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Resilience and elasticity of intertidal communities in response to harvesting of the alien mussel *Mytilus galloprovincialis*

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Abstract

Besides the direct impacts of exploitation on target species, indirect effects on non-target species are unavoidable and find expression in changes in community structure. We quantified the effects of experimental harvesting of *Mytilus galloprovincialis* on intertidal communities on the South African west coast. In the mid- and low-shore, four months of harvesting at intensities greater than $F=0.3$ and $F=0.6$ respectively, resulted in significant changes in community composition. These changes were driven by progressively greater spatial dominance by the macroalgae *Cladophora flagelliformis*, *Porphyra capensis* and *Ulva* species as harvesting intensity increased. Four months after cessation of harvesting, community structure had not recovered and even areas subjected to as little as $F=0.3$ supported significantly altered communities in both zones. The fact that substantial community changes were induced by even low-intensity exploitation is indicative of low resilience to harvesting. The densities and cover of the dominant taxa returned to a pre-harvest state 16 months after the cessation of harvesting, but multivariate analyses indicated that the overall community composition required 32 months for Cover Letter full recovery. Although these communities displayed elasticity within three years, it is recommended that should a *M. galloprovincialis* fishery be established in the region, harvesting be implemented at a maximum intensity of $F=0.3$. This approach would maximise yields and protect associated intertidal communities.

Keywords: Alien species; Community effects; Harvesting; Mussel; *Mytilus galloprovincialis*; South Africa

1. Introduction

On a global scale shellfish have been exploited by humans for many thousands of years (Walter et al., 2000), and the potential ecological impacts of such utilisation are well recognised (Branch 1975; Castilla and Durán 1985; Keough et al., 1993). The direct consequences of intertidal harvesting typically include reductions of biomass, density, size distribution, reproductive output, demography or geographic distribution of both the target species and associated organisms (Castilla and Durán 1985; Hockey and Bosman 1986; Castilla and Bustamante 1989; Lasiak and Dye 1989; Keough et al., 1993). Species associated with target species may also inadvertently be removed, altering species diversity and richness within and among communities, with intense exploitation tending to cause convergence of communities in terms of abundance and composition diversity (Hockey and Bosman 1986; Durán and Castilla 1989; Fairweather 1990).

The response of the community can be considered in terms of resilience and elasticity. Resilience, defined as the ability of a system to absorb changes and still persist (Holling, 1973), offers a measure of how resistant communities are to changes induced by harvesting. Elasticity is the speed with which a system returns to its former state following a perturbation (Orians, 1975). The stability of exploited systems reflects interaction between fishing intensity and frequency, and the resilience and elasticity of the community (Keough and Quinn, 1998).

In South Africa, harvesting of intertidal resources is focused in the Eastern Cape (the former Transkei) and northern KwaZulu–

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Natal (Hockey et al., 1988; Lasiak, 1992; Kyle et al., 1997; Harris et al., 2003) where the brown mussel *Perna perna* forms the major portion of catches (Kyle et al., 1997). As harvesting in this region has occurred over generations and over a wide area, studies considering the effects of exploitation have been limited to comparing utilised areas with those protected by nature reserves. Collectively these studies demonstrated significant changes in target species populations in exploited areas (Branch, 1975; Siegfried et al., 1985; Hockey and Bosman, 1986; Lasiak and Dye, 1989; Lasiak, 1991; Lasiak and Field, 1995). Considering these dramatic changes, it is not surprising that harvesting has also altered the overall intertidal community (Hockey and Bosman, 1986) and resulted in a convergence of exploited communities towards a common state, regardless of the pre-exploitation condition. Typically these changes are manifested in shifts in primary space dominance from mussel beds towards an open algal matrix (Lasiak and Dye, 1989) and are most pronounced in the low-shore zone, where harvesting is concentrated. These communities exhibit extremely low elasticity in response to disturbance, and full recovery has not been observed even after 13 years (Lasiak and Dye, 1989; Dye, 1995).

