
Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems

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Abstract :

Aim

Assessing the spatial structure and dynamics of marine populations is still a major challenge in ecology. The need to manage marine resources from ecosystem and large-scale perspectives is recognized, but our partial understanding of oceanic connectivity limits the implementation of globally pertinent conservation planning. Based on a biophysical model for the entire Mediterranean Sea, this study takes an ecosystem approach to connectivity and provides a systematic characterization of broad-scale larval dispersal patterns. It builds on our knowledge of population dynamics and discusses the ecological and management implications.

Location

The semi-enclosed Mediterranean Sea and its marine ecosystems are used as a case study to investigate broad-scale connectivity patterns and to relate them to oceanography and population dynamics.

Methods

A flow network is constructed by evenly subdividing the basin into sub-regions which are interconnected through the transport of larvae by ocean currents. It allows for the computation of various connectivity metrics required to evaluate larval retention and exchange.

Results

Our basin-scale model predicts that retention processes are weak in the open ocean while they are significant in the coastal ocean and are favoured along certain coastlines due to specific oceanographic features. Moreover, we show that wind-driven divergent (convergent, respectively) oceanic regions are systematically characterized by larval sources (sinks, respectively). Finally, although these connectivity metrics have often been studied separately in the literature, we demonstrate they are interrelated under particular conditions. Their integrated analysis facilitates the appraisal of population dynamics, informing both genetic and demographic connectivities.

Main conclusions

This modelling framework helps ecologists and geneticists to formulate improved hypotheses of population structures and gene flow patterns and to design their sampling strategy accordingly. It is also useful in the implementation and assessment of future protection strategies, such as coastal and offshore marine reserves, by accounting for large-scale dispersal patterns, a missing component of current ecosystem management.

Keywords : Larval dispersal, local retention, marine connectivity, marine ecosystems, marine protected areas, Mediterranean Sea, population dynamics, population genetics, self-recruitment, source/sink dynamics

1 Introduction

Efficient management strategies should be proposed and applied to maintain the values and services of marine ecosystems that are impacted at both regional and global scales by increasing anthropogenic stressors. Such strategies require a global view encompassing the large dimensions of oceanic systems and a good knowledge of complex ecosystem dynamics (instead of mono-specific focus). A good understanding of large-scale biogeography and spatial dynamics of marine populations is thus a prerequisite to scale-up regional management planning and to optimize the conservation of marine ecosystems heterogeneously distributed across large scales.

Marine populations are commonly structured as a “metapopulation” in which discrete “subpopulations” are linked to each other via the exchange of individuals (adults, juveniles, larvae, eggs...) [Cowen & Sponaugle 2009; Calò *et al.* 2013]. This *population connectivity* (i.e. the exchanges of individuals among subpopulations) can be evaluated with the study of *genetic connectivity*, defined as the degree to which gene flows affect evolutionary processes within subpopulations. Another closely related concept, often used in conservation plans, is *demographic connectivity*. It accounts for the impact of dispersal processes on growth and mortality rates of a subpopulation [Lowe & Allendorf 2010]. A good understanding of population connectivity, together with genetic and demographic connectivities, is fundamental for predicting the replenishment of a site after disturbance (population persistence), for the maintenance of biodiversity and overall for the management of marine ecosystems [Palumbi 2003; Cowen *et al.* 2006; Hastings & Botsford 2006; Cowen & Sponaugle 2009].

Since movements of adults are quite limited for a great majority of marine species [Cowen & Sponaugle 2009], the exchanges among subpopulations occur primarily through the pelagic dispersion of early life stages (eggs, larvae) transported by ocean currents over large distances [Kinlan & Gaines 2003; Shanks *et al.* 2003; Gaines *et al.* 2007; Siegel *et al.* 2008; Moffitt *et al.* 2009]. Even for species whose adults are highly mobile (e.g. large pelagic), oceanic circulation can play a crucial role in controlling the success of spawning, dispersal and settlement [Reglero *et al.* 2012], with implications for the structure and conservation of these populations [Rodriguez *et al.* 2013]. Indeed, both the magnitude and modality of larval dispersal by ocean currents are theoretically expected to affect both genetic and demographic connectivities. Consequently, studying the transport of larvae with biophysical models and discussing its managerial and genetic implications have received growing interest to delimit hydrodynamical provinces [Rossi *et al.* 2014], to characterize connectivity in various marine environments [e.g. Mitarai *et al.* 2009; Guizien *et al.* 2012; Tremblay *et al.* 2012; Young *et al.* 2012; Wood *et al.* 2014] or to investigate their effect on genetic connectivity [Kool *et al.* 2011; Foster *et al.* 2012].

Depending on the rate of migration, previous studies simplified the contrasting connectivity occurring in the real ocean by distinguishing *open* subpopulations that receive/export individuals from/to other subpopulations, while *closed* subpopulations do not exchange individuals to an appreciable extent [e.g. Hixon *et al.* 2002; Pinsky *et al.* 2012]. This implies that open subpopulations are primarily maintained through network persistence (i.e the exchange of individuals with neighbouring subpopulations) while closed subpopulations mainly survive through self-persistence (i.e local birth rate higher than death rate). Another distinction among geographically separated subpopulations that are not completely isolated from each other was introduced by Pulliam [1988] with the concept of *Source/Sink* dynamics. Habitat heterogeneity and variable dispersal ability lead to different demographic and exchange rates in each subpopulation, having key implications for conservation goals [Roberts 1997; Crowder *et al.* 2000]. Estimating the extent to which subpopulations are open/closed or sources/sinks has led to the definition of various local connectivity metrics that are related to larval transport. Particular attention was given to Self-Recruitment (*SR*), which measures the proportion of all local larval recruits that originated from the source population [e.g. Jones *et al.* 1999; Planes *et al.* 2009; Saenz-Agudelo *et al.* 2011]. Other studies estimated the Local Retention (*LR*) defined as the proportion of local larval production retained on a site [Carson *et al.* 2011; Hogan *et al.* 2012]. Because *SR* is a function of the number of larvae arriving from elsewhere and *LR* depends on the number of those leaving, these two metrics do not inform on population connectivity similarly [Burgess *et al.* 2014]. Concerning proxies of exchange in the marine realm, Cowen &

47 Sponaugle [2009] defined a source population as a subpopulation in which the net export of individuals is
48 greater than the net import; the reverse is a sink. Since larvae are the most dispersive stage of many marine
49 species, Roberts [1997] proposed to simplify the source/sink character by focusing on the directional movement
50 of larvae in ocean currents. Although this simplification might not hold for all marine species, it was later
51 supported by Bode et al. [2006] who identified source/sink subpopulations primarily driven by larval dispersal
52 and only marginally by local demography.

53 Despite the crucial information brought by these open/closed and source/sink proxies applied to larval
54 transport, they have not been investigated at large-scale. Furthermore, although they are often employed to
55 describe local subpopulations or to make management recommendations, the link with oceanographic processes
56 and their inter-relationships remain unclear.

57 In this study we propose a modelling framework to systematically characterize larval dispersal and connec-
58 tivity at large-scale, providing the necessary information to evaluate their effects on marine populations. Based
59 on a flow network built in the Mediterranean basin, we compute different connectivity metrics inspired from
60 concepts of population dynamics. A series of simulations allows for the analysis of the spatio-temporal variabil-
61 ity of these proxies, their links with oceanographic processes and the investigation of their global relationships.
62 While this setting is equally applicable to any target species and to any oceanic area, the general connectivity
63 patterns evidenced here are particularly relevant to several key organisms from Mediterranean ecosystems. Our
64 results are finally discussed in the context of population genetics and ecosystems conservation, with implications
65 for ecologists, biogeographers and managers.

66 2 Materials and Methods

67 2.1 Lagrangian flow network

68 To study large-scale connectivity patterns, we simulated the dispersal of free-swimming larvae by ocean currents
69 using the Lagrangian Flow Network methodology which is briefly described here while further details are found
70 in [Rossi et al. 2014; Ser-Giacomi et al. 2015].

71 A Lagrangian model simulates passive particle trajectories in the upper-ocean through the off-line integration
72 of the surface velocity field produced by an operational hydrodynamical model at $1/12^\circ$ horizontal resolution
73 over years 2002 – 2011 [Oddo et al. 2009]. The surface ocean was divided into 3270 equal-area boxes of $1/4^\circ$
74 horizontal-resolution (Fig. SI-6). For each experiment, 500 Lagrangian particles were seeded evenly in each
75 box, so that about 1635000 trajectories were computed with a *Runge-Kutta 4* algorithm with two parameters:
76 the starting time t_0 and the time of integration τ which simulate respectively the period of spawning and
77 the Pelagic Larval Duration (PLD). We retained two PLDs of 30 and 60 days and both winter and summer
78 spawning by considering three successive starting times t_0 for each season ($t_0 = 1^{st}, 15^{th}$ and 31^{st} of January and
79 $t_0 = 1^{st}, 15^{th}$ and 31^{st} of July) to account for episodic and variable spawning events. A total of 120 numerical
80 experiments (6 starting times over 10 years for 2 PLDs) allows the analysis of robust basin-scale connectivity
81 patterns, focusing on species with a wide geographical range and potential for large-distance dispersal (see
82 additional references in *Appendix 1* and Table SI-1 *Appendix 3*).

83 Marine populations are not uniformly distributed and panmictic but are rather organized as a network of
84 discrete subpopulations whose persistences depend strongly on self-replenishment and asymmetric exchanges of
85 individuals among heterogeneously distributed habitat patches [Kool et al. 2013]. Assuming those exchanges
86 occur mainly during the larval phase, each box (i.e. hereafter “node” of our flow network) can be seen as a
87 discrete habitat which supports the long-term survival of a local subpopulation through larval retention and
88 exchange with its neighbours.

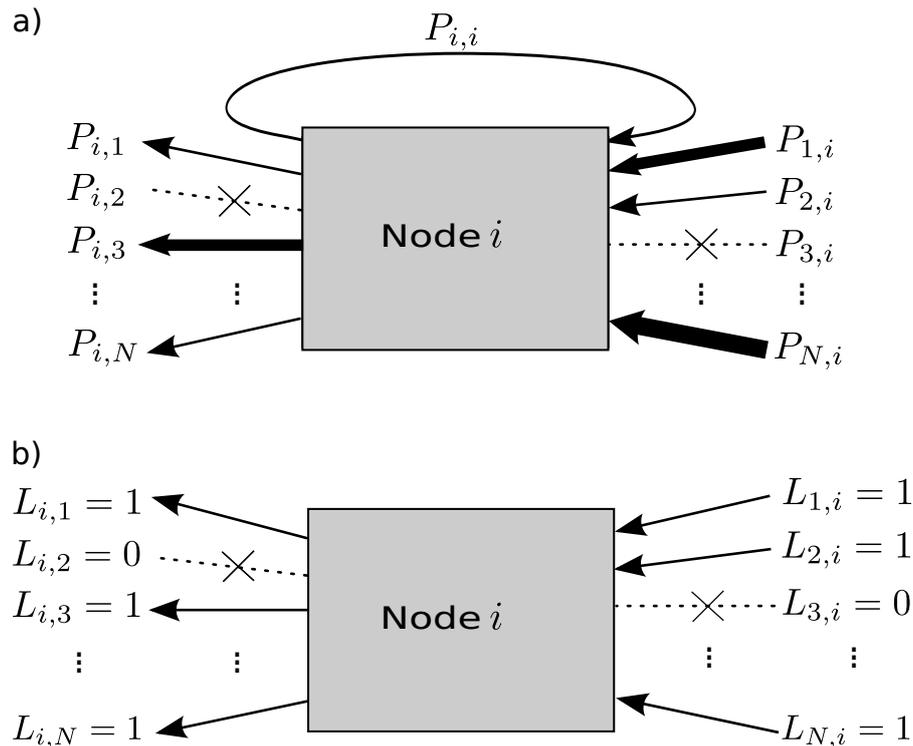


Figure 1: Schematic representation of larval exchanges through a node. (a) The elements $P_{x,y}$ constitute a matrix of larval fluxes used to compute the *strength* variables (i.e. from the amount of exchanged larvae). (b) The elements $L_{x,y}$ constitute a binary matrix used to compute the *degree* variables (i.e. from the number of connections, independently of their weights). Notations are consistent with the main text.

