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The richness of small pockets

Boada, Jordi; Pages Fauria, Jordi; Gera, Alessandro; Macpherson, Enrique; Santana, Yaiza; Romero, Javier; Alcoverro, Teresa

Marine Environmental Research

DOI:

[10.1016/j.marenvres.2018.09.012](https://doi.org/10.1016/j.marenvres.2018.09.012)

Published: 01/11/2018

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Boada, J., Pages Fauria, J., Gera, A., Macpherson, E., Santana, Y., Romero, J., & Alcoverro, T. (2018). The richness of small pockets: Decapod species peak in small seagrass patches where fish predators are absent. *Marine Environmental Research*, 142, 1-6.
<https://doi.org/10.1016/j.marenvres.2018.09.012>

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1 **The richness of small pockets: decapod species peak in small seagrass patches where fish**
2 **predators are absent**

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4 **Jordi Boada ^{a,*^}, Jordi F. Pagès ^{a,b^}, Alessandro Gera ^{a^}, Enrique Macpherson ^a, Yaiza**
5 **Santana ^a, Javier Romero ^c, Teresa Alcoverro ^{a,d}**

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7
8 ^a Centre d'Estudis Avançats de Blanes. CEAB-CSIC. C/ Acc. Cala St. Francesc 14, 17300 -
Blanes. Girona. Spain

9 ^b School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, United Kingdom

10 ^c Departamento de Ecología, Facultad de Biología, Universidad de Barcelona, Av. Diagonal
645, 08028 - Barcelona. Spain

11 ^d Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, 570 002 Mysore,
12 Karnataka (India)

* Corresponding author: Ph. +34 972336101; Fax. +34 972337806; E-mail:

jboada@ceab.csic.es

[^] These authors have contributed equally to this work

13 **Abstract**

14 Patchy landscapes behave differently from continuous ones. Patch size can influence species
15 behaviour, movement, feeding and predation rates, with flow-on consequences for the diversity
16 of species that inhabit these patches. To understand the importance of patchiness on regional
17 species pools, we measured decapod richness and abundance in several seagrass patches with
18 contrasting sizes. Additionally, we evaluated potential drivers of patch-specific species
19 distribution including resource abundance, predator habitat use and the structural complexity of
20 patches. Our results showed a non-random distribution of decapod species: small patches were
21 clear hotspots of diversity and abundance, particularly of larger-bodied epifaunal decapods.
22 Interestingly, these hotspots were characterized by lower nutrient resources, lower canopy
23 height, but also lower predator use. Small fish invertivores such as *Coris julis* and several
24 species of *Symphodus* were mostly restricted to large patches. These resident predators may be
25 critical in clumping predation in large patches with consequences for how biodiversity of their
26 prey is distributed across the seascape. Our results highlight the idea that a habitat mosaic with
27 both large and small seagrass patches would potentially bolster biodiversity because preys and
28 predators may seek refuge in patches of different sizes.

29

30 **Keywords:** Biodiversity, Fish use, Top down control, Mediterranean Sea, Patch size, species
31 richness, *Posidonia oceanica*, predation

32

33 1. Introduction

34 Vegetated seascapes are often spatially heterogeneous, typically occurring as mosaics of
35 vegetated patches surrounded by a matrix of sand that separates each patch from other vegetated
36 areas. Patchy landscapes behave very differently from continuous ones. Patch size can influence
37 species recruitment, behaviour, movement, feeding and predation rates, with flow-on
38 consequence for the diversity of species that inhabit these patches (Andren 1992, Williams
39 1964; Connor & MacCoy 1979, Pittman 2011). Unsurprisingly then, in patchy interconnected
40 landscapes, patch size has been one of the principal metrics used to predict local and regional
41 species abundance and distribution. Basic island biogeography principles applied to these
42 patches suggests that the number of species at a location could be predicted by patch size and
43 isolation merely by considering immigration and extinction probabilities, with larger patches
44 typically accumulating a higher species richness (MacArthur and Wilson, 1967). However,
45 island biogeography predictions cannot easily be ported to landscape and seascape scales, where
46 other factors likely play vital roles in determining assemblage patterns. Patches may not always
47 behave like islands. For one, populations in patches are more connected through individual
48 dispersal from adjacent patches than are populations between islands (Menendez & Thomas
49 2000). This connectivity is often species specific, with life history traits fundamental in
50 determining species-area relationship outcomes. Small isolated patches will likely affect the
51 survival of habitat specialists with limited dispersal abilities much more than vagile generalist,
52 for whom a fragmented landscape may be perceived as sufficiently connected (Thomas 2000).
53 Additionally, most benthic species, even those with low mobility, have planktonic phases of
54 dispersal, for which habitat fragmentation may not typically determine settlement (Gaines et al.
55 2007; Robertson and Butler Iv 2009). Finally, where spatial heterogeneity interacts with
56 ecosystem processes (i.e. predatory-prey interactions, competition), the distribution of vagile
57 fauna can be determined at small scales (Boström, Jackson & Simenstad 2006). Landscape
58 configurations can therefore drive a potentially predictable clumping of trophic processes (hot
59 and cold predation spots, Nelson & Boots, 2008; Temming, Floeter, & Eherich, 2007).

