INTERTIDAL PATTERNS AND PROCESSES: TRACKING THE EFFECTS OF COASTLINE TOPOGRAPHY AND SETTLEMENT CHOICE ACROSS LIFE STAGES OF THE MUSSELS *PERNA PERNA* AND *MYTILUS GALLOPROVINCIALIS*

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ABSTRACT

Within landscapes, spatial heterogeneity is common and specific landscape features can influence propagule dispersal by wind or water, affecting population connectivity and dynamics. Coastline topographic features, such as bays and headlands, have a variety of biophysical effects on nearshore oceanography, larval transport, retention and supply, and the processes of larval settlement and recruitment. Although this has been demonstrated in several parts of the world, engendering a perception of a general 'bay effect', few studies have investigated this generality in a single experiment or region, by replicating at the level of 'bay'.

The Agulhas biogeographic region of the south coast of South Africa is a useful system within which to test for such generality. Using the intertidal mussels *Mytilus galloprovincialis* and *Perna perna* as model organisms, patterns of adult distribution were surveyed across four large 'half-heart' bays and intervening stretches of open coast, providing replication at the level of 'bay' and duplication of ecologically similar species. In support of a general, pervasive influence of bays on intertidal populations, mussel cover was found to be greater in bays than on the open coast for both species, although the effect was strongest for *M. galloprovincialis*.

To explain this adult distribution, settlement, post-settlement mortality and recruitment were examined over 12mo at the same sites, with the prediction that rates of each would favour larger bay populations. Contrary to this, an interaction between month and bay-status was found, with greater settlement and recruitment on the open coast than in bays reflecting extreme settlement and recruitment events at 3 westerly open coast sites during summer. Re-analysis excluding these outliers, revealed the expected effect, of greater settlement and recruitment in bays. While this indicates the broad generality of the bay effect, it highlights exceptions and the need for replication in time and space when examining landscape effects.

Measuring post-settlement mortality required testing small-scale settlement behaviour on established and newly deployed settler collectors. It was found that all settlers preferred collectors with biofilm, but that primary settlers avoided conspecific settlers, while secondary settlers were attracted to them. With discrepancies in settler attraction to new and established collectors accounted for, initial (over 2d) and longer-term (over 7d) post-settlement mortality rates were found to be substantial (ca 60 %) for both species. No topographic effect on p-s mortality was evident.

Finally, recruit-settler, adult-recruit and interspecies correlations were examined at regional and local scales. Synergistic (or neutral) effects maintained the initial settlement pattern in recruit and adult populations regionally, but not at local scales; striking interspecies correlations suggested the influence of common regional transport processes. Ultimately, the results emphasize the importance of the direction of effects in different life stages and at different spatial scales, and the possibility that antagonistic effects may mask even strong patterns.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Pattern and process in ecology

Ecological study is founded on the understanding of pattern and process over a wide range of spatial and temporal scales. Historically however, most branches of ecology have studied processes with a view to explaining spatial patterns (Turner 1989). Surprisingly, past studies often assumed spatial homogeneity, regarding spatial complexity to be a complication (Pickett & Cadenasso 1995), rather than one of the most striking features of natural systems, as well as possibly one of the most important (Kareiva et al. 1990). As inclusion of spatial complexity and dynamics in ecological disciplines has increased over the last 3 decades (White 1979, Paine & Levin 1981, Schlosser 1991, Moilanen & Nieminen 2002), landscape ecology has arisen as a discipline in which the reciprocal effects of spatial pattern and ecological process on one another are recognised and explicitly examined (Turner 1989). As such, within landscape ecology, spatial dynamics are afforded the importance of a central causal factor (Pickett & Cadenasso 1995).

Although landscape ecology generally focuses on broad spatial scales, the term ‘landscape’ often seems rather vague because it is used in several different ways. Pickett and Cadenasso (1995: 332) hold that landscapes are either used as km scale “ecological systems” with identifiable features, or as an abstract “ecological criterion” represented at any given scale. Broadly then, a landscape is any spatially heterogeneous area at whatever scale (Turner 1989). Simplistically but usefully, landscapes are often broken down into 3 components: patches, corridors and the surrounding matrix (Forman & Godron 1981, Wiens 1997). Patches are areas of homogenous hospitable habitat situated within the less habitable matrix, and are connected by corridors of generally hospitable habitat that allow dispersal.

Within landscape ecology 3 key reviews address the main components of the discipline, namely: the characterisation of spatial landscape heterogeneity (Turner 1989), the influence of this heterogeneity as a causal agent on ecological processes (Turner 1989, Kareiva et al. 1990) and developing models and theories to explain landscape-scale ecological processes (Dunning et al. 1992). Forman and Godron (1986) characterised landscape ecology by way of three terms, "structure" (the distribution of resources and organisms with respect to landscape elements and their dimensions and configuration), "function" (the flow of these resources and organisms amongst landscape elements) and "change" (the temporal dynamics of structure and function within a landscape).

Together, landscape ecology studies have shown empirically and theoretically that spatial heterogeneity, in terms of landscape structure and function, not only form important ecological patterns but also influence ecological processes (see Turner 1989, Kareiva et al. 1990, Dunning et al. 1992, Wiens 2002 for review). Recent empirical examples of this (in the marine environment) include those of habitat patch (kelp holdfast) number and proximity on associated invertebrate assemblages (Goodsell & Connell 2002, 2008), and seagrass patch size on invertebrate population composition (Tanner 2006). Similar spatial effects are seen in modelling studies such as that of Lindenmayer and Possingham (1996) who showed that the spatial configuration of habitat patches affects the probability of extinction of Leadbeater's possum.

1.2 Dispersal, connectivity and population dynamics

The pattern of structural elements in a landscape often interacts with the process of dispersal, affecting population connectivity and thus population dynamics (e.g. Van Dorp & Opdam 1987, Bond et al. 2000). Propagule dispersal in terrestrial and marine environments is essentially the movement of seeds or larvae from a natal site to a final settlement/development site (e.g. Gerrodette 1981, Nathan & Muller-Landau 2000). In this usage, dispersal is distinguished from 'transport' by the requirement of movement from a natal to a settlement site rather than movement between any random points (Pineda et al. 2007). A multitude of bio-physical factors determine dispersal, and the resultant spread of propagules is described by the term connectivity (Cowen et al. 2006, Gawarkiewicz et al. 2007). In essence, the connectivity of two patches of habitat is the degree to which bio-physical characteristics of the environment and organism allow dispersal to occur successfully between them at a given scale. In this sense, connectivity could be said to represent realised dispersal over a particular scale. There are several formal definitions of connectivity, often highlighting the aspect or scale of interest (e.g. landscape connectivity vs. metapopulation connectivity), resulting in the use of different measures of connectivity (see Tischendorf & Fahrig 2000, Moilanen & Hanski 2001, Tischendorf & Fahrig 2001 for discussion). For example, landscape connectivity is defined as the "degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993: 571). In marine populations, connectivity at the scale of a species' range may be similarly defined as the linkage of populations (or metapopulations) by the exchange of larvae, recruits, juveniles or adults (Palumbi 2003). The idea of 'reproductive connectivity' – defined as the number of dispersing larvae moving among subpopulations that survive to reproduce – has also been recently introduced as a more meaningful measure of connectivity (Pineda et al. 2007).

The distribution and population dynamics of organisms that undertake a dispersive phase, particularly through fluid media (air or water), are the result of complex and often non-linear interactions between multiple factors over multiple scales (Cowen et al. 2000, Michener et al. 2001, Nathan et al. 2005, Pineda et al. 2009). In the broadest terms however, only births, deaths, emigration and immigration bring about changes in a population's size (Gaines & Lafferty 1995), ultimately determining the population's survival in a particular habitat and thus its distribution and structure. While birth and death rates can certainly be the product of multiple interacting factors, they are localised processes that are relatively easy to measure. In contrast, dispersal is affected in complex ways by many interacting factors at various scales.

The ability of organisms to disperse influences many ecological patterns and processes making dispersal a central and profoundly important aspect of population dynamics. This centrality can be seen in theoretical and empirical works linking attributes of dispersal to past and present species' distributions (Hansen 1980, Jablonski & Lutz 1983, Carlon & Olson 1993), physiological trends (Etienne & Olff 2004), interspecific competition and metacommunity coexistence (Leibold et al.

2004, Noda 2009), gene flow (Perrin et al. 2004, Sotka et al. 2004), predation (Wieters et al. 2008), species diversity (Forbes & Chase 2002), colonization (Gaylord & Gaines 2000) and recovery after disturbance (Sousa 1984, Johnson & Preece 1992), and evolution (Palumbi 1994). Perhaps most importantly, dispersal establishes the scale at which these population/community processes occur, particularly with respect to the physical environment or landscape (Wiens 1997, Tischendorf & Fahrig 2000, Kinlan & Gaines 2003, Kinlan et al. 2005, Levin 2006).

The process of dispersal is complex, but is strongly linked to the physical environment in 5 primary ways. Most fundamentally, the physical environment (or medium) determines the dimensions available for movement and dispersal. This may seem obvious, but is of considerable relevance to the basic shape of any dispersal kernel – the spatial probability density function describing propagule deposition/settlement with respect to natal location (Gerrodette 1981, Nathan & Muller-Landau 2000). Thus, as described by Gawarkiewicz and co-workers (2007), a fluid environment such as air or water allows 3-dimensional dispersal, while non-flying/floating organisms are restricted to 2-dimensional dispersal. In cases where the adult habitat is different from the juvenile habitat, the final adult distribution depends on the former. This is of particular relevance to intertidal invertebrates which are ultimately limited to 1-dimensional dispersal described by the linear land-sea boundary (Gawarkiewicz et al. 2007); perhaps more correctly this should rather be considered 2-dimensional dispersal, but with very limited movement in the cross-shore direction.

Secondly, the physical attributes of the medium (most importantly density and viscosity) have energetic implications for the buoyancy and movement of dispersing organisms; terrestrial organisms must work harder against gravity, but expend less energy overcoming aerodynamic friction than aquatic organism do hydrodynamic friction (Denny 1990).

Thirdly, for passive dispersers the ‘vector load’ – essentially the carrying capacity – of the medium (designated Q) affects the dispersal kernel (Nathan et al. 2008). For example, ocean currents by which floating or rafting seeds disperse provide a very large carrying capacity and therefore theoretically increase the number of long-distance dispersal events (Nathan et al. 2008).

A fourth fundamental aspect of the medium, particularly pertinent to passive dispersal, is its provision of transport. For atmospheric and oceanographic transport, both the mean flow and deviations around it are important determinants of dispersal (Nathan et al. 2005, Cowen & Sponaugle 2009). Related to this, landscape features and heterogeneity in various forms can further shape dispersal through their influence on transport processes at various scales (Nathan et al. 2005, Roughan et al. 2005). Examples of small scale landscape effects may be seen in cases of seeds becoming non-randomly trapped by emergent substrates in a river (Schneider & Sharitz 1988), or simply by vegetated relative to barren ground (Andersen 1991). Topography can have micro-scale effects with seeds accumulating in wind-protected sites and broader scale effects such as seeds being more easily washed off steep slopes than level ground (Bertiller 1992). In recognition of topographic effects on wind dispersal, elevation is incorporated into models of seed dispersal potential (Tackenberg et al. 2003). Even the dispersal of large terrestrial mammals can be affected by landscape features, as seen in the white-tailed deer for which average and maximum dispersal distances relate to forest cover (Long et al. 2005). Examples from studies applying landscape ecology concepts to within-river processes show how the spatial configuration of so-called 'dead-water zones' (i.e. pools or eddies) affects the dispersal of riparian plant propagules (Johansson et al. 1996), aquatic insects (Bond et al. 2000) and materials (Kling et al. 2000). These examples demonstrate that the geometric arrangement or configuration of structural landscape features and habitat patches can influence dispersal and overall connectivity.

Finally, underpinning dispersal is the interaction between the organism's behaviour and the medium (Cowen & Sponaugle 2009). Migration and dispersal occur via a spectrum of active and passive means (e.g. Maguire 1963, Savidge & Taghon 1988, Cowen et al. 2006). In the terrestrial environment, movement is often active; a purposeful movement of juveniles away from the natal habitat to establish a new territory (e.g. Scandinavian wolverines Vangen et al. 2001), determined largely by choices of the animal. Dispersal through fluid environments (air and water) can be entirely passive, with propagules, seeds or non-motile larvae, being transported solely by wind or water currents as the case may be (Myers et al. 2000, Tackenberg et al. 2003). Alternatively, dispersal may involve some active behaviour or swimming, such as diel and other vertical migrations in aquatic organisms (Hill 1998, Helfrich & Pineda 2003, Shanks & Brink 2005, Fiksen et al. 2007, North et al. 2008) or body positioning in some terrestrial insects (e.g. Washburn & Washburn 1984), which modifies the individual's usage of the fluid transport mechanism. Other behaviours may simply enhance lift, as seen in terrestrial wind dispersers such as some species of spider which use 'ballooning' techniques (Duffey 1956, Schneider et al. 2001, Bonte et al. 2003) analogous to the byssus drifting used by post-larval mussels (Lane et al. 1985). Both have developed the ability to use the fluid environment around them to enhance dispersal to new habitats. Therefore, connectivity – the ability of organisms to move between 'patches' – is governed by the interactions between structural landscape features and configuration, the biophysical nature of the route (the medium and its properties) and the biology and behaviour of the organism (Henein & Merriam 1990). Ultimately, dispersal (and thus connectivity) is said to be landscape- and species-dependent since even structurally connected areas of habitat are not necessarily functionally connected for species with differing behaviours and abilities (With 1997, Tischendorf & Fahrig 2000). Likewise**,** structurally disconnected areas are not necessarily functionally disconnected for all species.

1.3 Metapopulation connectivity in the marine environment

The various marine environments - pelagic, demersal, and benthic, including the intertidal - each offer a very specific array of unique bio-physical characteristics. Similarly, marine organisms employ a wide variety of reproductive and developmental modes (Strathmann 1990, Levin & Bridges 1995) and differ at small-scales in their methods of dispersal (*sensu* Negrello Filho et al. 2006).

Marine taxa, especially fish and some sessile/sedentary invertebrates, are generally capable of dispersing over greater distances (for bivalves and anemones this can be 20 - 500km) than terrestrial analogues such as plants (<1m – 100m) (Carr et al. 2003, Kinlan & Gaines 2003, Shanks et al. 2003a). Since mean dispersal distance is a key determinant of demographic connectivity (Kinlan &

Gaines 2003), populations of marine taxa with long distance dispersal capabilities have the potential for a high degree of connectivity, similar to the within-stream connectivity of lotic systems (Wiens 2002). In general terms, a high degree of connectivity should have several implications for population structure, demography and distribution, such as less predictability (Carr et al. 2003) and greater decoupling of local adult stocks from local larval or post-larval supply (e.g. Lipcius et al. 1997).

The remarkably wide range of reproductive behaviours and developmental modes of marine invertebrates (Levin & Bridges 1995) is generally broken down into 4 key modes, each identifying a characteristic extreme within the continuum of developmental types (Thorson 1946, 1950, Mileikovsky 1971, Vance 1973). These include feeding (planktotrophic) and non-feeding (lecitotrophic) free-swimming pelagic larval forms, a direct development form in which the larval stage takes place within an egg mass or brooding parent, and a non-pelagic (demersal) feeding form. By completing the classification introduced by Scheltema (1989), Levin and Bridges (1995) provide a more exhaustive classification scheme which includes categorisation of developmental mode according to 'dispersal potential' (i.e. teleplanic or aplanic). This category is based solely on larval duration so as to circumvent inconsistencies with classification based on nutritional mode or type of morphogenesis (Levin & Bridges 1995). Although the pelagic larval duration (PLD) is still upheld as a reasonable predictor of dispersal (Kinlan & Gaines 2003, Siegel et al. 2003), the rigidity of the paradigm that extended larval duration implies long distance dispersal and thus very open populations, is now being challenged (reviewed by Levin 2006). Recent modelling and empirical studies have shown dispersal distances to be shorter (e.g. McQuaid & Phillips 2000), and self-recruitment (Cowen et al. 2000, Swearer et al. 2002) and retention (Wolanski et al. 1989, Largier 2004) to be more common than previously thought.

At local scales benthic marine organisms disperse into patches of habitat by horizontal crawling on the substratum, by vertical settling from the water column, or by burrowing in the case of soft sediment substrata (Negrello Filho et al. 2006). Thus, the application of terrestrially derived landscape components (patch, corridor and matrix) to marine environments will differ according to the environment and organism. In the case of sedentary benthic intertidal invertebrates, areas of suitable substrata are patches, while inhospitable substrata form the matrix. For these organisms, habitat corridors in the traditional sense are not important since adults do not move among patches, and larvae cross discontinuities in adult habitat by pelagic dispersal (Carr et al. 2003). If however, the idea of a dispersal corridor is applied to the water through which larvae disperse, the pelagic environment must be viewed as key determinant of connectivity in the same way as structurally connected terrestrial or riverine landscapes. It is through these 'marine corridors' that larval transport and dispersal occur.

The sessile or sedentary nature of adult intertidal invertebrates such as barnacles and mussels, is distinctive, having no real equivalent in terrestrial systems (Paine 2005). This means that all dispersal occurs during the larval stage, making the colonization, connectivity and persistence of intertidal invertebrates critically reliant upon the pelagic dispersive phase.

Larval transport is influenced by various physical mechanisms acting either in the cross-shore or along-shore direction, the latter being particularly relevant to population connectivity (Pineda et al. 2007). Physical mechanisms include wind-induced flows (McQuaid & Phillips 2000, Tapia et al. 2004) and oceanographic features such as internal waves (Shanks & Wright 1987), tidal currents (Queiroga et al. 2006) or bores (Pineda 1991, 1994a), upwelling/downwelling events (Shanks & Brink 2005) and in particular, the various frontal systems associated with these features (Franks 1992, Helfrich & Pineda 2003, Scotti & Pineda 2007). Oceanographic mechanisms often interact with, or are produced by, coastal topography and bathymetry (Wolanski & Hamner 1988, Geyer & Signell 1992, McCulloch & Shanks 2003, Schmidt et al. 2005), and have been shown to enable nearshore retention of larvae and plankton (e.g. Murdoch 1989, Wing et al. 1998b, Roughan et al. 2005).

Larval use of, and behavioural interaction with, ocean flows adds an additional level of complexity to dispersal and population connectivity. This is because, while most marine larvae have some swimming capabilities, swimming speeds are generally weak (< 1mm s^{-1}) and incapable of directly opposing ocean flows or powering dispersal, making larvae reliant on ocean currents (Underwood

& Keough 2001). Modelling (Franks 1992, Witman et al. 2003) and empirical studies (DiBacco et al. 2001, Helfrich & Pineda 2003, Paris & Cowen 2004, Tapia & Pineda 2007) have demonstrated that vertical swimming and migratory behaviours interact with directional transport mechanisms and alter dispersal, often resulting in increased retention. In this sense, larval behaviour has as important an influence on larval transport as advection and diffusion (Pineda et al. 2007), and in this capacity has important effects on population connectivity.

While coastline topography and shelf bathymetry influence the physical transport mechanisms themselves, coastal heterogeneity (km scales) and substratum heterogeneity (cm scales) are especially crucial to intertidal organisms that must settle and reproduce along the land-sea interface (e.g. Archambault & Bourget 1996). For intertidal organisms inhabiting hard substrata, the availability of space to settle and grow is often a key resource (Roughgarden et al. 1985, Paine 2005). In addition, rocky substrata along many coasts are fragmented, to a greater or lesser extent, by sand. Rocky intertidal invertebrates therefore face very particular configurations of habitat that are often highly fragmented.

In light of the broad determinants of dispersal and connectivity (landscape features and configuration, the biophysical nature of the route, and biology and behaviour of the organism), the unique intricacies of nearshore and intertidal marine environments and the dispersing organisms that inhabit them, create widely varying and complex patterns of connectivity.

1.4 Coastline topography and nearshore oceanography

Bays and their associated headlands are common features of coastlines around the world. The presence of bays and headlands, and the width of the continental shelf influence nearshore oceanography (Goschen & Schumann 1988) and the creation of coastal retention zones (Largier 2004). In this capacity, these features have been used as predictors of the retentiveness of coastal sites (Reaugh 2006). As landscape scale features, bays and headlands produce persistent eddies and interact with or create oceanographic features such as fronts (Pingree et al. 1978) and upwelling shadows (Roughan et al. 2005).These features therefore affect both the along- and cross-shore transport upon which dispersal and connectivity depend (Gawarkiewicz et al. 2007). The implications of this are that certain areas of coast are likely to be more retentive than others. Relative to the open coast, bays have been characterised by very particular biophysical environments, differing in wave exposure (Burrows et al. 2008, von der Meden et al. 2008), temperature structure (Graham et al. 1992, Schumann et al. 1995) and food availability (Archambault et al. 1999); bays have also been shown to retain locally, and entrain externally, produced larvae (Murdoch 1989, Wing et al. 1998a, 1998b, Largier 2004). Topographically mediated differences in populations (von der Meden et al. 2008) have now also been shown to extend to the genetic structure of intertidal mussel populations, with genetic evidence revealing bays to have greater genetic endemism (Nicastro et al. 2008b). Persistent biophysical differences between bays and the open coast are likely to produce persistent ecological patterns of settlement, recruitment and adult abundance. These persistent bio-physical differences are also likely to affect post-settlement mortality – which is a fundamental aspect of reproductive connectivity (Pineda et al. 2007).

Although greater larval densities, settlement, recruitment and adult abundances in bays relative to the open coast have been demonstrated in various parts of the world (Gaines & Bertness 1992, Helson & Gardner 2004, Roughan et al. 2005, Mace & Morgan 2006)**,** little replication at the level of ‘bay’ has been attempted. Notable exceptions are the studies of Archambault and Bourget (1996, 1999), Archambault and colleagues (1998, 1999) and those of Wing and colleagues (1995, 1998a, 1998b), who used sites and nearshore transects extending alongshore across multiple bays and headlands.

1.5 Study aims

As Pineda and colleagues (2009) describe, the complexity of processes affecting benthic life is immense, comprising of at least 4 categories of process: those important to the larval pool, larval transport, and those acting at settlement and during post-settlement life. An ideal experiment examining these processes – testing multiple interacting factors and repeated in a wide range of environments over many years – would be logistically and financially prohibitive (Pineda et al. 2009). In accordance with suggestions of Pineda and colleagues (2009), the present study takes somewhat of a reductionist approach in seeking to establish landscape (topography) related patterns in populations of intertidal mussel settlers, recruits and adults as evidence of fundamental ecological processes acting at each life stage and the relative importance of these processes. Furthermore, the study duplicates species, testing two very similar and co-occuring mussel species in an attempt at finding evidence of common mechanisms (Lagos et al. 2005) and takes account of the potential openness of metapopulations of these organisms by using a broad scale of study (Underwood & Keough 2001, Kinlan et al. 2005).

The present study aimed to establish if there are general patterns of settlement, recruitment, post-settlement mortality and adult abundance related to coastline topography, thereby assessing the role of topography across different life stages of mussels. Specifically, patterns were examined with respect to the presence of large 'open' bays and their associated headlands relative to the open coast. The qualification of habitat (as sheltered bay or exposed open coast) was therefore primarily based on topography, but was confirmed by quantitative measurements of wave exposure in each habitat type. In addition, correlations between settlement, recruitment and adult mussel cover were examined at regional and local scales in order to identify causal processes. Based on the nature of these relationships, the relative importance of each parameter, at each scale, is discussed. The use of multiple (4) bays and intervening stretches of open coast, and the duplication of species, provides some much needed repetition/replication within a single biogeographic region. The varied size and shape of the bays should serve only to increase the generality of results, much as repetition of experiments in different regions would.

In synthesis, this thesis is comprised of 4 working chapters beginning with adult distribution. Successive chapters examine topography-related patterns in preceding life stages with a view to explaining the adult distribution. Chapter 2 therefore surveys and compares adult mussel cover in bays and on the open coast. The third chapter establishes spatial and temporal patterns of settlement and recruitment, and investigates relationships between settlement, recruitment and adult cover.

Specifically, the chapter tests the hypothesis that settlement and recruitment rates will be greater in bays than along the open coast. The fourth chapter tests the hypothesis that mussel settlement on artificial substrata (collectors) will be increased by the presence of biofilm and conspecific settlers, both individually and in combination; this chapter forms a prerequisite study needed to clarify methodological problems related to the use of artificial settlement substrata (collectors) used in the fifth working chapter of the thesis. The final (fifth) working chapter uses a new method to establish the levels of post-settlement mortality in bay and open coast habitats. Using these data the hypothesis that post-settlement mortality will be lower in bays than on the open coast was tested.

1.6 Study region

The warm-temperate south coast is one of three distinct biogeographic regions in South Africa (Bustamante & Branch 1996). Extending west from the eastern margin of this region, the study area encompasses a 550km section of coastline (Fig 1). This section of coast is characterised by 4 prominent 'half-heart' or log-spiral bays (Field & Griffiths 1991), which are south facing and open to the sea. Each bay is composed of a rocky headland at the western end with a sweeping curve or 'notch' running eastward, often made up by sandy beaches. The range in straight-line distance across the bay mouths range from 16km (Plettenberg Bay) to 61km (Algoa Bay) – as measured from tip of the headland to nearest section of straight coast. A total of 22 sites, divided equally between bay and open coast habitats, see Fig 1) and separated by 10s of kilometres, were selected between Kenton-on-Sea (34˚ 41´S, 26˚ 40´E) and Mossel Bay (34˚10´18˝S, 22˚7´41˝E). Bay sites were defined as those lying within the notch of the bays; open coast sites were positioned along the intervening stretches of open coast. Sites were simply selected where there were mussels and where access allowed; the quantity of rocky habitat present was not a criterion. Each of the studies and experiments presented are based on work done at these sites, or a subset of them.

On a large scale, the Agulhas current is the chief oceanographic feature of the region and flow follows the shelf-break diverging from the coast around the eastern Agulhas Bank (Lutjeharms 2006). Within the study region, boundary flow of the current interacts with landward waters to produce mesoscale circulation phenomena including meanders, eddies and plumes (Lutjeharms et al. 1989). These features do extend their influence into the nearshore environment, as demonstrated by the intrusion of plume (warm), and eddy (cold) water into Algoa Bay (Goschen & Schumann 1994). In addition, persistent upwelling is associated with interactions between the Agulhas current and the area of increased shelf width in the vicinity of Port Alfred (Lutjeharms et al. 2000). Continental shelf water is further modified by local wind and tidal forcings, bathymetry and topographical coastline characteristics (Goschen & Schumann 1988). Pockets of upwelling, initiated in part by the presence of the capes (headlands) in the study region (Schumann et al. 1982, Beckley 1983, Walker 1986), occur between December and May (Schumann et al. 1982). In terms of the very nearshore, the south coast is generally exposed to high levels of wave action, although some areas (particularly within bays) are relatively sheltered (McQuaid et al. 2000, Erlandsson et al. 2005).

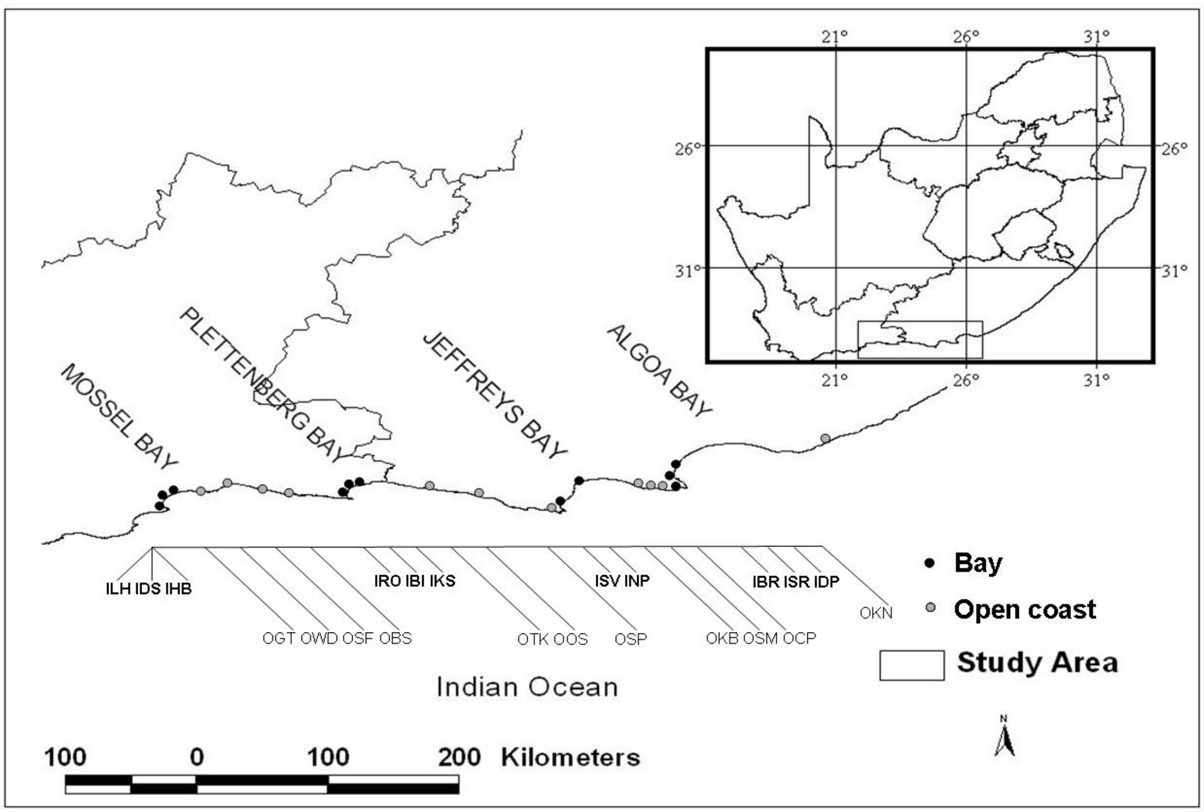

Figure 1.1 Study sites along the south coast of South Africa. Bay site codes indicated in bold text with prefix 'I' and open coast sites are those with prefix 'O'. For full names and coordinates of sites, see Appendix 1.1.

1.7 Study species

Intertidal assemblages have been extensively used as model systems to examine a wide variety of ecological processes (Bertness & Leonard 1997, Connolly & Roughgarden 1998). Mussels in particular have been used successfully as model organisms (Gosling 1992) and are the focus of the present study. The brown mussel *Perna perna* (Linnaeus 1758) and the Mediterranean blue mussel *Mytilus galloprovincialis* (Lamarck 1819) are bivalve molluscs belonging to the family Mytilidae. The mytilid evolution and retention of byssal threads, allowing mussels of this family to attach to hard substrata, together with their unique heteromyarian body form, has resulted in their domination of rocky shores in many regions of the world (Suchanek 1985, van Erkom Schurink & Griffiths 1991, Seed & Suchanek 1992).

As dominant space occupiers, mussels fulfill an important role as ecosystem engineers (Bertness & Leonard 1997, and for review see Gutiérrez et al. 2003). In this context mussel populations have several implications for the intertidal community as a whole. Mussel beds provide unique habitat for a host of associated organisms, and are therefore of great importance to intertidal biodiversity. Being highly productive filter feeders, mussels also afford a strong link between the primary production of the pelagic environment and the intertidal benthic community (Seed et al. 2000). Further to this, it has been observed that the release of reproductive (gametic) material during spawning forms a significant energy contribution to the surrounding community that may affect the "entire economy of the shore" (van Erkom Schurink & Griffiths 1991).

Of the two species considered in this study only *P. perna*, a warm-water form, is indigenous to South Africa and extends in range from Mozambique down to the southwestern Cape (van Erkom Schurink & Griffiths 1991). The invasive *M. galloprovincialis* has a current range of ca 2050km of coastline from southern Namibia to the Eastern Cape (Kidds Beach), and is the dominant intertidal organism within much of this area (Branch & Steffani 2004, Robinson et al. 2005). Both species are found extensively within the study area of the south coast, which is the only region of South Africa in which *P. perna* and *M. galloprovincialis* co-exist (Branch & Steffani 2004). Along this coast, *P. perna* and *M. galloprovincialis* display partial habitat segregation, forming three mussel zones on the low shore. The upper mussel zone is dominated by *Mytilus*, the low zone by *Perna* and the mid zone is a mixed zone where the two species overlap and co-exist (Bownes & McQuaid 2006). Most mussel beds along the south coast are monolayered (McQuaid et al. 2000) and discrete, often occupying alongshore distances of no longer than 25m and separated by sandy beaches (Erlandsson et al. 2005).

For *P. perna* 3 to 4 spawning events occur per year, most often in winter and spring (McQuaid and Phillips 2007), but these are variable and have been shown to occur in summer as well (Zardi et al. 2007). Interestingly, it seems that spawning of *P. perna* and *M. galloprovincialis* is somewhat asynchronous, with spawning of *M. galloprovincialis* peaking in October and April (Zardi et al 2007). These peaks may be protracted as observed by van Erkom Schurink and Griffiths (1991), who showed extended spawning periods (October – February and April – July). Peaks in primary settlement of *P. perna* on this coast usually occur during April and between September and November (Beckley 1979, McQuaid & Phillips 2007). The same is true of *M. galloprovincialis*, which on the west coast, settles in the summer months and particularly in April (van Erkom Schurink & Griffiths 1991).

Appendix 1.1

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

Code	Name	Latitude	Longitude	Code	Name	Latitude	Longitude
Bay					**Open coast**		
ILH	Lighthouse	-34.1811	22.15765	OGT	Glentana	-34.0523	22.32204
IDS	Dias Strand	-34.1717	22.12804	OWD	Wilderness	-33.9970	22.56628
IHB	Hartenbos	-34.1273	22.11931	OSF	Sedgefield	-34.0292	22.76841
IRO	Robberg	-34.0991	23.37729	OBS	Brenton-on-Sea	-34.0747	23.02041
IBI	Beacon Isle	-34.0545	23.37974	OTK	Tsitsikamma	-34.0239	23.89663
IKS	Keurboomstrand	-34.0050	23.45823	OOS	Oubosstrand	-34.0730	24.22423
ISV	Sea Vista	-34.1708	24.83461	OSP	Seal Point	-34.2099	24.82544
INP	Noordkloofspunt	-34.0263	24.93112	OKB	Kini Bay	-34.0223	25.38007
IBR	Bird Rock	-33.9841	25.67201	OSM	Skoenmakerskop	-34.0412	25.53365
ISR	Shark Rock Pier	-33.9799	25.65851	OCP	Chelsea Point	-34.0465	25.63431
IDP	Deal Party	-33.8996	25.62003	OKN	Kenton-on-Sea	-33.6833	26.66667

CHAPTER 2

THE END IS THE BEGINNING: A SURVEY OF ADULT COVER

* This chapter is a modified version of a published manuscript (von der Meden CEO, Porri F, Erlandsson J, McQuaid CD (2008) Coastline topography affects the distribution of indigenous and invasive mussels. MEPS 372: 135 – 145), and includes contributions of Dr Erlandsson to the semivariogram analyses (see sections 2.2.3 and 2.3.3).

