EXECUTIVE SUMMARY [1]

This synthesis, outlined during the course of the workshop was developed and consolidated in the following months on the basis of further inputs provided by the participants under the coordination of Salud Deudero. Frederic Briand, who reviewed and edited the entire Monograph, is grateful to Céline Barrier for overseeing the entire physical production of this volume.

1. INTRODUCTION

The dynamics and function of a given ecosystem will very much rely on the intensity, frequency and patterns of interactions among its biotic and abiotic components across space and time. These elements all constitute the matrix of marine connectivity which will also include the multiple linkages among related ecosystems, as those between mangroves, coral reefs and seagrasses habitats depicted in the simplified diagram below (Figure.1).

Such interactions are complex and particularly difficult to investigate in marine systems where data collection at different scales poses even greater challenges than in terrestrial or freshwater environments. Such is the context of this volume is the outcome of a workshop that was conducted by Dr Frederic Briand, Director General of the Mediterranean Science Commission, together with Dr Salud Deudero, co-chair of CIESM Committee on living resources, precisely to explore and discuss the latest findings to match challenges and key issues in the broad sector of marine connectivity. To this end, 14 scientists from diverse horizons and disciplines were invited by CIESM in the early spring of 2016 in Sóller on the island of Majorca. Exchanges during and following the workshop were rich, collective, and are well reflected in this opening, synthetic chapter.

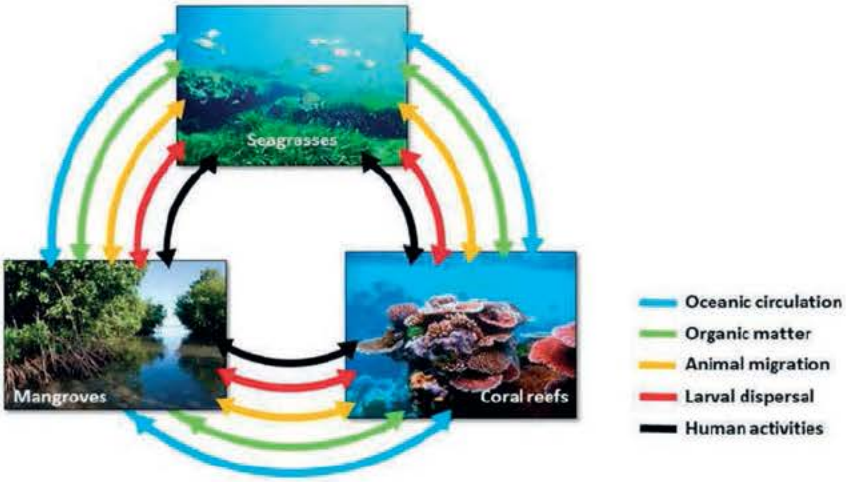

Figure 1. Some of the multiple interactions linking coastal ecosystems.

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[1] to be cited as:

Deudero S., Arnaud-Haond S., Di Franco A., Fromentin J-M., Gucu A.C., Hilário A., Mariani P., Panigada S., Pascual M., Rossi V., Soldo A., Villamor A., Zalota A.K. and F. Briand. 2016. – Executive Summary. pp. 5 - 18 *In* CIESM Monograph 48 [F. Briand ed.] Marine connectivity – migration and larval dispersal, 172 p., CIESM Publisher, Monaco.

Trophic interactions among marine species have received much scientific attention in the last 20 years; resulting in increasingly complex depictions of marine food webs and a better understanding of their vulnerability to human pressure and climatic change (see Figure. 2). While an exhaustive review of empirical studies embracing marine food web topology, diversity and ecosystem function is clearly beyond the perimeter of this volume, it is called for and will be the focus of a future CIESM workshop. For its part, this Monograph will largely concentrate on the mechanisms and processes like adults migrations and passive dispersal of larvae and propagules, genes flows, anthropogenic transport (ballast, aquaculture, etc.) – which connect populations, stocks or cohorts to distinct geographic areas, such as feeding grounds, spawning grounds or nurseries.

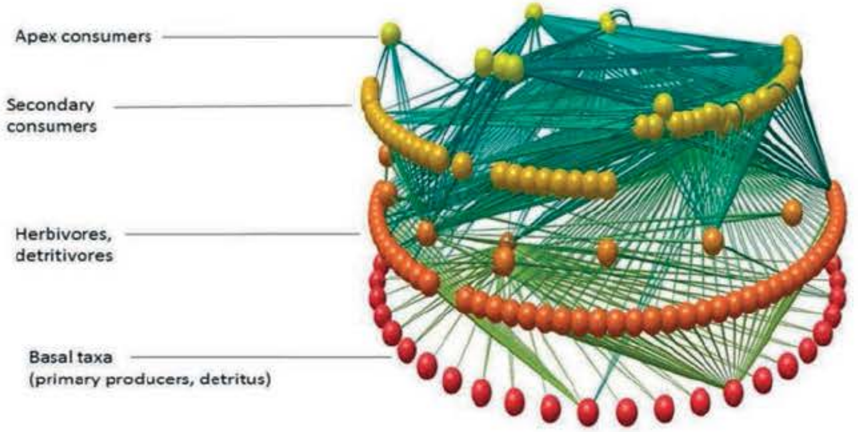

Figure 2. Main linkages among the 142 trophic species of a marine food web in the northeastern Pacific Ocean (Adapted from Dunne *et al.,* 2008).

The dynamics and high variability of seawater masses have marked effects on the connectivity of marine systems. The ocean can be described as a strongly heterogeneous medium in perpetual movement with non-linear processes occurring at various scales, from diffusive processes and small eddies to basin scale currents. The transport of materials by ocean current extends the spatial scale of many processes such as propagules dispersal (Shanks *et al.,* 2003); so that marine systems tend to be more "open" than their terrestrial counterparts. This relatively high "openness" of marine populations has marked influences on their spatial, genetic and demographic structures and dynamics (Carr *et al.,* 2003). In recent years, oceanographers recognized the prominence of mesoscales and sub-mesoscales structures (i.e. scales spanning approximatively 1 to 100km, and 1 day to 1 year) in oceanic flows (see CIESM, 2005), revealing both the presence of barriers (which prevents the dispersion of propagules) and of preferential corridors of transport (favoring efficient connection) with important consequences for the dispersal and retention of non-swimming larval stages (e.g. Harrisson *et al.,* 2013).

Even for actively and highly mobile life-stages (e.g. large pelagic organisms), oceanic circulation governs the spatial distribution of environmental variables and planktonic food and plays a crucial role in controlling the location, timing and success of spawning, dispersal and settlement (Mariani *et al.,* 2010; Reglero *et al.,* 2012). Part of this Monograph is dedicated at characterizing (often with numerical models) transport and dispersion processes in the ocean with consideration for integrating the physical environment in the design of Marine Protected Areas (MPAs). Due to the inherent turbulent and unpredictable nature of geophysical flows, transport and mixing phenomena in the ocean remain difficult to evaluate clearly.

For most marine organisms, connectivity is essential, providing access to feeding and nursery grounds, and protection against predators. Furthermore, the level of connectivity between distant ecological regions can drive biomass exchanges and metapopulation structure, regulating biodiversity and community structure in the ocean, and hence ecosystem functioning and its resilience to perturbations.

For a number of large migratory species, the presence of accessible migratory corridors is essential to gain access to suitable conditions for feeding or reproduction. Changes in the structure of such corridors, due for example to environmental changes or direct anthropogenic pressures (e.g. fishing, ship traffic), will affect the level of recruitment success for the population. The importance of the stability of connecting corridors is well illustrated by the case of the Atlantic bluefin tuna, developed in the next section.

2. THE SCALE OF MARINE CONNECTIVITY

Marine connectivity is a process operating over multiple temporal and spatial scales. Species can show substantial variability in the spatial extent of dispersal and connectivity among different life stages (e.g. larvae, juveniles and adults in fish species), with planktonic drifting stages usually considered as major determinant of connectivity in a species (Burgess *et al.,* 2014) despite exceptions (see Di Franco and Guidetti, this volume). Marine species have generally complex life cycles that include multiple life stages with differential behavior driving connectivity at multiple spatial scales.

At temporal scales, connectivity is a process operating along a continuum that, for the sake of simplicity, can be divided in two elements: historical and contemporary. Within the historical time frame, marine connectivity usually operates over large spatial scales and may depend on frequent but also rare events over long or intermediate time periods that may not be contemporary. Historical processes have a large impact in species distribution and may leave footprints of adaptation to the local environment but also of random processes, whether or not mediated by demographic events. Contemporary processes of connectivity may operate at a variety of scales that are extant, or have occurred recently and can affect the future in a short term but also at an historical level (Leis *et al.,* 2011).

Connectivity patterns are most likely the result of interacting processes operating at different geographic (e.g. small and large) and temporal scales (e.g. historical and contemporary). Thus historical processes can have a large impact in selection mediated by adaptation and influence contemporary processes. Temporal genetic changes observed across oceanographic discontinuities in the crab *Liocarcinus depurator* have been related to changes in water masses circulation showing the existence of contemporary gene flow; nonetheless the transiency of the change seems to respond to over-imposed selection (Pascual and Macpherson, this volume). Similarly, persistent contemporary connectivity can influence evolutionary processes.

For these reasons, investigating the patterns of dispersal and connectivity at multiple spatial and temporal scales is crucial to unveil the complexity of all the processes involved. Since connectivity studies will have different objectives (e.g. biodiversity conservation, fisheries management, marine spatial planning, the design of networks of marine protected areas), integrating information about processes at specific temporal and spatial scales is required. To this end, one must select one, or a combination of those complementary methods, as a function of the scientific questions or management objectives to be addressed.

3. HOT RESEARCH TOPICS IN MARINE CONNECTIVITY

3.1 Connectivity of highly migratory species

The last couple of decades have seen the development of technological tools which allow the tagging and tracking of several mobile large vertebrates, (see for example Block *et al.,* 2011). Satellite tags have been deployed on a large variety of apex predators, including sea turtles, sword fish, bluefin tuna, giant devil rays and cetaceans, providing invaluable data on migration routes and movement patterns and allowing the identification of breeding/feeding areas.

3.1.1 Sharks and rays

Cartilaginous fishes are generally K-selected. In other words, they are characterized by low fecundity, large juveniles, slow growth, late maturity, long life and high survival at all age classes. Thus, they have a low reproductive potential and a low capacity for population increase which makes them poor candidates for sustainable fisheries exploitation. Hence, many of them have advanced characteristics such as placental reproduction and live birth, homeothermy, very large brains and, especially, extremely sophisticated sensory capacity that allows them to migrate vast distances through our seas and oceans, swimming across a number of national and international jurisdictional boundaries in the process. Our current knowledge is vastly inadequate, even to identify conclusively all migratory sharks. As most of these species have not been the subject of tagging studies, data are missing on their migratory routes. Hence, even when conventional tagging studies have included large numbers of a single species, results did not provide much information on the migratory movements between capture events. The low number of electronic tracking studies carried out so far suggests that many theories about the migration of sharks could be incorrect. For instance, a female great white shark tagged in South African waters revealed the first known transoceanic trip for an individual shark that was travelling farther than any other shark known; more than 20,000 kilometers to the coast of Australia and back (see more in Soldo, this volume). Out of more than 1000 chondrichthyan species, 95 are identified as migratory. Within that group, according to the IUCN Red list of threatened species, 46% (44 species) are found to be threatened, 21% (20 species) Near Threatened, and only 9% (9 species) are Least Concern. This exceeds the current estimates of threat to all other marine and vertebrate taxa, with the exception of reef-building corals and amphibians. Stated/reported/official levels of threat are likely underestimated due to our poor knowledge of migratory chondrichthyans, where data deficiency amounts to a very high 34%.

3.1.2 Bony fish

Until the late 1990s, our understanding of the spatial dynamics of highly migratory bony fish, such as tuna and billfish, was based on fisheries data and conventional tagging until the late 1990s. This knowledge remained incomplete and, for many species, the spawning and feeding grounds were only partially identified or known while the main migratory routes were mostly speculated. In the space of a few years, the emergence of electronic tagging led to a tremendous progress and strongly modified our perception of the spatial dynamics of these species (Block *et al.,* 2005; Bestley *et al.,* 2009; Wilson *et al.,* 2015). As in marine mammals, unexpected migratory behavior has been depicted, with strong variations from year-to-year as well as among individuals of the same population (e.g. Galuardi *et al.,* 2010; Dewar *et al.,* 2011). At the same time, the accumulation of information allowed the identification of recurrent patterns: the mixing in given areas of different populations, the long residency in specific feeding grounds as well as homing behavior (e.g. Walli *et al.,* 2009, Fromentin, in this volume). The major difficulty with electronic tagging relates to the representativeness of the sampled fish to the population as a whole (electronic tagging remaining very expensive, with a relatively small sample size). Furthermore, electronic tagging does not provide the location of birth of the migrating fish - key information needed for a greater understanding of the spatial dynamics and population structure.

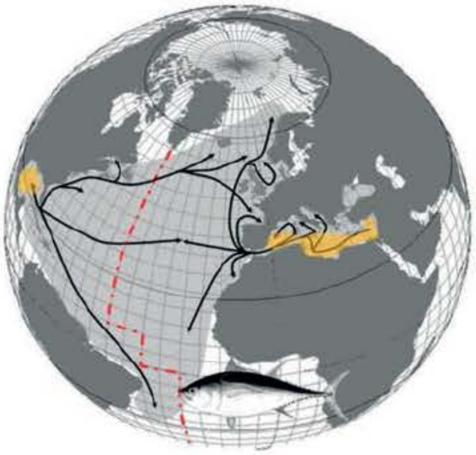

Figure 3. Spatial distribution of the Atlantic bluefin tuna between the two ICCAT management units separated by the red dotted line. The main migratory routes (in black) and the major spawning ground (in yellow) are indicated (Adapted from Fromentin and Powers, 2005).

There would be a significant gain to use biochemical, genetic and tagging techniques (see Arnaud-Haon, Pascual and Macpherson, Di Franco and Guidetti, this volume) simultaneously. This would enable scientists to obtain information on population structure and on key ecological processes (e.g. identification of the spawning and foraging sites, detection of natal homing, migration patterns and connectivity between main areas). Therefore it might be possible to investigate residency/migratory behavior among different sub-populations as well as the level of adaptation of some key biological processes to local/regional environments. By combining individual markers, one may obtain complementary information, as well as higher validation and precision, since genetic, chemical and electronic markers display different limitations and performances.

Throughout its thousand years of exploitation, catches of Atlantic bluefin tuna (ABFT) have exhibited notable changes in both time and space (Mather *et al.,* 1995), likely reflecting the high mobility of the species illustrated in the figure opposite (Figure. 3).

During the 20th century, large Nordic and Japanese fisheries reached unexpected fishing grounds, i.e., the North and Norwegian Seas and the equatorial Atlantic, to suddenly disappear after a few years or decades. Those variations seem to be primarily due to environmentally driven changes in ABFT migration patterns that could act in synergy with local/regional overfishing (Fromentin, 2009). One of the most striking changes in ABFT spatial distribution was the so-called "Brazilian episode", during which Japanese longline fishing boats caught large quantities of ABFT (a temperate species) in the equatorial Atlantic, where they were targeting tropical tunas (Fromentin *et al.,* 2014). Analysis of an extensive dataset of catch and environmental variables from 1960 to 2009 showed that favorable environmental conditions for ABFT prevailed in the western equatorial Atlantic during the 1960s, exactly where the Japanese vessels caught ABFT. The 1960s were the only decade in the last 50 years that exhibited relatively high probability of ABFT occurrence around the equator. ABFT could have thus migrated from the southeastern Atlantic to the western spawning grounds of the Gulf of Mexico through this "ecological bridge" created by strong oceanographic anomalies. However, this bridge was broken in the late 1960s because of oceanographic changes affecting sea surface temperature and possibly the equatorial current and counter-current, making ABFT migration from/to the South Atlantic more difficult and probably affecting the productivity of the western Atlantic ABFT (Fromentin *et al.,* 2014). Current global warming can also open up new corridors and habitat expansion towards northern areas (e.g. Greenland) (Mariani, this volume).

3.1.3 Cetaceans

The technology is evolving rapidly and the resolution of the data collected, either by archival or satellite-linked instruments, is becoming more precise and highly defined, and allowing fine scale description of habitat use and behavioral patterns. Satellite-linked transmitters have recently revealed unpredicted and undescribed migration routes which alter our knowledge of migration patterns. For example, Mate (2015) reported that a female western gray whale (*Eschrichtius robustus*) living off Russia's Sakhalin Island, where these cetaceans feed every year, swam from there to Mexico and back again – a total of 22,500 km – in 172 days. Western gray whales are critically endangered and little information is available on these animals' migratory path. In fact, many researchers previously suspected that the whales migrated in a loop from Russia to the South China Sea. This extreme migration route would have remained undiscovered without the deployment of satellite transmitters on western gray whales off Sakhalin Island. Satellite transmitters have been also applied on Mediterranean fin whales, providing evidence of movement patterns not described previously and providing conservation and mitigation tools to address anthropogenic pressures and threats within the Basin (Panigada and Pierantonio, this volume). Advanced statistical modelling, coupled with satellite derived data is now available to integrate movement data with behavioral patterns so as to better understand and quantify the complex processes of individuals' dispersal at multiple spatial and temporal scales.

3.2 Connectivity of habitat-forming species

Coralligenous assemblages are considered among the most important endemic ecosystems found in the Mediterranean Sea. They are characterized by a high diversity of species, but also by their vulnerability to environmental changes, namely temperature, and acidification, due to their calcareous nature. These assemblages are formed by a mixture of calcareous algae and corals, which provide habitats for many other sessile and vagile species, adult phases, larval and juveniles of commercially important species (see review by Ballesteros, 2006). Due to their importance for the maintenance of Mediterranean biodiversity, the connectivity patterns of several species of the Mediterranean coralligenous assemblages have been studied.

Among the most important habitat-forming species, the gorgonian coral *Paramuricea clavata* forms dense aggregations between 15 and 2000 meters depth and is subject to recurrent mass mortality events putatively related to climate change, as reported in several areas of the northwestern Mediterranean (Garrabou *et al.,* 2009). Basic biological traits of this species are known, such as its reproductive cycle and early life demographic parameters (Coma *et al.,* 1995; Linares *et al.,* 2008), complemented with observations on the larval behavior and dispersal capacity, which is very short. Fine scale molecular studies have evidenced a significant genetic differentiation at very small scales of a few meters, probably related to a combination of hydrographic factors such as the depth and seasonality of the thermocline (Mokhtar-Jamaï *et al.,* 2011). Molecular tools also allowed identifying recent colonization events, attributing the origin of the migrants to different areas, and showing that contemporary connectivity is higher than previously thought, while genetic drift strongly impacts the evolutionary makeup of populations (Arizmendi-Mejia *et al.,* 2015). Modelling tools have been recently developed to study the connectivity of this species, explicitly fitting the demographic traits of a metapopulation with hydrographic data (Padrón and Guizien, 2015). At larger geographic scales, the genetics of this gorgonian fits a pattern of isolation by distance, although most of its differentiation is attributable to mesoscale processes (Mokhtar-Jamaï *et al.,* 2011).

Interestingly, very similar patterns of connectivity have been described for the Mediterranean red coral *Corallium rubrum*, another habitat-forming species of the coralligenous. This long-lived species is known for its economic value, and hence has been subject to a long history of intensive exploitation along the Mediterranean coast, leading to a dramatic shift in the size structure of its populations and local extinction of commercial banks (Santangelo and Abbiati, 2001; Garrabou and Harmelin, 2002). The reproductive cycle of the early stages of this species is well known and complex (Santangelo *et al.,* 2012), indicating low recruitment rates and differential growth rates in the early life stages, probably affected by small scale environmental conditions. In this case as well, the low capacity for larval dispersal would advocate for small scale genetic structuring (Costantini *et al.,* 2007; Ledoux *et al.,* 2010). Last but not least, the combination of empirical data with passive dispersion models turned out useful to integrate the biophysical environment in the full description of this species connectivity patterns (Aurelle and Ledoux, 2013). To date the connectivity patterns of other habitat-forming species or taxa inhabiting coralligenous habitats have not received much attention. Among the few exceptions, the widespread sponge *Crambe crambe* showed contrasting connectivity patterns depending on the molecular marker and the spatial scale of analysis. To overcome this problem, exploratory studies should aim to identify the relevant scales for the processes affecting connectivity at contemporary and historical times (Pascual and Macpherson, this volume).

These emblematic species provide examples of multidisciplinary approaches for the successful study of connectivity within and among the endemic coralligenous assemblages. Demographic, hydrographic and genetic data are necessary at several geographic and temporal scales to properly define patterns of connectivity, but these data are lacking for virtually any other benthic invertebrates in the Mediterranean Sea. The connectivity patterns of a broader range of taxa, including common, rare, colonial, solitary species, etc., and covering a variety of feeding modes, dispersal potential, and life history traits, should be properly described in order to fully understand the dynamics of such crucial ecosystems (Villamor *et al.,* this volume).

3.3 Connectivity in alien species

Alien species transfer around the globe is directly related to human mediated vectors. The introduction of non-indigenous species in the marine environments is most commonly associated with ballast water transfer and hull fouling related to high shipping traffic, aquaculture activities; intentional introductions by humans and aquarium trade (see CIESM, 2002; 2007). These human activities contribute to the homogenization of biodiversity worldwide at an increasing speed. Understanding the areas with high risk of invasion, potentially successful alien species and the vectors of introduction connecting these areas will be crucial for the mitigation of invasions, monitoring and management activities.

Further, once a new species has been successfully introduced in a given area, it is essential to understand the means (natural and human mediated) of its further spread. Different seas have different levels of vulnerability to alien species, due to their natural disconnection from the world oceans and native biodiversity levels. In the Mediterranean Sea, the Suez Canal and the Gibraltar strait do not represent barriers to connectivity for most species, resulting in one of the most invaded seas worldwide. Zalota and Spiridinov (in this volume) address several case studies of secondary spread. The same species, for example *Rhithropanopeus harrisii*, can have different patterns and speed of secondary spread within nearby basins. In the Mediterranean, this species is restricted to a small number of brackish water lagoons (Mizzan and Zanella, 1996; Noël P., 2001; Ben Souissi *et al.,* 2004). In the Baltic Sea, this species shows similar distribution patterns and very slow (~100 years) eastwards spread. On the other hand, the speed of extension of this species in the Black, Azov and Caspian seas is very rapid (10 – 15 years), resulting in vast, occupied territories (the whole Sea of Azov) (Spiridinov and Zalota, in press). These seas have different hydrodynamical properties: the Mediterranean Sea shows high level of mesoscale activity, the Baltic Sea less so, the Black, Caspian and Azov seas even lower. Together with other abiotic and biotic factors, the Harris mud crab may have very weak links within a basin (Baltic and Mediterranean) or strong and highly interconnected network of vectors within an other (Black, Azov, and Caspian). Manmade structures (piers, breakwaters, harbours, ship hulls, aquaculture…) are new artificial substrates acting as steppingstones, especially for hard substrate species. This is illustrated by the Mediterranean bivalve *Pinna nobilis*: their shells are a suitable substrate for the alien macroalga *Lophocladia lallemandii* (Vazquez-Luis *et al.,* 2014) facilitating its spread over seagrass beds.

To understand the fundamental properties of connectivity, research efforts should not be restricted to one basin, but engage in a comparison of different seas. Invasive species provide an interesting and useful model for such studies.

3.4 Connectivity in the Deep Sea

In the deep sea, knowledge on large-scale processes is extremely fragmentary and mesoscale processes remain prohibitively expensive to parameterize, seriously limiting the resolution and accuracy of predictive modelling. Further, among the thousand deep sea species described, knowledge on larval biology is only available for a handful of them, adding potential errors to biophysical models. Therefore, genetics remains the main method in use to provide indirect estimates of connectivity, mainly on benthic species due to the difficulty of sampling mobile species. Since accurate estimates require large sample sizes, studies have been mostly limited to species that dominate the ecosystem in terms of biomass and density (e.g. bivalves, shrimp, corals…). Real important advances have been made and benchmark studies have shown that, in the continuum of high endemism suspected among biogeographic provinces, genetic differentiation occurs on a regular basis and the environment is less homogeneous than initially thought; these different elements appear to support the metapopulation scheme as the best adapted to those environments (Hilario *et al.,* this volume).

Finally, we must emphasize that deep sea studies have thus far mostly focused on ecosystems associated to geologic *anomalies* (such as hydrothermal vents, cold seeps, seamounts) that are detectable from the surface with tools developed for geological exploration of the seafloor, while the abyssal plain that represents about 75% of the ocean floor remains seriously overlooked (Teixeira *et al.,* 2013).

As human activities increasingly impact the deep sea ecosystems, it becomes crucial to understand their spatial distribution and the factors susceptible to impact their spatio-temporal dynamics. Indeed, commercial trawling ploughs more than one million square kilometers of the seafloor below 200m (Priede *et al.,* 2011) and the next decade will see an expansion of oil, gas and mineral extraction into deeper and deeper waters (Van Dover, 2011). At risk are ecosystems that provide a diversity of supporting, provisioning, regulating and cultural services The deep sea remains the least studied biome on our planet (see CIESM, 2003) with very large gaps of knowledge on all aspects related to connectivity (Hilário, this volume).

3.5 Connectivity of exploited species

Estimates of dispersal and connectivity patterns are a key to understand marine populations/stocks dynamics and ultimately properly manage exploited species. In that perspective, management strategies traditionally adopted, differ, in a very large generic sense, in Small-Scale Fisheries (SSF) usually associated with coastal fishes and in Large-Scale Fisheries (LSF) which target pelagic and demersal fishes found in the open sea. LSFs are usually managed by regularly assessing the state of the stocks with respect to the fishery catches and more specifically to the fishing effort. For SSFs, where assessment is a cumbersome practice due to dispersed nature of the fishery, Marine Protected Areas (MPAs) are seen as a proper tool to replenish population of target species.

Stocks refer to geographically distinct units with homogeneous vital rates, and isolated from adjacent resources. They are elementary units in an assessment. Identification of stock unit is the most crucial step when the state of the resource targeted by LSF is to be assessed. This traditional stock concept is violated when different populations exist in the same geographic area, periodically mix, and thus display sympatric structure.

Disregarding the population structure of an exploited fish distributed and mixed in different management areas would lead evidently to overfishing and/or severe stock decline (Ying *et al.,* 2011). However, in practice, in certain regional fisheries management frameworks, as in the Mediterranean and the Black seas, political concerns too frequently dismiss science in the delineation of stock boundaries (i.e. GSAs of GFCM). The outcomes therefore are very seldom scientifically accurate. Some of the stocks arbitrarily identified are in reality composed of multiple populations. In other cases, multiple stocks belong to a single population (Hauser and Carvalho, 2008).

Ignoring the spatial scale of a fishery resource and erroneously merging the stocks will reduce our understanding of the behavior of the stock and of recruitment variability in particular. Likewise segmenting the stock unit and neglecting connectivity may lead to erroneous results with detrimental consequences, such as overestimation of spawning stock biomass (SSB) and underestimation of fishing mortality (Guan *et al.,* 2013).

One may also underestimate the spawning stock when the variability in the dispersal patterns and in the migration routes is disregarded. As documented for the Black Sea anchovy fishery (see Gucu *et al.,*, this volume) very low catch in certain years which could erroneously be linked to low SSB otherwise, may in fact be associated with changes in the migration routes and/or with a temporary, climate-driven shift in the overwintering grounds. In that perspective, patterns of dispersal and connectivity are major determinant of populations/stocks structure and dynamics.

Accurate management advice would therefore require clear identification of stock components, incorporate migration and determine the degree of reproductive isolation. An important step taken forward with respect to accounting for spatial population structure in stock assessment is to track the groups of fish, with different capabilities and life-cycle patterns (contingents). Methodologies such as tagging, genetics, otoliths, and micro-chemistry allow discriminating contingents that have potentially different life history traits like migration patterns, habitats and reproduction. This approach has proven to be useful for large pelagic fishes, such as bluefin tuna (Fromentin, this volume).

An important biological mechanism which influences the rates of exchange among subpopulations of marine organisms and hence the exploited stocks seems to be the transfer of knowledge from one generation to the next. This involves learning, social behavior on migration routes and life cycle patterns. The steady increase in the southern Black Sea anchovy stock is linked, among a few other factors, to depletion of old individuals "social" interactions. Similarly, the transfer of knowledge among contingents carries significant information in large pelagics (Soldo, this volume). For what concerns MPAs and MPAs networks, the management-oriented need for information on dispersal and connectivity was recently recognized at policy level, as reflected by the implementation of the California Marine Life Protection Act in the USA and by the "Marine Strategy Framework Directive" in the EU.

Information on connectivity patterns is key to set (a) the proper size of each MPA in order that the populations/stocks of exploited species can be protected effectively throughout their life cycles and (b) the optimal distance between MPAs within a network so that they can be ecologically connected and achieve their core ecological objective of maintaining populations and providing benefits to unprotected areas (e.g. CIESM, 1999; Di Franco and Guidetti, this volume). Connected MPAs within a network have higher possibility to support the persistence and the recovery of local populations from disturbance (Di Franco and Guidetti, this volume). When MPAs are isolated from one another and not connected by dispersal, they become more vulnerable to local extinctions as they cannot be replenished by immigrants (Gaines *et al.,* 2010).

A Mediterranean example of connectivity patterns aimed at designing MPAs and at managing SSF is provided by research carried out on the white seabream *Diplodus sargus sargus* and on the two banded seabream *D.vulgaris* in the SW Adriatic Sea: based on dispersal assessment at multiple life stages (i.e. propagule, juvenile and sub-adult), it has been estimated that for both fish a network of relatively small MPAs (8 km of coastline), spaced 100-200km apart, would provide significant benefits in terms of population recovery and SSF enhancement (Di Franco and Guidetti, this volume).

3.6 Collective behavior and individual adaptation in migratory routes

The behavioral traits regulating the ability of marine organisms to migrate are largely unknown, but are likely dependent on a balance between individual preferences and collective decisions processes when moving in large groups. Migrations between widely separated but geographically stable locations of spawning and feeding sites raise several questions about how marine animals manage to learn and remember these often-complex migration routes. Where is the information on the path stored? How is it retrieved, shared and elaborated by a migrating group? Are the tasks significantly better when performed by the group than by isolated individuals?

Examples of such a complex decision-making problem can be found in the structure of the migration routes of several species of crustaceans (e.g. crabs), fish (e.g. tunas, mackerels) and marine mammals (e.g. cetaceans). For example, large numbers of Bluefin tunas used to migrate into the Norwegian and North Seas, but the species has become extremely rare in these regions since the mid-1960s and 1970s (Tiews, 1978; Fromentin, this volume). Reasons for the disappearance are still unknown but the loss of collective memory within tuna schools caused by heavy fishery has been suggested as a possible mechanism triggering a sudden shift in migrations and hence loss of habitat connectivity (De Luca *et al.,* 2014). Alternatively, after being introduced into two regions, some invertebrate species with less complex societal structures than fish (e.g. the Chinese mitten crabs) can discover new migrations routes by the exploratory adaptive behavior of single individuals entering rivers and channels in search of suitable reproductive conditions. In certain instances, these crabs will not find appropriate conditions and continue to migrate along the river quite deep into the continent (Zalota and Spiridinov, this volume). Then, when a suitable site is discovered, a new population is established and the new migratory route repeated over time.

Questions arise on the ability of these species moving in groups or in isolation to store information on specific routes and on the level of adaptation of the individuals to environmental changes and anthropogenic pressures. It has been hypothesized that collective memory, transmission of social information and decision-making processes might all play an important role in migratory behavior for a large range of species and can drive connectivity between distant habitats (Mariani, this volume; De Luca *et al.,* 2014; Petigas, 2010). Shedding light on the functioning of these mechanisms is not only of importance in ecology but may be relevant as well in fields such as sociology and economy (Surowiecki, 2005).

3.7 Human impacts on marine connectivity

3.7.1 Future connectivity

Human-induced climate change is projected to increase ocean temperature and modify circulation patterns, with potential implications for the transport and survival of marine planktonic larvae and for the migration routes of marine vertebrates (Gerber *et al.,* 2014). Recent studies suggest that changes in the physical and spatial structure of the environment will likely reduce potential dispersal distance and the spatial scale of connectivity, implying that we will need more proximate MPAs (Cetina-Heredia *et al.,* 2015). Others, combining climate velocity trajectories (Burrows *et al.,* 2014) with information on thermal tolerances and habitat preferences, (Garcia-Molinos *et al.,* 2015) project changes in global patterns of marine species richness, with range expansions prevailing over contractions, producing a net local increase in richness globally driven by redistribution rather than by loss of diversity. In addition, more frequent ocean and climate extreme events, such as heat waves, storms, etc., will affect oceanic circulation and mixing and potentially altering connectivity. Studying rare and extreme hydro-climatic events in dispersion, instead of focusing on the mean patterns, will improve our understanding of how species invade new habitats and how they disperse across such large distances in the ocean.

3.7.2 Pollution (noise, plastic litter)

Underwater noise now presents a major threat for cetaceans worldwide, and recent research demonstrated a broad range of negative effects in a variety of marine groups (see review by Williams *et al.,* 2015). Cetaceans are known to be highly acoustically oriented animals, relaying on sounds to navigate, communicate and find their preys through echolocation. They are therefore particularly vulnerable to acoustic pollution. In the Mediterranean Sea in particular, backgrounds noise levels are higher than in any other ocean basin (Ross, 2005), with ship noise and seismic surveys among the primary sources of noise (Maglio *et al.,* 2015). Seismic airguns, for example, can deter fin whales from feeding or breeding grounds (Castellote *et al.,* 2009). Marine litter represents a new important way of dispersal for many species (ranging from viruses, bacteria, to invertebrates). Floating and rafting marine litter (mainly plastics) act as vectors for dispersal and colonization over long distances (CIESM, 2014). Benthic habitats are also highly impacted by marine litter, favoring the propagation of hard-substrate species (Barnes and Milner, 2005).

3.7.3 Man-made interference with marine connectivity

Nowadays, numerous marine corridors and steppingstones enhance species spreading and propagation: man-made structures (harbours, breakwaters), maritime traffic (hulls, ballast water), cables and pipes (sewage, electrical cables), artificial structures (artificial reefs, oil and gas platform), oceanographic buoys, fishing gears, marine litter, etc. Too little attention is paid to these new marine substrates which might drastically affect benthic interlinkages.

3.7.4 Deep-sea mining

Deep-sea mining on seamounts, hydrothermal vents and in mineral-rich provinces of the abyssal plain are becoming real due to new technological developments and pressure to discover new resources. Several countries have been granted permits for deep-sea mining exploration by the International Seabed Authority (ISA) in the Atlantic, Pacific and Indian oceans in abyssal plains and mid-oceanic ridge systems. The short and long-term impacts on environment remain largely unknown.

In all cases, the extraction of deep-sea mineral resources will result in extensive habitat destruction. It may also irreversibly interrupt gene flow among populations, mostly through the local extinction of stepping-stone populations or the disruption of migration pathways. Many deep-sea habitats extend over large areas, but the extent of individuals species and habitat ranges are largely unknown, as 95% of the deep-sea remains unexplored. Further, certain habitats such as hydrothermal vents are distributed over long distances, and may be particularly vulnerable to mining impacts. Cold seeps harbor a large amount of long lived and slow growing species and may thus suffer extremely long term consequences of even punctual impacts.

As regulatory frameworks for the exploitation of mineral resources are being developed by individual countries and ISA, it is crucial to provide reliable, scientific information on basic environmental and ecological requirements for marine spatial planning, including on population connectivity.

4. APPLICATIONS OF CONNECTIVITY STUDIES

4.1 Conservation of large migratory species

International law recognizes the sovereignty of maritime States over their natural resources and their responsibility in terms of conservation in their respective Exclusive Economic Zone (EEZ). In the high seas, beyond the EEZ, in the absence of other specific international treaties, the principle of freedom of the oceans applies. The Mediterranean Sea poses legal problems for highly migratory species: due to the proximity of other shores, national jurisdiction covers far less than the usual 200 nautical miles. Therefore, migratory species will fall under the sovereignty of many different states situated along their migration route, meaning that their conservation will be subject to the legislation of each of these states in succession. International cooperation is therefore crucial, with the adoption of common rules governing the management, conservation, or fishing of migratory species, as was the case with the 1995 UN Agreement on the Conservation and Management of Straddling Fish Stock and Highly Migratory Fish Stocks. However, the scarce knowledge on the biology and ecology of highly migratory species remains a major constraint for the implementation of such rules. Further knowledge on migration patterns, breeding, feeding and on nursery areas is required.

4.2 Design of Marine Protected Areas

Information about dispersal and connectivity is essential for designing networks of adequate marine protected areas (MPAs) that are deemed a crucial management/conservation tool for restoring the biodiversity of coastal ecosystems. By acquiring information on dispersal and connectivity processes, it will be possible to predict which species will likely (1) be effectively protected within an MPA of a given size, (2) produce propagules having a chance to be exported, and (3) actively move towards unprotected areas during the different life stages. This information is useful in order to define the proper size of an MPA depending on the protection goals and the species involved (Moffitt *et al.,* 2011). In that perspective, a number of different investigation methods are currently available. They are summarized in Table 1.

Networks of MPAs are a prominent strategy in marine conservation, and current paradigms suggest they could yield a number of benefits to biodiversity and fisheries. In order to work, MPAs networks must be designed with a spacing between single MPAs that will match the scale of dispersal and connectivity (CIESM 1999), allowing MPAs to be connected among them. Ecologically connected MPAs reduce the risk of local functional extinction due to overexploitation and/or local disasters/hazards, ensuring the long-term persistence of populations better than single sites.

Table 1. Comparative advantages of methods available for the study of connectivity in marine systems.

Sector	Method	Temporal scale	Spatial scale (km)	Strength	Weakness
Observational	Natural tagging (photo ID, parasites)(1)*	Contemporary	10-1000	Individual movements; Site fidelity; estimate population size.	Only in certain species; depends on life-cycle.
	Conventional tagging	Contemporary	10-1000	Individual movements; estimate mortality.	Difficult to generalize at population level.
	Electronic tagging (e.g. satellite, acoustics)	Contemporary	10-1000	True pathway; 3D behaviour; individual information; identification of essential habitats.	Can be difficult to deploy; difficult to generalize at population level; size-dependent.
Genetics	Sibling analyses (2,3,4)	Contemporary	<10-100	Give direct empirical dispersal; estimate self-recruitment.	Large sample sizes.
	Population analyses (5,6)	Contemporary	<10-100	Estimate origin and number of migrant.	Lack temporal samples.
		Historical	10-1000	Re-trace demographic history; detect selection.	Lag between demography and genetics.
Modelling	Biophysical modelling (7,8,9,10,11,12,13,14)	Contemporary	10-1000	Set null hypotheses; Allow to hind- and forecast; Includes behaviour.	Low reliability at small spatial scales, lack of biological information to implement in models.
		Historical (15)	100 -1000	Estimate multi-generational connectivity.	Uncertainties difficult to set apart.
	Ecological modelling, metapopulation trophodynamics, network theory, spatial planning socioeconomic models	Both (16,17,18,19,20)	All	Allow testing scenarios, analysing mechanistic effects, providing predictions.	Can be seen as "too theoretical".
Elemental fingerprinting	Geochemistry of calcified structures (e.g. otoliths) (21,22,23,24)	Contemporary	10-100	Multiple life-stages; natal origin.	Potential lack of spatial variability in elemental fingerprint.
	Pollutants (POPs, heavy metals...) (25)	Contemporary	10-1000	Multiple life-stages.	
	Soft tissue stable isotopes	Contemporary	10-100	Multiple life-stages	

* References in table 1 : CIESM, 2004 (1); Schunter *et al.*, 2014 (2); Pascual and Macpherson (this volume) (3); Schunter *et al.*, 2011 (4); Palero *et al.*, 2011 (5), García-Merchán *et al.*, 2012 (6); Mitarai *et al.*, 2009 (7); Kool *et al.*, 2011 (8); Guizien *et al.*, 2012 (9); Treml *et al.*, 2012 (10); Andrello *et al.*, 2013 (11); Wood *et al.*, 2014 (12); Rossi *et al.*, 2014 (13); Dubois *et al.*, 2016 (14); White *et al.*, 2010 (15); Beger *et al.*, 2010 (16) ; Smith et al., 2009 (17); Colleter *et al.*, 2012 (18); Lett *et al.*, 2015 (19); Moffit *et al.*, 2009 (20); Di Franco *et al.*, 2012 (21), 2015 (22); Calò *et al.*, 2016 (23); Di Franco and Guidetti (This issue) (24); Madigan *et al.*, 2012 (25).

5. THE WAY FORWARD

Estimating connectivity in marine ecosystems requires the understanding of the biological and physical processes regulating dispersal, settlement and recruitment, and is therefore an intrinsically multidisciplinary task. Furthermore, understanding how these processes are coupled across scales, both spatial and temporal, requires a suite of complementary tools that are only available through an interdisciplinary concerted effort.

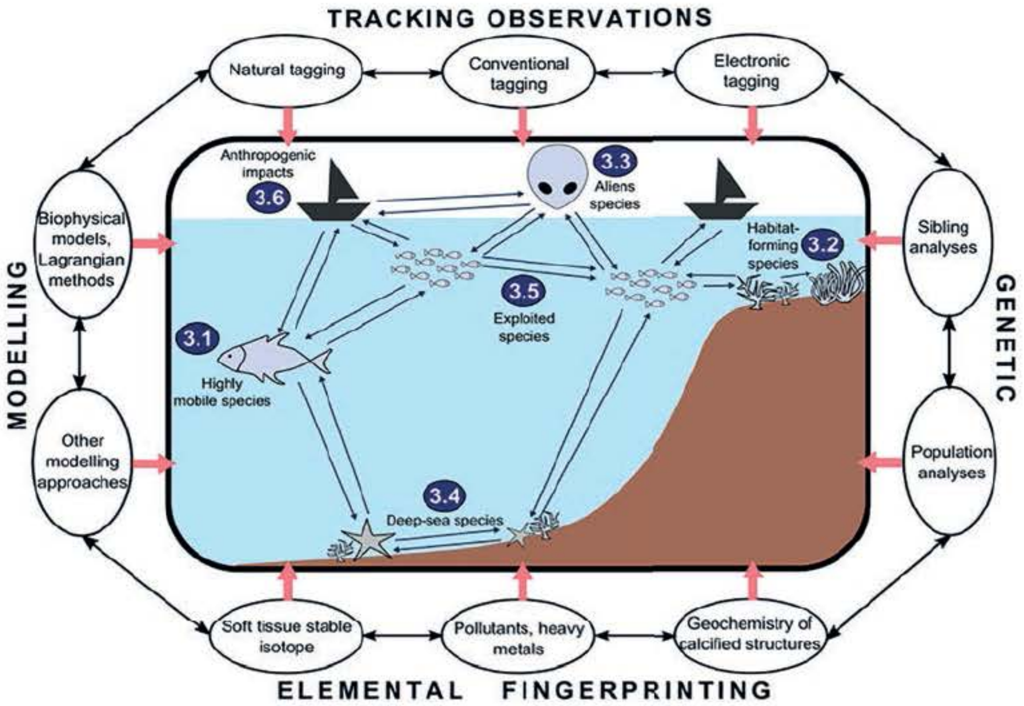

Figure 4. Diagram summing up the main issues and the various methodologies covered in this chapter.

Given the recognized importance of connectivity to design effective conservation and management plans, and the existential threats posed by the continuing industrialization of oceans, including the poorly understood deep sea, now is the time to establish the baselines necessary to accurately assess and protect marine connectivity. This can only be achieved through a coordinated research network that must be strongly committed to accomplish the following:

1. Develop a coordinated plan for international cooperation to study connectivity and provide comprehensive data to build coherent, transboundary networks of MPAs and produce effective management plans for transboundary resources.
2. Expand the ongoing scientific exploration at regional and global scales.
3. Promote data access and data sharing.
4. Facilitate the application of findings to manage deliberations.

Future challenges to address connectivity studies will need to include as depicted above (Figure 4):

A collaborative multidisciplinary effort throughout the entire Basin to:

- Build databases centralizing information on the localization of samples collection, data repositories, and a handbook of experts.
    - Collect biopsy samples.
    - Collect oceanographic data.
    - Collect data on early life traits and their spatio-temporal variability.
    - Deploy satellite transmitters.
    - Collect trophic data.
    - Multi-models comparison and validation exercises.
- Combination of individual markers:
    - Deploy electronic tags and get biochemical and/or genetic information.
- Combination of markers and models:
    - Develop state-space models aiming at reconstructing unobserved state sequence, using information from biochemical/tagging/genetic analyses.
    - Combine mechanistic bio-energetic models to reproduce individual behavior (e.g. growth, vertical migration) with oceanic model to obtain more realistic Lagrangian simulations of larval drift.
- Observation/sampling at multiple scales with technology development:
    - Set in a framework to study connectivity in an integrated way, include all compartments from genes to ecosystems.
    - Rapid stock assessment of connectivity and transfer to managers.

