



Functional uniformity underlies the common spatial structure of macrofaunal assemblages in intertidal seagrass beds

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Previous work has shown that the intertidal seagrass macrobenthos at three geographically and ecologically disparate localities (in the north-east Atlantic, south-west Indian and south-west Pacific Oceans) possess similar relative species occurrence distributions and uniform species densities. These common features are here demonstrated to be related to the presence in those assemblages of: (1) similar functional diversities and evennesses, (2) the same set of dominant component functional groups, and (3) similar ranked relative occurrence distributions both of those groups and of the component genera within each of the larger groups. The two lower-latitude systems were particularly similar in all these respects. Although sharing the same subset of individual functional groups, however, the relative importance of members of that subset varied from locality to locality and even within a single locality, whilst still maintaining the same ranked relative functional-group occurrence distribution. Therefore the broad structure of available macrobenthic functional roles and the relative occurrences of the component taxa in intertidal seagrass beds (and hence, granted stochastic assembly, the total numbers of taxa supported by unit area) are likely to be linked causally, although the form of the relationship is unclear. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 114–126.

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INTRODUCTION

Small-scale spatial variation of macrobenthic assemblage composition, structure and abundance is a well known phenomenon in shallow-water marine soft sediments (Morrissey *et al.*, 1992; Chapman, 1998; Paiva, 2001; Varfolomeeva & Naumov, 2013; *etc.*). Patchy distribution and abundance of the component taxa and consequent spatial variation in assemblage

composition seem universal. This includes within the beds of seagrass (Boström & Bonsdorff, 1997; Bowden, Rowden & Attrill, 2001; Borg *et al.*, 2010; Arponen & Boström, 2012) that play such a major role in the provision of ecosystem services in many areas (Cullen-Unsworth & Unsworth, 2013) yet are currently declining at an unprecedented rate (Fourqurean *et al.*, 2012). It was recently reported, however, that notwithstanding significant variation in the assemblage components over the same space, overall macrofaunal species density and diversity showed uniform magnitudes per sample across

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expanses of intertidal eelgrass meadow in South Africa (*Zosterella capensis*), in eastern England (*Z. noltei*) and, over distances of up to 6.5 km, in Queensland (*Z. capricorni*) (Barnes, 2013a, 2014a). As would be expected, the sizes of the total species pools, magnitudes of overall macrofaunal abundance, and levels of species diversity and density were very different in the three localities: N_0 γ diversity, for example, ranged from 30 to 140, total numbers from < 2500 to > 60 000 ind m^{-2} , and N_1 α diversity from < 3 to > 35. But nevertheless, not only did each 0.0275 m^2 seagrass sample from within a given site contain the same statistically constant number of macrofaunal species but the number supported at each locality was very similar, within a range of 14–23 across cool-temperate England, warm-temperate South Africa and subtropical Australia. A second feature common to all three systems was that the individual component species were assorted independently of each other (Barnes & Ellwood, 2011a), presumably as a result of being maintained below carrying capacity by predation from the largely nektonic consumers for which seagrass beds provide nurseries (Reise, 1985; Valentine & Duffy, 2006; Moksnes *et al.*, 2008; Lewis & Anderson, 2012). Barnes & Barnes (2014b) showed that these two features were causally related: numbers of species per sample will be statistically constant if the members of the available species pool are assorted randomly, the precise constant number per unit area then being dependent on the shape of the frequency of occurrence curve. The comparable numbers of species per unit area in the disparate macrofaunal seagrass assemblages above is therefore a direct reflection of sharing similar frequency of species occurrence distributions.

What then is responsible for the evolution of these particular occurrence distributions in the first place, and why are they similar in localities that are so contrasting in abundance and overall biodiversity? Even though resource-induced competition may be a rarity, there would still appear to be a somewhat limited number of potential categories of resource available to a benthic invertebrate in an intertidal seagrass bed, and examination of the faunas recorded from such habitats indicates that there are also both: (1) a rather limited number of middle-ranking taxa (families and superfamilies) that occur repeatedly (are preadapted to life) in this habitat across a range of localities through all oceans and across all latitudes, and (2) a relatively small number of life styles displayed by those taxa. This suggests that addressing the following null hypotheses at the three seagrass localities above could yield information contributing to an explanation of the common frequency of occurrence distributions observed. Primarily, (1)

that the form of these distributions is not related to the presence of similar patterns of functional diversity and to the sharing of a standard series of specific life styles or functional groups. And, subsidiary to the above, (2) that the functional diversities and sets of functional groups at the two localities that shared a particularly similar uniform level of biodiversity (those in South Africa and Australia) are not particularly similar when expressed in terms of relative functional-group occurrence frequencies; and (3) that lack of variation in these frequencies along the coast at the Australian locality, notwithstanding significant change in assemblage composition, does not correspond to uniformity of functional groups though space. In addition, a marked estuarine gradient occurs adjacent to the South African locality along which the macrofaunal seagrass assemblages are deterministically structured (Barnes & Ellwood, 2012) leading to a related null hypothesis that (4) variation in the frequency of taxon occurrence patterns along that environmental gradient does not correspond to changes in the frequencies of functional groups.

MATERIALS AND METHODS

NATURE OF THE DATA

Comparable data on the taxa comprising each benthic macrofaunal assemblage and on their relative importance were obtained from the datasets underlying recent published work in intertidal *Zosterella* habitats carried out at equivalent times of the year (Włodarska-Kowalczyk *et al.*, 2014) and with the same methodology: (1) on Scolt Head Island (within the Scolt Head National Nature Reserve) in the northwestern European North Sea at 53°N01°E (Barnes & Ellwood, 2011a; Barnes, 2014a), (2) at Knysna (within the Garden Route National Park) on the Indian Ocean coast of South Africa at 34°S23°E (Barnes & Ellwood, 2011b, 2012; Barnes, 2013a; Barnes & Barnes, 2014a) and (3) on North Stradbroke Island (within a Habitat Protection Zone of the Moreton Bay Marine Park) Queensland at 27°S153°E (Barnes & Barnes, 2012; Barnes & Hamylton, 2013; Barnes, 2014a). All sites are hence enclosed within areas of high conservation status. As the present study sought to account for the similar frequency of taxon occurrence patterns at these sites (see Barnes, 2014a, Fig. 5), the data used in comparisons were the individual relative frequencies of occurrence, instead of the more usual measure of relative abundance in species abundance distributions (SADs) or Whittaker plots (Whittaker, 1965; White, Thibault & Xiao, 2012). [NB Some alternative names for 'occurrence', i.e. for the frequency of presences in presence–