2.1 Introduction

For rocky intertidal organisms, patterns of adult distribution and abundance are the culmination of successful settlement governed by supply-side factors (Morgan 2001, Underwood & Keough 2001), and successful recruitment governed by local post-settlement factors such as competition, predation and disturbance (Connell 1961, Dayton 1971, Keough & Downes 1982). Of course, the adult populations continue to be influenced by these post-settlement processes. The surviving adult population is therefore an integrated record of the sum of these life history elements – settlement, recruitment and adult life. Despite the difficulty of dissecting this 'sum' into its respective parts, the meso-scale pattern and size of adult populations describing where, and how large populations are (as well as where they are not), is a good starting point for investigating the influence of 'landscape-scale' features (bays and headlands) on such populations. This is because bays and headlands are known to physically alter both the pre- and post-settlement environments in a variety of ways, including retention, wave exposure, productivity and food availability (Archambault & Bourget 1999, Largier 2004, Nicastro et al. 2008a), and any pervasive effects of these alterations should be reflected in the integrated signal of adult populations (e.g. Guichard et al. 2003). In this respect, patterns in adult populations may be especially important for sedentary organisms, which by virtue of their immobility, are relatively less dynamic than other life history stages, making them a fixed reference point from which to view the other stages.

Physical variables such as wave exposure (Hammond & Griffiths 2004, Westerbom & Jattu 2006), wind (McQuaid & Phillips 2000, Tapia et al. 2004), surface rugosity (Petraitis 1990), large oceanographic mechanisms (Shanks 1983) and micro-hydrodynamics (Pineda 2000, Dobretsov &

Wahl 2008) have key roles in either or both the pre- and post-settlement periods, and therefore produce variability in adult benthic marine populations. Several of these physical variables, including coastal oceanography, wind and wave exposure relate to, or are influenced by, topography at various scales (Schumann et al. 1982, Delafontaine & Flemming 1989, Guichard et al. 2001, McCulloch & Shanks 2003).

Bays and headlands have been implicated in the creation of meso-scale adult distribution patterns, with explanations suggesting larval retention and greater settlement rates as the underlying cause (e.g. Helson & Gardner 2004). Much new evidence supports this explanation, with recent studies of larval distribution, abundance and settlement showing topographically-mediated larval accumulation zones and greater settlement at embayed sites (Roughan et al. 2005, Mace & Morgan 2006).

In a different context, several studies have shown that the exposure of intertidal locations to different levels of wave action affects the distribution, biomass, and composition of rocky shore communities (Kingsbury 1962, Bustamante & Branch 1996, Underwood & Chapman 1998, Hammond & Griffiths 2004). Although there seems to be a general positive correlation between wave exposure and the overall biomass of intertidal assemblages (McQuaid & Branch 1984, Bustamante et al. 1997), biomass is usually highest at intermediate levels of exposure (Steffani & Branch 2003, Westerbom & Jattu 2006). At intermediate levels of exposure, the risk of sedimentation and harm to sessile or sedentary organisms via the dislodging action of waves are reduced. In contrast, intense water action or extreme occasional physical disturbance, such as storms or floods, can affect community structure heavily by removing large patches of assemblages (e.g. Jenkins et al. 2005, Erlandsson et al. 2006). In such circumstances, biological interactions, particularly between native and invasive species, may play a fundamental role in the re-structuring of intertidal communities (Erlandsson et al. 2006). The indirect effects of wave action extend to the maintenance of food supply and feeding efficiency through effects of water velocity and diffusion (Jumars & Nowell 1984, Frechette et al. 1989, McQuaid & Lindsay 2000, Steffani & Branch 2003, Westerbom & Jattu 2006).

Both meso-scale investigations of larval distribution and settlement, and localised studies addressing *in situ* effects of wave exposure are linked directly to coastline topography. This chapter attempts to understand better the overarching effect of topography on intertidal populations by examining wave exposure and adult mussel distribution in relation to topographic features.

In order to do this, a survey of percentage adult mussel cover of the 2 study species (*Perna perna* and *Mytilus galloprovincialis*) was undertaken across bay and open coast habitats of the study region. Similarly, wave exposure was measured in winter and summer at a subset of sites to give a quantitative picture of wave action in the study region. Due to the more sheltered nature of bays and because of possible larval retention, I tested the hypothesis that bays will, in general, support greater cover of mussels. Furthermore, the study tested whether the weaker attachment strength of *Mytilus* on this coast (Zardi et al. 2006) pre-disposes the species to greater wave induced losses. Hence, a second hypothesis was put forward: differences in cover between bay and open coast sites will be most pronounced for *Mytilus* because of its weaker attachment strength on this coast. Finally, the hypotheses that there is spatial dependence of variability in the distribution of both *Perna* and *Mytilus* along the south coast of South Africa and that the variability patterns of the 2 species are related were tested.

2.2 Materials and methods

2.2.1 Wave exposure

A bay environment implies a habitat more sheltered from wave action than the open coast, and levels of wave exposure were quantified at a representative subset of sites. Two approaches were required for this, as both wave force and overall water movement/flux needed to be assessed (Bell & Denny 1994). The former indicates the hydrodynamic forcing to which organisms living in each habitat are subjected; the latter quantifies the flux, diffusion and turbulence of the passing water. Maximal wave force was measured using dynamometers (Bell & Denny 1994), while water movement was assessed by calculating mass loss from cement balls (adapted from Kaehler 1999). Dynamometers (4 site^{-1} in June and 5 site^{-1} in November) and cement balls (5 site^{-1} in both months) were deployed simultaneously at 5 bay and 5 open coast sites and collected after 24 hours. This was done once in November (summer) and once in July (winter). In an attempt to relate wave force to potential disturbance, lift forces for each species were calculated for mussels living in beds and related to mean attachment strengths (N) recorded in Plettenberg Bay by Zardi and co-workers (2006). Lift forces, those acting normal to the substratum due to a difference in pressure created by a wave passing over a mussel bed, were calculated by converting maximal wave force data to velocity values. This was done according to the equation, $F_{lift} = ½ \rho U^2 C_l A_{min}$, where ρ is the density of sea water (1.024kg m^{-3}), U is the water velocity (m s^{-1}), C_l is the coefficient of lift (0.88) and A_{min} is the cross-sectional area of a mussel projected perpendicular to the substratum (Denny 1987), as is the case for mussels in beds. The A_{min} used here was that of a medium sized (4.5cm shell length - SL) individual of each species, calculated as an ellipse from the shell height and width data given in Zardi and co-workers (2006). Summer lift forces at each site were then related to the mean summer attachment strengths of 4.5cm individuals of each species from Plettenberg Bay, obtained from Zardi and co-workers (2006). Winter lift forces were likewise related, with attachment strength calculated from summer values, based on a 40% seasonal increase for each species (Zardi et al. 2007), thereby showing how close each species was to detachment under the given conditions. It is important to note that attachment strengths of both species are consistently greater on the open coast than in bays throughout the year (G. I. Zardi et al. unpubl. data). The use of bay attachment strengths is therefore a conservative measure provided merely to demonstrate the relative differences in attachment strength between species.

2.2.2 Mussel cover

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

2.2.3 Data analysis

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

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

Variability indicates changes in the value of a variable, while heterogeneity refers to the structure in variability across different scales. Instead of using a regular distance between sites, and estimating semivariance as a function of different spatial scales or lags (e.g. Dale 2000, Erlandsson et al. 2005), we used spatial tags for the different sites (1 to 22 from west to east) to estimate semivariance as a function of closeness/separation of sites. The semivariance was estimated from the sum of differences in mussel cover between sites at each separation: (1) between the sites closest to each other, (2) between sites with 1 site in between, and (3) between sites with 2 sites in between, etc. (see Appendix 2.1 for equations). Fractal scaling analysis was used to estimate heterogeneity of mussel distributions along the coast. The fractal dimension D = (4-absolute slope)/2 was calculated from the logarithmic semivariogram, i.e. the regression between semivariance and site separation 1 to 11 (since only up to half of the separation can be used, see Erlandsson et al. 2005). D varies between 1 and 2, and higher heterogeneity gives a flatter slope of the regression line in the semivariogram and a higher D-value. To detect significant scaling regions in the semivariogram a 3-step procedure was followed (see Erlandsson et al. 2005 for more details) for each semivariogram: (1) analysis of patterns among residuals (i.e. estimated differences between observed data points and the fitted regression line) was done to distinguish partial regression lines with different slopes and to determine the separation between sites at which the slopes changed; (2) regression analysis of the different slopes; and (3) t-tests comparing different slopes.

To describe the relationship between the variability of *Mytilus* and *Perna* cover in the high and low zones, respectively, along the coast, we used cross-semivariogram analysis, which is related to semivariogram analysis (Dale 2000, see equations in Appendix 2.1). Positive cross-semivariance values indicate a positive relationship between the variables at each separation between sites (i.e. co-variation in abundance) and a negative value indicates a negative relationship. Cross-semivariance values approaching 0 indicate no relationship between variables.

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

2.3 Results

2.3.1 Wave exposure

The 2-way ANOVA of maximal wave force showed no significant effect of month ($F_{1, 44} = 1.7$, $p >$ 0.05) and no interaction between bay status and month ($F_{1, 44} = 4.0$, $p > 0.05$). However, there was an effect of bay status, with forces being significantly greater on the open coast ($F_{1, 44}$ =, 4.4, p <0.05). Mean wave forces ranged from 14.5N (in June at IDS, Fig 2.1a) to 46.24 (in June at OSM, Fig 2.1a).

No significant interaction between bay status and month was found for water flux ($F_{1, 76} = 0.3$, p >0.05). Water flux was significantly lower in bays than on the open coast ($F_{1, 76} = 110.6$, p <0.0001). Month also had a significant effect ($F_{1, 76} = 4.6$, p <0.05), with mean water flux in June being lower than in November. Proxies of flux values ranged between 8.94% mass loss (again in June at IDS, Fig 2.1b) and 33.4% mass loss (in June at OSM, Fig 2.1b).

Despite the temporal limitation of once off physical measurements, the lack of interaction effects in both analyses suggests a consistent difference in wave exposure regardless of sampling time, which allows a clear quantitative distinction between the bay and open coast sites used in the present study.

Figure 2.2 clearly shows that *Mytilus* experiences greater lift forces than *Perna* and, due to its lower attachment strength (Zardi et al. 2006) is closer to detachment. November lift forces were greater than those recorded in June (7 of the 10 sites had values > 20N for both species). Surprisingly, the strongest November forces were recorded at a bay site, ISR (*Mytilus* 43.4N, *Perna* 34.1N), while the lowest values were recorded at IRO (*Mytilus* 15.8N, *Perna* 12.4N). The strongest lift forces were recorded for *Mytilus* in June, at the open coast sites OBS (49.4N) and OSM (48.5N), where they exceeded the “bay” level of attachment strength of this species.

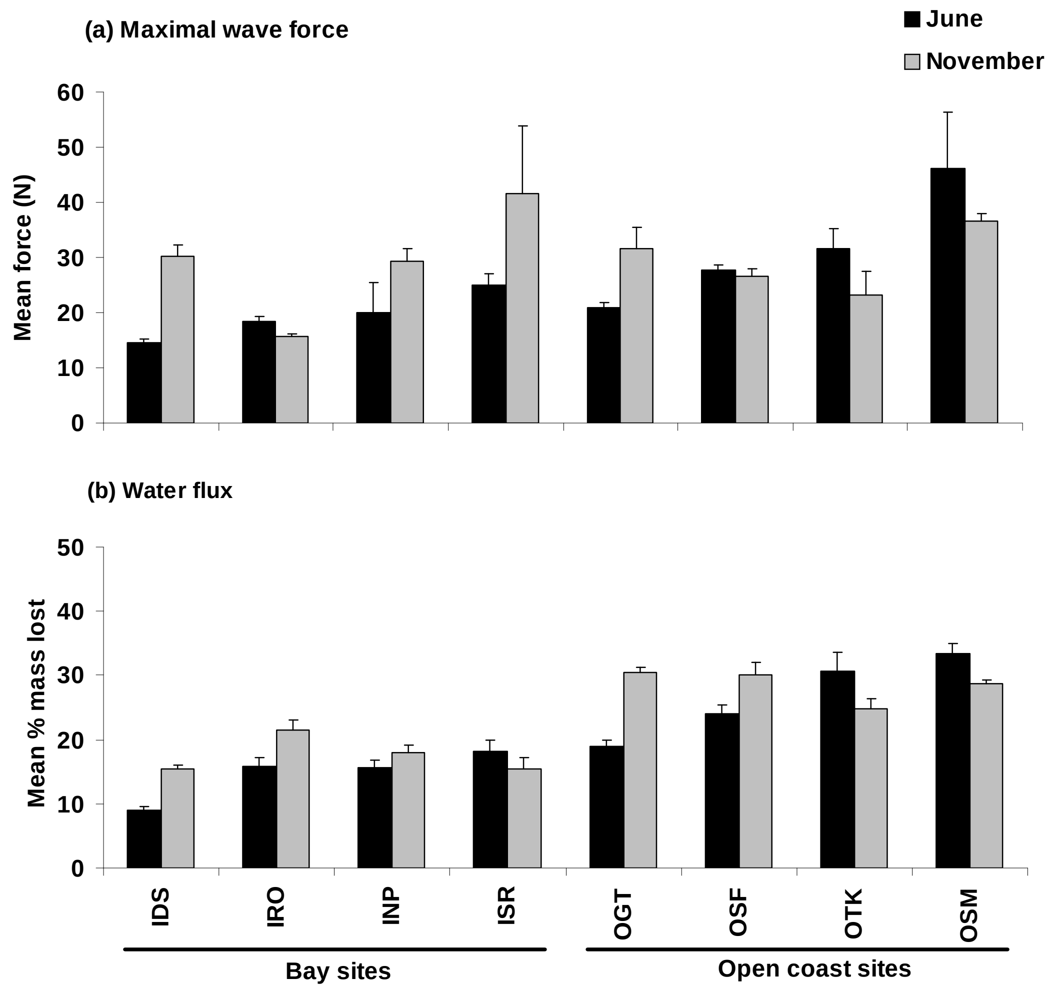

Figure 2.1 (a) Mean (+SE, $n = 3$) 'snap-shot' maximal wave force (N) for November and June, and (b) mean (+SE, $n = 5$) water flux (percentage mass eroded from cement balls) at selected bay and open coast sites. For full list of site names and coordinates see Chapter 1, Appendix 1.1.

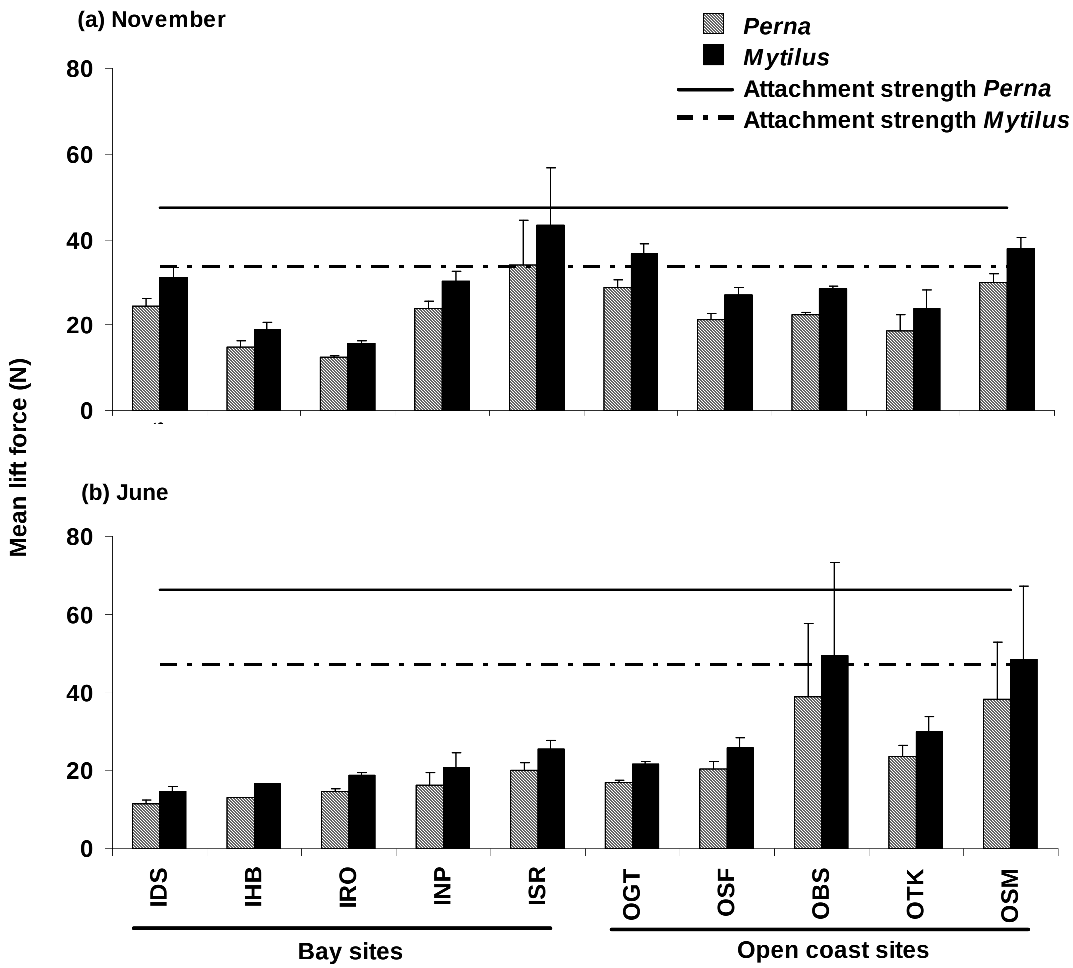

Figure 2.2 (a) Mean (+SE; n = 5) November and (b) June lift forces acting on bed mussels (*Mytilus galloprovincialis* and *Perna perna*, 4.5cm in shell length (SL), of each species. Solid and dashed lines indicate attachment strengths of these mussels, as measured by Zardi et al. (2006 and 2007) in Plettenberg Bay.

2.3.2 Bay and zone effects

Bays were found to have significantly greater *Mytilus* cover than the open coast ($F_{1,\ 324} = 8.1$, $p < 0.05$, Table 2.1a). As expected, there was a significant zone effect ($F_{2,324} = 31.1$, $p < 0.001$, Table 2.1a), with the greatest *Mytilus* cover occurring in the high zone and decreasing across the mid and low zones, as confirmed by the SNK test. Figure 2.3 illustrates both of the main effects, particularly the striking decrease in mean cover from the high to the low zone over bays and the open coast. The figure also shows the large difference in mean high zone cover between bay (18%) and open coast (9%) shores. Corresponding mean percentages for the low zone, bay (0.4%) and open coast

(0.2%), were the lowest. Although figure 2.3 suggests that the greatest difference between bay and open coast was in the high zone, no significant interaction between bay and zone was found ($F_{2,324} = 2.9$, $p > 0.05$, Table 2.1a).

Table 2.1. Results of 2-way ANOVAs of percentage cover estimates for (a) *Mytilus galloprovincialis* and (b) *Perna perna*. Student-Newman Keuls (SNK) post-hoc test results in both cases shown using codes representing B: bay; OC: open coast; H: high zone; M: mid zone; L: low zone.

(a) *Mytilus*

Source	**df**	**MS**	**F**	***p***
Bay (B, OC)	1	1237.3	8.1	< 0.05*
Zone (H, M, L)	2	4736.6	31.1	<0.001**
Bay x Zone	2	437.2	2.9	>0.05
Error	324	152.3		
SNK	B>OC; H> M > L			

(b) *Perna*

Source	**df**	**MS**	**F**	***p***
Bay (B, OC)	1	1062.3	17.9	<0.001**
Zone (H, M, L)	2	5691.7	95.3	<0.001**
Bay x Zone	2	3207.3	5.4	<0.05*
Error	324	590.5		
SNK	B(L) > OC(L), OC(M), B(M) > B(H), OC(H)			

Perna cover was affected significantly by the interaction between bay status and zone ($F_{2,324} = 5.4$, $p < 0.05$, Table 2.1b). SNK tests revealed 3 groups: mean bay low zone cover was the greatest, followed by the open coast low zone, which grouped with the mid zone (bay and open coast). The high zone had the lowest mean cover and, like the mid zone, cover was similar for bays and the open coast. Mean *Perna* cover (Fig 2.3) increased from the high to low zone, with differences between bay (65%) and open coast (41%) being most pronounced in the low zone. High zone percentages were far lower, with a mean for bays of 11% and for the open coast of 7% (Fig 2.3a).

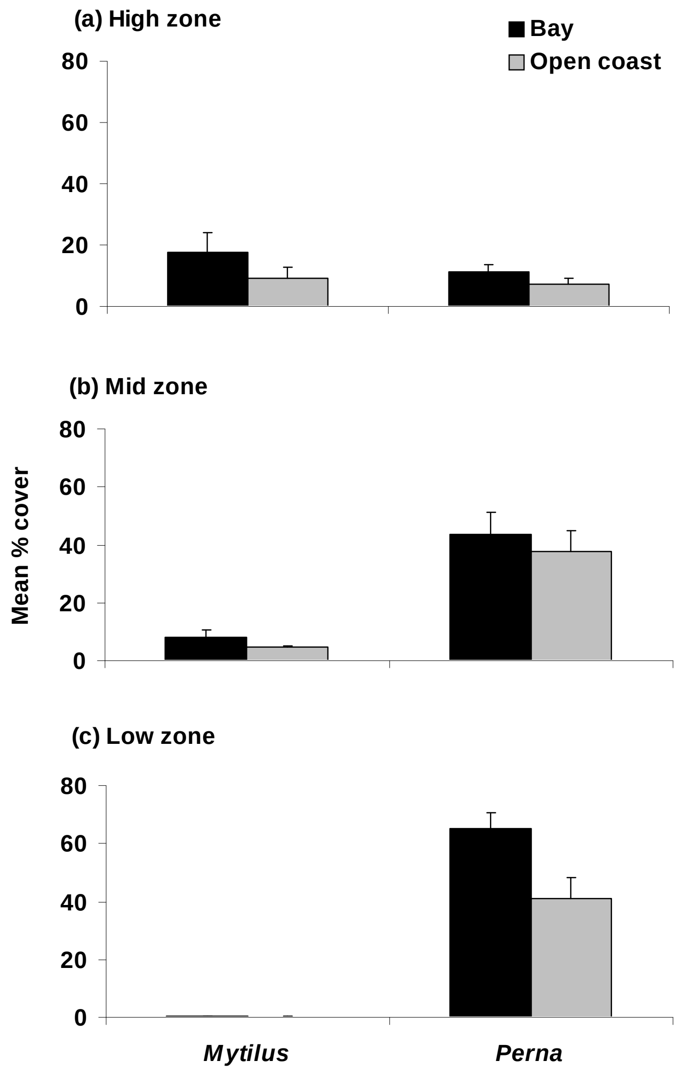

Figure 2.3 Mean (+SE; n = 220) percentage cover of *Mytilus galloprovincialis* and *Perna perna* at bay and open coast sites for each mussel zone: (a) high, (b) mid and (c) low.

2.3.3 Mussel distribution

Mean cover of *Mytilus* in the high zone ranged from 0 to 50.4%, while *Perna* had a range of 0 to 22.5%. Although *Mytilus* often dominated the upper zone, *Perna* had greater cover at 9 of the 22 sites. These deviations from *Mytilus* dominance were site-specific, with no gradient between sites strongly dominated by *Mytilus* and those dominated by *Perna* (Fig. 2.4a). As expected, abundance of *Mytilus* was highest in the upper zone, reaching maximal cover at the 3 sites inside Plettenberg Bay (IKS, IBI and IRO) and at the closest open coast site to the west of Plettenberg Bay (OBS). However, total mussel cover was generally lowest within this zone (Fig. 2.4a).

In the mid-zone, *Perna* dominated nearly all sites, with up to 87.7% cover. The only exception was 1 site in Mossel Bay (IHB), where cover of *Mytilus* was marginally (0.4%) greater than that of *Perna*. *Mytilus* cover was again highest in and around Plettenberg Bay, while *Perna* cover was greatest at Tsitsikamma (OTK), an open coast site. Other areas of notably high *Perna* cover were Algoa Bay (ISR and IBR) and Jeffery's Bay (INP and ISV) (Fig. 2.4b).Although there were sites where mid zone *Perna* cover was greater than low zone cover, generally cover was greatest (2.0 to 85.4%, Fig. 2.4c) in the low zone. *Mytilus* was present at less than half the sites in the low zone and always at ≤ 2% cover.

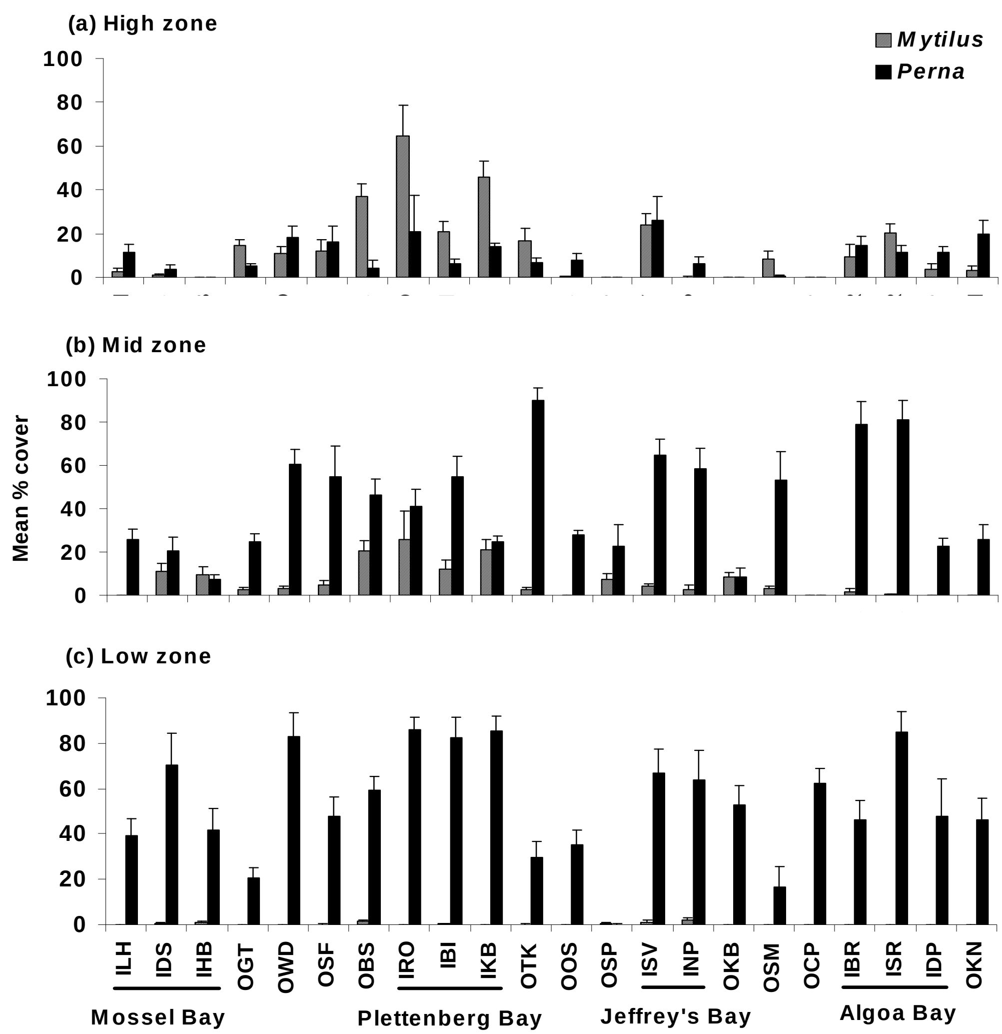

Fig. 2.4 Mean (+SE; n = 5) percentage cover of *Mytilus galloprovincialis* and *Perna perna* at each site (west-east) between Kenton – on – Sea (OKN) and Mossel Bay (ILH) in each mussel zone: (a) high, (b) mid and (c) low.

The semivariograms showed that variability in the distribution (% cover) of *Mytilus* along the coast increased with greater separation between sites, i.e. there was less difference in mussel cover among sites that were close together (Fig. 2.5a). In contrast, *Perna* distribution showed no such spatial structure, with variability being at the same level regardless of the spatial separation between sites (Fig. 2.5b). Thus, heterogeneity among sites was lower for the *Mytilus* distribution in general (D=1.84) and in particular for locations within 5 sites of each other (1st scaling region: D=1.74), while the *Perna* distribution showed a random pattern (D=1.98; random pattern=1.97 to 2.00, Erlandsson et al., 2005) of mussel cover along the coast (Fig. 2.5a-b). Still, in general, there was a positive relationship (i.e. positive values; with the spatial structure from the semivariogram also visible in the cross-semivariogram) between *Mytilus* cover in the high zone and *Perna* cover in the low zone, regardless of the separation among sites; in other words *Mytilus* and *Perna* cover co-varied along the coast (Fig. 2.5c).

2.3.4 Strength of the bay effect

Absolute differences in mean cover between bay and open coast populations (Table 2.2) were greater for *Mytilus* (8.1%) than *Perna* (4.2%) in the high zone, but lower in the mid (*Mytilus* = 3.2%; *Perna* 6.0%) and low zones (*Mytilus* = 0.2%; *Perna* 23.8%). The ratio of mean percentage cover in bays to mean percentage cover on the open coast (Table 2.2) was higher for *Mytilus* than *Perna* in the high (*Mytilus* = 1.90; *Perna* = 1.60), mid (*Mytilus* = 1.7; *Perna* = 1.6) and low zones (*Mytilus* = 2.0; *Perna* = 1.60). Comparison of the high zone *Mytilus* ratio to the low zone *Perna* ratio shows that the strength of the bay effect was greater for *Mytilus* than for *Perna*. However, these results must be interpreted carefully in light of the spatial structure found in *Mytilus* cover around Plettenberg Bay (see results of the semivariograms, section 2.3.3).

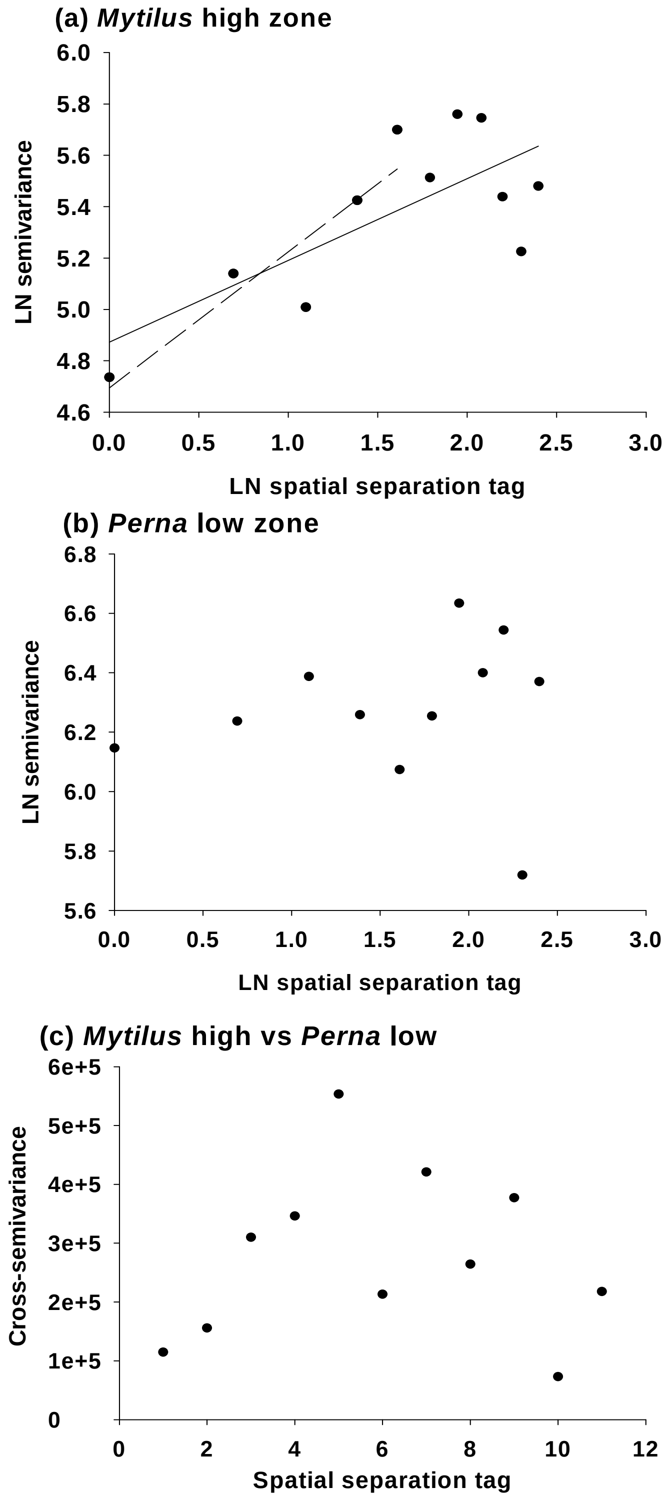

Figure 2.5 Logarithmic semivariograms of (a) *Mytilus galloprovincialis* high zone distribution (whole regression - solid line: r^2=0.54, p=0.01; first scaling region – dashed line: r^2=0.82, p=0.036) and (b) *Perna perna* low zone distribution (r^2=0.01, p=0.74) along the south coast, and (c) cross-semivariogram of *M. galloprovincialis* high zone vs *Perna perna* low zone distributions.

Table 2.2 Absolute differences (bay – open coast) and ratios (bay : open coast) of mean percentage cover of *Mytilus galloprovincialis* and *Perna perna* in each zone. B: bay; OC: open Coast.

