

Scale-dependent patterns and processes of intertidal mussel recruitment around southern Africa

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ABSTRACT: Different processes shape ecological communities at different physical scales. Their relative importance is central to ecology, particularly in the case of foundational species like mussels. For 5 yr at 8 locations across 5 bioregions spanning 3200 km of the southern African coast, we monitored recruitment and adult populations of 4 intertidal mussel species. At most locations, mussel bed width and percent cover were surprisingly constant, but declines did occur at 3 locations. Recruitment rates displayed a strong geographic gradient: exceptionally high on the West Coast, low on the South Coast and intermediate on the East Coast. At a regional scale, significant positive relationships existed between the magnitude of annual recruitment maxima and (1) adult abundance, (2) intertidal primary productivity and (3) the magnitude of upwelling. Recruitment was highest at locations with large adult populations, high productivity and more upwelling. Within locations, recruitment varied inconsistently among sites, years and seasons. Sea temperature and recruitment were seasonal at all locations except in the southern Benguela, suggesting they are linked. At the medium scale (<1 km), at which local hydrology is believed to be important, relationships between recruitment and adult abundance were observed at only 2 locations, while at the smallest scale (<1 m), significant positive relationships were more common. Two of the 3 locations with lowest recruitment were recruit-limited. This has important management implications because low-recruitment and recruit-limited locations in southern Africa occur where human exploitation is most intense.

KEY WORDS: Mytilid mussel settlement · Supply-side ecology · Large-scale coastal processes · *Mytilus galloprovincialis* · *Perna perna* · *Semimytilus algosus* · *Aulacomya ater*

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INTRODUCTION

Problems of pattern and scale are central to ecology. Many ecologists consider the influence of scale on processes underlying patterns to have been insufficiently addressed, despite its importance being raised repeatedly and with increasing exposure (e.g. Huffaker 1958, Wiens 1989, Sandel & Smith 2009). In particular, conclusions from local experiments should not be spatially extrapolated without understanding the processes operating across multiple

scales (Levin 1992). Scale-dependence is of special importance in the case of 'foundational species' (sensu Dayton 1972) that affect species of management concern. This includes, for example, interactions between forest fauna and resident birds (e.g. Smith et al. 2008) and the impact of shrub mounds on desert plant communities (e.g. Wright et al. 2006). Recognizing this issue, ecologists have begun to investigate interactions at multiple scales, often using a 'comparative-experimental approach' (e.g. Menge et al. 2002).

In the rocky intertidal, mussels have been shown to be foundational species because mussel beds provide habitat for many other intertidal organisms. The understanding of community dynamics and the spatio-temporal scales at which mussel populations operate has evolved from an initial focus on top-down control by predators (Paine 1974) to incorporate 'supply-side' processes that affect community interactions in a bottom-up manner (Underwood & Fairweather 1989). Both models and experiments have been used to examine effects of the arrival of pelagic larvae to shore (i.e. settlement) on community structure (e.g. Xavier et al. 2007). This body of work has been strengthened by large-scale inter-regional and long-term inter-annual studies of both larval settlement and the maturation of settlers into the adult population, i.e. recruitment (e.g. Hyder et al. 2001, Navarrete et al. 2005, Schoch et al. 2006).

We report patterns and underlying processes of the recruitment of several intertidal mussel species, measured over 5 yr at 8 locations that lie across 5 bioregions covering 3200 km around the coast of southern Africa. Previous studies of rocky-shore invertebrate recruitment over large spatial scales include barnacles in Europe (e.g. Jenkins et al. 2000, Hyder et al. 2001), corals in the Great Barrier Reef (Hughes et al. 1999, 2000), mussels and barnacles in California and Oregon, USA (Connolly et al. 2001), and mussels and barnacles in Chile (Navarrete et al. 2002). At an even larger scale, researchers have spanned hemispheres (Menge et al. 2002, Navarrete et al. 2008).

The results of these studies indicate that large-scale differences in recruitment intensity of benthic intertidal species arise from a combination of oceanographic, climatic and biological conditions, all of which operate at multiple, and often differing, spatial scales. Although ocean currents and coastal winds are strongly directional, local hydrography can be retentive or dispersive depending on shoreline topography and inter-annually variable offshore and nearshore conditions (Graham & Largier 1997, Connolly & Roughgarden 1998, Botsford 2001, Navarrete et al. 2002, 2005). Recruitment success is influenced at regional scales both before and after settlement by biological factors including local spawner stock biomass (Fisk & Harriott 1990), spawner fecundity (Hughes et al. 2000), larval condition and degree of starvation (Olson & Olson 1989), larval duration in the water column (Grantham et al. 2003), predation by conspecific adults (Porri et al. 2008a) and physical disturbance (Hunt & Scheibling 1996). Settlement and recruitment also vary temporally on multiple scales, linked to changes in the physical environment. For example, El Niño-Southern Oscillation (ENSO) events help explain inter-annual differences in recruitment rates in some

areas (Botsford 2001), while seasonal and daily differences in settlement or recruitment have been correlated with shorter-term hydrographic events for several species (e.g. Porri et al. 2008b, Shanks 2009a,b).

The relative importance of these effects varies among taxa and sites at all scales and can even co-vary (Menge et al. 2003). As a result, the relationship between adult abundance and recruitment rates has been investigated at multiple scales for a variety of marine organisms with short- and long-dispersing larvae (e.g. Yoshioka 1982, Hughes et al. 2000), although the scales at which recruitment is studied often have not matched the scale at which populations transition from 'open' to 'closed' (Roughgarden et al. 1985), thus complicating our understanding of adult-recruit relationships. Further, attempts to explicitly select an observation scale are problematic because genetic evidence challenges the long-held idea that pelagic larval duration affects dispersal distance and therefore indicates the diameter of closed intertidal populations (Weersing & Toonen 2009). Nevertheless, we know that, even within a closed population, adults and arriving recruits influence each other at multiple scales. For example, Roughgarden et al. (1985) demonstrated that barnacle settlement rate directly affects the size distribution of cohorts at the scale of the rocky shore and that the variety of cohorts in a given area in turn influences the settlement of additional cohorts at small scales. In contrast, at a biogeographic scale, Hughes et al. (2000) found that recruitment of corals was best explained by adult fecundity, rather than simply by adult density, year, or sector of the reef, indicating that recruits and adults influence one another at medium spatial scales.

Thus, the choice of size, distribution and replication of sampling units can all strongly influence conclusions about processes that underlie recruitment patterns and the relationship of recruitment to adult abundances (Underwood & Petraitis 1993). This has been addressed for coral reefs and rocky shores by examining and comparing adult abundance and recruitment at multiple spatial scales (e.g. Hughes et al. 1999, Methratta & Petraitis 2008), and we take a similar approach here.

A crucial issue in the ecology of benthic invertebrates is the degree to which populations are recruitment-limited. In addition to exploring relationships between recruitment intensity and adult abundance at different spatial scales, we examined whether recruit-limitation is linked to recruitment intensity. Working with barnacles, Connell (1985) has argued that settlement rates will only be related to recruitment levels when settlement levels are low, because it is only then that the supply of settlers will limit the number of recruits. Taking one further step, Caley et al. (1996) have

restricted the term 'recruitment limitation' to circumstances when recruitment 'adds to or subtracts individuals from a population'. Thus, a population can be regarded as recruit-limited when recruitment appreciably affects the density of juveniles or subadults at a later time. Menge (2000) has demonstrated that for barnacles, direct adult-recruit relationships are species-specific and can be masked by post-settlement effects such as heat and desiccation.

The coastal environment of southern Africa is characterized by strong temperature and productivity gradients (Bustamante et al. 1995, Lombard et al. 2004) and a variety of types and intensities of upwelling. Wind-driven upwelling on the West Coast supports high levels of primary productivity (Bustamante & Branch 1996). On the South and East Coasts, upwelling is absent from many areas, but persistent topographically induced upwelling cells draw relatively nutrient-rich waters into small retentive eddies in the Natal Bight and at Port Alfred and Port Elizabeth (Roberts 2005); these cells are supplemented by the interaction of wind and topography around prominent headlands (Schumann et al. 1982, Schumann 1999).

In 1995, 6 institutions in Namibia and South Africa began a 5 yr study of mussel recruitment around southern Africa. Four intertidal mussel species were monitored: *Mytilus galloprovincialis* (Lamarck), *Perna perna* (Linnaeus), *Semimytilus algosus* (Gould) and *Aulacomya ater* (Molina). Harris et al. (1998) reported on the first year of data for 7 locations. They found significantly greater recruitment densities on the West than on the South or East Coasts and a strong correlation between recruitment and adult densities at this spatial scale. Data collection continued for 4 more years, incorporating an eighth location and increasing the number of sites per location. The present study includes the full data set and investigates the recruitment of intertidal mussels at multiple spatial and temporal scales. It has clear relevance for coastal conservation and mussel fishery management, as recruitment patterns and processes influence community structure and functioning, harvesting effects and the replenishment of depleted mussel beds.

This paper addresses 3 principal objectives, providing (1) a description of patterns of variation in recruitment among sites, locations, seasons, years and species; (2) tests of possible causes of these patterns;

and (3) an investigation of the impacts of recruitment on adult beds.

