Coastline topography affects the distribution of indigenous and invasive mussels

Charles E. O. von der Meden[1],*, Francesca Porri[1], Johan Erlandsson[2,3],
Christopher D. McQuaid[1]

**[1]Coastal Research Group, Department of Zoology and Entomology, Rhodes University, PO Box 94, Grahamstown 6140,
South Africa**

[2]Dept. of Systems Ecology, Stockholm University, 106 91 Stockholm, Sweden

**[3]*Present address:* ARONIA Coastal Zone Research Team, Åbo Akademi University / Novia University of Applied Sciences,
10600 Ekenäs, Finland**

ABSTRACT: Coastline topography has important effects on nearshore oceanography, larval transport, settlement and the adult distribution of benthic organisms. The resultant physical regime also influences interactions between invasive and indigenous species. Such interactions can alter intertidal communities dramatically, including the local extinction and replacement of native species. We examined the effect of bays and their associated headlands on the distribution of indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels along 500 km of the south coast of South Africa. Within this single biogeographic region, mussel cover was estimated at 22 sites across 4 bays and the intervening open coast. Given that mussel biomass is greater at intermediate levels of wave exposure and that wave exposure is strongly dependent upon coastline topography, we hypothesised that mussel cover would be greater in bays, and that bays would specifically favour *M. galloprovincialis* which is more easily disturbed by strong waves. The 2 species show partial vertical separation into 3 zones within the lower eulittoral zone. Both species had significantly greater cover within bays. There was, however, an interaction between bay and zone for *P. perna*, and the effect of bays was strongest within the preferred zones of each species. Although the overall effect of bay was stronger for *M. galloprovincialis* than for *P. perna*, this resulted from the strong spatial structure identified for the *M. galloprovincialis* distribution using semivariogram analysis. Overall findings illustrate how coastline topography and local processes operate in synchrony to affect the dynamics of invasive and indigenous intertidal species.

KEY WORDS: *Perna perna* · *Mytilus galloprovincialis* · Bay effect · Coastal morphology · Topography ·
Intertidal zone · Retention · Invasive species

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INTRODUCTION

Marine intertidal populations and assemblages owe much of their complexity and variability to several biotic and abiotic factors operating at widely ranging spatial and temporal scales. For example, intertidal assemblages can be strongly affected by larval supply (Morgan 2001, Underwood & Keough 2001, Porri et al. 2006), and predation, competition and disturbance can influence recruitment, recovery and adult mortality (Keough & Downes 1982, Palmer et al. 1996, Erlandsson et al. 2006). Physical variables, such as wave expo-

sure (Hammond & Griffiths 2004), wind (McQuaid & Phillips 2000), surface rugosity (Petraitis 1990), large oceanographic mechanisms (Shanks 1983) and microhydrodynamics (Pineda 2000), also produce variability in benthic marine populations and communities. Of great present concern is the capacity of invasive species to alter species diversity and community structure due to the way they respond to physical disturbance and interact with indigenous species (Reusch & Williams 1999, Grosholz 2002, Lee & Klasing 2004).

On land and sea, topography influences the forces of wind and water movement that transport propagules

(Wolanski & Hamner 1988, Tackenberg 2003), and so has the potential to influence the structure and dynamics of assemblages. Bays and associated headlands are common features of coastlines around the world, and have a strong influence on coastal oceanography (Geyer & Signell 1992, Gan & Allen 2002). Due to their enclosed or semi-enclosed nature, bays experience different circulation and often experience reduced wave action relative to the open coast. The exposure of intertidal locations to different levels of wave action can affect the distribution, biomass and composition of organisms and the structure of assemblages on rocky shores (Kingsbury 1962, Bustamante et al. 1995, Underwood & Chapman 1998). Although there seems to be a general positive correlation between wave exposure and the overall biomass or cover of intertidal assemblages (Menge 1976, McQuaid & Branch 1984, Bustamante et al. 1997), biomass is usually highest at intermediate levels of exposure (Steffani & Branch 2003, Westerbom & Jattu 2006). At intermediate levels of exposure, the risk of sedimentation is absent and harm to sessile or sedentary organisms via dislodging action of waves is reduced. In contrast, intense water action or extreme occasional physical disturbance, such as storms or floods, can affect community structure heavily by removing large patches of assemblages (e.g. Jenkins et al. 2005, Erlandsson et al. 2006). In such circumstances, biological interactions, particularly between native and invasive species, may play a fundamental role in the re-structuring of intertidal assemblages (Erlandsson et al. 2006).

It has been suggested that the distribution of adult benthic organisms may be determined by coastline topography (here defined as the alongshore shape of the coast rather than any relief features) through larval retention, with greater settlement rates and adult abundances associated with headlands and related embayments (Roughan et al. 2005, Mace & Morgan 2006). For example, Helson & Gardner (2004) showed that planktonic larval densities and recruitment rates of 3 mussel species were significantly greater within Wellington Harbour (New Zealand) than at coastal sites, with adults showing the same pattern.

A reservation about earlier studies is that in each case a single bay is compared to the open coast (e.g. Mace & Morgan 2006), so that there is no replication at the level of 'bay' and conclusions about generality of the effect are difficult. The warm-temperate south coast is 1 of 3 distinct biogeographic regions in South Africa (Bustamante & Branch 1996) and offers the possibility of comparing multiple bays with open coast sites. The south coast is the only area in South Africa where the invasive *Mytilus galloprovincialis* (hereafter *Mytilus*) and the indigenous *Perna perna* (hereafter *Perna*) co-occur, allowing replication of bays and

duplication of mussel species. The 2 species display partial habitat segregation, forming 3 mussel zones on the low shore. The upper zone is dominated by *Mytilus*, the lower zone by *Perna* and the mid-zone is mixed, where the 2 species overlap and co-exist (Bownes & McQuaid 2006).