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

2.4 Discussion

It is difficult to find a system within which to replicate large-scale sampling programmes or experiments (Archambault & Bourget 1999), but in a biogeographical and ecological sense, the south coast of South Africa provides a relatively homogenous testing ground. The persistent finding of higher mussel abundance in bays than outside bays, obtained from sites including four bays of varied size, shape and geographic location, supports my first hypothesis of a general positive effect of bays on mussel abundance. The fact that the trend was evident in two different species reinforces the generality of our results and, given that the bay effect was observed in adult populations, suggests a pervasive influence on community structure. As expected, the difference in abundance was dependent on zone, with the bay effect being most pronounced for each species primarily within its preferred zone: the high zone for *Mytilus* and the low zone for *Perna*. Also striking was the lack of a geographic gradient, with mussel cover being strongly site specific. This was particularly true of *Mytilus*, which lacked a west to east gradient of decreasing abundance, despite having colonised the south coast from the west (C. D. McQuaid unpubl. data) and despite reaching its eastern limit within approximately 100km of the study area (Robinson et al. 2005). A possible reason for the lack of a distribution gradient is the more recent introduction of *Mytilus* to Algoa Bay (Branch & Steffani, 2004), which has enabled colonisation from the east. Although cover of the two species generally co-varied, they showed maximum and minimum cover in different regions of the coast. *Perna* had areas of high cover in and around each of the 4 bays, while *Mytilus* showed a clear centre of gravity around Plettenberg Bay (Fig 2.4). The increased variability with larger separation among sites for *Mytilus* cover in the high zone indicates the presence of spatial structure, while no such pattern was evident for *Perna* cover in the low zone (Fig 2.5a-b). In fact, the first scaling region found in the *Mytilus* distribution suggests that heterogeneity of *Mytilus* cover was lower amongst closely situated sites (within a 5 site distance) than among sites with larger separation. This pattern mainly arises from the greater *Mytilus* cover at the 5 sites in and around Plettenberg Bay, i.e. at OTK, IKS, IBI, IRO and OBS where *Mytilus* cover ranged between ca 20 to 50 %. The co-variation between *Mytilus* and *Perna* cover in the high and low zones respectively, revealed by the cross-semivariogram (Fig 2.5c), supports the idea that bays affect these two species in a similar way.

Differences in mussel cover between bays and the open coast can be linked to three primary mechanisms: wave exposure (McQuaid & Lindsay 2000), larval retention (Roughan et al. 2005) and larval transport (Shanks et al. 2003b). Differences in water temperature and salinity between bay and open coast sites may also be important for larval growth, and thus mortality since slow growth rates could increase time spent in the plankton and the associated risks of offshore loss, predation and starvation (Schumann et al. 1982, His et al. 1989).

Wave exposure is one of the most important factors affecting the abundances and community composition of sessile intertidal species (Dayton 1971, Bustamante & Branch 1996, Westerbom & Jattu 2006). Mortality of *Perna* is increased on exposed shores (McQuaid & Lindsay 2000), an effect that is more pronounced for *Mytilus* because of its lower attachment strength and wider shell (Rius & McQuaid 2006, Zardi et al. 2006, 2008). Similarly, *Perna* has been shown to have significantly greater growth rates (McQuaid & Lindsay 2000), and to contribute more to total biomass (Bustamante & Branch 1996), on exposed than sheltered shores. On the west coast of South Africa, growth, cover and biomass of *Mytilus* have been shown to be highest at intermediate levels of exposure (Steffani & Branch 2003, Hammond & Griffiths 2004). In the present study, bays provide habitats of lower wave exposure relative to the open coast, but are not enclosed; breaking waves in the bays should therefore keep food particles in suspension, without the negative effects of increased wave induced mortality that is likely on the open coast. Thus, bays along the south coast may provide an environment of intermediate wave exposure that allows greater mussel cover.

The hypothesis that *Mytilus* is more strongly affected by bays than *Perna* (Table 2.2) was supported and agrees well with the predictions of Zardi and co-workers (2006) and Erlandsson and colleagues (2006) that, due to its lower attachment strength and greater cross-sectional area, *Mytilus* will be better able to compete with *Perna* under conditions of intermediate wave exposure where the most can be gained from its superior growth and reproductive capabilities. The relationship between lift forces and attachment strength suggests the ability of sites such as IRO, in Plettenberg Bay, to provide (at times) 'ideal' environments for competitive invasion by *Mytilus*. While it is possible that this second hypothesis – a more pronounced bay effect on *Mytilus* – is supported only where *Mytilus* occurs in high numbers, it is also plausible that a differential bay effect occurs only at small scales, possibly due to localised synergistic interactions between topography, zonation, and disturbance level.

In a broad context, this study shows that adult mussel distribution is strongly affected by coastline topography. The importance of the 'configuration of occupied habitat' in relation to directional advective transport has been discussed by Gaylord and Gaines (2000). In their model, aspects of flow and coastline topography were, by necessity, significantly simplified. With greater understanding of the generality of the effects of coastline topography, models may be able to take more realistic account of this important factor.

The implications of this study are two-fold. Primarily, the non-random distribution of mussels in relation to topography provides evidence for a strong distinction between bay and open coast habitats. One of the suggestions for this pattern is that populations within bays are demographically more closed systems, with enhanced stock-recruitment relationships (McQuaid & Phillips 2007). Greater larval supply, and the often advantageous environmental conditions found in bays, also induce greater settlement and recruitment success (e.g.Gaines & Bertness 1992). In this way, positive feed-back may be established between adult and juvenile mussel populations. Alternatively, or in combination with the retention effect, the less severe daily wave action experienced by bays may favour mussel aggregation at bay sites, protecting the beds from wave-induced dislodgment. This result has important implications for the location of experiments and marine protected areas with respect to bays.

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

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

Appendix 2.1

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

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

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

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

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

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

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

where N is the total number of data points; $N_{(h)}$ is the number of pairs of data points separated by the distance or lag h, or in this case separated by a certain number of sites; X_i and X_{i+h}, and Z_i and Z_{i+h} are the values of two different variables (e.g. percent cover of *Mytilus* and *Perna*) at points i and i+h.

CHAPTER 3

TOPOGRAPHIC AND SEASONAL REGULATION OF SETTLEMENT AND RECRUITMENT RATES

3.1 Introduction

Intertidal mussels are amongst the majority of benthic marine invertebrates that have a pelagic larval stage. Life for these organisms is therefore not only dependent on local bio-physical conditions and interactions within the benthic environment but also, ultimately on the vagaries of the coastal ocean and nearshore hydrodynamics. This means that the population dynamics of such organisms may be influenced by processes acting within both the pelagic and benthic environments (Roughgarden et al. 1988, Eckman 1996).

Settlement and recruitment of larvae are considered to be two distinct processes (Keough & Downes 1982). Following Keough and Downes (1982) and Rodríguez and co-workers (1993) settlement is defined as the sequence of events during which competent larvae leave the pelagic environment by attaching to the substratum. Subsequent to attachment, the process may also include metamorphosis (Seed & Suchanek 1992). In this context, competent larvae are those that have the ability to detect and respond to stimuli and hence, to find suitable substrata on which to settle (Coon et al. 1990). Recruitment intensity is then the number of these settlers surviving a period of time or to a particular size after initial settlement (Keough & Downes 1982, Roegner 1991).

In light of the dual environmental influences, larval settlement occupies a pivotal position in the life-history of mussels, situated at the interface of pelagic and benthic life (Underwood & Fairweather 1989, Rodríguez et al. 1993, Eckert 2003). At this interface, settlement is influenced by pre-settlement factors such as larval supply (the combination of larval production, transport and mortality), larval quality, and habitat availability (Schmitt & Holbrook 2000, Underwood & Keough 2001, Jarrett 2003, Emlet & Sadro 2006, Marshall & Keough 2006). Here, habitat availability may be particularly significant given the potential for intensification of settlement in areas with limited suitable habitat (*sensu* Pineda 1994b, Pineda & Caswell 1997, Rilov et al. 2008). On the other side of this interface however, an equally formidable set of physical and biological post-settlement factors including disturbance, competition and predation are introduced (Dayton 1971, Caley et al. 1996). The importance of larval settlement as a pivotal life event is emphasised by its potential to introduce density dependent effects, and thereby determine whether pre- or post-settlement factors will be most influential in shaping adult population structure (Connell 1985). At low settlement rates, pre-settlement factors are likely to be the dominant drivers of population structure, but high settlement rates should mean that post-settlement factors, including density dependence, are more important agents of control (Underwood & Keough 2001). Thus, the nature of the determinants of recruitment can be shaped by initial settlement rate, making settlement an influential factor in the formation of adult benthic populations (Roughgarden et al. 1985). For all of these reasons larval settlement, its determinants, and resultant recruitment are central to the ecology of intertidal benthic organisms. In the case of mussels, the situation can be complicated by secondary settlement – an event in which settlers detach from their initial settlement site and enter a second phase of pelagic dispersal (Bayne 1964a). Although this is not a mandatory life history event (McGrath et al. 1988, Reaugh et al. 2007) it is common and so-called secondary settlers (in the present study this refers to any settlers having undergone a second period of dispersal – confirmed by the presence of large settlers on newly deployed collectors) make an important contribution to overall recruitment.

The presence of a pelagic stage has several important implications such as introducing the potential for long distance dispersal of propagules. As a result of dispersal, populations have been considered demographically and/or genetically "open", with weak stock-recruitment relationships (Roughgarden et al. 1988, Caley et al. 1996, Thorrold et al. 2002, Grantham et al. 2003). Ultimately, the pelagic stage and the broad array of so-called supply-side factors that influence the number and timing of arrival of larvae to suitable habitats (Lewin 1986, Underwood & Keough 2001) promote the variability of settlement, and influence the structuring of adult intertidal populations (Thorson 1950, van Erkom Schurink & Griffiths 1991, Gaines & Bertness 1992, Morgan 2001, Eckert 2003).

Recently however, the nature and extent of these implications have been re-assessed (see Levin 2006 for review). Specifically, retention of larvae near natal populations (due to increased residence time - Largier 2004) and therefore increased self-recruitment of these larvae back to their natal populations have been found to be far more common than previously thought (McQuaid & Phillips 2000, Swearer et al. 2002). It is likely too, that larval exchange has been overestimated, as evidence from biophysical modelling points to more limited scales of dispersal and the presence of isolated populations (Cowen et al. 2000, Cowen et al. 2006). Furthermore, at a population level, the idea of the pelagic stage as a source of variation is questioned by several authors including Eckert (2003) who demonstrated smaller fluctuations in populations of species possessing a larval stage, than in those that did not. These findings have been hailed as evidence of important paradigm shifts away from the long held views that pelagic dispersal of marine larvae results in open and highly variable populations, with long distance dispersal being the norm, and populations rarely showing self-recruitment (Levin 2006).

At a metapopulation level however, examples of the episodic and highly variable nature of supply/settlement/recruitment in dispersing invertebrates abound and cannot be ignored (e.g. Forward et al. 2004). In fact, recent modelling and field studies have specifically recognised the stochasticity inherent in larval dispersal, connectivity and settlement (Dixon et al. 1999, Siegel et al. 2003, Mitarai et al. 2008). These studies have attempted to integrate this unavoidable uncertainty into their models and theory, rather than assuming simple dispersion. For example, Dixon and co-workers (1999) make allowance for deterministic *and* stochastic processes in their accounting of variability in larval supply, suggesting the "nonlinear amplification by biological processes of stochastic physical forcing" (Dixon et al. 1999: 1530).

The event of settlement itself may be seen as the culmination of a hierarchical set of 'telescoping' factors (Pineda 2000). Conceptually, this begins with large scale influences acting on the larval pool and therefore, larval supply. Specifically, these processes may include pulsed shoreward transport by internal waves, tidal bores, and frontal features (Ebert & Russell 1988, Farrell et al. 1991, Pineda 1991, Alexander & Roughgarden 1996, Pineda 1999, Pineda & Lopez 2002, Helfrich & Pineda 2003). The process continues under the influence of smaller scale biotic (e.g. larval behaviour, Butman 1987, Hunt & Scheibling 1996), physico-chemical (e.g. temperature and salinity, His et al. 1989) and hydrodynamic factors acting on supplied larvae and settlers (Harvey et al. 1995a, Lemire & Bourget 1996, Dobretsov & Wahl 2008). In particularly, wave exposure and turbulence (McQuaid & Lindsay 2000, Hammond & Grifiths 2004, Dobretsov & Wahl 2008) are highly influential hydrodynamic factors that together with local substratum topography (Delafontaine & Flemming 1989, Chiba & Noda 2000), are especially crucial to successful settlement and recruitment. Within Pineda's (2000) hierarchy of factors, physical transport processes, predominantly oceanographic and meteorological (wind), are some of the most important. This is mainly because they act directly on the larval pool, and together with larval production and mortality, act on large numbers of larvae to determine larval supply (Pineda 2000, Morgan 2001, Underwood & Keough 2001). Certainly, large scale oceanographic features, particularly those related to upwelling, have been shown to drive mussel recruitment and population structure via "subsidies" of larvae and particulate food to the nearshore environment, relative to regions dominated by downwelling (Guichard et al. 2003, Menge et al. 2003). At more localised scales, nearshore oceanography in the form of wave exposure and turbulence continues to influence settlement and recruitment by way of its effects on diffusion of food and larvae, on settlement cues and through physical disturbance (Denny 1987, Abelson & Denny 1997)**.** Settlement and recruitment are therefore inherently linked to nearshore oceanography which is important in terms of both the pre- and post-settlement environments.

Despite the stochastic nature of larval supply and settlement, a consistent ranking of settlement rate across nearby sites (≤ km scales) has repeatedly been observed (Connell 1985, Porri et al. 2006, Rilov et al. 2008). As may be expected, a common explanation for this consistency is the influence of local oceanography (Alexander & Roughgarden 1996, Connolly & Roughgarden 1998, Menge et al. 2003, Lagos et al. 2005). At face value this is a curious suggestion since local physical/oceanographic forces are essentially stochastic, especially when coupled with complex biological factors (Dixon et al. 1999). However, in the nearshore environment the along shore shape of the coast (coastline topography), particularly the presence of bays and headlands or capes, and bathymetric features have long been shown to influence nearshore oceanography consistently (Pingree et al. 1978, Jury 1985, Wolanski & Hamner 1988, Mann & Lazier 1991, Geyer & Signell 1992, Largier 2004, Narváez et al. 2006). It may be that coastline topography has a sufficiently deterministic influence on nearshore oceanography to produce concomitantly regular biological patterns.

In terms of settlement and recruitment, Gaines and Bertness (1992) found greater barnacle settlement rates inside Narragansett Bay (USA) than on the open coast when bay flushing times were long. Greater larval accumulation and settlement rates in upwelling shadows associated with headlands and embayments, particularly under upwelling/relaxation conditions, have also been reported (Wing et al. 1995, 1998a, 1998b, Mace & Morgan 2006). Recruitment has likewise been correlated with topographic features, with differences in sea urchin recruitment on the leeward and windward sides of headlands (Ebert & Russell 1988). In addition, Helson and Gardener (2004) and McQuaid and Phillips (2007) demonstrated greater mussel recruitment in bays (Wellington Harbour – New Zealand and Algoa Bay - South Africa respectively) than at nearby open coast sites. Again, each of these studies examined only a single bay, with no replication of the topographic feature being investigated.

This study uses the unique opportunity provided by the configuration of the south coast of South Africa, to examine settlement and recruitment rates of two study species, across multiple bays and open coast sites, within this single biogeographic region. This is done across seasons over a 12 month period, attempting to elucidate the generality and spatio-temporal consistency with which topography influences settlement and recruitment levels. The study asks the question: do bays consistently have greater settlement and recruitment rates than the open coast, or are topographic effects superseded by other (local) factors? I hypothesise that settlement and recruitment rates will generally differ between bays and the open coast, with higher rates of both occurring in bays.

Although there is likely to be a strong effect of season, not only on larval densities, but also on nearshore hydrodynamics because of changing wind patterns, I hypothesise that topography-related patterns of settlement and recruitment will be consistent through time.

3.2 Materials and methods

3.2.1 Experimental setup

Monthly collections of settlers (< 360µm) and recruits (> 360µm) of the study species (*Perna perna* and *Mytilus galloprovincialis*) were carried out over 12 months, between March 2005 to March 2006. This was undertaken at each of the 22 sites on the south coast of South Africa, between Mossel Bay (34.18°S; 22.16°E) and Kenton-on-Sea (33.68°S; 26.67°E) (see Chapter 1, Fig 1.1 and Appendix 1 for details). Due to secondary settlement, the recruit size class includes primary settlers that have grown during the collector deployment period as well as older 'secondary' settlers arriving from the water column.

At each site, twenty galvanised eye-bolts (6x100mm), each passing through the centre of a small plastic disc were screwed into the low intertidal rock, within the low mussel zone. The low mussel zone was used as it receives the highest numbers of settling larvae of the two study species (Porri et al. 2007). The bolts were haphazardly spread within an area of approximately 2m radius. Each accompanying disc provided 4 small holes to which a collector could be attached using cable-ties. Collections were made using plastic mesh pot-scourers (Ø = 15cm), referred to from here on as collectors. Twenty collectors were deployed at each site in the hope that at least ten would survive *in situ* for a month.

Although a variety of artificial larval collectors have been used to estimate settlement and recruitment rates, for example, polyester-wool filled mesh pouches (Hunt & Scheibling 1996), nylon rope (Cáceres-Martínez et al. 1993, 1994) and folded shade cloth (Helson & Gardner 2004), Ramirez and Cácerez-Martínez (1999) reported a tendency for mesh scouring collectors to be more successful than other types such as the rope collectors. These plastic mesh scouring collectors are now widely used as standardised artificial substrata (e.g. Gilg & Hilbish 2000, Porri et al. 2006, Porri et al. 2007, Rilov et al. 2008). It is however important to note that abundance and size distribution of mussel settlers on artificial collectors has been found to be distinctly different from those on natural substrata (Hunt & Scheibling 1996), meaning that these collectors provide relative (rather than natural) estimates of settlement and recruitment.

High numbers of settlers and recruits, and the time consuming nature of processing the collectors, limited the number of samples that could be examined. As a result, collectors from 4 months (April 2005, July 2005, October 2005 and January 2006) were selected for processing as representatives of the 4 seasons. This enabled a broad investigation of topographic/seasonal interactions and effects across all 22 sites. During the course of this processing, the raw data revealed extraordinarily high levels of settlement and recruitment at 3 open coast sites centred around Glentana, east of Mossel Bay (OGT, OSF, OBS – Fig 3.1 and 3.2). These sites periodically attained levels of settlement and recruitment at least one order of magnitude greater than any other sites, forming a group of extreme outliers. This situation provided a rationale for examining data with, and without the influence of these Glentana area sites. To investigate the regularity of extreme settlement and recruitment events on this section of open coast, processing of samples from the remaining 8 months for the 3 'extreme' Glentana area sites was undertaken. For comparative purposes, nearby bay sites in Mossel Bay itself (IDS and IHB) were also processed. Therefore, the statistical analysis and results sections are divided into two sub-sections. The 'seasonal study' covers the initial selection of 4 months, examining both the full data-set of 20 sites (complete seasonal analysis – see *Data preparation* section 3.2.4 below for explanation of site loss), and the reduced data-set of 14 sites (reduced seasonal analysis). The reduced data-set excluded the 5 Glentana area (OGT, OSF, OBS) and Mossel Bay sites (IDS, IHB), as well as 2 additional sites from within this area (ILH and OWD) which were removed in order to balance the number of bay and open coast sites (refer to map Chapter 1, Fig 1.1). Here, site OWD replaces the previously excluded site OCP, allowing OCP to be included in the reduced data-set while maintaining the balanced design. In this way, the reduced data-set included Plettenberg Bay and all sites east of it. The seasonal study section also includes descriptions of the regional and local scale spatial variability and correlations, examining the relationships among mussel settlement, recruitment and adult cover within and between species based on the complete data-set. The 'temporal study' isolates and examines 5 of the 7 Glentana/Mossel Bay sites over the full year's data-set (IDS, IHB, OGT, OSF and OBS).

3.2.2 Sample collection and processing

While shorter sampling intervals are preferable (Connell 1985, Minchinton & Scheibling 1993), monthly sampling has been used successfully by Ramirez and Cácerez-Martínez (1999). Due to the number of sites and their significant geographical separation, the monthly approach was necessary. Each collection trip took between 3 to 5 days depending on tidal levels. This meant that there were no more than 5 days between the collection of the first and last collectors. At each site the collectors were cut free and placed in individual plastic bags. These were kept as cool as possible and frozen at over-night stops. In the laboratory, samples were stored at -20°C until processing. In all cases, 3 replicate collectors were processed per site and any exceedingly large samples (>200 larvae) were sub-sampled using small custom made sample splitters of various sizes.

Processing involved the careful unrolling and washing of each collector. Included in this washing was the bag, which was inverted so that any material lost from the collector during transport was kept. All material was then sieved through a stack of three sieves (4mm, 300µm, 75µm). All mussels (settlers and recruits) were removed from the sieved material using a dissecting microscope, and were stored in 95% alcohol for later identification.

3.2.3 Identification

Recent developments of immunological and DNA-based techniques now provide advantageous alternatives to traditional, morphological methods for species-level identification of bivalve larvae (see Garland & Zimmer 2002 for review). However, the mussel species dealt with in the present study are sufficiently distinct in colour and shell morphology, even at the settlement stage, so as to be distinguishable (Bownes et al. 2008). Although some phenotypic plasticity is possible, accuracy of identification of *Mytilus* and *Perna* based on morphology, rather than genetic techniques, has been confirmed by Bownes and co-workers (2008), and has been used for *Mytilus* and *Perna* by

Porri and co-workers (2006, 2007). *Perna* and *Mytilus* individuals were therefore identified by shell morphology and colour, and measured using a dissecting microscope (25X magnification). All individuals were counted and grouped into four size-classes. These were: 200µm – 360 µm; 360µm – 1mm; 1mm – 5mm; > 5mm. The first of these classes was considered to be primary settlers, while the three remaining classes contained recruits (either primary or secondary).

3.2.4 Data preparation

Due to the fact that collectors were not collected simultaneously, total numbers of mussels in each size were converted to daily rates of settlement or recruitment per collector. Quantifying settlement and recruitment by collector rather than by unit area has been used by Navarrete and co-workers (2005). For the recruitment size classes, this was done by dividing the total number of recruits in each collector by the exact number of days the collectors had been deployed on the shore (i.e. this differed slightly between sites). For primary settlers, the total number of settlers on each collector was divided by 2 days for all sites. This decision was based on the fact that settlers of such small size could only have arrived over the 48 hour period prior to collection (given size at settlement of ca 260µm Bayne 1965). Where only two collectors were retrieved from a site, an average value was substituted as the third value; sites with one or no collectors retrieved were excluded from analyses. Averaging to provide a third value was only necessary in two instances (in Apr '05 – IBR and Jan '06 – OGT), while one site (ISR) had to be excluded as no collectors were retrieved in April '05.

3.2.5 Statistical analysis – Seasonal study

Complete seasonal analyses - Separate two-way analyses of variance (ANOVA) were conducted on settlement and recruitment rate data for each species across the 4 months. Analyses examined bay status (fixed, 2 levels) and month (random, 4 levels). In all cases data were non-normal (Shapiro-Wilk's, $p < 0.05$) with heterogenous variances (Cochran's, $p < 0.05$). Data (log) transformation did not improve this situation in the majority of cases. Thus, data were not transformed, but the analyses were considered valid due to the high number of treatments and replicates (Underwood 1997, Quinn & Keough 2002). Analyses included all sites but ISR, for which no collectors were recovered in April 2005, and a randomly selected nearby open coast site (OCP) - omitted to balance the loss of ISR. These are the most inclusive analyses (20 sites), and are here-after referred to as 'complete'.

Reduced seasonal analyses - To remove the influence of the extreme settlement sites in the Mossel Bay area, all analyses were repeated using the reduced data-set which excluded the 7 sites described earlier (see *section* 3.2.1). The total number of sites for these analyses was thus 14, allowing comparison of 7 bay sites to 7 open coast sites. This set of analyses is referred to as 'reduced'. Student Newman-Keuls (SNK) post-hoc tests were used in both sets of analyses to examine pair wise comparisons (Zar 1974).

Spatial relationships - Focusing on the two (peak) summer months, the spatial relationships between mussel settlement and recruitment, and between recruitment and adult cover (from Chapter 2) of each species were examined in terms of the 'raw' data, the regional trend and local-scale site variation. In the same way, the relationship between settlement of one species and the other, and between recruitment of one species and the other (hereafter, inter-species relationships) were investigated to assess the existence of common processes governing settlement and recruitment. For each variable this was done according to the method of Lagos and co-workers (2005) and Navarrete and co-workers (2005), by which the log (n +1) transformed means from all 20 sites were plotted against distance from the western-most site (ILH in Mossel Bay, see chapter 1, Fig 1.1); these transformed data form the 'raw' data-set. A LOWESS (Locally Weighted Scatterplot Smoothing, Cleveland 1979) regression was then fitted to each 'raw' data plot. The resulting LOWESS regressions produced the regional trend in each variable as a function of distance from the western-most site (ILH) providing the 'regional trend' data-set. To determine the correct degree of smoothing or tension, the regressions were repeatedly fitted using a range of smoothing values. The correct fit was one producing normally distributed and geographically (distance) independent LOWESS residuals. Finally, the residual variation – the difference between the LOWESS 'trend' and the 'raw' data – generated the 'local-scale' data-set, indicating local (site-level) variation around the trend. The respective correlations (recruitment by settlement; adult cover by recruitment and the inter-species relationships) were then carried out on these raw, regional trend and local-scale data-sets using *r*-Pearson correlations.

3.2.6 Statistical analysis – Temporal study

A two-way ANOVA, examining month (random, 12 levels) and site (fixed, 5 levels), was done on settlement and recruitment data for each species. Again, data were non-normal (Shapiro-Wilk's, $p < 0.01$) and variances were heterogenous (Cochran's $p < 0.01$). Like the seasonal study analyses, the data were not transformed since transformation did not significantly improve the heterogeneity of variances. The number of treatments and sample size allows for departures from the usual assumptions required by ANOVA (Underwood 1997).

3.3 Results

3.3.1 Seasonal study

Complete data-set – Figures 3.1 and 3.2 show that settlement and recruitment rates of both species generally increased from autumn (Apr)/ winter (Jul) to summer (Jan). In April and July settlement rates peaked in Plettenberg Bay, while elsewhere settlement was relatively low (Fig 3.1). A distinct peak in recruitment occurred in Jeffreys Bay in April, but in July, peaks were isolated to very particular sites within each of the 3 easterly bays (Plettenberg, Jeffreys and Algoa, Fig 3.2). Over the summer months, extremely high settlement and recruitment rates (as much as 1 order of magnitude greater than other sites) were recorded at sites in and around Glentana (Fig 3.1 and 3.2 - OGT, OWD, OSF, OBS). In early summer (October), these settlement and recruitment peaks were limited to the Glentana area and decreased to the west into Mossel Bay and to the east into Plettenberg Bay. Later in summer (January) however, a dramatic increase in these rates was seen, as well as an expansion of extreme rates (especially in recruitment) to sites inside Mossel Bay and Plettenberg Bay. Other slightly lesser peaks in recruitment were seen in January in Jeffreys Bay and

Algoa Bay. An important finding was that periods of maximum settlement and recruitment differed among areas, such as different bays. While adjacent sites were often synchronised with regard to peak periods in settlement and recruitment, this was not true across broader areas; settlement and recruitment events were out of phase in different sections of the coast. In the easterly bays such peaks generally occurred in autumn and winter, and shifted to the westerly sites of the Mossel Bay/Glentana area in the summer months. Furthermore, within the easterly section of coast, peaks were out of phase and occurred in different bays at different times.

Patterns of mean settlement over the full set of 20 sites summarise the general trends described above, being similar for both species. The highest settlement rates were observed in the summer months (October and January), and *Perna* generally settled at higher rates than *Mytilus* (Fig 3.3). During April the mean settlement rate of both species was marginally greater in bays than on the open coast (Fig 3.3 $Perna_{\text{bay}}$ = 5.04 ± 0.9, $Perna_{\text{open coast}}$ = 2.92 ± 0.9; $Mytilus_{\text{bay}}$ = 7.83 ± 2.2, $Mytilus_{\text{open coast}}$ = 1.15 ± 0.3). Differences in mean settlement rate between bays and the open coasts were even less pronounced over July, but generally in the same direction (Figure 3.3 $Perna_{\text{bay}}$ = 1.77 ± 0.7, $Perna_{\text{open coast}}$ = 0.95 ± 0.2; $Mytilus_{\text{bay}}$ = 0.25 ± 0.1, $Mytilus_{\text{open coast}}$ = 0.25 ± 0.1). Although there was a general increase in settlement rate during the summer months in bays and on the open coast, settlement patterns reversed during these months, with the mean bay rates being markedly lower than those of the open coast. Differences in mean settlement rate between bays and the open coast were greatest in January, most particularly for *Perna* settlers (Figure 3.3 $Perna_{\text{bay}}$ = 176.1 ± 51.8, $Perna_{\text{open coast}}$ = 796.27 ± 225.4; $Mytilus_{\text{bay}}$ = 52.32 ± 15.9, $Mytilus_{\text{open coast}}$ = 142.7 ± 46.9). Statistical analyses of settlement data indicated that a significant month x bay status interaction was present for both species (Table 3.1 (a) *Perna*, $F_{3, 232} = 4.97$, $p < 0.01$; (b) *Mytilus* $F_{3, 232} = 3.25$, $p < 0.05$). The post hoc SNK comparisons showed that these interactions were significant only in January, when settlement rates were significantly greater on the open coast than in bays.

Patterns of recruitment were less consistent across species than those of settlement, but the trend of lower rates in April and July than in October and January was largely maintained (Fig 3.3 c and d), especially for *Perna*. Recruitment of *Perna* was also greater than that of *Mytilus*. As with settlement, a general increase in recruitment rate was accompanied by a reversal of the bay/open coast pattern in October and January. This reversal was most acute in January (Fig 3.3 (c) $Perna_{bay} = 52.58 \pm 11.4$, $Perna_{open\ coast} = 82.52 \pm 20.8$; (d) $Mytilus_{bay} = 4.2 \pm 1.3$, $Mytilus_{open\ coast} = 5.57 \pm 1.5$), and as Fig 3.3(d) shows, was limited to *Perna*.

The results of ANOVAs of recruitment data showed that there was no interaction of month and bay status for either species (Table 3.1 (c) *Perna*, $F_{3,\ 232} = 1.47$, $p > 0.05$; (d) *Mytilus* $F_{3,\ 232} = 2.00$, $p > 0.05$). However, a significant effect of month on *Perna* recruitment rate was found (Table 3.1 (c) *Perna*, $F_{3,\ 232} = 17.48$, $p < 0.05$); specifically, the SNK comparisons showed that significantly greater recruitment occurred in January (Table 3.1).

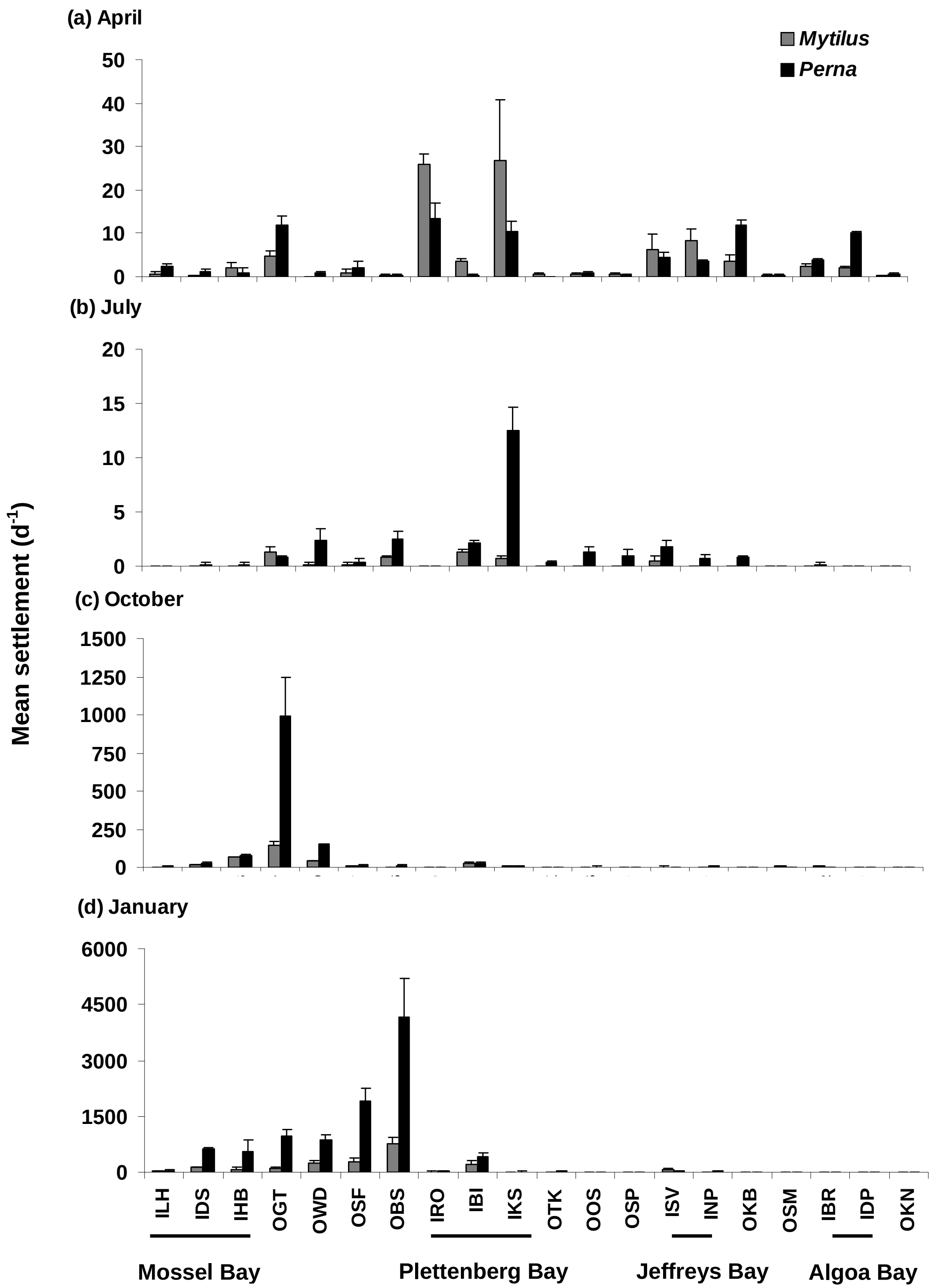

Figure 3.1 Mean settlement per collector.d^{-1} (+SE) of *Mytilus galloprovincialis* and *Perna perna* across bay and open coast sites in (a) April 2005 (b) July 2005 (c) October and (d) January 2006. Note that different scales were used on y-axis.

