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1 **Habitat continuity effects on gradients of fish biomass across marine**
2 **protected area boundaries.**

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8 **ABSTRACT**

9 Marine Protected Areas (MPAs) could be useful as fisheries management tools
10 for the exportation of pelagic eggs, larvae and adult fish. A decreasing gradient of fish
11 biomass across MPAs boundary may indicate export. We determine whether gradients
12 of decreasing biomass of fish assemblage occurred in Tabarca Marine Reserve over two
13 habitats with different continuity across the boundaries, to test if the patchy nature of
14 the marine environment might act as a barrier for the fish export. In general, significant
15 decreasing gradients in total fish biomass and biomass of some species were observed
16 on *P. oceanica* and rocky substrates, independently of their different continuity through
17 the reserve boundaries. Changes in the multivariate structure of the fish assemblage
18 were correlated with the distance from integral reserve. All of these results support the
19 hypothesis that the exportation of adult fish from Tabarca Marine Reserve occurs, and
20 this process may influence the surrounding fished areas.

21 **Keywords:** marine protected areas, fish, spillover, habitat continuity, visual census,
22 fisheries management.

23 1. INTRODUCTION

24 In recent years, most coastal fish resources have been overexploited (Castilla,
25 2000), raising doubts about the long-term sustainability of certain fisheries (Pauly et al.,
26 2002; Worm et al., 2006). In addition, fish habitats have also been strongly altered by
27 widely used impacting fishing gears (trawls, dredges, ...) resulting in reduced seabed
28 complexity and removal of macrobenthic organisms that provide shelter for others
29 (Sumaila et al., 2000). The poor effectiveness of conventional fisheries management has
30 led to increased interest among marine resource managers in marine protected areas
31 (MPAs) (Bohnsack, 1998; Caddy, 2000), because they are considered a potential means
32 of enhancing the long-term sustainability of many fisheries (Gell and Roberts, 2003;
33 Sobel and Dahlgren, 2004; Ramos-Esplá et al., 2004). However, while the use of MPAs
34 for this purpose is becoming popular, their ability to restock the fishing areas
35 surrounding MPAs is also controversial (Willis et al., 2003; Hilborn et al., 2004; Sale et
36 al., 2005).

37 A number of studies have explored the effect of the cessation of fishing within
38 MPAs and in general, abundance, biomass and mean size of exploited fish populations
39 are higher within protected areas than in nearby non-reserve areas (see Halpern, 2003
40 for review). However, to be useful as fisheries management tools, MPAs need to affect
41 outside fished areas in a positive manner (Russ, 2002; Gell and Roberts, 2003). To
42 benefit fisheries, MPAs are predicted to support adjacent fisheries through two
43 mechanisms: net emigration of adults and juveniles across borders, termed “spillover”,
44 and with the increased production and exportation of pelagic eggs and larvae (Rowley,
45 1994; Kaunda-Arara and Rose, 2004; Abesamis and Russ, 2005).

46 A decreasing gradient of fish biomass across MPAs boundaries, from high inside
47 to low outside, may indicate spillover (Rakitin and Kramer, 1996). Net emigration of
48 adult fish from the MPA, combined with fishing mortality outside, may produce such a
49 decreasing pattern of biomass (Rakitin and Kramer, 1996; Abesamis and Russ, 2005).
50 Protection increases the abundance of the most targeted species by fisheries (e.g. big
51 serranids and big sparids), favouring changes in the fish assemblage structure (Ojeda-
52 Martinez et al., 2007). Therefore, if spillover occurs the structure of fish assemblage
53 will change related with the distance from the MPA. Reporting MPA effectiveness only
54 by total or by individual species biomass is important but not sufficient from an
55 ecosystem-based perspective, being necessary to study the changes in the fish
56 assemblage structure to evaluate precisely the recovery effects of protection. Decreasing
57 gradients of fish biomass across MPA boundaries were observed in a number of studies
58 in tropical and temperate regions, using underwater visual census (Russ and Alcala,
59 1996; Ashworth and Ormond, 2005), catch rates (Kaunda-Arara and Rose, 2004; Goñi
60 et al., 2006) or both (Rakitin and Kramer, 1996; Russ et al., 2003, 2004; Abesamis and
61 Russ, 2005). However, these studies did not account for differences in habitat between
62 the reserve and the fished sites. Therefore, the patterns could have been due to spillover
63 or to habitat differences, which affect fish density (Chapman and Kramer, 1999;
64 Abesamis et al., 2006). Nevertheless, it is still unclear whether a decreasing gradient of
65 fish biomass across a reserve boundary indicates spillover. Many environmental factors
66 may explain spatial and temporal variability of littoral fish local assemblages. Habitat
67 structure in the form of habitat complexity and/or heterogeneity (McCoy and Bell,
68 1991), and also variations in depth (Bell, 1983), are often related to fish population size
69 and assemblage structure (Ruitton et al., 2000; García-Charton and Pérez-Ruzafa, 2001;
70 Letourneur et al., 2003). Thus, gradients of decreasing biomass across MPAs

71 boundaries may reflect better habitat characteristics inside than outside reserves, rather
72 than effects of protection from fishing in the reserve. Disentangling the effects due to
73 habitat structure will avoid “ecological confounding” in the interpretation of results
74 (Hurlbert, 1984; Underwood, 1997), as well as increase the chance of correctly
75 interpreting the observed spatial and temporal heterogeneity of fish populations due to
76 protection.

77 In addition, if gradients of decreasing biomass away from MPAs are due to
78 spillover, the availability of a continuous habitat suitable for fish adjacent to reserves
79 may have been important in promoting the net emigration of some fish from the
80 reserves. Spillover benefits are more likely if reserves and their immediate surroundings
81 occur in relatively homogeneous habitat (Chapman and Kramer, 2000; McClanahan and
82 Mangi, 2000; Kaunda-Arara and Rose, 2004), because many fishes are habitat specific
83 and are reluctant to disperse across “foreign” habitats (Chapman and Kramer, 2000).
84 For this reason, spillover will also be influenced by the habitat bordering a reserve
85 (Rowley, 1994).

86 The ideas of protecting breeding stocks, improving recruitment to neighbouring
87 areas, and restocking marine species of commercial interest, were the most important
88 initial goals of the creation of Tabarca Marine Reserve (Ramos-Esplá, 1985). This MPA
89 was established in 1986, and it has already yielded a large background of data showing
90 the presence of higher biomass inside. Overall fish abundance and biomass were
91 respectively 92% and 317% higher in Tabarca Marine Reserve with reference to control
92 fished areas (Forcada, 2005). Moreover, different traditional fishing grounds are
93 distributed around Tabarca Marine Reserve, which are mainly used by the artisanal fleet

94 causing a concentration of fishing effort close to the reserve boundaries (Goñi et al., *in*
95 *press*).

96 The main objective of this work was to assess spillover examining gradients of
97 fish biomass across Tabarca Marine Reserve boundaries. As a second objective, with
98 the aim to test if the patchy nature of the marine environment might act as a barrier for
99 the movement of fish, we investigated the gradients over two habitats: *Posidonia*
100 *oceanica* seagrass meadow (continuous through reserve boundaries) and rocky substrate
101 (discontinuous through reserve boundaries). Furthermore, we explored the relationship
102 between the fish assemblage and habitat structure, as an environmental factor likely to
103 account for an important part of the variability along the gradient. We statistically
104 control the effects of habitat correlates of fish assemblage to test the hypothesis that
105 gradients are due to reserve protection rather than measured habitat differences. Finally,
106 changes in the structure of the fish assemblage were assessed at different distances from
107 the integral reserve to test the effect of spillover.

108 2. MATERIALS AND METHODS

109 2.1. AREA DESCRIPTIONS

110 This study was carried out during June-July in 2005 and 2006 in Tabarca Marine
111 Reserve (South-western Mediterranean Sea, Spain). Tabarca Marine Reserve was
112 created in 1986 and is 1 400 ha. This MPA is zoned in three management zones with
113 different levels of protection (Ramos-Esplá, 1985; Fig. 1): (I) the Integral reserve area
114 (100 ha), where all human uses and activities are prohibited, except the scientific
115 research; (II) the Buffer area (630 ha), in which some selective fishing methods are
116 allowed; and (III) the Transitional area (670 ha), in which a number of activities are
117 permitted (selective fishing techniques, swimming, SCUBA diving, mooring of yachts).

118 The main habitat, *Posidonia oceanica* meadows, is highly extended outside the borders
119 in a continuous way, furthermore rocky bottoms also have a patchy distribution over the
120 area of study.

121 2.2. STUDY DESIGN AND METHODS

122 To test our hypothesis, 7 localities were positioned at increasing distances from
123 the core of the integral reserve and with different protection status (4 inside the MPA
124 and 3 in fished areas) (Fig. 1). In each locality, 3 sites were randomly located at a scale
125 of 100s of metres. Finally, six random visual counts (replicates) separated by 10s of
126 metres were done in each site. The surveys were carried out over one continuous habitat
127 (*Posidonia oceanica* seagrass meadow) and another discontinuous (rocky substrate). To
128 assess for the temporal consistency in the results, we repeated this sampling procedure
129 two times, resulting in a total of 504 replicates in the data set.

