

SIMPLE, SCALE-DEPENDENT PATTERNS EMERGE FROM VERY COMPLEX EFFECTS—AN EXAMPLE FROM THE INTERTIDAL MUSSELS *MYTILUS* *GALLOPROVINCIALIS* AND *PERNA PERNA*

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Understanding species distributions and patterns of coexistence is a basic aim of ecology and fundamental to understanding not only how communities have come to be as they are but also how they will change in the future. This is particularly important when trying to predict biological responses to rapid and extreme changes in environmental conditions. Our perception of community dynamics depends on the temporal and the spatial scales at which we make our observations and the taxonomic resolution we use. Thus, observations and empirical approaches that allow for variability in time and space of multiple, interacting drivers are essential to counteract the assumption that simple patterns of species' arrangement are driven by similarly simple processes. By altering the structure of resident communities, invasive species allow us to observe the development of new distributional equilibria and identify how variation in time and space of biotic and abiotic factors determines patterns of coexistence with native species. Here, we use the example of an invasive and an indigenous intertidal mussel to achieve this. We identify rather simple patterns of distribution of an exceptionally successful marine invasive species, the mussel *Mytilus galloprovincialis*, in its distribution along the coast of South Africa, examining relevant processes at multiple scales. In particular, we draw together research on its coexistence with an indigenous mussel, *Perna perna*. Over the last 40 years, *Mytilus galloprovincialis* has spread along thousands of kilometres of the southern African coast. *Mytilus galloprovincialis* has now reached at least a temporary equilibrium in its eastern limit and in its pattern of coexistence with the native mussel *Perna perna*. We synthesize a comprehensive body of literature on these two species that addresses processes occurring from centimetres to thousands of kilometres and from minutes to evolutionary timescales to develop a more robust understanding of the relative contributions of the deterministic and stochastic processes that structure the dynamics of coexistence. The review shows that the development and maintenance of simple distributional patterns emerge from and are maintained by variations in multiple biotic and abiotic interactions that occur at different and sometimes-nested scales. These include species-specific effects of environmental factors, such as not only high temperatures, wave action, desiccation, and sand scour or sand burial but also biological effects such as predation, parasitism, larval supply, and recruitment. Importantly, abiotic conditions can modulate species interactions, including interference and exploitation competition, so that species-specific responses

to environmental conditions are important. Viewed across the environmental gradient offered by the intertidal landscape, direct interactions include examples of initial facilitation followed by later competitive exclusion. Although in a state of flux at small scales, the present patterns of distribution and coexistence have been relatively stable at larger scales for decades and reflect place-specific balances among the interacting factors, with different factors assuming prominence in different places. Detailed observation and experimentation are necessary to avoid assuming that species' arrangements emerge from a single driver or a few simple drivers, and this has clear implications for attempts to predict species distributions under conditions of climate change. In addition, the same pattern can emerge for different reasons. For example, recruitment of both mussel species is weak in the high mussel zone, but for different reasons. For *Perna perna*, this is because of poor survival of few settlers, while for *Mytilus galloprovincialis*, it reflects good survival of few settlers. With so many interacting factors achieving fluctuating local balances, the surprise is not that the pattern is so clear, but that there is any pattern at all.

Introduction

Ecological problems are often approached by identifying and explaining patterns in the distributions and abundances of organisms. Our ability to detect patterns in nature and the patterns that we perceive are entirely dependent on the scales at which we make our observations, and scale can include not only time and space but also the level of taxonomic resolution considered (Díaz & McQuaid 2014). A fundamental danger is to assume that simple patterns have simple explanations and reflect the outcome of simple processes. Here, we show how extremely simple patterns emerge as the result of a balance among multiple effects, with the balance shifting either subtly or profoundly, in direct or indirect response to differences in environmental conditions among places.

Species live in a balance of positive (Bruno et al. 2003, Espeland & Rice 2007) and negative interactions, with facilitation receiving increasing attention, while competition has received considerable consideration in the past (Bertness et al. 1999, Mack et al. 2000). This perspective is essentially summarized in the concept of succession. In the past, there was a view of some sort of theoretical climax community as the end point of succession, but this perspective changed with the recognition of the dynamic nature of communities and the importance of patchiness and patch dynamics (Pickett 1985). Nevertheless, we have an unconscious or even conscious sense of the balance of nature, with organisms finely adjusted to living with one another. A perception of balanced communities is challenged by the phenomenon of biological invasions during which a non-indigenous species colonizes and eventually may totally dominate a community to which it is introduced. Biological invasions are now perceived as one of the greatest threats to biodiversity (Bax et al. 2003, Molnar et al. 2008, Gallardo & Aldridge 2013). Interestingly, while there are many examples of non-indigenous species causing species extinctions in freshwater systems (e.g., Vitule et al. 2009), there are no examples of such extinctions of indigenous marine species at anything other than local scales (Gurevitch & Padilla 2004, Reise et al. 2006, Briggs 2007, Galil 2007). This contrast may reflect the greater expanse and connectedness of marine systems. Given that biological invasions are studied at relatively short, ecological scales that necessarily preclude evolutionary events, we can use them to gain insight into how species coexist in non-invasive situations.

Among marine species, a few stand out as unusually successful at invading new places, and this can lead to attempts to characterize the properties required to be a successful invasive. In a way, this is obvious; rare species with low fecundities and poor competitive abilities are unlikely to fit the bill. Nevertheless, such attempts have been largely unsuccessful (Lodge 1993, Meiners et al. 2004), and there is little or no consistency in the characteristics of invasive species (Colautti et al. 2006). Instead, it seems to be more useful to examine higher-level characters as it may be possible to identify which broad groups are more likely to be successful as invaders. For example, while there

are a number of marine predators that are successful as invasive species (Abelló & Hispano 2006, Brousseau & Goldberg 2007), most invasions are attributable to low-trophic-level organisms, such as detritivores and deposit-feeders (Byrnes et al. 2007). It may also be possible to identify within-group characteristics that are associated with success as invasive species. For example, among the bivalves, body size seems to be important (Roy et al. 2002). The critical point is that, whatever its nature, whenever a non-indigenous species colonizes a new community, it faces new challenges, interacting with different species under novel environmental conditions. How is this possible, and how are patterns of species distribution rearranged when a community is invaded?

Invasive species belonging to lower trophic levels, such as macroalgae, detritivores, or deposit-feeders, are often ecological engineers that must compete for space with the local species, potentially altering habitat availability for the community as a whole. For example, the Asian brown seaweed *Sargassum muticum* has invaded several temperate regions worldwide, causing major changes to the ecosystem; it forms dense stands that may decrease flow, increase sedimentation, and dampen light and ambient nutrient concentrations for the native algae (e.g., Britton-Simmons 2004), all of which can indirectly affect the native fauna (e.g., Salvaterra et al. 2013).

Among animals, one of the most successful invasive species is the mussel *Mytilus galloprovincialis*. There is considerable literature on *M. galloprovincialis*, reflecting the fact that it has successfully colonized shores on every continent except Antarctica. *Mytilus galloprovincialis* is presumed to be indigenous to the Mediterranean and has an antitropical distribution (Hilbish et al. 2000). It has been recorded from Chile (Toro et al. 2005), to the Black Sea (Gosling 1992), Australia, California (McDonald & Koehn 1988), New Zealand (Westfall & Gardner 2010), Japan (Wilkins et al. 1983, Brannock et al. 2009), England (Hilbish et al. 2002), and southern Africa (Grant & Cherry 1985). The age of individuals found in the sea chest of the South African polar vessel SA Agulhas indicates they have even survived multiple trips into Antarctic waters (Lee & Chown 2007). Identification can be complicated by the fact that its genetic status can be unclear as it can hybridize with the congeneric *Mytilus edulis* (Bierne et al. 2003) and *M. trossulus*, though introgression may be limited (Rawson et al. 1999, Braby & Somero 2006), but the Mediterranean has been the sole source of propagation of *M. galloprovincialis* around the world (Westfall & Gardner 2010).

One could ask what properties it has that allow it to colonize such a wide range of communities. These include the usual suspects of ease of transport either as larvae in ballast water or as adults fouling the hull and seawater chests of ships (Lee & Chown 2007), the ability to compete aggressively for space (Erlandsson et al. 2006), and high fecundity (Van Erkom Schurink & Griffiths 1991, Griffiths et al. 1992). In most cases, the distribution of *Mytilus galloprovincialis* within invaded localities is clear; it occupies the part of the shore normally reserved for indigenous mussels, either exclusively or with habitat partitioning.

