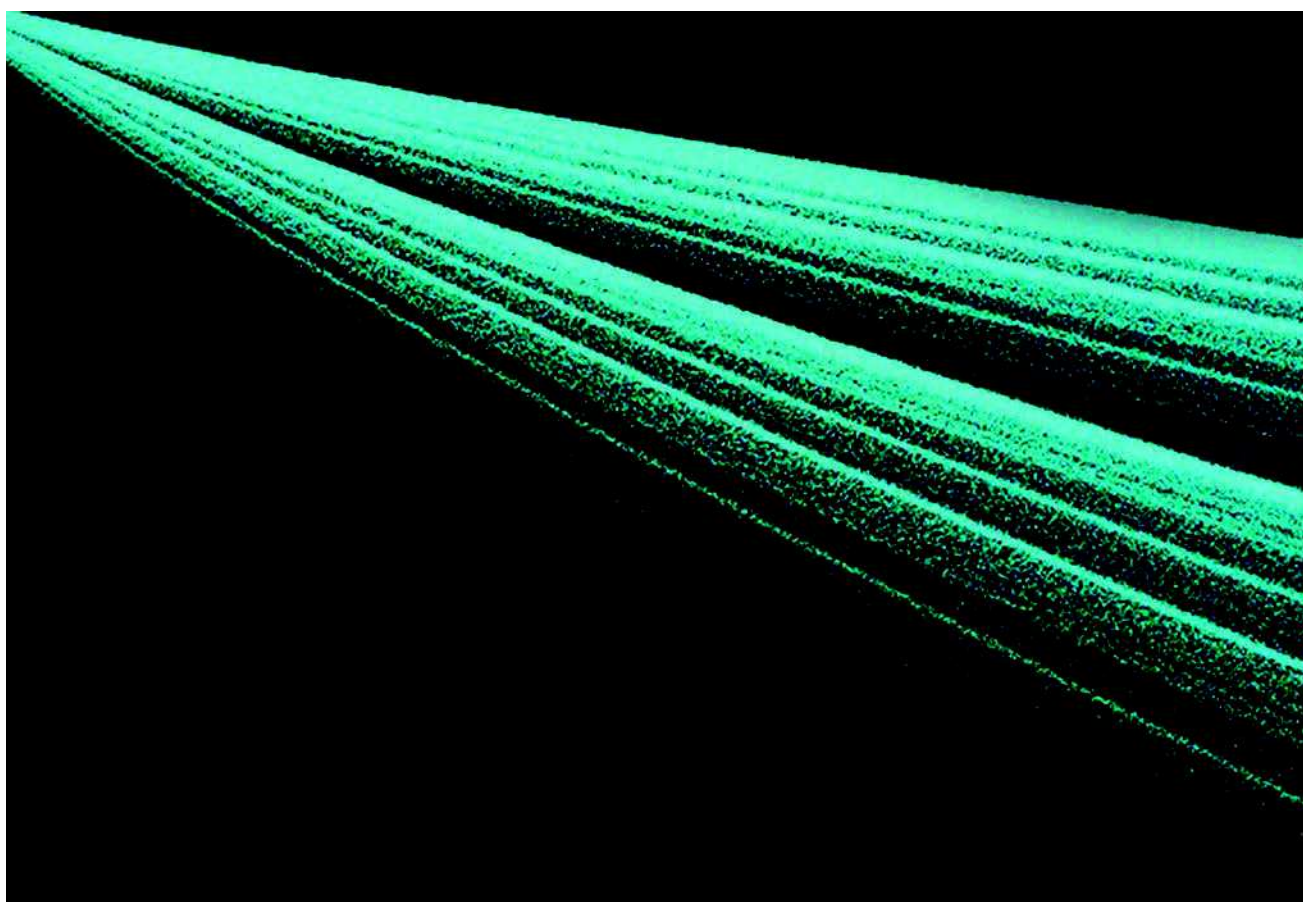


48

Marine connectivity – migration and larval dispersal

Sòller (Spain)
9 - 12 March 2016



C I E S M W o r k s h o p M o n o g r a p h s



Marine connectivity – migration and larval dispersal

Sòller, Spain, 9 - 12 March 2016

CIESM Workshop Monographs ◊ 48.

To be cited as:

CIESM 2016. Marine connectivity – migration and larval dispersal. CIESM Workshop Monograph n° 48 [F. Briand ed.], 172 p., CIESM Publisher, Monaco.

This collection offers a broad range of titles in the marine sciences, with a particular focus on emerging issues. The Monographs do not aim to present state-of-the-art reviews; they reflect the latest thinking of researchers gathered at CIESM invitation to assess existing knowledge, confront their hypotheses and perspectives, and to identify the most interesting paths for future action.

A collection founded and edited by Frédéric Briand.

