AGU PUBLICATIONS

Geophysical Research Letters

RESEARCH LETTER
10.1002/2014GL059540

Key Points:
- Method coupling Lagrangian transport and network theory to study connectivity
- Provinces delimited by oceanic features organize basin-scale larval dispersal
- New connectivity metrics to assess existing MPAs and design future ones

Supporting Information:
- Readme
- Figure S1
- Figure S2
- Text S1
- Text S2
- Text S3

Correspondence to:
V. Rossi,
vincent@ifisc.uib-csic.es

Citation:
Rossi, V., E. Ser-Giacomi, C. López, and E. Hernández-García (2014), Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves, *Geophys. Res. Lett.*, *41*, 2883–2891, doi:10.1002/2014GL059540.

Received 6 FEB 2014
Accepted 20 MAR 2014
Accepted article online 1 APR 2014
Published online 23 APR 2014

Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves

Vincent Rossi[1], Enrico Ser-Giacomi[1], Cristóbal López[1], and Emilio Hernández-García[1]

[1]Institute for Cross-Disciplinary Physics and Complex Systems, CSIC-UIB, Palma de Mallorca, Spain

Abstract Oceanic dispersal and connectivity have been identified as crucial factors for structuring marine populations and designing marine protected areas (MPAs). Focusing on larval dispersal by ocean currents, we propose an approach coupling Lagrangian transport and new tools from Network Theory to characterize marine connectivity in the Mediterranean basin. Larvae of different pelagic durations and seasons are modeled as passive tracers advected in a simulated oceanic surface flow from which a network of connected areas is constructed. Hydrodynamical provinces extracted from this network are delimited by frontiers which match multiscale oceanographic features. By examining the repeated occurrence of such boundaries, we identify the spatial scales and geographic structures that would control larval dispersal across the entire seascape. Based on these hydrodynamical units, we study novel connectivity metrics for existing reserves. Our results are discussed in the context of ocean biogeography and MPAs design, having ecological and managerial implications.

1. Introduction

Oceanic ecosystems are impacted by multiple human-induced stressors, including habitat destruction, pollution, overfishing, and global climate change. Marine protected areas (MPAs), used for the management and conservation of marine ecosystems, are considered effective to mitigate some of these impacts [*Lester et al.*, 2009]. Successful MPA design is, however, complicated primarily due to the difficulties in quantifying the movements of organisms, especially at larval stage [*Shanks*, 2009], 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].

Marine population connectivity, i.e., the exchange of individuals among geographically separated subpopulations, depends on numerous factors including spawning outputs, larval dispersal, habitat availability, trophic interactions and adult movements [*Cowen and Sponaugle*, 2009; *Game et al.*, 2009]. Among them, larval dispersal has been identified as a crucial factor for structuring oceanic populations [*Cowen et al.*, 2006] and for determining broad-scale ecological connectivity [*Treml et al.*, 2012]. It also plays a major role in assuring population persistence in a MPA network [*Moffitt et al.*, 2011], especially when target species show long-distance dispersal [*Shanks*, 2009]. As such, patterns and magnitude of larval connectivity have been used to design MPAs [*Lester et al.*, 2009] and assess their efficiency [*Pelc et al.*, 2010]. This paper focuses on the dispersion of larvae by ocean currents at basin scale, assuming they are passively transported by the flow (i.e. neglecting larval behavior), to inform the design of marine reserves.

Many biophysical modeling studies [e.g. *Cowen et al.*, 2006; *Siegel et al.*, 2008], including Lagrangian approaches, examined marine connectivity from the so-called "connectivity matrix" which represents the probability of larval exchange between distant sites. Previous analyses were mainly limited to the strengths of pairwise connections, i.e., the links from one coastal site, or MPA, to another distant one [e.g. *Corell et al.*, 2012; *Vaz et al.*, 2013]. Another perspective to investigate connectivity is the analysis of dispersal network topologies [*Treml et al.*, 2012; *Kool et al.*, 2013]. Recent studies applied tools derived from Graph Theory to document regional connectivity of near-shore MPAs in the Baltic Sea [*Nilsson-Jacobi et al.*, 2012], the Mediterranean Sea [*Andrello et al.*, 2013], and in the Great Barrier Reef region [*Thomas et al.*, 2014]. While our understanding of connectivity at small and regional scales has improved, previous efforts focused mainly on coastal/insular areas and did not provide a characterization of the seascape connectivity.

The significance of this shortcoming is emphasized by the growing interests for the implementation of MPAs in the pelagic ocean [*Pala*, 2013; *Guidetti et al.*, 2013] which also shelters biodiversity and important

©2014. American Geophysical Union. All Rights Reserved.

ecological processes [*Game et al.*, 2009; *Kaplan et al.*, 2010]. Designing open ocean MPAs is challenging partly because larval connectivity and pelagic habitats are difficult to assess in such vast and dynamic environment.

Here we use an approach coupling Lagrangian modeling and new tools from Network Theory [*Newman*, 2010] to characterize marine connectivity at basin scale in the Mediterranean Sea. Larvae of different pelagic larval durations (PLDs) are modeled as passive Lagrangian particles advected in a simulated oceanic surface flow from which a network of connected areas can be constructed. Hydrodynamical provinces extracted from this transport network are delimited by frontiers which match mesoscale and regional oceanographic features. We then identify the spatial scales and structures of larval dispersal across the entire seascape and analyze connectivity metrics for the existing Mediterranean MPAs. We finally discussed the usefulness of our results for the design of marine reserves and the characterization of oceanic biomes.