89 2.2 Definition and computation of connectivity metrics

90 Our weighted and directed network is analyzed from its *adjacency matrix*, an equivalent of the *connectivity*
 91 *matrix*, to describe both the pathways and fluxes of larvae between all sub-areas of the surface ocean. Each
 92 element of the connectivity matrix $P_{i,j} \in [0, 1]$ represents the probability that a particle released at t_0 from
 93 node i settles in node j after the integration time τ . A diagonal element of the matrix represents the probability
 94 that a particle released from node i stays or returns at the same location after integration. The non-diagonal
 95 elements represent the transport probabilities between each pair of nodes, considering the origin (destination)
 96 node as a row (column, respectively) of the connectivity matrix. Similarly, one can build a simplified binary
 97 connectivity matrix L with elements $L_{i,j} = 0$ if $P_{i,j} = 0$ (i.e. no larval flow from node i to j) and $L_{i,j} = 1$ when
 98 $P_{i,j} \neq 0$ (Fig. 1).

99 A number of studies were based on matrices which only depicted the connectivity between various coastal
 100 sites or MPAs [e.g. Trembl et al. 2012; Andrello et al. 2013; Mitarai et al. 2009] or among shelf regions [e.g.
 101 Nilsson-Jacobi et al. 2012]. In contrast, we aim to provide a global framework for the integrative management
 102 of both coastal and pelagic ecosystems. While Rossi et al. [2014] studied the global properties of the network
 103 to unveil hydrodynamical provinces organizing basin-scale larval dispersal, here we focus on local (node-scale)
 104 features to describe larval retention and exchange. For each node, one can examine the number (*degree*) and
 105 weight (*strength*) of all links emanating from it, referred to as the *OUT-degree* and *OUT-strength*, and those
 106 arriving in it, called the *IN-degree* and *IN-strength* (Fig. 1).

107 Botsford et al. [2009] defined the Local Retention (*LR*) as the ratio of locally produced settlement to local
 108 larval release. Since the local larval release and the success of recruitment are here assumed to be homogeneous
 109 in space, *LR* can be approximated for each node by the proportion of locally retained particles (i.e. diagonal

110 elements of P):

$$Local\ Retention_i = LR_i = P_{i,i} \in [0, 1]. \quad (1)$$

111 Botsford *et al.* [2009] defined the Self-Recruitment (SR) as the ratio of locally produced settlement to the
 112 overall settlement. With our assumptions, SR corresponds to the ratio of retained particles in each box to the
 113 total incoming particles from all origins (including those produced locally):

$$Self-Recruitment_i = SR_i = \frac{P_{i,i}}{\sum_{x=1, x \neq i}^N (P_{x,i}) + P_{i,i}} = \frac{P_{i,i}}{\sum_{x=1}^N (P_{x,i})} \in [0, 1]. \quad (2)$$

114 For each node, we also compute the local *OUT-strength* (*IN-strength*) which measures the proportion of par-
 115 ticles released (arriving) locally that were transported (originated from, respectively) elsewhere. It is calculated
 116 by summing the rows (columns, respectively) of the connectivity matrix, excluding the diagonal element:

$$OUT-strength_i = OUT_i^s = \sum_{x=1, x \neq i}^N (P_{i,x}) = \sum_{x=1}^N (P_{i,x}) - P_{i,i}, \quad (3)$$

117

$$IN-strength_i = IN_i^s = \sum_{x=1, x \neq i}^N (P_{x,i}) = \sum_{x=1}^N (P_{x,i}) - P_{i,i}. \quad (4)$$

118 The *IN-degree* and *OUT-degree* were computed similarly as the “strength” case but using the binary con-
 119 nectivity matrix L :

$$OUT-degree_i = OUT_i^d = \sum_{x=1, x \neq i}^N (L_{i,x}) = \sum_{x=1}^N (L_{i,x}) - L_{i,i}, \quad (5)$$

120

$$IN-degree_i = IN_i^d = \sum_{x=1, x \neq i}^N (L_{x,i}) = \sum_{x=1}^N (L_{x,i}) - L_{i,i}. \quad (6)$$

121 Following the simplification of Roberts [1997]; Bode *et al.* [2006], we finally examine the relative importance
 122 of larval export versus import to characterize the local source/sink dynamics. The Source Sink (SS) metrics
 123 are defined by:

$$Source\ Sink-strength_i = SS_i^s = \frac{IN_i^s}{IN_i^s + OUT_i^s} \in [0, 1]. \quad (7)$$

124

$$Source\ Sink-degree_i = SS_i^d = \frac{IN_i^d}{IN_i^d + OUT_i^d} \in [0, 1]. \quad (8)$$

125 They evaluate the source or sink character, in terms of the total amount of larvae (*strength*) or in terms of
 126 the spatial diversity of origins and destinations (*degree*). These metrics are restricted between 0 and 1 by
 127 construction and their negative (positive) deviations from 0.5 allow the quick appraisal of the nodes behaving
 128 as sources (sinks, respectively).

129 2.3 Spatio-temporal variability

130 Spatial patterns of each connectivity metric over the entire Mediterranean basin (Fig. SI-4) are studied through
 131 the mapping of their local (node-by-node) time-averages across all 120 simulations. Considering the intra-annual
 132 variability of the Mediterranean circulation [e.g. Bakun & Agostini 2001; Pinardi & Masetti 2000] (see also Fig.
 133 SI-5), we investigate how these spatial patterns change with the spawning season. To do this, we compute
 134 temporal averages over a subset of the simulations considering the two seasons separately.

135 To evaluate the confidence of the averages reported on the maps, we calculate the standard deviation σ of
 136 our local metrics and we then relate the variance σ^2 to the temporal mean μ by means of the so-called *index*
 137 of dispersion. The local mean is considered non-informative if $\sigma^2/\mu > 0.5$ (see pink crosses on Fig. 2, 3, 4).

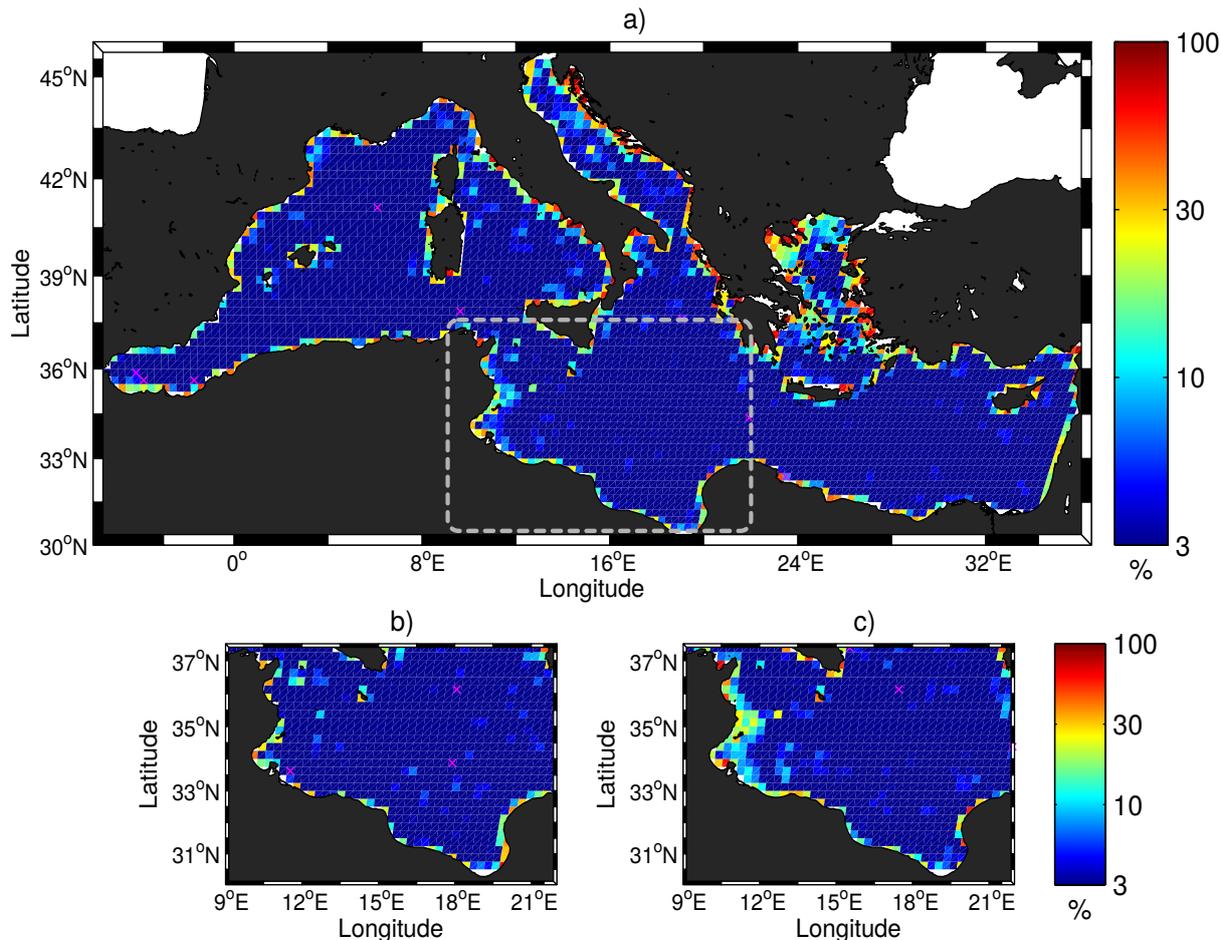


Figure 2: (a) Mean Local Retention (LR) for a Pelagic Larval Duration (PLD) of 30 days averaged across 60 (winter and summer) connectivity matrices; (b) mean LR over the southern Ionian Sea averaged across 30 winter matrices and (c) 30 summer matrices. Pink crosses in some boxes indicate particularly large temporal variability ($\sigma^2/\mu > 0.5$). For color version of this figure, the reader is referred to the online version of the article.

138 Nodes with a particularly high temporal variability are indicative of oceanic regions where the stochasticity of
 139 the circulation does not permit a robust characterization of connectivity.

140 3 Results

141 3.1 Global connectivity metrics

142 The global distributions of our connectivity metrics and their robustness to the most relevant biological and
 143 physical parameters have been investigated in *Appendix 2* (Fig. SI-1 to 3). In particular, our results are
 144 insensitive to the scale of spatial discretization (Fig. SI-2) and to the initial density of particles (Fig. SI-3).

145 3.1.1 Mapping retention metrics

146 Despite significant variability, maps of mean LR and SR over the Mediterranean basin (Fig. 2) reveal strongly
 147 contrasted patterns of retention rates. The largest LR or SR ($> 30\%$) are observed along the continental and
 148 insular coastlines while moderate values ($10\% < LR$ or $SR < 30\%$) are also found slightly offshore in nodes
 149 located over the continental shelf (depths < 200 m). In contrast, most open ocean boxes (depths > 200 m)
 150 show on average null or very low ($> 1\%$) LR or SR (Fig. 2a).

151 While these global patterns are observed for all simulations, some seasonal differences are noticeable. For
 152 instance, elevated values of LR and SR are found over the Tunisian shelf during summer whereas they are more
 153 restricted to the near-coastal boxes in winter (Fig. 2b and c).

