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Coastal topography drives genetic structure in marine mussels

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ABSTRACT: Understanding population connectivity is fundamental to ecology, and, for sedentary organisms, connectivity is achieved through larval dispersal. We tested whether coastal topography influences genetic structure in *Perna perna* mussels by comparing populations inside bays and on the open coast. Higher hydrodynamic stress on the open coast produces higher mortality and thus genetic turnover. Populations on the open coast had fewer private haplotypes and less genetic endemism than those inside bays. Gene flow analysis showed that bays act as source populations, with greater migration rates out of bays than into them. Differences in genetic structure on scales of 10s of kilometres show that coastal configuration strongly affects selection, larval dispersal and haplotype diversity.

KEY WORDS: Dispersal · Coastal topography · Connectivity

INTRODUCTION

A key role of genetic studies in ecology lies in discerning scales of propagule dispersal through determination of population connectivity. An understanding of connectivity is central to predicting responses to habitat fragmentation and long-term climate change. For marine organisms with sedentary or sessile adult stages, connectivity depends almost entirely on larval dispersal. Coastal heterogeneity (e.g. bays vs. open coasts) offers a range of environmental conditions and can potentially enhance or limit dispersal of larvae through its effect on direction and speed of flow of the dispersing medium and, thus, alter patterns of population connectivity (Gaines & Bertness 1992), population dynamics (McCulloch & Shanks 2003, Shanks et al. 2003) and the population structure (McKindsey & Bourget 2000) of sedentary marine organisms. Theoretical (Carr et al. 2003) and empirical (Gaines & Bertness 1992, Caley et al. 1996, Swearer et al. 2002, Sotka et al. 2004) studies have reported a wide range of possible dispersal distances for marine larvae, which can vary within the same species (Cowen et al. 2003, Sotka et al. 2004).

Bays are a common topographic feature of marine coastlines, and can act as retention zones. Some studies have observed higher settlement and recruitment patterns in bays than in surrounding areas such as headlands and open coasts (Gaines & Bertness 1992, Wing et al. 1995, Archambault & Bourget 1999, McQuaid & Phillips 2006) and have also reported increased zooplankton abundance in fronts and eddies generated by headlands associated with bays (Rankin et al. 1994, Graham & Largier 1997, Wing et al. 1998). Indirect evidence suggests that species with planktonic larvae could also show genetic differences between bay and nearby open coast populations (Stauber 1950, Loosanoff & Nomejka 1951, Bertness & Gaines 1993). For example, Bertness & Gaines (1993) show that rock temperatures are greater in bays and that barnacle mortality due to thermal stress is higher at bay locations, suggesting a strong signature on the genetic structure of marine populations. Defining the degree of gene flow between bay and open coastal habitats can help to explore mesoscale migration of larvae and consequently give new insight into the dynamics of marine populations.

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Bay morphology influences oceanography, not only by retaining water and, thus, changing circulation patterns and consequently affecting larval dispersal (Roughan et al. 2005), but also by creating different selective environments from those of the open coast. In bays, populations are often subjected to high thermal stress, different food concentrations and lower salinities compared to open coast sites (Ricketts & Calvin 1968, Castilla et al. 2002, Largier 2004). However, wave action, which can be the major cause of mussel dislodgement in the intertidal habitat (Paine & Levine 1981), is higher on the open coast than in bays (Ricketts & Calvin 1968).

In the present study, we test the hypothesis that the influence of coastal topography on larval dispersal and selective regime produces a discernible and predictable effect on the genetic structure of mussel populations. Our null hypothesis is that open coast sites have the same genetic diversity and number of private haplotypes as sites in bays. Mussels disperse by means of planktotrophic larvae that can stay in the water column for a period of weeks to months before settling to the substratum and being recruited into adult populations (Hicks & Tunnell 1995). In addition, wave force was measured at the same sites on 4 different occasions. Mortality rates of *Perna perna* were measured at 2 bay and 2 open coast sites after a storm to determine the role of hydrodynamic stress in genetic turnover.

