1 **Functional uniformity underlies the common spatial structure of**

2 **macrofaunal assemblages in intertidal seagrass beds**

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21 Running title: Functional uniformity in seagrass habitats

22 **ABSTRACT**

23

24 Previous work has shown the intertidal seagrass macrobenthos at three geographically and

25 ecologically disparate localities (in the NE Atlantic, SW Indian and SW Pacific Oceans) to

26 possess similar relative species occurrence distributions and uniform species densities.

27 These common features are here demonstrated to be related to the presence in those

28 assemblages of (i) similar functional diversities and evennesses, (ii) the same set of dominant

29 component functional groups, and (iii) similar ranked relative occurrence distributions both

30 of those groups and of the component genera within each of the larger groups. The two

31 lower latitude systems were particularly similar in all these respects. Although sharing the

32 same subset of individual functional groups, however, the relative importance of members of

33 that subset varied from locality to locality and even within a single locality, whilst still

34 maintaining the same ranked relative functional-group occurrence distribution. Therefore

35 the broad structure of available macrobenthic functional roles and the relative occurrences of

36 the component taxa in intertidal seagrass beds (and hence, granted stochastic assembly, the

37 total numbers of taxa supported by unit area) are likely to be linked causally, although the

38 form of the relationship is unclear.

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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 (Morrisey *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 *et al*., 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 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 <2,500 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;

68   Valentine & Duffy, 2006; Moksnes *et al.*, 2008; Lewis & Anderson, 2012). Barnes and

69   Barnes (2014b) showed these two features to be causally related: numbers of species per

70   sample will be statistically constant if the members of the available species pool are assorted

71   randomly, the precise constant number per unit area then being dependent on the shape of the

72   frequency of occurrence curve. The comparable numbers of species per unit area in the

73   disparate macrofaunal seagrass assemblages above is therefore a direct reflection of sharing

74   similar frequency of species occurrence distributions.

75   What then is responsible for the evolution of these particular occurrence distributions

76   in the first place, and why are they similar in localities so contrasting in abundance and

77   overall biodiversity? Even though resource-induced competition may be a rarity, there

78   would still appear to be a somewhat limited number of potential categories of resource

79   available to a benthic invertebrate in an intertidal seagrass bed, and examination of the

80   faunas recorded from such habitats indicates that there are also both (i) a rather limited

81   number of middle-ranking taxa (families and superfamilies) that occur repeatedly (are

82   preadapted to life) in this habitat across a range of localities through all oceans and across all

83   latitudes, and (ii) a relatively small number of life-styles displayed by those taxa. This

84   suggests that addressing the following null hypotheses at the three seagrass localities above

85   could yield information contributing to an explanation of the common frequency of

86   occurrence distributions observed. Primarily, (i) that the form of these distributions is not

87   related to the presence of similar patterns of functional diversity and to the sharing of a

88   standard series of specific life styles or functional groups. And, subsidiary to the above, (ii)

89   that the functional diversities and sets of functional groups at the two localities that shared a

90   particularly similar uniform level of biodiversity (those in South Africa and Australia) are

91   not particularly similar when expressed in terms of relative functional-group occurrence

92   frequencies; and (iii) that lack of variation in these frequencies along the coast at the

93   Australian locality, notwithstanding significant change in assemblage composition, does not

94   correspond to uniformity of functional groups though space. In addition, a marked estuarine

95   gradient occurs adjacent to the South African locality along which the macrofaunal seagrass

96   assemblages are deterministically structured (Barnes & Ellwood, 2012) leading to a related

97   null hypothesis that (iv) variation in the frequency of taxon occurrence patterns along that

98   environmental gradient does not correspond to changes in the frequencies of functional

99   groups.

100

MATERIALS AND METHODS

102   *NATURE OF THE DATA*

103   Comparable data on the taxa comprising each benthic macrofaunal assemblage and

104   on their relative importance were obtained from the datasets underlying recent published

105   work in intertidal *Zosterella* habitats carried out at equivalent times of the year (Wlodarska-

106   Kowalczuk *et al*., 2014) and with the same methodology: (i) on Scolt Head Island (within

107   the Scolt Head National Nature Reserve) in the northwestern European North Sea at

108   53ºN,01ºE (Barnes & Ellwood, 2011a; Barnes, 2014a), (ii) at Knysna (within the Garden

109   Route National Park) on the Indian Ocean coast of South Africa at 34ºS,23ºE (Barnes &

110   Ellwood, 2011b, 2012; Barnes, 2013a; Barnes & Barnes, 2014a) and (iii) on North

111   Stradbroke Island (within a Habitat Protection Zone of the Moreton Bay Marine Park)

112   Queensland at 27ºS,153ºE (Barnes & Barnes, 2012; Barnes & Hamylton, 2013; Barnes,

113   2014a). All sites are hence enclosed within areas of high conservation status. Since the

114   present study sought to account for the similar frequency of taxon occurrence patterns at

115   these sites (see Barnes, 2014a, Fig. 5), the data used in comparisons were the individual

116   relative frequencies of occurrence, instead of the more usual measure of relative abundance

117   in SADs (Species Abundance Distributions) or Whittaker Plots (Whittaker, 1965; White *et*

118   *al*., 2012). [*N.B.* a number of alternative names for 'occurrence', i.e. for the frequency of

119   presences in presence-absence datasets, are in current common ecological usage, for example

120   'occupancy' (e.g. Jenkins, 2011), 'incidence' (e.g. Gotelli & Chao, 2013) and 'constancy' (e.g.

121   Dengler *et al*., 2009)]. When arranged in rank order, such frequency of occurrence

122   distributions are equivalent to the RSOCs of Jenkins (2011) ('ranked species occupancy

123   curves') but constructed in the same format as SADs, i.e. as the percentage of the total taxon-

124   occurrences comprised by each taxon (Barnes, 2014b), instead of as proportions of the total

125   number of samples taken. In all cases, the basic unit of comparison was the percentage

126   relative presence of individual taxa in series of 0.0275 m^2 samples, with a minimum of 90

127   such samples or 25,000 individual animals in total from each locality, whichever was the

128   smaller. The specific South African site used in comparisons with the North Sea and

129   Queensland ones was the shoreline of the sheltered, marine Steenbok Channel in the lee of

130   Leisure Isle within the outer basin of the Knysna estuarine bay (Barnes & Ellwood, 2011b;

131   Barnes, 2013a), a site environmentally equivalent to those in the lee of Scolt Head and along

132   the lee (Rainbow Channel) coast of North Stradbroke. Comparison of sites within the

133   Knysna estuarine bay as a whole were between the significantly different local variants of

134   the seagrass fauna there identified along its long axis by Barnes & Ellwood (2012) and

135   Barnes (2013b). The basal taxon adopted was genus since no individual species occurred

136   beyond a single locality although genera did; there being no reason to believe that the types

137   of comparison undertaken here are sensitive to precise level of taxonomic resolution

138   (Chapman, 1998; Tataranni *et al*., 2009). All nomenclature, including of higher taxa, is as

139   per the World Register of Marine Species (www.marinespecies.org), assessed October 2014.

140   *IDENTIFICATION OF 'FUNCTIONAL GROUPS'*

141   There have been a number of attempts to identify the most ecologically relevant

142   properties of benthic marine species for use in estimation of functional diversity of their

143   assemblages (e.g. Gerino *et al*., 2003; Bremner *et al*., 2003; Norling *et al*., 2007). Few,

144   however, seem appropriate to intertidal seagrass faunas, not least because of the limited

145   range of ecological niche-types referred to above and because many seagrass animals appear

146   opportunistic and relatively generalist (Boström *et al*., 2006; Reed & Hovel, 2006). Most of

147   those under consideration here fall into only a few of the 23 feeding guilds recognised by

148   Macdonald *et al*. (2010), for example. Pavoine & Bonsall (2011), and in a somewhat

149   different context Törnroos *et al*. (2013), have also argued a strong general case for using

150   measures that combine information from both ecological and taxonomic diversity. The

151   limited *Zosterella* faunas under consideration here, however, do fall into a series of some 30

152   different taxonomic/ecological categories or life styles on the basis of a combination of their

153   morphology, method and location of feeding, mobility, and preferred habitat stratum within

154   seagrass beds; i.e. on features that can be expected strongly to influence relative organismal

155   performance (McGill *et al*., 2006). The simple system set out in Table 1 was therefore used

156   as a proxy for 'functional groups' in the calculation and comparison of functional diversities

157   across *Zosterella* localities.

