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Marine protected areas export larvae of infauna, but not of bioengineering mussels to adjacent areas

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ABSTRACT

Populations of organisms that create habitat can often be fragmented throughout landscapes by anthropogenic disturbances such as harvesting and loss or change to the identity of such bioengineers may lead to large changes in biodiversity. Using the fauna associated with a bioengineer, the intertidal mussel *Perna perna*, we tested hypotheses about the relative importance of larval export from protected populations in marine reserves. Harvesting led to the replacement of *P. perna* and the domination of shores outside reserves by turf-forming coralline algae, mostly *Corallina* spp. We determined whether the diverse fauna recruiting onto artificial units of habitat placed within mussel beds differed between reserves and non-reserve areas or whether shores outside reserves, and open to harvesting, received recruits through larval export from reserves. Furthermore, we determined whether this was affected by the distance away from reserves and whether colonisation was achieved by movement of adults from surrounding biogenic habitats or via the plankton. Overall, we found no effect of increasing distance away from a reserve on the cover of adult mussels or associated fauna. We found strong effects of the presence of marine reserves on abundances of molluscs and polychaetes but not crustaceans. There were greater densities of molluscs in sites with a reserve (i.e. inside reserves, and up to 5 km outside reserve boundaries), but more polychaetes in exploited sites. For molluscs, this pattern was driven by gastropods rather than bivalves. Furthermore, although reserves had greater cover of adult mussels than non-reserve areas, recruitment of mussels was not greater inside or near to reserves. Our study illustrates the effectiveness of these reserves in protecting stocks of adult mussels, and although there was no evidence that reserves provided export of the larvae of mussels (the target species), they did provide larval export of non-targeted associated species. By protecting a harvested bioengineer and through export of the larvae of its associated fauna, these reserves fulfil some, but not all the conservation aims of a marine protected area.

1. Introduction

There are concerns about how anthropogenic transformation of landscapes will lead to loss of species (Lindborg and Eriksson, 2004), so that we need to understand how fragmentation and connectivity affect ecological processes and the abundance and distribution of species in time and space. Usually habitat destruction refers to loss of biogenic habitat and consequent alteration of both habitat structure and abiotic conditions, rather than direct alteration of environmental conditions. Work has begun clarifying the effects of landscape fragmentation and the addition of corridors among habitat patches by focussing on individual species and the processes that threaten them (e.g. Beier and Noss, 1998; Bélisle, 2005), with previous studies illustrating delayed responses to habitat destruction (Hanski, 1998). Models of metapopulation dynamics propose that the probability of re-colonisation of patches that have been destroyed and of "rescue-effects" depend on the proximity of neighbouring patches (see Hanski (1998) for review).

Extinction cascades are likely if populations of keystone species or entire functional groups become fragmented (Fischer and Lindenmayer, 2007). Organisms that create habitat are an important functional group in many landscapes and their populations can often be fragmented by anthropogenic or natural disturbances (Fahrig and Merriam, 1994). These habitat-forming species often facilitate increased diversity of smaller organisms (Bruno et al., 2003). Such biogenic habitats have also been referred to as resulting from "ecosystem engineering" (Jones et al., 1997). Ecosystem engineers are important because they may have widespread impacts on the structure of assemblages in time and space (Jones et al., 1994). On intertidal rocky shores, mussels and turf-forming coralline algae provide habitats for diverse assemblages (e.g. Seed, 1996; Kelaher et al., 2001; Borthagaray and Carranza, 2007). In addition to supporting greater diversity than substrata devoid of biogenic habitats, different types of bioengineers support distinctly different assemblages (Borthagaray and Carranza, 2007; Cole et al.,

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2007). If bioengineers are lost, the overall biodiversity of rocky shores will change due to the loss of the habitat they provide and their replacement by other taxa (Paine and Levin, 1981), leading to changes in habitat quality (Hanski, 1998). This is particularly problematic if populations of bioengineers become highly fragmented as small populations are more likely to go extinct than larger ones. Risk of extinction of small populations may, however, be decreased due to immigration from larger neighbouring populations (Hanski, 1998).

An important management response to concerns about loss of species is the establishment of reserves (Halpern, 2003; Halpern and Warner, 2003). The use of marine protected areas (MPAs) is often couched in terms of the conservation of biodiversity, although a large proportion of studies on MPAs have focussed on harvested or target species rather than biodiversity *per se* (Russ and Angel, 2011). The consensus of these studies is that reserves have rapid and long lasting positive effects (Roberts et al., 2001; Halpern and Warner, 2002; Halpern, 2003), although recovery of benthic communities after the establishment of reserves may be seriously delayed by indirect effects (Parravicini et al., 2010). Reserves, particularly in marine systems where there are commercial fisheries, have often been considered as important sources of fish that "spill-over" beyond reserve boundaries (Rowley, 1994; Palumbi, 2004). The size of spill-over relative to residual populations outside the reserves is important, because managers may rely on such information to determine the size and extent of future reserves (McNeill and Fairweather, 1993). Previous studies that have investigated spill-over effects have mostly been on large mobile taxa, e.g. fish (see Roberts et al., 2001 for review). The few studies that have investigated similar effects due to the larval export of sessile taxa (e.g. Pelc et al., 2009) have been on habitat forming taxa (e.g. mussels and barnacles). Investigation of multispecies assemblages, particularly those that are associated with harvested taxa, is more complex. This is important because harvesting will have indirect effects on the biodiversity associated with bioengineers, as well as on the target species themselves.