MATERIALS AND METHODS

Sampling, DNA extraction, amplification, and sequencing. Populations of *Perna perna* (shell length 4 to 5 cm) were sampled at 3 sites inside bays (Plettenberg Bay, Jeffreys Bay, Algoa Bay) and 3 open coast sites (Cape St. Francis, Cape Recife, Kenton-on-Sea; n = 15 each population; Fig. 1) from low intertidal rocky shores of South Africa. These bays are typical of a series of half-heart or log-spiral bays found on this coast. They include a long stretch of sandy beach, with patches of sand-influenced granite rock (Bownes & McQuaid 2006). All populations belong to the same genetic lineage (Zardi et al. 2007). Mussels were opened in the laboratory, and a piece of gonad tissue was examined under the microscope to determine the sex of the animal by the presence of eggs or sperm. Because of doubly uniparental inheritance in mussels (DUI; Zouros et al. 1994), only female individuals were used in the present study. This phenomenon involves the presence of 2 mtDNA lineages, one transmitted from mothers to both daughters and sons, and the other transmitted from fathers to sons. Thus, female mtDNA inheritance is uniparental and male mtDNA inheritance is biparental, as females receive mtDNA from only the mother and males receive mtDNA from both parents (Zouros et al. 1994). Whole genomic DNA was extracted from approximately 1 mm^3 of gonad tissue (attached to the mantle) using a standard phenol-chloroform extraction method and re-dissolved in 50 µl of water. The primers LCOI1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG-3′) and HCO2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′; Folmer et al. 1994) were used in a polymerase chain reaction (PCR; Mullis et al. 1986, Saiki et al. 1988) to amplify a portion of the mitochondrial cytochrome oxidase subunit I gene (mtDNA COI). Amplifications were performed in a 100 µl solution containing 2 µl of genomic DNA extractions, 0.4 µM of each primer, 5 µl of Qiagen PCR buffer, 200 µM of each deoxynucleoside triphosphate (dNTP) and 2.5 U of *Taq* DNA polymerase (Qiagen). The PCR cycling profile comprised an initial denaturation step at 94°C for 2 min, 35 cycles of denaturation at 94°C for 60 s, annealing at 54°C for 60 s, extension at 72°C for 90 s, and a final extension at 72°C for 5 min. PCR products from each individual were purified with a Qiaquick gel extraction kit (Qiagen), and each cycle was sequenced in both forward and reverse directions with the same primers used in the amplification, using the BigDye Terminator v.3.1 Cycle Sequencing kit (Applied Biosystem) and sequenced on an ABI 3100 genetic analyzer.

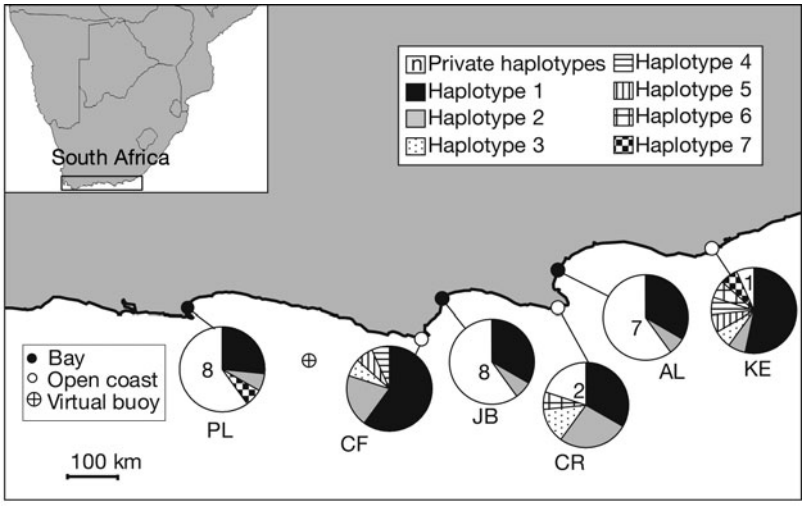

Fig. 1. *Perna perna.* Haplotype frequencies at each sample location (n = 15 each population). PL: Plettenberg Bay, CF: Cape St. Francis, JB: Jeffreys Bay, CR: Cape Recife, AL: Algoa Bay, KE: Kenton-on-Sea