absence datasets, are in current common ecological usage, for example ‘occupancy’ (e.g. Jenkins, 2011), ‘incidence’ (e.g. Gotelli & Chao, 2013), and ‘constancy’ (e.g. Dengler, Löbel & Dolnik, 2009)]. When arranged in rank order, such frequency of occurrence distributions are equivalent to the RSOCs of Jenkins (2011) (‘ranked species occupancy curves’) but constructed in the same format as SADs, i.e. as the percentage of the total taxon occurrences comprised by each taxon (Barnes, 2014b), instead of as proportions of the total numbers of samples taken. In all cases, the basic unit of comparison was the percentage relative presence of individual taxa in series of 0.0275 m² samples, with a minimum of 90 such samples or 25 000 individual animals in total from each locality, whichever was the smaller. The specific South African site used in comparisons with the North Sea and Queensland ones was the shoreline of the sheltered, marine Steenbok Channel in the lee of Leisure Isle within the outer basin of the Knysna estuarine bay (Barnes & Ellwood, 2011b; Barnes, 2013a), a site environmentally equivalent to those in the lee of Scott Head and along the lee (Rainbow Channel) coast of North Stradbroke. Comparison of sites within the Knysna estuarine bay as a whole were between the significantly different local variants of the seagrass fauna there identified along its long axis by Barnes & Ellwood (2012) and Barnes (2013b). The basal taxon adopted was genus as no individual species occurred beyond a single locality although genera did; there being no reason to believe that the types of comparison undertaken here are sensitive to precise level of taxonomic resolution (Chapman, 1998; Tataranni *et al.*, 2009). All nomenclature, including of higher taxa, is as per the World Register of Marine Species (<http://www.marinespecies.org>), assessed October 2014.

IDENTIFICATION OF ‘FUNCTIONAL GROUPS’

There have been a number of attempts to identify the most ecologically relevant properties of benthic marine species for use in estimation of functional diversity of their assemblages (e.g. Bremner, Rogers & Frid, 2003; Gerino *et al.*, 2003; Norling *et al.*, 2007). Few, however, seem appropriate to intertidal seagrass faunas, not least because of the limited range of ecological niche-types referred to above and because many seagrass animals appear opportunistic and relatively generalist (Boström *et al.*, 2006; Reed & Hovel, 2006). Most of those under consideration here fall into only a few of the 23 feeding guilds recognised by MacDonald *et al.* (2010), for example. Pavoine & Bonsall (2011), and in a somewhat different context Törnroos, Nordström & Bonsdorff (2013), have also argued a strong general case for using measures that

combine information from both ecological and taxonomic diversity. The limited *Zosterella* faunas under consideration here, however, do fall into a series of some 30 different taxonomic/ecological categories or life styles on the basis of a combination of their morphology, method and location of feeding, mobility, and preferred habitat stratum within seagrass beds; i.e. on features that can be expected strongly to influence relative organismal performance (McGill *et al.*, 2006). The simple system set out in Table 1 was therefore used as a proxy for ‘functional groups’ in the calculation and comparison of functional diversities across *Zosterella* localities.

Probable food sources of individual genera were taken from works such as Gambi *et al.* (1995), Farlin *et al.* (2010), MacDonald *et al.* (2010) and the specialist literature, and it was assumed that in these intertidal habitats most so-called ‘detritus’ feeders are mainly dependent on the living microphytobenthos within or on the surface of the sediment and on the seagrass leaves (Hillebrand *et al.*, 2002; Lebreton *et al.*, 2011; *etc.*). Animals potentially feeding on the same type of material but collecting it by use of contrasting techniques that probably influence the precise food species selected, e.g. feeding on phytobenthos via ciliated ‘tentacles’, via a rasping radula, or via a pair of cutting jaws, were placed in different categories (see, e.g., Aberle *et al.*, 2009). No attached sessile animals were included in the analyses. Nor were any large species (see De Bie *et al.*, 2012): all animals were from 8 cm diameter cores (five of which totalled the unit 0.0275 m²) and therefore included the smaller and most numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity (Albano, Sabelli & Bouchet, 2011), their dimensions being of the order of smallest < 1.5 mm and largest < 3 cm except for the length of various long thin worms such as *Lumbrineris*, *Onuphis* and some nemertines.

STATISTICAL PROCEDURES

The univariate and non-parametric multivariate techniques of the distance-based linear modelling package (DistLM) contained in PRIMER 6.1 (PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research) were used to explore locality-specific relative frequencies of macrofaunal functional-group occurrences. Similarities of functional-group occurrences between the localities were examined using PERMANOVA, based on square-root transformed data in Bray–Curtis similarity matrices, followed by post-hoc pairwise tests to highlight similarities. DistLM was employed to verify relationships between the functional groups from each site. DistLM produces a sequential test, which assesses the variation

Table 1. Macrofaunal life-style categories within *Zosterella* beds to which the individual genera were allocated as a proxy for functional groups in the estimation of assemblage functional diversity

