

Lagrangian Flow Networks: a new framework to study the multi-scale connectivity and the structural complexity of marine populations

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Abstract:

Assessing the spatial structure and dynamics of marine populations, especially considering the various and interlocked scales typical of oceanic systems, is still a major challenge in Ecology. We present a novel framework based on the construction and analysis of *Lagrangian Flow Network* (LFNs) which results in a systematic characterization of dispersal and connectivity of early life history stages of marine organisms. The network is constructed by subdividing the basin into an ensemble of sub-regions which are interconnected through the transport of propagules by ocean currents. The analysis of such networks allows the identification of hydrodynamical provinces and the computation of connectivity proxies measuring retention and exchange of larvae at multiple scales. Due to our spatial discretization and subsequent network representation, as well as our Lagrangian approach, further methodological improvements are handily accessible. It permits a better characterization of population connectivity and allows improving the management and protection of marine ecosystems.

1. Introduction

Marine populations are structured as a large "metapopulation" in which discrete "subpopulations" are linked to each other via the exchanges of individuals (Figure 1), occurring essentially during the embryo phase (eggs and larvae) for most marine organisms [Cowen and Sponaugle, 2009]. This population connectivity (i.e. exchange of individuals among subpopulations) is difficult to observe and quantify [Calò et al., 2013; Di Franco and Guidetti, *this issue*]. Nevertheless, it can be inferred from different approaches as it influences other biological processes. In particular, it is related to the concepts of genetic connectivity (defined as the degree to which gene flows affect evolutionary processes within subpopulations) and of demographic connectivity (which takes into account the impact of dispersal processes on the growth and mortality rates of a subpopulation). Indeed, 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 interests [e.g. Mitarai et al. 2009; Kool et al., 2011; Guizien et al. 2012; Trembl et al. 2012; Andrello et al. 2013; Wood et al. 2014; Rossi et al. 2014; Fach et al., *this issue*].

The contrasting connectivity occurring in the real ocean has been simplified by distinguishing, according to the specific migration rates, open subpopulations that receive/export individuals from/to other subpopulations and closed subpopulations that do not exchange individuals to an appreciable extent (Figure 1) [e.g. Hixon et al., 2002; Pinsky et al., 2012]. This implies that open subpopulations are primarily maintained through network persistence while closed subpopulations survive through self-persistence. Another distinction 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, so that a source

population is characterized by a net export of individuals greater than the net import; the reverse is a sink [Cowen & Sponaugle 2009]. Characterizing the connectivity of marine subpopulations led to the definition of various local connectivity metrics related to larval transport: Self-Recruitment (SR) measures the proportion of all local larval recruits that originated from the source population [e.g. Planes et al. 2009]; Local Retention (LR) is defined as the proportion of local larval production retained on a site [Hogan et al., 2012; Burgess et al., 2014].

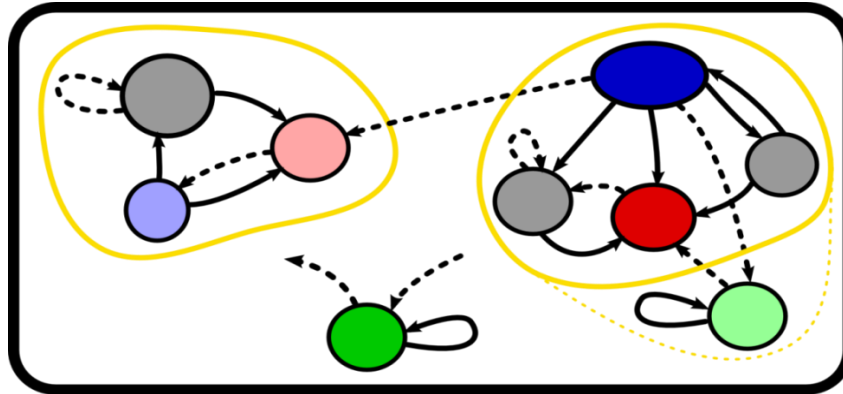


Figure 1: Schematic meta-population (black rectangle) composed of several sub-populations (black-outlined ellipses) with different connectivity behaviors (intensity is proportional to the darkness of the coloring). Green ellipses represent relatively “closed” subpopulations while the rests are “open” subpopulations. The latter group is further distinguished: blue ellipses illustrate “source” subpopulations while “sink” ones are red. Yellow contours identify “communities” within the meta-population system. Black arrows symbolize exchange of individuals, here assumed to be mainly due to larval transport (dotted arrows exemplify smaller larval fluxes than plain ones).

Understanding the connectivity of these complex subpopulations has crucial ecological and managerial implications [Dubois et al. 2016]. The need to manage marine resources from a large-scale perspective and considering the whole ecosystem is now accepted. The adequacy of such strategies requires a global view encompassing the large dimensions of oceanic systems and a characterization of connectivity processes relevant for organisms with contrasting life histories within a given ecosystem (instead of mono-specific focus). However, the absence of appropriate tools to face these challenges limits the implementation of globally pertinent conservation plans.

We present here a new modelling framework to characterize larval dispersal and connectivity in the marine realm. After briefly presenting the LFN methodology (section 2), we highlighted three case-studies focused on different scales and we examined the effects of larval dispersal for population ecology and genetics (section 3). Then, we reported the robustness of selected results (section 4). We finally discussed the implications of previously analyzed connectivity processes for the conservation and management of marine populations and ecosystems (section 5).

2. Materials and Methods

We study larval dispersion based on a *Lagrangian Flow Network* (LFN) [Rossi et al. 2014; Ser-Giacomi et al. 2015] that is composed of an ensemble of nodes interconnected by directed and weighted links. Each node corresponds to a geographical subarea of the oceanic surface and can be seen as a discrete habitat patch. Each link symbolizes an effective mass transport driven by ocean currents between two subareas during a given time interval, representing larval transport pathways. This framework is ideal to study the structure of marine populations which are commonly organized as heterogeneously distributed subpopulations whose respective persistence depends on self-replenishment and asymmetric exchanges of individuals among discrete habitat patches [Kool et al. 2013]. Assuming this connectivity is mainly mediated by larval transport, each node represents a discrete habitat supporting the long-term survival of a local subpopulation through larval retention and exchanges with its neighbors.

To characterize the transport of free-swimming larvae, the Lagrangian approach is appropriate [Siegel et al. 2008; Corell et al., 2012; Paris et al. 2013]. Lagrangian particles (simulating passively drifting larvae) are dispersed using any eddy-resolving velocity field produced by well-validated hydrodynamical models. Trajectories are computed through the offline integration of the velocity field, bilinearly interpolated at any sea point, using a Runge-Kutta 4 algorithm [Ser-Giacomi et al. 2015]. The exemplary outputs presented here used the daily horizontal flow field generated by the Copernicus (ex-MyOcean) operational model implemented in the Mediterranean at 1/16° horizontal resolution over the last 30 years [Oddo et al., 2009]. Dispersal at various depths can be examined by selecting adequately the corresponding vertical layer of the model. As in [e.g. Corell et al. 2012; Andrello et al. 2013], Lagrangian particles are dispersed as two-dimensional passive drifters. The implementations of both complex larval behavior (e.g. vertical migration, mortality, and settlement, e.g. [Lett et al. 2008; Mariani, *this issue*]) and 3-dimensional trajectories (e.g. [Kool et al. 2015]) are envisaged for future work.

The LFN tool has 4 modules (Figure 2): 1) builds the network grid and initialize evenly the particles field; 2) computes Lagrangian trajectories and stores final positions; 3) calculates the full connectivity matrix (i.e. adjacency matrix of the LFN); 4) consists in various and complementary post-processing of the matrices to examine connectivity. Besides the oceanic domain of interests, the selected depth for deploying the particles and the corresponding velocity field, the main parameters required by the software are the size of the nodes (ocean boxes), the spawning time(s) at which particles are released, and the duration of tracking, simulating the Pelagic Larval Duration (PLD), that is the amount of time larvae drift with ocean currents.

