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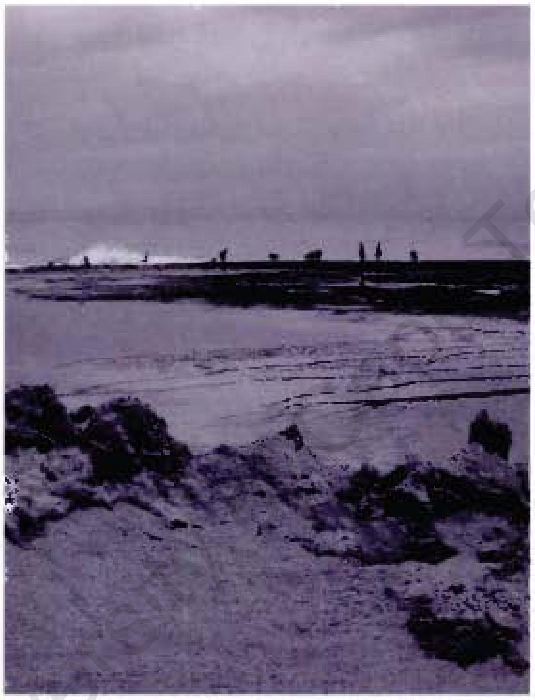
Recruitment patterns and processes and the connectivity of rocky shores in southern Africa



Mussel harvesters at Dog Point,
Maputaland, KwaZulu-Natal

University of Cape Town

Kathleen E. Reaugh

Thesis Presented for the Degree of
Doctor of Philosophy
in the Department of Zoology
University of Cape Town
August 2006

DECLARATION

I hereby declare that all of the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate

Kathleen E. Reaugh

28 Nov 06

Date

University of Cape Town

DEDICATION

This dissertation is dedicated (in no particular order):

to my Great Uncle Cliff, who took me clamming and crabbing for the first time in Oysterville, Washington, when I was seven,

to Dad, who let me play with the worms rather than put them on hooks when we were fishing, and took me to the zoo or the Exploratorium almost every time I asked

and to Mom, who let me keep pet snails and slugs, even when they made my room slimy, and who believes in the value of smart, uppity women.

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When any dissertation is lifted up and shaken gently, lots of names should fall out with loud and celebratory crashes: the acknowledgements of collaboration and assistance by colleagues and students, thanks for guidance to advisors and friends and references to previous researchers should clatter together to the floor in joyful cacophony. The SANCOR data presented in Chapter 1 is a remarkable testament to the collaborative efforts of the marine science community, involving seven institutions in Namibia and South Africa over the six years of data collection and processing. One of the most extraordinary aspects of my own field work (Chapters 2-4) was the number of people, both students and professionals, who I found ready and willing donate their time: approximately eighty people traveled all the way to Manzengwenya specifically to help with some aspect of my study! Additional equipment, support and consultation during data collection, sample processing, analyses and interpretation were provided by individuals at several universities and institutions, detailed below. I tried to note everyone's name carefully, and apologize for any omissions or misspellings. It's a lot of names. I therefore strongly advise against shaking this dissertation in the library. Librarians abhor a cacophony, joyful though it may be!

I cannot overstate how privileged I feel to have worked with my supervisors, Jean Harris, George Branch and Gavin Hough. Each in their way taught me important lessons (multiple times, when required) about academics, science, conservation and professionalism. Profound thanks go to my parents and my brothers, whose support and love I have never once in my whole life doubted. Also to Todd Flower, who talked me through more challenging moments then I choose to count, and has shown infinite patience through these final stretches. The liters of tea and coffee that I dedicated to this project I have rarely drunk alone. The tradition of shop-talk-and-tea started with Roni Jackson (then Brereton-Stiles) on the steps of the Manzengwenya house, and was carried cheerfully forward by Luisa Riato, Cloverley Lawrence, Kerry Sink, Gugu Zama, Stix Ngubane, Maya Pfaff, Marta Machado de Ponte, Evie Wieters, Vuyi Radebe, Baja Ngcobo, Minna Balbas, Desiree Marimuthoo, Tamsyn Livingstone, Judy Ratner, Ronel Nel and Ruth Branch. These special times have sustained me through the challenging ones. Finally, to all these friends and more that I have made over these five years in South Africa, thank you, dankie, ngiyabonga kakulu. I believe that your love for this country is now rivaled by my own, and I learned everything about it from you.

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ABSTRACT

This thesis addresses the recruitment patterns of barnacles and mussels at a range of spatial and temporal scales and attempts to relate them to larval and adult abundance, as well as to local productivity and oceanographic conditions that would influence larval transport and the connectivity of adult populations. In Chapter 1, I investigated the spatial and temporal patterns of mussel recruitment and adult bed dynamics of four mussel species (*Aulacomya ater, Mytilus galloprovincialis, Perna perna* and *Semimytilus algosus*) across 2500 km of the southern African coast. A coast-wise gradient of recruitment intensity was evident, with high recruitment rates on the West Coast and lower rates on the South and East Coasts. At the largest scale (100s of km), populations appear closed, as adult biomass was significantly and positively correlated with recruitment density. Although neither nearshore productivity nor meso-scale oceanic features were significantly correlated with among-location variability in recruitment intensity, an index that combined the two explained 62% of the variability, indicating that, taken in conjunction, both of these factors are important in understanding recruitment processes of benthic organisms with meroplanktonic larval stages. High inter-annual variability in recruitment was recorded, with low recruitment on the West Coast in years with Benguela Niño or Niño-like warming events. At most locations and for most species, sites were more variable in the density than in the timing of recruitment events. This study represents a first critical step in identifying and comparing large and meso-scale recruitment patterns and processes in southern Africa, and created a framework for the detailed investigations in the following three chapters.

Chapters 2-4 examine patterns and processes of the recruitment of mussels and barnacles along a 25-km stretch of shoreline in the Maputaland Marine Reserve (MMR) in northern KwaZulu-Natal (KZN), South Africa. The investigations in these chapters not only extend our knowledge of recruitment in South Africa into an under-studied bioregion, but also address marine reserve management-related questions of benthic-pelagic coupling and the connectivity of rocky shores in this important conservation area.

Knowledge of the shape, patchiness and density of the meroplanktonic larval pool, and how these are controlled by local processes such as productivity and onshore transport mechanisms, is critical to interpret both recruitment rates and connectivity between areas. Chapter 2 examines the spatial and temporal patchiness of the pool of mytilid, bivalve and cyprid meroplankton in the MMR. This is the first study of this kind in this region. The size and density of the patches were analyzed in relationship to the *in situ* biomass of zooplankton and phytoplankton, several physical parameters and the adult density of the mussel *Perna perna* on adjacent headlands. There is a strong sea-breeze effect and wind-driven upwelling, although weak, was present at this site; nearshore phytoplankton concentrations responded positively to decreases in water temperature.

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Bivalves and mytilids were vertically unstratified, positively correlated with water temperature and negatively correlated with phytoplankton concentration, indicating that they may be closer to shore during periods of upwelling-neutral or downwelling-positive winds. Cyprids aggregated near the bottom of the water column and were negatively correlated with temperature and positively correlated with phytoplankton, indicating that upwelling may be an important onshore transport mechanism for cyprids. Larvae of barnacle and mussel groups were, on average, denser at the inshore than the offshore stations, but very few nauplii were found, indicating that competent larvae may be using behavioral or swimming adaptations to aggregate nearer the shore. Cyprids were not denser at rocky headland points, where the adults occur, than in the bays between. Mytilids were found in highest densities proximate to two rocky headlands, however, suggesting that both accumulating mechanisms and associations with adult biomass are important in explaining the spatial structure of the mytilid larval pool.

Chapter 3 reports the recruitment rates of two mussels (*Brachidontes semistriatus* and *Perna perna*) and three barnacles (*Chthamalus dentatus, Tetraclita serrata* and *T. squamosa rufotincta*) onto natural and artificial substrates. These were recorded monthly for 18 months at each of five sites in the MMR, simultaneous to the collection of larval data presented in Chapter 2. Recruitment rates of mussel species in northern KZN were lower than those recorded anywhere else in southern Africa. Recruitment was strongly seasonal for all species, with *B. semistriatus, P. perna* and *C. dentatus* recruiting in spring/summer and *Tetraclita* spp. in autumn/winter. Locality, site and intertidal zone were less important than season in explaining recruitment variability, although locality was also often a significant factor for barnacles. Mean monthly temperature was generally the most important predictor for the recruitment variability of all species, which was expected due to the seasonal pattern of both water temperatures and recruitment in this region. Nearshore larval density was also a significant predictor for barnacles and for *B. semistriatus*, establishing benthic-pelagic coupling. The relationship between recruitment rate and adult density was found to be weak and non-significant for *P. perna*, implying that the population may be open at the scale of the study area (approx. 25 km), although it may reflect harvesting pressure on adult stocks.

To explore connectivity of the rocky shore communities, Chapter 4 investigates nearshore hydrography in the MMR. Dominant meso-scale patterns in SST were found to be more closely linked to offshore forcing at the confluence of currents joining to form the Agulhas Current than to local wind events. These dominant patterns were found to explain 10% and 15% of recruitment variability of the mussels *P. perna* and *B. semistriatus*, and 16% and 48% of the recruitment variability of the barnacles *C. dentatus* and *Tetraclita* spp., respectively. Analyses of the dominant current structures found this coast to be driven by coastal boundary, wave direction, wind and tidal forcing mechanisms. While the across- and alongshore currents were strongly sheared, the principal components of their patterns were not related to the patterns revealed by empirical orthogonal function analysis of SST. Alongshore velocity data and knowledge of across-shore transport and

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processes were then combined to estimate larval dispersal distances for mussels and barnacles, as well as other organisms, within the MMR. A semi-stochastic Lagrangian simulation was constructed to predict dispersal kernels of passive drifters during the recruitment season for mussels and *C. dentatus*. In all cases, the dominant direction of travel was southward, and mean dispersal distances for the various models ranged from 30-122 km south along the coast. Using these results, together from those in the previous chapters, three alternate examples of the spacing of no-take areas using dispersal distances were proposed, with recommendations for improvement of the management of the rocky shores within the MMR.

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GENERAL INTRODUCTION

As our understanding of community theory of rocky intertidal shores continues to improve, we have learned that conclusions from experimental investigations must consider not only mechanisms of top-down control (Strong 1992), but also key processes that affect the relative and absolute strength of community interactions from the bottom-up (Menge 2000b). This means that variability in population dynamics and community structure may be explained not only by the ways in which predators and/or herbivores control prey assemblages, but also by differences in the food or nutrient supply, or the arrival of newcomers to the assemblage via settlement and subsequent recruitment (Connell 1985; Menge 1991; Schiel 2004; Wieters 2006). The supply of dispersive recruits to communities of benthic adults has been investigated for decades (e.g. De Wolf 1973), but models and experiments that examine post-settlement effects on community structure are a relatively recent innovation (e.g. Gaines and Roughgarden 1985; Minchinton and Scheibling 1991; Menge 1995, 2000b; Menge et al. 1999; Underwood and Keough 2001; Forde and Raimondi 2004; Wieters 2005).

To focus investigations, Connell (1985) subdivided settlement and recruitment patterns of sessile invertebrates into four specific sub-questions: (1) What environmental factors affect the supply of settlers to the shore? (2) How does the density of settlers impact recruitment rates? (3) How do recruitment rates relate to adult densities? (4) How do recruitment rates vary over different scales of space or time? The structure that Connell (1985) provided has proved essential. For example, Berry (1978) previously noted the potential role of an anomalously high recruitment event in 1976 in shaping the rocky intertidal mussel population on the east coast of South Africa, but did not follow-up by testing his hypotheses. Bottom-up processes have, however, been investigated in South Africa for a long time. In fact, at the same time that Roughgarden described this suite of recruitment processes as part of 'supply-side ecology' in North America (Lewin 1986), researchers in South Africa were demonstrating the importance of key supply-side factors such as nutrient supply, primary productivity and food subsidies in controlling or altering community structure (Bosman and Hockey 1986; Branch et al. 1987; Bustamante et al. 1995a). These approaches were followed by studies of the settlement and recruitment of benthic rocky-shore organisms. All of Connell's questions are under continuing investigation in South Africa (e.g. Harris et al. 1998; Erlandsson and McQuaid 2004; Erlandsson et al. 2005a, b; McQuaid and Lawrie 2005; Porri et al. 2006; Pfaff et al. in prep), and this thesis addresses the third and fourth questions at varying spatial and temporal scales, extending Connell's questions to examine the processes that underlie recruitment patterns.

In southern Africa, the harvest of intertidal shellfish stocks has been an integral part of the coastal social and economic environment for at least 120,000 y, and continues to be important

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around the entire coast today (Griffiths and Branch 1997; Griffiths et al. 2004). The diverse impacts of human activities on these resources, including mussels and other sessile benthic invertebrates, are well documented (Lasiak and Dye 1989; Lasiak 1991b, 1993; Kyle et al. 1997a; Hauck and Sweijd 1999; Sink 2001; Cockcroft et al. 2002; Branch and Odendaal 2003) and have come to the fore of management concerns in the last fifteen years (Lasiak 1991b, 1993; Dye et al. 1997; Griffiths and Branch 1997; Tomalin and Kyle 1998; Cockcroft et al. 2002; Harris et al. 2002b; Hauck and Sowman 2003). Whereas the wild mytilid resources on the West Coast (*Choromytilus meridionalis*, *Aulacomya ater* and *Mytilus galloprovincialis*) are still not heavily harvested today (Robinson 2005), the smaller stocks of *Perna perna* along the South and East Coasts are heavily exploited by subsistence and recreational harvesters (Griffiths and Branch 1997; Kyle et al. 1997a; Lasiak 1999; Clark et al. 2002). To predict the effects that human activities will have in different coastal areas, we must first understand the patterns and processes of their replenishment through in-depth studies of larval transport, settlement and recruitment.

The first chapter in this thesis investigates the recruitment of four mussel species around the coast of southern Africa at a regional scale. Understanding of pattern and process at local scales, where supply-side and biological community dynamics come into play, requires contextualization through study at a larger scale that takes into account oceanographic and biogeographic gradients. The coastal environment of southern Africa is characterized by strong gradients in both temperature and productivity (Lombard et al. 2004), and several previous researchers have taken advantage of these gradients to examine community responses to them at a biogeographic scale (Bustamante et al. 1995a; Bustamante and Branch 1996; Sink et al. 2005, in prep). As illustrated in Figure i, the West Coast is dominated by the cold, northward flowing Benguela current and a pulsed, seasonal, highly productive upwelling system (Andrews and Hutchings 1980). In the southern Benguela, the coast consists of active upwelling cells and downstream sites. In the northern Benguela, upwelling is more consistent both spatially and temporally, with persistent winds that continually drive surface waters offshore. In contrast, the warm, nutrient-poor waters of the southward Agulhas Current dominate the East Coast, flowing adjacent to the narrow continental shelf (Lutjeharms et al. 2000a, b; Meyer et al. 2002). The two currents mix along the south coast over the Agulhas Bank and around the Cape Peninsula in the Cape Cauldron (Boebel et al. 2003; Richardson et al. 2003).

Moving from west to east, the coastal waters become generally warmer and more nutrient-poor. Upwelling on the West Coast enhances nutrient levels that support the highest levels of primary productivity on the coast, and this food becomes available to intertidal organisms both as phytoplankton and kelp detritus (Bustamante et al. 1995b). Previous studies at a biogeographic scale have shown that intertidal rocky shores become more diverse as biomass decreases, with the lowest intertidal biomass and highest diversity on the north-east coast (Bustamante and Branch 1996; Sink et al. 2005). At discrete points along the shoreward edge of the Agulhas Current, where the continental shelf widens on both the South and East Coasts, persistent topographically-induced

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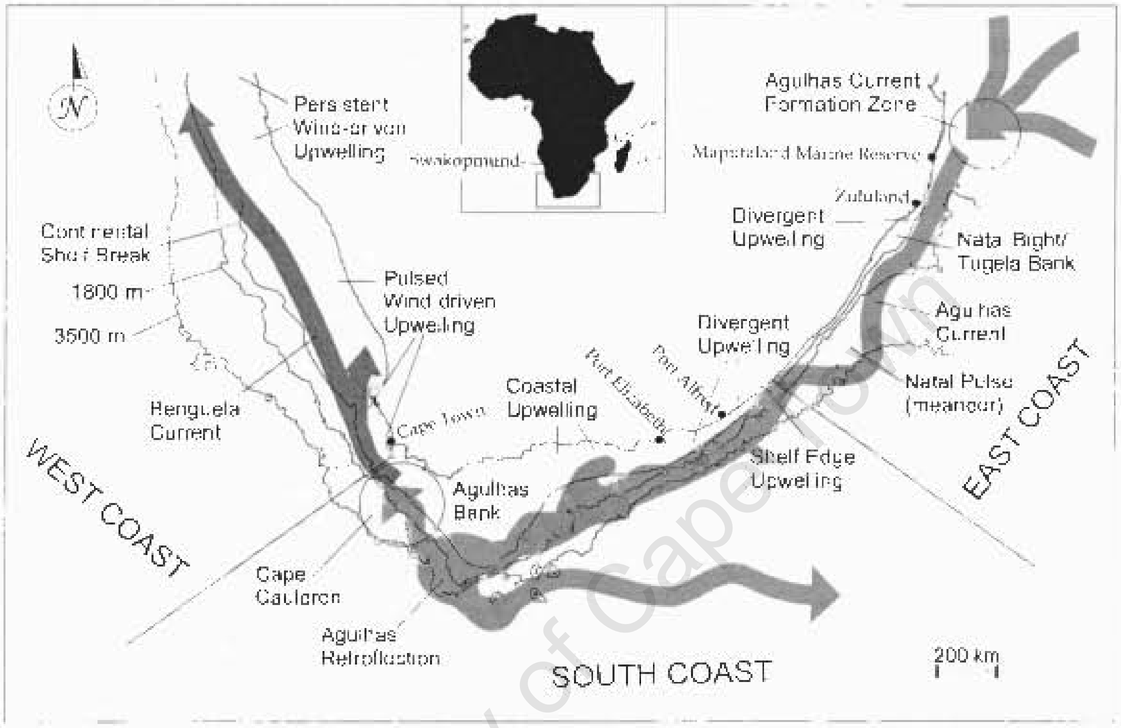

Figure i Map of southern Africa, with offshore bathymetry from Lombard et al. (2004), and relevant inshore features of the major currents around the coast from Roberts (2005). Bioregional divisions for the rocky intertidal are presented in Figure 1.1.

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upwelling cells draw relatively nutrient-rich waters into small eddying retention cells in the Natal Bight, as well as near Port Alfred and Port Elizabeth (Lutjeharms et al. 2000a; Meyer et al. 2002). These supply the South Coast, flanked by the widened shelf of the Agulhas Bank, and the East Coast's Tugela Bank with intermediate nutrient levels (Roberts 2005).

Studies addressing the connectivity of areas or populations examine the spatial paths along which food or propagules travel (e.g. Sheaves 2005; Mumby 2006). In most systems, the ecological linkages between spawners, larvae, settlers and recruits continue to remain elusive for benthic organisms with dispersive larvae despite vastly improved methods and experimental design. Knowledge has nevertheless been slowly built via *in-situ* experimentation (Olson and McPherson 1987; Levin et al. 1993; Chiswell and Booth 1999; Natunewicz and Epifanio 2001), inferential methods (Barber et al. 2002; Gilg and Hilbish 2003; McQuaid and Lawrie 2005) and modeling (Largier 2003; Siegel et al. 2003; Ellien et al. 2004; Schiel 2004). Additionally, the rates of spread of alien species have allowed us to create hypotheses about indigenous species with similar physical and behavioral characteristics (e.g. McQuaid and Phillips 2000; Armonies 2001; Branch and Steffani 2004; Kinlan and Hastings 2005).

Chapters 2-4 of this thesis focus in from the biogeographic perspective to examine patterns and processes of mussel and barnacle recruitment at a smaller scale. The experiments and observations I relate in these chapters were all based in the Maputaland Marine Reserve, in the northern half of the Greater St. Lucia Wetland Park and World Heritage Site, in northern KwaZulu-Natal, South Africa. This area is characterized by its proximity to the region of formation of the Agulhas Current, a typical western boundary current, and has a narrow continental shelf, a relatively straight stretch of coastline and warm nutrient-poor water (Heydorn et al. 1978; Schumann 1987; Carter and Schleyer 1988; Martin and Flemming 1988; Schumann 1988; Ridderinkhof et al. 2001; Quartly and Srokosz 2002; Roberts 2005). It is also a region of South Africa that, as a former homeland area, is still socio-economically underdeveloped. People living within the park continue to depend on coastal resources for food, frequenting the coast to exploit both benthic rocky-shore and sandy-beach organisms (Kyle et al. 1997a, b; Sink et al. 2005). The high level of exploitation, and its effects on community structure, are of increasing management concern (Tomalin and Kyle 1998; Robertson 2003; Sink et al. 2005). The relative influences of natural and anthropogenic effects on community structure cannot be distinguished, however, without investigation of community patterns and processes (Clarke 1993). Investigations such as mine are therefore fundamental to successful ecosystem-based management of coastal resources.

Supply-side experiments at smaller scales, more common than biogeographic investigations, have illuminated the physical factors that influence both larval survival and delivery in specific locales. These factors are now known to include winds (Almeida and Queiroga 2003; Navarrete et al. 2005), seasonal temperature cues or conditions (Broitman et al. 2005), upwelling or downwelling (Roughgarden et al. 1991a; Navarrete et al. 2005), including the influence of

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upwelling on nutrient concentrations (Lotze and Worm 2002; Broitman et al. 2005) and the presence of smaller-scale hydrographic features such as internal waves (Shanks 1983; Roughgarden et al. 1991a), tidal bores (Vargas et al. 2004; Ladah et al. 2005), reduced or sheared currents following topographic coastal features (Lagos et al. 2005) and wave exposure (Archambault and Bourget 1999; McQuaid and Lindsay 2005; Menge et al. 2005; Westerbom and Jattu 2006).

The way in which each of these physical factors influences the transport, life history and dynamics of the pool of larvae can affect the temporal and spatial heterogeneity of recruitment along a coastline (Narváez et al. 2004; Lagos et al. 2005; Navarrete et al. 2005; Wieters 2005), but there are also important biological factors at play. Larvae may actively choose the zone and exposure level on the rocky shore in which they will settle (Kingsford et al. 2002), through their position in the water column (Grosberg 1982; Satumanatpan and Keough 2001) and by seeking adult conspecifics (Keough 1998; Hills and Thomason 2003; Manríquez et al. 2004). Upon reaching the rocky shore, larvae may actively choose a preferred substrate according to its rugosity (Crisp and Barnes 1954; Petraitis 1990) or to avoid competitive dominants (Grosberg 1981), perhaps using chemical cues (Crisp 1974; Davis and Moreno 1995; Wright and Boxshall 1999), and may be influenced by the density of adult conspecifics or congenerics (Keough 1998). Whenever or wherever settlement occurs in numbers, there will be an element of competition, among conspecifics or individuals of different species, which can influence both pre-settlement larval choice and post-settlement mortality (Grosberg 1981). Survival can also be influenced by predation (Navarrete and Wieters 2000; Osman and Whitlatch 2004; Alfaro 2006a) or physical effects such as heat stress or desiccation at the edges of the adult range (Power et al. 2001; Chan and Williams 2003). The density of the larval pool and the rates at which larvae settle (bottom-up effects), as well as the density of adults on the shore (a top-down effect) will influence the relative importance of each of these factors in the ultimate recruitment of individuals (Menge 2000b; Wieters 2005).

All of the recruitment studies in my thesis compare recruitment rates among natural and artificial substrates. Competent larvae actively choose among substrates during settlement (Crisp et al. 1985; Raimondi 1988a, b, 1990; Holm 1990a; Raimondi and Keough 1990; Lasiak and Barnard 1995; Moreno 1995; Berntsson et al. 2000). As a result, there can be an interaction between the substrate offered and larval settlement densities, which is independent of the nearshore density of competent meroplanktonic larvae, especially under settlement-saturated conditions (Bertness et al. 1992). This variability can have an important effect on the interpretation of recruitment patterns among and between species, locations and regions. Standardized artificial substrates have become a common means for comparing settlement and recruitment rates among sites (Caceres-Martinez et al. 1993; Almeida and Queiroga 2003; Helson and Gardner 2004; Broitman et al. 2005; Navarrete et al. 2005; Porri et al. 2006) and even between hemispheres (Menge et al. 2002), although few studies exist that compare between simultaneous recruitment onto natural and artificial substrates (but see Strathman and Branscomb 1979; Raimondi 1988a; Bulleri 2005).

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In Chapter 1, I use a hierarchically-nested design to characterize the spatial, seasonal and annual variation in mussel recruitment rates across 2500 km and five bioregions along the southern African coastline, stretching from Swakopmund, Namibia around to Zululand on the east coast of South Africa. Using data collected seasonally over five years from four sites at each of eight locations, I examined how well coastal productivity and retention at biogeographic scales were able to explain recruitment rates. I then investigated the relationship between recruitment and densities of adult stocks at multiple scales, and compared theories of recruitment limitation in low-, medium- and high-level recruitment environments with the empirical data, focusing on recruitment limitation as it related to the adult:recruit ratio among species and locations. Finally, I provided some hypotheses about recruitment processes arising from these patterns, which guided the more process-oriented, smaller-scale studies that followed.

In Chapters 2-4, I present the first ever study of simultaneous larval supply, recruitment dynamics and nearshore hydrography in the Maputaland Marine Reserve (MMR) in South Africa. The study site is to the north of Zululand, the northeastern-most site investigated in Chapter 1, and these chapters extend our knowledge of recruitment dynamics across a biogeographic break into a new, understudied area. The MMR falls in the northern half of the Greater St. Lucia Wetland Park and extends from the coastline to 3 nautical miles seaward. The coastline is zoned to allow different types of activities in different areas. This zonation is currently being reviewed, so my study is timely. I also provide data for two species, the mussel *Brachidontes semistriatus* and the barnacle *Tetraclita squamosa rufotincta*, whose recruitment patterns were previously unknown. The data for these three chapters were collected simultaneously, but the results are broken into three inter-connected sections.

In Chapter 2, I examine several biological and physical parameters relating larval supply to the density of adult benthic rocky-shore organisms and patchiness of the larval pool. First, I characterized the spatial and temporal patchiness of mytilid, bivalve and cyprid meroplankton in the water column from oblique tows and related it to *in situ* phytoplankton concentration, temperature and salinity, as well as to the density of adult stocks on the shore. Then, using satellite imagery, I quantified the scale of patchiness of sea surface temperature and phytoplankton and compared these with the results for the plankton tows. Finally, using wind and subsurface temperature data, I examined the role of wind, tides via tidal bores and slicks as possible onshore or offshore transport mechanisms for the larval pool in this area.

In Chapter 3, I report the monthly recruitment rates of two species of mussels (*Perna perna* and *Brachidontes semistriatus*) and two taxa of barnacles (*Chthamalus dentatus* and *Tetraclita* spp.) onto natural and artificial substrates in two intertidal zones. Using physical and biological parameters from Chapter 2, I established levels of onshore-offshore coupling between larval density, phytoplankton concentration, physical processes and recruitment. However, predictions

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about alongshore connectivity, one ultimate goal of this investigation, could not be established without information about the velocity and variability of alongshore currents in Maputaland.

To provide this information, in Chapter 4, I measured current velocities in Maputaland from the swash zone to depths of 20 m using three types of oceanographic technology: drogues, an acoustic Doppler current profiler (ADCP) and videography. These are the first inner-shelf hydrographic measurements ever taken beyond the surf zone in this region, and the first application of video technology to current measurements in South Africa. Hoping to dispel the hypothesis that the nearby Agulhas Current drives nearshore processes, I analyzed these currents in relation to meso-scale events evident from remotely-sensed sea surface temperature. I then compared these events to recruitment rates measured in Chapter 3 to investigate what, if any, role the formation of the Agulhas Current might play in restricting or enhancing larval supply to Maputaland. Using the current measurements taken in each of the zones and some emerging theory of larval behavior and dispersal, I developed a semi-stochastic Lagrangian model for dispersal of passive drifters, and interpreted the results of this model to examine possible dispersal paths of species such as mussels and barnacles that have a meroplanktonic dispersive stage. Then, I provided examples of how this model might be interpreted to guide decision-making about the spacing of no-take areas within the Maputaland Marine Reserve.

Finally, I provide a synthesis of the results of my studies and draw general conclusions about the supply-side ecology and recruitment dynamics of mussels and barnacles over small to regional scales, highlighting the ways these will inform both further ecological research and coastal management.

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CHAPTER 1

Mussel recruitment around the coast of southern Africa at multiple scales and relationships with adult mussel stocks

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1.1 INTRODUCTION

Large-scale differences in recruitment intensity of benthic intertidal species arise from a combination of oceanographic and biological conditions. Teasing these apart is complicated, as their relative importance varies among taxa and sites at all scales and can even co-vary (Menge et al. 2003). However, they do group into two general categories: bottom-up, including pre-recruitment processes and local productivity, and top-down, including predation and grazing (Menge et al. 1997b). Ocean currents vary at multiple scales, and can be locally retentive or extractive depending on the oceanic environment and the local shoreline topography, ultimately influencing community composition (Connolly and Roughgarden 1998). Many studies have found physical conditions to be important for successful recruitment, including the dominant offshore and nearshore hydrographic conditions (Hicks and Tunnell 1995; Graham and Largier 1997; Archambault and Bourget 1999; Navarrete et al. 2005). These are temporally variable (Wing et al. 1995a, b; Connolly and Roughgarden 1999a; Botsford 2001), and most often the parameter used to indicate this variability is temperature (Bayne 1976; Navarrete et al. 2002; Broitman et al. 2005). Productivity is positively correlated with the following biological factors, all found to be important to recruitment success at regional scales: local spawner stock biomass (Fisk and Harriott 1990), spawner stock fecundity or other reproductive traits (Urho 1999; Hughes et al. 2000; Brante et al. 2003; Hills and Thomason 2003) and larval condition and rates of starvation (Bayne 1976; Olson and Olson 1989; Roberts and Lapworth 2001). Productivity varies temporally as well as spatially. For example, productivity linked to El Niño Southern Oscillation (ENSO) events helps explain inter-annual recruitment rates in some areas (e.g. Botsford 2001). Finally, recruitment is affected by benthic pre-settlement effects, such as larval predation by conspecifics (Navarrete and Wieters 2000), or post-settlement effects, such as physical disturbance on the rocky habitat (Hunt and Scheibling 1996).

Underwood (2000) asserts that it is impossible to understand how patterns and processes vary without valid inter-regional and inter-annual comparisons. Large-scale studies of intertidal ecology over 100s to 1000s of km are uncommon, but have been undertaken around the coast of southern Africa. For example, Bustamante and Branch (1996) investigated community structure at exposed headlands, semi-exposed rocky shores and sheltered bays at 15 locations between Lüderitz, Namibia and Inhaca Island, Mozambique, spanning ~3700 km of coastline. This study and others have highlighted differences in patterns and processes among bioregions, and as a result, single-model management is generally discouraged across a biogeographically complex region (McQuaid

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and Payne 1998; Lombard et al. 2004). Elsewhere, recruitment processes have also occasionally been studied over large spatial scales, including the recruitment of barnacles over a European scale (Jenkins et al. 2000; O'Riordan et al. 2004) and the recruitment of mussels and barnacles over 900 km in Chile (Rivadeneira et al. 2002). Similar inter-regional comparisons have been made via analyses of independently collected data and meta-data sets (e.g. Connell 1985; Hughes et al. 2002). Finally, for even larger-scale contrasts, researchers have spanned hemispheres, studying recruitment and community dynamics using the 'comparative-experimental approach' (Menge et al. 2002; Wieters 2006).

Lombard et al. (2004) have defined five inshore marine bioregions around southern Africa (Figure 1.1). Several mussels inhabit these shores, including the native brown mussel *Perna perna*, ribbed mussel *Aulacomya ater* and black mussel *Choromytilus meridionalis*, and the invasive mussels *Semimytilus algosus* and *Mytilus galloprovincialis* (van Erkom Schurink and Griffiths 1990; Bustamante and Branch 1996). In 1990, the overall standing stock of mussels in South Africa was estimated at 114,000 t whole wet mass, approximately 69% lying on the West Coast, 24% along the South Coast, and 7% on the East Coast (van Erkom Schurink and Griffiths 1990).

The brown mussel, *Perna perna*, has a widespread distribution, and has been studied along the southwest and southeast coasts of Africa, as well as the east coast of South America and the Gulf of Mexico. It is heavily exploited on the southern African coast (Dye et al. 1994), where it has a disjunct distribution, being found along the entire coastline except for 800 km between southern Namibia and the Cape Peninsula in South Africa (van Erkom Schurink and Griffiths 1990). In most areas, it forms dense monolayer beds from the intertidal to the very shallow subtidal (Branch et al. 1994). Grant et al. (1992) studied allozyme frequencies for *P. perna* over its southern African distribution and found a general lack of micro-geographic heterogeneity, although the Namibian population was slightly divergent. There is now a large body of literature investigating various aspects of its life history in southern Africa, including growth rates (Berry 1978; Crawford and Bower 1983; van Erkom Schurink and Griffiths 1993; Tomalin 1995; Kaehler and McQuaid 1999b; McQuaid and Lindsay 2000), the ecological effects of parasites (Calvo-Ugarteburu and McQuaid 1998a, b; Kaehler and McQuaid 1999a), population dynamics (McQuaid et al. 2000; Lawrie and McQuaid 2001; Erlandsson and McQuaid 2004; Erlandsson et al. 2005a, b), the timing of spawning periods on the South and East Coasts (Lasiak 1986; van Erkom Schurink and Griffiths 1991a; Ndzipa 2002), the impacts of harvesting and reseeding on population size structure (Lasiak and Dye 1989; Lasiak 1991b; Dye 1992a; Lasiak 1993; Dye et al. 1997; Kyle et al. 1997a; Dye and Dyantyi 2002), the settlement and recruitment of plantigrades into algae (Beckley 1979; Lasiak and Barnard 1995; Erlandsson and McQuaid 2004; McQuaid and Lindsay 2005), the recruitment of juveniles into mussel bed and bare rock (Bayne 1976; Crawford and Bower 1983; Barnard 1995; Lasiak and Barnard 1995; Dye et al. 1997; Harris et al. 1998; McQuaid and Phillips 2000; Porri 2003; Erlandsson and McQuaid 2004; McQuaid and Lindsay 2005) the changing population dynamics due

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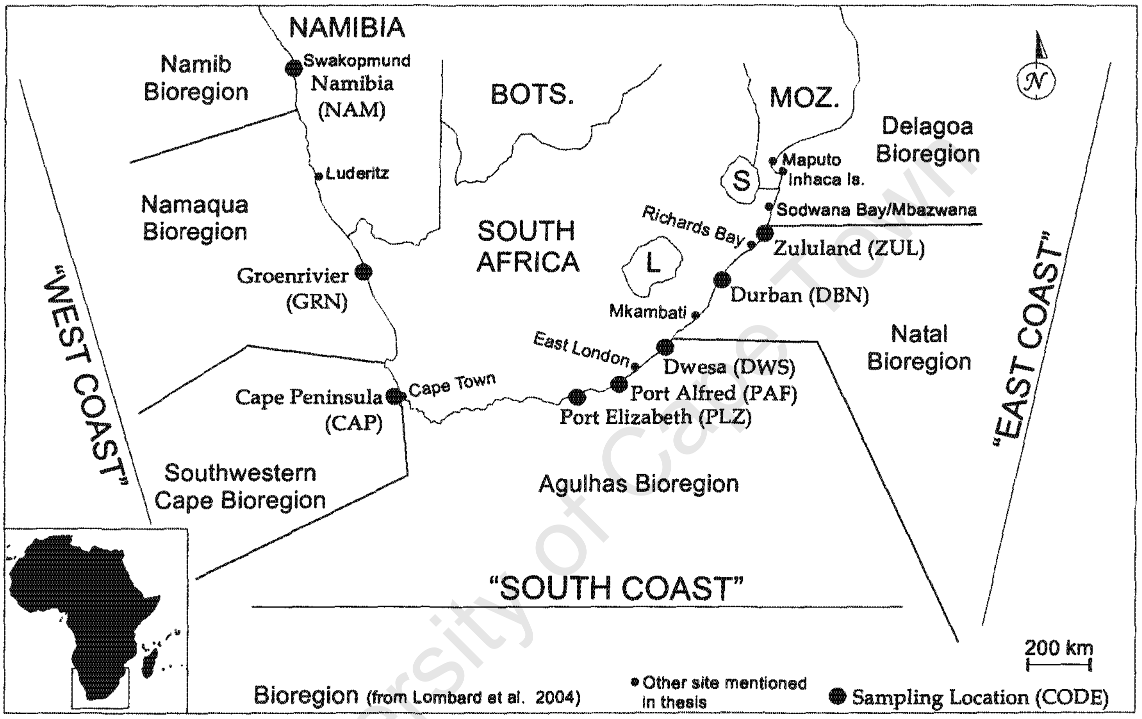

Figure 1.1 Map of sampling locations and bioregions of southern Africa, with names of other places mentioned in the thesis. BOTS. = Botswana, MOZ. = Mozambique, S = Swaziland, L = Lesotho.

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to its invasion by *M. galloprovincialis* on the South Coast (Bownes and McQuaid 2006), and its predicted dispersal distance (Table 1.1). Additional information on the species comes from its invasion into the Gulf of Mexico (Hicks and Tunnell 1993; Hicks and Tunnell 1995; Hicks et al. 2001).

Table 1.1 Details of dispersal-related larval ecology of the focal species of this chapter (*S. algosus* is unknown).

Species	Planktonic larval duration	Feed-ing?	Max disp. dist. y^{-1}	Average disp. dist. y^{-1}	Data from...	Reference(s)
Aulacomya ater	14-28 d	Yes	--	<10 km	Chile, South Africa (SA)	(Harris et al. 1998; Castilla and Guiñez 2000)
Mytilus galloprovincialis	30-32 d [a]	Yes	42 km east, 19 km west	5 km	South Coast, SA	(McQuaid and Phillips 2000; Grantham et al. 2003; Branch and Steffani 2004)
			115 km north, 25 km south	--	West Coast, SA	(Hockey and van Erkom Schurink 1992; Branch and Steffani 2004)
			56 km east, 46 km north;		Swakopmund, Namibia to Kidds Beach, SA	(Robinson 2005)
			--	< 10 km	South Africa	(Harris et al. 1998)
Perna perna	15-20 d	Yes	235 km south, 36 km north	--	Gulf of Mexico	(Hicks and Tunnell 1995)
			95 km		Gulf of Mexico	(Branch and Steffani 2004)
			--	< 10 km	South Africa	(Harris et al. 1998)

[a] based on estimate from *Mytilus edulis* (McQuaid and Phillips 2000)

In Namibia, beds of *P. perna* are now densely invaded by the small bisexual mussel *Semimytilus algosus*, of assumed Chilean origin (Branch et al. 1994; Tokeshi and Romero 1995), but little is known about its life history, recruitment patterns, or the timing of its invasion into Africa. This species can form a double layer in the intertidal, and extends subtidally to 15 m depth (B. Currie, pers. com.). It appears not to have spread south from Namibia into South Africa.

The native ribbed mussel, *Aulacomya ater*, is of intermediate size and lives in the intertidal and subtidally to 40 m depth, extending from East London westward and up into Namibia (Griffiths and King 1979; Branch et al. 1994). This mussel has a trans-Atlantic distribution, occurring in central Chile and Antarctica as well as South Africa (Castilla and Guiñez 2000). Its range in South Africa corresponds with another native mussel, *Choromytilus meridionalis*, and most southern African studies of their reproduction and adult physiology, including the timing of spawning and settlement periods, compare the two species (Griffiths 1977; Barkai and Branch 1989; van Erkom Schurink and Griffiths 1990, 1991a, 1991b; van Erkom Schurink and Griffiths 1993). *A. ater* is an important prey item of the rock lobster *Jasus lalandii* (Pollock 1979; Wickens and Field 1988) and the black oystercatcher *Haematopus moquini* (Hockey and Underhill 1983).

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In the last three decades, the west coast of southern Africa has been invaded by the alien Mediterranean mussel *Mytilus galloprovincialis* (de Moor and Bruton 1988; McQuaid and Phillips 2000; Steffani and Branch 2004; Robinson 2005), which now dominates rocky intertidal mussel beds on the West Coast (Robinson 2005). Its adult physiology has been examined in comparative studies with local mytilids (van Erkom Schurink and Griffiths 1991b, 1991a; van Erkom Schurink and Griffiths 1993). Although its spread northward into Namibia seems to have halted naturally (B. Currie, pers. com.), a secondary introduction has moved it into the range of *P. perna* on the south coast of South Africa (McQuaid and Phillips 2000; Robinson 2005; Bownes and McQuaid 2006) and dispersal distances have been estimated based on its invasion rate (Table 1.1). Dense in the intertidal, *M. galloprovincialis* rarely extends below the infratidal (Branch et al. 1994).

Localized recruitment studies on mussels have been limited to three of the six bioregions in southern Africa: Namaqua (Steffani and Branch 2004; Robinson 2005), Agulhas (Crawford and Bower 1983; Barnard 1995; Lasiak and Barnard 1995; Dye et al. 1997; McQuaid and Phillips 2000; Lawrie and McQuaid 2001; Erlandsson and McQuaid 2004; Bownes and McQuaid 2006; Porri et al. 2006) and Natal (Berry 1978; Lambert and Steinke 1986). At a larger scale, Harris et al. (1998) compared the recruitment of mussels at seven locations across five bioregions around the coast of southern Africa, from Swakopmund, Namibia to Zululand, South Africa. They found a gradient of recruitment intensity, with significantly higher densities on the West than on the South or East Coasts, and that maximum recruit intensities and simultaneous adult densities showed strong significant correlations. Additionally, they found high within- and among- site variability of recruitment events, concluding that dispersal processes influence recruitment patterns at a relatively small scale. Data collection then continued for a further four years, incorporating one more location, as well as one additional site at six of the original locations. This chapter includes the full five years of data in an inter-annual and inter-regional investigation into the recruitment of intertidal mussels around the coast of southern Africa, and addresses the following hypotheses:

1. There will be a regional-level gradient of recruitment intensity around the coast from high on the West Coast to low on the East Coast.
2. At the scale of 100s of km, a positive and significant correlation will exist between recruitment intensities and adult mussel biomass.
3. A combination of primary production and meso-scale oceanographic properties will explain relative recruitment intensity among locations.
4. During each species' period(s) of high recruitment, different species will have different ratios of recruits to adults, but these will be consistent within species among locations.
5. Low-recruitment locations will be recruit-limited, with relatively large recruitment events causing a significant increase in the density of juvenile mussels in the following season, whereas high-recruitment locations will not be recruit-limited.
6. Recruitment patterns will differ among sites within locations due to local conditions.

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7. Recruitment will show seasonal patterns at each location and for each species, but these will be strongest on the East Coast, as it has the highest seasonal temperature fluctuation. Significant differences among seasons and years will relate to seasonal or inter-annual temperature fluctuations.

In addition to testing the above hypotheses about larval recruitment patterns and processes, this study is relevant to the management of exploited mussel stocks and the design of marine protected areas, as recruitment dynamics and the scale of connectivity between mussel populations will influence the effects of harvesting and the speed with which depleted mussel beds are replenished.

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1.2 METHODS

Data collection

Mussel recruitment and adult mussel abundance were investigated at eight locations (100-950 km apart) around the coast of southern Africa (Figure 1.1), using a hierarchical design (Underwood 2000), following the methods outlined in Harris et al. (1998). Four unharvested sites were selected at each location (except three at Dwesa, due to a scarcity of suitable habitat), spaced 1-25 km apart (Table 1.2).

At each site, a permanent 20-m transect was installed in the middle of the intertidal mussel bed parallel to the shoreline. At 4-m intervals, this transect was intersected by six perpendicular transects, each spanning the width of the mussel bed. Every three months, the area of the mussel bed and the percent cover of mussels of standardized size classes (Table 1.3) were scored in 50 × 50 cm quadrats at 1-m intervals along the perpendicular transects. The mussel bed was defined as areas where mussel cover exceeded 5%. Sites were not visited on the same day, but usually within the same tide series. Mussel bed cover was measured pooling species wherever multiple species were present (i.e. at all west coast locations). However, each of these three locations had a dominant adult species present: *M. galloprovincialis* at Groenrivier and the Cape Peninsula and *P. perna* (primary cover) and *S. algosus* (secondary cover) at Namibia.

Recruitment was measured in dense mussel clumps (100% cover) by removing three replicate 10 × 10 cm^2 samples at each site from randomly selected positions (1-20 m apart) within 1 m of the horizontal transect. The samples were sorted and all mussels were measured, counted and identified to species level. Mussels form a monolayer at most of the locations in this study, except Namibia and Zululand. At Namibia, *S. algosus* often formed a secondary layer over both conspecifics and other species. In Zululand, *P. perna* sometimes formed a secondary layer. Beds at these two sites were therefore more structurally complex. Recruits were defined as late plantigrades or early juveniles 0.5-5.0 mm shell length. To compare among regions and seasons, samples for each season were collected within 2-month periods, i.e. winter (Jun/Jul), spring (Sep/Oct), summer (Dec/Jan) and autumn (Mar/Apr).

Spawning periods were determined for most of the locations from published literature. In Namibia, no previous data were available on spawning periods for any of the mussel species. Instead, adults of *P. perna* were collected and assessed as being 'ripe' (visibly mature gonads) or 'unripe' (not visibly mature) in each month from January 1994 to September 2000. The percentage of the collected individuals that were ripe was calculated as a ripeness index, and plotted against time (B. Currie, unpubl. data). Months that showed a mean reduction greater than 4% from the previous month were defined as spawning periods.

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Table 1.2 Characteristics of rock ledges and sampling periods at each location. Additional criteria used to ensure consistency in site selection are described in Harris et al. (1998).

Location	Site	Mussel spp.[a]	Longitude (E)	Latitude (S)	Dist to next loc.	Nearshore oceanog. climate	Sampling Period	
							Start	End
Namibia (NAM)	Badewanne	S,M,P	14° 31' 31.2"	22° 42' 02.0"	951 km	Persistent year-round upwelling cell[c]	Jun 95	Dec 99
	Langstrand North		14° 32' 58.9"	22° 48' 70.6"				
	Langstrand South		14° 32' 58.9"	22° 48' 70.6"				
	Mile Four		14° 31' 28.2"	22° 37' 36.1"				
Groen-rivier (GRN)	Esterhuizen	M,A	17° 37' 51.48"	30° 56' 32.94"	375	Seasonal upwelling downstream site[d]	Jul 95	Sep 99
	Gert Joseph		17° 31' 48.47"	30° 45' 11.77"				
	Island Point		17° 36' 12.08"	30° 54' 54.95"				
	Island Wreck		17° 36' 09.60"	30° 55' 00.66"				
Cape Pen-insula (CAP)	Blouberg	M,A	18° 25' 25.15"	34° 19' 39.73"	795	Active seasonal upwelling cell[d]	Jul 95	Oct 99
	Kommetjie		18° 19' 13.22"	34° 08' 27.12"				
	Scarborough North		18° 22' 11.89"	34° 12' 26.99"				
	Scarborough South		18° 22' 26.50"	34° 13' 08.89"				
Pt Eli-zabeth (PLZ)	Hougham North	P	25° 45' 54.01"	33° 45' 26.02"	101	Within Algoa Bay, proximate to divergent upwelling[ef]	Oct 96	Oct 99
	Houghham South		25° 45' 05.90"	33° 45' 53.51"				
	Humewood		25° 40' 53.09"	33° 59' 40.17"				
	Summerstrand		25° 41' 23.32"	34° 00' 23.35"				
Pt Alfred (PAF)	Kenton East	P	26° 41' 56.68"	33° 40' 47.32"	278	Divergent topographical upwelling[e]	Jul 95	Jul 99
	Kenton West		26° 41' 12.53"	33° 40' 58.68"				
	Kowie		26° 52' 41.39"	33° 31' 29.17"				
	Old Woman's River		27° 06' 51.09"	33° 37' 14.42"				
Dwesa (DWS)	Dwesa North	P	28° 52' 06.86"	32° 17' 23.07"	371	Straight coast, narrow shelf, no upwelling[g]	Jun 95	Mar 00
	Dwesa South 1		28° 49' 30.27"	32° 18' 58.34"				
	Dwesa South 2		28° 49' 01.80"	32° 19' 31.19"				
Durban (DBN)	Mdloti South	P	31° 07' 47.6"	29° 38' 52.8"	183	Center of Natal Bight trapped clockwise gyre[h]	Jun 95	Jul 00
	Newsell North		31° 07' 12.0"	29° 40' 12.0"				
	Newsell South		31° 07' 12.0"	29° 40' 12.0"				
	Peace Cottage South		31° 05' 48.0"	29° 42' 30.0"				
Zululand (ZUL)	Crayfish	P	32° 25' 36.7"	28° 25' 11.5"	--	Divergent topographical upwelling[h]	Mar 95	Sep 99
	Railway[b]		32° 24' 59.0"	28° 28' 06.9"			Aug 94	Sep 99
	Sandy		32° 24' 25.2"	28° 30' 20.0"			Feb 95	Feb 00
	Zavini		32° 25' 10.2"	28° 26' 54.4"			Jun 95	Sep 99

[a] Dominant mussel species present: M (*Mytilus galloprovincialis*), S (*Semimytilus algosus*), P (*Perna perna*), A (*Aulacomya ater*),
[b] Sampled monthly, [c] (Shillington et al. 1990; Demarq et al. 2003), [d] (Shannon 1985), [e] (Lutjeharms et al. 2000a), [f](Lutjeharms et al. 2000b), [g] (Roberts 2005), [h] (McLachlan et al. 1981)

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Table 1.3 Size classes for each sampling method and species sampled.

Method	Data	Species	Max length (mm)	Recruit length	Sub-adult length	Adult length (mm)	
						Small	Large
50 × 50 cm² quadrat	% cover	All species pooled		2-10 mm	10-35 mm	35-70	>70
10 × 10 cm² quadrat	counts	*A. ater*	70[a]	0.5-5	5-10	10-15	>15
		S. algosus	50[b]	0.5-5	5-10	10-15	>15
		M. galloprovincialis	85[a]	0.5-5	5-35	35-70	>70
		P. perna	90[a]	0.5-5	5-35	35-70	>70

[a](van Erkom Schurink and Griffiths 1990), [b](Branch et al. 1994)

The relative recruitment rates of *P. perna* into mussel bed and algal turf was investigated simultaneously at the four eastern locations. Algal turf was sampled three-monthly by removing three replicate 10 × 10 cm^2 sections from randomly-selected patches of 100% algal cover in the central mussel bed. All *P. perna* were removed from the algae and counted into size classes.

Nylon-bristle brushes were used as a standardized recruitment substrate at two sites ($n = 3$ per site) at five locations (Namibia, Groenrivier, Cape Peninsula, Pt. Alfred and Dwesa). These were installed three-monthly on the day that mussel data were collected, left out for one month, and then collected. At Railway, Zululand, nine brushes were installed monthly in three groups (North, Mid, South) from August 1994 to December 1998. After collection, brushes were cleaned and all mussels counted into size classes.

Statistical Analyses

All statistics were computed using Statistica 7.0 (StatSoft, Inc. © 1984-2004).

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Large-scale (among-location) spatial and annual variability of recruitment into mussel beds

The relative contributions of location, site and year to the annual variability of recruitment peaks for all species combined around the coast of southern Africa were tested using a partly-nested mixed-model analysis of variance (ANOVA) (Quinn and Keough 2002). Location (L) and Year (Y) were designated as a fixed factors, while Site nested within Location [S(L)] was a random factor. Whether time is calculated as a fixed or random factor depends largely on the *a priori* hypotheses. When the Year factor is intended to represent all possible years in which the experiment could have been run, then it is appropriate to regard it as a random factor. However, in the case of my observations, the years were intended to represent particular years, so that in the event of a significant Year-effect, differences detected among years could be linked to anomalous events in those years in a process-oriented interpretation of post-hoc tests (Quinn and Keough 2002; R. Clarke, pers. com.). Thus, all ANOVAs in this chapter use Year as a fixed effect. Location was also fixed, as locations were selected within different bioregions to span a range of oceanographic conditions. Sites were designated as random, selected to represent all possible sites within that location. The interaction Y*L was therefore fixed and Y*S(L) was random. Null hypotheses were associated with each factor (Table 1.4a), and were tested using a general linear model, and accepted or rejected at $p < 0.05$ (Table 1.4b). The mathematical model was:

$$X_{ijkl} = \mu + Y_i + L_j + S(L)_{k(j)} + L{*}Y_{ij} + Y{*}S(L)_{ik(j)} + \varepsilon_{ijkl}$$

where i refers to the year, j to the location, k to the site within each location and l to replicate, X is the observed magnitude of the response variable (number of recruits per 0.01m^2), μ is the overall mean of the response variable, and ε is the unexplained variance, or residual (Quinn and Keough 2002).

Table 1.4 (a) Null hypotheses and (b) calculations for the general linear models used for ANOVAs for the whole-coast comparison of annual recruitment peaks.

(a) Factor	H_0:
Location	No difference between locations in the mean number of recruits per quadrat, pooling years
Site(Location)	No added variance in the mean number of recruits per quadrat due to the effects of differences between all possible sites within each location
Year	No difference between years in the mean number of recruits per quadrat, pooling locations
Loc*Year	No interaction between years and locations on the mean number of recruits per quadrat, i.e. the effect of the location on the mean number of recruits per quadrat was the same in all the years
Year*Site(Loc)	No interaction between all possible sites within all locations and all years on the mean number of recruits per quadrat, i.e. the effect of all possible sites within the locations on the mean number of recruits per quadrat was the same in all years

(b) Factor		Effect	*df*[1]	*F*-value[2]
Intercept				$MS_{B(A)}$
Location	A	Fixed	p-1	$MS_A/MS_{B(A)}$
Site(Location)	B(A)	Random	p(q-1)	$MS_{B(A)}/MS_{B(A)C}$
Year	C	Fixed	r-1	$MS_C/MS_{B(A)C}$
Loc*Year	A × C	Fixed	(p-1)(r-1)	$MS_{AC}/MS_{B(A)C}$
Year*Site(Loc)	B(A) × C	Random	p(q-1)(r-1)	$MS_{B(A)C}/MS_{Resid.}$
Residual			pqr(n-1)	

[1] p = number of locations, q = number of sites, and r = number of years in each analysis

[2] For this mixed model, Statistica 7.0 calculated 99-100% of a synthesized MS-denominator for the *F*-value according to the above formulae, while the final 0-1% was due to the MS_{Resid} term, following Satterthwaite (1946).

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I balanced this model by adding a few virtual replicates to the data set. Although virtual replicates may increase the risk of type I error, they do reduce type II error and the risk of type I error can be compensated by increased degrees of freedom in the model (Underwood 1997). In general, data were well-balanced and few individual replicates were missing from any cell in any model. Because a balanced ANOVA is robust to slight variations in sample size (Quinn and Keough 2002), virtual replicates were not added if > 50% of the replicates were present in any individual cell. However, some cells lacked data at almost all of the locations, and in these cases cells were filled with virtual replicates, following Underwood (1997) and according to the following criteria:

1. When two sites close to each other followed the same trends (means or relative means and variances) in other years, virtual replicates were added to mimic the matching site in the missing season, not to exceed 15% of the overall data in the model.
2. When the site had no similar sites within the location, virtual replicates were added to mimic trends in other years at that same site.
3. Data were added such that their variance matched other cells with similar means.

Data fourth-root transformed to meet the assumptions of normality (examined graphically with a normal probability plot) and equal variances (examined graphically with a box-plot and statistically with Cochran's test, $\alpha = 0.05$), following Quinn and Keough (2002).

The interpretation of main effects for these models can be difficult, especially when the interaction effects are significant (Underwood 1997). However, when the Mean Squares denominator-value in the ratio used to calculate the F-statistic for the main effect incorporates the variability of the significant interaction, the main effects can be calculated with cautious confidence (Quinn and Keough 2002). Using the model prescribed by Statistica 7.0, the denominators for the main effects all incorporated $MS_{Interaction}$ values, and so I proceeded with post-hoc analyses of the main effects even when one or both interaction terms were significant.

For the unplanned post-hoc comparisons of significant between-plot main effects (L and S(L)), I used Tukey's HSD test (Quinn and Keough 2002). For within-plots comparisons (Y, L*Y and S(L)*Y), Quinn and Keough (2002) recommend a Bonferroni-type adjustment of significance levels for multiple testing and I therefore used a Bonferroni test.

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Large-scale (among-location) spatial and annual variability of recruitment into brushes

The deployment and collection of brushes at most locations was sporadic, and at some locations, brushes were not collected in all four seasons of each year. Recruitment into brushes and mussel bed could not be directly compared among locations as the collection of these treatments was not simultaneous at any site but Zululand. However, there were sufficient data collected in three of the years during recruitment seasons for a comparison of relative recruitment rates among locations. From each site, the deployment in each year with the highest recruitment was selected for analysis, and the number of mussel recruits (< 2 mm total length) per day for all species combined was used for a comparison among locations and years, with all brushes at all sites at each location being used as replicates.

The relative importance of location and year to the recruitment variability of mussels into brushes was tested using a partly-nested mixed-model ANOVA (Quinn and Keough 2002). In this model, Location (L) and Year (Y) were designated as fixed factors; the interaction Y*L was therefore fixed. Site was not considered in this model because of the sparse nature of these data. Null hypotheses associated with each factor were tested as above. The mathematical model used was:

$$X_{ijk} = \mu + Y_i + L_j + L{*}Y_{ij} + \varepsilon_{ijk}$$

where *i* refers to the year, *j* to the location and *k* to replicate. *X* is the observed magnitude of the response variable (recruits.day^{-1}), μ and ε were as above. Data were fourth-root transformed to meet the assumptions of normality (examined graphically with a normal probability plot) and equal variances (examined graphically with a box-plot and statistically with Cochran's test, $\alpha = 0.05$). Because both factors were fixed, Statistica did not use a Satterthwaite correction and instead followed a standard model, whereby the denominators of all three MS terms are the $MS_{Residual}$ value (Quinn and Keough 2002).

Productivity and nearshore circulation features per location versus recruitment

Both productivity and nearshore circulation patterns vary dramatically around the coast of southern Africa, and descriptions from literature were used to rank the eight locations in the study for each of these variables (Table 1.5). The productivity of the nearshore environment for each site was estimated using *in situ* or remotely-sensed chlorophyll climatologies (Demarq et al. 2003), nearshore nutrient samples and epilithic microalgal production measurements in the intertidal (Bustamante et al. 1995a) and *in situ* ship-based measurements (Meyer et al. 2002). The nearshore circulation was described according to three measurable features:

1. Relative persistence of upwelling (wind- or topographically-induced)
2. Continental shelf width
3. Relative degree of embayment

Locations were ranked for each of these three criteria, with the highest values given to the least persistent and active nearshore upwelling features (Demarq et al. 2003; Roberts 2005), the widest shelf (measured at 200 m depth) and the most embayment-like topography surrounding the selected sites. Although there are other oceanographic features that could potentially affect larval retention among sites and locations, such as relative exposure, wind speed or dominant swell direction or height, these data were not consistently available for all sites and locations and therefore were not included in the comparison. The results of this analyses must therefore be interpreted with some caution. These ranks were then summed to give an overall score (Table 1.5). Rankings were plotted against the significant ranks of mean annual recruitment rates for the locations examined with the mussel-bed ANOVA above, and their relationship examined using Pearson product-moment correlation.

Large-scale stock-recruit relationships

The relationship between recruitment rates and several parameters of the adult mussel bed per location (width, percent cover, and mean mussel stock size measured as the number of mussels per 1-m swath of mussel bed) was examined by combining species and sites. Maximum recruitment season and the parameters of the mussel bed measured simultaneously in each location and year were examined using Pearson product-moment correlation analysis.

Size-structure of the mussel bed during recruitment events

The size structure of each species in the mussel bed during recruitment events was investigated by graphing a size-frequency plot during the peak recruitment event for each species at

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each location in the 5-year sampling period. The ratio of adults to recruits in 0.01m^2 quadrats was examined graphically and using Pearson product-moment correlation.

Table 1.5 Ranking of the locations with respect to productivity and neasrshore circulation

Location	Upwelling type	Upwelling ranks [a]	Shelf width [b]	Degree of embayment [c]	Sum	Rank of sums	Productivity ranks [d]	Total
NAM	Persistent	1	8	8	17	7	8	15
GRN	Pulsed	5	7	4	16	5	7	12
CAP	Pulsed	5	4	6	15	4	7	11
PLZ	Persistent	3	6	8	17	7	5	12
PAF	Divergent, persistent	3	5	3	11	1	4	5
DWS	Occasional	8	2	1	11	1	3	4
DBN	Occasional	8	4	6	18	8	1	7
ZUL	Divergent, occasional	8	1	3	12	3	3	6

Refs: (Shannon 1985; Bustamante et al. 1995a; Meyer et al. 2002; Demarq et al. 2003; Roberts 2005); [a] 1 is the most persistently upwelled, 8 is the least, [b] 1 is the narrowest shelf, 8 is the widest, [c] 1 is the least embayed, 8 is the most, [d] 1 is the least productive, 8 is the most.

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Smaller-scale stock-recruit relationships

Three specific hypotheses relating to the stock-recruit relationship were tested at smaller scales. (1) Recruitment is higher into denser patches of mussel bed. (2) Recruitment is higher into mussel beds with larger biomass at the scale of the mussel bed (a measure that combines bed width and bed density). (3) Recruitment events will have a measurable positive effect on the density of the mussel bed in the following season. The first two concern the arrival and subsequent recruitment of mussels into existing mussel bed, and the third relates to the effect that a recruitment event will have on the density of juvenile mussels in the following season, exploring the role of recruitment limitation at the various locations. These hypotheses were tested for each location as follows:

(1) The ratio of recruits ($\leq$ 5 mm) to adults (> 5 mm) and the size-structure of the mussel bed during recruitment events for each species was compared graphically and using Pearson product-moment correlation. Recruitment events were defined per location: $\geq$ 3 individuals per 0.01m^2 (DBN, DWS), $\geq$ 5 individuals (PAF, PLZ, ZUL), $\geq$ 10 individuals (CAP, NAM, GRN). Each 0.01m^2 quadrat with at least the minimum number of recruits was taken as an individual replicate for the correlation analyses.

(2) Using Pearson product-moment correlation analysis, I explored the relationship between recruitment rates and the density and cover of available spawner stock at the time of recruitment (0 lag) and 3 months prior to recruitment (-3 month lag). Calculations were restricted to the following species, which were pooled: *P. perna, A. ater* and *M. galloprovincialis*. Recruitment events were

defined as above. N_{ts} is the number of adults in a 1-m strip of the mussel bed perpendicular to shore at t and s, and was calculated with the following formula:

$$N_{ts} = A_{ts} * 100 * C_{ts} * W_{ts}$$

A_{ts} is the mean number of individuals > 5 mm counted in the three 0.01m^2 quadrat squares of mussel bed taken simultaneously to the large quadrat sampling (at time t and site s), multiplied by 100 to extrapolate to 1 m^2. C_{ts}, is the mean percentage cover of adults at each sampling time (t) and site (s), determined from the large quadrat sampling. A_{ts} was then multiplied by C_{ts}, expressed as a decimal, to give an approximate number of individuals in the mussel bed at the given cover. This figure was then multiplied by W_{ts}, the mean width of the mussel bed (in m) measured in the 6 perpendicular transects, to give the overall stock size in an average perpendicular strip of mussel bed of 1-m width.

(3) The effect of large recruitment events on the mussel bed was examined using Pearson product-moment correlation. Recruitment events here were defined for each location as > 20% of the maximum number of recruits (< 5 mm) recorded in a 0.01m^2 patch over the sample period. Recruitment limitation was assessed by examining the change in juvenile mussel (5-10 mm) cover three months after a recruitment event. Following Caley et al. (1996), a location was defined as recruitment-limited if the density of the juvenile population increased (the relationship was positive and significant) following the recruitment event. A location was defined as recruitment-regulated if the measured recruitment event was not significantly related to the change in density of juveniles. A location was defined as neither recruitment regulated nor limited if the population decreased (the relationship was negative and significant) following recruitment events, implying that other factors superseded recruitment in their control of the abundance of juvenile mussels.

Within-location variability in recruitment intensity – spatial and temporal trends

The relative importance of site, year and season to the recruitment variability of each mussel species at each location was tested using a full-factorial mixed-model ANOVA (Quinn and Keough 2002). In my model, Year (Y) and Season (Sn) were designated as fixed factors, while Site (St) was random, representing all possible sites at each location. The interactions Y*St, Sn*St and Y*Sn*St were thus random, while Y*Sn was fixed (Table 1.6). The mathematical model used to explain the variance from the recruitment mean of each species at each location with respect to the effects of Season, Year and Site was:

$$X_{ijkl} = \mu + Y_i + Sn_j + St_k + Y{*}Sn_{ij} + Y{*}St_{ik} + Sn{*}St_{jk} + Y{*}Sn{*}St_{ijk} + \varepsilon_{ijkl}$$

where i refers to the year, j to the season, k to the site and l to replicate, X is the observed magnitude of the response variable (number of recruits per 0.01m^2) and μ and ε were as above.

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Table 1.6 Calculations for ANOVAs within locations and species.

Factor		Effect	*df*	*F*-value
Site	A	Random	p-1	$MS_A/MS_{AB}+MS_{AC}-MS_{ABC}$
Season	B	Fixed	q-1	MS_B/ MS_{AB}
Year	C	Fixed	r-1	MS_C/ MS_{AC}
Site*Season	A × B	Random	(p-1)*(q-1)	MS_{AB}/ MS_{ABC}
Site*Year	A × C	Random	(p-1)*(r-1)	MS_{AC}/ MS_{ABC}
Season*Year	B × C	Fixed	(q-1)*(r-1)	MS_{BC}/ MS_{ABC}
Site*Season*Year	A × B × C	Random	(p1)* (q-1)*(r-1)	MS_{ABC}/ MS_{Resid}
Residual			pqr(n-1)	

* For this mixed model, Statistica 7.0 calculated 99-100% of a synthesized MS-denominator for the *F*-value according to the above formulae, while the final 0-1% was due to the MS_{Resid} term, following Satterthwaite (1946).

Data were fourth-root transformed. When a relevant interaction not in the MS-denominator of a significant main effect was not significant or relatively unimportant compared to the main effect, Tukey's HSD test was used for unplanned comparisons of the main effect. If linear transformations failed to sufficiently reduce the heterogeneity of variances, I examined any significant results with post-hoc comparisons and graphic representations of the data to control for the increased chances of type I error following Quinn and Keough (2002).

Among-species temporal variability in recruitment intensity

At the three locations with more than one species present (Namibia, Groenrivier and Cape Peninsula), simultaneous recruitment rates were compared between species at each location using Pearson product-moment correlation.

Recruitment into turf algae, brushes and mussel beds

Pearson product-moment linear correlation and lagged-correlation analyses were used to explore relationships between the recruitment of mussels into mussel beds and turf algae for the four eastern locations, and between the recruitment of mussels into brushes and into mussel beds at Zululand.

1.3 RESULTS

Large-scale (among-location) spatial and annual variability of recruitment into mussel beds

When comparing peak annual recruitment events into mussel beds, Location (L) and Site nested within Location (S[L]) had significant effects while Year (Y) did not (Table 1.7). As the MS-denominator of the location effect incorporated the variability of the significant L*Y interaction, I used an unplanned Tukey HSD post-hoc test to examine this effect ($\alpha = 0.05$). This revealed that each of the west-coast locations was significantly different from all the others (Figure

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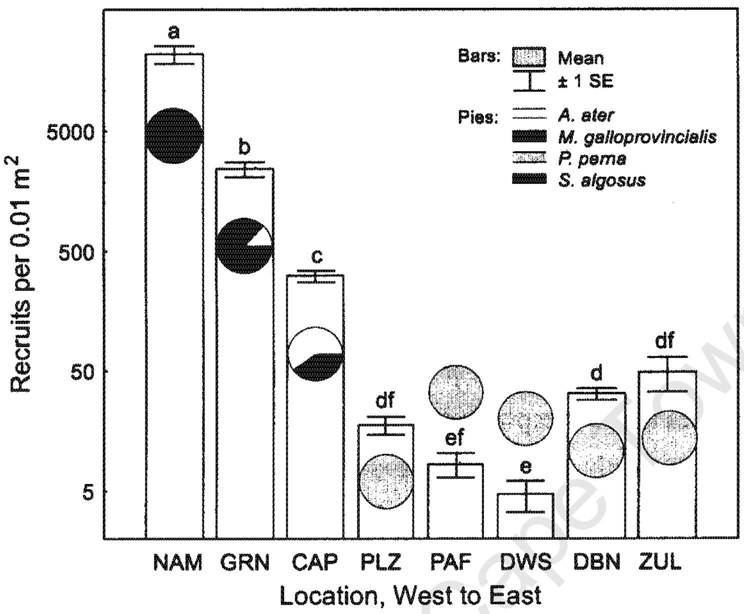
(a) Recruitment into mussel bed, 1995-1999



(b) Recruitment into brushes, 1996-1998

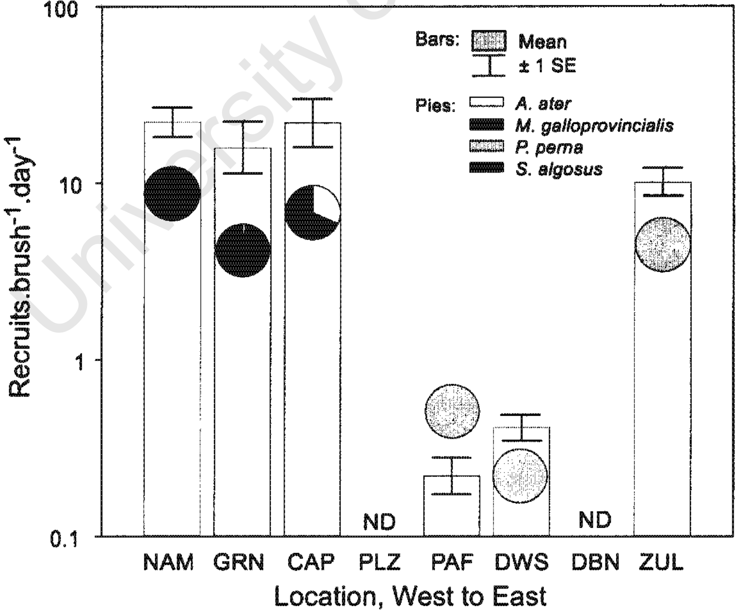


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Figure 1.2 (a) Mean (+SE) number of recruits per 0.01m^2 of mussel bed during peak recruitment events at each location over all 5 years. Letters are significant groups ($p < 0.05$, Tukey HSD post-hoc). (b) Mean (+SE) number of recruits.brush^{-1}.day^{-1} at 6 locations over 3 years. There were no testable significant groupings, as the interaction term was significant for this analysis. For both (a) and (b), pies show the proportion of recruits of each species. *P. perna* was present in Namibia, but too rare to be visible in the pies. Note that data are expressed on a logarithmic scale.

1.2a). Pooling years and sites, Namibia had the highest recruitment, followed by Groenrivier and then the Cape Peninsula. None of the south and east coast sites were completely independent of the others, but all were significantly lower than the west coast sites, and Dwesa and Port Alfred had the lowest inter-annual recruitment rates overall. The presence of *S. algosus*, a small invasive mussel that recruits in remarkably high numbers accounted largely (> 90%) for the high recruitment rates at Namibia. The recruitment rates of the other two species there, *P. perna* and *M. galloprovincialis*, resembled those of *A. ater* and *M. galloprovincialis* at the Cape Peninsula.

Table 1.7 Around-the-coast ANOVA of annual recruitment peaks into mussel beds; L = location, S = site replicate within location, Y = year (1995-1999); *p < 0.05, **p < 0.01, ***p < 0.001, ns = not significant.

Factor	*df*	MS	*F*	p
L	7	558.90	22.41	***
S(L)	24	24.96	8.15	***
Y	4	7.25	2.37	ns
L*Y	28	17.60	5.74	***
S(L)*Y	96	3.07	1.45	*
Error	317	2.12		

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Large-scale (among-location) spatial and annual variability of recruitment into brushes

For the comparison of peak recruitment events into brushes, all terms were significant in the model (Table 1.8). Due to the presence of an important interaction term, and because the denominator of neither main effect incorporated the variability of the interaction term, post-hoc analyses could not be pursued. For comparison with the mussel bed data, untransformed recruitment data were plotted, pooling years (Figure 1.2b). Recruitment into brushes among the three west-coast locations (Namibia, Groenrivier and Cape Peninsula) did not appear to be significantly different. In contrast, there to appeared to be differences among the south and east coast locations, with lower recruitment levels at Pt Alfred and Dwesa than at Zululand. This resembled the differences for recruitment into mussel bed among south and east coast locations. The interaction between location and year was examined graphically (Figure 1.3), revealing that most locations had reduced recruitment in 1997; Zululand and Namibia were the exceptions.

Table 1.8 Around-the-coast ANOVA of annual recruitment peaks into brushes; L = location, Y = year (1996-1998); ***p < 0.001.

Factor	*df*	MS	*F*	p
L	5	5.20	22.54	***
Y	2	3.23	14.02	***
L*Y	10	6.09	26.41	***
Error	142	0.23		

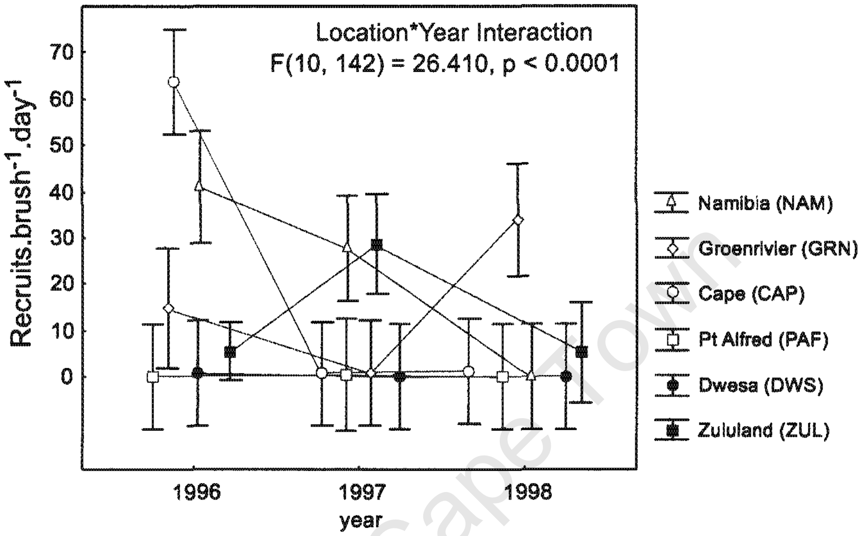

Figure 1.3 Significant interaction term of the Location*Year ANOVA for recruitment into brushes. Data were transformed for analysis but are presented here untransformed. Vertical bars denote 95% confidence intervals.

