

Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations

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ABSTRACT: The effect of wave exposure on the growth of low-shore populations of *Perna perna* (Linnaeus) was determined using 3 independent approaches at 6 sites on the south coast of South Africa: (1) Individual marking; notches were filed on the growing edges of mussels *in situ*. After 111 d, growth from the mark to the new growing edge was measured. (2) Internal shell-growth bands; mussels from the mark-recapture experiment were used to establish that growth bands are laid down tidally. Unmarked individuals were then used to measure growth over the last 60 tides. (3) Shepherd's length-composition analysis (SLCA); growth rates were determined from length-frequency distributions in 11 samples collected at 6 wk intervals over 15 mo. All 3 approaches showed that growth rate was approximately twice as fast on exposed as on sheltered shores (ANCOVA, $p < 0.05$ in all cases). Mean length for the first year of growth (averaged for the 3 methods) was 47 and 22 mm, respectively. There were, however, considerable differences among methods. Marking provided the lowest estimates of growth rates, and SLCA the highest. The mean mortality index ($Z \text{ yr}^{-1}$) was significantly higher and annual survival rate lower for exposed shores, indicating faster turnover under exposed conditions. Mean longevity on exposed shores (2.6 yr) was only one-third of estimated longevity on sheltered shores (6.7 yr). These findings show that degree of exposure has important interactions with growth and mortality of mussels on the low shore, and that these effects are independent of the effects of exposure on density. The findings also indicate strong bottom-up regulation of mussel populations.

KEY WORDS: Growth · Mortality · Mussels · *Perna perna* · Wave exposure · Bottom-up regulation

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INTRODUCTION

Mussels are an important ecological component of rocky shore communities around the world (Dayton 1971, Menge 1976, Frechette & Bourget 1985, Suchanek 1985, Griffiths & Hockey 1987, Grant et al. 1993, Dye et al. 1994), and often show differences in population structure with different degrees of wave action. This may be a species- or site-specific effect. In some areas, mussels are smaller on shores with strong

wave action (Seed 1969, Jørgensen 1976, Alvarado & Castilla 1996), while in South Africa the opposite is true. Low-shore populations of *Perna perna* on the south coast of South Africa differ markedly between exposed and sheltered shores. Both mean and maximum sizes of mussels are greater on exposed shores (McQuaid et al. in press). This could be due to different growth rates and/or different mortality rates and implies that population dynamics differ between these 2 shore types. Given the importance of mussels as a staple in a subsistence-level fishery in parts of South Africa (Dye 1988, Lasiak & Dye 1989, Lasiak 1991), this could have important implications for management of an exploited natural resource.

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The growth rate of a population in a fishery can be estimated by several methods, and at the outset there is often uncertainty about which approach is best. The primary advantage of using more than 1 technique is corroboration of results from independent measurements. In this study we used 3 independent approaches to measure growth rates of *Perna perna* under different exposure regimes on shores in close proximity to one another. Mortality may be as important as growth in the dynamics of mussel production (Dickie et al. 1984), and our growth findings were coupled with estimates of mortality to clarify the interactions of degree of exposure with growth and turnover.

MATERIALS AND METHODS

Studies were undertaken on the south coast of South Africa in the vicinity of Port Alfred (33°S, 27°E). The sites are approximately 3 to 30 km apart and span 70 km of coastline. This coast has equal semi-diurnal tides, with a maximum tidal range of ~2 m. Most shores are relatively exposed to wave action, but the degree of exposure varies. Six localities were classified both qualitatively and quantitatively, using dynamometers (Palumbi 1984), as either exposed (Diaz Cross, Kwaai Hoek, Fish River) or sheltered (Rufanes, Mgwalana, Riet River; authors' unpubl. data). Exposed and sheltered sites were interspersed along the coast. Growth rates of *Perna perna* (Linnaeus) were measured at each site along a 20 m stretch of low-shore mussel bed with 100% cover. During analysis, normality of data was examined using the Kolmogorov-Smirnov test and homogeneity of variance using the Bartlett test. Growth rates were measured using 3 independent techniques based on fundamentally different approaches: individual marking, growth-band analysis and length-frequency distributions.

Individual marking. Mussels were marked *in situ* at each site ($n = 245$ to 330) by filing a small notch (1 mm) in the growing edge of the shell (Ekaratne & Crisp 1982). After 111 d, the mussels were removed and the initial shell lengths (apex to notch) and the final lengths (apex to growing edge) were measured to the nearest 0.1 mm with vernier callipers. Mussels <25 mm were difficult to handle and were excluded. The sex of each mussel was determined by examination of the gonad colour (Lasiak 1986). Growth rates were calculated separately for males and females at each site.

