

Connectivity patterns of coastal fishes following different dispersal scenarios across a transboundary marine protected area (Bonifacio strait, NW Mediterranean)

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Abstract :

The Strait of Bonifacio constitutes one of the rare transboundary Marine Protected Areas (MPA) of the Mediterranean Sea (between Sardinia, Italy and Corsica, France). Based on the hypothesis that no-take zones will produce more fish larvae, compared to adjacent fished areas, we modeled the outcome of larvae released by coastal fishes inside the no-take zones of the MPA in order to: (i) characterize the dispersal patterns across the Strait of Bonifacio; (ii) identify the main potential settlement areas; (iii) quantify the connectivity and the larval supply from the MPAs to the surrounding areas. A high resolution hydrodynamic model (MARS 3D, Corse 400m) combined to an individual based model (Ichthyop software) was used to model the larval dispersal of fish following various scenarios (Pelagic Larval Duration PLD and release depth) over the main spawning period (i.e. between April and September). Dispersal model outputs were then compared with those obtained from an ichthyoplankton sampling cruise performed in August 2012. There was a the significant influence of PLD to the connectivity between coastal areas. The synchronization between spawning and hydrodynamic conditions appeared to be determinant in the larval transport success. Biotic and abiotic parameters affecting the dispersal dynamic of fish larvae within the Strait of Bonifacio were identified and synthesis maps were established as a tool for conservation planning.

Keywords : biophysical model, early life stages, reproductive timing, pelagic larval duration, Corsica, ichthyoplankton

1. Introduction

1.1. Larval dispersion & early life history traits of fish

Most coastal marine fish species have a bipartite life cycle, divided in a relatively sedentary juvenile/adult stage and a dispersive pelagic early life stage (eggs/larvae) ([Heath, 1992](#); [Leis, 2002](#)). Dispersal distances of Early Life stages of Fish (ELF) can reach up to 10 to 100s' of km, as shown in previous studies on reef fishes ([Cowen et al., 2006](#); [Kinlan and Gaines, 2003](#); [McCleave et al., 1987](#); [Purcell et al., 2009](#)). The dispersal process of ELF is thus generally considered to be the principal driver of population connectivity and subpopulation persistence in marine fish populations ([Cowen and Sponaugle, 2009](#)). The replenishment of subpopulations will greatly rely on the recruitment process of newly settled individuals ([Doherty and Fowler, 1994](#); [Hastings and Botsford, 2006](#); [Hjort, 2014](#)). However, more recent studies have provided the evidence that dispersal distances of ELF are less important than previously thought and that local recruitment plays an important role in the larval supply of coastal fish populations ([Saenz-Agudelo et al., 2011](#); [Shanks, 2009](#)). The larval dispersal is in fact a complex process difficult to predict as it relies on physical factors, such as the advection and diffusion, but also on biological factors ([Pineda et al., 2007](#); [Werner et al., 1996](#)), such as egg buoyancy, Pelagic Larval Duration (PLD), availability of food and predation

59 pressure operating at different spatial and time scales (Pineda et al., 2009; Scheltema,
60 1986) as well as on the behavior of ELF linked to their swimming and orientation abilities
61 (Leis, 2006; Leis and Lockett, 2005; Staaterman et al., 2012).

62 **1.2. The Mediterranean Sea and its marine protected areas**

63 The Mediterranean Sea is one of the world's marine biodiversity hotspots (Bianchi and
64 Morri, 2000; Coll et al., 2010) and concentrates between 4 to 18 % of known marine
65 species (Mouillot et al., 2011). It is also one of the most impacted ecosystems by
66 fisheries (Tudela, 2004) and considered as a highly vulnerable sea (Cognetti and
67 Curinigalletti, 1993; Coll et al., 2012). With the aim to sustainably protect and to ensure
68 marine biodiversity and related ecosystem goods and services, following the Convention
69 on Biological Diversity and the Barcelona Convention, a target of 10% protection of the
70 marine and coastal Mediterranean waters representative of the Mediterranean diversity
71 has been set to reach by 2020 (Olsen et al., 2013). To date, 677 Marine Protected
72 Areas (MPAs) have been identified in the Mediterranean Sea covering 87 500 km², i.e.
73 1.1% of the sea surface of the Mediterranean and up to 4.6%, including the Pelagos
74 Sanctuary for marine mammals (Gabrié et al., 2012). Marine Protected Areas are
75 particularly suited management tools for coastal areas, as they protect simultaneously
76 the living resources from extraction, but also the essential habitats on which they rely
77 (Agardy, 1994). Since the implementation of the first MPA around 1920- 1930 along the
78 Californian coasts (Sobel and Dahlgren, 2004), evidence has been provided by MPAs
79 around the world, that these management tools induce biological responses, mainly
80 increasing the densities of populations, biomass, average organism size and diversity
81 (Halpern, 2003; Halpern and Warner, 2002).

82 One future target identified within the framework of the Barcelona Convention, will be to
83 design networks of MPAs at a seascape scale rather than isolated MPAs at a regional or
84 national scale (Olsen et al., 2013). These MPA networks will consist of individual MPAs
85 sufficiently interconnected to provide genetic, demographic and ecological stepping-
86 stones. According to the IUCN-WCPA (International Union for Conservation of Nature -
87 World Commission on Protected Areas), the synergistic operation of these
88 interconnected MPAs will help to implement more efficiently their ecological aims (Olsen
89 et al., 2013). At present, the designation and the size of MPAs is still very uneven across

90 Mediterranean countries, being mostly located in the northern basin (96% in Spanish,
91 French, Italian and Greek waters). These MPAs range between 0.003 and 4000 km², but
92 most of them are small ranging between 11 and 25 km².

93 In a context promoting ecological coherent MPA networks in the Mediterranean, an
94 international marine park was established in 2012 in the Strait of Bonifacio - SB (PMIBB,
95 2012) which separates the island of Corsica (France) and of Sardinia (Italy). This marine
96 park links together both the French MPA of the “Bouches de Bonifacio” and the Italian
97 MPA of the “Archipelago de la Maddalena” and constitutes nowadays one of the rare
98 transboundary MPAs of the Mediterranean sea (Gabrié et al., 2012).

99 The general purpose of this work was thus to characterize the effects of the
100 hydrodynamic system of the SB on larval dispersal in order to provide fundamental
101 guidelines for the marine spatial planning in the recently established international marine
102 park of the SB. Based on the hypothesis that no-take zones or MPAs with enhanced
103 protection will produce more fish larvae, compared to adjacent fished areas, due to a
104 higher reproductive output and fitness and a denser population of spawners/brood stock,
105 we modeled the outcome of larvae released by coastal fishes inside the areas of
106 enhanced protection of the SB in order to: (i) characterize the dispersal patterns across
107 the SB, (ii) identify the main potential settlement areas, and (iii) quantify the connectivity
108 and the larval supply from the MPAs to the surrounding areas. Larval dispersal was
109 modeled following various scenarios in order to investigate the effect of the seasonal
110 variability and of biological parameters of early life stages, such as the pelagic larval
111 durations (PLDs) and the egg type (benthic or pelagic). Additionally, dispersal patterns
112 were compared with those obtained by a larval dispersal model based on the distribution
113 of fish larvae issued from a sampling campaign.

114 **2. MATERIAL and METHODS**

115 **2.1. Study area and hydrographic conditions**

116 The Strait of Bonifacio (SB) is a 13 km wide strait separating the islands of Corsica in
117 the North and of Sardinia in the South, located at the meeting-point between the western
118 Mediterranean and Tyrrhenian basin (Fig. 1). Straits are considered as naturally formed
119 passage, narrow enough to constrain surface flows (Astraldi et al., 1999). These choke

120 points are characterized by high seasonal variability of currents (Astraldi et al., 1999).
121 Due to its geomorphological configuration, bathymetry and the presence of numerous
122 islands and islets, the SB is a complex area in term of currents (Gérigny, 2010). These
123 currents have an average intensity of 0.5 m.s^{-1} and can reach up to 1.46 m.s^{-1} (Gérigny
124 et al., 2011). The general circulation in this area is mainly influenced by two prevailing
125 orographically controlled winds, a western wind (52-54% of the winds) and an eastern
126 wind (26%); (De Falco et al., 2011).