Group no.	Diagnosis of group
1	Subsurface-feeding, free-living, predatory worms (some nemertines & some errant polychaetes e.g. nephtyids, glycerids & goniadids)
2	Surface-feeding predatory worms (e.g. polyclads, many nemertines & errant polychaetes)
3	Surface-feeding, tubicolous or burrow-dwelling, omnivorous worms (e.g. errant polychaetes such as many nereids)
4	Deposit-feeding, tubicolous or burrow-dwelling worms with ciliated feeding palps, tentacles, etc., that collect material from the sediment surface (e.g. most canalpalpatan polychaetes, sipunculans & echiurans)
5	Suspension-feeding, infaunal, tubicolous worms (e.g. sabellid & chaetopterid polychaetes)
6	Subsurface, free-living or burrow-dwelling, microbe-, protist- or sediment-ingesting worms (e.g. most scolecidan polychaetes & tubificine oligochaetes)
7	Subsurface, free-living, omnivorous worms (e.g. errant polychaetes such as lumbrinerids)
8	Mobile, suspension-feeding ostracod crustaceans
9	Sedentary and often tubicolous, suspension-feeding peracaridan crustaceans (e.g. many corophiideans)
10	Omnivorous, free-living peracaridan crustaceans (e.g. apseudomorphs and sphaeromatoids)
11	Algivorous, free-living or occasionally 'nest'-building peracaridan crustaceans (e.g. many amphithoids & idoteids)
12	Predatory, free-living peracaridan crustaceans (e.g. anthuroids & phoxocephaloids), consuming small (often meiofaunal) prey
13	Large, free-living, predatory decapod crustaceans (e.g. portunioids) taking macrofaunal prey
14	Microphytobenthically-feeding, burrow-dwelling decapod crustaceans (e.g. many ocypodioids & axiideans)
15	Omnivorous, free-living decapod crustaceans (e.g. many paguroids)
16	Suspension-feeding, burrow-dwelling decapod crustaceans (e.g. gebioids)
17	Periphyton- and leaf-browsing, free-living gastropod molluscs (e.g. neritimorphs, trochoids & litiopids)
18	Microphytobenthos-grazing, free-living microgastropod molluscs (e.g. truncatelloids & rissoids)
19	Larger, deposit-feeding, free-living gastropod molluscs (e.g. batillariids & littorinoids)
20	Sedentary, infaunal, suspension-feeding gastropod molluscs (e.g. turritellids)
21	Predatory/scavenging, free-living molluscs (e.g. most neogastropods, epitonoids, nudibranchs)
22	Ectoparasitic gastropod molluscs (e.g. pyramidelloids)
23	Algivorous, free-living gastropod molluscs (e.g. saccoglossans & haminoeids)
24	Sedentary, infaunal, burrow-dwelling or buried, suspension-feeding bivalves (most bivalve molluscs & lingulatan brachiopods)
25	Carnivorous, epifaunal, free-living echinoderms (e.g. asterinid asteroids)
26	Burrowing, deposit-feeding echinoderms (e.g. apodidan holothurians)
27	Deposit-feeding, infaunal, free-living bivalves (e.g. protobranchs)
28	Free-living, sedentary animals dependent in whole or part on chemosynthetic symbionts (e.g. solemyoid & lucinoid bivalves, see, e.g., van der Heide <i>et al.</i> , 2012)
29	Suspension-feeding, free-living echinoderms (e.g. many ophiuroids)
30	Algal-grazing, free-living echinoderms (e.g. many echinidian echinoids)

that each predictor (functional group) has on its own, and a conditional test, assessing the variation across all the groups (McArdle & Anderson, 2001). The most parsimonious model was identified using the selection criterion R^2 . The DistLM was based on the various frequencies of occurrence, classified as 'other data', with 4999 permutations. Overall diversity of the functional-group distributions was estimated by Hill's N_1 , considered by Micheli & Halpern (2005), Schleuter *et al.* (2010), etc. to be appropriate in the ecological and analytical circumstances, relative func-

tional evenness by Pielou's J , as recommended by Jost (2010), and functional redundancy by within-functional-group evenness (Hewitt, Thrush & Dayton, 2008).

RESULTS

COMPARISONS BETWEEN LOCALITIES

Distribution of the relative frequencies of occurrence of the various functional groups of Table 1 varied

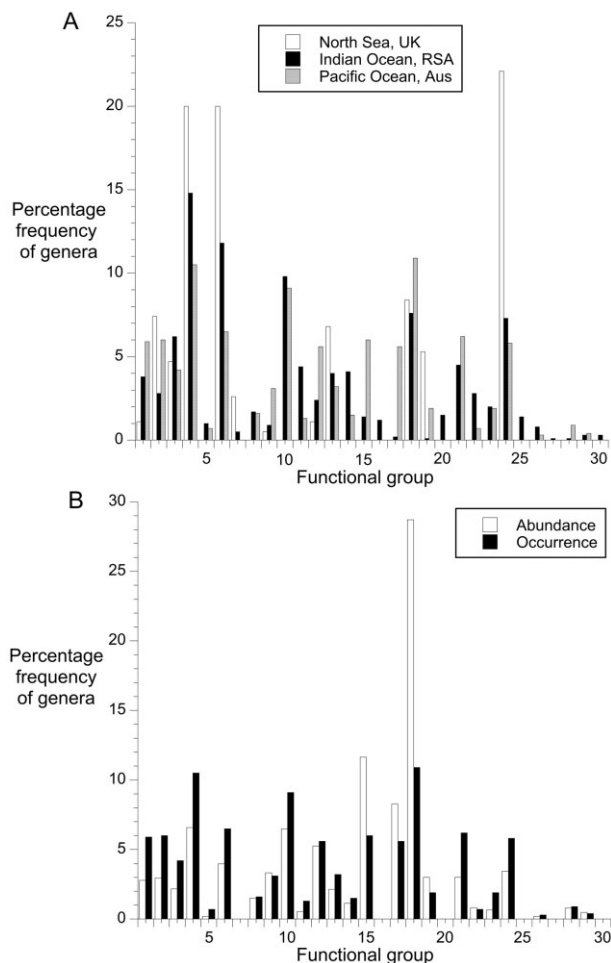


Figure 1. A, The importance (relative frequency of occurrence of the contained genera) of the different functional groups as defined in Table 1 in intertidal *Zosterella* beds on Scott Head Island in the North Sea (UK), along the Steenbok Channel coast of Leisure Isle in the marine basin of the Knysna estuarine bay (RSA), and along the Rainbow Channel coast of North Stradbroke Island, Moreton Bay (Australia). B, General correspondence between the dominant functional groups as assessed: (i) by relative occurrence of their contained genera; and (ii) by relative abundance of those genera, as exemplified by the North Stradbroke locality.

