Spatial distribution of juvenile fish along an artificialized seascape, insights from common coastal species in the Nor....

Article *in* Marine Environmental Research · February 2018

DOI: 10.1016/j.marenvres.2018.02.030

9 authors, including:

Manon Mercader
Université de Perpignan
7 PUBLICATIONS **10** CITATIONS
SEE PROFILE

Adrien Cheminée
Septentrion Environnement, Marseille, France
43 PUBLICATIONS **161** CITATIONS
SEE PROFILE

Jérémy Pastor
Université de Perpignan
41 PUBLICATIONS **299** CITATIONS
SEE PROFILE

Alexandre Mercière
Ecole Pratique des Hautes Etudes
11 PUBLICATIONS **12** CITATIONS
SEE PROFILE

Marine Environmental Research xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Spatial distribution of juvenile fish along an artificialized seascape, insights from common coastal species in the Northwestern Mediterranean Sea

Manon Mercader[a,b,*], Mary Rider[a,b], Adrien Cheminée[a,b,c], Jérémy Pastor[a,b], Audrey Zawadzki[a,b], Alexandre Mercière[a,b], Romain Crec'hriou[a,b], Marion Verdoit-Jarraya[a,b], Philippe Lenfant[a,b]

[a] *Université Perpignan Via Domitia, Centre de Formation et de Recherche sur les Environnements Méditerranéens, UMR 5110, F-66860 Perpignan, France*
[b] *CNRS, Centre de Formation et de Recherche sur les Environnements Méditerranéens, UMR 5110, F-66860 Perpignan, France*
[c] *Septentrion Environnement, Port des Goudes, 13008, Marseille, France*

ARTICLE INFO

Keywords:
Juvenile fish habitat
Coastal urbanization
Harbor
Coastal management
Mediterranean

ABSTRACT

Along the littoral, a growing number of anthropogenic structures have caused substantial habitat destruction. Despite their detrimental impact, these constructions could play a role in the functioning of coastal ecosystems. The objective of this work was to assess the distribution of juvenile coastal fish along a seascape composed of various natural and artificial habitats in order to determine the potential role of coastal infrastructures as juvenile habitat. We surveyed juvenile populations on various infrastructures and natural sites along a 100 km shoreline of the French Mediterranean coast. Juvenile densities varied according to the level of artificialization of the sites. Densities were the highest on coastal defense structures, intermediate in natural sites and lowest in harbors. Focusing inside harbors revealed highly variable densities depending on the type of habitat, with densities on ripraps or jetties that were equivalent to those of natural sites. Our results underline the importance of anthropogenic structures as potential juvenile habitats, which is too often not considered in management plans.

1. Introduction

Due to an ever growing global population and a general migration to the coast, coastal areas already concentrate more than 60% of the human population while they represent less than 15% of the planet's land surface (EEA, 1999) and this proportion is expected to reach 75% by 2025 (Airoldi and Beck, 2007; Creel, 2003). As a result, the land-sea interface is subject to an unprecedented variety and magnitude of anthropogenic pressures making them particularly vulnerable. This translates into a multitude of consequences such as resource overexploitation, pollution, invasive species and habitat modifications (Crain et al., 2009; Dugan et al., 2011). The latter is known to be one of the greatest threats to marine biodiversity and ecosystems (Coll et al., 2010; Dafforn et al., 2015; Halpern et al., 2008) and is exacerbated by the flourishing number of coastal anthropogenic structures (e.g. harbors, marinas, coastal defense structures such as seawalls, breakwaters, groins, etc.) triggered by urbanization, commerce, industry, tourism and the need to protect the coast from erosion and flooding (Bulleri and Chapman, 2010; Gerland et al., 2014; Scyphers et al., 2015). The main consequence of coastal hardening is that it destroys, transforms or homogenizes the natural seascape mosaic, replacing the original patchiness of heterogeneous subtidal environments by homogenous and often less complex artificial habitats. It has been shown that the reduction of complexity and heterogeneity of seascapes leads to lower abundances and the increased mortality of organisms (August 1983; Brokovich et al., 2006; Fisher et al., 2007). One of the essential functions offered by coastal habitats is their nursery role for marine organisms. The coastal seascape mosaic offers a wide variety of habitats, which provides suitable food and shelter essential for the juvenile stages of many different species (Beck et al., 2001).

Most coastal fish have a complex life cycle composed of two phases, a pelagic and a benthic (Armsworth, 2002; Jones, 1988; Mora and Sale, 2002; Öhman et al., 1998). The former is also known as the dispersive phase in which eggs are released into the water column and then hatch to produce larvae that disperse in open waters. After a period of about one month, during a transition called settlement, the larvae may reach the shore (Di Franco et al., 2013) and become a post-larva that will establish in its new benthic juvenile habitat. Newly settled juveniles will then grow in their juvenile habitat for approximately six months (variable upon taxa) until they reach a size permitting them to avoid

---

[*] Corresponding author. Université de Perpignan Via Domitia, Centre de Formation et de Recherche sur les Environnements Méditerranéens, UMR 5110, Bat.R, 52 Avenue Paul Alduy, 66000, Perpignan, France.
E-mail address: manon.mercader@univ-perp.fr (M. Mercader).

https://doi.org/10.1016/j.marenvres.2018.02.030
Received 15 November 2017; Received in revised form 24 February 2018; Accepted 26 February 2018

Please cite this article as: Mercader, M., Marine Environmental Research (2018), https://doi.org/10.1016/j.marenvres.2018.02.030

most predation (around 8 cm), at which point they actively leave this habitat to recruit into the adult population (Vigliola and Harmelin-Vivien, 2001). The juvenile stage is critical as mortality is great (Houde and Hoyt, 1987; Macpherson et al., 1997; Planes et al., 1999; Vigliola et al., 1998) and the number of individuals that will eventually contribute to the renewal of adult populations is highly dependent of the quality of juvenile habitat. According to Beck et al. (2001), nurseries are habitats that contribute a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other juvenile habitats. The "nursery value" of a given habitat, which is a relative value, results from a combination of four parameters: (1) the initial density of juveniles, (2) their survival rate, (3) their growth rate and (4) their ability to migrate from the juvenile habitat and recruit into adult habitats. As it is logistically difficult to assess parameters (2), (3) and (4), the number of juveniles present in a given habitat at a given time between settlement and recruitment has often been used as a proxy of its nursery value (Cheminée et al., 2017a; Cuadros et al., 2017a; Macpherson and Zika, 1999; Pastor et al., 2013) and permits comparison between sites. Besides, the concept of "effective juvenile habitats" (Dahlgren et al., 2006) brings complementary information. Those habitats are habitats whose densities of juveniles are small, but have a high overall contribution to adult population due to the large surface they might represent in the seascape, which might be the case of coastal anthropogenic structures.

Because the alteration of nursery habitats can have direct adverse effects on juvenile survival and the subsequent maintenance of adult populations, it is of prime importance to identify and localize them in order to focus conservation efforts. Some recent studies have focused on these goals (Cheminée et al., 2013, 2014; Cuadros et al., 2017b) but anthropogenic structures were only slightly taken into consideration. However, structures such as breakwaters have been shown to host high juvenile densities of certain coastal fish (Dufour et al., 2009; Pastor et al., 2013; Pizzolon et al., 2008; Ruitton et al., 2000). Therefore, their potential role as juvenile habitat should not be neglected especially in the context of their growing ubiquity in the coastal seascape.

The main objective of this study was to assess the spatial distribution of juvenile coastal fish in a seascape composed of natural habitats and various anthropogenic structures. This was undergone by working on a relatively large spatial scale (around 100 km of coastline) permitting the inclusion of different artificialized and natural sites. We focused on Mediterranean coastal species settling in shallow heterogeneous rocky habitats. We first compared different levels of artificialization using a snap-shot of juvenile densities found in natural habitats *versus* those present on Coastal Defense Structures (CDS) and inside harbors (i.e. the two most widespread coastal anthropogenic structures in the area). Furthermore, as very little is known about these urban ecosystems despite their universality, we then concentrated inside harbors where we assessed the effect of habitat type on juvenile densities.

2. Material and methods

2.1. Study area and sampling strategy

The study was conducted on the southernmost French Mediterranean coast in the Gulf of Lion (NW Mediterranean). The sampled area stretches from Leucate to Cerbère (at the border between France and Spain) for approximately 100 km. This coast can be divided in two different types of regions, a sandy coast (SC) to the north, and a rocky coast (RC) to the south (Fig. 1-a). The entire study area is included in the Gulf of Lion Natural Marine Park (GLNMP) and encompasses the Cerbère-Banyuls Natural Marine Reserve (CBNMR). Within this area harbors are scattered along the entire studied shoreline and represent around 20 km of shoreline, which is approximately the same amount of linear coast as the RC. Juvenile habitats were identified and measured by the use of aerial images as in Cheminée et al. (2017a, 2017b): identification criteria of juvenile habitats consisted of shallow, protected from strong swell, gently sloping habitats with a heterogeneous substrate consisting of small blocks and rocks. Among the 83 sites identified as potential nurseries, 29 natural sites (Fig. 1-b) and 10 CDS (Fig. 1-c) were randomly chosen for sampling. Additionally, seven harbors (Fig. 1-d) were added to this sampling array, out of the nine present in the study area, for a total of 46 sampled sites. Within each harbor, random samples were performed among the different types of habitat: outer jetty, inner jetty, natural (which can consist of a hard or soft bottom depending on the region), dock (concrete walls) and riprap (see Fig. 1-e to h for description). Each harbor contained between four and five habitat types. Minimums of three replicates were performed for each habitat type in each harbor.

2.2. Studied species

This study focused on species that use the above described heterogeneous rocky and sandy habitats as a nursery ground (Harmelin-Vivien et al., 1995). For the first part of our study, comparing natural, CDS and harbor sites, we considered the following eight species for our surveys as a previous study showed they were present in the study area (Cheminée et al., 2017a) and are strongly affiliated to the studied habitat (Cheminée et al., 2011; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Vigliola, 1998): white seabream (*Diplodus sargus sargus* (Linnaeus, 1758)), sharpsnout seabream (*Diplodus puntazzo* (Walbaum, 1792)), yellowmouth barracuda (*Sphyraena viridensis* (Cuvier, 1829)), ornate wrasse (*Thalassoma pavo* (Linnaeus, 1758)), dusky grouper (*Epinephelus marginatus* (Lowe, 1834)), zebra seabream (*Diplodus cervinus* (Lowe, 1838)), red porgy (*Pagrus pagrus* (Linnaeus, 1758)) and common dentex (*Dentex dentex* (Linnaeus, 1758)). In the second part of our study, we focused within harbors and as very little is known about juvenile assemblages in those infrastructures, we decided to extend our selection for those sites. We considered all observed species with the exception of those forming large mobile schools (eg. *Sarpa salpa*, *Pagellus* spp.) and those of the labrid family (only *T. pavo* is included as it is part of the original sampling list of species) as the youngest individuals are hard to observe and might require a different sampling procedure. The sampled species for each part of the study are recorded in Table 1.

