

# Wave exposure effects on population structure and recruitment in the mussel *Perna perna* suggest regulation primarily through availability of recruits and food, not space

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## Abstract

Recruitment and population structure of *Perna perna* in low shore mussel beds were investigated over 15 months at six sites along the south coast of South Africa. Initial, subjective classification of sites as wave exposed or wave sheltered (three of each) was confirmed using the dissolution of cement blocks to measure average water flux and dynamometers for maximum wave force. Recruitment occurred throughout the year, but recruit (1–5 mm) densities were significantly higher from January to April 1996 on both shore types. Recruit densities were positively correlated with adult (>15 mm) densities for both shore types ( $P < 0.05$ ) but the correlations were extremely weak ( $r^2 < 0.06$  in each case). In areas with 100% cover, adult size (mean and maximum lengths) was greater on exposed sites, but density showed the reverse and was negatively correlated with maximum wave strength ( $r = -0.84$ ). Despite differences in adult densities and sizes, biomass, which is a product of the two, showed no significant difference between the two shore types (ANOVA  $P > 0.05$ ). Thus wave exposure dramatically affects density, recruitment and mussel size, but not recruitment timing or biomass where there is 100% cover, and mediates a three-way interaction among food supply, larval supply and intraspecific competition for space. In contrast to shores with saturation recruitment, mussel biomass here appears to be limited by recruit supply and constraints of food, especially on sheltered shores, while density is regulated through intraspecific competition for space primarily on exposed shores and at small spatial scales.

## Introduction

Of the many factors that shape the intertidal biota, water movement, including the degree of wave exposure, is among the most important, influencing the biology of individual organisms, of species and even the trophic structure of the entire community (McQuaid and Branch 1985; Alvarado and Castilla 1996; Bustamente and Branch 1996). Wave exposure can act on a broad scale by influencing the species composition of communities (Ballantine 1961), and on finer scales by affecting virtually all aspects of a marine organism's life history (Jørgensen 1976; Bertness et al. 1992). As filter feeders, mussels are especially sensitive to wave climate. Differences in food availability, feeding time, suspensoid load and physical removal can have direct effects on their biology (Harger 1970; Harger and Landenberger 1971; Hunt and Scheibling 2000). Indirect effects are often more subtle and can be difficult to isolate from the effects of tidal height, temperature, biotic interactions, etc. (Griffiths 1981; Van Erkom Schurink and Griffiths 1990), but have, nevertheless, been well documented (Menge 1991; Petraitis 1991; Bertness et al. 1992; McQuaid and Lindsay 2000). The most obvious direct negative physical effect of wave action on mussels is dislodgement through lift and drag, with the effects of lift being greater in dense, firmly packed beds than in loosely packed, sparse ones (Denny 1987; Gaylord 2000). The comparison of mussel populations living under different conditions of wave exposure is, however, made difficult by variation in time and space and the degree of interaction that occurs between recruitment, size, growth, density and biomass (Peterson and Beal 1989). In sedentary organisms, particularly those limited by space and food, density-dependent interactions are likely to be strong (Griffiths and Hockey 1987; Hughes and Griffiths 1988), so that spatial dominance in mussels is maintained by recruitment, growth and mortality (Petraitis 1995). The same cover can be maintained either by achieving high densities of small mussels where growth rates have been suppressed by crowding, or by lower densities of larger mussels that have been thinned by physical disturbance, predators or natural mortality coupled with poor settlement.

Wave exposure is likely to affect not only adult survival and growth, but also recruitment. The rate of larval supply can be one of the most important determinants of population processes in marine ecosystems and can have a strong biogeographic component (Harris et al. 1998; Jenkins et al. 2000), but there is evidence that local effects can be more important at smaller scales (McKindsey and Bourget 2000; Lawrie and McQuaid 2001; Connolly et al. 2001; Erlandsson and McQuaid 2004). The prediction of recruitment success, mussel size, carrying capacity, and longevity is important for biological understanding of, and management of bivalve populations (Grant et al. 1993). As these processes are likely to be influenced by wave action, it follows that the vulnerability of a mussel population to exploitation may depend on the degree of wave exposure.

The mussel *Perna perna* is a primary occupier of space on South African shores. It provides habitats for a range of infauna (Hammond and Griffiths 2004) and is extensively harvested for food by subsistence level fisherfolk, often to the point of overexploitation (Lasiak 1991, 1993). *P. perna* experiences higher rates of growth and mortality on relatively exposed shores than on sheltered shores (McQuaid et al. 2000; McQuaid and Lindsay 2000). In this paper, we examine the effects of wave action on the timing and intensity of recruitment in *P. perna*, and on its population structure, particularly the density of juveniles and adults, adult size and total biomass.