The model is tunable to any species whose biological traits are known. For instance, we study the subsurface dispersal of hake's larvae simulating successive spawning events during autumn with a PLD of 40 days and with the currents at about 100 m. On the other hand, it can also be used in a generic configuration for an ecosystem approach to connectivity using ecologically-relevant values of parameters [Dubois et al. 2016].

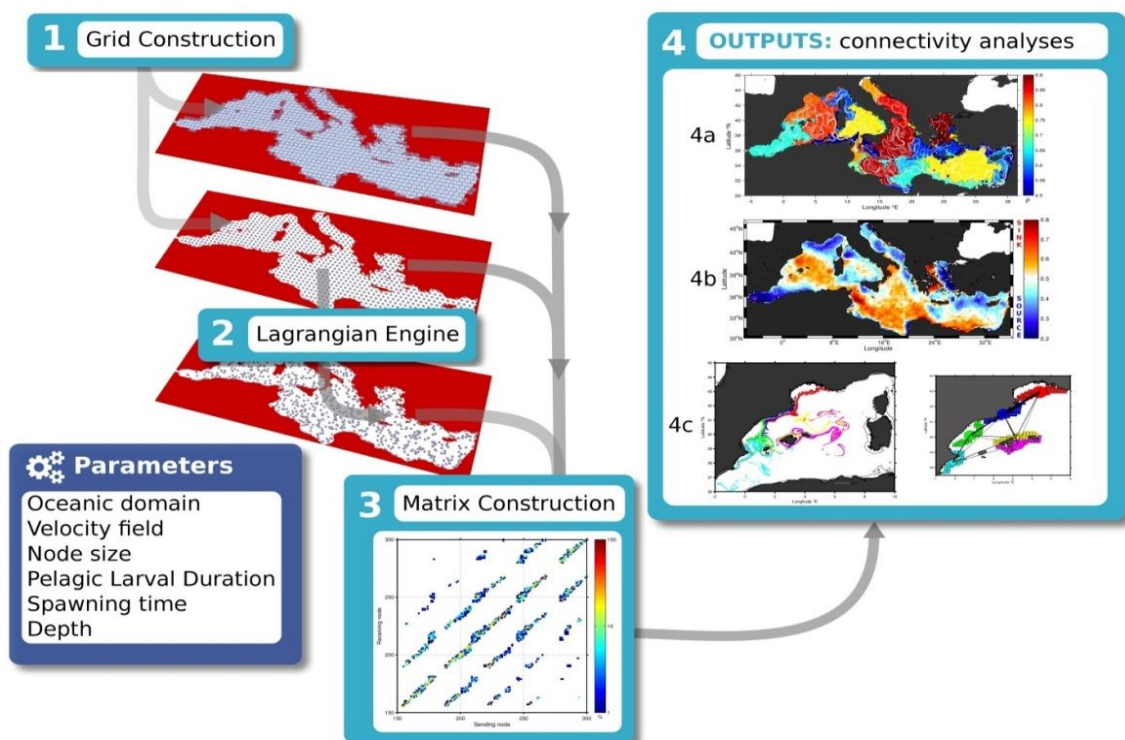


Figure 2: Simplified diagram of the *Lagrangian Flow Networks* set-up with 4 modules (light blue boxes). Key parameters (dark blue box) are the domain of interest, the velocity field (from any ocean model), the node size, the starting dates (spawning events), the vertical layer of the model (depth of dispersion) and the tracking time (Pelagic Larval Duration).

Network Theory tools permit the examination of both local and global properties of such network [Newman, 2010; Ser-Giacomi et al. 2015; Shtilerman and Stone, 2015]. The *Infomap* algorithm is applied to the connectivity matrix to detect communities in the LFN. It allows subdividing the oceanic surface in hydrodynamical provinces (Figure 3), which are well connected internally but with minimal exchanges of larvae between them [Rossi et al. 2014]. Focusing on local (node-scale) features and inspired from concepts of Population Dynamics, we also describe larval transport and exchange by computing indices of retention and source-sink proxies (Figure 4) at basin-scale [Dubois et al. 2016]. The connectivity matrix is manipulated to examine, for each node, the number and fluxes of all links emanating from it and entering it. Through a combination of these basic variables, and by assuming that local larval release, larval mortality and success of recruitment are homogeneous, Dubois et al. [2016] computed four complementary connectivity metrics. Local Retention (LR) is the ratio of locally produced settlement to local larval release [Botsford et al. 2009], i.e. the proportion of locally retained particles. Self-Recruitment (SR) is the ratio of locally produced settlement to the overall settlement [Botsford et al. 2009], i.e. the ratio of retained particles in each box to the total incoming particles from all origins (including those produced locally). Following [Bode et al. 2006], we also examine the relative importance of larval export versus import to characterize the local Source/Sink (SS) dynamics. Two local metrics evaluate the source/sink character in terms of the total number of larvae (SS-strength, SSs) or in terms of the diversity of origins and destinations (SS-degree, SSd). They are restricted to values between 0 and 1 and their negative (positive) deviations from 0.5 allow the quick appraisal of sources (sinks).

3. Case-studies: studying connectivity using Lagrangian Flow Network tools

a. Large-scale connectivity and its implications for population genetics

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

The LFN framework presents many advantages to help resolving these shortcomings. First, it allows delimiting the seascape in different hydrodynamical provinces (Figure 3) in which larvae disperse efficiently, while little exchange occurs with neighboring provinces [Rossi et al. 2014]. Those provinces can be extracted by different manners, depending essentially on which connectivity matrices are used to detect communities and on how is treated the temporal variability. On one hand, several snapshots matrices can be averaged “element-by-element” and then the community detection algorithm *Infomap* is applied to this averaged matrix, returning the mean hydrodynamical provinces for a given PLD (Fig. 3a, b). Following the same process, one can artificially remove from the matrices all elements representing the open-ocean nodes to obtain the mean provinces considering only coastal and shelf regions (Fig. 3c). On the other hand, it is also possible to apply the community detection method on several snapshot matrices, and then to map the mean frequency of boundaries apparition (Fig. 3d).

Future work using these synthetic provinces explores their potential roles in controlling large-scale gene flows [Arnaud-Haond, *this issue*; Villamor et al. *this issue*]. In collaboration with molecular ecologists, we are investigating if the dispersal regionalization is consistent with patterns of genetic differentiations in the Mediterranean Sea. Another perspective concerns the estimation of multi-generational connectivity among sites to be compared to a compilation of pair-wise genetic distances in an improved “isolation-by-distance” analysis.

