PUBLISHED IN *Marine and Freshwater Research* -

http://dx.doi.org/10.1071/MF14311

Diversity and abundance of epibiota on invasive and native estuarine gastropods depend on substratum and salinity

Jakob Thyrring[1*], Mads Solgaard Thomsen[2,3], Ane Kirstine Brunbjerg[4], Thomas Wernberg[3]

[1]Arctic Research Centre, Department of Bioscience, Aarhus University, C. F. Møllers Allé 8, building 1110, DK-8000 Aarhus C, Denmark

[2]Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

[3]UWA Oceans Institute and School of Plant Biology, University of Western Australia, Hackett Drive, Crawley 6009 WA, Australia

[4]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom

*Corresponding author: email: thyrring@bios.au.dk, phone: +45 8715 6697

Keywords

Batillaria, biodiversity, epibiosis, fouling, *Gracilaria,* invasive species

Running head

Diversity and abundance of epibiota on gastropods

Abstract

Epibiosis is a common life form in estuarine ecosystems, where shell structures provide important attachment substrate for sessile species. Many studies have quantified variation in epibiota communities, but few studies have related this variability to multiple concurrent environmental factors. In this study, we determined the relative importance of salinity, depth, wave exposure, habitat and 'shell type' (shell type combined species, size, morphology and mobility traits) for community structure of sessile epibiota on gastropods in the Swan River Estuary, Western Australia. We quantified distribution, biofouling patterns, and detailed epibiota community structures on dominant gastropod species in the estuary - the native *Nassarius pauperatus* and *Bedeva paiva* and the invasive *Batillaria australis*. The invasive *Batillaria* was much more abundant, and more often biofouled, than any of the native species, thereby supporting orders of magnitude more epibiota in the estuary. Generalized linear models were used to partition variation in richness and abundance of epibiota among the above listed environmental factors. The five factors accounted for 3-34% of the total deviance explained in these models, with shell type and salinity being the only significant factors in nine of 14 models. These results highlight (1) that a single invasive species can dramatically alter epibiota communities on a large system-wide scale, (2) an overwhelming importance of shell type and salinity in explaining estuarine epibiota communities, and (3) that additional environmental factors need to be included in future studies to provide better predictive models of distribution for epibiota communities.

1. Introduction

Benthic life is prolific in estuarine ecosystems, where abiotic and biotic hard surfaces are used as substratum by a variety of sessile species competing for space (Anderson and Underwood 1994; Harder 2009; Vasconcelos *et al.* 2007; Wahl 1989). Epibiosis (life on another living organism) is a direct consequence of this competition for space, and settlement and growth of epibiota species on other organisms (the 'basibiont' or 'host') is widespread in both intertidal and subtidal habitats (Creed 2000; Davis and White 1994; Wahl and Mark 1999).

Research has shown that the distribution, abundance and composition of epibiota species depend on the size and behaviour (Becker and Wahl 1996; Creed 2000; Gribben *et al.* 2009; Wernberg *et al.* 2010), species identity and shell morphology (Sandford 2003; Thyrring *et al.* 2013), and anti-fouling mechanisms (Wahl 1989; Wahl *et al.* 2010) of the host. Additionally, it has been shown that epibiota communities can change seasonally (Davis and White 1994; Sandford 2003) and are affected by interspecific competition between solitary and colonial species (Jackson 1977), external grazing pressure (Buschbaum 2000) and various habitat characteristics (e.g. tidal zones) (Bell 2005; Mclean 1983). Many factors associated with the host and the external abiotic and biotic environment are therefore likely to influence epibiota in estuaries, but most studies have only focused on one or a few factors at a time (see above references). Consequently, there is little understanding of the relative importance of individual factors influencing epibiotic community structure.

Estuaries are ecotones between marine and freshwater habitats. In estuaries, gradients in salinity, light, temperature hydrodynamic forces and physico-chemical conditions vary at small and large spatio-temporal scales. In general, such fluctuating environments restrict species richness (Mclusky and Elliott 2004). Estuaries are dominated by soft sediments, and hard substrates (suitable for colonization by sessile organisms) are often limited to mollusc

69 shells (Creed 2000; Olabarria 2000). Epibiosis may therefore be a particularly important
70 estuarine process, for example, compared to rocky reefs, where epibiota can also occupy
71 abiotic surfaces (e.g., shells in estuaries can facilitate entire sessile communities that would
72 otherwise be non-existent or very rare) (Harder 2009; Knott *et al.* 2004).
73 The Swan River Estuary is the largest estuary in Western Australia (Fig. 1) and is, like other
74 estuaries, characterized by strong environmental gradients (Brearley 2005). The Swan River
75 Estuary is therefore a good model system to study the relative importance of multiple
76 environmental factors on epibiotic community structures. Seagrass beds, dominated by the
77 small stress-resistant and fast growing species, *Halophila ovalis*, are widely distributed in the
78 otherwise sandy and muddy sediments (Brearley 2005). The non-indigenous invasive
79 gastropod *Batillaria australis* is, together with two native gastropods (*Nassarius pauperatus*
80 and *Bedeva paiva*) abundant throughout most of the Swan River Estuary, providing the vast
81 majority of shell substrates available for colonization by sessile epibiota (Thomsen *et al.*
82 2010b).
83 Our objective was to characterize epibiota communities on seven shell types of various sizes
84 (cf. Table 1) with four environmental conditions, including habitat types (seagrass vs.
85 mudflat), water depth, salinity and wave exposure. More specifically, we hypothesized that
86 epibiota communities would be richer and more abundant (i) on large shells with more space
87 and time for colonization (compared to small shells), (ii) on 'live/moving' shells that are more
88 likely to remain at the sediment surface (compared to dead shells), (iii) near the mouth of the
89 Swan River Estuary where salinity stress is smallest (compared to upstream sites), (iv) at
90 shallow depth with more light and reduced risk of becoming buried by sediments (compared
91 to deep sites), (v) at protected sites with lesser risk of epibiota being dislodged (compared to
92 exposed sites) and (vi) in seagrass beds that also support an epibiota community (compared to

93 'barren' mudflats). Furthermore, partitioning variation in epibiota community structure based
94 on their host shell type and the external environment, within a single analytical framework,
95 allowed us to rank test factors according their relative importance.
96

97 **2. Materials and Methods**
98
99 *2.1 Field sampling.*
100 All gastropod shells (*Batillaria australis, Nassarius pauperatus, Bedeva paiva)* were
101 collected in late austral spring and early summer, between October and early December 2011
102 in the Swan River Estuary, Perth, Western Australia (31° 59' 30.96"S, 115° 48' 59.82"E; Fig.
103 1).
104
105 *2.1.1 Shell size, density and fouling*.
106 We quantified size-structures, densities, and degree of fouling on shells of the three gastropod
107 species from three quadrats (0.058 m^2) haphazardly placed within each of nine sites (Fig. 1).
108 These samples were only collected from seagrass beds because here the three gastropod
109 species were found together in much higher densities compared to adjacent mudflats
110 (Thomsen *et al.* 2010b).
111
112 *2.1.2 Epibiota.*
113 We quantified epibiota communities on 3,226 gastropod shells collected from 13 sites (each
114 site ~ 150 × 150 m) distributed throughout the lower estuary (Fig. 1). *B. australis* shells were
115 divided into five types commonly found in the Swan River Estuary (Table 1). At each site
116 shells were collected haphazardly from two habitats (seagrass beds vs. mudflats, but one site
117 did not have a seagrass bed) and two different depths (ca. 0.5 vs. 1.5 meter). Most shell types

