



Interspecific abundance-occupancy relations along estuarine gradients

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ABSTRACT

Do interspecific abundance-occupancy (*A-O*) relationships vary systematically along environmental gradients? *A-O* relationships of macrobenthic assemblages of seagrass and adjacent bare-sediment were compared at series of sites along two types of estuarine gradient; the longitudinal one of the main axial channel, and a transverse one from that channel into progressively smaller channels and creeks enclosed within fringing saltmarsh. Three general features emerged: *A-O* regression slopes were remarkably uniform across all the disparate assemblages and sites (1.04 ± 0.08); values of R^2 were very high (≈ 0.96); and where small but significant differences between sites occurred, they were associated with the stronger gradients (i.e. those with the larger differentials in abundance and smaller compositional similarities). In two such cases, slope values were correlated with position along the gradient (although only at the margin of statistical significance). Variation in *A-O* relationships along estuarine gradients does clearly occur, but their constancy leaves the stronger impression.

1. Introduction

One of the most pervasive, robust and fundamental of macroecological patterns is the interspecific abundance-occupancy (*A-O*) relationship (Gaston et al., 2000; Roney et al., 2015); abundance being measured as mean number of individuals per unit area and occupancy as the probability of occurrence in unit sample. Indeed it has proved possible to estimate values of occupancy with great accuracy solely from abundance data (He and Gaston, 2003). If log abundance and log occupancy of each component species in a given assemblage are plotted together, a straight-line or curvilinear power-law relationship is characteristic. The same is often true within individual species, although this relationship is often much looser and may not be present at all (Bijleveld et al., 2018; Barnes, 2022a).

This pattern has been demonstrated across a wide range of types of organism and habitat. Most studies have been terrestrial in nature (Blackburn et al., 2006), although classical *A-O* relationships are known in estuarine macrobenthos (Foggo et al., 2003; Barnes, 2021a) and in the few other shallow-water coastal benthic systems that have so far been investigated (Webb et al., 2009; Barnes, 2022a; van Genne and Scrosati, 2022). Hitherto, such interspecific graphs have generally been produced for whole individual localities or taxa, without regard to local habitat variation. As emphasised by McGill et al. (2006, 2007), however, axes of environmental variation provide ideal natural experiments for

confirming ecological theories about assemblage structure; and estuaries, being transitional habitats, are typified by marked environmental gradients. Thus studies of individual sites in the warm-temperate Knysna estuary in South Africa's Western Cape, for example, have shown wide variation in such macroecological variables as assemblage abundance and species richness/density per unit area along both the axial estuarine gradient and that oriented perpendicular to that axis from the main estuarine channel into fringing saltmarsh-enclosed backwaters (Barnes, 2021b). Although by definition estuaries mark the transition from fresh to salt waters, estuarine gradients are not solely those of salinity. Changes in silt and organic content of the substratum, in shelter from wave action, and in width and slope of the shore and width of the channel are all characteristic, and these also might be expected to impinge on the distribution and abundance of the fauna (Terrados et al., 1998; Tagliapietra et al., 2012; Gross et al., 2019; Magni et al., 2022). Further, different component estuarine habitats and assemblage types (e.g. seagrass versus bare sediment, and intertidal versus subtidal assemblages) may show differential responses to any given gradient (Barnes and Claassens, 2020; Barnes, 2022b).

Recently, Sen and Akçakaya (2022) have suggested that *A-O* patterns are amongst those general ecological features that might be expected to respond to environmental gradients. Granted that the macroecological variables that are used to construct *A-O* relationships, or that might be expected to impinge on them in some way, are known to vary along

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estuarine gradients, they therefore provide an opportunity to test whether the form of the dependent *A-O* curves is also affected by position along zones of such environmental change. This was carried out on seagrass and adjacent bare-sediment macrobenthic assemblage data from environmental gradients in the Knysna estuarine bay.

