Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa

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Intensity of intertidal mussel recruitment was compared across a range of different spatial and temporal scales around the coast of southern Africa between June 1995 and October 1996. Comparison of the east and west coasts revealed significantly higher recruit densities on the west coast, corresponding to larger adult densities. This difference between the two coasts reflects biogeographic disparities in mussel species composition, growth rates and spawning intensities, oceanographic conditions and productivity. Significant spatial variations in recruitment were recorded between regions 100–1000 km apart and between localities 1–25 km apart. Results suggest that the influence of dispersal processes on recruitment patterns acts at a relatively small scale, and may affect the distribution and abundance of adults among shores only a few kilometres apart. The high variability in recruitment intensities at a scale of metres indicates that larval supply to the shore may be locally patchy, or that settlement preferences of recruits may be sensitive to subtle small-scale differences in adult density within mussel clumps. Small-scale differences in post-settlement mortality (e.g. owing to patchy predation pressure) may also play a role. This small-scale variability in recruitment is likely to reinforce the mosaic distribution of mussels evident on many of the shores. Significant temporal variability in recruit density was recorded, both between 3-monthly sampling intervals and interannually. Seasonal differences were absent for the north-west regions, whereas asynchronous seasonal patterns were displayed in the other regions. Results suggest that temporal cycles of recruitment are irregular and episodic, which may have important consequences for the dynamics of adults. Significant positive correlations were obtained between maximal recruitment and adult abundance, measured by density, or total number of adults on the shore (stock). This could be explained by the density-dependent role of adult conspecifics in providing suitable settlement habitat, or supply-side recruit limitation. These results have important implications for the management of exploited populations of mussels around the coast of southern Africa. Exploitation may influence recruitment success via at least two processes: reduction of larval supply by depletion of adult stock, and alteration of habitat suitable for settlement. Thus, over-exploitation will compromise recruitment, which is itself the only mechanism of recovery. The west-coast mussel populations are likely to be more resilient to exploitation as recruitment is more predictable over time, stocks are larger and recruitment intensities high. This brings into question the present regulations for mussel harvesting because, paradoxically, more lenient regulations are applied on the east coast, where stocks and recruitment are low, than on the west coast, where biomass, recruitment and potential for recovery are high.

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The relative importance of recruitment processes and adult population dynamics in shaping the community structure of marine benthic ecosystems continues to fuel debate, and has spawned much current interest in the field of 'supply-side ecology' (Gaines & Roughgarden 1985; Menge & Farrell 1989; Holt 1990; Menge 1991; Grosberg & Levitan 1992). The paradigm that placed biological factors, such as preda-tion, competition and herbivory at the centre of population regulation and community interactions, has been challenged by strong evidence that recruitment processes often control adult populations (Grosberg & Levitan 1992) and are major determinants of community structure (Roberts, Rittschof, Holm & Schmidt 1991, Eckman 1996).

Most benthic invertebrates have a pelagic larval stage

which contributes to the uncertainty of recruitment. Larval supply depends on larval production, and thus on the size and condition of the adult population and the impacts of environmental variables on spawning (e.g. Starr, Himmelman & Therriault 1990; Chase & Thomas 1995). Dispersal introduces the influence of oceanographic processes (e.g. Butler & Keough 1990; Kingsford 1990), and narrows the odds of safe return to adult habitat, inflicting heavy mortality through predation and exposure to unfavourable conditions (Strathman 1974; Olson & Olson 1989). Integrated, these factors cause spatial variation in larval concentrations and in settlement patterns (Gaines, Brown & Roughgarden 1985). Once larvae have arrived at the adult habitat, settlement is affected by the availability of suitable substrata (Petraitis 1990; Lohse 1993) and a variety of chemical, biological and physical factors (Roberts et al. 1991; Pawlik 1992; Rodriguez, Ojeda & Inestrosa 1993). Survival involves running the gauntlet of physical conditions (McKillup, Butler & McKillup 1995) and biological interactions (including density-dependent processes) in the adult habitat, which impose a high mortality (Olson & Olson 1989).

Considering the number of perilous steps involved in recruitment it is not surprising that dramatic variability in recruitment over time and space at a number of different scales has been reported for some benthic marine invertebrates (e.g. Raimondi 1988; Michener & Kenny 1991; Pennings 1991; Petraitis 1991; McKillup et al. 1995). The extent to which this variability is reflected in adult populations remains unclear, and the nature and strength of the adult (stock)-recruit relationship is an issue of contention. Studies suggest that temporal and spatial variability of larval settlement and recruitment account for a substantial proportion of the variations observed in the distribution and abundance of adults (Holm 1990; McShane & Smith 1991; Moreno, Reyes & Asencio 1993). Adults potentially influence recruitment at three crucial stages; as suppliers of spat, by altering habitat availability during settlement (e.g. Nielson & Franz 1995; Osman & Whitlatch 1995a, b), and by influencing survival of recruits (e.g. Alverado & Castille 1996; Petraitis 1991). Examination of recruitment intensity and adult abundance at a number of different spatial and temporal scales is required to address these questions.

Supply-side ecology is of particular relevance to the management of exploited benthic organisms (Fairweather 1991), because management of harvested populations requires an understanding of the nature and magnitude of temporal and spatial variability of individuals of exploitable size, which may be influenced both by perturbations (e.g. harvesting) and by settlement and recruitment processes (Fogarty, Sissenwine & Cohen 1991). Evidence suggests that alteration of adult habitat influences both settlement and recruitment success (Hurlbut 1991; Lohse 1993). The implications of a stock-recruit relationship for an exploited species are therefore two-fold: the ability to predict recruitment on the strength of stock assessments, and the possibility of a negative feed-back in which a reduction in adult stock influences the ability of the stock to recover, by influencing both the supply of recruits and survival after settlement. Predicting the response of a population to exploitation therefore requires an understanding of the magnitude of recruitment variability, as well as the influence of adult stock depletion on recruitment (Fogarty et al. 1991; Menge, Farrell, Olson, Tamelin Van & Turner 1993).

