RESEARCH ARTICLE

Is artificial habitat diversity a key to restoring nurseries for juvenile coastal fish? Ex situ experiments on habitat selection and survival of juvenile seabreams

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Man-made infrastructures have become ubiquitous components of coastal landscapes, leading to habitat modification that affects the abundance and diversity of marine organisms. Marine coastal fish have a complex life cycle requiring different essential habitats. One of these habitats is known as a nursery, a place where juveniles can settle in large numbers, survive, and grow to contribute to the adult population. Nurseries are mainly found in shallow, sheltered zones and are thus particularly impacted by urbanization, notably by harbors. The vertical featureless structure of docks is very unlikely to be used by juveniles, which need complex habitats to find food and shelter from predators. Recent attempts to rehabilitate the nursery function in such environments by using artificial habitats have proven efficient in increasing juvenile densities. However, nothing is known about the survival of juveniles in these habitats, preventing any conclusions on the effectiveness of this means of restoration from being drawn. Here, we set up tank experiments to test the relationship between habitat preferences and the survival rate of two species of seabream when facing stalk-attacking combers. Habitat choice was consistent with survival results, indicating that artificial habitats might not represent unintended ecological traps for juveniles. However, the artificial habitats' effect on survival was variable between species. Therefore, our results suggest that habitat diversity might be of prime importance to sustain juveniles of different species and stress the need for the development of diverse artificial habitats to counteract the effects of seascape homogenization.

Key words: artificial habitat, habitat selection, marine restoration, nursery, seascape homogenization, survival rate

Implications for Practice

- The effectiveness of artificial habitats as nurseries is species dependent. An artificial habitat can have a beneficial effect by being selected by juveniles and enabling a good survival rate or represent a potential "equal-preference trap" by leading to a lower survival rate and not being avoided. Additionally, the rehabilitation of nursery function should favor diverse artificial habitats to benefit multiple species and developmental stages.
- Management efforts to maintain coastal fish populations should include the conservation of remaining natural nursery habitats and the rehabilitation of degraded environments.
- To gain efficiency, marine coastal restoration requires the implementation of a diversity of solutions, which need to be developed and tested in a collaborative way among engineers, managers, and scientists.

Introduction

Landscape modification resulting from habitat degradation, fragmentation, or loss is known to be a key driver of species extinction leading to biodiversity loss in all ecosystems (Foley 2005; Hewitt et al. 2010). Homogenized landscapes impact not only the abundance of organisms but also the structure of communities and the functioning of ecosystems (Brokovich et al. 2006; Fischer & Lindenmayer 2007), reducing valuable functions and services (Cardinale et al. 2012). For marine ecosystems, this threat is particularly intense in coastal areas, where the human population and its ensuing pressures are concentrated

(Airoldi & Beck 2007) while being crucial for the early life stages of many species. Indeed, the heterogeneity of the coastal seascape results in a large variety of habitats providing food and shelter essential for juveniles (Beck et al. 2001). Habitat homogenization and simplification might then threaten the nursery function played by coastal areas (Piko & Szedlmayer 2007; Cheminée et al. 2016). The nursery value of a habitat is given by its relative contribution to the adult population by comparison to other nearby habitats. This contribution is the result of four factors: (1) initial density (better settlement), (2) survival rate, (3) growth rate, and (4) migration toward adult habitats (recruitment; Beck et al. 2001). Mortality during early fish life is high, reaching more than 90% by the end of the larval stage (Houde & Hoyt 1987), and postsettlement processes, such as juvenile growth and survival, which are directly linked to habitat availability and quality, are known to be of prime importance in the sustainability of populations (Nagelkerken et al. 2015). In recognition of the risk that coastal development might pose to marine populations, increasing efforts are being made to restore coastal habitats (Paalvast et al. 2012; Brown & Chapman 2014; Sella & Perkol-Finkel 2015). On the shoreline, harbors are the most common coastal infrastructures, and they have serious detrimental environmental impacts (Meinesz et al. 1991; Falandysz et al. 2002; Martin et al. 2005; Neira et al. 2011). With regard to coastal fish population maintenance, they may represent a risk, notably by acting as traps in which larvae can arrive but will not find suitable habitat to settle and survive. Indeed, the featureless nature of docks is very unlikely to provide them the food and shelter they need (Mercader et al. 2018). To mitigate this effect, programs of rehabilitation of the nursery function for coastal fish have been initiated within harbors. The first results showed that increasing habitat complexity by using small artificial habitats leads to increased juvenile densities (Bouchoucha et al. 2016; Mercader et al. 2017; Patranella et al. 2017). However, the observation of higher juvenile densities is not enough to draw a conclusion about the nursery role of artificial habitats or the success of rehabilitation. Indeed, the observation of higher densities could be the result of a simple concentration effect (Brickhill et al. 2005), which might induce adverse effects if the fitness of the juveniles on artificial habitats is lower than that on other available habitats. Preferential settling on artificial habitats could, for example, make juveniles more accessible to predators or induce greater competition for nutritional resources, inducing higher mortality. In such cases, the use of artificial habitats for harbor rehabilitation could lead to the formation of ecological traps (habitats preferred by animals but in which their fitness is lower than that in other available habitats; Robertson & Hutto 2006). Rehabilitation would not only be unsuccessful but could also compromise population persistence and increase extinction risk (Battin 2004; Hale et al. 2015a). Traps are known unintended consequences of management and restoration activities (Robertson et al. 2013; Hale et al. 2015b). Additionally, assessing the survival rate and habitat preference is a key element to guide restoration efforts because successful restoration results from the provision of suitable habitats (providing required resources to targeted species), which animals must perceive as appropriate and colonize (Van

Dyck 2012; Andrews et al. 2015; Hale & Swearer 2017). In that context, the main objective of this work was to determine whether artificial habitats used for harbor rehabilitation could represent ecological traps for juvenile fish. To do so, we tested the following hypotheses: (1) mortality of juvenile fish is not higher on artificial habitats than on other habitats and (2) juveniles are selecting the habitat that provides lower mortality (i.e. the better survival rate).

