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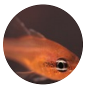

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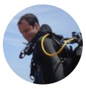

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# Shallow rocky nursery habitat for fish: Spatial variability of juvenile fishes among this poorly protected essential habitat

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ABSTRACT

Coastal nursery habitats are essential for the renewal of adult fish populations. We quantified the availability of a coastal nursery habitat (shallow heterogeneous rocky bottoms) and the spatial variability of its juvenile fish populations along 250 km of the Catalan coastline (France and Spain). Nurseries were present in 27% of the coastline, but only 2% of them benefited from strict protection status. For nine taxa characteristic of this habitat, total juvenile densities varied significantly between nursery sites along the coastline, with the highest densities being found on the northern sites. Recruitment level (i.e. a proxy of nursery value) was not explained by protection level, but it was moderately and positively correlated with an anthropization index. Patterns of spatial variations were taxa-specific. Exceptional observations of four juveniles of the protected grouper *Epinephelus marginatus* were recorded. Our data on habitat availability and recruitment levels provides important informations which help to focus MPA management efforts.

## 1. Introduction

Due to an ever growing global population and a general migration to coastal areas, oceans and seas are experiencing an unprecedented variety and magnitude of anthropogenic pressures. The Mediterranean, a semi-enclosed basin surrounded by inhabited land, is particularly susceptible to the effects of human induced pressures (Coll et al., 2010). This translates into a greater use of resources and increased modification of natural habitats, just to name a couple of the many consequences. In this context, coastal areas represent great stakes: they contain habitats essential for species life cycles as well as concentrating a maximum of anthropogenic disturbances.

Many coastal fish have a complex life cycle composed of a pelagic and a benthic stage. For many Mediterranean necto-benthic coastal species, eggs are released into the water column and generally hatch after two days, producing larvae that develop in pelagic waters for more than a month before migrating towards the shore (Di Franco et al., 2013). At the shore, post-larvae undergo "settlement", i.e. the transition from the pelagic larval habitat and establishment to the benthic juvenile habitat. Among juvenile habitats, nursery habitats are the one(s) that, for a particular species, have a greater "nursery value", i.e. contributes a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other habitats. The "nursery value" of a habitat results from a combination of four parameters: (1) the initial density of juveniles ("settlers"), (2) their survival rate, (3) their growth rate within these habitats and (4) their ability to move from the juvenile habitat and recruit into the adult habitat at the end of the post-settlement phase (Beck et al., 2001). The settlement period and juvenile nursery habitat can vary depending on the species to avoid inter-specific as well as intra-specific competition (Harmelin-Vivien et al., 1995).

In the Mediterranean, various Sparidae species of commercial and ecological importance use nurseries characterized as shallow coastal areas comprised of a heterogeneous rocky and sandy substrate (Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). In the case of *Diplodus* species, after about 4 to 6 months, when the juveniles have reached about 6 to 8 cm of total length (TL), the recruitment stage occurs. The now sub-adults ("recruits") leave the nursery habitat and disperse into the different and/or more diverse adult habitat(s) where they are integrated into shoals of older individuals (MacPherson, 1998; Vigliola and Harmelin-Vivien, 2001). The number of juveniles remaining in a nursery area before recruitment, at a given time, can be used to assess the nursery settlement success and final recruitment "level" (Macpherson and Zika, 1999), as a proxy of its nursery value, and can be compared between sites.

The alteration or transformation (let alone destruction) of a nursery habitat directly affects the life cycle of many species of fish by reducing

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its nursery value, and ultimately is detrimental to conservation efforts (Cheminée et al., 2016; Harmelin-Vivien et al., 1995). Because nursery habitats are essential in the life cycle of fish and the renewal of adult populations, protecting them should be a priority. Nevertheless, data on nursery habitat localization and site nursery value are often missing, preventing coastal managers from efficiently focusing their conservation efforts (Cheminée et al., 2014).

We studied one type of Mediterranean nursery habitat for fish, consisting of shallow (0 to 2 m depth) heterogeneous rocky bottoms made of blocks, pebbles and sand. We aimed to assess at a large spatial scale (>200 km long stretch of coastline) (1) the availability of this key habitat, (2) the spatial variation of juvenile fish population descriptors among this habitat (i.e. between sites displaying this given habitat) and (3) their response to anthropization and protection levels. The overall goal was to better understand nursery habitat efficiency and provide key data and proposals to coastal managers.

## 2. Materials and methods

### 2.1. Study sites and sampling strategy

The sampled area spans 238.3 km of Mediterranean coastline from Leucate, France (FR) to Roses, Spain (ES). First, nursery sites were identified using aerial images and confirmed in situ (in a subset of sites) during surveying. Nurseries are defined as portions of the coast displaying suitable habitat according to the following criteria: protected from strong swell, shallow (0–2 m depth), gently sloping heterogeneous bottoms of mixed substratum composed of blocks, pebbles and sand

