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Recent innovations in marine biology

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Abstract

Modern ecology arose from natural history when Vito Volterra analysed Umberto D'Ancona's time series of Adriatic fisheries, formulating the famous equations describing the linked fluctuations of a predator-prey system. The shift from simple observation to careful sampling design, and hypothesis building and testing, often with manipulative approaches, is probably the most relevant innovation in ecology, leading from descriptive to experimental studies, with the use of powerful analytical tools to extract data (from satellites to molecular analyses) and to treat them, and modelling efforts leading to predictions. However, the historical component, time, is paramount in environmental systems: short-term experiments must cope with the long term if we want to understand change. Chaos theory showed that complex systems are inherently unpredictable: equational, predictive science is only feasible over the short term and for a small number of variables. Ecology is characterized by a high number of variables (e.g. species) interacting over wide temporal and spatial scales. The greatest recent conceptual innovation, thus, is to have realized that natural history is important, and that the understanding of complexity calls for humility. This is not a return to the past, because now we can give proper value to statistical approaches aimed at formalizing the description and the understanding of the natural world in a rigorous way. Predictions can only be weak, linked to the identification of the attractors of chaotic systems, and are aimed more at depicting scenarios than at forecasting the future with precision. Ecology was originally split into two branches: autecology (ecology of species) and synecology (ecology of species assemblages, communities, ecosystems). The two approaches are almost synonymous with the two fashionable concepts of today: 'biodiversity' and 'ecosystem functioning'. A great challenge is to put the two together and work at multiple temporal and spatial scales. This requires the identification of all variables (i.e. species and their ecology: biodiversity, or autoecology) and of all connections among them and with the physical world (i.e. ecosystem functioning, or synecology). Marine ecosystems are the least impacted by human pressures, compared to terrestrial ones, and are thus the best arena to understand the structure and function of the natural world, allowing for comparison between areas with and areas without human impact.

The Science of Environment

Ecology has been studied since the dawn of culture. Humans depended on the natural world for survival: knowing about both animals and plants was vital to draw resources from the environment, and our ancestors had to learn where to get the animals and plants they needed. Our understanding of environmental functioning, however, was aimed at exploitation and did not care about management and conservation. In the Pleistocene,

humans pushed many terrestrial species to extinction simply by hunting them (Alroy 2001), and then, with agriculture (Diamond 2002), they devastated pristine habitats for millennia, leading to environmental catastrophes that resulted in the disappearance of the civilizations that caused them (e.g. Jansen & Scheffer 2004). Only recently have humans started to understand that nature is limited and that exploitation of its resources requires proper management and conservation (Malthus 1798). The response of human populations to environmental devastation, until now, has simply been demographic collapse due to famine, disease, or war. Even if the origin of taboos is linked with a perceived need to preserve some precious and delicate species or habitats (Colding & Folke 1997), non-formalized science rarely attempted to conserve natural resources. This was particularly true for the marine environment, originally presumed to be inexhaustible (Huxley 1884). Only recently, again, have humans perceived that the exploitation of marine populations cannot proceed indefinitely.

The precondition of a proper understanding to perform proper management has led to deeper studies of marine ecosystems, with great conceptual innovations based on a philosophical revolution in marine ecology. Everything started from fisheries.

Reductionistic Fisheries Science

Modern ecology started with Vito Volterra's models of fisheries (Kingsland 1995; Gatto 2009). However, the famous equations, obtained independently by Lotka, accounted for just two species. It is a common approach, especially in physics, to consider variables in couples, assuming that the rest of the system remains unvaried. Complex systems, thus, are analysed as simplified subsets to reduce their complexity, the subsets then eventually re-assembled to make inferences about the structure and function of the system while considering all its variables. This attitude stems also from the famous Poincaré's 'problem of the three bodies' (Poincaré 1890), postulating that when more than two variables (bodies) are considered, their behaviour becomes inherently unpredictable after just a few interactions. The same conclusion was reached later by chaos theory. In fisheries science, the two variables were the abundance of the target species and the fishing effort of humans. The target species (the prey) was considered as a single item, and its population dynamics were studied by considering the succession of cohorts extrapolated from the measurement of individuals. Humans, with fisheries, are the main source of mortality for the target species. It is true that overfishing is an overwhelming source of mortality for many species, but this scenario is far too simple. Fisheries management resulted in tragic failure (Jackson et al. 2001), partly due to the oversimplification of models and partly due to the lack of responsiveness by both artisanal and industrial fisheries to the advice of fishery scientists. The fish-human approach, thus, required a drastic change in attitude, and the European Union embraced the ecosystem approach, proposed in 1992 by the Rio Convention on Biological Diversity. Humans and fish cannot be extracted from the ecosystem(s) they inhabit. This means that the number of variables is much greater than two. Another innovation, stemming from the unavoidable uncertainty of the sciences of complexity, was the precautionary principle. To prevent is better than to cure: it is always safer to consider the worst case scenario when the available knowledge is not sufficient to perform safe predictions about the effects of our action.

Fisheries Statistics

Although the modelling of fisheries is not reliable in terms of predicting the future, fisheries statistics are a precious source of information to understand the present by analysing the past. Another great innovation was thus the synthesis of fisheries statistics worldwide to assess the health of fish populations. After all, fisheries is a sort of sampling, and from fisheries data we have a continuous quantitative evaluation of fish populations. Samples, however, should not disturb the investigated system, whereas in the case of fisheries, sampling is highly destructive. The late Ransom Myers, a mathematician, became famous by collecting the scattered data of fisheries yields worldwide and by analysing them to estimate the global conditions of fish populations. His sampling effort was negligible, the samples were there, in the drawers of fisheries scientists. He 'just' retrieved the pieces of the puzzle and put them together. The derived picture was appalling (Myers & Worm 2003). Large fish are quickly disappearing and, as Pauly et al. (1998) said, we are 'fishing down marine food webs', as the higher levels of food webs are almost exhausted. In the Pleistocene, human hunters depleted the terrestrial megafauna and drove many species to extinction. Now we are doing the same to the marine megafauna. Our ancestors, however, did not know the consequences of their actions and aimed at proximate advantages, not having a perception of the ultimate disadvantages. Today, we do know what will happen. Maybe our models are not so accurate as to predict with precision when the collapse will take place, but we can be pretty sure that it will take place.