60 Seagrass habitats range from large contiguous meadows to highly patchy seascapes. In the
61 latter, multiple seagrass patches are embedded in a matrix (e.g. sediment) that affects animal
62 movement and survival depending on habitat size and relative isolation (Tanner 2006, McNeill
63 & Fairweather 1993, Bell et al. 2001, Orth et al. 2006). This spatial heterogeneity can be the
64 result of natural or anthropogenic fragmentation or colonization processes (Gera et al. 2014,
65 Tamburello et al. 2012), and can strongly influence the diversity of flora and fauna within the
66 seascape (Bell *et al.* 2001; Hovel 2003; Arponen & Boström 2012). This is particularly true for
67 species associated with seagrass leaves and rhizomes, many of which are highly site attached

68 (Gacia *et al.* 2009, Manjón-Cabeza *et al.* 2009; Ramírez and García Raso 2012). Causes of local
69 spatial patchiness include differential recruitment, differential access to food resources, active
70 and passive dispersal or differential growth and mortality. Recruitment may be patch size
71 dependent with medium sizes having more recruits than small and large patches (Reusch 1998).
72 This patch dependency has also been observed in growth rates of filter-feeding bivalves for
73 which less vegetation and smaller patches may be more beneficial (Carroll & Peterson 2013).
74 Patch configuration can influence the way resources are distributed in the seascape. Small
75 patches capture or retain less detrital material, making them relatively poorer in nutrient
76 availability (Ricart *et al.* 2015) and potentially affecting plant growth and habitat structure (see
77 Gera *et al.* 2013). Predator-prey interactions, acting at local scales, can also drive heterogeneous
78 diversity patterns (Boström *et al.* 2011), for instance when the distinctive distributions of
79 predatory fish within fragmented meadows cause variations in predation impact (Fernández *et*
80 *al.* 2005). In highly mobile predator species, predation hotspots result in a non-random
81 distribution of their prey in patchy seascapes (Farina *et al.* 2017). This has also been observed in
82 fish herbivores, where landscape attributes determine the non-random distribution of herbivores
83 (Pagès *et al.* 2014). However, this predation distribution is not always consistently linked to
84 patch size within the meadows. Highly fragmented seascapes may not provide adequate shelters
85 and the relationships between predation intensity and vegetation cover may not always be linear
86 (Böstrom *et al.* 2011). Other factors such as the within-patch composition and location of the
87 patch on the shore can also influence the effect of the patch size (Mills & Berkenbusch 2009).

88 What is clear is that understanding how marine organisms respond to seagrass seascape
89 configurations is complex, the result of several drivers acting simultaneously, and at different
90 spatial scales. If predation is the main driver, we should expect prey distribution to be linked to
91 predator abundance that in turn may be related to landscape attributes (Farina *et al.* 2017).
92 However, if other factors such as differences in resource availability or competition are the main
93 drivers, patch size may be critical in determining species distribution, with diversity and
94 abundance increasing with patch size. Our objective in this study was to understand how the
95 patchiness of a seascape influences the regional species pool of decapods. We estimated
96 decapod richness and abundance associated with the leaves of patches of contrasting sizes in
97 highly heterogeneous seagrass meadows. Additionally, we evaluated potential drivers of patch-
98 specific species distribution including resource abundance, predator habitat use and the
99 structural complexity of patches.