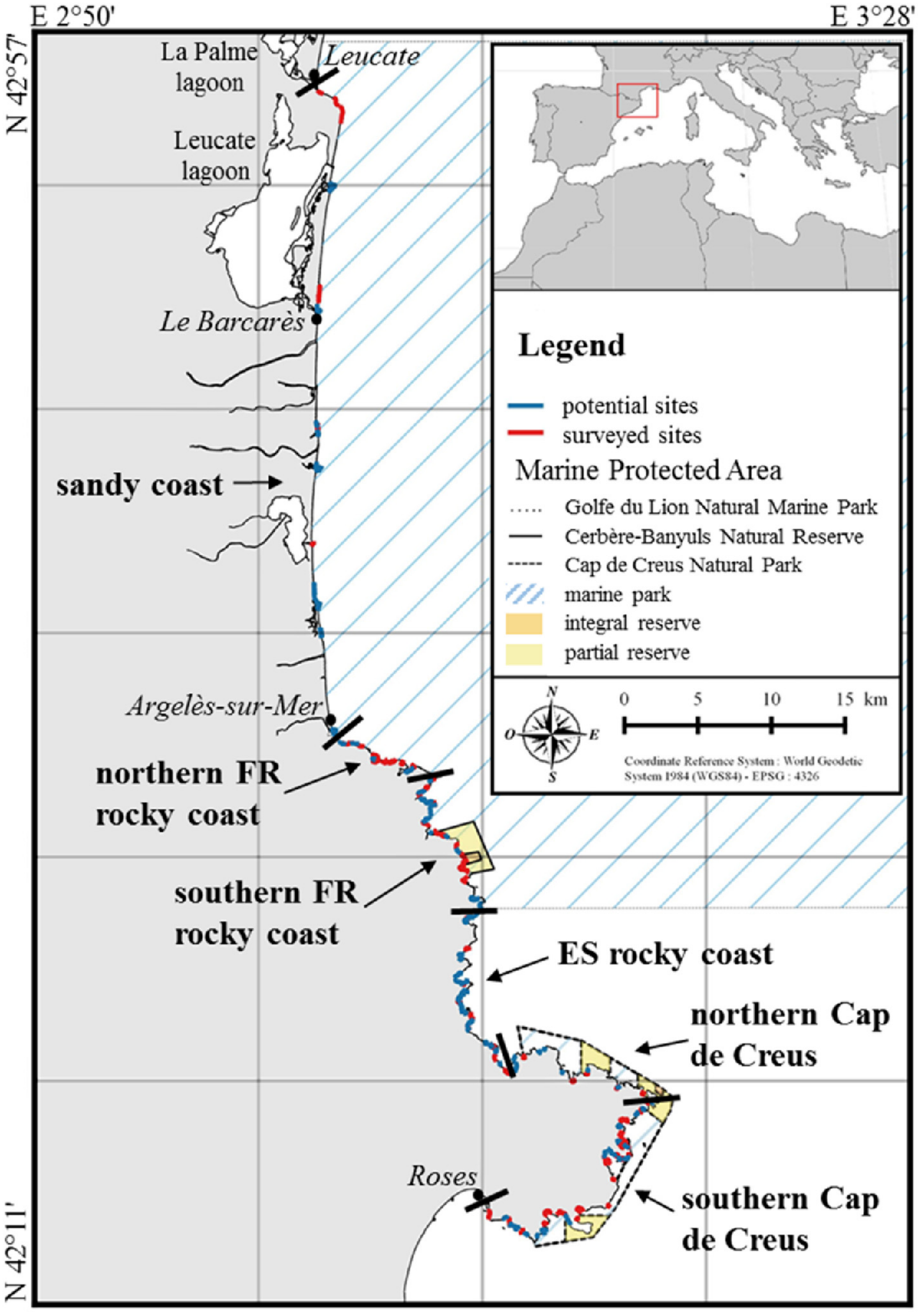

**Fig. 1.** Study area and all nursery sites that were identified along the coastline (red and blue stretches). Presented data comes from surveyed sites (in red). Other non-surveyed nurseries are indicated (in blue). Coastline was divided into 6 sectors for analysis (black arrows). Protection levels (Marine Protected Area zones) are identified (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

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**Table 1**
Length, percentage of nursery habitats and juvenile abundance by sector. Taxa: dc = *Diplodus cervinus*; dd = *Dentex dentex*; dp = *Diplodus puntazzo*; ds = *Diplodus sargus*; em = *Epinephelus marginatus*; pa = *Pagellus* spp.; pp = *Pagrus pagrus*; sv = *Sphyraena viridensis*; tp = *Thalassoma pavo.*

| Sector | Length (km) | Surveyed nurseries (km) (number of sites) | Other potential nurseries (km) (number of sites) | Total nurseries (km) | % of coastline that is nursery (number of sites) | Number of juvenile individuals surveyed per taxa | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ds | pa | sv | dp | em | dd | dc | pp | tp | Total |
| Sandy coast | 56.7 | 3.4 (16) | 8.3 (24) | 11.7 | 21% (39) | 2499 | 1878 | 135 | 7 | 0 | 1 | 1 | 0 | 0 | 4521 |
| Northern FR rocky coast | 16.7 | 4.8 (10) | 1.8 (4) | 6.6 | 39% (14) | 620 | 26 | 112 | 63 | 0 | 0 | 0 | 0 | 0 | 821 |
| Southern FR rocky coast | 26.3 | 8.0 (17) | 4.9 (13) | 12.9 | 49% (30) | 611 | 246 | 102 | 7 | 1 | 0 | 0 | 0 | 0 | 967 |
| ES rocky coast | 40.5 | 4.1 (9) | 9.0 (26) | 13.1 | 32% (35) | 524 | 11 | 76 | 33 | 0 | 1 | 0 | 0 | 0 | 645 |
| Northern Cap de Creus | 60.8 | 6.3 (13) | 3.6 (18) | 9.9 | 16% (31) | 560 | 379 | 151 | 61 | 0 | 0 | 0 | 1 | 0 | 1152 |
| Southern Cap de Creus | 37.3 | 6.9 (17) | 3.8 (17) | 10.7 | 29% (34) | 1273 | 240 | 416 | 110 | 3 | 1 | 0 | 0 | 1 | 2044 |
| **Total** | **238.2** | **33.5 (82)** | **31.4 (102)** | **64.9** | **27.2% (184)** | **6087** | **2780** | **992** | **281** | **4** | **3** | **1** | **1** | **1** | **10,150** |

(knowing that sand alone is not the most suitable habitat) (Cheminée et al., 2011; Cuadros et al., 2017; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). See Cuadros et al. (2017) for a pictured illustration of the suitable habitat. Nursery sites were identified and measured on ortho-photographs at a scale of 1:7000. As in Cheminée et al. (2014), a nursery site was identified as a stretch of coastline displaying a continuous portion of suitable habitat (see Sup. Fig. SF1). The length of nursery sites is therefore variable, although another study estimated that the length of nursery sites in 16 different Mediterranean zones was on average 62 m ± 6.8 m (SE) (Authors unpublished data). Aerial picture analysis was performed using QGIS 2.14 (QGIS Development Team, 2016). These sites can consist of natural or artificial structures as long as they adhere to the aforementioned requirements. A total of 184 nursery sites were located through aerial picture analysis (see Results). Their full cartography (see Sup. Fig. SF1) has been provided to MPA managers of the area (Zawadzki et al., 2015). Of these, we randomly sampled 82 sites spread in 6 sectors along this coast (Fig. 1, Table 1). This field work allowed us to validate the picture analysis criteria and to conduct a visual census of juvenile fish. Afterwards, once ground validation had been done in this subset of sites, the remaining 102 sites were considered as potential nurseries (even though not surveyed). Studied sectors displayed sites with similar habitat type. For example, sites from the sector "sandy coast" were selected to include both some breakwaters as well as rocky natural sites. This allowed us to further discuss density patterns of juveniles between sectors without any bias of habitat type since it is considered constant.