## Materials and methods

### Study sites and wave exposure

The south-east coast of South Africa consists of long sandy beaches, which are interspersed with rocky stretches, so that mussel beds occur on scales of tens of metres in length (usually less than 100 m), rather than on 100 m or km scales. Two complimentary approaches to measuring wave exposure were undertaken in the lowest zone of intertidal mussel occurrence at six sites that were subjectively categorised as exposed (Diaz Cross, Kwaai Hoek, Fish River) or sheltered (Mgwalana, Rufanes, Riet River; Fig. 1). Maximum wave force was estimated using dynamometers, modelled on Palumbi (1984). Results were obtained from a total of 39 dynamometers, each deployed for 1 day over three consecutive days, and analysed using one-way ANOVA. Average water movement was estimated by measuring the percentage mass loss of cement blocks ( $50 \times 35 \times 40$  mm) glued to asbestos plates ( $100 \times 100$  mm) and dried to constant weight at  $60^\circ\text{C}$  before and after exposure on the shore for 2–4 days. Weight loss was standardised to 1 day. A total of 45 blocks were used, but losses led to insufficient replication within sites, so that the data could not be analysed statistically.

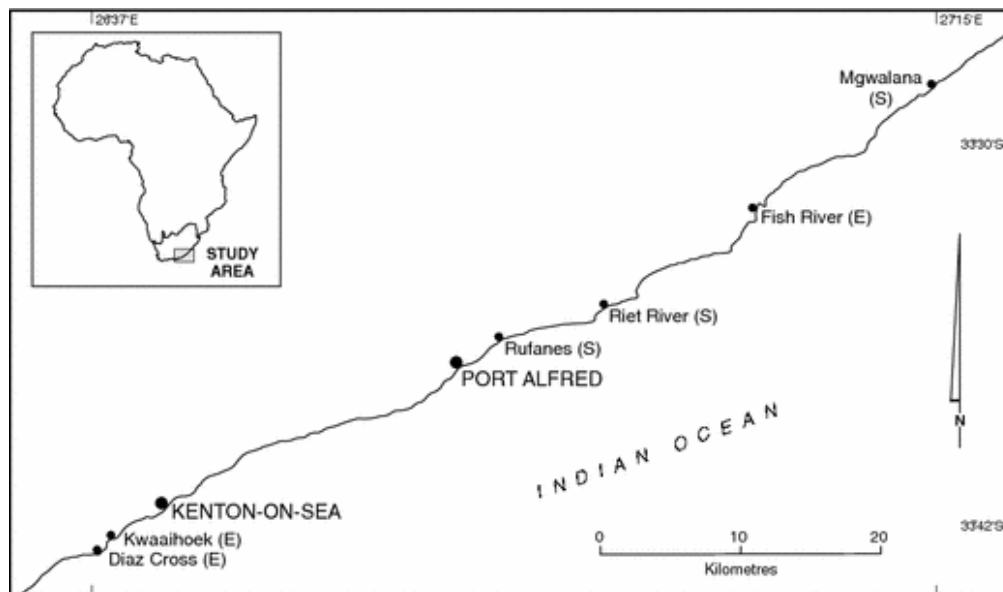


Fig. 1 Location of study area. Study sites are labelled as exposed (E) or sheltered (S)

Mussel beds of 100% cover were sampled at 6 week intervals (11 sampling occasions, for convenience referred to as months) from July 1995 to October 1996. Four quadrats of 10 × 10 cm were placed randomly within areas of approximately 100% cover at each shore on each sampling occasion and all mussels and macroalgae were removed. Macroalgae were carefully searched for small mussels. All mussels >1 mm were measured in the laboratory to the nearest 0.1 mm using the image analysing program, PC Image. The program measured mussels with a high degree of accuracy, giving a regression coefficient of 0.9996 ( $P < 0.05$ ) for values obtained by measuring the same mussels using vernier callipers and image analysis (size range 2–80 mm;  $n = 63$ ). Mussels were divided into adults (>15 mm; above this size population numbers stabilise); juveniles (1–15 mm); and recruits (1–5 mm).

Density data were analysed using ANOVA. In all analyses involving month, this was treated as a fixed factor as sampling was conducted at regular, rather than random intervals. When it was necessary to transform data, this is indicated. Significant results were further examined using Tukey's multiple range test.

#### Timing of recruitment

Data from length frequency distributions were used to determine the months of peak recruitment (1–5 mm) and whether this was exposure-dependent. For each site, the number of recruits in each month was calculated as a percentage of total recruits over the entire sampling period. The data were arcsine transformed and analysed using two-way ANOVA (factors exposure and month, both treated as fixed).

#### Adult and juvenile densities

Linear regression of adult densities (independent) against recruit densities (dependent) was undertaken using least squares analysis of data pooled for each shore for each sampling occasion. Correlation analysis was undertaken to test for significant relationships between mean monthly densities of mussels (juveniles plus adults) and mean monthly lengths of mussels. Sample size was thus  $11 \times 6 = 66$ . A further correlation analysis was undertaken on the relationship between the mean adult (>15 mm) density and the mean maximum wave force ( $N m^{-2}$ ) at each site.

