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RESEARCH ARTICLE

Testing source-sink theory: the spill-over of mussel recruits beyond marine protected areas

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Abstract Source-sink theory has contributed to our understanding of the function of protected areas, particularly due to their role as population sources. Marine reserves are a preferred management tool for the conservation of natural populations, creating areas of good quality habitat and thus improving population connectivity by enhancing larval supply and recruitment among shores. Despite recent advances in the study of protected areas in the context of the source-sink theory, rigorous and empirical testing of marine reserves as metapopulation sources for the adjacent areas remain largely unexplored. We investigated the role of marine reserves as population sources, whether there was spill-over beyond the reserve boundaries and if so, whether spill-over was directional. We measured percentage cover and recruitment of mussels (*Perna perna*) at two reserves and two comparably sized exploited control areas on the south-east coast of South Africa where unprotected populations are severely affected by artisanal exploitation. Adult abundances were enhanced within reserves, but decreased towards their edges. We predicted that recruitment would mirror adult abundances and show directionality, with northern shores having greater recruitment following the prevalent northward flow of near-shore currents. There were, however, no correlations between adult abundances and recruitment for any months or shores, and no clear spatial patterns in recruitment (i.e. similar patterns occurred at reserves and controls). The results emphasise that, while reserves may act as important refuges by protecting adult abundances, their influence on promoting recovery of near-by exploited shores through larval spill-over may be overestimated.

Keywords Connectivity · Intertidal · Metapopulation · Marine reserve · Mussels · Source-sink

Introduction

Source-sink theory has been a central topic of landscape connectivity for the last 20 years, when ecologists realised the role of demographics and habitat quality in the regulation of populations

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(Lipcius et al. 1997; Pulliam 1988). Given the broad scales at which marine propagules can potentially disperse, their connectivity dynamics fit into metapopulation models through a complex network of exchanges, deliveries and interactions with the habitat (Leibold et al. 2004; Lipcius et al. 2008). Characteristics of the habitat, dispersal routes, and rates of dispersal are therefore the major determinants of source-sink processes (see Diffendorfer 1998 for review). Suitable habitat is among the most limiting resource and is declining due to human induced loss (Tuck and Possingham 2000; Lipcius et al. 1997, 2008). The constant increase in anthropogenic pressure through over-fishing and exploitation of resources has also resulted in a need for effective strategies of restocking and restoration, leading to the application of the theoretical principles of the source-sink theory to the development of marine protected areas (MPAs) (Lipcius et al. 2008; Hansen 2011).

Marine protected areas (MPAs) or marine reserves have been proposed as a management strategy to conserve marine populations, combat habitat loss and declining biodiversity (Halpern 2003). Despite recent advances in the study of MPAs in the context of the source-sink theory (see Hansen 2011 for review), rigorous and empirical testing of marine reserves as metapopulation sources of juveniles for the adjacent areas remain largely unexplored (Palumbi 2004; Sale et al. 2005; Lipcius et al. 2008). This is particularly true for the consideration of the links between subpopulations inside reserves and the scales and rates of recruitment at adjacent places at different distances outside the reserves. MPAs are often considered as important source populations that ‘‘spill-over’’ beyond reserve boundaries (Rowley 1994; Palumbi 2004). Studies of spill-over have mostly been on large mobile taxa, e.g. fish (see Roberts et al. 2001 for review), and few studies on marine invertebrates (e.g. Palumbi 2004, Pelc et al. 2009; Cole et al. 2011).

For many marine invertebrates which have a dispersive larval stage and a non-mobile adult stage, their metapopulations dynamics become relatively complex due to the existence of stochastic corridors, and sources and sinks that vary in size, rate and direction (Lipcius et al. 2008). Subsequently, given the complex nature of larval dispersal, restocking, restoration and management strategies are challenging. In regions of overexploitation where the natural habitat has been degraded, measurements of connectivity appear, however, to be simplified due to almost complete isolation of the protected area.

