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A conceptual framework for marine biodiversity and ecosystem functioning

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Abstract

The meaning of 'biodiversity' ranges from genetic makeups to communities, covering almost all biological phenomena, still remaining linked to species diversity. Ecosystems function through three basic cycles of matter and energy: *extraspecific* cycles (biogeochemical cycles), *intraspecific* cycles (life cycles and histories), and *interspecific* cycles (food webs). In an evolutionary framework, ecology is characterised by change: evolutionary processes never stop. Change is either structural or functional, or both. Palaeontology and long-term ecological series show that stable ecosystems do not exist, at least in structure. In non-linear systems like environmental ones, even small changes in biodiversity can cause sharp changes in ecosystem functioning, changing the shape of environmental attractors. The currently accepted definition of ecosystem functioning (the efficiency of biogeochemical cycles) is insufficient to account for ecosystem health. The efficiency of extra-, intra- and interspecific cycles must be taken into consideration in order to know 'who does what'. To account for the historical nature of ecological phenomena, the Historical Biodiversity Index is proposed, considering not only the present status of a given habitat type (in terms of species composition) but also its history. This will allow biodiversity crises to be identified, including potential extinction. Natural history and experimental ecology must cooperate to help untangle ecological complexity, merging biodiversity with the functioning of ecological systems.

What is biodiversity?

'Biodiversity' has different meanings in different disciplines, ranging from the 'all species' approach of taxonomists, to 'charismatic and conspicuous species only' of socio-economists, to the 'functional units' of ecological modellers. The species concept itself is widely debated, and no clear-cut and universal definition of species, valid for all living forms, is currently available. Ecologists, furthermore, widened to communities and ecosystems the species-based approach to biodiversity, whereas geneticists restricted it to intraspecific variation in genetic makeups (see Heywood & Watson 1995 for a review). In this framework, biodiversity might become a one-size-fits-all

concept that can be stretched in every direction, according to the convenience of those who use it. The importance of biodiversity, however, became widely accepted due to the publication of papers asking questions such as: 'How many species are there on Earth?' (May 1988). This question is far from being answered. Biodiversity crises are first perceived in terms of the reduction of species pools, possibly leading to further modifications affecting the functioning of ecosystems.

What is Ecosystem Functioning?

Species are a nonsense-concept if not placed into an environmental context, involving the functioning of

ecosystems. Species survive and flourish because the ecosystems they inhabit do function, but it is also true that ecosystems (including the abiotic environment) function because the species that make up their biotic component thrive. The functioning of ecosystems is based on an efficient circulation of matter and energy through various levels of biological organisation, involving primary, secondary (and higher) production and decomposition. The (non-living) nutrients deriving from decomposition, and flowing as biogeochemical cycles, are essential to fuel primary production. Biotic (production and decomposition), and abiotic (biogeochemical cycles) processes and patterns are essential for the functioning of ecosystems and are deeply interconnected (Bonsdorff *et al.* 1995). Hence, it is possible to take one of these processes and patterns as an indication of the functioning of the whole ecosystem. Following this line of reasoning, ecosystem functioning is often represented by the efficiency of biogeochemical cycles (see Naeem & Wright 2003 for a review). This view, however, considers only the abiotic side of ecosystem functioning, disregarding the intricate biological patterns and processes that make it possible, resulting in too reductive a view to account for the complexity of communities and ecosystems. Three basic cycles of matter and energy concur to the functioning of ecological systems: biogeochemical (*extraspecific*) cycles, life (*intraspecific*) cycles, and food webs (*interspecific* cycles) (Boero 1999) (Fig. 1).

