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Quantifying larval export from South African marine reserves

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ABSTRACT: Marine reserves may not only protect populations within their borders but also subsidize harvested populations outside through the spillover of either adults or planktonic larvae. The conservation benefits of marine reserves are well documented, and a growing body of evidence suggests that the spillover of large adults from reserves can enhance fisheries for highly mobile species. However, the proposed benefit to fisheries through larval export, a crucial benefit for the many marine species without highly mobile adults, remains controversial. We tested for larval export by estimating larval production and recruitment patterns of a harvested intertidal mussel, *Perna perna*, inside— and a range of distances outside—3 marine reserves in South Africa. Within the borders of 2 reserves, mussels were more abundant and larger than outside the reserves, with significantly higher expected production. Recruitment was highest inside these reserves and declined exponentially with distance. In the third region, where harvest outside reserve boundaries is carefully managed by community members, no differences in production or recruitment inside versus outside the reserve were found. Where production and recruitment were enhanced, we used the inverse relationship of recruitment with distance from the reserves to determine the spatial scale and magnitude of larval export. Our results suggest that larval export from these reserves enhances recruitment to fished areas within several kilometers. This study supports the idea that increased production in reserves may subsidize fisheries outside their borders, even for species with immobile adults.

KEY WORDS: Larval export · Marine protected area · Larval dispersal · Mussel · *Perna perna* · Recruitment · Spillover · Conservation

INTRODUCTION

Marine reserves have been shown to harbor denser populations, larger individuals, and higher biomass of exploited species (Halpern 2003). The higher densities and larger individuals in reserves are expected to lead to greater production of larvae than in nearby fished areas (Palsson & Pacunski 1995, Manriquez & Castilla 2001, Branch & Odendaal 2003). Therefore, reserves are predicted to enhance adjacent fisheries through not only the movement of adults (Kellner et al. 2007)

but also the export of larvae produced in reserves to sites outside their boundaries (Gell & Roberts 2003, Halpern & Warner 2003). Recent studies have found evidence that the spillover of mobile adults protected inside reserves may enhance nearby exploited populations (McClanahan & Mangi 2000, Roberts et al. 2001, Russ et al. 2004). What is less clear is how reserves influence unprotected populations through the export of larvae released by the more productive populations in reserves (Stobutzki 2000, Palumbi 2004, Gaylord et al. 2005). Whether larval export can substantially

enhance fished populations remains controversial and depends in part on the scale of connectivity by larval dispersal (Halpern & Warner 2003, Hilborn et al. 2004). Determining whether this potential fisheries benefit occurs, and on what spatial scale, has been defined as one of the major research gaps in marine reserve science (Sale et al. 2005).

Despite the importance of this information, few studies have measured larval export from reserves. Studies of scallops in Georges Bank (Murawski et al. 2000), scallops and murex in the Gulf of California (Cudney-Bueno et al. 2009), and clams in Fiji (Tawake et al. 2001, 2002) found increased larval abundances near reserves after the onset of protection. Settlement and larval abundances were higher at sites near reserves than at more distant sites for harvested Queen conch in the Bahamas (Stoner & Ray 1996, Stoner et al. 1998) and scallops in the Isle of Man (Beukers-Stewart et al. 2005). Hockey & Branch (1994) found a decline in juvenile limpet abundance with distance from a refuge site in Tenerife, suggesting that the larvae produced in the reserve may spill over outside its boundaries. However, the evidence for larval export from reserves remains remarkably scarce (Sale et al. 2005), and in general the studies that have found a signal for larval export do not address the spatial scale and magnitude of this effect.

Here we take advantage of the abrupt change in expected production of larvae found near the edge of many marine reserves with intense fishing outside to test the prediction that marine reserves act as enhanced sources of larvae to surrounding areas. We predict that reserves with enhanced production of larvae will export larvae to nearby fished areas, thereby benefitting the exploited sites. While measuring larval abundance is often infeasible, recruitment or settlement of newly metamorphosed larvae into appropriate adult habitat may reflect patterns of larval abundance (Gaines et al. 1985). We predict that where expected larval production is substantially higher inside marine reserves, recruitment will be enhanced near reserves because of larval export, but for species or regions where there wais no difference in production inside versus outside reserves, recruitment will not be affected by distance from the reserve. In addition, where larval export is occurring, the spatial pattern of recruitment near the reserve will provide insight into the magnitude and spatial scale of the larval export effect.

The focal species for this study is the brown mussel *Perna perna* (Linnaeus, 1758), a common intertidal mussel in South Africa. Though not commercially harvested, it has been subject to subsistence harvest in South Africa for thousands of years (Marean et al. 2007), is an important food source for subsistence harvesters throughout South Africa today, and is found in

significantly reduced abundances and sizes where heavily harvested (Siegfried et al. 1985). *P. perna* is a broadcast spawner, with a pelagic larval duration (PLD) of approximately 10 to 20 d (Siddall 1979, 1980). While this PLD gives the mussel the potential for moderately long-distance dispersal, with an estimated mean dispersal distance of about 26 to 65 km based on oceanographic models (Siegel et al. 2003), larvae of coastal species with PLDs in this range may be retained in the coastal boundary layer for days and may on average disperse only a few kilometers from source populations (Swearer et al. 2002, Largier 2003). Therefore, we expect recruitment of *P. perna*, which lives only in the very nearshore environment, to decline with distance over several kilometers from reserves if production is higher inside reserves than outside and larval export is occurring.

In addition, within one region, we measure the abundance and recruitment of the unharvested eight-shell barnacle *Octomeris angulosa* (Sowerby, 1825), which has a PLD of about 10 to 30 d, to serve as a comparison. Because *O. angulosa* is not harvested in the region, we expect that the abundance of the barnacle will be similar inside and outside the reserve, and there will be no pattern of recruitment with distance from the reserve. Overall, this comparison of unharvested and harvested species within a region as well as the harvested species across regions allows this study to distinguish reserve effects on recruitment.

MATERIALS AND METHODS

Study sites. The rocky coast of South Africa is subject to intense harvesting of a wide range of intertidal invertebrate species (Griffiths & Branch 1997), yet boasts a set of monitored, enforced, and well-managed marine reserves (Branch & Odendaal 2003). This situation creates an ideal environment for studying dispersal from protected areas of high abundance to intensely harvested surrounding areas. The intertidal system is particularly well-suited for this study, because the distributions of intertidal species are approximately linear (alongshore), allowing settlement patterns to be more clearly discerned.

