

Typology of fish nurseries in shallow Mediterranean coastal zones: all habitats matter

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1 **Typology of fish nurseries in shallow Mediterranean coastal zones: all habitats matter.**

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23

24 **Abstract**

25 Coastal zones are ecosystems of high economic value but exposed to numerous disturbances,
26 while they represent nurseries for many fish species, raising the issue of the preservation of their
27 functions and services. In this context, the juvenile fish assemblages of all types of habitats
28 present in shallow coastal zones were studied on the south-east coast of France using underwater
29 visual censuses. The abiotic and biotic descriptors of the 14 habitat types individualized did not
30 vary with time, except for a higher cover percentage and canopy height of macrophytes in the
31 warm period, which increased the three-dimensional structure of some habitats. The taxonomic
32 composition and density of juvenile fish assemblages were analyzed using both multivariate and
33 univariate descriptors, after grouping the 57 fish species recorded into 41 well-individualized
34 taxa. Juvenile fishes were recorded in all habitat types, with higher mean species richness and
35 abundance during the warm than the cold period. The richest habitats in terms of both species
36 richness and abundance were the natural rocky substrates and the interfaces between *Posidonia*
37 beds and the other habitats. Although juvenile fish assemblages differed among habitat types and
38 between periods, the most abundant fish species (*Atherina* sp., *Sarpa salpa*, Gobiidae,
39 *Symphodus* spp., *Pagellus* spp. and several *Diplodus* species) colonized different habitat types
40 (from 7 to 14) during their juvenile life. This study provided evidence of the role of all types of
41 shallow coastal habitats as fish nurseries and their varying pattern of occupation in space and
42 time by the different juvenile stages. It highlighted the importance of the mosaic of habitats and
43 interfaces for the complete development of all juvenile life stages of fishes, and for the
44 preservation of a high diversity of coastal fish assemblages and fisheries resources in the
45 Mediterranean Sea.

46

47

48 **Introduction**

49 Coastal areas have long been known as high commercial value areas^{1,2} but also as the zones most
50 impacted by anthropogenic disturbances^{3,4}, including habitat destruction⁵, chemical pollution^{6,7},
51 artisanal and recreational fishing^{8,9}, and more recently anthropogenic noise pollution¹⁰. However,
52 coastal zones also represent nursery sites for numerous fishes, including commercial species¹¹⁻¹³.
53 Most benthic and demersal fish species present a bipartite life cycle with a dispersive pelagic
54 larval phase and a more sedentary benthic adult phase¹⁴. Depending on the species-specific
55 planktonic larval phase duration (PLD)¹⁵, reproduction products may be dispersed on a more or
56 less extensive stretch of coastline, ranging from a few hundred meters to hundreds of
57 kilometers¹⁶⁻¹⁸. When competent, the surviving larvae metamorphose into juveniles and settle in
58 specific habitats (settlement phase) where they grow for a few months, before being recruited
59 into adult populations (recruitment phase) generally in deeper and more diverse habitats, as
60 juveniles and adults often occupy different habitat types^{11,19,20}. As the replenishment of local
61 adult fish populations depends on the success of their larval and juvenile phases, juvenile
62 survival in nursery habitats means that they are of paramount importance with regard to the fish
63 life cycle, stock conservation and fisheries exploitation²¹⁻²⁴. Settlement in nurseries may occur at
64 different times of the year according to species^{25,26}. Moreover, although some alternatives may
65 exist, the settlement-recruitment process usually follows similar patterns: during settlement, one
66 main or several cohorts of settlers may occur, resulting in a uni- or pluri-modal settlement peak.
67 This peak may be quantified as the density of new settlers per unit area of habitat and is referred
68 to as “settlement intensity” or “settlement success”^{20,27}. The settlement peak is then followed by
69 a period where juveniles grow inside nursery habitats, and during which they may display
70 ontogenic habitat changes, switching between various nursery habitats as they grow and require

71 new resources¹⁹. Ultimately, surviving juveniles (recruits) may join adult populations and
72 habitats (i.e. recruitment). The quantity of surviving juveniles inside nurseries after an arbitrary
73 period of time following settlement has been used as a measure of “recruitment level”²⁷. Beck
74 and collaborators^{11,28} describe the “nursery value” of a given habitat as a more comprehensive
75 view of these descriptors: the nursery value of a given habitat is the quantity of new individuals
76 produced per unit area and provided to adult populations as an outcome of the combination of
77 four components: the initial number of settlers provided to a nursery, their growth and survival,
78 and their capacity to join the adult population (functional and structural connectivities) (but see
79 other works for alternative points of views^{13,24}).

80 Numerous studies have been undertaken on the role of particular shallow coastal habitats as fish
81 nursery sites in the Mediterranean Sea. One approach was to focus on one type of habitat, such
82 as coastal lagoons^{29,30}, soft bottoms^{31,32}, *Cymodocea nodosa* meadows^{33–36}, *Posidonia oceanica*
83 beds^{37–41}, shallow rocky reefs more or less colonized by macrophytes assemblages^{42–49} and
84 shallow heterogeneous rocky substrates^{50,51}. Another approach was to focus on specific fish
85 species such as the gilthead seabream *Sparus aurata*⁵², sparids of the genus *Diplodus*^{25,53–57},
86 flatfishes such as *Solea solea*^{58,59}, the dusky grouper^{60–63}, or labrid species^{64–66}.

87 While a few studies were focused on multiple habitats^{26,67–69}, no study has been yet
88 systematically carried out on all habitat types encountered along the coast without any *a priori*
89 assumption regarding their potential role as nurseries for fishes. The present study was thus
90 designed to explore the potential contribution of all shallow (<6m) coastal habitats and their
91 interfaces (i.e. ecotones) as fish nurseries on the coasts of Provence (France, NW
92 Mediterranean), whatever the type and intensity of human pressures. The aims of the present
93 study were to 1) define the environmental characteristics of the habitat types present in shallow

94 coastal habitats and their main temporal variations, 2) characterize the juvenile fish assemblages
95 associated with the different habitats and relate or not their seasonal variations to environmental
96 changes in habitat structure, and 3) determine the potential of the different habitat types as
97 nurseries for juvenile Mediterranean coastal fishes.

98

99 **Material and methods**

100 **Ethics statement**

101 The observational protocol was submitted to the regional authority 'Direction interrégionale de
102 la mer Méditerranée' (the French administration in charge of Maritime Affairs), which did not
103 require a special permit since no extractive sampling or animal manipulations were performed
104 (only visual censuses in natural habitats), since the study did not involve endangered or protected
105 species and since the surveyed locations were not privately owned.

106 **Sites and sampling methods**

107 Juvenile fish were monitored by underwater visual censuses (UVC)⁷⁰ in a wide variety of
108 habitats from 0 to 6 m depth at 42 stations randomly spread along a 100 km long stretch of the
109 Provence coastline (Fig. 1). A random sampling design was adopted to encompass the natural
110 characteristics and spatial variability of shallow coastal habitats during the warm (June-July
111 2014) and cold (April 2015) seasons (Table 1), as fish settlement shows wide seasonal
112 variation^{26,42,71}. A total of 2 101 UVC samples were undertaken. Each sample was *a priori*
113 attributed to one of 14 habitat types defined according to the main types of substrates present in
114 shallow sublittoral Mediterranean coastal areas, i.e. natural and artificial rocky substrates, soft
115 bottoms and seagrass beds, along with their main ecotones (hereafter named interfaces) (Table
116 1), according to previous studies on juvenile fish settlement in the Mediterranean Sea^{25,36,37,45}.

117 Fishes were recorded on 2 x 1 m (2 m²) quadrates on natural rocky substrates (RS), 5 x 2 m
118 (10 m²) belt transects in *C. nodosa* meadows (CY and POCY) and 10 x 1 m (10 m²) transects in
119 all other habitats, including *P. oceanica* beds, adapted according to the spatial extent, variability
120 and heterogeneity of habitat characteristics^{72,73}. All fishes smaller than 10 cm in total length (TL)
121 were identified at species or genus level, and their abundance and size (TL, to the nearest cm
122 between 4-10 cm, to 0.5 cm under 4 cm TL) were recorded. In addition, a set of habitat
123 descriptors were recorded in order to verify *a posteriori* that the sampling units (visually
124 selected) were appropriately classified into meaningful and objectively-defined habitat types.
125 After each fish count, a set of 26 habitat descriptors were recorded in quadrates or when
126 swimming back along transects in order to describe precisely the abiotic and biotic habitat
127 characteristics: depth (m), slope (integer scale from 1 to 6), percent coverage of substrate types
128 (6 types), rugosity classes (4 classes), vegetal types (3 types of seagrasses and 5 types of other
129 macrophytes), and height (cm) of the canopy^{26,72,74} (Table 2). For convenience we used the term
130 *Cystoseira* forest although the genus has been recently divided into three⁷⁵. Whatever the genus
131 actually used, *Carpodesmia*, *Treptacantha* or *Cystoseira*, all species display erect arborescent
132 thalli and functionally form a forest^{76,77}.

133 For statistical analyses, only the juvenile individuals of the species recorded were considered
134 following literature information, as the size limit between juvenile and adult stages varies among
135 species depending on their maximum size and biology^{57,72,74}.

136

137

138

139 **Data analysis**

140 Our sampling effort produced a data-frame containing 2 101 lines (one per sample) with data
141 ordered by columns for each fish (taxa: densities per species and per size-class) and habitat
142 descriptors (i.e. metrics describing habitat characteristics).

143

144 ***Habitat descriptor analysis***

145 A first set of analyses was performed on a subset of this data-frame, displaying only habitat
146 descriptors for each sample. Multivariate descriptors of habitat were previously standardized and
147 the Euclidean distance was used as a measure of dissimilarity due to the different nature and
148 variation range of the descriptors used⁷⁸. Ordination methods were applied to the distance matrix
149 calculated from this data-frame in order to verify whether samples would be grouped by clusters
150 in accordance with their *a priori* habitat types. Since a first visual interpretation of ordination bi-
151 plot indicated that samples were in effect grouped by habitat types (see results), we calculated a
152 new matrix of distance between centroids for the grouping factor “Habitat-Station-Period”,
153 which enabled us to display a clearer visual representation using ordination. To represent
154 dissimilarities between samples of habitat descriptor assemblages, we performed a Principal
155 Coordinate Analysis (PCoA) ordinations plot of centroids of descriptor samples of the dummy
156 factor combining station, habitat type and period^{79,80}. Arrows were superimposed onto PCoA bi-
157 plots to represent the Spearman’s rank correlations between biplot axes and habitat descriptors⁷⁸.
158 Complementarily, in order to test whether samples would indeed significantly differ in terms of
159 metrics assemblages as a function of their habitat types, we applied to this last distance matrix a
160 PERMutational multivariate ANalysis Of VAriance (PERMANOVA) using the algorithm
161 developed by Anderson et al.⁸⁰. The PERMANOVA model included two factors: (i) “Habitat”

162 was fixed and included 14 levels (Table 1) and (ii) “Period” was fixed and included two levels
163 (warm and cold).

164

165 *Juvenile fish assemblage analysis*

166 We applied the same model (Habitat x Period) in order to test the effect of both factors on the
167 descriptors of the juvenile fish assemblages. We used both univariate (taxa richness, total
168 assemblage density) and multivariate (composition and relative densities of taxa) descriptors as
169 response variables. In order to represent dissimilarities between samples in terms of juvenile fish
170 multivariate assemblages, according to habitats and period, we performed Principal Coordinate
171 Analysis (PCoA) ordinations plot of samples. Arrows were superimposed onto PCoA bi-plots to
172 represent the Spearman’s rank correlations between bi-plot axes and taxa densities^{78,79}.