The Transkei coast of South Africa and the intertidal mussel *Perna perna* provide a suitable testing ground for replicated large scale experiments on the effectiveness of marine reserves due to the existence of multiple reserves and surrounding areas that are subject to heavy harvesting pressure of mussels (Siegfried 1985), with macroalgae often taking over on these exploited shores (Lasiak and Field 1995). Besides this socio-ecological importance, mussels also play an important role ecologically (Paine 1996; Cole and McQuaid 2010) by providing unique habitat for a wide range of associated organisms (Stephens and Bertness 1991; Hunt and Scheibling 1996; Seed 1996), and are the preferred settlement habitat for mussels themselves (Lasiak and Bernard 1995; Erlandsson and McQuaid 2004).

In this study we investigated the role of marine reserves as sources of mussel larvae, whether there was spill-over of mussel larvae beyond the reserve boundaries and if so, whether spill-over was directional. First, we predicted that as sources, marine reserves would have a greater cover of adult mussels than outside of reserves. Second, we hypothesised that recruitment of mussels would be greatest in the centre of reserves and decrease with increasing distance from a reserve. Third, we predicted directionality in this effect because wind driven surface currents in this area would tend to transport larvae to the north.

Materials and methods

Study species and sites

Perna perna extends from central Mozambique (Berry 1978) to the southern parts of the west coast reappearing in Northern Namibia (van Erkon Shurink and Griffiths 1990). The first larval stage, (D-larva-type) appears in this species 14–18 h after fertilization. Pediveligers produce the first byssal threads about 3 weeks after fertilization indicating the onset of metamorphosis and reaching of competency for settlement (Siddall 1980).

This study was conducted on the southeast coast of South Africa in the Transkei region. This area is typically heavily harvested, and boasts multiple marine reserves (Branch and Odendaal 2003), making