118 were found at most sites, in seagrass beds and sediments, and in shallow and deep waters.
119 However, *B. australis* recruits were only found at site 1, 2, 4 and 6 (see Fig. 1). Four or five
120 sites were sampled within each of three salinity regions, based on annual minimum salinities
121 obtained from the Swan River Trust (http://www.swanrivertrust.wa.gov.au): *Inner estuary*
122 (1 ‰), *Central estuary* (5 ‰) and *Outer estuary* (30 ‰). Within each salinity region, site-
123 specific wave exposure was calculated as 'Effective Fetch' (Ruuskanen *et al.* 1999) based on
124 15 distance measurements from the site centre to the opposite shore. Measurements were
125 made on a Swan River Estuary chart in scale 1:25,000. The site-specific wave exposure
126 ranged from fully protected (effective fetch = 0) to highly exposed (effective fetch = 5)
127 (online supplementary S1).
128
129 *2.2 Laboratory procedures.*
130 All shells were carefully brought ashore and to the laboratory to ensure attached species did
131 not break off.
132
133 *2.2.1 Shell size, density and fouling*.
134 We measured shell length and width to nearest mm with digital callipers of the first 50 shells
135 of each adult species encountered in the quadrate. Length and width was converted to a
136 univariate shell dimension using Appleton's (1980) formula: Shell Dimension = Log shell
137 height x Log shell width. We subsequently counted all the randomly collected gastropods and
138 quantified the degree of biofouling - classifying a shell as 'fouled' if a least one epibiota
139 species was found attached.
140
141 *2.2.2 Epibiota*.

142 Attached sessile epibiota were identified and quantified under a dissection microscope at 40x
143 magnification. We estimated percentage cover of encrusting species per shell (e.g. *Ralfsia* sp.,
144 *Membranipora* sp.) and counted the number of foliose algae (e.g. *Gracilaria comosa*) and
145 solitary invertebrates (e.g. *Pomatoceros* sp.). The length and width of each shell was
146 measured and converted to shell dimension as described in the previous paragraph.
147
148 *2.3 Statistical analyses.*
149 *2.3.1 Shell size, density and fouling*.
150 One-way ANOVA was used to test if sizes differed between the three gastropod species and
151 two-way ANOVA tested if shell density and degree of fouling varied between species and
152 salinity regions. Homogeneity of variances was evaluated with Barletts and Brown-Forsythe
153 tests and data were square-root transformed when necessary to meet assumptions of
154 homogeneity of variances and normal distribution. Finally, Tukey HSD test was used to
155 compare significant treatment effects ($p < 0.05$).
156
157 *2.3.2 Epibiota*.

158 Generalized linear models (GLM) were used to model correlations between the explanatory
159 factors and taxonomic richness and abundance of all epibiota species combined, encrusting
160 species, foliose algae, and solitary invertebrates, and of the abundances of the most common
161 epibiota taxa. Prior to analysis we tested if shell-sizes (within each of the 7 shell-types)
162 differed between habitats, salinity, water depth and wave exposure (using 3-factorial
163 ANOVA's with wave exposure as co-variate). These tests showed that sizes (of a shell-type)
164 were statistically similar between environments (online supplementary S2). Data exploration
165 was then carried out following the protocol of Zuur *et al.* (2010). Relationships between co-

166 variates were assessed using boxplots and Pearson correlation coefficients (Zuur *et al.* 2010).
167 The two variables 'shell type' and 'shell size' showed a high level of collinearity (r = 0.79),
168 and we therefore excluded shell size from further analysis to eliminate correlation between
169 co-variates. Cook's plot and boxplots were used to identify outliers and to investigate
170 relationships between variables; as a result we eliminated one extreme value of abundance of
171 *Gracilaria comosa* because it would otherwise have made pattern detection in the data more
172 difficult (Quinn and Keough 2002). We found no indication of zero-inflation or over-
173 dispersion for richness data, which were therefore analyzed using GLM with Poisson
174 distributions. By contrasts, abundance data was characterized by over-dispersion (without
175 zero-inflation) and was therefore analyzed using GLM with negative binomial distributions
176 (Hilbe 2011). Shell type, salinity, wave exposure, habitat and water depth were included as
177 explanatory variables in the full models, and the models were reduced to final best-fit-models
178 using Akaike Information Criterion (AIC) with Δ AIC <2 (Burnham and Anderson 2002).

179

180 **3. Results**
181
182 *3.1 Shell size, density and fouling*.

183 The average shell surface area of the non-indigenous *Batillaria australis* was 7.25 ± 0.33 cm^2
184 (n=50), and significantly larger than the native gastropods *Bedeva paiva* (5.07 ± 0.14 cm^2,
185 n=50) and *Nassarius burchardi* (1.06 ± 0.04 cm^2, n=50) (ANOVA: $F_{2,147} = 597.8$; $p < 0.001$;
186 Online supplementary S3). *B. australis* shells were also more abundant (all sub-types
187 combined) with a maximum density of 1,767 shells m^{-2} found in the Outer estuary (ANOVA:
188 $F_{2,78} = 153.2$; $p < 0.001$; Fig. 2a). The highest density of shells from native gastropods was
189 found in the Central estuary with 285 m^{-2} of *N. burchardi* and 116 m^{-2} of *B. paivae* (Fig. 2a).
190 A significantly higher proportion of *B. australis* shells were fouled compared to *B. paivae* and

191 *N. burchardi* in all salinity regions (e.g. the maximal average fouling was 70% of *B. australis*
192 shells (all sub-types combined) in the Central estuary) (ANOVA: $F_{2,78} = 14.74$; $p < 0.001$; Fig.
193 2b).
194
195 *3.2 Epibiota*.
196 A total of 10 epibiota taxa were identified on the 3,226 gastropod shells examined,
197 represented by three foliose algae (*Gracilaria comosa*, *Chaetomorpha linum*, *Grateloupia* sp.),
198 three solitary invertebrates (*Pomatoceros* sp., *Ascidiacea* sp., *Anthozoa* sp.) and four
199 encrusting species (*Ralfsia* sp., *Membranipora* sp., coralline algae sp. 1, coralline algae sp. 2).
200 Generally, shell type and salinity were the most important variables that explained patterns in
201 epibiota richness (Table 2) and abundances of common taxa (Table 3, 4). The highest
202 taxonomic richness and abundances was found on 'Bat-Gra+' and 'Bat-Hermit' followed by
203 'Bat-Gra-', and 'Bat-Empty' shells. In comparison, 'Bat-Small', 'Bed' and 'Nas' shells
204 generally had lower richness and abundances (Fig. 3, 4, 5).
205
206 *Taxonomic richness*. We found significant effects of shell type and salinity on total epibiota
207 richness (Model 1: Explained deviance = 25 %; $p < 0.001$; Table 2). Most taxa were found on
208 'Bat-Gra+', followed by 'Bat-Hermit', 'Bat-Gra-' and 'Bat-Empty' shells, with more species
209 found on shells from the Outer estuary compared to shells from the Inner estuary (Fig. 3a,
210 salinity effect could not be evaluated for 'Bat-Small' from the Inner estuary because we did
211 not find this shell-type here). Richness of encrusting species was affected by shell type,
212 salinity and habitat (Model 2: Explained deviance = 8 %; $p < 0.001$; Table 2). 'Bat-Gra+'
213 and 'Bat-Hermit' shells had the highest richness, whereas no differences were found among
214 'Bat-Empty', 'Bat-Small', 'Nas' and 'Bed' (Fig. 3b). Richness was higher on shells from the

