The richness of small pockets

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

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

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Jordi Boada [a*^]**, Jordi F. Pagès** [a,b^]**, Alessandro Gera** [a^]**, Enrique Macpherson** [a]**, Yaiza Santana** [a]**, Javier Romero** [c]**, Teresa Alcoverro** [a, d]

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

8
[b] School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, United Kingdom

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

9
[d] Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, 570 002 Mysore,
10
Karnataka (India)

11
12

* Corresponding author: Ph. +34 972336101; Fax. +34 972337806; E-mail: jboada@ceab.csic.es

^ These authors have contributed equally to this work

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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.

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30   **Keywords:** Biodiversity, Fish use, Top down control, Mediterranean Sea, Patch size, species

31   richness, *Posidonia oceanica,* predation

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1. Introduction

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

Seagrass habitats range from large contiguous meadows to highly patchy seascapes. In the latter, multiple seagrass patches are embedded in a matrix (e.g. sediment) that affects animal movement and survival depending on habitat size and relative isolation (Tanner 2006, McNeill & Fairweather 1993, Bell et al. 2001, Orth et al. 2006). This spatial heterogeneity can be the result of natural or anthropogenic fragmentation or colonization processes (Gera et al. 2014, Tamburello et al. 2012), and can strongly influence the diversity of flora and fauna within the seascape (Bell *et al.* 2001; Hovel 2003; Arponen & Boström 2012). This is particularly true for 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 ($> 10m^2$) randomly chosen seagrass patches (n=6 of each). Patches were selected

104   on a ~15km stretch of the Western Mediterranean dominated by highly heterogeneous meadows

105   (41°41' N, 002°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 ~5m), 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   (40x20cm), with a 50 cm long handle, with a net (mesh size 250 μm) 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 1x1 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.

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 70ºC

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).

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).

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 ($\leq 3m^2$) and large ($>10m^2$)

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).

3. Results

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/m^2 for small patches, while
179 the abundance in large patches was 28±3 individuals/m^2 (Fig. 1b, Table 1). Similarly, small
180 patches hosted a significantly greater species richness with an average of 2.9±0.5 species/m^2
181 compared to 1.3±0.1 species/m^2 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 garciarasoi* 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).

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 ~49.1±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 (<1km^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).

3.3. Seagrass nutrient content

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

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3.4. Habitat structure

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

4. Discussion

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

Small patches have their limitations. Refuge, resources retention and nutrients are often limiting (Gera et al 2013, Ricart et al 2015), and as species scramble to appropriate them, competitive exclusion should likely leave smaller patches with fewer species (Murray and Baird 2008; Keymer et al. 2012). As resources decline, competitive exclusion alone can predictably explain the local extinction of species in smaller, putatively less nutritious and unprofitable patches (Kolb 2008). For a range of groups, from infaunal macroinvertebrates, decapods and fish, studies have shown a positive species-area relationship (Bowden et al. 2001, Boström et al. 2006). Similarly, nutrient limitation or physical degradation of small patches caused by habitat fragmentation can seriously impact the survival of non-mobile fauna due to changes in food availability and increased predation risk (Villafuerte et al. 1997). The prevailing assumption then is that decreasing patch sizes should result in lower species diversity of decapods communities (Reed et al 1982, Birkely & Gulliksen 2003). Surprisingly, our results showed the opposite trend, with a clear peak of decapod diversity and abundance in small, less structured *Posidonia oceanica* patches. Earlier studies on seagrass systems have documented similar 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 *Diplodu*s
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.