Mussels are recognized as key species in structuring communities on temperate intertidal rocky shores worldwide (Suchanek 1985). Their exploitation therefore has important implications for rocky shore community structure and conservation of biodiversity, and knowledge about the factors that influence their abundance and recovery from exploitation are essential for effective management. While substantial information exists about stock size, growth rates, larval biology and physiology of the four species that occur intertidally on southern African shores (van Erkom Schurink & Griffiths 1990, 1992), there is little information on their role in community dynamics and the relative importance of recruitment and post-recruitment processes in the temporal and spatial dynamics of mussel populations (Griffiths 1981; Crawford & Bower 1983; Lasiak & Barnard 1995). In addition, most studies are site specific, or conducted over a short time period or in different seasons, reducing their usefulness in understanding large-scale variations.

In this study we examine temporal and spatial variability in recruitment of mussels onto intertidal rocky shores around the coast of southern Africa, and the relationship between adult abundance (stock size) and recruitment intensity. This study is part of a 5-year programme to investigate and compare the importance of biological and physical factors in regulating intertidal community structure, and the implications for management of intertidal marine resources. The execution of experiments and monitoring at seven sites around the coast, each season over five successive years, provides the opportunity to examine variability in natural systems at a number of temporal and spatial scales. This will allow examination of the variability of biological responses around the coast, and the effects of large-scale geographic differences on processes influencing the dynamics of exploited populations. Here we report on the initial findings of the first year-and-a-half of the study, focussing specifically on the results gained by monitoring mussel recruitment.

Materials and methods

Spatial variability was investigated by estimation of mussel recruitment and adult mussel abundance in seven regions (100–1000 km apart) around the coast of southern Africa (Figure 1). In each region three localities 1–25 km apart were selected (except in the Transkei and at Durban where availability of sites necessitated selection of sites closer than 1 km), namely: Badewanne, Langstrand and Mile 4 near Swakopmund in Namibia (Namibia); Esterhuisen, Island Point and Gert Joseph near the Groenrivier mouth on the northwest coast of South Africa (Groen); Scarborough, Blouberg Strand and Kommetjie on the Cape Peninsula (W. Cape); Kenton, Kowie River and Old Woman's River in the Eastern Cape (E. Cape); Dwesa North, Dwesa South 1 and Dwesa South 2 inside the Dwesa Nature Reserve in the Transkei (Transkei); Peace Cottage, Mdloti and Newsell in central KwaZulu-Natal (Durban), and Crayfish Point, Zavini and Railway ledges alongside the Mapelane Nature Reserve on the northern KwaZulu-Natal coast (Zululand) (Table 1). All localities were selected to represent exposed rock platforms (slope < 30°) on

the open coast. The topography of most of the rock surfaces was smooth, while a variety of rock types were represented.
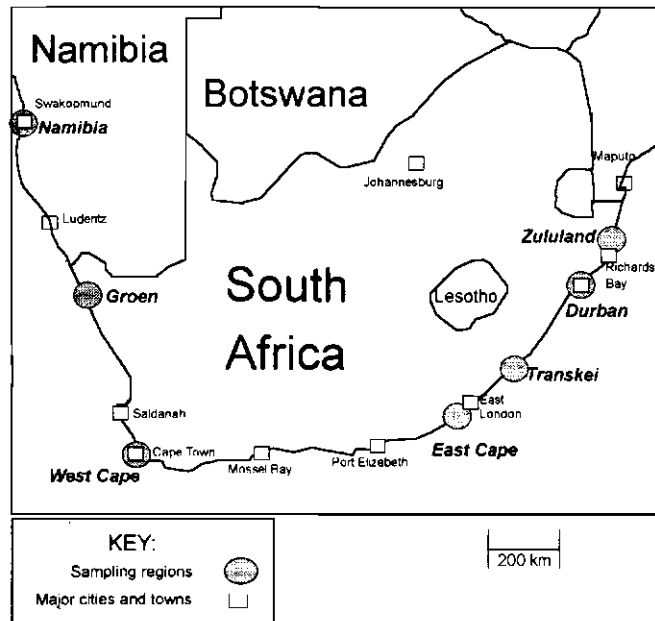
Figure 1 Map showing the position of the seven regions under study around the coast of southern Africa.

The length of rock ledge ranged from 5 km at Groen to 30 m in the E. Cape, and the extent of mussel bed on the rock ledge at each locality ranged from 3 km to 20 m (Table 1).

At each of the three localities in each region, a fixed 20 m transect in the middle of the intertidal mussel bed parallel to the shoreline, and six fixed transects perpendicular to the shoreline and intersecting the 20-m transect at 4-m intervals, were established. On each sampling occasion the per cent cover of mussels in the middle of the mussel bed was estimated using 0.5 × 0.5 m quadrats (n = 20) at 1-m intervals along the 20-m transect (hereafter referred to as 'mid-bed mussel cover'). The area of the mussel bed and total area of mussel cover in the stretch of shore covered by the transects was obtained by scoring per cent cover in 0.5 × 0.5 m quadrats at 1-m intervals along the six perpendicular transects from the spring low-water mark up the shore until mussel cover dropped to < 5% (i.e. to the upper edge of the mussel zone). The number of quadrats per transect was used to determine width of the mussel bed and thus to calculate the area covered by the mussel bed. For each perpendicular transect, the per cent cover was used to estimate the area of mussel cover in the 0.5-m strip up the shore. This value was multiplied by eight to provide an estimate of mussel cover for a 4-m section of shore, and the area of mussels for each of the 4-m sections summed to provide an estimate of mussel cover for a 24-m stretch of shore (hereafter referred to as 'area of

Table 1 Characteristics of rock ledge at each locality in each region. Topography is described as smooth, dimpled (irregularities < 5 cm deep), rough (ridges > 5cm) and cracked (deep fissures > 10 cm). Aspect indicates the direction towards which the shore faces. Rock type: TM, Q and VC Sandstone equals Table Mountain, Quartzitic and Vryheid Complex Sandstone, respectively. Slope is approximate

