However the fact that there was often more mussel bed available over the whole shore meant that this substratum received as many recruits as the algae did.

Early plantigrades (recruits <1mm) (Tables 2.18, 2.19)

Of the 10 possible comparisons (5 at Diaz Cross and 5 at High Rocks), four showed significantly ($p<0.05$) greater numbers of recruits on the mussel bed than on algae substrata. Five of the comparisons showed significantly ($p<0.05$) higher numbers of early plantigrades on algae than on mussel bed. There was no significant difference between the numbers of recruits on algae and mussel at the high shore exposed zone at Diaz Cross. The equivalent analyses to these for early plantigrades at 100% cover of substratum, revealed no cases where the number of recruits were significantly greater on mussel bed than they were on algae.

Late plantigrades (recruits 1-4.99mm) (Tables 2.20, 2.21)

A similar pattern to that for early plantigrades was observed for the late plantigrades. Of the 10 comparisons, three showed significantly ($p<0.05$) greater numbers of late plantigrades on mussel substrata than on algae substrata and five showed the opposite with significantly more ($p<0.05$) plantigrades occurring on algae than on the mussel bed. On the high exposed zone at Diaz Cross and the mid exposed zone at High Rocks there was no significant difference ($p>0.05$) between the mean density of late plantigrades on algae and on the mussel bed.

In summary, while the density of recruits on algae was always greater than or equal to that on mussels, the total proportion of the recruit population on algae was often less than that on mussels because of the cover by different substrata (Table2.22).

Table 2.18 Comparison of the mean number (per m^2 of shore, ± std. dev) of early plantigrades (<1mm) on mussel and algal substrata at each tidal level and for each shore at Diaz Cross. * indicates a significant difference in mean density at a tidal height, n.s. indicates a non-significant result ($p>0.05$). Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	471.8 (224.8)	1497.8 (636.7)	*	algae ↑
Mid	93.3 (48.2)	912.4 (717.8)	*	algae ↑
High	127.7 (66.7)	140.5 (35.5)	n.s.	algae ↑
Sheltered				
Mid	212.8 (147.1)	57.1 (28.1)	*	mussel ↑
High	135.3 (85.7)	228.8 (81.5)	*	algae ↑

Table 2.19 Comparison of the mean number (per m^2 of shore, ± std. dev) of early plantigrades (<1mm) on mussel and algal substrata at each tidal level and for each shore at High Rocks. * indicates a significant difference in mean density at a tidal height, n.s. indicates a non-significant ($p>0.05$) result. Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	636.8 (239.9)	1460.1 (728.4)	*	algae↑
Mid	165.6 (75.7)	83.4 (40.9)	*	mussel ↑
High	133.7 (43.5)	65.2 (25.4)	*	mussel ↑
Sheltered				
Mid	233 (118.6)	76.7 (23.1)	*	mussel ↑
High	27.4 (10.9)	55.7 (27.4)	*	algae ↑

Table 2.20 Comparison of the mean number (per m^2 of shore, ± std. dev) of late plantigrades (1-4.99mm) on mussel and algal substrata at each tidal level and for each shore at Diaz Cross. * indicates a significant difference in mean density at a tidal height, n.s. indicates a non-significant ($p>0.05$) result. Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	346.2 (48.5)	1459.7 (476.3)	*	algae ↑
Mid	105.9 (41.4)	954.4 (419.4)	*	algae ↑
High	173.3 (39.8)	156.7 (48.6)	n.s.	mussel ↑
Sheltered				
Mid	251.5 (146.1)	92.3 (57.9)	*	mussel ↑
High	99.2 (81.1)	324.8 (67.4)	*	algae ↑

Table 2.21 Comparison of the mean number (per m^2 of shore, ± std. dev) of late plantigrades (1-4.99mm) on mussel and algal substrata at each tidal level and for each shore at High Rocks. * indicates a significant difference in mean density at a tidal height, n.s. indicates a non-significant result ($p>0.05$). Algae ↑ indicates that the average settler density was higher on algae than it was on mussel. Results are from a series of one-way ANOVA's.

Zone	Mussel (±std. dev.)	Algae (±std. dev.)	Significance	Comment
Exposed				
Low	1566.6 (393.9)	2321.8 (483.8)	*	algae ↑
Mid	245 (78.4)	174.8 (36.9)	n.s.	mussel ↑
High	252.1 (110.3)	115.5 (25.8)	*	mussel ↑
Sheltered				
Mid	566.5 (203)	111.9 (37)	*	mussel ↑
High	52.5 (14)	85.4 (48.9)	*	algae ↑

Table 2.22 Summary of the results obtained for analysis d. A comparison of the densities of plantigrades on algae and on mussels for 100% cover and adjusted densities. The number of cases falling into the density criteria appear under the relevant headings.

