

2010

Turban Snails as Habitat for Foliose Algae: Contrasting Geographical Patterns in Species Richness

Thomas Wernberg
Edith Cowan University

Fernando Tuya
Edith Cowan University

Mads Thomsen
Edith Cowan University

Gary Kendrick

[10.1071/MF09184](https://doi.org/10.1071/MF09184)

This article was originally published as: Wernberg, T., Tuya, F., Thomsen, M., & Kendrick, G. (2010). Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness. *Marine and Freshwater Research*, 61(11), 1237-1242. Original article available [here](#)

This Journal Article is posted at Research Online.

<http://ro.ecu.edu.au/ecuworks/6268>

1 *Running head: Epiflora on Turbo*

2

3 **Turban snails as habitat for foliose algae: contrasting geographical patterns in species**
4 **richness**

5

6

7 Thomas Wernberg^{1,2,3*}, Fernando Tuya^{3,4,5}, Mads S. Thomsen^{3,6}, Gary A. Kendrick¹

8

9

10 ¹ School of Plant Biology, University of Western Australia, Crawley WA 6009, Australia

11

12 ² Australian Institute of Marine Science, Oceans Institute, Crawley WA 6009, Australia

13

14 ³ Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup WA 6027,
15 Australia

16

17 ⁴ CIIMAR, Rua dos Bragas, 289-4050-123, Porto, Portugal

18

19 ⁵ BIOGES, Department of Biology, University of Las Palmas, Las Palmas 35010, Spain

20

21 ⁶ Marine Department, National Environmental Research Institute, University of Aarhus, P.O.
22 Box 4000, Roskilde, Denmark

23

24 * Corresponding author:

25

26 Email: thomas.wernberg@uwa.edu.au, Ph. +61 8 6488 4648, Fax +61 8 6488 1001

27

28

29

30 **Abstract**

31 Understanding patterns of species richness is a major goal for ecologists, especially in space-
32 limited habitats where many organisms live on top of others (epibiosis) exemplified by algae
33 growing on gastropods in marine environments. We tested the hypotheses that species
34 richness of epiflora on the gastropod *Turbo torquatus* would not differ between regions with
35 similarly rich algal floras, and that epifloral richness would increase with increasing
36 gastropod size. Macroalgal floras of Hamelin Bay, Marmion, Jurien Bay and Kalbarri,
37 Western Australia, ranged from ~20 - 40 species reef¹ (JB = HB = M ≥ K). Epiflora on small
38 *T. torquatus* (shell area <150 cm²) did not differ among regions but epifloral richness
39 increased with increasing basibiont size. Large *T. torquatus* (>150 cm²) were only found in
40 Hamelin Bay and Marmion, where epifloral richness differed substantially. Epifloral richness
41 was positively related to basibiont size in Marmion but not in Hamelin Bay. However,
42 densities of patellid limpets on large *T. torquatus* were ~4 times higher in Hamelin Bay than
43 in Marmion, implying that limpet grazing suppresses epifloral richness. Epifloral richness on
44 turbinids is not simply associated with regional species pools or gastropod size. Rather,
45 biological interactions at the scale of individual basibionts apparently govern broad scale
46 patterns of epibiosis.

47

48 **Key words:** Epibiosis; Turbinid snails; *Turbo torquatus*; Western Australia; Grazing

49

50 **Introduction**

51 Space is often a limiting resource in marine environments, where epibenthic sessile species
52 rely on hard substrata for a significant part of their life cycle. Consequently, hard surfaces are
53 usually rapidly fouled by invertebrates or algae (Wahl 1989). Macroalgae generally dominate
54 on upward facing surfaces where there is sufficient light and low-enough grazing pressure
55 (Irving and Connell 2002). Where grazing is intense, the substratum is usually devoid of erect
56 vegetation, comprising mainly crusts of coralline algae ('barrens') (Fletcher 1987; Coleman *et*
57 *al.* 2006).

58

59 Shell-producing gastropods are 'islands' of hard substratum, and they often provides habitat
60 to a rich epibiota of algae and sessile animals. More generally, epibiotic associations are
61 defined by a basibiont (the host) that provide habitat for attached or mobile species (the
62 epibionts). Animal basibionts are usually slow-moving or sessile, non-burrowing, long-lived,
63 large and often with a biologically inactive external body surface (Wahl and Mark 1999).