Compartmentalized Marine Ecology

For many years ecology was a no-man's land. The general principles were drawn from observations on natural systems, usually carried out at easily reachable places, where manipulations are possible. The intertidal, instead of being what it is, an ecotone, became the paradigm of all environments, and the 'rules' inferred there became generalized. This naturalistic approach had little connection with the branches of marine studies that had some link with human activities. These worked in almost total isolation from the 'naturalistic' branch. Fisheries studies, on the one hand, considered only human-impacted systems, almost divorcing them from the rest of nature, whereas the rest of marine studies considered non-impacted systems only, as if man did not exist. The two fields grew separately, with different scientists publishing in different journals and speaking different languages. Then, studies on pollution became popular, especially after the occurrence of Minamata disease, and heavy metals took their toll in marine science, together with oil and sewage pollution. When humans started to realize their own impact on marine habitats, they started to protect some areas and the era of marine conservation began, with flourishing studies on Marine Protected Areas. The link of without-humans ecology with with-humans ecology is probably one of the greatest revolutions of the environmental sciences. Compartmentalizations began to be broken down.

Fisheries and Aquaculture

Aquaculture is commonly perceived as a way to save natural fish populations from the overexploitation of fisheries (Anonymous 2003). Looking back on human history, we can see that the passage from hunting and gathering to agriculture did not save terrestrial natural populations but, instead, further impacted on them. Natural environments and populations were drastically modified as sites for agriculture. In the sea, this process is even more acute. On land, in fact, the only animals we rear for feeding purposes are herbivores, whereas in the sea, we mainly rear carnivores, the tigers of Navlor & Burke (2005). What do we feed them with? There are three possible answers: (i) pellets made of smaller fish, coming from natural populations, (ii) pellets of plant food such as soybean, as a substitute for animal proteins, (iii) pellets made with the remnants of terrestrial animals that we use for food. In the first case, the use of fish food to sustain farmed fish represents an unwise way of solving the problem of the overexploitation of marine resources, as the conversion coefficient of this food is low and the impact on nature great (Brunner et al. 2009). After having depleted the populations of large fish, we are fishing down the food web to feed captive specimens of those same depleted species. To transfom carnivores into herbivores, furthermore, is a forcing of nature that may have unpredictable effects, as happened on land when we tried to transform herbivores into carnivores (and cannibals). Similar outcomes might result also from the third option. It is very probable that the farming of large carnivores will not solve the problem of food demand due to our numerical increase, as this practice is evidently unsustainable from an environmental point of view, not to speak of the impact of fish farming on the natural environment (Pusceddu *et al.* 2007) and the vulnerability of farmed fish to both disease and predators such as jellyfish (Boero *et al.* 2008a).

From a Fish to a Jellyfish Ocean

The ecosystem approach can teach us that the standing biomass of a given ecosystem is more or less stable, but that its repartition among the species that make up that ecosystem changes constantly. If we remove biomass from an ecosystem, the absence of a sink (the target species, seen as a resource simply because of its abundance) will channel production towards other species, leading to an overall biomass similar to the pre-impact stage. Quantity is more or less the same, once the carrying capacity of the system is reached, but quality can change drastically. The constant reports of lack of large vertebrates worldwide are counterbalanced by the continual reports of jellyfish blooms worldwide. We are witnessing the shift from a fish to a jellyfish ocean! We catch the large fish? The biomass that was once channelled towards them can move in another direction, for instance jellyfish. If jellyfish prevail, they are a further blow to fish populations, as they prey upon the prey of fish larvae (crustacean plankton) and on the larvae themselves, acting as both competitors and predators of fish (Boero et al. 2008a).

A Ctenophore Lesson

When the alien ctenophore *Mnemiopsis leyidi* reached the Black Sea, the impact of the new arrival on fish populations was more severe than that of industrial fisheries (CIESM 2002b). The collapse of Black Sea fisheries, in fact, did not result from a long history of human pressures, but from the sudden presence of an alien ctenophore! The blooms of gelatinous plankton are an essential variable to assess the causes leading to the viability of fish populations. A similar scenario might occur for cod at Georges Bank, where the enormous numbers of floating colonies of the hydroid *Clytia gracilis* are probably impairing the recruitment of the fish, by feeding on cod larvae and on their crustacean food (Bollens *et al.* 2001).

Jellyfish blooms are not considered in fisheries models! Larval mortality is taken into consideration as a more or less constant toll that the populations have to pay, but it is becoming obvious that this toll can change from year to year, and if jellyfish are present in great numbers, they cause catastrophic larval mortality! Jellyfish, furthermore, can also cause adult fish mortality. A recent bloom of Pelagia noctiluca drove the farmed salmon of Ireland to extinction, showing that cage aquaculture is extremely vulnerable to jellyfish blooms. Before this episode, it was thought that larger fish escaped from jellyfish predation: small fish are vulnerable but, as they grow, their size makes them invulnerable to jellyfish weapons. Evidently this is not the case. Fish escape jellyfish when they shift from planktonic larvae and juveniles to nektonic adults simply because they are faster swimmers, they escape by... escaping. If kept in a cage, they cannot escape from jellyfish and are killed by them. In nature, a jellyfish bloom affects fish populations by impairing their recruitment; with cage mariculture, jellyfish blooms impact on the adults (whereas eggs and larvae are safe in artificial hatcheries and nurseries).

Gelatinous plankters, thus, are not freaks in marine biology and ecology. Their irregular, sudden, and massive presence is the shuffling of the cards of the ecological play, probably preventing the prevalence of a few, extremely successful, nektonic species by reducing their population via predation on their larvae and on their food (Boero *et al.* 2008a).

