

Linking ecosystems, habitats, and biodiversity: from the grand picture to the tiny details, and back

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ABSTRACT

Natural sciences usually proceed through the analysis of facts that are then assembled into a general framework, often called a “theory”. I have tried here to assemble the “tiny facts” that I have uncovered in my career and to organize them into a holistic perspective. I have chosen to start from the “big picture”, *i.e.*, the functioning of ecosystems, to focus then on details regarding the expression of biodiversity, from the role of life cycles in ecosystem functioning, to the way of assessing biodiversity based on the accurate knowledge of its evolution in time. The Historical Biodiversity Index allows to compare the potential biodiversity (all the species recorded from the studied habitat type) with the realized biodiversity (the species found by sampling in that habitat). The study of natural history might lead to unexpected ecological connections, such as the dynamics of plankton (the most important ecological phenomenon of the whole planet) and the composition of resting stage banks, or the keystone role of the interstitial fauna in determining the diversity of plankton. The oceanic realm is in three dimensions and must be considered as a volume rather than as an area. Living systems, though, change constantly and a fourth dimension (time) is crucial to understand their structure and function. The cells of ecosystem functioning, based on connectivity, are proposed as natural spatial units for both management and protection from human impacts.

INTRODUCTION

The Italian Association of Oceanography and Limnology (AIOL) invited me to summarize my work in the field of marine biology and ecology, a path that started in 1976 with a joint paper with Norberto Della Croce (Della Croce and Boero, 1976), one of the founders of AIOL. Necessarily, the number of self-citations will prevail in the references. I have tackled issues regarding Biodiversity and Ecosystem Functioning (BEF) in a series of papers that I will assemble here, synthesizing my own views on how to deal with BEF. In most cases, I simply put together pieces of knowledge that were produced by other authors, that are cited in my papers and that I will not cite here, if not directly relevant. I will cite papers that I overlooked, while expressing as original what was not original at all. Such as the papers that I did not cite in my contribution on fluctuations and variations in the marine environment (Boero, 1994), namely Fauvel (1901) and Parenzan (1934).

I like very much the say “you are what you eat”, and I extend it somehow to “you are who you meet”. I met many interesting people, and learnt a lot from them, absorbing their wisdom like a sponge. I spent long periods in places that are at the opposite ends of what we call civilization: California and Papua New Guinea. The places where we live are also important in shaping us. Having met so many people, in so many countries, contributed to the way I see things.

I want to cite a single person here: Frank Zappa. Frank was a composer, and he formalized his approach to music with two concepts: the Big Note, and Conceptual Continuity.

When we hear a piece of music played by an orchestra, we hear a Big Note. The “little notes” of the players,

once blended, produce the music, perceived as a single combination of vibrations. If we listen to a single instrument at a time, we do not hear the music. The “little notes” are linked by a Conceptual Continuity that leads to what we hear. The composer writes the scores for each instrument so as to produce the Big Note as a final result.

I like music and when I learnt about the way Zappa saw it, I realized that science is the same.

With reductionism, scientists split a complex reality into a suite of less complex objects that are investigated in isolation from the rest. This led to prodigious scientific advances in all fields of science, whose branches are just like the instruments of an orchestra, each one playing its own “little notes”. Of course, each player thinks that s/he is playing the most important part of the music.

After almost a century of specialization, we realized that the whole is more than the sum of the parts: the appreciation of emerging properties is the trademark of ecology. Reductionism, then, should evolve into a holistic approach, identifying the Conceptual Continuity that links the little notes of each science branch into the Big Note, *i.e.*, the natural world.

There is a difference between music and science, though. The composer is the creator of the music. Scientists analyse phenomena that are not the result of their action. Steve Vai is a guitar player that, listening to the intricate guitar solos improvised by Frank Zappa, transcribed them and produced scores that did not exist before. We are like Steve Vai, let us say. But we do not transcribe the scores played by a single instrument. Music can be composed on a single instrument, to be then orchestrated. Zappa composed The Black Page as a drum solo, and then he wrote the scores for a whole band, so as to enhance its “statistical density”.

The challenge of this paper is to build a conceptual continuity that links all the things I have done in almost half a century. The problem, with science, is that we cannot listen to the message of 20 scientists, as we do when musicians play orchestral music. We listen to them one at a time. Words cannot convey a holistic vision because they are necessarily reductionistic: we hear one word at a time. But figures can deliver a visual message that can be holistic. I drew figures in my papers but, when I met the artist Alberto Gennari, I stopped producing drawings and I asked him to transform my concepts into visual objects that might deliver a holistic message.

HOW TO DEPICT AN ECOSYSTEM

The ocean covers 71% of the planet, but the oceanic space is not a surface, it is a volume. With an average depth of about 4.000 m, the volume of the ocean is more

than 90% of the life-inhabited space. Hence, the ocean is the rule, and the land is an exception, even though we tend to use the term ecosystem to label terrestrial ecosystems, and we use the adjective “marine” when dealing with oceanic ecosystems (Boero, 2021a).

If we want to depict the functioning of an ecosystem, then, it is scientifically sound to describe a marine ecosystem, considering mostly the water column, *i.e.*, the three-dimensional space that makes up the bulk of “terrestrial” ecosystems. The main characters that play a role in the functioning of an ecosystem and the relationships that link them to one another are illustrated in Figure 1.