| Region | Locality | Rock ledge | | | | | Mussel bed | Distance to next |
		length (m)	slope (°)	rock type	topography	aspect	length (m)	locality (km)
Namibia	Badewanne	1200	15	Marble	rough, cracks	W	800	8. 2
	Langstrand N	2000	10	Granite	rough, cracks	W	1000	12.6
	Mile 4	1500	25	Sandstone	smooth, cracks	W	1000	8.2
Groen	Esterhuizen	5000	20	TM Sandstone	smooth	W	3000	6
	Island Pt	3000	15	TM Sandstone	smooth	W	3000	6
	Gert Joseph	500	20	TM Sandstone	smooth	W	500	16
W. Cape	Blouberg	2000	30	TM Sandstone	smooth	NW	500	25
	Kommetjie	2000	12	TM Sandstone	smooth	W	1000	25
	Scarborough N	3000	-12	TM Sandstone	smooth	W	1000	10
E.Cape	Kenton E	30	0	Aeolianite	dimpled	SSE	30	25
	Kowie	30	10	Q Sandstone	smooth	W	20	25
	Old Woman's River	50	0	Q Sandstone	cracked, pools	SW	30	25
Transkei	Dwesa S2	50	10	Shale	dimpled	SE	1000*	0.1
	Dwesa S1	50	10	Shale	dimpled	SE	1000*	0.1
	Dwesa N	1000*	10	Shale	dimpled	SE	1000*	0.5
Durban	Peace Cottage S	100	10	Aeolianite	smooth	E	100	1.5
	Newsell S	300	5	Dolerite	rough	E	300	0.9
	Mdloti S	40	10	VC Sandstone	rough	SE	40	0.9
Zululand	Railway	900	0	Aeolianite	smooth	E	900	1.8
	Zavini	500	10	Aeolianite	smooth	E	500	1.8
	Crayfish	400	15	Aeolianite	smooth	E	400	2.4

* Owing to a lack of ledges with mussel beds, all 3 localities are within the same 1000 m stretch of coast.

mussel population'). The total number of adult mussels (> 35 mm length) in the 24-m stretch of shore was estimated by multiplying the area of adult mussel population by the mean number of adult mussels per 0.01 m² (n = 3) (referred to hereafter as 'size of adult mussel population'). This estimation assumes even adult mussel density across the width of the mussel bed, and it is likely that variation in mussel density across the bed will result in some over- or under-estimation of the adult mussel population (stock) size.

Sampling was conducted at three monthly intervals between June 1995 and September 1996 to determine temporal variability and detect any seasonality in mussel recruitment and population dynamics. To allow comparison between regions, sampling in all of the regions was conducted within a two-month period each season, i.e. winter = June/July, spring = September/October, summer - December/January. autumn = March/April.

On each sampling occasion at each locality, three replicate samples of mussels (1–20 m apart) were collected from the middle of randomly selected dense mussel clumps within 1 m of the fixed 20-m transect. All mussels occurring within each of three 10 × 10 cm quadrats were removed, counted and measured to provide the number of adult mussels (> 35 mm length) and number of recruits per 0.01 m². Recruits were defined as individuals of 1 10 mm length, and thus included post-settlement (late plantigrade) mussels only (Lasiak & Barnard 1995). Hereafter, these measures are referred to as 'mussel density' and 'recruit density', respectively.

One-way analysis of variance (ANOVA) was used to test for significant differences in recruitment on different sampling occasions (seasons) in each region (temporal variability), with data from all the three localities in each region analysed together (n = 9) for this analysis. To investigate scales of spatial variability, ANOVA was used to test whether there were significant differences in maximum mean recruitment (during the month in which peak recruitment was recorded in each region) between (1) the west and east coast (the regions on each coast being analysed together); (2) the regions (data from the localities analysed together, n = 9); and (3) between localities within regions (n = 3). If significant (p < 0.05) differences were detected, the ANOVA was followed by a Tukey multiple range test to allow comparison of means (Zar 1984). The relationships between mussel recruit density and the various estimates of mussel abundance (mussel density. size of mussel population, area of mussel population, mid-bed mussel cover), in the month of peak recruitment in each region. were investigated by simple correlation analysis. All statistical analyses were conducted using the Statgraphics software package (STSC, Inc. 1985 U.S.A).

It should be noted that the dominant intertidal mussel species differ between regions (van Erkom Schurink & Griffiths 1990; Griffiths, Hockey, Van Erkom Schurink & Le Roux 1992). In E. Cape, Transkei, Durban and Zululand *Perna perna* is the only abundant species. In Namibia, *Semimytilus algosus* outnumbers the other species but contributes minimally to biomass, and the invasive alien *Mytilus galloprovincialis* is occurring in increasing densities. At Groen and W. Cape *Aulacomya ater* and *M. galloprovincialis* are present both as adults and recruits in the intertidal. While the recruitment pattern for the different species in each region is pre-

sented, for the purposes of the above analyses the different mussel species are treated as one functional group, and adult and recruit densities and per cent cover for the different species are combined. Later papers will deal with interspecific differences and interactions in detail.

Results

Temporal and spatial variability in recruitment intensity

Mussel recruits were present in the mussel beds in all months sampled in all regions except the Transkei, where no recruits were recorded in June and December 1995 and September 1996 (Figure 2). Extreme spatial variation at the regional scale was recorded and maximum mean recruit densities ranged in magnitude from 5 246.22 (±4 576.71)/0.01 m² at Groen to 15.33 (±14.66)/0.01 m² in the E. Cape (Table 2). Similarly, the minimum mean recruit density recorded at Groen was 616.78 (±580.07)/0.01 m² compared to zero recruitment in the Transkei (Table 2). Recruitment intensity differed significantly (ANOVA, p < 0.05) between regions in
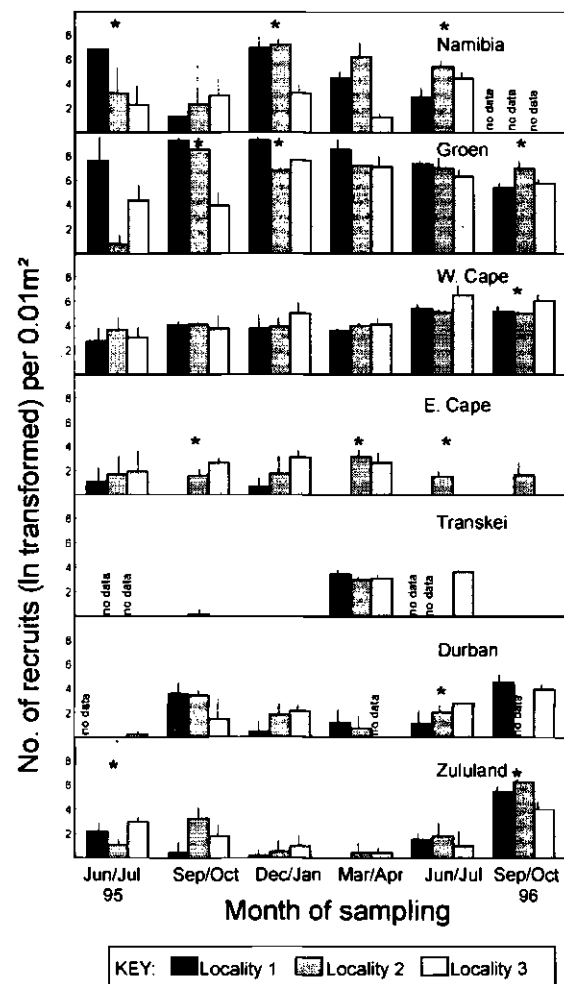
Figure 2 Mean (± SD) density of mussel recruits per 100 cm² of adult mussels at each of three localities (1–25 km apart) in the seven regions sampled around the southern African coast at 3-monthly intervals between June 1995 and October 1996. Occasions where no data exist are represented by 'no data', while blanks indicate that there were no recruits present. Significant differences in recruitment intensity between localities within regions are denoted by * (ANOVA, p<0.05).

