



The Cells of Ecosystem Functioning: Towards a holistic vision of marine space

Ferdinando Boero^{a,b,c,d,*}, Francesco De Leo^{c,e},
Simonetta Fraschetti^{a,c,d}, Gianmarco Ingrosso^{c,f}

^aDepartment of Biology, University of Naples Federico II, Naples, Italy

^bConsiglio Nazionale delle Ricerche, Istituto per lo Studio degli Impatti Antropici e sostenibilità in Ambiente Marino (CNR-IAS), Genoa, Italy

^cConsorzio Nazionale Interuniversitario per le Scienze del Mare (CoNISMa), Rome, Italy

^dStazione Zoologica Anton Dohrn, Napoli, Italy

^eConsiglio Nazionale delle Ricerche, Istituto di Scienze Marine (CNR-ISMAR), Bologna, Italy

^fDipartimento di Scienze e Tecnologie Biologiche ed Ambientali (DiSTeBA), University of Salento, Lecce, Italy

*Corresponding author: e-mail address: ferdinando.boero@unina.it

Contents

1. Summary	130
2. Introduction: Plankton, nekton and benthos	131
3. The four dimensions of marine systems	131
4. A very dynamic system	135
5. Habitats and ecosystems	136
6. Assembling the components into ecosystems	137
7. Life cycles: Intra-specific fluxes	139
8. Food webs: Inter-specific fluxes	141
9. Biogeochemical cycles: Extraspecific fluxes	142
10. Putting ecosystems into a spatial framework: The cells of ecosystem functioning	142
11. Identifying the Cells of Ecosystem Functioning	148
12. Challenges	150
Acknowledgements	151
References	152

Abstract

Marine space is three dimensional, the turnover of life forms is rapid, defining a fourth dimension: time. The definition of ecologically significant spatial units calls for the spatio-temporal framing of significant ecological connections in terms of extra-specific (biogeochemical cycles), intra-specific (life cycles), and inter-specific (food webs) fluxes. The oceanic volume can be split in sub-systems that can be further divided into smaller sub-units where ecosystem processes are highly integrated. The volumes where

oceanographic and ecological processes take place are splittable into hot spots of ecosystem functioning, e.g., upwelling currents triggering plankton blooms, whose products are then distributed by horizontal currents, so defining Cells of Ecosystem Functioning (CEFs), whose identification requires the collaboration of physical and chemical oceanography, biogeochemistry, marine geology, plankton, nekton and benthos ecology and biology, food web dynamics, marine biogeography. CEFs are fuzzy objects that reflect the instability of marine systems.



1. Summary

Marine space is usually represented in terms of areas (e.g. Marine Protected Areas), whereas oceanic environments are typically three dimensional (i.e. Marine Protected Volumes). In the ocean, furthermore, the turnover of plankton (the driving machine of marine ecosystems) is very rapid and the fourth dimension (time) is very relevant in defining space. Management and conservation initiatives in the oceanographic realm call for the definition of ecologically significant spatial units, where measures are to be implemented. Such units are proposed here as Cells of Ecosystem Functioning (CEFs). Their identification calls first for the definition of significant ecological connections that define marine ecosystems. Such connections are: extra-specific fluxes (biogeochemical cycles), intra-specific fluxes (life cycles), and inter-specific fluxes (food webs). Connectivity can be appreciated by superimposing these fluxes in oceanic volumes, also framing them in time. The world ocean is connected through the Great Ocean Conveyor, but this mega-system can be split in sub-systems that, in their turn, can be further split in smaller sub-systems, so as to identify the elemental spaces where ecosystem processes are highly integrated (i.e. CEFs). This exercise is proposed here for the Mediterranean Sea, essentially a miniature ocean, due to the presence of sites of deep water formation that are analogous to the polar systems that trigger the Great Ocean Conveyor. It is shown that two sub basins of the Mediterranean Sea (the Tyrrhenian and the Adriatic Seas) are very different in their oceanographic and ecological features, being further divisible into hot spots of ecosystem functioning (e.g. those volumes where upwelling currents favour the onset of plankton blooms) whose products are then distributed by horizontal currents, so defining CEFs.

The identification of CEFs requires the collaboration of disciplines that often evolve in isolation from each other, namely: physical oceanography, chemical oceanography and biogeochemistry, marine geology and geomorphology,

plankton, nekton and benthos ecology and biology, food web dynamics, and marine biogeography. Due to the high temporal variability of marine systems, in terms of seasonal and annual fluctuations and variations, CEFs are fuzzy objects that must reflect the intrinsic fluctuations of marine systems. Their definition in all portions of the world ocean requires a timely collaboration of all marine sciences in order to reach a holistic appreciation of highly connected systems that are still artificially kept separate by reductionistic analyses.



2. Introduction: Plankton, nekton and benthos

Textbooks divide the biological component of marine systems into plankton, nekton, and benthos. Plankton and nekton inhabit the water column: plankters can swim but cannot oppose the movement of major water masses, whereas nekton can move actively against the motion of currents; benthos comprises the organisms that live in contact with the sea bottom.

The three domains are further divided into several categories, based either on size (e.g. micro-, meso-, macro- and megaplankton), on functional attributes (e.g. phyto- vs zooplankton), and even on the consistency of its representatives (e.g. gelatinous plankton). Benthos, in its turn, is divided into a sessile and vagile component, or into phyto- and zoobenthos, or, again, on the basis of the inhabited substratum, e.g., hard-bottom vs soft-bottom benthos. Further divisions are based on size, such as micro- meio- and macrobenthos.

Other divisions of the marine domain consider the relationships with the coast, distinguishing coastal systems from off-shore to deep-sea systems.



3. The four dimensions of marine systems

The measurement of marine space as surfaces reflects a typically terrestrial approach. The term Marine Protected Areas is referred to the sea surface, as is the claim that the ocean covers 71% of the surface of the earth. But, the ocean is not a surface, it is a volume. The average depth of the ocean is 3500m and the resulting volume is the largest habitat of the planet: the habitat of plankton and nekton. The third dimension of depth, almost irrelevant on land, is paramount in the sea. Almost all organisms depend on what happens in the water column, those who do not live suspended in it

for at least a portion of their lives in any case derive their resources from it. If measured in terms of volume, most of the life-inhabited space of the planet is the water column.

Time adds a fourth dimension that, in the marine realm, is more important than on land. Terrestrial environments, in fact, are usually defined based on the vegetation, a spatially defined feature that changes with seasons but that is nevertheless clearly recognizable. This is far from being true in the marine realm, where important marine ecological processes are based on the primary production of microbes that live suspended in the water column of the euphotic zone. These do not contribute to form a perceivable landscape (at least for us) and cannot be equated to the vegetation that we use to define terrestrial or benthic habitats. The seasons of the sea define periods of intensive primary production, just like on land. Terrestrial plants, however, give shape to landscapes even in periods of quiescence, as happens in deciduous forests during winters or dry seasons. The bulk of marine primary production, in contrast, is due to the microbes of the phytoplankton that, in turn, support zooplankton pulses, followed by nekton pulses. Hence, submarine landscapes remain more or less constant on the sea bottom, but change dramatically in the water column, during seasonal fluctuations.