64 With ~80 described host species, Gastropoda is the animal class with the largest number of
65 known basibionts (Wahl and Mark 1999). However, an abundance of epibiota is also common
66 on many other benthic invertebrates (e.g., Davis and White 1994). Obligate epibionts are rare
67 - the majority of epibionts are facultative (i.e., not host or substratum selective), and are
68 usually also found living on other suitable surfaces in the vicinity of their hosts (Wahl and
69 Mark 1999). The ecological significance of epibiosis varies greatly (Wahl 1989); for example,
70 for gastropod basibionts it has been associated both with positive effects of reducing
71 predation rates (Thornber 2007) and negative effects of increased mortality (Schmitt *et al.*
72 1983; Warner 1997) and reduced reproductive performance and fitness (Buschbaum and
73 Reise 1999).

74

75 Turbinid gastropods (family Turbinidae) are conspicuous elements of intertidal and subtidal
76 habitats in tropical and temperate zones (Fletcher 1987; Foster and Hodgson 2000;
77 Vanderklift and Kendrick 2004). In temperate waters of Australasia, the large *Turbo*
78 *torquatus* (up to 12 cm shell height) is often the dominant gastropod. In Western Australia, *T.*
79 *torquatus* is found on most subtidal reefs (5-15 m depth) from Kalbarri (27°S) in the Indian
80 Ocean, and south into the Southern Ocean (Vanderklift and Kendrick 2004; Wernberg *et al.*
81 2008). Herbivory is generally not intense on these rocky reefs (Wernberg *et al.* 2008;
82 Vanderklift *et al.* 2009), and a dense cover of macroalgae dominated by the small kelp
83 *Ecklonia radiata* and fucallean algae characterise most sunlit surfaces (Wernberg *et al.* 2003;
84 Smale *et al.* 2010). The southwest coast of Western Australia is one of the most species-rich
85 areas for macroalgae in the world (Bolton 1994). The composition and structure of algal
86 assemblages differ among regions at different latitudes in this region (Wernberg *et al.* 2003;
87 Smale *et al.* 2010), and between reefs of different geology (Harman *et al.* 2003),
88 geomorphology (Toohey *et al.* 2007), and wave exposure (Kendrick *et al.* 1999). However,
89 the taxonomic richness of foliose species with a thallus >0.5 cm remains roughly consistent
90 across the region, typically with 15-30 species 0.25 m⁻² (Kendrick *et al.* 1999; Harman *et al.*
91 2003; Wernberg *et al.* 2003; Toohey *et al.* 2007).

92

93 Understanding the mechanisms that drive patterns of species richness is a major research
94 agenda for ecologists (Brown 1995). Many studies have investigated patterns of epibiosis
95 within a location (e.g., between different basibiont taxa, Davis and White 1994), but rarely
96 have patterns among locations been assessed. Because of the facultative nature of epibiosis
97 (Wahl and Mark 1999), the epibiota of basibionts such as *T. torquatus* represent ‘samples’ of

98 local communities. Patterns of epibiota richness on widespread basibionts may thus be
99 informative of regional and local drivers of community structure more generally as well as for
100 epibiota specifically. The species richness of local communities depends on an interplay
101 between broad-scale biogeographical and evolutionary processes that determine the regional
102 species pool, and small-scale ecological processes that excludes, or promotes, subsets of
103 species through biotic and abiotic interactions (Keddy 1992). Still, across ecosystems and taxa
104 two general patterns have emerged: strong positive relationships between (a) the richness of
105 regional species pools and that of their local assemblages (Witman *et al.* 2004; Briggs 2007),
106 and (b) the size of a habitat patch and its species richness (MacArthur and Wilson 1967;
107 Whittaker and Fernández-Palacios 2007).

108

109 Here, we assess the model that epibiota richness on turbinid gastropods is positively related to
110 the richness of the regional species pool and the size of the basibiont. As the species richness
111 of regional algal floras in our study area are similar, this model predicts that (1) there will be
112 no differences in the species richness of epiflora among different regions, and (2) species
113 richness of the epiflora will increase with increasing size of basibiont.

114

115 **Methods**

116 Foliose macroalgae and gastropods were sampled from reefs within four regions (Hamelin
117 Bay, 34°S; Marmion, 32°S; Jurien Bay, 30°S; Kalbarri, 28°S) evenly spaced by ~2° of latitude
118 (~300 km coastline), along the southwest coast of Western Australia. All reefs were similar
119 with respect to depth (10-12 m), kelp canopy cover (60-80%), wave exposure (exposed) and
120 geomorphology (low relief platforms with 1-2 m vertical sections interspersed) (e.g., Tuya *et al.*
121 2009a). The latitudinal gradient encompassed in this study is characterised by a gradual 2-
122 3°C change in ocean temperature, but there is no upwelling and water nutrient concentrations
123 are consistently low (Smale and Wernberg 2009).