130 Fish assemblage was sampled by means of underwater visual census techniques.
131 The abundance and size (total length in classes of 2 cm) of each fish species was
132 recorded by a SCUBA diver within a 25×5 m transect in rocky substrate, and a 50×5 m
133 transect in *P. oceanica* meadow as fish were more dispersed in this habitat (Harmelin-
134 Vivien et al., 1985). This procedure is quite precise after a training period (Bell et al.,
135 1985). Each observation was assigned to one of nine predetermined abundance classes
136 (Harmelin, 1987), the limits of which coincide approximately with the terms of a base 2
137 geometric series. Geometric means of each fish abundance class were used for further
138 calculations. This system of recording numbers, which is usual for fish censuses, leads
139 to similar degrees of error over a wide range of abundances, and insures the
140 homogeneity of variances when performing analyses with log-transformed data
141 (Frontier, 1986).

142 Habitat was described using substrate variables, distinguishing between vertical
143 complexity (estimated as number of rocky boulders and verticality), horizontal
144 heterogeneity (cover of different substrate) and depth (García-Charton and Pérez-
145 Ruzafa, 2001). After counting fish, the same observer covered the transect length in the
146 opposite direction to count the number of rocky boulders classified by the size of their
147 major length: small (major length: 50-100 cm), medium (major length: 100-200 cm),
148 and large (major length: >200 cm). The observer completed measuring the minimum
149 and maximum depth, and verticality (was estimated as the vertical distance between the
150 deepest and the shallowest point inside each transect). Finally, habitat heterogeneity was
151 estimated visually within each transect as the relative percentage cover of different
152 substrate types: rock, sand and *P. oceanica* meadow. Because the location of each
153 sampling *site* was randomly selected, its geographical position was denoted by means of
154 a global positioning system (GPS). Subsequently for each *site*, distance from the centre
155 of the integral reserve and distance from Tabarca Marine Reserve boundary were
156 calculated by means of a geographic information system (GIS).

157 The seasonality is an important environmental variable on fish assemblage in
158 temperate systems (Ansari et al., 1995; Magill and Sayer, 2002). For this reason, the
159 surveys were done in the same season to reduce the natural variance between replicates
160 thus providing better evidence of spatial patterns of distribution. The warm season is the
161 most suitable period for visual counts in the Mediterranean, as fish communities are
162 more diverse and stable during this period (Harmelin, 1987). Fish censuses were then
163 performed during June and July, between 10:00-15:00 h, and with optimal seawater
164 conditions of turbidity and swell.

165 2.3. DATA ANALYSIS

166 Fish parameters

167 Fish assemblage structure was specified for each transect by total biomass.
168 Individual weights of fish were estimated from published length–weight relationships
169 (Valle et al., 2003). For each species we estimated its relative frequency of occurrence,
170 separately for each habitat considered in the experimental design.

171 ‘Total reduced biomass’ was also estimated by excluding from the calculations
172 all pelagic species (Atherinidae, Centracanthidae, Pomacentridae and the Sparidae
173 *Boops boops* and *Oblada melanura*). These species are often abundant and gregarious,
174 and their high variability in spatial distribution may mask the effect of protection or
175 habitat (Harmelin, 1987; Garcia-Charton et al., 2004). Species belonging to Gobiidae
176 and Scorpaenidae are particularly cryptic or hidden and they require a sampling
177 procedure specially adapted to their characteristics (Willis, 2001). For this reason, these
178 species were not analysed and were also removed from the estimation of ‘total reduced
179 biomass’.

180 Influence of habitat characteristics

181 Linear regression was used to assess whether habitat variables (cover of different
182 substrate types, number of rocky boulders, depth and verticality) were related with
183 distance from integral reserve centre. An analysis of variance (ANOVA) of the
184 regressions was performed in order to determine whether the association between the
185 variables was statistically significant. Moreover, to explore the relationship between
186 fish assemblage parameters — total reduced biomass and species biomass (ln-
187 transformed) — and the previous habitat structure descriptors (and their quadratic and
188 cubic terms to explore the possible nonlinear relationship), multiple regression analyses

189 were performed in the framework of generalized linear models (GLM) (McCullagh and
190 Nelder, 1989; Chapman and Kramer, 1999; Letourneur et al., 2003; García-Charton et
191 al., 2004). Fish variables were examined at a replicate level using multiple linear
192 regressions. In each case, stepwise forward selection of variables was run, with the aim
193 of maximizing the deviance reduction, followed by a stepwise backward elimination to
194 prevent the loss of statistical significance of some variables due to the latter
195 incorporation of new variables into the model. Before accepting any model, an analysis
196 of residuals was performed to detect outliers with high influence on the models. We
197 measured the leverage and the Cook statistic of each sampling unit (McCullagh and
198 Nelder, 1989), so that any one with high values of leverage and influence was removed
199 and the model refitted to insure consistency.

200 **Gradients of fish biomass**

201 Gradients of fish biomass across MPA boundaries were analysed using linear
202 regressions. Average total reduced biomass and species biomass (ln-transformed) at
203 each *site* were tested versus distance from integral reserve centre. Analyses were
204 performed only on those non-pelagic taxa sufficiently frequent throughout the study, i.e.
205 with a frequency of $\geq 10\%$. These regressions were performed separately for two times
206 sampled at each habitat. An ANOVA of the regressions was performed in order to
207 determine whether the association between the variables was statistically significant.

208 To quantify the spatial variation after extracting the variability due to the
209 influence of habitat variables, residuals of multiple linear regression analyses (defined
210 as corrected biomass) were used as dependent variables repeating the linear regression
211 with distance from integral reserve centre. This process was done in order to ensure that

212 gradients were related to protection and not to differences in habitat features (Chapman
213 and Kramer, 1999; García-Charton et al., 2004).

214 **Changes in multivariate structure of fish assemblage**

215 We used multivariate techniques that are suited for ecological data because this
216 allowed the production of a diagnostic on the change of the entire fish assemblage.
217 Therefore, non-parametric approaches were selected by combining non-metric
218 multidimensional scaling (MDS) and hierarchical cluster (Clarke, 1993; Clarke and
219 Warwick, 2001), to assess differences in the biomass of the structure of the community
220 within each *locality*, with regard to the different habitats and times considered by our
221 sampling design.

222 With the aim of incorporating the influence of environmental variables in the
223 assessment of the effect of distance from integral reserve over the fish assemblage, we
224 perform BEST and LINKTREE routines included in PRIMER v6 software (Clarke and
225 Gorley, 2006). A first appraisal of the relationships between species biomass and
226 environment was provided by BEST, which was used to select the subset of
227 environmental variables which best explains the multivariate pattern of the fish
228 assemblage. In order to carry out a full search of all possible combinations of
229 environmental variables, BIO-ENV procedure was run using Spearman coefficient
230 (Kendall, 1970) as rank correlation method. Moreover, a global BEST match
231 permutation test (using 999 permutations) was applied to test agreement between fish
232 assemblage and the subset of environmental variables selected. The associated
233 Pearson's correlation coefficient of pairs of environmental variables was examined to
234 identify variables strongly correlated. All subsets of variables strongly collinear (with
235 values >0.95 or <-0.95) were reduced to a single representative in the BEST run (Clarke

236 and Warwick, 2001). In a second step, only the environmental variables selected by
237 BEST were included as explicative variables in LINKTREE procedure (a non-
238 parametric multivariate form of classification and regression trees; De'ath, 2002). This
239 non-parametric multivariate discrimination technique constructs a hierarchical tree
240 through successive dichotomies of the set of observations. Each division is
241 characterised by one or more variables, and ranges of their values, that appear to be
242 responsible for discriminating each different assemblage grouping. LINKTREE is
243 capable of demonstrating that an environmental variable is important for internal
244 assemblage structuring of one group of samples but not for another group (with similar
245 values range).

246 The “similarity profile” permutation test (SIMPROF) (Clarke and Gorley, 2006),
247 which test for significant evidence of multivariate structure among samples that have no
248 pre-defined grouping, was combined with hierarchical cluster and LINKTREE to justify
249 identification and interpretation of clusters. The significance level was conventionally
250 taken as 5%, and 1000 permutations were used to calculate the mean similarity profile,
251 with 999 to generate the null distribution of the departure statistic, π .

252 For the overall multivariate testing technique, similarities among fish
253 assemblage were calculated using the Bray-Curtis similarity index (Bray and Curtis,
254 1957) on the log-transformed biomass data by species. Censuses from *P. oceanica*
255 meadow and from rocky substrate were computed together. For protection status, a
256 dummy variable of ‘1’ was assigned to transects inside the MPA, and ‘0’ for those in
257 fished areas. Again, for habitat factor, another dummy variable of ‘0’ was assigned for
258 transects over rocky substrate, and ‘1’ for those carried out on *P. oceanica* meadow.
259 These two dummy variables (called MPA and habitat respectively), distance from the

260 integral reserve centre, and distance from MPA boundary were included in the
261 environmental data matrix with the substrate variables collected during the visual
262 census. Environmental variables similarity matrix used in the prior analysis was
263 calculated within *localities* using Normalised Euclidean distance (Clarke and Warwick,
264 2001).