Story-telling *versus* Experimental Approaches and Mathematical Modelling

There was a demise of natural history at the dawn of modern ecology, because of its story-telling approach, lacking precision and aimed more at the description of patterns and processes with verbal models (the stories) than at predictive mathematical modelling based on experimental tests of hypotheses. This led to the reductionistic approach that divided ecology into many subecologies and transformed the discipline into an oxymoron. Reductionistic ecology loses the very spirit of ecology: the identification of the nework of intricate interactions leading to the emerging properties of complex systems.

Story-telling and descriptive approaches have been and still are ridiculed by experimentally and mathematically oriented scientists (Gardner et al. 2007). This led to the relegation of descriptive ecology to local journals with no impact factor, and into peripheral institutions, with low funding availability and low attractivity for bright new students. Paradoxically, knowing animals and plants was less mandatory for the young generations of ecologists than knowing complex mathematics and statistics. 'Theoretical' approaches were invariably mathematically oriented and aimed at making predictions that were obtained by the

identification of general rules (laws). The quest for ecological laws was great and stemmed from the Popperian approach to the natural sciences. Each rule (law), in fact, is to be universal and thus applicable to all situations. If it fails to explain a situation that should follow its command, then the law is falsified and is to be rejected. The universal laws of ecology and evolution do not exist, and when they operate, they are the laws of physics and chemistry! The 'laws' that predict the development of a community are three (at least) and each time one is valid, the others are falsified. What is the 'law' that predicts the development of a community? There are no universal laws in ecology, the laws are existential: they predict the existence of a given set of events, but do not postulate their universality (Boero et al. 2004). There are no sharks in the bay is a universal statement that can be only falsified, it cannot be verified, falling into what is demanded by Popperian science, whereas There are sharks in the bay is an existential statement that can be only verified but cannot be falsified. Ecology and marine biology are based on existential rules that sometimes are valid and sometimes are not. At the same time, mathematical modelling becomes too rigid and cumbersome to account for such situations, and its precision is so low anyway that there is not much difference between it and verbal modelling. Of course the mathematical make-up has the allure of precision for any attempt at modelling nature, but confidence in such approaches is slowly fading, as we recognize that ecology is a historical discipline and that the mathematical modeling leading to predict future history is just an illusion.

Story-telling, as remarked by Gardner et al. (2007), is essential to generate hypotheses which then are to be tested with the most rigorous experiments. It is important, however, to understand whether we are looking for universal or existential statements. Asking for universal solutions in a domain of existential problems leads nowhere.

The 'grand picture' of ecology has still to be depicted, but the various components are slowly emerging, first as single elements. Here are some of the recently discovered ones.

The Microbial Loop. Or is it a Pathway?

It has been known for a very long time that the bulk of production of the biosphere is based on the activity of the microscopic protists we call phytoplankton. Textbook knowledge teaches that nutrients are taken up by photosynthetic microbes, which in their turn feed herbivorous plankton (mainly crustaceans). These then fuel a food web leading to the largest fish and mammals. The flow of energy thus should go from microbes to metazoa. Very few people considered that the heterotrophic microbes, besides

decomposing bacteria, play an essential role in the turnover of organic matter. Heterotrophic protists such as ciliates and flagellates feed upon bacteria and phytoplankton and represent a powerful sink of marine production. The appreciation of this component led to considering the microbial world as a loop (Azam et al. 1983) in which organic matter flows indefinitely, independent of contact with larger organisms. This microscopic world was, indeed, self sufficient (and thus a loop) for billions of years, before multicellular organisms evolved. The source of mortality of bacteria, when no 'higher' organisms were present, was presumably viruses, as still happens in a massive way in the deep sea (Danovaro et al. 2008). Since the Cambrian explosion, however, metazoa dominate the seas. Certainly, they depend on microbes for both primary production and decomposition but in doing so, they broke the microbial loop, transforming it into a pathway. As higher metazoans, it is obvious that, while giving proper importance to the basic role of microbial worlds, we are more interested in the parts of the biosphere that are more directly connected with us, taking for granted that the basal part will work, as it did for some billion years! After a period of oblivion, the microbial world has been given the importance it merits.

The study of marine viruses focused on even smaller worlds and is just opening new perspectives, leading to a better appreciation of the structural and functional complexity of marine realms (Danovaro *et al.* 2008).

Marine Ecology from Molecules to Space

The exploration of the microbial world required a thorough change in the techniques employed. The microscope was not enough. Molecular studies started to reveal unexpected worlds in microbial diversity (e.g. Delong 1992) with strong insights also in human health. The discovery of the association of Vibrio species with copepods (e.g. Rawlings et al. 2007) and other chitin-wrapped organisms (Stabili et al. 2008), both in the plankton and in the benthos, is suggesting new scenarios for human epidemics. Molecular studies have enhanced taxonomy (see below) and especially biogeography to even a greater extent. The study of both historical ecology and phylogeography is allowing further insights for understanding present-day situations of marine biodiversity (Wares & Cunningham 2001). The use of electronic tracking by satellite, coupled with molecular analyses, is providing precious information on the patterns and processes that lead to the distribution of organisms such as the blue fin tuna (Boustany et al. 2008).

Alien Species

Human activities, from shipping to aquaculture, to the opening of new connections among basins, are widening

the distribution of species, allowing the crossing of previously unsurmountable geographic barriers. The problem of alien, or, better, Non-Indigenous-Species (NIS), and their transport is a key issue in understanding the patterns and processes involved in marine biodiversity (CIESM 2002b). Molecular techniques are crucial to reconstruct the patterns of introduction of NIS, their sites of origin, and the viability of their newly founded populations (e.g. McIvor et al. 2001).

What about Pathogens and Parasites?