Growth-band analysis. The frequency with which internal growth bands were laid down in the shell was determined for mussels from the marking experiment, which had been in the field for a known period of 111 d. Ten individuals (34 to 82 mm) were used from each of the Kwaai Hoek (exposed) and Mgwalana

(sheltered) localities. Growth bands were identified using acetate peels, following Pentilla et al. (1988) and Richardson (1989). Growth was measured to the nearest 0.01 mm. The mean number of bands per day was $1.87 (\pm \text{SD } 0.19)$ at Mgwalana and $1.89 (\pm 0.23)$ at Kwaai Hoek, indicating a tidal pattern, i.e. 2 low tides d^{-1} . There was no significant difference in the number of bands laid down at the 2 sites (1-way ANOVA; $F = 0.04$, $df = 18$, $p = 0.85$).

The distance between successive tidally induced bands has been shown to represent the actual linear increase in shell length (Richardson et al. 1990). Once it was established that internal growth bands were laid down tidally (2 d^{-1}), growth over the last 60 bands was measured for unmarked mussels. Three mussels in each of 3 size classes (20 to 25, 40 to 45 and 70 to 75 mm) were used for each site. The initial length and growth over the last 60 tides were measured for each mussel. Failure in the acetate stage, resulting in indistinct slides, made it necessary to pool the results for each exposure category. Thus, the effects of exposure could be ascertained but not of site. The effects of exposure on growth rate were analysed using ANCOVA (with initial length as a covariate) on data from individual marking and on growth-band data. Growth rates from the marking method were also examined at the finer scale of site. Normality and homogeneity were achieved ($p > 0.05$) after $\log_{10}(n+1)$ -transformation.

For the marking and growth-band methods the Gulland-Holt plot (Gayanilo et al. 1996) was used to generate the parameters K (growth coefficient) and L_{∞} (theoretical maximum length), required for the von Bertalanffy growth equation, which converts length data to estimated age (see Sparre & Venema 1993). These parameters were also used to generate values for phi prime (Φ^1), which gives an index of overall growth performance (Pauly & Munro 1984, Tomalin 1995).

Length-frequency distribution. Length frequencies at each site were obtained at approximately 6 weekly intervals (11 occasions) over a period of 15 mo (July 1995 to October 1996). Samples of >200 mussels per site were collected using 4 or 5 10×10 cm quadrats placed randomly in areas of approximately 100% mussel cover. All mussels >1 mm were measured in the laboratory, using an image-analysing program (see McQuaid et al. in press). Regression of lengths obtained for the same individuals (size range 2 to 80 mm; $n = 63$) using vernier callipers and image-analysis gave a regression coefficient of 0.9996.

Shepherd's length-composition analysis (SLCA; Shepherd 1987) was carried out on 3 mm size classes using the software package FiSAT (Gayanilo et al. 1996). L_{∞} was estimated using the Powell-Wetherall plot (Wetherall 1986) on pooled length-frequency data

Table 1. *Perna perna*. Two-way ANCOVA on effect of sex and site on growth rate. Growth and initial length were \log_{10} -transformed

Source of variation	df	SS	MS	F	p
Initial length (co-variate)	1	23.90	24.90	632.30	<0.0001
Site (factor)	5	40.77	8.15	207.01	<0.0001
Sex (factor)	1	0.01	0.01	0.34	0.5656
Interaction of factors	5	0.64	0.13	3.25	0.0065
Residual	710	27.96	0.04		

for each site. The optimal combination of L_{∞} and K for each site was inserted into a von Bertalanffy equation.

Mortality. Size-distribution data were used to generate catch curves for each site, using FiSAT (see Pauly 1990). Total mortality (Z) was estimated from the gradient of the catch curve after excluding the first size class, as it appeared to be undersampled (see Pauly 1990, Pauly et al. 1995). Percentage survival rate per annum and longevity were calculated for each site as: survival rate (%) = $e^{-Z} \times 100$ and longevity = $-\ln(0.01)/M\%$ where M = natural mortality. This assumes no fishing mortality, which is true for the study areas.

RESULTS

The results from all 3 methods showed faster growth rates for *Perna perna* at exposed shores than sheltered shores and in younger mussels than older ones.