Density at 100% cover		DENSITY CRITERIA	Adjusted density	
Early plantigrades	**Late plantigrades**		**Early plantigrades**	**Late plantigrades**
6 cases	6 cases	algae>mussels	5 cases	5 cases
4 cases	3 cases	algae=mussels	1 case	2 cases
0 cases	1 case	algae<mussels	4 cases	3 cases

DISCUSSION

The suggestion of direct settlement of larvae from the plankton onto the mussel bed supports other work on *Perna perna* (Phillips, 1994; Lasiak & Barnard, 1995) indicating that the primary settlement of larvae onto algae followed by secondary settlement onto the mussel is not the only means of mussels recruiting onto the shore. Bayne (1964) first quantified primary and secondary settlement occurring on beds of *Mytilus edulis*, but since then few authors have been able to confirm his findings (Bøhle, 1971; Dare, 1976; King *et al.*, 1990). In many studies on mytilids, authors have noted that, in addition to direct settlement onto the mussel bed, plantigrades move onto the mussel bed after a growth period on algae (Berry, 1978; Beckley, 1979; Crawford & Bower, 1983; Beukema & de Vlas, 1989; King *et al.*, 1989; King *et al.* 1990; McGrath & King, 1991; Cáceres-Martinez *et al.* 1993, 1994; Phillips, 1994). Settling on algae may be advantageous to juvenile survival as algae provide a cryptic habitat that may reduce predation (Shepherd & Turner, 1985), competition between plantigrades and adults would be reduced (Bayne, 1964; Petersen, 1984a) and possible mortality of larvae due to filter feeding of larvae by adults is avoided (Andre *et al.* 1993; Phillips, 1994).

In this study there was no evidence of large numbers of late plantigrades leaving the algal substrata and suddenly appearing on the mussel beds and it must therefore be concluded that secondary settlement did not occur on a large scale. Lasiak & Barnard (1995) concluded that secondary settlement of *Perna perna* from algae to mussel bed did not occur at their sites. Of the other studies involving the secondary settlement of *Perna perna*, few offer conclusive evidence for the movement of recruits from algae substrata to the mussel bed. Phillips (1994) attributed the "disappearance" and "occasional settlement" of late *Perna perna* plantigrades in some of her samples to secondary settlement, however the decrease or increase of late plantigrades at a site could just as easily be ascribed to previous patchy settlement events. Referring to secondary settlement in *Perna perna*, Phillips (1994) states that indirect evidence from her study suggests that this phenomenon does occur, however she seems more inclined to conform to Bayne's (1964) findings than to look at alternatives. Crawford & Bower (1983) calculated the proportion of *Perna perna* <10mm at regular intervals over a two year period along the South African south coast. From this they were able to conclude that there was a greater proportion of mussels <10mm through mid spring and early winter, however they also cite this as evidence of secondary settlement during these months. Beckley (1979) does not state that *Perna perna* undergo secondary settlement, but she does imply it in her concluding paragraph. The only evidence given to support her assumptions is that, of the plantigrades found on *Gelidium*, 82% were less than 5mm. In terms of research on *Perna perna* in South Africa, Berry (1978) is perhaps the most cited author, unfortunately he has made general statements regarding secondary settlement that were based on studies undertaken at monthly intervals (rather than at a finer scale) and did not include studies on algal substrata. From his study (undertaken on the south coast of South Africa) it is only possible to conclude that increases in the frequency of plantigrades of 1-10mm, on mussel beds, were abundant in certain months.

Late plantigrades of *Choromytilus meridionalis* have been recorded in the plankton above sub-tidal mussel beds in southern African waters, indicating that at least sub-tidal populations of this mussel undergo a secondary pelagic stage (du Plessis, 1977). Whether intertidal late plantigrade *Choromytilus meridionalis* undergo secondary settlement is not certain, however migration of plantigrades up shore has been recorded for this species (Griffiths, 1981a). No evidence of secondary settlement was observed in *Mytilus californianus* mussel beds (Petersen, 1984b). So although most mussel species seem to be able to recruit secondarily into the adult population, in some species secondary settlement is vital to successful recruitment. For example populations of *Macoma balthica*, in the Wadden Sea (Beukema & de Vlas, 1989; Armonies & Hellwig-Armonies, 1992), and *Mytilus edulis*, in Morecambe Bay, Britain (Dare, 1976) may arise solely from secondarily settled individuals.