As a first step to understanding the effect of coastline topography on invasive and indigenous mussels, the present study examines the percentage cover of *Mytilus* and *Perna*, at a number of bay and open coast sites, testing for differences in mussel cover and for species-specific variability between these habitats. Due to the more sheltered nature of bays and because of possible larval retention, we tested the hypothesis that bays will, in general, support greater cover of mussels. Furthermore, we tested whether the weaker attachment strength of *Mytilus* on this coast (Zardi et al. 2006) pre-disposes the species to greater wave-induced losses. Hence, a second hypothesis is put forward: differences in cover between bay and open coast sites will be most pronounced for *Mytilus* because of its weaker attachment strength on this coast. Finally, we tested the hypotheses that there is spatial dependence of variability in the distribution of both *Perna* and *Mytilus* along the south coast of South Africa and that the variability patterns of the 2 species are related.

MATERIALS AND METHODS

Study sites. The south coast of South Africa is generally exposed to high levels of wave action, although some areas (particularly within bays) are comparatively sheltered (McQuaid et al. 2000, Erlandsson et al. 2005). Mussel beds along this coast, both within bays and on the open coast, are mostly monolayered (McQuaid et al. 2000) and discrete, often occupying alongshore distances of no longer than 25 m and separated by sandy beaches (Erlandsson et al. 2005).

A total of 22 rocky shore sites (11 in bays and 11 on the open coast), separated by 10s of kilometres, were selected on the south coast of South Africa between Kenton-on-Sea (34° 41′ S, 26° 40′ E) and Mossel Bay (34° 10′ 18″ S, 22° 7′ 41″ E), spanning a distance of ca. 500 km (Fig. 1; see Appendix 1 for a full list of coordinates). This stretch of coastline includes 4 large 'half-heart' or log-spiral bays (Field & Griffiths 1991), namely Algoa Bay, Jeffreys Bay, Plettenberg Bay and Mossel Bay. All of these are south facing with a headland at the western end and a pronounced 'notch' to the east of the headland. The coast runs eastwards from the notch as a gentle curve, often composed of sandy beaches (Fig. 1). These bays are thus open to the sea rather than semi-enclosed, with distances across their mouths ranging from 16 km (Plettenberg Bay) to
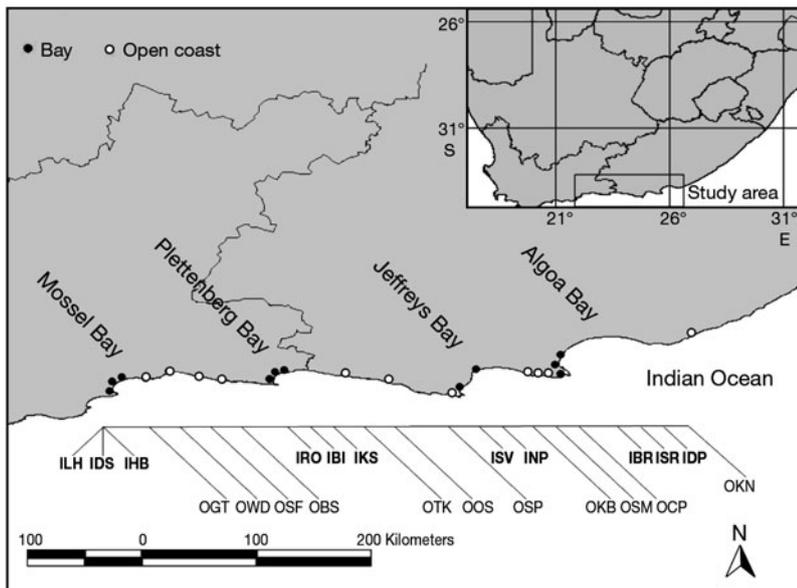
Fig. 1. Study sites along the south coast of South Africa. Bay sites are those in bold text with prefix 'I' and open coast are those with prefix 'O'. For full names of sites and coordinates, see Appendix 1

sity of seawater (1.024 kg m^{-3}), U is the water velocity (m s^{-1}), C_1 is the coefficient of lift (0.88) and A_{min} is the cross-sectional area of a mussel projected perpendicular to the substratum (Denny 1987), as is the case for mussels in beds. The A_{min} used here was that of a medium sized (4.5 cm shell length [SL]) individual of each species, calculated as an ellipse from the shell height and width data given in Zardi et al. (2006). Summer lift forces at each site were then related to the mean summer attachment strengths of 4.5 cm individuals of each species from Plettenberg Bay, obtained from Zardi et al. (2006). Winter lift forces were likewise related, with attachment strength calculated from summer values, based on a 40% increase for each species (Zardi et al. 2007), thereby showing how close each species was to detachment under the given conditions. It is important to note that attachment strengths of both species are consistently greater on the open coast than in bays throughout the year (G. I. Zardi, R. Nicastro, C. D. McQuaid unpubl. data). The use of bay attachment strengths is therefore a conservative measure provided merely to demonstrate the relative differences in attachment strength between species.