MATERIALS AND METHODS

Field data. Mussel recruitment and adult mussel abundance were measured seasonally at 8 locations around the coast of southern Africa (Fig. 1, Table 1). No known harvesting took place at any of the locations because they were inaccessible or located in protected areas. Sites were selected to ensure consistency of slope (<30°), topography (rock faces were smooth, although rock type varied) and wave action (all open-coast wave-exposed; see Harris et al. 1998). Sampling methods followed those detailed in Reaugh et al. (2007) and Reaugh-Flower et al. (2010). At each location, 4 sites 1 to 25 km apart were selected, except at Dwesa (3 sites) and Zululand (5 sites). At each site, a fixed 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 6 perpendicular transects, each spanning the width of the mussel bed. Every 3 mo, the width of the mussel bed was measured and the percent cover of mussels (for all species pooled) was scored using 50 × 50 cm quadrats placed at 1 m intervals along the perpendicular transects.

Recruitment was measured in 3 randomly selected 10 × 10 cm quadrats with 100% cover of mussels within 1 m of the horizontal transect. Samples were sorted and all mussels measured, counted and identified. 'Recruits' were defined as late plantigrades or early juveniles with a 0.5 to 5.0 mm shell length; 'subadults' as individuals 5 to 10 mm (for the smaller species *Aula-*

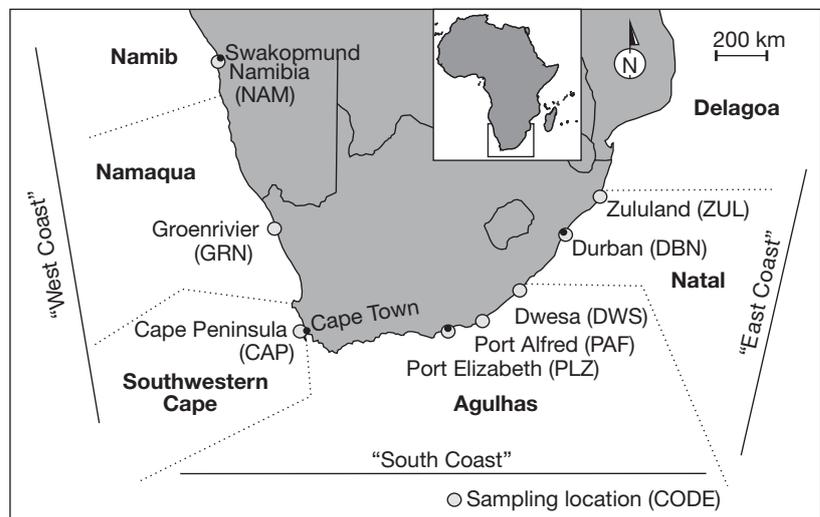


Fig. 1. Sampling locations and bioregions (**bold**, from Lombard et al. 2004) in southern Africa. Abbreviated codes for location names are given in parentheses

Table 1. Characteristics of sites and sampling periods at each location

Location (CODE) Site	Mussel spp. ^a	Longitude (E)	Latitude (S)	Distance to next location (km)	Nearshore ocean climate	Sampling period Start	End
Namibia (NAM)							
Badewanne	S,M,P	14° 31' 31.2"	22° 42' 02.0"	951	Persistent year-round upwelling ^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"				
Groenrivier (GRN)							
Esterhuizen	M,A	17° 37' 51.5"	30° 56' 32.9"	375	Seasonal upwelling downstream site ^d	Jul 95	Sep 99
Gert Joseph		17° 31' 48.5"	30° 45' 11.8"				
Island Point		17° 36' 12.1"	30° 54' 55.0"				
Island Wreck		17° 36' 09.6"	30° 55' 00.7"				
Cape Peninsula (CAP)							
Blouberg	M,A	18° 25' 25.2"	34° 19' 39.7"	795	Active seasonal upwelling cell ^d	Jul 95	Oct 99
Kommetjie		18° 19' 13.2"	34° 08' 27.1"				
Scarborough North		18° 22' 11.9"	34° 12' 27.0"				
Scarborough South		18° 22' 26.5"	34° 13' 08.9"				
Port Elizabeth (PLZ)							
Houghham North	P	25° 45' 54.0"	33° 45' 26.0"	101	Within Algoa Bay, close to divergent upwelling ^e	Oct 96	Oct 99
Houghham South		25° 45' 05.9"	33° 45' 53.5"				
Humewood		25° 40' 53.1"	33° 59' 40.2"				
Summerstrand		25° 41' 23.3"	34° 00' 23.4"				
Port Alfred (PAF)							
Kenton East	P	26° 41' 56.7"	33° 40' 47.3"	278	Divergent topographical upwelling ^e	Jul 95	Jul 99
Kenton West		26° 41' 12.5"	33° 40' 58.7"				
Kowie		26° 52' 41.4"	33° 31' 29.2"				
Old Woman's		27° 06' 51.1"	33° 37' 14.4"				
Dwesa (DWS)							
Dwesa North	P	28° 52' 06.9"	32° 17' 23.1"	371	Straight coast, narrow shelf, no upwelling ^f	Jun 95	Mar 00
Dwesa S 1		28° 49' 30.3"	32° 18' 58.3"				
Dwesa S 2		28° 49' 01.8"	32° 19' 31.2"				
Durban (DBN)							
Mdloti South	P	31° 07' 47.6"	29° 38' 52.8"	183	Center of Natal Bight, no upwelling ^g	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		31° 05' 48.0"	29° 42' 30.0"				
Zululand (ZUL)							
Crayfish	P	32° 25' 36.7"	28° 25' 11.5"	–	Divergent topographical upwelling ^g	Mar 95	Sep 99
Railway ^b		32° 24' 59.0"	28° 28' 06.9"				
Sandy		32° 24' 25.2"	28° 30' 20.0"				
Zavini		32° 25' 10.2"	28° 26' 54.4"				

^aDominant mussels: M = *Mytilus galloprovincialis*, S = *Semimytilus algosus*, P = *Perna perna*, A = *Aulacomya ater*
^bSampled monthly at 2 sites (north and south)
^cDemarcq et al. (2003)
^dAndrews & Hutchings (1980)
^eLutjeharms et al. (2000)
^fRoberts (2005)
^gMcLachlan et al. (1981)

comya ater and *Semimytilus algosus*) or 5 to 35 mm long (for the larger species *Mytilus galloprovincialis* and *Perna perna*); 'small adults' as respectively 10 to 15 mm or 35 to 70 mm long; and 'large adults' as respectively >15 mm or >70 mm long. The size range we used to define recruits is larger than that generally employed in studies measuring recruitment at shorter time intervals because we needed to ensure incorpora-

tion of all settlers that arrived over the period. Samples were collected in winter (June–July), spring (September–October), summer (December–January) and autumn (March–April), except for 2 sites in Zululand, where sampling was monthly.

Analysis of recruitment patterns. We used 3 descriptors of recruitment. 'Recruitment intensity' is defined as the number of recruits counted per unit area of sub-

stratum. 'Peak annual recruitment' is the maximum recruitment intensity measured annually at each location (averaging across replicates and sites) in each year. Because absolute amounts of recruitment differed so much around the coast, 'recruitment events' are defined as all occasions when we recorded >20% of the maximum density of recruits at a given location.

We began investigating recruitment patterns by testing for differences in recruitment intensities among sites, years and seasons for each mussel species at each location using a full-factorial Model II ANOVA. The main effects of year (Y), Season (Sn) and Site (St) were all treated as random factors. Season was included as a main factor so that differences among seasons could be examined—despite the lack of true sampling replication within seasons. Significant results for Season were consequently interpreted cautiously. Data were 4th-root transformed to achieve normality and equality of variance. To make direct comparisons among locations, identical models must be used (Petraitis 1998, Underwood & Petraitis 1993). For locations with 4 collection sites and sufficiently low number of missing data points (Namibia, Groenrivier, Cape Peninsula, Port Alfred and Zululand), identical models were constructed, incorporating 4 yr of data (September–October 1995 to June–July 1999), although for Cape Peninsula, only 3 yr of data (June–July 1995 to March–April 1998) could be incorporated into a $Y \times Sn \times St$ model. Models for the remaining locations were developed according to data characteristics and temporal coverage. These latter models are useful for the information they provide about the individual locations, but are not intended for comparison with the previous set. At Port Elizabeth, Dwesa and Durban, where missing cells or zero values could have led to bias, 4 yr of data (September–October 1995 to June–July 1999) were used, but sites were pooled, leaving a crossed $Y \times Sn$ model. Estimates of components of variance and their percentage contribution were calculated for each factor using restricted maximum likelihood methods. Negative components were set to zero and the remaining factors recalculated following Fletcher & Underwood (2002).

At the 3 locations with more than 1 species present (Namibia, Groenrivier and Cape Peninsula), differences in recruitment intensity were examined among sites and species. The simultaneity of recruitment among species was compared at each location using Kendall's tau (τ) correlations.