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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 ± 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)
Hippolyte prideauxiana	27.8±2.9	28.7±3.8	1.6-4.2
Cestopagurus timidus	0.4±0.2	2.2±1.1	1.5-2.4
Macropodia rostrata	0	0.3±0.1	7.0-7.5
Palaemon xiphias	0	1.1±0.4	4.6-11.3
Hippolyte garciarasoi	0	3.7±2.7	1.5-3.5
Pisa nodipes	0	0.1±0.1	12.5-12.7
Thoralus cranchii	0	3±1.4	2.0-3.6
Pisa tetraodon	0	0.2±0.1	11.5-12.2
Eualus occultus	0	0.3±0.3	1.8-3.2
Galathea bolivari	0	0.6±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
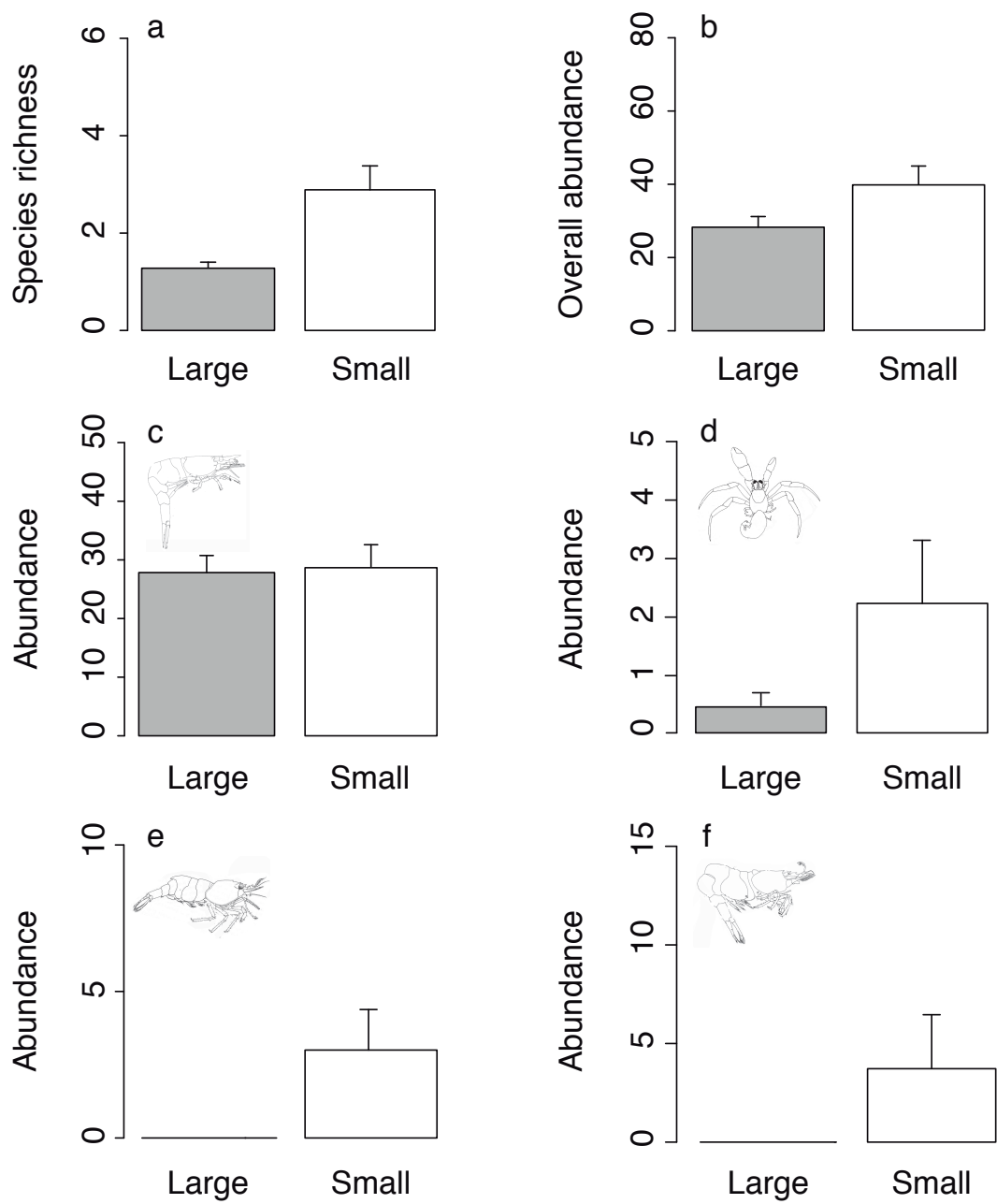
510 used in model for fish use.

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 ± 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 ± SE. The rest of the plots represent the mean abundance

516   ± SE found for each of the species c) *Hippolyte prideauxiana*, d) *Cestopagurus timidus*, e)

517   *Thoralus cranchii* and f) *Hippolyte garciarasoi* 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 ± SE (see methods) while empty bars represent the

525   percentage use of small patches ± SE by predatory fish species, a) *Coris julis*, b) *Symphodus*

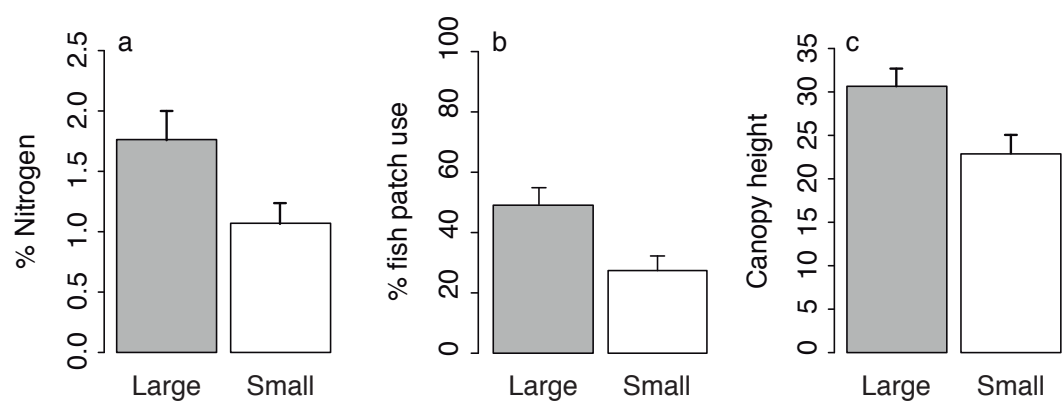526   *spp*, c) *Diplodus spp*.

527

528

529

530 **Fig. 1.**

531

532

533 **Fig. 2.**

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535
536

537 **Fig. 3.**

538