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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.

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**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*, Rafinesque 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<sup>®</sup>"). 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 m<sup>2</sup>. 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. 4m<sup>2</sup>. 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  $5 \times 0.8$  m ( $4 \text{ m}^2$ ) 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  $4 \text{ m}^2$  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  $\text{m}^2$  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  $1.33 \text{ m}^2$  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 the *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<sup>-1</sup>) 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) (Dufrene & 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  $\text{Abundance}_{ijk}$  is the mean abundance per count of the development stage  $i$  of the species  $j$  in the  
214 AH  $k$  and  $\text{Abundance}_{ij}$  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 m<sup>2</sup> per marina,  
234 instead of 12 m<sup>2</sup> 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  $3.29^\circ\text{C}$ ), respectively, than in the three other marinas ( $19.76 \pm 3.40^\circ\text{C}$  in Port-Barcarès,  $20.49.76 \pm$   
240  $3.16^\circ\text{C}$  in Cap d'Agde and  $20.56 \pm 3.21^\circ\text{C}$  in Le Brus).

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:  $0.73 \pm 0.14$   
256  $\text{ind. count}^{-1}$ ) 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 ( $1.08 \pm 0.18$   
270 ind. count<sup>-1</sup>) in Cap d'Agde and a minimum ( $0.04 \pm 0.003$  ind. count<sup>-1</sup>) in the marinas of Mèze and  
271 Port-Barcarès, while similar intermediate values were obtained for Le Brusc and Port-Vendres  
272 (respectively of  $0.85 \pm 0.24$ ,  $0.96 \pm 0.15$  and  $0.98 \pm 0.14$  ind. count<sup>-1</sup>, 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* ( $0.53 \pm 0.14$  ind. count<sup>-1</sup>),  
279 in Port-Vendres for *D. puntazzo* ( $0.24 \pm 0.05$  ind. count<sup>-1</sup>), in Port-Barcarès for *D. sargus* ( $0.67 \pm$   
280  $0.23$  ind. count<sup>-1</sup>) and in Cap d'Agde for *D. vulgaris* ( $0.55 \pm 0.16$  ind. count<sup>-1</sup>). 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:  $1.02 \pm 0.12$  ind. count<sup>-1</sup>) than on the nearby bare vertical  
285 surfaces used as controls (mean:  $0.52 \pm 0.12$  ind. count<sup>-1</sup>). 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<sup>-1</sup>) (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<sup>-1</sup>  
407 <sup>1</sup> on average, it has the highest density of use after the marina of Le Brusc (99.5 rings. ha<sup>-1</sup>). 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 ( $\pm 3.5$  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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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 Brusç (Sources MEDAM 2015).

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<b>Marina</b>	<b>Construction date</b>	<b>Surface area (ha)</b>	<b>Number of rings</b>	<b>Average depth (m)</b>	<b>Connection(s)</b>	<b>Coast type</b>
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 <sup>th</sup> 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<sup>-1</sup>) 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)
<b><i>Diplodus spp.</i></b>				
Month (Mo)	4	1.3285	1.8282	0.1718
Marina (Ma)	4	6.2927	23.643	<b>0.0001</b>
Artificial Habitat Type (AH)	3	3.4027	4.0546	<b>0.0309</b>
*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	<b>0.0005</b>
Mo x AH	12	0.6153	1.7594	0.0881
*Mo x DB-v-DC	4	0.74754	6.2743	<b>0.0036</b>
*Mo x PB-v-PC	4	0.27934	0.88306	0.4933
Ma x AH	12	0.84719	3.183	<b>0.0004</b>
*Ma x DB-v-DC	4	0.96961	3.2608	<b>0.0117</b>
*Ma x PB-v-PC	4	0.99439	4.2266	<b>0.0022</b>
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			
<b><i>D. annularis</i></b>				
Month (Mo)	4	2.9147	5.4272	<b>0.0052</b>
Marina (Ma)	4	1.2478	20.884	<b>0.0001</b>
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	<b>0.0001</b>
Mo x AH	12	0.5233	3.3548	<b>0.0011</b>
*Mo x DB-v-DC	4	0.79985	5.4357	<b>0.0053</b>
*Mo x PB-v-PC	4	0.76441	3.4679	<b>0.0286</b>
Ma x AH	12	0.31205	5.2228	<b>0.0001</b>
*Ma x DB-v-DC	4	0.26008	4.7304	<b>0.0011</b>
*Ma x PB-v-PC	4	0.59113	9.1692	<b>0.0001</b>
Mo x Ma x AH	48	0.15884	2.6584	<b>0.0002</b>
*Mo x Ma x DB-v-DC	16	0.15041	2.7356	<b>0.001</b>
*Mo x Ma x PB-v-PC	16	0.22453	3.4827	<b>0.0004</b>
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	<b>0.0001</b>
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	<b>0.0084</b>
Mo x AH	12	5.5525E-2	2.0167	<b>0.0413</b>
*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	<b>0.0001</b>
*Ma x DB-v-DC	4	2.5248E-2	1.0828	0.3637
*Ma x PB-v-PC	4	0.40952	9.4409	<b>0.0001</b>
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	<b>0.0156</b>
Marina (Ma)	4	0.7363	9.4466	<b>0.0001</b>
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	<b>0.0002</b>
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	<b>0.0001</b>
*Ma x DB-v-DC	4	1.2007E-2	0.40495	0.8068
*Ma x PB-v-PC	4	0.49567	3.9417	<b>0.0042</b>
Mo x Ma x AH	48	0.15413	1.9775	<b>0.0007</b>
*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	<b>0.0001</b>
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	<b>0.0017</b>
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	<b>0.0001</b>
*Ma x DB-v-DC	4	0.50927	2.3585	0.0509
*Ma x PB-v-PC	4	0.1903	9.3036	<b>0.0001</b>
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	<b>0.0028</b>
Residuals	796	0.1177		
Total	895			