154 3.1.2 Mapping Source/Sink metrics

155 All σ computed over 60 (global mean; Fig. 3) or 30 (seasonal mean; Fig. 4) connectivity matrices are of the
 156 same order of magnitude for both PLDs and reveal that less than 1% of nodes have $\sigma^2/\mu > 0.5$. Their locations
 157 do not show any consistent pattern, except in the western Alboran Sea which has thus been disregarded from
 158 our analyses ¹.

159 SS -degree and SS -strength show relatively similar spatial patterns (Fig. 3), with a slightly smaller magnitude
 160 for larval sinks in the SS -strength variable ². This holds true for both PLDs (not shown). As such, we only
 161 analyze the patterns observed in both SS -degree and SS -strength using a PLD of 60 days (as longer dispersal
 162 tends to accentuate patterns of exchange, see also sect. 3.1 and SI sect. 1).

163 Some regions are characterized by relatively stable behaviour throughout the year. For instance, larval
 164 export (source) is observed over most of the Ligurian Sea, intensified in near-shore areas (Fig. 3). The Gulf
 165 of Lion can be divided into two sub-regions: the north-east gulf which behaves as a larval source and the
 166 south-western coastlines which act as sinks. This “dipole” pattern is clearly visible in SS -degree (and to a lesser
 167 extent in SS -strength) and is similar for both seasons (Fig. 3), with the greatest differences observed during
 168 winter (Fig. 4a, b). The Adriatic Sea has a persistent larval sink along the southern Italian shores (Puglia
 169 coasts and the gulf of Taranto). Coastlines of Lybia, Egypt, Israel and Lebanon behave primarily as larval sinks
 170 throughout the year (Fig. 3), with an intensification along the Egyptian coastlines in summer (Fig. 4a, c).

171 Others regions are marked by two very distinct seasonal patterns. For instance, during summer most of
 172 Balearic Sea behaves as a quite homogeneous larval sink (Fig. 4a, b), whereas it shows disparate sources and
 173 sinks in winter. The northern Ionian Sea and the coastlines of Calabria and Sardinia behave as sources during
 174 winter while the western Greek shores are sinks (Fig. 4c). During summer, there is the opposite situation.
 175 The same pattern is observed in the Aegean Sea (Fig. 4a, c): in winter its eastern side acts as a larval sink
 176 while its western side is a source. The reverse is observed in summer. At smaller-scales, the Gulf of Taranto in
 177 wintertime acts as a sink on its north-eastern coast and as a source on its south-western side but it appears as
 178 a strong sink in summer (Fig. 4a, c).

179 Finally the central Ionian Sea, central Levantine Sea and Algerian Basin are characterized by heterogeneous
 180 patterns of both SS -degree and SS -strength (Fig. 3), with a particularly weak signal close to 0.5, making it
 181 difficult to discern clear sources or sinks in these open ocean regions.

182 3.2 Relationships among connectivity metrics

183 When we plot LR versus SR considering each box and each simulation independently, we find a rather loose
 184 relationship (Fig. 5a) with a correlation coefficient R^2 of 0.69, indicating a significant spread of the variables.
 185 However, by locally averaging LR and SR over all simulations (for a fixed PLD), they appear positively corre-
 186 lated through a more compact linear relationship (Fig. 5b). In this case, the R^2 coefficient is 0.89, suggesting
 187 that LR and SR are on average nearly equal at a given site (under our assumptions of homogeneous larval
 188 production and mortality).

189 To investigate if there is a global relationship between retention and exchange metrics we distinguished each
 190 point of the LR versus SR scatterplots according to its value of SS -degree and SS -strength (Fig. 6). We find
 191 that a sink site ($SS \leq 0.4$) tends to have higher LR than SR whereas a source site ($SS \geq 0.6$) is characterized

¹This “edge effect” is due to the lack of constant particle seeding despite the continuous entrance of Atlantic water through the Gibraltar strait.

²This maybe due to the almost incompressible character of the surface velocity field at these short time-scales.

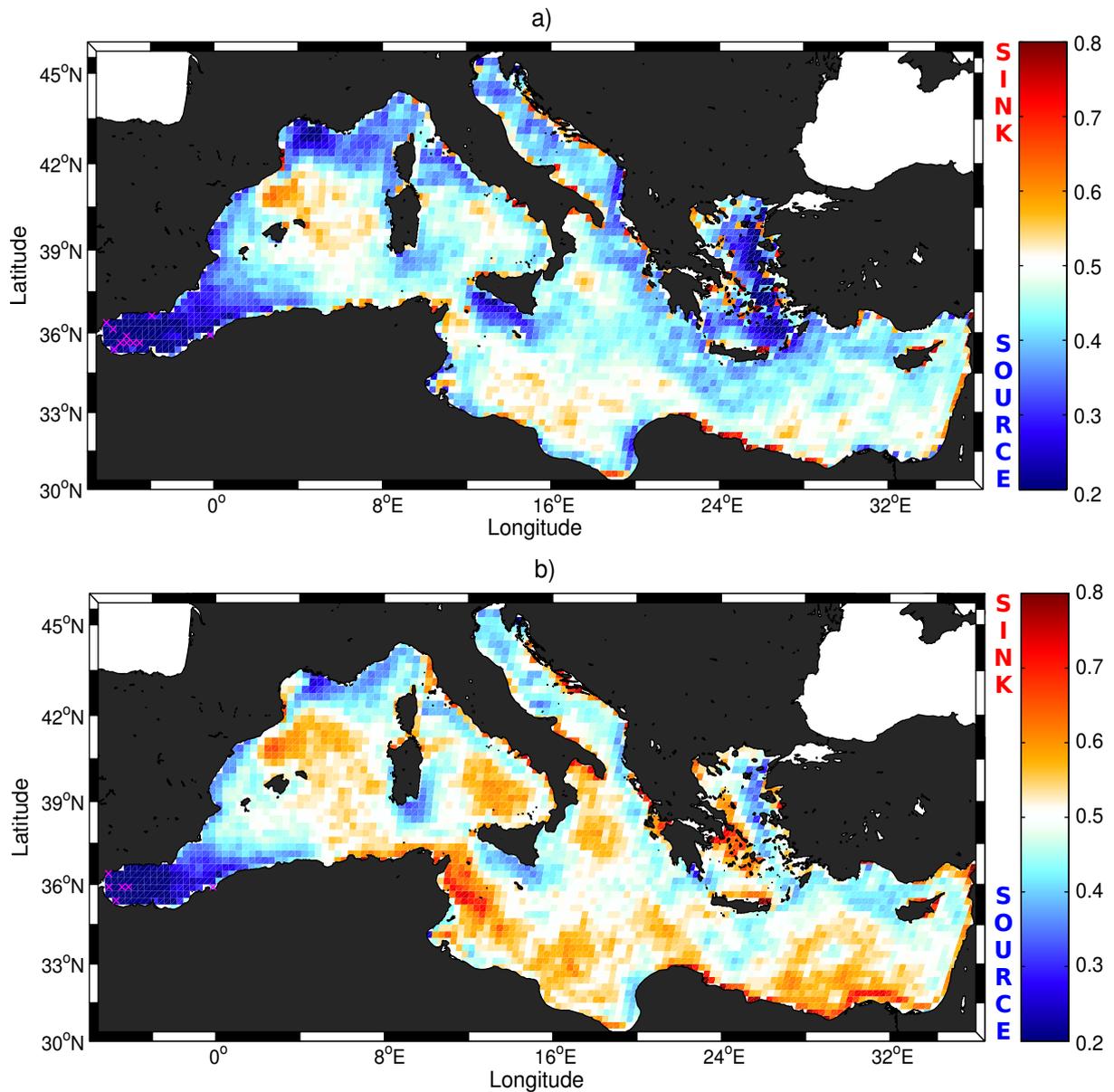


Figure 3: (a) Mean *Source Sink-strength* (relative importance of larval export versus import, computed from larval fluxes following Eq. [7]) and (b) mean *Source Sink-degree* (relative importance of larval export versus import, computed from the numbers of links independently of their weights following Eq. [8]) averaged across 60 (winter and summer) connectivity matrices for a PLD of 60 days. Pink crosses in some boxes indicate particularly large temporal variability ($\sigma^2/\mu > 0.5$). For color version of this figure, the reader is referred to the online version of the article.

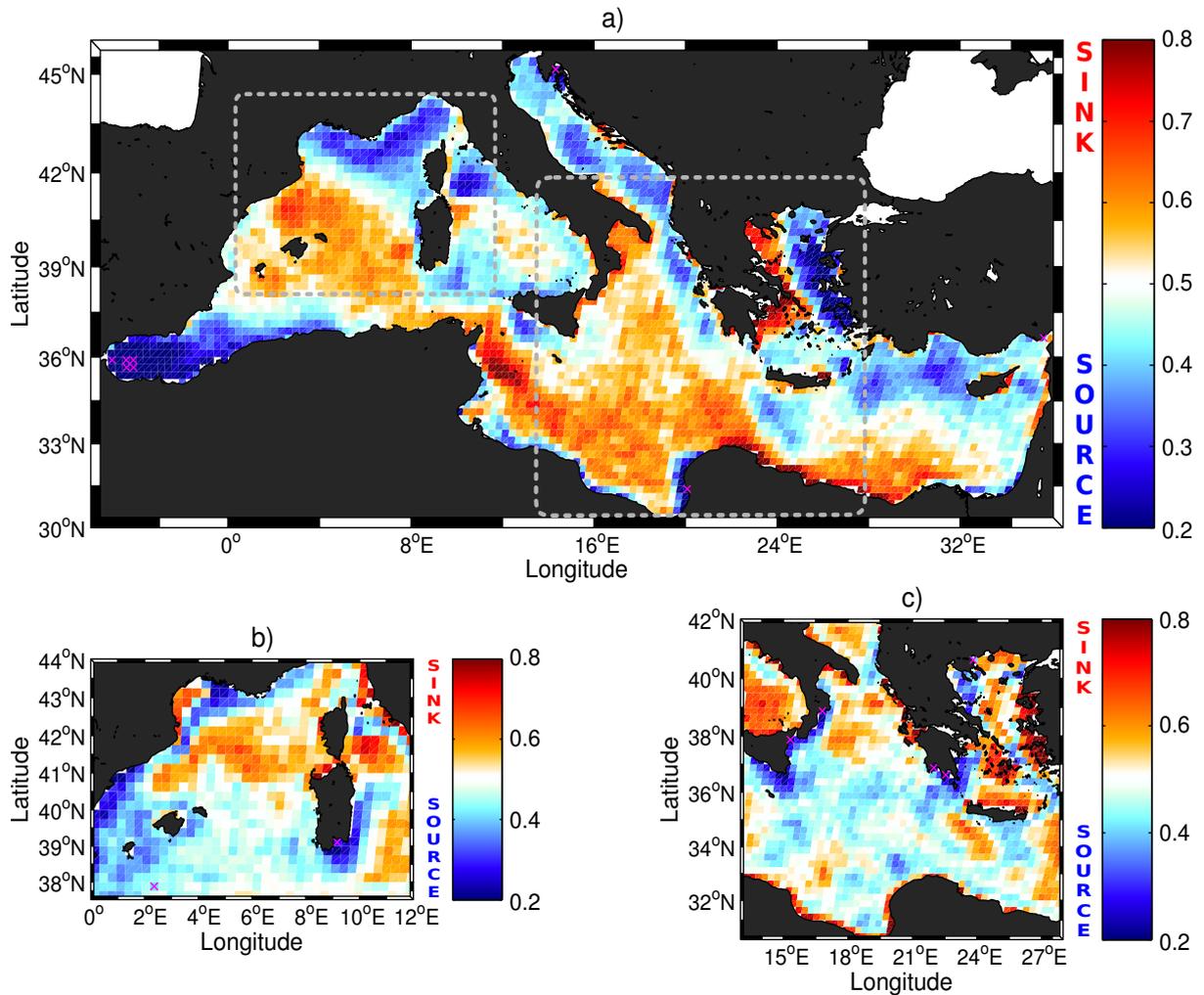


Figure 4: (a) Mean *Source Sink-degree* (relative importance of larval export versus import, measuring the number of links) averaged across 30 summer matrices and averaged across 30 winter matrices (b) over the north-west Mediterranean and (c) over the Ionian Sea for a PLD of 60 days. Pink crosses in some boxes indicate particularly large temporal variability ($\sigma^2/\mu > 0.5$). For color version of this figure, the reader is referred to the online version of the article.