Analysis of causes of recruitment patterns. We examined primary productivity and upwelling characteristics as possible drivers of the observed recruitment patterns. Local upwelling characteristics (Table 1) were used to group the locations *a priori* into 1 of 4 categories: (1) wind-induced year-round upwelling (Namibia), (2) wind-induced seasonal upwelling

(Groenrivier and Cape Peninsula), (3) topographically-induced year-round upwelling (Port Elizabeth, Port Alfred and Zululand) and (4) little or no upwelling (Dwesa and Durban). Data for all recruitment events at each site were 4th-root transformed for normality and homoscedascity and coded according to these groups. A 1-way ANOVA was then applied to them, followed by a Tukey's HSD post hoc test.

Published data on primary productivity were compared to peak annual recruitment intensities at each location. As measurements of pelagic productivity were not available at a scale appropriate to our sampling locations, we employed measurements of epilithic intertidal algal production, quantified as mg m^{-2} chlorophyll (chl) a per month (Bustamante et al. 1995). Productivity measurements were compared to annual maximum recruitment rates across all years at each location. Data were $\log_{10}(x + 1)$ transformed to meet assumptions of normality. Species were pooled at locations with multiple species. The relationship was tested for significant differences using a 1-way ANOVA and then for linearity using a regression with replication approach (Zar 1999).

Analysis of impacts of recruitment variation on adult beds. Adult abundance was measured 3 ways: (1) mussel bed width, (2) percentage cover of adult mussel size classes and (3) the number of individual mussels in 0.01 m^2 quadrats of 100% cover was used with information on bed width and cover to estimate the total number of mussels in the mussel bed.

Because we were interested in annual trends, temporal changes in mussel bed width at each location were examined with 1-way ANOVAs with Year as a fixed categorical factor. Seasons and sites were pooled within years. Data were 4th-root transformed to meet assumptions. For bed width, years with too few measurements (i.e. <5) were excluded from the analysis. For locations with a significant result, Tukey's HSD post hoc tests were used to identify significant groupings. Where different time periods were used for different locations, results are indicative for a particular location only and not for comparisons among locations.

Differences in mussel bed percentage cover were compared among locations with a 1-way ANOVA using data from September–October 1996 to March–April 1998 (when all 8 locations were regularly sampled). Seasons and years were pooled. Percent cover data were $\arcsin(0.01x^{0.5})$ transformed to meet assumptions for parametric testing. Significant groupings were identified with Tukey's HSD post hoc tests.

Relationships between recruitment intensity and adult abundance during recruitment events were examined using correlation analyses at 3 scales, which were selected to inform about processes that act at different scales (Underwood & Petraitis 1993). At the

largest scale (1000s of km, or among locations) and medium scale (<1 km, or within sites), adult abundance was defined as the mean number of post-recruit mussels in a 1 m strip of the mussel bed perpendicular to shore at that site, as measured in the larger-quadrat samples, and species were pooled. The large-scale analysis examines the possibility that overall adult abundance influences recruitment. The medium-scale assessment investigates whether local oceanographic conditions may over-ride any large-scale adult-recruit relationship. At the smallest scale (<1 m, within locations), adult abundance was defined as the number of post-recruit mussels in 10 × 10 cm quadrats, and species were examined individually. At this scale, the analysis examines the likelihood that adults influence recruitment via small-scale processes such as larval selectivity or larval consumption by adults.

To examine evidence for recruitment limitation (*sensu* Caley et al. 1996), we used the correlation between recruitment intensity during recruitment events and the change in cover of subadult mussels in 50 × 50 cm quadrats over the subsequent 3 mo. Locations were identified as 'recruit-limited' if the relationship between recruit density and change in subadult density was positive and significant. At Namibia, *Semimytilus algosus* was excluded from this calculation so that results for the other 2 species, *Perna perna* and *Mytilus galloprovincialis*, could be compared to other locations in the study.

RESULTS

Recruitment patterns

Within-location variability in recruitment intensity was plotted over time for each species at each site (Fig. 2) and tested with multi-way ANOVAs (Table 2). At Namibia, Year was the highest-contributing main factor for *Mytilus galloprovincialis* and *Perna perna*, whereas Site was most important for *Semimytilus algosus*. At Groenrivier, Site was the most explanatory factor for both *M. galloprovincialis* and *Aulacomya ater*, and the same was true at Port Alfred for *P. perna*. In contrast, Season was the most important factor for *P. perna* at Zululand. At Cape Peninsula, where species could be compared, Year was the most important contributing factor for both *M. galloprovincialis* and *A. ater*. For the remaining locations, comparisons of variance components among locations could not validly be undertaken because the time periods and models for these locations were not the same. Sites were pooled for these 3 locations (see 'Materials and methods—Analysis of recruitment patterns'). Season contributed more than Year to variance for *P. perna* at Port Eliza-

beth and Durban; the opposite was true at Dwesa. In summary, Site and Year effects were more important on the West Coast, whereas Season effects tended to be more important on the South Coast and particularly the East Coast.

Year interacted significantly with at least 1 other main factor at all locations except Port Elizabeth, indicating that even strong Site or Season effects are frequently obscured by annual fluctuations in the influencing environment (e.g. pre- and post-settlement effects).

Recruitment was synchronous between *Mytilus galloprovincialis* and *Aulacomya ater* at all sites at Cape Peninsula and Groenrivier ($\tau = 0.405$ to 0.589 , $n > 33$, $p < 0.0001$ in all cases), indicating a relative homogeneity of pre- and post-recruitment effects among sites at these 2 locations. In Namibia ($n = 54$ in all tests), recruitment was not synchronized between any species at Langstrand South, but was synchronous between all species at Badewanne ($\tau = 0.198$ to 0.451 , $p < 0.05$ in all cases). At Mile Four, *Perna perna* and *Semimytilus algosus* recruitment was synchronized ($\tau = 0.264$, $p = 0.0037$), and at Langstrand North, *P. perna* and *M. galloprovincialis* recruitment was synchronized ($\tau = 0.241$, $p = 0.0102$).

Causes of recruitment patterns

There was a strong gradient of recruitment intensity around the coast, with high levels of recruitment on the West Coast, low levels on the South Coast, and intermediate levels on the East Coast. Recruitment differed significantly among level of productivity ($F_{6,364} = 149.2$, $MS = 89.4$, $p < 0.0001$). A Tukey's HSD test revealed that all South and East Coast locations (which had low levels of productivity) differed significantly from those on the West Coast, and that Namibia and Groenrivier, with the highest values for productivity and recruitment, were significantly different from Cape Peninsula (Fig. 3). The relationship between productivity and recruitment was not, however, linear ($F_{6,363} = 31.5$, $MS = 18.8$, ns).

Recruitment intensity was also clearly related to the intensity and predictability of upwelling (Fig. 4). A 1-way ANOVA indicated significant differences among the 4 categorical ranks of upwelling ($F_{3,1203} = 134.0$, $MS = 872.5$, $p < 0.0001$). A Tukey's HSD post hoc test revealed that recruitment was highest in the location with year-round, wind-induced upwelling (Namibia), intermediate in locations with seasonal wind-induced upwelling (Groenrivier and the Cape Peninsula) and lowest in the remaining locations, which had topographically-induced (divergent) upwelling or no upwelling.