100 **2. Materials and Methods**

101 *2.1. Study design and sampling site*

102 We assessed the species richness and abundance of decapods in seagrass canopies in small (\leq
103 3m^2) and large ($> 10\text{m}^2$) randomly chosen seagrass patches ($n=6$ of each). Patches were selected
104 on a $\sim 15\text{km}$ stretch of the Western Mediterranean dominated by highly heterogeneous meadows
105 ($41^\circ 41'$ N, $002^\circ 50'$ E, Gera et al. 2013). All of our selected patches were embedded in a sandy
106 matrix separated by at least 2 m from other patches (average distance between patches $\sim 5\text{m}$), to
107 ensure a similar degree of isolation. At each of the patches we additionally measured seagrass
108 nutrient content (resource abundance), predatory fish habitat use and canopy height (structural
109 complexity).

110 2.2. Decapod abundance and diversity

111 We sampled canopy-dwelling decapod diversity and abundance in *P. oceanica* patches in
112 summer using a towed hand net sampling method. The device consisted of a rectangular frame
113 ($40 \times 20\text{cm}$), with a 50 cm long handle, with a net (mesh size $250\ \mu\text{m}$) long enough to prevent the
114 escape of fauna caught in its folds (130cm) and a small plastic jar attached to its end (Russo
115 1985). We marked off a 1×1 meter quadrat for each sample, sampling the seagrass canopy with
116 30 constant strokes of the hand net per quadrat (see Russo et al. 1985 for details of the sampling
117 technique). We sampled a total of 36 quadrats (3 replicates per patch, 6 patches per size, 2
118 sizes). To avoid variability caused by potential edge effects, all samples were situated along the
119 patch edge since the small patches were too small to sample their centre.

120 2.3. Fish patch use

121 We measured fish habitat use to estimate the presence of potential decapod predatory fish in the
122 patches. We sampled the same small and large patches from which decapods were sampled (see
123 above). We additionally sampled two more patches per size class since we expected larger
124 variability in fish habitat use ($n=8$ patches per size, a total of 16 samples). We set GoPro (Full
125 HD) cameras in patches attached to an iron bar at a fixed distance (60cm) from the edge of the
126 patch (see Boada 2015 for details). We recorded videos for 30 min in each patch (the first and
127 last 5 min were discarded to avoid SCUBA divers' effect, effective video duration = 20 min).
128 For each video we calculated fish patch use of the most common and abundant associated
129 predatory fish species (i.e. *Coris julis*, *Symphodus spp*, *Diplodus spp*, Bell & Harmelin-Vivien
130 1983, Guidetti 2000). Fish use of habitats was expressed as the percentage of time a given fish
131 species was present in a patch. We calculated the percentage of time spent by each fish species
132 in a given patch by adding the number of individuals of each species for the time they were
133 present within the patch (in minutes), and then dividing it by the total video sampling time (20
134 minutes). The overall time of predatory fish use was obtained by adding the time of all fish
135 species together related to the total time video sampling time (20 min). In addition, although our

136 sampling was not designed for larger-ranging shoaling species, we checked all videos to
137 quantify any *Sarpa salpa* (the predominant herbivore fish in these waters, Prado et al 2007)
138 recorded.

139 2.4. Seagrass nutrient content

140 Most species of decapods we recorded were mesograzers (feeding on epiphytes) and deposit
141 feeders (Gambi et al. 1992). To evaluate potential competitive exclusion related to nutrient
142 limitation (resource quality) in different patch sizes, we measured the nutrient content (nitrogen)
143 in *P. oceanica* rhizomes. This is a highly reliable and integrative method to detect differences in
144 nutrient availability in the water and the environment (see Roca et al 2015 for more details). We
145 collected two seagrass shoots per patch. The top 2 cm of rhizome were separated, dried at 70°C
146 for 48 hours and ground to a fine powder and pooled to obtain an adequate amount of sample
147 for subsequent analysis. Rhizome nitrogen concentration was measured using an Elemental
148 Analyzer FlashEA1112 (ThermoFinnigan Unidade de Técnicas Instrumentais de Análise,
149 Universidade de Coruña). Two of the patches, one for each treatment were not found at the end
150 of the experiment and only 5 patches were sampled for this variable. However, given the low
151 variability of this measurement we are confident that if there were differences in this variable
152 due to patch size they would be detected despite the lower sample size (see Gera et al. 2013).

153 2.5. Seagrass structure

154 We evaluated differences in habitat structure between patch size as a potential driver of species
155 richness and abundance by measuring canopy height at each of the patches. We did this at the
156 same time as our other sampling to ensure there were no seasonal changes. The length of *P.*
157 *oceanica* leaves influences the degree to which the habitat offers prey species chances to hide
158 from predators (Farina et al. 2009, Pagès et al 2012). We estimated canopy height (cm) in the
159 patches sampled for decapod fauna by measuring the vertical distance between the substrate and
160 the top of the standing leaves in two different randomly selected areas within each patch. Since
161 we could not find one patch of each treatment (see above) only 5 patches were sampled for this
162 variable (2 replicates, 5 patches, 2 size classes).