2. Materials and Methods

2.1. Oceanic Transport and Connectivity From a Network Theory Approach

The basic ingredients are (i) the tracking of passive Lagrangian particles (a model for larval transport) and (ii) the construction and analysis of a network of flow-mass transport. We study dispersal processes in the ocean based on a transport network in which a *node* corresponds to a geographical subarea of the oceanic surface, and a *link* (or *edge*) symbolizes an effective mass transport driven by ocean currents between two subareas during a given time interval.

The transport network is thus composed of an ensemble of nodes (subareas), covering the entire oceanic domain of interest, which are interconnected by a number of links (transport pathways). Each link is *directed* in accord with the effective direction of the flow and *weighted* proportionally to the amount of water flowing from one node to another. Many tools of Network Theory were designed to examine both local and global properties of such network [e.g., *Newman*, 2010], allowing us to explore geophysical flows and connectivity in a new fashion.

The Mediterranean Sea, a quasi-closed basin with its own physical circulation and ecological functioning under important human pressure [*de Madron et al.*, 2011], constitutes a natural laboratory for this study. In addition, it shelters already a hundred MPAs (whose locations were downloaded from the MedPan database) implemented for protection and conservation purposes. In this context, we aim at partitioning the surface Mediterranean seascape in hydrodynamical provinces, i.e., a set of oceanic subregions in which larvae/particles are much more likely to disperse efficiently within each other than among them at a given time scale. This spatial subdivision in provinces is tantamount to detecting *communities* within the hydrodynamical network [*Newman*, 2010].

2.2. Lagrangian Biophysical Modeling

The Lagrangian approach is a natural perspective to characterize transport phenomena affecting free-swimming larvae [*Corell et al.*, 2012; *Vaz et al.*, 2013]. Particles are advected in an eddy-resolving velocity field generated by the Nucleus for European Modeling of the Ocean hydrodynamical model implemented in the Mediterranean at a 1/16° horizontal resolution [*Oddo et al.*, 2009] (see also Text S1 in the supporting information). We focus on the upper ocean dynamics over years 2002–2011 with the use of daily horizontal flow fields at 8 m depth (Figure S1), representing the surface mixed layer in which larvae are assumed to be homogeneously distributed.

Horizontal trajectories are simulated by integrating the velocity field, bilinearly interpolated at any sea point, using a *Runge-Kutta 4* algorithm with a time step of 1 day, matching the resolution of the simulated currents. As assumed by *Corell et al.* [2012] and *Andrello et al.* [2013], Lagrangian particles are dispersed as two-dimensional passive drifters. Note that due to the non–fully incompressible horizontal flow field, vertical velocities may become significant in regions of strong divergence (e.g., coastal upwelling) and convergence (e.g., deep water formation). Neglecting vertical movements is, however, a reasonable assumption here because most particles remain in the selected layer over short time scales ($\leq$ 2 months) since horizontal velocities are several orders of magnitude higher than vertical ones [*d'Ovidio et al.*, 2004]. Another simplification is the passive character of the particles, the implementation of more complex larval behavior (e.g., vertical migration, mortality, and settlement) being envisaged for future work. Under these assumptions, larval dispersal is modulated by the PLD, the period of spawning and the time-varying oceanic circulation.

©2014. American Geophysical Union. All Rights Reserved.

Initial (t_0) and integration ($\tau \sim$ PLD) times are chosen according to the typical biological traits of marine organisms. Given the limited knowledge of their life cycles [*Shanks*, 2009], we investigate basin-scale larval connectivity from an ecosystem-based approach [e.g., *Coll et al.*, 2012; *Guidetti et al.*, 2013], rather than focusing on a particular target species. To do so, we retain two different PLDs ($\tau = 30, 60$ days) and consider winter (t_0 = 1 January) and summer (t_0 = 1 July) spawning [*Macpherson and Raventos*, 2006; *Shanks*, 2009; *Andrello et al.*, 2013] over the years 2002–2011. These modeling choices are ecologically meaningful for a number of Mediterranean organisms, especially those with wide geographical range and potential for large-distance dispersal (see also Text S2). Sensitivity of our results to the parameter τ was tested by performing additional simulations for $\tau = 45$ days. A total of 60 factorial experiments (with starting times covering two seasons over 10 years, for each of the three PLDs) allow the construction of 60 connectivity matrices from which hydrodynamical provinces are extracted (section 3.1). They are then temporally averaged to describe robust spatial patterns of larval connectivity in the entire Mediterranean basin (section 3.2) finally interpreted in the context of MPA design (section 3.3).

2.3. Construction and Analysis of a Transport Network

2.3.1. Connectivity Matrix

The nodes of the transport network are defined by discretizing the surface ocean into 3270 quasi-square boxes of 1/4° horizontal resolution (Figure S2), allowing the consideration of important mesoscale features of the Mediterranean circulation [*de Madron et al.*, 2011]. This procedure and the numerical diffusion it introduces [*Froyland and Dellnitz*, 2003] are detailed in Text S1.