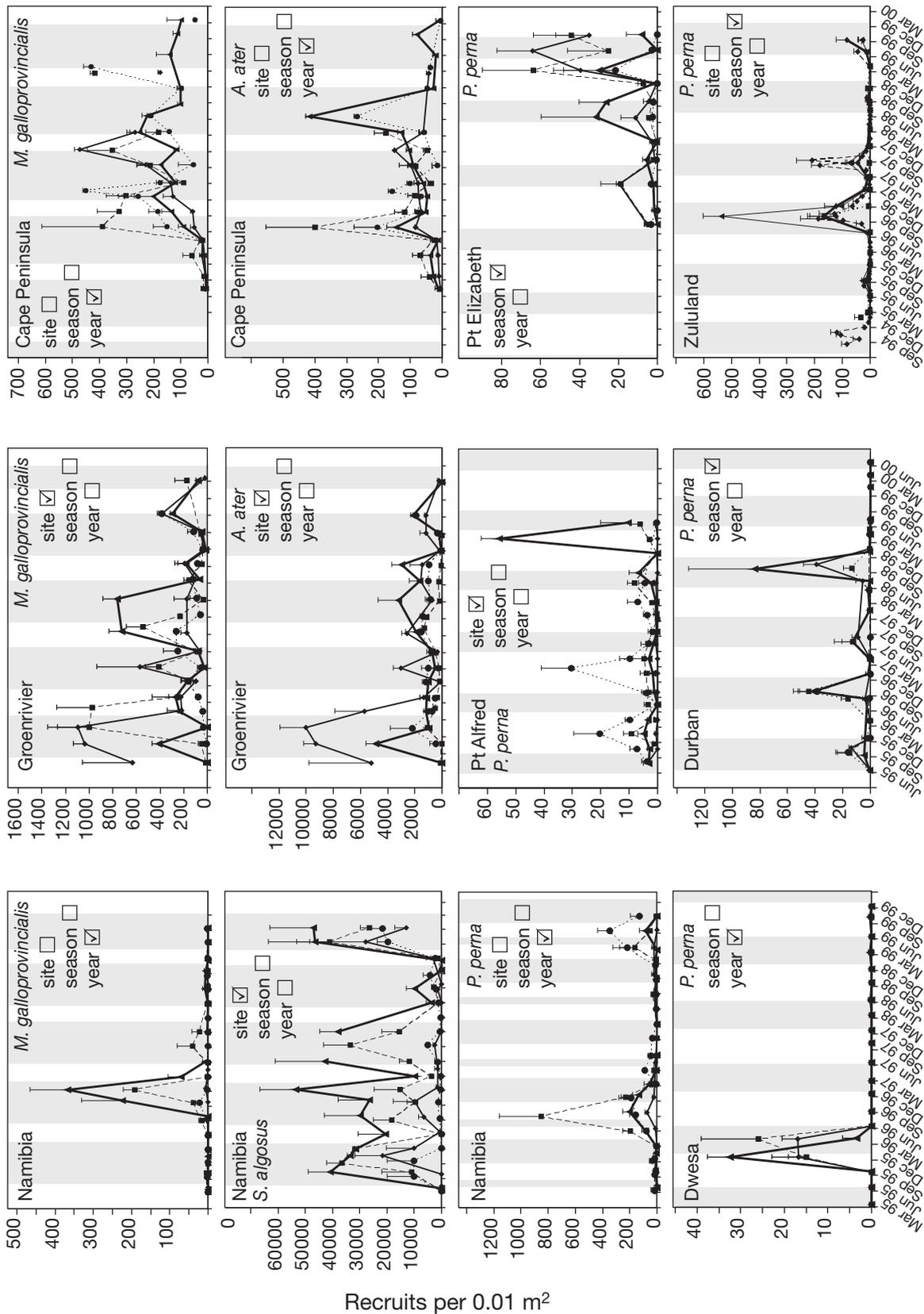


Fig. 2. Mussel recruits (mean + SE) per 0.01 m² for each species and site per location. Vertical shaded bars denote spawning periods for *Perna perna*: Namibia (B. Currie, unpubl. data); Port Elizabeth and Port Alfred (from data for Port Alfred; Ndzipa 2002); Dwesa (from data for adjacent Hlukeka, Eastern Cape; Lasiak 1986); Zululand and Durban (Berry 1978, J. M. Harris unpubl. data). For the Cape Peninsula, bars denote spawning periods of *Mytilus galloprovincialis* and *Aulacomya ater* combined (van Erkom Schurink & Griffiths 1991). For Groenrivier, bars denote upwelling season: spawning there is expected to be similar to that of the Cape Peninsula—protracted and without a strong seasonal cycle. For Namibia, bars denote recruitment season for *Semimytilus algosus* and *M. galloprovincialis*. Main effects contributing at least 20% to variance (from Table 2) are indicated with a tick in a box below species names. Line styles indicate sites (see Fig. 5)

Effects of recruitment variation on adult beds

Mussel bed width was examined graphically (Fig. 5) and using 1-way ANOVA. The mussel beds at 6 locations maintained a steady overall width over the years sampled, however, 2 beds diminished significantly over time, perhaps indicating a 'winding down' process. At Dwesa ($F_{5,48} = 4.57$, $MS = 0.067$, $p = 0.002$), the bed was significantly wider in 1995, intermediate in 1996 and 1998, and narrower in 1997, 1999 and 2000. Zululand, which was marginally non-significant ($F_{4,71} = 2.47$, $MS = 0.051$, $p = 0.052$), showed a pattern of diminishment followed by recovery across 5 yr.

A 1-way ANOVA among locations showed that there were clear biogeographic differences in mussel cover ($F_{7,189} = 48.23$, $MS = 1.24$, $p < 0.0001$), which declined from the West Coast through the South Coast sites of Port Elizabeth, Port Alfred and particularly Dwesa, where cover was consistently lowest (Fig. 6a,b). Cover at the East Coast sites was intermediate. Most sites also maintained a consistent total percentage cover of mussels among years, apart from Zululand, where the cover steadily decreased (Fig. 6a). In almost all cases the relative contributions of different size categories changed systematically over time.

At the largest scale (1000s of km), there was a strong and significant relationship between peak recruitment intensity and adult abundance ($r = 0.677$, $n = 125$, $p < 0.001$) and between peak recruitment intensity and total mussel percent cover ($r = 0.648$, $n = 125$, $p < 0.001$).

At the medium scale (within sites, i.e. < 1 km), recruitment during recruitment events was significantly positively correlated to adult abundance at only 1 of the 8 locations: Port Alfred (Table 3).

At the smallest scale (< 1 m), recruitment intensity was significantly correlated with adult density in 6 of the 12 cases (Table 4), with 3 significant relationships for *Perna perna* (Port Elizabeth, Durban and Namibia), 2 for *Mytilus galloprovincialis* (Namibia and Groenrivier) and 1 for *Semimytilus allosus* (Namibia). No significant rela-

tionships were detected for *Aulacomya ater*, probably due to low adult densities, as the mussel beds it occupied were dominated by *M. galloprovincialis*.

Table 2. Within-location ANOVAs for recruitment of each species; *Sn* = season, *St* = site, *Y* = year. **Bold:** significant results ($p < 0.05$). Numbers of sites and dates following each location indicate the segment of the dataset that was selected to allow robust and comparable ANOVAs. Data were 4th root transformed for analysis. Note that only locations with the same analyzed number of sites and sampling period can be directly compared with one another

Species	Factor	df	MS	F	p	Variance component	% Variance
Namibia (4 sites, Sep–Oct 1995 to Jun–Jul 1999)							
<i>Mytilus galloprovincialis</i>							
	<i>St</i>	3	5.536	3.177	0.1235	0.083	6.1
	<i>Sn</i>	3	3.439	1.597	0.2911	0.019	1.4
	<i>Y</i>	3	21.923	5.967	0.0128	0.403	29.7
	<i>St</i> × <i>Sn</i>	9	0.655	0.614	0.7730	0	
	<i>St</i> × <i>Y</i>	9	2.152	2.019	0.0819	0.108	8.0
	<i>Sn</i> × <i>Y</i>	9	2.566	2.407	0.0415	0.146	10.8
	<i>St</i> × <i>Sn</i> × <i>Y</i>	24	1.066	2.559	0.0004	0.179	13.2
	Error	122	0.417			0.417	30.8
<i>Semimytilus allosus</i>							
	<i>St</i>	3	414.203	6.170	0.0175	8.601	29.0
	<i>Sn</i>	3	157.515	8.901	0.0347	2.836	9.6
	<i>Y</i>	3	130.743	1.905	0.2051	1.621	5.5
	<i>St</i> × <i>Sn</i>	9	17.235	0.959	0.4959	0	
	<i>St</i> × <i>Y</i>	9	67.788	3.772	0.0044	4.873	16.5
	<i>Sn</i> × <i>Y</i>	9	18.432	1.026	0.4484	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	24	17.972	2.066	0.0055	2.980	10.1
	Error	122	8.697			8.697	29.4
<i>Perna perna</i>							
	<i>St</i>	3	10.215	3.327	0.0696	0.190	9.2
	<i>Sn</i>	3	5.096	0.622	0.6154	0	
	<i>Y</i>	3	34.386	4.248	0.0338	0.701	33.8
	<i>St</i> × <i>Sn</i>	9	2.181	1.936	0.0949	0	
	<i>St</i> × <i>Y</i>	9	2.013	1.787	0.1234	0.041	2.0
	<i>Sn</i> × <i>Y</i>	9	7.148	6.346	0.0001	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	24	1.126	2.118	0.0043	0	
	Error	122	0.532			1.144	55.1
Groenrivier (4 sites, Sep–Oct 1995 to Jun–Jul 1999)							
<i>M. galloprovincialis</i>							
	<i>St</i>	3	4.239	1.362	0.4049	0.074	5.1
	<i>Sn</i>	3	1.435	0.369	0.7814	0	
	<i>Y</i>	3	1.429	0.281	0.8376	0	
	<i>St</i> × <i>Sn</i>	9	2.742	0.766	0.6483	0	
	<i>St</i> × <i>Y</i>	9	3.956	1.105	0.4010	0	
	<i>Sn</i> × <i>Y</i>	8	4.716	1.317	0.2885	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	21	3.581	8.742	< 0.0001	0	
	Error	114	0.410			1.365	94.9
<i>Aulacomya ater</i>							
	<i>St</i>	3	35.411	5.339	0.0744	0.864	21.0
	<i>Sn</i>	3	1.673	0.156	0.9212	0.085	2.1
	<i>Y</i>	3	15.711	0.946	0.4591	0	
	<i>St</i> × <i>Sn</i>	9	2.949	0.558	0.8152	0	
	<i>St</i> × <i>Y</i>	9	8.941	1.693	0.1534	0	
	<i>Sn</i> × <i>Y</i>	8	12.958	2.454	0.0475	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	21	5.281	4.214	< 0.0001	0	
	Error	114	1.253			3.163	76.9

Table 2 (continued)