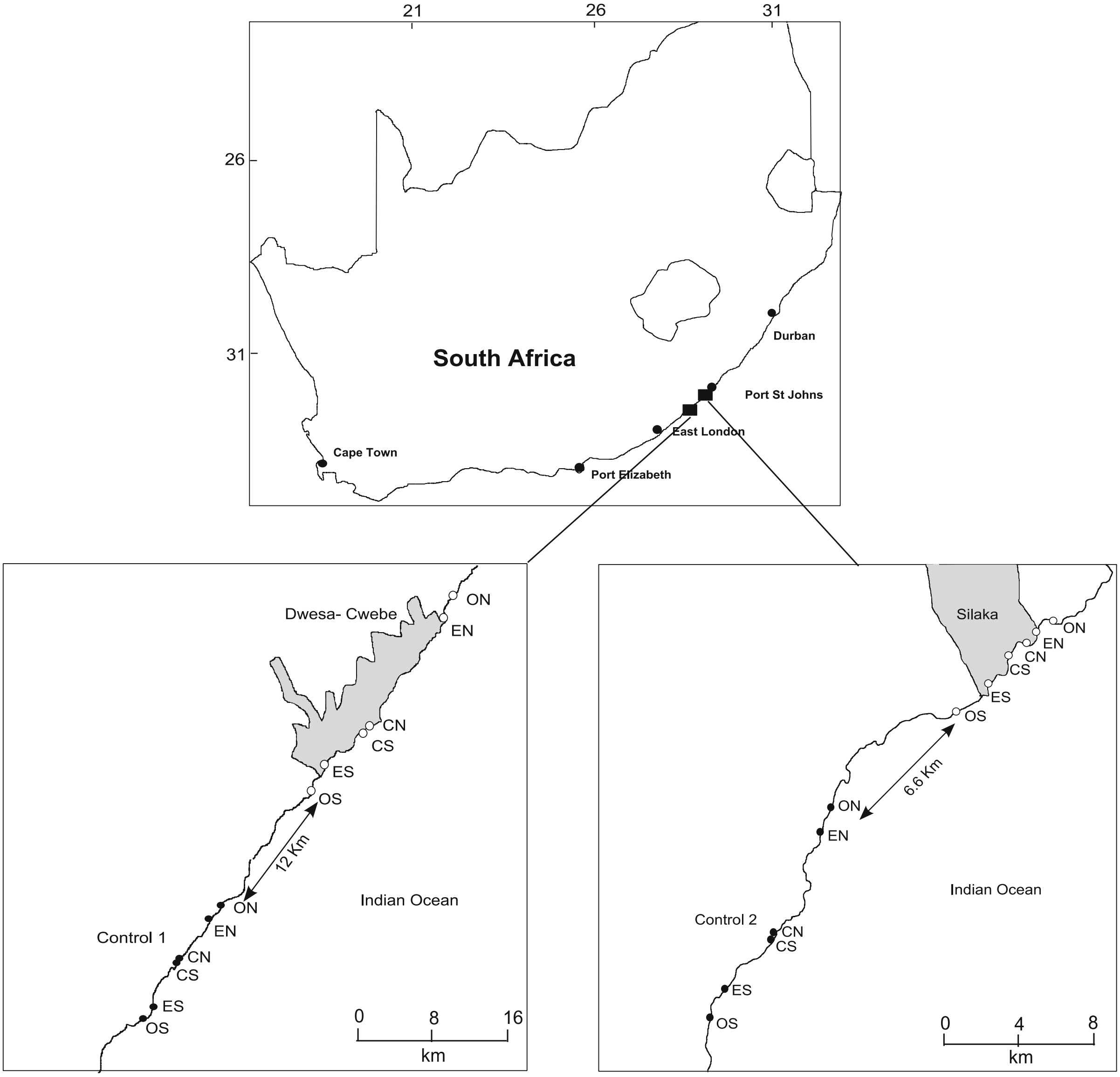

Fig. 1 Study sites with location and relative position of shores along the south-east coast of South Africa. Reserves in *grey*. *N* North, *S* South, *O* Outside, *E* Edge, *C* Centre. *Closed circles* indicate controls, *open circles* indicate reserves

it an ideal system for a study of connectivity between marine reserves and exploited areas. To test the effectiveness of marine reserves in protecting adult populations and supplying recruits to neighbouring areas at different distances and in different directions from reserves, sampling was done at two reserves, Dwesa-Cwebe (32° 15′S, 28° 54′E) and Silaka (31° 39′S, 29° 30′E), and at two controls (Fig. 1). Controls were situated south of each reserve (to ensure that they were far enough away from reserves to remain independent) and at least 5 km from all other shores to ensure independence (McQuaid and Phillips 2000; Cole et al. 2011). To test the effect of direction from a source, shores were sampled to the north and south of a reserve or control. To test the effect of distance away from a source, shores were sampled at three different positions, the centre, the edge or the outside of a reserve and control. In the case of reserves, the outside shores were approximately 2 km from the reserve edge. All study shores had similar aspect and topography. Due to the very different sizes of the two reserves, the sizes of controls were similar to make the controls comparable to each other as well as the reserves (Fig. 1). It was also necessary to have two controls and two reserves, each with two shores to successfully investigate whether the presence of a marine reserve was having an effect over and above spatial variability among shores.

Mussel cover

Adult stocks of the mussel *Perna perna* were estimated as percentage cover. Once-off surveys have been shown to estimate abundance adequately as cover may change at small scales, but remains fairly constant at larger scales (Reaugh-Flower et al. 2010) and Dwesa-Cwebe, Silaka with their respective controls were sampled in August and September 2009 respectively. Twenty-five 50 × 50 cm quadrats were haphazardly thrown within the mussel zone at each shore. Shores were sampled approximately every 100 to 400 m along the shore within each reserve, depending on the size of the reserve, where this was possible (some spots were inaccessible or comprised sand). The point intercept method (Meese and Tomich 1992) was used to determine percentage cover of mussels within each quadrat, with 100 evenly spaced points within each quadrat.