158   Probable food sources of individual genera were taken from works such as Gambi *et*

159   *al*. (1995), Farlin *et al*. (2010), Macdonald *et al*. (2010) and the specialist literature, and it

160   was assumed that in these intertidal habitats most so-called 'detritus'-feeders are mainly

161   dependent on the living microphytobenthos within or on the surface of the sediment and on

162   the seagrass leaves (Hillebrand *et al*., 2002; Lebreton *et al*., 2011; etc.). Animals potentially

163   feeding on the same type of material but collecting it by use of contrasting techniques that

164   probably influence the precise food-species selected, e.g. feeding on phytobenthos via

165   ciliated 'tentacles', via a rasping radula, or via a pair of cutting jaws, were placed in different

166   categories (see, e.g., Aberle *et al*., 2009). No attached sessile animals were included in the

167   analyses. Nor were any large species (see De Bie *et al*., 2012): all animals were from 8 cm

168   diameter cores (five of which totalled the unit 0.0275 m^2) and therefore included the smaller

169   and most numerous members of the macrofauna that constitute the large majority of

170   invertebrate biodiversity (Albano *et al*., 2011), their dimensions being of the order of

171   smallest <1.5 mm and largest <3 cm except for the length of various long thin worms such as

172   *Lumbrineris*, *Onuphis* and some nemertines.

173   *STATISTICAL PROCEDURES*

174   The univariate and non-parametric multivariate techniques of the distance-based

175   linear modelling package (DistLM) contained in PRIMER 6.1 (PrimerE Ltd: Plymouth

176   Routines in Multivariate Ecological Research) were used to explore locality-specific relative

177   frequencies of macrofaunal functional-group occurrences. Similarities of functional-group

178   occurrences between the localities were examined using PERMANOVA, based on square-

179   root transformed data in Bray-Curtis similarity matrices, followed by *post-hoc* pair-wise tests

180   to highlight similarities. DistLM was employed to verify relationships between the functional

181   groups from each site. DistLM produces a sequential test, which assesses the variation each

182   predictor (functional group) has on its own, and a conditional test, assessing the variation

183   across all the groups (McArdle & Anderson, 2001). The most parsimonious model was

184   identified using the selection criterion R^2. The DistLM was based on the various frequencies

185   of occurrence, classified as 'other data', with 4999 permutations. Overall diversity of the

186   functional-group distributions was estimated by Hill's N_1, considered by Micheli & Halpern

187   (2005), Schleuter *et al.* (2010), etc. to be appropriate in the ecological and analytical

188   circumstances, relative functional evenness by Pielou's *J*, as recommended by Jost (2010),

189   and functional redundancy by within-functional-group evenness (Hewitt *et al*., 2008).

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RESULTS

COMPARISONS BETWEEN LOCALITIES

Distribution of the relative frequencies of occurrence of the various functional groups of Table 1 varied 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 lower-latitude localities, North Stradbroke and Knysna, were not significantly different (Pairwise PERMANOVA t = 1.02; P >0.05), but that on Scolt 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 (a) their relative occurrences and (b) 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: Scolt 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

214   orders differed even in respect of the nine most important groups of the not otherwise

215   significantly different North Stradbroke and Knysna (Spearman $R = 0.75$; $P < 0.02$). The

216   most important functional groups at the separate localities are shown in Table 2. In

217   descending order of importance, groups 4, 6 and 24 best characterised Scolt Head (DistLM

218   Pseudo-F >6.5; $P < 0.01$), 4, 2, 24, 10, 6 and 3 Knysna (DistLM Pseudo-F >10; $P < 0.001$),

219   and 2, 24, 4, 18, 21 and 10 North Stradbroke (DistLM Pseudo-F $\geq$20; $P < 0.001$). Overall at

220   the two low-latitude localities, phytobenthos feeders comprised 41-46% of the total,

221   suspension feeders 12-14%, omnivores 18-19%, predators 19-27% and others 2-3%. At the

222   higher latitude Scolt Head, basal trophic-level categories were more important

223   (phytobenthos feeders 54%; suspension feeders 23%), whilst higher trophic-levels were less

224   so (omnivores 7%; predators 16%).

225   As would be expected from the differing sizes of the available pools, the total

226   numbers of genera in each functional group varied widely from locality to locality (Fig. 2A):

227   for example, group 2 only comprised 3 genera on Scolt Head, 12 in Knysna, but 30 on North

228   Stradbroke. Excluding the tail of 'satellite' (Hanski, 1982) or 'excess rare' genera (Magurran

229   & Henderson, 2003) with relative percentage frequencies $\leq$0.1 so as to confine the data to

230   those most responsible for the general form of the relationships, however, functional groups

231   4 (6-11 genera), 6 (6-7) and 24 (5-8) were remarkably similar in component generic

232   numbers across localities (Fig. 2B). Scolt Head supported only 12 different functional

233   groups and 30 genera. The two lower-latitude localities, each supporting at least twice as

234   many functional groups, however, showed very similar ranked relative group frequency

235   distributions notwithstanding differences in the identity of the component groups concerned.

236   As would be expected from a greater value of Fisher's α or Hubbell's θ, their curves tended

237   towards the log-normal form in contrast to the more geometric nature of that of depauperate

238   cool-temperate Scolt Head, but approximating them by an exponential decline (Jenkins,

239　2011) yields a common exponent of some -0.15 (Knysna R^2 0.99; North Stradbroke R^2 0.95;

240　Fig. 3).　Further, within each of the more important functional groups represented, the rank

241　order distributions of the component genera showed similar approximately exponentially

242　decreasing forms (Fig. 4), with a mean value of the exponent of -0.20 (and with that of -0.15

243　lying within 1 standard deviation of that mean).　Functional redundancy levels within each

244　such genus-rich functional group were:　Knysna 0.71-0.95 (mean 0.81) and North

245　Stradbroke 0.70-0.85 (mean 0.78).　The genera with the largest individual relative

246　occurrences at both Knysna and North Stradbroke all (or almost all) represented different

247　functional groups:　at Knysna the nine genera with the greatest occurrences each represented

248　a different group (groups 3, 10, 4, 21, 13, 14, 6, 11, 18 in descending order of importance),

249　and at North Stradbroke the eight most widely occurring genera represented seven different

250　groups (15, 18, 12, 10, 18, 1, 13, 21), with the exception, group 18, supporting two dominant

251　microgastropod genera (i.e. *Calopia* and *Pseudoliotia* which, however, are divergent in

252　shape, belong in different families, and probably occupy rather different niches).

253　　　　　Unlike in the various soft-sediment assemblages investigated by Ellingsen et al.

254　(2007), there was a very strong relationship between abundance and frequency of occurrence

255　of the component taxa (Spearman Rank R >0.98; P <<0.0001) (R^2 >0.55 *vs* Ellingsen *et al.*'s

256　R^2 of 0.195) (Fig. 5).　As would be expected, the importance of satellite genera increased

257　with decreasing latitude:　zero at Scolt Head, 23% of the total at Knysna, and 39% at North

258　Stradbroke.　Neither those at Knysna nor at North Stradbroke, however, departed from the

259　pattern of frequency of functional groups shown by the core genera (PERMANOVA Pseudo-

260　$F = 0.5$; P >0.05) although at North Stradbroke the satellite set did include more types of

261　predatory worms and of suspension-feeding bivalves although fewer of omnivorous

262　peracaridan crustaceans.