Mussel cover. Adult mussel cover was estimated at each site during a once-off survey (28 to 31 March 2006). Intensive temporal cover estimation was not deemed necessary, since mussel bed cover around the coast of South Africa has been stable over scales of 5 yr (Reaugh 2006). At each site, ten 20×20 cm quadrats were haphazardly thrown in each of the 3 mussel zones. These zones were identified by the characteristic patterns of vertical distribution of the 2 mussel species on the south coast of South Africa. *Mytilus* prevalence indicated the high zone; *Perna* prevalence, the low zone; with a mid-zone where the 2 species co-occur. In addition, the low zone was also characterised by the presence of the limpet *Scutellastra cochlear* and/or the alga *Hypnea spicifera*. The percentage cover of primary space occupied by *Mytilus* and *Perna* in each quadrat was estimated visually by 2 different observers using a grid, after moving any obstructing algal canopy aside. Identification of the 2 species was based mainly on shell colour and shape, with *Perna* being brown, while *Mytilus* is more robust and a darker colour (from blue to black) with narrow blue lines (Branch et al. 1994, Bownes 2005).

Data analysis. Each wave exposure parameter (maximal wave force and water flux) was analysed using a

61 km (Algoa Bay). Bay sites were defined as those lying within the notch of the bays; open coast or out-of-bay sites were positioned along the intervening stretches of open coast.

Wave exposure. A bay environment implies a habitat more sheltered from wave action than on the open coast, and levels of wave exposure were quantified at a representative subset of sites. Two approaches were required for this, as both wave force and overall water movement/flux needed to be assessed (Bell & Denny 1994). The former indicates the hydrodynamic forcing to which organisms living in each habitat are subjected; the latter quantifies the flux, diffusion and turbulence of the passing water. Maximal wave force was measured using dynamometers (Bell & Denny 1994), while water movement was assessed by calculating the mass loss from cement balls (adapted from Kaehler 1999). Dynamometers (4 site^{-1} in June and 5 site^{-1} in November) and cement balls (5 site^{-1} in both months) were deployed simultaneously at 5 bay and 5 open coast sites and were collected after 24 h. This was done once in November (summer) and once in July (winter). In an attempt to relate wave force to potential disturbance, lift forces for each species were calculated for bed mussels and related to mean attachment strengths (N) recorded in Plettenberg Bay by Zardi et al. (2006). Lift forces, those acting normal to the substratum due to a difference in pressure created by a wave passing over a mussel bed, were calculated by converting maximal wave force data to velocity values. This was done according to the equation, $F_{lift} = \frac{1}{2}\rho U^2 C_1 A_{min}$, where ρ is the den-

2-way ANOVA comparing the bay with the open coast sites (fixed, 2 levels) in June and November (fixed, 2 levels). Data for both analyses did not need transformation as they were homogenous (Levene's test, p > 0.05). In order to maintain independence of cover estimates, 5 of the 10 quadrats sampled in each zone were randomly allocated to each species. For each species, separate 2-way ANOVAs assessed differences in cover according to bay status and zone. The factor zone (fixed, 3 levels) was crossed against bay status (fixed, 2 levels). Following significant results, post hoc comparisons (Student-Newman-Keuls [SNK]) were carried out to test for homogeneous groupings. Although variances were heterogeneous (Levene's test, p < 0.05), even after arcsine transformation, the large sample size (n = 5 in each zone at each site), which included 6 treatments, together with the fact that the data were balanced meant that the experiment could be considered large enough to allow departure from the assumptions (Underwood 1997, Quinn & Keough 2002). Therefore, analyses of cover were done on untransformed data.

Mean percent cover of the 10 samples for each site was calculated for the 2 zones where each species dominated: the high zone for *Mytilus* and the low zone for *Perna*. This allowed us to estimate the spatial structure of mussel cover along the south coast using the geostatistical technique semivariogram analysis, which estimates the spatial dependence of the variability in a variable (e.g. Dale 2000).

Variability indicates changes in the value of a variable, while heterogeneity refers to the structure in variability across different scales. Instead of using a regular distance between sites, and estimating semivariance as a function of different spatial scales or lags (see e.g. Dale 2000, Erlandsson et al. 2005), we used spatial tags for the different sites (1 to 22 from west to east) to estimate semivariance as a function of closeness/separation of sites. The semivariance was estimated from the sum of differences in mussel cover between sites at each separation: (1) between the sites closest to each other, (2) between sites with 1 site in between and (3) between sites with 2 sites in between, etc. (see Appendix 2 for equations). Fractal scaling analysis was used to estimate heterogeneity of mussel distributions along the coast. The fractal dimension — $D = (4 - \text{absolute slope})/2$ — was calculated from the logarithmic semivariogram, i.e. the regression between semivariance and site separation 1 to 11 (since only up to half of the separation can be used, see Erlandsson et al. 2005). *D* varies between 1 and 2, and higher heterogeneity gives a flatter slope of the regression line in the semivariogram and a higher *D*-value. To detect significant scaling regions in the semivariogram a 3-step procedure was followed (see e.g. Erlandsson et al. 2005 for more details) for each semivariogram: (1) analysis of patterns among residuals (i.e. estimated differences between observed data points and the fitted regression line) was done to distinguish partial regression lines with different slopes and to determine the separation between sites at which the slopes changed; (2) regression analysis of the different slopes; and (3) *t*-tests comparing different slopes.

To describe the relationship between the variability of *Mytilus* and *Perna* cover in the high and low zones, respectively, along the coast, we used cross-semivariogram analysis, which is related to semivariogram analysis (Dale 2000, see equations in Appendix 2). Positive cross-semivariance values indicate a positive relationship between the variables at each separation between sites (i.e. co-variation in abundance), and a negative value indicates a negative relationship. Cross-semivariance values approaching 0 indicate no relationship between variables.

The strength of the bay effect on each species was assessed by calculating the mean absolute differences for each zone: (mean percent cover in bays) – (mean percent cover on open coast), and the ratio of cover in bays to open coast: (mean percent cover in bays / mean percent cover on open coast), for each species in each zone.