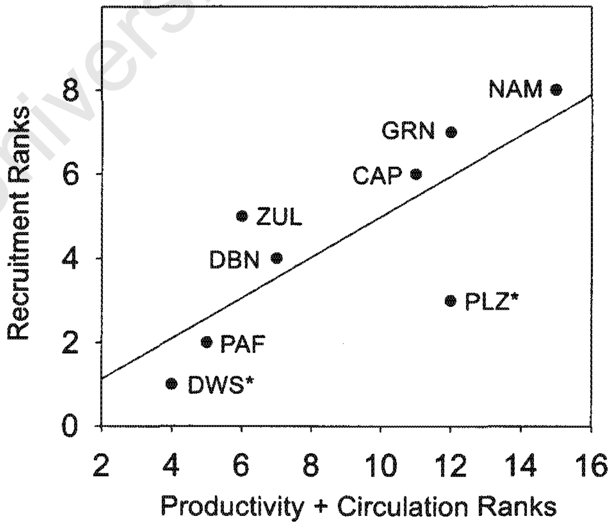

Figure 1.4 Ranking of recruitment plotted against the productivity plus circulation ranks for each of the locations. The trend is indicated by the least-squares fitted value ($r = 0.787$, $p < 0.05$). *denotes recruitment-limited location, as determined in this study (Figure 1.7).

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Productivity and nearshore circulation features per location versus recruitment

The relationship between recruitment, productivity and nearshore circulation features was plotted and evaluated using Pearson product-moment correlation analysis (Figure 1.4). The relationships between recruitment and productivity alone, or between recruitment and circulation alone, were not significant. There was, however, a significant linear relationship between recruitment and the summed value for circulation and productivity ($r = 0.787$, $n = 8$, $p < 0.05$).

Large-scale stock-recruit relationships

When all the species and all the locations were examined together at the scale of the entire coast to explore bioregional patterns, there were strong and significant relationships between recruitment rates and the following simultaneous variables: mean mussel bed width per site ($r = 0.585$, $n = 125$, $p < 0.001$), mean percent cover of adult mussels in the mussel bed ($r = 0.648$, $n = 125$, $p < 0.001$), and number of adult mussels in a 1-m swath perpendicular to the shoreline ($r = 0.677$, $n = 125$, $p < 0.001$). These relationships were much less strong when *S. algosus* was removed from the calculations: mussel bed width (not significant), percent cover adults ($r = 0.427$, $n = 99$, $p < 0.001$), and number of adults per 1-m swath ($r = 0.445$, $n = 99$, $p < 0.001$).

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Size-structure of the mussel bed during recruitment events

Size-structure at the time of the maximum recorded recruitment event was plotted for each species at each location to examine the ratio of adults to recruits, and yielded a unimodal or bimodal distribution (Figure 1.5). Three species-specific features emerged. First, over most of its range, recruits of *P. perna* never achieved high densities. Additionally, the maximum density of juvenile and adult *P. perna* was below the size at maturity at most locations, indicating that the post-recruit stocks in most areas were predominantly young. Second, recruits of both *S. algosus* and *A. ater* tended to achieve extremely high densities, but their adults were rare. Third, although adults of *M. galloprovincialis* were abundant wherever it occurred, its recruits were denser than adults in ratios that were intermediate between *S. algosus* and *P. perna.*

Smaller-scale stock-recruit relationships

Three hypotheses were tested that related spawner stock to recruitment densities at scales within locations. The first was that recruitment of mussels will be higher in denser patches of mussel bed. Examining the simultaneous ratio of adult density to recruit density among locations and species with correlation and linear regression analyses, I found that this relationship varied not only among species but also among locations (Figure 1.6a-d). In six of the twelve cases, there was no significant relationship between adults and recruits. There were three significant correlations for *P. perna* (Port Elizabeth, Durban and Namibia), two weak but significant correlations for *M.*

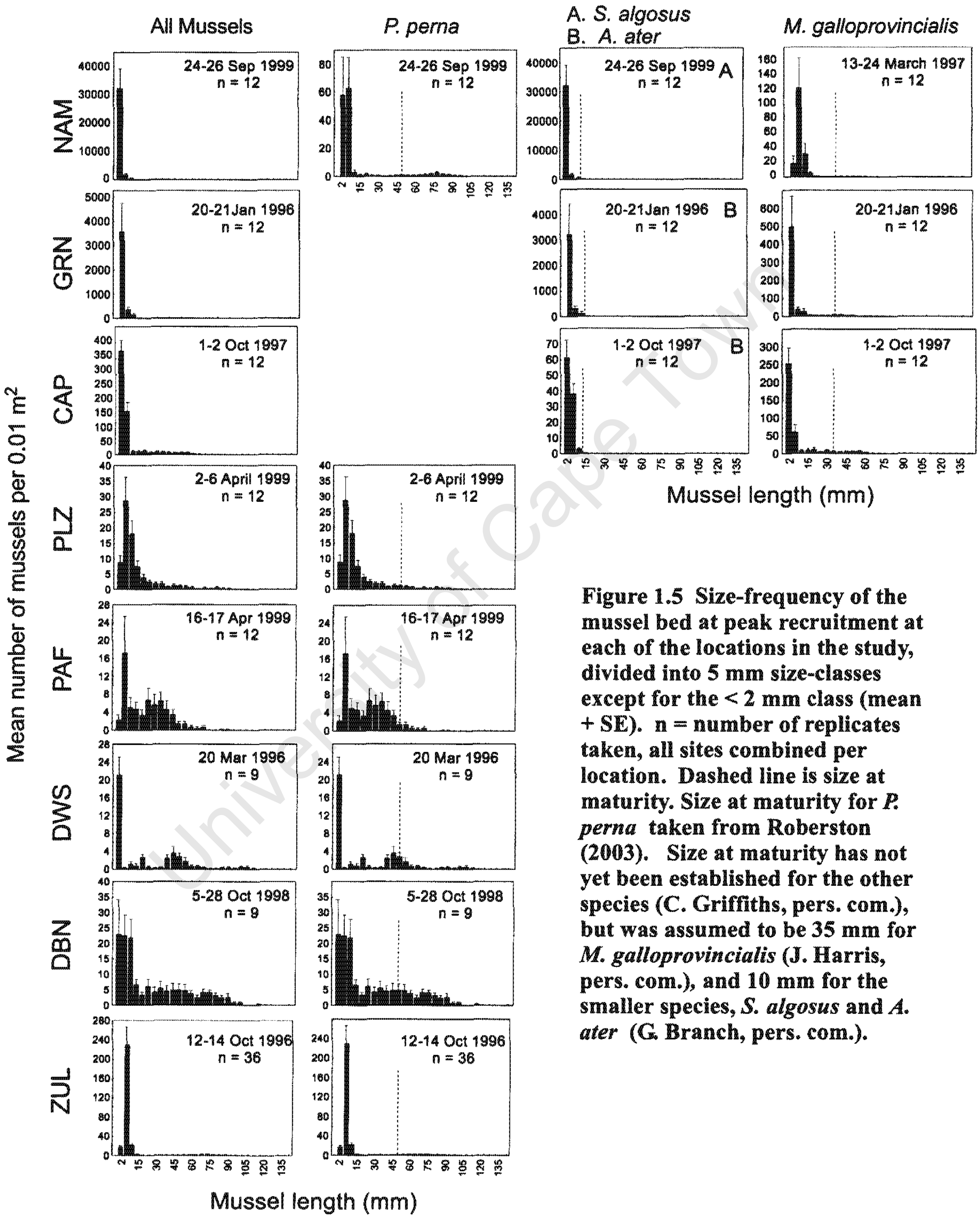

Figure 1.5 Size-frequency of the mussel bed at peak recruitment at each of the locations in the study, divided into 5 mm size-classes except for the < 2 mm class (mean + SE). n = number of replicates taken, all sites combined per location. Dashed line is size at maturity. Size at maturity for *P. perna* taken from Roberston (2003). Size at maturity has not yet been established for the other species (C. Griffiths, pers. com.), but was assumed to be 35 mm for *M. galloprovincialis* (J. Harris, pers. com.), and 10 mm for the smaller species, *S. algosus* and *A. ater* (G. Branch, pers. com.).

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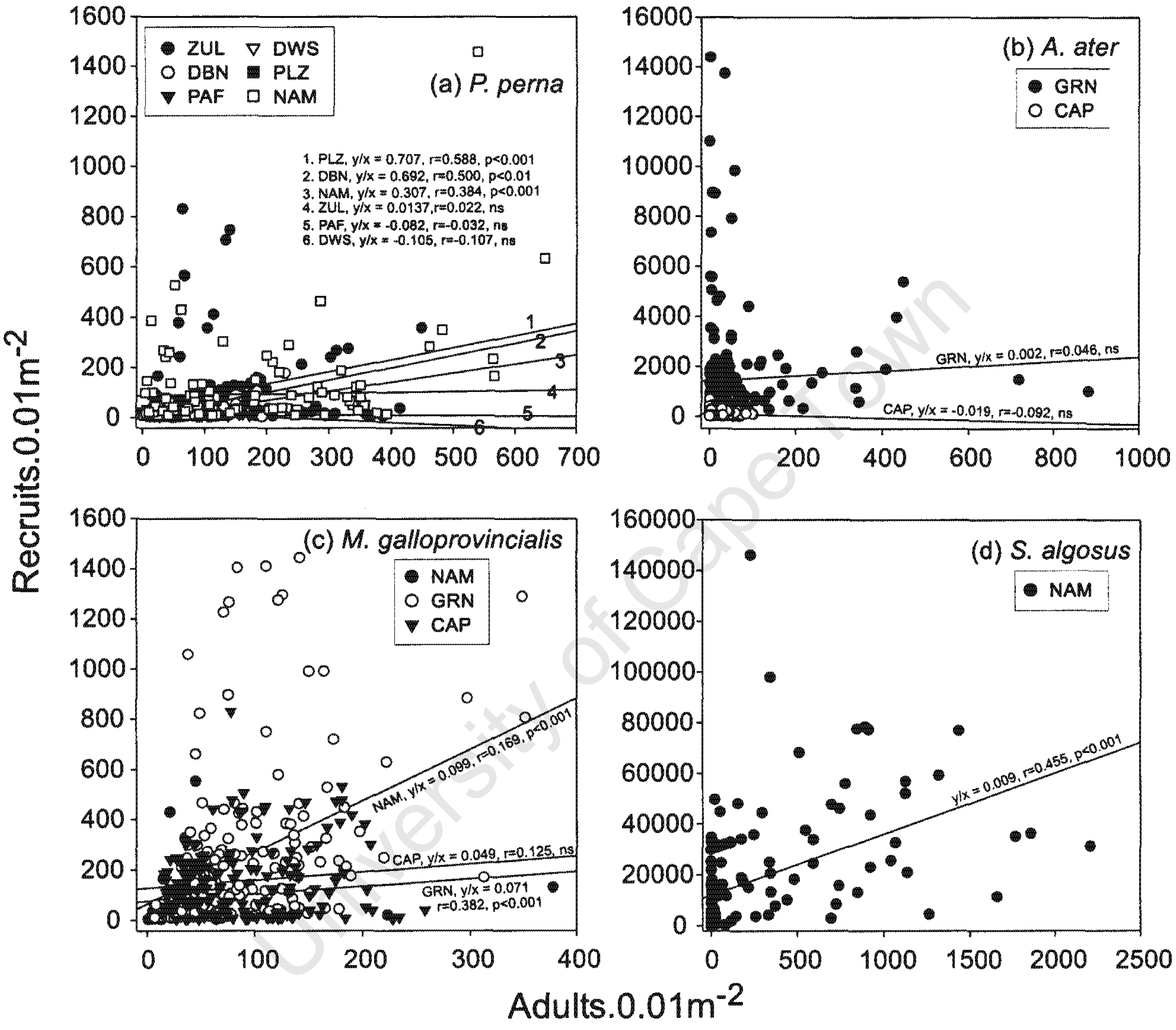

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Figure 1.6 a-d Linear regression lines of the simultaneous adult (> 5 mm) and recruit (≤ 5 mm) densities in 0.01 m^2 quadrats during recruitment events. y/x = the slope of the regression line, indicating the ratio of recruits to adults for each species at each location, ns = the regression line was not statistically significant.

galloprovincialis (Namibia and Groenrivier) and a significant correlation for *S. algosus* at Namibia. Of these, only those for *P. perna* were strong.

The second hypothesis was that recruitment of mussels is higher into mussel beds with greater numbers of mussels at the scale of the mussel bed, and was evaluated using measurements taken simultaneously (0 lag) and with the mussel bed measured 3 months prior to recruitment (-3 lag). Only Dwesa had no significant correlations, but this may have been due to the high number of years without recruitment events, which resulted in a severely reduced sample size for this calculation (Table 1.9). All other locations had significant relationships with either cover or number per meter, but never both. In all significant cases except Zululand and Pt Elizabeth, results were similar for the two lags examined.

The final hypothesis was that recruitment events will have a measurable positive effect on the density of juveniles in the mussel bed in the following season. In this test, Port Elizabeth and Dwesa showed positive significant relationships, Port Alfred had a significant negative relationship, and all other locations were not significant (Figure 1.7).

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Table 1.9 Correlations between recruitment and adult densities during recruitment events per location. For Lag -3, recruitment was compared to mussel bed variables 3 months prior to recruitment. *p < 0.05, **p < 0.01, ***p < 0.001, ns = not significant.

Location	Correlate Lag	% Cover^{d} 0	% Cover -3 mo.	# per 1m^{e} 0	# per 1m -3 mo.
NAM^{a}	r	0.015	0.024	0.442	0.364
	p	ns	ns	***	***
	n	90	93	90	93
GRN^{a}	r	0.080	0.026	0.207	0.272
	p	ns	ns	*	**
	n	149	117	149	117
CAP^{a}	r	0.245	0.249	0.052	-0.152
	p	**	*	ns	ns
	n	131	75	131	75
PLZ^{b}	r	-0.368	-0.326	0.635	0.388
	p	ns	ns	**	ns
	n	18	11	18	11
PAF^{b}	r	0.380	0.388	0.223	0.247
	p	*	*	ns	ns
	n	37	27	37	27
DWS^{b}	r	0.689	0.432	0.174	-0.332
	p	ns	ns	ns	ns
	n	7	8	7	8
DBN^{c}	r	-0.029	0.353	0.473	0.792
	p	ns	ns	**	***
	n	44	16	44	16
ZUL^{b}	r	-0.040	0.130	-0.086	0.237
	p	ns	ns	ns	*
	n	157	108	157	108

^{a,b,c}Recruitment event defined as (^{a}) > 9, (^{b}) > 4, or (^{c}) > 2 recruits (< 5 mm) into 0.01 m^2 of mussel bed.

^{d}Mean percentage cover of mussels ≥ 5 mm in mussel bed.

^{e}Number of mussels ≥ 5 mm in an average 1-m wide strip through the mussel bed, perpendicular to the shore, a measure of stock size.

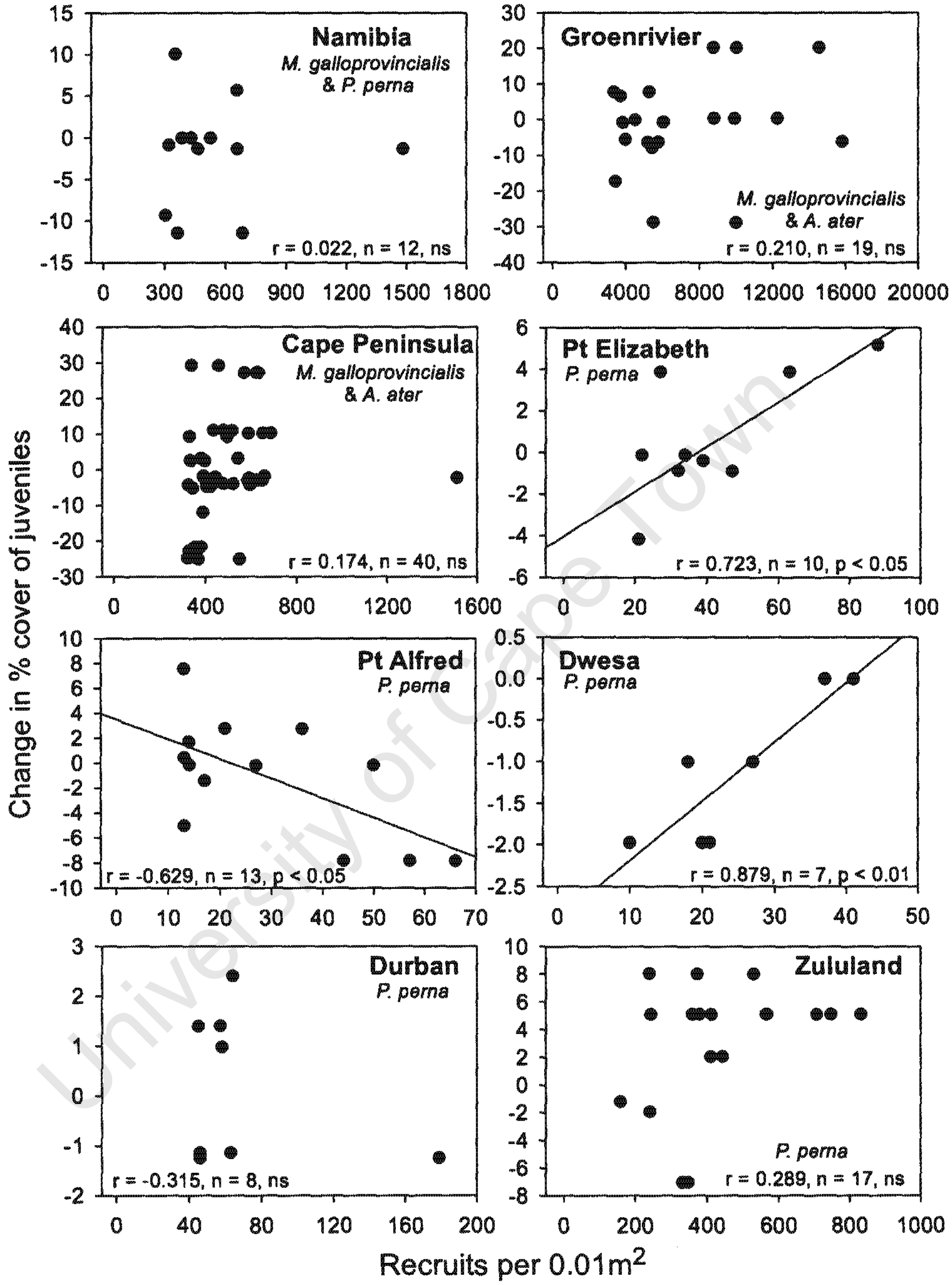

Figure 1.7 Pearson product-moment correlations between recruit densities in 0.01 m^2 quadrats and the change in the % cover of juveniles (5-10 mm) in the mussel bed in the 3 months following measurement of recruitment. This analysis only uses data from large recruitment events, when the number of recruits into the 0.01m^2 patch exceeded one-fifth of the maximum recruitment event recorded for that site.

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Within-location variability in recruitment intensity, seasonal and annual trends

The recruitment time-series was plotted for each species at each site (Figures 1.8a and 1.9) and analyzed within-locations using ANOVAs. Only Groenrivier lacked any significant effects of Year, Season or Site, and no location was completely without significant interactions (Table 1.10). Significant differences in recruitment rate among sites were found only at Namibia and Port Alfred, and the effects were generally weak. Pooling years, the species and the sites fell into four general categories or 'cases', illustrated in Figure 1.10, and the cases for each ANOVA are listed in Table 1.10. Half of the species/locations fell into the category of Case 2, whereby sites were temporally synchronized but did not maintain consistent ranks in recruitment density among years, implying a general mixing of larvae among these sites (i.e. a given species at a given location is 'open' at this spatial scale). Two species/locations belonged to Case 1, in which both site and season were significant, and these were both at Namibia. For *P. perna* and *S. algosus*, the sites maintained their rankings in recruitment density over time, indicating either that the sites are closed at this scale, or that there are physical or biological processes that maintain this distinction. Port Alfred fell into Case 3, whereby its sites maintained their rankings over time (and had a strong stock-recruit relationship at the scale of the mussel bed, Table 1.8), but had no temporal pattern. *M. galloprovincialis* at the Cape and *M. galloprovincialis* and *A. ater* at Groenrivier fell into Case 4, with neither synchrony nor consistent rankings among sites.

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Figure 1.8 – Overleaf

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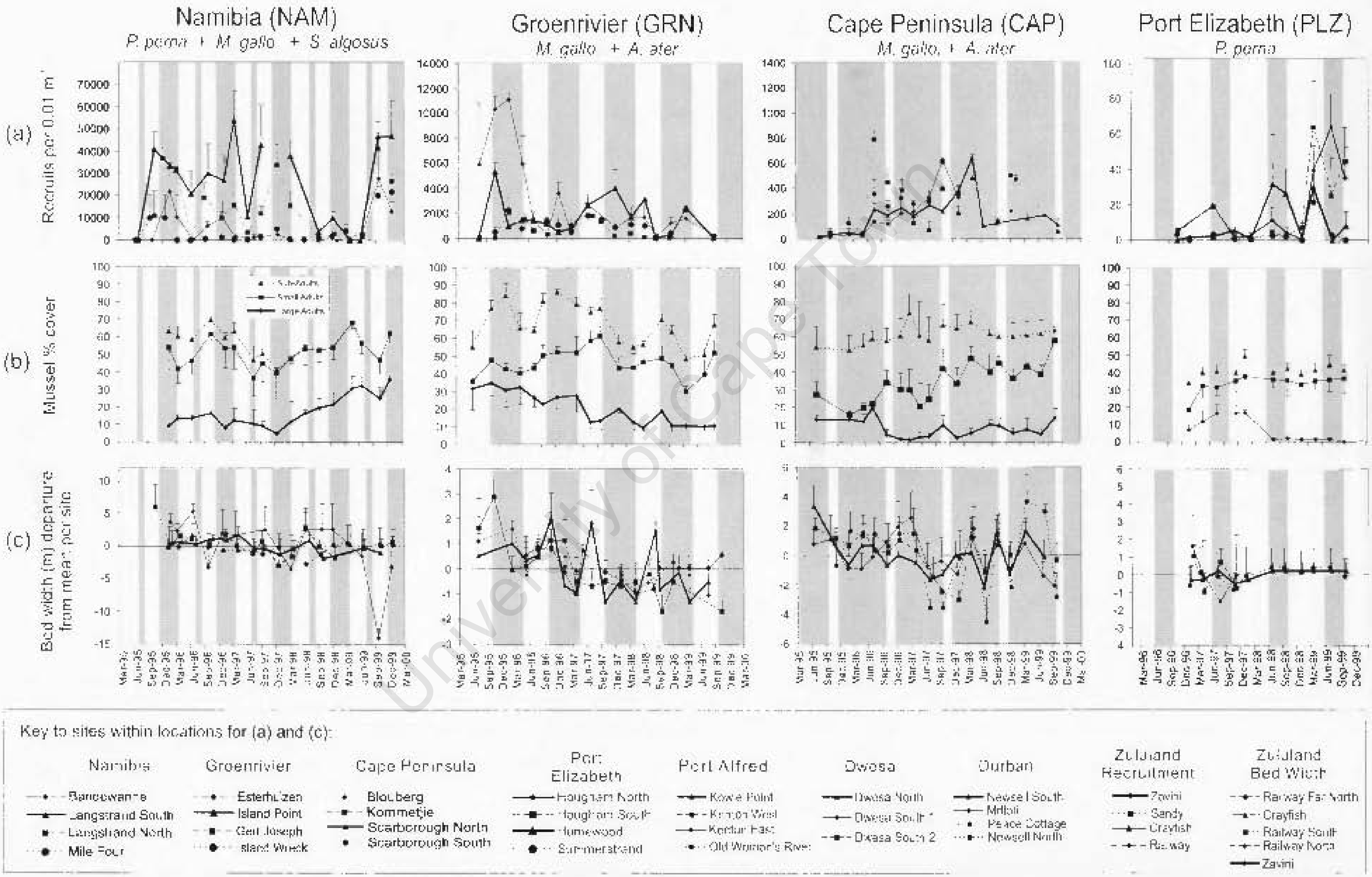

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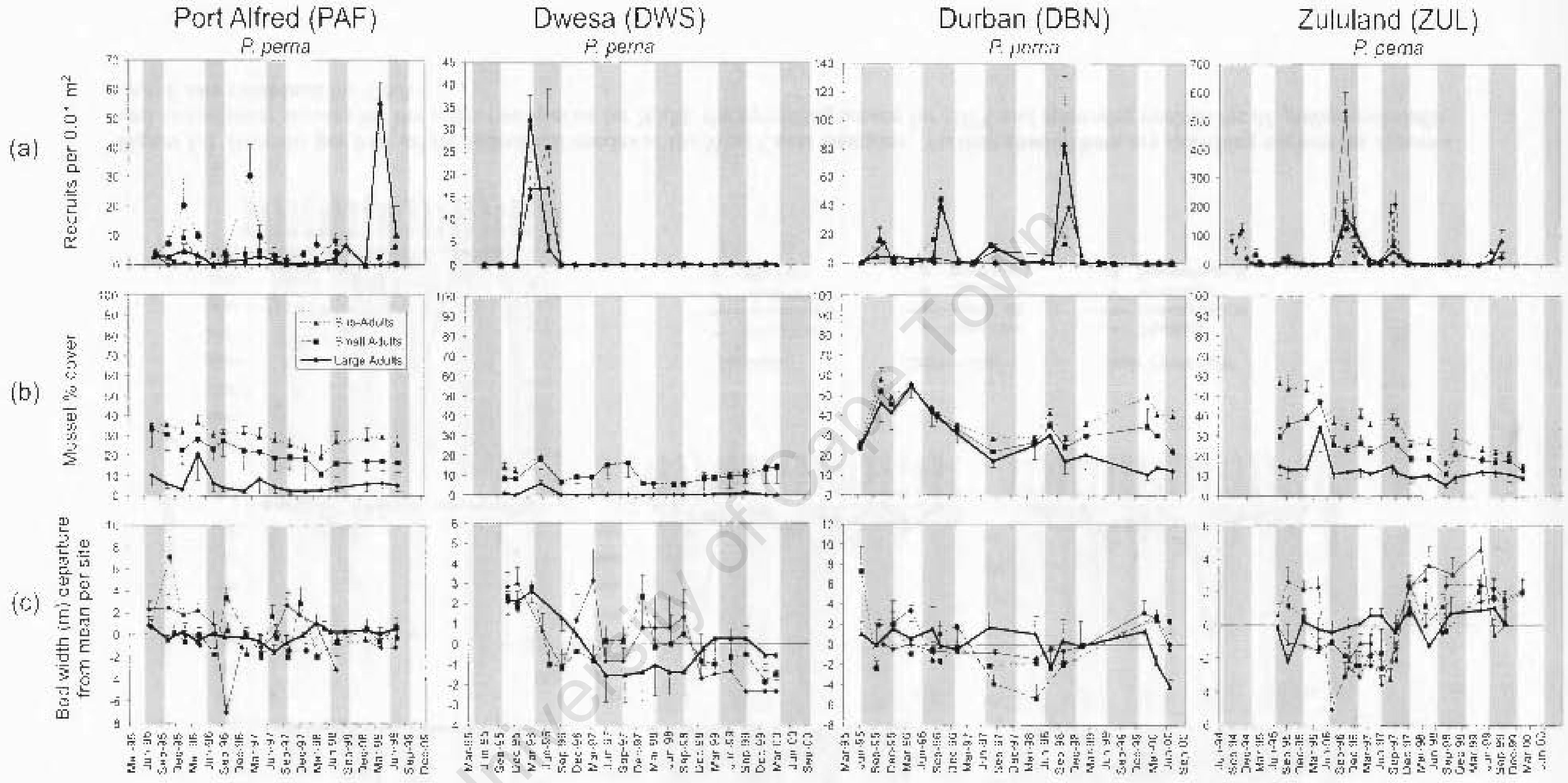

Figure 1.8 (a) Recruits +SE per 0.01 m^2, (b) mean percent cover of size classes in the mussels bed and (c) Bed width (m) −SE. For Namibia, Cape Peninsula and Port Elizabeth, vertical shaded bars denote spawning periods: Namibia: *P. perna* (B. Currie, unpublished data). Cape Peninsula: *M. galloprovincialis* and *A. ater* from Oudekraal and Bloubergstrand combined (van Erkom Schurink & Griffiths 1991), Port Elizabeth: *P. perna* from Port Alfred (Ndzipa 2002), Zululand and Durban: *P. perna* Durban (Berry 1978), Dwesa: *P. perna* Hluleka, Eastern Cape (Lasiak 1986), Port Alfred: *P. perna* Port Alfred (Ndzipa 2002). For Groenrivier, vertical shaded bars denote upwelling season, but spawning here is expected to be similar to that of the Cape Peninsula: protracted and without a strong seasonal cycle.

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Table 1.10 Within-location and within-species ANOVAs (west coast locations); Y = year, Sn = Season, St = Site; *p < 0.05, **p < 0.01, ***p < 0.001, ns = not significant.

Location	Species	Factor	*df*	MS	*F*	*p*	Sn-St case*
Namibia	*M. galloprovincialis*	Site	3	4.5	6.73	ns	2
		Season	3	4.9	8.97	**	
		Year	4	11.2	9.51	**	
		Site*Sn	9	0.5	0.52	ns	
		Site*Yr	12	1.2	1.11	ns	
		Sn*Yr	12	4.2	3.95	***	
		St*Sn*Yr	36	1.1	2.91	***	
		Error	159	0.4			
	S. algosus	Site	3	484.2	12.27	**	1
		Season	3	378.1	17.95	***	
		Year	4	131.9	3.38	*	
		Site*Sn	9	21.1	1.02	ns	
		Site*Yr	12	39.0	1.89	ns	
		Sn*Yr	12	47.9	2.33	*	
		St*Sn*Yr	36	20.6	2.30	***	
		Error	160	9.0			
	P. perna	Site	3	21.8	3.70	*	1
		Season	3	8.1	4.15	*	
		Year	4	32.4	7.27	**	
		Site*Sn	9	2.0	3.83	**	
		Site*Yr	12	4.5	8.75	***	
		Sn*Yr	12	3.8	7.49	***	
		St*Sn*Yr	36	0.5	0.88	ns	
		Error	160	0.6			
Groenrivier	*A. ater*	Site	3	46.7	5.70	ns	4
		Season	3	2.6	1.14	ns	
		Year	3	13.0	1.13	ns	
		Site*Sn	9	2.3	0.41	ns	
		Site*Yr	9	11.5	2.05	ns	
		Sn*Yr	9	18.9	3.36	*	
		St*Sn*Yr	27	5.6	4.09	***	
		Error	128	1.4			
	M. galloprovincialis	Site	3	6.2	1.31	ns	4
		Season	3	1.5	0.69	ns	
		Year	3	1.9	0.33	ns	
		Site*Sn	9	2.1	0.68	ns	
		Site*Yr	9	5.8	1.87	ns	
		Sn*Yr	9	7.5	2.44	*	
		St*Sn*Yr	27	3.1	6.34	***	
		Error	128	0.5			
Cape Penin.	*A. ater*	Site	3	0.7	0.71	ns	2
		Season	3	1.7	4.49	*	
		Year	2	23.0	19.73	**	
		Site*Sn	9	0.4	0.63	ns	
		Site*Yr	6	1.2	1.97	ns	
		Sn*Yr	6	4.2	7.14	***	
		St*Sn*Yr	18	0.6	2.51	**	
		Error	99	0.2			
	M. galloprovincialis	Site	3	1.2	0.41	ns	4
		Season	3	2.0	2.27	ns	
		Year	2	44.3	17.15	**	
		Site*Sn	9	0.9	1.63	ns	
		Site*Yr	6	2.6	4.78	**	
		Sn*Yr	6	0.5	0.89	ns	
		St*Sn*Yr	18	0.5	2.05	*	
		Error	99	0.3			

*Refers to Figure 1.10

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Table 1.10 continued (south and east coast locations)

Location	Species	Factor	*df*	MS	*F*	p	Sn-St case*
Pt Elizabeth	*P. perna*	Site	3	3.6	8.2	ns	2
		Season	3	11.6	20.9	***	
		Year	2	0.2	0.3	ns	
		Site*Sn	9	0.6	0.7	ns	
		Site*Yr	6	0.7	0.9	ns	
		Sn*Yr	6	0.5	0.5	ns	
		St*Sn*Yr	18	0.8	1.9	*	
		Error	95	0.4			
Pt Alfred	*P. perna*	Site	3	10.9	6.83	*	3
		Season	3	0.7	0.43	ns	
		Year	3	0.4	0.89	ns	
		Site*Sn	9	1.6	3.41	**	
		Site*Yr	9	0.4	0.93	ns	
		Sn*Yr	9	1.6	3.40	**	
		St*Sn*Yr	27	0.5	1.81	*	
		Error	128	0.3			
Dwesa	*P. perna*	Site	2	0.1	0.45	ns	2
		Season	3	1.6	16.35	**	
		Year	4	1.8	10.76	**	
		Site*Sn	6	0.1	0.75	ns	
		Site*Yr	8	0.2	1.22	ns	
		Sn*Yr	12	2.9	21.33	***	
		St*Sn*Yr	24	0.1	1.39	ns	
		Error	120	0.1			
Durban	*P. perna*	Site	3	0.1	0.39	ns	2
		Season	3	51.3	114.00	***	
		Year	4	1.6	5.12	*	
		Site*Sn	9	0.5	1.13	ns	
		Site*Yr	12	0.3	0.78	ns	
		Sn*Yr	12	1.4	3.62	**	
		St*Sn*Yr	36	0.4	1.54	*	
		Error	159	0.3			
Zululand	P. perna	Site	3	13.7	4.46	ns	2
		Season	3	69.9	51.37	***	
		Year	4	25.2	6.46	**	
		Site*Sn	9	1.4	0.62	ns	
		Site*Yr	12	3.9	1.79	ns	
		Sn*Yr	12	14.9	6.82	***	
		St*Sn*Yr	36	2.2	4.46	***	
		Error	632	0.5			

*Refers to Figure 1.10

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The season effect contained the Site*Season but not the Site*Year interaction terms in its MS-denominator, so not all seasonal effects could be interpreted with post-hoc comparisons. Those that were strong enough to be interpreted appear in Table 1.11. Both east-coast locations had highest recruitment in spring, and both south-coast locations had recruitment peaks in autumn, while on the West Coast there was no consistent pattern.

In Namibia, significant differences among sites were found for both *P. perna* and *S. algosus*, but not for *M. galloprovincialis*. Post-hoc test revealed that the rankings among sites were not the same for the two species, indicating that the site effect was not consistent among species (Table 1.12). The two most proximate sites (Langstrand North and South, lying within 1 km of each other) were significantly different for both species. This was also true at Port Alfred, for the proximate sites Kenton East and Kenton West.

Table 1.11 Results of Tukey's HSD post-hoc tests for seasonal effects. Letters indicate significant groupings, a being highest and c being lowest in each case.

		Season			
Location	**Species**	**Spring**	**Summer**	**Autumn**	**Winter**
Namibia	*M. galloprovincialis*	bc	b	a	c
	S. algosus	b	a	b	c
Port Elizabeth	*P. perna*	c	c	a	b
Dwesa	*P. perna*	b	b	a	a
Durban	*P. perna*	a	b	d	c
Zululand	*P. perna*	a	c	c	b

Table 1.12 Ranking of sites based on Tukey's HSD post-hoc tests for Site effects. $\overline{R}$ = mean number of recruits (individuals < 5 mm) per 0.01m^2 mussel bed per site.

	Rank	**1**		**2**		**3**		**4**	
Location	**Species**	**Site**	$\overline{R}$	**Site**	$\overline{R}$	**Site**	$\overline{R}$	**Site**	$\overline{R}$
NAM	*P. perna*	Mile 4	25.04	Langstrand North	10.61	Langstrand South	2.42	Bade-wanne	0.57
NAM	*S. algosus*	Langstrand South	13454.35	Langstrand North	4472.85	Badewanne	624.58		
						Mile 4	539.78		
PAF	*P. perna*	Old Woman's River	3.03	Kowie Point	0.87	Kenton East	0.001		
				Kenton West	0.74				

A year effect was found to be significant at five of the locations (Table 1.10). For the locations with multiple species (Namibia and Cape Peninsula), the year effect was significant (with or with out a significant interaction term) for all the species. Post-hoc tests could only be applied at three of the locations (Table 1.13), and revealed that 1996-97 appeared to have been a year of consistently high recruitment, while the years 1995-96 and 1998-99 were the lowest.

Table 1.13 Results of the Tukey's HSD post-hoc tests for Year effects; years ran June to May. In all cases, a is the group with the highest mean value and c is the lowest.

		Year				
Location	**Species**	**95-96**	**96-97**	**97-98**	**98-99**	**99-00**
NAM	*M. galloprovincialis*	c	a	b	bc	bc
CAP	*M. galloprovincialis*	b	a	a	--	--
	A. ater	b	a	a	--	--
DBN	*P. perna*	ab	ab	a	b	c

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Population structure and width of the mussel bed

Changes in the population structure of the mussel bed in relation to spawning and recruitment events were observed by plotting the percentage cover of the combined species at each location over the five years of the study, as recorded in the permanent 0.25 m^2 quadrat-transects (Figure 1.8b). Most sites maintained a consistent cover among years, with the noted exception of Zululand, where the cover steadily decreased despite fairly consistent annual recruitment events and an overall increase in bed width. The growth of cohorts within the mussel bed could be observed at Namibia, Groenrivier, Cape Peninsula, and Durban, while the other sites appeared to maintain a more consistent inter-annual ratio of sub-adults, small adults and large adults.

Changes in the width in the mussel bed were tracked by plotting the departure in the width at each site from that site's mean width over time. In most cases, the width of the bed varied from season to season, but maintained a steady overall width over the five years (Figure 1.8c). Noted exceptions were Groenrivier and Dwesa, where the beds at all sites decreased in width, and Zululand, where it steadily increased from June 1996 to the end of the study. Periodic and apparently radical dips at individual sites, followed by a complete recovery in the next season, such as the one in September 1996 at Kenton East, Port Alfred, were due to events when sand covered mussel bed and then was washed away. At Railway North, Zululand, sand covered the mussel bed and remained, killing large patches within the mussel bed. In this case, the bed slowly recovered its width over the following two years.

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Among-species temporal variability in recruitment intensity

Recruitment was found to be synchronous among species at some, but not all, locations. At Namibia, the recruitment periods of *P. perna* and *M. galloprovincialis* were synchronous among the sites (season-site cases 1 or 2, Figure 1.10), but the recruitment of the two species was not simultaneous at any of the sites. At Cape Peninsula, in contrast, the recruitment periods of *M. galloprovincialis* and *A. ater* were strongly, significantly and positively correlated over time at all but one site (Blouberg: $r = 0.817$, $p < 0.01$, $n = 12$; Kommetjie: $r = 0.574$, $p < 0.05$, $n = 11$; Scarborough North: $r = 0.555$, $p < 0.05$, $n = 16$; Scarborough South: $r = 0.336$, not significant, $n = 12$), and the recruitment rates of these two species were not significantly different from each other (student's t-test for independent samples, data fourth-root transformed, $\overline{X}_{Aula} = 57.6$, $\overline{X}_{Mytilus} = 131.3$, $t_{22} = -1.3$, not significant). The recruitment of *A. ater* and *M. galloprovincialis* was also significantly positively correlated at three of the four sites at Groenrivier (Esterhuizen: $r = 0.939$, $p < 0.001$, $n = 16$; Gert Joseph: $r = 0.637$, $p < 0.01$, $n = 16$; Island Point: $r = 0.659$, $p < 0.01$, $n = 16$; Island Wreck: $r = 0.417$, not significant, $n = 15$), but the mean recruitment of *A. ater* was significantly higher than that of *M. galloprovincialis* during this sampling period (student's t-test for

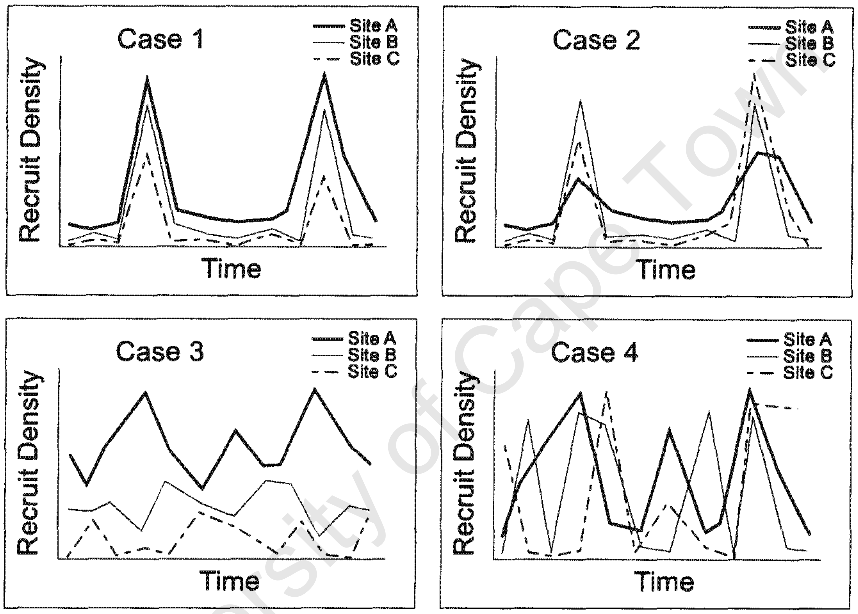

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Figure 1.10 Conceptual diagram of the four types of relationships among sites as revealed by ANOVA (Table 1.10). Case 1: both the site (St) and the season (Sn) effects were significant, indicating that sites are temporally synchronous and maintain a consistent ranking in recruitment density over time. (Year (Y) interactions are relatively weak or absent) 2: Sn significant, St is not, Y-interactions are weak or strong. 3: St is significant, Sn is not, Y-interactions are weak or absent. 4: Neither St nor Sn is significant, Y-interactions are weak or strong.

independent variables, data fourth-root transformed, $\overline{X}_{Aula} = 991.0$, $\overline{X}_{Mytilus} = 117.6$, $t_{28} = 7.2$, $p < 0.001$).

Simultaneous recruitment into turf algae, brushes and mussel beds

Recruitment into turf algae and mussel beds was strongly and significantly positively correlated over time at Dwesa and Port Alfred, but was not correlated at Port Elizabeth and Zululand (Table 1.14). At Railway, Zululand, both algal-turf and mussel-bed samples were collected monthly for 4 years. To investigate whether recruitment into algae was followed by secondary settlement into the mussel beds, I explored time-lagged correlations between densities of recruits into algae and densities of small adults (10-35 mm individuals) in the mussel bed (Table 1.15). Results indicated significant correlations between the density of recruits in algae and the density of small adults in the mussel bed 2 and 3 months afterwards. When the same analysis was performed for both recruits and small-adults within the turf algae, no significant correlations were found at any lag from -5 to +5 months. As there was no correlation between the simultaneous recruitment into algae and the mussel bed at this location, these results suggest a secondary movement from the algae into the mussel bed at Zululand.

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Table 1.14 Pearson product-moment correlations of the recruitment into turf algae and recruitment into mussel bed at lag 0. A =Turf Algae, M = Mussels (*P. perna*). $\overline{R}$ = the mean number of mussel recruits < 5 mm found in 10 × 10 cm^2 quadrats of mussel bed or algae. Significant correlations were both positive, *** $p < 0.001$, ns = not significant.

Location	A/M	$\overline{R}$	SD	r^2	p	n	Sampling frequency
Port Elizabeth	A	7.42	9.82	0.009	ns	36	Three-monthly
	M	9.21	12.60				
Port Alfred	A	8.33	22.22	0.471	***	43	Three-monthly
	M	4.30	9.48				
Dwesa	A	2.24	7.04	0.861	***	46	Three-monthly
	M	2.41	7.08				
Zululand	A	28.75	43.04	0.009	ns	78	Monthly
	M	37.68	77.28				

Table 1.15 Lag-correlations between recruitment into algae and sub-adult densities in the mussel bed at Railway, Zululand. *p < 0.05, ns = not significant.

Lag (months)[a]	$\overline{R}$ [b]	$\overline{A}$ [c]	r^2	p	n
-5	26.57	11.27	0.0002	ns	37
-4	25.42	10.84	0.0004	ns	37
-3	23.47	11.24	0.0429	ns	38
-2	24.85	11.59	0.0000	ns	38
-1	24.04	12.03	0.0002	ns	41
0	23.77	12.20	0.0036	ns	43
+1	23.96	12.68	0.0922	ns	38
+2	24.72	13.45	0.1347	*	37
+3	25.21	14.29	0.1126	*	38
+4	25.78	14.16	0.0436	ns	39
+5	27.21	14.96	0.0910	ns	36

[a] Negative lags indicate data taken from the mussel bed before recruitment into algal turf, positive lags indicate data taken from the mussel bed after recruitment into algal turf

[b] $\overline{R}$ = mean number of *P. perna* recruits (< 5 mm) per $0.01m^2$ turf algae

[c] $\overline{A}$ = mean number of sub-adults (10-35 mm) per $0.01m^2$ mussel bed.

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Due to sampling constraints, simultaneous recruitment into brushes and mussel bed was measured only at Zululand. A strong, significant linear relationship was found between recruitment into brushes and into the mussel bed ($r^2 = 0.523$, $n = 69$, $p < 0.001$), resulting in the regression model:

$$R_{bed} = 1.64 + 4.02 * R_{brush}$$

Synthesis of results

For ease of reference in the discussion, a summary of results appears in Table 1.16.

Table 1.16 Summary of results from this chapter. ND = no data, n/a = not applicable.

Location:	NAM			GRN		CAP		PLZ	PAF	DWS	DBN	ZUL
Recruitment ranking[a]	A			B		C		DF	EF	E	D	DF
Productivity[b]	↑			↑		↑		↔	↔	↓	↓	↓
Circulation[c]	↑			↔		↔		↑	↓	↓	↑	↓
P-C rank[d]	↑			↑		↑		↑	↓	↓	↔	↔
Rec v. adult densities (lag -3)[e]	#			#		%		none	%	none	#	#
Bed width[f]	↔			↓		↔		↔	↔	↓	↔	↑
Mean % cover[g]	60			70		65		42	31	12	35	32
% cover status[h]	↔			↔		↔		↔	↓	↔	↓	↓
Site effect varies amg. Spp[i]	y			n		n		n/a	n/a	n/a	n/a	n/a
Species[j]	*Pp*	*Mg*	*Sa*	*Mg*	*Aa*	*Mg*	*Aa*	*Pp*	*Pp*	*Pp*	*Pp*	*Pp*
Ad:rec y/x[k]	0.31	0.10	0.01	0.07	< 0.01	0.05	-0.02	0.71	-0.08	-0.11	0.69	0.01
Ad:rec r-value[l]	0.38*	0.17	0.46*	0.38*	0.05	0.13	-0.09	0.59*	-0.03	-0.11	0.50*	0.02
Site/season case (Fig 1.10)[m]	1	2	1	4	4	4	2	2	3	2	2	2
Peak rec season(s)	none	aut.	sum.	none	none	none	none	aut.	none	aut.-win.	spr.	spr.
Year effect[n]	n	y	n	n	n	y	y	n	n	n	y	n
Synch. with other spp. at site[o]	n	n	n	y	y	y	y	n/a	n/a	n/a	n/a	n/a
Rec. synch. into algae[p]	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n	y	y	ND	n
Rec limited[q]	n	n	ND	n	n	n	n	y	n	y	n	n

[a] Recruitment rankings are result of large-scale ANOVA post-hoc (Figure 1.2a), A is highest mean value;

[b,c,d] Productivity, Circulation and Productivity-Circulation (P-C) ranks: ↑ (high) = rank 7-8, ↔ (mid) = 4-6, ↓ (low) = 1-3 (Table 1.5);

[e] Correlation between recruit and adult densities at lag -3 months is significant for: # = no. of adults per meter, % = percent cover of adults (Table 1.8);

[f] Bed width: ↑ = increased over time, ↔ = did not change, ↓ = decreased (Figures 1.8c);

[g] Mean percentage cover of the mussel bed (Figures 1. 8b);

[h] Percentage cover status: ↔ = % cover did not change over time, ↓ = % cover decreased (Figures 1. 8b);

[i] Site effect, significant in ANOVA, varies among the different species at that location (Table 1.10);

[j] Species: *Pp = P. perna, Mg = M. galloprovincialis, Sa = S. algosus, Aa = A. ater*;

[k] Adult:recruit ratio as indicated by y/x (Figure 1.6);

[l] r-value of adult:recruit ratio (Figure 1.6), * significant r-value indicates recruitment is density-dependent for this species/location;

[m] Site/season cases are illustrated in Figure 1.10 and defined by within-location ANOVAs (Table 1.10);

[n] Year effect is significant in within-location and species ANOVAs (Table 1.10);

[o] Recruitment events at each location are generally synchronized among species;

[p] Recruitment into mussel bed and algae is synchronous;

[q] Species or pair of species is recruitment-limited at this location.

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1.4 DISCUSSION

Large-scale (among location) variability of recruitment into mussel beds

The high spatial variability in mussel recruitment noted by Harris et al. (1998) persisted in my 5-year study, with consistent and significant differences in peak annual numbers of recruits spanning three orders of magnitude among locations and species (Figure 1.2a). This extreme variation within species among locations is not uncommon. In their study of barnacle recruitment among four sites in northern Europe, Jenkins et al. (2000) found two orders of magnitude differences between shores in southwest England and those in Sweden. In a survey of the recruitment of two chthamaloid barnacles covering most of Europe, O'Riordan et al. (2004) found comparable differences between locations over a similar spatial scale (100s to 1000s of km), spanning two orders of magnitude, with the maximum recruitment levels falling at different locations for each of the species. Connolly and Roughgarden (1999a) also found two orders of magnitude difference among locations in the recruitment of chthamaloid barnacles across 5° latitude in California, USA, although the proportions among sites varied among years. Navarrete et al. (2002) found two orders of magnitude difference among 11 sites in the recruitment of chthamaloid barnacles and three orders of magnitude for mytilid mussels across 900 km of the Chilean coast. Differences among the three years of the study appeared less important than among sites, despite an ENSO event in one of the years radically affecting the oceanic climate. Hughes et al. (2002) recorded a 20-fold difference in recruitment levels of corals in their meta-analysis of studies along the Great Barrier Reef, Australia. As for Navarrete et al. (2002) and Connolly and Roughgarden (1999), the rankings of sites with regards to their recruitment intensity were not necessarily consistent among years for most locations. Finally, Menge et al. (2003) found a two-orders of magnitude difference for the recruitment of barnacles and a three-orders of magnitude difference for mussels between the east and west coasts of New Zealand.

When Harris et al. (1998) examined the large-scale stock-recruit relationship for all species at all locations together, they found a strong, positive and significant relationship between recruitment rates and the spawner density or biomass. The larvae of many taxa are known to be gregarious settlers, actively seeking adult conspecifics in settlement process (Raimondi 1988b; Harris et al. 1998), and this can confound conclusions about the open or closed nature of a population at smaller scales (Caley et al. 1996). As mussels in southern Africa can show gregarious recruitment at the small scale, as was demonstrated in Figure 1.6, weak stock-recruit relationships should be interpreted with caution. In their review, Caley et al. (1996) suggest that strong stock-recruit relationships indicate that populations are largely reproductively distinct, at this larger scale. As hypothesized, when I repeated these calculations with all species grouped together for the whole five years, I achieved similar results: all the examined relationships were positive and significant, although not always as strong as those of Harris et al. (1998). The positive significant relationship was not unexpected for several reasons. Firstly, mussel recruitment into mussel beds at the meta-

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population scale was anticipated to be reproductively isolated (Caley et al. 1996). The cycle from spawner to larva to recruit and back to spawner is dampened by loss of recruits in the water column (Olson and McPherson 1987; Young and Gotelli 1988; Morgan 1995a; Morgan and Christy 1996; Navarrete and Wieters 2000) and post-settlement mortality in the mussel bed (Griffiths 1981; Hunt and Scheibling 1997; Hunt and Scheibling 2001). Nevertheless, the size and fecundity of the adult stock plays an important role in determining the size and density of the larval pool which, once transported to its adult habitat, will influence settlement rates (Hughes et al. 2000), and therefore adult community structure, through the process of recruitment (Connell 1985). The overall fecundity of the population may be density-dependent (Hughes et al. 2000; Hills and Thomason 2003), and increased fecundity will, at least to a point, increase the number of larvae in the water column, which may then settle preferentially into mussel bed (Harris et al. 1998). On the West Coast, all species were pooled for this investigation due to the pooled stock percent cover data available. While comparisons of pooled species may mask some individual species effects, this pooling was necessary to make coast-wise conmparisons across biogeographic regions. A discussion of the smaller-scale per-species investigation of the stock-recruitment relationship follows below. At the coast-wise or meta-population scale, then, a strong positive relationship between stock and recruit densities was both anticipated and realized, and confirms our broad-scale understanding of this process.

The magnitude of the recruitment peaks for *P. perna, A. ater* and *M. galloprovincialis* varied among locations (Figures 1.8a and 9), and this variability was consistent with previous studies, with very high values on the West Coast, low values on the South and East Coasts, and extremely low levels at Dwesa in particular. Recruitment rates of *P. perna* in the Eastern Cape near Dwesa have been previously reported as two to three orders of magnitude lower than those elsewhere along the South and East Coasts (Dye et al. 1997). Lasiak and Barnard (1995) studied the recruitment of *P. perna* into mussel bed at Dwesa, and found the density of late plantigrades (0.5-3.5 mm) was 5-60 individuals.0.01m^{-2} of mussel bed, which falls within the densities measured in this study. McQuaid and Lawrie (2005) recorded recruitment densities of 10-50 individuals.0.01m^{-2} of mussel bed at Port Alfred in 1998-99, which also match recruitment intensities reported here. Berry (1978) reported 'normal' recruitment of 1-9 mm plantigrades and juveniles as being 46 individuals.0.01m^{-2} at Durban in June 1976, which was similar to values he recorded in the three previous years and to the densities I recorded in two of the years. In July 1976, however, which was the following month, Berry recorded an extraordinary 1700 individuals.0.01m^{-2} recruiting into mussel bed (and onto everything else, for that matter, including bare rock). It is worthwhile noting that while recruitment levels during this event were spectacularly high on the East Coast and had important ecological consequences, they were far less than the mean recruitment of *S. algosus* in Namibia, or even of *A. ater* at Groenrivier during my

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study. Finally, the recruitment rates I recorded for *M. galloprovincialis* at Groenrivier were similar to those reported by Robinson (2005) for the same location, recorded in 2004-05.

Nearshore primary productivity (including phytoplankton, epilithic algae and algal detritus), a bottom-up factor, is thought to influence differences in rocky intertidal community structure, and this link has been demonstrated through correlative experiments (Bustamante et al. 1995a; Menge et al. 1997a; Navarrete et al. 2005). Additionally, large-scale oceanographic features can control the delivery and retention of subsidies (particulate matter, nutrients and propagules) to the rocky shore, and also therefore control community structure and the strength of adult interactions (Menge et al. 2003; Navarrete et al. 2005). In my study, differing levels of primary productivity alone failed to explain variability in recruitment intensity around the coast of southern Africa. A hierarchical assessment of measurable meso-scale oceanographic features that might influence nutrient supply and hydrographic retention also failed to explain this variability. The two added together, however, explained 62% of the among-location variability in recruitment intensity (Figure 1.4). These results were similar to those of (Menge et al. 2003), who found mussel recruitment to be strongly and significantly correlated to both upwelling and phytoplankton concentration when comparing the east and west coasts of New Zealand.

The year effect was significant for several of the locations in the smaller-scale within-location ANOVAs. Examination of the data (Figures 1.8-9) and the post-hoc tests (Table 1.13) revealed that recruitment rates were generally highest in the 1996-97 recruitment season, and lowest in 1995-96 and 1998-99, with intermediate values for the remaining two years. Dye et al. (1997) also reported recruitment of *P. perna* into artificial substrates at five sites in the Eastern Cape, including two at Dwesa, as lower in 1995 than in 1996. The two years with the lowest recruitment in my study were marked by anomalous extreme warm events in the southeast Atlantic Ocean. The 1995 event was a Benguela Niño, and 1999 had properties similar to a Benguela Niño, including both nearshore oceanic warming and the relaxation of southerly winds at the equator (Hardman-Mountford et al. 2003). These events, centered at the intersection of the Angola and Benguela Currents, are known to have serious impacts on the offshore biological and oceanic environment (Shannon et al. 1986; Florenchie et al. 2003), but their impact on the nearshore environment in South Africa is little-known. Previous recruitment studies in upwelling regions have used correlation to examine the effects of long-period cycles in the oceanic climate such as that of the 1997 ENSO event in the northern hemisphere (Connolly and Roughgarden 1999a) and the southern hemisphere (Navarrete et al. 2002). Connolly and Roughgarden measured the recruitment of three barnacle species in 1996 and 1997 across 5° latitude and found strong evidence for increased recruitment in 1997, indicating that large-scale anomalies might affect the oceanographic transport of meroplanktonic larvae. In contrast, Navarrete et al. examined the recruitment rates of two chthamaloid barnacles and three mussels in 1997-2000 and found that the inter-annual variation in recruitment was not greater than the spatial variation for all species except the mussel *Perumytilus*

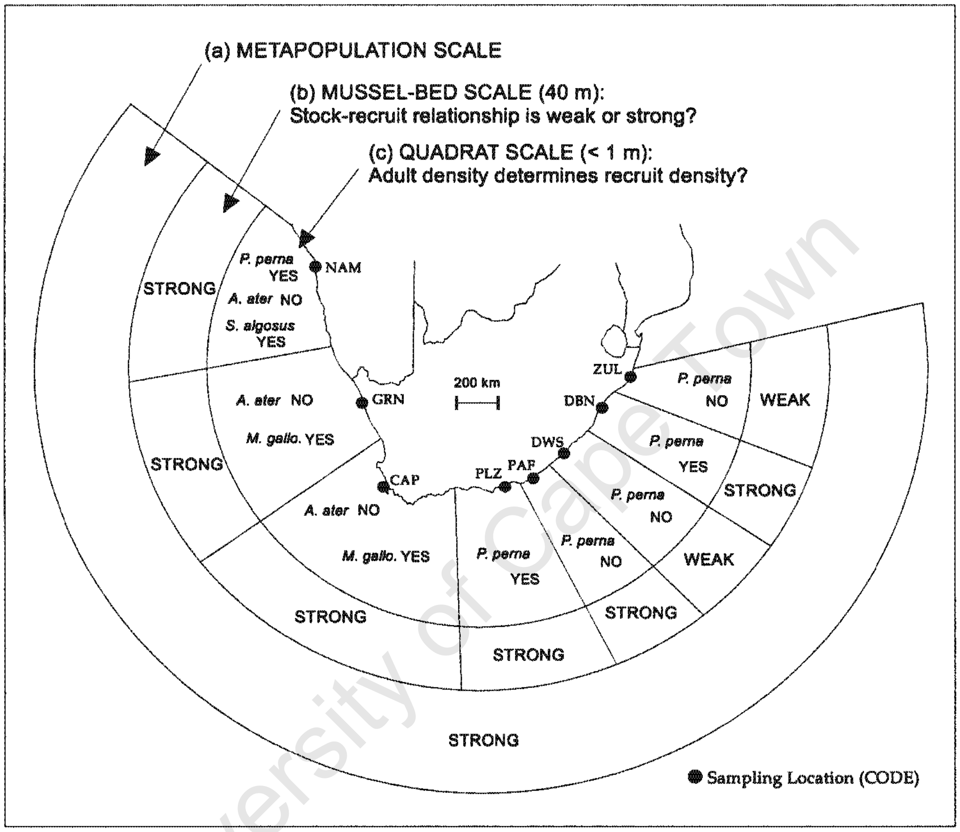

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Figure 1.11 Scales of the stock-recruit relationship investigated in this chapter. When stock and recruit densities are significantly positively correlated at a particular scale, then the relationship is 'strong'. When stock and recruit densities are 'weak', i.e. not significantly or are significanly negatively correlated, then conclusions are less clear, as other density-independent factors may be involved that mask the nature of the relationship. At the smallest scale (c), a significant stock-recruit relationship explains the strength of gregarious recruitment to adults. In this case, the non-significant relationship for *A. ater* is most likely due to the scarcity of adult conspecifics living within intertidal mussel beds on the West Coast.

Sampling location codes are: NAM (Namibia), GRN (Groen Rivier), CAP (Cape Peninsula), PLZ (Port Elizabeth), PAF (Port Alfred), DWS (Dwesa), DBN (Durban), ZUL (Zululand).

P. perna and *M. galloprovincialis* recruitment varied in its density-dependence at the quadrat scale among sites (Figure 1.6a,b). The weak relationship between adult *P. perna* densities and the density of its late plantigrades at Port Alfred was consistent with recent findings at that location (Erlandsson and McQuaid 2004). When recruitment is density-dependent, recruitment rates are sensitive to alterations in the density of the mussel bed caused by predation or harvesting. In her study near Groenrivier in 2004-05, Robinson (2005) experimentally manipulated the densities of the adult *M. galloprovincialis*, and found, as I did, that the recruitment of *M. galloprovincialis* at Groenrivier was density-dependent at the scale of meters. The recruitment of *A. ater* and *S. algosus* appeared to be density-independent. It is possible that the density-independent recruitment and low adult densities of *A. ater* were indicative of the high post-recruitment mortality caused by the invasion of *M. galloprovincialis*. The other potential cause of density-independent recruitment of *A. ater* is its subtidal distribution, extending to 40 m on rocky reef (Branch et al. 1994). Robinson (2005) did not, however, record *A. ater* recruiting in nearly such high numbers in 2004-05 as those recorded here, indicating more recent recruitment failure of this species.

Connell (1985) examined the relationship between settlement and recruitment with daily sampling of barnacle settlers on the rocky shore. He theorized that settlement and recruitment are positively correlated when settlement levels are low. When settlement levels are high, he continued, post-settlement mortality would be high, breaking the link between settlement and recruitment. The two would then become independent. Likewise, the link between recruits and juvenile or adult mussels could assume a similar relationship: adult density may be dependent on recruit density at low recruitment levels but independent of it at high levels (Caley et al. 1996). To evaluate this hypothesis, the Pearson product-moment correlation coefficient from Figure 1.6, describing the strength of the relationship between recruits and adult stocks, was compared to the maximum recruitment density for each species at each location (Figure 1.12). No significant exponential or logarithmic relationship was found between the two, indicating that the relationship is more complex than that predicted by Connell (1985) or Caley et al. (1996). Connell's general settlement hypothesis may not be extrapolated to describe the recruitment situation for mussels in southern Africa.

Recruitment limitation

Caley et al. (1996) define limitation as occurring when a process 'adds to or subtracts individuals from a population'. However, density-dependent recruitment, at whatever scale, does not necessarily indicate that a population is recruit-limited. McQuaid et al. (2000), deduced that near Port Alfred *P. perna* might be recruit-limited due to the low density of adults and significant correlations between recruit and adult densities. In my study, *P. perna* (at 3 of 6 locations), *M. galloprovincialis* (1 of 3 locations) and *A. ater* (1 of 2 locations) showed density-dependent recruitment (Figure 1.6). When the species were pooled within locations, most locations showed

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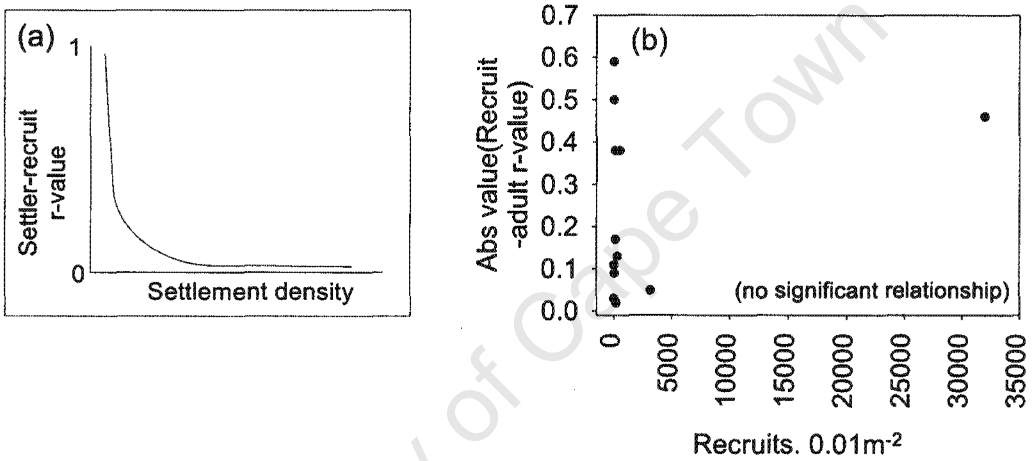

Figure 1.12 Comparison of (a) the settlement-recruitment hypothesis for barnacles (Connell 1985) with (b) the relationship between recruitment rates and recruitment density-dependence for mussels in southern Africa.

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density-dependent recruitment at the scale of the site, and two locations showed density-dependent recruitment at the location scale. In the final analysis, it was only Port Elizabeth and Dwesa that were found to actually be recruitment limited in the sense that juvenile abundance was influenced by recruit densities (Figure 1.7). The other six, including Port Alfred, appear to be recruitment regulated. Two of the four locations with low recruitment were recruit-limited, whereas none of the locations with high recruitment were recruit-limited. Although low recruitment levels may increase the probability of recruitment limitation, adult:recruit ratios and the density-dependence of recruitment are not reliable indicators of recruitment limitation for the mussel stocks around southern Africa.

Large-scale variability of recruitment into brushes

Erlandsson and McQuaid (2004) hypothesized that apparent high among-site variability in recruitment of mussels is derived from the small-scale recruitment heterogeneity associated with small-scale heterogeneity in the structural complexity of mussel beds. I employed brushes as a settlement substratum to standardize for differences in the depth and structural complexity of the mussel bed among locations, and a few important differences did emerge between recruitment into mussel beds and into brushes. These results must be interpreted with caution, however, due to limited sample sizes and the large and significant interaction term in the Location*Year ANOVA (Table 1.8). On the West Coast, the differences in recruit densities between the three locations were significantly reduced in brushes relative to mussel-bed samples, suggesting that structural complexity in mussel beds does play a role increasing the heterogeneity of recruitment for these species. Secondly, the ratio of *A. ater* to *M. galloprovincialis* was substantially different, with larger proportions of *M. galloprovincialis* recruiting into brushes than into mussel bed at both Groenrivier and the Cape. This may reflect differences in larval choice or post-settlement competition. On the South and East Coasts, in contrast, the relative among-site recruitment rates of *P. perna* into brushes more closely reflected the relative recruitment rates into mussel bed, indicating that the clumping of adults, competition with other species, and/or substrate effects may not be as important in these areas. This may be due to a lack of variation in structural complexity within and among *P. perna* beds on the South and East Coasts. In their study of *P. perna* in Port Alfred, where the layering of mussels is 'virtually absent', Lawrie and McQuaid (2001) found no evidence of the influence of habitat complexity on recruitment. In a more recent study of recruitment and spatial structure of *P. perna* in the same area, Erlandsson and McQuaid (2004) found that the densities of late plantigrades and recruits were both strongly positively associated with the density of adult mussels, with the strongest associations for late-stage recruits. Nevertheless, they concluded that there was no spatial structure in the distribution of numbers of recruits over local scales. In contrast, at Groenrivier, Robinson (2005) measured the recruitment of *M. galloprovincialis* into plots with experimentally manipulated densities of adult conspecifics, and

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found a significant correlation between adult and recruit density in the manipulated and control plots in both years of her study. The role of structural habitat complexity in determining recruit density may then vary among locations or species, and further comparative-experimental investigation would be required to fully understand these processes.

Alternate recruitment substrates and primary **versus** ***secondary settlement/recruitment***

Two locations yielded positive significant correlations between recruitment into algae and the mussel bed, while the other two showed no significant correlation (Table 1.16). Different algal species were dominant within the mussel bed at the different locations, and this may have had an important influence on the results. The results may thus genuinely reflect a preference for recruitment into turf algae at some sites but not others, or for some algal species over others (McQuaid and Lindsay 2005).

Dwesa was the location with the highest simultaneous correlation between recruitment into turf and in to mussel bed. However, when Lasiak and Barnard (1995) studied the recruitment of *P. perna* into filamentous algal turf and mussel bed at this location in 1992-93, they found that recruitment into the two substrates was not simultaneous, with the mussel recruiting into mussel bed in winter (June to September) and into algae in spring/early summer (October to December). This disparity may be due to the differences in scales used in the two sets of observations, as Lasiak and Barnard examined mussels < 3.5 mm only, covered 70 m of coastline and sampled every 4-6 weeks, whereas I considered mussels < 5 mm, sampled sampled 3-monthly, and covered over 1000 m of coastline.

At Railway, Zululand, monthly algal sampling allowed for an exploration of the potential role of coralline turf algae (*Jania* and *Corallina* spp.) in facilitating settlement or recruitment of *P. perna*. Recruitment was denser into mussel bed than into algae at this location, so recruitment facilitation via algae is probably secondary to the primary mechanism of direct recruitment into mussel bed. Recruitment events were not simultaneous into mussel bed and turf algae. However, significant correlations were found between recruitment rates into algae and the density of juveniles in the mussel bed 2 and 3 months later. In contrast, there was no correlation between the density of recruits and small adults within the turf algae at any lag. This suggests that the mussels that recruit into the algae do not mature there, but instead migrate across into the mussel bed at a larger size, and that turf algae may therefore sometimes facilitate recruitment into mussel beds. Lasiak and Barnard (1995) refuted the primary-secondary settlement hypothesis for *P. perna* in Dwesa, concluding that *P. perna* recruits both directly into mussel bed and also uses algae as a facilitation mechanism; my results support their findings.

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Within-location spatial and temporal variability in recruitment

One of the most interesting results is that some locations were more variable among their replicate sites than others. Sites can vary in two ways, temporally or in the relative magnitude of recruitment (Figure 1.10). Temporal patterns were detected at all sites for all species, except for *P. perna* at Pt. Alfred and *M. galloprovincialis* and *A. ater* at Groenrivier. In two cases (*P. perna* and *S. algosus* at Namibia), there was not only a strong temporal pattern but the sites were also consistent in their ranking from year to year and season to season within species. However, when the recruitment levels of *P. perna* and *S. algosus* were compared among sites, the sites were ranked differently (Table 1.12). This might have been predicted, as these two species had different seasonal recruitment patterns, with *S. algosus* recruitment peaking in summer and *P. perna* showing a significant seasonal pattern that could not be interpreted with a post-hoc test, but appeared to peak in spring. Oceanographic conditions that change seasonally and thus favor the delivery of larvae to different sites in different seasons might ultimately drive these spatial patterns. The implication of these results from Namibia is that the ranking of sites in terms of their recruitment density can be species-specific even for organisms falling within the same functional group (e.g. mytilid bivalves).

Persistent differences in recruitment density among locations are common (e.g. Hughes et al. 2002; Navarrete et al. 2002) and may be attributed to the relative levels of spatial heterogeneity that in turn influence local hydrographic phenomena (wave action, current speeds, water temperature, onshore/offshore transport or retention mechanisms, nutrient supply). Other studies that address the spatial patterns of recruitment on medium scales (100 m to 10 km) have also found variability in patterns of recruitment, due to variable current speeds attributed to shoreline heterogeneity. Archambault and Bourget (1999), in their study of larval recruitment in the St. Lawrence Estuary, found that shoreline heterogeneity, particularly in terms of its influence on nearshore current speeds, significantly affected the relative recruitment rates of individual species at different sites. In fact, they found that shoreline heterogeneity was much more important than larval flux in predicting recruitment rates. Ebert and Russell (1988) used the size-structure of populations of the purple sea urchin, *Strongylocentrotus purpuratus*, to infer recruitment patterns in northern California and southern Oregon, USA, where upwelling is topographically predicable. They found evidence for low recruitment at capes and headlands, sites with upwelling, and high recruitment in regions between headlands that lacked upwelling. McCulloch and Shanks (2003) also found that very nearshore oceanography, determined by shoreline topography, had strong effects barnacle recruitment, and weaker effects on mussel recruitment. Finally, in their investigation of the latitudinal gradient in the recruitment of barnacles along the coast of California and Oregon, Connolly et al. (2001) found that meso-scale oceanographic features, which are in part driven by shoreline heterogeneity, were more important in explaining recruitment variability than latitude.

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Within-location temporal variability in recruitment – seasonal trends

Harris et al. (1998) reported no clear seasonal patterns of recruitment intensity in Namibia (*P. perna* and *M. galloprovincialis* combined, excluding *S. algosus*) or Groenrivier (*M. galloprovincialis* and *A. ater* combined), but detected autumn and winter peaks for the Cape Peninsula (*M. galloprovincialis* and *A. ater* combined). They also reported two annual recruitment events for *P. perna* on the East Coast, the first and larger one in spring and the second in winter. Although the coarse temporal scale of recruitment sampling may have masked some seasonal or intra-seasonal patterns, my longer-term data revealed several important trends that may crucial to understanding patterns among locations at the three-monthly scale.

In Namibia, *P. perna* showed a clear seasonal trend, recruiting in the second half of the year in three of the five years sampled (Figure 1.9), while *M. galloprovincialis* recruited in one large autumn and then one small spring peak in 1997 and has not recruited again to date (B. Currie, pers. com.). *S. algosus* showed a strongly significant seasonal pattern, peaking in summer and with diminished recruitment in June to September of each year.

In contrast to other studies that have shown increased recruitment during the upwelling seasons on the west coast of South Africa (van Erkom Schurink and Griffiths 1990; Robinson 2005; M.C. Pfaff and G.M. Branch, unpubl. data), neither Groenrivier nor the Cape showed a strong seasonal recruitment pattern for either *M. galloprovincialis* or *A. ater* (Figure 1.9). Spawning events on the West Coast may have been linked to patterns of *in-situ* temperature, as the protracted asynchronous spawning events evidenced at the Cape Peninsula for both *M. galloprovincialis* and *A. ater* are consistent with the limited annual signal in the temperature cycle at these locations (van Erkom Schurink and Griffiths 1991a). Here, pulsed upwelling-positive wind events can cause temperatures to fluctuate widely and rapidly, varying up to 9°C between one day and the next. These fluctuations are more common in the summer upwelling season, and mean temperatures are cooler in the summer than in the winter (Andrews and Hutchings 1980; Demarq et al. 2003). A more constant supply of larvae into the water column during protracted spawning periods, in combination with persistent onshore-transport mechanisms (i.e. regular relaxation events in this pulsed upwelling system) could explain the near-absence of any temporal pattern of recruitment at these two locations. On-offshore current velocities caused by upwelling are very slow, and a larva might be able to retain its position in the nearshore simply by swimming up or down against that current, however, as shown by Shanks and Brink (2005) in the more weakly upwelled Duck, North Carolina, USA. The coarse temporal sampling regime could also be the cause of the disparity between the observed patterns and previously published data (Caley et al. 1996), as most other studies of recruitment on the West Coast have sampled recruitment on a monthly (or more frequent) basis (e.g. Robinson 2005; M.C. Pfaff and G.M. Branch, unpubl. data).