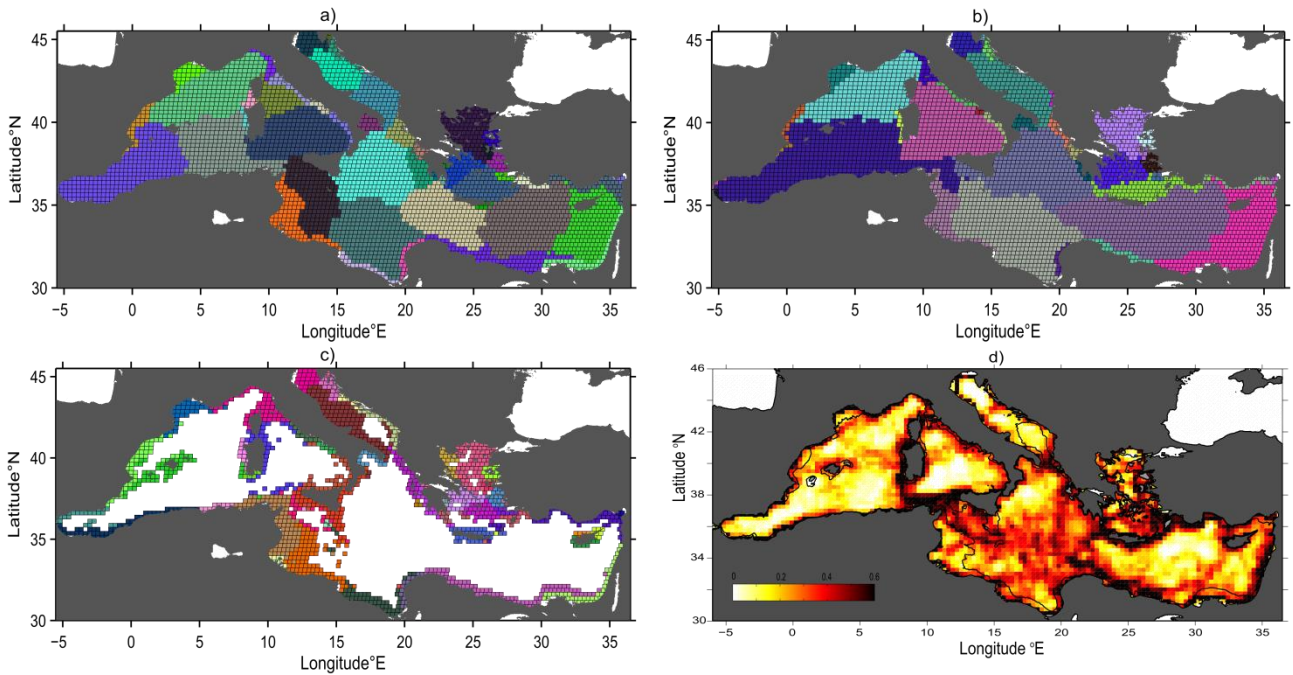


Figure 3: Hydrodynamical provinces in the Mediterranean. Annual mean provinces (across the ensemble of 20 experiments, covering all winters/summers over 2002-2011) for a) a PLD of 30 days and b) 60 days using the full matrix; c) a PLD of 60 days but considering only the shelf-nodes; d) frequency of occurrence of province boundaries at each node for a PLD = 60 days (black contour represents the 200 m isobaths). Panel (d) adapted from Rossi et al. [2004].

Others outputs of LFN analysis that are useful for geneticists are the mapping of our proxies of larval retention and exchange (Figure 4). Through the direct incorporation of population genetic concepts into a basin-scale biophysical model we propose a common platform for geneticists and oceanographers to explore connectivity issues [Dubois et al. 2016].

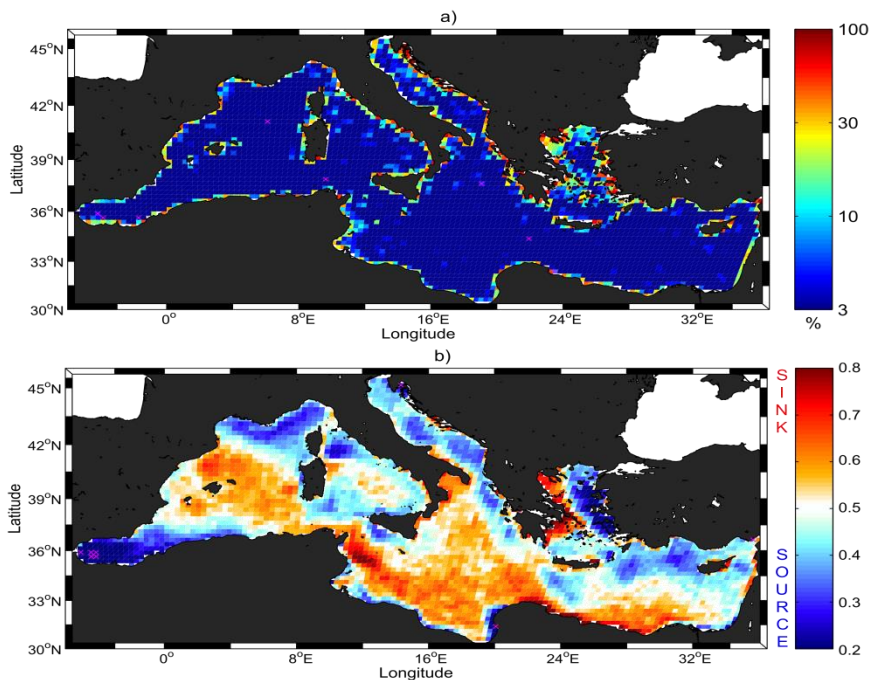


Figure 4: a) Mean Local-Retention (LR) for a PLD of 30 days averaged across 60 (winter and summer) connectivity matrices; b) Mean SS-degree (SSd: relative importance of larval export versus import, measuring the number of links) averaged across 30 summer matrices for a PLD of 60 days. Pink crosses in some boxes indicate particularly large temporal variability. Panels adapted from Dubois et al. [2016].

Our basin-scale model predicts that retention processes are weak in the open ocean while they are significant in the coastal ocean and are favored along certain coastlines due to specific oceanographic features (Fig. 4a). Moreover, we show that wind-driven divergent (convergent, respectively) oceanic regions are systematically characterized by larval sources (sinks, respectively) (Fig. 4b). Our results, and more generally the tunable modelling framework proposed here, should allow (1) formal testing of the effects of specific oceanographic processes on population genetics by

integrating the most relevant biological traits for a group of species [e.g. Pascual and Macpherson, *this issue*], and (2) targeting of sub-regions with dissimilar connectivity behaviors as predicted here, whose effects on connectivity in relation to species distribution and life-history traits could be evaluated.

b. Inter-annual regional-scale connectivity within the metapopulation of an harvested species

In this case study, we adapted the LFN methodology to the European hake *Merluccius merluccius*. It is a demersal fish largely distributed across continental shelves of the Mediterranean with important landings in all countries. Its spawning occurs during autumn, its PLD is about 40 days and its larvae are supposedly drifting at the subsurface. We aim at addressing the following questions: how inter-connected are Balearic and mainland sub-populations? What are the consequences of connectivity processes for the management of hake's stocks?

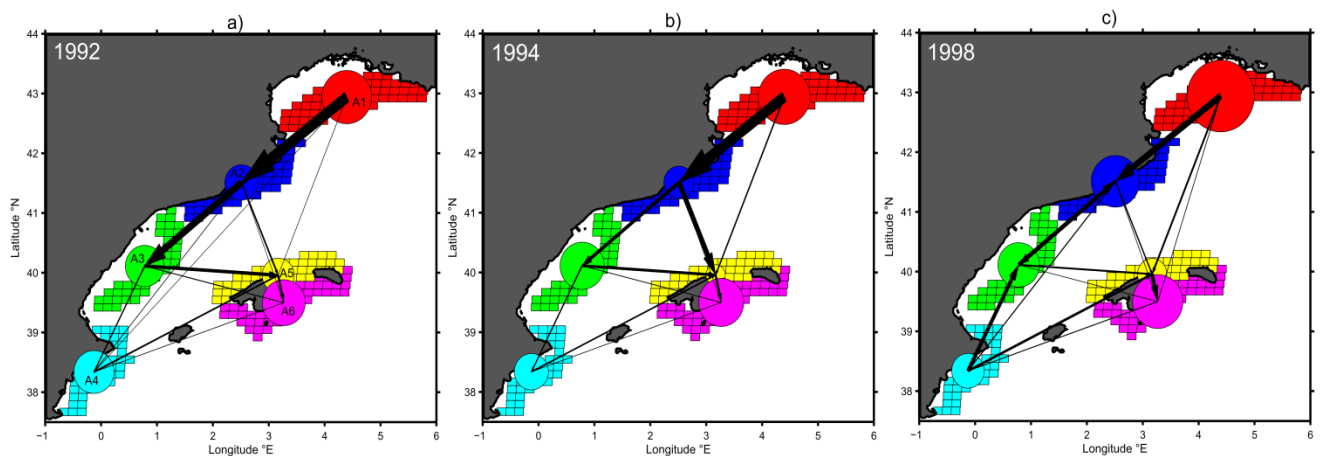


Figure 5: Normalized estimates of larval exchanges (arrows) and retention (circles) among the different sub-population of hake averaged over 7 successive spawning events in a) 1992, b) 1994 and c) 1998. Widths of arrows (diameters of circles) are proportional to the strength of connection (larval retention, respectively). Different sub-areas (representative of Hake's subpopulations) are: A1, Gulf of Lion (red); A2, Catalan coast (dark blue); A3, Ebro delta (green); A4, Ibiza channel (light blue); A5, north Balearic Islands (yellow); A6, south Balearic Islands (magenta).

