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: (1) characterize the dispersal patterns across the Strait of Bonifacio; (2) identify the main potential settlement areas; (3) quantify the connectivity and the larval supply from the MPAs to the surrounding areas. A high resolution hydrodynamic model (MARS 3D, Corse 400 m) 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 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.

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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 10–100s' of km, as shown in previous studies on reef fishes (McCleave et al., 1987; Kinlan and Gaines, 2003; Cowen et al., 2006; 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 (Shanks, 2009; Saenz-Agudelo et al., 2011). 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 (Werner et al., 1996; Pineda et al., 2007), such as egg buoyancy, Pelagic Larval Duration (PLD), availability of food and predation pressure operating at different spatial and time scales (Scheltema, 1986; Pineda et al., 2009) as well as on the behavior of ELF linked to their swimming and orientation abilities (Leis and Lockett, 2005; Leis, 2006; Staaterman et al., 2012).

1.2. The Mediterranean Sea and its marine protected areas

The Mediterranean Sea is one of the world's marine biodiversity hotspot (Bianchi and Morri, 2000; Coll et al., 2010) and concentrates between 4 and 18 % of known marine species (Mouillot et al., 2011). It is also one of the most impacted ecosystems by fisheries (Tudela, 2004) and considered as a highly vulnerable sea (Cognetti and Curinigalletti, 1993; Coll et al., 2012). With the aim to sustainably protect and to ensure marine biodiversity and related ecosystem goods and services, following the Convention on Biological Diversity and the Barcelona Convention, a target of 10% protection of the marine and coastal Mediterranean waters representative of the Mediterranean diversity has been set to reach by 2020 (Olsen et al., 2013). To date, 677 Marine Protected Areas (MPAs) have been identified in the Mediterranean Sea covering 87 500 km^2, i.e. 1.1% of the sea surface of the Mediterranean and up to 4.6%, including the Pelagos Sanctuary for marine mammals (Gabrié et al., 2012). Marine Protected Areas are particularly suited management tools for coastal areas, as they protect simultaneously the living resources from extraction, but also the essential habitats on which they rely (Agardy, 1994). Since the implementation of the first MPA around 1920–1930 along the Californian coasts (Sobel and Dahlgren, 2004), evidence has been provided by MPAs around the world, that these management tools induce biological responses, mainly increasing the densities of populations, biomass, average organism size and diversity (Halpern and Warner, 2002; Halpern, 2003).

One future target identified within the framework of the Barcelona Convention, will be to design networks of MPAs at a seascape scale rather than isolated MPAs at a regional or national scale (Olsen et al., 2013). These MPA networks will consist of individual MPAs sufficiently interconnected to provide genetic, demographic and ecological stepping-stones. According to the IUCN-WCPA (International Union for Conservation of Nature – World Commission on Protected Areas), the synergistic operation of these interconnected MPAs will help to implement more efficiently their ecological aims (Olsen et al., 2013). At present, the designation and the size of MPAs is still very uneven across Mediterranean countries, being mostly located in the northern basin (96% in Spanish, French, Italian and Greek waters). These MPAs range between 0.003 and 4000 km^2, but most of them are small ranging between 11 and 25 km^2.

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

The general purpose of this work was thus to characterize the effects of the hydrodynamic system of the SB on larval dispersal in order to provide fundamental guidelines for the marine spatial planning in the recently established international marine park of the SB. Based on the hypothesis that no-take zones or MPAs with enhanced protection will produce more fish larvae, compared to adjacent fished areas, due to a higher reproductive output and fitness and a denser population of spawners/brood stock, we modeled the outcome of larvae released by coastal fishes inside the areas of enhanced protection of the SB in order to: (1) characterize the dispersal patterns across the SB, (2) identify the main potential settlement areas, and (3) quantify the connectivity and the larval supply from the MPAs to the surrounding areas. Larval dispersal was modeled following various scenarios in order to investigate the effect of the seasonal variability and of biological parameters of early life stages, such as the pelagic larval durations (PLDs) and the egg type (benthic or pelagic). Additionally, dispersal patterns were compared with those obtained by a larval dispersal model based on the distribution of fish larvae issued from a sampling campaign.

2. Material and methods

2.1. Study area and hydrographic conditions

The Strait of Bonifacio (SB) is a 13 km wide strait separating the islands of Corsica in the North and of Sardinia in the South, located at the meeting-point between the western Mediterranean and Tyrrhenian basin (Fig. 1). Straits are considered as naturally formed passage, narrow enough to constrain surface flows (Astraldi et al., 1999). These choke points are characterized by high seasonal variability of currents (Astraldi et al., 1999). Due to its geomorphological configuration, bathymetry and the presence of numerous islands and islets, the SB is a complex area in term of currents (Gérigny, 2010). These currents have an average intensity of 0.5 m s^{-1} and can reach up to 1.46 m s^{-1} (Gérigny et al., 2011). The general circulation in this area is mainly influenced by two prevailing orographically controlled winds, a western wind (52–54% of the winds) and an eastern wind (26%); (De Falco et al., 2011).

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

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

2.2. Larval dispersal modeling

2.2.1. Biophysical model

Larval dispersal was modeled using Ichthyop, a coupled biophysical Lagrangian particle tracking tool (Lett et al., 2008). The CORSE-400 m hydrodynamic model is based on the MARS-3D code, the 3D hydrodynamic Model for Application at the Regional Scale (Lazure and Dumas, 2008). CORSE-400 m was implemented with a configuration of 400 m horizontal resolution and 30 sigma layers, which covers the entire Corsican Island, the SB and the most southern part of Sardinia Island. CORSE-400 m takes its boundary conditions on the North-western Mediterranean configuration –
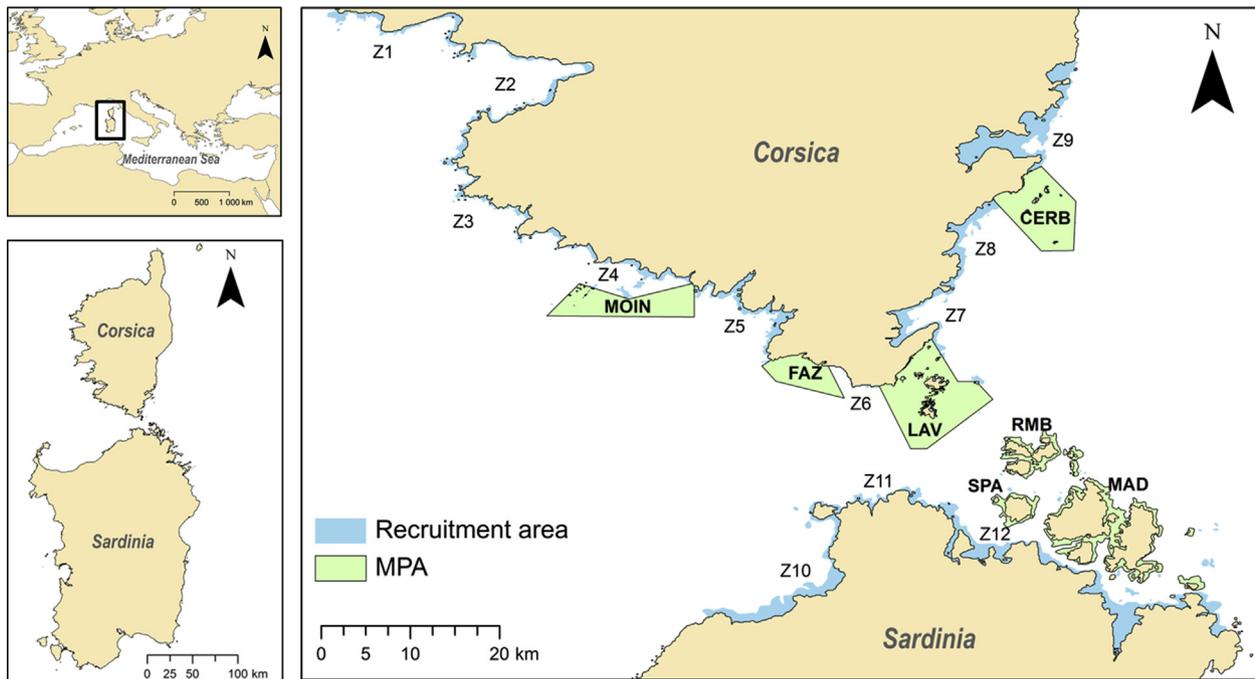
Fig. 1. Study location with the MPAs and the favorable settlement areas for coastal Mediterranean fishes of the Strait of Bonifacio (Corsica, France).

MENOR (André et al., 2005; Rubio et al., 2009). The CORSE-400 m hydrodynamic model was calibrated for temperature, salinity and hydrodynamic structures around Corsica during the MOMAR project (Faure et al., 2012) and during the Stella Mare 1 cruise in the SB in August 2012 (Gérigny and Coudray, 2013).

