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Potential use of marinas as nursery grounds by rocky fishes: insights from four *Diplodus* species in the Mediterranean

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Abstract :

The construction of marinas along the shoreline has caused substantial habitat destruction within the sheltered coastal areas previously used as nursery grounds by many fish species. However, although the negative ecological impacts of these constructions have been reported extensively, their potential roles in the functioning of the coastal zone remain largely unknown. Here, we surveyed the juveniles of 4 *Diplodus* species in 5 marinas located along the French Mediterranean coast to assess whether rocky fishes can successfully settle inside these artificialized coastal areas. Inter-specific differences in the spatiotemporal use of the various artificial habitats provided by marinas were investigated between April and August over 2 consecutive years. We also tested the potential benefit of pegging additional artificial habitats (Biohuts) on docks and pontoons to increase their value as fish nursery grounds. Our results suggest that although variations in marina and artificial habitat preferences exist between species, *Diplodus* juveniles repeatedly colonize marinas. Their average abundances on added Biohut habitats were twice as high as on nearby bare surfaces. This suggests that increasing the complexity of the vertical structures of marinas can considerably enhance their suitability for juvenile rocky fishes, especially at the youngest stages, when mortality is highest. Therefore, as long as marina water quality is well controlled, ecological engineering within these man-made habitats might reduce the ecological consequences of urban development by providing suitable alternative artificial nursery grounds for rocky fishes.

Keywords : Coastal areas, Habitat anthropization, Fish juveniles, Sparids, Habitat preferences, Ecological engineering, Biohut

1 1. Introduction

2 Until recently, most research in urban ecology has focused on terrestrial habitats (e.g., Clergeau et al.
3 2006, Hobbs et al. 2006). However, more than three billion people currently live within 200 km of the
4 sea, and this number is predicted to double by 2025 (Creel 2003). As a result, the destruction of
5 coastal habitats is one of the main threats to marine ecosystems (Lotze et al. 2006, Airoidi & Beck
6 2007, Seaman 2007, Halpern et al. 2008), through its combined effects on biodiversity and ecosystem
7 functioning (Beck et al. 2001, Courrat et al. 2009, Verdiell-Cubedo et al. 2013, Seitz et al. 2014,
8 Sundblad et al. 2014). Although many different types of man-made structures dominate the shoreline,
9 ecological issues relating to the introduction of infrastructures in shallow coastal waters have received
10 little attention so far (Chapman & Blockley 2009, Bulleri & Chapman 2010) and we are just beginning
11 to understand their impact on marine organisms, especially fishes (Duffy-Anderson et al. 2003).

12 Marinas are among the most common man-made infrastructures found on the shoreline. Their
13 construction not only leads to the direct destruction of natural shallow water habitats, but also causes
14 indirect damage through changes to currents and sediment loads that both have a dramatic impact on
15 the composition of benthic communities (Meinesz et al. 1991, Martin et al. 2005) and fish larval
16 dispersal and recruitment (Roberts 1997). Moreover, the industrial and yachting activities associated
17 with marinas result in chronic biological and chemical pollutions of both the sediment and the water
18 column inside and in the vicinity of marinas, which can have long-term consequences on living
19 organisms (Bech 2002, Falandysz et al. 2002, Neira et al. 2011). All these factors lead to
20 modifications of the ecological functions of the zones where marinas are built (Airoidi et al. 2005).
21 However, the new shallow water habitats created within marinas might support new ecological
22 functions.

23 The identification of nursery habitats is particularly important for stock conservation because mortality
24 rates in fish are maximal during the early phases of their life cycles (Macpherson et al. 1997, Jennings
25 & Blanchard 2004). Until now, very few studies have investigated the fish populations associated with
26 marina structures. However, the peripheral breakwaters of marinas are often colonized by marine
27 rocky fishes, at both the juvenile (Ruitton et al. 2000, Pizzolon et al. 2008, Dufour et al. 2009, Pastor

28 et al. 2013) and adult stages (Guidetti 2004, Clynick 2006, Pizzolon et al. 2008, Cenci et al. 2011).

29 Fish species richness on these artificial structures is generally equivalent to that of natural zones, and

30 fish abundances are sometimes higher (Perez-Ruzafa et al. 2006). The number of fish species and the

31 abundances of the most common rocky species inside marinas also seem to be similar to those found

32 in natural habitats (Clynick et al 2008). As a result, shallow and protected habitats on the inshore sides

33 of marina breakwaters **could provide** suitable nursery grounds for some of these fish species (Dufour

34 et al. 2009). In theory, fish nursery grounds are defined according to four parameters: they support

35 high abundances of juveniles, sustain faster somatic growth rates, allow higher survival and their

36 populations contribute more to the final adult stock (Beck et al. 2001). At first sight, featureless and

37 steep sloping marina structures, provided for example by docks and floating pontoons, seem unlikely

38 to meet these definition criteria. Nevertheless, high abundances of juvenile rocky fishes have been

39 observed on these artificial structures (Clynick 2008). Although not a definitive test, many authors

40 (e.g., Cheminee et al. 2013, Pastor et al. 2013) have used the abundance criterion alone to identify

41 nursery grounds among juvenile habitats. In this context, we decided to investigate the condition for

42 the potential use of marina vertical structures as nursery grounds by rocky fish species, by surveying

43 small-scale spatiotemporal changes in juvenile abundances for four sparids of the same genus

44 (*Diplodus*, *Raffinesque* 1810) within five contrasting marinas located along the French Mediterranean

45 coast (North-West Mediterranean). The main aims of this study were: (1) **to see whether** certain infra-

46 littoral rocky fishes could successfully settle on the artificial vertical structures commonly found

47 inside the marinas, and (2) to investigate how the juveniles of different species make use of the

48 artificial habitats available. However, we also wanted to (3) test the potential benefit of ecological

49 engineering within marinas to increase their value as rocky fish nursery grounds. Indeed, increasing

50 the complexity of vertical structures has been shown to augment biodiversity in artificial aquatic

51 habitats (Browne & Chapman 2014). For rocky fishes, this could also enhance juvenile survival by

52 providing shelter against predators (Bulleri & Chapman 2010). Therefore, increasing the complexity

53 of vertical structures inside marinas could enhance their value as fish nursery grounds, with potentially

54 important consequences in terms of population dynamics.

57 2. Materials and methods

58 2.1. Species studied

59 This study focused on the juveniles of four species of the *Diplodus* genus: the annular seabream *D.*
60 *annularis* (Linnaeus, 1758), the sharp snout seabream *D. puntazzo* (Cetti, 1777), the white seabream
61 *D. sargus sargus* (Linnaeus, 1758), hereafter *D. sargus*, and the two-banded seabream *D. vulgaris*
62 (Geoffroy Saint-Hilaire, 1817). These species are common in the Mediterranean and have high
63 ecological and commercial value (Coll et al. 2004, Morales-Nin et al. 2005, Lloret et al. 2008). They
64 are highly abundant in both natural and artificial rocky coastal areas (Tortonese 1965) and their
65 juveniles are present in high abundances inside marinas, at least along the internal side of peripheral
66 breakwaters (Clynick 2006). Natural settlement patterns are fairly well described for all four species:
67 *D. annularis*, *D. puntazzo* and *D. sargus* all settle in one pulse, in June-July, October-November and
68 May-June respectively, while *D. vulgaris* settles in two pulses, in November-December and in
69 January-February, the first pulse being the more predominant (García-Rubies & Macpherson 1995,
70 Harmelin-Vivien et al. 1995, Vigliola et al. 1998, Cheminee et al. 2011, Ventura et al. 2014). In
71 *Diplodus* species, physical habitat characteristics (substrate, depth, level of protection from the
72 prevailing winds, etc.) strongly determine both settlement success and pre-recruitment mortality
73 (Harmelin-Vivien et al. 1995, MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Cheminee et al.
74 2011, Ventura et al. 2014). *Diplodus puntazzo* and *D. sargus* both usually settle in very shallow parts
75 (< 1 m) of small crannies characterized by gentle slopes covered with pebbles or sand. *Diplodus*
76 *vulgaris* seems to prefer deeper waters (1-6 m) and can settle on a wider range of substrates (coarse
77 sand, gravel, pebbles or boulders). Finally, settlement in *Diplodus annularis* occurs at even greater
78 depths (> 5 m) but almost exclusively on seagrass beds (Harmelin-Vivien et al. 1995, Ventura et al.
79 2014). The species is thought to remain sedentary on the same seagrass bed for the entire duration of
80 its juvenile life, while in *D. puntazzo*, *D. vulgaris* and *D. sargus*, substrate specificity disappears
81 progressively during juvenile life, resulting in horizontal then vertical migrations (MacPherson 1998,

82 Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). Given the differences in settlement dates and
83 natural habitat preferences between these four species, the investigation of the variation in their
84 respective abundances and habitat preferences between different types of marina should allow
85 reaching global conclusions on the conditions of use of these man-made habitats by juvenile rocky
86 fishes.

87

88 2.2. Study area

89 One hundred and fifty five marinas are listed along the French Mediterranean coast (Pinar Genc &
90 Guler 2012). Our study was carried out within five of them, located at distances ranging from 20 to
91 180 km along the coasts of the Gulf of Lions and the French Riviera, in the towns of Port-Vendres,
92 Port-Barcarès, Cap d'Agde, Mèze and Le Brusc (Fig. 1). These five marinas have all been in operation
93 for over forty years and each harbors more than 200 pleasure craft; however, they have different
94 surface areas, depths and surrounding environmental characteristics (Table 1). Port-Vendres marina is
95 the deepest (8 m on average). Surrounded by a rocky coast, it covers a surface of 33 ha. The Cap
96 d'Agde marina was also built on a rocky peninsula but it can harbor up to 3 100 boats (on 53 ha), so it
97 is the most artificialized of the five. Le Brusc marina is the smallest (8 ha), but also the closest to
98 natural conditions. It was constructed on a rocky shore, near one of the last four *P. oceanica* barrier
99 reefs remaining in the French Mediterranean (Boudouresque et al. 1985). With a surface area of 81 ha,
100 Port-Barcarès marina is very shallow (2 m on average). It was constructed in the channel connecting
101 the Salses-Leucate lagoon to the sea and therefore communicates easily with the two habitats. The
102 Mèze marina is also linked to a lagoon (Thau) but has no direct link with the sea (although it
103 ultimately communicates with it through the three exits of the lagoon). Because these five marinas all
104 have very different topographies and levels of human impact, the study of their respective use by fish
105 juveniles should allow generalizing our results.

106

107 2.3. Surveys

108 Juvenile fish abundances and sizes were monitored along with water temperature (T in °C) in all five
109 marinas, every two weeks for five consecutive months (April - August) in 2013 and in 2014. Due to
110 logistic constraints, this timespan could not be extended to include the settlement dates for *D. puntazzo*
111 (October-November) and *D. vulgaris* (November-December) (Harmelin-Vivien et al. 1995, Vigliola et
112 al. 1998). However, it corresponds to the main period when the juveniles of all four species are found
113 in natural coastal areas (Harmelin-Vivien et al. 1995, MacPherson 1998, Vigliola et al. 1998).

114 Therefore we expected it to also cover most of the period for their joint presence in the marinas.

115 Two different artificial vertical structures frequently found in marinas were compared in our work:
116 vertical docks and floating pontoons. For each of them, two types of conditions were investigated: the
117 structure (i.e. docks or pontoons) left bare (for control) or equipped by patented multifaceted devices
118 specially designed to increase substrate complexity and facilitate fish post-larval settlement in man-
119 made coastal habitats ("Biohut[®]"). The latter were consistently positioned under the surface of the
120 water on both structures and immersed at least one month before the start of the annual surveys to
121 harmonize benthic fauna densities between Biohut and controls. For each marina, three distinct zones
122 containing only docks and three distinct zones containing pontoons were used as replicates. They were
123 consistently separated by at least 20 m and positioned to encompass most of the local variability in
124 physico-chemical conditions.

125 The sizes and locations of the surface areas of docks and pontoons dedicated respectively to Biohut
126 positioning and to control surveys in each zone were chosen to harmonize Biohut surfaces between
127 artificial structures and based on the minimum dimensions of the docks and the pontoons across all
128 marinas. As a result, the Dock Biohut (DB) consisted of eight pegged cages measuring $0.5 \times 0.8 \times$
129 0.25 m grouped along a 5 m long dock section and covering a total vertical surface of 4 m². Each DB
130 cage was composed by two inseparable parts: an empty part and a part filled with oyster shells to
131 maximize the surface for benthic fauna development (Fig. 2.a and 2.c). The Pontoon Biohut (PB)
132 consisted of three cages measuring $0.5 \times 0.8 \times 0.34$ m suspended under the pontoons by polyurethane
133 ropes to provide a total vertical surface of ca. 4m². Each PB cage was composed of three inseparable
134 parts: one part filled with oyster shells surrounded by two empty ones (Fig.2 b and 2d). Each replicate

135 dock zone contained one DB and one control, the later consisting in a 5×0.8 m (4 m^2) vertical surface
136 of bare dock (hereafter DC for Dock Control). Similarly, each replicate pontoon zone contained one
137 PB and one control, the later consisting in a vertical surface of 4 m^2 positioned on the upper part of a
138 pile used to anchor the pontoon (hereafter PC for Pontoon Control). In all replicate zones (dock or
139 pontoon), the distance between the Biohut and the control was always of at least 10 m.