265 3. RESULTS

266 3.1. FISH ASSEMBLAGE

267 During this study, a total of 47 fish species were observed (belonging to 16
268 families), of which 38 appeared in *P. oceanica* and 45 on rocky substrate (Appendix A).
269 The most representative family was Sparidae followed by Labridae, with 13 and 12
270 species respectively. Total biomass averaged 2213 ± 307 (SE, standard error) g 125 m^{-2}
271 on *P. oceanica*, and 10225 ± 1003 (SE) g 125 m^{-2} in rocky substrate. Total reduced
272 biomass — i.e. excluding from the summation pelagic and cryptic species — attained
273 values of 1503 ± 278 (SE) and 8874 ± 971 (SE) g 125 m^{-2} , in *P. oceanica* and rocky
274 substrate respectively.

275 3.2. INFLUENCE OF HABITAT STRUCTURE ON THE FISH ASSEMBLAGE

276 Some variables of habitat structure showed significant linear trends with
277 distance from integral reserve. On *P. oceanica* meadow, cover of rock (Time 1:
278 $R^2=0.433$, $p<0.01$; Time 2: $R^2=0.387$, $p<0.01$), maximum depth (Time 1: $R^2=0.221$,
279 $p<0.05$), and number of small (Time 1: $R^2=0.405$, $p<0.01$; Time 2: $R^2=0.488$, $p<0.001$)
280 and medium-sized (Time 1: $R^2=0.365$, $p<0.01$) rocky boulders, declined significantly
281 across the reserve boundary. In addition, verticality increased significantly with distance
282 from integral reserve (Time 1: $R^2=0.591$, $p<0.001$; Time 2: $R^2=0.189$, $p<0.05$). On the

283 other hand, on rocky substrate, a significant linear decrease of rock cover was obtained
284 across the reserve boundary (Time 1: $R^2=0.293$, $p<0.05$), whereas seagrass cover
285 showed the opposite trend (Time 1: $R^2=0.315$, $p<0.01$). Furthermore, medium-sized
286 (Time 2: $R^2=0.310$, $p<0.01$) and large (Time 2: $R^2=0.517$, $p<0.001$) rocky boulders
287 increased significantly with distance from integral reserve.

288 The parameters of fish assemblage responded to combinations of complexity and
289 heterogeneity of habitat. The analyses of residuals confirm the goodness-of-fit of the
290 models, so that no further reference will be given to these procedures. The regression
291 model constructed on the observed values of total reduced biomass on *P. oceanica*,
292 incorporated four habitat variables to explain 32.5% of the variation (Table 1). Biomass
293 responded to variations in rock cover, minimum and maximum depth and number of
294 small boulders. Similarly, on rocky substrate, the multiple regression analysis of
295 reduced biomass accounted for 28.4% of the variation, but the model incorporated rock
296 cover, verticality and number of large boulders (Table 1).

297 Significant models were obtained for 11 of the 12 most frequent non-pelagic
298 species on *P. oceanica*, when exploring the relationship between their biomass and
299 habitat variables (Table 1). The fitted models accounted for 1.9-16.2% of the observed
300 variation in species biomasses, although the explained variance was substantial (>10%)
301 for only 5 species. Sand cover did not explain variation in any species biomass, while
302 maximum and minimum depth were the habitat variables most included in the models.
303 On rocky substrate, 20 non-pelagic species had a frequency of occurrence $\geq 10\%$, and all
304 of them showed significant models, but the proportion of variance explained exceed
305 10% only for 14 species (Table 1). In general, models incorporated more than two
306 habitat variables and explained 2.3-29.3% of total variation of species biomasses.

307 3.3. GRADIENTS OF FISH BIOMASS

308 As the prior results exhibit, there was a significant spatial variation in habitat
309 structure, and fish assemblage responded to changes in habitat heterogeneity and
310 complexity. Therefore to try to distinguish between the effects of habitat and protection,
311 we did the linear regressions using the values of original variables after correcting for
312 the effect of habitat by using residuals of multiple regression analyses as dependent
313 variables. By doing so, we found some changes compared with the analyses performed
314 on raw data. In general, the slope of the linear regression and the proportion of variation
315 explained by distance from integral reserve decreased after removing the effect of
316 habitat. Moreover, after correcting for the effect of habitat, values of biomass of two
317 species on *P. oceanica*, and four on rocky substrate, had lost the significance of the
318 trend related with distance from integral reserve (Table 2). Additionally, two species on
319 *P. oceanica*, and one on rocky substrate, did not maintain the expected pattern over
320 time.

321 Corrected total reduced biomass decreased significantly across Tabarca
322 boundaries on both *P. oceanica* and rocky substrates, and this pattern was observed over
323 time (Fig. 2). Distance from integral reserve explained 26.1-38.8% of total variation of
324 corrected biomass on *P. oceanica*, and 24.7-67.3% on rocky substrate (Table 2).
325 Concerning the most frequent non-pelagic species on *P. oceanica*, only 6 of them
326 decreased significantly across Tabarca boundaries (Table 2). The gradient was
327 significant in both sampling periods for *Labrus merula* (Fig. 3a) and *Thalassoma pavo*
328 (Fig. 3c). However, it was significant only in one sampling time for *Serranus scriba*
329 (Fig. 3e), *Symphodus ocellatus* (Fig. 3g), *D. vulgaris* (Fig. 3i) and *S. salpa* (Fig. 3k). On
330 the other hand, on rocky substrate, corrected biomasses of 5 of the most frequent non-

331 pelagic species had a significant decreasing trend (Table 2): *Diplodus sargus* (Fig. 3b)
332 in two sampling times, and *S. salpa* (Fig. 3d), *Symphodus ocellatus* (Fig. 3f), *E.*
333 *marginatus* (Fig. 3h) and *Diplodus cervinus* (Fig. 3j) in only one. On the contrary,
334 corrected biomass of *Symphodus rostratus* (Fig. 3l) increased across Tabarca
335 boundaries, but it was significant only in one sampling time.

336 3.4. SPATIAL VARIATION IN THE MULTIVARIATE STRUCTURE OF FISH 337 ASSEMBLAGE

338 MDS clearly separated the two habitats sampled, except for localities 1 (during
339 both times) and 3 (only during time 1) of *P. oceanica*, which had a similarity of 70%
340 with the assemblage observed on rocky substrate (Fig. 4). SIMPROF test corroborated
341 these results ($\pi=4.29$, $p<0.001$). The pattern related with distance from integral reserve
342 was observed only on rocky substrate. Fish assemblage in the integral reserve differed
343 significantly ($\pi=1.11$, $p=0.015$) from that censused on the other localities. Moreover, fish
344 assemblages of the rest of localities were split significantly ($\pi=1.93$, $p<0.001$) in two
345 groups: the first one enclosed localities 2, 3 and 4, and the second included localities 5,
346 6 and 7. In the last group were also included the fish assemblage of the integral reserve
347 of *P. oceanica*, which had a structure different to those observed in the other localities
348 of seagrass.

349 The environmental variables, habitat, rock cover and maximum depth were
350 strongly collinear with *P. oceanica* cover, number of small boulders and minimum
351 depth respectively (Pearson's correlation coefficient >0.95). BEST results showed that
352 the combination of substrate cover, number of medium-sized boulders, and distance
353 from integral reserve was the most correlated with fish assemblage structure ($\rho=0.674$,
354 $p<0.001$). The inclusion of these variables in LINKTREE analysis (Fig. 5) resulted that

355 distance from integral reserve explained the differences found among localities of rocky
356 substrate. On rocky habitat, substrate cover was also important in the differences found
357 between the integral reserve and the localities 2, 3 and 4.

358 **4. DISCUSSION**

359 Total reduced biomass of fish assemblage and biomass of some specific species
360 exhibited a decreasing gradient across Tabarca Marine Reserve boundaries, which
361 persisted even though the effects of the habitat structure were removed. Changes in the
362 multivariate structure of the fish assemblage were also related with distance from
363 integral reserve. The pattern was observed on both habitats studied, and persisted over
364 time for total reduced biomass and some studied species.

365 The exploration of the relationship among fish assemblage parameters and
366 environmental variables in this study corroborates that habitat structure is an important
367 factor likely to explain the spatial distribution of Mediterranean fish assemblages.
368 Whereas visual counts were performed on areas with habitat structure as comparable as
369 possible, multiple linear regressions demonstrated that habitat characteristics, at the
370 smallest spatial scale, influenced significantly the fish community parameters studied.
371 Other studies also attribute a substantial part of the observed spatial variability in fish
372 assemblages to habitat (Ruitton et al., 2000; García-Charton and Pérez-Ruzafa, 2001;
373 Letourneur et al., 2003). Greater habitat heterogeneity and complexity result in a bigger
374 variety of substrates and greater surface availability, therefore additional and a
375 diversification of resources for individual fish are provided (food, refuge against
376 predation or light, as well as resting or mating sites; García-Charton and Pérez-Ruzafa,
377 2001). We found that each of the habitat structure variables considered was significant
378 in explaining the spatial distribution of the studied fish assemblage. This implies that all

379 of them should be taken into account because only this approach may give the most
380 comprehensive view of the fish assemblage-habitat relationship (Ruitton et al., 2000). In
381 this sense, Mediterranean MPAs were usually established in zones that already harbour
382 intrinsic structurally complex habitats (Ramos-Esplá et al., 2004), which favour the
383 development of abundant fish fauna. Additionally, protection may also enhance the
384 quality of habitat which is preserved inside MPAs from negative impacts (e.g.
385 destructive fishing practices; Sumaila et al., 2000). In fact, the present study
386 demonstrated that Tabarca Marine Reserve had some differences in habitat structure
387 compared to surrounding areas. Most of the habitat variables that explain part of the
388 variability of the fish assemblage had significant linear trends from inside to outside the
389 marine reserve, and this influence was taken into account. The decrease in the number
390 of significant gradients related to distance from integral reserve, when calculated after
391 extraction of variation due to habitat, confirmed that habitat characteristics were, in
392 some cases, more important than protection in explaining the pattern of the data. Note,
393 however, that statistically controlling for habitat correlates may attribute effects of
394 reserve protection to spuriously correlated habitat characteristics, increasing the
395 potential for type II error when testing for significant effects of reserve protection
396 (Chapman and Kramer, 1999). Our results indicating no significant effect of reserve
397 status based on this approach should therefore be interpreted cautiously.