124

125 The species richness of the regional algal floras was assessed by harvesting and identifying all
126 foliose macroalgae >0.5 cm from 0.25-m² quadrats ($n = 6$ from each reef) from six reefs (>1
127 km apart) within each region in November 2005. Quadrats were pooled for each reef and the
128 numbers of taxa tallied. One-way ANOVA, followed by *post hoc* Student-Newman-Keuls
129 tests, tested for differences in species richness among regions. Variance homogeneity was
130 assessed by Cochran's *C*-test.

131

132 *Turbo torquatus* individuals ($n = 156$) were collected in January – March 2006 (austral
133 summer) from at least three of the six reefs in each region. *T. torquatus* were easily
134 recognisable from other turbinids because of the characteristic ‘shoulders’ on the shell (a
135 feature peculiar to the West Australian subspecies, *T. torquatus* subs. *whitleyi*) and their
136 distinctly grooved operculum. Gastropods were collected by SCUBA divers and brought to
137 the boat, where their total shell length was measured with callipers as the distance from the
138 protoconch to the base of the outer lip (Wernberg *et al.* 2008). Epiflora attached to their shells
139 were visually identified, as accurately as possible, before releasing the snails unharmed.
140 Encrusting algae were not included because these were ubiquitous and could not be
141 distinguished on live *T. torquatus* in the field. Although it was often difficult to ascertain the
142 exact identity of each epibiont (many algae require reproductive structures, sectioning and
143 microscopy for proper identification), it was always possible to distinguish the number of
144 different macroscopic species. In addition to foliose algae, we also counted epibiotic
145 gastropod grazers (e.g., small limpets living on top of the turban snails). The number of *T.*
146 *torquatus* collected varied between reefs, and all gastropods were pooled within their
147 respective region. Consequently, in this study we are not able to assess patterns that might
148 exist among reefs within each region. However, our general observations while working with
149 gastropods on these reefs (e.g., Wernberg *et al.* 2008; Tuya *et al.* 2009b) suggest that such
150 differences are negligible.

151
152 The surface area of a gastropod shell cannot easily be determined due to its complex
153 geometry. We used stereo-photography to assess the relationship between total shell length,
154 an easily obtainable measure of size, and shell surface area for *T. torquatus* ($n = 20$
155 individuals across a range of sizes). Stereo-photography was used to generate a 3-dimensional
156 image of the shell from which surface area could be measured by triangulation between points
157 on the shell surface (Abdo *et al.* 2006). Data were fitted to a power function by non-linear
158 regression.

159
160 The relationship between gastropod size (shell surface area) and species richness was
161 explored separately for small ($<150 \text{ cm}^2$, 79.5 mm total shell length) and large ($>150 \text{ cm}^2$)
162 gastropods. The cut-off between small and large gastropods was chosen as the size threshold
163 characterising the latitudinal distribution of *T. torquatus* populations in Western Australia
164 (Wernberg *et al.* 2008); with the exception of one individual from Jurien Bay which was
165 excluded from the analyses, large individuals were only found at the two southern regions;

166 Hamelin Bay ($n = 40$) and Marmion ($n = 20$). Pooling all gastropods within a region, one-way
167 ANOVA tested for differences in epifloral richness among regions for small gastropods and t -
168 tests (uneven variances) tested for differences in basibiont size, epifloral richness and limpet
169 density on large *T. torquatus* between Hamelin Bay and Marmion. Variance homogeneity was
170 assessed by Cochran's C -test. Pearson product-moment correlation assessed the degree of
171 covariation between basibiont size, epibiotic limpet density, and epifloral richness.

172

173 **Results**

174 Total shell length was a good predictor of shell surface area ($r^2 = 0.98$, $P < 0.0001$; Fig. 1),
175 and the regression model was used to calculate the shell surface area of all *Turbo torquatus*
176 from field measurements of total shell length.

177

178 Mean species richness of regional algal floras ranged from 18.3 – 41.0 species reef⁻¹, and
179 there were significant differences among regions ($F_{3,20} = 6.47$, $P = 0.003$), although *post hoc*
180 SNK tests were unable to establish an unambiguous pattern of differences between regions
181 (Fig. 2; Jurien Bay = Hamelin Bay = Marmion \geq Kalbarri). Importantly, for the comparison of
182 epifloras on large gastropods, there was no difference in regional species richness between
183 Hamelin Bay and Marmion.

