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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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Abstract :

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.

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

62 **Implications for Practice:**

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

75

76 **Introduction**

77 Landscape modification resulting from habitat degradation, fragmentation or loss is
78 known to be a key driver of species extinction leading to biodiversity loss in all
79 ecosystems (Foley 2005; Hewitt et al. 2010). Homogenized landscapes impact not only
80 the abundance of organisms but also the structure of communities and the functioning
81 of ecosystems (Brokovich et al. 2006; Fischer & Lindenmayer 2007), reducing valuable
82 functions and services (Cardinale et al. 2012). For marine ecosystems, this threat is
83 particularly intense in coastal areas, where the human population and its ensuing
84 pressures are concentrated (Airoldi & Beck 2007) while being crucial for the early life
85 stages of many species. Indeed, the heterogeneity of the coastal seascape results in a
86 large variety of habitats providing food and shelter essential for juveniles (Beck et al.
87 2001). Habitat homogenization and simplification might then threaten the nursery
88 function played by coastal areas (Cheminée et al. 2016; Piko & Szedlmayer 2007). The
89 nursery value of a habitat is given by its relative contribution to the adult population by
90 comparison to other nearby habitats. This contribution is the result of four factors: (i)
91 initial density (better settlement), (ii) survival rate, (iii) growth rate and (iv) migration
92 toward adult habitats (recruitment) (Beck et al. 2001). Mortality during early fish life is
93 high, reaching more than 90% by the end of the larval stage (Houde & Hoyt 1987), and
94 post-settlement processes, such as juvenile growth and survival, which are directly
95 linked to habitat availability and quality, are known to be of prime importance in the
96 sustainability of populations (Nagelkerken et al. 2015). In recognition of the risk that
97 coastal development might pose to marine populations, increasing efforts are being
98 made to restore coastal habitats (Brown & Chapman 2014; Paalvast et al. 2012; Sella &
99 Perkol-Finkel 2015). On the shoreline, harbors are the most common coastal

100 infrastructures, and they have serious detrimental environmental impacts (Meinesz et
101 al. 1991; Martin et al. 2005; Neira et al. 2011; Falandysz et al. 2002). With regard to
102 coastal fish population maintenance, they may represent a risk, notably by acting as
103 traps in which larvae can arrive but will not find suitable habitat to settle and survive.
104 Indeed, the featureless nature of docks is very unlikely to provide them the food and
105 shelter they need (Mercader et al. 2018). To mitigate this effect, programs of
106 rehabilitation of the nursery function for coastal fish have been initiated within harbors.
107 The first results showed that increasing habitat complexity by using small artificial
108 habitats leads to increased juvenile densities (Bouchoucha et al. 2016; Mercader et al.
109 2017; Patranella et al. 2017). However, the observation of higher juvenile densities is
110 not enough to draw a conclusion about the nursery role of artificial habitats or the
111 success of rehabilitation. Indeed, the observation of higher densities could be the result
112 of a simple concentration effect (Brickhill et al. 2005), which might induce adverse
113 effects if the fitness of the juveniles on artificial habitats is lower than that on other
114 available habitats. Preferential settling on artificial habitats could, for example, make
115 juveniles more accessible to predators or induce greater competition for nutritional
116 resources, inducing higher mortality. In such cases, the use of artificial habitats for
117 harbor rehabilitation could lead to the formation of ecological traps (habitats preferred
118 by animals but in which their fitness is lower than that in other available habitats)
119 (Robertson & Hutto 2006). Rehabilitation would not only be unsuccessful but could also
120 compromise population persistence and increase extinction risk (Hale et al. 2015a;
121 Battin 2004). Traps are known unintended consequences of management and
122 restoration activities (Robertson et al. 2013; Hale et al. 2015b). Additionally, assessing
123 the survival rate and habitat preference is a key element to guide restoration efforts
124 because successful restoration results from the provision of suitable habitats (providing

125 required resources to targeted species), which animals must perceive as appropriate
126 and colonize (Hale & Swearer 2017; Van Dyck 2012; Andrews et al. 2015). In that
127 context, the main objective of this work was to determine whether artificial habitats
128 used for harbor rehabilitation could represent ecological traps for juvenile fish. To do so,
129 we tested the following hypotheses: (i) mortality of juvenile fish is not higher on
130 artificial habitats than on other habitats, and (ii) juveniles are selecting the habitat that
131 provides lower mortality (i.e., the better survival rate).

132 For juvenile coastal fish predation, competition for shelter and starvation are the main
133 causes for density-dependent mortality (Hixon & Jones 2005). While other causes of
134 mortality exist (pollution, diseases...), we focused our study on predation-induced
135 mortality. Juvenile depletion from a given habitat results from two distinct processes,
136 mortality and emigration, which are difficult to differentiate in open environments.
137 Previous studies revealed that in the Mediterranean Sea, artificial habitats used for
138 harbor restoration are mainly used by *Diplodus* spp. (seabream) (Bouchoucha et al.
139 2016). At the juvenile stage, these species do not undergo large displacement, but they
140 can still move at the scale of a whole cove (Macpherson 1998), which prevents accurate
141 study of their mortality on the smaller scale represented by artificial habitats.
142 Furthermore, visibility inside harbors is often poor, making it difficult to precisely follow
143 cohorts. Given these ecological constraints, tank experiments represent a good
144 alternative for studying the mortality of juvenile seabreams. A first set of experiments
145 permitted (i) the estimation of predation-induced mortality rates of juveniles on
146 different habitat types and (ii) the exploration of the influence of those habitats on prey
147 and predator behavior. A second set of experiments was designed (iii) to determine the
148 habitat preferences of juveniles. Based on the criteria outlined by Robertson & Hutto
149 (2006), the combination of the results allowed us to test our hypothesis and to assess

150 the relationship between habitat selection and survival to identify if these habitats could
151 represent potential ecological traps.