The Study System

Of the 86 introduced and 39 cryptogenic species identified from the South African coast, only 4 have been found on the open coast (Mead et al. 2011), and of these, the one with most striking ecological effects is *Mytilus galloprovincialis* (Robinson et al. 2005). The coast of South Africa comprises three broad biogeographic regions, with smaller subregions that can be identified on the basis of the invertebrate fauna (Emanuel et al. 1992). The three major regions correspond with the cool-temperate western coast, the warm-temperate southern coast, and the subtropical eastern coast. The western coast has the lowest levels of species richness, while the southern coast has unusually high levels of both richness and endemism (Awad et al. 2002). *Mytilus galloprovincialis* is believed to have arrived on the western coast of South Africa via shipping relatively recently, probably in the 1970s (Grant & Cherry 1985). It subsequently spread both north and south, with northerly spread being more rapid under the influence of the north-flowing Benguela Current, and its northern limit appears to be between the northern border of Namibia and southern Angola (Hockey & Van Erkom

Schurink 1992, Branch & Steffani 2004, Zupan et al. in press). *Mytilus galloprovincialis* has been enormously successful on the species-poor western coast, where it has become the dominant mussel, replacing the indigenous *Aulacomya ater* and *Choromytilus meridionalis*, and extending from the subtidal to higher on the shore than the indigenous species (Robinson et al. 2007). Consequently, the overall biomass of mussels on these shores has increased (Griffiths et al. 1992), with positive knock-on effects for mussel consumers such as the African oystercatcher (Vernon 2004, Brown & Hockey 2007, Coleman & Hockey 2008), but negative effects for other space occupiers, including not only competing mussels, of course, but also limpets (Griffiths et al. 1992, Steffani & Branch 2003a, Steffani & Branch 2005). More recently, another invasive mussel, *Semimytilus algosus*, has appeared on the western coast. This species was first reported in 2009 and now has a range of approximately 500 km, where it occupies the lower mussel zone, while *Mytilus galloprovincialis* occupies the higher mussel zone (de Greef et al. 2013). As a result, shores on the western coast are now totally altered from their original state by the presence of introduced species.

While the western coast is powerfully influenced by the Benguela Current, the offshore environment of the southern coast is dominated by the warm, oligotrophic Agulhas Current and supports a biota that includes species with Indian Ocean and Atlantic affinities, as well as a high proportion of endemics (Awad et al. 2002). This places *Mytilus galloprovincialis* in an environment that is both physically and biologically quite different from the western coast. On the southern coast, *M. galloprovincialis* interacts with the mussel *Perna perna*, a species that is naturally missing from the western coast. On the southern coast, *Mytilus galloprovincialis* has a much more patchy distribution, being abundant at some sites but rare at others, with an epicentre of abundance around Plettenberg Bay (von der Meden et al. 2008; Figure 1). The southern coast is characterized

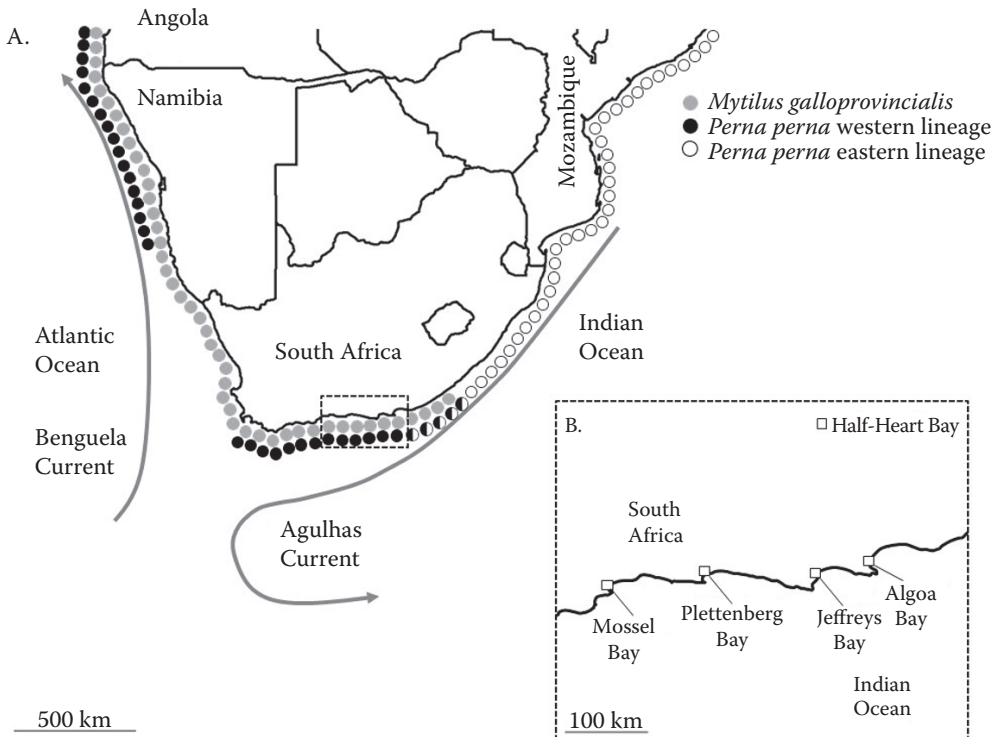


Figure 1 Map of the study area. (A) Main oceanographic features and southern African distribution of *Mytilus galloprovincialis* and of the two genetic lineages of *Perna perna* (as in Zardi et al. 2007a); (B) detail of the southern coast coastal topography, characterized by four half-heart bays.

by a series of log-spiral or half-heart bays, and like *Perna perna*, *Mytilus galloprovincialis* shows generally higher abundances in bays than on the open coast, but the effect is stronger for the invasive species. Finally, within sites, *M. galloprovincialis* shows partial habitat segregation with *Perna perna*, dominating the upper mussel zone, while the indigenous species dominates the lower mussel zone. The two show mixed populations in the mid-mussel zone (Bownes & McQuaid 2006, Hanekom 2008).

Being so widely spread around the globe, *Mytilus galloprovincialis* coexists with species of *Perna* in a number of situations, and in each case, we see essentially the same pattern of habitat segregation: *Mytilus galloprovincialis* occurring higher in the mussel zone and *Perna* lower down. This is true where *Mytilus galloprovincialis* coexists with *Perna perna* in southern Africa (Bownes & McQuaid 2006) and in northern Africa, where both species are indigenous (Abada-Boudjema & Dauvin 1995, Lourenço 2012), as well as where it coexists with *P. canaliculus* in New Zealand (Menge et al. 2007). Ironically, *P. perna* is itself invasive in the Gulf of Mexico (Hicks et al. 2001).

Here, we describe the wide variety of processes involved in establishing and maintaining across- and along-shore patterns of abundance of *Mytilus galloprovincialis* and *Perna perna* along the southern coast of South Africa. We begin with dispersal and recruitment, then examine how the fundamental niches of *P. perna* and *Mytilus galloprovincialis* overlap and how they differ, then consider how the potential distribution of these two species is modified by biological interactions.

Dispersal

The vast majority of marine organisms have external fertilization, followed by the dispersal of planktonic propagules (Thorson 1964), which may be long or short lived, giving them different dispersal potentials (e.g., Kinlan & Gaines 2003). Dispersal of pelagic larvae of benthic animals is a key feature of marine connectivity (Pineda et al. 2010) that is naturally variable and powerfully driven by large- and small-scale hydrodynamics (Pineda 1994, Porri et al. 2014). For intertidal species, the strength and direction of nearshore currents are especially important (Shanks & Eckert 2005, Byers & Pringle 2008). Although dispersal will generally be in the predominant flow direction, there are mechanisms that allow the persistence of upstream populations through self-recruitment: counterflow recruitment during the main reproductive season and recruitment from reversed current flow during the off season (Carson et al. 2011). Byers & Pringle (2008) have identified three main biological features that counteract downstream advection and promote retention and “upstream spill”. These include multiple spawning seasonality, prolonged larval duration, and high fecundity. *Mytilus galloprovincialis* exhibits all of these to a greater extent than some of the native mussel species with which it interacts (Van Erkom Schurink & Griffiths 1991, Wonham 2004), although not *Perna perna*. Scales of dispersal also depend of course on larval duration. For *Mytilus galloprovincialis*, this is believed to be a matter of weeks (Bayne 1975), and we assume it is similar for *Perna perna* so that for coexisting populations, we would expect similar dispersal of the two species. In fact, it is possible that this is not the case. We discuss below, the fact that the two species show differences in the timing of reproduction (Zardi et al. 2007b), and it is possible for this to result in differences in dispersal vectors (Carson et al. 2011).