127 Across the marine park of the SB, various protection levels are applied (Sorgente et al.,
128 2012), where gears and the fishing catches are limited (artisanal fishing, spear fishing),
129 depending on the levels of protection. In the enhanced protection areas of the MPA, all
130 recreational fishing activities are forbidden. The SB counts in total seven distinct
131 enhanced protection areas, each of them are include small fully protected zones where
132 all kinds of fishing activities are prohibited.

133 Habitat mapping in the SB shows that rocky substratum and *Posidonia oceanica* sea
134 grass are the predominant habitat types between 0 and 30m depth (Pasqualini et al.,
135 1998), which is the bathymetric preferendum for most Mediterranean coastal fish
136 species (Harmelin-Vivien et al., 1995). *P. oceanica* seagrass meadows are particularly
137 dense and extensive along the coasts of the Island of Corsica compared to other coastal
138 French Mediterranean areas (Pasqualini et al., 1998). *P. oceanica* sea grass meadows
139 are recognized to be essential habitats for many coastal fishes at the adult stage (Bell
140 and Harmelin-Vivien, 1982; Kalogirou et al., 2010; Moranta et al., 2006), but are also
141 perceived as an important nursery habitat for the early life stages (Garcia-Rubies and
142 Macpherson, 1995; Harmelin-Vivien et al., 1995).

143 **2.2. Larval Dispersal Modelling**

144 **Biophysical model.** Larval dispersal was modeled using Ichthyop, a coupled
145 biophysical Lagrangian particle tracking tool (Lett et al., 2008). The CORSE-400m
146 hydrodynamic model is based on the MARS-3D code, the 3D hydrodynamic Model for
147 Application at the Regional Scale (Lazure and Dumas, 2008). CORSE-400m was
148 implemented with a configuration of 400 m horizontal resolution and 30 sigma layers,
149 which covers the entire Corsican Island, the SB and the most southern part of Sardinia

150 Island. CORSE-400m takes its boundary conditions on the North-western Mediterranean
151 configuration - MENOR (André et al., 2005; Rubio et al., 2009). The CORSE-400m
152 hydrodynamic model was calibrated for temperature, salinity and hydrodynamic
153 structures around Corsica during the MOMAR project (Faure et al., 2012) and during the
154 Stella Mare 1 cruise in the SB in August 2012 (Gérigny and Coudray, 2013).

155 ***Dispersal scenarios & model parameterisation.*** Larval dispersal was modeled
156 following various scenarios for 2012, in order to account for the great variability of life
157 traits of early fish stages (Table 1). Three scenarios of pelagic larval durations (PLDs)
158 were therefore modeled: 'PLDmax', 'PLDmed' and 'PLDmin' corresponding respectively
159 to 35, 25 and 17 days of dispersal (Table 1). PLDs were computed based on the
160 median, the upper and lower quartile of known PLD for coastal Mediterranean fish
161 (Macpherson and Raventos, 2006; Raventos and Macpherson, 2001). Two release
162 depth scenarios were also modeled to simulate the dispersal for pelagic eggs ('Surface
163 scenario': release depth between 0 and 10 m) and benthic eggs ('Bottom scenario':
164 release depth between 10 and 30m depending on bathymetry; Table 1). In
165 Mediterranean coastal fish communities, most species have pelagic eggs (Olivar and
166 Sabates, 1997), such as most sparids (Macpherson and Raventos, 2006). Benthic eggs
167 attached or not to substrate, are representative of most Labridae (Yliff, 2000) and many
168 Gobidae (Macpherson and Raventos, 2006). Models for each scenario were run over
169 the main spawning period of Mediterranean coastal fish species, i.e. from April to
170 September (Tsikliras et al., 2010) to account for seasonal variability in the dispersal
171 pattern across the SB (Table 1). A total of 36 simulations were run corresponding to the
172 six different tested scenarios for each of the principal spawning months (April to
173 September).

174 In our case study, larval transport was modeled across the SB considering the
175 boundaries of the Corse-400m model (40.72° - 43.32° N and 8.15° - 9.95°E) and release
176 areas of particles (i.e. spawning areas) were parameterized as the seven MPA zones
177 with enhanced protection within the SB (Fig. 1). Four of them are located on the French
178 side of the SB, from west to east: the Islands of Moines (Moin), Fazio (Faz), Lavezzi
179 (Lav) and the Cerbicales (Cerb). Three of them are located on the Italian side of the SB
180 and constitute the 'Archipelago de la Maddalena': the Maddalena Island (Mad), the

181 Islands of Razzoli, Maria and Budelli (RMB) and the Island of Spargi (Spa). Settlement
182 areas were defined following the habitat preferences of coastal fish species, i.e. rocky
183 and vegetated substrates, mainly with sea grass meadows (Guidetti, 2000; La Mesa et
184 al., 2011) and within the upper bathymetric range from 0 to 20 m depth (Harmelin-Vivien
185 et al., 1995). As *P. oceanica* sea grass meadows were present nearly continuously on
186 the coasts of the study area, settlement areas were divided into 19 zones (Fig. 1),
187 numbered Z1 to Z12 from West to East and North to South plus the subset zones of the
188 MPA release zones favorable for larval settlement (Moin, Faz, Lav, Cerb, Mad, RMB,
189 SPA).

190 Particle tracking was performed with Ichthyop following an Eulerian advection method.
191 Due to a lack of biological and behavioral data of early life stages of coastal
192 Mediterranean fish species, larvae were considered as passive particles, assuming thus
193 that larval transport was mainly driven by physical forces. Eggs and larvae were
194 considered as neutrally buoyant and bouncing back when moving to land boundaries of
195 the model. A total of 80 000 particles were released for each spawning month. These
196 particles were released in four times at a 7 days interval (i.e. 20 000 particles per week)
197 with an equal density distribution across all release areas.

198 **Transport success & data analysis.** Transport success (i.e. proportion of larvae
199 released that reached a suitable settlement habitat within their settlement window) was
200 computed for each pair of release and settlement zones and for each tested scenario
201 (by PLDs, depth, months). Transport success was used as an estimate for larval
202 dispersal (which includes additionally behavioral processes linked to settlement; Pineda
203 et al. 2007) and connectivity (which includes as well post-settlement processes such as
204 density dependence, mortality due to predation or low food availability, affecting survival
205 of settlers). Prior to analysis, settlement success was standardized by the number of
206 particles released by each MPA, to account for unequal size of MPAs. Settlement
207 success was visually inspected using connectivity matrices between release and
208 settlement areas. Transport success data was non-normally distributed, even after
209 transformation efforts, and included repeated measures of transport success per
210 settlement area. GLMMs represent a suitable technique for analyzing non-normal data
211 with random effects (Zuur et al., 2009). The effect of PLD, release depth, month, and

212 area on the variability of transport success was thus tested using a GLMM using a
213 Gaussian distribution and an identity link after a box-cox transformation (Zuur et al.,
214 2009). GLMMs were computed using the package 'lme4' for the R statistical
215 environment (R Core Team, 2013). Settlement areas were considered as random
216 factors. PLD, release depth, month, and area were considered as fixed categorical
217 factors. In each model, the normality of residuals and the model performance were
218 visually examined using residual distributions and quantile - quantile plots of residuals
219 against fitted values. P-values were computed using the Kenward-Roger approximation
220 method using the R-package 'pbkrtest' (Halekoh and Højsgaard, 2012).