Vegetation is a key component of benthic communities in the euphotic zone, both as algal beds, kelp forests and seagrass meadows, whereas animals tend to prevail below the euphotic zone, forming animal forests (Rossi et al., 2017). At tropical latitudes, furthermore, animals form the landscape as coral formations, having symbiotic zooxanthellae that make them physiologically autotrophic. Besides sustaining benthic vegetation, however, the light of the euphotic zone allows for the growth of microbial primary producers: the phytoplankton formed by both photosynthetic bacteria and microalgae such as diatoms and phytoflagellates. The bulk of marine ecological processes takes place in the water column, the most widespread suite of habitats of the planet (Fig. 1).

All living beings die, and are decomposed by bacteria that, in their turn, are killed by viruses. The mineralization ensuing from bacterial metabolism produces the nutrients that, thanks to the energy of light, sustain phytoplankton blooms: pulses of primary production that use the nutrients deriving from decomposition and terrestrial runoffs, reviving matter. The microbial pathway comprises the decomposers (bacteria), the phytoplankton and the protists that feed on them (Fig. 1, centre). Microbes, during blooms, can give typical colours to the water, according to species. Red tides are the result of dinoflagellate blooms, whereas other microalgal blooms lead to either brown or green waters (Fig. 1, upper right corner). Crystal clear



Fig. 1 Trophic connections in the water column. Centre: the microbial pathway. Upper right corner: microbe bloom. Lower right corner: the microbe-crustacean-fish-human pathway. Lower left corner: the microbe-herbivorous gelatinous plankton pathway; upper left corner: the microbe-crustacean-fish-carnivorous gelatinous plankton pathway. Carbon is deposited on the sea bottom, where carbon sequestration takes place. See text for further explanation. *Concept: F. Boero; Artwork: Alberto Gennari.*

waters are not very productive, even though bacteria are invariably present. Microbes are also the food for benthic filter feeders, such as sponges, bivalves and tunicates. The typical grazers of phytoplankton are, however, in the water column where copepods are the most widely studied group.

Other crustaceans and rotifers are also very efficient grazers of phytoplankton. These small life forms are not the bulk of the landscape that humans can perceive. The secondary producers are food for the larvae and juveniles of most fish which, as such, play the role of tertiary producers and, once grown up, higher producers (Fig. 1, lower right corner). The larvae and juveniles of some fish species, in fact, grow and become large fish, whereas other species remain small: the large fish eat the small fish, but all of them, when larvae, eat the secondary producers. The life forms visible to us in the water column, those that are part of our diets, are almost invariably predators that can be quaternary producers or even much higher in the food chain. Sharks do not pass through larval stages and are born already as predators. The crustacean–fish pathway, however, does not represent the only fate of what is produced by the microbial pathway. Gelatinous herbivores (mostly thaliaceans, Fig. 1 low left corner), in fact, can be dominant for short periods, when they tap very efficiently into the microbial component, making up the microbial–herbivorous macrozooplankton pathway. Carnivorous gelatinous plankton, mostly jellyfish and ctenophores, represents fourth pathway, the microbial–crustacean–fish–carnivorous macrozooplankton pathway. Gelatinous carnivores, in fact, are top predators that feed on fish eggs and larvae (even those of the largest fish) and on their crustacean food (Fig. 1 upper left corner). Gelatinous macrozooplankters, both herbivorous and carnivorous ones, can be very large, and are part of the water column landscape.

The general perception of life in the water column, thus, is that of a world of predators, something that is ecologically impossible. The larval bottleneck is a crossroad that leads fish to the higher levels of the food web. Fish, besides feeding on each other, are also food for gelatinous predators (as larvae and juveniles), sharks, marine birds and mammals. The largest sharks (whale and basking sharks) and mammals (whales), however, tap into the base of food webs, feeding on secondary or tertiary consumers.

The greatest part of the water volume lies below the euphotic zone and is, thus, deprived of primary producers. The secondary producers of the plankton can perform daily vertical migrations, moving to surface levels to feed, and then going back to the dark deep to escape visual predators. The dead bodies of both plankton and nekton sink towards the sea bottom and, during their descent, are decomposed by bacteria and can eventually be incorporated in the sediments where carbon sequestration can occur. The marine snow ensuing from the sinking particulate organic matter brings energy to the sea bottom and to the water column above it.



4. A very dynamic system

Marine systems therefore are highly dependent on what happens in the water column. This very dynamic system does not remain the same even over the course of a single day, due to zooplankton vertical migrations and passive transport by currents. The movement of the water and of the organisms living in it, especially plankters, drive a continuous change that is difficult to represent in a map, as can be easily done for terrestrial habitats and the vegetation that makes them up.

The tendency to “fix” the living environment in terms of habitat maps considers mostly benthic habitats, because the water column, due to its variability, is mapped as current flows but not as large ecosystem patterns and processes. Primary production in terms of phytoplankton does not occur in the same way throughout the euphotic layer of the water column. Besides light, microalgae need nutrients, and these can have two origins. One part arrives into the sea through terrestrial runoff from rivers: estuaries are highly productive because of nutrient abundance. Second, nutrients reach the euphotic zone through upwelling of two kinds: nearshore or offshore upwellings. These nutrient inputs, together with light, lie at the base of microbial primary production and of the series of energy transfers that make up marine food webs (Fig. 1). The places where nutrient abundance allows for primary production pulses are veritable hot spots of ecosystem functioning and sustain much larger volumes as horizontal currents transport primary, secondary and higher producers in several ways (Hays, 2017). Fronts push organisms in a single direction, whereas gyres concentrate them and favour energy transfers at the various levels of food webs (Acha et al., 2015; Godø et al., 2012). The ensuing ecological scenario is, thus, very dynamic: the effects of processes that take place at a given spot (e.g. the hot spots of nutrient availability and primary production) can reach distant places both horizontally (fronts and gyres) and vertically (up- and down-wellings). The sinking of particles, furthermore, is not necessarily vertical since currents can concentrate them according to the geomorphological features of the sea bottom. Marine canyons, for instance, are sinks of sediments and of all the objects that fall to the bottom from the upper water column but, especially during upwellings, they are also distributors of nutrients towards the surface, where they support phytoplankton production.

Plankton samples are not identical if taken at the same place at different times of the day, due to the daily migrations along the water column of many

plankters. Plankton abundance and composition vary significantly, furthermore, even within a few metres since Langmuir currents concentrate suspended objects, from floating litter to live plankton, in longitudinal stripes that move (Barstow, 1983): plankton is abundant in Langmuir cells, whereas it is poor in the space between adjacent cells. Furthermore, plankters can migrate vertically during the day-night period. Water stratification, especially in the summer, is a barrier to exchanges along depth gradients.

This intertwining of physical and biological drivers leads to a fuzzy landscape that cannot be defined in space with the same accuracy of terrestrial or benthic landscapes. This difficulty should not lead to oversimplifications that allow for artificially precise reconstructions (and models that are often labelled as “predictive”) but which lack accuracy. The mismanagement of the environment often results from misrepresentations of the various components, and of their interactions.