2. Methodology

Recent historical datasets of the distribution and abundance of the soft-sediment benthic macrofauna of the Knysna estuarine bay (34°02'40"S, 23°01'29"E), part of South Africa's Garden Route National Park, are available for the intertidal seagrass beds and adjacent areas of bare sediment along its main axial channel (Barnes, 2022b), for the subtidal seagrass beds along the same channel (Barnes and Claassens, 2020), and for both the seagrass and bare-sediment fauna along the transverse gradient within the marine embayment section of the estuarine bay from the main channel through to the beds of small landwards saltmarsh creeks in the lee of a large island (Barnes and Barnes, 2014) (Fig. 1).

All sites were sampled using the same methodology during the austral summer: series of 0.0054 m² cores sieved through 710 µm mesh, 32 per site in respect of the subtidal samples, 40 per site for the intertidal axial ones, and 44 per site along the transverse gradient; a 'site' being a local area of some 50 m². Because of taxonomic uncertainty, identification of collected fauna was generally attempted only to morphologically-based operational taxonomic units ('morphotaxa'), an appropriate procedure to detect spatial patterns of numbers of taxa and their differential abundance (Dethier and Schoch, 2006; Gerwing et al., 2020). Although this incurs a risk of failing to distinguish any closely similar species, experience of taxonomic resolution/sufficiency in equivalent soft-sediment macrobenthic studies (e.g. Warwick, 1988; Tataranni et al., 2009; Brind'Amour et al., 2014) indicates that operating at various levels from species up to family all produce similar conclusions. Morphotaxa were distinguished under a ×25 binocular microscope, were counted, and individuals were then returned to their habitat. Sessile and mobile species can differentially influence spatial

patterns of biodiversity (Davidson et al., 2004), and this study excluded any sessile or semi-sessile animals that had become detached from the seagrass leaves during sampling. Further methodological details are available in the original reports cited above, and the full datasets upon which the following analyses are based are available online at Mendeley Data, VI, <https://doi.org/10.17632/y58skv2b7g.1>.

Occupancies are presented as logit transformed values (i.e. occupancy/1-occupancy; Williamson and Gaston, 1999) with values in cases of 100% occupancy (that result in a denominator of zero) being accorded a nominal value of 99.99; abundances are all mean numbers per m². Differences in *A-O* relationship slopes across sites were tested by ANCOVA using PAST 4.0.9 software (Hammer et al., 2021). All nomenclature below is as given by the World Register of Marine Species (WoRMS, www.marinespecies.org, accessed July 2022), except in respect of the small gastropods referred to as 'Assiminea' which still await generic placement within the Assimineidae (see Barnes, 2018).

3. Results

Overall, 159 infaunal and epifaunal animal morphotaxa were identified along the Knysna gradients, 47 of them annelid, 42 crustacean and 44 molluscan, spanning all estuarine invertebrate feeding guilds and body sizes from <2 mm long ostracods to >50 mm long worms. Individual sites varied widely from macrofaunal abundances of >35,000 individuals m⁻² to <2000 and from species densities of >60 to <20 per site (see Table 1).

Regression slopes of the 24 site *A-O* relationships assessed, however, were markedly uniform, with a mean value of 1.044 and standard deviation of only 0.079, and were characterised by very high values of adj. R², i.e. ≥0.90 with a median of 0.96 (Figs. 2 and 3). All 913 datapoints could be fitted to a single regression line with an adj. R² value of 0.95. Neither was there any difference along either the intertidal axial or transverse gradients in the regression slopes of the overall seagrass and bare-sediment macrobenthic *A-O* relationships (ANCOVA $F < 2.4$, $P > 0.12$).