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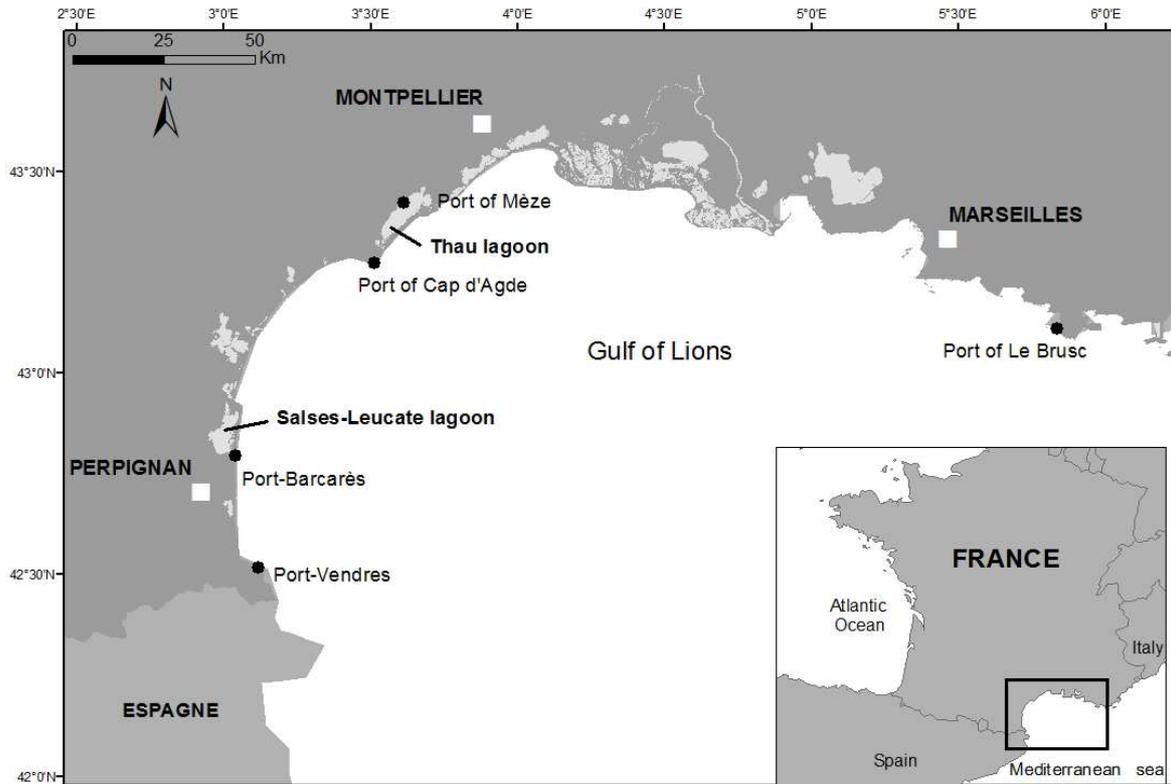
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848 Fig. 1: Location of the five marinas studied along the French Mediterranean coast.