On the South and East Coasts, the nearshore sea temperatures differ approximately 6°C between the warmer summer and cooler winter (Roberts 2005; Chapter 2, Figure 2.11). Most

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locations on the South and East Coasts had significant seasonal patterns with regular annual recruitment events. On the East Coast, the primary recruitment peak was in spring with a secondary autumnal peak. Berry (1978) reported spawning events towards the end of the year for *P. perna* in Durban, as water temperatures rise from the winter minimum to the summer maximum (July to December). At Dwesa, a single event was recorded in March-June 1996. Lasiak (1986) found that *P. perna* spawns earlier in the year (March to Sep) near Dwesa. These annual spawning patterns were consistent with the local recruitment patterns found on the East Coast and at Dwesa (Figure 1.8a). Ndzipa (2002) recorded spawning in June to November for *P. perna* at Port Alfred, although recruitment there did not follow any seasonal pattern. At Port Elizabeth recruitment peaks occurred in autumn of each of the years of my study, just before the spawning times reported by Ndzipa (2002). Therefore, spawning and recruitment times at these locations were not synchronized, and spawning at Port Alfred may be disconnected from recruitment at Port Elizabeth, reinforcing the hypothesis that these populations are largely reproductively independent despite being only 100 km apart on a relatively straight stretch of coatline. McQuaid and Lawrie (2005) recorded recruitment peaks in autumn and spring at Port Alfred, but with higher recruitment of plantigrades in autumn than in spring, and this matches the results for Port Elizabeth, but not Port Alfred, in this study. This could indicate either that the recruitment of Port Alfred is highly variable, or that it was anomalous during the years measured here.

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Implications for management of mussel stocks

Low recruitment and proximate harvesting at Dwesa

In terms of conservation, the mussel beds at Dwesa appear to be the most critical of all the locations, with very low levels of recruitment and mussel density, and recruitment limitation. Mussel beds in and surrounding Dwesa have been of concern to managers and researchers for almost two decades (Lasiak 1991a; Dye 1992a; Dye et al. 1997; Dye and Dyantyi 2002). In an analysis of contemporary coastal shell middens from 1987-89 in areas near Dwesa, Lasiak (1991b) noted that although *P. perna* is susceptible to depletion through unsustainable harvesting practices, the stocks have persisted despite heavy harvesting and showed no sign of recruitment failure, suggesting that the stocks must be maintained, at least in part, by larval supplies from populations beyond the exploited areas. As Dwesa is a small reserve, heavy harvesting of mussels on proximate ledges could cause the opposite effect – a significant reduction in larvae potentially available to settle in the reserve, thus limiting recruitment. Both legal and illegal harvesting have previously been implicated as a serious threat to mussel stock maintenance and recovery on the rock ledges surrounding Dwesa, and northern areas within Dwesa were heavily impacted by poachers in 1994 (Dye et al. 1997). High levels of legal harvesting outside and poaching within the reserve may explain the low recruitment rates that I recorded at Dwesa. If the possibility of replenishment from proximate sites is reduced, and if recruitment levels and bed density at Dwesa remain as low as they were during my study, this has important implications for management of mussel stocks in the area.

Mussel bed dynamics and diminishing returns in low recruitment environments

The width, percent cover and size structure within mussel beds are never constant over time, and can vary at multiple temporal scales. Wave action and the concussion of large objects against the rocky shore can dislodge portions of the mussel bed (Shanks and Wright 1986). The intense and rapid fluctuations of the bed width at Island Wreck, Groen, may have been due to such events (G.M. Branch, pers. com.). Predation by various terrestrial and marine organisms (Hockey and Underhill 1983), parasites and disease (Calvo-Ugarteburu and McQuaid 1998a, b), competition for space and resources within the mussel bed or at the edges (Steffani and Branch 2004), and smothering by sand and sand scour (van Erkom Schurink and Griffiths 1993) can all cause mortality, thereby reducing mussel bed width, density or cover. Sanding events were observed during my study, including one at Kenton East, Port Alfred from which the bed recovered immediately, and one at Railway North, Zululand, which caused severe mortality and a slow (2-year) recovery to the previous bed width.

The mortality of adult mussels, when not sufficiently replenished with adequate levels of annual recruitment, will cause a slow 'winding-down' of the mussel bed. This was evident for mussel cover at Port Alfred, Durban and Zululand (Figure 1.8b) and for bed width at Groenrivier and Dwesa (Figure 1.8c). Additionally, a reduction in the proportion of small adults in the mussel bed was evident at Namibia, the Cape, Dwesa and Zululand, indicating a lack of sufficient replenishment of young individuals into the mussel bed over the course of the study.

Thus, evidence of winding-down, direct or indirect, was present at every location in the study. So how do the mussel beds persist? Mussel beds can increase in width in several ways, including the settlement and recruitment of early and late plantigrade mussels directly into the mussel bed. Additionally, plantigrades may settle into adjacent algae or other substrates and then migrate into the bed at a larger size (Lasiak and Barnard 1995; Baker and Mann 1997; McQuaid and Lindsay 2005; Alfaro 2006b), and secondary settlement of large mats dislodged from other areas may land and attach, blanketing and smothering the organisms that were there before (G.M. Branch, S. Eekhout and F.J. Odendaal, unpubl. data). My study demonstrates that the magnitude of recruitment events varied temporally in both low and high-recruitment environments and for both low and high-recruiting species. Organisms with high fecundity and high pre-reproductive mortality that spawn in unpredictable nearshore environments can occasionally experience 'sweepstakes' recruitment events, in which, seemingly by chance, unusually high numbers of individuals recruit in a single year (e.g. Flowers et al. 2002). On the West Coast, these sweepstakes blanket-recruitment events are fairly common, on intra-decadal (3-6 year) time scales (G.M. Branch, pers. com.). It is certain, however, that my study did not record the full variability of recruitment densities on the East Coast, as evidence suggests that mussel stocks recover with large blanketing settlement events on a multi-decadal time scale. As described above, Berry (1978) reported normal June recruitment of *P. perna* in Durban in 1973, 1974 and 1975, with settlement predominantly on and around pre-existing mussel clumps. In 1976, he described a normal June settlement, followed by an anomalous 'massive' recruitment event in October, which extended along the entire coast of the Natal bioregion (including both Durban and Zululand), and was so dense that late plantigrades attached to every available surface, blanketing the entire intertidal zone. Where mussel beds had previously disappeared, they were fully re-established by this event. A second event occurred in the spring of 1994 in Zululand, whereby up to 100% of mussel beds and patches of coralline algae were densely covered by *P. perna* recruits, but this event did not extend to Durban (B. Tomalin, pers. com.). Similarly, Witman et al. (2003) report a massive recruitment event of subtidal mussels in the Gulf of Maine in 1995, which had important effects for both consumers and local competitors. Witman et al. concluded that episodic events such as these are important in marine community dynamics. A similar event has not been witnessed again in Natal to date, but it can only be concluded, as Berry (1978) did, that *P. perna*, and possibly other low-recruiting species as well, undergoes important natural fluctuations at intervals well beyond the temporal scope of my study.

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1.5 CONCLUSION

The hierarchically-nested design of this study of mussel recruitment around southern Africa allowed a detailed investigation of recruitment patterns and processes at multiple spatial scales. Recruitment patterns were found to vary bio-regionally, recruitment levels being extremely high on the West Coast but moderate to very low on the South and East Coasts. Whether and how these patterns are linked to processes at each of the locations will require further investigation, but recruitment intensity was correlated with a combination of relative productivity and nearshore meso-scale oceanographic features that may enhance retention. Two locations appeared to be recruitment limited, Port Elizabeth and Dwesa, and of these Dwesa is more critically in need of active management as it has experienced a sustained decrease in both bed width and cover. Recruitment patterns varied among sites at several locations, perhaps because of higher spatial heterogeneity causing differences in onshore-transport mechanisms such as internal tides and associated internal waves and bores, eddies and retention cells, areas of reduced alongshore current speed or the presence of rip currents in the surf zone. As these mechanisms are likely to vary among sites, or even among stretches of coastline within each site, they are thought to be associated with varying levels and scales of topographic heterogeneity. Recruitment also varied among species and among sites within species, reflecting both differences in reproductive strategy and adult survival among locations and bioregions. The density of recruitment peaks at most localities was persistent over time, and seasonal patterns matched those recorded in the literature for some but not all locations. The departures may indeed be real, as recruitment patterns remain somewhat unpredictable. The coarse temporal sampling and the use of natural substrata may have allowed post-recruitment density-dependent mortality to mask some recruitment peaks however. Studies at finer temporal scales using both natural and standardized artificial substrates are therefore essential to move towards a better understanding of site-level and intra-seasonal recruitment processes; these have already been undertaken at some locations subsequent to the collection of the data reported here (Porri 2003; Erlandsson and McQuaid 2004; McQuaid and Lawrie 2005; McQuaid and Lindsay 2005; Robinson 2005; M.C. Pfaff and G.M. Branch, unpubl. data; Chapters 2-4), and should be continued and expanded to the remaining understudied bioregions.

Southern African mussel stocks are important ecologically, economically and socially throughout the region. Their effective management relies on an understanding of their population dynamics, including the processes that limit or are limited by the supply of recruits. The coastal environment is under increasing pressure from human populations, and they grow and shift from the interior to the coast. In response, the South African Marine Living Resources Act of 1998 has mandated the protection and management of natural marine resources. The coastal areas of southern Africa are diverse (Lombard et al. 2004), and McQuaid and Payne (1998) argue that different regions should have different, specialized management strategies. These conclusions are not unique to southern Africa (e.g. Navarrete et al. 2005), and indeed, my findings support them.

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CHAPTER 2

A dip into the larval pool: spatial and temporal patterns of bivalve and barnacle meroplankton in the Maputaland Marine Reserve

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2.1 INTRODUCTION

It has long been understood that oceanic processes affect the recruitment of intertidal benthic organisms with a meroplanktonic larval stage, and are therefore a potential determinant of intertidal community structure (Roughgarden et al. 1988), although this is not always realized (Forde and Raimondi 2004). Researchers modeling settlement or recruitment processes often refer generally to a 'larval pool' of unknown but assumed constant density (e.g. Palmer et al. 1996; Pineda 2000), and a homogenous larval pool has been a necessary assumption for modeling exercises involving recruitment dynamics. However, the larval pool is, in reality, patchy, and an understanding of both the scale of patchiness and the shape of patches is important. Recently-spawned larvae may enter the water column as a cloud of constant density, but they are immediately both advected and diffused by currents (Largier 2003). Slow sheared currents may retain them in embayments or eddies, or accumulate and transport them in slicks associated with fronts or internal waves (Shanks 1983; Kingsford 1990; Archambault and Bourget 1999; Shanks et al. 2000; Paris et al. 2002), rip currents may shoot them offshore or entrain them in surf-zone cells (Smith and Largier 1995), and breaking internal waves or tidal bores can carry them shoreward (Pineda 1999). As a result of extended time in the water column, the actual shape of the larval pool may more likely resemble the spatial and temporal patchiness of a 'tattered curtain' (Roughgarden et al. 1991a). The physical conditions that will affect the spatial and temporal structure of the larval pool can be both local and regional, and will further interact with levels of predation and food availability (Morgan 1995a), as well as the life-history characteristics of the individual species (Grantham et al. 2003). There are some examples, such as particle-tracking models used in conjunction with three-dimensional hydrodynamic models for offshore fisheries management, which take into account hydrographic deformations of the larval pool (e.g. Huggett et al. 2003), but these have rarely been applied to coastal recruitment problems (but see Penven et al. 2000; Largier 2003). These characteristics ultimately influence connectivity, determining how larvae can interact with the available physical transport mechanisms that will return them to their adult habitat (Roughgarden et al. 1991a).

Once spawned, the alongshore distance that meroplanktonic larvae travel is influenced both by the distance that they are advected and diffused away from the shore and by the mechanisms by which they return (Largier 2003). Researchers in different coastal areas have attempted to characterize the nature of onshore and offshore transport mechanisms, as well as retentive features that are likely to enhance or reduce the diffusion and advection of the meroplankton of intertidal

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benthic invertebrates (e.g. Wing et al. 1995a, 1998; Epifanio and Garvine 2001; Narváez et al. 2004; Tapia et al. 2004). These meso-scale features vary in their appearance and importance among locations, and therefore must be investigated, described and considered in each region separately (Narváez et al. 2004). Roughgarden et al. (1991a) identified upwelling events associated with barnacle settlement pulses in central California, and these processes were subsequently incorporated into advection-diffusion models of larval transport and population dynamcis (e.g. Alexander and Roughgarden 1996). Upwelling and downwelling have thus been investigated, but not always identified, as transport mechanisms for other species with a meroplanktonic larval stage (e.g. Wing et al. 1995a, b; Shanks et al. 2000; Cudaback and Largier 2001; Poulin et al. 2002; Almeida and Queiroga 2003; Shanks et al. 2003b; Shanks and Brink 2005). Alongshore wind is largely responsible for the induction of Ekman transport and the on- or offshore transport of coastal water, but across-shore winds (sea-breeze effects) have also been associated with across-shore currents and could therefore affect larval transport (Tapia et al. 2004). Additionally, internal waves and internal tidal bores, with their associated surface-slicks, have been identified as potential onshore transport mechanisms (Shanks 1983; Kingsford 1990; Pineda 1991, 1994), and have been found to transport larvae in several locations, including Oregon (Shanks and McCulloch 2003), South Carolina (Shanks 1988), California (Pineda 1995; Pineda and Lopez 2002), and Baja California (Ladah et al. 2005). Finally, these onshore/offshore transport processes can be mitigated by shoreline features that shear alongshore currents, creating eddies, upwelling shadows, or topographically-generated convergences, providing retention zones inshore, or enhanced by features that create offshore jets or rip-currents, pushing larvae away from the shore (Graham and Largier 1997; Chiswell and Roemmich 1998; Wing et al. 1998; Chiswell and Booth 1999; Gibbons et al. 1999; Hutchings et al. 2002; McCulloch and Shanks 2003; Shanks et al. 2003c).

The Maputaland Marine Reserve lies within the Greater St. Lucia Wetland Park and World Heritage Site in KwaZulu-Natal, and comprises the entire South African portion of the Delagoa inshore marine bioregion (Lombard et al. 2004). The area is understudied, and supports great intertidal diversity on low-lying rocky semi-exposed to exposed headlands interspersed with long stretches of sandy beach (Sink 2001; Sink et al. 2005). Park residents of the Thonga ethnic group participate in a traditional subsistence fishery of the brown mussel, *Perna perna*, which requires co-management by the communities in conjunction with park administrators (Kyle et al. 1997a; Harris et al. 2002a, 2003). To address management needs, this study investigates the planktonic distribution of the larvae of mussels and barnacles to begin to understand the connectivity between rocky-shore populations in this protected area, and tests five hypotheses: (1) Because the area is energetic, with high winds and surf, the water column will be generally mixed, with no thermoclines or haloclines in depths of < 20 m. Because winds are generally alongshore, this will stimulate Ekman transport, and therefore some coastal upwelling and downwelling. (2) The larval pool, as well as pytoplankton measured at the surface with remote sensing or below the surface,

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measured in the field, will be patchy. Patches will either be associated with particular water temperatures or entrained (aggregated) in coastal embayments. (3) Strong along-shore winds will induce upwelling and downwelling, with associated changes in temperature and nutrients. (4) Based on evidence from other areas, cyprids will be generally found near the benthos and mytilids near the surface during daylight hours, so they are likely to be differently carried by onshore-offshore transport mechanisms, including upwelling. (5) Shore-parallel foam lines or slicks, observed regularly in this area and generated by topographic features, will be convergence zones for positively buoyant and swimming meroplanktonic larvae.

2.2 METHODS

I assessed the distribution of bivalve and barnacle larvae in the water column around and between five adjacent rock ledges within a 25-km stretch of the Maputaland Marine Reserve (MMR) in relationship to wind velocity, continuous subsurface temperature, temperature and salinity profiles, concentrations of phytoplankton determined using chlolophyll *a* (chl *a*) concentrations measured in the field, and surface temperature and surface phytoplankton measured with 1-km resolution satellite imagery of sea surface temperature (SST) and chl *a*. In the specific case of the brown mussel *Perna perna*, the abundance of mytilid larvae was then related to the density of the adult spawner stocks on adjacent rock ledges.

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Study Area

The Maputaland coastline runs NNE-SSW, and is gently scalloped by a series of regular, zeta-shaped sandy bays connecting low-lying platform headlands of aeoleonite or beachrock (Ramsay and Mason 1990; Miller and Mason 1994; Ramsay 1994). The bays vary in length from 5-10 km, and in width from 1-1.5 km (Figure 2.1), and are generally sandy, but contain some small patches of low-lying algal- or coral-dominated subtidal reef (Schleyer 1999; Lawrence 2005).

Black Rock lies at the center of the study area, where a near-pristine refuge of adult *P. perna* can be found on the southern half of the rock ledge. To investigate the potential for larval connectedness of Black Rock with its neighboring rocky headlands, zooplankton densities were measured directly off Black Rock and at two rocky points on either side, and also in the bays lying north and south of Black Rock (Figure 2.1).

Field Sampling Methods

All plankton sampling was completed during the day over running or slack low spring tides. The northern Maputaland coastline is exposed and rough (Sink 2001), lacking natural coves or harbors. For sampling trips, boats had to be towed onto the beach and launched through the surf.

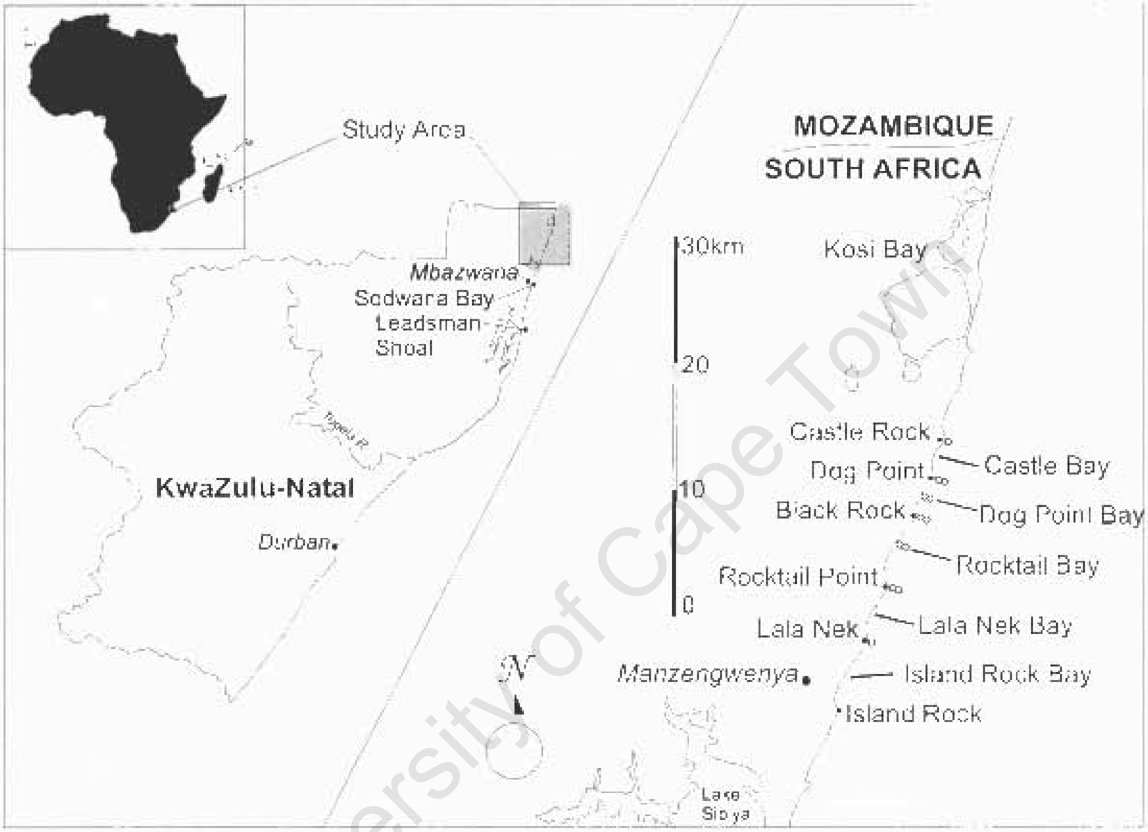

Figure 2.1 Map of the plankton sampling stations in the Maputaland study area, within the (Grey square). White dots represent the sampling stations, black dots represent the center of the rocky ledges.

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The study area lies across 'sanctuary' and 'restricted' zones of the park, where public access is restricted. Vehicle access onto the beach is allowed for management staff and permitted researchers only; driving is restricted to below the high-tide water mark and from three hours before to three hours after spring low tide. As the coastline lacks electric lighting, all nearshore boat operations are restricted to daylight hours.

Sampling stations were identified and relocated using a Garmin E-Trex GPS (WGS-84 datum, accurate ± 5 m) and a depth sounder. The sampling grid consisted of 12 stations, seven inshore (500 m from shore) and five offshore (750 m from shore), spanning 25 km from north to south, and was designed to be completed over two consecutive days on each sampling occasion. Additional hauls in the first year were made outside of this grid and are included in some analyses. All tows were necessarily made during favorable weather conditions, with winds under 15 kt and swell under 2.5 m, introducing an unavoidable weather-based bias into the data set. As sea conditions often deteriorated in the afternoon, plankton hauls were more successful in the mornings, and most days when the sampling set was completed had winds under 5 kt.

Launches were scheduled for three consecutive days per month during the *P. perna* spawning season, August to December of 2002 and 2003, plus three consecutive days in April 2003. Of the 33 scheduled launch days, launching was successful on only 18 days, and sampling was completed on 12 of those days. The entire sampling grid was completed in two days in only three of the prescribed months, December 2002 and April and November 2003.

Temporal and horizontal distribution of zooplankton

Horizontal plankton distribution is often assessed using vertical plankton hauls with circular conical nets (Wing et al. 1995a, b; McQuaid and Phillips 2000; Porri 2003), horizontal plankton net tows at various depths (Leis 1986; Le Fevre and Bourget 1991; Natunewicz and Epifanio 2001) or 12V submersible bilge pumps (Bertness et al. 1996; Graham and Sebens 1996; Caceres-Martinez and Figueras 1998), sampling in a grid pattern that includes replicates at various distances from shore and along the shore. A pilot study indicated that zooplankton densities are relatively low in Maputaland, so oblique vertical tows were used, integrating in both the vertical and horizontal plane in order to collect a sufficient amount of plankton per sample for valid analysis. Two independent oblique hauls, each lasting 3-5 minutes were carried out at each of the 12 stations (Figure 2.1, Table 2.1) using a 3-m long × 0.6-m diameter conical plankton net (surface area = 5.25 m^2) with a porous collar, 200-250 μm mesh, and an 11-cm diameter cod-end. Early-stage mussel larvae can be as small as 150 μm on the long axis (Bayne 1976), and so these youngest larvae may have escaped through the mesh of the net. Nets with a large pore size relative to the size of the target organism can significantly reduce a net's sampling efficiency for that size organism (Evans and Sell 1985). The results presented here therefore probably underestimate the true density of plankton < 300 μm, and should therefore be interpreted with caution. The net was fitted with a calibrated mechanical

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flow meter (General Oceanics Model 2030R with a low-speed 16.5 cm diameter rotor) placed asymmetrically in the mouth of the net, following Tranter and Smith (1968). For each tow, the net was lowered to the sandy bottom, the mouth lifted 50-100 cm, and the net then towed at less than 1 kt, slowly increasing the speed of the boat to lift the net higher and higher in the water, until it was towed just under the surface for the last 30 seconds at < 2 kt. Sand was trapped in some samples, but generally not more than 10-20 ml of sand was collected in any sample, indicating that this was of suspended, rather than benthic, origin. Following each tow, larvae were removed from the cod end and placed in a 600 ml jar. A 10 ml aliquot of 40% formaldehyde added and the container sealed. Samples were stored in a closed, darkened container to prevent sunlight bleaching.

Table 2.1 Summary of temporal and spatial distribution of zooplankton samples, showing the number of replicate oblique hauls (3-5 min long) taken at each station.

Site	Latitude	Longitude	Depth (m)	26 to 28 Aug 02	25 Sep 02	8 Oct 02	23 Oct 02	2 to 3 Dec 02	26 to 27 Apr 03	24 to 26 Aug 03	8 Oct 03	24 Oct 03	22 to 24 Nov 03
Lala Nek Point Inshore	27° 13.549' S	32° 47.855' E	10				2	2	2	2	2		2
Rocktail Point Inshore	27° 11.296'	32° 48.698'	10	1			2	2	2		2	2	2
Rocktail Point Offshore	27° 11.143'	32° 49.246'	15	1			2	2	2		2	1	2
Rocktail Bay Inshore	27° 09.471'	32° 49.140'	10	2				2	2		2	2	2
Rocktail Bay Offshore	27° 09.330'	32° 50.090'	15	2				2	2		2	2	2
Black Rock Point Inshore	27° 08.233"	32° 49.991'	10	1				2	2		2	2	8
Black Rock Point Offshore	27° 08.165'	32° 50.530'	15	1				2	2		2	2	6
Dog Point Bay Inshore	27° 07.496'	32° 50.323'	10	2	2			2	2			2	2
Dog Point Bay Offshore	27° 07.498'	32° 50.625'	15	2	1			2	2		2	2	2
Dog Point Point Inshore	27° 06.580'	32° 50.715'	10	1	2			2	2				2
Dog Point Point Offshore	27° 06.633'	32° 51.111'	15	2	2	2		2	2	2			2
Castle Rock Point Inshore	27° 04.775'	32° 51.078'	10		2	2		2	2	2			2

Three phytoplankton samples were taken per tow in all cases (one at 1 m, one at 3 m and one 1 m above the bottom). Single CTD dips were made at each station simultaneous to plankton sampling in sets from Oct to Dec in 2002 and Aug to Nov 2003. Supplementary samples within the study area, but outside of this sampling grid, were taken in 2002 and used in some analyses.

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Zooplankton - vertical stratification

On two occasions, the water column was sampled for vertical stratification of zooplankton using the same plankton net as above (Table 2.2). For each tow, the net was lowered to the selected depth and towed for 3-5 minutes at a constant speed, < 2 kt. At the end of the tow, the net was brought quickly to the surface, and the sample was processed as above.

Table 2.2 Zooplankton vertical stratification haul summary

Date	Location	Water depth (m)	Sampling depth (m)	Depth Category	n	Tow duration (min)	Mean volume filtered (m^3)
19 Sep 02	Black Rock Point	12	10	Bottom	3	3	105.2
		12	5	Mid	4	3	125.7
		12	1	Surface	4	3	179.3
19 Sep 02	Rocktail Bay	10	8	Bottom	3	3	111.7
		10	1	Surface	2	3	194.7
26 Nov 03	Black Rock Point	15	13	Bottom	1	5	143.6
		15	8	Mid	2	5	154.3
		15	1	Surface	2	5	166.4

Zooplankton – in and out of a topographically-induced foam line

A narrow shore-parallel foam line (1-2 m across) is regularly observed in the study area under conditions with along-shore wind velocities between 3-8 kt; above 10 kt it becomes masked by white horses and other surface features associated with higher winds. The foam line is generally formed 500-1000 m from shore at 10-20 m depths, and can span both headlands and bays. To assess its potential as a front line for zooplankton retention, oblique hauls were made beneath, shoreward and seaward of the foam line (Table 2.3). All samples were taken while traveling parallel to the foam line, directed into the wind. Samples taken outside of the foam line were randomly 20-40 m shoreward or seaward of the foam line.

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Table 2.3 Zooplankton foam-line oblique hauls in 15-20 m water depth; tow duration = 3 min. in all cases

Date	Location	In or outside of foam line	Water depth (m)	n	Tow duration (min)	Mean volume filtered (m^3)
17 Sep 02	Island Rock Bay	Out	15-20	3	3	276.2
		In	15-20	3	3	243.1
17 Sep 02	Rocktail Point	Out	15-20	2	3	163.5
		In	15-20	2	3	215.4
18 Sep 02	Rocktail Bay	Out	15-20	5	3	155.1
		In	15-20	7	3	170.4

Spatial and temporal patchiness of subsurface phytoplankton

Between the two plankton tows in each set at each station, duplicate water samples were taken 1 m below the surface, at 3-m depth, and at 1 m from the bottom. These samples were colleted in 500-ml darkened amber-glass pop-bottle containers, and stored in these containers in darkness until analysis.

In-situ *temperature and salinity measurements*

To assess stratification of the water, a temperature-salinity-depth profile (a 'dip') of the water column was measured at each sampling station using a Seabird Seacat SBE-19 Conductivity-Temperature-Depth (CTD) Profiler. Data were downloaded and processed using Sea Bird Electronics data-processing software (version 5.32a).

Benthic temperature

Benthic temperatures were taken every 30 min on a reef at 15 m depth in Sodwana Bay (27° 31.231' S, 32° 41.203' E, November 2002 to July 2005, 38 km from the study area) and at Leadsman Shoal (27° 52.419' S, 32° 36.216' E, August 2002 to May 2005, 100 km from the study area) with underwater temperature recorders (UTRs, Starmion Mini, manufactured by Star-Oddi, accuracy ± 0.05°C). As the coastline is fairly homogenous, and as these two loggers were within a reasonable distance from the study area, it was assumed that these measurements reflected conditions at the study area, so temperatures from these UTRs were used in calculations requiring continuous measurements.

The *in situ* sub-surface daily temperatures taken with the CTD at the observation sites (averaged over all stations for that day) were strongly correlated with simultaneous averaged daily benthic temperatures in Sodwana Bay ($r = 0.941$, $n = 8$, $p < 0.001$) and the Sodwana data strongly correlated with those on Leadsman Shoal ($r = 0.967$, $n = 45038$, $p < 0.0001$).

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Coastal winds

Hourly wind speed and direction were provided by the South African Weather Service from the Mbazwana Airfield (Climate Number 0412148-6, 27° 28.017' S, 32° 34.983' E, 61 m altitude), which lies 8 km west of the coast, 9 km NE of Sodwana Bay and 35 km SW of the study area (Figure 2.1).

Mussel adult stock density

The density of adult mussels on the shore was measured at each of the five rocky points in Oct-Nov 2003 and Nov-Dec 2004. Five or six shore-perpendicular transects were sampled, each 4 m apart and stretching from the top to the bottom of the mussel zone. Using quadrats of 100 × 50 cm, the number of mussels in one quadrat per meter was measured along each of the transects in the following size categories: adult *Perna perna* (> 35 mm), juvenile *P. perna* (10-35 mm), and small mussels (2-10 mm, *P. perna* and *Brachidontes semistratus* combined).

Laboratory procedures

Phytoplankton

Within eight hours of sample collection, the microalgal content of the water was filtered onto glass fiber filters (Whatman GF/F or Advantec GF 75). Chlorophyll was then extracted into 10 ml 90% acetone, and stored at 4°C in darkness. Within 72 h of filtration, the extract was transported on ice to Durban, and the supernatant analyzed using a Turner Design 10-AU fluorometer (narrowband, non-acidification method) following Welschmeyer (1994). The chl *a* content concentration was calculated using the formula:

$$\text{Chl } a = \frac{V_A}{V_W} * R$$

where V_W is the volume of water filtered in ml, V_A is the volume of acetone used in the extraction and R is the reading of the sample (converted to mg chl *a* with a calibration factor within the instrument). The concentration of chl *a* ($g.m^{-3}$) was thereafter used as an indication of phytoplankton biomass.

Zooplankton

To process the zooplankton samples, any large organisms (> 8 mm diameter) were first removed. Samples were then filtered through 200-µm mesh and resuspended in 4% formalin buffered with 1% sodium acetate ($NaC_2H_3O_2$) in de-ionized water, pH 7.0-7.5. The resuspended samples were then placed in a 100-ml graduated cylinder and allowed to settle undisturbed in the dark for 24 h. The settled volume was recorded and the sample then stored in buffered formalin in the dark for later analysis.

As each sample was large (settled volumes 4-75 ml), triplicate 5-ml subsamples were drawn off the samples for the identification and enumeration of organisms, following Kibirige and Perissinotto (2003). The sub-samples were placed in a channeled sampling dish tray. Using a stereo microscope, all bivalve larvae, mytilid larvae, cyprids and nauplii were measured and counted, although nauplii proved too scarce for analyses to be reported.

P. perna larvae have been identified in the plankton along the south coast of South Africa (McQuaid and Phillips 2000; Porri 2003; McQuaid and Lawrie 2005). The mytilid larvae I examined comprised veligers and pediveligers of the same size range and shape as those of *P. perna* in these studies. However, as mytilid bivalve larvae can closely resemble each other, my material may also have included larvae of other Maputaland mytilids including *Brachidontes semistriatus, Septifer bilocularis, Arcuatula capensis* and *Modiolus auriculatus* (Branch et al. 1994; Sink 2001). For the barnacles, descriptions of the naupliar stages of *Tetraclita serrata* (uncommon in Maputaland) and *Tetraclita squamosa rufotincta* (common) were made by Griffiths and King (1979) and Barnes and Achituv (1981) respectively, but cyprid illustrations were available for *T. serrata* only (Griffiths 1979). Cyprids were therefore not identified to species, but are likely to be

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T. squamosa rufotincta or other local species, including *Chthamalus dentatus* (common) and *Octomeris angulosa, Notomegabalanus cylindricus* and *Balanus amphitrite* (less common).

As the larvae of mytilids, other bivalves and barnacles could not be identified to the level of species, they were grouped into three taxa: all bivalves, mytilid bivalves, and cyprids. The bivalve group included all veligers and pediveligers (0.2-2.0 mm shell length) present in the sample.

Data Analysis

All statistics were computed using Statistica 7.0 (StatSoft, Inc. © 1984-2004).

Patterns of zooplankton biomass and density: horizontal and temporal

A Kruskal-Wallis test was used to examine temporal (monthly) and spatial patterns (by station). Data were transformed for homogeneity of variances. Nonparametric multiple post-hoc comparisons of the average ranks were then computed for each significant result.

To examine the inshore-offshore pattern of variability within the larval pool, a Student's t-test for dependent variables was employed, comparing density at the inshore station against that at the station immediately offshore ($n = 35$). Each response variable was $\ln(x+1)$ transformed to achieve normality (determined with normal probability plots) and homoscedascity (determined with the Brown and Forsythe's test) (Quinn and Keough 2002). Following this same method, the density within bays versus that at headlands was compared, averaging values for each day that had samples from both bays and points ($n = 11$).

Patterns of sub-surface phytoplankton distribution and temperature

Vertical stratification and horizontal and temporal patterns in the distribution of phytoplankton were explored. There were too many missing cells to warrant a multi-way ANOVA of these data, as this would have been a severely unbalanced design (Underwood 1997). However, as the log-transformed response variable was normally distributed with homogeneous variances for all three tests (horizontal, vertical, temporal), three one-way ANOVAs with type VI (unique) sum of squares were used, followed by Tukey's HSD for unequal n post-hoc tests ($\alpha = 0.05$) in cases of significant results. Tukey's HSD for unequal n post-hoc test is not robust to extremely variable sample sizes. Therefore, cells with less than 30% of the maximum n per cell were removed from each analysis.

Relationships between benthic temperature, phytoplankton concentration and larval density

Multiple linear regression analyses with the pairwise deletion of missing cells were used to investigate the relationships between zooplankton-density continuous response variables (settled volume, numbers of cyprids, all bivalves and mytilids), with specific physical variables (benthic temperature, *in situ* salinity and the station's longitude) and biological variables (zooplankton

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settled volume, numbers of cyprids, bivalves or mytilids) as independent parameters. As the benthic temperature data from Leadsman were most complete, these daily-averaged temperatures were substituted for the CTD data set for these calculations. The examination of the interaction terms available through a more complex general linear model was not pursued due to the problem of missing data points for each of the independent factors in the models. Data were examined for normality, co-linearity and heterogeneity of variances and the response variables were $\log_{10}(x+1)$-transformed to achieve normality. The model was checked to ensure that the residuals were normally distributed, and highly skewed independent biological variables that could affect the normality of the error term were log-transformed following Quinn and Keough (2002).

Zooplankton – in and out of a topographically-induced foam line

The data for zooplankton biomass (ml settled volume), numbers of cyprids, all bivalves and mytilid bivalves were compared in and out of the foam line using a two-way factorial ANOVA, with site as a random factor and in or out of slick as a fixed factor, using a type III (orthogonal) sum of squares. The data were transformed to meet assumptions ($\log_{10}(x+1)$ for biomass and mytilids, fourth-root for cyprids and bivalves). Post-hoc results were assessed visually using box-plot diagrams and non-parametric one-way comparison tests.

Zooplankton - vertical stratification

The stratification of zooplankton (biomass in ml settled volume, numbers of cyprids, all bivalves and mytilid bivalves) was investigated with a Kruskal-Wallis test, which is robust to non-normal distributions and varying sample sizes (Quinn and Keough 2002). Homogeneity of variance was examined using boxplot distributions and maximized using $\log_{10}(x+1)$ or fourth-root transformations (Quinn and Keough 2002). Significant results were examined using a nonparametric multiple post-hoc comparison of the average ranks, computed using normal z-values; post-hoc probabilities were corrected for the number of comparisons and computed for a two-sided test of significance in each case.

Remotely-sensed sea-surface temperature and phytoplankton

Biweekly 1-day to 3-day composite Advanced Very High Resolution Radiometer (AVHRR) 1-km resolution satellite sea-surface temperature (SST) and surface chlorophyll *a* (chl *a*) images, taken by the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite were used to investigate the patch scales of these two variables and their relationship. Like for the chl *a* measured in the field, surface chl *a* was used as an indication of phytoplankton concentration in surface waters.

SST data were first verified against the daily average subsurface (15 m) temperature data from the benthic temperature logger at Sodwana Bay using Pearson product-moment correlation. A

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square cell of nine pixels (9 km^2) lying over each of the loggers was selected. Surface chl *a* and temperature data were de-spiked (impossibly high or low values that indicated measurement errors were replaced with values using linear interpolation), and these nine pixels were then averaged and compared to the mean subsurface temperature for that day. Satellite SST data were strongly and significantly correlated to the simultaneous daily averaged subsurface (15 m) temperature data, and were on average ~1°C warmer ($r = 0.944$, $n = 15$, $p < 0.0001$, benthic temp = 3.806 + 0.816 * SST). Surface chl *a* was significantly negatively correlated with both temperature measurements (SST: $r = -0.706$, $n = 15$, $p < 0.01$; benthic: $r = -0.616$, $n = 15$, $p < 0.05$) (Figure 2.2a). As the relationship between daily surface and bottom temperatures was strong and significant, the daily mean of the running monthly benthic temperature anomaly record was used for time-lag correlation analysis between the concentration of chl *a* and temperature. No correlations were significant except for that at lag +1, comparing chl *a* to the temperature anomaly from the day before, indicating an increase in the chl *a* concentration 24 hours after a decrease in benthic temperature (Figures 2.2b and c).

Eight cells of two adjacent pixels closest to the coast spanning the study area were averaged for each date, as were eight cells of four adjacent pixels 5 and 10 km directly offshore from these, plus two cells of four adjacent pixels 17 km offshore (Figure 2.3). The simultaneous relationship between SST and surface chl *a* for all of the cells (within the study area, plus the two cells at Sodwana and Leadsman) was then examined with Pearson product-moment correlations. As surface and benthic temperatures were strongly positively correlated, the benthic temperatures were then used for time-lag correlation analysis between phytoplankton and the daily mean benthic temperature at Sodwana and Leadsman. The lag time-step was set as one day, and analysis was performed for ± 20 lags. The scales of patchiness of SST and surface phytoplankton were examined with a spatial autocorrelation analysis using multiple Pearson product-moment correlations with a pairwise deletion of missing cells. A matrix was created correlating the SST and the chl *a* concentration in each cell against every other. These r-values were then plotted against the distance between the cells to find the distance-scale at which the cells became de-correlated, indicating the patch size of the parameter in question.

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Patterns of winds and benthic temperature

The primary coastal winds in Maputaland are alongshore, switching between NNE and SSW at regular intervals (Hunter 1988). NNE winds are potentially upwelling-positive, as they induce offshore Ekman transport of the surface layer (Mann and Lazier 1996). The link between alongshore wind velocity and benthic temperature was first examined with time-lagged Pearson product-moment correlation analyses with a pairwise deletion of missing values. The hourly means of benthic temperature were de-trended with a running 30-day mean. These were then compared to the hourly mean of the 20° alongshore component of the wind velocity from Mbazwana Airfield at 80 time lags (lag = 1 hour). High r-values between upwelling-positive winds and a subsequent

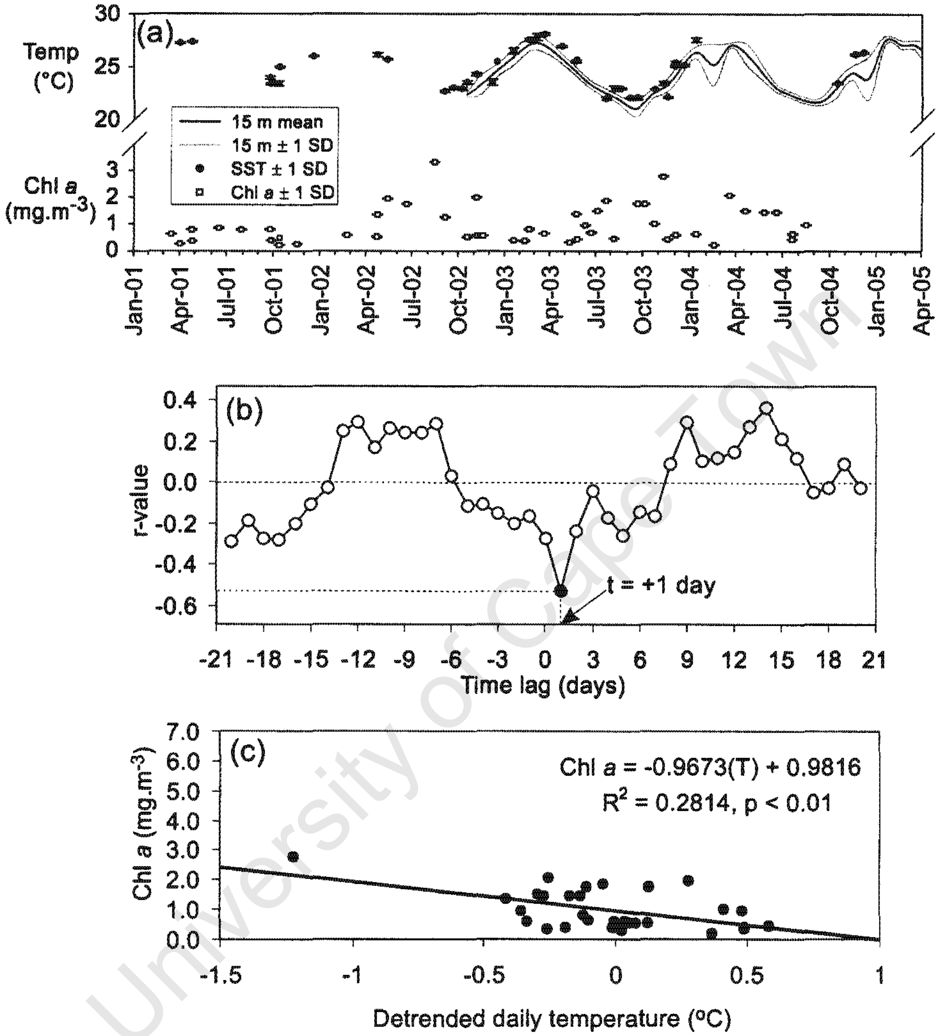

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Figure 2.2 (a) Surface and subsurface temperature and surface phytoplankton, measured using chl *a*, at the site of the Sodwana Bay underwater temperature logger (UTR). Black line is monthly subsurface temperature ± SD from UTR at 15 m depth. Black circles are the mean SST ± SD taken from the nine nearest 1 x 1 km^2 resolution pixels from bi-weekly satellite images (creating a 3 x 3 km^2 cell). White squares are the mean density of surface chl *a* ± SD measured in these same pixels. SST and phytoplankton were significantly negatively correlated. (b) Time-lagged correlation analysis of detrended subsurface temperature and phytoplankton. No correlations were significant except time lag +1, or chl *a* one day after subsurface temperature, indicating an upwelling response. (c) Pearson product-moment correlation of detrended daily temperature with phytoplankton at lag +1.

reduction in benthic temperatures (residual temperature after removal of the 30-day running mean) 12-36 hours following the wind was identified *a priori* as a potential upwelling response.

The relationship between wind and benthic temperature was then tested by examining the frequencies at which the power spectra of detrended hourly wind (along- and across-shore, or 20° and 110° from true north, respectively) and sub-surface temperature were significantly coherent. A climatology of the monthly winds and water temperature was compiled. A subset of the data was selected from the wind and temperature data sets to minimize missing values but maximize length; this set spanned 31 October 2003 to 8 July 2005. Although there were some missing data points in the wind data, there were never more than five consecutive missing values, and these were filled in using linear interpolation. No values were missing from the temperature record. Using the climatology, these data were then sub-divided, to examine the differences between the windy (July to Jan) and non-windy (January to July) seasons, and according to recruitment seasons (Chapter 3): September to April (recruitment season for mussels and *C. dentatus*) and April to September (recruitment season for *Tetraclita* spp.). All calculations were performed using Matlab v6 (© 1984-2000, The Math Works, Inc.).

A power spectral density estimate (PSD) of the detrended hourly temperature series was then computed with Welch's method (Welch 1967) with a window of 2048 values, an overlap of 1024 values and 2048 discrete Fourier transform points (nfft). The PSD was then plotted against frequency in the period window of 0.5-56 days to look for dominant patterns, specifically tidal (14 or 28 d), upwelling (3-10 d) or diurnal (1 d) signals.

Power spectra of the detrended whole data set (window = 1028, overlap = 512, nfft = 1028) and of the detrended subsets (window = 512, overlap = 256, nfft = 512) were then computed using Welch's method, and the values plotted against frequency. Estimates of the squared coherence of temperature and across-shore wind, and of temperature and along-shore wind, were calculated. The number of sections in each data set (s) was first determined using the original number of data points (n):

$$s = 2 * \left(\frac{n}{nfft} \right) - 1$$

The degrees of freedom (df) were then calculated:

$$df = \frac{36s^2}{19s - 1}$$

Finally, the level above which the squared coherence was significant was calculated using the desired significance level (α):

$$1 - \alpha^{2/(df-2)}$$

Significant coherence at frequencies higher or lower than the ecologically-relevant window (periods greater than 14 days or less than one day) was not reported. In cases where more than four of the

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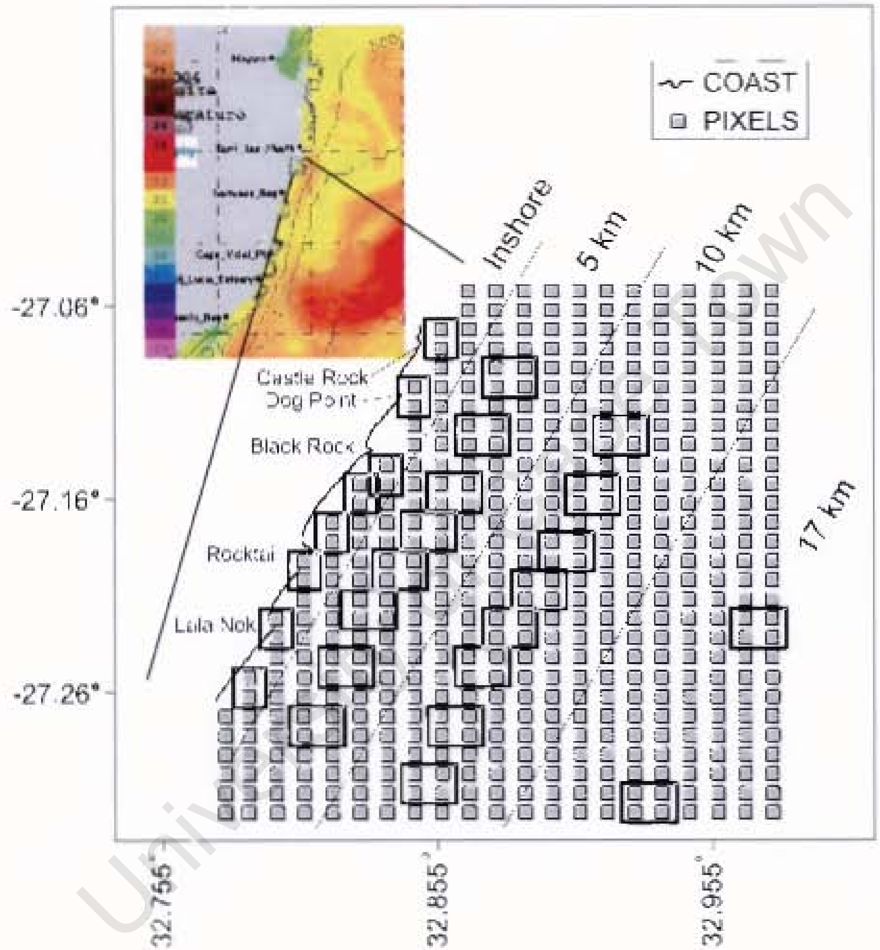

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Figure 2.3 Sampling grid of pixels selected from AVHRR 1-km resolution satellite images (Chl *a* and SST). Boxes indicate cells sampled.

coherence levels were significant, the four most important (highest coherence levels) were included in the table.

Patterns of adult mussel standing stock: 2003-2004

The mean density of adult mussels (> 10 mm shell length) per 0.5 m^2 quadrat was determined from each transect, yielding 5-6 replicates per site per year. These data were fourth-root transformed for normality and homogeneity of variances and the role of two factors, Site (random) and Year (random) were examined with a two-way factorial mixed model ANOVA with Type III (orthogonal) sums of squares. In the presence of a relevant significant interaction term, main effects were interpreted as in Chapter 1. Significant results were then compared with a Tukey's HSD for unequal n post-hoc test ($\alpha = 0.05$).

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2.3 RESULTS

Zooplankton biomass and density: spatial and temporal patterns

There were highly significant differences among months for zooplankton biomass and for the density of bivalves, mytilids and cyprids (Figure 2.4a-d, Table 2.4a). Mytilids and bivalves showed a similar pattern among months, but their densities did not necessarily correspond to months with the highest zooplankton biomass or cyprid densities, nor did cyprid densities correspond to zooplankton biomass. Zooplankton showed no seasonal pattern. Cyprids and mytilids were concentrated in the warmest month, with a peak in December, and bivalves were found in a wider range of months.

In the spatial comparison, there were significant differences among stations for zooplankton biomass and mytilid larvae, but not for all bivalves or cyprids (Table 2.4b). The highest density of mytilids was found at two points: Black Rock Point and Lala Nek Point. Again, the stations with the highest zooplankton biomass and the highest mytilid larvae did not necessarily correspond, although Lala Nek Point ranked highest for both categories. There was an increasing gradient in zooplankton biomass and mytilid density from north to south (Table 2.4b).

Bivalves, mytilids and cyprids were all more abundant inshore than offshore, while the overall biomass of zooplankton was not significantly different at the two distances (Figure 2.4, Table 2.5), indicating that meroplanktonic larvae are distributed differently from the general zooplankton pool, probably because they originate onshore and their dispersal is limited. None of the variables showed a significant bay-point pattern, disproving the second half of the first hypothesis of this study: although meroplanktonic larvae did accumulate closer to shore, they were not entrained in the bays as predicted, nor were they gathered near the points.

Table 2.4 Summary results of Kruskal-Wallis ANOVA by ranks tests for (a) temporal pattern and (b) spatial pattern of zooplankton distribution. H = Kruskal-Wallis test statistic (degrees of freedom, number of replicates), *p<0.05, ***p < 0.001, ns = not significant, n = number of replicates taken in a given month or site, $\Sigma R \cdot n^{-1}$ is the mean rank for each cell, MC = result of the multiple comparisons post-hoc tests ($\alpha = 0.05$).

(a)		Zooplankton[a]		Cyprids[b]		Bivalves[b]		Mytilids[b]	
Transformation		None		Log_{10}		Log_{10}		Log_{10}	
H (*df*, n)		38.4 (5,176)		35.0 (5,176)		72.4 (5,176)		47.4 (5,176)	
p		***		***		***		***	
Month	n	$\Sigma R \cdot n^{-1}$	MC	$\Sigma R \cdot n^{-1}$	MC	$\Sigma R \cdot n^{-1}$	MC	$\Sigma R \cdot n^{-1}$	MC
Aug 02	29	82.3	b	85.7	ab	46.0	c	50.2	c
Sep 02	37	52.9	b	90.9	ab	80.2	bc	64.0	bc
Dec 02	23	79.3	b	123.7	a	135.3	a	129.6	a
Apr 03	24	104.9	ab	64.7	b	130.9	a	112.6	a
Oct 03	32	93.7	ab	111.5	a	102.7	ab	98.9	ab
Nov 03	31	125.6	a	56.9	b	55.9	bc	93.6	ab

[a] Measured as settled wet volume (ml), [b] Measured as individuals per $100m^3$

(b)		Zooplankton[a]		Cyprids[b]		Bivalves[b]		Mytilids[b]	
Transformation		4th root		Log_{10}		Log_{10}		Log_{10}	
H (*df*, n)		16.4 (7,177)		8.2 (7,177)		13.6 (7,177)		18.5 (7,177)	
p		*		ns		ns		*	
Sites[c]	n	$\Sigma R \cdot n^{-1}$	MC	$\Sigma R \cdot n^{-1}$	MC	$\Sigma R \cdot n^{-1}$	MC	$\Sigma R \cdot n^{-1}$	MC
CRP	15	59.1	b	96.5	-	98.3	-	79.0	ab
CRB	13	66.2	ab	81.7	-	49.2	-	44.5	b
DPP	21	86.3	ab	99.2	-	97.6	-	81.1	ab
DPB	22	93.6	ab	101.5	-	83.5	-	77.3	ab
BRP	30	86.5	ab	73.3	-	81.3	-	103.3	a
RTB	38	86.1	ab	79.3	-	89.6	-	94.1	ab
RTP	25	108.4	ab	96.4	-	97.0	-	97.6	ab
LNP	13	119.9	a	100.5	-	114.2	-	113.2	a

[a] Measured as settled wet volume (ml), [b] Measured as individuals per $100m^3$, [c] Sites are listed from north to south; abbreviations of site names can be interpreted from Figure 2.1. P = rocky headland point, B = sandy bay

Table 2.5 Summary results of Student's t-test for matched pairs for inshore-offshore pattern of zooplankton distribution. All data were fourth-root transformed for analyses, but mean values are presented untransformed. Tr. = transformation of raw data, $\overline{X}$ = mean value of the response variable (in = inshore, off = offshore), t = Student's t-test for matched pairs statistic, **p < 0.01, *p < 0.05, ns = not significant.

Taxon	n	$\overline{X}_{in}$	$\overline{X}_{off}$	t	*df*	p
Mytilids[a]	35	287.2	181.3	3.11	34	**
All bivalves[a]	35	63.2	30.1	3.07	34	**
All cyprids[a]	35	45.3	28.4	2.30	34	*
Zooplankton[b]	35	202.1	224.1	-0.85	34	ns

[a] Measured as individuals $100m^{-3}$, [b] Measured as settled wet volume (ml)

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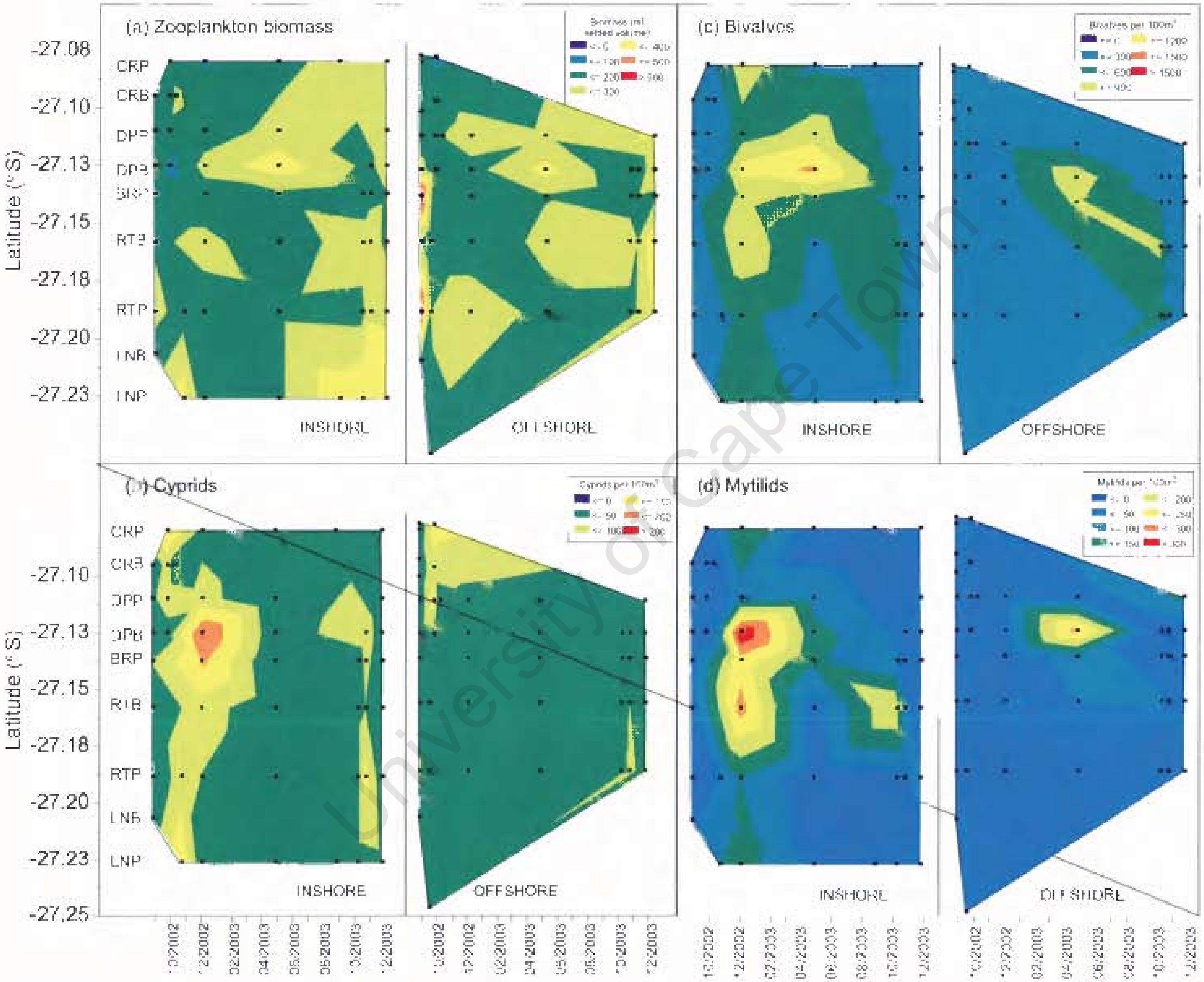

Figure 2.4 (a) Biomass of zooplankton, (b) densities of cyprid larvae (c) densities of bivalve larvae and (d) densities of mytilid larvae. Black dots represent sampling stations in space and time. Site codes: CRP/B – Castle Rock Point/Bay, DPP/B – Dog Point/Bay, BRP – Black Rock Point, RTB/P – Rocktail Bay/Point, LNB/P = Lala Nek Bay/Point.

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Phytoplankton concentration and temperature

Sub-surface phytoplankton concentration and temperature are summarized as spatio-temporal contour plots (Figure 2.5). There was no stratification in either the 10 or 15-m depth zones, indicating mixing throughout the water column. This was further supported by the lack of any consistent depth-pattern for phytoplankton concentration, measured using chl *a*, as the depth strata were not significantly different (One-way ANOVA, $F_{2,537} = 1.64$, not significant). Chl *a* varied significantly among dates (One-way ANOVA, $F_{12,497} = 142.36$, $p < 0.001$), and post-hoc analysis revealed that most dates were unique, including some sequential days (Figure 2.6a), indicating high temporal variability.

The concentration of subsurface chl *a* also differed significantly among sites (One-way ANOVA, $F_{6,501} = 3.35$, $p < 0.01$). Post-hoc analysis revealed that most sites were, however, not unique, with only Lala Nek Point (the southernmost site) and Castle Rock Point (the northernmost site) differing significantly from each other (Figure 2.6b). There was, however, a clear gradient from north to south, matching that of the zooplankton biomass and mytilid numbers. The distance between the northern and southernmost sites corresponds to the 23-km patch size indicated by the spatial autocorrelation of surface phytoplankton (Figure 2.7). This patch size was apparently independent of that of SST, which did not vary spatially at any scale considered in this analysis (Figure 2.7)

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Salinity

On all occasions when salinity was measured, there was no stratification at any station, and values varied between 35.3 and 35.5 ppt.

Temperature, phytoplankton concentration and larval density

Mytilid, bivalve and cyprid densities were all significantly predicted by the combination of water temperature, phytoplankton concentration and the densities of each other, but not by latitude or zooplankton biomass (Table 2.6). Mytilids and bivalves were positively correlated with water temperature and negatively correlated to phytoplankton, while the opposite was true for cyprids. Biomass of zooplankton was not predicted by any of the selected independent variables, as the model itself was not significant for zooplankton.

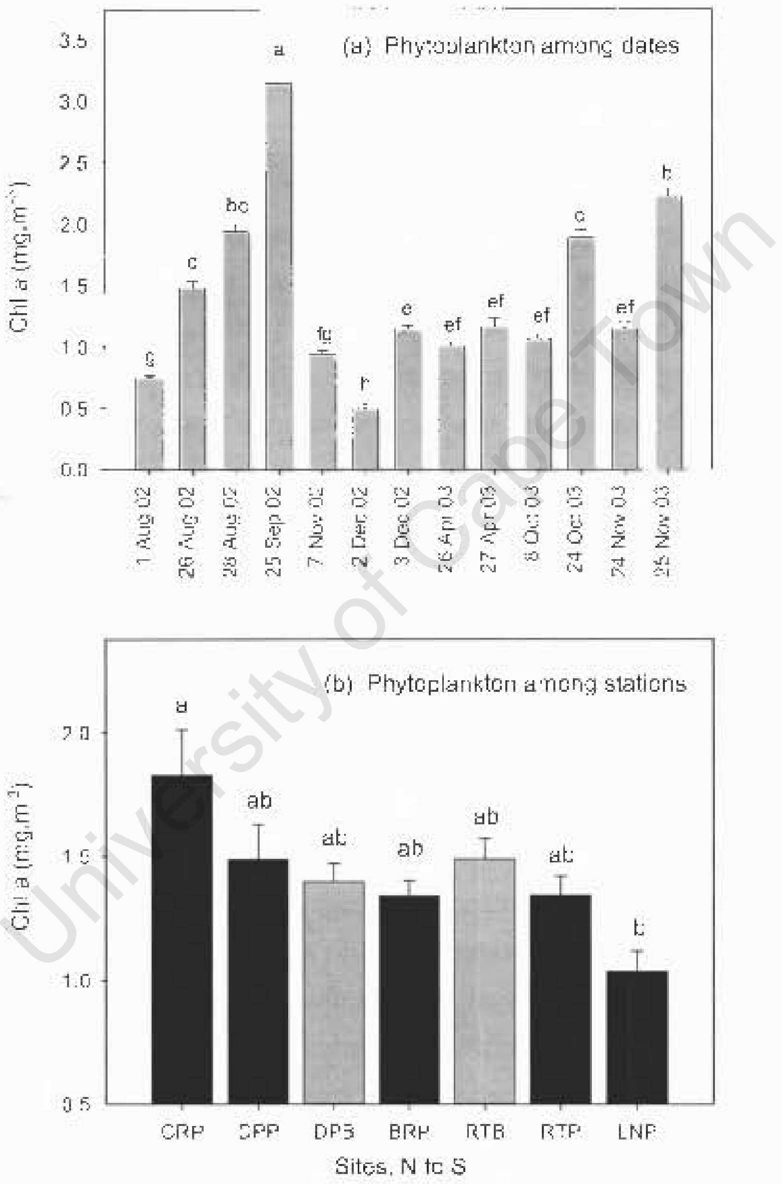

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Figure 2.6 Concentration (mg.m^{-3}) + SE of phytoplankton (measured with chl *a*) among (a) dates and (b) stations. Letters above bars differ when there were significant differences between days or sites (Tukey's HSD post-hoc test for unequal n). Data were $\mathrm{Log}_{10}(x+1)$ transformed for ANOVA, but are presented here untransformed. For (b), points are shown in black, bays in grey. Site codes: CRP (Castle Rock Point), DPP/B (Dog Point/Bay), BRP (Black Rock Point), RTB/P (Rocktail Bay/Point), LNP (Lala Nek Point).

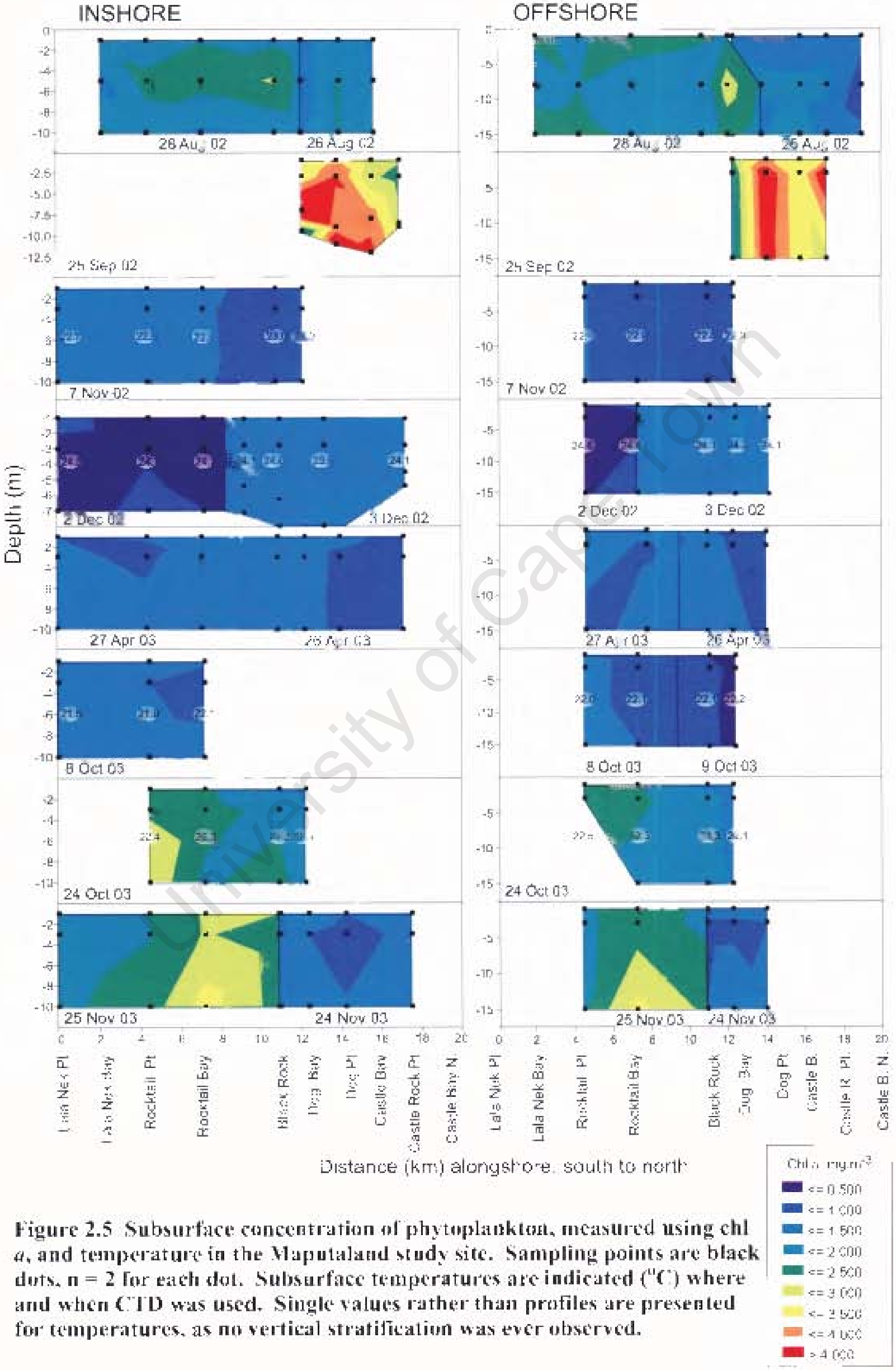

Figure 2.5 Subsurface concentration of phytoplankton, measured using chl *a*, and temperature in the Maputaland study site. Sampling points are black dots, n = 2 for each dot. Subsurface temperatures are indicated (°C) where and when CTD was used. Single values rather than profiles are presented for temperatures, as no vertical stratification was ever observed.

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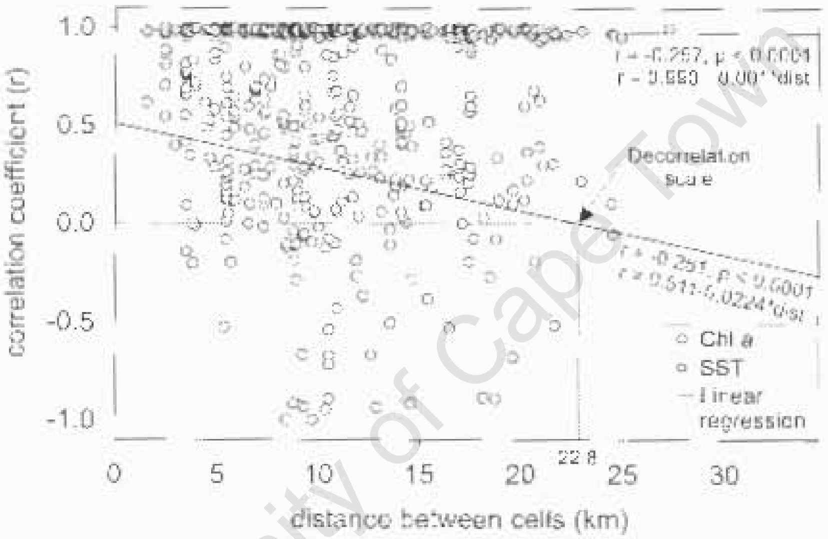

Figure 2.7 Pearson product-moment correlations and linear regressions of distance between satellite data cells and the correlations between SST values in different cells, or chl *a* values in different cells. Number of replicates (n) = 5-50 for each data point. For SST, all correlations but one were significant. For chl *a*, 65% of all correlations were significant. In this analysis, all data points were used, regardless of significance.

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Table 2.6 Summary results of multiple-regression analysis of larval densities (oblique grid tows only). All biological independent variables were $\log_{10}(x+1)$ transformed. ***$p < 0.001$, **$p < 0.01$, ns = not significant. Note that the model for zooplankton is marginally non-significant.

Independent variables		Const	Zoopl	Cyp	Myt	Biv	Phyto	Temp (°C)	Lat (°S)
	B	-32.742	X	-0.039	X	0.033	0.065	0.019	-1.236
Zooplankton	B_{SE}	12.468		0.066		0.056	0.134	0.017	0.458
	β			-0.075		0.075	0.062	0.132	-0.289
Adusted $R^2 = 0.057$	Tol.			0.664		0.673	0.647	0.738	0.920
$p = 0.080$ (ns)	t	-2.626		-0.594		0.599	0.485	1.103	-2.697
	Sig.	**		ns		ns	ns	ns	**
	B	4.184	-0.155	X	0.470	X	0.939	-0.121	0.046
Cyprids	B_{SE}	20.843	0.175		0.086		0.189	0.026	0.768
	β		-0.081		0.518		0.465	-0.439	0.006
Adusted $R^2 = 0.340$	Tol.		0.888		0.819		0.841	0.838	0.847
$p < 0.001$	t	0.201	-0.883		5.446		4.955	-4.671	0.060
	Sig.	ns	ns		***		***	***	ns.
	B	-10.903	0.216	0.555	X	X	-0.951	0.142	-0.292
Mytilids	B_{SE}	22.629	0.190	0.102			0.210	0.027	0.834
	β		0.102	0.504			-0.427	0.469	-0.032
Adusted $R^2 = 0.358$	Tol.		0.893	0.843			0.810	0.878	0.848
$p < 0.001$	t	-0.482	1.134	5.446			-4.530	5.180	-0.350
	Sig.	ns	ns	***			***	***	ns
	B	7.491	0.128	0.551	X	X	-1.091	0.129	0.344
Bivalves	B_{SE}	25.415	0.213	0.115			0.236	0.031	0.936
	β		0.057	0.468			-0.459	0.397	0.036
Adusted $R^2 = 0.290$	Tol.		0.893	0.843			0.810	0.878	0.848
$p < 0.001$	t	0.295	0.599	4.808			-4.630	4.163	0.368
	Sig.	ns	ns	***			***	***	ns

B = estimate of the raw coefficient, B_{SE} = standard error of this estimate, β = standardized coefficient and Tol = tolerance value (Tol. < 0.1 indicates strong co-linearity with another variable). t = tests the H_0 that $\beta = 0$ for that predictor variable. Sig. = significance level of this test. Const = model constant (intercept), Zoopl = settled biomass of zooplankton, Cyp = cyprids.100m^{-3}, Myt = mytilids.100m^{-3}, Biv = bivalves.100m^{-3}, Phyto = [chl *a*]. Temp = the mean benthic temperature on that sampling day, Lat = latitude. X indicates independent variables that were not used in the model, due to either non-relevance or co-linearity with another independent variable.

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Winds and benthic temperature

Most of the time-lagged correlations between the alongshore wind velocity and benthic temperature were negative and significant, but not very strong (Figure 2.8a). Significant r-values varied from +0.124 (lag -21, or temperature 21 hours before wind) to -0.333 (lag +34, or temperature 34 hours after wind), with 'positive' wind values (northerly and upwelling-positive) associated with lower temperatures (Figure 2.8b). The minimum significant r-value in this analysis fell within the *a priori* window for a wind-driven upwelling response, indicating weak offshore Ekman transport. The power spectral density analysis of the subsurface temperature supported the conclusion that wind-driven upwelling is present in this area, with secondary peaks ranging from 3.9-8.6 d (Figure 2.9). Despite a benthic upwelling response, a visible response in the SST satellite images was, however, rare (see Figure 2.10 for an example).

