



Provided by the author(s) and NUI Galway in accordance with publisher policies. Please cite the published version when available.

Title	Landscape effects in the intertidal around the coastline of Great Britain
Author(s)	Johnson, Mark P.; Maggs, Christine A.; Allcock, Louise A.; Blight, Andrew J.
Publication Date	2015-12-21
Publication Information	Johnson, Mark P., Maggs, Christine A., Allcock, A. Louise, & Blight, Andrew J. (2016). Landscape effects in the intertidal around the coastline of Great Britain. <i>Journal of Biogeography</i> , 43(1), 111-122. doi: 10.1111/jbi.12607
Publisher	Wiley
Link to publisher's version	http://dx.doi.org/10.1111/jbi.12607
Item record	http://hdl.handle.net/10379/7047
DOI	http://dx.doi.org/10.1111/jbi.12607

Downloaded 2018-12-12T12:25:54Z

Some rights reserved. For more information, please see the item record link above.



1 Original article

2

3 **Landscape effects in the intertidal around the coastline of Great Britain**

4

5

6 Mark P. Johnson*¹, Christine A. Maggs², A. Louise Allcock¹, Andrew J. Blight³

7

8 ¹*Ryan Institute and School of Natural Sciences, National University of Ireland Galway,*

9 *University Road, Galway, Ireland*

10 ²*School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast BT9*

11 *7BL, UK*

12 ³*Scottish Oceans Institute, East Sands, University of St Andrews, St Andrews, Fife, KY16 8LB,*

13 *UK*

14

15 *Corresponding author mark.johnson@nuigalway.ie

16 Ryan Institute and School of Natural Sciences, National University of Ireland Galway,

17 University Road, Galway, Ireland

18

19 Word count: (Abstract: 278) Abstract, main text, references 6665

20 Running head: intertidal landscape effects

21

22 Pre-print version

23 Final version at <http://onlinelibrary.wiley.com/doi/10.1111/jbi.12607/abstract>

24 DOI: 10.1111/jbi.12607

25 **ABSTRACT**

26 **Aim** We tested whether the size of habitat patches along the coastline of Great Britain
27 influences molluscan species richness.

28

29 **Location** Coastline of Great Britain.

30

31 **Methods** Intertidal mollusc data were compiled from the National Biodiversity Network to
32 derive a matrix of species presence/absence in 10 km × 10 km squares (hectads). Major
33 groupings within the coastal fauna were identified using clustering based on Simpson's
34 dissimilarity index. Contiguous hectads assigned to the same cluster were considered as
35 patches. Potential island biogeographical effects were investigated using regressions of
36 species density against patch size.

37

38 **Results** 598 hectads were clustered into 15 groups, with the three largest groups (94% of
39 hectads) having broad associations consistent with hectad dominance by rocky shore habitat,
40 sheltered sediment or sediment on exposed coasts. For all three main groups, there were
41 fewer species in larger patches than would be expected from a random sampling of hectads.
42 Species densities (species hectad⁻¹) increased with patch size in rocky shore-dominated
43 habitat. There was no support for a similar effect in sedimentary habitats, with higher than
44 expected species richness in isolated hectads of sheltered habitat.

45

46 **Main conclusions**

47 The increases in mollusc species density with patch size in rocky shore dominated habitat are
48 consistent with island biogeographical processes. The absence of similar effects in
49 sedimentary habitats may reflect more overlap between the species of intertidal and subtidal

50 in these habitats. Subtidal habitat may therefore act to change the hostility of the matrix
51 between intertidal patches of sedimentary habitat, diluting any island effects. As landscape
52 effects may change species richness at the scale examined, concerns that increased building
53 of artificial habitats will change the local patterns of species richness may be justified for
54 rocky habitats.

55

56 **Keywords:**

57 Beach, British Isles, cluster, inter-tidal, mollusc, rocky shore, patch size, sediment, species
58 area, species richness

59 INTRODUCTION

60 Several different processes may cause variation in the species richness of differently sized
61 patches of habitat. Larger segments of habitat may have greater species richness than smaller
62 areas of similar habitat as a consequence of holding more individuals (Preston, 1962). Larger
63 patches of habitat may also be associated with higher species richness as the increased area
64 samples a greater amount of environmental heterogeneity (Stein *et al.*, 2014). If the number
65 of species in comparable areas (e.g., same-size plots) within small patches and large patches
66 differs, this requires further explanation (Fahrig, 2013). One of the most widely known
67 explanations for an increase in species density (species per unit area) in larger fragments is
68 the theory of island biogeography (MacArthur & Wilson, 1967): larger islands have lower
69 extinction rates and/or higher species immigration rates than smaller islands, resulting in
70 more species at the equilibrium point between species extinction and species immigration.
71 Island biogeography has often been applied to habitat mosaics, where the matrix is not as
72 hostile as the sea is to inhabitants of true islands. Matrix effects can alter island
73 biogeographical processes by obscuring patterns of habitat specialists (Cook *et al.*, 2006).
74 The edge of habitat fragments can be areas of increased richness as ‘mass effects’ allow
75 species to persist in unfavourable habitats due to immigration from an adjacent favourable
76 matrix (Kunin, 1998). Positive or negative edge effects may arise from altered or
77 intermediate habitats around the perimeter of patches (Ewers & Didham, 2006).

78

79 Despite the wealth of theory related to patch, island and landscape effects, it is not always
80 clear how the different potential processes may be evident in different systems. This of
81 course reflects both scale-dependent differences across studies, variations in species traits
82 such as dispersal capacity and differences in the composition and heterogeneity of landscapes
83 (Sólymos & Lele, 2012). Studies of landscape effects in marine systems lag behind the

84 terrestrial literature (Boström *et al.*, 2011), and yet there are many concerns about changes in
85 marine habitats due to sea level rise, habitat loss and habitat modification (e.g., Bulleri &
86 Chapman 2010; Jackson & McIlvenny, 2011; Hawkins, 2012). Landscape effects on species
87 richness (e.g., Steffan-Dewenter, 2003) have implications for managing habitat change and
88 conservation planning.

89

90 To investigate how intertidal species richness may be linked to landscape structure we used a
91 clustering approach to identify the broad-scale structure of intertidal molluscan diversity
92 around Great Britain. Structure was defined at the grain scale of 10 km × 10 km squares
93 (hectads). Having identified a parsimonious description of heterogeneity at the hectad scale,
94 the links between patch size (based on neighbouring hectads of the same cluster) and species
95 richness were examined using null models (Gotelli, 2001). Null models, in the current study
96 as random selections of hectads into patches, can be used to generate an expectation for
97 patches in the absence of spatial structuring processes. For example, if there are Allee effects
98 (Gascoigne & Lipcius, 2004) or colonization–extinction dynamics that require local (within
99 patch) population sources, then larger patches may have more persistent populations and
100 higher species richness as envisioned by MacArthur & Wilson (1967). If edge or isolation
101 effects restrict the colonization and persistence of populations in small patches, then there
102 should be fewer species than expected in small groups of hectads.

103

104 The observed diversity of patches of habitat will be influenced by a number of processes.
105 Ideally these could be controlled by a standardized sampling programme, but it is not feasible
106 to generate contiguous coverage along extensive coastlines using such an approach. The
107 patterns of diversity in habitat patches were therefore examined using a proxy for collection
108 effort. An indented coastline may also reflect greater intertidal area or habitat heterogeneity,

109 for example by creating variance in wave exposure. This proxy was also examined using
110 coastline length as a possible influence on species richness. Considering the two additional
111 predictor variables led to a more robust test of the central question: whether species density
112 increased in larger patches of intertidal habitat. This was supplemented by a test of species
113 accumulation to test whether total species richness in patches was greater or lesser than
114 expected by chance selection of hectads.

115

116 **MATERIALS AND METHODS**

117 **Broad scale habitat structure**

118 Existing shoreline maps (Fig. 1) were used to help identify likely habitat associations of
119 clusters identified separately using species presence–absence in hectads. The available
120 shoreline maps are based on digitized coastlines, cross-referenced with satellite images;
121 <http://www.euroasion.org>. One of the major habitat distinctions is between sedimentary shores
122 (beaches) and rocky shores. The Euroasion categories emphasize a further group of habitats
123 generally found in estuaries. The category of ‘conglomerates and/or cliffs with rock and
124 sediment on shore’ is intermediate between sedimentary and rocky shores. The match to rock
125 or sediment dominance for the conglomerates category is dependent on local factors.