We focused on 3 reserves in South Africa. The Goukamma Nature Reserve is located on the southern coast in the Eastern Cape province. The Dwesa-Cwebe Nature Reserve is in the Transkei region of the Eastern Cape. The Mapelane Nature Reserve is on the northeast coast in Kwazulu-Natal (Fig. 1). We conducted the field research in April and May 1999 in Dwesa-Cwebe, July and August 2005 in Goukamma, and August and September 2006 in Mapelane. The 3 reserves sampled in this study are located in distinct
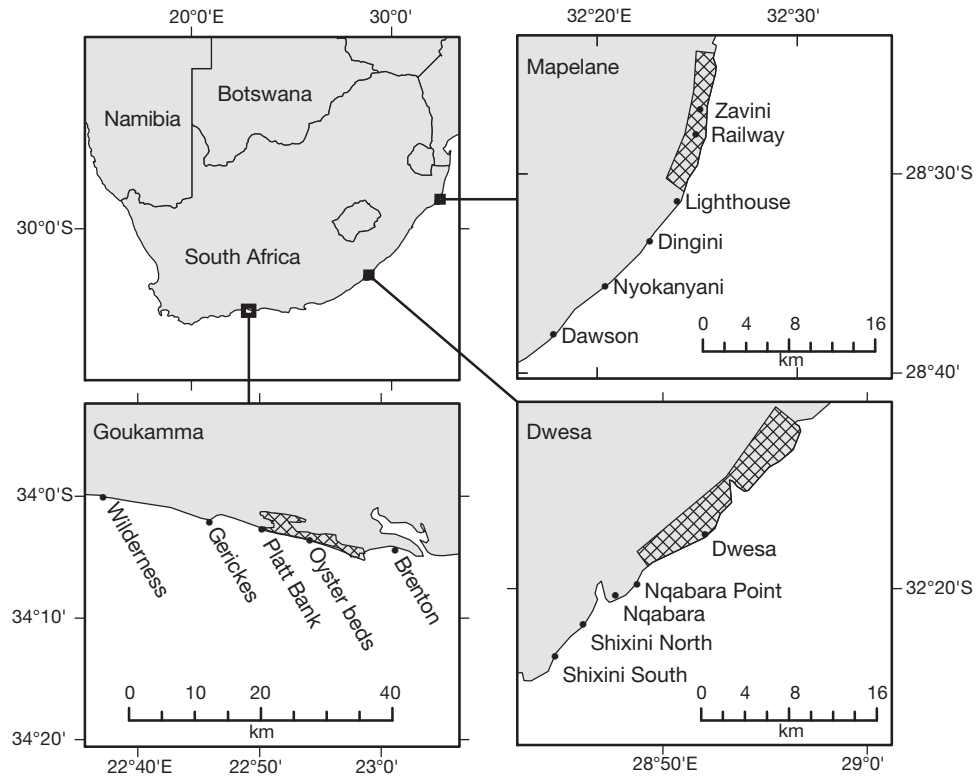
Fig. 1. Study sites and regions in South Africa. Hatch marks denote reserve areas: Goukamma (est. 1990), Dwesa-Cwebe (est. 1975), and Mapelane (est. 1984)

biogeographic provinces, with vastly different productivity and oceanographic regimes as well as characteristic mussel densities and recruitment rates (Harris et al. 1998, Reaugh 2006).

Because of the effects of biogeography, inter-annual variability, and differences in methodology (see below), we did not directly compare the magnitude of recruitment across regions. Instead, we directly compared recruitment rates within regions, while comparing spatial patterns of recruitment (e.g. whether recruitment declines with distance from reserves) across regions. The inclusion of 3 reserves helps clarify whether spatial patterns result from reserve protection or natural spatial variability.

The Goukamma Nature Reserve has been protected since 1990. Reserve regulations, which permit line fishing but prohibit taking of all rocky intertidal organisms, are closely enforced by rangers during all spring tides. In addition, the middle of the reserve is inaccessible by car without assistance from the reserve staff, granting it further protection from poaching. Recreational harvesting in the intertidal zone is common outside the reserve. We sampled recruitment and production at one site at the reserve center (Oyster Beds), one site at the reserve boundary (Platt Bank), and 3 sites at various distances outside the reserve (Brenton,

Gerickes, and Wilderness). We selected 4 subsites at Platt Bank and 2 subsites at Oyster Beds. Subsites were 100 to 500 m apart, and all data were averaged across subsites.

The Dwesa-Cwebe Nature Reserve has been protected from harvesting since 1975, while surrounding areas have a long history of exploitation, with pressures increasing in recent years (Branch & Odendaal 2003). We estimated abundance and biomass density of *Perna perna* in this region from previously published literature (Lasiak 1999) and sampled recruitment at Dwesa, located inside the reserve, and 4 exploited sites south of the reserve: Nqabara Point, Nqabara, Shixini North, and Shixini South. At each site except Shixini South, 2 subsites about 100 m apart were selected.

The Mapelane Nature Reserve, protected since 1984, is located on the southern end of the Greater St. Lucia Wetlands Park and bordered by the St. Lucia estuary to the north. The local Sokhulu community harvests *Perna perna*, an important subsistence resource for the community, from the mussel beds south of the reserve, while only very restricted recreational harvest is permitted in the reserve. We measured production and recruitment at 2 protected sites in the reserve (Railway and Zavini) and 4 exploited

sites south of the reserve (Lighthouse, Nyokanyani, Dingini, and Dawson), each separated by about 5 km, with 2 subsites between 100 and 500 m apart at all sites except Lighthouse and Dawson.

Within each region, we chose sampling locations inside and outside reserves for similarity in wave exposure and topography. Substrate types were similar at all sites within and outside the Dwesa-Cwebe and Mapelane reserves. In the Goukamma region, substrate type was highly variable, and we selected continuous sandstone bench and sand-scoured sandstone patch sites (all sites shown in Fig. 1) for recruitment and production sampling, as well as limestone sites for production sampling only, with all substrate types represented both inside and outside the reserve. Due to logistical constraints of the study, we were not able to have subsites at all sampling sites, and were able to sample only at sites on one side of each the Mapelane and Dwesa reserves, with all but one of the sites outside Goukamma on one side of the reserve. In addition, the environmental (e.g. substrate type) differences between regions as well as set sampling standards within individual reserves led to different procedures for measuring production and recruitment for each region, detailed below.

Production and the reserve effect. *Goukamma:* In Goukamma, we estimated gonad mass per area inside and outside the reserve using survey data on size structure, abundance, and the function of gonad mass at length, and we used gonad mass per area as a proxy for larval production. We estimated adult (>15 mm) *Perna perna* abundance by counting individuals in a 0.25 m² quadrat at 1 m intervals along 20 m transects parallel to shore in the mussel zone. We determined mussel length to the nearest 0.1 mm using dial calipers by measuring 150 ind. randomly chosen along the transect. In addition, we haphazardly selected 50 mussels spanning a range of sizes to dissect for gonad mass measurements to determine the function of gonad mass at length. Using an estimated function for gonad mass at length rather than comparing direct measurements of gonad mass among sites reduced the uncertainty introduced by high temporal and spatial variability in reproductive output.

As a comparison with the harvested mussels, we also measured the percent cover of the unharvested barnacle *Octomeris angulosa* inside and outside the Goukamma reserve from photo quadrats taken at 1 m intervals along the transect.

Of all regions in our study, only Goukamma had a highly heterogenous habitat distribution, with differing habitat quantity and quality inside versus outside the reserve. Production of larvae may be affected not only by protected status but also by the distribution of suitable mussel habitat. We therefore analyzed pro-duction in the Goukamma region by accounting for 2 factors, substrate type and protection status (see 'Data analysis'), to determine how production varied with both factors. To account for the effect of habitat, in addition to sampling at each rocky substrate type (limestone, sandstone bench, and sandstone patch) both inside and outside the reserve, we used geo-referenced satellite imagery from Google Earth (http://earth.google.com) to determine and record substrate type for alongshore locations at 0.016 km intervals across the entire Goukamma region, and calculated average production estimates for each protection status/substrate type combination. Then we used these values to create an array of estimated production values across each study region. This allowed us to convert the production estimated from quadrats placed within mussel habitat ('local production') to an estimated production per unit length of coastline, by accounting for the abundance of suitable habitat per unit length of coastline. Within each substrate type, comparisons of local production inside the reserve versus outside the reserve serve as an indicator of the reserve effect, while comparisons of production per unit length of coastline inside versus outside the reserve are more appropriate for predicting differences in overall larval production inside and outside the reserve. These calculations were conducted for both estimated larval production of mussels and barnacle percent cover data.