Five hundred Lagrangian particles evenly distributed in each oceanic box are advected, corresponding to a total of $\sim$ 1.6 million trajectories in the Mediterranean basin for each experiment. The connectivity matrix is built using the initial and final positions of these particles. Each matricial element $\mathbf{P}_{ij}^{t_0,\tau}$, i.e., the link between nodes i and j, is proportional to the fraction of particles leaving box i at time t_0 and arriving in box j at time $t_0 + \tau$. $\mathbf{P}_{ij}^{t_0,\tau} = \#$ particles from box i to box $j/N_i \in [0, 1]$ is interpreted as the probability for a particle selected randomly in box i at the initial time ending up in box j at the final time. N_i is a local normalization coefficient equal to the number of particles still within the oceanic domain after integration. Due to numerical limitations, some trajectories may indeed abort prematurely with the "beaching" of particles onto land areas. With this normalization, which concerns less than 5% of all particles for $\tau = 60$ days, the stochasticity of the matrix (i.e. its rows sum to 1) is ensured and the constraint of mass conservation fulfilled.

2.3.2. Community Detection

To locate coherent regions in time-varying flows, the transport matrix approach has been proposed by *Froyland and Dellnitz* [2003]. Such objects are extracted by examining eigenvalues [*Nilsson-Jacobi et al.*, 2012] or singular vectors [*Froyland et al.*, 2012] of the transport (connectivity) matrix which approximates the continuous advection operator. These concepts, along with other community detection algorithms, were recently used to study ecological connectivity [*Nilsson-Jacobi et al.*, 2012; *Thomas et al.*, 2014].

Here we analyze the topology of the transport network to subdivide the surface ocean in hydrodynamical provinces. Based on the connectivity matrix $\mathbf{P}^{t_0,\tau}$, an equivalent of the network adjacency matrix, we detect communities using the *Infomap* algorithm [*Rosvall and Bergstrom*, 2008]. Random walkers are considered to move in the network according to the statistical description of the surface flow contained in the connectivity matrix. From these synthetic trajectories and using information theory concepts, *Infomap* decomposes the network into a number of communities that define oceanic provinces well connected internally but with minimal exchanges of particle between them. The method is described and compared with its alternatives in Text S3.

To evaluate the significance of the spatial partitioning, we define a coherence ratio [*Froyland et al.*, 2012] associated with each province k by the following: $\rho_k = \sum_{i,j \in \mathcal{I}_k} N_i \mathbf{P}_{ij}^{t_0,\tau} / \sum_{i \in \mathcal{I}_k} N_i$ where $\mathcal{I}_k$ is the set of indices that identify all boxes constituting province k. Physically, $\rho_k \in [0, 1]$ is interpreted as the fraction of particles initially released within a given province which remained in it after integration. Its complement $1 - \rho_k$ measures the proportion of particle leaking across the boundaries of each province.

3. Results and Discussion

3.1. Time-Dependent Hydrodynamical Provinces

The provinces and their boundaries are dynamical objects that evolve in space and time with different dimensions, shapes and locations (e.g., Figure 1), due to the important variability of the ocean circulation

©2014. American Geophysical Union. All Rights Reserved.