263   *COMPARISONS WITHIN LOCALITIES*

264   Within the North Stradbroke locality, the close correspondence, though again not in

265   relative magnitude, of the dominant functional groups at the three component sites is clear

266   from Fig. 6 (PERMANOVA Pseudo-F = 0.33; P >0.05). The most parsimonius model

267   explained 98% of the variation. The 6.5 km apart Deanbilla and Capembah sites in particular

268   showed effectively identical functional N_1 diversities (16.93 and 16.98 respectively),

269   although that of the intermediately sited Goompi was somewhat larger, at 18.80. Relative

270   functional evennesses were all within the very narrow range of 0.90-0.92. Although

271   different groups were obviously dominant at different sites (Fig. 6), a DistLM sequential test

272   showing that, in descending order of importance, groups 4, 10, 18, 3, 24 and 17 explained

273   >50% of the variation, the curves of their ranked relative occurrence at each site were

274   effectively identical (Fig. 7).

275   Functional-group frequencies were not evenly distributed within any site across the

276   whole Knysna estuarine bay (PERMANOVA Pseudo-F 83-166; P<0.001) but there were no

277   significant differences between their frequencies at the various sites (pairwise

278   PERMANOVA t = 0.58-0.76; P >0.05), the most parsimonious model explaining 98% of the

279   variation. Nevertheless, there was a significant trend from high to low functional diversity

280   and a decrease in the component functional groups, both in total and in the number of local

281   dominants, from the marine outer basin into the lagoonal and brackish zones (Spearman $R \geq$-

282   0.9; P <0.04) (Fig. 8). In particular, functional groups 6 and 11 were important only in the

283   marine and lagoonal sections, 4, 10 and 13 only extended into the lower section of the

284   estuary, whilst conversely groups 21 and 24 were more dominant within the estuary. It was

285   only in the upper estuary that there was a marked change in relative functional evenness,

286   however: over the rest of the system this was in the range 0.85-0.91 but within the upper

287   estuary it fell to 0.68 consequent on the overwhelming dominance there of the group 18

288   microgastropods *Hydrobia* and "*Assiminea*" (*sensu* Miranda *et al*., 2014) comprising 35% of

289   the total genus-occurrences and 65% of the overall abundance.

290

291   **DISCUSSION**

292   Notwithstanding that they are located in different oceans across 87º of latitude and

293   152º of longitude, the three disparate sheltered marine seagrass localities all supported very

294   similar suites of macrobenthic taxa and life styles. Intertidal seagrass clearly provides a

295   standard suite of niches and a standard set of animals have evolved to fill them. Amongst

296   these, surface-feeding predatory worms (e.g. polyclads, nemertines and some eunicid and

297   nereid polychaetes), worms collecting free-living surface microphytobenthos, etc.

298   (particularly spionids but also cirratulids and fabriciids), subsurface sediment-ingesting

299   worms (particularly capitellids, orbiniids and paraonids), microphytobenthos grazing

300   gastropods (particularly truncatelloids), and infaunal suspension-feeding bivalves

301   (particularly tellinoids, cardioids and/or galeommatoids) dominated all three, whilst

302   scavenging nassariid gastropods and omnivorous peracarids such as sphaeromatoids and/or

303   apseudomorphs were also important at the two lower-latitude localities. Further, although, in

304   those lower latitude localities at least, some eight genera comprised each dominant

305   functional group, most genera were rare such that a total of only some 21-26 had an index of

306   numerical importance (Barnes, 2014b) ≥1%. This was also evidenced by the most

307   widespread genera at Knysna and North Stradbroke each representing a different functional

308   group. The frequency of occurrence distributions within each dominant group mirrored

309   those of the assemblage as a whole. In essence, the ranked relative occurrence distributions

310 of component taxa (Barnes, 2014a) and of component functional groups (this paper) were of

311 similar form.

312   As argued by Bremner *et al*. (2006) and by Frid *et al*. (2008), analysis of the relative

313 importance of their various functional roles proved useful for identifying whether

314 assemblages in similar habitats but different geographical locations are constructed, and

315 hence presumably operate ecologically, in the same manner. It showed the South African

316 and Queensland seagrass beds to have evolved an almost identical overall N_1 functional

317 diversity and functional structure in terms of relative occurrences (and of relative

318 abundances), and all three localities to have very similar frequency of functional group

319 occurrence distributions and relative evennesses of those functional groups. Nevertheless, it

320 was evident that the relative importance of the individual shared dominant groups was

321 significantly different across localities, including at the otherwise similar Knysna and North

322 Stradbroke, and even varied across sites within the latter locality: the details varied from

323 place to place without changing the overall pattern of construction. The single most

324 important group at the South African site was surface-deposit collecting (spionid and

325 cirratulid) polychaetes, whereas in Queensland overall it was microphytobenthos-grazing

326 microgastropods; indeed, such microgastropods were effectively absent from the specific

327 South African site investigated by Barnes (2013a), although they were the dominant

328 components at other nearby sites (Barnes & Barnes, 2014a). Within the Queensland locality,

329 the single most important group also differed between the three component sites: surface

330 deposit-feeding worms at one, microphytobenthos-grazing microgastropods at another, and

331 omnivorous peracaridan crustaceans at the third. Cool-temperate Scolt Head, with only 30%

332 of the genera and 40% of the functional groups present at warm-temperate Knysna, and 16%

333 and 50%, respectively, of those on subtropical North Stradbroke, maintained a lower

334 functional diversity (only 45%) than that at the two lower latitude localities as would be

335 expected.

336 Those individual functional groups that each supported several genera displayed

337 moderate to high levels of within-group functional evenness, and if this does equate with

338 relatively high levels of functional redundancy (and if such redundancy is a valid concept;

339 Loreau, 2004), they should also show considerable resilience. Very little is known, however,

340 about for example the precise diets of seagrass macrofauna, and the extent to which they

341 overlap or are complementary in species within the same functional group (Duffy *et al*.,

342 2001; Jaschinski *et al*., 2009). The increasing number of genera within functional groups

343 such as that of surface-feeding predatory worms along the Scolt Head – Knysna – North

344 Stradbroke latitudinal and climatic-zone series could reflect, not increasing functional

345 redundancy, but increasing diversity of prey sources supporting an increasingly diverse set of

346 consumers. These (apparently) high redundancy levels from seagrass systems contrast with

347 those found by Micheli & Halpern (2005) from hard substrata, although values will clearly

348 vary across studies dependent on the inclusivity of the chosen functional groups.

349 Therefore at each of the three marine localities investigated to date, (a) the number of

350 macrofaunal species per unit 0.0275 m^2 area within the intertidal seagrass beds has proved to

351 be uniform across distances of up to 6.5 km, (b) its magnitude has been shown to be similar,

352 particularly in respect of those at Knysna and North Stradbroke, notwithstanding large

353 differences in the sizes of the local species pools (Barnes, 2013a, 2014a), and (c) the form of

354 the frequency of relative species occurrence distributions are closely similar (Barnes, 2014a).

355 In this paper, close similarity, again especially between Knysna and North Stradbroke, has

356 been demonstrated in (d) the subset of functional groups that dominated the macrofaunal

357 assemblage occurrences, (e) the pattern of the ranked relative occurrence distributions of

358   those groups, and (f) the overall functional diversities and relative evennesses of the

359   assemblages. Features (a)-(c) above have already been shown to be linked causally (Barnes

360   & Barnes, 2014b) and the close relationship between those and (d)-(f), i.e. between the

361   nature and number of possible macrobenthic functional roles and the relative occurrence

362   distributions of the component taxa filling those roles (and hence the total numbers of taxa

363   supported by unit area), indicates a wider causal network. Granted, however, that the precise

364   members of the limited series of functional groups that dominated individual localities and

365   sites were not the same, the relationship is clearly not a straight-forward one.