Putting together the pieces of the puzzle: combining multiple approaches to better understand patterns of fish dispersal and connectivity

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ABSTRACT

Estimates of dispersal and connectivity patterns are crucial to properly manage fish stocks and to design effective networks of marine protected areas. However, quantifying dispersal and connectivity patterns is a complex task due to the difficulty of following individuals throughout their entire life cycle. Multiple approaches are available to assess dispersal and connectivity of fishes, among which biophysical models, population genetics, tagging and assessment of the spatio-temporal distribution of larvae and settlers. However, each of these different approaches measures different things, often over different time scales, and has some drawbacks that could potentially impair our ability to provide reliable estimates of dispersal and connectivity in the marine environment. Therefore, combining multiple approaches is likely the best option to study dispersal and connectivity patterns as each method compensates the limits and constraints of the others. Although very time consuming and costly, the use of multiple and multidisciplinary approaches for assessing fish dispersal and connectivity in the Mediterranean Sea is a priority in order to better inform management and conservation initiatives.

Dispersal is the process by which living organisms expand actively and/or passively the space or range where they live and is one of the fundamental life-history traits affecting the dynamics of spatially structured populations (Cote *et al.,* 2010). Dispersal is a multi-stage process including departure, movement, and settlement which results in the net displacement of an individual through space (Burgess *et al*., 2015).

Connectivity can be defined as the demographic link between local populations through the exchange of individuals at whatever life stage (Cowen and Sponaugle, 2009) and is intrinsically dependent on species dispersal capacity (Jones *et al*., 2007; Botsford *et al*., 2009).

Dispersal and connectivity are among the few traits shared by virtually all species, both animal and vegetal (Gaines *et al*., 2007). In fact, although many species (e.g. plants and benthic species) seem permanently locked to a particular site, they inevitably move at some stage(s) of their life cycles.

Individuals can move for a multitude of reasons (e.g. to avoid competition with conspecifics, reduce the risk of inbreeding, seek food, avoid predation, pursue favorable environmental conditions or find a mate; Gaines *et al*., 2007; Burgess *et al*., 2015) but in the marine realm, dispersal and related connectivity can also occur as a by-product of life strategies aimed at supporting population dynamics (Burgess *et al*., 2015). Most coastal fish species have a bipartite life cycle characterized by a pelagic phase (i.e. at the stages of eggs and larvae, overall called propagules) followed by metamorphosis and settlement into a benthic juvenile and later joining the adult at a phase named recruitment (Tresher *et al*., 1989). Nearly all fish produce propagules (eggs and larvae) that grow by feeding on planktonic prey. Larvae (but not all species follow this life strategy) can spend long periods (up to several months) in the open water and commonly increase in size by an order of magnitude. Fish can also move at later phases (i.e. juvenile and adult) so that dispersal and connectivity, on the whole, can occur at several life stages: propagule (i.e. eggs and larvae), juvenile and / or adults stage depending on the species.

Dispersal and connectivity play significant roles in a wide range of ecological and evolutionary processes (Davidson *et al*., 2004; Gaines *et al*., 2007) by driving changes at distant sites. As a result, the population dynamics of a species at any location often depends on processes and interactions occurring at distant locations.

Measures of dispersal and connectivity between local populations are also essential to the successful design of marine protected areas (MPAs) and so that MPA networks may achieve their core ecological objective of maintaining population persistence and providing benefits to unprotected areas: each individual MPA should be adequately connected to the others to support the persistence and the recovery of local populations from disturbance (Planes *et al*., 2009; Gaines *et al*., 2010). If MPAs are isolated from one another and not connected by dispersal between them, MPAs are more vulnerable to local extinctions because of local perturbations, as they cannot be replenished by immigrants (Kritzer and Sale, 2004; Gaines *et al*., 2010). The management-oriented need for information on dispersal and connectivity is now recognized at policy level, as highlighted for example by the implementation of the California Marine Life Protection Act in the USA and by the 'Marine Strategy Framework Directive' in the EU.

Measurements of dispersal and connectivity at multiple life stages are therefore extremely important to better understand marine population dynamics and to better manage marine fish populations, although such measurements are extremely difficult (Palumbi, 2003).

Despite the variety of approaches currently used to tackle this issue, tracking the movements of marine fauna and quantifying dispersal and connectivity patterns is a complex task due to the difficulty of following individuals throughout their entire life cycles (Calò *et al*., 2013). Origins and destination points provide the basic data in dispersal and connectivity studies (Cowen *et al*., 2006). Direct and exhaustive measures of larval dispersal in the ocean, for instance, require the ability to track minuscule larvae through the pelagic environment, from spawning locations to settlement sites. Most marine species with pelagic larvae spawn huge quantities of propagules that are then subjected to significant advection, diffusion, and mortality in vast volumes of seawater, making traditional mark-recapture approaches virtually impossible (Levin, 2006; Thorrold *et al*., 2007).

As a consequence, remarkably few measures of dispersal or population connectivity in ocean environments do exist (i.e. only 21 estimates of larval connectivity globally, Burgess *et al*., 2014), almost all of them concerning tropical species (Burgess *et al*., 2014).

For all this, patterns of dispersal and population connectivity are the big "black box" in the field of marine ecology (Buston and D'Aloia, 2013; Burgess *et al*., 2014; Castorani *et al*., 2015). However, recent advances in technology are providing new insights. In particular, fundamental knowledge of larval dispersal and connectivity can be gained from i) bio-physical models (i.e. Lagrangian models, Cowen *et al*., 2006; Di Franco *et al*., 2012a; Pujolar *et al*., 2013; Andrello *et al*., 2013, 2015; Rossi *et al*., in this volume; Hilário, in this volume), which are particularly effective when they are parameterized with contextualized information about species life history traits (e.g. pelagic larval duration (PLD) and spawning date (SpD)) and oceanographic data (Pujolar *et al*., 2013), ii) population genetics (Weersing and Toone, 2009; Planes *et al*., 2009; Almany *et al*., 2013; Arnaud-Haond, in this volume; Pascual and Macpherson, in this volume) and iii) tagging (both natural and artificial, Thorrold *et al*., 2002; Di Lorenzo *et al*., 2014). In addition, the assessment of the spatio-temporal distribution of larvae and settlers has provided useful information (Crechriou *et al*., 2010; Leis *et al*., 2011; Calò *et al*., 2013; Di Franco *et al*., 2013a).

These different approaches measure different things, often over different time scales. Reviews thoroughly describing the specific features, the pros and cons of each of these approaches are available (e.g. Leis *et al*., 2011; Calò *et al*., 2013), and so we will provide here a brief description of the issue.

Distributional studies of larvae (i.e. by means of plankton tows and/or light traps) and settlers (i.e. by means of underwater visual census, uvc) can allow reconstructing patterns of dispersal and connectivity by assessing their outputs at different stages. Their conclusions must be considered with caution as surveys are typically snapshots that capture only a small fraction of the spawning season (Leis *et al*., 2011). In addition, when focusing on larvae, we should bear in mind that the final portion of the pelagic period plus settlement and all post-settlement events are excluded from any connectivity estimates, therefore impairing our ability to describe the full process. On the other hand, when focusing on settlers, spatial patterns could be biased by active movements during the post-settlement phase (Di Franco *et al*., 2012b; 2015). In addition, such assessments (especially for larvae) are very time consuming and expensive. Therefore, studies on the distribution of larvae and settlers are probably more appropriate to ground-truth outputs from biophysical models than for providing robust dispersal and connectivity estimates per se (Leis *et al*., 2011; Calò *et al*., 2013).

Bio-physical models allow the integration of physical hydrodynamic models with data on key biological traits. Biological information is typically represented by the knowledge of the distribution ranges of species (especially large reproducers), timing of release of propagules (i.e. spawning dates for fishes) and the time spent in the plankton (i.e. PLD), that, along with information about swimming speed, orientation and patterns of vertical migration, may help refine estimates of dispersal patterns. However modelling commonly used in the available literature is often based on fairly unrealistic assumptions, such as the absence of larval active behavior that on the contrary has been shown to significantly affect models outputs (Irisson *et al*., 2004; Mariani, in this volume), and spatial and temporal invariability of the early life traits needed to feed the model and that are often extrapolated from a highly different context (i.e. spatial location and time) from the one investigated. This is partially understandable due to the effort (time and resource consumption) and specific competences (e.g. ability to analyze otolith microstructure) required to get reliable information on PLD and spawning or birth dates, but there is the risk to provide unrealistic scenarios, that could mislead management decisions (e.g. how far to create MPAs from each other in a network). There is increasing evidence, in fact, that these biological traits significantly change in time and space (Di Franco *et al*., 2011; 2013b; Di Franco and Guidetti, 2011), suggesting the need to use spatially and temporally proper (i.e. contextual) data to refine local predictions on dispersal patterns of propagules. In addition, bio-physical models outputs can be weakened by the absence of fine spatial scales resolution of hydrodynamics (Nickols *et al*., 2015, see Tintoré *et al*., in this volume). Dispersal modelling approaches to estimating connectivity are rather low-cost once the biological inputs they require are available (Leis *et al*., 2011) but bio-physical model exercises risk to be futile if not attached to spatio-temporal resolute information about early life traits and spawning areas and without any field-validation of their outputs.

Population genetics represents a powerful tool to estimate dispersal distances and connectivity patterns from molecular data (Planes *et al*., 2009; Saenz-Agudelo *et al*., 2009; Almany *et al*., 2013). It describes the spatial scale at which populations can be differentiated into discrete units due to the process of genetic drift (Leis *et al*., 2011). In the marine realm, however, genetic studies generally have limited success in inferring connectivity, due to the recurrent absence of spatial genetic structure in species exhibiting high fecundity and dispersal capabilities

(Gagnaire *et al*., 2015). The majority of marine species, in fact, show life history traits (e.g. high fecundity, large population sizes, high dispersal potential) causing weak patterns of genetic differentiation, if any (Palumbi, 2003; Hedgecock *et al*., 2007). A lack of genetic differentiation may result from an array of situations ranging from practically total demographic independence among large-sized populations to the existence of a unique panmictic population (see Gagnaire *et al*., 2015 for a detailed discussion about this issue). When the number of individuals exchanged between populations per generation (N_em) is high (> 25), the gene flow is considered high, and genetic panmixia is increasingly likely. However, from an ecological point of view (i.e. at ecological timescale), the arrival of 25 individuals per generation from an external source is likely insufficient to replenish a population that has been reduced by a natural or an anthropogenic stress (Leis *et al*., 2011). Reliable estimates of N_em can be obtained only when genetic differentiation is strong and sample size adequate (e.g. 20 independent markers, 100 individuals per location) and this is not always the case due to sampling constraints and analytical costs (Leis *et al*., 2011). We must bear in mind that classical population genetics assesses the so-called evolutionary connectivity (Leis *et al*., 2011, but see Pascual and Macpherson, in this volume) that represents the movement of genes through populations, and this movement may be contemporary and/or historical (i.e. the result of dispersal and connectivity over multiple generations).

Nowadays novel genetic techniques are available, which directly estimate connectivity by parentage analysis (e.g., Jones *et al*., 2005; Planes *et al*., 2009), and assign individual larvae/juveniles to specific parents (Leis *et al*., 2011). They can estimate ecological connectivity, i.e. the movement of individuals between spatially separated locations at ecological timescales (Leis *et al*., 2011). However, they require a significant effort for all sampling potential sources (parents or populations), because a large proportion of the parental population must be sampled and genetically characterized before assigning individual larvae to specific parents (Leis *et al*., 2011; Calò *et al*., 2013). A less effort-demanding alternative is sibship analysis (identification of sibling) that can allow direct measurements of dispersal (see Schunter *et al*., 2014; Pascual and Macpherson, in this volume).

Among artificial tagging techniques, acoustic telemetry represents a useful method able to provide fine scale estimates of movement patterns in time (Alós *et al*., 2012; Di Lorenzo *et al*., 2014; Di Lorenzo *et al*., 2016). Acoustic telemetry is applicable generally to adult or subadult coastal fishes in relation to individual size (the ratio tag weight/ fish weight should not exceed 2%). Among natural tags, otolith chemical signatures have proven to be a valuable approach to both tracking fish movements and modelling dispersal patterns (Elsdon *et al*., 2008; Gillanders 2009; Di Franco *et al*., 2012b). Otoliths (ear bones) are carbonate structures usually in the form of aragonite located in the inner ear of fishes and grow by the daily accretion of calcium carbonate increments throughout the fish entire lifetime (Campana, 1999).

Otolith chemistry reflects the water chemistry of the surrounding environment, and once laid down, increments (that can be referenced to specific ages) remain unaltered (Campana, 1999; Elsdon *et al*., 2008). The chemical information acquired locally within the otoliths can be used to derive profiles of the movement history of an individual fish (Campana, 1999; Green *et al*., 2009). Despite some limitations (see Elsdon *et al*., 2008 for detailed description of the method), otolith chemistry is nowadays largely accepted as a useful method for unravelling fish dispersal and connectivity patterns (Calò *et al*., 2013; Starrs *et al*., 2014). The essential proviso to use geochemical tag is based on the existence of substantial variation in the elemental composition of those tags among locations of interest (Thorrold *et al*., 2002). This variability is often found in species inhabiting estuaries because of substantial differences in salinity, temperature, and water chemistry among estuarine waters (Thorrold *et al*., 2007). On the other hand, significant variability can be more rarely detected in fully marine species, probably because gradients in oceanographic conditions can be more subtle, thus obscuring the generation of unique geochemical tags (Starrs *et al*., 2014).

Otoliths are also ideal repositories for artificial chemical markers that are used to tag embryos or larvae before dispersal from natal locations (Jones *et al*., 1999; Thorrold *et al*., 2006; Almany *et al*., 2007). Fluorescent compounds such as tetracycline or calcein, elemental markers (e.g., rare earth elements), and radioactive isotopes have all been used to tag calcified structures by immersing developing larvae (or their food) in a solution containing the target marker (reviewed by Thorrold *et al*., 2002). The marked larvae can then be released from a source population and, if recaptured, they can be screened for presence of the artificial tag so to assess the dispersal from the location of release to that of recapture (Thorrold *et al*., 2007). However, the logistic difficulties associated with tagging a large proportion of the total larval production from an area has proved difficult to overcome. A new approach for marking fish larvae relies upon transgenerational transfer of enriched Ba isotopes from females to the embryonic otoliths of their offspring. TRAnsgenerational Isotope Labeling (TRAIL) technique, based on maternal transmission of an enriched stable Ba isotope that is incorporated in the embryonic otoliths of larval fish, may help to overcome this limitation (Thorrold *et al*., 2006). The TRAIL approach represents a significant advance from earlier artificial tagging methods and multiple tags can be applied (Thorrold *et al*., 2007). However, the use of artificial tag into otoliths is an application still in its infancy. Due to the huge effort that it requires, it has been very rarely used, never in the Mediterranean Sea.

In summary every approach can provide information on dispersal and connectivity (e.g. on a specific life stage, at a particular temporal and spatial scale) and involves limitations. Hence the need to combine multiple approaches to cross-check multiple evidence. A multidisciplinary approach could allow us to capture the whole spectrum of dispersal and connectivity patterns and related processes (e.g. evolutionary or genetic, and ecological or demographic processes). Evolutionary connectivity in the marine environment is typically at large spatial scales, may depend on rare events over long or intermediate time periods and may not be contemporary. Ecological connectivity in the marine environment may operate at a variety of scales; is dependent on regular, albeit stochastic, events; and is extant, or has occurred recently (Leis *et al*., 2011).

Here, we want to give strength to the largely unheeded call (e.g. Sale and Kritzer, 2008; Leis *et al*., 2011; Calò *et al*., 2013) for the use of multiple approaches in assessing dispersal and connectivity. This could be perceived as a general rule of thumb applicable to the whole ecology but it seems to be particularly relevant in dispersal and connectivity estimates, considering that each single approach has drawbacks and limitations that could impair our ability to unravel the real patterns.

In our opinion the most comprehensive assessment of dispersal and connectivity of a marine fish would require to 1) simulate via modelling larval dispersal (based on spatial-temporal contextualized information about species life-traits and information about species presence and abundance as a proxy of spawning potential), 2) estimate larval dispersal (by using otolith microchemistry with natural or artificial markers, or by using genetic parentage analysis), 3) investigate dispersal and connectivity at subsequent life stages (i.e. juvenile and adult) by using tagging (natural or artificial), 4) assessing the effects on populations (by using underwater visual census and estimating density at multiple life stages on a relevant spatial scale), 5) assess the effects of dispersal and connectivity at multiple life stages on genetic structure of investigated populations. The numbering does not imply any temporal and/or relevance order.

Along with the importance of using multiple approaches, we point out the need to focus not just on propagule stage and consider also post-settlement stages. Post-settlement movements are often disregarded in dispersal and connectivity assessment based on the largely untested assumption that fish dispersal and connectivity takes chiefly place during the larval phase, with this habit potentially hiding a convenient choice due to the inherent difficulties in estimating dispersal at post-settlement stages (e.g. impossibility of using biophysical models). But this assumption seems to be more and more questionable considering both the evidence indicating higher rates of larval retention than expected, by considering PLD and biophysical model outputs and the increased body of evidence highlighting extensive dispersal at post-settlement stages (Di Franco *et al*., 2012b; Reis Santos *et al*., 2013; Di Franco *et al*., 2015).

Unfortunately, up to now, very few examples of multidisciplinary approaches to dispersal and connectivity assessment for Mediterranean fishes exist. As reported in Calò *et al*., 2013, among these we can find evidence that the genetic structure of *Serranus cabrilla* matched perfectly with the outputs of dispersal models highlighting the effect of two oceanographic barriers to species dispersal (Schunter *et al*., 2011). Another example of the use of multiple approaches is the one focusing on the bluefin tuna *Thunnus thynnus*. Genetics and electronic tags highlighted that despite extensive dispersal among populations inhabiting Mexican Gulf, Eastern and Western Mediterranean Sea, significant genetic structure among populations occurs, suggesting strong natal homing to individual spawning grounds (Boustany *et al*., 2008).

More recently it has been showed that, for the saddled seabream *Oblada melanura* along the Mediterranean Spanish coast, population genetics and otolith microchemistry provided concordant evidence highlighting extensive larval dispersal (Calò *et al*., 2016) able to induce genetic homogeneity (Calò *et al*., 2016).

A multidisciplinary approach integrating fishery data, population genetics, and otolith microchemistry analyses has been applied to investigate population and stock structure of Atlantic mackerel (*Scomber scombrus*) in the northern–central Adriatic Sea (Papetti *et al*., 2013). Landings data highlighted recurrent monthly–seasonal variations in catch, suggesting stock migrations potentially related to the use of a common spawning ground as evidenced by otolith microchemistry, and with this driving to the existence of a panmictic population in the northern–central Adriatic Sea as pointed out by genetics. This mix of approaches allows therefore to gain a critical piece of information needed to answer relevant fishery science questions.

Among the most comprehensive assessments of patterns of fish dispersal and connectivity and their effects on populations in the Mediterranean Sea we can mention the case studies on the white seabream *Diplodus sargus sargus* and the two-banded seabream *D. vulgaris* in the southwestern Adriatic Sea. Both case studies deal with the potential role of a MPA, i.e. Torre Guaceto (hereinafter TGMPA), in providing recruitment subsidy to external unprotected locations. The two case studies encompass the same geographical area (i.e. approximately 200 kms of Apulian Adriatic coastline) and adopted 1) field surveys to estimate density and biomass of fish at multiple life stages (settlers, recruits and adults, Di Franco *et al*., 2012a; Di Franco *et al*., 2013a), 2) reproductive biology to estimate reproductive potential (Turnone, 2011), 3) biophysical models fed with ecological information contextualized in space and time (i.e. spawning dates and PLD assessed by analyzing otolith microstructure, Di Franco *et al*., 2012a; Pujolar *et al*., 2013), 4) otolith microchemistry to investigate larval and juvenile (i.e. between settlement and recruitment) dispersal (Di Franco *et al*., 2012b; Di Franco *et al*., 2015), 5) population genetics to assess homogeneity/heterogeneity over the study area (Di Franco *et al*., 2012a; Pujolar *et al*., 2013). In addition, for what concerns the white seabream, acoustic tagging was used to investigate adult movement patterns at the TGMPA (Di Lorenzo *et al*., 2014; Di Lorenzo *et al*., 2016).

Evidence is similar for the two species and suggests the potentially relevant role of TGMPA in contributing to replenish seabreams local populations both within and outside the MPA. The findings can be summarized as follows:

1) The basic assumption to expect an effective egg/larval export from a MPA is the recovery of populations within the MPA itself. In this perspective, as highlighted by underwater visual census, TGMPA hosts the highest biomass of spawners of the two species all along the sampling area (i.e. 200 km along the South Apulian Adriatic coast) (Di Franco *et al*., 2012a; Di Franco *et al*., 2013a).

2) The high biomass value recorded within TGMPA, along with the higher abundance of large-sized adults (that for white seabream display an high site-fidelity within the TGMPA, Di

Lorenzo *et al.*, 2014), lead to an high eggs/larval production (Turnone 2011), potentially replenishing both TGMPA itself and the unprotected coast as highlighted by biophysical models (Di Franco *et al.*, 2012a; Pujolar *et al.*, 2013). Propagule dispersal was estimated for the two species to be in the order of few hundreds of kms (Di Franco *et al.*, 2012a; Pujolar *et al.*, 2013), with model estimates matching evidences from otolith microchemistry (Di Franco *et al.*, 2012b; Di Franco *et al.*, 2015). For what concerns the white seabream *D. sargus* a strong directionality (i.e. southward) in propagule transport has emerged from model simulations and perfectly matched the spatial distribution of settlers described using underwater visual census (Di Franco *et al.*, 2012a).

3) The spatial pattern at settlement can be deeply modified at post-settlement stages by extensive juvenile dispersal (i.e. tens of kilometers) that has been showed for the two species (Di Franco *et al.*, 2012b; Di Franco *et al.*, 2015) (Figure. 1). For the white seabream adult within TGMPA showed high site fidelity (Di Lorenzo *et al.*, 2014).

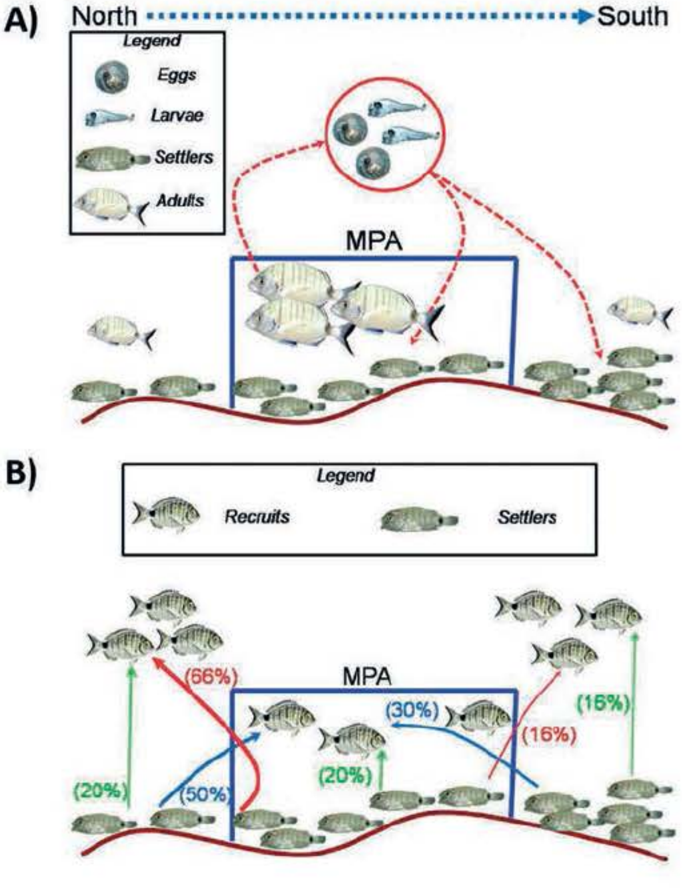

Figure 1 Representation of larval retention/export processes at the Torre Guaceto MPA. The blue dotted line represents the direction of the dominant sea current in the South-Western Adriatic Sea: Post-settlement dispersal in Torre Guaceto MPA and in flanking unprotected coastal areas. Green lines represent settlers recruiting in the same sites where they settled. Blue lines represent settlers from unprotected areas recruiting into Torre Guaceto MPA. Red lines represent settlers from Torre Guaceto MPA recruiting in unprotected areas. Percentages were estimated through otolith chemistry analysis; line thickness is proportional to percentages (from Di Franco, 2011).

Such findings suggest that, under hydrographic conditions (i.e. sea-currents) similar to those characterizing the study area, a network of MPAs sized as TGMPA (i.e. about 8 km) and placed at distance of 100-200 kilometers could be effective for both conservation and fishery goals of the seabream species investigated in the south-western Adriatic area.

As demonstrated by these examples, multidisciplinary approaches are likely the best option as each method compensates the limits and constraints of the others, and outputs deriving from each approach can reciprocally corroborate results.

Acknowledgements

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Modeling habitat connectivity: migrations and larval dispersal

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1. INTRODUCTION

Movement of organisms is widespread in nature and it happens at all scales from bacteria moving in chemical gradients, to plankton searching for food and mates, to fish and birds that can travel thousands of kilometers between distant habitats (Turchin, 1998). Often this movement is a result of an active and directed behavior (e.g., migrations) but it can also result from the passive transport of propagules and larvae by wind and ocean currents (Dingle, 2014).

Many terrestrial and marine species can alternate passive and active type of movements through their life cycle. For example, most fish have a pelagic phase when they are passively transported by ocean currents as eggs or small larvae before they settle and recruit in distant suitable habitats (Cowen and Sponaugle, 2009). At the juvenile phase many fish can show some degree of residency that can also last for several years (e.g., cod). In these phases diel vertical migrations can be present, resulting as an active behavior to balance feeding opportunities and predator avoidance. Finally as adult and mature individuals, the same fish can migrate back to its initial spawning location either travelling alone (e.g., eels, turtles) or as part of a school of conspecifics (e.g., tunas).

The combination of active movements of the organisms and passive transport regulates connectivity between spatially distant habitats. The resulting species dispersal can favor gene flow and horizontal gene transfer within and among species; hence connectivity can affect speciation, community structure and evolution at several spatial scales.

Irrespective of the details of the species dispersal, all the resulting tracks have a general common characteristic in that they will have some very small scales where the trajectory tends to remain constant in direction while a degree of randomness appears at some larger scales (Taylor, 1921; Visser and Kiørboe, 2006). Moreover if any migration is undertaken, the individual will show again a highly correlated path until the destination habitat is reached. The tortuosity of the migration path and the time needed to complete the migration will depend on local conditions of the currents and the navigation ability of the migrant. These different movement strategies might be showed using a simple cartoon that compares random behavior and migrations with and without a cross-flow (Figure 1).

Has a start we can consider the case of individuals moving with a random walk within a confined domain in no flow conditions (Figure 1, blue lines). In such cases, it might take a very long (but finite) time for individuals to move from their birth-place (black habitat) to one other of the settling habitats on the eastern part of the domain. The net displacement (*l*, the Euclidian distance from the starting point of the individual to one of the point along the trajectory) for short time range will tend to increase linearly with time (t, $l \approx t$), while for longer time scales it will grow as: $l \approx t^{1/2}$. This diffusive motion has implication on the connectivity in the region since the probability to reach distant settling habitats will only increase slowly if the dispersal time is increased. Hence only the closest, nearby habitat can be effectively reached.

When a cross flow is added to the random motion, the time needed to move into a settling habitat can decrease substantially (Figure 1 green lines). This could be the case of fish larvae transported in the ocean currents or spores passively transported by the wind. For these cases the net displacement will follow a curve similar to the pure diffusive case discussed above, with a swimming speed, u. But when a current (or wind) of comparable speed is encountered on the track, the net displacement will show a quasi-linear increase over time. Hence the track is more correlated because of the directionality of the flow.

Introducing migration in the case above will result in an even further increase of the correlated movement (Figure 1, red lines). In this case we assume that individuals move randomly in the flow until a certain migration time is reached. Then they oriented their movement towards the target habitat (green habitat) and when the migration period is over they will start to move randomly again. This can be the case of long distant migrants typically travelling through cross flow, such as sea turtles or several bird species. Interestingly when migrating in a cross flow the individual need to invest some time or energy in adjusting their heading, since the flow will displace them off of the shortest path (Figure. 1 red lines). The way specific individuals can operate such control will substantially alter the trajectories displayed (Hays *et al*., 2014).

Although simple, the example above contains some of the typical processes observed in real organisms' dispersal. In particular, when organisms relay on passive transport from their birth-place to the settlement habitat, local flow conditions will generally regulate the success of this dispersal strategy. Hence changes in the flow can alter settlement success and population connectivity (Cowen and Sponaugle, 2009). Below, I will introduce the case of Atlantic cod spawning in the North Sea and show how the dispersal trajectories of the larvae are altered by the combination of vertical swimming behavior and local ocean circulation, which can in turn be linked to wind conditions.

The migration case used in the example above is also a crude synthesis of a series of complex factors driving migrations, among which: the timing of migration, the navigation capability of the individuals, school formation and collective behavior, etc. While a detailed description of such processes is out of the scope of the present contribution, I will briefly introduce below a theoretical framework to describe migration dynamics and habitat connectivity for the Atlantic bluefin tuna and will show an application to describe tuna migrations under climate change.

I will then conclude with a summary and some thoughts on future research directions regarding migration behavior and habitat connectivity.

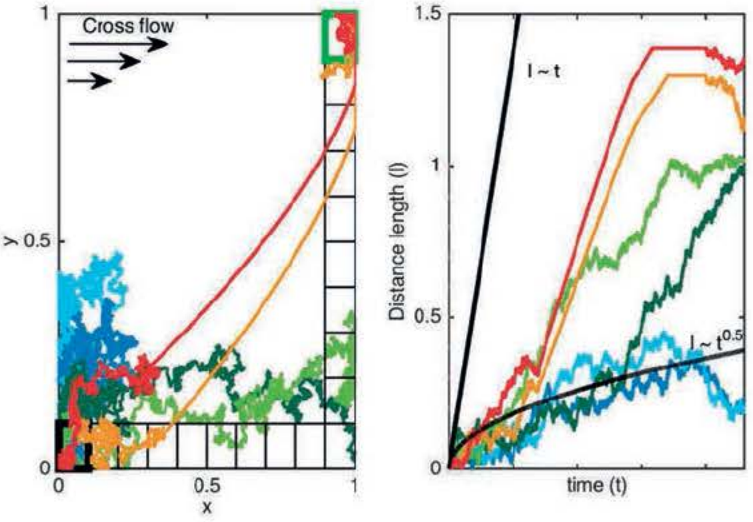


Figure 1. Example of biological dispersal for a set of six trajectories resulting from: random walk (blue lines) random walk in cross-flow (green lines) and random walk and migration in cross flow (red lines). (a) Map of the tracks. Note that a number of settling habitats are defined at the boundaries (black boxes) of the domain, while the birth habitat (tick black box) is distant from the target habitat for migration (green box). (b) Time evolution of the net displacement, *l*, for each track. The black lines are the time-dependent net displacement expected for: a ballistic motion, $l \approx ut$; or a continuous random walk in two dimensions, $l \approx \left(\frac{4}{3}u^2\tau t\right)^{1/2}$, where *t* is the time, *u* the swimming speed, *τ* the correlation time scale.

2. NORTH SEA COD

The pelagic phase of eggs and larvae of several marine species can promote large-scale dispersal and reduce genetic differentiation of metapopulations. Ocean transport in early life stages can indeed promote mixing of spatially separated populations of fish, thus favoring interbreeding and damping speciation processes (Bradbury *et al.*, 2008). Therefore genetic differentiation is often expected to be low among fish populations. Nevertheless, evidence is mounting that fine-scale as well as large-scale genetic structures are widespread in fish (Hoffman *et al.*, 2012). This counterintuitive outcome comes from the difficulty in clearly discerning genetic boundaries as well as from a limited understanding of the physical and biological factors driving gene flow patterns among marine populations (Palumbi *et al.*, 1997).

The analyses of genetic markers have been widely used to identify structures in fish populations, i.e. units of reproductively isolated individuals (Nielsen *et al.*, 2009), and Atlantic cod is one of the most intensively studied species in marine fish population genetics. Several studies have identified significant levels of population structure in North Atlantic cod both at large and local geographical scales. For example, small but statistically significant genetic differences have been identified among Norwegian coastal cod in samples collected within a few kilometers (Knutsen *et al.*, 2003; 2011). Often the genetic variability coincides with observed differences in the ecology or in the life history of the species (Olsen *et al.*, 2008). Recently, Poulsen *et al.* (2011) examined a number of genetic markers linked to genes that are potentially important for fish physiology and found significant genetic differences between offshore and inshore locations in one specific gene (see also Hemmer-Hansen, 2011). These findings suggest possible adaptations to local environmental conditions in cod population living in the North Sea.

In the North Sea cod larvae can, potentially, be transported over long distances and such transport can limit population divergence but could also contribute to local recruitment far away from the breeding grounds. On the other hand different areas of the North Sea can be characterized by contrasting transport regimes (retention or dispersion) and small displacement in the spawning ground can result in large changes in transport conditions. This mechanism can contribute to producing genetically divergent subpopulations in cod as have indeed been identified throughout the range of the North Sea (Knutsen *et al.,* 2011).

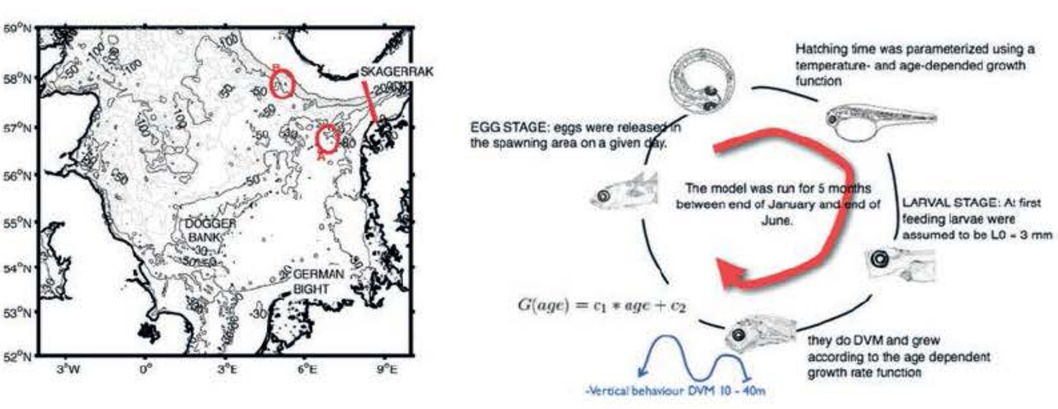
The transport of cod eggs and larvae across the North Sea has been extensively investigated in models (Fiksen *et al*., 2007) as well as in surveys (Fox *et al*., 2008; Munk *et al*., 2009; Höffle, 2012). However, theoretical studies have focused on larval dispersion as passive particles and less attention has been paid to the interactions of hydrographic processes with larval swimming behaviour (Jenkins *et al*., 1999; Leis, 2007). A common assumption in the modelling of dispersion processes is that larval swimming and orientation abilities are so limited that they will be irrelevant to dispersion. On the other hand it has been shown that diel vertical migration (Neilson & Perry, 1990; Emsley *et al*., 2005) and horizontal movements (Leis, 2006) can play a significant role in regulating larval dispersion. Even minor changes in the vertical positions of the larvae may expose them to different circulation conditions (Fiksen *et al*., 2007) and hence in contrasting dispersion and/or retention environments. Moreover location and spawning time are both crucial factors to determine the fate of cod larvae.

We investigate here cod larvae dispersion in the North Sea and adjacent areas integrating knowledge of spawning and behavioral components in cod populations. We determine the spawning time and location based on recent observations in the North Sea and investigate the sensitivity of transport and connectivity in metapopulations to larval diel vertical behavior. The ocean currents are derived from a general circulation model: a hydrostatic 3-dimensional circulation model originally developed by the German Federal Maritime and Hydrographic Agency (BSH). The model has been running operationally at DMI since 2001 and the details about performance and model results verification are reported elsewhere (e.g. She *et al*., 2007).

A particle tracking algorithm combining egg development and diel vertical migrations of fish larvae with the ocean current is used to simulate particle trajectories. This particle-tracking algorithm has previously been applied to compute sandeel larval transport patterns in the North Sea (Christensen *et al*., 2008) and is now used to analyse cod larvae transport.

2.1 Egg phase

From observed distributions of cod eggs and larvae (Höffle, 2012) we calculate a spatial probability density function for the North Sea that regulates the number of particles released in the specific numerical box. Although the time of spawning, i.e., time of particle release in the model, is an important factor affecting larval transport and size distribution, only limited information about spawning period in different areas of the North Sea is available (Brander *et al*., 1994; Fox *et al*., 2008). The time of particle release is then obtained assuming temperature-dependent effects on the maturation of adult cod, similarly to a method used to identify spawning period for other fish species in the North Sea (Lange & Greve, 1997). In particular, we assume that adult cod tend to be resident in a given area during winter time and that the higher is the upper ocean temperature in that area the sooner is the time of spawning. We then assume the existence of a temperature threshold above which cod will start spawning. Using the integral of the first 30 m temperature from January 1st of each year we set the threshold temperature as $T = 340^{o}C$ and use the date when that threshold is passed as the mean of a gaussian distribution with standard deviation of one week (total spawning period extent is two weeks).



(a) (b)

Figure 2. (a) Study area with indication of topography and the coastal (A) and offshore (B) study sites. Also shown is the transect between Skagerrak and North Sea. (b) Schematic presentations of the processes included in the individual based model of cod.

2.2 Larval phase

The obtained spawning period simulates typical patterns observed in cod population in the North Sea (Figure 2a): 1) main spawning happening in February each year; 2) existence of a North to South gradient in the time of spawning. After release cod eggs have a development period of ca. two weeks when they are not feeding and exposed to passive dispersion (Figure 2b). After entering the larval stage (hatching at size of 3 mm) they start growing according to a simple linear function of age (Figure 2) that closely reproduces observed data on cod larvae growth in the North Sea (Nielsen and Munk, 2004). At this stage they can also employ diel vertical migrations (DVM) and we assume that they swim close to the surface (10 m) at night and dusk while deeper (40 m) during the day.

2.3 Results: Spatial patterns in displacement

Although exposed to an important year-to-year variability, simulations of larval dispersion in the North Sea show consistent patterns (Figure 3). An area of low dispersion is present for all simulations in the central North Sea with larvae spawned around 56N 3E often displaced less than 50 km in simulated period (Jan-Jun). The more we move towards the boundary of the basin the more larvae are subject to transport, typically with displacement within 200 km from the spawning origin.

The largest transport and final displacement is in correspondence of the German Bight and the Jutland currents (south and east North Sea) where larvae generally travel more than 350 km from their spawning ground.

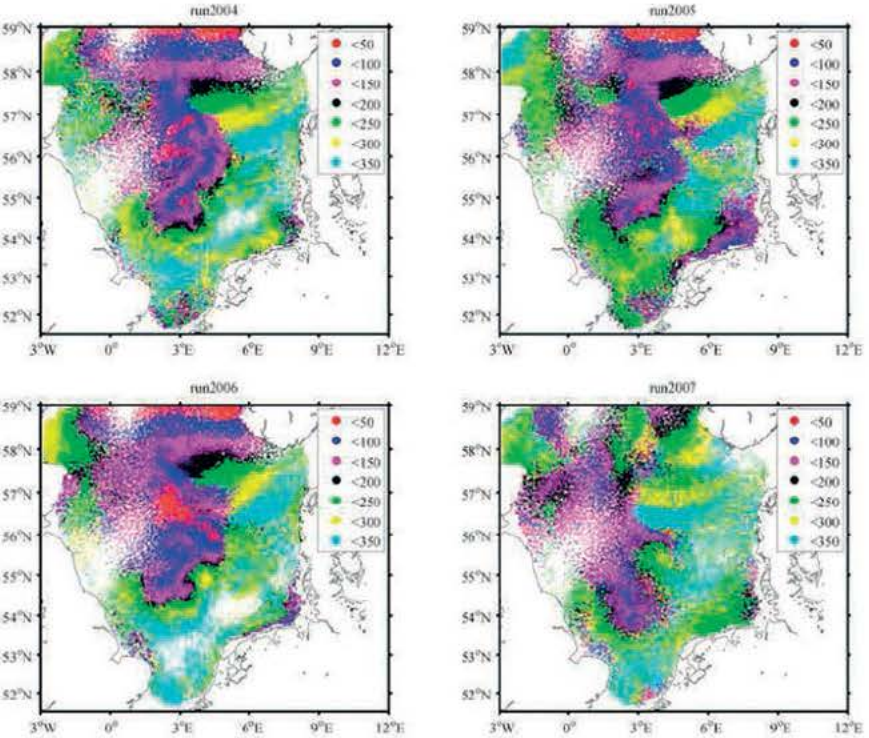
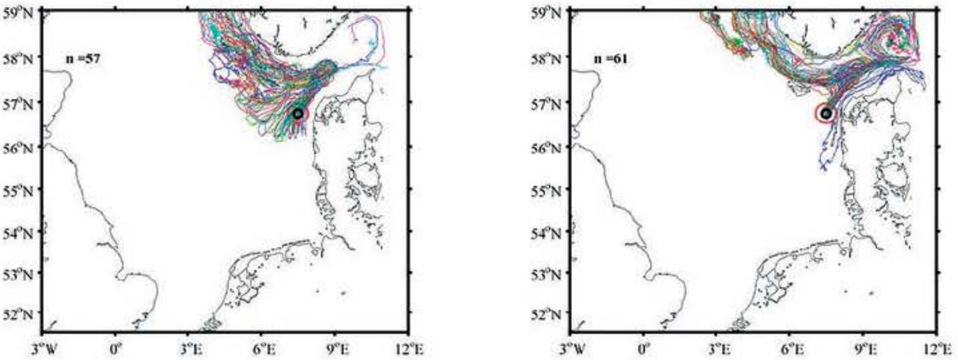


Figure 3. Maps of the final distribution of larvae for the period 2004-2007- different colors indicate the total displacement (in km) of the larvae from the spawning origin.

For all the analysed years (2004-2007) larvae spawned close to the Danish coast enter the Skagerrak in some period during their dispersal. But this connectivity is highly variable. For some year the connectivity is very strong (2004, 2005 and 2007) while in other years (2006) the larvae pelagic phase is mainly confined in the North Sea (Figure 4). In contrast, larvae spawned in more offshore sites do not show any connectivity to the Skagerrak area but tend to disperse along the northwest direction. The changes in connectivity between the North Sea and adjacent seas can be generally explained by the seasonal variability of the surface ocean transport, which is mainly controlled by wind regimes.



(a) (b)

Figure 4. Transport of larvae at a coastal site in the North Sea showing variable connectivity with the Skagerrak: (a) 2006; (b) 2007.

3. MIGRATION DYNAMICS IN TUNA

Long distance migration is a widespread phenomenon that has evolved independently in several animal groups in terrestrial and marine ecosystems. Many factors can contribute to the migration process; of primary importance are intra-specific competition and seasonality in the resource distribution. The ideal free distribution (IFD) has been suggested as an evolutionary stable state to reduce competition and maximize fitness (Krivan *et al.*, 2008) but less attention has been given to the effects of seasonality and intra-specific variability on this equilibrium distribution. Recently, a game theoretical approach has been used to model the migration process of an age-structured population under seasonal environmental changes (Mariani *et al.*, 2015).

The model assumes that given a network of habitats and a population of unequal competitors then an equilibrium distribution can be reached according to the IFD among locally connected habitats. This equilibrium solution does depend on the cost of moving between habitats and the seasonality of resources within the habitat.

When the model is applied to Atlantic bluefin tuna it is able to capture several migratory dynamics of this pelagic population (Mariani *et al.*, 2015). The Atlantic bluefin tuna (*Thunnus thynnus*) has evolved a migratory behavior in which spawning and feeding sites are separated by large distances, typically spanning 100s-1000s of km and several degrees of latitude (Mather, 1995; Cury, 1998). Spawning sites are located in temperate-tropical waters (e. g., Mediterranean Sea, Gulf of Mexico), but feeding sites used by the largest and oldest individuals are located in northern temperate-boreal waters (Mather, 1995). During the narrow reproductive period individuals often display fast trans-Atlantic migrations to reach the Mediterranean spawning ground (Block *et al.*, 2005; Fromentin *et al.*, 2009). The seasonal south-north migratory behavior exhibited by bluefin tuna has likely evolved to allow the species to benefit from large biomasses of prey species in these regions (Cury, 1998).