2.3. Sampling procedure

Sampling was performed according to the widely used Underwater Visual Census (UVC) protocols (Harmelin-Vivien et al., 1985). Trained and inter-calibrated divers snorkeled along the coast at a slow and steady pace and identified, counted, and estimated the size of juvenile individuals from any of the target species along a 1 m wide belt transect parallel to the coast. Transects were defined on a waterproof map depicting the coastline so divers knew were to begin and stop their transects. Observations were recorded on the same map, which also provided examples of different juvenile sizes (in increments of 5 mm) to aid in size estimations. We used 5 mm size classes to estimate Total Length (TL). Which is consistent with a previous study that estimated the precision of such underwater size estimation to be of ± 3.5 mm (Macpherson, 1998). For most rocky reef fishes in the Mediterranean, size at settlement is around 10 mm TL (Cheminée et al., 2013; Crec'hriou et al., 2015; Garcia-Rubies and Macpherson, 1995). The smallest specimens of the taxa studied were considered newly settled individuals. Our visual censuses took into account only the young of the year (YoY or y0 individuals), which might be newly settled individuals (for species settling during spring and summer) or individuals having settled a few months prior (for species settling during fall and winter) (maximum sizes retained for each species are available in supplementary material 1).

Sampling was performed during the last two weeks of July 2015 and 2016 which corresponds to one or two months after the known settlement or post-settlement periods of many Mediterranean species

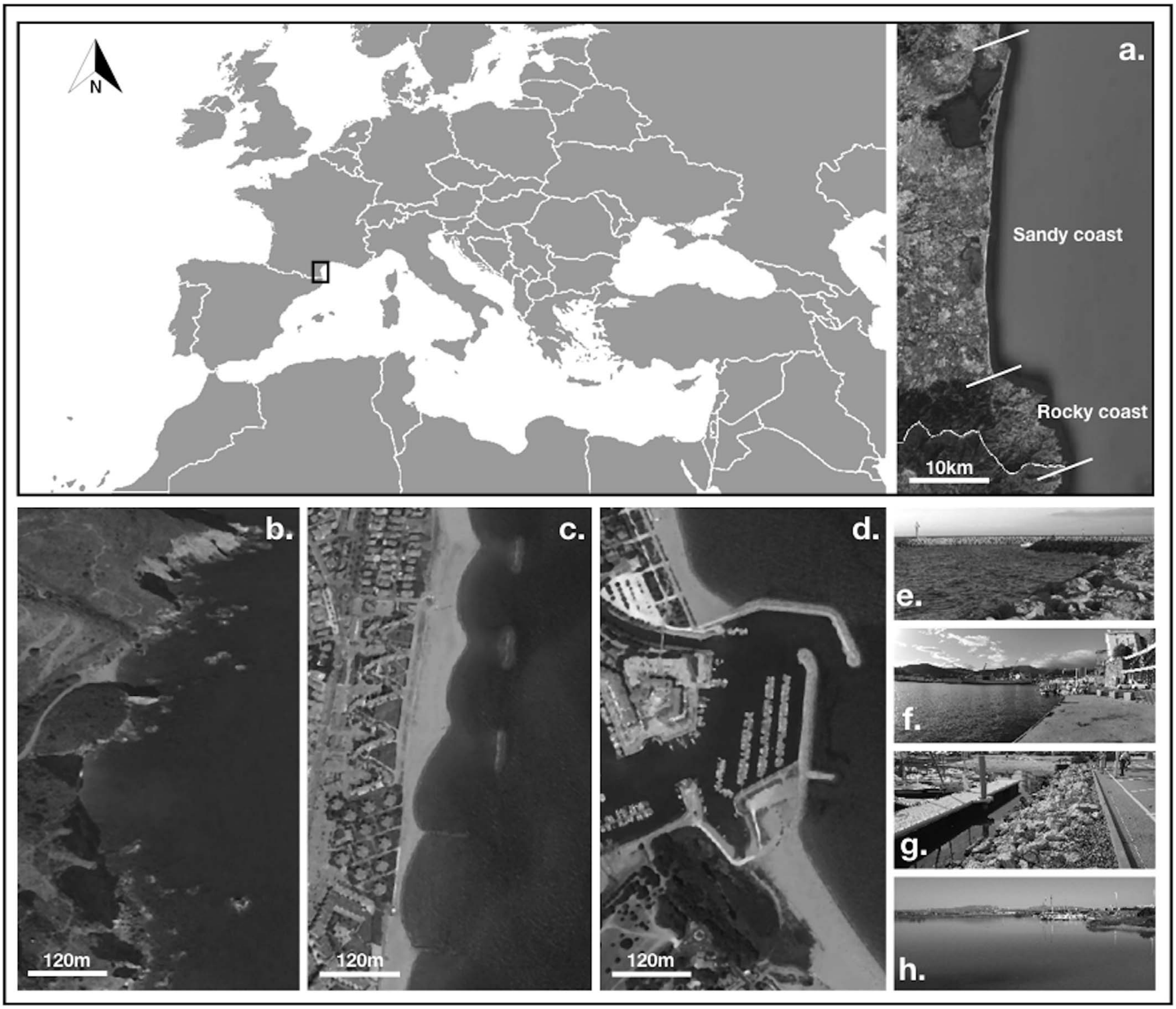

Fig. 1. (a.) Location of the study area in the Northwestern Mediterranean and delimitation of the two regions (rocky and sandy coasts noted respectively RC and SC). Examples of (b.) natural site, (c.) coastal defense structures (CDS), (d.) harbor. Examples of the different habitat types, (e.) jetties, (f.) dock, (g.) riprap and (h.) natural.

Table 1
Species considered for sampling in all sites (natural, CDS and harbors) and for the focus within harbors.

	all sites	within harbors
Chromis chromis		+
Dentex dentex	+	+
Dicentrarchus labrax		+
Diplodus annularis		+
Diplodus cervinus	+	+
Diplodus puntazzo	+	+
Diplodus sargus	+	+
Diplodus vulgaris		+
Epinephelus marginatus		+
Mullus sp.		+
Oblada melanura		+
Pagrus pagrus	+	+
Sparus aurata		+
Sphyraena viridensis	+	+
Spondyliosoma cantharus	+	+
Thalassoma pavo	+	+

(Crec'hriou et al., 2015; García-Rubies and Macpherson, 1995; Raventos and Macpherson, 2001). In this context, we can consider that the main part of the total observed individuals will integrate into the local population and provides a snapshot of the future recruitment as most of the mortality as already occurred (Macpherson and Zika, 1999). Sampling days with rough seas and poor visibility were avoided.

2.4. *Study design and data analysis*

To test the influence of the level of artificialization of the habitat on response variables describing juvenile assemblages, three different levels of artificialization were defined (in increasing order of modification and loss of 3D structure): natural sites (high structural complexity), which consist of unmodified rocky areas composed of small bays and small boulder beaches with shallow waters interspersed with steeper portions (for the SC such habitat is found at the northern most of the sampling area), CDS, and highly modified harbors. For the most abundant species, we analyzed the variability of response variables

Table 2
Sampled area, species richness and taxa-specific abundances in sampled natural sites, CDS and harbors in 2015 and 2016.

Sampled area in m^2	2015								2016								**Total**
	Rocky coast			Sandy coast			**Total**	**Total**	Rocky coast			Sandy coast			**Total**	**Total**	
	Natural	Harbor	**Total**	Natural	CDS	Harbor			Natural	Harbor	**Total**	Natural	CDS	Harbor			
	12324	589	**12913**	1695	1670	11550	**14915**	**27828**	9506	5289	**14796**	1484	1985	11598	**15067**	**29863**	**57691**
Richness	**5**	**4**	**6**	**3**	**5**	**5**	**5**	**7**	**6**	**3**	**5**	**3**	**4**	**4**	**5**	**7**	**8**
Dentex dentex	–	3	**3**	–	1	2	**3**	**6**	–	–	**-**	1	5	3	**9**	**9**	**15**
Diplodus cervinus	–	–	**-**	–	1	1	**2**	**2**	3	–	**3**	–	–	–	**-**	**3**	**5**
Diplodus puntazzo	68	78	**146**	1	6	86	**93**	**239**	103	29	**132**	11	10	139	**160**	**292**	**531**
Diplodus sargus	1210	259	**1469**	976	1514	1857	**4347**	**5816**	4559	860	**5419**	3349	11026	8887	**23262**	**28681**	**34497**
Epinephelus marginatus	1	–	**1**	–	–	–	**-**	**1**	–	–	**-**	–	–	–	**-**	**-**	**1**
Pagrus pagrus	–	–	–	–	–	–	**-**	**-**	1	–	**1**	–	18	–	**18**	**19**	**19**
Sphyraena viridensis	213	30	**243**	85	50	34	**169**	**412**	29	13	**42**	–	–	17	**17**	**59**	**471**
Thalassoma pavo	2	–	**2**	–	–	–	**-**	**2**	5	–	**5**	–	–	–	**-**	**5**	**7**
Total	**1494**	**370**	**1864**	**1062**	**1572**	**1980**	**4614**	**6478**	**4700**	**902**	**5602**	**3361**	**11059**	**9046**	**23466**	**29068**	**35546**

(species composition, taxa-specific densities and mean size) according to the following model with three fixed factors: "year" (with two levels: 2015 and 2016), "region" (with two levels: RC and SC) and "artificialization level" (with two levels on the RC (natural and harbor) and three levels on the SC (natural, CDS and harbor)). Replication units used for this model were the entire sites (i.e. the whole cove, CDS or harbor, with each site representing one continuous transect). Sites were replicated for each combination of the three forcing factors (year x region x artificialization, the total sampled area for each combination is given in Table 2). Abundance data was then divided by the sampling area of each site (ranging from 123 m to 4646 m) to obtain comparable densities (expressed in ind./10 m^2).

The degree of openness of a bay is known to have an effect on juvenile fish densities (Cuadros et al., 2017a). Thereby, for our data sampled among habitats inside the harbors, the distance to the entrance of the harbor might affect the distribution of juveniles. Indeed, all habitats were not situated at equal distance from the entrance (see supplementary material 2), which might confound the results. Consequently, a second model was used to test the relative effect of distance from the entrance and habitat type within harbors on the same response variables. Replication units were transects of each habitat type with three to nine transects per habitat type per harbor (lengths between 14 m and 446 m) and the data was expressed in ind./10 m^2 as previously noted. Similar to the first model, we used three fixed factors: "year" (with two levels: 2015 and 2016), "region" (with two levels: RC and SC) and "habitat" (with five levels: outer jetty, inner jetty, natural, dock and riprap). In this model, we added distance from entrance as a covariate in order to disentangle the variability of the response variables due to both factors (habitat and distance). Distances were estimated (to the nearest meter) on Google Earth (version 7.1.2.2041) by tracing the shortest possible path between the entrance and the middle of each transect.