Visually, carnivores dominate the water column, as exemplified by the white shark eating the tuna, eating the mackerel, eating the sardine. Such an environment cannot persist, even though fisheries science often focuses on fish and disregards other components of the ecosystems, for instance, jellyfish (Boero, 2013). In the euphotic zone, the coastal landscape is dominated by algae and seagrasses,

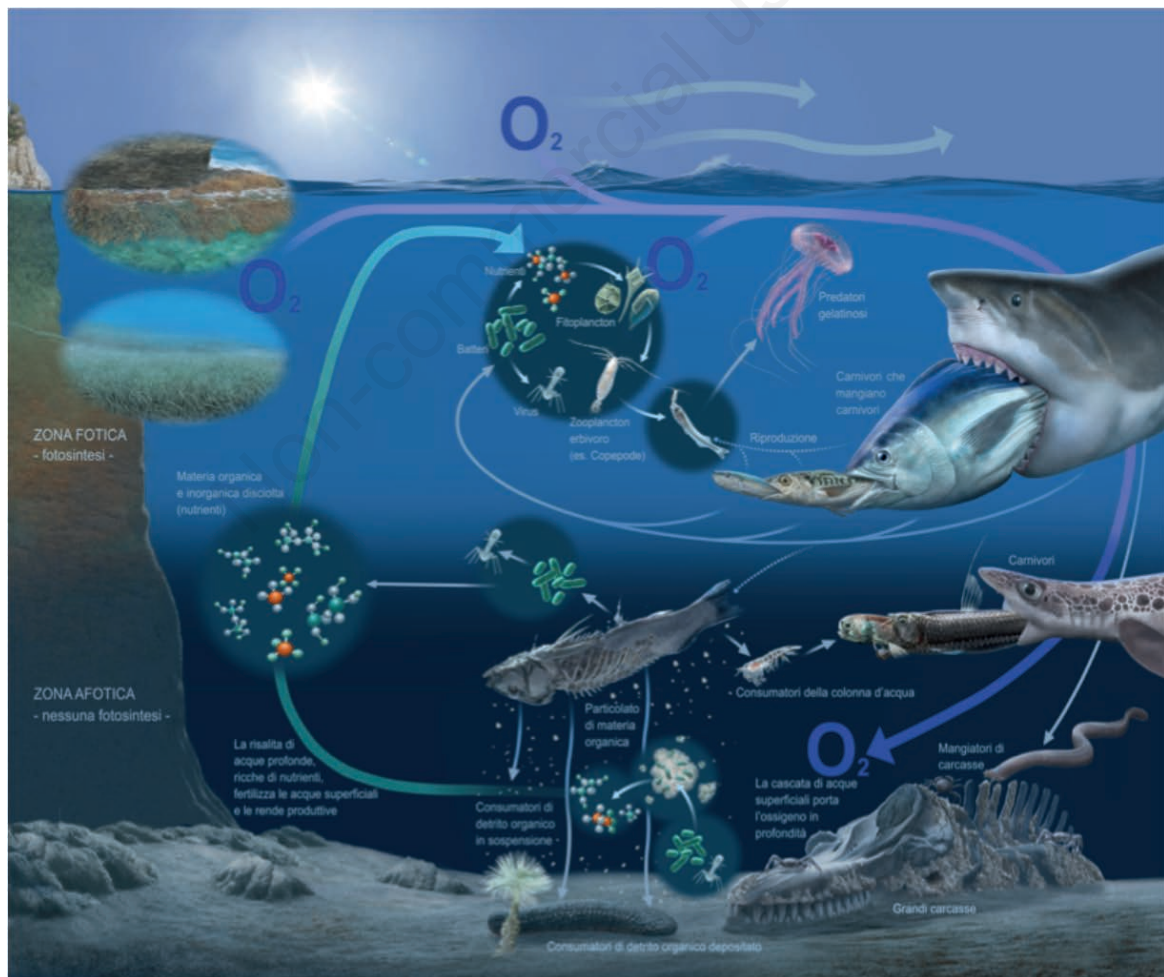


Figure 1. The structure and function of an ecosystem (*concepts: F. Boero; artwork: Alberto Gennari; from the exhibit of the Darwin Dohrn Museum, Naples, Italy*).

and by zoobenthos (not shown), but the vast majority of the water column, *i.e.*, the pelagic domain, is not characterized by primary producers that we can see. The adult bony fish we see, apparently making up most of the whole trophic network, start their life as eggs, embryos, larvae, and juveniles. These early stages feed on herbivorous zooplankton (here exemplified by a copepod) that, in their turn, feed on phytoplankton (here shown as dinoflagellates and diatoms). These are the herbivores and the primary producers: contrary to terrestrial ecosystems, they are microscopic. Jellyfish eat both the herbivores and the eggs, larvae, and juveniles of fish. If one tuna is considered as a life cycle, it is highly probable that jellyfish kill more tuna (when they are eggs, larvae and juveniles) than white sharks do. All living beings eventually die and are decomposed by bacteria that make nutrients available to phytoplankton. Viruses are a cause of bacterial mortality. The “microbes” (*i.e.*, phytoplankton, bacteria, and viruses) are the core of ecosystem functioning and are often labelled as the microbial loop. Microbes, however, are not only a loop, but they are also the pillars of all ecosystems.