366   Two of the common features stand out as being likely to be critical to the evolution

367   (both generation and persistence) of this pattern. First, that despite their compositional

368   differences, the rank-order distributions of the dominant functional groups, and within them

369   of the component genera, at both Knysna and North Stradbroke fell on effectively the same

370   curve, and the equivalent distribution at Scolt Head was also essentially similar if allowance

371   is made for its high-latitude poverty in genera and functional groups steepening the curves

372   (see, e.g., Hubbell, 1997: Fig. 4). Secondly, that the eight or nine genera that dominated the

373   relative occurrence distributions at each site were representative of as many, or almost as

374   many, different functional groups, i.e. the common genera showed no functional redundancy

375   at the inter-group level. The detailed circumstances bringing about these states in a system

376   otherwise lacking significant structural interactions between species may not yet be clear, but

377   in general the intertidal *Zosterella* macrobenthos appears to comprise a simple system that is

378   capable of supporting up to 8 or 9 different major functional units as well as maybe up to

379   twice as many minor ones, although any one site is likely to be relatively conducive only to

380   some of these in a rankable order of potential favourability, presumably dependent on

381   environmental and structural features of each local area (Matias *et al*., 2007). Local regimes

382   of current speed, light penetration to the sea bed, and even the potential success rates of

383   different types of nektonic predator could all influence the relative importance of, for

384   example, suspension versus phytobenthic feeders, shelled versus unshelled body plans, etc.

385   Most research into marine soft-sediment functional diversity and assemblage

386   structure has been devoted to changes in diversity patterns in response to major changes in

387   habitat type, including those induced anthropogenically (e.g. Bremner *et al*., 2003, 2006;

388   Bremner, 2008; Afli *et al*., 2008; Aloui-Bejaoui & Afli, 2012). Virtually all studies of

389   marine assemblage structure have also been concerned with patterns of relative component

390   numbers (i.e. density) (Hughes, 1984; Hubbell, 1997; Magurran & Henderson, 2003;

391   Törnroos *et al*., 2013; etc.) not with those of relative component spatial distribution (i.e.

392   occurrence) (Jenkins, 2011; Barnes, 2014b). Nevertheless, under many — probably most —

393   circumstances (including here assessment of the relative importance of the various functional

394   groups on the two bases), abundance and distribution are clearly interdependent and closely

395   related phenomena (Hanski, 1982), and the present results from the deterministically-

396   structured estuarine assemblages at Knysna would seem to conform to the patterns seen in

397   relative importance from other marine systems elsewhere (e.g. Scrosati *et al*., 2011). Less

398   research has concerned similarity of overall pattern across contrasting systems, although

399   Hewitt *et al*. (2008), studying soft-sediment macrofaunas in two marine bays in New

400   Zealand, 500 km apart and supporting different faunas, have commented on the similar

401   representation of functional traits across localities and the relative unimportance of the size

402   of local pools of taxa. Hewitt *et al*.'s (2008) results show a number of parallels with the

403   present study. They also found differences between their sites to be mainly a matter of

404   relative importance of different shared elements, showed marked differences of detail both

405   within and between sites, and found high within-functional-group values of evenness. Why

406   it is that assemblages of different functional groups in different areas, and even assemblages

407   of genera within single functional groups, should all show such similar ranked relative

408 distributions, regardless of the specific nature of the component groups, is not obvious. This

409 could be considered unexpected in that it occurs in a system lacking potential niche-related

410 structural forces like interspecific competition, if indeed interspecific competition can be

411 described as 'structuring' (Loreau & de Mazancourt, 2013), but Hubbell's (1997, 2001)

412 neutral model shows that apparent structure can be achieved stochastically, and that dispersal

413 within larger metacommunities can stabilise local and regional assemblage structure over

414 wide areas without any assumptions of deterministic niche assembly. Neutral models may

415 also be particularly relevant to seagrass assemblages because of the possibility of their being

416 especially associated with suites of generalist species (Pandit *et al.*, 2009).

417

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423

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612

LEGENDS FOR FIGURES

613
614

615   1.   A, The importance (relative frequency of occurrence of the contained genera) of the

616   different functional groups as defined in Table 1 in intertidal *Zosterella* beds on Scolt

617   Head Island in the North Sea (UK), along the Steenbok Channel coast of Leisure Isle in

618   the marine basin of the Knysna estuarine bay (RSA), and along the Rainbow Channel

619   coast of North Stradbroke Island, Moreton Bay (Australia). B, General correspondence

620   between the dominant functional groups as assessed (i) by relative occurrence of their

621   contained genera and (ii) by relative abundance of those genera, as exemplified by the

622   North Stradbroke locality.

623   2.   The numbers of genera represented in each functional group across the three

624   localities of Fig. 1A: A, total numbers; B, numbers of core genera (those with percentage

625   frequencies >0.1).

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

627   localities.

628   4.   Ranked relative occurrence distributions of the component genera comprising each of

629   the four functional groups that supported the largest intra-group generic diversity (groups

630   2, 4, 10 and 24; see Fig. 2) at Knysna (open circles) and North Stradbroke (filled circles).

631   5.   Relationship between percentage relative abundance and percentage relative

632   occurrence amongst the genera at the two most genera-rich localities, Knysna and North

633   Stradbroke.

634   6.   Percentage frequency of occurrence of the different functional groups at three sites

635   within the North Stradbroke locality, distributed over a distance of some 6.5 km. Note the

636   common peaks of groups 4, 6, 10, 12, 15, 18, 21 and 24, but their differing relative

637   magnitudes.

638   7.   Ranked relative occurrence distributions of the various functional groups present at

639   the three component sites of the North Stradbroke locality.

640   8.   Response of N_1 functional diversity and of both the total number of component

641   functional groups and the number of those that dominated the assemblages (i.e. comprised

642   >4% of the total) to the long-axis gradient of the Knysna estuarine system, as exemplified

643   by the upstream chain of five stations, the sites within each of which supported a

644   significantly-different macrobenthic assemblage, as identified and as numbered in Barnes

645   (2013b: Fig. 3). [The Steenbok Channel locality, used to represent Knysna in comparisons

646   with Scolt Head and North Stradbroke, forms part of station 2.]

647

648   **Table 1**. Macrofaunal life-style categories within *Zosterella* beds to which the individual

649   genera were allocated as a proxy for functional groups in the estimation of assemblage

650   functional diversity.

651

652   <u>Group No.</u>   <u>Diagnosis of group</u>

653

654   1   Subsurface-feeding, free-living, predatory worms (some nemertines & some

655   errant polychaetes e.g. nephtyids, glycerids & goniadids)

656   2   Surface-feeding predatory worms (e.g. polyclads, many nemertines & errant

657   polychaetes)

658   3   Surface-feeding, tubicolous or burrow-dwelling, omnivorous worms (e.g.