Individual marking

Growth rates did not differ significantly between males and females (2-way ANCOVA, $p > 0.05$, Table 1). However, for 1 site, Mgwalana, there was a small, significant difference (1-way ANOVA, $p = 0.045$; male growth > female growth). This resulted in a significant interaction between factors (Table 1). As sex did not generally have a significant effect on the growth rates for the remaining sites, all further analyses were undertaken on combined male and female data. Growth decreased with initial size and was faster at the exposed sites (Fig. 1). One-way ANCOVA

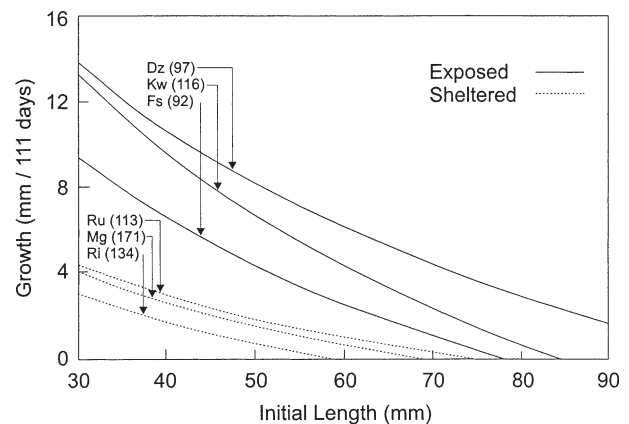


Fig. 1. *Perna perna*. Growth of marked mussels using untransformed data. Exposed sites are Dz (Diaz Cross), Kw (Kwaai Hoek), and Fs (Fish River); sheltered sites are Ru (Rufanes), Mg (Mgwalana), and Ri (Riet River). Sample size is given in parentheses for each site

showed that both site and the co-variate (initial length) had significant effects on growth ($p < 0.05$, Table 2). There were significant differences among all sites (Tukey's multiple-range test, $p < 0.05$), with sheltered sites ranking below exposed sites. Likewise, 1-way ANCOVA on data pooled for sites showed a significant effect for exposure (Table 3A).

The growth parameters Φ^1 and K were significantly higher on the exposed shores (Student's t -tests, $p < 0.05$ in both cases). Although L_{∞} was lower at sheltered sites (Table 4), the difference was not significant ($p > 0.05$). The higher Φ^1 and K values indicate that, on exposed shores, mussels show higher growth performance and reach their maximum theoretical lengths (L_{∞}) faster.

Table 2. *Perna perna*. One-way ANCOVA on relationship between site, initial length and growth rate. Data from mark-recapture method were \log_{10} -transformed

Source of variation	df	SS	MS	F	p
Site (factor)	5	41.45	8.29	207.13	<0.0001
Initial length (co-variate)	1	25.06	25.06	626.16	<0.0001
Residual	716	28.66	0.04		

Table 3. *Perna perna*. One-way ANCOVA on relationship between exposure, initial length and growth rates for (A) Data from individual marking method (data were \log_{10} -transformed) and (B) data from growth bands

Source of variation	df	SS	MS	F	p
A					
Exposure (factor)	1	35.74	35.74	748.66	<0.0001
Initial length (co-variate)	1	20.63	20.63	432.15	<0.0001
Residual	720	34.37	0.05		
B					
Exposure (factor)	1	23.74	23.74	107.92	<0.0001
Initial length (co-variate)	1	9.61	9.61	43.67	<0.0001
Residual	31	6.82	0.22		

Von Bertalanffy growth curves showed that, at 1 and 2 yr of age, mussels were twice as long at exposed as at sheltered sites (Fig. 2). Conversely, individuals of similar lengths were substantially older at sheltered sites.

Growth-band analysis

Sample sizes per shore were low, and results were pooled as exposed or sheltered. Both initial length and exposure had significant effects on mussel growth rate (Table 3B; 1-way ANCOVA, $p < 0.05$). Growth was faster for smaller mussels and under exposed conditions (Fig. 3). Φ^1 , L_∞ and K were all higher at exposed sites (Table 4).