Using the time series of wind and temperature, a climatology was compiled for the area (Figure 2.11) and used to assign 'windy' and 'non-windy' seasons. There was significant coherence in the frequencies between alongshore wind and across-shore wind and temperature for all data sets examined (Table 2.7). Coherence levels increased in the shorter data sub-sets, indicating the

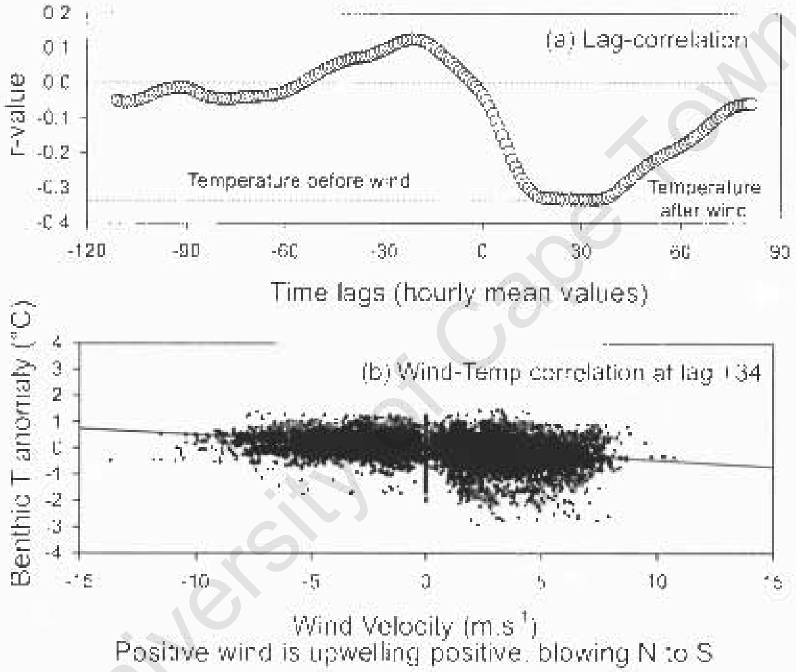

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Figure 2.8 **(a) Time-lagged cross-correlations of the alongshore component of hourly wind velocity and the hourly benthic temperature anomaly at Sodwana Bay. (b) Wind velocity and benthic temperature anomaly at lag with minimum r-value. Linear regression is $T = 0.01658 - 0.0485 * v_{20}$ ($r^2 = 0.111$, $n = 10150$, $p < 0.0001$), where T is temperature anomaly from the running monthly mean and v_{20} is the alongshore component of the wind velocity in $m.s^{-1}$.**

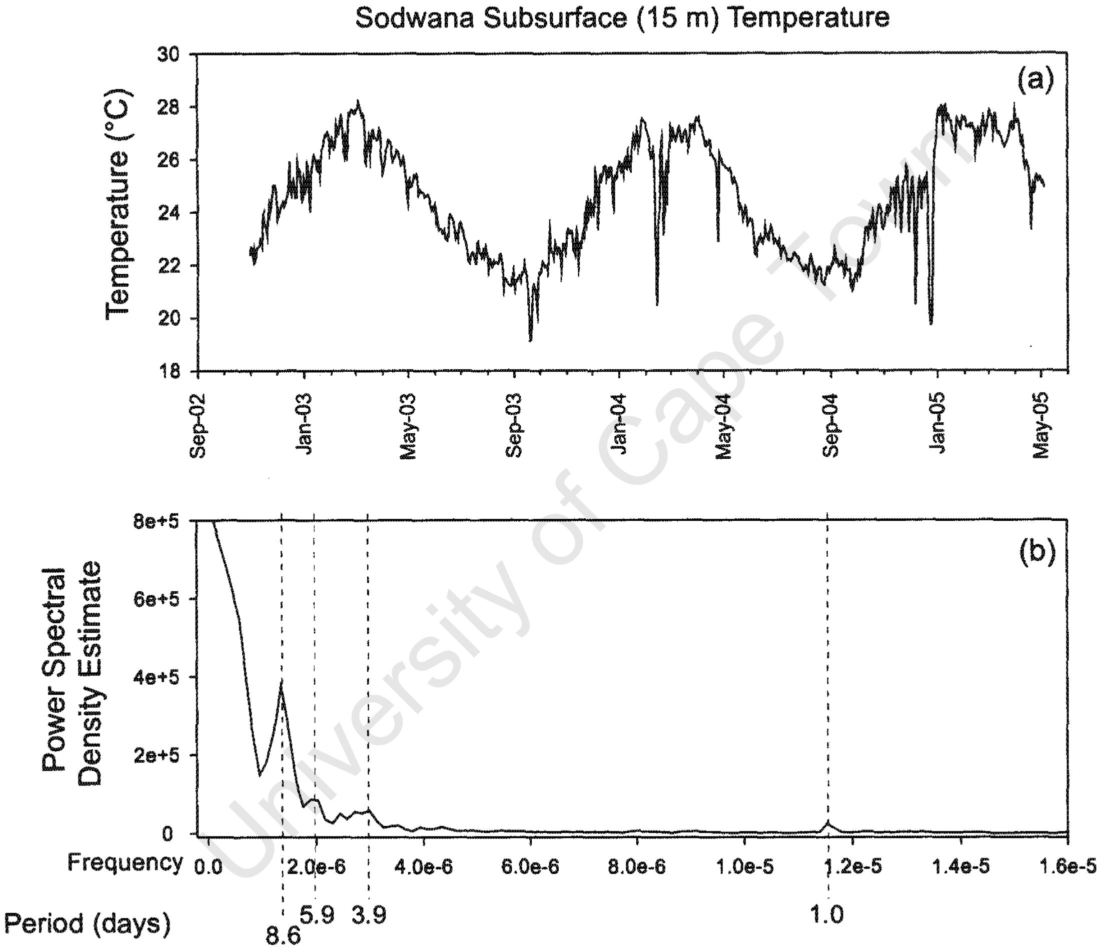

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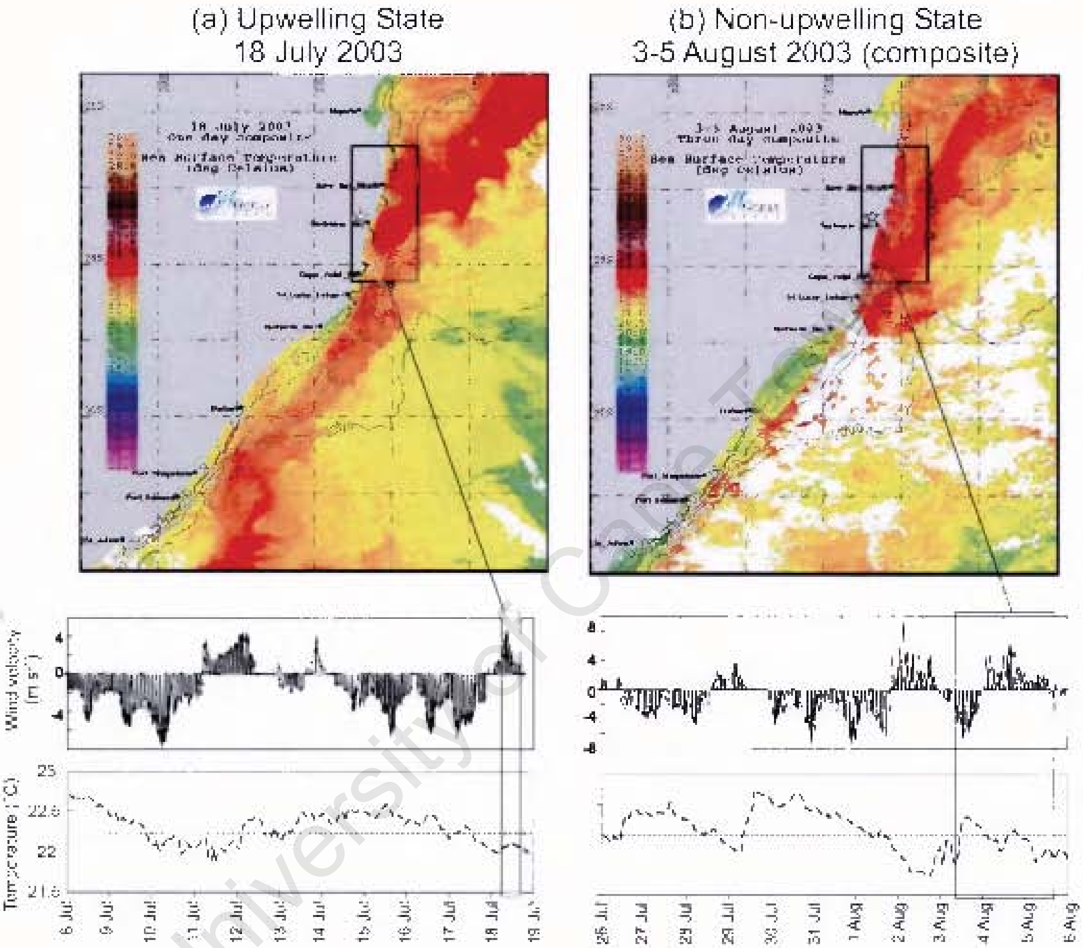
Figure 2.9 (a) Sodwana half-hourly subsurface (15 m) temperatures over 2.5 years, (b) Power spectral density of the hourly measurements taken between Oct 03 - July 05, using a 2048 window. Strong peaks were converted from frequency to period. Peaks at 3.9-8.6 days indicate the influence of wind-driven effects such as upwelling. The peak at 1.0 days indicates diurnal warming or a cross-shore sea breeze effect.



(a) Upwelling State
18 July 2003

(b) Non-upwelling State
3-5 August 2003 (composite)

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Figure 2.10 **Subsurface temperature time series, and two examples of near-shore relationships between the Agulhas Current, alongshore winds, and benthic temperature. Satellite SST images are AVHRR, 1 and 3-day composites at 1-km resolution. Wind was recorded at Mbazwana (marked with a white star), and positive values are for NNE winds, which are upwelling-positive. Benthic temperature was measured at Sodwana Bay, on a 15-m deep reef. In (a), very near-shore surface waters within the study area (marked by box) appear to be cooler than offshore waters during periods of sustained north-northeasterly winds, indicating that these winds are inducing offshore Ekman transport and therefore upwelling.**

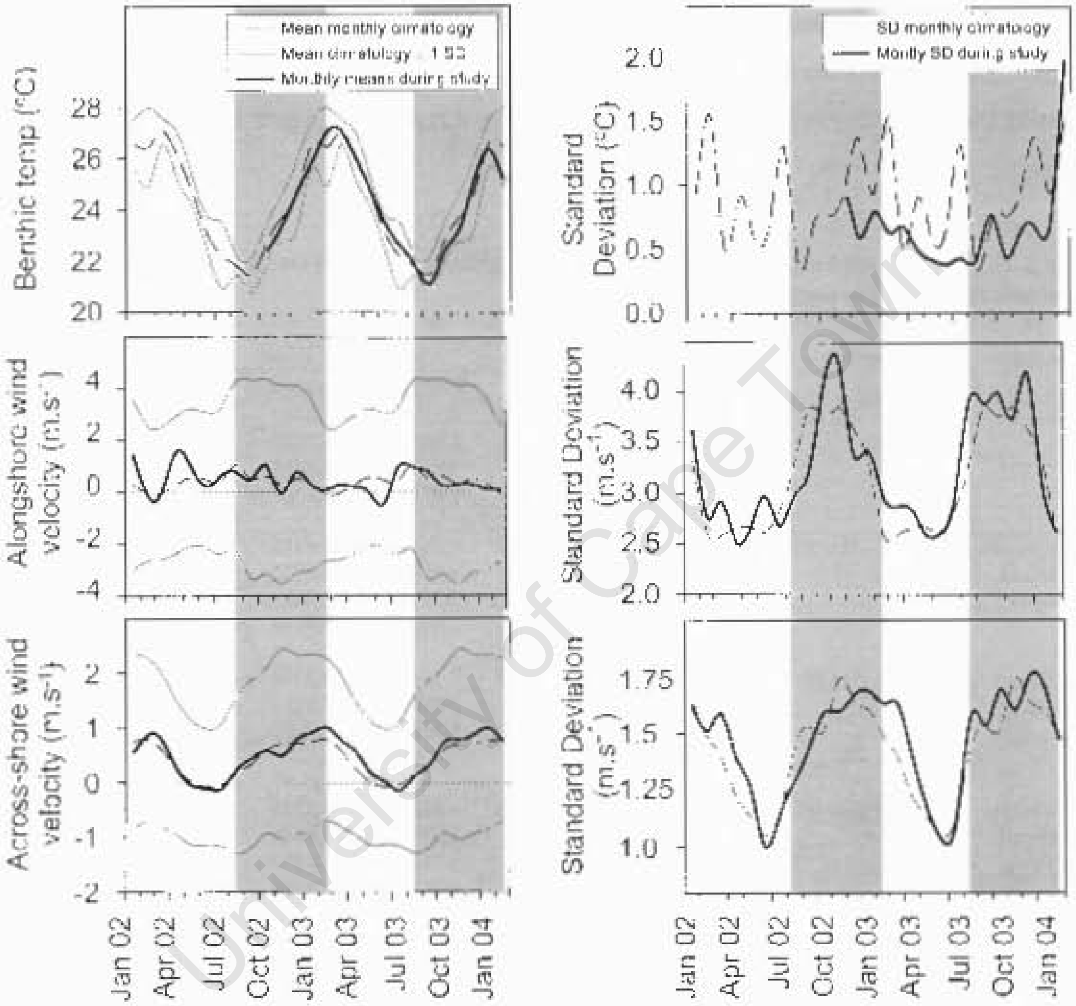

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Figure 2.11 Recorded monthly benthic temperature and winds over the period of observation (heavy black lines, 2002-2003) superimposed on a 4-year climatology for benthic temperature (2002-2005) and a 6-year climatology for wind (2000-2005) from Mbazwana airfield, mean + 1 SD. Positive alongshore wind is NNE'ly, positive across-shore wind is ESE'ly. Shaded areas highlight the recruitment season for mussels and the barnacle *C. dentatus* (Chapter 3).

maximum frequencies of this relationship were not stable among seasons. The strongest period for the coherence of across-shore winds with benthic temperature was nearly always one day, suggesting that the daily sea-breeze effect may influence diurnal warming at all times of the year. The period with the maximum coherence was more variable among data sets for the alongshore wind, but was often of a similar period to the across-shore wind (less than two days). However, there were significant coherences at longer periods also, suggesting that the periodic reversals in alongshore winds influence temperature by inducing on- or offshore Ekman transport, again indicating that upwelling or downwelling is important in this system (Figure 2.12 shows one example).

Table 2.7 The four highest significant values from coherence analysis relating sea temperature to winds; period is measured in days.

Season	Months	nfft	n	df	α	Alongshore wind		Across-shore wind	
						Period	Coherence	Period	Coherence
Full Data Set	Nov 03 Jun 05	1024	14076	50	0.01	8.5333	0.2465	8.5333	0.3421
						5.3333	0.2622	3.8788	0.3091
						3.8788	0.2891	1.0159	0.6293
						1.7778	0.3306	0.9922	0.6516
Recruitment: mussels and *C. dentatus*	Nov 03 – Mar 04	512	3310	11	0.05	5.3333	0.4218	10.6667	0.3089
						4.2667	0.4231	5.3333	0.3675
						1.7778	0.3944	1.1228	0.3209
						1.6410	0.5318	1.0159	0.4093
Recruitment: *Tetraclita* spp.	Apr 04 – Sep 05	512	4392	15	0.05	7.1111	0.3374	7.1111	0.4178
						2.6667	0.2113	4.2667	0.3428
						1.1228	0.1900	1.0159	0.7009
								0.9697	0.6085
Recruitment: mussels and *C. dentatus*	Oct 04 – Mar 05	512	4368	14	0.05	4.2667	0.3356	10.6667	0.2458
						1.9394	0.3018	7.1111	0.2463
						1.7778	0.3695	4.2667	0.2781
						1.0159	0.6469	1.0159	0.8204
Windy	Nov 03 Jan 04	512	1486	9	0.05	5.3333	0.6969	5.3333	0.7827
						4.2667	0.7784	4.2667	0.8364
						1.6410	0.7479	1.1852	0.8867
						1.0159	0.6506	1.0159	0.7455
Non-windy	Jan 04 Jul 04	512	4367	14	0.05	4.2667	0.2546	1.9394	0.2735
						2.6667	0.3068	1.7778	0.2398
						1.9394	0.3917	1.1228	0.2559
						1.7778	0.4069	1.0159	0.4415
Windy	Jul 04 Jan 05	512	4416	14	0.05	2.6667	0.2822	1.0159	0.8028
						1.9394	0.3188		
						1.7778	0.2570		
						1.0159	0.4826		
Non-windy	Jan 05 Jan 05	512	3867	12	0.05	3.5556	0.3691	4.2667	0.3800
						3.0476	0.3048	3.5556	0.6076
						1.1228	0.2452	3.0476	0.4415
						1.0159	0.3696	1.0159	0.7997

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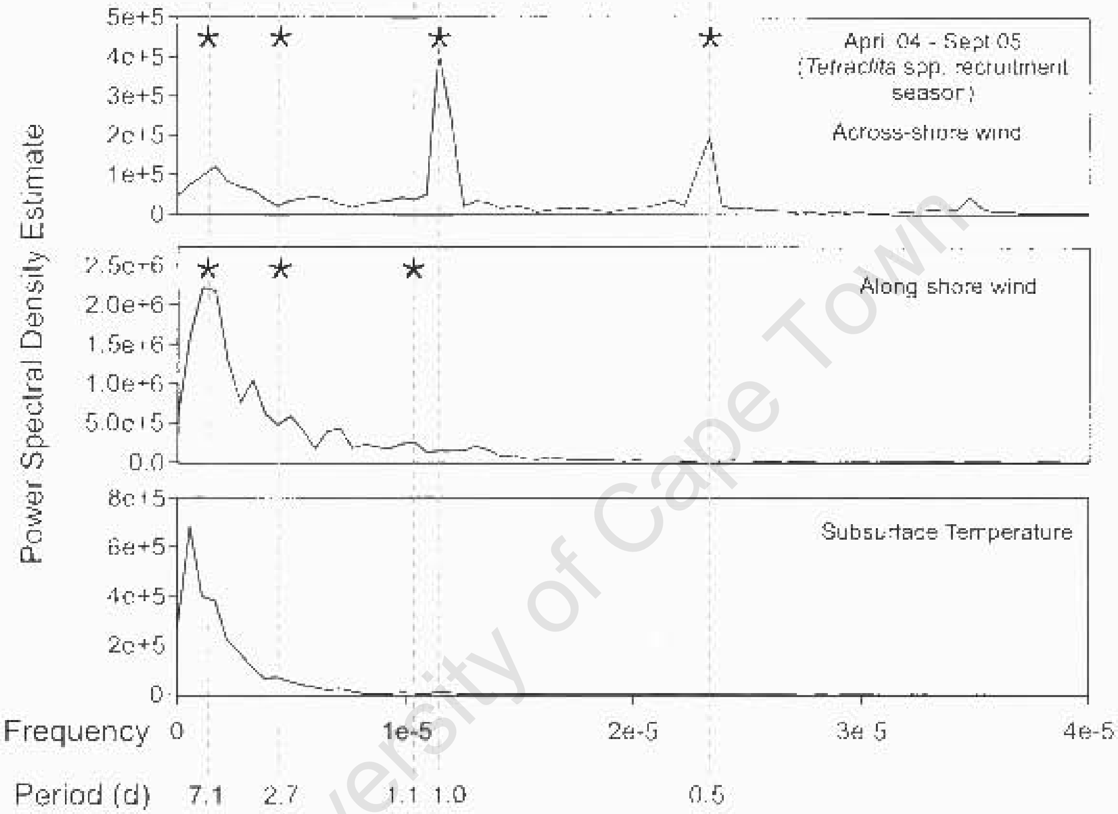

Figure 2.12 Example of the power spectra of alongshore and across-shore wind and subsurface temperature taken at Sodwana bay (data are presented in Figure 2.9). Some significant coherence frequencies are highlighted with vertical lines, and the periods (in days) are given. Stars indicate when wind vectors were significantly coherent with temperature ($\alpha=0.05$).

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Zooplankton – in and out of a topographically-induced foam line

Neither the overall zooplankton biomass nor the density of mytilid bivalves were significantly different in or out of the foam line or among sites (Figure 2.13, Table 2.8), and the interaction term was also not significant for these variables. Only the interaction term (Treatment*Site) was significant in the case of cyprids: although cyprids appeared to be denser within the foam lines, there was a significant interaction with the site of the sampling because only Rocktail Bay had a significant difference in cyprid density. Only bivalves showed significant differences both between treatments and among sites, with the highest densities beneath the foam lines on every sampling occasion.

Table 2.8 Summary results of Site*Treatment two-way factorial ANOVA of meroplankton in and out of the shore-parallel foam line. Site was a random factor and treatment was fixed. Data were $Log_{10}(x+1)$ or fourth-root transformed. ***$p < 0.001$, *$p<0.05$, ns = not significant.

Taxon	Factor	*df*	MS	*F*	p
Zooplankton	Treatment	1	0.146	3.64	ns
	Site	2	0.001	0.01	ns
	Treatment*Site	2	0.040	0.26	ns
	Error	16	0.156		
Cyprids	Treatment	1	0.596	1.20	ns
	Site	2	0.396	0.75	ns
	Treatment*Site	2	0.532	5.73	*
	Error	16	0.093		
Mytilids	Treatment	1	0.156	3.37	ns
	Site	2	0.03	0.57	ns
	Treatment*Site	2	0.046	0.37	ns
	Error	16	0.125		
Bivalves	Treatment	1	0.337	35.04	***
	Site	2	0.046	24.58	*
	Treatment*Site	2	0.002	0.019	ns
	Error	16	0.098		

Zooplankton - vertical stratification

Kruskal-Wallis tests failed to detect any significant differences in the abundances of zooplankton, mytilids or bivalves at different depths, indicating that these were not stratified when the samples were collected. Cyprids, however, were significantly stratified (Kruskal-Wallis test, $H_{2,21} = 7.18$, $p < 0.05$). Higher densities were found at the middle and bottom, which were not significantly different, and fewer cyprids were found at the top (multiple comparisons tests, Figure 2.14).

Patterns of adult mussel standing stock: 2003-2004

Two-way ANOVA revealed no significant differences between sites or years in the adult stock of *P. perna* at each of the rocky points (Year: MS = 0.013, $F_{1,47} = 0.032$, not significant; Site: MS = 0.223, $F_{4,47} = 0.542$, not significant; Year*Site: MS = 0.411, $F_{4,47} = 4.437$, $p < 0.05$). This analysis necessarily excluded the Black Rock South site as it was sampled only in 2003. Years

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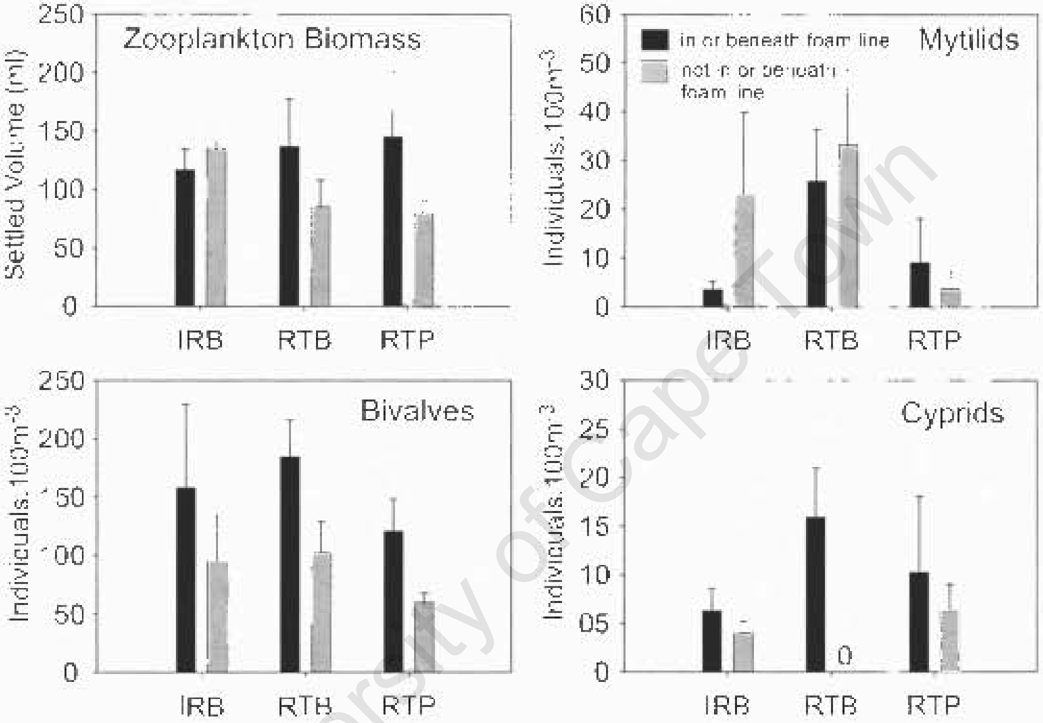

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Figure 2.13 Abundance of zooplankton and meroplankton in and out of shore-parallel foam line. Locations are Island Rock Bay (IRB), Rocktail Bay (RTB) and Rocktail Point (RTP). Treatments are within the foam line (black) and > 40 m away from the foam line (grey). Neither site nor treatment was significant for zooplankton biomass or for mytilids. For bivalves, both factors were significant, while for cyprids only the interaction term was significant. Data were transformed for analyses but are presented here untransformed. Values are means + SE.

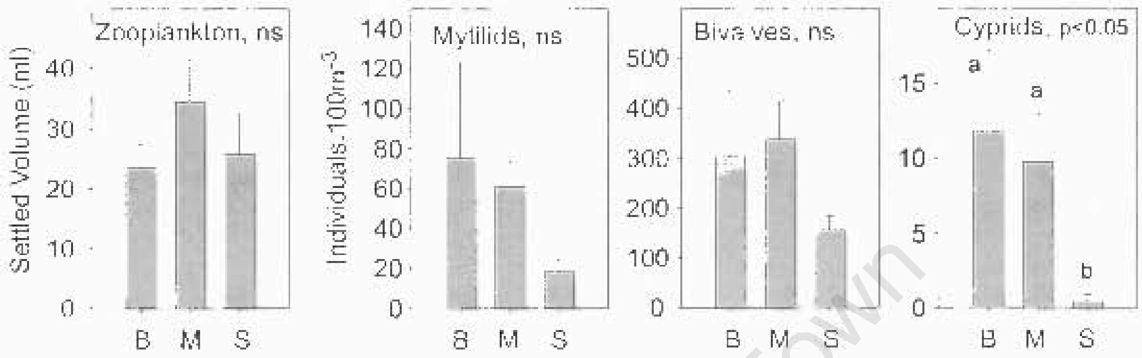

Figure 2.14 Vertical stratification of zooplankton and meroplankton, all replicate sampling events are pooled. Results of Kurskal-Wallace comparisons: different letters above bars for cyprids indicate significant differences ($\alpha = 0.05$), ns – test was not significant. Data were transformed for analyses but are presented here untransformed, values are means + SE. B = bottom, M = midwater, S = surface

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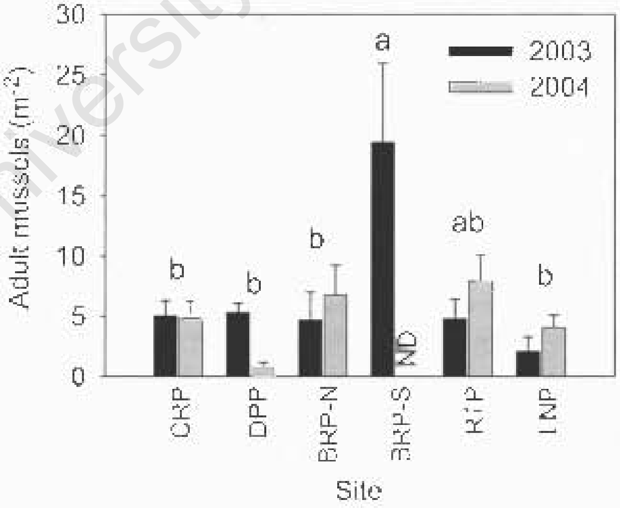

Figure 2.15 Adult stock of *P. perna* on each of the rock points during the mussel recruitment seasons of 2003 and 2004. Factorial two-way ANOVA (excluding BR-S site) revealed no significant difference between years, so data were combined for one-way ANOVA. Letters show results of Tukey's HSD for unequal n post-hoc test. Data were fourth-root transformed for analyses, but are presented here untransformed. Site codes: CRP – Castle Rock Point, DPP = Dog Point, BRP-N/S – Black Rock Point North/South, RTP – Rocktail Point, LNP = Lala Nek Point. There were no data (ND) for BRP-S in 2004.

were then combined for a one-way ANOVA with site as a random factor, including the data from Black Rock South. There was then a significant difference between sites (MS = 0.861, $F_{5,61}$ = 6.630, $p < 0.001$), with the unharvested Black Rock southern site having significantly higher densities of adult mussels than any of the other sites except Rocktail Point (Figure 2.15). There were also significant differences in the alongshore densities of mytilid larvae (Table 2.4b), which achieved greater densities at Black Rock Point (where the density of adult mussels was highest) and at Lala Nek Point (where the density of zooplankton was highest).

2.4 DISCUSSION

The larval pool

Temporal variability

Densities of zooplankton and larval taxa all varied significantly among months (Table 2.4a). The densities of mytilid and bivalve larvae did not, however, correspond to high recruitment periods for *Perna perna* or *Brachidontes semistriatus* (Chapter 4, this study). This situation corresponds with that reported by McQuaid and Lawrie (2005), who found three periods of significantly higher than normal mytilid larval densities, but no correlation with spawning times or settlement peaks at sites they examined on the south coast of South Africa. Multiple regression analyses in my study did show that mytilids and bivalves were significantly and positively correlated with warmer water that was lower in phytoplankton, while cyprids were correlated to cooler water that was higher in phytoplankton, and variability in these factors associated with wind events (and therefore the presence or absence of upwelling) might explain the higher or lower densities of these taxa during different months of the year (Table 2.6).

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Patterns of abundance

The densities of cyprids, mytilids, bivalves and zooplankton were all very low compared to those recorded in other regions of South Africa. I found mean (and maximum) values of approximately 0.04 (3), 0.2 (15) and 0.1 (5) m^{-3} for mytilids, bivalves, and cyprids, respectively. In 1990-91, McQuaid and Phillips (2000) investigated the spatial distribution of *P. perna* larvae in waters < 400 m from shore near Port Alfred on the south coast of South Africa and found densities of larval *P. perna* varying between 0 and 140 m^{-3}. In the same area, Porri (2003) found mean (max) densities of ~20 (300) m^{-3} for *P. perna* in 2000, two orders of magnitude greater than the mytilid densities I recorded in Maputaland. These densities were highly pulsed, as Porri found no larvae on most sampling occasions. McQuaid and Lawrie (2005), working in a similar area to Porri, found equivalent mean (max) densities of ~10 (400) m^{-3}, but, as in my study, larvae were present at least in low numbers on 80% of their sampling dates from February 1998 to April 1999. On the west coast of South Africa, in the cooler Benguela Current where wind-driven upwelling is prevalent, larval bivalve densities of 25000-200000 m^{-3} were recorded nearshore in St Helena Bay, an additional step up of three orders of magnitude from the South Coast (Gibbons et al. 1999).

The maximum values found in Maputaland were also lower than those found in studies in other parts of the world. In the Outer Banks of North Carolina, USA, another oligotrophic western boundary current system influenced by wind-induced upwelling, the densities of inshore larvae spanned 5-746 m^{-3} for barnacle cyprids and 0-516 m^{-3} for bivalves, with both taxa peaking in density near-simultaneously (Garland and Zimmer 2002). The authors concluded that in this shallow depth the two taxa were moving in a single larval patch. In a 3-hourly study at a similar location but at deeper depths (3, 9 and 12 m in 21-m water) the following year, bivalve larvae densities spanned 100-10000 m^{-3} (Garland et al. 2002). In another part of the same study, the veligers of the bivalve *Mya arenaria* were found in densities to 300 m^{-3} in depths up to 14 m (Shanks et al. 2000). On the west coast of North America, in Oregon, USA, a study of mussel larvae and barnacle cyprids reported densities of mussel larvae ranging across 0-817 m^{-3}, with less than 50 m^{-3} on most sampling occasions, and densities of cyprids averaging 40-70 m^{-3} with maximum densities of 140-400 m^{-3} (McCulloch and Shanks 2003). Finally, in southern California, USA, cyprid densities were found to span 0.3-22 m^{-3}, at a distance of 300 m from the shore (Tapia 2005), considerably fewer then in the studies in North Carolina, and more consistent with the results I recorded.

If larval densities are as temporally pulsed as some studies indicate (e.g. Porri 2003), the low values in my study could simply be due to low sampling frequency. This is unlikely, however, as sampling was repeated on six occasions over 12 days during peak spawning periods.

Patterns of spatial variability

Despite the low values for the density of all the planktonic groups I considered, there were nevertheless significant spatial patterns that indicate patchiness on scales smaller than that of the study area (Tables 2.4 and 2.5, Figure 2.4). The overall biomass of zooplankton was not correlated with the densities of any of the variables examined, as the multiple-regression model describing their effects was not significant (Table 2.6). There was, however, a significant increase from north to south, with greater concentrations around Lala Nek, the southernmost site (Table 2.4b). Although the densities of the larval taxa were not correlated with each other in the multiple regression analysis, the three contributed significantly to the variability of each other when temperature and phytoplankton were added to the model (Table 2.6). All three showed significant spatial patterns in the study area, although these differed among the taxa. All these were concentrated more inshore than offshore, and at particular sites along the coast (Figure 2.4, Table 2.4). In contrast, McQuaid and Lawrie (2005) did not find any significant differences in *P. perna*

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larval densities among transects (on/offshore or alongshore) on any occasion. The lack of alongshore pattern in their study could be due to the much smaller scale of their sampling, with replication within a study area of only 600 × 600 m^2. McCulloch and Shanks (2003), in contrast, sampled at 0.2, 0.6 and 1.5 km from shore and found both mussel and barnacle larvae to exhibit spatial structure, being consistently least abundant at the most inshore sampling station, and they attributed this to the presence of a topographically-generated front at the mouth of the bay.

The physical environment and phytoplankton concentration

Large-scale onshore transport mechanisms

In winter, northeasterly (upwelling-positive) and southwesterly (upwelling-negative) winds are generally equally frequent in KZN, but in the summer the northeasterly winds dominate (Hunter 1988). Southwesterly wind speeds are slightly greater than northeasterly, but mean wind speeds have previously been recorded as being 7-8 m.s^{-1} in both directions (Hunter 1988), and were slightly lower during the course of my study (monthly means spanned 1.5-4.0 m.s^{-1}). This could be due to the position of the anemometer I used, which was approximately 2 km inland and behind the coastal dunes. Alongshore winds, offshore Ekman transport and upwelling have important influences on the provision of nutrients and the transport or retention of meroplanktonic larvae in other western-boundary current systems in the world (Shanks et al, 2000; Garland et al. 2002; Shanks et al. 2003b; Shanks and Brink 2005). This led to the generation of the hypothesis that the strong alongshore winds in Maputaland stimulate upwelling inshore of the Agulhas Current. Just to the south of Maputaland the increased width of the Natal Bight trains the Agulhas Current away from the coast, topographically inducing a center where cooler upwelled water is then entrained and eddied as far south as Durban (Lutjeharms et al. 2000a; Meyer et al. 2002), as evident in the satellite images in Figure 2.10. Nearby, in southeast Madagascar, another upwelling cell has been identified inshore of the southern arm of the East Madagascar current (Lutjeharms and Machu 2000). However, I have found no previous mention of wind-induced offshore Ekman transport in the literature for the Maputaland region. In my study, upwelling-positive winds and reductions in benthic temperature at Sodwana were most positively and significantly correlated after lags of 12-36 hours, that is, benthic temperatures decreased ~24 hours after the onset of upwelling-positive wind events. This is a strong indication that upwelling does occur along this coastline. This was confirmed with observations of satellite images in conjunction with temperature and wind records (e.g. Figure 2.10), as well as the significant coherence between temperature and alongshore wind at periods between 2-9 days (Table 2.7).

There are two other potential deliverers of pulsed upwelled water to the nearshore environment. The first is internal tidal bores, or breaking internal tides associated with spring tides which could push up benthic water from further offshore (Pineda 1994). These would be signaled by a regular fortnightly occurrence of cooler water (Pineda 1995). A 14 or 28-day (tidal) cycle of

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warming and cooling was not evident in the temperature power spectrum, indicating that tidal bores are probably not a dominant feature in this area (Figure 2.9). The other is internal waves that can generate the observed foam lines or slicks, and are a potential onshore-transport mechanism for both positively and negatively buoyant meroplanktonic larvae (Shanks 1983; Waldron 1988; Kingsford 1990). Although internal waves could be present in Maputaland, they were not evident, as I never observed their characteristic series of shore-parallel slicks moving shoreward.

The final local oceanographic feature that could cause benthic cool water intrusion into the nearshore is a pulse, a solitary ocean-wards meander of an otherwise stable current such as the Agulhas, similar to the Natal Pulse that originates in the Natal Bight eddy (Lutjeharms and Roberts 1988; Lutjeharms and Connell 1989; Lutjeharms et al. 2000b; Lutjeharms et al. 2001), but originating further north, perhaps from the Delagoa Bight eddy (Lutjeharms and Da Silva 1988). Natal Pulses may enhance upwelling at the inshore edge of the main stream of the Agulhas Current; if pulses were to form as far north as Maputaland, originating with the Delagoa Bight eddy, they could cause both upwelling and inshore counter-currents as they travel by (M. Roberts, pers. com.). No information is currently available on the incidence of eddy-induced pulses north of Cape Vidal, but a record of these pulses, taken from satellite SST imagery or altimetry, analyzed together with the benthic temperature data presented in this chapter, might reveal the influence of Mozambique Channel or Delagoa Bight eddies on inshore dynamics in Maputaland (T. Lamont, pers. com.).

Phytoplankton concentration

Very few studies describe the characteristics of phytoplankton concentration in Maputaland waters, but the values that have been recorded are almost always very low (reviewed in Carter and Schleyer 1988). Generally, researchers consider plankton dynamics in the region of the Agulhas Current to be physically mediated, and Meyer et al. (2002) describe nutrient levels in the Agulhas Current region as relatively low, peaking in the northern part of the Natal Bight. M. C. Pfaff (unpubl. data) recorded chl *a* concentrations of 0.08-1.87 $mg.m^{-3}$ proximate to rocky shores within my study area between August 2003 and August 2004; this is slightly lower than the offshore measurements reported in my study. Although phytoplankton concentrations continually remained low compared to other regions in southern Africa, they did respond positively to decreases temperature in the previous day (Figure 2.2b,c). This indicates that the upwelled water may not only be cooler, but also may transport nutrients into this otherwise nutrient-poor environment. The significant simultaneous correlation between increased surface phytoplankton and reduced surface temperature derived from the satellite data at Sodwana and Maputaland confirms this relationship. In their investigation of the patch sizes of *in situ* phytoplankton along coastal Chile, Wieters et al. (2003) found persistent differences between sites 10s of km apart, and attributed that to localized upwelling cells. The patch size of phytoplankton was larger in my study, being ~23 km (Figure 2.7). The Maputaland coastline is much less spatially heterogeneous than that of central Chile, so

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upwelling is not expected to be as localized. However, if localized upwelling does not drive the patchiness of phytoplankton in Maputaland, heterogeneous physical drivers (bottom-up effects) or variation in consumption (top-down effects) may nevertheless exist along the length of the coastline that will alter the density of phytoplankton at meso-scales such as these.

The low levels of nutrients and phytoplankton in the nearshore waters of Maputaland could have important effects on zooplankton growth and survivorship. Most mussel and barnacle larvae, including most of those in this study, are planktotrophic, although larvae of the barnacle *Tetraclita squamosa rufotincta* are thought not to be so (Barnes and Achituv 1981). For planktotrophic organisms, food limitation during the larval stage can be the most important source of larval mortality where primary production is low (Olson and Olson 1989; Shanks 1995; Anil et al. 2001; Desai and Anil 2002), and the timing and abundance of food can affect both the development and competency of pelagic larvae (Rodriguez et al. 1993). A grazing effect could therefore explain the negative partial correlation found between both mytilids and bivalves and phytoplankton in the multiple regression analysis. Interestingly, the general biomass of zooplankton was not correlated with phytoplankton, either positively or negatively. The species composition of the zooplankton pool was highly variable among the samples taken in this study (pers. obs.), and ranged from herbivore-dominated (mostly copepods) to predator-dominated assemblages (chetognaths and others), and this could explain the lack of correlation.

Smaller-scale onshore transport mechanisms

The larval pool was sampled for vertical stratification at three depths offshore and two depths inshore on one day, and then at one offshore site at three depths on a second day in the following year, always during the recruitment period for *P. perna*. Cyprids were the only taxa that showed a significant vertical pattern, with higher densities in the middle and bottom strata (Figure 2.14). These results agree with previous studies elsewhere. In their study of *P. perna* on the south coast, McQuaid and Phillips (2000) found no vertical stratification on 9 of 11 sampling occasions, and concluded that *P. perna* does not undergo diel vertical migration. In a study of chthamaloid barnacle larvae in southern California, Tapia (2005) found that although the naupliar phases were more abundant near the surface, cyprids aggregated nearer the bottom.

Shore-parallel or curvilinear slicks or foam lines in the nearshore, although all similar in appearance, may be caused by a suite of different mechanisms, all of which could be important for the physical hydrography that influences meroplankton dynamics (Kingsford 1990). The first mechanism is wind-driven Langmuir circulation cells that accumulate buoyant particles and upward-swimming organisms as they subduct (Langmuir 1938; Kingsford 1990). The second is topographically-generated fronts that form as two water masses move vertically against each other (McCulloch and Shanks 2003; Shanks et al. 2003c), also causing the accumulation of buoyant particles and upward-swimming organisms at the interface, although these can be wider than those

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observed in my study (Kingsford 1990). Finally, sets of slicks or foam lines may be created, and then pushed shoreward, by internal waves passing underneath (Ewing 1950; Waldron 1988). These slicks have been found to push the larvae of fishes and invertebrates shoreward in other parts of the world (Shanks 1983, 1988). Other oceanographic mechanisms have also been hypothesized to transport larvae in the nearshore environment, such as upwelling, the relaxation of upwelling and active downwelling (Farrell et al. 1991; Roughgarden et al. 1991a; Shanks et al. 2000; but see Shanks and Brink 2005) and breaking internal tidal waves, or tidal bores (Pineda 1994, 1995; Vargas et al. 2004; Ladah et al. 2005), but neither of these alone cause shore-parallel foam lines or slicks.

All of the three oceanographic processes that cause shore-parallel foam lines will accumulate buoyant particles at the surface, but only internal waves or topographically-generated fronts could potentially also accumulate denser particles below the slicks through turbulent eddying at the pycnocline boundary. I could find no differences in zooplankton biomass or mytilid densities in and out of the shore-parallel slicks, but the densities of all bivalves (which were generally vertically unstratified) were significantly higher inside all the foam lines sampled and cyprids (which were found to accumulate near the bottom) were significantly higher in some of them (Table 2.8, Figure 2.13). This suggests that some, but not all, of the shore-parallel slicks sampled in this study were accumulating denser particles such as larvae, and therefore might be caused by fronts or internal waves rather than wind-driven Langmuir circulation cells. For internal waves to be present, a pycnocline is required in the water column (Mann and Lazier 1996). Unfortunately, no salinity- or temperature-with-depth measurements were taken on the days that the slicks were sampled to indicate whether or not a pycnocline was present, but all days with measurements showed no pycnocline in this depth of water. In addition, sets of shore-parallel slicks, indicative of internal waves, were never observed, so it is likely that this is a topographically-generated front. Rather than driving cross-shore transport, this front would act as a barrier to advection for meroplanktonic larvae (McCulloch and Shanks 2003; Shanks et al. 2003c). These patterns require further observation through careful larval sampling and oceanographic measurements before drawing any conclusions about the process that formed them and their role in the onshore-transport of meroplanktonic larvae.

The role of larval behavior in transport processes

In their study of the meroplanktonic larvae of *Concholepas concholepas* in Chile, Poulin et al. (2002) concluded that the distribution of competent larvae was determined both by physical transport mechanisms (in this case, downwelling caused by alongshore winds) and by larval behavior, which maintained competent larvae near settling areas despite the presence of mechanisms that might have transported them away. In my study, all taxa were found to be more dense inshore than offshore, perhaps due to the presence of a topographically-generated front at 12-

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17 m depth that prohibited offshore advection of the larvae. Of these, mytilids were found to be most dense nearest two particular rock points, Black Rock and Lala Nek. The study area as a whole was selected because of its repeated pattern of small rocky headlands and long shallow sandy bays along a straight contiguous coastline, so that the rocky headlands are nearly physical replicates of one another. Biologically, they are not replicates, as the central ledge, Black Rock, has a significantly higher density of the mussel, *P. perna*, than exists for 15 km in either direction along the coastline. Additionally, a second, smaller area of high-density of *P. perna* has been reported on a small island 50 m offshore of the rock point just south of Lala Nek, called Island Rock (Sink 2001). The significantly greater densities of mytilid larvae inshore near the adult populations at Black Rock and Lala Nek could be an indication of associations with adults related to either spawning or settlement events. In contrast, cyprids were found to be more densely inshore in the absence of nauplii, which may therefore indicate behavioral adaptations of the competent larvae that allow them to return to areas nearer their preferred settlement habitat. An examination of the current patterns around these rock ledges would be required to further investigate these hypotheses.

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2.5 CONCLUSION: a conceptual model of the larval distribution and local transport near Maputaland rocky shores

The meroplanktonic larvae and coastal phytoplankton investigated in this study did exhibit spatial patterns, accumulating inshore and around some headlands, while the general pool of zooplankton did not. This is probably because the zooplankton pool was dominated by forms such as copepods and chaetognaths, which are open-ocean neritic species, whereas the barnacle and bivalve larvae belonged to species whose adults are confined to the intertidal zones of rocky shores. Phytoplankton increased in density 24 h after the appearance of cooler water, which appeared 12-48 h after the onset of upwelling-positive northeasterly winds, suggesting that wind-induced upwelling transports nutrients into the nearshore. Wind-driven upwelling may also be important for the onshore transport of bottom-dwelling larvae such as cyprids, and relaxation of upwelling may transport larvae onshore if they occur in the upper strata. Neither mytilids nor phytoplankton had an alongshore spatial pattern, disproving the hypothesis that eddying or slowing of currents within the bays is retentive for phytoplankton or larvae. Even though vertical stratification of the water column was not measured in the brief investigation of foam lines, the aggregation of negatively buoyant larvae within some foam lines indicates that a topographically-generated frontal convergence zones may accumulate larvae in this area. The density of adults may influence the spatial patchiness of meroplanktonic larvae, as noted with the increased densities of mytilid larvae nearest to Black Rock; whether this aggregation was related to spawning or to settlement was not determined. Additional sampling, plus further study at a fine temporal scale of larval settlement, associated with a rapid collection of subsurface temperature and salinity information, would be necessary to test these hypotheses. This would resolve whether upwelling, topographically-generated fronts or internal waves are mechanisms of larval retention, transport and aggregation and are therefore important for onshore or offshore transport of mussels and cyprids in the Maputaland Marine Reserve.

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CHAPTER 3

Recruitment patterns of mussels and barnacles and benthic-pelagic coupling in Maputaland

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3.1 INTRODUCTION

Many benthic invertebrates rely on pelagic larvae for dispersal, and the amount of propagules that then recruit into or from other locations forms the basis of inter-generational connectivity. Benthic-pelagic coupling has been reported in studies correlating hydrography with both meroplanktonic distribution and larval settlement (Yoshioka 1982; Minchinton and Scheibling 1991; Bertness et al. 1992, 1996; Archambault and Bourget 1999; Wing et al. 2003). These authors found that when larvae converge or are driven inshore by dominant hydrologic or wind regimes, larval density in the plankton is a good predictor of settlement density. Although these results seem intuitive, some researchers have failed to find direct evidence of coupling between larval densities and settlement, at the scale of meters (De Wolf 1973) or 100s of meters (Porri et al. 2006), while others have found direct links at some locations but not at other proximate sites (McQuaid and Lawrie 2005).

The connectivity of adult populations both in and out of marine protected areas has become a topic of increased research in the past decade, and is important because the factors that connect larval and adult ecology are central to conservation and management (Warner and Cowen 2002; Lubchenco et al. 2003; Roberts et al. 2003). In particular, improving our understanding of connectivity within and among marine protected areas has become timely in South Africa (e.g. Wieters 2006), especially under a new climate of ecosystem-based management and systematic conservation planning (e.g. Lombard et al. 2004; Pierce et al. 2005). Of all the marine protected areas in South Africa, the largest falls within the Greater St. Lucia Wetland Park, in northern KwaZulu-Natal, and is now known to span two intertidal bioregions (Lombard et al. 2004). Re-assessment, with regard to placement and size of sanctuaries and permissible activities (including extractive use) of the Parks zonation is currently underway as part of a legislative requirement for development of an Integrated Management Plan for the World Heritage Site.

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In previous decades, most scientists describing the intertidal and nearshore subtidal marine biogeography of the KwaZulu-Natal (KZN) coastline grouped it with the rest of the east coast of South Africa into a single region called the Natal Biogeographic Province (Hommersand 1986; Field and Griffiths 1991; Emanuel et al. 1992; Bustamante and Branch 1996). These descriptions, based mostly on species presence/absence data, were recently revised by Sink et al. (2005), who took both species composition and abundance into consideration. Further, Bolton et al. (Bolton et al. 2004) identified Cape Vidal as a biogeographic break for seaweed. Both Sink et al. (2005) and Bolton et al. (2004) confirmed Jackson's (1976) suggestion of an important biogeographic break in intertidal populations at Cape Vidal, within the Greater St. Lucia Wetland Park. Systematically ruling out the influences of sea temperature and wave exposure, Sink (2001) identified two correlates for this break. The first was riverine input: 99% of KZN province's annual rainfall runs into the Natal marine province to the south of Cape Vidal, whereas a mere 1% flows into the Delagoa marine province to the north in Maputaland, mostly through the Kosi Lakes system in the extreme north of the province. The other factor was the impact of human harvesting of intertidal invertebrates: harvesting offtake in Maputaland was 18 times higher than that in the Natal bioregion. One of the most heavily targeted species in Maputaland is the brown mussel, *Perna perna* (Kyle et al. 1997a), a focal species in this study. Sink's conclusion was supported by Lombard et al. (2004) who described two distinct inshore bioregions based on both intertidal community structure and geomorphological data: the Natal bioregion extending south from Cape Vidal and the Delagoa bioregion extending north into Mozambique, through a coastal area known as Maputaland or Thongaland (Figure 3.1). This break also appears to exist for subtidal communities (Lawrence 2005).

Recruitment rate is a reproductive parameter that is strongly influenced by connectivity, and is a compound measurement of several important factors that influence the early life history of benthic invertebrates. Biotic and abiotic factors affecting benthic recruitment influence each of the following periods in this complex life cycle: (1) initial release of gametes or larvae into the water column (including fecundity, spawning synchrony, fertilization success), (2) emigration and the pelagic larval phase (navigation and orientation), (3) metamorphosis and settlement (immigration, settlement cues, settlement choice), (4) post-settlement survival and recruitment, and (5) juvenile growth and maturation (Morgan 2001). At each of these stages, there are intrinsic properties of each species and even each individual organism (type of larval development, behavior, condition, growth, sensory capabilities) that will influence its dispersal path and recruitment success, as well as extrinsic selective biotic factors (predation, food availability, competition, mutualism) and abiotic factors (temperature, advection, diffusion, accumulation, water chemistry, nutrients) that play strong roles in survivorship during the various periods (Morgan 1995a, b, 2001; Shanks 1995; Morgan and Christy 1996; Pineda 2000; Kingsford et al. 2002; Menge et al. 2004; Navarrete et al. 2005; Wieters 2005). In recruit-limited environments, settlement and recruitment rates reflect the subsequent density of adults on the shore (Connell 1985; Gaines and Roughgarden 1985), and will influence the relative strength of community-level processes (Nielsen and Navarrete 2004; Navarrete et al. 2005; Wieters 2005). Previous studies have shown substantial temporal and spatial variability in recruitment among species (Navarrete et al. 2002), substrates (Bulleri 2005), proximate sites (Helson and Gardner 2004), different levels of wave intensity (McQuaid and Lindsay 2005) and intertidal zones (McQuaid and Lindsay 2005).

This chapter investigates the recruitment patterns of the mussel species *P. perna* and *B. semistriatus* and the barnacle taxa *C. dentatus* and *Tetraclita* spp. onto natural and artificial

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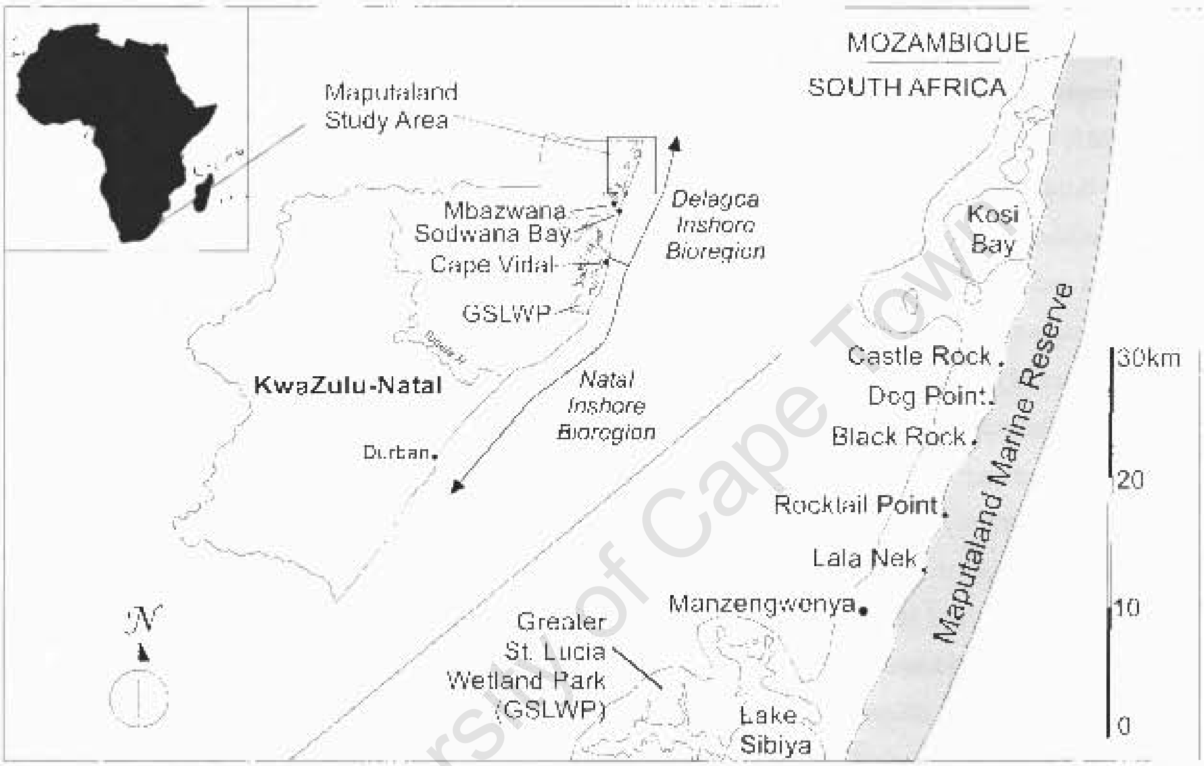

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Figure 3.1 Map showing the biogeographic divide between the Natal and Delagoa bioregions at Cape Vidal and the position of the study area adjacent to the Greater St. Lucia Wetland Park World Heritage Site (left) and an enlargement of the study area with sites (right), each of which has two localities, north and south. Shading indicates the Maputaland Marine Reserve, which extends 3 nautical miles offshore. Other locations mentioned in this chapter are indicated in Figure 2.1.

substrates at five adjacent rocky headlands in Maputaland. The most important intertidal mussel in KZN is the brown mussel *Perna perna*. Mature beds of *P. perna* support coastal biodiversity: as ecosystem engineers, they transform simple rock face into a complex three-dimensional matrix that houses numerous other organisms (Suchanek 1985; Alper 1998). As filter feeders, mussels actively transfer energy from the nearshore pelagic ecosystem into the intertidal, transforming it into a food source for coastal predators including starfish, whelks, seabirds, inshore linefish and humans (Pollock 1979; Griffiths 1981; Hockey and Underhill 1983; Hockey and Bosman 1986). Mussels are an important traditional food resource for human coastal communities (Bigalke 1973; Siegfried et al. 1985; Lasiak 1993; Kyle et al. 1997a; Cockcroft et al. 2002; Harris et al. 2003), and in some areas in South Africa their consumption prevents nutrition-related diseases like kwashiorkor that affect childhood development (Siegfried et al. 1985). *P. perna* is also one of the two most important recreational fisheries in KZN (Tomalin and Kyle 1998; Robertson 2003). Finally, mussels accumulate marine pollutants in their tissues, and can play an important role as bioindicators of the coast's health (e.g. Gregory et al. 2002). Because of its high offtake by subsistence harvesters in Maputaland, *P. perna* is of special conservation concern to managers and harvesters alike (Kyle et al. 1997a; Tomalin and Kyle 1998; Robertson 2003), and additional information is required to assist the successful co-management of local stocks established in several areas around the coast of South Africa (Cockcroft et al. 2002; Harris et al. 2003).

Settlement and recruitment patterns of *P. perna* have been previously investigated in South Africa in the Natal bioregion (Berry 1978; Harris et al. 1998; and see Chapter 1), and in the Agulhas Bioregion to the south (Figure 1.1) (Beckley 1979; Crawford and Bower 1983; Lasiak 1991a; Dye 1992a; Barnard 1995; Lasiak and Barnard 1995; Dye et al. 1997; Harris et al. 1998; Lawrie and McQuaid 2001; Porri 2003; Erlandsson and McQuaid 2004; McQuaid and Lindsay 2005; Porri et al. 2006; and see Chapter 1). These studies have included settlement and recruitment into both natural substrates (mussel beds, algae and bare rock) and artificial substrates (scouring pads and brushes). In general, *P. perna* has shown a strong seasonal recruitment pattern, with spring peaks in KZN and winter peaks along the south coast of South Africa (Berry 1978; Harris et al. 1998; and see Chapter 1). No recruitment studies of benthic intertidal invertebrates to date have extended north of Cape Vidal into the Delagoa bioregion in South Africa, although some studies of the settlement and recruitment of brachyuran crabs (Paula et al. 2001, 2003) and their larval distribution (Paula et al. 2004) have been undertaken at Inhaca Island, in southern Mozambique (26° 02' S, 32° 54' E). Aspects of the distribution, recruitment and growth of *P. perna* have also been studied in Brazil and Venezuela, where the species is commercially farmed (Velez and Epifanio 1981; Pompa et al. 1990; Marques et al. 1998; Holland 2001), and in Texas, USA, where it has become invasive (Hicks and Tunnell 1995; Hicks et al. 2001; Holland 2001). Finally, settlement and recruitment studies on the wild and farmed greenshell or green-lipped mussel *Perna canaliculus* in New Zealand have added

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to knowledge of the genus (e.g. Booth 1977; Hayden and Kendrick 1992; Menge et al. 2002; Alfaro and Jeffs 2003; Helson and Gardner 2004; Alfaro 2006b).

A second, smaller mussel species, *Brachidontes semistriatus*, co-occurs with *P. perna* throughout KZN, and is the other bivalve species in this study. A unexploited mussel that can grow up to 30 mm, its range it presently thought to extend from South Africa to the Mediterranean and throughout the eastern Indian Ocean basin. Its taxonomy is currently in revision, however. The two names used previously in South African literature for this species are *B. variabilis* (e.g. Davies 1980) and, more recently, *B. semistriatus* (e.g. Lasiak 1999), but both are junior homonyms and therefore invalid (Herbert and Warén 1999). While Herbert and Warén (1999) refrained from recommending an alternative name, other researchers have begun to refer to this species as *B. pharaonis* across its distribution (e.g. Oliver et al. 2004). There is some suspicion that this may be more than one species (Rilov et al. 2004; G. Oliver, pers. com.). Given the current taxonomic confusion, I have opted to retain the name *B. semistriatus* in my thesis, as it links the southern populations of this species to the name used previously in South African ecological literature. In a comparison of adjacent exploited and non-exploited rocky shores at the Mkambati Nature Reserve in the Eastern Cape (Figure 1.1), *B. semistriatus* contributed numerically very strongly to the average dissimilarity because it was found more commonly on exploited rocky shores (Lasiak 1999). With the exception of studies on *B. pharaonis* in the Mediterranean Sea (Nakhlé et al. 2006), little else is known about the ecology of the species. There are, however, many studies on the physiology and the ecology of some congenerics, including *B. solisianus* and *B. darwinianus* in Brazil (Tanaka and Magalhães 2002), *B. exustus* and *B. recurvus* in Texas (Hoese 1960) and Florida, USA (Lee and Foighil 2004), *B. rodriguezii* in Argentina (Adami et al. 2004) and a recruitment study of *B. granulata* in Chile (Navarrete et al. 2002).

In addition to the two mussel species, I investigated the recruitment patterns of the dominant mid-shore barnacles *Tetraclita squamosa rufotincta* and *Chthamalus dentatus*, as well as the less common *Tetraclita serrata*. All of the species are indigenous to South Africa and Mozambique and are sessile as adults but have a dispersive planktonic larval stage. Plantigrades or nauplii and cyprids remain in the water column for 10-20 days before settling onto hard substrata in the mid to low intertidal (Griffiths 1979; Barnes and Achituv 1981; Anderson 1994; Hicks and Tunnell 1995; Chapter 2).

The reproductive season of *Tetraclita serrata*, has been studied in the Western Cape by Griffiths (1979), and the intensity of its regular annual recruitment was found to be significantly related to the mean abundance of adults in the Eastern Cape Province (Dye 1992b). Dye concluded that this indicated limited dispersal for this species. I have found very little published material on any of these barnacle species, so instead have largely consulted the literature on congeners. The recruitment of *T. squamosa* and *T. japonica* in Hong Kong are known to be controlled by heat stress at the upper limits of their zonation and by predation at the lower limit (Chan and Williams 2003),

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and *Tetraclita panamensis* is thought to be recruitment-limited in Costa Rica (Barnes and Achituv 1981; Sutherland 1987). Aspects of the settlement and recruitment ecology of other *Chthamalus* species have been studied in Mexico (Raimondi 1988b, 1990), California and Oregon, USA (Menge 2000a; Connolly et al. 2001; Forde and Raimondi 2004; Broitman et al. 2005), Japan (Apolinário 1999), the UK (Kent et al. 2003), Portugal (Cruz 1999; Cruz et al. 2005) and across Europe (O'Riordan et al. 2004).

This is the first intertidal recruitment study in the Delagoa bioregion of South Africa. Incorporating the recruitment data presented here plus the physical, larval and adult density data presented in Chapter 2, five hypotheses are tested. (1) As in other areas of KZN, mussels will show regular seasonal recruitment patterns while barnacles will not show a regular seasonal pattern. (2) At the scale of the study, recruitment among sites will be synchronous, but unpredictable differences in intensity of recruitment will exist among sites. (3) Recruitment rates for each species will be correlated between adjoining natural and artificial substrates, as well as among zones on the shore. (4) Interannual and spatial patterns of mussel recruitment will be correlated with the density of adult stock on the shores. (5) Variability in recruitment rates will be explained by simultaneous larval densities in the nearshore, and/or by physical conditions including prevailing water temperature, recent temperature anomaly and along- and across-shore winds.

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3.2 METHODS

Study Area

The study area comprised a 25-km stretch of coast within the Maputaland Marine Reserve in KZN, South Africa, and is the same as that described in Chapter 2 (Figure 3.1, Table 3.1). Five intertidal rock ledges with a limited range of wave impacts, from exposed to very exposed (Sink 2001, Sink et al. 2005) were investigated. Sink (2001) recorded wave forces spanning 4.8 to 18.1 × 10^3 N.m^{-2} in Maputaland, with the most exposed sites falling between Castle Rock and Lala Nek (ranging from 15.5 at Black Rock to 18.1 × 10^3 N.m^{-2} at Dog Point), ranking my study area as the most wave-exposed region of Maputaland. In comparison with measurements taken by Bustamante et al. (1997) and Steffani and Branch (2003), these values are higher than those previously measured on the south and west coasts of South Africa (1.1 to 10.0 and 1.5 to 15.0 × 10^3 N.m^{-2}, respectively), and fall within the measurements on the north-west coast of South Africa (2.5 to 18.0 × 10^3 N.m^{-2}), indicating that the rocky shores in this study are among the most wave-exposed in South Africa.

Table 3.1 Station positions for rocky shore sampling.

Site name	Main platform length (m)	North		South	
		Latitude	Longitude	Latitude	Longitude
Castle Rock	400	27° 04.700' S	32° 50.967' E	27° 04.725' S	32° 50.977' E
Dog Point	1100	27° 06.372'	32° 50.598'	27° 06.395'	32° 50.608'
Black Rock	800	27° 08.025'	32° 49.868'	27° 08.045'	32° 49.880'
Rocktail	400	27° 11.145'	32° 48.520'	27° 11.193'	32° 48.532'
Lala Nek	600	27° 13.538'	32° 47.732'	27° 13.553'	32° 47.718'

The five ledges have similar shapes and geological substrata (aeoleonite sandstone), and are separated by sandy zeta-shaped bays 5-10 km long and 0.5-1.5 km deep. All of the rock ledges consist of an exposed sea-level notch, forming a flat horizontal intertidal platform of aeoleonite carbonate-cemented beachrock 2-12 m wide. An armored rim lies at the seaward edge of most of the platforms (Miller and Mason 1994). Shoreward, the platform may be backed by sandy beach (Lala Nek, Rocktail, Dog Point, and the south locality at Castle Rock) or rocky cliffs (Black Rock and the north locality at Castle Rock). The average position of the platform-beach interface varies horizontally by as much as 10 m seasonally (pers. obs.), but has been noted to change by as much as 40 m (Miller and Mason 1994).

Vertical zonation patterns in KZN were first described at Isipingo Beach, Durban (Eyre and Stephenson 1938), then at multiple other sites including Black Rock (Jackson 1976), and most recently and more extensively along the entire coastline (Sink 2001; Sink et al. 2005). In addition, there is also an important horizontal variability in community structure at a scale of 1-10 m (Sink 2001). The mussel and barnacle zones in my study are equivalent to those alternatively called 'lower balanoid' and 'upper balanoid' (Branch and Branch 1981).

Field Methods

Monthly recruitment was investigated for 18 months from July 2002 to February 2004. In July 2002, one set of treatments of 5 brushes, 5 plates, and 10 scraped patches was installed at each of the 5 designated rock points. Each of these treatments was located 100-300 m south of the main point of the ledge (Figure 3.2). Brushes and plates were placed on the main rock ledge with an aspect < 20° from the horizontal. This first set of treatments was surveyed monthly through to February 2003. In February 2003, the treatment replication was reduced to 3 brushes, 3 plates, and 6 bare rock patches, and duplicated at each rock point by the addition of localities lying 100-150 m north or south of the original locality. Sampling took place monthly through to February 2004.

Brushes were manufactured by Addis®, with nylon-bristles, identical to those used for the study in Chapter 1. The brushes measured 16 × 5.5 cm, but were cut in half. A stainless steel coach (hex-head) bolt was used to attach each half-brush to a hole drilled into the rock and fitted with a plastic wall plug. Some brushes were lost, reducing sample sizes.

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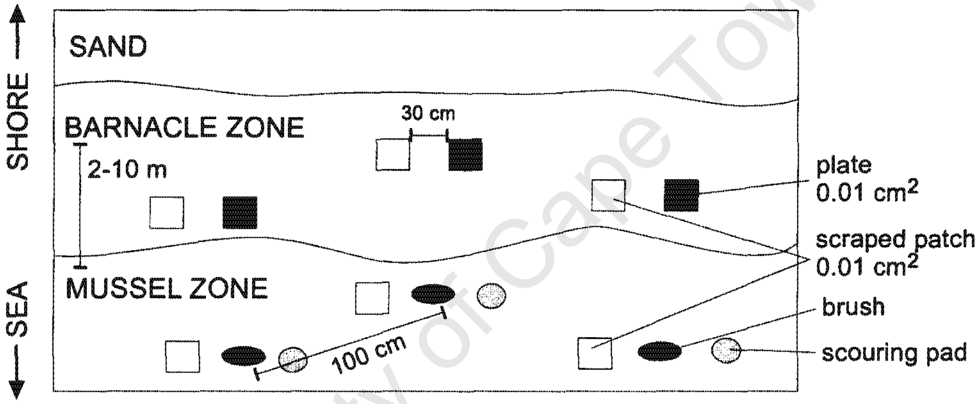

Figure 3.2 Schematic of the recruitment treatments used in this study: plates, scraped patches, brushes, and scouring pads or Chuffies.

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Plates were constructed of clear 3-mm shatter-resistant acrylic, cut into 10 × 10 cm squares, affixed with 3M® grey Safety-Walk tape and attached to the rocks using stainless steel bolts (Menge et al. 1994). Plate loss was lower than brush loss, but there were two incidents of theft or vandalism at Black Rock (June and July 2003).

Each plate and brush had a corresponding 10 × 10 cm^2 patch of bare rock situated 30-40 cm away that was scraped and scoured with a steel brush and then surveyed for recruits a month later. All barnacles > 500 µm sitting on plates or scraped rock patches were identified, counted, and assigned to 1-mm size classes. No mussels were found attached to the bare rock patches in the either zone throughout the survey.

On two occasions and at two sites, blue scouring pads called 'Chuffies', Chilean-made versions of Tuffy® scouring pads, used to record recruitment in Chile, South Africa and the USA (Navarrete and Castilla 1990; Menge et al. 1994) were installed 100-120 cm from each brush, left out for one month and then removed on the same day as the brushes. The surface area of these scouring pads, when unrolled, was approximately 100 cm^2, and they occupied about 48 cm^3 when rolled and deployed (6 × 4 × 2 cm).

Laboratory methods

After retrieval, brushes and Chuffies were stored frozen at -4°C. They were then placed in a bucket of 8 liters fresh water with 1 ml commercial bleach and soaked for ~ 1 h before being cleaned with a comb and/or forceps to remove all biological material. The biological material was seived through a 250 µm mesh strainer and stored in 70% ethanol in darkness until analysis. The cleaned brushes and Chuffies were soaked overnight in a mild bleach solution, rinsed with fresh water, sun-dried, and stored prior to the next installation. The biological material was examined using a stereo-microscope and all *B. semistriatus* and *P. perna* counted and measured in 1-mm size classes. Recruits were defined as individuals 0.5-2.0 mm shell length. Over 95% of all the bivalves in the samples were either *P. perna* or *B. semistriatus*, and other rarer species were not counted.

To process the plates, any *C. dentatus* and *Tetraclita* spp. that had settled on them were counted and measured across the maximum diameter in 1-mm size classes. Cyprids were not identified to species, but were counted. Following analysis, plates were soaked overnight in a mild bleach solution, brushed, dried in the sun, brushed vigorously to remove all biological remnants, checked under the microscope and stored for future use.

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Data analysis

All statistics were computed using Statistica 7.0 (StatSoft, Inc. © 1984-2004).

Temporal and spatial recruitment patterns

Recruitment rates were plotted for each taxon at each locality. Although all treatments were collected every 26-30 days, data are standardized and presented as recruits per sampling unit per day.

For the brushes, counts of mussel recruits of *B. semistriatus* or *P. perna* were included in the analysis. For the plates and bare rock treatments, counts of barnacle recruits of *C. dentatus* or *Tetraclita* spp. < 4 mm were included. Other species and cyprids were not examined, as their appearance was too infrequent for statistical analysis. For each of the target species on each substrate, I tested the relative importance of site, locality (north or south) on the headland and season to the recruitment variability using a mixed-model three-way partly-nested ANOVA (Quinn and Keough 2002). Season (Sn) and Locality (Loc) were designated as fixed factors. Often time is regarded as a random factor in models such as these. However, as the data were grouped *a priori* into seasons with the intent of finding specific temporal effects, I treated season as a fixed factor. Site (St) was designated as a random factor and thus locality nested within site [Loc(St)] also became a random factor. The interactions Sn*St and Sn*Loc(St) were therefore both random factors (Table 3.3a).

This analysis was only possible for the period March 2003 to February 2004, following the addition of a second locality to each site in Febrary 2003. 'Seasons' (used here to designate three-month blocks of time, rather than actual seasons) were designated as follows: Autumn 03 (Mar-May 2003), Winter 03 (Jun-Aug 2003), Spring 03 (Sep-Nov 2003) and Summer 04 (Dec 2003-Feb2004).

In general, data were well-balanced and few individual replicates were missing from any cell for any species. Cells were considered to be the monthly values, and three cells for each locality were combined to give a seasonal mean ($n_{cell} = 3$, $n_{season} = 9$) and to allow temporal replication within seasons. Because a balanced ANOVA is robust to slight variations in sample size (Quinn and Keough 2002), virtual replicates were not added if > 50% of the replicates were present in any individual cell. However, cells for the artificial substrates were occasionally vacant. In this case, as in Chapter 1, the models were balanced by adding a few virtual replicates to the data sets following Underwood (1997) and according to the following criteria: (1) When two localities close to each other followed the same trends (means or relative means and variances) in other seasons, virtual replicates were added to mimic the matching locality in the missing season, not to exceed 10% of the overall data in the model. (2) Data were added such that their variance matched other cells in the same season with similar means.

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Table 3.3 Calculations for the general linear models used in (a) the split-plot three-way mixed-model ANOVAs, (b) four-way partly-nested mixed-model ANOVAs and (c) two-way mixed-model factorial ANOVAs

(a) Factor		Effect	*df*	*F*-value*
Intercept		Fixed		MS_A
Site	A	Random	p-1	$MS_A/MS_{B(A)}+MS_{AC}-MS_{B(A)C}$
Locality(Site)	B(A)	Random	p*(q-1)	$MS_{B(A)}/MS_{B(A)C}$
Season	C	Fixed	r-1	MS_C/MS_{AC}
Season*Site	A × C	Random	(p-1)*(r-1)	$MS_{AC}/MS_{B(A)C}$
Locality(Site)*Season	B(A) × C	Random	p*(q-1)*(r-1)	$MS_{B(A)C}/MS_{Resid.}$
Residual			pqr*(n-1)	

(b) Factor		Effect	*df*	*F*-value*
Intercept		Fixed		MS_A
Site	A	Random	p-1	$M_A/MS_{AB}+MS_{C(A)}-MS_{BC(A)}+MS_{D(A)}-MS_{CD(A)}+MS_{BCD(A)}$
Season	B	Fixed	q-1	MS_B/MS_{AB}
Site*Season	A × B	Random	(p-1)*(q-1)	$MS_{AB}/MS_{BC(A)}+MS_{BD(A)}-MS_{BCD(A)}$
Zone(Site)	C(A)	Random	p*(r-1)	$MS_{C(A)}/MS_{BC(A)}+MS_{CD(A)}-MS_{BCD(A)}$
Season*Zn(Site)	B × C(A)	Random	p*(q-1)*(r-1)	$MS_{BC(A)}/MS_{BCD(A)}$
Locality(Site)	D(A)	Random	p*(s-1)	$MS_{D(A}/MS_{BD(A)}+MS_{CD(A)}-MS_{BCD(A)}$
Season*Loc(Site)	B × D(A)	Random	p*(q-1)*(s-1)	$MS_{BD(A)}/MS_{BCD(A)}$
Zone (Site)*Loc(Site)	C(A) × D(A)	Random	p*(r-1)*(s-1)	$MS_{CD(A)}/MS_{BCD(A)}$
Ssn* Zn (Site)*Loc(Site)	C(A) × D(A) X B	Random	p*(q-1)*(r-1)*(s-1)	$MS_{BCD(A)}/MS_{Resid}$
Residual			pqrs*(n-1)	

(c) Factor		Effect	*df*	*F*-value*
Intercept		Fixed		MS_A
Site	A	Fixed	p-1	MS_A/MS_{AB}
Season	B	Random	q-1	MS_B/MS_{AB}
Site*Season	A × B	Random	(p-1)*(q-1)	MS_{AB}/MS_{Resid}
Residual			pq*(n-1)	

*For all of these models Statistica 7.0 calculated 97-100% of a synthesized MS-denominator for the *F*-value according to the above formulae, while the final 0-3% was due to the MS_{Resid} term, following Satterthwaite (1946). The model in (c) closely resembles the unrestricted full-factorial mixed-model presented by Quinn and Keough (2002).