221 **2.3. Matching of dispersal model with fish larvae distribution**

222 **Sample collection and identification.** During an oceanographic cruise performed in
223 2012, between August 4th and 8th, 64 plankton samples were taken at 32 stations across
224 the SB. At each station, ichthyoplankton was collected using a 60cm bongo net mounted
225 with 200 μm and 500 μm mesh size on each side. Oblique tows were performed at two
226 knots from above the bottom to the surface with a depth meter attached to the net.
227 Volumes filtered were calculated from calibrated flowmeters attached to the mouth on
228 each side of the bongo net. Immediately after capture, samples were fixed whether in
229 ethanol for 500 μm mesh and in 3.7% buffered formalin for 200 μm mesh. At the
230 laboratory, ichthyoplankton was classified according to fish families and life stages were
231 defined according to Griocche *et al.* (2000) (i.e. stage 1 as the yolk-sac larvae, stage 2
232 the preflexion larvae, stage 3 the flexion larvae and stage 4 the post-flexion larvae). Size
233 class identification was used for an estimation of the age of larvae for further analyses.
234 Among the 15 fish families identified, only Sparidae and Labridae larvae were
235 considered, as they were the most abundant coastal fishes in the samples, and are
236 often considered as indicator species of Mediterranean coastal fish communities
237 (Guidetti et al., 2002; Mouillot and Culioli, 2002).

238 **Distribution of fish larvae in the SB.** The potential geographic distribution of Labridae
239 and Sparidae larvae was estimated for the entire SB by characterizing the
240 environmental predictors and conditions suitable for larvae belonging to these two fish
241 families. For this purpose, different ecological meaningful environmental variables were

242 collected, to be used as predictors of fish larval densities, namely subsurface
243 temperature, salinity, bathymetry, atmospheric pressure (issued from PREVIMER data
244 <http://www.previmer.org/>), Chlorophyll A (issued from MODIS satellite data obtained by
245 OC5 algorithm), and distance to coast computed additionally using GIS-tools. The
246 environmental point data for each variable was then used to produce continuous raster
247 maps by interpolation using a krigging method (Geostatistical Analyst for ArcGIS 10.1).
248 A correlative species distribution model was fitted, using generalized linear models, to
249 predict the likelihood of the density of fish larvae based on environmental predictors. A
250 forward stepwise selection of the best model was performed using the Akaike
251 Information Criterion AIC (Akaike, 1981). This information-theoretic method uses
252 deviance as a measure of fit (Burnham and Anderson, 2002; Burnham et al., 2011). The
253 final selected model for Labridae and Sparidae was then used to predict their density
254 distribution across the SB. The Jenks optimization method was used to classify the
255 predicted density distribution and areas of highest Labridae and Sparidae densities were
256 delineated using GIS.

257 ***Larval dispersal model and scenarios.*** Dispersal simulations were then run
258 corresponding to the sampling period of larvae (i.e. August 2012), considering the
259 highest density areas of Labridae and Sparidae as release areas (Table 1). As for the
260 dispersal models with larvae released from the MPAs, we considered three PLD
261 (PLDmax, PLDmed, PLDmin) to test the effect of the dispersal duration on larval
262 transport (Table 1). The age estimate of larvae, based on their larval stage, was
263 however first subtracted to the different PLDs (95% of stage 2 for Labridae and
264 Sparidae). The effect of PLD and release area on the variability of transport success in
265 august 2012 was tested for Labridae and Sparidae using a GLMM with a Gaussian
266 distribution and an identity link after a Box-Cox transformation (Zuur et al., 2009),
267 following the same method described for the MPA scenarios (S1 to S6). Settlement
268 areas were considered to be random factors and PLD and release areas as fixed
269 categorical factors. Transport success from the dispersal models of August 2012 based
270 on field data were then compared with the results from the dispersal model with larvae
271 released from the MPAs of the SB.

272 **3. RESULTS**

273 **3.1. General retention characteristics of the SB and its MPAs**

274 The mean retention of the Strait of Bonifacio (SB), for all simulation scenarios and
275 across all spawning months, was of $3.56\pm 2.31\%$, i.e. a mean of 3.56% of larvae
276 released inside the MPAs of the SB reached a favourable settlement habitat within their
277 settlement window. The other 96% of released particles were dispersed out of the
278 studied system or did not reach a favourable settlement habitat during their settlement
279 window. The degree of retention for each MPA was considerably lower, even if a great
280 variability can be noticed between scenarios and months. Highest retention rates were
281 found for the MPAs Cerb, Faz and Lav (respectively 0.26 ± 0.43 , 0.22 ± 0.36 , $0.19\pm 0.27\%$)
282 and lowest for the MPAs Moin, Mad, RMB and Spa (respectively 0.11 ± 0.17 , 0.10 ± 0.17 ,
283 0.10 ± 0.19 , $0.11\pm 0.23\%$).

284 **3.2. Spatio-temporal variability and influence of biological parameters on** 285 **transport success**

286 A significant temporal variability was noticed in the contribution of MPAs to the transport
287 success of larvae (Fig. 2; Table 2). Temporal variations are particularly marked for
288 MPAs contributing the most to the transport success, such as Cerb, Faz and Lav, for
289 which the transport success was markedly lower in June than for the other months (Fig.
290 2). Low transport success was also occurring at the MPAs Mad, Moin, RMB and Spa,
291 particularly during late summer months, August and/or September, depending on the
292 tested scenario (Fig. 2). Among the overall tested scenarios, monthly larval transport
293 success varied significantly across PLD and release area (Table 2), with the lowest
294 transport success occurring for most PLDs and release areas in June (mean \pm sd:
295 $0.06\pm 0.12\%$) and the highest in April (mean \pm sd: $0.06\pm 0.12\%$; see Fig. 2).

296 Transport success of larvae released in the surface layer (i.e. pelagic eggs) seems to be
297 slightly lower than for larvae released close to the bottom (i.e. benthic eggs; Fig.2).
298 Significant differences of transport success according to depth are however observed
299 only across PLDs and months (Table 2). The contribution of the different MPAs, i.e.
300 release areas of the system, to overall transport success remained unaffected by
301 release depth of particles (Fig. 2; Table 2).

302 In terms of spatial dispersal patterns, no differences were observed between the three
303 tested PLD, which explains that we pooled the three scenarios in Figure 3. In contrast,
304 differences in dispersal patterns are observed between the two release depth scenarios
305 (Fig.3), mainly for the Lavezzi Islands (Lav) and the western Italian side of the SB (Z12),
306 which settle respectively more with the 'Bottom' than the 'Surface' scenario. The value of
307 transport success is also notable with the 'Bottom' scenario at the western Italian part of
308 the SB (Z10), whereas for the 'Surface' scenario settlement is also notable at the
309 western French part of the SB (Z1-Z3; Fig.3).

310 **3.3. Matching of dispersal model with fish larvae distribution**

311 The results from the species distribution model using the observed distribution of fish
312 larvae (Fig. 4A), which were sampled during the oceanographic campaign in August
313 2012, revealed different areas of high larval densities for Sparidae and Labridae. Nine
314 areas were isolated for Sparidae and seven for Labridae. Sparidae were located all
315 across the SB, but mainly in shallow coastal areas on the French and the Italian side,
316 especially around the Archipelago of the Maddalena (Fig. 4B). Labridae larvae were
317 located off the coasts in the western part of the SB, but also present on the Italian
318 coasts of the SB and around the Lavezzi Islands on the French side (Fig. 4B).

319 For the dispersal model, the transport success did not differ significantly across PLD and
320 release area (Table 3), but similarly as with previous results with the MPA release sites,
321 transport success increased for both, Labridae and Sparidae, as the PLD decreased
322 ($PLD_{max} < PLD_{med} < PLD_{min}$; Fig. 5). The transport success was however only
323 significantly different between PLD_{max} and PLD_{min} for both species ($PLD_{max} <$
324 PLD_{min} ; Table 3). The transport success for Labridae was generally higher than for
325 Sparidae in August 2012, independently of release area and PLD (Fig. 5).