RESULTS

Wave exposure

The 2-way ANOVA of maximal wave force showed no significant effect of month ($F_{1,44} = 1.7$, p > 0.05) and no interaction between bay status and month ($F_{1,44} = 4.0$, p > 0.05). However, there was an effect of bay status, with forces being significantly greater on the open coast ($F_{1,44} =, 4.4$, p < 0.05). Mean wave forces ranged from 14.5 N (in June at IDS; Fig. 2a) to 46.24 (in June at OSM; Fig. 2a).

No significant interaction between bay status and month was found for water flux ($F_{1,76} = 0.3$, p > 0.05). Water flux was significantly lower in bays than on the open coast ($F_{1,76} = 110.6$, p < 0.0001). Month also had a significant effect ($F_{1,76} = 4.6$, p < 0.05), with mean water flux in June being lower than in November. Flux values ranged between 8.94 % mass loss (again in June at IDS; Fig. 2b) and 33.4 % mass loss (in June at OSM; Fig. 2b).

Despite the temporal limitation of once-off physical measurements, the lack of interaction effects in both analyses suggests a consistent difference in wave exposure regardless of sampling time, which allows a clear quantitative distinction between the bay and open coast sites used in the present study. Fig. 3 clearly
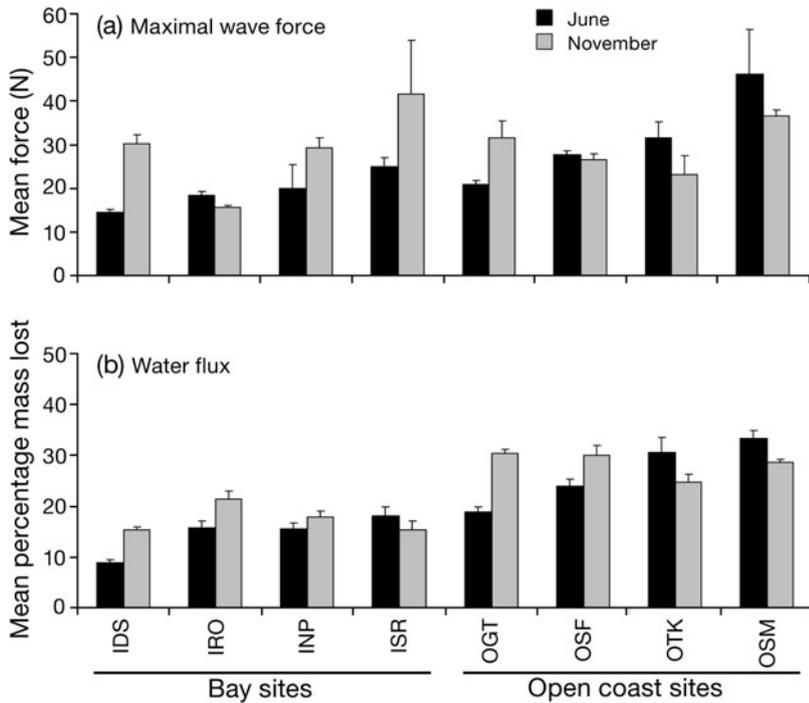
Fig. 2. (a) Mean (+SE; n = 3) 'snap-shot' (November and June) maximal wave force (N) and (b) mean (+SE, n = 5) water flux (percentage mass eroded from cement balls) at selected bay and open coast sites. For full names of sites, see Appendix 1
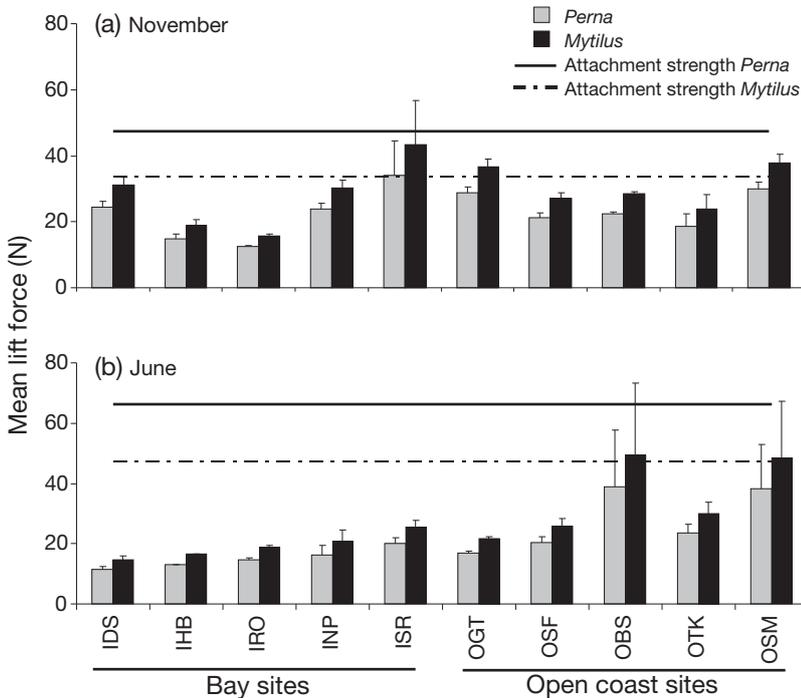

Fig. 3. *Mytilus galloprovincialis* and *Perna perna*. Mean (+SE; n = 5) lift forces acting on bed mussels (4.5 cm in shell length) of each species at selected bay and open coast sites: (a) November, (b) June. Solid and dashed lines indicate attachment strengths of these mussels, as measured by Zardi et al. (2006, 2007) in Plettenberg Bay. For full names of sites, see Appendix 1

shows that *Mytilus* experiences greater lift forces than *Perna*, and, due to *Mytilus*' lower attachment strength (Zardi et al. 2006), it is closer to detachment. November lift forces were greater than those recorded in June (7 of the 10 sites had values >20 N for both species). Surprisingly, the strongest November forces were recorded at a bay site, ISR (*Mytilus* 43.4 N, *Perna* 34.1 N), while the lowest values were recorded at IRO (*Mytilus* 15.8 N, *Perna* 12.4 N). The strongest lift forces were recorded for *Mytilus* in June, at the open coast sites OBS (49.4 N) and OSM (48.5 N), where they exceeded the 'bay' level of attachment strength of this species.