659   errant polychaetes such as many nereids)

660   4   Deposit-feeding, tubicolous or burrow-dwelling worms with ciliated feeding

661   palps, tentacles, etc., that collect material from the sediment surface (e.g. most

662   canalipalpatan polychaetes, sipunculans & echiurans)

663   5   Suspension-feeding, infaunal, tubicolous worms (e.g. sabellid & chaetopterid

664   polychaetes)

665   6   Subsurface, free-living or burrow-dwelling, microbe-, protist- or sediment-

666   ingesting worms (e.g. most scolecidan polychaetes & tubificine oligochaetes)

667   7   Subsurface, free-living, omnivorous worms (e.g. errant polychaetes such as

668   lumbrinerids)

669   8   Mobile, suspension-feeding ostracod crustaceans

670   9   Sedentary and often tubicolous, suspension-feeding peracaridan crustaceans

671   (e.g. many corophiideans)

672	10	Omnivorous, free-living peracaridan crustaceans (e.g. apseudomorphs and
673		sphaeromatoids)
674	11	Algivorous, free-living or occasionally 'nest'-building peracaridan crustaceans
675		(e.g. many ampithoeids & idoteids)
676	12	Predatory, free-living peracaridan crustaceans (e.g. anthuroids &
677		phoxocephaloids), consuming small (often meiofaunal) prey
678	13	Large, free-living, predatory decapod crustaceans (e.g. portunioids) taking
679		macrofaunal prey
680	14	Microphytobenthically-feeding, burrow-dwelling decapod crustaceans (e.g.
681		many ocypodioids & axiideans)
682	15	Omnivorous, free-living decapod crustaceans (e.g. many paguroids)
683	16	Suspension-feeding, burrow-dwelling decapod crustaceans (e.g. gebioids)
684	17	Periphyton- and leaf-browsing, free-living gastropod molluscs (e.g.
685		neritimorphs, trochoids & litiopids)
686	18	Microphytobenthos-grazing, free-living microgastropod molluscs (e.g.
687		truncatelloids & rissooids)
688	19	Larger, deposit-feeding, free-living gastropod molluscs (e.g. batillariids &
689		littorinoids)
690	20	Sedentary, infaunal, suspension-feeding gastropod molluscs (e.g. turritellids)
691	21	Predatory/scavenging, free-living molluscs (e.g. most neogastropods,
692		epitonioids, nudibranchs)
693	22	Ectoparasitic gastropod molluscs (e.g. pyramidelloids)
694	23	Algivorous, free-living gastropod molluscs (e.g. saccoglossans &
695		haminoeoids)

696	24	Sedentary, infaunal, burrow-dwelling or buried, suspension-feeding bivalves
697		(most bivalve molluscs & lingulatan brachiopods)
698	25	Carnivorous, epifaunal, free-living echinoderms (e.g. asterinid asteroids)
699	26	Burrowing, deposit-feeding echinoderms (e.g. apodidan holothurians)
700	27	Deposit-feeding, infaunal, free-living bivalves (e.g. protobranchs)
701	28	Free-living, sedentary animals dependent in whole or part on chemosynthetic
702		symbionts (e.g. solemyoid & lucinoid bivalves, see, e.g., van der Heide *et al*.
703		2012)
704	29	Suspension-feeding, free-living echinoderms (e.g. many ophiuroids)
705	30	Algal-grazing, free-living echinoderms (e.g. many echinidian echinoids)
706		

707   **Table 2**. Variation in the nine most important functional groups (numbered as in Table 1)

708   across the three localities in terms of relative frequency of occurrence (percentage of the total

709   genus-occurrences within each group being given in parentheses). Note that groups 4, 6 and

710   18 appear in the top four at all three localities.

711

712 Rank	Scolt Head	Knysna	North Stradbroke
713 1	24 (22.1%)	4 (14.8%)	18 (10.9%)
714 2	6 (20%)	6 (11.8%)	4 (10.5%)
715 3	4 (20%)	10 (9.8%)	10 (9.1%)
716 4	18 (8.4%)	18 (7.6%)	6 (6.5%)
717 5	2 (7.4%)	24 (7.3%)	21 (6.2%)
718 6	13 (6.8%)	3 (6.2%)	2 (6.0%)
719 7	19 (5.3%)	21 (4.5%)	15 (6.0%)
720 8	3 (4.7%)	11 (4.4%)	1 (5.9%)
721 9	7 (2.6%)	14 (4.1%)	24 (5.8%)