152

153 **Methods**

154 Studied fishes

155 We focused on the juveniles of two sparid species: the two-banded seabream (*Diplodus*
156 *vulgaris* (Geoffroy Saint-Hilaire, 1817)) and the white seabream (*Diplodus sargus*
157 (Linnaeus, 1758)), which were used as model prey species. These species are common
158 in Mediterranean coastal waters, and their high commercial value places them among
159 the most harvested species by local artisanal fisheries (Coll et al. 2004; Lloret et al.
160 2008). The juveniles settle in shallow heterogeneous rocky habitats made of small
161 blocks, pebbles or coarse sand, and their life cycle and behavior at settlement are
162 representative of those of most coastal nektobenthic fish species (Planes et al. 1998;
163 Macpherson 1998; Harmelin-Vivien et al. 1995). Both species can also be found in high
164 densities on artificial structures such as breakwaters or jetties (Clynick 2008; Pastor et
165 al. 2013) and have been observed inside harbors (Bouchoucha et al. 2016; Mercader et
166 al. 2018, 2017). If they use the same habitats as nurseries, they do not settle during the
167 same time period: *D. vulgaris* post-larvae reach the shore from December to March,
168 while *D. sargus* post-larvae arrive between May and June, which avoids competition
169 between these two species. *D. vulgaris* is also more opportunistic and can settle slightly
170 deeper in the ecotone between rocky bottom and shallow meadows (Vigliola &
171 Harmelin-Vivien 2001).

172 We used the comber (*Serranus cabrilla* (Linnaeus, 1758)) as a predator model. This
173 abundant species mainly lives around rocky substrates and meadows, which constitute
174 suitable habitats for its stalk-attacking strategy to predate. The comber is an

175 opportunistic macrocarnivore and one of the most important predators of small fish
176 (Cresson et al. 2014; Stergiou & Karpouzi 2002). Its small size (10 to 25 cm as an adult)
177 and its aggressive nature also make it a good model for predation tank experiments.

178

179 Fish collection and housing

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

188 After collection, juveniles were held in 500 L tanks with a maximum of 200
189 individuals/tank to minimize damage and stress. Combers were placed individually in
190 tanks of 45 L to avoid any aggressive behavior among them. All tanks (housing and
191 experimental, see next section) were connected to the same filtration system filled with
192 natural seawater. The water temperature was different between the expeditions to
193 mirror natural conditions: 17 °C in February and 22 °C in June. The salinity (37), pH (8),
194 and photoperiod (12 h/day of artificial light) were constant throughout all experimental
195 expeditions. Physicochemical parameters (pH, NH₃, NO₂, NO₃, salinity and temperature)
196 were checked and adjusted twice a week. Fish were acclimated for two weeks before
197 starting the experiments to allow them to recover from catching. Juveniles were fed
198 twice a day with defrosted *Artemia* sp.; combers, once a day with defrosted *Atherina* sp.
199 Combers were not fed for 48 h before each experiment to ensure that they were all in

200 the same starvation state at the beginning of all trials. At the time of experiments, the
201 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
202 sizes of *S. cabrilla* were 15.1 ± 1.8 cm and 15.5 ± 1.4 cm for experiments with *D. vulgaris*
203 and *D. sargus*, respectively. Once the experiments were performed, all predators and
204 juveniles that had not been eaten were released alive at their capture site.

205

206 Experimental design

207 All experiments were held in 100x50x40 cm tanks connected to the same filtration
208 system as the holding tanks. For mortality experiments, an activated carbon filter was
209 added to each experimental tank between each trial to clear away dissolved fish
210 chemicals from trial to trial (Martin et al. 2010). To avoid any disturbance, filtration and
211 air pumps were turned off during the whole duration of the experiments.

212 The bottom of all tanks was covered with a green velour carpet; the back and the sides
213 of the tanks were masked with auto-adhesive blue film to prevent exterior perturbations
214 during experimental trials. We conceived of four different types of habitats, two of which
215 mimicked typical natural nursery habitats for sparids: rocky chaotic clusters (R) and
216 *Posidonia oceanica* meadow (M), one artificial habitat similar to those used in recent
217 ecological restoration projects (AH) and a control (C) (Figure 1). Each habitat was
218 conceived to occupy a 60 dm³ volume, dividable into two equivalent parts (of 30 dm³),
219 so it could be used in both experiments (mortality and habitat selection). Rocky chaotic
220 clusters consisted of quarry stones randomly placed in the aquarium to provide
221 heterogeneous shapes and sizes of cavities. The stones were piled up to form a
222 25x25x100 cm habitat. Meadows were made of plastic algae fixed to two 50x25 cm
223 Plexiglas planks (for a total dimension of 25x25x100 cm). Each plank was composed of
224 12 feet with 20 leaves of 20 cm height and 10 feet with 12 leaves of 25 cm dispersed

225 randomly. The total leaf density resulting from the dispersal was 2880 leaves/m² for
226 95% to 100% recovery, corresponding to a medium-density meadow (Buia et al. 2004),
227 which is representative of what can be found in the area between 0 and 3 m depth
228 (Rotini et al. 2013). The artificial habitat used was composed of a pair of stainless steel
229 alloy cages of different mesh sizes (5 cm for the outer cage, 2.5 cm for the inner), the
230 inner cage being filled with oyster shells (see Bouchoucha et al. (2016) for full
231 description). The original version of this habitat was an 80x25x50 cm rectangle. Here,
232 we used two smaller versions of 30x25x35 cm, which were hung from the top of the
233 tank, leaving a 5 cm space between the tank bottom and the habitat. For the control, two
234 weighted plastic tubes (L=20 cm, \varnothing =8 cm) were placed in the tanks to avoid comber
235 stress due to the total absence of habitat.