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The denominators for the main effects all incorporated $MS_{Interaction}$ values (Table 3.3a), so post-hoc analyses of the main effects were carried out even when the interaction term was significant (Quinn and Keough 2002). For the unplanned post-hoc comparisons of significant main between-plots effects (St and Loc[St]), Tukey's HSD test for unequal n was used following Quinn and Keough (2002) and the recommendations in Statistica 7.0. For unplanned within-plots comparisons (Sn, Sn*St and Sn*Loc[St]), I used a Bonferroni test to allow adjustment of significance levels for multiple testing (Quinn and Keough 2002).

For the bare rock treatments, zone (*Z*), nested within site, was examined as a fourth fixed factor in the models (Table 3.3b). There were no missing cells for these data sets. Data were fourth-root transformed to achieve normality (examined graphically with a histogram and a normal probability plot) and homoscedascity (examined graphically with a box-plot, and statistically with Cochran's test, $\alpha = 0.05$). The data set for *P. perna* recruitment into brushes contained multiple zero-values. Although transformation did improve the normality of these data, the results were interpreted conservatively, using graphic representations of the data to control for the increased chances of Type I error.

In cases when the Loc(St) term was not significant in this model, this term was removed from the analysis and the localities were subsequently combined within each site (Table 3.3c). This allowed a comparison with the earlier data, in which only one locality on each rock point was sampled. Each of the models was balanced by adding a few virtual replicates as above, and fourth-root transformations were applied to meet assumptions. Post-hoc analyses of the main effects were carried out even when the interaction term was significant, as above.

Recruitment density among species, substrates and zones

The simultaneous difference in recruitment density between any two taxa recruiting onto the same substrate was tested with a matched-pair student's t-test. Data were fourth-root transformed for normality and heterogeneity of variances. Recruitment synchrony among species and zones was examined with Pearson product-moment correlation analyses (Zar 1999).

Coupling of recruitment with larval densities and physical processes

To explore correlations between recruitment and the density of meroplankton or the zooplankton biomass sampled in the same month at the same rocky headlands, I used the inshore zooplankton data in Chapter 2 and Pearson product-moment correlation analysis (Zar 1999).

Hourly wind velocity and direction data from January 2000 to December 2005 taken at Mbazwana Airfield (Climate Number 0412148-6; 27° 28' 01" S, 32°34'59" E, 61 m altitude) were provided by the South African Weather Service, and are the same as those used in Chapter 2. From these, the vector components of the hourly wind data were calculated so that a positive velocity corresponded to a north-northeasterly wind (20° clockwise from north) for the alongshore component and an east-southeasterly wind (110°) for the across-shore component. Benthic (15 m) temperature was measured hourly from 2002-2005 at Sodwana Bay, using the recorder described in Chapter 2. These data were used to compile a monthly climatology of subsurface temperature, and alongshore and across-shore winds for the region (Chapter 2, Figure 2.11). Using these hourly data, the mean values for the 27 days previous to the collection of recruitment samples each month were calculated for the following variables: along- and across-shore wind velocity, benthic temperature, and benthic temperature anomaly. Temperature anomalies were calculated by taking the mean temperature calculated for those 27 days previous to the collection of recruitment data and subtracting from them the mean temperature for those 27 days from all the years of data collection.

Multiple regression analyses with the pairwise deletion of missing cells were then used to determine the relative importance of winds, water temperature, temperature anomaly and nearshore larval densities in explaining recruitment rates. Mean daily recruitment rates for each species on each substrate were used as the dependent variable in the models, and independent variables were

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temperature, wind, larval densities and latitude. Before running the model, the individual linear relationships between the physical and biological variables were examined for co-linearity using Pearson product-moment correlation analysis (Zar 1999). Interaction terms available through a more complex general linear model were not pursued due to the problem of missing data points for each of the independent factors in the models. Data were examined for normality and heterogeneity of variances and the response variables. Independent biological variables were fourth-root transformed to achieve normality, as skewed variables could affect the normality of the error term (Quinn and Keough 2002). The model was checked to ensure that the residuals were normally distributed, and that the tolerance among the independent variables was sufficiently high (a tolerance < 0.1 indicating strong co-linearity with another variable). If redundant independent variables were indicated, they were removed and the model re-run.

Coupling of recruitment with adult stock densities

Pearson product-moment correlation analysis was used to compare mean recruitment levels per brush per day for *P. perna* during its spring/summer recruitment season with the numbers of adults.m^{-2} recorded at each site (taken from Chapter 2). A regression line was fitted using the least-squares method.

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3.3 RESULTS

Temporal and spatial recruitment patterns

Recruitment patterns for both *Brachidontes semistriatus* and *Perna perna* showed consistent and similar inter-annual trends, with peaks in the second half of both 2002 and 2003 (Figures 3.3 and 3.4). All sites showed the same temporal pattern, but differed in intensity. Only season significantly affected recruitment of *P. perna*, while site and season were significant for *B. semistriatus* (Table 3.4a). The northern and southern sites within each location were not significantly different for either species of mussel, so they were pooled for comparison with the first year's data (Table 3.4b), which confirmed that season was the only factor significantly affecting *P. perna* and that both season and site affected *B. semistriatus*. Post-hoc analysis revealed that spring was the peak recruitment season for both species (Figure 3.5). Recruitment of mussels onto plates or bare rock was too uncommon to warrant analysis (< 15 individuals of *B. semistriatus* over the course of the entire study, and no *P. perna*). Recruits of *B. semistriatus* were observed settling densely in patches of colonial diatoms on bare rock in the barnacle zone, especially in colonies trapping sand to a depth of 1 cm, but their densities there were not enumerated.

The recruitment patterns of barnacles were much more complex than for mussels (Figures 3.6 and 3.7). There was a significant seasonal effect for both species (Table 3.4a,c, Figure 3.8); *C. dentatus* showed a spring recruitment peak in both years, with an additional peak in winter 2003, and *Tetraclita* spp. had a peak in autumn 2003. A significant Locality(Site) effect for both substrates revealed that localities separated by only 100-150 m within sites were different, reflecting spatial heterogeneity in barnacle recruitment at a smaller spatial scale than for mussels. This precluded a pooling of localities and hence a comparison with the earlier phase of sampling when only one locality was sampled per site. There was no clear north-south trend, indicating a lack of consistent alongshore pattern in recruitment density among rock ledges (Figure 3.8)

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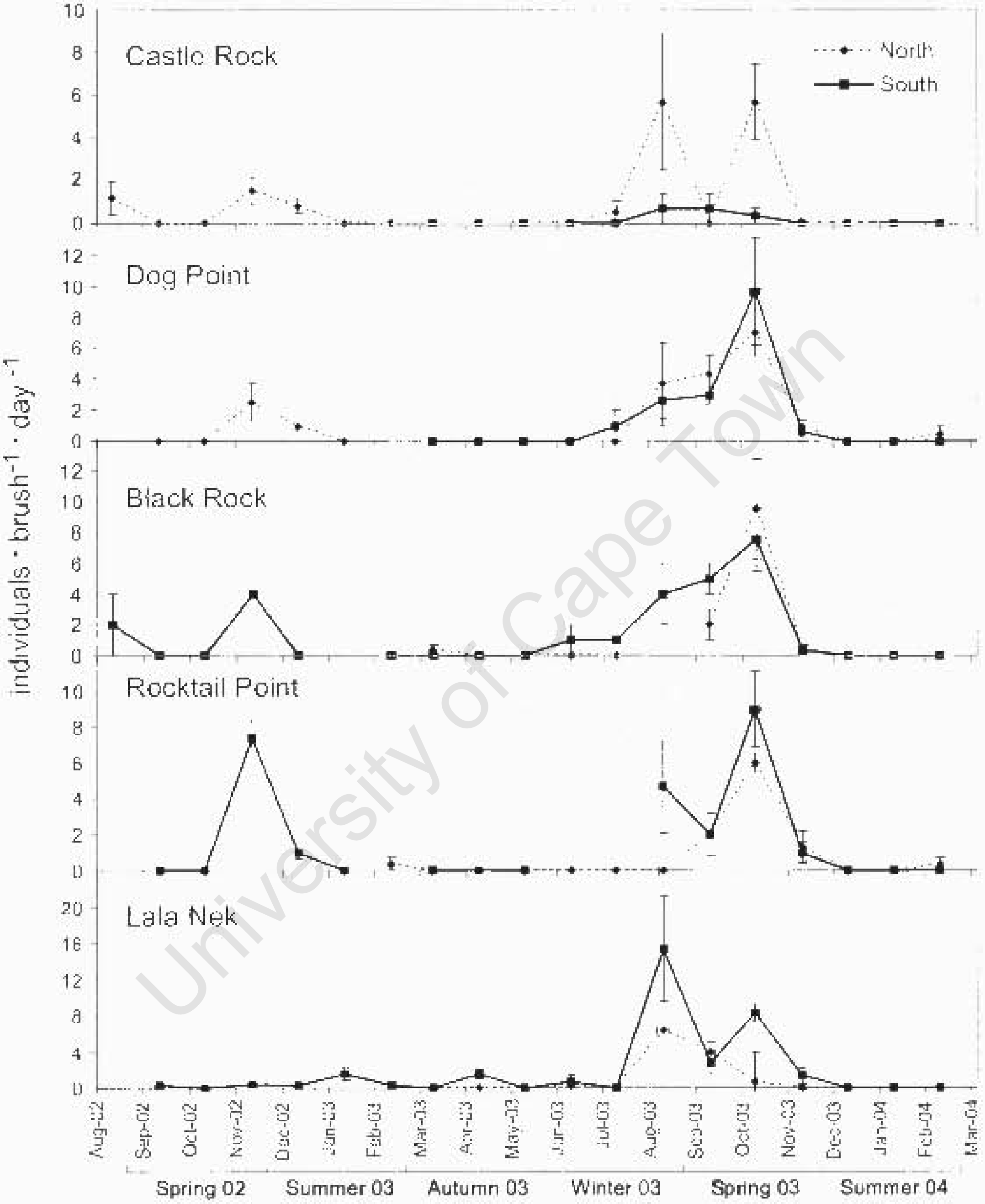

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Figure 3.3 Recruitment of *Brachidontes semistriatus* into brushes (mean ± SE). Prior to February 2003, samples were collected at one locality only (north or south) at each site (n = 5); thereafter, they were taken both north and south (n = 3).

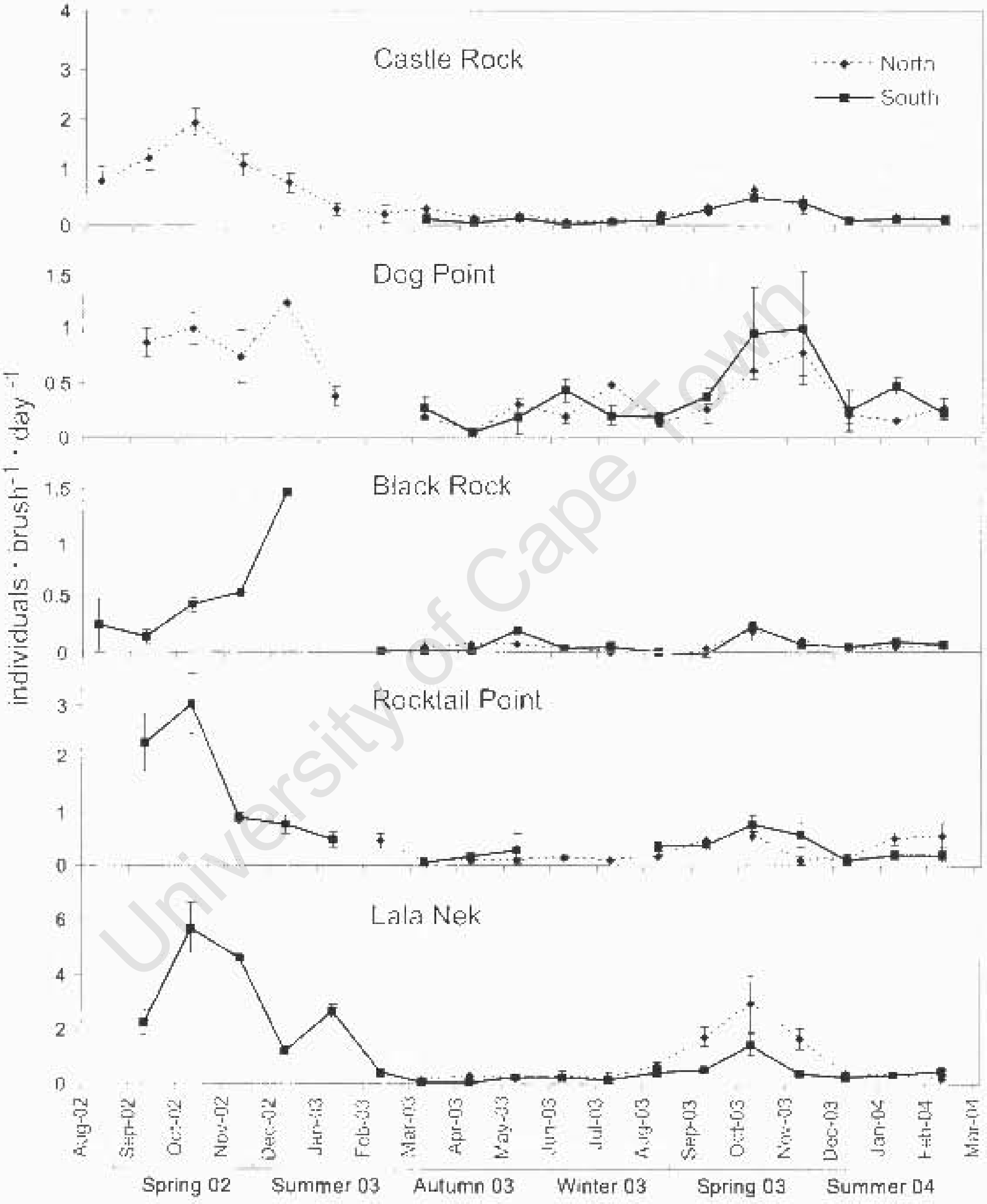

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Figure 3.4 **Recruitment of *Perna perna* into brushes (mean ± SE). Prior to February 2003, samples were collected at one locality only (north or south) at each site (n = 5); thereafter, they were taken both north and south (n = 3).**

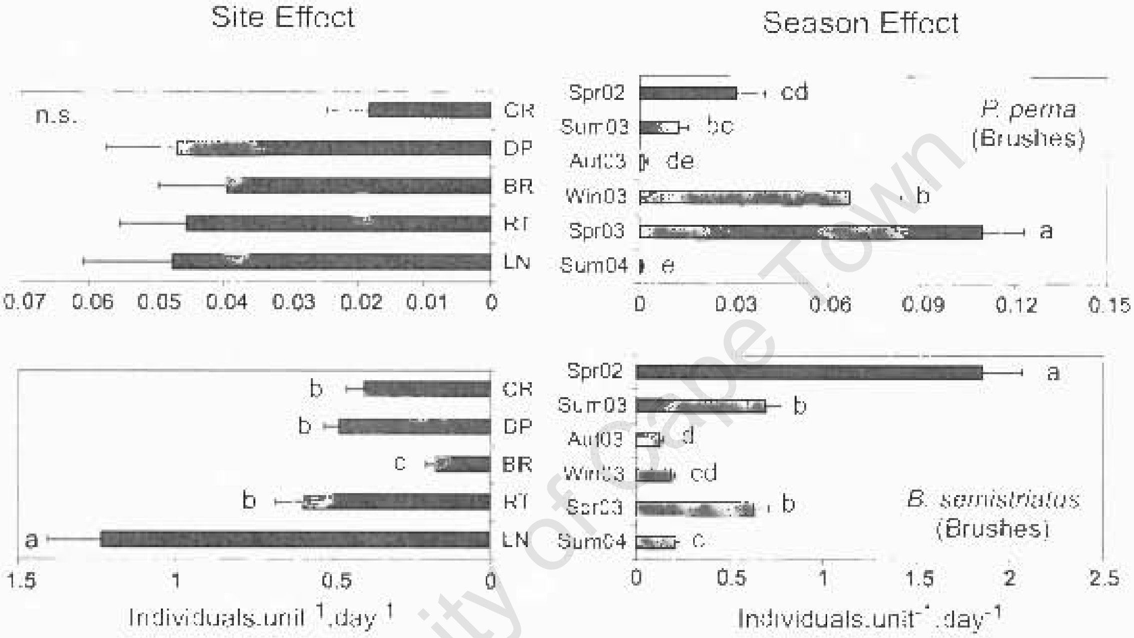

Figure 3.5 Spatial (left) and temporal (right) patterns of mussel recruitment. Site codes: CR (Castle Rock), DP (Dog Point), BR (Black Rock), RT (Rocktail) and LN (Lala Nek). Site effect was tested with Tukey's HSD for unequal n, seasonal effect was tested with a Bonferroni test; letters show significant groupings ($\alpha = 0.05$). Data were fourth-root transformed for analyses, but are presented here untransforme as mean ± SE.

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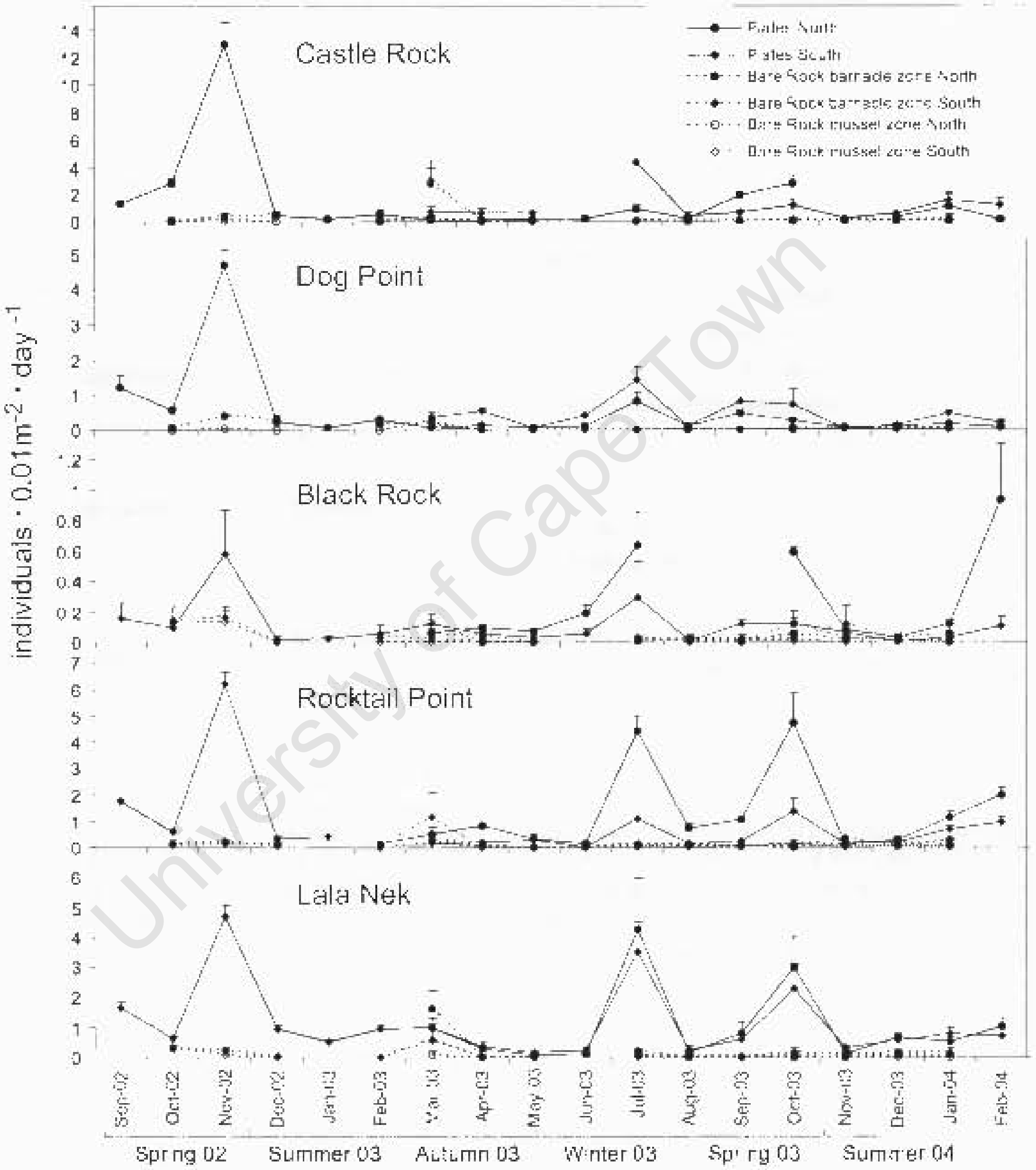

Figure 3.6 Recruitment of *Chthamalus dentatus* onto plates (mean ± SE). Prior to February 2003, samples were collected at one locality only (north or south) at each site (n = 5); thereafter, they were taken both north and south (n = 3).

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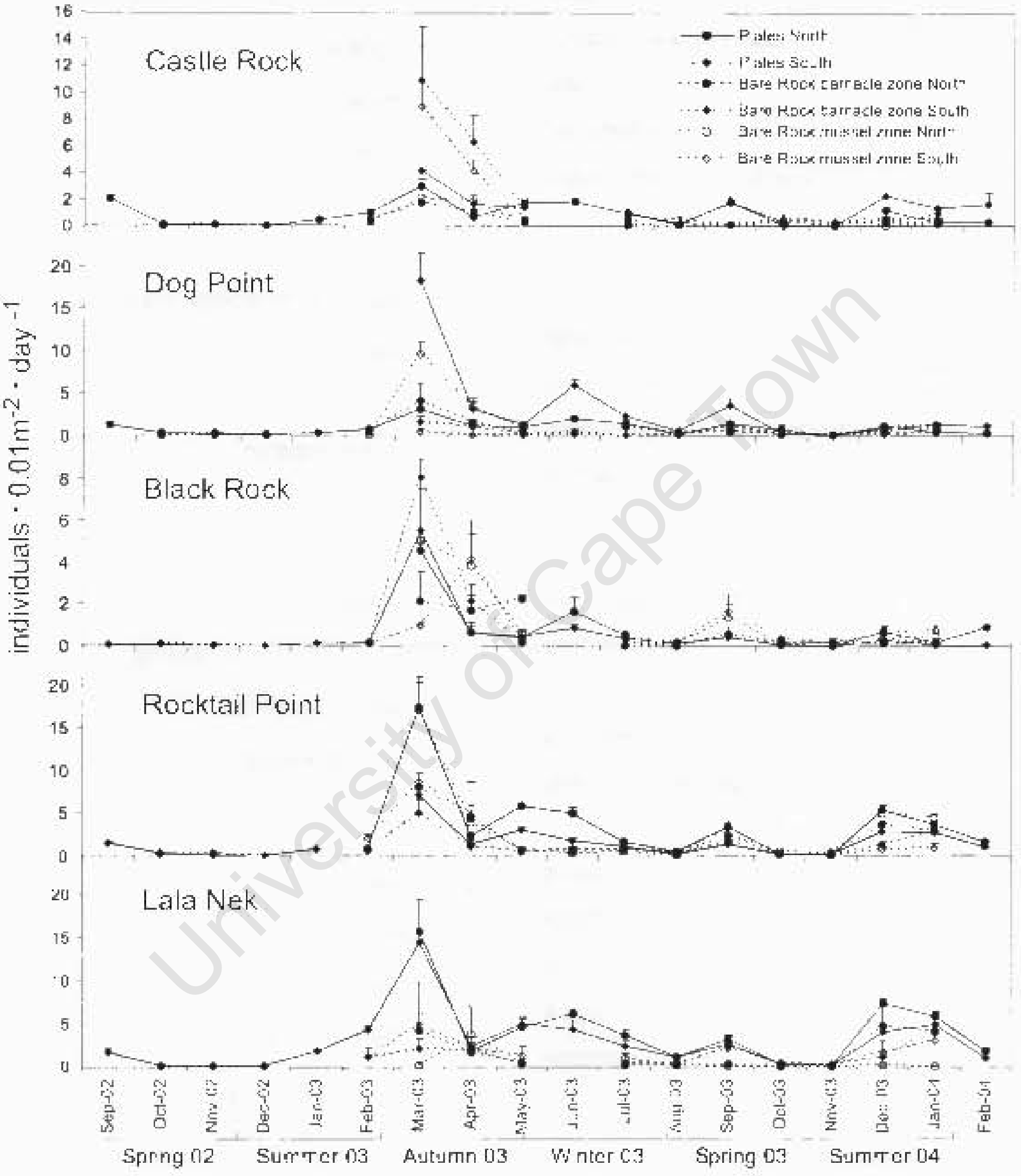

Figure 3.7 Recruitment of *Tetraclita* spp. onto plates (mean ± SE). Prior to February 2003, samples were collected at one locality only (north or south) at each site (n = 5); thereafter, they were taken both north and south (n = 3).

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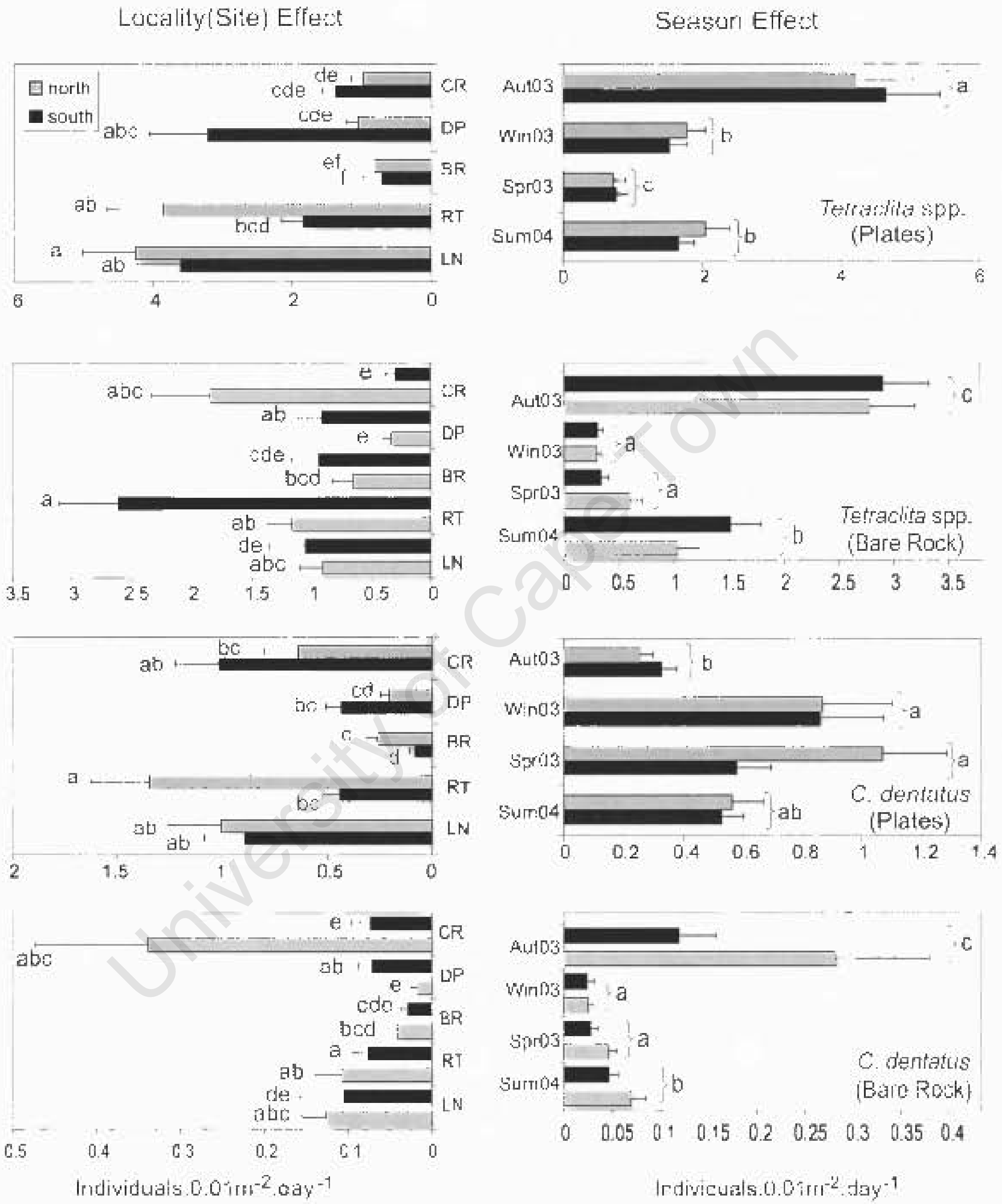

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Figure 3.8 Spatial and temporal patterns of recruitment for *C. dentatus* and *Tetraclita* spp., merging zones. Site codes: CR (Castle Rock), DP (Dog Point), BR (Black Rock), RT (Rocktail) and LN (Lala Nek). Site effect was tested with Tukey's HSD for unequal n, seasonal effect was tested with a Bonferroni test. Letters show significant groupings at $\alpha = 0.05$ level. Data were fourth-root transformed for analyses, but are presented here untransformed as mean ± SE.

Table 3.4 Results of the (a) partly-nested three-way, (b) two-way mixed-model factorial and (c) partly nested four-way mixed-model ANOVAs. Significance: *p < 0.05, **p < 0.01, ***p < 0.001, n.s. = not significant.

(a) Species	Substrate	Factor*	*df*	MS	*F*	p
Brachidontes semistriatus	Brush	Site	4	1.2469	10.0321	*
		Locality(Site)	5	0.1089	1.6141	ns
		Season	3	1.6248	19.6173	***
		Season*Site	12	0.0832	1.2298	ns
		Loc(Site)*Season	15	0.0677	1.8899	*
		Error	278	0.0358		
Perna perna	Brush	Site	4	0.1619	1.0376	ns
		Locality(Site)	5	0.0940	2.0902	ns
		Season	3	2.8919	26.9864	***
		Season*Site	12	0.1075	2.3922	ns
		Loc(Site)*Season	15	0.0450	1.0080	ns
		Error	282	0.0446		
Chthamalus dentatus	Plate	Site	4	1.5921	2.8512	ns
		Locality(Site)	5	0.5786	7.0860	**
		Season	3	0.3676	5.9849	**
		Season*Site	12	0.0614	0.7522	ns
		Loc(Site)*Season	15	0.0817	1.0156	ns
		Error	321	0.0804		
***Tetraclita* spp.**	Plate	Site	4	3.3134	7.7232	*
		Locality(Site)	5	0.3805	3.4684	*
		Season	3	5.6542	35.7398	***
		Season*Site	12	0.1582	1.4420	ns
		Loc(Site)*Season	15	0.1097	1.0566	ns
		Error	321	0.1038		

(b) Species	Factor ª	*df*	MS	*F*	p
Brachidontes semistriatus	Site	4	2.2232	19.0556	***
	Season	5	3.2149	27.4328	***
	Site*Season	20	0.1176	2.5890	***
	Error	418	0.0454		
Perna perna	Site	4	0.1128	1.1978	ns
	Season	5	1.7800	18.8143	***
	Site*Season	20	0.0948	2.0093	**
	Error	422	0.0472		

(c) Species	Substrate	Factor*	*df*	MS	*F*	p
Chthamalus dentatus	Bare Rock	Site	4	2.1572	0.7450	ns
		Season	3	8.9032	15.4757	***
		Site*Season	12	0.5761	1.2957	ns
		Zone(Site)	5	0.3366	0.9678	ns
		Season*Zn(Site)	15	0.2100	0.9391	ns
		Locality(Site)	5	2.7924	4.7293	*
		Season*Loc(Site)	15	0.4585	2.0506	ns
		Zn(Site)*Loc(Site)	5	0.3611	1.6263	ns
		Ssn*Zn(Site)*Loc(Site)	15	0.2236	1.4120	ns
		Error	534	0.1583		
***Tetraclita* spp.**	Bare Rock	Site	4	2.1572	0.7450	ns
		Season	3	8.9032	15.4757	***
		Site*Season	12	0.5761	1.2957	ns
		Zone(Site)	5	0.3366	0.9678	ns
		Season*Zn(Site)	15	0.2100	0.9391	ns
		Locality(Site)	5	2.7924	4.7293	*
		Season*Loc(Site)	15	0.4585	2.0506	ns
		Zn(Site)*Loc(Site)	5	0.3611	1.6263	ns
		Ssn*Zn(Site)*Loc(Site)	15	0.2236	1.4120	ns
		Error	534	0.1583		

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Recruitment density among species, substrates and zones

The recruitment of *B. semistriatus* was denser than that of *P. perna* at all sites and into both substrates (Table 3.5). Statistical comparisons of mussel recruitment between zones or between substrates were not possible as both species rarely settled on bare rock and never on plates. *Tetraclita* spp. recruited more densely than *C. dentatus* onto all substrates, and both barnacle taxa recruited more densely into the barnacle zone than into the mussel zone when comparing recruitment onto bare rock.

Table 3.5 Summary results of matched-pair student's t-tests between taxa recruiting onto the different substrates. Significance: ***p < 0.001, **p < 0.01.

Taxa	Substrate	Zone	Mean.day^{-1}	SD	*df*	t	p
B. semistriatus	Brushes	Mussel	0.746	0.325	734	37.48	***
P. perna			0.190	0.281			
B. semistriatus	Scouring Pads	Mussel	0.608	0.382	47	3.22	**
P. perna	(Chuffies)		0.424	0.329			
C. dentatus	Plates	Barnacle	0.851	0.309	722	-5.95	***
***Tetraclita* spp.**			0.990	0.509			
C. dentatus	Bare Rock	Barnacle	0.270	0.339	803	-22.43	***
***Tetraclita* spp.**			0.732	0.542			
C. dentatus	Bare Rock	Mussel	0.147	0.282	790	-25.15	***
***Tetraclita* spp.**			0.673	0.616			
***Tetraclita* spp.**	Bare Rock	Barnacle	0.661	0.483	387	2.72	**
		Mussel	0.592	0.542			
C. dentatus	Bare Rock	Barnacle	0.276	0.341	387	6.56	***
		Mussel	0.149	0.283			

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Correlation analysis of simultaneous recruitment of barnacles onto plates *versus* bare rock in the barnacle zone revealed a positive correlation for *Tetraclita* spp. ($r = 0.20$, $n = 727$, $p < 0.0001$) and a weak but still significant positive relationship for *C. dentatus* ($r = 0.096$, $n = 727$, $p < 0.01$). *Tetraclita* spp. recruitment was denser than *C. dentatus* on all substrates, and the proportion varied between substrates more than between zones. *Tetraclita* spp. recruitment was 2-3 times as dense as *C. dentatus* on bare rock but less than twice as dense on plates. The correlation between mussel species recruiting into brushes and Chuffies was positive and strong (for *B. semistriatus*, $r = 0.85$, $n = 40$, $p < 0.0001$; for *P. perna*, $r = 0.36$, $n = 40$, $p < 0.05$); recruitment was approximately three times greater into brushes than into Chuffies.

Comparing between zones, there was a strong correlation of barnacle recruitment rates on bare rock between the mussel and barnacle zones (for *Tetraclita* spp., $r = 0.48$, $n = 782$, $p < 0.0001$; for *C. dentatus*, $r = 0.36$, $n = 782$, $p < 0.0001$). This was supported by the lack of significant result for any factor involving zone in the ANOVA analyses (Table 3.4).

Comparing between species, *Tetraclita* spp. was negatively correlated with *C. dentatus* on plates ($r = -0.10$, $n = 804$, $p < 0.0001$), which is to be expected as their recruitment rates occurred at different times of the year. Surprisingly, their recruitment onto bare rock was correlated ($r = 0.38$, $n = 804$, $p < 0.0001$). Despite the similar recruitment seasons of *B. semistriatus* and *P. perna*, the recruitment of these two species was not correlated ($r = 0.005$, $n = 743$, not significant), indicating that there may be competition or mutually exclusive settlement at a small spatial scale between these two species. Recruitment of *C. dentatus* onto plates was positively correlated with recruitment of both *P. perna* and *B. semistriatus* into Chuffies ($r = 0.13$, $n = 671$, $p < 0.001$ and $r = 0.23$, $n = 671$, $p < 0.001$ respectively) and *Tetraclita* spp. recruitment onto plates was negatively correlated with that of either of these mussels into Chuffies ($r = -0.19$, $n = 671$, $p < 0.001$ and $r = -0.17$, $n = 671$, $p < 0.001$ respectively). Both sets of results could have been predicted as *C. dentatus* shares its breeding season with the mussels, whereas *Tetraclita* spp. does not. These comparisons between barnacles and mussels must, however, be treated cautiously as they were made across zones and substrates.

Coupling recruitment rates with larval densities and physical processes

The linear relationships between recruitment rates and the densities of zooplankton, cyprids, mytilid larvae, and bivalve larvae were first examined using Pearson product-moment correlation analysis (Table 3.6). The measured biotic and abiotic factors that were thought to influence recruitment rates were then examined for co-linearity (Table 3.7). Due to the high correlation between mytilid and bivalve larval densities, the bivalve larvae independent variable was removed from further analyses.

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Table 3.6 Pearson product-moment correlation matrix of recruitment levels on different substrates with mean inshore zooplankton densities measured at the same rock points in the same month. Significance: ***p < 0.001, **p < 0.01, *p < 0.05, ns = not significant.

		Nearshore Plankton Density			
	Taxon **Zone** **Substrate**	**Zooplankton Biomass[a]** **Inshore Point Zooplankton**	**Cyprids[a]** **Inshore Point Zooplankton**	**Mytilid Larvae[a]** **Inshore Point Zooplankton**	**Bivalve Larvae[a]** **Inshore Point Zooplankton**
Recruitment Rate	***C. dentatus*** [b] **Mussel** **Bare Rock**	r = 0.149 n = 250 *	0.223 250 ***	X[c]	X
	***Tetraclita* spp.** **Mussel** **Bare Rock**	-0.167 250 *	-0.279 250 ***	X	X
	C. dentatus **Barnacle** **Bare Rock**	ns	0.267 258 ***	X	X
	***Tetraclita* spp.** **Barnacle** **Bare Rock**	-0.178 258 **	-0.291 258 ***	X	X
	C. dentatus **Barnacle** **Plate**	ns	0.182 255 **	X	X
	***Tetraclita* spp.** **Barnacle** **Plate**	ns	ns	X	X
	B. semistriatus **Mussel** **Brush**	0.266 244 ***	X	0.179 244 **	ns
	P. perna **Mussel** **Brush**	0.226 244 ***	X	-0.207 244 **	-0.212 244 ***

[a] Zooplankton data are samples collected at inshore point stations from Chapter 2 (biomass is ml settled volume, meroplankton are larvae.100 m^{-3})

[b] Recruitment data are recruits.100 cm^{-2}.day^{-1}

[c] Correlation analysis was not performed

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Table 3.7 Pearson product-moment correlations of potential independent predictor variables for multiple regression analyses. Significance: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns = not significant.

Correlate	Along-shore Wind	Across-shore Wind	Mean Temperature	Temperature Anomly	Latitude	Biomass	Mytilid Larvae	Bivalve Larvae	Cyprids
Along-shore Wind [a]	X	r =-.281 n =907 ***	-.563 740 ***	-.125 740 **	ns	.432 280 ***	-.609 280 ***	-.549 280 ***	.192 280 **
Across-shore Wind [a]	r =-.281 n =907 ***	X	.603 740 ***	-.496 740 ***	ns	-.121 280 *	.398 280 ***	.267 280 ***	ns
Mean Temperature [b]	-.563 740 ***	.603 740 ***	X	-.141 740 ***	ns	-.526 234 ***	.311 234 ***	.490 234 ***	-.178 234 **
Temperature Anomaly [c]	-.125 740 **	-.496 740 ***	-.141 740 ***	X	ns	-.233 234 ***	.293 234 ***	.293 234 ***	.214 234 **
Latitude [d]	ns	ns	ns	ns	X	-.459 280 ***	ns	ns	ns
Zoopktn sett vol [e]	.432 280 ***	-.121 280 *	-.526 234 ***	-.233 234 ***	-.459 280 ***	X	-.341 280 ***	-.396 280 ***	ns
Mytilid Larvae [f]	-.609 280 ***	.398 280 ***	.311 234 ***	.293 234 ***	ns	-.341 280 ***	X	.809 280 ***	.339 280 ***
Bivalve Larvae [f]	-.549 280 ***	.267 280 ***	.490 234 ***	.293 234 ***	ns	-.396 280 ***	.809 280 ***	X	.157 280 **
Cyprids [f]	.192 280 **	ns	-.178 234 **	.214 234 **	ns	ns	.339 280 ***	.157 280 **	X

[a] Wind = the alongshore and across-shore components of the mean of the hourly coastal winds from the 27 days previous to the date of the recruitment sample collection; positive alongshore wind is north-northeasterly and induces offshore Ekman transport, positive across-shore wind is east-southeasterly

[b] Mean Temperature = the mean of the benthic temperature at Sodwana Bay (°C) from the 27 days previous to the date of the recruitment sample collection

[c] Temperature Anomaly = the difference between the Mean Temperature[b] and the mean temperature for those 27 days in all years measured (2002-2005)

[d] Latitude = the latitude of each site

[e,f] All zooplankton data are from Chapter 2, and are the mean values of the two replicates from the inshore station at the associated rock point taken in the same month as month as the recruitment data. Zoopktn sett vol = ml settled volume of zooplankton

[f] Mytilid Larvae, Bivalve Larvae and Cyprids are $100m^{-3}$

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**Table 3.8 (a) Results of multiple regression analyses for recruitment of barnacles into substrates and zones, with pairwise deletion of missing cells. Significance: ***p < 0.001, **p < 0.01, *p < 0.05,
ns = not significant.**

Dependent variable, fit of model	Independent variables	Trans-formation	B	B_{SE}	β	Tol.	t	Valid n	Signif-icance (p)
Recruitment of	Const.		-35.683	15.806			-2.258		*
C. dentatus	Alg. Wind	None	-0.046	0.060	-0.062	0.613	-0.775	907	ns
onto plates	Acs. Wind	None	0.261	0.131	0.233	0.287	1.999	907	*
	Mean T	None	-0.084	0.031	-0.442	0.146	-2.707	740	**
Adusted R^2 =	T Anomaly	None	0.109	0.091	0.098	0.578	1.195	740	ns
0.091	Latitude	None	-1.444	0.611	-0.213	0.481	-2.365	907	*
$F(7,226)=4.33$	Pktn biomass	4th root	-0.392	0.223	-0.225	0.238	-1.757	280	ns
$p < 0.001$	Cyprids	4th root	0.025	0.084	0.032	0.337	0.298	280	ns
Recruitment of	Const.		32.092	12.964			2.475		*
C. dentatus	Alg. Wind	None	-0.175	0.049	-0.254	0.613	-3.564	907	***
onto bare rock	Acs. Wind	None	-0.146	0.107	-0.141	0.287	-1.358	907	ns
(Barnacle zone)	Mean T	None	0.108	0.025	0.618	0.146	4.251	740	***
Adusted R^2 =	T Anomaly	None	-0.196	0.075	-0.192	0.578	-2.624	740	**
0.277	Latitude	None	1.338	0.501	0.215	0.481	2.671	907	**
$F(7,226)=13.78$	Pktn biomass	4th root	0.676	0.183	0.422	0.238	3.696	280	***
$p < 0.0001$	Cyprids	4th root	0.475	0.069	0.659	0.337	6.868	280	***
Recruitment of	Const.		63.883	10.615			6.018		***
C. dentatus	Alg. Wind	None	-0.166	0.040	-0.290	0.613	-4.144	907	***
onto bare rock	Acs. Wind	None	-0.306	0.088	-0.356	0.287	-3.484	907	***
(Mussel zone)	Mean T	None	0.128	0.021	0.883	0.146	6.167	740	***
Adusted R^2 =	T Anomaly	None	-0.142	0.061	-0.167	0.578	-2.322	740	*
0.301	Latitude	None	2.573	0.410	0.496	0.481	6.274	907	***
$F(7,226)=15.32$	Pktn biomass	4th root	1.260	0.150	0.945	0.238	8.419	280	***
$p < 0.0001$	Cyprids	4th root	0.434	0.057	0.723	0.337	7.663	280	***
Recruitment of	Const.		16.448	17.840			0.922		ns
***Tetraclita* spp.**	Alg. Wind	None	0.135	0.067	0.130	0.613	2.004	907	*
onto plates	Acs. Wind	None	-1.195	0.147	-0.770	0.287	-8.104	907	***
	Mean T	None	0.369	0.035	1.404	0.146	10.545	740	***
Adusted R^2 =	T Anomaly	None	-0.211	0.103	-0.138	0.578	-2.056	740	*
0.423	Latitude	None	0.988	0.689	0.105	0.481	1.433	907	ns
$F(7,215)=24.28$	Pktn biomass	4th root	1.122	0.252	0.466	0.238	4.463	280	***
$p < 0.0001$	Cyprids	4th root	0.466	0.095	0.430	0.337	4.896	280	***
Recruitment of	Const.		-123.101	17.187			-7.162		***
***Tetraclita* spp.**	Alg. Wind	None	0.171	0.065	0.155	0.613	2.624	907	**
onto bare rock	Acs. Wind	None	0.677	0.142	0.410	0.287	4.767	907	***
(Barnacle zone)	Mean T	None	-0.149	0.034	-0.534	0.146	-4.426	740	***
Adusted R^2 =	T Anomaly	None	-0.107	0.099	-0.066	0.578	-1.085	740	ns
0.504	Latitude	None	-4.859	0.664	-0.487	0.481	-7.317	907	***
$F(7,226)=34.81$	Pktn biomass	4th root	-1.642	0.242	-0.640	0.238	-6.774	280	***
$p < 0.0001$	Cyprids	4th root	-1.116	0.092	-0.968	0.337	-12.178	280	***
Recruitment of	Const.		-119.158	21.850			-5.453		***
***Tetraclita* spp.**	Alg. Wind	None	0.122	0.083	0.097	0.613	1.476	907	ns
onto bare rock	Acs. Wind	None	0.773	0.181	0.412	0.287	4.279	907	***
(Mussel zone)	Mean T	None	-0.188	0.043	-0.592	0.146	-4.395	740	***
Adusted R^2 =	T Anomaly	None	-0.130	0.126	-0.070	0.578	-1.036	740	ns
0.380	Latitude	None	-4.753	0.844	-0.419	0.481	-5.630	907	***
$F(7,226)=21.43$	Pktn biomass	4th root	-1.701	0.308	-0.583	0.238	-5.521	280	***
$p < 0.0001$	Cyprids	4th root	-1.174	0.117	-0.895	0.337	-10.075	280	***

B = estimate of the raw coefficient, B_{SE} = standard error of this estimate, β = standardized coefficient, Tol. = tolerance value (Tol. < 0.1 indicates strong co-linearity with another variable), t and p test the null hypothesis that the given coefficient equals zero, Valid n = the number of evaluated cases that contained a value for this variable, Const. = model constant (intercept), Alg. Wind = mean alongshore vector component of wind velocity ($m.s^{-1}$) from the previous 27 days (positive is NNE'ly and upwelling-positive), Acs. Wind = mean across-shore vector component of wind velocity from the previous 27 days (positive is ESE'ly), Mean T = mean benthic water temperature from the previous 27 days (°C), T Anomaly = difference between Mean T for those previous 27 d and the Mean T for those previous 27 days over 4 years (2002-2005). Latitude = degrees latitude (negative is increasing southward), Pktn biomass = biomass ($ml.100m^{-3}$) of all zooplankton collected in the same month at the same inshore rock point as the recruitment data, Mytilids/Cyprids = density of mytilid bivalve/cyprid larvae ($100m^{-3}$) recorded in the zooplankton same month and at the same inshore rock point as the recruitment data.

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Table 3.8 (b) Results of multiple regression analyses for recruitment of mussels. See Table 3.8 (a) for further interpretation.

Dependent variable, fit of model	Independent variables	Trans-formation	B	B_{SE}	β	Tol.	t	Valid n	Signif-icance (p)
Recruitment of	Const.		-21.478	10.027			-2.142		*
B. semistratus	Alg. Wind	None	0.273	0.077	0.413	0.233	3.531	907	***
into brushes	Acs. Wind	None	-0.057	0.152	-0.058	0.134	-0.375	907	ns
Adusted R^2 =	Mean T	None	-0.041	0.019	-0.242	0.253	-2.157	740	*
0.258	T Anomaly	None	-0.126	0.091	-0.129	0.368	-1.389	740	ns
$F(6,227)=14.52$	Latitude	None	-0.828	0.377	-0.138	0.803	-2.198	907	*
$p < 0.0001$	Mytilid larvae	4th root	0.438	0.140	0.451	0.153	3.125	280	**
Recruitment of	Const.		-3.332	7.509			-0.444		ns
P. perna	Alg. Wind	None	-0.033	0.058	-0.057	0.233	-0.565	907	ns
into brushes	Acs. Wind	None	0.094	0.114	0.109	0.134	0.826	907	ns
Adusted R^2 =	Mean T	None	-0.114	0.014	-0.779	0.253	-8.099	740	***
0.454	T Anomaly	None	-0.152	0.068	-0.179	0.368	-2.236	740	*
$F(6,227)=33.27$	Latitude	None	-0.227	0.282	-0.043	0.803	-0.804	907	ns
$p < 0.0001$	Mytilid larvae	4th root	0.053	0.105	0.063	0.153	0.505	280	ns

The relative importance of the remaining physical and biological factors for recruitment was then examined with multiple regression analyses. The residual values for all models fell within the standard requirements for normality. All models were significant, but differed in their ability to explain recruitment variability, with adjusted R^2 values ranging from 0.091 to 0.504 (Table 3.8a, b). Adjusted R^2 values were higher for *Tetraclita* spp. and *P. perna* than for *C. dentatus* and *B. semistriatus*, and lowest of all for *C. dentatus* recruitment onto plates. The relative importance of each of the independent factors was compared using the relative values of β (the standardized coefficient); β values were tested with the statistic t. The responses of the taxa in the various substrates and zones to the independent factors were not consistent, indicating a high level of variability in the processes that can influence recruitment. No single factor considered was non-significant in all models.

The previous 27 days' mean subsurface temperature was generally the most important abiotic factor, with cooler temperatures predicted higher levels of recruitment for mussels in all cases and for barnacles in most cases (exceptions being *C. dentatus* recruiting on bare rock and *Tetraclita* spp. on plates). This value was not detrended, and mean monthly temperature in Maputaland varies seasonally (Chapter 2). As recruitment is also seasonal, this relationship could have been predicted. Strong positive associations between recruitment and larval abundance also emerged, although the association was negative in the case of *Tetraclita* spp. on bare rock.

The relationships between mean temperature, the availability of larvae and the recruitment of barnacles onto plates and mussels into brushes were examined graphically (Figure 3.9). Although only two of the independent variables were plotted for each model, the three-dimensional plots demonstrate the interaction between the two independent variables and their non-linear relationships with recruitment.

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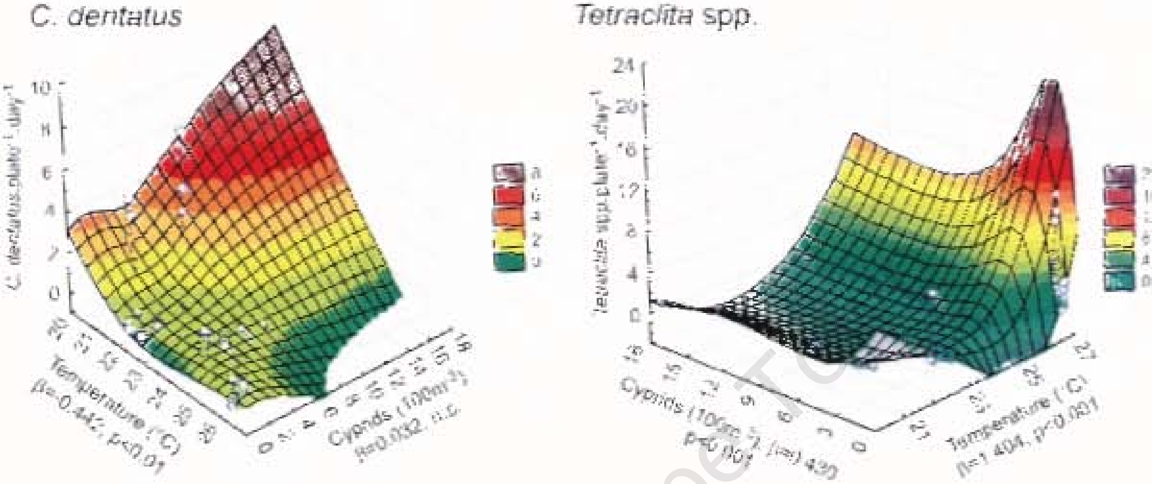
(a) Barnacle recruitment onto plates



(b) Mussel recruitment onto brushes

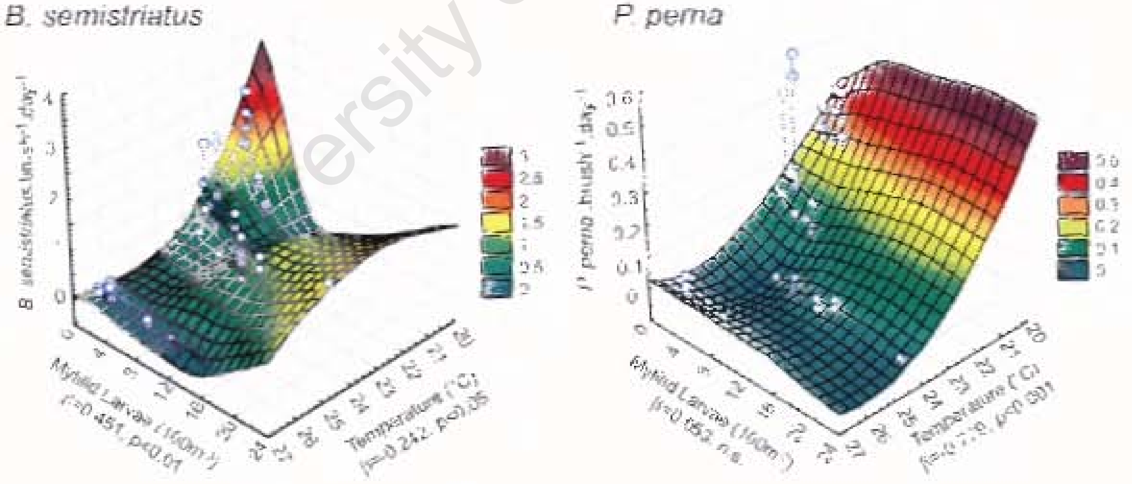


Figure 3.9 Two important predictors of recruitment: temperature and larval abundance. β = standardized coefficient from the multiple regression model (Table 4.8). Shape is the least-squares fitted values to the three-dimensional scatter plot of observed values. Data are presented untransformed. Temperature is the mean benthic temperature at Sodwana for the 27 days previous to the collection of recruitment plates or brushes. Note that axes are the same in each plot, but are rotated differently for the best visibility.

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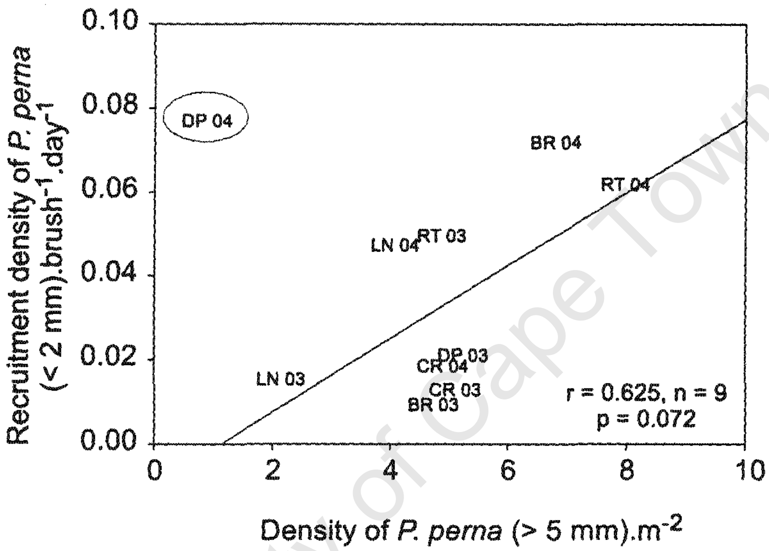

Figure 3.10 Relationship between adult stock and recruitment densities of *P. perna* in Maputaland study area. Rock headland codes: CR (Castle Rock), DP (Dog Point), BR (Black Rock), RT (Rocktail) and LN (Lala Nek). Year codes: 03 (Aug 2002 to Feb 2003), 04 (Aug 2003 to Feb 2004). DP 04 (circled) was excluded from this relationship as an outlier, as explained in text.

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3.4 DISCUSSION

This chapter focuses on temporal and spatial patterns in intertidal recruitment variability and the coupling between recruitment rates and larval supply in the Maputaland Marine Reserve (MMR), testing hypotheses about spatial and temporal recruitment variability advanced in Chapter 1. Table 3.9 summarizes patterns arising from this and previous chapters, and relates them to factors that appear to be driving them.

Table 3.9 Synthesis of the patterns of larval abundance and recruitment variability in Maputaland. Larval data and patterns are synthesized from Chapter 2.

Taxon	***Chthamalus dentatus***	***Tetraclita* spp.**	***Perna perna***	***Brachidontes semistriatus***
Relative recruitment density	Low	High	Low	High
Larval pattern (spatial)	Cyprids near bottom, higher densities inshore than offshore, no alongshore differences (bay/point, latitudinal)		No vertical pattern, higher densities inshore than offshore, no bay/point pattern, more larvae at Lala Nek and Black Rock than other sites	
Larval pattern (temporal)	Most abundant in spring and summer, less in autumn and winter		Most abundant in summer and winter, less in spring and autumn	
Larval density drivers	Temperature (-), Phytoplankton (+). Larvae may be transported shoreward by upwelling and internal waves		Temperature (+), Phytoplankton (-). Larvae may be transported shoreward by downwelling or relaxation of upwelling	
Spatial recruitment pattern (sites and localities)	Localities within sites are different. No latitudinal pattern	Localities within sites are different; higher recruitment southwards	Localities within sites are the same; no difference among sites; weak association with adult stock	Localities within sites are the same; higher recruitment southwards
Recruitment peak (temporal)	Winter and spring/ summer, synchrony among sites	Autumn/winter, synchrony among sites	Spring/summer, synchrony among sites	
Recruitment pattern (substrates)	No recruitment into brushes; no clear association between bare rock and plates; drivers differ among substrates	No recruitment into brushes; weak correlation between bare rock and plates; drivers are the same but have opposite signs	No recruitment onto bare rock or plates; strong correlation between brushes and scouring pads	
Recruitment pattern (between zones)	Moderate correlation between zones, drivers are the same		Not examined	Not examined
Recruitment pattern (between species)	More co-recruitment between taxa evident on bare rock than on plates, but co-recruitment rare as recruitment seasons are not the same for the two taxa		Although recruitment season is the same, individual brushes were generally dominated by one species or the other rather than containing similar ratios of both	
Recruitment drivers (significant independent variables with $\beta > 0.2$ or < -0.2)	Plates: Across-shore wind (+), Mean temp (-) Latitude (-) Bare Rock: Alongshore wind(-), Mean temp (+), Latitude (+), Plankton biomass (+), Cyprids (+)	Plates: Across-shore wind (-), Mean temp (+), Plankton biomass (+), Cyprids (+) Bare Rock: Across-shore wind (+), Mean temp (-), Latitude (-), Plankton biomass (-), Cyprids (-)	Brushes: Mean temp (-), Temp anomaly (-)	Brushes: Alongshore wind (+), Mean temp (-), Latitude (-), Mytilid larvae (+)

β = standardized coefficient from multiple regression analysis
+/- = sign of β: indicates whether association is positive or negative

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For all the species examined, recruitment was strongly seasonal. This was predicted for mussels, as mussel recruitment was found to be strongly seasonal at both the Durban and Zululand locations in Chapter 1. Beneath this overarching seasonal recruitment pattern, recruitment rates varied among sites, species, substrates and zones, and this variability related to both biotic and abiotic pre- and post-settlement effects. Sites and zones were generally synchronous within species, as initially hypothesized, but substrates were not. In Chapter 1, seasonal recruitment on the south and east coasts of South Africa was attributed to seasonal cycles in the production of larvae, which in turn can be linked to the seasonal nature of the prevailing conditions that cue larval release and mediate transport and delivery of larvae to their targeted habitat, as well as to the relative homogeneity of the shoreline along this coast.

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Temporal recruitment patterns

Both *P. perna* and *B. semistriatus* had a well-defined seasonal pattern of recruitment, with peaks in spring in both years (Figures 3.3-3.5), consistent with previous descriptions of the reproductive cycle of *P. perna* in southern KZN (Berry 1978; Harris et al. 1998; Chapter 1). However, due to the course nature of the temporal sampling in this study, and the relative brevity of this data set (1.5 years), these results must be interpreted with some caution. The temporal recruitment pattern was strongly correlated between the two mussel species investigated. This is in different from the situation in multi-species mussel beds on the west coast of South Africa, where none of the species showed clear seasonal patterns and the timing of their recruitment peaks was not coherent among species (Chapter 1). This may be attributed to the physical heterogeneity and irregular pulsing of upwelling on the West Coast, coupled with a limited seasonal temperature signal there.

Recruitment rates of *C. dentatus* peaked in September, coincident with the spring recruitment of both mussel species (Figures 3.6 and 3.8). Working in the Dwesa Nature Reserve, ~600 km south-west of my study site (Figure 1.1), Dye (1988) reported consistent recruitment of *C. dentatus* in late winter and early spring (August-September) over a five year period, with one exceptional second settlement in January 1985. In Maptualand, *Tetraclita* spp. recruited mainly in autumn (March-April) with minor peaks in June and December, a pattern that was consistent at all sites (Figure 3.7). At Dwesa, Dye (1988) reported that *T. serrata* exhibited peak recruitment in winter (July-September). However, this difference may simply be due to species differences, as the dominant intertidal *Tetraclita* species in Maputaland is *T. squamosa rufotincta* rather than *T. serrata.*

Although *Tetraclita* spp. recruited more densely than *C. dentatus* throughout my study, this ratio may not be stable over time. After a further 9-year continuance of his study, at Dewsa, Dye (1998) reported high interannual variability in settlement rates of both *C. dentatus* and *T. serrata* associated with longer-term cycles of alternating adult dominance on the scale of 4-8 years. For example, he recorded a massive settlement of *T. serrata* at two of the three sites in his study in 1984. Despite high post-settlement mortality, this event changed the structure of the communities at these two sites, with *Tetraclita* spp. overtaking *C. dentatus* to become proportionally denser. Dye also monitored *C. dentatus* over 8-9 years in undisturbed plots at Dwesa and Mkambati (180 km NE of Dwesa, Figure 1.1), concluding that adult densities there also fluctuate on a scale of 3-9 years (Dye 1993). The role of massive settlement events in mussel communities, such as the one described by Berry (1978) for *P. perna* in KZN is discussed in Chapter 1. Large but intermittent recruitment events, like those described by Dye (1998), may also be important for the long-term maintenance of barnacle densities in eastern South Africa, although they fall beyond the scope of my study.

Recruitment events for both *C. dentatus* and *Tetraclita* spp. were synchronous among sites and on both bare rock and plates, which could be due to onshore-transport processes acting at scales larger than the study site (Table 3.4a). In a study of the daily and two-daily settlement of *Chthamalus* spp. in Baja California, Mexico, Ladah et al. (2005) similarly reported that settlement peaks were synchronous but spatially heterogeneous. They proposed that the spatial heterogeneity could have been due to a variety of factors, including a non-uniform larval pool, variability in transport processes, or differences in substrate among the sites, and attribute temporal synchrony to pulses of recruitment associated with breaking internal tidal bores, which would have operated at a scale larger than that of their study.

While recruitment can be an integrated sample that represents the settlement densities, the signals of settlement pulses that may operate on the scale of days (e.g. Ladah et al. 2005) or weeks, showing fortnightly peaks (e.g. Porri et al. 2006) can be masked by post-settlement mortality. Without further, detailed study of the settlement rates of these taxa, it is possible that the observed seasonal recruitment pattern is driven by the effects of seasonal post-settlement mortality, rather than by seasonal spawning or settlement. Nevertheless, as the seasonal nature of the recruitment patterns observed for the taxa I investigated were similar to those reported for the same taxa in different bioregions, the seasonality of recruitment is probably accurately described, even if the underlying patterns that cause it are not yet fully understood.

Spatial recruitment patterns

Mussel recruitment patterns were similar between the two species and among localities and sites, with no significant spatial pattern in the recruitment of *P. perna* (Table 3.4b). This was similar to the recruitment of *P. perna* in Zululand and Durban (Chapter 1), where this species showed low levels of spatial heterogeneity among sites within locations. *B. semistriatus* did show a significant spatial pattern, with highest recruitment rates at Lala Nek in the south. When the recruitment rates were compared between and among species, sites and locations on the west coast

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of South Africa in Chapter 1, patterns were far more localized, with spatial heterogeneity at a scale of less than 10 km.

The recruitment rates of both barnacles were much more heterogeneous spatially than those of the mussels (Table 3.4). Not only were there significant differences in recruitment rates among sites, but also among localities within sites. This high variability at small spatial scales is common for barnacles. Dye (1988) reported high spatial variability in the recruitment of *C. dentatus* and *T. serrata* among four randomly placed 0.25 m^2 experimentally denuded plots at each of three sites located 2-8 km apart in Dwesa Nature Reserve. In an eight-year study of *T. serrata* at 11 sites spanning 200 km in the Eastern Cape, in and out of exploited areas, Dye (1992b) reported high levels of spatial and temporal variability in the populations of this species. However, he did find a significant linear relationship between the long-term detrended mean adult abundance and the maximum observed recruitment at each of the sites. He concluded that this indicated limited dispersal of the larvae, and attributed any observed departures from this relationship to both biotic top-down effects (predation) and physical bottom-up effects (temperature and desiccation). Spatial heterogeneity of barnacle recruitment also has been reported in several other areas around the world. Lagos et al. (2005) found that the biweekly recruitment of both balanoid and chthamaloid barnacles in Chile was seasonally pulsed and showed significant spatial structure. Chthamaloid recruitment levels appeared spatially consistent over time, linked to upwelling-related nearshore processes. Balanoid recruitment was, however, not spatially consistent, and the authors attributed this to processes acting at more local scales. At a larger scale, the spatial heterogeneity of barnacle recruitment on the Chilean coast appears to be more consistent than among-year heterogeneity at each site, even during oceanic anomalies such as El Niño Southern Oscillation (ENSO) events (Navarrete et al. 2002). This is in contrast to the recruitment pattern on the west coast of the USA, where an ENSO event was more important than spatial heterogeneity in explaining recruitment variability (Connolly and Roughgarden 1999a).

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Recruitment density among species

Tetraclita spp. consistently recruited more densely than *C. dentatus* onto all substrates (Table 3.5). At three sites at Dwesa, monitored between 1982 and 1996, *C. dentatus* and *T. serrata* alternated dominance of the upper balanoid zone interannually, switching in 1985 and again in 1989 and 1990 (Dye 1988, 1998), indicating that the ranking of these species, in terms of either recruit or adult density, may also not persist in Maputaland. Maximum recruitment densities of *T. serrata* into the uncleared barnacle zone in the Eastern Cape varied between 600 m^{-2} at Mkambati and 7000 m^{-2} at Dwesa (Dye 1992b). The maximum recruitment of *Tetraclita* spp. ranged 500-1200 m^{-2} onto bare rock and 400-1800 m^{-2} onto plates among sites in my study, falling within the range of the lower-recruiting sites in the Eastern Cape.

Although recruitment levels of *C. dentatus* were low compared to other locations in South Africa, they did fall into the range of recruitment rates for *Chthamalus* spp. worldwide, as recorded in studies spanning both large and small spatial and temporal scales. In Baja California, Mexico, daily settlement rates of *Chthamalus* spp. varied between 1750 (mean) and 17500 (peak) m^{-2}.day^{-1} (Ladah et al. 2005). This is 1-2 orders of magnitude greater than the recruitment rates observed in Maputaland; however, as settlement was recorded daily, it can be expected to be higher than values obtained from cumulative recruitment rates recorded over longer periods in other studies because of post-settlement mortality (Connell 1985). In Europe, O'Riordan et al. (2004) studied the monthly recruitment of *Chthamalus montagui* and *C. stellatus* onto bare rock between Ireland and NE Italy. Mean rates for *C. montagui* varied between 57 in Ireland and 2800 m^{-2}.day^{-1} in Portugal, and *C. stellatus* varied between 0 in Portugal to 81 m^{-2}.day^{-1} in NW Spain. Mean *C. dentatus* recruitment fell within values for *C. stellatus* and at the low end of those for *C. montagui*. However, these studies included cyprids and barnacles < 0.5 mm in diameter, whereas my study did not. In Chile, (Navarrete et al. 2002) found that annual recruitment rates of Chthamaloid barnacles onto plates identical to those used in my study varied significantly among both sites and years, ranging from 0 to 2300 m^{-2}.day^{-1}. The recruitment rates of *C. dentatus* onto plates in Maputaland spanned a comparable range of values.

Too few patches of mussels existed in the mid-shore in Maputaland to allow observations of recruitment of *P. perna* into mussel patches such as those in Chapter 1. However, using the regression formula from the Zululand brush recruitment rates (R) in Chapter 1 ($R_{bed} = 1.64 + 4.02*R_{brush}$) and data from Figure 3.4, the recruitment peaks for *P. perna* into mussel beds in my study area can therefore be calculated to be 2600 m^{-2}.day^{-1} at Lala Nek in September 2002. This is lower than the equivalent values for any other location described in Chapter 1 (see Figure 3.11). The low values for *P. perna* recruitment in Maputaland may be due to the lack of a dense local source population. If the population is recruit limited, adult stocks, the source of nearshore larvae, that have been depleted by intense harvesting will reduce local recruitment, such as in the case for Dwesa (Chapter 1). Mean (and peak) recruitment rates of *B. semistriatus* were 0.5 (6.0) brush^{-1}.day^{-1} at most sites in my study. Using the linear regression formula from the correlation analysis ($R_{Chuffy} = 0.1393 + 0.3061*R_{Brush}$), this can be converted to 0.3 (2.0) Chuffy^{-1}.day^{-1}. In their study of recruitment rates of the congener *B. granulata* in Chile, (Navarrete et al. 2002) report mean annual recruitment rates among 12 sites varying between 0 and 0.12 Chuffy^{-1}.day^{-1}, so recruitment rates of *B. semistriatus* in Maputaland appears to be higher than those for *B. granulata* in Chile.

While some mussel species appear to recruit in very high numbers, others have lower intrinsic recruitment rates (Chapter 1). In Namibia, the recruitment rates of the small bisexual mussel *Semimytilus algosus* were orders of magnitude greater than for *P. perna*, but the shore was dominated by adult *P. perna*. On the west coast of South Africa, at Groenrivier, the very high recruitment rates of *Aulacomya ater* similarly did not result in it out-competing the invasive *Mytilus*

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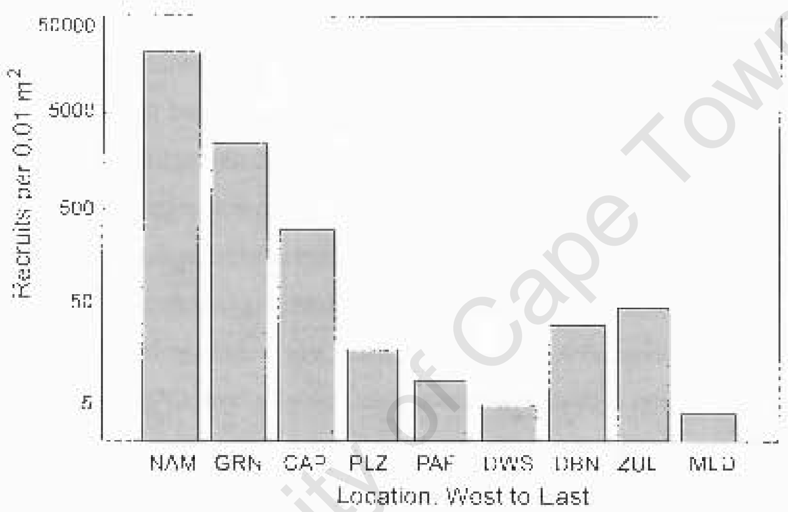

Figure 3.11 Comparison of Maputaland (MLD) mean annual recruitment peaks for mussels compared with those at other locations around the coast of southern Africa, adapted from Figure 1.2a. Maputaland data converted to recruits per 0.01 m^2 using brush-to-mussel bed regression formula in Chapter 1. Location codes are the same as in Chapter 1 (refer to Figure 1.1): NAM (Swakopmund, Namibia), GRN (Groen Rivier, Namaqualand, South Africa), CAP (Cape Peninsula), PLZ (Port Elizabeth), PAF (Port Alfred), DWS (Dwesa), DBN (Durban), ZUL (Zululand), MLD (Maputaland).

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galloprovincialis for adult habitat (Branch and Steffani 2004). Throughout my study, *B. semistriatus* recruited in significantly higher densities than *P. perna*, but adult beds of *B. semistriatus* were much rarer on the shore, and never existed without at least some adult *P. perna* among them (pers. obs.). Lasiak (1999) reported that rocky shores adjacent to the Mkambati Nature Reserve in the Eastern Cape, which had been denuded of *P. perna*, became numerically dominated by *B. semistriatus*. *B. semistriatus*, like *S. algosus*, may therefore be a 'weedy' species that exploits disturbed habitats, but does not persist well as an adult stock, relying on high recruitment levels, dispersion and the colonization of disturbed habitats, rather than on the intergenerational stability of long-lived adults in mature mussel beds, to maintain its presence in the intertidal environment.