215 Outer estuary, compared to Inner estuary shells for all shell types (Fig. 3b). Richness of
216 foliose algae was significantly affected by shell type and salinity (Model 3: Explained
217 deviance = 34 %; $p < 0.001$; Table 2); 'Bat-Gra+' had highest richness, and significantly
218 fewer species were found on 'Bat-Gra-' and 'Bat-Hermit' shells in the Inner estuary (Fig. 3c).
219 Taxonomic richness of solitary invertebrates were also affected by shell type and salinity
220 (Model 4: Explained deviance = 10 %; $p < 0.001$; Table 2). Richness was generally higher in
221 the Outer estuary than Inner estuary on 'Bat-empty', 'Bat-Gra-', 'Bat-Gra+', 'Bat-Hermit'
222 and 'Bed', but significant effects was only found for 'Bat-Hermit' (Fig. 3d).
223
224 *Group abundances.* We found significant effects of shell type and salinity on total epibiota
225 abundances (Model 5: Explained deviance = 6 %; $p < 0.001$; Table 3). Highest abundances
226 were found on shell type 'Bat-Gra+', 'Bat-Hermit' and 'Bat-Gra-'(Fig. 4a). Significantly
227 higher epibiota abundances were found on all shell types in the Outer estuary compared to
228 shells from the Inner estuary (Fig. 4a). Abundance of encrusting taxa was also only affected
229 by shell type and salinity (Model 6: Explained deviance = 3 %; $p < 0.001$; Table 3). 'Bat-
230 Hermit' shells had significant higher epibiota cover compared to 'Bat-Small', whereas no
231 differences were found among the other shell types (Fig. 4b). Furthermore, cover was higher
232 on shell types (except 'Bat-Small') in the Outer estuary compared to the Inner estuary (Fig
233 4b). Abundance of foliose algae was also significantly affected by shell type and salinity
234 (Model 7: Explained deviance = 27 %; $p < 0.001$; Table 3). 'Bat-Gra+' had the highest
235 abundance of foliose algae, and there was significantly more foliose algae on 'Bat'Gra+' and
236 'Bat-Gra- in the Outer than Inner estuary (Fig. 4c). Abundances of solitary invertebrates were
237 also affected by shell type and salinity (Model 8: Explained deviance = 16 %; $p < 0.001$;

238 Table 3), with highest abundances on ‘Bat-Hermit’ shells in the Central and Outer estuary
239 (Fig. 4d).
240
241 *Taxonomic abundances*. The red alga *Gracilaria comosa* was significantly affected by shell
242 type and salinity (Model 9: Explained deviance = 6 %; $p < 0.001$; Table 4). *G. comosa* was
243 most common on ‘Bat-Gra+’ followed by ‘Bat-Hermit’ shells, but were rare on ‘Bat-Small’,
244 ‘Bed’ and ‘Nas’ (Fig. 5a). There was a (non-significant) trend of more *G. comosa* attached to
245 shells in the Outer estuary (Fig. 5a). The green alga *Chaetomorpha linum* was affected by
246 shell type, salinity, depth and wave exposure (Model 10: Explained deviance = 19 %; $p <$
247 0.001; Table 4), but the two latter factors accounted for very little of the likelihood ratio test
248 (LRT). *Chaetomorpha linum* was most abundant on *B. australis* shells (except ‘Bat-Small’)
249 with the highest densities found in the Outer estuary (Fig. 5b). The alga *Grateloupia* sp. was
250 the only taxon not affected by salinity, but it was affected by shell type and wave exposure
251 (Model 11: Explained deviance = 25 %; $p < 0.001$; Table 4), being most common on ‘Bat-
252 Hermit’ and ‘Bat-Gra+’ shells (Fig. 5c). Wave exposure only accounted for a low LRT
253 compared to shell type (5.9 vs. 239.5). The tube-building annelid *Pomatoceros* sp. was
254 significantly affected by shell type and salinity (Model 12: Explained deviance = 16 %; $p <$
255 0.001; Table 4). Highest densities were found on ‘Bat-Hermit’, ‘Bat-Gra+’, ‘Bat-Dead’ and
256 ‘Bed’ (Fig. 5d), and for ‘Bat-Hermit’ shells, with lowest density in the Inner estuary (Fig. 5d).
257 The encrusting brown alga *Ralfsia* sp. was significantly affected by shell type, salinity and
258 wave exposure (Model 13: Explained deviance = 5 %; $p < 0.001$; Table 4). Highest cover
259 were found on ‘Bat-Hermit’ and ‘Bat-Gra+’ followed by ‘Bat-Dead’ and ‘Bat-Gra-’ (Fig. 5e).
260 Percentage cover per shell of *Ralfsia* sp. was higher on shells from the Outer than Inner
261 estuary (Fig. 5e), and on shells from wave protected sites compared to exposed sites (Online

262 supplementary S4). Finally, *Membranipora* sp. was affected by shell type, salinity and wave
263 exposure (Model 14: Explained deviance = 13 %; $p < 0.001$; Table 4). 'Bat-Gra-', 'Bat-Gra+
264 and 'Bat-Hermit' shells had the highest cover (Fig. 5f). In contrast to other taxa, cover of
265 *Membranipora* sp. were generally highest in the Central estuary, although only significant on
266 'Bat-Gra-', 'Bat-Gra+' and 'Bat-Hermit' (Fig. 5f) and on shells from wave exposed sites
267 (Online supplementary S5).

268

269 **4. Discussion**

270 It is important to understand how environmental factors influence epibiota communities to
271 better understand general processes that affect biodiversity in estuarine ecosystems. Here, we
272 documented significant relationships between biogenic substrates, multiple environmental
273 conditions and taxonomic richness and abundance of shell-associated epibiota in the Swan
274 River Estuary, Western Australia. More specifically, we found that shell type and salinity
275 were the most important factors (explaining most of the data variability in GLM models)
276 affecting richness and abundances across epibiota taxa and form-groups.

277

278 In the Swan River Estuary, the most abundant shell substrata for epibiota communities were
279 provided by only three gastropod species; the native *Nassarius pauperatus* and *Bedeva paivae*
280 and the non-indigenous *Battilaria australis.* Of these species, *B. australis* shells were both
281 more heavily fouled and were 13 times more abundant than the native species. Indeed, *B.*
282 *australis* shells occurred in densities exceeding 1,700 shells m^{-2}, more than twice the density
283 reported in 2007 (Thomsen *et al.* 2010b), suggesting a continued rapid population expansion
284 over the last few years. The invasive gastropod is thereby orders of magnitude more important

285 as a biogenic habitat former throughout the estuary, compared to all native shell-formers
286 combined.
287 We also found that taxonomic richness and abundance of the shell-associated epibiota were
288 significantly correlated with shell type, salinity, habitat, water depth and wave exposure,
289 although only shell type and salinity were consistently significant in all models (and
290 explaining most of the data variability in the models, salinity excepted in model 11).
291
292 Biofouling typically depends on substrate availability and we therefore expected more species
293 and higher epibiota population abundances on larger than smaller shell hosts (Creed 2000).
294 For example, Wernberg *et al.* (2010) found more epibiota species on large *Turbo torquatus*
295 shells, and Vasconcelos *et al.* (2007) found a higher colonization score of epibiotic
296 polychaetes on large *Hexaplex trunculus*. Our results support these data; when abundance and
297 richness were evaluated per cm^2 shell we found no differences among shell types (data not
298 shown) but we generally found less species and low abundances associated with small shell
299 types (*N. pauperatus* and small *B. australis*) compared to larger shell types. Importantly,
300 small *B. australis* had much less epibiota than larger con-specifics (including live, empty, and
301 hermit-crab-occupied *B. australis* shell types, cf. Fig. 4-6) highlighting the importance of
302 substrate-availability in explaining variability of host-specific epibiota communities. However,
303 the small *B. australis* shells are also younger than the large *B. australis* shells and have
304 therefore had shorter exposure time for settlement of fouling species. Thus, we cannot
305 distinguish if facilitation of epibiota relate more to *host size* or *host longevity* (i.e., substrate
306 availability in space and time, respectively), as also noted in other epibiota studies (Creed
307 2000; Vasconcelos *et al.* 2007; Wernberg *et al.* 2010). Clearly manipulative experiments are