The model shows typical patterns of migration of BFT with spawning areas generally occupied throughout all seasons and owning the majority of younger stages, while distant feeding areas (e.g., northern North Sea) are occupied on a seasonal basis by larger individuals (Figure 5). Moreover patterns of migrations and biomass distribution can change depending on the cost of migrations and the reproduction success. For high costs of migration and low reproduction success, connectivity and migration routes are significantly reduced (Figure 5b).

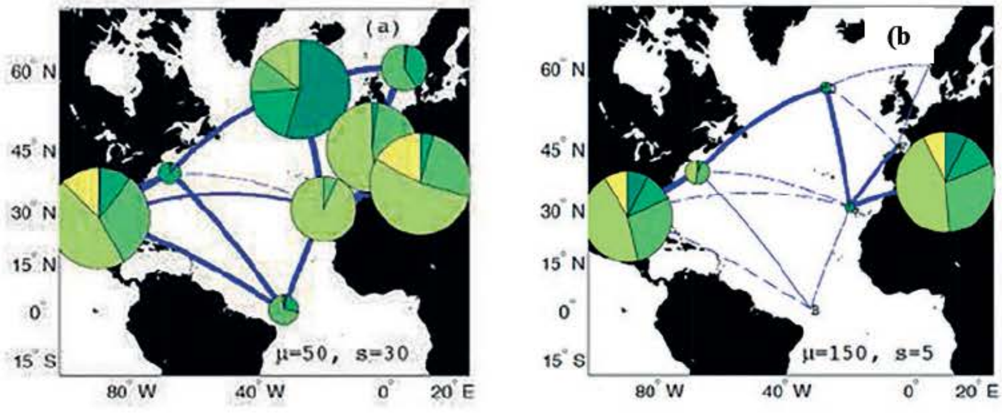


Figure 5. Modelled network of bluefin tuna feeding and spawning habitats at different values of spawning intensity (s) and migration cost (μ): (a) μ =50; s = 30; (b) μ =150; s = 5. Histograms are proportional to tuna biomass with different colors for different age classes, while the thickness of lines is proportional to the strength of migration fluxes between those habitats.

3.1 Climate scenarios

In the model the benefits of migrations towards different habitats are proportional to the relative habitat quality (e.g., food abundance). A measure of habitat quality can be obtained from the tuna habitat index provided by the biogeochemical model SEAPODYM (Lehodey *et al.*, 2010). This index accounts for temperature effects as well as tunas' prey availability in the North

Atlantic. SEAPODYM can be used to make scenarios simulations. Future climate scenarios are simulated based on the IPSL CM4 Earth Climate model with the parameterization for bluefin tuna used by SEAPODYM. The climate projection is the IPCC SRES A2 scenario, i.e., an increase of atmospheric CO2 concentrations reaching 850 ppm in the year 2100.

In the North Atlantic, the habitat index for bluefin tuna shows large seasonal variability as well as year-to-year changes (Figure 6). Generally more tropical areas are less varying seasonally but show a clear deterioration of the habitat quality in future scenarios, whereas northern areas (e.g., around Iceland) have a strong seasonal cycle and they appear to have better conditions for tuna in the future. In particular by 2050 the total suitable area in the western Atlantic (60 – 20 W, 28.5 – 48.5 N) available for bluefin tuna feeding and growth (calculated as index larger than 0.8) would be reduced by 80% compared to the 1950 conditions.

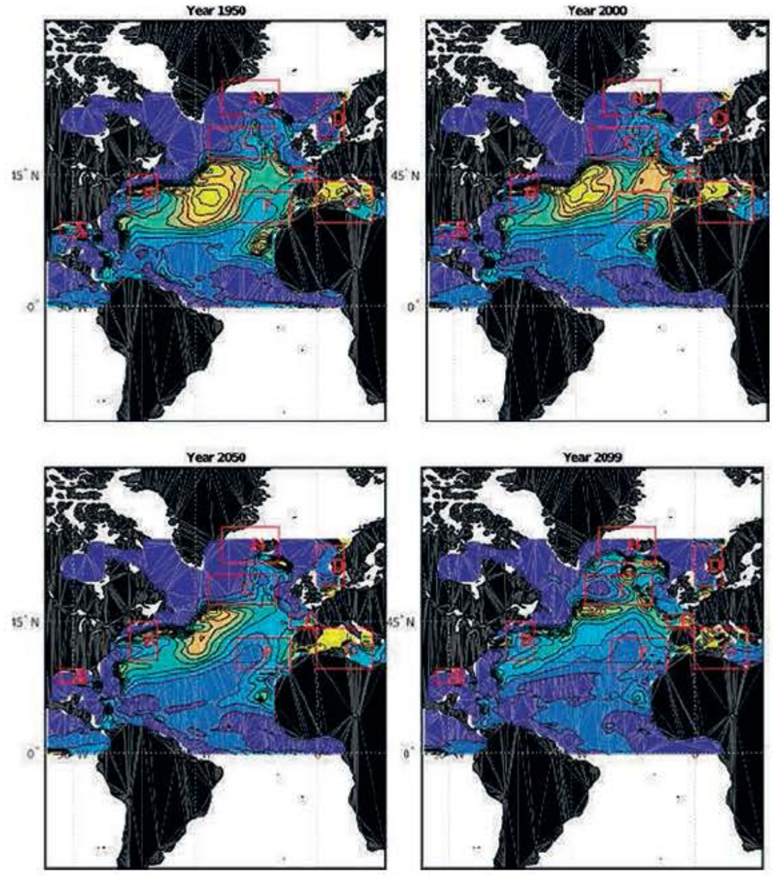
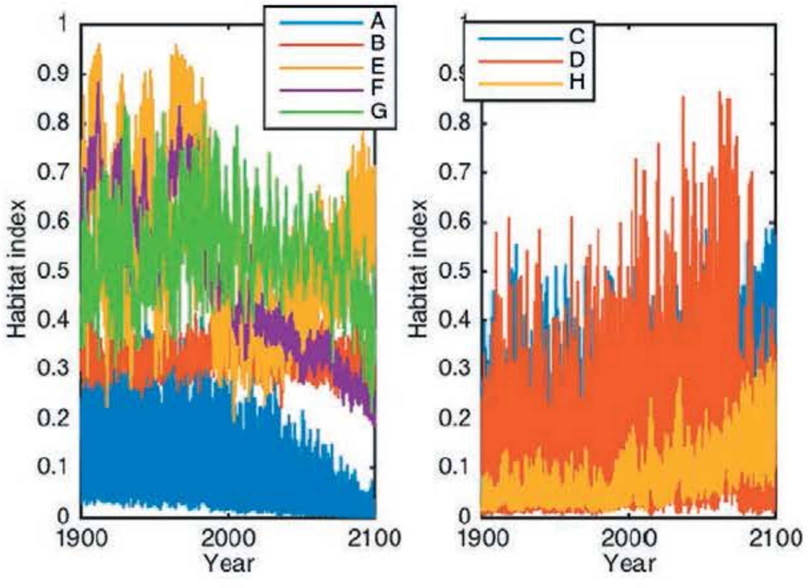


Figure 6. Bluefin tuna feeding habitat predicted using IPSL forcing for the time period 1900-2099. Maps are showed for the year (a) 1950 (b) 2000 (c) 2050 (d) 2099. Also shown are the regions considered as feeding habitat for the migration game. The resolution of these data is 2deg longitude x 1deg latitude x 1month and color ranges between 1 (yellow) and zero (dark blue). This prediction is the results of a simulation based on parameterization obtained for MERCATOR reanalysis and starting from year 2000 the forcing follows IPCC-A2 scenario (Lehodey *et al.*, 2010).

To apply the migration model we focus on the bluefin tuna habitat hotspot as indicated by tagging data and historical catches. We also include potential future habitats such as northwest of Iceland and close to the Greenland coast (Figure 6). Changes of habitat index in those habitats (Figure 7) are quite marked for the southern regions, which generally tend to be worst. In particular Gulf of Mexico is very close to zero by 2100, while the other present spawning area in the Mediterranean Sea decreases by about 50% of its historical conditions (Figure 7a). Conversely northern habitats, have a more seasonal pattern with strong oscillations but they generally seem to improve regarding temperature and food conditions for bluefin tuna, especially after 2030.



(a) (b)

Figure 7. Monthly time series of the habitat index at (a) southern (b) northern feeding habitats as shown in the maps above. In the legend the names of the different habitats are: (A) Gulf of Mexico, (B) Gulf of Maine, (C) central North Atlantic, (D) northern North Sea, (E) Gulf of Biscay, (F) central-eastern Atlantic, (G) Mediterranean Sea, (H) Iceland/Greenland.

We use the index to modulate the carrying capacity in the different areas and we then apply the migration game model to simulate past, present and future scenarios (Figure 8).

Under a constant fishing mortality on tuna (F = 0.7), the model predicts a total biomass in the simulated habitats of 350 kton until the year 2000. Then the total biomass steadily decreases to about 150 kton by 2100. The western Atlantic appears to have the major decrease in tuna biomass both in the Gulf of Mexico (Figure 8A) and Gulf of Maine (Figure 8B). The decrease is between 80% to 90% of the reference biomass and it affects all stages from young-of the year to mature and old tunas. On the eastern Atlantic, the Mediterranean Sea shows the largest biomass, which stays almost unaffected by changing climate (Figure 8G). The Bay of Biscay (Figure 8E) has also an important total biomass and large seasonal fluctuations. After the year 2020 the presence of tunas appears to be consistently lower than average but then biomass recovers by the end of the century.

This has potential implications for the connectivity between the different habitats. All northern habitats show increases in the biomass of bluefin tuna mainly after 2080 (Figure 8C, D, H). In particular the central North Atlantic appears to have a dynamic very similar to the Gulf of Biscay, with a significant reduction of tuna in the period 2020 – 2080 but then a recovery by 2100 (Figure 8C). Further our model suggests that the habitat around Iceland and Greenland can be visited by migratory tunas but generally at low biomass (~1.5 kton). However, by the end of this century we predict a 3-fold biomass increase in the area to about 5 kton (Figure 8H). Moreover all northern areas have been historically very seasonal habitats with a significant presence of tuna occurring only for few (generally summer) months. Under changing climate the seasonal signal will be weaker with a general migration in northern habitats during summer but with some presence of the species also in winter periods.

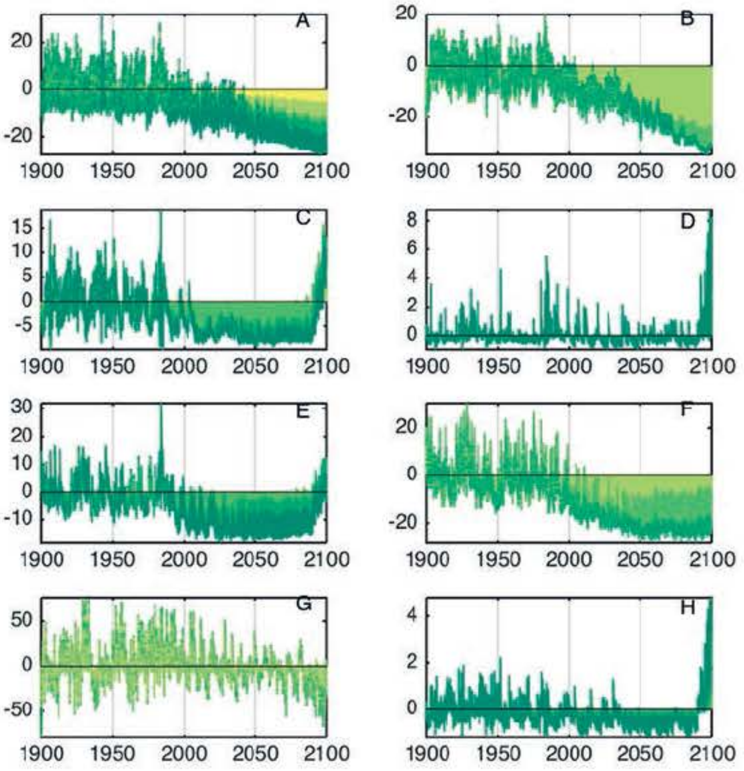


Figure 8. Monthly values of bluefin tuna biomass anomalies (kton) for the eight habitats considered in the period 1900 – 2099. The reference value is a stage dependent average over the period 1900 – 1950. Different colors are for different stages: young of the year (yellow), juvenile (light yellow), adult (light green), mature (green), old (dark green). The habitats are: (A) Gulf of Mexico, (B) Gulf of Maine, (C) central North Atlantic, (D) northern North Sea, (E) Gulf of Biscay, (F) central-eastern Atlantic, (G) Mediterranean Sea, (H) Iceland/Greenland

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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 volume). 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 has received growing interests (e.g. Mitarai *et al.*, 2009; Kool *et al.*, 2011; Guizien *et al.*, 2012; Treml *et al.*, 2012; Andrello *et al.*, 2013; Wood *et al.*, 2014; Rossi *et al.*, 2014; Fach *et al.*, this volume).

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).

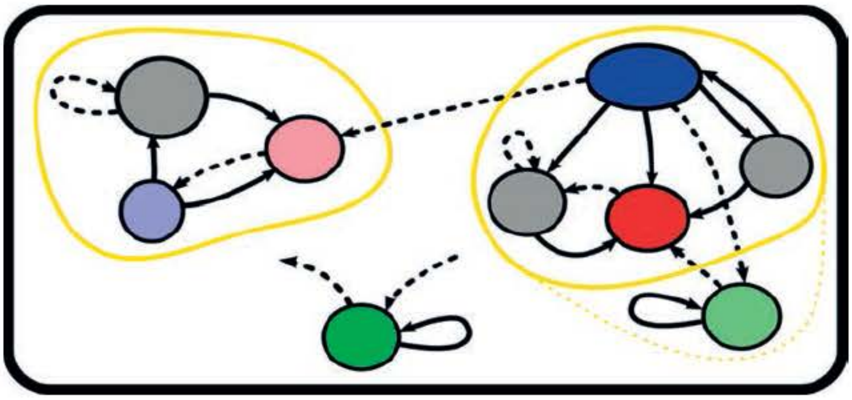

Figure 1: Schematic meta-population (black rectangle) composed of several sub-populations (black-outlined ellipses) with different connectivity behaviors (intensity is proportional to the darkness of the coloring). Green ellipses represent relatively "closed" subpopulations while the rests are "open" 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 highlight three case-studies focused on different scales and we examine the effects of larval dispersal for population ecology and genetics (section 3). Then, we report the robustness of selected results (section 4). We finally discuss 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 sub-area 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 sub-areas 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 that 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 volume) and 3-dimensional trajectories (e.g. (Kool *et al*. 2015)) are envisaged for future work.

The LFN tool has four modules (Figure 2): (1) builds the network grid and initializes 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 studied 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. 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).

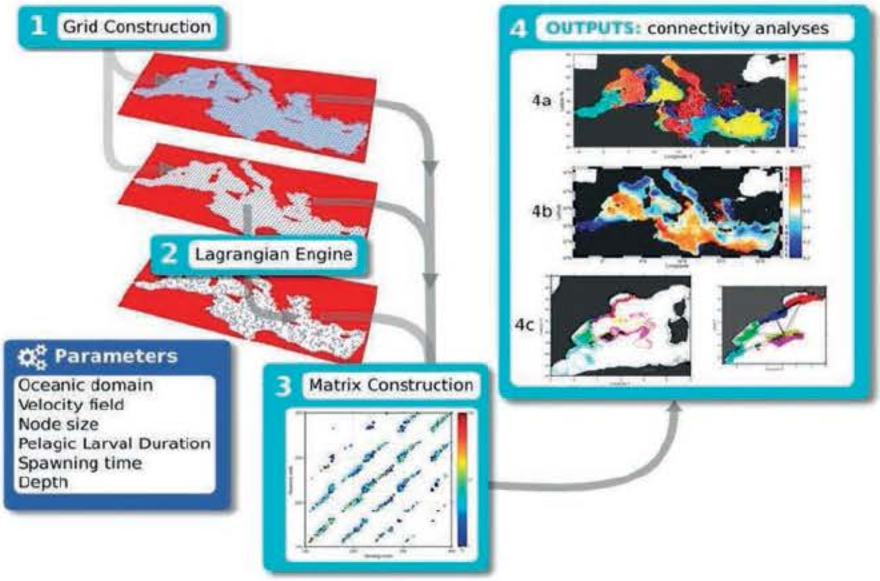

Figure 2: Simplified diagram of the Lagrangian Flow Networks set-up with 4 modules (light blue boxes). Key parameters (dark blue box) are the domain of interest, the velocity field (from any ocean model), the node size, the starting dates (spawning events), the vertical layer of the model (depth of dispersion)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

3.1 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 (Figure. 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 (Figure. 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 (Figure. 3d).

Future work using these synthetic provinces explores their potential roles in controlling large-scale gene flows (Arnaud-Haond, this volume; Villamor *et al.*, this volume). 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.

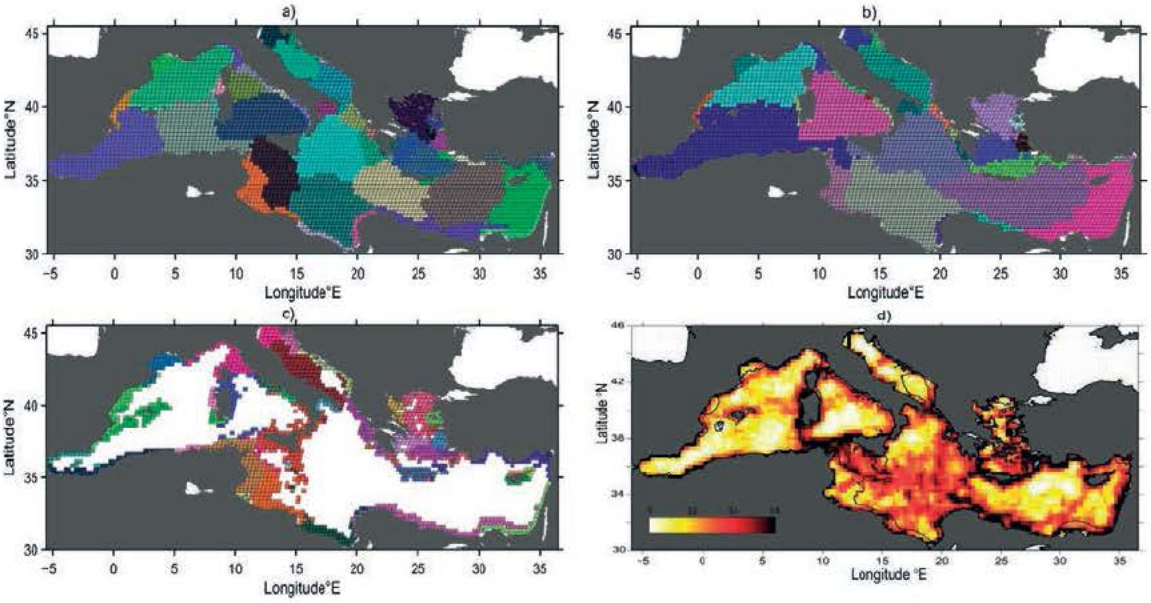

Figure 3: Hydrodynamical provinces in the Mediterranean. Annual mean provinces (across the ensemble of 20 experiments, covering all winters/summers over 2002-2011) for a) a PLD of 30 days and b) 60 days using the full matrix; c) a PLD of 60 days but considering only the shelf-nodes; d) frequency of occurrence 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).

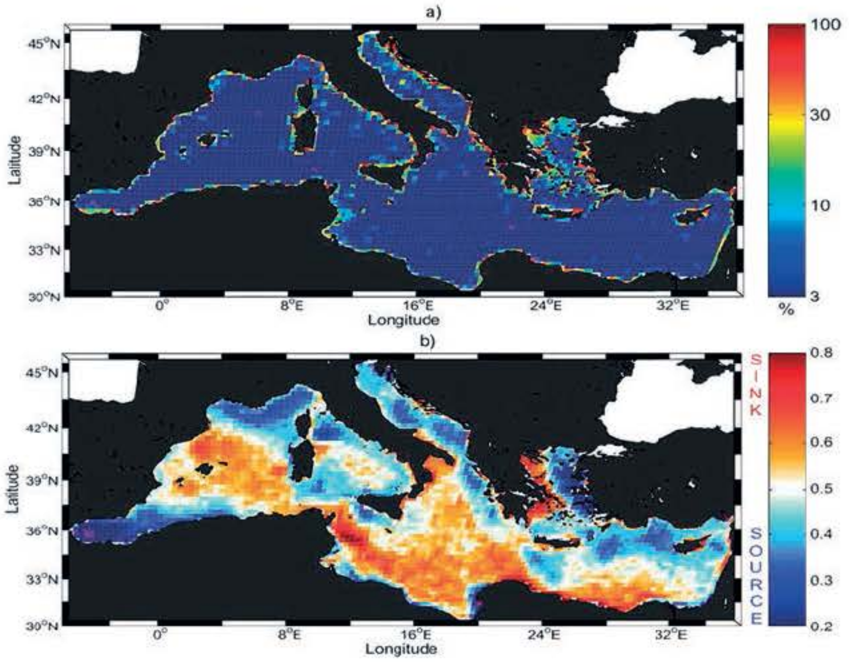

Figure 4: a) Mean Local-Retention (LR) for a PLD of 30 days averaged across 60 (winter and summer) connectivity matrices; b) Mean SS-degree (SSd: relative importance of larval export versus import, measuring the number of links) averaged across 30 summer matrices for a PLD of 60 days. Pink crosses in 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 (Figure. 4a). Moreover, we show that wind-driven divergent (convergent, respectively) oceanic regions are systematically characterized by larval sources (sinks, respectively) (Figure. 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 volume), 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.

3.2 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?

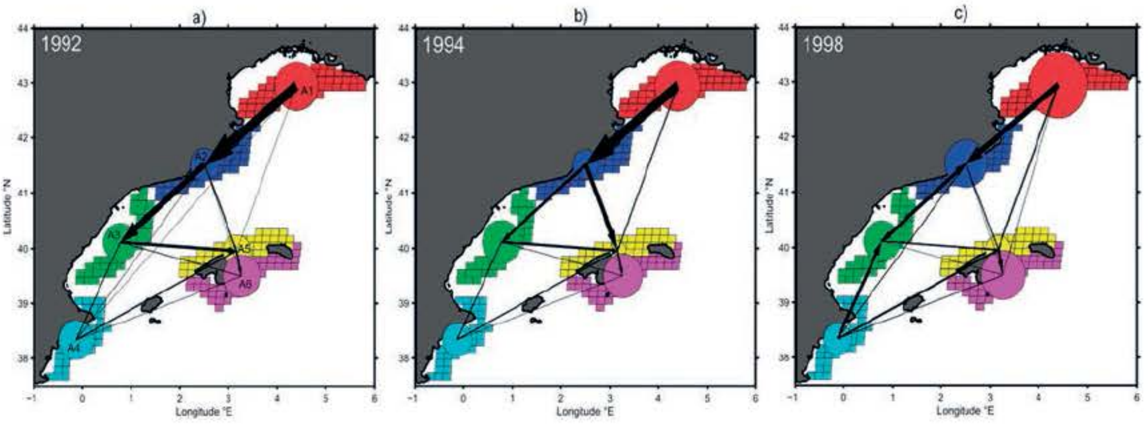

Figure 5: Normalized estimates of larval exchanges (arrows) and retention (circles) among the different sub-populations of hake averaged over seven successive spawning events in a) 1992, b) 1994 and c) 1998. Widths of arrows (diameters of circles) are proportional to the strength of connection (larval 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 (Figures. 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 together explain 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).

3.3 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 subpopulations 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° 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

4.1 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 (Figure. 6a) and the quantity of initial particles (Figure. 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.

4.2 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.

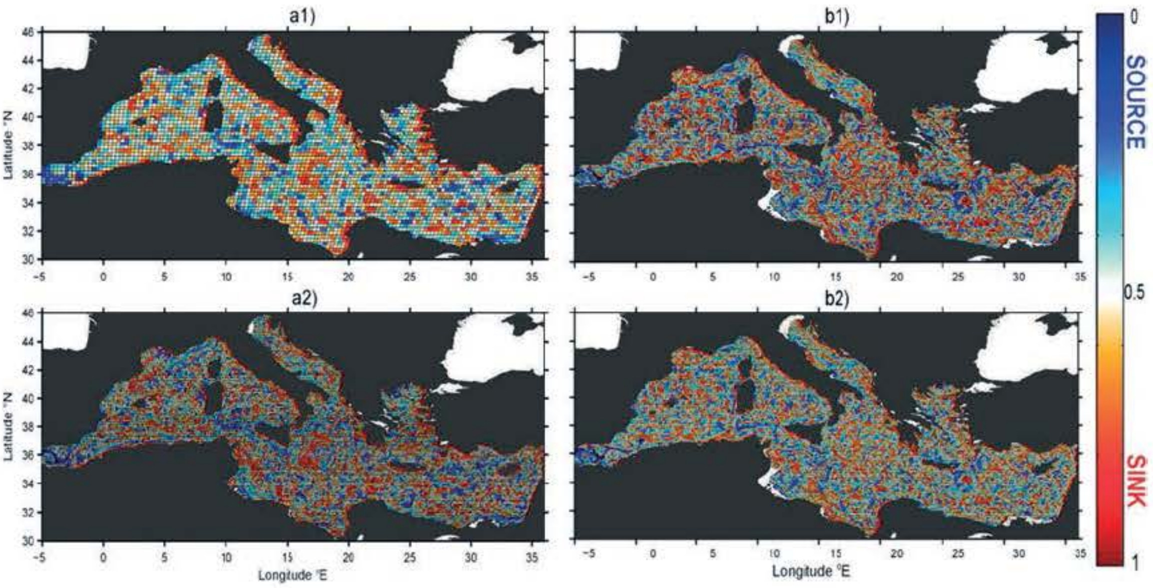

Figure 6: Sensitivity studies for the "physical" parameters. Snapshot maps of the SourceSink-degree (SSd) generated with the same parameters but: a) for network grids of (a1) medium 1/4° and (a2) high 1/8° resolution; b) for different particles initial density (b1) 1000 particles per node and (b2) 100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

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 (Figure. 7a). The long PLD experiment reveals lower retention of particles in the Gulf and stronger southward export as well as a more intense eastward retroflection (Figure. b7). Note however that the main patterns (yellow-to-reddish colors) remain essentially unchanged.

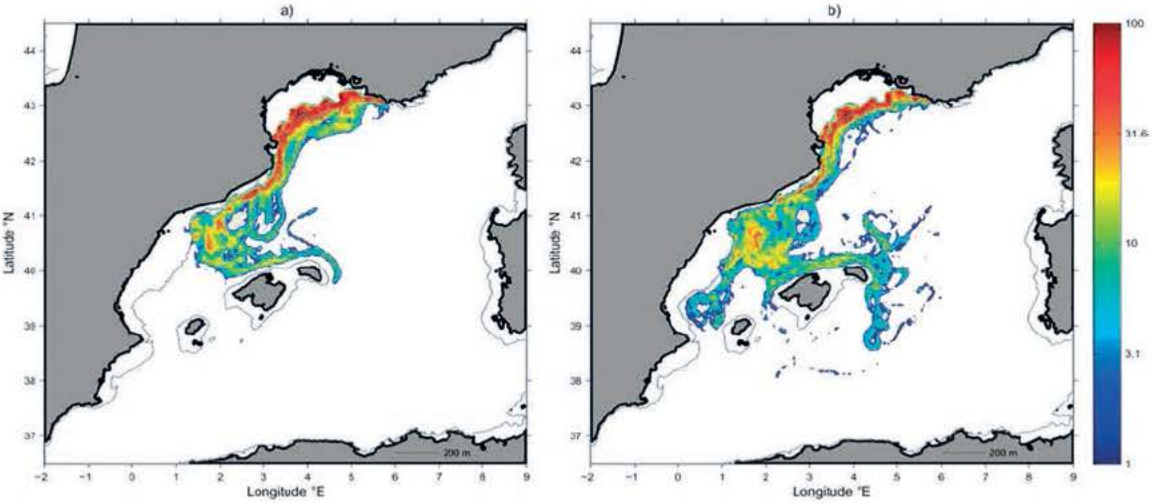

Figure 7: Probabilities Density Functions of particles released in autumn 2001 (summed up over 7 spawning events) from the Gulf of Lion and tracked during a PLD of a) 30 days and b) 50 days.

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).

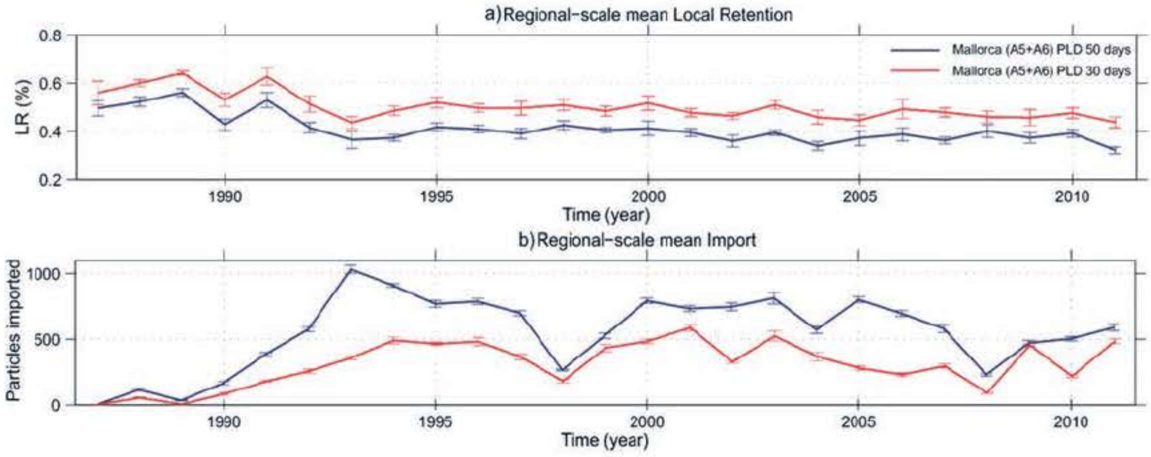

Figure 8: 27 year-long time-series of regional connectivity indices for the hake case-study. Panel a) is spatially averaged LR for larvae released in the Balearic archipelago. Panel b) is the total number of particles reaching the Balearic archipelago after their released from the Gulf of Lion and the 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 volume) so that their dispersal is expected to be very different from those drifting at or close to the surface.

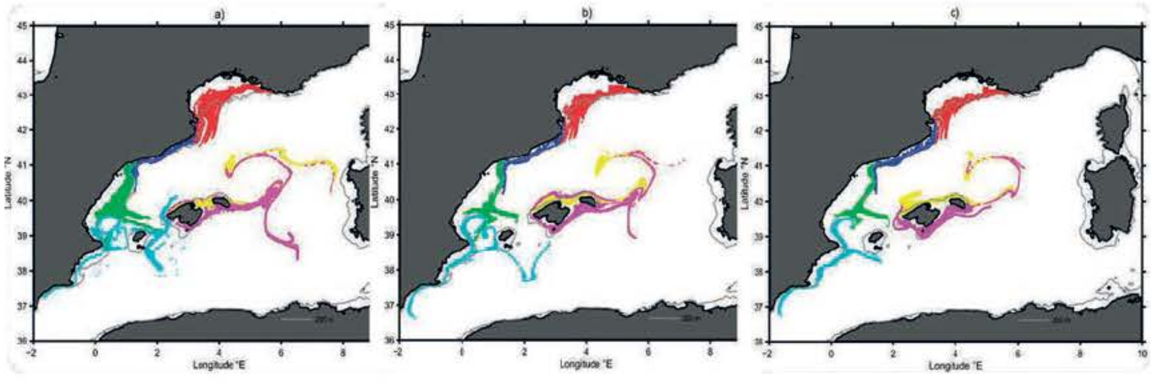

Figure 9: Final positions of particles released from distinct sub-populations of hake (according to the color code) and tracked during a PLD of 30 days at different depths: a) 60 m, b) 90 m and c) 120 m.

5. IMPLICATIONS FOR THE MANAGEMENT AND 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 and/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 due primarily 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 hardly 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.

5.1 Marine Protected Areas design

The geographical structure of larval dispersal across the seascape largely influences 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 ($\leq 5\times10^4$ km^2), 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 km^2). 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 ($\geq 7\times10^4$ km^2). 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 (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 (≥ 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 ($\leq 5\times10^4$ km^2). 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 (Figure. 10).

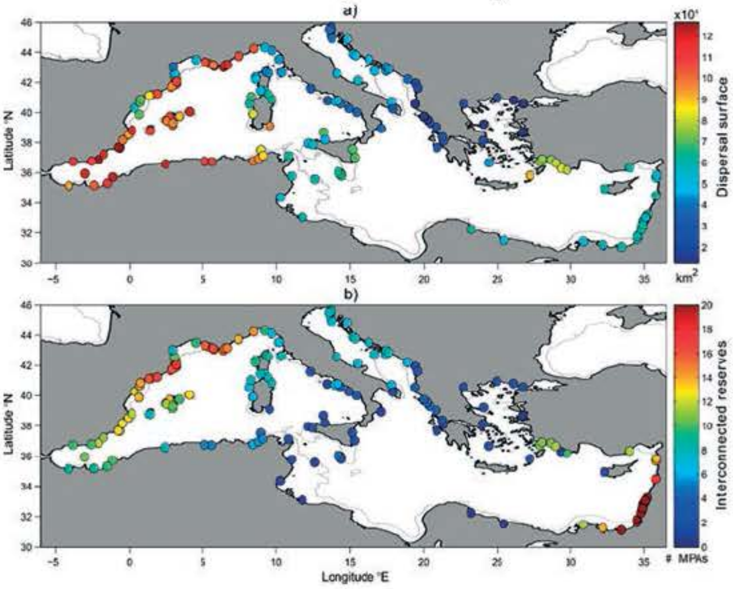

Figure 10: Spatial variability of MPAs connectivity derived from three complementary metrics averaged across all winter/summer experiments over 2002–2011 using a PLD of 30 days. (a) Mean area (in km^2) and (b) mean number of interconnected MPAs (i.e. number of reserves situated within the same hydrodynamical 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.

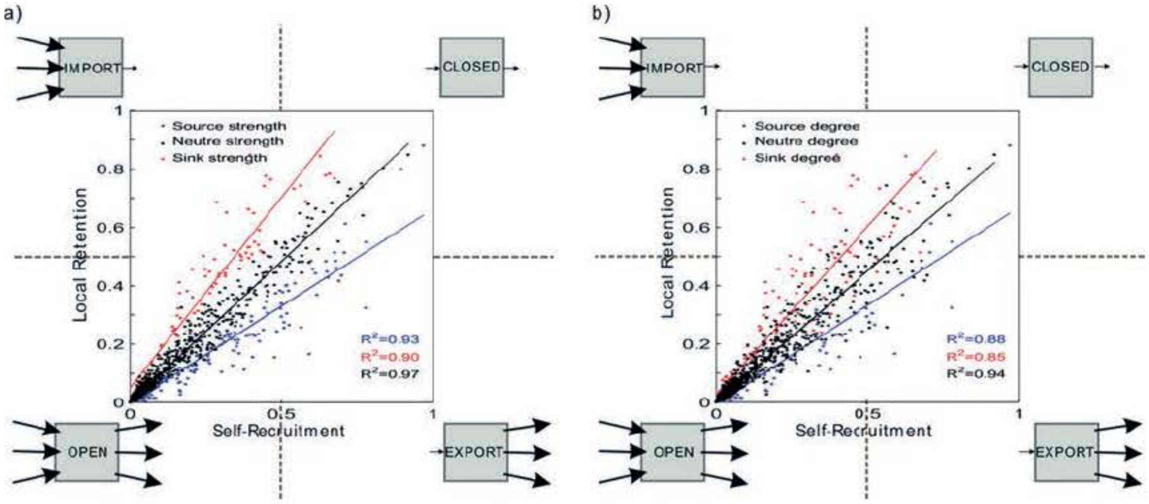

Figure 11: Inter-relationship among connectivity metrics for a PLD of 30 days. Mean relationship between LR and SR distinguishing "source" (blue), "sink" (red) and "neutral" (black) nodes based on (a) Source-Sink index computed from larval fluxes and (b) Source-Sink index computed from the number of 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 MPAs (Dubois *et al.*, 2016). They give insight into how subpopulations are connected through larval transport and as such help predict the effects of management measures or disturbances on both local and surrounding subpopulations. For instance, establishing a MPA on a site where 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 (Figure. 11) provide relevant information for managers and scientists to discuss implementation guidelines "case-by-case", in accord with conservation objectives (Dubois *et al.*, 2016).

5.2 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 volume). 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*., 2013).

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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Present day limitations and future paths for the identification of barriers to gene flow and the reliable appraisal of present day dispersal in the marine realm

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As global biodiversity is facing a sixth wave of extinction, marine species and ecosystems are highly vulnerable to anthropogenic perturbation and global change: their decline follows a rate twice to ten times higher than the ones reported in terrestrial environments (Lotze *et al.,* 2006), and nearly no area in the ocean is immune to anthropogenic impact (Halpern *et al.,* 2008; Ramirez-Llodra *et al.,* 2011). The sea is subject to large direct physicochemical perturbations (increasing coastal demography associated to pollution, acidification, warming, introduction of alien species, direct destruction of habitat for construction or resources preemption including fisheries, aquaculture installations, mineral and oil extraction...) and 90% of top marine predators disappeared since the transition to industrial era.

Oceans cover 70% of Earth surface and encompass almost all major living phyla. Yet, they are clearly understudied with 10% of research effort in 2006 (Hendriks *et al.,* 2006). A collateral consequence of this disequilibrium is the lagging protection of the marine environment: the Aichi targets defined by the Convention for Biological Diversity for 2020 realistically set 10% as an objective for the conservation of coastal and marine areas by 2020, whereas 17% is aimed for terrestrial and land waters. The conservation of marine species may require measures sharing some similarities with those followed in the terrestrial realm, including the establishment of network of protected areas. Yet, the establishment of networks needs to account for the diversity and specificity of life cycles and connectivity patterns of marine species, preventing a simple transfer of terrestrial recipes in the marine environment and calling for enhanced knowledge.

Most species are heterogeneously organized across their distribution range, with groups of individuals forming subpopulations more or less interconnected by migratory flows. The distribution, importance and direction of these flows - a set of parameters designed as '*connectivity*' - plays a major role in population and community dynamics both on the long and the short run, by determining the demographic, ecological and evolutionary inter-dependency of populations (Botsford *et al.,* 2001; Cowen *et al.,* 2007). Migratory movements allow the persistence of populations of limited size, temporarily impacted demographically (rescue effect, or source-sink systems), or genetically impoverished (limiting drift), and thus strongly influence their capacity to cope with spatially and temporally fluctuating environmental conditions. While fragmentation is an important concern in conservation genetics and has been the subject of a large number of empirical studies and theoretical development in continental species (Lindenmayer and Fischer, 2006), the problem remains poorly understood in the marine realm, probably owing to its widespread but excessive perception as an highly homogeneous and dispersive environment. In this increasingly altered environment, subject to cumulative impacts across all its three dimensions favoring habitat alteration and fragmentation, it is now essential to assess, analyze and understand the patterns of connectivity as reliably as possible. The management of fisheries resources, the control and prevention of invasive species and the conservation plans for threatened species or vulnerable ecosystems (some already suffering well characterized declines such as coral reefs –Aichi target 10-, seagrass, mangroves…) require the knowledge of interconnection and interdependency of stocks, populations and communities constituting these ecosystems.

Although emblematic marine species are often top predators with migration encompassing the large and periodic movements of adults toward feeding or reproductive grounds, the majority of marine organisms exhibit a complex life cycle with two phases, including an adult stage with limited movements and a larval dispersive stage. The direct observation and study of migratory movements is almost impossible in the oceans due to i) the limits to full access of the marine environment, ii) the often extreme population sizes *sensu stricto*, and iii) the generally extensive migration distances, at adult or larval stages, with no strict *a priori* relation between life history traits suspected to influence dispersal potential and the scale of realized migrations (Riginos *et al.,* 2011). Therefore, tracking and indirect inferences of connectivity patterns are needed. Systems allowing the direct estimates of spatial movements such as Mark-Recapture (MR) or electronic tags are at present realistic for a very low percentage of marine species (mostly top predators and large pelagic – marine mammals, turtles, sharks…). Molecular methods, direct approaches using microchemistry or individual tags, and modeling of dispersal have a central role to play in the study of marine connectivity (Gagnaire *et al.,* 2015).

In recent decades, the use of molecular markers to test for the predictions and hypotheses formalized for nearly one century in theoretical population genetics has allowed large progress in the understanding of connectivity in the marine environment, but also revealed loopholes calling for further theoretical and empirical developments. The aim of this paper is to summarize briefly, taking Mediterranean cases as examples, the advantage, pitfall and time scales associated to population genetic studies. The aim is also the identification of the possible pathways for improvement in the identification of the drivers of genetic differentiation and the access to reliable estimates of contemporary connectivity, in order to inform the management of resources and the design of coherent networks of Marine Protected Areas.

FROM SPECIES TO POPULATION LEVEL: PROVIDING EVIDENCE FOR THE LACK OF CONNECTIVITY AND RETRACING HISTORY

Among the major advances offered by the use of molecular tools in the theoretical framework of population genetics, the main one may be the support offered to describe and recognize taxonomic groups, particularly through several initiatives such as the barcode of life (Hebert *et al.,* 2003) that gave rise to the fast-improving field of integrative taxonomy (Puillandre *et al.,* 2012; Pante *et al.,* 2014). Based on the initially proposed biological concept of species ("*Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups*" Ernst Mayr, 1940), it is clear that the knowledge of species boundaries is a prerequisite to delineate the set of populations among which assessing contemporary gene flow is meaningful (i.e. among populations of the same species). Although such a recommendation may appear obvious, a number of cases were reported where the use of molecular markers revealed the occurrence of either synonymous (Johnson *et al.,* 2009; Teixeira *et al.,* 2009) or, frequently in the marine environment, cryptic species (Appeltans *et al.,* 2012; Pante *et al.,* 2015). A proposed definition for these taxonomic inconsistencies is as follows: cryptic species are "*two or more species lacking obvious morphological diagnostic features that are classified as a single nominal species; it is the opposite situation compared to synonyms for which different scientific names are given to the same species*" (Pante *et al.,* 2015).

The former case corresponds to the morphological description of specimens belonging to the same species as different taxonomic entities, which if remaining undetected, would a priori and logically prevent engaging into any connectivity study among taxonomic entities thought to correspond to distinct species. A contrario, such studies would lead to the erroneous interpretation of large genetic structure estimate as resulting from strong present day barriers to gene flow, when past rather than present barriers are involved in event of divergence, often through vicariance, responsible for the contemporary observed genetic differentiation (see the area of taxonomic uncertainties in Figure 1).

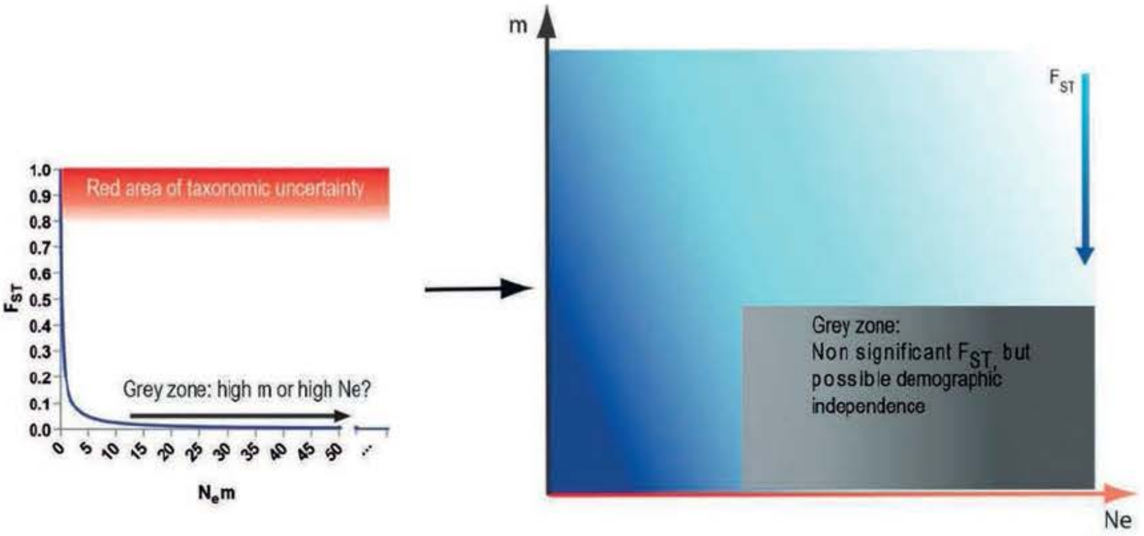

Figure 1: limitations to the interpretation of Fst estimates in terms of contemporary connectivity. The red zone indicates the cases where at least partial reproductive isolation render Fst estimates more impinged by historical events, and the grey zone illustrates the usual area of uncertainties where populations may be demographically inter-independent, but genetically homogeneous.