140 For each replicate dock and pontoon zone, a submersible data logger (IbCod 22L) was positioned to
141 record water temperature (T in °C) hourly during the five months of the study (April -August) and
142 surveys of juvenile fish abundances and sizes were scheduled every two weeks on all four artificial
143 habitat types (AH, referring to DB, DC, PB and PC).

144 Abundances for all species were estimated by underwater visual census using stationary point counts,
145 as they are particularly appropriate in restricted areas with homogeneous habitats (Bohnsack &
146 Bannerot 1986, Clynick 2008, La Mesa et al. 2011). To do this, individual fish were always counted
147 for three minutes. The surveys were carried out between 10:00 am and 4:00 pm and poor visibility and
148 evident chemical or bacterial pollution conditions were consistently avoided. For each replicate zone,
149 the survey of the docks was designed to include four successive stationary point counts per AH (one
150 per pair of cages for DB and one per m^2 of bare dock surface for DC), so both DB and DC were each
151 surveyed for 12 minutes. Moreover, for each replicate zone, the survey of the pontoons consisted of
152 three successive point counts per AH (one point count per cage for PB and one per 1.33 m^2 of pile for
153 PC), so their survey took nine minutes each. As a result, fish counts took 24 minutes in a dock zone,
154 18 minutes in a pontoon zone, and underwater visual censuses of 126 minutes were needed for the
155 complete survey of each marina.

156 During the visual censuses, the juveniles of the four species were discriminated according to the
157 morphological and size criteria given in Fishbase.com (Froese & Pauly 2014). All the juveniles
158 identified were counted and their sizes (total length, TL) were estimated to the nearest 5 mm. To
159 minimize bias in this estimation, fish silhouettes of different sizes were printed on plastic slates and
160 used *in situ* by the divers (García-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995). When *in*

161 *situ* identification was difficult, pictures and videos of individuals were taken and interpreted once
162 back at the laboratory, with the assistance of expert Underwater Visual Census (UVC) divers. The
163 same two divers worked throughout the sampling period.

164 In order to investigate changes in habitat use within the marinas, the juveniles of all species were also
165 classified *a posteriori* into three successive development stages, according to the size ranges provided
166 by Vigliola & Harmelin-Vivien (2001) for *D. sargus*, *D. vulgaris* and *D. puntazzo*, and by Ventura et
167 al. (2014) for *D. annularis* (Table S1). Irrespective of the species, the "post-settlement" stage refers to
168 the smallest individuals found during the short time-period that immediately follows benthic
169 settlement (Vigliola & Harmelin-Vivien 2001). The "intermediate" stage is longer and includes
170 juveniles of medium sizes that usually colonize all suitable habitats within the nursery ground. Finally,
171 the "pre-dispersal" stage refers to the largest individuals that have acquired adult-like morphology and
172 are ready to leave the nursery ground.

173

174 2.5. Statistical analysis

175 All calculations and statistical analyses were performed using the PRIMER 6 software with the
176 PERMANOVA add-on (Clarke & Warwick 2001) or using the R software (R Core Team 2014) and
177 *indicspecies* package. The significance level for the tests was consistently set at $\alpha = 0.05$.

178 Preliminary data analyses showed that the sampling year had no significant effect on juvenile
179 *Diplodus* abundances and produced negative variance component estimates in all models but one (that
180 for *D. sargus*). Therefore, following Fletcher & Underwood (2002), the data for the two consecutive
181 years sampled in this work were consistently analyzed pooled, to reduce the effect of random
182 variability in fish abundances among fish counts for certain AH and species, and thereby give a more
183 robust image of the overall patterns of marina use by juvenile rocky fishes.

184 As the corresponding data were not normally distributed, spatial differences in water temperatures
185 during the period studied (April-August) were investigated using a non-parametric Kruskal-Wallis test

186 followed by Steel-Dwass-Critchlow-Fligner bilateral pairwise tests. Spatio-temporal variations in fish
187 abundances (in numbers of individuals per count, hereafter ind. count⁻¹) were analyzed for all four
188 species, separately or grouped, according to the month, the marina and the AH. For this, we performed
189 three-way univariate PERMANOVAs since this method allows the handling of complex, unbalanced
190 and multiple-factors designs, considers interaction among factors and does not assume a normal
191 distribution of errors (Anderson 2001). Fish abundances were log(X+1) transformed prior to the
192 generation of Euclidean distance similarity matrixes, and the factors 'Month' (with five levels: April
193 to August) and 'AH' (with four levels: DB, DC, PB and PC) were treated as fixed, while the 'Marina'
194 factor (with five levels: Port-Vendres, Port-Barcarès, Cap d'Adge, Mèze and Le Brusce) was treated as
195 random. In addition to the main PERMANOVA test, contrasts were used to compare fish abundances
196 between DB and DC and between PB and PC (Glasby 1997). P-values were calculated by 9999
197 random permutations of residuals under a reduced model and Type III sum of square (Anderson 2001).

198 For each species, ontogenetic changes in habitat use during juvenile life in marinas were also
199 investigated, by identifying the type(s) of AH(s) preferred at each development stage using the
200 Indicator Value index (IndVal) (Dufrière & Legendre 1997). This composite index was originally
201 developed to compare populations between sites and link species to communities based on habitat
202 conditions (De Cáceres & Legendre 2009). It combines two estimates of habitat use for each species:
203 specificity (S) and fidelity (F), based respectively on the species' relative abundance and its relative
204 frequency of occurrence among sites or habitat types. Therefore it gives precise and accurate
205 information on species habitat preferences (Legendre & Legendre 1998). In the present study, we
206 applied it to explore differences in AH preferences within the marinas between all the development
207 stages of the four species. Therefore development stages (post-settlement, intermediate and pre-
208 dispersal) by species were used instead of species in IndVal calculations per AH, following the
209 formula:

$$210 \text{ IndVal}_{ijk} = 100 \times S_{ijk} \times F_{ijk}$$

211 with specificity S_{ijk} defined by:

212 $S_{ijk} = \text{Abundance}_{ijk} / \text{Abundance}_{ij}$.

213 where Abundance_{ijk} is the mean abundance per count of the development stage i of the species j in the
214 AH k and Abundance_{ij} is the sum of the mean abundances per count of the same stage i of the same
215 species j over all AH.

216 and with fidelity F_{jk} defined by:

217 $F_{jk} = N_{ijk} / N_{.k}$

218 where N_{ijk} is the number of the survey with at least one individual of the development stage i of the
219 species j in the AH k , and $N_{.k}$ is the total number of surveys for this AH during the all study.

220 In order to generalize our results, IndVal was also calculated per development stage for all four species
221 grouped. Differences in IndVal values between AH were tested by 9999 random permutations among
222 groups (De Cáceres & Legendre 2009).

223

224 3. Results

225 Due to unexpected adverse environmental conditions in the marinas (e.g., occasional days with poor
226 underwater visibility, pollution events) or logistic constraints on some of the sampling dates scheduled
227 during the two years of the study, finally only 896 surveys were performed of the 1 200 initially
228 planned. This did not however prevent accurate investigation of fish AH use in the five marinas, since
229 all the sites were fully surveyed at least twice per month over the whole duration of the study when
230 considering the two years pooled. [However, pooling data from the two years can bias estimates of](#)
231 [variance in some analyses and caution should be taken when interpreting the results.](#) Similarly,
232 logistic constraints in 2013 allowed performing only one stationary count per replicate zone for the
233 controls, so the vertical surfaces investigated for DC and PC in this year covered only 4 m² per marina,
234 instead of 12 m² in 2014. This should not however affect our conclusions since fish abundances on

235 controls for 2014 were similar (PERMANOVA, $p > 0.5484$) when using one or all stationary counts,
236 irrespective of the species or the marina.

237 Water temperatures in April-August differed significantly according to the survey site ($p < 0.0001$,
238 Fig. S2), with higher and lower averages in Mèze ($22.37 \pm 3.77^\circ\text{C}$) and in Port-Vendres ($19.39 \pm$
239 3.29°C), respectively, than in the three other marinas ($19.76 \pm 3.40^\circ\text{C}$ in Port-Barcarès, $20.49.76 \pm$
240 3.16°C in Cap d'Agde and $20.56 \pm 3.21^\circ\text{C}$ in Le Brusç).

241

242 3.1. Juvenile fish abundances in the marinas

243 Over the time period surveyed, the maximum number of *Diplodus* juveniles observed throughout one
244 point count was 60 individuals (on 15/04/2013 on a DB habitat in the Cap d'Agde marina). However,
245 single counts with no observation were very frequent (83 %), and occurred irrespective of month or
246 location. Finally, a total of 1 766 observations of *Diplodus* juveniles were made within the five
247 marinas. However, most of the juveniles counted were *D. vulgaris* (N= 653) or *D. annularis* (N= 520),
248 while observations were less frequent for *D. sargus* (N= 388) and *D. puntazzo* (N= 205).

249 Spatiotemporal patterns of marina use varied greatly between species (Table 2, Fig. S1). Significant
250 interactions between the 'Month' and 'Marina' factors in the PERMANOVAs for all four species,
251 whether grouped or not (Table 2), also indicated that the temporal variations in juvenile abundances
252 were not consistent across locations. Although this complicated data interpretation, some general
253 temporal and spatial trends could still be discerned.

254 Temporal variations in juvenile abundances were significant only for *D. annularis* and *D. sargus*
255 (Table 2), with the highest abundances for these species being reached in August (mean: 0.73 ± 0.14
256 ind. count^{-1}) and in July (mean: $0.48 \pm 0.14 \text{ ind. count}^{-1}$), respectively. Temporal trends in the
257 abundances of the post-settlement juveniles of the two species allowed identifying their respective
258 periods of settlement in the marinas, in June-July for *D. sargus* and in July-August for *D. annularis*
259 (Fig. 3). Similarly, a detailed analysis of the temporal variations in abundance for the post-settlement
260 and pre-dispersal development stages of *D. puntazzo* and *D. vulgaris* suggested that settlement in the

261 marinas probably occurred before the sampling period (April-August) for both these species, and
262 suggested that their departure from the marinas started from July at certain locations (in particular
263 Port-Vendres, Fig. 3). It is probable that sampling was stopped well before *D. annularis* dispersal
264 because very few pre-dispersal individuals were observed for this species and most of its juveniles
265 were still at the intermediate stage in August (Fig. 3).

266 Regarding general spatial trends, the number of observations of *Diplodus* juveniles varied
267 considerably between marinas, with a total of 646 individuals being counted in Cap d'Agde, 393 in Le
268 Brusc, 387 in Port-Vendres, 337 in Port-Barcarès, and only three in Mèze. Accordingly, juvenile
269 abundance differed significantly between locations ($p < 0.001$, Table 2), with a maximum (1.08 ± 0.18
270 ind. count⁻¹) in Cap d'Agde and a minimum (0.04 ± 0.003 ind. count⁻¹) in the marinas of Mèze and
271 Port-Barcarès, while similar intermediate values were obtained for Le Brusc and Port-Vendres
272 (respectively of 0.85 ± 0.24 , 0.96 ± 0.15 and 0.98 ± 0.14 ind. count⁻¹, respectively).

273 Species composition also depended on location, with spatial variations in juvenile abundance
274 concerning all four species (Table 2), but differently (Fig. S1). Indeed, juveniles from all four species
275 were observed in Port-Vendres, Port-Barcarès, Cap d'Agde and Le Brusc, while only three individuals
276 of *D. vulgaris* were seen in Mèze (one post-settler in April and two pre-dispersal juveniles in June,
277 observed on a DC and on a DB, respectively). Over the April-August period, the global average
278 abundance of juveniles per count was maximum in Le Brusc for *D. annularis* (0.53 ± 0.14 ind. count⁻¹)
279 ¹), in Port-Vendres for *D. puntazzo* (0.24 ± 0.05 ind. count⁻¹), in Port-Barcarès for *D. sargus* ($0.67 \pm$
280 0.23 ind. count⁻¹) and in Cap d'Agde for *D. vulgaris* (0.55 ± 0.16 ind. count⁻¹). This may suggest
281 differences in habitat suitability for *Diplodus* juveniles between the five marinas investigated, with
282 further variation between the marinas according to species.

283 With regards effects of the artificial habitat type, abundances for the four species grouped were on
284 average twice higher on the Biohut (mean: 1.02 ± 0.12 ind. count⁻¹) than on the nearby bare vertical
285 surfaces used as controls (mean: 0.52 ± 0.12 ind. count⁻¹). The significance of the interactions $Ma \times$
286 $DB-v-DC$ ($p = 0.012$) and $Ma \times PB-v-DC$ ($p = 0.002$) suggested that *Diplodus* abundances were

287 higher on Biohut than on controls irrespective of the artificial structure considered (dock or pontoon)
288 but also revealed that this effect was strongly dependent on the location. Considering species
289 separately revealed that, on the pontoons, this pattern concerned all four species ($Ma \times PB-v-PC$, $p <$
290 0.004). On the docks however, the interaction was significant for *D. annularis* ($Ma \times DB-v-DC$, $p =$
291 0.001), approached statistical significance for *D. vulgaris* ($p = 0.050$), but was not significant for *D.*
292 *puntazzo* ($p = 0.364$) and *D. sargus* ($p = 0.807$). As a result, for docks, the month also had a significant
293 effect on the global difference in *Diplodus* spp. abundances between Biohut on controls ($Mo \times DB-v-$
294 DC , $p = 0.004$).