The lower part of Figure 1 shows the deep sea, where light is either absent or not sufficient for photosynthesis. The living matter produced “above” changes status and, after the death of the organisms, sinks towards the deep and is decomposed by bacteria, becoming particulate organic matter (marine snow). Also, faecal pellets (not shown) are important in this transfer from the surface to the deep, as are the migrations of organisms that move towards the surface to search for food. Marine snow sustains a host of detritivores and suspension feeders, here exemplified with pelagic crustaceans and benthic echinoderms and annelids. The large carcasses, in this case, killer whales, fall to the sea bottom and are consumed by scavengers.

This dark domain is the vast majority of the space available for life. The oxygen is produced by the primary producers and is also dissolved to the water through air-water exchanges. Both phenomena occur near the surface. Downwelling currents bring the oxygen to the deep sea and trigger upwelling currents that bring nutrients from the deep to the surface, where they will sustain the primary producers. The scenario depicted in Figure 1 can be further defined in terms of pathways (Figure 2).

The center of the figure represents the microbial loop: all living beings die (the central black circle with corpses) and are decomposed by heterotrophic bacteria that, in their turn, can be killed by viruses. Bacterial decomposition leads to the production of nutrients that are used by phytoplankton (here as diatoms and dinoflagellates). Nutrients are brought to the sea also by terrestrial runoffs. Heterotrophic microbes (here as a ciliate protozoan) feed on the other microbes. For millions of years, life functioned in this way. It still can happen that microbes pre-

vail, and the microbial loop leads to a microbial pathway, as is the case of red tides, *i.e.*, abnormal proliferations of phytoplankters such as dinoflagellates (top right). The evolution of Metazoa led to the consumption of microbes by filter feeders, such as the small crustacean, a copepod, that is at the margin of the microbial core.

A second pathway (bottom right), thus, involves microbes, herbivores, fish larvae and juveniles that, in their turn, become adult fish and feed on each other. This is our favorite pathway and leads directly to us, through fisheries.

A third pathway (bottom left) involves gelatinous herbivores, here depicted as a salp chain. When these animals develop huge populations, they overexploit the microbial component and compete with the copepods, thus having an impact on the pathway that leads to the fish.

A fourth pathway (top left) involves gelatinous carnivores, here depicted as a cnidaria jellyfish and two ctenophores. These predators feed upon the herbivores and the eggs, larvae, and juveniles of fish, being themselves top predators. Gelatinous plankton can be represented by huge populations that can re-direct the functioning of ecosystems, as argued by Boero *et al.* (2008) and Boero (2013). Not all living matter is recycled and portions of it can become incorporated in the sediments, where carbon seques-

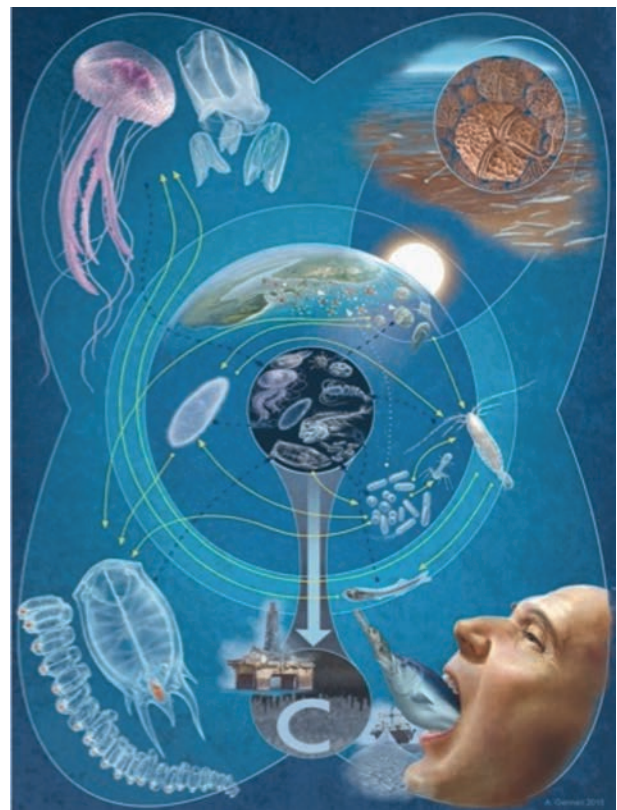


Figure 2. The four pathways of living matter in marine ecosystems (concepts: F. Boero; artwork: Alberto Gennari).

tration occurs (bottom center). Figure 2 shows the pathways that characterize the photic zone.

A fifth pathway is shown in Figure 1 for the deep sea, where marine snow triggers a trophic network based on detritus, with species that can perform diel migrations from the deep sea to the surface and back.

INTRA- INTER- AND EXTRA-SPECIFIC FLUXES

Figures 1 and 2 can be formalized in an abstract fashion (without showing the organisms) so as to illustrate the fluxes of matter across food webs. Ecology is usually divided into several branches that tackle single topics. Life cycles, for instance, deal with the flux of living matter across generations of the same species (intraspecific fluxes). Trophic networks, instead, deal with the flux of living matter from one species (the producer) to another species (the consumer) (interspecific fluxes) (Boero and Bonsdorff, 2007).