163 2.5. Statistical Analysis

164 To determine the effects of patch-size on the dependent variables ‘decapod species richness’
165 and ‘decapod species abundance’ we performed general linear models with a Poisson
166 distribution and the explanatory variable ‘Patch Size’: 2 levels small ($\leq 3\text{m}^2$) and large ($>10\text{m}^2$)
167 and patch (3 replicates per patch) as a random factor. A negative binomial distribution was used
168 to deal with over-dispersion when necessary (i.e. for ‘total decapod abundance’). Similarly, we

169 used generalized linear models with either Poisson or Gaussian distributions (as required) to
170 assess the effect of ‘Patch Size’ to the three different processes analysed; i) fish habitat use, ii)
171 nutrient resources and iii) canopy height. Patch was included as a random factor in the nutrient
172 resources and canopy height model. All the statistical analyses were performed in R using *lme4*
173 package for the general linear model analyses (R Development Core Team 2013, Bates et al.
174 2016).

175 **3. Results**

176 *3.1. Decapod diversity*

177 Decapod species richness and abundances were significantly higher in small patches. The
178 average number of total individuals per patch was 39 ± 5 individuals/m² for small patches, while
179 the abundance in large patches was 28 ± 3 individuals/m² (Fig. 1b, Table 1). Similarly, small
180 patches hosted a significantly greater species richness with an average of 2.9 ± 0.5 species/m²
181 compared to 1.3 ± 0.1 species/m² in large patches (Fig. 1a, Table 1). The most common and
182 abundant species (*Hippolyte prideauxiana*) was ubiquitously distributed regardless of patch size
183 (Fig. 1c). In contrast, other species were mainly present in the small patches (i.e. *Cestopagurus*
184 *timidus*, *Hippolyte garciaraso* and *Thoralus cranchii*, Fig. 1d,e,f). Additionally, the three
185 largest decapod species were only present in the small patches, despite being relatively scarce in
186 general (i.e. carapace length: *Macropodia rostrata* 7.0-7.5mm, *Pisa tetraodon* 11.5-12.2mm,
187 *Pisa nodipes* 12.5-12.7mm, Table 2).

188 *3.2. Fish patch use*

189 The overall predatory fish use of patches was greater in large patches. The average use of large
190 patches by predatory guilds was $\sim 49.1 \pm 5.5$ %, compared to 27.4 ± 4.8 % in small patches (Fig.
191 2b, Table 3). This trend resulted from the high % use of large patches by *Coris julis* and by
192 species of the genus *Symphodus* (see Fig 3a, b). However, species from the genus *Diplodus*,
193 which are known to be very territorial and display restricted home ranges ($< 1 \text{ km}^2$) (Aspillaga et
194 al. 2016), appeared to use both patch sizes similarly (Fig. 3c). No shoals of the herbivorous fish
195 *Sarpa salpa* were recorded in the videos. However, video recording might not be the best
196 technique to determine the abundance of shoaling fish species, with relatively large home
197 ranges (Pagès et al. 2013).

198 *3.3. Seagrass nutrient content*

199 We found nutrient content to be higher in larger patches with average values of $\sim 1.75 \pm 0.2$ %N
200 compared to small patches in which the %N was $\sim 1.07 \pm 0.2$ (Fig. 2a, Table 3).

201 3.4. *Habitat structure*

202 Finally, we also found differences in canopy height between patches of different sizes (Fig. 2c,
203 Table 3). Large patches had, in general, higher canopy height with an average of 30.6 ± 2 cm long
204 leaves compared to smaller patches, where leaves were 22.9 ± 2 cm long, on average (Fig. 2c).