Effects of intertidal zone

Comparisons of recruitment between zones were limited to the two barnacle species on bare rock, as no other substrates were situated in both zones, and mussels failed to recruit on bare rock. Although the matched-pairs t-tests indicated significantly more recruitment into the barnacle zone than the mussel zone (Table 3.5), the effect of zone was reduced to non-significance in the ANOVAs (Table 3.4c), and the levels of recruitment in the barnacle zone were temporally correlated with those in the mussel zone. Dye (1998) monitored the recruitment of barnacles into undisturbed and periodically denuded 0.25 m^2 plots in the upper and lower balanoid zones at three sites over 13 years at Dwesa, and showed that recruitment rates for both *C. dentatus* and *T. serrata* generally fell within the same order of magnitude into all plots, with no clear pattern of denser recruitment levels in either zone or onto either treatment. As adult barnacles are less dense in the mussel zone than in the barnacle zone (pers. obs.), this implies that although recruitment is approximately equal in both zones, post-recruitment mortality eliminates more barnacles in the mussel zone (Connell 1985).

Effects of substrate

Substrate was more important in explaining barnacle recruitment rates than zone. The correlation between recruitment onto bare rock and plates for *Tetraclita* spp. in the barnacle zone was positive and significant, but weaker than that between the two zones for bare rock. For *C. dentatus*, the relationship between recruitment onto bare rock and plates was even weaker, and in one case not significant. Additionally, the recruitment of the two taxa on plates was negatively correlated, indeed nearly mutually exclusive, but was positively correlated on bare rock in both the mussel and the barnacle zones. Substratum structure has often been reported to explain settlement variability in barnacles (Crisp and Barnes 1954; Crisp 1974; Chabot and Bourget 1988; Herbert and Hawkins 2006), as well as differences in post-recruitment survivorship and thus community structure (Herbert and Hawkins 2006), and cyprids have a demonstrated preference for relatively smooth over rough surfaces, but not over those that are totally smooth (Crisp and Barnes 1954;

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Anderson and Underwood 1994; Berntsson et al. 2000). The material of the substrate has been found to influence the settlement of both cyprids and mussel veligers, with both taxa favoring materials to which they can better adhere (Crisp et al. 1985). In his study comparing the colonization of space on rocky shores and seawalls, Bulleri (2005) presented both cleared bare-rock patches and settlement panels on both structures at three locations in Sydney Harbour, Australia. While he generally concluded that structure was more important than substratum in explaining colonization patterns, he did find significant interactions between location, structure and substratum, as well as for patch nested within these factors. Bulleri (2005) presented two plausible hypotheses for the variability in settlement among substrata: (1) panels, which are not flush with the substratum, dry more rapidly than cleared rock, favoring organisms more resistant to heat stress or desiccation, and (2) as herbivores and predators were not excluded from the treatments, their preference for one substrate over another may have contributed to recruitment variability. Indeed, both of these factors apply to my study. Some of my cleared rock treatments could never be completely dried due to depressions or pits in the rock surface, differentially favoring some organisms over others. Secondly, I often found limpets (*Helcion concolor* or *Cellana capensis*) and snails (*Oxystele tabularis*) grazing on cleared rock patches, more frequently in the mussel than in the barnacle zone. Although occasionally present on the plates, grazers were substantially less common there. Connell (2001) found that even when predation or disturbance levels are large, they may not explain the differences in community structure between different nearby substrata. Nevertheless, Bulleri (2005) attributed the difference in settlement and colonization between adjacent substrata, if not between structures, to the differential presence of molluscan herbivores.

This suggests that artificial recruitment panels may not accurately reflect either the actual recruitment rates onto rock or the ratio of recruitment rates among species. Despite the utility of standardized artificial recruitment plates in comparing among proximate or distant locations (e.g. Menge et al. 2002; Bulleri 2005; Navarrete et al. 2005), these must be ground-truthed against natural substrate to understand the relationship between the arrival of settlers onto plates and their settlement and recruitment into, and subsequent ecological effects on, the surrounding community.

Examination of mussel recruitment into brushes versus mussel beds in Chapter 1 revealed that recruitment rates into brushes accurately reflected the recruitment of *P. perna* into mussel beds. In this chapter, *P. perna* and *B. semistriatus* recruited into brushes and Chuffies with similar temporal patterns and in similar proportions, although the total number of recruits into brushes was generally three times that in adjoining Chuffies. However, no mussels were ever observed recruiting directly on scraped patches of bare rock in either the mussel or the barnacle zone. In fact, the only recorded incidence of *P. perna* settling directly onto bare rock in KZN was in the anomalously high recruitment event in 1976 along the coast of Natal (Berry 1978), in which recruits blanketed the shore, radically changing the mid- and low-shore ecosystems along this entire stretch of coastline. Prior studies relating to the practices of subsistence harvesters in the Eastern Cape

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have also revealed that neither mussel settlers nor recruits attach directly to bare rock, and this is one of the reasons why *P. perna* beds can take up to 10 years to recover from denudation (Dye 1992a, 1998; Dye et al. 1997). Working in Dwesa Nature reserve, Dye (1988) reported that denuded patches in the upper and lower balanoid zone were much more unstable during their recovery in terms of diversity and species composition than adjacent control patches. This has important implications for the choice of harvesting practices employed by subsistence and recreational mussel fishers, as their top-down practices can influence the bottom-up effects of the mussel beds on recruitment (Harris et al. 2003; Robinson 2005).

Coupling of recruitment and larval densities

Two important patterns emerged from multiple-regression investigation of the association between cyprid density in the nearshore waters and the recruitment of barnacles in the intertidal (Table 3.8a). The first was that the abundance of cyprids was an important factor explaining the variability of the recruitment of *C. dentatus* onto bare rock in both zones. Similar benthic-pelagic coupling has been observed for barnacles in other parts of the world, as noted in the introduction. This relationship was negative, however, for the recruitment of *Tetraclita* spp. onto bare rock. I could not identify the cyprids to species-level, so it is possible that the pool of competent cyprids collected in the nearshore zooplankton samples largely comprised *C. dentatus*. The absence of this relationship, or the negative relationship, might also be due to sampling error. Cyprids in Maputaland are stratified and occupied mainly the bottom layer (Chapter 2), and the oblique tows used in Chapter 2 may have inaccurately sampled the density of cyprids in the nearshore by not sampling the bottom 1 m.

However, this leads to the second important pattern, which was that the relationship between the density of cyprids and the recruitment of both taxa onto plates was totally different from that between cyprid densities and recruitment onto bare rock. There was no significant relationship between cyprid density and the recruitment of *C. dentatus* onto plates, and the relationship for *Tetraclita* spp. recruitment onto plates was positive (and highly significant) rather than negative. Although they may be due to error related to low sampling levels, these confounding results between plates and bare rock imply, as discussed above, that cyprid settlement behavior as it relates to substrate choice and the relative strength of post-settlement mortality on the different substrates are important processes influencing recruitment.

Pearson product-moment correlation revealed that nearshore mytilid larval density was positively correlated with the recruitment of *B. semistriatus* and negatively correlated with that of *P. perna* (Table 3.6). Multiple regression analyses showed that mytilid larval densities were a significant positive indicator of recruitment density for *B. semistriatus* but not for *P. perna* (Table 3.8b). The identification of larval-recruit coupling has been somewhat elusive in other regions of South Africa (e.g. Porri 2003) but has nevertheless been established for *P. perna* at some sites on

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the South Coast (McQuaid and Lawrie 2005). The collection of larval data was limited and less consistent compared to the other data sets used in my study, and comprised snapshot samples interpreted to represent a month-long process. Despite this, a strong pattern of benthic-pelagic coupling emerged for *B. semistriatus*, which recruited much more densely than *P. perna*. Mytilid larval densities may still predict mussel recruitment of *P. perna* in Maputaland, but, due to their relative rarity, more complete and consistent larval collections would be required to demonstrate this. One of the first studies that successfully showed coupling between larval and adult population densities for nearshore organisms with a meroplanktonic larval stage was that of the bryozoan *Membranipora membranacea*, which adheres to kelp blades along the coast of California, USA. Yoshioka (1982) reported that upwelling conditions and the presence predators explained 55% of larval abundance, and that larval abundance and surface temperature, in turn, explained 79% of recruitment variability. Finally, recruitment was found to be the major factor (with predation) that explained population fluctuations, and also explained 75% of the variability of the reproductive output of the bryozoan colonies. Similar coupling between hydrography, larvae, settlement and adult community dynamics has thereafter been demonstrated for barnacles (Connell 1985; Gaines and Roughgarden 1985), urchins (Ebert and Russell 1988) and mussels (Menge et al. 2004).

Coupling of recruitment and physical processes

Multiple regression analyses revealed that mean monthly water temperature was the most important factor for the recruitment of barnacles. Again, however, the sign of this relationship varied among not only species but also substrates, complicating the interpretation of the physical processes (Table 3.8). For example, cooler temperatures predicted recruitment of *Tetraclita* spp. onto bare rock, but warmer temperatures predicted recruitment of *Tetraclita* spp. onto plates. In Chapter 2, a hypothesis was advanced relating cyprid densities to the onshore transport mechanism of upwelling, driven by alongshore winds, which predicted that barnacle recruitment would be higher during periods with cooler water temperatures and stronger northerly winds. Northerly alongshore wind was more important for *Tetraclita* spp., but across-shore wind was even more important, and the peak recruitment period for *Tetraclita* spp. fell in March 2003, in the month with the maximum onshore wind (Figure 2.11). For *C. dentatus*, the effect of along- and across-shore winds varied in their relative importance among the substrates and zones, but recruitment was generally highest with moderate northerly winds. Although the mean monthly wind showed no seasonal pattern, the variability of the wind was highly seasonal, peaking in August and September. Strong intermittent northerly winds during this period could therefore be related to the recruitment peaks for *C. dentatus*.

Mean temperature was also the most important indicator of the recruitment of mussels (Table 3.8). The annual cycle was not removed from the mean temperature value, and both variables showed a strong seasonal cycle (see climatology in Figure 2.11), so this relationship was

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anticipated. Alongshore wind, which was linked to temperature and upwelling in Chapter 2, but has no strong seasonal cycle, was a negative indicator of recruitment for *P. perna*. As predicted, the recruitment of *P. perna* in Maputaland may have occurred during times with upwelling relaxation or even downwelling conditions. Onshore wind, which can also promote downwelling-type conditions, was found to be an important factor in other studies (e.g. Tapia et al. 2004), and was also important in explaining the recruitment rate of *P. perna*. For *B. semistriatus*, northerly alongshore wind was significant but of low importance, and neither across-shore wind nor the temperature anomaly were significant factors in the model, leaving water temperature as the only process-related factor. This indicates that season was more important than smaller-scale wind-based events for the recruitment of this species, in contrast with many previous studies of recruitment dynamics occurred in regions where wind-based events, such as upwelling and downwelling, or the relaxation of upwelling and downwelling, are more important than seasonality in controlling nearshore coastal processes (e.g. Roughgarden et al. 1991a; Botsford et al. 1994; Wing et al. 1995a; Bertness et al. 1996; Miller and Emlet 1997; Almeida and Queiroga 2003).

Role of shoreline homogeneity in spatial and temporal recruitment patterns

In Chapter 1 and here, recruitment was shown to be temporally pulsed and much more spatially homogenous on the east than on the west coast of South Africa. Two mussel species recruit in Maputaland just as there were two (different) species at Groenrivier and the Cape Peninsula (Chapter 1). On the West Coast, recruitment at each site was synchronous between species, but there was a distinct lack of temporal synchrony among sites. In the MMR, in contrast, recruitment at each site was synchronous between mussel species, and the sites were also synchronous. As described above, one important factor controlling temporal synchrony of recruitment is spawning period, or larval supply, which is known to be pulsed for *P. perna* on the East Coast (Berry 1978). The spawning period is unknown for *B. semistriatus*.

In addition to seasonality (discussed above), the final important factor found previously to control the synchrony of recruitment is shoreline heterogeneity in relation to the distribution of meso- and local-scale hydrographic events (e.g. Ebert and Russell 1988; Palma et al. 2006). Local coastal topography can shape and channel winds, which will influence wind-driven currents, Ekman transport, and Langmuir circulation cells. Below the surface, bathymetry will likewise channel currents and flows, changing current speed and direction, mediating the influence of tides, internal waves, upwelling, rip currents and other features. Many of these have been shown to be important for larval transport, accumulation and retention (Vargas et al. 2004; Queiroga and Blanton 2005; Shanks and Brink 2005). Various onshore-transport mechanisms have been shown to be strongly related to shoreline shape and topography, including sheared currents within bays (Graham and Largier 1997; Archambault and Bourget 1999), upwelling (Lagos et al. 2005), internal waves (Shanks 1983; Shanks and Wright 1987; Kingsford 1990) and internal tidal bores (Pineda 1999;

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Vargas et al. 2004; Ladah et al. 2005), resulting in a settlement pattern that is temporally pulsed on the scale of days. When these effects are seasonal, such as on the east coast of South Africa, this may explain the seasonal nature of recruitment. Spatial heterogeneity of recruitment rates among sites has been attributed to bottom-up processes that are mediated by the shape of the coastline (Roughgarden et al. 1991a; Wing et al. 1995a; Archambault and Bourget 1999; McCulloch and Shanks 2003). The lack of alongshore physical spatial heterogeneity in the MMR, and even along the entire coast of KZN, may strongly influence the marked temporal and spatial homogeneity of mussel recruitment.

Coupling of recruitment with adult stock densities

The densities of adult stocks of *P. perna* in Maputaland are currently very low compared to other regions of South Africa. I recorded mean densities of subadults and adults (i.e. individuals > 5 mm) equaling about 5 m^{-2} and mean cover equaling about 3% (Chapter 2, Figure 2.15). In the non-exploited area of southern Black Rock, mean densities reached 15-25 m^{-2}, or about 6% cover. Dwesa had the lowest densities of *P. perna* of all the locations investigated in Chapter 1, with a cover that averaged around 15%. One factor that contributes to the low value for Maputaland is the greater horizontal patchiness within the low-shore zone (Sink 2001), reducing the overall values. At the locations surveyed in Chapter 1, the permanent transects were placed within patches of mussel bed, whereas the mussel surveys in Maputaland (Chapter 2) were randomly placed and often fell upon other biotypes. Within the densest patches of the mussel biotope in Maputaland, densities reached 50 adults m^{-2} and 25% cover in the exploited areas and 110 m^{-2} and 60% cover in the non-exploited areas (Black Rock South). This is higher than the mean values, but not higher than the maximum values that were recorded in Dwesa from 1995-2000. Stocks of mussels in Maputaland are clearly low relative to all other regions of the southern African coast. The top-down control of mussel density in Maputaland by high levels of human harvesting has been well documented (Kyle et al. 1997a; Tomalin and Kyle 1998; Sink 2001; Cockcroft et al. 2002; Robertson 2003), and this probably accounted for to the significant difference in the density of *P. perna* between adjacent exploited and non-exploited areas.

I disproved my hypothesis for a positive significant stock-recruit relationship for mussels in Maputaland. Ecologically, the relationship between stock and recruit is important at two points in a mussel's life history. Firstly, a reduction in adult densities, especially the removal of the largest or most fecund individuals of the population, reduces the number of larvae produced (Hughes et al. 2000). Secondly, mussel settlement and recruitment is enhanced by the three-dimensional matrix of the mussel bed (Harris et al. 1998; Robinson 2005; Chapter 1). With such a significantly reduced density of adult mussels in Maputaland, it is not surprising that recruitment rates are so low. Nevertheless, the correlation between adult stocks and recruitment was (marginally) non-significant ($p = 0.07$ after removal of an outlying point).

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In situations with high or superfluous settlement, (Connell 1985) predicted that the stock-recruit relationship could be masked by non-density-dependent post-settlement (or post-recruitment) mortality. In Maputaland, however, recruitment is very low, and this scenario is unlikely to explain the observed pattern. In recruitment-limited environments, settlement rate is a good predictor of recruit density (Connell 1985; Caley et al. 1996), and even of adult densities and community structure (Gaines and Roughgarden 1985; Menge et al. 2003). These bottom-up indicators may be rendered non-predictive in some environments by density-dependent top-down community-level effects such as competition and predation (Menge 1995, 2000b; Menge et al. 1999, 2002; Wieters 2005). Both Dye (1998) and Harris et al. (1998) interpreted a significant relationship between adult stock densities and recruitment rates as evidence for limited dispersal, as it implies that the system is closed at the scale of the study. However, even in a closed system, stock densities and recruitment rates can be decoupled if mortality of either the adult stock or the larvae is stochastic rather than density-dependent. In Chapter 1, most of the locations examined had significant, positive, linear stock-recruit correlations. All of the sites chosen for that study were protected from human harvesting. Human harvesting behavior, when not economically driven (i.e. recreational or subsistence), is not density-dependent, as time invested in fishing is not considered in the individual's cost-benefit analysis (Clark 1985). Therefore, if one considers harvesting on the rocky shores in Maputaland to be a non-density-dependent source of mortality to the adult stock, this could explain the non-significant relationship between stock and recruitment in this area.

Finally, there may be no significant relationship between stock and recruitment if the system is open at the scale of this study, as was concluded for many locations in Chapter 1. In some environments, larvae may be able to avoid advection and remain close to their parental stock using vertical swimming or horizontal orientation behaviors (Kingsford et al. 2002). However, larvae are small, and they are weak swimmers (Bayne 1976). If the alongshore currents are not amenable to retention (i.e. highly advective and not sheared), no swimming behavior will allow them to remain close to their origins. As described in this chapter and in Chapter 2, the coastline of Maputaland is exposed and rough, with strong winds and potentially strong currents as well, and a low potential for eddying in the bays. More information about currents and oceanography of the area is required to resolve whether these rocky shores are likely to be open or closed at the scale of this study (Gaines et al. 2003), and an investigation into the advective properties of the surface and sub-surface currents in Maputaland is the focus of Chapter 4.

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3.5 CONCLUSION

Recruitment of barnacles and mussels in the Maputaland Marine Reserve is seasonal. Seasonal recruitment patterns for *Perna perna* and *Chthamalus dentatus* were similar to those of conspecifics in other bioregions. There are no previous records of recruitment rates of *Tetraclita serrata rufotincta* or *Brachidontes semistriatus*, so no comparisons could be made for these species. Benthic-pelagic coupling was demonstrated for both mussels and barnacles, with larval densities explaining a significant portion of recruitment variability for each species. The seasonally pulsed nature of recruitment was linked to seasonal spawning, driven by the strongly seasonal patterns of sub-surface temperature. *B. semistriatus* recruited simultaneously with *P. perna*, which is different from the situation for the multi-species systems described for the West Coast in Chapter 1, and this may be due to similarly timed spawning or to a lack of spatial heterogeneity along the Maputaland coast.

Recruitment rates were only very loosely coupled to adult stock densities in both years of the study. Human harvest of adult mussels on these rocky shores is having a clear impact on the adult densities in the MMR. Several lines of evidence support this. Firstly, harvesting may explain the absence of a stock-recruit relationship. At unharvested sites with low levels of *P. perna* recruitment in other parts of South Africa, the small-scale stock-recruit relationship was generally strong (Chapter 1). In addition, *P. perna* recruitment rates were among the lowest in the country, as are the stocks of adult mussels. Finally, the recruitment density of *B. semistriatus* was consistently higher than *P. perna*. *B. semistriatus* is a 'weedy' species that relies on high recruitment and the continued invasion of disturbed habitats, and is an indicator of disturbed rocky shores on the east coast of southern Africa (Lasiak 1999). As these areas are subject to regular harvesting, these factors together indicate that disturbance of the mussel stocks is having a transformative effect on the intertidal environment.

The establishment of controlled or no-take areas could counteract the harvesting pressure currently exerted on rocky shores in the MMR. To contribute to the determination of scales and spacing of these closed areas for replenishment of mussel both in and out of sanctuary areas, an investigation into the potential for advection by nearshore currents in the study area is required. The results of such an investigation are presented in Chapter 4.

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CHAPTER 4

Hydrography of the inner shelf and the connectivity of rocky shores in Maputaland

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4.1 INTRODUCTION

Conservation biologists have for decades understood the importance of the connectedness of disjunct populations for their maintenance (Saunders et al. 1991, for review). However, while connectivity via corridors and buffer areas have become a focal area of research for terrestrial ecologists (e.g. Wegner and Merriam 1979) and island biogeographers (e.g. Whitcomb et al. 1976), marine ecologists have until recently simply referred to benthic populations as either 'open' or 'closed'. Some have regarded rocky shores as being 'open' and connected by a large homogenous larval pool that is transported onshore by little-understood and therefore unpredictable hydrographic mechanisms (e.g. Berry 1978; Roughgarden et al. 1985). Others have treated them as 'closed', or disconnected, with recruitment dynamics being completely locally controlled (e.g. Suchanek 1985). Perhaps this is because marine organisms can disperse on average so much further than their terrestrial counterparts, making the connection between adult stocks and larval settlement less readily discernable (Kinlan and Gaines 2003). Marine studies have, however, lately shown that populations are rarely either totally open or closed. Instead, scales of connectedness between disparate populations vary in ways that depend on multiple factors, some of which are scalar (Kinlan et al. 2005). Some of these factors are becoming increasingly understood and predictable; others are not. At the same time, there is a continuing appreciation that insurance of continued connectedness of benthic adult populations via their larvae, or via various life stages that occupy different habitats, is essential for conserving ecosystems and sustaining fisheries (Botsford et al. 1998; Gaines et al. 2003; Lubchenco et al. 2003; Mumby et al. 2003; Carson and Hentschel 2006).

The minimum ecologically required dispersal distance at the population level is only hundreds to thousands of meters from the parental stock (Strathmann et al. 2002). While stepping-stone models indicate that this might be accomplished in a matter of days (Palumbi 2003), the meroplanktonic phase of dominant intertidal species such as mussels and barnacles is on the order of 1-4 weeks (Grantham et al. 2003; Shanks et al. 2003a). A pelagic larval stage lasting weeks may have therefore evolved not for long-distance dispersal, but rather in response to selective forces that inhibit alternative modes of early life development (Strathmann et al. 2002). As a result, Strathmann et al. (2002) suggest that the long-distance dispersal evident from large-scale genetic homogeneity may not be a direct result of selection, but simply a by-product of the selective advantage of a prolonged early life at sea. Byers and Pringle (2006) support this view, and demonstrated that long-distance dispersal may simply result from the prodigious larval production required to allow sufficient retention. Recent experimental evidence suggests that many species

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with dispersive larvae show strong stock-recruit relationships and even larval return (Harris et al. 1998; Castilla and Guiñez 2000; Swearer et al. 2002; Warner and Cowen 2002; Branch and Steffani 2004). In addition, studies of larval behavior indicate that many meroplankers may have the ability to orient themselves and navigate through the water column (Kingsford et al. 2002; Shanks and Brink 2005).

Studies identifying the physical and biological mechanisms that drive larval dispersal have contributed to a better understanding of adult population dynamics (Roughgarden et al. 1988; Bertness et al. 1996; Botsford et al. 1998). Although maximal distance of propagule dispersal maintains genetic homogeneity among populations (Mills and Allendorf 1996), it is the average realized dispersal distance that will effectively replenish neighboring (or distant) populations from one generation to the next (Kinlan and Gaines 2003). Maximum and average dispersal distances do not necessarily co-vary, and both can vary among populations and also among years, and therefore both require our study and understanding (Kinlan et al. 2005). The important intrinsic biological components of the dispersive phase have been generally identified, if not precisely explained, and these include both inter-specific differences (reviewed by Underwood and Keough 2001) and intra-specific plasticity (Holm 1990b; Raimondi and Keough 1990) of dispersal and settlement behavior (Morgan 1995a, 2001). These interact with a suite of extrinsic biological and physical factors that include adult density (Hills and Thomason 2003), timing of fecundity and spawning (Lasiak 1986; van Erkom Schurink and Griffiths 1991a; Ndzipa 2002; McQuaid and Lawrie 2005), life history parameters (Grantham et al. 2003; Carson and Hentschel 2006), mortality in the water column (Olson and Olson 1989; Morgan 1995a; Anil et al. 2001; Morgan 2001; Johnson and Shanks 2003), meso-scale retentive oceanographic features (Wing et al. 1998), water velocity (Archambault and Bourget 1999), accumulation by slicks or fronts (Shanks 1983), and onshore transport by various mechanisms such as internal waves, tidal bores, or the onset or relaxation of pulsed upwelling (Shanks 1983, 1988; Pineda 1994; Shanks et al. 2003b; Tapia et al. 2004; Vargas et al. 2004; Ladah et al. 2005; Shanks and Brink 2005). Additionally, all of these vary with inter-annual fluctuations in the oceanic environment (Connolly and Roughgarden 1999a; Marinovic et al. 2002; Navarrete et al. 2002). Of course, the relative importance of these factors to local communities will vary in a scalar manner, underscoring the importance of generating local hypotheses to explain local community dynamics, and creating local, as well as national, management strategies (McQuaid and Payne 1998; Carson and Hentschel 2006; Chapter 1, this study). Finally, the study of larval dispersal has been greatly enhanced by mathematical modeling (e.g. Gaines et al. 2003), although most models that predict larval dispersal have been created to describe straight stretches of coastline, an assumption that is inappropriately simple for most coasts (Largier 2003; Siegel et al. 2003).

The east coast of South Africa is, however, an ideal location to apply these models of larval dispersal as it contains relatively straight stretches of coastline. The area selected for this study falls

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just south of Maputo Bay, Mozambique, and is proximate to where the Agulhas Current is formed (Figure 4.1). The flow of the western Indian Ocean was previously thought to include a southward branching of the South Equatorial Current (SEC) at Madagascar. The SEC was then thought to run poleward and west towards the African continent, where it diverted again southward and joined the poleward Mozambique Current to form the Agulhas Current between 23° and 27°S (Quartly and Srokosz 2004). The strength of the Mozambique Current was known to vary seasonally with the onset of monsoons (Schumann 1998). A recent ship-based survey has indicated that, at the time of measurement, the Mozambique Current and the East Madagascar Current respectively contributed 27% and 30% to the Agulhas Current; the balance was contributed by the westward limb of the subtropical Indian Ocean Gyre south of 25°S (Donohue and Toole 2003). These inputs change over time, due to variable features such as eddies within the Mozambique Channel (Quartly and Srokosz 2004) and the East Madagascar Retroflection (Quartly and Srokosz 2002) which, to date, have produced no clear consistent signal (Quartly and Srokosz 2004).

Dominant features of inshore hydrography on the east coast of South Africa can be grasped from 1-km resolution Advanced Very High Resolution Radiometer (AVHRR) images, comparing typical summer and winter conditions (Figure 4.2). Firstly, the Maputo (formerly Delagoa) Bay, near Maputo, Mozambique, lies at the mouth of several rivers and smaller streams and its waters are the same temperature as the surrounding water in summer, but considerably cooler in winter, due in part to the addition of cooler water via riverine input. Maputo Bay is shallow, with restricted circulation (Paula et al. 2004), and is known for the proximate formation of lee eddies in the Delagoa Bight (Lutjeharms and Da Silva 1988; Quartly and Srokosz 2004). Riverine inputs may inflate nutrient (and therefore phytoplankton) levels. There are two other areas with higher nearshore levels of phytoplankton concentration year-round. The first is the Natal Bight, between Richards Bay and Durban. Here, a topographically-induced upwelling cell, in addition to input of freshwater via the Tugela River, reduces inshore temperatures and increases nutrient levels, thereby increasing nearshore productivity (Meyer et al. 2002). A second topographically-induced upwelling cell south of Port Shepstone, has similar, if less obvious, consequences (Roberts 2005).

The area selected for this study is the same as that described in Chapters 2 and 3, extending from Castle Rock to Island Rock in the Maputaland Marine Reserve (MMR), northern KwaZulu-Natal (KZN), South Africa, from the shoreline to 20 m depth (Figure 4.3). In satellite images, the area appears relatively featureless, with nearshore SST within 1°C of the offshore temperatures, and no obvious proximate sources of nutrient subsidies that would affect nearshore phytoplankton levels. Due to its remoteness, little of the area's inshore hydrography has been described (but see Mitchell et al. 2005). The coastline is nearly straight, allowing an empirical comparison of dispersal estimates with previous dispersal models that assume a straight coastline, and has a series of rocky headland isolated by intervening sandy bays, permitting questions about the connectedness of rocky-shore fauna on these points by larval dispersal. Using data presented here, as well as

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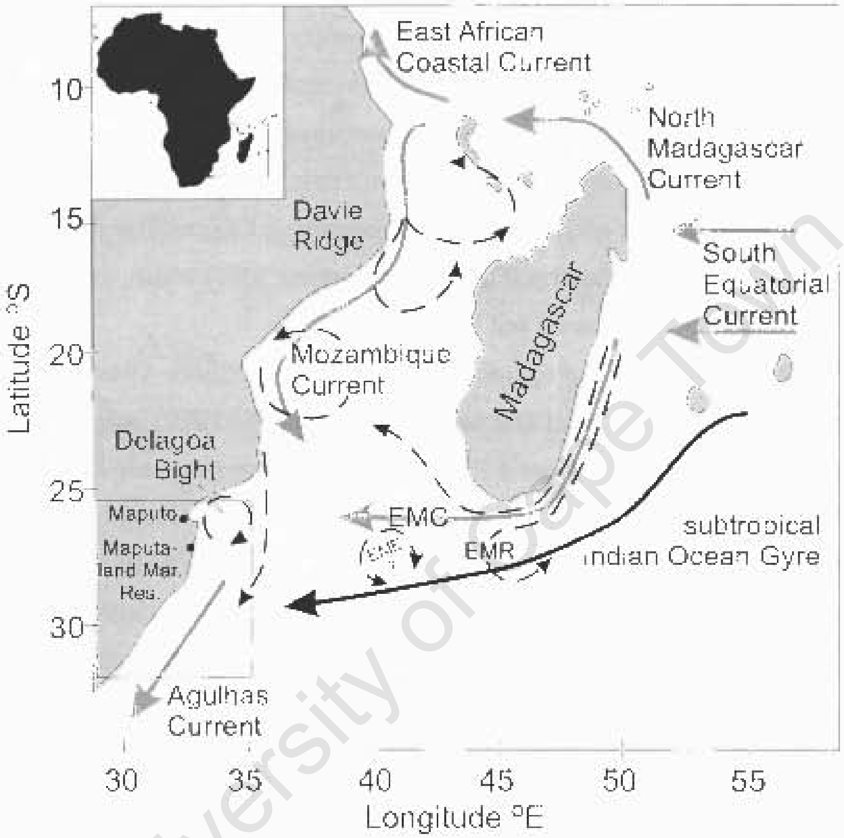

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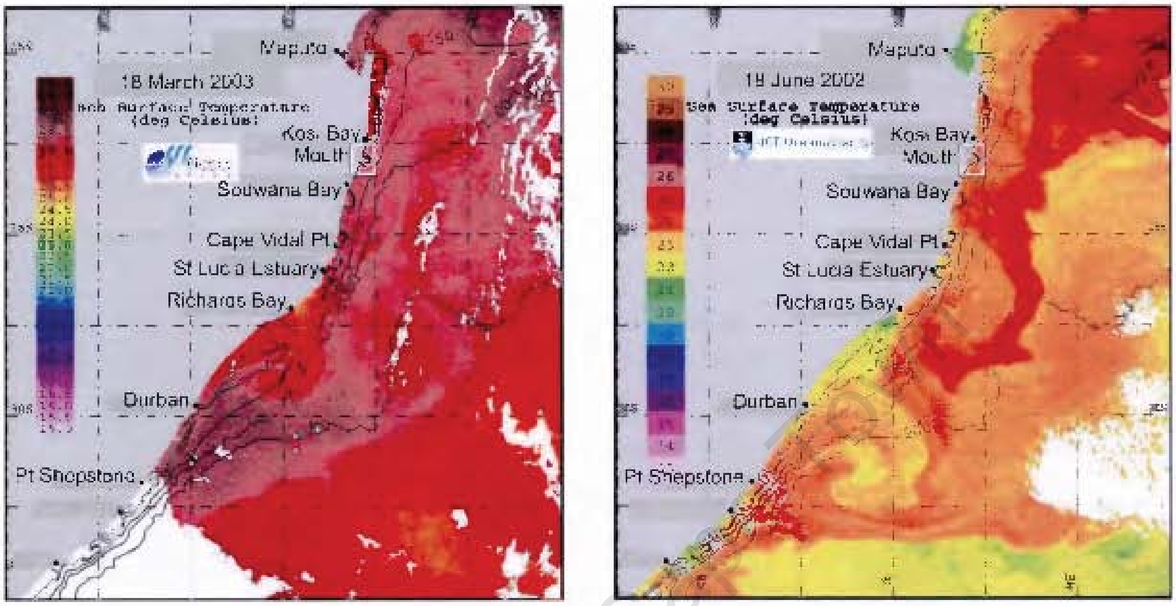
Figure 4.1. **Schematic of oceanic circulation around Madagascar, Mozambique and NE South Africa and the formation of the Agulhas Current. Thick grey arrows show traditional view of circulation (long-term mean flows from wind forcing and water properties). Thin dashed arrows show variability in the features derived from satellite imagery (from Quartley and Srokosz 2004). The thick black line shows additional water input into Agulhas Current (up to 30%) from the westward limb of the subtropical Indian Ocean Gyre (Donohue and Toole 2003). Box shows area detailed in satellite images in Figure 4.2.**

EMC = East Madagascar Current , EMR = East Madagascar Retroflection, EME = East Madagascar Eddies shed by retroflection.

Sea surface temperature - Summer

Sea surface temperature - Winter



Chlorophyll *a* - Summer

Chlorophyll *a* - Winter

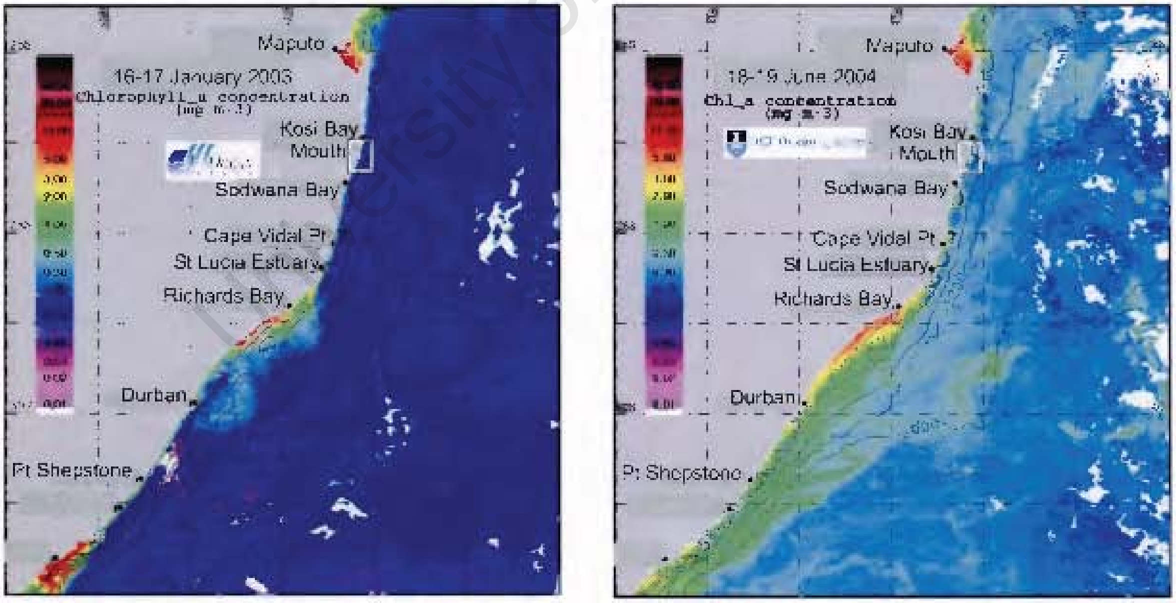


Figure 4.2 Typical summer and winter conditions on the KwaZulu-Natal coast. White box indicates study area.

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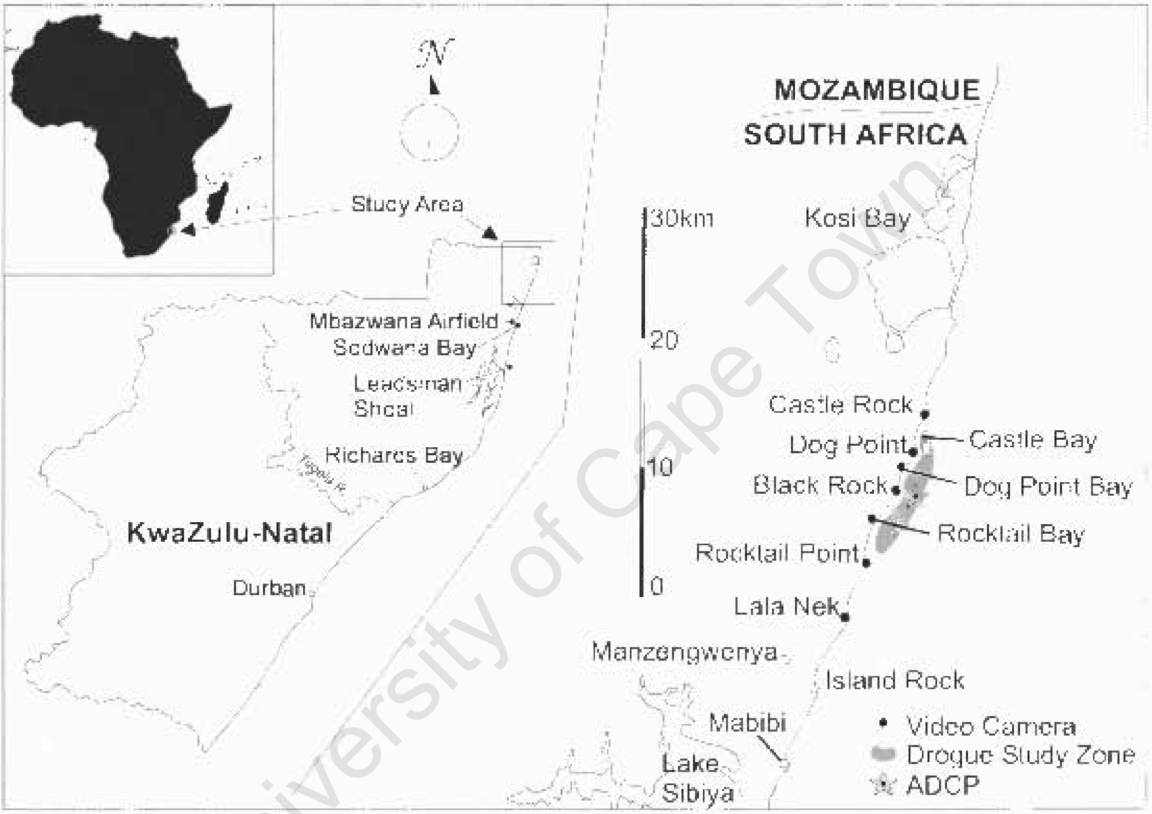

Figure 4.3 Map of hydrographic and wind sampling stations in the Maputaland study area (filled circles), as well as other locations mentioned in the text (white circles)

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selected data from Chapters 2 and 3, this study examines the roles of meso- and small-scale hydrodynamic forcing on recruitment dynamics, and the connectedness of rocky shores in the MMR, in three parts. First, to dispel the hypothesis that the Agulhas Current dominates nearshore dynamics in areas with narrow continental shelves, which would effectively eliminate any means of retention along the coast, the role of meso-scale forcing on nearshore currents and recruitment patterns was investigated at the scale of the Agulhas Current using remote sensing. Second, nearshore currents were measured and examined in relation to coastline shape and wind and tidal forcing. These empirical measurements were then used to create a model of along- and across-shore dispersal for passive drifters. This section of the MMR falls both in an out of sanctuary zones, but the entire coast and the adjacent Kosi Bay Estuary are subject to subsistence-level harvesting of many invertebrate species including the mussel *Perna perna* and the tunicate *Pyura stolonifera*, as well as fish (Kyle et al. 1997a, b; Kyle 1999). The outcomes of the model are therefore relevant to the management of rocky shore organisms with complex lifestyles; three examples of its potential use in recommending spacing of sanctuary areas for the management of rocky-shore fisheries within the MMR are provided at the end of this chapter.

4.2 METHODS

Study Area

Launching constraints and bathymetry of the nearshore area of the Maputaland Marine Reserve (MMR) are described in Chapter 2, and the geomorphology of the rocky shores, including the special characteristics of Black Rock, the headland at the center of this study, in Chapter 3. The continental shelf is generally narrow (2-7 km) with a shelf break depth of 45-112 meters (Martin and Flemming 1988). I partitioned the inner shelf into five zones (Figure 4.4). The first three zones, which comprise the nearshore, are the swash (0-50 m from shore), the surf (50-100 m) and the region just behind the surf (100-150 m). In the bays, where sand bars create a second surf zone behind the first, two additional zones were included -- the second surf zone (125-150 m) and the region behind the second surf zone (150-200 m). The final two zones are the inshore (200-450 m from shore, depths of 7-12 m) and the offshore (450-800 m, 12-18 m deep).

Maputaland is microtidal (< 2 m tidal range) and experiences storm surges ≥ 2 m approximately once annually (Mitchell et al. 2005). Tidal currents are small and thought to have a minor influence on coastal processes. Using 30 years of ship data from the South African Data Centre for Oceanography (SADCO), Mitchell et al. (2005) report seasonal mean swell conditions that vary between southerly and south-easterly (January: 140° direction, 1.6 m height, 6.5 s period; July: 170°, 1.9 m, 7.8 s). Winter southerly swells refract strongly, producing northward swash- and surf-zone alongshore currents. These currents are pulsed, with storm swells of Cape origin arriving approximately weekly, lasting 2-3 days and driving alongshore northward currents exceeding

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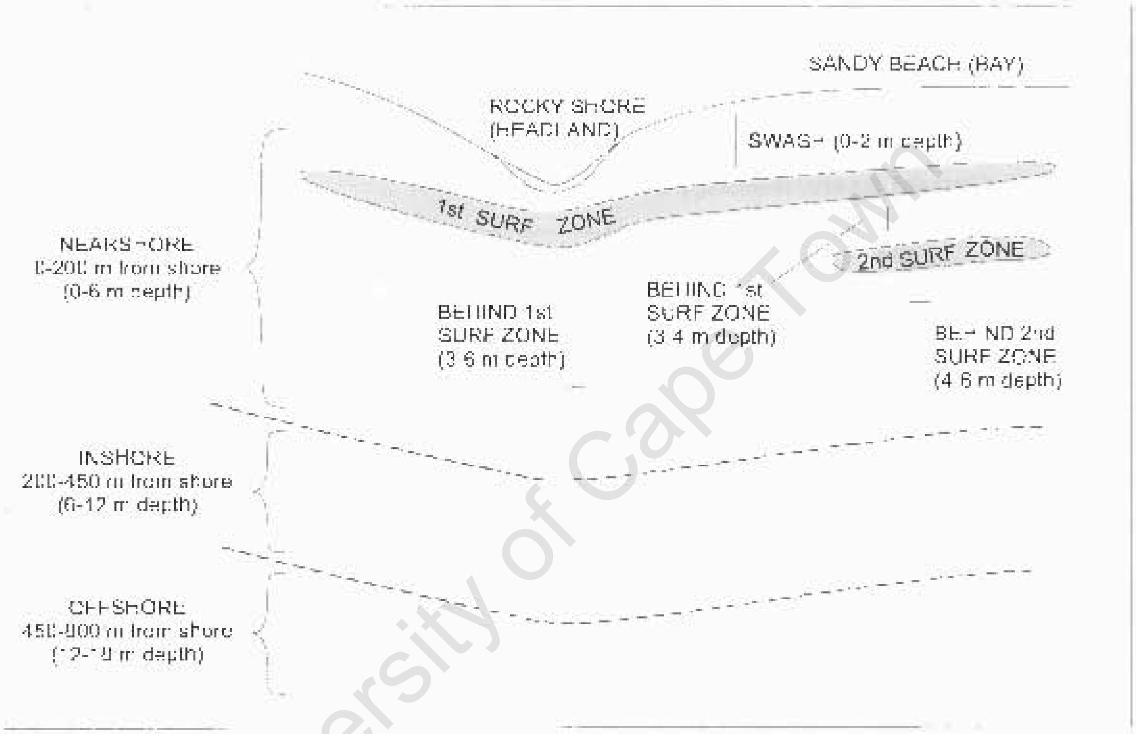

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Figure 4.4 Schematic drawing of the zonation of inner shelf waters used in this chapter. The second surf zone forms only in bays and when a sandbar is present.

$1\ m.s^{-1}$. Using the Enguelund-Fredsoe equation, Mitchell et al. (2005) deduce that alongshore swash- and surf-zone currents are energetic, and can mobilize a northward 'river' of sand, greater than $10^5\ m^3$ per year.

Field-based environmental measurements

Current speed and velocity in the inner shelf zones were measured three ways: videography, drogues, and ADCP (Table 4.1) at various depths during four field trips of four consecutive days, two in 2002 and 2003, one near the beginning and one near the end of the *P. perna* spawning period on the east coast of South Africa (Berry 1978).

Table 4.1 Current measurement types by zone

Zone	**Video**	**Drogue**	**ADCP**
Water depth	**All**	**2-15 m**	**17 m**
Measurement depth	**Surface**	**2-10 m**	**1-15 m**
Swash	X		
First surf zone	X		
Behind first surf zone (bays only)	X		
Second surf zone (bays only)	X		
Behind all surf	X		
Inshore	X	X	
Offshore	X	X	X

Current measurements using videography

Following methods developed during a pilot study (den Oudendammer 2002), filming of surface waters took place at each of seven sites (Table 4.2), recording for 10 minutes at three specified times on each day at each of three angles in 2002 and four angles in 2003 (Table 4.3, Figure 4.5). The video footage was then used to measure the velocity of the surface layer of the water in each of the nearshore zones using a *keogram*, or time-stack. The use of video-based visual time-stacks to study hydrodynamics at small and medium scales is a relatively new trend in nearshore oceanography. The method, usefulness and accuracy of the time-stack method for alongshore current measurements from a single, fixed location have been recently described (Chickadel et al. 2003). My study extends this method to involve multiple cameras filming simultaneously from several fixed locations, giving an array of current speeds spanning a substantial section of coast. Modifications and extensions of the method described by Chickadel et al. (2003) are detailed in Appendix 1. Videographic methods for measurements of surface currents are particularly valuable for investigations in isolated areas such as the Maputaland Marine Reserve, where location, access to electricity, cost, equipment security, the need for very-nearshore current measurements and other factors prohibit or exclude more permanent and costly options.

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Table 4.2 Description of the filming sites.

Site	Latitude, Longitude	Camera height (m)*	Substrate
Castle Rock	27° 04' 42.2" S, 32° 50' 57.1" E	5.2	Solitary rock
Dog Point	27° 06' 26.9", 32° 50' 30.0"	27.5	Heavily vegetated dune
Dog Bay	27° 07' 18.2", 32° 49' 56.2"	19.3	Slightly vegetated dune
Black Rock	27° 08' 04.0", 32° 49' 53.1"	11.6	Rock headland
Rocktail Bay	27° 09' 36.4", 32° 48' 43.6"	25.8	Slightly vegetated dune
Rocktail Point	27° 09' 28.8", 32° 48' 49.6"	19.0	Moderately vegetated dune
Lala Nek	27° 13' 30.6", 32° 47' 39.0"	15.6	Moderately vegetated dune

*The height of each filming point was measured using a theodolite and reflecting prism (accuracy ± 25 cm), corrected using hourly tide tables (Anon. 2002, 2003), and expressed as height in meters above MLWS.

Table 4.3 Details of the video current measurements and drogue deployment schedule on each day (n = the number of drogues deployed on that day).

		Video		Drogues			
Date	Tide state [a]	Filming angles	Start times	Sites [c]	Deployment depths (m)	Drogue lengths (m)	n
17 Sep 02	M	NE, E, SE	9:30, 13:00, 15:00	DB-S, BRP, RTB-N	7, 14	5, 10	20
18 Sep 02	M	NE, E, SE	10:00, 12:00, 15:00	DB-N, DB-C, DP-S	7-8, 14-16	5, 10	27
19 Sep 02	M	NE, E, SE	9:00, 12:00, 15:00	DB-N, DB-C, BRP	7-8, 14	5, 10	20
20 Sep 02	S	NE, E, SE	9:30, 12:00, 15:00	DB-S, BRP, RTB-N	7	2, 5, 10	8
1 Dec 02	M	NE, E, SE	9:00, 12:00, 15:00	DB-S, BRP, RTB-N	7	5, 10	20
2 Dec 02	S	NE, E, SE	9:00, 12:00, 15:00	DB-S, BRP, RTB-N	10-11, 15-16	5, 10	12
3 Dec 02	S	NE, E, SE	9:00, 12:00, 15:00	CRB-S, DP, DB-N, BRP	15	5, 10	10
4 Dec 02	S	NE, E, SE	9:00, 12:00, 15:00	DP, DP-N	12, 15-16	5, 10	12
23 Aug 03	M	NNE, ENE, ESE, SE	9:00, 12:00, 15:00	DB-S	15	5, 10	6
24 Aug 03	M	NNE, ENE, ESE, SE	9:00, 12:00, 15:30	DB	10, 15	5, 10	6
25 Aug 03	M	NNE, ENE, ESE, SE	9:00, 12:00, 15:00	DB	10, 15	5, 10	2
26 Aug 03	S	NNE, ENE, ESE, SE	9:00 [b]	DB	10, 15	5, 10	16
23 Nov 03	S	NNE, ENE, ESE, SE	9:00, 12:00, 15:00	DB-N, DB-C, DB-S	10, 15	2, 5, 10	12
24 Nov 03	S	NNE, ENE, ESE, SE	9:00, 12:00, 15:00	DB-N, DB-C, DB-S	10, 15	5, 10	12
25 Nov 03	S	NNE, ENE, ESE, SE	10:00, 12:00, 15:00	DP-N, DB-C, BRP	10, 15	2, 5, 10	10
26 Nov 03	S	NNE, ENE, ESE, SE	9:00, 12:00, 15:00	DB-N, DB-C, BRP-C	10, 15	5, 10	14

[a] Tide state: S = spring tide, M = midway between spring and neap

[b] 12:00 and 15:00 filmings cancelled due to high winds.

[c] BPR (Black Rock Point), CPB-S (Castle Rock Bay – Southern third), CRP (Castle Rock Point), DP (Dog Point), DP-N (Dog Bay – Northern third), DP-C (Dog Bay, Central third), DB-S (Dog Bay – Southern third), RTB-N (Rocktail Bay – Northern third)

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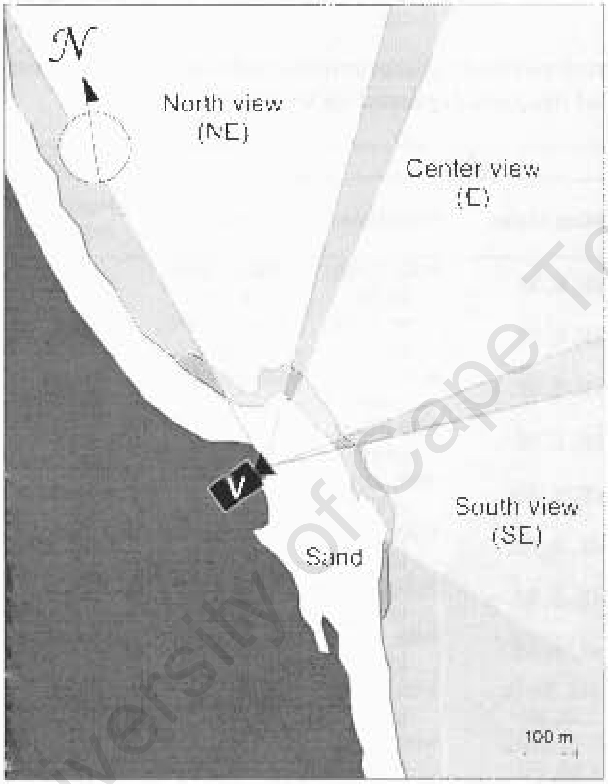

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Figure 4.5 Aerial view of Rocktail Point, exemplifying the placement of the video camera (V) and the three fields of view at this location in 2002. The bay in the north view was relatively sheltered, while the headlands in the center and south views were exposed to the dominant swell direction. In 2003, four rather than three fields of view were employed.

Subsurface temperature

Subsurface temperature data were taken from Chapters 2 and 3, collected half-hourly at 15 m depth at Leadsman Shoal and Sodwana Bay from 2002-2005.

Data analysis

All statistics, unless otherwise stated, were computed using Statistica 7.0 (StatSoft, Inc. © 1984-2004).

Meso-scale hydrographic patterns and their influence on recruitment dynamics

One-km resolution 1- to 3-day Advanced Very High Resolution Radiometer (AVHRR) satellite data were the same as those used in Chapter 2. In this exercise, however, a larger block, 40 km wide (E-W) and 80 km long (N-S), centered at its western edge just below Black Rock, was extracted for analysis. Satellite data were selected approximately biweekly from March 2001-December 2004. Images with > 30% cloud cover were rejected. Missing pixels were interpolated using ordinary kriging (EasyKrig3.0, © 2004 Dezhang Chu and Woods Hole Oceanographic Institution, running in Matlab 6.0, © 1984-2000, The Math Works, Inc.). Semi-variograms were computed using a general exponential-Bessel model. Kriging was cross-validated statistically to ensure that the distribution of the deviation for the mean fell within acceptable criteria. The data were then detrended spatially (within each date) and an Empirical Orthogonal Function (EOF) analysis, equivalent to Principal Component Analysis, was performed, using a covariance matrix following Armstrong (2000). The distribution of the days among the first two eigenvectors, or factors, was examined graphically.

A moderate separation of the images was observed between 'summer' (Sept-Feb, the recruitment season of mussels *Perna perna* and *Brachidontes semistriatus* and the barnacle *Chthamalus dentatus*) and 'winter' (Mar-Aug, recruitment season of the barnacles *Tetraclita* spp.). The detrended data were therefore separated for two analyses, one of only the summer months, and one of the winter months. For each factor, the factor loadings for each pixel were plotted, yielding a spatial representation of the dominant surface temperature patterns. The factor loadings of the dates were plotted, and Pearson product-moment correlations were used to relate these loadings to the daily, previous 3-days' and previous 7-days' mean along- and across-shore wind velocities, as well as daily mean subsurface temperatures.

To investigate whether dominant SST conditions could explain the variability of recruitment events, these factor loadings for the summer and winter months were also compared to recruitment rates of the four species mentioned above, drawing on recruitment data in Chapter 3. For these calculations, the date in the middle of the recruitment month was matched to its temporally closest satellite image. The factor loadings of these dates for Factors 1, 2 and 3 were

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Current measurements using drogues

The drogues used in my study were the same as those used by the Council for Scientific and Industrial Research (CSIR, Stellenbosch, South Africa), and their velocities have previously matched well with simultaneous ADCP measurements (CSIR, unpubl. data). For four days of each field excursion, drogues were tracked directly offshore but in view of the central video cameras. The drogues were deployed with the overarching goal of describing the current structure between Castle Bay and Rocktail Bay, with a focus on Black Rock (Figure 4.3). Sampling on all days but 18 September 2002 occurred over low slack tides. Window-shade type drogues measuring 100 cm long × 50 cm wide reaching to three depths (2, 5 or 10 m) were deployed at the localities indicated in Table 4.3. Generally, two groups of drogues were tracked simultaneously; one set along the 15-m isobath in the offshore zone, and the other in the inshore zone. The inshore drogues were placed just behind the surf backline, generally in depths of 7-10 m. Drogue velocities were calculated by recording drogue positions and times at 10-15 min intervals using a boat-based Lowrance LCX 15MT GPS in the WGS-84 datum.

Current measurements using ADCP

A 1200 kHz RD Instruments Workhorse Sentinel ADCP was deployed on sand using a 240-kg aluminum and lead frame designed for a sandy substrate. A lead-lined rope attached the frame to a 50-kg sand anchor and a 10-kg angel, which were then attached to a subsurface buoy. The apparatus was installed at 17-m depth on 26 November 2003 directly offshore the central headland at Black Rock (27° 08.114'S, 32° 50.116'E) with the following settings: 0.5 m bins, 90 days, 3 measurements.hr^{-1} (20 min ensemble interval), 22°C, 35 ppt salinity, 350 pings.ensemble^{-1} (SD 0.37), transducer depth 17 m, magnetic variation -19.3°, magnetic error 6.7. Pre-deployment settings were configured using WinSE (ver 1.28). The ADCP was deployed for 111 days. ADCP data were analyzed by Janelle Reynolds-Fleming, following methods described in Reynolds-Fleming (2003) and Reynolds-Fleming and Luettich (2004). As the ADCP was deployed after all other current measurements and not during the recruitment season for mussels, data from its deployment are used only for validation of the other current measurement techniques (see Appendix 2).

Wind data

Wind speed and direction were recorded hourly on each filming day at Black Rock using a Silva Wind Watch (accurate ± 4%), a directional flag and a compass adjusted for magnetic declination. Additional hourly wind speed and direction were provided by the South African Weather Service from the Mbazwana Airfield (Climate Number 0412148-6, 27° 28.017' S, 32° 34.983' E, 61 m altitude), which lies 8 km west of the coast and 35 km SW of the study area (Figure 4.3).

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then plotted against the recruitment rate of each species. Replicates with zero-values for recruitment in that month were excluded. Recruitment of *P. perna*, *B. semistriatus* and *C. dentatus* was plotted against the factor loadings for summer, and the recruitment of *Tetraclita* spp. was plotted against the factor loadings for winter.

Measurement verification and processes driving currents

Data from the drogues, videography, and winds measured in the study area were validated (Appendix 2). Wind data collected at Mbazwana Airfield (presented in Chapters 2 and 3) and vertical tidal velocities were then used to determine to what extent these processes were driving currents by applying Pearson product-moment correlation analyses at various time lags. Hourly predicted tide levels (Anon. 2002, 2003) were used to determine vertical tidal velocity (V_T, in $m.s^{-1}$) using the formula

$$V_T = \frac{H_1 - H_0}{t}$$

where H_0 is the tidal height at the beginning of the 1-hour time bin in meters, H_1 the tidal height at the end of the time bin, and t is the elapsed time in seconds.

Inshore hydrography and current variability

The current data were then compiled to deduce dominant current patterns around headlands and in bays. The spatial velocity data were very patchy, and data points were added to some missing cells according to the following *a priori* rules. (1) Alongshore current speeds within the same 2-hour period in the inshore and offshore zones were assumed constant at all depths, based on field observations. (2) In the nearshore stations (surf and swash zones), when data collected at ≥ 3 rock points were similar, the mean values were substituted for missing cells for remaining rock points. (3) Data in the surf and swash zones were only collected in two of the bays. If data were missing for one bay, and if data collected later or earlier in the day indicated that both bays displayed similar current patterns, then the alongshore current velocity measured in one bay was substituted for the other bay. The alongshore component vectors of current speeds were binned by 1-hour time window, depth, station and distance from shore; only currents measured behind the surf zone were used in substitutions for this zone. These data were then detrended temporally to investigate the daily patterns of current structures using EOF analysis with a covariance matrix, as for the satellite imagery. The factor loadings of the first three principal components, or factors, were compared both spatially and temporally. The temporal factor loadings were then compared to the dominant factors from the satellite images to contextualize the study on smaller-scale currents.

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Larval density and alongshore current speeds

On days where current speeds and *in situ* larval densities were measured simultaneously, Pearson product-moment correlations were calculated between along- and across-shore current velocities and zooplankton biomass and meroplanktonic larval densities, using larval data from Chapter 2.

Dispersal models for mostly-passive drifters in Maputaland

Using the alongshore velocity vectors obtained empirically from drogue (inshore and offshore) and video (nearshore) current measurements in summer, a model similar to a stochastic Lagrangian simulation (e.g. Siegel et al. 2003) was constructed to describe the advection paths of passive drifters during summer within the Maputaland Marine Reserve. Five pre-competent planktonic larval durations (PLD) were examined (10, 13, 16, 19 and 22 days), typical of many meroplanktonic larvae of intertidal benthic organisms in Maputaland (Table 4.4). The path that was modeled involved movement among the nearshore, inshore and offshore zones (Figure 4.6).

Table 4.4 Planktonic larval duration (PLD) of dominant Maputaland benthic intertidal rocky-shore organisms, measured or inferred from 'Comparison spp.'

Species	PLD	Comparison spp.	Plankto-trophic?	Harvested?	Reference(s)
Balanus amphitrite (striped barnacle)	11-15 d at 20°C 13-22 d at 30°C	--	Yes	No	(Anil et al. 2001)
Fissurella spp. (keyhole limpet)	11 d	*Fissurella volcano*	No	Yes	(Grantham et al. 2003)
Idanthyrsus pennatus (reef worm)	49 d	*Sabellaria cementum*	Yes	No	(Grantham et al. 2003)
Perna perna (brown mussel)	15-20 d	--	Yes	Yes	(Hicks and Tunnell 1995)
Pyura stolonifera (red bait tunicate)	2-35 h	--	No	Yes	(Griffiths 1976; Castilla and Guiñez 2000)
Scutellastra pica (limpet)	21 d	*Lottia* spp.	No	Yes	(Grantham et al. 2003)
Stomopneustes variolaris (pot-hole urchin)	35 d, 60 d	*Strongylocentrotus droebachiensis*, *Lytechinus anamesus*	Yes	Yes	(Grantham et al. 2003)
Striostrea margaritacea & *Saccostrea cucullata* (oysters)	7 d	*Ostrea lurida*	Yes	Yes	(Grantham et al. 2003)
Tetraclita squamosa rufotincta (pink volcano barnacle)	6-8 d from naupliar stages I to IV	--	No	No	(Barnes and Achituv 1981)

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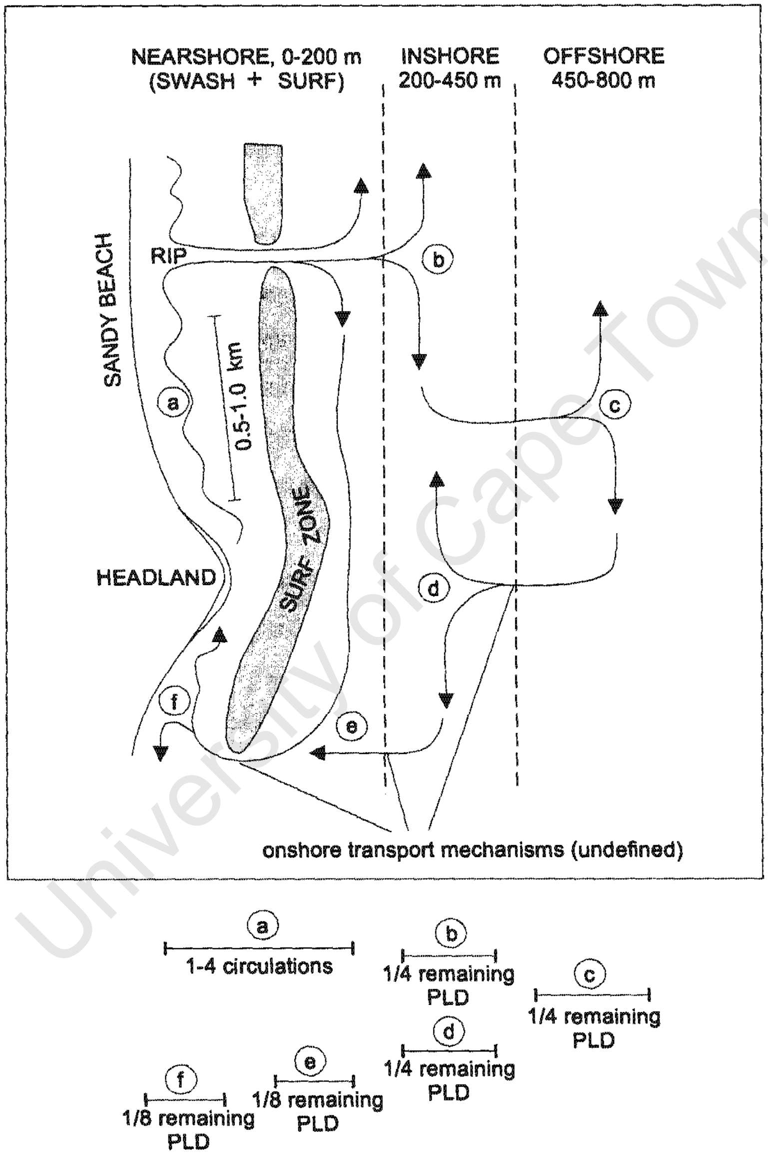

Figure 4.6 Conceptual diagram of empirical Lagrangian advection model for a passive drifter. Sensitivity of the model to variations in time spent in the nearshore *versus* inshore/offshore (steps b-e) as well as to variation in distance from release to rip currents, are reported in the text. PLD = planktonic larval duration.

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The following assumptions are contained in the model:

1. The nearshore contains a series of rip currents that form 0.5-1.0 km from headlands and 0.5-1.0 km apart; these are capable of ejecting particles from the nearshore into the inshore zone, although they may instead recycle into the swash zone (Largier 2002; Largier and George, unpubl. data).
2. Velocity measurements taken by drogue and video represent typical days during August to December; velocities within zones are similar along the entire modeled stretch of coast.
3. In each of the nearshore zones, surface and subsurface velocities were the same.
4. Passive drifters are not subject to benthic counter-currents that oppose mid-shore current velocities.
5. Despite the dominant cyclic pattern of wind events (Chapter 2) and their relationship with subsurface alongshore currents (this chapter), these patterns have high levels of variability (Chapter 2), so that the actual current direction and speed that a larva encounters in any given zone is selected randomly from the measurements taken in that zone.
6. Drifters are more able to control their distance from shore as they reach the end of their planktonic larval duration (PLD) and capitalize on onshore transport mechanisms to return to the surf zone.
7. Once returned to the surf zone, the competency window is sufficiently plastic to allow postponement of settlement until arrival at a rocky headland (e.g. Chicharo and Chicharo 2000).
8. No drifters are lost. This exercise models the hypothetical path of drifters that successfully return to the swash zone when they are competent to settle.
9. No diffusion occurs – drifters move with the same velocity as the patch of water they are found in.

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For each model, 19180 particles were released from the rocky headland. Each modeled drifter traveled along the beach until encountering a rip current. The velocity of the water in the swash zone was selected at random from the mean three-hourly values derived empirically using the video measurements. The drifter was advected with the swash zone current for a randomly generated distance of 0.5-1.0 km until it entered a rip current. The rip current released the drifter into the region behind the surf zone, where it was advected for the same distance by a velocity selected at random from the values for this zone from the video analysis. The particle was then re-circulated back into the surf zone 1-4 times (number randomly generated). If the particle had not yet reached the end of its prescribed PLD, it emerged into the inshore zone. From here, it spent one quarter of its remaining PLD in the inshore, one quarter in the offshore, one quarter back in the inshore, one eighth behind the surf zone, and one eighth in the swash zone. Five alternate scenarios were examined for the inshore and offshore zones: (a) the drifter always remains in the middle depths of the water column, (b) the drifter always remains in the surface, (c) the drifter migrates between the surface and midwater, spending one-third of its time at the surface and two-thirds of its time in the subsurface in both zones, (d) the drifter migrates between midwater and the bottom, spending one-third of its time at the bottom and two-thirds of its time in the midwater in both zones, (e) the drifter migrates between surface, midwater and the bottom, spending one-quarter of its time at the surface, one-quarter of its time at the bottom and one half of its time in the midwater in both zones. All alongshore current velocities were randomly selected from the empirically measured values, using 5-10 m drogues measurements for rates at middle depths and videography for the surface rates. Current speeds near the bottom were estimated using a ratio obtained from the ADCP data: on average, currents 1 m above the bottom flowed at 68% the speed and in the same direction as the midwater currents. The total alongshore distance traveled for the duration of the life of the particle was then summed (subtracting total southward travel from total northward travel), and alongshore dispersal kernel distributions plotted as histograms. Finally, holding the larval life span constant at 13 d, the sensitivity of the model to the effects of shorter or longer nearshore entrapments was examined using scenario (e).

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4.3 RESULTS

Meso-scale hydrographic patterns and their influence on recruitment

Analysis by Empirical Orthogonal Function (EOF) revealed that there were dominant patterns in SST in the nearshore environment. The first factor, or eigenvector, explained 42% of the total variance, while the second and third factors explained 11.3% and 9.1%, respectively. When the satellite images were plotted according to the first two factors, some divergence between those falling in 'summer' (spring/summer, 16 August to 15 February) and 'winter' (autumn/winter, 16 February to 15 August) became apparent (Figure 4.7a). The dominant (Factor 1) pattern was one in which water masses of different temperatures were arranged linearly in a pattern that was parallel to the coast, with a gradient of water temperature from east to west (e.g. Figure 4.7b). Factors 2 and 3 were less linear, with circular patterns that resembled eddies (e.g. Figures 4.7c-d).

To determine the dominant SST patterns in summer and winter, the satellite raw data were split between the two seasons and detrended, and the EOF analysis re-run. Again, the dominant (Factor 1) patterns for both seasons were more linear, but Factor 1 explained much more of the variability in the summer (49.8%) than in winter (27.8%) (Figures 4.8 and 4.9). Additionally, the longitudinal temperature gradient spanned 7°C for summer (Figure 4.8a), but only 3.5°C in the winter (Figure 4.9a). In both cases, Factor 2 represented a condition with patterns that more closely resembled eddying at the inshore or offshore edges of the images. Importantly, satellite images with strongly positive factor loadings resembled these figures, with cooler water inshore and warmer water offshore, while images with strongly negative loadings resembled their inverse, with warmer water inshore and cooler water offshore.

In Chapter 2, I concluded that wind-induced onshore or offshore Ekman transport could affect subsurface temperatures in the nearshore environment. The structure of the SST in Factor 1 resembled an upwelling condition with cooler water inshore (and its inverse, therefore, a downwelling or non-upwelling condition). The hypothesis that these patterns were related to nearshore wind events was tested by comparing various aspects of the continuous wind and temperature data sets with the Factor 1 loadings of each of the dates to determine whether coastal wind primarily explained the variability in SST patterns, either by Ekman transport or wind forcing. However, wind was only weakly associated with SST variability. For the summer season (Table 4.5a, Figure 4.8c), there was a weak but significant negative correlation between the factor loadings and the mean alongshore velocity of the previous three days' winds. As positive (northerly) alongshore wind is upwelling-positive, a negative correlation indicates that it was southerly winds that were associated with the dominant pattern with cooler water inshore (Figure 4.7). For the winter, Factor 1 was correlated more strongly with winds (Tables 4.5b and Figure 4.9c), negatively to cross-shore winds and positively to alongshore winds; Factor 1 was also negatively correlated with same-day subsurface temperature.

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Table 4.5 Pearson product-moment lag correlations between Factor 1 Eigenvector and the along- and across-shore wind velocity, plus that day's subsurface water temperature taken at Sodwana Bay.

Season	Correlates	Mean [a]	SD	r [b]	n	p
(a) Summer	Same-day mean alongshore wind	1.888	2.215	-0.241	35	ns
	Same-day mean across-shore wind	0.567	0.601	0.249	35	ns
	Three days' previous alongshore wind	0.837	1.662	-0.392	35	*
	Three days' previous across-shore wind	0.695	0.397	0.041	35	ns
	One-week's previous alongshore wind	0.723	1.189	-0.196	35	ns
	One-week's previous across-shore wind	0.636	0.313	-0.109	35	ns
	Same-day mean subsurface temperature	24.037	1.807	0.098	21	ns
(b) Winter	Same-day mean alongshore wind	1.901	1.756	0.052	26	ns
	Same-day mean across-shore wind	-0.128	0.630	-0.329	26	ns
	Three days' previous alongshore wind	0.653	1.428	0.327	26	ns
	Three days' previous across-shore wind	0.118	0.538	-0.461	26	*
	One-week's previous alongshore wind	0.358	1.211	0.446	26	*
	One-week's previous across-shore wind	0.164	0.449	-0.542	26	**
	Same-day mean subsurface temperature	24.283	2.099	-0.624	15	*

[a] Positive alongshore wind is upwelling-positive (NNE'ly), positive across-shore wind is onshore.

[b] A negative r-value implies correlation between the factor and downwelling-positive (SSW'ly) alongshore wind, offshore (WSW'ly) across-shore wind, or reduced temperature.