The LFN model provided the inter-annual variability of connectivity proxies (i.e. larval retention and exchanges) among six different areas of the Western Mediterranean Sea: Gulf of Lions, Catalan coast, Ebro delta, Ibiza channel, northern and southern Balearic Islands (Figure 5). We also use time-series of hake recruitment over 1980-2014 from assessment groups to assess the potential influence of connectivity in the population dynamics of hake, in combination with additional hydro-climatic drivers such as the IDEA index [Monserrat et al. 2008]. Our study provides evidence of directional connectivity following the main pathways of the most prominent currents flowing through the study area. However, important inter-annual variability of connectivity is observed both for the retention and exchange of larvae (Fig. 5, 8). Overall, the Gulf of Lion is a main source contributing to the Spanish mainland coast, while the Balearic Sea appears as a sink receiving particles from several areas of the mainland [Hidalgo et al. 2016]. This suggests a potential complex metapopulation system with three main components: a source (Gulf of Lion), a sink (Balearic Islands) and a transition area (Spanish mainland coastlines).

The inter-annual variability of the connectivity processes and the temporal evolution of the IDEA index explain together the inter-annual variability of recruitment estimated in the assessment groups and those observed by the scientific trawl surveys. Both connectivity processes and the IDEA index influenced the hake density at the main nursery areas in the north of the Balearic archipelago: maxima of recruits are observed when connectivity is high and the IDEA favored the survival of larvae. In contrast, the nursery area in the south seems more stable through time and is more dependent on SR. Overall, both the degree of connectivity that takes place from the end of

autumn to early winter, and the IDEA index that represents the hydro-climatic scenario affecting the survival of early life stages and pre-recruits from the end of winter to spring, shape together the spatial pattern of hake recruits in spring [Hidalgo et al. 2009; 2016].

c. Local-scale connectivity and its implications on demographic connectivity of an emblematic species

For sessile species such as *Pinna nobilis*, the exchanges of individuals among subpopulations occur only during the larval phase [Lorena-basso et al. 2015]. Understanding the mean patterns and magnitude of connectivity processes, and its temporal variability, for the sub-populations of *Pinna nobilis* heterogeneously distributed across the Balearic seascape have ecological and managerial implications [Dubois et al. 2016].

The LFN framework will be tuned according to the most relevant biological traits of *Pinna nobilis* and will be focused on the western Mediterranean with the use of a velocity field for the Balearic Sea with the highest-resolution possible to take into account small-scale processes. The node size would be $1/8^\circ$ or smaller (to be chosen in accord with the resolution of the circulation model). Successive starting dates in May/June each year will simulate episodic and variable spawning events of *Pinna nobilis* and larvae will drift at the surface during 15 days, i.e. the PLD of *Pinna nobilis* [Lorena-basso et al. 2015]. Focusing on local features, we will describe larval transport by computing indices of retention and exchanges [Dubois et al. 2016] at the smallest scales reachable by the simulated velocity field. Proxies of larval connectivity (SR, LR and SS) and their variability will be computed among a-priori known subpopulations, such as the ones identified around the Balearic Archipelago for *Pinna nobilis* [Vazquez-Luis et al. 2014]. In addition, more sophisticated diagnostics are handily accessible through the post-processing of the full connectivity matrices. It could consist in selecting and/or weighting a subset of nodes depending on the presence of favorable habitats, on the density of mature adults or on the age structure of the local population [Vazquez-Luis et al. 2014, Deudero et al. 2015].

4. Sensitivity and robustness

a. Numerical parameters:

The most relevant numerical parameters influencing connectivity metrics derived from the LFNs are the node size and the initial density of particles (Figure 6). They should be determined according to the spatio-temporal scales of interests and the effective resolution of the ocean model. When changing the resolution of the nodes (Fig. 6a) and the quantity of initial particles (Fig. 6b), both spatial patterns and magnitudes of connectivity proxies are consistent over the entire basin. It confirms the robustness of the LFN tool with respect to changes in these quantities. We refer to [Putman and He, 2013] and [Simons et al. 2013] to read more about the sensitivity of connectivity estimates to the resolution of modelled currents and to tracking parameters, respectively.

a. Bio-physical parameters:

Key bio-physical parameters are the spawning time (unique or successive spawning events can be considered, e.g. [Kough and Paris, 2015]), the Pelagic Larval Duration (PLD) and the mean depth of dispersion. The sensitivity of our analyses to these parameters depends on many factors, including which proxies are examined. By performing experiments varying one of the parameters alone, we provide below illustrative examples of the potential impacts on specific outputs.

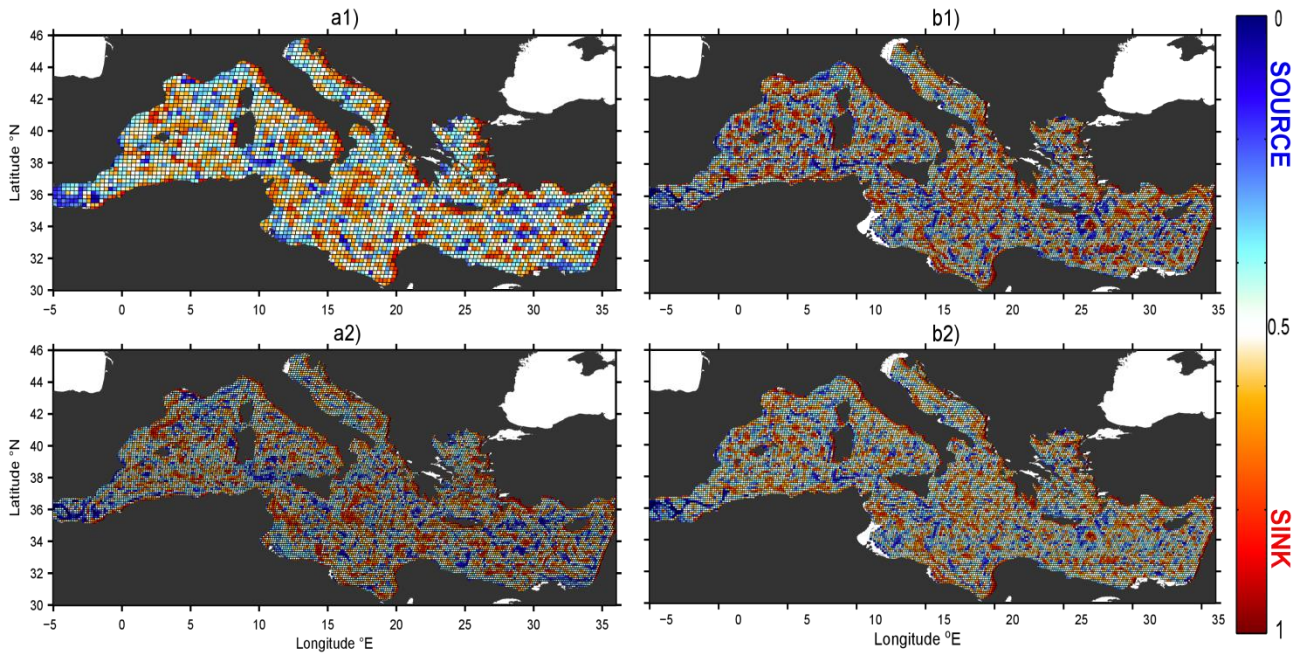


Figure 6: Sensitivity studies for the “physical” parameters. Snapshot maps of the SourceSink-degree (SSd) generated with the same parameters but: a) for network grids of (a1) medium $1/4^\circ$ and (a2) high $1/8^\circ$ resolution; b) for different particles initial density (b1) 1000 particles per node and (b2) 100 particles per node (of $1/8^\circ$).