184

185 A total of 156 gastropods were sampled across the study area; 95 were small (<150 cm²) and
186 61 were large (>150 cm²). There were no differences among locations in mean size ($F_{3,91} =$
187 1.89, $P = 0.140$) or epiflora species richness ($F_{3,91} = 0.11$, $P = 0.96$) for small *T. torquatus*. On
188 average, the size of small gastropods was 75 ± 3 cm² and they hosted 0.91 ± 0.1 (SE, $n = 95$)
189 species of foliose algae. Across all regions, there was a positive relationship between
190 gastropod size and species richness of the epiflora on small *T. torquatus* ($r = 0.61$, $P < 0.0001$,
191 $n = 95$; Fig. 3). Large (>150 cm²) *T. torquatus* were only found in Hamelin Bay and Marmion
192 (Fig. 3). Large individuals from Marmion (238 ± 9 cm², mean surface area \pm SE, $n = 20$) were
193 significantly larger (ca. 14%) than those from Hamelin Bay (208 ± 4 cm², SE, $n = 40$) ($t_{56} =$
194 3.00, $P = 0.006$; Fig. 3). The species richness of epiflora was 2.5 times higher in Marmion
195 (8.3 ± 0.7 species *Turbo*⁻¹, SE, $n = 20$) than in Hamelin Bay (3.4 ± 0.5 species *Turbo*⁻¹, SE, n
196 = 40), and this was statistically significant ($t_{56} = 6.74$, $P < 0.001$). The epiflora in Marmion
197 continued to accumulate species with increasing basibiont size, as we found for small
198 gastropods, which resulted in a positive relationship there between epifloral richness and
199 basibiont size ($r = 0.13$, $P = 0.590$, $n = 20$; Fig. 3). The relatively low value of the correlation

200 coefficient was considerably influenced by two individuals with very low species richness
201 (i.e., outliers clearly outside the general pattern); the correlation coefficient increased to $r =$
202 0.49 ($P = 0.044$, $n = 18$), when these two samples were omitted. In contrast to Marmion, the
203 richness of the epiflora on large *T. torquatus* did not increase with increasing shell size in
204 Hamelin Bay ($r = -0.17$, $P = 0.284$, $n = 40$).

205

206 Epibiotic gastropods were entirely dominated by 10-20-mm patellid limpets (mainly
207 *Patelloida alticostata*), and their average density in Marmion (0.7 ± 0.21 limpets *Turbo*⁻¹, SE,
208 $n = 20$) was less than one quarter of densities in Hamelin Bay (3.05 ± 0.31 limpets *Turbo*⁻¹,
209 SE, $n = 40$) ($t_{56} = -6.31$, $P < 0.001$). Across all large *T. torquatus*, there was a negative
210 correlation between limpet density and the species richness of foliose epiflora ($r = -0.44$, $P =$
211 0.0004 , $n = 60$; Fig. 4).

212

213 **Discussion**

214 *Turbo torquatus* was found to host a rich epiflora comprising up to 13 different species of
215 foliose macroalgae per individual. For small *T. torquatus*, the species richness of the epiflora
216 did not differ between regions and species richness increased with increasing basibiont size.
217 For large *T. torquatus*, there were significantly fewer epiflora species in Hamelin Bay than in
218 Marmion despite no differences in the regional species pools of macroalgae. Moreover,
219 whereas the species richness of epiflora increased with increasing basibiont size in Marmion,
220 it did not in Hamelin Bay. Consequently, our data does not support the model that epifloral
221 richness simply reflects the richness of the regional species pool and the size of the basibiont.
222 Substantially higher densities of epibiotic limpets in Hamelin Bay, and a negative relationship
223 on large snails between limpets and algal species richness, suggest that limpets maintain a
224 disproportionately low species richness of the epiflora in Hamelin Bay. Thus, our study
225 indicates that biological interactions between limpets and algae (presumably grazing) modify
226 the expected richness patterns.

227

228 No epiflora was found on gastropods smaller than 49.3 cm^2 (41 mm TSL). Assuming an
229 annual growth rate of $12.9 \text{ mm year}^{-1}$ (Joll 1975), this implies that *T. torquatus* are around 3.2
230 years old before they start to become fouled by macroalgae. The relatively long delay before
231 the onset of fouling suggests that the epibiosis requires some sort of preconditioning of the
232 shell such as damage from failed predation attempts (Schmitt *et al.* 1983), facilitation by
233 earlier colonisers such as serpulid worms (Warner 1997) or encrusting coralline algae

234 (Thornber 2007). Indeed, both serpulids and encrusting corallines were often seen on small
235 shells otherwise devoid of epibionts.