Table 2 Mean (± SD) recruit density (number of recruits per 0.01 m²) in each region at 3-monthly intervals between June 1995 and October 1996 (n = 9, alternatively (SD)⁴ denotes n = 4, etc.); nd = no data

| Region	Date					
	Jun/Jul	Sep/Oct	Dec/Jan	Mar/Apr	Jun/Jul	Sep/Oct
Namibia	190.71 (368.92)[7]	185.43 (438.55)[7]	965.51 (969.76)	39.25 (16.65)	124.33 (115.29)	nd
Groen	2011.67 (5213.16)	5246.22 (4575.71)	4740.78 (5125.01)	3002.00 (3051.46)	1227.78 (777.72)	616.78 (580.07)
W. Cape	34.11 (30.39)	58.89 (24.91)	105.00 (94.35)	54.22 (23.14)	415.44 (443.78)	271.11 (185.60)
E. Cape	9.00 (8.75)	6.89 (6.62)	12.22 (13.07)	15.33 (14.66)	1.78 (2.64)	6.78 (9.55)
Transkei	0.00 (0.00)[3]	0.33 (0.71)	0.00 (0.00)	25.25 (8.24)[8]	39.00 (2.83)[2]	0.00 (0.00)
Durban	0.83 (0.75)[6]	27.78 (22.84)	6.33 (5.70)	3.40 (3.13)[5]	9.56 (5.83)	77.17 (41.89)[6]
Zululand	11.67 (9.41)	13.78 (19.59)	2.11 (2.03)	1.11 (1.36)	5.89 (4.68)	285.67 (224.42)

all seasons sampled except winter 1995 (June/July), a period of medium recruitment intensity in all regions (Table 3). In the months sampled between September 1995 and July 1996 mean recruitment intensity was significantly higher in the Groen region than in all other regions. Significant within-region differences, between localities 1–25 km apart (ANOVA, p < 0.05), were obtained in all regions (Figure 2), although significant variability was not detected on the majority of sampling occasions. In the Transkei, no significant differences in recruitment intensity between localities was detected, possibly reflecting the fact that these localities were closer together than in the other regions. These results suggest that spatial variability in recruitment is very high, and is significant at both the regional (100–1 000 km) and local (1–25 km) scales.

Significant temporal variability in recruitment intensity (between 3-monthly sampling periods) was observed in most regions (ANOVA, p < 0.05, Table 3), although clear seasonal patterns of recruitment did not emerge for all regions (Figure 2). No seasonal pattern of recruitment was apparent in Namibia, Groen, and E. Cape. Significantly higher recruitment (ANOVA, p < 0.05) was recorded in autumn and winter in the Transkei in 1996, and in winter and spring in the W. Cape in 1996, while recruitment peaks occurred in spring in both 1995 and 1996 in Durban and Zululand. Peak recruitment over the period sampled was recorded in December 1995 in Namibia, in September 1995 in Groen, July 1996 in W. Cape, March 1996 in E. Cape and March 1996 in Transkei (Table 2). Significant interannual differences (ANOVA, p < 0.05) were obtained in the W. Cape, Transkei, Durban and Zululand, corresponding to the month of peak recruitment and reflecting the substantially higher recruitment pulse recorded in 1996 compared to 1995 in all these regions.

To compare recruitment intensity between regions, the month of peak recruitment over the period sampled was selected for each region and data for the three localities pooled (Figure 3). Highly significant differences in maximum recruitment intensity (ANOVA, F = 9.357, df 58, p < 0.01)

Table 3 ANOVA and Tukey range test results showing significant regional and temporal (seasonal) differences in recruitment of mussels around the coast of southern Africa. Identical letters (a, b) indicate no significant differences (p < 0.05) between regions

(a) Regional differences

	Season					
	Jun/Jul 95	Sep/Oct 95	Dec/Jan 95	Mar/Apr 96	Jun/Jul 96	Sep/Oct 96
ANOVA						
F-ratio	0.998	11.091	7.449	7.523	14.41	5.705
df	51	60	61	56	58	47
p (sig. level)	0.438	0.000	0.000	0.000	0.000	0.000
Tukey test						
Namibia	a	a	a	a	a	no data
Groen	a	b	b	b	b	b
W. Cape	a	a	a	a	a	ab
E. Cape	a	a	a	a	a	a
Transkei	a	a	a	a	a	a
Durban	a	a	a	a	a	a
Zululand	a	a	a	a	a	ab