Species	Factor	df	MS	F	p	Variance component	% Variance
Cape Peninsula (4 sites, Jun–Jul 1995 to Mar–Apr 1998)							
<i>M. galloprovincialis</i>							
	<i>St</i>	3	0.850	0.500	0.6943	0	
	<i>Sn</i>	3	1.758	0.441	0.7313	0	
	<i>Y</i>	2	18.818	4.157	0.0551	0.425	45.1
	<i>St</i> × <i>Sn</i>	9	0.656	1.651	0.2072	0	
	<i>St</i> × <i>Y</i>	6	1.385	3.500	0.0309	0	
	<i>Sn</i> × <i>Y</i>	6	3.519	8.907	0.0007	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	12	0.395	1.633	0.0970	0	
	Error	87	0.242	0.500	0.6943	0.518	54.9
<i>A. ater</i>							
	<i>St</i>	3	1.486	0.588	0.6428	0	
	<i>Sn</i>	3	2.686	2.490	0.1641	0.039	2.6
	<i>Y</i>	2	35.739	14.669	0.0039	0.939	62.9
	<i>St</i> × <i>Sn</i>	9	0.789	1.569	0.2307	0	
	<i>St</i> × <i>Y</i>	6	2.148	4.288	0.0154	0	
	<i>Sn</i> × <i>Y</i>	6	0.765	1.530	0.2494	0.038	2.8
	<i>St</i> × <i>Sn</i> × <i>Y</i>	12	0.501	1.740	0.0718	0	
	Error	87	0.288			0.477	31.9
Port Alfred (4 sites, Sep–Oct 1995 to Jun–Jul 1999)							
<i>P. perna</i>							
	<i>St</i>	3	8.724	7.181	0.0136	0.209	31.1
	<i>Sn</i>	3	1.015	0.422	0.7408	0	
	<i>Y</i>	3	0.388	0.239	0.8670	0	
	<i>St</i> × <i>Sn</i>	9	1.236	2.611	0.0305	0	
	<i>St</i> × <i>Y</i>	9	0.462	0.975	0.4853	0	
	<i>Sn</i> × <i>Y</i>	9	1.645	3.474	0.0076	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	23	0.473	1.741	0.0292	0	
	Error	120	0.272			0.462	68.9
Port Elizabeth (4 sites, Sep–Oct 1996 to Jun–Jul 1999)							
<i>P. perna</i>							
	<i>Sn</i>	3	5.839	23.320	<0.0001	0.330	34.6
	<i>Y</i>	2	0.074	0.262	0.7724	0	
	<i>Sn</i> × <i>Y</i>	5	0.186	0.283	0.9216	0	
	Error	103	0.657			0.624	65.4
Dwesa (3 sites, Sep–Oct 1995 to Jun–Jul 1999)							
<i>P. perna</i>							
	<i>Sn</i>	3	2.193	0.974	0.4467	0	
	<i>Y</i>	3	6.123	2.721	0.1068	0.162	34.6
	<i>Sn</i> × <i>Y</i>	9	2.251	18.030	<0.0001	0	
	Error	128	0.125			0.306	65.4
Durban (4 sites, Sep–Oct 1995 to Jun–Jul 1999)							
<i>P. perna</i>							
	<i>Sn</i>	3	23.421	14.638	0.0012	0.593	55.9
	<i>Y</i>	3	0.565	0.354	0.7874	0	
	<i>Sn</i> × <i>Y</i>	8	1.644	4.170	0.0002	0	
	Error	134	0.394			0.467	44.1
Zululand (4 sites, Sep–Oct 1995 to Jun–Jul 1999)							
<i>P. perna</i>							
	<i>St</i>	3	18.446	3.804	0.0518	0.151	9.6
	<i>Sn</i>	3	64.043	2.960	0.0962	0.477	30.4
	<i>Y</i>	3	15.812	0.645	0.6029	0	
	<i>St</i> × <i>Sn</i>	9	1.519	1.255	0.3124	0.020	1.3
	<i>St</i> × <i>Y</i>	9	4.546	3.753	0.0050	0	
	<i>Sn</i> × <i>Y</i>	8	21.253	17.548	<0.0001	0	
	<i>St</i> × <i>Sn</i> × <i>Y</i>	23	1.211	3.072	<0.0001	0	
	Error	471	0.394			0.921	58.7

Only 2 locations (Port Elizabeth and Dwesa) yielded evidence of recruitment limitation (Fig. 7). These were among the 3 locations with the lowest recruitment levels. No significant positive relationships were found for the remaining 6 locations.

DISCUSSION

Recruitment patterns and causes

Persistent differences in recruitment density at large spatial scales, such as those we detected among locations, are common (e.g. Hughes et al. 2002, Navarrete et al. 2002) and have been variously attributed to latitude, wind patterns and differences in coastal topography, which in turn influence local hydrography. In our study, strong west-to-east gradients of intertidal primary productivity and differences in both the intensity and type of upwelling explained much of the continental-scale variability in recruitment. Mussel recruitment was highest in areas identified as having high productivity (Bustamante et al. 1995, Bustamante & Branch 1996, Lombard et al. 2004) and constant wind-driven upwelling (Shannon 1985), and lowest in areas with low productivity and topographically induced or no upwelling (Schumann 1999, Roberts 2005). Reaugh-Flower et al. (2010) have previously noted this gradient of recruitment. On the West Coast, where multiple species recruited at each location, intrinsic differences among the species involved may have contributed to this pattern. Nevertheless, when comparing individual species, the pattern holds, with greater recruitment for *Mytilus galloprovincialis* and *Aulacomya ater* at Groenrivier than at Cape Peninsula, and greater recruitment for *Perna perna* at Namibia than at any of the South and East Coast sites.

Our results parallel those of Menge et al. (2003), who found mussel recruitment to be strongly and significantly correlated with both upwelling and the concentration of chl *a* when

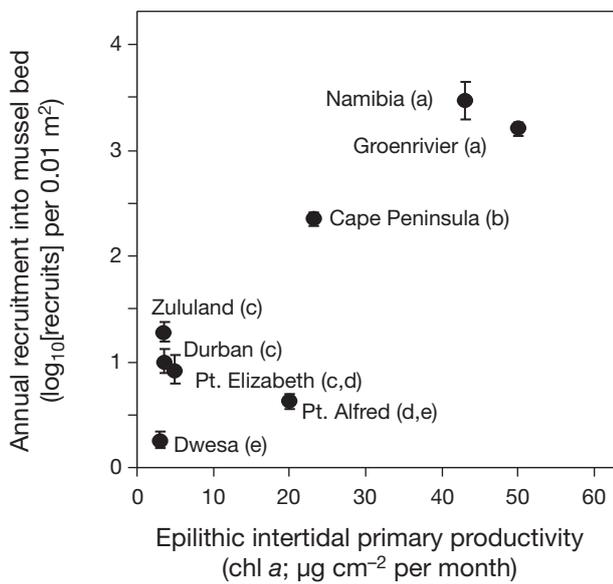


Fig. 3. Annual recruitment (mean maximum ± SE) versus epilithic primary productivity around the coast of southern Africa. Primary productivity data are from Bustamante et al. (1995). Productivity data for Durban were used for both Durban and Zululand. Significant groupings from a Tukey's HSD post hoc test are indicated by lower-case letters in parentheses following location name

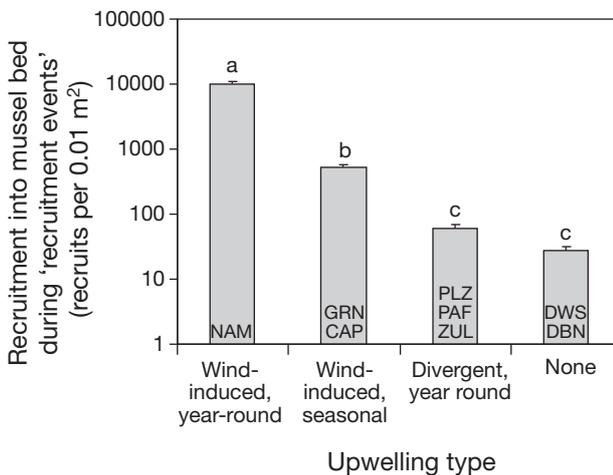


Fig. 4. Recruitment intensities (mean + SE) at all recruitment events, grouped according to type of nearshore upwelling. Lower-case letters express significant groupings from post hoc tests ($p < 0.05$). Location abbreviations within bars are explained in Fig. 1

they compared locations on the east and west coasts of New Zealand. Several correlative studies have documented how nearshore primary productivity strongly influences rocky intertidal community structure (Bustamante et al. 1995, Menge et al. 1997a, Navarrete et al. 2005). Coastal oceanographic features such as upwelling and retention cells control

the delivery of particulate matter, nutrients and propagules to rocky shores, thus influencing community structure and the strength of adult interactions (Navarrete et al. 2005).