A-O slopes of neither the intertidal seagrass nor the bare-sediment

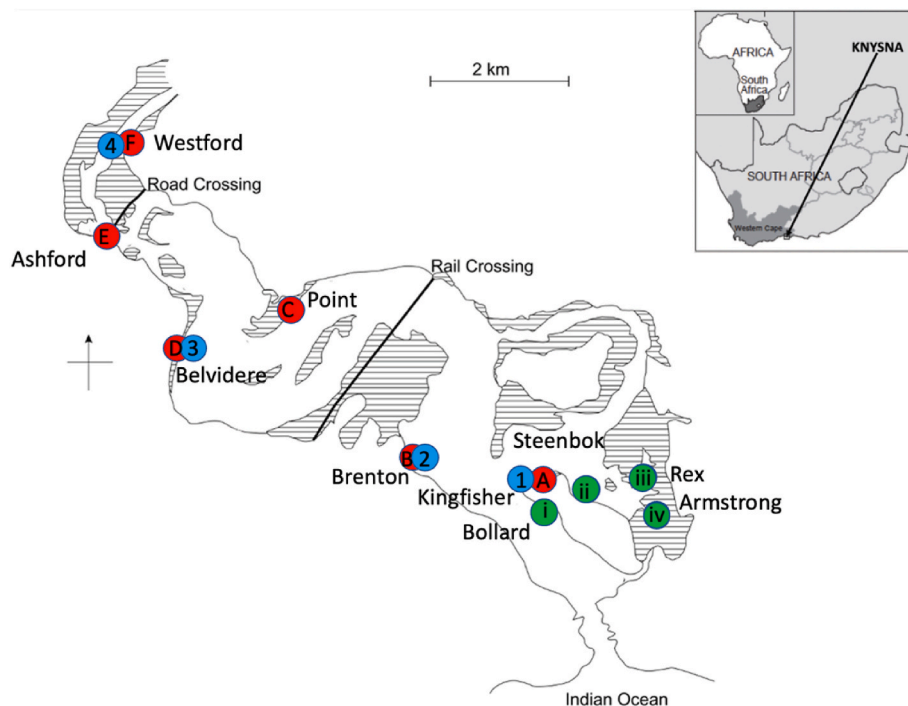


Fig. 1. Location of the series of sampling sites along environmental gradients in Knysna estuarine bay: (i) intertidally along the main axial channel where both seagrass and adjacent bare-sediment sites were sampled separately in 2021/2022 (A–F); (ii) subtidally along the same axial channel where seagrass sites were sampled in 2020 (1–4); and along the transverse gradient where creek-bed seagrass and bare sediments were sampled separately in 2014 (i–iv).

Table 1

Magnitude of differences between macrobenthic assemblages at sites at each end of habitat gradients in the Knysna estuarine bay along: the intertidal longitudinal axis (sites 'A' and 'F' in Fig. 1); the subtidal longitudinal axis (sites '1' and '4' in Fig. 1); and the transverse gradient from axial channel into fringing marshes (sites 'i' and 'iv' in Fig. 1). For ratios between values of abundance and species density, values at distal sites 'F', '4' and 'iv' are set at 1.

Gradient	Abundance ratio	Species density ratio	Bray-Curtis similarity	The 3 most numerically dominant taxa at each end of the gradient (distal versus proximal)
AXIAL				
intertidal seagrass	1 : 1.09	1 : 1.92	0.26	<i>Prionospio</i> , <i>Salmacoma</i> & <i>Simplisetia</i> versus <i>Orbinia</i> , <i>?Cylindroleberis</i> & <i>Paramoera</i>
intertidal bare sediment	1 : 3.47	1 : 2.39	0.23	<i>Salmacoma</i> , <i>Prionospio</i> & <i>Nassarius</i> versus <i>Prionospio</i> , <i>Orbinia</i> & <i>Simplisetia</i>
subtidal seagrass	1 : 6.82	1 : 3.20	0.03	<i>Nassarius</i> , <i>Arcuatula</i> & <i>Paratyloidiplax</i> versus <i>Alaba</i> , <i>Grandidierella</i> & <i>Paridotea</i>
TRANSVERSE				
seagrass	1 : 0.18	1 : 1.81	0.03	' <i>Assimineae</i> ' <i>capensis</i> , <i>Hydrobia</i> & ' <i>Assimineae</i> ' <i>globulus</i> versus <i>Turritella</i> , <i>Alaba</i> & <i>Cylindroleberis</i>
bare sediment	1 : 0.14	1 : 2.08	0.03	' <i>Assimineae</i> ' <i>capensis</i> , <i>Hydrobia</i> & <i>Simplisetia</i> versus <i>Turritella</i> , <i>Paradoneis</i> & <i>Pseudopolydora</i>

