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Causes of rarity and range restriction of an endangered, endemic limpet, *Siphonaria compressa*

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Abstract

The pulmonate limpet *Siphonaria compressa* is South Africa's most endangered marine mollusc. It is endemic to just two localities: Langebaan Lagoon on the west coast, and Knysna Estuary on the south coast, and occurs only on the eelgrass *Zostera capensis*. In Langebaan Lagoon, eelgrass has fluctuated substantially over the last 34 years, and *S. compressa* has twice approached extinction. *S. compressa* is largely confined to the lower edge of the eelgrass beds there, being replaced higher up by another small gastropod, *Assiminea globulus*. We explored the physical and biological factors underlying the limpet's narrow habitat, using field observations, translocations, caging and transplant experiments. Abundance of *S. compressa* was positively correlated with *Z. capensis* cover and negatively correlated with shore height. When moved to the upper portions of the eelgrass bed, *S. compressa* had lower rates of persistence and survival than in the lowest zone. The lower limit of zonation for *S. compressa* was set indirectly by bioturbation by the sandprawn *Callianassa kraussi*, which excluded eelgrass from intertidal sandbanks. Transplants of eelgrass into the sandbanks proliferated provided *C. kraussi* was experimentally eliminated, and supported densities of *S. compressa* 20-fold greater than in control eelgrass beds, suggesting that high-shore eelgrass beds to which *S. compressa* is normally confined are suboptimal for the limpet. *A. globulus* showed patterns opposite to those of *S. compressa*: its persistence and survival were greatest in the upper zone and it actively avoided the lower sections of these beds and never colonised eelgrass transplanted into sandflats lower on the shore. There was no evidence that competition between *S. compressa* and *A. globulus* influenced the zonation or abundance of either species. Rarity of *S. compressa* and its endangered status seem dictated by its extremely narrow and temporally changeable habitat-range, which is defined by physical stress in the high-shore and bioturbation by *C. kraussi* in the low-shore. Fluctuations in eelgrass abundance and limitation of *S. compressa* to just two localities add substantially to the risks of extinction for this embattled stenotypic limpet.

Keywords: *Assiminea*; *Callianassa*; Eelgrass; Habitat restriction; Rarity; Seagrass; *Siphonaria*; *Zostera*

1. Introduction

Three types of rarity are recognised: low abundance, habitat specialisation and narrow geographic range (Pimm et al., 1993; Manne and Pimm, 2001). All predispose species to extinction (Simberloff, 1988; Gaston, 1994), and extreme biological traits such as limited dispersal or intolerance of changes in physical conditions exacerbate vulnerability to extinction (Carlton, 1993; Purvis et al., 2000). Conservationists seek to understand these factors to predict which species are threatened with extinction, and to take ameliorative

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actions (Manne and Pimm, 2001). Studies of the population dynamics of naturally rare species also elucidate processes that influence declines of more common species. However, our understanding of the processes driving rarity is based mainly on terrestrial species (Karr, 1977; Bevill and Louda, 1999; Ricklefs, 2000; Gillespie, 2000). There have been few studies of rarity in marine animals (e.g. Angermeier, 1995), and even fewer on marine invertebrates specifically, possibly because of their small size and cryptic nature (Carlton, 1993; Sanderson, 1996; Herbert, 1999; Chapman, 1999). Moreover, the majority of rarity studies have been of a correlative nature: few probe the causes of rarity experimentally. All of these issues impede our understanding of rarity (New, 1993; Gaston, 1994).

This study focuses on a pulmonate limpet, *Siphonaria compressa* Allanson, which has a restricted range and habitat (Allanson, 1958a,b) and has been identified as South Africa's most threatened marine invertebrate, being the only South African marine mollusc listed as 'critically endangered' (Herbert, 1998). In particular, it addresses the association of *S. compressa* with the Cape eelgrass *Zostera capensis* Setchell, and the physical and biological factors restricting its habitat, including potential interactions with another gastropod, *Assiminea globulus* (Connolly) and with the sandprawn *Callianassa kraussi* Stebbing.