126

127 **Clustering of species assemblages**

128 Species presence records in 10 km × 10 km hectads in the UK National grid system were
129 extracted from the National Biodiversity Network (NBN; <http://data.nbn.org.uk; records>
130 [accessed 19/11/2008](#)). The data were examined to remove ambiguous records (e.g., those
131 with genus name only) and filtered to include intertidal records only, as described in Blight *et*
132 *al.* (2009). Molluscs were used as a suitable indicator phylum for distributional patterns as
133 this group is relatively widely collected and identified, occurs in both hard and soft shore

134 habitats and has been found to act as a surrogate for other littoral species (Smith, 2005).
135 Species authorities follow the World Register of Marine Species (WoRMS Editorial Board,
136 2015).

137

138 There were 598 hectads with data on mollusc presence. It is not possible to extrapolate the
139 existing habitat classification for the UK intertidal (JNCC biotopes, Connor *et al.*, 2004) to
140 hectads as this would require a greater coverage of biotope maps than currently exists and
141 additional decisions on how to deal with mixtures of biotopes at the 10 km × 10 km grain size
142 of the available species data. Clustering was therefore applied directly to the matrix of
143 species records to define groups of hectads with similar species (Kreft & Jetz, 2010).

144 Dissimilarities between hectads were calculated using Simpson's dissimilarity index (β_{sim} ,
145 Koleff *et al.*, 2003). The advantage of Simpson's index in this context is that it summarizes
146 information on the turnover element of beta diversity (Baselga, 2010). In cases such as the
147 NBN data, where details of collection effort are variable and often unknown, a reduced
148 species list for a hectad is more likely to represent under-collection than an absence of
149 species. We are interested in fairly broad habitat classifications so that, on balance, a hectad
150 with just the most common species for, say, rocky shores will cluster with a hectad with a
151 longer species list containing the same common species. In such cases, Simpson's index is
152 preferable to other common indices like Sørensen's, which are also influenced by the change
153 in species number, even if all species in the species-poor hectad are also found in the species-
154 rich area.

155

156 The matrix of Simpson's dissimilarities among hectads was clustered using average
157 dissimilarities among groups (UPMGA) using the HCLUST package in R (R Development
158 Core Team, 2013). A stopping rule is needed to judge the number of clusters that represents a

159 parsimonious description of structure in the data. Methods for finding an ‘elbow’ in cluster
160 dispersion data (Kreft & Jetz, 2010) did not work satisfactorily in this study: the decline in
161 within-cluster dispersion with group number was too smooth. We attempted to find a cluster
162 number using a technique based on resampling the locations to create a null expectation of
163 cluster structure (cf. Dudoit & Fridlyand, 2002). A conventional r^2 statistic was used to judge
164 the degree to which clusters represent the distances between hectads. The squared distances
165 from cluster centroids required to calculate r^2 can be obtained from the sum of squared
166 distances between cluster members divided by the number of sites in the cluster (Anderson &
167 Thompson, 2004). The expectation is that r^2 will rise more or less asymptotically to 1 as the
168 number of clusters approaches the number of hectads. This will occur even as hectads are
169 randomly assigned to clusters of the same size as those defined from hierarchical clustering.
170 The difference between the r^2 from hierarchical clusters defined by group averaging and
171 clusters assembled randomly gives an estimate of the degree of structure for any given
172 number of groups. To estimate the expectation from random allocation of hectads to clusters,
173 the average r^2 was calculated after 100 randomizations for each node in the hierarchical
174 clustering using the ‘sample’ command in R to reallocate cluster membership.

175

176 **Patch size effects**

177 By defining an informative clustering of hectads, the spatial structure within cluster groups
178 could be examined. Hectads from the same cluster group were considered to form patches
179 when they were contiguous (using an eight cell neighbourhood). For the most common
180 clusters, this led to a relatively large number of fragments (patches), separated by areas of
181 different habitat. The number of hectads of the same cluster in each patch defines the patch
182 size hereafter.

183

184 In any heterogeneous system, species richness will increase with an increasing sample area or
185 number of independent sample quadrats, reflecting the increased effort. The term species
186 accumulation is used to refer to this effect (Gotelli & Colwell, 2001). We therefore expect
187 overall species richness to be linked to patch size. An appropriate null model of species
188 accumulation is needed to test for the presence of additional influences on species richness in
189 patches. A null model for the expected rate of increase of species in the absence of spatial
190 structure can be estimated from a random resampling process. Hectads within each habitat
191 group were randomly reassigned to patches to generate a species accumulation in the absence
192 of any island biogeographical effects. Simulations were carried out using POPTOOLS (Hood,
193 2010). The size of any observed departure from the null expectation was expressed using z -
194 scores, the difference between observed and mean resampled species number for each patch
195 divided by the SD from 100 randomizations. Extended tests indicated that the null
196 expectations were stable at 100 simulations and larger resampling trials were not needed. If
197 there are no patch effects, then the z -scores should lie close to zero with no trend associated
198 with changes in patch size.

199
200 An alternative means of examining the patch size effect is to test the average number of
201 species for a fixed area in different sized fragments (Fahrig, 2013; called D-SAR in Giladi *et*
202 *al.*, 2014). This was tested using regressions of the mean species richness hectad⁻¹ in patches,
203 as a function of the patch size for different habitats. If patch-related processes help species
204 establish or persist at the hectad scale, then the regression of mean hectad richness should
205 have a positive slope.

206
207 Alongside any landscape effects at the patch scale, two alternative predictors were also
208 examined to evaluate other potential influences on average richness hectad⁻¹ in patches. The

209 collection effort in the NBN database is uneven as the data reflect the amalgamation of
210 different surveys. Details like the number of individuals examined or survey effort in
211 different contributions to the NBN data are generally not known. Blight *et al.* (2009) found
212 that the number of survey records in a hectad helped explain variation in species richness.
213 ‘Survey records’ in this context includes repeat observations of the same species so that data
214 of this sort includes information on the total effort expended in the hectad. A further variable
215 that may influence species richness in patches of hectads is the length of coastline found there.
216 A hectad containing a relatively longer fragment of coastline may contribute more species to
217 a patch if a longer coastline implies a more convoluted shoreline where habitat heterogeneity
218 results in increased species richness. A longer coastline also implies a greater intertidal area
219 within a hectad. Greater area within a hectad may also boost species richness if island
220 biogeographical processes operate at this scale. The average coastline length per hectad
221 within a patch was therefore examined as a third potential predictor of patch species richness.

222

223 **Analysis of patch effects**

224 The species accumulation (z -scores) relationships with patch size were examined using
225 ANCOVA with group as a fixed factor and patch size as the covariate. Residual plots were
226 examined for departures from normality and homoscedasticity and these assumptions were
227 supported by the diagnostic plots. Full ANCOVA models (including the group \times patch size
228 interaction term) were fitted and compared with models containing the main effects only. The
229 optimum model to describe the data was subsequently chosen on the basis of the lowest small
230 sample corrected Akaike Information Coefficient (AIC_c). Akaike weights were used to
231 compare candidate models. The Akaike weight indicates the relative support for a model,
232 while the ratio between the weights of different models (the evidence ratio) indicates the

233 likelihood that one model is a better fit to the data than the comparator (Burnham and
234 Anderson, 2002).

235

236 Calculating the mean species hectad⁻¹ involved estimates with varying precision (dependant
237 on the number of heactads in a patch). Estimates from patches with low numbers of hectads
238 were more variable. This heterogeneity creates an issue for ordinary least squares regression
239 and was addressed by using weighted regression: based on the variance in a patch size of n
240 hectads being s^2/n , where s^2 is the variance of species richness across all hectads in a habitat
241 group. The relative influences of competing models using combinations of the three predictor
242 variables (patch size, average coastline length of hectads in patch and total records in patch)
243 were also compared using AIC_c values from competing linear regression models.

