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From coast to coast: simulating the connectivity of marine ecosystems

Abstract – Given the openness of marine environments, connectivity is not only inherently fundamental to the ecology of seascape communities, but is also a crucially important component of marine ecosystems health. Preserving genetic diversity, rescuing species from habitat deterioration or loss, enhancing resilience to local unfortunate environmental events are just few notable examples of the many reasons why connectivity must be understood and quantitatively assessed over possibly large spatial domains and sufficiently long temporal scales. Here we summarize the potentiality of Lagrangian simulation-based approaches by revising four case studies recently contributed by our research group. Integrating high-resolution Earth Observations to physically based oceanographic models, the most up-to-date available re-analyses permit, in an informative way, to deal with fundamental topics of marine ecology. Our research has focused on species that provide important ecosystem services (such as the habitat former *Posidonia oceanica* and its fish community or the European eel *Anguilla anguilla*) and/or have been performed in areas of special interest for biodiversity protection (from the Northern Line Islands in the Pacific ocean to the Mediterranean sea). Inter-annual variability of connectivity can systematically be accounted for by using the presented approaches, and the statistical significance of temporal trends in connectivity can also be identified. In cases where the auto-ecologies of species under study are sufficiently well known (in terms, for example, of their suitable habitat, timing of spawning and larval/seed transport duration or movement behavior of larval stages), biophysical simulations like those presented here permit to incorporate them into modelling, thus improving the realism of obtained connectivity patterns. Since prioritizing interventions may be key in marine management programs, that are typically budget-limited, we also show how our modelling approach can help decision makers to plan actions for marine protection based on communities rather than single-species ranking.

Keywords: coupled physical-biological models, marine conservation, movement ecology, propagule dispersal, seascape connectivity.

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Introduction

Seascape connectivity is a key process affecting the dynamics of marine communities and a major ecological principle for ecosystem-based planning. However, connectivity is a very general term that describes a complex process including many components. Although both adult movement and larval dispersal can characterize connectivity, the latter is considered the most important phenomenon for many species of marine organisms. Here, we will deal with this kind of connectivity, which however leaves out all those species whose adults are highly mobile, such as big pelagic fish and marine mammals. The elements of larval connectivity are sketched in Figs. 1 and 2.

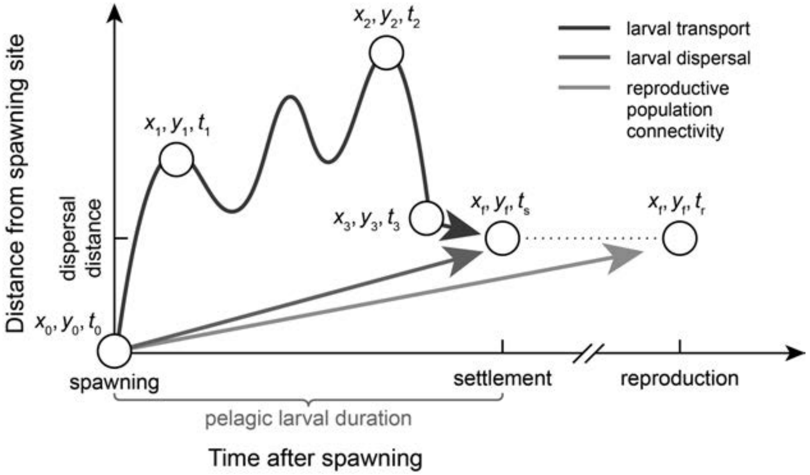

Fig. 1. Relationship between the spatial and temporal components of larval transport, larval dispersal and reproductive population connectivity for a sessile species. White circles are locations in space with coordinates *x-y* at time *t*. Initial (x_0) and final (x_f) locations are benthic, while the others are pelagic. Redrawn after [10].

There are several possible approaches to studying connectivity in marine ecosystems. Very broadly, they can be classified into three categories:

- Mark-recapture methods, tagging, chemical signatures etc.
- Genetic markers
- Individual-based simulation

In this brief correspondence, we are going to explore the third approach with reference to the early life history stages of marine organisms, mainly the larval stage, its dispersal and the eventual settlement. Individual-based, coupled physical-biological models are increasingly used to investigate marine dispersal; the physical engine is provided by ocean re-analyses assimilating Earth Observation data, however, studying passive transport is not sufficient in many cases and thus it is necessary to