(b) Temporal differences

	Region						
	Namibia	Groen	W.Cape	E.Cape	Transkei	Durban	Zululand
ANOVA							
F-ratio	3.354	2.253	5.249	1.990	12.171	14.838	13.776
df	39	53	53	53	38	43	53
p(sig. level)	0.020	0.064	0.001	0.097	0.000	0.000	0.000
Tukey test							
Jun/Jul 95	ab	a	a	a	a	a	a
Sep/Oct 95	ab	a	a	a	ab	a	a
Dec/Jan 95	b	a	a	a	ab	a	a
Mar/Apr 96	ab	a	a	a	c	a	a
Jun/Jul 96	a	a	b	a	a c	a	a
Sep/Oct 96	no data	a	ab	a	ab	b	b
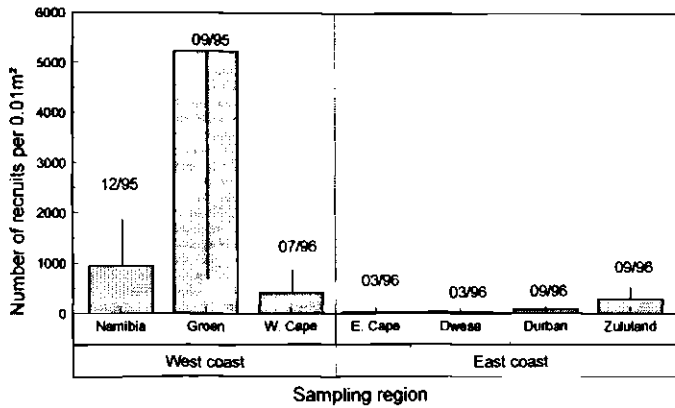
Figure 3 Comparison of maximum mean (± *SD*) recruitment recorded between June 1995 and October 1996 in the different regions around the southern African coast (*n* = 9).
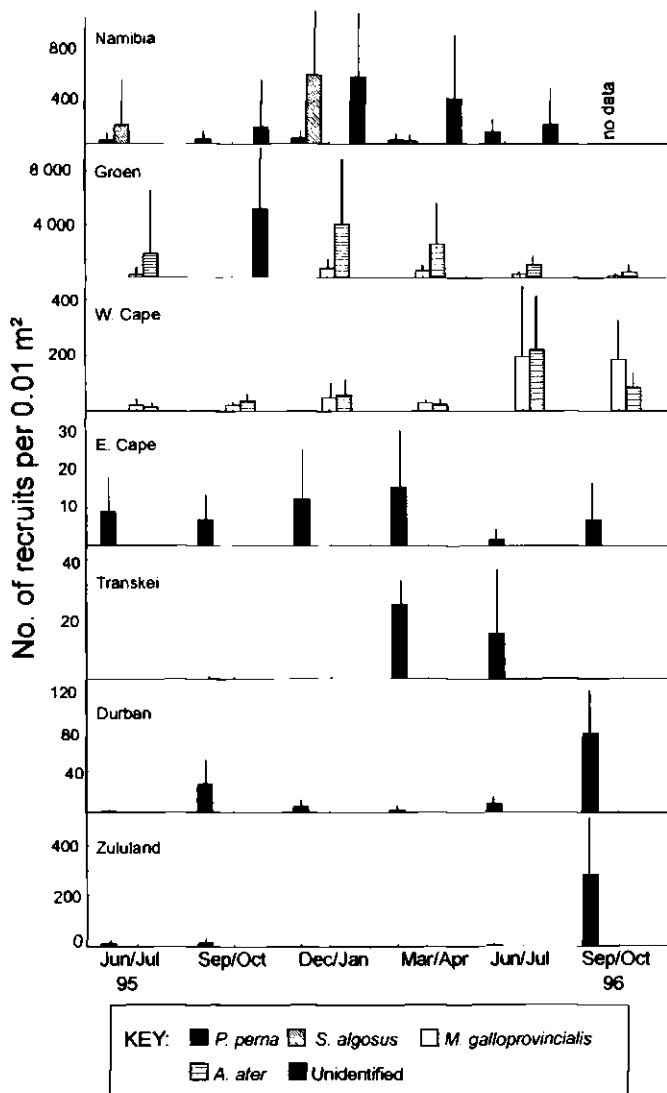
Figure 4 Mean (± *SD*) density of individual species of mussel recruits per 100 cm² of adult mussels at each of the seven regions (100–1 000 km apart) sampled around the southern African coast at 3-monthly intervals between June 1995 and October 1996. Occasions where no data exist are represented by 'no data', while blanks indicate that there were no recruits present. Refer to Table 2 for number of samples per region.

were found between regions, with recruitment intensity at Groen an order of magnitude higher than in any other region.

Maximum recruitment intensities in the E. Cape and Transkei were similar and extremely low, and that in Durban was also much lower than in the other regions investigated (Figure 3). Furthermore, maximum recruitment intensity on the west coast (Namibia, Groen and W. Cape combined) was significantly higher than on the east coast (data from all east coast regions combined) (ANOVA, $F = 12.178$, $df\, 58$, $p < 0.01$).

Whereas only *P. perna* recruits were present in all east coast regions, both *M. galloprovincialis* and *A. ater* were represented at Groen and in the W. Cape (Figure 4). In the W. Cape similar recruit densities and temporal patterns of settlement for the two species were obtained, and thus the patterns described above are reasonable for the individual species. At Groen *A. ater* recruits occurred in much higher densities than did those of *M. galloprovincialis*, and the intensity of recruitment and temporal pattern described above can thus largely be attributed to *A. ater*. In Namibia the dominant species represented by the recruits were *P. perna* and *S. algosus*. *P. perna* exibited minimal seasonal differences, while *S. algosus* displayed a peak in summer. The difficulty experienced in this study in distinguishing recruits of the different species however obviates clear conclusions about the seasonality of their recruitment in this region.

Adult-recruit relationship

The abundance of adult mussels at the time of maximum recruitment was compared between regions. Adult abundance expressed as density (numbers/0.01 m²), per cent cover, or by population size (area and number of mussels on the 24 m length of shore), varied significantly (ANOVA, $p < 0.05$) on the scale of 100 km, i.e. between regions (Table 4). Mussel abundance was significantly higher (ANOVA, $p < 0.05$) in Namibia and at Groen than in the W. Cape and the east coast regions (Figure 5).

Analysis of the means of recruit density and adult abundance per locality from all regions during the period of maximum recruitment, revealed positive stock-recruit relationships with significant correlations between recruitment intensity and adult density, as well as the size of the adult mussel population (numbers) during the period of maximum recruitment (Table 5). However, no significant correlations were obtained between recruitment intensity and adult abundance as estimated by per cent cover in the middle of the mussel bed, or by area of mussel bed on the shore.

Discussion

Recent studies of intertidal and subtidal benthic systems suggest that the biological and physical processes influencing variability in recruitment patterns operate across multiple temporal and spatial scales. Conclusions concerning the coupling of recruitment and adult dynamics and community structure, and the geographic generality of interactions, consequently require that a number of scales be examined (Menge 1991; Michener & Kenney 1991; Ebert *et al*. 1994).