326 The connectivity matrices show that the dispersal pattern for Labridae and Sparidae
327 remains generally unaffected by the PLD, only the intensity of the transport success
328 varies (i.e. decreasing transport success as the PLD increases; Fig. 6). The main
329 settlement areas, for the Labridae and Sparidae in August 2012, are the eastern Italian
330 part of the SB (i.e. Z12) and then the Lavezzi Islands (Lav), which are both supplied by
331 larvae from all release areas of Labridae (Lab1-Lab7) and Sparidae (Spa1-Spa9; Fig. 6).

332 Additionally, Labridae are also highly dispersed to the western and central part of the
333 Italian side of the SB (Z10 and Z11), which are only supplied by the western release
334 areas of labrids located in deeper parts of the SB (Lab4-Lab7; Fig. 6).

335 **4. DISCUSSION**

336 **4.1. The Strait of Bonifacio: a highly dispersive system**

337 The low degree of larval retention inside the Strait of Bonifacio (SB) is characteristic of a
338 highly dispersive system. More than 96 % of larvae released from the MPAs inside the
339 strait were washed out of the monitored system (77.7 ± 12.2 % of non-settling particles
340 left the system boundaries) or died (22.3 ± 12.2 % of non-settling particles died) due to a
341 mismatch between the settlement habitat and their settlement window. The proportion of
342 mismatch between favorable settlement habitat and larval stage is even higher as the
343 PLD increases, implying that the settlement of species with shorter PLD is favored
344 inside the SB. Furthermore, self-recruitment of MPAs were rather low compared to the
345 contribution of MPAs to other non-protected settlement areas, supporting the idea that
346 connectivity patterns inside the SB are mainly driven by dispersal processes rather than
347 retention processes.

348 The degree of self-recruitment of fish larvae varies widely from one study system to
349 another (James et al., 2002; Jones et al., 1999; Saenz-Agudelo et al., 2011) with values
350 ranging from 5% (Siegel et al., 2003) to up to 60% in some cases (Almany et al., 2007).
351 Compared to those values reported in the literature, the percentage of self-recruitment
352 within the SB (around 4%) is situated at the lower range limit and can mainly be
353 explained by the hydrographic conditions of this area. Strong and highly variable
354 currents are known to occur in strait configurations (Astraldi et al., 1999; Plus et al.,
355 2009). The tightening in the middle of the SB, both horizontally (between Corsica and
356 Sardinia) and vertically, where water masses with an Atlantic affinity and from the
357 Tyrrhenian basin are exchanged, induces an acceleration of these water masses, which
358 induces a Venturi effect and the formation of eddies (Gérigny, 2010; Gérigny et al.,
359 2011). These effects are amplified in the SB due to a very jagged coastline, and a wide
360 continental shelf on the eastern part of the SB and a narrow shelf on the western part
361 with a steep bathymetric slope (Gérigny et al., 2011). Furthermore, a strong bi-modal

362 wind system occurring in this area (De Falco et al., 2011) amplifies also the small scale
363 spatio-temporal variability of currents in the SB (Gérigny, 2010; Gérigny and Coudray,
364 2013). All these factors favor the presence of strong currents with a high spatio-temporal
365 variability within the SB and explain its dispersive nature for fish larvae.

366 However, the main hydrographic and larval flows identified suggest that a considerable
367 amount of particles are drifting along the western Corsican and the eastern Italian
368 coasts. Both coasts mainly occupy the 0 to 20 m bathymetric range of rocky substrates
369 or *Posidonia* seaweeds, which are favorable habitats for larval settlement for most
370 coastal Mediterranean fish species (Garcia-Rubies and Macpherson, 1995). It is likely,
371 that the transport success of larvae exported from the SB would be greater if we
372 consider a greater spatial scale, beyond the SB. Great dispersal distances at scales of
373 tens or even hundreds of kilometers are not uncommon and have already been noticed
374 for coastal species in several ecosystems (Kinlan and Gaines, 2003). Moreover, even if
375 the specific hydrodynamic conditions of this strait area might seem to act as a major
376 forcing on the larval dispersal, self-recruitment in the SB might have also been
377 underestimated due to the lack of behavioral information in our dispersal model.
378 Previous studies have shown that the ability of larvae to orient themselves and actively
379 choose their settlement habitat reduces their dispersal from the release locations
380 (Basterretxea et al., 2013; Codling et al., 2004; Irisson et al., 2004; Staaterman et al.,
381 2012; Wolanski et al., 1997).

382 **4.2. Early life history traits and larval transport success**

383 Early life history traits of fish species are highly variable across species and have been
384 shown to determine the connectivity of several marine populations (Hanski, 1998;
385 Possingham and Roughgarden, 1990; Simons et al., 2013; Treml et al., 2012). The PLD
386 of Mediterranean coastal fish species is one of these highly variable traits, ranging from
387 only couple of days for *Symphodus ocellatus* (min. 8 days) to more than one and a half
388 month for *Pagellus erythrinus* (max. 49 days; Macpherson and Raventos, 2005). This
389 variability is as important within a same fish family (mean PLD of Labridae ranges
390 between 10 and 39 days) as it is among fish families (Macpherson and Raventos, 2005).
391 As supported by our results and by previous studies (Simons et al., 2013), the PLD

392 greatly influences the degree of dispersion and transport success of fish larvae. Coastal
393 species with shorter PLD will have greater chances to encounter a favourable settlement
394 habitat within their settlement window, as species with longer PLD will more likely drift
395 outside their favourable settlement habitat range. This is particularly true in isolated
396 areas with strong currents, such as the Islands of Corsica and Sardinia, and more
397 specifically the SB.

398 Our results in fact show that the transport success within the SB decreases consistently
399 as the PLD increases regardless of the season. The dispersal model results based on
400 the distribution of Labridae and Sparidae in the SB in August 2012 supports also this
401 result. They show that the transport success is higher for labrids which have for most of
402 them shorter PLDs than for sparids (Raventos and Macpherson, 2005b), but also that
403 their settlement areas within the SB are less wide spread than those of sparids. Most
404 sparid species occurring frequently in the SB such as *Diplodus puntazzo*, *D. sargus*, *D.*
405 *vulgaris* or *Sarpa salpa* have long mean PLDs of respectively 32, 27, 40 and 31 days
406 (Raventos and Macpherson, 2005a). In turn, most labrids occurring in the SB, such as
407 *Symphodus cinereus*, *S. doderleini*, *S. mediterraneus*, *S. ocellatus*, *S. roissali*,
408 *Symphodus tinca* present rather short average PLDs of respectively 11, 13, 13,10, 12
409 and 10 days (Raventos and Macpherson, 2005a). Fewer are the sparids with shorter
410 PLDs (e.g. *D. annularis* with a PLD of 18 days), and the labrids with longer PLDs (e.g.
411 *Thalassoma pavo* and *Labrus viridis*, with respectively a PLD of 39 and 31 days;
412 (Raventos and Macpherson, 2005a).