Given a comprehensive sampling and a reasonable knowledge of the life cycle of studied organisms, a complementary sets of markers will thus allow to simultaneously ensure the study of a single taxonomic entity, and ascertain the pattern of genetic structure across its entire geographic range (Pante *et al.,* 2015).

ASSESSING BARRIERS TO GENE FLOW USING MOLECULAR MARKERS: DISTINGUISHING THE DRIVERS OF ANCIENT DIVERGENCE AND THE BARRIERS MAINTAINING PRESENT DAY DIFFERENTIATION

The use of molecular markers provides information on processes facilitating or impeding gene flow potentially integrating a broad range of time scales. Their use in a phylogenetic or phylogeographic framework informs about the ancient patterns of divergence (disruption of gene flow) that have shaped the Tree of Life through nearly 4 billion years of evolution. When accurately circumscribed to the infra-specific level, their use in a population genetics framework permits, along a continuum from high to low differentiation, the reconstitution of biogeographic history and the study of the first steps of divergence. However, identifying both the role of ancient barriers to migration and the present-day factors limiting gene flow is not an easy task.

First, the nature, strength and location of barriers fluctuate across evolutionary time scale, particularly in the marine environment, and the identification of ancient barriers requires the knowledge of the paleo-environment across a series of evolutionary time scales (Hewitt, 2004). Partial knowledge of such conditions allowed already major advances in the understanding of the long lasting signature of paleo-environments on present day phylogeny (among species) or phylogeography and population genetics (within species). This allowed comparing the history of plate tectonics to the ancient divergence of hydrothermal fauna (Hurtado *et al.,* 2004; Moalic *et al.,* 2012), and the putative influence of paleo-currents (Benzie and Williams, 1997) or more recently the influence of sea level changes during the last glacial periods (Grant and Bowen, 1998; Hewitt, 2004; Marko *et al.,* 2010) in the present-day pattern of differentiation. As for Mediterranean taxa, the influence of long term vicariance, particularly during the Last Glacial Maximum but also as anciently as the Messinian crisis, is reflected in a large amount of sister species or extremely differentiated populations of the same species found on both sides of the Gibraltar Straight or of the Almeria Oran oceanographic front. One of these two boundaries acts, depending on species, as barrier to gene flow between the Atlantic and the Mediterranean, as underlined though a compilation of data on 70 species (Patarnello *et al.,* 2007). This meta-analysis exemplified the fact that genetic structure is the resultant of multiple processes spanning from possible past divergence to present day lack of gene flow. In such conditions, the maintenance of species differentiation may owe to present-day exogenous barriers to gene flow (physical barrier to dispersal, environmental barrier preventing local adaptations…) adding or not to the accumulation of endogenous (Bierne *et al.,* 2011) genetic barriers. Among the species showing genetic structure around Gibraltar Straight or Almeria Oran Front, some may thus suffer limitation to dispersal owing to the physical barriers imposed by the emerged lands or water masses, whereas others may disperse across those boundaries but be submitted to limited gene flow owing to partial reproductive isolation among sister clades. Discriminating present-day exogenous barriers from anciently developed endogenous incompatibilities is now realistic provided that a sufficient amount of markers is available to interpret patterns of genetic differentiation (Bierne *et al.,* 2011; Gagnaire *et al.,* 2015).

Beyond the Almeria Oran front, several studies within the Mediterranean Sea have unraveled a strong East-West differentiation. Although few studies could rely on a sampling allowing to define the location of barriers to gene flow, a majority of those supported a strong incidence of the Siculo-Tunisian Straight in creating and/or maintaining disruption to gene flow in a range of taxonomic groups spanning from macrophytes to vertebrates (Borsa, 1997; Bahri-Sfar *et al.,* 2000; Arnaud-Haond *et al.,* 2007; Alberto *et al.,* 2008; Zitari-Chatti *et al.,* 2009; Bahri-Sfar *et al.,* 2011; Fadhlaoui-Zid *et al.,* 2012). A pattern of isolation by distance was also reported among locations of the western basins for several vertebrates and invertebrate species (Kotoulas *et al.,* 1995; Zulliger *et al.,* 2009; Ledoux *et al.,* 2010; Aurelle *et al.,* 2011; Fratini *et al.,* 2013; Arizmendi-Mejia *et al.,* 2015), while the eastern basin appeared as characterized by more frequent and less predictable disruptions to gene flow, particularly in the Aegean Sea and the Adriatic (Bahri-Sfar *et al.,* 2011; Borrero-Perez *et al.,* 2011; Barbieri *et al.,* 2014).

Besides the influence of straights and of distance on the limitation to gene flow observed in these species, a handful of studies also suggests the possible influence of the movements and composition of water masses (Franchini *et al.,* 2012; Lo Brutto *et al.,* 2013; Clusa *et al.,* 2014). Yet, the few studies reported thus far in the Mediterranean, the often limited sampling evenness and density and the extremely difficult access to almost half the Mediterranean coasts spanning from Morocco to Turkey (and more particularly in the south of the Eastern basin), are still needed to obtain a robust appraisal of the global pattern of differentiation and the identification of the local drivers of connectivity.

TRANSLATING GENETIC ESTIMATES INTO DEMOGRAPHIC CONNECTIVITY: PANMIXIA AND THE GREY ZONE OF GENETIC DIFFERENTIATION

Given the usual underlying assumptions (population do not strongly depart the equilibrium migration-drift ; no endogenous barriers to gene flow occur) the pattern of genetic differentiation among populations can be interpreted as the occurrence of very limited gene flow and shed light on the present environmental conditions acting as barriers to gene flow. Under these conditions, the pattern of genetic differentiation allows the successful identifying groups of populations that are genetically and thus demographically inter-independent-a precious information to manage population of exploited, invasive or endangered species in particular.

The situation is highly different in the case when no genetic differentiation is detected among studied populations. This case is unfortunately very common in marine species due to their peculiar life history traits (e.g. high fecundity, large population sizes, high dispersal potential), most often leading to weak or no differentiation (Waples, 1998; Hedgecock *et al.,* 2007). In fact, the accumulation of genetic differentiation (through the independent evolution of allelic frequencies) theoretically depends on the per generation number of migrants exchanged (N_em, with N_e the effective population size and m the rate of migration), whereas the level of demographic inter-dependency depends on the rate of migrants (m) exchange (Lowe and Allendorf 2010). Genetic panmixia in most marine species can therefore be the outcome of a wide range of very distinct demographic situations, spanning from a nearly negligible contemporary rate of demographic exchanges among populations with a large effective size (N_e), to a rate m high enough to ensure both genetic homogeneity and strong demographic interdependency even among small populations (Figure 1).Depending on the effective size of populations, the minimum per-generation number of migrants required to lead to genetic panmixia may thus allow neither demographic interdependency nor rescue effect (Waples and Gaggiotti, 2006).

Here also the molecular progresses owed to New Generation Sequencing and the spectacular developments of bioinformatics analysis including Bayesian computations open large perspectives. The recently generalized access to high density genome scan is expected to allow the improved inference of parentage or kinship through coalescent analyses and to expand analyses based on linkage disequilibrium (Hellberg, 2009), to refine the interpretation of the patterns of genetic differentiation (but seeWaples, 2015). Besides, recent advances also showed such improvement could also be gained by extracting information from those outlier loci influenced by endogenous barriers to gene flow (Bierne *et al.,* 2011; Gagnaire *et al.,* 2015).

PROMPTING MULTIDISCIPLINARY APPROACHES: THE NEED FOR AN INTEGRATIVE FRAMEWORK

The prediction of patterns of gene flow in marine species is still far from straightforward and the influence of life history traits embedded in complex life cycles is not clearly understood in the marine realm, as meta-analysis often lacks statistical power due to the heterogeneous sampling they rely on. Two meta-analyses (Riginos *et al.,* 2011; 2014) however detected a significant influence of dispersal potential on the extent and scale of population genetic structure for benthic fishes, although the part of the variance it explains is limited and clearly calls for other explanatory variables. Progresses in ocean circulation modelling deliver predictions of patterns of effective dispersal expected under approximated duration and mode of larval dispersal (deYoung *et al.,* 2004; Treml *et al.,* 2007; Lett *et al.,* 2008), and some theoretical bridges between oceanographic features and metapopulation models are emerging (Watson *et al.,* 2011; Andrello *et al.,* 2013).

All fields of research dealing with connectivity rely on the interpretation of data under restrictive underlying hypotheses or models. The combination of results issued from these distinct fields may help, when obtaining a convergence of estimates, overcoming some of the limitations inherent to each of those hypothesis and models. Whereas genetic methods estimate the number of migrants per generation, or ideally target the rate of migration, stable isotopes and biochemical tags can be used to assign individuals to characterized environments corresponding to their populations of origin or to feeding areas (Thorrold *et al.,* 2007), electronic tags to directly track the movement individuals and oceanographic models to predict dispersal. A pioneer work by Abaunza *et al.*(2008) showed that combining information from different methods within a single study (e.g., genetic data, morphological traits, chemical signatures, parasites) and using multivariate analysis can reduce type I errors and enhance the reliability of estimates. Also, the simultaneous characterization of host population genetics and associated bacterial communities has the potential to contribute to the understanding of migratory pathways, as when tracking the source of an invasion (Aires *et al.,* 2013).

Such information is thus required not only to enhance the theoretical framework for the study of the dynamics and evolution of marine metapopulations, but also to improve the management of exploited resources (fisheries, aquaculture), the protection of the environment (invasive species, impact studies) and the preservation of biodiversity, among others through the development of coherent networks of Marine Protected Areas. Additionally, the predictions of consequences of global changes require an accurate knowledge of connectivity in order to estimate colonization and range shift and adaptive abilities (Mumby *et al.,* 2011), to identify the main conservation and management units (Gerber *et al.,* 2014), the and to forecast the effect of environmental change on realized (McLeod *et al.,* 2013).

The generalization of Next Generation Sequencing now allows producing high-resolution population genomic data, which will allow the reconstruction of networks of connectivity with increased accuracy. The next step is now to pursue the development of statistical methods that can combine these different sources of information in a common statistical inference framework (Thorrold *et al.,* 2007) , both in order to improve connectivity estimates and to identify the main barriers to gene flow.

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Population genetic connectivity among marine species; a matter of dispersal, selection and drift

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Protecting marine isolated habitats is not enough to maintain biodiversity. The establishment of networks of marine protected areas is fundamental to enhance species resilience in front of environmental disturbances (Botshford *et al.,* 2009). Population connectivity refers to the exchange of individuals among geographically separated subpopulations that comprise a metapopulation and is the base for building those networks. For most littoral marine organisms, with restricted adult movement, pelagic larvae represent the most important dispersal phase (Cowen *et al.,* 2007). Thus, measuring marine connectivity, although important for the management of biodiversity, is not an easy task. Assessing genetic connectivity implies identifying gene flow; individuals that disperse, even over long distances, but do not contribute with their genes to the next generation in the areas visited during their lifespan will not be relevant in ensuring the long term persistence of those populations. Genetic diversity and similarity among areas is a frequently used proxy of connectivity. Most studies of marine organisms have used this indirect approach based on classical population genetics comparing allele frequency distributions between populations (Palumbi, 2003; Duran *et al.,* 2004b; Carreras *et al.,* 2007; Schunter *et al.,* 2011b) and only a few studies have directly measured connectivity through parentage or sibship analyses (Planes *et al.,* 2009; Schunter *et al.,* 2014).

Population genetic studies on marine species have steadily increased in the last 20 years and the molecular markers used have changed through time and will continue doing so as new technological advances allow using them in non-model organisms (Milano *et al.,* 2014; Shinzato *et al.,* 2015). Several misconceptions, based on the use of different genetic markers, have arisen. They will be discussed using case examples from different marine organisms.

MOLECULAR MARKERS

The molecular markers most frequently used to infer connectivity in marine organisms are mitochondrial DNA (mtDNA), restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), allozymes, microsatellites and single nucleotide polymorphism (SNP). They can be grouped according to their inheritance as maternal (mtDNA) free of recombination, or biparental (the rest) presenting recombination between markers related to their physical distance on the chromosomes. Thus mtDNA is not only depicting female connectivity as selection acting on one of its genes will leave also a footprint on the other genes of this circular molecule. Biparental inherited markers can be further subdivided into dominant (RFLP and AFLP), scored as presence and absence of amplified fragments, and codominant (allozymes, microsatellites and SNPs) where the two alleles of a diploid individual can be scored-one from paternal and the other from maternal origin. For biparental markers selection would be only identified in adaptive genes or neighboring genes whose linkage to them is not broken by recombination, although false positives may arise if populations are not at equilibrium (Lotterhos and Whitlock, 2014). It has been claimed that different genetic markers are appropriate for drawing inferences at different temporal scales, with mtDNA being most suitable to unveil historical processes and microsatellite and AFLP loci for contemporary processes (Wang, 2010). However, the lag between demography and population genetic structure is dependent on generation time, mutation rates and population-sizes among other factors affecting the ability to detect connectivity after perturbations-and should not be neglected when interpreting landscape genetic studies (revised in Epps and Keyghobady, 2015).

PLD, BATHYMETRY AND MIGRATION

Life history traits of dispersive stages are expected to affect population genetic structuring and thought to correlate with gene flow. For most littoral species where larvae are the main dispersive phase, pelagic larval duration (PLD) is assumed to determine connectivity. However mixed results are observed in different empirical studies. No significant relation between gene flow and early-life-history traits (egg type, pelagic larval duration, and inshore-offshore spawning) was observed in seven Mediterranean fish species sampled in the same area using microsatellite markers (Galarza *et al.,* 2009). In the European spiny lobster (*Palinurus elephas*) ,despite its long PLD from 6 months to 1 year, populations from the Atlantic and Mediterranean basins showed small but significant genetic differentiation among them with microsatellite loci (Palero *et al.,* 2011). Larval behavior and retentive oceanographic environments could account for these results as suggested to constrain dispersal in the Caribbean Sea in *Palinurus argus*, also with long-lived larvae (Butler *et al.,* 2011). Differences in genetic structure were observed in 35 codistributed species in the Hawaiian archipelago where regional structuring was the pattern most commonly found and isolation by distance the least common despite the stepping stone configuration of the islands (Selkoe *et al.,* 2014). These authors further observed that all species presenting chaotic structuring were non-endemic generalists. Nonetheless other factors were suggested to impact genetic structure in that archipelago such as abundance across islands and depth ranges. A comparative study along the Atlantic-Mediterranean transition using seven crustacean decapod species with different bathymetric distributions identified higher levels of population structure in shallow-water species, but no relation to the number of larval stages, as proxy for PLD (García-Merchán *et al.,* 2012). However, the haplotypes within the different species coalesced at times that could be related with past climatic events occurring before, during and after the last glacial maximum indicating that historical processes are important in shaping the diversity and the ability to identify connectivity. A reassessment of different datasets revealed a moderate fit between PLD and genetic proxies of dispersal (IBD slope and global F_{ST}), moreover important effects on identifying this relation were detected for the marker type, the number of individuals, the number of populations sampled and their geographic scale (Selkoe and Toonen, 2011). Isolation by distance was best observed at small scales in the red gorgonian *Paramuricea clavata* (Mokhtar-Jamaï *et al.,* 2011) while it saturates with distance (Selkoe and Toonen, 2011). Thus, to estimate connectivity several factors contribute to their identification such as a robust sampling design, the marker used, the demographic and historical processes determining the distribution of the species, the oceanographic discontinuities separating populations and the geographic distance between the populations assayed.

OCEANOGRAPHIC DISCONTINUITIES

Oceanographic fronts in the Western Mediterranean have been shown to represent major barriers to gene flow for many marine species (Patarnello *et al.,* 2007; Galarza *et al.,* 2009). However, the barrier effect is not general across species since contrasting population differentiation associated to oceanographic fronts was observed for even closely related species which could not be easily predicted from their early-life history traits nor the genetic markers used (Galarza *et al.,* 2009). Seasonal changes in current patterns and the relationship between ocean circulation patterns and spawning season may also play an important role in population structure around oceanographic fronts. In *Serranus cabrilla* directional gene flow was observed matching simulations of passive particles drifting with currents (Figure 1) from west to east over the Almeria-Oran front, from north to south on the Ibiza channel and from south of the channel towards the Balearic Islands (Schunter *et al.,* 2011). Similarly, for *Carcinus aestuarii*, genetic differentiation reflects an oceanographic subdivision in the Adriatic Sea into three sub-basins, with circulation patterns allowing the exchange of larvae through permanent connections linking north Adriatic sites and ephemeral connections like those linking the central Adriatic with northern and southern locations (Schiavina *et al.,* 2014). A significant effect of the Strait of Gibraltar was found in the crabs *Liocarcinus depurator* and *Macropipus tuberculatus*, but no differentiation was observed in two hermit crabs nor in two shrimp species using mtDNA, indicating that demographic or selective historical processes could prevent identifying the current connectivity among populations (García-Merchán *et al.,* 2012).

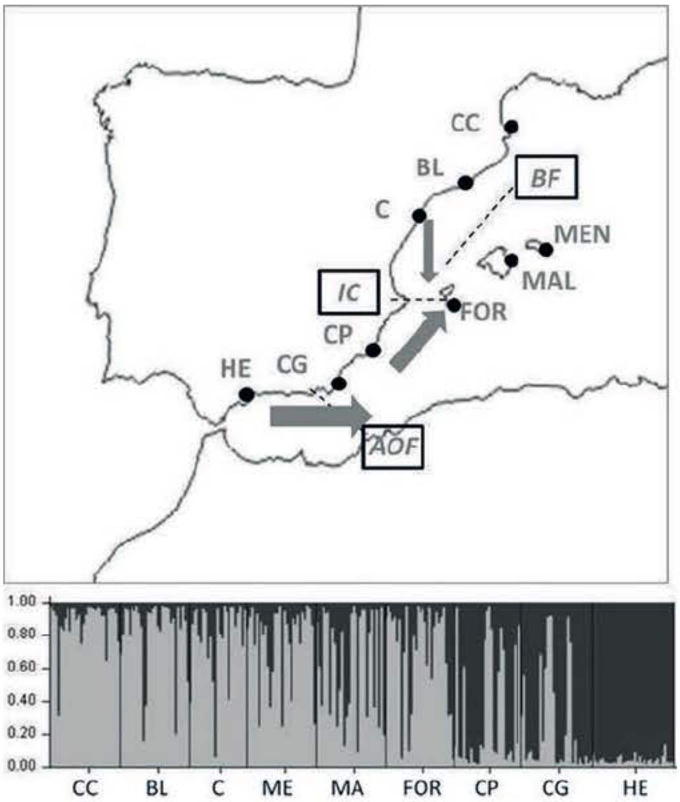

Figure 1. Top: Gene flow (arrow) in *Serranus cabrilla* matching particle dispersal simulation across three oceanographic discontinuities: Almeria Oran front (AOF), Ibiza Channel (IC) and Balearic front (BF). The size of the arrow reflects the intensity and direction of the flow. Bottom: Probability of each individual in each population to belong to one of the two clusters identified with STRUCTURE, reflecting influence of Atlantic waters (dark grey) or Mediterranean waters (light grey). Adapted from Schunter *et al.* (2011a).

HISTORICAL AND CONTEMPORARY PROCESSES

The relative importance of historical and current processes on the spatial distribution of genetic diversity is difficult to ascertain, since both time and space may not be independent. Changes in the environmental conditions (estimated from paleoclimatic data) and historical shifts of species distributions significantly structure genetic variation, as shown by spatially-explicit demographic modeling of genetic differentiation (He *et al.,* 2013). Many phylogeographic studies identify genetically differentiated units that can be attributed to vicariance or selection reducing gene flow (Kelly and Palumbi, 2010). For instance the separation of eastern and western Australian populations of the ascidian *Microcosmus squamiger* during the Pleistocenic glaciations left a footprint on the present population genetic structure; however this species has recently invaded populations worldwide with admixed founders from these two Australian regions and thus some broadly separated areas are genetically more similar than geographically close localities (Rius *et al.,* 2008; 2012). Surprisingly these two gene pools seem to be moderately unmixed in the invaded areas without compromising post-border colonization processes (Ordóñez *et al.,* 2013).

Temporal genetic variation has also been detected in a few marine organisms using mtDNA and nuclear markers. For instance, significant changes among years were detected in the blue crab *Callinectes sapidus* in the northern Gulf of Mexico (Yednock and Neigel, 2014). Similarly, a significant differentiation was observed between discrete size classes of the Caribbean spiny lobster *Panulirus argus* indicating temporal variation among genotypes of larval recruits (Truelove *et al.,* 2015). Temporal differences were observed in the western Mediterranean for the sea urchin *Paracentrotus lividus* and the crab *Liocarcinus depurator* that could be associated with changes in circulation patterns associated to oceanographic discontinuities (Calderón *et al.,* 2012, Pascual *et al.,* 2016). Some of these reported temporal changes were attributed to selection, to drift, and/or to dispersal due to changes in oceanographic currents.

THE CASE STUDY OF *CRAMBE CRAMBE*

The encrusting sponge *Crambe crambe* was the first sponge species for which microsatellite loci were isolated (Duran *et al.,* 2002). It is commonly found in the sublittoral rocky zones of the western Mediterranean. It reproduces sexually and releases lecitotrophic larvae that, according to laboratory experiments, can swim for 24-72h before settlement and with its behavior be carried away into the water column (Uriz *et al.,* 1998). Asexual reproduction was also described in adult individuals by fission (Turon *et al.,* 1998). Three different molecular markers were analyzed from locations separated by distances from 20 to more than 3,000 km encompassing most of the Atlanto-Mediterranean range of the species: the mtDNA gene cytochrome oxidase subunit I (COI), the nuclear ribosomal internal transcribed spacers (ITS-1 and ITS-2) and microsatellite loci. Extreme low nucleotide diversity (π=0.0006) was found for COI; the frequencies of the only two haplotypes found significantly differed between close populations suggesting low gene flow, although some distant populations had the same haplotype fixed indicating that probably drift played an important role in shaping the population structure in this species (Duran *et al.,* 2004c). ITS and microsatellite markers revealed for the same populations highly structured populations and isolation-by-distance (Duran *et al.,* 2004a; 2004b). Identical genotypes were found in some locations, although samples collected were separated by at least 5 m. Thus, other asexual processes besides fission events were invoked to explain its distribution such as accidental fragmentation with subsequent dispersal of the fragments or rafting on algal thalli (Duran *et al.,* 2004b). Asexual reproduction proved to play an important role in structuring populations in *C. crambe* since 76 out of 177 individuals were identified as clones of 24 groups in a fine scale study, where the mean intraclone distance was 20 cm and the maximum distance 1m (Calderón *et al.,* 2007). Spatial autocorrelation analyses showed a drastic decrease in genetic relatedness within the first distance classes (30–40 cm) once the contribution of clonality was eliminated, while genetic similarities with sponges from other Mediterranean localities were within the same range as those found in sponges 2–7 m apart (Calderón *et al.,* 2007). Thus asexual reproduction has a higher impact than previously thought in shaping the population structure of this species, isolation by distance is detected at small scales although at large scales distances are saturated and genetic drift during colonization processes should also be considered when analysing the structure of long lived sessile organisms with potential low dispersal capabilities.

THE CASE STUDY OF *TRIPTERYGION DELAISI*

Tripterygion delaisi is a common littoral fish in the Mediterranean Sea, living always in rocky habitats, preferentially in biotopes of reduced light, between 6 and 12 m (Zander, 1986). Adult individuals are highly territorial, showing high levels of homing behaviour, parental care of the eggs and cannot swim even short distances (tens of meters) in open water or on sandy bottoms (Wirtz, 1978). Larvae of *Tripterygion delaisi* remain in plankton for 16-21 days (Raventós and

Macpherson, 2001), almost exclusively in coastal waters (Sabatés *et al.,* 2003), suggesting that larvae remain close to adult habitats. Thus, the dispersal capability of *T. delaisi* might be low, consequently constituting an interesting model for investigating differentiation in marine fishes. The population structure of this species was analysed in different studies, indicating that large discontinuities (>30 km) of sand or deep-water channels could be acting as effective barriers, preventing larval and adult exchange between populations (Carreras-Carbonell *et al.,* 2006). Furthermore, the existence of oceanographic discontinuities enhances this genetic differentiation, as observed with the. Almeria-Oran Front (Galarza *et al.,* 2009). Due to their scarce dispersal capability, a high proportion of the larvae of *T. delaisi* remain close to, or never leave, their natal spawning area as revealed by the use of assignment tests among western Mediterranean populations (Carreras-Carbonell *et al.,* 2007). This study showed that the self-recruitment in the NW Mediterranean population was that ca. 75%, and most of other recruits belonged to the geographically nearest ones (Figure 2). Thus, some retention mechanisms must be acting in these larvae during the mobile phase, since self-recruitment results imply that a significant percentage of spawned larvae come back to, or never leave, their natal population.

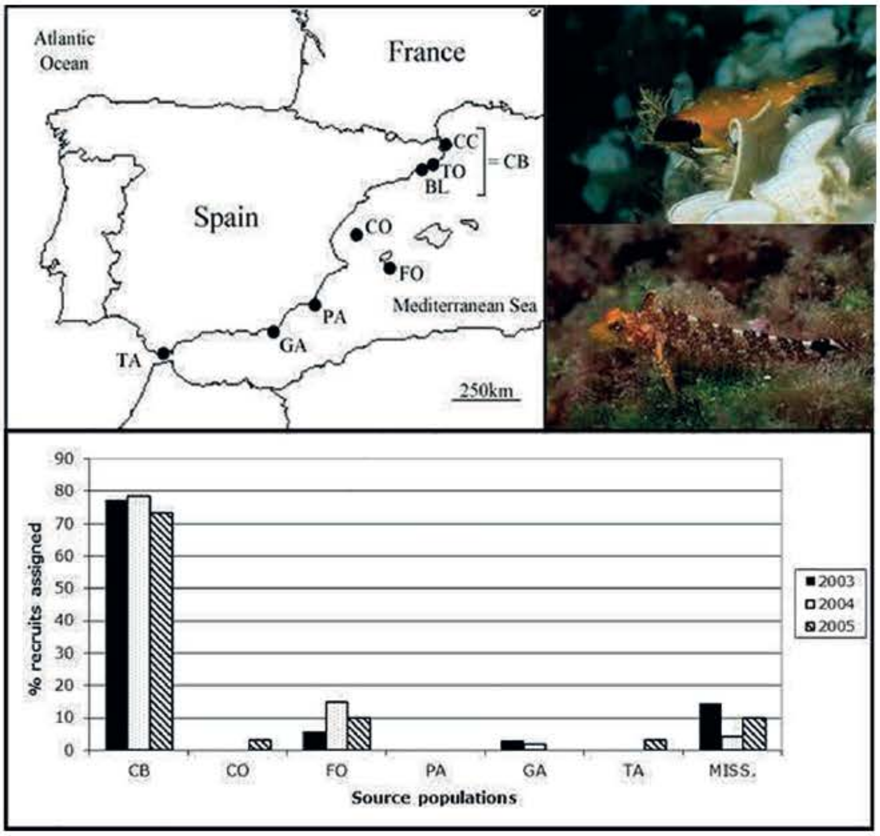

Figure 2. Male (above) and female (below) photographs of *Tripterygion delaisi* and assignment test to identify recruits from 2003, 2004 and 2005 from Blanes (BL) and map location of source localities used. (MISS.): miss assigned individuals.

However, direct measurements of dispersal are essential to understanding connectivity patterns and show the degree of self-replenishment and sustainability of populations. Recently, due to the technical difficulties of tracking larvae, parentage analysis has provided a means to address this question effectively. In *T. delaisi,* after using SNP markers to perform parentage and sibship reconstruction, some interesting results were obtained. The analysis revealed a decrease in dispersal success in the focal area over 1 km distance and approximately 6.5% of the juveniles were identified as self-recruits. Sibship reconstruction analysis found that, in general, full siblings did not recruit together to the same location, and that the largest distance between recruitment locations was much higher (11.5 km) than found for parent/offspring pairs (1.2 km) (Schunter *et al.,* 2014).

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Comparative genetic structure of shallow water benthic invertebrates as a proxy to marine connectivity in the Mediterranean Sea

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CONNECTIVITY AND DISPERSAL OF BENTHIC INVERTEBRATES

Coastal areas represent a small proportion of the marine realm; yet they host a large extent of marine biodiversity (Coll *et al.*, 2010), together with a complex synergy of threats far greater than in offshore waters (UNEP, 2006). The most species-rich marine ecosystems worldwide are located in near-shore demersal and benthic habitats, from the tropical coral reefs to the Mediterranean coralligenous assemblages. These rich habitats are formed by a myriad of taxa, all of them interconnected by complex networks of direct and indirect interactions (Dayton, 1971). Invertebrates largely contribute to benthic biodiversity with a variety of body plans and adaptations. They include more than 15 phyla, each of them with different evolutionary histories, life history traits, feeding modes and habitat requirements. In benthic habitats, competition for space and available resources increases the specialization, therefore even closely related species might show contrasting traits, as a result of unique adaptations to occupy specific ecological niches (Mendonza *et al.,* 2014; Keogh *et al.,* 2016). The large diversity of benthic invertebrates includes many keystone species, as for instance corals, due to their habitat-forming capacity, or several species of echinoderms, due to their feeding activity, either herbivores or specialist carnivores, able to provoke large trophic shifts. In spite of this vast diversity of life history traits, most benthic invertebrates have in common a bipartite life cycle: a planktonic larval stage and a sessile or slightly mobile adult life. So dispersal and hence effective connectivity occurs mainly during larval and/or juvenile phases. Larvae show a large variety of features and dispersal capability, from long lasting pelagic planktotrophic larvae, which feed on the plankton and have a long dispersal potential, to lecitotrophic larvae, feeding on the yolk and having a more limited dispersal potential. It has long been assumed that the pelagic larval duration (PLD) should directly relate to the realized dispersal potential. However, in recent year, more and more empirical evidence seems to indicate that this correlation is not always true, since many other biotic and abiotic factors play a relevant role in shaping the effective dispersal of the species (e.g. Palumbi, 2003; Kelly and Palumbi, 2010; Riginos *et al.*, 2011). The effective connectivity between benthic invertebrates' populations is the result of their larval dispersal, pre- and post- settlement processes, until the achievement of the adults' sexual reproduction. At the same time, complex biological and environmental features affect these processes, as larval behavior, near shore water currents, space availability, competitive interactions etc. (Figure 1).

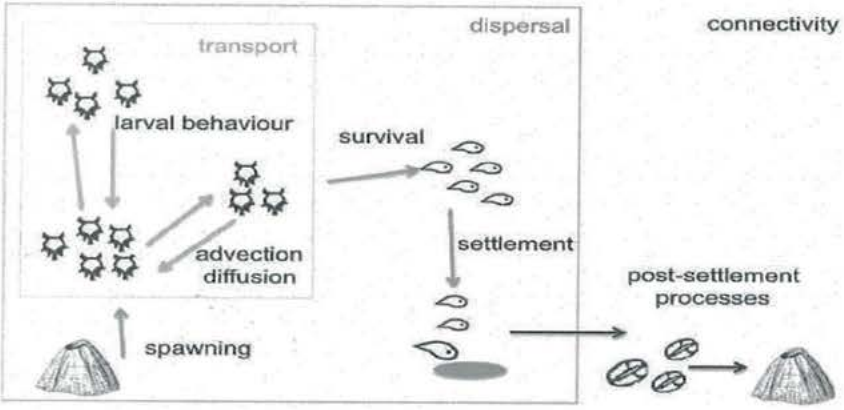

Figure1: The factors directly influencing the larval transport, larval dispersal, the population connectivity and the correlation between these three concepts. Adapted from Pineda *et al.* (2007).

Population connectivity, understood as the exchange of individuals among geographically separated populations, might be sufficient to impact the demographic rates of local populations (Cowen, 2007). It represents a crucial process to guarantee and promote diversity and hence resilience against perturbation, either natural or anthropogenic, promoting the recovery from local extinctions. According to the effective connectivity patterns, populations or metapopulations are considered open, if there is an exchange of individuals between distant populations, or closed, if sustained by self-recruitment and no exchange occurs with other populations. The exchange of individuals among populations guarantees the maintenance and enhancement of genetic diversity, which increases the fitness and resilience against disturbances, whereas the lack of exchange will eventually produce a genetic impoverishment, which may lead to local extinctions.

These considerations have major implications for conservation, as one of the main objectives of any management policy is to preserve biodiversity at each level from genetic diversity to species and habitats. The main factors controlling connectivity patterns in the marine realm are the dispersal potential of the species, the water currents, the geomorphology, the space availability, and the biophysical integration of them (Cowen and Sponaugle, 2009). In this contribution we will focus on the measure of genetic diversity and structure among marine populations as estimates of genetic connectivity, and indirectly of population connectivity.

GENETIC DIVERSITY AND CONNECTIVITY ASSESSMENT

Based on its importance and on the difficulty of tracking larvae in the sea, the direct assessment of connectivity among benthic invertebrates' populations seems an elusive issue. However, with the advent of molecular tools, some problems have been overcome, allowing estimates of genetic connectivity among coastal organisms and habitats. The genetic connectivity assesses the spatial and temporal changes of genetic diversity, quantifying the genetic structure of populations. In the least years, assessment, protection and maintenance of the genetic diversity is increasingly taking a role in management plans (Miller and Ayre, 2008). In fact, it is now acknowledged that a proper diversity assessment must include both the taxonomic and the genetic approaches, which are complementary, and conservation planning should incorporate information on both dimensions of biodiversity (Moritz and Faith, 1998).

Two distinct approaches or analytical frameworks can be used to assess connectivity using genetic tools (Chenuil, 2013). The direct approach, through a genetic fingerprinting, allows detecting individual migrants from the possible source and destination populations. This approach has not been widely used in studies on marine organisms, as it requires the development of species-specific genetic markers, which are costly and time consuming. Furthermore, for many benthic invertebrates with large population size and where the age cohorts cannot be identified, these methods present major difficulties and discriminating cohorts and migrants. However, recent technological progress is allowing the development of a large number of genetic markers with a reduction of costs and lab work, and the near future may promote the extensive application of the direct approach. Indirect approaches, more widely applicable, assess the exchange of genes among populations by comparing allele frequency distributions between populations. These approaches have been widely used, and among their advantages is the wide applicability across virtually any species, the cost-effectiveness and the availability of large public databases (e.g. Genbank), that provide a priceless source of data to compare with.

Each marker and approach has its advantages, and ultimately the choice has to be related to the main question of interest, the temporal (evolutionary vs. ecological) and spatial scales of connectivity addressed, the need to compare different taxa, availability of markers, the coasts of marker development, etc. In ideal conditions, direct approaches are preferred as they provide further details on the identification of individual migrants and of their population of origin, and at the same time the data used in the direct approaches can be analyzed with frequency distribution approaches (Table 1). However, combining different approaches and markers might provide an overall picture of connectivity patterns, less biased than using one single marker.

Table 1: Scheme of different molecular approaches according to the main question, evolutionary or ecological scales considered, with indication of the most commonly used markers, their strengths and weaknesses. Adapted from von der Heyden *et al.* (2014).

Time scales	Study questions	Marker/analytical approach	Geographic scale	Strengths	Weaknesses
Evolutionary	Phylogeography	Sequences of mt and nuclear DNA/Fst	Species range, basin scales.	- Evolutionary significant units ESUs - Genetic breaks - Fst comparable across studies - True biodiversity estimate	- Neutral and adaptive markers may provide different structures, need for multiple markers.
	Biogeographic barriers		Large scales, explicitly incorporating biogeographic knowledge on sampling design		
	Cryptic species	Same as before plus microsatellites	Depending on cases		
Ecological	Parentage analysis	Microsatellites and/or SNPs/Fst and fingerprinting	Depending on study question	- Identification of parent-offspring relationships - Connectivity at contemporary time scales	- High sample sizes of adults and recruits - Marker development costs - May underestimate connectivity and self-recruitment in high gene flow conditions.
	Assignment tests			- No need for recruits - Larger range of time and spatial scales	

MEDITERRANEAN GENETIC CONNECTIVITY STUDIES

In the Mediterranean Sea, genetic connectivity studies have been connectivity studies have been conducted mainly on commercial fishes and invertebrates, given the direct implications of such data for their management and sustainable exploitation (see review in Chenuil, 2013). The genetic structure of several flagship species, many of which are exploited, has been studied. That is the case of the large crustaceans *Scyllarides latus* (Faria *et al.,* 2013) and *Palinurus elephas* (Palero *et al.,* 2008), or the cephalopods *Sepia officinalis* (Pérez-Losada *et al.,* 2007) and *Octopus vulgaris* (Casu *et al.,* 2002). Among these species, with populations decimated by different degrees of harvesting, only *S. latus* showed a panmictic pattern, whereas the rest presented different levels of structuring, which would require specific stock assessment and management plans. Genetic diversity and connectivity studies have been applied in other invertebrates, noteworthy cases of endangered or heavily threatened species, as *Pinna nobilis* (Sanna *et al.,* 2013), *Patella ferruginea* (Casu *et al.,* 2011), *Corallium rubrum* (Costantini *et al.,* 2007; Aurelle *et al.,* 2011), or *Dandropoma petraeum* (Calvo *et al.,* 2009).

Genetic connectivity of the most important Mediterranean habitat-forming species has also received some attention. Among them, several habitat-forming species of the coralligenous (subtidal biogenic reefs) assemblages (see review in Abbiati *et al.,* 2009; Mokhtar-Jamai *et al.,* 2011) or the *Posidonia oceanica* meadows (Serra *et al.,* 2010). However, as also shown by Abbiati *et al. (2009),* most of these studies are localized in the north-western Mediterranean Sea. Indeed, the knowledge on the Mediterranean genetic diversity and connectivity patterns is largely biased by taxa and geographic area covered by the studies, which is obviously driven by the presence of research institutions and experts in one or another field (Coll *et al.,* 2010).

In many cases, observed connectivity patterns in the same area can vary depending on the species studied. Contrasting patterns across species have been detected in the Ionian Sea and Strait of Sicilia (which includes the Sicily, Malta and Pantelleria Channels), where the transition between eastern and western basins occurs. In this area, the main genetic break has been detected in differing positions depending on the species: across the Siculo-Tunisian Strait (Serra *et al.,* 2010), across the Messina Strait (Sa-Pinto *et al.,* 2012), in the mid-Ionian Sea (Sa-Pinto *et al.,* 2005), and even in the eastern Ionian (Pérez-Losada *et al.,* 2007; Boissin *et al.,* 2011; Dailianis *et al.,* 2011). The location of genetic breaks might have importance for the management and conservation of the species and habitats; however single species genetic structure might not provide a full picture valid to infer general patterns.

COMPARATIVE APPROACHES AND THE DEFINITION OF GENERAL PATTERNS

The evidence that patterns of genetic structuring and connectivity are extremely complex, has led to the need of comparative and multidisciplinary approaches. The integration of tools and species is becoming mandatory for ecosystem inferences, in order to take account seasonality, life history traits, differences in PLD, demographic histories (impact of past history events), etc. This framework would allow overcoming the limitation of the “single species” genetic approach, focusing on genetic diversity itself (Moritz and Faith, 1998).

In recent years, several studies addressing multispecies genetic connectivity provided general inferences on genetic structure and connectivity patterns, useful for conservation planning. Among many others, comparative genetic structure has been used for ecosystem-based management purposes in the Hawaiian archipelago (Toonen *et al.,* 2011), in the Indo-Pacific (von der Heyden *et al.,* 2014), in the Coral Triangle (Carpenter *et al.,* 2011) or in the northeastern Pacific (Kelly and Palumbi, 2010). However, to date in the Mediterranean Sea comparative genetic connectivity studies are lacking. There are few exceptions, which include the critical review by Patarnello *et al.* (2007), where they analyzed the available data for several species, and provided the background to define the Almeria-Oran front as the main phylogeographical break between the Atlantic Ocean and the Mediterranean Sea. A review on genetic connectivity in coralligenous assemblages provided straightforward evidence that larval dispersal of coralligenous species is often limited to few tens of meters, supporting the hypothesis of limited connectivity and fragility of these habitats (Abbiati *et al.,* 2009). Few other comparative genetic studies have been developed, and most of them are focused on the Atlanto-Mediterranean transition (several molluscs in Fernandez *et al.,* 2015, and decapods in Garcia-Merchan *et al.,* 2012).

MEDITERRANEAN BIOGEOGRAPHICAL AND PHYLOGEOGRAPHICAL TRANSITIONS

Several ecoregions or biogeographic areas are defined in the Mediterranean Sea based on species composition and distribution (Bianchi, 2007; Spalding *et al.,* 2007), or on biophysical features (Notarbartolo di Sciara and Agardy, 2010; Rossi *et al.,* 2014) (Figure 3). Although genetic structuring across the two main Mediterranean basin (western and eastern) has been repeatedly described for bivalves (Nikula and Väinölä, 2003; Cordero *et al.,* 2014), cnidarians (Costantini *et al.,* 2007; Aurelle *et al.,* 2011), crustaceans (Yebra *et al.,* 2011), echinoderms (Borrero-Pérez *et al.,* 2011) and sponges (Dailianis *et al.,* 2011), little is known on the genetic diversity and connectivity patterns across most of the Mediterranean ecoregions.

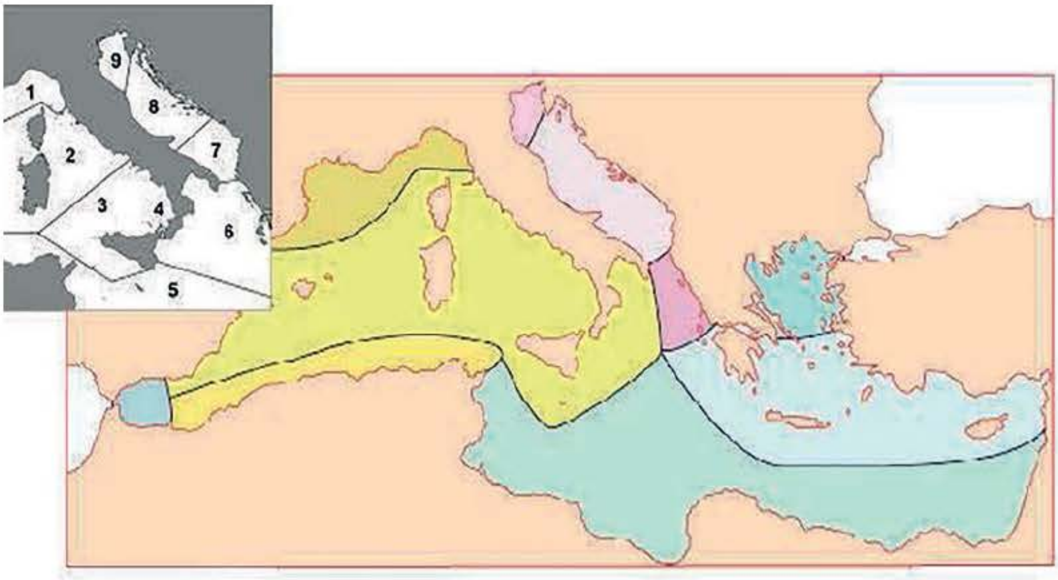

Figure 2: Mediterranean biogeographic areas defined in Pèrez (1972). In the small square, the biogeographic areas around the Italian peninsula as defined by Bianchi (2007) (modified from Bianchi, 2007).

To address this issue Villamor *et al.* (2014), aimed to reveal the genetic structure and diversity across several biogeographic boundaries in the Central Mediterranean by analysing genetic patterns of several invertebrates' species, differing in their life history traits. Seven species of common benthic shallow water invertebrates were sampled at each side of three biogeographic boundaries (see Figure 2, detail, between areas 1-2, 3-6, and 6-7). Samples were analyzed using the mitochondrial COI marker, which has a fair mutation rate, and allows comparison between species but also detects infra-specific variation. The study revealed the existence of a genetic break across one of the hypothesized boundaries (Tyrrhenian/Ionian boundary) for two of the species analyzed (*Patella caerula* and *Hexaplex trunculus*). Furthermore, an unexpected genetic break, across the Ionian Sea was detected according to the genetic structure of other two species (*Chondrosia reniformis* and *Osilinus turbinatus*). Overall, four out of seven species showed two different patterns of genetic structuring in the same area. To address this complex pattern across species, a multivariate statistical analysis of multispecies genetic data was implemented, in an attempt to provide an overall picture of the connectivity patterns in the area, independently of the species (Figure 3).