In Chapter 3, temperature was an important correlate explaining recruitment variability of the four invertebrate taxa, *P. perna*, *B. semistriatus*, *C. dentatus* and *Tetraclita* spp. But can the larger-scale variability in sea surface temperature also help to explain the timing and density of recruitment events? Factor loadings were plotted against recruitment densities for the summer and winter (Figure 4.10). In both seasons, Factor 1 explained the highest, significant proportion of

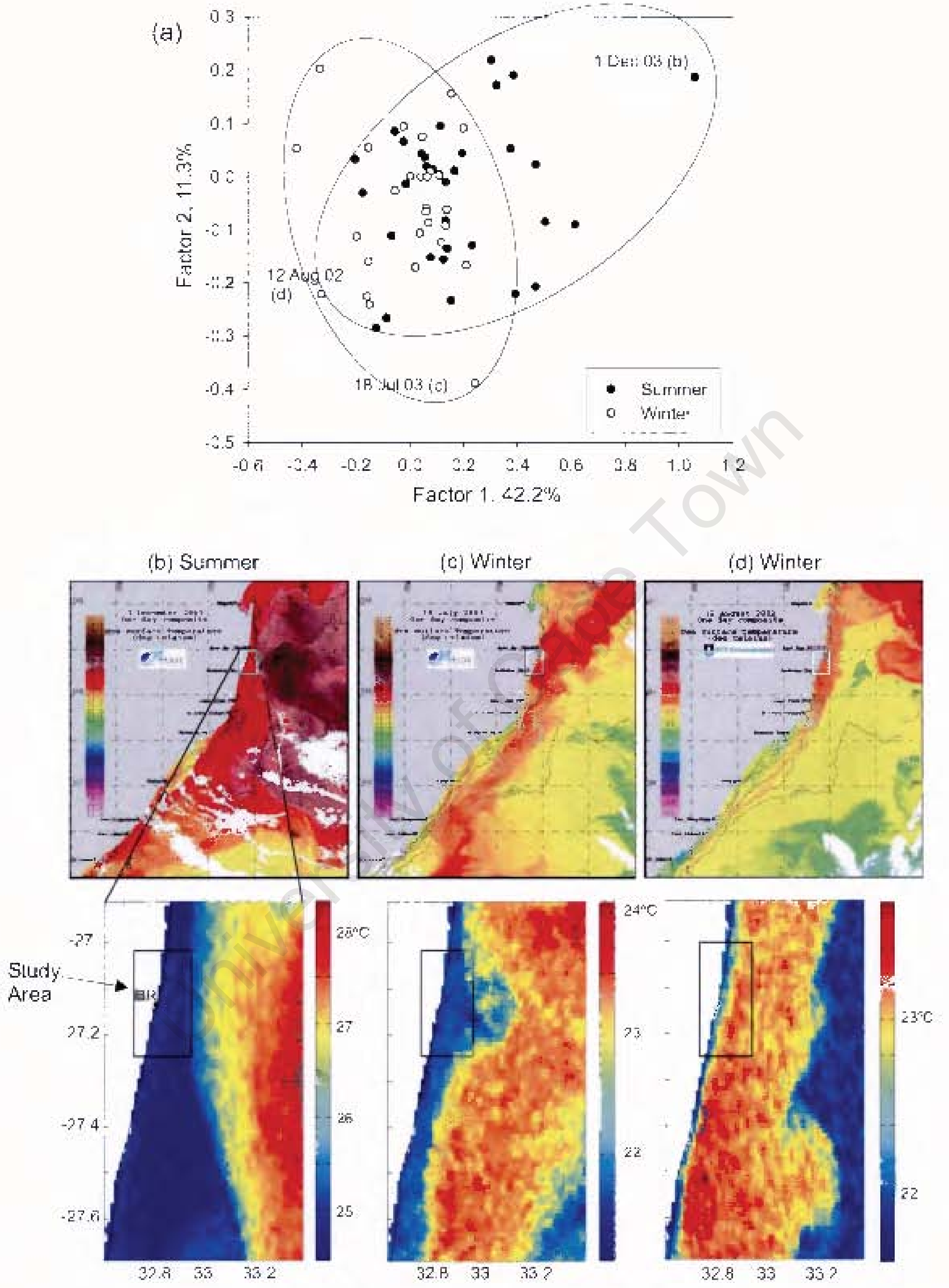

Figure 4.7 (a) Results of Empirical Orthogonal Function using all available satellite images of the study area, comparing patterns of sea surface temperature (SST) in summer and winter. (b-d) Selected examples of three outlying dates, showing the surrounding SST distribution (middle) and the detailed SST distribution (below). Note that color scales are not equal among images. BR = Black Rock Point

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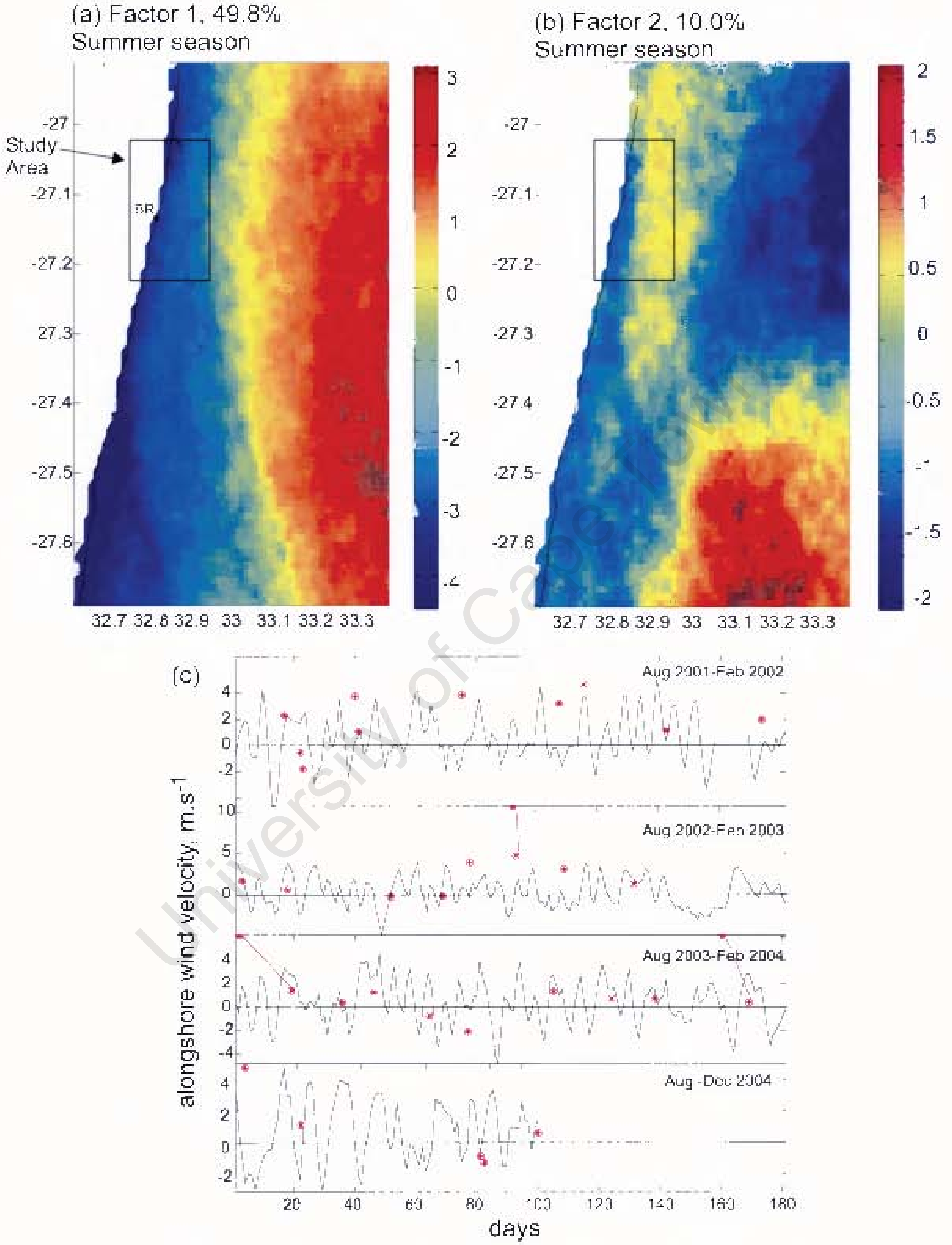

Figure 4.8 a-c Factor loadings per pixel of Factor 1 (a) and Factor 2 (b) from Empirical Orthogonal Function analysis of the summer satellite images. BR = Black Rock.
(c) Significant negative correlation between previous 3-days' mean alongshore wind and Factor 1. Factor loadings (dotted circles) are multiplied by ten for plotting. Positive wind is NNE'ly or upwelling-positive.

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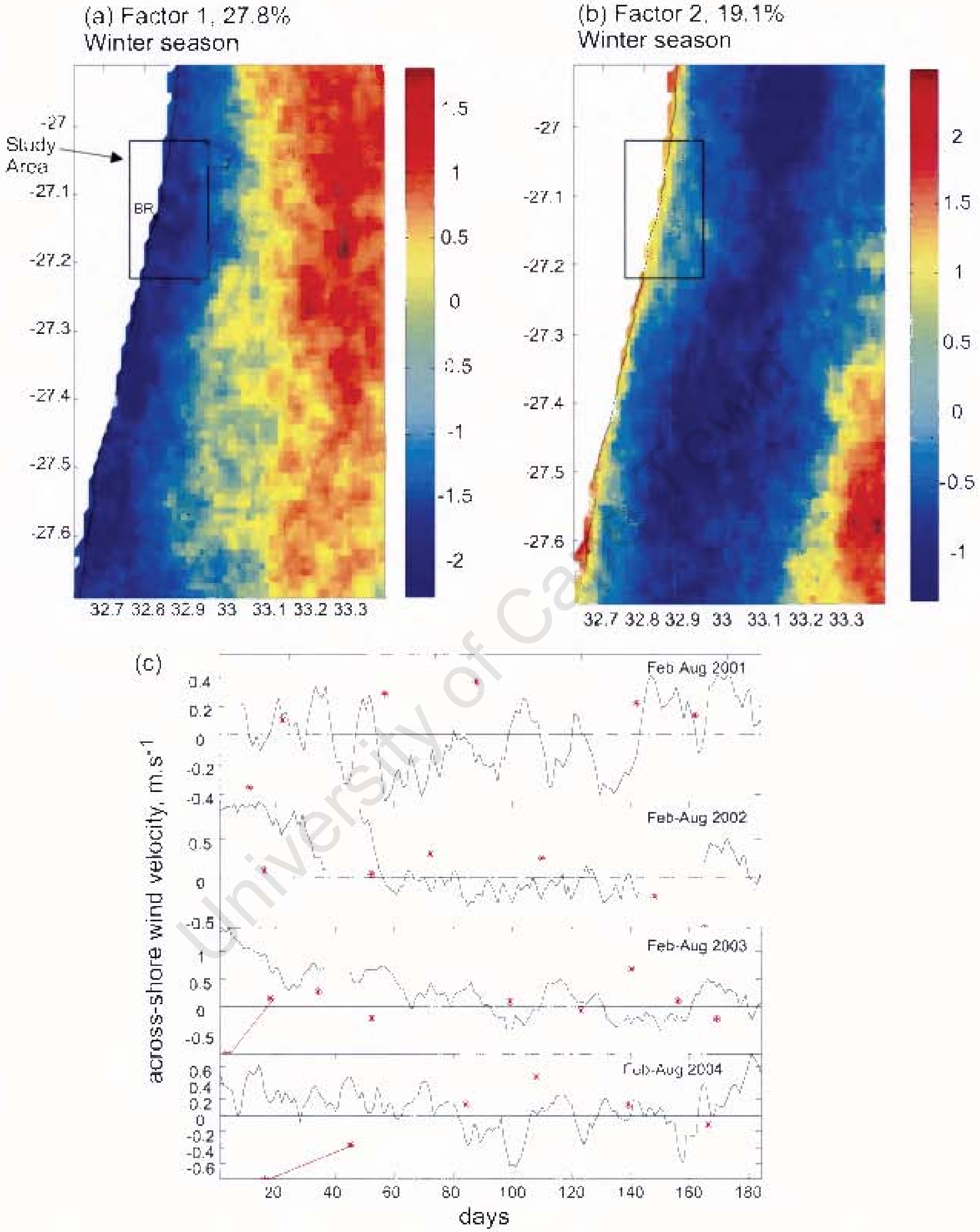

Figure 4.9 a-c Factor loadings per pixel of Factor 1 (a) and Factor 2 (b) from Empirical Orthogonal Function analysis of the winter satellite images. BR – Black Rock. (c) Significant negative correlation between the previous 7-days' mean across-shore wind and Factor 1. Factor loadings (dotted circles) are multiplied by ten for plotting. Positive wind is offshore.

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recruitment density, but the relationships were never linear. Recruitment of the mussel *P. perna* had a hump-shaped relationship with Factor 1, but the majority of recruitment events occurred in months with positive Factor 1 loadings (Figure 4.10a), which resembled the image in Figure 4.8a, with cooler water inshore and a linear longitudinal pattern of SST. Recruitment of the barnacle *C. dentatus* onto bare rock in the barnacle zone and recruitment of the mussel *B. semistriatus* into brushes were approximately equally well explained by the meso-scale pattern of SST, with recruitment of both species falling in months with positive Factor 1 loadings (Figure 4.10a). Recruitment of *C. dentatus* onto plates or bare rock in the mussel zone was not significantly explained by any of the first three factors from the EOF analysis. Recruitment of the barnacle *Tetraclita* spp. in winter onto both substrates (plates and bare rock) and in both zones (mussel and barnacle zone) was best explained by Factor 1, with the majority of recruitment occurring with negative factor loadings (Figure 4.10b). Satellite images with strongly negative loadings for Factor 1 more resembled the inverse of the image in Figure 4.9a, retaining the linear shape but with warmer surface water inshore and cooler water offshore.

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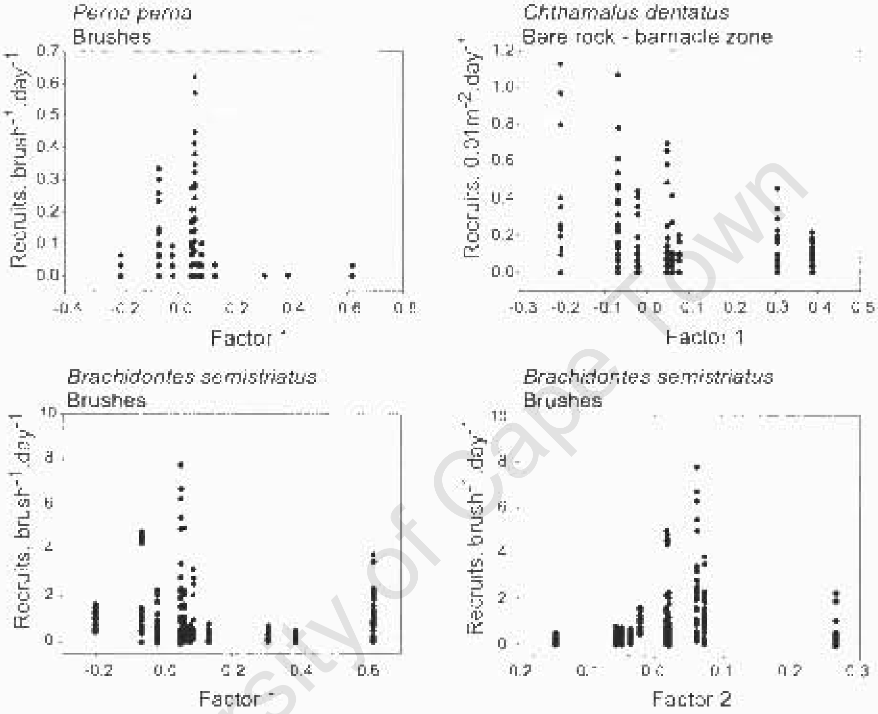
Processes driving currents

Wind, tidal height and tidal velocity on the dates of current measurements are presented in Figure 4.11. Alongshore currents were most strongly correlated to alongshore wind ($n = 14\text{-}132$, $r = 0.36\text{-}0.83$, $p < 0.05$), while across-shore currents were most strongly correlated to tidal velocity ($n = 25\text{-}30$, $r = 0.37\text{-}0.56$, $p < 0.05$). Alongshore currents behind the surf zones were negatively and significantly correlated with the alongshore wind component (surface: $n = 126$, $r = -0.38$, $p < 0.001$; 5-m depth: $n = 85$, $r = -0.78$, $p < 0.001$), indicating that the wind and surface water flowed in the same direction. Alongshore current velocities in the swash and surf zones were not significantly correlated with either along- or across-shore wind. Across-shore surface currents in the inshore zone were positively associated with alongshore winds ($n = 252$, $r = 0.15$, $p < 0.05$), indicating a slight offshore flow in northerly winds. For both along- and across-shore currents, the strongest correlations for the surface currents were at shorter time intervals (same-hour to 6-hour), while the strongest correlations for the subsurface currents were at a longer (12-hour) time interval. Alongshore current was only associated once with tidal velocity and never with tidal range. Across-shore currents were more strongly and significantly correlated with both tidal velocity (negative association, strongest at 5-m depth, both inshore and offshore) and tidal range (positive association, strongest at 2-m depth, offshore). Detailed methods and results for these investigations are presented in Appendix 2.

(a) Summer season



(b) Winter season

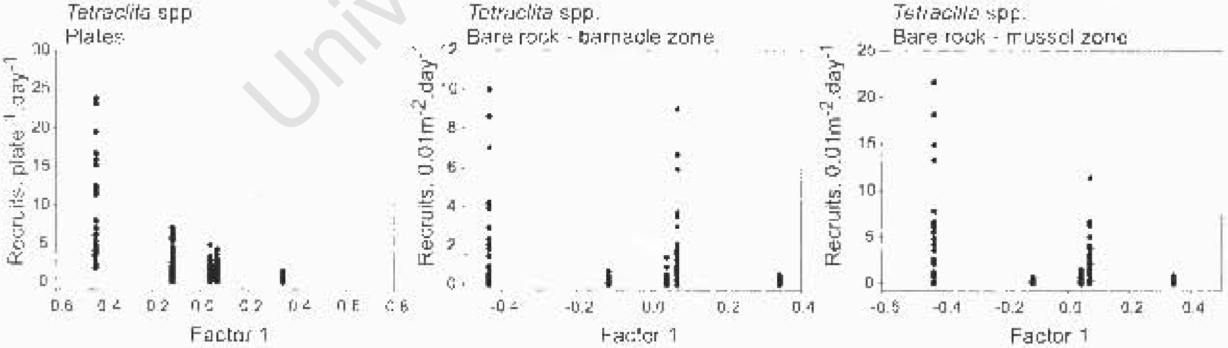


Figure 4.10 Factor loadings of satellite images in the (a) summer and (b) winter seasons, compared to non-zero recruitment densities (see Chapter 3) in that same month.

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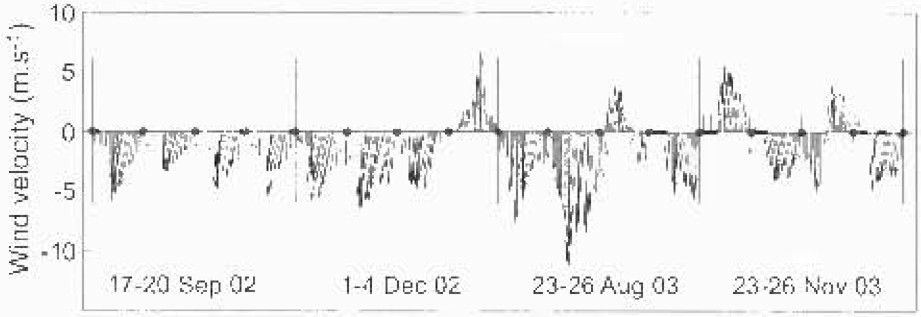

Figure 4.11a Hourly wind measurements at the Mbazwana airfield during drogue and videography data collection periods in 2002 and 2003. Arrows indicate the direction the wind is going *to*.

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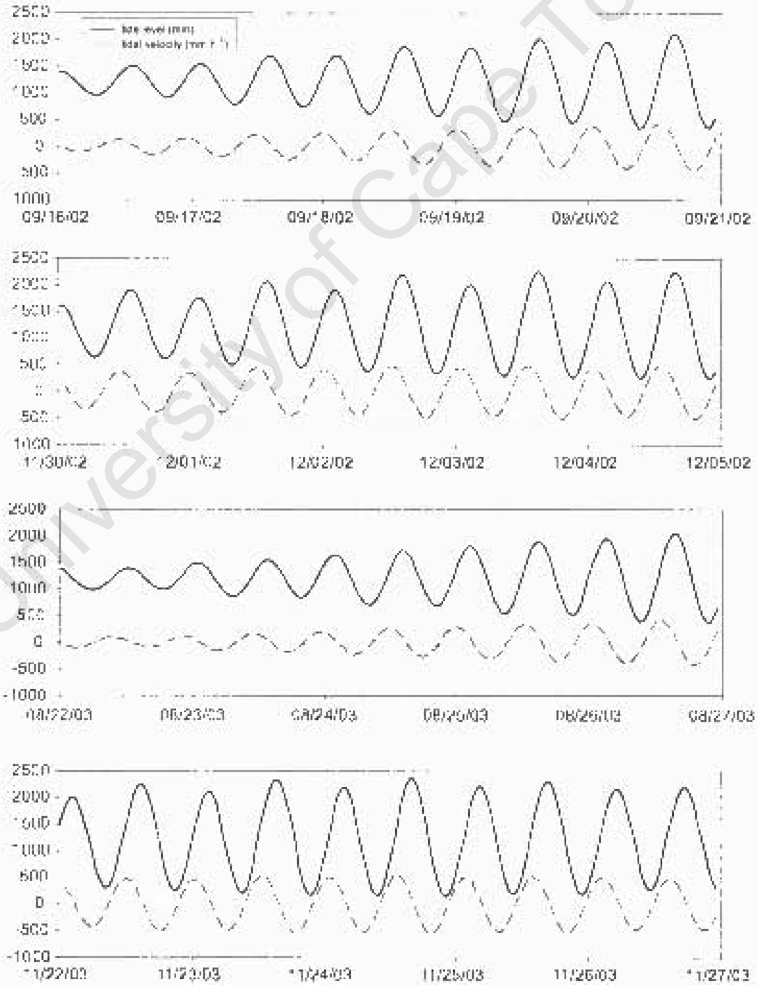

Figure 4.11b Hourly predicted tides (level, solid lines, and velocity, dashed lines) in KZN during drogue and videography data collection periods in 2002 and 2003. Positive velocities indicate a flowing tide, and negative velocities indicate an ebbing tide.

Inner shelf hydrography and current variability

The first three factors of the EOF analysis of surface and subsurface alongshore currents described a cumulative 78% of the variability (Figure 4.12). These plots describe the *relative* current speeds, or shear, in each case, not the actual current directions. For example, a current structure that falls strongly positive for Factor 1 could have currents all flowing southward, but with a sheared flow, such that the nearshore currents are much slower than the offshore ones. In all three cases (Factors 1, 2 and 3), the subsurface currents were coherent, flowing either 'southwards' or 'northwards' relative to the nearshore currents. Current measurements in the very nearshore almost always opposed the dominant subsurface offshore directions. For Factor 3, relative subsurface current speeds were highest at Black Rock.

Each day and time of current measurement was plotted according to its Factor 1 and Factor 2 loadings (Figure 4.13). The current measurements were compared to satellite images from the day closest to that on which the currents were measured. Of these four images, three had positive Factor 1 loadings (19 September 02, 14 December 02 and 1 December 03), while the fourth (16 August 03) had a negative Factor 1 loading in the EOF for both the whole data set and for the data split into summer and winter seasons. In the plots of the current velocity factors in Figure 4.13, the August 2003 velocity measurements were set slightly apart from the other dates.

Larval density and alongshore current speeds

When the densities of meroplanktonic larvae were compared with along- and across-shore current speeds on the day of sampling (Table 4.6), cyprids emerged as negatively related to alongshore currents (Figure 4.14a), indicating that they were most dense in faster, southward-flowing subsurface water. In contrast, the total zooplankton pool was denser in northward-flowing water, although this relationship was never significant. There were few significant relationships between meroplanktonic larvae and across-shore currents, and the sign of the relationship varied among taxa, zones and depths. Cyprids were always negatively associated (e.g. Figure 4.14b), indicating higher densities in water flowing towards shore. Conversely, the zooplankton pool was denser in onshore-flowing surface water and offshore-flowing deeper water. Mytilids were not significantly related to either alongshore or across-shore currents (e.g. Figure 4.14c,d).

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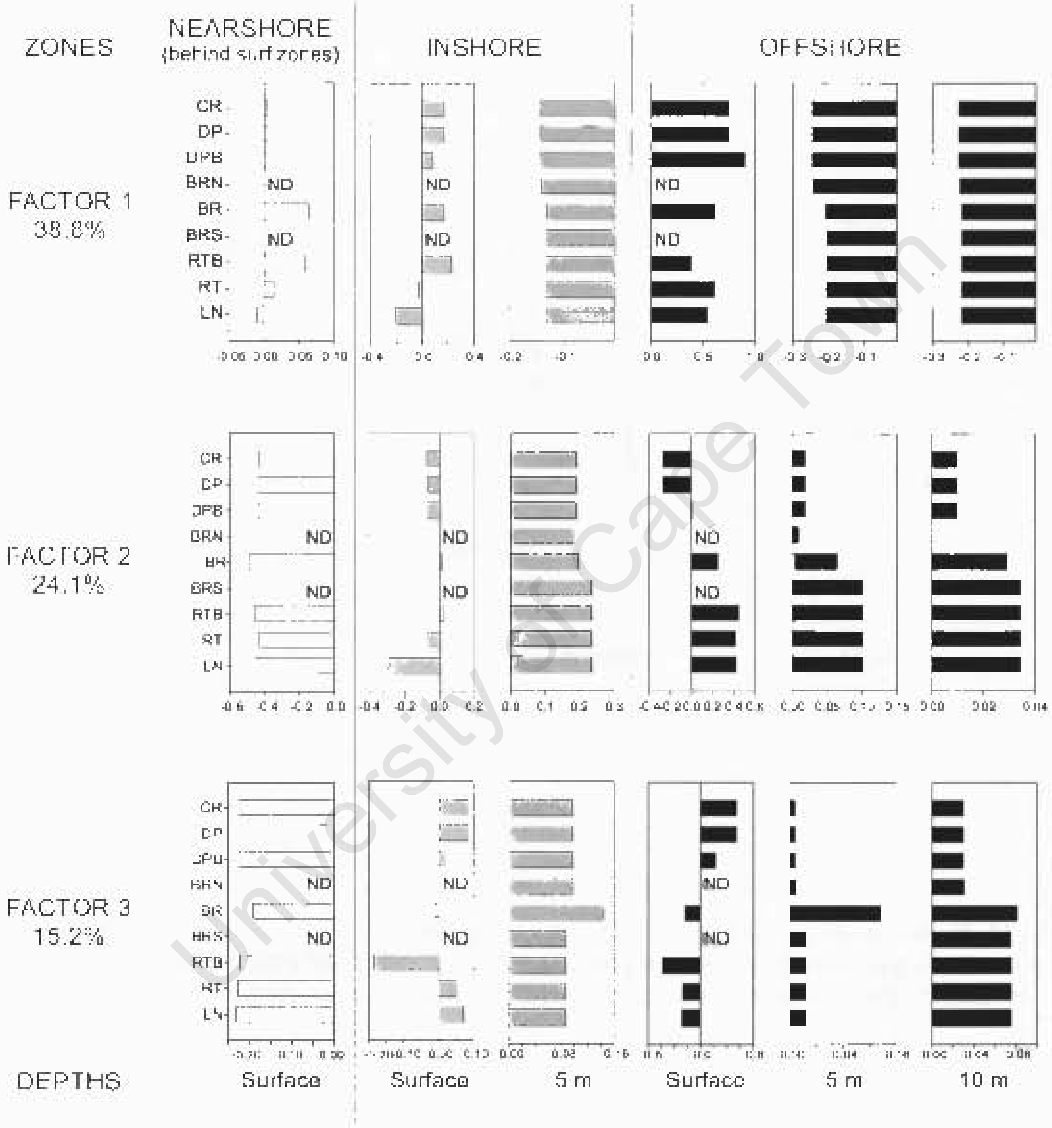

Figure 4.12 Factor loadings of the three most important factors from EOF of hourly measurements showing *relative* shear of currents in Maputaland during drogue and videography data collected in 2002 and 2003. ND = no data
Station codes: CR (Castle Rock), DP (Dog Point), DPB (Dog Point Bay), BRN (Just north of Black Rock), BR (directly offshore Black Rock), BRS (just south of Black Rock), RTB (Rocktail Bay), RT (Rocktail Point), LN (Lala Nek).

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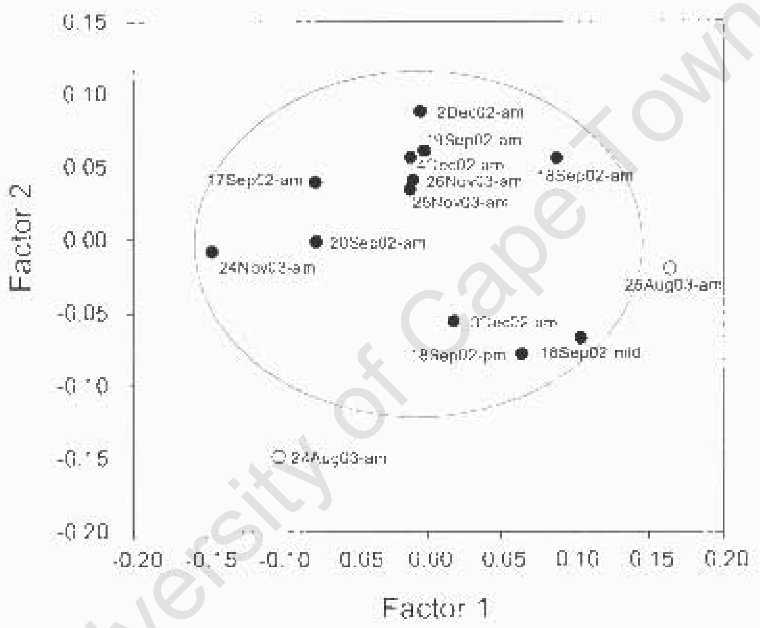

Figure 4.13 Factor loadings for dates of current measurements. Dates with positive Factor-1 loadings for the temporally closest satellite image from the SST EOF analysis are marked with a black dot and circled, those with a negative factor loading are marked with a white dot.

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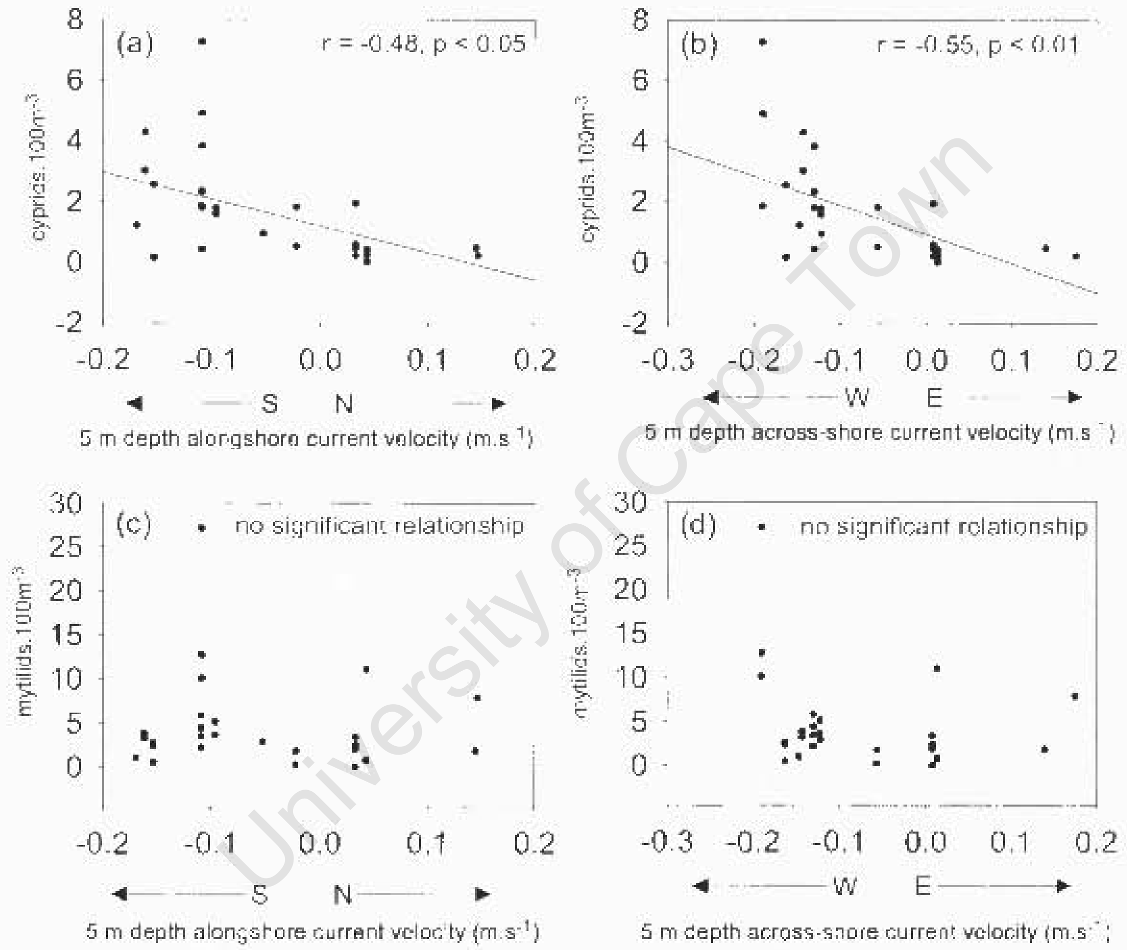

Figure 4.14 Selected relationships between meroplanktonic larval densities (from Chapter 3) and along- and across-shore current speeds measured in the same day, station and zone.

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Table 4.6 Correlations between larval densities (Chapter 2) and along- and across-shore current speeds at depths and within zones. Correlations between cyprids and surface currents were not tested (X), as cyprids are generally not found in surface waters in Maputaland (Chapter 2). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns – not significant.

		Larval taxon	Zooplankton	Mytilids	All bivalves	Cyprids
Current Direction	Measurement depth	Units	ml.100m^{-3}	no.100m^{-3}	no.100m^{-3}	no.100m^{-3}
Alongshore	Surface	r	-.0565	-.2036	-.2585	
		n	20	20	20	X
		p	ns	ns	ns	
	2 m	r	.4305	.4258	.2171	-.3497
		n	9	9	9	9
		p	ns	ns	ns	ns
	5 m	r	.2827	-.1144	-.2160	-.4780
		n	27	27	27	27
		p	ns	ns	ns	*
	10 m	r	.3255	-.0329	-.4817	-.6468
		n	15	15	15	15
		p	ns	ns	ns	**
Across-shore	Surface	r	-.4378	.2156	.3888	
		n	20	20	20	X
		p	ns	ns	ns	
	2 m	r	.4511	.4083	.1200	-.4341
		n	9	9	9	9
		p	ns	ns	ns	ns
	5 m	r	.3809	-.2587	-.3743	-.5467
		n	27	27	27	27
		p	*	ns	ns	**
	10 m	r	.2907	-.0599	-.3764	-.4592
		n	15	15	15	15
		p	ns	ns	ns	ns

Dispersal models for mostly-passive drifters in Maputaland

Histograms of the empirical current velocities in each depth and zone for all measurement days are presented in Figure 4.15. In the swash and first surf zones, currents were generally low-speed and northward. In all other zones and depths, however, currents were either evenly distributed between northward and southward or were predominantly southward. For the inshore and offshore surface currents, the distributions were slightly bimodal, with fewer measurements of lower current speeds than of intermediate ones. Maximum speeds increased with distance offshore and decreased with depth.

The majority of drifters in the model traveled south after their release, although some did travel north in all five scenarios outlined in the methods (Figures 4.16 and 4.17). The maximum southward distances were approximately four times the northward. The standard deviations and maximum distances became larger for particles with longer PLDs (Figure 4.17), and the model results for particles with longer PLDs were more normally distributed (Figure 4.16). For particles that remained in the middle of the water column, scenario (b), mean (± SD) dispersal values for particles of 10 and 22 d PLDs were 36 ± 25 and 95 ± 56 km to the south, respectively, while values for particles remaining only at the surface, scenario (a), traveled farther (43 ± 90 and 116 ± 227 km to the south, respectively). Thus, remaining in middle water depths appears to limit dispersal

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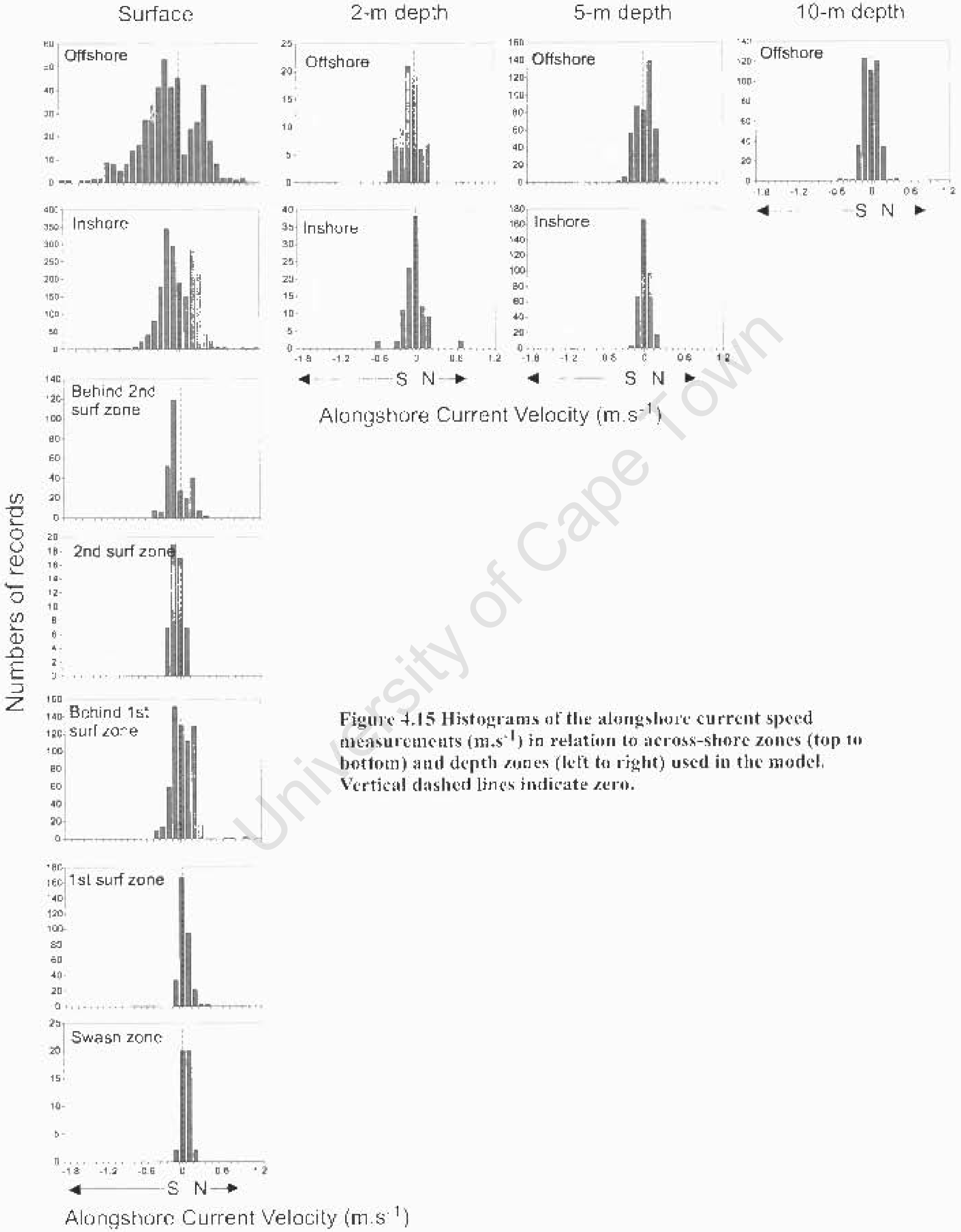

Figure 4.15 Histograms of the alongshore current speed measurements ($m.s^{-1}$) in relation to across-shore zones (top to bottom) and depth zones (left to right) used in the model. Vertical dashed lines indicate zero.

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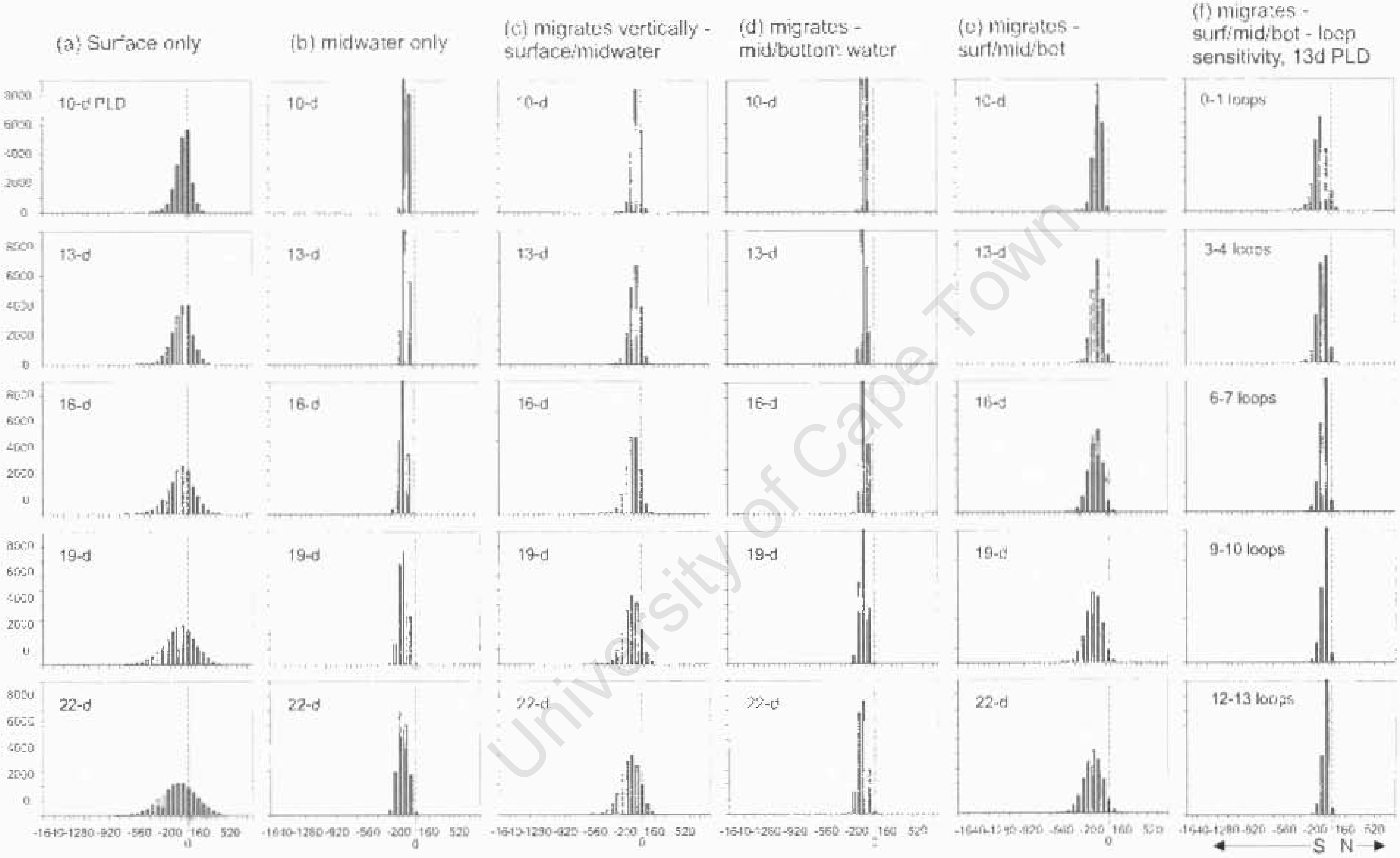

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Figure 4.16 (a-e) Dispersal kernels (km north or south) from alongshore advection models for passive drifters of 10, 13, 16, 19 and 22-d planktonic larval durations (PLD) that successfully return to (or remain in) the swash zone. n = 19180 for each histogram. (a) offshore drifters remain at surface; (b) offshore drifters remain in midwater; (c) offshore drifters migrate vertically between surface and middle depths; (d) offshore drifters migrate vertically between middle and bottom depths; (e) offshore drifters migrate vertically between surface, middle and bottom depths; (f) sensitivity of model to nearshore loops: histogram outputs from passive drifters of 13-d PLD, using scenario (e) and varying number of nearshore loops each drifter does in the model before leaving the nearshore.

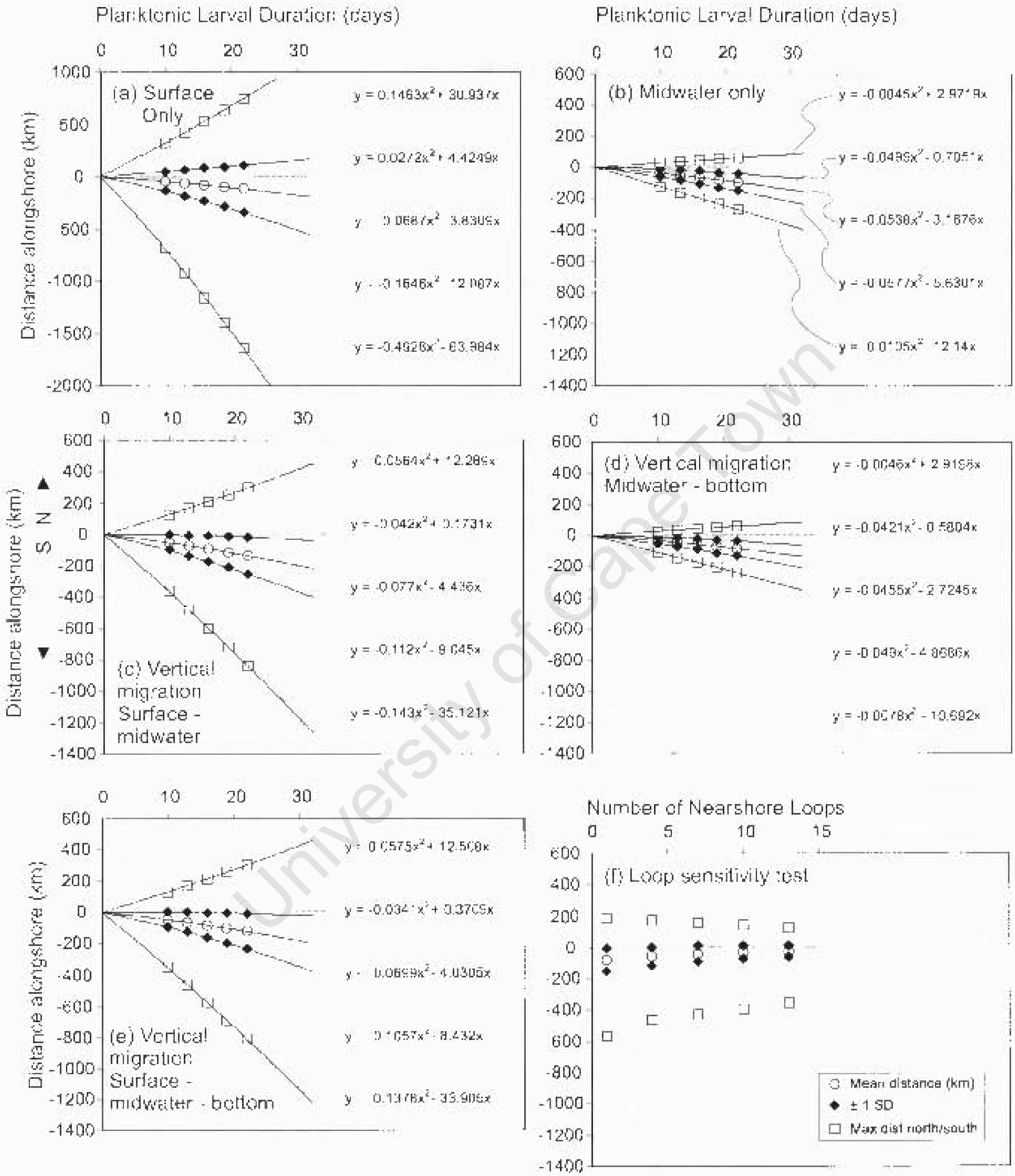

Figure 4.17 (a-e) Outputs from alongshore advection models for passive drifters of 10, 13, 16, 19 and 22 d planktonic larval durations (PLDs) that successfully return to (or remain in) the swash zone: mean ± 1 SD and maximum values. Negative values are southward, positive values are northward. Equations are second-order polynomials fitted to data, each with an intercept of zero: (f) sensitivity of model to nearshore loops: histogram outputs from passive drifters of 13-d PLDs in scenario (e), varying number of nearshore loops each drifter before moving into the inshore.

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distance and also allows fewer particles to travel north, while remaining at the surface vastly increased dispersal and allowed a higher percentage of northward travel (Figure 4.17).

Migration between layers (scenarios c-e) did not consistently result in intermediate dispersal distances. The shortest dispersal distances were for particles migrating between the middle and bottom layers (30 ± 22 and 81 ± 48 km to the south, respectively), and dispersal distances were comparable to those in scenario (a) for particles migrating through the middle and top layers (scenario c), 50 ± 49 and 112 ± 100 km to the south, respectively, and through all three layers (scenario e), 16 ± 47 and 122 ± 114 km to the south, respectively.

Dispersal distance was very sensitive to the number of nearshore loops, as retention in the nearshore prevented particles from joining the faster (and more southward-flowing) offshore surface and benthic currents, but the relationship between number of loops and the mean dispersal distance was nearly linear (Figure 4.17f). The number of particles that remained within one km of the headland where they were released (i.e. 'self-recruiting') was very low (≤ 3%), even when a high percentage of particles were entrained in the nearshore, but was never zero (always > 0.5%), even when the number of nearshore loops was reduced to 0-1 (Table 4.7).

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Table 4.7 Retention of passive particles in model.

Scenario	Depth offshore	Drifter life span (days)	Near-shore loops	Retained in nearshore	Self recruiting
(a)	Surface only	10	1-4	4.87%	2.79%
		13		2.02	1.57
		16		0.70	0.88
		19		0.00	0.44
		22		0.00	0.38
(b)	5-10 m only	10	1-4	4.87	3.03
		13		2.02	1.67
		16		0.70	0.92
		19		0.00	0.54
		22		0.00	0.44
(c)	Vertically migrating between surface and 10 m	10	1-4	4.87	2.71
		13		2.02	1.57
		16		0.70	0.88
		19		0.00	0.51
		22		0.00	0.43
(d)	Vertically migrating between 5 m and bottom	10	1-4	4.87	3.05
		13		2.02	1.73
		16		0.70	0.99
		19		0.00	0.65
		22		0.00	0.51
(e)	Vertically migrating through full water column	10	1-4	4.87	2.90
		13		2.02	1.61
		16		0.70	0.88
		19		0.00	0.52
		22		0.00	0.40
(f)	Vertically migrating through full water column	13	0-1	0.00	0.55
		13	3-4	4.07	2.63
		13	6-7	18.01	7.37
		13	9-10	27.47	12.97
		13	12-13	36.96	19.55

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4.4 DISCUSSION

Meso-scale hydrographic patterns and their influence on recruitment

There was an evident relationship between meso-scale patterns of SST variability and mussel and barnacle recruitment in Maputaland, the key features of which are synthesized in Table 4.8. Varying modes of Agulhas Current formation, as well as the relative temperatures of the inner-shelf versus oceanic water, may drive this relationship. Models of the offshore/onshore transport of meroplanktonic larvae have previously linked temperature-related patterns of nearshore hydrography to recruitment dynamics (Roughgarden et al. 1991a), and remote sensing has been employed to investigate temporally-variable features in the nearshore environment as they relate to coastal transport processes for meroplankton (Roughgarden et al. 1991b). Other studies have reported relationships between nearshore-hydrography and recruitment dynamics across latitudinal gradients (Navarrete et al. 2005) or gradients of upwelling intensity and productivity (Menge et al. 2003; Broitman et al. 2005). However, these studies have all taken place in strongly upwelled west-coast systems.

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Table 4.8 Synthesis of relationships between recruitment rates and meso-scale oceanic factors, as measured in EOF analysis

Species	*Perna perna*	*Brachidontes semistriatus*	*Chthamalus dentatus*	*Tetraclita* spp.
Recruitment Substrate	Brushes	Brushes	Bare Rock & Plates	Bare Rock & Plates
Recruitment season (Chapter 3)	Summer	Summer	Summer	Winter
Associated recruitment processes (Chapter 3	For all species, seasonal effects were more important that temperature-related events on shorter time scales			
Associated larval processes (Chapter 2)	Bivalve larvae more abundant in warmer water poorer in phytoplankton		Cyprids more abundant in cooler water richer in phytoplankton	
Factor 1 important (inshore water flows from Mozambique Channel)	Yes	Yes (strong association)	Yes*	Yes
Loading on Factor 1 is positive (cooler coastal than oceanic water)	Yes	Yes	No	No
Factor 2 important (inshore water from Mozambique Channel is blocked)	No	Yes (weak association)	No	No
Loading on Factor 2 is positive (cooler coastal than oceanic water)	--	Yes	--	--

* No relationship when settling on plates

Both Factor 1 and Factor 2 emerged as important in the EOF analysis. Whether a satellite image had a strong loading for either factor was related to the water masses that converged to form the Agulhas Current on that date. Images with strong Factor 1 loadings appeared very linear, a pattern that portrays the direct nearshore input of water from the Mozambique Channel. Images with strong Factor 2 loadings, in contrast, showed an eddying pattern that indicated a disruption of flow out of the Mozambique Channel, whereby the Agulhas was formed predominantly by its other water sources, the East Madagascar Current and the westward limb of the Indian Ocean subtropical gyre (Donohue and Toole 2003).

The predominantly southward current along this coastline indicates that the pool of larvae that is delivered to Maputaland must originate to the north. Of the three water masses that join to form the Agulhas Current, only water from the Mozambique Current or the East Madagascar Current could recently have been near a coastal environment. Of these, only water from the Mozambique Current could be carrying competent larvae of short to medium planktonic larval durations that might successfully recruit in Maputaland. Thus, water flowing southward from coastal Mozambique that is trapped along the coast and undiluted by waters from the other two currents (as in Factor 1) is most likely to bring high concentrations of coastal larvae southward without dilution of the larval pool. For all four mussel and barnacle species, recruitment rates were highest when the satellite image had a strong Factor 1 loading (synthesis, Table 4.8). Thus, elevated recruitment rates in Maputaland may be due to a successful delivery of propagules from the eastern Mozambique channel.

The second pattern revealed by EOF analysis related to the temperature gradient between coastal and oceanic surface water (Table 4.8). If an image had a positive factor loading for either Factor 1 or Factor 2, coastal water was cooler than oceanic surface water (Figures 4.8 and 4.9). If an image had a negative factor loading for either factor, then the coastal water was warmer than the offshore water. The generally positive loadings of Factor 1 associated with the recruitment of the mussels *Perna perna* and *Brachidontes semistriatus* during the summer (the mussel recruitment season) suggest that recruitment was enhanced both by a reduced mixing between the Mozambique and East Madagascar Currents and also by relatively cooler nearshore water (Figure 4.10). The positive loading of *B. semistriatus* recruitment densities onto Factor 2 indicates that some mixing of waters may also have enhanced recruitment, provided that cooler water was still maintained inshore. The generally negative loadings on Factor 1 for recruitment for both *Chthamalus dentatus* (in summer) and *Tetraclita* spp. (in winter) imply that recruitments of barnacles were enhanced by warmer inshore water in addition to a reduced mixing of the currents.

These results might appear to contradict those found in Chapter 2, wherein the abundance of cyprid larvae in the water column was *negatively* associated with benthic temperature, while both all-bivalve and mytilid larvae were *positively* associated with benthic temperature (see synopsis in Chapter 3, Table 3.9). These results are not, however, contradictory, as the temperature

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measurement in Chapter 2 explained the seasonal component of temperature, whereas the factor loadings from the satellite images explained temperature patterns that exclude seasonality and are related to relative spatial temperature variability. In Chapter 3, recruitment of *C. dentatus*, *B. semistriatus* and *P. perna* were all enhanced by cooler mean temperatures and *P. perna* recruitment was also correlated with negative (cooler) temperature anomalies, which does correspond to the negative Factor 1 loadings for these species.

The recruitment of *Tetraclita* spp. onto different substrates was inconsistently related to temperature in Chapter 3, with recruitment onto plates positively correlated with temperature and negatively with temperature anomaly, and recruitment onto bare rock negatively correlated with temperature and not significantly correlated with temperature anomaly (Chapter 3, Table 3.9). This was reflected in the factor loadings for this taxon, with a much clearer association with warmer inshore temperatures for recruitment onto plates than for bare rock in either zone.

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Does the Agulhas Current dominate inner-shelf hydrography in Maputaland?

Dominant patterns of meso-scale sea-surface temperature (SST) variability were revealed in the EOF analysis and varied temporally (Figures 4.8 and 4.9). In strongly upwelled regions such as the Benguela Current system on the west coast of South Africa, wind-induced Ekman transport can drive meso-scale longitudinal temperature gradients with an obvious signal in remotely-sensed SST (e.g. Demarq et al. 2003). However, only weak onshore and offshore Ekman transport was evidenced in Chapter 2, and winds that might induce offshore Ekman transport were not highly correlated with the remotely-sensed larger-scale SST patterns in this chapter. Even in strongly upwelled systems, alongshore hydrography on the inner shelf is largely independent of essentially slow-moving across-shore transport events such as upwelling driven by offshore Ekman transport (Mann and Lazier 1996). This suggests that inner shelf currents in Maputaland are independent of meso-scale hydrography, including the formation of the Agulhas Current. This view is supported by evidence that instead links currents velocity with wind and tides as drivers, standard mechanisms in other inner-shelf systems. While the varying modes of Agulhas Current formation may influence recruitment rates via nutrient and larval supply, it is unlikely that they influence smaller-scale transport processes such as alongshore current direction and speed, and onshore-offshore transport mechanisms.

The Agulhas Current, although very near the inner shelf in Maputaland, has a reduced effect on nearshore hydrography because the coastal boundary layer modifies the effects of mechanisms that influence current velocities. Shanks (1995) reviews several elements of the coastal environment that contribute to the formation of the coastal boundary layer. Firstly, cross-shore momentum is absorbed or diverted into alongshore components when met with the coastline boundary. This translation can cause eddies in the coastal currents, stretching parallel to the shore. In addition, friction and dissipation are stronger in shallower depths, slowing currents. Strong stratification can lead the formation of features such as coastal jets. Finally, factors such as runoff and solar heating in the shallowest water can cause thermohaline flow. Of these, neither strong stratification (Chapter 2) nor runoff or riverine inputs (Sink 2001) are common in Maputaland.

Inner-shelf hydrography and current variability

The three most important factors in the EOF analysis of current variability involved inshore counter-currents or strongly sheared currents as part of their across-shore pattern, whether the dominant offshore current direction was southwards (Factor 1) or northwards (Factors 2 and 3). Both northward and southward currents were observed in the 10-15 m depth range, and varied with alongshore wind direction.

These results agree with previous studies along the KwaZulu-Natal coast, all of which have indicated that northward dispersal is possible despite a mean southward advective flow, via either current reversals or nearshore counter-currents. First, Steinke and Ward (2003) released passive drifters resembling mangrove propagules at a river mouth near Richards Bay and demonstrated that 18% of these traveled northwards inshore of the Agulhas Current. Second, over a 5-day study by Jury et al. (2001), the only evidence of a nearshore eddy was a drogue closest to shore, which revered its trajectory from north to south. Third, Mitchell et al. (2005) recorded 8% southeastwards currents, 28% northeast, 54% northwest, and 10% southwest. In my study, alongshore currents in the surf and swash zone were more often southwards than in results reported by Jury et al. (2001) and Mitchell et al. (2005), but this could be explained by the strong northerly winds experienced on many of the sampling days.

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Larval density and alongshore current speeds

Although it has long been assumed that fast-swimming meroplanktonic larvae may move against the dominant current (Shanks 1995; Genin et al. 2005), it is unlikely that even slow-swimming or non-swimming larvae act as completely passive drifters (Shanks and Brink 2005). Recent evidence suggests that veligers of at least some bivalves can remain near the coast in the presence of both up- and downwelling conditions (Shanks et al. 2002, 2003c; Shanks and Brink 2005). To predict the along- and across-shore advection of larvae by currents, we must understand the associations between meroplanktonic larvae and current speeds on the inner shelf.

In the quest to identify the onshore-transport mechanisms at specific locations, most previous studies relating larval concentrations to current speeds focus on the associations between the meroplanktonic larvae of various taxonomic groups and the across-shore component of wind, tide, or internal wave-generated transport on the inner shelf measured *in situ* (e.g. Shanks 1998; Shanks et al. 2000; Garland et al. 2002; Shanks et al. 2002; 2003b). Some studies have also examined the relationship between larvae and the alongshore component of *in situ* current velocities (e.g. Johnson 1995; Archambault and Bourget 1999; Garland and Zimmer 2002; Shanks et al. 2002;

Shanks et al. 2003b). In my study, cyprids had the strongest correlations with both the along- and across-shore components of current velocities, being associated with southward and onshore-flowing water. In his investigation of the distribution of post-larval crabs and shrimp at Duck, North Carolina, USA, Shanks (1998) found relationships between larvae and cross-shore currents that differed among genera, time lags (days) and measurement depths. For two genera, significant negative relationships existed with cross-shore currents at 4-m depth (more individuals in onshore flows); for one genus, a significant positive relationship was detected with cross-shore currents at 18-m depth (more individuals in offshore flows); for another genus, a significant positive relationship existed with alongshore currents (more individuals in northward flows); for a final genus, no relationships were evident with any current measurements.

Two subsequent studies at Duck have investigated the relationship between current velocities and the densities of various invertebrate taxa during downwelling and upwelling events. In an analysis of a downwelling event in August 1994, Shanks et al. (2002) studied several bivalve species and found varying relationships with along- and across-shore flows. The veligers of the mussel *Mytilus edulis*, for example, were significantly positively correlated with cross-shore flow (more larvae in offshore-flowing water) and with depth, and significantly negatively correlated with depth and with temperature, but had no significant relationship with alongshore flow. Larvae from *M. edulis* were found both above and below the pycnocline, and were hypothesized to act as passively drifting particles. In an upwelling event during the same period, Shanks et al. (2003b) found *M. edulis* to be uncorrelated with across-shore flow, depth and temperature, but positively correlated with alongshore flow (more larvae in northward-flowing water). In both studies, the densities of *M. edulis* larvae differed from those of other bivalve species (mostly clams) in terms of their correlations with physical environmental variables, and their correlations with both along- and across-shore flows were different during upwelling and downwelling events. Thus, the relationships of individual taxa with their physical environment can differ according to the larger-scale hydrographic climate (e.g. upwelling *vs.* downwelling). A spatially-explicit understanding of these relationships is essential to interpret advective and diffusive mechanisms, and further study will be required before these data can be incorporated into a more comprehensive model of larval dispersal.

Dispersal models for mostly-passive drifters in Maputaland

The real advection of larvae is weaker than anticipated and diffusion is stronger than predicted in many models of larval dispersal (Largier 2003). Largier (2003) adds that two-dimensional (alongshore) models of larval transport often ignore the cross-shore component, an essential aspect of dispersal. Coupling alongshore and cross-shore dispersal therefore results in a more realistic (and nonlinear) relationship between alongshore dispersal distance and larval planktonic duration. Advective models (e.g. Roberts 1997) and stochastic Lagrangian descriptions

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(e.g. Siegel et al. 2003) of larval dispersal have been previously employed to gain understanding of the potential connectivity of coastal environments, and are valuable for the ease with which they may be compared with field-based observations (Siegel et al. 2003). Although my model does not incorporate specific cross-shore transport mechanisms, it does incorporate the coupling between across- and alongshore dispersal in sheared nearshore flows, as well as the retentive nature of slowed currents within the bays along the nearshore region of the coastal boundary layer (Largier 2004). However, my model probably overestimates alongshore larval displacement, as it neglects the effects of vertically sheared flow within 1 m of the bottom, diffusion and the role of larval behavior in controlling along- or across-shore travel by modifying the time a larva will spend at any depth (Largier 2003, 2004). Nevertheless, the increase in downstream alongshore dispersal that I detected with increased planktonic larval duration (PLD) agrees with most (but not all) previous analyses (Largier 2003; Shanks et al. 2003a; Siegel et al. 2003). In their more complex stochastic Lagrangian model, Siegel et al. (2003) predicted a Gaussian distribution for the dispersal trajectories for pre-competent planktonic larval durations of 5 and 42 d. The estimates of dispersal in my model for particles of shorter planktonic duration more closely resembled a Poisson distribution due to the extra nearshore retention built into my model, but my model became more Gaussian with longer larval durations. The flow field in the analysis by Siegel et al. (2003) comprised a current of 0.05 m.s^{-1} with stochastic fluctuations of $\pm 0.15 \text{ m.s}^{-1}$, and their mean dispersal values for larvae of short and long duration were 8 km and 208 km downstream, respectively. My study site meets their assumption of a straight coastline and my current measurements and model outputs fall within their ranges of values.

My model assumes that alongshore currents switch in a nature that is stochastic from the perspective of the larva, so there is an equally probable chance of encountering any current velocity and direction in any zone, regardless of what the current was in the previous zone. However, analyses in Chapter 2 revealed that alongshore winds (which are strongly linked to alongshore currents and changes in subsurface temperature) do reverse at regular intervals (4-5 days) during the spring and summer (Chapter 2, Table 2.7). Because current measurements were always restricted to four consecutive days, these measurements cannot reveal the extent to which the system is event-dominated (i.e. its stationarity). For this, more detailed analysis of continuous current measurements, such as the ADCP data, would be required. If there was a high level of stationarity in this system, the model might be modified to predict the probability with which a drifter would encounter currents of the same direction and similar speed as it moved into each subsequent zone.

My model also assumes that larvae are retained in the nearshore for some of their duration in the plankton, but not all of it. This assumption is currently being examined in Oregon, but there are no results to date (A.L. Shanks, pers. com.). Some researchers believe that the surf zone is a dangerous and stressful place for early-stage larvae, who can be damaged by the turbulence and the presence of air bubbles in the water, driving larvae to eject themselves as quickly as possible through the surf zone and into the relatively calmer water offshore (A.L. Shanks, pers. com.). However, experiments measuring dye or pollution released from shore have shown that the surf zone effectively entraps particles in the very nearshore (Grant et al. 2005), and so other researchers believe that the surf zone could be an important mechanism for retaining early larvae in the very nearshore (J.L. Largier, pers. com.).

Further investigation involving experimentation and more complex mathematical modeling would be required to verify whether my empirically-derived semi-stochastic Lagrangian model will accurately predict the advective component of larval dispersal. Nevertheless, it is reasonable to assume that the net transport of the majority of meroplanktonic larvae, if they do leave the nearshore zone, will travel southward a distance less than the mean value predicted by the advective models. In the case of a larva with a 16-day PLD, the mean dispersal distance would be less than 63 km south, with limited dispersal to the north (Figure 4.17), well within the boundaries of the Greater St. Lucia Wetland Park, but beyond the study area. It is possible, then, that this net southward displacement of the passive drifters, with limited northward travel, may explain the higher bivalve larval densities and bivalve recruitment at Lala Nek and Rocktail Point recorded in Chapters 2 and 3, respectively, as these regions lie south of the largest population of potential spawners at Black Rock.

In my dispersal model I assumed that no successful drifters would enter the Agulhas Current, although it is likely that some larvae will do so, whether by advection or diffusion. As noted above, Steinke and Ward (2003) dropped drift cards into an estuarine river mouth in Maputaland. Their results both corroborated the output from my model and explained the fate of larvae not considered in my model: those that disperse too far offshore and into the Agulhas Current. While the cards used by Steinke and Ward (2003) were substantially larger than the larvae considered in my study, they were passive drifters of neutral buoyancy. As they were released on an outgoing tide, it is likely that many were ejected in a jet through the surf zone and into the inshore currents, and their trajectory can be compared to my passive drifters after their release from circulation in the nearshore environment. Of the cards recovered, 18% traveled north (perhaps having remained in the nearshore zone, or in northward currents in the inshore), 12% were recovered within 2-3 km of the river mouth (perhaps never having drifted out of the nearshore and being quickly deposited back onto the beach), and the remaining 70% traveled south. Although 32% of the southward-traveling drift cards remained within KwaZulu-Natal, others traveled very quickly south, presumably having entered and been carried in the swift Agulhas Current. Four cards came ashore 700 km to the south after 14-15 days, i.e. within the expected lifespan of a mussel larva, providing evidence of a potential (if rare) long-distance connection between Maputaland mussels and those on rocky shores far to the south. This potential long-distance dispersal of meroplanktonic larvae in South Africa is supported by the lack of coast-wide genetic heterogeneity of *P. perna* (Grant et al. 1992).

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Implications for size and spacing of no-take areas in Maputaland

The entirety of the South African section of the Delagoa marine bioregion, extending from Cape Vidal to the Mozambique border, falls under protection as the Maputaland Marine Reserve under both the Greater St. Lucia Wetland Park World Heritage Site Authority and the conservation organization Ezemvelo KwaZulu-Natal Wildlife. The zonation of the MMR is currently under revision, and includes recreational-use and sanctuary areas. Nevertheless, there are, to date, no legislated no-take areas between Mabibi and the Mozambique border, as even 'sanctuary' areas are open to monitored, but unregulated subsistence-level harvesting. This is in conflict with the current best-practice advocated by conservation professionals in South Africa who emphasize ecosystem-based conservation via systematic protection of habitats and biotypes in every bioregion (e.g. Lombard et al. 2004; Pierce et al. 2005). There have been several reports detailing the type of impact subsistence harvesting currently has on rocky shores in Maputaland, with varying conclusions. Kyle et al. (1997a) argued that harvesting levels were sustainable, as the catch per unit effort of key organisms such as *Perna perna*, as well as oysters *Striostrea margaritacea* and *Saccostrea cucullata* and the tunicate *Pyura stolonifera* did not change over seven years of observation. However, Sink et al. (2005) noted that the harvesting offtake in Maputaland was 18 times higher than in the Natal bioregion to the south, and invoked harvesting as a covariant in the biogeographic separation of communities north and south of Cape Vidal. In my study at Black Rock (Chapter 3), adult mussel densities were much higher in the unharvested area than in the harvested section < 100 m away. Harvesting at current rates has altered adult mussel densities, with important implications for both rocky-shore communities (Lasiak 1999) and the supply of mussel larvae to the region (Chapter 2). Clearing experiments have shown that recovery of *P. perna* beds can take up to ten years (Dye 1992b, 1998; Dye et al. 1997), and often wholesale clearing of previously dense mussel beds (> 65% cover) results in the establishment of stable alternate communities comprising elements such as barnacles, macroalgae and bare rock (Lasiak and Dye 1989).

It is therefore possible that the stable state observed by Kyle et al. (1997a), which led them to declare offtake levels as sustainable, was one that had already been altered by years of harvesting, and low densities were being maintained by continued high harvesting levels, lending to a stable but suboptimal offtake. Also, the relatively high recruitment of *Brachidontes semistriatus* compared to *Perna perna* reported in Chapter 3 indicates high levels of disturbance in this area, as Lasiak (1999) demonstrated enhanced recruitment of *B. semistriatus* following removal of *P. perna* from the South Coast. Fisheries resources must be managed not for constancy of harvest, but for optimal sustainability. The harvesting of intertidal resources in South Africa is an ancient tradition, and the food gathered is nutritionally important for coastal communities, and optimization of the offtake should be an implicit goal of management (Siegfried et al. 1985; Hockey et al. 1988; Hauck

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and Sowman 2003; Griffiths et al. 2004). Many efforts are currently underway to regulate these fisheries in a way that is equitable and culturally appropriate (e.g. Branch et al. 2002a, b; Clark et al. 2002; Harris et al. 2002b; Hauck et al. 2002; Branch and Clark 2006). While formalization of the fishery is an important first step, the establishment of no-take areas in the Delagoa bioregion (i.e. north of Sodwana Bay) is essential to conserve representative ecosystems and to foster adult stocks that can provide propagules to harvested areas. Additionally, no-take areas provide benchmarks against which the effects of harvesting can be judged. One final added benefit of no-take areas is that they may encourage local community participation in conservation through education, as has been demonstrated in other areas within KwaZulu-Natal (Harris et al. 2003).

There is a wide range of issues that affect which management options are desirable for any protected coastal area, and my study offers some comment on the rocky-shore component of the coastline. My data provide some options for the size and spacing of no-take areas within the Maputaland Marine Reserve, based on projected dispersal distances for important harvested or habitat-forming rocky-shore organisms. Compiling meta-data on the life-spans and dispersal distances of 25 marine taxa, Shanks et al. (2003a) found a bi-modal distribution of dispersal distances, with a gap between 1 and 20 km. For propagules with planktonic durations of < 4.5 d, dispersal distances were < 1 km, whereas those that were planktonic for > 12.5 days generally dispersed > 20 km. In my study, passive drifters with planktonic larval durations of 10-22 days were modeled, representing the expected range of planktonic duration for mussels and barnacles in the region. Although mean dispersal distance for the propagules in every scenario in was greater than 20 km, even the modeled propagules with the longest life-spans had a few individuals (albeit < 1 %) that remained within 1 km of the release point. With decreasing PLD, an increasingly large number of drifters were both retained in the nearshore and self-recruited (Table 4.7), and one might imagine that a large proportion of drifters with very short PLDs (i.e. < 4 d) would never emerge from nearshore circulation into the inshore or offshore regions, reflecting the data for reduced dispersal reported by Shanks et al. (2003a). Largier (2003) supports this argument, adding that the diffusion component of larval transport can further mitigate advective transport to prevent 'wash-out' of even those species with intermediate PLDs such as those examined here.

Some particles traveled northward in all five of the scenarios I explored, despite a dominant southward alongshore current. The largest proportion of these occurred in the case of particles that remained only on the surface (Figure 4.17a). Byers and Pringle (2006) assert that 'upstream' travel by dispersing larvae is possible in advective environments via stochastic current reversals. In order to take advantage of this stochasticity, larvae must meet three observable criteria: (1) spawning over several seasons or years, (2) short pelagic period and (3) 'prodigious' larval production. My model agrees with their prediction that stochastic current reversals provide a mechanism for passive upstream drift, which could indeed be enhanced by larval behavior that increases associations with upstream currents. Additionally, my model confirms their second criterion for upstream travel, as

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particles with longer planktonic larval durations had proportionally fewer particles that were transported upstream (Figures 4.17 b-e).

Shanks et al. (2003a) used meta-data on larval dispersal distance and planktonic duration to recommend a framework for the spacing of sanctuaries along a coast. They suggest that reserves be of sufficient size that larvae with short planktonic durations may self-recruit, and that the reserves be spaced sufficiently closely along a coast to allow larvae with longer durations to disperse and settle into one or many downstream protected areas. They propose that reserves be at least 4-6 km in diameter and spaced ≤ ~20 km apart, resulting in a conservation target of 25% coverage of the coast. In the case of harvested species in the Maputaland Marine Reserve (MMR), such as that of the mussel *P. perna*, the desire is that both sanctuary and non-sanctuary areas must be replenished with propagules, to optimize fishing in the non-sanctuary areas. *P. perna* has an estimated planktonic larval duration (PLD) of 15-20 d (Table 4.4), and mussel larvae were found to be present at all depths (Chapter 2). In Maputaland, the modeled 13- and 16-day pre-competent passive drifters at all depths (Figures 4.16e and 4.17e) had mean (± SD) dispersal distances of 64 (± 63) and 83 (± 80) km, respectively. Barnacle cyprids, in contrast, were found mostly in the middle and bottom layers and have a likely PLD of 12-18 d at 25° C (Table 4.4). My model predicts that 13- and 16-day pre-competent passive drifters remaining at middle and bottom depths (Figures 4.16c and 4.17c) will have mean (± SD) dispersal distances of 43 (± 28) and 56 (± 35) km, respectively. If diffusion and larval behavior reduced the model's predicted distances by 50%, these estimates would fall between 32 (± 31.5) and 41.5 (± 40) km for mussels and 21.5 (± 14) and 28 (± 17.5) km for barnacles. Thus, 95% of the mussel propagules would travel 2-73 km south of the source, and 95% of the cyprids would travel 9-41 km south. The dispersal distance estimated for *P. perna* here is substantially less than the 235 km reported by Hicks and Tunnell (1995). However, their method consisted of tracking the invasion of *P. perna* in the Gulf of Mexico, recording the furthest distances individuals successfully dispersed. Their estimation does fall within the maximum downstream dispersal estimated by my model for mussel propagules (450 km).