413 Release depth of eggs, i.e. bottom vs. surface release, which we used in our model as a
414 proxy for respectively benthic and pelagic eggs, also affects the transport success of fish
415 larvae across the SB, notably in association to PLD and month. Oceanographic
416 circulation studies conducted previously in the SB have provided evidence that surface
417 currents in this area (average speed \pm SD = 50 ± 28 cm.s⁻¹; maximum speed 146 cm.s⁻¹)
418 are generally stronger than bottom currents (average speed \pm SD = 16 ± 12 cm.s⁻¹;
419 maximum speed = 81 cm.s⁻¹) which are weaker and more diffusive (Gérigny, 2010;
420 Gérigny et al., 2011). Most sparids having pelagic eggs and most labrids benthic eggs,
421 the 3D circulation pattern of this area, in combination to differences in PLD, would
422 explain the lower transport success of sparids compared to labrids. Although there is a

423 general lack of information on the swimming abilities of Sparids and Labrids occurring in
424 the Mediterranean Sea, regarding the swimming abilities of other temperate Sparid and
425 Labrid species, their critical swimming speeds range from a few cm up to 20 cm.s⁻¹
426 depending on species and larval size (Clark et al., 2005; Patrick and Strydom, 2009;
427 Trnski, 2002). This reveals their potential of influencing their dispersal in low surface
428 current conditions and average bottom current conditions in the SB.

429
430 In sum, our model results seem to indicate that species with benthic eggs and short PLD
431 emitted inside the SB will have greater chances to settle inside this area with low spread
432 rates, whereas species with pelagic eggs and long PLD will be dispersed over larger
433 distances throughout the SB and exported outside this area (Blaxter, 1986; Leis and
434 Miller, 1976; Macpherson and Raventos, 2006; Siegel et al., 2003; Snelgrove et al.,
435 2008; Suthers and Frank, 1991). However, species might present local adaptations to a
436 specific region such as a reduced PLD (Bay et al., 2006), which makes it difficult to
437 assign specific species to a particular scenario of the biophysical model tested. Given
438 the geographical isolation of the Corsican and Sardinian Islands, it could however be
439 likely that Sparid and Labrid subpopulations of these islands are well differentiated from
440 those in less dispersive and isolated regions of the Mediterranean Sea and might
441 present local adaptations such as shorter PLDs. If this is the case, dispersal patterns in
442 the SB would correspond better to scenarios with short PLDs (PLD_{min} = 17 days) than
443 with long PLDs (PLD_{max} = 35 days).

444 **4.3. Match-mismatch: the spatio-temporal synchronization between larval supply** 445 **and hydrographic currents**

446 In the SB, larval transport success is not only dependent on early life history traits such
447 as the PLD, release depth and egg type, but also highly fluctuates in time and space.
448 The strong monthly variations of transport success highlight the essential contribution of
449 the synchronization between hydrographic conditions and reproductive timing.
450 According to Dixon et al. (1999), the episodic fluctuations in larval supply and the lack of
451 relationship between spawning output and transport success often observed in coastal
452 species can mainly be explained by the non-linear physical processes operating during

453 larval life stage. The circulation system of the Mediterranean Sea varies at different
454 spatio-temporal scales (Fernandez et al., 2005; Millot, 1999; Pinardi and Masetti, 2000):
455 at an annual, seasonal and small daily scale. Earlier hydrographic investigations
456 conducted in the SB have in fact shown that this area follows the average hydrographic
457 conditions present in the Mediterranean Sea (Gérigny, 2010), i.e. strong currents in
458 winter induced by winds and lower flow intensities in summer conditions (Astraldi et al.,
459 2002; Millot, 1999). Furthermore as shown in other Mediterranean areas, as for instance
460 in the Tyrrhenian basin (Iacono et al., 2013), summer hydrographic conditions in the SB
461 are characterized by frequent eddy structures (Gérigny, 2010).

462 The presence of stronger currents in the SB during winter than summer conditions could
463 suggest lower transport success during early spring than summer. Furthermore, the
464 increase of eddies structures in summer should favor transport success as these
465 structures are known to be centers of food retention (Logerwell and Smith, 2001).
466 Despite this, in the SB the stronger currents in spring seem to favor larval transport all
467 through the SB, from the Corsican East coast (Z7 to Z9 and 'Cerb' MPA) and the
468 Maddalena Archipelago ('RMB', 'Spa', 'Mad' MPAs) to the Corsican West coast (Z1 to
469 Z4; Fig. 7 A). This could explain the higher transport success in April than in the summer
470 months. In summer the main current drifting from North to South along the Eastern
471 Corsican coast getting weaker, connectivity between the East and West coast of the SB
472 was reduced compared to spring (Fig. 7). As shown before in Gérigny (2010), the
473 hypothesis behind that would be that the stronger the currents are, the more directional
474 they are, whereas lower currents tend to be more diffusive which would increase the
475 random dispersion of larvae outside the bounds of the SB system and explain the lower
476 larval transport success observed in summer and the higher transport success in spring.
477 This reduced transport success could also be linked to the formation of eddy structures
478 in summer which would disperse larvae away from favorable settlement habitats to
479 oceanic areas. Previous studies have also suggested that eddies can act as dispersion
480 mechanisms (Rodriguez et al., 2004). An important eddy structure in the western outer
481 part of the SB present in summer (Gérigny and Coudray 2013) would particularly explain
482 the low transport success in the western part of the SB in this time of the year.
483 Furthermore, compared to other potential settlement zones inside the SB, our model

484 highlights a relative high transport success around the MPAs of the Lavezzi Islands and
485 the complex of the Maddalena Archipelago and Z12 (the closest Sardinian coast located
486 to this archipelago; Fig. 7). The local bathymetry and the presence of numerous islands
487 and islets in these parts of the SB could increase the phenomenon of larval retention
488 and explain their relative high transport success particularly marked in early spring and
489 late summer (Fig. 7 A & C) compared to June (Fig. 7 B). These principal larval flow
490 patterns shown in Figure 7 are consistent with those based on the high density areas of
491 Labridae and Sparidae issued from our distribution model. In August, sparids and labrids
492 larvae across the SB, including those located in the western part of the SB, settle mainly
493 around the Lavezzi Island and the complex of the Maddalena Archipelago and Z12 (Fig.
494 8). The MPAs of the French Lavezzi Islands (Lav) and the Italian Maddalena
495 Archipelago (RMB, SPA and Mad) appear as two key areas concerning both, larval
496 supply and as settlement area. These results are generally consistent with the
497 management conducted until now in the SB. The Italian east coast of the SB close to the
498 Maddalena Archipelago (Z12) should however be further considered in future
499 management plans of the international marine park of the SB. Labrid larvae identified in
500 the eastern part of the SB further off shore or on the western Italian coast, settled
501 however also along the western Italian coast of the SB (Z10 see Fig. 8). Further
502 investigations including the entire Corsican and Sardinian Islands would thus be
503 required to assess the larval supply of the SB to other coasts of these two Islands.

504 The strong spatio-temporal variability of transport success of fish larvae observed in the
505 SB can furthermore have important ecological implications on their population dynamics.
506 Temperate-water species have generally restricted spawning seasons (Pavlov et al.,
507 2009) and can consequently be more affected by recruitment variability according to the
508 match-mismatch theory (Cushing, 1990; Wright and Trippel, 2009). Given our results,
509 we can hypothesize that late spring or early summer spawning species, such as *Dentex*
510 *dentex* or *Oblada melanura*, will be particularly sensitive to the dispersal process in the
511 SB and require thus particular attention in the management of these areas. The
512 spawning season of *D. dentex* occurs mainly between April and June (Marengo et al.,
513 2014). For instance, under the hydrodynamic configuration observed in 2012 in the SB,
514 if one year the main spawning peak of *D. dentex* shifted towards spring (and for early

515 spawners in general), then reproductive timing and hydrodynamic conditions would
516 match, as a greater part of produced larvae will reach a suitable settlement habitat
517 within the SB. In contrast, if the spawning peak occurs in early summer (and for late
518 spawners in general), there will be a mismatch between reproductive timing and the
519 hydrodynamic conditions leading to a very low transport success of larvae and most
520 particles being washed out of the boundaries of the system of the SB. A simulation
521 should be run over several years to produce a more generalized view of the
522 hydrographic regimes and their effects on dispersal processes in the SB. Although we
523 could only compute a dispersal model for one year (i.e. 2012) due to the availability of
524 data at time of the study, the summer circulation observed in the SB in 2012 (Gérigny
525 and Coudray, 2013) corresponds to that observed during previous oceanographic
526 cruises (Gérigny, 2010) and does not appear as an atypical situation, arguing that low
527 larval transport success highlighted in early summer in the SB is not only an isolated
528 phenomenon in 2012.