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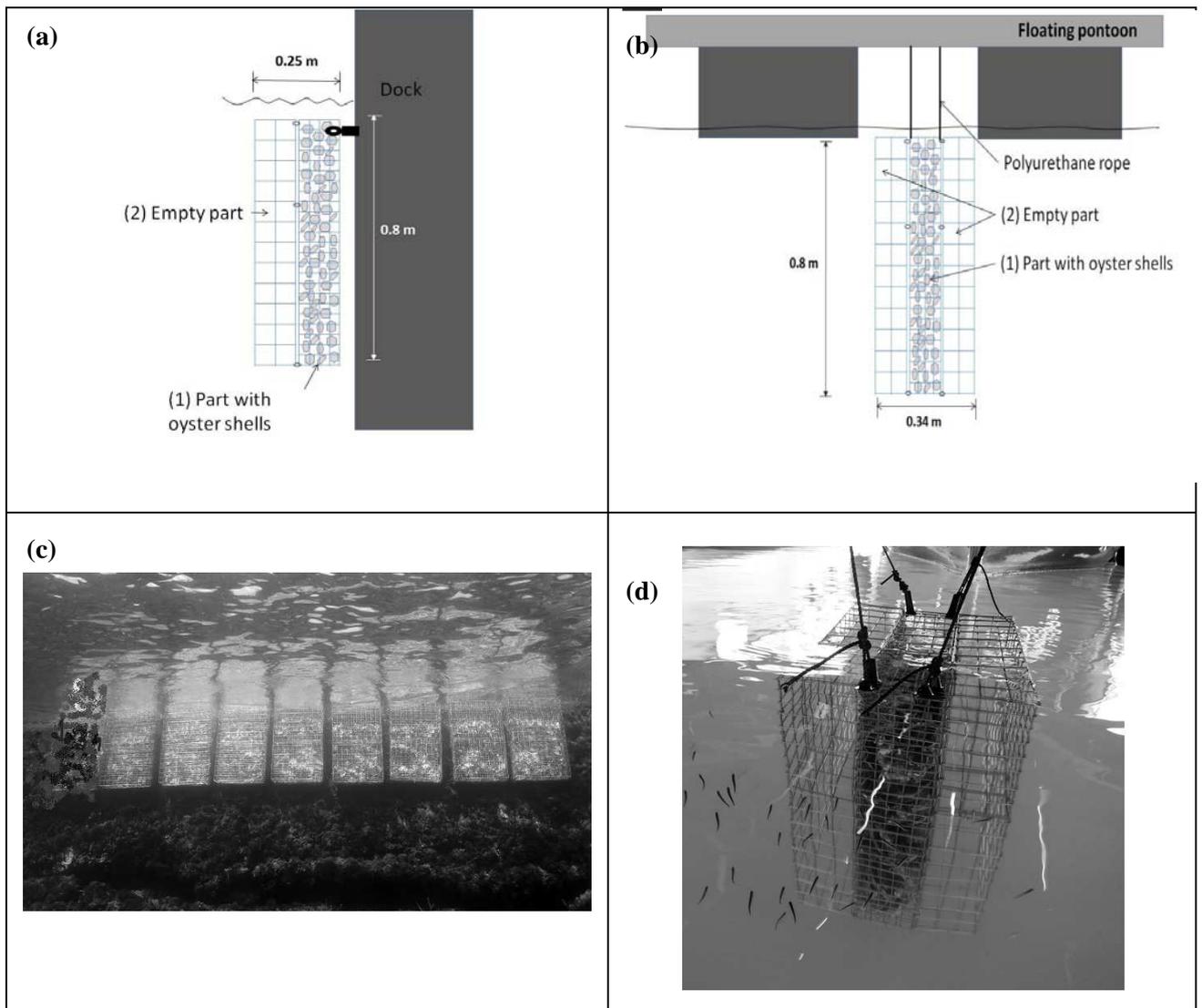
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859 Fig 2. (a) Dock Biohut<sup>®</sup> steel cage including (1) a part filled with oyster shells (0.5 x 0.8 m, 2.5 cm  
 860 mesh size) and (2) an empty part (0.5 x 0.8 m, 5 cm mesh size). (b) Pontoon Biohut<sup>®</sup> steel cage  
 861 including (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.