Spatial variability

The high spatial variability in mussel recruitment recorded between regions (scale of 100–1 000 km) and within regions (scale of 1–25 km) (Figure 2) mirrors the findings for a number of other intertidal (Caffey 1982; Michener & Kenny

Table 4 ANOVA and Tukey range test results showing significant differences in adult (> 35 mm) abundance of mussels in the different regions around the coast of southern Africa. Identical letters (a, b) depict no significant differences (p < 0.05) between regions
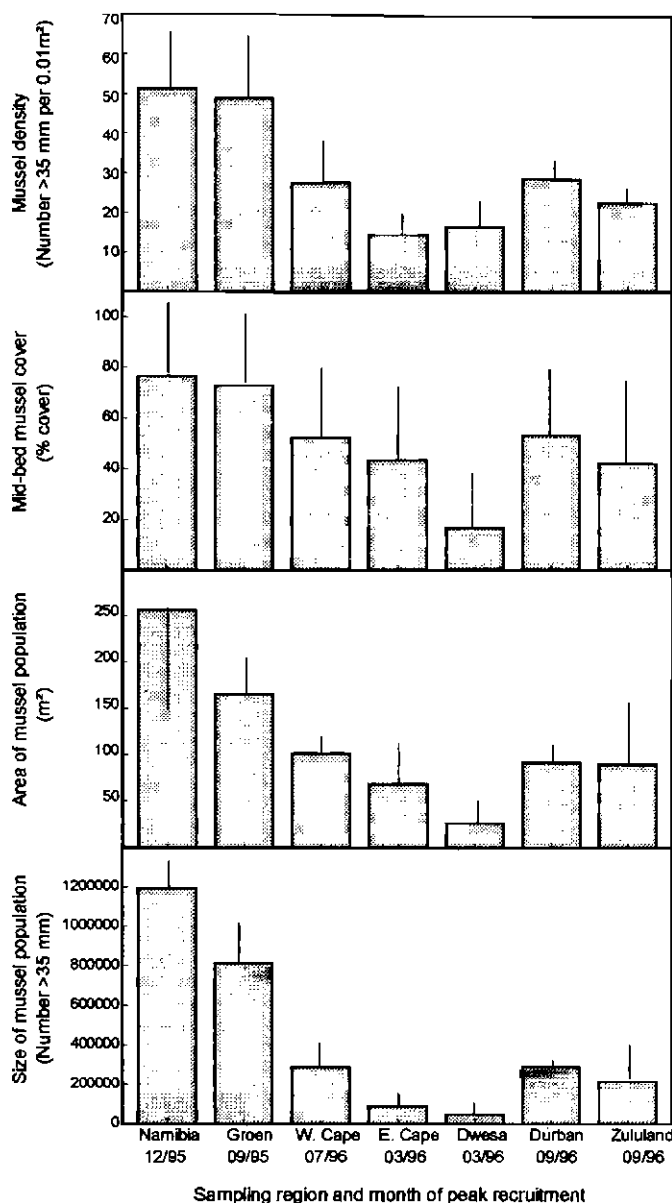
	Mussel density	Mid-bed mussel cover	Area of mussel population	Size of mussel population
ANOVA				
F-ratio	15.96	30.42	4.94	30.48
df	58	419	20	19
p (sig. level)	0.000	0.000	0.007	0.000
Tukey test				
Namibia	a	a	a	a
Groen	a	a	ab	b
W. Cape	b	b	ab	c
E. Cape	b	b	b	c
Transkei	b	b	b	c
Durban	b	b	b	c
Zululand	b	c	b	c

Table 5 Results of correlation analyses between maximum recruitment intensity and adult mussel abundance (data from all regions combined). The significance level is depicted by * (p < 0.05) or ** (p < 0.01)

Correlations	n	r (correl. coeff.)	p (sig. level)
Recruit density (number of recruits/0.01 m^2) versus:			
Mussel density (number of adults/0.01 m^2)	63	0.437	0.000**
Mussel density (number of adults/0.01 m^2; means for localities)	21	0.483	0.027*
Mid-bed mussel cover (%)	21	0.315	0.165
Area of mussel population (m^2/24 m shore)	21	0.378	0.091
Size of mussel population (number of adults/ 24 m shore)	21	0.502	0.020*

1991) and subtidal benthic invertebrates (McShane & Smith 1991; Pennings 1991). While the substantial regional differences may, in part, be explained by asynchronous recruitment patterns around the coast, comparison of recruitment intensity in the period of maximal recruitment in each region still revealed clear differences, spanning three orders of magnitude, among regions (Figure 3). Maximum recruitment in Namibia, W. Cape and Zululand were an order of magnitude lower than at Groen, and those in the E. Cape and Transkei were yet another order of magnitude lower.

The regional differences in recruitment intensities are of relevance in understanding the degree to which recruitment influences the large-scale differences in community structure observed around the coast of southern Africa (Bustamante, Branch & Eekhout 1996). Menge (1991) found that where recruitment density is low its importance in influencing the structure of intertidal communities was amplified. Spatial differences in recruitment intensities may therefore affect the relative importance of recruitment compared to post-recruitment processes such as competition and predation. The highly

Figure 5 Comparison of adult mussel abundance in the seven regions during the month of maximum recruitment (three localities combined). Mussel density is expressed as number of mussels per 0.01 m^2 (n = 9), mid-bed mussel cover is mean per cent mussel cover in middle of mussel bed (n = 60), area and size of mussel population are expressed respectively as m^2 and number of mussels in a 24-m stretch of shore (n = 3).

significant difference in recruitment intensity between the east and west coast (at a scale of > 1 000 km apart), (Figure 3), suggests that recruitment is likely to play a very different role on the west coast, compared to the east coast, where recruit densities are an order of magnitude lower.

The smaller-scale variability in recruitment between localities within regions is of interest with regard to the role played by recruitment in the distribution and abundance of mussel populations along fairly homogenous stretches of coastline. It could explain the disjoint distribution of some mussel populations and the large differences in mussel abundance between shores only a few kilometres distant, even when they do not discernably differ physically (Harris, pers. obs.). This suggests that recruitment may exert a significant influence on

adult distribution and abundance, and may act at scales as small as a few kilometres, delivering larvae differentially to adjacent shores only a short distance apart. Topical in the literature at present is the issue of the range of larval dispersal (Strathman 1974; Menge *et al.* 1993), and there is some evidence that supply distances in many benthic invertebrates are much shorter than previously assumed (Butler & Keough 1990), with larvae becoming entrained in very localized circular current systems (Dye, pers. comm.). Consequently stock and recruit may be more closely coupled than previously thought.