within each locality (PERMANOVA Pseudo- F ranging from 22 to 51; in all cases $P < 0.001$) but showed a broadly similar pattern across localities, groups 2, 4, 6, 10, 18, 21 and 24 peaking at two or all three (Fig. 1A). Together these peak functional groups included 55–78% of the total genus occurrences and were responsible for 53% of the similarity between localities (DistLM sequential test Pseudo- $F > 32$; $P < 0.001$). The most parsimonious model for the three localities explained 85% of the variation. The distributions of functional groups at the two

Table 2. Variation in the nine most important functional groups (numbered as in Table 1) across the three localities in terms of relative frequency of occurrence (percentage of the total genus-occurrences within each group being given in parentheses)

Rank	Scotl head	Knysna	North stradbroke
1	24 (22.1%)	4 (14.8%)	18 (10.9%)
2	6 (20%)	6 (11.8%)	4 (10.5%)
3	4 (20%)	10 (9.8%)	10 (9.1%)
4	18 (8.4%)	18 (7.6%)	6 (6.5%)
5	2 (7.4%)	24 (7.3%)	21 (6.2%)
6	13 (6.8%)	3 (6.2%)	2 (6.0%)
7	19 (5.3%)	21 (4.5%)	15 (6.0%)
8	3 (4.7%)	11 (4.4%)	1 (5.9%)
9	7 (2.6%)	14 (4.1%)	24 (5.8%)

Note that groups 4, 6 and 18 appear in the top four at all three localities.

lower-latitude localities, North Stradbroke and Knysna, were not significantly different (Pairwise PERMANOVA $t = 1.02$; $P > 0.05$), but that on Scott Head did differ from both the other two ($t \geq 1.25$; $P < 0.05$), with groups 10 and 21, for example, being important only in Knysna and North Stradbroke (Fig. 1A). Groups 2, 4 and 24 accounted for 31% of the total variation (DistLM sequential test). At each locality there was a close correlation between the relative importance of the various functional groups as determined on the basis of: (1) their relative occurrences; and (2) their relative abundances (Pearson $R > 0.72$; $P < 0.0001$), and likewise in respect of the rank orders of importance of the groups assessed on the two bases (Spearman $R_s > 0.93$; $P < 0.0001$) (Fig. 1B). N_1 functional diversities at the three localities were: Scott Head 8.01; Knysna 17.94; North Stradbroke 17.83; relative evenness values of the distributions were more uniform: 0.84–0.91.

The relative importance of these specific shared dominant functional groups was not the same across localities, however (PERMANOVA Pseudo- $F = 1.6$; $P < 0.01$), and rank orders differed even in respect of the nine most important groups of the not otherwise significantly different North Stradbroke and Knysna (Spearman $R = 0.75$; $P < 0.02$). The most important functional groups at the separate localities are shown in Table 2. In descending order of importance, groups 4, 6 and 24 best characterised Scott Head (DistLM Pseudo- $F > 6.5$; $P < 0.01$), 4, 2, 24, 10, 6 and 3 Knysna (DistLM Pseudo- $F > 10$; $P < 0.001$), and 2, 24, 4, 18, 21 and 10 North Stradbroke (DistLM Pseudo- $F \geq 20$; $P < 0.001$). Overall at the two low-latitude localities, phyto-benthos feeders comprised 41–46% of the total, suspension feeders 12–14%, omnivores 18–19%,

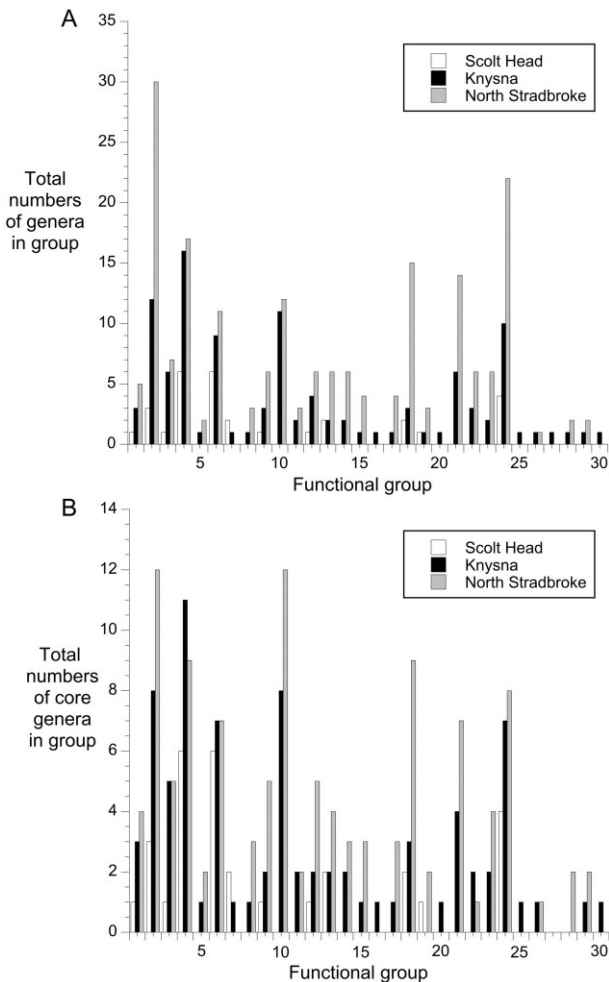


Figure 2. The numbers of genera represented in each functional group across the three localities of Figure 1A: A, total numbers; B, numbers of core genera (those with percentage frequencies > 0.1).

predators 19–27% and others 2–3%. At the higher latitude Scolt Head, basal trophic-level categories were more important (phytobenthos feeders 54%; suspension feeders 23%), whilst higher trophic levels were less so (omnivores 7%; predators 16%).