Any population must be capable of recruitment to sustain itself, and recruitment may be an especially important driver of mussel abundance in South Africa. Densities of recruits tend to be extremely low compared to many other parts of the world (McQuaid & Phillips 2006), so that these populations may be limited by recruitment rates rather than space or food (McQuaid & Lindsay 2007, Reaugh-Flower et al. 2011). We examine settlement and recruitment of *Perna perna* and *Mytilus galloprovincialis* across three nested spatial scales as this forms the first step in establishing patterns of abundance of the two species.

Recruitment within shores

Mytilus galloprovincialis has much higher levels of fecundity than the indigenous South African mussels (Van Erkom Schurink & Griffiths 1991), and this is energetically balanced against the need for attachment to resist wave action; attachment is markedly stronger in *Perna perna* (see 'Abiotic drivers' below). On the southern coast, coexisting populations of the two species also differ in the timing of spawning (Zardi et al. 2007b), and studies elsewhere have shown how the timing of reproduction influences population connectivity if the currents affecting eggs and larvae change regularly (Carson et al. 2011). This implies that the timing of settlement will differ between these species. This has not been tested for the southern coast, although in Namibia, the two species show synchronized recruitment (Reaugh-Flower et al. 2011).

A high proportion (>60%) of mussel larvae settle on macroalgae on these shores (McQuaid & Lindsay 2005). This is likely to be linked to the need to avoid predation by filter-feeding adults and might be interpreted as supporting Bayne's (1964) primary/secondary hypothesis. This was developed for *Mytilus edulis* in the United Kingdom and postulates primary settlement on macroalgae followed by a period of growth, detachment, and secondary settlement among adult beds. In fact, it seems impossible to test this directly as it is not feasible to mark or track mussel recruits as they disappear from macroalgae, but several lines of indirect evidence indicate that the vast majority of larvae settling on algae in South Africa are lost to the population (Erlandsson et al. 2008).

Where overexploitation of mussels results in their replacement by extensive algal beds, as occurs widely in parts of South Africa (Lasiak & Dye 1989, Dye 1992), settlement of larvae on macroalgae and subsequent loss of recruits as they grow may be a mechanism preventing recovery of mussel beds (Erlandsson et al. 2011). This is linked to spatial structure in *Perna perna* beds. Adults show no spatial structure on topographically unstructured shores, but distinct spatial structure on topographically structured shores. Adult mussels and algae show a strong negative relationship, presumably because of competition for space, with mussels more associated with depressions, increased slope, and orientation towards waves (Erlandsson et al. 2005). While plantigrades occur on both macroalgae and adult mussels and exhibit no spatial structure, larger recruits disappear from algae and are found only among adults, exhibiting the same spatial structure as adults do (Erlandsson & McQuaid 2004). Consequently, recruits often show significant, if weak, relationships with adult densities (McQuaid & Lindsay 2007, Reaugh-Flower et al. 2011).

Experiments linking the spatial complexity of mussel beds and rates of recruitment across scales ranging from kilometres to centimetres indicated that a high proportion of the variability in recruit densities occurs at very small (<10 cm) scales. This proportion increases as recruits age and disappear from macroalgae. As a result, it seems that recruitment is not directly affected by the physical complexity of mussel beds, but rather that recruitment influences complexity (Lawrie & McQuaid 2001).

These findings hint at the importance of the behaviour of larvae and early recruits, and data comparing the onshore larval pool and settlement have also implicated the importance of behaviour in determining patterns of settlement (Hoffmann et al. 2012). Shifts in recruitment of mussels seem to be reflected in differences in community structure (Demello & Phillips 2011), but at within-shore scales, the species segregation observed between adults of *Mytilus galloprovincialis* and indigenous mussel species cannot be explained by patterns of settlement in either California or South Africa (Johnson & Geller 2006, Porri et al. 2007, Bownes & McQuaid 2009). Within southern Africa, the relationship between adults and recruits seems in any event to vary with scale. At the largest (1000 km) scales, the relationship is positive, being driven by the productivity associated with regional upwelling. At medium (<1 km) scales, local hydrographic features seem to override any links between adults and recruits, while at small (<1 m) scales there is a positive correlation between adult and recruit abundances (Reaugh-Flower et al. 2011). Fine-scale ontogenetic shifts in response to conspecifics have been shown for mussels in the laboratory and in the field (Dobretsov

1999, von der Meden et al. 2010). In the laboratory, larger recruits are much more ready to move off algae towards adults (Erlandsson et al. 2008). This is supported by experiments using artificial spat collectors in the field that were prepared with or without biofilm and seeded with early-stage mussel recruits or not. The results indicated that primary settlers are attracted to biofilm while secondary settlers prefer a combination of biofilm and the presence of other mussel recruits (von der Meden et al. 2010).

These combined findings help to explain aggregation among mussels, but not habitat segregation between species. Field experiments using natural mussel beds, artificially created mussel patches, and artificial spat collectors showed that both *Mytilus galloprovincialis* and *Perna perna* predominantly settle low on the shore, with no discrimination between adults or attraction to conspecific adults (Porri et al. 2007, Bownes & McQuaid 2009). This is quite different from the strong attraction to conspecifics of sessile animals such as barnacles and oysters (Zimmer-Faust & Tamburri 1994, Jenkins 2005). The absence of conspecific attraction at settlement presumably reflects the fact that, although they have limited mobility, mussels are sedentary rather than sessile and are capable of rearranging themselves at small scales after settlement. The overall conclusion is that, at within-shore scales of shore height, patterns of settlement and adult abundance are matched for *P. perna* but not for *Mytilus galloprovincialis*, so that habitat segregation at this scale can only be partially explained by settlement.

Among shores and regional-scale effects

Differences among shores in settlement will reflect the rates at which larvae arrive and there is good evidence that, at scales of hundreds of metres, these can reflect differential delivery from a common offshore larval pool (Porri et al. 2006). This presumably stems from the effects of bottom topography on very nearshore currents and larval delivery. Consequently, shores that are separated by hundreds of metres can show consistent ranking by daily settlement rates (Porri et al. 2008b). Larval delivery will also be affected by site-specific rates of bulk water flow, including the effects of wave exposure. Wave action has long been recognized as a key driver of intertidal community structure (Newell 1979), and the degree of wave exposure has a significant effect on recruitment in these populations. Recruitment rates are greater on wave-exposed than wave-sheltered shores for *Perna perna* on the southern coast (e.g., McQuaid & Lindsay 2007) and under semi-exposed conditions for *Mytilus galloprovincialis* on the western coast, with overall mediating effects on the composition of the intertidal community (Branch et al. 2008, 2010).

The larger-scale setting or context of shores has a strong effect on recruitment rates. The southern coast of South Africa is characterized by a series of large log-spiral or so-called half-heart bays (Figure 1B), and oceanographic models indicate a relatively high level of particle retention off this coast (Lett et al. 2006, Miller et al. 2006). The log-spiral bays themselves are believed to have a mesoscale topographic effect on nearshore currents that is reflected in a degree of particle or larval retention within the bays (McQuaid & Phillips 2006, von der Meden et al. 2008). This results in a significant effect of coastal topography on recruitment rates.

Gaines & Bertness (1992) demonstrated the importance of water retention within bays for rates of barnacle settlement. A comparison of multiple sites within a single bay against sites on the open coast in South Africa confirmed this for mussels, with much stronger cohorts of recruits within bays, suggesting that bays and the open coast act as semidiscrete elements of a larger metapopulation (McQuaid & Phillips 2006). The generality of a topographic effect was confirmed in a large-scale study across 500 km of coastline encompassing four log-spiral or half-heart bays on the southern coast. Recruitment was measured monthly for 12 months and was higher at within-bay sites than at open-coast sites. This applied to both *Mytilus galloprovincialis* and *Perna perna*, but interestingly only for three of the four bays. For the most westerly fourth bay, Mossel Bay, recruitment was higher

on the open coast, possibly because this part of the coast is characterized by cold bottom water (Boyd & Shillington 1994) and stratification throughout the year (Swart & Largier 1987).