#### Mean and maximum lengths

The mean lengths of adults (>15 mm) were calculated from length frequency data. Data analysis was performed on a UNIX computer using the statistical package, BMDP. A Welch Brown–Forsythe's test established that homogeneity of variance was achieved after  $x^{0.5} + 1$  transformation ( $P > 0.05$  in all cases). Normality was assumed due to the large sample size ( $n = 10,547$ ) (Zar 1996). Mean maximum lengths were estimated using the ten largest mussels for each sampling event at each site. The large, uniform sample size avoids possible problems of bias related to sample size. Both data sets were analysed using two-way ANOVA.

#### Biomass

Regressions of length against dry mass were calculated for each site using mussels collected in March 1995. Regressions were used to calculate biomass from the lengths of collected mussels, allowing total biomass for each quadrat, at each site and on each sampling occasion to be calculated. Data were analysed using two-way ANOVA.

## Results

An ideal ranking of the sites should include wave action measurements repeated under a variety of sea conditions, but analysis of maximum wave forces from dynamometer data confirmed the subjective categorisation of sites. Site had a significant effect on wave exposure ( $F_{5,33} = 14.98, P < 0.05$ ); sites identified as exposed experienced significantly higher wave forces than sheltered sites (Fig. 2).

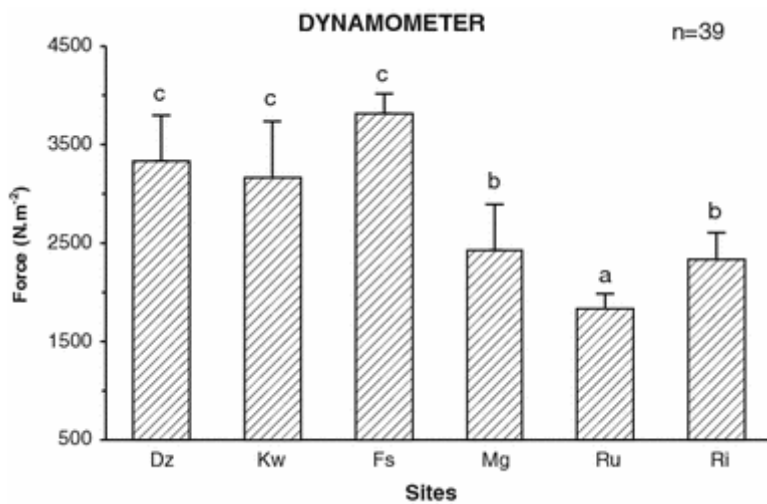


Fig. 2 Mean of maximum wave forces (+SD) measured using dynamometers. Site abbreviations are: Diaz Cross *Dz*, Kwaai Hoek *Kw*, Fish River *Fs*, Mgwalana *Mg*, Rufanes *Ru* and Riet River *Ri*.  $N = 6-8$  per site. Letters indicate homogenous groups ( $P < 0.05$ ) identified using Tukey tests

Of the 45 cement blocks deployed, only 17 were recovered, preventing statistical analysis. Nevertheless these results too supported the original categorisation. The mean percentage mass loss (standardised to 1 day) was greatest at the two exposed sites Kwaai Hoek and Diaz Cross followed by the sheltered sites Rufanes, Mgwalana, and Riet River (Fig. 3). No blocks were recovered from Fish River, indirectly indicating the strong wave action there.

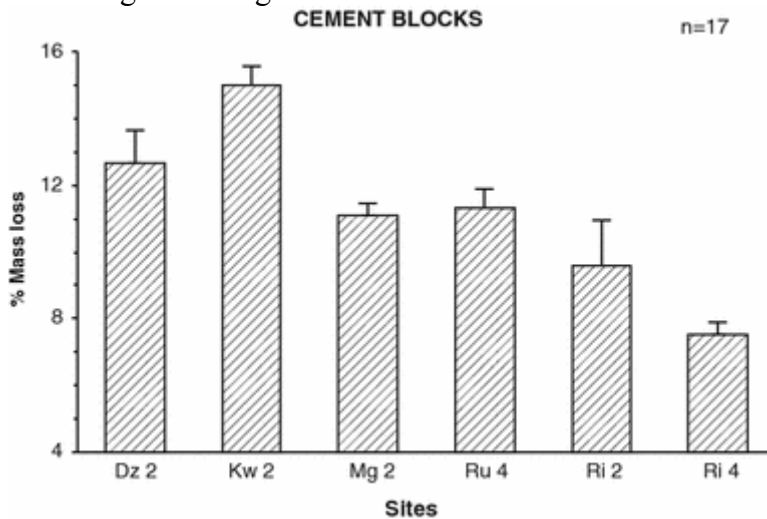


Fig. 3 Mean percentage mass loss per day (+SD) of cement blocks at five sites (abbreviated as in Fig. 2). Blocks were recovered from Dz, Kw, Mg and Ri on day-2 and from Ru and Ri on day four