As would be expected from the differing sizes of the available pools, the total numbers of genera in each functional group varied widely from locality to locality (Fig. 2A): for example, group 2 only comprised three genera on Scolt Head, 12 in Knysna, but 30 on North Stradbroke. Excluding the tail of 'satellite' (Hanski, 1982) or 'excess rare' genera (Magurran & Henderson, 2003) with relative percentage frequencies ≤ 0.1 so as to confine the data to those most responsible for the general form of the relationships, however, functional groups 4 (6–11 genera), 6 (6–7) and 24 (5–8) were remarkably similar in component generic numbers across localities (Fig. 2B). Scolt Head supported only

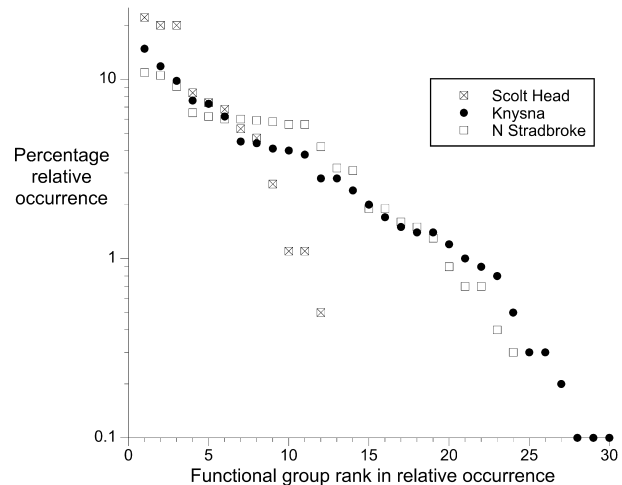


Figure 3. Ranked relative occurrence distributions of the various functional groups at the three localities.

12 different functional groups and 30 genera. The two lower-latitude localities, each supporting at least twice as many functional groups, however, showed very similar ranked relative group frequency distributions notwithstanding differences in the identity of the component groups concerned. As would be expected from a greater value of Fisher's α or Hubbell's θ , their curves tended towards the log-normal form in contrast to the more geometric nature of that of depauperate cool-temperate Scolt Head, but approximating them by an exponential decline (Jenkins, 2011) yields a common exponent of some -0.15 (Knysna R^2 0.99; North Stradbroke R^2 0.95; Fig. 3). Further, within each of the more important functional groups represented, the rank-order distributions of the component genera showed similar approximately exponentially decreasing forms (Fig. 4), with a mean value of the exponent of -0.20 (and with that of -0.15 lying within 1 standard deviation of that mean). Functional redundancy levels within each such genus-rich functional group were: Knysna 0.71–0.95 (mean 0.81) and North Stradbroke 0.70–0.85 (mean 0.78). The genera with the largest individual relative occurrences at both Knysna and North Stradbroke all (or almost all) represented different functional groups: at Knysna the nine genera with the greatest occurrences each represented a different group (groups 3, 10, 4, 21, 13, 14, 6, 11, 18 in descending order of importance), and at North Stradbroke the eight most widely occurring genera represented seven different groups (15, 18, 12, 10, 18, 1, 13, 21), with the exception, group 18, supporting two dominant microgastropod genera (i.e. *Calopia* and *Pseudoliotia* that, however, are divergent in shape, belong in different families, and probably occupy rather different niches).

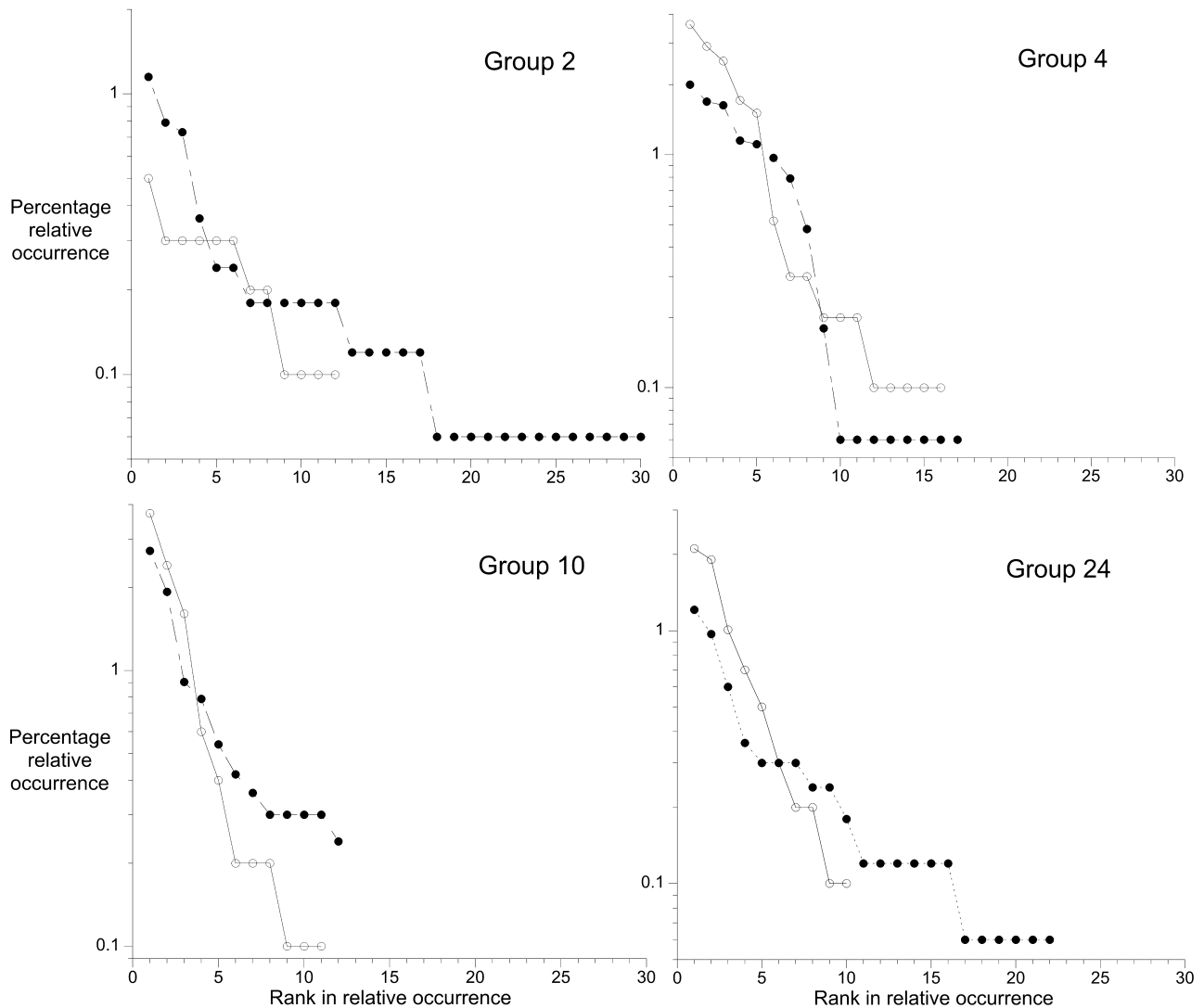


Figure 4. Ranked relative occurrence distributions of the component genera comprising each of the four functional groups that supported the largest intra-group generic diversity (groups 2, 4, 10 and 24; see Figure 2) at Knysna (open circles) and North Stradbroke (filled circles).