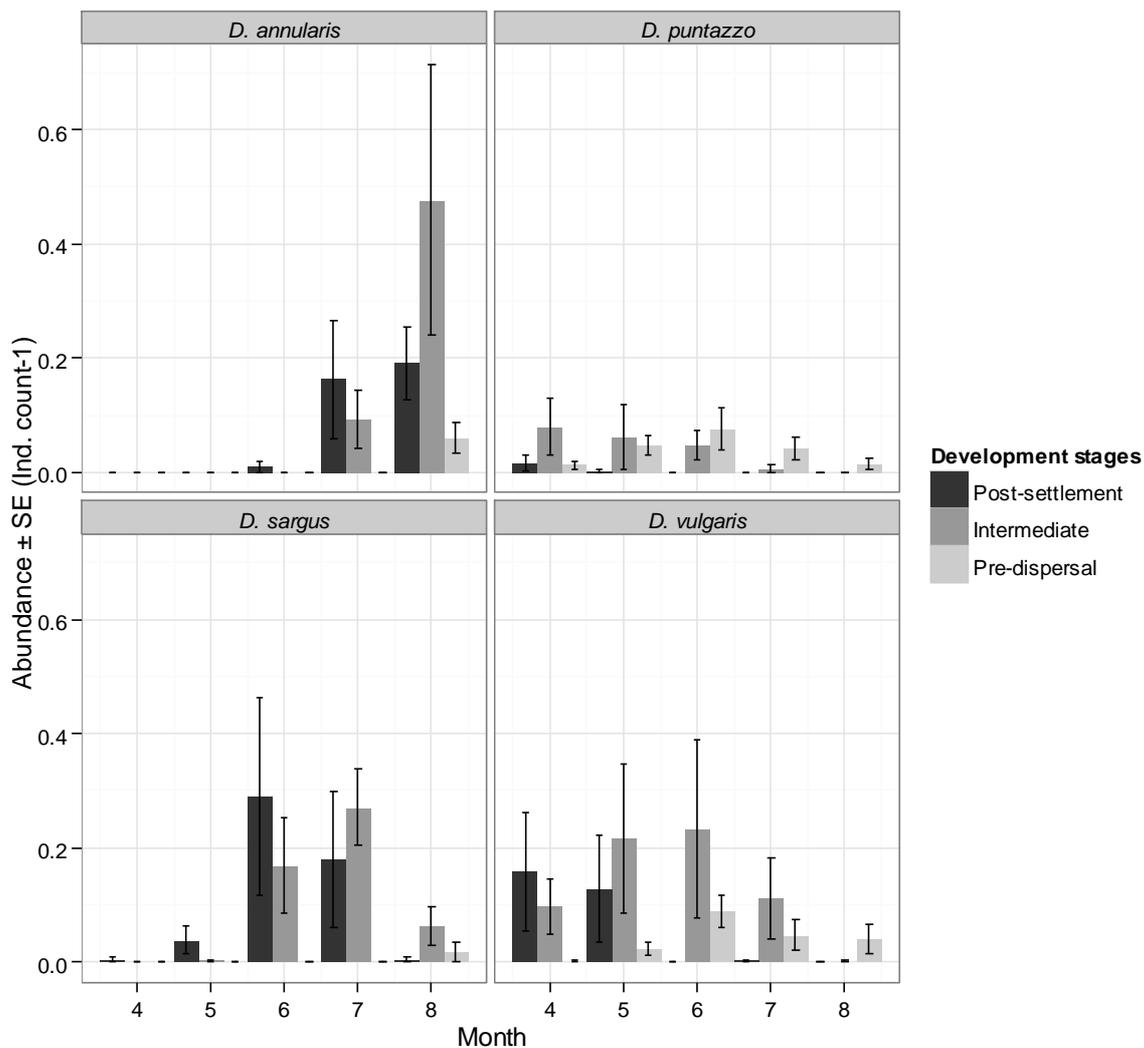
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869 Fig. 3: Average monthly abundances of juveniles (expressed in ind. count<sup>-1</sup>) at the post-settlement,  
 870 intermediate and pre-dispersal stages observed for the four *Diplodus* species investigated. Results for  
 871 all locations,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



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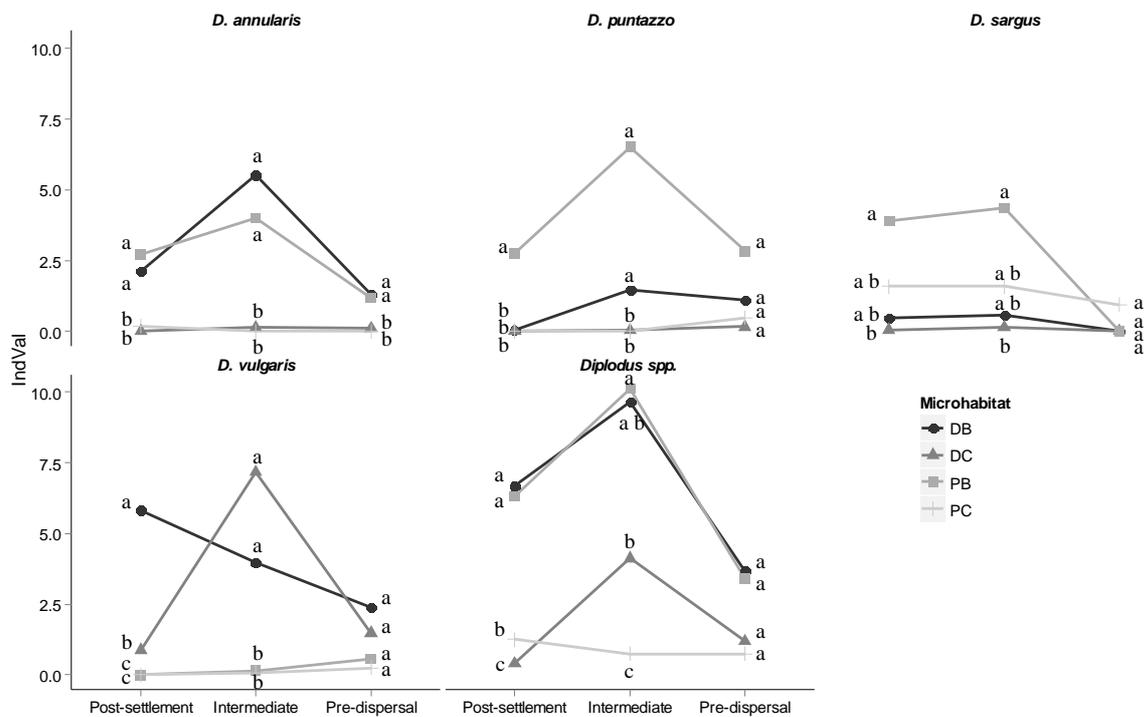
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880 Fig. 4: Indicator Value indexes (Dufrêne & Legendre 1997) per habitat type obtained for all three  
 881 development stages (post-settlement, intermediate and pre-dispersal) in the four *Diplodus* species  
 882 considered grouped or separately.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