244

245 The influence of patch size on species identity was estimated using the matrix of Simpson's
246 dissimilarities for each habitat type. The null hypothesis here is that hectads drawn from
247 patches of similar sizes will be more similar than hectads from differently sized patches. This
248 was tested using the RELATE test within the PRIMER package, which calculates the rank
249 correlation between the matrix of dissimilarities and a distance matrix of difference in patch
250 size, using a randomization equivalent to a Mantel test to evaluate the significance of the
251 observed correlation (Clarke & Gorley, 2006).

252

253 The presence of edge effects on isolated hectads can also be tested by examining the structure
254 in the Simpson's dissimilarity matrix. Under the null hypothesis of no edge effects, the
255 average dissimilarity between a hectad and all hectads not in the same habitat group should
256 not change when comparing means from isolated hectads with means from hectads
257 contiguous with at least one hectad of the same habitat group. If the species composition in

258 isolated hectads is influenced by the surrounding habitat, then isolated hectads should be
259 more similar to hectads from other habitat groups than is the case for hectads from larger
260 patches.

261

262 **RESULTS**

263 The relationship between group number in the cluster analysis and explanatory power (r^2)
264 rose to an asymptote, but the profile contained jumps, with a pronounced plateau (Fig. 2).

265 The difference between the observed r^2 and the average profile from resampling also reached
266 a plateau, indicating that much of the pattern in the data could be explained by relatively few
267 groups. The most informative division was therefore taken to occur at 15 clusters, the
268 inflection point in the profiles.

269

270 With 15 clusters providing a parsimonious description of structure in the dataset, the three
271 largest identified clusters contained 94% of the 598 hectads with data. These three groups
272 were used to examine patch effects after identifying contiguous hectads with the same cluster
273 type. Although cluster members were found all around the coastline of Great Britain (Fig. 3),
274 there appeared to be some general associations with broad-scale habitat conditions. Hectads
275 in group A ($n = 358$) were generally found on open coasts and in positions consistent with the
276 likely presence of at least some rocky shore (including what EuroSION classed as
277 ‘conglomerates’). Group B (130 hectads) was concentrated around sheltered areas,
278 particularly estuarine areas like the Wash in the east of England, the Solent on the south coast
279 and the Solway Firth. The 73 hectads of group C seemed to be associated with predominantly
280 sedimentary shores in open coast areas. A cross referencing of hectads in separate clusters
281 with the nearest EuroSION category showed strong associations (G-test of association, $G_6 =$
282 338, $P < 0.001$, clusters not random across EuroSION habitat types).

283

284 The total species lists in the three largest groups were overlapping in content, with an average
285 intergroup Simpson's dissimilarity of 6%. Within the small number of species exclusive to
286 each group, there was some evidence to support the broad-scale environmental associations
287 suggested from Fig. 3. For example, the saltmarsh and seagrass specialists *Assiminea*
288 *grayana* and *Haminoea navicula* were found exclusively in group B. Relative frequencies of
289 species in the separate groups were also suggestive of a coarse separation into dominant shore
290 types: characteristic rocky shore species such as *Patella vulgata*, *Nucella lapillus*,
291 *Melarhappe neritoides* and *Gibbula umbilicalis* were more than four times more likely to be
292 found in group A than in the other two groups.

293

294 Pairs of hectads within the same habitat group became more dissimilar with distance (Fig. 4).
295 In contrast, distances between hectads within a patch were relatively small, reflecting the
296 sizes of patches overall. This meant that the average beta dissimilarity between hectads was
297 greater than the dissimilarities within patches. Observed species lists in patches are therefore
298 accumulated from less distinct species lists than is the case for random allocations: as patches
299 are made up of neighbouring hectads more similar than the average for the coastline as a
300 whole. This phenomenon was reflected by larger habitat patches having fewer species than
301 would be expected on the basis of random allocation of hectads to patches (Fig. 5, Table 1).
302 The model with an interaction between patch size and habitat type had an evidence ratio
303 suggesting that it was more than twice as likely as more simple models. The relative decline
304 in accumulated species was greatest in habitat B, associated with estuarine habitats. This
305 grouping also had a standardized species number above one for single hectad patches:
306 indicating that single hectad patches were richer than might be expected by chance (mean
307 standardized species richness for single hectad patches = 0.65, SE 0.288). By comparison,

308 single hectad patches of habitat C had close to the expected number of species (mean
309 standardized richness -0.09 , SE 0.1176). Single hectad patches of habitat A had fewer species
310 than would be expected from random selection of single hectads (mean score -0.42 , SE
311 0.173).

312

313 Unsurprisingly, the proxy for collection effort, number of records, was a consistent predictor
314 of the average species richness hectad⁻¹ in different patches (Fig. 6). Patch size was also
315 supported as a predictor for species density, although the effects were not consistent in
316 different habitat groups (Table 2). For group A, the evidence ratio suggests that the optimum
317 model was over three times as likely as the next best alternative. For this habitat, consistent
318 with rocky shore dominated areas, species density increased with patch size (slope 0.00254 ,
319 SE 0.000781). In contrast, species density declined with patch size in habitat group B
320 (estuarine areas). The optimum model for habitat group B had overwhelming support
321 compared to competing models and included all three predictor variables. This habitat group
322 therefore had evidence for an additional effect of coastline length. Species density was higher
323 in more convoluted estuarine areas. The final habitat group had less support for an optimum
324 model, although the effect of species record number was still positive for species density. The
325 weakly supported alternative model ($w_iAIC_c = 0.298$) had a negative relationship between
326 patch size and species density, although the estimated error around the slope was relatively
327 high (habitat C, model averaged slope for patch size = -0.03 , SE 0.023).

328

329 The dissimilarity between hectads did not seem to be a function of the relative patch size for
330 habitat A (RELATE test, correlation between dissimilarity matrices = 0.001 , $P > 0.05$). In
331 contrast, greater differences in patch size were related to the degree of difference in species
332 composition within habitat B (correlation 0.039 , $P < 0.05$) and habitat C (correlation = 0.084 ,

333 $P < 0.05$). Aside from intra habitat changes in dissimilarity, inter habitat dissimilarity was
334 also affected by patch size for two habitat groups (Table 3). Isolated hectads of both habitat
335 groups B and C were more similar to hectads from other groups when compared to the means
336 from larger patches. In contrast, isolated hectads of habitat A were no less dissimilar to non-
337 A habitat than larger patches.

338

339 **DISCUSSION**

340 There were habitat-specific differences in the way species accumulated in patches of different
341 size and in the influence of patch size on species richness hectad⁻¹. In the case of habitat
342 group A (rocky shore dominated), the increase in species density with patch area in larger
343 patches of group A habitat is an effect consistent with patterns seen in island biogeography.
344 An island effect is also suggested by the pattern for single hectad fragments of habitat A to
345 have fewer species than expected from a random selection of hectads. Habitat B had the
346 opposite pattern, relatively species rich single hectads, with a decline in species density in
347 larger patches. In contrast, there was less evidence for patch size effects on species richness
348 in the third habitat grouping (associated with sedimentary shores in open coast areas).

349

350 It is not clear why the habitat group consistent with rocky shores had an island
351 biogeographical effect of increasing species density in hectads from larger patches. The
352 inference from island biogeography is that species extinction is lower and/or immigration to
353 hectads is higher in larger patches. Immigration of molluscan species to areas of newly
354 established artificial hard shores far smaller than hectads seems relatively rapid (Dethier *et al.*,
355 2003; Krone *et al.*, 2013). Other studies, however, suggest that recolonization can take
356 decades for species with direct development (Johnson *et al.*, 2008). The converse of a
357 positive effect of patch size on the supply of colonists to individual hectads would be an

358 increase in extinction in small fragments of rocky shore. For example, if being surrounded by
359 sedimentary areas increases stress on rocky shores (e.g., by sedimentation or scouring,
360 Airoidi, 2003), this may cause greater local extinction rates with lower associated mollusc
361 diversities.

362

363 Both greater immigration to larger patches and greater loss of species in isolated hectads can
364 affect the species density–patch size relationship in the same way: it is therefore difficult to
365 separate these potential effects in the current study. Little is known about the extinction–
366 colonization dynamics of intertidal species at the scale of hectads. Considerable turnover has
367 been observed in areas of 4 m² monitored over a decade (Dye, 1998); for reasons of
368 tractability, most monitoring occurs at a similar scale. If larger patches reflect an increased
369 potential for source populations to supply colonists for recovery of local extinctions, this may
370 lead to greater local species densities. As the habitats are large relative to the movement
371 capacity of intertidal molluscs, a link between habitat extent and hectad-scale extinction
372 colonization dynamics would require a metapopulation effect with local populations linked
373 by larval dispersal or rafting. Repeated surveys of areas with different habitat extents could
374 test a recolonization rate and local extinction rate hypotheses, but this would be a challenging
375 project and not one that appears to have been attempted as yet.