722

723   Fig. 1

A

Percentage
frequency
of genera

North Sea, UK
Indian Ocean, RSA
Pacific Ocean, Aus

Functional group

B

Percentage
frequency
of genera

Abundance
Occurrence
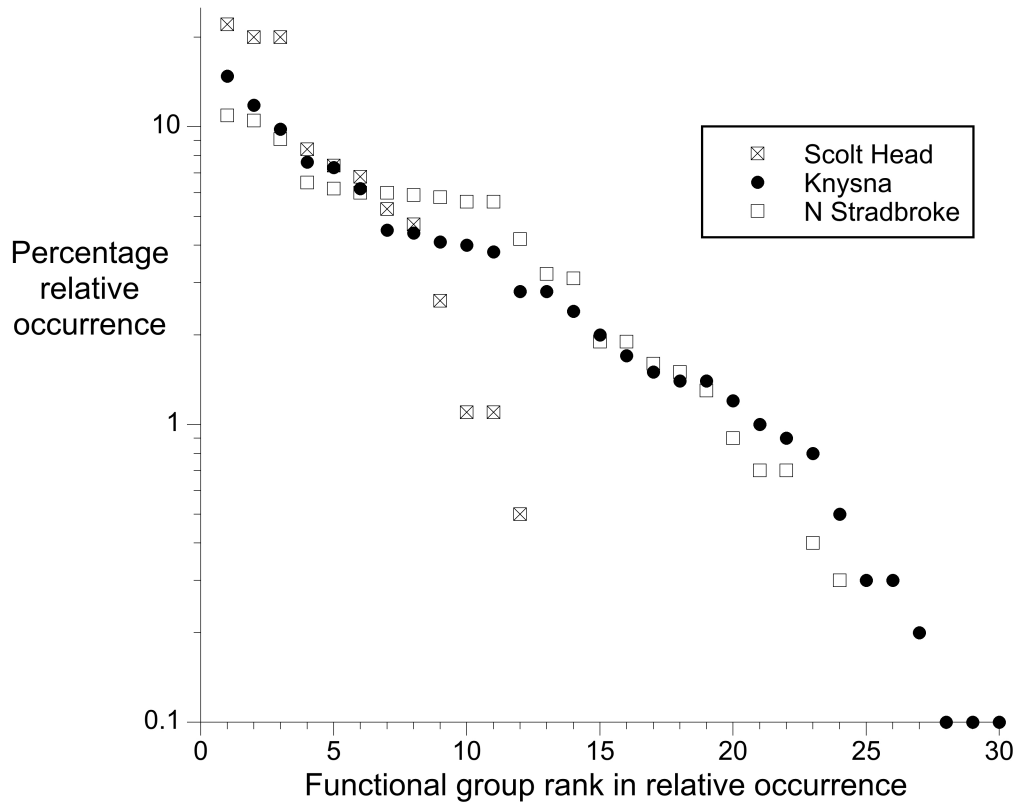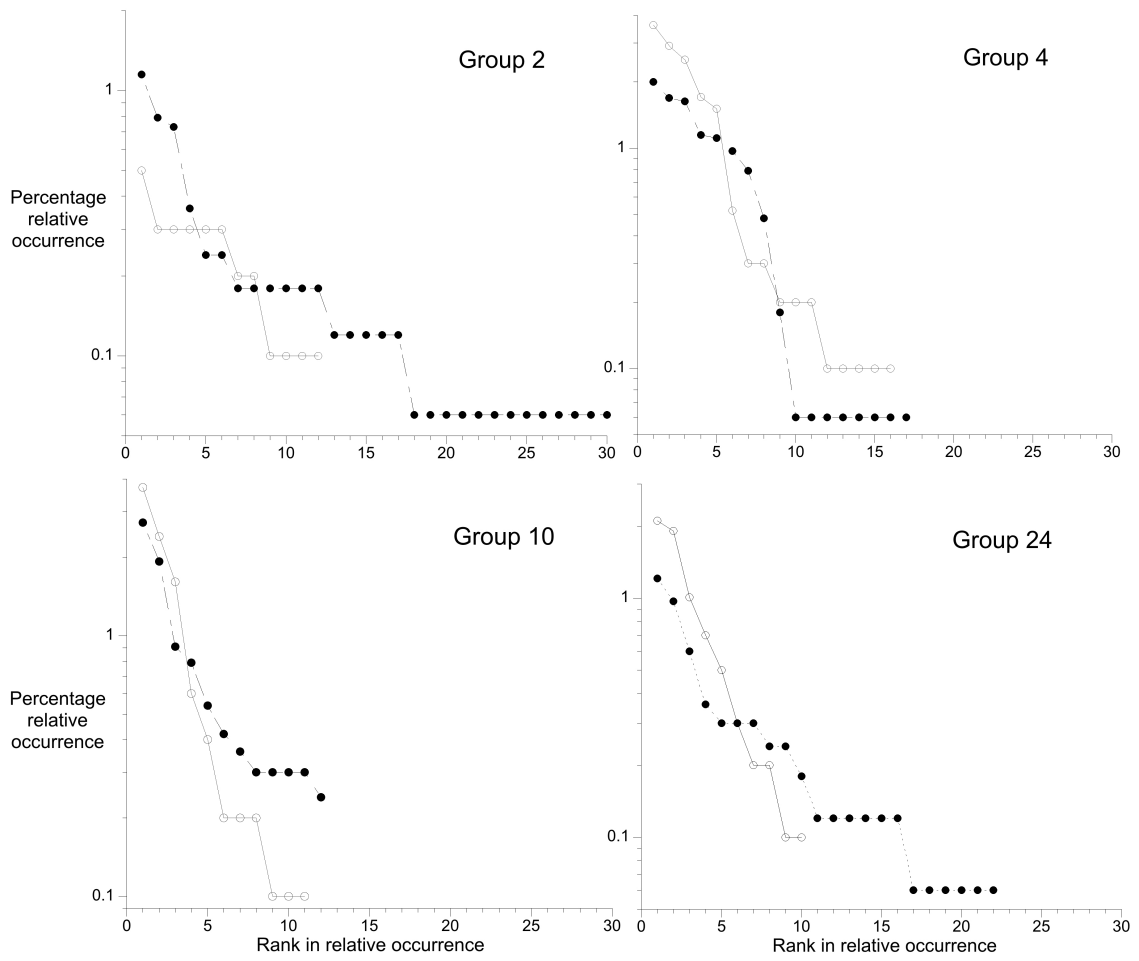
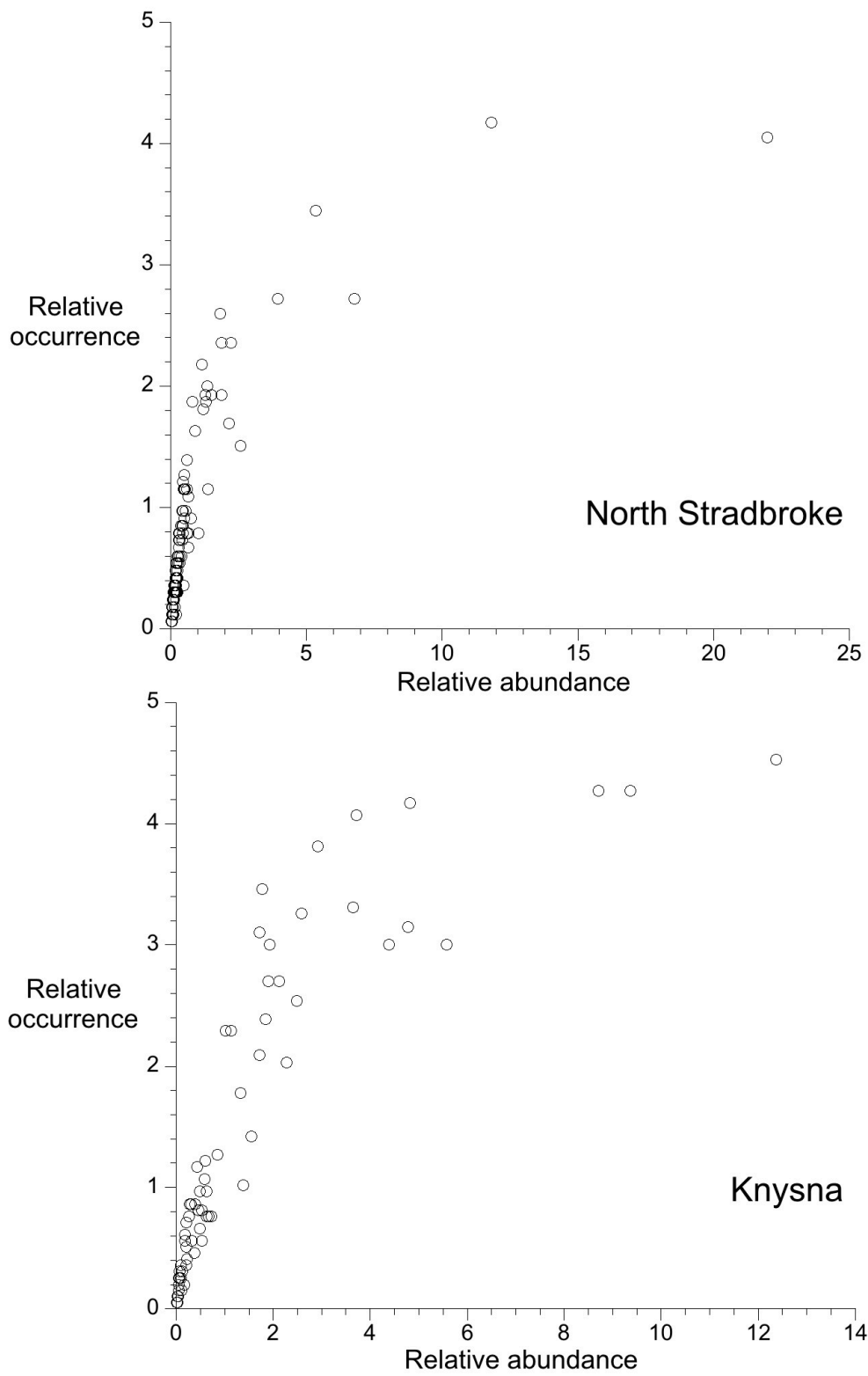Functional group