236

237 Survival

238 Four tanks were used, each presenting a habitat (AH, M, R or C) occupying a volume of
239 60 dm³ (Fig. 1a - d). A see-through plastic plank was placed in the middle of the tank to
240 divide it into two halves, preventing encounters between prey and predator but letting
241 them see each other. Five juveniles were placed on one side and a predator on the other
242 for 30 min, allowing them time to recover from manipulation, acclimate to the new tank
243 and explore the habitat. The position (right or left) of the juveniles and the predator
244 during this acclimation was switched for each replicate. After 30 min, the plastic plank
245 was removed and experimentation began. For 2 h, tanks were recorded using a camera
246 (GoPro HERO3) placed in front of the tank, allowing the measurement of the exact time
247 of every predation event. In addition, behavioral data (numbers of approaches, attacks
248 and escapes, *cf.* Table S1 for the description of each behavior) were recorded every 30 s
249 by direct observation during the first 30 min of experimentation. At the end of the

250 experiment, surviving juveniles and predators were removed from experimental tanks.
251 Predators were replaced in their individual tanks, and juveniles were put in a new
252 housing tank to avoid using them a second time. For each habitat type and each prey
253 species, eight trials were run. To ensure complete randomization, each habitat was
254 placed in a tank for two runs and then moved to the next tank until it had been placed
255 twice in each tank. To prevent predators from encountering the same habitat twice (and
256 thus risking the predators learning the environment) and to limit potential bias due to
257 interindividual behavioral variability, two combers were randomly assigned to a tank in
258 such a way that each of them would run the experiment once for each habitat.

259

260 Habitat selection

261 Habitat selection was investigated for juveniles of the two species, *D. vulgaris* and *D.*
262 *sargus*. Experiments were held in a unique tank. Habitats were arranged in the tank in
263 combinations of two (M/AH, R/AH, M/R), with each habitat occupying half of the tank
264 and representing a volume of 30 dm³ (Fig. 1e - g). In addition to the three combinations,
265 three control experiments were carried out in which the same habitat was present in the
266 whole tank (AH1/AH2, M1/M2, R1/R2) (Fig. 1h - j). Five juveniles were placed in the
267 middle of the tank, and observations began 1 min after their introduction. The same
268 camera as the one used for survival experiments was placed in front of the tank and was
269 set to take a picture every 2 s for 5 min to determine the position of the juveniles (*cf.*
270 next section). As with the previous experiments, all fishes were removed from the tank
271 and placed in a separate housing tank to avoid using the same fish twice. Eight replicates
272 were run for each habitat type for both species.

273

274 Data acquisition

275 Videos of survival experiments were used to report the time at which each lethal
276 interaction occurred and to allow the calculation of the mortality kinetics. As mentioned
277 previously, qualitative behavioral data were recorded only for the first 30 min.

278 For habitat selection, pictures were first corrected for the distortion due to the fish eye
279 of the camera using Photoshop (version CC 2015). The position of the fish in an X-Y
280 plane was then incremented using ImageJ (version 1.51j8). Due to battery issues, only 4
281 min 30 s (out of the intended 5 min) could be analyzed for all trials, which still
282 represents 130 pictures, 650 coordinates per replicate and 5200 coordinates per
283 treatment (M/AH, R/AH, M/R, AH1/AH2, M1/M2, R1/R2). The intermediate area
284 separating the two habitats in a tank was used as a limit to evenly divide each tank into
285 two parts corresponding to the different habitats. Each pair of coordinates was then
286 assigned to a habitat.

287

288 Statistical analysis

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

294

295 Effect of habitat on juvenile survival

296 To compare the survival of the juveniles between the four habitats (AH, R, M and C), we
297 determined juvenile survival probabilities in each habitat using the Kaplan-Meier (KM)
298 method. This method allows to nonparametrically estimate the survival probability for
299 censored and uncensored survival times (Kaplan & Meier 1958). Equality of the survival

300 function between habitats was tested using the Peto and Peto modification of the Gehan-
301 Wilcoxon test because the hazard ratio was not constant over time and was not
302 proportional between habitats (Diez 2013). If the hypothesis of equality was rejected,
303 pairwise comparisons were performed using the Peto and Peto test with BH-adjusted p-
304 values (Benjamini & Hochberg 1995). All survival analyses were performed using the
305 “survival” package (Therneau 2015) for the R environment.

306

307 Fish Behavior

308 To compare the behavioral patterns of the fishes between habitats, we used the total
309 number of observed behaviors for each behavioral variable (Approach, Attack and
310 Escape) in each trial as response variables. Multivariate analyses of variance were
311 performed on Bray-Curtis dissimilarity matrices with the addition of a dummy variable.
312 P-values were calculated by 999 random permutations of unrestricted raw data, as our
313 design contained only one factor (habitat), and Type III sum of squares (Anderson
314 2001a). The Monte Carlo test was used when fewer than 200 permutations were
315 generated. Post hoc pairwise tests were performed when relevant. SIMPER analyses
316 were conducted when PERMANOVAs were significant to determine the relative
317 contribution of each behavioral variable to differences between habitats.

318

319 Habitat selection

320 Jacob's Selection Index (SI) (Jacobs 1974) was used to determine which habitat (AH, M
321 or R) juvenile fishes preferentially chose. For each of the height replicates, SI was
322 calculated with 650 points (X-Y coordinates) corresponding to the position of each of
323 the five juveniles every two seconds. This index is based on the following formula:

324 $SI = (nH1 - nH2)/(nH1 + nH2)$, where n refers to the number of points observed in
325 habitat 1 (H1) and in habitat 2 (H2). This index ranges between -1 and 1. SI = -1
326 indicates a preferential choice for habitat 1, SI = 1 for habitat 2, SI = 0 indicates no
327 particular choice. SI values were then used as response variables and compared to zero
328 (for controls and combinations) using a one-sample Wilcoxon test. If controls differ from
329 zero, observed choices are not linked to habitat type but to other unknown factors. If
330 controls do not differ from zero but a combination does differ from zero, juvenile fish
331 made a significant choice toward a habitat.