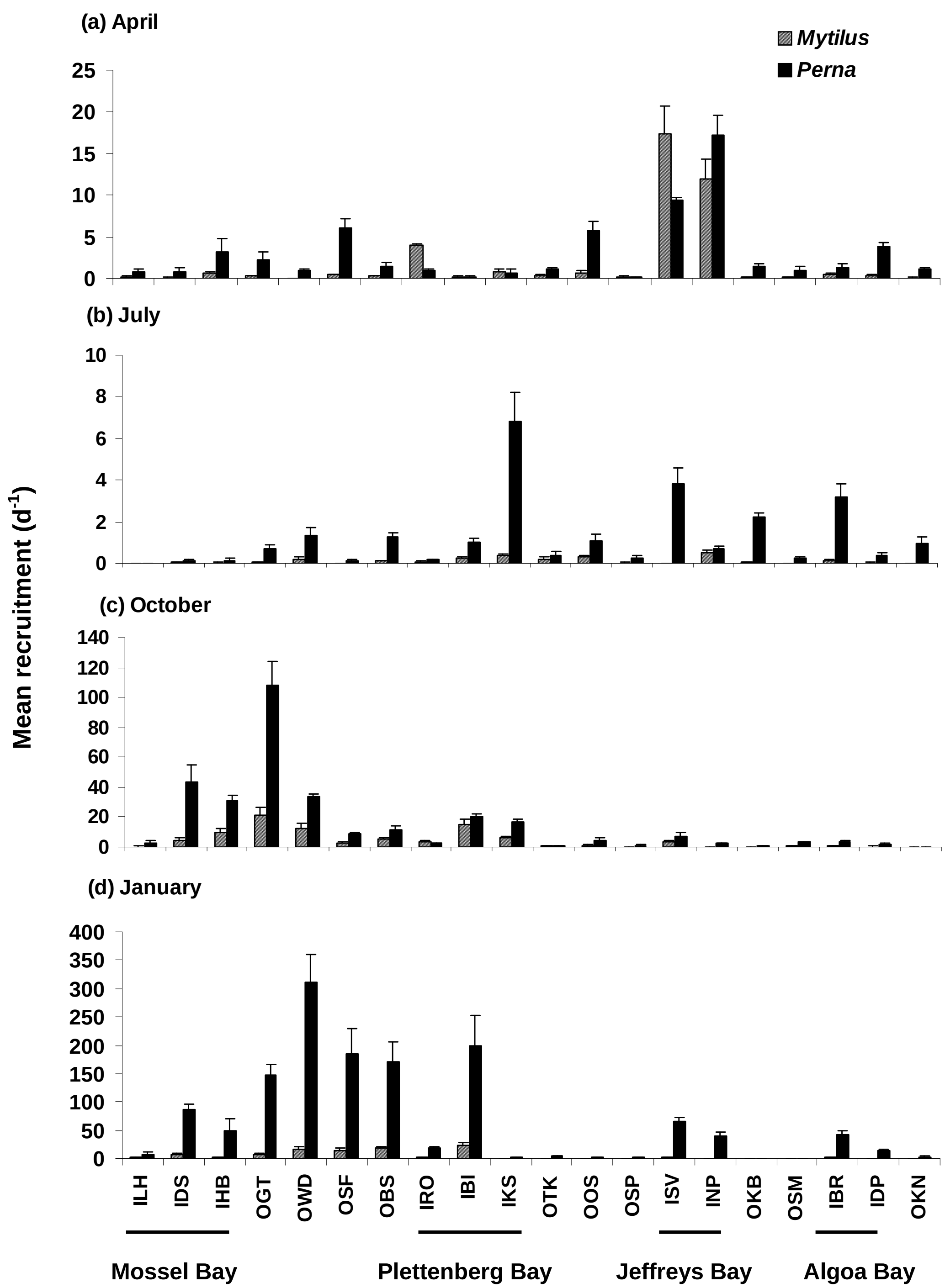

Figure 3.2 Mean recruitment per collector.d^{-1} (+SE) of *Mytilus galloprovincialis* and *Perna perna* across bay and open coast sites in (a) April 2005 (b) July 2005 (c) October and (d) January 2006. Note that different scales were used on y-axis.

Table 3.1 Results of 2-way ANOVAs of settlement (d^{-1}) data for (a) *Perna perna* and (b) *Mytilus galloprovincialis*, and recruitment rate data for (c) *P. perna* (d) *M. galloprovincialis* based on the complete data-set. The SNK results use abbreviations for bay status B: bay, OC: open coast.

(a) *Perna* settlement

Source	**Df**	**MS**	**F**	***p***
Month	3	3260818	2.45	>0.05
Bay status	1	1935325	1.46	>0.05
Month x Bay	3	1329211	4.97	< 0.01
Error	232	267639		
SNK (Mo x B)	OC (Jan 06) > B (Jan 06) = all other bay status x month combinations			

(b) *Mytilus* settlement

Source	**Df**	**MS**	**F**	***p***
Month	3	125464.2	4.05	>0.05
Bay status	1	31025.3	1.0	>0.05
Month x Bay	3	30989.6	3.25	<0.05
Error	232	9530.9		
SNK (Mo x B)	OC (Jan 06) > B (Jan 06) = all other bay status x month combinations			

(c) *Perna* recruitment

Source	**Df**	**MS**	**F**	***p***
Month	3	58253.2	17.48	<0.05
Bay status	1	3773.7	1.13	>0.05
Month x Bay	3	3332.7	1.47	>0.05
Error	232	2273.1		
SNK (Mo)	Jan 06 > all other months			

(d) *Mytilus* recruitment

Source	**Df**	**MS**	**F**	***p***
Month	3	298.37	4.98	>0.05
Bay status	1	16.0	0.27	>0.05
Month x Bay	3	59.97	2.0	>0.05
Error	232	29.84		
SNK	No significant effects			

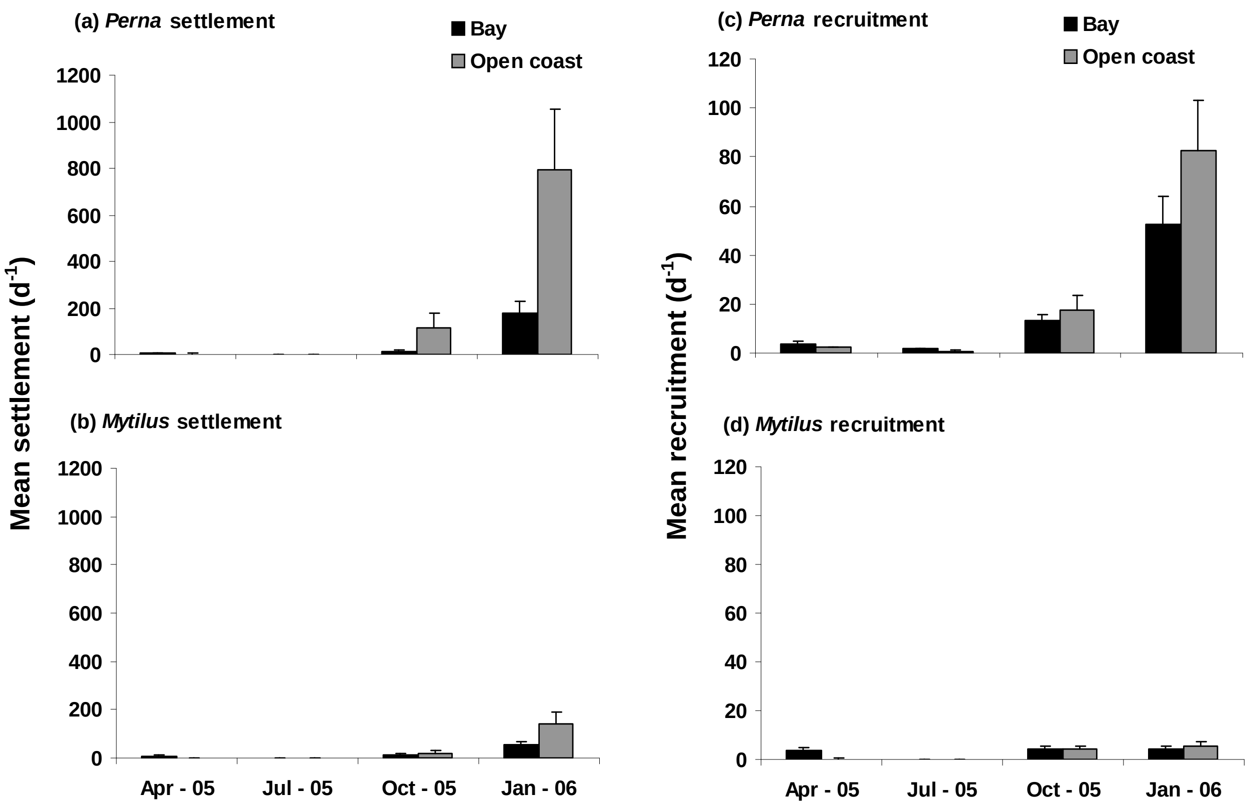

Figure 3.3 Mean settlement (+SE) of (a) *Perna perna* and (b) *Mytilus galloprovincialis*, and mean recruitment (+SE) of (c) *P. perna* and (d) *M. galloprovincialis* at bay and open coast sites for each of four months. (Means calculated from the complete data-set of 20 sites).

Reduced data-set – In the absence of extreme settlement and recruitment of the Glentana area sites, patterns of settlement and recruitment along the remaining stretch of coast can be more clearly seen (Fig 3.4 and 3.5). In April, settlement was highest in each of the bays with maximal rates reached in Plettenberg Bay (Fig 3.4a). Corresponding patterns of recruitment for this month differed from those of settlement in that peak recruitment occurred in Jeffreys Bay while recruitment at all other sites remained low (Fig 3.5a). During July, settlement and recruitment were low (< 20 indiv.d^{-1}) across all sites (Fig 3.4b and 3.5b). In the summer months, peaks in settlement and recruitment followed topographic patterns more closely than in autumn and winter. Maximum rates of settlement and recruitment were recorded in Plettenberg Bay in October and January, with lesser peaks appearing in both of these months at Jeffreys Bay and Algoa Bay (Fig 3.4c and d; Fig 3.5c and d). Rates comparable to these lesser peaks were however found at the open coast sites on either side of Jeffreys Bay (OOS and OSM) in October (Fig 3.4c and Fig 3.5c).

Using the reduced data-set, mean settlement and recruitment rates clarify general patterns on bay and open coast shores. Mean settlement of both species at bay and open coast sites was lowest in July. However, while mean open coast levels were low in April, mean bay rates increased to levels comparable to those in October. During April and July the pattern of higher bay than open coast rates remained similar to that found using the complete data-set (higher settlement rate in the bays than out, Fig 3.6a and b). The general increase in settlement expected in October and January was found to be limited primarily to bay sites (Fig 3.6a and b). As a result of this differential increase, and in contrast to the rates calculated from the complete data-set, mean settlement rates remained greater in bays than on the open coast during October and January, for both species. Over the four months, mean settlement rates on the open coast remained low and changed relatively little (*Perna*: 0.5 – 4.3 settlers.d^{-1}; *Mytilus*: 0.02 – 2 settlers.d^{-1}). The most striking differences in settlement rates between bays and the open coast were in January (Figure 3.6a $Perna_{\text{bay}} = 76.97 \pm 33.65$, $Perna_{\text{open coast}} = 4.29 \pm 1.53$ settlers.d^{-1}, and 3.2b $Mytilus_{\text{bay}} = 44.02 \pm 20.51$, $Mytilus_{\text{open coast}} = 1.98 \pm 1.02$ settlers.d^{-1}). Statistical analysis of the reduced data-sets found a significant interaction between month and bay status for settlement rate of each species (Table 3.2a *Perna*, $F_{3,\,160} = 4.14$, $p < 0.01$; 3.2b *Mytilus* $F_{3,\,160} = 3.26$, $p < 0.05$). Although mean settlement was greater in bays than on the open coast for each of the four months (Fig 3.6), SNK comparisons show these differences to be significant in January only (Table 3.2).

In terms of recruitment, patterns differed between species. Although lower in magnitude, recruitment patterns of *Perna* closely followed those of settlement. The lowest mean rates were recorded in July (Fig 3.6c $Perna_{\text{bay}} = 2.3 \pm 0.5$, $Perna_{\text{open coast}} = 0.8 \pm 0.2$ recruits.d^{-1}), but increased recruitment to bay shores was seen in April, October and most dramatically, in January (Fig 3.6c $Perna_{\text{bay}} = 54.5 \pm 15.4$, $Perna_{\text{open coast}} = 2.1 \pm 0.3$ recruits.d^{-1}). Recruitment on open coast shores remained consistently low in all four months (*Perna*: 0.8 – 2.1 recruits.d^{-1}; *Mytilus*: 0.09 – 0.4 recruits.d^{-1}).

In contrast, seasonal trends of *Mytilus* recruitment did not follow those of settlement. Mean recruitment on bay shores was maintained at a rate of ca 4.5 recruits.d^{-1} during April, October and January, while July saw the lowest rates for both shore types (Fig 3.6d $Mytilus_{bay}$ = 0.2 ± 0.05 recruits.d^{-1}; $Mytilus_{open\ coast}$ = 0.1 ± 0.03 recruits.d^{-1}). On the open coast, mean recruitment rates were low in the remaining three months. Recruitment rates of *Perna* were found to be significantly affected by a month x bay status interaction (Table 3.2c *Perna*, $F_{3,\ 160}$ = 9.95, $p < 0.0001$). As was the case with settlement of this species, SNK tests showed the high recruitment rate in bays during January to be responsible for this interaction effect. Neither bay status nor month affected the recruitment rate of *Mytilus*, and no significant interaction was found (Table 3.2d).

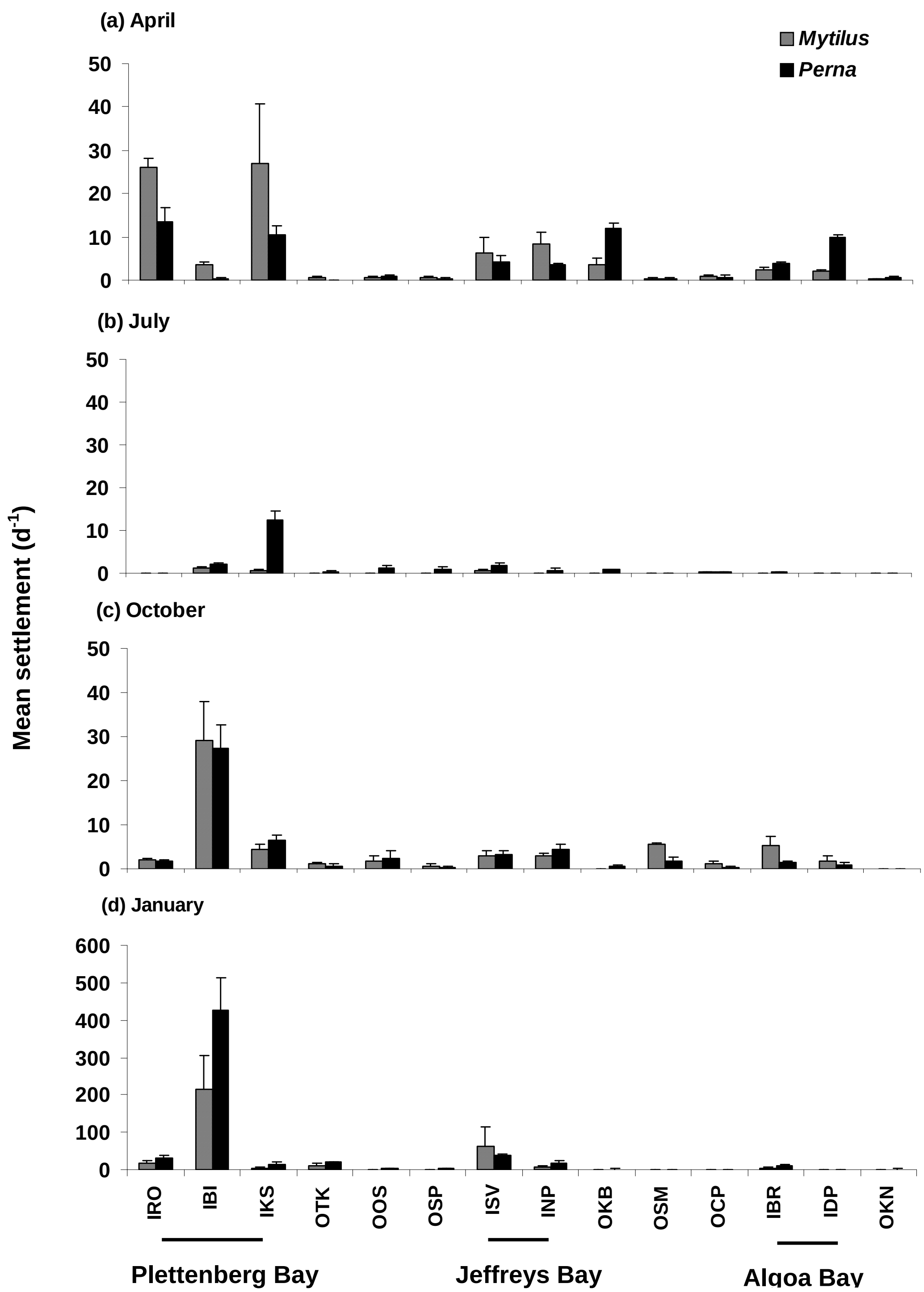

Figure 3.4 Mean settlement per collector.d^{-1} (+SE) of *Mytilus galloprovincialis* and *Perna perna* across bay and open coast sites east of Brenton-on-Sea in (a) April 2005 (b) July 2005 (c) October and (d) January 2006. Note that different scales used on y-axis.

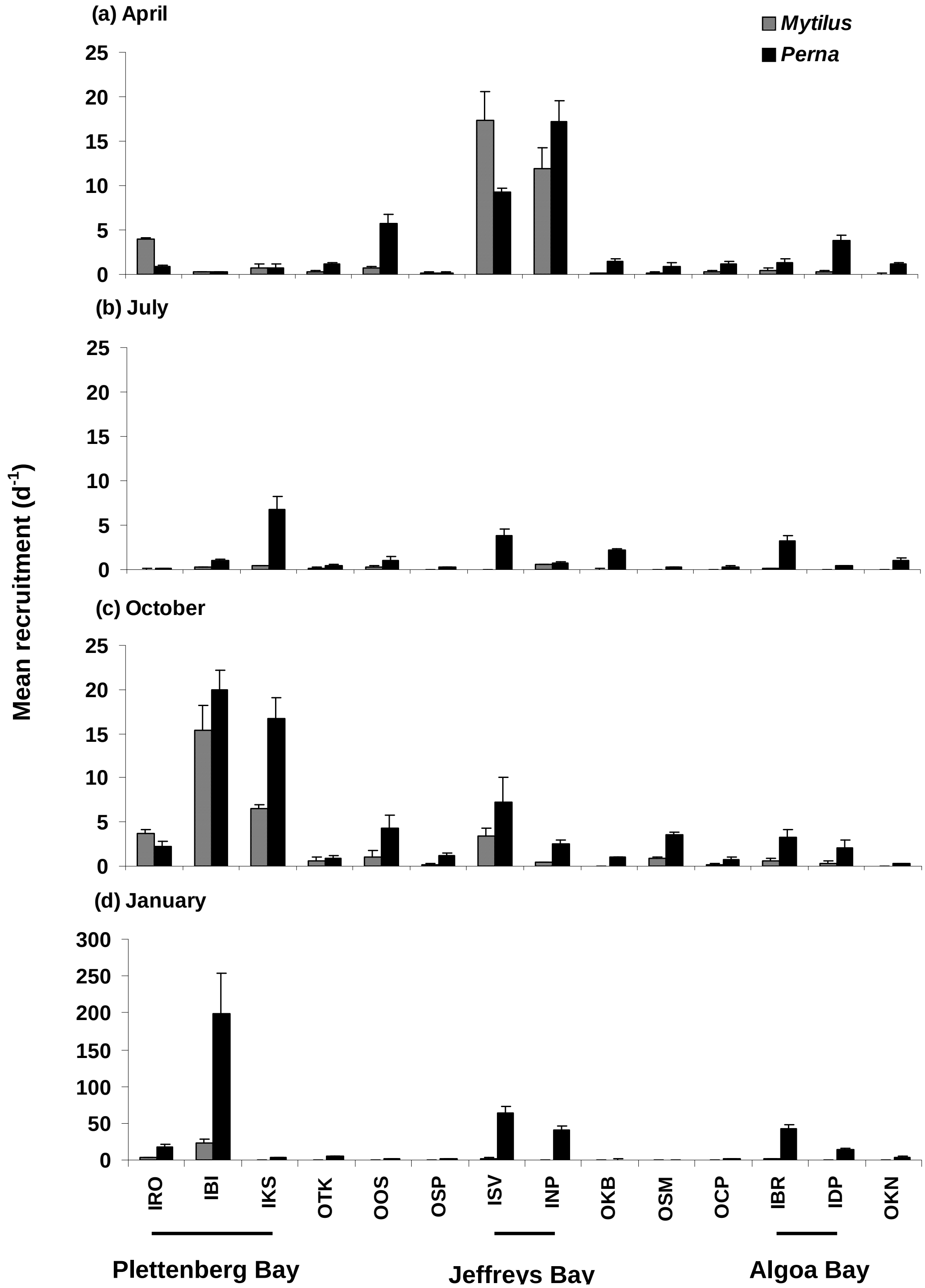

Figure 3.5 Mean recruitment per collector.d^{-1} (+SE) of *Mytilus galloprovincialis* and *Perna perna* across 14 sites east of Brenton-on-Sea bay and open coast sites in (a) April 2005 (b) July 2005 (c) October and (d) January 2006. Note that different scales used on y-axis.

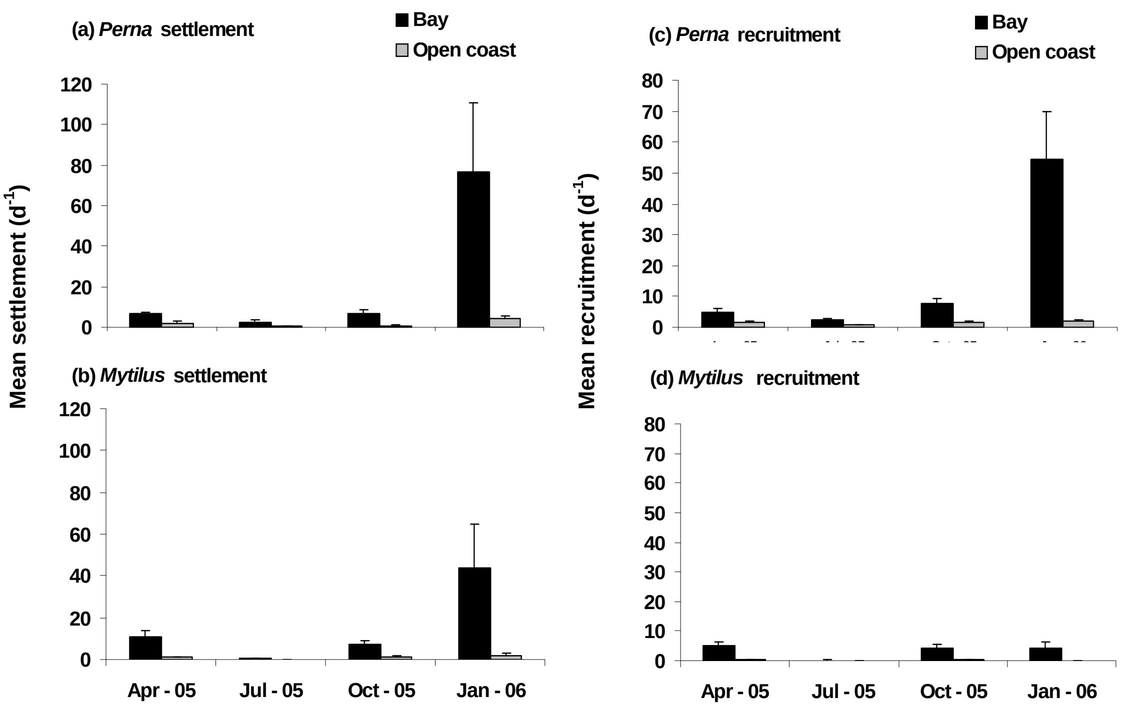

Figure 3.6 Mean settlement (+SE) of (a) *Perna perna* and (b) *Mytilus galloprovincialis*, and mean recruitment (+SE) of (c) *P. perna* and (d) *M. galloprovincialis* at bay and open coast sites for each of four months. Means calculated from the reduced data-set of 14 sites, which excludes the 7 sites in and around Mossel Bay.

Table 3.2 Results of 2-way ANOVAs of monthly settlement (d^{-1}) data for (a) *Perna perna* and (b) *Mytilus galloprovincialis*, and recruitment data for (c) *P. perna* (d) *M. galloprovincialis* based on the reduced data-set. The SNK results make use of abbreviations for bay status B: bay, OC: open coast.

(a) *Perna* settlement

Source	Df	MS	F	p
Month	3	14800.11	1.2	> 0.05
Bay status	1	18864.82	1.5	> 0.05
Month x Bay	3	12400.68	4.1	< 0.01
Error	160	2997.8		
SNK (Mo x B)	B (Jan 06) > all other bay status month combinations			

(b) *Mytilus* settlement

Source	Df	MS	F	p
Month	3	4265.8	1.1	> 0.05
Bay status	1	8725.7	2.3	> 0.05
Month x Bay	3	3721.5	3.3	< 0.01
Error	160	1143.2		
SNK (Mo x B)	B (Jan 06) > all other bay status month combinations			

(c) *Perna* recruitment

Source	Df	MS	F	p
Month	3	6710.3	1.1	> 0.05
Bay status	1	10461.2	1.7	> 0.05
Month x Bay	3	6313.4	9.9	< 0.001
Error	160	634.6		
SNK (Mo x B)	B (Jan 06) > all other bay status month combinations			

(d) *Mytilus* recruitment

Source	Df	MS	F	p
Month	3	55.6	1.2	> 0.05
Bay status	1	444.7	9.4	> 0.05
Month x Bay	3	47.3	2.6	> 0.05
Error	160	18.5		
SNK	No significant effects			

Spatial relationships – The LOWESS smoothing function fitted to log (n+1) summer settlement data revealed that regional trends in settlement of both species followed a strikingly similar pattern in both months (Fig 3.7). Settlement generally increased from Mossel Bay to a distinct peak (maximum rate) over the Glentana area sites (OGT, OWD, OSF, OBS; between 60-100km east of ILH in Mossel Bay, Fig 3.7), followed by a decreasing trend towards OOS (at 241km) on the open coast between Plettenberg Bay and Jeffreys Bay. Within this decreasing section, a small localised change in the direction of the trend can be seen in Plettenberg Bay (ca 150km). Moving from OOS, settlement increased to a point around 350km indicating Jeffreys Bay, from which settlement gradually decreased across Algoa Bay and on to OKN (at 544km). In October, high settlement of *Mytilus* in Algoa Bay (ca 450km) resulted in a small change to the general trend, with settlement increasing from Jeffreys Bay to a small peak within Algoa Bay. The other noticeable difference in regional trend between months is the shift in maximum settlement from OWD (at 58km) in October to OBS (at 105km) in January. Overall however, at the regional scale, log (n +1) settlement rates decreased as distance from Mossel Bay increased.

The regional trends in recruitment of *Mytilus* and *Perna* also showed the influence of extreme recruitment rates in the Glentana area, and a general decrease in recruitment from this region towards the east (Fig 3.8). Like settlement, the trend changed direction slightly at Plettenberg Bay (ca 150km) and again around Jeffreys Bay (ca 350km), producing overall trends similar to those of settlement.

A somewhat different regional pattern emerged for adult cover of both species with cover increasing from low levels in Mossel Bay across the Glentana sites to a peak in Plettenberg Bay at around 150km (Fig 3.8c and d). From there, cover decreased sharply until beyond Jeffreys Bay. Thereafter, cover increased and levelled out from Algoa Bay (ca 420km) onwards to the most easterly site at Kenton-on-Sea (OKN at 544km).

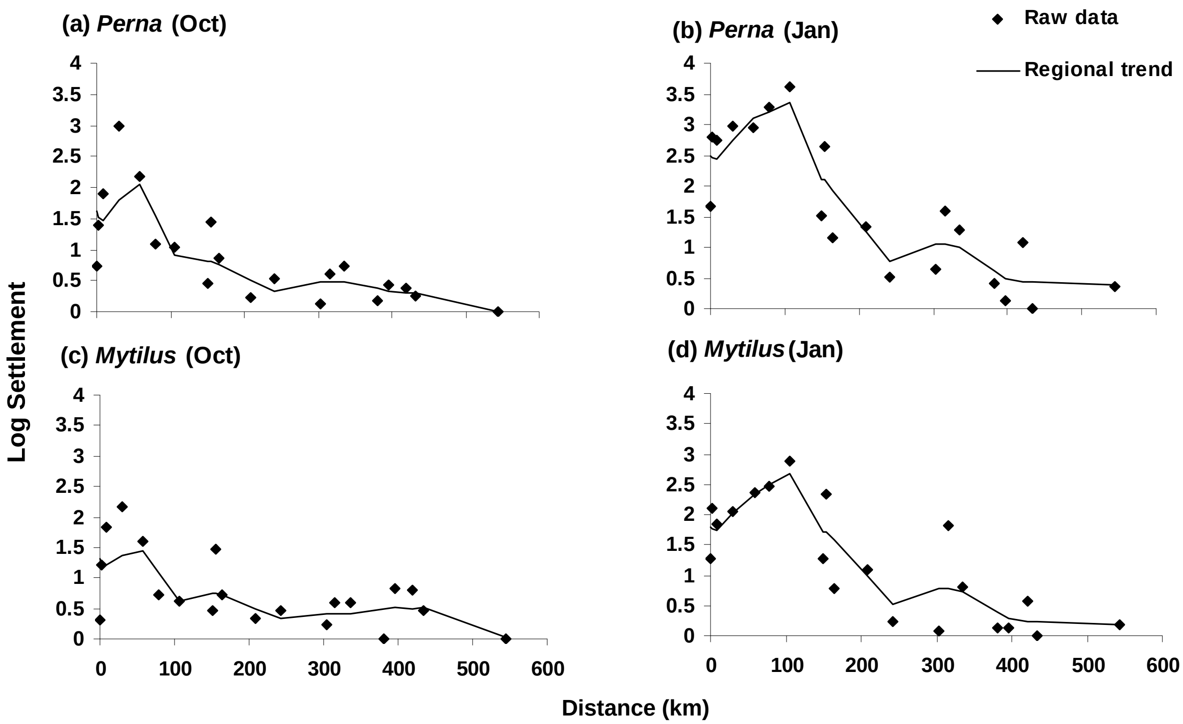

Figure 3.7 Log-scaled settlement (d^{-1}) and the LOWESS fit (regional trend) in relation to distance from the study region's most westerly site (ILH) for all 20 sites. In each case the fitted line shows the regional trend in settlement of (a) *Perna perna* in October 2005 and (b) in January 2006. (c) and (d) show the corresponding plots for *Mytilus galloprovincialis*.

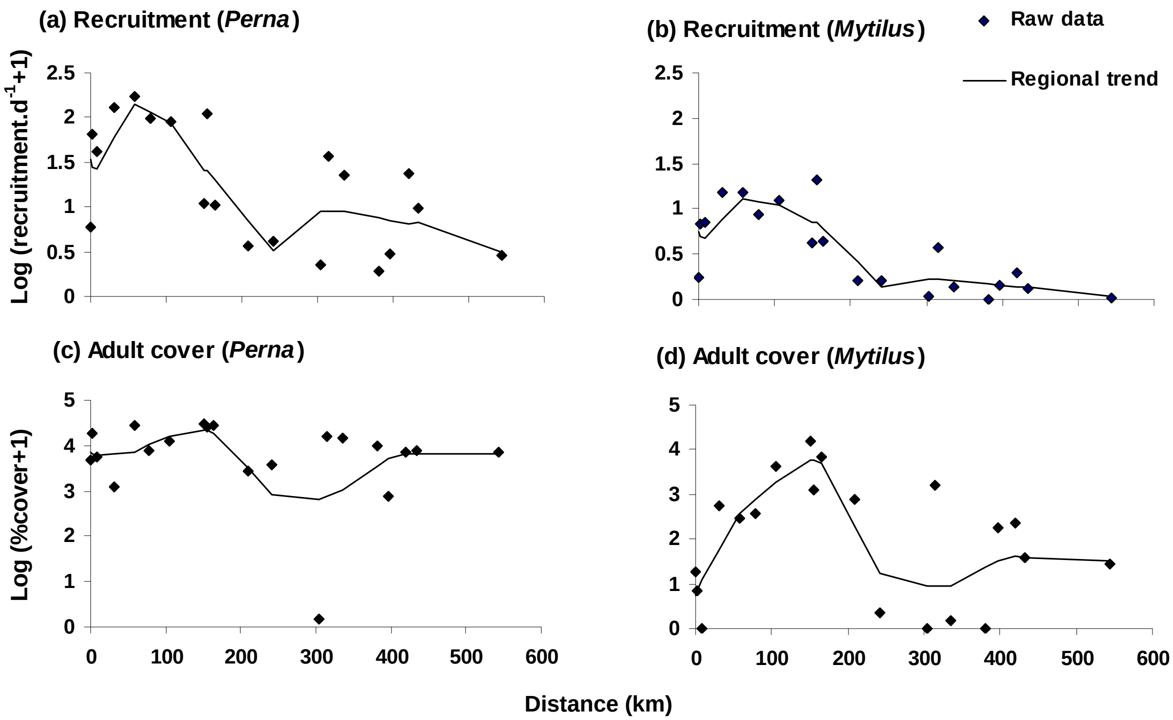

Figure 3.8 Log-scaled mean recruitment (d^{-1}) (average of October 2005 and January 2006) and LOWESS fit (regional trend) over the complete 20 sites in relation to distance from the study region's most westerly site (ILH) for (a) *Perna perna* and (b) *Mytilus galloprovincialis*. Panel (c) and (d) show the log-scaled mean adult cover and LOWESS fit for *P. perna* (in the low mussel zone) and *M. galloprovincialis* (in the high mussel zone) respectively.