398 After extracting the effect of habitat, significant decreasing gradients of total fish
399 biomass and most of the species studied were observed on *P. oceanica* and rocky
400 substrate, and some of them were consistent over time. Changes in the structure of the
401 fish assemblage were correlated with distance from integral reserve and not with
402 protection status (inside-outside MPA). These gradual changes in fish assemblage
403 related with distance from integral reserve, rather than a sudden change across the

404 reserve boundary, indicate good evidence of biomass export. About the species that did
405 not maintain the same pattern over time, it is part of the natural variability of the fish
406 assemblage (Holbrook et al., 1994), which obliges to incorporate a suitable temporal
407 replication in order to differentiate adequately the effects of protection. Net emigration
408 of adult fish from Tabarca Marine Reserve combined with the high concentration of
409 fishing effort around its boundaries (Goñi et al., *in press*) produce the observed
410 decreasing patterns of biomass. These results corroborate the hypothesis of spillover
411 (Rakitin and Kramer, 1996) around Tabarca Marine Reserve. On the contrary, the
412 opposite pattern was obtained for *S. rostratus*, which increased significantly with
413 distance from the centre of the Tabarca integral reserve. Similar results were found in
414 other studies (Watson and Ormond, 1994; Kaunda-Arara and Rose, 2004; Ashworth and
415 Ormond, 2005), where for some species greater abundance in fished areas have been
416 observed, suggesting that this could be due to reduced competition or predation outside
417 the reserve. Theoretically, some families and species might be expected to experience
418 negative effects from reserves, because species interactions may also have important
419 effects (Pinnegar et al., 2000; Jennings, 2001).

420 Although significant decreasing gradients has been detected in both habitats, we
421 found some differences between the results obtained in *P. oceanica* meadow and on
422 rocky substrate. Distance from integral reserve explained greater proportion of variance
423 of total reduced biomass on rocky substrate than in *P. oceanica* meadow. Moreover, the
424 multivariate structure of the fish assemblage showed a gradual change related with
425 distance from integral reserve on rocky substrate, meanwhile over *P. oceanica* only the
426 assemblage of the integral reserve was different to those of the other localities. These
427 results suggest that, contrary to what we expected, evidence of spillover seem to be
428 clearer on rocky substrate even though it has a big discontinuity between inside to

429 outside Tabarca Marine Reserve. Although the multivariate structure of fish assemblage
430 was significantly different between *P. oceanica* and rocky substrate, 80% of the species
431 were observed at both habitats. The relative lack of specificity of most species for
432 bottom features could be the result of the combination of a relatively wide home range
433 and flexibility on resources use in general. Although, another likely explanation is that
434 most of the target species (e.g. *E. marginatus*, *S. umbra*, *D. cervinus*, etc) seek shelter
435 during daytime hours on rocky substrates, increasing their residence time in this habitat,
436 hence responses to protection would be intrinsically stronger to detect on rocky
437 substrates relative to *P. oceanica* meadows. In this sense, the diet and pattern of space
438 occupation of species may vary depending on age (Harmelin-Vivien et al., 1989),
439 resulting in morphological changes, learning, social rank, reproductive state and sex (in
440 the case of sequential hermaphrodite species) (Forrester, 1991; McCormick, 1998).
441 Furthermore, most fish species would be sufficiently flexible in their feeding and space
442 requirements to adapt to resources available at each site and to avoid competing for
443 them with conspecifics or individuals of other species, as suggested by a few studies in
444 the Mediterranean Sea (Harmelin-Vivien et al., 1989; Jennings et al., 1997). Therefore,
445 it can be suggested that movements of fish among rocky patches could occur easily
446 through *P. oceanica* meadows which acts as a suitable path. It has been pointed out
447 (Roberts, 2000) that habitat continuity through MPAs limits is important for biomass
448 export to open fished areas. An extensive tagging study carried out in Apo Reserve
449 (Chapman and Kramer, 2000) supports this assessment. When reserve boundaries are
450 set at natural barriers where costs of moving increase, relocation across the boundaries
451 should be reduced, and conversely, fish may readily move from reserves to fished areas
452 when these areas are connected by continuous suitable habitat (Chapman and Kramer,
453 2000). However, this assumption does not seem to be useful for the fish assemblage

454 associated to rocky patches located inside *P. oceanica* beds. Our results suggest that fish
455 could move easily among rocky patches when they are located inside *P. oceanica*
456 meadows. To obtain spillover effects, habitat continuity of rocky bottoms is not as
457 important as their presence inside and outside the MPA, only if they are properly
458 connected. Defining and understanding the mosaic of habitats and their connection
459 within the ecosystem is critical. MPAs need to be viewed in the larger context of the
460 entire ecosystem and their design needs to consider the habitat requirements and life
461 histories of the species of interest, as well as the extent to which these habitats interact
462 at larger spatial scales.

463 **5. CONCLUSIONS**

464 This study detected gradients of decreasing biomass of fish across the
465 boundaries of Tabarca Marine Reserve, which continued even after removing the effects
466 of the habitat structure. This pattern persisted over time for total reduced biomass and
467 some studied species. Decreasing gradients appeared in both habitats studied, *P.*
468 *oceanica* meadow and rocky substrate, and independently of their different continuity
469 through the reserve boundaries. These gradients ultimately culminated in progressive
470 change in the structure of fish assemblages, particularly on rocky substrate. All of these
471 results support the hypothesis that the export of fish from Tabarca Marine Reserve
472 occurs. This process should provide local benefits to the artisanal fleet which operates
473 in fishing grounds just around Tabarca Marine Reserve, achieving the main objective of
474 the creation of this MPA.

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652

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653 CAPTIONS

654 Table 1. Results of multiple linear regression analysis of mean biomass (ln-transformed)
655 ($\ln \text{ g}/125 \text{ m}^2$) against habitat structure descriptors for total reduced biomass and the 12
656 and 20 species most frequent on *P. oceanica* meadow and on rocky substrate
657 respectively. For full species names see Table 2.

658 Table 2. Linear regressions analyses for mean corrected biomass (residuals) versus
659 distance (m) from integral reserve at each time of total reduced biomass and the 12 and
660 20 species most frequent on *P. oceanica* meadow and on rocky substrate respectively.

661 Figure 1. Tabarca Marine Reserve location, including limits and zonation (I: integral
662 reserve area, II: buffer area, III: transitional area), and main habitat distribution. The
663 position of the seven localities (L1: locality 1, L2: locality 2, ..., L7: locality 7) sampled
664 at each habitat (P: *P. oceanica* seagrass meadow, R: rocky substrate) are also indicated.

665 Figure 2. Mean corrected total biomass (residuals) at each site as a function of distance
666 from integral reserve centre (IR) on a) *P. oceanica* meadow and b) rocky substrate. A
667 linear regression is showed for each time sampled when it was significant. Error bars
668 indicate standard error.

669 Figure 3. Mean corrected biomass (residuals) at each site as a function of distance from
670 integral reserve centre (IR), on *P. oceanica* meadow for a) *Labrus merula*, c)
671 *Thalassoma pavo*, e) *Serranus scriba*, g) *Symphodus ocellatus*, i) *Diplodus vulgaris* and
672 k) *Sarpa salpa*, and on rocky substrate for b) *Diplodus sargus*, d) *Sarpa salpa*, f)
673 *Symphodus ocellatus*, h) *Epinephelus marginatus*, j) *Diplodus cervinus* and l)
674 *Symphodus rostratus*. A linear regression is showed for each time sampled when it was
675 significant. Error bars indicate standard error.

676 Figure 4. Two dimensional nMDS ordination of biomasses (log-transformed) of the
677 species observed at each locality at each time. Cluster results were superimposed,
678 grouping with similarity levels of 60% and 80%. For each point, the first digit indicates
679 the time (1: time 1, 2: time 2) and the letter and number represent the locality (L1:
680 locality 1, L2: locality 2,..., L7: locality 7).

681 Figure 5. LINKTREE of biomass (log-transformed) of the species observed at each
682 locality within each time. The plot displays only those divisions for which SIMPROF
683 test was significant ($p < 0.05$). For each split the ANOSIM test statistic (R: rank
684 similarity index) is showed. B%: absolute measure of group differences. For each
685 sample, the first digit indicates the time (1: time 1, 2: time 2), the next letter the habitat
686 (R: Rocky substrate, P: *P. oceanica* meadow), and the last letter and number the locality
687 (L1: locality 1, L2: locality 2,..., L7: locality 7).