### 2.2. Study species

We counted every necto-benthic species that we observed in the studied habitat. In study sites, juvenile fish assemblages were described using several descriptors: total abundances (all studied taxa together), assemblage composition (relative abundances of the studied taxa), and taxa-specific abundances. We present data for eleven species that utilized heterogeneous rocky and sandy habitats as nurseries. They were grouped into the following nine taxa (Table 2, Sup. Fig. SF2): white seabream (*Diplodus 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), common dentex (*Dentex dentex*, Linnaeus 1758) and *Pagellus* spp. (including the axillary seabream (*Pagellus acarne*, Risso 1827), common pandora (*Pagellus erythrinus*, Linnaeus 1758) and the blackspot seabream (*Pagellus bogaraveo*, Brünnich 1768) which are difficult to differentiate at the juvenile stage). *Pagellus* spp. was studied separately and then excluded from the average densities (all taxa together) and assemblage structure analyses because *P. acarne* and *P. bogaraveo* are not found exclusively on rocky habitats and are often found in large schools. Opportunistic species, which have previously been documented as more ubiquitous in term of juvenile habitat choice, were excluded from the presented data. This includes *Sarpa salpa*, *Diplodus vulgaris* and *Oblada melanura* (Cheminée et al., 2011; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; Vigliola, 1998).

**Table 2**
Code and maximum juvenile Total Length (TL) considered for each of the nine surveyed taxa (eleven species in total).

| Genus | Species | Code | TL (mm) |
|---|---|---|---|
| *Diplodus* | *sargus* | ds | 80 |
| *Diplodus* | *puntazzo* | dp | 90 |
| *Sphyraena* | *viridensis* | sv | 150 |
| *Dentex* | *dentex* | dd | 90 |
| *Diplodus* | *cervinus* | dc | 90 |
| *Epinephelus* | *marginatus* | em | 200 |
| *Pagellus* | spp. | pa | 90 |
| *Pagrus* | *pagrus* | pp | 90 |
| *Thalassoma* | *pavo* | tp | 50 |

### 2.3. Fish sampling procedure

In each of the 82 surveyed sites (i.e. replicates), for each studied species, juvenile abundances were monitored once, during the last ten days of July 2015. This allowed us to take into account not only settlers from July but juveniles from a longer period of time as well (from previous September to July) (Crec'hriou et al., 2015; Froese and Pauly, 2011; Garcia-Rubies and Macpherson, 1995; Lejeune, 1985; Raventos and Macpherson, 2001). By doing so, we did not aim to consider the settlement peak of a given species, but rather we performed an estimate of the recruitment level for a variety of species, i.e. quantifying the remaining juveniles after an arbitrary period of time following settlement (sensu Macpherson and Zika (1999)). Juveniles were counted along 1-meter-wide belt-transects parallel to the shoreline, among the previously described habitat. The same divers, previously inter-calibrated, performed underwater visual censuses (UVC) of juvenile fishes as described in previous works (Cheminée et al., 2011; Cuadros, 2015; Cuadros et al., 2017; MacPherson, 1998; Pastor et al., 2013; Vigliola et al., 1998). The diver recorded the abundance and size per taxa of benthic juveniles. The total length (TL) of individuals (±0.5 cm) was estimated with the help of fish silhouettes of different sizes on a submersible slate. TL estimates were used *a posteriori* in order to study only juvenile individuals (Table 2). Rough sea and poor visibility days were avoided.

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 the young of the year (y0 individuals) and size-classes that may correspond to young of the previous year (y + 1) (Table 2). At this stage most of the mortality has already occurred so the densities observed are a proxy of what should recruit into the adult population (Macpherson and Zika, 1999). *Thalassoma pavo* is a stenotherm species affiliated to warmer waters from southern parts of the Mediterranean. However, data from the last 20 years suggest a

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shift in its geographical range concomitant with global change and the warming of the Mediterranean (Guidetti et al., 2002; Milazzo et al., 2016). In the northern Mediterranean coasts, juveniles are still very rare and the detection of adult specimens is important data, as it indicates the shift of its expansion range towards the north. For this reason, we recorded all sizes of this species.

### 2.4. Study design and data analysis

Using sites ($n = 82$) as replication units, we tested the effect of explaining factors (i.e. spatial location, protection level and anthopization level of sites) on the descriptors of juvenile assemblages (i.e. total abundances (all taxa together), assemblage composition (relative abundances of the studied taxa), and taxa-specific abundances). This sampling strategy aimed to test for the variability of juvenile descriptors, at a given time, for a given habitat type, for a given set of species. We did not aim to compare e.g. absolute abundance between species. This would have been irrelevant since different species settle at different time of the year. It is rather the spatial pattern of each descriptor that is discussed and differences between species are only discussed in terms of the relative differences in spatial patterns.

First, the eighty-two surveyed nursery sites (i.e. replicates) were grouped into 6 spatial sectors: sandy coast, northern French (FR) rocky coast, southern French (FR) rocky coast, Spanish (ES) rocky coast, northern Cap de Creus and southern Cap de Creus (Fig. 1, Table 1). Within each sector, sites displayed similar topography, orientation, protection and/or jurisdiction.

Secondly, there exist three Marine Protected Areas (MPAs) along this zone: the Gulf of Lion Natural Marine Park (established 2011, 4019 $km^2$), the Cerbère-Banyuls Natural Marine Reserve (est. 1974, 6.5 $km^2$), and the Cap de Creus Natural Park (est. 1998, 30.7 $km^2$). For a subset of three sectors that contain sites in both levels of protection (southern FR rocky coast, northern Cap de Creus, southern Cap de Creus), sites were classified into two categories according to protection levels: (P1) sites situated outside of heavily regulated or monitored water (including the Gulf of Lion Natural Marine Park) and (P2) sites situated within the partial or reinforced protection of a MPA, i.e. with protection enforced by law.

Finally, two anthropization indices, MedImpact (Mannoni et al., 2014) and Micheli et al. (2013), were used to assess the putative effect of anthropization on juvenile densities. First, we used the MedImpact index. It is derived from intertidal algal community composition along the French rocky coasts. This assessment is based on a methodology for monitoring water quality constructed from the cartography of littoral and upper-sublittoral rocky-shore communities (CARLIT, in short) (Ballesteros et al., 2007). Only the sites located on the FR rocky coast had available MedImpact data. Therefore, we tested the effect of the MedImpact anthropization index only on this spatial subset of juvenile density data. Secondly, we used the index by Micheli et al. (2013). This index aims to map the cumulative human impact on the Mediterranean Sea and Black Sea by taking into account twenty-two different drivers and seventeen different marine ecosystems and calculating the cumulative impact score for each 1 $km^2$. It designates ecologically meaningful categories to the cumulative impact scores, i.e. ecosystems that are subject to: very high (>15.52); high (12–15.52); medium high (8.47–12); medium (4.95–8.47); low (1.4–4.95); and very low impact (<1.4). Both indices are available in raster layers compatible with geographic information systems. For each index, each study site was assigned an anthropization value according to the pixel closest to or overlapping the nursery habitat. If the habitat transected several pixels, or lacked values, the average of the transected or closest pixels was calculated.