Recruitment

Monthly recruitment of *Perna perna* was examined during Austral spring and early summer (October, November and December 2009) when settlement rates are relatively high (Lasiak and Dye 1989; Dye et al. 1997; Harris et al. 1998). The experiment was repeated in multiple months to gain temporal replication and therefore months were analysed separately. Sampling was done by attaching standardised units of habitat (plastic scouring pads with a diameter of 10–11 cm and a thickness of 2 cm) to the rocks with eye bolts. Previous studies have found that within regions (Reaugh-Flower et al. 2010), these are suitable substrata for estimating recruitment of mussels (Menge 1992; Porri et al. 2006, 2007). At each shore, six collectors were haphazardly placed approximately 1 m apart from each other within low-intertidalmussel beds. Collectors were collected and deployed during the first spring low tide of each month. A minimum of three collectors were obtained from each shore, except control 2 edge south where all collectors were stolen in October. Collectors were preserved in 70 % ethanol and washed in the laboratory to remove mussels. Settlers (<400 μm) and recruits (>400 μm) were identified by size (Bownes et al. 2008), counted and measured using a dissecting microscope with a micrometer.

Data analysis

Adult percentage cover and numbers of recruits were analysed separately, using four-factor analysis of variance (ANOVA). The first factor “Reserve” (2 levels; Reserve or control) was fixed, factor 2 “Shore” (2 levels; reserve 1, reserve 2, control 1, control 2) was random and nested in “Reserve”, factor 3 “Position” (3 levels; centre/edge/out) was fixed and orthogonal and factor 4 “Direction” (2 levels; North or South) was fixed and orthogonal to reserve and position. When the lowest interaction term was non-significant ($P > 0.25$), it was pooled post hoc with the residual to allow a more powerful test of individual factors (Underwood 1997). All variances were heterogeneous (Cochran’s test) but no transformations produced homogeneous variances. As large, balanced ANOVA is relatively robust to heterogeneity of variances, untransformed data were analysed (Underwood 1997). Post hoc Student–Newman–Keuls (SNK) tests were done for significant sources of variation to examine differences relevant to hypotheses of interest. In October 2009, all of the standardised units of habitat were stolen at the Control 2 southern edge shore. In order to retain the symmetrical design, all edge shores were removed from the analysis and factor 3 “Position” was reduced to 2 levels (centre and out). The decision to remove the edge shores and not the southern shores was based on the data, which showed clear directionality in settler abundance that could not be ignored.

Correlation analyses were done to determine the relationship between adult cover and recruitment rates. Pearson’s correlation coefficient, r, was calculated for: 3 months combined for each reserve and each control (4 analyses), three months combined for reserves and separately for controls (2 tests) and 3 months combined, reserves and controls combined (1 test).

Results

Adult cover

There was a significant interaction between the factors Shore (nested in Reserve), Direction and Position. At Dwesa-Cwebe reserve, the predicted pattern was observed, with the cover of adult mussels being greatest at the centre, followed by the edge and least out, in both north and south directions (Table 1; Fig. 2). The magnitude of this pattern did, however, differ with the southern edge having much greater cover than the northern edge (Fig. 2). At Silaka reserve, the predicted pattern was not observed, for both directions the centre shores had the greatest cover and the edges had the least (Table 1; Fig. 2). Furthermore, to the north, the outside shore had greater cover than the edge, and to the south, the cover did not differ between the centre and the outside (Table 1; Fig. 2). In the controls there was, as predicted, no clear pattern in adult percentage cover (Table 1; Fig. 2). The controls did, however, generally have much lower percentage cover than the shores within reserves (Fig. 2).