Overall, settlement and recruitment rates at specific sites are influenced by the amount of water arriving at the shore and the density of larvae within that water. Water flux reflects very nearshore currents and the degree of wave action, while larval densities are influenced by the fact that sites exist within a larger, mesoscale topographic context that may promote larval retention or advection. Taken overall, along this coast, there is a ubiquitous, but inconsistent, effect of coastal topography on mussel recruitment (von der Meden et al. unpublished).

Post-settlement mortality (i.e., mortality within weeks of settlement) can powerfully reshape the patterns of distribution and abundance established at settlement (Connell 1961) and can, for example, drive a sharp decline in the genotype of *Mytilus galloprovincialis* in the Irish hybrid zone. This strong differential selective pressure against particular genotypes occurs within the first few weeks after initial settlement and may be driven by developmental malfunctions during metamorphosis (Gilg & Hilbish 2000). In the case of our two study species, however, mortality immediately after settlement does not seem to differ markedly between them at either within-shore scales (Bownes & McQuaid 2009) or mesoscales (Hoffmann et al. 2012, von der Meden et al. 2012).

Biogeographic effects

Just as shores exist within a regional, topographic context, regions exist within a biogeographic context. The coastline of South Africa spans three biogeographic regions that are aligned with two globally important currents and characterized by very different levels of primary production, with a clear decrease of upwelling intensity and frequency, and primary production from west to east (Lutjeharms 2006, Hutchings et al. 2009). These are the upwelling-driven Benguela Current on the western coast (Andrews & Hutchings 1980, Branch & Griffiths 1988) and the warm, oligotrophic Agulhas Current that follows the eastern and southern coasts (Lutjeharms 2006). Although the differences in recruitment on the different coasts confound primary production and species identity, there is a strong gradient from west to east, with up to five orders of magnitude more recruitment on the western than the southern and eastern coasts (Harris et al. 1998). This clearly reflects the relationship between recruitment intensity and the nature of upwelling, specifically its intensity and predictability (Reaugh-Flower et al. 2011).

Apart from its effects on primary productivity, and thus larval food availability, upwelling is believed to have strong effects on the advection of larvae between coastal waters and the intertidal. The earlier paradigm of a negative influence of upwelling on the recruitment of intertidal invertebrates, encapsulated by the upwelling-relaxation hypothesis (Roughgarden et al. 1988, Farrell et al. 1991, Alexander & Roughgarden 1996), has recently been reassessed, and in regions where *Mytilus galloprovincialis* has become successfully established, a positive relationship between upwelling (or intermittent upwelling) and settlement of this mussel has been identified (Xavier et al. 2007, Broitman et al. 2008, Shanks & Shearman 2009, Peteiro et al. 2011, Pfaff et al. 2011).

Overall, differences in patterns of settlement and recruitment exist between the two study species mostly at within-shore scales. Looking across decreasing spatial scales, the effects on settlement of biogeography, coastal topography, upwelling, wave action, and height on the shore seem to be similar for the two species. Post-settlement mortality rates appear to differ mainly at the within-shore scales and can explain the within-shore distribution of *Perna perna*, but not *Mytilus galloprovincialis*.

Abiotic and biotic drivers: overlap in the fundamental niche

The traditional assertion that species limits are generally established and maintained by species interactions in productive habitats and physiological limits in stressful habitats (e.g., Connell

1961) has been challenged. A number of exceptions to this oversimplification have been identified (Bertness 1989, Wootton 1992, Robles & Desharnais 2002). Its place is now taken by a more complex view in which the inseparable interaction of multiple physical and biotic processes delineates the realized limits of species (Denny & Wethey 2001). The upper vertical distribution limits of many rocky intertidal organisms were thought to be defined by thermal or desiccation stress related to aerial exposure, while biotic factors generally determined the lower limits (Connell 1961, Paine 1974). A major advance in our understanding of intertidal biotic zonation on rocky shores has been the evidence that lower and upper vertical distribution limits, and community dynamics in general, are largely driven by the intricate networks of dynamic environmental stresses and species interactions (e.g., Bertness & Callaway 1994, Tomanek & Helmuth 2002, Arakelova & Michel 2009, Zardi et al. 2011b).

In addition, organisms can alter the physical conditions they experience through behavioural responses, and these form the first and least demanding in a hierarchy of responses to stress (Heinrich 1981). Behaviour is most elaborate and complex in large, motile animals but is important even in plants, and the simple behavioural repertoires of sedentary animals can be remarkably effective in minimizing stress (Nobel 1983, Nicastro et al. 2012).

An understanding of mechanisms of species interaction and how biotic and abiotic environments affect competing species is a prerequisite for understanding how species can co-occur. Spatial and temporal variation in environmental conditions interact with the diverse biological attributes and tolerances of species, playing a decisive part in coexistence dynamics (Hu & Tessier 1995, Gerlach & Rice 2003, Leicht-Young et al. 2007). Sympatric species might be advantaged at different times and in different places because of the different ways and strengths with which they respond to fluctuations of stressful physical environments. These variations are particularly crucial in setting the distribution of an invasive species in a native community. As both indigenous species and invaders respond to environmental variations, it is the difference in their responses that ultimately determines the success of the invader and how it interacts with native species (Chesson 2000, Shea & Chesson 2002).

Microclimatic gradients provide an ideal situation for exploring questions concerning the determinants of habitat segregation among coexisting species. Species distributions over large geographic scales are often replicated over smaller scales on local gradients, but the local scale is more tractable when examining species responses to environmental factors (Bailey 1995, Zardi et al. 2011b). Intertidal organisms are regularly covered and uncovered by the tides that subject them to a transition from aquatic to terrestrial conditions over very small (metre) spatial scales. The resultant pattern is usually one of biological zonation of species (e.g., Knox 2001, Heaven & Scrosati 2008): Organisms are intermittently exposed to environmental extremes and generally exist at or close to the limits of their physiological tolerances (e.g., Tomanek & Helmuth 2002, Helmuth et al. 2006).

In the past, the effects of abiotic or biotic factors have generally been described and tested separately, although it is now recognized that the separation of ecological drivers into separate categories can lead to questionable and incomplete understandings. Here, we review the responses of *Perna perna* and *Mytilus galloprovincialis* to separate abiotic and biotic stresses, but, when assessing biotic factors (e.g., predation, parasitism, or direct interaction between the two species), we discuss how these are moderated by the physical environment.

Abiotic drivers

The domination of the upper and the lower areas of the mussel zone by *Mytilus galloprovincialis* and *Perna perna*, respectively, along the southern coast of South Africa (Bownes & McQuaid 2006) can partially be explained by their different responses to environmental clines and spatio-temporal variability in those responses. Although the rocky intertidal is often characterized by a dynamic mosaic pattern of interacting abiotic stressors, a few persistent vertical environmental gradients

occur within this habitat. In general, the intensity of hydrodynamic and sand stress decreases from the lowest to the highest portions of the shore, while this pattern is reversed for thermal and desiccation stress (Thompson et al. 2002, Denny & Gaines 2007). Because the intertidal habitat is regularly covered and uncovered by the tides, the vertical distribution of intertidal communities reflects steep gradients in temperature, desiccation, and oxygen availability (Newell 1979, Wethey 1983, Zandee et al. 1986, Hays 2007, Contreras-Porcia et al. 2011, Zardi et al. 2011b). The two study species show contrasting responses to and tolerances of each of these stresses. Furthermore, patterns in the temperatures experienced by intertidal organisms are often highly intricate, and effective temperatures can differ dramatically even among individuals in close proximity to one another (Helmuth & Hofmann 2001). Heat exchange between these organisms and their environment can vary strikingly with size, behaviour, and morphology, and two organisms exposed to identical climatic conditions can experience very different body temperatures (Helmuth 1998, Fitzhenry et al. 2004, Jost & Helmuth 2007, Denny et al. 2011).

Life in the high intertidal requires a well-coordinated set of adaptive responses (physiological, behavioural, biochemical, and molecular), such as increased thermal resistance (e.g., Sokolova et al. 2000, Zardi et al. 2011b); increased extracorporeal water storage; reduced evaporation (e.g., McQuaid & Scherman 1988); and stress-induced expression of heat stress proteins (Hsps) (Hofmann et al. 2002, Miller et al. 2009, Marshall et al. 2011). The fact that *Mytilus galloprovincialis* has a greater tolerance to emersion stress than indigenous South African mussels (Nicastro et al. 2010b) reflects such adaptations. As a response to air exposure, *M. galloprovincialis* produces high levels of Hsps (Nicastro et al. 2010b), which prevent aggregation of damaged proteins and facilitate their refolding following stress (Parsell & Lindquist 1993). In contrast, the indigenous *Perna perna* expresses lower levels of Hsps and suffers higher mortality rates when exposed to air in the laboratory.