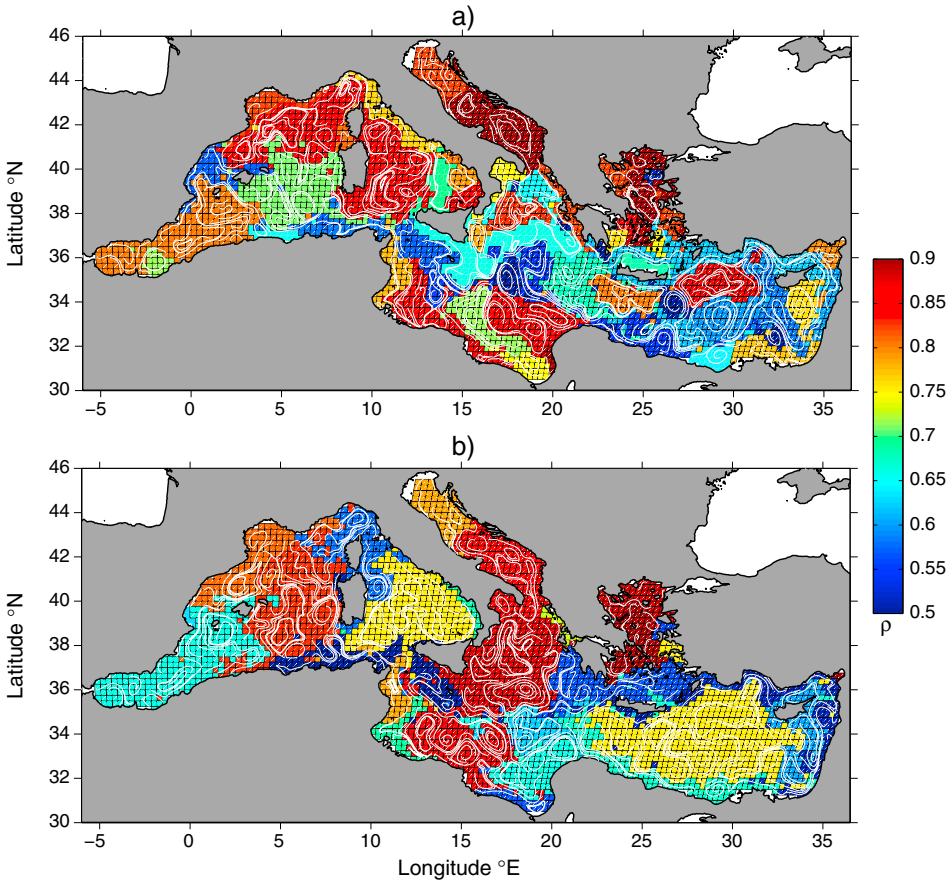


Figure 1. Hydrodynamical provinces extracted from the connectivity matrices of (a) winter 2011 (t_0 = 1 January) using $\tau \simeq$ PLD = 30 days and (b) summer 2011 (t_0 = 1 July) using $\tau \simeq$ PLD = 60 days. Each province is colored according to its ρ value (ranging from 0.5 to 0.9). White streamlines represent the simulated flow averaged over the period of integration (i.e., Figure 1a for 1–30 January 2011 and Figure 1b for 1 July to 29 August 2011).

[*Millot and Taupier-Letage*, 2005]. The method captures an elevated number of communities in the network, with 65 provinces using a PLD = 30 days and only 32 for PLD = 60 days on the exemplary calculations displayed in Figure 1. Intuitively, the longer the tracking time, the lower the number of provinces detected and the larger their mean area. On average over the ensemble of experiments, community detection results in 61, 46, and 36 provinces characterized by a mean area of 4.12×10^4, 5.5×10^4, and 6.8×10^4 (in km^2) for $\tau = 30, 45, 60$ days, respectively. Because of the time-varying flow [*Siegel et al.*, 2008], both release time and tracking duration (simulating respectively the initiation and duration of the pelagic larval phase) affect the spatial partitioning.

Most province boundaries match very well the mean flow streamlines (Figure 1), suggesting high-oceanographic relevance. While isolated streamlines are found in the cores of provinces, dense ones usually coincide with the detected boundaries. Hydrodynamical provinces are delimited by intense oceanic mesoscale structures such as jets, meanders, fronts and eddies. These features, which influence the topology of the transport network and thus the community detection, were recently reported to strongly impact connectivity [*Vaz et al.*, 2013]. For instance, some mesoscale eddies are extracted as quasi-circular single provinces (e.g., in the Alboran Sea and in the southern Levantine basin), in good agreement with the flow streamlines (Figure 1a). Other mesoscale structures are contained in larger provinces. The method allows the optimal detection of coherent oceanic subregions originating from the ocean circulation and its multiscale variability.

The coherence ratios are generally elevated ($\rho \in [0.5, 1]$) and variable (Figure 1). Although it depends on both the local leaking processes and the area of a given province, there is no apparent relationship between the size of the subregion and its coherence ratio. Overall, $\rho \geq 0.8$ are often seen in the Aegean and

©2014. American Geophysical Union. All Rights Reserved.