Figure 3 assembles three approaches to the study of the fluxes of matter across ecosystems. Biogeochemical cycles represent fluxes of matter that is not organized in a living form, *i.e.*, into species, and can be defined “extra-specific” fluxes. Primary producers, plants, protists and monerans, with photo- and chemosynthesis, organize the “nutrients” in a living form. These organisms, like all other organisms, perpetuate the existence of their species through life cycles that represent “intra-specific” fluxes across generations. The fate of primary producers is double. They die and are recycled by decomposers, represented by fungi and monerans that disassemble them, contributing to the production of “nutrients”, fuelling extra-specific fluxes. Besides decomposing the materials, these organisms consume them also to synthesize their bodies (bacterial and fungal synthesis). All other components of food webs are subjected to the same fate if they

are not consumed by organisms at higher trophic levels. Decomposers, like all other components of the food webs, perpetuate themselves with intraspecific fluxes, *i.e.*, their life cycles. The primary producers can also be consumed by secondary producers, *i.e.*, animals and heterotrophic protists (protozoans). In this case, living matter flows from the primary to the secondary producers giving rise to “inter-specific” fluxes. The guts of secondary producers decompose the primary producers, often with the aid of heterotrophic bacteria, and then synthesize their food into their own bodies (zoo-synthesis) besides using their food as a source of energy for their body functions. Secondary producers, *i.e.*, the herbivores, are in their turn consumed by tertiary producers, the carnivores, and these can be consumed by higher trophic levels that can be again predators or, in alternative, parasites, *i.e.*, micro-predators that do not kill their prey.

In marine systems, the food webs can be very long, as shown in Figure 1, where a white shark eats a tuna that eats a mackerel, that eats a sardine, and where the larvae of all bony fish eat herbivorous zooplankton that feeds upon phytoplankton. The same species, furthermore, can occupy much different trophic positions during its life cycle. A tuna, for instance, can be preyed upon by a white shark as an adult large fish, but, as a larva, it can be eaten by a jellyfish (Figure 1 and 2). The diet of a tuna, moreover, can be based on herbivores at larval and juvenile stages, whereas it shifts to much higher trophic levels as size increases.

The linkages between the three branches of ecology that are often kept separate, *i.e.*, life cycles, trophic networks, biogeochemical cycles are illustrated in Figure 3.

FOCUSING ON IMPORTANT PROCESSES

The functioning of oceanic ecosystems is the most important ecological process on Earth, since the ocean covers more than 70% of the planet. Contrary to terrestrial systems, marine systems function in pulses, with seasonal plankton blooms.

Figure 4 shows the seasonal pulses at the base of the functioning of marine systems. In spring, phyto- and zooplankton proliferate (in Figure 1 it is shown how “microbes” sustain higher trophic levels, dominated by carnivores). In summer, the plankton that has not been consumed by planktivorous organisms dies off and falls to the bottom. In fall, mild mixing triggers secondary plankton blooms. In winter, turbulence is maximal, and the nutrients are resuspended, so fuelling the spring blooms of phytoplankton that, in turn, fuel the zooplankton in the following spring. A series of papers (Boero, 1994; Belmonte *et al.*, 1995; Boero *et al.*, 1996; Marcus and Boero, 1998, among others) complements the biogeo-

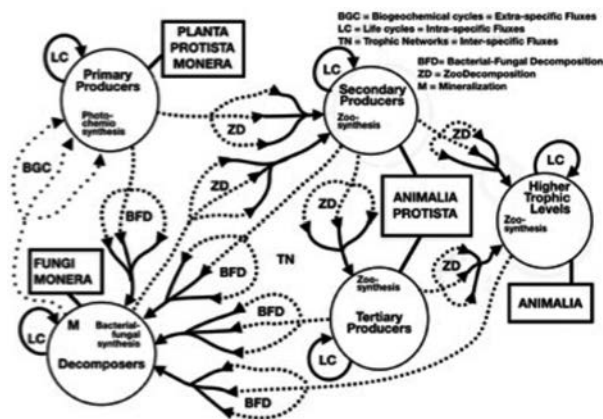


Figure 3. The fluxes of matter across ecosystems.

chemical explanation of ecosystem functioning with a life cycle approach that recognizes a crucial role to benthic stages of planktonic organisms. Many coastal plankters, in fact, are represented by huge biomasses for short periods, to disappear shortly thereafter. The traditional answer to the question “Where are they when they are not there?” is “Somewhere else” or, in alternative, “they are very rare and then become abundant again”. The fate of plankters that form true swarms and then disappear is not a mystery if jellyfish are concerned. Boero *et al.* (2008) answered this question for gelatinous plankton and especially jellyfish. Some jellyfish are holoplanktonic, but most of them have benthopelagic life cycles that involve both planktonic (jellyfish) and benthic (polyps) stages. These, however, were often studied by different scientists that focused either on the benthic or the planktonic stages. Bouillon *et al.* (2006) tried to put some order in the Hydrozoa, proposing a single classification that unites both polyps and medusae but, for many planktonic taxa, from copepods to rotifers, diatoms and dinoflagellates, benthic stages are given almost no ecological relevance. Figure 4 also shows the benthic resting stages and introduces life cycles so as to complement the biogeochemical approach to the explanation of plankton dynamics. Phytoplankton does not come from nutrients, and zooplankton does not come from phytoplankton! As illustrated in Figure 3, biogeochemical cycles, life cycles and trophic networks must be considered altogether, so as to fully understand the functioning of ecosystems.

DO PLANKTON, NEKTON AND BENTHOS REALLY EXIST?