Perna perna and *Mytilus galloprovincialis* also have contrasting behavioural strategies that strongly modulate their physiological resilience to desiccation. During emergence in air, some mussel species close the two valves of their shell and undergo anaerobic metabolism, while others display alternate closure and opening of the shell (gaping), which allows the maintenance of aerobic respiration (Widdows et al. 1979, Famme & Kofoed 1980). The first behaviour leads to reduced evaporative water loss at the cost of inefficient use of stored energy; gaping allows more efficient functioning of the metabolic machinery, but valve movements force water out of the mantle cavity, increasing water loss and the risk of desiccation. *Mytilus galloprovincialis* is a non-gaping species, while *Perna perna* exhibits gaping (Nicastro et al. 2010b). Despite the higher stress and energy demands involved, valve closure allows the invasive species to lose relatively lower amounts of water and thus to colonize and dominate higher portions of the intertidal where *P. perna* cannot survive because of water loss during gaping (Nicastro et al. 2010b).

Hydrodynamic forces from breaking waves are among the most important causes of mortality in the rocky intertidal zone (Paine & Levin 1981). The capacity of an organism to resist wave-induced damage or displacement is a prerequisite for survival in wave-swept intertidal environments. Several studies have reported differences in the strength of byssal attachment for coexisting mussel species that compete for space (Willis & Skibinski 1992, Brazee 2006, Zardi et al. 2006a, Pearce & LaBarbera 2009). Relatively strong attachment to the substratum could promote competitive dominance both seasonally, during winter storms, and geographically, along gradients of wave exposure among shores and vertically within shores (Carrington 2002). *Perna perna* has more and thicker byssal threads than *Mytilus galloprovincialis*, resulting in a comparatively more secure attachment; thus, hydrodynamic stress contributes to the vertical zonation of these two species, consigning the more weakly attached *M. galloprovincialis* to the higher mussel zone, where water movement is less severe (Zardi et al. 2006a) The benefit of being more firmly attached to the substratum is especially noticeable when populations of the two mussel species are subjected to particularly harsh wave conditions. After intense winter storms, mortality rates of *M. galloprovincialis* are substantially higher than those of the indigenous species (Zardi et al. 2006a), although in some

cases storm-induced effects reflect compensatory mortality (Connell et al. 1984), with the more abundant species in mixed beds showing the highest mortality (Erlandsson et al. 2006).

Optimal fitness involves maximization of survival and reproduction at all ages and ontogenetic stages of an organism. Trade-offs among traits that contribute to lifetime fitness are, however, common elements of models of life-history evolution (Stearns 1992). Trade-offs occur when organisms pay a fitness cost, such as delaying sexual maturation to acquire higher chances of survival later in life (e.g., Blomquist 2009). For intertidal mussels, byssal production and gonad maturation are among the most energetically demanding physiological processes (Griffiths & King 1979, Seed & Suchanek 1992, Carrington 2002). The production of byssal threads leads to high attachment strength, allowing organisms to endure stressful hydrodynamic conditions, while gonadal development contributes to recruitment rates and successful colonization.

During an 18-month survey, peaks in attachment strength coincided with periods of comparatively low gamete production for both *Mytilus galloprovincialis* and *Perna perna*, suggesting that neither species can afford to spend energy simultaneously on the two processes (Zardi et al. 2007b). The two coexisting species adopt different energetic strategies, however. *Perna perna* attachment strength is always higher than that of *Mytilus galloprovincialis*, while the latter has greater reproductive output (Zardi et al. 2007b) and the two spawn over different periods. Interestingly, this trend is true only on shores that experience moderate-to-low wave exposure, such as bays. Bays offer more shelter from wave action, emphasizing the capacity of *M. galloprovincialis* to have high gamete production and to colonize free space more rapidly than *Perna perna* (Erlandsson et al. 2006). On shores where waves impose high hydrodynamic forces, the invasive species loses this ecologically significant advantage over the indigenous species (von der Meden et al. 2008, Nicasastro et al. 2010a). Thus, high attachment strength is a necessary requirement to survive on strongly wave-swept shores, where the energetic demands it places on the invasive species come at the cost of lower reproductive output (Nicasastro et al. 2010a), and it grows faster, with better body condition, on shores with intermediate levels of wave action (Steffani & Branch 2003b).

Waves not only are associated with hydrodynamic stress but can also carry heavy loads of sand, periodically disturbing intertidal shores through sand burial or sand scour (Taylor & Littler 1982). Acting as an agent of disturbance, sand removes plant tissue, epiphytes, or invertebrates with poor attachment to the rock surface through scouring and decreases light, oxygen, and substratum available to organisms through burial. Sand stress can maintain an equilibrium between sand-tolerant and sand-intolerant competitors, determining habitat segregation and zonation of intertidal mussels (Marshall & McQuaid 1989). It can lead to temporary species impoverishment by selective elimination of maladapted species (Daly & Mathieson 1977, D'Antonio 1986), but in the longer term, it may also enhance species richness by increasing habitat heterogeneity, allowing within-shore coexistence of sand-intolerant species and those associated with sand deposits (McQuaid & Dower 1990).

Surprisingly, sand stress strongly affects the survival of *Mytilus galloprovincialis* and *Perna perna* individuals but is not related to their physiological tolerances and does not explain their vertical zonation. When buried under sand, *P. perna* mortality rates are higher than those of *Mytilus galloprovincialis* in both laboratory and field experiments, yet it is *Perna perna* that dominates the low shore where sand inundation is recurrent (Zardi et al. 2006b). Although both species accumulate sediments within the shell valves while still alive and sand buried, the quantities are much greater for *P. perna*, causing intense visible damage and clogging of the gills, explaining its higher mortality rates. Presumably, the accumulation of sand within the shell of *P. perna* is linked to its gaping behaviour.

Wave and sand stress vary also in time, altering the timing and mortality rates of the two mussel species (Zardi et al. 2008). During periods of high sand accumulation in mussel beds, the indigenous species has increased mortality rates that are higher than those of *Mytilus galloprovincialis*, while the pattern is reversed during winter, when wave action is high (Zardi et al. 2008). When sand stress is high, the less-stable secondary substratum of sand and shell fragments weakens the

attachment strength of mussels living within a bed. Consequently, the indigenous species loses its advantage in attachment strength over the invasive species, and this results in a seasonal shift in the competitive balance between the two.

Large-scale mortality, and even the stochastic death of individuals, free space within beds; because they are sedentary, mussels can respond to this. Following mortality events, mussels react to the increased availability of space and decreased attachment to neighbours by increasing their movement to reorganize into safer arrangements and more secure attachment. Under field conditions, higher movement rates of *Mytilus galloprovincialis* (Nicastro et al. 2008) combined with its weaker attachment strength make the invasive species both more susceptible and more responsive to wave action, contributing to a shift in competitive advantage between more sheltered shores within bays and shores that are more wave exposed on the open coast. In contrast, *Perna perna* has evolved a resistance strategy characterized by minimal movement but markedly higher attachment strength. The efficacy of each strategy depends on environmental conditions and how these fluctuate in time and space. The higher hydrodynamic stresses experienced in open coast habitats are disadvantageous to the invasive species that are more active and less strongly attached. The high reproductive output of *Mytilus galloprovincialis* is a crucial attribute of its success worldwide. This promotes its capabilities as an exploitation competitor, able to recolonize free space more quickly through settlement than, for example, *Perna perna* (Erlandsson et al. 2006). It comes, however, at the price of lower byssal thread production (Zardi et al. 2007b), weakening its capacity for interference competition on wave-exposed shores.