Spatial correlations – In each of the two summer months, settlement intensities for *Mytilus* and *Perna* were highly positively correlated with each other in terms of the raw data (Table 3.3 Jan: r = 0.97, $p < 0.0001$; Oct: $r = 0.93$, $p < 0.001$) and at regional scale (LOWESS fit – Jan: $r = 0.99$, $p <$ 0.0001; Oct: $r = 0.97$, $p < 0.0001$) and local scales (residual data – Jan: $r = 0.89$, $p < 0.0001$; Oct: r = 0.93, $p < 0.0001$). Likewise, significant correlations were found between mean recruitment of *Mytilus* and *Perna* in raw ($r = 0.91$, $p < 0.001$), regional trend ($r = 0.95$, $p < 0.0001$) and local scale residual data ($r = 0.86$, $p < 0.0001$).

For *Perna*, recruitment in January was significantly correlated with settlement in the preceding October in terms of the raw data (r =0.64, $p < 0.05$) and at the regional scale (Table 3.3 $r = 0.83$, p < 0.0001), but not at the local scale ($r = 0.34$, $p > 0.05$). A similar relationship existed for *Mytilus* with recruitment in October correlating significantly with settlement in January at the regional scale

(r = 0.49, p < 0.05) but not at local scales (r = 0.11, p > 0.05) nor in the raw data (r = 0.39, p > 0.05).

Mean recruitment and mean adult cover of *Perna* (low shore) were significantly correlated regionally (r = 0.54, p < 0.05) and locally (r = 0.48, p < 0.05), but no correlation for the raw data was found (r = 0.43, p > 0.05). In equivalent correlations, mean recruitment and adult cover of *Mytilus* were meaningfully correlated regionally (r = 0.62, p < 0.04) and in terms of the raw data (r = 0.50, p < 0.05) but were not locally correlated (r =0.18, p > 0.45).

Table 3.3 Pearson's r statistic and significance level for the interspecies (a) settlement and (b) mean recruitment (Oct/Jan) correlations; (c) correlations of settlement in October (2005) with recruitment in January (2006) for each species, and (d) correlations of adult cover of each species (*Perna* – low zone; *Mytilus* – high zone) with mean recruitment (Oct/Jan) of each. In all cases correlations were carried out on raw data, the LOWESS (regional) trend data and on the residual (local scale) data.

(a) Interspecies Settlement	**Pearson's *r***	***p***
Mytilus by *Perna*		
(Jan) Raw	0.97	< 0.001
(Jan) Residual	0.89	< 0.001
(Jan) Trend	0.99	< 0.001
(Oct) Raw	0.93	< 0.001
(Oct) Residual	0.93	< 0.001
(Oct) Trend	0.97	< 0.001
(b) Interspecies Recruitment		
Mytilus by *Perna*		
(Mean) Raw	0.91	< 0.001
(Mean) Residual	0.86	< 0.001
(Mean) Trend	0.95	< 0.001
(c) Settlement vs Recruitment		
Settlement (Oct) by Recruitment (Jan)		
(*Perna*) Raw	0.64	< 0.01
(*Perna*) Residual	0.34	> 0.05
(*Perna*) Trend	0.83	< 0.001
(*Mytilus*) Raw	0.39	> 0.05
(*Mytilus*) Residual	0.11	> 0.05
(*Mytilus*) Trend	0.49	< 0.05
(d) Recruitment vs Adult Cover		
Recruitment (Mean) by Cover (Mean)		
(*Perna*) Raw	0.43	> 0.05
(*Perna*) Residual	0.49	< 0.05
(*Perna*) Trend	0.54	< 0.05
(*Mytilus*) Raw	0.50	< 0.05
(*Mytilus*) Residual	0.18	> 0.05
(*Mytilus*) Trend	0.62	< 0.01

3.3.2 Temporal study

Over the 12 months of sampling at the 5 Mossel Bay area sites, relatively consistent temporal patterns of settlement and recruitment emerged for both species. All peaks, including the maximal settlement and recruitment rates (*Perna* = 5162 ± 314.3 settlers.d^{-1}, *Perna* = 457 ± 39.3 recruits.d^{-1}; *Mytilus* = 779 ± 171.7 settlers.d^{-1}, *Mytilus* = 53 ± 18.7 recruits.d^{-1}, see Fig 3.9 and 3.10), occurred during the period from October 2005 to January 2006. Outside this period, the months April through September 2005 and February and March 2006, settlement and recruitment of both species was far lower (< 30.d^{-1}). Although this trend was consistent for both species, the magnitude of settlement and recruitment rates differed between them. In general *Perna* settled and recruited at far greater rates (at times as much as two orders of magnitude greater) than *Mytilus*, and during peak settlement/recruitment months, settlement rates exceeded recruitment of both species (Figs 3.9 and 3.10).

Thus, the extreme levels of settlement and recruitment, previously noted at the 3 open coast sites (OGT, OSF and OBS), did not occur throughout the year. Rather, these were isolated events happening only between October 2005 and January 2006. Within this period, two distinct pulses of settlement of both species occurred across all 5 sites. During the first of the main pulses, which took place in November 2005, settlement of *Perna* and *Mytilus* was greatest at OGT (Fig 3.9 *Perna* = 5162 ± 314.3 settlers.d^{-1}; *Mytilus* = 256 ± 64 settlers.d^{-1}). The second pulse happened in January 2006, and settlement rates were highest at OBS (Fig 3.9 *Perna* = 4170 ± 1044.2 settlers.d^{-1}; *Mytilus* = 779 ± 171.7 settlers.d^{-1}).

Extreme recruitment periods were similarly restricted to the months October 2005 through January 2006. Broadly, two pulses of recruitment were recorded, but peaks, especially of *Perna* did not occur concurrently at all sites. The main peak in *Perna* recruitment was recorded at OGT in November (Fig 3.10 OGT = 457 ± 39.3 recruits.d^{-1}). The pulses of *Mytilus* recruitment, seen most strikingly at OGT in October (Fig 3.10 OGT = 22 ± 4.9 recruits.d^{-1}) and December (Fig 3.10 OGT = 53 ± 18.7 recruits.d^{-1}), were more synchronous in nature.

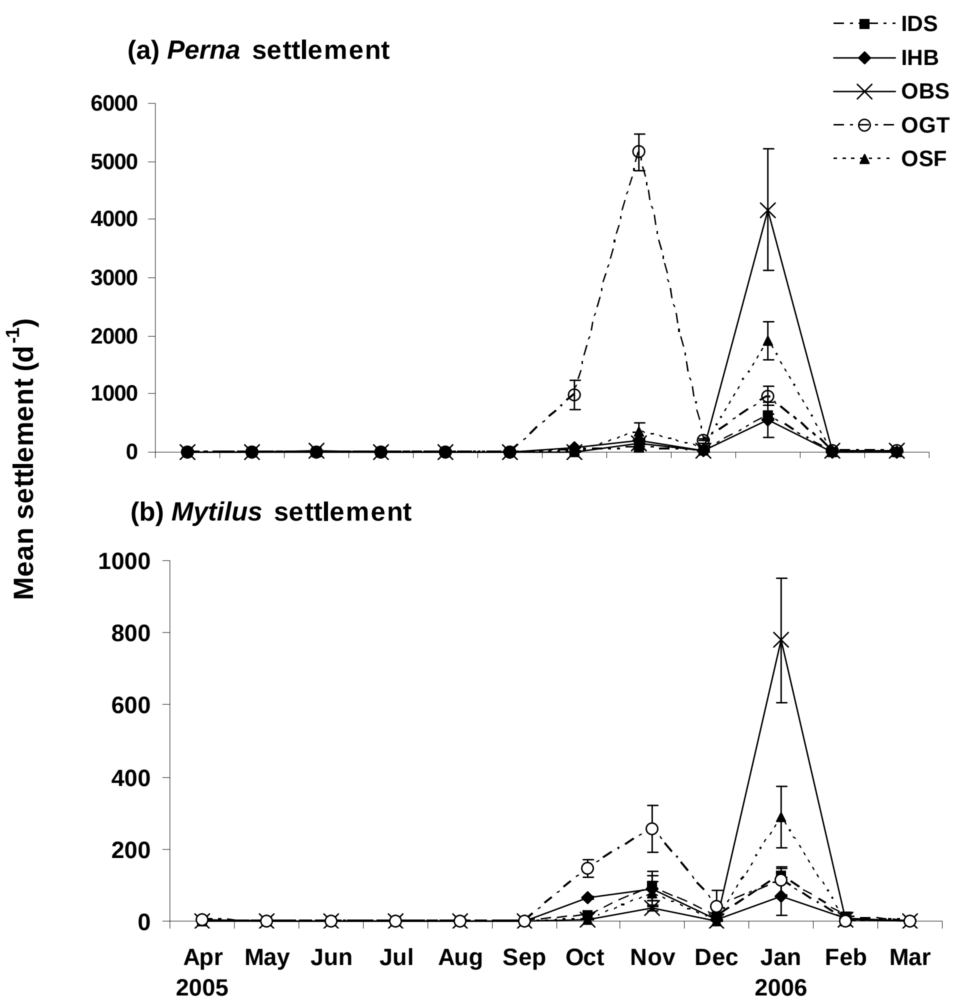

Figure 3.9 Mean daily settlement (±SE) for April 2005 through March 2006 for (a) *Perna perna* and (b) *Mytilus galloprovincialis* at the three open coast sites immediately east of Mossel Bay and the two bay sites inside Mossel Bay. Note that y-axis scales are not equivalent.

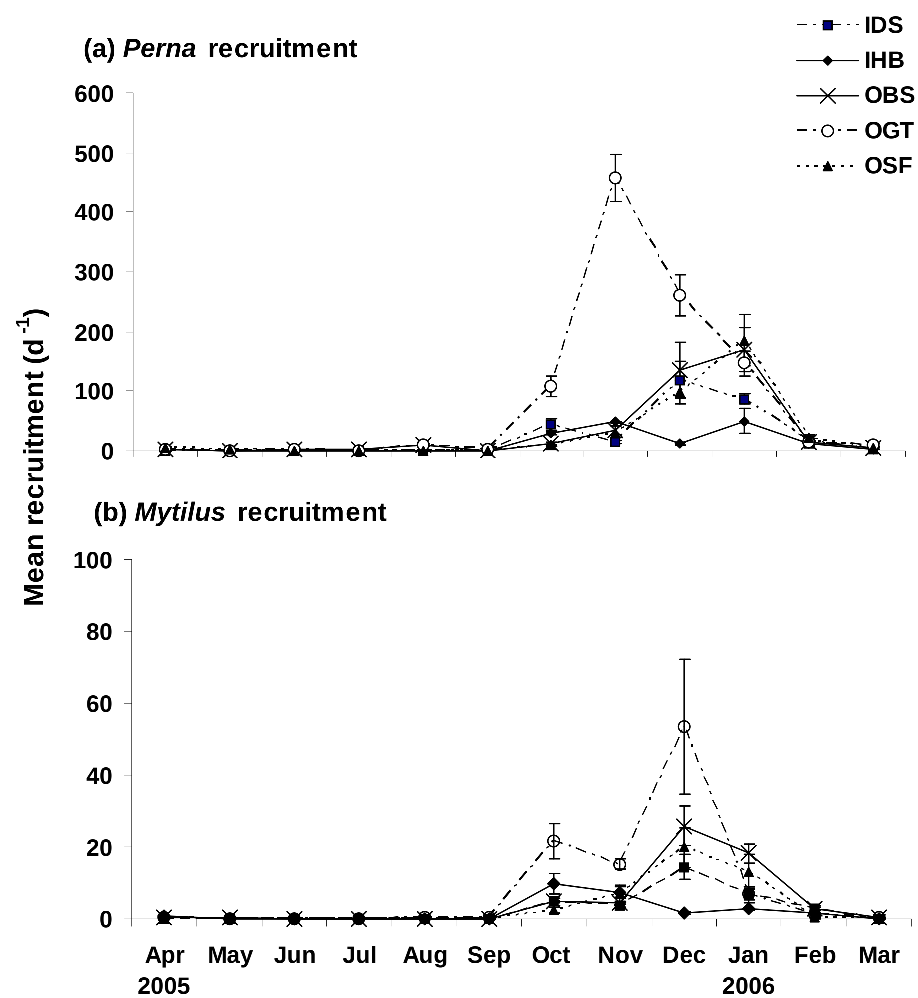

Figure 3.10 Mean daily recruitment (±SE) for the months April 2005 through March 2006 for (a) *Perna perna* and (b) *Mytilus galloprovincialis* at the three open coast sites immediately east of Mossel Bay and the two bay sites inside Mossel Bay. Note that y-axis scales are not equivalent.

ANOVAs (examining the factors month and site) showed significant month x site interactions for settlement (Table 3.4 (a) *Perna*, $F_{11, 120} = 24.36$, $p < 0.001$; (b) *Mytilus*, $F_{11, 120} = 9.81$, $p < 0.001$) and recruitment (Table 3.4 (a) *Perna*, $F_{11, 120} = 19.5$, $p < 0.001$; (b) *Mytilus*, $F_{11, 120} = 4.4$, $p < 0.001$) for both species. SNK comparisons revealed that settlement of *Perna* and *Mytilus* was, in some months, significantly greater at the 3 open coast sites than for other month x site combinations (Table 3.4 (a) *Perna* OGT (Nov 05) > OBS (Jan 06) > OSF(Jan 06) > other combinations; (b) *Mytilus* OBS(Jan 06) > OSF(Jan 06) > OGT(Nov 05) > other combinations). The post-hoc analyses of *Perna* recruitment data showed that the highest level of recruitment occurred at OGT during November 2005. This was found to be significantly greater than the second highest level of recruitment, which also happened at OGT, but in December 2005. For each of these month x site combinations, recruitment was significantly different from all other combinations.

For *Mytilus*, SNK comparisons showed a very similar month x site interaction in which recruitment, at OGT during December 2005, was significantly greater than that in any other month x site combination (Table 3.4).

Table 3.4 Results of 2-way ANOVAs, (month x site) of temporal settlement (d^{-1}) of (a) *Perna perna* and (b) *Mytilus galloprovincialis* and temporal recruitment (d^{-1}) of (c) *P. perna* (d) *M. galloprovincialis* at 5 Mossel Bay sites. Abbreviations used in the SNK results show the month, followed by a three-letter site code. For site codes, the prefix 'I' denotes a bay site, while 'O' denotes an open coast site. The sites examined were: IDS – Dias Strand, IHB – Hartenbos, OGT – Glentana, OSF – Sedgefield and OBS – Brenton-on-Sea.

(a) *Perna* settlement

Source	**Df**	**MS**	**F**	***p***
Month	11	4562648	2.47120	< 0.05
Site	4	1952554	1.05754	> 0.05
Month x Site	44	1846325	24.35751	< 0.0001
Error	120	75801		
SNK (Mo x Site)	Nov(OGT) > Jan(OBS) > Jan(OSF) > all other Mo x site combinations			

(b) *Mytilus* settlement

Source	**Df**	**MS**	**F**	***p***
Month	11	99891.7	3.964187	< 0.001
Site	4	14899.4	0.591282	> 0.05
Month x Site	44	25198.5	9.808799	< 0.0001
Error	120	2569.0		
SNK (Mo x Site)	Jan(OBS) > Jan (OSF); Nov(OGT) > all other Mo x site combinations			

(c) *Perna* recruitment

Source	**Df**	**MS**	**F**	***p***
Month	11	42663.6	3.90781	< 0.001
Site	4	27440.3	2.51342	< 0.05
Month x Site	44	10917.5	19.49069	< 0.0001
Error	120	560.1		
SNK (Mo x Site)	Nov(OGT) > Dec(OGT) > all other Mo x site combinations			

(d) *Mytilus* recruitment

Source	**Df**	**MS**	**F**	***P***
Month	11	727.185	6.484575	< 0.0001
Site	4	220.379	1.965201	> 0.05
Month x Site	44	112.141	4.393791	< 0.0001
Error	120	25.523		
SNK (Mo x Site)	Dec(OGT) > all other Mo x site combinations			

3.4 Discussion

The most immediately noticeable result of this study is an intersection of geography and time. The complete data-set showed that the open coast sites just east of Mossel Bay, centred on Glentana (OGT, OSF, OBS) behaved distinctly differently from other open coast sites, particularly in summer. This was most conspicuous in the extraordinarily high mean settlement rates of *Mytilus* and *Perna* in this area during October and January (Fig 3.3). The resultant reversal of summer settlement patterns of both species, to a situation of higher settlement on the open coast than in bays (significant in January only), is in direct contrast to both of my hypotheses. This indicates that the positive effect of topography (bays) on settlement and recruitment, demonstrated in previous studies, is not a ubiquitous occurrence. Consequently, two questions were raised: (1) what would the results be without the influence of the extreme outlier values of the three anomalous open coast sites and (2) when and how regularly does extreme settlement and recruitment occur at these three sites? These questions were answered by analysis of the reduced data-set, and of the temporal (12mo) data-set respectively.

From the reduced data-set, it was seen that settlement and recruitment patterns across the section of coast east of OBS were much closer to what was predicted by the original study hypothesis. In general, a consistent pattern of greater settlement and recruitment in the 3 bays (Plettenberg, Jeffreys and Algoa bay) than on the open coast was observed across all four months for both species, although rates on both shore types in July were often so low as to be negligible (Figs 3.4 and 3.5). In terms of statistical significance however, this trend was strongly dependent on month. Here it is important to note that it was the bay sites that were dependent on month (season), rather than the open coast sites. In other words, settlement and recruitment rates (bar *Mytilus* recruitment) on the open coast remained relatively constant over time, while bay rates increased dramatically (by as much as an order of magnitude in January) in the summer. Although the general trend is of direct interest, this seasonal pattern in bays, and its conspicuous absence from the open coast, may provide some insight into the causal relationships underlying the overall effect of topography.

As to the second question, the temporal study showed that within the Glentana area, the extreme levels of settlement and recruitment observed in the seasonal study were temporally isolated events (Fig 3.9 and 3.10). In terms of settlement, two very distinct pulses, in November and January, were observed to occur simultaneously across all five sites, while recruitment pulses were not geographically simultaneous, and were spread out between October and January. Both of these temporal patterns however, agree well with what is known about reproductive output in the study area. McQuaid and Phillips (2007) and Porri and co-workers (2006) recorded significant spawning and settlement events occurring up to four times a year. The months May through October were designated as having a high probability of spawning, while January to March were described as low probability months (McQuaid & Phillips 2007). Given the capacity of mytilid larvae to delay metamorphosis and settlement for up to a month (Pechenik 1990), these spawning times generally match up well with the timing of settlement/recruitment pulses observed in the present study (allowing for some natural variability in spawning and settlement times of course). Outside of the months when pulses occurred, settlement and recruitment were low (< 30 individuals.d^{-1}).

Theoretically, the general trend of greater settlement/recruitment in bays relative to the open coast, and the seasonal pattern of settlement/recruitment in bays may be explained by differences in larval dynamics (production, mortality or transport), settler mortality (post-settlement mortality) and/or local hydrodynamics between bay and open coast habitats. Additionally, if a habitat-specific bias in substratum availability exists, settlement intensification possibly forms part of the explanation. Localised differences in any of these factors, may also account for the spatial disparity between the Mossel Bay/Glentana area and the rest of the coast. On a localised scale, wave exposure may be important in terms of settler mortality, and is certainly important to factors dependent on diffusion rate such as food and propagule supply (Bell & Denny 1994, Abelson & Denny 1997). While the seasonal peaks in settlement and recruitment seen in bays seem to be clearly linked to the pulsed spawning described for the study species (McQuaid & Phillips 2007, Nicastro 2007), the question of why similar peaks were not seen on the open coast remains.

Larval production or at least reproductive output has been previously examined on the south coast of South Africa by McQuaid and Phillips (2007) who showed average gamete output of *Perna perna* and *Choromytilus meridionalis* (estimated from individual weight loss) within Algoa Bay to be significantly greater than at open coast sites east of the bay. In a multiple-bay study on the same coast, Nicastro (2007) generally found the gonad index of *Mytilus galloprovincialis* to be greater in bays than on the open coast. However, the study of Nicastro (2007) did not find a similar situation for *Perna*. In fact the inverse was often the case, with reproductive output of this species on the open coast being greater than or equal to that in bays throughout the year studied.

Neither of these studies therefore introduced any evidence of differences in seasonal patterns of output between habitats. Logically then, general seasonal changes in reproductive output and settlement (as described by McQuaid & Phillips 2007, Nicastro 2007) should be discernable in *both* habitats, and should be similar in trend, if not in magnitude. Thus, the findings of the present study indicate that seasonal changes in reproductive intensity on the open coast were not translated into noticeable changes in settlement or recruitment. Critically, this de-coupling of settlement/recruitment from reproductive output on the open coast suggests that differences in settlement/recruitment between bays and the open coast are likely driven by factors other than larval production. This leaves differential larval transport and mortality, differential post-settlement mortality, settlement intensification and the spectrum of effects associated with local hydrodynamics – including wave exposure – as possible explanations for the observed settlement and recruitment patterns.

Given the enormous complexity of biological phenomena such as settlement and recruitment, the idea of singling-out a cause or process responsible for the spatial and temporal patterns of such phenomena is unrealistic (Pineda et al. 2009). Since no quantification of rocky habitat was undertaken here and no larval mortality data exist for the current study area, it is not possible to rule-out effects of larval mortality or settlement intensification. However, select correlations between key life stages that span vulnerable, changeable or ‘high flux’ periods can be very informative and help to rule out certain processes (*sensu* Lagos et al. 2005).

The data available allowed the relationships between settlement and recruitment, recruitment and adult cover, and interspecies relationships in settlement and recruitment to be examined. Perhaps most usefully, strikingly high interspecies correlations – those between settlement of *Perna* and settlement of *Mytilus*, and between recruitment of each – were found to occur at regional and local scales in both of the months examined (Table 3.4). The two most important aspects of these results are that 1) the correlations remained consistently strong after a post-settlement period (i.e. interspecies recruitment correlations are as high as interspecies settlement correlations, Table 3.4), and curiously 2) the correlations were equally strong at regional and local scales (differences between regional and local *r* values of between 0.042 and 0.108). Interspecies correlations such as these, between similar, co-occurring species, may be considered indicative of common larval transport processes (Pineda 1994a, Connolly et al. 2001, Lagos et al. 2005). Given the maintenance of strong interspecies correlations at recruitment, any such process is one that has the same effect on settlement and as it does on recruitment. This could happen in 2 ways; either the process acts early on and has a pervasive impact, or the process simply acts continuously, affecting settlers and recruits. In light of the seemingly scale-independent nature of the process, it should also be a process that has common effects at regional and local scales. As with its consistent impact on settlement and recruitment, the process may be a basal one that sets the pattern regionally, but is important enough for this pattern to trickle down to the local scale, or it may be that the process actually acts in the same way at both scales. Based on these deductions, if a common process is responsible, it should be one that is basally important to settlement of both species, has the same effects regionally as it does locally, and is able to supersede subsequent factors acting after settlement, either by direct action or by the strength of its initial effect.

Although generally weaker, the correlations found between settlement and recruitment and recruitment and adult cover help to narrow down the identification of the process further. Recruitment was correlated with settlement for both species, but only at the regional scale, showing that at least in terms of regional pattern, post-settlement mortality or other post-settlement processes are not important enough to de-couple recruitment from settlement. The inverse of this is that at local scales, post-settlement processes could be important. Adult mussel cover was likewise correlated with recruitment in both species at the regional scale, but this correlation extended to the local scale for *Perna*. These findings also suggest that post-settlement/post-recruitment factors do not change the initial distribution/abundance setup at settlement.

Together, the correlations generally depict a situation in which the regional patterns of recruitment and adult cover are strongly related to the pattern of settlement – the initial pattern of successfully returned and settled larvae. They also provide some evidence of a regionally strong stock-recruitment relationship for these species. Local scale patterns and relationships however, are clearly more variable. Finally, these results discount a strong influence of mesoscale topography-related post-settlement processes (such as post-settlement mortality due to wave exposure) on settlers and recruits, with the possible exception of the Glentana area sites. In taking this discussion further, it is important to recognise the inadequacies of inferring larval transport mechanisms from settlement data (Pineda et al. 2007). Rather than attempting to speculate as to specific mechanisms, it may simply be said that bays can have a strong influence on settlement and recruitment, but the precise nature of this influence is not always straightforward, as the Mossel Bay/Glentana sites demonstrate.

With larval production ruled out, and indirect support for the presence of common transport mechanisms (strong interspecies correlations), one explanation may be that topographically-mediated larval transport processes drive settlement. The possibility of density independent settlement may then account for the relative unimportance of post-settlement processes (Connell 1985), and therefore also account for the persistence of the initial settlement pattern to recruit and adult levels (at least regionally). Locally however, recruit-settler and adult-recruit relationships were poor. For instance, assuming that extreme settlement and recruitment events are characteristic of the Glentana area, (given that sites can rank consistently over time - *sensu* Connell 1985, Porri et al. 2006, Rilov et al. 2008), the absence of correspondingly extreme adult cover in this region (relative to the rest of the coast) is particularly indicative of this local decoupling. Here the idea of density-dependence may form part of the explanation. High settlement over a ‘short’ time period can cause density dependent competition, increased mortality and therefore a decoupling of settler and adult populations (Connell 1985). This scenario fits well with the extreme peaks of primary settlement recorded at Glentana area sites, which individually would have occurred over a period of approximately 2 days. Therefore at these sites, post-settlement processes may be crucial, in response to the extraordinary, temporally localised pulses of settlement.

It seems likely that some level of interaction of nearshore oceanography with local shelf features is responsible for the different regional biological patterns. This view is based firstly on the generalisations that a wider shelf should mean greater retention (Reaugh 2006), as should a concave coastline (Largier 2004). More specifically, within the study region, widening of the continental shelf alters boundary flow interactions of the Agulhas Current with nearshore water, affecting upwelling features (Lutjeharms et al. 2000). Furthermore, the nearshore oceanographic regime in the Mossel Bay/ Glentana area is distinctly different from the eastern section of the study region, with wind-induced upwelling shown to occur in association with the prominent headlands at Algoa Bay, Jeffreys Bay and Plettenberg Bay, but not at Mossel Bay (Schumann et al. 1982). These oceanographic differences should mean differential larval transport (and possibly nutrient regimes), thus explaining the extreme settlement events observed on the open coast (Glentana area sites) in terms of greater larval supply.

While density-mediated processes may help to explain the lack of correspondingly extreme adult cover at the Glentana area sites, this de-coupling could also be attributed to any number of other local factors. For example, disturbance by sand inundation or storms strongly affects mussel populations (e.g. Erlandsson et al. 2006, Zardi et al. 2008). Another possibility is some sort of synergistic interaction between density-mediated and local disturbance factors, whereby high densities may increase vulnerability of populations to disturbance (e.g. Harger & Landenberger 1971, Paine & Levin 1981). These explanations may of course be contingent upon the temporal dynamics of extreme settlement; although sites generally rank consistently, settlement was not always high in the Glentana area.

In conclusion, inferences drawn from the recruit-settler and adult-recruit correlations, together with the fact that a strong relationship exists between coastline topography and nearshore oceanography within the study region (Schumann et al. 1982, Beckley 1983, Goschen & Schumann 1988), seem to point to a strong and pervasive influence of supply-side factors stemming primarily from regional patterns of larval transport. This kind of bottom-up influence of coastal oceanography on rocky intertidal population dynamics has certainly been demonstrated (e.g. Menge et al. 2003). Apart from identifying the limits of generalisations about positive bay/headland effects on settlement and recruitment, the unusual settlement and recruitment patterns at the Glentana area sites may reinforce the notion of topography and oceanography-mediated settlement. This is because the dramatic changes in settlement and recruitment rates fit precisely with changes in coastal oceanography (related to coastline topography and shelf bathymetry) between the eastern and western sections of the study region (Schumann et al. 1982, Walker 1986); upwelling centres are associated with the 3 easterly headlands, but are not found west of Mossel Bay. Finally, deviation from the general trends and the breakdown of correlations at local scales highlight the importance of integrating local and regional data, as patterns of settlement, recruitment and adult cover may be governed by different processes at each of these scales.

CHAPTER 4

THE DICHOTOMOUS ROLES OF BIOFILM AND CONSPECIFIC SETTLERS ON SETTLEMENT

4.1 Introduction

For marine invertebrate larvae, including those of bivalves, the sheer number of studies examining the process of settlement speaks to the complexity of this event (see Rodríguez et al. 1993 for review of settlement studies). Several models have been proposed and tested, particularly with respect to the influences of hydrodynamics (e.g. André et al. 1993, Abelson & Denny 1997). These models fall into two broad groups, split between those that suggest settlement is largely a passive process (Eckman 1990, Armonies & Hellwigarmonies 1992, Cáceres-Martínez et al. 1994, Harvey et al. 1995a) and those that postulate active larval choice and behaviour-determined settlement (e.g. Keough & Downes 1982, Pawlik 1992, Arnold et al. 2005, Dobretsov & Wahl 2008). Settlement behaviours are, however, not mutually exclusive as Harvey and colleagues (1995a: 103) note; passive delivery of larvae does not preclude active behaviour which may occur at microhabitat scales or in response to various "chemical or textural differences". Furthermore, switching between active and passive settlement in mussel and abalone species has been shown to be regulated by hydrodynamic conditions (Boxshall 2000, Pernet et al. 2003, Dobretsov & Wahl 2008), with larvae actively selecting microhabitats under low flow, but being increasingly relegated to passive behaviour under higher flow conditions. In line with such findings, perhaps the most realistic way of viewing settlement is as a changeable continuum of behaviour with varying degrees of activity (André et al. 1993).

In short, the details of settlement behaviour differ between individuals and species, both of which are influenced by fundamental endogenous and exogenous factors (Hadfield 1986). Endogenous factors are the inherent genetic, physiological or developmental characteristics of individuals, and are often most influential in terms of the timing of settlement. For instance, larval age and size affect the 'readiness' of larvae to settle (Satuito et al. 1997, Marshall & Keough 2003a, 2003b); older larvae settle more readily, while larger larvae – presumably with greater energy reserves - are able to delay settlement in favour of being more discerning in terms of settlement substrate and other cues. These changes in larval selectivity and responsiveness to settlement cues, with increasing age and/or decreasing energy reserves, are better known as the 'desperate larva' hypothesis (Toonen & Pawlik 2001). Exogenous factors are usually physical or chemical properties of the environment in which the larvae occur, and may affect passive and active settlement via physical forcing or attractant/repellent cues respectively. Hydrodynamic forces drive passive settlement (Abelson & Denny 1997), but have also been shown to influence active settlement behaviour (e.g. Mullineaux & Garland 1993, Pernet et al. 2003). Other physical factors influencing active settlement behaviour include attributes of the substratum (e.g. Crisp & Ryland 1960), water temperature (Hidu & Haskin 1978) and light (Marsden 1984). The influences of chemical factors (as cues for metamorphosis and/or settlement) are well documented and are becoming better understood (see Pawlik 1992, Steinberg et al. 2002 for review) with more effort recently being given to the identification and characterisation of ecologically relevant compounds and chemicals (e.g. Harder et al. 2002, Bao et al. 2007, Soares et al. 2008).

The involvement of chemical cues, either as inducers (attractants - Keough & Raimondi 1995) or inhibitors (repellents - Maki et al. 1989, Wieczorek & Todd 1998) of metamorphosis or attachment, has been shown for several organisms. The cues tested (or suggested) in such studies stem mostly from macroalgae (Pearce & Scheibling 1991, Huggett et al. 2005), biofilms (for an early review see Meadows & Campbell 1972), closely associated or host organisms (Krug & Zimmer 2000) or conspecific adults (Crisp & Meadows 1962, Highsmith 1982, Zhao & Qian 2002). In general, it is suggested that inducers are usually primary metabolites (sugars, carbohydrates, amino acids and/or proteins) of macro-organisms, while inhibitors or deterrents are more likely to be non-polar secondary metabolites (Steinberg et al. 2002). Various macroalgal species or extracts thereof have been shown to increase settlement of mussel larvae. Examples include work on *Mytilus edulis* (Dobretsov 1999, Dobretsov & Wahl 2001, 2008) and that on *Perna perna* (Soares et al. 2008) and

P. canaliculus (Alfaro et al. 2006). As Dobretsov (1999) notes however, there is often some difficulty in entirely separating the effects of macroalgae from those of the biofilms growing on them. Indeed, several studies have demonstrated that biofilms isolated from the surface of various macroalgal species, rather than the algae themselves, are the attracting agents (Johnson & Sutton 1994, Negri et al. 2001). Furthermore, Dobretsov (1999) points out that biofilms growing on macroalgae could potentially be contaminated through their uptake of secondary algal metabolites. With this caveat in mind, it was shown that biofilm gathered from filamentous algae (*Cladophora rupestris*) produced significant positive chemotactic movement of *M. edulis*. Regardless of the source of the cue, Dobretsov (1999) argues that larval behaviour observed in this study, by definition, constituted taxis in response to water soluble cues. One other concern discussed by various authors is that of concentration of cues and their detection in the field, particularly by very small (1-2mm) larvae (Meadows & Campbell 1972). However, at least some field (Dobretsov & Wahl 2008) and laboratory (Marsden 1991) evidence points to the ability of larvae to detect and respond to cues at distances of at least 3-10cm. With evidence of the ability for ecologically relevant detection of, and chemotactic response to chemical cues, this chapter focuses specifically on the effects of cues associated with biofilms and conspecifics in the field.

4.1.1 Biofilm

The presence of biological "films" in the marine environment was first demonstrated in the 1930's, most notably by Zobell and Allen (1935). Their work recorded the ability of the films to colonise submerged surfaces rapidly and described the films as consisting mostly of bacteria and diatoms. This work is also one of the earliest instances of an explicit link being made between microbial films and settlement: "…such films favour the subsequent attachment of the larger and more inimical fouling organisms" (Zobell & Allen 1935: 249). More recently, the presence and importance of microalgae in biofilms has been established (Pearce & Scheibling 1991). Thus, biofilm is defined here as a microscopic biological film colonising submerged or intertidal surfaces, comprised mostly of bacteria, diatoms and microalgae.

Biofilms, or specific components thereof, have been shown to increase settlement of many marine invertebrates, including polychates (Williams 1964, Meadows & Campbell 1972, Lau & Qian 2001, Harder et al. 2002), barnacles (Olivier et al. 2000), the green sea urchin - *Strongylocentrotus* sp (Pearce & Scheibling 1991), oysters (Tritar et al. 1992) and limpets (Zhao & Qian 2002). Similar evidence exists for the mussels *Mytilus galloprovincialis* (Hrs-Brenko 1973, Satuito et al. 1997, Bao et al. 2007), *M. edulis galloprovincialis* (Satuito et al. 1994) and *Mytilus edulis* (Dobretsov 1999) under field and laboratory conditions. Comparable results have been shown for the freshwater mussel, *Dreissena polymorpha* in the field (Wainman et al. 1996). The precise nature of biofilm cues possibly differs between organisms, since work by Dobretsov and Wahl (2008) indicates waterborne chemical detection of biofilm by mussel larvae, but other workers (polychaetes - Williams 1964 , limpets - Zhao & Qian 2002) demonstrated that tactile detection was necessary, suggesting that the relevant biofilm cues were not waterborne.