At a regional scale, the relationship between adult abundance and recruitment was very strong. Parallel patterns have been detected in large-scale observations on other continents (e.g. Menge et al. 2003, Navarrete et al. 2005), and are likely to have 2 root causes. (1) Enhanced food supplies will increase larval survival and hence settlement and recruitment; they will also improve conditions for adults, thus elevating reproductive output and, ultimately, larval abundance (Hughes et al. 2000). (2) The retentive or extractive nature of local environments has been shown to significantly influence settlement and thus both recruitment success (Byers & Pringle 2006) and adult abundances (von der Meden et al. 2008). In a comparative study of South Africa and Chile, Wieters et al. (2009) have shown that nearshore hydrographic conditions exert a strong influence on community structure, with recruitment as a likely driver (e.g. Porri et al. 2008b). However, Xavier et al. (2007), working on the West Coast of South Africa, failed to find strong links between mussel recruitment and most measures of adult abundance.

Upwelling is, therefore, a two-edged sword. It enhances productivity, but it can also transport food materials and larvae offshore. At the scale of the whole coast, one edge of the sword — productivity — emerges as the dominant element influencing recruitment. But at more local scales, the transport and supply of materials and larvae is likely to cause smaller-scale geographic differences in population dynamics due to reduction of recruitment at focal points of upwelling and its concentration in downstream 'upwelling-shadows' where larvae are returned to the shore during relaxation after the passage of upwelling events (Andrews & Hutchings 1980, Pfaff et al. 2010). Upwelling aside, coastal topography *per se* can also significantly affect recruitment over medium scales (10s to 100s of km) (Gaines & Bertness 1992).

We predicted that locations with strong seasonal temperature patterns (i.e. those on the South and East Coasts) would have strong seasonal recruitment patterns, whereas locations with weaker seasonal temperature patterns and greater day-to-day variability (the West Coast locations of Cape Peninsula, Groenrivier and Namibia) would not show any obvious seasonality in recruitment. In Namibia, Season did not contribute as strongly as Year to recruitment of *Mytilus galloprovincialis* or *Perna perna*. The strong year effect was likely due to recruitment failures in several years. Site explained most of the recruitment variability for *Semimytilus algosus*, indi-

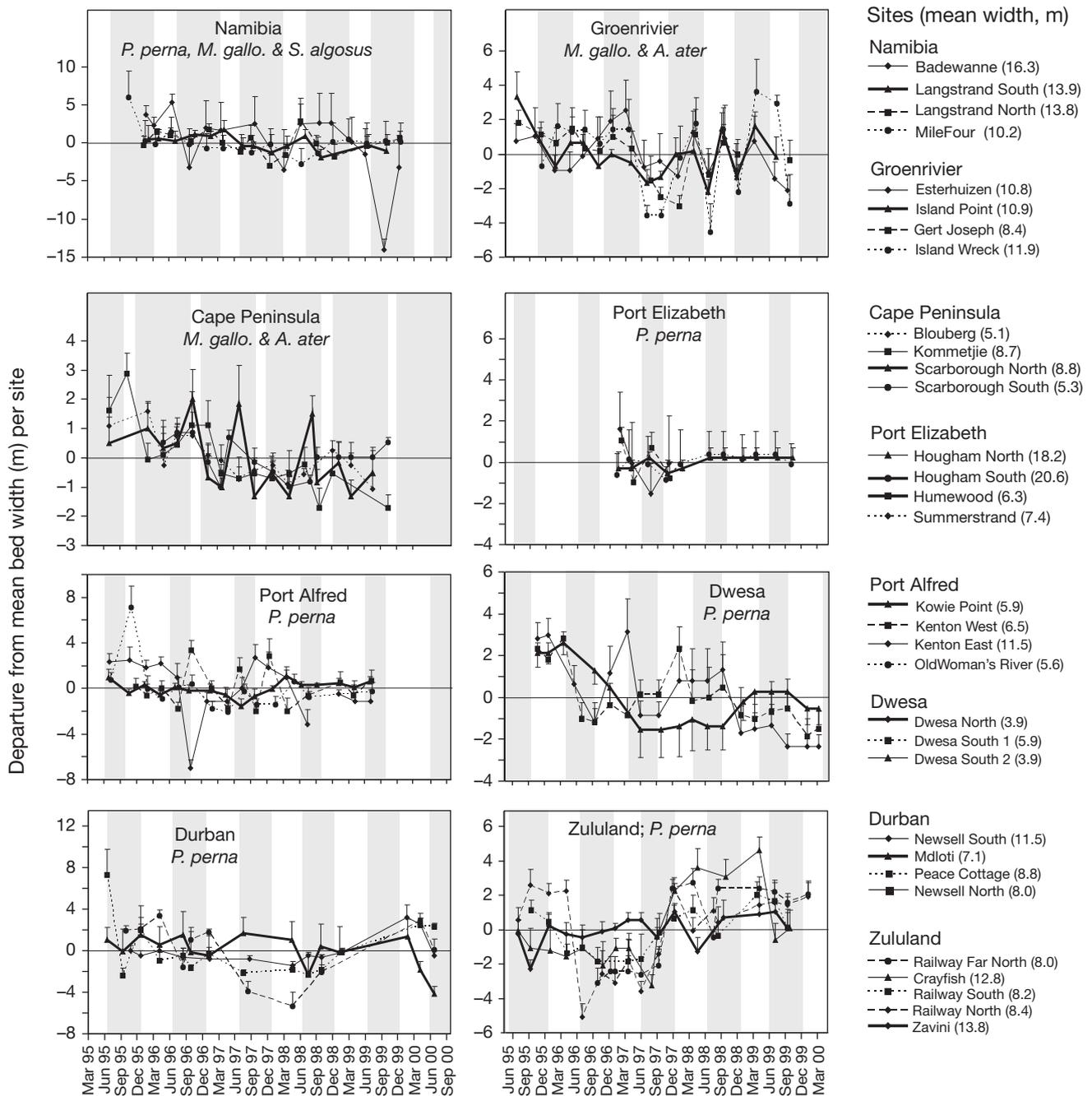


Fig. 5. Departures from mean mussel bed width (m) +SE or -SE at each site sampled per location for the 4 species *Perna perna*, *Mytilus galloprovincialis*, *Semimytilus algosus* and *Aulacomya ater*. Occasional radical dips at individual sites, followed by recovery within 1 to 6 seasons, were due to sand inundating the mussel beds and then washing away, allowing recovery. Vertical shaded bars denote seasons as in Fig. 2

cating that local hydrographic conditions are important for this species, which exhibits year-round recruitment and differences among sites in Chile (Navarrete et al. 2008).

In contrast to shorter-term studies that have suggested increased recruitment during the upwelling season

on the West Coast of South Africa (van Erkom Schurink & Griffiths 1990, Robinson et al. 2007), recruitment of *Mytilus galloprovincialis* and *Aulacomya ater* was not correlated with or explained by Seasons at Groenrivier or Cape Peninsula (Table 2). Pulsed upwelling-positive wind events during the summer