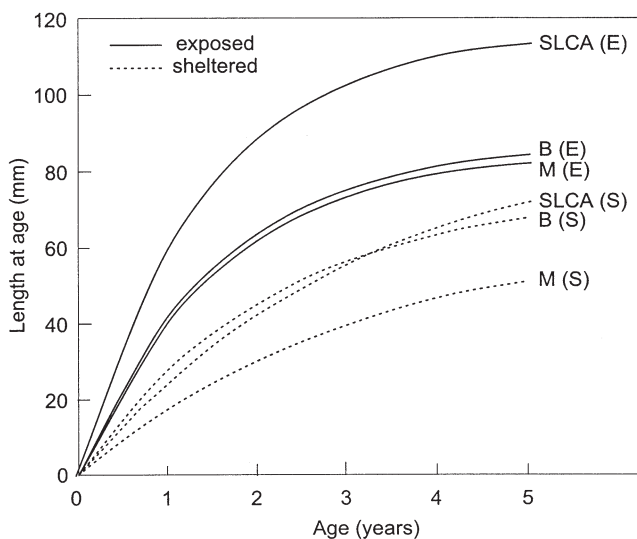


Fig. 2. *Perna perna*. Von Bertalanffy growth curves generated from growth rates obtained by individual marking method (M), growth band (B) and cohort analysis (SLCA) (sites pooled). E = exposed shores; S = sheltered shores. Mean lengths in mm (pooled for all methods) for 1 yr of age are exposed = 47.06 (\pm SD 10.50), sheltered 23.07 (\pm 5.13); and for 2 yr of age are exposed = 71.24 (\pm 14.96), sheltered = 39.14 (\pm 7.88)

Length-frequency distributions

Although cohorts were not easy to identify, there was 1 cohort at all sites which could be traced from recruitment in November 1995/January 1996 through to August/September 1996. Mean length at 1 yr was greater at exposed sites (Fig. 2). Younger mussels grew faster than older ones on both shore types. Φ^1 , L_∞ and K were all significantly higher for the exposed shores than for the sheltered shores (Table 4; t -tests, $p < 0.05$ in all cases).

Φ^1 values were positively correlated with wave force at individual sites (methods pooled) ($r = 0.71$, $p < 0.05$, $n = 6$). Φ^1 , calculated from marking and SLCA, was negatively correlated with adult density ($r = -0.68$, $p < 0.05$, $n = 12$, Fig. 4). Although there was a general trend of decreasing Φ^1 with increasing density ($r^2 = 0.68$), the degree of exposure was important. Packing densities at Mgwalana (sheltered) and Fish River (exposed) were almost identical, but Φ^1 values were very different (Fig. 4).

Table 4. *Perna perna*. Comparison of L_∞ , K , and Φ values generated at exposed and sheltered shores using mark-recapture (MR), growth band (GB), and Shepherd's length-composition analysis (SLCA). Means are presented for mark-recapture and Shepherd's method, as replication of sites was undertaken

Method	L_∞	K	Φ
Exposed			
MR	85.85	0.64	3.69
GB	88.05	0.64	3.70
SLCA	117.44	0.70	3.98
Sheltered			
MR	65.61	0.31	3.14
GB	76.98	0.44	3.42
SLCA	91.94	0.31	3.40

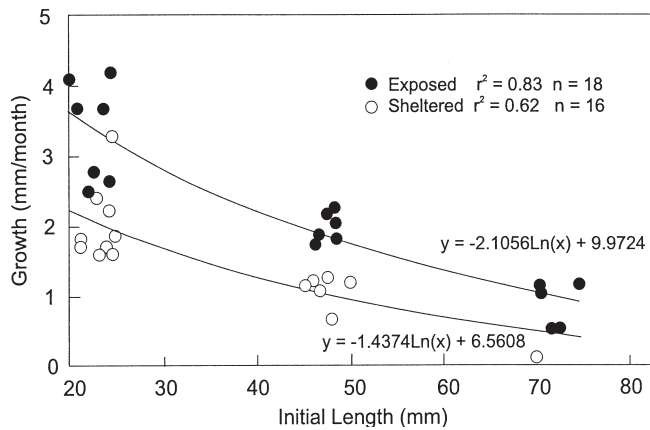


Fig. 3. *Perna perna*. Pooled growth rates for exposed and sheltered sites obtained from growth-band data for a 30 d period (60 tides)

Mortality

Total mortality rates (Z^{-1}) were significantly higher at the exposed shores (Table 5; $t = 4.8338$, $p = 0.0084$). As a result, calculated longevity was significantly higher (in fact 2.6 times greater) for sheltered shores ($t = 3.295$, $p = 0.0301$, Table 5). There was a significant linear relationship between the estimates of growth performance (Φ^1) and corresponding estimates of mortality (Z ; $p < 0.05$, $r^2 = 0.9239$).