173 Complementarily, for each assemblage descriptor (i.e. multivariate taxa densities, richness, total
174 densities), in order to test whether samples would indeed significantly differ in terms of
175 assemblage descriptors as a function of their habitat types and/or period, we applied to each
176 respective distance matrix a PERMutational uni/multivariate ANalysis Of VAriance
177 (PERMANOVA) using the algorithm developed by Anderson et al.⁸⁰. The PERMANOVA
178 model included two factors: (i) “Habitat” was fixed and included 14 levels (Table 1) and (ii)
179 “Period” was fixed and included two levels (warm and cold). For univariate descriptors (richness
180 and total densities), we used the Euclidian distance while for the multivariate assemblage
181 descriptor (relative taxa densities), we used the Modified Gower distance measure as suggested
182 by Anderson et al.⁸⁰. Additionally, for a set of 6 Sparidae taxa whose juvenile habitats have been
183 particularly described in the past²⁵, mean individual sizes (TL, cm) were compared between

184 treatments using t-tests (*Diplodus annularis*, *D. vulgaris*, *D. sargus*, *Oblada melanura*, *Pagellus*
185 spp., *Sarpa salpa*).

186 Sums of squares (SS) for all PERMANOVA designs were performed as a fully partial analysis
187 (type III). P-values were obtained by 999 permutations of residuals under a reduced model.
188 Monte Carlo P-values were considered when there were not enough possible permutations
189 (<200). Terms were pooled as suggested by Anderson et al.⁸⁰. Due to the intrinsic variability of
190 ecological data, tests were considered significant for P-values <0.1. Multivariate exploratory
191 analyses and both multivariate and univariate inferential tests were performed using the PRIMER
192 6 software and PERMANOVA + B20 package^{79,80}. Dataset manipulations, basic tests (t-tests)
193 and others graphical visualizations were performed in R Environment⁸¹ using the library
194 `ggplot2`⁸².

195

196 **Results**

197

198 **Typology of habitats**

199 Mean habitat descriptors significantly differed between the habitat types *a priori* defined, while
200 Period and the interaction (Habitat x Period) had no significant effect (PERMANOVA, P-value <
201 0.001, Table 3, Fig. 2). Among the 91 habitat pairs, 88 pair-wise tests resulted in a significant
202 difference of descriptor assemblage between pairs of habitat types (PERMANOVA, pair-wise
203 tests, all P < 0.1). Such results *a posteriori* confirmed the validity of the 14 habitat types defined
204 for the fixed factor “habitat”, which remained stable over time whatever the season. These
205 habitat types could be grouped into 3 main categories: rocky substrates, soft bottoms and
206 seagrass beds, with all their interfaces.

207 The first two axes of the PCoA explained 63.4 % of the variance (81.7 % for the first five axes).
208 Rocky substrates (natural and artificial) gathered tightly on the positive part of axis 1 and were
209 correlated not only with rocks and boulders, but also with high slope, high rugosity, and most
210 macrophyte categories. Natural rocky habitats (RS) were characterized in particular by
211 *Cystoseira* forests (21 % mean coverage), other arborescent macroalgae (7 %; i.e. *Halopitys*
212 *incurvus*), and bushland communities (49 %; i.e. Sphacelariales) (Table S1). Artificial rocky
213 substrates (AR) differed from natural ones by the absence of any type of erect perennial
214 macrophyte forest, but the amount of turf/encrusting algae cover (42 %) and bushland (58 %).
215 All soft bottoms (SB) clustered on the positive part of axis 2 and were mainly correlated with
216 gravel and floating algal detritus. They were scattered along axis 1 from pebbles (positive part)
217 to sand (negative part) depending on their granulometry. They were also characterized by a low
218 slope and the absence or rarity of algal cover (5 % of turf/encrusting algae only). Unlike rocky or
219 soft bottoms, seagrass bed habitats, and particularly those associated with *Posidonia oceanica*
220 (PO), were highly dispersed on the PCoA plan (Fig. 2), in relation with the type of substrate *P.*
221 *oceanica* is growing on. Stations where *P. oceanica* was growing on rocky substrates clustered
222 on the positive part of axis 1, but on the negative part of axis 1 where it was growing on sandy
223 substrates. Habitats associated with *P. oceanica* barrier reef structure were scattered along axis 2
224 from high depth and seagrass cover percentage on the barrier reef outer slope (POEX) to a high
225 percentage of sand in the shallow inner slope (POIN) and associated *Cymodocea nodosa*
226 meadows (CY and POCY). POIN was also characterized by the presence of algal wrack, which
227 offered shelter to juvenile fish.
228 On the plan defined by axes 1 and 2, some PODM stations were gathered with rocky habitats due
229 to a high cover percentage of macrophytes, especially bushland communities (Table S1), but all

230 PODM stations tightly clustered together on the positive part of axis 4, which was correlated
231 with a high dead matte percentage. All interfaces were positioned on the PCoA plan at a logical
232 but well-individualized place testifying to their particular identity: IPR between *Posidonia* and
233 rocky substrates on the positive part of axis 1 and negative part of axis 2, IRS between rocky and
234 soft substrates on the positive parts of both axes, IPS and IPM on the negative part of axis 1, as
235 correlated to high sand and dead matte percentages respectively. Mean values (\pm SE) of the
236 abiotic and biotic descriptors of the 14 individualized habitat types are given in Table S1, along
237 with their significant seasonal variations. Abiotic descriptors rarely changed with period
238 whatever the habitat and were related to the haphazard position of sampling units, while biotic
239 habitat descriptors presented consistent seasonal variations linked to the biology and growth of
240 macrophytes. Higher cover percentages and canopy height of seagrasses and macroalgae were
241 generally recorded in warm rather than in cold period, except for turf/encrusting and wrecked
242 algae, which increased the three-dimensional structure of these habitats (Table S1). However,
243 differences were statistically significant only in a few habitats due to the high variance of data.

244

245 **Juvenile fish assemblages**

246 A total of 526 014 juvenile individuals, belonging to 57 different fish species/taxa and 22
247 families were recorded (Table S2). As small juveniles of particular genera such as *Symphodus*, or
248 families such as blenniids and gobiids, were difficult to identify precisely underwater, they were
249 grouped into 41 taxa for analysis. A higher total species richness of juvenile fish was recorded
250 during the warm (37 taxa, $n = 1\ 376$) than the cold (27 taxa, $n = 725$) period and differed among
251 habitats (Table 4). The highest total number of taxa was recorded on soft bottoms (25 taxa, $n =$
252 426), followed by rocky substrates and *Posidonia* beds (22 taxa each, $n = 428$), while the lowest

253 number of juvenile fish species was observed in *Cymodocea* beds (6 taxa, n = 116). The most
254 abundant taxa included by decreasing order of importance unidentified larvae, *Atherina* sp.,
255 *Sarpa salpa*, Gobiidae, *Symphodus* spp., *Diplodus vulgaris*, *Pagellus* spp., *Diplodus annularis*,
256 *Oblada melanura* and *Diplodus sargus* (Fig. 3). They were observed in most habitats (from 7
257 habitats for *Pagellus* spp. to 14 for *D. vulgaris*), while 13 taxa were recorded in only one habitat
258 type, generally with low abundance (Table S3). Four taxa were only recorded on rocky substrates
259 (*Boops boops*, *Epinephelus marginatus*, *Thalassoma pavo* and Tripterygiidae) and four on soft
260 bottoms (*Arnoglossus* spp., *Bothus* sp., *Solea* sp. and Trachinidae). Most species (23 spp.) were
261 observed at both periods, and a higher number were recorded only in warm than only in cold
262 periods (14 spp. vs 4 spp., respectively) (Fig. 3).

263 Mean species richness varied from 0.25 to 3 taxa per 10 m² and differed according habitats and
264 periods. The significant interaction of the two factors indicated that between-habitat variability
265 differed between seasons (PERMANOVA, F = 6.506, P < 0.001, Table 5). Mean species
266 richness was highest on natural and artificial rocky substrates and lowest in *Cymodocea* beds
267 (Fig. 4). Interfaces *Posidonia*/other habitats (IPR, IPS and IPM) presented a higher mean species
268 richness than the different habitats of *P. oceanica* bed and barrier reef, demonstrating the
269 particular importance of ecotones for juvenile fishes. The mean species richness tended to be
270 higher during the warm than the cold period, in all but POIN habitat, where a lower mean species
271 richness was recorded in summer (data not shown).

272 As schools of larvae and *Atherina* sp. could be numerous and haphazardly dispersed in space and
273 time, they might mask the effect of period or habitat on relative abundance. *Atherina* sp. were
274 more abundant during the warm period and were present in 12 habitats, while undetermined
275 larvae were observed in higher abundance during the cold period and present in 13 habitat types.

276 They were thus excluded from the analysis of juvenile abundance to obtain clearer patterns. The
277 total density of juvenile fishes also varied significantly between habitats and periods, with
278 different patterns according to the period (PERMANOVA, $F = 6.028$, $P < 0.001$; Fig. 5; Table
279 6). In most habitats, except POIN and IPS, juvenile fish abundance was higher during the warm
280 season, especially in *Posidonia* seagrass beds and barrier reef outer slope (POEX) and lagoon
281 (POCY). The mean abundance of juvenile fish, all habitats combined, did not differ significantly
282 with period (Table 6), reaching 8.48 ± 0.69 individuals per 10 m^2 during the warm period and
283 9.59 ± 0.94 individuals per 10 m^2 during the cold period.

284

285 **Variability of juvenile fish assemblages in habitats**

286 The assemblage composition of juvenile fishes in terms of relative taxa-specific densities
287 significantly differed between periods, and these differences were specific to each habitat as a
288 significant interaction between the two factors was evidenced (PERMANOVA, $F = 7.743$,
289 $P < 0.001$; Fig. 6 ; Table 7). Seasonal differences in juvenile assemblage occurred in most habitat
290 types, except CY, POCY and IRS. On rocky substrates (RS), no difference in juvenile fish
291 assemblage according to the relative importance of macroalgal cover types (*Cystoseira* forest,
292 bushland or turf/encrusting) was observed (PERMANOVA, $F = 0.87$, $p = 0.531$). While the
293 assemblage differed with period (pair-wise test, $t = 1.594$, $p = 0.025$), *Sarpa salpa* was the
294 dominant species in both periods, followed by *Diplodus annularis*, *Boops boops* and *Symphodus*
295 spp. in the warm period, and by *D. sargus*, *Mugil* spp., and *Thalassoma pavo* in the cold period
296 (Fig. 6). *S. salpa* also dominated on artificial structures (AR) in warm period, with *Symphodus*
297 spp., *Oblada melanura* and *Coris julis*. On soft bottoms (SB), Gobiidae followed by *S. salpa*
298 dominated in both periods, while the assemblage statistically differed ($t = 3.406$, $p < 0.001$).