5. Habitats and ecosystems

The habitat concept usually applies to benthic systems, where habitat mapping is widely adopted to define the features of marine environments. Marine Protected Areas, however, should be termed Marine Protected Volumes, and should fully comprise habitats and ecosystems. The adoption of the ecosystem approach led to a suite of different representations of marine space, planning human uses with Networks of Marine Protected Areas, Maritime and Marine Spatial Planning, and Coastal Zone Management. The spatial representations of these approaches, often applied independently to the same ecological space, are usually bi-dimensional and only consider areas.

Biogeography studies the distribution of life in space. Living matter is organized as individuals that are ascribed to different categories that should reflect phylogenetic affinities: species and higher taxa. Species are further fragmented into populations that inhabit different portions of the environment. Populations can be more or less connected with each other, so as to form metapopulations, i.e., populations of populations. Some endemic species are represented by small populations or metapopulations and their management and protection occurs within the space of their distribution. More widely distributed species, however, can have distinct metapopulations that have less chances to exchange genes.

This led to the concept of connectivity as a measure of the connections that link the populations into metapopulations. This intraspecific approach, considering connections within species, must be upgraded to a community level, identifying assemblages of species that coexist within the ecological space. These assemblages are often termed communities, so as to suggest a common ecological background, based on coevolutionary processes, and not a simple assemblage. Species can distribute in space simply to find places where their ecological requirements in terms of abiotic variables are met. If, while co-occurring, they form relationships with each other in terms of cooperation, predation (including parasitism) and, also, competitive networks, then a co-evolved community becomes established.

Each community usually occurs in a habitat but, from an ecological point of view, habitat fragmentation can lead to metahabitats (collections of the same habitat that occurs in different portions of space) inhabited by metapopulations. As explained in the previous section, however, it is seldom the case that a habitat type does not have links with other habitats, both in terms of life cycles of the various species, and of nutrient or prey inputs from the water column which, in itself, is a three dimensional (Sayre et al., 2017) and very dynamic suite of habitats. The ensemble of habitats and populations, and their interactions with the abiotic variables, allows us to identify ecosystems.

Biogeography describes the patterns of biodiversity distribution, identifying areas characterized by similar species assemblages based on biogeochemical provinces (Longhurst, 2010) while still keeping coastal and shelf systems (Spalding et al., 2007) separated from pelagic ones (Spalding et al., 2012). The link of biogeography and ecology led to macroecology (Brown, 1995) which, indeed, might be a way to adopt the ecosystem approach.



6. Assembling the components into ecosystems

The hierarchy of populations—metapopulations—species assemblages—communities—habitats—metahabitats—ecosystems links all the components of marine systems. These are sampled with different techniques and are studied by different scientists, often working in different portions of the ocean (i.e. deep sea vs coastal areas). However, it is well known that the portions interact with each other so as to form ecosystems that overcome the artificial boundaries that have been built by mere convenience.

This vision of the ecosystem requires the assemblage of the components, integrating parts that are usually kept separate. A wealth of knowledge has been gathered already on these parts, and time is ripe to assemble them. But these divisions are not natural, and depend on the tools we use to study them. Samples are collected from a specific domain and studied with specific techniques and only rarely do the approaches comprise the whole space in which species play their roles during their life cycles. The ecosystem approach, thus, should consider the processes that link a much-fragmented representation of the life in the seas.

If the biology and ecology of organisms calls for a shift from a reductionistic to a holistic approach that recognizes the links across artificial biological and ecological subdivisions, then a further effort is required to frame these processes in wider spaces. Boero and Bonsdorff (2007) proposed consideration of marine ecosystems as being the intertwining of three fluxes of matter that changes state from living to non living and back to living, flowing within species (intra-specific fluxes, i.e., life cycles), among species (inter-specific fluxes, i.e., food webs) and outside species (extra-specific fluxes, i.e., biogeochemical cycles) (Fig. 2). Naming them “fluxes” conveys a dynamic approach that describes the flow of matter across permeable compartments that should not be considered as isolated units.

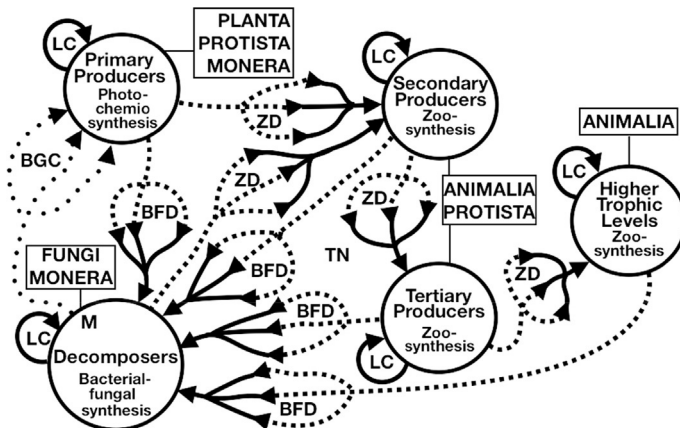


Fig. 2 Ecosystem functioning occurs via connections that involve biogeochemical cycles (BGC = Extra-specific Fluxes: dotted arrows), life cycles (LC = Intra-specific Fluxes: solid arrows), and trophic networks (TN = Inter-specific Fluxes: dashed arrows). BFD = Bacterial-Fungal Decomposition; ZD = ZooDecomposition; M = Mineralization.



7. Life cycles: Intra-specific fluxes

Species have life cycles, and cannot be considered as adults only. Species persist because matter flows from one generation to the next, remaining “organized” as individuals of that species: hence “intra-specific fluxes”.

The life cycles of marine organisms cross the boundaries of plankton, nekton and benthos. Benthic organisms often do have planktonic larvae (e.g. most echinoderms) or adults (e.g. the sexually reproducing medusae are the planktonic adults in a life cycle with both planktonic and benthic larvae: the planulae and the polyps). Nektonic fish usually start their life as planktonic eggs, zygotes, embryos, larvae and juveniles, shifting to nekton later in their life span (Pepin et al., 2015).

Connectivity is often represented in terms of life cycles, measuring the fluxes of propagules that link distinct populations of the same species so as to form a metapopulation (Boero et al., 2016b).

If trophic interactions are considered, furthermore, most benthic organisms depend on processes that take place in the water column, from where they draw most resources, so influencing the ecology of plankton.

To cope with high environmental variability, many planktonic organisms have evolved life cycles that allow them to spend even long periods in a resting stage, waiting for the onset of favourable conditions to spring into action (Marcus and Boero, 1998) (Fig. 3).

Sudden plankton blooms are usually not the product of sustained reproductive processes that gradually increase the size of the population but, instead, result from the contemporary hatching of benthic resting stages that give rise of abundant populations that, then, increase further in size with reproductive processes, to return into a resting state when resources become scarce, predation is too intensive, or abiotic conditions become hostile. The resting stages of plankton are veritable propagules that connect the water column with the sea bottom. Resting stages can travel with currents and, once hatched, the resulting organisms are further transported by water movement.