308 needed to separate the relative influence of 'habitat-size' vs. 'habitat-longevity' in future
309 epibiota studies.
310
311 Epibiota communities can also be modified by the behaviour and movement patterns of the
312 biogenic host (Becker and Wahl 1996; Wahl 1989), e.g., documented in several studies that
313 compared epibiota communities on gastropod shells alive vs. occupied by hermit crabs (Bell
314 2005; Creed 2000; Wonham *et al.* 2005). Our data support previous studies as we also found
315 differences between epibiota communities inhabiting live shells, dead shells and shells
316 occupied by hermit crabs. In depositional habitats in Swan River, empty shells are more likely
317 to become buried, live *B. australis* snails are typically partly buried in sediments, but hermit
318 crabs move around on the sediment surface (i.e., their shells are constantly exposed to
319 epibiota fouling). These differences co-varied with epibiota patterns, as we generally found
320 higher densities, and sometimes also higher richness, on hermit crab shells compared to
321 empty or live *B. australis* shells.
322
323 Salinity was the second most important determinant of epibiota communities in our models.
324 Salinity determine distribution patterns of most estuarine organisms (Mclusky and Elliott
325 2004; Middelboe *et al.* 1998), because estuarine species are better adapted to marine than
326 freshwater conditions and because saltwater intrusions, and connectivity to the adjacent sea
327 facilitate dispersal of marine species into estuaries (Roegner 2000). Similar patterns have
328 been documented for estuarine epibiota, e.g., Hardwick-Witman and Mathieson (1983) found
329 a decrease in the abundance and richness of epibiota along a salinity gradient into the Great
330 Bay Estuary System (New Hampshire, U.S.A.). We also documented strong salinity effects
331 on epibiota in the Swan River Estuary; most taxa were more abundant in the high than the low

332 salinity region and this pattern was consistent across shell types. One exception was the
333 bryozoa *Membranipora* sp., which was most abundant in the Central estuary. Some bryozoans
334 are eurythermal and adapted to survive and colonise estuarine ecosystems (Menon and Nair
335 1972; O'Dea and Okamura 1999), potentially explaining why *Membranipora* sp. was most
336 abundant in the Central estuary. We did not sample the fresh water streams (constant salinity
337 of ~ 0-1 ‰) farther into the Swan Rivers and salinity effects would likely have been even
338 stronger if low salinity areas had been included. However, these areas contain few gastropod
339 hosts, i.e., the salinity threshold of the hosts limited the areas in which we could sample
340 epibiota. We finally note that salinity often co-vary with other environmental factors. For
341 example: flow rates, suspended food particles, water clarity, and sediment grain sizes are
342 typically higher (and nutrient levels lower) near the high-salinity estuary mouth (Mclusky and
343 Elliott 2004; Thomsen *et al.* 2006). Nevertheless, we suggest that salinity generally is more
344 important than these co-variates, although manipulative experiments are needed to verify this
345 hypothesis.
346
347 In our initial hypotheses, we suggested that water depth, wave exposure and habitat type
348 (seagrass vs. mudflats) would, in addition to shell type and salinity, influence epibiota
349 community structures. For example, Barnes and Clarke (1995) found that percentage cover of
350 bryozoan epibiota on the limpet *Nacella concinna* increased with depth, and Rossi *et al*.
351 (2000) found higher abundances of hydroids on their hosts at more sheltered sites. However,
352 in our models, those test-factors were rarely significant, and only explained a small proportion
353 of the data variability (i.e. were of no or relative low importance in determining epibiota
354 richness and abundance). There may be several reasons why we found few effects of depth,
355 wave exposure and habitat type. Importantly, *B. australis, N. pauperatus* and *B. paivae* and

hermit crabs are active species that move around. Effects of water depth and habitat could therefore be diluted by host-movements between habitats and depths. For example, seagrasses are patchily distributed around mudflats, and the living shell types might move in and out of patches to obscure differential settlement patterns of epibiota propagules. Furthermore, currents around seagrass beds and mudflats may mix and disperse propagules to reduce inter-habitat differences in epibiota communities. Finally, waves and currents can entrain both live and dead shell types and move them passively between habitats and depths. Indeed, after storms we have often observed large quantities of *B. australis* on the beach, suggesting passive drift across depth levels. Note also that we compared effects of water depth within a narrow interval (0.5 vs. 1.5 m). Sampling a larger depth gradient, including shells from shallower and deeper strata, would likely have increased the importance of this test factor. For example, at increasing depth light decrease thereby limiting survival of autotrophic epibiota (Rohde *et al.* 2008). Furthermore, like salinity 'depth' typically co-varies with light levels, wave exposure, currents, turbidity, sediment grain size, re-suspension, etc. Some co-variates might thereby facilitate but other inhibit epibiota communities with increasing depth, and thereby potentially cancel out depth-effects. Again, manipulative experiments are essential to test if co-varying factors modify epibiota community structures differently along depth gradients. Finally, wave exposure also only explained little data variability, probably because the Swan River Estuary is relatively protected from waves. Thus, in comparisons to open coastlines, estuarine wave exposure gradients are typically weak and likely to be of less importance in determining epibiotic community structures.

Shell substratum provided by *Battilaria* species has previously been shown to facilitate sessile communities (Chan and Chan 2005; Thomsen *et al.* 2010a; Thomsen *et al.* 2010b; Wonham

380 *et al.* 2005). Of the different epibiota taxa observed in our study, *Gracilaria comosa* is likely
381 to be particular important, because it is common throughout the estuary on different shell
382 types and because it is the only epibiota species that form a large 3-dimensional structure.
383 Indeed, *G. comosa*, like other estuarine *Gracilaria* species, can itself facilitate a range of
384 sessile and mobile invertebrates, thereby increasing biodiversity and productivity through
385 cascading habitat formation (Thomsen *et al.* 2012; Thomsen *et al.* 2010a). However, research
386 is needed to better understand processes whereby shell-forming hosts directly and indirectly
387 facilitate epibiota and control biodiversity, e.g., by testing if intermediate habitat-formers (like
388 *G. comosa*) can have negative impacts on other epibiota through competition for nutrients or
389 light or by altering water flow (Miller and Etter 2008; Tanner 1995). However, our data did
390 not indicate negative effects of *G. comosa* on other epibiota, because abundances and richness
391 were generally higher on *B. australis* with, than without, large *G. comosa* fronds.
392
393 In summary, our results highlight that shell type and salinity are particularly important in
394 determining community structures of estuarine sessile epibiota. Our models only explained 3-
395 34% of the total data variability, but generalized linear models are nevertheless a powerful
396 tool to investigate the relatively importance of multiple processes influencing richness and
397 abundance of epibiota communities. We finally suggest that future epibiota studies that test
398 for effects of multiple environmental factors include (i) more explanatory factors in their
399 models, (ii) wider ranges of each gradients, (iii) manipulative experiments to identify
400 underlying mechanisms and (iv) analysis and test of how individual epibiota species affect
401 each other - and the host itself.
402
403
404
405

406 **Acknowledgements**
407
408 JT was supported by a travel grant from Oticon Fonden, MST was supported by a Rising Star
409 travel grant from the Australian National Network in Marine Science and the Marsden Fund
410 of the Royal Society of New Zealand (13-UOC-106), AKB was supported by the Carlsberg
411 Foundation and TW was supported by the Australian Research Council.

412

References

Anderson, M.J., and Underwood, A.J. (1994) Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *J Exp Mar Biol Ecol* **184**(2), 217-236.

Becker, K., and Wahl, M. (1996) Behaviour patterns as natural antifouling mechanisms of tropical marine crabs. *J Exp Mar Biol Ecol* **203**(2), 245-258.

Bell, J.J. (2005) Influence of occupant microhabitat on the composition of encrusting communities on gastropod shells. *Mar Biol* **147**(3), 653-661.

Brearley, A. (2005) 'Ernest Hodgkin's Swanland: estuaries and coastal lagoons of south-western Australia.' (University of Western Australia Press: Crawley, Western Australia) 550

Burnham, K.P., and Anderson, D.R. (2002) 'Model Selection and Multimodel Inference: A Practical Information - Theoretic Approach.' (Springer-Verlag: New York) 488

Buschbaum, C. (2000) Direct and indirect effects of *Littorina littorea* (L.) on barnacles growing on mussel beds in the Wadden Sea. *Hydrobiologia* **440**(1-3), 119-128.