For juvenile coastal fish predation, competition for shelter and starvation are the main causes for density-dependent mortality (Hixon & Jones 2005). While other causes of mortality exist (pollution, diseases …), we focused our study on predation-induced mortality. Juvenile depletion from a given habitat results from two distinct processes, mortality and emigration, which are difficult to differentiate in open environments. Previous studies revealed that in the Mediterranean Sea, artificial habitats used for harbor restoration are mainly used by *Diplodus* spp. (seabream; Bouchoucha et al. 2016). At the juvenile stage, these species do not undergo large displacement, but they can still move at the scale of a whole cove (Macpherson 1998), which prevents accurate study of their mortality on the smaller scale represented by artificial habitats. Furthermore, visibility inside harbors is often poor, making it difficult to precisely follow cohorts. Given these ecological constraints, tank experiments represent a good alternative for studying the mortality of juvenile seabreams. A first set of experiments permitted (1) the estimation of predation-induced mortality rates of juveniles on different habitat types and (2) the exploration of the influence of those habitats on prey and predator behavior. A second set of experiments was designed (3) to determine the habitat preferences of juveniles. Based on the criteria outlined by Robertson and Hutto (2006), the combination of the results allowed us to test our hypothesis and to assess the relationship between habitat selection and survival to identify if these habitats could represent potential ecological traps.

Methods

Studied Fishes

We focused on the juveniles of two sparid species: the two-banded seabream (*Diplodus vulgaris* [Geoffroy Saint-Hilaire, 1817]) and the white seabream (*Diplodus sargus* [Linnaeus, 1758]), which were used as model prey species. These species are common in Mediterranean coastal waters, and their high commercial value places them among the most harvested species by local artisanal fisheries (Coll et al. 2004; Lloret et al. 2008). The juveniles settle in shallow heterogeneous rocky habitats made of small blocks, pebbles, or coarse sand, and their life cycle and behavior at settlement are representative of those of most coastal nektobenthic fish species (Harmelin-Vivien et al. 1995; Macpherson 1998; Planes et al. 1998). Both species can also be found in high densities on artificial structures such as breakwaters or jetties (Clynick 2008; Pastor et al. 2013) and have been observed inside harbors (Bouchoucha et al. 2016; Mercader et al. 2017, 2018). If they use the same habitats as nurseries, they do not settle during

the same time period: *D. vulgaris* postlarvae reach the shore from December to March, while *D. sargus* postlarvae arrive between May and June, which avoids competition between these two species. *D. vulgaris* is also more opportunistic and can settle slightly deeper in the ecotone between rocky bottom and shallow meadows (Vigliola & Harmelin-Vivien 2001).

We used the comber (*Serranus cabrilla* [Linnaeus, 1758]) as a predator model. This abundant species mainly lives around rocky substrates and meadows, which constitute suitable habitats for its stalk-attacking strategy to predate. The comber is an opportunistic macrocarnivore and one of the most important predators of small fish (Stergiou & Karpouzi 2002; Cresson et al. 2014). Its small size (10–25 cm as an adult) and its aggressive nature also make it a good model for predation tank experiments.

Fish Collection and Housing

Individuals were collected in the natural environment. None of these species are endangered or protected, and sampling did not include any sites within marine protected areas. Fishing protocols and sites were approved by the Direction Inter-Régionale de la Mer (DIRM, the French administration of maritime affairs) under permit number 560. Fishes were captured on two expeditions, corresponding to the prey model's arrival on the coast, in February (for *D. vulgaris*) 2016 and June (for *D. sargus*) 2017. For both expeditions, captures were performed at the same sites of the French Catalan coast using hand nets for seabreams and lines and hooks for combers.

After collection, juveniles were held in 500-L tanks with a maximum of 200 individuals/tank to minimize damage and stress. Combers were placed individually in tanks of 45 L to avoid any aggressive behavior among them. All tanks (housing and experimental, see next section) were connected to the same filtration system filled with natural seawater. The water temperature was different between the expeditions to mirror natural conditions: 17°C in February and 22°C in June. The salinity (37), pH (8), and photoperiod (12 hours/day of artificial light) were constant throughout all experimental expeditions. Physicochemical parameters (pH, NH_3, NO_2, NO_3, salinity, and temperature) were checked and adjusted twice a week. Fish were acclimated for 2 weeks before starting the experiments to allow them to recover from catching. Juveniles were fed twice a day with defrosted *Artemia* sp.; combers, once a day with defrosted *Atherina* sp. Combers were not fed for 48 hours before each experiment to ensure that they were all in the same starvation state at the beginning of all trials. At the time of experiments, the fish were at a mean size of 2.4 ± 0.1 cm for *D. vulgaris* and 2.3 ± 0.2 cm for *D. sargus*. The sizes of *S. cabrilla* were 15.1 ± 1.8 cm and 15.5 ± 1.4 cm for experiments with *D. vulgaris* and *D. sargus*, respectively. Once the experiments were performed, all predators and juveniles that had not been eaten were released alive at their capture site.

Experimental Design

All experiments were held in $100 \times 50 \times 40$ cm tanks connected to the same filtration system as the holding tanks. For mortality experiments, an activated carbon filter was added to each experimental tank between each trial to clear away dissolved fish chemicals from trial to trial (Martin et al. 2010). To avoid any disturbance, filtration and air pumps were turned off during the whole duration of the experiments.