In Maputaland, hard substrate is limited, with rocky headlands of < 1 km length regularly spaced 4-7 km apart. Although the Maputaland Marine Reserve (MMR) is currently protected from recreational and commercial harvest of all coastal species, subsistence harvesting still occurs at varying levels along its entire length, with important community effects (Kyle et al. 1997a, Chapter 3). Results from my model can be used to imagine various scenarios for the spacing of no-take areas within the reserve that would allow self-recruitment and connectivity from protected to unprotected areas. For example, if the recommendations of Shanks et al. (2003a) were to be used without modification, this would entail closing approximately every fourth headland to all harvesting. In my model, barnacle propagules were estimated to disperse, on average, 5 km farther than the minimum 20 km established by Shanks et al. (2003a), and mussels 10 km farther than that. Additionally, rocky substrate is limited: within any 4-6 km of contiguous coastline available for

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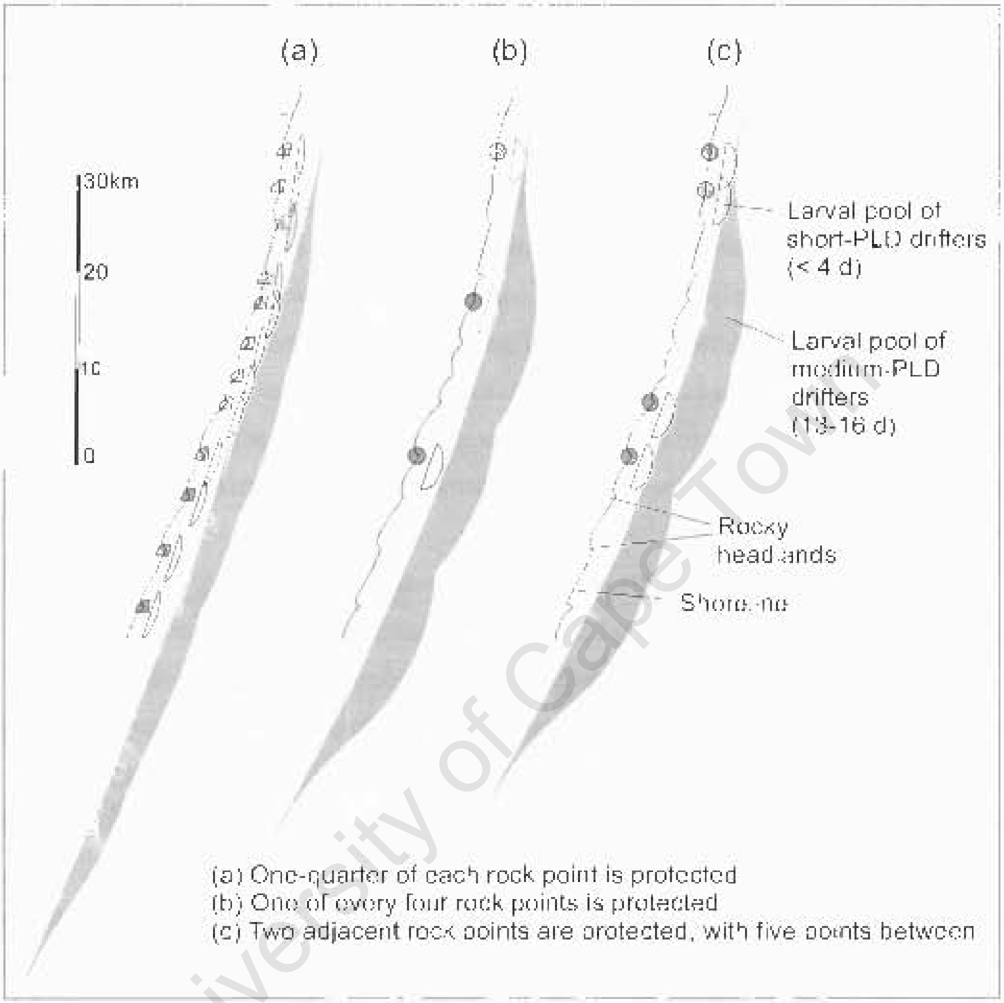

(a) One-quarter of each rock point is protected
(b) One of every four rock points is protected
(c) Two adjacent rock points are protected, with five points between

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Figure 4.18 Three alternate options for placement of no-take areas based on larval dispersal kernals (grey circles for (b) and (c), one-quarter circles for (a)), with predicted dispersal kernels for medium-PLD drifters (grey areas) and for short-PLD drifters (white half-circles). The relative advantages and disadvantages of each scenario are discussed in the text.

4.5 CONCLUSION

Rocky shores in the Maputaland Marine Reserve are connected, and this connectivity is not unidirectional. However, the movement of propagules that emerge from the nearshore environment will be generally southward. Estimating the connectivity of rocky shores enhances our understanding of population dynamics and improves our ability to protect and conserve both individual species and communities. However, this first requires knowledge of linkages and how they are affected by both local and meso-scale phenomena. In this chapter, inshore currents behind the surf zone were predominantly (but not exclusively) southward. Meso-scale hydrography was found to influence larval supply, as the varying confluence of the three water masses that create the Agulhas Current probably controls the arrival of larvae from coastal Mozambique. However, smaller-scale processes such as current speed and direction on the inner shelf were strongly influenced neither by the source of the upstream water masses nor by the proximity of the Agulhas current, but rather by wind and tides. This is consistent with patterns seen in other nearshore systems throughout the world.

Although sheared currents were common, there was little evidence of retentive eddying within the shallow bays. When empirical current measurements in the nearshore zones were used to produce a Lagrangian model of larval dispersal, however, dispersal kernels provided evidence for nearshore retention, self-recruitment and upstream advection despite a predominant southward flow. These models can be used to strategically place no-take areas within the current Maputaland Marine Reserve protection scheme, and some examples of their application are provided in this chapter. The establishment of no-take areas, in conjunction with controls in the harvested areas, would increase the spawner biomass of targeted animals, augmenting the density of propagules to areas that remain open to harvesting, with a further advantage being the provision of baseline area for education and research.

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SYNTHESIS

In this thesis, I address mussel and barnacle recruitment in southern Africa at multiple spatial and temporal scales, relating them to both bottom-up and top-down processes including larval and adult abundance and local hydrography and productivity. Recruitment can have important effects in both the short and long-term structure of rocky shore communities (Berry 1978; Connell 1985; Menge 1991; Caley et al. 1996; Forde and Raimondi 2004; Schiel 2004). Both adult populations and recruitment are influenced by bottom-up factors such as local and meso-scale hydrography and top-down processes such as predation and competition (Menge 1995; Menge et al. 1997b, 1999, 2003; Connolly and Roughgarden 1999b; Menge 2000b; Wieters 2005; O'Connor et al. 2006). Their relative strength will differ among sites, populations and regions, as will their influence on species and on species assemblages (Botsford et al. 1994; Botsford 2001; Connolly et al. 2001; Menge et al. 2002; Navarrete et al. 2005; Wieters 2006). They will also vary temporally, from scales of days to decades (Connolly and Roughgarden 1999a; Wing et al. 2003; Tapia et al. 2004; Vargas et al. 2004; Ladah et al. 2005; Alfaro 2006b). Understanding recruitment dynamics and the ways that they vary in specific regions, and then scaling-up our understanding using both inference and large-scale comparative experimentation allows us to create and test theories about the generality of these processes, the scales at which they operate, and the ways in which they shape our natural world (Harris et al. 1998; Hughes et al. 2002; Menge et al. 2002; Rivadeneira et al. 2002; Wieters 2006). Ultimately, there are two types of benefits from these investigations. The first is theoretical, as each experiment allows us to further understand or challenge existing paradigms. The second is applied, as the increasingly general theories and resultant predictive ecological models assist us to become more strategic in the conservation, protection and management of species, communities and habitats sensitive to the ever-mounting threats of human population density and climate change.

The southern African coastline, with its gradients of physical and biological features, has proved ideal for geographic comparative studies spanning multiple bioregions (e.g. Bustamante 1994; Bustamante et al. 1995a, 1997; Bustamante and Branch 1996; Hammond and Griffiths 2005; Lawrence 2005; Sink et al. 2005; Wieters 2006). In Chapter 1, I examined mussel recruitment patterns at a biogeographic scale spanning southern Africa. A synergistic combination of meso-scale hydrographic features and nearshore productivity explained 62% of the variation in mussel recruitment into mussel bed. As the mussel species assemblages differed among locations, the biology of the individual species was also important in explaining recruitment variability. In particular, mussel bed complexity, fecundity and adult competitiveness in the mussel bed all have the potential to influence recruitment. The roles of the invasive species *Mytilus galloprovincialis* and *Semimytilus algosus* on the West Coast emerged as important in these dynamics, as they appear

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to out-recruit and/or out-compete native mussel species *Choromytilus meridionalis* and *Aulacomya ater*, as well as the intertidal limpet *Scutellastra argenvillei* which was previously dominant on west coast shores (Steffani and Branch 2003, 2004; Robinson 2005).

Investigation of the stock-recruit relationship at various spatial scales allowed some inferences about dispersal and recruitment at each of the locations. At the largest scale (100s of km), adult stocks were correlated with recruitment, implying that populations are reproductively isolated at this scale. At the smallest scale (meters), a significant relationship between mussel stock density and recruitment, evident at some locations, was caused by the suitability of adult mussel clumps as a recruitment substrate. Reducing mussel bed complexity will reduce mussel recruitment, and mussels do not normally recruit directly onto bare rock. If mussel beds are removed by harvesting, recruitment is severely retarded, with obvious implications for management.

Temporal and spatial patterns vary among locations in their relative importance in explaining large-scale recruitment patterns (e.g. Connolly and Roughgarden 1999a; Navarrete et al. 2002). The large spatial scale of the biogeographic recruitment study facilitated the comparison of patterns at large and medium temporal scales. An inter-annual pattern of periodically reduced mussel recruitment was evident on the West Coast and appeared to be linked to Benguela Niño or Niño-like anomalous warming events in the Benguela Current region. Such events have previously been shown to affect pelagic fisheries and the offshore environment (Shannon et al. 1986; Florenchie et al. 2003), but mine is the first study that proposes that these events may also have bottom-up impacts on west-coast community processes. This has important implications for models that predict the influences of large-scale temporal events and climate change on rocky-shore community structure in southern Africa. Mussel recruitment appeared to be much more strongly seasonal on the South and East Coasts than on the West Coast. Again, this temporal pattern appears linked to temperature-related physical factors. On the West Coast, the greatest source of nearshore temperature variability is wind-induced upwelling operating in cycles of about seven days, with seasonality playing a secondary role. Here, spawning and recruitment are periodic, but do not show a strong seasonal trend among or within species. On the South and East Coasts, coastal subsurface temperature is strongly seasonal, differing 6-8°C between summer and winter, and any effects of upwelling or other local-scale temperature-related events are secondary to the annual cycle. Both spawning and recruitment events are also markedly seasonal on these coasts, although the peak spawning and recruitment seasons differ among regions.

In this study, recruitment was measured not just into mussel bed, but also in to brushes and, at four east coast locations, into turf algae found within the mussel bed. While brushes were found to work well as a standardized treatment for the measurement of recruitment at most locations, algae was not. Although sample sizes at three of the four locations were low, the recruitment of *P. perna* into algae and into mussel bed appeared to be asynchronous. At Zululand, where recruitment

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into both algae and mussel bed were measured monthly, a migration of mussels that recruited into turf algae from the algae to the mussel bed was apparent. This movement is, however, secondary to the strongly seasonal spring recruitment into mussel bed evidenced at this location.

Finally, comparisons among replicate sites within locations led to an appreciation of smaller-scale spatial patterns of mussel recruitment. On the West Coast, where multiple species were recruiting at each site and the coastline is heterogeneous at small spatial scales, proximate sites (even those < 1 km apart) were often not synchronous. At the same time, there was temporal and spatial synchrony among the species at each site. On the South and East Coasts, where the coastline is more homogenous, sites tended to be more strongly temporally synchronized. This led to the hypothesis that increased spatial heterogeneity on the West Coast causes differences among sites in the process that delivers propagules from the larval pool, whereas these processes are more uniform in regions that are spatially homogenous.

The Delagoa bioregion (Lombard et al. 2004) was the only one of the six southern African bioregions not included in the mussel recruitment study in Chapter 1. In Chapters 2-4, I examined the recruitment patterns and processes in this bioregion, specifically in the Maputaland Marine Reserve, and was able to test various hypotheses generated in Chapter 1 about the nature of recruitment there. This is an area that lacks large or medium-sized embayments, has a narrow continental shelf, and is known to be extremely nutrient-poor (Schumann 1987, 1988; Carter and Schleyer 1988; Martin and Flemming 1988). The coastline is relatively homogenous and straight. Sub-surface (15 m benthic) temperatures were strongly seasonal, as were local winds, with warmer water and windier conditions in the spring and summer (Chapter 2). Two mussel species recruit to the intertidal here: *Perna perna* and *Brachidontes semistriatus*, the former being a large and heavily harvested species and the latter a small mussel with a known affinity for highly disturbed rocky shores (Lasiak 1999). I also included two barnacle taxa, *Chthamalus dentatus* and *Tetraclita* spp. for comparison. The basic hypotheses about this system, generated from the findings of Chapter 1, were that mussel recruitment rates would be low and strongly seasonal, with a high level of synchrony among both species (*B. semistriatus* and *P. perna*) and sites. Limited retention would result in low-levels of self-recruitment on individual headlands, and thus intra-headland connectivity among mussel populations was expected to be high.

Indeed, the results of Chapters 2 and 3 confirmed these hypotheses about recruitment pattern and process. Recruitment of both *P. perna* and *B. semistriatus* was synchronous within and among sites, but very low compared to other bioregions. Barnacle recruitment was also strongly seasonal but peak recruitment seasons, spatial heterogeneity, and the role of substrates varied more strongly among barnacle than among mussel species. Recruitment of all species was coupled to nearshore larval densities which, although low, varied spatially and temporally with temperature and the concentration of phytoplankton, indicating that bottom-up processes are important in controlling recruitment in Maputaland.

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Various onshore-transport mechanisms have been previously described for meroplankton in other coastal areas, and include upwelling or downwelling, onshore wind, internal waves and internal tidal bores (Shanks 1983; Pineda 1994; Shanks et al. 2000; Almeida and Queiroga 2003; Tapia et al. 2004; Vargas et al. 2004; Shanks and Brink 2005). In Chapter 2, two onshore-transport mechanisms were identified in Maputaland: upwelling and internal waves. Of these, the more important was coastal upwelling, and its role as a bottom-up process enhancing recruitment was confirmed in Chapter 3. Wind-induced upwelling in Maputaland has not been previously reported, and although it is not strong, it does appear to be important for the onshore-transport of benthic cooler water from further offshore, and may carry benthic propagules with it. Barnacle cyprids were found in the middle and bottom layers of the water column, and barnacle recruitment was enhanced by both northerly (upwelling-positive) winds and a reduction in onshore winds, both of which might facilitate the approach of cyprids towards the coast. In contrast, mytilid larvae were found in all layers of the water column, and southerly or downwelling-positive wind was found to enhance recruitment for both mussel species. *B. semistriatus* recruited in greater numbers than *P. perna* throughout the study.

The results of Chapter 4 confirmed the connectivity of both adjacent and distant rocky shores in Maputaland for benthic organisms with a planktonic phase in their life cycles. Using a Lagrangian model to predict dispersal kernels for drifters with varying strategies of vertical migration and planktonic larval durations, estimates for drifters fell within those hypothesized for low-retention areas by Harris et al. (1998), with mean ranges of 30-45 km south for mussels and 20-30 km south for barnacles. In Chapter 2, I reported that the southern half of Black Rock, the headland in the center of the study area, contained an un-harvested population of *P. perna* that was significantly more dense than any other in the study area. There was a significant latitudinal gradient of mytilid larval densities (Chapter 2) and mussel recruitment (Chapter 3), with higher levels south of Black Rock. This evidence supports the dispersal kernels predicted by the model. Although the majority of passive drifters traveled southwards in every model, there were some that remained within 1 km of the release site and some that traveled northwards, confirming the results of other nearshore models in the literature that provide a mechanism for passive upstream dispersal in advective environments, by way of stochastic current reversals (e.g. Byers and Pringle 2006). Larval behavior that enhances retention or upstream travel will further increase the probability of localized recruitment.

Implications for the conservation and management of mussel stocks in southern Africa

The South African Marine Living Resources Act of 1998 mandates the protection and management of the country's natural marine resources. McQuaid and Payne (1998), in reference to the publication of the first 15 months of the data set used in Chapter 1 (Harris et al. 1998), emphasize that the coastal areas in different regions of South Africa are diverse, and that to fulfill

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this mandate effectively, regions should have different management strategies. In Chapter 1, I confirm that populations appear relatively reproductively isolated at the biogeographic scale. Mussel recruitment patterns and processes differed in important ways among regions, coasts and species, and were influenced by location- and even site-specific processes. As our understanding of the patterns and processes of the variability of mussel recruitment among regions increases, so must practices be modified to conserve and manage stocks, tailoring them to the specific needs within each bioregion to ensure continued persistence and optimal utilization of intertidal stocks such as mussels around the entire coast of southern Africa.

Of all the locations I investigated, Dwesa on the South Coast (Chapter 1) and Maputaland on the East Coast (Chapter 3) had the lowest recruitment levels. These two areas are similar in many ways: they are regions with a narrow continental shelf with limited upwelling, low levels of nearshore nutrients and phytoplankton. Additionally, these two areas are the most socio-economically depressed, with coastal communities that depend on intertidal resources and harvest them under limited control by conservation authorities. Dwesa is a small marine reserve surrounded by shores that are heavily harvested, and this intense harvesting may have important effects on both maintenance of populations inside the reserve and their recovery after disturbance (Dye et al. 1997).

In Maputaland, it is clear that mussel harvesting is having an important and deleterious effect on both adult mussel bed density and local recruitment rates. Kyle et al. (1997a) reported that harvesting levels were stable over seven years of observation, i.e. there was no observed change in catch per unit effort. From this they concluded that harvesting was sustainable. However, although current harvesting levels may be sustaining the population at a fixed (if low) density, there are strong indications that harvesting levels are above those that would optimize offtake (Sink 2001). This is substantiated by many lines of evidence that emerged in Chapters 2-4. In Chapter 2, I reported no significant difference in mussel density among harvested areas, all of which had significantly lower densities than mussel beds in the southern half of Black Rock, an area that is not harvested due to a local taboo. There was a decoupling of stock and recruitment rates among sites, which can indicate the presence of some density-independent factor. Human harvesting of mussels, when not economically driven, is density-independent (Clark 1985), and so harvesting pressure may have erased any significant stock-recruit relationship. In Chapter 3, I recorded recruitment densities for *P. perna* that are lower than any other population examined thus far in southern Africa, implying that adult *P. perna* stocks are recruit-limited like Dwesa (Chapter 1). Furthermore, *P. perna* was consistently out-recruited by the small 'weedy' mussel *B. semistriatus* in Maputaland. On the South Coast, *B. semistriatus* has been found to be an indicator of high-disturbance due to *P. perna* harvesting (Lasiak 1999), and its dominance also suggests high harvesting pressure here. Finally, in Chapter 4, I provided evidence for the potential for upstream and downstream connectivity of rocky shores in Maputaland between both proximate (< 5 km) and distant (20-45 km) headlands with a predominantly southward flow. In Chapters 2 and 3, I demonstrated high densities of mytilid larvae

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and recruitment south of Black Rock, suggesting that its small protected adult population may be providing propagules to headlands < 15 km south. That these high densities were detectable through time in a recruit-limited environment further supports the argument that the spawner stock at Black Rock is providing propagules to downstream sites, and this source requires continued local and increased governmental protection.

My findings indicate that there could be several benefits to establishing a number of strategically placed no-take areas within the Maputaland Marine Reserve, including increases in spawner biomass, and the provision of baseline areas against which harvesting effects may properly be judged. Shanks et al. (2003a) recommend that such fully protected areas should be spaced to benefit organisms that are both long-dispersing (such as *P. perna*) and short-dispersing (such as the tunicate *Pyura stolonifera*). Using current velocity information and modeled dispersal kernels presented in Chapter 4, I provided examples of how this model might be interpreted to guide decision-making about the spacing of no-take areas within the Maputaland Marine Reserve. Based on the findings in Chapter 1, it is possible that areas of the South Coast, specifically those near Dewsa, might also benefit from such a protection scheme. Of course, it is important to remember that because *P. perna* larvae do not settle on bare rock, the closure of areas to harvesting may not have an immediate effect. In the absence of sweepstakes recruitment events, which appear to occur on the scale of 10-20 years on the East Coast (Chapter 1), *P. perna* beds could take up to 10 years to recover (Dye et al. 1997).

The coastal benthic communities of southern Africa, including mussel stocks, are important ecologically, economically and culturally in all bioregions around the coast. Their effective management relies upon an understanding of population and community dynamics, including recruitment processes. Human populations from the interior of South Africa are shifting to the coast and continue to increase in size, placing intertidal stocks under increasing pressure. Additionally, climate is changing at an unprecedented rate. The results recorded in this thesis are thus not just of intrinsic interest in advancing knowledge about recruitment patterns and their underlying causes, but contribute to the pool of information needed for the conservation and management of resources demanded by the country's Marine Living Resources Act and its commitment to international protocols that call for protection and sustainable use of the coast.

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APPENDICES

APPENDIX 1 Keogram analysis methodology

Current measurements using video time-stacks (keograms)

The *keogram* is a time-stack of visual data, taken with a video camera, which allows the measurement of nearshore surface current speeds within a field of view. The use of video to study hydrodynamics at small and medium scales is a relatively new trend in nearshore oceanography, with a wide range of applications (Foote et al. 2002; Govender et al. 2002; Chickadel et al. 2003). The technique I used is similar to that described by Chickadel et al. (2003) and the descriptions in this appendix highlight departures from their methods.

My study extends the method from Chickadel et al. (2003) to involve multiple cameras filming simultaneously from fixed locations, giving an array of current speeds. Six analog cameras (Sony Handycam CCD-TR648E PAL) and one digital camera (Sony Digital Handycam DCR-TRV340E PAL) were fitted with Prinz 37mm UV filters. Hi-8 tapes were selected for their versatility, availability and visual integrity; tripods were chosen to be light and portable. All footage was taken with the camera completely zoomed out (maximizing the scene in the view).

A pilot study of the videographic method was undertaken prior to the data collection presented here. From 12 May to 12 June 2002, videos of the surface currents and wind data were collected every second day at Lala Nek (den Oudendammer 2002).

Video footage processing

The video data were accessed via an Ellips Rio capture card and Coastal Dynamics software (G. Hough, Envirovision Solutions, 2002). The software displays the video footage in a video window for the creation of time stacks. Two to three sampling lines, each 1-pixel wide and of varying length, were then positioned in the sampling window (Figure A1.1a) according to certain rules: (1) The vertical sampling line was placed first, in the middle third of the image to minimize error due to lens distortion. Its length was adjusted, if necessary, so that it crossed both the horizon and a calibration point centrally located in the image. (2) If any obvious features could be seen in the top third of the water in the image, a horizontal sampling line was placed through this region. (3) If no features in the top third stood out, both sampling lines were placed in the bottom two-thirds of the image. (4) If features such as a foam line were present, these were targeted for analysis. (5) In the absence of any features that would clearly produce a signature, the sampling lines were placed just beyond and just inside the backline of the breaking surf. These locations were selected because they most consistently produced detectable bubble-raft signatures when the vertical and horizontal keograms were run.

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When creating a keogram, all sampling rates have the potential to give signatures. Not all the signatures represent surface currents, however, as some could be shadows from clouds moving overhead, or the paths of white horses or sea foam pushed by the wind. Using drogue and ADCP results, as well as surface current calculations from other sources, the likely range of current speeds that was expected to be seen on the surface of the water was estimated. The sampling rate was then adjusted within the Coastal Dynamics software so that the slowest signatures in the horizontal keogram (the alongshore currents) would generally appear at an angle of at least 25° from the horizontal (time) axis, and the fastest currents would appear at an angle of not more than 70°. This range of angles made the signatures easier to both identify and measure in the keogram. The ideal sampling rate was calculated to be 600-750 $\text{ms}\cdot\text{frame}^{-1}$ for current speeds ranging 0.05-1.5 $\text{km}\cdot\text{h}^{-1}$. Keograms whose timing fell below 450 or above 850 $\text{ms}\cdot\text{frame}^{-1}$ were re-set and re-run. Examples of two time-stack keograms and marked 'signatures' are presented in Figures A1.1b-e.

The alongshore and on/offshore components of the velocity of three replicate signatures of the selected feature were calculated using a series of variables and constants (Tables A1.1 and A1.2) that were compiled into a software algorithm called the KeoImporter (v1.0, G. Fouche, K. Reaugh and G. Hough, Envirovision Solutions, 2005) following the mathematical sequence below. The resultant velocity measurements were then plotted and used to measure surface current speeds in the nearest 1000 m from shore.

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References

References are found in the main reference list for the thesis.

Table A1.1 Variables used in keogram analysis

Variable	Definition
Δd	$= d_s - d_f$; change in distance of signature (this is the distance traveled by a signature on vertical keoline), negative value indicates movement southwards, if top of keoline is to the north
ΔR	change in range of signature (this is the distance traveled by a signature on vertical keoline), negative value indicates movement away from camera
Δt	$t_f - t_s$
$\Delta\delta$	slue angle of one pixel on horizontal sampling line
$\Delta\Theta$	angular dip - the angle that subtends one pixel in a vertical keoline
C_i	column number i in keogram (one pixel wide)
C_f	column of end of signature
C_s	column of start of signature
d	distance along horizontal keoline from centre to feature (m)
d_f	distance to end of signature
d_i	distance to any pixel i from the centre pixel of the horizontal keoline
d_s	distance to start of signature
H	height from Mean Low Water Springs, in meters
H_c	calibration point height
H_v	video camera height

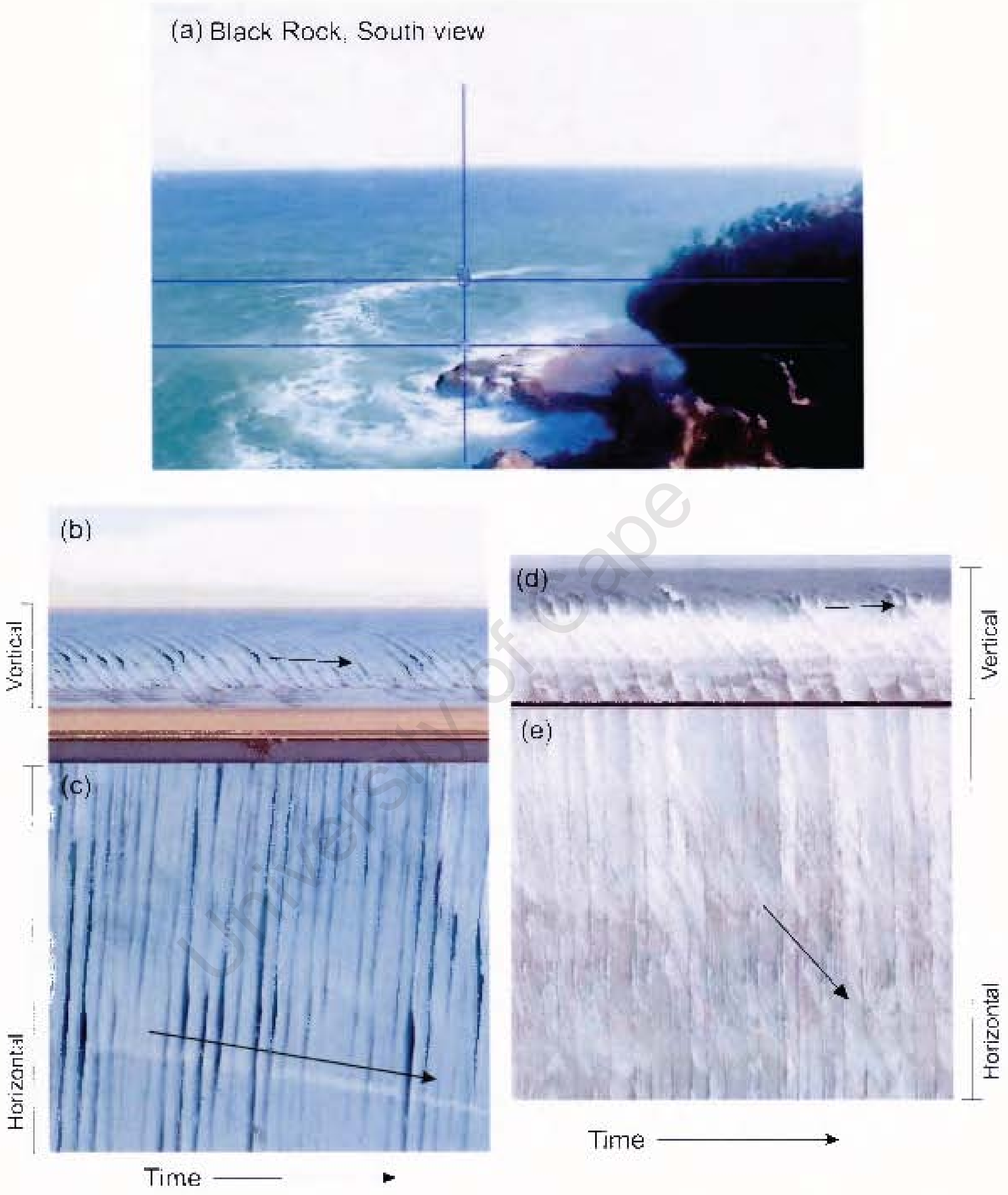

Figure A1.1 Examples of (a) placement of data collection keo-lines along current signatures in the vertical and horizontal keograms of (b) and (c) foam line ($0.018\ m.s^{-1}$) and (d) and (e) white water movements following a breaking wave ($2.169\ m.s^{-1}$). Arrows indicate signatures used for velocity calcuations

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Variable	**Definition**
L_e	latitudinal distance between camera and feature, in meters
L_n	longitudinal distance between camera and feature, in meters
n	number of pixels in the whole original picture
n_x	number of horizontal pixels
n_y	number of vertical pixels)
p_c	centre row of the horizontal keoline
p_i	number of pixels from centre of horizontal keoline to feature
P_x	width of picture on the screen
P_y	height of picture on the screen in mm
R	range (horizontal distance from camera to another point), in meters
r	pixel row in keoline (denotes an individual pixel; the top pixel in the keogram is always 1)
R_c	range to cal point
r_c	row of cal point
R_f	range to end of signature
r_f	row of end of signature
R_h	range to horizon
r_h	row of keoline that crosses horizon
r_i	any row in the keoline
R_k	range to keoline
R_p	range to a pixel in question on the horizontal sampling line
R_{pf}	range to the pixel at the end of the signature in horizontal keogram
R_{ps}	range to the pixel at the start of the signature in horizontal keogram
R_s	range to start of signature
r_s	row of start of signature
r_{sf}	central r of the signature
SR	sampling rate in ms/frame
t	time in decimal hours
t_i	time at column number i
t_f	time at last column of signature
t_s	time at first column of signature
V_v	velocity of the signature as measured in the vertical keoline (radial component)
V_h	velocity of the signature as measured in the horizontal keoline (azimuthal component)
V_{sig}	velocity of the signature using combined radial and azimuthal components
γ_v	camera angle, in degrees (= angle measured by videographer in field plus/minus declination)
γ_i	actual direction in degrees to feature
γ_{sig}	bearing of the signature with relation to true north
δ	slue angle, angle from center of horizontal sampling line (which lies on the vertical sampling line) to feature, in degrees
δ_f	slue angle to end of signature
δ_s	slue angle to start of signature
δ_{sig}	angle that subtends the signature in the horizontal sampling line
θ	dip angle from horizontal line from camera to another point on the ground, in degrees
θ_c	dip angle to cal point
θ_f	dip angle to end pixel (row) in the signature
θ_h	dip angle to horizon
θ_{hc}	difference in angle from horizon to cal point
θ_i	dip angle to some pixel (row) in the signature
θ_k	dip angle to keoline
θ_{kc}	difference in angle from keoline to cal point
θ_s	dip angle to the start pixel (row) in the signature
θ_{sf}	central Θ of the signature (= $\Theta(s)$ - $\Theta(f)$)
θ_{sig}	angle that subtends the signature

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Table A1.2 Constants used in calculations

Constant	Definition
a	equatorial radius of the earth = 6378140 meters
27° S	subtends 98794 meters
32° E	subtends 111096 meters

Coastal Imaging Geometry:

Use the camera height to calculate the horizon dip angle (preferred method)
θ_h can be determined trigonometrically (Figure A1.2):

1.
$$\cos \theta_h = \frac{a}{a+H_v}$$

$$H_v = \cos^{-1}\left(\frac{a}{a+H_v}\right)$$

Use the camera height to calculate the horizon dip angle (alternate method)
Assume $L = R_h$ (Figure A1.3).

2.
$$a^2 + R_h^2 = (a + H_v)^2 \quad \text{(Pythagoras)}$$

$$R_h = \sqrt{2aH_v + a^2}$$

3.
$$\tan \theta_h = \frac{R_h}{a}$$

$$\theta_h = \tan^{-1}\left(\frac{R_h}{a}\right)$$

Calculate θ_c, the dip angle from the horizontal to the calibration position. Lat_n and $Long_n$ are the latitude and longitude of a point in space in decimal degrees. ΔLat is a change in latitude measured in degrees, and Δy is a change in latitude measured in meters; $\Delta Long$ and Δx are similarly equivalent. At this particular location, the 27th degree latitude South subtends 98784 m, while the 32nd degree longitude East subtends 111096 m (Figure A1.4)

4.
$$\Delta Lat_{vc} = Lat_c - Lat_v$$

5.
$$\Delta y_{vc} = \Delta Lat_{vc} \cdot (98784\text{m})$$

6.
$$\Delta Long_{vc} = Long_c - Long_v$$

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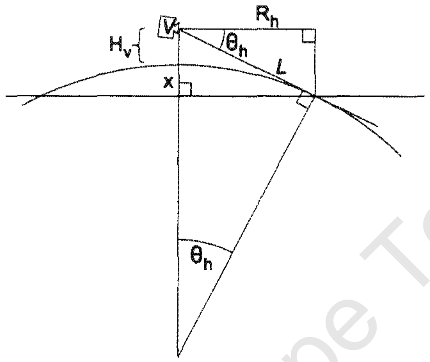

Figure A1.2 Camera height is used to calculate the horizon dip angle trigonometrically (preferred method). V = position of video camera

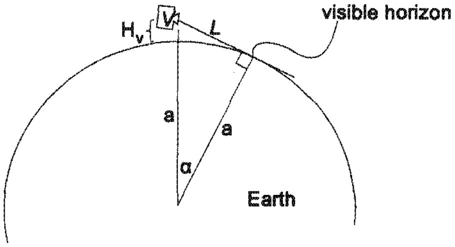

Figure A1.3 Camera height is used to calculate the horizon dip angle using Pythagorean method, assuming L = R_h (alternate method)

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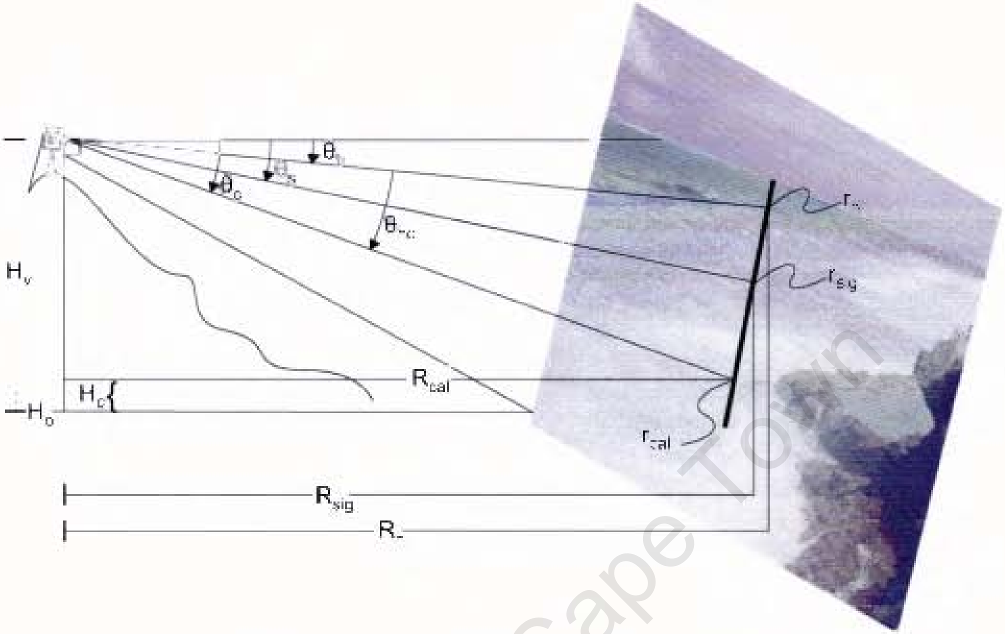

Figure A1.4 Variables used in the calculation of velocity for the vertical sampling line

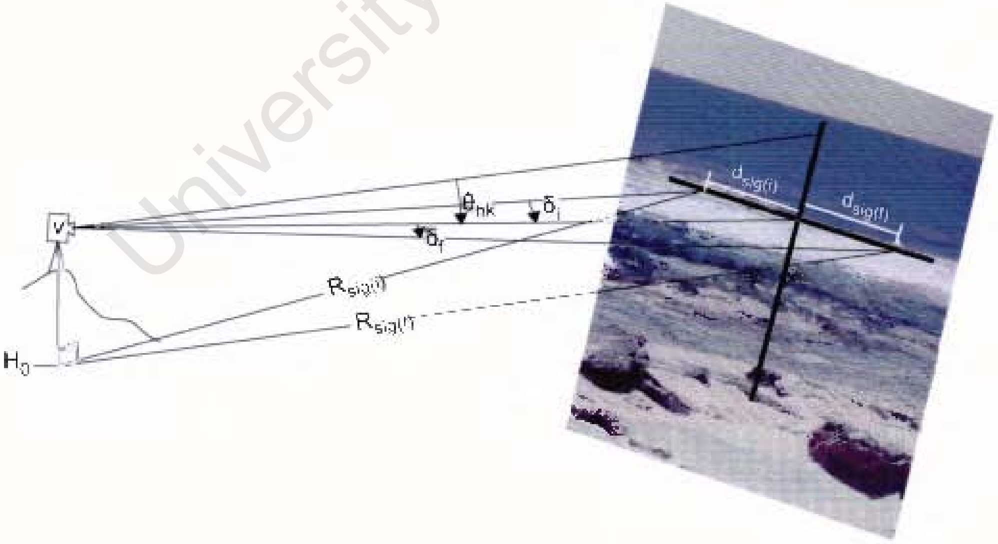

Figure A1.5 Variables used in the calculation of velocity for the horizontal sampling line

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19. $\Delta R = R_s - R_f$

Here, a negative value for ΔR indicates a movement east, or away from the camera.

Calculate the velocity vector for the signature from the vertical keogram:

20. $V_v = \dfrac{\Delta R}{\Delta t}$

Calculate the latitude and longitude of the centre of the signature measured. Find the average distance from the camera to the signature in meters:

21. $\overline{R} = \dfrac{R_s + R_f}{2}$

Calculate the difference in latitude and longitude in decimal degrees between the signature and the camera

22. $\Delta Lat_{sig} = \dfrac{\overline{R} \cdot \cos(180 - \gamma)}{98784m}$, negative result is movement north

23. $\Delta Long_{sig} = \dfrac{\overline{R} \cdot \sin(180 - \gamma)}{111096m}$, negative result is movement east

Calculate the latitude and longitude of the signature

24. $Lat_{sig} = Lat_v - \Delta Lat_{sig}$

25. $Long_{sig} = Long_v + \Delta Long_{sig}$

Use the horizontal keogram to get the azimuthal *component of the velocity vector.* Assume that pixels are square, and therefore let $\Delta\theta = \Delta\sigma$. Calculate the bearing, relative to true north, from the camera to the start and the end of the signature (Figure A1.5).

26. $\gamma_s = \gamma_v + (p_c - p_s) \cdot \Delta\sigma$

27. $\gamma_f = \gamma_v + (p_c - p_f) \cdot \Delta\sigma$

Calculate Δd, the distance in meters that this change in bearing for the distance traveled by the signature subtends:

28. $\theta_k = \Delta\theta \cdot (r_h - r_k) + \theta_h$

29. $R_k = \dfrac{H_v}{\tan \theta_k}$

30. $\sigma_{sig} = (r_s - r_f) \cdot \Delta\sigma$

31. $\Delta d = R_k \cdot \tan \sigma_s$

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Calculate Δt for the signature following formulae 13 and 14.

Calculate the azimuthal velocity component for the signature:

32. $$\mathrm{V_h} = \frac{\Delta d}{\Delta t}$$

Calculate the latitude and longitude of the signature.

33. $$\sigma_i = (r_i - r_c) \cdot \Delta\sigma$$

34. $$d_i = R_k \cdot \tan \sigma_i$$

35. $$\overline{d} = \frac{d_s + d_f}{2}$$

36. $$R_{sig} = \sqrt{R_k^{\ 2} + \overline{d}^2}$$

Calculate the difference in latitude and longitude in decimal degrees between the signature and the camera

37. $$\Delta Lat_{sig} = \frac{R_{sig} \cdot \cos(180 - \gamma_v)}{98784m}$$, negative result is movement north

38. $$\Delta Long_{sig} = \frac{R_{sig} \cdot \sin(180 - \gamma_v)}{111096m}$$, negative result is movement east

Calculate the latitude and longitude of the signature as per equations 24 and 25.

Find the velocity vector of the signature using V_v and V_h.
If the signature is a round object, such as a bubble raft, this equation should be used:

39. $$V_{sig} = V_h^{\,2} + V_v^{\,2}$$

If the signature is a streak that lies approximately parallel to a sampling line (an angular difference of <15°, such as a shore-parallel slick or the wake of a boat, then this alternate formula should be used:

40. $$\frac{1}{V_{sig}} = \frac{1}{V_h^{\ 2}} + \frac{1}{V_v^{\ 2}}$$

Calculate the bearing of the signature with relation to true north

41. $$\gamma_{sig} = 90 - \tan\frac{V_h}{V_v}$$

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APPENDIX 2 Validation of current velocity measurements and determination of processes driving currents

Methods

Validation of current measurements

Current data from the drogues and videography were compared using Pearson product-moment correlation analysis for validation and corroboration of the along- and across-shore current measurements. Where multiple correlations were employed, a sequential Bonferroni adjustment (Holm 1979) following the recommendations of Quinn and Keough (2002). These data were also compared with the ADCP measurements for further corroborative evidence. Finally, surface and sub-surface current speeds were compared with wind and tidal velocity measurements to describe the variability in the current speed and direction that is related to these two factors. All statistics were calculated with Statistica 7.0 (© 1984-2004, StatSoft, Inc.).

Processes driving currents

Wind data from Black Rock and Mbazwana airfield were compared to determine the validity of applying remote data recorded at Mbazwana to the study area. Hourly alongshore wind data collected at Mbazwana Airfield were significantly and positively strongly correlated with data taken at Black Rock during the videography ($r = 0.741$, $n = 103$, $p < 0.0001$). The across-shore component was positive and significant, but very weak ($r = 0.283$, $n = 103$, $p < 0.01$, $U_{MB} = 0.789 + 0.189 * U_{BR}$). Across-shore winds were generally stronger at Black Rock than at Mbazwana, probably due to the inland and protected position of the Airfield and the headland position on Black Rock. As the Black Rock wind data were not complete, the Mbazwana wind data were used for analyses requiring continuous wind measurements, and were compared to the mean hourly along- and across-shore current velocities by zone and depth.

The along and across-shore current velocities were filled in following the procedures above and data from all stations were pooled into hourly time bins and compared with the along- and across-shore wind components and with tidal range and velocity measurements by using Pearson product-moment correlation analyses (Zar 1999). Wherever multiple tests were used, Holm's (1979) sequential Bonferroni adjustment was used to accept or reject the value for p following Quinn and Keough (2002).

Tidal velocities were calculated as in Chapter 4.

Results

Validation of current measurements

Alongshore surface current data derived from videos were compared with simultaneous subsurface alongshore current measurements obtained from drogues (Figure A2.1). Surface current speeds determined by video generally fell within the range of those of the drogues, although they

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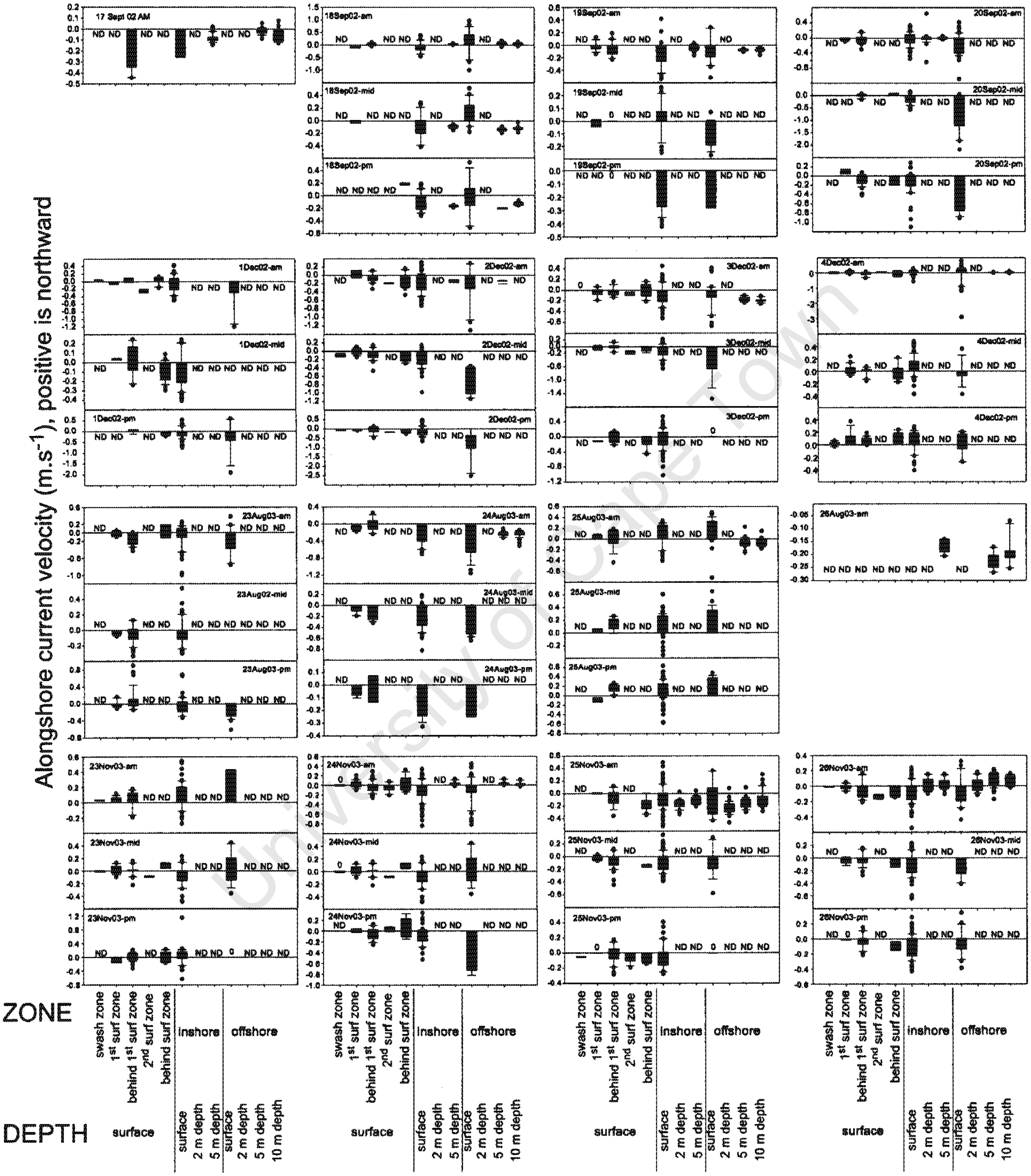

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Figure A2.1 Alongshore median current speed (positive is northwards), all stations combined (m.s^{-1}), 50th percentile (box), 90th percentile (whiskers) and outliers (dots). Data are presented by zone and water depth. Surface currents were measured with video, sub-surface currents were measured with drogues.

were much more variable. Inshore video measurements of surface currents were significantly and positively correlated with the behind-surf and offshore surface video measurements, as well as with velocities of the 2-m drogues (Table A2.1). In contrast, the offshore surface video measurements were not correlated with the behind-surf measurements. Insufficient offshore video data prevented correlation analysis with the offshore drogue measurements. Drogue measurements in both zones and at all depths were strongly significantly positively correlated with each other, indicating coherence of velocity direction with depth on all days.

Table A2.1 Correlations between drogue (subsurface) and video (surface) alongshore current measurements at the same station and within the same hour. n = number of replicate measurements, r = Pearson product-moment correlation coefficient. The value for p was accepted or rejected using a sequential Bonferroni procedure for multiple testing (α = 0.05, c = 6). * test was significant at the adjusted level, ns = test was not significant.

Data type	Depth	Zone		Video Surface Behind surf	Video Surface Inshore	Video Surface Offshore	Drogue 2 m Inshore	Drogue 5 m Inshore	Drogue 2 m Offshore	Drogue 5 m Offshore	Drogue 10 m Offshore
Video	**Surface**	**Behind surf**	r		.4333	.1862	--	--	--	--	--
			n	X	41	22	1	2	1	2	2
			p		*	ns					
Video	**Surface**	**Inshore**	r	.4333		.4349	.9973	.6102	.9981	.4081	.2900
			n	41	X	124	3	4	3	6	6
			p	*		*	ns	ns	ns	ns	ns
Video	**Surface**	**Offshore**	r	.1862	.4349		--	--	--	--	--
			n	22	124	X	0	0	0	1	1
			p	ns	*						
Drogue	**2 m**	**Inshore**	r	--	.9973	--		.9908	.9912	.9834	.9585
			n	1	3	0	X	8	5	5	5
			p		ns			*	*	*	*
Drogue	**5 m**	**Inshore**	r	--	.6102	--	.9908		.9926	.9789	.9622
			n	2	4	0	8	X	5	14	15
			p		ns		*		*	*	*
Drogue	**2 m**	**Offshore**	r	--	.9981	--	.9912	.9926	X	.9942	.9752
			n	1	3	0	5	5		5	5
			p		ns		*	*		*	
Drogue	**5 m**	**Offshore**	r	--	.4081	--	.9834	.9789	.9942		.9651
			n	2	6	1	5	14	5	X	28
			p		ns		*	*	*		*
Drogue	**10 m**	**Offshore**	r	--	.2900	--	.9585	.9622	.9752	.9651	
			n	2	6	1	5	15	5	28	X
			p		ns		*	*	*	*	

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Mean (standard deviation) alongshore current velocities varied from approximately +0.025 (0.26) m.s^{-1} at 1-5 m depth to -0.015 (0.18) m.s^{-1} nearest the bottom (Table A2.2); positive velocities are northward. Results of the ADCP analysis indicated that both the M2 (12.42 h) and M4 (6.21 h) tidal ellipses had a predominant effect on the alongshore flow, most pronounced in shallower water (depths to 10 m). While alongshore wind and alongshore current direction and speed appeared to be correlated through the water column, there were some periods when across-shore water velocities corresponded to alongshore wind velocity, indicating possible offshore Ekman transport. Spectral coherence analyses of the ADPC data revealed a significant coherence between cycles of alongshore wind and both along- and across-shore velocity at low frequencies (i.e. 2-4 d time scales) (Reynolds-Fleming and Reaugh, unpublished data).

Table A2.2 Velocity summary from ADCP deployment from 26 Nov 2003 to 18 Mar 2004, rotated 20° clockwise into along- and across-shore components. Height is meters above the bottom, in half-meter depth bins. Velocities are m.s^{-1}. Positive across-shore velocity is eastwards (offshore), positive alongshore current velocity is northwards.

	Across-shore velocity		Alongshore velocity	
Height (m)	Mean	Std Dev	Mean	Std Dev
13.76	-0.033	0.076	-0.019	0.274
13.26	-0.007	0.055	-0.025	0.267
12.76	0.003	0.043	-0.026	0.265
12.26	0.004	0.040	-0.025	0.262
11.76	0.004	0.038	-0.023	0.260
11.26	0.003	0.036	-0.021	0.258
10.76	0.003	0.035	-0.019	0.256
10.26	0.002	0.034	-0.017	0.254
9.76	0.002	0.033	-0.015	0.251
9.26	0.002	0.032	-0.013	0.249
8.76	0.001	0.032	-0.010	0.246
8.26	0.001	0.032	-0.008	0.243
7.76	0.001	0.032	-0.006	0.240
7.26	0.001	0.032	-0.003	0.237
6.76	0.001	0.032	-0.001	0.233
6.26	0.002	0.033	0.001	0.230
5.76	0.002	0.034	0.004	0.226
5.26	0.003	0.035	0.006	0.222
4.76	0.004	0.036	0.009	0.217
4.26	0.005	0.037	0.011	0.212
3.76	0.006	0.039	0.013	0.206
3.26	0.007	0.041	0.015	0.200
2.76	0.009	0.042	0.016	0.193
2.26	0.010	0.043	0.017	0.185
1.76	0.012	0.044	0.016	0.175
1.26	0.013	0.043	0.014	0.160

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Along- and across-shore velocities measured by ADCP during the period of video and drogue data collection (7:00 to 17:00, 26 November 03) were compared with drogue and videography measurements from Rocktail Bay, Black Rock, and Dog Bay (Table A2.3). Additionally, wind along- and across-shore components taken at Black Rock were compared to wind data taken at the Mbazwana Airfield. Surface currents were nearly always faster than the 1-m measurements from the ADCP. Generally, alongshore surface currents were directionally associated with wind, while across-shore surface currents were directionally associated with the subsurface current measurements. Current measurements taken by the drogues and ADCP were similar in direction and speed. Winds measured at Mbazwana, as compared to those measured on the headland at Black Rock, were often higher in the alongshore component and lower in the across-shore component, but also generally fell within the same direction and order of magnitude of measurement.

Table A2.3 Simultaneous drogue, video and ADCP along- and across-shore current velocity measurements, plus wind ($m.s^{-1}$). Drogue measurements from the offshore sets were used for comparison; video measurements from both inshore and offshore zones were used. For comparison, positive across-shore velocity is east-wards (offshore), positive alongshore current velocity is north-wards for both wind and current measurements. Blank cells indicate that no data were available.

Direction	Instrument	Station[a]	Depth	8:00	9:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00
Along-shore	Wind watch	BR	Wind			-2.13	-2.98	-2.96	-2.65	-2.48	-2.78	-5.64
	Anomometer	Mbaz	Wind	-1.60	-2.40	-3.90	-4.92	-4.69				-4.94
	Video (mid+offshore)	DPB	Surface		0.07			-0.21			0.10	
		BR	Surface		-0.11							
		RTB	Surface			-0.31	-0.27	-0.13			-0.17	
	ADCP (offshore)	BR	1 m		0.2	0.2	0.2	0.3	0.1	0.1	0.1	0.1
			2 m		0.2	0.2	0.2	0.3	0.3	0.2	0.1	0.1
			5 m		0.2	0.2	0.2	0.3	0.3	0.2	0.1	0.1
			7 m		0.2	0.2	0.3	0.3	0.3	0.2	0.1	0.1
			10 m		0.1	0.1	0.2	0.2	0.2	0.2	0.1	0.1
			13 m		0	0.1	0.2	0.2	0.2	0.2	0.1	0.1
	Drogue (offshore)	DPB	2 m	-0.065		-0.017						
			5 m	-0.006		0.025						
			10 m	0.018		0.074						
		BR	2 m		0.127							
			5 m		0.145							
			10 m		0.148							
Across-shore	Wind watch	BR	Wind			-4.01	-5.23	-5.55	-4.98	-4.66	-5.23	0.30
	Anomometer	Mbaz	Wind	0.58	0	0	0.87	-1.71				-2.85
	Video (mid+offshore)	DPB	Surface		0.47			0.45			0.69	
		BR	Surface		0							
		RTB	Surface			0.22	0.22	0			0.25	
	ADCP (offshore)	BR	1 m		-0.1	-0.1	-0.1	0.03	0.03	0.03	0.03	0.03
			2 m		0.1	0.03	0.03	0.1	0.1	0.1	0.1	0.1
			5 m		0.1	0.03	0.03	0.03	0.03	0.03	0.1	0.1
			7 m		0.1	0.03	0.03	0.03	0.03	0.03	0.03	0.03
			10 m		0.1	0.03	0.03	0.03	0.03	0.03	0.03	-0.1
			13 m		0.1	0.03	0.03	0.03	0.03	0.03	0.03	-0.1
	Drogue (offshore)	DPB	2 m	-0.046		0.023						
			5 m	-0.024		0.089						
			10 m	0.012		0.082						
		BR	2 m		0.081							
			5 m		0.139							
			10 m		0.179							

[a] Station codes: BR = Black Rock, Mbaz = Mbazwana Airfield, DPB = Dog Bay, RTB = Rocktail Bay

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Processes driving currents

The relative influences of tidal velocity and Mbazwana wind speed on current speeds and directions were investigated using Pearson product-moment correlation analyses. Several scales were considered for both parameters. For wind, the directionless velocity was considered, as well as the along- and across-shore components, and values for the same hour, as well as the mean values for the 2, 4, 6, 12 and 24 hours previous to the measurement of the current velocity.

Table A2.4a Correlations between *alongshore wind* records from Mbazwana Airfield and the *alongshore* current measurements derived from drogue and video per station and per hour. Positive winds are from the north, positive currents are northwards. The significance of the value for p was accepted or rejected using a sequential Bonferroni procedure for multiple testing ($\alpha = 0.05$, $c = 6$). * test was significant at the adjusted level, ns = test was not significant.

					Wind measurement					
Current direction	**Data type**	**Depth**	**Zone**		**Same hour**	**Prev 2 hours**	**Prev 4 hours**	**Prev 6 hours**	**Prev 12 hours**	**Prev 24 hours**
Alongshore	**Video**	**Surface**	**Behind surf (points)**	r	-.3636	-.3749	-.3806	-.3762	-.3742	-.2502
				n	124	124	126	126	126	126
				p	*	*	*	*	*	*
	Video	**Surface**	**Behind surf (bays)**	r	-.3599	-.3844	-.4374	-.4700	-.4957	-.4301
				n	44	44	45	45	45	45
				p	ns	ns	*	*	*	*
	Video	**Surface**	**Inshore**	r	-.4579	-.4521	-.4482	-.4410	-.4028	-.2111
				n	256	256	261	261	261	261
				p	*	*	*	*	*	*
	Drogue	**2 m**	**Inshore**	r	-.4214	-.4093	-.4256	-.4498	-.4761	-.3561
				n	29	29	29	29	29	29
				p	*	ns	*	*	*	ns
	Drogue	**5 m**	**Inshore**	r	-.6427	-.7045	-.7610	-.7828	-.8022	-.5786
				n	85	85	85	85	85	85
				p	*	*	*	*	*	*
	Video	**Surface**	**Offshore**	r	-.3640	-.3822	-.4016	-.4142	-.3951	-.1802
				n	128	128	132	132	132	132
				p	*	*	*	*	*	ns
	Drogue	**2 m**	**Offshore**	r	-.5769	-.6998	-.7689	-.7740	-.8327	-.8122
				n	14	14	14	14	14	14
				p	ns	*	*	*	*	*
	Drogue	**5 m**	**Offshore**	r	-.5510	-.6121	-.6927	-.7250	-.7973	-.6242
				n	102	102	102	102	102	102
				p	*	*	*	*	*	*
	Drogue	**10 m**	**Offshore**	r	-.6296	-.6757	-.6970	-.7049	-.8040	-.6780
				n	112	112	112	112	112	112
				p	*	*	*	*	*	*

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Alongshore current velocities were nearly all negatively and significantly correlated with the alongshore wind component (Table A2.4a), indicating that the wind and water were flowing in the same direction. Across-shore sub-surface currents were also generally significantly negatively correlated with alongshore winds (Table A2.4b) but were much less frequently significant, implying an onshore flow with northerly (upwelling-positive) winds in some zones. Across-shore surface currents in the inshore zone were positively associated with winds, indicating an offshore flow in northerly winds. For both along- and across-shore currents, the strongest correlations for the surface currents were at shorter time intervals (same-hour to 6-hour), while the strongest correlations for the subsurface currents were at a longer (12-hour) time interval.

Table A2.4b Correlations between *alongshore wind* records from Mbazwana Airfield and the *across-shore* current measurements derived from drogue and video per station and per hour. Positive winds are from the north, positive currents are northwards. The significance of the value for p was accepted or rejected using a sequential Bonferroni procedure for multiple testing (α = 0.05, c = 6). * test was significant at the adjusted level, ns = test was not significant.

Current direction	Data type	Depth	Zone		Wind measurement					
					Same hour	Prev 2 hours	Prev 4 hours	Prev 6 hours	Prev 12 hours	Prev 24 hours
Across-shore	Drogue	2 m	Inshore	r	-.5843	-.7051	-.7626	-.8037	-.8840	-.8548
				n	29	29	29	29	29	29
				p	*	*	*	*	*	*
	Drogue	5 m	Inshore	r	-.5483	-.5986	-.6604	-.7097	-.7998	-.7532
				n	99	99	99	99	99	99
				p	*	*	*	*	*	*
	Drogue	2 m	Offshore	r	-.4261	-.5974	-.7047	-.7448	-.8575	-.8915
				n	14	14	14	14	14	14
				p	ns	*	*	*	*	*
	Drogue	5 m	Offshore	r	-.3800	-.4413	-.5285	-.5596	-.7047	-.6613
				n	115	115	115	115	115	115
				p	*	*	*	*	*	*
	Drogue	10 m	Offshore	r	-.4555	-.5113	-.5641	-.5778	-.7162	-.6517
				n	121	121	121	121	121	121
				p	*	*	*	*	*	*

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Across-shore winds were also compared to both along- and across-shore current velocities (Table A2.5). Several parameters were not significantly correlated and therefore not presented. For the alongshore currents, relationships were generally stronger at longer time scales (more than 6 hours), and strongest for the 2-m drogues. For the across-shore currents, correlations were again strongest for the 2-m drogues, and weaker or non-significant for the deeper drogues and the surface currents.

Table A2.5 Correlations between *across-shore wind* records from Mbazwana Airfield and the (a) *alongshore* and (b) *across-shore* drogue (subsurface) and video (surface) current measurements per station and per hour. Positive across-shore wind is easterly, positive alongshore currents are north-wards and positive across-shore currents are west-wards). The significance of the value for p was accepted or rejected using a sequential Bonferroni procedure for multiple testing (α = 0.05, c = 6). * test was significant at the adjusted level, ns = test was not significant

					Wind measurement					
Current direction	Data type	Depth	Zone		Same hour	Prev 2 hours	Prev 4 hours	Prev 6 hours	Prev 12 hours	Prev 24 hours
(a) Alongshore	Video	Surface	Behind surf	r	.2318	.2686	.2594	.2756	.2437	.0532
				n	124	124	126	126	126	126
				p	*	*	*	*	*	ns
	Drogue	5 m	Inshore	r	.0508	.1332	.2029	.2437	.4207	-.0657
				n	85	85	85	85	85	85
				p	ns	ns	ns	ns	*	ns
	Drogue	2 m	Offshore	r	.6805	.5794	.7581	.7693	.7452	-.7196
				n	14	14	14	14	14	14
				p	*	*	*	*	*	*
	Drogue	5 m	Offshore	r	.1350	.0681	.0612	.1347	.2817	.2032
				n	102	102	102	102	102	102
				p	ns	ns	ns	ns	*	ns
	Drogue	10 m	Offshore	r	.0426	.0626	.1104	.1676	.3222	.0580
				n	112	112	112	112	112	112
				p	ns	ns	ns	ns	*	ns
(b) Across-shore	Drogue	2 m	Inshore	r	.8366	.8348	.8558	.8820	.8496	.2755
				n	29	29	29	29	29	29
				p	*	*	*	*	*	ns
	Drogue	2 m	Offshore	r	.6977	.6800	.8149	.8261	.7605	-.7183
				n	14	14	14	14	14	14
				p	*	*	*	*	*	*
	Drogue	5 m	Offshore	r	.0057	-.0390	-.0519	.0243	.2648	.2277
				n	115	115	115	115	115	115
				p	ns	ns	ns	ns	*	ns
	Drogue	10 m	Offshore	r	-.0398	-.0354	-.0135	.0568	.2872	.1394
				n	121	121	121	121	121	121
				p	ns	ns	ns	ns	*	ns

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Tides in Maputaland are diurnal and approximately symmetrical. Along- and across-shore current velocities were compared to the tidal velocity at three time scales and the absolute value of current velocity was compared to the tidal range (Table A2.6). Alongshore current was only associated once with tidal velocity and never with tidal range. Across-shore currents were more strongly and significantly correlated with both tidal velocity (negative association, strongest at 5 m depth, both inshore and offshore) and tidal range (positive association, strongest at 2 m depth, offshore).

Table A2.6 Correlations between along- and across-shore drogue (subsurface) current measurements per station per hour and vertical tidal velocities (in the z-direction). Positive alongshore current is northwards, positive across-shore current is eastwards, positive tidal velocity is ebbing, measured in $mm.h^{-1}$. Tidal range is a measure of variability, larger numbers indicate larger (spring) tides, and was correlated with directionless current speed. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

Current direction	Measurement depth	Zone		Tidal Velocity			Tidal Range (mm)
				Same hour	Prev 2 h mean	Prev 4 h mean	Prev 12 h
(a) Alongshore	Surface	Behind surf	r	.1347	.1838	.2299	-.1724
			n	14	14	14	126
			p	ns	ns	ns	ns
	2 m	Inshore	r	.1623	.1665	.1208	.6844
			n	8	8	8	8
			p	ns	ns	ns	ns
	5 m	Inshore	r	-.3817	-.4070	-.3856	-.2409
			n	25	25	25	30
			p	ns	*	ns	ns
	2 m	Offshore	r	-.0629	-.0949	.0333	.6844
			n	5	5	5	8
			p	ns	ns	ns	ns
	5 m	Offshore	r	-.2571	-.2815	-.2786	-.2409
			n	30	30	30	30
			p	ns	ns	ns	ns
	10 m	Offshore	r	-.2556	-.2666	-.2426	-.2115
			n	30	30	30	30
			p	ns	ns	ns	ns
(b) Across- shore	2 m	Inshore	r	-.2407	-.3074	-.2957	.5734
			n	8	8	8	8
			p	ns	ns	ns	ns
	5 m	Inshore	r	-.5437	-.5650	-.5067	-.2539
			n	25	25	25	25
			p	**	**	*	ns
	2 m	Offshore	r	.0458	.0040	-.0347	.9303
			n	5	5	5	5
			p	ns	ns	ns	*
	5 m	Offshore	r	-.4293	-.4749	-.4788	-.3568
			n	30	30	30	30
			p	*	**	**	ns
	10 m	Offshore	r	-.3612	-.3904	-.3806	-.2932
			n	30	30	30	30
			p	*	*	*	ns

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Discussion

Validation of current measurements

Drogue measurements on each day were highly correlated among zones and depths, and some non-significant results were probably due to low sample sizes rather than lack of correlation (Table A2.1). The surface (video) and drogue measurements of alongshore currents were also positively correlated, though not as strongly. This could have been predicted, as surface currents are much more subject to the changing orientation and speed of wind and offshore swells. When the simultaneous sub-surface drogue measurements were compared with the ADCP measurements at Black Rock and Dog Point Bay, the recorded current direction was the same, and the measurements fell within those taken by the ADCP (Table A2.3). It is likely that drogue measurements of both the across- and alongshore velocity components were biased due to the stress of surface winds, currents and occasional breaking waves and varying surface velocity on the drouges' lines and floats, but these biases are not quantified here.

Currents at Black Rock were faster than those taken in Dog Point Bay, 2.5 km north and in the same water depth. These differences are due to the shape of the coastline: Black Rock is a relatively large headland, forcing winds and currents to accelerate as they move around it, while the bays provide wider channels for the same volume of air and water and are therefore likely dissipative, allowing both alongshore wind and currents to slow (Mann and Lazier 1996).

The Agulhas Current is one of the fastest boundary currents in the world; its core generally lies just offshore of the shelf break and attains speeds of 0.6 $m.s^{-1}$ 35 km from shore in the study area, increasing by 0.06 $m.s^{-1}$ every 100 km as it travels southward (Schumann 1988; 1998). In their shipboard ADCP measurements nearest the Maputaland coastline, Donohue and Toole (2003) recorded speeds of approx. 0.2 $m.s^{-1}$ at a water depth of 100-300 m over seafloor depths of 1000-2000 m. To the north, current speeds in the Mozambique Channel have been recorded in excess of 2 $m.s^{-1}$ (Saetre and da Silva 1984). Alongshore subsurface coastal (in- and offshore) currents in my study were generally one to two orders of magnitude slower than in the Agulhas, due to the shear forces at the coastal boundary layer – as is typical of nearshore environments (Mann and Lazier 1996).

Steinke and Ward (2003) released plastic drift cards of the same buoyancy as mangrove propagules from the mouths of three rivers, including the Mhlathuze River (28.50°S) near Richards Bay, south of the study area (see Chapter 4, Figure 4.3). The maximum travel rates from release to recovery on the beach for cards released from the Mhlathuze River were 0.004 $m.s^{-1}$ to the north and 0.020 $m.s^{-1}$ to the south. The most rapidly traveling card in the study (> 0.036 $m.s^{-1}$) was released from a second river near Durban, south of the Mhlathuze, and recovered from Ponta Dobela in Mozambique (26.52°S), north of my study area. It is unknown whether these cards were restricted to the nearshore longshore drift or were transported alongshore further offshore before they returned to the beaches and were recovered, but velocity measurements in both the nearshore and offshore environments fall within the estimates from my survey. In an investigation of the role of embayments in relation to meroplanktonic larvae and benthic community dynamics in the St. Lawrence Estuary, Archambault and Bourget (1999) found median surface current speeds of < 0.05 $m.s^{-1}$ at 3 m depth within bays and 0.1 to 0.5 $m.s^{-1}$ outside bays and along straight stretches of coast. The range of current speeds measured in my study by the 2-m drogues fell within these two sets of measurements. Other current measurements on the inner shelf include alongshore

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speeds of 0.02 $m.s^{-1}$ (mean) and 0.06 to 0.1 $m.s^{-1}$ (max) at Duck, NC, USA (Garland and Zimmer 2002), and alongshore current speeds of 0.02-0.08 $m.s^{-1}$ and cross-shore current speeds of 0-0.02 $m.s^{-1}$ at the same location (Shanks et al. 2002). These measurements match those of my study for the alongshore component of the velocity, but are slower in the across-shore component.

In a study of wind-forced surface currents and the dispersal of crab larvae in Chesapeake Bay, Johnson (1995) measured surface currents of 0-0.25 $m.s^{-1}$ in both the across- and alongshore components, somewhat slower than I recorded. However, the wind stress measured in his study ranged 0-1.5 $dyn.cm^{-2}$, from which I calculated wind velocities of 0-8 $m.s^{-1}$, using equations provided by Mann and Lazier (1996). Therefore, both wind speed and surface currents at Chesapeake Bay were slower than those measured using the video method in my study.

In the nearshore environment (between the surf zone and the shore), alongshore currents matched previous velocity measurements in the area. In a previous drogue survey over five days (27 Nov to 2 Dec 2000) in a small bay just north of Mabibi Point (see Figure 1.1 for location), Jury et al. (2001) found current speeds that were similar in range to the nearshore surface currents measured using video (Table A2.7). Integrated results over several years confirmed nearshore speeds of 0.01 to 1.0 $m.s^{-1}$, with a mode of 0.3 $m.s^{-1}$ (Mitchell et al. 2005). In calibrated optical measurements of the nearshore and surf zone environment, Chickadel et al. (2003) recorded nearshore speeds of 0.35 to 1 $m.s^{-1}$ and swash and surf-zone alongshore speeds of 0.1 to 0.8 $m.s^{-1}$ (Table A2.7).

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Table A2.7 Nearshore current speeds measured *in situ* in other studies

Data source	Instrument	Location	Distance from shore	Zone	Direction	Speed ($m.s^{-1}$)
Jury et al. (2001)	Drogue	Mabibi, KZN, South Africa	10-20 m	Nearshore	North, then reverses to south	0.19
			60-80 m	Nearshore	North	0.20
			70-80 m	Nearshore	North	0.33
			150-180 m	Behind surf?	North	0.42
Chickadel et al. (2003)	Optical	Duck, NC, USA	120 m	Nearshore	South	0.1
			140 m	Nearshore	South	0.3
			160 m	Nearshore	South	0.5
			180 m	Surf zone	South	0.7
			200 m	Behind surf	South	0.6
			220 m	Behind surf	South	0.4

Processes driving currents

Along- and across-shore velocity, measured using all available methods, showed coherence with wind speed and direction, indicating wind forcing as a major determinant of current velocities. In some periods during the ADCP deployment, wind-induced Ekman transport was observed, but these events were uncommon, and Ekman transport was secondary to wind stress in determining directional flow of the subsurface waters. The wind stress required to set up Ekman transport is about 0.26 $dyn.cm^{-2}$ (caused by wind speeds of ~3 $m.s^{-1}$) (Shanks 1995). While the effects of

Ekman transport can be visible in coastal waters < 100 m depth, Shanks (1995) notes limitations to Ekman theory, notably that if water depth is shallower than the depth of the wind's direct influence, or if the presence of land retards the flow of water at the coastal boundary, then the entire water column will tend to move roughly downwind rather than in the net left-perpendicular direction predicted by the Ekman spiral in the southern hemisphere. This has important implications for recruitment studies.

Schumann (1998) reports few estimates of tidal currents on the shelf of southern Africa. In analyses of current-meter records in 29 m water off Port Edward (31°S, just south of KZN), Schumann and Perrins (1982) reported tidal fluctuations were less important than the influence of the Agulhas Current, although Welsh (1964, reviewed in Schumann 1998) found evidence of inertial currents even further south on the Agulhas Bank. My study site was much further north of the Port Edwards measurements, however, where the power and velocity of the Agulhas Current are reduced (Donohue and Toole 2003). In my offshore ADCP study (17 m depth), as on the Agulhas Bank, current measurements showed a tidal influence on both along- and across-shore current velocities. I found no correlations between nearshore current speeds and tidal velocity in the drogue or video measurements, however. This corresponds to the situation described by Mitchell et al. (2005), who observed that the very nearshore current at Mabibi was persistently northward and was coupled neither to tidal events nor to wind events except during strong north-northeasterly winds. Instead, very nearshore currents were most likely driven by the dominant swell direction on that day relative to the position of the measurements along the coastline (whether on the exposed or lee side of the headland) and the tidal height (Mann and Lazier 1996).

Conclusion

Current measurements taken by each of the techniques were similar in direction and velocity to each other and to previous measurements taken in the Maputaland area, and are driven by nearshore coastal processes such as winds (very nearshore) and winds and tides (further offshore). Therefore, these measurements were accepted as valid and used without correction in the empirical advection model presented in Chapter 4.

References

References are found in the main reference list for the thesis.

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