Dwesa: In the Dwesa region, we used previously published estimates of biomass inside and outside the reserve as a proxy for larval production. Several previous reserve studies have found that changes in estimated larval production or reproductive output in reserves were similar in magnitude to changes in biomass (Kelly et al. 2000, Paddack & Estes 2000, Beukers-Stewart et al. 2005, Evans et al. 2008), although in other cases production has increased more than biomass in protected areas (Sluka et al. 1997, Manriquez & Castilla 2001, Branch & Odendaal 2003, Willis et al. 2003, Kamukuru & Mgaya 2004). The difference in biomass inside versus outside the Dwesa reserve therefore serves as a conservative proxy for the difference in larval production.

Mapelane: In the Mapelane region, as in Goukamma, we estimated gonad mass per area and used this calculation as a proxy for larval production. To estimate gonad mass per area, we measured the length of each adult mussel (>15 mm) collected in three 100 cm² samples of 100%-cover mussel bed during each tide series at each sampling location to determine size structure and counted *Perna perna* adults in a 0.25 m² quadrat along a transect to determine abundance. We dissected haphazardly collected mussels of a range of sizes to estimate gonad mass at length.

Recruitment, dispersal, and larval export. We measured recruitment of mussels in a combination of natural, *in situ* substrate and standardized collectors at each site. Although recruitment of larvae may be highly episodic and reflects not only larval supply but also transport and delivery events (Pineda et al. 2007), large and consistent differences in larval supply (as when there is a strong gradient in production due to protection in a reserve) are expected to be reflected in patterns of recruitment. Patterns of recruitment across the different collector and substrate types were qualitatively similar within each region, so we combined recruitment data from various collector types into a standardized recruitment index. Where production was enhanced in the reserves and recruitment declined with distance from reserves (the Goukamma and Dwesa regions), we then used the spatial patterns of production and recruitment to estimate 3 characteristics of the system: (1) how far, on average, mussel larvae in the system disperse (mean dispersal distance), (2) the distance over which larval export from the reserves enhances recruitment to populations outside the reserves (the scale of the larval export effect), and (3) the proportional increase in recruitment in the enhanced regions due to larval export (the magnitude of the larval export effect).

Recruitment: Goukamma: In the Goukamma region, we collected two 100 cm^2 samples of red algal turf, known to be a settlement site for *Perna perna* larvae (Lasiak & Barnard 1995), and counted all recruits (<4 mm) in each turf sample. We also deployed 2 plastic scouring pads (tuffies) as mussel recruit collectors and 2 PVC tiles as barnacle recruit collectors at each sampling site, to provide a standardized substrate for comparison across sites. Barnacles on tiles were counted under a dissecting microscope, and tuffies were rinsed over a 250 µm sieve, and the contents viewed under a microscope. We collected substrate samples and replaced tuffies and tiles at 2 wk intervals during 2 sampling periods, and took the average of the recruitment at both sampling periods.

Dwesa: In the Dwesa region, we deployed 4 nylon brushes as mussel recruit collectors at each sampling location and collected them after 1 mo. The brushes were placed in an ultrasonic bath in a dilute bleach solution, and materials found in the brushes were sorted through a series of sieves. Mussels were counted under a dissecting microscope.

Mapelane: In the Mapelane region, we deployed 3 tuffies and collected three 100 cm^2 samples of 100%-cover mussel bed and three 100 cm^2 samples of algal turf at each sampling location. We rinsed tuffies over a 250 µm sieve after retrieval and counted mussel recruits (<5 mm) in tuffies and substrate samples using a dissecting microscope. We collected substrate samples and replaced tuffies at 2 wk intervals during 3 sampling periods, and averaged recruitment from the 3 sampling periods.

Estimated mean dispersal scale: To estimate mean dispersal scale in the Goukamma and Dwesa regions, we fit a dispersal model to the spatial pattern of production and recruitment data. We created an array of estimated production values across each study region by recording substrate (sand or rock at Mapelane and Dwesa, and sand, limestone, sandstone bench, or sandstone patch at Goukamma) at 0.016 km intervals using Google Earth, and using average production estimates for each substrate type/protection status combination from our data in each region. Production estimates were continued for at least 100 km beyond the boundaries of each study region to reduce edge effects. We then used non-linear least squares model fitting in R (R Development Core Team 2005) to fit an array of the recruitment data from all sites within each region to an array of predicted recruitment, calculated using the following equation:

$$R_y = z \sum_x P_x k(x, y) \tag{1}$$

where x and y are alongshore locations, R_y is recruitment at any location y, z is a scaling factor (accounting for the conversion of our biomass or gonad mass proxies for production to number of larvae produced, and incorporating larval and post-settlement mortality, to convert estimated gonad mass or biomass per unit length of coastline to larval recruitment), P_x is production at location x, and $k(x,y)$ is the larval dispersal kernel describing the frequency distribution of larvae from each location x arriving at each location y. Because suitable *Perna perna* habitat may not always be distributed continuously, we used the double geometric dispersal kernel for a discrete analogue of exponential decay, previously used to model dispersal in marine reserves (Botsford et al. 2001, Lockwood et al. 2002, Baskett et al. 2007):

$$k(x, y) = \frac{(1-A)^{|x-y|}A}{2} \tag{2}$$

where A is a parameter describing dispersal scale, such that the mean dispersal distance is:

$$\frac{1-A}{A} \tag{3}$$

Subtidal and/or inaccessible mussel beds may also contribute to production of mussel larvae, particularly in the Dwesa region, where (owing to its topography and substrate availability) subtidal subsidies are most likely. Therefore, we ran the model with a range of supplemental production, assumed to be homogenously distributed inside and outside the reserve, and

reported the resulting range of dispersal estimates for the Dwesa region. The model was sensitive to varying the amount of subtidal subsidy, although the estimated dispersal scale remained within the same order of magnitude. Because we are unable to calculate or determine robust estimates of production in these subtidal or inaccessible zones, we can use this model only to determine rough estimates of dispersal scale. These rough approximations are probably more appropriate than precise estimates of the mean dispersal scale when sampling is limited, given that dispersal scales of the same species may be highly variable across space and time.

Spatial scale and magnitude of larval export: We defined the spatial scale of the larval export effect as the distance (calculated from the reserve center in one direction) over which recruitment was significantly higher than an estimated background or baseline level of recruitment that would be expected in the absence of larval export from the reserve. We estimated the larval export effect scale as the distance from the reserve center where the one-tailed lower 95% confidence curve on the regression of recruitment by distance intersects background recruitment levels, approximated as recruitment at the farthest site from the reserve, in the absence of actual baseline data for recruitment.

To calculate the magnitude of the larval export effect, we divided total recruitment within the region enhanced by larval export (defined as the region outside the reserve but within the spatial scale of the larval export effect, as calculated above) by total recruitment that would be expected within the same region in the absence of larval export. For any regions with significant larval export from the reserve, we calculated the definite integral of recruitment from the reserve edge to the measured spatial scale of the larval export effect in each region to approximate total recruitment within the region enhanced by larval export. We estimated expected total recruitment in the absence of larval export by multiplying the length of this enhanced region by the baseline level of recruitment, approximated as recruitment at the most distant site from the reserve, as above.