Biogeochemistry accounts for the production and availability of the building blocks of life deriving from

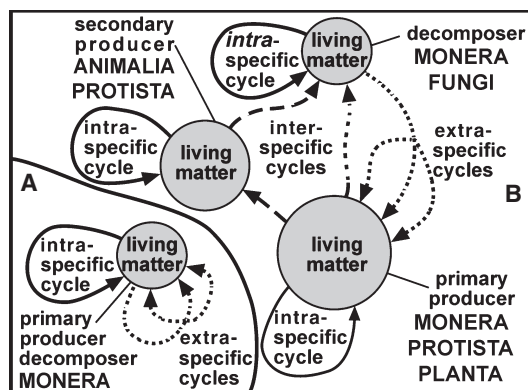


Fig. 1. Types of ecosystem functioning. A: the functioning of the first ecosystem, represented by the first species that evolved. Its role was both primary production and decomposition. B: The evolution of biodiversity increased the complexity of ecosystems, with different organisms performing different functions. Intra-specific cycles are life cycles, allowing the persistence of species (depicted as closed circles); inter-specific cycles occur through food webs and are trophic relationships, with fluxes among species; extra-specific cycles are biogeochemical cycles, when matter is not organised in a living state.

decomposition; food webs account for all types of production, and decomposition and life cycles account for the persistence of the species.

If we consider the history of ecosystems, we might ask what were the patterns and processes allowing the functioning of the first ecosystem. If life is monophyletic, as suggested by the common genetic language spoken by all living beings, in the beginning there was just one species (in fact, from a philosophical point of view, this may still be viewed as being so). The first ecosystem, then, functioned with a very low diversity (Fig. 1A). It can be hypothesised that this first species was both a primary producer and a decomposer, as some present-day bacteria still are. When biodiversity evolved, and the number of both species and species roles, *i.e.* functions, increased (Fig. 1B), new types of functioning evolved and the ecosystems became more complex. This relationship between species number (minimum number of required species) and abundance patterns was analysed in some detail by Sugihara (1980). It is evident that the concept of diversity and ecosystem functioning in relation to both temporal (long-term) and spatial scales needs specific attention (Tilman & Kareiva 1997; Ieno *et al.* 2006; Naeem 2006).

The continuity of life (*omne vivum ex vivo*) is guaranteed by intraspecific cycles. Each generation will eventually die and the persistence of species relies on the efficiency of their life cycles and histories, and on their resilience to environmental change or plasticity to adapt. Some clonal species (mainly plants) may live as 'individuals' for an equivalent of multiple generations of long-lived organisms. It is not known how these adapt genetically to a changing environment, but their role in the ecosystem may certainly change. The number of intraspecific cycles represents the diversity of the species pool in the ecosystem. Primary producers take energy and matter from non-living sources. The nutrients they use are not organised in a living fashion and are, thus, outside of species (*i.e.* extraspecific). Besides primary producers, present-day ecosystems have also secondary, tertiary and even higher producers. They rely on the energy and matter produced by other species, so being a part of interspecific cycles, with passage of energy and matter from one species to another. For ease of analysis, ecologists have used a reductionistic approach, splitting the complexity of the intertwining of these three basic cycles into separate disciplines, with scant attempts to a timely synthesis and with conceptual gaps that make the re-assembly of the various parts difficult.

From the above, it is clear that biodiversity does not have much to offer to ecosystem functioning if this is exemplified by the efficiency of biogeochemical cycles, as biogeochemistry (being extraspecific) does not consider species (and the supra- and sub-specific approaches to

biodiversity). This position might be correct because ecosystems have worked since the very beginning of life, when there was just one species and biodiversity was, therefore, very low. And they continued to function even after the catastrophic mass extinctions of the past. However, if we consider the three types of cycles, the extinction of a species means the malfunction of the ecosystem in one of its components, *i.e.* the intraspecific cycle of that species. A species loss, furthermore, is also the loss of one node of food webs, and the interactions between species-assemblages and the functioning of the ecosystem are often both delicate and hard to identify, emphasising the need for experimental research within the field of functional marine biodiversity (Bulling *et al.* 2006; Ieno *et al.* 2006; Solan *et al.* 2006). The same is valid for the arrival of a new species, or the change in the relative abundances of the various species, including non-native species that may enter an ecosystem by means of unnatural immigration (Reise *et al.* 2006). Of course the ecosystem as a whole will continue to have efficient biogeochemical cycles after these modifications, but does this mean that the modifications will not affect it?