376

377 The lower species richness hectad⁻¹ in larger patches of estuarine habitat (group B) is not
378 surprising given the general tendency for estuarine habitats to be species poor (Attrill, 2002).
379 However, this alone does not explain why a landscape effect similar to rocky shores does not
380 seem to be present in habitat B. The positive influence of average coastline length implies
381 that more convoluted coastlines promote species richness. A more convoluted coastline could
382 promote species richness hectad⁻¹ by an effect of habitat area, but this is not consistent with

383 the decline in species density in larger patches of habitat B. It therefore seems more likely
384 that the positive effect of coastline length reflects greater habitat heterogeneity. As single
385 hectads of habitat B had higher species richness than expected by chance alone (Fig. 5), this
386 implies an edge effect of enrichment from surrounding, non-estuarine, habitat or that the
387 isolated fragments have a greater chance of including diverse habitat types, with larger
388 patches being more homogenous. Such edge effects are supported by the observation that
389 isolated hectads of habitat B are more similar to the surrounding habitat than is the case for
390 hectads from larger patches (Table 3).

391

392 Habitat C seemed to have few influences of patch size on species richness. The decline in
393 accumulated species in larger patches is consistent with patches undersampling the available
394 diversity among hectads in the dataset, as occurred for the other habitat groups. Similar to
395 Habitat B, there was some suggestion for enrichment from surrounding habitat in isolated
396 hectads of Habitat C, along with some patch size related changes in assemblage composition.

397

398 A distinction that may explain the differences between predominantly hard (group A) and
399 soft habitats (groups B and C) is that relatively more species in soft habitats are also found
400 subtidally. For example, the sediment dwelling genera *Abra*, *Cerastoderma* and *Mya* are
401 given as characteristic components of both littoral and subtidal biotopes in the marine habitat
402 classification for Britain and Ireland (Connor *et al.*, 2004). In contrast, *Littorina* species
403 occurred more frequently in habitat A than any other habitat group, are listed as components
404 of over 50 intertidal biotopes, but only mentioned in one uncommon subtidal biotope
405 (Connor *et al.*, 2004). With additional source areas available, patch size may not be such a
406 good proxy for potential source populations in sedimentary habitats as it is in rocky habitats.

407

408 The theory of island biogeography relies on changes in colonization–extinction dynamics
409 related to island size. Colonization and extinction are also related to life history traits, with
410 the presence or duration of a pelagic dispersal stage potentially influencing molluscan species
411 distributions at a number of scales (Johnson *et al.*, 2001). The absence of a larval stage
412 generally restricts the estimated average dispersal distance of marine species (Kinlan and
413 Gaines, 2003). Under the inference that direct developers are poor dispersers, one might
414 expect this group of species to benefit more from the presence of alternative source
415 populations in a larger habitat patch. This idea was examined by calculating the average
416 patch size where each species was found and then comparing means between the different
417 dispersal modes. If large patches favour direct developers, this group should have a higher
418 average patch size than planktonic dispersers. The result of this comparison was not
419 significant (e.g., average patch size where direct developers found in habitat A = 28.6 hectads
420 (SE 1.31), $n = 54$; equivalent values for planktonic dispersers: mean 26.4 hectads (SE 0.69), n
421 = 214). It is difficult, however, to interpret the lack of a difference between dispersal modes
422 in the face of examples where direct developing species have been shown to reach isolated
423 habitat patches (Johannesson, 1988; O’Foighil, 1989); observations that undermine the
424 assumption behind a simple distinction in colonization range between dispersal modes. The
425 RELATE test makes a further point with respect to the differences between patch sizes: there
426 was not a clear pattern for different assemblages on different sized patches of habitat A.
427 Some influence of patch size on species turnover was evident in habitat types B and C. This
428 may reflect the influences of surrounding habitat on patches of different sizes, particularly the
429 edge effects proposed for habitats B and C earlier.

430

431 As emphasized by Giladi *et al.* (2014), the different techniques of species density and species
432 accumulation applied in the current study emphasize separate mechanisms affecting species

433 richness. The patterns are also likely to be grain-size dependent. Experience of resampling
434 species occurrence grids at different scales suggests that measures of turnover decrease as
435 grain size increases (Lennon *et al.*, 2001). By collating the information at larger scales, the
436 turnover of species at smaller scales is lost, in the same way that widely spaced temporal
437 sampling can miss species turnover (the residency effect, Burns, 2014). If the data were
438 available to subdivide hectads, larger levels of turnover would therefore be expected. This
439 might be expected to lead to greater definition of habitat classes and a wider diversity of
440 landscape effects ranging from none to strong effects depending on target habitat and context.

441

442 It is possible to move to analyses at larger grain scales. As predicted, this decreases the
443 average turnover among locations (e.g., mean Simpson's dissimilarity declines from 0.47
444 among hectads to 0.33 when using 50 km × 50 km cells). Lower discrimination between
445 locations results in the definition of fewer groups that explain less of the observed structure
446 (compare 15 groups with a difference of 0.45% between observed and resampled r^2 in Fig. 2
447 to a difference of 0.19% for five groups with 50 km × 50 km cells, results not shown). A
448 consequence of moving grain size is that different habitats are identified. This restricts the
449 comparisons that can be done across scales. For example, Habitat C is split almost evenly
450 across the two largest groupings of 50 km × 50 km cells.

451

452 The effect of patch size on hard-shore communities suggests that increased use of shore
453 armoring and artificial structures will affect biogeographical patterns by increasing hard
454 shore habitat. One of the concerns about novel structures in the sea is that this will facilitate
455 the establishment of invasive species (Mineur *et al.*, 2012). The inferred island
456 biogeographical effects from species density are consistent with this hypothesis, although the
457 pattern is likely to be a positive relationship between native and introduced species density

458 (Mineur *et al.*, 2008) unless the novel structures lead to a greater degree of habitat
459 homogeneity at the patch scale.

460

461 For conservation planning, the results suggest that reserve spacing and sizes should be
462 considered differently for the different habitat groups. Soft sediment areas maintain species
463 richness in small fragments, so relatively small protected areas (1 hectad) may be functional,
464 with the highest diversity achieved by spacing around the coastline. In contrast, the more
465 rocky shore dominated areas have landscape effects, suggesting that landscape context should
466 also be considered when selecting areas for protection.

467

468 Overall, the results suggest that the presence of landscape and edge effects depends on the
469 type of habitat defined at the scale of analyses. The patch size of rocky habitat appears to
470 promote mollusc species density, possibly by increasing the pool of potential local source
471 populations and/or by reducing local extinction rates. This does not appear to result in a
472 different assemblage in larger patches of rocky habitat, so the majority of associated species
473 appear to benefit. In contrast, species density in soft sediments appears to benefit most from
474 heterogeneity of habitats in adjoining hectads. Intertidal molluscs associated with rocky and
475 sedimentary habitats have different relationships to potential source habitat. The results are
476 consistent with the observation of stronger island effects when species have a higher degree
477 of specialization on the focal habitat (cf., Cook *et al.*, 2006, Lövei *et al.*, 2006). It is likely
478 that other intertidal groups will have different responses, reflecting other relationships with
479 potential source habitats, including variation in the fidelity of species to particular habitats.

480

481 **Acknowledgements**

482 A.J.B. was funded by a Department of Employment and Learning studentship. The referees
483 improved the manuscript through their perceptive comments.

484

485 **References**

486 Airoidi, L. (2003) The effects of sedimentation on rocky coast assemblages. *Oceanography*
487 *and Marine Biology: an Annual Review*, **41**, 161–236.

488 Anderson, M. J. & Thompson, A. A. (2004) Multivariate control charts for ecological and
489 environmental monitoring. *Ecological Applications*, **14**, 1921–1935.

490 Attrill, M. J. (2002) A testable linear model for diversity trends in estuaries. *Journal of*
491 *Animal Ecology*, **71**, 262–269.