299 During the warm period, *Mugil* spp., *D. sargus* and *D. puntazzo* were also abundant on SB and
300 particularly associated with high percentages of pebbles and gravel, while *Pagellus* spp.,
301 *Lithognathus mormyrus*, *Mullus* spp., Trachinidae, *Bothus* sp. and *Solea* sp. were more
302 associated with sand. During the cold period, *D. vulgaris* was particularly abundant on SB and
303 mainly associated with pebbles and gravel. In *Posidonia* beds (PO), the juvenile fish assemblage
304 slightly differed according to the type of substrate *P. oceanica* was growing on. Higher
305 abundances of *D. annularis* and *Symphodus* spp. were recorded when the seagrass was growing
306 on sand, and of *O. melanura* and *S. salpa* when growing on rocky substrates. A seasonal
307 variation was observed in PO ($t = 3.298$, $p < 0.001$) with high abundances of *Pagellus* spp., *S.*
308 *salpa*, *Symphodus* spp. during the warm period, and the dominance of *D. vulgaris* in the cold
309 period. *Oblada melanura* remained abundant all the year in PO. In the different barrier reef
310 habitats, the juvenile assemblage differed with periods, while some species dominated in both
311 periods, such as *S. salpa* in POBR ($t = 2.335$, $p < 0.001$) and PODM ($t = 2.048$, $p = 0.007$),
312 *Symphodus* spp. in POEX ($t = 2.651$, $p < 0.001$), and Gobiidae plus *Pagellus* spp. in POIN ($t =$
313 3.174 , $p < 0.001$) (Fig. 6). Each type of interface was dominated by the abundance of some
314 species, and presented seasonal variations, except IRS ($t = 1.101$, $p = 0.289$) dominated by
315 Gobiidae, *Serranus cabrilla* and *O. melanura*. At IPR, *C. julis* was the dominant species in both
316 periods, but with a far higher abundance in the warm period ($t = 2.083$, $p = 0.005$) followed by
317 *O. melanura* and *Symphodus* spp., and by *S. salpa* and *S. cabrilla* in the cold period. At IPS, the
318 juvenile assemblage was dominated by *Symphodus* spp., *D. annularis*, and *O. melanura* during
319 the warm period, and by Gobiidae, *D. vulgaris* and *Pagellus* spp. in the cold period ($t = 1.608$, p
320 $= 0.038$). At IPM, the dominant species was *S. salpa* in the warm period, and *Symphodus* spp. in
321 the cold period ($t = 3.331$, $p < 0.001$). Noteworthy was the higher presence of predators

322 (*Serranus cabrilla*, *S. scriba*, *Scorpaena porcus*, *Dentex dentex* and *Labrus viridis*) in interface
323 habitats (Fig. 6). In *Cymodocea* meadows (CY and POCY) no statistical difference was observed
324 with period ($t = 1.221$, $p = 0.212$ and $t = 1.297$, $p = 0.162$, respectively) and the assemblage was
325 dominated by *D. vulgaris* in CY and by *Pagellus* spp., *D. vulgaris* and Gobiidae in POCY. Thus,
326 several species dominated in different juvenile habitats in both periods. However, the mean size
327 of juvenile fishes could differ between periods as illustrated in Fig. 7 for some of the most
328 abundant species. Smaller-sized juveniles were observed during the warm period for *D.*
329 *annularis*, *D. sargus*, *O. melanura* and *Pagellus* spp., and during the cold period for *D. vulgaris*
330 and *S. salpa*.

331

332 **Discussion**

333

334 **Habitats used by juvenile fish in Mediterranean shallow coastal zones**

335 All the sites surveyed hosted juveniles whatever the period, highlighting the crucial functional
336 role of the very shallow coastal bottoms as fish nurseries. In contrast to findings based on the
337 habitat- and species-centered approaches, in the present study juvenile fish assemblages were
338 recorded in all types of habitats encountered in Mediterranean shallow coastal zone. A total of 14
339 different habitat types were characterized, which could be grouped into three broad categories,
340 rocky substrates (natural RS and artificial AR), sedimentary bottoms (SB) with all levels of
341 granulometry, and seagrass beds including *Cymodocea nodosa* and *Posidonia oceanica*
342 meadows (CY, PO, PODM) (Table 1). The ecotones or interfaces between the three broad
343 habitat categories (IPM, IPR, IPS and IRS), were individualized as particular habitat types. We
344 evidenced that if the structural characteristics of habitat types did not vary with period, the

345 biological characteristics did vary with higher cover percentages and canopy height of seagrasses
346 and macroalgae in the warm period (Table S1).

347 The presence of juveniles was evidenced in every type of sampled habitat. While the habitat
348 types were well individualized, it appeared that one third of fish species occupied more than 7
349 habitat types when juveniles and were the most abundant species (34.1 % of total species
350 richness and 95.2 % of total abundance), while the one third of species characteristic of only one
351 habitat type were rather rare (31.7 % of total species richness and 1.1 % of total abundance). If
352 atherinids and larvae were excluded, the relative abundance of the common and restricted species
353 remained similar (90.8 % and 2.0 % respectively). Habitat and seascape tri-dimensional structure
354 can be qualified by its heterogeneity and complexity^{83,84}. Generally high quality habitats for
355 juvenile fishes are recognized to be associated with high degrees of three-dimensional
356 structuration⁸⁵, in terms of both complexity^{46,48,86,87} and/or heterogeneity³⁶. Natural rocky
357 habitats (RS) presented a high structural and biological complexity due to different macrophytes
358 assemblages, and indeed supported the highest mean species richness and abundance of juvenile
359 fishes whatever the period. However, SB while presenting a lower structural complexity than RS
360 or PO, supported the highest total species richness (24 spp.) of juvenile fish owing to an
361 intermixed diversity of granulometry and the ability it offers to the juveniles to blend in with the
362 bottom. It was also evidenced that interfaces represented highly favorable habitats for juveniles
363 in terms of both species richness and abundance (Fig. 4 and 5). Ecotones (i.e. interfaces) have
364 long been known as increasing the diversity of fish communities⁸⁸ and their role in the dynamics
365 of rocky fish assemblages associated with *Cystoseira* forests was recently studied in the
366 Mediterranean Sea^{47,89}. Interfaces, particularly between *Posidonia* beds and adjacent habitats
367 (IPS, IPR, IPM), harbored a high number of juveniles of piscivorous fishes such as *Serranus*

368 *cabrilla*, *Scorpaena porcus*, *Dentex dentex*, and *Labrus viridis*, which found here a suitable place
369 for predation. This is consistent with previous studies highlighting the suitability of ecotones for
370 various predation strategies (ambush, stalk-attack, etc.)⁸⁹ and for avoidance of predators by their
371 juvenile prey⁸⁷. In the case of the *Posidonia oceanica* barrier reef complex, we provided
372 evidence that different juvenile fish assemblages were associated with the different parts of the
373 barrier reefs including reef flat, slopes and lagoon (POBR, POEX, POIN, and POCY). The
374 barrier reef complex is by nature a juxtaposition of various habitat patches along with their
375 interfaces; this habitat diversity allows various species to find suitable juvenile habitats, as
376 illustrated in the case of tropical reef habitat systems^{90,91}.

377

378 **Temporal succession of nursery use by juvenile fishes**

379 We observed that juvenile fish assemblages presented higher species richness and abundance
380 during the warm than the cold period in most habitat types. The specific composition of the
381 juvenile assemblage is directly linked to the reproductive cycle of coastal fish species. Juvenile
382 fishes settling in coastal nurseries during the warm period were issued from adults reproducing in
383 spring or early summer, as the duration of larval life for most Mediterranean coastal fish species
384 ranges from 2 to 6 weeks^{15,59,92}. Those arriving during the cold period resulted from the
385 reproduction of adults in late summer, autumn and winter. We observed in effect the smallest *D.*
386 *annularis* and *D. sargus* juveniles during the warm period and the smallest *D. vulgaris* and *S.*
387 *salpa* during the cold period (Fig. 7), following a well-known temporal succession of juvenile
388 fish species in coastal nurseries^{26,42,56,64,68,93}. If juvenile fishes settle sometimes in highly specific
389 habitats, they rapidly expand their home range when growing and increasing their swimming
390 capacities, colonizing deeper or adjacent habitats²⁰, and leaving settlement sites available for the

391 successive arrival of fish post-larvae^{54,56,93}. By performing such ontogenetic habitat shifts as they
392 grow, juveniles tend to switch to using the habitat best fitting their needs in terms of food *versus*
393 refuge against predation availability (the “habitat quality” ratio)¹⁹. We observed in effect the
394 presence of juveniles of >34% fish species in more than half of the habitat types individualized
395 indicating that they were used by fishes at various stages of their juvenile life. Thus, for most
396 species, the presence of a mosaic of different habitats is essential for the success of juvenile fish
397 recruitment^{46,47}.

398

399 **Importance of both local habitat characteristics and large-scale environmental**
400 **conditions**

401 However, the higher abundance of juveniles in seagrass bed habitats and rocky substrates during
402 the warm period could be related to the greater protection and food resources provided by the
403 greater canopy height of *Posidonia oceanica* and macroalgae communities^{45,46,48}. The role of
404 highly complex *Cystoseira* forest canopies with regard to the composition of juvenile fish
405 assemblage was well studied by Cheminée et al.^{45,46}, Cuadros et al.⁴⁷ and Hinz et al.⁴⁸, who
406 demonstrated that *Symphodus* spp., *Labrus* spp. and *Serranus* spp. were more abundant in dense
407 complex forests, while *C. julis* and *T. pavo* preferred less complex patches of bare substratum
408 located at the edges of the forests. In our study, *Cystoseira* forests were not extensive enough to
409 form large, dense forests such as those studied by these authors in Corsica and the Balearic
410 Islands, but were mixed with patches of other erect macroalgae, bushland and turf algae. This
411 was the reason why no correlation was found between the cover percentages of these macrophyte
412 assemblages and the composition of the juvenile fish assemblages on the coasts of Western
413 Provence (authors’ unpublished data). The decline and scarcity of erect macroalgae forests

414 (notably *Cystoseira* spp.) has been documented in the last two decades in different parts of the
415 Mediterranean coasts⁹⁴⁻⁹⁷. Decline of forests occurs through ecosystem shifts resulting from
416 cascading effects from a wide array of anthropogenic pressures⁹⁸⁻¹⁰⁰. Such profound
417 transformations of the seascape is known to have damaging effects on habitats' nursery
418 role^{45,47,49,72}. Therefore, in those altered areas, the habitat quality available nowadays for juvenile
419 fishes is probably several orders of magnitude below what it could be⁴⁶. This highlights the
420 importance of preserving what is left of the nursery function of coastal areas. In order to preserve
421 this function, habitats should in particular be protected against destruction but also against any
422 kind of transformation of their tri-dimensional structure and composition.
423 On the other hand, juvenile fishes' abundance⁵⁶, growth¹⁰¹ and mortality¹⁰² vary considerably in
424 space and time due to natural stochastic processes linked to both environmental conditions
425 (currents, winds, hydrological parameters)^{44,53} and the success of adult reproduction¹⁰³, being
426 high or low at one place from one year to another. The same nursery site can therefore perform
427 as a 'good' nursery site one year and not the following one⁵⁶. Similarly, the same habitat can
428 perform as a 'good' nursery at a given site but not in another location¹⁰⁴. Thus, the success of
429 fish nurseries does not depend only on the local characteristics of habitats but also on large scale
430 environmental phenomena that determine the initial intensity and trajectory of the flux of fish
431 larvae^{71,105}.

432

433 **Importance of the mosaic of habitats for coastal fishes**

434 We provided evidence that the most abundant fish species in Mediterranean shallow coastal
435 areas used several habitat types as nurseries whatever the period, even if juvenile fish
436 assemblages presented specificities in composition and relative abundance of species in each

437 habitat type (Fig. 6). It could be thus claimed that all habitat types present an actual potential as
438 nursery sites for Mediterranean coastal fishes, and that a diversified mosaic of habitats would be
439 the most efficient way to promote high and successful juvenile fish recruitment by providing
440 contiguous shelters and food resources for the different stages of fishes' juvenile life. These
441 results are in agreement with the seascape nursery approach developed by Nagelkerken et al.¹⁰⁶,
442 which conceptualizes the role of functionally connected multiple mosaics of habitats for fish
443 nursery management.