Bay and zone effects

Bays were found to have significantly greater *Mytilus* cover than the open coast ($F_{1,324} = 8.1$, $p < 0.05$; Table 1). As expected, there was a significant zone effect ($F_{2,324} = 31.1$, $p < 0.001$; Table 1), with the greatest *Mytilus* cover occurring in the high zone and decreasing across the mid- and low zones, as confirmed by the SNK test. Fig. 4 illustrates both of the main effects, particularly the striking decrease in mean cover from the high to the low zone over both the bay and the open coast. The figure also shows the large difference in mean high-zone cover between bay (18%) and open coast (9%) shores. Corresponding mean percentages for the low zone, bay (0.4%) and open coast (0.2%), were the lowest. Although Fig. 4 suggests that the greatest difference between bay and open coast is in the high zone, no significant interaction between bay and zone was found ($F_{2,324} = 2.9$, $p > 0.05$; Table 1).

Perna cover was affected significantly by the interaction between bay status and zone ($F_{2,324} = 5.4$, $p < 0.05$; Table 1). SNK test revealed 3 groups: mean bay low-zone cover was the greatest, followed by the open coast low zone, which grouped with the mid-zone (bay and open coast). The

Table 1. Results of 2-way ANOVAs of percentage cover estimates for *Mytilus galloprovincialis* and *Perna perna*. Student-Newman-Keuls (SNK) post hoc test results in both cases. B: bay; OC: open coast; H: high zone; M: mid-zone; L: low zone

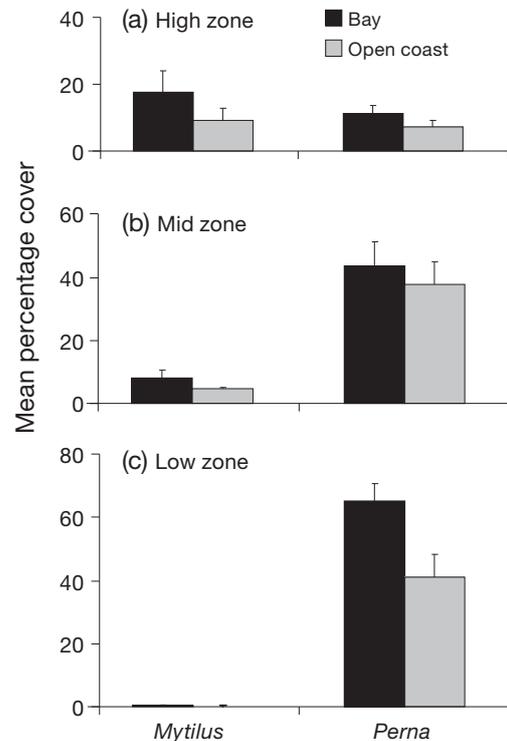| Source	df	MS	F	p
Mytilus				
Bay (B, OC)	1	1237.3	8.1	<0.05
Zone (H, M, L)	2	4736.6	31.1	<0.001
Bay × Zone	2	437.2	2.9	>0.05
Error	324	152.3		
SNK B > OC; H > M > L				
Perna				
Bay (B, OC)	1	1062.3	17.9	<0.001
Zone (H, M, L)	2	5691.7	95.3	<0.001
Bay × Zone	2	3207.3	5.4	<0.05
Error	324	590.5		
SNK B(L) > OC(L), OC(M), B(M) > B(H), OC(H)				

Fig. 4. *Mytilus galloprovincialis* and *Perna perna*. Mean (+SE; n = 220) percentage cover of *M. galloprovincialis* and *P. perna* at bay and open coast sites for each mussel zone: (a) high, (b) mid and (c) low

high zone had the lowest mean cover and, like the mid-zone, cover was similar for the bay and the open coast. Mean *Perna* cover (Fig. 4) increased from the high to low zone, with differences between the bay (65%) and open coast (41%) being most pronounced in the low zone. High-zone percentages were far lower, with means for the bay of 11% and for the open coast of 7% (Fig. 4).

Mussel distribution

Mean cover of *Mytilus* in the high zone ranged from 0 to 50.4%, while *Perna* had a range of 0 to 22.5%. Although *Mytilus* often dominated the upper zone, *Perna* had greater cover at 9 of the 22 sites. These deviations from *Mytilus* dominance were site specific, with no gradient between sites strongly dominated by *Mytilus* and those dominated by *Perna* (Fig. 5). As expected, abundance of *Mytilus* was greatest in the high zone, reaching maximal cover at the 3 sites inside Plettenberg Bay (IKS, IBI and IRO) and at the closest open coast site to the west of Plettenberg Bay (OBS). However, total mussel cover was generally lowest within this zone (Fig. 5).

In the mid-zone, *Perna* dominated nearly all sites, with up to 87.7% cover. The only exception was 1 site in Mossel Bay (IHB), where cover of *Mytilus* was marginally (0.4%) greater than that of *Perna. Mytilus* cover was again highest in and around Plettenberg Bay, while *Perna* cover was greatest at Tsitsikamma (OTK), an open coast site. Other areas of notably high *Perna* cover were Algoa Bay (ISR and IBR) and Jeffreys Bay (INP and ISV) (Fig. 5).