Connectivity is usually considered as the link among populations that inhabit the same habitat types at disjunct locations via propagule transport (Pineda et al., 2007) (Fig. 4). Usually this is the prevailing view

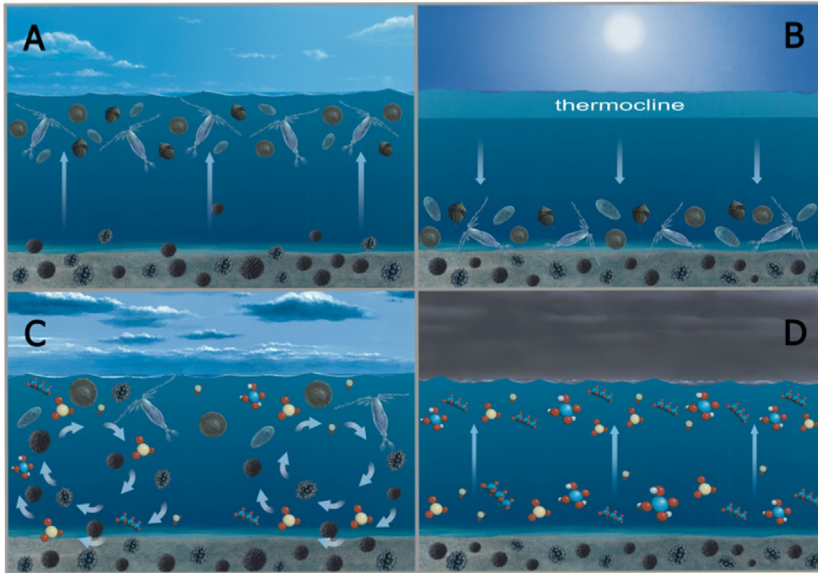


Fig. 3 Plankton pulses. (A) in the spring resting stages hatch and lead to phyto- and zooplankton blooms. (B) in the summer, with the onset of stratification and thermocline formation, plankters produce resting stages that fall to the sea bottom; (C) in the fall minor blooms occur due to mixing caused by storms; (D) in the winter resting stages remain in the sediments, to be then resuspended together with nutrients in the following spring. *Art: Alberto Gennari.*

of connectivity and is often used to design management schemes of marine populations (Boero et al., 2016b). In this case, however, communities are simple assemblages of species that are analysed separately from each other and that do not form coherent ecological units. The distribution of organisms, furthermore, coincides with the sum of the records of their occurrence, throughout their life cycle. Some migratory species, such as eels, can colonize a suite of habitats during their life span, when they travel across the Atlantic as larvae, enter the Mediterranean Sea, and then come back to their birth place as adults. Important fish, such as salmon, pass from the sea to rivers, where they spawn until they die. Their larvae and juveniles going back to the ocean where they grow until maturity, then heading for the place where they were born, to spawn and die. The connectivity through resting stages, linking the sea bottom and the water column, remains mostly unexplored.

Taking just some species to represent ecological connections does not give justice to the complexity of marine systems.

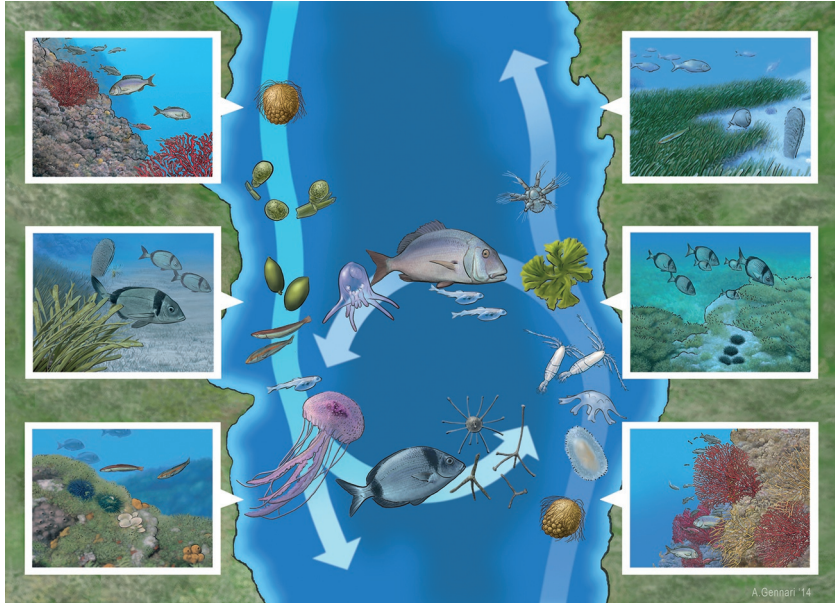


Fig. 4 Connectivity with several propagule types. Habitats accommodate populations that, together, form communities. Currents transport propagules that ensure colonization of new sites and that are food for predators. Propagules can be either adults (like many fish), or seeds, larvae and juveniles, and asexual fragments. Intra-specific connectivity links populations of a given species and leads to metapopulations. Food webs are the result of inter-specific connectivity and defines metacommunities. *Artwork by Alberto Gennari.*



8. Food webs: Inter-specific fluxes

Inter-specific fluxes (Fig. 2) involve a passage of matter from prey species to predatory species and, eventually, to species that play the role of decomposers. When a heterotrophic species uses the matter of other species, it decomposes it and then organizes matter into own organization (species are what they eat). Animals decompose their prey in their guts (zoo-decomposition), usually with the aid of symbiotic microbes, then they assemble it according to their genetic specifications (zoo-synthesis) or use it for their physiological requirements and reproduction. Inter-specific fluxes are a form of connectivity that adds to the intra-specific fluxes of life cycles. Propagules, in fact, are not only the objects that allow for the connections among different populations of the same species: they are also prey for organisms of different species that feed on them; propagules, furthermore, can feed on other prey

items. Predators, of course, can also feed on fixed organisms that cannot be considered as propagules (e.g. nudibranchs feeding on sponges, or sea urchins feeding on algae). When species interact with each other through persistent food web dynamics, they form coevolved communities (Guzman et al., 2019) and when species inhabit different habitats throughout their life cycles, they eventually participate in metacommunities. Pati et al. (1999), for instance, suggested that the interstitial fauna might control plankton composition by feeding on the resting stages of the dominant species of a given season, so preventing them from monopolizing future plankton blooms, so acting as a keystone guild. Plankton and meiobenthos communities, in this case, should be considered as parts of highly connected metacommunities.

Eventually all organisms die (Figs 1 and 2) and are decomposed by heterotrophic bacteria and fungi that use the matter of other species to build up their bodies and to carry out physiological and reproductive processes. These metabolic patterns involve mineralization, with the release of simple chemicals into the environment, where they are no longer organized in a living state. Primary producers use these resources and revive matter either via photo- or chemosynthesis.



9. Biogeochemical cycles: Extraspecific fluxes

Biogeochemistry studies the distribution of chemicals that are of crucial importance for primary producers, often called with the general term “nutrients”. These derive from decomposition of previously living matter by bacteria and fungi, or from terrestrial runoff. Biogeochemical cycles are extensively studied and their bearing on ecosystem functioning is crucial. The efficiency of biogeochemical cycles is often taken as a measure of ecosystem functioning (e.g. Naeem and Wright, 2003) and is obviously a convenient measure of ecological processes, but extra-specific fluxes cannot be considered as separated from intra- and extra-specific fluxes in depicting ecosystem functioning, the three fluxes contributing to ecological processes (Fig. 2).