688 Appendix A. Mean total biomass \pm standard error (g/125 m²) and percentage of
689 frequency of occurrence (Freq.) of the species observed in *P. oceanica* meadow and
690 rocky substrate.

691

692 Table 1.

Species	n	Adj.R ²	F ^a	Const	<i>P.oce</i>	<i>P.oce</i> ³	Rock	Rock ²	Rock ³	Sand	D.min	D.min ²	D.min ³	D.max	D.max ²	D.max ³	Vert	Vert ²	Vert ³	sml.b	sml.b ³	med.b	med.b ²	med.b ³	larg.b	larg.b ²	larg.b ³	
<u><i>P. oceanica</i> meadow</u>																												
Reduced biomass	252	0.325	25.181***	9.411	-	-	0.176	-	-	-	-	-	-0.001	-0.657	-	0.003	-	-	-	0.179	-	-	-	-	-	-	-	-
<i>C. julis</i>	252	0.162	25.212***	2.593	-	-1.5E-6	-	-	-	-	0.228	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>D. annularis</i>	252		ns	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>D. sargas</i>	251	0.123	12.723***	2.266	-	-	-	-	-	-	-0.348	-	-	-	-	0.002	-	-	-	-	-	-	-	-	-	-	0.822	
<i>D. vulgaris</i>	250	0.047	13.342***	9.078	-0.076	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>L. merula</i>	252	0.021	6.395*	0.675	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.222	-	-	-	-	-	-	-	
<i>S. salpa</i>	252	0.125	18.888***	1.709	-	-	0.320	-	-	-	-	-	-	-	-	-	-	-	-	0.462	-	-	-	-	-	-	-	
<i>S. scriba</i>	252	0.101	15.141***	1.550	-	-	0.146	-	-	-	-	-	-	-	-	0.001	-	-	-	-	-	-	-	-	-	-	-	
<i>S. cantharus</i>	252	0.028	4.669*	-0.527	-	-	-	-	-	-	0.200	-	-	-	-	-0.001	-	-	-	-	-	-	-	-	-	-	-	
<i>S. ocellatus</i>	251	0.063	9.448***	2.932	-	-1.8E-6	-	-	-	-	-	-	-	-	-	-	-	-	-0.133	-	-	-	-	-	-	-	-	
<i>S. rostratus</i>	252	0.019	5.927*	0.072	-	-	-	-	-	-	-	-	2.8E-4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. tinca</i>	252	0.025	4.153*	1.444	-	-	-	-	-	-	-	-	-	0.138	-	-	-	-	-	-	-	-	-	-0.028	-	-	-	
<i>T. pavo</i>	249	0.156	46.928***	0.193	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.318	-	-	-	-	-	-	
<u>Rocky substrate</u>																												
Reduced biomass	251	0.284	20.481***	6.961	-	-	-	-	1.6E-6	-	-	-	-	-	-	0.443	-	-0.006	-	-	-	-	-	-	-	-0.012	0.001	
<i>A. imberbis</i>	249	0.187	10.487***	-1.075	-	-	-	4.3E-4	-5.0E-6	-	0.22	-	-	-	-	-3.7E-4	0.168	-	-	-	-	-	-	-	-	0.069	-	
<i>C. julis</i>	251	0.115	33.561***	3.078	-	-	-	-	-	-	-	-	-	0.106	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>D. dentex</i>	250	0.074	20.992***	-0.183	-	-	-	-	2.1E-6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>D. annularis</i>	251	0.153	23.603***	3.597	-	-	-	-	-2.7E-6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.7E-4	-	-	
<i>D. cervinus</i>	252	0.293	35.674***	4.709	-	-7.4E-6	-	-0.003	2.6E-5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>D. puntazzo</i>	252	0.184	29.225***	0.611	-	-	-	3.6E-4	-	-	-	-	-	-	-	-3.4E-4	-	-	-	-	-	-	-	-	-	-	-	
<i>D. sargas</i>	252	0.118	34.621***	3.506	-	-	-	-	3.0E-6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>D. vulgaris</i>	252	0.225	15.589***	3.141	-	-	0.017	-	-	-	-	-	-	-	-	-0.001	0.732	-0.075	-	-	-	-	-	-	-	0.075	-	
<i>E. marginatus</i>	252	0.168	26.423***	0.452	-	-	-	-	3.9E-6	-	-	-	-	-3.4E-4	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>L. merula</i>	252	0.148	15.570***	3.748	-	-	0.015	-	-	-	-	-	-	-0.604	0.021	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. salpa</i>	249	0.099	7.779***	4.240	-	-	-	-	-	-	-	-	-	-	-	0.692	-	-	-	-	-1.9E-4	-	-	-	-	-0.036	0.003	
<i>S. umbra</i>	248	0.141	14.548***	0.300	-	-	-	-	-	-	-	-	-	-	-	-2.8E-4	0.641	-	-	-	1.6E-4	-	-	-	-	-	-	
<i>S. scriba</i>	252	0.027	8.064**	2.923	-	-	-	1.2E-4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. cantharus</i>	252	0.111	16.732***	-0.262	-	-	-	-	-	-	-	-	-	0.085	-	-	-	-	-	-	-0.023	-	-	-	-	-	-	
<i>S. mediterranean</i>	251	0.023	6.927**	0.110	-	-	-	-	-	-	0.054	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. ocellatus</i>	251	0.112	8.901***	0.722	-	-	0.042	-	-4.4E-6	-0.097	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.055	-	-	
<i>S. roissali</i>	252	0.177	18.992***	3.369	-	-	-	-	-6.9E-7	-	-	-	-	-0.386	0.012	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. rostratus</i>	252	0.035	5.587**	0.928	-	-	-1.9E-6	-	-	-7.7E-7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. tinca</i>	250	0.074	20.917***	5.609	-	-	-	-	-	-	-0.137	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>T. pavo</i>	252	0.245	14.597***	0.730	-	-	-	1.6E-4	-	-	-	0.009	-	-	-	-0.001	0.651	-0.064	-	-	-	0.053	-	-	-	-	-	

693 Habitat structure descriptors: *P.oce*, *P. oceanica* cover; Rock, rock cover; Sand, sand cover; D.min, minimum depth; D.max, maximum depth; Vert, verticality; sml.b, small boulders; med.b, medium-sized boulders;

694 larg.b, large boulders. Superscripts refer to quadratic and cubic terms.

695 ^aProbability: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant.

696 Table 2.

Variables	Time 1				Time 2			
	Const.	Slope	R ²	F ^a	Const.	Slope	R ²	F ^a
<u><i>P. oceanica</i> meadow</u>								
Reduced biomass	0.677	-0.0001	0.261	6.733*	0.554	-0.0002	0.388	12.090**
<i>Coris julis</i>	-0.005	-1.1E-5	0.003	0.059	0.187	-3.6E-5	0.012	0.239
<i>Diplodus annularis</i> ^d	3.998	-9.8E-6	0.001	0.023	4.290	-1.2E-4	0.143	3.161
<i>Diplodus sargus</i> ^c	0.036	5.8E-5	0.026	0.517	0.068	-8.0E-5	0.092	1.918
<i>Diplodus vulgaris</i>	0.068	-2.7E-5	0.004	0.079	0.826	-2.0E-4	0.198	4.687*
<i>Labrus merula</i>	0.261	-1.1E-4	0.185	4.321*	1.436	-3.2 E-4	0.556	23.760***
<i>Sarpa salpa</i> ^b	1.994	-4.7E-4	0.376	11.464**	0.826	-2.6E-4	0.137	3.014
<i>Serranus scriba</i> ^b	0.725	-2.0E-4	0.284	7.519*	0.664	-1.5E-4	0.151	3.371
<i>Spondyllosoma cantharus</i> ^c	-0.201	1.2E-4	0.156	3.524	0.018	-7.4E-5	0.111	2.370
<i>Symphodus ocellatus</i>	-0.384	4.3E-6	0.001	0.010	0.898	-1.3E-4	0.178	4.119*
<i>Symphodus rostratus</i>	-0.034	-1.0E-5	0.017	0.322	0.064	3.0E-6	0.000	0.009
<i>Symphodus tinca</i>	-0.325	7.6E-6	0.000	0.006	0.655	-9.3E-5	0.044	0.878
<i>Thalassoma pavo</i>	0.285	-8.5E-5	0.318	8.845**	0.504	-1.2E-4	0.595	27.930***
<u>Rocky substrate</u>								
Reduced biomass	0.746	-0.0002	0.673	39.196***	0.079	-7.7E-5	0.247	6.239*
<i>Apogon imberbis</i> ^c	0.135	-3.3E-6	0.000	0.004	-0.073	-1.1E-5	0.002	0.037
<i>Coris julis</i>	-0.157	2.9E-5	0.017	0.331	-0.015	2.5E-5	0.019	0.365
<i>Dentex dentex</i> ^c	0.839	-1.5E-4	0.118	2.548	-0.285	-1.5E-5	0.004	0.086
<i>Diplodus annularis</i> ^c	-0.172	1.1E-4	0.080	1.650	-0.568	1.3E-4	0.141	3.110
<i>Diplodus cervinus</i>	0.474	-1.0E-4	0.179	4.150*	-0.175	2.1E-6	0.000	0.001
<i>Diplodus puntazzo</i>	0.749	-9.3E-5	0.040	0.793	-0.178	-9.9E-5	0.051	1.020
<i>Diplodus sargus</i>	1.210	-2.8E-4	0.297	8.015*	0.270	-2.1E-4	0.253	6.441*
<i>Diplodus vulgaris</i>	0.395	-6.4E-5	0.053	1.059	-0.109	-3.2E-5	0.011	0.202
<i>Epinephelus marginatus</i> ^b	0.547	-1.7E-4	0.153	3.440	0.767	-2.6E-4	0.309	8.485**
<i>Labrus merula</i>	-0.161	-4.3E-5	0.022	0.423	0.525	-8.0E-5	0.059	1.192
<i>Sarpa salpa</i>	2.236	-6.7E-4	0.580	26.192***	-0.876	2.0E-4	0.080	1.642
<i>Sciaena umbra</i>	0.068	-1.1E-4	0.128	2.796	0.920	-2.1E-4	0.122	2.629
<i>Serranus scriba</i>	0.010	2.7E-5	0.009	0.175	-0.231	4.7E-5	0.031	0.617
<i>Spondyllosoma cantharus</i>	0.114	-1.0E-5	0.002	0.038	-0.215	4.5E-5	0.067	1.355
<i>Symphodus mediterraneus</i>	0.056	-1.3E-5	0.005	0.103	0.051	-2.3E-5	0.014	0.267
<i>Symphodus ocellatus</i>	-0.411	-1.1E-4	0.187	4.372	0.653	3.6E-5	0.016	0.306
<i>Symphodus roissali</i>	-0.074	1.0E-5	0.004	0.074	-0.001	1.4E-5	0.004	0.086
<i>Symphodus rostratus</i>	0.001	-4.4E-7	0.000	0.000	-0.411	1.3E-4	0.381	11.697**
<i>Symphodus tinca</i>	-0.004	-6.6E-5	0.042	0.831	0.306	-3.8E-5	0.017	0.330
<i>Thalassoma pavo</i> ^c	0.270	-8.8E-5	0.096	2.026	0.350	-1.2E-4	0.173	3.977