444 The effective management of coastal zones often consists in a non-fair trade-off between
445 destructive or impacting human activities (harbor and marina constructions, sewage and
446 industrial outflow, etc.) and efforts for environmental protection mainly represented by the
447 implementation of marine protected areas^{107,108}. A pernicious consequence of the current
448 awareness of the economic value of ecosystems and their ecological services to human
449 populations¹⁰⁹ often resides in a hierarchical view of ecosystems or habitats depending on the
450 intended goals of users. For example, in the Mediterranean Sea *Posidonia oceanica* seagrass
451 beds benefit from a particular protection status¹¹⁰, and coralligenous reefs merit special
452 attention¹¹¹. The results of the present study evidence the importance of all types of shallow
453 coastal habitats as nursery sites for Mediterranean fishes whatever the period considered, which
454 strongly supports the general seascape nursery theory of Nagelkerken et al.¹⁰⁶ and the views of
455 Cheminée et al.¹¹² and Cuadros et al.⁴⁷ for the Mediterranean Sea, regarding the importance of
456 protecting the mosaic of habitats for the good health and functioning of coastal ecosystems. The
457 preservation of a mosaic of habitats along the coast, notably in very shallow waters, therefore
458 constitutes the best way to preserve both fish biodiversity and fishery resources. This study
459 highlights that conservation in France is often disconnected from biological reality with, except

460 in a few Marine Parks (which represent a small portion of coastline¹¹³), most of the shallow
461 habitats not taken into account in any protection plan.

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463

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772 **Author Contributions**

773 All authors contributed extensively to the work presented in this paper. AC, LLD, ER, PA, AG,
774 AB, LC, JYJ, SR, TT and MHV performed the field work. AC, ER, PA, AG, DB, LC compiled
775 the data. AC, LLD and MHV analyzed output data. AC, LLD and MHV designed, wrote and
776 revised the manuscript. All authors discussed the results and implications and commented on the
777 manuscript at all stages.

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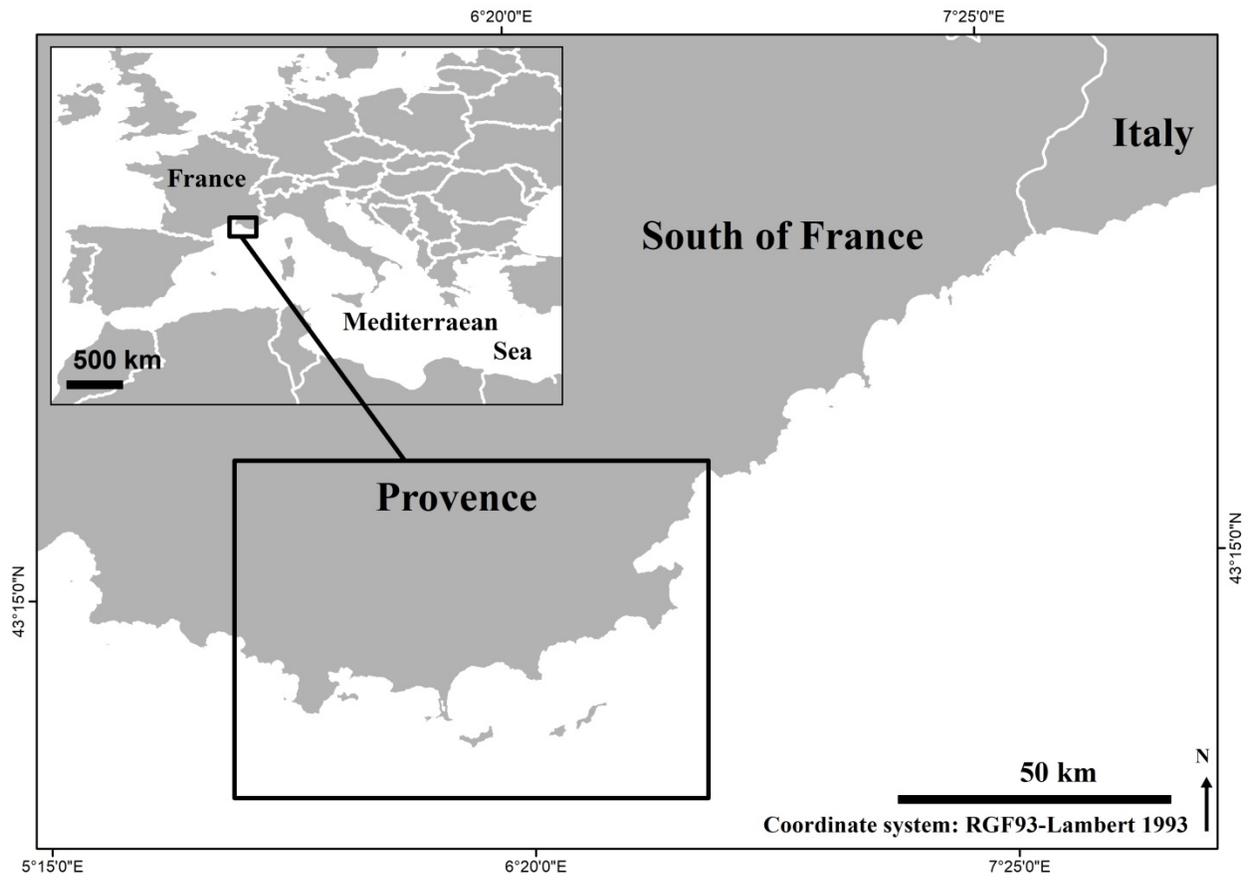
779 **Competing Financial Interests statement:**

780 The authors declare no competing financial interests, and no non-financial competing interest.

781

782 **Additional Information**

783 Supplementary information accompanies this paper at <http://www.nature.com/srep>



785

786 Figure 1. Map of the studied area: 42 stations were sampled along the 100 km stretch of the
787 studied portion of the French Riviera coastline (red rectangle)

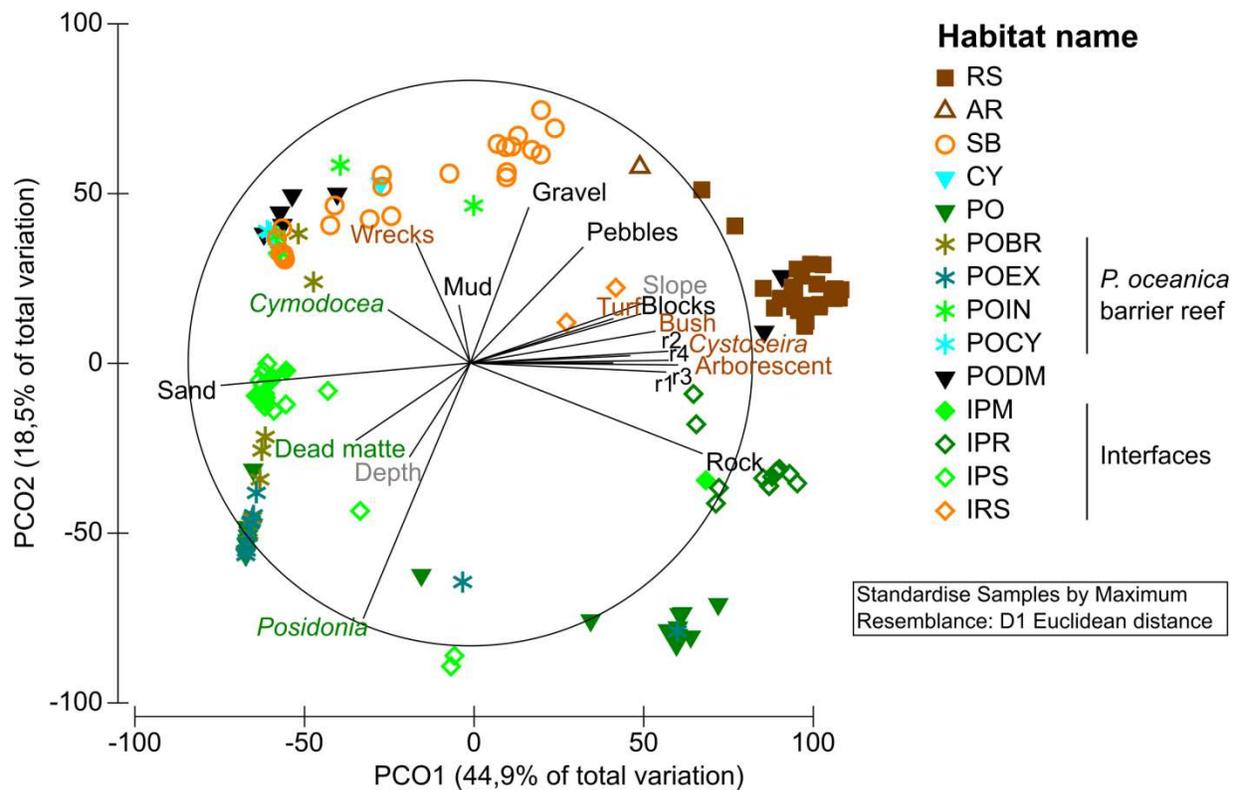
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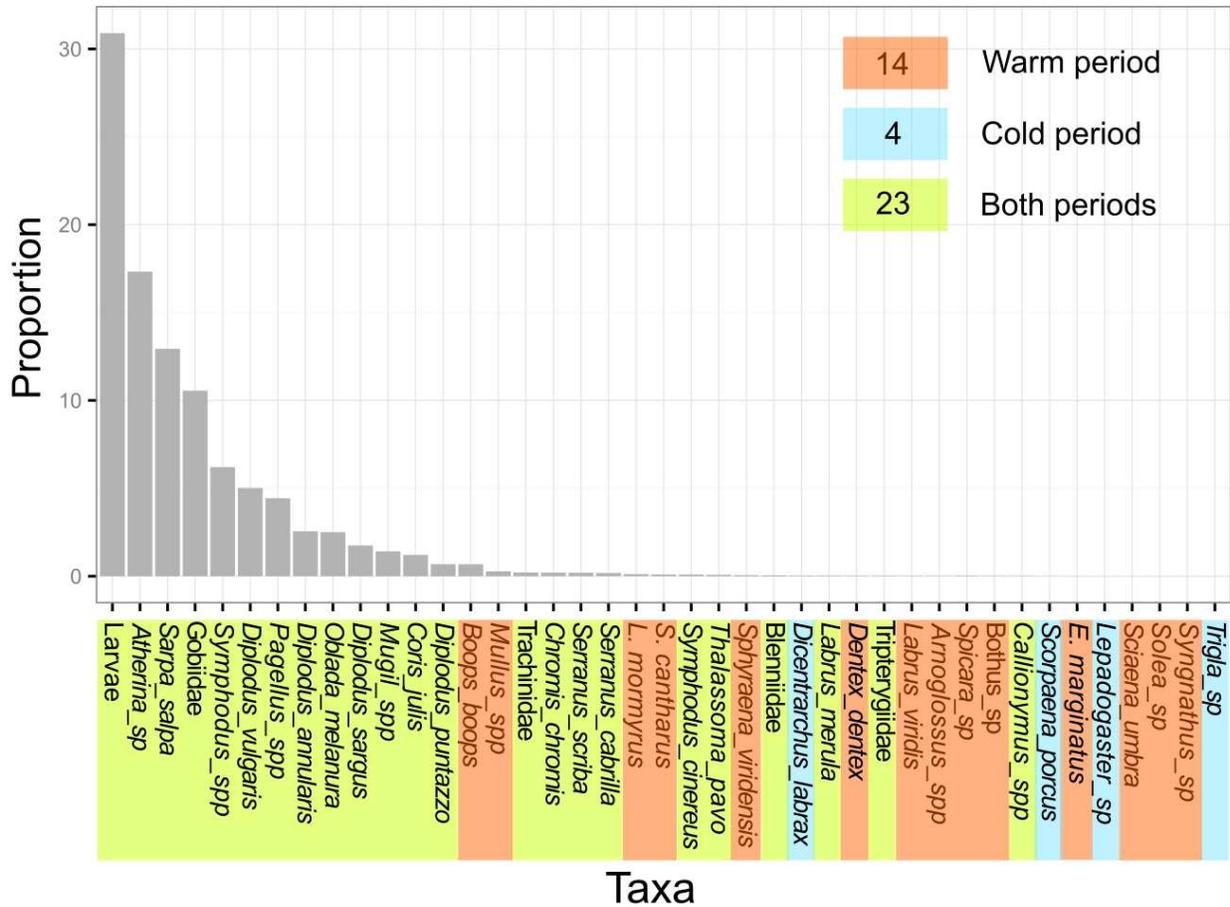
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 795 assemblages according to habitat types. Correlation vectors (Spearman) of descriptors are plotted
 796 (correlations >0.2). RS: Rocky substrates; AR: Artificial rocky reefs; SB: soft bottoms; CY:
 797 *Cymodocea nodosa* beds; PO: *Posidonia oceanica* beds; POBR: *Posidonia* barrier reef flat;
 798 POEX: *Posidonia* barrier reef outer slope; POIN: *Posidonia* barrier reef inner slope; POCY:
 799 Barrier reef lagoon with *Cymodocea*; PODM: *Posidonia* dead matte; IPR: Interface
 800 *Posidonia*/Rocky substrates; IPS: Interface *Posidonia*/Soft bottoms; IPM: Interface
 801 *Posidonia*/Dead matte; IRS: Interface Rocky substrates/Soft bottoms.

