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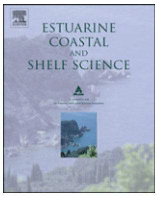

Spatial variation in the macrobenthic assemblages of intertidal seagrass along the long axis of an estuary

R.S.K. Barnes [a], [*], M.D.F. Ellwood [b]

[a] Knysna Basin Project Field Laboratory & Department of Zoology and Entomology, Rhodes University, Downing Street, Grahamstown 6140, South Africa
[b] Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

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ABSTRACT

Invertebrate macrofaunal biodiversity within intertidal seagrass meadows was investigated over a salinity gradient of <5–35 in the Knysna estuarine system (Garden Route National Park, South Africa). Rather than the classic gradual decline in species richness with distance from the mouth there were zones of considerable faunal stability separated by relatively sharp discontinuities. At the point upstream at which salinity regularly falls below 30, the rich, diverse and highly spatially variable downstream faunal assemblage changed to a less rich, less diverse and more uniform one that dominated the upstream stretch without any further upstream reduction in richness. Nevertheless, without loss of overall richness, assemblage composition changed, again rapidly, in the upper region of the upstream stretch to a zone dominated by the microgastropod *Hydrobia*, which otherwise occurs in the Knysna system only in highly sheltered regions of the downstream stretch where it is also dominant. The upstream faunal assemblage was a subset of that in the marine-influenced downstream region not a different replacing one. Position along the estuarine gradient accounted for 29% of total assemblage variation. Overall faunal abundance declined with distance upstream until the *Hydrobia* zone where it rose sharply, but there was no evidence of increase in density of those species remaining on putative release from competition.

1. Introduction

Ever since the classic papers of Remane (1934) and Alexander et al. (1935), organisms that occur in estuarine systems have been portrayed largely as a series of predominantly marine species that penetrate into brackish waters to differing degrees, each dependent on its tolerance limit to lowering salinity — or more likely to the degree of salinity fluctuation (Montague and Ley, 1993; Attrill, 2002) — with the consequence that species richness continually declines with increasing distance upstream until the onset of freshwater conditions (Cognetti and Maltagliati, 2000; Attrill, 2002; Attrill and Rundle, 2002; Whitfield et al., 2012). Although this 'Remane paradigm' (Remane, 1934, 1971) has become 'the recognized textbook model for diversity patterns in tidal estuaries' (Attrill, 2002) and 'central … in estuarine ecology' (Whitfield et al., 2012), it is clearly subject to a number of qualifications when applied to estuaries (Day, 1981; Attrill, 2002; de Biasi et al., 2003; Teske and Wooldridge, 2004; Whitfield et al., 2012). One potential caveat is that the occurrence of the phenomenon in estuarine benthos has been based on data from, e.g. unvegetated soft sediments (Schlacher and Wooldridge, 1996), rocky outcrops (Bassindale, 1943) or the whole benthic system (Rodrigues et al., 2011), but never specifically on the benthic faunal assemblages supported by seagrass. Earlier work (Barnes and Ellwood, 2011; Barnes and Barnes, 2012) has shown that the equivalent textbook paradigm of declining species richness and diversity with progression from the sublittoral up the intertidal zone applies poorly within stands of two seagrasses, *Nanozostera capensis* and *Nanozostera muelleri*, possibly in some measure because the vegetation mitigates the usual effects of decreasing tidal cover on sediment-dwelling animals. Correspondingly, the presence of seagrass along an estuarine axis might, for example, have an additional dampening effect on the already reduced salinity variation within the sediment compared to that in the overlying water (Alexander et al., 1932; Kinne, 1967) and thereby also affect distributions. In the light of this, the manner and extent to which faunal richness and diversity within intertidal estuarine seagrass beds decrease upstream is open to question, as is the degree of change within seagrass faunal assemblages along the upstream gradient.

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[*] Corresponding author.
E-mail addresses: r.barnes3@uq.edu.au, R.Barnes@ru.ac.za, rsb1001@cam.ac.uk (R.S.K. Barnes).

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Notwithstanding that much work has been done on the importance of both salinity and seagrass to estuarine faunal abundance and diversity (e.g. Collett et al., 1984; Edgar and Barrett, 2002), it appears that the sole study partly to address these questions has been that of Yamada et al. (2007) on the Akkeshi-ko system in northern Japan, although this investigation was only semi-quantitative and confined to the seagrass epibenthos. Concentrating on beds of the subtidal *Zostera marina*, these authors did find a significant relationship between salinity and species richness of epifaunal malacostracans and gastropods (the only taxa studied) in the seagrass. But they found little evidence of different species assemblages occurring in different regions of the gradient, and there was no relationship between overall faunal abundance and salinity. This combination of results could be taken to indicate that faunal assemblages in the upstream regions of estuarine seagrass may be little more than impoverished versions of those in more marine areas, with a few, particularly tolerant species reacting there to their release from competition by increasing in density.