697 ^aProbability: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.698 ^bRegression lost the significance in one time sampled after correcting for the effect of habitat.699 ^cRegression lost the significance in both times sampled after correcting for the effect of habitat.700 ^dRegression was done using mean biomass ($\ln \text{ g/125 m}^2$) because not significant relationship with habitat
701 was found.

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703

704 Appendix A.

Family	Species	<i>P. oceanica</i> meadow		Rocky substrate	
		Biomass	Freq.	Biomass	Freq.
Muraenidae	<i>Muraena helena</i> Linnaeus, 1758	3.14 ± 3.14	0.40	100.66 ± 35.22	4.76
Serranidae	<i>Anthias anthias</i> (Linnaeus, 1758)	0.03 ± 0.03	0.40	0.09 ± 0.09	0.40
	<i>Epinephelus costae</i> Valenciennes, 1828	3.36 ± 3.36	0.40	26.91 ± 10.75	3.17
	<i>Epinephelus marginatus</i> (Lowe, 1834)	187.03 ± 119.46	2.78	1339.01 ± 431.57	23.41
	<i>Mycteroperca rubra</i> (Bloch, 1793)	8.37 ± 8.37	0.40	67.43 ± 29.87	3.17
	<i>Serranus cabrilla</i> (Linnaeus, 1758)	0.20 ± 0.15	0.79	0.23 ± 0.23	0.40
	<i>Serranus scriba</i> Linnaeus, 1758	32.59 ± 5.42	71.03	80.52 ± 5.23	82.54
Moronidae	<i>Dicentrarchus labrax</i> Linnaeus, 1758	-	0.00	12.87 ± 9.41	1.98
Apogonidae	<i>Apogon imberbis</i> Lacepède, 1801	-	0.00	15.17 ± 2.45	30.95
Haemulidae	<i>Pomadasys incisus</i> (Bowdich, 1825)	-	0.00	7.35 ± 2.81	3.97
Sciaenidae	<i>Sciaena umbra</i> Linnaeus, 1758	15.75 ± 6.42	5.95	320.02 ± 61.07	23.02
Mullidae	<i>Mullus surmuletus</i> Linnaeus, 1758	1.94 ± 0.82	7.54	1.53 ± 0.64	4.37
Sparidae	<i>Boops boops</i> (Linnaeus, 1758)	218.05 ± 35.21	38.10	159.89 ± 42.83	11.90
	<i>Dentex dentex</i> (Linnaeus, 1758)	110.84 ± 44.67	5.95	486.25 ± 202.24	11.90
	<i>Diplodus annularis</i> Rafinesque, 1810	81.97 ± 5.33	97.62	53.06 ± 4.77	64.68
	<i>Diplodus cervinus</i> Lowe, 1841	0.22 ± 0.22	0.40	45.43 ± 10.58	11.51
	<i>Diplodus puntazzo</i> , Cetti, 1789	5.31 ± 2.50	5.16	161.25 ± 21.38	38.10
	<i>Diplodus sargus</i> (Linnaeus, 1758)	42.38 ± 14.91	23.41	585.50 ± 63.32	82.54
	<i>Diplodus vulgaris</i> (Geoffroy Saint-Hilaire, 1817)	42.41 ± 7.82	47.22	803.38 ± 139.87	91.67
	<i>Oblada melanura</i> (Linnaeus, 1758)	248.72 ± 72.20	62.30	672.94 ± 171.12	63.49
	<i>Pagellus acarne</i> (Risso, 1827)	-	0.00	0.02 ± 0.02	0.40
	<i>Pagrus pagrus</i> (Linnaeus, 1758)	-	0.00	87.44 ± 27.61	7.94
	<i>Sarpa salpa</i> (Linnaeus, 1758)	828.90 ± 203.86	32.14	4109.46 ± 720.12	63.89
	<i>Sparus aurata</i> Linnaeus, 1758	3.02 ± 1.57	1.59	39.41 ± 13.38	4.76
	<i>Spondyliosoma cantharus</i> (Linnaeus, 1758)	4.44 ± 0.80	23.81	3.66 ± 0.88	10.71
Centranchidae	<i>Spicara maena</i> (Linnaeus, 1758)	1.35 ± 0.55	4.37	6.89 ± 6.82	1.19
	<i>Spicara smaris</i> (Linnaeus, 1758)	9.42 ± 4.25	5.16	35.30 ± 16.32	4.37
Pomacentridae	<i>Chromis chromis</i> (Linnaeus, 1758)	166.21 ± 33.59	84.13	418.56 ± 57.18	85.71
Labridae	<i>Coris julis</i> (Linnaeus, 1758)	37.40 ± 2.16	90.08	88.63 ± 4.19	94.84
	<i>Labrus merula</i> (Linnaeus, 1758)	21.47 ± 4.22	17.06	91.21 ± 14.45	24.60
	<i>Labrus viridis</i> (Linnaeus, 1758)	1.39 ± 0.55	3.57	2.76 ± 1.26	1.98
	<i>Symphodus cinereus</i> (Bonnaterre, 1788)	-	0.00	0.05 ± 0.04	0.79
	<i>Symphodus doderleini</i> (Jordan, 1981)	0.09 ± 0.07	0.79	0.23 ± 0.11	2.38
	<i>Symphodus mediterraneus</i> (Linnaeus, 1758)	0.84 ± 0.23	6.35	4.99 ± 0.91	16.27
	<i>Symphodus melanocercus</i> (Risso, 1810)	0.30 ± 0.09	5.95	1.25 ± 0.30	9.52
	<i>Symphodus ocellatus</i> Forsskal, 1775	6.90 ± 0.83	48.02	29.56 ± 2.72	57.94
	<i>Symphodus roissali</i> (Risso, 1810)	0.39 ± 0.13	4.37	6.17 ± 0.99	25.00
	<i>Symphodus rostratus</i> (Bloch, 1797)	1.05 ± 0.22	11.90	3.12 ± 0.57	15.48
	<i>Symphodus tinca</i> (Linnaeus, 1758)	48.95 ± 4.05	72.22	228.80 ± 15.81	89.29
	<i>Thalassoma pavo</i> (Linnaeus, 1758)	2.30 ± 0.72	11.51	36.26 ± 3.58	79.76
Gobiidae	<i>Gobius cruentatus</i> Gmelin, 1789	-	0.00	0.03 ± 0.02	0.79
Sphyraenidae	<i>Sphyraena sphyraena</i> (Linnaeus, 1758)	2.68 ± 2.68	0.40	-	0.00
Mugilidae		6.97 ± 3.49	1.98	34.09 ± 11.63	7.94
Atherinidae	<i>Atherina hepsetus</i> Linnaeus, 1758	66.17 ± 8.81	44.05	55.21 ± 11.79	24.60
Scorpaenidae	<i>Scorpaena notata</i> Rafinesque, 1810	-	0.00	0.41 ± 0.41	0.40
	<i>Scorpaena porcus</i> Linnaeus, 1758	0.14 ± 0.14	0.40	-	0.00
	<i>Scorpaena scrofa</i> (Linnaeus, 1758)	-	0.00	1.55 ± 1.55	0.40