Accordingly, two factorial models and two correlation models were used to test the influence of the explanatory variables on the spatial variation of descriptors of juvenile assemblages (total abundances, composition, taxa-specific abundances) (Supplementary Table ST1). The first model tested the influence of the fixed factor "sector" (six levels: sandy coast, northern French (FR) rocky coast, southern French (FR) rocky coast, Spanish (ES) rocky coast, northern Cap de Creus and southern Cap de Creus) on the spatial variability of the total juvenile density, assemblage structure and taxa-specific densities along the Catalan coast from Leucate, France to Roses, Spain. The second model tested the crossed effects of the fixed factor "sector" (three levels: southern FR rocky coast, northern Cap de Creus, southern Cap de Creus) and the fixed factor "protection" (two levels: P1: no regulatory protection, P2: regulatory protection) on the total juvenile density and assemblage structure in the three sectors that contain sites under both levels of protection. The third model tested the correlation between the MedImpact anthropization index (Mannoni et al., 2014) and the total juvenile density found at sites on the northern FR rocky coast and the southern FR rocky coast. The fourth model tested the correlation between the Micheli et al. (2013) anthropization index and the total juvenile density at all 82 sites.

For the factorial models, the effect of the design factors on the total juvenile density and taxa-specific densities (univariate data), was analyzed using permutational univariate ANOVAs (PERANOVAs) with the Euclidean distance. The effect of the design factors on the assemblage structure (multivariate data) was analyzed using permutational multivariate ANOVAs (PERMANOVAs) with a preliminary square root transformation of the data and the Bray-Curtis dissimilarity measure. PERANOVA and PERMANOVA pair-wise comparisons were carried out on all designs obtaining significant results from the global tests. Significant results from the assemblage structure PERMANOVAs were complimented with SIMPER tests to determine the relative contribution of each taxa to the variations in assemblage structure. p-Values were calculated by 999 random permutations of residuals under a reduced model (Anderson, 2001; Anderson and Millar, 2004). Due to the intrinsic variability of ecological data, tests were considered significant for p-values < 0.1. All factorial analyses were performed using the PERMANOVA + package for PRIMER 6 software (Anderson et al., 2008; Clarke and Gorley, 2006). The correlation models were tested using linear regression *t*-tests in R. Data pre-treatment and graphical visualizations were performed in R Environment (R_Development_Core_Team, 2013) using the library ggplot2 (Wickham, 2009).

## 3. Results

### 3.1. Nursery habitat availability and protection

We identified 184 sites (i.e. stretches of coastline) on the studied shoreline (238.3 km long) which displayed nursery habitat characteristics. These were therefore considered to be potential nurseries. These sites (including sites surveyed in situ and potential sites not surveyed) represented 64.9 km of coast, or 27% of the studied coast from Leucate to Roses (Table 1, Fig. 1). Of these 64.9 km of nursery habitat, 20.5 km (31%) were under no form of protection, 37.6 km (58%) were under limited protection in the form of natural marine parks, 5.9 km (9%) were within a partial reserve and only 1.3 km (2%) were within an integral reserve.

### 3.2. Spatial variation of juvenile populations

Among the 82 sampled sites, the overall juvenile abundances were dominated by four taxa (in decreasing order): *D. sargus*, *Pagellus* spp., *S. viridensis* and *D. puntazzo* (Table 1). Fewer than 5 individuals were seen for each of the other five species throughout the entire study area (Table 1).

#### 3.2.1. Total juvenile density

The total juvenile fish densities were unevenly repartitioned among the different sectors (Fig. 2; Table 3; PERANOVA, $F = 11.324$, $p \leq 0.001$) with the sector "sandy coast" containing the highest average density

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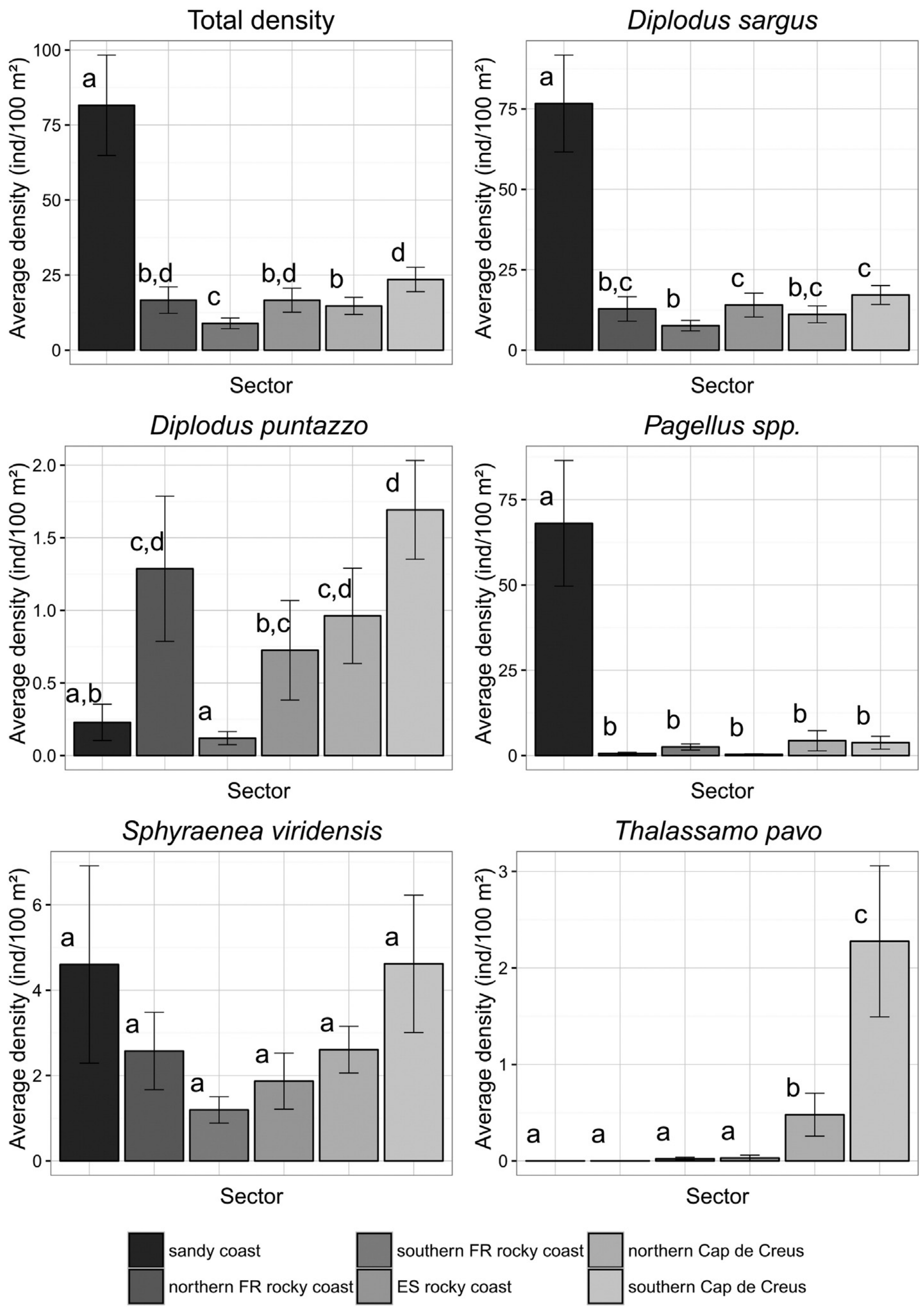