The bottom of all tanks was covered with a green velour carpet; the back and the sides of the tanks were masked with auto-adhesive blue film to prevent exterior perturbations during experimental trials. We conceived of four different types of habitats, two of which mimicked typical natural nursery habitats for sparids: rocky chaotic clusters (R) and *Posidonia oceanica* meadow (M), one artificial habitat similar to those used in recent ecological restoration projects (AH), and a control (C; Fig. 1). Each habitat was conceived to occupy a 60-dm^3 volume, dividable into two equivalent parts (of 30 dm^3), so it could be used in both experiments (mortality and habitat selection). Rocky chaotic clusters consisted of quarry stones randomly placed in the aquarium to provide heterogeneous shapes and sizes of cavities. The stones were piled up to form a $25 \times 25 \times 100$ cm habitat. Meadows were made of plastic algae fixed to two 50×25 cm Plexiglas planks (for a total dimension of $25 \times 25 \times 100$ cm). Each plank was composed of 12 ft with 20 leaves of 20 cm height and 10 ft with 12 leaves of 25 cm dispersed randomly. The total leaf density resulting from the dispersal was 2,880 leaves/m^2 for 95% to 100% recovery, corresponding to a medium-density meadow (Buia et al. 2004), which is representative of what can be found in the area between 0 and 3 m depth (Rotini et al. 2013). The artificial habitat used was composed of a pair of stainless steel alloy cages of different mesh sizes (5 cm for the outer cage, 2.5 cm for the inner), the inner cage being filled with oyster shells (see Bouchoucha et al. 2016 for full description). The original version of this habitat was an $80 \times 25 \times 50$ cm rectangle. Here, we used two smaller versions of $30 \times 25 \times 35$ cm, which were hung from the top of the tank, leaving a 5 cm space between the tank bottom and the habitat. For the control, two weighted plastic tubes (L = 20 cm, $\emptyset = 8$ cm) were placed in the tanks to avoid comber stress due to the total absence of habitat.

Survival

Four tanks were used, each presenting a habitat (AH, M, R, or C) occupying a volume of 60 dm^3 (Fig. 1A–D). A see-through plastic plank was placed in the middle of the tank to divide it into two halves, preventing encounters between prey and predator but letting them see each other. Five juveniles were placed on one side and a predator on the other for 30 minutes, allowing them time to recover from manipulation, acclimate to the new tank, and explore the habitat. The position (right or left) of the juveniles and the predator during this acclimation was switched for each replicate. After 30 minutes, the plastic plank was removed and experimentation began. For 2 hours, tanks were recorded using a camera (GoPro HERO3, GoPro, Inc., San Mateo, CA, USA) placed in front of the tank, allowing the measurement of the exact time of every predation event. In addition, behavioral data (numbers of approaches, attacks, and escapes, cf. Table S1, Supporting Information, for the description of each
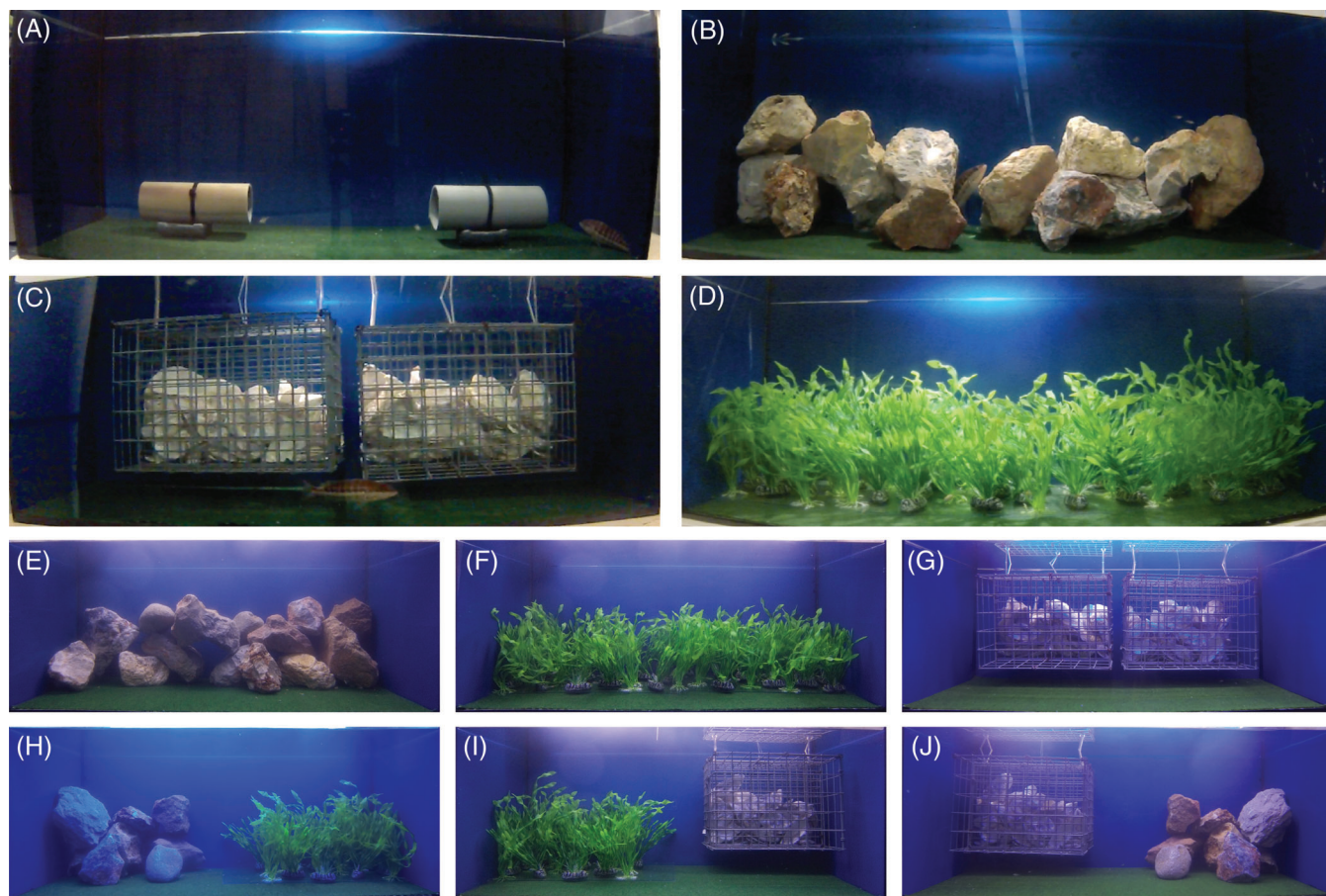
Figure 1. Habitat types used for survival experiments (A to D) and habitat selection experiments (E to J). Artificial habitat (A), rock (B), control (C), meadow (D), combination rock-meadow (E), meadow-artificial habitat (F), artificial habitat-rock (G), and controls (H to J).