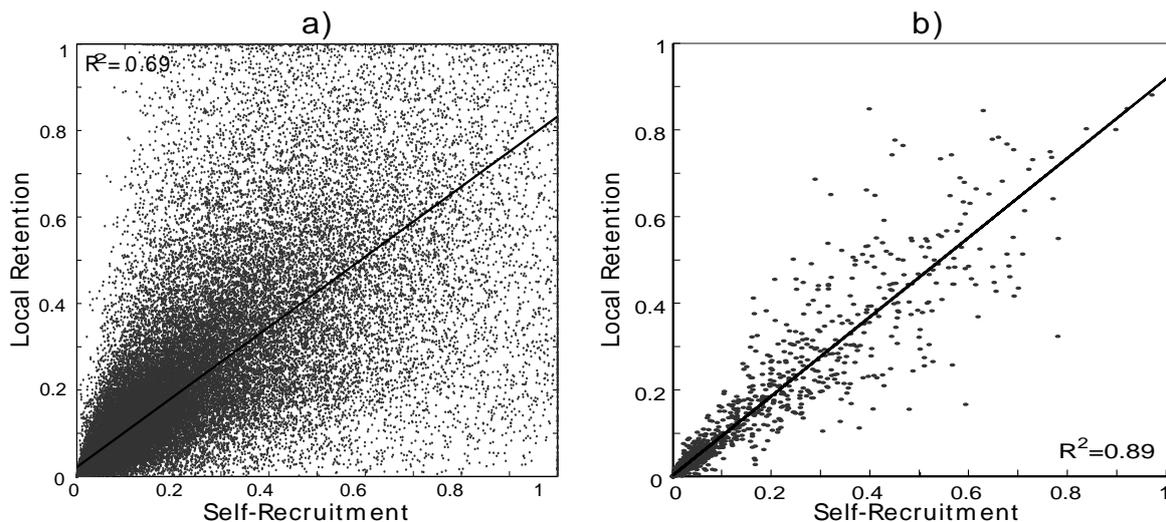


Figure 5: Relationship between LR (Local Retention) and SR (Self-Recruitment) for a PLD of 30 days when (a) considering each node (3270) and each simulation (60) independently, and (b) when averaging our proxies locally across all simulations.

192 by *SR* higher than *LR*. A tight linear relationship between *SR* and *LR* (R^2 of 0.96) is found for the sites
 193 characterized by neutral *SS* (i.e. with similar larval import and export $0.4 \leq SS \leq 0.6$).

194 4 Discussion

195 4.1 Linking broad-scale connectivity patterns and oceanography

196 From a basin-scale perspective, our study highlights common oceanographic conditions which would favour
 197 retention processes in any oceanic region. Extended continental shelves and complex bathymetry (e.g. islands,
 198 capes, large bays, Fig. SI-4) in association with relatively weak currents (Fig. SI-5) lead to high retention near
 199 the coast. Specific locations of enhanced *LR* and *SR* are the Gulf of Lion, the Gulf of Valencia/Ebro delta, the
 200 Tuscan archipelago, the Croatian coastlines and the insular and near-shore sub-regions of the Aegean Sea. This
 201 is consistent with the elevated retention processes that were documented in coral reef environments using high
 202 resolution biophysical models [e.g. Paris & Cowen 2004; Tremblay et al. 2012]. Retention is however diminished by
 203 large-scale energetic currents flowing close to the shore (e.g. the narrow continental shelves of the french “Côte
 204 d’Azur”) and by long-lived mesoscale structures travelling offshore (e.g. the Algerian coast). The seasonal
 205 change of *LR* or *SR* observed over the Tunisian shelf illustrates clearly these two behaviours (Fig. 2b, c). The
 206 high *LR* observed in summer decreases during winter due to the acceleration and intrusion over the shelf of the
 207 Sicily-Strait-Tunisian-Current [Millot & Taupier-Letage 2005] (Fig. SI-5).

208 The variability of *SS-degree* and *SS-strength* metrics appears also primarily determined by the oceanographic
 209 setting as most larval sources (sinks) identified here match well-known divergence (convergence) zones. For
 210 instance, the “sink” character of the Balearic Sea could be related to the dominant wind regimes that forces
 211 convergent surface transport and downwelling in the centre of the gyre, especially in summer [Bakun & Agostini
 212 2001]. In contrast, atmospheric patterns change during winter with the intensification of the Cierzo wind in
 213 the Ebro valley, resulting in a cyclonic wind stress curl producing an area of Ekman divergence and associated
 214 upwelling [Bakun & Agostini 2001] in the southern part of the Balearic Sea. The permanent retentive character
 215 of the north-eastern Balearic Sea is consistent with the results of Poulain et al. [2012] who documented the
 216 highest residence times of geolocated surface drifters in this area over the last decade. Offshore sources such as

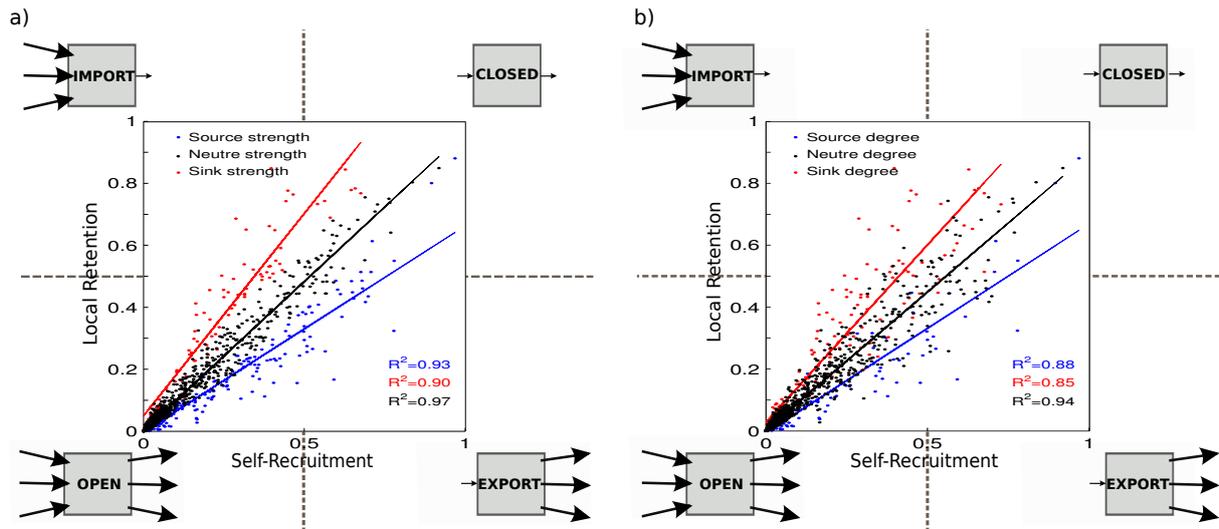


Figure 6: Inter-relationship among connectivity metrics for a PLD of 30 days. Mean relationship between LR (Local Retention) and SR (Self-Recruitment) distinguishing “source” (blue), “sink” (red) and “neutral” (black) nodes based on (a) $SS - strength$ (Source-Sink index computed from larval fluxes) and (b) $SS - degree$ (Source-Sink index computed from the number of links). Annotations represent schematically the behaviour of a node according to its location on the plot. Source (sink) nodes are characterized by $SS - strength$ or $SS - degree$ smaller than 0.4 (larger than 0.6, respectively). For color version of this figure, the reader is referred to the online version of the article.

217 in the Adriatic and Tyrrhenian Sea are also reasonably well explained by the oceanographic context with the
 218 three cyclonic gyres in the Adriatic Sea and the summer strengthening of the northern Tyrrhenian cyclonic gyre
 219 (Fig. SI-5). Whereas the larval sinks observed along the Lybian/Egyptian shores are due to the dominance of
 220 coastal convergence all year long [Bakun & Agostini 2001].

221 The impact of a boundary current on connectivity properties is another relevant mechanism that is clearly
 222 evidenced in the north-western Mediterranean. The dominant circulation pattern in the region is the Liguro-
 223 Provençal Current (Ligurian sector) which extends into the Northern Current off the Gulf of Lion (Fig. SI-5).
 224 It intensifies and narrows during winter [Millot & Taupier-Letage 2005] which would favour larval export along
 225 the main axis of the jet. This provides a good explanation for the narrow larval source observed in winter along
 226 the French coastline as well as the blue vein (source) further west that sharply separates the Gulf of Lion from
 227 the Balearic Sea. In contrast, during summer the source region (Ligurian Sea) extends further offshore due to
 228 the slower and less defined current associated with the “Mistral” wind which tends to veer eastward, forcing
 229 coastal upwelling [Bakun & Agostini 2001].

230 The Gulf of Lion is characterized by a shallow bathymetry that often maintains the core of the Northern
 231 Current off the shelf-break. As such, the inner-shelf circulation is primarily influenced by the “Tramontane” and
 232 “Mistral” winds which produce a divergent zone associated with upwelling along the Provence/Camargue coast-
 233 lines (north-eastern parts of the Gulf) and a convergent zone with downwelling along the Languedoc-Roussillon
 234 coast (south-western parts of the Gulf) [Millot & Taupier-Letage 2005]. These divergence/convergence zones
 235 are closely aligned with the source/sink dynamics previously described. Note that the accentuated source/sink
 236 pattern observed in the Gulf during winter is also consistent with the seasonal intensification of “Mistral”
 237 and “Tramontane” winds [Bakun & Agostini 2001]. Similarly, other “dipoles” of upwelling/downwelling forced
 238 by seasonal wind regimes are in agreement with our proxies (Fig. 3, 4): for example the source/sink dipole
 239 documented along the northern Ionian and Aegean coastlines [Pinardi & Masetti 2000] and the winter dipole
 240 observed in the Gulf of Taranto [Bakun & Agostini 2001].

241 Although relatively stable circulation is consistently associated with larval sources/sinks, it is worth men-
 242 tioning that some regions such as the central Levantine Sea and the Algerian Basin are characterized by chaotic

243 and turbulent transport [Millot & Taupier-Letage 2005; Poulain et al. 2012] preventing a clear depiction of their
244 connectivity patterns.

245 4.2 Unifying hydrodynamic and genetic connectivity

246 Despite numerous attempts to characterize the interplay between the complex life history traits of marine
247 organisms, their distribution ranges and their realized dispersal [e.g. Riginos et al. 2011; Mora et al. 2012],
248 the respective roles of intrinsic and extrinsic factors that determine population connectivities remain unclear
249 [Botsford et al. 2009]. Previous research revealed that the relationship between PLDs and geographic distances
250 alone have a limited influence, if any, on observed genetic structuring [e.g. Weersing & Toonen 2009; Riginos
251 et al. 2011], calling for a better appraisal of biological and extrinsic factors, such as hydrodynamics, that drive
252 both species range and population connectivity [e.g. Baums et al. 2006; Jolly et al. 2009; White et al. 2010;
253 Schunter et al. 2011; Kool et al. 2011; Soria et al. 2012; Foster et al. 2012].