The influence of the PLD on larval transport is quite intuitive: long PLD favors larger dispersion characterized by stronger larval fluxes and more dispersive pathways. Considering for instance the release of hake’s larvae within the Gulf of Lion (Figure 7), the short PLD experiment shows retention of larvae within the Gulf and moderate larval transport through the Northern (Catalan) current (flowing southwestward along the continental margin) until it retroflects toward the Balearic archipelago (Fig. 7a). The long PLD experiment reveals lower retention of particles in the Gulf and stronger southward export as well as a more intense eastward retroflexion (Fig. b7). Note however that the main patterns (yellow-to-reddish colors) remain essentially unchanged.

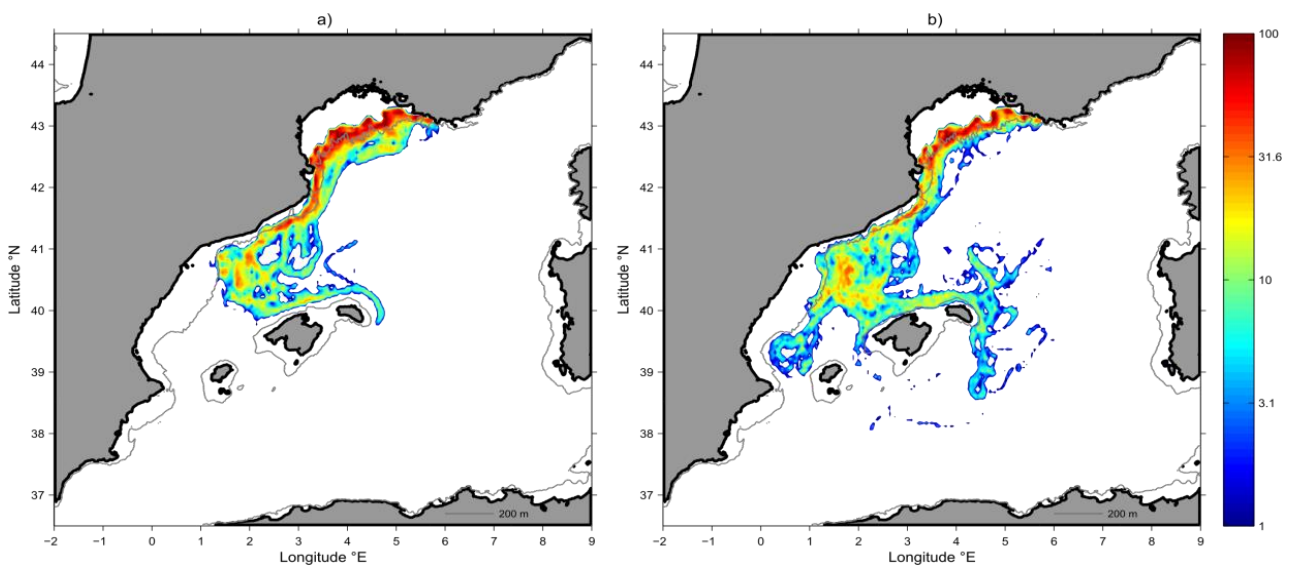


Figure 7: Probabilities Density Functions of particles released in autumn 2001 (summed up over 7 spawning events) from the Gulf of Lion and tracked during a PLD of a) 30 days and b) 50 days.

When computing synthetic and spatially averaged connectivity indices such as LR and Import (total number of particles imported from other subpopulations) for the hake case-study, the PLD duration affects the mean estimates: long PLD diminishes LR and increases the amount of imported larvae. Note however it only marginally impacts the inter-annual variability of these quantities as both time-series show similar temporal evolution (Figure 8).

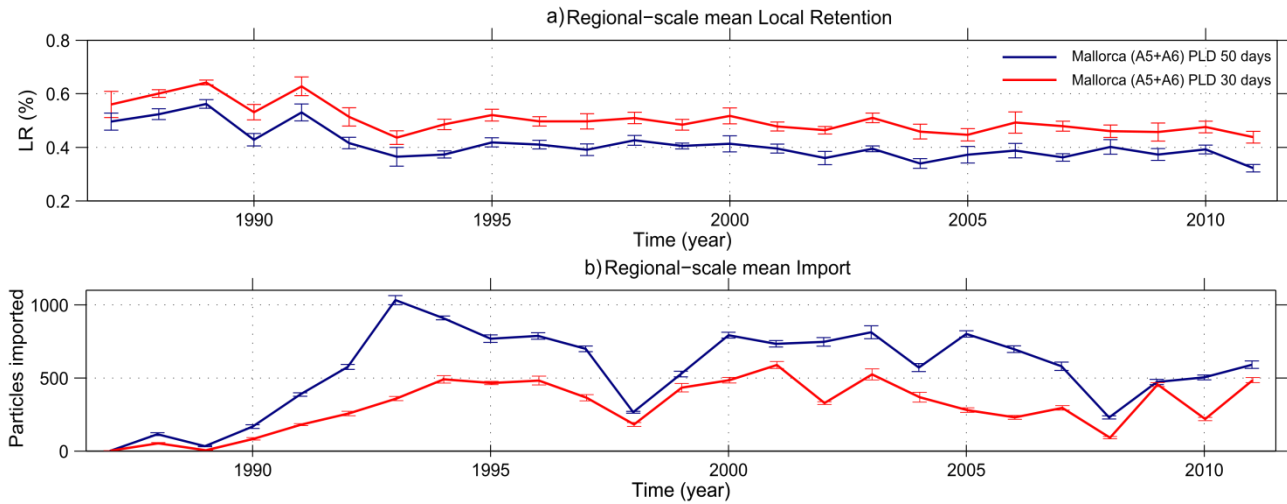


Figure 8: 27 year-long time-series of regional connectivity indices for the hake case-study. Panel a) is spatially averaged LR for larvae released in the Balearic archipelago. Panel b) is the total number of particles reaching the Balearic archipelago after their released from the Gulf of Lion and the Catalan continental shelves. Red lines represent a PLD of 30 days while blue lines are for 50 days. Error bars indicate the variability among several spawning events.

The vertical structure of ocean currents (ranging from homogeneous barotropic flow to strongly baroclinic currents) and its spatio-temporal variability determine how the drifting depth would impact dispersal patterns. In hydrodynamical models, the structure depends on the vertical resolution and the parametrization used to resolve vertical mixing and mixed boundary layers. The final positions of particles released concomitantly (in early winter) but tracked at different depths in [Oddo et al. 2009]’s model reveal quite identical spatial patterns (Figure 9). It suggests that those simulated currents have relatively similar profiles in the top 100 m, representing a “well mixed layer” in which most surface larvae could be assumed to be homogeneously distributed. Note however that some benthic organisms have deep-drifting larvae [e.g. Hilario, *this issue*] so that their dispersal is expected to be very different than those drifting at or close to the surface.