492 Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity.
493 *Global Ecology and Biogeography*, **19**, 134–143.

494 Blight, A. J., Allcock, A. L., Maggs, C. A. & Johnson, M. P. (2009) Intertidal molluscan and
495 algal species richness around the UK coast. *Marine Ecology Progress Series*, **396**,
496 235–243.

497 Boström, C., Pittman S. J., Simenstad, C. & Kneib, R. T. (2011) Seascape ecology of coastal
498 biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series*,
499 **427**, 191–217.

500 Bulleri, F. & Chapman, M. G. (2010) The introduction of coastal infrastructure as a driver of
501 change in marine environments. *Journal of Applied Ecology*, **47**, 26–35.

502 Burnham, K. P. & Anderson, D. R. (2002) *Model Selection and Multimodel Inference. A*
503 *Practical Information-Theoretic Approach*. 2nd edn. Springer-Verlag, New York.

504 Burns, K. C. (2014) Pitfalls in quantifying species turnover: the residency effect. *Frontiers of*
505 *Biogeography*, **6**, 3–8.

- 506 Chapman, M. G. (2013) Constructing replacement habitat for specialist and generalist
507 molluscs—the effect of patch size. *Marine Ecology Progress Series*, **473**, 201–214.
- 508 Clarke, K. R. & Gorley, R. N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E,
509 Plymouth.
- 510 Connor, D. W., Allen, J. H., Golding, N., Howell, K. L., Lieberknecht, L. M., Northen, K. O.
511 & Reker, J. B. (2004) *The Marine Habitat Classification for Britain and Ireland*.
512 Version 04.05. JNCC, Peterborough, UK.
- 513 Cook, W. M., Lane, K. T., Foster, B. L. & Holt, R. D. (2006) Island theory, matrix effects
514 and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619–623.
- 515 Dethier, M. N., McDonald, K. & Strathmann, R. R. (2003) Colonization and connectivity of
516 habitat patches for coastal marine species distant from source populations.
517 *Conservation Biology*, **17**, 1024–1035.
- 518 Dye, A. H. (1998) Dynamics of rocky intertidal communities: analyses of long time series
519 from South African shores. *Estuarine Coastal and Shelf Science*, **46**, 287–305.
- 520 Dudoit, S. & Fridlyand, J. (2002) A prediction–based resampling method for estimating the
521 number of clusters in a dataset. *Genome Biology*, **3**, research0036–research0036.21.
- 522 Ewers, R. M. & Didham, R. K. (2006) Confounding factors in the detection of species
523 responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.
- 524 Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis.
525 *Journal of Biogeography*, **40**, 1649–1663.
- 526 Gascoigne, J. & Lipcius, R. N. (2004) Allee effects in marine systems. *Marine Ecology*
527 *Progress Series*, **269**, 49–59.
- 528 Giladi, I., May, F., Ristow, M., Jeltsch, F. & Ziv, Y. (2014) Scale-dependent species–area
529 and species–isolation relationships: a review and a test study from a fragmented
530 semi-arid agro-ecosystem. *Journal of Biogeography*, **41**, 1055–1069.

- 531 Gotelli, N. J. (2001) Research frontiers in null model analysis. *Global Ecology and*
532 *Biogeography*, **10**, 337–343.
- 533 Gotelli, N. J. & Colwell, R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the
534 measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- 535 Hawkins, S. J. (2012) Marine conservation in a rapidly changing world. *Aquatic*
536 *Conservation: Marine and Freshwater Ecosystems*, **22**, 281–287.
- 537 Hood, G. M. (2010) *PopTools version 3.2.5*. Available on the internet. URL
538 <http://www.poptools.org>
- 539 Jackson, A. C. & McIlvenny, J. (2011) Coastal squeeze on rocky shores in northern Scotland
540 and some possible ecological impacts. *Journal of Experimental Marine Biology and*
541 *Ecology*, **400**, 314–321.
- 542 Johannesson, K. (1988) The paradox of Rockall: why is a brooding gastropod (*Littorina*
543 *saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L.*
544 *littorea*)? *Marine Biology*, **99**, 507–513.
- 545 Johnson, M. P., Allcock, A. L., Pye, S. E., Chambers, S. J. & Fitton, D. M. (2001) The effects
546 of dispersal mode on the spatial distribution patterns of intertidal molluscs. *Journal of*
547 *Animal Ecology*, **70**, 641–649.
- 548 Johnson, M. P., Pye, S. & Allcock, L. (2008) Dispersal mode and assessments of recovery on
549 the shores of Gruinard, the 'anthrax island' *Biodiversity and Conservation*, **17**, 721–
550 732.
- 551 Kinlan, B. P. & Gaines, S. D. (2003) Propagule dispersal in marine and terrestrial
552 environments: A community perspective. *Ecology*, **84**, 2007–2020.
- 553 Koleff, P., Gaston K. J. & Lennon, J. J. (2003) Measuring beta diversity for presence–
554 absence data. *Journal of Animal Ecology*, **72**, 367–382.

- 555 Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on
556 species distributions. *Journal of Biogeography*, **37**, 2029–2053.
- 557 Krone, R., Gutow, L., Joschko, T. & Schröder, A. (2013) Epifauna dynamics at an offshore
558 foundation - implications of future wind power farming in the North Sea. *Marine*
559 *Environmental Research*, **85**, 1–12.
- 560 Kunin, W. E. (1998) Biodiversity at the edge: A test of the importance of spatial “mass
561 effects” in the Rothamsted Park Grass experiments. *Proceedings of the National*
562 *Academy of Sciences USA*, **95**, 207–212.
- 563 Lennon, J. J., Koleff, P., Greenwood, J. J. D. & Gaston, K. J. (2001) The geographical
564 structure of British bird distributions: diversity, spatial turnover and scale. *Journal of*
565 *Animal Ecology*, **70**, 966–979.
- 566 Lövei, G. L., Magura, T., Tóthmérész, B., Ködöböcz, V. (2006) The influence of matrix and
567 edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in
568 habitat islands. *Global Ecology and Biogeography*, **15**, 283–289.
- 569 MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton
570 University Press, Princeton, NJ.
- 571 Mineur, F., Johnson, M. P. & Maggs, C. A. (2008) Non-indigenous marine macroalgae in
572 native communities: a case study in the British Isles. *Journal of the Marine Biological*
573 *Association of the United Kingdom*, **88**, 693–698.
- 574 Mineur, F., Cook, E. J., Minchin, D., Bohn, K., MacLeod, A. & Maggs, C. A. (2012)
575 Changing coasts: Marine aliens and artificial structures. *Oceanography and Marine*
576 *Biology: an Annual Review*, **50**, 187–232.
- 577 O’Foighil, D. (1989) Planktotrophic larval development is associated with a restricted
578 geographic range in *Lasaea* a genus of brooding hermaphrodites bivalves. *Marine*
579 *Biology*, **103**, 349–358.*et al.*

- 580 Preston, F.W. (1962) The canonical distribution of commonness and rarity: Part II. *Ecology*,
581 **43**, 410–432.
- 582 Quinn, G. P. & Keough, M. J. (2002) *Experimental Design and Data Analysis for Biologists*.
583 Cambridge University Press, Cambridge.
- 584 R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation
585 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- 586 Smith, S. D. A. (2005) Rapid assessment of invertebrate biodiversity on rocky shores: where
587 there's a whelk there's a way. *Biodiversity and Conservation*, **14**, 3565–3576.
- 588 Sólymos, P. & S. R. Lele (2012) Global pattern and local variation in species–area
589 relationships. *Global Ecology and Biogeography*, **21**, 109–120.
- 590 Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species
591 richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*,
592 **17**, 1036–1044.
- 593 Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver
594 of species richness across taxa, biomes and spatial scales. *Ecology Letters*, **17**, 866–
595 880.
- 596 WoRMS Editorial Board (2015) *World Register of Marine Species*. Available from
597 <http://www.marinespecies.org> at VLIZ.
598
599

600 **Biosketch**

601 **Mark Johnson** is a marine ecologist with interests in the spatial ecology of benthic and
602 pelagic systems.