Parasites, along with pathogens, are extremely important in controlling the populations of the various species, and their study is still at its dawn in all branches of ecology, not only marine ecology (Mattiucci & Nascetti 2008). Pathogens and parasites are among the future frontiers of marine ecology. They might be the equal of predators (after all, parasites are micropredators) in controlling natural populations but this aspect of marine ecology is still far from being incorporated into ecological theory (and practice) (see Rhode 2005, for a comprehensive treatise on marine parasitology).

Life Cycles and Life Histories

The succession of stages that an organism undergoes throughout its existence makes up its life cycle. The quantities of these stages (from gametes, to zygotes, larval stages, juveniles, reproductive adults) make up its life history. Most of the life cycles of known marine organisms are unknown, and we know even less about their life histories (Giangrande et al. 1994). Every stage of life history has its own ecological niche, and the sum of the ecological niches of all stages makes up the ecological niche of the species. These aspects are studied by population dynamics and are very advanced in fisheries studies, even though egg and larval mortalities of fish are a black hole in the knowledge of their population dynamics. We still have to describe a great quantity of unknown species, to properly evaluate marine biodiversity and, for each of them and for the already known ones, we still have to describe the life cycle and reconstruct the life history.

Looking for Links

Life-cycle dynamics have only been incorporated into ecological studies for a short time. The biology of coastal plankters, for instance, taught us that many species spend the adverse season as resting stages in coastal sediments, and even on the bottom of marine canyons (Boero *et al.* 1996; Marcus & Boero 1998; Della Tommasa *et al.* 2000). Benthic pelagic coupling started as a biogeochemistry

issue, with nutrients flowing from the water column to the bottom and then to the water column again. However, it is evident that this coupling also concerns life cycles and that many so-called holoplankters are the reverse of the commonly perceived meroplankton. Meroplankton, in fact, is the larval component of plankton and, after this stage, it becomes either benthos or nekton. But there are organisms that have a planktonic life as adults and spend their egg, or zygote or larval life in the benthos, as resting stages. These species can be either protists or metazoans. The boundaries between benthos and plankton are no longer clear, and the two domains are too connected to each other to be properly understood by approaches that are too tightly focused. The appreciation of these links might lead to even subtler connections. such as that hypothesized between plankton diversity and the predation of meiobenthos on resting stage banks, giving a keystone role to the meiobenthos (Pati et al. 1999). Other unexpected connections might be, for instance, that mollusc overfishing prevents shell deposits on beaches, leading to coastal erosion (see below).

Putting the Pieces Together

It is evident that fisheries, aquaculture and jellyfish biology are important parts of ecosystems and that, sooner or later, they must be merged so as to have a proper appreciation of the complexity of marine systems (Pauly et al. 2008). This exercise is very hard, though, as complexity hinders our comprehension and, furthermore, what has been listed so far is just a small portion of the variables that make up marine ecosystems. In recent years, we discovered that life is expressed in many unexpected ways. The importance of microbes, taken for granted but never explored in detail, led to the recognition of the microbial loop. The exploration of the deep sea led to the discovery of hydrothermal vent communities, virtually independent of sunlight as a source of energy. The exploration of interstitial environments led to the discovery of new phyla and of unexpected connections among marine domains that had previously been regarded as very separate. If the meiobenthos can feed on the resting stages of plankters, then the meiofauna can be a keystone guild controlling the diversity of plankton! A still almost completely neglected aspect of marine biology is the ecological importance of marine parasites. They are studied by parasitologists, but their ecological role is rarely taken into account when dealing with the dynamics of marine populations, contributing to ecosystem functioning. Behavioural ecology, furthermore, is well developed on land but is still at its dawn in the marine world, with the exception of a very few obvious species such as cetaceans. For the overwhelming majority of species whose existence we are aware of, we know neither the life cycle nor the ecological role. It is obvious that our level of ignorance is still very great.

These aspects, and many others, do not stem from a theoretical approach that is aimed at depicting a grand scenario that is then to be explored in detail, component by component. The approach is purely inductive. It is discovered that hydrothermal vents exist, and then they are explored. It is realized that microbes are important and then they are studied. The general synthesis occurs later, from an almost random assemblage of disconnected pieces.

Goods and Services

A common, human perception of nature is that everything is there for us to take advantage of. Biodiversity is there to provide us with the 'goods and services' so essential for our well-being. This is still the notion that is usually put forward to convince people that biodiversity is important (Hooper et al. 2005). The vision is anthropocentric, and does not consider the 'right' of nature to continue to thrive. As we are part of nature, our impact is natural. We are like the first organisms that started to produce oxygen as a by-product of their metabolism. They made the world less hospitable for the anaerobic biota. Nature knows no compassion. Maybe we could shift from the merely utilitaristic approach to biodiversity to a deeper vision, paradoxically sometimes expressed more by religion than by science. As people tend to listen more to religious authorities than to scientists (Wilson 2006), we are running the risk of being surpassed by some religious community in explaining why biodiversity is to be protected.

Habitats

If biodiversity is usually perceived as 'species' by the lay people, it is commonplace within the scientific community that the other two levels (the genetic and the habitatecosystem) are equally important (Gray 1997). A very long time will be required to answer May's (1988) question: How many species are there on Earth? But it may be easier to answer the question: How many habitats are there on Earth (Fraschetti et al. 2008)? Once the list is made, we will have to answer the question: Where do they occur? Another great innovation is the introduction of GIS in ecology and biogeography. We can now locate single individuals and follow them in their migrations (Block et al. 2001). And we can reconstruct maps of habitat distribution in extreme detail, and monitor the boundaries of these habitats to see whether they are stable, or are growing or regressing. The exploration of the environment is crucial and there is, also at this stage, a passage from an imprecise and descriptive account of habitat distribution to a precise and experimental way to draw information from the environment so to have repeatable observations.