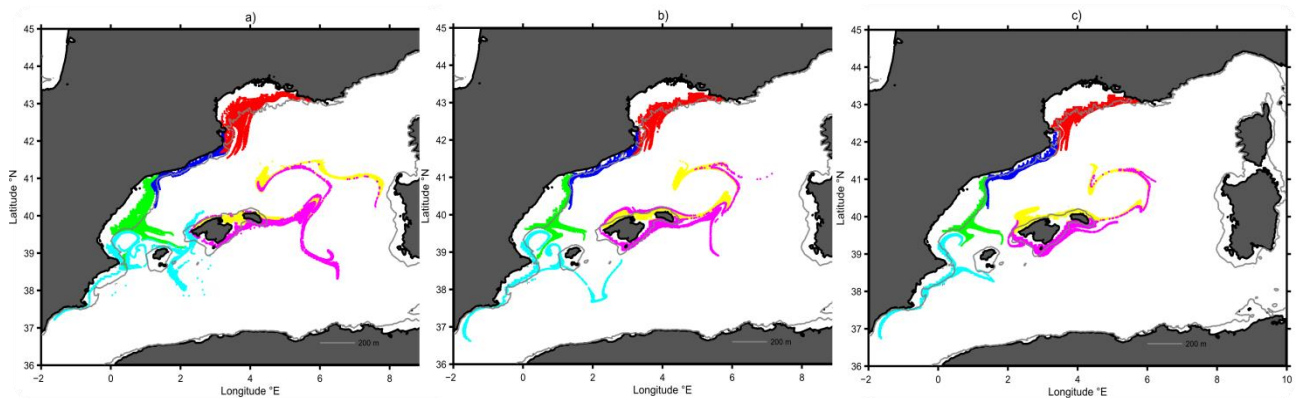


Figure 9: Final positions of particles released from distinct sub-populations of hake (according to the color code) and tracked during a PLD of 30 days at different depths: a) 60 m, b) 90 m and c) 120 m.

5. Implications for the management and the protection of marine ecosystems

Marine ecosystems are impacted by multiple human-induced stressors, including habitat destruction, pollution, overfishing and climate change. The main strategies implemented to counteract these negative factors, to maintain biodiversity and to ensure the persistence of marine populations consist (i) in creating marine reserves which ban deleterious activities within their perimeters or (ii) in regulating potentially harmful activities such as fishing [Lester et al., 2009]. While Marine Protected Areas (MPAs) are considered effective to mitigate some of these impacts [Edgar et al. 2014], their successful design is still complicated primarily due to the difficulties in quantifying the movements of organisms, especially at larval stage [Shanks et al., 2003], in

resolving the multiscale variability of ocean currents [Siegel et al., 2008] and in apprehending the spatial scales and biogeography of the seascape [Hamilton et al., 2010].

Moreover, the impact of oceanic connectivity on the spatial structuring of marine populations has been largely demonstrated. However, an important question poorly explored from the fisheries assessment perspective is which species and which management units' boundaries are sensitive to the connectivity processes. This question is considerably relevant in the Mediterranean Sea due to the small size of the management units used to assess harvested species.

a. Marine Protected Areas design

The geographical structure of larval dispersal across the seascape influences largely the connectivity of marine reserves [Rossi et al. 2014]. The MPAs located within large and stable hydrodynamical units (Figure 3) are interconnected, in good agreement with Andrello et al. [2013] who identified similar MPA clusters in the Algerian, Balearic, Adriatic, and Tyrrhenian Seas, respectively. Further information is obtained with the mean spatial scales of larval dispersal (by averaging over several experiments the area of the time-dependent province encompassing each MPA) and the mean number of interconnected MPAs (i.e. temporally averaged number of MPAs encountered within the same time-dependent province). Larval connectivity and dispersal potentials are highly variable among the Mediterranean MPAs (Figure 10). Reserves in the Adriatic and Aegean Seas are characterized by small dispersal surface ($\leq 5 \times 10^4$ km²), suggesting a low connectivity also reflected in the few interconnected MPAs (≤ 8) despite their relatively high density. MPAs located around isolated islands are associated with modest dispersal surface (4 to 8×10^4 km²). Typical of these insular environments [Vaz et al., 2013], complex circulation patterns (islands' wake, eddies, retention, etc.) result in a moderate connectivity. MPAs implemented within narrow continental shelves bounded by energetic currents are characterized by rather large provinces ($\geq 7 \times 10^4$ km²). These reserves are situated along the French Côte d'Azur with the Liguro-Provencal Current, the Catalan coast with the Northern Current, the Moroccan/Algerian coastlines impacted by the Algerian Current, and in the eastern Levantine basin with the jet-like intensifications of its gyre circulation [Milot and Taupier-Letage, 2005]. This elevated connectivity is driven by the adjacent currents that regularly intrude onto the shelf, enhancing larval dispersal along the current axis, as suggested by the numerous interconnected MPAs (≥ 15) along the French, Catalan, and Israelian coastlines. In contrast, MPAs located along extended continental shelves, such as the Gulf of Lion, are characterized by rather small dispersal area ($\leq 5 \times 10^4$ km²). Unless exceptional intrusion events, the inner shelf remains isolated by the shallow bathymetry holding the current off the shelf break, and resulting in a limited connectivity (Fig. 10).

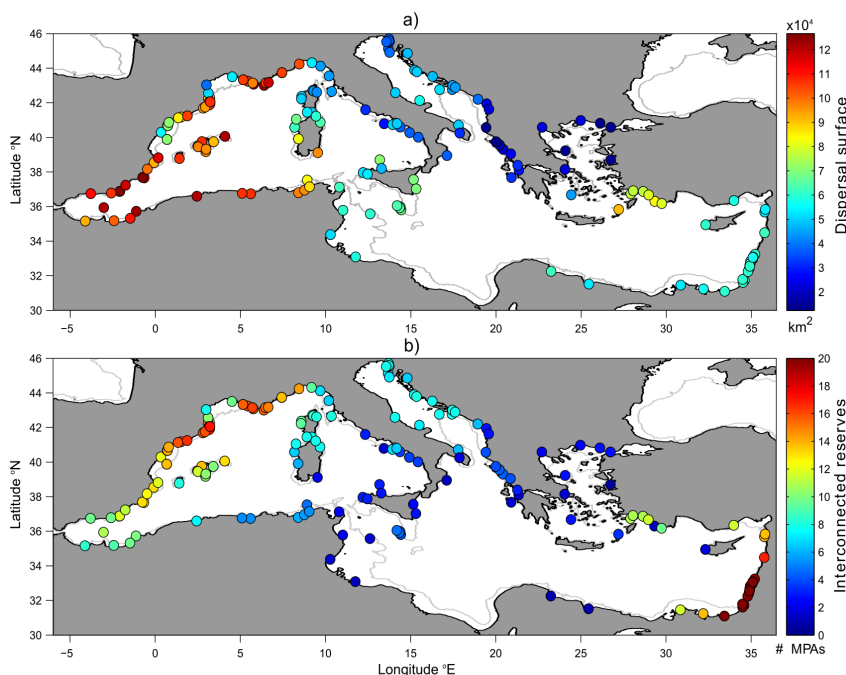


Figure 10: Spatial variability of MPAs connectivity derived from three complementary metrics averaged across all winter/summer experiments over 2002–2011 using a PLD of 30 days. (a) Mean area (in km²) and (b) mean number of interconnected MPAs (i.e. number of reserves situated within the same hydrodynamical province). Light grey contours represent the 200 m isobath. Results for longer PLD are qualitatively similar with a slight increase of the mean area and the number of interconnected reserves. Figures adapted from Rossi et al. [2014].