603

604 Author contributions: M.J., C.A.M. and A.L.A conceived the project. A.J.B. collated the data
605 and was involved with the other authors in discussions over the patterns within the data. M.J.
606 carried out the final analyses and wrote the first draft with subsequent contributions from the
607 other authors.

608

609 Editor: Michael Dawson

610 **Table 1.** Ranking of alternative models for the change in standardized intertidal molluscan
 611 species richness in patches of different sizes, with habitat type considered as a categorical
 612 variable. Records were extracted in 2008 for the coastline of Great Britain with habitats
 613 defined by clustering (distributions shown in Fig. 3). Variables shown as Patch: log number
 614 of hectads in patch and Habitat: Habitat group. The small sample corrected AIC (AIC_c) was
 615 used to compare models. ΔAIC_c is the difference between the model with the lowest AIC_c
 616 and other models, $w_i AIC_c$ are Akaike weights used to compare the support for different
 617 models.

618

Predictor variables in model	r_{adj}^2 (%)	AIC_c	ΔAIC_c	$w_i AIC_c$
Habitat, Patch, Habitat \times Patch	15	445.2	0.00	0.585
Habitat, Patch	13	447.1	1.88	0.229
Patch	11	447.5	2.30	0.186
Habitat	4.4	458.3	13.16	0.001

619

620 **Table 2.** Evaluation of alternative models for the average intertidal molluscan species
 621 richness hectad⁻¹ in patches of different size around the coast of Great Britain. Predictor
 622 variables are the average coastline length of hectads in a patch (coastline), the log of the total
 623 number of species records in the patch (Records) and the number of hectads in the patch
 624 (Patch). The small sample corrected AIC (AIC_c) was used to compare models. ΔAIC_c is the
 625 difference between the model with the lowest AIC_c and other models, $w_i AIC_c$ are Akaike
 626 weights used to compare the support for different models. Colinearity of predictor variables
 627 was minimal, variance inflation factors (VIFs) were below 1.4

628 a) Habitat group A

Coastline	Records	Patch	r_{adj}^2 (%)	AIC_c	ΔAIC_c	$w_i AIC_c$
	x	x	70	-14.4	0.00	0.737
x	x	x	70	-12.1	2.31	0.233
x	x		66	-6.8	7.63	0.016
	x		65	-6.5	7.94	0.014
		x	15	47.9	62.29	0.000
x		x	14	50.2	64.59	0.000
x			2	56.8	71.24	0.000

629

630 b) Habitat group B

Coastline	Records	Patch	r_{adj}^2 (%)	AIC_c	ΔAIC_c	$w_i AIC_c$
x	x	x	81	-1.6	0.00	0.946
	x	x	78	5.1	6.76	0.032
x	x		77	5.9	7.52	0.022
	x		71	15.0	16.64	0.000
x			28	55.2	56.81	0.000
x		x	26	57.6	59.23	0.000
		x	-2	70.6	72.19	0.000

631

632 c) Habitat group C

Coastline	Records	Patch	r_{adj}^2 (%)	AIC_c	ΔAIC_c	$w_i AIC_c$
	x		55	16.3	0.00	0.413
	x	x	56	17.0	0.65	0.298
x	x		55	17.8	1.51	0.195
x	x	x	55	19.3	2.95	0.094
x			3	42.9	26.57	0.000
		x	-1	44.3	28.03	0.000
x		x	0	45.3	28.93	0.000

633

634 **Table 3.** Mean hectad dissimilarities between each of the three main habitat groups defined
 635 for intertidal molluscs and all hectads not in the focal habitat group. Records were collated
 636 for hectads around the coast of Great Britain, as described in the text. Dissimilarities were
 637 calculated with the Simpson's index, where larger values indicate greater species turnover
 638 between the hectads being compared. Means were calculated for single hectad patches and for
 639 all larger patches of the same habitat. Differences between means within a habitat were
 640 examined with t-tests (equal variances not assumed).

641
 642

Mean dissimilarity between habitat group and hectads not in same group (SE)				
Habitat group	Isolated hectads	Patches with more than one hectad	t value (df)	p
A	0.57 (0.024)	0.58 (0.006)	0.32 (26)	>0.05
B	0.51 (0.034)	0.62 (0.016)	3.03 (33)	<0.01
C	0.48 (0.018)	0.57 (0.023)	3.04 (60)	<0.01

643
 644

645 **Figure legends**

646 **Figure 1.** Simplified shoreline types for Great Britain derived from the Euroasion dataset
647 (<http://www.euroasion.org/>) hosted by the European Environment Agency. For simplicity, the
648 20 morpho-sedimentological codes of Euroasion have been amalgamated into rocky shores
649 (including artificial substrate), sedimentary shores (beaches), estuarine-type habitats and
650 conglomerates/cliffs with rock and sediment on the shore. The latter category is intermediate
651 between rocky and sedimentary shore. Locations mentioned in the text are labelled.

652

653 **Figure 2.** Degree of variation accounted for (as r^2) as a function of the number of clusters
654 defined in the hectad data for intertidal molluscs around the coast of Great Britain. The
655 observed pattern is derived from clusters defined by UWPGA averaging of the matrix of
656 dissimilarities among hectads. The random group allocation line is generated by permuting
657 the group labels randomly across hectads (mean of 100 randomizations for each group
658 number). The dotted line for observed-random indicates the information content over and
659 above the expected increase in r^2 with group number. Profiles show a sharp inflection at 15
660 groups, which was taken to give a parsimonious description of structure in the data.

661

662 **Figure 3.** Distribution of hectads allocated to the three most common habitat groups (A, B, C)
663 defined by clustering of intertidal mollusc data for Great Britain. The three groups contain 94%
664 of the 598 hectads with data and were defined in the most informative grouping based on the
665 proportion of variance explained (r^2).

666

667 **Figure 4.** Comparison between (a) the distribution of separation distances between hectads
668 within patches and (b) the average turnover of mollusc species between hectads separated by
669 different distances (as mean Simpson's dissimilarity, error bars SE). The majority of within-

670 patch separations are less than 25 km, at which point turnover is lower than the asymptotic
671 value. Data are shown for habitat group A only, but the patterns are similar in groups B and C.

672

673 **Figure 5.** Relationship between patch size and the accumulated number of intertidal mollusc
674 species found in the patch. The species list for each patch is expressed as a standardized score
675 with reference to the mean and standard deviation from a random allocation (within each
676 habitat group) of hectads to patches. If species richness is unaffected by landscape-related
677 processes, the data are expected to have a mean of 0 and no slope. The separate lines
678 represent the patch size \times habitat group interaction found in the best supported model (r_{adj}^2
679 15%).

680

681 **Figure 6.** Residual variation in mollusc species density (species hectad⁻¹) as a function of
682 predictor variables in the optimum model (identified using AIC_c in a multiple regression
683 analysis). Plots separate the influence of variables controlled for the influence of other
684 predictors. Rows in the figure show the patterns for different habitats, distinguished as open
685 circles (habitat A), filled triangles (habitat B) and shaded squares (habitat C). Each column
686 relates to a separate predictor variable. As only the variables contained in the optimum model
687 for each habitat are shown, gaps in the figure indicate where a no contribution was estimated
688 for a predictor of variation in mollusc species density for a particular habitat.