2.2.2. Dispersal scenarios & model parameterization

Larval dispersal was modeled following various scenarios for 2012, in order to account for the great variability of life traits of early fish stages (Table 1). Three scenarios of pelagic larval durations (PLDs) were therefore modeled: 'PLDmax', 'PLDmed' and 'PLDmin' corresponding respectively to 35, 25 and 17 days of dispersal (Table 1). PLDs were computed based on the median, the upper and lower quartile of known PLD for coastal Mediterranean fish (Raventos and Macpherson, 2001; Macpherson and Raventos, 2006). Two release depth scenarios were also modeled to simulate the dispersal for pelagic eggs ('Surface scenario': release depth between 0 and 10 m) and benthic eggs ('Bottom scenario': release depth between 10 and 30 m depending on bathymetry; Table 1). In Mediterranean coastal fish communities, most species have pelagic eggs (Olivar and Sabates, 1997), such as most sparids (Macpherson

and Raventos, 2006). Benthic eggs attached or not to substrate, are representative of most Labridae (Ylieff, 2000) and many Gobidae (Macpherson and Raventos, 2006). Models for each scenario were run over the main spawning period of Mediterranean coastal fish species, i.e. from April to September (Tsikliras et al., 2010) to account for seasonal variability in the dispersal pattern across the SB (Table 1). A total of 36 simulations were run corresponding to the six different tested scenarios for each of the principal spawning months (April to September).

In our case study, larval transport was modeled across the SB considering the boundaries of the Corse-400 m model (40.72°–43.32°N and 8.15°–9.95°E) and release areas of particles (i.e. spawning areas) were parameterized as the seven MPA zones with enhanced protection within the SB (Fig. 1). Four of them are located on the French side of the SB, from west to east: the Islands of Moines (Moin), Fazio (Faz), Lavezzi (Lav) and the Cerbicales (Cerb). Three of them are located on the Italian side of the SB and constitute the 'Archipelago de la Maddalena': the Maddalena Island (Mad), the Islands of Razzoli, Maria and Budelli (RMB) and the Island of Spargi (Spa). Settlement areas were defined following the habitat preferences of coastal fish species, i.e. rocky and vegetated

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

substrates, mainly with sea grass meadows (Guidetti, 2000; La Mesa et al., 2011) and within the upper bathymetric range from 0 to 20 m depth (Harmelin-Vivien et al., 1995). As *Posidonia oceanica* sea grass meadows were present nearly continuously on the coasts of the study area, settlement areas were divided into 19 zones (Fig. 1), numbered Z1 to Z12 from West to East and North to South plus the subset zones of the MPA release zones favorable for larval settlement (Moin, Faz, Lav, Cerb, Mad, RMB, SPA).

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

2.2.3. Transport success & data analysis

Transport success (i.e. proportion of larvae released that reached a suitable settlement habitat within their settlement window) was computed for each pair of release and settlement zones and for each tested scenario (by PLDs, depth, months). Transport success was used as an estimate for larval dispersal (which includes additionally behavioral processes linked to settlement; Pineda et al., 2007) and connectivity (which includes as well post-settlement processes such as density dependence, mortality due to predation or low food availability, affecting survival of settlers). Prior to analysis, settlement success was standardized by the number of particles released by each MPA, to account for unequal size of MPAs. Settlement success was visually inspected using connectivity matrices between release and settlement areas. Transport success data was non-normally distributed, and included repeated measures of transport success per settlement area. GLMMs represent a suitable technique for analyzing non-normal data with random effects (Zuur et al., 2009). The effect of PLD, release depth, month, and area on the variability of transport success was thus tested using a GLMM using a Gaussian distribution and an identity link after a box–cox transformation (Zuur et al., 2009). GLMMs were computed using the package 'lme4' for the R statistical environment (R Core Team, 2013). Settlement areas were considered as random factors. PLD, release depth, month, and area were considered as fixed categorical factors. In each model, the normality of residuals and the model performance were visually examined using residual distributions and quantile–quantile plots of residuals against fitted values. P-values were computed using the Kenward–Roger approximation method using the R-package 'pbkrtest' (Halekoh and Højsgaard, 2014).

2.3. Matching of dispersal model with fish larvae distribution

2.3.1. Sample collection and identification

During an oceanographic cruise performed in 2012, between August 4th and 8th, 64 plankton samples were taken at 32 stations across the SB. At each station, ichthyoplankton was collected using a 60 cm bongo net mounted with 200 μm and 500 μm mesh size on each side. Oblique tows were performed at two knots from above the bottom to the surface with a depth meter attached to the net. Volumes filtered were calculated from calibrated flowmeters attached to the mouth on each side of the bongo net. Immediately after capture, samples were fixed whether in ethanol for 500 μm mesh and in 3.7% buffered formalin for 200 μm mesh. At the laboratory, ichthyoplankton was classified according to fish families

and life stages were defined according to Grioche et al. (2000) (i.e. stage 1 as the yolk-sac larvae, stage 2 the preflexion larvae, stage 3 the flexion larvae and stage 4 the post-flexion larvae). Size class identification was used for an estimation of the age of larvae for further analyses. Among the 15 fish families identified, only Sparidae and Labridae larvae were considered, as they were the most abundant coastal fishes in the samples, and are often considered as indicator species of Mediterranean coastal fish communities (Guidetti et al., 2002; Mouillot and Culioli, 2002).

2.3.2. Distribution of fish larvae in the SB

The potential geographic distribution of Labridae and Sparidae larvae was estimated for the entire SB by characterizing the environmental predictors and conditions suitable for larvae belonging to these two fish families. For this purpose, different ecological meaningful environmental variables were collected, to be used as predictors of fish larval densities, namely subsurface temperature, salinity, bathymetry, atmospheric pressure (issued from PREVIMER data http://www.previmer.org/), Chlorophyll A (issued from MODIS satellite data obtained by OC5 algorithm), and distance to coast computed additionally using GIS-tools. The environmental point data for each variable was then used to produce continuous raster maps by interpolation using a kriging method (Geostatistical Analyst for ArcGIS 10.1). A correlative species distribution model was fitted, using generalized linear models, to predict the likelihood of the density of fish larvae based on environmental predictors. A forward stepwise selection of the best model was performed using the Akaike Information Criterion AIC (Akaike, 1981). This information-theoretic method uses deviance as a measure of fit (Burnham and Anderson, 2002; Burnham et al., 2011). The final selected model for Labridae and Sparidae was then used to predict their density distribution across the SB. The Jenks optimization method was used to classify the predicted density distribution and areas of highest Labridae and Sparidae densities were delineated using GIS.

2.3.3. Larval dispersal model and scenarios

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

3. Results

3.1. General retention characteristics of the SB and its MPAs

The mean retention of the Strait of Bonifacio (SB), for all simulation scenarios and across all spawning months, was of 3.56 ± 2.31%, i.e. a mean of 3.56% of larvae released inside the MPAs of the SB reached a favorable settlement habitat within their settlement window. The other 96% of released particles were

dispersed out of the studied system or did not reach a favorable settlement habitat during their settlement window. The degree of retention for each MPA was considerably lower, even if a great variability can be noticed between scenarios and months. Highest retention rates were found for the MPAs Cerb, Faz and Lav (respectively 0.26 ± 0.43, 0.22 ± 0.36, 0.19 ± 0.27%) and lowest for the MPAs Moin, Mad, RMB and Spa (respectively 0.11 ± 0.17, 0.10 ± 0.17, 0.10 ± 0.19, 0.11 ± 0.23%).

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

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

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

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

settlement is also notable at the western French part of the SB (Z1–Z3; Fig. 3).

3.3. Matching of dispersal model with fish larvae distribution

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

For the dispersal model, the transport success did not differ significantly across PLD and release area (Table 3), but similarly as with previous results with the MPA release sites, transport success increased for both, Labridae and Sparidae, as the PLD decreased (PLDmax < PLDmed < PLDmin; Fig. 5). The transport success was however only significantly different between PLDmax and PLDmin for both species (PLDmax < PLDmin; Table 3). The transport success for Labridae was generally higher than for Sparidae in August 2012, independently of release area and PLD (Fig. 5).