## Timing of recruitment

Peak recruitment occurred from January 1995 to April 1996 at both exposed and sheltered shores (Fig. 4). Month had a significant effect ( $F_{10,242} = 14.62$ ,  $P < 0.05$ ) on the proportion of total recruits, but exposure did not ( $F_{1,242} = 0.07$ ,  $P > 0.05$ , with no significant interaction). Thus both shore types showed the same patterns of recruitment over time. Tukey's multiple range tests revealed that the number of recruits was significantly higher from January to April 1996, than during most other months ( $P < 0.05$ , Fig. 4). Approximately 60% of all recruits were found during these 4 months. The remaining 40% were approximately evenly distributed throughout the rest of the year.

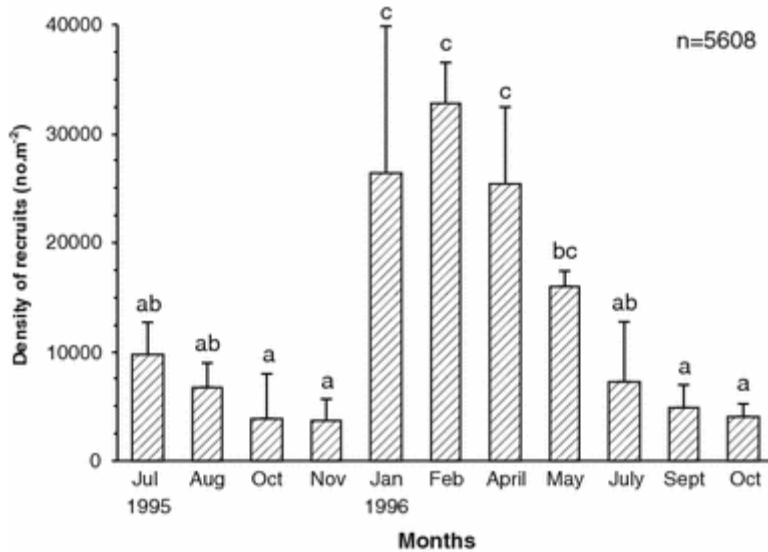


Fig. 4 Mean recruit (<5 mm) densities (+SD), data pooled for all sites for 11 sampling occasions. A total of 44 quadrats per site were sampled. Letters indicate homogenous groups ( $P < 0.05$ )

## Effects of exposure, site and month on densities of juveniles and adults

The mean density of juveniles (1–15 mm,  $\log_e(x + 1)$  transformed data pooled for sites) was significantly higher on exposed shores ( $5,896 \text{ m}^{-2}$ ) than sheltered shores ( $2,986 \text{ m}^{-2}$ ) ( $P = 0.0002$ ; Table 1), though Fish River, an exposed site, had densities similar to those at Riet River, which was sheltered (Fig. 5). The month  $\times$  exposure interaction was not significant.

Table 1 Two-way ANOVA on the effect of exposure and month on juvenile (1–15 mm) and adult (>15 mm) densities

Source of variation	df	Juveniles			Adults		
		MS	F	P	MS	F	P
Exposure	1	14.56	13.87	0.0002	8.11	39.71	<0.0001
Month	10	7.67	7.31	<0.0001	0.21	1.05	0.4006
Interaction	10	0.75	0.72	0.7061	0.26	1.26	0.2558
Residual	242	1.05			0.20		

Data were  $\log_e(x + 1)$  transformed

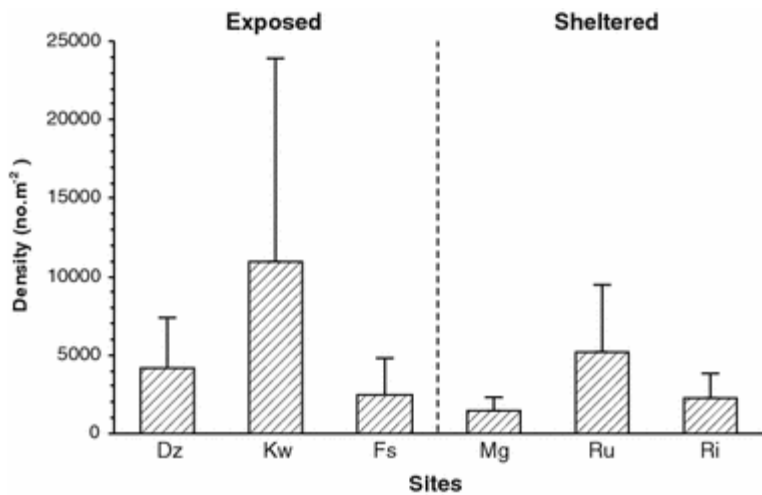


Fig. 5 Mean (+SD) densities of juveniles (1–15 mm) at six sites, abbreviated as for Fig. 2. Data pooled for 11 sampling occasions.  $n = 44$  quadrats per site