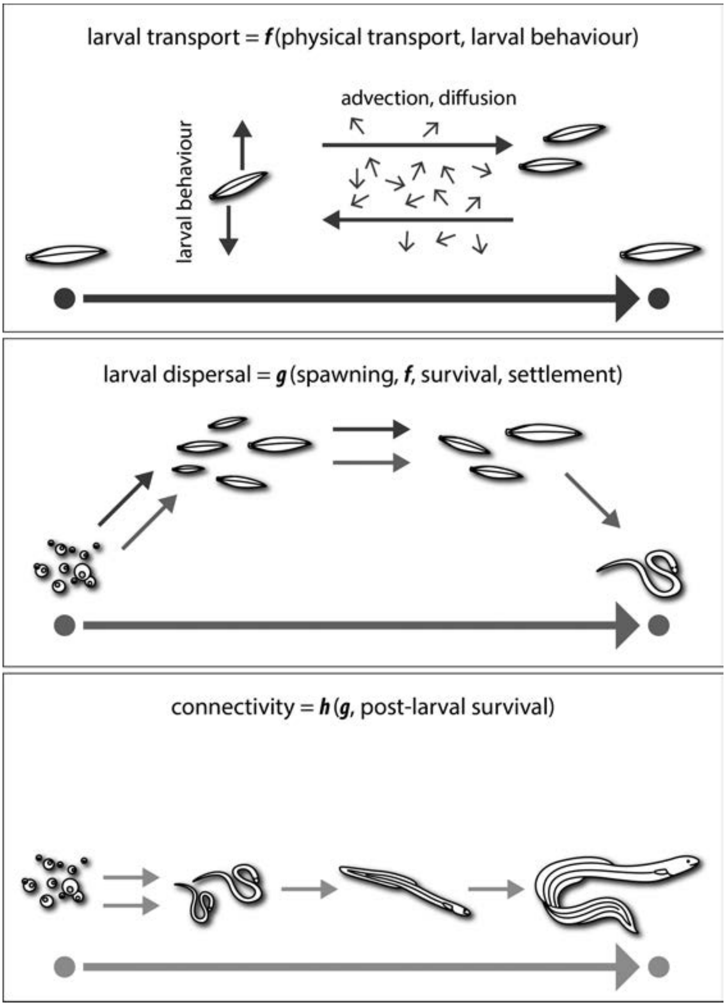

Fig. 2. The concepts of larval transport, larval dispersal and reproductive population connectivity. *f*, *g* and *h* are suitable functions. Redrawn after [10].

introduce specific biological characteristics of the organisms being investigated, including their ability to autonomously move and their post-larval survival. We will not make a general review of the topic, rather we will illustrate some of the recent results of the work performed by our research group. More specifically, we will deal with cases of increasing biological complexity.

– Pure larval transport (larvae as drifters): the case of Northern Line Islands in the Central Pacific Ocean

– Species-specific dispersal and connectivity: *Posidonia* beds in the Mediterranean Sea

– Making drifters alive: impacts of long-term changes in oceanic circulation on European eel recruitment

– Ecosystems connectivity: the *Posidonia* fish community in the Adriatic Sea.

Connectivity in the Northern Line Islands

Assessing ecological connectivity is of the uttermost importance in marine regions where there exist several species that risk extinction, but might be rescued by means of Marine Protected Areas (MPAs). These can serve as refuges for adult organisms, nurseries for juveniles and sources of propagules for other unprotected areas. The potential of MPAs to effectively operate can be assessed by studying larval transport within MPAs, and between MPAs and non-protected locations that are, however, suitable as nurseries. A paradigmatic example that we have studied [4] is that of the Northern Line Islands (Fig. 3). This archipelago is located in the Central Pacific Ocean and is one of the longest island chains of the planet. The northernmost

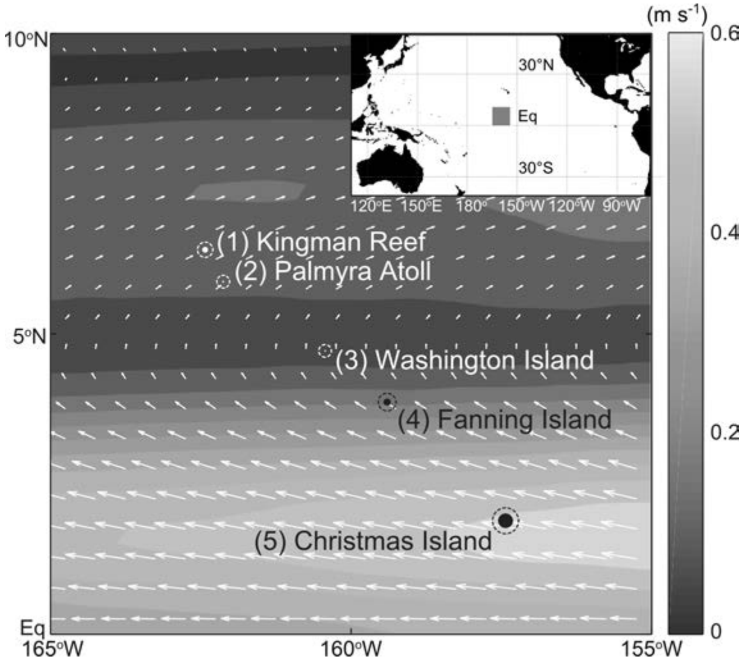

Fig. 3. The Northern Line Islands. Filled dots indicate positions and areal extents of the five islands of the archipelago, from where larvae were released for Lagrangian simulations, while dashed circles enclose the area used as retention zone of each island. The background gray scale represents the magnitude of the surface velocity field (global average 1991-2010), while arrows indicate average flow direction. The study area is highlighted as a gray square in the Central Pacific region (inset). Redrawn after [4].

islands, Kingman Reef and Palmyra Atoll (territories of the United States) are uninhabited and are among the most pristine tropical marine environments worldwide. Both are part of the Pacific Remote Islands Marine National Monument, the largest MPA in the world. The southern part of the archipelago, instead, belongs to the Republic of Kiribati and consists of inhabited islands, whose residents heavily depend on fishing for their subsistence. Thus, there is a strong latitudinal gradient of human impact.

Potential connectivity patterns in the Northern Line Islands archipelago were investigated via individual-based simulations, in which fish larvae were described as passive Lagrangian particles. The Ocean General Circulation Model NEMO v.3.2 was used as the hydrodynamic engine for numerical simulations. A wide range of spawning seasons (month of larval release) and pelagic larval durations (PLD, the amount of time a larva can spend in open waters before eventually settling on a reef), two typical life traits of fish species that heavily influence dispersal dynamics, was used to investigate the effect of intra-annual variability. Inter-annual variability was instead accounted for by performing simulations over a long temporal span, from 1991 to 2010. Based on individual larval trajectories, pairwise between-island connectivity was measured as the fraction of particles released at one island whose trajectories crossed the retention region (defined as a round patch centered at the island coordinates with a radius corresponding to that of the island plus a buffer of 10 km) of another island at any time before the end of the PLD (see e.g. [9]).