**Fig. 2.** Barplots of mean juvenile densities by sector. Total juvenile densities (all taxa together) and taxa-specific densities for *Diplodus sargus*, *Pagellus* spp., *Diplodus puntazzo*, *Sphyraena viridensis* and *Thalassoma pavo* (for this taxa densities include adults and juveniles); error bars = standard error. Pairwise results are given by lowercase characters: treatments sharing at least one character do not differ significantly. Note that the y-axis scales vary between graphs.

(81.6 ind/100 $m^2$ ± 16.7 (mean density ± standard error)) and being significantly different from all other sectors. The sector "southern FR rocky coast" had a significantly lower mean density than all of the other sectors (8.9 ind/100 $m^2$ ± 1.8). The sectors "northern FR rocky coast" (16.7 ind/100 $m^2$ ± 4.4), "ES rocky coast" (16.6 ind/100 $m^2$ ± 4.0), "northern Cap de Creus" (14.7 ind/100 $m^2$ ± 2.9) and "southern Cap de Creus" (23.5 ind/100 $m^2$ ± 4.1) were all situated in-between these two values with varying significant differences (pairwise tests, Fig. 2).

### *3.2.2. Assemblage structure and taxa-specific density*

There was a significant difference in juvenile composition between sectors (Table 3; PERMANOVA, $F = 4.600$, $p \leq 0.001$). The sandy coast was the only sector that was significantly different from all other sectors. All other sectors shared a significant resemblance with at least two other sectors always including the adjacent sector(s). The northern FR rocky coast was not significantly different from all other rocky coast sectors in terms of species compositions. In all cases *D. sargus* (SIMPER, 45%–75% contribution) is principally responsible for the dissimilarity, followed by *S. viridensis* (18%–31% contribution) and *D. puntazzo* (5%–23% contribution). The combination of these three species always makes up for >90% of the dissimilarity between sectors.

A closer look at the taxa-specific variations shows widely varying spatial patterns depending on the species. *D. sargus* and *Pagellus* spp. showed patterns very similar to that of the total juvenile density. This is not particularly surprising since *D. sargus* represented 83% of the total abundance observed in 2015. In contrast, there was no significant difference in average density of *S. viridensis* between the sectors and *D. puntazzo* had a global north to south increasing gradient but with an elevated average density in the northern French rocky coast sector (Fig. 2).

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**Table 3**
PERANOVA/PERMANOVA table of results: effects of explanatory factors on univariate descriptor of juvenile fish assemblage (total density) and multivariate juvenile assemblage structure.

| Source | Df | MS | Pseudo-F | P (perm) |
|---|---|---|---|---|
| **Model 1. Sector** | | | | |
| **Response variable: total density** | | | | |
| Secteur (Se) | 5 | 1.1426 | 11.324 | **0.001**$^{***}$ |
| Res | 76 | 0.1009 | | |
| Total | 81 | | | |
| **Response variable: assemblage structure** | | | | |
| Secteur (Se) | 5 | 4419 | 4.5996 | **0.001**$^{***}$ |
| Res | 76 | 960.74 | | |
| Total | 81 | | | |
| **Model 2. Protection** | | | | |
| **Response variable: total density** | | | | |
| Secteur (Se) | 2 | 5.29E-02 | 3.3944 | **0.052** · |
| Protection (Pr) | 1 | 1.14E-02 | 0.73282 | 0.365 |
| Sex Pr | 2 | 1.03E-02 | 0.66405 | 0.452 |
| Res | 41 | 1.56E-02 | | |
| Total | 46 | | | |
| **Response variable: assemblage structure** | | | | |
| Secteur (Se) | 2 | 1776.7 | 2.2123 | **0.053** · |
| Protection (Pr) | 1 | 488.58 | 0.60834 | 0.601 |
| Sex Pr | 2 | 726.93 | 0.90512 | 0.437 |
| Res | 41 | 803.13 | | |
| Total | 46 | | | |

Significance = ·p ≤ 0.1; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

A single juvenile of the *T. pavo* species (50 mm TL) was observed, located in one of the most southern sites ("Cadaques" bay, in southern Cap de Creus sector). Taking into account both juveniles (<55 mm TL) and adults a total of 176 individuals of this species were observed (from 50 to 150 mm TL). The southern Cap de Creus had the highest average density (2.28 ind/100 $m^2$ ± 0.78) and mean densities showed a strong south to north decreasing gradient (Fig. 2). No individuals were observed on the two northern sectors (the northern FR rocky coast and sandy coast). The mean densities observed on the southern FR rocky coast (0.02 ind/100 $m^2$ ± 0.02) and the ES rocky coast (0.03 ind/100 $m^2$ ± 0.03), were not significantly different from 0 (Fig. 2).

We observed four juvenile *E. marginatus* in natural habitats: one in the southern FR rocky sector (Paulilles cove, 70 mm TL) and three in the southern Cap de Creus sector, at Peligri cove (120 mm TL), Joncols cove (110 mm TL) and Roses (80 mm TL) (see illustration in Sup. Fig. SF2). In each case they were located at a depth of about 1.5 to 2.0 m, sheltering in crannies between blocks and boulders of the heterogeneous rocky substratum. Finally, we observed three juvenile individuals of *D. dentex* (50, 70 and 70 mm TL), one of *D. cervinus* (50 mm TL) and one of *P. pagrus* (90 mm TL) in the entire study area (Table 1).