Genetic data analysis. Sequence data (400 bp in length) from 90 *Perna perna* individuals were analysed using the program IM (Hey & Nielsen 2004), which estimates migration rates between 2 populations by taking into account their effective population sizes and times of divergence under the coalescent model (Kingman 1982). This model assumes that an ancestral population has been divided into 2 descendant populations that have maintained gene flow. One group contained all of the bay populations, and the other, all open coast populations. We specified the HKY model (Hasegawa et al. 1985) with an inheritance scalar of 0.25 for mitochondrial DNA. After a number of exploratory runs to determine suitable upper bounds for each model parameter, we used the following search strategy: –b500000 –q1100 –q2200 –qa50 –qu1 –t2.5 –m15 –m210 –fg –n20 –g10.01 –g22 –k20 (Population 1: bay; Population 2: open coast; see program manuals for details). To ensure consistency of results, 10 independent runs with random starting seeds and at least 2 million genealogical steps were performed. The final estimates of the migration rates were calculated using the run with the highest effective sample sizes. Migration rate estimates were converted to number of female migrants per generation by multiplying each population's mean migration rate parameter (m) by its mean effective population size parameter (θ).

ARLEQUIN 3.1 (Excoffier et al. 2005) was used to calculate Φ_{st} values (sequence divergence among haplotypes; Excoffier et al. 1992) among bay and open coast populations using pairwise differences among sequences.

One-way ANOVA was used to evaluate the effects of topography (bays and open coast) on number of haplotypes and the endemism index (see Table 2). The calculation of the endemism index and number of haplotypes was repeated 5 times with approximately half the number of samples (n = 7, randomly chosen). Each time a 1-way ANOVA was performed to test the effects of topography (bays and open coast).

Wave force measurements. During both rough and calm sea conditions, degree of wave exposure was quantified on 4 different occasions (4 October, 9 October, 3 November, 22 November 2006) by measuring maximum wave force using dynamometers modelled on those used by Palumbi (1984). Five dynamometers were placed at each location (Fig. 1) in the lower balanoid zone and removed the following day. Wave height values were obtained from data from a virtual buoy located at 34° 51′ S, 23° 53′ E (90 km perpendicular to the South African southern coastline) as recorded by the USA National Data Buoy Centre (www.ndbc.noaa.gov). Each dynamometer gave a single measurement of maximum wave force during 2 tidal cycles, which was expressed in N m^{-2}. Offshore wave height values on the 4 occasions were correlated with bay and open coast wave forces measured in the field (n = 60 each for bays and open coast). One-way ANOVA was used to evaluate the effects of topography (bays and open coast) on wave force measurements.

Mortality measurements. Mortality rates of *Perna perna* were measured at 2 bay (Plettenberg Bay, Algoa Bay; Fig. 1) and 2 open coast sites (Robberg, Cape Recife). Due to logistic constraints, we were obliged to replace Kenton-on-Sea with Robberg (34° 06′ 08″ S, 23° 22′ 49″ E) as an open coast site at which mortality was measured. At each site, digital pictures of 24 quadrats (20 × 20 cm) were taken before and after a storm (>5 m swells) that hit the study sites on the 18 and 19 March 2007 (South African Weather Service). In each quadrat, 20 mussels were selected, and their mortality was recorded after the storm. A Kruskal-Wallis test was used to evaluate the effects of topography (bays and open coast) on mussel mortality, regardless of the particular cause.