236

237 Patterns in species richness of epiflora growing on *T. torquatus* followed the expected
238 patterns for small gastropods and large gastropods in Marmion, but not for large gastropods in
239 Hamelin Bay. Overall, the mean number of epifloral species in Marmion (8.3) was higher
240 than the median epibiota richness (4.8) reported for molluscs as a group (Wahl and Mark
241 1999). Given that *T. torquatus* are large relative to most other gastropods, this is consistent
242 with an overall positive relationship between basibiont size and epibiont richness. Conversely,
243 the markedly lower epifloral richness in Hamelin Bay (3.4) clearly sets this region apart from
244 the general patterns of epibiosis. Large *T. torquatus* were slightly bigger in Marmion than in
245 Hamelin Bay, but the difference was relatively small (14%), and despite the positive
246 relationship between richness and size in Marmion, size differences seem unlikely to be a
247 significant contributor to the large (~250%) difference in epifloral richness between the two
248 regions. Moreover, size differences do not explain the lack of correlation between size and
249 species richness in Hamelin Bay.

250

251 The division between small and large *T. torquatus*, where they would be ~6.2 years old
252 assuming 12.9 mm growth year⁻¹ (Joll 1975), was based on biogeographical patterns of
253 population structure (Wernberg *et al.* 2008). However, this threshold also appears to
254 correspond well to the onset of change in the epifloral richness pattern in Hamelin Bay (cf.
255 Fig 3). There have been relatively few experimental tests to distinguish between multiple
256 competing models of what drives epifloral assemblages. Abbot and Bergey (2007) found that
257 grazing from other molluscs, not nutrients or chemical defences (antifouling), controlled algal
258 growth on a freshwater snail. Grazing is also a plausible driver of the observed patterns of
259 epifloral species richness on large *T. torquatus*. Limpets and small gastropods have some of
260 the greatest per capita interaction strengths with macroalgae (Sala and Graham 2002), and
261 their ability to control algal communities is well documented (e.g., Fletcher 1987; Coleman *et*
262 *al.* 2006). The mean density of limpets on large *T. torquatus* in Hamelin Bay (~3 limpets
263 *Turbo*⁻¹ of 208 cm²) is equivalent to ~140 limpets m⁻², which is in the same order of
264 magnitude as has been recorded to cause a significant impact on the cover of foliose
265 macroalgae across temperate rocky coasts (Coleman *et al.* 2006). Moreover, a range of
266 invertebrates including limpets, chitons and abalone are known to cue their recruitment to
267 coralline algae (see references in Pearce and Scheibling 1990). If coralline algae start to

268 recruit onto and develop in ~4 year old *T. torquatus*, then limpets may be attracted to recruit
269 onto *T. torquatus* and develop a capacity (density and size) for top-down control as *T.*
270 *torquatus* approaches the threshold size between small and large, thus explaining the lack of
271 impacts on small *T. torquatus* and the relatively sudden onset of grazing control. The
272 implication is that broad-scale processes that dictate the presence of limpets may indirectly
273 control the patterns of epibiosis on *T. torquatus*. A range of mechanisms could account for
274 regional differences in limpet densities between Hamelin Bay and Marmion. For example,
275 substantial differences across latitudinal gradients, of several hundred kilometres, in adult
276 populations of limpets and other rocky reef invertebrates have been associated with
277 oceanographic control of recruit delivery (Connolly *et al.* 2001) and recruitment and recruit
278 performance (Gilman 2006).

279

280 Where the rich epiflora on large gastropods from Marmion can best be described as lush
281 growth, sometimes with attached kelps and fucoids as large as 30-50 cm, the large gastropods
282 from Hamelin Bay resemble ‘mini-barrens’, i.e., hard substratum dominated by encrusting
283 corallines devoid of foliose algae. This classical ‘top-down state’ is interesting because it
284 contrasts with the organisation of subtidal reef assemblages across most of temperate
285 Australia (west of Wilsons Promontory, Connell and Irving 2008), where grazing pressure
286 generally is too low to influence landscape and assemblage structure (Connell and Irving
287 2008; Wernberg *et al.* 2008; Vanderklift *et al.* 2009).

288

289 In conclusion, we found substantial differences in epifloral richness despite similarly rich
290 regional algal floras, and richness did not always increase with increasing basibiont size. As
291 such, the generalisations about species richness did not apply unequivocally to the epiflora on
292 turbinids in Western Australia. We propose that limpets are responsible for the geographical
293 differences in epifloral richness. Our study adds to the mounting evidence that regional
294 differences in biological interactions, perhaps mediated by environmental conditions such as
295 ocean circulation patterns or temperature, is likely to play an important role in influencing
296 broad-scale patterns of biodiversity.

297

298 **Acknowledgements**

299 This research was supported by a Discovery grant from the Australian Research Council to
300 TW and GAK (DP0555929). MST was partially funded by the Danish Research Academy.
301 We thank K. Cook for field assistance and D. Abdo for help with measuring *Turbo* surface

302 areas. We also thank the Editor (Boulton), an Associate Editor, A. Davis and an anonymous
303 reviewer for comments that have improved the manuscript.

