Research Letters

A newly discovered population of the critically endangered false limpet *Siphonaria compressa* Allanson, 1958 (Pulmonata: Siphonariidae), with observations on its reproductive biology

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The endangered false limpet, *Siphonaria compressa,* originally described by Allanson in 1958 from Langebaan Lagoon, Saldanha, has been found living in intertidal eelgrass meadows in the embayment of the Knysna River estuary at Bollard Bay, Leisure Isle, Knysna, South Africa. This represents only the second known site of occurrence of the species. Although classified by the IUCN as critically endangered, the Knysna population is viable.

Introduction

The plight of the critically endangered eelgrass limpet, *Siphonaria compressa* Allanson, 1958,[1] was highlighted by Herbert.[2] At that time, the only locality from which living specimens were known was Langebaan Lagoon on the Atlantic coast of South Africa, a relatively pristine habitat, potentially threatened by industrial developments at Saldanha. Beach-drift specimens in the Natal Museum, closely resembling those of *S. compressa,* suggested that the species may have once occurred on the Cape south coast, in the Knysna Lagoon and Keurbooms estuary. However, despite requests for assistance and information, and personal surveys, no evidence of extant populations at either of these localities, or at any others in the southern Cape, was forthcoming. The evidence available suggested that Langebaan Lagoon contained the only surviving population of the species. It has a specialized mode of life and is to be found living only on the leaves of eelgrass (*Zostera capensis* Setchell).[2]

A new survey of the present diversity of macro-invertebrate fauna in the Knysna estuary, initiated by the first author at the same time that R.S.K. Barnes of Cambridge University was extending his investigations of the hydrobiid gastropod, *Hydrobia knysnaensis,* in the lagoon,[3] found viable colonies of *S. compressa* on eelgrass at mid-tide level in Bollard Bay, Leisure Isle. This note describes the structure of the present population and provides a voucher specimen description of the species. The original description was made on ethanol-preserved material.

Materials and methods

Samples of *S. compressa* were collected from eelgrass meadows at a number of localities in the course of a survey of the macro-invertebrate fauna of the Knysna estuary. Population densities were determined from two, low water of neap tide (LWNT) collections in the eelgrass meadow of Bollard Bay (34°03′55′′S; 23°03′13′′E) in seawater of 34 psu, using a 1/16 m^2 quadrat (25 × 25 cm). Six replicates were collected on 23 April 2004 and three on 17 May 2004. Within each quadrat, the leaves of eelgrass were cut at ground level and placed in plastic bags. In the first sample series the leaves, while wet, were procumbent. In the second

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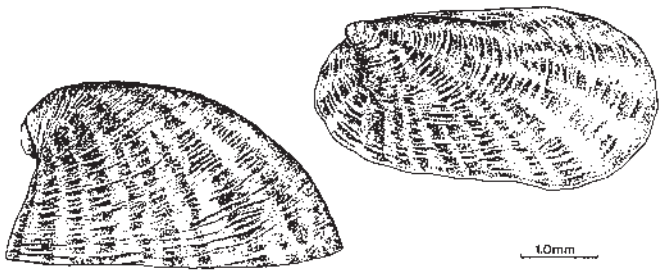

Fig. 1. *Siphonaria compressa* drawn by L. Davis, Natal Museum, Pietermaritzburg.

sampling, the samples were drawn from erect leaves in 300 mm of water. The overall area sampled was 0.563 m^2, from which a wet leaf biomass of 348 g was harvested.

The collected material was placed in 4% formalin seawater overnight to allow release of the pulmonates from the leaves. Subsequent collection of individuals was done by gently washing the leaves into a net using a stream of tap water. The washed leaves were examined to ensure that all individuals had been removed. The sample was then stored in 70% ethanol. The long axis of the shell was used as a measure of animal size. The length of the shell was measured in millimetres using a stage micrometer. Pieces of leaves with living individuals of *S. compressa* attached were removed, prior to treatment with formalin, and placed in seawater in covered micro-aquaria for further observation.

Distribution and population structure

To date, *S. compressa* (Fig. 1) has been found at three sites within the Knysna estuary (Fig. 2), namely: Bollard Bay (1) (34°03′55′′S; 23°03′13′′E), Kingfisher Creek (2) (34°03′42′′S; 23°03′10′′E) and the lower Ashmead Channel (3) (34°03′33′′S, 23°04′03′′E). Thus far, the limpet has not been found in the upper Ashmead Channel (4) (34°02′23′′S, 23°04′01′′E), nor in the lagoon sector of the estuary at The Point (5) (34°02′18′′S, 23°00′48′′E). These latter sites are subject to considerable variation in salinity, ranging from 5 psu during river floods and flooding of stormwater canals, to 34 psu when tidal flow is re-established. The lower embayment is not normally subject to such wide salinity variation.