Although there were sites where mid-zone *Perna* cover was greater than low-zone cover, it was generally greatest (2 to 85.4%) in the low zone. *Mytilus* was present at less than half the sites in the low zone and always at ≤2% cover.

The semivariograms showed that variability in the distribution of *Mytilus* along the coast increases with greater separation between sites, i.e. there was less difference in mussel cover among sites that are close together (Fig. 6a). In contrast, *Perna* distribution showed no such spatial structure, with variability being at the same level regardless of the spatial separation between sites (Fig. 6b). Thus, heterogeneity among sites was lower for the *Mytilus* distribution in general (D = 1.84) and in particular for locations within 5 sites of each other (first scaling region: D = 1.74), while the *Perna* distribution showed a random pattern (D = 1.98; random pattern = 1.97 to 2.00; Erlandsson et al. 2005) of mussel cover along the coast (Fig. 6a,b). Still there was a general positive relationship (i.e. positive values; with the spatial structure from the semivariogram also visible in the cross-semivariogram) between *Mytilus* cover in the high zone and *Perna* cover in the low zone, regardless of the separation among sites, i.e. *Mytilus* and *Perna* cover co-varied along the coast (Fig. 6c).
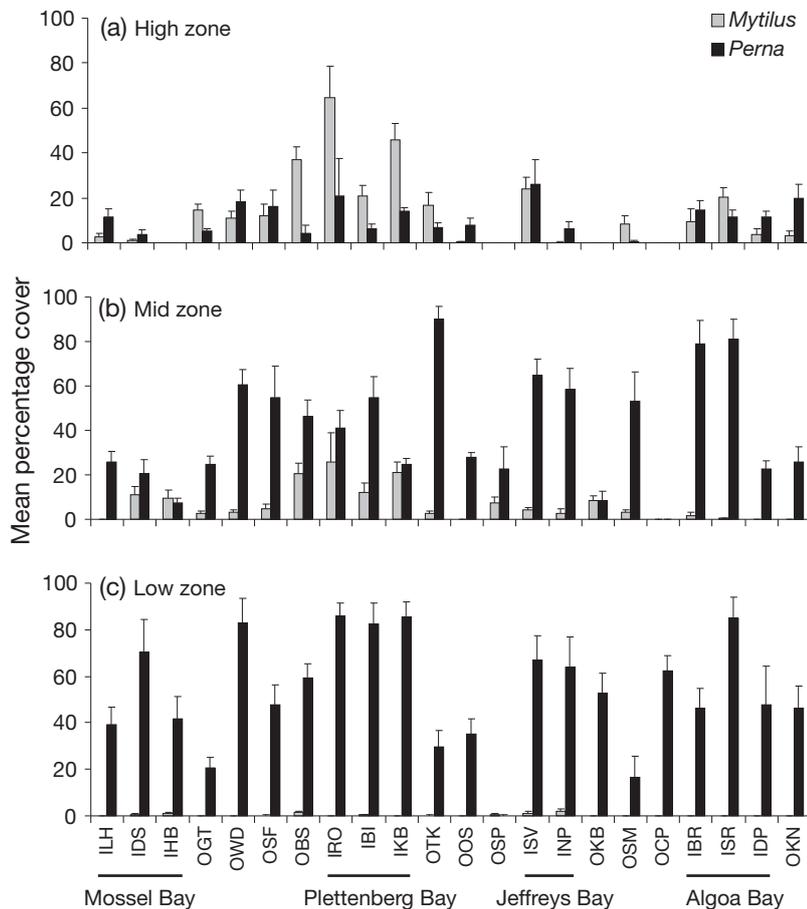
Fig. 5. *Mytilus galloprovincialis* and *Perna perna*. Mean (+SE; n = 5) percentage cover of *M. galloprovincialis* and *P. perna* at each site (west to east) between Kenton-on-Sea (OKN) and Mossel Bay (ILH) for each mussel zone: (a) high, (b) mid and (c) low. On the *x*-axis the site code prefix 'I' denotes bay and 'O' denotes open coast sites. For full names of sites, see Appendix 1

DISCUSSION

The persistent finding of greater mussel abundance in bays than outside bays supports the idea of a general effect of bays on mussel abundance and, therefore, a general effect of coastline topography on adult assemblages. As expected, the difference in abundance was dependent on zone, with the bay effect being most pronounced for each species primarily within its preferred zone: the high zone for *Mytilus* and the low zone for *Perna*. Also striking was the lack of a geographic gradient, with mussel cover being strongly site specific. This was particularly true of *Mytilus*, which lacked a west to east gradient of decreasing abundance, despite having colonised the south coast from the west (C. D. McQuaid unpubl. data) and despite reaching its eastern limit within approximately 100 km of the study area (Robinson et al. 2005). Although cover of the 2 species generally covaried, they showed maximum and minimum cover in different regions of the coast. *Perna* had areas of high cover in and around each of the 4 bays, while *Mytilus* showed a clear centre of gravity around Plettenberg Bay (Fig. 5). The increased variability with larger separation among sites for *Mytilus* cover in the high zone indicates the presence of spatial structure, while no such pattern was evident for *Perna* cover in the low zone (Fig. 6a,b). In fact, the first scaling region found in the *Mytilus* distribution suggests that heterogeneity of *Mytilus* cover was lower amongst closely situated sites (within a 5-site distance) than among sites with larger separation. This pattern mainly arises from the greater *Mytilus* cover at the 5 sites in and around Plettenberg Bay, i.e. at OTK, IKS, IBI, IRO and OBS, where *Mytilus* cover ranged between ca. 20 and 50%. The co-variation between *Mytilus* and *Perna* cover in the high and low zones, respectively, revealed by the cross-semivariogram (Fig. 6c), supports the idea that bays affect these 2 species in a similar way.