Data analysis. In the Goukamma region, both substrate type and protection status were important factors that varied inside versus outside the reserve and could affect production, while in the Dwesa and Mapelane regions, substrate type was similar at all our sampling sites, and habitat distribution was similar inside and outside the reserves. To separate effects of substrate type and protection status in the Goukamma region, we used a 2-way ANOVA to analyze mussel length, density, and production and barnacle percent cover data from within the sampled habitat. Mussel

production data and barnacle percent cover data were square root-transformed to conform to the assumption of normality. Standardized mussel production and barnacle percent cover within the sampled habitat ('local production') were combined with habitat distributions determined from Google Earth to estimate production and percent cover per unit length of coastline. We performed a bootstrap test to determine confidence intervals of these estimates of production (for mussels) and percent cover (for barnacles) per unit length of coastline and determine whether these values were significantly different inside versus outside the Goukamma reserve.

A 1-way ANOVA was used to analyze the effect of reserve protection on mussel length and density data from Mapelane. Mussel production data from Mapelane were square root-transformed to meet the assumption of normality and analyzed with a Welch ANOVA due to heterogeneity of variances. All tests were 2-tailed with an alpha level of 0.05.

For all regions, we tested the relationship between recruitment and distance from each reserve with a linear regression with a natural log transform on recruitment. We used the log transform to determine if exponential decay is a reasonable approximation for the shape of the decline. Recruitment values were averaged across both spatial (subsite) and temporal (tide series) replicates within sites; therefore, their underlying distribution approaches normality. We analyzed the relationship between mussel recruitment and mussel adult density, production, and juvenile abundance with Pearson's product-moment correlation tests.

RESULTS

In the Goukamma region, because both habitat distribution and protection status may have influenced production, we present data on local production (indicating reserve effectiveness) as well as estimated production per unit length of coastline (indicating differences in expected larval production per standard length of coast). Mussel density, length, and production (standardized for substrate) within the sampled habitat, indicators of reserve effectiveness, were significantly higher inside the reserve than outside (density: $F_{(1,186)}$ = 14.72, p = 0.0002, Fig. 2A; length: $F_{(1,3231)}$ = 28.88, p < 0.0001, Fig. 2B; production: $F_{(1,186)}$ = 36.63, p < 0.0001, Fig. 3A). In addition, there was a greater proportion of suitable mussel habitat inside the reserve (46% rocky substrate) compared with outside the reserve (37% rocky substrate). Production per length of coastline, a metric taking into account both production per area of mussel habitat and amount of mussel habitat per length of coastline,
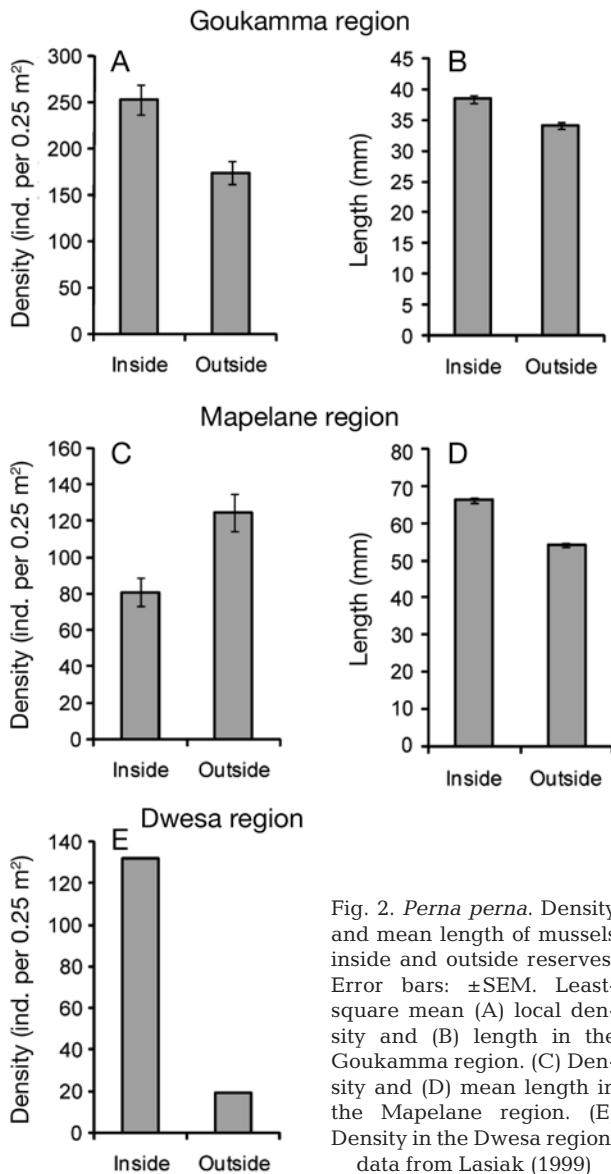
Fig. 2. *Perna perna*. Density and mean length of mussels inside and outside reserves. Error bars: ±SEM. Least-square mean (A) local density and (B) length in the Goukamma region. (C) Density and (D) mean length in the Mapelane region. (E) Density in the Dwesa region; data from Lasiak (1999)
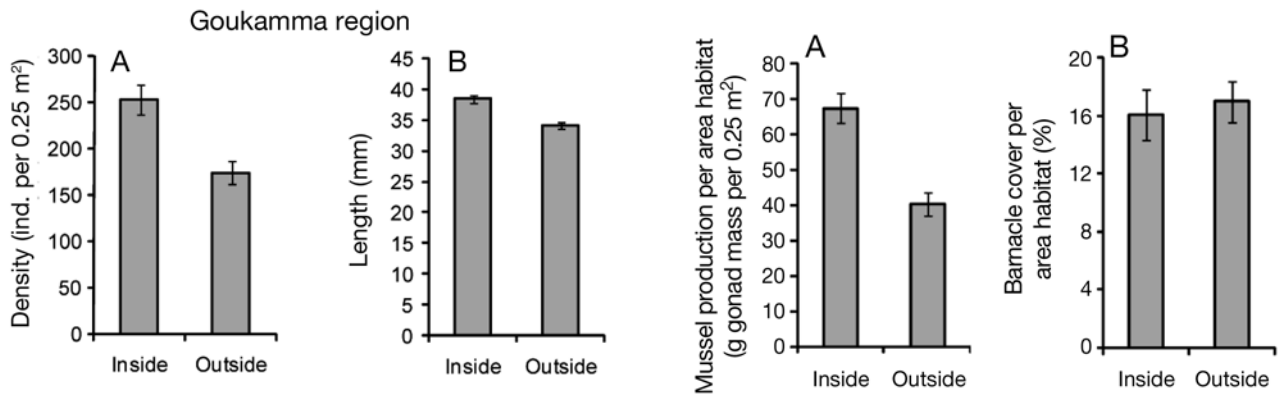

Fig. 3. *Perna perna* and *Octomeris angulosa*. Estimated (A) production of mussels and (B) percent cover of barnacles within sampled habitat inside and outside the Goukamma reserve. Error bars: ±SEM

was higher inside Goukamma reserve than outside (p = 0.0001, Fig. 4A). Coincident with these patterns of production, mussel recruitment declined exponentially with distance from the reserve's center ($F_{(1,3)}$ = 30.25, R^2 = 0.910, p = 0.0118, Fig. 4B). Mussel recruitment was not correlated with adult density (ρ = 0.2517, p = 0.5135) or estimated production (ρ = −0.0347, p = 0.9294) across sites. The mean dispersal scale of mussel larvae in this region was estimated at about 4.4 km (±1 SE interval: 1.6 to 51.9 km). The scale of the larval export effect, estimated from the point where the lower 95% confidence interval of recruitment crossed the baseline recruitment level, was approximately 20 km from the reserve center. Total recruitment within the subsidized region outside the Goukamma reserve was >12 times higher than

background levels. In contrast to these results, percent cover of unharvested barnacles showed no differences either within sampled habitat ($F_{(1,124)}$ = 0.2838, p = 0.5952, Fig. 3B) or by length of coastline (p = 0.7382, Fig. 4C), and barnacle recruitment showed no relationship with distance from the reserve ($F_{(1,2)}$ = 0.43, R^2 = 0.178, p = 0.5784, Fig. 4D).