The relative abundance of large recruits (>5mm) found on coralline algae and the mussel bed and not on *Gelidium* may be related to the higher quality of refuge sites afforded by the coralline algae and the mussel bed. Late plantigrades on algae were nearly always situated nearer the alga's holdfast (pers. obs.). This area of the plant would afford better refuge for mussels and provide greater protection from wave action. The denser foliage and larger holdfast area found associated with coralline algae may be responsible for the greater numbers of late recruits found on this algae, when compared to those found on *Gelidium*. A question that now arises is: what happens to settlers once they reach larger sizes on a particular substratum? Conventional ideas suggest that the late plantigrades release their hold on the alga and re-enter the water column until they can attach onto the mussel bed. Most literature on *Perna perna* gives little substantial evidence of this occurring (Berry, 1978; Beckley, 1979; Crawford & Bower, 1983; Phillips, 1994). *Perna perna* plantigrades may never "voluntarily" release from a substratum. With plantigrade growth and increased size, drag on the juvenile mussel, caused by wave action, would increase (see Denny, 1987). The increase in drag may result in the removal of plantigrades from particular substrata and not from others. Removed plantigrades, now in the surf zone are likely to wash up onto the shore and die. *Perna perna* plantigrades do not seem to be able to attach directly to the rock surface (Lambert & Steinke, 1986), and if there is no secondary settlement of plantigrades from algae to the mussel bed, then it must be concluded that settlement onto algae is wasted settlement. Studies on settlers re-entering the water column and entering a secondary bysso-pelagic were undertaken on northern hemisphere shores where huge tidal differences and sub-tidal mussel beds occur (Bayne, 1964; Dare, 1976; Lane *et al.* 1985). Little wave action and strong ebbing tidal currents, rather than exposed conditions with low tidal ranges, may be more conducive to plantigrades entering a second pelagic stage.

Early plantigrade densities were greater at Diaz Cross than at High Rocks, however this was not the case for the late plantigrades (except for the densities on algal substrata). Settlement intensity (especially low intensity) can influence the abundance of recruits and ultimately adult intertidal organisms (Connell, 1985). Certain areas can repeatedly experience lower settlement than others due to a lower density of larvae in the water adjacent to the settling area (Raimondi, 1988). The larval pool is influenced by local environmental conditions such as water currents (Scheltema, 1975; Connell, 1985; Minchinton & Scheibling, 1991; Young *et al.* 1996) sea temperatures (Muus, 1981) and salinity (Bayne, 1965). However, it has been suggested that stochastic events can also influence the number of larvae arriving at certain shores at different times (Sebens & Lewis, 1985; Phillips, 1994; Leeb, 1995). The timing of settlement events at Diaz Cross and High Rocks sites showed little synchrony, and there tended to be greater synchrony among substrata within a zone, than on the same substrata among zones. This implies that that larvae are dumped in a zone and settle on the available substrata within that zone, rather than selecting a more preferred substratum in another zone. Patchiness of larvae in the water column as well as local hydrographic conditions, probably prevent synchrony of settlement events among shores (Raimondi, 1988).

In most cases the densities of early and late plantigrades were greater on the low and mid shore than they were on the high shore. This was probably due to a greater submergence time and greater water depth on the low and mid shores, which resulted in more time for settlement in these zones (Menge, 1991; Bertness *et al.* 1992; Leeb, 1995).