CONTENTS

I – EXECUTIVE SUMMARY5

1. Introduction
2. The scale of marine connectivity
3. Hot research topics in marine connectivity
 - 3.1 Connectivity of highly migratory species
 - 3.2 Connectivity of habitat – forming species
 - 3.3 Connectivity of alien species
 - 3.4 Connectivity in the deep sea
 - 3.5 Connectivity of exploited species
 - 3.6 Collective behavior and individual adaptation in migratory routes
 - 3.7 Human impacts on marine connectivity
4. Applications of connectivity studies
 - 4.1 Conservation of large migratory species
 - 4.2 Design of Marine Protected Areas
5. The way forward

II – WORKSHOP COMMUNICATIONS

Multiple approaches to quantify dispersal and connectivity patterns

- Putting together the pieces of the puzzle: combining multiple approaches to better understand patterns of fish dispersal and connectivity.....21
Antonio Di Franco and Paolo Guidetti

- Modeling habitat connectivity: migrations and larval dispersal.....29
Patrizio Mariani

- Lagrangian Flow Networks: a new framework to study the multi-scale connectivity and the structural complexity of marine populations.....39
Vincent Rossi, Enrico Ser-Giacomi, Mélodie Dubois, Pedro Monroy, Manuel Hidalgo, Emilio Hernandez-García, Cristóbal López

Passive dispersal - genetic flux

- 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.....53
Sophie Arnaud-Haond

- Population genetic connectivity among marine species: a matter of dispersal, selection and drift.....	59
<i>Marta Pascual and Enrique Macpherson</i>	

- Comparative genetic structure of shallow water benthic invertebrates as a proxy to marine connectivity in the Mediterranean Sea.....	65
<i>Adriana Villamor, Federica Costantini and Marco Abbiati</i>	

Case studies across taxa and geography

- Estimating larval dispersal and population connectivity in the deep-sea.....	73
<i>Ana Hilário</i>	

- The Black Sea anchovy – new perspectives regarding their spawning, nursery and overwintering behavior.....	81
<i>Ali Cemal Gucu, Serdar Sakinan, Özgür Emek Inanmaz, Meltem Ok, Murat Dağtekin, Yaşar Genç, Orhan Ak, İlhan Aydın</i>	

- Connectivity, migratory routes and population structure of Atlantic bluefin tuna	89
<i>Jean-Marc Fromentin</i>	

- Migratory patterns and strategies of Mediterranean marine mammals and relation to intersystem connectivity.....	95
<i>Simone Panigada and Nino Pierantonio</i>	

- Modeling ecological connectivity and dispersal in the Black Sea: seasonal and interannual variability.....	105
<i>Bettina A. Fach, Sinan S. Arkin, Baris Salihoglu</i>	

Marine connectivity and man

- Vectors of introduction and pathways of dispersal of alien decapod species in Black, Azov, Caspian and Baltic seas.....	115
<i>Anna K. Zalota, Vassily A. Spiridonov</i>	

- Knowledge on migration routes and patterns as a prerequisite for good fisheries management.....	121
<i>Alen Soldo</i>	

III - BIBLIOGRAPHIC REFERENCES.....	127
--	------------

IV - LIST OF PARTICIPANTS.....	169
---------------------------------------	------------

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.

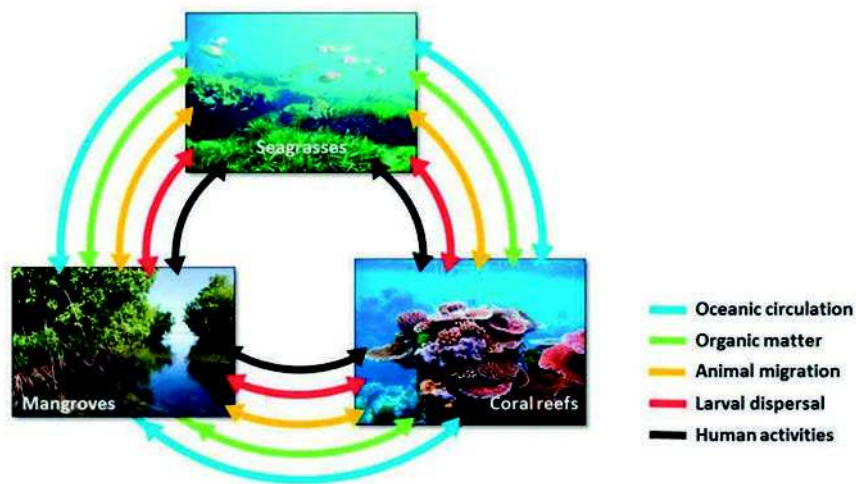


Figure 1. Some of the multiple interactions linking coastal ecosystems.

¹to 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.