Furthermore, the patchy distribution of mussels within some shores, with mosaics typically developing (Paine & Levin 1981; Tokeshi & Romero 1995; Hunt & Scheibling 1996), is likely to be enhanced by the highly variable recruitment recorded over the beds in the current study. There is evidence that mussel recruits preferentially settle in adult clumps (e.g. Petraitis 1990; Hunt & Scheibling 1996). However, the fact that such high small-scale variability in recruitment was obtained even when considering this single substratum suggests that local adult population characteristics (density, size structure, etc.) may influence recruit settlement or survival. The ability of larvae to orientate and position themselves on the shore and to select preferred substrate has been well demonstrated (e.g. Pawlik 1992; Minchinton & Scheibling 1993; Lemire & Bourget 1996), as has improved survival of recruits on conspecifics (Nielson & Franz 1995). However, our observations may simply reflect uneven dispersal of larvae on the shore at the scale of metres, as high variability in larval concentrations in the water at small scales has also been reported for some benthic invertebrates (Gaines *et al.* 1985).

Consistent large-scale regional differences in settlement of benthic organisms may reflect regional differences in physical conditions, biological factors (mortality/growth) or constraints on larval exchange by physical oceanographic processes (Ebert, Schroeter, Dixon & Kalvass 1994). When considering the reasons why recruitment is much higher on the west coast than the east coast, a number of fundamental differences between the two coasts should be noted. The much higher productivity of the waters of the west coast compared to the east coast (Branch & Griffiths 1988; Bustamante *et al.* 1995) could have profound effects on recruitment, as it may influence both larval supply and survival. Invertebrate spawning (Starr *et al.* 1990; Bertness, Gaines, Bermudez & Sanford 1991) and prevention of larval starvation (Sale 1990) have both been coupled with nutrient availability and phytoplankton blooms. Furthermore, the disparate oceanographic conditions on the two coasts (Branch & Griffiths 1988, Emanuel *et al.* 1992) may influence recruitment intensities on the east versus west coasts: factors such as temperature have been shown to affect recruitment (Kingsford 1990). The two coasts also differ in terms of the species of mussels that predominate, each with different biological attributes. Differences between the species may influence larval supply (reproductive output, growth rate, age to maturity) as well as settlement (substrate preferences) and recruit survival (density-dependent effects, early mortality and growth). Growth rates may be a factor in the present study as they are reported to be very variable and affected by region (van Erkom Schurink & Griffiths 1993). For example, a lower growth rate may influence

competitive dominance and thus reduce availability of adult substrate for recruits which settle preferentially among adults. However, the spawn rates of the four species of mussel investigated in the present study (measured as kg wet mass of gametes/m²/year) are not markedly different (van Erkom Schurink & Griffiths 1991) when measured at the same locality. Thus spawn rate could be a factor only if there is significant intraspecific spatial variation, for which insufficient information currently exists.

The question of whether the enhanced recruitment on the west coast is due to a greater biomass of mussels on the west coast requires examination. Van Erkom Schurink & Griffiths (1990) noted that most of the southern African mussel biomass occurs on the west coast (69%), while relatively small stocks are present in the Transkei (4%) and Natal (7%). At the specific sites investigated in the present study (Figure 5), mussel abundance was also highest in two of the west coast regions, Groen and Namibia, but the third west coast region (W. Cape) supported stocks of similar magnitude to those on the east coast (Durban and Zululand), suggesting that the relationship between adult stock size and recruitment intensity is not entirely straightforward.

We examined adult abundance in four different ways: i.e. density of adults in established clumps, per cent cover of mussels in the middle of the mussel bed, and total adult stock on the shore, expressed either as the area of shore covered or by total number of mussels. Of interest are the significant positive correlations between recruitment and within-clump density (Table 5). Higher adult densities were recorded on the west coast compared to the east coast (Table 4), reflecting the pattern obtained for recruitment. This suggests that density-dependent effects and adult habitat complexity contribute significantly to the differences in recruitment intensity around the coast. The size of the adult mussel populations in this analysis is a function of density within mussel clumps on the shore and the area of shore that the mussel clumps cover. The significant relationship between stock size and recruit density suggests that recruitment may be limited *a priori* by larval supply, and that regions with very low adult abundance may experience recruitment limitation. This appears to be the case in Transkei, where severe depletion of stocks outside reserve areas (Lasiak & Dye 1989) may be coupled with very low and intermittent recruitment. The lack of correlation between recruitment and either area of mussels on the shore or per cent mussel cover (Table 5) may be related to the fact that area is not a good measure of total mussel abundance. Adult density on the west coast is greater, since mussels are packed in multiple layers, while on the east coast this is seldom the case. This is not a species-specific phenomenon, because *P. perna* forms multi-layered hummocks on the west coast, and mono-layered clumps on the east coast. Thus, independent of the species involved, mussel beds on the west coast provide more sheltered and more complex settlement habitats than on the east coast (see Petraitis 1991).

There is ample evidence that settling benthic larvae show substratum preferences (e.g. Petraitis 1990; Caceres-Martinez, Robledo & Figueras 1994; Hunt & Scheibling 1996; Raimondi 1988; Lohse 1993), and that adult conspecifics influence the settlement and survival of recruits by providing a protected habitat (Nielson & Franz 1995). Adult conspecifics

may, however, also have a negative impact, for example by consumption of gametes and larvae (Osman & Whitlatch 1995a, b). While these results suggest that adult stocks may significantly influence recruitment around the coast of southern Africa, the converse influence of recruitment on reinforcing adult abundance patterns should not be overlooked. A number of studies provide evidence that recruitment processes control the distribution and abundance of adults (Butler & Keough 1990; Grosberg & Levitan 1991; McShane & Smith 1991; Menge 1991).