Wave exposure influenced the density of early and late plantigrades on algae, with more recruits being present on algae at exposed sites than at sheltered sites. This difference was most pronounced on the low shore, but not so on the mid and high shores. In chapter one (this study), differences in adult population structure between exposed and sheltered sites were also found to be greatest on the low shore. The algal beds at the low shore sheltered zones were only about 15mm high, while at the low shore exposed sites they were from 40-60mm high (pers. obs.). Algae at the low shore exposed sites could possibly snare more settlers. The difference in plantigrade densities between exposed and sheltered low shores could also have been related to the scarcity of adult mussels on the low shore sheltered sites, which in some way inhibited the settlement of larvae. Higher plantigrade densities on algal substrata than on the mussel bed, were probably a result of more larvae "choosing" to settle on algal substrata. Higher settlement onto algae was a trend observed throughout this study. Other studies have found similar trends and it is usually suggested that the larvae actively select to settle on algae for a short growth period (Bayne, 1964, King *et al.*, 1990). In contrast to this Bourget & Harvey (1998) suggest that hydrodynamic processes are sufficient in explaining large scale (>3cm) recruitment patterns. When the area of the algae was taken into account the importance of this substratum to settlers was still great, with 63% of the total settlement occurring on algae. Most of this settlement (45%) occurred on coralline algae. The high cover of this alga combined with the high settlement onto it were responsible for this. Phillips (1994) recorded a similar phenomenon with high settler numbers on algae, especially corallines. Algae, as a refuge for recruits, are probably ecological dead end substrata for mussels. *Perna perna* is not able to colonise areas which are already dominated by algae (Lambert & Steinke, 1986). Why would larval *Perna perna* settle on algae? Cáceres-Martinez and co-workers (1994) suggest that the settlement of *Mytilus galloprovincialis* is a passive process. Contact mucus threads produced by late pediveliger and post-larvae stages are more likely to snag filamentous surfaces, this results in a higher number of settlers occurring on algae when compared to those settling on the mussel bed. The filtering effect of algae is more efficient than that of byssus threads at trapping settling larvae (Lane *et al.*, 1985).

The fact that exposure had no effect on densities of early and late plantigrades at the mid and high shore zones, suggests that the difference between exposed and sheltered low shore zones may be indirectly linked to exposure. For example, if exposure affected the quality of the settling sites (in this case algae on the low shore) the resulting density of recruits could be affected in a complex way. Petraitis (1991) working on *Mytilus edulis* found that exposure and settler density were not related. In another study the density of *Perna perna* early plantigrades was not affected by the degree of wave action (Phillips, 1994). Contrary to the above studies, Leeb (1995) found that densities of *Mytilus galloprovincialis* recruits were greatest at exposed sites and proposed that exposed shores received a greater supply of larvae than sheltered shores, as they were submerged for longer, however she had no replication of sites. High settlement rates in areas of increased wave action resulted in high recruitment rates (Leeb, 1995). Patterns of recruitment may not always be as simple as this. In this study the greatest difference between exposed and sheltered sites occurred on the low shore and on algal substrata. A similar pattern was noted by Menge (1991), where recruitment of barnacles was highest at low and mid shore exposed sites, but on the high shore there was no difference between recruitment on exposed and sheltered sites.

A possible scenario for a *Perna perna* settlement event begins with a pocket of larvae of settling size arriving at a shore (Figure 2.24). With the wave action having increased upon reaching the intertidal zone, it is possibly only a matter of minutes before a larva that has not settled would wash up onto the shore. Algae offer an easy attachment site and probably act as a sieve for larvae, 63% of settlers attach to them. The coarser byssal threads of the adult mussels are not as easy to attach to and only 37% of the larvae settle into the mussel bed. The larvae metamorphose and begin growing, survivors in the mussel bed recruit into it and become adults. Survivors on the algae grow, as they become larger the increased drag on their shells results in them being removed by wave action, they now have at the most a couple of minutes before being washed ashore, most of this time is probably spent in partial suspension. Most of these mussels die and only a very small proportion become secondarily attached to the mussel bed.

Generally the settlement rates of *Perna perna* appear to be lower than those of other mussels, however these low rates are able to sustain mussel beds (Berry, 1978; Phillips, 1994; Lasiak & Barnard, 1995). Recruitment rates for *Perna perna* may be even lower than expected if settlers on algae die so that secondary settlement does not occur.

It is important not to make generalisations and assumptions about a species' life history style without relating them to local conditions. Regarding the secondary settlement of late plantigrades from algae onto mussel beds, some authors seem to have been swayed by the findings of scientists working on different species of mussels subjected to totally different environmental conditions. By trying to make their data conform to "accepted" patterns, the true patterns may be overlooked.

Although exposure does not seem to affect the density of plantigrades directly, it may affect the algal substrata particularly on the low shore. This could affect the density of larvae settling on the substrata and in turn effect the densities of plantigrades and adult mussels.