### 3.3. Protection level and anthropization index effect

The level of protection had no significant effect on the total juvenile density (Table 3; PERANOVA, $F = 0.733$, $p = 0.365$) and it had no significant effects on the assemblage structure (Table 3; PERMANOVA, $F = 0.608$, $p = 0.601$).

The MedImpact anthropization index showed a significant interaction with the overall density (Fig. 3; linear regression *t*-test, $F = 5.184$, $p = 0.032$); the most degraded sites displayed the highest juvenile densities. However the $R^2$ value of the linear regression was very low ($R^2 = 0.17$, $y = -0.3883x + 0.3415$) meaning that <20% of the variability was described by the linear model. The regression using the Micheli et al. (2013) index was not significant ($p = 0.176$).

## 4. Discussion

One fourth of the 240 km long coast that was evaluated displayed nursery habitat for the species on which this study focused. However, only a small portion (11%) of this essential fish habitat was under protection (marine park, natural park or partial reserve), and even a smaller portion (2%) benefited from the highest protection level (integral reserve). Juvenile densities among nurseries varied in space but not as a function of protection level. On the other hand, they were moderately and positively correlated with an anthropization index. Juvenile densities displayed contrasting spatial patterns according to taxa. As regards rare species, it is worthwhile to note that individuals of the protected grouper *E. marginatus*, not reported in the last 20 years in this area, were seen on four occasions during this study in 2015.

### 4.1. Nursery habitat availability and protection

We highlighted that a small portion of the existing nursery habitat benefited from strict protection (only 2% of the nursery habitat is located in integral reserves). Furthermore, it is important to remember that protection by MPAs does not necessarily protect juvenile fish habitat from transformation or destruction. And yet it has been demonstrated

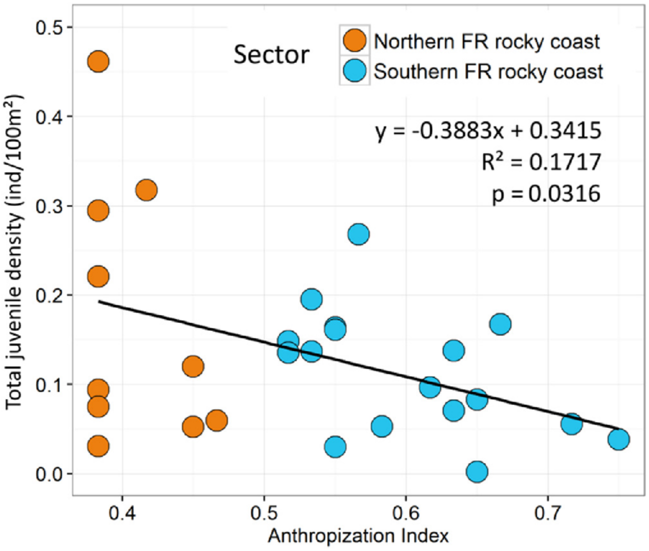

**Fig. 3.** MedImpact anthropization index in relation to total juvenile density per site. One dot = one site; x-axis: the index varies from 0 (most degraded) to 1.2 (least degraded).

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that habitat transformation (e.g. homogenization) is detrimental for its nursery value (sensu Beck et al., 2001; Cheminée et al., 2016). From a socio-economic point of view the implementation of strong regulation in juvenile zones is difficult as they are mainly located on beaches and creeks where touristic activities and coastal developments are concentrated. In the future, managers should focus their efforts on setting up measures to adequately protect this essential habitat, notably in buffer zones or outside of regulated core areas (integral reserve). Co-management (David et al., 2003; Granek and Brown, 2005) could avoid habitat transformations by promoting alternate coastal use and management practices, for example, by avoiding beach nourishment which is a common practice that tends to homogenize habitat and may reduce its nursery value (Cheminée et al., 2014; Cuadros, 2015). For this purpose, our data has been made available to MPA managers through the edition of an atlas displaying the full cartography of nursery sites of the area (Zawadzki et al., 2015). An extract of this atlas is given as an example in Supplementary Fig. SF1.

On the other hand, the results of this study show that the protection level of sites had no significant effects on either total density of juveniles or juvenile assemblage structure. This is not surprising considering that current MPA regulation tends to focus on adult catch limitations. However some indirect effects could be expected since protection may favor potential predators of juveniles and thus influence their survival and abundances (Tupper and Juanes, 1999).

### *4.2. Spatial variability of juvenile population descriptors: anthropization level impact*

Juvenile densities among nurseries were moderately and positively correlated with the MedImpact anthropization index. However, index values were not homogeneously spread among sites with southern sites being the most impacted. Consequently any correlation between juvenile densities and anthropization should be regarded cautiously since it might be linked to a confounding effect of space. The MedImpact anthropization index is calculated on the base of the composition of the photophilic macrophyte assemblages present in the medio-littoral (intertidal) level (Mannoni et al., 2014). The correlation between total juvenile density and the MedImpact anthropization index values, although weak, suggested that sites where composition of macroalgae assemblages, i.e. a proxy of water quality, was the most impacted supported higher densities of juveniles. However, any further correlation between juvenile densities and water quality cannot be conducted since this index may be subject to various biases. For example, this correlation may simply reflect the habitat preferences of the juveniles studied because they are known to prefer heterogeneous rocky and sandy habitats to macroalgae habitats. It would be interesting to find a way to get a direct measure of pollution and of other human pressures. This would allow a closer look at the anthropogenic pressures along this coastline to determine if and how they may have an effect on juvenile populations and habitat nursery value. In contrast with Micheli et al. (2013), others indexes could be developed at a finer spatial scale to better assess pressures such as levels of human site attendance, water and substratum contamination by micro-plastics (de Sá et al., 2015; Šiljić et al., 2015), etc.

### *4.3. Spatial variability of juvenile population descriptors: other possible drivers*

Our results are based on samples from one single year and therefore observed patterns should be interpreted cautiously since juvenile descriptors are known to vary between years. Nonetheless, our data is useful to discuss, at a large spatial scale, for a given year, juvenile density variability and its link with possible drivers.

Our data showed that there was a significant spatial variation in the total juvenile density and assemblage structure of the juvenile assemblages along the Catalan coastline depending on the sector. The "sandy coast" sector hosted the highest average total density of juvenile fish and a unique assemblage structure, due mainly to a very high density of *D. sargus*. The five other sectors had much lower total juvenile densities and their assemblage structures were never significantly different from those of the adjacent sector(s). These results demonstrate a spatial variation of recruitment level between sites, for a given species in a given juvenile habitat. For a given juvenile habitat, nursery value and its proxy (i.e. recruitment level) are known to vary in space and time (Beck et al., 2001; Cheminée, 2012; Macpherson and Zika, 1999). For scientists and managers, the challenge is to understand what factors drive such variability. The following paragraphs aim to present some possible explanations that should be further investigated.