My personal answer is no. These domains have been recognized based on the tools we use to study marine bi-

ology and ecology. Jellyfish are collected in the water column, with plankton nets or plastic bags, whereas their polyps are collected from the sea bottom, with scuba diving or with dredges and grabs, and those who study the very same animals consider just one stage of the life cycle. The same is true for fish, studied by fisheries biologists as nektonic adults, whereas their larvae are studied by planktonologists. Benthic organisms with planktonic larvae are almost the rule. Even if the larval and juvenile stages are often short-lived, they make choices that are vital for the benthic adults that develop from them (Fraschetti *et al.*, 2003).

Pati *et al.* (1999), furthermore, demonstrated the coexistence of the meiofauna and the resting stages of plankters in marine sediments. Meiofauna and resting stages, however, are extracted with different techniques by different specialists, and are rarely considered as a whole. Consequently, the relationships that might occur among these coexisting species are almost entirely unknown. Many members of the meiofauna do have piercing mouthparts and sucking pharynxes: what do they pierce and suck? Resting stages are “seeds” and, at the same time, are rich in nutrients and, thus, represent a potential food source for the meiofauna. Pati *et al.* (1999) hypothesized that, as shown in Figure 5, after a plankton bloom the resting stages of the dominating species would fall on the sea bottom and become incorporated into the sediments. The resulting massive amounts of resting stages might guarantee the re-occurrence of the bloom in the following favourable seasons, thus acting as “seeds”. This is seldom the case, and the meiofauna might play a keystone role with predation on the resting stages (which thus are also a food source) of the previously dominant species, so enhancing or the diversity of plankton.

The links among plankton, benthos and nekton are pervasive, but the connections among these domains are

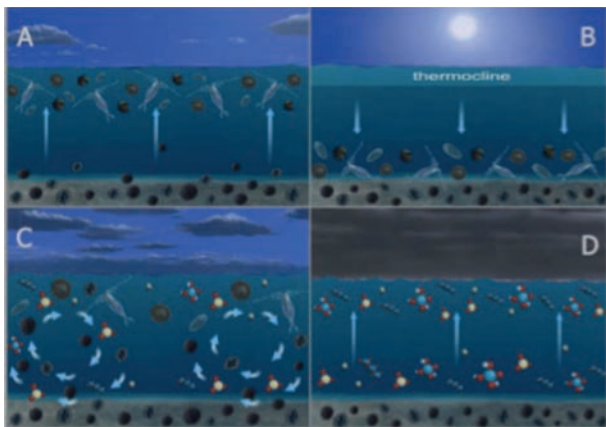


Figure 4. Plankton seasonality. A: spring; B: summer; C: fall; D: winter (concepts: F. Boero; artwork: Alberto Gennari).



Figure 5. The predation of meiofauna on resting stage banks (concepts F. Boero; artwork Alberto Gennari).

often neglected and this artificial separation hinders a holistic comprehension of the functioning of marine ecosystems. Boero (*e.g.*, 1994, 1996, 2021a, 2021b) and Boero *et al.* (2004, 2019b) have repeatedly stressed the need for the unification of these approaches which, however, remain separated from each other in most research projects.

FROM ECOSYSTEM FUNCTIONING TO BIODIVERSITY AND BACK

The former section depicts the functioning of ecosystems in terms of connections through “artificial” compartments, defined for ease of analysis and seldom united into a single, holistic vision.

This functional approach must be complemented with a structural counterpart. In recent decades the acronym BEF (Biodiversity and Ecosystem Functioning) became fashionable, with the aim of linking structure and function (Heip *et al.*, 2009).

This is realized in the Marine Strategy Framework Directive of the EU and the eleven descriptors of Good Environmental Status (GES) therein. The pillars of GES are just biodiversity and ecosystem functioning (Boero, 2016). The holistic approach defined above is the result of reductionistic analyses, but I preferred to sketch the whole picture before entering structural details, even if these are the factual basis for the synthesis.

BIODIVERSITY

The assemblage of species living in a given ecosystem, often colonizing different habitats throughout their life cycles, is the most obvious definition of biodiversity. Each species has an inner diversity in terms of genetic make ups, and the different combinations and abundances of species produce a higher level of diversity, with emerging properties that do not equal to the simple sum of the species that can be found in a given ecological space. This has led to many diversity indexes, translating into numbers the information that can be drawn by sampling at a given place.

Biodiversity can be considered as a “structure” that is conducive to a “function”, the functioning of ecosystems the previous section dealt with. The acronym BEF (Biodiversity and Ecosystem Functioning) links structure and function, patterns, and processes. Since the times of Darwin, it is assumed that high biodiversity leads to high efficiency in the functions of ecological systems (Boero, 2015a).

The aim of a BEF approach is to reach a holistic vision of the marine environment, assembling reductionistic approaches so as to understand the whole after having carefully inspected the parts. This stems from the say that “the whole is more than the sum of the parts”, namely the emerging properties that should be the main object of eco-

logical studies. At present, however, marine ecology is still mostly reductionistic.