As an example, the in/outbound connectivity scores for Palmyra Atoll in year 2000 are shown in Fig. 4. Local larval retention is present for the months from January to June (except for May). Palmyra Atoll appears to act as a potential propagule source for Kingman Reef (from January to May, but mostly in February-April), while no outbound connectivity to the other islands is observed. As a sink, Palmyra Atoll receives propagules from all the other islands of the archipelago. Connectivity to Palmyra Atoll is especially strong for larvae released during January-April. Some connectivity is also observed from the three southernmost islands between October and December. In general, longer PLDs are found to favor between-island connectivity. Remarkably, average connectivities within the Pacific Remote Islands Marine National Monument (i.e. between Kingman Reef and Palmyra Atoll) are typically stronger than connections between Palmyra Atoll and the southern islands of the archipelago.

Potential connectivity can significantly fluctuate from year to year, following interannual variations of the circulation fields. As an example, Fig. 5 shows how connectivity patterns from Palmyra Atoll to Kingman Reef and from Christmas Island (the southernmost island of the archipelago) to Palmyra Atoll have changed over a twenty-year period. Interannual variations appear to be at least partially associated with the El Niño–Southern Oscillation. Specifically, yearly averages of the South-to-North connectivity scores are negatively correlated with the yearly averages of the El Niño–Southern Oscillation signal [4].

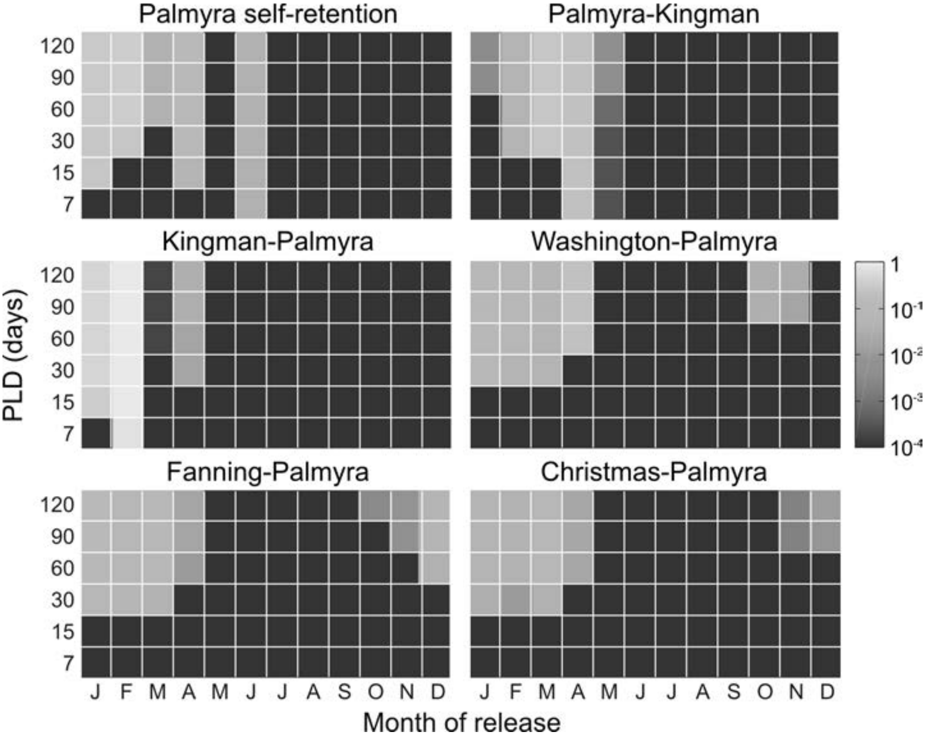

Fig. 4. Connectivity scores for Palmyra Atoll as a function of spawning season and PLD (year 2000). Connectivity patterns to the other islands are not shown because connectivity scores are less than 1% for every combination of PLD and release season. Redrawn after [4].

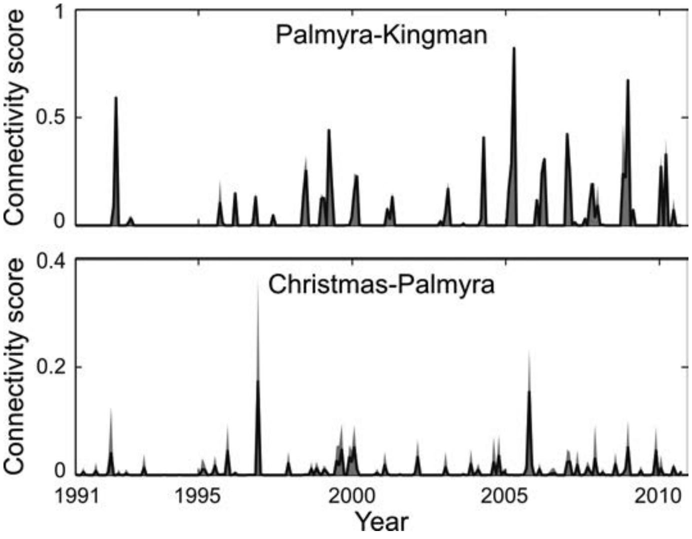

Fig. 5. Inter-annual variability of connectivity patterns within the Northern Line Islands archipelago for the period 1991-2010. Black solid lines represent monthly connectivity scores averaged over the set of PLDs considered in Fig. 4, while the gray shaded areas report the min-max range of the PLD-specific connectivity scores. Redrawn after [4].