As our data did not follow normal distribution and our designs were unbalanced and contained interactions of factors, we used permutational MAN(C)OVAs, ANOVAs and AN(C)OVAs. Permutation tests were used because they can handle this kind of complex design and have no assumption on data distribution as long as observational units might be exchangeable (Anderson, 2001). Analyses were performed on Euclidian distance matrixes for the univariate total and taxa-specific densities and TL and on Bray-Curtis dissimilarity matrixes for the multivariate assemblage composition with the addition of a dummy variable. P-values were calculated by 999 random permutations of residuals under a reduced model and Type III sum of square (Anderson, 2001) for the first model. For the second model, Type I sum of square was used and covariate was introduced in the first place into the model (without including the interaction terms between covariate and factor). It allowed the assessment of the variations in the response variable(s) that are due to variations in the covariate, prior to test the putative effects of other factors (Anderson et al., 2008). The order of factors was defined as follows: Distance (covariate), Habitat, Region, Year and their interactions Region*Habitat, Year*Habitat, Year*Region and Year*Region*Habitat. The Monte-Carlo test was used when less than 200 permutations were generated. Post-hoc pairwise tests were performed on all designs obtaining significant results from the global tests.

SIMPER analyses were conducted when PERMANOVAs on species composition were significant in order to determine the relative contribution of each taxa to differences between groups of samples. The significance level was consistently set at a level of 0.1 for all tests due to the intrinsic variability of ecological data. All statistical analyses were performed using PRIMER 6 software with the PERMANOVA add-on (Clarke and Gorley, 2006; Clarke et al., 2014) and R software (R version 3.0.3- Rstudio Version 0.99.486) using the ggplot library (Wickham, 2009).

3. Results

3.1. Effect of the artificialization level (natural, CDS and harbor sites)

Although all eight studied species were observed, there were large disparities in abundances with *Diplodus sargus* being by far the most numerous species while some others were very rare. This was the case of the dusky grouper (one surveyed individual), the zebra seabream (five individuals) and the ornate wrasse (seven individuals) (Table 2). A PERMANOVA on species composition showed there were significant differences in juvenile composition according to the three interactions Year*Region (p-value = 0.003), Year*Anthropization level (p-value = 0.001) and Region* Anthropization level (p-value = 0.003) and SIMPER analysis confirmed that *D. sargus,* was responsible for almost all the observed dissimilarity and similarities between and among the tested factors (always more than 80%). Accordingly, we present the results for this species as well as for *D. puntazzo* and *S. viridensis* as they were present in large enough number to run the analysis. Analyses were not run for the other five species since less than 20 individuals were observed for both years pooled. However, we noted that while *D. dentex* and *D. cervinus* were present both years in both regions, *P. pagrus* was observed only in 2016 and almost exclusively on the RC, *T. pavo* was observed only on the RC both years and the unique observation of *E. marginatus* happened in 2015 on the RC as well (Table 2).

Concerning *D. sargus* there was a significant Year*Artificialization level interaction (Table 3) with densities in harbors being the lowest for both years. Natural sites and CDS did not differ in 2015, but in 2016

Table 3
Results of the univariate 3-way PERMANOVAs tests performed to compare *D. sargus* and *S. viridensis* densities (ind./10 m^2) between Years (2015, 2016), Regions (RC and SC) and Artificialization levels (natural, CDS and harbor). df and MS respectively degree of freedom and Mean square. Significance = °p ≤ 0.1; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

Source	df	MS	Pseudo-F	P(perm)	
***D. sargus* density**					
Year	1	50.6650	51.549	0.001	
Region	1	9.15260	9.3123	0.008	***
Artificialization level	2	21.5000	21.875	0.001	**
Ye*Re	1	2.88460	2.9349	0.088	***
Ye*Art	2	12.3540	12.57	0.001	°
Re*Art	1	3.03460	3.0875	0.082	***
Ye*Re*Art	1	0.61258	0.45966	0.418	°
Res	80	0.98285			
Total	89				
***S. viridensis* density**					
Year	1	0.01090	7.74	0.009	
Region	1	0.00508	3.60	0.077	**
Artificialization level	2	0.00523	3.71	0.053	°
Ye*Re	1	0.00575	4.08	0.060	°
Ye*Art	2	0.00506	3.59	0.056	°
Re*Art	1	0.00724	5.13	0.045	°
Ye*Re*Art	1	0.00809	5.74	0.043	*
Res	80	0.00141			*
Total	89				

CDS hosted significantly higher densities (Fig. 2-a). For all three artificialization levels, the densities in 2016 were significantly higher than in 2015 (pairwise tests, p-value = 0.002, p-value = 0.025 and p-value = 0.001 for natural, harbor and CDS respectively). The Region*Artificialization level interaction was also significant (Table 3), however this significant interaction might result from the absence of CDS on the RC as in both regions harbors hosted significantly lower densities than natural sites. On the SC naturals sites and CDS did not differ one from the other (Fig. 2-b). The effect of region varied depending on the year with a significant Year*Region interaction (Table 3). *D. sargus* densities were higher on the SC than on the RC for both years but this difference was of a greater amplitude in 2016 (pairwise tests, p-value = 0.009 in 2015 and p-value = 0.026 in 2016) and they were significantly higher in 2016 than in 2015 for both regions (pairwise tests, p-value = 0.001 on the RC and p-value = 0.002 for the SC) (Fig. 2-c).

D. sargus mean TL was significantly different depending on the year and the artificialization level (PERMANOVA, p-value = 0.001 and p-value = 0.003 respectively). Individuals were bigger in 2015 than in 2016 (pairwise test, p-value = 0.001) and in harbors than in natural sites or CDS (pairwise test, p-value = 0.001 and p-value = 0.009 respectively) (supplementary material 3).

D. puntazzo was the second most abundant species but its contribution to dissimilarity between artificialization levels was very low and its densities differed only according to the year factor (PERMANOVA, p-value = 0.09) with higher densities in 2015.

As the second contributor to dissimilarity and the third most abundant species *S. viridensis* showed densities that varied significantly according to the triple interaction Year*Region*Artificialization level (Table 3). For both regions and either year, no significant difference was observed between artificialization levels. However, densities were significantly higher in 2015 than 2016 for the natural sites of the RC and the CDS of the SC. In 2015, the densities of natural sites were significantly higher on the SC than on the RC (pairwise tests, p-value = 0.037) while no significant difference was observed for the harbor sites. In 2016, there was no significant difference between the two regions for either the natural or harbor sites (Fig. 2-d).

The size of *S. viridensis* differed according to the Year*Artificialization level and Year*Region interactions (PERMANOVA, p-value = 0.001 and p-value = 0.003 respectively). There was no significant difference in size between the different artificialization levels in 2015 but in 2016 observed individuals in harbors had a longer average TL than those of natural site (pairwise tests, p-value = 0.003) (no observations were made on CDS). Concerning differences between regions, there was no difference between regions in 2015 but juveniles were bigger on the RC in 2016 (pairwise tests, p-value = 0.001). Globally, individuals were longer in 2015 than 2016 but this difference was significant only for natural sites and the RC (pairwise tests, p-value = 0.03 and 0.041 respectively) (Supplementary material 4).

3.2. Focus on the inside of harbors: effect of habitat type

After looking at the effect of the artificialization level, we then focused on within harbor variations according to habitat type. In total, 12 species were observed, with a maximum of 10 species and a minimum of four per habitat, region and year (Table 4).

3.2.1. Species composition

Distance to the entrance of the harbor significantly influenced species composition. Moreover, independently from distance to entrance, composition varied significantly according to the triple interaction Year*Region*Habitat (Table 5). In both regions and for both years, the main differences in assemblages were observed for outer and inner jetties, which differed significantly from most of the other habitats, while those habitats showed only some differences between them that varied depending on the year and the region.

This variability in assemblages is corroborated by the SIMPER analysis, which showed a relatively low level of similarity (< 29%) among a same habitat and a relatively high level of dissimilarity (> 74%) between habitats. *D. sargus* was always the main contributor to dissimilarity between habitats (> 40%) followed by *D. vulgaris*, *Mullus* sp., *D. labrax*, *O. melanura* and *D. puntazzo* in different orders depending on the combination of tested habitats. Regions also showed a high level of dissimilarity (83.37%) mainly due to *D. sargus* (47.54%) and to a lesser extent to the above-cited species. Both regions exhibited relatively low levels of similarity (20.74% for the RC, 21.33% for the SC). The same pattern was observed between years with similarity being higher for 2016 than 2015 (25.89% and 14.77% respectively), and the same species were responsible for the dissimilarity, which was rather high (82.38%).

3.2.2. Taxa-specific densities

Since they were the main contributors to the dissimilarity between habitats, regions and years, variations in taxa-specific densities for *D. sargus*, *D. vulgaris*, *Mullus* sp., *D. labrax*, *O. melanura* and *D. puntazzo* were analyzed.

D. sargus and *O. melanura* showed similar patterns (Fig. 3-a and b) with densities that were significantly influenced by distance from the entrance and significantly differed according to the triple interaction Year*Region*Habitat (Table 5) once controlled for the effect of the covariate.

For *D. sargus*, the effect of habitat was different between the regions with densities being significantly higher on jetties and ripraps on the SC while on the RC the higher densities were hosted by natural habitats and ripraps (Fig. 3-a). As a mean of comparison, it should be noted that densities observed on outer jetties in 2016 were higher than those observed in natural sites outside of the harbors on the same coast (respectively 33.9 ± 11.3 ind./10 m^2 and 29.7 ± 11.1 ind./10 m^2, cf. above part about artificialization level). Densities on outer and inner jetties of the SC were significantly higher than on the RC and those on natural habitats significantly higher on the RC than on the SC. The effect of habitat and region was, however, relatively consistent between years (Fig. 3-a). Globally, densities were higher in 2016 than in 2015 (significantly for all habitats on the SC, for natural and docks only on the RC).