254 Through the direct incorporation of population genetic concepts into a bio-physical modelling approach at
255 basin-scale, we propose a common framework for geneticists and oceanographers to explore connectivity issues
256 [Botsford et al. 2009]. Our results, and more generally the tunable modelling framework proposed here, should
257 allow i) to formally test the effects of specific oceanographic processes on population genetics by integrating the
258 most relevant biological traits for a group of species into this general framework and ii) to target sub-regions
259 with dissimilar connectivity behaviours as predicted here, whose effects on connectivity in relation with species
260 distributions and life history traits could be evaluated.

261 As shown by Thomas & Bell [2013], the persistent larval sources/sinks that we identified have the potential
262 to impact the genetic connectivity of local subpopulations. For instance, the genetic homogeneity found among
263 the sea-bream *Diplodus sargus* populations of the Italian, French and Spanish coasts [Lenfant & Planes 1996]
264 could be related to the efficient gene flows occurring among those source areas. In contrast, genetic samples
265 originating from the south-western part of the Gulf of Lion were found differentiated from the surrounding areas
266 for *D. sargus* [Lenfant & Planes 1996] and the sessil red gorgonian *Paramuricea clavata* [Mokhtar-Jamaï et al.
267 2011]. A strong influence of oceanographic features on larval dispersal was hypothesized to explain the genetic
268 differentiation observed in the south-west Gulf. This was later supported by a small-scale study [Guizien et al.
269 2012] as well as by our basin-scale model, both predicting a marked larval sink in this region. It is important to
270 note that with our assumptions, which differ from those of Pulliam [1988], a subpopulation is characterized as a
271 sink under two contrasting situations. On one hand, a subpopulation is classified as a sink when it sends almost
272 no emigrant elsewhere (i.e. weak exportation, high LR), suggesting it is mainly genetically influenced by itself
273 and that significant levels of genetic differentiation with its neighbouring subpopulations may be established
274 [Jolly et al. 2009]. On the other hand, a sink is also identified when importation from neighbouring source(s)
275 are particularly high (i.e. low SR), that would suggest potential inputs of genetic materials from surrounding
276 subpopulations and could possibly result in weak genetic differentiation between the connected source/sink
277 subpopulations [Gaggiotti 1996]. Such sink subpopulations could be further distinguished into those influenced
278 by a single or by several sources, potentially maximizing its genetic diversity [Pannell & Charlesworth 1999].
279 Indeed subpopulations of the Balearic Sea have been often described as a “mixed genes pool” with diverse
280 genetic influences from the Alboran, Catalan and Ligurian seas [Ledoux et al. 2010; Mokhtar-Jamaï et al. 2011].
281 Our results consistently suggest that the Balearic Sea is a basin of attraction for drifting larvae as evidenced
282 by a strong influx (*strength*) from diverse origins (*degree*), potentially leading to a mixture of local genes and
283 those from the surrounding sources.

284 4.3 Interpretation of connectivity metrics for management purposes

285 As recently shown by Lett et al. [2015] (by using a metapopulation model combined with genetic data of Saenz-
286 Agudelo et al. [2011]) and the genetic study of Hogan et al. [2012], we confirm SR is a good predictor of LR ,
287 especially when averaging the stochasticity of ocean currents.

288 Our models demonstrate that LR , which is a crucial parameter to infer population persistence but is rather
289 hard to access [Burgess et al. 2014], can be reliably estimated for “neutral” subpopulation through SR , generally
290 much easier to measure through empirical approaches. However, when a population is characterized by large
291 relative differences between its exportation and importation, LR and SR are still linearly correlated but with
292 a slope > 1 for sinks and < 1 for sources. This is because a site characterized by high SR (i.e. low “Openness”
293 [Hixon et al. 2002]) rarely receives larvae from elsewhere (weak import) and inversely, a site with high LR
294 would have very low exportation. Consequently, a subpopulation with both high SR and LR can be considered
295 as “closed” due to the limited upstream and downstream exchanges, while “open” subpopulation would be
296 characterized by low retention rate (Fig. 6). In other words, the greater the relative difference between SR
297 and LR , the larger are the deviations of $SS-degree$ or $SS-strength$ from 0.5, and the more pronounced is the
298 source or sink behaviour. While these conclusions based on $SS-strength$ are straightforward, we also show they
299 hold when considering $SS-degree$: a site which tends to import from distinct geographical regions but export
300 to only a few (a sink in terms of $degree$) is also characterized by LR higher than SR , which would have
301 consequences for the local genetic and phenotypic diversities.

302 The integrated interpretation of retention and exchange large-scale connectivity indices has implications
303 for the implementation of coastal and pelagic Marine Protected Areas (MPAs). They give insight into how
304 subpopulations are connected through larval transport and as such, help to predict the effects of management
305 measures or disturbances on both local and surrounding subpopulations. For instance, establishing a MPA on
306 a site whose larval supply originates from several non-protected “upstream” subpopulations may be ineffective
307 [Roberts 1997; Crowder et al. 2000], especially if retention rates are not sufficient to allow for self-persistence
308 of source sub-populations. Another strategy could be to position new MPAs within regions characterized by
309 both significant retention and exchange of larvae, thus favoring together self- and network persistence. Overall,
310 an accurate depiction of both local and broad-scale connectivity, as is allowed by our model, is necessary to
311 appropriately implement MPAs.

312 4.4 Modelling limitations and future developments

313 Rather than developing a realistic model for a single species [e.g. Kool et al. 2011; Foster et al. 2012], we retained
314 a range of parameters in accord with well-known ecological traits of various Mediterranean organisms to describe
315 large-scale connectivity patterns from an Ecosystem Approach. The “true” connectivity of marine populations
316 depends however on numerous species-specific biological processes such as the production of larvae, its swimming
317 behaviour, its natural mortality, the duration of the pelagic phase (PLD), the success of recruitment, the trophic
318 interactions, etc., all of which are also influenced by abiotic factors such as the variable oceanic circulation and
319 the heterogeneity of littoral and pelagic habitats [Cowen & Sponaugle 2009]. Despite resolving only some
320 of these processes, we highlight specific oceanographic processes that control larval connectivity, potentially
321 affecting both demographic and genetic connectivities of many marine organisms. Furthermore, it is worth
322 emphasizing that this modelling framework is indeed adaptable to any species whose biological traits and
323 ecological preferences are precisely known.

324 For instance, homogeneous larval production in both coastal and open ocean regions is a strong assumption
325 since some organisms spend most of their life-cycle in shallow areas (Tab. SI-1). Nevertheless, our source/sink
326 metrics can be re-calculated to restrict larval release over the continental shelves by selecting only the corre-
327 sponding nodes within the full connectivity matrices (Fig. SI-6). In this case, very similar spatial patterns are
328 observed (Fig. SI-7), suggesting that offshore processes only marginally affect the connectivity of continental

shelves [Rossi et al. 2014]. One could also incorporate the effects of habitat patchiness on population connectivity [Pinsky et al. 2012; Anadón et al. 2013] by adjusting local larval production and success of recruitment according to the proportion of favourable habitat in each node.

Realistic larval traits, such as active swimming, could be also implemented, but only large vertical migrations (outside of the surface mixed layer) are expected to significantly change the dispersal schemes [Corell et al. 2012]. Nevertheless, little information exists about the behaviour and the spatial distribution of larvae of most organisms [Calò et al. 2013], and even when it is relatively well-known, Trembl et al. [2012] found little impact of biological parametrizations on broad-scale connectivity. Lastly, although near-shore areas are not particularly well resolved by the basin-scale model we used, most patterns are in agreement with regional studies based on dedicated high-resolution models [e.g. Guizien et al. 2012].

5 Conclusions

Describing the connectivity of marine subpopulations, thought to be governed largely by the dispersal of pelagic larval stages, has ecological and managerial implications. We propose a modelling framework including Lagrangian simulations, tools from Network Theory and concepts of population dynamics to characterize marine connectivity at basin-scales. Various connectivity metrics and their spatio-temporal variability are related to local oceanography. We show that retention processes are favoured along coastlines with sluggish circulation and over extended continental shelves. We also demonstrate that convergence/divergence areas generated by alongshore winds are often associated with larval sinks/sources. Furthermore, studying the relationship among the connectivity metrics sheds light on their integrated interpretation for conservation planning. Overall, our results offer opportunities to (i) improve the sampling strategy of genetic studies, (ii) formulate and test hypotheses pertaining to the role of larval dispersal in the spatial and genetic structuring of populations and (iii) systematically depict retention and transport processes at multiple scales, which is propitious to their adequate consideration in the management of marine ecosystems.

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510 **7 Biosketch**

511 Mélodie Dubois was a master student at IFISC and is now enrolled in a PhD at CRIOBE. Her research
512 focuses on modelling ecological and social dynamics to improve fisheries management. Dr. Vincent Rossi
513 (<http://ifisc.uib-csic.es/users/vincent/>) is a post-doctoral researcher at IFISC. He is interested in
514 multidisciplinary and contemporary issues encompassing Physical & Biological Oceanography and Marine Ecology. Enrico Ser-Giacomi has just completed his PhD that takes Dynamical Systems and Complex Networks
515 perspectives to investigate geophysical flows. This research team composed of physicists (E.S.-G., C.L. and
516 E.H.-G.), oceanographer (V.R.), marine ecologist (M.D.) and evolutionary ecologist (S.A.-H.) aims to study
517 the spatial structure and dynamics of marine populations from ecosystemic and multidisciplinary approaches
518 to propose globally pertinent conservation plans and management strategies.
519

520 **Appendix 1: Data sources**

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Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems.

SUPPORTING INFORMATION

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Appendix 2: Connectivity proxies distribution and sensitivity analysis

To explore the variability of the connectivity metrics and their sensitivity to the most relevant parameters, we study their mapping and their probability distribution function with the Complementary Cumulative Distribution Function (CCDF) given by $F(x) = \text{Prob.}(X > x)$. In other words, $F(x) \in [0, 1]$ represents the proportion of values X that are strictly higher than the threshold x . The CCDFs of *strengths*, *degrees* and *SourceSink* are computed using a binning with regular intervals of 0.002 (corresponding to the numerical resolution of the model $1/500$), 1 and 0.005, respectively.

We also investigate the sensitivity of the CCDFs for each connectivity metric depending on the parameters $\tau = PLD$ and $t_0 =$ spawning period considered independently. For instance, to highlight the effect of the *PLD* on the distribution of $P_{i,j}$ and $L_{i,j}$, we build a single CCDF taking into account all 60 simulations that used the same integration time $\tau = PLD = 30$ days and we compare it to the CCDF build with the other 60 simulations using $\tau = PLD = 60$ days. Similarly, we test the seasonal effect alone, the inter-annual variability alone, and finally the full variability considering all effects together on every connectivity proxy.

2.1 Statistical distributions

Our two retention metrics (LR and SR) show very similar density functions. On average over all simulations (Fig. SI-1a), more than 50% of boxes have null LR and SR, indicating they never retain particle in their core at the end of the simulations. High values of LR and SR ($> 50\%$) are rarely found in less than 3% of oceanic boxes (which corresponds approximatively to 95 nodes with our discretization). Considering the *SourceSink* metrics, the CCDFs indicate that about 30% of all sites tend to behave as larval sink (≥ 0.6) and 30% as larval source (≤ 0.4) in terms of degree (SS^d). In terms of strength (SS^s), less than 20% of all nodes appear as sink and 35% are sources (Fig. SI-1b and c).