332

333 **Results**

334 **Survival**

335 Habitat type significantly influenced juvenile survival probabilities for both species
336 (Peto & Peto test, p-value 0.002 for *D. vulgaris* and p-value = 0.0053 for *D. sargus*), but
337 this effect was very different depending on the species. For *D. vulgaris*, the mean survival
338 time was the lowest on the meadow habitat (88.88 ± 6.06 min), significantly lower
339 (pairwise Peto & Peto p-value = 0.009) than that on the AH, which provided the best
340 survival time (108.16 ± 5.18 min). Survival on the control and rock was intermediate
341 (98.43 ± 6.70 min and 93.38 ± 6.92 min, respectively) (Fig. 2a; Table S2a). For *D. sargus*,
342 survival was equivalent on the control (115.40 ± 2.60 min), meadow (115.23 ± 2.84
343 min) and rock (115.22 ± 2.41 min) but lower on the AH (98.23 ± 6.24 min, pairwise Peto
344 & Peto p-value = 0.038 for all three combinations) (Fig. 2b; Table S2b). Mortality was
345 globally lower for *D. sargus* than for *D. vulgaris* (14 and 29%, respectively, of total
346 juveniles were eaten). It is also interesting to note that the lowest survival probability
347 (at the end of the 120 min experiment) for *D. sargus* (on the AH) was equivalent to the
348 survival probability for *D. vulgaris* on rock (upper 0.86, mean 0.70, lower 0.57).

349

350 Fish behavior

351 Behavioral patterns varied slightly according to habitat type. For *D. vulgaris*, these
352 differences were significant (PERMANOVA p-value = 0.004): only the control habitat
353 significantly differed from all other habitat types (pairwise test p-value = 0.026, 0.015
354 and 0.005 when compared to the AH, M and R respectively), which did not differ one
355 from one another (Table S3). Fish in the control habitat were less active overall, but the
356 difference resulted mainly from a lower number of approaches, which was responsible
357 for most of the dissimilarity between the control and other habitats (SIMPER results:
358 59.11, 44.18 and 47.39% for M, R and AH respectively) (Fig. 3a).

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

362

363 Habitat selection

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

371

372 **Discussion**

373 Our study revealed interspecific variations concerning the effect of habitat type on
374 survival and on the efficiency of the AH as a nursery rehabilitation tool. The survival of
375 *D. vulgaris* juveniles on the AH was equivalent to that observed on their natural nursery
376 habitat (rock). This species selected the AH as often as rocks while slightly dismissing
377 meadows, on which survival was the lowest. Therefore, for this species, there was
378 coherence between survival and habitat selection, which coupled with the densities
379 observed in the field (Bouchoucha et al. 2016), makes AH an efficient solution to
380 mitigate the impact of nursery habitat loss caused by the presence of harbors (Hale &
381 Swearer 2017). The structure of the AH might then provide comparable functionality to
382 those of heterogeneous and complex natural rocky bottom (Bouchoucha et al. 2016),
383 which is corroborated by the absence of a difference in behavioral patterns between
384 both habitats. On the other hand, *D. sargus* juveniles experienced the lowest survival
385 rate on the AH, and this species did not show any habitat preference. As they were not
386 preferentially choosing the AH, the implementation of such habitats could result in the
387 formation of an “equal-preference trap” (Robertson & Hutto 2006). These results are
388 concordant with an *in situ* study that found that, within Mediterranean marinas,
389 juveniles of *D. vulgaris* use more AH than juveniles of *D. sargus* (Bouchoucha et al. 2016).
390 The contrasting response observed between two close species implies that the
391 formation of eventual traps cannot be discarded. However, as natural, better quality,
392 habitat are usually not available within harbors (as this is the reason why restoration is
393 undertaken), further studies are needed to draw conclusions about the potential
394 benefits of the use of AH to rehabilitate the nursery function for juvenile coastal fishes
395 notably. These studies should include the assessment of the fitness of individuals on the
396 long term, take into account the landscape surrounding the AH and should also be led on
397 species naturally settling in different habitats (e.g., *D. annularis* individuals that settle in

398 meadows and *Chromis chromis* individuals that settle on steep slopes of rocky reefs) or
399 with more cryptic behavior (e.g., *Epinephelus marginatus* or juveniles from the *Gobiidae*
400 and *Blenniidae* families). For cryptic juveniles, the type of AH used in this study might be
401 of particular interest. Indeed, during all experimental trials, combers never entered the
402 AH. Likewise, in the field, predators have never been observed inside AH placed in
403 harbors, with the exception of small gobies (authors' personal observations). This
404 suggests an efficient refuge role from at least predators larger than 15 cm. This is not the
405 case for all AH designs, as mentioned by Patranella et al. (2017), which sustains the
406 hypothesis of an adapted structure to provide protection to juveniles. Therefore, the size
407 of the cavities seems to be of prime importance to prevent the establishment of stalk
408 attack and ambush predators (Patranella et al. 2017; Almany 2004). In the wild, most
409 nursery habitats (e.g., seagrass meadows) also attract many predators. However, their
410 structural complexity provides adequate refuge for juveniles, which limits the
411 effectiveness of predators and thus limits the mortality of juveniles despite high
412 densities of predators (Anderson 2001b). The number and diversity of the cavities (i.e.,
413 the complexity of a habitat) might also be a determining factor favoring multiple species
414 and size classes (Rogers et al. 2014). In that sense, an AH might be a powerful tool to
415 rehabilitate nursery function for many species if the size, number and diversity of their
416 cavities are well designed. Not only should one particular AH be designed with a variety
417 of cavities but also various AH designs should be used to mimic the heterogeneity of the
418 seascape and thus furnish complementary habitats for juveniles of different species or
419 even for different developmental stages of the same species. Indeed, in all ecosystems,
420 prey might adapt their habitat use depending on the presence of predators, which is an
421 indirect effect of predation on the prey population known as risk effect (Hamilton &
422 Heithaus 2001). In our study, juveniles faced variable mortality rates depending on the

423 habitat but did not have the possibility to change habitat when facing predation.
424 Additionally, if evolving in a heterogeneous seascape, they might use different habitats
425 depending on the presence and nature of the predators, which might increase their
426 survival. For instance, associating an AH designed to mimic a seaweed forest or
427 phanerogam meadow with one mimicking complex rocky bottom could increase
428 interhabitat connectivity and thus increase restoration efficiency (Baillie et al. 2015;
429 Traut 2005).