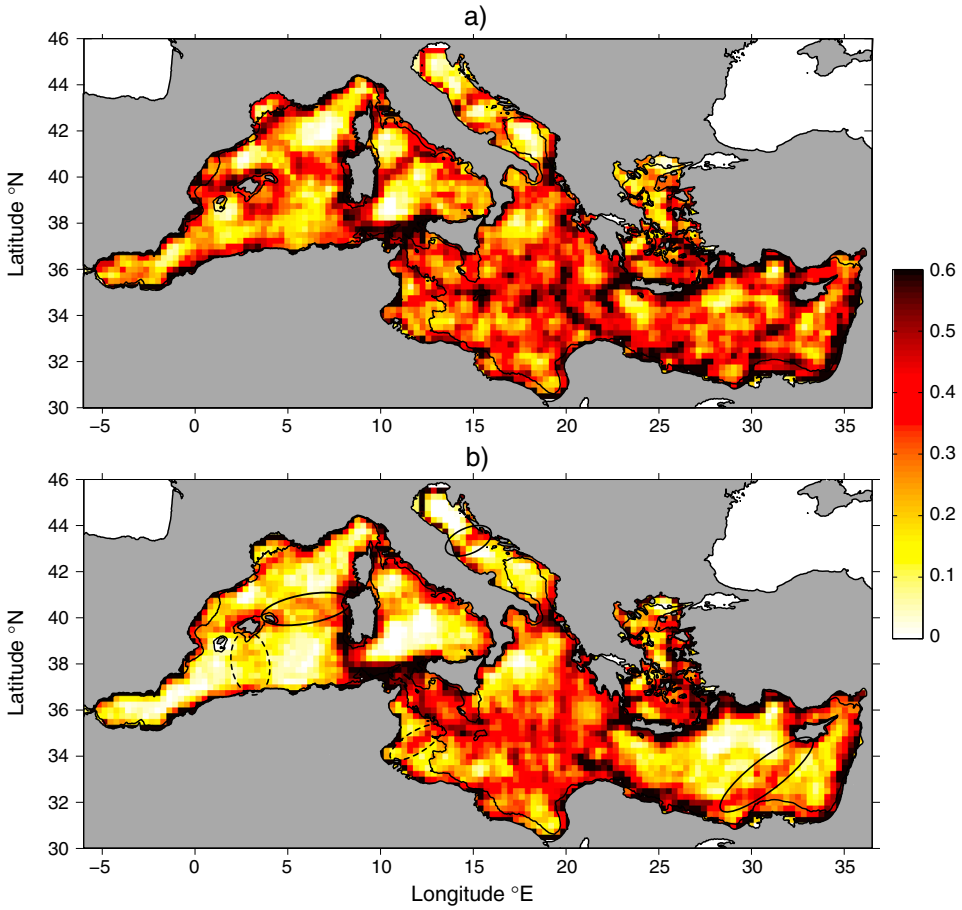


Figure 2. Frequency of occurrence of province boundaries at each ocean node across the ensemble of 20 experiments (all winters/summers of 2002–2011) for each PLD: (a) $\tau \simeq$ PLD $=$ 30 days and (b) $\tau \simeq$ PLD $=$ 60 days. Black ellipses in Figure 2b highlight the frontiers which show a significant seasonality: plain ellipses indicate a preferential occurrence in winter and dotted ellipses in summer. Black contour represents the 200 m isobath.

Adriatic Seas. The Alboran, Balearic, Tyrrhenian, and Adriatic Seas are characterized by relatively large provinces, whereas the Levantine, Aegean, south Ionian and Libyan Seas are subdivided in rather small ones. Note also that some provinces are composed of noncontiguous boxes. This occurs especially within the pathways of fast-flowing currents as the Algerian Current, the Atlantic-Ionian stream (south Ionian, Libyan and southeast Levantine Seas), and the Liguro-Provencal Current (Ligurian sector).

3.2. Spatial Scales and Geographic Structure of Larval Dispersal

The frequency of occurrence of province boundaries is now examined across the ensemble of experiments to identify recurrent frontal systems and relatively stable hydrodynamical units which would organize larval dispersal. Over most coastal/shallow regions, boundaries occur in various locations and orientations, resulting in no apparent structure (dark red patches). These disorganized patterns characterize oceanic environments with complex circulation in which spatial scales of connectivity are highly variable [*Siegel et al.*, 2008]. They are observed in most insular regions (Balearic, Tuscan, and Aegean archipelagos, Corsica, Sardinia, Crete, and Cyprus), in the Tunisian-Sicilian strait (also punctuated by small islands) and over narrow continental shelves (Italian, French, Catalan, Libyan-Egyptian, and Israelian-Lebanon shelves) (Figure 2a). In contrast, wide continental shelves are organized as coherent hydrodynamical units whose offshore limits match the 200 m isobath. The Gulf of Lion is delimited by a frontier coinciding with the Catalan front and associated Northern Current (an extension of the Liguro-Provencal Current) [*Bouffard et al.*, 2010]. For long PLDs only, the Tunisian-Libyan shelf appears as two units in summer (Figure 2b), merging into a single one in winter. The oceanic frontiers constituted by such currents/fronts are likely to prevent coastal larvae from escaping wide continental shelves.

©2014. American Geophysical Union. All Rights Reserved.

In the open ocean, clear hydrodynamical units emerge (Figure 2), organized as large "gyre" systems with rare occurrence of boundaries (white/yellow colors) in their center and semipersistent frontiers (light/dark red colors) aligned along their perimeters. Elevated connectivity within each subdivision, but little exchange between them, is expected, thus providing basin-scale patterns of larval dispersal. Large hydrodynamical units are found in the western Mediterranean basin, the Adriatic Sea, the Tyrrhenian Sea (Figures 2a and 2b), and only at longer time scales in the north Ionian and Levantine Seas (Figure 2b). Most of these open ocean frontiers are located along well-known oceanographic features [*Millot and Taupier-Letage*, 2005], some of them recognized as partial transport barriers. For instance, the so-called Oran-Almeria front separates the Alboran Sea from the rest of the Mediterranean Sea. It appears here rather extending from Oran to Cartagena, some 200 km away than previously documented [*de Madron et al.*, 2011, and references therein]. The Balearic front is another semipermament transport barrier [*Mancho et al.*, 2008] passing north of the Balearic archipelago in the Balearic Current [*Bouffard et al.*, 2010] and elongating eastward in winter. North of this quasi-zonal boundary, a large hydrodynamical unit composed of the Lion gyre and Ligurian Sea is separated from the Balearic Sea at short time scale. The Tyrrhenian Sea is consistently organized as a two-gyre system using both PLDs. For the 30 day integration the Adriatic Sea is subdivided by bathymetric gradients ($\sim$ 100 and 200 m isobaths, i.e., off the Gargano promontory) into a northern, central, and southern Adriatic gyres, the two latter units merging for PLDs of 60 days.

Surprisingly, some open ocean areas, such as the Ionian, Levantine and Aegean basins (Figure 2a), are characterized by disorganized dispersal patterns and stochastic larval connectivity [*Siegel et al.*, 2008]. They become more structured at longer time scales with the emergence of the western Ionian gyre, the Shikmona gyre, and a large system encompassing the Rhodes, Ierapetra, and Mersa-Matruh gyres [*Millot and Taupier-Letage*, 2005]. The eastern Aegean Sea has disorganized dispersal patterns whereas small hydrodynamical units appear in its northern and western parts, in good agreement with its thermal structure [*Poulos et al.*, 1997].

More generally, regions with no apparent spatial patterns at short PLDs see the emergence of spatial structures for longer integration time. Oceanic areas already identified as gyral systems for short time scales have their diameter increasing with the integration time, ultimately merging with their neighbors.