DISCUSSION

Intertidal animals can show great plasticity in growth (Seed 1968, 1976, Cerrato & Keith 1992, van Erkom Schurink & Griffiths 1993), and earlier studies, including transplantation experiments, have shown that local conditions strongly influence growth rates of mussels (e.g. Seed 1969, Kautsky et al. 1990, Arnold et al. 1991). Although it is difficult to isolate the effect of 1

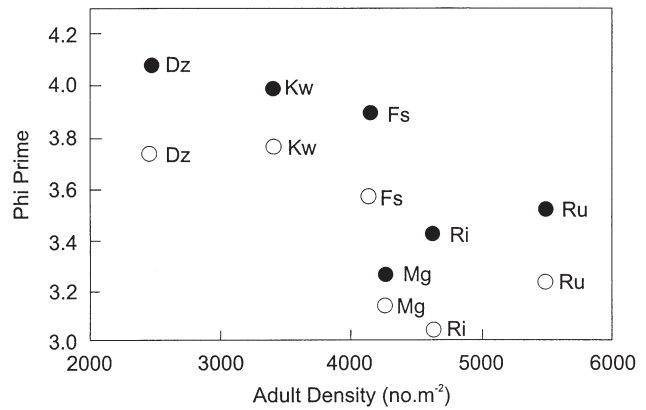


Fig. 4. *Perna perna*. Relationship between mean density of mussels and Φ^1 (index of overall growth performance) obtained for each site using marking method (O) and cohort analysis (SLCA) (●). Site abbreviations as in Fig. 1

particular factor in natural populations, several authors have documented the importance of wave action to growth rates (Jones & Demetropoulos 1968, Raubenheimer & Cook 1990). The effect of wave action may be species specific, as an increase in wave exposure may lead to either increased (van Erkom Schurink & Griffiths 1993), or decreased (Seed 1968, Jørgensen 1976) growth rate. We found that significant differences in growth rates in populations of *Perna perna* separated at scales of 10s of kilometers were unequivocally linked to variations in wave action.

The 3 methods used all showed higher growth rates for smaller mussels, as expected, but they also all showed that mussels grew twice as fast on exposed as on sheltered shores. There were differences in the absolute values obtained, but the 3 methods were ranked in the same order under both exposure regimes (Fig. 2). Length-frequency analysis was laborious and produced the highest estimates of growth rate, while mark-recapture produced the lowest, presumably because filing the growing margin caused a growth

Table 5. *Perna perna*. Total annual mortality (Z) calculated from total length-frequency data obtained over 15 mo. Correlation coefficient for each curve for each site is included

Site	Z^{-1}	r^2	Survival (%)	Longevity (yr)	Mean \pm SD
Exposed					
Diaz Cross	1.82	0.83	16.20	2.53	
Kwaai Hoek	2.12	0.87	12.00	2.17	2.59 \pm 0.47
Fish River	1.48	0.96	22.76	3.11	
Sheltered					
Rufanes	0.94	0.98	39.06	4.90	
Mgwalana	0.51	0.92	60.05	9.03	6.72 \pm 2.11
Riet River	0.74	0.93	47.71	6.22	

check. The use of chemicals such as tetracycline and calcein as internal shell markers offers a better alternative (Dey & Bolton 1978, Kaehler & McQuaid 1999a). Estimates of maximum theoretical length (L_{∞}) obtained by the 3 techniques showed the same ranking as growth estimates: SLCA > growth bands > marking. In fact the largest mussels measured were longer (by up to 10 mm) than the highest estimate of L_{∞} for 3 of the 6 shores.

As well as significant effects of wave action on growth rates, we found a positive correlation between the maximum wave force measured by dynamometers and overall growth performance (Φ^1). Food supply is perhaps the single most important factor in determining mussel growth rates (Seed 1969, Griffiths 1980a,b, Tsuchiya 1980, Newell & Shumway 1993). Greater water flow over the gills increases growth in mussels (van Erkom Schurink & Griffiths 1993), while wave action and tidal currents maintain food in suspension and could make more food available (Griffiths 1980a,b, Bayne 1993). When food is limited, intraspecific competition becomes important and the number of individuals competing for it can affect growth rates (Kautsky 1982, Bertness & Grosholz 1985). We found a negative relationship between growth performance (Φ^1) and the density of adults (>15 mm), which is in accordance with this suggestion. However, our results indicate that this relationship is simply a correlation and that the real effect on Φ^1 is caused by wave action. Although densities at 100% cover were similar at Mgwalana and Fish River (which is much more wave-exposed), Φ^1 values were quite different (Fig. 4). This implies that, although mean packing densities were significantly greater on sheltered shores, the lower growth recorded for these shores was actually a response to wave action and independent of density. Growth performance and density are likely to respond independently to wave action through the latter's effects on food availability and recruitment/wave-induced mortality respectively (Jones & Demetropoulos 1968, Berry 1978, Griffiths 1980a, Eyster & Pechenik 1987, van Erkom Schurink & Griffiths 1993, McQuaid & Lindsay unpubl. data).