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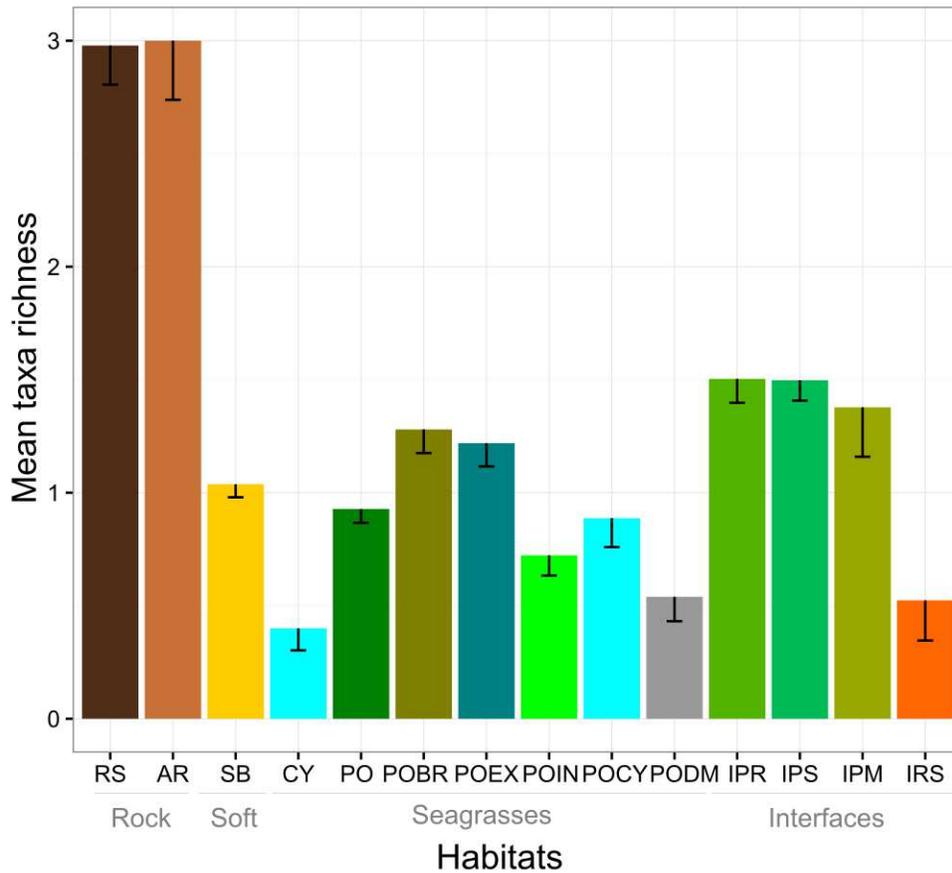


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804 Figure 3. Proportion of each observed taxa in the total abundance of juvenile fishes recorded in
 805 all samples and habitats combined; *E.* = *Epinephelus*, *L.* = *Lithognathus*, *S.* = *Spondylisoma*.

806 Period(s) of observation of each taxa and total number of taxa observed per period are indicated
 807 with colored boxes.

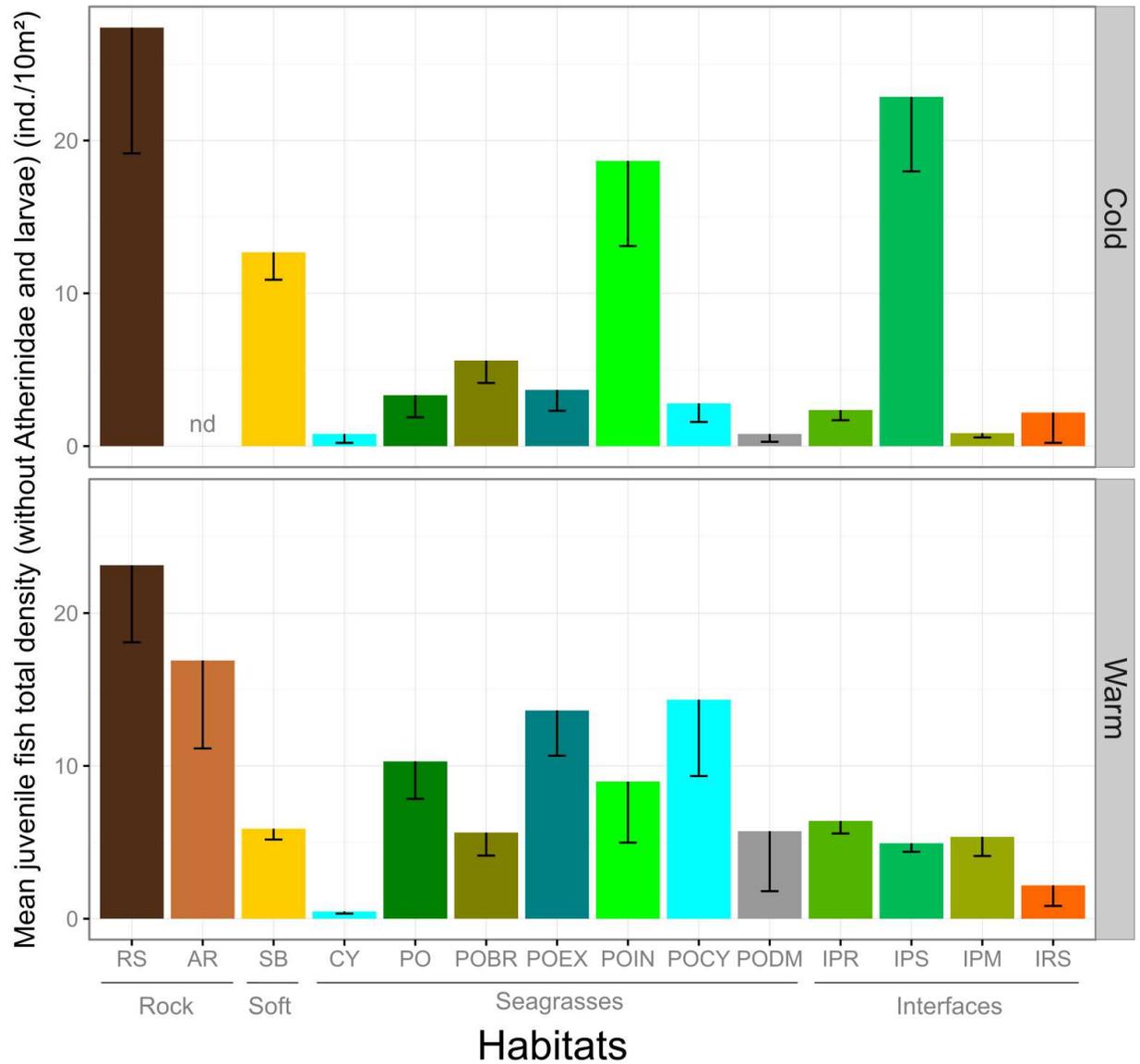
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811 Figure 4. Mean taxa richness (\pm SE) of juvenile fishes per 10m² in shallow coastal juvenile
 812 habitats. RS: Rocky substrates; AR: Artificial rocky reefs; SB: soft bottoms; CY: *Cymodocea*
 813 beds; PO: *Posidonia oceanica* beds; POBR: *Posidonia* barrier reef flat; POEX: *Posidonia* barrier
 814 reef outer slope; POIN: *Posidonia* barrier reef inner slope; POCY: Barrier reef lagoon with
 815 *Cymodocea*; PODM: *Posidonia* dead matte; IPR: Interface *Posidonia*/Rocky substrates; IPS:
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 817 substrates/Soft bottoms. Main habitat categories are indicated in grey.

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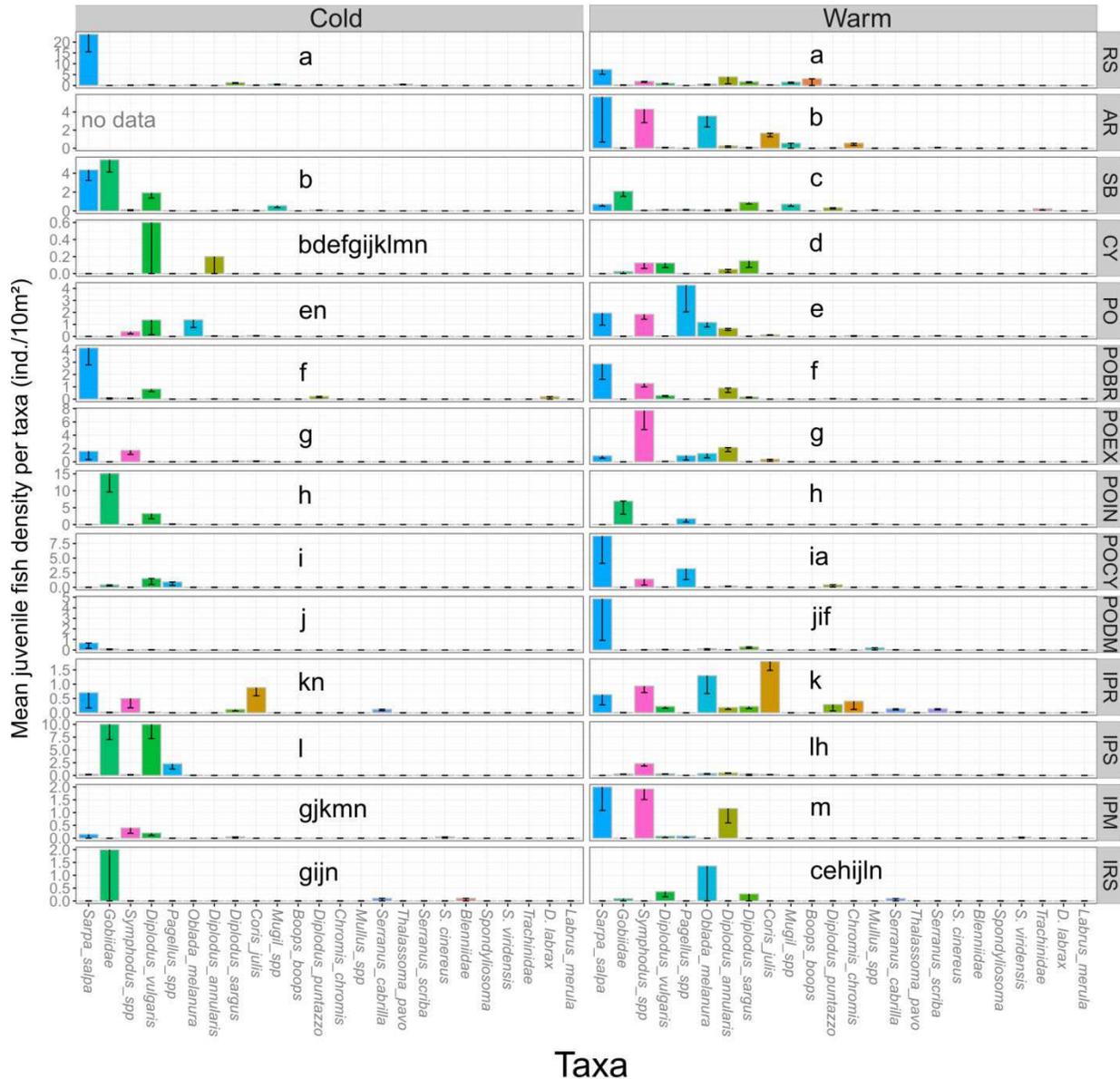


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820 Figure 5. Mean (\pm SE) total density (without Atherinidae and larvae) of juvenile fishes among
 821 habitats for both periods (Cold and Warm). Main habitat categories are indicated in grey; “nd” =
 822 no data available.