Biotic drivers

Understanding the distribution patterns exhibited by *Perna perna* and *Mytilus galloprovincialis* in South Africa is linked to understanding how *M. galloprovincialis* has been so successful in colonizing shores around the world and invasion processes generally. Inevitably, an invasive species must tolerate abiotic conditions in its new range, but importantly, it must interact with the indigenous species. Such interactions can be central to the success or failure of a potential invasion. There is considerable debate about how, or whether, diversity in the recipient community promotes biotic resistance to invasions (McQuaid & Arenas 2009). In marine systems, both large-scale correlative and small-scale manipulative studies have produced either equivocal or contrasting results (Stachowicz et al. 2002, Dunstan & Johnson 2004, Klein et al. 2005, Wasson et al. 2005), and functional group diversity may be more important than richness (Ceccherelli et al. 2002, Arenas et al. 2006, Britton & Simmons 2006). For marine macroalgae, the link between invasion resistance and richness appears to concern resource availability. However, resource depletion interacts with facilitation (Bulleri et al. 2008), and the interaction between *M. galloprovincialis* and *Perna perna* provides a good example of how competition and facilitation can form two sides of the same coin.

Direct interactions between *Mytilus galloprovincialis* and *Perna perna* include competition and facilitation. Competition has been a target for ecological research for decades following the classic paper by Hairston et al. (1960). In the case of intertidal species, there appears to be a difference between competition for food, a renewable resource, and for space, a non-renewable resource (Branch 1984), but models predict that the strength of interspecific competition is mediated by the effects of offshore larval advection on recruitment rates (Connolly & Roughgarden 1999). Space, however, is commonly a critical limiting factor for sessile or highly sedentary species in the intertidal where occupancy often approaches 100% (Sousa 1984, McGroarty & Goss-Custard 1995). Consequently, for mussels, competition is primarily for space. Even within a species, there are enormous losses between settlement and sexual maturity due to intraspecific competition (Branch & Steffani 2004), and the intensity of competition is closely linked to growth rates (Griffiths & Hockey 1987), which are also directly affected by wave exposure (Steffani & Branch 2003b).

Perna perna grows markedly faster on wave-exposed than wave-protected shores (McQuaid & Lindsay 2000), and field experiments manipulating water flux around mussel patches on within-shore scales of tens of centimetres indicated that growth rates respond directly and strongly to changes in small-scale hydrodynamics, indicating that food supply can limit growth rates and so will affect the intensity of competition for space (McQuaid & Mostert 2010). Experiments commonly identify clear dominants and subdominants among competing species (Hill 1998), but while we can estimate growth rates (and thus potential competitive ability) of our two mussel species, the competitive hierarchy is not as inflexible as this implies. In fact, competitive hierarchies can change with height on the shore and the degree of wave action (Connell 1961, Lubchenco 1980), as well as with time.

Settlement on the South African coast tends to be much less strongly pulsed than at higher latitudes (McQuaid & Phillips 2006), but in monospecific beds of *Perna perna*, it is common to see doming of small (<1 m) patches, where smaller, younger mussels in close contact with the substratum grow up underneath their older conspecifics, forcing them into unstable configurations that bulge up from the main mussel bed (personal observation). Intraspecific competition is also strongly implicated in the self-organization of mussel beds on soft sediments (van de Koppel et al. 2005), where facilitation through protection from water movement at small spatial scales, combined with competition for food at larger scales, results in beds of *Mytilus edulis* on soft sediments forming distinct, regularly spaced rows.

In the case of an invasive mussel, however, interspecific competition with indigenous species is critical. We have already seen how the high fecundity of *Mytilus galloprovincialis* makes it an effective exploitation competitor, able to settle on and colonize large areas of free space effectively (Erlandsson et al. 2006). But, these species also interact through interference competition. Because they are sedentary, rather than truly sessile, adult mussels are able to respond to freeing of space on very small scales, for example, through the loss of a single individual or the growth of neighbours. As adults, *Perna perna* and *Mytilus galloprovincialis* show remarkably different behaviours in response to small- (centimetre-) scale availability of space. Both species exhibit higher mortality at the edges of mussel patches than in the centre (Nicastro et al. 2008). Mussels attach to both the primary substratum and to each other, providing a mutually supportive network of byssal attachments. Loss of neighbours disrupts this network, and survivors respond by showing greater movement than individuals in the centre of a patch. This presumably reflects a need to find a safer arrangement and reattach when a neighbour has been lost. As described in the 'Abiotic drivers' section above, *Mytilus galloprovincialis* is less strongly attached and more mobile than *Perna perna* (Nicastro et al. 2008). These differences in tenacity and mobility presumably influence competitive interactions between the two, as wave action is a major driver of habitat segregation between them (Zardi et al. 2006a).

A series of manipulative experiments involving treatments that tested for interspecific and intraspecific competition in *Perna perna* and *Mytilus galloprovincialis* across the shore showed a competitive hierarchy that depended on height on the shore. As well as competing, the two species also exhibit interspecific facilitation (Rius & McQuaid 2006, 2009). They show different tolerances of physical stress, with *M. galloprovincialis* more tolerant of heat and desiccation and more vulnerable to wave action. Across the stress gradient of high wave action and low heat/desiccation stress on the lower shore to the reverse in the high mussel zone, tolerance of abiotic conditions shifts from favouring *Perna perna* to favouring *Mytilus galloprovincialis*. This not only shifts the competitive hierarchy but also means that at each height on the shore, the more tolerant species provides a degree of protection to the less tolerant, facilitating its survival, at least initially. On the low shore, *M. galloprovincialis* suffers 100% mortality when transplanted to monospecific plots but shows improved survival when combined with the more strongly attached *Perna perna*, although it is later eliminated through competition. *Perna perna* transplanted to the high mussel zone died in all treatments. In the mid-mussel zone, where the two naturally coexist, *P. perna* survived better

at higher densities and survived even better in combination with the invasive species. Again, this initial facilitation was followed by competitive exclusion. Rius & McQuaid (2009) concluded that because facilitation occurred strongly on the low shore (*P. perna* facilitated survival of *Mytilus galloprovincialis*), weakly on the midshore (the reverse), and not on the high shore, facilitation was not linearly related to stress, but rather was minimal where stress was low, maximum at intermediate stress levels, and overridden by abiotic factors where stress was high.

Although we have no data on the up-shore limits of *Perna perna* before the arrival of *Mytilus galloprovincialis*, it seems that the invasive species has allowed an up-shore spread of the indigenous species, and that the mixed zone is now rather higher on the shore than the original limit for *Perna perna*. Certainly, the arrival of *Mytilus galloprovincialis* has resulted in an up-shore shift in overall mussel distribution on the western coast (Hockey & Van Erkom Schurink 1992).

Inter- and intraspecific facilitation dynamics can also be observed in terms of protection against heat and desiccation stress. The gaping behaviour of *Perna perna* has no effect on the body temperatures of isolated individuals, but when in aggregations, this behaviour strongly modifies temperature and humidity, resulting in cooler body temperatures (Nicastro et al. 2012). Thermoregulation through *P. perna* aggregation can also modulate levels of desiccation stress for coexisting *Mytilus galloprovincialis* in mixed beds. During periods of particularly intense heat conditions, mortality rates of mussels surrounded by gaping *Perna perna* individuals are lower than those of mussels surrounded by non-gaping *Mytilus galloprovincialis* (Nicastro et al. 2012). Competitive hierarchies driven by intrataxon differences, like the differential biotic effect of the two lineages of *Perna perna* on *Mytilus galloprovincialis*, can further emphasize the complexity of how the distributions of organisms are determined.

Lest this appear too simple, there is a further complication: unpublished data from field experiments indicate that the eastern limit of distribution for *Mytilus galloprovincialis* on the South African coast is set not only by unfavourable abiotic conditions but also by interaction with *Perna perna*. *Perna perna* exists as two distinct genetic lineages on the South African coast that overlap for approximately 200 km of the southern coast of the country (Zardi et al. 2007a; Figure 1) in precisely the region where *Mytilus galloprovincialis* reaches its eastern limit (Robinson et al. 2005). The two lineages are non-sister taxa, with the southern coast the scene of secondary contact between them (Cunha et al. 2014), and they have different tolerances of heat, desiccation, and sand inundation (Zardi et al. 2011a). Field experiments indicated that, while *M. galloprovincialis* can outcompete the western lineage of *Perna perna* in the mid-mussel zone, it is outcompeted by the eastern lineage (unpublished data).

A second interaction that is likely to shape the interaction of the two species is predation. Predation can have enormous effects on communities, as epitomized by the idea of the keystone predator. This was originally developed in the context of predation of mussels by the starfish *Pisaster ochraceus* and conceptualized as a species that prevents habitat monopolization by a competitively dominant species by preferentially consuming that species (Paine 1969). The keystone predator concept was later refined by Power et al. (1996) to include an estimate of how much a community changes in response to alterations in the abundance of the predator.