724

725

726   Fig. 2

A

B
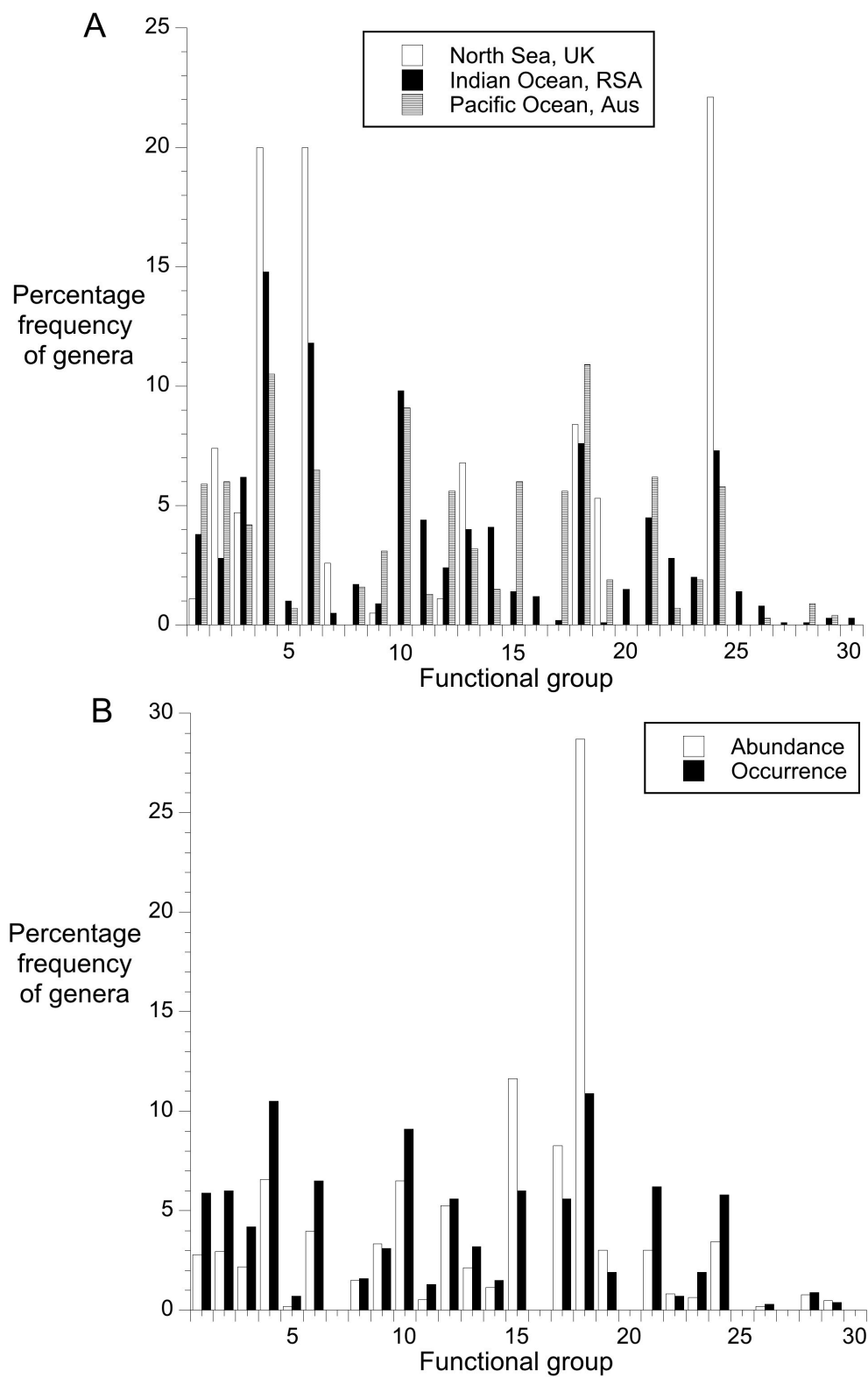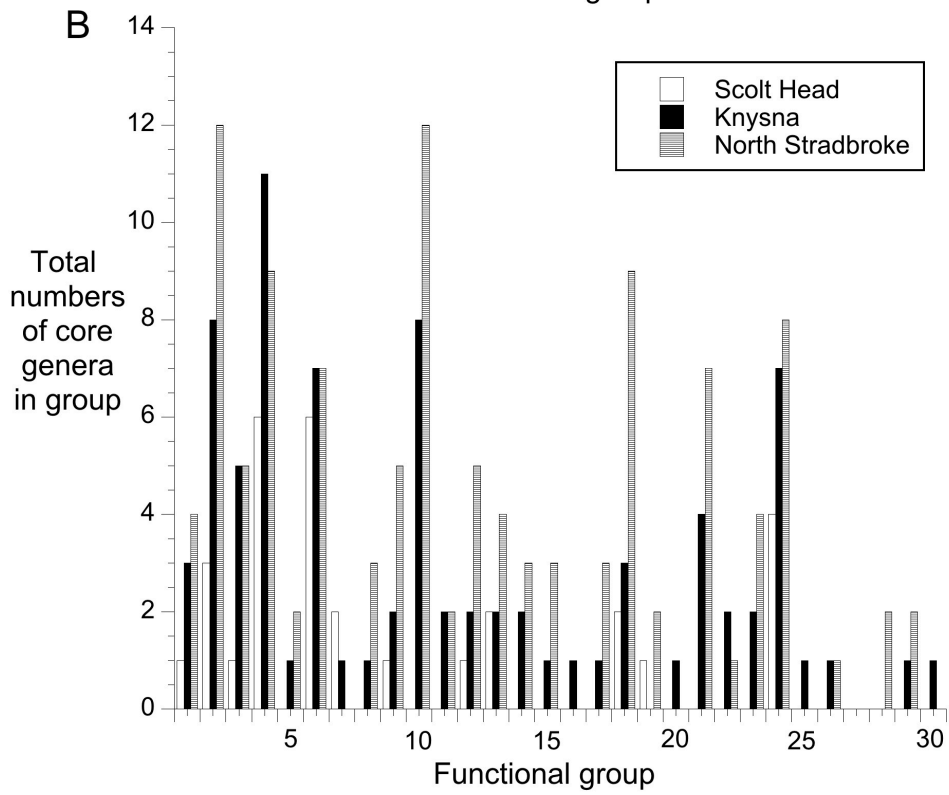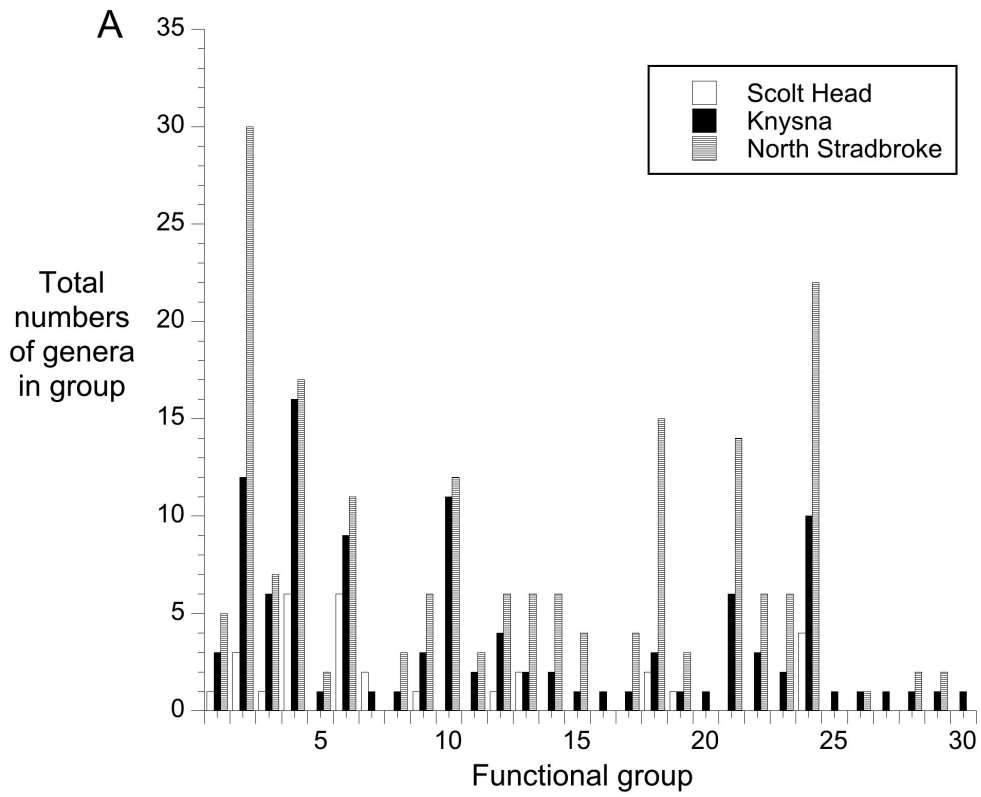
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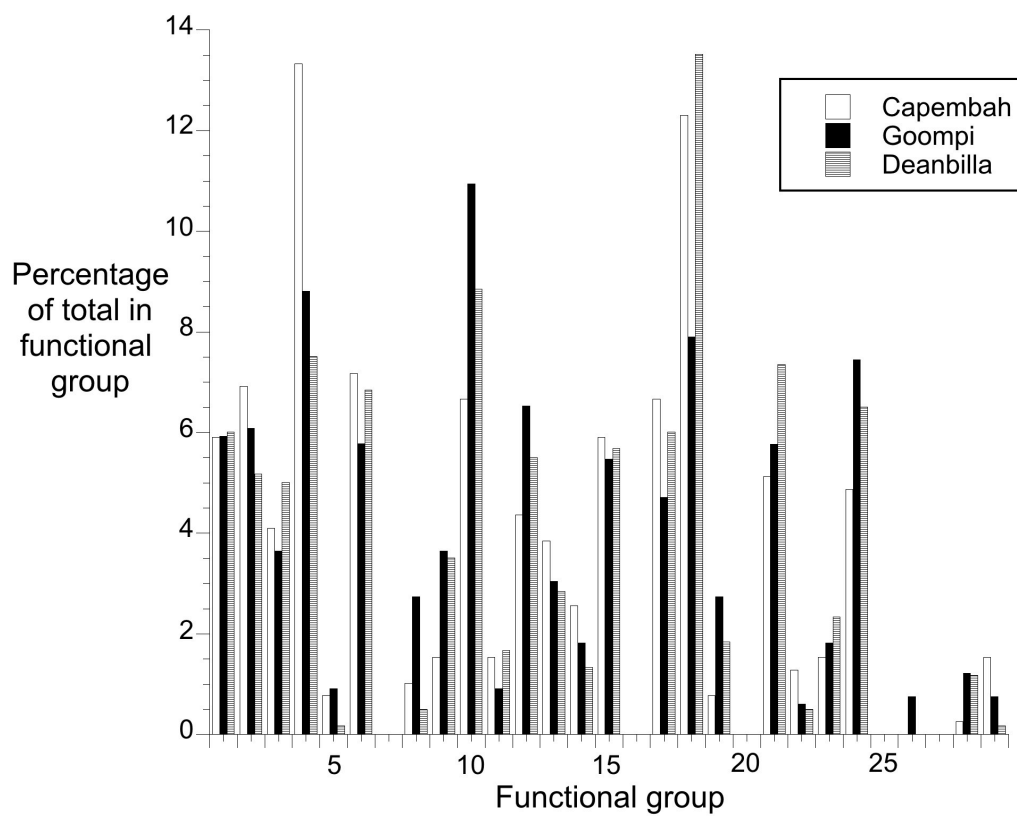
728