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827 Figure 6. Mean (\pm SE) juvenile density of each taxa in juvenile habitats for both periods (Cold
 828 and Warm). Atherinidae and larvae, as well as the 15 least abundant taxa, were removed for a
 829 clearer representation. Note that vertical axes display different scales. *S. cinereus* = *Symphodus*
 830 *cinereus*; *S. viridensis* = *Sphyræna viridensis*; *D. labrax* = *Dicentrarchus labrax*; Details of taxa
 831 are given in Table S2. For each period, comparisons of juvenile fish assemblages between
 832 juvenile habitats (pairwise tests results) are given (treatments that share at least one lower case
 833 character do not significantly differ).

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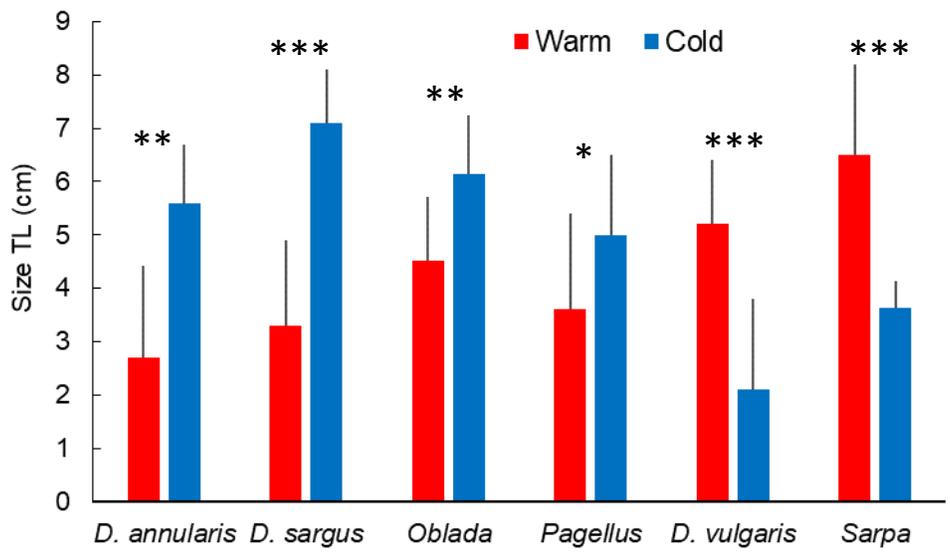


Figure 7. Mean size (TL cm \pm SD) of some fish species juveniles settling in Mediterranean shallow coastal habitats. *D.* = *Diplodus*; *Oblada* = *Oblada melanura*; *Pagellus* = *Pagellus* spp.; *Sarpa* = *Sarpa salpa*. Warm: warm period (summer 2014); Cold: cold period (winter 2015). Results of t-test for difference in mean size of a given species according to period: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

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857

858 Table 1. Habitat types, codes and number of samples (N) in warm (summer 2014) and cold
 859 (winter 2015) periods.

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Habitat type	Code	Warm period N	Cold period N
Rocky substrates	RS	328	150
Artificial rocky reefs	AR	20	0
Soft bottoms	SB	271	155
<i>Cymodocea nodosa</i> beds	CY	40	5
<i>Posidonia oceanica</i> beds	PO	174	90
<i>Posidonia</i> barrier reef flat	POBR	75	50
<i>Posidonia</i> barrier reef outer slope	POEX	64	50
<i>Posidonia</i> barrier reef inner slope	POIN	71	30
Barrier reef lagoon with <i>Cymodocea</i>	POCY	51	20
<i>Posidonia</i> dead matte	PODM	33	30
Interface <i>Posidonia</i> /Rocky substrata	IPR	87	50
Interface <i>Posidonia</i> /Soft bottoms	IPS	126	65
Interface <i>Posidonia</i> /Dead matte	IPM	25	20
Interface Rocky substrates/Soft bottoms	IRS	11	10
TOTAL		1376	725

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863 Table 2. Abiotic and biotic habitat descriptors of shallow coastal nurseries.
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Descriptor	Type	Units, scales or levels
Depth	Continuous	Meters
Slope (Integer scale)	Numerical scale of integers from 1 to 6:	1 (0-15°); 2 (16-30°); 3 (31-60°); 4 (61-<90°); 5 (90°); 6 (>90°)
Substrate (6 types)	% cover for each of 6 types	Rock, blocks, pebbles, gravel, sand, mud
Rugosity (4 types)	% cover of each of 4 types	Low, medium, high, very high
Vegetal coverage: Seagrasses (3 types)	% cover for each of 3 types	<i>Posidonia oceanica</i> , dead matte, <i>Cymodocea nodosa</i>
Vegetal coverage: Macrophytes (5 types)	% cover for each of 5 types	- <i>Cystoseira sensus lato</i> forest (<i>Carpodesmia brachycarpa</i> , <i>Carpodesmia crinita</i> , <i>Treptacantha barbata</i> , <i>Cystoseira compressa</i>) - Other arborescent algae (<i>Halopitys incurva</i> , <i>Spaerococcus coronopifolius</i>) - Bushland (<i>Halopteris scoparia</i> , <i>Padina</i> sp., Dictyotales, <i>Corallina</i> sp., <i>Acetabularia acetabulum</i> , <i>Laurencia</i> spp.) - Turf/encrusting algae - Wrecked algae
Canopy height	Continuous	Height (cm) of canopy (only for each seagrass or macrophytes types)

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Table 3. PERMANOVA table of results: comparison of habitat descriptors assemblage per station between habitats and period. Table gives degrees of freedom (df), Mean Squares (MS), calculated pseudo-F, and P-values (P). P-values were obtained by 999 permutations of residuals under a reduced model (perm) or through Monte Carlo test (MC, see methods).

Source of variation	df	MS	Pseudo-F	P(perm)
Habitat type (Ha)	13	72942	18.367	0.001
Period (Pe)	1	3352.3	0.84415	0.502
Ha x Pe	12	3889	0.9793	0.518
Residuals	130	3971.2		
Total	156			

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Table 4. Total number of fish taxa recorded in the different juvenile habitats of shallow coastal areas, and during the warm (summer 2014) and cold (winter 2015) periods.

Habitat type	Total	Warm period	Cold period
RS	22	22	15
AR	14	14	-
SB	25	22	15
CY	6	6	2
PO	22	21	10
POBR	15	14	8
POEX	16	15	9
POIN	14	13	6
POCY	16	15	3
PODM	12	10	4
IPR	21	20	8
IPS	21	21	12
IPM	11	8	6
IRS	8	7	3
TOTAL	41	37	27

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Table 5. PERMANOVA table of results: comparison of taxa richness of juvenile assemblages between habitats and periods. Table gives degrees of freedom (df), Mean Squares (MS), calculated pseudo-F, and P-values (P). P-values were obtained by 999 permutations of residuals under a reduced model (perm) or through Monte Carlo test (MC, see methods).

Source	df	MS	Pseudo-F	P(perm)
Ha	13	28,253	22,632	0,001
Pe	1	53,082	42,52	0,001
HaxPe	12	7,4477	5,9658	0,001
Res	1689	1,2484		
Total	1715			

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Table 6. PERMANOVA table of results: comparison of total juvenile density between habitats and periods. Table gives degrees of freedom (df), Mean Squares (MS), calculated pseudo-F, and P-values (P). P-values were obtained by 999 permutations of residuals under a reduced model (perm) or through Monte Carlo test (MC, see methods). Atherinidae and larvae have been removed for a clearer representation.

Source	df	MS	Pseudo-F	P(perm)
Ha	13	3002,7	6,0563	0,001
Pe	1	9,7155	0,019596	0,878
HaxPe	12	2364,2	4,7686	0,001
Res	1689	495,79		
Total	1715			

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Table 7. PERMANOVA table of results: comparison of multivariate assemblage of juvenile density between habitats and periods. Table gives degrees of freedom (df), Mean Squares (MS), calculated pseudo-F, and P-values (P). P-values were obtained by 999 permutations of residuals under a reduced model (perm) or through Monte Carlo test (MC, see methods).

Source	df	MS	Pseudo-F	P(perm)
Ha	13	17,591	10,738	0,001
Pe	1	19,628	11,982	0,001
HaxPe	12	7,8712	4,8049	0,001
Res	1689	1,6382		
Total	1715			