4.1.2 Conspecifics

Chemical cues from conspecifics have been implicated in the gregarious settlement of many marine invertebrate species in multiple phyla (reviewed by Meadows & Campbell 1972, Burke 1986). Wilson (1968) considered conspecific influence to be the principal signal to which larvae respond, resulting in metamorphosis and attachment.

As with biofilm cues, the nature of the interaction between larva and cue seems to be specific to the organism involved. Some studies point to waterborne cues (Marsden 1991, Toonen & Pawlik 1996, Bryan et al. 1997, Zhao & Qian 2002, de Vooys 2003), while others suggest cue detection to be dependent on physical contact with conspecifics (Crisp & Meadows 1962, Wilson 1968). Although the occurrence and importance of conspecific attraction is well documented, few studies have examined this effect in mussels. Some of what is known about conspecific attraction in mussels comes from the study of freshwater species, particularly the Zebra mussel *Dreissena polymorpha*. Most notably, greater settlement of *D. polymorpha* (270-390µm) has been shown to occur on live conspecific adults and dead shells than on other inanimate substrata with similar textural properties

(Wainman et al. 1996). Likewise, the presence of adult conspecifics stimulated the attachment of larger individuals (> 10mm) of this species (Kobak 2000). Here, waterbourne cues were suggested since no necessity for physical contact was demonstrated. In a similar laboratory study, contact between immature freshwater mussels (*Limnoperna fortunei*) was shown to stimulate byssus secretion (Uryu et al. 1996). For marine species, increased recruitment of "small" mussels (0-5mm) on collectors containing adult conspecifics has been shown for the ribbed mussel, *Geukensia demissa* (Nielsen & Franz 1995). Similarly, selection of adult conspecifics over a competitor species (Petersen 1984) and movement towards conspecific signal (de Vooys 2003) has been shown for *Mytilus edulis*. However, some doubt is thrown on the broad applicability of such results since settlement of Mytilid species seems not to be driven by conspecific attraction in the field (Johnson & Geller 2006, Porri et al. 2007) or in the laboratory (Davis & Moreno 1995).

In addition, conspecific cues are not necessarily limited to those exuded by adults; certainly settler/larval interactions and attraction has been shown in two species of serpulid polychaete (Marsden 1991, Bryan et al. 1997), barnacle species (Clare et al. 1994) and in the American oyster *Crassostrea virginica* (Hidu 1969). Although such evidence lends credibility to the idea that early settlers and/or juveniles may have an attractant effect on conspecific larvae or juveniles, some contrary findings do exist for barnacles and ascidians (Keough 1998, Jeffery 2002). These latter studies found the attraction of larvae to established settlers and recruits to be weak or nonexistent. To my knowledge however, no studies have examined this kind of settler/larva relationship in any mussel species. Understanding such interactions, particularly in the case of strong attractant (or inhibitory) effects, will be important to artificial or experimental surfaces where an initial settler presence may well influence subsequent settlement.

Since biofilms are ecologically important and ubiquitous colonisers of marine surfaces (Zobell & Allen 1935, Pearce & Scheibling 1991), including sediments (Meadows & Campbell 1972), there are probably no entirely non-living surfaces in the marine environment (Steinberg et al. 2002). This, together with significant evidence for ecologically relevant detection of, and chemotactic response to, chemical cues compels examination of the effects that the presence of biofilms and conspecific settlers have on subsequent settlement of mussel larvae on artificial substrata. This is of particular importance for the following chapter, or whenever experimental design involves serial removal and replacement of collectors and comparison of these to more established substrata.

Hence, this study tests the effect of biofilm, conspecific settlers and a combination of the two on subsequent primary and secondary settlement of *Perna perna* and *Mytilus galloprovincialis*. It is hypothesised that biofilm and conspecifics will increase settlement individually and in combination.

4.2 Methods and materials

4.2.1 Experimental setup

For the purposes of the present study, the term "conspecific" refers to either of the two study species, *Mytilus galloprovincialis* and *Perna perna*, while the term "biofilm" refers to the whole assemblage of bacteria, diatoms and microalgae that first colonise submerged substrata. The attraction of primary and secondary settlers to epilithic biofilm, conspecific settlers and a combination of the two was investigated at two 'high' settlement sites (see Chapter 1, Fig 1.1; also Chapter 3, Fig 3.1 and 3.2) on the south coast of South Africa. Brenton-on-Sea (OBS 34.07°S; 23.02°E) was sampled in April 2008 and the experiment was repeated the following month at Sedgefield (OSF 34.03°S; 22.77°E). The experiments compared settlement over 24hr on various 'established' or pre-treated plastic pot scourers (larval collectors as used in Chapter 3) with that on untreated 'new' collectors.

4.2.2 Preparation

Three experimental treatments and one control treatment were developed over a 5 day preparatory period in the field, immediately prior to the experiment. For each treatment, 10 larval collectors were randomly deployed within the low mussel zone. This zone on the shore was chosen as it receives highest levels of settlement of both study species (Porri et al. 2007). Each collector was attached to an eye-bolt screwed into the rock. The treatments were: 1) Biofilm (*B*): settlers were excluded from collectors by means of 15x15cm 200µm nylon mesh bags, thus allowing development of biofilm in the absence of settlers. 2) Settlers (*S*): collectors were used to gather primary and secondary settlers over the first 4 days of the preparatory period. At the field laboratory on the 5th day, settlers from each collector were washed off and 'seeded' onto a clean collector in order to exclude biofilm (numbers of settlers varied; e.g. for Brenton-on-Sea there were between 66 – 118 per collector, with 4 of the 6 collectors used, having around 100 settlers each). Once seeded, each collector was placed into a 250ml jar and maintained in aerated sea water for the remaining 24hr of the preparatory period. This allowed settlers time to attach fully to the collector. 3) Biofilm-Settlers (*BS*): natural settlement and biofilm development was allowed to occur on these collectors during the 5 days. In addition a control treatment was prepared: Biofilm-Settlers$_{\text{shaded}}$ (BS_{shaded}): 200µm mesh discs, 10cm Ø, were sewn onto the top of collectors to control for possible effects of shading created by the mesh bags in the biofilm (B) treatment. This partial covering of the collectors allowed settlement, and maintained biofilm development at levels comparable to those found on the 'bagged' biofilm treatment collectors. Although the quantity of biofilm could not be directly controlled or standardised across all preparatory treatments, 3 of the 10 collectors in each of the above treatments were randomly designated as 'chlorophyll testers'. These collectors were kept aside at the end of the preparatory period, wrapped in aluminium foil and immediately frozen to allow quantification of biofilm on bagged (*B*), shaded (BS_{shaded}) and unshaded (*BS*) treatments. This meant that any effects of the 200µm mesh on chlorophyll-a (chl-a) levels in the biofilm could be identified.

4.2.3 Staining

On the 5th day, all treatments (except the settler (*S*) treatment which had already been collected on day 4) were removed to the field laboratory where each collector was placed into a 250ml plastic jar. In order to mark settlers, each jar was filled with a 200mg/l solution of calcein in sea water and aerated for 24hrs to allow maximum uptake of the stain by the settlers. This fluorescent staining technique has been shown to mark calcium carbonate shelled organisms such as abalone, gastropods and mussels (Pirker & Schiel 1993, Day et al. 1995, Kaehler & McQuaid 1999, Moran 2000, Eads & Layzer 2002). Although Eads and Layzer (2002) did record high mortality of juveniles younger than 2 months while using the calcein stain, they ascribed this to human error rather than lethal effects of the stain itself. Choice of concentration and staining time was based on work conducted on juvenile freshwater mussels by Eads and layzer (2002). Lastly, two additional control treatments were created using brand new collectors: 1) New Washed$_{\text{stained}}$ ($NW_{stained}$) for which 10 new collectors were submerged in calcein solution for 24hrs; and 2) New Unwashed$_{\text{unstained}}$ ($NUW_{unstained}$) for which 10 new collectors were simply rinsed in fresh water and left to dry. This setup allowed comparison of settlement and biofilm development between stained and unstained collectors.

4.2.4 Experiment (24hr field deployment)

On day 6, all prepared collectors (except those kept aside for chl-a analysis) were re-deployed haphazardly on the shore, without their various treatment preparation coverings. All treatments and controls were left for 24hrs, after which collectors of each were retrieved and individually stored in 70% ethanol for later processing.

4.2.5 Laboratory

Each collector, apart from those kept for chlorophyll analysis, was thoroughly rinsed and a 75µm sieve used to retain all mussel settlers. *Mytilus* and *Perna* settlers were then identified, measured and grouped into four size classes (<360µm, 360 – 440µm, 441 – 590µm, > 590µm) and counted, using a stereo microscope at 25X magnification. These size classes were chosen to represent primary settlers, potential weekly growth at a low and a high growth rate and secondary settlers respectively. Growth rates used here are those of Bownes (2005).

Treatments that could have contained stained settlers (i.e. treatments: *S*, *BS*, and BS_{shaded}) were examined using an Olympus fluorescence microscope with a 460-490nm excitation filter (U-MWIB Cube) as described by Kaehler and McQuaid (1999). The number of calcein-stained individuals in each size class was recorded. Subtraction of the number of stained settlers from total settlers gave the number of (unstained) new settlers arriving on the collectors over the 24hr experiment. The number of settlers in each of the remaining treatments, i.e. those not containing settlers prior to the experiment (*B*, $NUW_{unstained}$ and $NW_{stained}$) directly indicated the number of settlers arriving over the 24hr experiment. The rate of settlement over 24hr could then be compared across treatments.

4.2.6 Chlorophyll-a analysis

Although biofilms consist largely of bacteria and diatoms (Zobell & Allen 1935, Dobretsov 1999), a microalgal spore component is also present (Pearce & Scheibling 1991). Concentration of chl-a has been used as an indicator of quantity or biomass of epilithic biofilm in several studies (Nagarkar & Williams 1997, Thompson et al. 1999). In the present study, chlorophyll extraction was done using room temperature analytical grade (99%) methanol in accordance with the protocol described by Thompson and colleagues (1999). Surface area of each collector was calculated using the weight of *Johnsons & Johnsons Baby Oil* adhering to them (Mapstone et al. 1984). This allowed the concentrations of chl-a to be expressed as μg/cm^2 and compared among treatments *B*, *BS* and BS_{shaded}. Chlorophyll analysis was undertaken only on samples from the experiment at Brenton-on-Sea.

4.2.7 Statistical analysis

Separate two-way ANOVAs were run using the factors site (random, 2-levels) and treatment (fixed, 6-levels, n = 6), comparing the number of settlers across treatments and sites, for each species/size-class combination. Significant results were further examined using Student Newman Keul's (SNK) post-hoc tests. Since data for both species and all size classes came from single collectors, correlations of settlement between species, and between size-classes within species, were checked to determine the independence of the data. This involved examining the correlation of primary settlement of *Perna* (across all treatments and sites) with that of *Mytilus*, and repeating this with the secondary settlement data. Size class correlations were done, examining all possible combinations of size class within each species. For example, the correlation of primary *Perna* settlers (size class 1) with size class 2, class 3 and class 4 were individually examined, showing whether the number of settlers in classes 2, 3 or 4 were dependent on the number of class 1 settlers. Overall, primary settlement of *Perna* correlated with primary settlement of *Mytilus* (r = 0.66, p < 0.05), showing that species data were not independent. No overall correlation was found between large secondary settlers of *Perna* and *Mytilus* (r = -0.0075, p > 0.05). Similarly, no correlation was found between numbers of primary (<360µm) and large secondary settlers (>600µm) of *Perna* ($r = 0.248$, $p > 0.05$) or *Mytilus* ($r = -0.166$, $p > 0.05$). The size class data were therefore considered independent, but primary settlement data for the two species were dependent.

Based on these correlations, separate ANOVAs were done for each species and size class, using only the smallest (primary settler) and largest (secondary settler) classes. Equivalent correlations for the Sedgefield site were more variable, but in the interests of using an analysis that included site as a factor, the corresponding size class data from Sedgefield were used.

This brought the total number of analyses to four (two size-classes for each of two species). Using the Shapiro-Wilks test, none of the data were found to be normally distributed ($p < 0.001$ in all cases). The homogeneity of variances was checked in each ANOVA and none were homogeneous (Cochran's test, $p < 0.05$ in all cases). Transformation of the data did not improve heteroscedasticity, hence all analyses were done on untransformed data. This was considered valid due to the large overall sample size drawn from 2 sites, including 6 treatments with 6 replicates each (Underwood 1997).

A 1-way ANOVA (fixed 3-levels, $n = 3$) was performed to determine whether chlorophyll-a concentrations differed between the bagged (B), shaded (BS_{shaded}) and unshaded (BS) treatments at Brenton-on-Sea. This analysis was done on untransformed data as variances were homogenous (Cochran's C = 0.78, df = 2, $p = 0.16$; Zar 1974).

The effects of biofilm and conspecific attraction were then quantified by examining differences in mean settlement between the relevant (significant post-hoc groups) treatments and clean ($NUW_{unstained}$) collectors. In this way a 'multiplier' or 'correction factor' was calculated for primary and secondary settlement, determining the factor by which mean settlement was greater on the treatment collectors than on the clean collectors, using the equation:

$$\text{Correction factor} = \frac{\text{Mean settlers on treatment}}{\text{Mean settlers on } NUW_{unstained}}$$

This factor was also expressed as a percentage increase, calculated by obtaining the difference between mean settlement on the significant treatment and clean collectors as a percentage of the mean settlement on the clean collectors:

$$\text{Percent increase} = \frac{(\text{Mean treatment} - NUW_{unstained})}{NUW_{unstained}} \times 100$$

These calculations were only done on data from Brenton-on-Sea, due to the low settlement at Sedgefield.

4.3 Results

4.3.1 Shading and staining controls

Chlorophyll-a level did not differ significantly between the bagged (*B*), shaded (BS_{shaded}) and unshaded (*BS*) treatments ($F_{2,\ 6} = 0.5$, $p > 0.05$, mean pooled across treatments = 0.044µg.cm^2), indicating comparable biofilm growth on all treatments. Similarly, the ANOVAs and post-hoc tests on primary and secondary settlement data revealed that there were no significant differences between new stained ($NW_{stained}$) and unstained ($NUW_{unstained}$) collectors. Thus the calcein staining technique did not affect primary or secondary settlement of either species.

4.3.2 Primary settlement

Patterns of primary settlement across treatments were strikingly similar for *Perna* and *Mytilus* at Brenton-on-Sea. For both species the BS_{shaded} control treatment had the greatest mean number of primary settlers (Fig 4.1a *Perna* = 6.5 ± 0.43; Fig 4.1b *Mytilus* = 4.3 ± 0.61). The next highest mean settlement occurred on the Biofilm (*B*) treatment (Fig 4.1a *Perna* = 4.5 ± 1.28; Fig 4.1b *Mytilus* = 3.2 ± 0.70). The lowest settlement in both species was found to occur on treatments using new collectors (Fig 4.1a *Perna* = 1.2 ± 0.40; Fig 4.1b *Mytilus* = 0.2 ± 0.17).

In comparison to Brenton-on-Sea, primary settlement of both species was far lower at Sedgefield (Fig 4.1c and d, all treatments ≤ 1.5 settlers). The settlement patterns across treatments were also less consistent between species than at Brenton-on-Sea. As was seen at Brenton-on-Sea, the highest settlement of *Perna* was found on the BS_{shaded} treatment collectors (Fig 4.1c *Perna* = 1.3 ± 0.49). Surprisingly however, the next highest settlement occurred on new-unstained collectors $NUW_{unstained}$ (Fig 4.1c *Perna* = 1 ± 0.37). The Biofilm treatment followed this, with a mean of 0.83 ± 0.40 *Perna* settlers. For *Mytilus*, primary settlement was greatest on the Biofilm treatment collectors (Fig 4.1d *B* = 1.5 ± 0.81), with the Biofilm-Settler treatment getting the next highest number of settlers (Fig 4.1d *BS* = 1.17 ± 0.48). There was therefore some similarity in settlement pattern between sites, with the Biofilm treatments receiving the greatest numbers of primary settlers.

Statistical analysis of the primary settlement data revealed significant treatment x site interactions for both species (Table 4.1a *Perna* $F_{5,\ 60}$ = 5.51, p < 0.001; Table 4.1b *Mytilus* $F_{5,\ 60}$ = 5.92; p < 0.001). Student-Newman Keul's (SNK) tests showed these interactions to be the same for both species, with significantly greater settlement on the Biofilm and Biofilm-Settler$_{\text{shaded}}$ treatments at Brenton-on-Sea (Table 4.1a *Perna* $BS_{shaded} > B >$ all other treatment x site combinations; Table 4.1b *Mytilus* $BS_{shaded} = B >$ all other treatment site combinations), but with no treatment effects at Sedgefield. Therefore at Brenton-on-Sea, the Biofilm (*B*) and Biofilm-Settler$_{\text{shaded}}$ (BS_{shaded}) treatments had significantly higher primary settlement over 24 hours than the four other treatments ($NW_{stained}$ $NUW_{unstained}$, *BS* and *S*) all of which had similar levels. If the BS_{shaded} treatment is excluded (see section 4.3.4 below for explanation of this exclusion), post-hoc groupings from the experiment at Brenton-on-Sea showed that new collectors and those with an initial settler presence at the start of the experiment ($NW_{stained}$ $NUW_{unstained}$, *BS* and *S*), had significantly less primary settlement than the treatment with biofilm only. Therefore, the presence of settlers in the *S* and *BS* treatments did not induce higher primary settlement than occurred on new collectors.

4.3.3 Secondary settlement

The levels of secondary settlement over the 24hr experiment were generally substantially greater than those of primary settlement. Within each site, the pattern of secondary settlement across treatments was similar for both species. At Brenton-on-Sea, the numbers of settlers of both species were generally higher on treatments that included an initial settler presence (*S*, *BS* and BS_{shaded}). Figure 4.2a shows that for *Perna* the highest mean number of settlers was recorded on the Biofilm-Settler treatment (*BS* = 55 ± 12.04), followed by the Settler treatment (*S* = 32.2 ± 3.80), while the lowest occurred on new collectors ($NW_{stained}$ = 9.83 ± 1.89 and $NUW_{unstained}$ = 8.33 ± 1.96). The mean number of secondary settlers on the Biofilm treatment (Fig 4.2a *B* = 14.2 ± 1.25) shows that secondary settlement on these collectors was numerically closer to that on the new collectors than on either of the experimental treatments with a settler presence (*S* and *BS*).

Secondary settlement of *Mytilus* at Brenton-on-Sea was low (relative to *Perna*) for all treatments. Although the highest mean number of settlers came from New $\text{UnWashed}_{\text{unstained}}$, the high error within this treatment should be noted. Excluding this, a trend similar to that seen in the *Perna* data, of higher settlement on those treatments containing initial settlers can be seen, with the highest mean number of settlers coming from the Biofilm-Settler treatment (Fig 4.2b *BS* = 1 ± 0.25). The lowest settlement occurred on the Biofilm and New $\text{Washed}_{\text{stained}}$ treatments (Fig 4.2b *B* and $NW_{stained}$ = 0.33 ± 0.21).

To some extent the pattern of maximum secondary settlement occurring on treatments with an initial settler presence was also recorded at Sedgefield. At this site the *BS* and BS_{shaded} treatments had the highest numbers of settlers for both species. For *Perna*, maximum secondary settlement was recorded on the BS_{shaded} collectors (Fig 4.2c BS_{shaded} = 27.7 ± 6.90), with *BS* having the second highest settlement (Fig 4.2c *BS* = 22.3 ± 4.91). For *Mytilus*, maximum secondary settlement was found on the *BS* treatment collectors (Fig 4.2d *BS* = 7.5 ± 1.82), followed by the BS_{shaded} treatment (Fig 4.2d BS_{shaded} = 6 ± 1.69). In contrast to the pattern established at Brenton-on-Sea however, the level of secondary settlement on the Settler treatment collectors was lower than on the Biofilm treatment collectors for both species. In fact, the Settler treatment received similar or lower secondary settlement than the treatments using new collectors (Fig 4.2c *Perna* $S = 10.83 \pm 1.25$, Fig 4.2d *Mytilus* $S = 3.67 \pm 0.92$); for *Mytilus*, this was the lowest number of settlers out of all treatments.

ANOVA results showed a significant treatment x site interaction for *Perna*, but not for *Mytilus* (Table 4.1c *Perna* $F_{5, 60} = 4.68$, $p < 0.01$; Table 4.1d *Mytilus* $F_{5, 60} = 1.37$, $p > 0.05$). Post-hoc tests showed that secondary settlement of *Perna* was significantly greater on the Biofilm-Settler treatment collectors at Brenton-on-Sea than for any other treatment x site combination (Table 4.1c). Therefore, the Biofilm-Settler treatment had a significant effect on secondary settlement, but only for *Perna* at Brenton-on-Sea. For *Mytilus*, only a significant site effect was found (Table 4.1d $F_{5, 60} = 42.72$, $p < 0.01$).

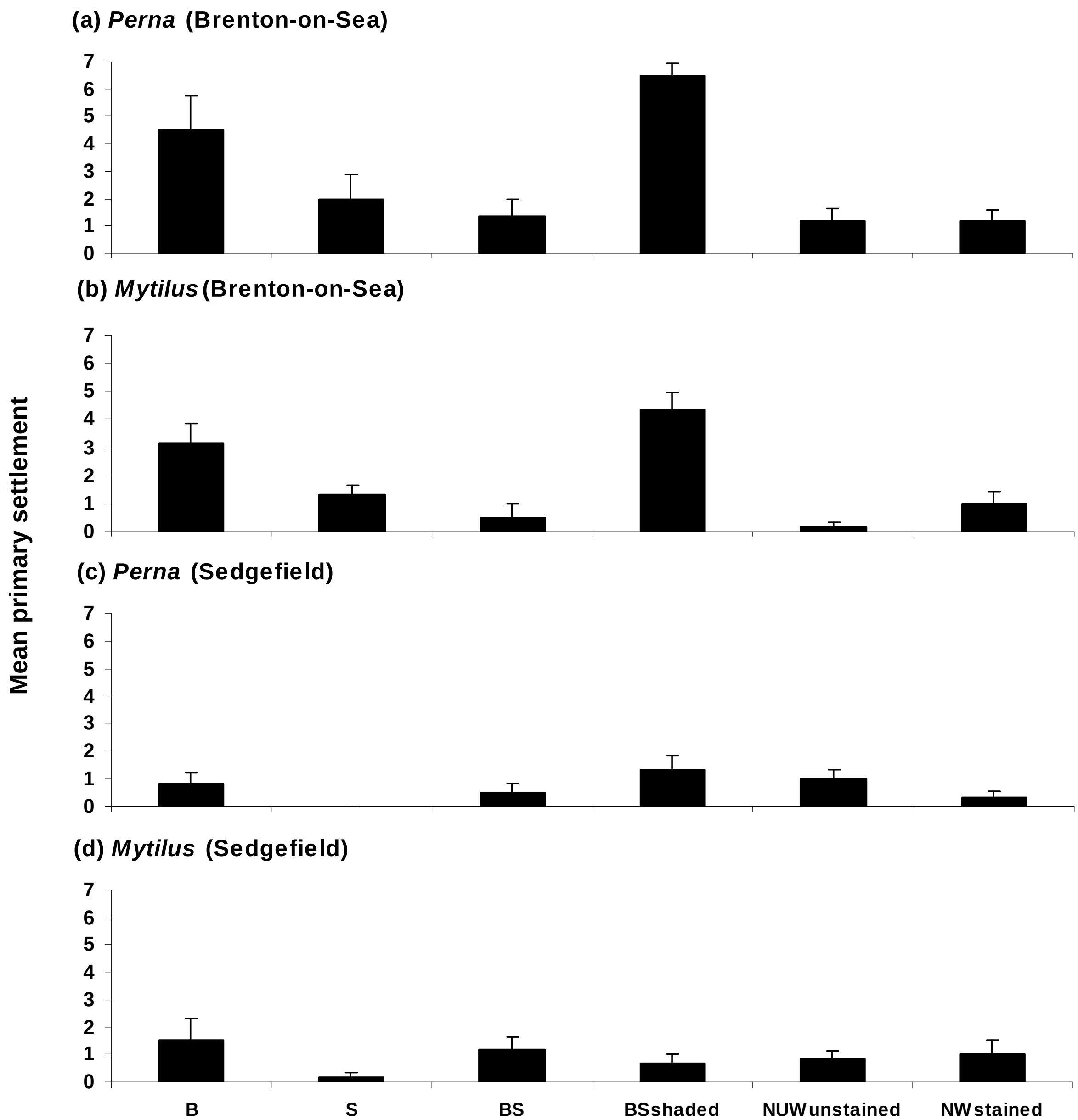

Figure 4.1 Mean primary settlement (+SE) on the 6 treatments over the experimental 24hr period at two sites. Panels (a) *Perna* and (b) *Mytilus* show settlement at the Brenton-on-Sea, while panels (c) and (d) show settlement of these species at Sedgefield. Treatments: *B* = Biofilm, *S* = Settler, *BS* = Biofilm-Settler, $NUW_{unstained}$ = New $\text{Unwashed}_{\text{unstained}}$; and Controls: BS_{shaded} = $\text{Biofilm-Settler}_{\text{shaded}}$ (shading control), $NW_{stained}$ = New $\text{Washed}_{\text{stained}}$ (staining control).

Table 4.1 Two-way ANOVA and Student Newman Keul's post-hoc test results for primary settlement of (a) *Perna* and (b) *Mytilus*. Panels (c) and (d) show the corresponding results for analyses of secondary settlement data.

(a) *Perna* (primary settlement)

Source	**df**	**MS**	**F**	**p**
Treatment	5	19.76	1.75	> 0.05
Site	1	80.22	7.11	< 0.05*
Treatment x Site	5	11.29	5.51	< 0.001***
Error	60	2.050		
SNK	BS_{shaded} > B > all other treatment site combinations			

(b) *Mytilus* (primary settlement)

Source	**df**	**MS**	**F**	**p**
Treatment	5	9.01	1.07	> 0.05
Site	1	13.35	1.59	> 0.05
Treatment x Site	5	8.41	5.93	< 0.001***
Error	60	1.42		
SNK	BS_{shaded} > B > all other treatment site combinations			

(c) *Perna* (secondary settlement)

Source	**df**	**MS**	**F**	**p**
Treatment	5	1647.81	12.25	< 0.0001****
Site	1	1503.35	11.18	< 0.01**
Treatment x Site	5	629.41	4.68	< 0.01**
Error	60	134.50		
SNK	BS > all other treatment site combinations			

(d) *Mytilus* (secondary settlement)

Source	**df**	**MS**	**F**	**P**
Treatment	5	7.01	0.88	> 0.05
Site	1	342.34	42.72	< 0.01**
Treatment x Site	5	8.01	1.37	> 0.05
	60	5.85		
SNK	Sedgefield > Brenton-on-Sea (site effect only)			

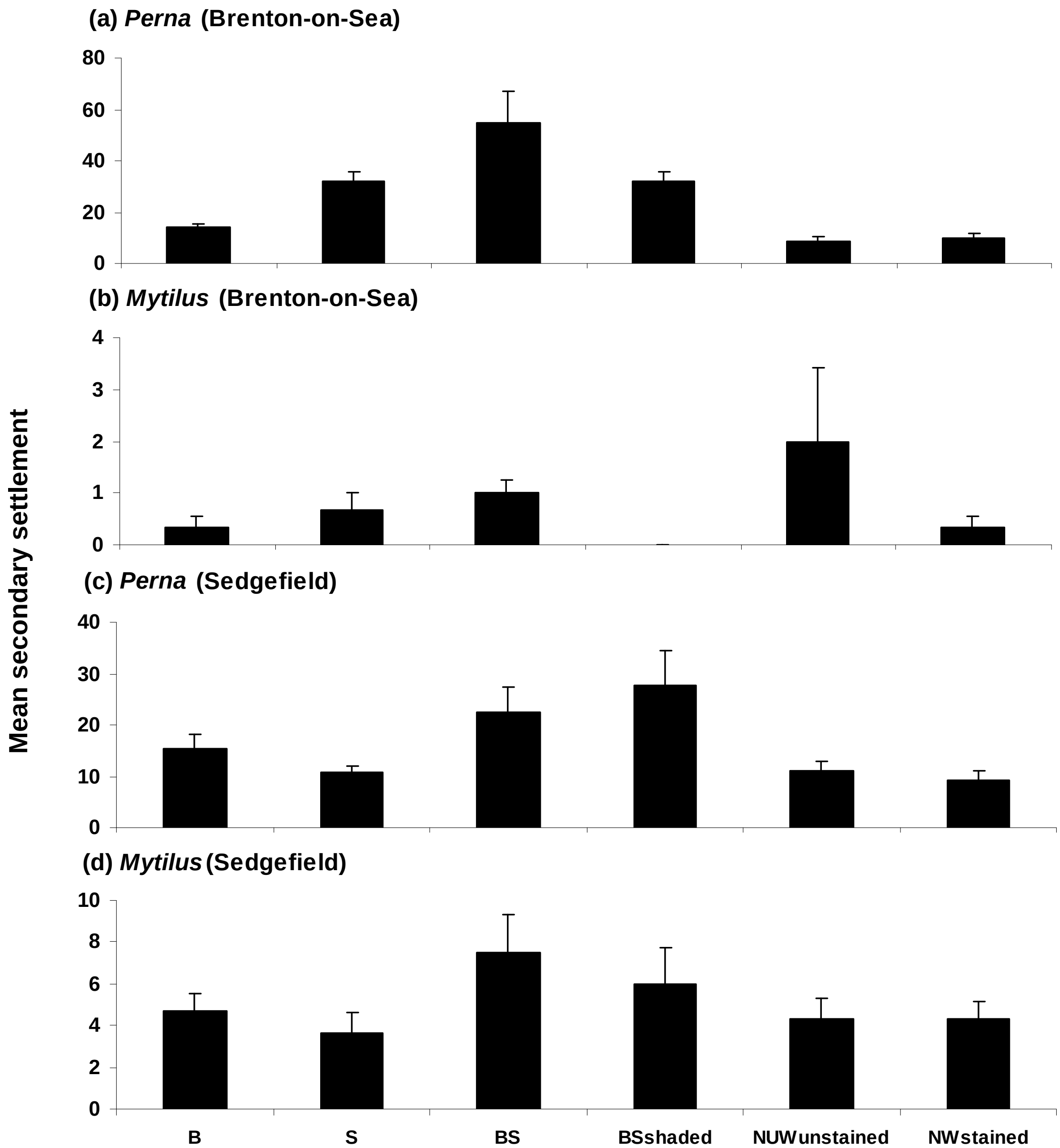

Figure 4.2 Mean secondary settlement (+SE) on 4 experimental and 2 control treatments, at two sites. Panels (a) *Perna* and (b) *Mytilus* show secondary settlement at the Brenton-on-Sea site, while panels (c) and (d) show settlement of these species at the Sedgefield site. Treatments: *B* = Biofilm, *S* = Settler, *BS* = Biofilm-Settler, $NUW_{unstained}$ = New Unwashed$_{\mathrm{unstained}}$; and Controls: BS_{shaded} = Biofilm-Settler$_{\mathrm{shaded}}$ (shading control), $NW_{stained}$ = New Washed$_{\mathrm{stained}}$ (staining control). Note: y-axis scales not equal.

4.3.4 Discredited shading control

In terms of primary settlement, the BS_{shaded} treatment had significantly more settlers than any other treatment in all cases except for *Mytilus* at Sedgefield. The pattern was however less commonly seen in the secondary settlement data. If mean primary settlement of the BS_{shaded} treatment is compared to that of the *BS* treatment, an identical treatment apart from the half mesh covering, it can be seen that the shaded treatment accumulated well over double the number of settlers at both sites (Fig 4.1).

During the preparatory period the presence of mesh discs on the BS_{shaded} treatment could have had two effects: 1) shading and 2) netting. Since larvae, including *M. edulis* pediveligers, may respond photonegatively to light intensity (Bayne 1964b) both the shading and netting effects may potentially have increased settlement of conspecifics over the preparatory period. Given that no significant difference in chl-a was found among shaded, bagged and unshaded treatments however, it is unlikely that light intensity was significantly altered by the mesh discs. Rather, a strong 'netting effect' is plausible since the collectors were able to orientate themselves slightly with water movement creating a mesh 'net', resulting in abnormal accumulations of conspecific settlers, sediment and organic detritus. Although the mesh discs were not present during the 24hr experiment itself, these abnormal accumulations, particularly of conspecifics, seem to have had strong effects on subsequent settlement. Due to the uncertainty of these effects the BS_{shaded} treatment is excluded from discussion and interpretation of settlement results.

4.3.5 Summary: Primary and secondary settlement

In summary, if the discredited BS_{shaded} treatment is removed, primary settlement was always greatest on the Biofilm treatment, with the exception of *Perna* at Sedgefield, where settlement was low and the $NUW_{unstained}$ treatment inexplicably received the most primary settlement. Although the trend of high settlement on the Biofilm treatment was common to both sites, the effect was only statistically significant for Brenton-on-Sea. Using a similar exclusion (of the BS_{shaded} treatment) for secondary settler data, secondary settlers attached in greatest numbers to the Biofilm-Settler at both sites (with the exception of *Mytilus* at Brenton-on-Sea). At Brenton-on-Sea the numbers of *Mytilus* secondary settlers were generally low and the $NUW_{unstained}$ treatment received the highest settlement. The general pattern of maximum secondary settlement on the *BS* treatment was common to both sites, but was statistically significant only at Brenton-on-Sea for *Perna*.

4.3.6 Correction factors

Finally, correction factors were calculated using the site for which significant treatment effects were found - Brenton-on-Sea. As Table 4.2 shows, mean primary settlement of *Perna* increased 3.8 fold from 1.17 on clean collectors to 4.5 on Biofilm treatment collectors, an increase of 284 %. A larger change was seen in mean secondary settlement which increased 6.6 fold from 8.3 on the clean collectors to 55 on Biofilm-Settler treatment collectors, an increase of 560 % (Table 4.2). For *Mytilus* a much larger increase in primary settlement was seen (Table 4.2, 18.6X, 1765%). With no significant treatment effects on secondary settlement for *Mytilus*, no correction factor was calculated.