Published data from the Transkei region shows that the Dwesa-Cwebe Nature Reserve, the only protected site in the southern part of the Transkei, harbored 7 times the abundance (Fig. 2E) and >22 times the biomass of *P. perna* compared with nearby exploited sites (Fig. 4E; Lasiak 1999). Data from the present study indicate that recruitment declined with distance from the reserve, and this relationship was well described by an exponential decay curve ($F_{(1,3)}$ = 19.41, R^2 = 0.866, p = 0.0217, Fig. 4F). Mean dispersal distance was estimated as 12.6 km (±1 SE interval: 10.2 to 16.2 km) when accounting only for production at intertidal beds, and ranged as low as 2.4 km when assuming a subtidal production subsidy throughout all the rocky substrate in the region, both inside and outside the reserve, of equal magnitude to the production at protected intertidal beds. As in Goukamma, the larval export effect scale was estimated as 20 km. Total mussel recruitment within the region with enhanced recruitment outside Dwesa-Cwebe was approximately 1.8 times higher than background recruitment levels at more distant sites.

Mussels inside the Mapelane Nature Reserve were less numerous ($F_{(1,188)}$ = 11.31, p = 0.0009, Fig. 2C) but larger ($F_{(1,3232)}$ = 154.0613, p < 0.0001, Fig. 2D) than mussels outside the reserve. In contrast to the Dwesa-Cwebe and Goukamma reserves, there was no difference in estimated larval production of mussels inside versus outside the Mapelane reserve ($F_{(1,178.83)}$ = 0.405, p = 0.5252, Fig. 4G), and there was no relationship between recruitment and distance from the Mapelane
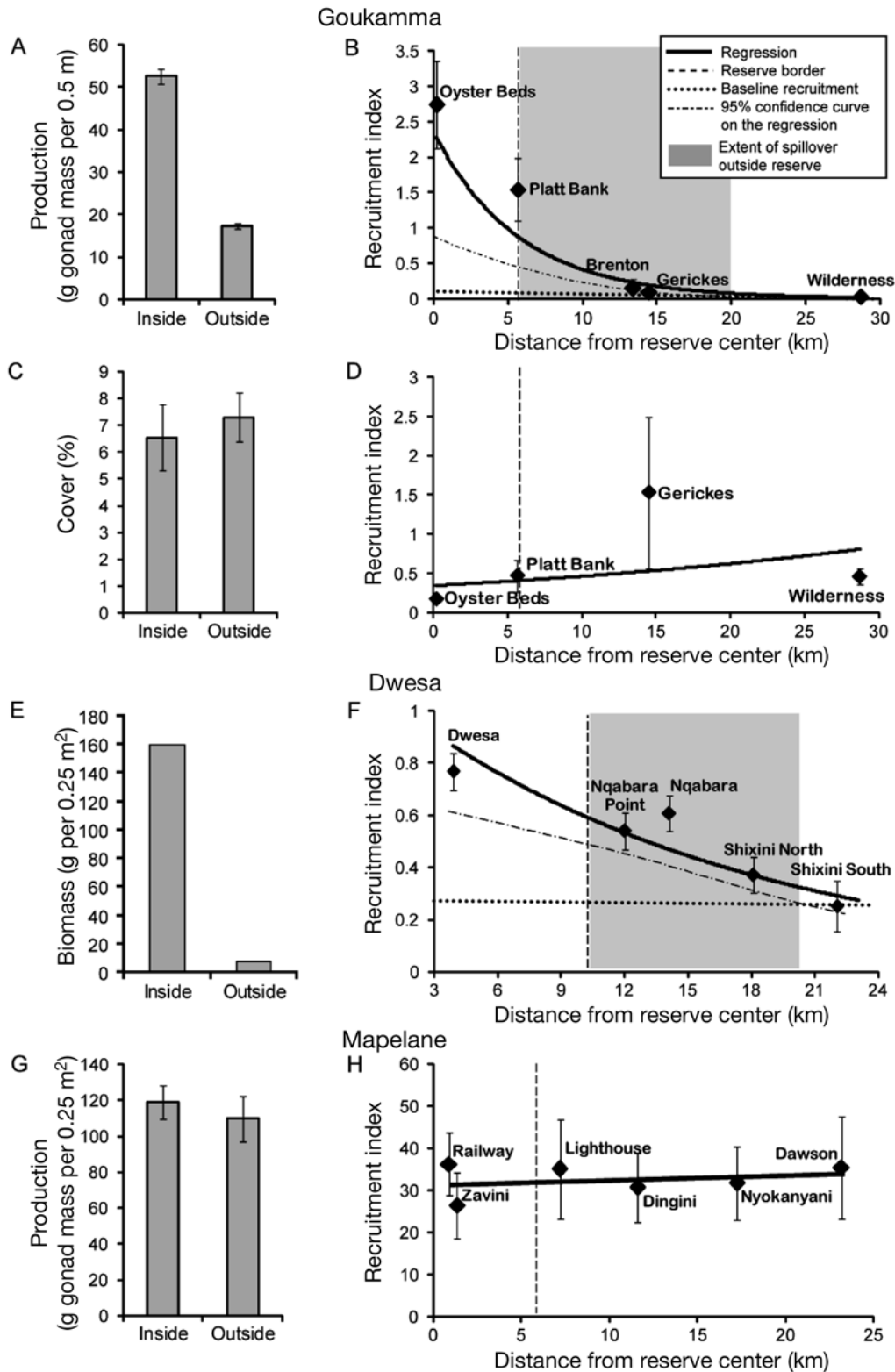
Fig. 4. *Perna perna* and *Octomeris angulosa*. Production and recruitment inside and outside reserves. Error bars: ± SEM. (A) Standardized mussel production per length of coastline inside and outside the Goukamma reserve. (B) Mussel recruitment declines exponentially with distance from the center of the Goukamma reserve. (C) Estimated standardized barnacle percent cover per length of coastline inside and outside the Goukamma reserve. (D) Barnacle recruitment shows no decline with distance from the center of the Goukamma reserve. (E) Mussel biomass inside and outside Dwesa-Cwebe reserve. Data from Lasiak (1999). (F) Mussel recruitment declines exponentially with distance from the center of the Dwesa-Cwebe reserve. (G) Mussel production inside and outside the Mapelane reserve. (H) Mussel recruitment shows no decline with distance from the center of the Mapelane reserve

reserve ($F_{(1,4)}$ = 0.32, R^2 = 0.075, p = 0.6003, Fig. 4H). As in Goukamma, recruitment across sites in the Mapelane region was not correlated with either local production (ρ = 0.2285, p = 0.6633) or mussel density (ρ = 0.3406, p = 0.5088). On the scale of mussel bed samples (100 cm^2 scale), recruitment was not significantly correlated with adult mussel density (ρ = 0.0958, p = 0.3979).

DISCUSSION

Production, recruitment and the reserve effect

Patterns of recruitment and production within each region support our hypothesis that where larval production is greater inside reserves, recruitment will decline with distance from reserves. For the harvested mussel *Perna perna*, but not for unharvested barnacles, recruitment declined with distance in the Goukamma and Dwesa regions, where larval production was enhanced by the protection of larger, more abundant adults. The elevated larval production inside reserves and the gradient in recruitment with distance from reserves suggest that larval export subsidizes fished areas. With our method of quantifying larval export, we find that this spillover benefit extends several kilometers from the reserves. The lack of a spatial pattern of recruitment for unharvested barnacles in Goukamma, which were no more abundant inside the reserve than outside, supports the hypothesis that for the harvested mussel, patterns of declining recruitment with distance from the Goukamma and Dwesa reserves are driven by larval export due to protection and subsequently enhanced production in the reserves.