Unlike in the various soft-sediment assemblages investigated by Ellingsen, Hewitt & Thrush (2007), there was a very strong relationship between abundance and frequency of occurrence of the component taxa (Spearman Rank $R > 0.98$; $P < 0.0001$) ($R^2 > 0.55$ versus Ellingsen *et al.*'s R^2 of 0.195) (Fig. 5). As would be expected, the importance of satellite genera increased with decreasing latitude: zero at Scolt Head, 23% of the total at Knysna, and 39% at North Stradbroke. Neither those at Knysna nor at North Stradbroke, however, departed from the pattern of frequency of functional groups shown by the core genera (PERMANOVA Pseudo- $F = 0.5$; $P > 0.05$) although at North Stradbroke the satellite set did include more types of predatory worms and of

suspension-feeding bivalves although fewer of omnivorous peracaridan crustaceans.

COMPARISONS WITHIN LOCALITIES

Within the North Stradbroke locality, the close correspondence, though again not in relative magnitude, of the dominant functional groups at the three component sites is clear from Figure 6 (PERMANOVA Pseudo- $F = 0.33$; $P > 0.05$). The most parsimonious model explained 98% of the variation. The 6.5 km apart Deanbilla and Capembah sites in particular showed effectively identical functional N_1 diversities (16.93 and 16.98 respectively), although that of the intermediately sited Goompi was somewhat larger, at

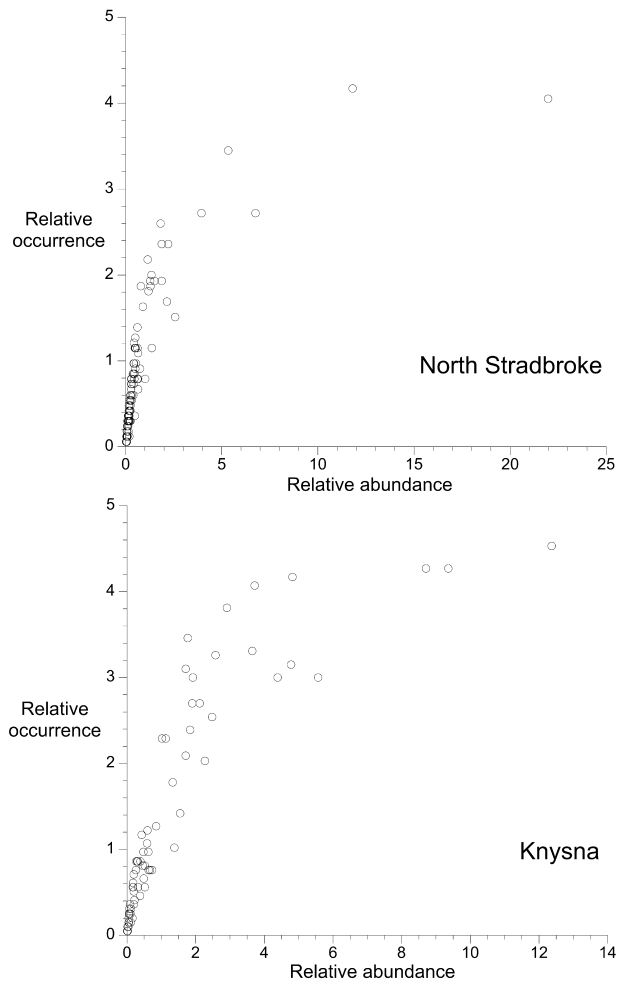


Figure 5. Relationship between percentage relative abundance and percentage relative occurrence amongst the genera at the two most genera-rich localities, Knysna and North Stradbroke.

18.80. Relative functional evennesses were all within the very narrow range of 0.90–0.92. Although different groups were obviously dominant at different sites (Fig. 6), a DistLM sequential test showing that, in descending order of importance, groups 4, 10, 18, 3, 24 and 17 explained > 50% of the variation, the curves of their ranked relative occurrence at each site were effectively identical (Fig. 7).

Functional-group frequencies were not evenly distributed within any site across the whole Knysna estuarine bay (PERMANOVA Pseudo- F 83–166; $P < 0.001$) but there were no significant differences between their frequencies at the various sites (pairwise PERMANOVA $t = 0.58$ – 0.76 ; $P > 0.05$), the most parsimonious model explaining 98% of the variation. Nevertheless, there was a significant trend from high to low functional diversity and a decrease in the component functional groups, both in total and

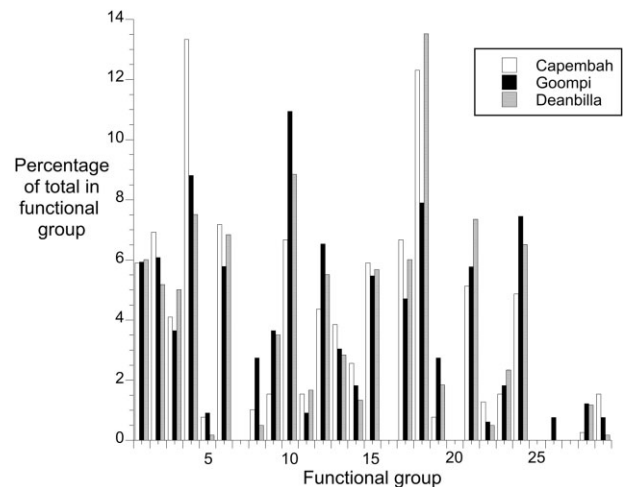


Figure 6. Percentage frequency of occurrence of the different functional groups at three sites within the North Stradbroke locality, distributed over a distance of some 6.5 km. Note the common peaks of groups 4, 6, 10, 12, 15, 18, 21 and 24, but their differing relative magnitudes.