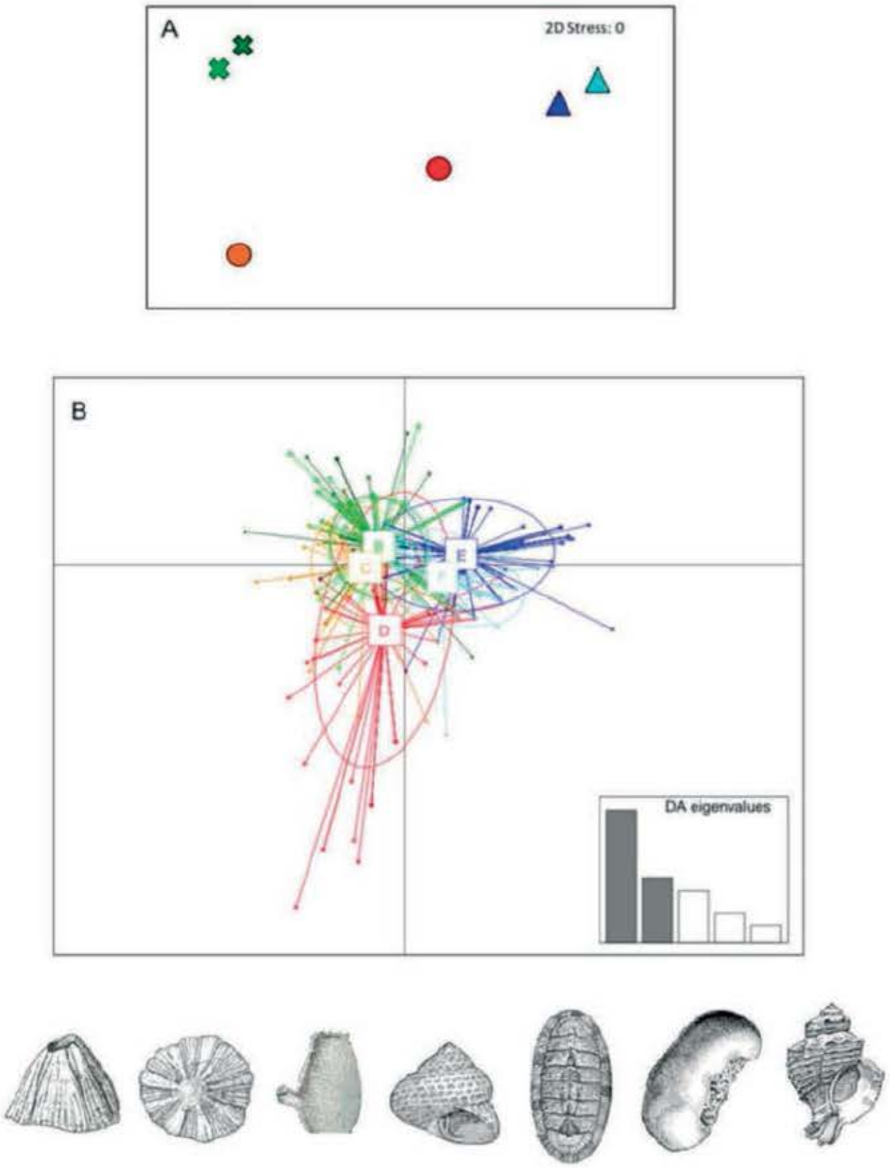

Figure 3: Multivariate analysis performed on genetic data of the seven invertebrate species represented below the graphs: on the top, MDS of Bray-Curtis dissimilarities of haplotype frequencies, and in the middle, a DAPC, transforming sequences to polymorphisms. Colors represent the six sampled locations, in pairs across the three putative barriers to gene flows (green, red and blue colors from Tyrrhenian to Adriatic, see text and Figure 2). Modified from Villamor *et al.* (2014).

The following step would be to analyze genetic connectivity patterns according to different genetic markers, with higher mutation rates, which would allow inferences on ecological connectivity and migration rates, or to ecological of selection, sex-biased dispersal, homoplasy etc. (Larmuseau *et al.,* 2010). Different genetic structures revealed by different markers have been detected in the Mediterranean for Pinna nobilis (Katsares *et al.,* 2008), for *Palinurus elephas* (Elphie *et al.,* 2012) and for cephalopods (Garoia *et al.,* 2004) for instance.

FINAL REMARKS AND DISCUSSION POINTS

Despite the importance of genetic connectivity for the conservation and sustainable management of Mediterranean biodiversity, this tool is not yet integrated in a practical way in an ecosystem-based management and marine spatial planning at local and international levels. To reach this goal, a series of gaps should be filled.

First, a full picture on genetic connectivity patterns in Mediterranean benthic invertebrates is needed as baseline knowledge. Collaboration among Mediterranean scientists is needed to raise the level of knowledge across the whole basin. In particular, where there is a scarcity of data on the southern and eastern part of the Mediterranean (but see for example Dailianis *et al.,* 2011; Boissin *et al.,* 2011), with better coverage of the Aegean and Levantine seas). This full picture of the genetic connectivity should take account a variety of species, abundant and less abundant, and cover a wide range of life history traits and taxa. The multispecies approach should be integrated by a multimarker approach: mitochondrial sequences or frequency-based approaches are still useful, depending on the species and may provide good levels of resolution, while at the time they allow direct comparisons with data available in the literature. However, the increase of genomic data, an of the reduction of analysis costs, will allow in the near future to extend the direct approaches to many species, increasing shared data in public databases.

Second, genetic information should be enclosed in a multidisciplinary study, including oceanography, geology, and ecology among other fields. The seascape genetics approach aims at addressing these issues, by coupling environmental parameters (both abiotic and biotic) affecting the population demography and connectivity, with molecular results.

Third, scientists should be able to transfer to managers and policy makers in a scientifically sound, easy and effective way, the contribution that molecular tools can provide to address conservation and management issues. Studies by Kelly and Palumbi (2010), Micheli *et al.* (2013), van der Heyden *et al.* (2014) are good examples of how a scientific method and background may act as a decision support tool to set conservation priorities. Moreover, van der Heyden *et al.* (2014) give full evidence that this kind of approach can be successfully and practically applied.

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Estimating larval dispersal and population connectivity in the deep-sea

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1. INTRODUCTION

The deep-sea is the largest ecosystem on Earth, comprising 90% of the habitable volume and 63% of the surface area, but remains one of the least studied because of its remoteness and the technological challenges presented for its investigation (Ramirez-Llodra *et al.,* 2010). Despite being recognized as one of the largest reservoirs of biodiversity, the deep-sea is particularly poorly represented in biodiversity surveys. The paucity of taxonomic information on the deep-sea fauna (Broekeland and George, 2009) hinders accurate species identification, which limits inferences about geographic distributions, ecology, evolutionary history and connectivity. The misconception that the deep-sea is largely an homogenous environment with no obvious dispersal barriers and early evidence that deep-sea species have larger geographic ranges than their shallow counterparts (e.g. Etter and Rex, 1990; Allen and Sanders, 1996) led to the long-standing notion that deep-sea organisms disperse over large distances (reviewed in Rex and Etter, 2010). However, evidence amassed during the last decades has revealed a much greater diversity of deep-sea habitats than previously suspected (reviewed in Ramirez-Llodra *et al.,* 2010), and as anthropogenic impacts on the deep-sea increase, possibly leading to habitat fragmentation, it has become increasingly important to test this paradigm.

With the depletion of mineral and biological resources on land and in coastal waters, resource extraction has been extending into the water column and the seafloor of the deep sea. Oil and gas have long been extracted in waters deeper than 200 m. The *Deepwater Horizon* blowout in the Gulf of Mexico, which occurred directly on the deep sea bed, was the largest oil spill in history and affected deep-sea communities that were not even known before the accident (Fisher *et al.,* 2014). The continuous expansion of oil and gas exploration onto the continental margins largely enhances the threat for similar accidents and impacts. Trawl fisheries, which have major effects on biogenic seafloor structure (e.g. Watling and Norse, 1998), as well as targeted and bycatch species (e.g. Dayton *et al.,* 1995; Myers and Worm, 2003) now extend to depths of at least 3000 m (Ramirez-Llodra *et al.,* 2011). Exploration leases have been granted for the mining of seafloor manganese nodules at abyssal depths, as well as for the mining of cobalt-rich manganese crusts on seamounts and polymetallic sulfide mining near hydrothermal vents (ISBA, 2014; Mengerink *et al.,* 2014). Global phenomena such as climate change and ocean acidification are further threats to the deep-sea ecosystem as a whole (Ramirez-Llodra *et al.,* 2011).

Because the spatial and temporal scales of these impacts are not known, and because the deep-sea biological communities and the drivers that regulate them are also unknown, international efforts have begun to focus on the protection of deep-sea fauna and habitats (e.g. Mengerink *et* *al.,* 2014). A number of factors must be considered when designing marine reserves (CIESM, 1999), including habitat representation and replication, patterns of species richness and endemism, protection of unique areas, and reserve location, size and spacing (reviewed in Green *et al.,* 2014). Connectivity - the demographic linking of local populations through the dispersal of individuals as larvae, juveniles or adults - is a key ecological factor due to its important implications for the persistence of metapopulations and their recovery from disturbance (Cowen *et al.,* 2007).

Many marine species, particularly benthic species, have complex life cycles that include a planktonic larval stage and sessile adult (Thorson, 1964). For these species, larval transport is the main process connecting populations; yet, we still know very little about dispersal distances or connectivity in the deep ocean (Hilário *et al.,* 2015; Figure 1). Two main approaches have been used to estimate population connectivity by larval dispersal in coastal systems: i) biophysical modelling of larval dispersal, ii) use of geochemical tracers and genetic markers to derive larval origins and dispersal pathways. Both have advantages and limitations (reviewed in Levin, 2006; Cowen and Sponaugle, 2009), but only the first addresses the mechanisms. Further, it has the benefit of addressing connectivity at multiple spatial and temporal scales.

On contemporary time scales biophysical models can provide insight into current metapopulation management and demographic dynamics (Cowen and Sponaugle, 2009). Modelling can be used to define the average route and distance of dispersal paths from a release site (Cowen *et al.,* 2007; Kool *et al.,* 2013) and provide retention estimates and thus inform marine protected area networks (Paris and Cowen, 2004; Treml and Halpin, 2012). Most modelling studies explore the effect of physical drivers on dispersal (e.g. Soria *et al.,* 2012; Young *et al.,* 2012) but, in a system where knowledge on life-history traits is lacking, they can also be built to test null hypotheses.

Here I review the current knowledge on larval dispersal and population connectivity in the deep sea and the application of biophysical models to study them.

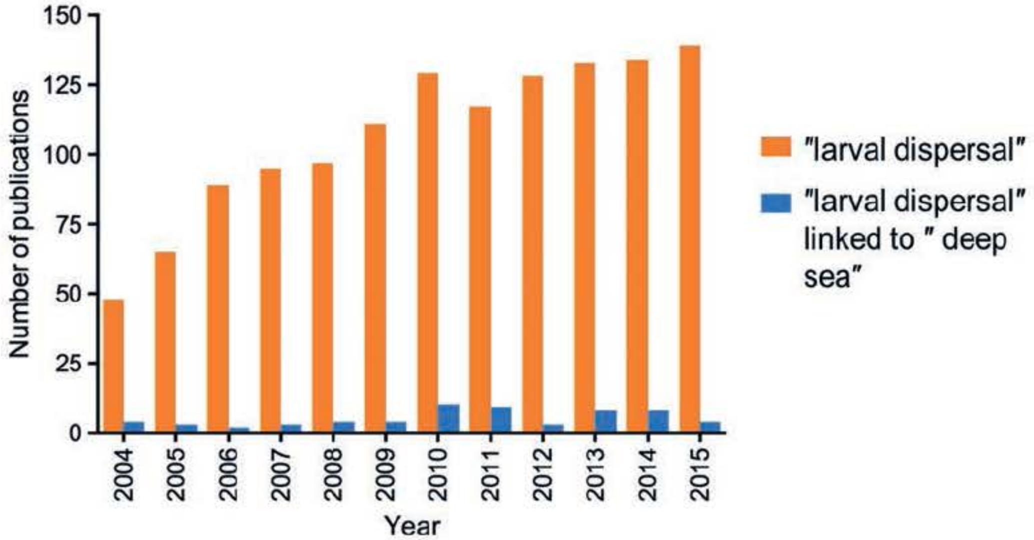

Figure 1. The number of articles published over the last 11 years whose title or abstract contained the term "larval dispersal" or "larval dispersal" linked to "deep-sea". Data from 1977 to 2003 can be found in Levin (2006). Based on a Web of Science survey.

2. DEEP-SEA CONNECTIVITY

Studies about connectivity in the deep-sea have been placed in the context of two long-standing and partially contradictory hypotheses:

1- Due to the uniform physical and chemical conditions throughout the deep ocean there should be no dispersal barriers, resulting in high connectivity;

2- Deep-sea animals should undergo direct development, by-passing the pelagic embryonic and larval stages (also known as the Thorson's Rule), resulting in limited connectivity.

The expansion in deep-sea exploration capability of the last fifty years, in particular the development of seafloor mapping and imaging tools, brought about the recognition of the deep-sea as a highly complex and heterogeneous landscape of contrasting geological and ecological settings. Ecosystems within the deep sea often occur over large geographic scales, yet are spatially fragmented across the entire range with stretches of unsuitable habitat separating prime habitat patches (e.g. hydrothermal vents, methane seeps, cold-water coral reefs) and many ecological patterns observed in these ecosystems can be explained by metapopulation dynamics as conceived by Levins (1969). Under this scenario, species occur within patchy habitats that undergo local extinction and recolonization, those patches are connected via dispersal and migration, and the resilience of the metapopulation increases as the availability of suitable habitat patches increases, local extinction decreases, and migration/dispersal between patches increases.

Although much less is known about patterns of connectivity in the deep-sea than in shallow-water, recent studies have shown some similarities between both systems, including the applicability of the stepping-stone model (Kimura and Weiss, 1964). Several deep-sea species show evidence for a stepping-stone mode of dispersal between neighbouring populations, particularly those arranged linearly along continental margins (Le Goff-Vitry, 2004), mid-oceanic ridge axes (reviewed by Vrijenhoek, 2010), or relatively linear arrays of seamounts (Samadi *et al.,* 2006). But when interruptions to these linear arrays occur, they may create effective barriers to dispersal, and an abrupt decrease in creating regionally isolated populations. Suggested connectivity barriers include landmasses, large expanses of deep water, deep-water sills, structuring of the water column (density layers), rugged topography (canyons and seamounts) and oxygen minimum zones. For example, work on genetic connectivity at hydrothermal vents along ridge axes reveals little evidence for genetic structure on moderate to large scales along the axes of ridges (reviewed by Vrijenhoek, 2010) but shows significant structure on opposite sides of biogeographic barriers such as microplates (Won *et al.,* 2003), transform faults (Johnson *et al.,* 2006; Young *et al.,* 2008) and fracture zones (O'Mullan *et al.,* 2001). Regional differentiation of deep-sea fauna is not limited to benthic organisms: even highly mobile species, such as fishes (Aboim *et al.,* 2005) and squid (Shaw *et al.,* 1999), show regional structuring.

One factor that may uniquely influence connectivity among deep-sea organisms is depth. As depth increases there are strong physiological gradients that can result in locally adapted populations and enhanced genetic differentiation (Rogers, 2002). Depth-related divergence has been identified in several groups including molluscs (Goffredi *et al.,* 2003; Etter *et al.,* 2005; Zardus *et al.,* 2006; Jennings *et al.,* 2013), polychaetes (Lundsten *et al.,* 2010; Cowart *et al.,* 2014) and corals (Lindner *et al.,* 2008; Baco and Cairns, 2012).

In addition to physical barriers, species-specific life history strategies may also act to limit exchange of individuals between populations. From the earliest days of deep-sea exploration, it was assumed that animals living in this presumably hostile environment should show life-history attributes and reproductive modes differing from those of their shallow-water counterparts. Nevertheless, with few exceptions, deep-sea invertebrates lack special reproductive adaptations, suggesting that phylogeny constrains reproduction (reviewed in Young, 2003). Further, contrary to the initial prediction (see above), both planktotrophic and lecithotrophic larvae occur in deep-sea invertebrates. Although the prevalence of lecithotrophic dispersal could limit dispersal potential, long lecithotrophic development is known in some echinoderms (Shilling and Manahan, 1994; Young *et al.,* 2012), and low metabolism in cold water has been shown to greatly extend the larval lives of Antarctic species.

3. USING BIOPHYSICAL MODELS TO PREDICT DISPERSAL IN THE DEEP-SEA

External environmental factors, the distribution of disjunct habitat, and demographic factors, all play roles in determining genetic structure in the deep-sea, but larval or adult dispersal by oceanic currents has been identified as the fundamental mechanism of connectivity in virtually every species that has been examined. Therefore, understanding the biological and physical processes regulating larval dispersal, and how these processes interact on different spatial and temporal scales, is of paramount importance to estimate population connectivity in the deep-sea (reviewed by Hilário *et al.,* 2015). Because sampling over all relevant scales is presently not (yet) possible, numerical models that incorporate both physical dynamics and biological traits are critical tools to quantify larval transport and assess its role in regulating population connectivity. In coastal and shallow areas, such coupled biophysical models have provided information of relevance to decision-makers in determining the spatial arrangement of marine reserves (e.g., Guizien *et al.,* 2012; Treml *et al.,* 2012). However, in the deep sea, this field of research is still in its infancy and only very few studies have attempted to model larval dispersal in the deep sea, most of them restricted to chemosynthetic habitats (Table 1). Because of the paucity of data on life histories of deep-sea fauna, most modeling exercises have been experiments that attempt to identify the biological values required to produce a given distributional or genetic pattern, rather then models integrating biological parameters to estimate dispersal distances and potential connectivity among populations (reviewed by Hilário *et al.,* 2015).

Components such as vertical migration, buoyancy of embryos, mortality, food availability, developmental rate, and physiological tolerances, can all play an important role in dispersal patterns (Metaxas and Saunders, 2009), but most of these factors have not been studied in deep-sea species. To date, the only biological variable to be included in biophysical models to study connectivity in the deep sea is the planktonic larval duration (PLD). Although the validity of the prevailing hypothesis that species with long larval duration also have greater dispersal potential remains equivocal (Weersing and Toonen, 2009), PLD can be used to set maximal and minimal bounds of dispersal ranges (Selkoe and Toonen, 2011) and models integrating estimated PLD have already generated important information to understand dispersal and connectivity in the deep sea (Marsh *et al.,* 2001; Young *et al.,* 2012).

Table 1. List of studies addressing larval dispersal in the deep sea using biophysical models. Shaded rows indicate studies using empirical estimates of biological parameters. LTM: Lagrangian transport model; PFM: Propagule flux model; PVD: progressive vector diagram; ROM: Regional ocean models system. (a) LTRANS: Lagrangian larval transport model; (b) ARIANE.

Reference	**Species**	**Region**	**Habitat**	**Model type**	**Biol.param.**	**Disp.dist. (km)**
Chevaldonné *et al.* (1997)	*Alvinella pompejana*	NE Pacific	Hydrothermal vents	PFM	(Population size; fecundity; mortality)	8 – 40
Marsh *et al.* (2001)	*Riftia pachyptila*	NE Pacific (9ºN)	Hydrothermal vents	PVD	PLD = 38d	~100
Mullineaux *et al.* (2002)	*Riftia pachyptila*	NE Pacific (13ºN)	Hydrothermal vents	PVD	PLD = 38d	~200
McGillicuddy *et al.* (2010)	*Riftia pachyptila*	NE Pacific (9ºN)	Hydrothermal vents	ROM + Online LTM	PLD = 38d	50 – 100
Yearsley and Sigwart (2011)	Polyplacophoran molluscs	S Pacific	Sunken wood	ROM + Online LTM	PLD = 50d PLD = 100d PLD = 250d PLD = 500d	29 – 162 40 – 378 48 – 565 74 – 692
Young *et al.* (2012)	*Sclerasterias tanneri* *Cidaris blakei* *Stylocidaris lineata* *Bathymodiolus childressi* *Bathynerita naticoidea* *Lamellibrachia luymesi* *Phascolosoma turnerae*	NW Atlantic (Intra-American Seas)	Cold seep Continental margin Continental margin Cold seep Cold seep Cold seep Sunken wood	ROM + Offline LTM$^{(a)}$	PLD = 660d PLD = 120d PLD = 120d PLD = 390d PLD = 210d PLD = 21d PLD = 210d	724 – 1184 160 – 422 160 – 422 423 – 507 2182 – 2377 102 – 113 2182 – 2377
Sala *et al.* (2013)		NE Atlantic	Continental margin	ROM + Offline LTM$^{(b)}$		
Etter and Bower (2015)	Protobranch bivalves	NW Atlantic	Continental margin	ROM + Offline LTM	PLD = 30d PLD = 180d PLD = 365d PLD = 1820d	

In the context of spatial planning, connectivity is often not considered for single species, but rather between different areas. In this case, models can 1) be used to estimate the durations that would be required to connect particular metapopulations, which is limited by insufficient data on species distribution, or 2) incorporate PLD values that guarantee a minimum dispersal distance for a wide range of species (Hilário *et al.,* 2015). Based on a review of PLD data of species found at depths below 200 m, Hilário *et al.* (2015) showed that the incorporation of a PLD of 35 and 69 days ensures a minimum distance for 50 and 75% of deep-sea species. Despite its utility, the authors acknowledged that the high variability in PLD between and within taxonomic groups underscores the limitations of such proposal and limits generalizations that are often attractive to decision-makers.

PLD is an important parameter for all dispersal models, but the estimation and use of this parameter are fraught with potential errors, especially when information on larval behavior is lacking (Shanks, 2009). The problems are compounded for deep-sea species. For example, whereas shallow-water larvae may experience only minor fluctuations in temperature while dispersing, deep-sea larvae potentially can move into water of different temperatures (Young *et al.,* 1996; 1998), thereby experiencing changes in metabolism, feeding rate, and other vital processes. Even when PLD is known it is easy to make large errors in estimating dispersal potential unless realistic oceanographic data are used. In one of the first attempts to place upper and lower limits upon potential dispersal of larvae, McClain and Hardy (2010) plotted most of the known PLDs for deep-sea animals against rough estimates of high and low current speeds in the deep sea. Plotting the same values against realistic dispersal rates based on models of deep-ocean circulation (Yearsley and Sigward, 2011; Young *et al.,* 2012; Sala *et al.,* 2013; Etter and Bowden, 2015) reveals differences of 100's to 1000's of kilometres in the dispersal potential of these species (Figure 2), without taking in account current reversals that can greatly limit dispersal distance. Regarding the PLD value of 35 days estimated by Hilario *et al.* (2015), it is evident that such larval duration will yield different dispersal distances according to location and depth.

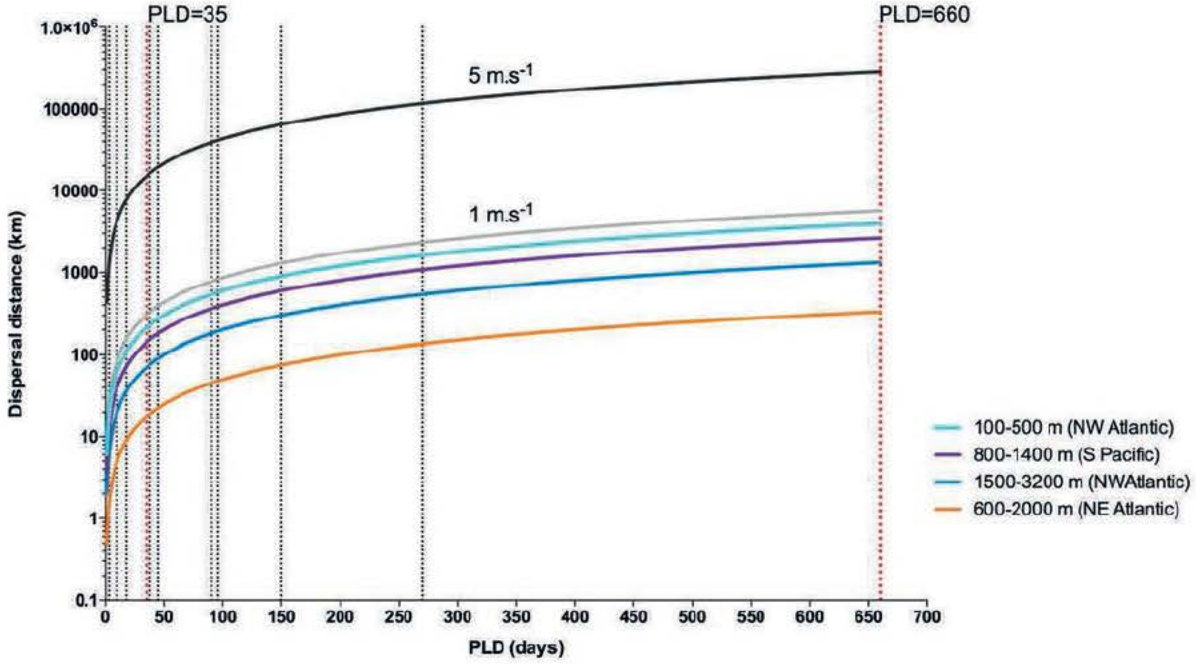

Figure 2. Potential larval dispersal distance of deep-sea fauna based on current speed (from McClain and Hardy 2010), dispersal rates (Etter and Bower, 2015, Sala et al., 2013, Yearsley and Sigward, 2011, Young et al., 2012), and published estimates of planktonic larval duration (from McClain and Hardy, 2010). PLD=35 days is PLD estimated to ensure a minimum distance for 50% of the deep-sea species for which PLD is known (Hilário et al., 2015); PLD=660 is the longest PLD known for a deep-sea invertebrate (Young et al., 2012).

The physical components of biophysical models are limited by scale and computational capacity. Large-scale processes are well understood and parameterized within model equations, but it is the local and fine scale processes there are most relevant for larval dispersal (Metaxas and Saunders, 2009). These small-scale phenomena, however, are prohibitively expensive to parameterize within a large spatial scale model. For this reason, a sub-gridscale parameterization is usually considered an adequate enough approximation for most purposes although this is difficult to estimate in itself (Fossette *et al.,* 2012). There are additional conflicts of resolution, such as poorly represented topography, and consequential flow modifications that result from low resolution in bathymetry data (Werner *et al.,* 2007). One of the most important physical components and yet one of least understood is vertical velocity, often reduced to secondary calculation in line with the conservation of energy. Without improved understanding of vertical velocities, the potential for passive vertical migration of larvae and consequent exposure to different current speeds, temperature, etc, also remains elusive (reviewed by Hilário *et al.,* 2015).

4. MOVING FORWARD: STUDYING LARVAL DISPERSAL AND CONNECTIVITY IN THE DEEP-SEA IN THE NEXT DECADE

While considerable advances have been made in recent years in understanding population connectivity in the deep-sea, there are very few studies is non-chemosynthetic habitats, and particularly no single study in the abyssal plains, where large areas have been identified as potential mining sites. In the last few years various organizations have applied for deep sea-bed mining licenses, and mining operations are expected to start by 2025 (Smith *et al.,* 2008). Like for most deep-sea ecosystems currently under threat of major disturbances, our limited understanding on the resident species and communities and the mechanisms that regulate them can compromise our ability to manage these areas sustainably.

As anthropogenic pressure is rapidly increasing, there is an urgent need to fill our knowledge gaps on the factors that regulate larval dispersal and connectivity in the deep sea. The development of new tools and technologies over the past decades will undoubtedly allow us do to so (Danovaro *et al.,* 2014) if there is a strong commitment from science-policy makers and funding bodies.

Of all methods to estimate larval dispersal, biophysical modelling uniquely addresses the mechanisms of dispersal rather than the effects, with the benefit of addressing multiple spatial and temporal scales of connectivity. However, because of the paucity of data on life histories and larval behaviour of deep-sea fauna as well as deep-sea circulation, accurate modelling and precise validation are not feasible at this point. Currently available molecular tools allow robust taxonomy and the resolution of cryptic species, offering new opportunities to investigate species distributions. New technologies that can facilitate the quantification of PLD and swimming behaviour include pressure and temperature-controlled sampling vessels and holding facilities (e.g., Pradillon *et al.,* 2004; Mestre *et al.,* 2009; 2013; Ravaux *et al.,* 2013). Precision plankton sampling using remotely operated (ROVs) and autonomous underwater vehicles (AUVs) and association of such sampling systems with larval identification by high- throughput molecular techniques have the potential to transform our understanding of spatial and temporal scales of patchiness in larval distributions. Moreover, the rapid advances in temporal observation potential with cabled observatories can fundamentally change our view of reproductive and recruitment dynamics. From the point of view of oceanography, the refinement of multibeam acoustics and related tools allows high quality bathymetry down to a scale of meters that result in higher-resolution models. Further, with the use of AUVs it is now possible to acquire such data at large scales. Long-term and long-scale current measures are now also possible due to the development of seafloor observatories and underwater gliders (Rudnick, 2016).

Finally, combining coupled biophysical models with genetic data will lead to a better understanding of processes that underlie larval dispersal and, therefore, connectivity.

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The Black Sea anchovy – new perspectives regarding their spawning, nursery and overwintering behavior

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The anchovy family (Engraulidae), according to FAO, alone contributes more than 10% of the global fisheries landings. The stocks of the members of this family display unpredictable but not so surprising variations as they are fast growing short-lived fishes very sensitive to their surroundings. What is surprising though, is that some of the variations observed on opposite sides of the globe are thought to be tele-connected via large scale climatologic forcing, such NAO, AO (Alheit and Bakun, 2010). Understanding the causes behind their variability, even in a regional sea, would be highly valuable.

The Black Sea anchovy, *Engraulis encrasicolus*, is the third (after *E. ringens* and *E. japonicus*) most important anchovy species harvested, accounting for 1/3 of the global anchovy landing in the early 1980s. However the catches soared to 566,000 tons in 1984; remained at high levels until 1988 (526,000 tons) and abruptly dropped to only 86,000 tons in 1989. From 1995 to 2013 catches ranged with wide oscillations from year to year within the range of 135,000-400,000 tons even though the fishing effort basically remained the same (STECF, 2013). These fluctuations in the fishery as opposed to a *status quo* indicate that environmental drivers are no less important than fisheries in influencing the biomass of a species.

Niermann *et al.* (1999) linked these variabilities in the Black Sea with NAO-induced large scale atmospheric variability, demonstrating the similarities in the long-term climate-plankton-anchovy connection in different regions of the world ocean. Fluctuations in the landings were sometimes very dramatic, adversely affecting the local communities by causing significant economic losses. According to Campbell (1993) and Caddy (1992), the economic loss due to the decline in anchovy catches in late 1980s to early 1990s ranged between US$240e6 and US$309e6, if not more (Knowler, 2005).

Various factors adversely affecting the survival and in turn, recruitment success have emerged in the Black Sea during the last few decades. A decrease in the trophic state to dystrophy at the spawning grounds (Zaitsev, 1993) and intensified predation and competition pressure incurred by an exotic ctenophore (Vinogradov *et al.,* 1989; Vinogradov *et al.,* 1995; Vinogradov *et al.,* 2005) are among the most crucial reasons listed. If such non-fishery impacts on recruitment success are disregarded in stock assessment and fisheries management decisions, the ecological and economic consequences would undoubtedly be misleading (STECF, 2013).

The Black Sea is a huge catchment basin receiving freshwater (hence nutrients) via river drainage from a considerable area of Eastern Europe (Lancelot *et al.,* 2000). Rivers played a crucial role in the biological evolution of the Black Sea; initially by nourishing very rich biological resources; later by overloading the sea mainly with phosphorus and nitrogen due to intensified agricultural activities, and finally by altering the trophic state of the sea. As a characteristic response of an ecosystem to advanced eutrophication, hypoxia occurred in the zone where the rivers enter the Black Sea. The hypoxic conditions were first recognized on the broad NW continental shelf in the mid-1970s and developed very rapidly. In the 1990s the size of hypoxic areas measured 40 000 km^{-2} causing 60 million tons of benthic life to perish (Mee, 2006). The most devastating effect was that these hypoxic areas were essentially the major spawning and nursery grounds for a diverse range of fish species, including the Black Sea anchovy.

Towards the end of the 1980s, when the Black Sea ecosystem was still lingering with the effects of this catastrophic event, an exotic ctenophore appeared in the Black Sea with a massive outbreak following shortly afterwards. Its biomass was estimated as 4.7 kg m-2 throughout the anchovy spawning grounds during the summer of 1989 (Shushkina and Vinogradov, 1991). This ctenophore species was claimed to predate the early life stages of the anchovy (Tzikhon-Lukanina *et al.,* 1993; Shiganova and Bulgakova, 2000) and was even listed amongst the suspects responsible for the collapse of anchovy stocks observed in the late 1980s (Vinogradov *et al.,* 1989; Shiganova *et al.,* 2001).

It is believed that there are at least two distinct anchovy spawning grounds (Ivanov and Beverton, 1985). The Azov anchovy spawns in the Azov Sea and migrates southward through the Kerch strait to overwinter (Figure 2). This group is fished by the Ukrainian, Russian, Georgian and, to a lesser extent, by the Turkish fishing fleets. The Black Sea anchovy (BS) spawns in the north-western shelf and migrates south in winter (Ivanov and Beverton, 1985). The fishing season of BS anchovy usually begins in late autumn and lasts throughout the winter. They are fished almost exclusively in the Turkish and Georgian waters. However in the past, until the late 1980s, Romanian and Bulgarian fishermen used to catch anchovy when they formed schools and migrated towards the south. During the pristine state of the Black Sea before the mid-1970s, the ecological features driving the life cycles of the anchovy were quite clear; the main spawning and feeding areas of the species were located in the most productive regions of the Black Sea (Ivanov and Beverton, 1985; Shulman, 2002). Cooling at the feeding grounds in late autumn was herding the species towards the warmest region of the basin during winter. The Black Sea anchovy were reported to follow the west coast while Azov anchovy pursued the east coast during the winter migration towards the overwintering grounds (Ivanov and Beverton, 1985). It may also be worth noting that in a basin wide ichthyoplankton survey conducted in the 1950s, a noticeable quantity of anchovy eggs and larvae were observed in the south and open sea (Einarsson and Gürtürk, 1960). This indicates that the anchovy's spawning areas were not solely limited to the NW Shelf and Azov Sea even during the pristine state of the Black Sea.

In the 1990s, a series of international ichthyoplankton surveys covering the whole basin were conducted. In these surveys, anchovy egg numbers found in the southern and particularly in the south-eastern Black Sea were significantly higher than those found in the north-western shelf which was essentially the main spawning area of anchovy (Niermann *et al.,* 1994). In 1993 and 1996, two additional ichthyoplankton surveys were conducted covering only the southern half of the Black Sea and it was found that the number of eggs spawned in the south was higher than those previously reported (Kideys *et al.,* 1999). The authors explained this situation with the outburst of the recently introduced ctenophore *Mnemiopsis leidyi* and supported the hypothesis that this invader had played a major role in diminishing the Black Sea anchovy fisheries, by noting that the drastic changes in the Black Sea ecosystem (due to eutrophication, heavy fishing, etc.) might also have had an effect (Niermann *et al.,* 1994; Kideys *et al.,* 1999).

Later, international efforts and particularly the Danube River Protection Convention seemed to work particularly in the NW shelf area, where the major spawning activities of BS anchovy used to take place. Several key littoral ecosystem components such as Zernov's *Phyllophora* fields (Tkachenko *et al.,* 2009), associated benthic communities (Mee, 2006) and mussel beds (Mee *et al.,* 2005) were reported as having revived in the 2000s. Also, the anchovy stocks seemingly recovered to pre-collapse levels. The signs of revival in the Black Sea ecosystem have also been attributed to various other factors; such as the sudden appearance of a new ctenophore *Beroe sp*. predating the former invader *Mnemiopsis leidyi* (Shiganova *et al.,* 2000; Vinogradov *et al.,* 2000) and the relocation of the fishing fleet towards new fishing grounds beyond the Black Sea (Gucu, 2002). Despite evidence reporting recovery in essential habitats and in key species of the NW shelf area mentioned above, it is not known whether or not the change in the spawning grounds of anchovy first reported by Niermann *et al.* (1994) was merely a temporary response and following revival of the ecological state they returned to their former spawning grounds. In this study, we present the current situation two decades later and discuss possible reasons behind the changes addressing similarities and dissimilarities observed in populations of the same species in other seas.

More recently three ichthyoplankton surveys were carried out in July 2013, July 2014 and July 2015 on the Turkish EEZ, which essentially covers the southern Black Sea. The surveys followed exactly the methodology previously applied in the same area (Niermann *et al.,* 1994; Kideys *et al.,* 1999).

Two main points emerged from this study; first, the number of anchovy eggs laid in the southern region of the Black Sea has increased compared to the 1990s. This is due in part to import from adjacent areas, such as the NW shelf area, which is one of the two most important spawning areas of the species. Another proportion of the eggs found in the southern Black Sea had been transported from the Sea of Marmara. However neither of these sources seems to play a significant role on the recruitment success since egg/larvae and live/dead egg ratios are low within the respective area. Another source, with a better chance of survival, lies somewhere in the north, possibly near the Crimean coast (Gucu *et al.,* 2016a).

In addition to the imports, a new spawning ground was found on the southeast coast. Hydrographic properties, characterised by anti-cyclonic eddies located between the coast and the rim current, seem to play a role in the development of the new site. Also when the counts of gelatinous organisms in recent years were compared with previous surveys carried out in the same area, the maximum *Mnemiopsis leidyi* density observed in 2013 was quasi identical to the value found in 1992; however the average density is double (Mutlu *et al.,* 1994; Gucu *et al.,* 2016a). The opposite situation was found for *Aurelia aurita*; the basin average density was almost the same as in the 1990's; but the maximum density had now doubled. In this respect, distribution of *M. leidyi* appears to have expanded lately, while *A.aurita* is localized. Yet, the remoteness of the anchovy spawning sites from the surface gelatinous predator accumulation sites, such as those of Mnemiopsis leidyi and *Aurelia aurita*, is considered as an opportune loophole for the species (Gucu *et al.,* 2016a).

Whether the eggs and larvae observed in the south are prone to starvation death or whether they survive and recruit to the exploited stock remains an open question. Yet, the second most important point of the study is the significantly higher reproductive activity observed offshore today. It signifies the existence of a growing, and possibly non-migrating stock (Gucu *et al.*, 2016a).

The entrainment of the young population by the elders towards the spawning area, and the transfer of knowledge from repeat spawners to inexperienced recruits may help answer the question as to why the anchovy are spawning offshore and why those who refuse to migrate have increased in the last few decades. The collapse experienced towards the end of the 1980s and the continual removal of aged individuals from the stock through fisheries might possibly reduce the knowledgeable proportion of the population and weaken the continuity of the social transfer of knowledge (Gucu *et al.,* 2016a).

On the other hand all the "collapse" hypotheses summarized above relied on one single, somewhat bold assumption that the landings reflect the quantity of fish at sea and that the drastic drop displayed in the landing statistics points to an equally drastic drop in the size of the anchovy stock. Yet, none of the hypotheses proposed satisfactorily explain the very rapid and sharp increase in the anchovy landings seemingly exceeding the pre-collapse levels when all the factors listed were in effect.

The trends in landings and the "recovery" itself represent quite important information which may present some important hints towards understanding the situation experienced in the Black Sea. According to the FAO statistics (FishStatJ), the anchovy stock in the Black Sea had been exploited by four countries until the dissolution of USSR, namely Turkey, Romania, Bulgaria and the USSR. Following the drastic 1989 collapse, the anchovy fishery recovered in part in Turkey, Georgia and Ukraine, while remaining quasi inexistent in the other Black Sea countries (Figure 1). Gucu *et al.* (2016a) emphasized the opposite patterns in the landings of the north western (Bulgaria and Romania) and south eastern countries (Turkey), questioning possible changes in the spawning grounds and/or alternative migration routes (Figure 2). It must be noted that during the disintegration of USSR drastic changes were experienced in the structure of the fishing fleet (Khavtasi, 2010). The USSR fleet abandoned Georgia where they used to fish the largest part of their BS anchovy catch. Further, following their membership to the EU, some of the old anchovy fishing techniques were abandoned in Bulgaria and Romania. For instance, the number of pond nets, which was used to catch migrating anchovies declined from 140 units in 1965 to 21 units in 2014 (Totoiu *et al.,* 2015). These events might have, to a certain degree, played a role in the low level of catch in the post-collapse period; however the very fast recovery in the Turkish anchovy fishery after 1980s is evidently a sign of a drastic change in the behaviour of BS anchovy.

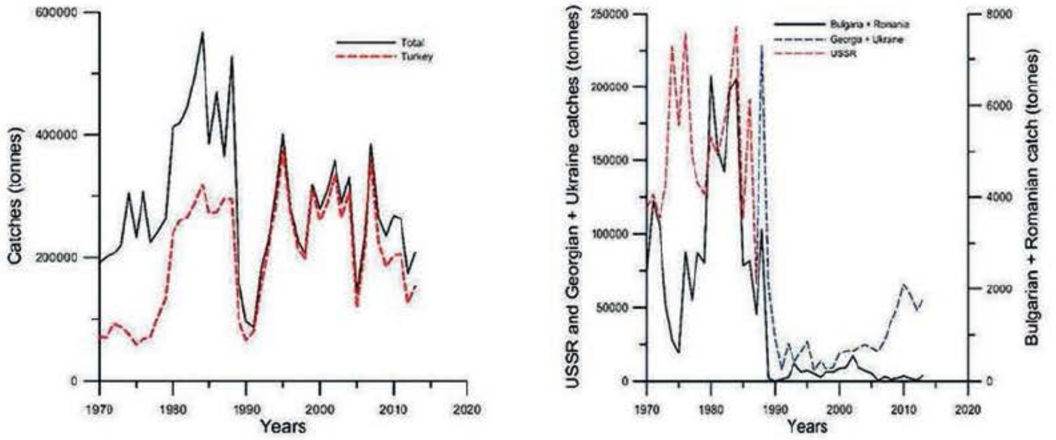

Figure 1.Total Black Sea anchovy landings, signalling dominant catches from Turkey (left) and landings of other Black Sea riparian countries (right). The data are taken from STECF (2015).

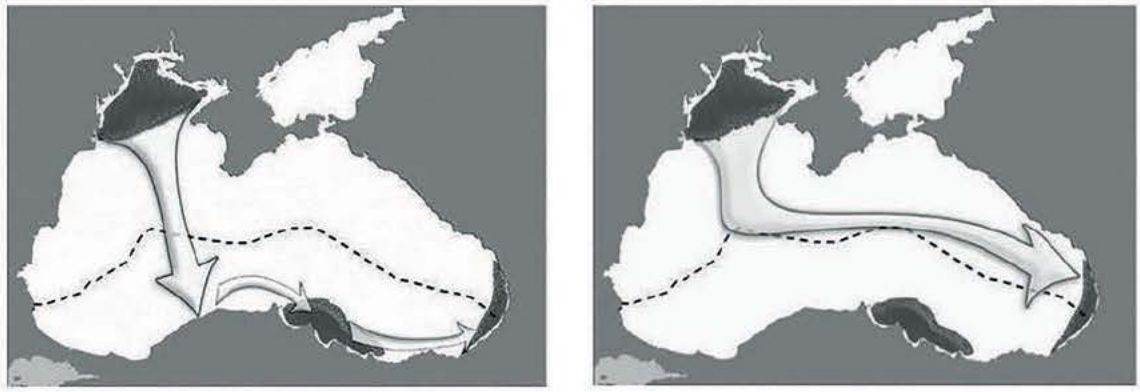

Figure 2.Two schematic alternative overwintering migration routes a) detouring the west coast and heading to central Anatolia; b) the offshore route heading straight to east detouring the Anatolian coast (grey zones are the spawning areas) Taken from Gucu *et al.* (2016b).

Although current fishermen and managers are quite confident that the destination of the migrating anchovies is in the east - within Georgian EEZ - there is contradicting information concerning the overwintering grounds of the BS anchovy. In some ancient reports the overwintering grounds are depicted near to the central part of the Turkish coast (Aasen and Akyüz, 1956). In an acoustical survey conducted towards the end of the overwintering season in the 1970s, Johannesson and Losse (1973) estimated almost a million tonnes of anchovy occupying the central part of the Turkish BS coast. These two reports show that anchovies have been overwintering in the south within Turkish waters. However, other observations such as the very first anchovies in Georgian waters appearing at the Turkish border (Chashchin *et al.,* 2015) support the fisher's thoughts.