The connectivity matrices show that the dispersal pattern for Labridae and Sparidae remains generally unaffected by the PLD, only the intensity of the transport success varies (i.e. decreasing transport success as the PLD increases; Fig. 6). The main settlement

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

	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**

Fig. 2. Contribution of each MPA of the Strait of Bonifacio to the larval transport success per PLD (max, med, min), release depth (Bottom, Surface), and for each of the principal spawning months in 2012 (April to September).
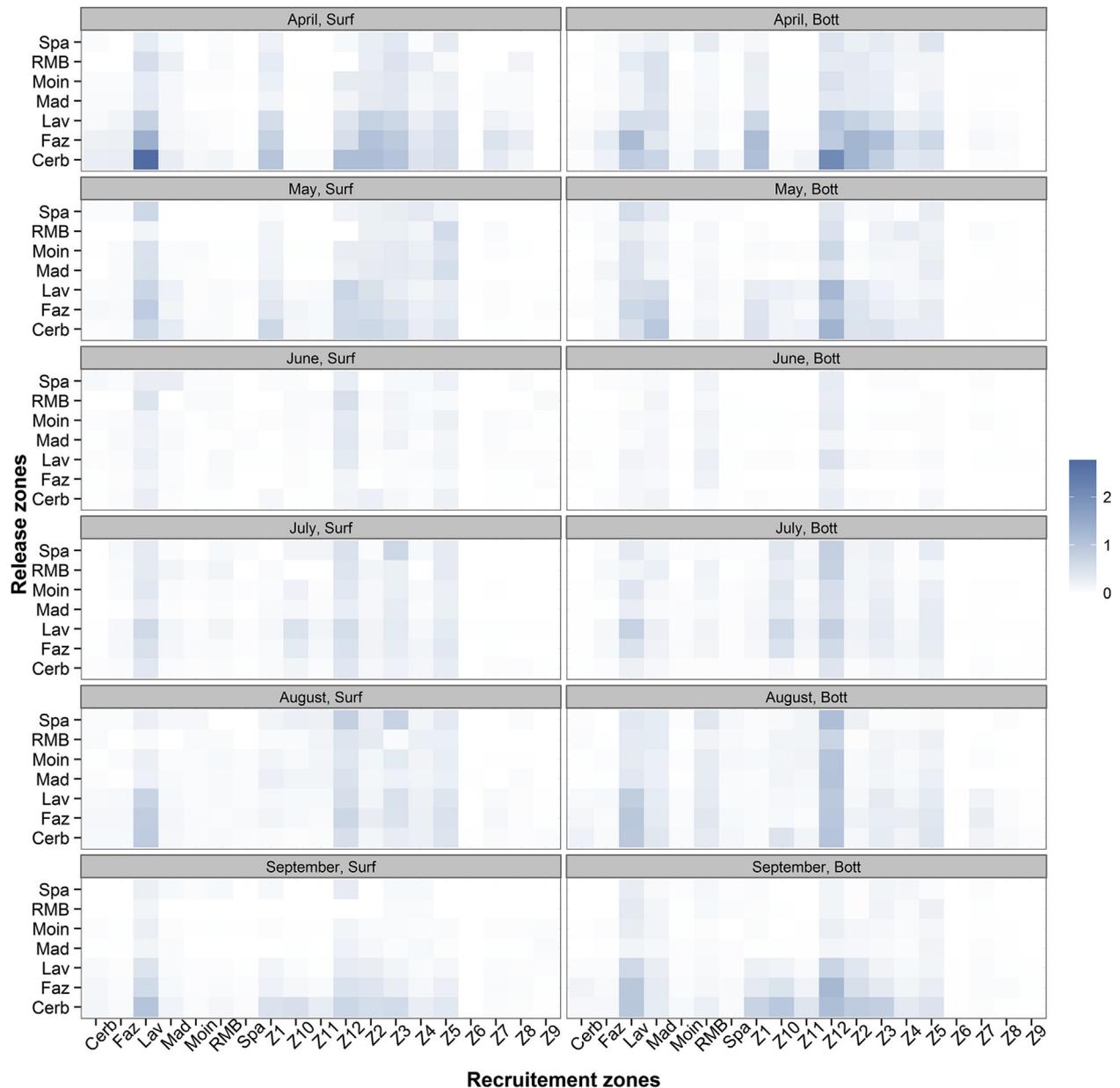
Fig. 3. Connectivity matrices of mean transport success (%) per principal spawning months and release depth (Surface, Bottom) between each pair of release and settlement areas.

areas, for the Labridae and Sparidae in August 2012, are the eastern Italian part of the SB (i.e. Z12) and then the Lavezzi Islands (Lav), which are both supplied by larvae from all release areas of Labridae (Lab1–Lab7) and Sparidae (Spa1–Spa9; Fig. 6). Additionally, Labridae are also highly dispersed to the western and central part of the Italian side of the SB (Z10 and Z11), which are only supplied by western release areas of labrids located in deeper parts of the SB (Lab4–Lab7; Fig. 6).

4. Discussion

4.1. The Strait of Bonifacio: a highly dispersive system

The low degree of larval retention inside the Strait of Bonifacio (SB) is characteristic of a highly dispersive system. More than 96% of larvae released from the MPAs inside the strait were washed out of the monitored system (77.7 ± 12.2% of non-settling particles left the

system boundaries) or died (22.3 ± 12.2% of non-settling particles died) due to a mismatch between the settlement habitat and their settlement window. The proportion of mismatch between favorable settlement habitat and larval stage is even higher as the PLD increases, implying that the settlement of species with shorter PLD is favored inside the SB. Furthermore, self-recruitment of MPAs were rather low compared to the contribution of MPAs to other non-protected settlement areas, supporting the idea that connectivity patterns inside the SB are mainly driven by dispersal processes rather than retention processes.

The degree of self-recruitment of fish larvae varies widely from one study system to another (Jones et al., 1999; James et al., 2002; Saenz-Agudelo et al., 2011) with values ranging from 5% (Siegel et al., 2003) to up to 60% in some cases (Almany et al., 2007). Compared to those values reported in the literature, the percentage of self-recruitment within the SB (around 4%) is situated at the lower range limit and can mainly be explained by the hydrographic
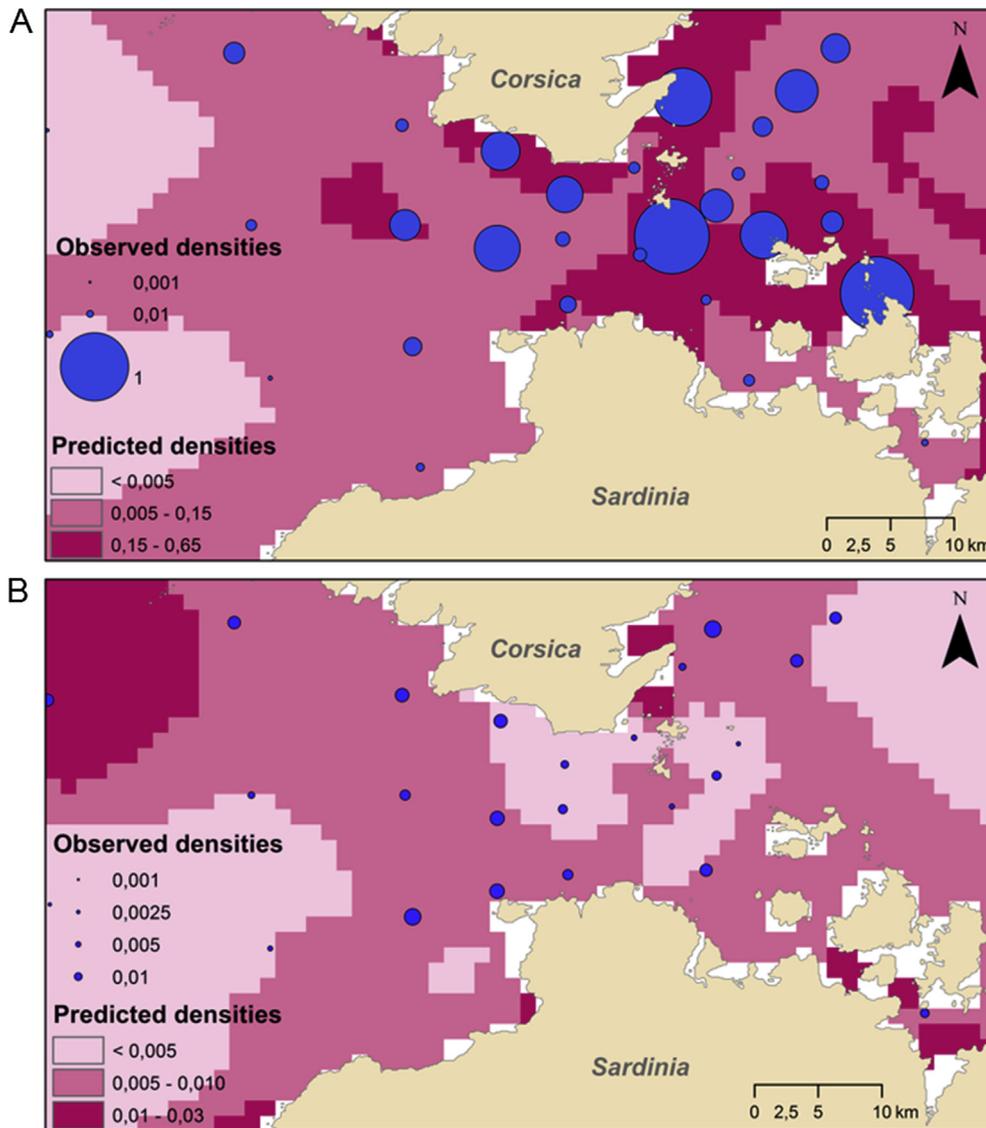
Fig. 4. Distribution maps of observed and predicted (A) Sparidae and (B) Labridae larval densities (ind m^{-2}). Areas of high densities were extracted as release polygons for the dispersal model based on the field data for Labridae and Sparidae.