Mean adult (>15 mm) densities were significantly higher on sheltered ( $4,796 \text{ m}^{-2}$ ) than exposed shores ( $3,348 \text{ m}^{-2}$ ;  $P < 0.0001$ , Table 1). Densities were highest at Rufanes and Riet River (both sheltered;  $5,495$  and  $4,630 \text{ m}^{-2}$ , respectively), intermediate at Mgwalana (sheltered) and Fish River (exposed) ( $4,264$  and  $4,148 \text{ m}^{-2}$ ) and lowest at Kwaai Hoek and Diaz Cross (both exposed) ( $3,409$  and  $2,486 \text{ m}^{-2}$ ; Fig. 6). Month did not have a significant effect on adult densities, nor was there a significant interaction ( $P > 0.05$ , Table 1).

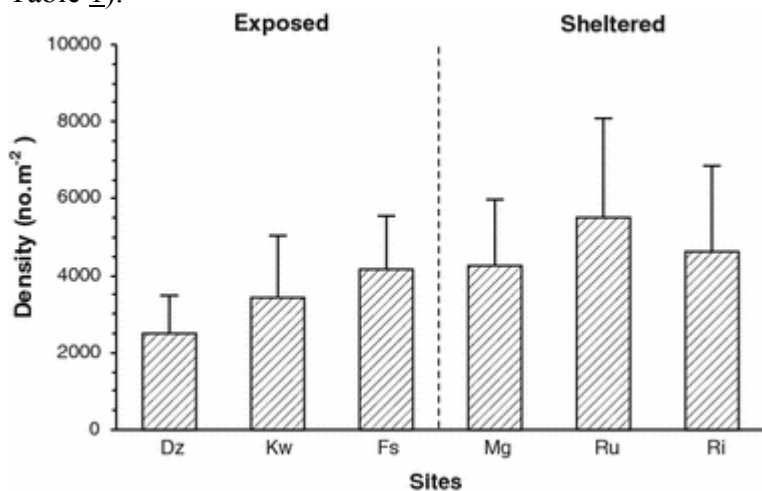


Fig. 6 Mean (+SD) densities of adults (>15 mm) at six sites, abbreviated as for Fig. 2. Data pooled for 11 sampling occasions.  $n = 44$  quadrats per site

On both sheltered and exposed shores, greater adult densities were associated with greater recruit densities (Fig. 7). Although significant ( $P < 0.05$  in both cases), the relationships were extremely weak for both sheltered and exposed shores ( $r^2 = 0.05$  and  $0.06$ , respectively). Generally, exposed shores had higher densities of recruits and lower densities of adults, and vice versa for sheltered shores, giving a higher slope for exposed shores (Fig. 7).

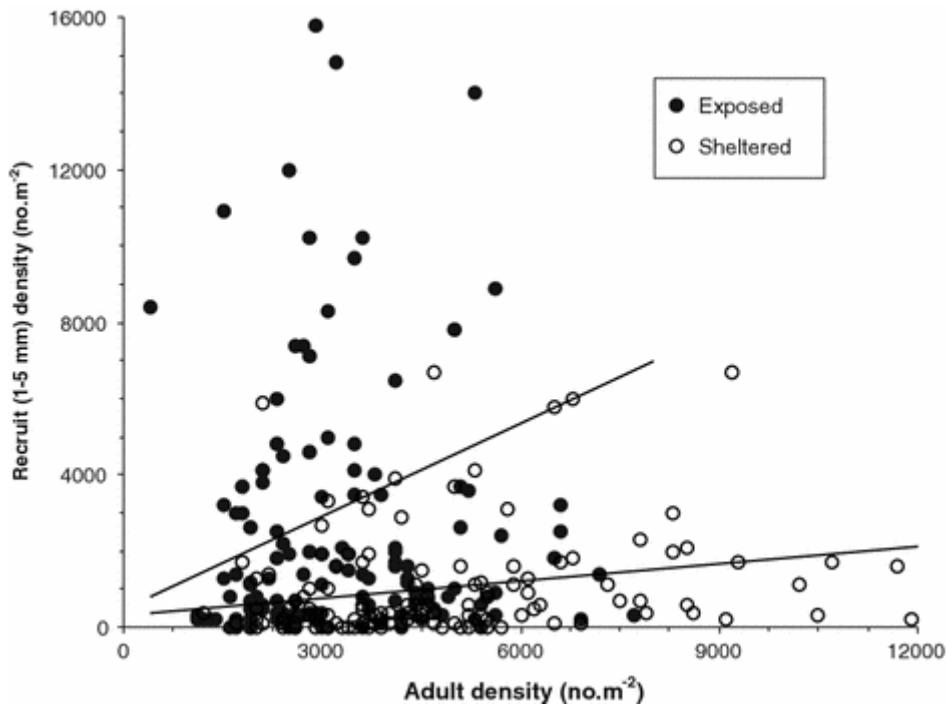


Fig. 7 Linear regression of recruit (1–5 mm) densities against adult (>15 mm) densities for sheltered and exposed shores. Four outlying data points have been excluded from the graph, but not the regression calculations. Exposed,  $y = 0.81x + 503$  sheltered,  $y = 0.15x + 316$   $n = 132$  for each