529 **4.4. Model limitations**

530 There are several shortcomings in the performed dispersal model which could be
531 improved in future studies. They concern mainly the fact that we considered larvae to be
532 passive particles due to a lack of biological information. The behavior of fish larvae has
533 in fact not been included; however several articles have shown the active orientation
534 and swimming abilities of fish larvae, particularly after reaching stage 4 of larval
535 development (Leis, 2006; Leis and Lockett, 2005; Staaterman et al., 2012). The
536 mortality or sublethal effects due to starvation of fish larvae has also not been included,
537 which can act as an important limiting factor in the larval supply (Faria et al., 2011).
538 Another limitation to our model is that we did not evaluate the efficient recruitment of fish
539 larvae as many biotic factors are involved in post-recruitment processes and mortality,
540 linked to habitat/resource availability or density dependent effects (Dixson, 2012; Planes
541 et al., 1998; Tupper and Boutilier, 1997). Instead of quantifying the effective recruitment
542 of fish populations, the aim of this work was in fact rather to quantify the potential larval
543 supply in order to identify the contribution of existing MPAs and to characterize the
544 general dispersal patterns in the SB. Further research on early life stages and juveniles
545 will thus be necessary in the future in order to implement more accurate and realistic

546 dispersal models. Among the different tools nowadays implemented, e.g. otolith
547 microchemistry and population genetics in general, transgenerational isotopic tagging
548 and genetic parentage analysis seem to be the most suitable tools to assess
549 connectivity (Leis et al., 2011; Thorrold et al., 2006) and should in future be coupled to
550 biophysical modelling of larvae (Gilg and Hilbish, 2003).

551 **5. Conclusions and Management Implications**

552 Despite some methodological shortcomings due to a lack of knowledge on the life
553 history and behavioral traits of early life stages of Mediterranean coastal fish species,
554 our work provides a first framework for conservation planning of the SB, integrating the
555 wide range of PLD and different egg types of coastal Mediterranean fish species. The
556 present work represents a groundwork resuming the connectivity between existing
557 MPAs and the main flow of larval supply in the SB influenced by hydrographic conditions
558 and life history traits. As highlighted by the connectivity between MPAs and by their
559 larval supply to French and Italian coastal areas, a transboundary management and
560 spatial planning of the SB is essential to sustainably protect fish resources in this area.
561 Similar transboundary MPA initiatives are nowadays still rare, but are necessary
562 especially in highly dispersive ecosystems where the persistence of populations strongly
563 relies on the dispersive life stages (i.e. on larval supply). Even if international
564 cooperation and agreements upon conservation and exploitation of natural resources
565 take time to get effective, they should be further encouraged in the future by politicians,
566 managers and stakeholders, for a more efficient management of marine coastal areas.

567 **Acknowledgements**

568 This study is part of the research Program "Halieutic Resources" introduced in 2012 by
569 the University of Corsica and its platform "Stella Mare" and was funded by the European
570 Union, the French Ministry of Environment and the Corsican Region through a CPER
571 (Contrat de Plan Etat-Région) and a FEDER (Fonds Européens de Développement
572 Régional) fund. We acknowledge Philippe Verley for his assistance with Ichthyop and
573 Chiara Lapucci from the LaMMA Consortium, Italy, for providing the Chlorophyll A data
574 used in the distribution model of fish larvae. We also wish to thank the crew of the
575 'Téthys II' for their valuable help on the field, as well as the environmental managers of

576 the marine park of the SB (“Réserve Naturelle des Bouches de Bonifacio”) for
577 exchanges conducted prior to this study. We would like to thank two anonymous
578 reviewers for providing helpful comments to this manuscript.

ACCEPTED MANUSCRIPT

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- 873
- 874

875 **Figure captions**

876 **Figure 1. Study location with the MPAs and the favorable settlement areas for**
877 **coastal Mediterranean fishes of the Strait of Bonifacio (Corsica, France).**

878
879 **Figure 2. Contribution of each MPA of the Strait of Bonifacio to the larval transport**
880 **success per PLD, release depth, and for each of the principal spawning months in**
881 **2012 (April to September).**

882
883 **Figure 3. Connectivity matrices of mean transport success (%) per principal**
884 **spawning months and release depth between each pair of release and settlement**
885 **areas.**

886
887 **Figure 4. Distribution maps of observed and predicted (A) Sparidae and (B)**
888 **Labridae larval densities (ind m⁻²). Areas of high densities were extracted as release**
889 **polygons for the dispersal model based on the field data for Labridae and Sparidae.**

890
891 **Figure 5. Contribution of each release polygon of Labridae and Sparidae to the**
892 **larval transport success per PLD for August 2012.**

893
894 **Figure 6. Connectivity matrices of Labridae and Sparidae transport success (%)**
895 **per PLD for August 2012.**

896
897 **Figure 7. Schematic map of main larval flows (of recruiting larvae) between**
898 **release (MPAs) and settlement areas for April (A), June (B) and August 2012 (C).**

899
900 **Figure 8. Schematic map of main larval flows between release areas (based on**
901 **field data, i.e. high larval density areas) and settlement areas for Labridae (A) and**
902 **Sparidae (B) during August 2012.**

903 **Tables**

904 **Table 1. Parameterization and aims of performed simulation scenarios. (SDM:**
 905 **Species Distribution Model, PLD: Pelagic Larval Duration, MPA: Marine Protected**
 906 **Area)**

Scenario code	Release area (Nb)	Release depth (m)	Number of particles	PLD (days)	Period	Release Frequency	Aims
S1	MPA (7)	Surface (0 - 10 m)	80 000	PLD max (35)	April to August 2012	Each week	Influence of biological parameters and temporal variability on larval dispersal (transport success)
S2				PLD med (25)			
S3				PLD min(17)			
S4	MPA (7)	Bottom (10 - 30 m)	80 000	PLD max (35)	April to August 2012	Each week	
S5				PLD med (25)			
S6				PLD min (17)			
S7	areas of high density of stage 2 Sparidae larvae issued from the SDM (9)	Surface (0 - 15 m)	100 000	PLD max (35 - 10 = 25)	August 2012	Each day (4th to 8th)	Comparison with in-situ data
S8				PLD med (25 - 10 = 15)			
S9				PLD min (17 - 10 = 7)			
S10	areas of high density of stage 2 Labridae larvae issued from the SDM (7)	Surface (0 - 15 m)	100 000	PLD max (35 - 10 = 25)	August 2012	Each day (4th to 8th)	
S11				PLD med (25 - 10 = 15)			
S12				PLD min (17 - 10 = 7)			

907

908

909

910 **Table 2. GLMM (Generalized Linear Mixed Model) of larval transport success by**
 911 **release MPA (rel), release depth (surface, bottom), PLD (max, med, min) and**
 912 **spawning months (April to September 2012). 'ns' $p > 0.05$, '*' $p < 0.5$, '**' $p < 0.01$,**
 913 **'***' $p < 0.001$**

	Df	AIC	LRT	Pr(Chi)	
		-1435.9			
PLD : Depth	2	-1431.2	8.76	0.012549	*
PLD : Month	10	-1329.1	126.88	< 2.2e-16	***
PLD : Release	12	-1300.7	159.25	< 2.2e-16	***
Depth : Release	6	-1443.7	4.25	0.642746	
Release : Month	30	-1169.9	326.06	< 2.2e-16	***
Depth : Month	5	-1430.6	15.33	0.009054	**