Despite the stochastic nature of larval dispersal [Siegel et al., 2008], local oceanographic characteristics result in the emergence of connectivity regimes. They should be in accord with the main conservation objectives to ensure successful implementations of coastal and offshore marine reserves. For instance, the allocation of MPAs within narrow shelves bounded by currents would favor larval export over large distances whereas reserves created within internal seas or large continental shelves would rather promote the restoration of local populations. Overall, the Mediterranean MPAs are not evenly distributed across the spatial partitioning of the seascape revealed by our analysis. Moreover, the “size and spacing” guidelines, studied theoretically by Moffitt et al. [2011], may differ depending on the local dispersal behavior. Our results suggest the use of few large MPAs located in each stable hydrodynamical unit of the western Mediterranean basin and of the Adriatic Sea, whereas numerous small MPAs evenly distributed across the fluctuating units of the Ionian and Aegean Seas might be preferable.

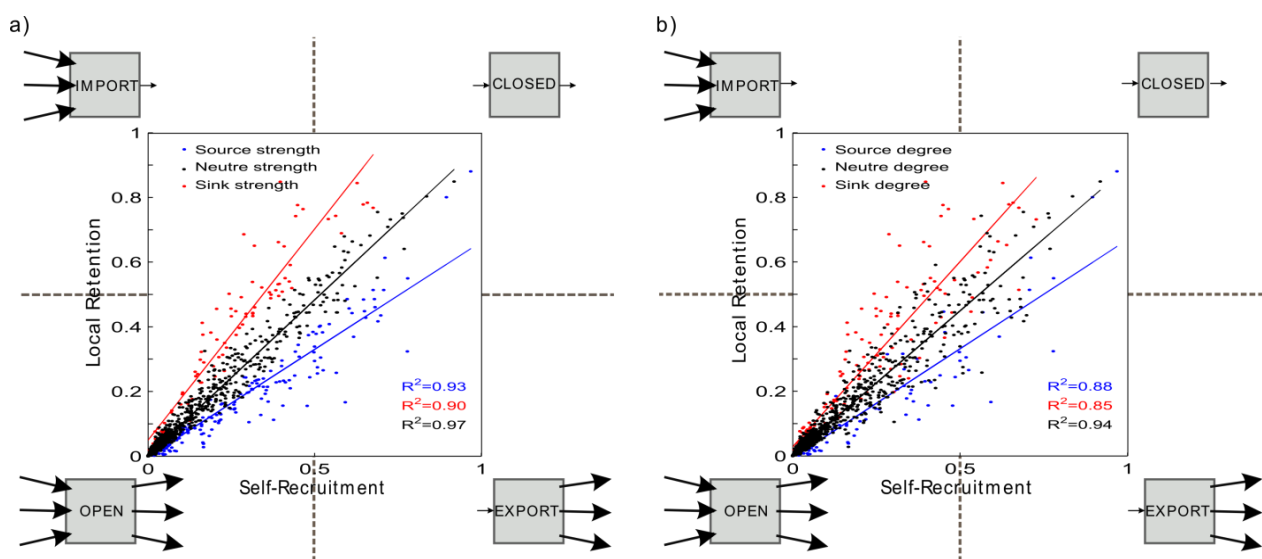


Figure 11: Inter-relationship among connectivity metrics for a PLD of 30 days. Mean relationship between LR and SR distinguishing “source” (blue), “sink” (red) and “neutral” (black) nodes based on (a) Source-Sink index computed from larval fluxes and (b) Source-Sink index computed from the number of links). Annotations represent schematically the behavior of a node according to its location on the plot. Source (sink) nodes are characterized by SS-strength or SS-degree < 0.4 (> 0.6 , respectively). Figures adapted from Dubois et al. [2016].

The integrated interpretation of retention and exchange large-scale connectivity indices (Figure 11) has implications for the implementation of coastal and pelagic Marine Protected Areas (MPAs) [Dubois et al. 2016]. They give insight into how subpopulations are connected through larval transport and as such, help to predict the effects of management measures or disturbances on both local and surrounding subpopulations. For instance, establishing a MPA on a site whose larval supply originates from several non-protected “upstream” subpopulations may be ineffective, especially if retention rates are not sufficient to allow for self-persistence of source sub-populations. Another strategy could be to position new MPAs within regions characterized by both significant retention and exchange of larvae, thus favoring together self- and network persistence (i.e. favoring the persistence of both local and surroundings populations). Overall, an accurate depiction of both local and broad-scale connectivity, as is allowed by our model, is necessary to appropriately implement MPAs. Our connectivity proxies (Fig. 11) provide relevant information for managers and scientists to discuss implementation guidelines “case-by-case”, in accord with conservation objectives [Dubois et al. 2016].

b. Fisheries assessment

Improving the assessment and management of harvested marine populations requires integrative frameworks that combine biological and physical processes taking place at different temporal and spatial scales [e.g. Gucu et al., *this issue*]. Indeed, there is mounting evidence that both the spatial and the demographic structure of marine populations are more complex than currently accounted for by management schemes. In the case of small management areas such as those in the Mediterranean Sea, multiple scales of connectivity and small-scale oceanographic processes may alter significantly the population dynamics assessed at regional scale throughout fluctuating variability of the connectivity processes [Snyder and Paris, 2014]. Our on-going study suggests that the understanding of hake sub-population dynamics in the Balearic Islands requires the integration of both oceanographic conditions and biological information from the mainland coast of the Western Mediterranean. We outline how large-scale fishery management could explicitly recognize metapopulation structure by considering larval transport dynamics [Kough et al. 2014].

6. Conclusions

The LFN framework allows studying the structure of marine populations through the delimitation of hydrodynamical provinces and the computation of complementary connectivity metrics. The LFN methodology also allows studying their spatio-temporal variability and discussing their relationships with both ecological and oceanographic processes. It permits depicting larval retention and exchange at multiple-scales, studying inter-relationships among connectivity metrics, informing the sampling strategy and interpretation of genetic datasets and appraising the implications of connectivity processes in the design of marine reserves and in the management of harvested populations.

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References:

- Andrello, M., Mouillot, D., Beuvier, J., Albouy, C., Thuiller, W., & Manel, S. (2013). Low connectivity between Mediterranean marine protected areas: a biophysical modeling approach for the dusky grouper *Epinephelus marginatus*. *PLoS ONE*, 8(7), e68564.
- Bode, M., Bode, L. & Armsworth, P.R. (2006) Larval dispersal reveals regional sources and sinks in Great Barrier Reef. *Marine Ecology Progress Series*, 308, 17–25.
- Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J.B., Largier, J., O'Farrell, M.R., Ralston, S., Soulanille, E. & Wespestad, V. (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries*, 19, 69–95.
- Burgess, S.C., Nickols, K.J., Griesemer, C.D., Barnett, L.A.K., Dedrick, A.G., Satterthwaite, E.V., Yamane, L., Morgan, S.G., White, J.W. & Botsford, L.W. (2014) Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. *Ecological Applications*, 24, 257–270.
- Calò, A., Félix-Hackradt, F.C., Garcia, J., Hackradt, C.W., Rocklin, D., Treviño Otón, J. & García-Charton, J.A. (2013) A review of methods to assess connectivity and dispersal between fish populations in the Mediterranean Sea. *Advances in Oceanography and Limnology*, 4, 150–175.
- Corell, H., P.-O. Moksnes, A. Engqvist, K. Doos, and P. Jonsson (2012), Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas, *Mar. Ecol. Prog. Ser.*, 467, 29–46.
- Cowen, R.K., and Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1, 443–466.
- Deudero S, Vázquez-Luis M, Álvarez E (2015) Human Stressors Are Driving Coastal Benthic Long-Lived Sessile Fan Mussel *Pinna nobilis* Population Structure More than Environmental Stressors. *PLoS ONE* 10(7): e0134530. doi:10.1371/journal.pone.0134530.
- Dubois, M., Rossi, V., Ser-Giacomi, E., Arnaud-Haond, S., López, C., and Hernandez-García, E. (2016), Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems, *Global Ecology and Biogeography*, *in press*, doi:10.1111/geb.12431.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., et al. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506, 216–220.
- Guizien, K., Belharet, M., Marsaleix, P. & Guarini, J.M. (2012) Using larval dispersal simulations for marine protected area design: application to the Gulf of Lions (northwest Mediterranean). *Limnology and Oceanography*, 57, 1099–1112.
- Hamilton, S., J. Caselle, D. Malone, and M. Carr (2010), Incorporating biogeography into evaluations of the Channel Islands marine reserve network, *Proc. Natl. Acad. Sci. U.S.A.*, 107, 18,272–18,277.
- Hidalgo, M., Tomás, J., Moranta, J., Morales-Nin, B. (2009) Intra-annual recruitment events for European hake off the Balearic Islands (NW Mediterranean) *Estuarine Coastal and Shelf Science* 83, 227–238.
- Hidalgo et al. (2016) Embracing marine connectivity and assessment estimates to manage a complex fish metapopulation. In prep.
- Hixon, M.A., Pacala, S.W. & Sandin, S.A. (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, 83, 1490–1508.
- Hogan, J.D., Thiessen, R.J., Sale, P.F. & Heath, D.D. (2012) Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia*, 168, 61–71.
- Kool, J.T., Paris, C.B., Barber, P.H., & Cowen, R.K. (2011). Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. *Global Ecology and Biogeography*, 20(5), 695–706.
- Kool, J.T., Moilanen, A., Treml, E.A. (2013). Population connectivity: recent advances and new perspectives. *Landscape Ecology*, 28, 165–185.
- Kool, J. T. and S. L. Nichol, (2015), Four-dimensional connectivity modelling with application to Australia's north and northwest marine environments, *Environmental Modelling & Software*, 65, 67–78.
- Kough, A. S. and Paris, C. B., (2015), The influence of spawning periodicity on population connectivity, *Coral Reefs*, 34 (3), 753–757, doi:10.1007/s00338-015-1311-1.
- Kough A. S., C. B. Paris and M. J. Butler (2013). Larval Connectivity and the International Management of Fisheries, *PLoS ONE*. 06/2013; 8(6):e64970. DOI: 10.1371/journal.pone.0064970.
- Lett C, Verley P, Mullon C, Parada C, Brochier T, Penven P, Blanke B (2008). A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling & Software*, 23(9), 1210–1214.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airame, S., & Warner, R.R. (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, 384(2), 33–46.

- Lorena-Basso, L., M. Vázquez-Luis, J. R. García-March, S. Deudero, E. Alvarez, Nardo Vicente, C. M. Duarte, I. E. Hendriks (2015). The Pen Shell, *Pinna nobilis*: A Review of Population Status and Recommended Research Priorities in the Mediterranean Sea, *Advances in Marine Biology*, 71, 109-160.
- Millot, C., and I. Taupier-Letage (2005), Circulation in the Mediterranean Sea, in *The Mediterranean Sea, Handbook of Env. Chem.*, vol. 5K, edited by A. Saliot, pp. 29–66, Springer, Berlin, Heidelberg.
- Mitarai, S., Siegel, D.A., Watson, J.R., Dong, C. & McWilliams, J.C. (2009) Quantifying connectivity in the coastal ocean with application to the Southern California Bight. *Journal of Geophysical Research – Oceans*, 114, C10026.
- Moffitt, E. A., J. W. White, and L. W. Botsford (2011), The utility and limitations of size and spacing guidelines for designing marine protected area networks, *Biol. Conserv.*, 144, 306–318.
- Monserat, S., Marcos, M., López-Jurado, J. (2008) Interannual variability of Winter Intermediate Water at the Balearic Islands. *Journal of Marine Systems* 71, 413–420.
- Newman, M. E. J. (2010), *Networks: An Introduction*, Oxford Univ. Press, New York.
- Oddo, P., Adani, M., Pinardi, N., Fratanni, C., Tonani, M. & Pettenuzzo, D. (2009) A nested Atlantic-Mediterranean Sea general circulation model for operational forecasting. *Ocean Science Discussions*, 6, 1093–1127.
- Paris, C.B., Helgers, J., VanSebille, E., Srinivasan, A. (2013). The Connectivity Modeling System: a probabilistic modelling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environ. Modell. Softw.* 42, 47–54.
- Pinsky, M.L., Palumbi, S.R., Andrefouet, S., & Purkis, S.J. (2012). Open and closed seascapes: where does habitat patchiness create populations with high fractions of self-recruitment? *Ecological Applications*, 22(4), 1257-1267.
- Planes, S., Jones, G.P. & Thorrold, S.R. (2009) Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences USA*, 106, 5693–5697.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist*, 652-661.
- Putman N. F. and R. He (2013). Tracking the long-distance dispersal of marine organisms: sensitivity to ocean model resolution, *J. R. Soc. Interface*, 10, 20120979; doi: 10.1098/rsif.2012.0979.
- Riginos, C., Douglas, K.E., Jin, Y., Shanahan, D.F. & Treml, E.A. (2011). Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography*, 34, 566–575.
- Rossi, V., Ser-Giacomi, E., Lopez, C., & Hernandez-García, E. (2014). Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. *Geophysical Research Letters*, 41(8), 2883-2891.
- Ser-Giacomi, E., Rossi, V., Lopez, C., & Hernandez-Garcia, E. (2015). Flow networks: A characterization of geophysical, fluid transport. *Chaos*, 25, 036404.
- Shanks, A.L., Grantham, B.A. & Carr, M.H. (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, 13, 159–169.
- Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters (2008), The stochastic nature of larval connectivity among nearshore marine populations, *Proc. Natl. Acad. Sci. U.S.A.*, 105(26), 8974–8979.
- Shtilerman E. and L. Stone (2015). The effects of connectivity on metapopulation persistence: network symmetry and degree correlations, *Proc. R. Soc. B*, 282, 20150203; doi:10.1098/rspb.2015.0203.
- Simons R. D., D. A. Siegel, K. S. Brown (2013). Model sensitivity and robustness in the estimation of larval transport: A study of particle tracking parameters, *Journal of Marine Systems*, 119/120, 19-29.
- Snyder, R.E., Paris, C.B., Vaz, A.C. (2014). How much do marine connectivity fluctuations matter? *American Naturalist*, 184, 523–530.
- 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. *Integrative and Comparative Biology*, 52(4), 525-537.
- Vázquez-Luis M., D. March, E. Alavarez, D. Alavarez-Berastegui and S. Deudero (2014). Spatial distribution modelling of the endangered bivalve *Pinna nobilis* in a Marine Protected Area, *Medit. Mar. Sci.*, 15 (3), 626-634.
- Vaz, A. C., K. J. Richards, Y. Jia, and C. B. Paris (2013). Mesoscale flow variability and its impact on connectivity for the island of Hawaii, *Geophys. Res. Lett.*, 40, 332–337.
- Weersing, K. & Toonen, R.J. (2009). Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series*, 393, 1–12.
- White, C., Selkoe, K.A., Watson, J., Siegel, D.A., Zacherl, D.C. & Toonen, R.J. (2010). Ocean currents help explain population genetic structure. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1685–1694.
- Wood, S., Paris, C.B., Ridgwell, A. & Hendy, E.J. (2014). Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography*, 23, 1–11.