295

296 3.2. Changes in habitat use during juvenile life

297 Our results revealed a generalized loss of habitat specificity during juvenile life in marinas in the four
298 fish species investigated (Fig. 4). Indeed, when considering all *Diplodus* spp. grouped, IndVal values
299 at the post-settlement stage were significantly higher ($p < 0.036$) for DB and PB than for DC and PC,
300 reflecting a preference for Biohut habitats than for bare structures. At the intermediate stage, although
301 IndVal values were still significantly higher ($p < 0.0001$) for DB and PB than for PC, the values for
302 DB and DC were no longer statistically different ($p = 0.067$). Finally, at the pre-dispersal stage, IndVal
303 did not differ significantly between any pair of habitat ($p > 0.057$), so no AH preference could be
304 detected. This general trend was, however, slightly complicated by differences in AH preference
305 between species, especially at the post-settlement and intermediate stages (Fig. 4). In *D. annularis*,
306 IndVal values for DB and PB were similar ($p > 0.611$), irrespective of the development stage, and
307 consistently higher ($p < 0.023$) than those of DC and PC. This indicated a preference for the Biohut
308 habitats (on both docks and pontoons) in this species throughout its juvenile life within marinas. For
309 the three other species investigated, ontogenetic shifts in habitat use were observed, all resulting in an
310 absence of AH preference at the pre-dispersal stage ($p > 0.073$). *Diplodus vulgaris* settled essentially
311 on DB, as indicated by the significantly higher ($p = 0.0001$) IndVal value found for this AH at the
312 post-settlement stage. At the intermediate stage, it enlarged its habitat use to all dock habitats, which

313 resulted in similar IndVal values for DB and DC ($p = 0.55$), both significantly higher ($p < 0.0003$) than
314 those of PB and PC. In *D. puntazzo*, juveniles showed a preference for PB ($p < 0.032$) at the post-
315 settlement stage, and then gathered preferentially around either of the two types of Biohut provided in
316 the marinas. Thus, at the intermediate stage, the IndVal indexes for DB and PB in this species were
317 significantly higher than those for DC and PC ($p < 0.014$) but did not differ significantly from each
318 other ($p = 0.059$). Finally, post-settlement and intermediate juveniles of *D. sargus* had similar AH
319 preferences. Their IndVal index for PB was significantly higher than that for DC ($p < 0.002$) but did
320 not differ significantly from those of PC and DB ($p > 0.162$).

321

322

323 4. Discussion

324 To our knowledge, this is the first time that the use of man-made structures inside marinas, such as
325 docks and pontoons found all around the world, by juvenile rocky fishes has been investigated this
326 thoroughly. Juvenile fishes of the *Diplodus* genus were present on docks and pontoons in several of
327 the marinas we investigated along the French Mediterranean coast. All four species were observed
328 inside the marinas, and at all development stages (i.e. from post-settlement to pre-dispersal). However,
329 even within these highly artificialized ecosystems, inter-specific variations in habitat preferences
330 (mostly associated with the complexity of the vertical substrate available) were evidenced, especially
331 at the youngest stages when mortality is highest (Macpherson et al. 1997). These findings have strong
332 implications for the evaluation of the potential suitability of marinas as fish nursery grounds.

333

334 4.1. Conditions for the use of marinas as juvenile fish habitats

335 Juveniles of *Diplodus* spp. have already been reported in high numbers in the peripheral breakwaters
336 of certain Mediterranean marinas (Ruitton 1999, Clynick 2006) but up to now no study has
337 investigated their abundances on the AH present inside them. Our work shows that they are also

338 present at all development stages on both the docks and the pontoons available inside the marinas.
339 This suggests that docks and pontoons (or at least parts of them) have the potential to meet the habitat
340 requirements for the successful settlement and juvenile growth of various *Diplodus* species in the
341 Mediterranean.

342 This result was relatively unexpected, in particular for *D. annularis* for which juveniles were
343 previously thought to be strongly associated with *P. oceanica* beds in the Mediterranean (Gordoa &
344 Moli 1997, Garcia-Charton et al. 2004, Ventura et al. 2014). During the two summer months
345 considered in this work, 520 juveniles of *D. annularis* were observed in the five marinas tested with
346 high inter-location variability (Fig. S1). 54% and 42% of these observations were made on DB and
347 PB, respectively. Since different protocols were used for the juvenile counts, the abundances measured
348 in this study cannot be compared directly to those observed in natural areas. However, this result
349 suggests that certain parts of marina ecosystems can allow the settlement of *D. annularis* juveniles.

350 Pelagic fish larvae are known to often settle in the first suitable habitat they encounter (Shapiro 1987).
351 Therefore, high abundances of *D. annularis* juveniles in certain marinas could partially result from an
352 absence of suitable natural habitat in their immediate vicinity. This could be the case in Port-Barcarès,
353 since this marina is located on a sandy coast, far from any *P. oceanica* bed. However, this explanation
354 is not valid for the two marinas where the species was the most abundant (Le Brusca and Cap d'Agde),
355 since they are both located in the neighborhood of one of the largest meadows of *P. oceanica*
356 remaining along the Mediterranean coast (Boudouresque et al. 1985, Descamp et al. 2011). Therefore,
357 our results suggest that plasticity in juvenile habitat requirements is probably higher than previously
358 thought in *D. annularis*, and is maybe close to that already pointed out in the three other *Diplodus*
359 species investigated (Guidetti 2004, Martin et al. 2005, Clynick 2006, Pastor et al. 2013). Further
360 research should be conducted to investigate this possibility since an active selection of man-made
361 artificial habitats by *Diplodus* larvae cannot be excluded, given the low levels of waving and the high
362 trophic productivity often found in marinas (Planes et al. 1999, Dufour et al. 2009). Marinas could also
363 act as light traps for the larvae at night (Doherty 1987). Whatever the case, plasticity in juvenile
364 habitat requirements apparently allows successful settlement and growth of the juvenile fishes of this

365 genus within certain marinas, despite the unavoidable pollution (by noise and by chemicals) associated
366 with these man-made ecosystems (CETMEF 2010). If so, marinas could provide alternative nursery
367 grounds for rocky fishes, at least in highly urbanized areas of the shoreline.

368 The presence and abundance of *Diplodus* juveniles varied greatly however according to the marina
369 investigated. With only three juveniles (of *D. vulgaris*) observed during the whole period of our study,
370 the marina of Mèze was barely colonized by the juveniles of this genus in 2013-14. The environmental
371 conditions in this marina were apparently particular, since monthly temperatures during the study
372 period were consistently at least 1°C higher in Mèze than in the four other sites investigated (Fig. S2).
373 For many fish species, juvenile abundances strongly depend on water temperature, especially at the
374 post-larval stage (e.g., Henderson & Seaby 1994, Félix-Hackradt et al. 2013). However, the juveniles
375 of at least *D. vulgaris*, *D. annularis* and *D. puntazzo* usually settle successfully in environments with
376 large differences in water temperature (18-29°C), salinities (18-39) and dissolved oxygen levels (2.7-
377 9.6 mg. l⁻¹) (Vinagre et al. 2010). Therefore, it is quite unlikely that the main reason for the absence of
378 *Diplodus* juveniles in Mèze lies in its environmental conditions. Another explanation could lie in the
379 fact that this marina is located within the Thau lagoon, which the post-larvae must cross before
380 reaching the marina. Indeed, in the nearby lagoon of Salses-Leucate, in which the salinity and
381 temperature conditions are very close to those observed in Thau (Ifremer 2012), a marked reduction in
382 the abundance of *D. sargus* juveniles has been noted over recent decades (Pastor et al. 2013). This
383 phenomenon was attributed either to the increasing collection of *D. sargus* larvae by the artificial
384 constructions built at the entrance of the lagoon, or to an augmentation of local juvenile mortality rates
385 due to the degradation of environmental conditions in it. All the channels connecting the Thau lagoon
386 to the sea are artificial and the Mèze marina is located at ca. 4 km from the nearest marine entrance.
387 Therefore, the hypotheses proposed to explain the decline of juvenile *D. sargus* in Salses-Leucate
388 (Pastor et al. 2013) could also apply in Thau and explain the lack of juveniles of the *Diplodus* genus in
389 the Mèze marina, which has no direct connection with the sea where the breeding of the four species
390 occurs (Harmelin-Vivien et al. 1995).

391 Juvenile fish abundances also varied between the four other marinas investigated, with almost twice as
392 many individuals counted in Cap d'Agde as in Le Brusc, Port-Vendres and Port-Barcarès. Several
393 hypotheses can be proposed to explain these spatial differences. For example, as the main direction of
394 local currents and the presence of gyres can influence the dispersion or retention of fish eggs and
395 larvae (Cheminee et al. 2011), pelagic larval inputs for each species may differ between marinas,
396 depending on the location of their nearest spawning grounds. Some marinas might also be close to
397 natural nursery areas and indirectly benefit from their attractiveness for the larvae. Another
398 explanation might lie in the differences in mean depth between our marinas as this factor governs
399 *Diplodus* spp. settlement in natural areas (Harmelin-Vivien et al. 1995). However, *Diplodus*
400 abundances in our study showed no significant relation with marina depth. For example, the maximum
401 abundances of *D. puntazzo*, a species known to naturally settle in very shallow coastal habitats
402 (Harmelin-Vivien et al. 1995), were observed in the deepest marina (Port-Vendres). Finally, post-
403 settlement mortality rates can differ between locations depending on both the physico-chemical
404 conditions and local inter-specific competition for available resources (Planes et al. 1998). Apparently,
405 of all the sites we studied, the vast (53 ha) and shallow (< 3 m) marina of Cap d'Agde is the most
406 favorable for the settlement and growth of *Diplodus* juveniles, despite the fact that, with 58.5 rings. ha⁻¹
407 ¹ on average, it has the highest density of use after the marina of Le Brusc (99.5 rings. ha⁻¹). This
408 might be due to its location on a primarily rocky shore, or to the fact that it is surrounded by several *P.*
409 *oceanica* meadows (Descamp et al. 2011). However, species composition also depended highly on
410 location and maximum juvenile abundances were found in Cap d'Agde for *D. vulgaris* only. For the
411 three other species, these abundances occurred in other marinas: in Le Brusc for *D. annularis*, in Port-
412 Vendres for *D. puntazzo* and in Port-Barcarès for *D. sargus*. Therefore the factors responsible for
413 spatial differences in juvenile abundances are probably multiple and depend on the species. They
414 require investigation to better understand the potential value of marinas as nursery grounds for rocky
415 fishes. However, our results clearly indicate that marinas do not all succeed in providing
416 environmental conditions favorable for the settlement and survival of *Diplodus* juveniles. Thus the
417 location and environmental characteristics of marinas should be considered first when trying to restore
418 the potential nursery function of the littoral ecosystems in which they were built.

419

420 4.2 Ecological engineering: a tool for improving the nursery potential of marinas

421 Each marina consists in a mosaic of different artificial habitats, each characterized by specific biotic
422 and abiotic features and supporting functionally different life stages or species. Our results showed
423 that increasing their diversity can have a significant impact on the value of marinas as fish nursery
424 grounds. Indeed, post-settlement stage juveniles were essentially found around the added Biohut
425 structures, irrespective of whether they were installed on docks or on pontoons. *But this result strongly
426 depends on the marina considered as, due to their location or physico-chemical conditions they
427 provide, some of them do not seem to meet environmental conditions for the successful *Diplodus*
428 juveniles settlement. Such marinas (for example Mèze) probably cannot function as *Diplodus* nursery
429 grounds and adding Biohut on docks or pontoons do not provide any ecological benefit.*

430 In a natural context, early mortality of *Diplodus* juveniles is driven both by density-dependent
431 processes linked to post-settlement intensity (Doherty 1981, 1991), and by density-independent
432 processes linked to predation and refuge availability (Hixon 1991, Vigliola 1998). Although this has
433 not yet been demonstrated, we can reasonably assume that these two types of processes also modulate
434 the abundances of rocky fish juveniles in marinas. For example, differences in abundance between
435 Biohut and controls in our study could be due to a reduction of juvenile mortality on Biohut, since
436 they provide more refuge against predators than the featureless vertical surfaces usually found on
437 docks and pontoons (Ammann 2004, Bulleri & Chapman 2010). In this case, the reason why habitat
438 preference for Biohut in marinas was particularly observable for the youngest stages may lie in the fact
439 that mortality by predation is highest at this period of life (Macpherson et al. 1997). Another
440 explanation could lie in the attraction offered by complex solid structures (in our case the Biohut) for
441 pelagic larvae, a behavior known as thigmotaxis (Ammann 2004). The two hypotheses are not
442 mutually exclusive and, even if the Biohut was originally designed to protect the youngest juveniles
443 from mobile predators, knowing whether they act on fish production by reducing post-settlement
444 mortality or on fish density by attracting fish larvae by thigmotaxis requires further investigation.

445 Interestingly, habitat preference at the post-settlement stage was the least marked in *D. sargus* for
446 which no significant differences in IndVal were observed between DB, PB and PC. This could be due
447 to the higher plasticity in this species' juvenile habitat requirements (Cheminee et al. 2011, Pastor et
448 al. 2013) or to a limitation in the availability of its most favorable habitats (Harborne et al. 2011).
449 Indeed, when pre-settlement *D. sargus* arrive in the marinas (in June-July), Biohut habitats are still
450 largely occupied by the post-settlement juveniles of *D. puntazzo* and *D. vulgaris* (Fig. S1). This might
451 partly explain why they also settle abundantly under the bare pontoons. Therefore, as in natural
452 habitats, high occupation rates of the most optimal habitats could lead to competitive interactions
453 between species within marinas and force the late-breeding ones to settle on sub-optimal habitats.