behavior) were recorded every 30 seconds by direct observation during the first 30 minutes of experimentation. At the end of the experiment, surviving juveniles and predators were removed from experimental tanks. Predators were replaced in their individual tanks, and juveniles were put in a new housing tank to avoid using them a second time. For each habitat type and each prey species, eight trials were run. To ensure complete randomization, each habitat was placed in a tank for two runs and then moved to the next tank until it had been placed twice in each tank. To prevent predators from encountering the same habitat twice (and thus risking the predators learning the environment) and to limit potential bias due to interindividual behavioral variability, two combers were randomly assigned to a tank in such a way that each of them would run the experiment once for each habitat.

Habitat Selection

Habitat selection was investigated for juveniles of the two species, *D. vulgaris* and *D. sargus*. Experiments were held in a unique tank. Habitats were arranged in the tank in combinations of two (M/AH, R/AH, M/R), with each habitat occupying half of the tank and representing a volume of 30 dm^3 (Fig. 1E–G).

In addition to the three combinations, three control experiments were carried out in which the same habitat was present in the whole tank (AH1/AH2, M1/M2, R1/R2; Fig. 1H–J). Five juveniles were placed in the middle of the tank, and observations began 1 minute after their introduction. The same camera as the one used for survival experiments was placed in front of the tank and was set to take a picture every 2 seconds for 5 minutes to determine the position of the juveniles (cf. next section). As with the previous experiments, all fishes were removed from the tank and placed in a separate housing tank to avoid using the same fish twice. Eight replicates were run for each habitat type for both species.

Data Acquisition

Videos of survival experiments were used to report the time at which each lethal interaction occurred and to allow the calculation of the mortality kinetics. As mentioned previously, qualitative behavioral data were recorded only for the first 30 minutes. For habitat selection, pictures were first corrected for the distortion due to the fish eye of the camera using Photoshop (version CC 2015). The position of the fish in an *x-y* plane was then incremented using ImageJ (version 1.51j8). Due

to battery issues, only 4 minutes 30 seconds (out of the intended 5 minutes) could be analyzed for all trials, which still represents 130 pictures, 650 coordinates per replicate, and 5,200 coordinates per treatment (M/AH, R/AH, M/R, AH1/AH2, M1/M2, R1/R2). The intermediate area separating the two habitats in a tank was used as a limit to evenly divide each tank into two parts corresponding to the different habitats. Each pair of coordinates was then assigned to a habitat.

Statistical Analysis

For all statistical analyses, the significance threshold was fixed at 0.05. The survival and habitat selection analysis, which respectively test the survival function and Jacob's selection index as response variables, were run in R (R Core Team 2017). Behavioral analysis of the multivariate response data (number of each behavior) was performed using PRIMER 6 software with the permutational multivariate analysis of variance (PERMANOVA) add-on (Clarke et al. 2014).

Effect of Habitat on Juvenile Survival

To compare the survival of the juveniles between the four habitats (AH, R, M, and C), we determined juvenile survival probabilities in each habitat using the Kaplan–Meier method. This method allows to nonparametrically estimate the survival probability for censored and uncensored survival times (Kaplan & Meier 1958). Equality of the survival function between habitats was tested using the Peto and Peto modification of the Gehan–Wilcoxon test because the hazard ratio was not constant over time and was not proportional between habitats (Diez 2013). If the hypothesis of equality was rejected, pairwise comparisons were performed using the Peto and Peto test with Benjamini-Hochberg-adjusted p values (Benjamini & Hochberg 1995). All survival analyses were performed using the "survival" package (Therneau 2015) for the R environment.

Fish Behavior

To compare the behavioral patterns of the fishes between habitats, we used the total number of observed behaviors for each behavioral variable (Approach, Attack, and Escape) in each trial as response variables. Multivariate analyses of variance were performed on Bray–Curtis dissimilarity matrices with the addition of a dummy variable. p Values were calculated by 999 random permutations of unrestricted raw data, as our design contained only one factor (habitat), and type III sum of squares (Anderson 2001*a*). The Monte Carlo test was used when fewer than 200 permutations were generated. Post hoc pairwise tests were performed when relevant. SIMPER analyses were conducted when PERMANOVAs were significant to determine the relative contribution of each behavioral variable to differences between habitats.

Habitat Selection

Jacob's selection index (SI; Jacobs 1974) was used to determine which habitat (AH, M, or R) juvenile fishes preferentially chose.