304

305 **References**

306 Abbott, L.L., and Bergey, E.A. (2007). Why are there few algae on snail shells? The effects of
307 grazing, nutrients and shell chemistry on the algae on shells of *Helisoma trivolvis*. *Freshwater*
308 *Biology* **52**, 2112-2120.

309

310 Abdo, D.A., Seager, J.W., Harvey, E.S., McDonald, J.I., Kendrick, G.A., *et al.* (2006).
311 Efficiently measuring complex sessile epibenthic organisms using a novel photogrammetric
312 technique. *Journal of Experimental Marine Biology and Ecology* **339**, 120-133.

313

314 Bolton, J.J. (1994). Global seaweed diversity: patterns and anomalies. *Botanica Marina* **37**,
315 241-245.

316

317 Briggs, J.C. (2007). Marine biogeography and ecology: invasions and introductions. *Journal*
318 *of Biogeography* **34**, 193–198.

319

320 Brown, J.H. (1995). 'Macroecology.' (University of Chicago Press: Chicago, USA)

321

322 Buschbaum, C., and Reise, K. (1999). Effects of barnacle epibionts on the periwinkle
323 *Littorina littorea* (L.). *Helgoland Marine Research* **53**, 56-61.

324

325 Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Aaberg, P., Arenas, F., *et al.* (2006).
326 A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* **147**,
327 556-564.

328

329 Connell, S.D., and Irving, A.D. (2008). Integrating ecology with biogeography using
330 landscape characteristics: a case study of subtidal habitat across continental Australia. *Journal*
331 *of Biogeography* **35**, 1608-1621.

332

333 Connolly, S.R., Menge, B.A., and Roughgarden, J. (2001). A latitudinal gradient in
334 recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* **82**, 1799–1813.

335

336 Davis, A.R., and White, G.A. (1994). Epibiosis in a guild of sessile subtidal invertebrates in
337 south-eastern Australia: a quantitative survey. *Journal of Experimental Marine Biology and*
338 *Ecology* **177**, 1-14.

339

340 Fletcher, W.J. (1987). Interactions among subtidal Australian sea urchins, gastropods and
341 algae - effects of experimental removals. *Ecological Monographs* **57**, 89-109.

342

343 Foster, G.G., and Hodgson, A.N. (2000). Intertidal population structure of the edible mollusc
344 *Turbo sarmaticus* (Vetigastropoda) at an unexploited and exploited sites along the coast of the
345 Eastern Cape Province, South Africa. *African Zoology* **35**, 173-183.

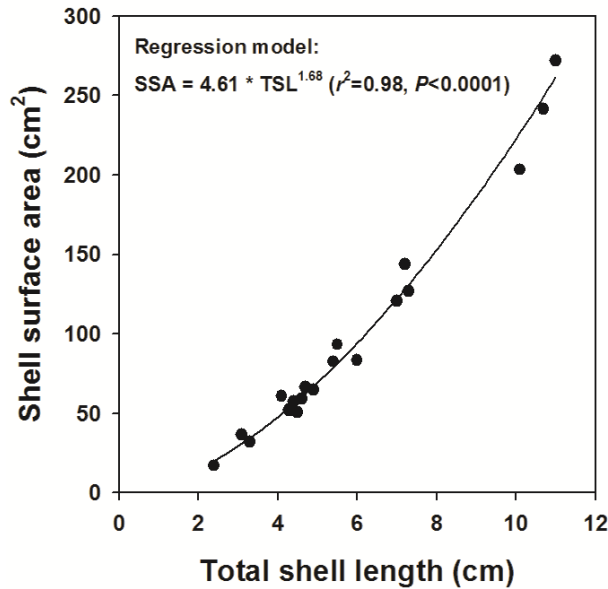
346

347 Gilman, S.E. (2006). The northern geographic range limit of the intertidal limpet *Collisella*
348 *scabra*: a test of performance, recruitment, and temperature hypotheses. *Ecography* **29**, 709-
349 720.