Chan, D.L., and Chan, B.K. (2005) Effect of epibiosis on the fitness of the sandy shore snail *Batillaria zonalis* in Hong Kong. *Mar Biol* **146**(4), 695-705.

Creed, J.C. (2000) Epibiosis on cerith shells in a seagrass bed: correlation of shell occupant with epizoite distribution and abundance. *Mar Biol* **137**(5-6), 775-782.

Davis, A.R., and White, G.A. (1994) Epibiosis in a guild of sessile subtidal invertebrates in south-eastern Australia - a quantitative survey. *J Exp Mar Biol Ecol* **177**(1), 1-14.

Gribben, P.E., Byers, J.E., Clements, M., McKenzie, L.A., Steinberg, P.D.*, et al.* (2009) Behavioural interactions between ecosystem engineers control community species richness. *Ecol Lett* **12**(11), 1127-1136.

Harder, T. (2009) Marine epibiosis: concepts, ecological consequences and host defence. In Marine and Industrial Biofouling. Vol. 4. (Eds. H-C Flemming, PS Murthy, R Venkatesan and K Cooksey) pp. 219-231. (Springer Berlin Heidelberg)

Hardwick-Witman, M.N., and Mathieson, A.C. (1983) Intertidal macroalgae and macroinvertebrates: Seasonal and spatial abundance patterns along an estuarine gradient. *Estuarine, Coastal and Shelf Science* **16**(2), 113-129.

Hilbe, J.M. (2011) 'Negative Binomial Regression.' 2nd edn. (Cambridge University Press: New York) 569

Jackson, J.B.C. (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am Nat* **111**, 743-767.

Knott, N.A., Underwood, A.J., Chapman, M.G., and Glasby, T.M. (2004) Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. *J Mar Biol Assoc Uk* **84**(06), 1117-1130.

Laudien, J., and Wahl, M. (1999) Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. *Marine Ecology* **20**(1), 35-47.

Mclean, R. (1983) Gastropod shells - a dynamic resource that selps shape benthic community structure. *J Exp Mar Biol Ecol* **69**(2), 151-174.

Mclusky, D.S., and Elliott, M. (2004) 'The Esturine Ecosystem.' 3rd edn. (Oxford University Press Oxford, New York) 214

Menon, R., and Nair, N.R. (1972) On the nature of tolerance to salinity in two euryhaline bryozoans *Victorella pavida* Kent and *Electra crustulenta* Pallas. *Proceedings of the Indian National Academy* **38**(B), 414-424.

Middelboe, A.L., Sand-Jensen, K., and Krause-Jensen, D. (1998) Patterns of macroalgal species diversity in Danish estuaries. *Journal of Phycology* **34**(3), 457-466.

Miller, R.J., and Etter, R.J. (2008) Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. *Ecology* **89**(2), 452-462.

O'Dea, A., and Okamura, B. (1999) Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati*. *Mar Biol* **135**, 581-588.

Olabarria, C. (2000) Epibiont molluscs on neogastropod shells from sandy bottoms, Pacific coast of Mexico. *J Mar Biol Assoc Uk* **80**(02), 291-298.

Quinn, G.P., and Keough, M.J. (2002) 'Experimental Design and Data Analysis for Biologists.' (Cambridge University Press: New York) 537

Roegner, G.C. (2000) Transport of molluscan larvae through a shallow estuary. *J Plankton Res* **22**(9), 1779-1800.

Rohde, S., Hiebenthal, C., Wahl, M., Karez, R., and Bischof, K. (2008) Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis. *European Journal of Phycology* **43**(2), 143-150.

Rossi, S., Gili, J.M., and Hugues, R. (2000) The effects of exposure to wave action on the distribution and morphology of the epiphytic hydrozoans *Clava multicornis* and *Dynamena pumila*. *Scientia Marina* **64**, 135-140.

Ruuskanen, A., Back, S., and Reitalu, T. (1999) A comparison of two cartographic exposure methods using *Fucus vesiculosus* as an indicator. *Mar Biol* **134**(1), 139-145.

Sandford, F. (2003) Population dynamics and epibiont associations of hermit crabs (Crustacea: Decapoda: Paguroidea) on Dog Island, Florida. *Memoires of Museum Victoria* **60**(1), 45-52.

Tanner, J.E. (1995) Competition between scleractinian corals and macroalgae - an experimental investigation of coral growth, survival and reproduction. *J Exp Mar Biol Ecol* **190**(2), 151-168.

Thomsen, M.S., de Bettignies, T., Wernberg, T., Holmer, M., and Debeuf, B. (2012) Harmful algae are not harmful to everyone. *Harmful Algae* **16**(0), 74-80.

Thomsen, M.S., McGlathery, K.J., and Tyler, A.C. (2006) Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. *Estuaries and Coasts: J ERF* **29**(3), 465-473.

Thomsen, M.S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D.*, et al.* (2010a) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integrative and Comparative Biology* **50**(2), 158-175.

Thomsen, M.S., Wernberg, T., Tuya, F., and Silliman, B.R. (2010b) Ecological performance and possible origin of a ubiquitous but under-studied gastropod. *Estuarine, Coastal and Shelf Science* **87**(4), 501-509.

Thyrring, J., Thomsen, M.S., and Wernberg, T. (2013) Large-scale facilitation of a sessile community by an invasive habitat-forming snail. *Helgol Mar Res* **67**(4), 789-794.

Vasconcelos, P., Cúrdia, J., Castro, M., and Gaspar, M. (2007) The shell of *Hexaplex (Trunculariopsis) trunculus* (Gastropoda: Muricidae) as a mobile hard substratum for epibiotic polychaetes (Annelida: Polychaeta) in the Ria Formosa (Algarve coast—southern Portugal). *Hydrobiologia* **575**(1), 161-172.

Wahl, M. (1989) Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar Ecol Prog Ser* **58**, 175-189.

Wahl, M., and Mark, O. (1999) The predominantly facultative nature of epibiosis: experimental and observational evidence. *Mar Ecol Prog Ser* **187**, 59-66.

Wahl, M., Shahnaz, L., Dobretsov, S., Saha, M., Symanowski, F.*, et al.* (2010) Ecology of antifouling resistance in the bladder wrack *Fucus vesiculosus*: patterns of microfouling and antimicrobial protection. *Mar Ecol Prog Ser* **411**, 33-48.

551 Wernberg, T., Tuya, F., Thomsen, M.S., and Kendrick, G.A. (2010) Turban snails as habitat
552 for foliose algae: contrasting geographical patterns in species richness. *Marine and*
553 *Freshwater Research* **61**(11), 1237-1242.
554
555 Wonham, M.J., O'Connor, M.O., and Harley, C.D.G. (2005) Positive effects of a dominant
556 invader on introduced and native mudflat species. *Mar Ecol Prog Ser* **289**, 109-116.
557
558 Zuur, A.F., Ieno, E.N., and Elphick, C.S. (2010) A protocol for data exploration to avoid
559 common statistical problems. *Methods in Ecology and Evolution* **1**(1), 3-14.
560
561

562 **Tables**

563

564 **Table 1** Shell types collected in the Swan River Estuary, based of their morphological

565 characteristics and ecological importance. n = number of each shell-type included in the data-

566 analysis of epibiota communities.