430 Juvenile *Diplodus* spp. are known to undergo ontogenic shifts in habitat use, enlarging
431 their niche by vertical (for *D. vulgaris*) or horizontal (for *D. sargus*) migration (Ventura
432 et al. 2014). Those shifts have also been observed on the AH within harbors
433 (Bouchoucha et al. 2016), and during experiments, most juveniles were observed under
434 the AH, which seems to be the same *in situ* (authors' unpublished data). Changes in
435 habitat use are a widespread behavior in juvenile fish in every ecosystem (Feary et al.
436 2011; Machado et al. 2003; Schlosser 1987; Kimirei et al. 2011). Additionally, placing AH
437 at different depths and different locations could enhance its refuge role in many
438 different restoration contexts (e.g., temperate and tropical coastal waters as well as
439 lagoons and even fresh water environments, such as lakes or deep rivers).

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

445 If AH might reduce the predation-induced mortality of juveniles, pollution within
446 marine urbanized areas might be greater than that in natural areas, which can increase
447 the mortality of juveniles. However, juvenile seabreams within harbors show levels of

448 contamination and growth rates comparable to those of individuals living in adjacent
449 natural areas (Bouchoucha et al. 2018). Additionally, the risks of over-mortality linked
450 to this factor might be low. Nevertheless, restoration projects should be considered only
451 once pressures have been reduced to the lowest possible level. Indeed, if increased
452 habitat complexity might increase juvenile survival, it is important to keep in mind that
453 anthropogenic disturbances often lead to biotic homogenization (Devictor et al. 2008;
454 Olden 2006). The set of species able to live in highly urbanized areas, such as harbors,
455 might then be restricted to generalist species (Fischer & Lindenmayer 2007).
456 Additionally, when possible, management efforts should first focus on the preservation
457 of diverse natural habitats.

458 Plasticity in fish settlement requirements might be greater than expected. Juveniles are
459 able to settle on artificial structures that can sometimes be very different from their
460 natural habitat (Guidetti 2004; Pastor et al. 2013). Even species that are only rarely
461 observed at the juvenile stage in natural habitats, such as the common dentex (*Dentex*
462 *dentex*), the black seabream (*Spondyliosoma cantharus*), pipefishes (*Syngnathus* spp.)
463 (authors' unpublished data) or even the protected dusky grouper (*Epinephelus*
464 *marginatus*) (Mercader et al. 2016), have been seen within harbors. This suggests that
465 even more specialized species could be able to live in those areas if suitable complex
466 habitats are present. Marine restoration is has more recent development than its
467 terrestrial or freshwater counterparts, and, probably due to the inherent properties of
468 marine systems (hardly accessible and highly dispersive), the range of tools available to
469 restore marine habitats remains restricted. However, projects using AH are increasing
470 (Seaman 2007; Brown & Chapman 2014; Paalvast et al. 2012; Sella & Shimrit Perkol-
471 Finkel 2015), and some attempts to transplant living organisms to restore marine
472 habitats are flourishing (Jaap 2000; Ng et al. 2015; Perkol-Finkel et al. 2012).

473 Nevertheless, if the restoration of coastal fish nurseries is to be effective, efforts have to
474 be made in designing new artificial habitats and nature-based solutions, which should
475 be tested in two phases: (i) an experimental approach in aquariums to understand the
476 use by juvenile species and (ii) complex field experiments taking into account all factors
477 potentially influencing juvenile mortality and their interactions. Such studies would
478 permit confirmation and extend this work on the effect of nursery habitat restoration.

479

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490

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675

676 **Figure captions:**

677 **Figure 1:** Habitat types used for survival experiments (A to D) and habitat selection
678 experiments (F to K). Artificial Habitat (A), Rock (B), Control (C), Meadow (D), Combination
679 Rock-Meadow (F), Meadow-Artificial Habitat (G), Artificial Habitat-Rock (H) and controls (I to
680 K).

681 **Figure 2:** Kaplan-Meier survival curves for each habitat with 95% confidence intervals.
682 Lowercase letters indicate the results of pairwise tests; habitats sharing at least one letter do
683 not differ. (A) *D. vulgaris* and (B) *D. sargus*.