Like growth rates, maximum lengths recorded over 15 mo were also greater for exposed shores, as found in a single, detailed survey of 18 sites along this coast (McQuaid et al. in press). Jones & Demetropoulos (1968) found that the average length of blue mussels *Mytilus edulis*, increased as exposure increased, but others have found the opposite (Seed 1969, Jørgensen 1976, Alvarado & Castilla 1996). The predominance of smaller individuals on more exposed shores could reflect greater predation on sheltered shores (Menge 1976), or dislodgment of large mussels by waves on exposed shores (Harger & Landenberger 1971, Griffiths 1981, Paine & Levin 1981, Denny 1987). Our

results indicate that mussels are larger on exposed shores because their much faster growth offsets the higher mortality rates and lower longevity which we measured.

Mortality may be as important as growth in the overall dynamics of mussel production (Dickie et al. 1984) and can vary enormously depending on environmental conditions. Mortality for *Mytilus edulis* ranges from 95 to 100% yr⁻¹ in Morecambe Bay (Dare 1976) and 6 to 7% yr⁻¹ in Scottish lochs (Stirling & Okumus 1994). Our entire study area stretched for approximately 70 km and we found that mortality differed dramatically on shores separated by 10s of kilometers. Longevity showed an inverse relationship with growth (see also Seed 1969, Bayne 1976, Dare 1976, Berry 1978) and was lowest on exposed shores, where growth was faster. The mean annual mortality rate was 83% for exposed shores, but only 51% for sheltered shores. These are comparable to the 74% calculated for *Perna picta* in Morocco (Shafee 1992). One cause of mortality which is known to be greater on exposed shores is shell degradation caused by endolithic cyanobacteria (Kaehler 1999, Kaehler & McQuaid 1999b).

In terms of occupying space, growth may offset mortality in mussels. Small *Mytilus edulis* can double their length in a year, and this is sufficient to compensate for 60% mortality yr⁻¹ without an increase in free space (Petraitis 1995). We found that the higher growth rates of *Perna perna* on exposed shores compensate for the higher mortality rates they experience. This allows them to maintain cover at levels similar to populations on sheltered shores, despite differences in size and density.

This is a second South African example of bottom-up regulation (Menge 1992) of intertidal communities. Bustamente et al. (1995) showed that densities of limpet populations on the west coast depended on the rate of kelp input. In this study we found that growth rates of mussels are affected by wave action (presumably as this dictates rates of food supply), and it has previously been shown that predator biomass in South Africa is correlated with filter-feeder biomass (McQuaid & Branch 1985, see also Menge 1992). Both filter-feeder and total animal biomass are significantly higher on exposed than sheltered shores (McQuaid & Branch 1985), and this may indicate the importance of energy subsidies into the system through the medium of wave action. Higher growth rates on exposed shores also provide a mechanism which can explain the shift in dominance between filter-feeders on exposed shores and algae on sheltered shores recorded for the South African coast (McQuaid & Branch 1985).

The degree of wave action is a continuous variable, but subjective classification of shores as exposed or

sheltered can be linked to real differences in populations. Both growth and mortality rates were much higher for mussels on more exposed shores, resulting in different size structures and suggesting much more rapid turnover rates in exposed populations. The implication is that wave action does not act only as a form of stress on the shore; indeed wave action favours some species (McQuaid & Branch 1984). More importantly, the effects of water movement on food supply for filter-feeders are analogous to the effects of nutrient supply to macroalgae, allowing bottom-up regulation of populations (cf. Menge 1992). A further implication is that shores with different degrees of wave action may also differ in their carrying capacity and the ability of mussel populations to sustain human exploitation.

Acknowledgements. We are very grateful to Jenny Gush, Chris Gray, Carol Simon and Gillian McGregor for their help in the field. We are also indebted to SANCOR, The Foundation for Research Development and the Joint Research Council of Rhodes University for funding.

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Editorial responsibility: Roger Hughes (Contributing Editor), Bangor, Wales, UK

*Submitted: September 22, 1999; Accepted: May 30, 2000
Proofs received from author(s): October 16, 2000*