Overall, our results suggest that, despite the temporal intermittency of some features, the main patterns of connectivity within the Northern Line Islands archipelago are quite clear in terms of their directions and intensities. Specifically, Kingman Reef and Palmyra Atoll act more as sinks of particles from the southern islands than as sources of larvae for them. Thus, the protected part of the archipelago extends its conservation reach well beyond its geographical borders. In fact, even larvae released from the more impacted southern islands can ultimately reach the northern sanctuary, which may therefore serve as a nursery for juveniles that were originally born elsewhere. Conversely, larval dispersal from North to South seems to be more sporadic, thus unlikely to be ecologically important. It is worth remarking that the increasing anthropogenic pressures in action on Washington, Fanning and Christmas islands might turn the South-to-North connectivity also into an emerging potential threat. In fact, any pollutants or alien species possibly departing from the southern islands, which are the most inhabited by humans, have non-negligible chances of reaching Palmyra Atoll and/or Kingman Reef.

Dispersal in Posidonia *beds of the Mediterranean Sea*

The seagrass *Posidonia oceanica* is considered the most important and well-studied seagrass species of the Mediterranean Sea. It supports fundamental marine food webs in all coastal areas of the Mediterranean large marine ecosystem. Unfortunately, this species, which is not only important *per se*, but also as a habitat forming organism for many other marine species, is declining at an alarming rate (about 1.5% every year in recent years). Within the framework of the H2020 Ecopotential Project (www.ecopotential-project.eu), we have evaluated the connectivity of *P. oceanica* beds in the whole Mediterranean from 1987 to 2016 on the basis of Earth-Observation guided ocean re-analyses. Given the long time span considered, we also aimed to detect possible impacts on connectivity of ongoing climate change.

Connectivity patterns were explored via Lagrangian simulations, in which purely passive transport of the seagrass fruits between locations that are suitable for *P. oceanica* beds was simulated, according to the species-specific reproductive schedule and dispersal traits. A general map of potential suitability for the seagrass was obtained from the MEDISEH-Marea project (Mediterranean Sensitive Habitats), while the physical engine for the biophysical simulations was provided by the Copernicus Marine Environment Monitoring Service (marine.copernicus.eu). Ecological connectivity was then evaluated according to an *ad-hoc* definition accounting not only for the strength of dispersal (evaluated as the number of trajectories linking directionally two suitable sites) driven by purely oceanographic factors, but also for the species-specific suitability scores of the release and settling sites. As an example, the suitability-weighted connectivity map for year 1995 is shown in Fig. 6.

Suitability-weighted connectivity was evaluated over time to single out the strongest and most time-persistent ecological connections for *P. oceanica* across the

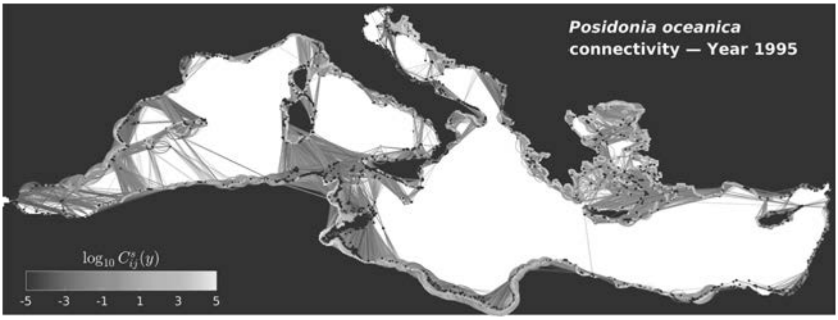

Fig. 6. Patterns of suitability-weighted connectivity for *P. oceanica* across the Mediterranean Sea for the year 2005. Connectivity between two sites (say, *i* and *j*) is defined as $C_{ij}^s = s_i\, n_{ij}\, s_j$, where n_{ij} is the numer of fruits released at site *i* reaching site *j*, whereas s_i and s_j are the suitability scores of the source and settling sites, respectively. In the map, dots represent self-retention C_{ii}^s, while links represent pairwise connectivity scores C_{ij}^s (with $i \neq j$).

Mediterranean Sea, specifically in terms of the possible functional roles that a local population can play. To characterize this role, we calculated the fluxes originating from and received by the same marine site (*retainer*), originating from a site and received by any other (*source*), and originating from any other and arriving to a site (*sink*). Following the methodology proposed by [7] we have produced connectivity rankings for the different Mediterranean sites, namely giving higher scores to locations that are better retainers, sources and sinks in terms of both sheer intensity and temporal persistence. In this way, we identified possible hotspots of *P. oceanica* ecological connectivity (Fig. 7). For instance, the top-100 hotspots appear to be unevenly distributed in all of the four principal sub-basins of the Mediterranean Sea, mainly along the Spanish coastline in the Balearic Sea, on the Western coast of Sardinia, in the Norhern Tyrrhenian Sea (Western Mediterranean region), along the coasts of Tunisia and Libya and in the Ionian Sea (Central Mediterranean region),

Fig. 7. Hotspots of ecological connectivity for *P. oceanica* in the Mediterranean Sea. Shown are the top-100 suitability-weighted connectivity hotspots.

in the North-Eastern Adriatic Sea (Adriatic region), and in the Aegean Sea and along the Egyptian coastline (Eastern Mediterranean region).