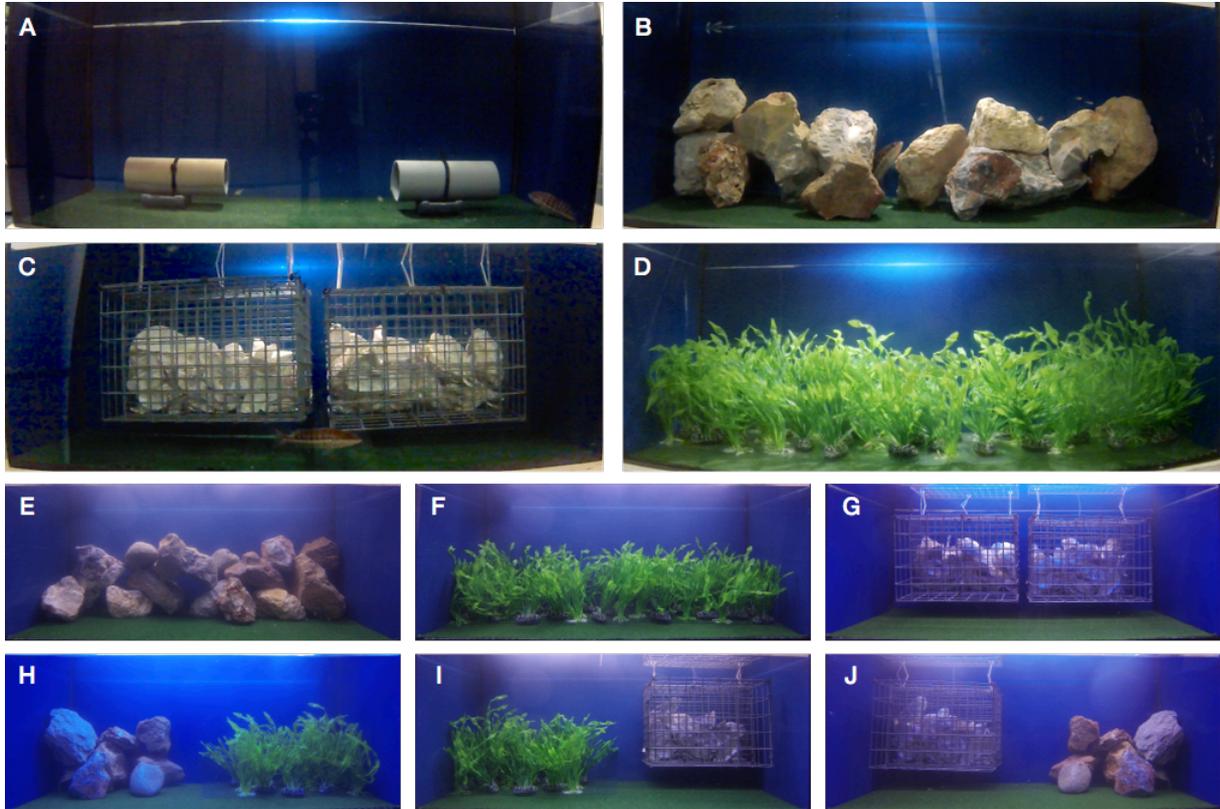
684 **Figure 3:** Mean number (error bar + SD) of behavioral observations for the comber
685 (approach and attack) and the juveniles (escape) for the first 30 min of the predation
686 experiments on (A) *D. vulgaris*, (B) *D. sargus*. Lowercase letters indicate the results of
687 pairwise tests; habitats sharing at least one letter do not differ.

688 **Figure 4:** Boxplots of the spread of Jacob's Selection index for (A) *D. vulgaris*, (B) *D. sargus*.
689 Vertical black lines indicate the median; the ends of the boxes, the first and third quartiles;
690 the whiskers, the values whose distance from the box is at most 1.5 times the interquartile
691 range; the points, extreme values and black crosses, the mean values.

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693 **Figures:**

694 **Figure 1:**



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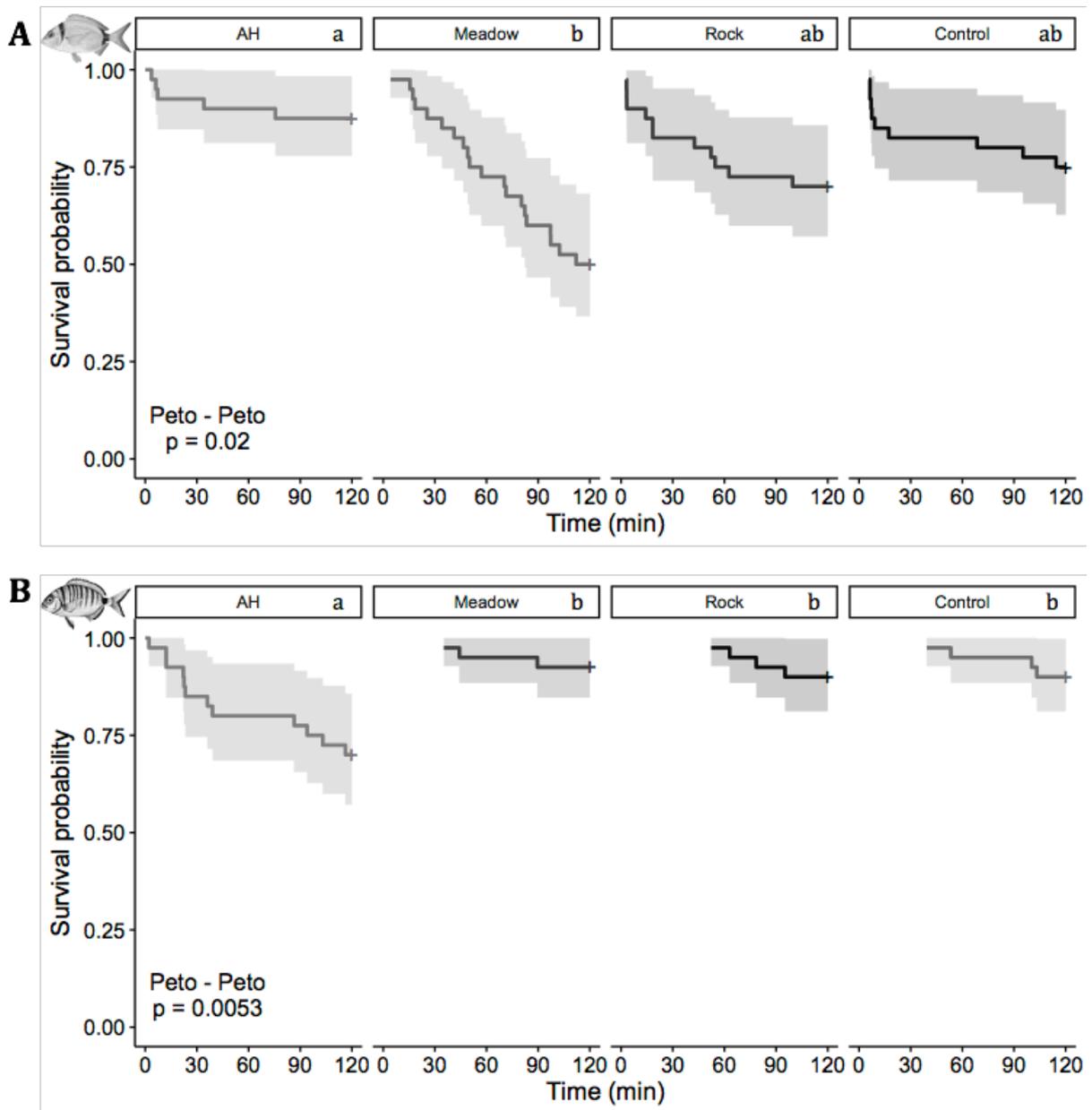
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703 **Figure 2:**