Table 1 ANOVA comparing the percentage cover of adult mussels between the presence of a Reserve (Re), of which there were two reserves (Dwesa-Cwebe and Silaka) and two controls (Control 1 and 2), each with two randomly chosen nested Shores (Sh), and in the Direction (Di) to the North (N) or South (S) of a reserve or control, and Positions (Po) at the Centre (C), Edge (E) or Outside (O) of a reserve or control

Source	d.f.	M.S.	*F*	*P*
Reserve = Re	1	35,167	68.37	**0.014**
Shore(reserve) = Sh(Re)	2	514	2.79	**0.063**
Direction = Di	1	95	0.02	0.893
Position = Po	2	18,796	3.05	0.157
Re × Di	1	836	0.20	0.697
Re × Po	2	11,458	1.86	0.269
Di × Sh(Re)	2	4,136	22.41	**0.000**
Po × Sh(Re)	4	6,163	33.39	**0.000**
Di × Po	2	8,726	3.38	0.138
Re × Di × Po	2	44	0.02	0.983
Po × Di × Sh(Re)	4	2,584	14.00	**0.000**
Residual	552	184		
Total	575			

SNK: Po × Di × Sh(Re)

Dwesa-Cwebe N: C > E > O; S: C > E > O Silaka N: C > O > E; S: C = O > E

Control 1 N: C > E = O; S: C < E = O Control 2 N: C = O > E; S: C = O > E

Prior to analysis, data were tested for homogeneity of variances (Cochran's *C* test), $C = 0.16$ ($P < 0.01$). Post hoc Student–Newman–Keuls (SNK) tests were done for significant sources of variation relative to our hypotheses of interest. Significant values are denoted in bold, $P < 0.05$

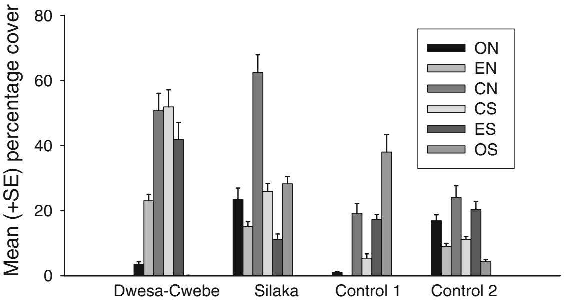

Fig. 2 Mean ($n = 25$, +SE) percentage cover of *Perna perna* at the marine reserves, Dwesa-Cwebe and Silaka, and the controls, Control 1 and 2. Key with codes representing *N* North, *S* South, *C* centre, *E* edge, *O* outside

Recruitment

In general, the predicted pattern of more recruits inside reserves and more to the north was not observed in any month (Table 2a–c). For October 2009, there was a significant interaction between reserve and position (Table 2a). In reserves, the centre shores were equal to the outside shores (Table 2a; Fig. 3). For controls the outside shores had more recruits than the centre shores (Table 2a; Fig. 3).

For November 2009, there was a significant interaction between the factors reserve and direction (Table 2b). For reserves, recruitment in both directions was equal, while for controls, south had greater recruitment than north (Table 2b; Fig. 3).

For December 2009, there was a significant interaction among the factors Shore (nested in Reserve), Direction and Position (Table 2c). Both reserves showed the same pattern with recruitment in the centre being equal to edge and outside in the north, while in the south centre shores had greater recruitment than edge which was equal to that outside (Table 2c; Fig. 3). In the controls there was, as predicted, no clear pattern in recruitment, with all shores being equal except for the Control 1 outside south shore which had greater recruitment than both centre and edge south shores (Table 2c; Fig. 3).

Table 2 ANOVA comparing recruitment of mussels between the presence of a Reserve (Re) of which there were two reserves (Dwesa-Cwebe and Silaka) and two controls (Control 1 and 2), each with two randomly chosen nested Shores (Sh), and in the Direction (Di) to the North (N) or South (S) of a reserve or control, and Positions (Po) at the Centre (C), Edge (E) or Outside (O) of a reserve or control