conditions of this area. Strong and highly variable currents are known to occur in strait configurations (Astraldi et al., 1999; Plus et al., 2009). The tightening in the middle of the SB, both horizontally (between Corsica and Sardinia) and vertically, where water masses with an Atlantic affinity and from the Tyrrhenian basin are exchanged, induces an acceleration of these water masses, which induces a Venturi effect and the formation of eddies (Gérigny, 2010; Gérigny et al., 2011). These effects are amplified in the SB due to a very jagged coastline, and a wide continental shelf on the eastern part of the SB and a narrow shelf on the western part with a steep bathymetric slope (Gérigny et al., 2011). Furthermore, a strong bi-modal wind system occurring in this area (De Falco et al., 2011) amplifies also the small scale spatio-temporal variability of currents in the SB (Gérigny, 2010; Gérigny and Coudray, 2013). All these factors favor the presence of strong currents with a high spatio-temporal variability within the SB and explain its dispersive nature for fish larvae.

However, the main hydrographic and larval flows identified suggest that a considerable amount of particles are drifting along the western Corsican and the eastern Italian coasts. Both coasts mainly occupy the 0—20 m bathymetric range of rocky substrates or

Posidonia seaweeds, which are favorable habitats for larval settlement for most coastal Mediterranean fish species (Garcia-Rubies and Macpherson, 1995). It is likely, that the transport success of larvae exported from the SB would be greater if we consider a greater spatial scale, beyond the SB. Great dispersal distances at scales of tens or even hundreds of kilometers are not uncommon and have already been noticed for coastal species in several ecosystems (Kinlan and Gaines, 2003). Moreover, even if the specific hydrodynamic conditions of this strait area might seem to act as a major forcing on the larval dispersal, self-recruitment in the SB might have also been underestimated due to the lack of behavioral information in our dispersal model. Previous studies have shown that the ability of larvae to orient themselves and actively choose their settlement habitat reduces their dispersal from the release locations (Wolanski et al., 1997; Codling et al., 2004; Irisson et al., 2004; Staaterman et al., 2012; Basterretxea et al., 2013).

4.2. Early life history traits and larval transport success

Early life history traits of fish species are highly variable across species and have been shown to determine the connectivity of

Table 3
(A) GLMM (Generalized Linear Mixed Model) of larval transport success by release area 'rel' and PLD (max, med, min) for the two fish families, Sparidae and Labridae, during August 2012 and (B) the pair-wise test for only the factor of PLD length. 'ns' p > 0.05, '*' p < 0.5, '**' p < 0.01, '****' p < 0.001.

(A)

	Df	AIC	LRT	Pr(Chi)	
Sparids	790.4				
PLD: rel	16	761.46	3.0617	0.9998	ns
Labrids	1096.2				
PLD: rel	12	1074	1.858	0.9996	ns

(B)

	Estimate	Std. error	z-value	Pr(>|z|)	
Sparids					
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	
Labrids					
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	

several marine populations (Possingham and Roughgarden, 1990; Hanski, 1998; Treml et al., 2012; Simons et al., 2013). The PLD of Mediterranean coastal fish species is one of these highly variable traits, ranging from only couple of days for *Symphodus ocellatus* (min. 8 days) to more than one and a half month for *Pagellus erythrinus* (max. 49 days; Macpherson and Raventos, 2005). This variability is as important within a same fish family (mean PLD of Labridae ranges between 10 and 39 days) as it is among fish families (Macpherson and Raventos, 2005). As supported by our results and by previous studies (Simons et al., 2013), the PLD greatly influences the degree of dispersion and transport success of fish larvae. Coastal species with shorter PLD will have greater chances to encounter a favorable settlement habitat within their settlement window, as species with longer PLD will more likely drift outside their favorable settlement habitat range. This is particularly true in isolated areas with strong currents, such as the Islands of Corsica and Sardinia, and more specifically the SB.

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

Release depth of eggs, i.e. bottom vs. surface release, which we used in our model as a proxy for respectively benthic and pelagic eggs, also affects the transport success of fish larvae across the SB, notably in association to PLD and month. Oceanographic circulation studies conducted previously in the SB have provided evidence that surface currents in this area (average speed $\pm$ SD = 50 $\pm$ 28 cm s^{-1}; maximum speed 146 cm s^{-1}) are generally stronger than bottom currents (average speed $\pm$ SD = 16 $\pm$ 12 cm s^{-1}; maximum speed = 81 cm s^{-1}) which are weaker and more diffusive (Gérigny, 2010; Gérigny et al., 2011). Most sparids having pelagic eggs and most labrids benthic eggs, the 3D circulation pattern of this area, in combination to differences in PLD, would explain the lower transport success of sparids compared to labrids. Although there is a general lack of information on the swimming abilities of Sparids and Labrids occurring in the Mediterranean Sea, regarding the swimming abilities of other temperate Sparid and Labrid species, their critical swimming speeds range from a few cm up to 20 cm s^{-1} depending on species and larval size (Trnski, 2002; Clark et al., 2005; Pattrick and Strydom, 2009). This reveals their potential of influencing their dispersal in low surface current conditions and average bottom current conditions in the SB.

In sum, our model results seem to indicate that species with benthic eggs and short PLD emitted inside the SB will have greater chances to settle inside this area with low spread rates, whereas species with pelagic eggs and long PLD will be dispersed over larger distances throughout the SB and exported outside this area (Leis and Miller, 1976; Blaxter, 1986; Suthers and Frank, 1991; Siegel et al., 2003; Macpherson and Raventos, 2006; Snelgrove et al.,
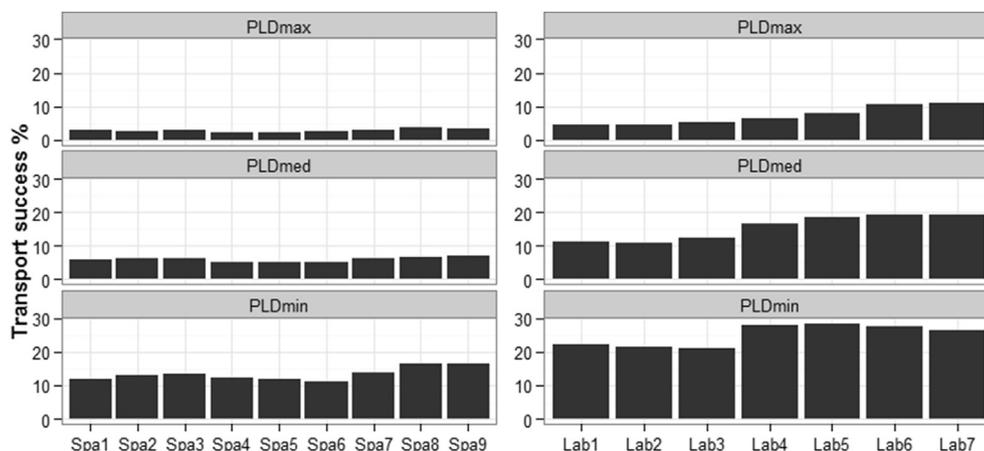
Fig. 5. Contribution of each release polygon of Labridae (Lab 1-7) and Sparidae (Spa 1-9) to the larval transport success per PLD for August 2012.
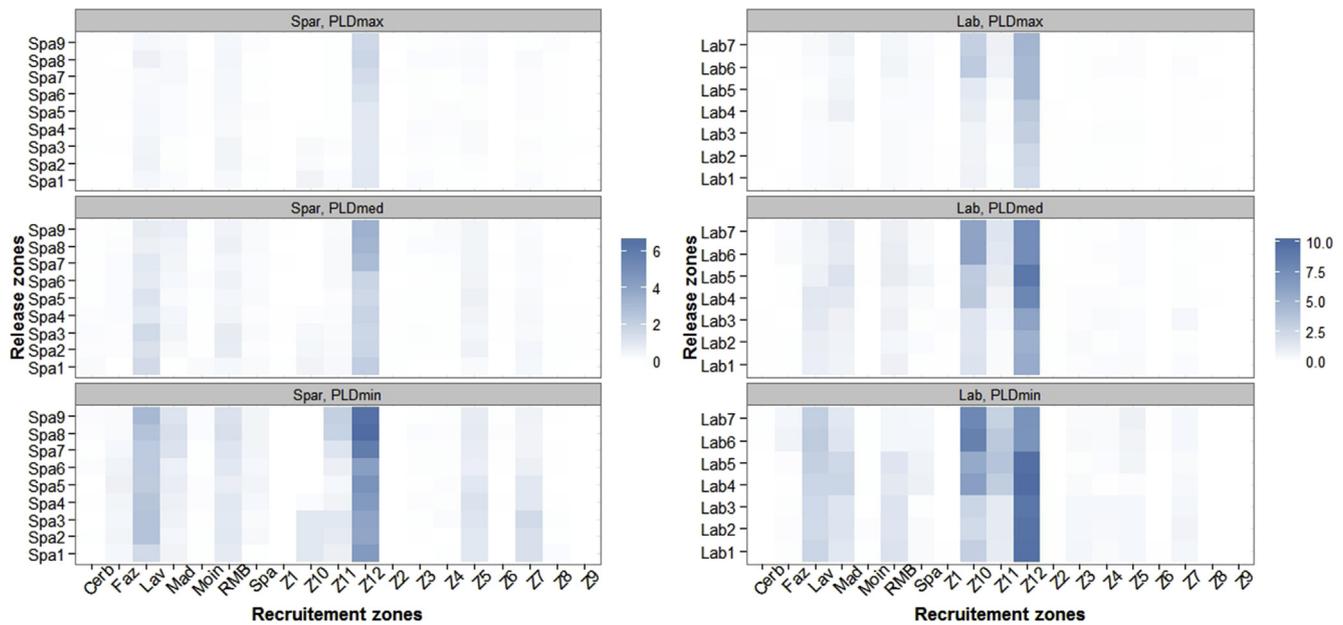
Fig. 6. Connectivity matrices of Labridae (Lab) and Sparidae (Spar) transport success (%) per PLD for August 2012.

