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Recruit/algal interaction prevents recovery of overexploited mussel beds: Indirect evidence that post-settlement mortality structures mussel populations

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ABSTRACT

The mechanisms maintaining community structure following an ecosystem shift are poorly understood and we propose that they must inherently be biological. Over-exploitation can provide a "natural experiment" with man as a predator driving a change in community structure, possibly an ecosystem shift. We examined a possible mechanism that maintains algal beds as an alternative state on the east coast of South Africa where the mussel *Perna perna* has been overexploited. Even on unexploited shores, about 50% of mussel larvae settle onto algae, but it is unclear whether they later recruit into adult beds. On such shores we used two indirect field approaches to understand the fate of recruits, testing whether inhibition of mussel recruitment by macroalgae could constitute a biological mechanism preventing reversion from the algal to the pre-disturbance mussel-dominated state. First, we examined possible ontogenetic migration of recruits from algae to adult mussels, testing the prediction that the ratio large:small recruits in adult beds is greater where algae are liberally interspersed with mussels. Second, we examined whether, like adults, recruits show spatial structure that is related to the distribution of topographic depressions, testing the hypothesis that large and small recruits show different co-variation with depressions, microhabitats where algae commonly occur. We found no evidence that recruits on algae actively move to nearby mussel beds as neither the ratio large:small recruits nor the abundances of small or large recruits showed any relationship with algal cover/variability. Small and large recruits showed different co-variation with topographic depressions on spatially structured transects. Like adults, large recruits commonly exhibited negative relationships with depressions. Thus, large recruits neither occur on algae nor migrate from algae to the primary substratum or onto adult beds. Consequently our results (a) highlight the importance of post-settlement mortality in structuring these mussel populations, and (b) suggest that the interception of larvae by algae forms a biological mechanism that can maintain macroalgal beds that develop following exploitative disturbance by man, thus preventing or at least drastically delaying the natural recovery of mussel beds.

1. Introduction

An ecosystem shift leads to different community structure that is characterized by different ecosystem processes and functions (Norström et al., 2009; Scheffer, 2009). Such shifts can be sudden, characterized by a threshold value (tipping point) where the specific system is driven away from equilibrium through positive feedback, and have been shown in a variety of ecosystems, including terrestrial, freshwater and coastal marine systems (Petraitis and Dudgeon, 2004; Hargeby et al., 2007; van Wesenbeeck et al., 2008; Scheffer, 2009). A shift occurs following some perturbation and the new ecosystem may be persistent for multiple generations of the species concerned (Beisner et al., 2003; Petraitis and Dudgeon, 2004; Scheffer, 2009). Perturbations can cause a shift in community structure due to the loss of top-down control (e.g. through overfishing and hence reduced herbivory) or due to changes in bottom-up dynamics (e.g. through nutrient loading and eutrophication), both processes seen in coral reefs (Norström et al., 2009; Lilliesköld Sjöö et al., 2011). Much of the literature on this subject concerns the factors or disturbances that cause a shift, but there is a recognition that the processes that lead to a particular ecosystem state may be quite different from those that maintain it (Drake, 1991; Scheffer, 2009) so that we can ask what factors prevent an assemblage returning to its original state after external disturbance ceases. Organisms inevitably alter their own environment (Peterson, 1984), but assuming no extrinsically driven

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change in environmental conditions, the mechanisms buffering the new state must presumably involve biological interactions (e.g. Barkai and McQuaid, 1988).

Arguably Man is a natural part of many if not all ecosystems, and here we are concerned with the mechanisms that may allow the persistence of a novel community structure after predation by man (i.e. human exploitation of a biological resource) has ceased; mechanisms that would exist even on unexploited shores. In many places around the world, unsustainable invertebrate harvesting is a major environmental and social problem, and molluscs, especially bivalves, are often the main target species for subsistence harvesters (Keough et al., 1993; Castilla, 1999; Rius et al., 2006). Along the east coast of South Africa (the Transkei region) heavy harvesting of mussels results in quite different overall community structure in exploited and protected areas (Lasiak, 1991; Dye, 1992; Lasiak and Field, 1995). The primary target species is the brown mussel *Perna perna* and over-exploitation has resulted in extremely low general *P. perna* abundance (in general, patches of a few small individuals remain providing cover of <2%; Calvo-Ugarteburu and McQuaid Unpubl. data) over long (10s–100s km) stretches of coastline where it used to dominate with >80% cover at densities of hundreds per square metre (Hockey and Bosman, 1986; Lasiak, 1991, pers. obs.). Where mussels have been removed, they have often been replaced by coralline algae and this situation has been maintained for many years (Siegfried et al., 1985; Calvo-Ugarteburu and McQuaid, Unpubl. data).