Fig. 1

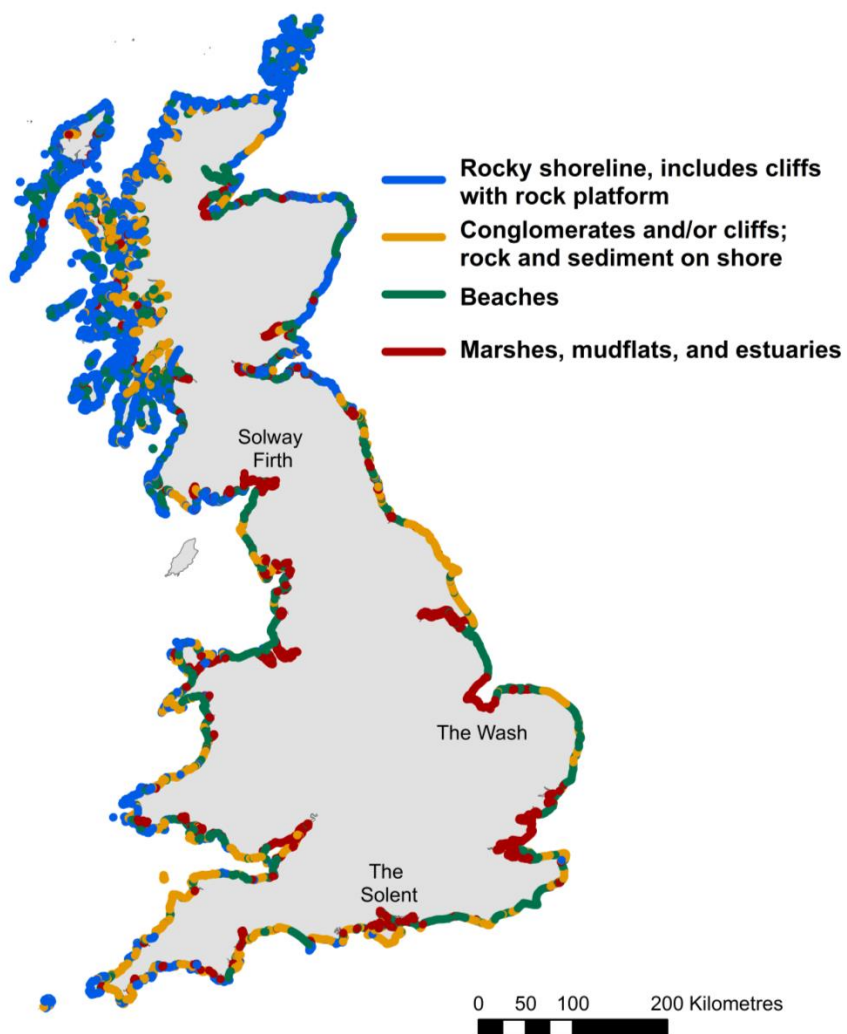


Fig. 2.

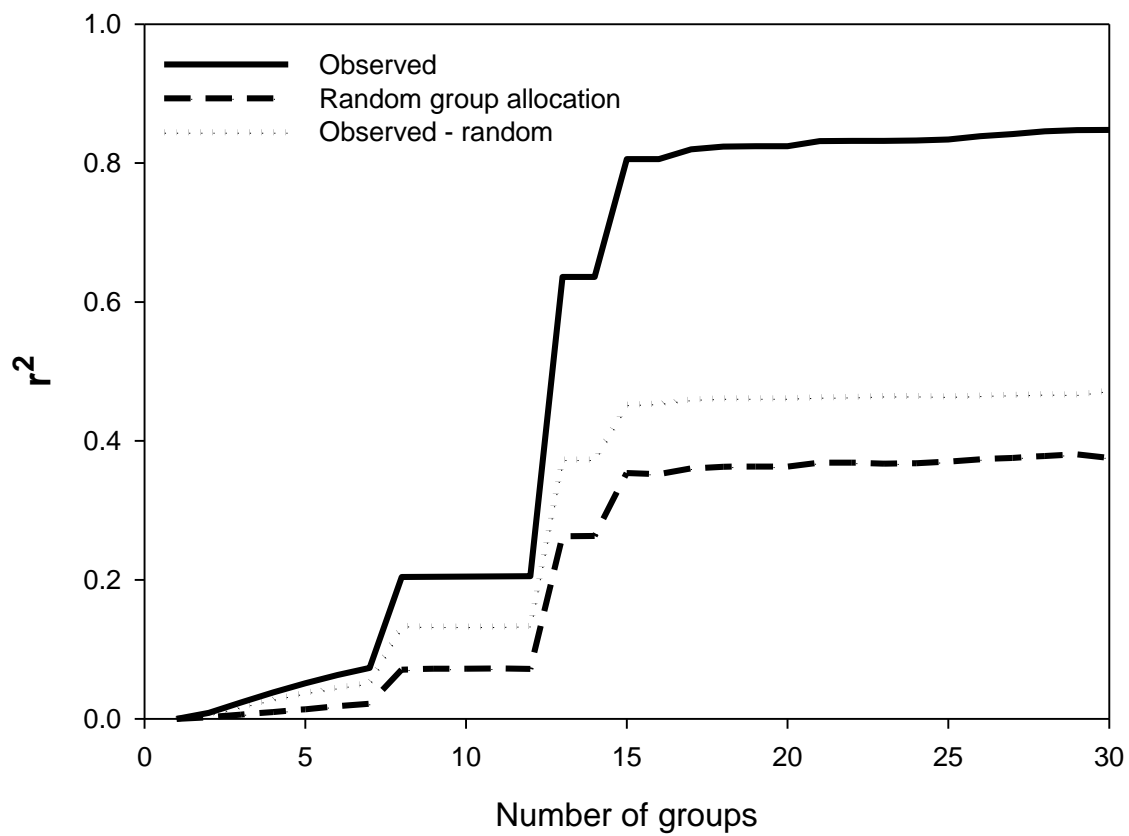


Fig. 3.