Adult mussels suffer high levels of predation in many parts of the world, from marine (both intertidal and subtidal) and terrestrial species. Among terrestrial predators, generally only birds have strong effects (Goss-Custard 1980), but see the work of Kurle et al. (2008) for an illustration of how birds and introduced rats interact to shape an intertidal community. These various predators have different effects on mussel populations and can set the low-shore limits for mussel distribution (e.g., Saier 2001, Robles et al. 2009), but the effects of predation are mediated by many factors. These include factors affecting predator abundance and performance, such as the availability of predator habitats like subtidal reefs (Rilov & Schiel 2006, 2007) and wave action (Menge 1978), as well as recruitment and growth rates of the mussels themselves (Griffiths & Hockey 1987, Menge

et al. 1999). Juvenile mussels can be particularly vulnerable to predators and can suffer extremely high rates of mortality (Dare & Edwards 1976), so that removal of predators can result in increases in the abundance of small mussels as well as down-shore shifts in distribution (Paine 1974).

To contribute to the distributional patterns seen on the South African southern coast, predators would have to exert different pressures and have different effects on our two species. Mussel predators in South Africa include starfish (Penney & Griffiths 1984), whelks (Griffiths 1981), rock lobsters (Griffiths & Seiderer 1980), and especially octopuses (Smale & Buchan 1981). These can have dramatic effects on mussel populations in the subtidal, altering overall community structure dramatically and excluding mussels where the abundances of large predators are high (Barkai & McQuaid 1988). In contrast, in the intertidal, adult mussels seem to suffer only low levels of predation, and most predators take only small size classes.

In trying to understand whether predation shapes habitat segregation between invasive and native mussels, we need to know if they have different vulnerabilities to predators. There is no evidence of such a difference for juvenile mussels, but one indirect effect of the spread of *Mytilus galloprovincialis* in South Africa has been that total mussel biomass has increased dramatically, particularly on the western coast (Griffiths et al. 1992). This in turn has been linked to increases in numbers of an endangered shorebird, the African black oystercatcher, *Haematopus moquini*. This species is endemic to southern Africa, and the total population is of the order of 6000 but has been increasing over the last 20 years, coincident with the spread of *Mytilus galloprovincialis* (Hockey et al. 2005), which seems to have had a positive effect on bird numbers (Hockey & Van Erkom Schurink 1992).

This effect has been strongest on the western coast, where *Mytilus galloprovincialis* dominates the entire mussel zone, but includes an eastward extension along the southern coast of oystercatcher breeding range (Vernon 2004, Brown & Hockey 2007). *Haematopus moquini* feeds intertidally on a range of species, primarily limpets and mussels (Kohler et al. 2009). A strong biogeographic gradient exists in the stable isotope values of suspended particulate matter in inshore waters around the coast of South Africa, with enrichment of $\delta^{15}\text{N}$ values from the east towards the west as one moves from the oligotrophic Agulhas Current-dominated eastern coast to the eutrophic Benguela Current-dominated west (Hill et al. 2006). This signal is reflected in the tissues of mussels (Hill & McQuaid 2008, Hill et al. 2008). In fact, the biogeographic signal in isotope values passes to the top of the food chain and can be detected in gannets (Jaquemet & McQuaid 2008). It can also be detected in oystercatchers.

Oystercatcher blood has $\delta^{13}\text{C}$ values between those of carbon-depleted mussels and carbon-enriched limpets, and across 2000 km of coastline, this signal reflects changes in the proportion of grazers and filter-feeders in the oystercatcher diet. Diet is dominated by mussels on the western coast, with mixed proportions of mussels and limpets on the south-eastern coast. This strongly reflects regionally high abundances of the invasive *Mytilus galloprovincialis* (Kohler et al. 2011), although there can be some refinement. African oystercatchers form strong pair bonds and on the southern coast males have a stable isotope signal that is closer to that of limpets, while their mates have isotope signals closer to that of mussels (Kohler et al. 2009). Interestingly, the difference between the sexes is minimal where *M. galloprovincialis* is abundant and increases towards the east, where it becomes rare (Kohler et al. 2014). Theoretically, predation by oystercatchers could influence habitat segregation on the southern coast because *Haematopus moquini* shows a preference for the more weakly attached invasive mussel than *Perna perna* (Kohler et al. 2009). Bird numbers are so low, however, that this seems unlikely to have any discernible effect on mussel populations except perhaps within the territory of a mating pair of birds.

A combination of benthic and pelagic intertidal predators, including fish, can have strong effects on small recruits and may limit recruitment (Plass-Johnson et al. 2010), but above a very small size, predation is not believed to be a major source of mortality in mussels on this coast, even when

growth rates are low so that individuals remain within a window of predation vulnerability for long periods (Griffiths & Hockey 1987). Perhaps one of the greatest predatory threats to juvenile mussels comes from their own kind.

Mussels are filter-feeders capable of dramatically reducing the particle content of the water (Norén et al. 1999). Although mussels feed primarily on phytoplankton, there is abundant evidence that they are capable of feeding on zooplankton (Wong et al. 2003, Lehane & Davenport 2004, 2006, Zeldis et al. 2004, Alfaro 2006). Mussel larvae are small particles within the size range consumed by adults, and larvae have to settle in the adult habitat, presenting a real danger of cannibalism. Porri et al. (2008a) counted the numbers of mussel larvae found in the guts of adults and compared these with estimates of the densities of settlers on the shore. They concluded that over 50% (maximum approaching 80%) of incoming larvae are lost through larviphagy by adults. The implications for adult diets are seasonal as Alfaro (2006), working in New Zealand, found that mussel larvae and juveniles formed 70% of the particles consumed by *Perna canaliculus* during the peak spawning period, but less than 1% during gametogenesis before gametes are released.

For the larvae, it is clear that cannibalism is a major threat as they approach adult beds during settlement and the ontogenetic changes in the behaviour of settlers and recruits described may be linked to the need to avoid larviphagy. While loss of larvae to adults is important, in the context of habitat segregation, there is no evidence that the larvae or newly arrived settlers of the two species show strong differences in behaviour or vulnerability to larviphagy.

Parasites are important components of natural communities and can potentially be crucial players in determining the outcomes of species' interactions (Dobson & May 1986, Gilbert 2002, Prenter et al. 2004, Malmstrom et al. 2006, Alison & Dunn 2009). For instance, two species that share a parasite may respond differently to the same weakening agent; metabolic costs, host growth, reproduction, and survivorship may be affected differently. Alternatively, parasites can influence interactions between species even if they do not share the parasite. For example, a parasite can potentially mediate the competitive strength of infected hosts against a non-host species (reviewed in Hatcher et al. 2006). Mussels are common hosts for many parasites, so parasitism could play a role in the interaction between coexisting species (e.g., Kim & Powell 2006, Thielges et al. 2009).

Digenetic trematodes (phylum Platyhelminthes) are parasitic flatworms. They are the most frequent and most important metazoan parasites of bivalves (Cheng 1967, Kinne 1980). A survey at nested spatial scales of trematodes in the indigenous mussel *Perna perna* and the invasive *Mytilus galloprovincialis* on the southern and eastern coasts of South Africa, as well as for indigenous populations of *M. galloprovincialis* in Spain, showed that *M. galloprovincialis* is free of trematodes, whilst *Perna perna* is commonly infected by trematodes (Calvo-Ugarteburu & McQuaid 1998a). The most common parasites infecting *P. perna* are two species of digenetic trematodes: metacercariae of the genus *Proctoeces* and bucephalid sporocysts, with infection rates of up to approximately 50%. Both *Proctoeces* and the bucephalid sporocysts have harmful effects on the ecological fitness of *Perna perna*, reducing the survival and competitive ability of this species (Calvo-Ugarteburu & McQuaid 1998b). The incidence of *Proctoeces* is higher in females than in males, and it negatively affects primarily growth; bucephalid sporocysts have powerful negative effects on reproduction, adductor muscle strength, and water loss. The harmful effects of bucephalid sporocysts on reproduction are particularly dramatic. All infected *Perna perna* individuals are completely castrated, with no trace of sex products left (Calvo-Ugarteburu & McQuaid 1998b).