The four graphs presented in Figure 4 were drawn based on daily catch registered at the landing port in four successive fishing seasons between 2011 and 2014. The vertical axis is the time scale starting from 1st of September. The quantity of fish landed is represented by the size of the circles. The points where the vertical lines meet the coastline on the background represent the position of the landing sites. These graphs show when and where the main fishery activity took place in a season. The very first landings are reported on the western side. As can be seen from the position of circles the fleet generally moves eastward as the season progresses. As a matter of fact, anchovy is not known as a strong migratory species because it is limited by several constraints, such as size spectrum in food selection, its shape, etc. (Bakun and Broad, 2003; Van der Lingen *et al.,* 2006). The reason why they migrate great distances in the Black Sea is apparently to utilize the nutritious food sources offered by the productive north in summer and but also to avoid lethal temperature of the northern winter. Therefore the rate of cooling, in a sense, determines how fast anchovy migrates during winter.

Figure 5 displays the dates of the highest fishing activity in the ports (longitudes). The positive linear relation (dotted line; $P>0.05$) confirms that the fish moves from lower longitudes to higher, or in another words migrates from west to east. The linear relation also shows that the distance covered in a day is almost constant but displays variation from season to season. The speed of the move estimated ranges between 7 and 25 n.mils/day. Moreover the speed of migration in a season seems to have linear relation with the cooling rate in the southwest; the faster it cools in the feeding grounds the faster they migrate to overwintering sites. Hence, the higher the speed of migration, the shorter the fishing season anchovy is fished.

The currents along the south coast are characterized by an alongshore peripheral current (Rim Current, RC; Figure 3). The current is located over the continental slope flowing in the same direction as the migrating anchovy. Its velocity accelerates and slows down ranging between 50–100 cm/s in the upper layer (Oguz and Besiktepe, 1999) depending on the strength of the heat loss from the sea to atmosphere (Korotaev *et al.,* 2001). The migration speed - being considerably slower than the velocity of RC (~25-50 n.miles/day) - shows that the anchovy do not use the RC, but to the contrary avoids it as a typical response of the pelagic fishes against strong currents (Freon and Misund, 1999). In association with the RC, several anticyclonic eddies (CAEs) are observed over the continental shelf, between the RC and the coast (Steneva *et al.,* 2001) and it seems that overwintering anchovy occupies these coastal eddies in order not to be drifted away by the RC. This also explains the difference presented in Figure 3a and Figure 3b, in which anchovy aggregations nestle up to the coastal at the sites under the influence of RC in the west while within the large CAEs on the east they form offshore aggregations. It may also worth to note that Gucu *et al.* (2016a) draws attention to the very same coastal anticyclonic structures selected as spawning areas by the southern anchovy population.

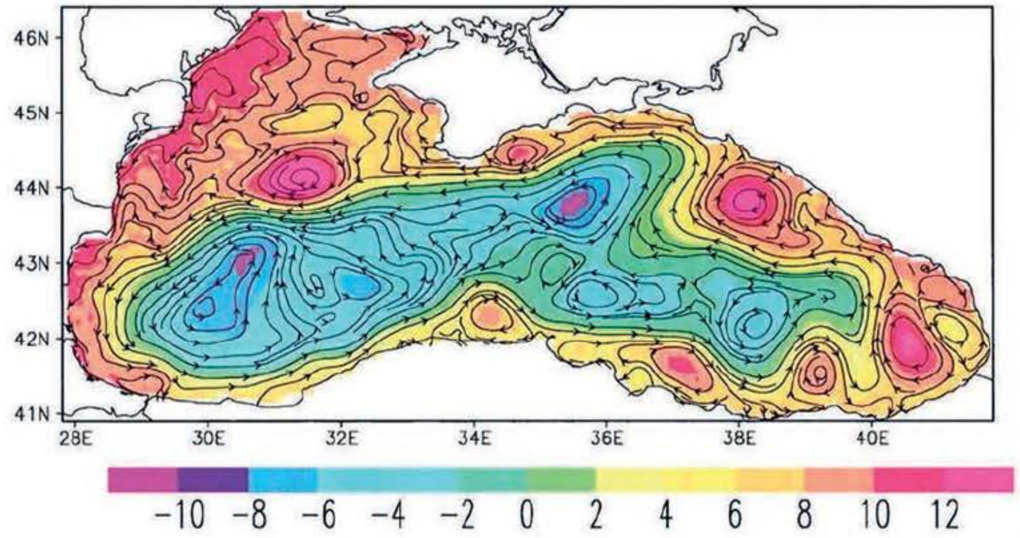

Figure 3.Schematic presentation of the main currents of the Black Sea and mean sea level height (taken from Staneva *et al.*, 2001).

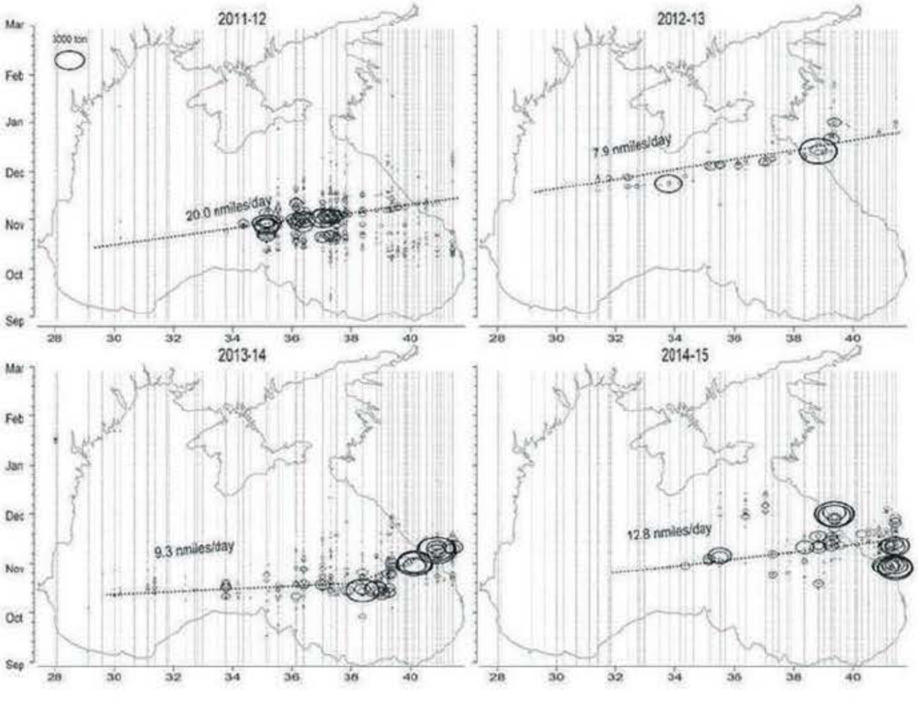

Figure 4.Landings by position of landing ports, by time and by size

As all these observations suggest, fast winter cooling has three effects on the anchovy; first, it drives anchovy faster so that migration is faster and second, it deepens the UML faster so that anchovy can approach to coast, settles on the overwintering grounds and form compact schools faster. In the case of fast cooling in autumn, they turn into easy targets for the fishers; they are fished out faster; the daily catch of the fleet is high; the over-all landing of the season is usually higher and the fishing season lasts less than the other years. In the case of slowly cooling winters, thermocline persists for a longer period and keeps the anchovy away from the coast, so that they migrate off the continental shelf in sparse surface aggregations. Consequently the daily quantity of fish removed by fishery is lower; the season prolongs and a larger part of the stock migrates to Georgian waters. Given that the strength of the RC is in a sense determined by cooling (heat loss from the sea to atmosphere; Korotaev *et al.,* 2001), fast cooling accelerates the RC, reduces the size of the CAEs which provides retention areas for the anchovy. Therefore the main implication of cooling rate on management of anchovy fishery might be that it determines the final destination of the transboundary migrating schools, and which would evidently influence the total level of landings by countries.

An acoustic survey conducted in autumn 2014 (10 October – 5 November) reveals the distribution of anchovies during the cooling period (Figure 5). Therefore the map also signals the location of anchovies in the southern Black Sea before or at the onset of the fishing season. Three main areas of accumulations draw attention on the map. The first is that one at the eastern most edge of the map. The second is in the central Turkish coast and possibly representing a part southern stock mentioned by Gucu *et al.,* (2016a). Finally, the third is located off the NW shelf, probably from where it was originated. Although they display different patch sizes, their densities are within the same order of magnitude. As the map is evaluated together with the position of the landings (Figure 4), it can be seen that the first group in the east seems to be there at the same spot even before the fishing season. The area in question located in effluent of the Batumi anticyclonic gyre and coincides with the spawning area noted by Gucu *et al.* (2016a). This one and the second accumulation were detected by the fishermen shortly and fished at two different sites.

An interesting point draws attention when comparing Figure 5 with the landings of the 2014-15 fishing season (Figure 4): fishery seems to target mainly the anchovy accumulations which were already on the south. On the other hand the same landing graphs do not give any indication that the western accumulation originated from the NW shelf was found and fished by the Turkish fleet. This group seems to follow an unusual route, heading straight to east along an offshore path not seen on the Turkish coast before they form dense schools sought by the fishermen and so that not fished on the Turkish coast (Figure 5). As a consequence, Turkish landing (70 000 tonnes) reported for the season is the lowest since the dramatic decline in 1990. In contrary, companies (except one) along the Caucasian coast filled their limits (GFCM, 2015), Georgia alone catching up with Turkish the landing first time in the history. The difference between TAC and the total landing of Georgian is due to some enterprise not being able to operate (GFCM, 2015). Besides as Ukraine lost the sovereignty of the Black Sea anchovy fishing grounds in Crimea, which used to be fished by their fleet, it is not known whether or not a part of the stock is overwintered in the north as they did in 2005.

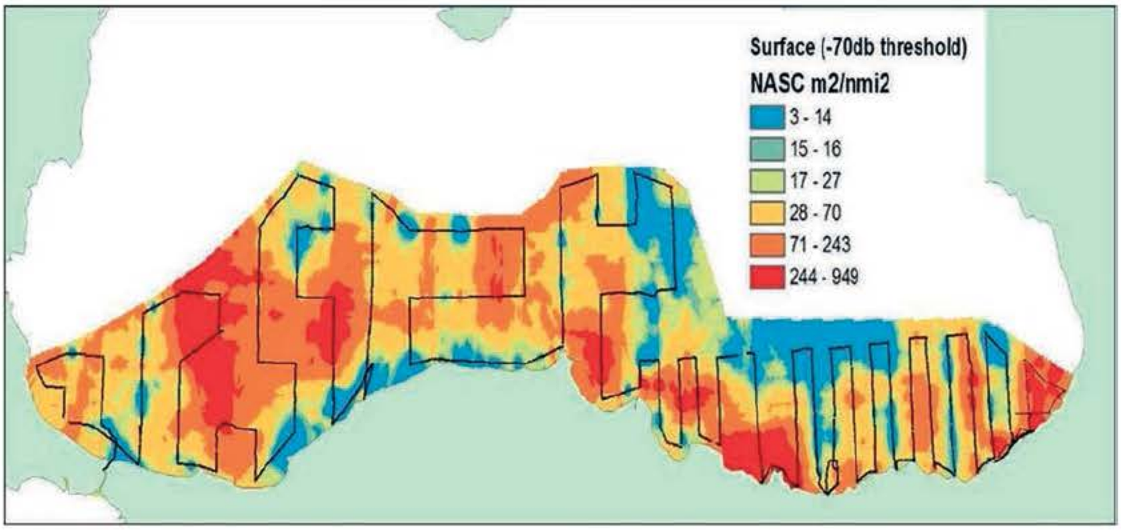

Figure 5.Distribution of anchovy in autumn 2014

There are two more similar significant drops in the Turkish anchovy landings (1989-1991 and 2005) experienced within the last 4 decades (Figure 1). The former is considered as a direct consequence of collapse of the stock which was attributed to various factors. In 2005, the landings decreased to a level lower than 100 thousand tonnes, and the stock unrealistically recovered the very next year. Interestingly, in contrary to regular overwintering pattern, a significant fraction of BS anchovy was reported to accumulate in the southern Crimea during the very same year (Chashchin *et al.,* 2015). Apparently, that year, a part of the BS anchovy stock was overwintered outside its range and the significant drop in the southern landings is, quite likely, a consequence of the temporal shift in the overwintering ground. This exceptional case raises the question as to whether the sharp decrease in the anchovy landings experienced in 1989-1991 might have resulted from a similar shift and the stock was not actually collapsed but simply anchovy overwintered outside the areas where they were expected. It may worth to note that the "collapse" in 1989-1991 coincided with the dissolution of USSR and during this period there were either no fishery in some areas like Georgia (Van Anrooy *et al.,* 2006), or fishery was not reported due to the lack of authority (Ulman and Divovich, 2015).

Finally, Figure 2 b is the output of an hypothetical migration model based on the assumption that the cooling in the upper mixed layer is the main driver of the Black Sea anchovy migrating south. The model suggests that the cooling pattern in the Black Sea is in fact facilitates the anchovies occupying the NW shelf area, taking a detour following an offshore route heading straight to the east coast.

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Connectivity, migratory routes and population structure of Atlantic bluefin tuna

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SPATIAL DISTRIBUTION

The Atlantic bluefin tuna thereafter referred as ABFT inhabit the pelagic ecosystem of the entire North Atlantic and its adjacent seas, primarily the Mediterranean Sea, i.e. from the equator to the North of Norway and from the Black Sea to the Gulf of Mexico (Figure 1). ABFT can sustain cold (down to 3°C) as well as warm (up to 30°C) temperatures while maintaining stable internal body temperature (Block *et al.,* 2001). Until recently, it was assumed that ABFT preferentially occupies the surface and subsurface waters of the coastal and open-sea areas, but electronic tagging showed that both juveniles and adults ABFT can dive to depth of 500m to 1000m (Brill *et al.,* 2001).

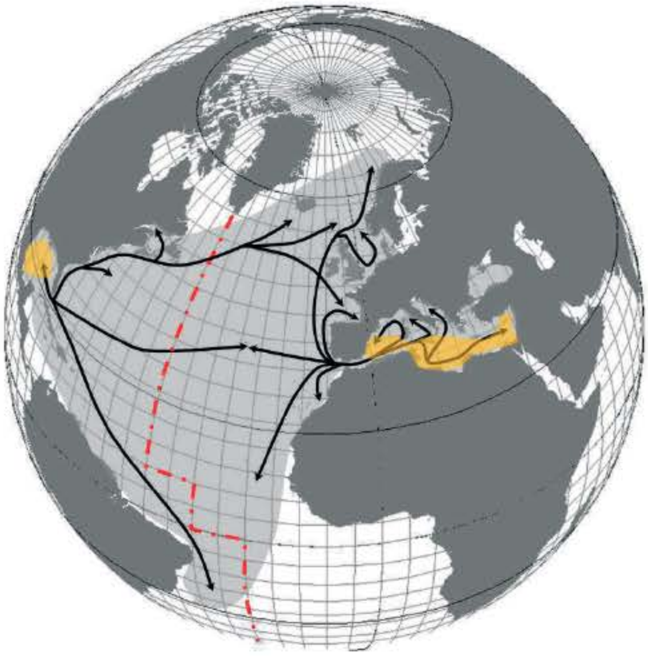

Figure 1: Spatial distribution of Atlantic bluefin tuna (gray shading) and main migration routes (black arrows). The orange areas depict the main spawning grounds and the vertical dashed dotted line depicts the stock delimitation between the two current ICCAT management units (from Fromentin and Powers, 2005)

The spatial distribution and movement of ABFT seem to be partly determined by preferential ranges and gradients of temperature and chlorophyll, with some preferential habitats in proximity to oceanic fronts (Royer *et al.,* 2004). This association is likely to be related to foraging, ABFT feeding on the abundant vertebrate and invertebrate prey concentrations of these areas (Boustany *et al.,* 2001). The types of ocean fronts known to be frequently visited by ABFT are the Moroccan and Portuguese upwelling areas, the meso-scale oceanographic structures associated with the general circulation of the North Atlantic and adjacent seas, e.g., the East coast of North America from Cape Hatteras to the Gulf of St Lawrence, the Bay of Biscay and the northwestern Mediterranean (Fromentin and Powers, 2005; Walli *et al.,* 2009).

ABFT REPRODUCTIVE MIGRATORY ROUTES

ABFT is known to do spawning migration between the North Atlantic and the Mediterranean or the Gulf of Mexico for a long time (Mather *et al.,* 1995). It displays a homing behavior, i.e. the adult comes back to spawn to the specific area where it was born an hypothesis that is supported by extensive electronic tagging surveys and chemical signatures in the otoliths (Rooker *et al.,* 2008). ABFT distribute themselves over a wide habitat (probably at a rather low density), so that aggregation of individuals at any given time and place appears necessary to ensure breeding and reproduction success. Ecologists usually distinguish between natal homing, i.e. a strict fidelity to the birth location due to imprinting of environmental cues during early life stages, such as salmon (Dittman and Quinn, 1996) and repeat homing (a process related to spatial learning of the younger from the older individuals, such as the herring (Dodson, 1988; McQuinn, 1997). Spatial learning would be advantageous when fish can repeat experiences (i.e. iteroparous reproduction) and when they live in unstable and unpredictable environments. ABFT is more likely to perform repeat homing, which is in agreement with several observations from fisheries and findings (Fromentin and Powers, 2005). Although spawning grounds are thought to be reasonably known (Mather *et al.,* 1995; Rooker *et al.,* 2007), two very recent studies are challenging our current knowledge. Following some intriguing results from electronic tagging studies, which showed that mature ABFT bluefin tuna do not always visit known spawning grounds during the spawning season, Richardson *et al.* (2016) showed that Western Atlantic bluefin tuna would have a differential spawning migration, with larger individuals spawning in the Gulf of Mexico and smaller individuals spawning in the Slope Sea of the northwestern Atlantic (similarly to what is assumed for Pacific Bluefin tuna). Using a different approach based on habitat modeling, Druon *et al.* (2016) displayed potential (but not yet validated) spawning grounds in the Azores area and off Morocco to Senegal during July and August when extrapolating the model settings from the Gulf of Mexico into the North Atlantic. These two very recent studies nonetheless demonstrate that our understanding of ABFT connectivity still relies on basic biological features, such as spawning locations, which remain uncertain.

VARIATIONS IN MIGRATION PATTERNS

The appearance and disappearance of past fisheries suggest that important changes in the spatial dynamics of ABFT (i.e. its migratory routes) may be environmentally driven (Ravier and Fromentin, 2004). Indeed, throughout its thousand-year old exploitation, catches of Atlantic bluefin tuna (ABFT, *Thunnus thynnus*) have never been stable, but exhibited conspicuous changes in both time and space domains, probably reflecting the high mobility of the species. During the 20th century, large Nordic and Japanese fisheries rapidly arose in unexpected fishing areas, i.e., the North and Norwegian Seas and the equatorial Atlantic, but suddenly disappeared after a few years or decades. The sudden disappearance of ABFT in 1963 from the North Sea and Norwegian Sea (after two to three decades of presence) was related to changes in migration routes that may have been induced by the synergy of local overfishing and a rapid cooling of the North Atlantic in the early 1960s that have affected Atlantic herring (the main ABFT prey in this area, Fromentin, 2009).

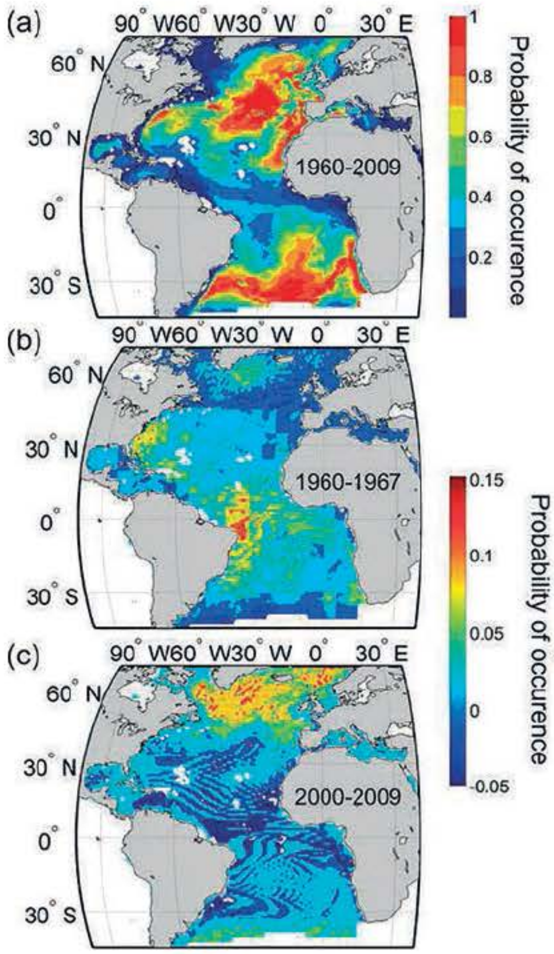

Figure 2. Maps of the probabilities of ABFT occurrence for: (a) the entire period (1960 to 2009); (b) map of the anomalies of the probabilities of ABFT occurrence during the "Brazilian episode" (i.e. 1960 to 1967); and (c) same as (b) for the period 2000 to 2009.

A recent study scrutinizing one of the most striking changes in ABFT spatial distribution, the so-called "Brazilian episode", during which Japanese fishing boats caught large quantities of ABFT (a temperate species) in the equatorial Atlantic where they were targeting tropical tunas, brings a few elements of understanding (Fromentin *et al.,* 2014). ABFT has indeed a remarkably large ecological niche in terms of temperature, salinity and bathymetry and display high probabilities of occurrence in the North Atlantic and adjacent seas (as expected) as well as in the South Atlantic at around 30°S and along the southwestern African coast (Figure 2). The niche model also detected favorable environmental conditions for ABFT in the western equatorial Atlantic during the 1960s, exactly when and where the Japanese LL caught ABFT. The 1960s were the only decade over the last 50 years that exhibited relatively high probability of ABFT occurrence around the Equator and no ABFT have been caught in the equatorial Atlantic since then, although the fishing effort from the Japanese fleets significantly increased in that area. ABFT could have thus migrated from their northern spawning grounds to the South Atlantic during the 1960s through the western equatorial Atlantic, playing the role of an "ecological bridge", i.e., a large-scale oceanographic structure between the central North and the central South Atlantic. Further analyses indicated that ABFT could have migrated, during that period, from the equatorial Atlantic to the western spawning ground of the Gulf of Mexico during the first semester and to a reverse north-south migration during the second part of the year (Fromentin *et al.,* 2014). During the last decade (Figure 2c), higher probabilities of ABFT mostly occurred above 45°N, which could be related to the global warming and is in agreement with a northward expansion of ABFT.

FEEDING MIGRATION AND SITE FIDELITY

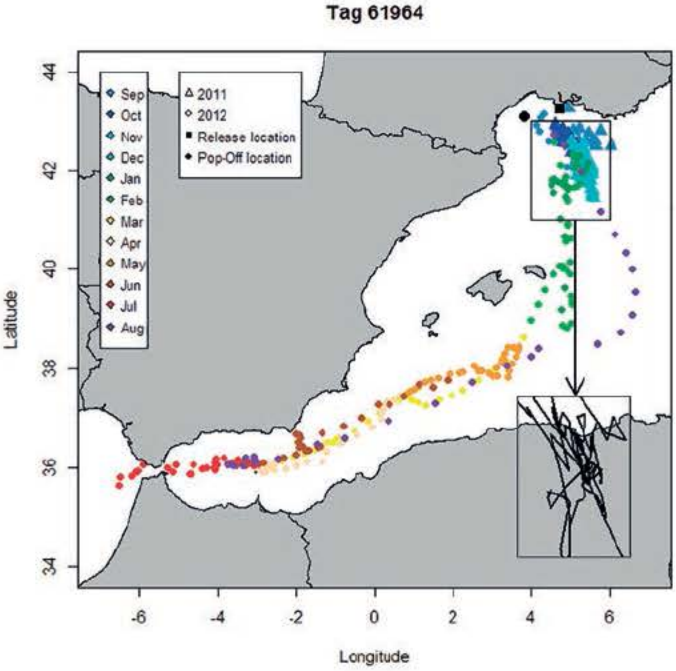

Figure 3. Track of tag 61964 with the release (black square) and pop-off (black circle) locations. Month and year information is given by color and symbol, respectively. The rectangle indicates the potential key area where details of the track are given in a subplot.

If electronic tagging surveys indicated that migration and movement patterns of ABFT vary considerably between individuals, years and areas (Sibert *et al.,* 2006), they also allowed us to identify clear hotspots where ABFT seem to seasonally concentrate for feeding (Walli *et al.,* 2009). Larger fish feed in the northern - high chlorophyll levels – latitudes up to the Norwegian Sea in the eastern Atlantic and to the Gulf of Saint Lawrence in the western basin, probably because of a wider temperature (Druon *et al.,* 2016). Permanent suitable habitat for juveniles ABFT feeding appeared to be mostly located in temperate latitudes in the North Atlantic and in the Mediterranean Sea, as well as in subtropical waters off north-west Africa. Two recent tagging studies in the Mediterranean Sea further tend to indicate that ABFT could be more resident than expected (Fromentin and Lopuszanski, 2014; Cermeño *et al.,* 2015). In those studies, the spatial distributions of ABFT showed little year-to-year variation as the fish (all mature) can aggregate in small areas of the western Mediterranean, where they may stay for several months (Figure 3). The individual tracks display sinuous trajectories in this area, indicating the possibility of feeding behavior. In those two studies (including about 80 individuals tagged over eight years), no fish went out to the North Atlantic, nor to the Eastern Mediterranean, but several fish displayed migrations to the Adriatic Sea and to the central Mediterranean during the spawning season. These tagging surveys also showed that strong site fidelity, sometimes with a "homing behavior" to some restricted feeding areas that are probably persistent from year-to-year (Figure 3). These persistent feeding areas for ABFT could result from local enrichment due to permanent meso-scale oceanographic features related to the North Mediterranean Current, the North Balearic front and the Rhône River discharge.

POPULATION STRUCTURE, MIGRATORY ROUTES AND CONNECTIVITY

The International Commission for the Conservation of Atlantic Tunas (ICCAT) currently manages ABFT as two stocks with the boundary between the two spatial units being the 45°W meridian (Figure 1). Most recent genetic, microchemistry studies are in agreement with the two stocks hypothesis, each with its distinct spawning area (i.e. the Mediterranean Sea and the Gulf of Mexico). Nonetheless, electronic tagging and retrospective analyses also advocate for overlapping between these two stocks, especially on North Atlantic feeding grounds (Block *et al.,* 2005). Fromentin (2009) postulated that the situation might be more complex, with at least three sub-populations: (1) a highly migratory stock over all the North Atlantic (which would preferentially spawn in the Western and Central Mediterranean), (2) a more resident stock in the Mediterranean (that would spawn in the Central and Eastern Mediterranean), and (3) a +/- migratory stock in the West Atlantic (that would spawn in the Gulf of Mexico). Latest tagging results (see above) tend to confirm the presence of more resident sub-populations in the Mediterranean, but there still remain some uncertainties about the status of the Eastern Mediterranean bluefin tuna. Past genetic studies advocate for two Mediterranean populations (Carlsson *et al.,* 2004). However, more recent and extensive genetic analyses do not unequivocally confirm this hypothesis and tagging of eastern Mediterranean individuals remains too scarce to get a comprehensive view of the migration patterns of this putative eastern Mediterranean sub-population.

Studies on salmon, herring and striped bass have opened new avenues for interpreting the complexity of fish dynamics, especially in those cases where both migration and residence seem to occur in the same population. For example, concepts of imprinting and Clark‘s contingent definition purport that divergent energy allocations during early life stages can cause divergent migration or habitat uses among groups of fish (Secor, 1999). These differences could further persist in case of reproductive isolation, phenotypic plasticity and/or heterogeneous distribution of the habitat. An alternative approach follows the concept of metapopulation theory from which ABFT would be seen as a collection of discrete local populations, occupying distinct and patchy suitable habitats, displaying their own dynamics but with a degree of demographic influence from other local populations through dispersal (Hanski, 1999, Kritzer and Sale, 2004). Within each local population, individuals would display similar migration or habitat uses, resulting from a common spatial learning among individuals (Olivieri *et al.,* 1990). Both hypotheses might provide a better explanation of the concomitance of residence, homing behavior and variations in migratory routes (that could lead to the occurrence of colonization and extinction in some areas) in ABFT populations. The main difference between Clark’s contingent hypothesis and the metapopulation approach finally lies with the importance given to the deterministic (imprinting) *versus* stochastic (behavioral) processes. More likely, there is no single factor but rather a mixture of mechanisms acting in ABFT populations (Fromentin and Powers, 2005).

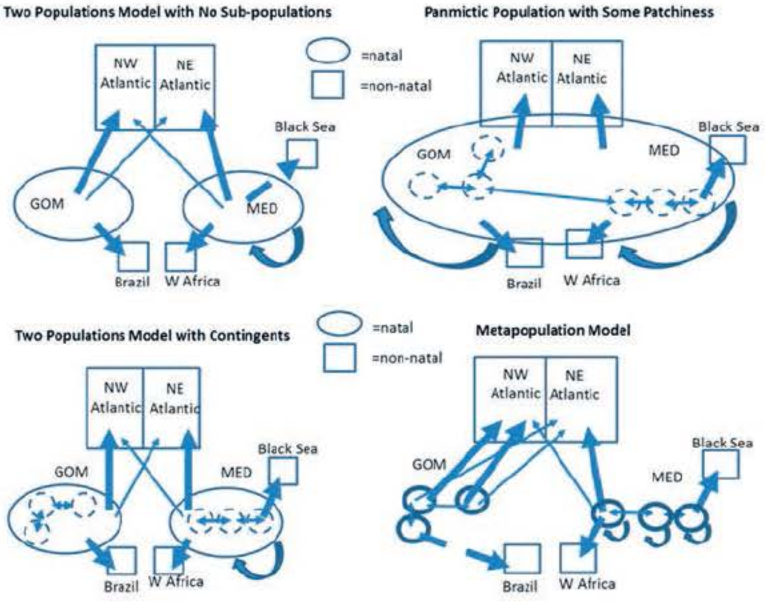

Figure 4. Schematic representation of four population structures and connectivity of ABFT that depend on self-reproducing entities (populations and sub-populations) and groups with similar lifetime migration behaviors, which do not necessarily depend on reproductive isolation (contingents) (ICCAT, 2014).

Connectivity, migratory patterns and population structure are thus closely related to each other. Based on current knowledge, a recent ICCAT WG proposed a range of four main population structures for ABFT (which are not exhaustive) and connectivity among them (Figure 4). Recent research outputs from genetic, otolith chemistry and tagging tend to support the model of "two populations with contingents", but there is not yet sufficient evidence, despite a tremendous research effort, to be fully conclusive.

CONCLUSION

ABFT connectivity, probably like all highly migratory species, is thus clearly related to the variations in its migratory routes. Migration patterns in ABFT seem to be both environmentally- and biologically-driven. The "homing behavior" induces a strong persistence in the ABFT migratory routes, especially those related to reproduction. However, environmental changes can impact ABFT reproductive and feeding migrations and thus change the connectivity of ABFT. For example, an oceanographic anomaly in the equatorial Atlantic during the 1960s probably induced an opportunity for ABFT to connect the northern and southern Atlantic (Fromentin *et al.,* 2014). Because ABFT displays a large ecological niche, it has potentially more abiotic opportunities (i.e., a larger ecological window) than other large pelagic fish, which may explain rapid changes in its connectivity. Nonetheless, our understanding of ABFT spatial dynamics (including its distribution, main migratory path and connectivity) also depends on our understanding of ABFT population structure. The implication of a "metapopulation model" *versus* a "two-population model" (with or without patchiness or contingents) is indeed important from a connectivity viewpoint, as it relates to the degree of fragmentation of the population into sub-groups, which are +/- connected to each other (Hanski, 1999).

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Migratory patterns and strategies of Mediterranean marine mammals and relation to intersystem connectivity

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ABSTRACT

This paper reviews and discusses the current knowledge on movement strategies and patterns of Mediterranean marine mammals. Emerging knowledge essential to overcome the existing gaps towards the identification of conservation strategies that systematically and explicitly account for the connectivity between populations, systems and realms is also presented.

INTRODUCTION

The exchange of individuals among populations through connectivity, e.g. dispersal, is an important life-history trait, critical to metapopulation dynamics, demography, persistence and expansion (see Gaylord and Gaines, 2000; Hastings and Botsford, 2006; James *et al.,* 2002; Roughgarden *et al.,* 1988; Simberloff and Wilson, 1969; Wright, 1931). Several factors can mediate the movements of organisms and the probability of their successful dispersal from one location to another (Casabianca *et al.,* 2012). It has been suggested that the knowledge of organisms' dispersal is essential to understand the response of populations and species to climate change, habitat loss and fragmentation, as well as biological invasions (e.g. Tesson and Edelaar, 2013). Understanding the complex dynamics of population connectivity and its relationship to environmental and anthropogenic factors is therefore a prerequisite for successful wildlife conservation and management (e.g. Botsford *et al.,* 2001; Bradbury *et al.,* 2008; Ruzzante *et al.,* 2006; Sale *et al.,* 2005).

While several examples exist for terrestrial species (e.g. Wiens, 2001), it is more difficult in marine systems to directly monitor the exchange of individuals among populations. The resulting limited understanding of the degree of connectivity among populations and systems creates a significant challenge for the management of nearly every marine species. The use of population genetics as a tool for indirectly estimating population and system connectivity (e.g. Bohonak, 1999; Howeth *et al.,* 2008; Lowe and Allendorf, 2010; Palumbi, 2003), despite significant advantages, often results in complex conclusions and possibly misinterpretations regarding connectivity, due to the complex genetic patterns among populations typically observed in marine systems (Bradbury and Bentzen, 2007). In fact, as recently reported, genetic methods provide valuable information on connectivity mostly when combined with alternative approaches, such as capture-mark-recapture methods or data on movement behavior, essential to elucidate the complex role of dispersal in natural populations (Lowe and Allendorf, 2010).

During the last decades, technological advances allowed the tagging and tracking of several marine species (e.g. Block *et al.,* 2011; Calò *et al.,* 2013; Hart and Hyrenbach, 2009; James *et al.,* 2005; Levin, 2006; Pittman *et al.,* 2014; Ropert Coudert *et al.,* 2009; Wood *et al.,* 2000). Concerning marine mammals, animal-borne satellite-linked tags have provided invaluable information on migration routes and patterns, as well as migration timing and distances of several species, contributing vital information to identify and mitigate anthropogenic impacts, and to inform the conservation of migratory species and their critical habitats (Mate, 2015; Rosenbaum, 2014). In particular, these studies, coupled with advanced statistical modelling (Jonsen *et al.,* 2013, 2003; Nielsen *et al.,* 2009; Silva *et al.,* 2014), greatly increase the possibility to integrate movement data to existing knowledge on behavior so as to better understand and quantify the complex processes of individuals' dispersal at multiple spatial and temporal scales, as well as the connectivity between populations and systems.

This paper reviews and discusses the current knowledge on movement strategies and patterns of Mediterranean marine mammals and presents emerging knowledge essential to overcome the existing gaps towards the identification of conservation strategies that systematically and explicitly account for the connectivity between populations, systems and realms.

MEDITERRANEAN SEA MARINE MAMMALS

Conservation status

A number of species of marine mammals have been reported to occur in the Mediterranean Sea over the course of centuries (e.g. Notarbartolo di Sciara and Birkun, 2010), but only few of them are currently considered to regularly inhabit this body of water. Eleven species of cetaceans, including the fin whale (*Balaenoptera physalus*), the sperm whale (*Physeter macrocephalus*), the Cuvier's beaked whale (*Ziphius cavirostris*), the Killer whale (*Orcinus orca*), the long-finned pilot whale (*Globicephala melas*), the Risso's dolphin (*Grampus griseus*), the rough-toothed dolphin (*Steno bredanensis*), the common bottlenose dolphin (*Tursiops truncatus*), the striped dolphin (*Stenella coeruleoalba*), the short-beaked common dolphin (*Delphinus delphis*) and the harbor porpoise (*Phocoena phocoena*) and one species of Pinniped, the Mediterranean monk seal (*Monachus monachus*) regularly occur in the Basin.

Recent genetic evidence suggests that some of the cetaceans occurring the Mediterranean Sea constitute distinct sub-populations from the North Atlantic, with little or no gene flow across the Strait of Gibraltar (Bérubé *et al.,* 1998; Drouot *et al.,* 2004a; Engelhaupt *et al.,* 2009; Gaspari *et al.,* 2013, 2007, 2006; Natoli *et al.,* 2008, 2005, 2004; Palsbøll *et al.,* 2004). The conservation status of these Mediterranean sup-populations (*sensu* IUCN) has been assessed according to the International Union for the Conservation of Nature (IUCN), resulting in one species classified as "*Critically Endangered*" (CR), four species classified as "*Endangered*" (EN), four species classified as "*Vulnerable*" (VU), and three species listed as "*Data Deficient*" (Table 1; IUCN, 2012).

Table. 1 Conservation status of the marine mammal species occurring in the Mediterranean and Black Seas

Species-subspecies	Region	IUCN Criterion	Year
Harbour porpoise *Phocoena phocoena ssp. relicta*	Black Sea subspecies	**Endangered** *A1d+4cde*	2008
Common bottlenose dolphin *Tursiops truncatus ssp. ponticus*	Black Sea subspecies	**Endangered** *A2cde*	2008
Short-beaked common dolphin *Delphinus delphis ponticus*	Black Sea subspecies	**Vulnerable** *A2cde*	2008
Sperm whale *Physeter macrocephalus*	Mediterranean subpopulation	**Endangered** *C2a(ii)*	2012
Short-beaked common dolphin *Delphinus delphis*	Mediterranean subpopulation	**Endangered** *A2abc*	2003
Fin whale *Balaenoptera physalus*	Mediterranean subpopulation	**Vulnerable** *C2a(ii)*	2012

Common bottlenose dolphin *Tursiops truncatus*	Mediterranean subpopulation	**Vulnerable** *A2cde*	2012
Striped dolphin *Stenella coeruleoalba*	Mediterranean subpopulation	**Vulnerable** *A2bcde*	2012
Risso's dolphin *Grampus griseus*	Mediterranean subpopulation	**Data Deficient**	2012
Long-finned pilot whale *Globicephala melas*	Mediterranean subpopulation	**Data Deficient**	2012
Cuvier's beaked whale *Ziphius cavirostris*	Mediterranean subpopulation	**Data Deficient**	2012
Mediterranean monk seal *Monachus monachus*	Mediterranean subpopulation	**Critically Endangered** *A2abc; C2a(i)*	2008

Mediterranean marine mammal populations live in precarious condition due to the high volume of pressures coming from human related activities and ever-increasing global changes, making this semi-enclosed sea one of the most degraded ecosystems worldwide (Bianchi and Morri, 2000; Coll *et al.,* 2010; Danovaro *et al.,* 2010; Piroddi *et al.,* 2015). Threats with actual and potential detrimental effects on Mediterranean marine mammals include injuries and mortality from shipping (e.g. Panigada *et al.,* 2006), chemical pollution (e.g. Borrell *et al.,* 2014; Fossi *et al.,* 2013, 2001; Panti *et al.,* 2011), interactions with fisheries (e.g. Lewison *et al.,* 2014; Reeves *et al.,* 2013), direct killings, noise pollution along with severe and widespread habitat loss and degradation.

In this context, the lack of critical information about abundance, trends, occurrence, distribution and movements, among other several ecological and life history traits, hampers the identification of management and conservation priorities.

Reported movements from the literature: examples from the Mediterranean Sea

Long- and mid-distance migrations are well known for several species of large cetaceans (e.g. Calambokidis *et al.,* 2001; Luschi and Luschi, 2013; Mate, 2015; Mizroch and Rice, 2013; Pomilla and Rosenbaum, 2005; Rasmussen, 2007; Stevick *et al.,* 2011; Stone *et al.,* 1990; Torres-Florez *et al.,* 2015) and to a lesser extent for smaller odontocete species. Marine mammals generally exploit resources across the world's oceans, but foraging grounds are often spatially and temporally separated from breeding grounds (Boyd, 2004). As an instance, most of the mysticete cetaceans utilize seasonally rich food supplies in the polar waters during the summer season, but migrate to sub-tropical waters during winter, when mating and birth take place (Block *et al.,* 2011). Migrations tend to follow predictable routes but often species with the largest body size undertake migration over the longest distances.

In the Mediterranean Sea, although marine mammals are well studied on their summer foraging grounds (e.g. Azzellino *et al.,* 2008; Druon *et al.,* 2012; Panigada *et al.,* 2011, 2005) and to a lesser extent on their winter grounds (Canese *et al.,* 2006), large knowledge gaps exist concerning their distribution and occurrence for much of the rest of the year. Accidental species have been reported from the Mediterranean Sea following exceptional migrations through the Atlantic and possibly the Northern Pacific Ocean (Bompar, 2000; Capellini, 1877; Gasco, 1878; Pouchet and Beauregard, 1888; Scheinin *et al.,* 2011).

The following paragraphs report on known movement patterns and migrations for five species of cetaceans occurring in the Mediterranean Sea, presenting novel information on the fin whale, recently obtained by means of satellite telemetry studies.

Sperm whale

Mediterranean sperm whales constitute a distinct sub-population from the North Atlantic stock (Drouot *et al.,* 2004a; Engelhaupt *et al.,* 2009). The systematic and extensive use of photo-identification methodology (Arnbom, 1987) across the Region over the last decades revealed how sexually mature male sperm whales undertake mid- to long-distance north–south migrations between the feeding grounds located in the Northern regions and the breeding grounds around the Balearic Islands (Drouot-Dulau and Gannier, 2007; Drouot *et al.,* 2004b; Gannier *et al.,* 2002) (Figure 1). Further extensive evidence have also been provided by Carpinelli *et al.,* (2014) (Figure 2), indicating long-range movements throughout the whole western Mediterranean Sea, with a maximum straight-line distance of about 1600 km. The same authors highlight the absence of photographic recaptures between the Mediterranean Sea and the North Atlantic Ocean, supporting earlier genetic evidence of a distinct Mediterranean sub-population. Finally, Frantzis *et al.* (2011) (Figure 3) provided the first ever conclusive evidence of inter-basin movements of this species following a rare mass stranding (Mazzariol *et al.,* 2011). The authors report that three of the seven stranded whales had been previously photo-identified in different locations of the Ligurian Sea, North Western Mediterranean, and the Hellenic Trench over two decades and have hence undertaken migrations of 1600-2100 km across the Strait of Messina or the Strait of Sicily, Central Mediterranean Sea. Although the authors do not provide exhaustive information on the migration routes, essential to possibly identify critical habitats and trigger protection actions, they provide crucial information on the inter-basin gene flow for the small Mediterranean sperm whale sub-population, that most likely amounts to hundreds (Rendell *et al.,* 2014).

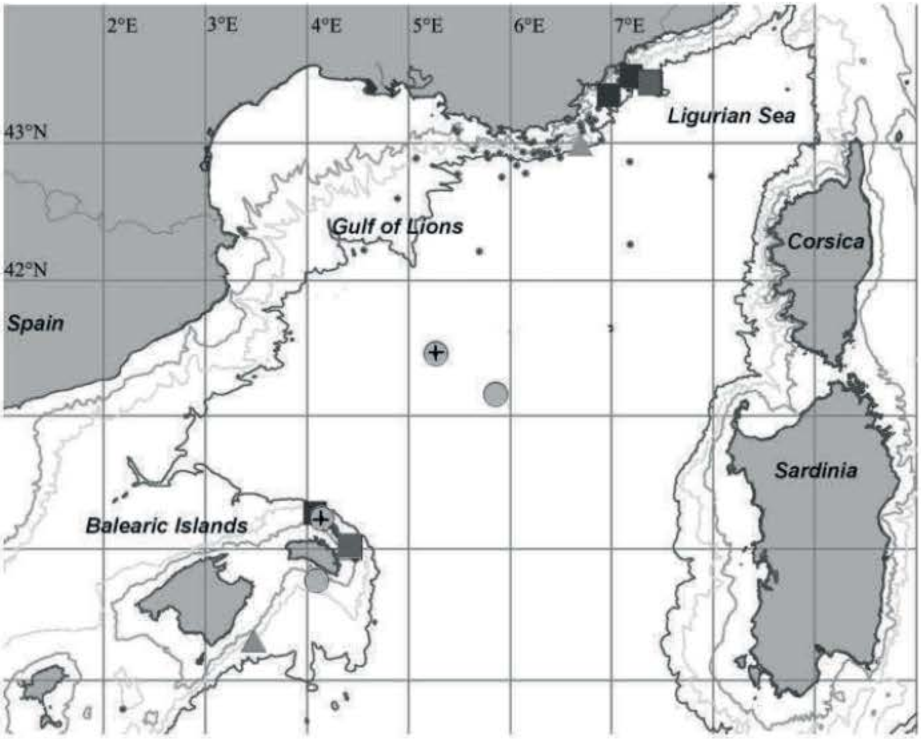

Figure. 1 - Photo-identified whales (dots) and long distance re-captures of sperm whales between the Balearic Islands and the North-Western Mediterranean Sea (from: Drouot-Dulau and Gannier, 2007).