Temporal variability

While a number of studies have examined temporal variations in the recruitment patterns of mussels around the coast of southern Africa, most were conducted for only one year and there are no published long-term records of recruitment at more than one temporal scale (months and years) for more than two consecutive years for any one species at any site (e.g. Griffiths 1977; Lasiak & Barnard 1995; van Erkom Schurink & Griffiths 1991). Thus, we know very little about interannual variability and the frequency and predictability of recruitment peaks.

In the present study, no clear seasonal patterns of recruitment intensity were found in Namibia and Groen, while the other west-coast region (W. Cape) experienced recruitment peaks in autumn and winter. At Groen and W. Cape the adult mussel populations are dominated by two co-existing species, i.e. *Mytilus galloprovincialis* and *Aulacomya ater*. Previous studies have reported asynchronous, intermittent settlements of *Choromytilus meridionalis* and *A. ater* on the west coast, with both species displaying protracted seasons of maximum recruitment, principally during spring and summer (Griffiths & King 1975; Griffiths 1977; van Erkom Schurink & Griffiths 1991). *Mytilus galloprovincialis* recruitment is also reported to occur over two protracted seasons (summer and winter), but these are not synchronous with those of the other two west coast species (van Erkom Schurink & Griffiths 1991). However, the lack of a seasonal pattern of mussel recruitment for Groen does not appear to be explained by the combination of recruits of the two dominant species in the analyses of the present study because both species displayed similar recruitment trends, albeit much higher intensities by *A. ater* (Figure 4). The two species present on the W. Coast, *M. galloprovincialis* and *A. ater*, exhibited similar seasonal recruitment patterns.

The lack of seasonality in recruitment intensity in Namibia is interesting, considering that the dominant adult mussel species, *Perna perna*, is reported to display clear seasonal peaks on the east coast, at least in years when measurable recruitment occurs. Our east coast results support previous reports of recruitment peaks for *P. perna* in spring and winter (Lambert & Steinke 1986; Lasiak 1986; Lasiak & Dye 1989; van Erkom Schurink & Griffiths 1991; Lasiak & Barnard 1995; Tomalin 1995; Harris unpubl. data), although the season may extend into summer on occasions (Crawford & Bower 1983; Lasiak & Dye 1989). In Namibia it appears that recruitment by *S. algosus* overshadows that of *P. perna*, although no clear seasonal trends were detected in the present study for the latter species (Figure 4). The radically different oceanographic conditions between the east and west coasts are the most

likely explanations for the different temporal patterns exhibited by *P. perna*.

In most of the regions sampled there were significant temporal variations between sampling periods (three months) as well as between years, with recruitment being higher in 1996 than in 1995. Large differences in recruitment intensity among years have been reported for other intertidal mussel species (e.g. Petraitis 1991), and seasonal patterns of settlement are subject to a high degree of temporal variability in many benthic marine invertebrates (Hurlbut 1991; Michener & Kenny 1991; Pennings 1991; Roberts *et al.* 1991). In general, recruitment on the west coast was more consistent, possibly just because it is much higher, but also because there is protracted spawning, whereas on the east coast recruitment is confined to specific seasons. However, intermittent and irregular settlements appear to characterise the recruitment patterns of the mussels both on the east and west coast (Griffiths 1981), particularly on the east coast (Berry 1978) where massive settlements occur sporadically. The importance of episodic recruitment events in community structure and dynamics of populations is highlighted by Reed, Laur & Ebeling (1988). Large flushes of recruitment may also affect the way recruitment processes operate. For example, small-scale settlement preferences of barnacles are masked when there is a massive settlement (Minchinton & Scheibling 1993).

Management implications

Understanding the relationship between exploited populations and their probable recruitment in subsequent years forms the cornerstone of models used to set harvest levels (Fairweather 1991). Thus, from the perspective of managing exploitation of mussels, the spatial and temporal variability in recruitment reported in this study have important implications. The clearest patterns to emerge are: (1) much higher recruitment on the west than the east coast; (2) considerable spatial variability at smaller scales varying from 10–100 km down to 1–10 m; (3) seasonal and interannual differences in recruitment intensities in the different regions; and (4) recruitment is correlated with adult density and stock size but not cover. The main factors likely to explain these patterns are larval supply, survival during dispersal (food, physical conditions), and conditions in the adult habitat (substrate availability for settlement and survival). While managers cannot readily influence survival during the larval dispersal phase, they are responsible for managing the harvesting of adults. Harvesting may reduce adult stocks to the point where larval supply is compromised, or may alter adult habitat, with consequences for the settlement and survival of recruits (Sale 1990). The different stock sizes and recruitment rates in the different regions must influence the vulnerability of the populations to harvesting, because those regions with very low biomass will be closer to recruitment failure considering the significant stock-recruit relationship recorded. Whether the underlying cause is because the supply of larvae is depressed, or because suitable adult habitat becomes limiting is immaterial.

Resilience of populations to exploitation depends on whether negative or positive feedback processes exist (Fogarty *et al.* 1991). The high small-scale variability in recruitment between shores at the scale of kilometres suggests a

vulnerability to small-scale/local perturbations if a reduction in the adult stocks leads to a reduction in suitable habitat for settlement. Such effects may be particularly acute in the case of intense harvesting which causes fairly large-scale decimation of populations, and may have long-lasting consequences if there is patchy and localised dispersal of larvae to shores only a few kilometres apart. Taken collectively, our results therefore indicate that the mussel populations on the east coast are more vulnerable to harvesting effects on recruitment, because of the low stock sizes and relatively low recruitment levels and, possibly, also because of greater temporal variability and seasonality.

This raises a legislative anomaly highlighted by Griffiths & Branch (in press). Despite the fact that the east-coast stocks are more vulnerable and more heavily exploited than those on the west coast (van Erkom Schurink & Griffiths 1990; Tomalin 1993), legislation there is more lenient: 50 mussels may be harvested per person per day on the east coast, but only 25 on the west coast.

The other important management issue that needs to be pursued further is whether adult mussels do indeed enhance settlement and survival of recruits. If this does prove to be the case, then the mode of harvesting becomes critical. Strip-removal with a large implement may be efficient in terms of short-term yield, but will destroy the adult mussel beds which promote recruitment, and is therefore not sustainable. Smaller implements may allow more selective removal of individual large mussels, preserving the integrity and complexity of the mussel beds. Implementation of such refinements will require more than legislation: education and co-operation of harvesters will be imperative.

Acknowledgements

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