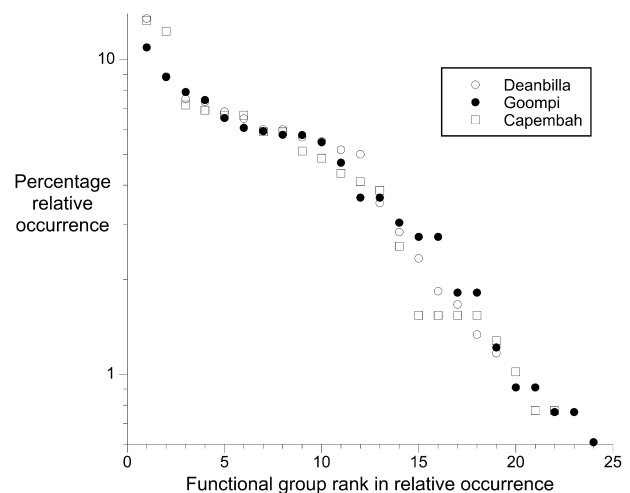


Figure 7. Ranked relative occurrence distributions of the various functional groups present at the three component sites of the North Stradbroke locality.

in the number of local dominants, from the marine outer basin into the lagoonal and brackish zones (Spearman $R \geq -0.9$; $P < 0.04$) (Fig. 8). In particular, functional groups 6 and 11 were important only in the marine and lagoonal sections, 4, 10 and 13 only extended into the lower section of the estuary, whilst conversely groups 21 and 24 were more dominant within the estuary. It was only in the upper estuary that there was a marked change in relative functional evenness, however: over the rest of the system this was in the range 0.85–0.91 but within the upper estuary it fell to 0.68 consequent on the overwhelming

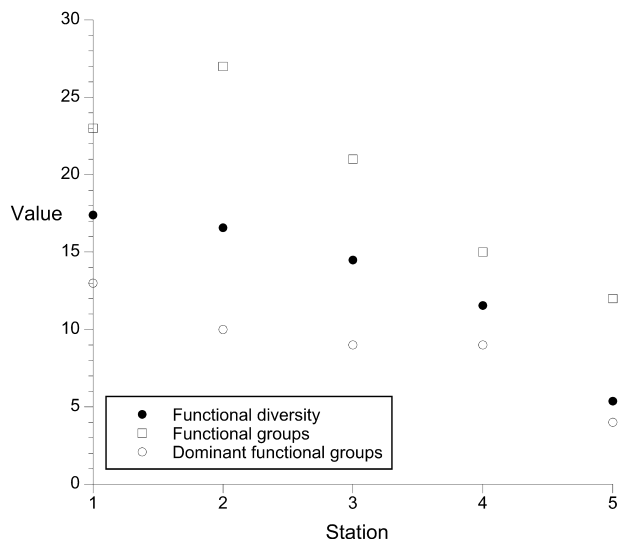


Figure 8. Response of N_1 functional diversity and of both the total number of component functional groups and the number of those that dominated the assemblages (i.e. comprised > 4% of the total) to the long-axis gradient of the Knysna estuarine system, as exemplified by the upstream chain of five stations, the sites within each of which supported a significantly different macrobenthic assemblage, as identified and as numbered in Barnes (2013b: Figure 3). [The Steenbok Channel locality, used to represent Knysna in comparisons with Scolt Head and North Stradbroke, forms part of station 2.]

dominance there of the group 18 microgastropods *Hydrobia* and '*Assimineae*' (*sensu* Miranda *et al.*, 2014) comprising 35% of the total genus occurrences and 65% of the overall abundance.

DISCUSSION

Notwithstanding that they are located in different oceans across 87° of latitude and 152° of longitude, the three disparate sheltered marine seagrass localities all supported very similar suites of macrobenthic taxa and life styles. Intertidal seagrass clearly provides a standard suite of niches and a standard set of animals have evolved to fill them. Amongst these, surface-feeding predatory worms (e.g. polyclads, nemertines and some eunicid and nereid polychaetes), worms collecting free-living surface microphytobenthos, etc. (particularly spionids but also cirratulids and fabriciids), subsurface sediment-ingesting worms (particularly capitellids, orbinids and paraonids), microphytobenthos-grazing gastropods (particularly truncatelloids), and infaunal suspension-feeding bivalves (particularly tellinoids, cardioids and/or galeommatoids) dominated all three, whilst scavenging nassariid gastropods and omnivo-

rous peracarids such as sphaeromatoids and/or apseudomorphs were also important at the two lower-latitude localities. Further, although, in those lower-latitude localities at least, some eight genera comprised each dominant functional group, most genera were rare such that a total of only some 21–26 had an index of numerical importance (Barnes, 2014b) $\geq 1\%$. This was also evidenced by the most widespread genera at Knysna and North Stradbroke each representing a different functional group. The frequency of occurrence distributions within each dominant group mirrored those of the assemblage as a whole. In essence, the ranked relative occurrence distributions of component taxa (Barnes, 2014a) and of component functional groups (this paper) were of similar form.

As argued by Bremner, Rogers & Frid (2006) and by Frid *et al.* (2008), analysis of the relative importance of their various functional roles proved useful for identifying whether assemblages in similar habitats but different geographical locations are constructed, and hence presumably operate ecologically, in the same manner. It showed the South African and Queensland seagrass beds to have evolved an almost identical overall N_1 functional diversity and functional structure in terms of relative occurrences (and of relative abundances), and all three localities to have very similar frequency of functional-group occurrence distributions and relative evennesses of those functional groups. Nevertheless, it was evident that the relative importance of the individual shared dominant groups was significantly different across localities, including at the otherwise similar Knysna and North Stradbroke, and even varied across sites within the latter locality: the details varied from place to place without changing the overall pattern of construction. The single most important group at the South African site was surface-deposit collecting (spionid and cirratulid) polychaetes, whereas in Queensland overall it was microphytobenthos-grazing microgastropods; indeed, such microgastropods were effectively absent from the specific South African site investigated by Barnes (2013a), although they were the dominant components at other nearby sites (Barnes & Barnes, 2014a). Within the Queensland locality, the single most important group also differed between the three component sites: surface-deposit-feeding worms at one, microphytobenthos-grazing microgastropods at another, and omnivorous peracaridan crustaceans at the third. Cool-temperate Scolt Head, with only 30% of the genera and 40% of the functional groups present at warm-temperate Knysna, and 16% and 50%, respectively, of those on subtropical North Stradbroke, maintained a lower functional diversity (only 45%) than that at the two lower-latitude localities as would be expected.