The mean number of individuals from the nine Bollard Bay samples (n = 202) was 22.4 ± 9.7 per 1/16 m^2 quadrat, which equates to 358 individuals per square metre of eelgrass meadow at LWNT. The total area over which the limpet occurs is approximately 4200 m^2. The number of individuals in size classes of 0.5 mm, from 0.5 mm upwards, is given in Fig. 3 The modal shell length fell within the 1.5–2.0-mm size class. Densities at Kingfisher Creek and the Ashmead Channel were lower at 4 and less than 2 individuals/quadrat, respectively (64 and <32 individuals per square metre).

Shell and soft part anatomy

The shells of this newly discovered population possess all the features described by Allanson,[1] and illustrated photographically by Herbert.[2] The shell is laterally compressed with a maximum long axis or diameter in the Knysna material of 4–4.5 mm, considerably larger than originally described (3 mm) in alcohol-preserved material from the Langebaan Lagoon, but comparable to that of specimens subsequently collected by Herbert[2] at that locality.

The genitalia anatomy conforms exactly to that described by Allanson (ref. 1, fig. 18). The radula formula varies from 9:1:9 to 12:1:12, which is less than that reported by Allanson[1] for the type material, 15:1:15. All the other species of *Siphonaria* in South Africa have a radula formula much larger than this, ranging from

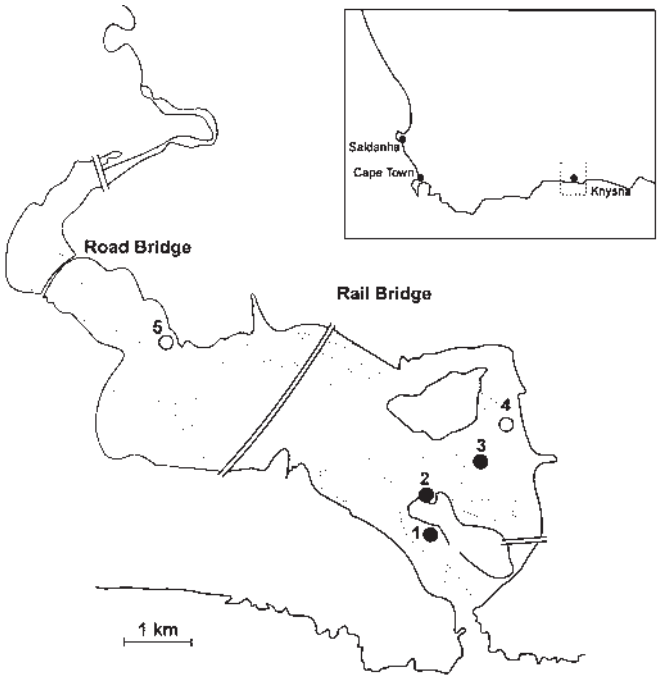

Fig. 2. Location of the Knysna River estuary, and collecting sites in the marine embayment: 1, Bollard Bay; 2, Kingfisher Creek; 3, Lower Ashmead Channel; 4, Upper Ashmead Channel; 5, The Point, in the lagoon sector of the estuary.

30:1:30 to 48:1:48. Warén[4] has shown in prosobranchs that the number of teeth per row in the radula increases during ontogeny. If *S. compressa* has evolved through paedomorphosis,[2] then it would quite logically retain the lower number of teeth/row characteristic of juveniles.

Eyes are present at the base of stubby tentacles. The presence of eyes was missed in the original alcohol-preserved material. Voucher specimens have been lodged in the Mollusca collection of the Natal Museum, Pietermaritzburg (NMSA W2299).

Some aspects of biology

A rich community of diatoms, filamentous algae and bacteria covers eelgrass leaves. This 'aufwuchs' supports a variety of animals, and the faecal pellets of *S. compressa* show that the

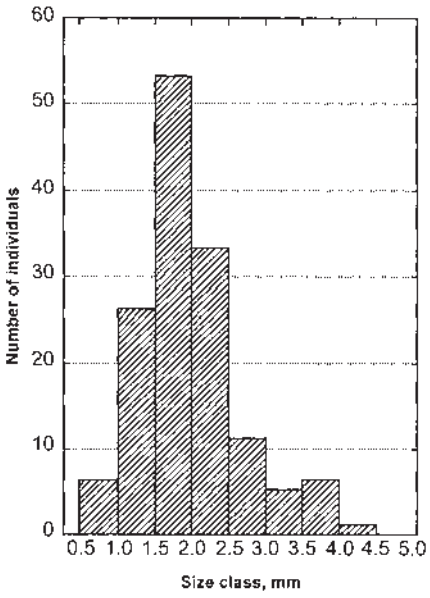

Fig. 3. Size distribution within a population of *Siphonaria compressa* in the intertidal eelgrass meadow of Bollard Bay, Leisure Isle, Knysna.