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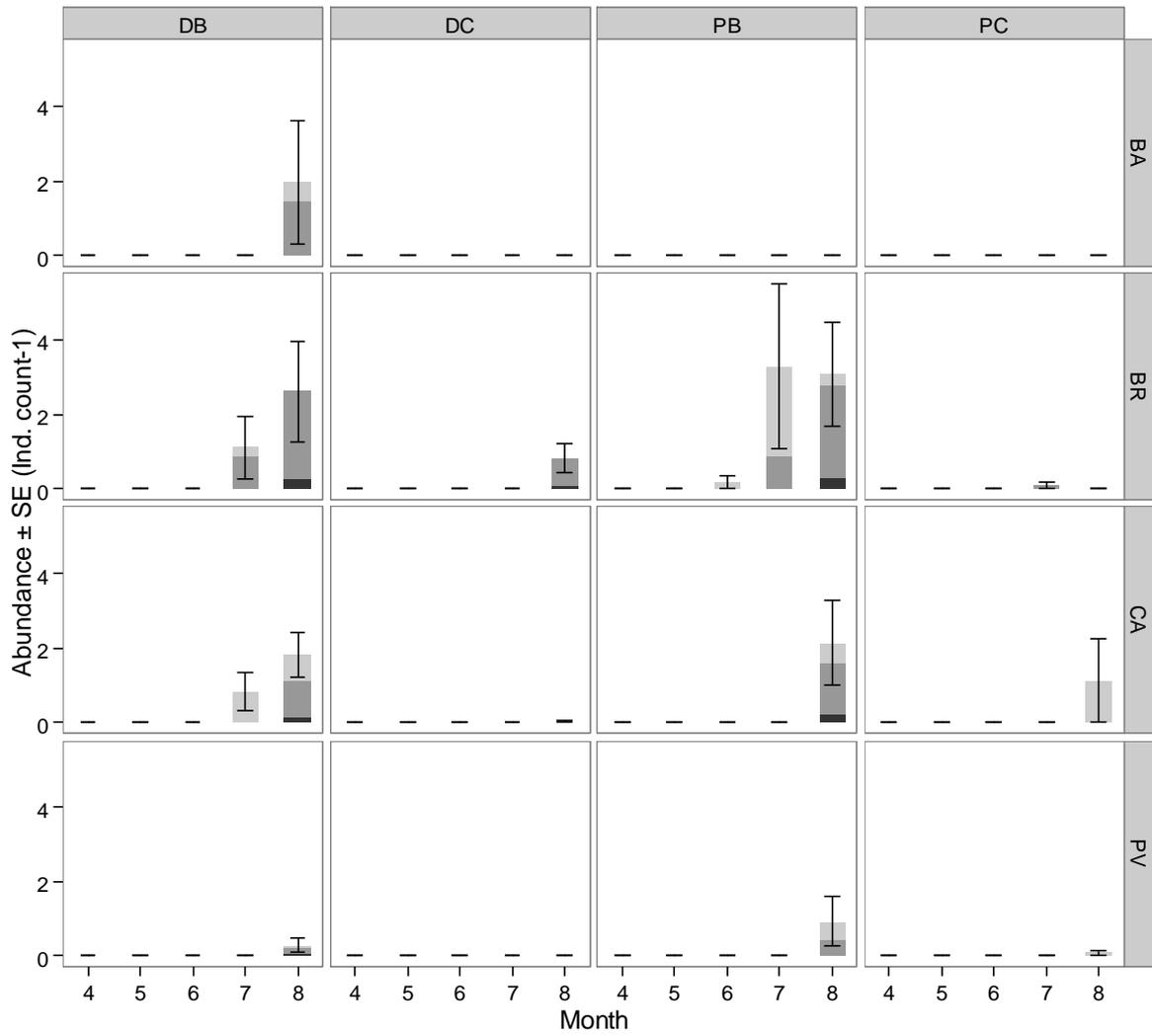
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896 Supplementary material

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898 Fig. S1: Mean abundances (ind. count<sup>-1</sup>) 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.