Mean monthly densities of juveniles + adults (all sites pooled; Fig. 8) were significantly negatively correlated with their mean monthly lengths ( $y = 561,141x^{-1.2963}$ ;  $n = 66$ ;  $r = -0.90$ ;  $P < 0.05$ ), i.e. as densities increased, lengths decreased non-linearly. There was also a clear, significant trend of decreasing density with stronger wave action ( $r = -0.84$ ;  $P < 0.05$ ). Omitting Fish River, which did not fit the pattern well (Fig. 9), raised the  $r$  value to a highly significant 0.99 ( $P < 0.001$ ).

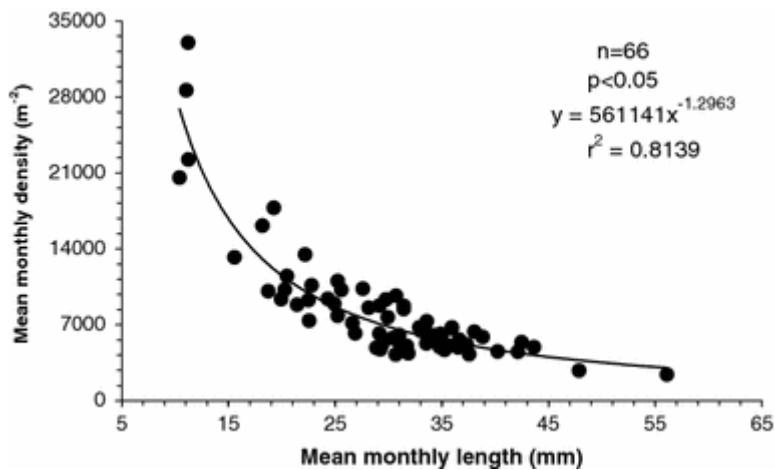


Fig. 8 Regression of mean monthly densities of mussels (juveniles + adults) against monthly mean lengths (juveniles + adults) for all sites pooled

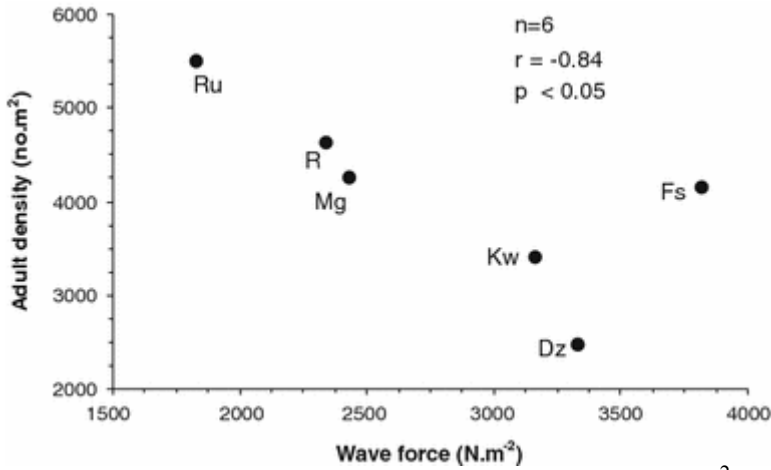


Fig. 9 Correlation of mean maximum wave force ( $\text{N.m}^{-2}$ ) at each site against mean adult density ( $>15$  mm) at each site. Sites abbreviated as for Fig. 2

### Mean and maximum lengths

Mean adult lengths were greater on exposed shores ( $52.9 \pm 23.1$  mm) than sheltered shores ( $41.6 \pm 16.6$  mm;  $P < 0.05$ , Table 2), though there was a significant interaction with month. Site also had a significant effect on mean length (two-way ANOVA,  $P < 0.05$ ). The greatest mean lengths were recorded at Diaz Cross (58.4 mm), followed by Fish River (51.1 mm), Kwaai Hoek (49.3 mm), Mgwalana (43.6 mm), Riet River (42.3 mm) and Rufanes (38.9 mm). Although month had a significant effect on mean lengths, no common trend was apparent among sites (significant month  $\times$  site interaction; Table 2). Likewise, exposure had a significant effect on mean maximum lengths (ANOVA,  $F_{1,638} = 949.52$ ,  $P < 0.0001$ ), which were greater at exposed shores ( $93.6 \pm 7.2$  mm) than sheltered shores ( $75.5 \pm 0.8$  mm; Fig. 10).