In Mapelane, production was similar inside and outside the reserve despite differences in size structure and density. It is possible that mussels in the Mapelane Nature Reserve grew to larger sizes due to lower mortality rates because of protection, and that the larger sizes led to lower densities inside the reserve through density-dependent competition for space. McQuaid and Lindsay (2007) found that decreased densities of *Perna perna* at sites with larger mussels compensated for increased size, leading to similar biomass across sites, presumably due to density-dependent competition for space. However, this relationship would not be expected to hold where mussels are severely depleted owing to heavy harvesting. In this study, estimated production was far higher in the Mapelane region than in the Goukamma and Dwesa regions, which is consistent with previously described biogeographic patterns in South Africa (Reaugh 2006). In addition to the effect of biogeography, high production in this region may

reflect relatively low harvest rates outside the reserve. Under a community-based management program in the region, instituted in 1995, local intertidal monitors set harvest quotas, enforce a closed season, and carefully monitor the mussel beds during all spring tides to prevent poaching (Harris et al. 2003).

With no difference in production inside versus outside Mapelane Nature Reserve, there is no expectation of a gradient in recruitment with distance from the reserve, and we found no spatial pattern in recruitment within the region. Because no reserve effect was found in Mapelane, this region functions as a useful comparison, suggesting that significant declines in recruitment with distance from reserves occur only where strong gradients in production occur. In addition, naturally high levels of larval supply in the region may swamp any effects of among-site differences, causing the relatively low among-site variability in recruitment in this region. In an analysis of a multiyear study of mussel recruitment along the South African coastline, Reaugh (2006) found far higher recruitment rates (as with the production mentioned above) in Kwazulu-Natal, where Mapelane is located, than in the study sites near the Dwesa and Goukamma reserves. Reaugh (2006) proposed that recruitment in this region may be enhanced by high retention of larvae, due to relatively little upwelling (compared with the southern coast where Goukamma is located), and a wider shelf and more embayed coastline than the region where Dwesa is located. Recruitment rates that we measured were consistent with this pattern, although methods differed across regions, and therefore the recruitment rates from our study cannot be directly compared among regions. Without larval supply limitation, microscale variation in larval delivery may be the main factor shaping recruitment patterns in the Mapelane region (McQuaid & Lawrie 2005, Porri et al. 2006). In contrast, differences in larval supply due to strongly differential production inside and outside the Dwesa-Cwebe and Goukamma reserves appear to determine recruitment patterns in those areas.

Effects of natural variability

The higher production inside Goukamma Nature Reserve compared with that outside the reserve was a product of both a reserve effect and heterogenous habitat distribution, with a greater proportion of suitable mussel habitat inside the reserve. While the habitat distribution alone is not sufficient to produce the strong decline in recruitment that we detected, the superior habitat within the reserve certainly contributed to differences in production per length of coastline, most likely making the decline in recruitment with distance

from the reserve more dramatic. Differences in habitat quality may frequently confound the effects of marine reserves, and explicit consideration of habitat is necessary to account for these effects (Garcia-Charton & Perez-Ruzafa 1999). The similarity between patterns of recruitment near Goukamma, where habitat was highly patchy, and Dwesa-Cwebe, characterized by continuous rocky habitat, suggests that the declines in recruitment that we detected are driven by reserve effects, and not solely by habitat. This hypothesis is also supported by the lack of a pattern in recruitment for unharvested barnacles in Goukamma, which also rely on rocky habitat for settlement, but were no more abundant inside the reserve than outside.

Mussels settle directly into adult mussel beds, and therefore adult mussel abundance may influence recruitment in 2 ways: (1) by providing settlement habitat, and (2) by influencing larval supply (Erlandsson & McQuaid 2004, Robinson et al. 2007). Robinson et al. (2007) found that with presumed high larval supply, experimental harvesting of adult *Mytilus galloprovincialis* reduced recruitment by decreasing settlement habitat. In our study, the use of standardized collectors in addition to natural substrate helped to eliminate this potentially confounding factor. In addition, we found no correlation between adult abundance and recruitment, even within our mussel bed samples. The effects described by Robinson et al. (2007) are specific to a species with high recruitment rates in a system where settlement habitat is saturated and larval supply is not limiting, conditions that do not apply in this study. However, the importance of intact adult beds as a settlement substrate suggests that in addition to protecting standing stocks in reserves, sustainable management strategies must include some protections outside reserves to allow exploited mussel populations to recover (Dye et al. 1997).

Post-settlement mortality may also affect the observed recruitment rates in this study. Because standardized collectors were replaced every 2 wk (tiles and tuffies) to 4 wk (brushes), recruits may have settled in these collectors up to 2–4 wk before they were counted. Similarly, we inferred, on the basis of the size of recruits measured in the natural substrate, that settlement may have occurred up to a few weeks before our *in situ* recruitment measurements. It is possible that post-settlement mortality affected the results if mortality rates differed among sites, for example, owing to differential predation rates inside versus outside the reserves or density-dependence at settlement. Because it was not possible to measure recruitment on a daily basis or to quantify settlement before post-settlement mortality had an effect, an effect of post-settlement mortality cannot be conclusively ruled out. However, we used standard methods commonly used in

explorations of larval supply, and we know of no reason to expect biases among sites in either abundance of predators of new settlers or density dependence at settlement that would lead to the patterns in recruitment observed here. While strong density-dependent mortality rates after settlement could have contributed to the lack of observed pattern in recruitment in the Mapelane region, recruitment in that region was driven almost entirely by very small, very recent settlers and is therefore unlikely to be strongly affected by post-settlement mortality.

A common criticism of marine reserve studies is that without data taken both before and after reserve establishment, it is impossible to determine whether observed spatial differences in abundance result from reserve protection or natural spatial gradients, a particularly important concern if reserves are generally placed in naturally more productive areas (Lester et al. 2009). No historical data are available to compare spatial patterns of recruitment before and after the establishment of the Goukamma, Dwesa-Cwebe, and Mapelane reserves. However, several attributes of this study suggest that the spatial patterns we detected are not merely artifacts of siting reserves in intrinsically high-settlement areas. First, the reserves sampled here are multi-purpose coastal nature reserves designated to protect a diversity of both terrestrial and marine habitats, and siting is unlikely to be based on the distribution of mussel stocks. In the Goukamma region, according to reserve management, the primary purpose of the marine reserve is to preserve 'marine and estuarine ecosystems that are representative of the warm temperate south coast' and 'the MPA [marine protected area] was not established where it is because of mussel populations and is rather a case of protection leading to a higher biomass' (M. Prophet, pers. comm). In Dwesa, the reserve's management plan lists the primary purposes of the nature reserve as the conservation of coastal forests and unique grassland habitat, as well as protection of a marine and estuarine habitat that is important for several collapsed fish stocks, notably including a number of reef fish species and abalone. More generally, a meta-analysis of marine reserve studies that use a Before-After-Control-Impact (BACI) design found no evidence that reserves are typically placed in superior habitat (Halpern et al. 2004). Finally, it is unlikely that the spatial patterns we detected—i.e. dramatic declines in recruitment with distance from reserves in the 2 regions where production was considerably higher inside reserves, but not in a region where production was no higher in reserves than outside—result from coincidental natural gradients in recruitment rates. While we cannot rule out the possibility that natural spatial gradients contribute to the observed patterns, the replication provided by

sampling 3 reserves strengthens our confidence in our conclusions, because recruitment declined with distance only near the reserves that harbored enhanced populations of mussels. In addition, the hypothesis that the declines in recruitment we observed are driven by larval export from reserves is further supported by the finding that barnacles, which are not harvested, were no more abundant inside the reserve than outside, and there was no spatial pattern of barnacle recruitment.