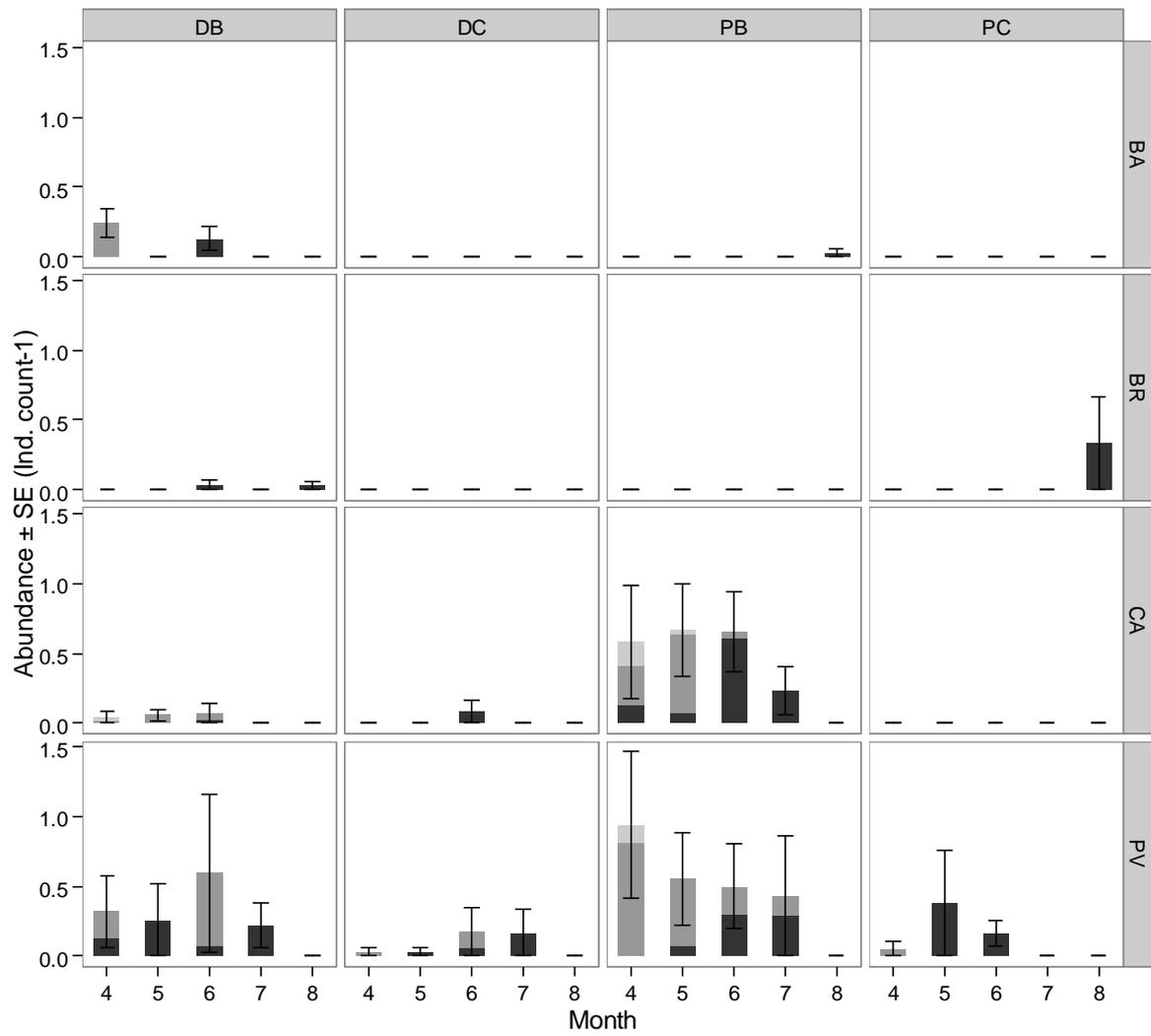
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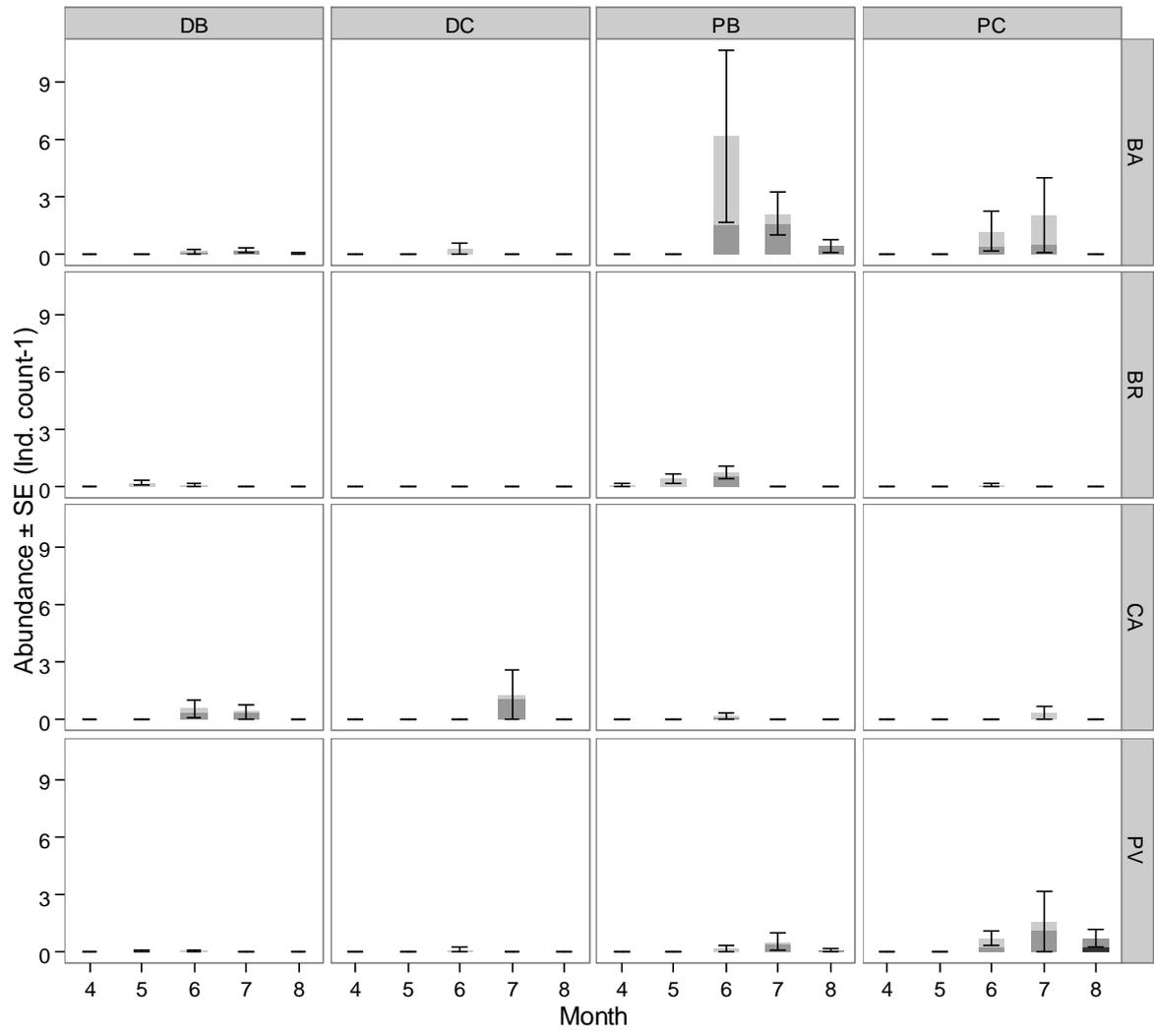
907 (A): *D. annularis*