Source	d.f.	M.S.	*F*	*P*
(a) October $C = 0.44^{***}$				
Reserve = Re	1	305	1.71	0.322
Shore(Reserve) = Sh(Re)	2	178	1.08	0.345
Direction = Di	1	143	0.72	0.485
Position = Po	1	77	0.47	0.498
Re × Di	1	150	0.76	0.476
Re × Po	1	744	4.51	**0.041**
Di × Sh(Re)	2	198	1.20	0.312
Po × Sh(Re)^{b}	2	186		
Di × Po	1	346	2.10	0.156
Re × Di × Po	1	6	0.04	0.850
Po × Di × Sh(Re)^{a}	2	31		
Residual^{a}	32	172		
Pooled 1^{b}	34	163		
Pooled 2	36	165		
Total	47			
SNK: Re × Po				
Reserve: C = O; Control: C < O				
(b) November $C = 0.37^{***}$				
Reserve = Re	1	50	0.46	0.568
Shore(Reserve) = Sh(Re)	2	109	3.45	**0.039**
Direction = Di	1	102	3.25	0.077
Position = Po	2	102	1.99	0.252
Re × Di	1	150	4.75	**0.034**
Re × Po	2	23	0.45	0.667
Di × Sh(Re)^{b}	2	21		
Po × Sh(Re)	4	51	1.63	0.180
Di × Po	2	2.1	0.07	0.937
Re × Di × Po	2	35	1.13	0.330
Po × Di × Sh(Re)^{a}	4	10		
Residual^{a}	48	33		
Pooled 1^{b}	52	31		
Pooled 2	54	31		
Total	71			
SNK: Re × Di				
Reserves N = S; Controls N < S				
(c) December $C = 0.40^{***}$				
Reserve = Re	1	72	2.96	0.228
Shore(Reserve) = Sh(Re)	2	24	1.85	0.169
Direction = Di	1	138	76.92	**0.013**
Position = Po	2	54	1.45	0.336
Re × Di	1	0.05	0.03	0.877
Re × Po	2	94	2.52	0.196
Di × Sh(Re)	2	1.8	0.14	0.872
Po × Sh(Re)	4	37	2.84	**0.034**
Di × Po	2	33	0.80	0.511
Re × Di × Po	2	68	1.64	0.303
Po × Di × Sh(Re)	4	42	3.20	**0.021**
Residual	48	13		
Total	71			
SNK: Po × Di × Sh(Re)				
Dwesa-Cwebe N: C = E = O; S: C > E = O Silaka N: C = E = O; S: C > E = O				
Control 1 N: C = E = O; S: C = E < O Control 2 N: C = E = O; S: C = E = O				

Separate analyses were done for (a) October, (b) November and (c) December 2009. Due to loss of samples from the Edge, in October, comparisons were made between only the Centre and the Outside. All variances were heterogeneous (Cochran's C test), *** indicates $P < 0.001$. Where interactions were extremely not significant ($P > 0.25$), interaction terms were pooled for a stronger test of the main effects of interest (Underwood 1997). Post hoc Student–Newman–Keuls (SNK) tests were done for significant sources of variation relative to our hypotheses of interest. Significant values are denoted in bold, $P < 0.05$

[a, b] Denotes post hoc pooling when $P > 0.25$. New *F* ratios are given for those tested against the pooled terms (pooled 1 and pooled 2)

There were no significant correlations between the number of recruits and adult cover in any of the combinations of months (Table 3a) or reserves (Table 3b) or among months and reserves (Table 3c).

Discussion

The pattern of distribution of adult mussels was as predicted for reserves, with an increased cover of mussels in the centre and decreasing outwards. The general pattern of greater cover of mussels within the boundaries of reserves, particularly at the centre of a reserve when compared to the edges and outside shores, may be explained by harvesting pressure and the protection that reserves provide. Differences in mussel cover among shores and between reserves and controls can be linked to mechanisms ranging from larval