Table 4.2 Mean settlement (over 24hr) on various treatment collectors at Brenton-on-Sea, including those with biofilm (*B*), conspecific settlers (*S*), both (*BS*, BS_{shaded}) or neither ($NUW_{unstained}$, $NW_{stained}$). Multipliers reflect the number of times greater mean settlement was on the relevant (* = significant) treatment than on clean collectors ($NUW_{unstained}$). The increase in settlement is also represented as a percentage in the final row.

Treatment	***Perna* primary**	***Mytilus* primary**	***Perna* secondary**	***Mytilus* secondary**
B	*4.5 ± 1.3	*3.17 ± 0.7	14.17 ± 1.2	0.33 ± 0.2
S	2 ± 0.9	1.33 ± 0.3	32.17 ± 3.8	0.67 ± 0.3
BS	1.3 ± 0.6	0.5 ± 0.5	*55 ± 12.0	1 ± 0.3
BS_{shaded}	6.5 ± 0.4	4.33 ± 0.6	32 ± 3.8	0 ± 0.0
$NUW_{unstained}$	1.17 ± 0.5	0.17 ± 0.2	8.33 ± 2.0	2 ± 1.4
$NW_{stained}$	1.17 ± 0.4	1 ± 0.4	9.83 ± 1.9	0.33 ± 0.2
Multiplier (*Treatment / $NUW_{unstained}$)	3.8 X	18.6 X	6.6 X	N/A
Percentage increase	284 %	1765%	560 %	

4.4 Discussion

This study has successfully tested, in isolation and in combination, the effects of biofilm and conspecific settler presence on mussel settlement. The problem of possible contamination of natural experimental substrata (such as algae) by biofilm, as noted by several authors (Alfaro et al. 2006, Dobretsov & Wahl 2008), was circumvented in this study by the seeding of clean substrata with mussel settlers. The positive (attractant) effects of biofilm and conspecific settlers on settlement were clearly demonstrated by the significant interaction of treatment and site. According to the original hypothesis, both primary and secondary settlement would be increased by biofilm and conspecific presence, both in isolation and combination. However, the results were not so straightforward. At Brenton-on-Sea, primary settlement of *Perna* and *Mytilus* was significantly greater only on the Biofilm treatment (Table 4.1a and c), while secondary settlement was significantly greater only on the treatment combining biofilm and conspecific settlers (*BS*), and then only for *Perna* (Table 4.2a and c). The low secondary settlement of *Mytilus* at this site may have reduced the ability to detect a treatment effect.

In addition to the lack of any treatment effects at Sedgefield, the pattern of primary settlement across treatments did not match precisely with that at Brenton-on-Sea. Some similarities did exist however; most importantly, the finding of maximum primary settlement of *Mytilus* on the Biofilm treatment collectors agreed well with the results of the Brenton-on-Sea experiment. Again, the low levels of settlement made decisive interpretation difficult.

The pattern of secondary settlement at Sedgefield followed that at Brenton-on-Sea more closely, with the Biofilm-Settler treatment receiving the greatest settlement of both species (after removal of the BS_{shaded} treatment). The similarities in secondary settlement between sites end, however, with the Biofilm treatment at Sedgefield having greater settlement than the Settler treatment in each species.

The most striking result, based on the statistical evidence of the interaction of a treatment effect at Brenton-on-Sea and numerical corroboration of this key pattern at Sedgefield, is therefore the distinctly different behaviours and responses to cues of primary and secondary settlers. In essence, it seems that primary settlers settled in greater numbers on collectors bearing biofilm (BS_{shaded} excluded here – see explanation in section 4.3.4) but not on those with an initial settler presence, even if these bore biofilm (i.e. treatment *BS*). This possibly suggests an avoidance of conspecifics by primary settlers. The fact that the Settler treatment at Sedgefield received the lowest number of primary settlers for both species supports this idea.

In contrast to this, secondary settlement (of *Perna*) was greatest on those treatments with a settler presence, namely the Biofilm-Settler combination treatment (*BS*). At Brenton-on-Sea, the seeded treatment (*S*) also received high numbers of secondary *Perna* settlers, but this pattern was not seen at Sedgefield for either species. Thus, it seems that secondary settlers were attracted to conspecific settlers, but most acutely in combination with biofilm.

Repetition of the experiment at two different sites demonstrated that the effects of biofilm and conspecifics are not always significant. It is likely however, that the low levels of settlement at Sedgefield meant that any treatment effects were not detectable. Although some evidence suggests that responses to cues are seasonal (de Vooys 2003), this is a study of boreal species which generally demonstrate strong seasonality in many aspects including settlement (Petraitis 1991, Cácerez-Martínez et al. 1993). In the southern hemisphere, and for the current study species, seasonality of reproduction and settlement is often less pronounced (Lasiak & Barnard 1995, McQuaid & Lawrie 2005). Therefore, no temporal effect was considered in the present study. Boreal studies also show that the abundance of epilithic microbiota can be seasonal (Hill & Hawkins 1991), but in the present study this is an unlikely explanation for differences in results between sites as both sites were examined in the same season.

The increase of settlement in response to biofilm and conspecifics relative to clean substrata compares remarkably well with the results of other works. Satuito and others (1997) showed 70% of *Mytilus galloprovincialis* pediveligers settled on biofilmed glass slides, but none settled on clean slides. Likewise, a significant proportion of *Mytilus edulis* pediveligers (50%) were shown to move toward epiphytic biofilm scraped from the alga *Cladophora rupestris* (Dobretsov 1999), not only indicating an attraction to biofilm, but also that the cue was waterbourne. Interestingly, Wainman and colleagues (1996) found significant attraction of *Dreissena polymmorpha* settlers (smaller than 390μm) to both biofilm and adult conspecifics. Although quoting a reduction in settlement of 10-20 % on treatments without biofilm (Wainman et al. 1996), re-working their calculation (using the same method used in Table 4.2) to produce correction factors comparable to the results of the present study, indicates a 3 fold increase from bare to biofilmed substrata, and a 5.2 fold increase from bare to biofilmed-conspecific substrata . These data agree well with the present findings (3.8 fold for *Perna* on Biofilm and 6.6 fold on Biofilm-Settler treatments).

Comparable support for conspecific attraction in marine mussels also exists, with Dobretsov and Wahl (2001) showing a 2 fold increase in settlement of *M. edulis* on artificial substrate placed in close proximity to adult beds, relative to controls. As with biofilm, detection of waterborne conspecific cues by *M. edulis*, resulting in a significant increase in movement towards the source, has been shown (de Vooys 2003). The study of Porri and colleagues (2007) is noteworthy as it investigated the attraction of *P. perna* and *M. galloprovincialis* settlers (< 3mm in size) to artificial clumps of adult mussels. The clumps were placed within natural mussel beds of each species and were either monospecific or mixed. No attraction of *Mytilus* or *Perna* to adult conspecifics was found relative to the surrounding natural bed; instead tidal height was found to be the most influential determinant of settlement (Porri et al. 2007). This study therefore required greater species specificity of selection than the present study, and did not compare selection of conspecifics relative to bare (clean) substrata. A further difference between the present study and that of Porri and co-workers (2007) is that the latter examined settler response to *adult* conspecifics rather than to conspecific settlers. The results of Porri and co-workers (2007) do not therefore contradict those of the present study, which examined conspecificity in a slightly broader manner (conspecific settlers in the present study were settlers of either species). Moreover, the present study made direct comparisons between treated and bare collectors, rather than to natural mussel beds. This may have allowed improved isolation of treatment effects.

The study of Hidu (1969), which found that the presence of 24hr-old oyster spat (*Crassostrea virginica*) significantly increased subsequent settlement, highlights the occurrence of juvenile (in this case, larval-settler) interactions. In contrast to this finding, Jeffery (2002) working with barnacles, showed that the presence of settlers and recruits did not increase subsequent settlement.

In many studies examining settlement cues, larval or settler age has not always been recognised as a critical factor. All too often, broad size-classes have been used, allowing for little or no ecologically relevant distinction between behaviours of early and late settlers (e.g. Davis & Moreno 1995, Kobak 2000). However, work by Marsden (1991) and by Satuito et al (1997) amongst others, provide some corroboration of the age-dependent responses found in the present study. Satuito and co-workers (1997) found that barnacle cyprids settle more readily with age, and suggested that larvae may require an initial period in which to acquire competence and respond to settlement cues. A contributory factor to this age-dependence would also likely be the increasing need of lecitotrophic cyprids to settle and begin feeding. Marsden (1991) however, working on a serpulid polychaete (*Spirobranchus polycerus*), found a very specific and far narrower age-related 'window' for response to conspecific cues. This consisted of attraction of 4-8 day old trocophores to larvae of the same age, but no similar response in early (2-3d), or late (9-10d) larvae. It must be noted that the validity of the 9-10d results were interpreted cautiously due to low numbers. The strongly age-dependent switching seen in the present study (primary settlers selecting biofilmed collectors; secondary settlers seeking the additional presence of other settlers), may possibly be explained in evolutionary terms by the need for very small primary settlers to avoid larviphagy (Porri et al. 2008) by adults. With size-refuge (from larviphagy) reached, conspecific attraction should no longer be selected against in mussels larger than primary settlers, explaining the well documented gregarious and clumping behaviours of larger mussels.

Ultimately, it seems that chemical signals on artificial substrates as small as the 10cm diameter plastic collectors used in this study, can significantly alter both primary and secondary mussel settlement patterns on them. It is not possible to say whether these cues were waterborne or if contact was necessary, but it is remarkable that such signals were detected against the background 'noise' of the surrounding mussel bed, and in the turbulent, highly diffuse field conditions. It seems likely that this substrate selection occurred actively through detailed discrimination at the attachment site scale, as suggested by Harvey and colleagues (1995b). Although haphazard settlement can occur through passive deposition, specific active selection can come about at localised scales through ‘ping-pong’ bouncing and drifting (André et al. 1993) and through crawling behaviour (Cáceres-Martínez et al. 1994).

Apart from adding to our understanding of mussel settlement behaviour, this study has important implications for the use of experimental and artificial settlement substrata. Biofilms develop rapidly, and have been shown to provide detectable cues within 3 days (Pearce & Scheibling 1991). Settler presence can be just as immediate and, depending on spatio-temporal supply of larvae, can have a significant influence on settlement within 5 days, as shown here. Although based on only one site, the multipliers calculated in the present study (Table 4.2) could be used as a ‘correction factor’ in subsequent work where the control of biofilm development and settler influence is not possible. This will be examined in the next chapter.

CHAPTER 5

POST-SETTLEMENT MORTALITY

5.1 Introduction

The potential for high mortality during early post-settlement life has long been suggested (Thorson 1966, Seed 1969), observed (Connell 1961) and amply demonstrated (see Gosselin & Qian 1997, Hunt & Scheibling 1997 for review). Citing work on various marine invertebrates, Gosselin and Qian's (1997) review describes early juveniles as "ecologically distinct" from other life stages. A large part of this distinction stems from increased vulnerability of early juveniles to negative environmental and biological factors. In the majority of studies this vulnerability results in more than 90% mortality (Gosselin & Qian 1997), identifying this period as especially critical in the life history progression of intertidal organisms. Studies have shown variable, but significant post-settlement mortality for numerous marine taxa: reef fish (Searcy & Sponaugle 2001, Doherty et al. 2004), mobile invertebrates such as crabs, abalone and other gastropod species (Ray & Stoner 1995, Moksnes et al. 1998, Naylor & McShane 2001) and a variety of sessile invertebrates including barnacles, a serpulid polychaete, an oyster and several ascidians and bryozoans (Hurlbut 1991, Gosselin & Qian 1996, Marshall & Keough 2003a).

While it is established that post-settlement mortality usually claims a large proportion of settlers, effort has been put to determining the ecological importance of post-settlement mortality in setting adult distributions, relative to that of larval supply and settlement. This is a critical issue since, in cases where post-settlement mortality de-couples recruitment from settlement, adult population dynamics may be regulated by this early mortality rather than supply-side factors or settlement (Hunt & Scheibling 1997).

Examinations of barnacles (Wethey 1985, Delany et al. 2003) and the mussel *Mytilus galloprovincialis* (Peteiro et al. 2007) showed early mortality to be a more important determinant of distribution than larval supply, while the opposite was true of a third barnacle species (Jeffery

2003). In the latter study, the adult distribution of *Chamaesipho tasmanica* was found to follow closely that of juveniles, despite heavy post-settlement losses (generally ≥ 50%), demonstrating the variable importance of early mortality. In broad terms, Hunt and Scheibling (1997) showed that, in the majority of studies on sessile or sedentary species, a positive relationship between numbers of recruits and settlers precludes a de-coupling effect of post-settlement mortality on this relationship. This situation seems to hold for the mussel species examined in the present study, as the strong correlations between settlement and recruitment in the previous chapter demonstrate.

Regardless of its changeable importance however, post-settlement mortality must be considered a dependent part of the *whole* life history progression. By necessity, many studies have examined a single life stage independently of the preceding or subsequent stages (Goater 1994). Such divisions between larval life, settlement, post-settlement mortality, and recruitment are not entirely valid as these 'stages' are not independent of one another (Phillips 2002, Gimenez 2004). An example of the general logic of this idea is seen in the fact that any extension of larval duration, due to exogenous or endogenous influences on growth rate, can affect not only survival to settlement, but subsequent post-settlement survival as well (Widdows 1991).

Most directly, the pre- and post-settlement stages are linked by density-mediated effects. These are a product of supply-side factors, and go on to affect density-dependent post-settlement processes (see for review Gimenez 2004). In addition, the ubiquitous presence of trait-mediated effects – physiological, developmental or phenotypic traits established during larval life that affect growth and survival in later stages, particularly during early post-settlement life - provide a similar but indirect link between pre- and post-settlement stages (Phillips 2002, Gimenez 2004, Phillips 2004, Marshall & Keough 2006, Meekan et al. 2006). Similarly, genotype-specific (endogenous) responses to environmental conditions have been found to cause differences in larval, juvenile and adult growth and survival, affecting individual performance in more than one life stage (Pedersen et al. 2000, Shields et al. 2008). Thus, to explain fully patterns of settlement, recruitment and adult abundance, and the relationships between these, knowledge of the post-settlement period in the study area is necessary if not critical.

Monitoring of early settlers must be frequent enough so as to allow separation of the initial settlement pattern from the mortality-altered post-settlement pattern (Hunt & Scheibling 1997). The requirement of high frequency sampling (Minchinton & Scheibling 1993), together with the small size of early settlers makes studies of mortality within the first 24 – 48hr exceedingly difficult (Hunt & Scheibling 1997). Much of our knowledge of post-settlement processes and their importance to benthic invertebrate populations comes from the study of barnacles (Foster 1971, Connell 1985, Wethey 1985, Jarrett 2000, Chan & Williams 2003). In fact, until recently, barnacles (Young 1991, Gosselin & Qian 1996) and ascidians (Davis 1987, Stoner 1990) were the only groups for which mortality within the first 2d of benthic life had been directly shown.

As is clear from the lack of studies on bivalves (and mussels in particular), establishing early mortality of mussels is especially difficult. This is due firstly to the microscopic size of mussel settlers and juveniles, and secondly to their relative mobility (crawling and drifting behaviour) in comparison to organisms such as barnacles. The latter makes distinguishing between real mortality and emigration-derived losses virtually impossible. Consequently, standard techniques of mapping or photographing experimental plates, such as are used for barnacles (Gosselin & Qian 1997), cannot be employed. Traditional cohort monitoring, or variants of the technique, have been used with some success, finding high rates of mussel mortality within various sampling intervals (Moreno 1995, Cole et al. 2000, McQuaid & Phillips 2007, Peteiro et al. 2007). Such studies however, produce integrated and rather general estimates of mortality between time 0 and time 1 – this period being weeks to months long.

Although previous methods of marking or tagging mussel settlers in the numbers necessary for meaningful experimentation have proved unsuccessful (Seed 1969), recent advances have made this method one of the most reliable. Working on *M. galloprovincialis*, Phillips (2002, 2004) successfully used fluorescent staining with calcein to study the effects of larval nutrition on post-settlement performance in the field, finding mortality after the first 2 weeks of benthic life to range from 70 – 97%. Other methods include that used by Shields et al. (2008), who successfully obtained estimates of monthly juvenile mussel mortality (75 – 100%), but these only explored certain sources of mortality as caged plots were used. Most notably, Bownes (2005) used a new method of sequential deployment of paired settler collectors to estimate juvenile mussel mortality over 6d. In addition, the number of dead mussels (empty shells attached to collectors) in each size class were used to give estimates of size-specific mortality. Losses from the primary ($\leq$ 400µm) settler class (ca. 40%) provided an estimate (albeit, an underestimate) of the earliest post-settlement mortality by virtue of the settlers maximum age - 48hr. To my knowledge this provides the first estimate of early (within 48hr) post-settlement mortality for mussels.

A great deal of work on a variety of marine organisms has shown early mortality to be influenced by several exogenous factors (for review see Hunt & Scheibling 1997). These include biological disturbance, physical (hydrodynamic) disturbance, physiological stress (e.g. food availability), predation and competition. The influence of these factors is not limited to direct effects on early settlers, as most factors begin their effect on larval growth and condition. Many of these factors have been specifically identified as influencing early mussel mortality. For example, tidal height, which relates to desiccation and emersion stress, affects juvenile survival of the green mussel *Mytilus viridis* (Tan 1975); similar physiological stress effects in Mytilid species have been shown by Iwasaki (1995). Larval food availability affects growth, condition and hence post-larval survival of *M. galloprovincialis* (Phillips 2002, 2004). Also, the effect of substratum type in relation to predation on *Choromytilus chorus*, is aptly illustrated by Moreno (1995). Of obvious relevance to the topic of topography-mediated effects, is wave exposure. In this respect, no studies have examined early mussel mortality, but a wave exposure effect has recently been implicated in adult mussel mortality (McQuaid & Lindsay 2000, Nicastro et al. 2008a). However, some evidence of such an effect on juvenile mortality comes from work on abalone (Naylor & McShane 2001). Many of these factors, especially wave exposure, are likely to differ between bay and open coast habitats, and thus are likely to affect post-settlement mortality accordingly.

This study therefore revolves around 3 points. 1) Very little detail is known about early mussel mortality; 2) The physical differences between bay and open coast habitats may well induce different post-settlement mortality regimes, knowledge of which would be pertinent to explaining distributions of recruits and possibly adults too, and 3) Despite the significant correlations between settlement and recruitment during the summer months (chapter 3), which suggest little ecological effect of post-settlement mortality in the study area, an understanding of early mortality is needed to disentangle topographically-related settlement patterns from any topographically-related post-settlement mortality patterns. To address these points, an adapted version of Bownes's (2005) technique is used to investigate post-settlement mortality across multiple bays and open coast sites. Although a more direct route, the method of Phillips (2002) was not used here because staining and out-planting of settlers over such a large spatial scale is impractical.

Three corresponding hypotheses are put forward. 1) Post-settlement mortality of the study species will be substantial (ca > 50% on average). 2) Mortality will be greater on the open coast than in bays. 3) In light of hypothesis 2, mortality patterns will reinforce topographically-related settlement patterns, maintaining these in recruit distribution and abundance.

5.2 Methods and materials

5.2.1 Experimental setup

Making use of the same plastic pot-scourer settler collectors as in preceding chapters, post-settlement mortality was estimated by adapting a technique developed by Bownes (2005). The method uses replicate pairs of collectors; one of each pair is removed and replaced every 24hr, while the other remains on the shore for the full duration of the experiment (in this case 7 days). In this way, the number of settlers on each of the 7 "daily" collectors can be summed to produce a "mortality-free" estimate of cumulative daily settlement. The number of settlers on the corresponding single "weekly" collector from each replicate gives an estimate of 7-day settlement that is inclusive of mortality. Mortality is then estimated by subtracting the mortality-inclusive total "weekly" settlement from the mortality-free cumulative "daily" settlement. The method is therefore fundamentally dependent on the idea that mortality on daily collectors within each 24 hour period is negligible or very low. Paradoxically, Bownes (2005) showed mortality of primary mussel settlers to be as much as 40%, indicating a substantial loss of 1-2d old settlers. As much as a 30% loss within the first 24hr of settlement is however verified by several works on barnacles and ascidians (see Gosselin & Qian 1997 for review), making the assumption of negligible 24hr mortality unlikely. Nevertheless, the relatively instantaneous measure of daily settlement is compared with the integrated measure of weekly settlement. In both cases, some immediate mortality of new settlers will occur each day. A usable mortality rate can be established due to the continued mortality of settlers in the weekly collectors relative to the daily collectors.

In order to test for a topographic effect on post-settlement mortality, a subset of 16 (8 bay, 8 open coast) of the original 22 sites surveyed in chapter 2 was used. At each site a total of 10 galvanised eye-bolts were screwed into low shore rocks within mussel beds. Two collectors were cable-tied onto each eye-bolt, giving one "daily" and one "weekly" collector. Eye-bolts were spaced at least 50cm apart and positioned roughly in a row running parallel to oncoming waves. This setup allowed easy deployment and retrieval of collectors in a consistent order, thereby making certain that sequential daily collectors came from the same position on the shore, within a given sampling week. This was very important since a set of daily collectors needed to correspond with each other as well as the weekly collector at a particular position on the shore.

To deal with the considerable distance over which sites were distributed (500km), the coast was subdivided into 3 sections. The most easterly of these sections included 7 sites, the middle 4, and the westerly 5. Each section was sampled over a week, collecting and replacing the daily collectors every morning during low tide. Sampling of the first section began on 18 January 2007, while sections 2 and 3 were sampled on the two subsequent tides (starting 31 January and 15 February respectively). This procedure was repeated directly after the completion of this first 3 section "cycle", starting with section 1 on 1 March and sampling sections 2 and 3, starting on 15 March and 1 April respectively. This produced two sampling cycles of 3 sections each: cycle 1 and 2. Collectors were stored in jars of 70% ethanol immediately after collection.

5.2.2 Laboratory procedures and data handling

Three replicate sets, each comprising 7 daily and 1 weekly collector, were processed per site in each section. Since collectors had been stored immediately in ethanol, settlers were found to be firmly attached and difficult to rinse out. Thus, collectors were soaked for 3 minutes in a weak solution of sodium hypochlorite to dissolve byssal threads (Davies 1974, Connolly et al. 2001). All mussel settlers were removed from the collectors and *Mytilus* and *Perna* individuals were identified and counted into 4 size classes: the primary settler class included all settlers smaller than 360µm while the largest, class C, covered all secondary settlers greater than 660µm. The two intervening size classes, 360 – 440µm (class A) and 440 – 660µm (class B), were based on potential weekly growth from an initial settlement size of 260µm, and were calculated using slow (28.6µm) and fast (32.5µm) growth rates respectively, as estimated for the study species by Bownes (2005).

5.2.3 Calculation of mortality

There are two differences between Bownes's (2005) calculation of post-settlement mortality and its adaptation in the present study. (1) In Bownes (2005), post-settlement mortality included that of recently settled individuals and larger secondary settlers (recruits). No separation of these sizes was made (apart from a calculation based on the number of empty shells in collectors). Mortality was thus calculated by subtracting the total number of live recruits in the weekly collectors at the end of the sample period from the cumulative daily settlement that occurred during that time. Mortality was then expressed as a percentage of the cumulative daily settlement. (2) The premise behind Bownes's (2005) calculation was therefore that there was no inherent difference between attraction of settlers to the "clean" daily collectors and the established weekly collectors. In reality, weekly collectors would have rapidly developed bacterial communities and biofilms, probably within the first 24hr of being deployed (Zobell & Allen 1935). In addition, weekly collectors would have had an accumulating presence of settlers. In Chapter 4 I demonstrated significant attractant effects of biofilm and conspecific settlers (developed over 5 days) on subsequent 24hr primary and secondary settlement on collectors.

In the present study, two calculations are used. One estimates post-settlement mortality of primary settlers (Eq. 1.3), while the other does not take size of settlers into account and like Bownes's (2005) calculation, gives an inclusive estimate of "total" post-settlement mortality (Eq. 2.3). Both equations introduce a correction factor, as described in Chapter 4, to adjust for the difference in "attractiveness" between daily and weekly collectors. Although the correction factor was calculated for only one species at one site, its application was deemed more important than possible variability associated with site or species. Application of the correction factor was necessary and results should be interpreted accordingly. In each case, the correction was applied only to daily collectors from day 2 onwards, allowing 24hr for the establishment of biofilms and arrival of conspecifics on the weekly collectors. Thus, the corrected cumulative primary settlement (D_{psT}) on daily collectors was calculated as follows:

$$D_{psT} = D_{1ps} + \sum D_{2\text{-}7ps} C_1 \qquad 1.1$$

Here, D_{1ps} is the primary settlement (ps) on the day 1 daily collector, and $\sum D_{2\text{-}7ps}$ is the sum of primary settlers from days 2-7. This sum is multiplied by the primary settler correction factor C_1 = 3.8 (see results section, Table 4.3, Chapter 4). The number of primary settlers arriving on weekly collectors early in the sampling period, and thus growing out of the primary settler class by the end of the week, was estimated and included in the calculation of total weekly primary settlement (W_{psT}) using the following equation:

$$W_{psT} = W_{ps} + (W_{sA} - \sum D_{1\text{-}7sA}) \qquad 1.2$$

Here W_{ps} is the number of primary settlers on the weekly collector; the term W_{sA} comprises those settlers of size class A on the weekly collector (this size class includes the maximum size to which a primary settler of size 260μm could have grown in a week based on Bownes's (2005) slow growth rate); and $\sum D_{1\text{-}7sA}$ is the sum of size class A settlers on the daily collectors over the week. The term in parentheses therefore estimates the number of primary settlers that had arrived on a weekly collector but grew out of the primary size class into class A during the sampling week. This is explained by the fact that weekly settlers of size A (W_{sA}) could have arrived either by growing to this size during the sampling period, or by immigrating to the weekly collector at this size (W_{sA}). Since there is no statistical evidence (see, results Chapter 4) of a difference in attraction of individuals of this size class (A) to daily versus weekly collectors, their rate of immigration is assumed to be equal on daily and weekly collectors. The subtraction is based on this assumption, together with the fact that settlers of size class A on daily collectors had to be immigrants, as daily collectors were only deployed for 24hr. Thus, equation 1.2 is the number of primary settlers on a weekly collector plus those primary settlers that had grown out of the primary settler class during the course of the week. It therefore provides an estimate of total primary settlement on a weekly collector, over the week-long sampling period. Putting equations 1.1 and 1.2 together, primary post-settlement mortality ($M_{primary}$) was estimated as follows:

$$M_{primary} \quad = \quad \frac{D_{psT} - W_{psT}}{D_{psT}} \quad X \quad 100 \qquad 1.3$$

The calculation of primary mortality as described by equations 1.1 – 1.3 has several difficulties and comes with 2 assumptions:

(1) In theory the calculation relies on the assumption that there is negligible mortality on daily collectors, within each 24hr deployment time, relative to the corresponding weekly collector. In reality, this assumption takes the form of an equivalent baseline mortality occurring on daily and weekly collectors, thus making daily mortality "negligible". Significant mortality (over and above this baseline) on daily collectors would mean an underestimate of mortality.

(2) The individuals of size class A on the weekly collector (W_{sA}, eqn 1.2) have in reality been exposed to mortality. Since there is no way of accounting for this mortality, the equation is forced to assume that mortality of this very narrow class is negligible. In reality, when

mortality in this class is moderate (i.e. W_{sA} is low but not lower than $\sum D_{1\text{-}7sA}$), primary mortality will be overestimated. Due to the setup of eqn 1.3, when W_{sA} is lower than $\sum D_{1\text{-}7sA}$ due to high mortality within class A, primary mortality may also be overestimated.

(3) Since it is impossible to distinguish settlers that migrate from a collector from those that actually die, it must be assumed that rates of immigration and emigration of settlers to and from collectors are similar if not equal and therefore balance each other. Based on this assumption, calculated mortality rates describe only those settlers that die.

Total post-settlement mortality (M_{total}) was calculated by subtracting the total number of settlers of all 4 size classes on the weekly collector (W_{TS}) from the total cumulative number of settlers (of all sizes) on the 7 daily collectors (D_{TS}). The correction factor (C_1) was again applied to the daily primary settlers, and a second correction factor ($C_2 = 6.6$) was introduced to correct the largest daily secondary settler class (class C) as was shown to be necessary in chapter 4. Thus, M_{total} was calculated using the corrected daily total settlement:

$$D_{TS} = (D_{1ps} + \sum D_{2\text{-}7ps} C_1) + \sum D_{1\text{-}7sA} + \sum D_{1\text{-}7sB} + (D_{1sC} + \sum D_{1\text{-}7sB} C_2) \qquad 2.1$$

And the weekly total settlement:

$$W_{TS} = W_{ps} + W_{sA} + W_{sB} + W_{sC} \qquad 2.2$$

To produce a percentage as follows:

$$M_{Total} = \frac{D_{TS} - W_{TS}}{D_{TS}} \times 100 \qquad 2.3$$

The terms for equation 2.1 – 2.3 are the same as in equations 1.1 – 1.3, with the additions of $\sum D_{1\text{-}7sB}$ = the cumulative sum of settlers of size class B (weekly growth based on Bownes's (2005) fast growth rate) on daily collectors 1 to 7; D_{1sC} = the number of settlers of size class C on daily collector 1; and finally W_{sA}, W_{sB} and W_{sC} are the total number of weekly settlers in size classes A, B and C respectively. Assumptions (1) and (3) above, also apply to the calculation of total post-settlement mortality

In each data-set (primary and total mortality), all mortality percentages falling outside the range 0 – 100% due to non-conformance with the equations' assumptions were discarded. In the case of primary post-settlement mortality, this approach drastically reduced the number of sites in each cycle: for *Perna* 6 usable sites remained in each cycle, while for *Mytilus* a total of 6 usable sites were obtained only by pooling cycles. For each species then, 3 bay sites were compared to 3 open coast sites. Since calculation of total post-settlement mortality inherently included those primary settlers that had grown and died, assumption 2 (above) was not necessary. Thus, far fewer sites had to be discarded, leaving a total of 10 usable sites per sampling cycle (5 bay vs. 5 open coast sites).

5.2.4 Statistical analysis

To examine the possibility of an effect of coastline topography on primary post-settlement mortality of *Perna*, a 2-way ANOVA compared 3 bay to 3 open coast sites across sampling cycles, examining the factors bay status (fixed, 2 levels) and sampling cycle (random, 2 levels). For *Mytilus* a 1-way ANOVA examined bay status in the pooled cycle data-set. With sufficient usable sites in each cycle, the two-way ANOVA (bay status – fixed, 2 levels; and sampling cycle – random, 2 levels) was undertaken on the total post-settlement mortality data-set for each species, comparing the 5 bay to the 5 open coast sites.

5.3 Results

5.3.1 Primary post-settlement mortality

No distinct topography-related pattern was discernable in the primary mortality data for either species (Fig 5.1 & 5.2). The overall mean mortality levels of *Perna* over sampling cycles 1 and 2 were remarkably similar, with respective percentages of 59% and 60%. Based on the pooled cycle data, primary *Mytilus* settlers suffered a similar level of mean mortality of 64%. In terms of mean primary mortality then, *Mytilus* suffered between 4 – 5% greater loss than *Perna*.

Looking at individual sites, the lowest mortality for *Perna* was 28% (OWD, cycle 2, Fig 5.1), while the greatest mortality was 92% (ISR, cycle 2, Fig 5.1). The maximum primary mortality suffered by *Mytilus* was 87%. Unlike *Perna*, this occurred at an open coast site (OKB, Fig 5.2), while the minimum mortality for this species was 43%, and was recorded at the bay site (INP, Fig 5.2).

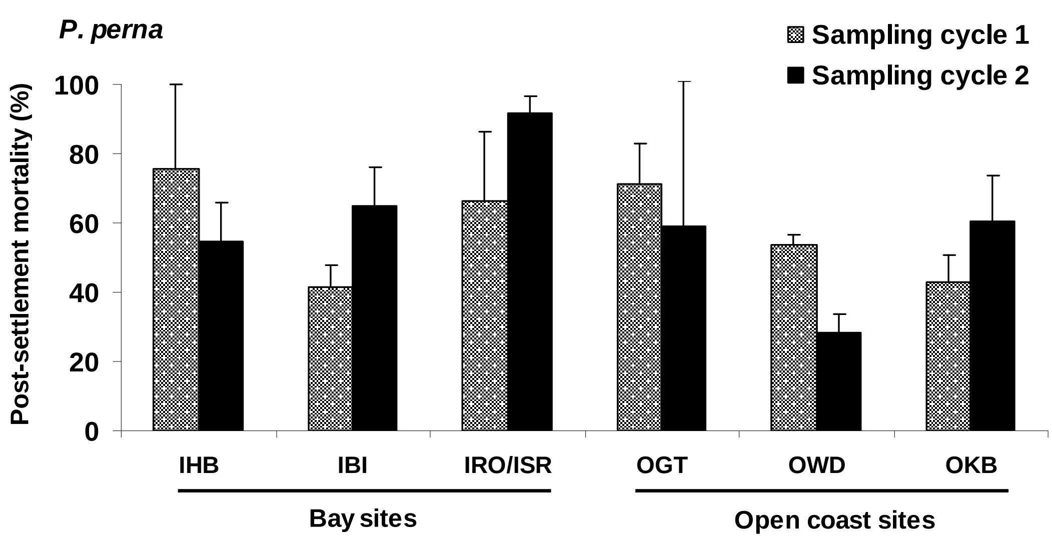

Figure 5.1 Mean primary 7d post-settlement mortality (+SE) of *Perna perna* at bay and open coast sites over two summer sampling periods. Sites arranged west-east within each habitat type.

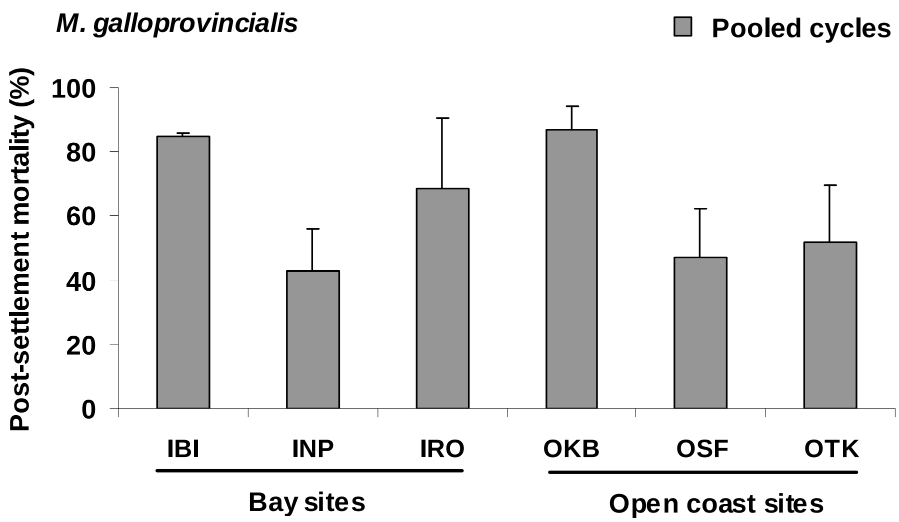

Figure 5.2 Mean primary 7d post-settlement mortality (+SE) of *Mytilus galloprovincialis* at bay and open coast sites. Sampling cycles are pooled. Sites arranged west-east within each habitat type.