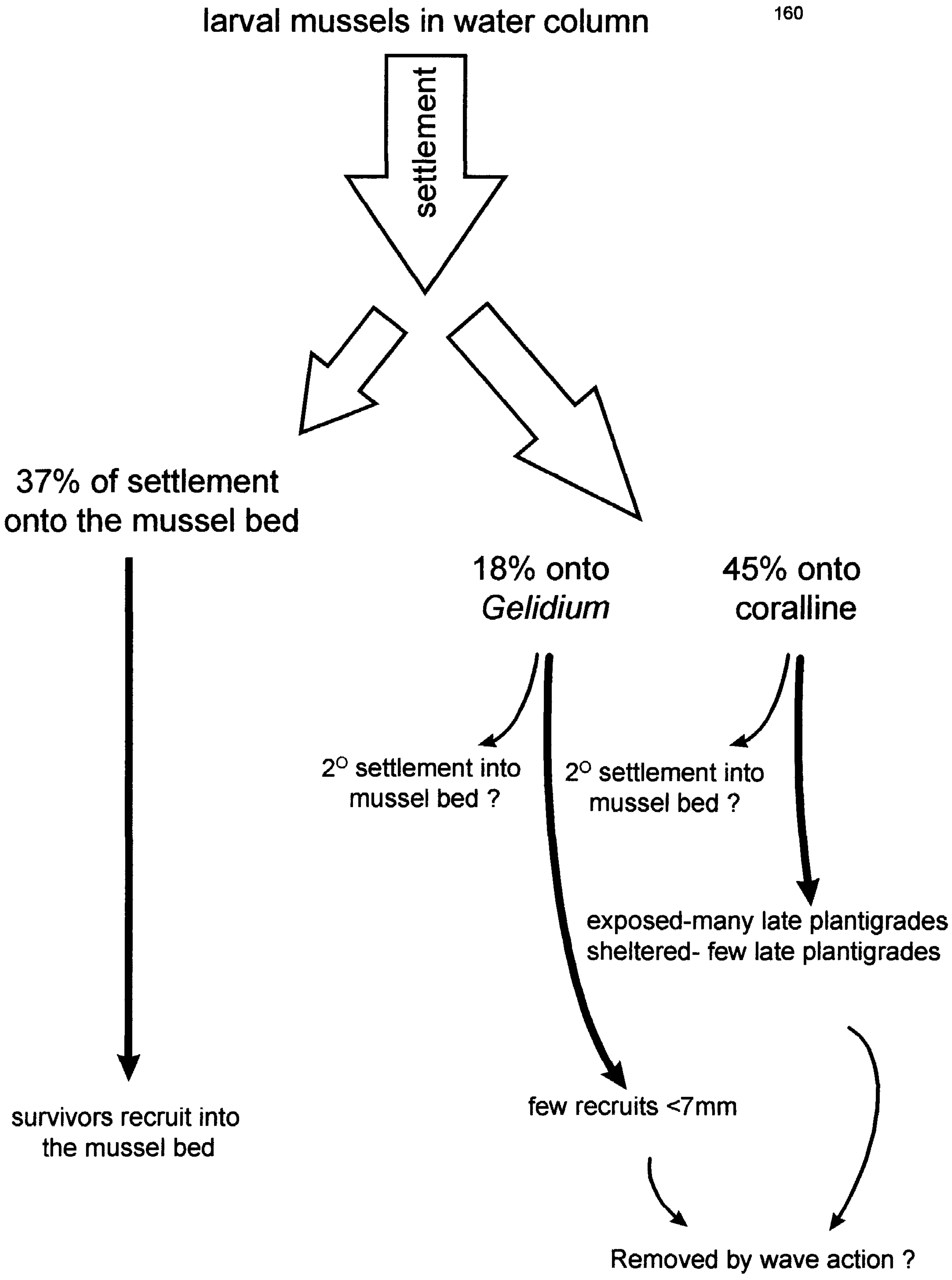


Figure 2.24 Summary of settlement onto different substrata. Unless stated, differences between exposed and sheltered sites and different zones are not included in this diagram.

GENERAL CONCLUSIONS AND DISCUSSION

The population dynamics of marine intertidal organisms with pelagic larvae are affected by different processes in different habitats. Studies in only one of the habitats may omit many factors influencing a population (Roughgarden *et al.* 1988). In mussels, such as *Perna perna*, this is complicated even more with mussels occurring in or on three habitats *i.e.* in the water column, on algae and on solid rock. Factors influencing mussels in or on any of these habitats may have an important role in structuring present and future mussel beds. For example the number of larvae reaching the shore may be limited by water currents (Scheltema, 1975; Jackson & Strathmann, 1981; Connell, 1985; Minchinton & Scheibling, 1991; Young, *et al.*, 1996), sea temperatures (Muus, 1981) and salinity (Bayne, 1965). Low settlement rates may result in density independent mortality (Connell, 1985; Menge, 1991), and this could influence the structure of the adult mussel bed (Connell, 1985). A single study dealing with just the larval, settling or adult mussel stage will tell little of the actual processes determining the population structure of the mussel bed.