Selection...s

As in ecology, reductionism is dominant in evolutionary biology, which, at its dawn, started with an exquisitely organismic and environmental approach, to evolve into a genetics-dominated discipline. Darwin's book on natural selection dealt with the effects of environmental forces upon the species, whereas Darwin's most popular contemporary follower, Ernst Haeckel, with his 'biogenetic law', put evolution into a developmental framework. It is telling that neither ecology nor developmental biology took part in the modern evolutionary synthesis: the dominating disciplines were taxonomy and biogeography, palaeontology, and genetics. The hierarchical levels here assigned to ecological cycles can also be assigned to evolutionary drivers, with natural selection covering what the environment outside the species (*i.e.* extraspecific pressures) does to select specimens; sexual and internal selection covering what individuals do within their own species (*i.e.* intraspecific pressures) to select specimens; and species selection regarding what species (*i.e.* interspecific pressures or the environment in general) do to select other species. In this framework, ecology represents the short-term result of selective pressures, whereas evolution covers the influence of selections over the long term.

Change

Change is the main feature of evolution and, thus, of ecology. Change in abiotic features of the environment indu-

ces change in the composition of species assemblages, possibly changing ecosystem functioning; biotic changes, furthermore, can change the features of the abiotic component. The result is a chain reaction of continuous change, possibly altering not only the structure but also the functioning of ecosystems. Ecosystem stability, from this point of view, is very unlikely (a kind of 'non-concept'), as it implies the cessation of evolutionary processes. Communities can face change with resistance and resilience, but the history of life shows that no systems are able to remain unmodified over the long term. For example, the Baltic Sea was formed only after the last glaciation some 10,000 years ago and gained its current brackish water conditions no more than 7000 years ago; it is still undergoing dramatic abiotic and biotic changes (Voipio 1981). Change can be of several types, usually reduced to two main ones: structural *versus* functional. They are not mutually exclusive. Palaeontology and long-term ecological series clearly show that stable ecosystems do not exist, at least in structure (Jackson & Johnson 2001). It commonly happens that rare species become abundant, abundant species become rare, new species arrive, other species become (totally or locally) extinct. This involves changes in both the abundance and the distribution of species (Boero 1994, 1996; Rumohr *et al.* 1996; Bonsdorff *et al.* 1997). The 'problem' of change, however, remains. Change, on the one hand, is a natural feature of all systems; on the other hand the rate of change can vary from slow to fast and, sometimes, it might become alarmingly fast, and described as unnatural.

Some questions

If we consider the amount of biodiversity change a community can bear, one question might be: *what is the minimal number of species allowing for the functioning of an ecosystem?* We have seen (Fig. 1A) that the answer is: at least one. The early ecosystem that worked with the first species, however, no longer exists, and the minimum number of species in present-day ecosystems is a result of the evolutionary processes that govern the interactions between species and their changing environment (Sugihara 1980). Ecosystems functioned with one species, and the global ecosystem continues to function with perhaps ten million species!

At this point, another question might be: *what is the maximal number of species that can be supported by a given ecosystem?* The first question considers how species make ecosystems function, the second one considers how ecosystem functioning can account for species existence. Other relevant questions might be:

What is the cost/benefit of rare species for an ecosystem?

What is the contribution of rare species to ecosystem functioning?

What is the impact of newly entered species to the functioning of an ecosystem?

What is the impact of changes in the relative abundances of species on ecosystem functioning?