REDUCTIONISTIC ECOLOGY: THE OXYMORON

Marine science is still practised by many sciences. Each branch focuses on portions of the marine space and of marine biodiversity and is often disconnected from other branches. The array of topics is overwhelmingly vast. Physical oceanography deals with the physics of the sea. It is studied with oceanographic vessels, automated vehicles, and satellites and it generates predictive models. The interaction with the atmosphere is often disregarded, as is the interaction with the sea bottom and the coastline. This calls for marine geology, whose main objective is to map the sea bottom and understand sediment transport along coasts. This involves physics, but it is often the case that geologists collaborate with hydraulic engineers, rather than with physical oceanographers. Marine chemistry deals with the chemical properties of seawater, firstly salinity which, indeed, interacts with temperature in generating thermohaline currents, such as the great ocean conveyor belt. Ocean acidification is also a matter of chemistry, and is an emerging field of marine chemistry, with a great bearing on marine biology. Marine biology, furthermore, is divided into three main domains: plankton, benthos, and nekton. They are further divided into many sub disciplines. Phytoplankton comprises autotrophic organisms, such as diatoms, flagellates, and bacteria: these tiny organisms are called microbes, whose study is labelled as microbial ecology. Zooplankton is divided into size categories that span from heterotrophic ciliates to the giants of macro-zooplankton which, in their turn, are also labelled as gelatinous plankton, comprising species that range from chordates (*e.g.*, the thaliacea) to cnidarians and ctenophores. The plankton, furthermore, comprises also species that spend just a period of their life in this domain, sometimes as larvae (*e.g.*, fish and many benthic animals) sometimes as adults (*e.g.*, the sexually competent jellyfish that have benthic polyps). The nekton is made of animals that can actively swim against the current. The nekton is also studied by fisheries biology, from a resource management point of view. Marine conservation deals with the protection of the marine environment. All these disciplines are based on the recognition of species, *i.e.*, on taxonomy, whose approaches can be either phenotypic or genotypic, or both.

The study of species must reconstruct their life cycles, and this clearly show that these domains are fading into each other for most species. Many supposed holoplankters (spending their whole life in the plankton) very often do have benthic resting stages and their blooms are fuelled

by a benthic resting stage bank (Boero *et al.*, 1996; Marcus and Boero, 1998). Trophic networks, in their turn, connect the three domains. Juvenile fish do feed on plankton, then change their diet when they grow up. As larvae or juveniles, fish are eaten by predators that then can be the prey of the adult stage.

Furthermore, the division between the deep sea, the high seas, and the coastal areas, each studied by different portions of the scientific community, is unnatural, since these domains are highly connected by vertical and horizontal currents, from the great ocean conveyor belt to the local up- and down-welling processes generated by winds and submarine canyons. The ocean is, instead, one.

Such a need for a holistic approach is often invoked, as the European Marine Board did in the introduction of Navigating the Future IV: “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 for Europe, but for human society as a whole” (Arnaud *et al.*, 2013).

THE EVOLUTION OF APPROACHES

The habitat approach embraced with the Habitats Directive, dealing exclusively with benthic habitats (Fraschetti *et al.*, 2008), eventually evolved into the ecosystem approach in the Marine Strategy Framework Directive and its 11 Descriptors of Good Environmental Status, having BEF as its pillar (Boero, 2016). “Biodiversity is maintained” is the first Descriptor. The other 10 list a series of impacts that must be kept below threshold, so as to maintain the functioning of the ecosystems in “good” status. Of course, the meaning of “good” in these measures is: good for us. So, the concept of goods and services emerged with ecological economics: nature is important because it supports us with goods and services that can be given a price. If we destroy nature, we will lose money! The argument here is that decision makers care only for money, so it is better to talk about money when talking about nature, often confusing value with price (Boero, 2008).

The words “maintain” and “conservation” imply that we should identify a reference status and that we should keep it. But what is the reference status we want to maintain? The present one? Almost all agree that the present one is not so good. So, the question is: what is the ocean we want? (Boero, 2021b). Do we want to maintain the current situation, or do we want it to go back to previous statuses? Is it wise to propose that things must not change, or that they must go back to previous statuses? This is what political conservation wants. The natural world,

however, is a changing world, whose trademark is evolution, *i.e.*, change. A challenge, thus, is to understand change, and to study it.

The marine realm has three dimensions, and must be studied in terms of volumes, but the processes studied by marine ecology are rapid. The water column makes up most of the ecological space available to life and living processes proceed in pulses: phytoplankton pulses are followed by zooplankton pulses, and the two sustain an apparently stable nektonic component. Microbial processes are the core of the functioning of marine ecosystems and sustain most of the deep-sea life, where photosynthesis is impossible due to lack of light.

Marine ecosystems, thus, are very dynamic. As terrestrial animals, we are attracted by landscapes that are part of our experience, such as algal, seagrass or animal forests that are as stable as most terrestrial vegetation, but the majority of the marine space is not linked to the sea bottom and there the processes are very dynamic.

FLUCTUATIONS AND VARIATIONS: THE FOURTH DIMENSION

The perception that natural systems do change within the short term, especially in the marine realm, is not new, and Fauvel (1901) and Parenzan (1934) were among the first to realize that even apparently stable benthic systems do vary in their species composition and that species that were previously rare can become suddenly abundant, whereas abundant species can become rare.

Boero (1994, 1996) reached their same conclusion, arguing that stability does not exist in natural systems, especially in marine ones, and that the situations we can depict with a given sampling session represents a “moment” that is part of a “story”. Regular fluctuations (*e.g.*, seasonal ones) are different from variations, when what is perceived as “normal”, in terms of the species composition at a specific location, changes and common species become rare whereas rare species become abundant. Boero (1994) argued that the species pool in a given basin tends to remain stable, but that each species contributes with different biomasses to the total biomass that the system can “express” which can remain stable in terms of quantity but not of quality.