914

915 **Table 3. (A) GLMM (Generalized Linear Mixed Model) of larval transport success**
 916 **by release area 'rel' and PLD (max, med, min) for the two fish families, Sparidae**
 917 **and Labridae, during August 2012 and (B) the pair-wise test for only the factor of**
 918 **PLD length.**

919 **(A)**

<i>Sparids</i>	Df	AIC	LRT	Pr(Chi)
		790.4		
PLD : rel	16	761.46	3.0617	0.9998 ns

<i>Labrids</i>	Df	AIC	LRT	Pr(Chi)
		1096.2		
PLD : rel	12	1074	1.858	0.9996 ns

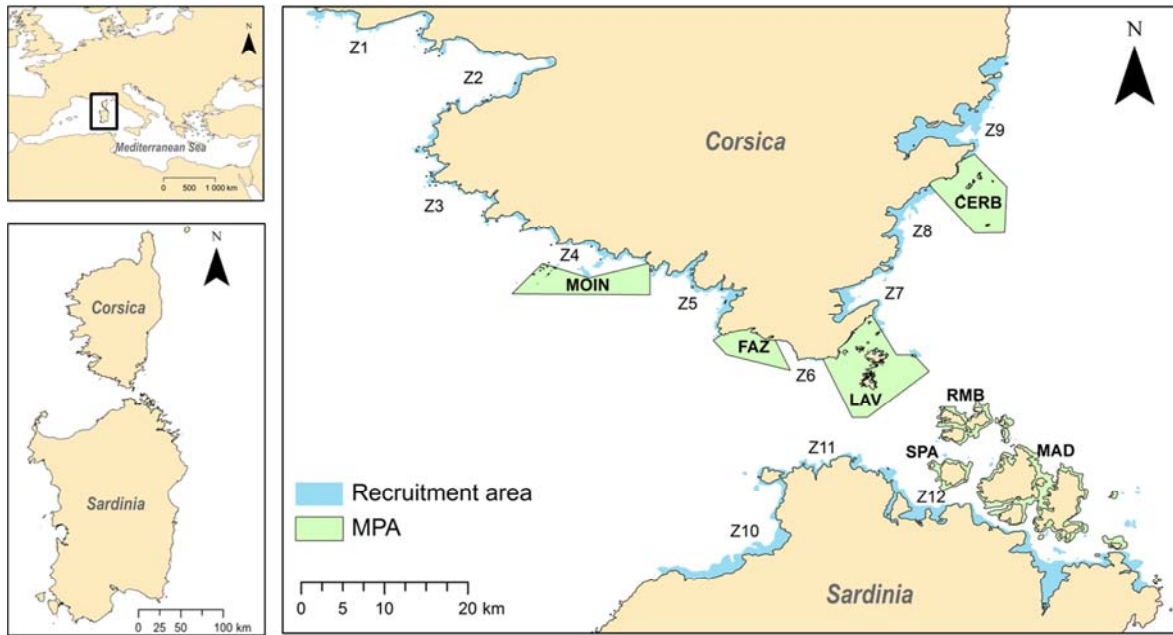
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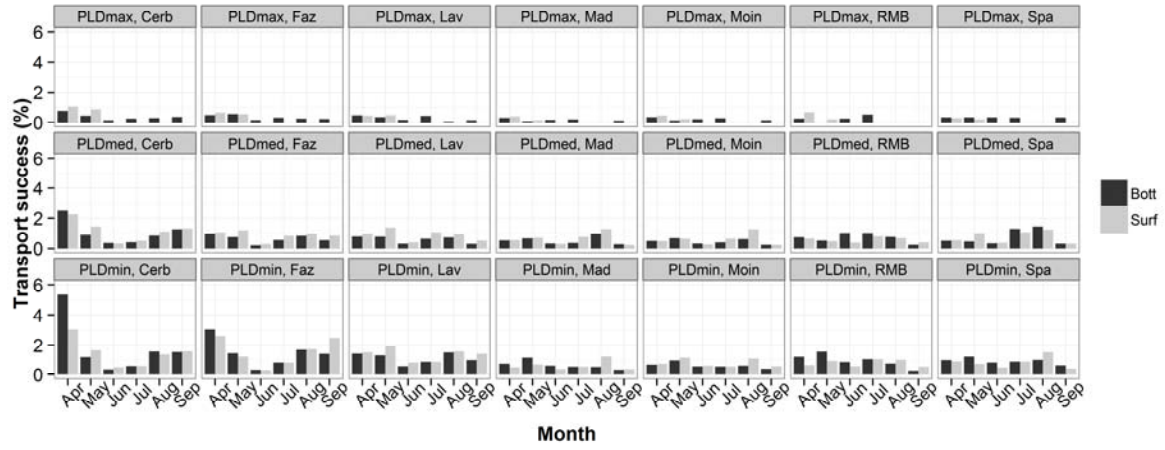
921 **(B)**

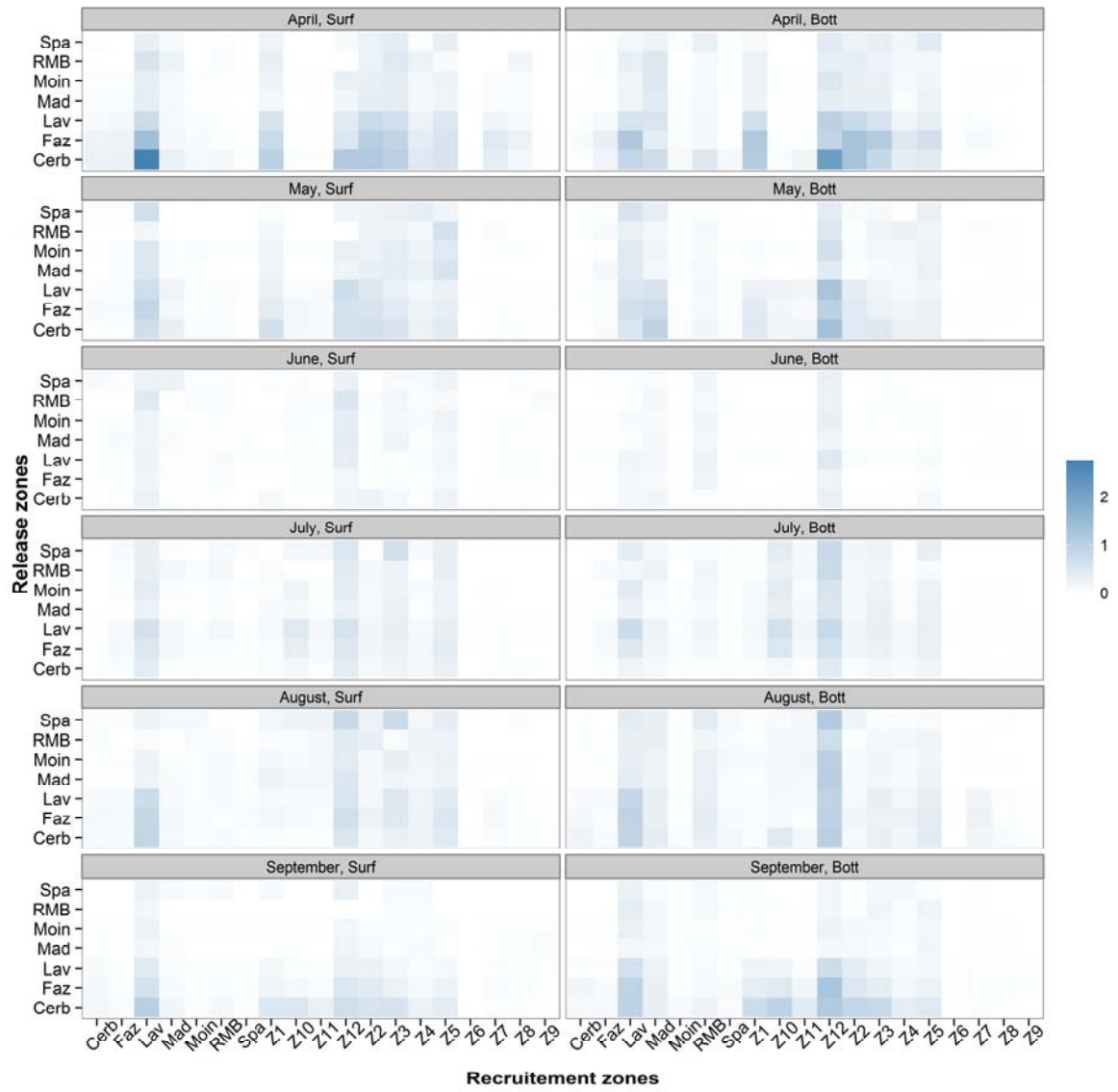
<i>Sparids</i>	Estimate	Std. Error	z-value	Pr(> z)
PLDmed : PLDmax	0.1714	0.1529	1.121	0.50119
PLDmin : PLDmax	0.4804	0.1529	3.142	0.00478 **
PLDmin : PLDmed	0.309	0.1529	2.021	0.10718