729   Fig. 3

730

731

732   Fig. 4

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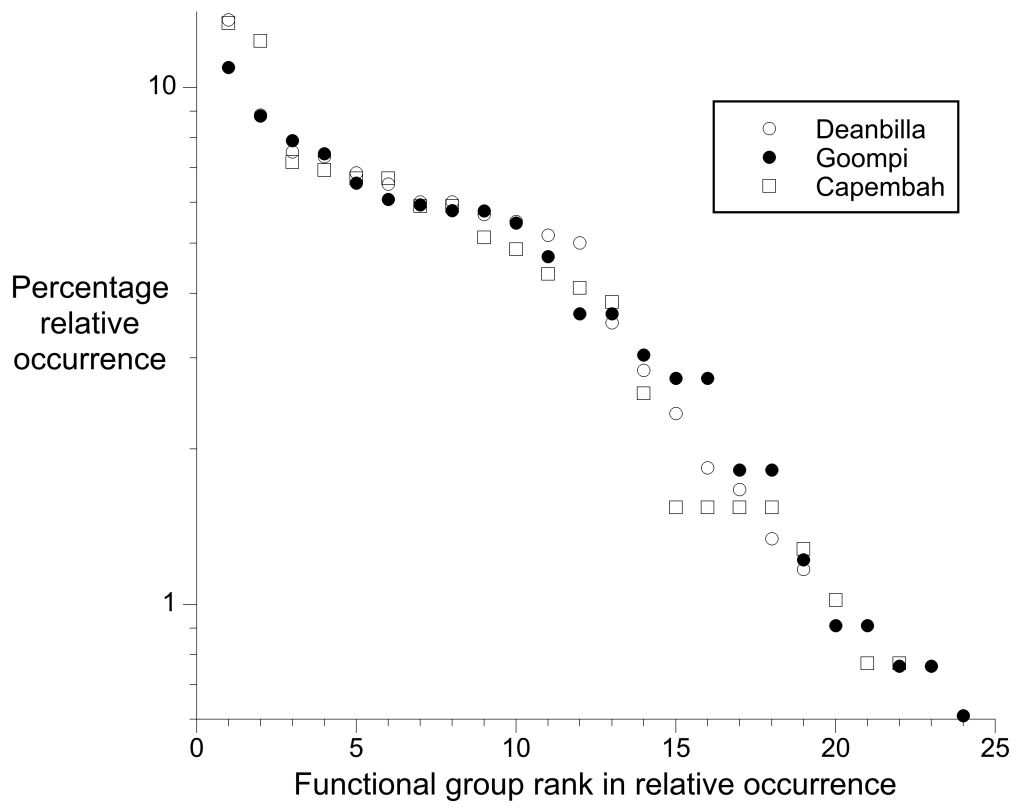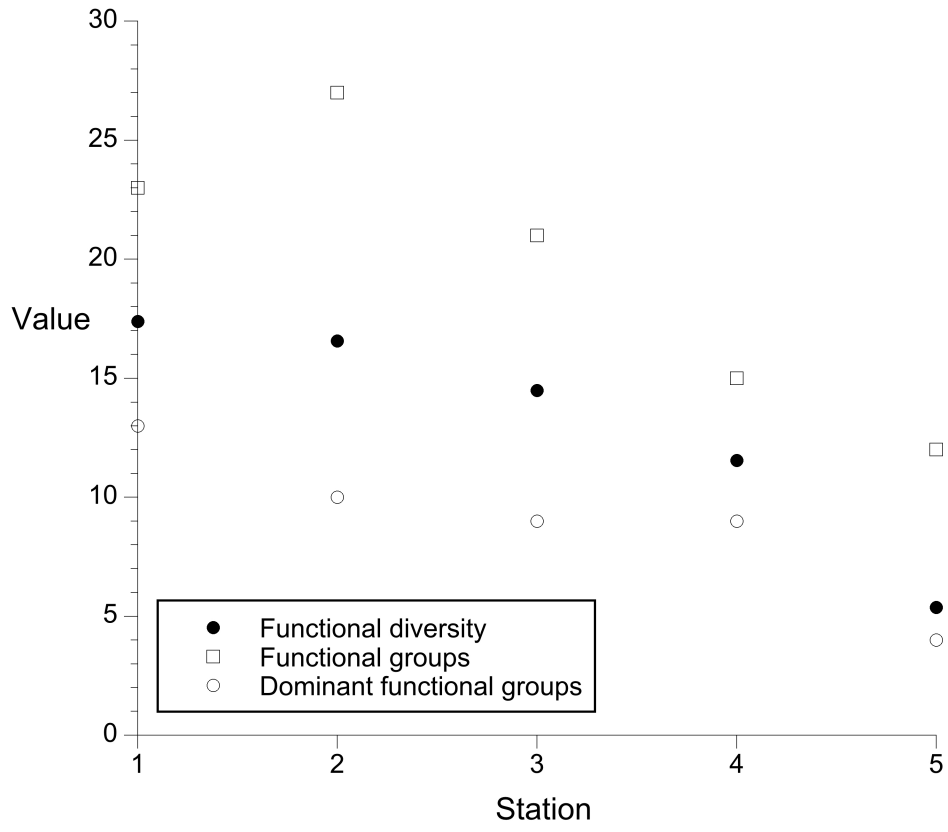734

735   Fig. 5

North Stradbroke

Knysna

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738   Fig. 6

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740

741   Fig. 7

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744   Fig. 8

745