Temporal trends in local connectivity metrics are shown in Fig. 8. The occurrences of statistically significant ($p < 0.05$) negative linear trends outnumber the occurrences of positive ones for both self-retention and indegree. Interestingly, *Posidonia* connectivity hotspots are characterized by relatively fewer occurrences of increased self-retention and more instances of decreased self-retention compared to the whole Mediterranean Sea. By contrast, positive indegree trends are more prevalent

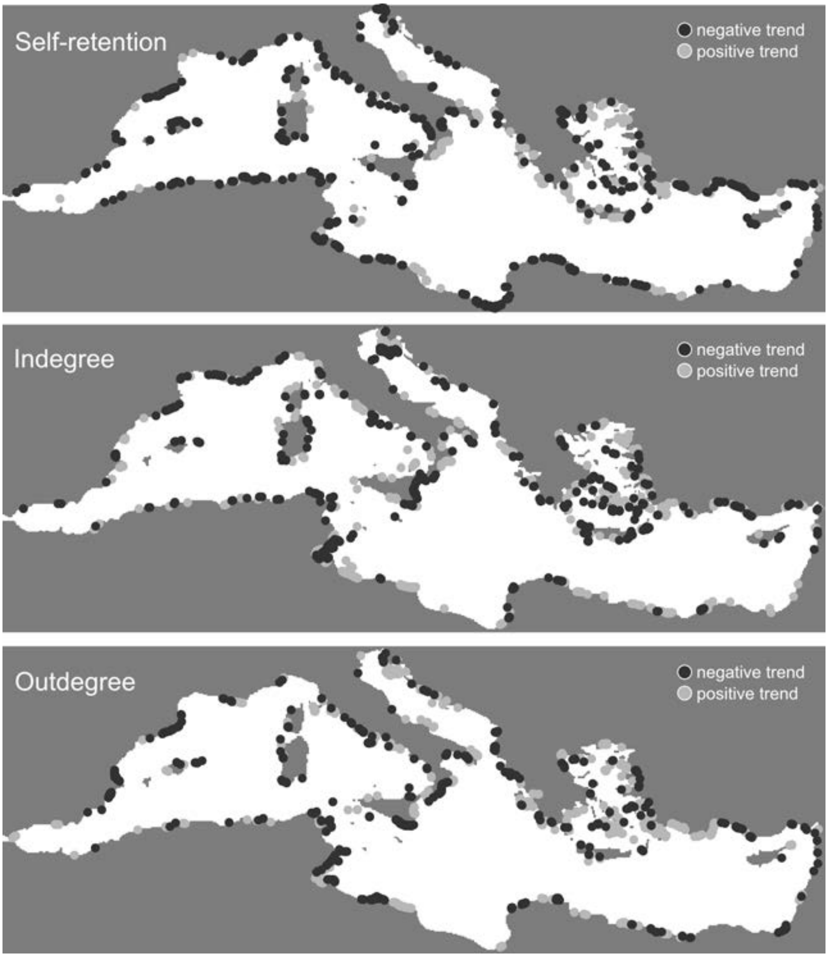

Fig. 8. Directions of change in local time series of *P. oceanica* connectivity metrics. Shown are the marine sectors for which statistically significant trends are detected over the period 1987-2016. With the term indegree (respectively, outdegree) we indicate the ability of different locations to act as sinks (sources).

among connectivity hotspots than in the whole Mediterranean Sea, while negative indegree trends are less frequent in connectivity hotspots. Outdegree trends appear to be less variable when evaluated over the whole Mediterranean Sea or restricted to connectivity hotspots, yet statistically significant trends (either positive or negative) in outdegree time series are more frequently observed in connectivity hotspots.

The results of our large-scale and long-term assessment suggest that spatiotemporal variability is an important component of *P. oceanica* connectivity in the Mediterranean. Clearly, such variability makes the identification of connections that are both sufficiently strong and time-persistent to be ecologically relevant a completely nontrivial task, especially in the heavily anthropized coastal ecosystems of the Mediterranean Sea [8]. Also, the finding that significant trends in connectivity are more frequently identified in connectivity hotspots suggest that the role played by these marine sites in structuring the dispersal dynamics of *P. oceanica* might be changing over time, with implications for the future of large-scale propagule exchange in the Mediterranean Sea. This, together with the prediction that the Mediterranean basin will be one of the regions most affected by global change [3], suggests that these hotspots might deserve special protection, and reaffirms the idea that decisions regarding marine protection should also aim to enforce resilience against climate change impacts [5].

Making drifters alive: the long trip of European eel

Up to now, we have considered passive transport alone, but in many cases propagules are also capable of active motion. Most fish larvae are not only transported by oceanic currents but can swim in specific directions. A case study that our research group has pursued for many years is that of the European eel, *Anguilla anguilla* L. This catadromous species has a very unique life cycle which is summarized in Fig. 9. In the past 50 years, a synergy of factors has led the European eel stock on the edge of collapse (recruitment has experienced a >99% drop with respect to historical levels): habitat loss, chemical contamination, parasitic diseases, over-exploitation, and possibly oceanic changes. It is this last factor that we have recently explored with reference to the dispersal of larvae (the so-called leptocephali) from the Sargasso Sea to the European shores. This dispersal phase can last up to 3-4 years. Therefore, our approach has explicitly accounted for larval body growth and the implications that body size has on the mortality rate of leptocephali, their swimming speed and the depth of diel vertical migration. We can thus term such a model as physical-biological, not purely physical (passive transport only).