At the population level, the negative effects of both parasites on *Perna perna* are exacerbated because they each target the size classes that direct most energy into the fraction of the energy budget affected by the parasite. *Proctoeces* affects growth only in the smaller individuals, which in normal conditions must compete for space and invest the most in growth (Griffiths & Hockey 1987); bucephalid sporocysts castrate the bigger mussels, which spend most energy on reproduction (Calvo-Ugarteburu & McQuaid 1998b). Interestingly, infestation does not affect the filtration or respiration rates of infested *Perna perna*, indicating that there is no compensation of the energy

budget by the host through either decreasing energy losses by reducing respiration or increasing energy gain by raising feeding rates. Instead, the energy gained by feeding is simply rerouted to the parasite, to the detriment of growth and reproduction. The high occurrence of both parasites in *P. perna* along the South African coast and the associated negative effects provide *Mytilus galloprovincialis* with an indirect competitive advantage and may be one of the reasons for its success on this coast. For a parasite community, the resource base is the host, so it will be important to follow future dynamics of trematode infestations to understand whether these parasites have the ability to develop in *M. galloprovincialis*, negatively affecting its competitive advantage, or whether their fate is indissolubly linked with that of *Perna perna*, a host whose competitive abilities they diminish.

In addition to trematodes, the shells of both mussels are attacked by shell-boring endoliths in what can be considered to be a form of parasitism (*sensu lato*; Prenter et al. 2004). Endolithic microorganisms, including heterotrophs (fungi) and phototrophs (cyanobacteria and algae), penetrate actively into hard minerals by biochemical dissolution (Golubic et al. 1981, Garcia-Pichel et al. 2010). A few species of cyanobacteria are able to excavate carbonate minerals, from limestone to biogenic carbonates, including coral reefs, skeletal materials, and the shells of living and dead organisms (Tribollet 2008). The damage caused by phototrophic endoliths was thought to be restricted to the periostracum, the outermost layer of molluscan shells (Laukner 1983). However, more recent studies demonstrated that boring activities of photosynthetic endoliths can cause extensive damage to their hosts (e.g., Raghukumar et al. 1991, Kaehler & McQuaid 1999). In mussels, photoautotrophic endolithic infestation can have devastating effects and can be responsible for 50% of total mortality by causing shell collapse, particularly when the area of the shell above the adductor muscle is badly eroded (Kaehler & McQuaid 1999, Zardi et al. 2009). In South Africa, endolithic infestation of mussels occurs in both *Mytilus galloprovincialis* and *Perna perna*, but with higher incidences in the invasive species. The higher levels of endolithic parasitism in *Mytilus galloprovincialis* mirror greater mortality rates attributed to parasitism in this species (Zardi et al. 2009), presumably affecting its ability to compete with *Perna perna*.

The key pressure exerted by endolithic parasitism may not only result in mortality events but can also have sublethal effects. The most evident sublethal effect is weakening of the shell, and this can become lethal through shell fracturing when endolithic boring activity is particularly intense (e.g., Kaehler & McQuaid 1999). Mussels with weakened shells are more vulnerable to both predation and the mechanical effects of wave action (Webb & Korrubel 1994). A number of studies have highlighted the ability of molluscs to restore damaged parts of the shell through the deposition of new shell material (reviewed by Wilbur 1964, Watanabe 1983). Shell repair is an energetically demanding process that can alter the energetic budget of an organism and can reduce the energy available for other important functions, such as reproductive output and tenacity (attachment force normalized to mussel size). In *Mytilus galloprovincialis* and in *Perna perna*, fitness-related traits are negatively affected by endolithic parasites, suggesting an energy trade-off between the more urgent need to maintain an intact shell and other physiological parameters. Given the higher rates of infection of *Mytilus galloprovincialis* by endoliths, again there should be competitive costs to its interaction with *Perna perna*.

Disturbance can interact positively or negatively with parasites (Dove 1997, Lafferty 1997); thus, parasites and introduced species may interact with environmental disturbances in a number of ways, generating complex and heterogeneous patterns of parasitism that change over different temporal and spatial scales. In mussels, the occurrence of endolithic infestation can be highly variable, generally following spatial gradients of wave exposure because physical damage to the outer shielding periostracum of mussels caused by abrasion by wave- or wind-borne sand may facilitate the first stages of endolithic shell excavation (Kaehler 1999). Thus, the highest infestation rates occur on wave-exposed, open coast sites rather than protected sites within bays. At a smaller, within-shore scale, the incidence of infested shells also varies, being high at the upper tidal levels of mussel distribution and low or absent on the low shore (Kaehler 1999). In addition, since many microborers

are photosynthetic (Golubic et al. 1975), the degree of light exposure is a key factor driving the species composition of endolithic assemblages. Light intensity within the intertidal is patchy due to the extreme heterogeneity of the 3-dimensional structure of this habitat. Mussels in shaded areas have lower infestation frequencies than those in non-shaded spots, indicating an important role for microscale variation of sun exposure in the control of endolithic infestation (Zardi et al. 2009). The strong link between environmental disturbance and endolithic prevalence suggests that, because *Mytilus galloprovincialis* has lower attachment strength and a thinner shell relative to coexisting *Perna perna*, its invasiveness will be limited at sun- and wave-exposed locations where endolithic activity, shell scouring, and risk of dislodgement are high. This underlines the crucial role of the physical environment in regulating biotic stress. These physical/biological interactions may explain site-to-site variability in the competitive balance between the invasive and the indigenous species.

The enemy release hypothesis (ERH), one of the most popular single-factor hypotheses proposed to explain the establishment and spread of introduced species, states that invasive species are successful because they escape from natural, coevolved enemies (Crawley 1987, Maron & Vilà 2001, Keane & Crawley 2002). In general, the process of invasion is characterized by a reduction in the parasite community and perhaps acquisition of native parasites (Bauer 1991, Dove 1997, 2000, Torchin et al. 2002). When tested for endolithic parasitism of *Mytilus galloprovincialis* populations from native (Portugal) and invasive (South Africa) ranges, the ERH hypothesis was clearly rejected (Marquet et al. 2013). The degree of endolithic infestation and mortality rates due to endoliths were strikingly higher in the invasive range than in the native range. In the most infested South African location, all individuals showed signs of endolithic infestation, and 60% of total mortality of that mussel population could be attributed to endoliths. Despite such dramatic effects, endoliths have not prevented the invasive *M. galloprovincialis* from successfully spreading along the South African coast and becoming the most successful invasive marine species in this country (Robinson et al. 2005). The dynamics of invasions are probably the result of multiple interactions between characteristics of the invaded community, properties of the invader, and again, the physical environment and intertidal heterogeneity.

Conclusions

The fundamental aim of ecology is to explain the distribution and abundance of organisms; this often translates as observing and understanding patterns in nature. Often, these patterns are rather simple; for example, there are generally more species at low than high latitudes or in shallow than deep waters. In our case, one species lives higher on the shore than the other, and they are affected differently by coastal topography and wave exposure. The danger is to assume that simple patterns reflect simple and predictable processes and to make predictions based on this assumption. In the case of latitudinal gradients in species richness, over 100 hypotheses have been put forward to explain this simple pattern, yet none has universal generality (Rahbek & Graves 2001).

While the ability to tolerate abiotic conditions is clearly *sine qua non*, we show that, within a shared fundamental niche, recruitment and interspecific competition are key drivers of species abundances. Patterns of settlement, post-settlement mortality, and recruitment can explain the vertical zonation of *Perna perna* but not of *Mytilus galloprovincialis*. Rather, this seems to be explained best by combinations of interference and exploitation competition between the two species. For exploitation competition, the high fecundity of the invasive *M. galloprovincialis* is advantageous; for interference competition, growth is critical. Importantly, the competitive hierarchy is moderated by abiotic conditions, altering in space and in time. In space, the competitive hierarchy differs with height on the shore and with coastal topography (bays vs. the open coast), and there is probably a degree of site specificity linked to wave action. In addition, the hierarchy can vary in time, particularly with seasonality of growth, which may reflect the biogeographic origins of the two species.

A final, but perhaps critical, point is the importance of phylogeography. The two genetic lineages of *Perna perna* have different competitive effects on *Mytilus galloprovincialis*, reemphasizing the complexity of how species distributions are determined.

In the context of predicting how biological communities will respond to long-term climate change, it is important to recognize the importance of biological effects. These effects are subtle and flexible; most important, they interact with environmental conditions and with each other.

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