Table 2 Two-way ANOVA on the effect of exposure and month on mean adult ( $>15$  mm) length (data were  $x^{0.5} + 1$  transformed) and biomass [data were  $\log_e(x + 1)$  transformed]

Source of variation	df	Length			Biomass		
		MS	F	P	MS	F	P
Exposure	1	1,293.05	610.86	<0.0001	0.08	1.01	0.3160
Month	10	22.52	10.64	<0.0001	0.17	2.13	0.0233
Interaction	10	6.74	3.18	0.0004	0.15	1.82	0.0575
Residual		2.12			0.08		

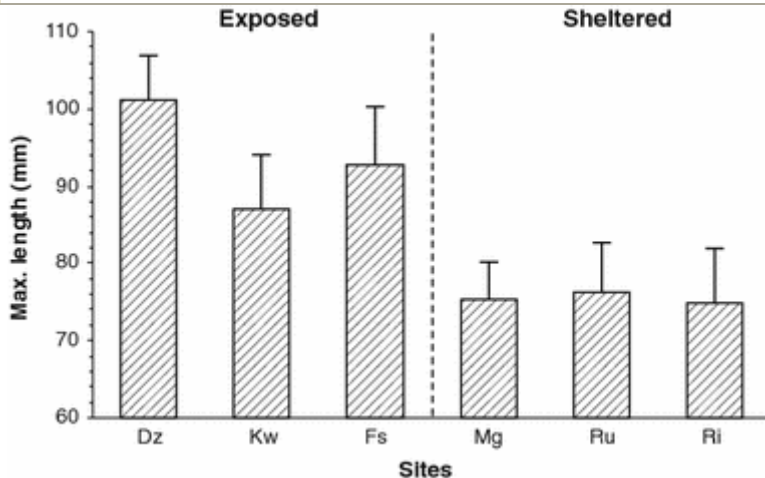


Fig. 10 Mean maximum lengths (+SD) for the ten largest mussels each sampling month for each site. Sites abbreviated as for Fig. 2. Sample size equals 110 mussels per site



## Biomass

Two-way ANOVA showed that both site and month had significant effects on biomass ( $F_{5,198} = 18.56$  and  $F_{10,198} = 2.94$ , respectively,  $P < 0.05$  in both cases), with no significant interaction. When sites were pooled into exposure categories, only month had a significant effect, while exposure did not ( $P > 0.05$ , Table 2); nor did it interact significantly with month.

## Discussion

We examined the effects of wave exposure on population structure and recruitment, recognising that different measures of water movement are required. For larval supply, measurements of bulk flow (estimated by mass loss of cement blocks) are appropriate, while the survival of adults is more likely to be governed by dislodgement by maximum wave forces than by overall water motion (Harger and Landenberger 1971; Denny and Gaines 1990). Both sets of measurements confirmed the *a priori* categorisation of shores and indicated that sites with higher mass flow also had higher maximum wave velocities. The values obtained for maximum wave forces were markedly lower than those found using the same technique in other studies in South Africa (Steffani and Branch 2003; Zardi et al. 2006), but were derived over a single brief period of three consecutive days. While our wave force values cannot be compared directly with those of Steffani and Branch, which were collected throughout a year, they do suggest that our shores do not lie near the extreme end of heavy wave action, where mussel populations are likely to be regulated by physical stress. The use of just two categories simplifies an exposed-sheltered continuum, and the response of mussels to a broader spectrum of wave exposures can be non-linear (Steffani and Branch 2003). Nevertheless, the use of two categories clearly indicated that the degree of wave action profoundly shaped most aspects of population structure and dynamics, though not the timing of recruitment or total biomass, and that this resulted in quite distinct populations on exposed and sheltered shores.

## Mean length and packing density

There are strong species and/or biogeographic influences on the relationship between mussel size and wave exposure. We found mussels on exposed shores were much larger than those on sheltered shores, as has been shown for *Mytilus edulis* in Britain (Jones and Demetropoulos 1968; Seed 1969). However, the reverse is true for *M. edulis* in the USA (Petraitis 1991), and for other mussel species in the Americas (Harger 1970; Alvarado and Castilla 1996). Correlations between size and wave exposure can be driven by a variety of factors including the influence of waves on predators (Menge 1983; Bertness et al. 2003), but predation is believed to be relatively unimportant on the west coast of South Africa (Griffiths and Hockey 1987) and there is no evidence of strong predation on the study shores. Wave-driven mortality can also influence mean sizes as the force required to remove mussels from rocks increases with mussel size, though the relationship differs among species (Harger 1970; Zardi et al. 2006). In the case of *P. perna*, stronger byssal threads are developed under more exposed conditions (Hepburn et al. 1979) and the species survives wave action well (Erlandsson et al. 2006; Rius and McQuaid 2006). A more likely explanation for the effect of exposure on mussel size concerns growth rates. Mean and maximum mussel lengths frequently depend on growth rates (Seed 1969; Jørgensen 1976), so that food availability may be the main factor determining the maximum size that a species or individual can attain (Jørgensen 1976; Kautsky 1982). Although size is not necessarily indicative of growth, for example it may be determined by predator selection (Seed and Brown 1978), *P. perna* grows twice as fast on exposed shores as on sheltered shores (McQuaid and Lindsay 2000) and growth presumably does determine maximum size.