205

206 **4. Discussion**

207 Our results show a clear non-random distribution of decapods with patch size across the
208 *Posidonia oceanica* seagrass seascape. We found large patches to be less rich in decapod
209 species and with lower abundances. Thus, small patches appear to be hotspots of decapod
210 diversity and abundance. Of the various hypotheses that could potentially explain how patch
211 size influences species richness and abundance, our observations point strongly to the role of
212 top-down control. As expected from previous studies in the same system (Gera et al 2013,
213 Ricart et al 2015), larger patches had more resources (i.e. nitrogen content in seagrass leaves,
214 detrital material) and were structurally more complex (i.e. taller canopies), factors typically
215 linked to enhanced diversity and abundance. However, these large patches had several resident
216 fish predators. Predators were much less frequent in small patches, making them refuges of
217 decapod diversity and abundance. In addition, the largest species of decapods, which were more
218 susceptible to mobile predatory fish, were only present in the small patches. Overall, our results
219 highlight the potential effect of predation in shaping decapod distribution.

220 Small patches have their limitations. Refuge, resources retention and nutrients are often
221 limiting (Gera et al 2013, Ricart et al 2015), and as species scramble to appropriate them,
222 competitive exclusion should likely leave smaller patches with fewer species (Murray and Baird
223 2008; Keymer et al. 2012). As resources decline, competitive exclusion alone can predictably
224 explain the local extinction of species in smaller, putatively less nutritious and unprofitable
225 patches (Kolb 2008). For a range of groups, from infaunal macroinvertebrates, decapods and
226 fish, studies have shown a positive species-area relationship (Bowden et al. 2001, Boström et al.
227 2006). Similarly, nutrient limitation or physical degradation of small patches caused by habitat
228 fragmentation can seriously impact the survival of non-mobile fauna due to changes in food
229 availability and increased predation risk (Villafuerte et al. 1997). The prevailing assumption
230 then is that decreasing patch sizes should result in lower species diversity of decapods
231 communities (Reed et al 1982, Birkely & Gulliksen 2003). Surprisingly, our results showed the
232 opposite trend, with a clear peak of decapod diversity and abundance in small, less structured
233 *Posidonia oceanica* patches. Earlier studies on seagrass systems have documented similar
234 results, showing that the density of faunal groups (decapods, fish, bivalves) either do not

235 respond or increased with reducing patch size, linked to positive edge effects (area/perimeter
236 relationship, Hirst and Attrill 2008; Arponen and Boström 2012). Although we did not record
237 herbivores in our video samples, herbivory on small patches could certainly interact with lower
238 nutrients to reduce overall canopy heights (Gera et al 2013). Our study does not test if
239 increased light availability in lower-canopied small patches could increase decapod diversity
240 and abundance, by favouring epiphyte growth. Given that some species of decapods are
241 consumers of the epiphyte community (Gambi et al. 1992), this potential feedback cannot be
242 ruled out and is an avenue for further studies.

243 The uneven distribution of diversity across a patchy seascape can be generated and
244 strengthened by predator-prey interactions responding to local-scale ecosystem processes
245 (Boström et al. 2011). In our study, predatory fish showed a clear preference for large patches;
246 thus, predation pressure clearly increased with increasing habitat size. In a similar study Hovel
247 and Fonseca (2005) show that smaller seagrass patches served as predation refugia for blue
248 crabs. This has also been observed in mobile insects that actively select larger patches to
249 forage, ignoring smaller patches (Lienert 2002, Haynes and Crist 2009). Since the ability to
250 perceive habitats is determined by the size, vision and movement characteristics of an animal,
251 the effects of patch size on predatory fish behaviour can be highly relevant (Macreadie et al.
252 2009). This was also proposed by Eggleston et al. (1999) as an explanation for higher predation
253 on grass shrimp (*Palaemonetes spp.*) and small, mobile crustaceans (i.e. amphipods and
254 isopods, but not of *Hippolytes spp* shrimps) in artificial seagrass habitats with different patch
255 sizes. Additionally, Micheli and Peterson (1999) found that medium sized predators may avoid
256 moving into fragmented areas of an habitat, since they have limited refuge and are potentially
257 more vulnerable to larger predators (also supported by Morales-Nin and Moranta 1997; Moranta
258 et al. 2006). The most abundant fish groups recorded in our study had distinct preferences for
259 larger patches, which are also potentially the best refuges. Small fish invertivores such as *Coris*
260 *julis* and several species of *Symphodus* that are important decapod consumers (Bell and
261 Harmelin-vivien 1983) were mostly restricted to large patches where they could potentially find
262 better refuge from their own predators. The exceptions were species from the genus *Diplodus*
263 that we found using small and large patches equally. This genus comprises several, very
264 different generalist species and are typically not seagrass-specific (i.e. *Diplodus sargus*,
265 *Diplodus vulgaris*, *Diplodus annularis*). Resident predators may be critical in maintaining
266 hotspots of predation in large patches with consequences for all larger species of leaf-associated
267 decapods that were absent.