2.2 Sensitivity to the Pelagic Larval Duration

For most proxies, the Pelagic Larval Duration (PLD) is the most important factor of variability as it has the largest impact on the shape of the CCDF curves. The longer the PLD, the larger larval dispersion and the smaller retention rates. This is evidenced by the smaller absolute values of SR and LR for PLDs of 60 days as compared to 30 days (Fig. SI-1d). Stronger dispersion is evidenced by a greater number of links (Fig. SI-1e), a larger spread of their distribution and by higher export rates for longer PLDs (not shown). The effect of the PLD on the source/sink dynamics is more complex. The distributions of both *SS* metrics suggest that longer PLDs are associated with slightly higher proportions of source versus sink regions (Fig. SI-1f), especially for the strength analyses. For instance, about 35% of boxes have $SS^s \leq 0.4$ (source) with a PLD of 60 days but less than 25% of boxes are source with a PLD of 30 days. These results confirm the fact that PLD of marine organisms is a good predictor of their larval dispersal potential [Shanks *et al.* 2003]. We also find that the strong dispersal potential for long PLD is evident with stronger larval fluxes (*strength*) and dispersive pathways with more diverse destinations and origins (*degrees*). Finally, while the impact of PLD on source/sink dynamics has apparently not been studied previously, our results suggest that organisms with longer PLDs would tend to be more characterized as larval sources than as sinks.

2.3 Sensitivity to the spawning time

For each proxy, the variability due to the season of spawning ($t_0 \in$ January or $t_0 \in$ July) is similar in magnitude to the inter-annual variability ($t_0 \in$ 2002-2011) (Fig. SI-1g, h, i and j, k, l). Apart from SR and LR, winter simulations tend to enhance the spread of the CCDFs with higher frequencies in high values. More specifically,

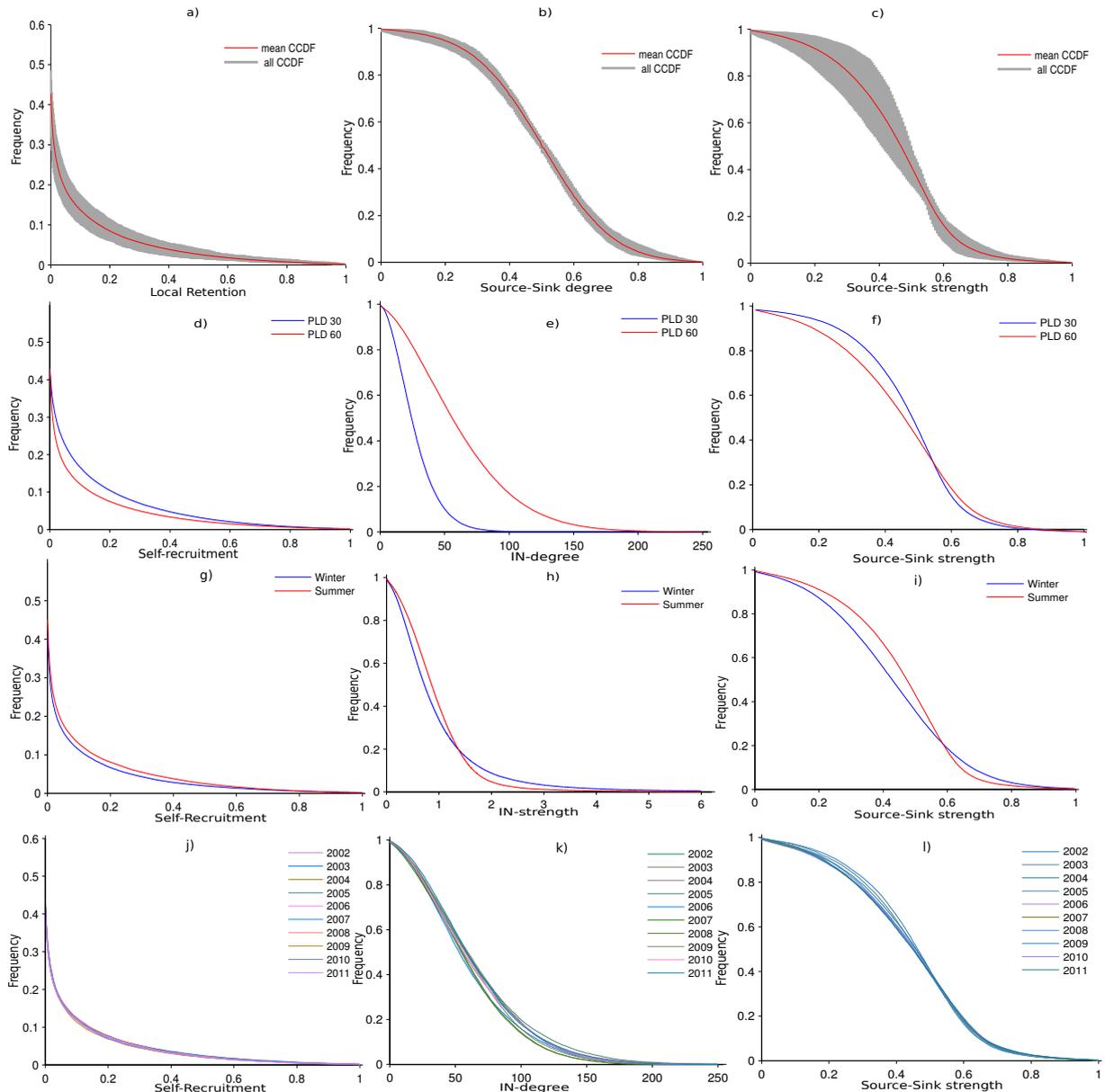


Figure SI-1: First row: mean Complementary Cumulative Distribution Function (CCDF) (red line) and its variability considering all experiments separately (grey shading) for (a) LR , (b) *SourceSink-degree* (SS^d) and (c) *SourceSink-strength* (SS^s). Second row: Effect of the *PLD* on CCDFs of (d) SR, (e) *IN - degree* and (f) SS^s . Third row: Effect of the season of spawning (t_0), considering a fixed *PLD* of 30 days, on CCDFs of (g) SR, (h) *IN - strength* and (i) SS^s . Fourth row: Effect of the year of spawning (t_0), considering a fixed *PLD* of 30 days, on CCDFs of (j) SR, (k) *IN - degree* and (l) SS^s (l).

42 it leads to stronger export during winter evidenced by lower retention (Fig. SI-1g) and of $IN^s > 1$ (Fig. SI-
43 1h). This is also observed on the degree analyses with higher occurrence of large degrees (not shown). This
44 is probably related to the enhanced winter mixing in the surface ocean [d'Ovidio *et al.* 2004] which leads to
45 stronger and more anisotropic larval dispersal in the surface ocean. As a consequence, slightly smaller LR and
46 SR are generally observed in winter times (Figure SI-1g). The seasonal variability of both *SS* metrics is more
47 puzzling. In terms of degree, winter simulations show a small increase of the proportions of sink boxes (not
48 shown), whereas *SS-strength* distributions reveal that source boxes are more frequent in winter than in summer
49 (Fig. SI-1i).

50 2.4 Sensitivity to the spatial discretization

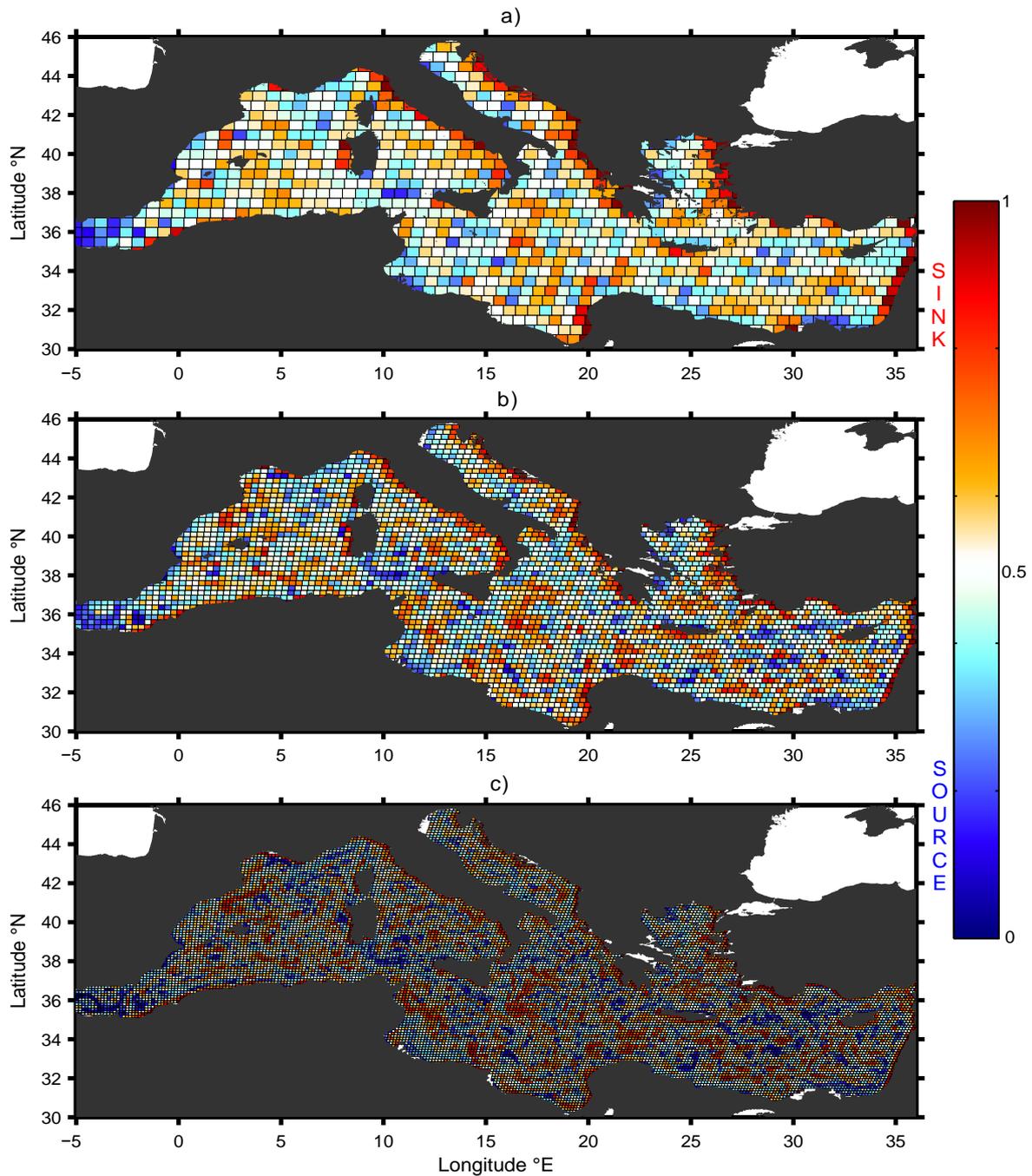


Figure SI-2: Snapshot maps of the SourceSink-degree (SS^d) generated with same parameters but for network grids of (a) low ($1/2^\circ$), (b) medium ($1/4^\circ$, i.e. the resolution used in the manuscript) and (c) high resolution ($1/8^\circ$). Note the very good agreement in the large-scale connectivity patterns among these snapshots, indicating no significant sensitivity of the averages depicted in the manuscript.