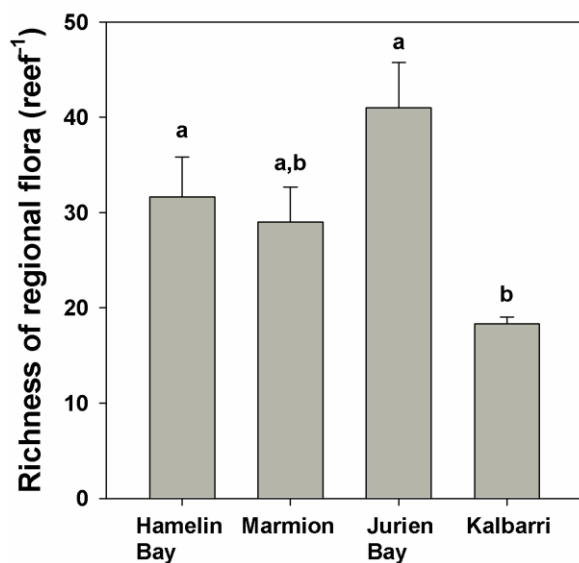
350
351 Harman, N., Harvey, E.S., and Kendrick, G.A. (2003). Differences in fish assemblages from
352 different reef habitats at Hamelin Bay, south-western Australia. *Marine and Freshwater*
353 *Research* **54**, 177-184.
354
355 Irving, A.D., and Connell, S.D. (2002). Sedimentation and light penetration interact to
356 maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages.
357 *Marine Ecology Progress Series* **245**, 83-91.
358
359 Joll, L.M. (1975). Reproduction and growth in two species of Turbinidae (Gastropoda
360 Prosobranchia). MSc thesis, University of Western Australia, Perth, Australia
361
362 Keddy, P.A. (1992). Assembly and response rules two goals for predictive community
363 ecology. *Journal of Vegetation Science* **3**, 157-164.
364
365 Kendrick, G.A., Lavery, P.S., and Philips, J.C. (1999). Influence of *Ecklonia radiata* kelp
366 canopy structure on macro-algal assemblages in Marmion Lagoon, Western Australia.
367 *Hydrobiologia* **399**, 275-283.
368
369 MacArthur, R.H., and Wilson, E.O. (1967). 'The Theory of Island Biogeography.' (Princeton
370 University Press: Princeton, USA)
371
372 Pearce, C.M., and Scheibling, R.E. (1990). Induction of metamorphosis of larvae of the green
373 sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. *Biological Bulletin* **179**,
374 304-311.
375
376 Sala, E., and Graham, M.H. (2002). Community-wide distribution of predator-prey interaction
377 strength in kelp forests. *Proceedings of the National Academy of Sciences of the United States*
378 *of America* **99**, 3678-3683.
379
380 Schmitt, R.J., Osenberg, C.W., and Bercovitch, M.G. (1983). Mechanisms and consequences
381 of shell fouling in the kelp snail, *Norrisia norrisi* (Sowerby): indirect effects of octopus
382 drilling. *Journal of Experimental Marine Biology and Ecology* **69**, 267-281.
383
384 Smale, D.A., Kendrick, G.A., and Wernberg, T. (2010). Assemblage turnover and taxonomic
385 sufficiency of subtidal macroalgae at multiple spatial scales. *Journal of Experimental Marine*
386 *Biology and Ecology* **384**, 76-86.
387
388 Smale, D.A., and Wernberg, T. (2009). Satellite-derived SST data as a proxy for water
389 temperature in near-shore benthic ecology. *Marine Ecology Progress Series* **387**, 27-37.
390
391 Thornber, C. (2007). Associational resistance mediates predator-prey interactions in a marine
392 subtidal system. *Marine Ecology* **28**, 480-486.
393
394 Toohey, B.D., Kendrick, G.A., and Harvey, E.S. (2007). Disturbance and reef topography
395 maintain high local diversity in *Ecklonia radiata* kelp forests. *Oikos* **116**, 1618-1630.
396
397 Tuya, F., Wernberg, T., and Thomsen, M.S. (2009a). Habitat structure affect abundances of
398 labrid fishes across temperate reefs in south-western Australia. *Environmental Biology of*
399 *Fishes* **86**, 311-319.