Densities of *O. melanura* were variable depending on the year and

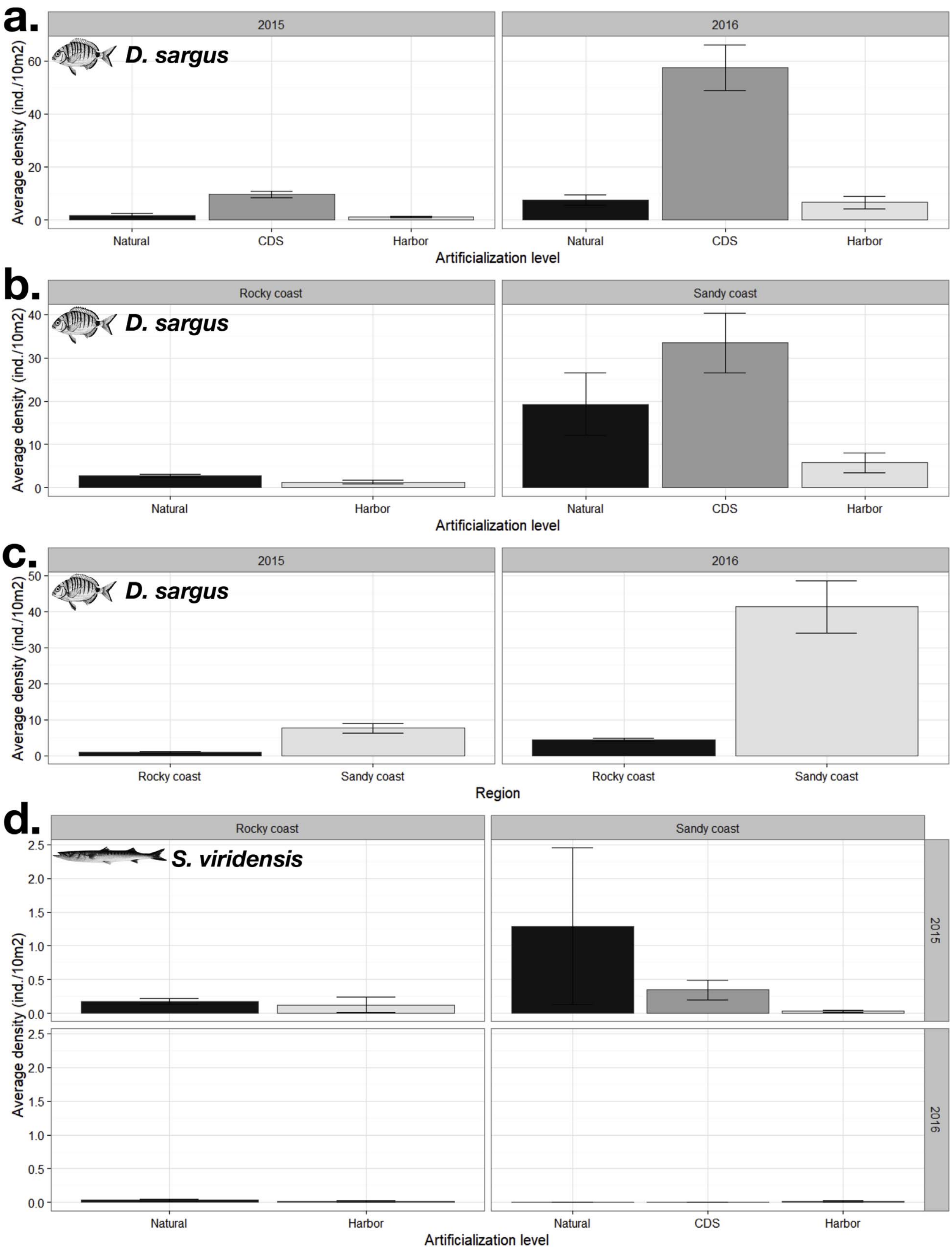

Fig. 2. Mean taxa-specific densities expressed in number of individuals per 10 m^2 for (a.) *D. sargus* according to Year and Artificialization level, (b.) Region and Artificialization level, (c.) Year and Region and for (d.) *S. viridensis* according to Year, Region and Anthropizaton level. Error bars = standard error. Lowercase characters give pairwise results: treatments sharing at least one character do not differ significantly. Note that the y-axis scales vary between graphs.

Table 4
Sampled area, species richness and taxa-specific abundances in sampled habitat type within harbors in 2015 and 2016 on the rocky and sandy coasts.

Sampled area in m^2	2015												
	Rocky coast						Sandy coast						Total
	Outer jetty	Inner jetty	Natural	Dock	Riprap	**Total**	Outer jetty	Inner jetty	Natural	Dock	Riprap	**Total**	
	702	404	1344	2469	371	**5289**	2238	1558	680	3962	2968	**11409**	**16696**
Richness	**6**	**6**	**8**	**8**	**6**	**11**	**10**	**9**	**4**	**10**	**9**	**11**	**11**
Chromis chromis	15	35	-	513	-	**563**	7	-	-	1	-	**8**	**571**
Dentex dentex	1	-	1	-	1	**3**	2	-	-	-	-	**2**	**5**
Dicentrarchus labrax	-	-	-	8	31	**39**	3	81	3	91	431	**609**	**648**
Diplodus annularis	1	-	-	-	-	**1**	-	23	-	15	4	**42**	**43**
Diplodus puntazzo	10	2	20	36	10	**78**	57	12	-	9	8	**86**	**164**
Diplodus sargus	-	2	108	116	33	**259**	765	535	1	78	482	**1861**	**2120**
Diplodus vulgaris	17	18	53	32	39	**159**	309	221	4	33	135	**702**	**861**
Mullus sp	-	2	2	6	11	**21**	146	283	19	98	149	**695**	**716**
Oblada melanura	11	210	93	45	-	**359**	642	82	-	10	6	**740**	**1099**
Sparus aurata	-	-	1	-	-	**1**	44	10	-	10	4	**68**	**69**
Sphyraena viridensis	-	-	6	24	-	**30**	11	15	-	1	7	**34**	**64**
Spondyliosoma cantharus	-	-	-	-	-	**-**	-	-	-	-	-	**-**	**0**
Total	**191**	**322**	**284**	**800**	**151**	**1748**	**2255**	**1276**	**27**	**348**	**1226**	**5132**	**6880**

Sampled area in m^2	2016													Total
	Rocky coast						Sandy coast						Total	
	Outer jetty	Inner jetty	Natural	Dock	riprap	**Total**	outer jetty	inner jetty	natural	dock	riprap	Total		
	702	404	1344	2469	371	**5289**	2238	1558	680	3962	2968	**11409**	**16696**	
Richness	**4**	**4**	**5**	**8**	**6**	**8**	**10**	**9**	**5**	**7**	**9**	**11**	**11**	**12**
Chromis chromis	-	-	-	-	-	**-**	-	-	-	-	-	-	**-**	**571**
Dentex dentex	-	-	-	-	-	**-**	1	1	-	-	1	3	**3**	**8**
Dicentrarchus labrax	-	-	-	3	21	**24**	16	41	13	35	262	367	**391**	**1039**
Diplodus annularis	-	-	-	-	-	**-**	-	3	-	12	5	20	**20**	**63**
Diplodus puntazzo	3	4	9	6	7	**29**	21	18	1	45	57	142	**171**	**335**
Diplodus sargus	42	75	297	298	148	**860**	3302	2426	59	473	2628	8888	**9748**	**11868**
Diplodus vulgaris	22	35	80	109	15	**261**	220	242	6	75	115	658	**919**	**1780**
Mullus sp	13	32	33	51	49	**178**	109	373	28	130	378	1018	**1196**	**1912**
Oblada melanura	-	-	-	3	12	**15**	88	-	-	-	-	88	**103**	**1202**
Sparus aurata	-	-	-	-	-	**-**	5	3	-	-	3	11	**11**	**80**
Sphyraena viridensis	-	-	11	2	-	**13**	17	-	-	-	-	17	**30**	**94**
Spondyliosoma cantharus	-	-	-	2	-	**2**	7	5	-	1	1	14	**16**	**16**
Total	**195**	**842**	**537**	**624**	**348**	**2546**	**4020**	**3551**	**107**	**800**	**3705**	**12183**	**14729**	**21609**

region. On the RC, in 2015, the highest densities were found on inner jetties followed by natural habitat, while there were found on ripraps in 2016. On the SC, in 2015 jetties hosted the higher densities and ripraps the lowest but there was no difference between habitats in 2016 (Fig. 3-b).

The densities of *D. vulgaris* were also significantly influenced by the covariate but varied significantly according to the double interaction Region*Habitat (Table 5). On the RC, densities were slightly different according to habitat type, one habitat always showing similar densities to at least two others. On the SC, jetties hosted the highest densities and docks the lowest with the other habitats being intermediate (Fig. 3-c). Concerning the differences between regions, outer and inner jetties hosted significantly higher densities on the SC, while natural habitats and docks of the RC hosted higher densities than those of the SC.

The distance from the entrance of harbor did not influence densities of *D. puntazzo*, which significantly differed only according to the Ye*Re interaction (Table 5). In 2015, densities were higher on the RC than on the SC, while there was no significant difference in 2016. On the RC, there was significantly more *D. puntazzo* in 2015 than in 2016, while it was the contrary for the SC with higher densities in 2016.

Similar to *D. puntazzo*, the distance to the entrance had no significant effect on *D. labrax* densities. Habitat was the only factor having a significant effect for this species (Table 5). Densities were significantly higher on ripraps than on docks, natural habitats and outer jetties (Fig. 3-d).

For *Mullus* sp., densities were significantly influenced by the distance to the entrance covariate and differed according to the Region*Habitat and Year*Habitats interactions (Table 5). On the RC, the pattern was similar to the one observed for *D. vulgaris* with densities which slightly differed according to habitat type, one habitat always showing similar densities to at least two others. On the SC, densities were the highest on inner jetties and the lowest on natural habitats and docks (Fig. 3-e). In 2015, densities on natural habitats and docks were significantly lower than those on inner jetties and ripraps. The same kind of pattern was observed in 2016 with significantly higher densities on inner jetties and ripraps than on natural habitats, docks and outer jetties (Fig. 3-f).

4. Discussion

Our results showed that human infrastructures such as harbors and CDS were used as juvenile habitats by certain coastal species typically settling on heterogeneous shallow rocky habitats, notably, during our sampling period, the white seabream *D. sargus*. The densities of juveniles were variable between regions and years but globally the highest on CDS (*versus* harbors and even natural sites). The densities found in harbors were lower than on CDS and natural sites but still not negligible as they represented between 50% and 90% of those in natural sites. They were also variable according to the type of habitat within the harbor with the least complex docks hosting the lowest densities.