Note that most of these hydrodynamical units are quite consistent with the trophic clusters obtained from satellite chlorophyll data [*d'Ortenzio and d'Alcalá*, 2009], suggesting they also delimit specific biogeochemical provinces [*Longhurst*, 2006]. Indeed, although this study focuses on passive larvae, the unveiling of well-known oceanic fronts and gyres hints that the spatial distribution of other tracers (e.g., salinity, temperature, chlorophyll-*a*, and dissolved nutrients) is also influenced by similar transport patterns.

3.3. Implications for the Design of Marine Reserves

The geographical structure of larval dispersal in the seascape influences largely the connectivity of marine reserves. The MPAs located within large and stable hydrodynamical units (Figure 2) 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 analysis of three complementary proxies of connectivity defined as follows. We analyze the mean spatial scales of larval dispersal (Figure 3a) and the mean local coherence (inversely related to leaking, Figure 3b) by averaging over the ensemble of experiments the area and the coherence ρ, respectively, of the time-dependent province encompassing each MPA. While these two metrics are solely influenced by the flow, the mean number of interconnected MPAs (i.e., temporally averaged number of MPAs encountered within the same time-dependent province, Figure 3c) depends also on the density of existing reserves.

Larval connectivity and dispersal potentials are highly variable among the Mediterranean MPAs (Figure 3). Reserves in the Adriatic and Aegean Seas are characterized by small dispersal surface ($\leq 5\times10^4$ km^2) and among the highest coherence ($\rho \geq 0.8$). This suggests a low connectivity which is also reflected in the few interconnected MPAs (≤ 8) despite their relatively high density. MPAs located around isolated islands are associated with modest dispersal surface ($\sim 4 - 8\times10^4$ km^2) and low coherence ($\rho \leq 0.7$). Typical of these insular environments [*Vaz et al.*, 2013], complex circulation patterns (islands' wake, eddies, retention, etc.) result in a moderate connectivity and high temporal variability (not shown). MPAs implemented within narrow continental shelves bounded by energetic currents are characterized by rather large provinces ($\geq 7\times10^4$ km^2) and moderate coherence ($0.65 \leq \rho \leq 0.8$). These reserves are situated along the French Côte d'Azur with the Liguro-Provencal Current, the Catalan coast with the Northern Current,

©2014. American Geophysical Union. All Rights Reserved.