454 Although our results suggest that ecological engineering in **some** marinas could increase their value as
455 nursery grounds for rocky fishes, this also implies the preservation or improvement of their water and
456 sediment quality. Indeed, in order to satisfy the definition of nursery area, habitats have to contribute
457 considerably to the adult stock (Beck et al. 2001). Juvenile fish can experience very stressful
458 environmental conditions in marinas (e.g., boat traffic, extensive pollutant loads, dredging, etc.) linked
459 to human activities (CETMEF 2010). Chemical contaminants in particular are known to adversely
460 affect fish physiology, growth, health and behavior, especially at young stages (e.g., Laroche et al.
461 2002, Marchand et al. 2003, Rowe 2003, Kerambrun et al. 2012). As in other organisms, sub-lethal
462 responses to contaminant exposure in fish commonly involve a decrease in feeding activity (Stephens
463 et al. 2000, Saborido-Rey et al. 2007) and a modification in energy allocation, which is preferentially
464 used to fight chemical stress rather than for body maintenance and growth (Rowe 2003). This can have
465 marked negative effects on global individual fitness, as fish juveniles with slow growth rates and
466 limited energy storage have lower survival rates and contribute less to the adult stock (Sogard 1997).

467 Therefore heavily contaminated marinas probably cannot function as fish nursery grounds. Since
468 between 337 and 646 *Diplodus* juveniles were observed at all development stages in all but one marina
469 (Mèze) tested for two consecutive years, the pollution in these particular locations is probably below
470 critical pollution thresholds. However, our results might overestimate the actual abundances of
471 *Diplodus* juveniles in marinas since the techniques applied in this study (underwater visual census by

472 snorkelers) excluded heavily polluted sites from our investigations. Therefore, the impact of
473 contaminant exposure during juvenile life (high and punctual or limited yet repeated) on the final
474 fitness of fishes will have to be explored before concluding on the real value of marinas as nursery
475 grounds.

476

477 4.3. Consistency in seasonality and changes in habitat use between natural and artificial habitats

478 In the Mediterranean, juvenile presence on nursery grounds is known to occur from May-June to late
479 September in *D. sargus*, from July to September in *D. annularis*, from October to May-June in *D.*
480 *puntazzo* and from November-December to June-July in *D. vulgaris*. Therefore, given our period of
481 survey within marinas (April to August), abundance peaks in juveniles linked to recruitment were
482 expected for *D. annularis* and *D. sargus* only. Similarly, artificial habitat preferences were estimated
483 solely from the individuals present within the marinas from April to August. As a result, they were
484 reliably assessed only for the post-settlement juveniles of *D. annularis* and *D. sargus*, the intermediate
485 juveniles of all four species and the pre-dispersal juveniles of *D. puntazzo*, *D. vulgaris* and *D. sargus*.
486 For the other fish groups, preferred habitat estimates should be considered with caution since they
487 were extrapolations based on a reduced number of observations.

488 Temporal abundance patterns for the post-settlement juveniles of *D. sargus* and *D. annularis* indicated
489 that, during the two years studied, their juveniles mainly arrived in the marinas in June and in July-
490 August, respectively. This timing is consistent with the information gathered so far on their respective
491 settlement periods in the Western Mediterranean, which can both show temporal variation of ca. one
492 month between sites and years (see Ventura et al. 2014 for review). For *D. puntazzo* and *D. vulgaris*,
493 post-settlement juveniles were observed only at the beginning of the survey period (from April to
494 June) and were consistently accompanied by older juveniles. This suggests that both species settled in
495 the marinas well before the start of the surveys (in April). Thus local adaptations to marina artificial
496 habitats in *Diplodus* spp. apparently do not involve a modification in recruitment dates. It should be
497 noted, however, that the observation of 12 post-settlement juveniles of *D. puntazzo* in several of the

498 marinas investigated in April was relatively unexpected since this species settles in November –
499 December on its natural nurseries (Harmelin-Vivien et al. 1995, Vigliola et al. 1998). Although errors
500 (± 3.5 mm) in the estimation of fish size by visual census cannot be excluded (MacPherson 1998), so
501 part of these *D. puntazzo* individuals could be at the boundary between post-settler and intermediate
502 juvenile classes, they were particularly small (< 30 mm TL). Therefore further research should be
503 conducted to investigate the reasons for their presence in the marinas at this period.

504 In Mediterranean natural coastal areas, ontogenetic shifts in habitat use are well documented for
505 *Diplodus* species (MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). In
506 general, morphologic modifications during fish growth in this genus are accompanied by habitat
507 changes, resulting in horizontal then vertical migrations (MacPherson 1998, Vigliola & Harmelin-
508 Vivien 2001). In *D. annularis* however, fidelity to *P. oceanica* meadows is usually strong throughout
509 juvenile life, except for the larger individuals that can be found on other substrates such as sandy areas
510 (Ventura et al. 2014). This high habitat fidelity was also observed in the marinas, where the species
511 was almost exclusively found in Biohut habitats, irrespective of the juvenile stage. Indeed, during the
512 two years of our survey, *D. annularis* juveniles were observed only twice on DC and only three times
513 on PC, and at very low abundances in both cases. Behavior in the artificial context of marinas is thus
514 close to natural behavior, the juveniles of the species being highly associated with the most sheltered
515 habitat available. Similarly, changes in habitat preferences during juvenile life for *D. sargus*, *D.*
516 *vulgaris* and *D. puntazzo* juveniles in marinas mirrored those described in natural areas (MacPherson
517 1998). With increasing body size juvenile fish are less vulnerable to predation (Houde & Hoyt 1987),
518 so their need for shelter decreases. They also diversify their diet toward bigger and more mobile prey,
519 and experience lower inter- or intra-specific competition for food (Ross 1986, MacPherson 1998),
520 driving them to enlarge their territory. Accordingly, in the marinas investigated, the youngest juvenile
521 stages of *D. sargus*, *D. vulgaris* and *D. puntazzo* were essentially associated with the most sheltered
522 (PB and/or DB), whereas the oldest ones were found to occur evenly on all the types of AH
523 investigated. This was not anticipated because the habitats available within the marinas and in natural

524 environments differ dramatically and fish species generally adapt their behavior to the habitat (Koeck
525 et al. 2013).

526

527

528 5. Conclusions

529 By studying the abundances of *Diplodus* spp. juveniles in five marinas located along the French
530 Mediterranean coast, we observed that these man-made littoral ecosystems, designed without
531 considering their potential value as fish habitats, can contain high numbers of juvenile rocky fish
532 which apparently remain there from settlement to dispersal. This had already been observed for other
533 artificial habitats found in the coastal zone, including the breakwaters commonly found at the entrance
534 of marinas. Nevertheless, the docks and pontoons commonly found inside marinas unexpectedly also
535 seem to be suitable for fish settlement and growth, especially if artificial multifaceted devices are
536 added to increase their structural complexity. This has important ecological implications since the
537 entire surface of marina ecosystems might participate in the maintenance of rocky fish stocks along
538 anthropized shorelines. However, water and sediment are often polluted in marinas, and the physical
539 damage caused by the replacement of natural substrates with built infrastructures is irreversible.
540 Therefore, even if some ecological functions can be conserved within man-made habitats, some are
541 definitively lost and it seems unrealistic to pursue the hope of restoring marinas to pristine conditions.
542 Public policies should therefore manage and protect natural fish nursery grounds prior to considering
543 the potential improvement of marina quality as such. Whatever the case, the rehabilitation of the
544 nursery function of the zones where marinas have been built cannot rely only on ecological
545 engineering. The immediate and long-term effects of fish exposure to the contaminants found in
546 marinas should also be studied to adequately improve their water and sediment quality. Finally,
547 connectivity between artificial and natural habitats must be evaluated in order to prioritize restoration
548 of the marinas that receive the highest numbers of larvae and contribute most to coastal adult stocks.

549

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565 Bibliographical references

566

- 567 Airoidi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. In: Gibson
568 RN, Atkinson RJA, Gordon JDM (eds) *Oceanography and Marine Biology*, Vol 45, Vol 45.
569 Crc Press-Taylor & Francis Group, Boca Raton, p 345-405
- 570 Ammann AJ (2004) SMURFs: standard monitoring units for the recruitment of temperate reef fishes.
571 *Journal of Experimental Marine Biology and Ecology* 299:135-154
- 572 Anderson JM (2001) Permutation tests for univariate or multivariate analysis of variance and
573 regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626-639
- 574 Bech M (2002) Imposex and tributyltin contamination as a consequence of the establishment of a
575 marina, and increasing yachting activities at Phuket Island, Thailand. *Environmental Pollution*
576 117:421-429

577 Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG,
578 Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MR (2001) The identification,
579 conservation, and management of estuarine and marine nurseries for fish and invertebrates.
580 *Bioscience* 51:633-641

581 Bohnsack J, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing
582 community structure of coral reef fishes, Vol Technical Report 41. NOAA

583 Boudouresque CF, Meinesz A, Lefevre JR (1985) Mapping the marine benthic communities in
584 Corsica. The *Posidonia oceanica* reef of Saint-Florent. *Annales de l'Institut Oceanographique*
585 61:27-38

586 Browne MA, Chapman MG (2014) Mitigating against the loss of species by adding artificial intertidal
587 pools to existing seawalls. *Marine Ecology Progress Series* 497:119-129

588 Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in
589 marine environments. *Journal of Applied Ecology* 47:26-35

590 Cenci E, Pizzolon M, Chimento N, Mazzoldi C (2011) The influence of a new artificial structure on
591 fish assemblages of adjacent hard substrata. *Estuarine Coastal and Shelf Science* 91:133-149

592 CETMEF L (2010) Bilan national du RÉPOM-Réseau national de surveillance de la qualité des eaux
593 et des sédiments des ports maritimes. 90 p

594 Chapman MG, Blockley DJ (2009) Engineering novel habitats on urban infrastructure to increase
595 intertidal biodiversity. *Oecologia* 161:625-635

596 Cheminee A, Francour P, Harmelin-Vivien M (2011) Assessment of *Diplodus* spp. (Sparidae) nursery
597 grounds along the rocky shore of Marseilles (France, NW Mediterranean). *Scientia Marina*
598 75:181-188

599 Cheminee A, Sala E, Pastor J, Bodilis P, Thiriet P, Mangialajo L, Cottalorda J-M, Francour P (2013)
600 Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes. *Journal of*
601 *Experimental Marine Biology and Ecology* 442:70-79

602 Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis
603 and interpretation. PRIMER-E Limited Plymouth, UK

604 Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki M-L, Dinetti M (2006) Avifauna
605 homogenisation by urbanisation: Analysis at different European latitudes. *Biological*
606 *Conservation* 127:336-344

607 Clynick BG (2006) Assemblages of fish associated with coastal marinas in north-western Italy.
608 *Journal of the Marine Biological Association of the United Kingdom* 86:847-852

609 Clynick BG (2008) Characteristics of an urban fish assemblage: Distribution of fish associated with
610 coastal marinas. *Marine Environmental Research* 65:18-33

611 Coll J, Linde M, García-Rubies A, Riera F, Grau AM (2004) Spear fishing in the Balearic Islands
612 (west central Mediterranean): species affected and catch evolution during the period 1975–
613 2001. *Fisheries Research* 70:97-111

614 Courrat A, Lobry J, Nicolas D, Laffargue P, Amara R, Lepage M, Girardin M, Le Pape O (2009)
615 Anthropogenic disturbance on nursery function of estuarine areas for marine species.
616 *Estuarine Coastal and Shelf Science* 81:179-190

617 Creel L (2003) Ripple effects: Population and coastal regions, Vol. Population Reference Bureau
618 Washington, DC

619 De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and
620 statistical inference. *Ecology* 90:3566-3574

621 Descamp P, Holon F, Ballesta L, Guilbert A, Guillot M, Boissery P, Raimondino V, Deter J (2011)
622 Fast and easy method for seagrass monitoring: Application of acoustic telemetry to precision
623 mapping of *Posidonia oceanica* beds. *Marine Pollution Bulletin* 62:284-292

624 Doherty PJ (1987) Light-traps: selective but useful devices for quantifying the distributions and
625 abundances of larval fishes. *Bulletin of Marine Science* 41:423-431

626 Doherty PP (1981) Coral reef fishes: recruitment-limited assemblages? *The Reef and Man*.
627 *Proceedings of the 4th International Coral Reef Symposium, Manila Philippines, 18-22 May*
628 *1981-pages: 2: 465-470. Marine Sciences Center, University of the Philippines*

629 Doherty PP (1991) Spatial and temporal patterns in recruitment *Ecology of coral reef fishes*.
630 Academic Press, p 261-293

631 Duffy-Anderson JT, Manderson JP, Able KW (2003) A characterization of juvenile fish assemblages
632 around man-made structures in the New York New Jersey Harbor Estuary, USA. *Bulletin of*
633 *Marine Science* 72:877-889

634 Dufour V, Cantou M, Lecomte F (2009) Identification of sea bass (*Dicentrarchus labrax*) nursery areas
635 in the north-western Mediterranean Sea. *Journal of the Marine Biological Association of the*
636 *United Kingdom* 89:1367-1374