The temptation of considering just the most 'important' species (habitat forming, keystone and ecosystem engineers) and discarding the rest of biodiversity is great (Piraino *et al.* 2002). This, however, would imply that some species are 'not important' and that, ultimately, biodiversity is not so important, because a majority of biodiversity is made of rare and/or inconspicuous species that apparently play no great roles in the functioning of ecosystems and are, therefore, disregarded by non-taxonomists, unless they are charismatic. This reasoning is important also from a conservation point of view (what do we preserve, and why), knowing that ecosystems change over time. Conservation should 'preserve' ecosystems in a manner that hinders unnatural variation/deviation from the anticipated successional patterns (if biodiversity really develops towards a specific state, which is far from generally true). In the open world (ocean) of today, human activities have broken many ecological barriers, artificially enhancing the spreading of species to new environments (*e.g.* 'alien' or invasive or non-native species). This potentially imposes significant changes in the functioning of the 'invaded' system (see Leppäkoski *et al.* 2002 for a comprehensive review). Aliens, furthermore, might be successful at degraded sites, filling the ecological void left by stressed populations of resident species, as envisaged by the 'passenger model' (Didham *et al.* 2005). The passenger model might explain why species-poor basins, such as the Baltic Sea and the Eastern Mediterranean (in respect to the Western Mediterranean), are so prone to be 'invaded', but the ecological effects of these invaders still remain debated (Reise *et al.* 2006).

Equilibrium versus change

Traditional ecology developed concepts, such as succession and climax, to indicate that, for every climactic state, communities tend to reach a dynamic equilibrium (Connell & Slatyer 1977) point that represents an optimum, the most desirable, but transient (non-stable) state. These ideas are still very popular and the 'breaking of ecological equilibria' is often seen as a terrible catastrophe. The species that make up 'climax communities' are not the same as those of the various steps that communities have to go through to reach their 'final state'. In other words, if the whole world would reach the climax, the species leading to the climax would disappear, overwhelmed by climactic ones! This led to ideas linked to

disequilibrium as a way to enhance diversity, with the development of concepts such as keystone predation and intermediate disturbance (see Piraino *et al.* 2002, for a review) and to alternative models of community development to the classical facilitation model (Connell & Slatyer 1977). Equilibrium ecology is somehow teleological: ecosystems develop towards a state, the supposedly optimal one, and they should resist any change from that state, or should try to go back to that state after any disturbance. Non-equilibrium ecology, while recognising the existence of multiple stable points in the organisation of communities, identifies disturbance (at an intermediate level) as a way to enhance diversity. Stability, in other words, is seen as a depression of biodiversity. This reasoning has profound importance for our perception of conservation ecology, as exemplified for *e.g.* the Baltic Sea by Jansson & Jansson (2002).

The evolution of biodiversity

Hutchinson (1959) asked the question: *why are there so many species?* The question is logical if one looks at the environment from a functional point of view. If ecosystems do function at a low species-diversity, with few, essential, ecological roles (niches) fulfilled by few species, how come there are so many species? The Baltic Sea in this respect provides a good example of gradual increases in species-diversity and functional properties from the more or less limnic inner reaches to the fully marine North Sea (Bonsdorff & Pearson 1999; Bonsdorff 2006). Boero *et al.* (2004) tried to provide an answer. The first species originated at one place and then expanded and reached new types of habitats, where it underwent allopatric speciation because of different pressures by environmental conditions. The expansion of the range of the new species eventually saturated the ecospace and they started to interact. A useful concept, at this stage, is Van Valen's (1973) Red Queen hypothesis: whenever a change affects a biological system, this system has to change if only to continue functioning (*i.e.* to remain stable). In a changing world, thus, every change fuels further change, so as to avoid a catastrophic change. This paradox envisages biodiversity evolution as a chain reaction. Once life started to become diverse, its diversity sparked further diversity and this arms race, or escalation, towards diversification is still going on (Vermeij 1993). The history of life, through cladogenesis, is characterised by a steady increase in species number, and the more they are the more they will become, in spite of extinctions. There is no functional reason for that, as all ecosystems function (if they do not function, they disappear), even the first one, based on a single species. Life is baroque, and its redundancy has no functional reason. Life is not teleological, it is tautological.