Furthermore, the species pool can change due to the arrival of non-indigenous species that can contribute to the maintenance of biodiversity (in terms of species numbers) in a changing ocean (Boero, 2021b). If a basin warms up, due to global warming, the indigenous species will suffer from the new conditions, but these will be conducive to the thriving of species that are adapted to higher temperatures. These species are often non-indigenous ones. This calls for the second descriptor of Good Envi-

ronmental Status: “non-indigenous species do not adversely alter the ecosystem”. Non-indigenous species are often labeled as noxious invaders, but they can also replace the species that cannot withstand new conditions, determined by global change, as Boero (2021b) suggested. Non-indigenous species, or aliens, can be noxious, such as the ship driven ones, that invade basins where they can outcompete indigenous species (Boero, 2002), but this is not the case for all “aliens”. The alteration of ecosystems, thus, can be due to changing physical conditions (e.g., global warming) or to the arrival of a noxious alien, as is the case of the ctenophore *Mnemiopsis leydi* that dramatically changed the Black Sea ecosystem (Boero *et al.* 2008; Boero, 2013). Boero *et al.* (2019), hence, proposed the concept of the Ocean in 4D: the surfaces of the sea bottom and sea surface are in 2D, the water column is in 3D, and the dynamics of marine systems add a fourth dimension to the system: time. Boero *et al.* (2015) stressed the importance of time series and labeled time as an affliction because, when a given situation seems to be described and understood... it changes, and our predictions fail. The historical nature of bio-ecology is not conducive to predictions stemming from mathematical models, at the press of a button (Boero *et al.* 2004): we cannot predict what will happen tomorrow even in our history which, in turn, depends on the history of natural systems, with innumerable feedbacks and interacting variables. Indeed, episodic events (Boero, 1996) can be important drivers of change that lead to different statuses of ecosystem structure and function.

MEASURING BIODIVERSITY, LINKING IT TO HABITATS

Boero and Bonsdorff (2007) proposed the Historical Biodiversity Index (HBI) to introduce time in the evaluation of the status of biodiversity. Its application requires a thorough knowledge of biodiversity from a historical perspective. The index is very simple:

$$\text{HBI} = \text{realized biodiversity} / \text{potential biodiversity}$$

Where realized biodiversity is the species pool resulting from a sampling session in a given habitat, and the potential biodiversity is the list of species that, in the biogeographical region where the samples have been collected, includes all species recorded in previous studies of the sampled habitat.

Checklists of species have been made for most biogeographic regions, the European Register of Marine Species (Costello *et al.*, 2001) being a significant example. Some work is still necessary to assemble a complete list of habitats (Fraschetti *et al.*, 2008) since benthic habi-

tats have received much attention, whereas pelagic ones are still less clearly defined.

For each biogeographic unit, thus, a matrix can be built, comprising both the species that have been recorded from that unit, and the habitats that are present in the very same unit. Each species is then to be assigned to the habitats where it has been recorded from. Some are exclusive to a single habitat (e.g., the species leaving only on seagrass leaves, or in specific symbiotic associations) whereas others are present across many habitats. The table leads to a species list for each habitat: the potential biodiversity. A sampling session in a given habitat leads to a species list: the realized biodiversity. This can be increasingly efficient also by using environmental DNA.

The value of HBI is 1 if the number of species found in sampling session (realized biodiversity) equals the number of species found throughout the study of the sampled habitat (potential biodiversity). If no species is found, the index is 0. The more the index approaches to 1, the more biodiversity is maintained, the more it approaches to 0, the more biodiversity is eroded.

Since the quantitative contribution of species varies in time (Boero, 1994) it is useless to focus much on the quantities of each species, since they undergo continuous change. The apparent disappearance of a previously dominant species might not be a tragedy if other species replace it.

Besides being assigned to one or more habitats, furthermore, each species should be classified based on its trophic role. The presence of species that have a basic role in trophic networks should be more constant, whereas the species occupying high trophic levels are more liable of being “eroded”. The disappearance of top predators, and the dominance of species with lower trophic roles, is now labelled as trophic downgrading (Britten *et al.*, 2014). The comparison of species lists, if accurate, provides a wealth of information about the history of a given ecosystem, and of its status.

The index, furthermore, provides a very useful information that is usually not considered in sampling sessions: it provides the list of species that have not been found, and that were found in the past. This information will allow the detection of species that are not being found anymore and that might be putatively extinct species (Boero *et al.*, 2013; Boero and Gravili, 2013; Gravili *et al.*, 2015). If the sampling leads to species that were previously unrecorded (e.g., non-indigenous species) they are to be added to both the potential and the realized biodiversity. Since the exploration of biodiversity is far from being complete, it is possible that species new to science are also found. These might be indigenous species that have been overlooked by previous sampling sessions, or non-indigenous species that have not been described from their sites of origin. The quite evident jellyfish *Pelagia benovici*, for instance, recently bloomed in the Adriatic

Sea and was described as a new species by Piraino *et al.* (2014). Since the jellyfish fauna of the Adriatic Sea is rather well known, it was hypothesized that *P. benovici* reached the Adriatic from elsewhere, even though, from a zoological point of view, the Adriatic is its typical locality. The revision of genera, furthermore, might lead to the splitting of a nominal species into a set of distinct species, as is the case of *Aurelia* (Scorrano *et al.*, 2017), whose diversity in the Mediterranean is much greater than previously recognized.