assemblages at individual sites along the axial channel differed (seagrass sites ANCOVA $F = 1.906$, $P = 0.094$; bare sediment sites ANCOVA $F = 0.124$, $P = 0.99$); but those of the axial subtidal seagrass sites and of both the seagrass and bare sediment sites along the transverse gradient although similar nevertheless did differ significantly from each other (ANCOVA $F > 4.6$, $P < 0.002$). Slopes of the intertidal axial-channel sites were also significantly steeper than those subtidal axial-channel and transverse gradient sites (ANOVA $F_{1,22} = 11.5$, $P = 0.001$). Slopes of the subtidal and of the transverse-gradient seagrass assemblages were correlated with position along the gradients concerned, slopes increasing upstream and decreasing landwards respectively, but with only four sites along each gradient the correlations were only around the margin of statistical significance ($P = 0.055$ and 0.03 respectively).

4. Discussion

Three general features of these results are apparent. One is the marked similarity of slopes of all the A-O relationships at sites across quite strong environmental gradients and contrasting faunal assemblages, ranging along the axial one from broad sandy marine intertidal flats to narrower, more strongly inclined and muddier regions subject periodically to low salinities, and along the other from the same broad sandy mudflats into the more sheltered, narrow and higher-level creeks within the fringing saltmarsh. This suggests that regardless of large differences in overall assemblage abundance, in species density and in species composition, the underlying processes structuring the assemblages are the same.

Secondly, relationships were also consistently very strong, with considerably smaller values of residual 'errors' than most reported in the literature from other assemblages (see, e.g., Gaston et al., 2000; Webb et al., 2009; van Genne and Scrosati, 2022; ten Caten et al., 2022), implying very tight structural control of the relative importances of the individual component species at each site.