4.1. Anthropogenic structures as a habitat opportunity for juveniles

This study showed contrasting densities of juveniles according to artificialization level but also a strong effect of the region factor with surprisingly higher mean densities on the SC. It would have been expected that the RC would host the highest densities as it displays more abundant natural habitat for the studied juveniles (shallow heterogeneous rocky habitat). However, this result is consistent with previous studies that found higher *D. sargus* densities on the SC or on CDS (Cheminée et al., 2017a; Pastor et al., 2013). Indeed, in this study, CDS hosted higher juvenile densities than natural and port sites, which might explain the differences between regions (CDS being absent of the RC). Nonetheless, Cheminée et al. (2017a) hypothesized that differences between regions were not due to what they named "habitat type" (here referred as artificialization level), because high densities were

Table 5
Results of the uni- and multi-variate 3-way PERMANOVAs tests performed to compare fish species composition, *D. sargus, D. vulgaris, O. melanura, D. puntazzo, Mullus* sp. and *D. labrax* densities (ind./10 m^2) between Years (2015, 2016), Regions (RC and SC) and Habitat type within harbor (outer jetty, inner jetty, riprap, natural and dock). df and MS respectively degree of freedom and Mean square. Significance = °p ≤ 0.1; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

Source	df	SS	MS	Pseudo-F	P(perm)	
Assemblages						
Distance	1	30862	30862	24.673	0.001	***
Habitat	4	48563	12141	9.7061	0.001	***
Region	1	21271	21271	17.005	0.001	***
Year	1	27406	27406	21.91	0.001	***
Re*Hab	4	49774	12444	9.9482	0.001	***
Ye*Hab	4	14552	3638.1	2.9086	0.001	***
Ye*Re	1	4806.9	4806.9	3.843	0.003	**
Ye*Re*Hab	4	7497	1874.2	1.4984	0.54	°
Res	245	3.06E+05	1250.8			
Total	265	5.11E+05				
Dicentrarchus labrax						
Distance	1	1.2864	1.2864	0.96816	0.347	
Habitat	4	46.194	11.548	8.6913	0.001	***
Region	1	3.6269	3.6269	2.7296	0.102	
Year	1	0.54425	0.54425	0.4096	0.571	
Re*Hab	4	2.8104	0.7026	0.52878	0.687	
Ye*Hab	4	1.1227	0.28066	0.21123	0.947	
Ye*Re	1	5.48E-02	5.48E-02	4.12E-02	8.49E-01	
Ye*Re*Hab	4	0.74955	0.18739	0.14103	0.97	
Res	245	325.54	1.3287			
Total	265	381.93				
Diplodus puntazzo						
Distance	1	1.07E-02	0.010690	0.20395	0.641	
Habitat	4	4.00E-02	0.009999	0.19077	0.951	
Region	1	0.23519	0.235190	4.4872	0.045	*
Year	1	2.59E-04	0.000259	4.95E-03	9.38E-01	
Re*Hab	4	0.37617	0.094043	1.7942	0.126	
Ye*Hab	4	0.30613	0.076532	1.4601	0.197	
Ye*Re	1	0.25845	0.258450	4.9309	0.033	*
Ye*Re*Hab	4	0.3219	0.081547	1.5558	0.184	
Res	242	12.684	0.052414			
Total	262	14.237				
Diplodus sargus						
Distance	1	1261.8	1261.8	9.2044	0.002	**
Habitat	4	3029.7	757.43	5.525	0.001	***
Region	1	1927.9	1927.9	14.063	0.001	***
Year	1	3351.1	3351.1	24.444	0.001	***
Re*Hab	4	3199.4	799.84	5.8344	0.002	**
Ye*Hab	4	2812.9	703.23	5.1297	0.001	***
Ye*Re	1	1152.9	1152.9	8.4095	0.004	**
Ye*Re*Hab	4	1931.5	482.87	3.5222	0.007	**
Res	243	33313	137.09			
Total	263	51980				
Diplodus vulgaris						
Distance	1	14.942	14.942	35.684	0.001	***
Habitat	4	12.336	3.084	7.37E+00	0.001	***
Region	1	0.77285	0.77285	1.8457	0.181	
Year	1	1.20E-02	1.20E-02	2.87E-02	0.854	
Re*Hab	4	11.844	2.961	7.0714	0.001	***
Ye*Hab	4	1.02	0.25499	0.60897	0.667	
Ye*Re	1	0.24587	0.24587	0.58719	0.459	
Ye*Re*Hab	4	1.1433	0.28583	0.68261	0.603	
Res	245	102.59	0.41873			
Total	265	144.91				
Mullus sp.						
Distance	1	4.2944	4.2944	5.8334	0.012	
Habitat	4	33.851	8.4629	11.496	0.001	
Region	1	8.4396	8.4396	11.464	0.003	
Year	1	8.3626	8.3226	11.36	0.001	
Re*Hab	4	9.1139	2.2785	3.095	0.018	
Ye*Hab	4	6.2626	1.5657	2.1267	0.072	
Ye*Re	1	1.6747	1.6747	2.2749	0.14	
Ye*Re*Hab	4	0.99414	0.24853	0.3376	0.859	

(continued on next page)

Table 5 *(continued)*

Source	df	SS	MS	Pseudo-F	P(perm)	
Res	245	180.36	0.73617			
Total	265	253.36				
Oblada melanura						
Distance	1	37.835	37.835	11.18	0.002	**
Habitat	4	50.963	12.741	3.7647	0.012	*
Region	1	2.532	2.532	0.74817	0.407	
Year	1	37.58	37.58	11.104	0.001	***
Re*Hab	4	75.172	18.813	5.559	0.004	**
Ye*Hab	4	72.172	18.043	5.3314	0.001	***
Ye*Re	1	2.4221	2.4221	0.71569	0.435	
Ye*Re*Hab	4	59.526	14.882	4.3972	0.002	**
Res	245	829.16	3.3843			
Total	265	1167.4				

observed for both CDS and natural sites on the SC. Their study was led on data surveyed only in 2015 and in the present study we also obtained no significant difference between CDS and natural sites for this year. However, there was a significant difference in 2016 suggesting that the effect of "habitat type" (i.e. artificialization level) might depend on settlement intensity, which was much higher in 2016. CDS would then be of a particular importance as nursery habitat in years of high settlement. It might be possible that when larval inputs are high, and natural habitats are saturated, CDS are then furnishing an alternative habitat. Even if they might be of lower quality (which is to be assessed), this anthropogenic structures may increase the adult stock by providing more juvenile habitat, especially in areas where nursery habitat is limited (such as the sandy coast) (Sundblad et al., 2014). The SC is characterized by long stretches of sandy bottom; therefore a concentration of individuals on the smaller amount of available habitat might then explain such higher densities. Settlement would thereby be limited by the availability of suitable habitat (Holbrook and Schmitt, 2002; Holbrook et al., 2000; Sale et al., 2005; Schmitt and Holbrook, 2000). However, the study by Cheminée et al. (2017a) cited above demonstrated that when multiplied by the total area of available nursery and standardized by the total area of the region, densities are still higher on the SC. A better survival rate on CDS could also be an explanation for this discrepancy between coasts. The very high mortality rate of settlers and juveniles is essentially due to predation pressure and food availability (Houde and Hoyt, 1987; Macpherson et al., 1997; Planes et al., 1999; Vigliola et al., 1998). It is also known that adult fish and benthic assemblages on this kind of structure are different than those on natural rocky shores (Clynick et al., 2008; Fowler and Booth, 2013; Lam et al., 2009; Moschella et al., 2005; Perkol-Finkel and Benayahu, 2004; Rilov and Benayahu, 2000). Predation pressure as well as food availability and quality might then differ between the two coasts inducing differences in mortality rate. However, our sites were selected in areas with similar fishing regulation and thus similar fishing pressure on predators or competitors. Consequently, another hypothesis, and maybe the most likely, is a difference in larval flux, the input being much higher on the SC. Hydrologic conditions at the regional scale have a determinant effect on the settlement success of juveniles along the coast through the dispersal and survival of the planktonic larvae (Hindell et al., 2003; Pineda et al., 2010; Roy, 1998). In the studied area, the dominant current (liguro-provençal current) goes from the northeast to the southwest and might bring with it larvae (Guizien et al., 2006; Pastor, 2008), which could then first settle on the northern nurseries of the SC. This would lead to a higher larval input on the SC

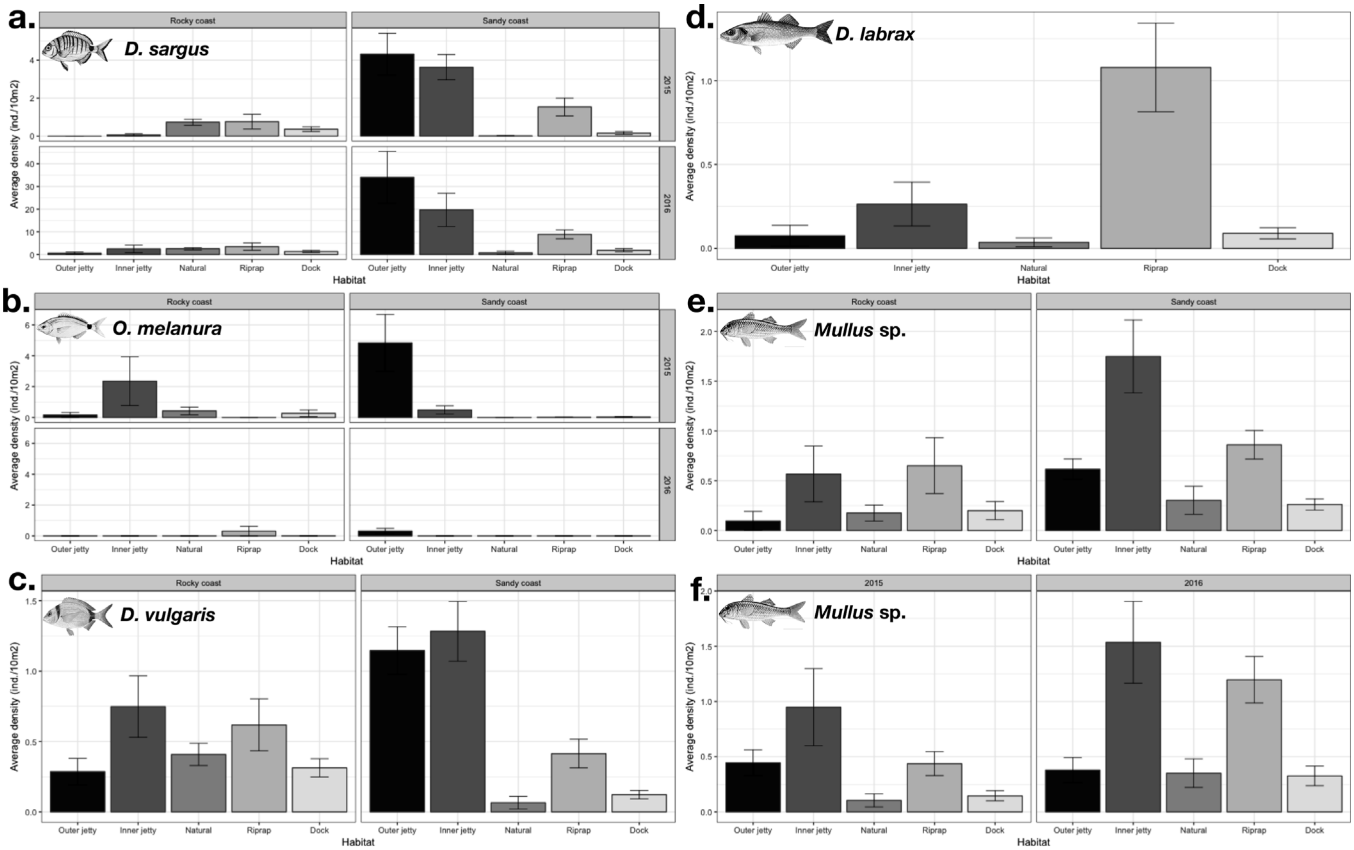

Fig. 3. Mean taxa-specific densities expressed in number of individuals per 10 m^2 for (a.) *D. sargus* and (b.) *O. melanura* according to Year, Region and Habitat type, (c.) for *D. vulgaris* according to Region and Habitat type, (d.) for *D. labrax* according to Habitat type and (e.) and (d.) for *Mullus* sp. according to Region and Habitat type and Year and Habitat type respectively. Error bars = standard error. Lowercase characters give pairwise results: treatments sharing at least one character do not differ significantly. Note that the y-axis scales vary between graphs and that presented densities are not corrected for the effect of the distance from the entrance of harbor, while the pairwise tests do.

and an impoverished larval flow to the RC (Pastor, 2008). CDS are also more "exposed" (-*census* (Cuadros et al., 2017a)) and so more accessible to the larvae, which can favor settlement. On the other hand, harbors are usually very enclosed, which might limit larval flow inside those infrastructures.