Shell type and species	Life stage	Characteristics	Ecological importance	n	Shell area (cm^2)
Covered *Batillaria australis* (Bat-Gra+)	Adult	Shells with attached dense fronds of coarsely branched red alga *Gracilaria Comosa*	A relatively common shell type. The large seaweed fronds may create novel micro-habitat on shells.	476	7.6
Normal *Batillaria australis* (Bat-Gra-)	Adult	Shells without *Gracilaria comosa.*	The most common shell type in Swan River	660	7.5
Dead *Batillaria australis* (Bat-Empty)	Adult	Empty shells	A non-moving common shell type; accumulate in massive 'graveyards'.	491	7.6
Hermit *Batillaria australis* (Bat-Hermit)	Adult	Shells inhabited by hermit crabs	Different movement than live adult *B. australis* shells	490	7.6
Juvenile *Batillaria australis* (Bat-Small)	Juvenile	Small shell size (<1.3 cm high)	Common but inconspicuous shell type; important component to understand effect of host size and age on epibiota	146	1.6
Bediva pavia (Bed)	Adult	Live shells from the largest native snail	Native snail of similar size as *B. australis*. 3rd most abundant snail in Swan River	398	5.0
Nassarius pauperatus (Nas)	Adult	Large shell from the smallest native snail	Small native snail, 2nd most abundant in Swan River.	565	1.0

567

Table 2 Generalized linear model results partitioning variation in taxonomic richness of all epibiotic taxa combined (model 1), encrusting taxa (model 2), foliose algae (model 3) and solitary invertebrates (model 4) using a Poisson distribution. Only significant explanatory variables are shown. For each model we show degrees of freedom (df), variables deviance (Deviance), likelihood ratio test value (LRT) and significant p-values ($p < 0.05$).

GLM Models (Poisson distribution)	df	Deviance	LRT	p -value
Model 1 (All taxa ~ Shell type + Salinity)				
Explained deviance = 25 %				
Shell type	6	4624.6	1119.8	<0.001
Salinity	2	3594.9	90.1	<0.001
Residuals	3217	3504.7		
Model 2 (Encrusting taxa ~ Shell type + Salinity + Habitat)				
Explained deviance = 8 %				
Shell type	6	2596.0	160.6	<0.001
Salinity	2	2495.9	60.4	<0.001
Habitat	1	2440.1	4.6	0.03
Residuals	3216	2435.5		
Model 3 (Foliose algae ~ Shell type + Salinity)				
Explained deviance = 34 %				
Shell type	6	3588.2	1221.7	<0.001
Salinity	2	2382.9	16.44	<0.001
Residuals	3217	2366.4		
Model 4 (Solitary invertebrates ~ Shell type + Salinity)				
Explained deviance = 10 %				
Shell type	6	2224.7	197.6	<0.001
Salinity	2	2059.5	32.4	<0.001
Residuals	3217	2027.1		

Table 3 Generalized linear model results partitioning variation in abundances of all epibiotic taxa (model 5), encrusting taxa (model 6), foliose algae (model 7) and solitary invertebrates (model 8) using a negative binomial distribution. Only significant explanatory variables are shown. For each model we show degrees of freedom (df), variables deviance (Deviance), likelihood ratio test value (LRT) and significant p-values ($p < 0.05$).

GLM Models (Negative binomial distribution)	df	Deviance	LRT	p -value
Model 5 (all taxa ~ Shell type + Salinity)				
Explained deviance = 6 %				
Shell type	6	3462.7	129.5	<0.001
Salinity	2	3446.5	113.3	<0.001
Residuals	3217	3333.1		
Model 6 (Encrusting taxa ~ Shell type + Salinity)				
Explained deviance = 3 %				
Shell type	6	2261.3	36.8	<0.001
Salinity	2	2269.6	45.2	<0.001
Residuals	3217	2224.4		
Model 7 (Foliose algae ~ Shell type + Salinity)				
Explained deviance = 27 %				
Shell type	6	2261.3	36.8	<0.001
Salinity	2	2269.6	45.2	<0.001
Residuals	3217	2224.4		
Model 8 (Solitary invertebrates ~ Shell type + Salinity)				
Explained deviance = 16 %				
Shell type	6	1954.3	129.5	<0.001
Salinity	2	1787.3	82.5	<0.001
Residuals	3217	1704.8		

Table 4 Generalized linear models partitioning variation in abundance of the most common epibiotic species found in the Swan River Estuary including *Gracilaria comosa* (model 9), *Chaetomorpha linum* (model 10), *Grateloupia* sp. (model 11), *Pomatoceros* sp. (model 12), *Ralfsia* sp. (model 13) and *Membranipora* sp. (model 14) using a negative binomial distribution. Only significant explanatory variables are shown. For each model we show degrees of freedom (df), variables deviance (Deviance), likelihood ratio test value (LRT) and significant p-values ($p < 0.05$).

GLM Models (Negative binomial distribution)	df	Deviance	LRT	p -value
Model 9 (*Gracilaria comosa* ~ Shell type + Salinity)				
Explained deviance = 6 %				
Shell type	6	3459.5	133.4	<0.001
Salinity	2	3437.5	111.4	<0.001
Residuals	3212	3326.1		
Model 10 (*Chaetomorpha linum* ~ Shell type + Salinity + Depth + Wave exposure)				
Explained deviance = 19 %				
Shell type	6	1729.4	254.0	<0.001
Salinity	2	1503.9	28.5	<0.001
Depth	1	1483.1	7.8	0.005
Wave exposure	1	1481.5	6.2	0.01
Residuals	3215	1475.4		
Model 11 (*Grateloupia* sp. ~ Shell type + Wave exposure)				
Explained deviance = 25 %				
Shell type	6	980.7	239.5	<0.001
Wave exposure	1	747.2	5.9	0.01
Residuals	3218	741.25		
Model 12 (*Pomatoceros* sp. ~ Shell type + Salinity)				
Explained deviance = 16 %				
Shell type	6	1909.3	243.5	<0.001
Salinity	2	1749.5	83.8	<0.001
Residuals	3217	1665.8		
Model 13 (*Ralfsia* sp. ~ Shell type + Salinity + Wave exposure)				
Explained deviance = 5 %				
Shell type	6	2012.3	51.5	<0.001
Salinity	2	2006.3	45.5	<0.001
Wave exposure	1	1967.0	6.2	0.01
Residuals	3216	1960.8		
Model 14 (*Membranipora* sp. ~ Shell type + Salinity + Wave exposure)				
Explained deviance = 13 %				
Shell type	6	596.1	41.0	<0.001

Salinity	2	581.9	26.7	<0.001	
Wave exposure	1	568.8	13.6	<0.001	
Residuals	3216	555.2			

688 **Figure Captions**

689 **Figure 1.** Map of the 13 study sites in the Swan River Estuary. Dotted lines divide the estuary
690 into three regions sampled and classified by their annual lowest salinity: *Outer estuary*
691 (annual lowest salinity >30 ‰), *Central estuary* (salinity >5 ‰) and *Inner estuary* (salinity
692 >1 ‰). *Outer estuary*: 1: Gilbert Fraser (0.40); 2: Leeuwin (0.16); 3: Chidley Point* (0.35); 4:
693 Freshwater Bay (3.49). *Central estuary:* 5: Point Resolution (1.15); 6: Charles Court* (4.06);
694 7: J.H Abrahams (2.04); 12: Jeff Joseph (3.32); 13: Point Walter (2.63). *Inner estuary:* 8:
695 Matilda Bay^{+} (2.60); 9: Mills Point* (4.97); 10: Como* (4.88); 11: Heathcote (3.89). *Sites
696 used to estimate shell abundance and degree of fouling. $^{+}$No seagrass beds at this location.
697 Effective fetch showed in brackets. Insert map: Location of the Swan River Estuary, Perth,
698 Western Australia. Shaded area: native distribution of *Batillaria australis.*

699

700 **Figure 2.** Shell density (shells m^{-2}) and degree of shells biofouled (% of shells with at least
701 one epibiotic taxa) for the three gastropod host-species (*Battilaria australis* (Bat), *Bedeva*
702 *paiva* (Bed) and *Nassarius pauperatus* (Nas)) from the three sampled regions (Outer, Central
703 and Inner estuary). Error bars indicate standard error. *Different letters* indicate a significant
704 difference ($p < 0.05$) among shell types. *Different numbers of stars* indicates a significant
705 difference ($p < 0.05$) among the salinity regions (Inner, Central, Outer).