Differences in mussel cover between bays and the open coast can be linked to 3 primary mechanisms: wave exposure (McQuaid & Lindsay 2000), larval retention (e.g. Roughan et al. 2005) and larval transport (Shanks et al. 2003). Differences in water temperature and salinity between bay and open coast sites may also be important for larval growth and thus mortality (Schumann et al. 1982, His et al. 1989).
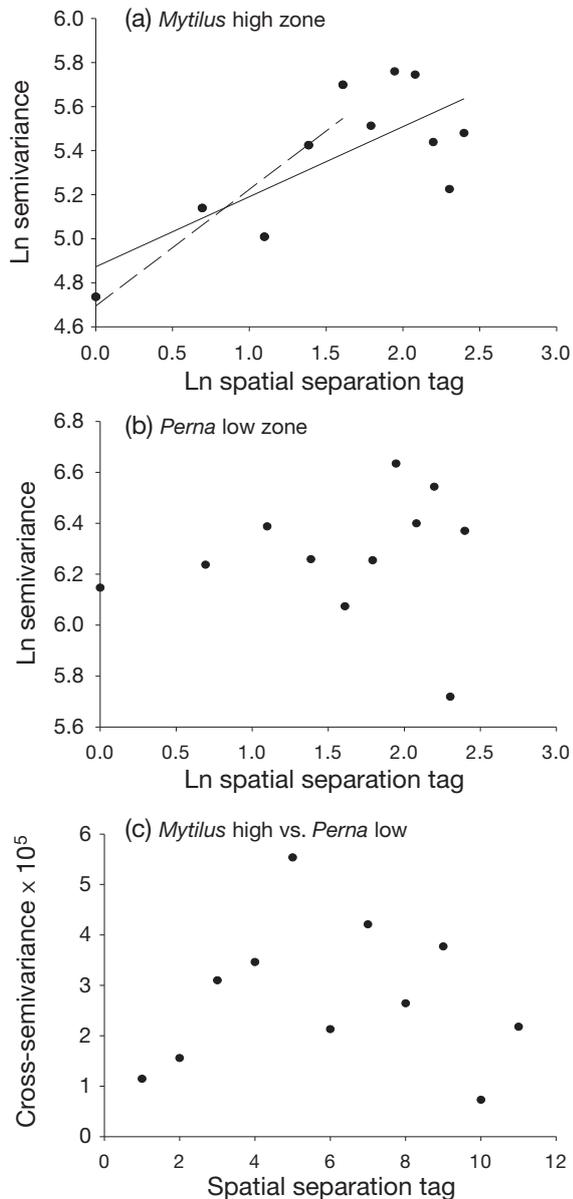
Strength of the bay effect

Absolute differences in mean cover between bay and open coast populations (Table 2) were greater for *Mytilus* (8.1%) than for *Perna* (4.2%) in the high zone, but lower in the mid (*Mytilus* = 3.2%; *Perna* = 6.0%) and low zones (*Mytilus* = 0.2%; *Perna* = 23.8%). The ratio of mean percentage cover in bays to mean percentage cover on the open coast (Table 2) was higher for *Mytilus* than for *Perna* in the high (*Mytilus* = 1.90; *Perna* = 1.60), mid (*Mytilus* = 1.7; *Perna* = 1.6) and low zones (*Mytilus* = 2.0; *Perna* = 1.60). Comparison of the high-zone *Mytilus* ratio to the low-zone *Perna* ratio shows that the strength of the bay effect was greater for *Mytilus* than for *Perna*. However, these results must be interpreted carefully in light of the structuring found in *Mytilus* cover around Plettenberg Bay (see subsection 'Mussel distribution', results of the semivariograms).

Table 2. *Mytilus galloprovincialis* and *Perna perna*. Absolute differences (bay – open coast) and ratios (bay:open coast) of mean percentage cover of *M. galloprovincialis* and *P. perna* in each zone. B: bay; OC: open coast

	Zone	*Mytilus*	*Perna*
Absolute difference			
(B – OC)	High	8.1	4.2
	Mid	3.2	6
	Low	0.2	23.8
Ratio			
(B:OC)	High	1.9	1.6
	Mid	1.7	1.7
	Low	2	1.6

Perna has been shown to have significantly greater growth rates (McQuaid & Lindsay 2000), and to contribute more to total assemblage biomass (Bustamante & Branch 1996), on exposed than on sheltered shores. On the west coast of South Africa, growth, cover and biomass of *Mytilus* have been shown to be highest at intermediate levels of exposure (Steffani & Branch 2003, Hammond & Griffiths 2004). Bays in the present study provide habitats of lower wave exposure relative to the open coast, but are not enclosed. Breaking waves in the bays should keep food particles in suspension, without the negative effects of increased wave-induced mortality that is likely on the open coast. Thus, bays along the south coast may provide an environment of intermediate wave exposure that allows greater mussel cover. The finding that *Mytilus* is more strongly affected by bays than *Perna* (Table 2) correlates well with the predictions of Zardi et al. (2006) and Erlandsson et al. (2006) that, due to its lower attachment strength and greater cross-sectional area, *Mytilus* will be better able to compete with *Perna* under conditions of intermediate wave exposure where the most can be gained from its superior growth and reproductive capabilities. The relationship between lift forces and attachment strength suggests the ability of sites such as IRO in Plettenberg Bay to (at times) provide 'ideal' environments for competitive invasion by *Mytilus*. While it is possible that our second hypothesis is supported only where *Mytilus* occurs in high numbers, it is also plausible that a differential bay effect occurs only at small scales, possibly due to localised synergistic interactions between topography, zonation and disturbance level.