Those individual functional groups that each supported several genera displayed moderate to high levels of within-group functional evenness, and if this does equate with relatively high levels of functional redundancy (and if such redundancy is a valid concept; Loreau, 2004), they should also show considerable resilience. Very little is known, however, about for example the precise diets of seagrass macrofauna, and the extent to which they overlap or are complementary in species within the same functional group (Duffy *et al.*, 2001; Jaschinski *et al.*, 2009). The increasing number of genera within functional groups such as that of surface-feeding predatory worms along the Scolt Head – Knysna – North Stradbroke latitudinal and climatic-zone series could reflect, not increasing functional redundancy, but increasing diversity of prey sources supporting an increasingly diverse set of consumers. These (apparently) high redundancy levels from seagrass systems contrast with those found by Micheli & Halpern (2005) from hard substrata, although values will clearly vary across studies dependent on the inclusivity of the chosen functional groups.

Therefore at each of the three marine localities investigated to date, (1) the number of macrofaunal species per unit 0.0275 m² area within the intertidal seagrass beds has proved to be uniform across distances of up to 6.5 km, (2) its magnitude has been shown to be similar, particularly in respect of those at Knysna and North Stradbroke, notwithstanding large differences in the sizes of the local species pools (Barnes, 2013a, 2014a), and (3) the form of the frequency of relative species occurrence distributions are closely similar (Barnes, 2014a). In this paper, close similarity, again especially between Knysna and North Stradbroke, has been demonstrated in (4) the subset of functional groups that dominated the macrofaunal assemblage occurrences, (5) the pattern of the ranked relative occurrence distributions of those groups, and (6) the overall functional diversities and relative evennesses of the assemblages. Features (1)–(3) above have already been shown to be linked causally (Barnes & Barnes, 2014b) and the close relationship between those and (4)–(6), i.e. between the nature and number of possible macrobenthic functional roles and the relative occurrence distributions of the component taxa filling those roles (and hence the total numbers of taxa supported by unit area), indicates a wider causal network. Granted, however, that the precise members of the limited series of functional groups that dominated individual localities and sites were not the same, the relationship is clearly not a straight-forward one.

Two of the common features stand out as being likely to be critical to the evolution (both generation and persistence) of this pattern. First, that despite

their compositional differences, the rank-order distributions of the dominant functional groups, and within them of the component genera, at both Knysna and North Stradbroke fell on effectively the same curve, and the equivalent distribution at Scolt Head was also essentially similar if allowance is made for its high-latitude poverty in genera and functional groups steepening the curves (see, e.g., Hubbell, 1997: Fig. 4). Secondly, that the eight or nine genera that dominated the relative occurrence distributions at each site were representative of as many, or almost as many, different functional groups, i.e. the common genera showed no functional redundancy at the inter-group level. The detailed circumstances bringing about these states in a system otherwise lacking significant structural interactions between species may not yet be clear, but in general the intertidal *Zosterella* macrobenthos appears to comprise a simple system that is capable of supporting up to 8 or 9 different major functional units as well as maybe up to twice as many minor ones, although any one site is likely to be relatively conducive only to some of these in a rankable order of potential favourability, presumably dependent on environmental and structural features of each local area (Matias, Underwood & Coleman, 2007). Local regimes of current speed, light penetration to the sea bed, and even the potential success rates of different types of nektonic predator could all influence the relative importance of, for example, suspension versus phytobenthic feeders, shelled versus unshelled body plans, etc.

Most research into marine soft-sediment functional diversity and assemblage structure has been devoted to changes in diversity patterns in response to major changes in habitat type, including those induced anthropogenically (e.g. Bremner *et al.*, 2003, 2006; Afli, Ayari & Brahim, 2008; Bremner, 2008; Aloui-Bejaoui & Afli, 2012). Virtually all studies of marine assemblage structure have also been concerned with patterns of relative component numbers (i.e. density) (Hughes, 1984; Hubbell, 1997; Magurran & Henderson, 2003; Törnroos *et al.*, 2013; etc.) not with those of relative component spatial distribution (i.e. occurrence) (Jenkins, 2011; Barnes, 2014b). Nevertheless, under many – probably most – circumstances (including here assessment of the relative importance of the various functional groups on the two bases), abundance and distribution are clearly interdependent and closely related phenomena (Hanski, 1982), and the present results from the deterministically structured estuarine assemblages at Knysna would seem to conform to the patterns seen in relative importance from other marine systems elsewhere (e.g. Scrosati *et al.*, 2011). Less research has concerned similarity of overall pattern across contrasting systems, although Hewitt *et al.* (2008),

studying soft-sediment macrofaunas in two marine bays in New Zealand, 500 km apart and supporting different faunas, have commented on the similar representation of functional traits across localities and the relative unimportance of the size of local pools of taxa. Hewitt *et al.*'s (2008) results show a number of parallels with the present study. They also found differences between their sites to be mainly a matter of relative importance of different shared elements, showed marked differences of detail both within and between sites, and found high within-functional-group values of evenness. Why it is that assemblages of different functional groups in different areas, and even assemblages of genera within single functional groups, should all show such similar ranked relative distributions, regardless of the specific nature of the component groups, is not obvious. This could be considered unexpected in that it occurs in a system lacking potential niche-related structural forces like interspecific competition, if indeed interspecific competition can be described as 'structuring' (Loreau & de Mazancourt, 2013), but Hubbell's (1997, 2001) neutral model shows that apparent structure can be achieved stochastically, and that dispersal within larger metacommunities can stabilise local and regional assemblage structure over wide areas without any assumptions of deterministic niche assembly. Neutral models may also be particularly relevant to seagrass assemblages because of the possibility of their being especially associated with suites of generalist species (Pandit, Kolasa & Cottenie, 2009).

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