Does this mean that biodiversity is useless (*i.e.* has no functional role as such)? On the one hand, the answer may be 'yes' (but this, nonetheless, does not give us the right to destroy it). On the other hand, even small changes in biodiversity can lead to enormous changes in ecosystem functioning. Species present, but with seemingly small or no ecological roles, may also be seen as the buffer of evolution in the case of a catastrophic event (such as occurred when the dinosaurs died and the birds and mammals took over). Such events dramatically alter the prerequisites for ecosystem functioning in the way it has functioned until a certain point in time.

Nonlinearity in ecosystem functioning: the jellyfish effect

The introduction of the alien ctenophore *Mnemiopsis leydi* in the Black Sea impaired recruitment in fish populations, leading to the collapse of fisheries, due to the predation of the comb-jelly on fish larvae and on the copepods they feed upon (CIESM 2001). The outbreaks of gelatinous plankton of the early 1980s possibly changed the functioning of the whole Adriatic Sea, showing that a

change in the abundance of resident species can also have an enormous impact (Boero 2001) (Fig. 2).

In the naturally species-poor Baltic Sea, modern 'invaders' may have a tremendous ecological impact today, as entire ecological functions may be lacking compared with the systems the invaders stem from. For instance, the deep-burrowing North American polychaete *Marenzelleria viridis* has invaded the entire Baltic Sea within some 20 years; it now occurs from the shoreline to 300 m deep, from the semi-marine conditions of the southern parts to the low-saline inner reaches, with profound implications for benthic sediment reworking and nutrient release. The Ponto-Caspian carnivorous pelagic branchiopod *Cercopagis pengoi* has had major effects on the entire pelagic food-web in the Gulf of Finland (Leppäkoski *et al.* 2002). An interesting aspect is that these invasive species gain a lot of attention among ecologists, whereas taxonomically (and, hence, ecologically) important findings may go unnoticed, such as the newly described fucoid (*Fucus radicans* sp. nov.; Bergström *et al.* 2005): until 2005, it had been treated as one more morphological adaptation to low salinity rather than a distinct species with distinct ecological requirements.