The presence of juvenile fish within harbors has already been documented (Bouchoucha et al., 2016; Clynick, 2006, 2008; Dufour et al., 2009; Mercader et al., 2017) but comparison of the observed densities with nearby natural sites is very often lacking, preventing the assessment of their potential nursery role. Here, we compared the densities in harbors with those of natural sites and CDS and found that if juvenile fish do settle in harbors; the densities observed are lower than those of the other sites (CDS and natural). In 2015, *D. sargus* densities in harbors were about 50% of those of natural sites and 15% of those of CDS. In 2016, when settlement was much higher, those proportions were different with densities in harbors representing almost 90% of those of natural sites (although still significantly different) but an even smaller proportion of CDS (densities in natural sites representing only 13% of those on CDS). These results suggest that, like CDS, the use of harbors as juvenile habitat is in part dependent on the intensity of settlement. On years of important larvae flux, the number of larvae arriving at the coast might be significant enough to allow some of them to arrive inside harbors despite their low accessibility. Lower densities inside harbors could also be explained by post-settlement processes influenced by higher levels of anthropogenic pressures. Indeed, pollution potentially caused by the presence of hydrocarbons, organic pollutants, anti-fouling paint and heavy usage as well as sound pollution are known to have adverse effects on juvenile survival and growth rates (Kerambrun et al., 2012; Marchand et al., 2003; Nichols et al., 2015; Simpson et al., 2016). However, Bouchoucha et al. (2018) showed that the concentrations of metallic trace elements in the muscles of juvenile *Diplodus* spp. settled in harbors were far below health safety thresholds. Also, their growth rate and condition were not different from those of juveniles settled outside the harbor. Another potential explanation, and maybe the most intuitive, for lower densities in harbors is the poor structural complexity and the relative homogeneity of the substrate. Indeed, it is known that the loss or reduction of complexity and/or heterogeneity leads to the reduced abundance and survival of organisms (August 1983; Brokovich et al., 2006; Cuadros et al., 2017b; Fisher et al., 2007). This point will be further discussed in the next section.

Although densities are lower in harbors, juvenile *D. sargus* tended to be bigger in those sites, which might suggest a faster growth rate. This is in concordance with the fact that *D. sargus* are known to have a preference for areas protected from strong swell and hydrodynamics (Harmelin-Vivien et al., 1995), conditions that are met inside harbors together with high productivity (more food) and higher temperatures, which are known to favor growth (Vigliola et al., 1998).

4.2. *Effect of small-scale habitat variations within harbors*

Most studies investigating the distribution of juveniles focus on only one spatial scale, however it has been shown that seascape attributes at different spatial scales might influence the densities of juveniles (Cuadros et al., 2017a). In our study, harbors in their totality (all habitats together) always show lower densities than other sites. However, when looking at a finer spatial scale within the harbors (habitat type), some habitats might host densities comparable to those observed in natural sites while others exhibit very low densities. Habitat choice could result from widely varying structural complexity since habitat complexity has an important effect on settlement and the abundance of juvenile fish with greater complexity supporting more species and individuals (Anderson and Millar, 2004; Cheminée et al., 2017b; Garcia_Charton et al., 2004; Horinouchi and Sano, 1999; Thiriet et al., 2014). It has been shown that a reduced tri-dimensional habitat complexity may reduce habitat quality, alter habitat choices and cause differential mortality of juveniles (Cheminée et al., 2016). Harbors are composed of a mosaic of habitats with different complexity and our results showed that the contribution of each habitat type to the global amount of juveniles of a site is highly variable. In this study, relatively complex jetties and ripraps represented approximately 50% of the habitat, while featureless vertical docks the other 50% (this proportion being variable from one harbor to the other). Docks do not provide essential habitat for juvenile fish. They provide them with neither the protection nor the foraging opportunities that are essential for their growth and survival thereby explaining the very low densities observed on docks and the resulting globally low densities of harbor sites. Jetties and riprap, on the other hand, structurally simulate the essential habitat of juvenile fish and may provide suitable nursery habitat, which explains why some of them supported densities of juvenile *D. sargus* equivalent to those observed in natural sites. However, the effect of habitat is highly contrasted between the two regions. Although jetties hosted the highest densities for most sampled species on the SC, it is not the case on the RC. The presence of nearby natural habitat could explain this difference as juveniles are known to settle on the first suitable habitat they encounter (Shapiro, 1987). However, juveniles were found in relatively high densities within the harbors of the RC suggesting that the low densities on jetties might rather result from hydrodynamic conditions or the fact that they are much steeper and deeper on the RC than on the SC (Authors' unpublished data). Densities on natural habitats within harbors were also very different, being high on the RC and low on the SC, but this was consistent with the nature of the substrate, which is different between the two regions. On the RC it is composed of rocky bottom, which represents the preferential habitat of the studied species, while on the SC it consists of sandy or muddy bottom, which doesn't provide the complexity needed by the sampled species. Ripraps are the only habitat showing a consistent response on both coasts with intermediate densities probably due to their complex structure but their lower accessibility. Indeed, as mentioned in the above section, accessibility might be a determining factor for settlement success. This is corroborated by the significant effect of the covariate distance from the entrance of the harbor. With the exception of some species, densities decreased as distance increased, which sustains the hypothesis according to which settlement is favored in exposed areas if suitable habitat is available (Brown et al., 2005; Jenkins and Wheatley, 1998; Pastor et al., 2013). Larval supply would then represent a limiting factor in highly sheltered areas such as inner reefs (D'Alessandro et al., 2007), upper parts of estuaries (Bell et al., 1988; Martins et al., 2007), narrow coves ()(Cuadros et al., 2017a) and lagoons (Pastor et al., 2013), and here, on the most enclosed part of the harbor.

Even if global patterns in terms of habitat use and the effect of distance are consistent between species, some variations are observed suggesting they might have different requirements and preferences. This is in concordance with the fact that many fish species are known to have taxon-specific microhabitat requirements for settlement (Cheminée et al., 2013; García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Macpherson and Zika, 1999; Vigliola and Harmelin-Vivien, 2001) which may evolve as juveniles grow (Dahlgren and Eggleston, 2000; Macpherson et al., 1997).

Within harbors and at the time of the survey (late July), *D. sargus* and *O. melanura* showed approximately the same distribution. They both tended to be more on jetties (which might be due to the above mentioned factors such as accessibility) but *D. sargus* uses ripraps more than *O. melanura*. This difference might be explained by the fact that ripraps are often located in very shallow areas and present a gentle slope (while it can be steeper on jetties) which might better correspond to the requirements of *D. sargus* than *O. melanura.* Indeed, in natural areas settlers of *D. sargus* are usually found in very shallow water close to the bottom, whereas those of *O. melanura* tend to be more on the surface even in habitat with deeper waters (Harmelin-Vivien et al., 1995).

D. vulgaris seemed to use the inside of the harbor more and a larger variety of habitats. Since this species settles during winter, individuals are already at an intermediate developmental stage or even at a predispersal stage during the sampling period. During these stages, juveniles use all suitable habitats available or are even ready to leave their nursery to join adult habitat (Bouchoucha et al., 2016; Ventura et al., 2014; Vigliola and Harmelin-Vivien, 2001). This less restrictive habitat requirement would explain the broader distribution of this species inside the harbors.

Supporting this hypothesis, the same pattern is observed for *D. puntazzo*, which is known to be more specialized than *D. vulgaris* and also settles during winter. It is to note that this species is not very abundant in the region and that densities observed in harbors are equivalent to those observed in natural sites, particularly in winter and spring when juveniles are at post-settlement and intermediate stages (authors unpublished data).

D. labrax are known to mainly settle in lagoons or estuaries (Cabral and Costa, 2001; Jennings and Pawson, 1992; Martinho et al., 2008), therefore the low hydrodynamic and high productivity found in harbors might furnish suitable conditions for settlement and development of this species. The highest densities of this species were observed in Port-Barcarès harbor, which is connected to a lagoon, and in Argelès harbor in which flows a small river, which supports this hypothesis. Surprisingly, within the harbors, juvenile *D. labrax* are mostly found on riprap, a rocky habitat quite different from the usually soft bottom or meadow found in lagoons.

The last species found in harbors in relatively large densities were *Mullus* sp., which were mainly observed on inner jetties and ripraps. Those habitats composed of structurally complex rocky substrate usually surrounded by a large portion of soft bottom, correspond well to the natural nursery of the species (García-Rubies and Macpherson, 1995).

4.3. Implications for management

In the Mediterranean Sea, nursery grounds are still poorly taken into account in protection measures. Indeed, coastal management historically focused on adult fish and only a small proportion of nursery habitat benefits from protection (Cheminée et al., 2017a). It is also to note that, even in Marine Protected Areas, juvenile habitat may still be transformed and impacted by human activities. Most nurseries are located in areas of intense touristic activities and coastal development (beaches and coves), which makes the implementation of substantial protection measures particularly difficult. However, co-management (Granek and Brown, 2005; Pinkerton, 1989) could encourage alternative coastal use and management in order to help to reduce habitat transformation notably by limiting practices that lead to habitat homogenization (Cheminée et al., 2014; Cuadros et al., 2017a). Our results showed that man-made infrastructures and CDS in particular could serve as juvenile habitats for some species. Despite this potential, the ecological consequences resulting from the construction of these structures, such as the loss of habitat essential to other species or changes in courants and sediment loads, should always be evaluated and taken into consideration (Bulleri and Chapman, 2010). In cases where their construction doesn't destroy highly complex ecosystems (i.e. seagrass meadow, coral reef), they might be seen as little oases of biodiversity (Clynick, 2006; Guidetti, 2004; Ruitton, 1999) that can increase connectivity (Koeck et al., 2013). In light of their potential as juvenile habitat and the importance of this function in the replenishment of fish populations (Beck et al., 2001; Mumby et al., 2004), these kinds of structures should be taken into account in future management plans. However, this requires keeping in mind that the diversity of habitat among the seascape mosaic is crucial to provide suitable essential habitat to different species and allow a true renewal of coastal biodiversity.