10. Putting ecosystems into a spatial framework: The cells of ecosystem functioning

Boero et al. (2016b) proposed the concept of cells of ecosystem functioning as an approach to design networks of Marine Protected Areas and based this concept on intraspecific connectivity, linking metapopulations

inhabiting different locations where the same habitat types occur. Connectivity was measured in terms of current patterns, comparisons of species lists (Beta diversity), propagule presence in the water column, and genetic connections across populations of selected species.

To fully account for ecosystem functioning, however, intraspecific fluxes are just one of the three essential components, requiring the upgrade of the approach to interspecific fluxes (food webs) and extra specific fluxes (biogeochemical cycles).

The concept of Cells of Ecosystem Functioning is based on the splitting of marine space into coherent units where ecosystem functions take place with the three fluxes described in Fig. 2. Current patterns are well known in their general dynamics and represent an initial hypothesis of what CEFs might be.

The water column is mapped in terms of currents, the largest one, the Great Ocean Conveyor (Broecker, 1991), which connects all oceans into a single, grand system generated by deep water formation at the poles, from where currents spread to the deep sea and go back to the surface again (Fig. 5).

In spite of this worldwide connectivity, the world ocean can be divided into basins that, in their turn, can be further split into parts that contain highly connected ecosystems: the cells of ecosystem functioning. The Mediterranean Sea can be considered as a replica of the world ocean, a miniature ocean (Lejeune et al., 2010) with a very rich biodiversity (Coll et al., 2010). As shown in Fig. 5, besides the poles, the only other sites of deep water formation are located in the Mediterranean, whose waters have higher salinity than Atlantic ones, and this difference triggers the Gibraltar Current that reaches the Eastern Mediterranean and flows back as the Intermediate Levantine Current, flowing back in the Atlantic Ocean. This flow renews the Mediterranean but, however, it occurs within 500 m depth, whereas the basin is much deeper, on average. Lack of water renewal should lead to anoxic crises in the deep sea, but this does not happen because of the cold engines of the Gulf of Lions, and the Northern Adriatic and Aegean (Fig. 6).

The cold engines, in fact, form cascading currents that flow to the deep through marine canyons (Fig. 6 inset), bringing oxygen-rich coastal waters to the deep and causing offshore upwellings that bring nutrients to the surface (Fig. 6). The canyons that are not drivers of cascading phenomena are the drivers of coastal upwellings (Fig. 6 inset).

These exchanges between the deep sea and the coast are essential to the survival of deep sea life in the Mediterranean in terms of oxygen, and

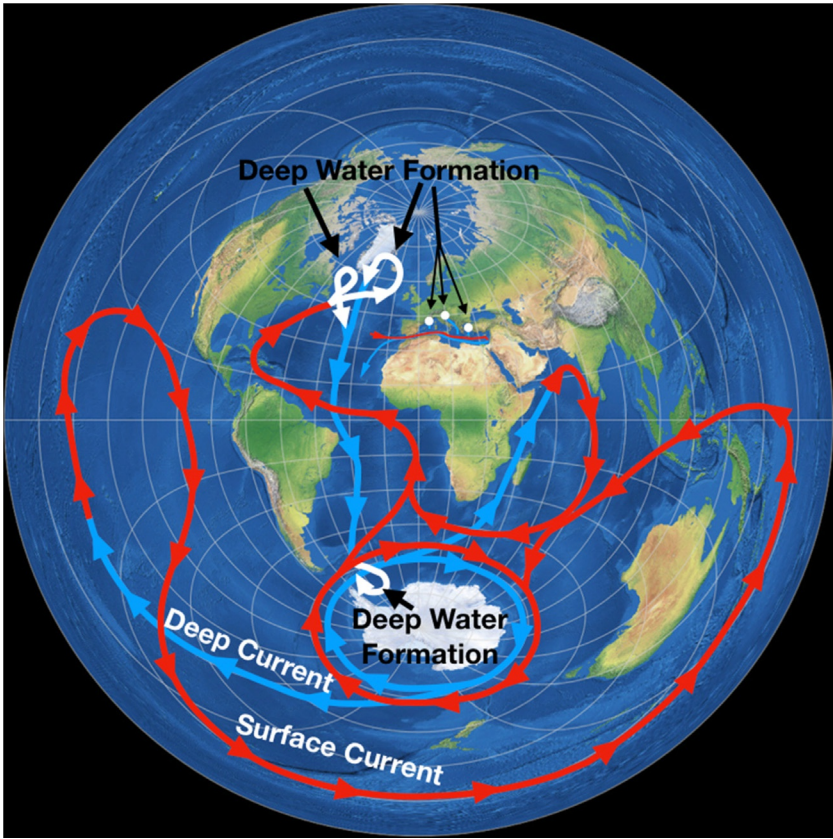


Fig. 5 The Great Ocean Conveyor. See text for explanations.



Fig. 6 The main horizontal and vertical currents of the Mediterranean Basin: GC, Gibraltar current; ILC, intermediate Levantine current; BIOS, Bimodal Oscillating System. Lower inset: canyon-generated cascading and upwelling currents. Right inset: gyre generated by coastal morphology. After Danovaro R., Boero F., 2019. Italian seas. In: Sheppard C. (Ed). *World Seas. An Environmental Evaluation (second ed.)*. Academic Press, London. pp. 283–306.

to the production of coastal systems in terms of nutrient and propagule injection. The Mediterranean, thus, can be divided into sub-basins with different ecosystem processes, generated by current patterns. Fig. 6 shows that the Tyrrhenian Sea is apparently not affected by the influence of the cold engines, hence water renewal should not be so intensive in this basin that, instead, is biodiversity rich in its deepest portions also.

The current patterns of the Tyrrhenian Sea, in fact, are somehow different from those of the rest of the basin, albeit depending on them via the surface and deep currents that enter from the northern coast of Sicily. The Tyrrhenian Sea, in its turn, influences the Ligurian Sea and the Western Mediterranean with its outflowing currents. In spite of these connections, however, the Tyrrhenian Sea can be considered as a compact entity determined by an internal connectivity that defines original environmental features and, possibly, ecosystem functions (Fig. 7).

The horizontal unidirectional currents and gyres of the Tyrrhenian Sea (MAW and LIW) must be coupled with the vertical currents driven by canyons as inshore upwellings and offshore downwelling (Fig. 7). Canepa et al. (2014) reported that marine canyons bring huge blooms of the scyphozoan jellyfish *Pelagia noctiluca* from the deep sea to the coasts of the Tyrrhenian Sea. Jellyfish, in this case, are tracers of current patterns. Boero et al. (2016a) showed that *P. noctiluca* is abundant in the Tyrrhenian Sea and suggested that its presence depends on the inocula of deep sea jellyfish that reach the coast with the canyon-generated upwellings and are then distributed along the coasts by horizontal currents. The circulation of the Tyrrhenian sea is very complex. It involves an incoming surface current that is a branch of the Gibraltar Current, named Modified Atlantic Water (MAW). This current enters the basin from the northern part of Sicily and flows along the coast to eventually enter the Ligurian Sea. At deeper levels, a current made of Levantine Intermediate Water (LIW), comes from the Eastern Mediterranean, being a branch of the Intermediate Levantine Current. LIW flows parallel to MAW and also enters the Ligurian Sea, but a branch of it flows southwards along the Sardinian Coast and exits the Tyrrhenian basin, together with Tyrrhenian Deep Water (TDW). The interaction of these currents with the conformation of the coast and the sea bottom forms a series of cyclonic and anticyclonic gyres. Furthermore, a cold downwelling current has been sometimes identified in correspondence with the Bonifacio Strait (between Corsica and Sardinia), even though its presence and intensity are still to be confirmed. The bottom of the Tyrrhenian Sea is indented by a high number of marine canyons that, during periods of homothermy,