The dominant seagrass in southern Africa is Cape dwarf-eelgrass, *N. capensis*, which is particularly associated with estuarine conditions (Bandeira and Gell, 2003; Whitfield et al., 2012). Its South African stronghold is the estuarine bay (*sensu* Whitfield, 1992) at Knysna, known locally as the Knysna Lagoon, within the Garden Route National Park (Russell et al., 2009). This system supports 350–390 ha of *N. capensis* (Maree, 2000; Bandeira and Gell, 2003); i.e. over half of the total national area. Like all *Nanozostera* species, *N. capensis* can certainly tolerate low salinity, down to some 2 (Iyer and Barnabas, 1993), and hence its usual categorisation as being estuarine in habitat. Nevertheless, like many ‘estuarine’ organisms (Barnes, 1989; Attrill and Rundle, 2002), dwarf-eelgrasses are probably more truly characteristic of sheltered coastal conditions in general and they occur in areas other than those of reduced salinity. Indeed they flourish in full-strength seawater in lagoons and bays, and a salinity of 35 is within their optimal growth range (Adams and Bate, 1994). With a field salinity range of some 2–40, *N. capensis* therefore provides an ideal subject for an examination of the extent to which intertidal seagrass faunal assemblages might vary along an estuarine axis. This paper then considers the effects on seagrass faunal biodiversity and related ecological features of the axial hydrographical gradient at the Knysna stronghold of *N. capensis*. The Knysna system is also an appropriate one for such an investigation on several grounds. It is, for example, the type of estuary in which salinity is likely to be an important factor structuring the fauna (Teske and Wooldridge, 2003), and its influence on biodiversity in several habitat types there has already been demonstrated (Day et al., 1952; Allanson et al., 2000a). Further, both *N. capensis* itself (Short et al., 2007, 2011) and the fauna that it supports at Knysna are of very high conservation importance (Hodgson and Allanson, 2000; Russell et al., 2009), and information on the spatial distribution of their biodiversity is of practical value to management strategy.

2. Study area

The permanently open, 18 km^2 Knysna estuarine bay ($34^{0}02'$S, $23^{0}01'$E) is ranked ecologically as the most important of South Africa’s 250+ estuaries (Turpie et al., 2002; Turpie and Clark, 2007). It contains a higher proportion of the total South African estuarine biodiversity than any other estuary (Turpie et al., 2002) and hosts a number of species for which Knysna is the only known African locality (Barnes, 2010; Barnes and Ellwood, 2011). In part this is due to its large size and wide range of habitat types, and also because, unusually amongst South African estuaries, it receives both seawater input with every high tide, supporting a diverse assemblage of marine species, and freshwater from a permanently inflowing river at its head. At the same time, however, it is also the most economically valuable of South Africa’s estuarine resources. In 2007, for example, it was the premier estuarine tourist destination (with an annual tourist revenue then equivalent to 150×10^6 US$) and premier estuarine residential area (with estuary-related property $\approx 0.2 \times 10^9$ US$), whilst still yielding an annual income $\approx 26 \times 10^6$ US$ from its use by line fish as a nursery-area and 120×10^3 US$ of harvested resources to subsistence fishers (Turpie and Clark, 2007). However, despite the considerable human impingement on the system (Russell et al., 2009), levels of environmental health are still ranked as ‘good’, the second-highest category on a four point, ‘excellent’ → ‘poor’ scale (Turpie, 2004; Turpie and Clark, 2007).

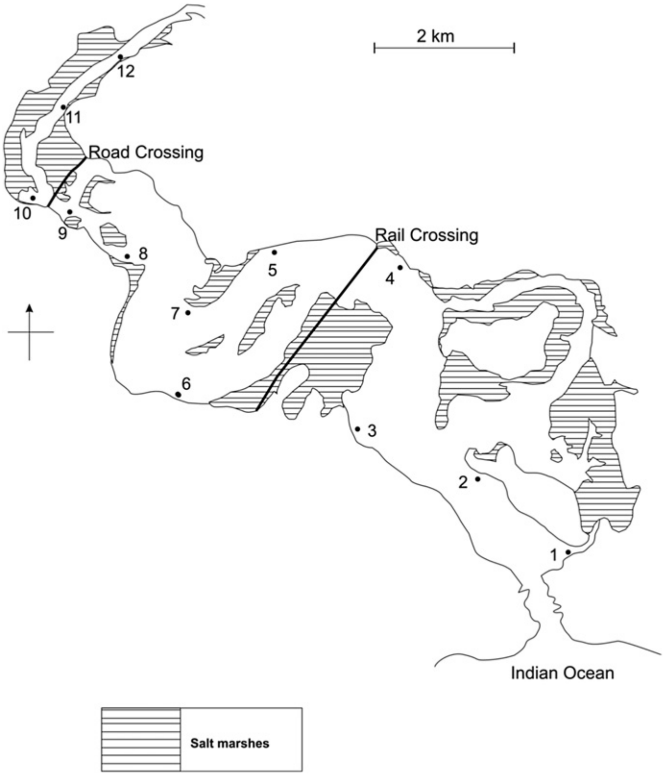

Fig. 1. The Knysna estuarine bay showing the location of the 12 sites close to the margins of the axial channel. The width of the axial seagrass beds is at most sites too narrow for them to be included on a map of this scale.

Hydrographically, the estuarine bay is divisible into a linear series of three units (Largier et al., 2000): (1) an outer marine system tidally flushed with cool water from the Indian Ocean (the spring tidal prism being some 19×10^6 m^3, the largest of any South African estuary; CSIR, 1974) and with salinities usually >34; (2) a middle, relatively isolated lagoonal section with not only a long residence time but also high salinity (30–34); and (3) an inner, stratified and well-flushed estuary with low (0–<30) and variable salinity as a result of the influence of the Knysna River. Several other freshwater streams and small rivers do enter all three units, but these do not normally affect the hydrography of the main water mass. Estuaries being dynamic systems, these hydrographic components are not constant in areal extent or geographical position. The estuarine regime shrinks and enlarges in response to variation in river flow, and the marine regime likewise expands (to 7.5 km upstream) and contracts (to 4 km upstream) in response to variation in high-tidal seawater incursion during spring (1.7 m range) versus neap (0.5 m range) tidal phases, forcing the intervening lagoonal regime to move accordingly (Largier et al., 2000).