Harbors also host juveniles but our results showed that the densities were highly dependent on the habitat considered. Given the amount of featureless docks inside harbors and the fact that juveniles only poorly use them due to their lack of complexity, it could be interesting to consider ecological engineering approaches on those structures. Recent studies showed that the use of small artificial habitats could enhance juvenile densities on docks and under pontoons (Bouchoucha et al., 2016; Mercader et al., 2017) and that even the protected dusky grouper (*Epinephelus marginatus*) could settle inside harbors (Mercader et al., 2016). Also, since harbors are usually seen as having a negative environmental impact, eco-engineering and restoration ecology approaches coupled with pollution reduction measures could represent another and complementary way, along with natural habitat preservation, to favor the nursery function of the Mediterranean coast even in highly urbanized areas.

5. Conclusion

The results of this study showed contrasting densities of juveniles depending on the level of artificialization and the region. Despite the habitat modifications they may cause, CDS hosted higher densities of certain coastal species, notably *D. sargus,* than most natural sites and so may be considered as important potential juvenile habitats. This seems to be particularly true when settlement numbers are high. Although densities in harbors were lower than on CDS and natural sites, they still hosted some juveniles, and densities found on jetties and riprap were equivalent to those in natural nurseries. The effect of the habitat type inside harbors seemed to be very dependent of the region, however, lower densities on featureless docks were a general pattern. These results suggest that despite their ecological impact, man-made infrastructures might represent alternative juvenile habitats, at least for some species whose juveniles usually settle on heterogeneous rocky bottoms. Taking them into account in management plans at the seascape scale is of prime interest for fish population maintenance. Ecological engineering in highly modified sites such as harbors could also represent an interesting complementary approach to conservation efforts particularly in the concerned coastal zone were protection isn't always possible.

Acknowledgements

This work was supported by the Total Foundation, the Fondation de France and the Conseil Départemental 66 in the frame of the e-Cate program (2014–2016), as well as the Agence de l'eau Rhône Méditerranée Corse for all sampling done in harbors. The authors would like to thank Gilles Saragoni, Quentin Thernon, as well as Amélie Foncuberta and Anaïs Gudefin from the Ecocean company for their help in fieldwork. We would also like to thank the MPAs' managers for facilitated access to the field and constructive exchanges. The authors also thank Marc Bouchoucha for constructive comments on the manuscript and are particularly grateful to Bob Clarke (PML – Primer-E) for his advises on data analysis. We also want to thank two anonymous reviewers for their constructive comments.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.02.030.

References

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr. Mar. Biol. Annu. Rev. 45, 345–405.

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. 58, 626–639.

Anderson, M.J., Millar, R.B., 2004. Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. J. Exp. Mar. Biol. Ecol. 305, 191–221.

Anderson, J.M., Gorley, R.N., Clarke, K., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.

Armsworth, P.R., 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology 83, 1092–1104.
August, P.V., 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64, 1495–1507.
Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., et al., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51, 633.
Bell, J., Steffe, A., Westoby, M., 1988. Location of seagrass beds in estuaries: effects on associated fish and decapods. J. Exp. Mar. Biol. Ecol. 122, 127–146.
Bouchoucha, M., Darnaude, A., Gudefin, A., Neveu, R., Verdoit-Jarraya, M., Boissery, P., Lenfant, P., 2016. Potential use of marinas as nursery grounds by rocky fishes: insights from four Diplodus species in the Mediterranean. Mar. Ecol. Prog. Ser 547, 193–209.
Bouchoucha, M., Brach-Papa, C., Gonzalez, J.-L., Lenfant, P., Darnaude, A.M., 2018. Growth, condition and metal concentration in juveniles of two Diplodus species in ports. Mar. Pollut. Bull. 126, 31–42.
Brokovich, E., Baranes, A., Goren, M., 2006. Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. Ecol. Indic 6, 494–507.
Brown, C.A., Jackson, G.A., Holt, S.A., Holt, G.J., 2005. Spatial and temporal patterns in modeled particle transport to estuarine habitat with comparisons to larval fish settlement patterns. Estuar. Coast Shelf Sci. 64, 33–46.
Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47, 26–35.
Cabral, H., Costa, M.J., 2001. Abundance, feeding ecology and growth of 0-group sea bass, Dicentrarchus labrax, within the nursery areas of the Tagus estuary. J. Mar. Biol. Assoc. U. K. 81, 679–682.
Cheminée, A., Francour, P., Harmelin-Vivien, M., 2011. Assessment of Diplodus spp. (Sparidae) nursery grounds along the rocky shore of Marseilles (France, NW Mediterranean). Sci. Mar. 75, 181–188.
Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., Cottalorda, J.-M., Francour, P., 2013. Nursery value of Cystoseira forests for Mediterranean rocky reef fishes. J. Exp. Mar. Biol. Ecol. 442, 70–79.
Cheminée, A., Feunteun, E., Clerici, S., Cousin, B., Francour, P., 2014. Management of Infralittoral Habitats: towards a Seascape Scale Approach. In Underwater Seascapes. Springer International Publishing, pp. 161–183.
Cheminée, A., Merigot, B., Vanderklift, M.A., Francour, P., 2016. Does habitat complexity influence fish recruitment? Mediterr. Mar. Sci. 17, 39.
Cheminée, A., Rider, M., Lenfant, P., Zawadzki, A., Mercière, A., Crec'hriou, R., Mercader, M., Saragoni, G., Neveu, R., Ternon, Q., et al., 2017a. Shallow rocky nursery habitat for fish: spatial variability of juvenile fishes among this poorly protected essential habitat. Mar. Pollut. Bull. 119, 245–254.
Cheminée, A., Pastor, J., Bianchimani, O., Thiriet, P., Sala, E., Cottalorda, J.-M., Dominici, J.-M., Lejeune, P., Francour, P., 2017b. Juvenile fish assemblages in temperate rocky reefs are shaped by the presence of macro-algae canopy and its three-dimensional structure. Sci. Rep. Nat. Publ. Group 7, 1–11.
Clarke, K., Gorley, R., 2006. PRIMER V6: User Manual/Tutorial. (Plymouth).
Clarke, K., Gorley, R., Somerfield, P., Warwick, R., 2014. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. PRIMER-E, Plymouth.
Clynick, B.G., 2006. Assemblages of fish associated with coastal marinas in north-western Italy. J. Mar. Biol. Assoc. U. K. 86, 847–852.
Clynick, B.G., 2008. Characteristics of an urban fish assemblage: distribution of fish associated with coastal marinas. Mar. Environ. Res. 65, 18–33.
Clynick, B.G., Chapman, M.G., Underwood, A.J., 2008. Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecol. 33, 140–150.
Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., et al., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS One 5 e11842.
Crain, C.M., Halpern, B.S., Beck, M.W., Kappel, C.V., 2009. Understanding and managing human threats to the coastal marine environment. Ann. N. Y. Acad. Sci. 1162, 39–62.
Crec'hriou, R., Garsi, Laure-Hélène, Lèbre, Laurie, Lozano, Laura, Pastor, Jérémy, Lecaillon, Gilles, Durieux, Eric, Simon, Gaël, Ternengo, Sonia, Bracconi, Jérémy, et al., 2015. Atlas of Post-larval Fish of the Northwestern Mediterranean Sea.
Creel, L., 2003. Ripple Effects: Population and Coastal Regions. Population Reference Bureau Washington, DC.
Cuadros, A., Moranta, J., Cardona, L., Thiriet, P., Pastor, J., Arroyo, N.L., Cheminée, A., 2017a. Seascape attributes, at different spatial scales, determine settlement and post-settlement of juvenile fish. Estuar. Coast Shelf Sci. 185, 120–129.
Cuadros, A., Cheminée, A., Thiriet, P., Moranta, J., Vidal, E., Sintes, J., Sagristá, N., Cardona, L., 2017b. The three-dimensional structure of Cymodocea nodosa meadows shapes juvenile fish assemblages at Fornells Bay (Minorca Island). Reg. Stud. Mar. Sci. 14, 93–101.
Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L., 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Front. Ecol. Environ. 13, 82–90.
Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81, 2227–2240.
Dahlgren, C., Kellison, G., Adams, A., Gillanders, B., Kendall, M., Layman, C., Ley, J., Nagelkerken, I., Serafy, J., 2006. Marine nurseries and effective juvenile habitats: concepts and applications. Mar. Ecol.-Prog. Ser 312, 291–295.
D'Alessandro, E., Sponaugle, S., Lee, T., 2007. Patterns and processes of larval fish supply to the coral reefs of the upper Florida Keys. Mar. Ecol. Prog. Ser 331, 85–100.
Di Franco, A., Qian, K., Calò, A., Di Lorenzo, M., Planes, S., Guidetti, P., 2013. Patterns of variability in early life traits of a Mediterranean coastal fish. Mar. Ecol. Prog. Ser 476, 227–235.
Dufour, V., Cantou, M., Lecomte, F., 2009. Identification of sea bass (Dicentrarchus labrax) nursery areas in the north-western Mediterranean Sea. J. Mar. Biol. Assoc. U. K. 89, 1367–1374.
Dugan, J.E., Airoldi, L., Chapman, M.G., Walker, S.J., Schlacher, T., 2011. Estuarine and coastal structures. In: Treatise on Estuarine and Coastal Science. Elsevier, pp. 17–41.
EEA, 1999. Coastal and Marine Zones. Chapter 3.14. Environment in the European Union at the Turn of the Century. State of Environment, Copenhagen.
Fisher, P., Weber, A., Heine, G., Weber, H., 2007. Habitat structure and fish: assessing the role of habitat complexity for fish using a small, semiportable, 3-D underwater observatory. Limnol. Oceanogr. Methods 5, 12.
Fowler, A.M., Booth, D.J., 2013. Seasonal dynamics of fish assemblages on breakwaters and natural rocky reefs in a temperate estuary: consistent assemblage differences driven by sub-adults. PLoS One 8 e75790.
Garcia_Charton, J.A., Pérez-Ruzafa, A., Sanchez-Jerez, P., Bayle-Sempere, J.T., Reñones, O., Moreno, D., 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Mar. Biol. 144, 161–182.
Garcia-Rubies, A., Macpherson, E., 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Mar. Biol. 124, 35–42.
García-Rubies, A., Macpherson, E., 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Mar. Biol. 124, 35–42.
Gerland, P., Raftery, A.E., ev ikova, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., et al., 2014. World population stabilization unlikely this century. Science 346, 234–237.
Granek, E.F., Brown, M.A., 2005. Co-management approach to marine conservation in Mohéli, Comoros Islands. Conserv. Biol. 19, 1724–1732.
Guidetti, P., 2004. Fish assemblages associated with coastal defence structures in south-western Italy (Mediterranean Sea). J. Mar. Biol. Assoc. U. K. 84, 669–670.
Guizien, K., Brochier, T., Duchêne, J., Koh, B., Marsaleix, P., 2006. Dispersal of Owenia fusiformis larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model. Mar. Ecol. Prog. Ser 311, 47–66.
Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.
Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Barnabé, G., Blanc, F., Chevalier, R., Duclerc, J., et al., 1985. Evaluation visuelle des peuplements et populations de poissons méthodes et problèmes.
Harmelin-Vivien, M.L., Harmelin, J.G., Leboulleux, V., 1995. Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. Hydrobiologia 300–301, 309–320.
Hindell, J.S., Jenkins, G.P., Moran, S.M., Keough, M.J., 2003. Swimming ability and behaviour of post-larvae of a temperate marine fish re-entrained in the pelagic environment. Oecologia 135, 158–166.
Holbrook, S.J., Schmitt, R.J., 2002. Competition for shelter space causes density-dependent predation mortality in Damselfishes. Ecology 83, 2855.
Holbrook, S.J., Forrester, G.E., Schmitt, R.J., 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. Oecologia 122.
Horinouchi, M., Sano, M., 1999. Effects of changes in seagrass shoot density and leaf height on abundances and distribution patterns of juveniles of three gobiid fishes in a Zostera marina bed. Mar. Ecol. Prog. Ser. 87–94.
Houde, E., Hoyt, R., 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2, 17–29.
Jenkins, G.P., Wheatley, M.J., 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. J. Exp. Mar. Biol. Ecol. 221, 147–172.
Jennings, S., Pawson, M.G., 1992. The origin and recruitment of bass, Dicentrarchus labrax, larvae to nursery areas. J. Mar. Biol. Assoc. U. K. 72, 199.
Jones, G.P., 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. J. Exp. Mar. Biol. Ecol. 123, 115–126.
Kerambrun, E., Henry, F., Courcot, L., Gevaert, F., Amara, R., 2012. Biological responses of caged juvenile sea bass (Dicentrarchus labrax) and turbot (Scophtalmus maximus) in a polluted harbour. Ecol. Indic 19, 161–171.
Koeck, B., Alós, J., Caro, A., Neveu, R., Crec'hriou, R., Saragoni, G., Lenfant, P., 2013. Contrasting fish behavior in artificial seascapes with implications for resources conservation. PLoS One 8 e69303.
Lam, N.W., Huang, R., Chan, B.K., others, 2009. Variations in Intertidal assemblages and zonation patterns between vertical artificial seawalls and natural rocky shores: a case study from Victoria Harbour, Hong Kong. Zool. Stud. 48, 184–195.
Macpherson, E., Zika, U., 1999. Temporal and spatial variability of settlement success and recruitment level in three blennoid fishes in the northwestern Mediterranean. Mar. Ecol.-Prog. Ser 182, 269–282.
Macpherson, E., Biagi, F., Francour, P., García-Rubies, A., Harmelin, J., Harmelin-Vivien, J., Jouvenel, J.Y., Planes, S., Vigliola, L., Tunesi, L., 1997. Mortality of juvenile fishes of the genus Diplodus in protected and unprotected areas in the western Mediterranean Sea. Mar. Ecol. Prog. Ser 160, 135–147.
Marchand, J., Tanguy, A., Laroche, J., Quiniou, L., Moraga, D., 2003. Responses of European flounder Platichthys flesus populations to contamination in different estuaries along the Atlantic coast of France. Mar. Ecol. Prog. Ser 260, 273–284.
Macpherson, E., 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. J. Exp. Mar. Biol. Ecol. 220, 127–150.
Martinho, F., Leitão, R., Neto, J.M., Cabral, H., Lagardère, F., Pardal, M.A., 2008. Estuarine colonization, population structure and nursery functioning for 0-group sea bass (Dicentrarchus labrax), flounder (Platichthys flesus) and sole (Solea solea) in a mesotidal temperate estuary. J. Appl. Ichthyol. 24, 229–237.
Martins, I.M., Dias, J.M., Fernandes, E.H., Muelbert, J.H., 2007. Numerical modelling of fish eggs dispersion at the Patos Lagoon estuary — Brazil. J. Mar. Syst. 68, 537–555.
Mercader, M., Fontcuberta, A., Mercière, A., Saragoni, G., Boissery, P., Bérenger, L., Dubas, R., Lecaillon, G., Pastor, J., Lenfant, P., 2016. Observation of juvenile dusky groupers (Epinephelus marginatus) in artificial habitats of North-Western Mediterranean harbors. Mar. Biodivers. 1–2.
Mercader, M., Mercière, A., Saragoni, G., Cheminée, A., Crec'hriou, R., Pastor, J., Rider, M., Dubas, R., Lecaillon, G., Boissery, P., et al., 2017. Small artificial habitats to enhance the nursery function for juvenile fish in a large commercial port of the