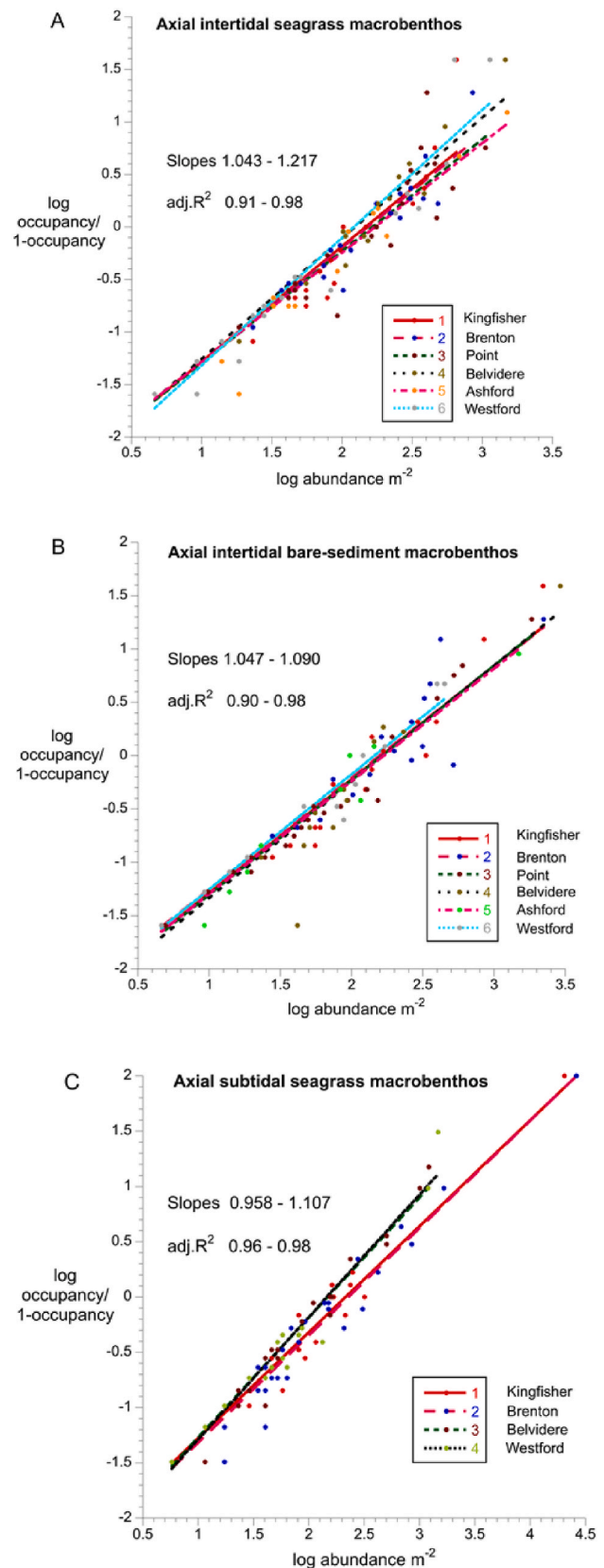


Fig. 2. Abundance-occupancy relationships of the macrobenthic assemblages at sites along the axial gradient of the Knysna estuarine bay associated with: (A) intertidal seagrass, (B) intertidal bare sediment, and (C) subtidal seagrass.

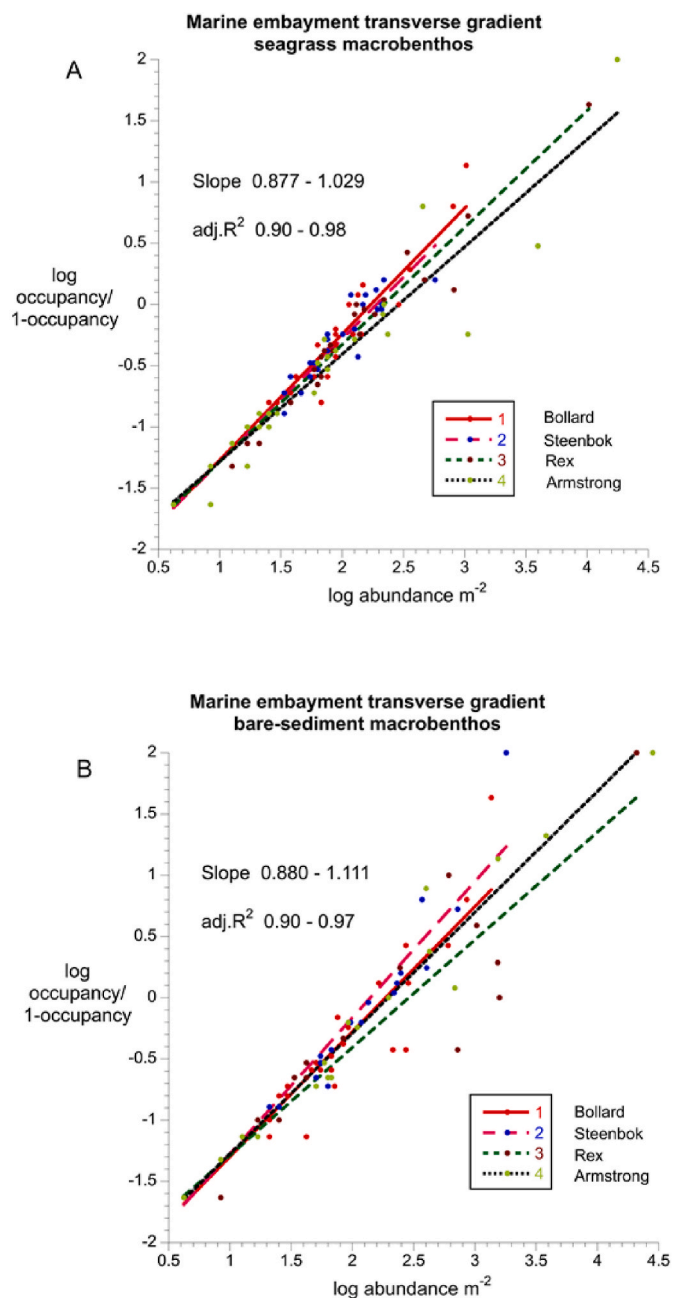


Fig. 3. Abundance-occupancy relationships of the macrobenthic assemblages at sites along the transverse gradient in the marine embayment region of the Knysna estuarine bay associated with: (A) seagrass and (B) bare sediment.