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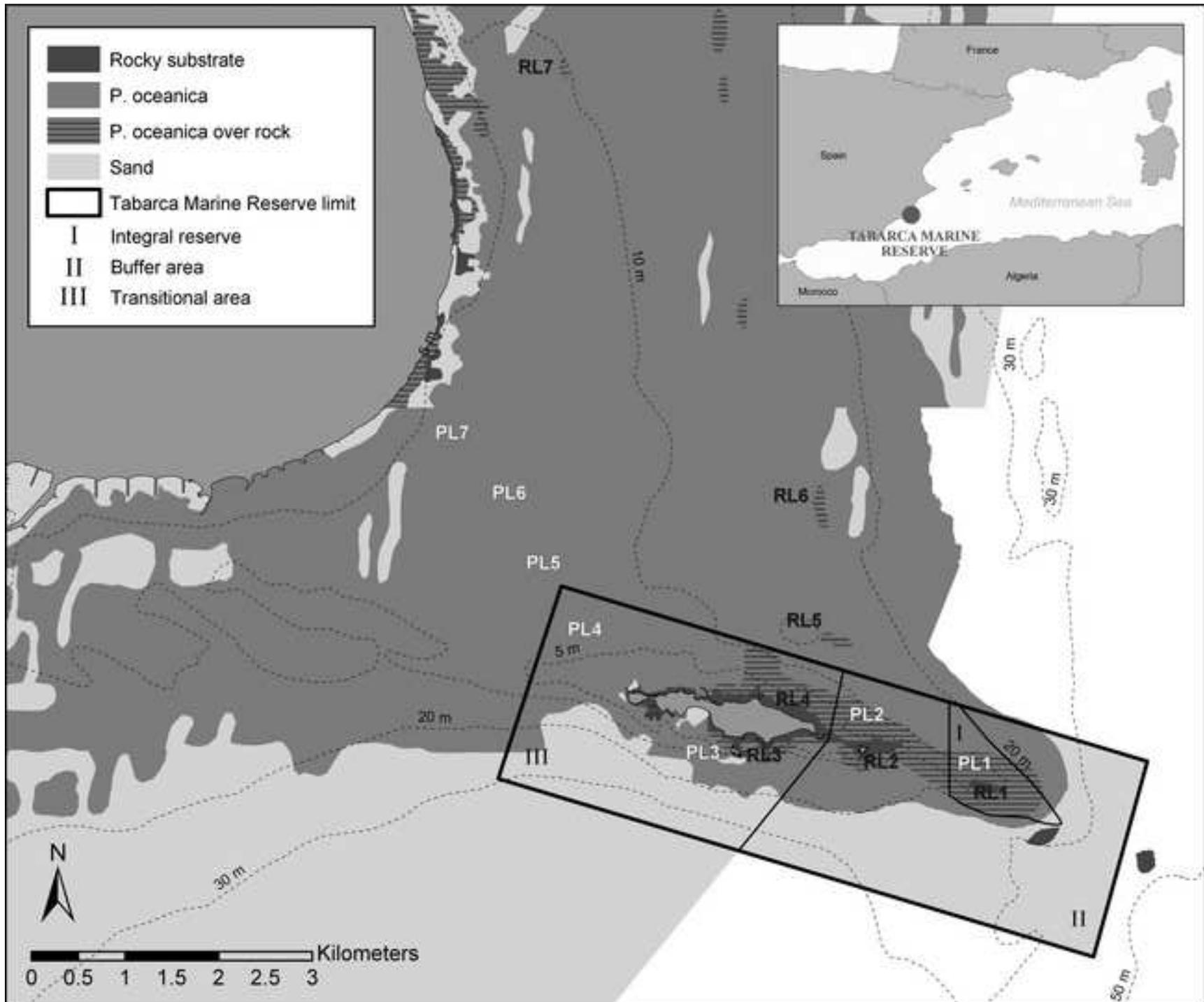


Figure 1

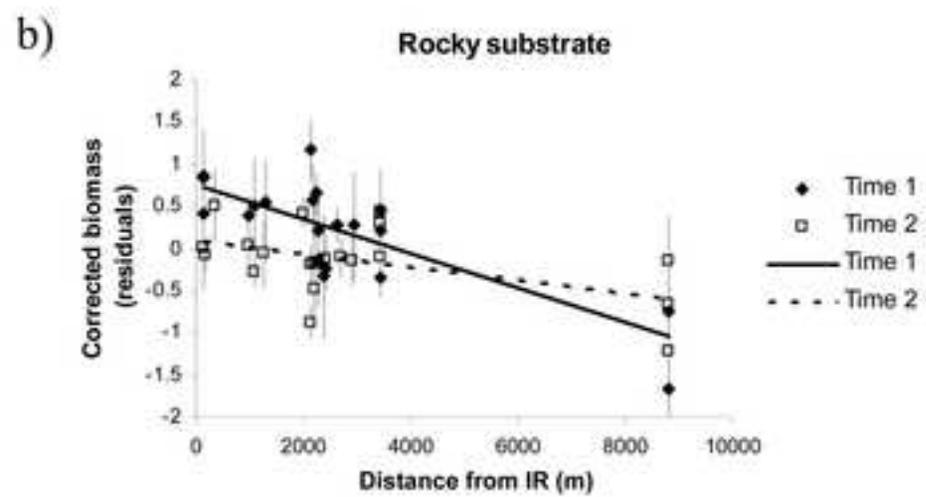
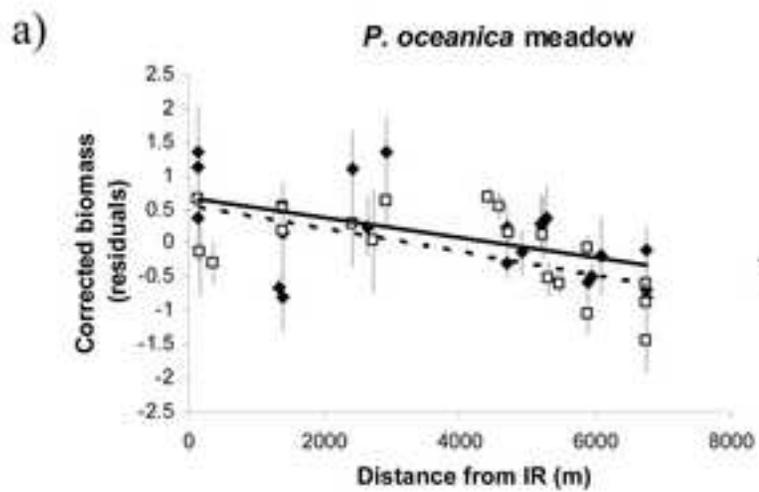