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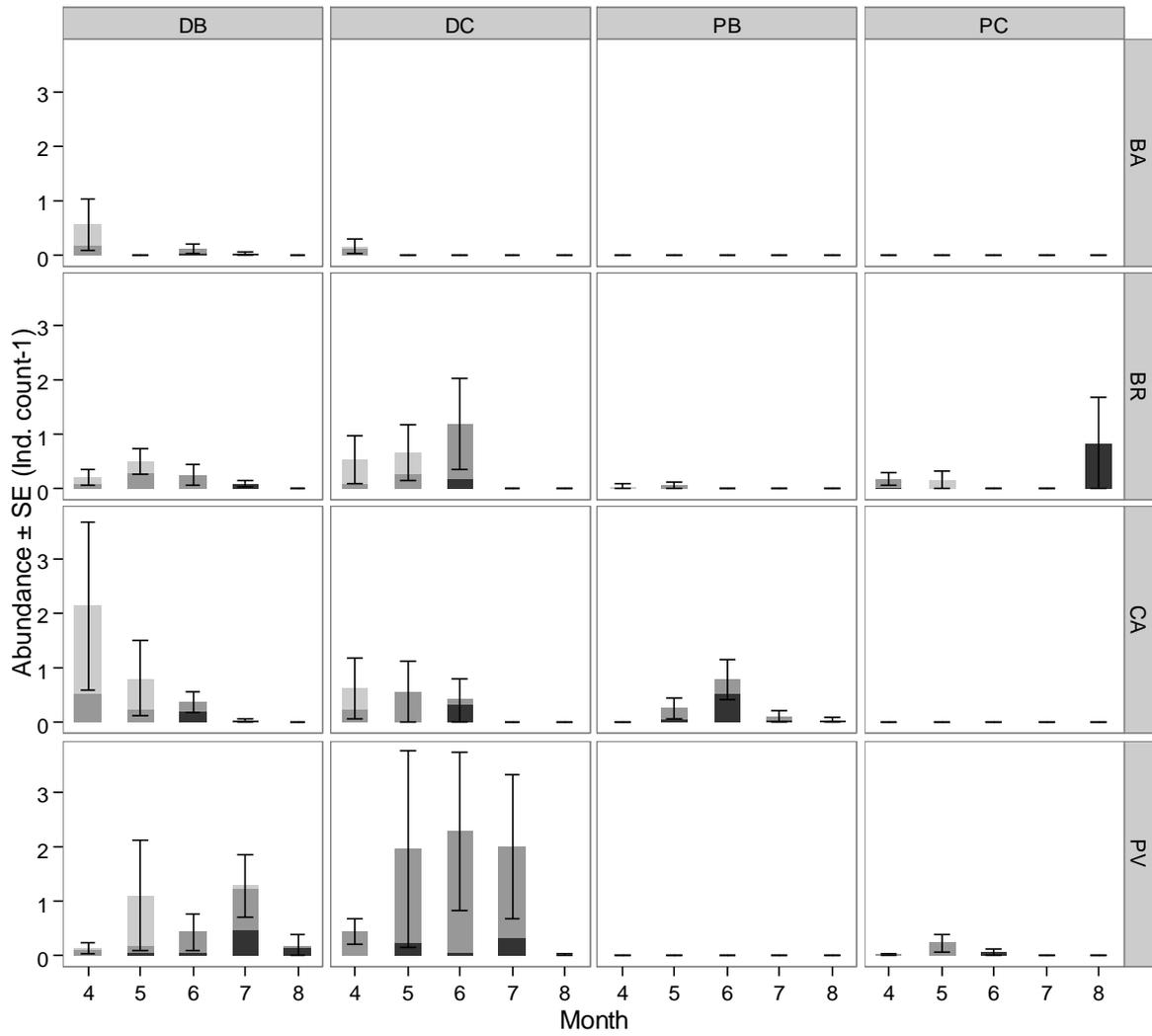
910 (B): *D. puntazzo*