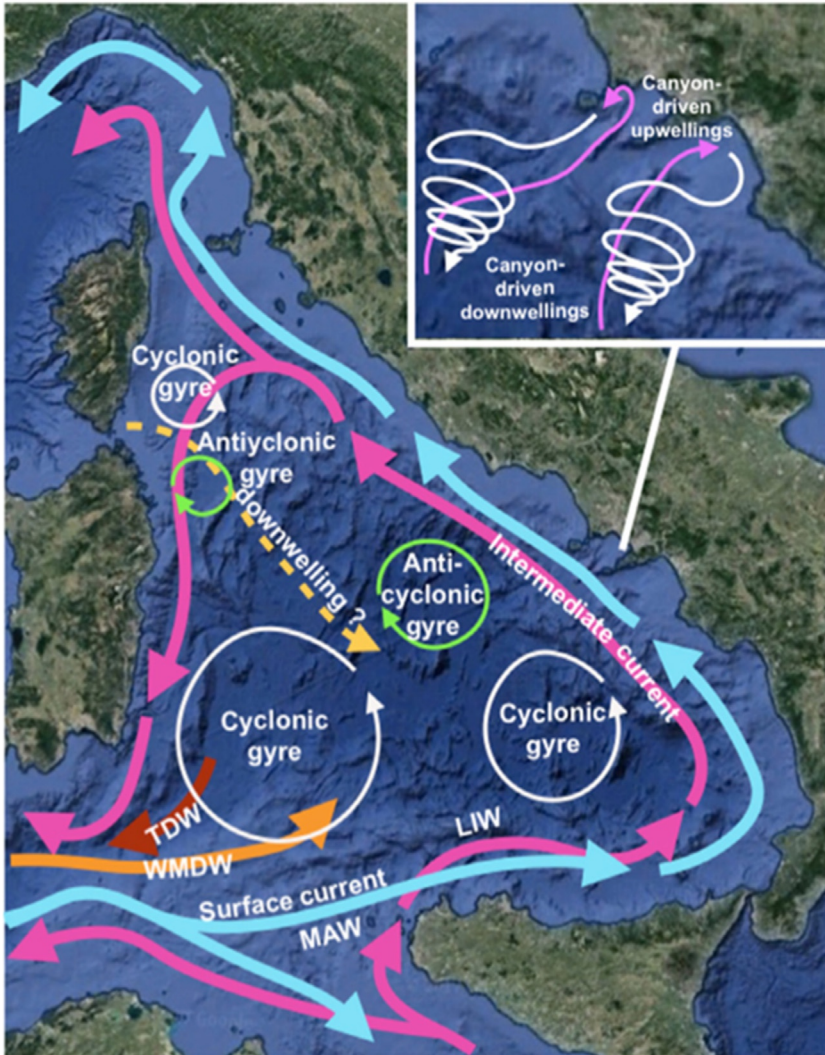


Fig. 7 The main currents of the Tyrrhenian Sea. LIV: Levantine Intermediate Water; MAW: Modified Atlantic Water; TDW: Tyrrhenian Deep Water; WMDW: Western Mediterranean Deep Water. Inset: Canyon-driven up- and down-welling. *From various sources, graphics: F. Boero. After Danovaro R., Boero F., 2019. Italian seas. In: Sheppard C. (Ed). World Seas. An Environmental Evaluation (second ed.). Academic Press, London. pp. 283–306.*

are usually driving deep water towards the coast, with upwelling currents (Fig. 7, inset). These upwellings bring deep sea nutrients towards the coast and cause offshore downwellings that should bring surface oxygenated waters towards the deep portion of the basin. The presence of sites of

deep-water formation near the coast is not recorded from the Tyrrhenian Sea so that, in this respect, it is somehow different from the Western and the Eastern Mediterranean.

The vertical currents link the deep sea with the coastal systems, and probably are hot spots of ecosystem functioning that trigger phytoplankton blooms at the end of the winter, when nutrient rich deep water reaches the coasts and support the blooms that restart the system, supporting the rest of the ecosystem processes. The products of the spring blooms are then distributed throughout the basin with the horizontal currents and are concentrated in the gyres, where production should be further enhanced, as [Godø et al. \(2012\)](#) demonstrated elsewhere.

The Tyrrhenian Sea megacell of ecosystem functioning, thus, can be divided in a series of cells that determine hot spots of ecosystem functioning, namely, the locations where upwellings take place, and the corresponding downwellings, and the offshore gyres. These are the places where ecosystem processes should be more intensive, whose products should be distributed throughout the megacell by the horizontal currents ([Danovaro and Boero, 2019](#)) ([Fig. 7](#)).

Even in the same basin (e.g. the Mediterranean Sea) the various portions, albeit connected with each other, acquire distinct features. The Adriatic Sea, for instance, is much shallower than the Tyrrhenian Sea and is characterized by the presence of a cold engine in its northern part ([Fig. 8](#)) that generates a current that flows along the Italian coast and enters the Ionian Sea, from where an incoming current flows northwards along the eastern coast of the basin. The conformation of the coast leads to the formation of three main gyres that connect the opposite shores of the basin and divide the basin into three portions. The circulation in the Adriatic Sea, furthermore, is influenced by the Bimodal Oscillating System (BiOS in [Fig. 6](#), [Civitarese et al., 2010](#)) that acts as a roundabout that regulates the exchanges between the two basins.

These oceanographic processes allow us to define marine volumes in which the ecological processes are supposed to be characterized by higher internal connectivity than connectivity with neighbouring basins.

This connectivity, however, is not the same for all organisms. Some species, in fact, are highly mobile and their populations are highly connected, whereas the populations of other, less vagile, species are more separated from each other, as far as intra-specific fluxes (i.e. life cycles) are concerned. Inter-specific fluxes can also vary according to the species. The white corals living in the Southern Adriatic, for instance, draw food from the cascading current



Fig. 8 The main currents of the three portions of the Adriatic Sea. After Danovaro R., Boero F., 2019. *Italian seas*. In: Sheppard C. (Ed). *World Seas. An Environmental Evaluation* (second ed.). Academic Press, London. pp. 283–306.

generated by the cold engine of the Northern Adriatic, with which they are trophically connected, even if their intra-specific fluxes have no relationship with that part of the basin.

These ecosystem processes take place seasonally and their spatial definition is not as precise as that of benthic habitats. The water column is dynamic and its features vary with the seasons, so the fourth dimension (time) is essential in defining the features of marine systems.