51 2.5 Sensitivity to initial density of particles

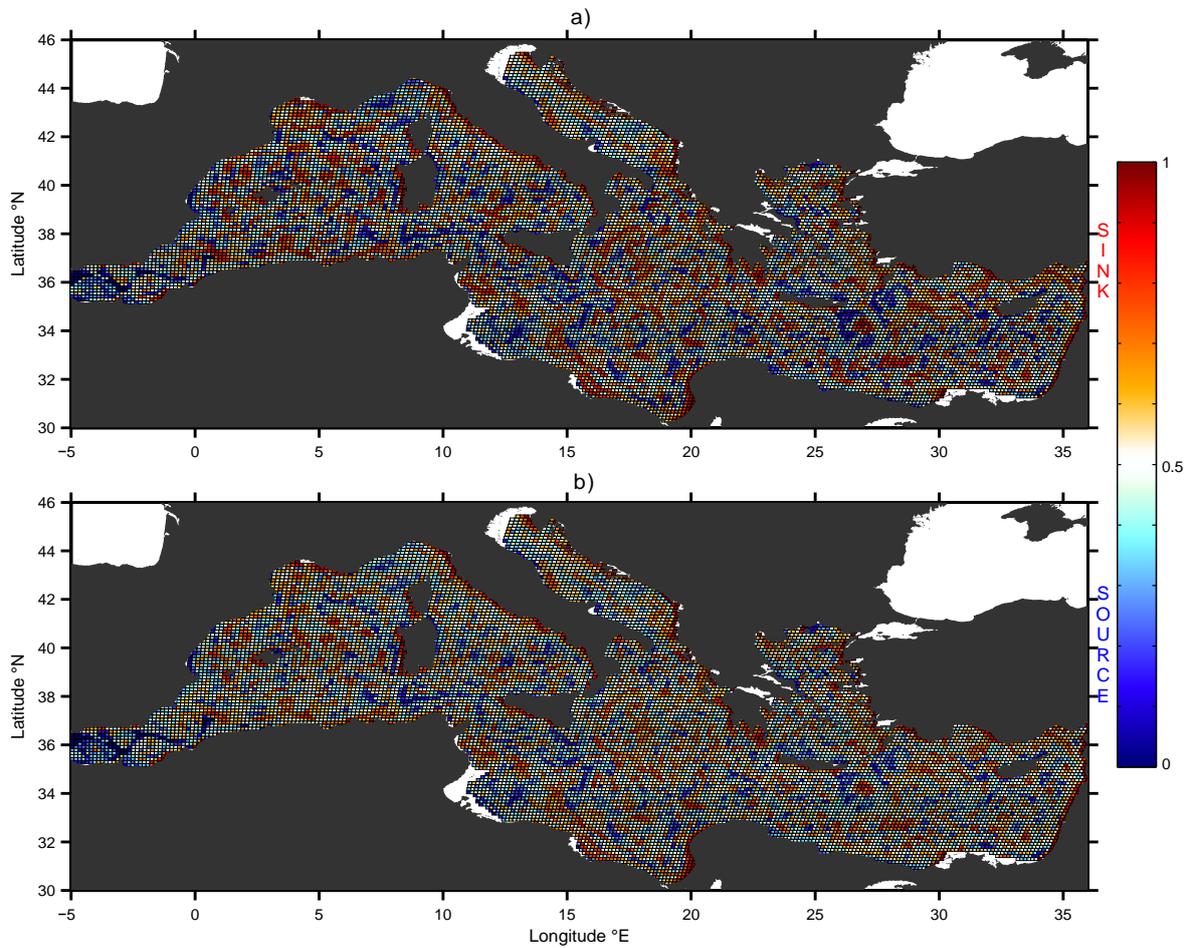


Figure SI-3: Snapshot maps of Source-Sink degree (SS^d) generated with same parameters but for different latitudinal spacing (the distance between two tracers in the initial grid) (a) of 0.0042° (corresponding to approximately 1000 particles per node of $1/8^\circ$), and (b) of 0.0125° (corresponding to about 100 particles per node of $1/8^\circ$). The spatial patterns and their magnitudes are very similar among those plots, suggesting no significant sensitivity of the averages described in the manuscript.

52 Appendix 3: Additional figures and table

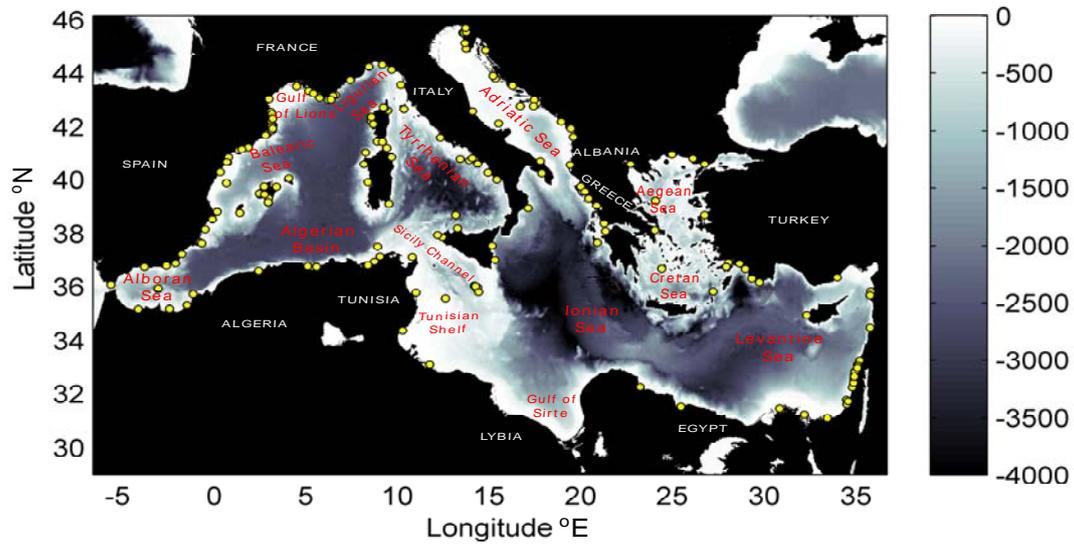


Figure SI-4: Overall geography and bathymetry (GEBCO) of the Mediterranean basin. Yellow dots represent the current network of Marine Protected Areas (MPAs coordinates were downloaded from the MedPan database).

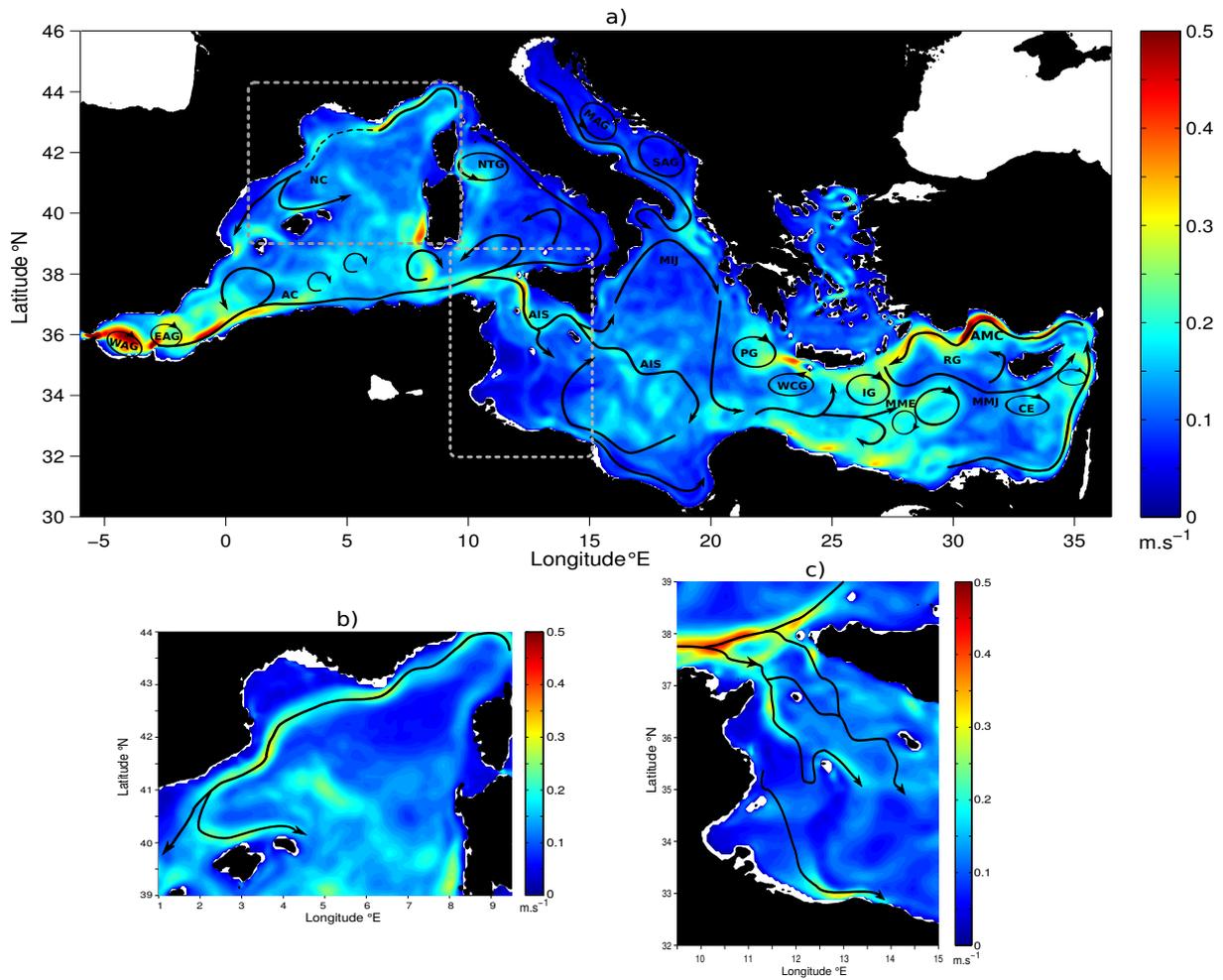


Figure SI-5: Schematic representation of surface currents adapted from Poulain *et al.* [2012], superimposed on the mean modulus ($m.s^{-1}$) of the surface velocity field produced by *MyOcean* hydrodynamical model averaged over 2002 – 2011 a) considering all summer months (July/August) and b) regional zooms (as indicated by the grey rectangles on the upper panel) using all winter months (January/February). AC = Algerian Current, AIS = Atlantic-Ionian Stream, AMC = Asian Minor Current, CE = Cyprus Eddy, EAG/WAG = Eastern/Western Alboran Gyre, IG = Iearapetra Gyre, MIJ = Mid-Ionian Jet, MME = Mersa-Matruh Eddy, MMJ = Mid-Mediterranean Jet, NC = Northern Current, PG = Pelops Gyre, RG = Rhodes Gyre, SAG/MAG = Southern/Middle Adriatic Gyre.

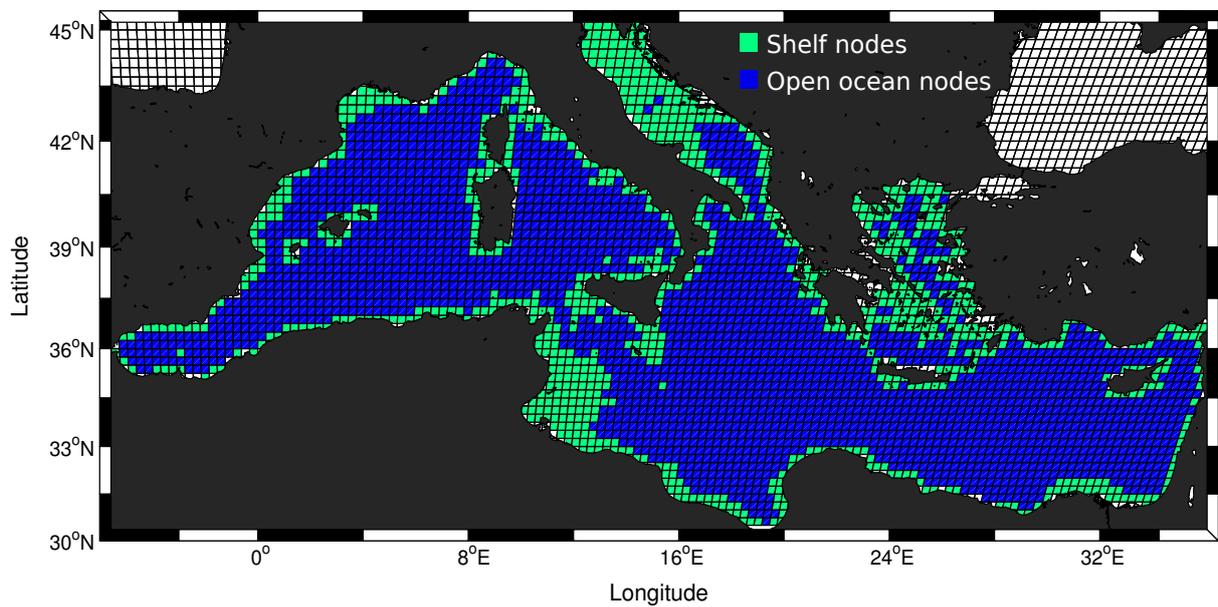


Figure SI-6: By co-locating the geographical coordinates of each node with a gridded bathymetry (GEBCO), one can distinguish the shelf and oceanic nodes (according to the color code). Following similar methodology, further ecologically-relevant distinction could be made in the future, such as separating the four main bathymetric floors (infra-, circa-littoral, bathyal and abyssal) or using the proportion of a specific benthic habitat in each node (see also Discussion sect. 4.4).