Both *D. sargus* and *Pagellus* spp. had very high average densities in all sites from the sandy coast sector compared to the five other sectors. In each studied sector (e.g. the sandy coast, the northern FR rocky coast, etc), we selected and studied sites so that, on average, sectors displayed similar habitat type (see Materials and methods section). For example, because strictly sandy beaches are not typical nursery habitats, nursery sites from the "sandy coast" sector included both artificial structures and three natural sites at Cap Leucate (a natural rocky outcropping situated in the middle of two long stretches of sandy beach). The artificial structures in the sandy coast sector are comprised of man-made structures placed in shallow zones, primarily in the form of breakwaters and jetties. In the sandy coast sector, high densities of juveniles were observed in both natural sites and artificial structures (see Results). Consequently, observed juvenile density patterns are linked with the sector but not with habitat type. During a three year study by Pastor et al. (2013) the breakwaters along the sandy coast sector had higher densities, every year, than sites from the northern and southern FR rocky coast sectors. It could be hypothesized that the juveniles along the sandy coast are simply concentrated in these sites due to the absence of suitable habitat along strictly sandy stretches of the shore. However, when these densities are extrapolated according to the total length of available nursery habitat, and standardized using the total length of each sector, the sandy coast sector truly seemed to be characterized by either a much higher input of juveniles and/or a much better survival rate (see Sup. Table ST2). In comparison, the northern Cap de Creus had an even lower relative percentage of nurseries along its coast but did not boast similar densities of juveniles in its nursery habitats. Thus, for the year 2015, high densities of *D. sargus* and *Pagellus* spp. on the sandy coast may be driven rather by a notably higher initial post-larvae input and/or a better juvenile survival inside nurseries. Initial post-larvae input is mainly driven by (a) adult reproduction location and intensity, (b) the local hydrodynamics, and (c) habitat availability and accessibility. On the other hand, juvenile survival is driven notably by (d) predation pressure and (e) food availability. We discuss these alternatives in the following paragraphs.

The location of *D. sargus* adult reproduction events (a) remains a poorly explored thematic in the Mediterranean. Telemetry research programs studying the movements of adult individuals could shed light on reproduction behavior for *Diplodus sargus* and *E. marginatus* (Koeck et al., 2014; Pastor et al., 2009).

Regional hydrology (b) has a major influence on the initial larval dispersal from breeding sites, the displacement and survival of planktonic larvae, and their input towards settlement sites along the coast (Hindell et al., 2003). In the Catalan region, hydrological data suggests that there is a dominant current coming from the northeast, the "liguro-provençal" current, which could bring with it larval flow (Guizien et al., 2006; Pastor, 2008). If the majority of larvae are grouped in this current, the northern nursery sites (on the sandy coast sector) might capture the post-larvae before they travel farther south (Pastor, 2008). This might explain why between the sandy coast and the rocky coast there is a significant decrease in density. Future research on spawning grounds and Langrangian models of larval transport should be performed and may be able to clarify some of the questions raised by this data.

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As regards habitat accessibility (c), most of the sites along the "sandy coast" sector are more "exposed" (i.e. accessible) since more opened towards the sea -*sensu* Cuadros et al. (2017)- than the sites from other sectors. In the area around Cap de Creus, for example, the sites are hidden within the morphology of the coastline. These enclosed coves may provide well-suited habitats for juveniles, but they may also be difficult for post-larvae to access at settlement (Cuadros, 2015; Cuadros et al., 2017). In comparison, the sandy stretches along the southern Gulf of Lion may be adapted for the success of artificial structures as potential juvenile nursery habitat because they provide easily accessible habitat where none exist. Artificial structures may even increase connectivity between natural rocky habitats and help to maintain, if not improve, biodiversity (McCormick and Makey, 1997). However it should not be forgotten that construction of any artificial structure also physically destroys previously present habitats, which may be functionally important for other species. For example, along the sandy coast, ports and jetties were often built in the opening of small estuaries connecting coastal lagoons to the sea. Such soft and flat sandy bottoms are known to be nursery grounds for flat fishes (Le Pape et al., 2003).

We used protection as a proxy of predatory pressure (d), but we could not detect any effect on juveniles (see above). On the other hand, food availability (e) can also play an important role in the quality and nursery value of juvenile habitats (Beck et al., 2001). The sandy coast and the northern FR rocky coast sectors have been subject to strong anthropic pressures resulting from the urbanization of this coastline. Development of a large agricultural industry (viticulture) has led to the input of chemical fertilizers along this coastline (Delay, 2015). Harbors and the protected areas of breakwaters are suitable for zooplankton expansion, which constitutes the staple food of juvenile fishes (Clynick, 2006). The addition of chemical fertilizers to the water around these sites might lead to blooms that could provide adequate food resources to support high densities of *Pagellus* spp. and *D. sagrus* along the sandy coast. Other species such as *D. puntazzo* might not be sensitive to this driver; i.e. may not be limited by food, since they do not usually settle in such abundant shoals as usually do *D. sargus* (Cheminée et al., 2011; Vigliola et al., 1998). Further studies would be required to test the effect of food availability.

Furthermore, although high juvenile densities may seem like a positive ecological outcome, it is also true that juvenile growth rates can be density-dependent. Macpherson et al. (1997) found that *D. sargus* was subject to density-dependent mortalities and that this caused the reduction in the variability of year-class strength. Even in nursery habitats with high food availability and low predation risk, an over-population of juveniles can cause diminished growth rates (Dahlgren and Eggleston, 2000) and may be important in limiting the population (Walters and Juanes, 1993). A more detailed study of juvenile TL could help to clarify any potential negative effects that the high densities observed on the sandy coast have on juvenile growth.

In the Mediterranean, recruitment into the adult populations for *D. puntazzo* begins the end of April (Harmelin-Vivien et al., 1995). Therefore we would expect some of the juveniles to have left the nursery habitat by the time of surveying in late July. However, many juveniles remained inside nurseries, with a general north to south increasing gradient. *D. sargus* and *D. puntazzo* occupy spatially different adult habitats and nutrition (Sala and Ballesteros, 1997) but juveniles of both species depend on the same nursery habitats (Vigliola, 1998). However, the temporal repartitioning of their installation within the nursery habitat along this coastline may limit competition for resources (Harmelin-Vivien et al., 1995). A study of *D. puntazzo* juveniles during their settlement peak in the nursery habitat (October/November), along with their size-class distribution, would help to clarify questions regarding their spatial distribution.