11. Identifying the Cells of Ecosystem Functioning

Connectivity (Zuercher and Galloway, 2019) is the key concept that defines the ecologically significant spaces. Intra-specific connectivity

throughout life cycles and inter-specific connectivity across food webs must be superimposed on extra-specific connectivity, i.e., biogeochemical cycles. These three fluxes are at the base of ecosystem functioning and can be framed spatially into Cells of Ecosystem Functioning (CEFs): the three-dimensional spaces in which connections of the three kinds (intra-inter- and extra-specific fluxes) are tighter than in neighbouring spaces. The definition of CEFs calls first for a good knowledge of physical oceanography, with the identification of the main currents, both horizontal and vertical. Currents, and the definition of water masses also in terms of stratification due to temperature changes, determine the distribution of nutrients in space and are the drivers of biogeochemical cycles, together with riverine inputs. Currents make nutrients available (extra-specific fluxes) and this triggers intra-specific fluxes with the sustainment of the populations of primary producers, i.e., phytoplankton, that allow for the passage from biogeochemistry to biology. The blooms of microbes determine proper conditions for the onset of inter-specific fluxes through food webs. At some places (e.g. canyons and the upwelling areas in their correspondence) link the deep and the coastal and open seas, triggering biogeochemical processes that sustain biological processes (i.e. production) that are then transported by horizontal currents across much wider spaces. Fronts bring plankton and nutrients in linear directions, while gyres concentrate or disperse them.

At present, the Cells of Ecosystem Functioning can only be hypothesized. Their actual distribution requires assembling a wealth of information that is starting to become available and whose refining and assemblage should be a priority in marine science. The disciplines involved in the definition of the Cells of Ecosystem Functioning are: physical oceanography, chemical oceanography and biogeochemistry, marine geology and geomorphology, plankton, nekton and benthos ecology and biology, food web dynamics, marine biogeography. These disciplines are studied by portions of the scientific community that rarely interact with each other in a holistic fashion. Furthermore, the approach to marine sciences still suffers from a terrestrial bias, focusing on benthic systems to define marine habitats, and disregarding the water column as a suite of highly variable habitats. The variability of marine systems, and the seasonal pulses of production, from phytoplankton to nekton, that characterize ecosystem functioning hinders a precise spatial definition of marine space. The Cells of Ecosystem Functioning are a fuzzy concept because they represent fuzzy systems. Disregarding this fuzziness for ease of analysis leads to a misrepresentation of the patterns and processes that characterize the functioning of marine ecosystems.



12. Challenges

The world ocean is highly connected (Fig. 5) but it can be divided into portions (Oceans and Seas) that can be further divided into highly connected volumes. The Mediterranean Sea (Fig. 6) is an example of how to divide a basin into sub-basins (as is the case of the Tyrrhenian and the Adriatic Seas) that, in their turn, can be divided into even smaller portions where internal connectivity is very intensive (Figs 7 and 8). At present, however, the measures of connectivity are almost invariably based on intra-specific fluxes, i.e., the exchange of propagules among different populations of the same species inhabiting different portions of the marine space. Fig. 9 shows an assessment of Marine Protected Area connectivity by a simulation of larval dispersal based on the modelling framework developed by Trembl et al. (2012). Statistically significant numbers of connections were obtained by performing larval dispersal simulations in 3 years (2015, 2016, 2017), considering four different seasonal periods for each year, and setting at 30 days the pelagic larval duration (PLD) of the released particles. Obviously not all propagules behave as inertial particles, and this modelled connectivity does not consider the inter-specific connections throughout food webs. Propagules can eat and be eaten, intra-specific connections, furthermore, do not occur only via larvae but also through adults and asexual propagules, as shown in Fig. 5. Extra-specific connections, in terms of nutrient distribution, are also disregarded in these connectivity models. Over-simplifications can lead to models that, however, do not represent the complexity of marine systems.

The concept of CEFs puts ecosystem functions in a spatial concept and represents a theoretical attempt towards the integration of the available knowledge and the filling of the gaps that still prevent the full understanding of the functioning of marine ecosystems so as to identify coherent units of management and conservation based on ecosystem features and not on our modes of using marine space.

The aim of this proposal is in line with a crucial sentence in Navigating the Future IV, of the European Marine Board: “To truly progress this knowledge, European scientists across a broad range of disciplines and domains must make a quantum leap towards holistic approaches and integrated research on a scale which will help us to much better understand, protect, manage and sustainably exploit the seas and oceans which surround us. This is a Grand Challenge; not just Europe, but for human society as a whole” (Arnaud et al., 2013 p. 5).

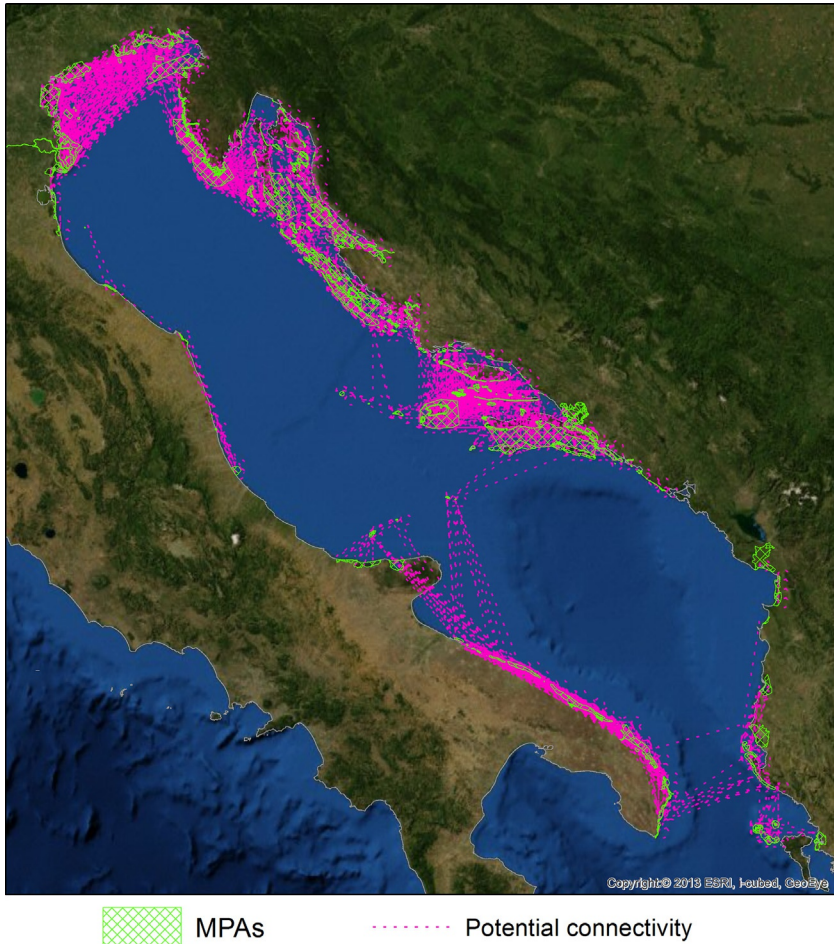


Fig. 9 Potential connectivity (purple tracks) of the Adriatic MPAs (in green) calculated from dispersal simulation analysis. Map was created using ArcGIS software by Esri (Environmental Systems Resource Institute, ArcMap 10.1, www.esri.com).