RESULTS

Sampling, DNA extraction, amplification and sequencing

A total of 33 haplotypes of *Perna perna* were identified, 26 of which were private (i.e. present in a single population only; Fig. 1, Table 1). Populations within bays had greater numbers of haplotypes and a higher endemism index than populations on the open coast (Table 2). Haplotype 1 was the most common and, together with Haplotype 2, was present at all locations. The number of shared haplotypes (shared index; Table 2) was higher among open coast than bay populations; only 3 haplotypes were shared between bay and open coast populations.

Genetic data analysis

Analyses of gene flow using the program IM revealed asymmetrical migration rates that were approximately 17 times as high from bay to open coast populations than in the opposite direction (see Fig. 2 for examples of posterior probability plots).

Although there was no significant genetic structure among bay populations and among open coast populations, the amount of genetic structure among the bay populations was nonetheless higher (Table 2). One-way ANOVA showed that the number of private haplotypes and the endemism index were significantly higher in bays than on the open coast (n = 15, $p < 0.01$; Table 2, and n = 7, $p < 0.01$ for each of the 5 runs; data not shown).

Table 1. *Perna perna*. Variable positions in 33 mtDNA haplotypes. Numbers indicate site position along the 400 bp cytochrome oxidase I fragment. Dots denote identity with the first sequence (site abbreviations see Fig. 1)

Haplo-type	Nucleotide position				
	11	1111111111	1111111222	2222223333	3333333
	2455667900	0233445666	6778899022	4567990011	2334578
	1207099325	6359149025	8270328158	9680786956	5072727
1	ACTACTTTCA	TCTACTCCGG	CTTGCTACGT	TCCGTTTTTT	TCTGCTG
2	....	....T.....	....	....	....
3	.T........	..C.T.....	.......T..	....	....
4	....	....	....	C	....
5	....	........A.	....	....	....
6	....	....T.....	....	....	..C....
7	....	....	....	..T.......	....
PL1	.T........	..C.T.....	..C....T..	....	......T
PL2	.......C..	....	........A.	....	....
PL3	.T......T.	....	....	.TT.......	.T.....
PL4	........T.	....	....	.TT.......	....
PL5	...G....T.	....T....A	....	....	....
PL6	...G......	........A.	C	....	....
PL7	......C...	....T.....	T...T.....	....	....
PL8	...G......	........A.	...A.....C	....	....
JB1	...G....T.	.T..T.....	....	....	....
JB2	...G......	........A.	....	....	....
JB3	....	....T.....	....	....	C...GC.
JB4	...GT...T.	....T..T..	....	....	....
JB5	...G......	........A.	T.........	....	....
JB6	...G.G....	...T......	T.........	....	....
JB8	........T.	....T.....	.C........	....	....
JB9	.T........	..C.T.....	....	....	....
CR1	...G....T.	....T.....	....	....	....
CR2	....	.....C....	.....C....	.....C....	....
AL1	....	....T.....	....	....C.....	....
AL2	....	....	....	.......C..	....
AL3	G.........	....	....	....	.T.....
AL4	....	C.........	....	....	....
AL5	..C.......	....	....	....	....
AL6	....	....T.....	....	C	....
AL7	.T.......G	..C.T.....	.......T..	....	....
KE1	........T.	.T..T.TT..	....T.G...	C..A..C.C.	...A...

Table 2. *Perna perna*. Φ_{st} values, number of haplotypes, endemism index and shared index at the sites sampled. Endemism index is calculated according to $E = e/n$, and shared index is calculated as $S = s/n - e$, where e and n are the numbers of putatively endemic haplotypes and the total number of haplotypes detected in each sample, respectively, while s is the number of non-endemic haplotypes shared by at least 2 locations. Site abbreviations see Fig. 1

	Φ_{ST}	Site	No. of haplotypes	Endemism index	Shared index	
Bay	0.032 (p = 0.06)	PL	11	0.73	0.29	0.43
		JB	10	0.8		
		AL	9	0.78		
Open coast	0.008 (p = 0.34)	CF	5	0	0.86	
		CR	6	0.33		
		KE	8	0.12		