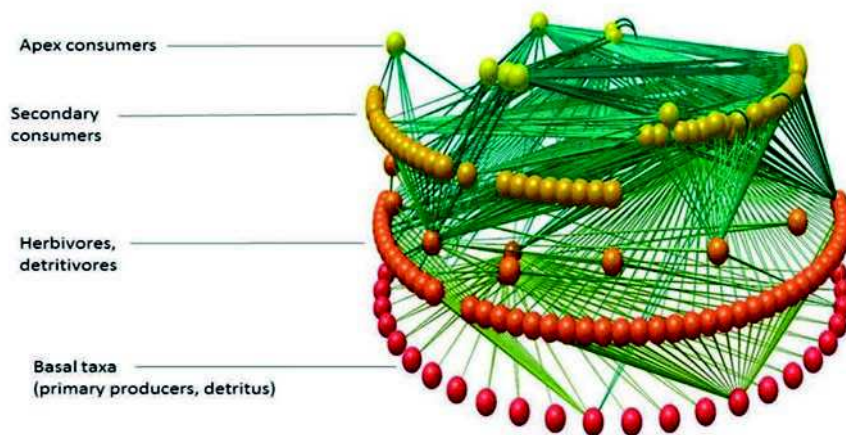


Figure 2. Main linkages among the 142 trophic species of a marine food web in the northeastern Pacific Ocean (Adapted from Dunne *et al.*, 2008).

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 approximately 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. Harrison *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.

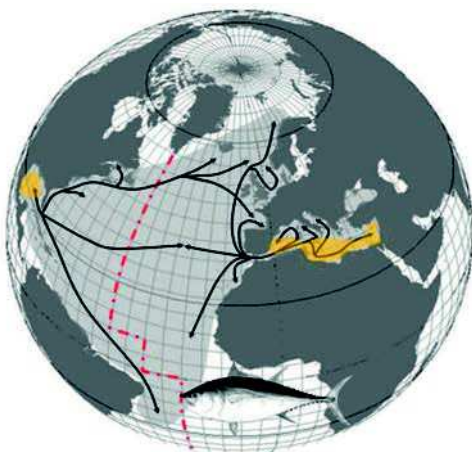


Figure 3. Spatial distribution of the Atlantic bluefin tuna between the two ICCAT management units separated by the red dotted line. The main migratory routes (in black) and the major spawning ground (in yellow) are indicated (Adapted from Fromentin and Powers, 2005).

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 harrisi*, 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, relying 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, background 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, Both 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), Garcia-Merchán *et al.*, 2012 (6); Mitarai *et al.*, 2009 (7); Kool *et al.*, 2011 (8); Guizien *et al.*, 2012 (9); Trembl *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.

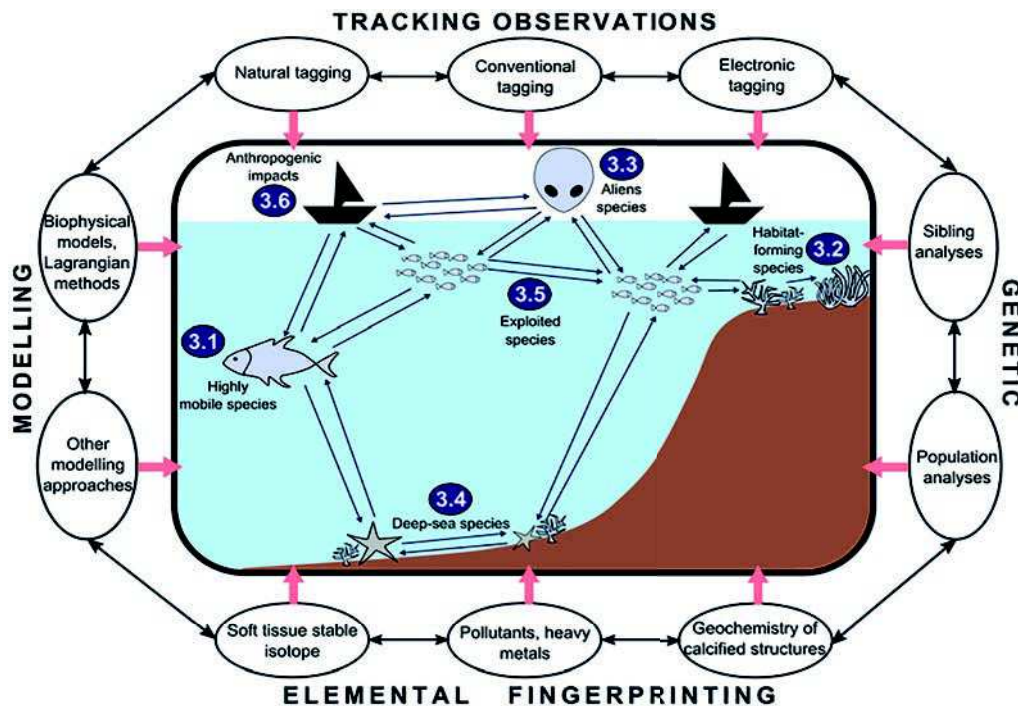


Figure 4. Diagram summing up the main issues and the various methodologies covered in this chapter.

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.