The 2-way ANOVA on primary mortality data for *Perna* showed no significant interaction between bay status and sampling cycle, nor any individual effects of either factor (Table 5.1a $F_{1, 32} = 0.0495$, $p > 0.05$). Analogous results were produced by the 1-way ANOVA on mortality data (sampling cycles pooled) for *Mytilus*, showing that bay status did not have an effect on early post-settlement mortality (Table 5.1b $F_{1, 16} = 0.0194$, $p > 0.05$).

Table 5.1 Results of ANOVAs carried out on post-settlement mortality of primary settlers of (a) *Perna perna* and (b) *Mytilus galloprovincialis*. Analysis of *P. perna* data considered topographic and sampling time factors (bay status and cycle). For *M. galloprovincialis* data were pooled over sampling cycles and a 1-way ANOVA was performed, examining the bay status effect.

(a) Primary post-settlement mortality (*Perna*)

Source	**df**	**MS**	**F**	***p***
Bay status	1	0.24186	5.245	> 0.05
Cycle	1	0.00388	0.084	> 0.05
Bay status*Cycle	1	0.04612	0.0495	> 0.05
Error	32	0.09309		
SNK	No significant effects			

(b) Primary post-settlement mortality (*Mytilus*)

Source	**df**	**MS**	**F**	***p***
Bay status	1	0.00222	0.0194	> 0.05
Error	16	0.11439		

5.3.2 Total post-settlement mortality

The more inclusive estimates of total post-settlement mortality, which consider mortality of settlers of all sizes and ages, did not differ drastically from those of primary post-settlement mortality. No particular trend was observed with respect to bay status for either species, and overall mean mortality estimates were > 60% for both species. *Perna* was found to suffer a maximum post-settlement mortality of ca 81% during each sampling cycle. These maximum estimates, however, occurred at different sites; the maximum percentage for cycle 1 was recorded at an open coast site (OBS, Fig 5.3), while the maximum in cycle 2 was recorded at a bay site (ISR, Fig 5.3). The minimum post-settlement mortality for this species was 11%, and was recorded during cycle 1 at a bay site (INP, Fig 5.3). The lowest mortality seen in cycle 2 (49%) also occurred at a bay site (IDS, Fig 5.3). Overall mean estimates of total post-settlement mortality for this species were 61% (cycle 1) and 66% (cycle 2).

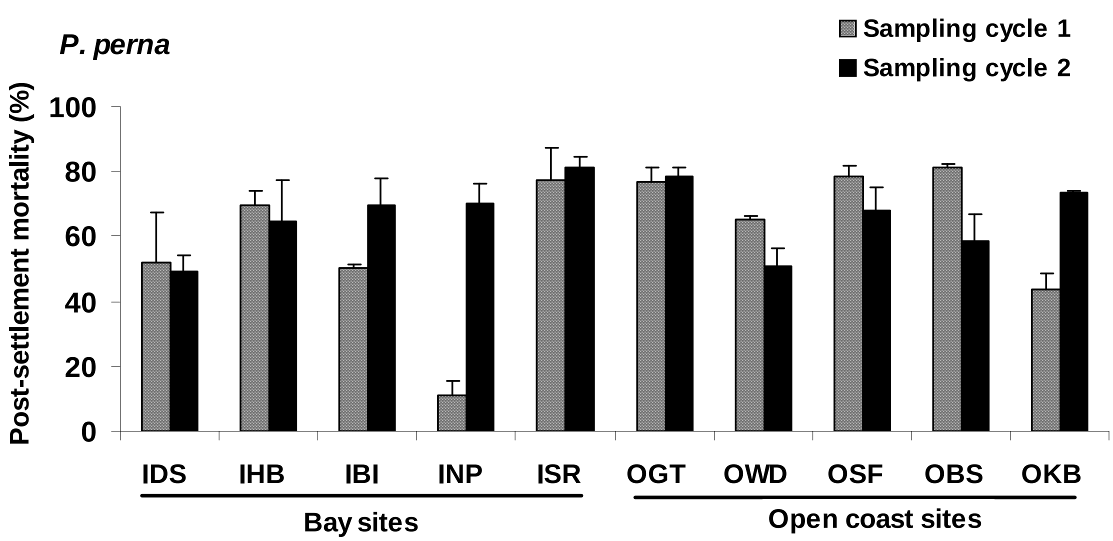

Figure 5.3 Mean total 7d post-settlement mortality (+SE) of *Perna perna* at bay and open coast sites. Grey dotted bars and solid black bars show sampling cycle 1 and 2 respectively. Sites arranged west-east within each habitat type.

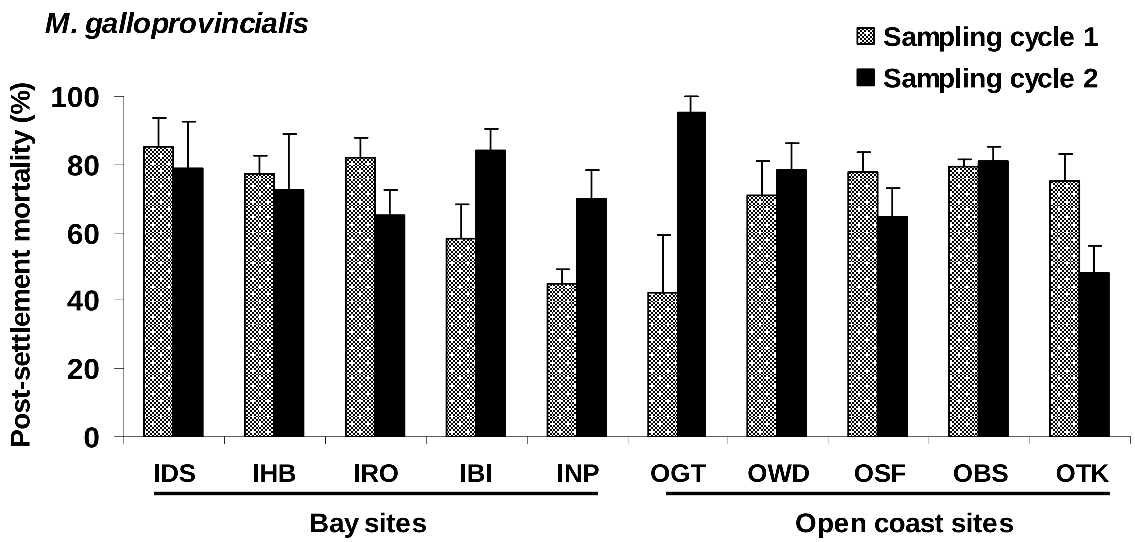

Figure 5.4 Mean total 7d post-settlement mortality (+SE) of *Mytilus galloprovincialis* at bay and open coast sites. Grey dotted bars and solid black bars show sampling cycle 1 and 2 respectively. Sites arranged west-east within each habitat type.

Mean total mortality of *Mytilus* was 8 – 9 % greater than that of *Perna*, with values of 69% (cycle 1) and 74% (cycle 2). The maximum estimates of total mortality for *Mytilus* were 85% for cycle 1 recorded at a bay site (IDS, Fig 5.4), and 95% for cycle 2, a value that came from an open coast site (OGT, Fig 5.4). The minimum percentages were observed at open coast sites in both cycles (Fig 5.4 cycle 1 = 42% at OGT; cycle 2 = 48% at OTK). Throughout the data there does not seem to be any pattern to the occurrence of minimum/maximum percentages at either bay or open coast sites. Moreover, there does not seem to be any discernable site-specific pattern, although inferences along these lines are limited by the loss and use of different sites between some cycles and certainly between species.

Statistical analyses (2-way ANOVA) of total post-settlement mortality data showed that no significant interactions between bay status and cycle existed for either species (Table 5.2a *Perna*: $F_{1, 56} = 3.73$, $p > 0.05$ & b) *Mytilus*: $F_{1, 56} = 0.0056$, $p > 0.05$). Furthermore, neither bay status nor sampling cycle had significant effects on post-settlement mortality of the study species (Table 5.2a & b). The lack of a topographic effect on post-settlement mortality is thus corroborated thorough the finding of similar patterns of primary and total post-settlement mortality in two species.

Table 5.2 Results of 2-way ANOVAs testing the effects of bay status and sampling time effects on total post-settlement mortality of (a) *Perna perna* and (b) *Mytilus galloprovincialis*.

(a) Total post-settlement mortality (*Perna*)

Source	df	MS	F	*p*
Bay status	1	0.11358	0.7083	> 0.05
Cycle	1	0.06353	0.3962	> 0.05
Bay status*Cycle	1	0.16035	3.7310	> 0.05
Error	56	0.04298		
SNK	No interaction			

(b) Total post-settlement mortality (*Mytilus*)

Source	df	MS	F	*p*
Bay status	1	0.00016	0.003	> 0.05
Cycle	1	0.06099	1.079	> 0.05
Bay status*Cycle	1	0.00557	0.099	> 0.05
Error	56	0.05653		
SNK	No interaction			

5.4 Discussion

Primarily, this study adds to the small number of works presenting estimates of early post-settlement mortality (within the first 2d of settlement) in marine invertebrates, obtained for barnacles (Young 1991, Gosselin & Qian 1996) and ascidians (Davis 1987, Stoner 1990). More specifically, results of the present work add to the even smaller number of studies providing estimates of early post-settlement mortality of bivalves, which includes the study of Roegner and Mann (1995) on the American oyster (*Crassostrea virginica*) and the work of Bownes (2005) on intertidal mussels. In agreement with previous studies (e.g. Gosselin & Qian 1997, Bownes 2005) and my first hypothesis, it is shown that mortality within the first 24hr of settlement is substantial, being greater than 50% in the present study.

Estimates of total mortality were similarly substantial (61 – 74%). These total mortality estimates vary in their agreement with other results obtained from studies using a similar sampling interval. For example, using a different technique, Phillips (2002, 2004) found mortality over 2 weeks to be between ca. 70 – 97% for *Mytilus galloprovincialis*. Bownes (2005) however, showed a far lower range of around 2 – 30% mortality over a 6d period, but with very high variability. This latter result is especially relevant to the present study as it describes mortality on the low shore, for the same species and from the same coast as the present work. It could be that these low percentages are a result of increased attraction to established weekly collectors, which was unaccounted for in Bownes's (2005) study. This increased attraction to weekly collectors relative to daily collectors would have the effect of decreasing the difference between the cumulative daily total settlement and total weekly settlement, thus decreasing estimates of mortality.

Contrary to the second hypothesis, no statistical evidence was found to suggest a topographic effect on post-settlement mortality. This was corroborated by the indiscriminate occurrence of maximum and minimum levels of mortality at both bay and open coast sites. By extension, wave exposure and possibly other physical factors that differ between these habitats did not have a strong effect on early mussel mortality. Consequently the third hypothesis, stating that early mortality patterns would reinforce the topography-related settlement/recruitment pattern, was not supported either.

In light of the study by Nicastro and co-workers (2008a), who showed a bay effect on adult mussel mortality, it seems that topographically driven effects, such as differential wave exposure, act directly on adult mortality, but, as seen in the present study, have little effect on post-settlement mortality. A possible explanation for the lack of a topographic effect on post-settlement mortality could be that the minimum 'fatal' level of wave exposure for settlers lies below the level of wave action commonly occurring in bays on the study coast. In other words, the range of wave exposure between bays and the open coast may not have been sufficient to capture differences in post-settlement mortality as settlers would have been equally disturbed by wave action in both habitats.

Genotype- and environment-dependent selection and mortality have been demonstrated (e.g. Gardner & Skibinski 1991, Rawson et al. 1999), and may be important determinants of species (and hybrid) distribution patterns, abundance and persistence (Sherwood & Petraitis 1998, Shields et al. 2008). Although not statistically tested in the present study, results indicate that, on average, both primary and total post-settlement mortality was greater for *Mytilus* than *Perna* by 4 – 9 %. This agrees well with the results of Bownes (2005) who demonstrated a mean percentage difference in post-settlement mortality of ca. 5% between low shore populations of *Mytilus* and *Perna*. This difference was however non-significant, due to high variability. A comparative (ca. 5%), and statistically significant, trend in adult mortality has been shown in some populations of these species (Nicastro et al. 2008a). The slight, but consistent difference in overall post-settlement mortality between species seems to fit well with the different life strategies adopted by *Mytilus* and *Perna*. These are essentially strategies of resilience and resistance (Nicastro et al. 2008a); *Perna* is more resistant to physical disturbance than *Mytilus*, which in contrast, ensures resilience through greater reproductive output (Zardi et al. 2006, 2007). It seems likely that a genotype-environment interaction, similar to the one suggested by Shields and colleagues (2008), may be the cause of the species-specific differences in post-settlement mortality.

The most enduring problem with studies of post-settlement mortality seems to be the separation of settler migration from actual mortality (Gosselin & Qian 1997, Cole et al. 2000). None of the methods outlined in the introduction, except the use of caged plots by Shields and co-workers (2008), are able to make this separation. The method used in the present study is no exception. Although it is argued (according to assumption 3) that rates of migration to and from experimental substrata are equal, in reality, field conditions, the complex dynamics of settlement behaviour and spatio-temporal variability of settlement make this assumption unlikely. This has the frustrating implication that most studies of early mortality, including the present one, could either under- or overestimate mortality depending on relative rates of emigration/immigration.

The method of out-planting calcein stained settlers, as done by Phillips (2002, 2004), is an improvement insofar as it allows immigrant settlers to be distinguished from original settlers. The loss of stained settlers however, can still not be categorically ascribed to either mortality or emigration, and the method may not be easily practicable on the large scale. Perhaps the most viable option for future research is some sort of adaptation of the method of Walters (1992); here silicone vacuum grease was applied to experimental plates thereby permanently attaching settling larvae. In a post-settlement mortality context this method would allow the use of mapping or photographic techniques to follow settlement and mortality at short intervals without the confounding factor of emigration. The silicone grease does not affect settlement or attachment, and has been successfully used in a recent recruitment study by Dobretsov and Wahl (2008). The application of practical methods for accurately establishing post-settlement mortality should allow future work to focus on better integrating information from all life stages.

CHAPTER 6

GENERAL DISCUSSION

The effects of coastline topography are varied and extend over a range of scales from centimetres to 100's of kilometres (Delafontaine & Flemming 1989, Lemire & Bourget 1996, Blanchard & Bourget 1999, Denny et al. 2004). As such, topography has many levels of influence, affecting patterns (e.g. distribution - Bourget et al. 1994, population structure - McQuaid & Phillips 2007) and processes (e.g. predation - Gosselin & Bourget 1989, dispersal - Jessopp & McAllen 2007) in the pelagic and benthic environments.

While coastlines are geometrically complex landscape forms (Andrle 1996), and encompass a variety of physical features at different spatial scales, the current thesis has presented a binary view of coastline topography. In this view, large-scale alongshore topographic heterogeneity was decomposed into two habitat types – bays and open coasts. Along the study coast, rocky intertidal habitat is arranged either within a bay in the lee of a headland, or linearly on the open coast. This configuration of available habitat brings about a specific spatial dynamic as it affects the possible distribution of mussel patches and other resources (landscape structure), and through the relationship with pelagic "corridors", creates a particular pattern of connection among patches (landscape function).

Using the intertidal mussels *Mytilus galloprovincialis and Perna perna* as model organisms, the patterns and processes existing in the two different habitat types were compared. The thesis therefore addressed: (1) the differential distribution pattern of adult mussels with respect to bays and the open coast, and the extent to which these patterns are general; (2) how topography affects preceding functional life-stages and how this knowledge helps to explain the adult pattern and (3) the magnitude of post-settlement mortality at meso-scales and its role as an intermediary process. An integrated interpretation of these results demonstrates the central tenet of landscape ecology – the reciprocal relationship between pattern and process (Turner 1989). More specifically, the relationship between landscape structure and function is identified, adding to our understanding of the influence of coastal topography on dispersal and intertidal population connectivity.

6.1 The effects of habitat and corridor quality

The spatial configuration of habitat is a key structural element of a landscape (Forman & Godron 1981), affecting dispersal, population dynamics and persistence (Turner 1989, Goodsell & Connell 2002, Roberts & Poore 2005). The broad effect of habitat configuration is, however, dependent on the relative quality of habitat patches within the arrangement, and on the quality of dispersal routes or corridors joining habitat patches (Fahrig & Merriam 1994, Fahrig 2002). Dispersal route quality, through its effect on dispersal success, can influence regional and local population abundance (Henein & Merriam 1990). The quality of a dispersal route essentially refers to the survival probability of organisms or propagules moving through corridor habitat, with zero quality reflecting a dispersal barrier (Fahrig & Merriam 1994). In the context of the present work, pelagic corridor habitat that enables substantial loss of invertebrate larvae to uninhabitable areas or offshore waters could be considered poor quality or even a dispersal barrier, if losses are absolute. Conversely, since bays are retentive environments (Largier 2004), corridor habitat provided by nearshore waters within a bay that limit the offshore loss of larvae, could be considered to be of higher quality.

At a landscape level the spatial structure of extant mussel populations followed coastline topography, with strongly habitat-dependent mussel cover (Chapter 2). Although habitat quality is usually measured in terms of patch area and isolation (see Fleishman et al. 2002), it is possible that the support of larger populations by bay-type habitats (assuming cover indicates abundance since mussel beds were mono-layered) is indicative of better quality habitat relative to the open coast. This notion is dependent on the definition used to establish “quality”, and raises the question of whether the habitat-dependent differences in mussel cover were due to environmental factors, substratum characteristics or food supply (directly associated with the quality of the habitat), or to larval supply (i.e. related to corridor-quality). In line with the hypothesis of settlement intensification, an additional influence may have been the amount of rocky space available in each habitat, with settlement being increased in areas with less available habitat (Pineda 1994b, Pineda & Caswell 1997, Pineda 2000, Rilov et al. 2008).

As Hunt and Scheibling (2001) discuss, habitat-specific environmental conditions are likely to influence patch dynamics through their effects on biological interactions. An example of this is the influence of wave exposure on predation and competition (Richardson & Brown 1990, Rius & McQuaid 2006). Moreover, environmental aspects of patch quality can supersede patch geometry in explaining metapopulation dynamics (Fleishman et al. 2002). Differences in physico-chemical properties between bay and open coast habitats have been identified, including differences in oceanographic characteristics, temperature and food supply (Geyer & Signell 1992, Graham & Largier 1997, Archambault et al. 1999). Of course wave exposure is also closely related to topography (Burrows et al. 2008), and in the case of bays versus open coasts, differences in exposure are often subjectively assumed (e.g. Coates 1998). Certainly, within the present study region, large scale oceanographic interactions with bays and headlands have been shown to produce characteristic differences in temperature structure and flow between bays and open coast stretches (Schumann et al. 1982). In the present thesis, quantitative wave exposure measurements showed definite environmental differences between habitat types, and supported the idea of environmental influence on the adult distribution pattern (Chapter 2). If these environmental aspects of patch quality are indeed able to supersede other characteristics of habitat quality and mediate biological interactions or other processes, their effects on population dynamics may be substantial.

Alternatively, evidence of higher settlement rates in bays than on the open coast, and the lack of a significant difference in post-settlement mortality rates between habitat types (Chapters 3 & 5), suggested that pre-settlement supply-side factors were the drivers of the observed population distribution. Although this pattern was not entirely consistent in time or space, the spatial inconsistencies in settlement pattern, seen at the Glentana area sites, may be coincident with meso-scale oceanographic changes previously observed in this area (Chapter 3, Schumann et al. 1982). If real, this coincident transition in settlement pattern is perhaps itself indicative of a strong supply-side influence. More specifically, the striking regional interspecies correlation of settlement highlighted the possibility of common transport mechanisms (Chapter 3). Based on the importance of supply-side factors (primarily larval transport), it seems likely that rather than, or in addition to, differential habitat quality, the quality of dispersal routes differed between bay and open coast habitats, and was an important determinant of the adult distribution pattern. In agreement with this, asymmetric dispersal due to physical dispersal media such as oceanographic features can supersede differences in habitat quality (Kawecki & Holt 2002). Applied to the present case, this could mean that even high quality habitat along the open coast would not necessarily be expected to support large populations.

Although no quantitative comparison of rocky habitat availability (quantity) was undertaken between bay and open coast environments, the log-spiral bays of the study region are each composed of a relatively small rocky headland with extensive sandy beaches extending to the east; in contrast, open coast sites are, for the most part, extensively rocky (pers. obs). Based on these observations, differences in availability of rocky habitat between bays and the open coast may form part of the explanation for intensified settlement in bays. However, the relative importance of habitat quality and asymmetric dispersal in relation to this intensification effect is as yet unknown.

6.2 Dealing with complex processes and scale

The complexity of a natural system such as that governing benthic intertidal life, makes attempts at the definitive assignment of individual causal factors difficult, if not futile (Pineda et al. 2009). This is especially true in the present case, where environmental conditions (wave exposure) and larval transport mechanisms (retention) are both closely tied to topography (Chapters 2 & 3), and are both likely to affect settlement (Denny & Shibata 1989, Eckman et al. 1990, Wing et al. 1995) and adult distribution (Gaines & Bertness 1992, Bustamante et al. 1997) in various ways.

The studies presented here provide direct and inferential support for strong habitat-specific effects on intertidal mussel populations via processes acting at multiple spatial scales and across life-stages. The strong correlations among life stages (settlement, recruitment, adults) at regional but not at local scales (Chapter 3), are suggestive of the changeable importance of processes at different scales. Certainly, processes are often linked to a specific spatial scale, and while a particular process may be locally influential at small scales, it may not be so at larger regional scales or vice-versa (Wiens 1989, Hughes et al. 1999). Consequently, the consideration of scale is paramount when searching out explanations for patterns (Chesson 1998, Huston 1999, Habeeb et al. 2005). The concept of hierarchical models however, has been put forward as a means of handling the complexities of scale (Allen & Starr 1982, de Boer 1992).

Hierarchical models of complex processes interacting across multiple scales have been used to simplify and explain population dynamics and ecosystem structure, simultaneously resolving pattern and process (Menge & Olson 1990, Fisher et al. 1998). Hierarchical approaches have been used in terrestrial and freshwater ecology (Rahel 1990, Tonn et al. 1990, Fisher et al. 1998, Noda 2004) and more specifically in several studies of intertidal systems (Pineda 1994b, Nakaoka et al. 2006, Lagos et al. 2008). While Denny and colleagues (2004) found no evidence of hierarchical spatial scales of intertidal variability over scales ranging from 10s' of centimetres to 100s' of metres, they recognised that their results were too limited by the spatial extent of the study to represent an unequivocal test of hierarchical models, such as those suggested by Menge and Olsen (1990).

The broader spatial extent of experiments and surveys in the present study (ca 500km) encompassed topographic features at meso-scales, while attachment-site selection by settlers was investigated at small (cm – m) scales. This range of scales enables a multi-scale (spatially explicit) and multi-life-stage (biologically explicit) explanation for the observed habitat dependent patterns. A hierarchical approach fits well with metapopulation studies since metapopulations are themselves hierarchical, being composed of 3 levels: individuals, local populations and the metapopulation (Noda 2004). Defining a metapopulation as a group of local populations of a species linked by dispersal (Gilpin & Hanski 1991), highlights the potential for links between regional and local scales, particularly the ability of local processes and patterns to influence collectively regional dynamics (Huston 1999, Leibold et al. 2004).

6.3 A hierarchical model

The 'telescoping' hierarchy of Pineda (1994b, 2000) and Pineda and colleagues (2009), already speculatively applied to the present thesis in Chapter 2, identifies 4 broad interlinking processes operating within a hierarchy of spatial scales, from large-scale processes acting on the larval pool and those determining larval transport, to small-scale settlement and post-settlement processes. Overlaying this hierarchy of processes and associated spatial scales onto the integrated results of the present study produces a good match. In the present thesis, coastline topography and the spatial intertidal patterns associated with it are shown to influence, through effects on different life-stages, each of these broad processes.

The combined possibilities of decreased fertilization on the open coast due to rapid dilution of gametes at higher levels of wave exposure (Chapter 2, Denny & Shibata 1989), and greater larval food availability in bays due to higher productivity and particulate subsidies (Archambault et al. 1999), mean that differences between the two habitat-types in the present study may have been initiated at large scales, early on in the hierarchy, having primary effects on the larval pool. Perhaps building on these early differences in the larval pool, it seems that topographically-related larval transport processes produced differential patterns of larval supply, creating habitat-dependent patterns of settlement (Chapter 3).

In terms of the settlement processes themselves, definite small-scale behavioural processes related to substratum selection were observed (Chapter 4). Although differences in behaviour of settlers between bay and open coast habitats were not assessed in this thesis, it is possible that differences in wave exposure, which affect the production of biofilm (Thompson et al. 2005), and potentially the detection of such cues by larvae (Abelson & Denny 1997), could mean habitat-specific settlement behaviour. At the scale of bays and open coasts in the present thesis however, such differences are unlikely because the effects of wave exposure on biofilm production and cue detection are counteractive, with wave exposure increasing production, but decreasing detection (Abelson & Denny 1997, Thompson et al. 2005).

As density-dependent interactions become increasingly important across the hierarchy, from large to small-scale processes (Pineda 1994b, 2000), the intensity of settlement is a critical input to the post-settlement level. In this regard, settlement intensification associated with less substratum availability (Pineda 1994b, Pineda & Caswell 1997, Rilov et al. 2008) may have played a role in increasing settlement in bays, potentially increasing the influence of density-dependent post-settlement processes.

Forming the final level of the hierarchy, post-settlement processes, including small scale biotic interactions and early post-settlement mortality, are the local determinants of population abundance (Pineda 1994b, 2000). While post-settlement mortality was substantial (around 60%), it was not habitat-dependent at the scale of bays (Chapter 5). However, the local scale de-coupling of the recruit-settler relationship did suggest the potential for small-scale influences of early post-settlement mortality on local recruitment and adult population distributions (Chapter 3). The role of density-dependence in these local interactions remains unclear.

With no differential effect of habitat (topography) on post-settlement mortality, the habitat-dependent settlement patterns reflected initial settlement and its presumed underlying cause, larval supply (Chapter 3). At the regional scale, strong recruit-settler and adult-recruit relationships were congruent with post-settlement mortality results and indicated a direct link between topographically driven settlement patterns and adult distribution. In agreement with Pineda (2000) and Lagos and colleagues (2005), these links across life-stages depict a hierarchy in which large-scale larval supply processes, connected to coastline topography, are strongly interrelated and have pervasive influences on regional adult patterns.

6.4 Spatial scale and coastline complexity

The integration of results in the hierarchical framework above serves to highlight the importance of scale, identifying clear regional trends and correlations in relation to topography, but variable local patterns. Thus, it seems that meso-scale topographic features are important drivers of regional, but not local scale processes and patterns. Moreover, the results demonstrate that local processes and variability can supersede regional trends (i.e. the anomalous Glentana area sites, Chapter 3).

While explanations for differences between regional and local scale patterns probably revolve around the relative importance of different processes at each scale (e.g. Tonn et al. 1990), there may also be scale-specific topographical causes (e.g. Jiang & Plotnick 1998, Denny et al. 2004). In this sense, the concept of a hierarchy may encompass topographic complexity across spatial scales. At a structural level, coastlines exhibit fractal geometry to varying degrees at different spatial scales (Mandelbrot 1967, Carr & Benzer 1991, Jiang & Plotnick 1998). At local scales there is a possibility that the highly fractal structure of shoreline topography may be responsible for the stochastic (1/f noise) variability of physical and biological factors (Denny et al. 2004). At the scale of continental coastlines however, some coasts are not very fractal ($D \approx 1$, Murray and Barton 2007), including that of South Africa (D =1.02, Richardson 1961 cited in Mandelbrot 1967). Although the bays and rocky headlands of the current study region should somewhat increase its fractal dimension (Jiang & Plotnick 1998), it is likely to be far lower than that of local scale, within-site level topography. This disparity in topographic complexity should mean that small-scale patterns will be inherently stochastic, while at larger scales, coastline topography will have a more deterministic effect, creating identifiable regional patterns.

6.5 The determinants of coastline connectivity

In terms of the 3 determinants of connectivity (organism behaviour, habitat configuration and the biophysical attributes of dispersal routes; Henein & Merriam 1990), there is evidence of active larval behaviour; both in terms of interactions between vertical positioning and oceanographic transport mechanisms in bivalve larvae (Shanks & Brink 2005), and in terms of small-scale substratum selection (Chapter 4, Lemire & Bourget 1996). As to the other 2 determinants, the present thesis demonstrates that the spatial configuration of habitat along the coast, with respect to topography, inherently links populations to particular “types” of corridor habitat. Due to their physical attributes, these corridors either make for high (retentive) or low quality (dispersive) dispersal routes (see section 6.1 above).

Since by definition, landscape connectivity is the extent to which a landscape enables dispersal (Taylor et al. 1993), the connectivity of patches within each habitat type, and among habitat types should differ considerably. Populations within bays should be strongly connected, a suggestion that has some genetic support, with bay populations having more private haplotypes and greater genetic endemism than those on the open coast (Nicastro et al. 2008b). However, entrainment of externally produced larvae into bays may increase connectivity with outside populations. In contrast, connectivity among populations on the open coast should be broader in extent, but weaker and more variable, being dependent on the vagaries of shoreward transport of larvae.

6.6 Coastline topography: a potential template for source-sink dynamics

The importance of connectivity has meant that a variety of models have attempted to describe and predict dispersal dynamics and population distributions in heterogeneous landscapes (reviewed by Kareiva et al. 1990). Dispersal and connectivity however, are species and landscape-dependent processes (Tischendorf & Fahrig 2000) that change according to the life history characteristics of the species involved, and the heterogeneity of the landscape through which the organisms move (Diffendorfer 1998).

In theory, populations of species that disperse passively, by way of wind or water currents, are most likely to display source-sink dynamics due to their inability to assess and respond to differences in habitat quality (Diffendorfer 1998). Moreover, although accurate empirical evidence for such dynamics is limited to a few plant species (Keddy 1981, Kadmon & Shmida 1990, Diffendorfer 1998), two key features of classical source-sink models fit with the conditions and patterns seen in the present study. These are 1) distinctively different habitat quality, and 2) differential dispersal (Diffendorfer 1998). The traditional definition of a source population requires that it be self-sustaining, a net exporter and have an average fitness greater than 1; a sink population is then defined as a net importer, entirely reliant on immigration with an average fitness less than 1 (Holt 1985, Pulliam 1988). Speculatively, in their strictest form, these definitions of sources and sinks are difficult to fully reconcile with the respective dispersal and population dynamics of bay and open coast populations in the present study. This is mainly because, in terms of post-settlement mortality, onshore fitness of settlers did not differ between habitats (Chapter 5). Differences in mortality between habitats may, however, have been introduced at the time of dispersal, with greater offshore loss of larvae from nearshore waters associated with open coast habitat than bay habitat. This reasoning changes the definition of a sink population from one in which average fitness is less than zero, to a population that simply loses more larvae than return to it via self-recruitment. In other words, one could say that the definition of "fitness" is extended to include the capacity of the population to avoid mortality due to offshore losses.

Secondly, the retentive nature of bays does not immediately fit with the idea of these populations being net exporters. In this case however, it is important to remember that retention does not mean that no larvae move out of bays, only that the time taken for them to move out is increased (Largier 2004, Jessopp & McAllen 2007). Of course, source-sink dynamics in intertidal populations could occur at scales unrelated to meso-scale topography. At small scales though, the ability of mussel larvae to assess habitat quality, enabling them to select habitat actively, should mean adherence to a more balanced dispersal pattern (*sensu* Diffendorfer 1998).

In a general sense then, bay and open coast populations may not behave precisely as source and sink populations all the time, but within the continuum of dispersal patterns (Diffendorfer 1998) they have more in common with a source-sink dynamic than with balanced dispersal. The applicability of source-sink models to the bay-open coast situation should depend on the strength of differences in habitat quality and consistency of dispersal patterns between them.

Trying to categorise bay and open coast populations as sources and sinks may be simplistic, but identifying systems in which source-sink dynamics occur is important to advancing our understanding of species population dynamics and conservation (Pulliam 1988, Lawton 1993, Dias 1996). Further research to determine the applicability of source-sink models to large-scale topographically-defined intertidal populations should allow the role of coastline topography in the areas of population dynamics and conservation to be assessed. This research will however require very particular data that allows true sink populations to be distinguished from pseudo-sinks and areas that simply have low carrying capacity (Watkinson & Sutherland 1995, Diffendorfer 1998). It should also take into account the possibility of correlations in recruitment of predator and prey species (White 2007).

6.7 Conclusion

Any scientifically meaningful experimentation or observation requires that spatio-temporal repeatability be demonstrated through replication (Underwood & Petraitis 1993). In line with the suggestion of Archambault and colleagues (1999), this thesis assessed the generality of a bay effect through large-scale replication within a single system, finding the pattern to be general, but certainly not without contingencies. An inseparable part of establishing generality in ecology, however, is the spatial scale of study. The merits of local-scale studies, such as apply to community ecology, and large-scale studies employed in macro-ecology, are discussed by Simberloff (2004) and Lawton (1999) respectively. While Lawton (1999) argues for small-scale detail to be ignored in favour of identifying key patterns or regularities, the present thesis demonstrates that identifying general patterns in ecology depends on knowledge of both local and large-scale patterns and processes, and the relative importance and variability of each. The present thesis also shows that while a general pattern may exist in one life-stage (i.e. adult mussel cover), it may be more variable in others (i.e. larval settlement and recruitment). Overall however, the effects of topography on the life-stages examined here were either synergistic or neutral (in the case of post-settlement mortality), depicting a regional influence of coastline topography across life-stages. Consequently, a final key point is that landscape patterns, resulting from a fundamental structural element such as topography, may be detectable when the element's effects are synergistic across life stages and scales, but may be hidden when effects are antagonistic.

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