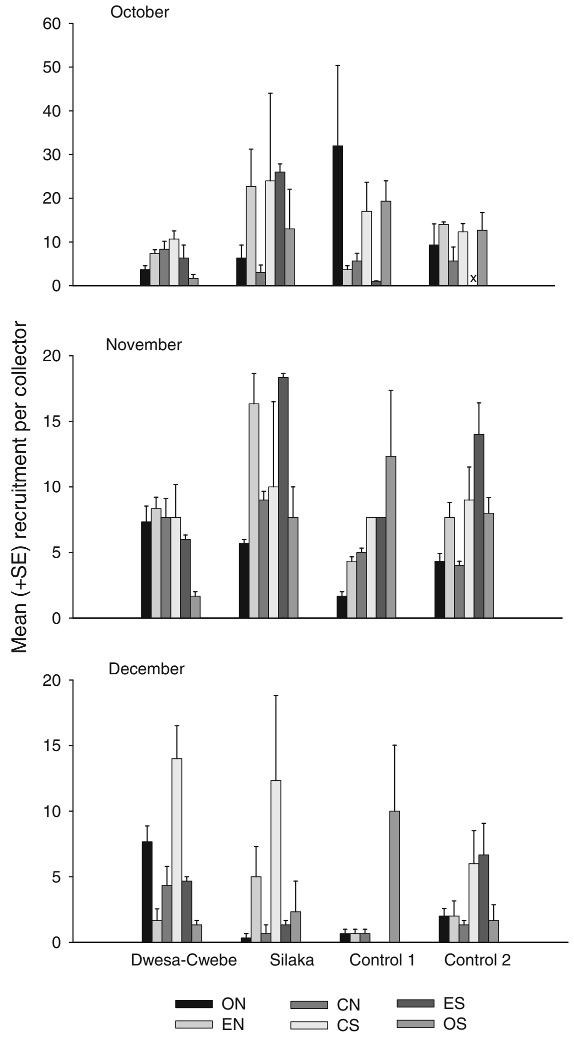

Fig. 3 Mean ($n = 3$, +SE) recruitment of *Perna perna* at Dwesa-Cwebe, Silaka, Control 1 and 2 for October, November and December 2009. Key with codes representing *N* North, *S* South, *C* centre, *E* edge, *O* outside. *X* shows missing data

Table 3 Correlations between number of recruits and adult abundance

	r crit.	*r* obs.	d.f.	*P*
(a) Combined months				
Dwesa-Cwebe	0.486	0.434	16	>0.05
Silaka		−0.359		
Control 1		0.306		
Control 2		−0.145		
(b) Combined reserves				
Reserves October	0.576	−0.229	10	>0.05
Reserves November		−0.099		
Reserves December		0.180		
Controls October		0.31		
Controls November		0.077		
Controls December		0.28		
(c) Combined reserves and months				
Reserves	0.32	−0.077	34	>0.05
Controls		0.162		

Combinations shown: (a) combined months, (b) combined reserves, (c) combined reserves and months. *r* critical, *r* observed, degrees of freedom (d.f.) and significance levels are shown

transport, supply (Pineda et al. 2009), relative landscape connectivity (Kindlmann and Burel 2008), and habitat availability (Lasiak and Bernard 1995; Erlandsson et al. 2008). The strongest explanation in this system may, however, be disturbance (Beukers-Stewart et al. 2005), and exploitation (Griffiths and Branch 1997). Disturbance, both natural and human induced (exploitation), can have a large effect on marine assemblages, and has been shown to cause switches in community structure (Sousa 1984; Lasiak and Field 1995; Petraitis and Latham 1999; Underwood 1999; Airoldi et al. 2005). The variability seen inside reserves may reflect the natural variation, also possibly combined with poaching near the perimeter of reserves (Lasiak and Dye 1989; Underwood and Kennelly 1990; Williamson et al. 2004). For example, Lasiak and Dye (1989) found that management strategies in the Transkei region were ineffective and poaching was prevalent, particularly on the edges of reserves.