S. compressa is the smallest species of the genus, reaching shell lengths of 3–5 mm. Some evidence suggest that it was at one time more widely distributed in South Africa, but for almost 50 years since its description, it was known only from Langebaan Lagoon on the West Coast of South Africa (Allanson, 1958a; Herbert, 1999). Recently it has been discovered at a second locality, Knysna Estuary on the South Coast, some 600 km distant from Langebaan Lagoon: no living populations have been found in any other estuaries (Allanson and Herbert, 2005) although beach-drift specimens from Keurbooms Estuary near Knysna suggest that it once occurred there (Herbert, 1999). In addition to its restricted range, *S. compressa* also has extremely narrow habitat requirements, being recorded only on blades of the eelgrass *Z. capensis*, where it feeds on epiphytic diatoms, filamentous algae and bacteria (Chambers and McQuaid, 1994; Herbert, 1999; Allanson and Herbert, 2005). *S. compressa* lays egg capsules, has the lowest fecundity of all nine South African members of the genus and has a direct mode of development (Chambers and McQuaid, 1994; Allanson and Herbert, 2005), in common with many lagoonal and freshwater gastropods, for which planktonic dispersal is unlikely to be adaptive (Barnes, 1988). The absence of a dispersal stage, low fecundity, isolated geographical distribution and restricted habitat are all characteristics related to rarity and the risk of extinction.

Three other species are known or suspected to influence the habitat breadth of *S. compressa*. The first (and most obvious) is the eelgrass *Z. capensis*. Because *S. compressa* lives exclusively on this eelgrass, its habitat is already narrow and specific. *Z. capensis* is limited to intertidal sandflats and estuaries in southern Africa (Edgcumbe, 1980; Adams et al., 1999). Seagrasses in general are associated with high species richness, abundance and biomass compared with adjacent, unvegetated habitats (Sand-Jensen, 1975; Stoner, 1980; Whitfield et al., 1989). Among possible reasons for this are habitat complexity, sediment deposition and stabilisation, dampening of wave action, nutrient trapping and recycling, and protection from predators (Fonseca et al., 1982; Lewis, 1984; Edgar, 1990; Fonseca and Cahalan, 1992; Lee et al., 2001). *Z. capensis* plays similar ecological roles (Day, 1959; Christie, 1981; Emmerson, 1986; Whitfield et al., 1989; Kalejta and Hockey, 1991), although in Langebaan Lagoon benthic richness and diversity are lower in beds of *Z. capensis* than in adjacent unvegetated sandflats, and the faunal composition very different in these two habitats (Day, 1959; Siebert and Branch, 2005b, in press).

The main factors limiting growth of *Zostera* spp. are light availability, abrasion by sand particles, salinity fluctuations, turbidity and fluvial siltation (Day, 1981; Hanekom and Baird, 1988; Talbot and Bate, 1987; Adams and Talbot, 1992). Periodic reductions associated with floods and cyclic patterns of growth, maturity and senescence are a feature in many estuaries (Talbot and Bate, 1987; Hanekom and Baird, 1988; Adams et al., 1999; Steinken, 1999; Turner et al., 1999). *Z. capensis* is patchily distributed on intertidal sandbanks, usually between high and low neap tides (Day, 1959, 1981; Adams et al., 1999). Its upper limit seems to be determined by desiccation, as is evidenced by stunted leaf growth where there is low retention of water by the sediment (Talbot and Bate, 1987). In Langebaan Lagoon, its lower limit appears to be set by interaction with the second of the species suspected of restricting the habitat breadth of *S. compressa*: the sandprawn *C. kraussi*, which is responsible for extensive bioturbation that conditions the sediment for the rest of the fauna (Day, 1959; Flemming, 1977; Branch and Pringle, 1987; Siebert and Branch, 2005a, in press). Rhoads and Young (1970) were the first to show that bioturbation by deposit feeders excludes many suspension feeders and sessile surface-dwelling species. Bioturbation alters