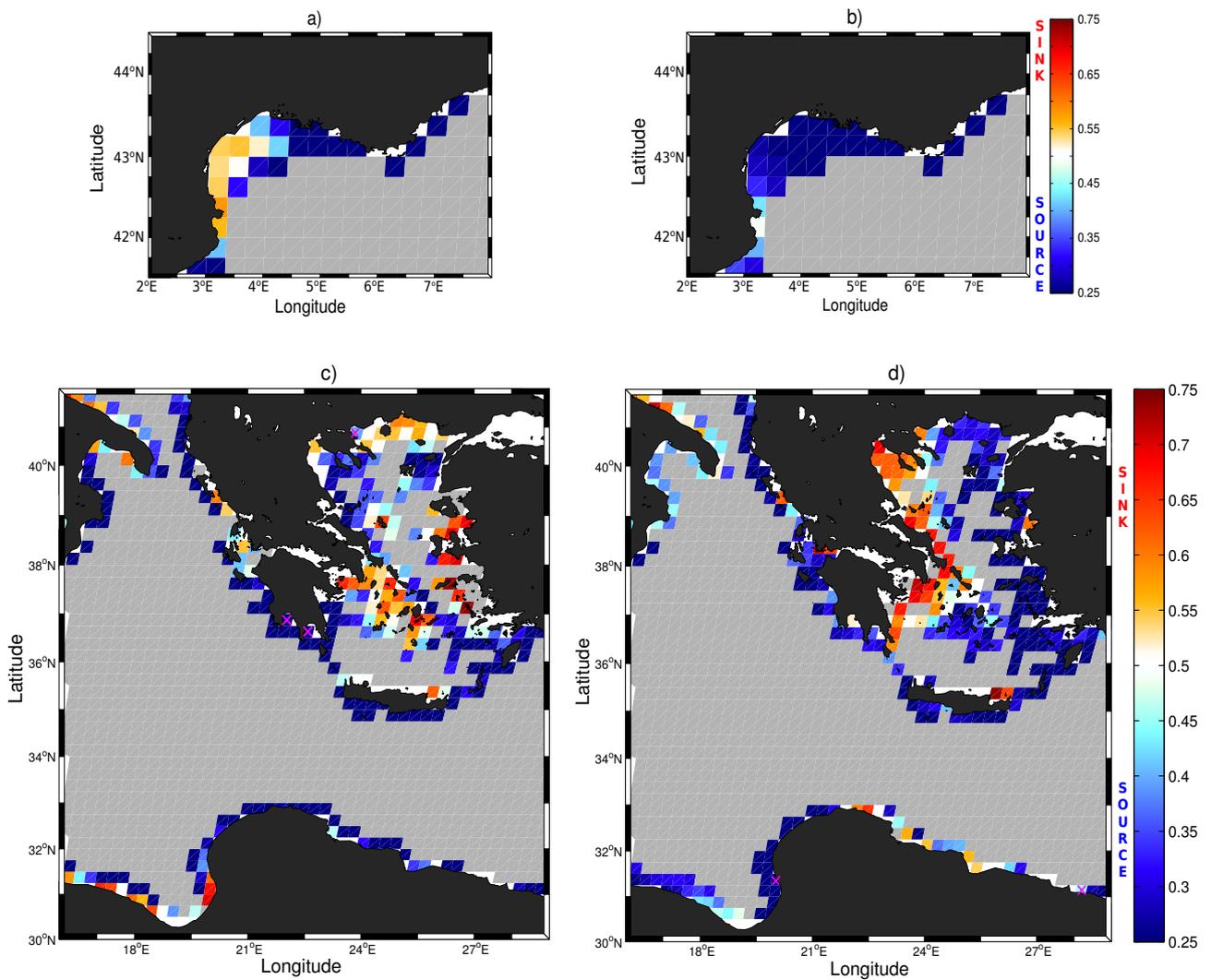


Figure SI-7: Regional zooms of the mean *Source Sink-degree* averaged over 30 winter (a, c) and 30 summer (b, d) connectivity matrices for a PLD of 60 days. Zooms on the Gulf of Lion (a,b) and Ionian and Aegean (c,d) regions. Grey areas represent the oceanic nodes that were disregarded from these analyses.

Marine species	Taxonomy	Category (adults habitats)	Larval distribu- tion	Estimated PLD (days)	Larval season (following spawning)	References
Blenny <i>Lipophrys trigloides</i>	Vertebrate, Fish	Littoral demersal (benthic)	Inshore	67	Winter	[MacPherson & Raventós 2006]
Blenny <i>Lipophrys canevai</i>	Vertebrate, Fish	Littoral demersal (benthic)	Offshore	30	Summer	[MacPherson & Raventós 2006]
Rainbow Wrasse <i>Coris julis</i>	Vertebrate, Fish	Littoral demersal (benthopelagic)	Offshore	21-34	Summer	[MacPherson & Raventós 2006; Torres <i>et al.</i> 2011]
Green Wrasse <i>Labrus viridis</i>	Vertebrate, Fish	Littoral demersal (benthopelagic)	Inshore	31-34	Spring/ Summer	[Bauchot & Quignard 1979; Raventós & MacPherson 2001; MacPherson & Raventós 2006]
Goat Fish <i>Mullus surmuletus</i>	Vertebrate, Fish	Littoral demersal (benthopelagic)	Offshore	30	Spring/ Summer	[MacPherson & Raventós 2006]
Dusky Groper <i>Epinephelus marginatus</i>	Vertebrate, Fish	Littoral demersal (benthopelagic)	Offshore	25-30	Summer	[MacPherson & Raventós 2006; Andrello <i>et al.</i> 2013]
Salema Porgy <i>Sarpa salpa</i>	Vertebrate, Fish	Littoral demersal (benthopelagic)	Offshore	32	Winter	[MacPherson & Raventós 2006]
Shore Rockling <i>Gaidropsarus mediterraneus</i>	Vertebrate, Fish	Littoral demersal (benthic)	Offshore	43	Winter	[MacPherson & Raventós 2006]
Two-banded Seabream <i>Diplodus vulgaris</i>	Vertebrate, Fish	Littoral/Shelf demersal (benthopelagic)	Offshore	29-58	Winter	[MacPherson & Raventós 2006]
White Seabream <i>Diplodus sargus</i>	Vertebrate, Fish	Littoral demersal (benthopelagic)	Inshore	28	Winter	[Bauchot & Hureau 1990; MacPherson & Raventós 2006]
Gilthead Seabream <i>Sparus aurata</i>	Vertebrate, Fish	Littoral/Shelf demersal (benthopelagic)	Offshore	40-50	Winter	[Bauchot & Hureau 1990]
Bullet Tuna <i>Auzis rochei</i>	Vertebrate, Fish	Shelf pelagic (epipelagic)	Offshore	16	Spring/ Summer	[Houde & Zastrow 1993; Reglero <i>et al.</i> 2012]
Sandsmelt Fish <i>Atherina spp.</i>	Vertebrate, Fish	Littoral pelagic (epipelagic)	Inshore	9-15	Spring/ Summer	[MacPherson & Raventós 2006; Torres <i>et al.</i> 2011]
Dolphin Fish <i>Coryphaena hippurus</i>	Vertebrate, Fish	Shelf pelagic (epipelagic)	Offshore	?	Spring/ Summer	[Dulčić 1999]
European Anchovy <i>Engraulis encrasicolus</i>	Vertebrate, Fish	Oceanic pelagic (epipelagic)	Offshore	37	Summer	[Houde & Zastrow 1993]
Bluefin Tuna <i>Thunnus thunnus</i>	Vertebrate, Fish	Oceanic pelagic (epipelagic)	Offshore	30	Summer	[Rooper <i>et al.</i> 2007]
Ray Breem <i>Brama brama</i>	Vertebrate, Fish	Oceanic pelagic (epipelagic)	Offshore	?	Summer	[Dulčić 1999]
Gilt Sardine <i>Sardinella aurita</i>	Vertebrate, Fish	Oceanic pelagic (epipelagic)	Offshore	60	Summer	[Ramirez <i>et al.</i> 2001; Sabatés <i>et al.</i> 2003; Torres <i>et al.</i> 2011]
European Hake <i>Merluccius merluccius</i>	Vertebrate, Fish	Shelf/Oceanic demersal (benthopelagic)	Offshore	40-60	Summer/ Autumn	[Morales-Nin & Moranta 2004]
Horse Mackerel <i>Trachurus mediterraneus</i>	Vertebrate, Fish	Shelf/Oceanic pelagic (epipelagic)	Offshore	?	Summer	[Smith-Vaniz 1986]
European Seabass <i>Dicentrarchus labrax</i>	Vertebrate, Fish	Littoral/Shelf demersal (benthopelagic)	Offshore	40	Winter	[Smith 1990]
Sea Star <i>Astropecten aranciacus</i>	Invertebrate, Echinoderms	Littoral demersal (benthic)	Inshore	60	Spring/ Summer	[Zulliger <i>et al.</i> 2009]
Marbled Crab <i>Pachygraptus marmoratus</i>	Invertebrate, Crustaceans	Littoral/Shelf demersal (benthic)	Inshore	30	Spring/ Summer	[Fratini <i>et al.</i> 2013]
Other crustaceans (e.g. Lobster)	Invertebrate, Crustaceans	Littoral/Shelf demersal (benthic)	Variable	~30-300	Variable	[Queiroga <i>et al.</i> 2007; Shanks 2009]
Other molluscs (e.g. Oys- ter)	Invertebrate, Molluscs	Littoral demersal (benthic)	Variable	~10-100	Variable	[Shanks 2009; Kough <i>et al.</i> 2013]

Table SI-1: Literature review of biological traits for some emblematic Mediterranean marine species with wide geographical range and potential for large-scale dispersal. With our parameter values and under our assumptions, the broad-scale connectivity patterns evidenced in this paper are applicable for those organisms that belong to different trophic levels of the Mediterranean food webs. Note that the vertical positioning of eggs/larvae may vary but for simplicity, they are assumed here to remain in the $\sim 50 - 150$ m thick Mixed Layer Depth, thus seeing relatively similar transport patterns (see also Discussion sect. 4.4). While we take here an "ecosystem approach" to study connectivity, following what has been recommended for the management of marine resources [e.g. Pikitch *et al.* 2004; Coll *et al.* 2013; Guidetti *et al.* 2013], one could obtain refined predictions by tuning our modelling framework to any target specie with well-known biological traits and to any oceanic area. Category: Littoral $\sim 0 - 50$ m; Shelf $\sim 50 - 200$ m; Oceanic ≥ 200 m. Larval distribution: Inshore $\sim 0 - 50$ m; Offshore ≥ 50 m (shelf and oceanic waters).

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