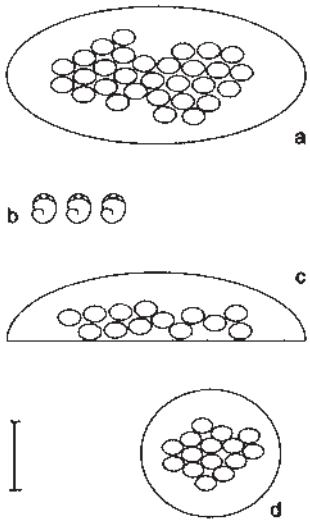

Fig. 4. The spawn of *Siphonaria compressa*, and of hatchlings with eyespots: **a, d**, near-elliptical and circular spawn; **c**, a lateral view of spawn showing the arrangement of the egg capsules relative to the convex surface; **b**, appearance of hatchlings. Scale bar = 0.5 mm.

limpets utilize this resource effectively.

Small gelatinous egg packets, or spawn,[5] circular or roughly elliptical in shape and containing between 16 and 30 eggs, each in a separate elliptical capsule have been found on the leaves and on the clear surface of the polyethylene micro-aquaria in which adults were kept, confirming the observation of the late Tex Reid that the species lays its eggs in capsules.[5] Figure 4 records the size and shape of the spawn as well as the arrangement of the egg capsules in the gelatinous matrix, and the appearance of hatchlings.

Development past the veliger to the teleoconch stage is passed within the egg capsule. There is no planktonic phase. There is a small but significant ($t = 2.35$, $P < 0.05$) increase in egg capsule size as the larva develops. Immediately after the spawn was laid, mean capsule length and diameter were 364 μm and 240 μm ($n = 7$). At the advanced teleoconch stage, capsule length and diameter increased to 395 μm and 276 μm ($n = 8$). Release of the juveniles from the egg capsules has been observed in a micro-aquarium 17 days after gastrulation (Fig. 4b). This period of development is similar to that of other siphonariids with direct development and considerably longer than those with planktonic development.[5]

Threatened species status

Siphonaria compressa remains listed as critically endangered in the most recent list of threatened species,[6] and is the only South African marine mollusc that falls into this category. In terms of the current red-listing criteria,[7] the finding of the additional extant population in the Knysna estuary does not materially affect its critically endangered status. The criteria for listing as CE B 1a,b, based upon its limited extent of occurrence (and area of occupancy), and threat to the extent and quality of its habitat, are still evidently met, although this will need to be confirmed by formal re-evaluation. Angel[8] has recently evaluated the factors that influence the rarity of *S. compressa* in Langebaan Lagoon, emphasizing the complete dependence on eelgrass. A period of invasive diatom growth that covered beds of *Zostera capensis* resulted in the loss of the limpets.

The eelgrass meadow in Bollard Bay has only recently returned: within the past eight years. Prior to 1996, the intertidal sand flats were bare and used to moor small craft and for bait collection. This is in contrast to the rich beds of eelgrass in the bay during 1947 and 1948,[9] when urbanization of the island was just beginning.

After the completion of the small boat harbour on Leisure Isle, where the majority of boats are now housed, trampling of the sand flats was reduced, and *Zostera capensis* slowly returned. Eelgrass now covers a substantial area of what previously was bare sand. It is in this 'new' meadow that *S. compressa* is found. As the Kingfisher Creek area (Fig. 2) has remained relatively unchanged since the surveys of J.H. Day and his colleagues[9] and the later investigations of the Knysna Basin Project in 1997,[10] it is possible that this site represents a refuge for the species from which it is now spreading into other suitable areas. Dispersal between sites is, however, likely to be slow in view of the direct larval development, compounding the threat of habitat destruction. The devastating floods of 22/23 December 2004 reduced the population to <2 individuals per quadrat (1/16 m^2). It is slowly recovering.

The support of a Council research grant from Rhodes University to B.R.A. is gratefully acknowledged. Our thanks are due to Linda Davis for her clear and accurate drawing of the shell of *S. compressa,* and to two reviewers for their constructive comments.

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