Petraitis and Dudgeon (2004) suggest that biologists should be concerned with the forces that maintain systems near some stable point. We believe that such forces must definitively be intrinsically biological. Here we examine how one population parameter (mussel recruitment) may change to allow the persistence of a new algal community state. The shift from a mussel-dominated intertidal state to an algal dominated state and vice versa is common globally, although it is debated whether these states are stable or not (Bertness et al., 2004; Petraitis and Dudgeon, 2004; Petraitis et al., 2009). The replacement of mussel beds by dense beds of macroalgae, such as on the east coast of South Africa (Siegfried et al., 1985; Lasiak and Field, 1995), means mussel recruits must mainly settle onto algae. After reaching a certain size, recruits will be unable to remain attached to algae (Erlandsson and McQuaid, 2004) and if they are unable to move onto the primary substratum (or to the few existing mussel patches) as they grow, then recruitment is inhibited or even prevented. This effect will be enhanced by an Allee effect, as low abundances of adult mussels will result in low densities of gametes released in the water and a reduction of fertilisation success (Gascoigne and Lipcius, 2004a,b; Kramer et al., 2009; Scheffer, 2009).

Larvae of *Perna perna* show roughly equal preference for mussel and algal (erect coralline or corticated red algae) habitats (Erlandsson and McQuaid, 2004; McQuaid and Lindsay, 2005). In the mid mussel zone on the southeast coast of South Africa, the corticated red alga *Gelidium pristoides* commonly occurs adjacent to or among mussels, but is more abundant at some locations than others. This red alga branches irregularly and is a dominant mid-shore alga, often occurring with heterogeneous distribution on a shore (Erlandsson et al., 2005). It can cover almost 100% of the primary substratum but often also occurs on limpet shells (Carter and Anderson, 1991). *Gelidium pristoides* and *P. perna* adults show negative co-variation at all spatial within-shore scales and contrasting relationships with the distribution of topographic depressions (gullies and crevices); adult *P. perna* shows negative co-variation, while *G. pristoides* shows positive or no co-variation with topographic depressions, depending on scale (Erlandsson et al., 2005). The spatial structure of large mussel recruits (3.5–10 mm) is similar to that of adults (i.e. high heterogeneity), and the two show positive co-variation at all within-shore scales (large recruits also show negative relationships with algae), so that patterns in adult mussel beds are already discernible among large recruits (Erlandsson and McQuaid, 2004). For small recruits of 0.5–3.5 mm (i.e. late plantigrades), the situation is different. Small recruits generally show positive co-variation with both adult mussels and *G. pristoides* and occur at similar abundances in both habitats (Erlandsson and McQuaid, 2004). Consequently small recruits show random spatial patterns rather than being clumped within a single habitat. Thus the spatial structure of *P. perna* adults is acquired between the small and large recruit stages and the fate of larvae that settle onto algae is critical to both population regulation and the spatial structure of mussel beds. We know how the two recruit habitats (adult mussels and algae) co-vary with topographic depressions, but not whether there is co-variation between the distribution of recruits (small or large) and the distribution of topographic depressions. Insight into this is needed to clarify what factors structure *P. perna* populations: primary settlement, movement of recruits and/or post-settlement mortality, i.e. whether the relationship with topographic depressions changes from the plantigrade stage to the adult stage. Furthermore, very large recruits (9–10 mm) actively move from algae to mussel patches in the laboratory, with no such movement by recruits <9 mm (Erlandsson et al., 2008) but it is unclear whether recruits of 3.5–5 mm (the critical size on algae) are capable of similar small-scale movement in the field.

Our overall hypothesis was that inhibition of mussel recruitment by macroalgae constitutes a biological mechanism that could maintain the algal community state of this system (following a disturbance), by inhibiting reversion to the pre-disturbance mussel-dominated state. As we can imagine no way of directly tracking individual mussel larvae settling onto or leaving algae, we combined two indirect field approaches to examine and understand their fate. First, we indirectly examined whether recruits show ontogenetic migration from algae to adult mussels, thus increasing the ratio of large to small recruits. To do this, we tested the hypothesis that the ratio of large:small recruits in adult beds is greater where algal cover is higher (see Materials and methods). Second, we examined whether, like adults, recruits show spatial structure that is related to the distribution of topographic depressions along the shore, testing the hypothesis that large recruits show mainly negative co-variation (i.e. a negative relationship) with depressions, while small recruits show no relationship with depressions.

2. Materials and methods

2.1. Description of mussel beds, recruit size classes and general approach

Mussels are almost non-existent and recruitment is extremely low where they have been overexploited on the east coast (though still settlement occurs at low levels) and therefore the study was carried out on the southeast coast of South Africa, in two relatively unexploited areas, Kenton-on-Sea (26°40′E, 33°41′S) and Port Alfred (26° 54′E, 33° 36′S), where *Perna perna* and *Gelidium Pristoides* are relatively abundant and mixed in the mid mussel zone. At Kenton-on-Sea two different sites were used (Middle Beach and High Rocks), separated by ca. 3 km. Likewise, in the Port Alfred area, two sites were sampled (Port Alfred and Riet Point) separated by ca. 15 km. Intertidal mussel beds on this coast are discrete, easily defined and often up to 25 m long. Individual beds are usually separated by 50–100 m and extend from just above the subtidal fringe to the low shore. The beds are monolayered, with the byssus threads of adults attached directly to the rock surface (McQuaid et al., 2000) and can be clearly divided into mid, low and upper