The third is that notwithstanding this relative uniformity a clear distinction was present between those assemblages showing unchanging slopes along a given gradient and those in which the slopes of different sites displayed small but nevertheless significant differences. Sites with unchanging slopes were those along the relatively weaker ecological gradients investigated, i.e. those with smaller differentials in abundance and greater compositional similarities. Those showing significant change along the gradients were all associated with the larger abundance differentials and smaller compositional similarities. Divergences tended to be manifested at the high-values end of the slopes; i.e. those sets showing such differences were all characterised by some of the component sites (those over the more marine half of the axial gradient and those of the landwards half of the transverse gradient) supporting relatively huge though locally variable numbers and almost if not complete occupancy of one or two species that were effectively absent at

sites over the other halves of the gradients concerned. Thus, the two subtidal seagrass sites nearer the mouth supported almost seven times more animals than those upstream, with a single species (the cerithioid gastropod *Alaba*) comprising 84% of the total individuals there compared to 3% at those sites nearer the head (Barnes and Claassens, 2020). Likewise, along the transverse gradient, both the seagrass and the bare sediment at the two landwards sites supported 5–6 times as many animals in total as the less enclosed ones, and the truncatelloid gastropods *Hydrobia* and *Assimineae* there comprised >87% of the individuals, compared with <2% nearer the main channel (Barnes and Barnes, 2014). In contrast, the intertidal seagrass and bare sediment habitats along the axial channel each supported more even overall macrofaunal and relative compositional abundances; the most numerous member of the axial intertidal fauna of both the seagrass and the bare sediment, the polychaete *Prionospio*, being more than three times as numerous as the next-most abundant species but nevertheless only comprising <27% of total individuals (Barnes, 2022a).

It has been considered (Bulafu, 2015) that one of the central problems in ecology is to understand spatial and temporal variation in A-O relationships. Temporal variation has indeed received considerable attention (e.g. Frisk et al., 2011; Manne and Veit, 2020), and the present results suggest that spatial variation along environmental gradients does occur, although perhaps not by as much as might have been expected — understanding the lack of spatial variation may therefore be equally important and could profit from more research. Seagrass beds, and other structurally complex systems (Hyman et al., 2019), support macrofaunal assemblages that generally display a considerable degree of spatial and temporal stability of abundance and composition, and high levels of resilience (Whanpetch et al., 2010; Blake et al., 2014; Gartner et al., 2015). This also appears to extend to the degree of intrinsic patchiness in seagrass macrobenthic systems (Barnes, 2019, 2020), and therefore granted the relationship between patchiness and abundance and occupancy (Barnes, 2021a), relative uniformity of A-O relations is perhaps not so much of a surprise.

Causality of the A-O relationship may still be debated and a considerable number of different models have been proposed in explanation (Holt et al., 2002; Verberk et al., 2010; Frisk et al., 2011; Webb et al., 2019; etc.), indeed many processes may interact to produce the effect (Sen and Akçakaya, 2022). In that context it is worth stressing, however, that these results were derived from the whole benthic macrofauna at each site, and include animals feeding below, on, and above the sediment surface, epibenthically, carnivorously, herbivorously, on suspended materials and on the microphytobenthos (see McGill et al., 2006); that develop directly or via planktonic larvae (see Foggo et al., 2007); that include both specialists and generalists (see Verberk et al., 2010); that inhabit tubes and burrows or are free-living; etc. Explanations based on a few specific trait types are therefore unlikely to be causal in this case. But whatever the ultimate explanation for these various inter-related macroecological phenomena may be, in the Knysna estuarine system its effects are clearly of sufficient magnitude to suffer minimal perturbation even by the local extreme superabundance of one or more component species. It may be no coincidence that on the one hand estuaries and coastal mudflats are generally considered to be harsh, extreme habitats for animals of essentially marine ancestry and characterised by very high mortality rates (e.g. Bachelet and Yacine-Kassab, 1987; Gosselin and Qian, 1997), and that on the other their macroecological assemblage structure such as A-O relationships appear to be under very tight control.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data uploaded to Mendeley Data.

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