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Figures

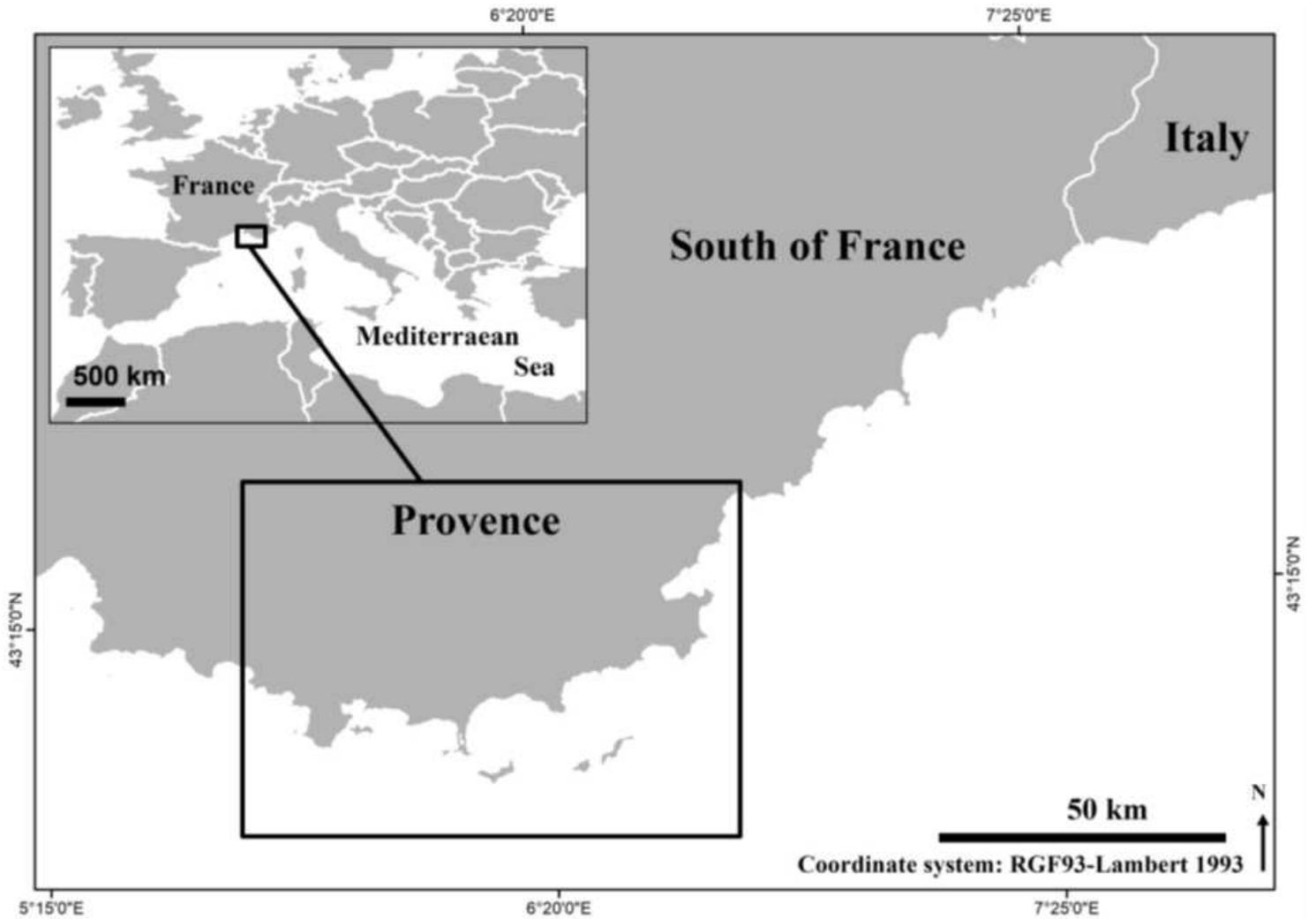


Figure 1

Map of the studied area: 42 stations were sampled along the 100 km stretch of the studied portion of the French Riviera coastline (red rectangle)

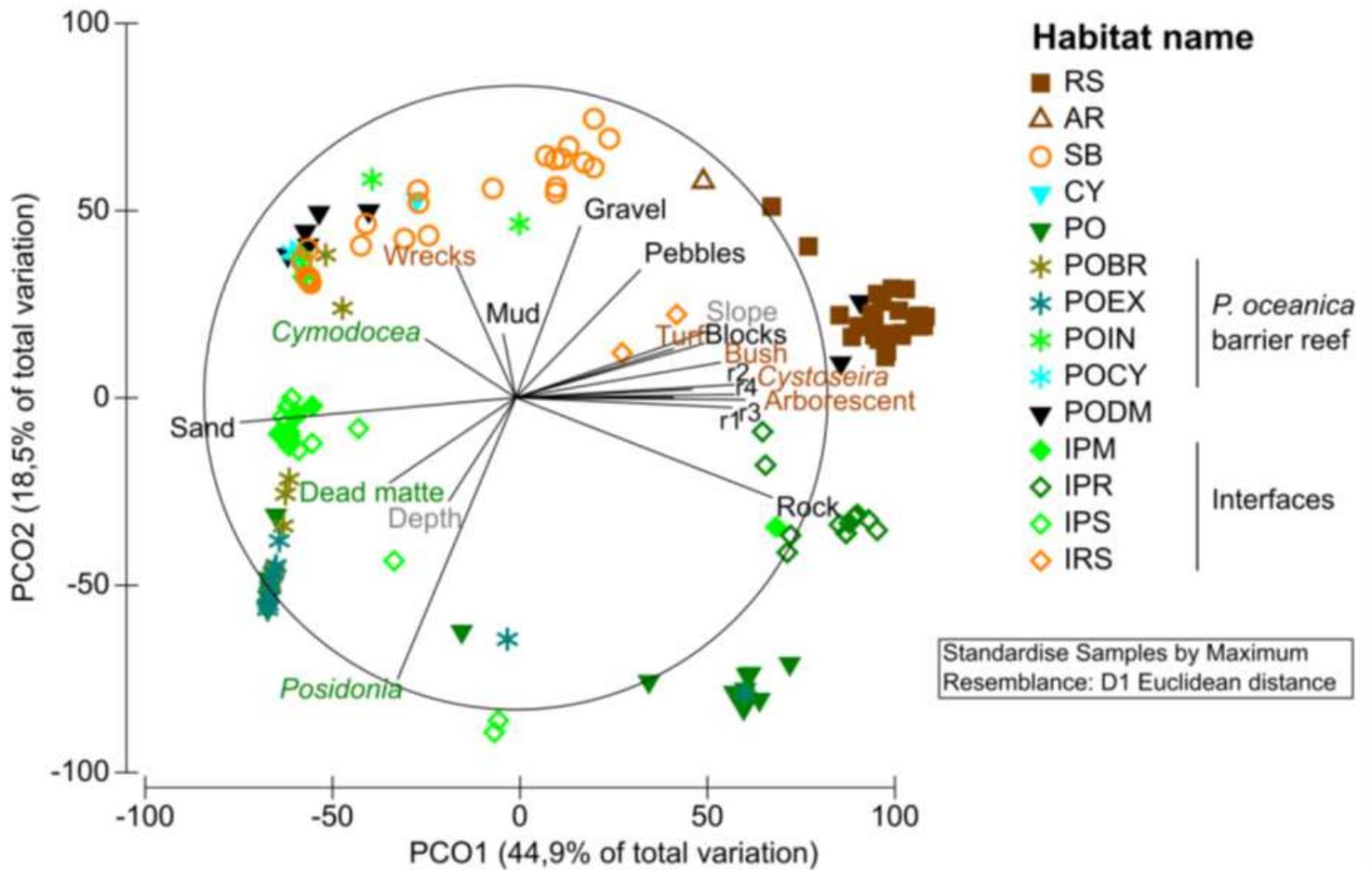


Figure 2

Principal coordinate analysis (PCoA) ordination plot of centroids of habitat descriptor assemblages according to habitat types. Correlation vectors (Spearman) of descriptors are plotted (correlations >0.2). RS: Rocky substrates; AR: Artificial rocky reefs; SB: soft bottoms; CY: *Cymodocea nodosa* beds; PO: *Posidonia oceanica* beds; POBR: *Posidonia* barrier reef flat; POEX: *Posidonia* barrier reef outer slope; POIN: *Posidonia* barrier reef inner slope; POCY: Barrier reef lagoon with *Cymodocea*; PODM: *Posidonia* dead matte; IPR: Interface *Posidonia*/Rocky substrates; IPS: Interface *Posidonia*/Soft bottoms; IPM: Interface *Posidonia*/Dead matte; IRS: Interface Rocky substrates/Soft bottoms.

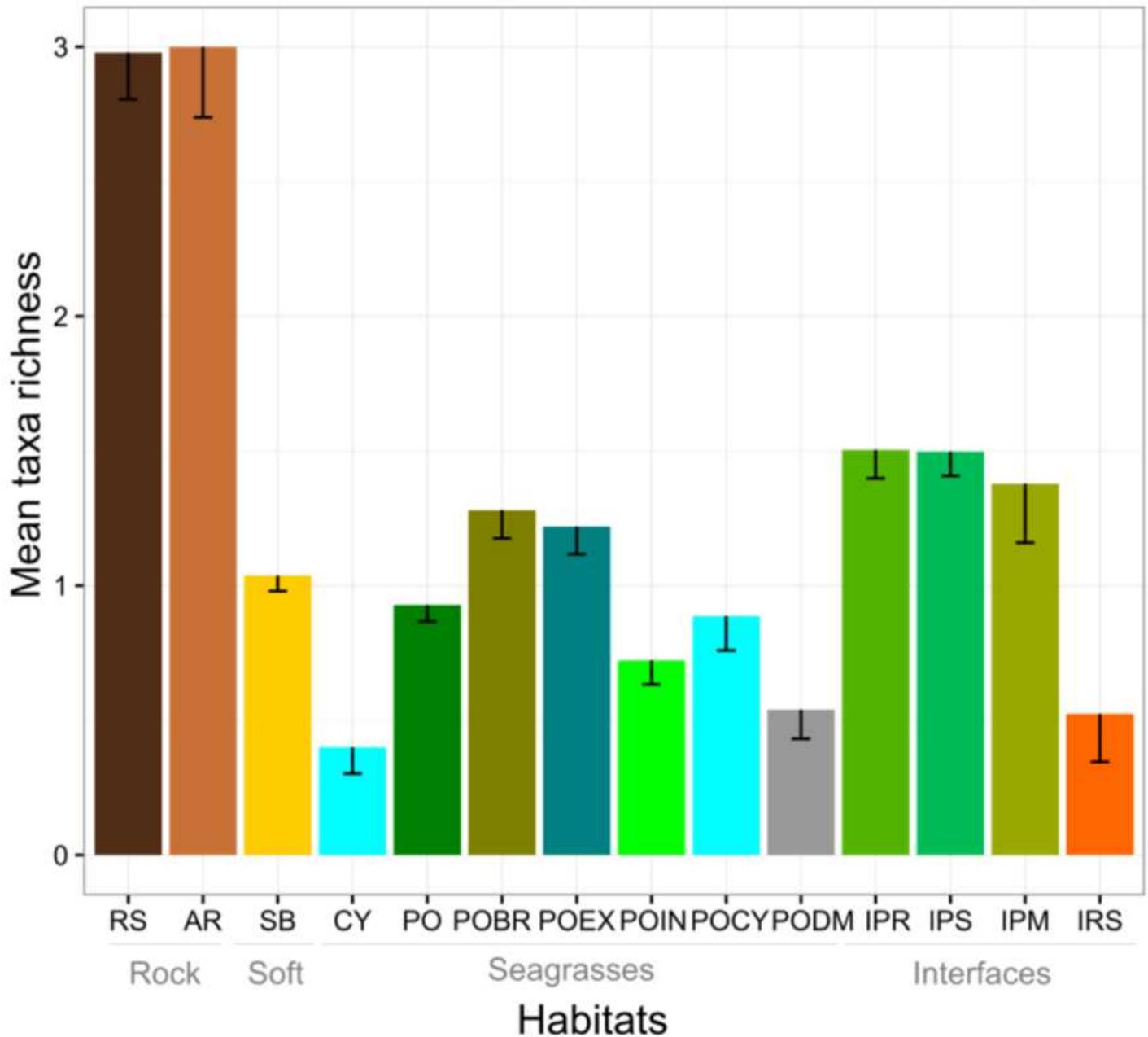


Figure 4

Mean taxa richness (\pm SE) of juvenile fishes per 10m² in shallow coastal juvenile habitats. RS: Rocky substrates; AR: Artificial rocky reefs; SB: soft bottoms; CY: Cymodocea beds; PO: Posidonia oceanica beds; POBR: Posidonia barrier reef flat; POEX: Posidonia barrier reef outer slope; POIN: Posidonia barrier reef inner slope; POCY: Barrier reef lagoon with Cymodocea; PODM: Posidonia dead matte; IPR: Interface Posidonia/Rocky substrates; IPS: Interface Posidonia/Soft bottoms; IPM: Interface Posidonia/Dead matte; IRS: Interface Rocky substrates/Soft bottoms. Main habitat categories are indicated in grey.