These approaches are relatively easy for benthic communities, but plankton and nekton also have their habitats in the water column, albeit less definite than benthic ones, within their boundaries. The definition of the boundaries of pelagic habitats is obviously based on current regimes, but these can change, too, and many strange patterns of water movement are constantly being discovered, such as the places where deep-water formation occurs at the surface of the sea (e.g. the Northern Adriatic and the Gulf of Lions for the deep Mediterranean waters) (Boero et al. 2008b).

History

Ecology and biology are characterized by never-ending change. All living things are born and eventually die, continents move, new seas are formed and old ones die. History is never the same, even though some patterns may recur. The long-term history of life is evolution, leading, for instance, to the origin of new species. Ecology must cope with a short-term history that, however, is affecting the structure and function of communities by local extinctions and immigrations, by climatic changes and, of course, by our impact. History is ruled by two opposite drivers: constraints and contingencies (Boero & Bonsdorff 2007). Our understanding of how the environment works is based, first of all, on the appreciation of constraints; as these set the 'rules' that allow for the perpetuation of life, they may be the 'general laws' sought by Popperian logic. Contingencies, however, are the expression of the quintessence of history: the beat of the wings of a butterfly that (sometimes) can lead to a hurricane. Chaos theory demonstrates that deterministic systems are ruled by constraints (attractors, in the terminology of the theory) but that the system has a great freedom to change within the limits of these constraints, and this change is often caused by contingencies (the existential side of the way life is regulated).

We are attracted by regularities, by norms and laws. We have thus dedicated great efforts to single out the constraints that rule the world. Now it is time to perceive that rules are broken all the time, and that, sometimes, irregularities rule the world. The best example is the already mentioned shuffling of the cards by massive blooms of gelatinous organisms (Boero et al. 2008a), but more and more evidence in this direction is accumulating (Benincà et al. 2008; Doak et al. 2008).

Bureaucracy

The way science proceeds is linked to fund availability. Projects are commonly short term, and are focused on specific topics leading to testable results that, usually, should be 'novel' and 'exciting'. Fashionable research topics, usually sustained by scientific lobbies, receive much funding, whereas other topics, not sustained by powerful lobbies, tend to disappear or, worst, are 'invaded' by other lobbies. The worst case is that of taxonomy. Molecular and computerized taxonomy is taking almost all the funding, leaving traditional taxonomy in almost complete poverty (Ebach & Holdrege 2005). It is often the case that the format of research projects is very complicated and the requirements to be fulfilled are so cumbersome that many scientists simply give up applying. Furthermore, results are seldom validated and controls focus on financial aspects only, often with costly financial audits. The outcome of all this is that the successful scientists are the ones good at managing large projects. Devoting most of their time to this, they obviously dedicate less time to research. As scientific validation is a useless optional, at least in some projects, funding policies often hamper scientific progress. Apparently, this behavioural pattern is not pursued in the USA, at least by the National Science Foundation. No wonder the scientific community of the USA is much more productive than the European one! We spend most of our time dealing with bureaucracy: they spend it on science. Our results are often validated by satisfying bureaucratic requirements, whereas theirs are validated by scientific excellence. This explains why the brain drain affecting many European countries is going towards the USA more than anywhere else (Boero 2001).

Publications

The impact factor frenzy has affected research trends for several decades, determining career and funding opportunities. Some areas of biological research have profited from this situation, others have been damaged by it. The need for scientific scoops in high impact journals is not supportive of long-term research: projects are usually short and are renewed on the basis of the scientific production in the 'best' tribunes (i.e. journals with high impact factor). Career and funding opportunities are based on the number of articles and the sum of their impact factors. A nicely conducted ecological experiment, based on an impeccable design and data treatment is usually publishable in good journals, and can be carried out in a relatively short time. A long series of observations, on the other hand, besides requiring more time, is usually labelled as 'descriptive' and has low viability in high impact journals. Paradoxically, however, these data

become invaluable to assess trends of change and reference conditions. Data-mining is becoming a fashionable activity in research projects, as the data readily available in bibliographic repertories, covering a limited set of journals, are often useless to make an assessment of the history of biota. In this period of global change, the possibility of retrieving data over long time spans is important to make assessments about the state of the environment. If all scientists had followed the predominant trends, we would know much less about the state of the environment. The lack of importance given to 'descriptive' studies is leading to a decreasing quality control (in the form of peer review) of their outcomes. Metanalyses, based on the so-called grey literature or on unpublished data, or on data published on journals that do not perform a severe control of what they publish, might be conducted with the most beautiful algorithms and rationales, but the old saying of statisticians - 'garbage in, garbage out' - cannot be circumvented by statistical formulations. Very few journals, if any, perform a strict control of the accuracy of the list of species that describes the biodiversity within ecological papers. Many journals do not even provide the list, whereas they publish impeccable treatments of data that might not be as reliable as the reputation of the journal might warrant.

Trendy Biodiversity Studies

The era of biodiversity started with the Rio de Janeiro Convention on Biological Diversity in 1992. Since then, the presence of the word 'biodiversity' in any project has been a warranty of success. Some calls were aimed at using biodiversity as a tool to understand the environment, other calls at promoting biodiversity research in a direct way, as it is obvious that biodiversity exploration is not complete and, anyway, the distribution of biodiversity changes all the time. In the same period, however, the science of biodiversity identification and description (i.e. taxonomy) started to enter into a deep crisis. There has been a great development of molecular taxonomy, with the birth of new journals dedicated just to it, but traditional taxonomy, based on morphology and developmental biology, started to be perceived as obsolete, partly because most of the journals dedicated to it (e.g. Museum journals) did not have any impact factor and, thus, publishing in them was not of great help in scientific careers and in applications for research funds. Most of the money dedicated to biodiversity went to molecular taxonomy and to the building of computer-based inventories (e.g. Arvanitidis et al. 2006), assuming that morphological approaches produced all possible fruits. Taxonomy became (and still is) synonymous with identification. Taxonomic sufficiency, furthermore, implies that the study of higher taxa is sufficient to appreciate biodiversity. This position is somehow ambiguous. Taxonomic sufficiency might be sufficient to detect impacts, but it does not by definition reflect biodiversity at species level and thus cannot be sufficient to appreciate the core of biodiversity – species (Terlizzi *et al.* 2009). Ecology and taxonomy should go together, as both can profit much from each other (*e.g.* Neto 1992).