637 Dufrière M, Legendre P (1997) Species assemblage and indicator species: the need for a flexible
638 asymmetrical approach. *Ecological Monographs* 67:345-366

639 Falandysz J, Brzostowski A, Szpunar J, Rodriguez-Pereiro I (2002) Butyltins in sediments and three-
640 spined stickleback (*Gasterosteus aculeatus*) from the marinas of the Gulf of Gdansk, Baltic
641 Sea. *Journal of Environmental Science and Health Part a-Toxic/Hazardous Substances &*
642 *Environmental Engineering* 37:353-363

643 Félix-Hackradt FC, Hackradt CW, Treviño-Otón J, Segovia-Viadero M, Pérez-Ruzafa A, García-
644 Charton JA (2013) Environmental determinants on fish post-larval distribution in coastal areas
645 of south-western Mediterranean Sea. *Estuarine, Coastal and Shelf Science* 129:59-72

646 Fletcher DJ, Underwood AJ (2002) How to cope with negative estimates of components of variance in
647 ecological field studies. *Journal of Experimental Marine Biology and Ecology* 273:89-95

648 Froese R, Pauly D (2014) Fishbase. Available: www.fishbase.org

649 Garcia-Charton JA, Perez-Ruzafa A, Sanchez-Jerez P, Bayle-Sempere JT, Renones O, Moreno D
650 (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on
651 Western Mediterranean rocky reef fish assemblages. *Marine Biology* 144:161-182

652 García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile
653 fishes of the Mediterranean littoral. *Marine Biology* 124:35-42

654 Glasby T (1997) Analysing data from post-impact studies using asymmetrical analyses of variance: A
655 case study of epibiota on marinas. *Australian Journal of Ecology* 22:448-459

656 Gordo A, Moli B (1997) Age and growth of the sparids *Diplodus vulgaris*, *D. sargus* and *D.*
657 *annularis* in adult populations and the differences in their juvenile growth patterns in the
658 north-western Mediterranean Sea. *Fisheries Research* 33:123-129

659 Guidetti P (2004) Fish assemblages associated with coastal defence structures in south-western Italy
660 (Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom*
661 84:669-670

662 Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert
663 C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding
664 M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems.
665 *Science* 319:948-952

666 Harborne AR, Mumby PJ, Kennedy EV, Ferrari R (2011) Biotic and multi-scale abiotic controls of
667 habitat quality: their effect on coral-reef fishes. *Marine Ecology Progress Series* 437:201-214

668 Harmelin-Vivien ML, Harmelin JG, Leboulleux V (1995) Microhabitat requirements for settlement of
669 juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia* 300-301:309-320

670 Henderson PA, Seaby RMH (1994) On the factors influencing juvenile flatfish abundance in the lower
671 Severn Estuary, England. *Netherlands Journal of Sea Research* 32:321-330

672 Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale P (ed) *The*
673 *Ecology of Fishes on Coral Reefs*. Academic press, p 475-508

674 Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA,
675 Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora
676 R, Zobel M (2006) Novel ecosystems: theoretical and management aspects of the new
677 ecological world order. *Global Ecology and Biogeography* 15:1-7

678 Houde E, Hoyt R (1987) Fish early life dynamics and recruitment variability. *American Fisheries*
679 *Society Symposium Series* 2:17-29

680 Ifremer (2012) Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2011. .
681 Report No. 12/2012

682 Jennings S, Blanchard JL (2004) Fish abundance with no fishing: predictions based on
683 macroecological theory. *Journal of Animal Ecology* 73:632-642

684 Kerambrun E, Henry F, Courcot L, Gevaert F, Amara R (2012) Biological responses of caged juvenile
685 sea bass (*Dicentrarchus labrax*) and turbot (*Scophthalmus maximus*) in a polluted harbour.
686 Ecological Indicators 19:161-171

687 Koeck B, Alos J, Caro A, Neveu R, Crec'hriou R, Saragoni G, Lenfant P (2013) Contrasting fish
688 behavior in artificial seascapes with implications for resources conservation. PLoS ONE 8
689 La Mesa G, Molinari A, Gambaccini S, Tunesi L (2011) Spatial pattern of coastal fish assemblages in
690 different habitats in North-western Mediterranean. Marine Ecology 32:104-114

691 Laroche J, Quiniou L, Juhel G, Auffret M, Moraga D (2002) Genetic and physiological responses of
692 flounder (*Platichthys flesus*) populations to chemical contamination in estuaries.
693 Environmental Toxicology and Chemistry 21:2705-2712

694 Legendre P, Legendre L (1998) Numerical Ecology, Volume 24, Developments in Environmental
695 Modelling, Vol. Elsevier Science

696 Lloret J, Zaragoza N, Caballero D, Font T, Casadevall M, Riera V (2008) Spearfishing pressure on
697 fish communities in rocky coastal habitats in a Mediterranean marine protected area. Fisheries
698 Research 94:84-91

699 Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX,
700 Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries
701 and coastal seas. Science 312:1806-1809

702 MacPherson E (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes.
703 Journal of Experimental Marine Biology and Ecology 220:127-150

704 Macpherson E, Biagi F, Francour P, Garcia-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel JY,
705 Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus *Diplodus* in
706 protected and unprotected areas in the western Mediterranean Sea. Marine Ecology Progress
707 Series 160:135-147

708 Marchand J, Tanguy A, Laroche J, Quiniou L, Moraga D (2003) Responses of European flounder
709 *Platichthys flesus* populations to contamination in different estuaries along the Atlantic coast
710 of France. Marine Ecology Progress series 260:273-284

711 Martin D, Bertasi F, Colangelo MA, de Vries M, Frost M, Hawkins SJ, Macpherson E, Moschella PS,
712 Satta MP, Thompson RC, Ceccherelli VU (2005) Ecological impact of coastal defence
713 structures on sediment and mobile fauna: Evaluating and forecasting consequences of
714 unavoidable modifications of native habitats. Coastal Engineering 52:1027-1051

715 MEDAM (2015) www.medam.org (assessed 04 April 2015)

716 Meinesz A, Lefevre JR, Astier JM (1991) Impact of coastal development on the infralittoral zone
717 along the southeastern Mediterranean shore of continental France. Marine Pollution Bulletin
718 23:343-347

719 Morales-Nin B, Moranta J, García C, Tugores MP, Grau AM, Riera F, Cerdà M (2005) The
720 recreational fishery off Majorca Island (western Mediterranean): some implications for coastal
721 resource management. ICES Journal of Marine Science: Journal du Conseil 62:727-739

722 Neira C, Mendoza G, Levin LA, Zirino A, Delgadillo-Hinojosa F, Porrachia M, Deheyn DD (2011)
723 Macrobenthic community response to copper in Shelter Island Yacht Basin, San Diego Bay,
724 California. Marine Pollution Bulletin 62:701-717

725 Pastor J, Koeck B, Astruch P, Lenfant P (2013) Coastal man-made habitats: Potential nurseries for an
726 exploited fish species, *Diplodus sargus* (Linnaeus, 1758). Fisheries Research 148:74-80

727 Perez-Ruzafa A, Garcia-Charton JA, Barcala E, Marcos C (2006) Changes in benthic fish
728 assemblages as a consequence of coastal works in a coastal lagoon: The Mar Menor (Spain,
729 Western Mediterranean). Marine Pollution Bulletin 53:107-120

730 Pinar Genc E, Guler N (2012) Assessment of marinas in the Mediterranean and the position of Turkey.
731 PROMET-Traffic&Transportation 18:207-213

732 Pizzolon M, Cenci E, Mazzoldi C (2008) The onset of fish colonization in a coastal defence structure
733 (Chioggia, Northern Adriatic Sea). Estuarine Coastal and Shelf Science 78:166-178

734 Planes S, Jouvenel JY, Lenfant P (1998) Density dependence in post-recruitment processes of juvenile
735 sparids in the littoral of the Mediterranean Sea. Oikos 83:293-300

736 Planes S, Macpherson E, Biagi F, Garcia-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel JY,
737 Tunesi L, Vigliola L, Galzin R (1999) Spatio-temporal variability in growth of juvenile sparid

738 fishes from the Mediterranean littoral zone. *Journal of the Marine Biological Association of*
739 *the United Kingdom* 79:137-143

740 R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for
741 *Statistical Computing*, Vienna, Austria

742 Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1454-1457

743 Ross ST (1986) Resource Partitioning in Fish Assemblages: A Review of Field Studies. *Copeia*
744 1986:352-388

745 Rowe CL (2003) Growth responses of an estuarine fish exposed to mixed trace elements in sediments
746 over a full life cycle. *Ecotoxicology and Environmental Safety* 54:229-239

747 Ruitton S (1999) Les communautés benthiques et nectobenthiques associées aux aménagements
748 littoraux en Méditerranée nord-occidentale. Structure et fonctionnement., Université d'Aix-
749 Marseille II

750 Ruitton S, Francour P, Boudouresque CF (2000) Relationships between algae, benthic herbivorous
751 invertebrates and fishes in rocky sublittoral communities of a temperate sea (Mediterranean).
752 *Estuarine Coastal and Shelf Science* 50:217-230

753 Saborido-Rey F, Dominguez-Petit R, Tomas J, Morales-Nin B, Alonso-Fernandez A (2007) Growth of
754 juvenile turbot in response to food pellets contaminated by fuel oil from the tanker 'Prestige'.
755 *Marine Ecology Progress Series* 345:271-279

756 Seaman W (2007) Artificial habitats and the restoration of degraded marine ecosystems and fisheries.
757 *Hydrobiologia* 580:143-155

758 Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal
759 habitats for commercially and ecologically important species. *ICES Journal of Marine*
760 *Science: Journal du Conseil* 71:648-665

761 Shapiro DY (1987) Inferring larval recruitment strategies from the distribution ecology of settled
762 individuals of coral-reef fish. *Bulletin of Marine Science* 41:289-295

763 Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of*
764 *Marine Science* 60:1129-1157

765 Stephens SM, Frankling SC, Stagg RM, Brown JA (2000) Sub-lethal effects of exposure of juvenile
766 turbot to oil produced water. *Marine Pollution Bulletin* 40:928-937

767 Sundblad G, Bergstrom U, Sandstrom A, Eklov P (2014) Nursery habitat availability limits adult stock
768 sizes of predatory coastal fish. *ICES Journal of Marine Science* 71:672-680

769 Tortonese E (1965) Biologie comparée de trois espèces méditerranéennes de Diplodus (Pisces
770 Sparidae). Rapport Commission Internationale pour l'Exploration Scientifique de la Mer
771 Méditerranée 189-192

772 Ventura D, Jona Lasinio G, Ardizzone G (2014) Temporal partitioning of microhabitat use among four
773 juvenile fish species of the genus Diplodus (Pisces: Perciformes, Sparidae). *Marine*
774 *Ecology*:1-20

775 Verdiell-Cubedo D, Oliva-Paterna FJ, Ruiz-Navarro A, Torralva M (2013) Assessing the nursery role
776 for marine fish species in a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea).
777 *Marine Biology Research* 9:739-748

778 Vigliola L (1998) Contrôle et régulation du recrutement des Sparidae (Poissons, Téléostéens) en
779 Méditerranée : importance des processus pré- et post-installation benthique. Université Aix-
780 Marseille II

781 Vigliola L, Harmelin-Vivien M (2001) Post-settlement ontogeny in three Mediterranean reef fish
782 species of the genus Diplodus. *Bulletin of Marine Science* 68:271-286

783 Vigliola L, Harmelin-Vivien ML, Biagi F, Galzin R, Garcia-Rubies A, Harmelin JG, Jouvenel JY, Le
784 Direach-Boursier L, Macpherson E, Tunesi L (1998) Spatial and temporal patterns of
785 settlement among sparid fishes of the genus Diplodus in the northwestern Mediterranean.
786 *Marine Ecology Progress Series* 168:45-56

787 Vinagre C, Cabral HN, Costa MJ (2010) Relative importance of estuarine nurseries for species of the
788 genus Diplodus (Sparidae) along the Portuguese coast. *Estuarine Coastal and Shelf Science*
789 86:197-202

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792 Table 1: Characteristics of the five marinas studied in this work. PV = Port-Vendres, BA = Port-
793 Barcarès, CA = Cap d'Agde, ME = Mèze, BR = Le Brusc (Sources MEDAM 2015).

Marina	Construction date	Surface area (ha)	Number of rings	Average depth (m)	Connection(s)	Coast type
PV	1853	33	253	8	Sea	Rocky
BA	1963	81	950	2	Sea and Salses-Leucate lagoon	Sandy
CA	1969	53	3 100	3	Sea	Rocky
ME	6 th century	18	200	2	Thau lagoon	Sandy
BR	1960	8	796	4	Sea	Rocky

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808 Table 2: Results of the univariate three-way PERMANOVAs performed to compare juvenile fish
809 abundances (ind. count⁻¹) between months (April to August), marinas (Port-Vendres, Port-Barcarès,
810 Cap d'Agde, Mèze and Le Brusc) and artificial habitat type (DB, DC, PB and PC). Contrasts were
811 used to compare juvenile fish abundances between DB vs DC and PB vs PC. Significant p values (<
812 0.05) are indicated in bold. A star (*) in the 'Source' column to indicates the results of contrast tests.