2008). However, species might present local adaptations to a specific region such as a reduced PLD (Bay et al., 2006), which makes it difficult to assign specific species to a particular scenario of the biophysical model tested. Given the geographical isolation of the Corsican and Sardinian Islands, it could however be likely that Sparid and Labrid subpopulations of these islands are well differentiated from those in less dispersive and isolated regions of the Mediterranean Sea and might present local adaptations such as shorter PLDs. If this is the case, dispersal patterns in the SB would correspond better to scenarios with short PLDs (PLDmin = 17 days) than with long PLDs (PLDmax = 35 days).

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

In the SB, larval transport success is not only dependent on early life history traits such as the PLD, release depth and egg type, but also highly fluctuates in time and space. The strong monthly variations of transport success highlight the essential contribution of the synchronization between hydrographic conditions and reproductive timing. According to Dixon et al. (1999), the episodic fluctuations in larval supply and the lack of relationship between spawning output and transport success often observed in coastal species can mainly be explained by the non-linear physical processes operating during larval life stage. The circulation system of the Mediterranean Sea varies at different spatio-temporal scales (Millot, 1999; Pinardi and Masetti, 2000; Fernandez et al., 2005): at an annual, seasonal and small daily scale. Earlier hydrographic investigations conducted in the SB have in fact shown that this area follows the average hydrographic conditions present in the Mediterranean Sea (Gérigny, 2010), i.e. strong currents in winter induced by winds and lower flow intensities in summer conditions (Millot, 1999; Astraldi et al., 2002). Furthermore as shown in other Mediterranean areas, as for instance in the Tyrrhenian basin (Iacono et al., 2013), summer hydrographic conditions in the SB are characterized by frequent eddy structures (Gérigny, 2010).

The presence of stronger currents in the SB during winter than summer conditions could suggest lower transport success during early spring than summer. Furthermore, the increase of eddies

structures in summer should favor transport success as these structures are known to be centers of food retention (Logerwell and Smith, 2001). Despite this, in the SB the stronger currents in spring seem to favor larval transport all through the SB, from the Corsican East coast (Z7 to Z9 and 'Cerb' MPA) and the Maddalena Archipelago ('RMB', 'Spa', 'Mad' MPAs) to the Corsican West coast (Z1 to Z4; Fig. 7A). This could explain the higher transport success in April than in the summer months. In summer the main current drifting from North to South along the Eastern Corsican coast getting weaker, connectivity between the East and West coast of the SB was reduced compared to spring (Fig. 7). As shown before in Gérigny (2010), the hypothesis behind that would be that the stronger the currents are, the more directional they are, whereas lower currents tend to be more diffusive which would increase the random dispersion of larvae outside the bounds of the SB system and explain the lower larval transport success observed in summer and the higher transport success in spring. This reduced transport success could also be linked to the formation of eddy structures in summer which would disperse larvae away from favorable settlement habitats to oceanic areas. Previous studies have also suggested that eddies can act as dispersion mechanisms (Rodriguez et al., 2004). An important eddy structure in the western outer part of the SB present in summer (Gérigny and Coudray, 2013) would particularly explain the low transport success in the western part of the SB in this time of the year. Furthermore, compared to other potential settlement zones inside the SB, our model highlights a relative high transport success around the MPAs of the Lavezzi Islands and the complex of the Maddalena Archipelago and Z12 (the closest Sardinian coast located to this archipelago; Fig. 7). The local bathymetry and the presence of numerous islands and islets in these parts of the SB could increase the phenomenon of larval retention and explain their relative high transport success particularly marked in early spring and late summer (Fig. 7A & C) compared to June (Fig. 7B). These principal larval flow patterns shown in Fig. 7 are consistent with those based on the high density areas of Labridae and Sparidae issued from our distribution model. In August, sparids and labrids larvae across the SB, including those located in the western part of the SB, settle mainly around the Lavezzi Island and the complex of the Maddalena Archipelago and
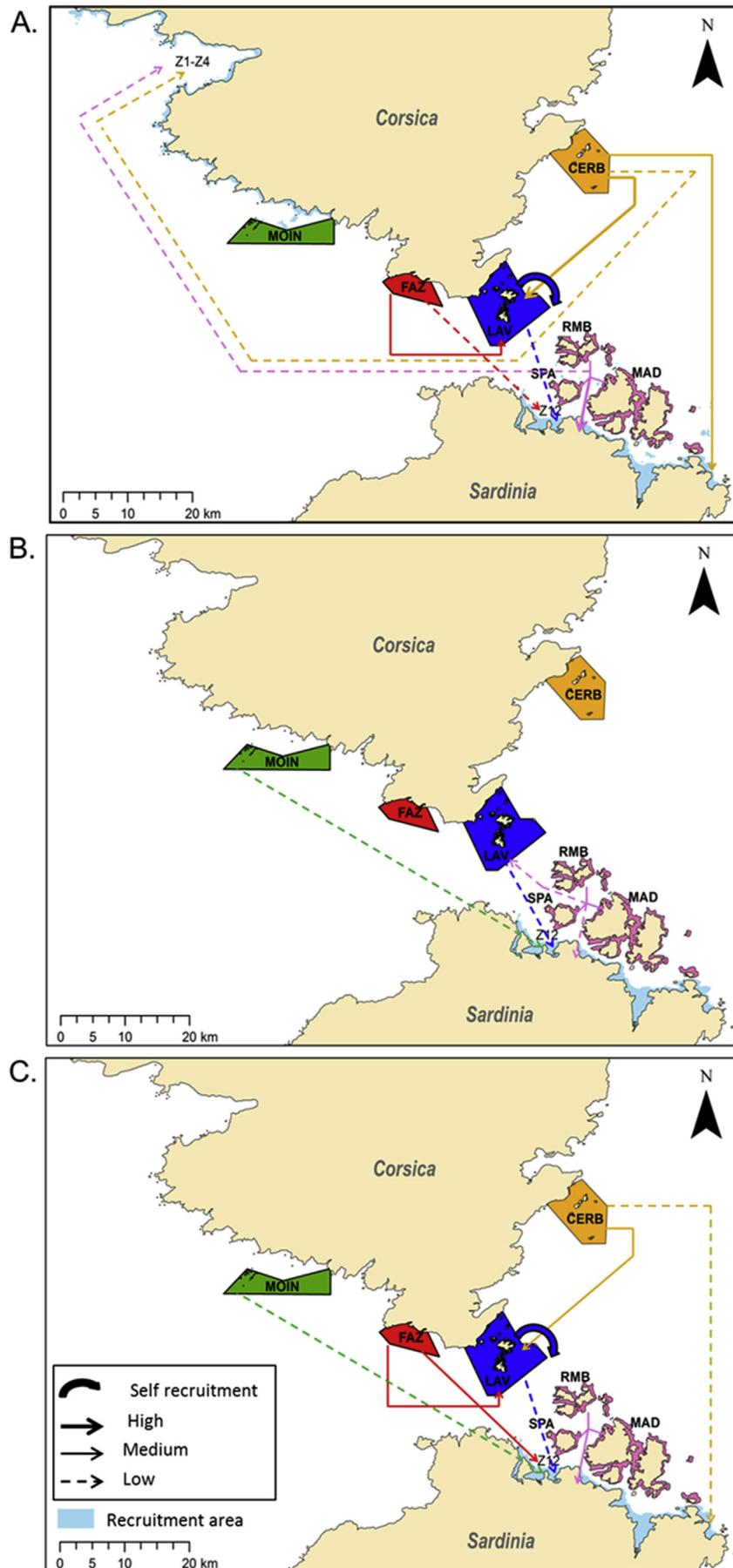
Fig. 7. Schematic map of main larval flows (of recruiting larvae) between release (MPAs) and settlement areas for April (A), June (B) and August 2012 (C).