For recruitment, there was a general lack of clear patterns at either reserves or controls, with no gradient of decreasing recruitment at greater distances from reserves or clear directionality. Recruitment was similar across shores, with a high degree of variability among and within shores for each of the sampling months. This pattern was in direct contrast with the three main hypotheses which predicted a clear effect of reserves as sources, effective spill-over from reserves and directionality in supply. Our findings are also in contradiction with previous studies done on recruitment inside and at different distances from reserves (Hockey and Branch 1994), including another study done in the same study region (Pelc et al. 2009). In general, similar recruitment in reserves and controls was observed for two (October and November) of the 3 months. There was some evidence for the pattern in December 2009, reserve centre south shores had more recruitment than edges and outside shores, and north shores having equal recruitment, may be the result of the extremely low recruitment. Low recruitment may highlight existing spatial patterns of adults, with high recruitment hiding this pattern due to saturation settlement (Connell and Keough 1985; Pelc et al. 2009). Given the generally low rates of recruitment in this region (Harris et al. 1998; Reaugh-Flower et al. 2011), and the very low abundances of settlers in this study, this is extremely unlikely. The lack of clear patterns in recruitment has multiple possible explanations including differences in larval production, transport or mortality (Pineda et al. 2009), fine scale local hydrodynamics (Morgan 2001; Underwood and Keough 2001; Porri et al. 2006), and early post-settlement mortality (Caley et al. 1996). Although reproductive output is assumed to be increased within reserves due to the presence of more adults and larger individuals inside reserves than in exploited areas (Manriquez and Castilla 2001; Branch and Odendaal 2003), our data show that any such increase in productivity is effectively not reflected in recruitment patterns. This indicates that differences between recruitment inside reserves and controls are not driven by the increased production within reserves, at least for a reliable restocking of the adult populations. Furthermore, the absence of natural recovery of exploited shores could be a consequence of increased early post-settlement mortality. Previous studies have suggested that mussel larvae settling on algae cannot subsequently move into existing beds or create new beds (McQuaid and Lindsay 2005; Erlandsson et al. 2008). This does, however, not explain the observed low and equal numbers of recruits between reserves and controls since we used artificial, standardised substrata, and there were plenty of available natural substrata for recruitment (i.e. adult mussels and coralline algae inside reserves and coralline algae outside reserves, Lasiak and Field 1995; Cole et al. 2011).

When comparing adult abundances and recruitment there were no similarities between patterns, or correlations between them, suggesting a de-coupling of adults and recruits in this area, and a strong influence of independent supply and early post-settlement processes. In contrast, to the classic view of population sources which concurrently self-replenish and contribute to larval export and restocking of adjacent sinks, our data suggest that the adult mussel population inside reserves behave more like “putatitve sources” (sensu Lipcius et al. 2008), where reserves may or not act as reliable sources, depending on the environment, but, most likely, in this case, on human impact due to harvesting. It is likely that the intertidal system we considered has reached a threshold of damage, under which the sources cannot recover to their optimum, and can only maintain the protected population without any power for restocking. Theoretical studies predict critical habitat levels that prevent population recovery, referring to them as ‘extinction thresholds’ (Fahrig 2001; Huggett 2005). Threshold values vary among species and regions, but the probability of survival of a species decreases sharply below the critical threshold value (Huggett 2005). Subsequently, reserves may be acting as “refuges” that are good quality habitats threatened by external conditions, large enough to favour just the persistence of a population but not its reproduction (Naves et al. 2003, Hansen 2011).

In order to be effective in supporting neighbouring exploited sinks, reserves need to consist of good quality habitats with high connectivity. To provide benefits to surrounding shores they must achieve two aims: (1) they must increase adult abundances and reproductive output; and (2) they must supply recruits to exploited shores outside of the reserves (Kellner et al. 2007). Clearly marine reserves can increase adult abundances (this study; Halpern 2003), but there is less evidence that they fulfil the second criterion. Our findings indicate that the ability of reserves to help the recovery of nearby shores may be overestimated. In a source-sink context, reserves may not act as a source habitat but rather as a refuge, ensuring the protection of adults within reserves through self replenishment, but potentially becoming non-viable sources to the outside and therefore ineffective for restocking of resources. Although confined to the Transkei region in South Africa, we are facing a localised example of protected areas as ineffective sources of stocks, which are driven to a local threshold and exposed to local extinction.

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