268 Predator behaviour can have major implications for diversity patterns across landscapes
269 (Lima and Zollner 1996) . If landscape attributes modify that behaviour, changes in landscape

270 can result in a very different distribution of species across space. Disentangling the relationship
271 between predator behaviour, landscape attributes and diversity patterns is essential to
272 understanding how processes like fragmentation are likely to affect ecosystem functioning,
273 particularly in strongly top-down controlled ecosystems (Lima and Zollner, 1996). For seagrass
274 meadows, seascape configurations can drive a potentially predictable clumping of medium size
275 fish predators in large patches that in turn can drive decapod leaf-associated species to
276 concentrate in small patches. These resident predators may be critical in maintaining hotspots of
277 predation in large patches with consequences for how biodiversity of their prey is distributed
278 across the seascape. Seagrass seascapes with a matrix of small and large patches may potentially
279 bolster biodiversity because preys and predators may seek or find refuge in patches of different
280 sizes.

281 **5.Acknowledgments**

282 This research was funded by the Spanish Ministry of Science and Innovation (CTM2017-
283 86695-C3-3-R) and supported J. B. (scholarship BES-2011-043630). Authors are also very
284 grateful to R. Arthur for his contributions to this manuscript. JFP acknowledges financial
285 support from the Welsh Government and Higher Education Funding Council for Wales through
286 the Sêr Cymru National Research Network for Low Carbon, Energy and Environment.

287 Symbols in Fig. 3 are courtesy of the Integration and Application Network, University of
288 Maryland Center for Environmental Science (ian.umces.edu/symbols/).

289

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496

497 **Table 1.** Mean values and SE for decapod species richness and abundance in large and small
 498 patches. P-values show the results from generalized linear models testing the effect of patch size
 499 (fixed factor) on decapod species richness and abundance (response variables). Patch number
 500 was included as random factor. Significant p-values are given in bold.

501

Patch Size	Species richness	SE	Total Abundance	SE
Large	1.28	0.11	28.28	2.91
Small	2.89	0.49	39.67	5.05
P value	<0.01		<0.03	

502

503 **Table 2.** Mean abundance value \pm standard error per patch size for each species. Carapace
 504 length in mm of each species is also given.

505

Site	Large patches	Small patches	Size Range (mm)
<i>Hippolyte prideauxiana</i>	27.8 \pm 2.9	28.7 \pm 3.8	1.6-4.2
<i>Cestopagurus timidus</i>	0.4 \pm 0.2	2.2 \pm 1.1	1.5-2.4
<i>Macropodia rostrata</i>	0	0.3 \pm 0.1	7.0-7.5
<i>Palaemon xiphias</i>	0	1.1 \pm 0.4	4.6-11.3
<i>Hippolyte garciaraso</i>	0	3.7 \pm 2.7	1.5-3.5
<i>Pisa nodipes</i>	0	0.1 \pm 0.1	12.5-12.7
<i>Thorulus cranchii</i>	0	3 \pm 1.4	2.0-3.6
<i>Pisa tetraodon</i>	0	0.2 \pm 0.1	11.5-12.2
<i>Eualus occultus</i>	0	0.3 \pm 0.3	1.8-3.2
<i>Galathea bolivari</i>	0	0.6 \pm 0.6	3.5

506

507 **Table 3.** Results from generalized linear model testing the effect of patch size (fixed factor) on
 508 nutrients, fish habitat use and habitat structure (response variables; processes). Patch number
 509 was used as a random factor in models for nutrients and structure. A Poisson distribution was
 510 used in model for fish use.

Response	DF	Chi Sq	P value	Factor
Nutrients	1	5.44	0.02	Patch size
Fish use	1	10.626	<0.01	Patch size
Structure	1	6.98	<0.01	Patch size

511

512 **Figure 1.** Decapod species richness and abundance (individuals per square meter) in large
513 (filled) and small (blank) seagrass patches. a) mean number of species \pm standard error (SE)
514 found in samplings (18 for large and 18 for small patches). b) mean number of individuals of all
515 the species pooled found in samplings \pm SE. The rest of the plots represent the mean abundance
516 \pm SE found for each of the species c) *Hippolyte prideauxiana*, d) *Cestopagurus timidus*, e)
517 *Thorulus cranchii* and f) *Hippolyte garciaraso* respectively.