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Source	df	MS	Pseudo-F	P(perm)
<i>Diplodus spp.</i>				
Month (Mo)	4	1.3285	1.8282	0.1718
Marina (Ma)	4	6.2927	23.643	0.0001
Artificial Habitat Type (AH)	3	3.4027	4.0546	0.0309
*DB-v-DC	1	2.6958	2.8197	0.1742
*PB-v-PC	1	7.3272	7.4131	0.0619
Mo x Ma	16	0.737	2.769	0.0005
Mo x AH	12	0.6153	1.7594	0.0881
*Mo x DB-v-DC	4	0.74754	6.2743	0.0036
*Mo x PB-v-PC	4	0.27934	0.88306	0.4933
Ma x AH	12	0.84719	3.183	0.0004
*Ma x DB-v-DC	4	0.96961	3.2608	0.0117
*Ma x PB-v-PC	4	0.99439	4.2266	0.0022
Mo x Ma x AH	48	0.3522	1.3233	0.0771
*Mo x Ma x DB-v-DC	16	0.11284	0.37948	0.9883
*Mo x Ma x PB-v-PC	16	0.31847	1.3536	0.1618
Residuals	796	0.26616		
Total	895			
<i>D. annularis</i>				
Month (Mo)	4	2.9147	5.4272	0.0052
Marina (Ma)	4	1.2478	20.884	0.0001
Artificial Habitat Type (AH)	3	1.0537	3.4146	0.0506
*DB-v-DC	1	1.5682	6.1272	0.0778
*PB-v-PC	1	1.5927	2.7135	0.1796
Mo x Ma	16	0.54779	9.1682	0.0001
Mo x AH	12	0.5233	3.3548	0.0011
*Mo x DB-v-DC	4	0.79985	5.4357	0.0053
*Mo x PB-v-PC	4	0.76441	3.4679	0.0286
Ma x AH	12	0.31205	5.2228	0.0001
*Ma x DB-v-DC	4	0.26008	4.7304	0.0011
*Ma x PB-v-PC	4	0.59113	9.1692	0.0001
Mo x Ma x AH	48	0.15884	2.6584	0.0002
*Mo x Ma x DB-v-DC	16	0.15041	2.7356	0.001
*Mo x Ma x PB-v-PC	16	0.22453	3.4827	0.0004
Residuals	796	5.9749E-2		
Total	895			

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Source	df	MS	Pseudo-F	P(perm)
<i>D. puntazzo</i>				
Month (Mo)	4	0.11838	1.7037	0.185
Marina (Ma)	4	0.58042	17.379	0.0001
Artificial Habitat Type (AH)	3	0.40819	2.1155	0.1367
*DB-v-DC	1	0.13055	5.1787	0.0947
*PB-v-PC	1	0.80851	1.9883	0.2246
Mo x Ma	16	7.0293E-2	2.1048	0.0084
Mo x AH	12	5.5525E-2	2.0167	0.0413
*Mo x DB-v-DC	4	2.2988E-2	2.6866	0.0726
*Mo x PB-v-PC	4	0.12138	2.6845	0.0708
Ma x AH	12	0.19517	5.8438	0.0001
*Ma x DB-v-DC	4	2.5248E-2	1.0828	0.3637
*Ma x PB-v-PC	4	0.40952	9.4409	0.0001
Mo x Ma x AH	48	2.7359E-2	0.8192	0.7967
*Mo x Ma x DB-v-DC	16	8.0345E-3	0.34458	0.99
*Mo x Ma x PB-v-PC	16	4.5265E-2	1.0435	0.4057
Residuals	796	3.3397E-2		
Total	895			
<i>D. sargus</i>				
Month (Mo)	4	1.3037	4.225	0.0156
Marina (Ma)	4	0.7363	9.4466	0.0001
Artificial Habitat Type (AH)	3	0.69136	1.5925	0.2432
*DB-v-DC	1	6.022E-2	4.8709	0.0998
*PB-v-PC	1	0.29581	0.60032	0.4789
Mo x Ma	16	0.31376	4.0256	0.0002
Mo x AH	12	0.17219	1.1333	0.354
*Mo x DB-v-DC	4	1.056E-2	0.33165	0.8579
*Mo x PB-v-PC	4	0.14321	1.0896	0.3924
Ma x AH	12	0.4391	5.6336	0.0001
*Ma x DB-v-DC	4	1.2007E-2	0.40495	0.8068
*Ma x PB-v-PC	4	0.49567	3.9417	0.0042
Mo x Ma x AH	48	0.15413	1.9775	0.0007
*Mo x Ma x DB-v-DC	16	3.1919E-2	1.0765	0.3708
*Mo x Ma x PB-v-PC	16	0.13158	1.0463	0.4124
Residuals	796	7.7943E-2		
Total	895			

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Source	df	MS	Pseudo-F	P(perm)
<i>D. vulgaris</i>				
Month (Mo)	4	0.56464	1.9424	0.1555
Marina (Ma)	4	1.4537	12.35	0.0001
Artificial Habitat Type (AH)	3	1.9162	3.709	0.0433
*DB-v-DC	1	1.5172E-3	3.0143E-3	0.9144
*PB-v-PC	1	1.3173E-3	0.0069712	0.9741
Mo x Ma	16	0.29459	2.5029	0.0017
Mo x AH	12	0.26063	1.4489	0.1845
*Mo x DB-v-DC	4	8.1717E-2	0.78894	0.5441
*Mo x PB-v-PC	4	6.4966E-2	1.2575	0.3328
Ma x AH	12	0.5222	4.4367	0.0001
*Ma x DB-v-DC	4	0.50927	2.3585	0.0509
*Ma x PB-v-PC	4	0.1903	9.3036	0.0001
Mo x Ma x AH	48	0.18172	1.5439	0.0149
*Mo x Ma x DB-v-DC	16	9.9605E-2	0.46128	0.9627
*Mo x Ma x PB-v-PC	16	5.2481E-2	2.5657	0.0028
Residuals	796	0.1177		
Total	895			

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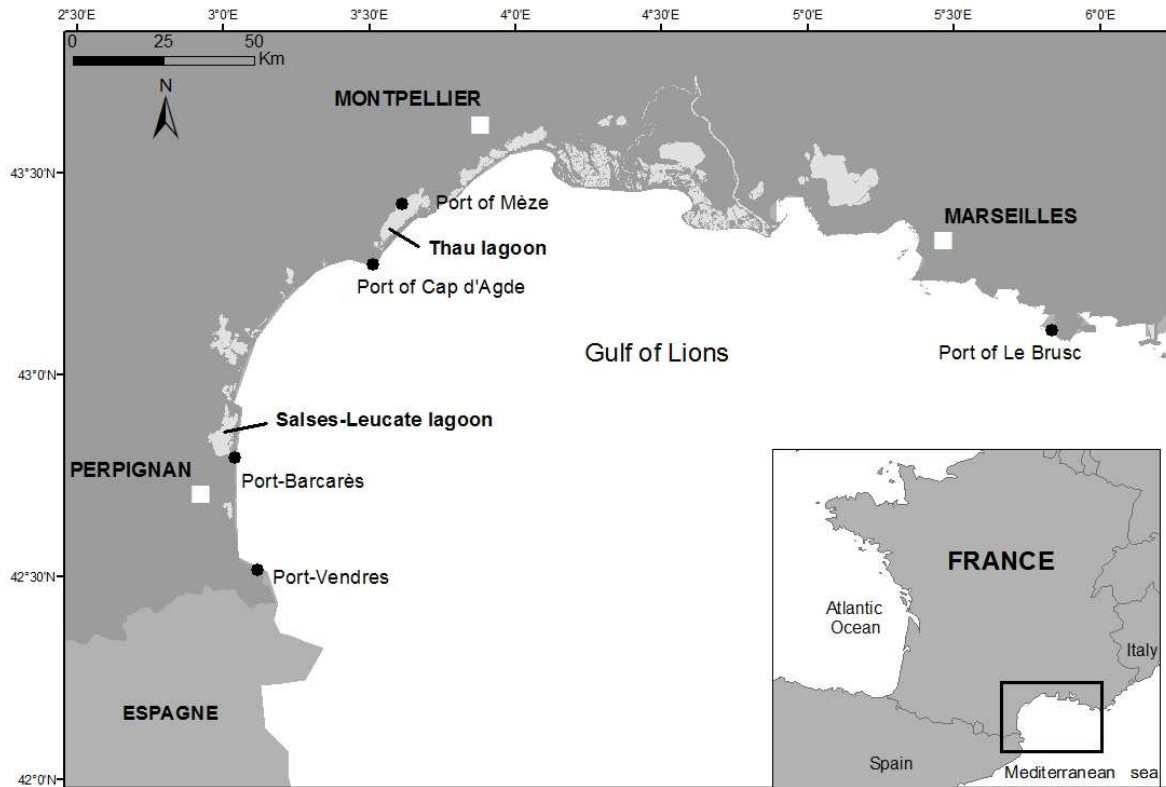
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848 Fig. 1: Location of the five marinas studied along the French Mediterranean coast.



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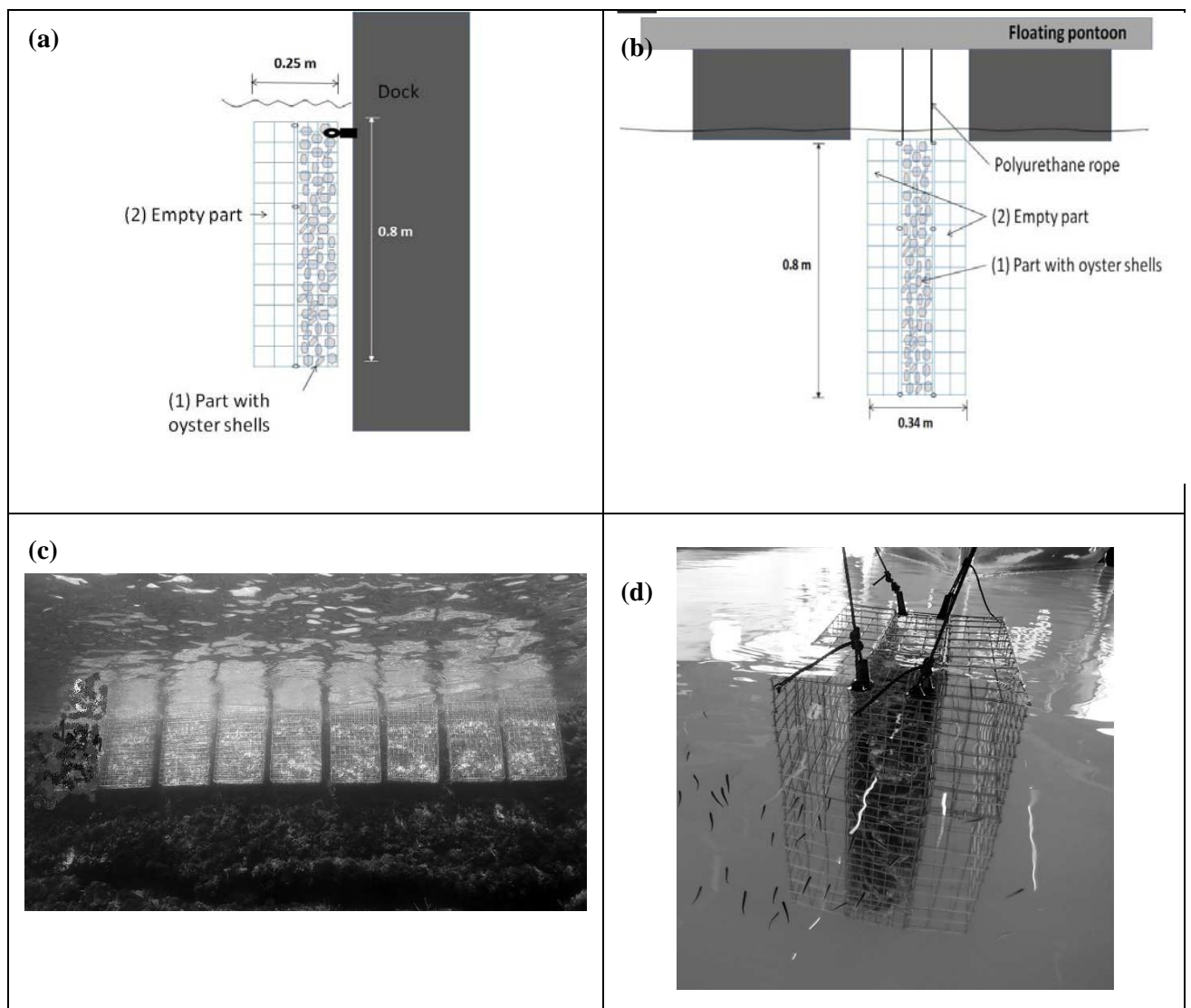
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859 Fig 2. (a) Dock Biohut[®] steel cage including (1) a part filled with oyster shells (0.5 x 0.8 m, 2.5 cm
860 mesh size) and (2) an empty part (0.5 x 0.8 m, 5 cm mesh size). (b) Pontoon Biohut[®] steel cage
861 including (1) a part filled with oyster shells (0.5 x 0.8 m, 2.5 cm of mesh size) and (2) two empty parts
862 (0.5 x 0.8 m, 5 cm of mesh size). (c) Dock Biohut sampling unit (DB) corresponding to eight adjacent
863 cages pegged on 5m of dock, (d) Pontoon Biohut (PB) cage fixed under a floating pontoon with
864 polyurethane ropes.