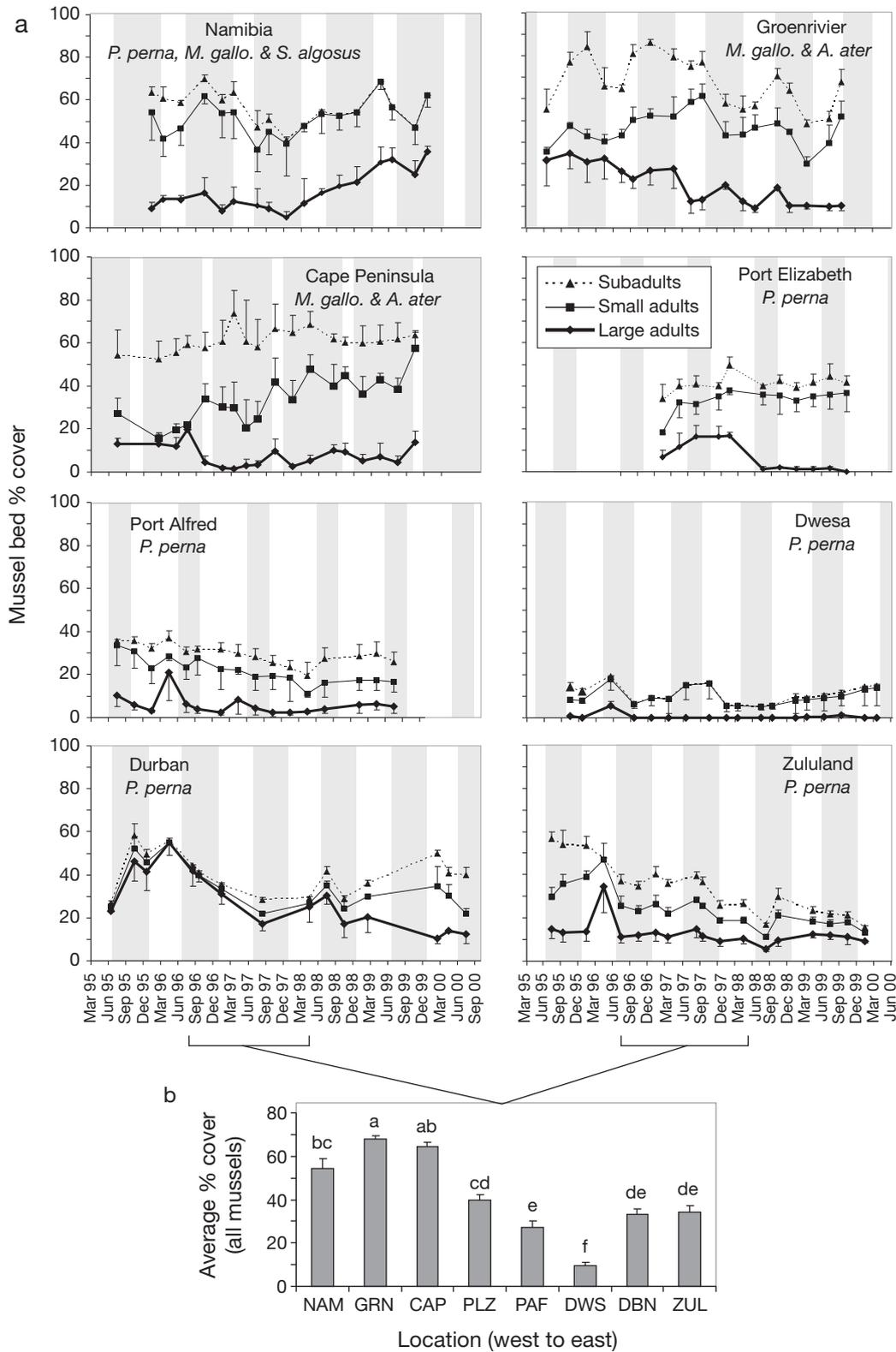


Fig. 6. (a) Percent cover of size classes of *Perna perna*, *Mytilus galloprovincialis*, *Semimytilus alkosus* and *Aulacomya ater* in the mussel beds, mean + SE or -SE. Because the graphs are additive, the subadult line also shows total cover. Vertical shaded bars denote seasons as in Fig. 2. Size classes are defined as subadult (5 to 35 mm long), small adult (35 to 70 mm) or large adult (>70 mm). (b) Mean percent cover of all mussels from September–October 1996 to March–April 1998. Location abbreviations are explained in Fig. 1. Letters denote significant groupings from Tukey’s HSD post hoc test ($p < 0.05$)

Table 3. Correlations between recruitment rates and adult abundance at medium scale (i.e. <1 km, within sites), for untransformed densities of post-recruit mussels (>5 mm) and densities of recruits (≤5 mm) during recruitment events. All species pooled at locations with multiple species. Significant results (p < 0.05) in **bold**

Location	r	n	p
Namibia	-0.286	105	0.003
Groenrivier	0.246	43	0.112
Cape Peninsula	0.113	96	0.271
Port Elizabeth	-0.199	11	0.557
Port Alfred	0.601	18	0.008
Dwesa	0.029	10	0.938
Durban	0.043	27	0.833
Zululand	0.020	20	0.933

upwelling season can cause temperatures to fluctuate daily by up to 9°C (Andrews & Hutchings 1980), and mean temperatures are cooler in summer than in winter (Demarcq et al. 2003). A more constant supply of larvae into the water column during protracted spawning, a limited seasonal temperature signal (van Erkom Schurink & Griffiths 1991) and persistent onshore transport of surface waters during regular relaxation events could all contribute to the near absence of any seasonal recruitment pattern at these 2 locations.

On the South and East Coasts, nearshore sea temperatures differ by approximately 6°C between the warmer summer and cooler winter, and day-to-day variability is relatively small (Roberts 2005, K. Reaugh-Flower unpubl. data). We predicted that recruitment would be strongly seasonal on these coasts. Indeed, Season was the greatest contributing factor to *Perna perna* recruitment variance at 3 out of the 5 locations on these coasts (Port Elizabeth, Durban and Zululand). All these locations had regular annual recruitment events and strong synchrony among sites within locations. This accords with previous studies showing highly seasonal spawning and/or recruitment at or near these locations (Berry 1978, Lasiak 1986, Zardi et

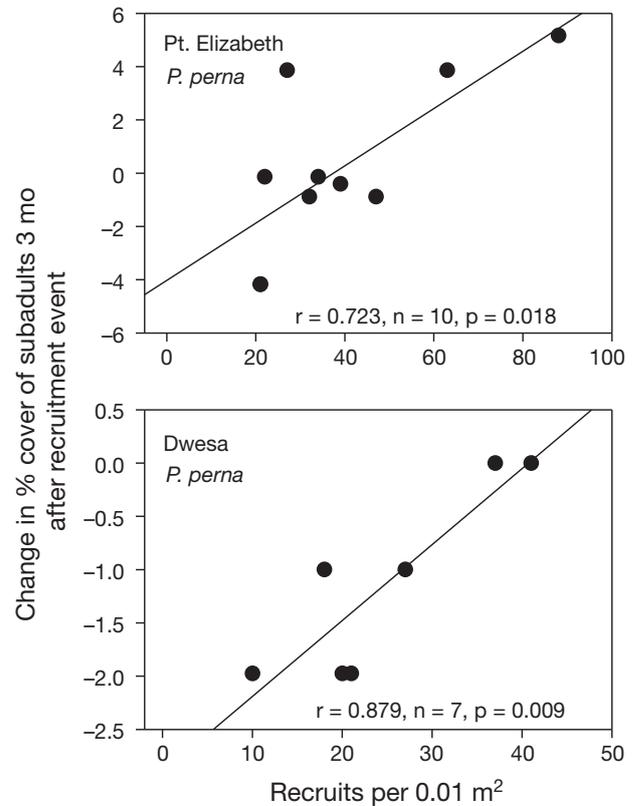


Fig. 7. *Perna perna*. Pearson product-moment correlations between recruit densities in 10 × 10 cm quadrats during recruitment events at Port Elizabeth and Dwesa, and the change in the percent cover of subadults in the mussel bed 3 mo later. Significant positive correlations indicate recruitment limitation

al. 2007). Port Alfred lacked a seasonal pattern, supporting previous reports of irregular seasonal and annual recruitment and spawning around this location (Ndzipa 2002, McQuaid & Lawrie 2005, Porri et al. 2006a,b). Any possible seasonal signal at Dwesa was masked by recruitment failure in 4 of the 5 years, a pattern supported by previous records of reproductive failure there (Lasiak 1986). Thus, although the exact

Table 4. Significant adult–recruit relationships at smallest scale (<1 m), indicating local influence of adult beds on recruitment. Lines of best fit describe the simultaneous relationship between untransformed densities of settled mussels (A, >5 mm) and untransformed densities of recruits (Rc, ≤5 mm) of individual species in 0.01 m² quadrats during recruitment events. The resulting models are descriptive of individual cases: where they differ among cases, they should not be used to compare among species or locations

Location	Species	Best fit	Formula	R ²	n	p
Namibia	<i>Perna perna</i>	linear	$Rc = 40.43 + 0.48 \times A$	0.148	93	0.0001
	<i>Mytilus galloprovincialis</i>	log-log	$\text{Ln}(Rc) = 1.94 + 0.56 \times \text{Ln}(A)$	0.314	34	0.0006
	<i>Semimytilus algosus</i>	log-log	$\text{Ln}(Rc) = 6.78 + 0.55 \times \text{Ln}(A)$	0.377	117	<0.0001
Groenrivier	<i>M. galloprovincialis</i>	log-log	$\text{Ln}(Rc) = 1.39 + 0.80 \times \text{Ln}(A)$	0.209	173	<0.0001
Port Elizabeth	<i>P. perna</i>	linear	$Rc = 4.53 + 0.49 \times A$	0.346	50	<0.0001
Durban	<i>P. perna</i>	linear	$Rc = -1.73 + 0.36 \times A$	0.250	38	0.0014

timing of spawning differed among studies, all but 1 location on the South and East Coasts (Port Alfred) showed seasonal recruitment. Any differences in recruitment months or seasonality between our study and those of others may also reflect the fact that we sampled at a relatively coarse temporal scale, whereas others have sampled at monthly (or shorter) intervals.

Impacts of recruitment variation on adult beds

Whereas there was a strong correlation between recruitment and adult abundance at the scale of the whole coast, relationships between adult abundance and recruitment intensity were rare at the medium scale (<1 km, or within-site), and occurred in only 50 % of cases at the small scale (<1 m, or within-quadrat), as summarized in Fig. 8. However, 4 patterns emerged. (1) At the medium scale, the relationship between adult abundance and recruitment was positive and strong at only 2 locations (Port Alfred and Namibia). Thus, as described above, we suggest that local geographic effects influence the adult-recruit relationship at medium scales even when comparing locations with the same species. (2) For *Perna perna*, the ratio of adults to recruits was always high. *P. perna* is known to have generally low recruitment in comparison with other mytilid species (Berry 1978, Erlandsson & McQuaid 2004), and the low recruitment rate is thought to limit adult abundance, although this is not

necessarily the case (see below). (3) For both *Semimytilus algosus* and *Mytilus galloprovincialis*, recruitment rates were very high and adult:recruit ratios were therefore low. The apparent overabundance of recruits implies that recruitment is unlikely to be limiting (Connell 1985). (4) Adults of *Aulacomya ater* were very rare in intertidal mussel beds, despite the fact that we recorded high levels of recruitment. Its low ratios of adults:recruits reflect post-recruitment competition with the invasive mussel *M. galloprovincialis* (Steffani & Branch 2005, Branch et al. 2008), whose high recruitment inputs are fueled by dense adult beds. However, since our data were gathered, Robinson et al. (2007) recorded much lower recruitment of *A. ater* between 2004 and 2005, hinting at more recent recruitment failure of this species.