Figure. 2 - Individuals from the Strait of Gibraltar re-sighted in the Mediterranean Sea. Numbers indicate chronological order of observation (from: Carpinelli *et al.*, 2014).

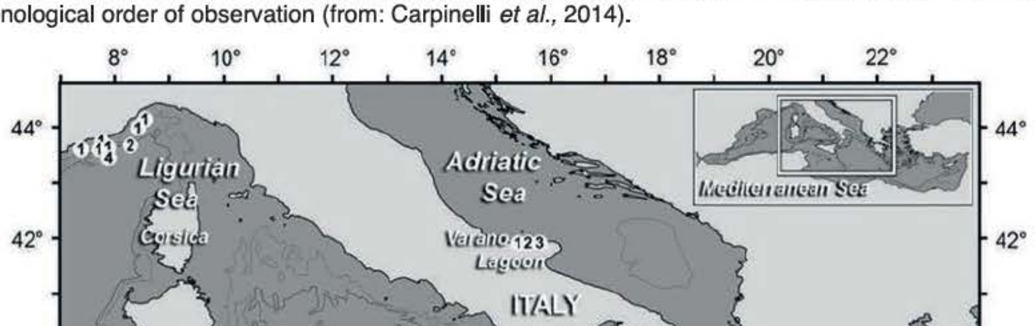

Figure. 3 - Map of the central Mediterranean, west and east of the Straits of Messina and Sicily. The position of the area presented in the map within the limits of the Mediterranean Sea is shown at the top right frame. Depth contours correspond to 1000 m (light grey) and 2000 m (dark grey). All observations of the whales identified in both the Western and Eastern Mediterranean basins and/or identified in the mass stranding are shown by numbered white dots (from: Frantzis *et al.*, 2011).

Common bottlenose dolphins

The common bottlenose dolphin (here after 'bottlenose dolphin') is one of the most frequently observed cetaceans in the Mediterranean Sea. The species occurs mostly in coastal waters within the entire basin. The total population size is unknown but may be in the low 10,000s based on observed densities in areas that have been surveyed. Most of the Mediterranean areas inhabited by these dolphins are subject to intensive human presence, and therefore severe detrimental pressures. The Mediterranean sub-population is distinct from those inhabiting the Eastern North Atlantic Ocean and the Scottish Sea (Natoli *et al.,* 2005). For a full review of the existing knowledge on the species ecology and conservation status in the Mediterranean Sea, please refer to Bearzi *et al.* (2009).

In the Mediterranean Sea, based on information obtained through photo-identification methods, bottlenose dolphins are primarily considered resident with some communities showing high levels of long-term site fidelity (Bearzi *et al.,* 1997). The lack of information on long-distance movements has resulted so far on higher emphasis on site fidelity, possibly underestimating the roaming abilities of the species and its potential to use and exploit alternative core habitats.

The longest movements reported in the Region are of 427 and 400 km, described by Gnone *et al.* (2011) in the North-Western Mediterranean, and followed by mid-distance movements of about 250 km presented by Bearzi *et al.* (2010) who present details on the movements of nine individuals photo-identified in different areas in western Greece (Figure 4). Moreover, one individual, photo-identified off Northern Corsica, was re-sighted in South-Eastern continental France, 228 km away from the original location (Dhermain *et al.,*1999). Mid-range movements were also observed among bottlenose dolphins photo-identified off the North-Western coast of Italy, where several individuals were re-sighted 100–130 km apart (Gnone *et al.,* 2006). Genov *et al.,* (2015) presented details on mid-distance re-sightings of a common bottlenose dolphin in the northern Adriatic Sea. One single adult bottlenose dolphin was observed and photographed alive off the Slovenian coast by the end of April 2014 and subsequently found dead on the shores of Goro, Italy, on 5 May 2014, about 130 km from the original sighting location. As reported by the authors, the fresh carcass suggests that the dolphin had died very recently prior to being found, indicating that the reported movement was not an artefact of currents. This further observation shows that bottlenose dolphins inhabiting the Northern Adriatic Sea can undertake substantial movements in relatively short time frames with such movements possibly being more common than documented to date. Very recently, using social network analysis Carnabuci *et al.,* (2016) investigated the association patterns of photo-identified common bottlenose dolphins and the macrostructure of the meta-population inhabiting the Pelagos Sanctuary for Mediterranean Marine Mammals and its connectivity in relation to the landscape characteristics. Their analysis of the network connectivity confirms previous knowledge that animals belonging to this meta-population tend to aggregate primarily with the individuals coming from the same sub-area. However, the same analysis also highlights that some animals tend to roam widely in the area connecting with different subgroups of the same meta-population. In fact, a few long travelling adult erratic males have been found to play an important role in connecting neighbouring clusters.

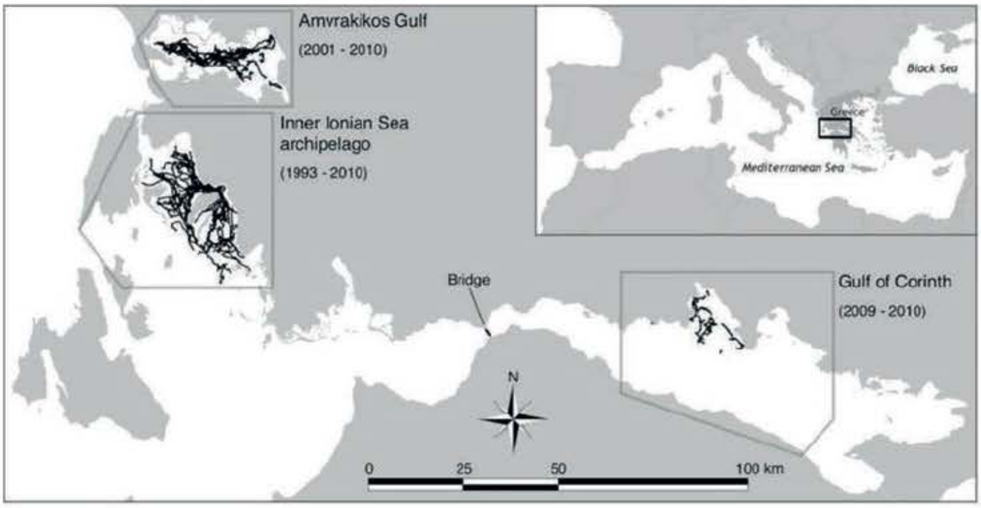

Figure. 4 - Location of the three study areas in Greece (delimited by grey lines). Black lines indicate movements by nine bottlenose dolphins (from: Bearzi *et al.,* 2010).

Humpback whale

The occurrence of the humpback whale (*Megaptera novaeangliae*), considered to be an occasional species in the Mediterranean basin, has been increasingly reported in the last decade with 14 sightings, 3 strandings and 2 by-caught individuals from different locations across the Region since, along with the first re-sighting of a lone individual in three different locations in the Mediterranean Sea between 2012 and 2013. A whale, approximately 8-9-meters long, was first observed in the Ligurian Sea, NW Mediterranean, in June 2012. The same animal was then re-sighted off Lampedusa Island, Sicily Channel, in March 2013 over 1000 km away in a straight line from the previous location and again in August 2013 in the Ligurian Sea (Figure 5).

The increased occurrence of this species in the Mediterranean Sea might be the result of the recent recovery of the North Atlantic humpback whale population, leading to increased migrations of individuals in the Mediterranean through the Gibraltar Strait. This range expansion, possibly leading to a (re)colonization of the Mediterranean in the future, could expose the species to severe anthropic pressures and urges appropriate mitigation measures to be considered and implemented also for this species.

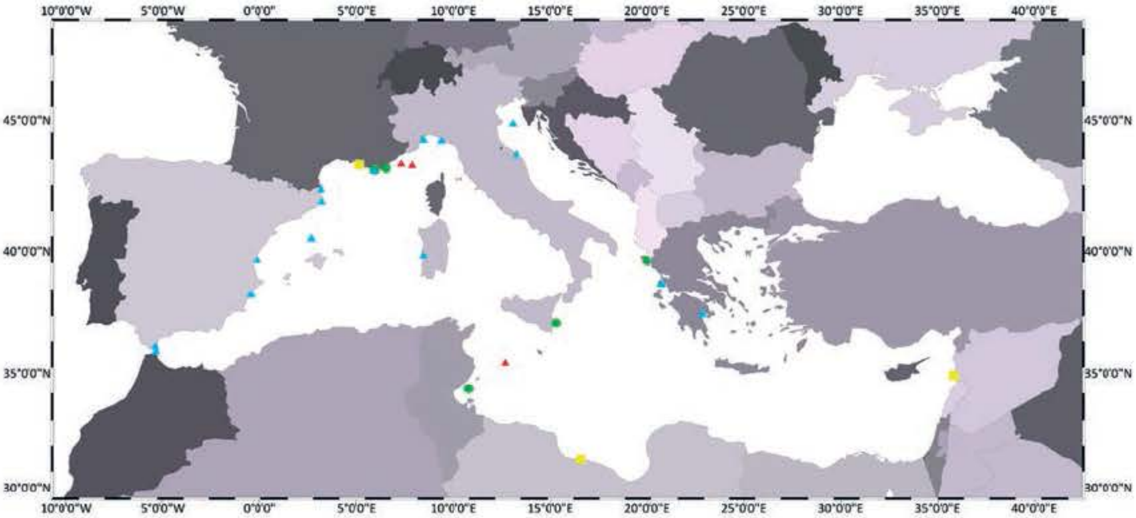

Figure. 5 Map showing the locations of sightings and strandings of humpback whales in the Mediterranean. The red triangles correspond to the re-sighted whale (from: Panigada *et al.,* 2014).

Short-beaked common dolphin

Once one of the most abundant cetacean species in the Mediterranean Sea, the short-beaked common dolphin (hereafter 'common dolphin'), constitutes a distinct sub-population from the North Atlantic (Natoli *et al.,* 2008). The species has declined throughout the region since the 1960s, likely due to overfishing and incidental mortality in fishing gear (Bearzi *et al.,* 2003). In the Mediterranean Sea, long-range movements have been reported only in one single occasion (Figure 6). Genov *et al.* (2012) describe a long-distance migration of one lone individual, encompassing a minimum of 1000 km across the Ionian and the Adriatic Seas, obtained through non-invasive photo-identification. This represents the longest documented movement for any individual of this species worldwide (Figure 6). While the authors could not reconstruct the possible migration route and stopovers, these data provide useful information in an area, the Northern Adriatic Sea, where common dolphins were historically abundant but had virtually vanished since the 1970s (Bearzi *et al.,* 2004; 2003).

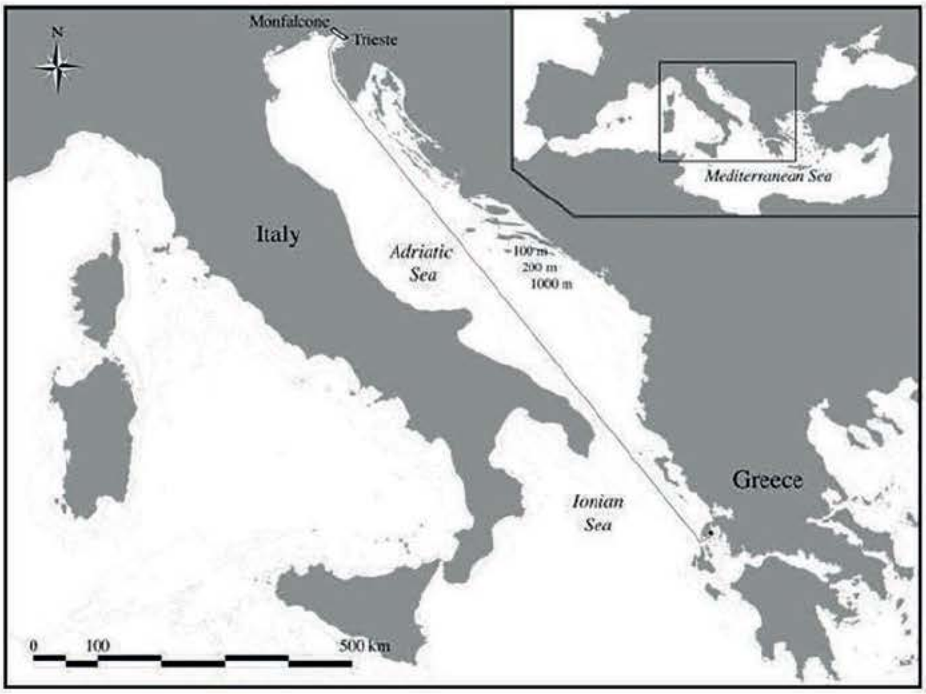

Figure. 6 - Minimum distance travelled by the adult common dolphin, with some of the locations cited in the text (from: Genov *et al.,* 2012).

Fin whale

The fin whale, mostly found in deep pelagic waters (Azzellino *et al.,* 2008; Notarbartolo di Sciara *et al.,* 2003; Panigada *et al.,* 2008), is abundant in the western basin with seasonal concentrations in highly productive areas such as the Ligurian Sea in the North-Western Mediterranean and the waters surrounding the Island of Lampedusa in Sicily Channel (Canese *et al.,* 2006; Notarbartolo di Sciara *et al.,* 2003; Panigada *et al.,* 2006). Genetic studies (Bérubé *et al.,* 1998; Palsbøll *et al.,* 2004) indicate differences between the Mediterranean population, which is thought to be resident, and fin whales in Atlantic coastal waters of Canada, Greenland, Iceland and Spain, with limited but recurrent gene flow between the Mediterranean and the North Atlantic populations. Recent acoustic studies (Castellote *et al.,* 2012) and stable isotope (Giménez *et al.,* 2014, 2013; Roubira *et al.,* 2015) have shed some light on the existence of two separate populations of fin whales utilizing primarily the Western Mediterranean, with one travelling back and forth between southern Spain and the actual Mediterranean sub-population. Ship strikes are reported to be the most detrimental threat and the main cause of direct mortality in the region (Panigada *et al.,* 2006).

In part due to a lack of information, or to often contradictory information, the knowledge and understanding of seasonal movements and migrations of Mediterranean fin whales across and outside the basin is scant and only limited to portions of the potential range of the species in the region. Fin whales are known to congregate in the Ligurian Sea during the summer months (Notarbartolo di Sciara *et al.,* 2003; Panigada *et al.,* 2005) and to possibly remain in the area if favorable conditions would occur, but no extensive and comprehensive information exist on yearly movement patterns. Castellote *et al.* (2012) reported consistent movements of Mediterranean fin whales from the Ligurian Sea towards the Alboran Sea and the northern coast of Algeria, with presence in these areas higher in spring and autumn, suggesting seasonal movements to and from the summer feeding areas located in the Ligurian Sea.

Recent information on large-scale movements describes the first north-south migration of one single animal between the Strait of Sicily and the Ligurian Sea through the Central and Southern Tyrrhenian Basin. The whale, equipped with a satellite transmitter, migrated in about five days between the two areas after spending several days in the only known winter feeding area around the Island of Lampedusa (Canese *et al.,* 2006). While the migration of one single individual might not represent conclusive evidence, and despite the lack of information on the identity of the whales occurring in the waters surrounding the Island of Lampedusa, it certainly shows a direct connection between the two feeding areas and highlights the need to preserve the migration route.

DISCUSSION

While connectivity plays a central role in sustaining marine populations, our understanding of this process and of its complexity is still largely underdeveloped.

From an ecological point of view, the understanding of demographic connectivity among populations is essential to understand the dynamics of populations and how they respond to natural and/or human disturbances (Hannah *et al.,* 2007; Lowe and Allendorf, 2010; Roberts, 1997; Roberts *et al.,* 2003; Saenz-Agudelo *et al.,* 2011; With *et al.,* 1997). Hence, quantifying the magnitude of retention within and connectivity among sub-populations is vital to metapopulation dynamics (e.g. Hixon *et al.,* 2002; Levin, 1974) and to model the effects of human pressures and natural fluctuations on marine ecosystems (Hughes *et al.,* 2005).

A detailed understanding of dispersal pathways and population connectivity in marine populations is necessary to trigger and guide the design of MPAs networks.

In the Mediterranean Sea, a hotspot of biodiversity, as well as one region most impacted by human activity (Coll *et al.,* 2010), natural fluctuation and anthropogenic stressors affect both the structural connectivity – the area and spatial configuration of habitats – and the functional connectivity – the rate of movement of individuals or genes among populations.

For marine mammals, in particular for cetaceans, it has been reported that high connectivity can buffer genetic diversity against demographic decline (Foote *et al.,* 2013). This is mostly relevant for the Mediterranean Sea where all the resident species of cetaceans constitute sub-populations that show distinctive genetic differences from the North Atlantic ones, with reduced gene flow between the two areas. The fragmentation and the general habitat loss and degradation of several Mediterranean ecosystems, primarily in coastal waters (Claudet and Fraschetti, 2010), is resulting into a general large-scale simplification and homogenisation of the marine environment, with potential severe detrimental effects at all levels and components of diversity.

Cetaceans are highly mobile species whose seasonal occurrence, site fidelity, movement patterns and connectivity are greatly determined by foraging and reproductive needs, with intrinsic barriers to movement being mainly represented by finding access to a suitable mate and/or breeding ground, as well as presence and seasonality of food resources (e.g., Foote *et al.,* 2009; Guzman *et al.,* 2015). Mediterranean cetaceans have been reported to perform short- to mid- and long-distance migrations with a high rate of seasonal or inter-annual site fidelity to some areas. For some of these species, a limited gene flow across the Strait of Gibraltar has been described, suggesting minimal genetic connectivity between separate sub-populations.

Further genetic fragmentation within the Region has only been investigated for the most accessible species and the lack of essential baseline data on this aspect is hampering further speculations. In this contest, the very recent gathering of movement data for some species such as the fin whale is therefore essential to integrate existing knowledge based on molecular techniques and to be complemented by the use of other remotely sensed information (e.g. Bauer *et al.,* 2015; Burtenshaw *et al.,* 2004; Druon *et al.,* 2012).

In this contest, modern technology can be essential to identify previously unknown movement corridors (Zeh *et al.,* 2016) which are often unknown (Hyrenbach *et al.,* 2000) or change following natural dynamics and processes (Grüss *et al.,* 2011; Lascelles *et al.,* 2014).

Investigating whales' migrations and movement patterns in conjunction with the presence of feeding grounds and the potential shift of prey occurrence could help identifying factors leading to isolation of populations on a timesòe not detectable by genetic analysis, hence providing critical information to conservation.

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Modeling ecological connectivity and dispersal in the Black Sea: seasonal and interannual variability

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ABSTRACT

Dispersal mechanisms of pelagic larvae across the Black Sea were studied with a series of Lagrangian particle trajectory simulations using surface currents calculated by a parallel configuration of the Princeton Ocean Model during a period of three years (2001-2003). Particles representing pelagic fish larvae were released across the Black Sea in winter, spring, and summer of each year to investigate seasonal and interannual variability. Particles were advected with different pelagic larval duration times between 30-60 days, representing a wide range of different pelagic larval species of importance in the Black Sea, such as e.g. anchovy, horse mackerel, and sprat. Connectivity patterns related to these species were derived from these simulations.

Simulations revealed that the northern part the northwestern shelf has continuously very high retention rates (> 80%) inside the area, while the Crimea peninsula region exhibits barely any retention but rather shows displacement onto the northwestern shelf from there. Further, the southern Black Sea coast regions are more isolated than the northern regions. In addition, the advection of particles on the northwestern shelf is strongly influenced by river inflow of the Dnieper in the north and the Bosporus plume in the north-west. Advection of larvae by these river plumes is seasonally dependent and variable from year to year. In the north-east Black Sea the water inflow through Kerch Strait, is however a constant source of larva displacement and may be one factor influencing fish migration in the region.

INTRODUCTION

Importance of dispersal during early life

Dispersal by ocean currents often occurs during early life when young individuals are not yet capable of active movement while older life stages exhibit behavior and active movement and can therefore often move on different spatial scales. This dispersal is known to structure marine populations through influencing population success and persistence. To be able to understand populations dynamics one must therefore assess the extent of exchange between populations (connectivity) and determine the factors driving it, which still remains a challenge today (Cowen *et al.,* 2006).

Larval dispersal by ocean currents and connectivity between different oceanic regions have been identified as crucial factors for structuring marine populations (Cowen *et al.,* 2006) as well as useful tools for designing networks of Marine Protected Areas (MPAs) (Moffit *et al.,* 2009; Lester *et al.,* 2009), or even understanding the spread of marine pests (Glasby and Lobb, 2008). While marine population connectivity depends on a variety of factors such as habitat availability, spawning efficiency, larval dispersal, trophic interactions and adult movements (Cowen and Sponaugle, 2009; Game *et al.,* 2009), 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). Therefore, patterns and magnitude of larval connectivity have been used as a tool to design MPAs (Lester *et al.,* 2009) and also assess their efficiency (Pelc *et al.,* 2010).

The aim of this study is to identify basin-scale pelagic larval connectivity using an ecosystem-based approach (e.g. Coll *et al.,* 2012; Guidetti *et al.,* 2013) as opposed to focusing on one target species, such as the commercially important anchovy (Fach, 2014). The common trait of many of these species is that they have pelagic larval stages that stay in the water for different lengths of time. Here, pelagic larvae are tracked in the simulated surface circulation of the Black Sea to assess the dispersal and retention of pelagic larvae in different regions.

Black Sea Circulation

The Black Sea is a nearly enclosed basin connected to the Sea of Marmara and the Sea of Azov only by the narrow Bosporus and Kerch Straits, respectively. The only major shelf region of the Black Sea is the northwestern shelf where the three largest rivers of the Black Sea, the Danube, Dniepr and Dniestr, discharge. The general circulation of the Black Sea is driven by this large freshwater input on the northwestern shelf as well as the curl of the wind stress field and is steered by the steep topography around its periphery that consists of narrow shelves and a maximum depth of around 2200 m (Oguz *et al.,* 2005). A permanent feature of the upper layer circulation is the meandering, cyclonic Rim Current that encircles the entire basin, forming a large cyclonic gyre and two cyclonic cells within the interior basin. Current speeds in the upper layer of the Rim Current are 50-150 cm/s (Oguz and Besiktepe, 1999) and meanders of the Rim Current have a typical time scale of persistence on the order of 50-150 days (Korotaev *et al.,* 2003). The Rim Current is most intense in winter-spring, forced by the seasonal wind stress curl variations. Along the Rim Current significant mesoscale variability occurs, forming a number of quasi-permanent anticyclonic eddies on the coastal side of the Rim Current. Dynamic events such as meandering of the Rim Current, eddy formation and detachment take place on weekly time-scales and may lead to considerable exchange between the coastal and offshore (Oguz *et al.,* 2002) and may be an important component of Black Sea circulation dynamics, likely to influence the spatial distribution of pelagic fish eggs and larvae.

METHODS

Circulation model and particle tracking

To assess dispersion via ocean currents, the surface velocity fields from 1990-2010 generated by the Stony Brook Parallel Ocean Model (sbPOM) based on the Princeton Ocean Model using the Mellor-Yamada level 2.5 turbulence parameterization (POM; Blumberg and Mellor, 1987) were used. The model domain encompasses the entire Black Sea with a 5km x 5km horizontal grid and a 35 level, sigma-coordinate, vertical grid. The model was forced using the atmospheric fields generated by the HIRHAM model of the Danish Meteorological Institute (DMI) and river discharge rates obtained from the Black Sea Commission's river database. The model was initialized using World Ocean Atlas fields, spun up for five years and then the hindcast simulation was performed for the period 1990-2009. Black Sea surface velocity fields for the years 2001 to 2003 were obtained for particle tracking from this hindcast simulation, which was set up and validated for the Black Sea in the framework of the European FP7 project OPEC (OPerational Ecology.Ecosystem forecast products to enhance marine GMES applications) (Allen *et al.,* 2013).

In each simulation Lagrangian drifters were released at 3km intervals in surface circulation fields at 10m depth (total of 45200 drifters per simulation) and moved individually at 1 hour intervals according to locally interpolated current velocity. This choice is representing the surface mixed layer in which larvae are assumed to be homogeneously distributed. Neglecting vertical movements is a reasonable assumption here because most particles remain in the selected layer over short time-scales (≤ 2 months) since horizontal velocities are several orders of magnitude higher than vertical ones (d'Ovidio *et al.,* 2004).

Pelagic Larvae Duration

In this study it is assumed that larval dispersal is dependent on different life traits common to all pelagic larvae: i) duration of larvae in the surface water, also refereed to as pelagic larval duration (PLD), ii) the timing of spawning and iii) the oceanic circulation. Spawning times and PDL are chosen to resemble pelagic larval species of importance in the Black Sea (Table 1).

Table 1: Important commercial fish species with pelagic larval stages in the Black Sea

Species	**Spawning Time**	**Spawning Area**	**PLD**	**Reference**
Anchovy *(Engraulis encrasicolus ponticus)*	June-August	North-western shelf and open water > 20°C	~36 days	Niermann *et al.,* 1994; Lisovenko and Adrianov, 1996; Sorokin, 2002; Dulcic, 1997
Sprat *(Sprattus sprattus)*	autumn-spring	Inshore areas of Black Sea until ~100 km offshore, river deltas	~70 days	Ojaveer, 1981; Houde, 1989; Ivanov and Beverton, 1985
Horse mackerel *(Trachurus mediterraneus ponticus)*	summer	Coastal areas	~25 days	Satilmis *et al.,* 2003, 2014
Red mullet *(Mullus barbatus ponticus)*	Summer (after May)	North-western shelf and off Kerch Strait	28-35 days	Satilmis *et al.,* 2003; Macpherson and Raventós, 2006; Galarza *et al.,* 2009b FISHreport 2015
Bluefish *(Pomatomus saltatrix)*	Spring - summer	Coastal regions (Turkish, Ukrainian, Bulgarian coasts)	18-25 days	Satilmis *et al.,* 2003; 2014; Ceyhan *et al.,* 2007; Gordina and Klimova, 1996; Hare & Cowen, 1997
Turbot *(Scophthalmus maeoticus)*:	Spring - summer		29-39 days	Satlimis *et al.,* 2014; Haynes *et al.,* 2007

To account for the above listed species of importance we investigate winter, spring and summer spawning times (1st of January, 1st of April, and 1st of July) as well as three different PLD times (30, 45 and 60 days) for the years 2001 to 2003 which are ecologically meaningful modeling choices for a number of Black Sea organisms. The specific years 2001 to 2003 were chosen after analysis of satellite data of the past two decades, which were very different in terms of temperature and surface circulation (Fach, 2014) and hence suitable to assess the influence of environmental conditions on this dispersal. 2001 was chosen because it was an anomalously warm year, compared to other years of the 1990s and 2000s, while 2003 was exceptionally cool in comparison (McQuatters-Gollop *et al.,* 2008). Hence, three consecutive years represented a wide variety of environmental conditions in the Black Sea.

For the purpose of this theoretical modeling study, the Black Sea was divided into 15 regions composed of 11 coastal regions with depths less than 1700m and four open ocean regions (Figure. 1). The north-western shelf and other coastal regions such as off Kerch Strait and the Turkish coast are generally accepted spawning regions of many Black Sea fishes such as anchovy, sprat, red mullet and other fish species listed in Table 1 (Einarson and Gürtürk, 1960; Ivanov and Beverton, 1985; Niermann *et al.,* 1994, STECF Report, 2015). However, observations also show that pelagic eggs and larvae are found in open water areas of most of the Black Sea as well, such as those of anchovy (Einarson and Gürtürk, 1960; Niermann *et al.,* 1994). For each simulation with changing life traits spawning time/year/PLD, 45200 drifters were tracked in the Black Sea.

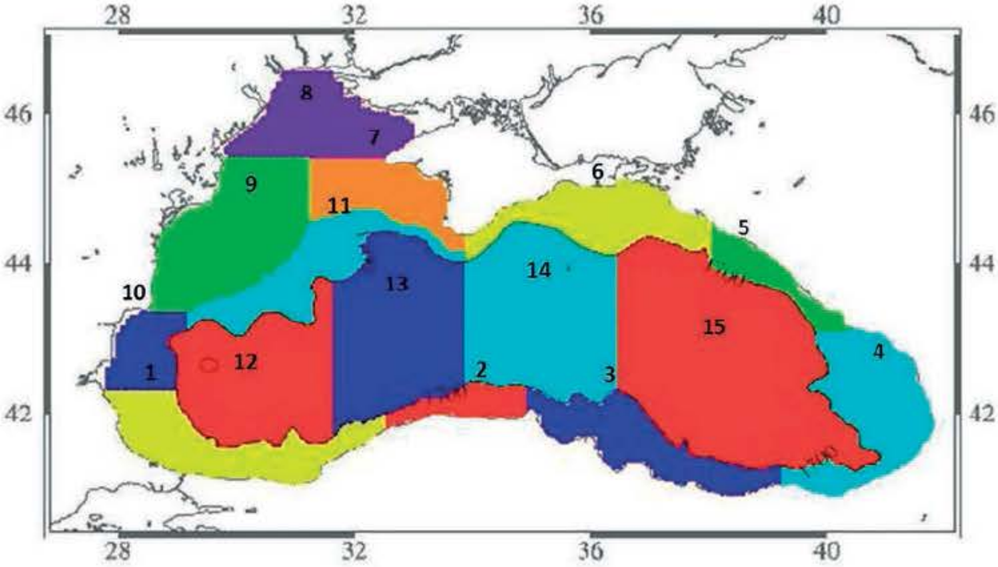


Figure 1: Color-coded release areas for modelled pelagic larvae in the entire Black Sea (total of 45200). The thin black line marks the 1700m isobaths.

RESULTS

Circulation model validation and skill assessment

The hindcast run of the circulation model output of temperature, salinity and the density derived variables, potential energy anomaly and mixed layer depth were validated using a database that was collated using data from cruises performed by the Institute of Marine Sciences of the Middle East Technical University (IMS-METU) as well as other cruises whose data are present within the pan-European infrastructure SeaDataNet. Both, observations and model results were monthly averaged and statistical metrics were computed by spatially interpolating model fields onto observations. Model validation of temperature over the entire basin using 191551 and salinity using 192982 data show that the model has a high degree of skill in reproducing both temperature and salinity observations as seen in the respective Taylor diagrams (Figure 2&3, left). Model performance indices indicate a high reliability (1.09 for temperature and 1.01 for salinity). The model shows a lower standard deviation than observations for both temperature and salinity but the correlation coefficients are high (0.904 for temperature and 0.88 for salinity). The unbiased RMSD is 2.1 for temperature and 0.66 for salinity. The target diagrams (Figure 5, 3 & 4, right) show that the normalized model bias is low and negative for temperature as well as salinity, with a normalized total RMSD of 0.45 and 0.52, respectively.

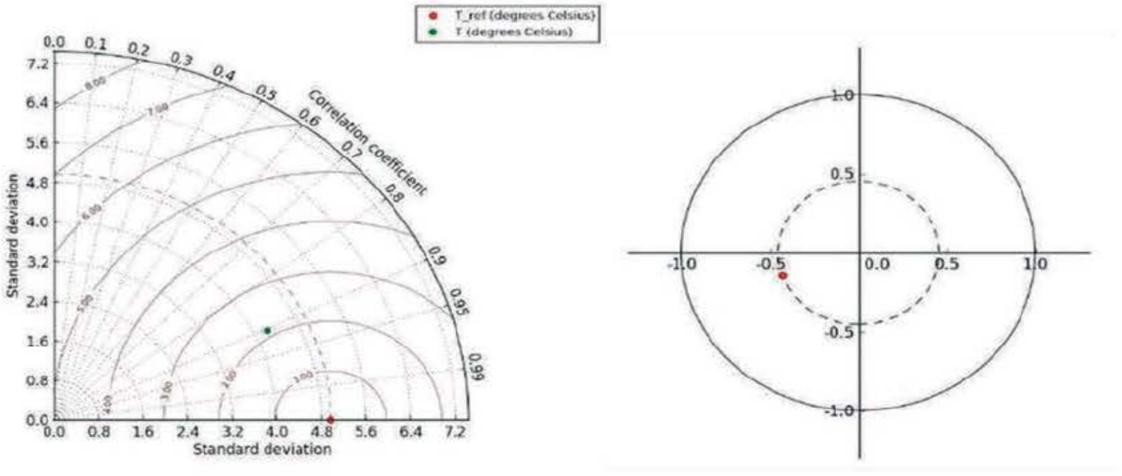


Figure 2: Point to point validation of the hindcast temperature on the entire domain vs. the in situ Black Sea database (N=191551). On the right the Taylor diagram, on the left the target diagram.

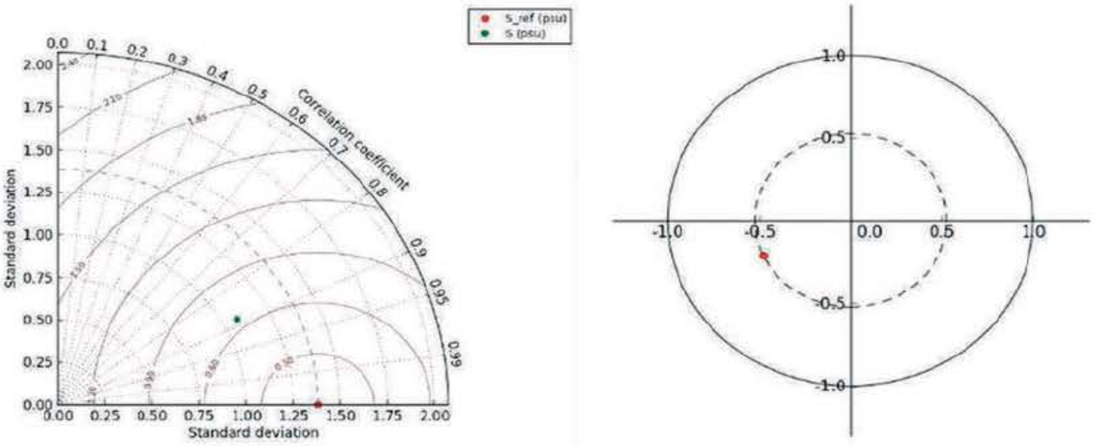


Figure 3: Point to point validation of the hindcast salinity on the entire domain vs. the in situ Black Sea database (N= 192982). On the right the Taylor diagram, on the left the target diagram.

The model performs slightly less well with respect to mixed layer depth (MLD) and potential energy anomaly (PEA) with the reliability index climbing to 1.44 and 1.56, respectively. MLD provided by the model has a lower standard deviation than observations, hence does not reproduce the observed variability. The correlation coefficient is 0.58 and the RMSD of the mixed layer depth lies at 12% of the natural variability of this parameter (Figure 5). The Target diagram shows that there is small positive bias with a normalized total RMSD of 0.81.

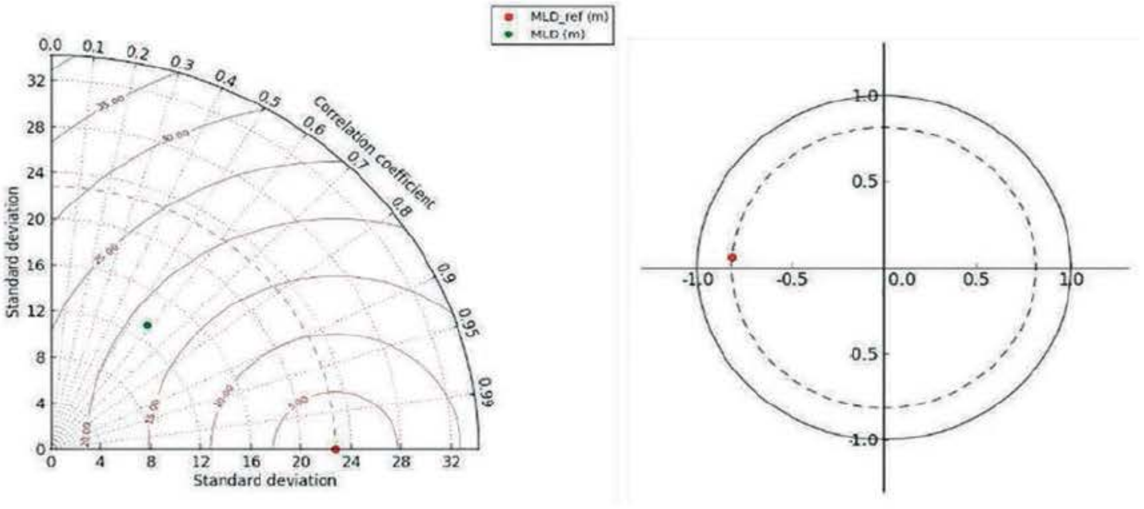
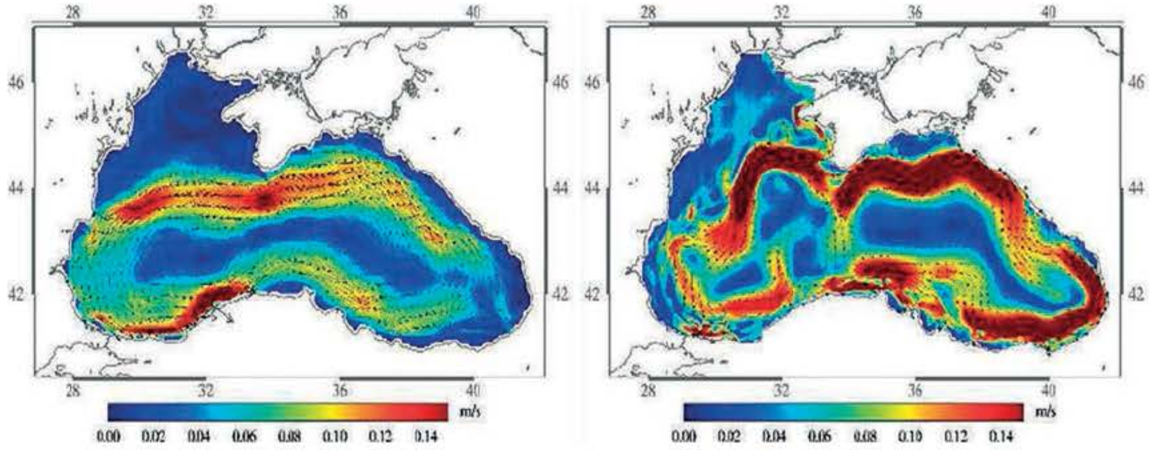


Figure 4: Point-to-point validation of the hindcast mixed layer depth on the entire domain vs. the in situ Black Sea database (N= 3625). On the right the Taylor diagram, on the left the target diagram.

In addition to above validation the ability of the circulation model to reproduce the general circulation patterns of the Black Sea, as well as the observed current speeds is of particular interest to this study. For this purpose, the 20-year mean surface circulation (1990-2010) of the model (Figure 5b) is compared to the mean current velocities computed from sea-level height fields extracted from AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) using the geostrophic approximation (Figure 5a). For details on the data and this calculation of geostrophic fields, please refer to Fach (1914).



(a) (b)

Figure 5: Mean 20-year surface velocity field (1990-2010) obtained from a) AVISO satellite data and b) the circulation model used in this study.

The model does capture the general circulation with a predominant cyclonic Rim Current well; simulated current speeds are of the same order of magnitude (Figure. 5). The modeled currents show higher variability of the Rim Current at Crimea, where the current shows stronger southward flow than the geostrophic currents, and in the western basin. In addition, the currents off Sinop at the Turkish coast and in the Batumi region are stronger than the mean flow field which should be kept in mind when evaluating connectivity results. However, it should also be noted that calculation of geostrophic flow from satellite data is only a rough approximation of the general surface circulation as it lacks representation of turbulent flow.

Variability in distribution patterns

Larval distribution is controlled by the general circulation and local circulation patterns at different scales and at different release times. As expected, the general circulation with the strong Rim Current as the main driver structures the distribution pattern of larvae leaving areas void of particles in its wake (Figure. 6). Local features such as the river plume of the Dnieper/Southern Bug rivers emptying into the Dnieper-Bug estuary and inflow from the Azov Sea through Kerch Strait (Figure. 6), as well as the Bosporus, the biggest river emptying into the Black Sea play a large role in advecting larvae. The Bosporus plume is not very visible in the July distributions because its outflow peaks earlier in spring and is hence more pronounced in the January (Figure. 6, left column) and April simulations. An accumulation of drifters at the western coast can be observed in the July simulations, and to a lesser extent in April simulations.

There are marked differences in the effect of river inflow between seasons and years (Figure. 6 rows vs columns). Interestingly, the north-western shelf area (shallower than 200m depth), which is a spawning ground for all of the fish species of interest in this study, is subject to strong variability in dispersal. In January, when sprat is likely to spawn on the shelf (STECF report, 2015) there is a tendency for particles to be advected off shelf (Figure. 6, left column), especially in 2002 and 2003, while in April, when Turbot and Bluefish are likely to spawn, much more retention on the shelf is seen, with the river plumes of both Danube and Dnieper/Southern Bug concentrating particles on the center of the shelf (Figure. 6, center column). In July, when anchovy and red mullet are likely to spawn, there is an accumulation of particles on the western coast of the northwestern shelf. The Azov Sea outflow through Kerch strait advects particles away from the coast at all times (Figure. 6), but this effect is most pronounced in July and least in January. In the July simulations an accumulation of particles along the western coast of the Black Sea is seen. These patterns do not change much for simulations with extended PLD's (not shown).

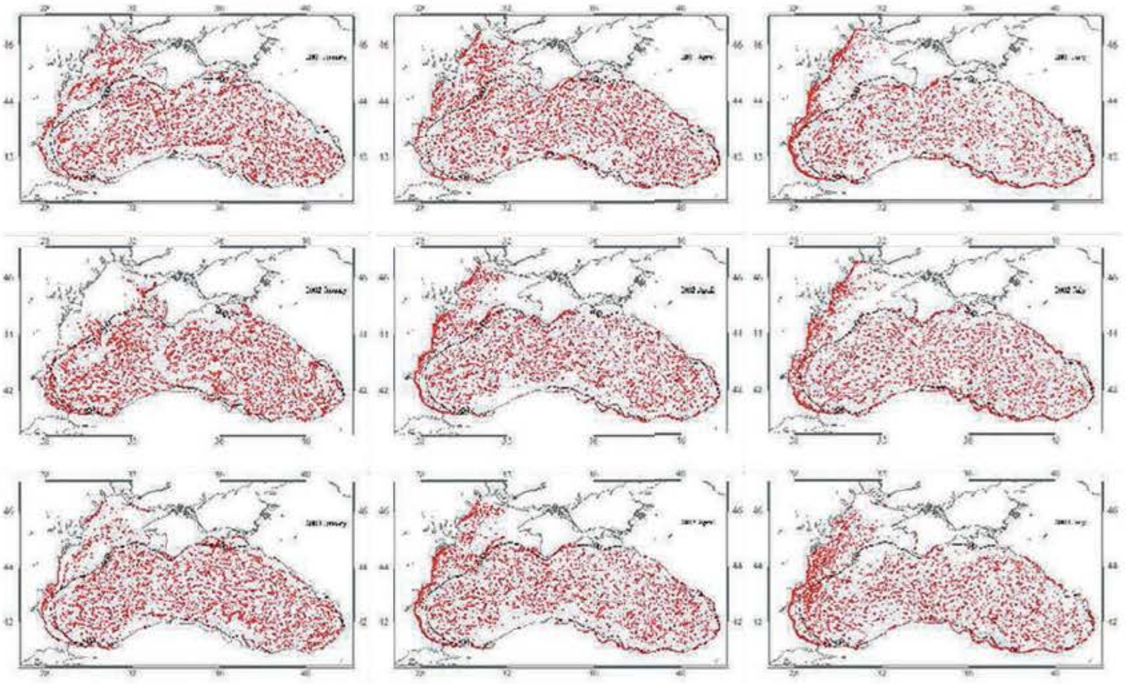


Figure 6: Seasonal and interannual particle distributions after 45 days of advection released on the 1th of January, April and July (1st to 3rd column) in each of the years 2001, 2002, and 2003 (1st to 3rd row).