Safe Topics

An ideal trend of research projects should be to propose something that has been already accomplished (at least in part), so to be sure to have results and fulfil the requirements of the project, and then invest the freshly available money into some innovative field, with no risks if the results do not fulfil our expectations. The risk of failure in a daring scientific project (such as the study of immortality in a jellyfish species able to perform ontogeny reversal, or the impact of meiofauna predation as a regulator of plankton diversity) is obviously great. If the results are positive, the scientific impact is great, but if the results are negative, then there is not much justification for the sustained economic effort. Of course, if the results are irrelevant in the evaluation of projects, and bureaucratic requirements are sufficiently met, the risk of its failure being 'discovered' is low. However, a study that does not produce any good results, leads to a lower publication score for the researcher, so diminishing his or her status in the scientific community. It is better to stick to well established procedures and tackle 'safe' topics. No wonder the investigations on the populations of limpets in the intertidal are extremely popular and successful (680 articles in the ISI Web of Science from 1986 to 2008, h-index 38), whereas studies on thaliacea are much less popular (79 papers, h-index 15).

The overall importance of limpet grazing on algal mats is almost irrelevant to ecosystem functioning, whereas the roles of thaliacea might be paramount in determining planktonic primary production. However, the risk of failure of thaliacean studies is great, due to their erratic presence, so it is much safer to stick to limpets, possibly shifting to barnacles (1990 papers, h-index 64), for a change.

From Knowledge to Management and Conservation

It is evident, from all the above, that we still know little of what should be known to properly evaluate marine biodiversity and its bearing on ecosystem functioning. The exploration phase has still to be accomplished (Bouchet *et al.* 2002), and the elucidation of mechanisms is even more in its infancy. Knowledge of the patterns and processes governing ecosystem functioning is a prerequisite

for management. Of course, we cannot wait to describe all species and to elucidate the relationships of each of them with the rest of the biosphere to start actions aimed at mitigating our evident impact on the natural world. There are some actions that can be taken even with very little knowledge (for instance, discharging nuclear waste in the environment is bad, and we do not need to understand perfectly all the facets of it to decide on its ban). On the other hand, there are very subtle ecological processes (such as the impact of thaliacean grazing on phytoplanktonic primary production, or jellyfish impact on fish populations, see Boero *et al.* 2008a) that might lead to undesirable situations; whereas with proper knowledge, we might avoid non-obvious environmental catastrophes.

Shellfish Overfishing and Coastal Erosion

Productive seas, such as the Adriatic Sea before the 1980s, sustain enormous populations of bivalve molluscs that are used as a food source by humans. At the end of the summer, the populations of many of these species go through catastrophic mortality and the dead shells are stranded on beaches, forming large masses of calcium carbonate. Wave action, instead of affecting the sand of beaches and causing erosion, impacts on the stranded shells, breaking them down and leading to the formation of biogenic sand grains. In other words, stranded mollusc shells are a natural beach replenishment, year after year.

Studies on the contribution of this process to sediment balances on beaches are rare (Lopez et al. 2008). However, it is suggestive that the populations of these molluscs are more and more depleted by overfishing, and shell stranding does not occur anymore, for example, along the Adriatic Sea. The whole Italian coast of the Adriatic, from the Gargano peninsula to the Gulf of Venice, is affected by severe beach erosion and, in the last two decades, it has been 'protected' by an almost continuous line of coastal defences: the great wall of the Adriatic. The causes of beach erosion are manifold, such as the irrational urban development along sandy shores and the barrage of rivers with dams, so preventing sediment input through riverine outflows (CIESM 2002a); railway tracks on the shore, furthermore, led to the perception that any change in coastline is a catastrophe. The overfishing of bivalves, in this complex scenario, ruled by multiple causality, might have been the last straw that broke the camel's back. And maybe it was not a straw!

The Wheel Re-invented: Biodiversity and Ecosystem Functioning

Some decades ago, ecology was divided into two main branches: autoecology and synecology. Autoecology was

the ecology of species and essentially concerned their biology. According to the organisms studied, autoecologists were either zoologists or botanists. A prerequisite for studying autoecology, in fact, was knowledge of the existence of species and, thus, the exploration of biodiversity. Synecology stemmed from the widely shared concept of the emerging properties of ecology, the whole being more than the sum of the parts. This means that synecology is not simply the sum of the autoecologies of each species. The ecology of species (biodiversity) contributes to the ecology of species assemblages within their physical environment (ecosystem functioning) in a complex way, and it is vain to pretend that knowledge of a species by species ecology might lead to understanding the functioning of the ecosystems. However, the perception of the value of species diversity calls for some justification. Biodiversity is important because it makes ecosystems function, but how? Do we know enough about species roles (the old autoecology) (Piraino et al. 2002)? Especially in the sea, we barely know the list of species living at a certain place, not to mention their roles. Lists and roles are better known for species-poor seas, such as the Baltic or the North Sea, whereas they are barely known in species-rich seas such as the Mediterranean Sea. This is why synecology is more advanced in Northern Europe than in Southern Europe: the systems are simpler.

The old paradigms are still valid. The first step is the exploration of biodiversity (how many species are there on Earth?). Then there is their autoecology (what are their life cycles, what are their ecological niches?) and synecology (how do ecosystems work?). In spite of having re-discovered auto- and synecology, the introduction of BEF (Biodiversity and Ecosystem Functioning) has the merit of having merged the two approaches, calling for a timely conceptual unification (Boero et al. 2004; Boero & Bonsdorff 2007). Ecology is the science of interactions, compartments are to be broken, reductionism to lead to multiscalar approaches, both in time and space. Ecology is the study of the processes leading to the patterns of distribution and abundance of organisms. Biogeography, faunisfloristics, macroecology, synecology, biology, autoecology, fisheries science, anthropology, economics and many other branches of the study of nature require a synthetic approach that does not see reductionism as the opposite of holism. All approaches are necessary and none is sufficient. Maybe, with a slightly modified meaning, the old term 'natural history' is the best one to depict the necessary unification of the life sciences.