518

519 **Figure 2.** Functional processes studied; resource limitation a) as percentage of nutrient content
520 in plant tissues, fish use of the landscape b) as percentage use of patches by the fish predatory
521 guild and the structural complexity of the habitat c) as canopy height (leaves length).

522

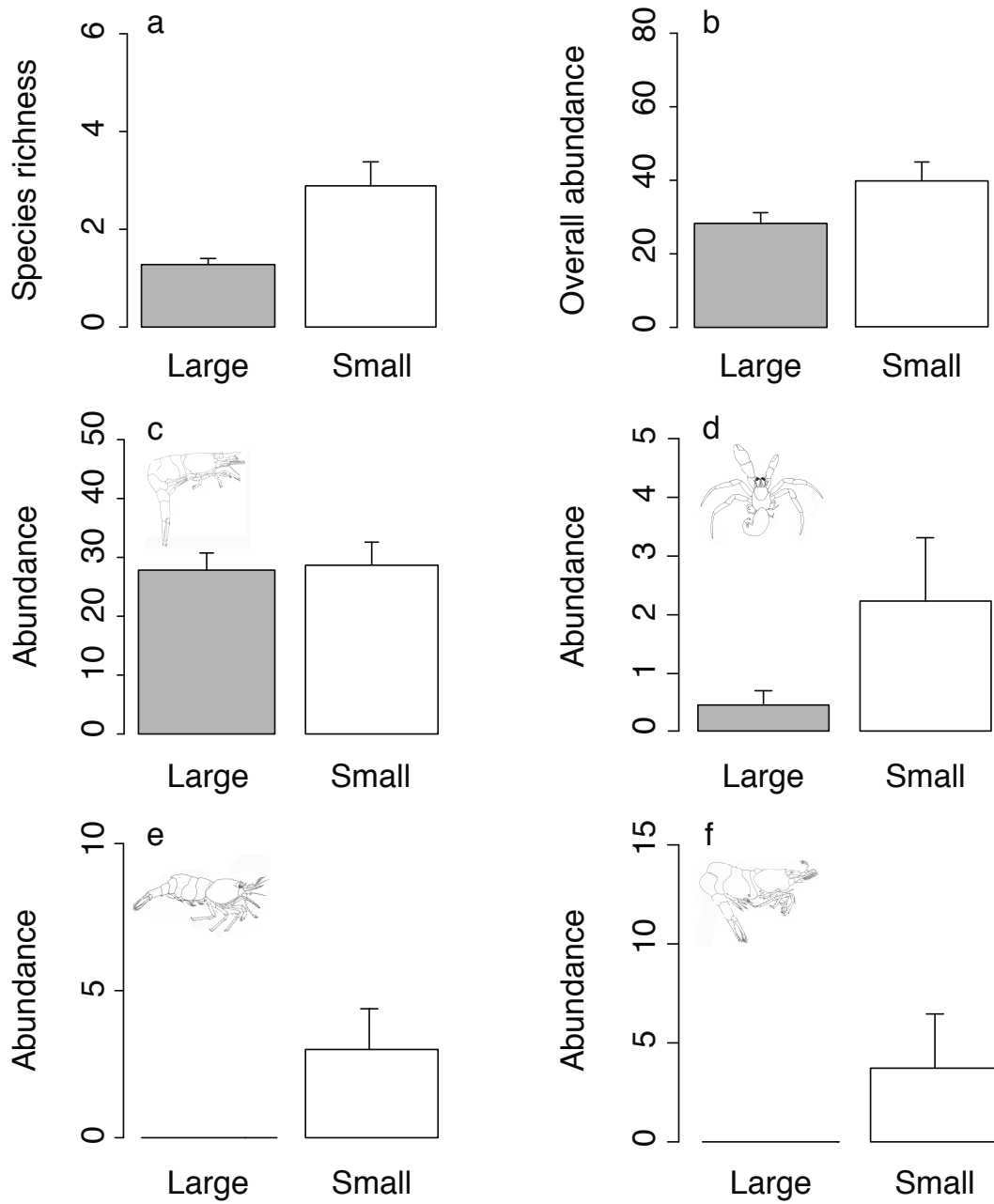
523 **Figure 3.** Fish habitat use of the landscape according to patch sizes. Filled grey bars represent
524 the mean percentage use of the large patches \pm SE (see methods) while empty bars represent the
525 percentage use of small patches \pm SE by predatory fish species, a) *Coris julis*, b) *Symphodus*
526 *spp.*, c) *Diplodus spp.*