Relying on ocean circulation models that performed physical reanalysis of ocean currents from 1958-2000, we have run Lagrangian simulations tracking the dispersal of millions of growing and actively swimming larvae departing from the spawning area of the Sargasso Sea. We have let the individual eel larvae be carried by the currents (as described by the circulation model), providing them with key biological

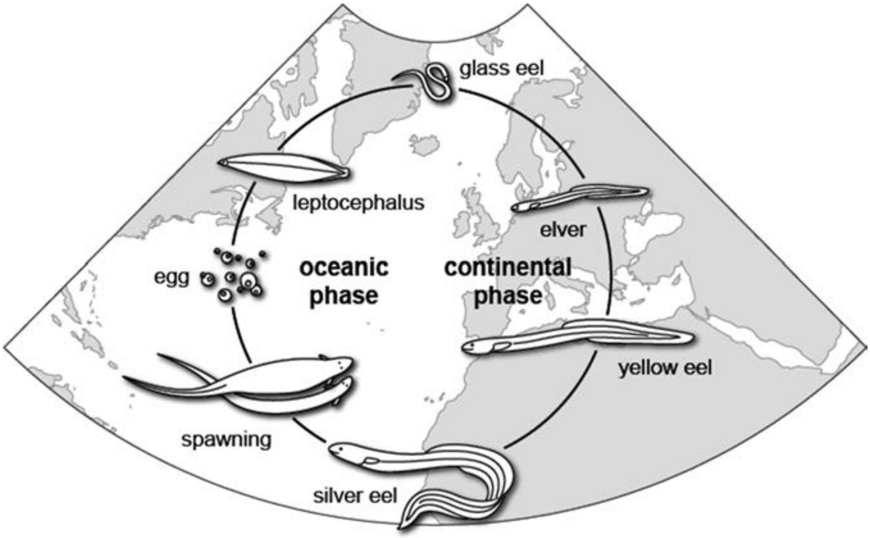

Fig. 9. Life cycle of the European eel *A. anguilla*. Modified from [1].

features that affect migration. These include the ability of larvae to swim autonomously and to move up and down in the water column to feed and avoid predators. We have first calibrated the model against field data from oceanic surveys conducted in the 1980s, including the distribution of larvae in the area of reproduction and near continental shores [6]. The calibrated model has then been used to simulate the migration of eel larvae along the time horizon 1958-2000, monitoring eel arrivals at the 15th meridian west [11]. Results are reported in Fig. 10 and can be summarized as follows:

- there is a weakly significant decreasing trend in migration duration
- the median migration duration has decreased by 6 days per year (7 months in 40 years)
- there is a strongly significant decreasing trend in the mean latitude of arrivals
- the mean latitude has moved southwards by 1/4° per year (10° in 40 years)

Ecosystems connectivity: the Posidonia *fish community in the Adriatic Sea*

Understanding connectivity patterns of single paradigmatic species with high cultural, economic or ecological role is important; however, biological conservation should adequately consider the complexity of ecosystems across a range of spatial scales instead of focusing on single species. For instance, marine protected areas increasingly aim to protect biodiversity in a holistic fashion. The COCONET project (towards COast to COast NETworks of MPAs - from the shore to the high and deep sea- coupled with sea-based wind energy potential) has recently investigated the role

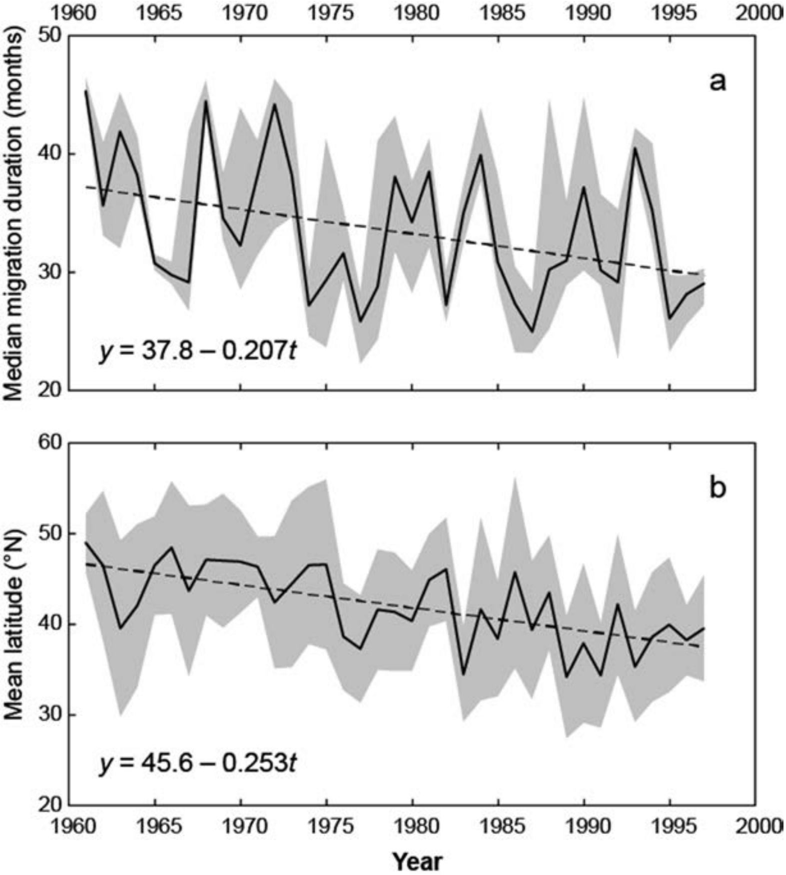

Fig. 10. Reconstructed time series of the main features of the oceanic migration of European eel larvae from the Sargasso Sea to the 15 °W meridian. (a) Median (solid line) and interquartile range (shaded area) of the median migration duration. (b) Mean (solid line) ± standard deviation (shaded area) of the latitude of arrival. Dashed lines indicate the corresponding regression lines. Modified from [11].

of networks of marine protected areas in guaranteeing ecological connectivity across the Mediterranean Sea [2].