Z12 (Fig. 8). The MPAs of the French Lavezzi Islands (Lav) and the Italian Maddalena Archipelago (RMB, SPA and Mad) appear as two key areas concerning both, larval supply and as settlement area. These results are generally consistent with the management conducted until now in the SB. The Italian east coast of the SB close to the Maddalena Archipelago (Z12) should however be further considered in future management plans of the international marine park of the SB. Labrid larvae identified in the eastern part of the SB further off shore or on the western Italian coast, settled however also along the western Italian coast of the SB (Z10 see Fig. 8). Further investigations including the entire Corsican and Sardinian Islands would thus be required to assess the larval supply of the SB to other coasts of these two Islands.

The strong spatio-temporal variability of transport success of fish larvae observed in the SB can furthermore have important ecological implications on their population dynamics. Temperate-water species have generally restricted spawning seasons (Pavlov et al., 2009) and can consequently be more affected by recruitment variability according to the match-mismatch theory (Cushing, 1990; Wright and Trippel, 2009). Given our results, we can hypothesize that late spring or early summer spawning species, such as *Dentex dentex* or *Oblada melanura*, will be particularly sensitive to the dispersal process in the SB and require thus particular attention in the management of these areas. The spawning season of *D. dentex* occurs mainly between April and June (Marengo et al., 2014). For instance, under the hydrodynamic configuration observed in 2012 in the SB, if one year the main spawning peak of *D. dentex* shifted towards spring (and for early spawners in general), then reproductive timing and hydrodynamic conditions would match, as a greater part of produced larvae will reach a suitable
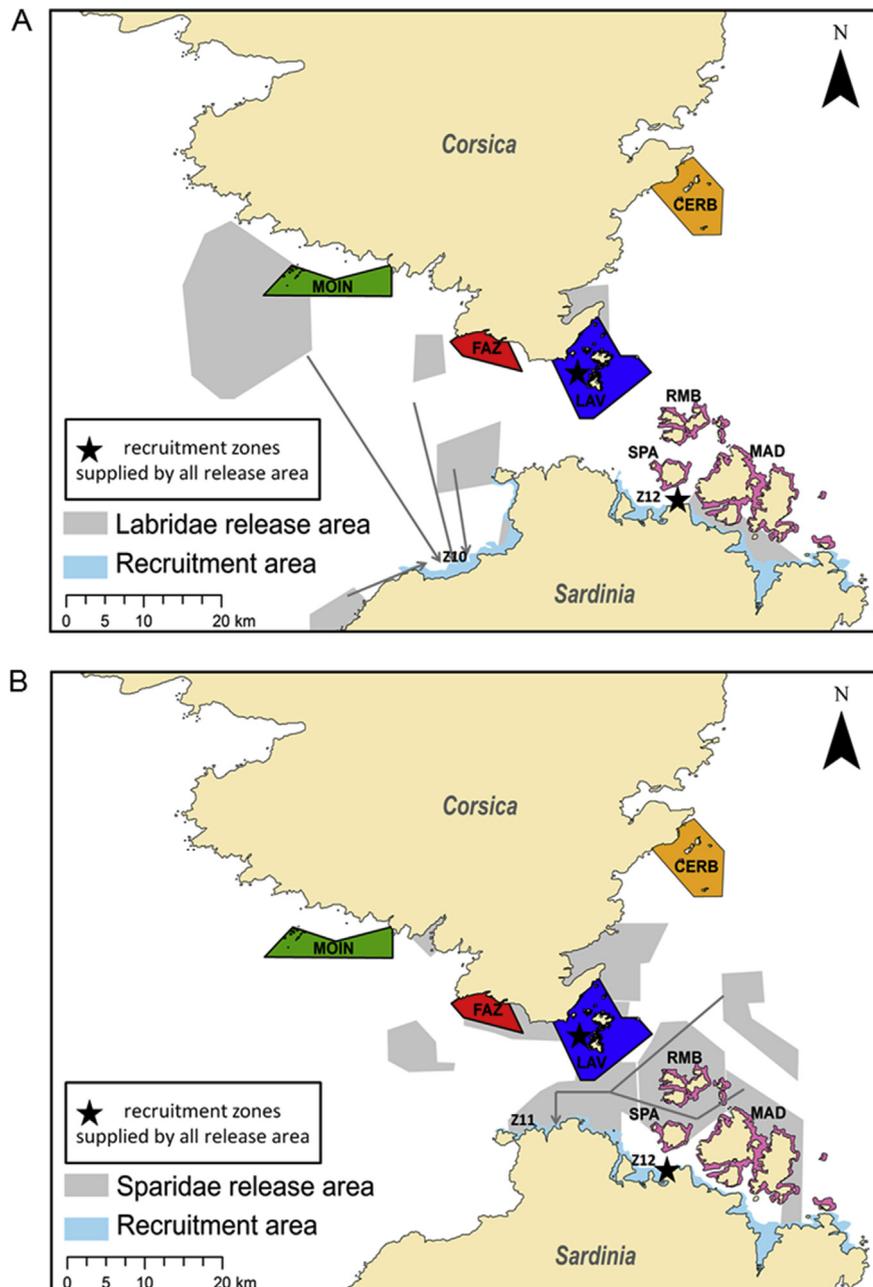
Fig. 8. Schematic map of main larval flows between release areas (based on field data, i.e. high larval density areas) and settlement areas for Labridae (A) and Sparidae (B) during August 2012.

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

4.4. Model limitations

There are several shortcomings in the performed dispersal model which could be improved in future studies. They concern mainly the fact that we considered larvae to be passive particles due to a lack of biological information. The behavior of fish larvae has in fact not been included; however several articles have shown the active orientation and swimming abilities of fish larvae, particularly after reaching stage 4 of larval development (Leis and Lockett, 2005; Leis, 2006; Staaterman et al., 2012). The mortality or sublethal effects due to starvation of fish larvae has also not been included, which can act as an important limiting factor in the larval supply (Faria et al., 2011). Another limitation to our model is that we did not evaluate the efficient recruitment of fish larvae as many biotic factors are involved in post-recruitment processes and mortality, linked to habitat/resource availability or density dependent effects (Tupper and Boutilier, 1997; Planes et al., 1998; Dixson, 2012). Instead of quantifying the effective recruitment of fish populations, the aim of this work was in fact rather to quantify the potential larval supply in order to identify the contribution of existing MPAs and to characterize the general dispersal patterns in the SB. Further research on early life stages and juveniles will thus be necessary in the future in order to implement more accurate and realistic dispersal models. Among the different tools nowadays implemented, e.g. otolith microchemistry and population genetics in general, transgenerational isotopic tagging and genetic parentage analysis seem to be the most suitable tools to assess connectivity (Thorrold et al., 2006; Leis et al., 2011) and should in future be coupled to biophysical modeling of larvae (Gilg and Hilbish, 2003).

5. Conclusions and management implications

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

References

Agardy, M.T., 1994. Advances in marine conservation – the role of marine protected areas. Trends Ecol. Evol. 9, 267–270.

Akaike, H., 1981. A new look at the statistical model identification. Curr. Contents/Eng. Technol. Appl. Sci. 22.

Almany, G.R., Berumen, M.L., Thorrold, S.R., Planes, S., Jones, G.P., 2007. Local replenishment of coral reef fish populations in a marine reserve. Science 316, 742–744.

André, G., Garreau, P., Garnier, V., Fraunie, P., 2005. Modelled variability of the sea surface circulation in the North-western Mediterranean Sea and in the Gulf of Lions. Ocean. Dyn. 55, 294–308.

Astraldi, M., Balopoulos, S., Candela, J., Font, J., Gacic, M., Gasparini, G.P., Manca, B., Theocharis, A., Tintore, J., 1999. The role of straits and channels in understanding the characteristics of Mediterranean circulation. Prog. Oceanogr. 44, 65–108.

Astraldi, M., Gasparini, G.P., Vetrano, A., Vignudelli, S., 2002. Hydrographic characteristics and interannual variability of water masses in the central Mediterranean: a sensitivity test for long-term changes in the Mediterranean Sea. Deep-Sea Res. I – Oceanogr. Res. Pap. 49, 661–680.

Basterretxea, G., Catalan, I.A., Jordi, A., Alvarez, I., Palmer, M., Sabates, A., 2013. Dynamic regulation of larval fish self-recruitment in a marine protected area. Fish. Oceanogr. 22, 477–495.