For each of the height replicates, SI was calculated with 650 points (*x-y* coordinates) corresponding to the position of each of the five juveniles every 2 seconds. This index is based on the following formula:

$$\mathrm{SI} = (n\mathrm{H1} - n\mathrm{H2}) \, / \, (n\mathrm{H1} + n\mathrm{H2})$$

where n refers to the number of points observed in habitat 1 (H1) and in habitat 2 (H2). This index ranges between −1 and 1. $\mathrm{SI} = -1$ indicates a preferential choice for habitat 1, $\mathrm{SI} = 1$ for habitat 2, and $\mathrm{SI} = 0$ indicates no particular choice. SI values were then used as response variables and compared to zero (for controls and combinations) using a one-sample Wilcoxon test. If controls differ from zero, observed choices are not linked to habitat type but to other unknown factors. If controls do not differ from zero but a combination does differ from zero, juvenile fish made a significant choice toward a habitat.

Results

Survival

Habitat type significantly influenced juvenile survival probabilities for both species (Peto & Peto test, p value 0.002 for *Diplodus vulgaris* and p value = 0.0053 for *Diplodus sargus*), but this effect was very different depending on the species. For *D. vulgaris*, the mean survival time was the lowest on the meadow habitat (88.88 ± 6.06 minutes), significantly lower (pairwise Peto & Peto p value = 0.009) than that on the AH, which provided the best survival time (108.16 ± 5.18 minutes). Survival on the control and rock was intermediate (98.43 ± 6.70 minutes and 93.38 ± 6.92 minutes, respectively; Fig. 2A; Table S2A). For *D. sargus*, survival was equivalent on the control (115.40 ± 2.60 minutes), meadow (115.23 ± 2.84 minutes), and rock (115.22 ± 2.41 minutes) but lower on the AH (98.23 ± 6.24 minutes, pairwise Peto & Peto p value = 0.038 for all three combinations; Fig. 2B; Table S2B). Mortality was globally lower for *D. sargus* than for *D. vulgaris* (14 and 29%, respectively, of total juveniles were eaten). It is also interesting to note that the lowest survival probability (at the end of the 120-minute experiment) for *D. sargus* (on the AH) was equivalent to the survival probability for *D. vulgaris* on rock (upper 0.86, mean 0.70, lower 0.57).

Fish Behavior

Behavioral patterns varied slightly according to habitat type. For *D. vulgaris,* these differences were significant (PERMANOVA p value = 0.004): only the control habitat significantly differed from all other habitat types (pairwise test p value = 0.026, 0.015, and 0.005 when compared to the AH, M, and R, respectively), which did not differ one from one another (Table S3). Fish in the control habitat were less active overall, but the difference resulted mainly from a lower number of approaches, which was responsible for most of the dissimilarity between the control and other habitats (SIMPER results: 59.11, 44.18, and 47.39% for M, R, and AH, respectively; Fig. 3A).
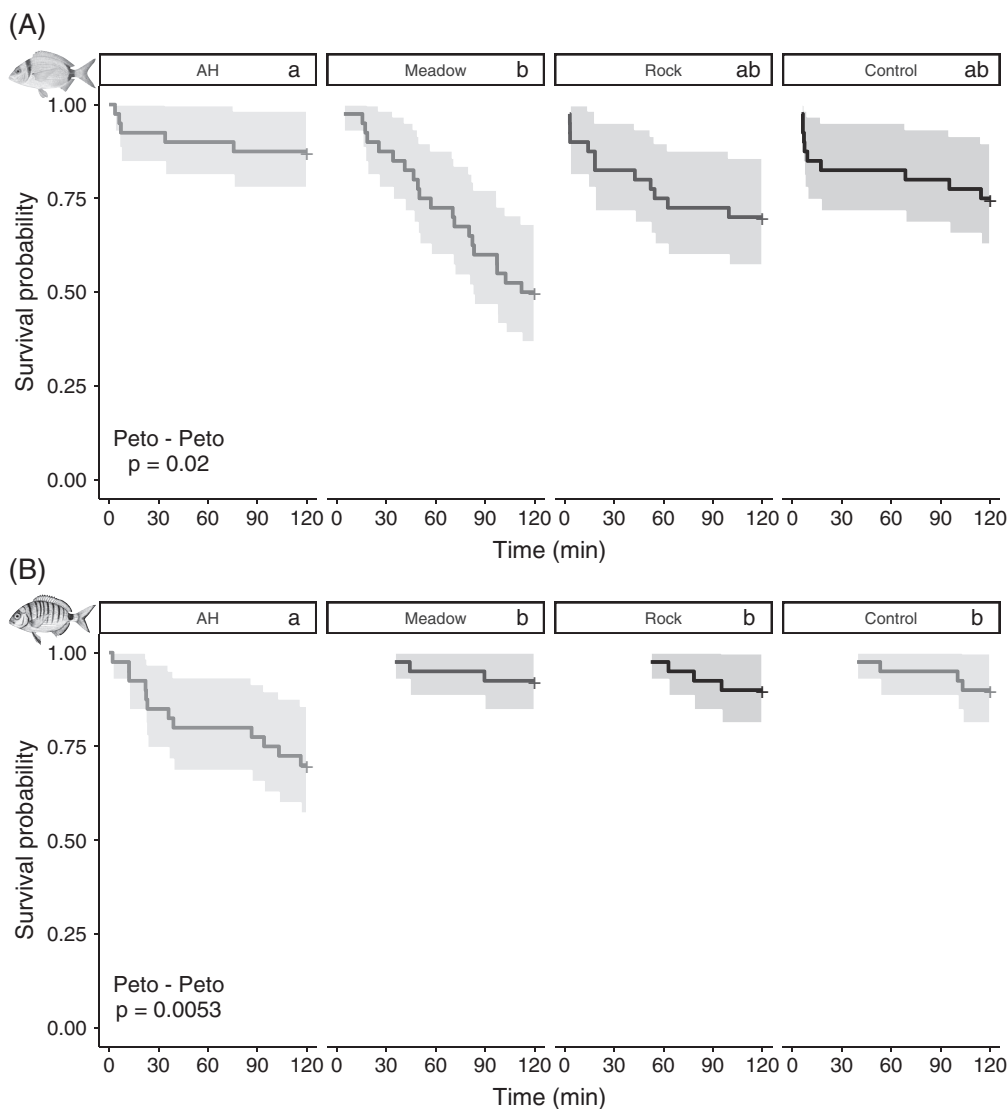
Figure 2. Kaplan–Meier survival curves for each habitat with 95% confidence intervals. Lowercase letters indicate the results of pairwise tests; habitats sharing at least one letter do not differ. (A) *Diplodus vulgaris* and (B) *Diplodus sargus*.