To establish MPA networks and assess their effectiveness, the concept of connectivity should be extended from a single-species to a community perspective. Within the COCONET project we have considered *P. oceanica* not only per se, but also as a primary producer and habitat former for the trophic web that it sustains [7]. We have focused on a set of key species belonging to the *P. oceanica* community: *P. oceanica* itself, as well as three fish species (*Sarpa salpa*, *Symphodus ocellatus* and *Scorpaena porcus*) occupying different trophic levels and characterized by different dispersing traits (Fig. 11a,b) as regards both season and depth at which propagules are

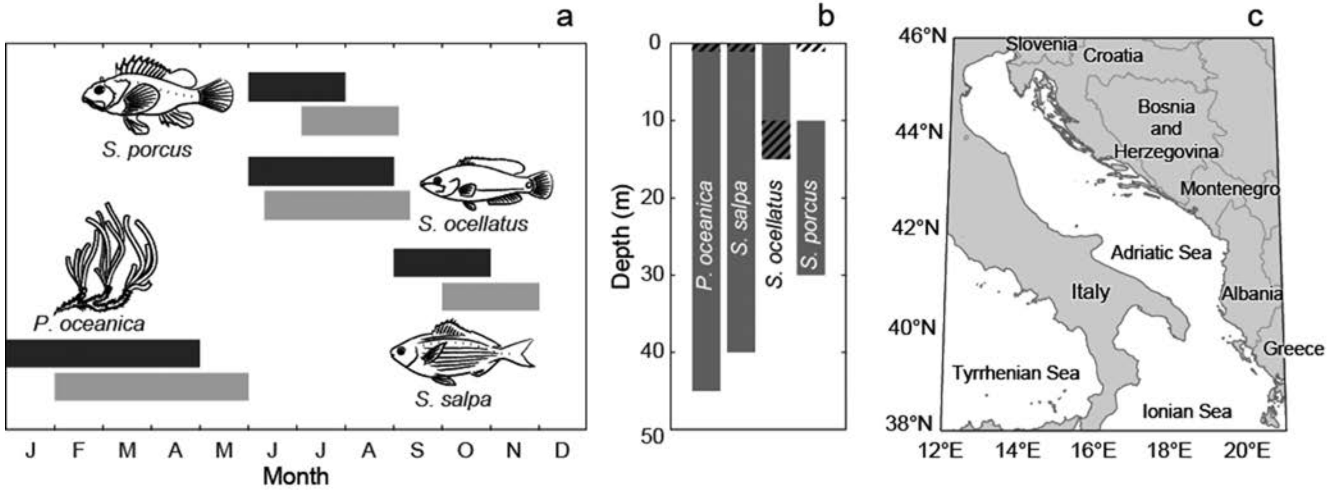

Fig. 11. (a,b) Dispersing features of each species: (a) period of propagule release (upper bar) and recruitment (lower bar); (b) suitable depth range for recruitment (bars) and dispersal depth of propagules (hatched areas). (c) Study area. Modified from [7].

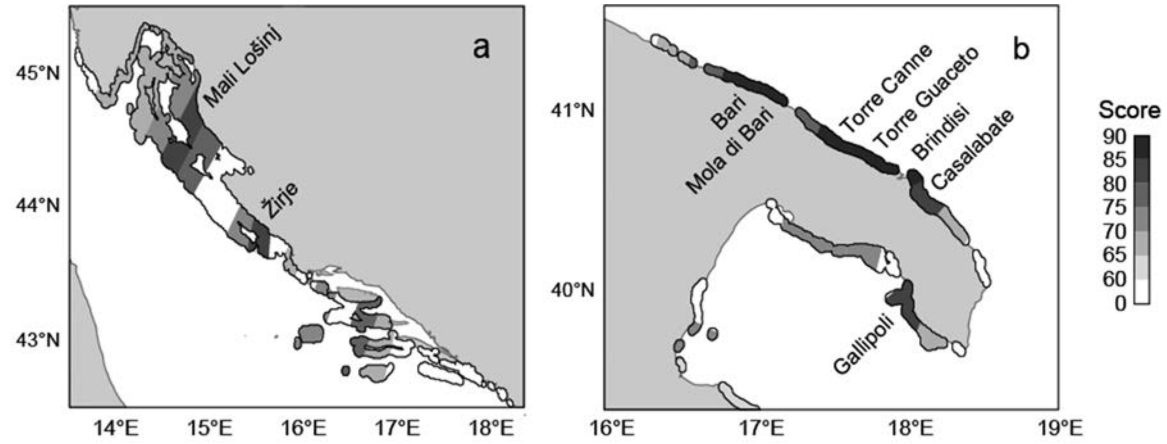

Fig. 12. Sectors of the Adriatic Sea characterized by the highest community connectivity score for an assemblage of four species (*Posidonia oceanica*, *Sarpa salpa*, *Symphodus ocellatus* and *Scorpaena porcus*). Modified from [7].

released. The salema, *S. salpa*, is almost exclusively herbivorous (trophic level 2); the ocellated wrasse, *S. ocellatus*, feeds on bryozoans, hydroids, tubiculous polychaete worms, shrimps, amphipods and molluscs (trophic level 3.5±0.5); the black scorpionfish, *S. porcus*, feeds on small fishes such as blennies and gobies, crustaceans and other bottom-dwelling invertebrates (trophic level 3.9±0.7).