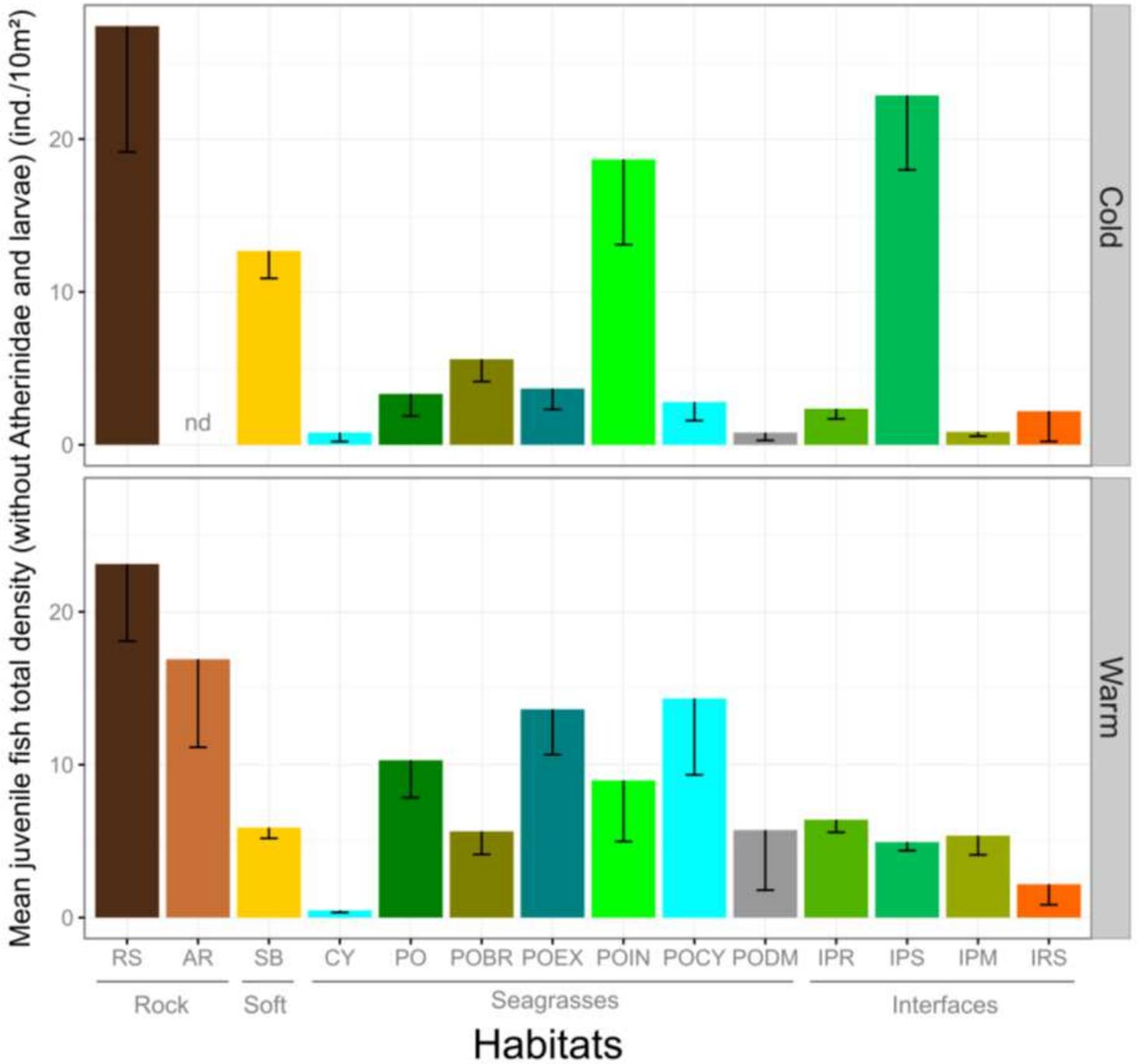


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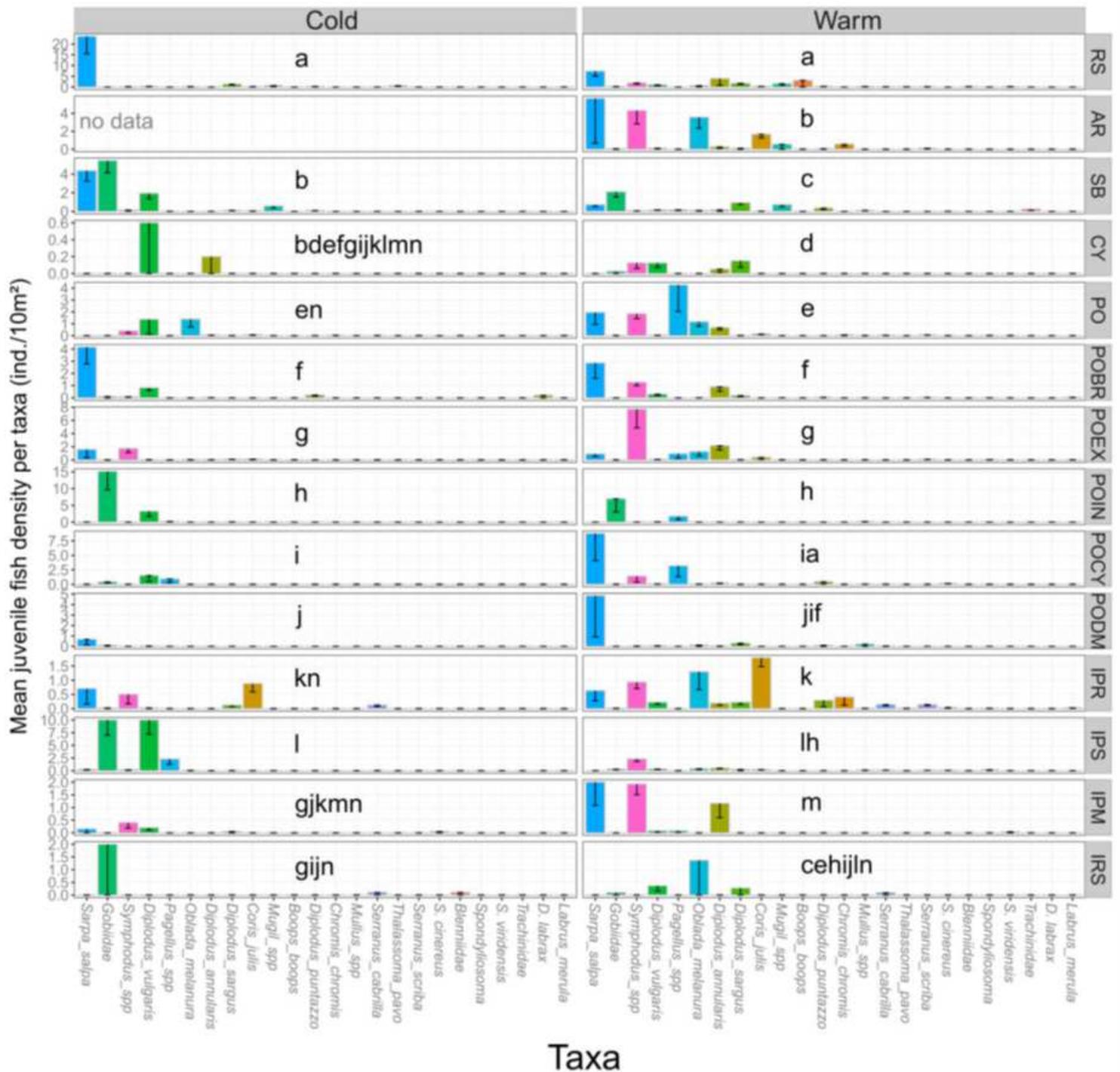


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Mean (\pm SE) juvenile density of each taxa in juvenile habitats for both periods (Cold and Warm). Atherinidae and larvae, as well as the 15 least abundant taxa, were removed for a clearer representation. Note that vertical axes display different scales. *S. cinereus* = *Symphodus cinereus*; *S. viridensis* = *Sphyræna viridensis*; *D. labrax* = *Dicentrarchus labrax*; Details of taxa are given in Table S2. For each period, comparisons of juvenile fish assemblages between juvenile habitats (pairwise tests results) are given (treatments that share at least one lower case character do not significantly differ).

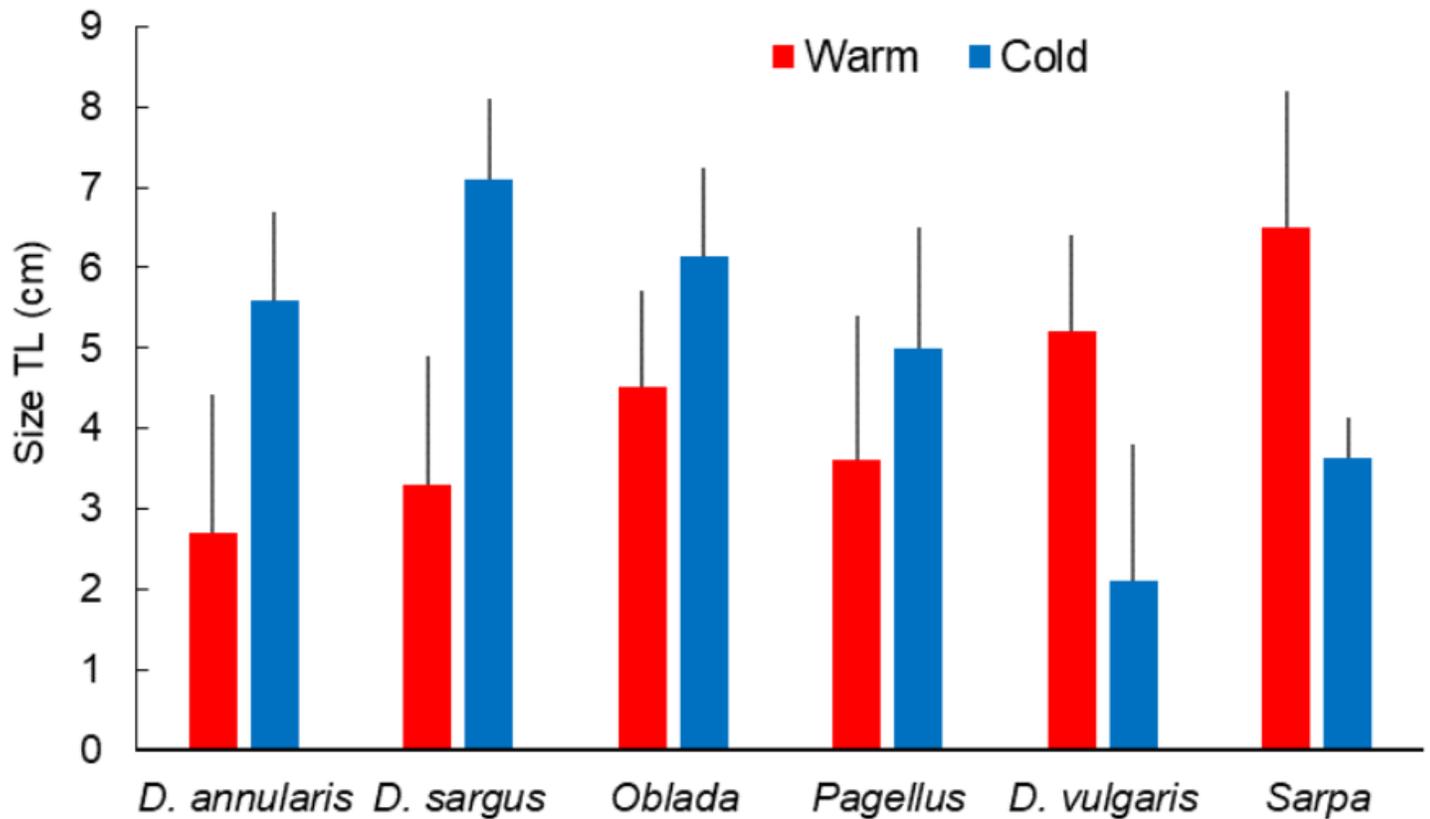


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