In the Transkei region on the east coast of South Africa (Fig. 1), intertidal organisms are harvested as a major source of protein (Lasiak, 1991). Within this region, there are a number of reserves where harvesting is prohibited (Hockey et al., 1988). Previous studies have shown that intertidal molluscs are the main target taxa for artisanal fishers (Hockey et al., 1988; Lasiak and Dye, 1989), and the brown mussel, *Perna perna* (Linnaeus 1758), often comprises greater than 80% of total shellfish offtake (Lasiak, 1992). Through the investigation of middens from coastal households in the region, Lasiak (1991) found that *P. perna*, the abalone, *Haliotis spadicea*, the turban snail, *Turbo sarmaticus*, and various patellid limpets were the preferred food for many people. Other molluscs were often (greater than 75% of the time) found in middens and included *Oxystele sinensis*, *Fissurella natalis*, *Thais capensis*, *Burnupena cincta* and *Burnupena lagenaria*, and *Dinoplax validofossus* (Lasiak, 1992). These taxa are also associated with beds of *P. perna* (Cole and McQuaid, 2010). Outside reserves, space freed by mussel collection is generally occupied by macroalgae (Lasiak and Field, 1995) and as

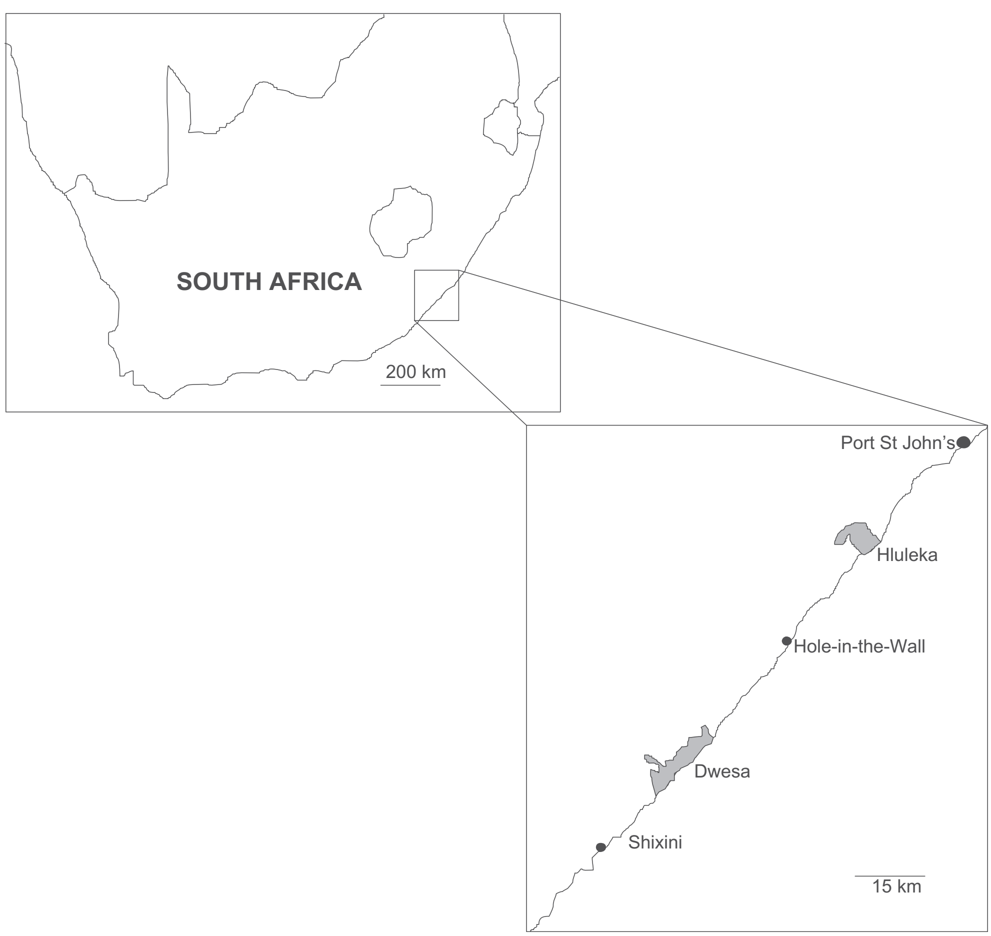

Fig. 1. Map of South Africa showing the Transkei Region. Shores in each of the sites with marine reserves at Hluleka and Dwesa and exploited sites at Hole-in-the-Wall and Shixini were sampled. Shores were also sampled 2 km and 5 km south of each of the reserves and exploited shores.