For *D. sargus,* habitat types did not significantly influence behavioral patterns. However, the fishes seemed to be more active on the AH, while almost no activity was recorded on the control (Fig. 3B).

Habitat Selection

For both species, all controls showed mean SI values that were not significantly different from zero, indicating that, when confronted with the same habitat in the whole tank, fishes did not show a preference for one side of the tank versus the other (Fig. 4A & 4B). Surprisingly, no significant deviation from zero was observed for any of the combinations of habitats and for both species. However, a trend close to significance was detected for *D. vulgaris*, which used slightly more AH than meadow (one-sample Wilcoxon test *p* value = 0.058).

Discussion

Our study revealed interspecific variations concerning the effect of habitat type on survival and on the efficiency of the AH as a nursery rehabilitation tool. The survival of *Diplodus vulgaris* juveniles on the AH was equivalent to that observed on their natural nursery habitat (rock). This species selected the AH as often as rocks while slightly dismissing meadows, on which survival was the lowest. Therefore, for this species, there was coherence between survival and habitat selection, which, coupled with the densities observed in the field (Bouchoucha et al. 2016), makes AH an efficient solution to mitigate the impact of nursery habitat loss caused by the presence of harbors (Hale & Swearer 2017). The structure of the AH might then provide comparable functionality to those of heterogeneous and complex natural rocky bottom (Bouchoucha et al. 2016), which is corroborated by the absence of a difference in behavioral patterns between both
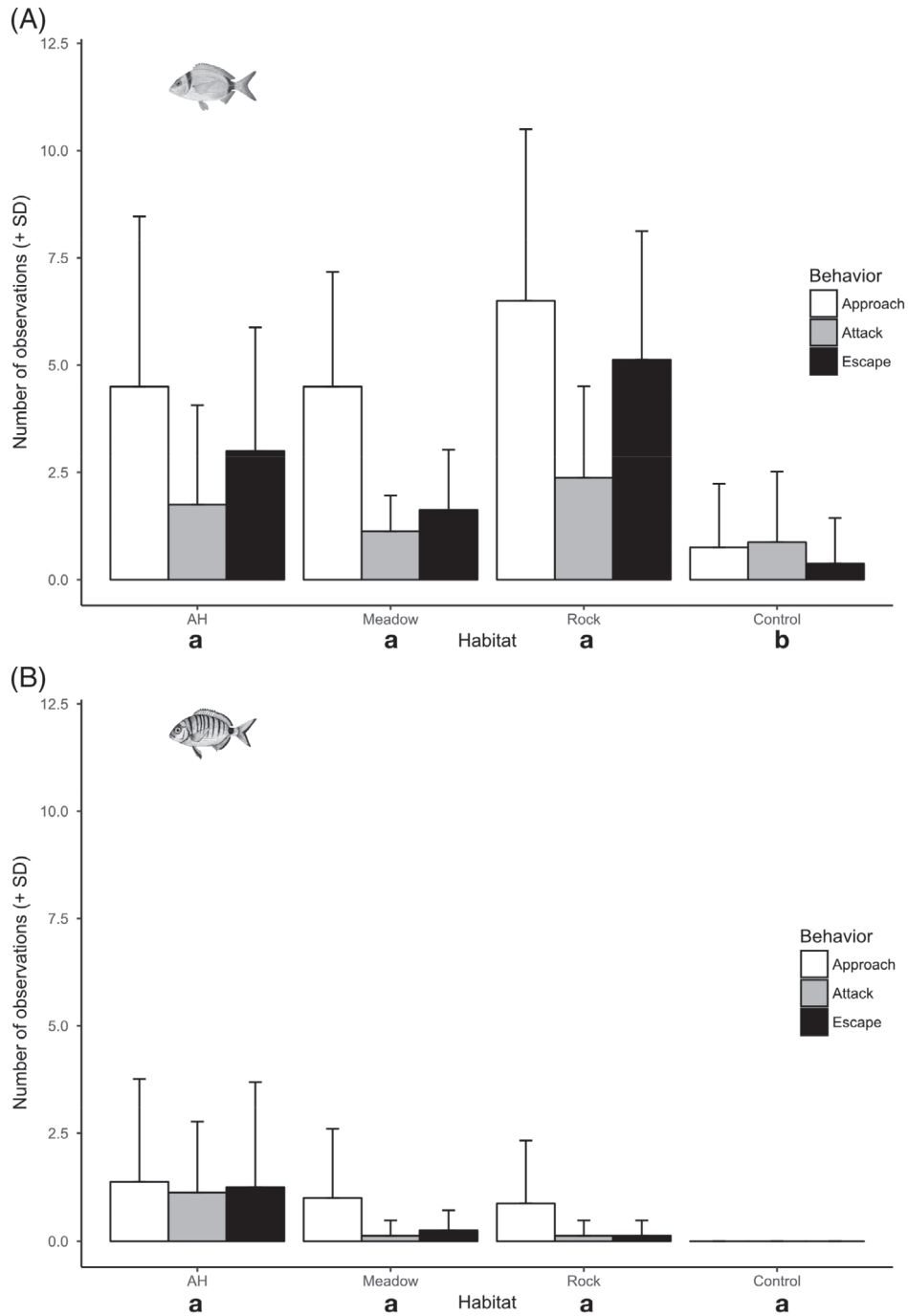
Figure 3. Mean number (+SD) of behavioral observations for the comber (approach and attack) and the juveniles (escape) for the first 30 minutes of the predation experiments on (A) *Diplodus vulgaris*, (B) *Diplodus sargus*. Lowercase letters indicate the results of pairwise tests; habitats sharing at least one letter do not differ.