Connell (1985) has suggested that local conditions at a site are responsible for maintaining community structure at a certain level. Physical conditions such as coastal morphology, wave action or currents and biological factors such as predation can remain fairly consistent over time. However many of the processes within a system are affected by stochastic events superimposed on local physical and biological factors (Phillips, 1994). For example unusually heavy settlement of *Perna perna* has resulted in the establishment of mussel beds previously devoid of mussels (Berry, 1978). Dare (1975) working on *Mytilus edulis* observed swarms of starfish (*Asterias rubens)* clear large areas of mussel bed, this phenomenon was not predictable and swarms seemed to appear at random. The results obtained in this study show some very clear patterns regarding mussel populations and certain physical factors. Although these physical conditions tend to shape communities over time, it is inevitable that other stochastic events could lead to dramatic changes in mussel communities. The effect of biological factors must also not be underestimated as these can be very important in influencing the settlement of marine organisms (Scheltema, 1974; Denley & Underwood, 1979; Watzin, 1983; Petersen, 1984; Johnson & Strathmann, 1989; Munday & Keegan , 1992; Dye, 1995) and the structure of adult populations (Seed, 1969b; Dare, 1975; Denley & Underwood, 1979; Munday & Keegan, 1992; Hunt & Scheibling, 1995).

Settlement rates of *Perna perna* are generally very low along the South African coastline, and seldom do the numbers of early plantigrades exceed 100 000 individuals per metre square of shore on the south and east coasts (Phillips, 1994, Harris, *et al.*, in press). In most cases densities are usually below 60 000 individuals per metre square (Chapter 2, this study; Phillips, 1994). At low levels of recruitment density independent mortality results in a correlation between adults and juveniles. However at high levels of recruitment, density dependant mortality uncouples this relationship (Connell, 1985). In this study the density of *Perna perna* early recruits was generally more site specific than it was related to the degree of wave exposure. An important exception was that on the low shore recruit densities on algae were greater on exposed than sheltered sites. This suggests that differences on the mid and high shore between the densities of adult *Perna perna* at exposed and sheltered shores are caused by post-recruitment processes. Wave exposure is probably the post-recruitment factor that influences this pattern. Wave exposure may have a thinning role whereby more mussels are removed by wave action on exposed shores than on sheltered shores. This could encourage mussels on exposed shores to grow faster and reach greater sizes and lower densities as a result of a reduction in food competition (Kautsky, 1982) and increased space for growth (Hughes & Griffiths, 1988). Or, more likely, wave exposure increases growth rates on exposed shores directly (see Lindsay, 1998), and this results in competition for space, slower growing mussels are forced out of the mussel bed and this results in larger mussels at lower densities on these shores because of limitations to packing density (Hughes & Griffiths, 1988). The maximum size attained by mussels on exposed shores exceeds the size of those attained on sheltered shores, and adds support to these theories (Chapter 1, this study).

Decreases in adult mussel densities (within the mussel zone, not at 100% cover, effectively cover) were noted with an increase in shore height, but showed no pattern with respect to exposure. This decrease in mussel density up the shore may be related to an increase in physical stress with increased shore height, but it may also be related to a decrease in the number of plantigrades on the high shore. High shore zones had lower plantigrade densities. This could reflect very high mortality immediately after settlement (*i.e.* within 12-48 hrs), or decreased settlement, caused by decreased tidal submergence *i.e.* fewer larvae reach the shore. The stress caused by aerial exposure on adult as well as juvenile mussels could enhance the effects of low settlement rates and result in a lower cover of mussels on the high shore.

Settlers appear to be more effectively snared by algae than by the mussel bed and this results in more plantigrades occurring on the algal substrata. Theoretically plantigrades grow on algae until a certain size is reached after which the drag caused by wave action removes them from the substratum. Late plantigrades may not find their way onto the mussel bed before being washed to the shore and this could result in very high mortality rates of these mussels. Frequency histograms revealed little evidence for secondary settlement of plantigrades from algae to the mussel bed.

The primary aim of this study was to investigate the effects of wave exposure on naturally occurring *Perna perna* populations. The importance of wave exposure, on adult mussels and to a lesser degree on early recruits has, been highlighted throughout this thesis. A pattern that was repeated in both sections of this study was that wave action strongly influenced mussel populations on the low shore while it did not have as great an effect on the mid and high mussel zones.

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