706

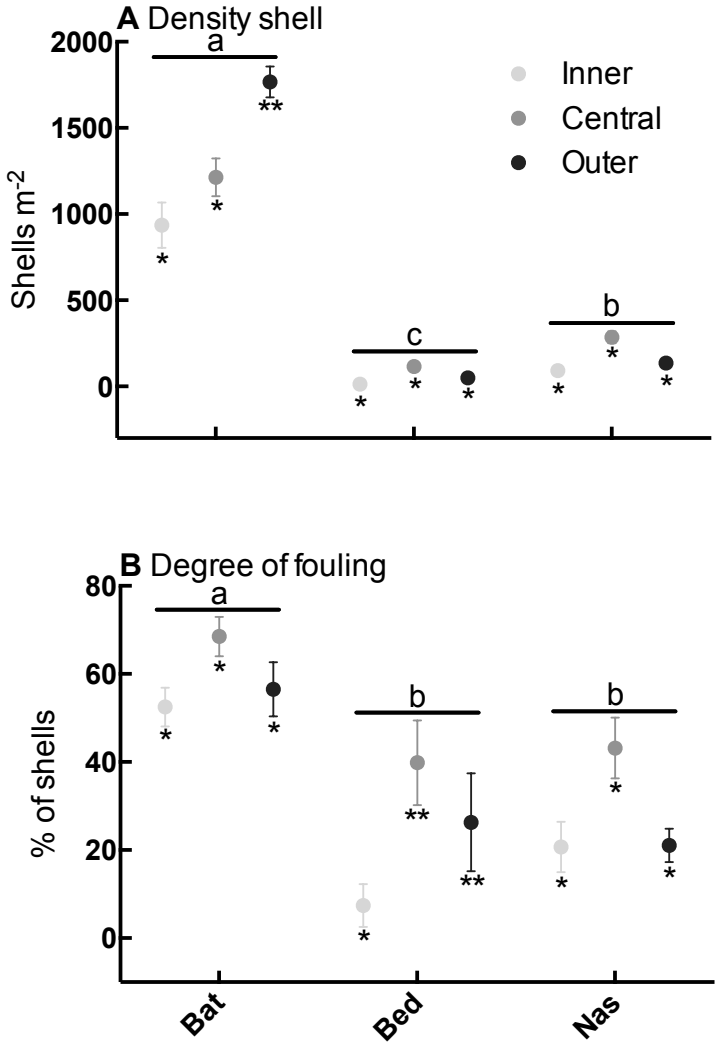
707 **Figure 3.** Taxonomic richness of epibiota attached to *Battilaria australis* (Bat), *Bedeva paiva*
708 (Bed) and *Nassarius pauperatus* (Nas) shell types in the Swan River Estuary. Taxonomic
709 richness of **a)** All epibiotic taxa combined; **b)** Encrusting taxa; **c)** Foliose algae and **d)**
710 Solitary invertebrates found on seven shell types. Error bars indicate standard error. *Different*
711 *letters* indicate a significant difference ($p < 0.05$) among shell types. *Different numbers of*

712 *stars* indicates a significant difference ($p < 0.05$) among the salinity regions (Inner, Central,
713 Outer). No *N. pauperatus* shells were found in the Outer region.
714
715 **Figure 4.** Abundance of epibiota attached to *Battilaria australis* (Bat), *Bedeva paiva* (Bed)
716 and *Nassarius pauperatus* (Nas) shell types in the Swan River Estuary. Abundance of **a)** All
717 epibiotic taxa combined; **b)** Encrusting taxa; **c)** Foliose algae and **d)** Solitary invertebrates
718 found on seven shell types. Error bars indicate standard error. *Different letters* indicate a
719 significant difference ($p < 0.05$) among shell types. *Different numbers of stars* indicates a
720 significant difference ($p < 0.05$) among the salinity regions (Inner, Central, Outer). No *N.*
721 *pauperatus* shells were found in the Outer region.
722
723 **Figure 5.** Abundance of dominant epibiota taxa attached to *Battilaria australis* (Bat), *Bedeva*
724 *paiva* (Bed) and *Nassarius pauperatus* (Nas) shell types in the Swan River Estuary.
725 Abundance of **a)** *Gracilaria comosa;* **b)** *Chaetomorpha linum*: **c)** *Grateloupia* sp.; **d)**
726 *Pomatoceros* sp.; **e)** *Ralfsia* sp. And **f)** *Membranipora* sp. Error bars indicate standard error.
727 *Different letters* indicate a significant difference ($p < 0.05$) among shell types. *Different*
728 *numbers of stars* indicates a significant difference ($p < 0.05$) among the salinity regions (Inner,
729 Central, Outer). No *N. pauperatus* shells were found in the Outer region.
730
731
732
733
734
735
736
737
738
739
740