Also, it should be noted that establishment of reserves may have concentrated effort outside the reserves, potentially increasing mortality and decreasing both production and recruitment outside reserves. Without historical data from these regions, we cannot conclusively compare recruitment and production before and after reserve establishment, and this presents the potential for overestimation of what we consider 'baseline' recruitment. However, despite concerns that displaced fishing effort may depress populations outside reserves after the onset of protection, meta-analysis of BACI studies has found no evidence of this effect (Lester et al. 2009). Because only sites south (downstream) of both the Dwesa and Mapelane reserves were sampled (Beckley & Vanballegooyen 1992), the patterns we detected may not necessarily be applicable to sites upstream of reserves. In Goukamma, only one site east of the reserve was included, which similarly limits the ability to extrapolate the results.

Scales of dispersion and larval export effect

In both the Dwesa and the Goukamma regions, the dispersal scales we estimated (12.6 and 4.4 km, respectively) are consistent with our expectations. In particular, they agree with stock-recruitment relationships that suggest self-recruitment in *Perna perna* on scales of about 10 km (Harris et al. 1998, Reaugh 2006), mirror the finding that larvae of the invasive mussel *Mytilus galloprovincialis* in South Africa generally settled within 5 km of the parent population (McQuaid & Phillips 2000), and are consistent with recent evidence that coastal mussels in California are retained within 20 to 30 km of source populations (Becker et al. 2007). While *P. perna* are clearly capable of long-distance dispersal events (Hicks & Tunnell 1995), the mean dispersal scales estimated here are more relevant for population replenishment from harvesting (Kinlan et al. 2005). Differences in dispersal scales between the 2 areas are not surprising given the local oceanography and coastal topography in each region. The highly embayed coastline and wide coastal shelf near Goukamma, where the estimated dispersal scale is shorter, suggest greater larval retention in the region,

and the Goukamma Nature Reserve is located within an embayment (Reaugh 2006). In contrast, the relatively straight coastline and narrow coastal shelf near Dwesa may facilitate longer-distance larval transport (Reaugh 2006). However, it is important to note that because subtidal sources of production could not be quantified, the estimates of production along the coastline are only rough approximations. As a result, the dispersal scale estimates, which depend on estimates of production, should be considered only order-of-magnitude approximations.

Implications for conservation and management

The estimated scale of the larval export effect was similar in Dwesa and Goukamma, about 20 km in each system. It is important to note, however, that this estimate is likely to be more conservative for the Dwesa region than the Goukamma region. Because baseline recruitment levels are not known, we used recruitment at the most distant site in each region as an estimate of baseline recruitment. Near Goukamma, this level of recruitment was very low and may well represent a true baseline. The spatial extent of our sampling around Dwesa was shorter, however, and recruitment even at our most distant site was relatively high given that other studies have found the Dwesa region to have the lowest recruitment levels in South Africa (Harris et al. 1998, Reaugh 2006). This suggests that the larval export effect in the Dwesa region may actually extend well beyond the spatial extent of our study.

The existence of recruitment subsidies in these regions has important implications for management of *Perna perna* in South Africa and species with similar life histories of nearshore planktonic larvae and sessile adults. Prior studies have found that *P. perna* is recruitment-limited in some parts of South Africa, including Dwesa and Port Elizabeth (near the Goukamma Nature Reserve; Reaugh 2006), suggesting that larval export from these reserves may help support the heavily harvested mussel populations nearby. Due to the widespread and diffuse nature of subsistence harvesting, the challenge of enforcement across broad spatial scales frequently limits the efficacy of traditional management and regulations. Spatial management, which allows managers to concentrate enforcement in closed areas, may be the most tenable strategy for sustaining this resource. More generally, our results indicate that reserves can protect source populations and export larvae to fished areas, which helps provide a buffer against uncertainty in fisheries management (Pauly et al. 2002), and our results from Mapelane suggest that such larval export benefits vary with natural recruitment rates and fishing pressure outside reserves.

The scale of benefit, however, is tied to the scale of larval dispersal (Hilborn et al. 2004). Knowledge of the scales of larval dispersal and export is critical to determining the optimal size and spacing of reserves and designing effective reserve networks (Halpern & Warner 2003, Palumbi 2004, Sale et al. 2005). Theoretical explorations have found that for larval export to occur and offset the effects of displaced fishing effort caused by closing an area to fishing, reserves should be no larger than twice the mean dispersal scale (Halpern et al. 2004). Although reserves are multispecies conservation tools and dispersal scales vary by orders of magnitude among species protected within a single reserve (Kinlan & Gaines 2003), results from this study suggest that the reserves in South Africa are an appropriate size for allowing larval export of *Perna perna* to benefit nearby fished areas. Estimates of the scale of the larval export effect from this study and approach can inform future efforts in the design, placement, and evaluation of networks of marine reserves.

Despite the expectation that larval export will occur wherever reserves enhance the production of planktonically dispersed larvae, empirical evidence for larval export has been sparse. Very broad dispersal in some species may obscure the spatial signal of larval export by diluting it over larger distances, or studies may not sample at the appropriate spatial or temporal scale to detect that signal. In addition, any signal of larval export in recruitment data may not appear for many years given the high temporal heterogeneity in productivity and recruitment characteristic of marine populations. In other cases, reserves may be too small relative to the neighborhood sizes of exploited species to contribute significantly to the local or regional larval pool (Palumbi 2004), and siting reserves in isolated or 'sink' locations may prevent larvae from successfully dispersing from reserves to non-reserve areas (Crowder et al. 2000, Lipcius et al. 2001). Further study is necessary to understand how larval export is affected by species life history, oceanography, and the design and placement of marine reserves. Nonetheless, for a heavily exploited species with pelagic larval dispersal, we have estimated the spatial scale of larval export from effective marine reserves.

LITERATURE CITED

Baskett ML, Weitz JS, Levin SA (2007) The evolution of dispersal in reserve networks. Am Nat 170:59–78

Becker BJ, Levin LA, Fodrie FJ, McMillan PA (2007) Complex larval connectivity patterns among marine invertebrate populations. Proc Natl Acad Sci USA 104:3267–3272

Beckley LE, Vanballegooyen RC (1992) Oceanographic conditions during 3 ichthyoplankton surveys of the Agulhas current in 1990/91. S Afr J Mar Sci 12:83–93

Beukers-Stewart BD, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR (2005) Benefits of closed area protection for a population of scallops. Mar Ecol Prog Ser 298:189–204

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Branch GM, Odendaal F (2003) The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. Biol Conserv 114:255–269

Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. Bull Mar Sci 66:799–820

Cudney-Bueno R, Lavin MF, Marinone SG, Raimondi PT, Shaw WW (2009) Rapid effects of marine reserves via larval dispersal. PLoS One 4:e4140, doi:10.1371/journal.pone.0004140

Dye AH, Lasiak TA, Gabula S (1997) Recovery and recruitment of the brown mussel, *Perna perna* (Linnaeus), in Transkei: implications for management. S Afr J Zool 32:118–123