Mediterranean. Ecol. Eng. 105, 78–86.

Mora, C., Sale, P.F., 2002. Are populations of coral reef fish open or closed? Trends Ecol. Evol. 17, 422–428.

Moschella, P.S., Abbiati, M., Åberg, P., Airoldi, L., Anderson, J.M., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., Frost, M., Gacia, E., et al., 2005. Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. Coast. Eng 52, 1053–1071.

Mumby, P.J., Edwards, A.J., Ernesto Arias-González, J., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., et al., 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427, 533–536.

Nichols, T.A., Anderson, T.W., Širović, A., 2015. Intermittent noise induces physiological stress in a coastal marine fish. PLoS One 10 e0139157.

Öhman, M.C., Munday, P.L., Jones, G.P., Caley, M.J., 1998. Settlement strategies and distribution patterns of coral-reef fishes. J. Exp. Mar. Biol. Ecol. 225, 219–238.

Pastor, J., 2008. Rôle des enrochements côtiers artificiels dans la connectivité des populations, cas du sar commun (Diplodus sargus, Linné, 1758) en Méditerranée nord-occidentale. Université de Perpignan; Ecole pratique des hautes études-EPHE PARIS.

Pastor, J., Koeck, B., Astruch, P., Lenfant, P., 2013. Coastal man-made habitats: potential nurseries for an exploited fish species, Diplodus sargus (Linnaeus, 1758). Fish. Res. 148, 74–80.

Perkol-Finkel, S., Benayahu, Y., 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23.

Pineda, J., Porri, F., Starczak, V., Blythe, J., 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. J. Exp. Mar. Biol. Ecol. 392, 9–21.

Pinkerton, E., 1989. Attaining better fisheries management through co-management prospects, problems and propositions. In: Co-operative Management of Local Fisheries: New Direction in Improved Management and Community Development. E. Pinkerton, Vancouver, BC, pp. 3–33.

Pizzolon, M., Cenci, E., Mazzoldi, C., 2008. The onset of fish colonization in a coastal defence structure (Chioggia, Northern Adriatic Sea). Estuar. Coast Shelf Sci. 78, 166–178.

Planes, S., Macpherson, E., Biagi, F., Garcia-Rubies, A., Harmelin, J., Harmelin-Vivien, M., Jouvenel, J.-Y., Tunesi, L., Vigliola, L., Galzin, R., 1999. Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. J. Mar. Biol. Assoc. U. K. 79, 137–143.

Raventos, R., Macpherson, E., 2001. Planktonic larval duration and settlement marks on the otoliths of Mediterranean littoral fishes. Mar. Biol. 138, 1115–1120.

Rilov, G., Benayahu, Y., 2000. Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Mar. Biol. 136, 931–942.

Roy, C., 1998. An upwelling-induced retention area off Senegal: a mechanism to link upwelling and retention processes. South Afr. J. Mar. Sci. 89.

Ruitton, S., 1999. Les communautés benthiques et nectobenthiques associées aux aménagements littoraux en Méditerranée nord-occidentale: structure et fonctionnement.

Ruitton, S., Francour, P., Boudouresque, C.F., 2000. Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a temperate sea (Mediterranean). Estuar. Coast Shelf Sci. 50, 217–230.

Sale, P.F., Danilowicz, B.S., Doherty, P.J., Williams, D.M., 2005. The relation of microhabitat to variation in recruitment of young-of-year coral reef fishes. Bull. Mar. Sci. 76, 123–142.

Schmitt, R.J., Holbrook, S.J., 2000. Habitat-limited recruitment of coral reef damselfish. Ecology 81, 3479.

Scyphers, S.B., Gouhier, T.C., Grabowski, J.H., Beck, M.W., Mareska, J., Powers, S.P., 2015. Natural shorelines promote the stability of fish communities in an urbanized coastal system. PLoS One 10 e0118580.

Shapiro, D.Y., 1987. Inferring larval recruitment strategies from the distributional ecology of settled individuals of a coral reef fish. Bull. Mar. Sci. 41, 289–295.

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C.O., Chivers, D.P., McCormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. Nat. Commun. 7, 10544.

Sundblad, G., Bergström, U., Sandström, A., Eklöv, P., 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES J. Mar. Sci. 71, 672–680.

Thiriet, P., Cheminée, A., Mangialajo, L., Francour, P., 2014. How 3D complexity of macrophyte-formed habitats affect the processes structuring fish assemblages within coastal temperate seascapes? In: Musard, O., Le Dû-Blayo, L., Francour, P., Beurier, J.-P., Feunteun, E., Talassinos, L. (Eds.), Underwater Seascapes. Springer International Publishing, Cham, pp. 185–199.

Ventura, D., Jona Lasinio, G., Ardizzone, G., 2014. Temporal partitioning of microhabitat use among four juvenile fish species of the genus *Diplodus* (Pisces: perciformes, Sparidae). Mar. Ecol. 36, 1013–1032.

Vigliola, L., 1998. Contrôle et régulation du recrutement des Sparidae (Téléostéens) en Méditerranée: importance des processus pré- et post- installation benthique. Université de la Méditerranée.

Vigliola, L., Harmelin-Vivien, M., 2001. Post-settlement ontogeny in three Mediterranean reef fish species of the genus Diplodus. Bull. Mar. Sci. 68, 271–286.

Vigliola, L., Harmelin-Vivien, M.L., Biagi, F., Galzin, R., Garcia-Rubies, A., Harmelin, J.-G., Jouvenel, J.-Y., le Direach-Boursier, L., Macpherson, E., Tunesi, L., 1998. Spatial and temporal patterns of settlement among sparid fishes of the genus Diplodus in the northwestern Mediterranean. Mar. Ecol. Prog. Ser 168, 45–56.

Wickham, H., 2009. Ggplot2: Elegant Graphics for Data Analysis. Springer, New York.