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912 (C): *D. sargus*

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915 (D): *D. vulgaris*

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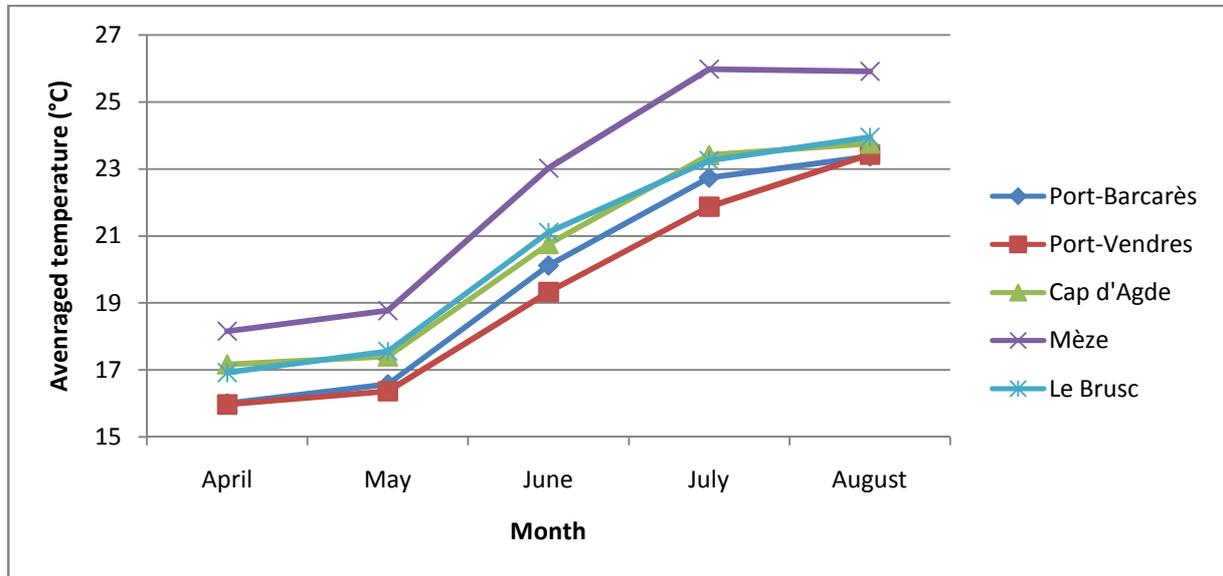
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924 Fig. S2: Evolution of monthly average temperatures in the five marinas studied during the sampling  
925 period (April-August).

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

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