Other authors have reported higher densities of mussels at exposed sites (Jones and Demetropoulos 1968; Beckley 1979; Crawford and Bower 1983), but we found the reverse and this reflects a simple interaction between mussel size and density. Our samples were collected from areas of 100% cover and so represent

packing densities. More small mussels can be packed into a given area than large ones (Griffiths 1981; Hughes and Griffiths 1988) and on our coast, adults were larger (both mean and mean maximum sizes) and at lower densities on exposed shores.

## Recruitment

Recruitment shows strong biogeographic trends around the coastline of South Africa, declining from the west coast towards the east (Harris et al. 1998). Densities of recruits in the study area are generally one or more orders of magnitude lower than in boreal systems (McQuaid and Phillips 2006) and we found that recruits (1–5 mm) occurred in low numbers throughout the year, with strong seasonality. Recruit density was highest from January to April (summer/autumn) and peaked in February. This accords with other studies in the region (Beckley 1979; McQuaid and Lawrie 2005), though seasonality of recruitment diminishes a few hundred km farther east (Lasiak and Barnard 1995). We found no differences between shore types in the timing of maximum recruitment, though there were marked differences in densities of recruits.

In contrast to adults, densities of juveniles (1–15 mm) were significantly higher on exposed than sheltered shores. Recruitment intensity has a huge influence on the structuring of marine communities (Hughes 1990; Menge 1991) and depends on both settlement rates and post-settlement mortality. Petraitis (1991) did not find consistent effects of exposure on the numbers of *Mytilus edulis* recruits in Maine, but recruitment was usually higher on wave-exposed shores, as in our study. Generally, we found adults were more abundant than juveniles, so that overall there was a negative correlation between maximum wave force and total (adult + juvenile) densities. Adults provide suitable settlement areas for juveniles in the form of byssal threads and crevices (Alvarado and Castilla 1996) and, on both exposed and sheltered shores, an increase in adult density was associated with an increase in recruit density. Connell (1985) noted that adult density is positively correlated with recruit density when recruitment is light but uncorrelated when it is heavy. In this study the relationship between adult and recruit densities was very weak, but nevertheless significant. The correlation was no weaker on exposed shores (where there were more recruits) than on sheltered shores, but the slope of the recruit versus adult curve was markedly steeper.

## Biomass

As biomass was estimated from length and density data, observed differences in mass were not the result of variations in gonad mass. Around the Cape of Good Hope, filter feeders, carnivores and omnivores all have significantly higher biomass under exposed conditions (McQuaid and Branch 1985). This contrasts with our findings, but we sampled areas of 100% cover, while the earlier study used random sampling and so dealt with average densities, not packing densities. Although our findings showed strong effects of wave exposure on both densities and sizes of mussels, there was no effect on biomass. Essentially, in areas with 100% cover, the higher densities of mussels on sheltered shores compensated for the larger sizes on exposed shores, resulting in similar overall biomass. So, where mussel beds are monolayered (as at all these sites except Fish River), carrying capacity is relatively constant, though it may be packaged differently. This presumably reflects the effects of faster growth rates leading to stronger intraspecific competition on exposed shores. As a result, exposure does not affect the biomass of mussels because of the compensating interaction of two factors it does influence: density and size.

## Population determination

Populations on both shore types tend to be limited by recruit availability, but this effect is stronger on sheltered shores, while exposed shores experience higher growth rates and higher density-dependent mortality (McQuaid and Lindsay 2000). Greater water flux brings in more food and more larvae, both of which will enhance intraspecific competition for space. Thus wave exposure mediates a three-way balance between food supply, larval supply and competition. More water flux brings in more larvae, but this does

not lead to greater adult densities because faster growth promotes density-dependant mortality. Likewise more bulk flow should bring in more food (Bustamante and Branch *1996a, b*), yet this does not lead to higher mussel biomass because multilayered beds are rare and biomass is simply “re-packaged” as fewer, larger mussels. Presumably multi-layered beds would develop if larval supply were better. Thus these populations are broadly recruit-limited, though in areas with 100% cover they are partly regulated by density-dependant mortality due to intraspecific competition for space.

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