Black Sea Connectivity

To summarize the impact of hydrodynamic processes on the dispersal of pelagic larvae shown in the section above and how these processes vary from year to year, model results were aggregated in geographic terms to help avoid too much focus on small-scale patterns that may be less reliable. Therefore, the dispersal of pelagic larvae was depicted as a measure of connectivity between all geographic regions and calculated as the percentage of particles that left from one area (source) and were transported to another area (sink) at the end of 45-day simulations, PLD = 45 days (Figure. 7). Coastal areas 1-6 showed generally higher retention rates than the regions 7-11 located in the northwestern shelf regions except in January and April 2003. All open ocean areas showed high dispersal in all months and years (Figure. 8) which was expected. Of the coastal regions, 1, 3, 6, and 8 had relatively high retention rates of between 40-80% in most simulations, with region 8 on the northwestern shelf having consistently high (>80%) rates of retention in the same area, except for January and July 2003 (Figure. 7). This is to be expected due to its location and current patterns in this region. Area 7 (off Crimea) showed very low to 0 retention at times, and virtual larvae left area 7 to be transported downstream onto the northwestern shelf (2003, Figure.7) Area 10 was connected to area 1 downstream. Open ocean regions however showed a high rate of dispersal and continuous inflow from coastal regions, mainly regions 2-4.

Connectivity matrices reveal that the lower northwestern shelf (area 9) is connected to the region on the southwestern shelf off the Bosphorus (area 1) with 22-40% of the virtual larvae reaching there within 45 days over the different years (Figure. 7). At the same time, the southern coast regions are more isolated that the northern Black Sea regions. In the cold year 2003 the effect of higher dispersal rates in almost all regions was found in simulations starting in January and April.

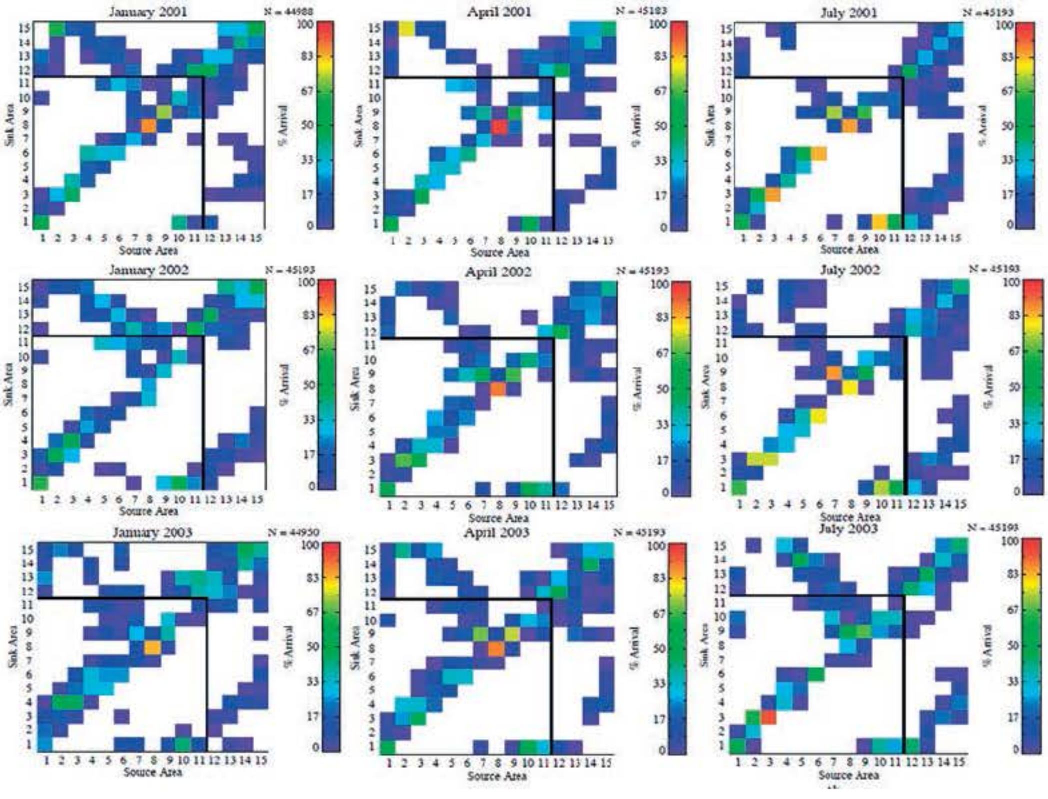


Figure 7: Connectivity matrices for modelled pelagic larvae released on the 1st of January, April and July (column) in each of the years 2001, 2002, and 2003 (row) with a PLD of 45 days. Matrices indicate the probability (%) for larvae originating from a source area (x-axis) to be transported to a sink area (y-axis)

estimated from individual 30-day trajectories. A thick black line separates shelf regions from open ocean regions > 1700m (areas 12-15).

Different Larval Stage Durations

Considering different pelagic larval durations of short (30 days) and long (60 days) it becomes obvious that shorter PLD means also higher retention probability of pelagic larvae in the source region (Figure. 8 A-C) for the case of July release. At 30 day PLD it is seen that the regions 1-6 show higher retention rates than the northwestern shelf regions. Again most dispersal is seen in open ocean regions.

High PLD of 60 days increases connectivity especially of regions 5, 6, and 7 to region 1 off the Bosporus and Igneda as well as region 10. In addition, shelf regions 9-11 do connect to these two regions.

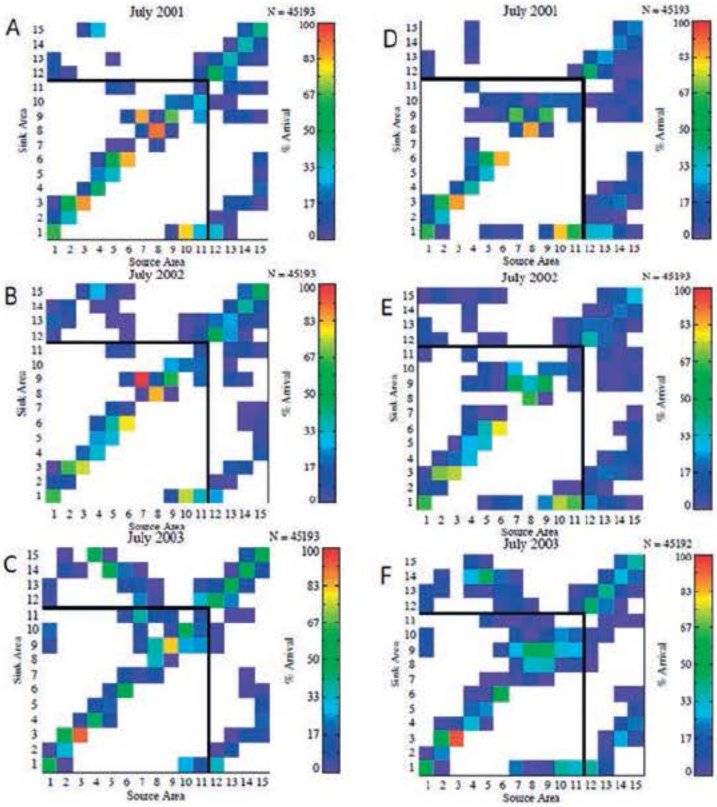


Figure 8: Connectivity matrices for modelled pelagic larvae released on the 1th of July of the years A) 2001, B) 2002, and C) 2003 with a PLD of 30 days and released on the 1st of July of the years D) 2001, E) 2002, and F) 2003 with a PLD of 60 days. Matrices indicate the probability (%) for larvae originating from a source area (x-axis) to be transported to a sink area (y-axis) estimated from individual 30-day trajectories. Thick black line separates shelf regions from open ocean regions > 1700m (areas 12-15).

DISCUSSION

Particle tracking simulations considering the entire Black Sea showed that the northern part on the northwestern shelf has continuously very high retention rates (> 80%) inside the area, while the Crimea peninsula region often had no retention whatsoever but rather showed displacement onto the northwestern shelf from there. In addition, the southern Black Sea coast regions were more isolated than the northern regions. Local features such as the river plume of the Dnieper/Southern Bug rivers emptying into the Dnieper-Bug estuary and the Bosporus plume on the north-western shelf play a large role in advecting larvae off the north-western shelf area, though this is seasonally dependent and variable from year to year. The water inflow through

Kerch Strait however, is a constant source of larvae displacement and may be one factor influencing fish migration in the region.

Above analysis can be a valuable tool when assessing the feasibility of where to establish Marine Protected Areas (MPAs). MPAs form a key element of the ecosystem-based approach to managing and safeguarding the Black Sea marine environment, including improving the sustainability of fisheries. For the establishment of a network of MPAs in the Black Sea this study elucidated that connectivity in the northern

Black Sea (except the north of the NW shelf, region 8) is higher and possibly MPAs can be spaced further apart than along the southern coast, where connectivity is considerably less. This is especially important to consider for species with a short PLD.

As Oztürk *et al.* (2013) pointed out several MPAs have been designated in the Black Sea riparian countries, however there is at present no MPA in the Turkish coast, which is spanning 1400km. Öztürk *et al.* (in review) used the above detailed modelling approach together with observational data to propose an optimal set of five MPA's to be established along the Turkish coast of the Black Sea.

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Vectors of introduction and pathways of dispersal of alien decapod species in Black, Azov, Caspian and Baltic seas

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ABSTRACT

In this paper we compare different routes and means of alien species penetration into the Black, Azov, Caspian and Baltic seas and compare them with the same alien species in the Mediterranean Sea. Main vectors of introduction are through shipping, although for the majority of species this is hard to confirm, especially for species found only once or rarely. Further dispersal of alien species in new territories depends on the biology of the species and environmental factors of the water body. In some cases species continue to disperse through a secondary shipping vector which often leads to a patchy distribution along the coasts. In other cases, such as Sea of Azov invasion by *Rhithropanopeus harrisii*, the dispersion is through natural migration of adults and larval drift, which leads to fast and even spreading of the species.

INTRODUCTION

Alien species constitute a well-known and recognized problem across the world and different biotopes (MEA, 2005; Grosholz, 2002; Perrings, 2002; Sala *et al.,* 2000; Wallentinus and Nyberg, 2007; Molnar *et al.,* 2008; Vilà *et al.,* 2010; EU, 2008). Marine invasive species have both negative and positive impacts on ecosystem services such as food provision and ocean nourishment, recreation and tourism etc (Sakai *et al.,* 2001; Schlaepfer *et al.,* 2005, 2012; Vilà *et al.,* 2010; Simberloff *et al.,* 2013; Katsanevakis Stylianos *et al.,* 2014). The debate is still open on the subject of impact and reasons to control certain economically important invaders, such as *Paralithodes camtschaticus* in the Barents Sea (Britayev *et al.,* 2010; Jørgensen and Spiridonov, 2013; Pereladov *et al.,* 2013), although it is generally assumed that new introductions should be prevented and further spread of already established species controlled (CBD, 2000).

The spread of non-indigenous species in marine environments is hard to observe and control due to low accessibility of the medium. Water dwelling species have no political and clear cut physical boundaries that can restrict their spread. Different life histories may result in different restriction factors.

Crustaceans are one of the most successful groups of invasive species and decapods are one of the main reasons (Galil *et al.,* 2011). They have pelagic larvae that can be transported via ballast water and currents, as well as adult forms that can hitch a ride on hull fouling. This makes this group one of the most successful invaders along with mollusks and fish (Katsanevakis *et al.,* 2013a).

A new alien species has to first reach the new territory through some vector, and once the species has made the journey to the new territory it goes through stages of establishing its population and spreading out further (Vermeij, 1996; Kolar and Lodge, 2001; Sakai *et al.,* 2001). It is essential to prevent the newcomer from reaching its destination through control of the vectors, for example ballast water treatment (Nunes *et al.,* 2014). Unfortunately very often this proves impossible or not enough. Further, it is essential to identify and monitor invasive hotspots, such as ports and eradicate or control alien species population in these places at low levels if possible (Thresher and Kuris, 2004; Vermeij, 1996; Nunes *et al.,* 2014). This is also very hard to do in aquatic environments, thus it is essential to understand further routes of alien species migration from these hotspots. These routes may be very different depending on the species in question and the water body where they have appeared (Molnar *et al.,* 2008; Katsanevakis *et al.,* 2013b; Galil *et al.,* 2014).

There is a substantial amount of published information on the presence, ecology and impact of alien species in European seas, especially in the Mediterranean. Most of these sources lack information about Russian waters due to low research effort and the fact that many of these projects concern EU countries. Nevertheless, political boundaries have no power over the migration of marine species, thus it is essential to have a better understanding of a water body as a whole, without political subdivision.

In this paper we will asses and compare different routes of dispersal of decapod species in Baltic, Mediterranean, Black, Azov and Caspian seas, using literature data and personal observations.

This work is a compilation of literature review and personal observations of authors throughout their research of alien Decapod species in the Black, Azov, Caspian, Baltic and Mediterranean seas in the past five years.

PHYSICAL DESCRIPTION OF THE SEAS

Mediterranean Sea

The Mediterranean Sea is a large enclosed oligotrophic basin. Its average depth is 1460 m, (maximum 5267 m), average surface temperatures are 14–16°C in winter and about 20–26°C in summer; salinity reaches up to 38‰ (DEVOTES, 2014).

Black Sea

The Black Sea is a eutrophic basin that is connected only to the Mediterranean and Azov Seas through narrow straits with a maximum depth of 2258 m, and average salinity 18‰ (maximum 22‰). Hydrogen sulphide deposits below 150 m restrict almost all benthic life forms to a narrow band around the coast. Temperatures can exceed 25°C in summer and down to 6-8°C in winter (-0,5 to -1 °C in shallow areas) (Zaitsev *et al.,* 2002; Dobrovolski and Zalogin, 1982).

Sea of Azov

The Sea of Azov is very small and shallow (maximum 14 m and an average of 7 m) water body with low salinity of approximately 11‰ (Lagutov, 2012; Borisov and Kapitonov, 1973). In winter water temperatures can be as low as +1 to -3 °C; summer temperatures can reach very high levels due to shallowness of the sea up to 25°C (or even 32 °C in shallows and bays) Dobrovolski and Zalogin, 1982).

Caspian Sea

The Caspian Sea is a completely enclosed water basin that stretches over several climatic belts: from continental in the north to subtropical and arid in the south. Due to this the water temperatures are also very different along this gradient: in winter from 0 °C in the north to +10 °C in the south; and in summer from 22-24 °C in the north to 28 °C in the south. In addition to the climate gradient, there is a higher freshwater discharge in the north of the sea as well as vast shallow area that decreases water salinity to 0.2—0.3‰ and it increases towards southern regions up to 13‰ (Dobrovolski and Zalogin, 1982).

Baltic Sea

The Baltic Sea is a shallow (mean depth is 60 m), narrow stretched out water basin with eutrophic water basin that is connected to the North Sea by a narrow and shallow strait. Maximum depth of 470 m with very uneven water temperatures and salinity gradient across the basin: from freezing to 0.7 - 2 °C in winter and 15-17 °C in summer (can exceed 25 °); salinity can vary from almost 0‰ in semi enclosed bays and change from 5 to 17‰ from east to west of the basin (Dobrovolski and Zalogin, 1982).

VECTORS OF INTRODUCTION

Number and list of alien Decapoda species in the Baltic, Black, Azov and Caspian seas are summarized in Tables 1 and 2; only species found in other seas are listed for the Mediterranean Sea. The staggering difference in the number of alien species between the Mediterranean Sea and the other seas under study is explained by differences in salinity, temperature, depth and most importantly a large and important vector of introduction through the Suez canal that is absent in other seas (Por, 1978; Galil, 2006; Rilov and Galil, 2009; Katsanevakis *et al.,* 2013b). A few of species sighted in the Black Sea only once are present in Mediterranean and have been most probably transported through Bosphorus channel: *Dispanopeus sayi, Hemigrapsus sanguineus, Palaemon macrodactylus*. Species seem to mainly enter the Black Sea, and rarely from Black to the Mediterranean. Since *Paleamon longirostris* and *Penaeus semisulcatus* have not been seen in the Mediterranean Sea, their vector of introduction is unknown and their presence is questionable. *Callinectes sapidus* has been first found in the Mediterranean Sea in 1949 (Giordani Soika, 1951), and it has been caught in the Black/Azov basin since the 1960s (Spiridonov and Zalota, in press). This crab could have been independently introduced to the Black/Azov sea basin as well as through secondary vectors of introduction from the established populations in the Mediterranean Sea.

Black and Azov sea basin is a recipient as well as a source of alien species. *Palaemon adspersus*, and *P. elegans*, native to Black/Azov seabasin were introduced intentionally to the Caspian Sea (Shorygin and Karpevich, 1948; Behning, 1936). *P. elegans* has also been introduced to the Baltic Sea, possibly through a shipping vector (Grabowsky *et al.,* 2005; Burukovsky, 2012; Berezina and Petryashov, 2012; Katajisto *et al.,* 2013).

Shipping (ballast waters and hull fouling) is considered to be the main vector of introduction in European seas and globally (Katsanevakis *et al.,* 2013b; Molnar *et al.,* 2008). Although most alien decapod species might have been transported via this vector, it is often very hard to confirm, thus most of the casual species have an unknown vector of introduction.

Table 1. Number of alien decapod species in the Mediterranean, Black, Azov Baltic and Caspian seas sorted by their origin.

Seas	No of alien Decapods	Origin of introduction					
		Black/Azov/ Med.	West Atlantic	East Atlantic	Pacific	Ido-Pacific	Indian/Red Sea
Med.	80		8	9	4	44	15
Black	8		3		4	1	
Azov	3		2		1		
Baltic	4		2		1	1	
Caspian	3	2	1				

Table 2. Alien Decapoda in Caspian, Azov, Black and Baltic Seas. Mediterranean alien species only present in these seas are shown. Adopted and modified from Spiridonov & Zalota (in press).

Taxa, species	Origin	Vector	Sea				
			Casp.	Azov	Black	Baltic	Med.
Suborder Dendrobranchiata							
Penaeus semisulcatus	Indo-Pacific	Unknown			Cas		
Suborder Pleocyemata, infraorder Caridea, family Palaemonidae, genus *Palaemon*							
Palaemon adspersus	Azov/Black Sea basin	Hitchhiker	Est				
P. elegans	Azov/Black/Med. Basin	Hitchhiker, Shipping	Est (HI)			Est (S?)	
P. longirostris	North West Pacific	Unknown			Cas		
P. macrodactylus	North West Pacific	Unknown			Cas		Est
Infraorder Brachyura, family Portunidae, Oregonidae, Panopeidae, Varunidae							
Callinectes sapidus	East North Atlantic	Dispersion		Mult	Mult	Cas	Est
Dispanopeus sayi	East North Atlantic	Unknown			Cas		Est
Eriocheirs sinensis	North West Pacific	Shipping	Mult	Mult	Mult	Mult	Cas
Hemigrapsus sanguineus	North West Pacific	Unknown			Cas		Cas
Rhithropanopeus harrisii	East North Atlantic	Shipping/ Dispersion	Est	Est	Est	Est	Est

Legend: Vector: Dispersion - Range expansion from initial introduction area, Hitchhiker - with intentional introduction of other species, Shipping –ballast waters and hull fouling; Status in the sea: Cas – Alien species, single or very rare sighting (in the sense of CIESM, http://www.ciesm.org/online/atlas/index.htm), Mult – Alien species, multiple sightings, status unknown, Est – Naturalized/Established alien species. Compiled from literature data, collections materials and results of field studies performed by authors. (Cuesta *et al.,* 2014; Zenetros *et al.,* 2010; Leppäkoski and Olenin, 2000)

DISPERSAL PATTERNS IN THE AREA OF INTRODUCTION

Following their successful introduction and naturalization in the initial area of introduction, such as ports, species tend to disperse further out within the basin and neighboring water bodies that meet their habitat requirements. This dispersal may be assisted through further shipping vectors, often via smaller local boats that travel short distances along the coast. Such migration can often be the reason for spotted distribution of alien species in the region as well as local physical and environmental factors.

The Harris mud crab, *Rhithropanopeus harrisii* is an alien species established in all seas under study. The nature and history of its establishment and distribution in these seas can be used as a model to show different modes of dispersal under different or similar environmental conditions. The distribution of *R. harrisii* in European waters is shown in Figure. 1. Within the Mediterranean Sea, in general not suitable of its reproduction, this species is restricted to a few regions with low salinity, although the adult form can tolerate high temperatures and salinity (Smith, 1967; Normant and Gibowicz, 2008) which allow it to travel between estuary habitats with secondary shipping vectors. Similarly, its distribution is patchy in the Baltic Sea, where this species is restricted to narrow, estuarine habitats along the coast and in bays where the depth is small. This species has been found for the first time in 1874 in European waters in the Zuiderzee lagoon (Province of North Holland) in the Netherlands (Buitendijk and Holthuis, 1949). From there it has spread west and east, through the Kiel Canal into the Baltic Sea. From historical data its gradual patchy distribution eastwards within the Baltic Sea can be seen. It has been only recently found in Finland and Estonia (Kotta and Ojaveer, 2012; Fowler *et al.,* 2013). Its dispersal is still ongoing and may continue further. Based in molecular genetic studies (Projecto-Garcia *et al.,* 2010; Hegele-Dryva *et al.,* 2015) the population in the North and Baltic Sea are similar to the native population with the exception of one haplotype (A) that is not found in the native population. It is reasonable to suggest that further spread of *Rhithropanopeus harrisii* in the Baltic Sea is through slow migration of local population rather than new settlements from native populations.

A very different situation can be seen in the Sea of Azov, where the crab has most probably appeared around the Second World War, although it has only been found in 1948 (Mordukhay-Boltovskoy, 1952) and by the 1950s it has became a common species throughout the entire sea (Reznichenko, 1967). The speed and extent of the Harris mud crab dispersal suggest natural larvae and adult migration within this basin. Due to suitable environmental biotic factors as well as small depth of the sea, nothing restricted this species from occupying almost all habitats within the sea. A similar fast dispersal occurred in the Caspian Sea, after initial unintentional introduction in 1958 (Nebolsina, 1959), by the early 1960s it was found throughout the extensive shallows of the northern part of the sea (Reznichenko, 1967). In the Black Sea on the other hand it has both a patchy and extensive distribution. In the north-western part of the sea, along the Ukrainian and Romanian coast where there is a substantial fresh water discharge and extensive shallow area it is widespread. On the other hand a very narrow coastal shelf along the Russian coast restricts this species to a few bays, limans and river estuaries (Spiridonov and Zalota, in press, and references within). On the Turkish and Georgian coasts it has not yet been found, probably due to insufficient research effort in the river estuaries.

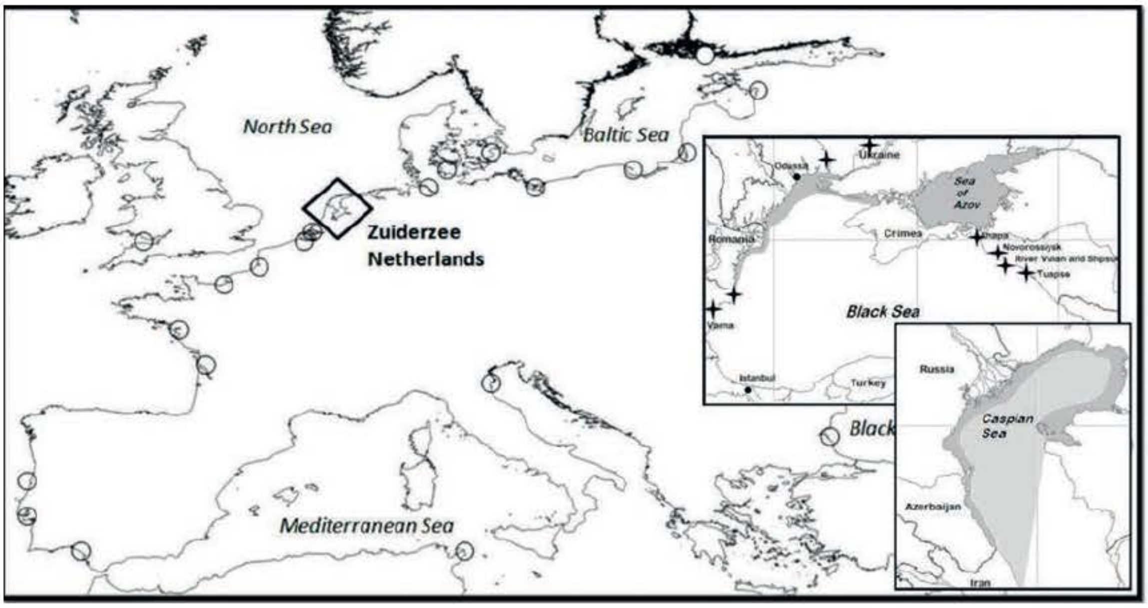

Figure 1. Distribution of *Rhithropanopeus harrisii* in European waters.

The Chinese mitten crab, *Eriocheir sinensis* is a special case of dispersal of an alien species in European waters, which involves catadromous migration. Europe has a vast inland waterways network that connects southern and northern sea through rivers and canals and creates an additional routs of species migration through via shipping active migration of adults or passive drift (Panov *et al.,* 2009). These routes are actively exploited by Chinese mitten crab which has established populations in Europe in the North Sea, but in the East Baltic, Black and Azov Russian waters there is no evidence of reproducing population (Spiridonov and Zalota in press and references within) although, it is one of the most widespread alien species in Eastern Europe (Figure. 2). These crabs are found deep in inland waters where they extend their range most probably by walking as they age together with possible transportation thru hull fouling on slow moving ships (Shakirova *et al.,* 2007).

Figure. 2. Records of Chinese mitten crab *Eriocheir sinensis* in Eastern Europe.

CONCLUSION

Overall it is clear that the same species can spread at very different rates and through different means within similar water bodies, restricted by different factors. Assuming that the biology of a potential invasive species would allow its naturalization in the Azov or Caspian and north-west Black seas, one can predict that similar fast and vast dispersal of the species will occur. On the other hand within the Baltic and Mediterranean seas, similar species may progress through slow patchy dispersal mode assisted by secondary vectors.

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Knowledge on migration routes and patterns as a prerequisite for good fisheries management

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When migration routes of marine species are debated, the subject of the interest is usually species in general or a species group of, very often, uncertain size related to some specific habitat or geographical area. On the other hand fisheries management is an integrated process which governs fisheries activities that are exploiting marine species, commercial as well as bycatch. In order to ensure the continued productivity of the resources, exploitation has to be sustainable. Accomplishment of desired fisheries objectives cannot be based on undefined and uncertain characteristics of a species group, so fisheries management is mainly based on "the stock concept". From a fisheries management point of view the most suitable definition of "stock unit" is probably the one provided by Gulland (1969; 1983) who, on operational criteria and practical grounds, proposed that a group of fish can be treated as a "stock" and managed as an independent unit if the results of assessment and the impact of management measures do not differ significantly from what they would be in the case of a truly independent stock.

Generally speaking, a "stock" is a subset of a species with similar growth and mortality parameters within a given geographical area and with negligible interbreeding with other stocks of the same species in adjacent areas (Maguire *et al.,* 2006). Furthermore, in practice, the application of the concept varies considerably depending on the knowledge available and acceptable complexity in management, so nowadays it is clear that the stock structure of many species is much more complex than is captured by stock definitions for management purposes. Consequently, of late stocks are being redefined on the basis of new information obtained by scientific research focused on different characteristics of the species or species group.

When the assessment is based on FAO statistics, the term "stock" is applied to species-area combinations with the resolution of statistical areas used for reporting capture production to the FAO Statistical Database (Maguire *et al.,* 2006). Due to the desire to describe more precisely a given stock, new terms have been introduced, such as "highly migratory stock", "high seas stock", "straddling stock" etc. (Figure 1). Highly migratory stocks are defined as those composed of highly migratory species, e.g. species having a capability of migrating relatively long distances, and stocks of these species are likely to occur both within EEZs (Exclusive Economic Zone) and on the high seas. The exploitation of high seas stocks is relatively recent and less is known about their biology and stock structure than is the case for the more traditional fishery resources on the continental shelves which have been exploited and studied for much longer. Individual aggregations of those high seas stocks may belong to isolated stocks, individual stocks with some mixing with other stocks, or a larger stock occupying an area much larger than that covered by individual aggregations (Maguire *et al.,* 2006). FAO (1994) used the term "purely high seas stocks" for stocks that are not found within EEZs. However, specifying that fish stocks not found within EEZs are "purely" or "entirely" high seas stocks seems redundant and could even be misleading since all the other fish stocks that may occur in the high seas are already described either as "straddling stocks", if occurring both within the EEZs and in the high seas, or as "highly migratory stocks", if composed of species listed in Annex 1 of UNCLOS (The United Nations Convention on the Law of the Sea), independently on whether they occur within the EEZs and/or in the high seas (it is noted that most if not all highly migratory stocks will represent a subtype of "straddling stock" subject to slightly different arrangements from those applicable to the other living marine resources of the EEZ as addressed in Part V of UNCLOS). The concept of straddling fish stock can cover a continuum from most of the fish being inside the areas of the EEZs under national jurisdiction to most of the fish being in an area beyond and adjacent to it, that is outside EEZs (in the high seas). No minimum portion outside or inside has been defined, but usage seems to indicate that as long as there is some directed fishing effort at catching the stock on either side of the EEZ line, it is considered to be straddling (Maguire *et al.,* 2006).

Although individuals of some species can travel of long distance, the term "migrations routes" of bony fish is mainly related to the groups/stocks. Grouping behavior is a widespread phenomenon in animal ecology and is thought to be an emerging property of the self-organization of individual organisms (Sumpter, 2010). Individuals are forming groups and benefit from several advantages, among which is a more efficient capacity in problem solving (Krause and Ruxton, 2002). Of particular interest is the ability of the group to make collective decisions but very often no obvious reason can be given to explain the social behavior of certain species, e.g. migrating from one area to another, except the fact that those groups are more efficient than single individuals in retrieving information from the environment (Berdahl *et al.,* 2013).

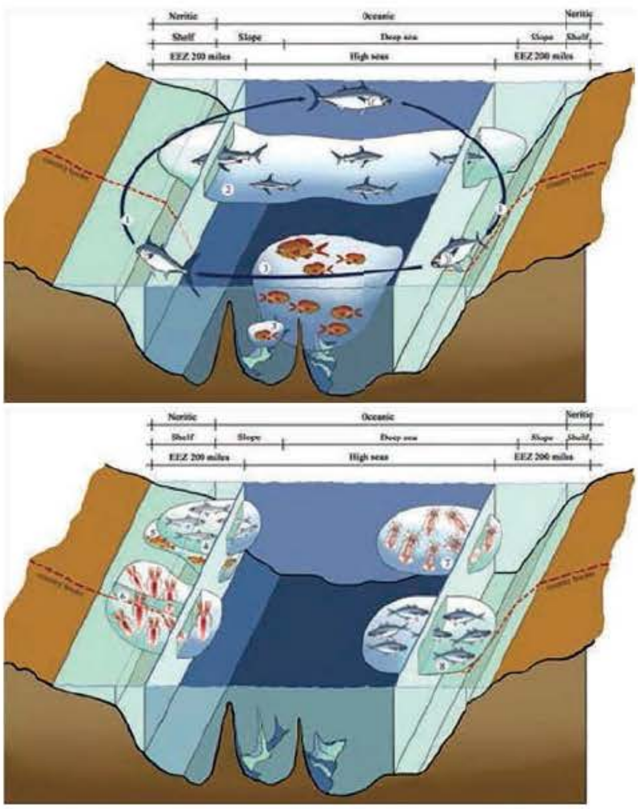

Figure 1. Types of stocks occurring partially or entirely in the high seas. Top panel: 1. highly migratory; 2. Straddling (extensive distribution); 3. High seas. Bottom panel: 4. pelagic straddling (mostly within EEZ); 5. Demersal straddling (mostly within EEZ); 6. Straddling (transboundary); 7. Straddling (mostly in high seas); 8. Straddling (evenly distributed); according to Maguire *et al.* (2006).

For groups on the move, such as fish schooling, it has been shown that information transfer and social interactions are important factors of group cohesion and can promote the ability of making consensus decisions. An example of such a collective decision-making problem is the structure of migration routes in some fish species. Migration between widely separated, but geographically stable locations of spawning and feeding sites raises several questions about how these animals manage to learn and remember the migration route between feeding and spawning sites. Where is the information on the path stored? How is it retrieved, shared and elaborated by a migrating group? De Luca *et al.* (2014) showed that abrupt changes in migratory patterns of animal groups can be caused by removal of knowledgeable individuals, e.g. by fisheries activities, from the group or by decreasing preference of the individuals towards a particular migratory destination. Fishing out informed individuals and their prey can exacerbate the loss of collective memory up to the point where a migratory pathway is suddenly interrupted. Authors assumed that each year young individuals join the group: among them a fraction are able to gather information and remember a migratory route, whereas the rest have a purely social behaviour. The "information-gatheringable" individuals behave as uninformed individuals, but learn a new migratory route during the first migration(s). If the group does not succeed in starting migration, or migrates towards a different location, the young "information-gatheringable" individuals will not learn the traditional migration route of the group and the social traditions of the group will not be transmitted to the new generations. The loss of collective memory in the group will then force the system to cross the critical line, and the migration towards the destination site will stop. The results of De Luca *et al.* (2014) are consistent with previous models suggesting that a small number of informed individuals can lead to large group migrations (Huse *et al.,* 2002). Consequently, poorly managed fisheries that is not bearing in mind an importance of knowledgeable individuals can diminish individual preference for a given migration site and break the already established migration process and consequently a reliability of proposed fishery management measures.

Breaking of a migration routes is not caused only by direct fisheries but also by indirect causes, through the prey-predator relationship. An example of a prey–predator collapse and subsequent abrupt disappearance of migratory route is provided by Atlantic bluefin tuna, *Thunnus thynnus*, and its main prey, the herring, *Clupea harengus*, in the Norwegian and the North Seas. During the 1950s to 1970s, both species were heavily exploited in these regions, resulting in the disappearance of both species. Since then, the herring populations in both regions have recovered to moderate to high levels, but bluefin tuna have been extremely rare during the 1980s to 2000s and apparently have not migrated back to these areas in large numbers since their disappearance several decades ago (ICCAT, 2012).

Moreover, during spring period, bluefin tuna perform long seasonal reproductive migrations between feeding areas in the Atlantic Ocean and spawning grounds, either in the Gulf of Mexico (western stock) or the Mediterranean Sea (eastern stock). Within the Mediterranean area a major hypothesis for a long time was that after spawning, Mediterranean bluefin tuna immediately initiate a trophic migration towards the Atlantic Ocean (De Metrio *et al.,* 2005). However, later findings were not consistent with that theory, e.g. Tudela *et al.* (2011) suggested that for some of the tuna associated to the Balearic Sea the Atlantic migration might either take place significantly later in the year or not happening at all in a given year. This is supported by another study (Fromentin, 2009) that suggested a higher residency time in the Mediterranean than expected. The tunas tagged in the south of France during Fromentin´s study were related to a possible foraging or overwintering area offshore the Gulf of Lions and one of them migrated to the central Mediterranean. Nevertheless, such new theory on tuna migration was again disputed as later results by Aranda *et al.* (2013) suggested that bluefin tuna following extended residency around the Balearic Islands crossed the Strait of Gibraltar heading for the North Atlantic. Discrepancies between the migratory tracks reconstructed from this and previous electronic tagging studies suggest that the bluefin tuna Mediterranean population may comprise distinct units exhibiting differing migratory behaviors. Some population subdivisions spawning in the central-eastern Mediterranean Sea and exhibiting resident behavior would intermingle with more mobile bluefin tuna spawning in the central-western Mediterranean. It would then be plausible that highly migrant subpopulations predominate over more resident ones in the westernmost Mediterranean area. According to Aranda *et al.* (2013) hypothesis, tagging surveys carried out at separate times in the western Mediterranean might target different reproductive units with differential migration patterns. Endless differences between results of different investigations are pointing that new data are required as reliable migratory routes and patterns of bluefin tuna are still unknown. One cannot conclude whether this is due to uncertainty of the data, or to unknown factors perhaps influencing/changing the migratory routes of bluefin tuna.

Another good example is the case of bonito, Sarda sarda, with spawning migrations in the Eastern Mediterranean thought to be well documented. According to the widely accepted hypothesis S. sarda overwinters in the Adriatic and Aegean seas and migrates through the Sea of Marmara to its spawning areas in the northern part of the Black Sea (Ivanov and Beverton, 1985). However, recent study where mitochondrial DNA D-loop gene sequencing was used to investigate genetic structure of 11 *S. sarda* populations from the Black Sea, Marmara, Aegean, Mediterranean Seas and Adriatic Sea showed that *S. sarda* was divided into three genetically different populations. The Black and Marmara Sea populations comprise one genetic unit, the Aegean and Mediterranean coast of Turkey populations constitute a genetically different second unit, while the Adriatic Sea population from Croatian coast is genetically different from these two units (Turan *et al.,* 2015), which is not in agreement with previous hypotheses.

A particular problem in the Mediterranean is a general lack of detailed information on exploited fish stocks, both commercial and bycatch (wanted and unwanted). Which raise an obvious: how to get reliable information on existing Mediterranean migration routes and patterns of migratory fishes in a situation where the possible sources of such information are so diverse from one area to another (more than 20 countries)?

Global warming is also causing the shifts and poleward migrations of many taxa that are now extending their biogeographical range (Perry *et al.,* 2005). This tendency is also observed in the Mediterranean Sea as some indigenous species, typically confined to the warmer parts of the Mediterranean, are currently colonizing the northern sectors. The increase of water temperature is also allowing the success of tropical non-indigenous/invasive species in the Mediterranean Sea, a phenomenon that has been called "tropicalization" (Bianchi and Morri, 2003; CIESM, 2008). Fish species are particularly sensitive to changes in water temperatures. Physiological processes caused by temperature changes directly alter behavior and trigger new movement and migratory patterns for these species. Other indirect effects of climate change, such as those related to the change of currents, could affect larval dispersal, retention and recruitment of fish species. However, a particular problem in determining migration routes and its consequences of tropical exotic species is the fact that migration patterns observed in one species can not be merely translated to another, even if it is a close relative. A typical example is a case of close relatives white grouper, *Epinephelus aeneus*, and orange-spotted grouper, *Epinephelus coioides*. Both species were observed for the very first time in the Adriatic in 1998. Since then, the white grouper has established a large population which is commercially exploited, while the orange-spotted grouper has not been recorded since.

Another problem is the validity of historic data that are considered reliable, thus used for creating different theories which are later confronted with new data, making it difficult to determine whether some changes actually happened or there is a case of former misinterpretation of the data. A noteworthy example is a case of the two Lessepsian herbivorous fishes *Siganus rivulatus* and *S. luridus* that were recorded for the first time in the Mediterranean Sea in 1924 and 1955, respectively. Since then, both species have established significant populations in the eastern basin and have spread westwards as far as Sicily and Tunisia (Rilov and Galil, 2009). The native herbivorous salema, *Sarpa salpa*, was relatively abundant, but nowadays, records of *S. salpa* from Lebanon are very scares and it has been suggested that the native species has been outcompeted by the Lessepsian invaders (Galil, 2007). Golani (2010) rejected this hypothesis as he considered that high abundance of *S.salpa* was formerly incorrectly reported due to misidentification with another common sparid *Boops boops*. Later, Kaligorou *et al.* (2012) considered that actually *S. salpa* was correctly identified. It is clear that knowledge on migration and causes of migrations is still scarce in the Mediterranean.

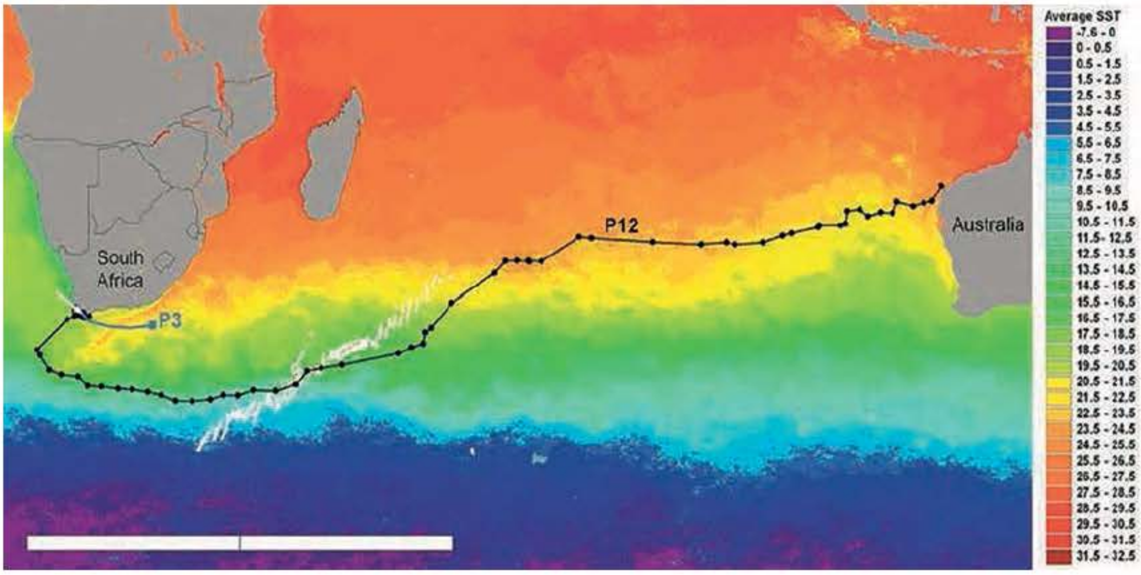

Figure 2. Transoceanic migration of a single female white shark, *Carcharodon carcharias* (according to Bonfil *et al.*, 2005).

As far as chondrichthyans are concerned, knowledge on their migration routes within the Mediterranean is extremely scarce or totally missing. A particular problem, especially within large sharks, which are usually highly migratory, is that those species, being key predators, have small populations where individuals are not grouping often, causing discrete and single migrations. For example, fidelity to an individually-specific distant location has been clearly demonstrated in a female white shark, *Carcharodon carcharias*, tagged in western South Africa, which completed a transoceanic migration circuit between Africa and Western Australia, extending over 20,000 km (Figure. 2). During the migration to Australia, the shark followed a remarkably straight course, which was reconstructed thanks to light-level data relayed by its pop-up transmitter. The shark was seen again at the original site 10 months after tagging, but unfortunately the path back to South Africa could not be tracked (Bonfil *et al.*, 2005).

In the Mediterranean, the distribution of chondrichthyans is not homogenous as many species have restricted range there. Available data spatial predicted patterns of species richness in the Mediterranean Sea, created on the AquaMaps model, calculating that the concentration of rays and sharks in coastal waters is high in central and western Mediterranean, but low in eastern areas (Coll *et al.*, 2010). On the other hand, behind establishing of CIESM Rare Sharks Program (Soldo *et al.*, 2016) was an hypothesis that such estimations reflect more a limited availability of the data from the eastern Mediterranean than a real situation. Data collected from CIESM RSP are currently supporting such hypothesis as most of the new and recent data on chondrichthyans are deriving from the eastern Mediterranean.

Knowing migration routes and patterns unfortunately will not reveal in which way marine fish manage to establish their position with respect to a given site during long trip away from it. A number of navigational mechanisms permitting such routines have been described in different animals, but not all of them can be reliably used by for explanation of movements taking place in the ocean. For a human eye, the open sea seems essentially featureless, being devoid of any signposts landmarks, or visual reference. Thus any navigational mechanism based on reliance on visual cues seems, therefore, unlikely. Yet, one cannot exclude that animals moving in the open sea may still refer some kind of signposts, perhaps of magnetic or olfactory nature, which would provide them with useful navigational information (Lushi, 2013).

Several different techniques are nowadays available to follow marine species in their long-distance movements and the results obtained have often revealed surprising patterns of migrations. Basin-wide oceanic movements are quite routinely recorded in various marine fish, but, unfortunately, experimental data are still scarce in the Mediterranean for many migratory fish. As field studies are expensive, fishermen's local knowledge of fish resources and migrations may be an important source of information, especially in the Mediterranean, where most data on fish biology, ecology, as well as exploitation are lacking. Data gathered from fishermen may provide inexpensive and prompt information, potentially applicable to fisheries management.

To conclude, it is obvious that fishery management should especially take account migration routes and patterns of managed stocks which are essential to acquire the necessary level of knowledge before exploitation proceeds too far. Such studies should be accompanied by others that will focus on the navigational mechanisms that are allowing migrations in order to comprehend the behavioral mechanisms underlying these migratory performances. Only such combined results will allow us to determine a more precise state of fish populations as well as a reliable prediction of migration changes caused by different factors that are impacting Mediterranean lately.

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