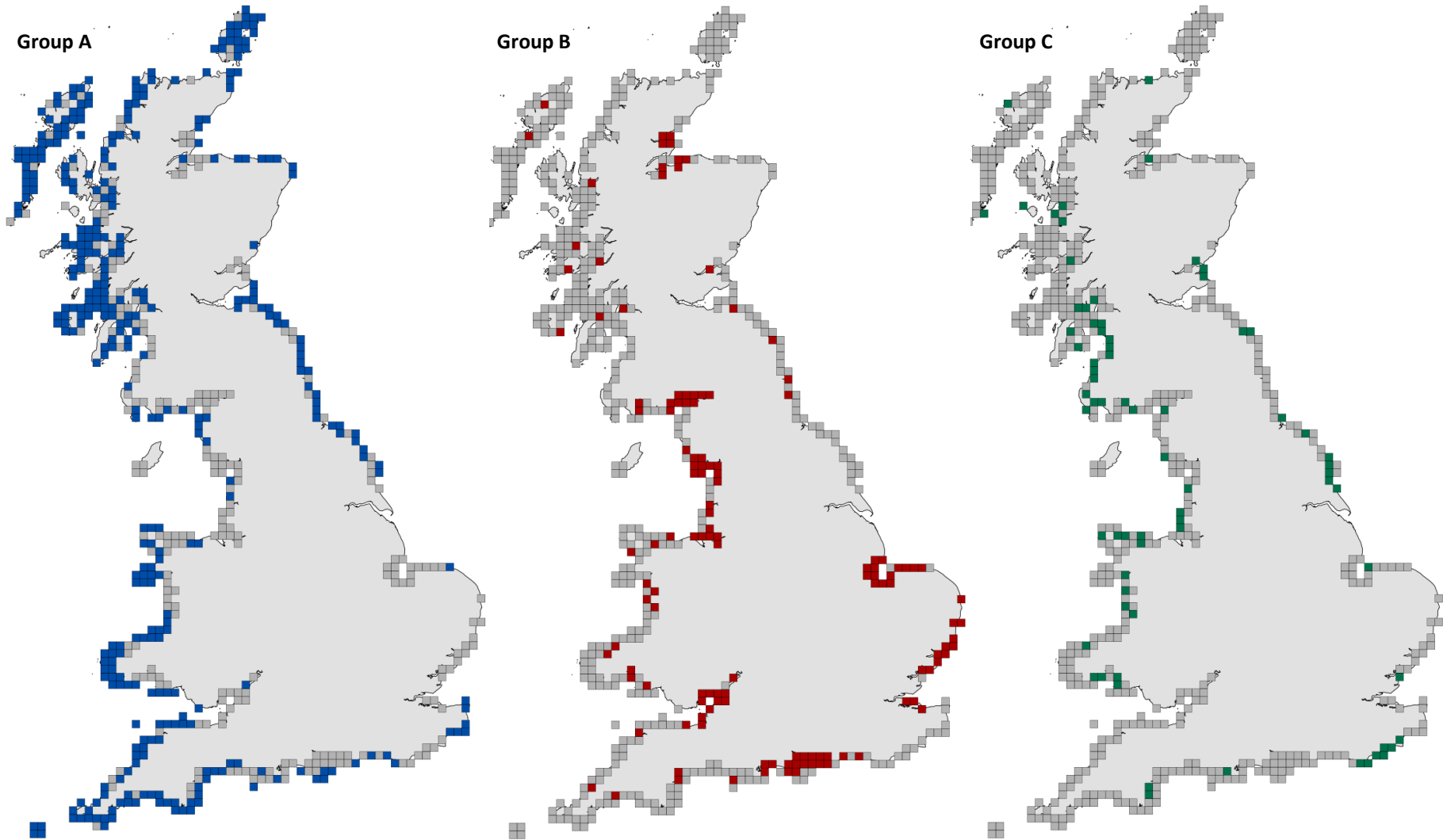
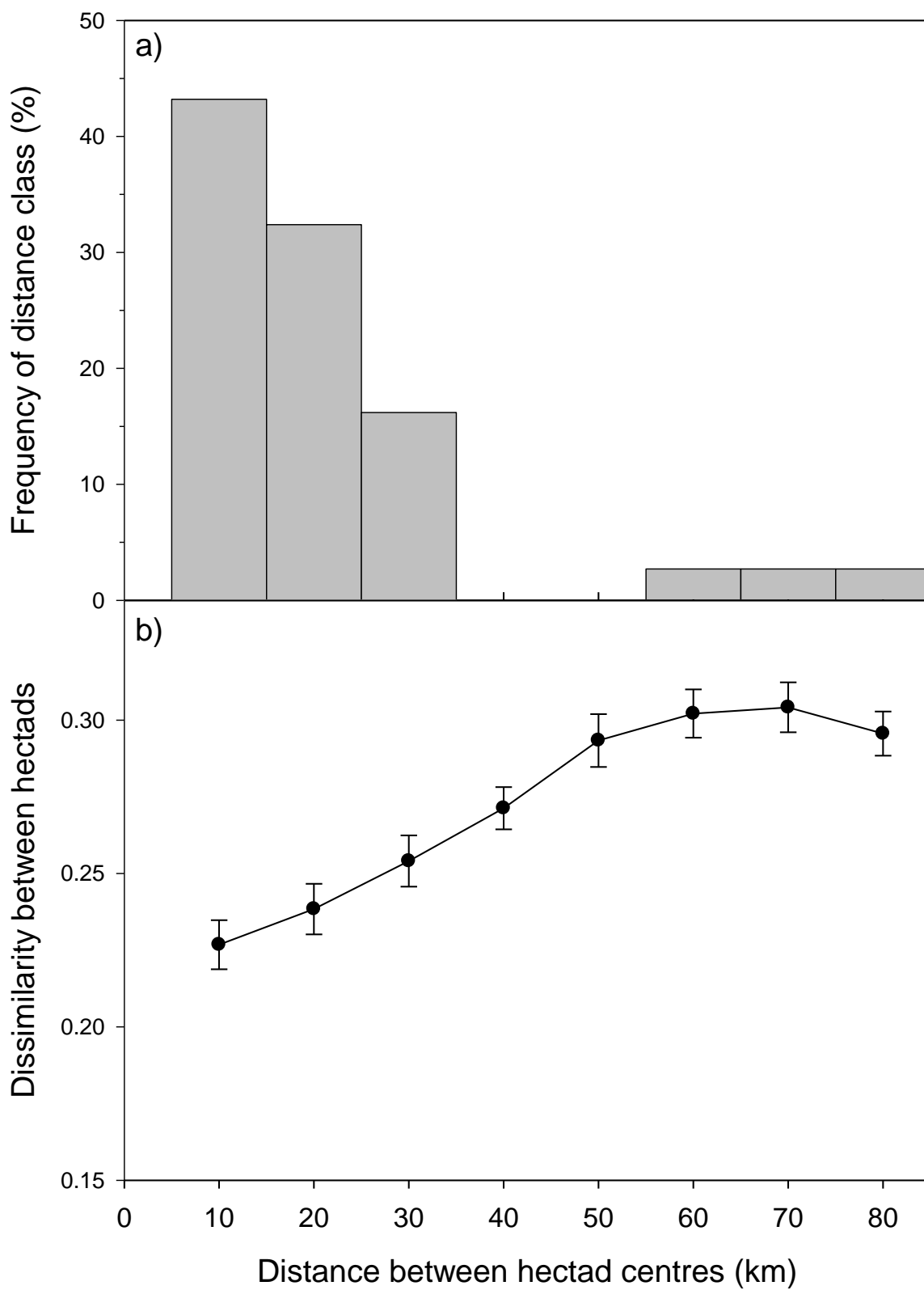


Fig. 4.



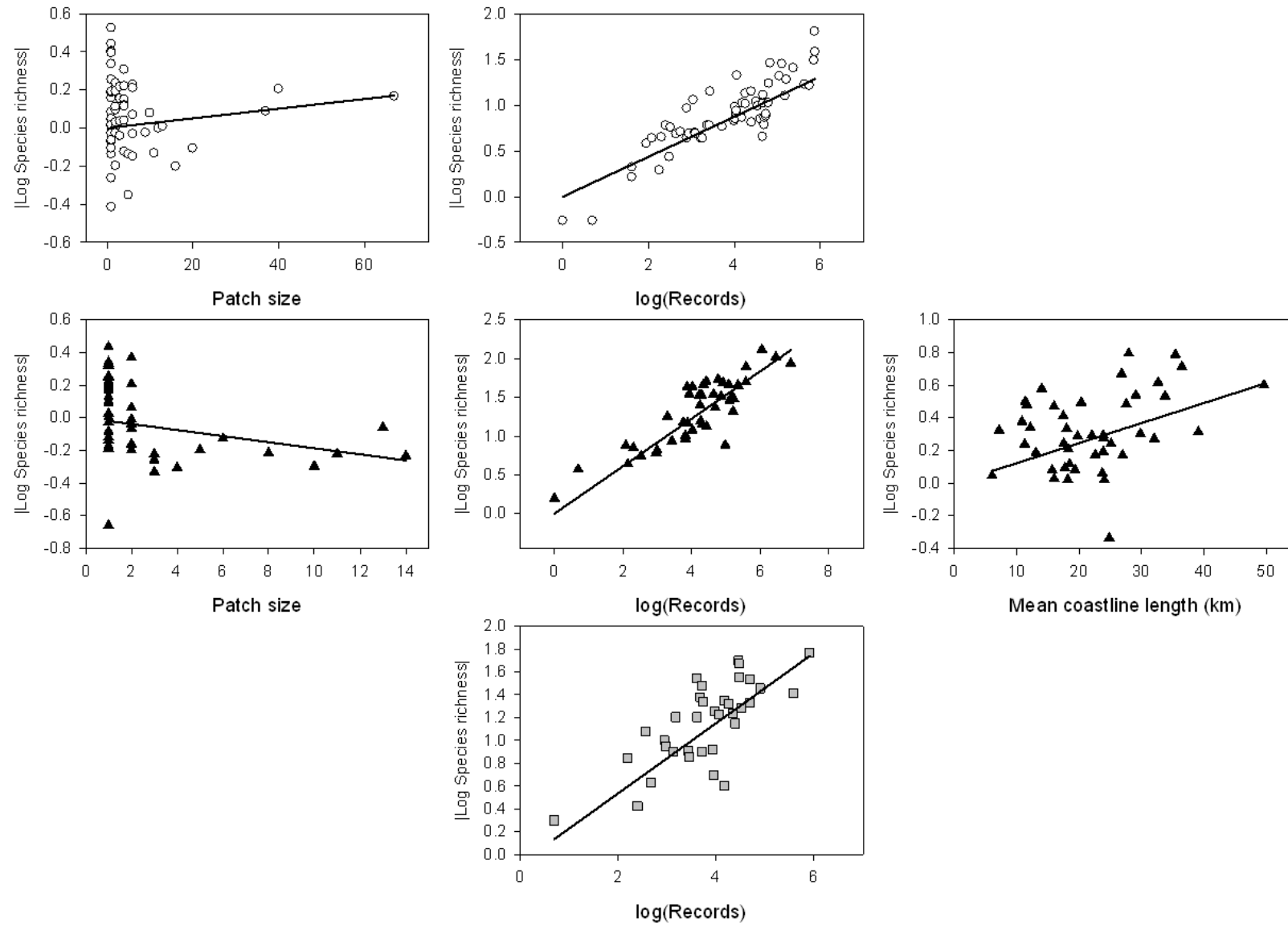


Fig 6.