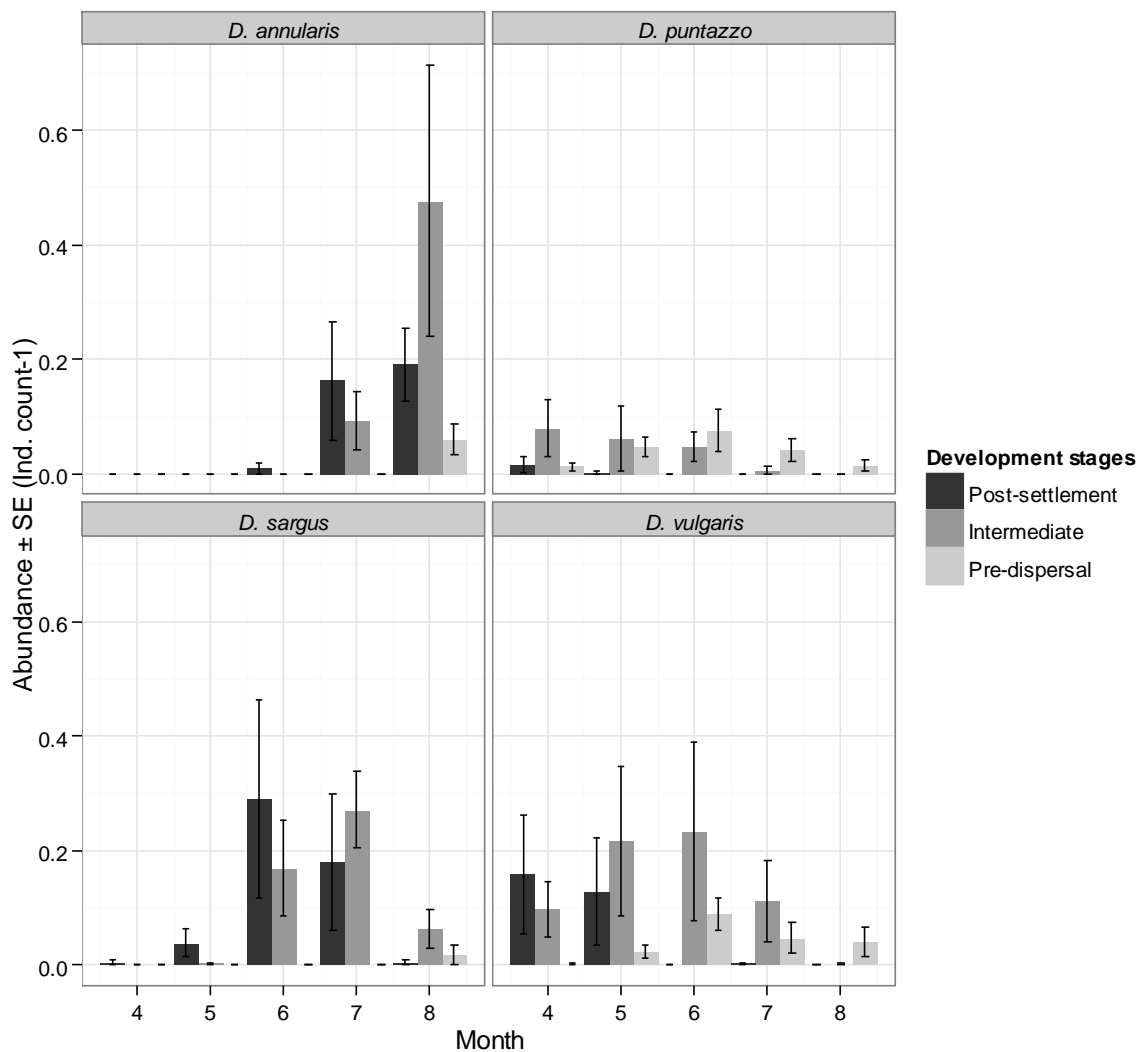
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869 Fig. 3: Average monthly abundances of juveniles (expressed in ind. count⁻¹) at the post-settlement,
 870 intermediate and pre-dispersal stages observed for the four *Diplodus* species investigated. Results for
 871 all locations, artificial structures and artificial habitats are pooled. Error-bars represent standard errors
 872 around the means.



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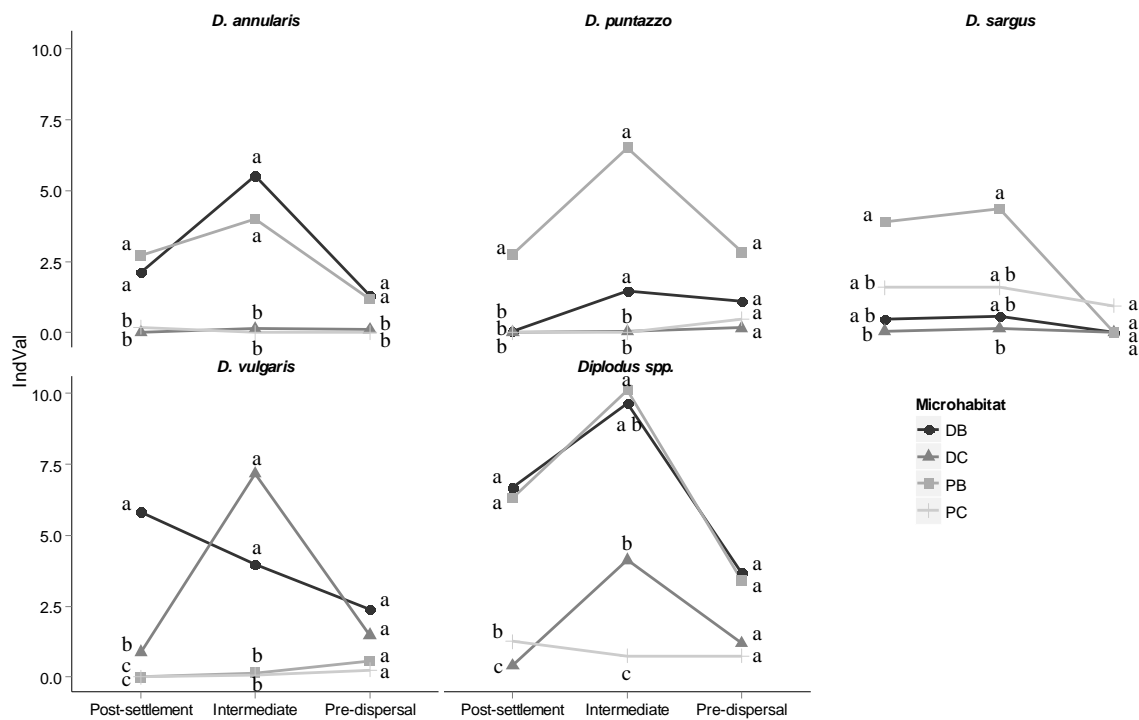
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880 Fig. 4: Indicator Value indexes (Dufrêne & Legendre 1997) per habitat type obtained for all three
 881 development stages (post-settlement, intermediate and pre-dispersal) in the four *Diplodus* species
 882 considered grouped or separately. For each development stage, artificial habitats presenting
 883 differences in their IndVal indexes are given different letters.



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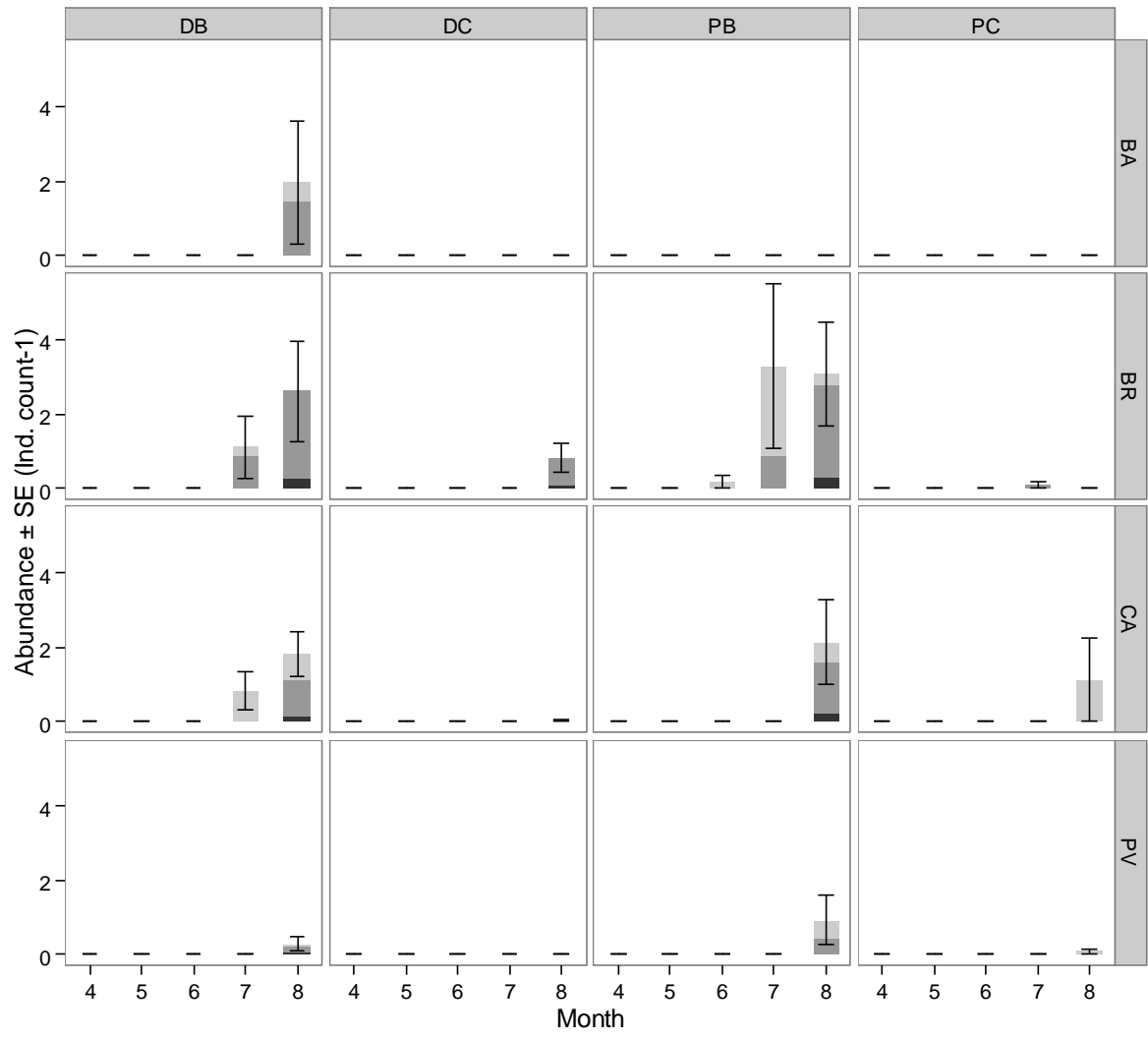
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896 Supplementary material

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898 Fig. S1: Mean abundances (ind. count⁻¹) of the juveniles of *D. annularis* (A) , *D. puntazzo* (B) , *D.*
899 *sargus* (C) and *D. vulgaris* (D) observed per month, marina (Port-Vendres -PV-, Port-Barcarès -BA-,
900 Cap d'Agde -CA- and Le Brusc -BR-) and habitat type (DB, DC, PB and PC). Results for Mèze are
901 not represented since a total of only 3 individuals were observed in this marina. Colors correspond to
902 the three development stages chosen in this study: post-settlement in light grey, intermediate in dark
903 grey and pre-dispersal in black. Error-bars represent the standard error around the mean abundance
904 found when all development stages were combined.