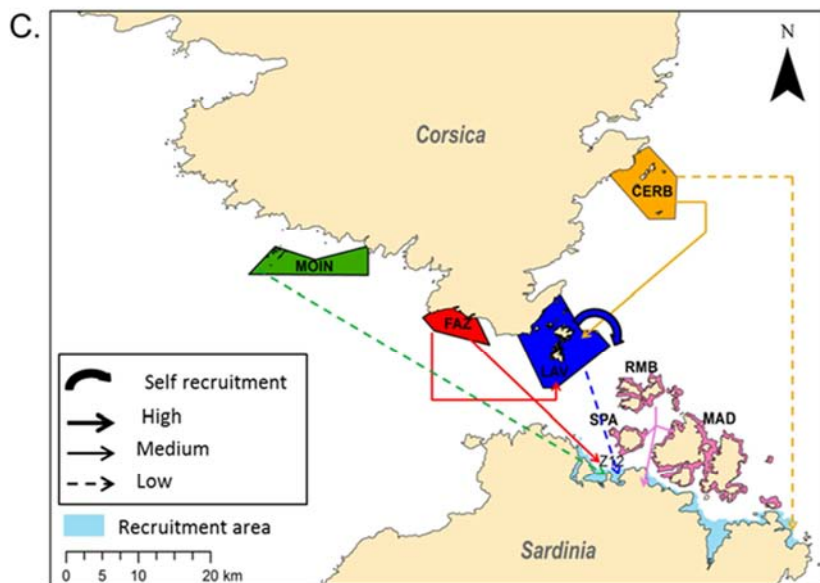
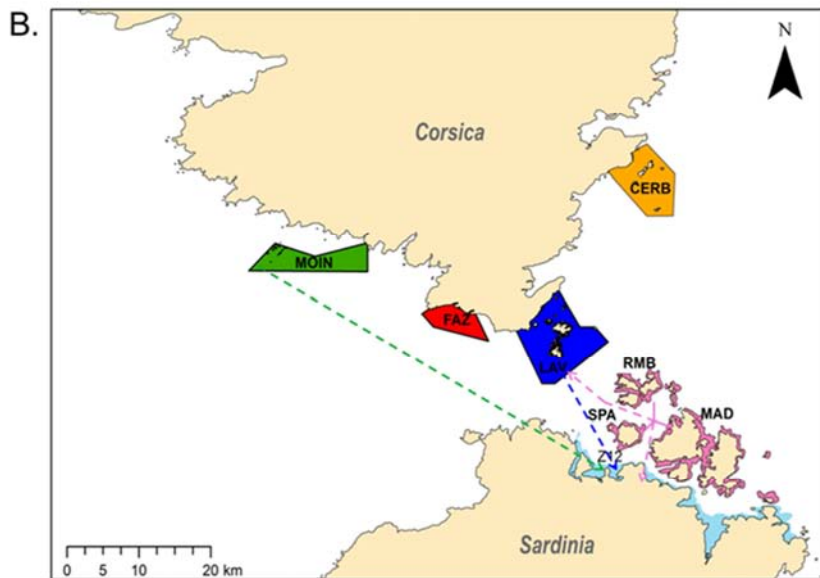
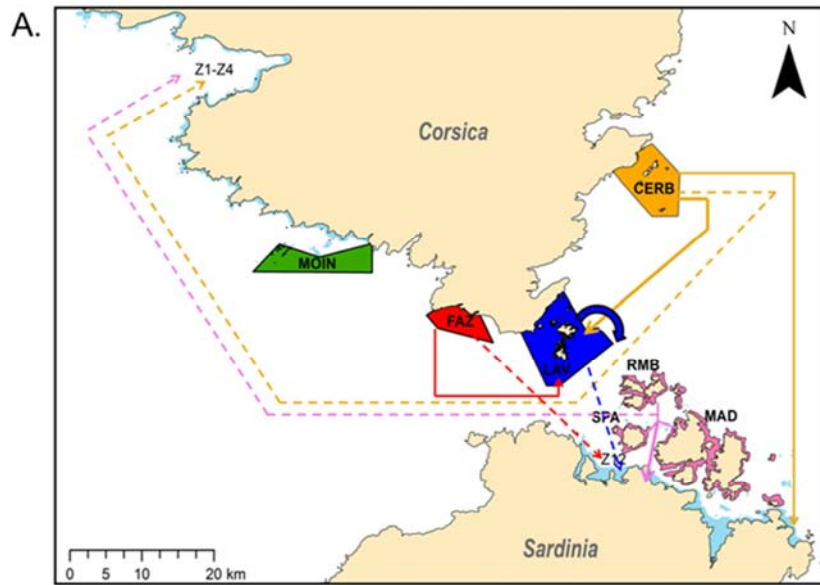
<i>Labrids</i>	Estimate	Std. Error	z-value	Pr(> z)
PLDmed : PLDmax	0.3505	0.2712	1.293	0.39926
PLDmin : PLDmax	0.9221	0.2712	3.401	0.00196 **
PLDmin : PLDmed	0.5716	0.2712	2.108	0.08829 .

922

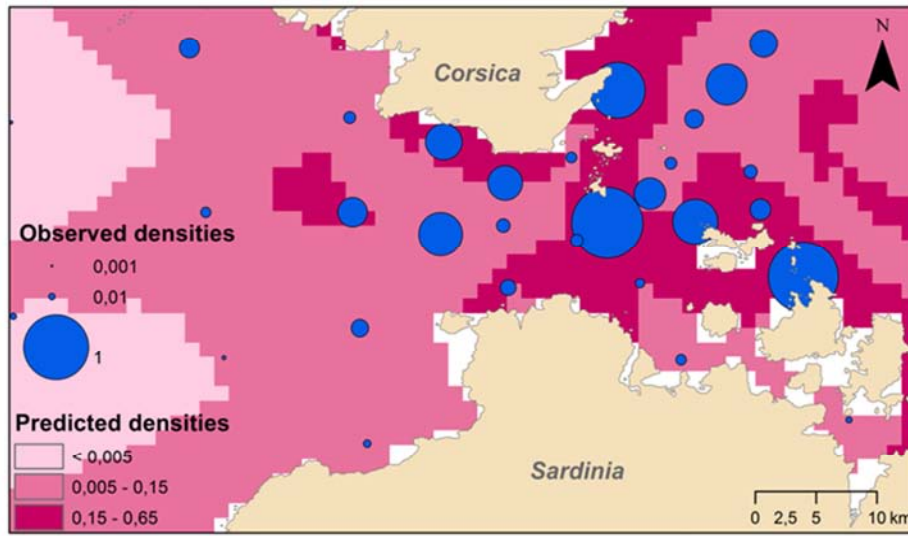








A



B