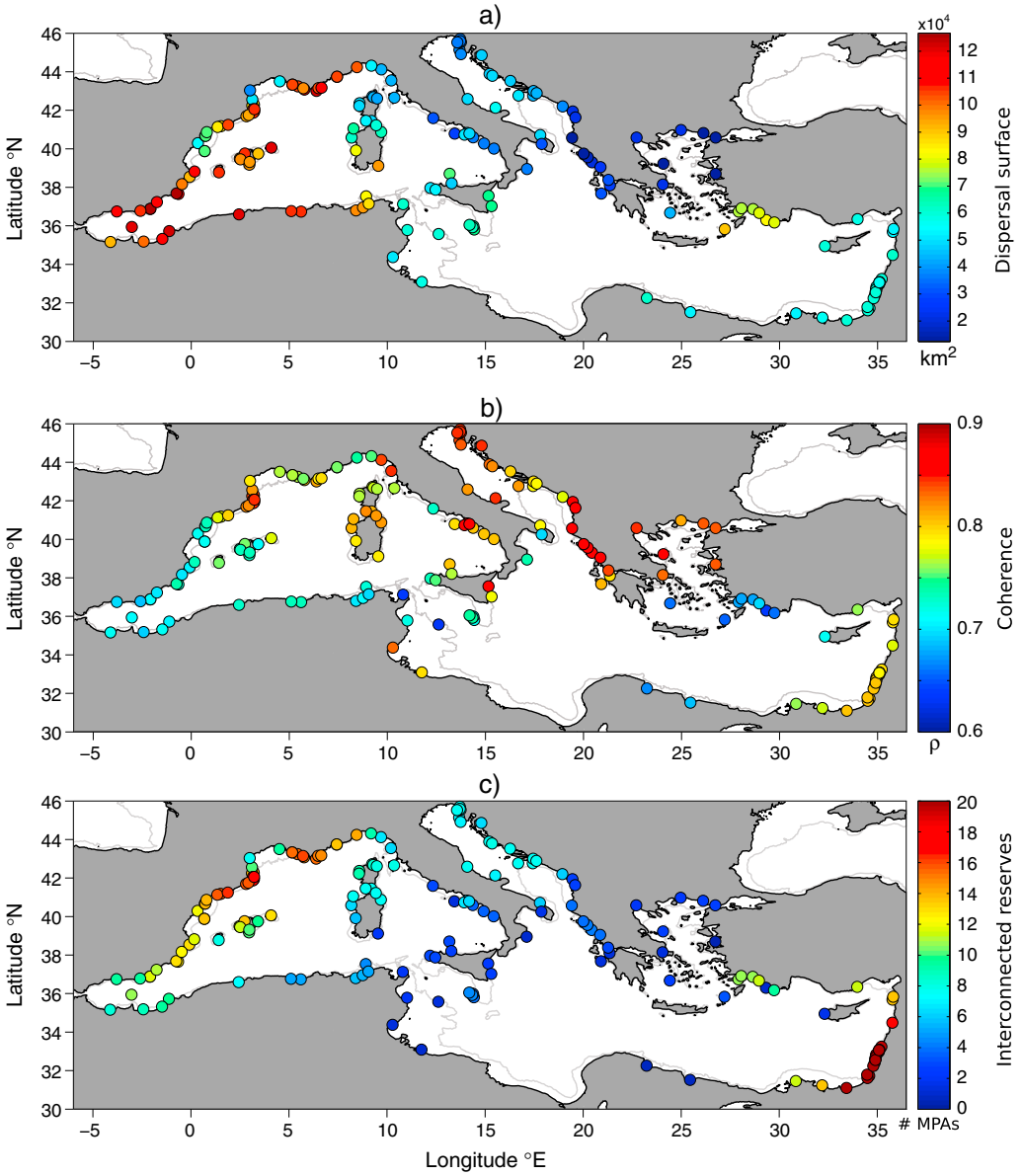


Figure 3. Spatial variability of MPAs connectivity derived from three complementary metrics averaged across all winter/summer experiments over 2002–2011 using $\tau \simeq$ PLD = 30 days. (a) Mean area (in km^2) and (b) mean ρ of the province sheltering the reserve of interest. (c) Mean number of interconnected MPAs (i.e. number of reserves situated within the same hydrodynamical province). Light grey contours represent the 200 m isobath. Results using a PLD of 45 and 60 days are qualitatively similar with a slight increase of the mean area and the number of interconnected reserves. Note that noncontiguous areas belonging administratively to a given reserve were treated here as a single MPA.

the Moroccan/Algerian coastlines impacted by the Algerian Current, and in the eastern Levantine basin with the jet-like intensifications of its gyre circulation [*Millot 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 ($\geq$15) along the French, Catalan, and Israelian coastlines. In contrast, MPAs situated within extended continental shelves, such as the Gulf of Lion and the Tunisian/Libyan shelf, are characterized by rather small dispersal area ($\leq 5 \times 10^4$ km^2) and large coherence ($\rho \geq 0.75$). Unless exceptional intrusion events (not shown), the inner shelf remains isolated by the shallow bathymetry holding the current off the shelf break, resulting in a limited connectivity. Note that most MPAs associated with narrow shelves and sluggish circulation (such as the Tyrrhenian, Corsican, and Sardinian coastlines) behave quite similarly to the latter group with small dispersal surfaces.

©2014. American Geophysical Union. All Rights Reserved.

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 [*Pelc et al.*, 2010] whereas reserves created within internal seas or large continental shelves would rather promote the restoration of local populations [*Pineda et al.*, 2007]. Overall, the Mediterranean MPAs are not evenly distributed across the spatial partitioning of the seascape revealed by our analysis (section 3.2) [*De-Juan et al.*, 2012]. 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.

4. General Conclusions and Perspectives

Using a method coupling Lagrangian trajectories and new tools from Network Theory, we study larval dispersal by surface currents in the Mediterranean Sea. Under our assumptions, a transport network is constructed from the horizontal advection of passive particles in a modeled oceanic flow, simulating larvae of different planktonic seasons and durations. The systematic detection of communities in the network extracts a set of hydrodynamical provinces which organize the surface dispersion of larvae in the entire Mediterranean basin. Their boundaries coincide with both mesoscale and regional-scale oceanographic features, comprehending the multiscale processes of ocean circulation. The repeated occurrence of these frontiers allows separating the seascape in different hydrodynamical units which provide the "backbone" of oceanic transport impacting larval dispersal and connectivity among existing MPAs. While the role of such large-scale dispersal patterns on the genetic structure of marine population remain to be determined, the hydrodynamical units evidenced may be used to optimize the sampling strategy of genetic studies. The similarity between our flow-driven boundaries and major environmental gradients commonly used to regionalize the Mediterranean seascape finally suggests they might also define oceanic biomes or even faunistic units. Future developments of the methodology would have to consider more realistic larval behavior for a given target species as well as full tridimensionality of the flow. These extensions may help incorporating large-scale biogeography and dispersal patterns to improve MPAs design toward efficient management and conservation of marine ecosystems.

Acknowledgments

The authors acknowledge support from MICINN and FEDER through the ESCOLA project (CTM2012-39025-C02-01) and support from ECs Marie-Curie ITN program (FP7-PEOPLE-2011-ITN) through the LINC project (289447). The simulated velocity field used in this study was generated by MyOcean (http://www.myocean.eu/), and the locations of Mediterranean MPAs were provided by MedPan (http://www.medpan.org/). The authors thank two anonymous reviewers who helped to improve the original manuscript.

The Editor thanks two anonymous reviewers for their assistance in evaluating this paper.

References

Andrello, M., D. Mouillot, J. Beuvier, C. Albouy, W. Thuiller, and S. Manel (2013), Low connectivity between Mediterranean marine protected areas: A biophysical modeling approach for the dusky grouper *Epinephelus marginatus*, *PLoS One*, *8*(7), e68564.

Bouffard, J., A. Pascual, S. Ruiz, Y. Faugère, and J. Tintore (2010), Coastal and mesoscale dynamics characterization using altimetry and gliders: A case study in the Balearic Sea, *J. Geophys. Res.*, *115*, C10029, doi:10.1029/2009JC006087.