habitats. On the other hand, *Diplodus sargus* juveniles experienced the lowest survival rate on the AH, and this species did not show any habitat preference. As they were not preferentially choosing the AH, the implementation of such habitats could result in the formation of an "equal-preference trap" (Robertson & Hutto 2006). These results are concordant with an in situ study that found that, within Mediterranean marinas,

juveniles of *D. vulgaris* use more AH than juveniles of *D. sargus* (Bouchoucha et al. 2016). The contrasting response observed between two close species implies that the formation of eventual traps cannot be discarded. However, as natural, better quality habitat is usually not available within harbors (as this is the reason why restoration is undertaken), further studies are needed to draw conclusions about the potential benefits of the use of AH
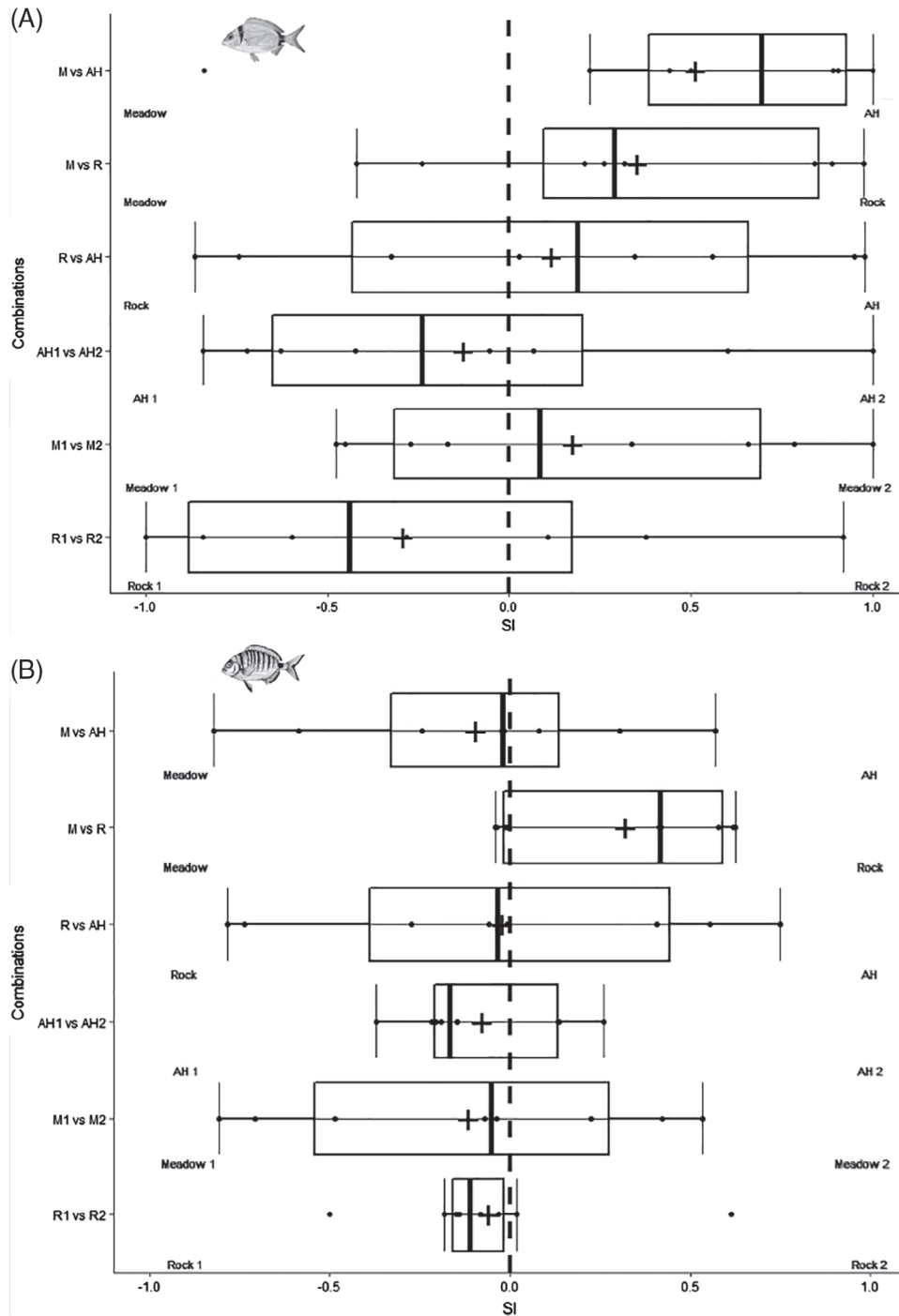
Figure 4. Boxplots of the spread of Jacob's selection index for (A) *Diplodus vulgaris*, (B) *Diplodus sargus*. Vertical black lines indicate the median; the ends of the boxes, the first and third quartiles; the whiskers, the values whose distance from the box is at most 1.5 times the interquartile range; the points, extreme values and black crosses, the mean values.

