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Research Online

1-1-2010

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

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1   *Running head: Epiflora on Turbo*

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

4   **richness**

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Abstract

Understanding patterns of species richness is a major goal for ecologists, especially in space-limited habitats where many organisms live on top of others (epibiosis) exemplified by algae growing on gastropods in marine environments. We tested the hypotheses that species richness of epiflora on the gastropod *Turbo torquatus* would not differ between regions with similarly rich algal floras, and that epifloral richness would increase with increasing gastropod size. Macroalgal floras of Hamelin Bay, Marmion, Jurien Bay and Kalbarri, Western Australia, ranged from ~20 - 40 species reef[1] (JB = HB = M ≥ K). Epiflora on small *T. torquatus* (shell area <150 cm2) did not differ among regions but epifloral richness increased with increasing basibiont size. Large *T. torquatus* (>150 cm2) were only found in Hamelin Bay and Marmion, where epifloral richness differed substantially. Epifloral richness was positively related to basibiont size in Marmion but not in Hamelin Bay. However, densities of patellid limpets on large *T. torquatus* were ~4 times higher in Hamelin Bay than in Marmion, implying that limpet grazing suppresses epifloral richness. Epifloral richness on turbinids is not simply associated with regional species pools or gastropod size. Rather, biological interactions at the scale of individual basibionts apparently govern broad scale patterns of epibiosis.

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

Introduction

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

Shell-producing gastropods are 'islands' of hard substratum, and they often provides habitat to a rich epibiota of algae and sessile animals. More generally, epibiotic associations are defined by a basibiont (the host) that provide habitat for attached or mobile species (the epibionts). Animal basibionts are usually slow-moving or sessile, non-burrowing, long-lived, 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^oS) 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 fucalean 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*

121 *al.* 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-m^2 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 neglible.

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 cm^2, 79.5 mm total shell length) and large (>150 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 cm^2) and

186   61 were large (>150 cm^2). 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 cm^2 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 cm^2) *T. torquatus* were only found in Hamelin Bay and Marmion

192   (Fig. 3). Large individuals from Marmion (238 ± 9 cm^2, mean surface area $\pm$ SE, $n = 20$) were

193   significantly larger (ca. 14%) than those from Hamelin Bay (208 ± 4 cm^2, 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 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 cm^2) 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

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

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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
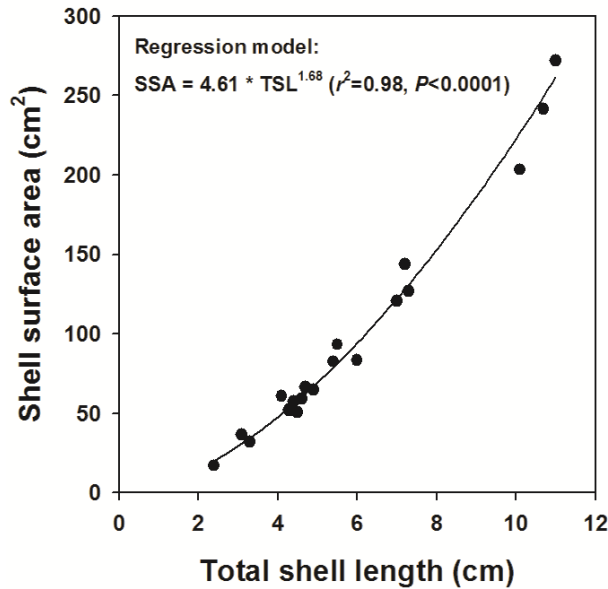
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446 **Fig. 2.** Species richness (mean + SE) of foliose macroalgae >0.5 cm in each region ($n = 6$