The implications of this study are 2-fold. Primarily, the non-random distribution of mussels in relation to topography provides evidence for strong distinction between bay and open coast habitats. One of the suggestions for this pattern is that populations within bays are demographically more closed systems, with enhanced stock-recruitment relationships (McQuaid & Phillips 2006). Greater larval supply and the often advantageous conditions found in bays also induce

Fig. 6. Logarithmic semivariograms of (a) *Mytilus galloprovincialis* high-zone distribution (whole regression — solid line: $r^2 = 0.54$, $p = 0.01$; first scaling region — dashed line: $r^2 = 0.82$, $p = 0.036$) and (b) *Perna perna* low-zone distribution ($r^2 = 0.01$, $p = 0.74$) along the south coast of South Africa. (c) A cross-semivariogram of *M. galloprovincialis* high-zone versus *P. perna* low-zone distributions

Wave exposure is one of the most important factors affecting the abundances and community composition of sessile intertidal species (Dayton 1971, Bustamante & Branch 1996, Westerbom & Jattu 2006). Mortality of *Perna* is increased on exposed shores (McQuaid & Lindsay 2000), an effect that is more pronounced for *Mytilus* because of its lower attachment strength and wider shell (Rius & McQuaid 2006, Zardi et al. 2006, 2008). Similarly,

greater settlement and recruitment success (Gaines & Bertness 1992). In so doing, positive feed-back may be established between adult and juvenile mussel populations. Alternatively, or in combination with the retention effect, the less severe daily wave action experienced by bays may favour mussel aggregation at bay sites, protecting the beds from wave-induced dislodgment.

Secondly, Branch & Steffani (2004) argue that *Mytilus* has so far had a minimal effect on *Perna*, and predict interactions between the 2 species along the south coast to be 'balanced', but slightly in favour of *Mytilus*. Our data suggest that any change in this balance would be most likely to manifest itself in bay environments. Hence, these sites would be the logical choice for monitoring the interaction between the 2 species. However, the spatial structure observed for *Mytilus* underlines the importance of local-scale effects, for example the case of the Plettenberg Bay area, which supports unusually high *Mytilus* cover. There are documented episodes of serious disturbance in this area, which may have favoured the development of an epicentre of high cover of the invasive species *Mytilus* because of its ability to recolonise faster than *Perna* (Erlandsson et al. 2006, C. E. O. von der Meden pers. obs.).

Thus, understanding interactions between the native and invasive species and making predictions about possible outcomes requires information on a combination of factors. In the case of interaction between *Perna* and *Mytilus* on this coast, the outcome will depend on coastline topography, degree of wave exposure, zone and occasionally extreme disturbances, which can act in different synergies to produce different competitive hierarchies. Our results highlight how scales of investigation and spatial structure of distribution of intertidal sedentary organisms can be important in predicting the colonisation success of invasive species and changes in the composition and organization of rocky shore assemblages.

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Appendix 1. Site codes, full names and coordinates (within respective groups, sites are arranged in the order west to east)

Code	Name	Latitude (°S)	Longitude (°E)	Code	Name	Latitude (°S)	Longitude (°E)
Bay				**Open coast**			
ILH	Lighthouse	34.1811	22.15765	OGT	Glentana	34.0523	22.32204
IDS	Dias Strand	34.1717	22.12804	OWD	Wilderness	33.997	22.56628
IHB	Hartenbos	34.1273	22.11931	OSF	Sedgefield	34.0292	22.76841
IRO	Robberg	34.0991	23.37729	OBS	Brenton-on-Sea	34.0747	23.02041
IBI	Beacon Isle	34.0545	23.37974	OTK	Tsitsikamma	34.0239	23.89663
IKS	Keurboomstrand	34.005	23.45823	OOS	Oubosstrand	34.073	24.22423
ISV	Sea Vista	34.1708	24.83461	OSP	Seal Point	34.2099	24.82544
INP	Noordkloofspunt	34.0263	24.93112	OKB	Kini Bay	34.0223	25.38007
IBR	Bird Rock	33.9841	25.67201	OSM	Skoenmakerskop	34.0412	25.53365
ISR	Shark Rock Pier	33.9799	25.65851	OCP	Chelsea Point	34.0465	25.63431
IDP	Deal Party	33.8996	25.62003	OKN	Kenton-on-Sea	33.6833	26.66667

Appendix 2. Equations for estimation of semivariance and cross-semivariance and for calculation of the fractal dimension

The semivariance ($Y_{(h)}$) was estimated as:

$$Y_{(h)} = 1/(2N_{(h)}) \sum_{i=1}^{N-h} (Z_{i+h} - Z_i)^2 \qquad (1)$$

where N is the total number of data points; $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h, or in this case separated by a certain number of sites; Z_i and Z_{i+h} are the values of a variable (e.g. percent cover of an organism) at points i and $i + h$. Fractal scaling analysis was used to estimate heterogeneity of spatial distributions along the coast. The fractal dimension (D) was calculated from the logarithmic semivariogram (which is a plot of $Y_{(h)}$ vs. h) as:

$$D = (4 - m)/2 \qquad (2)$$

where m is the absolute slope of the regression in the logarithmic semivariogram.

The cross-semivariance ($Y_{(h)}$) was estimated as:

$$Y_{(h)} = 1/(2N_{(h)}) \sum_{i=1}^{N-h} (X_{i+h} - X_i)(Z_{i+h} - Z_i) \qquad (3)$$

where X_i and X_{i+h}, and Z_i and Z_{i+h} are the values of 2 different variables (e.g. percent cover of *Mytilus* spp. and *Perna* spp.) at points i and $i + h$.