400
401 Tuyu, F., Wernberg, T., and Thomsen, M.S. (2009b). Colonization of gastropods on subtidal
402 reefs depends on density in adjacent habitats, not on disturbance regime. *Journal of*
403 *Molluscan Studies* **75**, 27-33.
404
405 Vanderklift, M.A., and Kendrick, G.A. (2004). Variation in abundances of herbivorous
406 invertebrates in temperate subtidal rocky reef habitats. *Marine and Freshwater Research* **55**,
407 93-103.
408
409 Vanderklift, M.A., Lavery, P.S., and Waddington, K.I. (2009). Intensity of herbivory on kelp
410 by fish and sea urchins differs between inshore and offshore reefs. *Marine Ecology Progress*
411 *Series* **376**, 203–211.
412
413 Wahl, M. (1989). Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Marine*
414 *Ecology Progress Series* **58**, 175-189.
415
416 Wahl, M., and Mark, O. (1999). The predominantly facultative nature of epibiosis:
417 experimental and observational evidence. *Marine Ecology Progress Series* **187**, 59-66.
418
419 Warner, G.F. (1997). Occurrence of epifauna on the periwinkle, *Littorina littorea* (L.), and
420 interactions with the the polychaete *Polydora ciliata* (Johnston). *Hydrobiologia* **355**, 41-47.
421
422 Wernberg, T., Kendrick, G.A., and Phillips, J.C. (2003). Regional differences in kelp-
423 associated algal assemblages on temperate limestone reefs in south-western Australia.
424 *Diversity and Distributions* **9**, 427-441.
425
426 Wernberg, T., White, M., and Vanderklift, M.A. (2008). Population structure of turbinid
427 gastropods on wave-exposed subtidal reefs: effects of density, body size and algae on grazing
428 behaviour. *Marine Ecology Progress Series* **362**, 169-179.
429
430 Whittaker, R.J., and Fernández-Palacios, J.M. (2007). 'Island Biogeography - Ecology,
431 Evolution and Conservation.' (Oxford University Press: London, UK)
432
433 Witman, J.D., Etter, R.J., and Smith, F. (2004). The relationship between regional and local
434 species diversity in marine benthic communities: A global perspective. *Proceedings of the*
435 *National Academy of Sciences of the United States of America* **101**, 15664-15669.
436
437
438

439 **Fig. 1.** Relationship between total shell length (distance from the protoconch to the base of
440 the outer lip) and shell surface area calculated from triangulations based on digital stereo-
441 photography ($n = 20$).
442



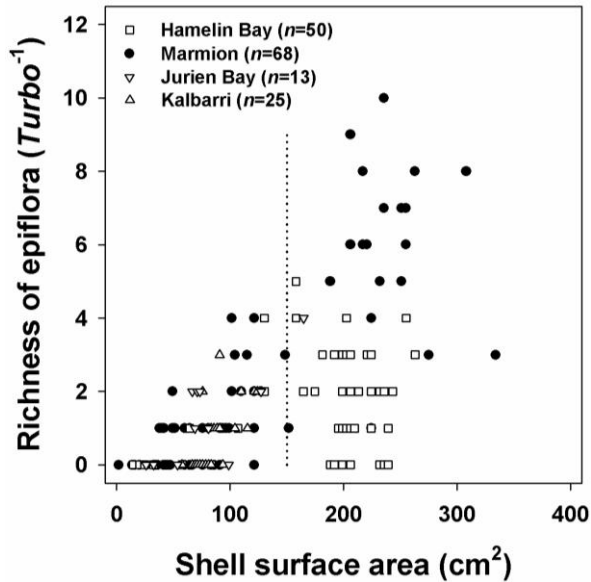
443
444
445
446 **Fig. 2.** Species richness (mean + SE) of foliose macroalgae >0.5 cm in each region ($n = 6$
447 reefs per region). Species richness does not differ among regions sharing a letter above the bar
448 ($P > 0.05$, SNK-tests).
449



450

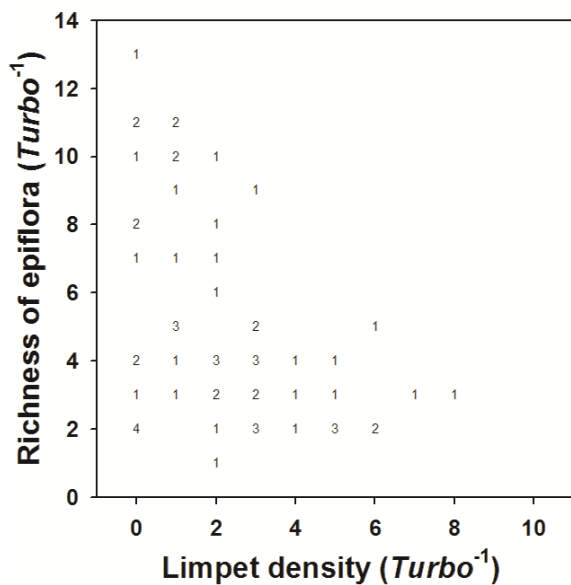
13

451 **Fig. 3.** Species richness of epibiotic foliose algae growing on *Turbo torquatus* sampled from
 452 subtidal habitats in four regions (Hamelin Bay, Marmion, Jurien Bay and Kalbarri) across
 453 south-western Australia. The dotted line indicate 150 cm² (79.5 mm total shell length); the
 454 cut-off between small and large gastropods used in the data analyses.
 455



456
 457

458 **Fig. 4.** Species richness of epibiotic foliose algae versus epibiotic limpet density for large
 459 (>150 cm²) *Turbo torquatus* from Hamelin Bay (n = 40) and Marmion (n = 20). Numbers
 460 indicate the frequency of overlapping data points.
 461



462
 463