We have explored the connectivity of this species assemblage over a decade (2003-2013) within a region of about 250,000 km^2 in the central Mediterranean, encompassing the Adriatic Sea and the northernmost part of the Ionian Sea (Fig. 11c). The methodology used to assess the connectivity of each single species is basically the same as the one we described above for the *Posidonia* beds of the whole Mediterranean. In fact, connectivity was characterized by the effectiveness, that is the capacity to retain/donate/receive propagules, and persistence, that is the continuity of the flux of propagules throughout the years. To single out the locations that are most prominent in terms of the conservation of the 4-species assemblage, we aggregated species-specific indicators into a set of indices characterizing connectivity at the community level. To account for the fact that poor connectivity in one species cannot be completely compensated by good levels of connectivity in other species, we calculated each community index as the geometric mean of the corresponding species-specific indicators. The geometric mean is a measure of central tendency that places more weight (compared with the arithmetic mean) on the lowest values, thus providing a conservative measure of community connectivity. In this way, we have been able to identify hotspots of community connectivity. Fig. 12 shows the sectors with the highest community connectivity score along Croatian (a) and Apulian (b) coasts.

Conclusions

Part of the complexity characterizing ecological systems is in that they display spatial and temporal patterns that depend on both local dynamics and the mechanisms of spatial connection. Such a complexity is particularly challenging in the marine environments because oceanic currents have the power of establishing ecologically relevant connections between locations that may be quite remote in terms of geographic distance (thousands of kilometres) and in a persistent (even if possibly fluctuating) manner for decades.

Big data provided by Earth Observation and the availability of incredible amounts of geo-referenced data at high resolution has made it possible to conceive the use of realistic space-explicit models that can provide scenarios, forecasts and guidelines for decision makers. Models of that kind can in fact incorporate climate variability too, thus making them very useful tools not only for the current management of marine ecosystems but also for a better planning of the management of our future environment.

Lagrangian simulations like those presented in the present paper allow in fact the study of the effects of long-term changes in species-specific connectivity patterns.

Connectivity is a factor of primary importance to design conservation programs for vulnerable communities as well as to understand changes of provisioning ecosystem services. According to the biological characteristics of each species (such as timing and depth of spawning, pelagic larval duration, …), the resulting *ecological connectivity* between marine ecosystems may be quite different from the *average oceanographic connectivity* between marine locations and can therefore be subject to species-specific (or community-specific) detectable and significant temporal trends. Such trends are not necessarily found by large-scale, purely oceanographic studies, because they may be averaged out in space and/or time with other significant trends of opposite sign or with a large majority of other patterns that show no significant trends at all. In other words, our work suggests that policy makers should inform their decisions on *ad hoc* designed connectivity studies accounting for the relevant ecological characteristics of the communities at hand.

Acknowledgments

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BIBLIOGRAPHY

[1] Bevacqua D., P. Melià, M. Gatto & G.A. De Leo (2015). A global viability assessment of the European eel. Global Change Biology 21: 3323-3335. doi: 10.1111/gcb.12972.

[2] Boero F., F. Foglini, S. Fraschetti, P. Goriup, E. Macpherson, S. Planes, T. Soukissian & the CoCoNet Consortium (2016). *CoCoNet: towards coast to coast networks of marine protected areas (from the shore to the high and deep sea), coupled with sea-based wind energy potential.* SCIRES-IT 6: 1-95. doi: 10.2423/i22394303v6Sp1.

[3] Lejeusne, C., P. Chevaldonné, C. Pergent-Martini, C.F. Boudouresque & T. Perez (2010). Climate change effects on a miniature ocean: The highly diverse, highly impacted Mediterranean Sea. Trends in Ecology & Evolution 25: 250-260. doi: 10.1016/j.tree.2009.10.009.

[4] Mari L., L. Bonaventura, A. Storto, P. Melià, M. Gatto, S. Masina & R. Casagrandi (2017). Understanding large-scale, long-term larval connectivity patterns: The case of Northern Line Islands in the Central Pacific Ocean. PLoS ONE 12: e0182681. doi: 10.1371/journal.pone.0182681.

[5] McLeod, E., R. Salm, A. Green & J. Almany (2009). Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment, 7:362-370. doi: 10.1890/070211.

[6] Melià P., M. Schiavina, M. Gatto, L. Bonaventura, S. Masina & R. Casagrandi (2013). Integrating field data into individual-based models for the migration of European eel larvae. Marine Ecology Progress Series 487: 135-149. doi: 10.3354/meps10368.

[7] Melià P., M. Schiavina, M. Rossetto, M. Gatto, S. Fraschetti, R. Casagrandi (2016). Looking for hotspots of marine metacommunity connectivity: A methodological framework. Scientific Reports 6:23705. doi: 10.1038/srep23705.

[8] Micheli F., N. Levin, S. Giakoumi, S. Katsanevakis, A. Abdulla, M. Coll, S. Fraschetti, S. Kark, D. Koutsoubas, P. Mackelworth, L. Maiorano & H.P. Possingham (2013). Setting priorities for regional conservation planning in the Mediterranean Sea. PLoS One 8: e59038. doi: 10.1371/journal.pone.0059038.

[9] Paris, C. B., R.K. Cowen, R. Claro & K.C. Lindeman (2005). Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. Marine Ecology Progress Series 296:93-106. doi: 10.3354/meps296093.

[10] Pineda, J., J.A. Hare & S. Sponaugle (2007). Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20(3):22–39. doi: 10.5670/oceanog.2007.27.

[11] Schiavina M., R. Casagrandi, M. Gatto, L. Bonaventura, S. Masina & P. Melià (2013). Has the ocean contributed to the decline of European eel recruitment? Results of a 40-year simulation experiment. *Prima Conferenza Annuale della Società Italiana per le Scienze del Clima (SISC)*, Lecce, Italy, 23-24 September 2013.