Figure 2

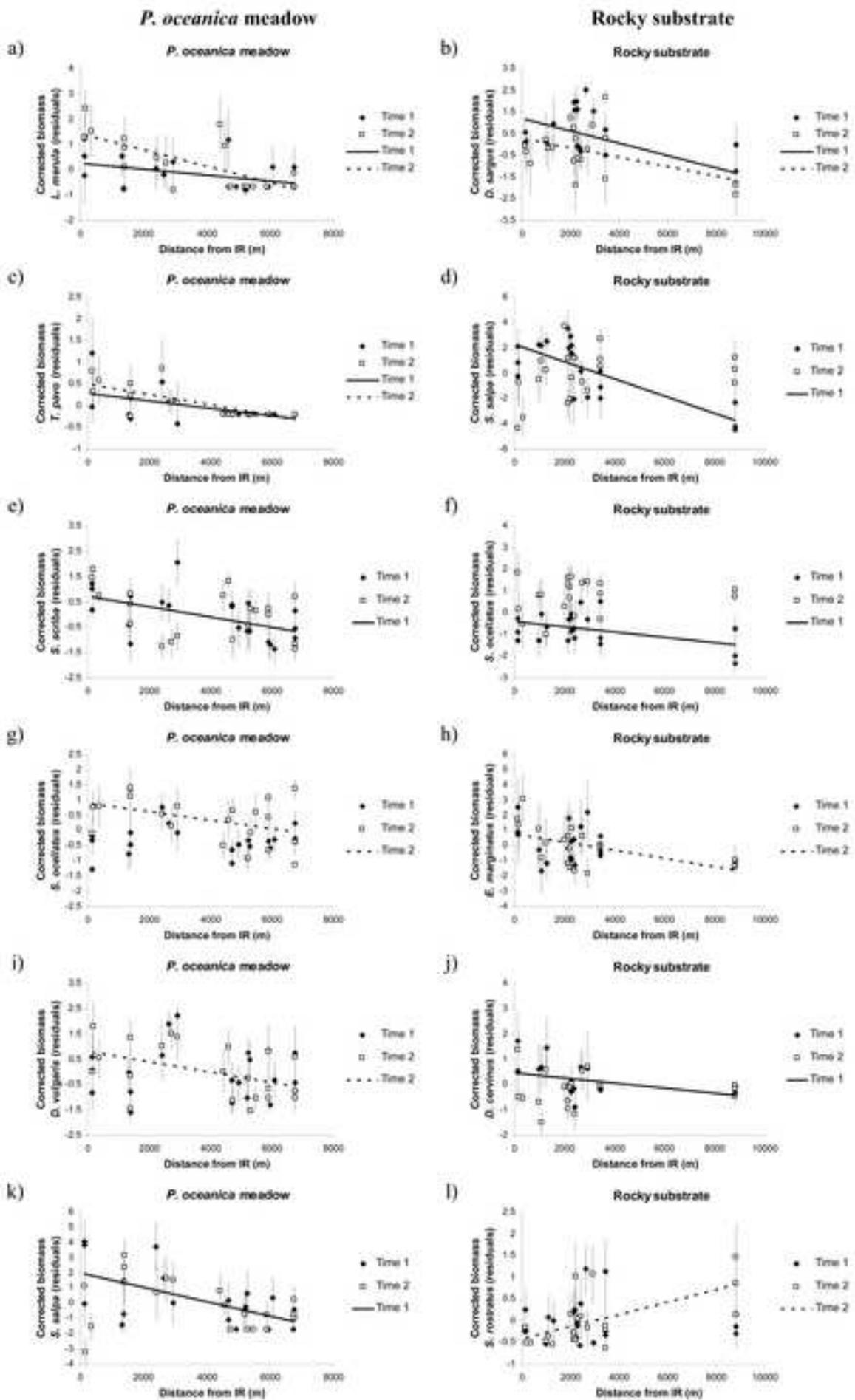


Figure 3

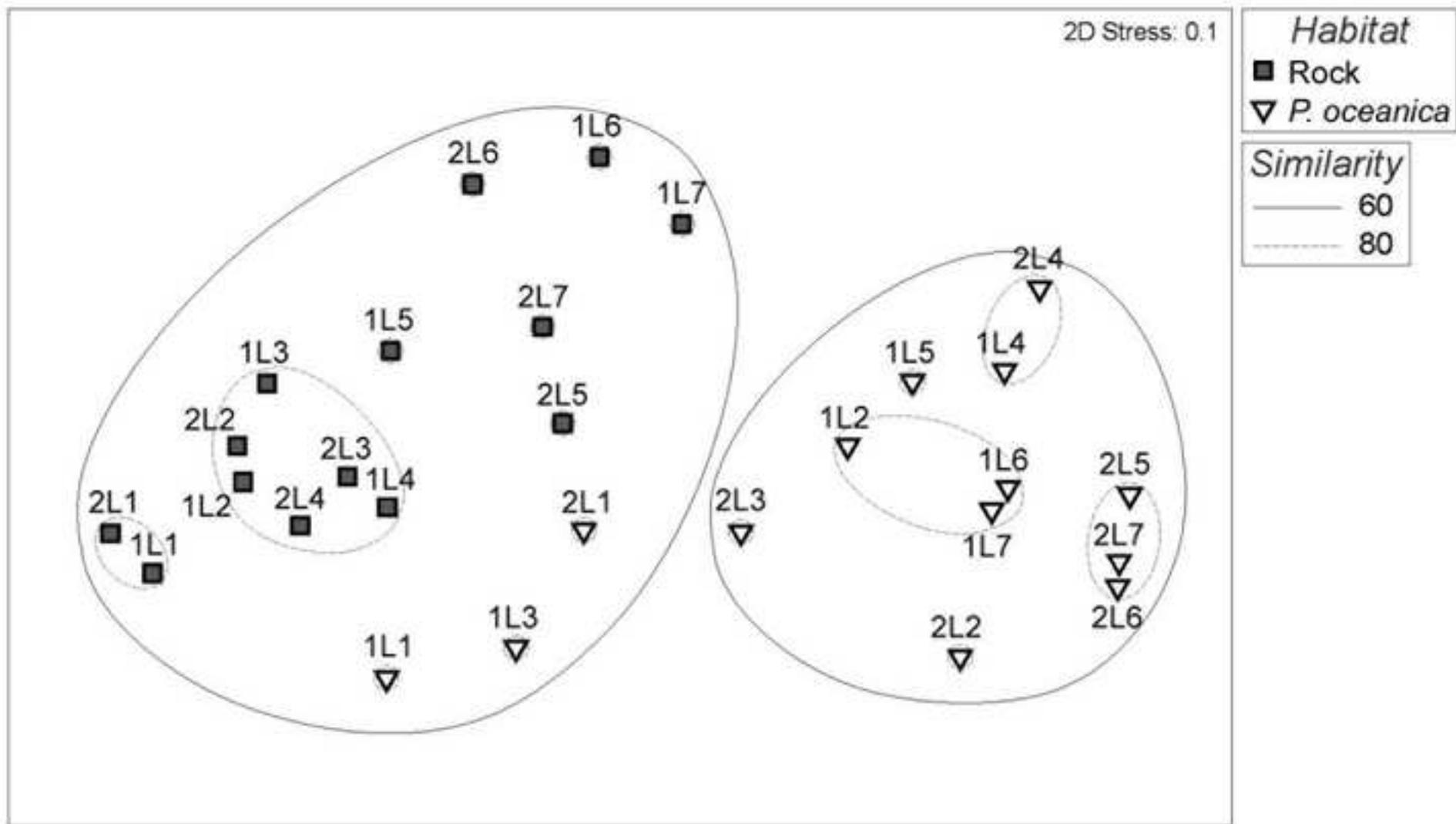


Figure 4

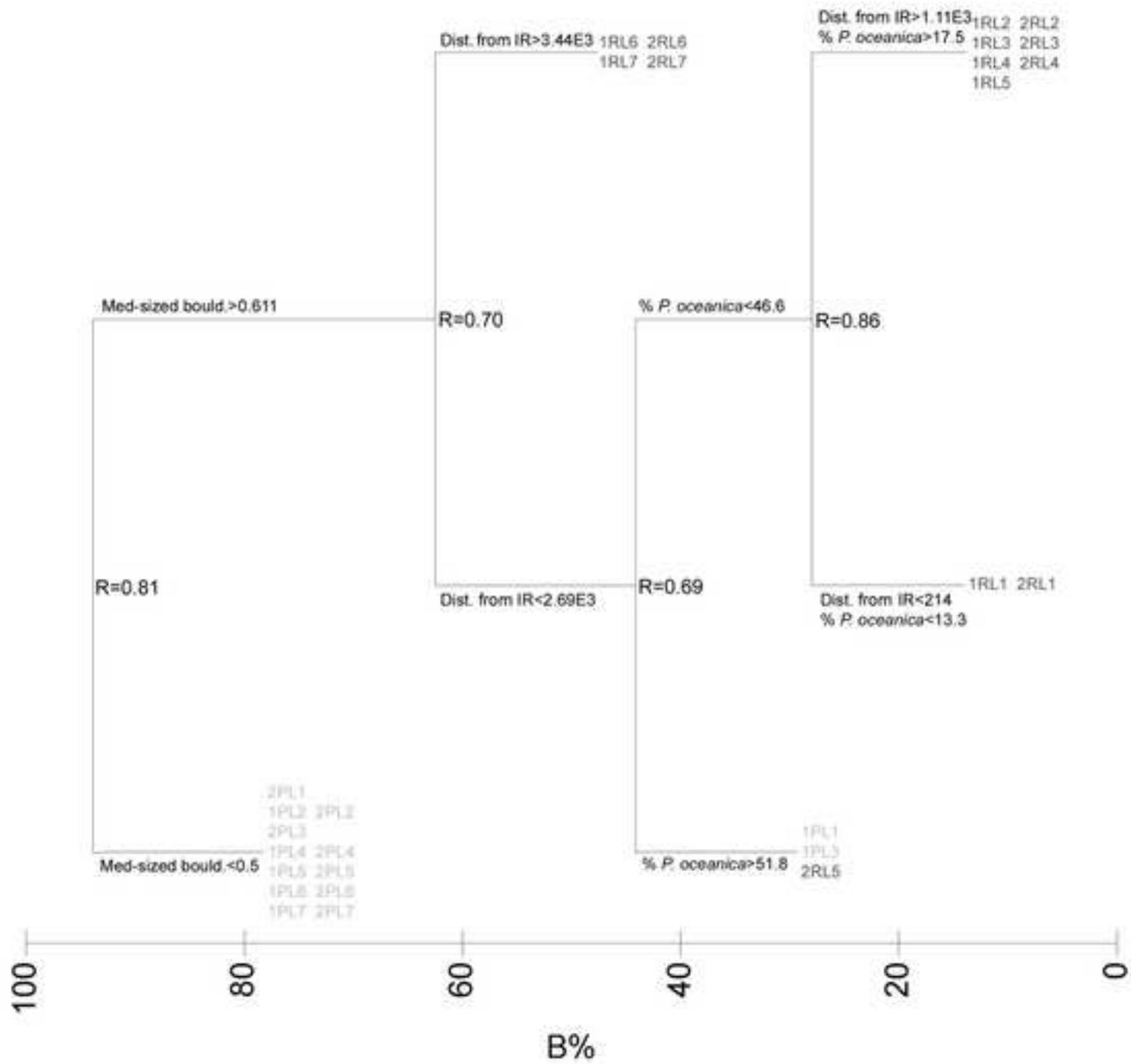


Figure 5