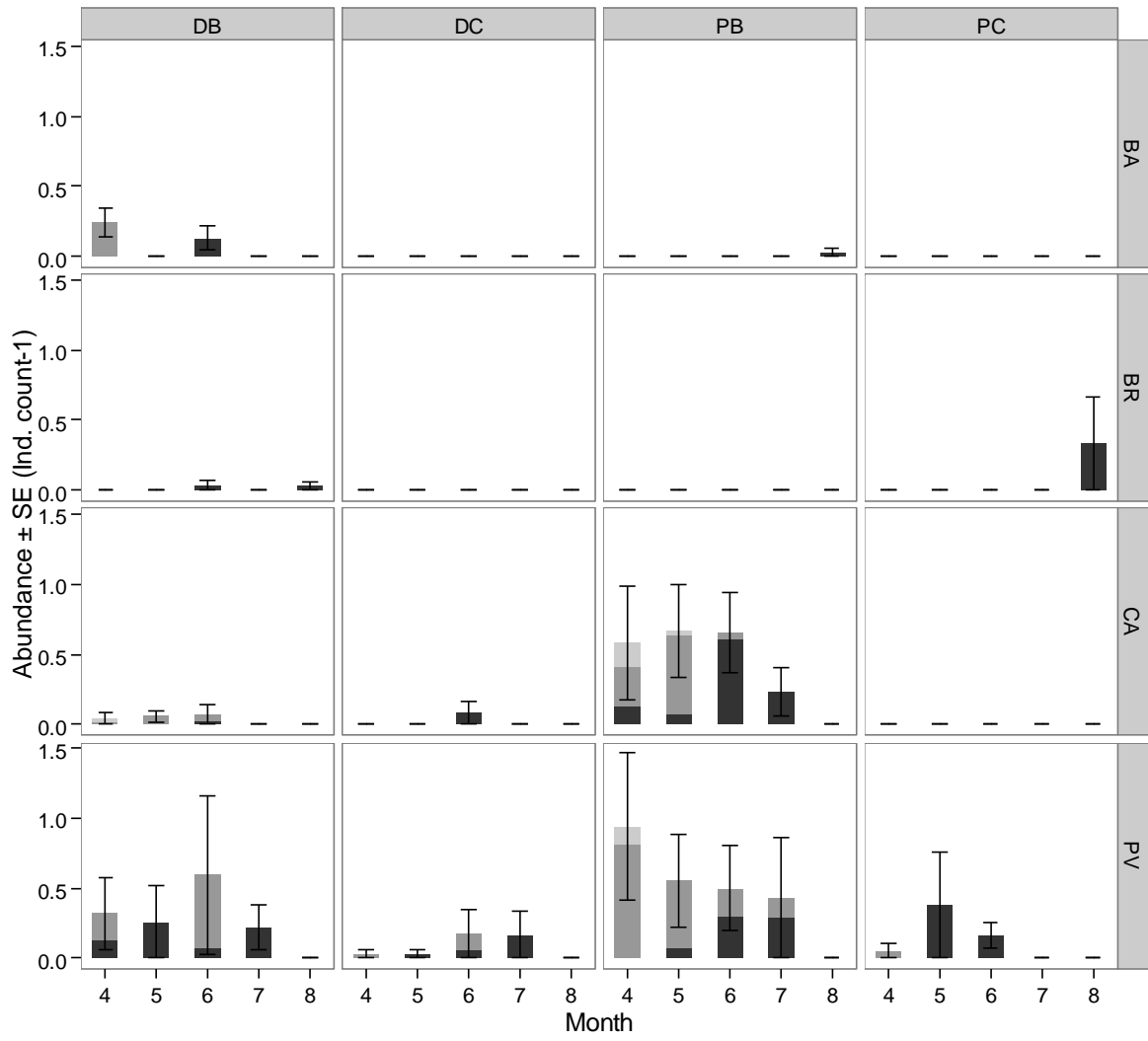
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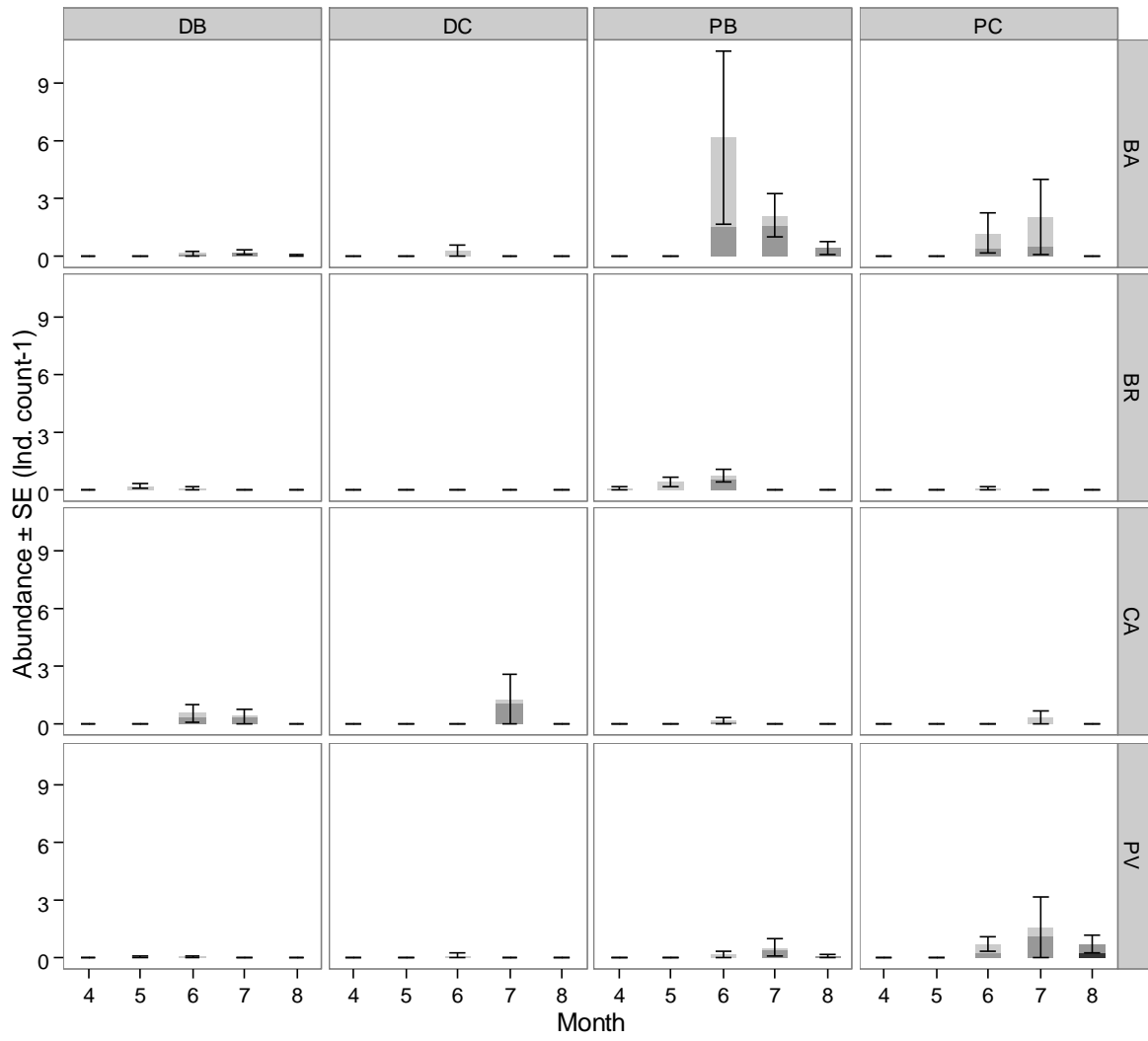
907 (A): *D. annularis*

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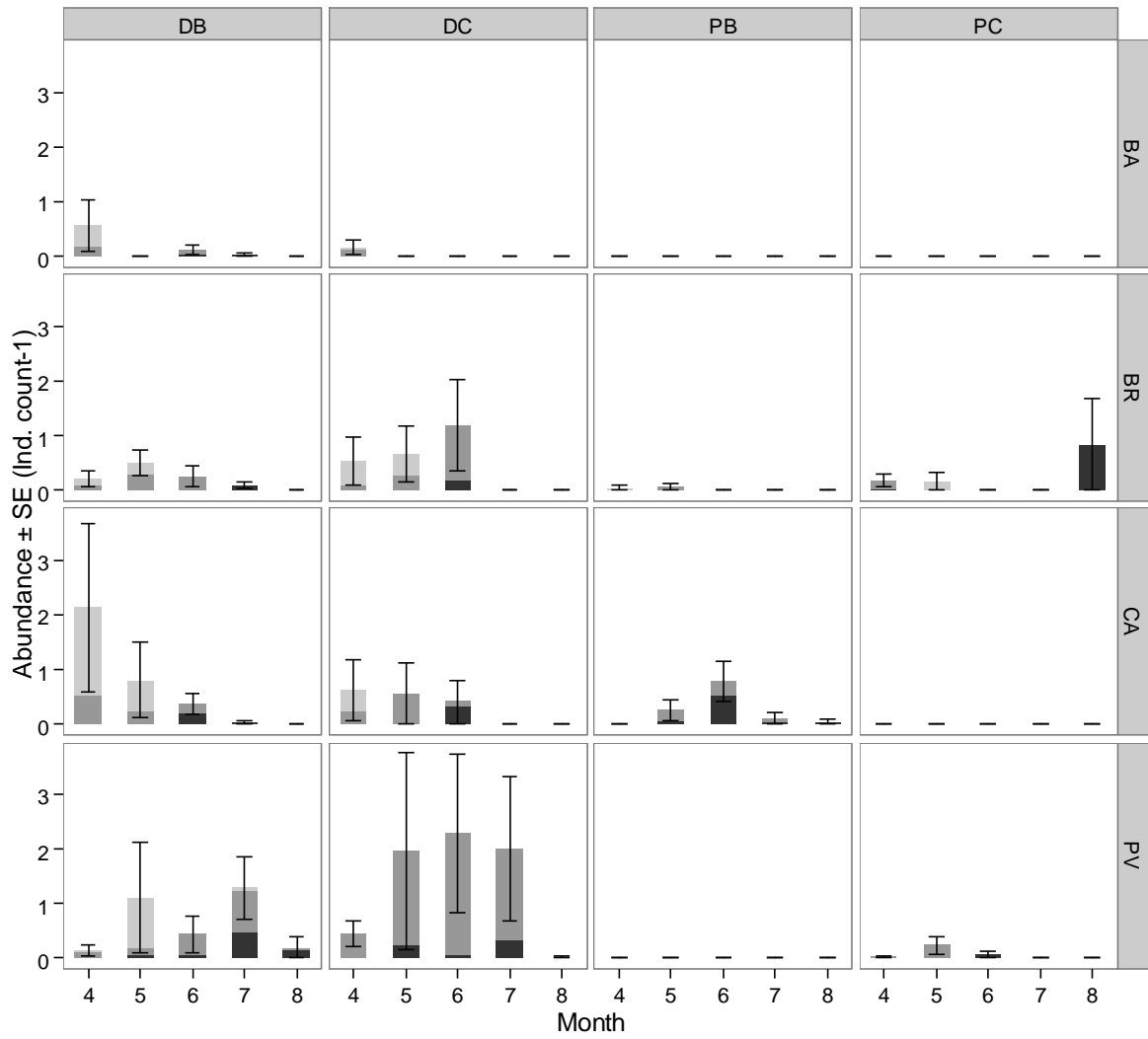
910 (B): *D. puntazzo*



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912 (C): *D. sargus*

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915 (D): *D. vulgaris*

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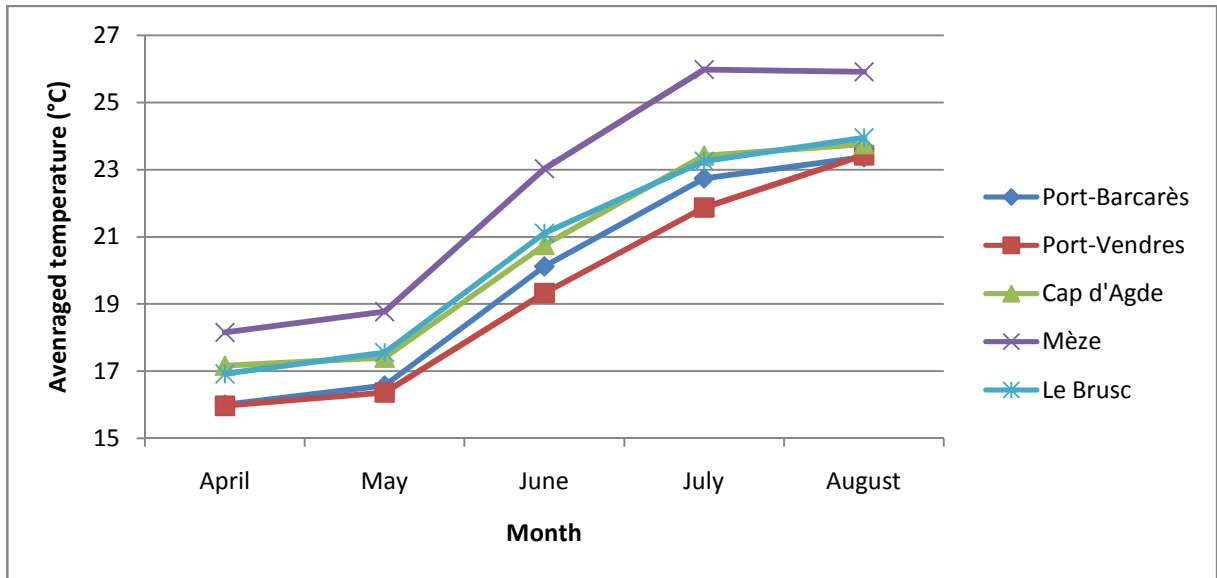
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924 Fig. S2: Evolution of monthly average temperatures in the five marinas studied during the sampling
925 period (April-August).

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941 Table S1: Definition of development stages for the four species studied. (a) Data from Ventura et al.
 942 (2014). (b), (c) and (d) Data from Vigliola & Harmelin (2001). SL = standard length. TL = total
 943 length. Length used for development stages in Vigliola & Harmelin (2001) are given in SL. We
 944 estimated TL in our study. Relation between SL and TL are given in (Vigliola 1998): $LT = a \cdot LS$ with
 945 $a = 1.257$ for *D. puntazzo*. $a = 1.290$ for *D. sargus*. $a = 1.283$ for *D. vulgaris*.

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Development stage	SL (mm)	TL (mm)
a) <i>D. annularis</i>		
Post-settlement		Settlement - 20
Intermediate		20 - 45
Pre-dispersal		>45
b) <i>D. puntazzo</i>		
Post-settlement	Settlement - 21	Settlement - 26
Intermediate	21 - 43	26 - 54
Pre-dispersal	> 43	> 54
c) <i>D. sargus</i>		
Post-settlement	Settlement - 23	Settlement - 30
Intermediate	23 - 49	30 - 63
Pre-dispersal	> 49	> 63
d) <i>D. vulgaris</i>		
Post-settlement	Settlement - 24	Settlement - 30
Intermediate	24 - 40	30 - 51
Pre-dispersal	> 40	> 51

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