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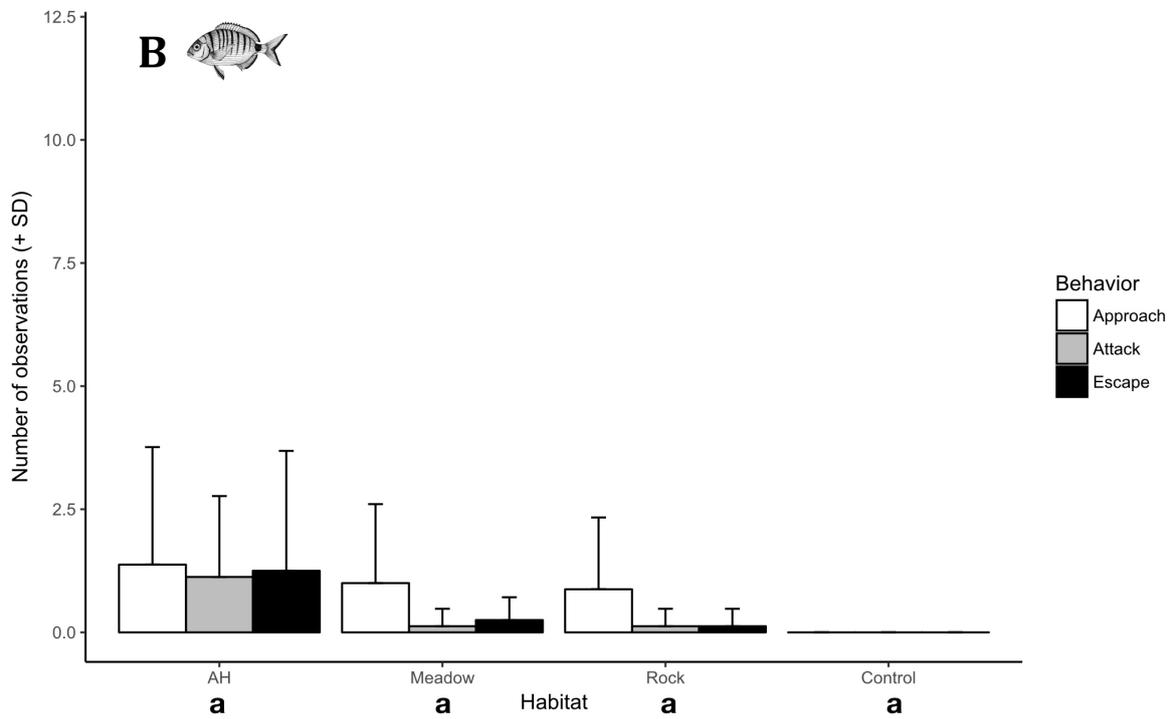
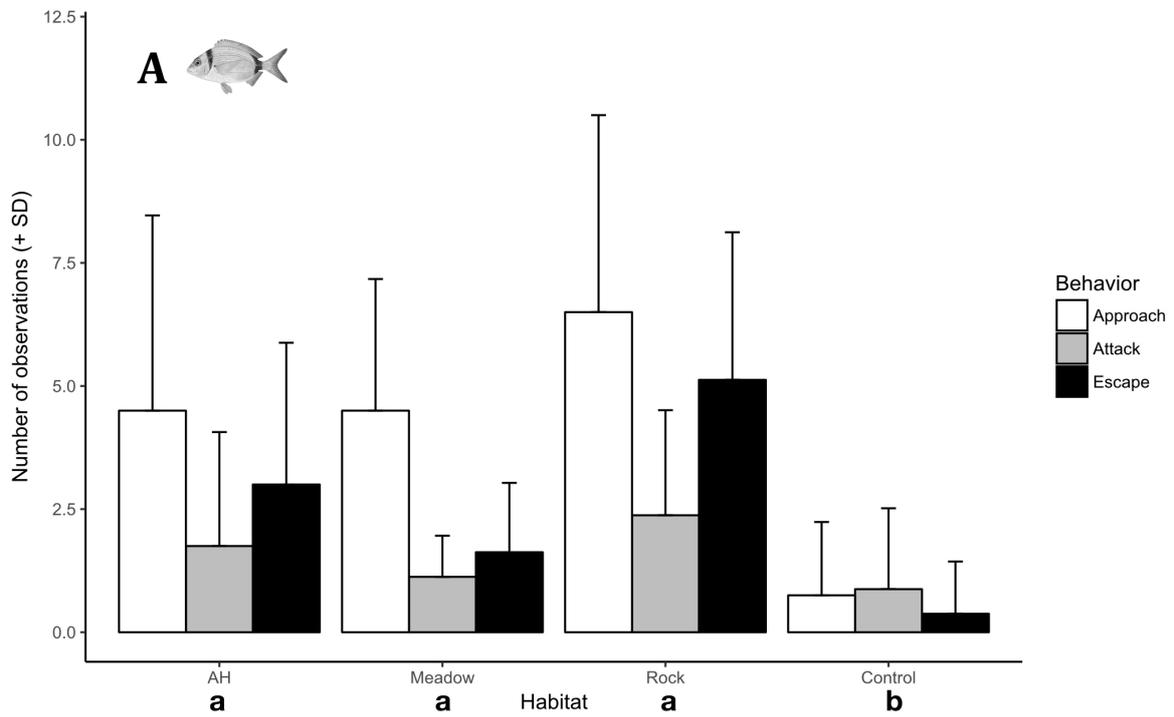
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709 **Figure 3:**