Wave force measurements

Regression between offshore wave height and maximum wave forces was significant for both bays and open coast (n = 60, $y = 4.1809e^{0.1859x}$, $R^2 = 0.5094$, $p < 0.01$ for bays; n = 60, $y = 7.066e^{0.2365x}$, $R^2 = 0.7308$, $p < 0.01$ for open coast). One-way ANOVA showed that during 4 different occasions, with an hourly offshore wave height ranging from 1.85 to 5.11 m, maximum wave force (N m^{-2}) was significantly higher ($p < 0.0001$; Fig. 3) at open coast than at bay sites.

Mortality measurements

After a severe storm, mortality rates were significantly higher (Kruskal-Wallis test, $p < 0.0001$; data not shown) at open coast than at bay sites.

DISCUSSION

Our results show that haplotype divergence can develop between bay and open coast mussel populations at mesoscale distances (i.e. distances of 10s of kilometres; see Fig. 1). Coastline topography can have an effect on both oceanographic features and the degree of environmental stress, consequently influencing the degree of larval dispersal and adult population dynamics.

The sheltering effect of within-bay habitats subjects mussels to a less stressful environment (e.g. lower wave action compared to the open coast), leading to lower mortality rates. Growth and mortality rates are much higher for mussels on more exposed shores, while percentage cover declines, suggesting much higher turnover rates in populations exposed to strong wave action (McQuaid & Lindsay 2000, Hammond & Griffiths 2004). Mortality rates after a single storm event

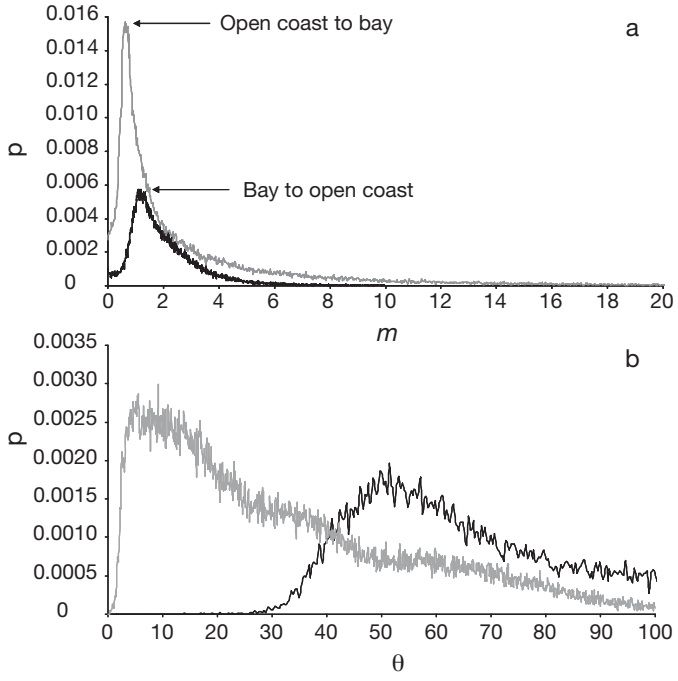

Fig. 2. *Perna perna*. Scaled migration rates and effective population size parameters of *P. perna* populations in bays (black) and on the open coast (grey): (a) pairwise estimates of gene flow and (b) effective population sizes scaled to neutral evolutionary rate using mitochondrial cytochrome oxidase subunit I sequence data. To convert these estimates to number of female migrants per generation, each population's mean scaled migration rate parameter (*m*) was multiplied by its mean effective population size parameter (θ). Marginal posterior probabilities (p) are depicted on the *y*-axis and indicate which values of *m* and θ are the most likely for a particular dataset