Although there appears to be no significant difference in juvenile densities between the sectors for *S. viridensis*, there has been some question as to whether species misidentification may have occurred. It is possible that the European barracuda (*Sphyraena sphyraena*, Linnaeus, 1758) is also present along this coast. These species are difficult to differentiate during their juvenile stage but juveniles of these two species have never been identified in the same juvenile habitat, suggesting habitat segregation between them (Di Blasi et al., 2013). Surveying in subsequent years could aim to clarify this point through the capture and rearing of juveniles for proper identification.

### *4.4. Scarce species: even punctual observations have meaningful implications*

Only one juvenile of the species *T. pavo* was observed in 2015, in the southern-most sector. Our results also show that adults in 2015 were present in the four southern-most sectors, with increasing densities towards the South. This stenotherm species is usually found on the southern Mediterranean coasts, in warmer waters. According to the maps presented in Guidetti et al. (2002) and Milazzo et al. (2016), the Gulf of Lion remain one of the last areas of the Mediterranean not populated by *T. pavo*. Generally *T. pavo* adults are the first to be observed colonizing a new area, followed by the juveniles (Figueiredo et al., 2005). Recent works highlighted the warming-related shifts of this species' distribution towards the north-western parts of the Mediterranean (Milazzo et al., 2016). Therefore the presence of a juvenile in this sector, along with the higher abundances of adults observed in the south part of the study area, may be strong indicators of this distribution shift. A yearly survey of this species would help to analyze and determine the extent and rapidity of this process.

We observed four juvenile *E. marginatus* in natural habitats in 2015, one in the southern FR rocky sector and three in the southern Cap de Creus sector. The southern FR rocky sector has been monitored during the past 20 years using a comparable method and absolutely no young-of-the-year groupers (<10 cm TL) had been reported there (Bodilis et al., 2003a, 2003b). Once highly hunted by spearfishers, this species suffered an alarming decrease in abundance in the north-western Mediterranean (Coll et al., 2004). Since its strict protection in France in the 90's it has been slowly recolonizing the area. However, along French coasts of the entire Gulf of Lion, only one young-of-the-year had been observed in natural habitats over the last twenty-five years (Bodilis et al., 2003a). Accordingly, our observation of four juvenile groupers over a short stretch of shoreline in the same year is exceptional. Moreover, another observation of a juvenile *E. marginatus* was documented in an artificial habitat in the same study area (Northern FR rocky coast, Port Vendres harbor) in 2015 and in two other artificial habitats placed in harbors in the northern Gulf of Lion in 2013 and 2014 (Mercader et al., 2016). As juveniles, dusky groupers tend to be easily frightened so their absence in previous years might not mean they were not present. However, the density of juveniles seems to have reached a threshold at which observations are more likely. This is a major observation in the context of the conservation and stock replenishment of this emblematic and protected species.

Only one individual of *D. cervinus* was observed during the surveys and it was located on the sandy coast. The low abundance of adults of this species in the NW Mediterranean, even inside MPAs (Derbal and Kara, 2006), is probably preventing strong reproduction and settlement events. Moreover, *D. cervinus* shows large inter-annual variations, peaking approximately every ten years (Authors unpublished data). Peaks in *D. cervinus* settlement typically coincide with peaks in *D. sargus* settlement but at much lower densities (Garcia-Rubies and Macpherson, 1995). It is known that if the appropriate meteorological conditions do not occur during the limited settlement period, larvae will be subject to massive mortality due to famine and predation, resulting in low juvenile populations. The random nature of these events explains why the settlement process of most organisms is unpredictable and why settlement intensity is highly variable through space and time (Vigliola et al., 1998).

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The very low densities of other species that were observed (*D. dentex*, *P. pagrus*) put into question our knowledge of their juvenile habitat preferences. Some previous studies (Cheminée, 2012; Thiriet et al., 2014) pointed out that these taxa may rather use transitional zones between different habitats, an illustration of the "edge-effect" (Smith et al., 2011).

### 4.5. Perspectives at the Mediterranean scale

In this study, we provide useful information regarding the ecology and management of some important species. However, due to the temporal variability of settlement events, further studies repeated in other years are needed to confirm or contrast trends observed in 2015. Furthermore, future objectives for the fundamental understanding of species life cycles and for management practices must be seen in the context of the complex seascape mosaic of coastal environments. First, the nursery value of other habitats, for other species, must be studied since the replenishment of coastal biodiversity relies not only on a few habitat types but on the complementarity of the seascape mosaic (Colloca et al., 2015). Secondly, pre-settlement and post-settlement factors and processes driving nursery value variability (between habitats, between sites for a given habitat) must be understood (Cuadros et al., 2017). For example, before settlement, these include, among others things, successful reproduction and egg and larval dynamics. After settlement, they include the effect of anthropogenic drivers (e.g. pollution, invasive species, habitat degradation as well as habitat restoration, etc.) on juvenile growth and survival. Thirdly, for the coastal management of a given area, protecting essential habitat from degradation is a multivariate task, since it must include not only the various nursery habitats corresponding to various species, but other functionally important habitats as well (breading and feeding grounds for example) (Cheminée et al., 2014). Furthermore it must take into account the possible failure of a given site a given year, which means acting among a network of connected managed areas. In this sense, both fundamental research and management require further studies of population connectivity at various life stages.

## 5. Conclusions

Regarding the ecological dynamics of the studied species, our results from 82 sites in 2015 underline that although the suitable habitat for juvenile fish was present, strong spatial differences in the final recruitment level exist between sites spread over a 240 km long coastline. Furthermore, only a small portion of these essential habitats was under efficient protection. This data stresses the need, first, to promote nursery habitat protection as a complement to adult stock management, and second, to implement protection in a variety of sites in order to prevent local failure of recruitment. Our results provide some insights into factors shaping recruitment level: it was not explained by protection level, but it was moderately and positively correlated with an anthropization index. Further studies of these driving factors, including over several years, will be required. By considering an even larger spatial scale, e.g. the entire Mediterranean, future work could allow a better comprehension of possible forcing factors, such as global warming, pollution or invasive species. Juvenile densities displayed contrasted spatial patterns according to taxa. As regards rare species, it is worth noting that individuals of the protected grouper *E. marginatus*, unseen in the last 20 years in this area, were seen on four occasions during this 2015 study. Additionally, our data will be useful for monitoring further the expansion of a stenotherm species, *T. pavo*, in response to global warming. In this way, our results underline the importance of setting up and maintaining long term monitoring.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marpolbul.2017.03.051.

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