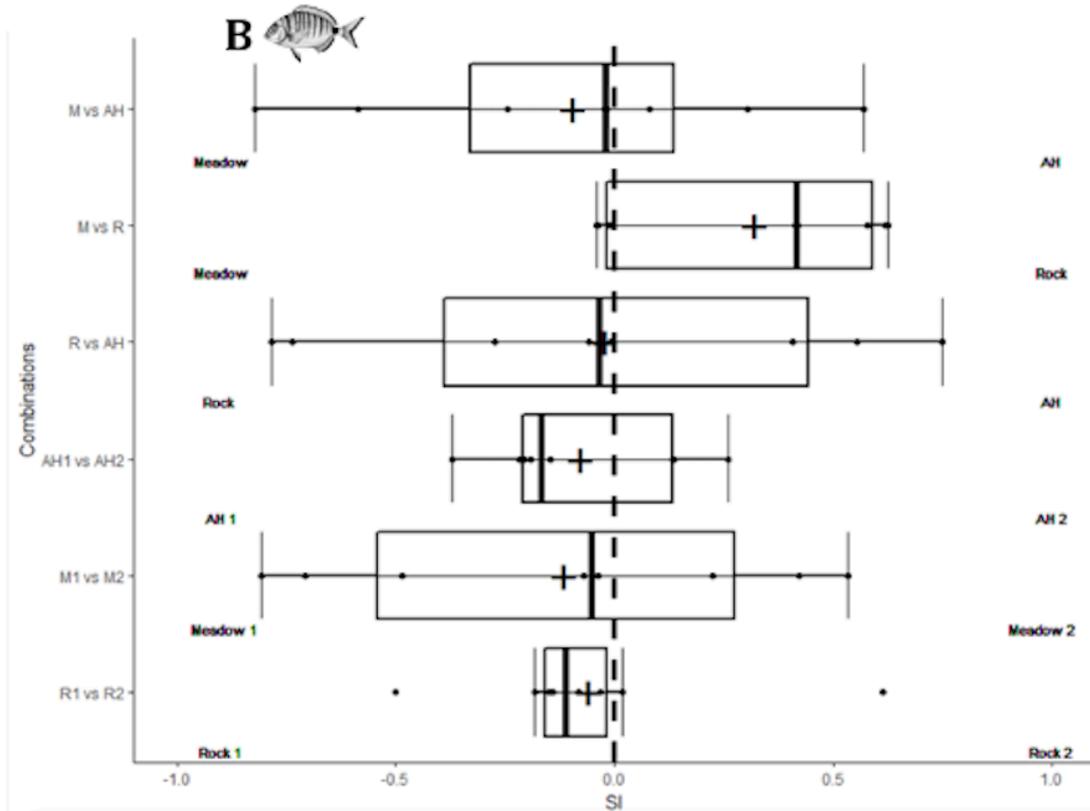
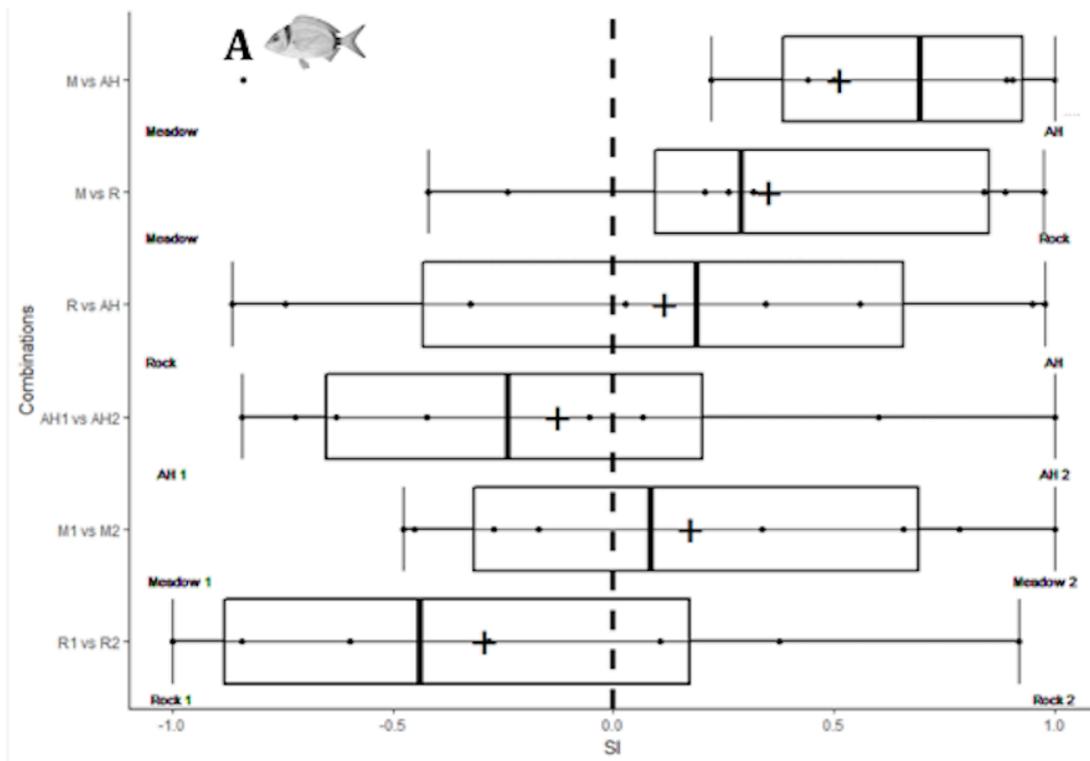


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713 **Figure 4:**



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