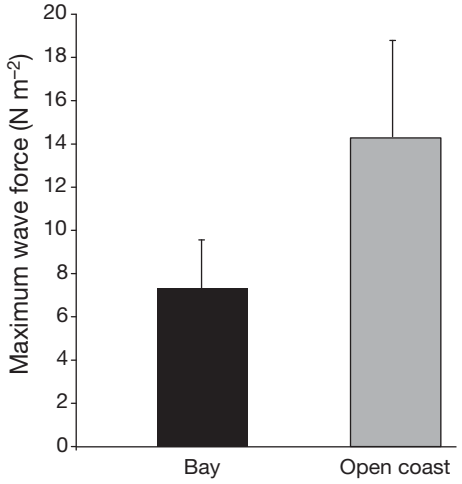

Fig. 3. Mean (+SD) maximum wave force (N m^{-2}) in bays and on the open coast

were much higher on the open coast. It is important to note that other biotic (e.g. predation) and abiotic (e.g. heat stress, sand inundation) factors can be responsible for mussel mortality; however, the close temporal relation between sudden increases in hydrodynamic stress and the observed mortality suggests indirectly but strongly that wave conditions are a determinant factor. In addition, whatever the causes, our results clearly show that mortality rates are higher on the open coast than in bays; this is supported by ongoing field surveys in the same bays showing that monthly mortality rates of *Perna perna* fluctuate in time, but are always significantly higher on the open coast than inside bays (authors' unpubl. data). At a genetic level, greater fluctuation in population sizes may result in the elimination of rare haplotypes (Nei et al. 1975). The high wave action experienced on the open coast subjects intertidal communities to frequent mass mortality, generating free space that can be colonized en mass by larvae in the water column, which comprise a subset of available haplotype diversity. The freeing of space makes primary substrata available for settlers that potentially arrive from different locations, allowing a more frequent and intense gene pool turnover. Genetic differentiation and the shared index showed a high degree of gene flow among open coast populations, while each of the bay populations was quite distinct. The higher gene flow from bay towards open coast populations than vice versa seems to contrast with the retention concept. Larvae do leave bays and colonize the open coast, but the high mortality rates of adult mussels cause more frequent genetic turnover and, consequently, a lower endemism index for open coast populations. Note that mussel larvae in this region are dispersed like passive particles and that the dispersal direction and ranges can be predicted from hydrographic data (McQuaid & Philips 2000).

Good-quality habitats with natality rates higher than mortality rates can be designated as sources, and low-quality habitats with a demographic deficit, as sinks, requiring migration in order to persist (Dias 1996). Adult mussels in bays could act as sources with higher spawning (McQuaid & Phillips 2006), and consequently may have a higher output of larvae than on the open coast. Open coast populations act as sinks, whereas larvae from bay populations are recruited into the free space generated by a more severe selective environment.

Clearly, topography is an important consideration when studying marine connectivity, and our results stress the importance of a careful choice of sampling sites for marine population genetics. For example, it is necessary to take into account possible differences between bays and open coast sites.

Mitochondrial DNA sequences for *Perna perna* indicate a strong phylogeographic break on the southern coast of South Africa, north of East London (approximately 300 km east of our site at Kenton-on-Sea), leading to the formation of an eastern and western lineage

(Zardi et al. 2007). No significant isolation by distance was found within lineages. In their paper there was no comment about a possible effect of embayment on the population genetic structure; however, examining those results retrospectively, it is evident that a higher number of private haplotypes is always associated with, and characteristic of, bay populations. Therefore, it is important to stress that population genetic studies should also consider the possible effects of mesoscale topography.

Topography has effects on both population genetics, through the creation of different selective environments, and on re-colonization patterns. That topography has these effects on genetic structure is remarkable and suggests that populations in bays and on the open coast may have quite different potentials for responding to long-term climate change and/or stochastic local extinctions associated with environmental events. For example, changes in atmospheric circulation due to global warming might also change storm frequency; an increase in the frequency of winter storms has already been observed in coastal oceans (Bromirski et al. 2003), and the trend is expected to continue (IPCC 2001). This could lead to a higher impact of storms on mussel populations, and consequently even higher mortality, on the open coast than in bays.

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