527

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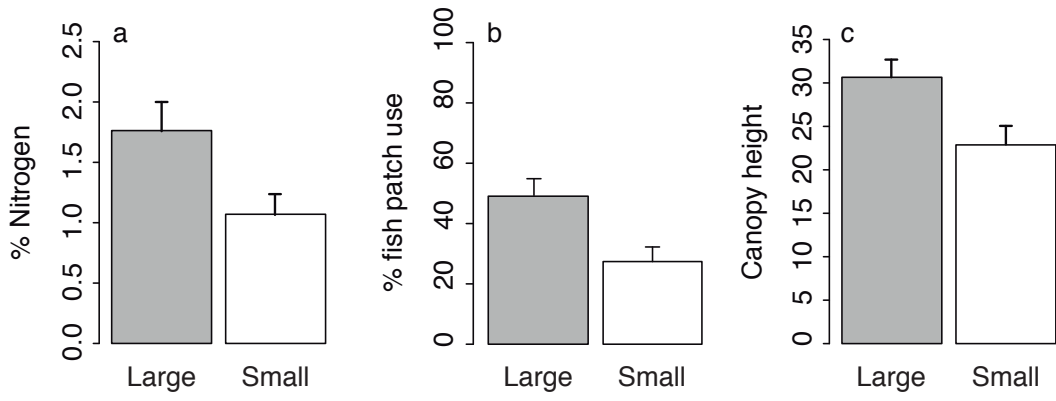
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530 Fig. 1.
531



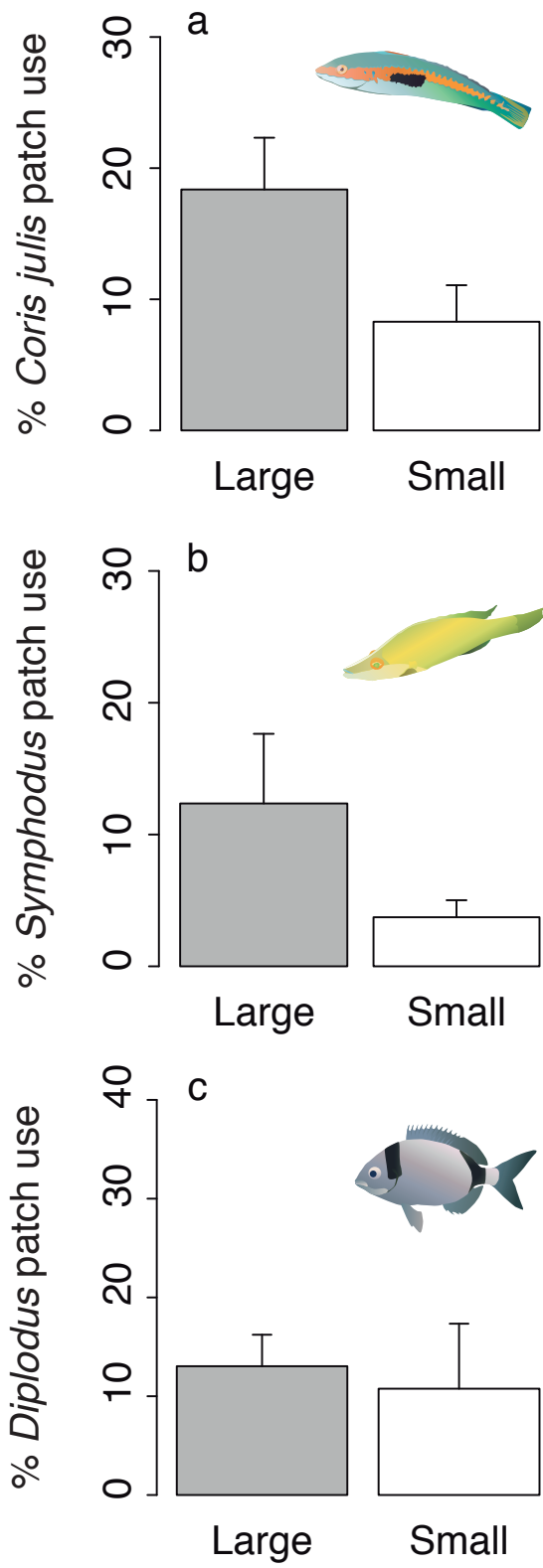
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533 **Fig. 2.**
534



535
536

537 Fig. 3.
538



539