Conclusion

The search for general rules and 'laws' governing environmental systems, with the aim of predicting their future behaviour, is crashing up against the wall of the intrinsic impredictability of complex systems. We must describe properly and try to understand, singling out the relevant variables and their interactions. This will lead to the proposal of very weak predictions, or scenarios, that will not pretend to predict future history but that will depict the possible shape of the main attractors of chaotic environmental systems. Regularities are extremely important, and we have dedicated most of our efforts to identifying them. Now it is the turn of irregularities. The drivers of change may be extremely subtle: e.g. the absence of stranded molluscs, leading to coastal erosion, or the predation of small jellyfish, leading to the impairment of fish recruitment, or the dredging of harbour sediments, leading to red tides by waking up dinoflagellate cysts buried in the sediments, or the grazing of a salp bloom. All these possible drivers have not been investigated as much as they deserve. It is time to make daring hypotheses on functional links, and it is time to start exploring again, passing from the computer and the laboratory into the field. We abandoned long-term series, and we must revive them: (natural) history can only be understood through archives (containing raw data); libraries (containing the elaboration of data) are not enough (after the available data have been elaborated).

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References

- Alroy J. (2001) A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science*, **292**(5523), 1893–1896.
- Anonymous (2003) The promise of a blue revolution. *The Economist*, **368**(8336), 19–21.
- Arvanitidis C., Valavanis V.D., Eleftheriou A., Costello M.J., Faulwetter S., Gotsis P., Kitsos M.S., Kirmtzoglou I., Zenetos A., Petrov A., Galil B., Papageorgiou N. (2006) MedOBIS: biogeographic information system for the eastern Mediterranean and Black Sea. *Marine Ecology Progress Series*, 316, 225–230.
- Azam F., Fenchel T., Field J.G., Gray J.S., Meyer-Reil L.A., Thingstad F. (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, **10**, 257–263.

- Benincà E., Huisman J., Heerkloss R., Jonk K.D., Branco P., Van Nes E.H., Scheffer M., Ellner S.P. (2008) Chaos in a long-term experiment with a plankton community. *Nature*, **451**, 822–825.
- Block B.A., Dewar H., Blackwell S.B., Williams T.D., Prince
 E.D., Farwell C.J., Boustany A., Teo S.L.H., Seitz A., Walli
 A., Fudge D. (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science*,
 293, 1310–1314.
- Boero F. (2001) Light after dark: the partnership for enhancing expertise in taxonomy. Trends in Ecology and Evolution, 16, 266.
- Boero F., Bonsdorff E. (2007) A conceptual framework for marine biodiversity and ecosystem functioning. *Marine Ecology: An Evolutionary Perspective*, **28**(Supl. 1), 134–145.
- Boero F., Belmonte G., Fanelli G., Piraino S., Rubino F. (1996) The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends in Ecology and Evolution*, 11, 177–180.
- Boero F., Belmonte G., Bussotti S., Fanelli G., Fraschetti S., Giangrande A., Gravili C., Guidetti P., Pati A., Piraino S., Rubino F., Saracino O., Schmich J., Terlizzi A., Geraci S. (2004) From biodiversity and ecosystem functioning to the roots of ecological complexity. *Ecological Complexity*, **2**, 101–109.
- Boero F., Bouillon J., Gravili C., Miglietta M.P., Parsons T., Piraino S. (2008a) Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*, **356**, 299–310.
- Boero F., Féral J.P., Azzurro E., Cardin V., Riedel B., Despalatović M., Munda I., Moschella P., Zaouali J., Fonda Umani S., Theocharis A., Wiltshire K., Briand F. (2008b) I Executive summary of CIESM Workshop 35 'Climate warming and related changes in Mediterranean marine biota'. CIESM Workshop Monographs, 35, 5–21.
- Bollens S.M., Horgan E., Concelman S., Madin L.P., Gallager S.M., Butler M. (2001) Planktonic hydroids on Georges Bank: effects of mixing and food supply on feeding and growth. *Deep-Sea Research Part II-Topical Studies in Ocean-ography*, **48**, 659–672.
- Bouchet P., Lozouet P., Maestrati P., Heros V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, 75, 421–436.
- Boustany A.M., Reeb C.A., Block B.A. (2008) Mitochondrial DNA and electronic tracking reveal population structure of Atlantic bluefin tuna (*Thunnus thynnus*). *Marine Biology*, **156**, 13–24.
- Brunner E.J., Jones P.J.S., Friel S., Bartley M. (2009) Fish, human health and marine ecosystem health: policies in collision. *International Journal of Epidemiology*, **38**, 93–100.
- CIESM (2002a) Erosion littorale en Méditerranée: dynamique, diagnostic et remèdes. *CIESM Workshop Monographs*, Vol. 18. CIESM Publishers, Monaco: 102 pp.