Acknowledgements

The CEF was developed from the EU FP7 CoCoNet project—“Towards Coast to COast NETworks of marine protected areas (from the shore to the high and deep sea), coupled with sea-based wind energy potential” (GA No. 287844), the Flagship Project RITMARE—“Ricerca ITaliana per il MARE (2012–2016)” the Tender project “Achieving coherent networks of marine protected areas (MPAs): analysis of the situation in the Mediterranean Sea”(DG-ENVC2/FRA/2016/0017—771344). Authors declare no competing interests.

References

- Acha, E.M., Piola, A., Iribarne, O., Mianzan, H. (Eds.), 2015. *Ecological Processes at Marine Fronts: Oases in the Ocean*. Springer.
- Arnaud, S., Arvanitidis, C., Azollini, R., Austen, M., Balguerías, E., Boero, F., Boyen, C., Boetius, A., Buckley, P., Calewaert, J., Canals, M., Chu, N., Cook, R., Danovaro, R., Denègre, J., Dupont, S., Ekebom, J., Freiwald, A., Fritz, J., Hammer, C., Heip, C., Henriot, J.P., Héral, M., Heussner, S., Koster, F., Kraus, G., Lampadariou, N., Larkin, K., Lemoine, L., Loeng, H., McDonough, N., Nolte, N., Olsen, E., Olsen, J., Philippart, K., Queguiner, B., Ramirez-Llodra, E., Roest, W., Santos, R., Seys, J., Sluijs, A., Solidoro, C., Souza Pinto, I., Steenbergen, J., Stomsem, K., Sultan, N., Tyler, P., van den Hove, S., van Hoof, L., Vanreusel, A., Viard, F., Volckaert, F., Wallmann, K., Weaver, P., Wood, J., Wood, L., 2013. Navigating the Future IV. Position Paper 20 of the European Marine Board, Ostend, Belgium, . ISBN: 9789082093100.p. 203.
- Barstow, S.F., 1983. The ecology of Langmuir circulation: a review. *Mar. Environ. Res.* 9 (4), 2011–2236.
- Boero, F., Bonsdorff, E., 2007. A conceptual framework for marine biodiversity and ecosystem functioning. *Mar. Ecol.* 28 (Suppl. 1), 134–145. An evolutionary perspective.
- Boero, F., Brotz, L., Gibbons, M.J., Piraino, S., Zampardi, S., 2016a. Impacts and effects of ocean warming on jellyfish. In: Laffoley, D., Baxter, J.M. (Eds.), *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*. Full Report. IUCN, Gland, Switzerland, pp. 213–237.
- Boero, F., Fogliani, F., Frascchetti, S., Goriup, P., Machpherson, E., Planes, S., Soukissian, T., Consortium, C.C.N., 2016b. CoCoNet: Towards Coast to Coast Networks of Marine Protected Areas (From the Shore and the High and Deep Sea), Coupled with Sea-Based Wind Energy Potential. *SCI-RES.IT* 6 (supplement). CASPUR-CIBER Publishing, pp. 1–95.
- Broecker, W.S., 1991. The great ocean conveyor. *Oceanography* 4 (5), 79–89.
- Brown, J., 1995. *Macroecology*. University of Chicago Press, p. 269.
- Canepa, A., Fuentes, V., Sabatés, A., Piraino, S., Boero, F., Gili, J.M., 2014. *Pelagia noctiluca* in the Mediterranean Sea. In: Pitt, K.A., Lucas, C.H. (Eds.), *Jellyfish Blooms*. Springer Science + Business Media Dordrecht, pp. 237–266.
- Civitaresse, G., Gačić, M., Lipizer, M., Eusebi Borzelli, G.L., 2010. On the impact of the bimodal oscillating system (BiOS) on the biogeochemistry and biology of the Adriatic and Ionian seas (eastern Mediterranean). *Biogeosciences* 7 (12), 3987–3997.
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Galil, F.C., BS, G.J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.S., Koukouras, A., Lampadariou, N., Laxamana, E., de la López-Fé Cuadra, C.M., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., San Vicente, C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS One* 5 (8), e11842.
- Danovaro, R., Boero, F., 2019. Italian seas. In: Sheppard, C. (Ed.), *World Seas. An Environmental Evaluation*, second ed. Academic Press, London, pp. 283–306.
- Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel, R., Hjøllø, S.S., et al., 2012. Mesoscale eddies are oases for higher trophic marine life. *PLoS One* 7 (1), e30161.
- Guzman, L.M., Germain, R.M., Forbes, C., Straus, S., O'Connor, M.I., Gravel, D., ... Thompson, P.L., 2019. Towards a multi-trophic extension of metacommunity ecology. *Ecol. Lett.* 22 (1), 19–33.
- Hays, G.C., 2017. Ocean currents and marine life. *Curr. Biol.* 27, R470–R473. <https://doi.org/10.1016/j.cub.2017.01.044>.

- Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C., Pérez, T., 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends Ecol. Evol.* 25 (4), 250–260.
- Longhurst, A. (Ed.), 2010. *Ecological Geography of the Sea*, second ed. Academic Press, San Diego, CA.
- Marcus, N., Boero, F., 1998. Production and plankton community dynamics in coastal aquatic systems: the importance of benthic-pelagic coupling and the forgotten role of life cycles. *Limnol. Oceanogr.* 43 (5), 763–768.
- Naem, S., Wright, J., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.* 6, 567–579.
- Pati, A.C., Belmonte, G., Ceccherelli, V.U., Boero, F., 1999. The inactive temporary component: an unexplored fraction of meiobenthos. *Mar. Biol.* 134, 419–427.
- Pepin, P., Robert, D., Bouchard, C., Dower, J.F., Falardeau, M., Fortier, L., Jenkins, G.P., Leclerc, V., Levesque, K., Llopiz, J.K., Meekan, M.G., Murphy, H.M., Ringuelette, M., Sirois, P., Sponaugle, S., 2015. Once upon a larva: revisiting the relationship between feeding success and growth in fish larvae. *ICES J. Mar. Sci.* 72, 359–373.
- Pineda, J., Hare, J.A., Sponaugle, S., 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20 (3), 22–39.
- Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.), 2017. *Marine Animal Forests*. Springer. 1336 pp.
- Sayre, R.G., Wright, D.J., Breyer, S.P., Butler, K.A., Van Graafeiland, K., Costello, M.J., Harris, P.T., Goodin, K.L., Guinotte, J.M., Basher, Z., Kavanaugh, M.T., Halpin, P.N., Monaco, M.E., Cressie, N., Aniello, P., Frye, C.E., Stephens, D., 2017. A three-dimensional mapping of the ocean based on environmental data. *Oceanography* 30 (1), 90–103.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57, 573–583.
- Spalding, M.D., Agostini, V.N., Rice, J., Grant, S.M., 2012. Pelagic provinces of the world: a biogeographic classification of the world's surface pelagic waters. *Ocean Coast. Manag.* 60, 19–30.
- Tremblay, E.A., Roberts, J.J., Chao, Y., Halpin, P.N., Possingham, H.P., Riginos, C., 2012. Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integr. Comp. Biol.* 52, 525–537. <https://doi.org/10.1093/icb/ics101>.
- Zuercher, R., Galloway, W.E., 2019. Coastal marine ecosystem connectivity: pelagic ocean to kelp forest subsidies. *Ecosphere* 10 (2), 1–35. Article e02602.