The species pool of a basin is made of all the species that have been recorded from its waters. Some species are known since the beginning of the study of biodiversity and are part of what is considered as the “native” species pool of a basin. Many of these species have been described in 1758 and in the following years, by the pioneers of the study of biodiversity, and they are usually quite evident. The original species pool is not very rich, but it increases with the refinement of biodiversity exploration. As long as species are discovered either as new species or as new records, the species pool increases in size. The HBI can, thus, identify putative extinctions.

MARITIME SPATIAL PLANNING

Once biodiversity and ecosystem functioning are framed into a conceptual framework, they must also be framed spatially, with the four-dimensional approach depicted above. This will allow to manage our activities in the marine environment, as required by the European Commission with the Directive on Maritime Spatial Planning.

The Habitats Directive is a prelude to maritime spatial planning, since it identifies the benthic habitats that deserve protection. Single states, furthermore, defined other important areas as national Marine Protected Areas, not necessarily based on the Habitats Directive. Boero (2017) argued that most MPAs are designed to protect charismatic habitats that do not necessarily comprise ecosystems. It is rarely the case, in fact, that a single habitat comprises an entire ecosystem. Protecting a habitat without protecting the ecosystem it depends on is not ecologically sound. For this reason, the European Commission shifted its focus from habitats and MPAs to ecosystems (the Marine Framework Directive and the Maritime Spatial Planning Directive) (Boero *et al.*, 2016). This approach led to the definition of “Cells of ecosystem functioning” (Boero *et al.*, 2019), based on ecological connectivity (Figure 6).

The cells of ecosystem functioning (CEFs), thus, are the natural units of management and conservation, and should be at the basis of maritime spatial planning.

The greatest challenge for marine science, as the sum of the various marine sciences, is to join forces and map

the marine environment from both a structural and a functional point of view, *i.e.*, mapping the cells of ecosystem functioning.

CONCLUSIONS

I have omitted here my direct contribution to the exploration of marine biodiversity, culminated with two monographs on the Hydrozoa of the Mediterranean and of the world (Bouillon *et al.*, 2004, 2006). The writing of such monographs is increasingly rarer, due to the unwise dismissal of traditional taxonomy (Boero, 2001, 2010) with the claim that genotypic approaches might replace phenotypic ones (Boero and Bernardi, 2014): both are necessary.

The sample of my scientific production cited here does not cover all the topics I tackled in my career. The apparent jumps from one topic to the other(s) occurred almost by chance, due to opportunities or, even, to the calls for projects that forced me to wrap up what I was doing, discovering *a posteriori* that what I did had emerging properties.

I would be a liar if I would say that I knew since the beginning where I wanted to go with my research. I focused on a specific topic, the polyp stage of the hydrozoa, then I had to deal with the medusa stage, passing from benthos to plankton, to arrive to nekton while considering the impact of jellyfish predation on fish larvae. The study of Marine Protected Areas led me to shift from the habitat to the ecosystem approach, and this led to the natural link of all facets of marine science. I jumped on “strange” phenomena, when they occurred, such as the mass mortalities of benthic organisms, linking them to climatic fluctuations (Rivetti *et al.*, 2014), as I did with the changes in the hydroid assemblage that I studied in my youth (Boero and

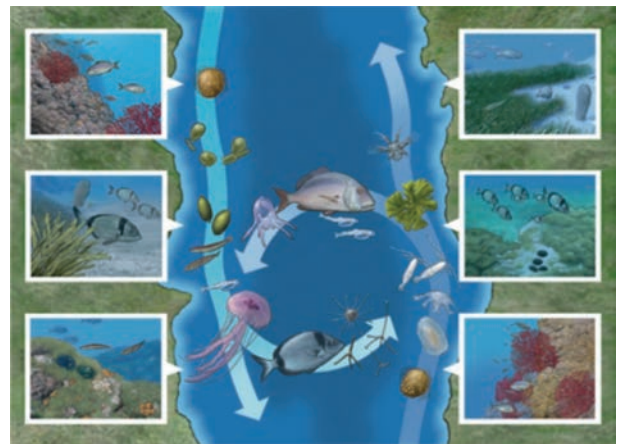


Figure 6. A hypothetical cell of ecosystem functioning in which currents link different habitats through propagule transport (the water column is also a suite of habitats) (concepts: F. Boero; artwork: Alberto Gennari).

Fresi, 1986) and that was the re-analyzed after decades (Puce *et al.*, 2009).

Philosophy of science attracted me since the very beginning of my career, but it took me a long time to understand that the Popperian paradigm of falsification, calling scientists to produce universal statements (that can be only falsified and cannot be verified) is not valid in historical disciplines (such as ecology and evolution) that are based on existential statements (that can be only verified and cannot be falsified) (Boero *et al.*, 2004). Gradual evolution, for instance, falsifies the universality of punctuate evolution, but not its existence (and vice-versa). Dealing with historical systems (dominated by existential statements) as if they were a-historical systems (dominated by universal statements) is hindering the development of both ecology and evolution. Despite the impossibility of performing predictions about the behaviour of ecological systems, it is anyway possible to understand them and to depict future scenarios (Boero, 2015b), and to act so as to drive future ecosystems into a desired status (Boero, 2021b).

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