Bay, L.K., Buechler, K., Gagliano, M., Caley, M.J., 2006. Intraspecific variation in the pelagic larval duration of tropical reef fishes. J. Fish Biol. 68, 1206–1214.

Bell, J.D., Harmelin-Vivien, M.L., 1982. Fish fauna of French Mediterranean Posidonia oceanica seagrass meadows. Tethys 10, 337–347.

Bianchi, C.N., Morri, C., 2000. Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. Mar. Pollut. Bull. 40, 367–376.

Blaxter, J.H.S., 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115, 98–114.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, second ed. Springer Verlag, New York.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35.

Clark, D.L., Leis, J.M., Hay, A.C., Trnski, T., 2005. Swimming ontogeny of larvae of four temperate marine fishes. Mar. Ecol. Prog. Ser. 292, 287–300.

Codling, E.A., Hill, N.A., Pitchford, J.W., Simpson, S.D., 2004. Random walk models for the movement and recruitment of reef fish larvae. Mar. Ecol. Prog. Ser. 279, 215–224.

Cognetti, G., Curinigalletti, M., 1993. Biodiversity conservation problems in the marine environment. Mar. Pollut. Bull. 26, 179–183.

Coll, M., Piroddi, C., Albouy, C., Lasram, F.B., Cheung, W.W.L., Christensen, V., Karpouzi, V.S., Guilhaumon, F., Mouillot, D., Paleczny, M., Palomares, M.L., Steenbeek, J., Trujillo, P., Watson, R., Pauly, D., 2012. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. Glob. Ecol. Biogeogr. 21, 465–480.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K.,

Kitsos, M.S., Koukouras, A., Lampadariou, N., Laxamana, E., de la Cuadra, C., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., San Vicente, C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. Plos One 5.

Cowen, R.K., Paris, C.B., Srinivasan, A., 2006. Scaling of connectivity in marine populations. Science 311, 522–527.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Annu. Rev. Mar. Sci. 1, 443–466.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations – an update of the match mismatch hypothesis. Adv. Mar. Biol. 26, 249–293.

De Falco, G., De Muro, S., Batzella, T., Cucco, A., 2011. Carbonate sedimentation and hydrodynamic pattern on a modern temperate shelf: the strait of Bonifacio (western Mediterranean). Estuar. Coast. Shelf Sci. 93, 14–26.

Dixon, P.A., Milicich, M.J., Sugihara, G., 1999. Episodic fluctuations in larval supply. Science 283, 1528–1530.

Dixson, D.L., 2012. Predation risk assessment by larval reef fishes during settlement-site selection. Coral Reefs 31, 255–261.

Doherty, P., Fowler, T., 1994. An empirical-test of recruitment limitation in a coral-reef fish. Science 263, 935–939.

Faria, A.M., Chicharo, M.A., Goncalves, E.J., 2011. Effects of starvation on swimming performance and body condition of pre-settlement *Sparus aurata* larvae. Aquat. Biol. 12, 281–289.

Faure, V., Gatti, J., Bensoussan, N., 2012. Analyse de la campagne MELBA et évaluation du modèle Mars3D-Corse400m. IPSO-FACTO-IFREMER.

Fernandez, V., Dietrich, D.E., Haney, R.L., Tintore, J., 2005. Mesoscale, seasonal and interannual variability in the Mediterranean Sea using a numerical ocean model. Prog. Oceanogr. 66, 321–340.

Gabrié, C., Lagabrielle, E., Bissery, C., Crochelet, E., Meola, B., Webster, C., Claudet, J., Chassanite, A., Marinesque, S., Robert, P., Goutx, M., Quod, C., 2012. Statut des Aires Marines Protégées en mer Méditerranée. In: Collection, M. MedPAN & CAR/ASP, p. 260.

Garcia-Rubies, A., Macpherson, E., 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Mar. Biol. 124, 35–42.

Gérigny, O., 2010. Hydrologie et hydrodynamisme dans les bouches de Bonifacio: mesure in-situ, modélisation, influence sur la biomasse. University of Corte – Pascal Paoli, p. 241.

Gérigny, O., Coudray, S., 2013. Campagne océanographique STELLAMARE1-août 2012. Analyse des données de courantologie. Première approche pour une compréhension de l'hydrodynamisme méso-échelle dans les Bouches de Bonifacio. RST.ODE/LERPAC.

Gérigny, O., Di Martino, B., Romano, J.C., 2011. The current dynamics inside the Strait of Bonifacio: impact of the wind effect in a little coastal strait. Cont. Shelf Res. 31, 1–8.

Gilg, M.R., Hilbish, T.J., 2003. The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. Ecology 84, 2989–2998.

Grioche, A., Harlay, X., Koubbi, P., Lago, L.F., 2000. Vertical migrations of fish larvae: Eulerian and Lagrangian observations in the Eastern English Channel. J. Plankton Res. 22, 1813–1828.

Guidetti, P., 2000. Differences among fish assemblages associated with nearshore Posidonia oceanica seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuar. Coast. Shelf Sci. 50, 515–529.

Guidetti, P., Fanelli, G., Fraschetti, S., Terlizzi, A., Boero, F., 2002. Coastal fish indicate human-induced changes in the Mediterranean littoral. Mar. Environ. Res. 53, 77–94.

Halekoh, U., Højsgaard, S., 2014. A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package pbkrtest. J. Stat. Softw. 59.

Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl. 13, S117–S137.

Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. Ecol. Lett. 5, 361–366.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.

Harmelin-Vivien, M.L., Harmelin, J.G., Leboulleux, V., 1995. Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. Hydrobiologia 300, 309–320.

Hastings, A., Botsford, L.W., 2006. Persistence of spatial populations depends on returning home. Proc. Natl. Acad. Sci. U. S. A. 103, 6067–6072.

Heath, M.R., 1992. Field investigations of the early-life stages of Marine fish. Adv. Mar. Biol. 28, 1–174.

Hjort, J., 2014. Fluctuations in the Great Fisheries of Northern Europe, Viewed in the Light of Biological Research. A. F. Høst & Fils.

Iacono, R., Napolitano, E., Marullo, S., Artale, V., Vetrano, A., 2013. Seasonal variability of the Tyrrhenian Sea surface geostrophic circulation as assessed by altimeter data. J. Phys. Oceanogr. 43, 1710–1732.

Irisson, J.O., LeVan, A., De Lara, M., Planes, S., 2004. Strategies and trajectories of coral reef fish larvae optimizing self-recruitment. J. Theor. Biol. 227, 205–218.

James, M.K., Armsworth, P.R., Mason, L.B., Bode, L., 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. Proc. R. Soc. B Biol. Sci. 269, 2079–2086.

Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C., 1999. Self-recruitment in a coral reef fish population. Nature 402, 802–804.

Kalogirou, S., Corsini-Foka, M., Sioulas, A., Wennhage, H., Pihl, L., 2010. Diversity, structure and function of fish assemblages associated with Posidonia oceanica

beds in an area of the eastern Mediterranean Sea and the role of non-indigenous species. J. Fish Biol. 77, 2338–2357.

Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84, 2007–2020.

La Mesa, G., Molinari, A., Gambaccini, S., Tunesi, L., 2011. Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Mar. Ecol. – Evol. Perspect. 32, 104–114.

Lazure, P., Dumas, F., 2008. An external-internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). Adv. Water Resour. 31, 233–250.

Leis, J.M., 2002. Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. Environ. Biol. Fishes 65, 199–208.

Leis, J.M., 2006. Are larvae of demersal fishes plankton or nekton? In: Alan, J.S., David, W.S. (Eds.), Advances in Marine Biology. Academic Press, pp. 57–141.

Leis, J.M., Lockett, M.M., 2005. Localization of reef sounds by settlement-stage larvae of coral-reef fishes (Pomacentridae). Bull. Mar. Sci. 76, 715–724.

Leis, J.M., Miller, J.M., 1976. Offshore distributional patterns of Hawaiian fish larvae. Mar. Biol. 36, 359–367.

Leis, J.M., Van Herwerden, L., Patterson, H.M., 2011. Estimating connectivity in marine fish populations: what works best?. In: Gibson, R.N., Atkinson, R.J.A., Gordon, J.D.M. (Eds.), Oceanography and Marine Biology: an Annual Review, vol. 49, pp. 193–234.

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., Blanke, B., 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environ. Model. Softw. 23, 1210–1214.

Logerwell, E.A., Smith, P.E., 2001. Mesoscale eddies and survival of late stage Pacific sardine (Sardinops sagax) larvae. Fish. Oceanogr. 10, 13–25.

Macpherson, E., Raventos, N., 2005. Settlement patterns and post-settlement survival in two Mediterranean littoral fishes: influences of early-life traits and environmental variables. Mar. Biol. 148, 167–177.

Macpherson, E., Raventos, N., 2006. Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. Mar. Ecol. Prog. Ser. 327, 257–265.