Despite considerable research on the effects of intertidal harvesting on the east coast of South Africa, this issue has not been considered on the west coast. This is primarily because the shores in this region have been subject to substantially less exploitation, as a result of low human population density and the fact that diamond-mining operations exclude the public from large areas. Nonetheless, large stocks of the alien mussel *Mytilus galloprovincialis* exist along these shores and in an effort to stimulate new fisheries-based industries and address historic imbalances in access to fishing rights in South Africa, a community-based project was initiated in 2002 to determine the potential for exploitation of this mussel in the Northern Cape Province of South Africa (Robinson et al., 2007b). As part of this project, unemployed people from local communities were trained to harvest *M. galloprovincialis*. Although there is a substantial body of knowledge about the effects of harvesting on the east coast, the west and east coast systems differ in a number of ways, so that extrapolation of findings from the east to the west coast is risky. Firstly, on the west coast, intertidal exploitation is focused on *M. galloprovincialis*, which is an aggressive alien invader, whereas indigenous species are harvested elsewhere. Secondly, the west coast itself is inherently different from the east coast, due to the dominance of the cold, nutrient-rich Benguela upwelling system (Hutchings et al., 1995), which generates a highly productive nearshore pelagic environment, and exceptionally productive rocky shores (Bustamante et al., 1995). Thirdly, probably as a consequence of this, mussel biomass on the west coast is about two orders of magnitude greater than on the east coast (Harris et al., 1998). Fourthly, on the east coast, because harvesting is pervasive, it has been difficult to implement controlled fishing at a suite of different fishing intensities to explore the consequences of fishing effort (Harris et al., 2003). In contrast, on the west coast there are large areas where mussels have never been harvested to any significant extent. This situation offered the opportunity to implement harvesting at a range of intensities, including zero harvest controls, to assess the resilience and elasticity of intertidal communities to mussel harvesting.

Considering the known effects of intertidal harvesting on the east coast and the differences in ecology between the coasts, the following *a priori* hypotheses were constructed: (1) Resilience of intertidal communities will be inversely proportional to the intensity of harvesting; (2) Communities on the west coast will demonstrate greater elasticity than those on the east coast due to their high productivity. Within this framework, our study quantified the effects of harvesting *M. galloprovincialis* on intertidal community structure as a whole, thus explicitly addressing the recognised need to move from single species fisheries management towards a broader ecosystem approach (Cochrane et al., 2004; Shannon et al., 2004).

2. Methods

2.1. Study site

The effects of harvesting on community structure were determined at Flat Rocks (29°48.862’ S; 17°04.472’ E), a rocky platform bordered below by beds of the kelps *Laminaria pallida* and *Ecklonia maxima*. As *M. galloprovincialis* beds along the South African west coast are concentrated in the mid- and low-shore, the study focused on the effects of harvesting in these zones. Prior to harvesting, the mid-shore was covered in a mussel–algal matrix dominated by *M. galloprovincialis* and the algae *Gigartina stiriata* and *Champia lumbricalis*. The low-shore was dominated by dense *M. galloprovincialis* beds.

2.2. Experimental design

Harvesting was done by hand and with screwdrivers and *M. galloprovincialis* individuals with a shell length greater than 50 mm were targeted. To assess the effects of a spectrum of harvesting intensities, five treatments were employed i.e. an unharvested control area (10 m), a once-off total clearance area (3 m) in which all *M. galloprovincialis* were removed, and areas of $F=0.3$ (23 m), $F=0.6$ (11.5 m) and $F=0.9$ (7.5 m), respectively referring to preset harvesting intensities whereby 30%, 60% or 90% of the total mussel biomass present were removed over four months of harvesting. The order of these areas was randomly allocated. Further details of the design of the overall project are given by Robinson et al. (2007b).

Initial data were collected in October 2003, before the commencement of experimental harvesting, in June 2004. Follow-up data were collected in October 2004, after four months of harvesting (Time 1), and in February 2005 (Time 2), April 2006 (Time 3) and finally in August 2007 (Time 4), four 16 and 32 months after the cessation of harvesting respectively.

Within each treatment area the mid-shore (MLWN–MHWN) and low-shore (MLWS–MLWN) were considered separately. In each of these zones, the primary and secondary percentage cover of sessile organisms and algae, and the numbers of mobile organisms were recorded in five randomly-placed replicate 0.25 m^2 quadrats in each zone in each area. Primary cover was defined as the area of primary rock covered by algal attachment