to rehabilitate the nursery function for juvenile coastal fishes. These studies should include the assessment of the fitness of individuals in the long term, take into account the landscape surrounding the AH, and should also be led on species naturally settling in different habitats (e.g. *Diplodus annularis* individuals that settle in meadows and *Chromis chromis* individuals that

settle on steep slopes of rocky reefs) or with more cryptic behavior (e.g. *Epinephelus marginatus* or juveniles from the Gobiidae and Blenniidae families). For cryptic juveniles, the type of AH used in this study might be of particular interest. Indeed, during all experimental trials, combers never entered the AH. Likewise, in the field, predators have never been observed inside AH

placed in harbors, with the exception of small gobies (authors' personal observations). This suggests an efficient refuge role from at least predators larger than 15 cm. This is not the case for all AH designs, as mentioned by Patranella et al. (2017), which sustains the hypothesis of an adapted structure to provide protection to juveniles. Therefore, the size of the cavities seems to be of prime importance to prevent the establishment of stalk attack and ambush predators (Almany 2004; Patranella et al. 2017). In the wild, most nursery habitats (e.g. seagrass meadows) also attract many predators. However, their structural complexity provides adequate refuge for juveniles, which limits the effectiveness of predators and thus limits the mortality of juveniles despite high densities of predators (Anderson 2001*b*). The number and diversity of the cavities (i.e. the complexity of a habitat) might also be a determining factor favoring multiple species and size classes (Rogers et al. 2014). In that sense, an AH might be a powerful tool to rehabilitate nursery function for many species if the size, number, and diversity of their cavities are well designed. Not only should one particular AH be designed with a variety of cavities but also various AH designs should be used to mimic the heterogeneity of the seascape and thus furnish complementary habitats for juveniles of different species or even for different developmental stages of the same species. Indeed, in all ecosystems, prey might adapt their habitat use depending on the presence of predators, which is an indirect effect of predation on the prey population known as risk effect (Hamilton & Heithaus 2001). In our study, juveniles faced variable mortality rates depending on the habitat but did not have the possibility to change habitat when facing predation. Additionally, if evolving in a heterogeneous seascape, they might use different habitats depending on the presence and nature of the predators, which might increase their survival. For instance, associating an AH designed to mimic a seaweed forest or phanerogam meadow with one mimicking complex rocky bottom could increase interhabitat connectivity and thus increase restoration efficiency (Traut 2005; Baillie et al. 2015).

Juvenile *Diplodus* spp. are known to undergo ontogenic shifts in habitat use, enlarging their niche by vertical (for *D. vulgaris*) or horizontal (for *D. sargus*) migration (Ventura et al. 2014). Those shifts have also been observed on the AH within harbors (Bouchoucha et al. 2016), and during experiments, most juveniles were observed under the AH, which seems to be the same in situ (authors' unpublished data). Changes in habitat use are a widespread behavior in juvenile fish in every ecosystem (Schlosser 1987; Machado et al. 2003; Feary et al. 2011; Kimirei et al. 2011). Additionally, placing AH at different depths and different locations could enhance its refuge role in many different restoration contexts (e.g. temperate and tropical coastal waters as well as lagoons and even freshwater environments, such as lakes or deep rivers).

One last factor that should be taken into account in AH conception is the material employed. For example, the use of particular concrete composition and surface texture is known to support enhanced fauna and flora (Perkol-Finkel & Sella 2014). Materials permitting the settlement of fouling organisms should be developed to enhance potential food provision and thus increase habitat quality.

If AH might reduce the predation-induced mortality of juveniles, pollution within marine urbanized areas might be greater than that in natural areas, which can increase the mortality of juveniles. However, juvenile seabreams within harbors show levels of contamination and growth rates comparable to those of individuals living in adjacent natural areas (Bouchoucha et al. 2018). Additionally, the risks of over-mortality linked to this factor might be low. Nevertheless, restoration projects should be considered only once pressures have been reduced to the lowest possible level. Indeed, if increased habitat complexity might increase juvenile survival, it is important to keep in mind that anthropogenic disturbances often lead to biotic homogenization (Olden 2006; Devictor et al. 2008). The set of species able to live in highly urbanized areas, such as harbors, might then be restricted to generalist species (Fischer & Lindenmayer 2007). Additionally, when possible, management efforts should first focus on the preservation of diverse natural habitats.

Plasticity in fish settlement requirements might be greater than expected. Juveniles are able to settle on artificial structures that can sometimes be very different from their natural habitat (Guidetti 2004; Pastor et al. 2013). Even species that are only rarely observed at the juvenile stage in natural habitats, such as the common dentex (*Dentex dentex*), the black seabream (*Spondyliosoma cantharus*), pipefishes (*Syngnathus* spp.; authors' unpublished data), or even the protected dusky grouper (*Epinephelus marginatus*; Mercader et al. 2016), have been seen within harbors. This suggests that even more specialized species could be able to live in those areas if suitable complex habitats are present. Marine restoration has a more recent development than its terrestrial or freshwater counterparts, and, probably due to the inherent properties of marine systems (hardly accessible and highly dispersive), the range of tools available to restore marine habitats remains restricted. However, projects using AH are increasing (Seaman 2007; Paalvast et al. 2012; Brown & Chapman 2014; Sella & Perkol-Finkel 2015), and some attempts to transplant living organisms to restore marine habitats are flourishing (Jaap 2000; Perkol-Finkel et al. 2012; Ng et al. 2015). Nevertheless, if the restoration of coastal fish nurseries is to be effective, efforts have to be made in designing new artificial habitats and nature-based solutions, which should be tested in two phases: (1) an experimental approach in aquariums to understand the use by juvenile species and (2) complex field experiments taking into account all factors potentially influencing juvenile mortality and their interactions. Such studies would permit confirmation and extend this work on the effect of nursery habitat restoration.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Behavioral repertoire describing prey and predator behavior during survival experiments.

Table S2. Results of the Peto & Peto main and pairwise tests performed to compare survival function.

Table S3. Results of the PERMANOVA test to compare behavioral patterns of *D. sargus* and *S. cabrilla*.