Marengo, M., Durieux, E.H., Marchand, B., Francour, P., 2014. A review of biology, fisheries and population structure of Dentex dentex (Sparidae). Rev. Fish. Biol. Fish. 24, 1065–1088.

McCleave, J.D., Kleckner, R.C., Castonguay, M., 1987. Reproductive sympatry of American and European eels and implications for migration and taxonomy. Am. Fish. Soc. Sym. 1, 286–297.

Millot, C., 1999. Circulation in the Western Mediterranean Sea. J. Mar. Syst. 20, 423–442.

Moranta, J., Palmer, M., Morey, G., Ruiz, A., Morales-Nin, B., 2006. Multi-scale spatial variability in fish assemblages associated with Posidonia oceanica meadows in the Western Mediterranean Sea. Estuar. Coast. Shelf Sci. 68, 579–592.

Mouillot, D., Albouy, C., Guilhaumon, F., Lasram, F.B.R., Coll, M., Devictor, V., Meynard, C.N., Pauly, D., Tomasini, J.A., Troussellier, M., Velez, L., Watson, R., Douzery, E.J.P., Mouquet, N., 2011. Protected and threatened components of fish biodiversity in the Mediterranean Sea. Curr. Biol. 21, 1044–1050.

Mouillot, D., Culioli, J.M., 2002. The sample size necessary to assess changes in fish biomass – a reply. Mar. Ecol.-Pubbl. Della Stn. Zool. Di Napoli I 23, 11–18.

Olivar, M.P., Sabates, A., 1997. Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. Mar. Biol. 129, 289–300.

Olsen, E.M., Johnson, D., Weaver, P., Goñi, R., Ribeiro, M.C., Rabaut, M., Macpherson, E., Pelletier, D., Fonseca, L., Katsanevakis, S., Zaharia, T., 2013. Achieving ecologically coherent MPA networks in Europe: science needs and priorities. In: Larkin, K.E., McDonough, N. (Eds.), Marine Board Position Paper. European Marine Board, Ostend, Belgium.

Pasqualini, V., Pergent-Martini, C., Clabaut, P., Pergent, G., 1998. Mapping of Posidonia oceanica using aerial photographs and side scan sonar: application off the Island of Corsica (France). Estuar. Coast. Shelf Sci. 47, 359–367.

Pattrick, P., Strydom, N.A., 2009. Swimming abilities of wild-caught, late-stage larvae of Diplodus capensis and Sarpa salpa (Pisces: Sparidae) from temperate South Africa. Estuar. Coast. Shelf Sci. 85, 547–554.

Pavlov, D.A., Emel'yanova, N.G., Novikov, G.G., 2009. Reproductive dynamics. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A., Moksness, E. (Eds.), Fish Reproductive Biology. Wiley-Blackwell Scientific Publications, Chichester, UK, pp. 48–90.

Pinardi, N., Masetti, E., 2000. Variability of the large scale general circulation of the Mediterranean Sea from observations and modelling: a review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 158, 153–174.

Pineda, J., Hare, J.A., Sponaugle, S., 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20, 22–39.

Pineda, J., Reyns, N., Starczak, V., 2009. Complexity and simplification in understanding recruitment in benthic populations. Popul. Ecol. 51, 17–32.

Planes, S., Jouvenel, J.Y., Lenfant, P., 1998. Density dependence in post-recruitment processes of juvenile sparids in the littoral of the Mediterranean Sea. Oikos 83, 293–300.

Plus, M., Dumas, F., Stanisiere, J.Y., Maurer, D., 2009. Hydrodynamic characterization of the Arcachon Bay, using model-derived descriptors. Cont. Shelf Res. 29, 1008–1013.

PMIBB, 2012. Création du Groupement Européen de Coopération Territoriale GECT et du Parc Marin International des Bouches de Bonifacio PMIBB. Press release, Bonifacio, France.

Possingham, H.P., Roughgarden, J., 1990. Spatial population dynamics of a marine organism with a complex life-cycle. Ecology 71, 973–985.

Purcell, J.F.H., Cowen, R.K., Hughes, C.R., Williams, D.A., 2009. Population structure in a common Caribbean coral-reef fish: implications for larval dispersal and early life-history traits. J. Fish Biol. 74, 403–417.

R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Raventos, N., Macpherson, E., 2005a. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus Symphodus. Mar. Ecol. Prog. Ser. 285, 205–211.

Raventos, N., Macpherson, E., 2005b. Environmental influences on temporal patterns of settlement in two littoral labrid fishes in the Mediterranean Sea. Estuar. Coast. Shelf Sci. 63, 479–487.

Rodriguez, J.M., Barton, E.D., Hernandez-Leon, S., Aristegui, J., 2004. The influence of mesoscale physical processes on the larval fish community in the Canaries CTZ, in summer. Prog. Oceanogr. 62, 171–188.

Rubio, A., Taillandier, V., Garreau, P., 2009. Reconstruction of the Mediterranean northern current variability and associated cross-shelf transport in the Gulf of Lions from satellite-tracked drifters and model outputs. J. Mar. Syst. 78, S63–S78.

Saenz-Agudelo, P., Jones, G.P., Thorrold, S.R., Planes, S., 2011. Connectivity dominates larval replenishment in a coastal reef fish metapopulation. Proc. R. Soc. B Biol. Sci. 278, 2954–2961.

Scheltema, R.S., 1986. On dispersal and planktonic larvae of benthic invertebrates - an eclectic overview and summary of problems. Bull. Mar. Sci. 39, 290–322.

Shanks, A.L., 2009. Pelagic larval duration and dispersal distance revisited. Biol. Bull. 216, 373–385.

Siegel, D.A., Kinlan, B.P., Gaylord, B., Gaines, S.D., 2003. Lagrangian descriptions of marine larval dispersion. Mar. Ecol. Prog. Ser. 260, 83–96.

Simons, R.D., Siegel, D.A., Brown, K.S., 2013. Model sensitivity and robustness in the estimation of larval transport: a study of particle tracking parameters. J. Mar. Syst. 119, 19–29.

Snelgrove, P.V.R., Bradbury, I.R., de Young, B., Fraser, S., 2008. Temporal variation in fish egg and larval production by pelagic and bottom spawners in a large Newfoundland coastal embayment. Can. J. Fish. Aquat. Sci. 65, 159–175.

Sobel, J., Dahlgren, C., 2004. Marine Reserves: a Guide to Science, Design, and Use. Island Press, Washington DC, p. 220.

Sorgente, B., Sorgente, R., Olita, A., Fazioli, L., Cucco, A., Perilli, A., Sinerchia, M., Ribotti, A., 2012. Effects of protection rules and measures in an important international strait area: the Bonifacio Strait. J. Oper. Oceanogr. 5, 35–44.

Staaterman, E., Paris, C.B., Helgers, J., 2012. Orientation behavior in fish larvae: a missing piece to Hjort's critical period hypothesis. J. Theor. Biol. 304, 188–196.

Suthers, I.M., Frank, K.T., 1991. Comparative persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova-Scotia, Canada. Mar. Biol. 108, 175–184.

Thorrold, S.R., Jones, G.P., Planes, S., Hare, J.A., 2006. Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Can. J. Fish. Aquat. Sci. 63, 1193–1197.

Treml, E.A., Roberts, J.J., Chao, Y., Halpin, P.N., Possingham, H.P., Riginos, C., 2012. Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. Integr. Comp. Biol. 52, 525–537.

Trnski, T., 2002. Behaviour of settlement-stage larvae of fishes with an estuarine juvenile phase: in situ observations in a warm-temperate estuary. Mar. Ecol. Prog. Ser. 242, 205–214.

Tsikliras, A.C., Antonopoulou, E., Stergiou, K.I., 2010. Spawning period of Mediterranean marine fishes. Rev. Fish. Biol. Fish. 20, 499–538.

Tudela, S., 2004. Ecosystem effects of fishing in the Mediterranean: an analysis of the major threats of fishing gear and practices to biodiversity and marine habitats. In: Mediterranean, G.F.C.f.t. (Ed.), Studies and Reviews. FAO, Rome, p. 44.

Tupper, M., Boutilier, R.G., 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Mar. Ecol. Prog. Ser. 151, 225–236.

Werner, F.E., Perry, R.I., Lough, R.G., Naimie, C.E., 1996. Trophodynamic and advective influences on Georges Bank larval cod and haddock. Deep-Sea Res. II — Topical Stud. Oceanogr. 43, 1793–1822.

Wolanski, E., Doherty, P., Carleton, J., 1997. Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. Naturwissenschaften 84, 262–268.

Wright, P.J., Trippel, E.A., 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish Fish. 10, 283–304.

Ylieff, M.C., 2000. Les stratégies de reproduction chez les poissons labridés méditerranéens. Cah. d'Ethologie 20, 113–138.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. In: Gail, M., Krickeberg, K., Samet, J.M., Tsiatis, A., Wong, W. (Eds.), Statistics for Biology and Health. Springer, New York.