741 **Figure 1**
742

743
744
745
746
747
748
749
750
751
752
753
754
755
756
757
758
759
760

761
762
763 **Figure 2**



764
765
766
767
768
769
770
771
772
773
774
775
776
777
778

Figure 3

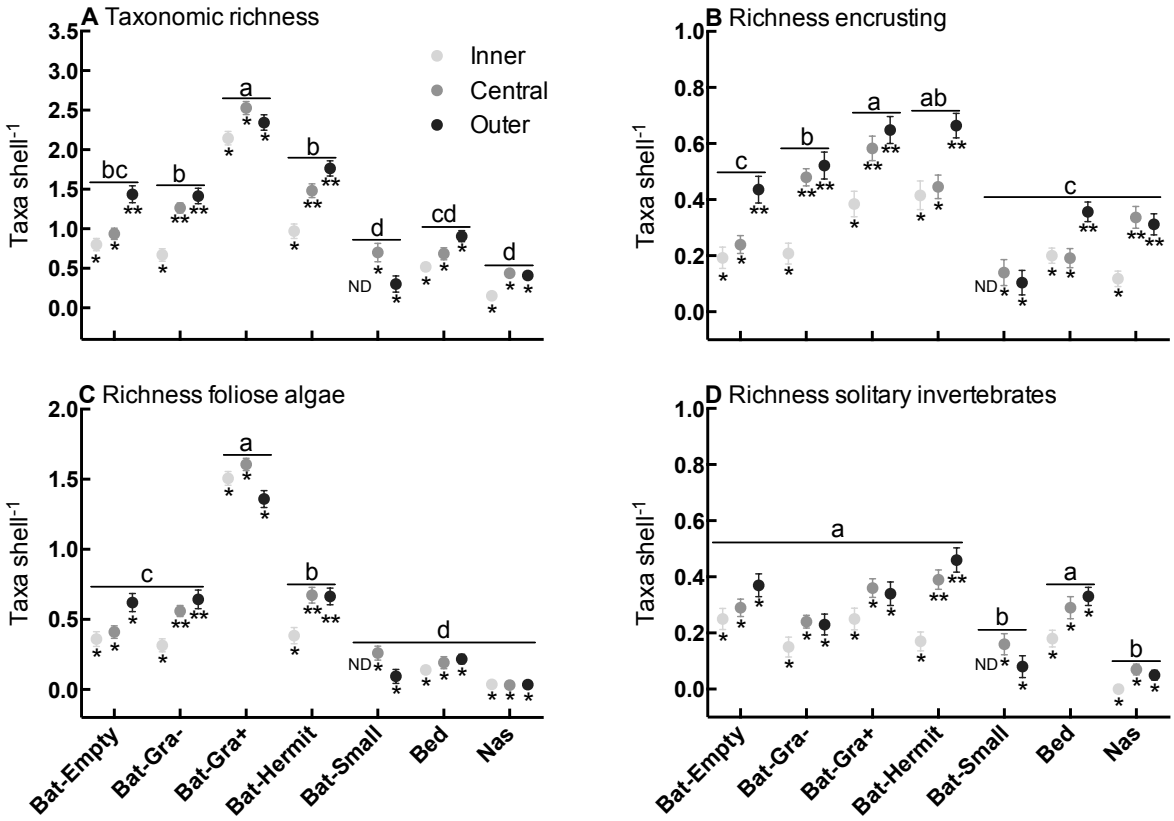
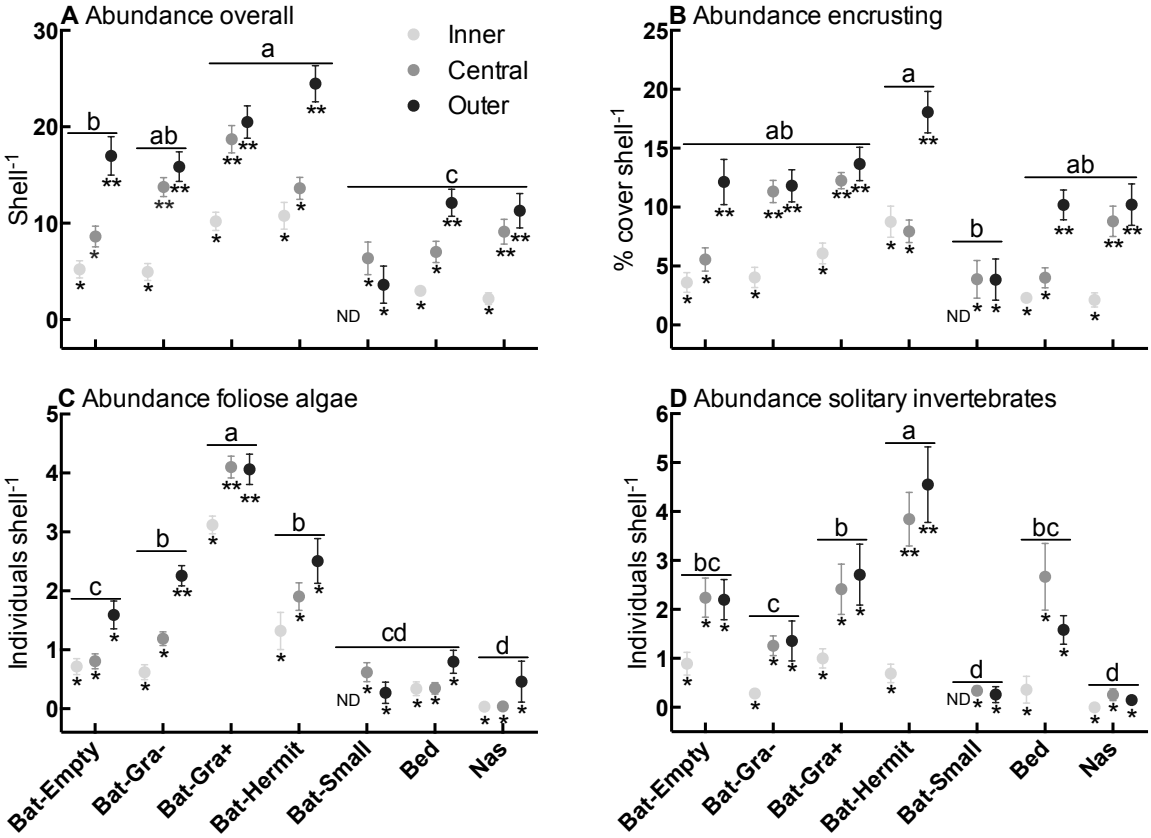
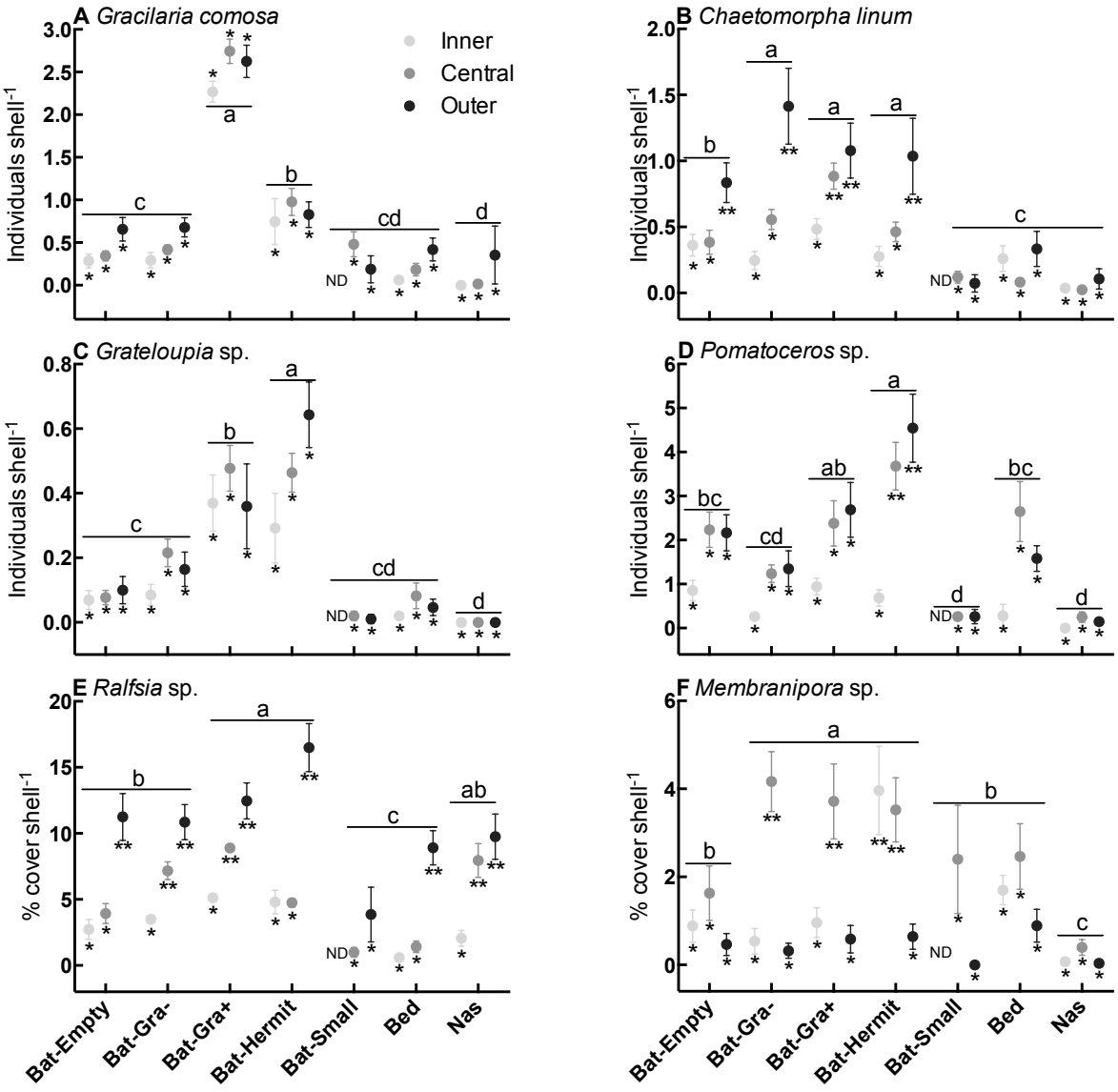

A Taxonomic richness
B Richness encrusting
C Richness foliose algae
D Richness solitary invertebrates
Taxa shell-1
Inner
Central
Outer
ND
Bat-Empty
Bat-Gra-
Bat-Gra+
Bat-Hermit
Bat-Small
Bed
Nas

Figure 4


A Abundance overall
Inner
Central
Outer
Shell-1
B Abundance encrusting
% cover shell-1
C Abundance foliose algae
Individuals shell-1
D Abundance solitary invertebrates
Individuals shell-1
ND
Bat-Empty
Bat-Gra-
Bat-Gra+
Bat-Hermit
Bat-Small
Bed
Nas

826 **Figure 5**



827