Coll, M., et al. (2012), The Mediterranean Sea under siege: Spatial overlap between marine biodiversity, cumulative threats and marine reserves, *Global Ecol. Biogeogr.*, *21*, 465–480.

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 S. Sponaugle (2009), Larval dispersal and marine population connectivity, *Annu. Rev. Mar. Sci.*, *1*, 433–466.

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

De-Juan, S., et al. (2012), A regional network of sustainable managed areas as the way forward for the implementation of an Ecosystem-Based Fisheries Management in the Mediterranean, *Ocean Coast. Manage.*, *65*, 51–58.

de Madron, X. D., et al. (2011), Marine ecosystems' responses to climatic and anthropogenic forcings in the Mediterranean, *Prog. Oceanogr.*, *91*, 97–166.

d'Ortenzio, F., and M. R. d'Alcalá (2009), On the trophic regimes of the Mediterranean Sea: A satellite analysis, *Biogeosciences*, *6*, 1–10.

d'Ovidio, F., V. Fernandez, E. Hernandez-García, and C. Lopez (2004), Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents, *Geophys. Res. Lett.*, *31*, L17203, doi:10.1029/2004GL020328.

Froyland, G., and M. Dellnitz (2003), Detecting and locating near-optimal almost-invariant sets and cycles, *SIAM J. Sci. Comput.*, *24*(6), 1839–1863.

Froyland, G., C. Horenkamp, V. Rossi, N. Santitissadeekorn, and A. S. Gupta (2012), Three-dimensional characterization and tracking of an Agulhas ring, *Ocean Model.*, *52*, 69–75, doi:10.1016/j.ocemod.2012.05.001.

Game, E. T., et al. (2009), Pelagic protected areas: The missing dimension in ocean conservation, *Trends Ecol. Evol.*, *24*(7), 360–369.

Guidetti, P., G. Notarbartolo-Di-Sciara, and T. Agardy (2013), Integrating pelagic and coastal MPAs into large-scale ecosystem-wide management, *Aquat. Conserv.*, *23*, 179–182.

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.

Kaplan, D., E. Chassot, A. Gruss, and A. Fonteneau (2010), Pelagic MPAs: The devil is in the details, *Trends Ecol. Evol.*, *25*, 62–63.

Kool, J., A. Moilanen, and E. Treml (2013), Population connectivity: Recent advances and new perspectives, *Landscape Ecol.*, *28*, 165–185.

©2014. American Geophysical Union. All Rights Reserved.

Lester, S., B. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. Gaines, S. Airamé, and R. R. Warner (2009), Biological effects within no-take marine reserves: A global synthesis, *Mar. Ecol. Prog. Ser.*, *384*, 33–46.
Longhurst, A. R. (2006), *Ecological Geography of the Sea*, 560 pp., Academic Press, San Diego, Calif.
Macpherson, E., and N. Raventos (2006), Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes, *Mar. Ecol. Prog. Ser.*, *327*, 257–265.
Mancho, A., E. Hernandez-Garcia, D. Small, S. Wiggins, and V. Fernandez (2008), Lagrangian transport through an ocean front in the north-western Mediterranean Sea, *J. Phys. Oceanogr.*, *38*, 1222–1237.
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.
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.
Newman, M. E. J. (2010), *Networks: An Introduction*, Oxford Univ. Press, New York.
Nilsson-Jacobi, M., C. André, K. Doos, and P. R. Jonsson (2012), Identification of subpopulations from connectivity matrices, *Ecography*, *35*, 1004–1016.
Oddo, P., M. Adani, N. Pinardi, C. Fratianni, M. Tonani, and D. Pettenuzzo (2009), A nested Atlantic-Mediterranean Sea general circulation model for operational forecasting, *Ocean Sci.*, *5*(4), 461–473.
Pala, C. (2013), Giant marine reserves pose vast challenges, *Science*, *339*(6120), 640–641.
Pelc, R. A., R. R. Warner, S. D. Gaines, and C. B. Paris (2010), Detecting larval export from marine reserves, *Proc. Natl. Acad. Sci. U.S.A.*, *107*(43), 18,266–18,271.
Pineda, J., J. Hare, and S. Sponaugle (2007), Larval transport and dispersal in the coastal ocean and consequences for population connectivity, *Oceanography*, *20*(3), 22–39.
Poulos, S., P. Drakopoulos, and M. Collins (1997), Seasonal variability in sea surface oceanographic conditions in the Aegean Sea (eastern Mediterranean): An overview, *J. Mar. Syst.*, *13*, 225–244.
Rosvall, M., and C. T. Bergstrom (2008), Maps of random walks on complex networks reveal community structure, *Proc. Natl. Acad. Sci. U.S.A.*, *105*(4), 1118–1123.
Shanks, A. L. (2009), Pelagic larval duration and dispersal distance revisited, *Biol. Bull.*, *216*, 373–385.
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.
Thomas, C. J., J. Lambrechts, E. Wolanski, V. Traag, V. D. Blondel, E. Deleersnijder, and E. Hanert (2014), Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef, *Ecol. Modell.*, *272*, 160–174.
Treml, E., J. Roberts, Y. Chao, P. N. Halpin, H. Possingham, and C. Riginos (2012), Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations, *Integr. Comp. Biol.*, *52*(4), 525–537.
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, doi:10.1029/2012GL054519.

©2014. American Geophysical Union. All Rights Reserved.