At the smallest scale (<1 m), there was a significant relationship between adult abundance and recruit density in 6 of the 12 instances. At this scale, we explored whether adults influence recruitment via small-scale processes. The strong relationships that we observed in Namibia and at Groenrivier are consistent with other findings. In a study near Groenrivier, Robinson et al. (2007) experimentally manipulated the densities of adult *Mytilus galloprovincialis* and found, as we did, that recruitment was dependent on the density of adults, as would be expected of aggregating species. The effects of adults may be positive, if they provide suitable settlement habitat, but also may be muted by larviphagy—the consumption of larvae by adults

(Porri et al. 2008a). The generally weak to non-significant relationships between adult and recruit *Perna perna* densities recorded on the South and East Coasts are consistent with the findings of Erlandsson & McQuaid (2004), who concluded that the role of intertidal algae, an important but inconsistent primary settlement substratum for *P. perna* (Reaugh et al. 2007), could obscure small-scale relationships between adult abundance and recruitment.

Management implications

Harvesting intertidal shellfish has been an integral part of coastal societies in southern Africa for at least 120 000 yr and continues to be important today (Griffiths & Branch 1997, Griffiths et al. 2004). The important and diverse impacts of human activities on these resources, especially mussels, are well documented (e.g. Kyle et al. 1997,

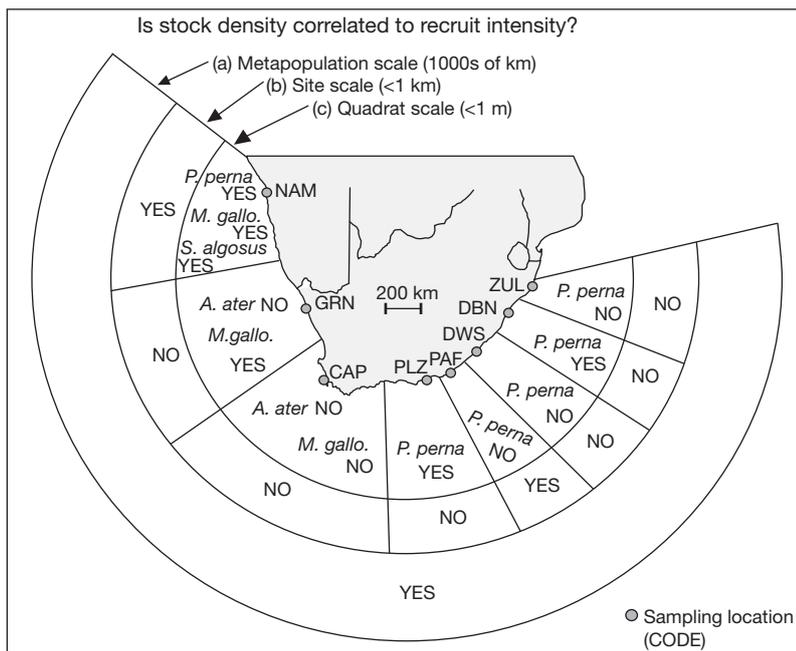


Fig. 8. Summary of stock-recruit relationships for *Perna perna*, *Mytilus galloprovincialis*, *Semimytilus algosus* and *Aulacomya ater* at 3 spatial scales. Location abbreviations are explained in Fig. 1

Branch & Odendaal 2003) and are at the fore of management concerns (e.g. Lasiak 1991, Griffiths & Branch 1997, Harris et al. 2007). Although mytilids on the West Coast are lightly harvested (Robinson et al. 2007), the smaller stocks of mussels along the South and East Coasts are heavily exploited (Griffiths & Branch 1997, Rius et al. 2006).

Recruit-limited populations are in particular need of management because of the risk of local extinction (Jones et al. 2009). We recorded 2 cases of possible recruit-limitation, at Port Elizabeth and Dwesa, which were among the 3 locations with the lowest intensities of recruitment. The third location with low recruitment, Port Alfred, has previously been hypothesised to be recruit-limited (McQuaid et al. 2000), but our results do not support this. As Connell (1985) previously argued for barnacles, while only populations with low recruitment are likely to be limited by the input of settlers or recruits, not all low-recruitment populations are recruit-limited.

In terms of conservation, Dwesa is the most critical location, as it is a marine reserve with low adult standing stocks, very low recruitment and demonstrable recruitment limitation. Mussel beds in and surrounding Dwesa have been of concern to managers and researchers for more than 2 decades (Lasiak 1991, Dye et al. 1997, Dye & Dyantyi 2002). As *Perna perna* rarely exists below the infratidal fringe on either the East Coast (Sink et al. 2007) or the South Coast (Fielding et al. 1994), replenishment of intertidal stocks from this source is not possible. Heavy harvesting on proximate sections of the coast could reduce larval settlement in the reserve, further limiting recruitment.

The mortality of adult mussels, when not sufficiently replenished with adequate levels of recruitment, will cause a slow 'winding-down' of the mussel bed. This was evident for bed width at Dwesa and Zululand (with a comparable but non-significant decline at Cape Peninsula). How do mussel beds persist in the face of such progressive diminishment? Our study demonstrated that the magnitude of recruitment events varied temporally; in 5 instances recruitment occurred largely in a single year. Organisms with high fecundity and high pre-reproductive mortality that spawn in unpredictable nearshore environments occasionally experience 'sweepstake' recruitment events, in which unusually high numbers of individuals recruit in a single year (e.g. Flowers et al. 2002). These events can be driven by oceanographic phenomena that vary on interannual scales, such as ENSO, and Paine & Trimble (2004) have even argued that they can drive a transition to an alternative stable state. On the West Coast, these sweepstake blanket-recruitment events are fairly common, occurring on intra-decadal (3 to 6 yr) time scales (Griffiths 1977). It is certain that our study

did not record the full variability of recruitment on the East Coast, where there is evidence that mussel stocks intermittently experience large blanketing settlement events on a multi-decadal time scale. Berry (1978) reported an anomalous 'massive' recruitment event for *Perna perna* in October 1976, which spanned the East Coast, blanketing the entire intertidal zone. A second such event occurred in Zululand in the spring of 1994, when up to 100% of mussel beds and patches of coralline algae became densely covered by *P. perna* recruits (B. Tomalin unpubl. data). In the Gulf of Maine, Witman et al. (2003) reported a massive recruitment of subtidal mussels that had important effects for both consumers and local competitors. They concluded that episodic events such as these powerfully influence marine community dynamics.

CONCLUSIONS

Our results document intertidal mussel recruitment and mussel-bed dynamics spanning 5 yr and multiple scales around the 3200 km coast of southern Africa and elucidate the processes that underpin patterns at different scales. At the largest scale, we observed a strong adult-recruit relationship, probably driven by an inter-regional gradient in primary productivity and differences in upwelling intensity, a known driver of primary productivity.

Understanding the effects of spatial and temporal scales influences how (or even whether) we perceive patterns, because the influence of different processes can vary across scales. This has critical implications for the management of exploited populations. Our data demonstrate that factors fundamental to management, such as adult-recruit relationships, vary with scale, with different processes coming into play. Relationships between adult abundance and recruitment ranged from a highly predictable relationship driven by productivity at the largest scale, through a much less predictable one influenced by selective recruitment to mussel beds at the smallest scale, to a virtually non-existent relationship dependent on local vagaries of hydrographic conditions at the medium scale.

Seasonal patterns were more common on the South and East Coasts than on the West Coast, where upwelling obscures seasonal temperature signals, affecting spawning and therefore recruitment. Synchrony among sites and species at given locations was also unpredictable—some sites and species were closely temporally coupled, while others were not. This may be due to variability in nearshore circulation patterns that affect retention and larval delivery among sites, as well as species-specific differences.

At the medium scale (<1 km), adult densities were strongly correlated with recruit densities at only 2 locations. At this scale, relationships potentially reflect (1) the influence of adult abundance on the production of locally retained larvae (and, hence, recruitment), (2) the attraction of larvae to mussel beds or (3) the effect of recruitment on subsequent subadult abundance, indicating recruit limitation, which was observed at only 2 localities. However, the absence of significant adult-recruit correlations in the large majority of cases argues that local hydrographic effects override any link between adults and recruits.

At the smallest scale (<1 m), simultaneous relationships between adult abundance and recruitment emerged in 6 instances and most likely indicate preferential recruitment to denser mussel patches, as demonstrated by Robinson et al. (2007).

Southern African mussels are important ecologically, economically and socially. McQuaid & Payne (1998) have argued that different regions should have different management strategies, designed for regional circumstances to embrace differences in productivity, recruitment intensity and variability, and human harvesting—all of which alter the resistance and resilience of adult populations to depletion. This principle is not unique, finding parallels in Chile (Castilla & Fernandez 1998, Navarrete et al. 2005) and North America (Schoch et al. 2006, Blanchette & Gaines 2007), and our results support its application in southern Africa.

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