Erlandsson J, McQuaid CD (2004) Spatial structure of recruitment in the mussel *Perna perna* at local scales: effects of adults, algae and recruit size. Mar Ecol Prog Ser 267: 173–185

Evans RD, Russ GR, Kritzer JP (2008) Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia. Coral Reefs 27:179–189

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula.* Oecologia 67: 267–272

Garcia-Charton JA, Perez-Ruzafa A (1999) Ecological heterogeneity and the evaluation of the effects of marine reserves. Fish Res 42:1–20

Gaylord B, Gaines SD, Siegel DA, Carr MH (2005) Marine reserves exploit population structure and life history in potentially improving fisheries yields. Ecol Appl 15: 2180–2191

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol 18: 448–455

Griffiths CL, Branch GM (1997) The exploitation of coastal invertebrates and seaweeds in South Africa: historical trends, ecological impacts and implications for management. Trans R Soc S Afr 52:121–148

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13(Suppl.):117–137

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc R Soc Lond Ser B Biol Sci 270:1871–1878

Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. Ecol Appl 14: 1248–1256

Harris JM, Branch GM, Elliott BL, Currie B and others (1998) Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. S Afr J Zool 33:1–11

Harris JM, Branch GM, Sibiya C, Bill C (2003) The Sokhulu subsistence mussel-harvesting project: co-management in action. In: Hauck M, Sowman M (eds) Waves of change: coastal and fisheries co-management in South Africa. UCT Press, Cape Town, p 61–98

Hicks DW, Tunnell JW (1995) Ecological notes and patterns of dispersal in the recently introduced mussel, *Perna perna* (Linnaeus, 1758), in the Gulf of Mexico. Am Malacol Bull 11:203–206

Hilborn R, Stokes K, Maguire JJ, Smith T and others (2004) When can marine reserves improve fisheries management? Ocean Coast Manag 47:197–205

Hockey PAR, Branch GM (1994) Conserving marine biodiversity on the African coast—implications of a terrestrial perspective. Aquat Conserv Mar Freshwat Ecosyst 4:345–362

Kamukuru AT, Mgaya YD (2004) Effects of exploitation on reproductive capacity of black-spotted snapper, *Lutjanus fulviflamma* (Pisces: Lutjanidae) in Mafia Island, Tanzania. Afr J Ecol 42:270–280

Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. Ecol Appl 17:1039–1054

Kelly S, Scott D, MacDiarmid AB, Babcock RC (2000) Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. Biol Conserv 92:359–369

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Divers Distrib 11:139–148

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecol Appl 13(Suppl.):71–89

Lasiak T (1999) The putative impact of exploitation on rocky infratidal macrofaunal assemblages: a multiple-area comparison. J Mar Biol Assoc UK 79:23–34

Lasiak TA, Barnard TCE (1995) Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary-secondary settlement hypothesis. Mar Ecol Prog Ser 120:147–153

Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J and others (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384: 33–46

Lipcius RN, Stockhausen WT, Eggleston DB (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. Mar Freshw Res 52:1589–1598

Lockwood DR, Hastings A, Botsford LW (2002) The effects of dispersal patterns on marine reserves: Does the tail wag the dog? Theor Popul Biol 61:297–309

Manriquez PH, Castilla JC (2001) Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas.* Mar Ecol Prog Ser 215:201–211

Marean CW, Bar-Matthews M, Bernatchez J, Fisher E and others (2007) Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449:905–908

McClanahan TR, Mangi S (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecol Appl 10:1792–1805

McQuaid C, Lawrie S (2005) Supply-side ecology of the brown mussel, *Perna perna*: an investigation of spatial and temporal variation in, and coupling between, gamete release and larval supply. Mar Biol 147:955–963

McQuaid CD, Lindsay TL (2007) Wave exposure effects on population structure and recruitment in the mussel *Perna perna* suggest regulation primarily through availability of recruits and food, not space. Mar Biol 151:2123–2131

McQuaid CD, Phillips TE (2000) Limited wind-driven dispersal of intertidal mussel larvae: in situ evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. Mar Ecol Prog Ser 201: 211–220

Murawski SA, Brown R, Lai HL, Rago PJ, Hendrickson L (2000) Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. Bull Mar Sci 66:775–798

Paddack MJ, Estes JA (2000) Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. Ecol Appl 10:855–870

Palsson WA, Pacunski RE (1995) The response of rocky reef fishes to harvest refugia in Puget Sound. In: Robichaud E (ed) Proc Puget Sound Research, Jan 12 1995, Bellevue, WA, Vol 1. Puget Sound Water Quality Authority, Olympia, WA, p 224–234

Palumbi SR (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annu Rev Environ Resour 29:31–68

Pauly D, Christensen V, Guenette S, Pitcher TJ and others (2002) Towards sustainability in world fisheries. Nature 418:689–695

Pineda J, Hare J, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography (Wash DC) 20:22–39

Porri F, McQuaid CD, Radloff S (2006) Spatio-temporal variability of larval abundance and settlement of *Perna perna*: differential delivery of mussels. Mar Ecol Prog Ser 315:141–150

R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reaugh K (2006) Recruitment patterns and processes and the connectivity of rocky shores in southern Africa. PhD thesis, University of Cape Town

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science 294:1920–1923

Robinson TB, Branch GM, Griffiths CL, Govender A (2007) Effects of experimental harvesting on recruitment of an alien mussel *Mytilus galloprovincialis.* J Exp Mar Biol Ecol 345:1–11

Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT (2004) Marine reserve benefits local fisheries. Ecol Appl 14:597–606

Sale PF, Cowen RK, Danilowicz BS, Jones GP and others (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80

Siddall SE (1979) Effects of temperature and salinity on metamorphosis in two tropical mussels. Proc Natl Shellfish Assoc 69:199

Siddall SE (1980) A clarification of the genus *Perna* (Mytilidae). Bull Mar Sci 30:858–870

Siegel DA, Kinlan BP, Gaylord B, Gaines SD (2003) Lagrangian descriptions of marine larval dispersion. Mar Ecol Prog Ser 260:83–96

Siegfried WR, Hockey PAR, Crowe AA (1985) Exploitation and conservation of brown mussel stocks by coastal people of Transkei. Environ Conserv 12:303–307

Sluka R, Chiappone M, Sullivan KM, Wright R (1997) The benefits of a marine fishery reserve for Nassau grouper *Epinephelus striatus* in the central Bahamas. Proc 8th Int Coral Reef Symp, Panama City 2:1961–1964

Stobutzki IC (2000) Marine reserves and the complexity of larval dispersal. Rev Fish Biol Fish 10:515–518

Stoner AW, Ray M (1996) Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. Fish Bull (Wash DC) 94:551–565

Stoner AW, Mehta N, Ray-Culp M (1998) Mesoscale distribution patterns of Queen Conch (*Strombus gigas* Linnaeus) in Exuma Sound, Bahamas: links in recruitment from larvae to fishery yields. J Shellfish Res 17:955–969

Swearer SE, Shima JS, Hellberg ME, Thorrold SR and others (2002) Evidence of self-recruitment in demersal marine populations. Bull Mar Sci 70:251–271

Tawake A, Parks J, Radikedike P, Aalbersberg B, Vuki V, Salafsky N (2001) Harvesting clams and data: involving local communities in monitoring can lead to conservation success in all sorts of unanticipated ways: a case in Fiji. Conserv Pract 2:32–35

Tawake A, Gell F, Roberts C (2002) Community-based closed areas in Fiji. In: Gell F, Roberts C (eds) The fishery effects of marine reserves and fishery closures. WWF-US, Washington, DC, p 59–62

Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. J Appl Ecol 40:214–227