447 reefs per region). Species richness does not differ among regions sharing a letter above the bar
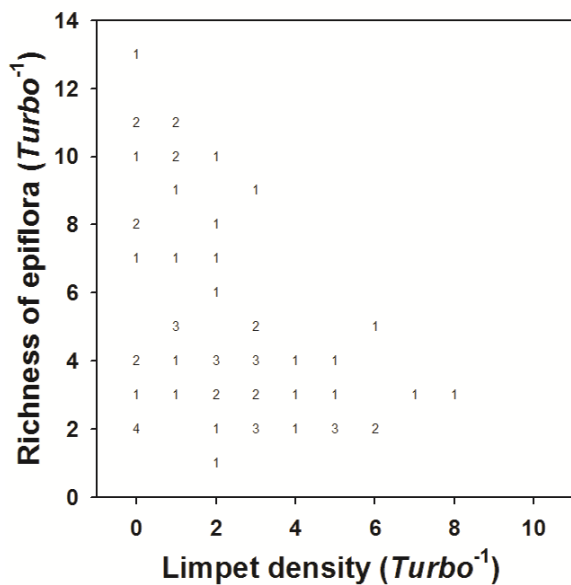
448 ($P > 0.05$, SNK-tests).

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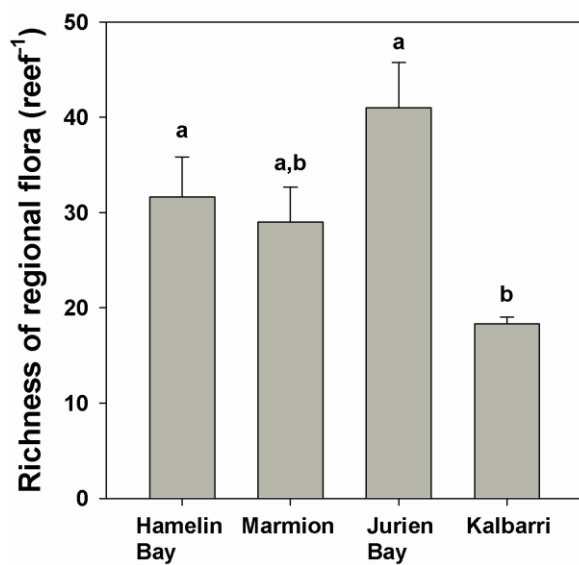
Fig. 3. Species richness of epibiotic foliose algae growing on *Turbo torquatus* sampled from subtidal habitats in four regions (Hamelin Bay, Marmion, Jurien Bay and Kalbarri) across south-western Australia. The dotted line indicate 150 cm^2 (79.5 mm total shell length); the cut-off between small and large gastropods used in the data analyses.
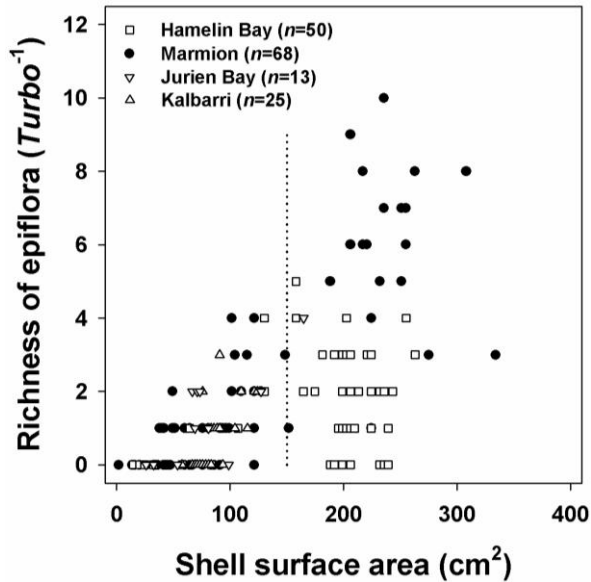
Fig. 4. Species richness of epibiotic foliose algae versus epibiotic limpet density for large (>150 cm^2) *Turbo torquatus* from Hamelin Bay ($n = 40$) and Marmion ($n = 20$). Numbers indicate the frequency of overlapping data points.

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