- CIESM (2002b) Alien marine organisms introduced by ships in the Mediterranean and Black seas. *CIESM Workshop Monographs*, Vol. 20. CIESM Publishers, Monaco: 135 pp.
- Colding J., Folke C. (1997) The relations among threatened species, their protection, and taboos. *Ecology and Society*, 1, 6 Available at: http://www.consecol.org/vol1/iss1/art6/.
- Danovaro R., Dell'Anno A., Corinaldesi C., Magagnini M., Noble R., Tamburini C., Weinbauer M. (2008) Major viral impact on the functioning of benthic deep-sea ecosystems. *Nature*, **454**, 1084–1087.
- Della Tommasa L., Belmonte G., Palanques A., Puig P., Boero F. (2000) Resting stages in a submarine canyon: a component of shallow-deep-sea coupling? *Hydrobiologia*, **440**, 249–260.
- Delong E.F. (1992) Archaea in coastal marine environments. Proceedings of the National Academy of Sciences of the USA, 89, 5685–5689.
- Diamond J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature*, **418**, 700–707.
- Doak D.F., Estes J.A., Halpern B.S., Jacob U., Lindberg D.R.,
 Lovvorn J., Monson D.H., Tinker M.T., Williams T.M.,
 Wootton J.T., Carroll L.I., Emmerson M., Micheli F., Novak M. (2008) Understanding and predicting ecological dynamics: are major surprises inevitable? *Ecology*, 89, 952–961.
- Ebach M.C., Holdrege C. (2005) DNA barcoding is no substitute for taxonomy. *Nature*, **434**, 697.
- Fraschetti S., Terlizzi A., Boero F. (2008) How many habitats are there on Earth (and where)? *Journal of Experimental Marine Biology and Ecology*, **366**, 109–115.
- Gardner J., Marsack P., Trueman J., Calcott B., Heinsohn R. (2007) Story-telling: an essential part of science. *Trends in Ecology and Evolution*, 22, 510.
- Gatto M. (2009) On Volterra and D'Ancona footsteps: the temporal and spatial complexity of ecological interactions and networks. *Italian Journal of Zoology*.**76**, 3–15..
- Giangrande A., Geraci S., Belmonte G. (1994) Live-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. *Oceanography and Marine Biology Annual Review*, **32**, 305–333.
- Gray J.S. (1997) Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, 6, 153–175.
- Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setala H., Symstad A.J., Vandermeer J., Wardle D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75, 3–35.
- Huxley T.B. (1884) Inaugural address. Fisheries Exhibition Literature, 4, 1–22.
- Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J., Warner R.R. (2001) Historical overfishing and

- the recent collapse of coastal ecosystems. *Science*, **293**, 629–638.
- Jansen M.A., Scheffer M. (2004) Overexploitation of renewable resources by ancient societies and the role of sunk-cost effects. *Ecology and Society*, 9, 6 Available at: http:// www.ecologyandsociety.org/vol9/iss1/art6/.
- Kingsland S.E. (1995) Modeling Nature, 2nd edn. The University of Chicago Press, Chicago: 306 pp.
- Lopez R.A., Penchaszadeh P.E., Marcomini S.C. (2008) Stormrelated strandings of mollusks on the northeast coast of Buenos Aires, Argentina. *Journal of Coastal Research*, 24, 925–935.
- Malthus T. (1798) An Essay on the Principle of Population. J. Jonson, London.
- 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. *Limnology and Oceanography*, **43**, 763–768.
- Mattiucci S., Nascetti G. (2008) Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host-parasite coevolutionary processes. *Advances in Parasitology*, **66**, 47–148.
- May R.M. (1988) How many species are there on Earth? *Science*, **241**, 1441–1449.
- McIvor L., Maggs C.A., Provan J., Stanhope M.J. (2001) rcbL sequences reveal multiple introductions of the Japanese red alga *Polysiphonia harveyi*. *Molecular Ecology*, 10, 911–919.
- Myers R.A., Worm B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature*, **423**, 280–283.
- Naylor R.L., Burke M. (2005) Aquaculture and ocean resources: raising tigers of the sea. *Annual Review of Envi*ronment and Resources, 30, 185–218.
- Neto A.I. (1992) Contribution to the taxonomy and ecology of the Azorean benthic marine algae. *Biological Journal of the Linnean Society*, **46**, 163–176.
- Pati A.C., Belmonte G., Ceccherelli V.U., Boero F. (1999) The inactive temporary component: an unexplored fraction of meiobenthos. *Marine Biology*, 134, 419–427.
- Pauly D., Christensen V., Dalsgaard J., Froese R., Torres F. Jr (1998) Fishing down marine food webs. *Science*, **5352**, 860–863.
- Pauly D., Graham W., Libralato S., Morissette L., Palomares M.L.D. (2008) Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia*, 616, 67–85.
- Piraino S., Fanelli G., Boero F. (2002) Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology*, **140**, 1067–1074.
- Poincaré H. (1890) Sur les équations de la dynamique et le problème de trois corps. *Acta Mathematica*, **13**, 1–270.
- Pusceddu A., Fraschetti S., Mirto S., Holmer M., Danovaro R. (2007) Effects of intensive mariculture on sediment biochemistry. *Ecological Applications*, 17, 1366–1378.
- Rawlings T.K., Ruiz G.M., Colwell R.R. (2007) Association of Vibrio cholerae O1 El Tor and O139 Bengal with the copepods Acartia tonsa and Eurytemora affinis. Applied and Environmental Microbiology, 73, 2926–7933.

- Rhode K. (Ed.) (2005) *Marine Parasitology*. CSIRO Publishing, Collingwood, Vic., Australia: 592 pp.
- Stabili L., Gravili C., Tredici S.M., Piraino S., Talà A., Boero F., Alifano P. (2008) Epibiotic *Vibrio* luminous bacteria isolated from some hydrozoa and bryozoa species. *Microbial Ecology*, **56**, 625–636.
- Terlizzi A., Anderson M.J., Bevilacqua S., Fraschetti S., Wlodarska-Kowalczuk M., Ellingsen K.E. (2009) Beta diversity
- and taxonomic sufficiency: do higher-level taxa reflect heterogeneity in species composition? *Diversity and Distributions*, **15**, 450–458.
- Wares J.P., Cunningham C.W. (2001) Phylogeography and historical ecology of the North Atlantic intertidal. *Evolution*, **55**, 2455–2469.
- Wilson E.O. (2006) The Creation: An Appeal to Save Life on Earth. W.W. Norton & Co., New York: 175 pp.