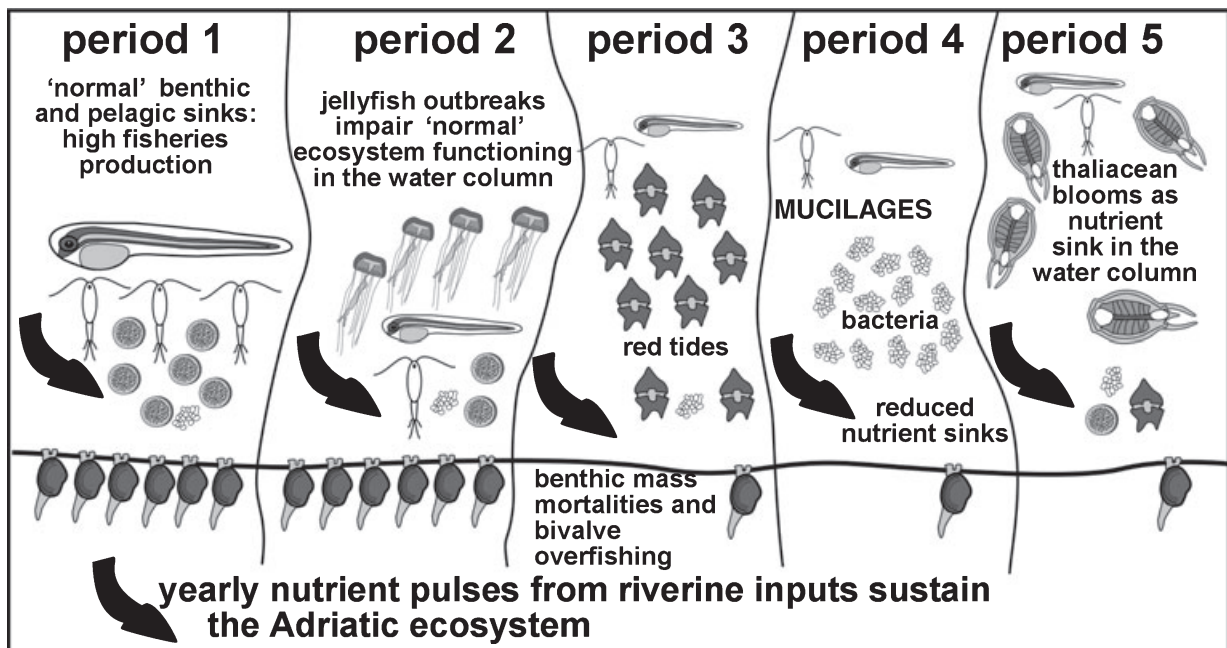


Fig. 2. Adriatic ecological history. Period 1: Nutrient pulses sustain diatom production that, in turn, sustains zoobenthic filter feeders and zooplankton, the latter sustaining nekton. In this period the Adriatic fisheries yields are very high. Period 2: Several years of outbreaks of *Pelagia noctiluca* strongly impact the communities in the water column, removing zooplankton and fish larvae. Period 3: The reduction of pelagic nutrient sinks, due to *Pelagia* outbreaks, leaves space for opportunistic dinoflagellates, leading to red tides in the water column and to benthic mass mortalities. The reduction in fisheries yields leads to increased fishery efforts (for instance with hydraulic dredges). Both pelagic and benthic nutrient sinks are reduced. Period 4: In the absence of relevant nutrient sinks, nutrient pulses are used by bacteria that produce mucilages as a side effect of their metabolism. Period 5: Blooms of pelagic tunicates filter phytoplankton (including bacteria) and restore, albeit temporarily, the pelagic nutrient sinks.

If viewed in the light of the chaos theory, ecological systems seem to be governed by nonlinear dynamics, so that apparently irrelevant episodic events (like the bloom of a resident species or the arrival of a single alien) can redirect the history of a system with changes in the shape of the main environmental attractors (Boero 1996). If ecosystems function in this way (as palaeontology and long-term series teach us), it is tenuous to infer on their future, as the sources of change can be initially too small to be detected. Clearly, one of the currently accepted definitions of ecosystem functioning (*i.e.* the efficiency of biogeochemical cycles) is insufficient to account for ecosystem health. It might be possible, for instance, that the biogeochemistry of the Black Sea continues to be extremely efficient in spite of the blooms of the comb-jelly, so that the ecosystems continue to perform their functions even while having a completely different structure. It is clear, at this point, that the efficiency of at least three types of cycles (*i.e.* extra-, intra- and interspecific cycles) must be taken into consideration to better understand the state of an ecosystem. Changes driven by humans must also be considered over large areas and long time periods (Jackson 2001; Worm *et al.* 2002). The complexity of natural systems does not allow for their precise, equation-based, modelling unless one considers just the function and disregards structure, losing information on 'who does what', and 'when', and 'how'.

Relevance and modelling

It is often said that modelling helps to untangle the complexity of the modelled systems and that, step after step, the approximation of early models will lead to increasingly refined models, eventually allowing almost complete understanding – and even prediction about the future conditions – of the modelled systems.

All modellers maintain, however, that algorithms cannot transform a poor set of data into a goldmine of information and insight. Relevance of what is put in the model is paramount in yielding a good model. This calls for identifying the relevant components of ecological systems, bearing in mind that they are regulated by multiple causality and that simple correlation does not imply direct causation.

It is very tempting, for example, to explain phytoplankton blooms by simple nutrient availability and increased light intensity (extraspecific cycles), with an approach based on bottom up control, and/or by the pressure of grazers (interspecific cycles), *i.e.* the top-down control, while forgetting that living matter needs continuity (intra-specific cycles) to persist. This has led us to neglect the ecological importance of benthic resting stage banks of planktonic organisms in explaining the cycle of plankton

(Viitasalo & Katajisto 1994; Boero *et al.* 1996; Katajisto 1996; Marcus & Boero 1998).

Furthermore, the relevance of benthic resting stage banks might lead to the consideration of the hypothesis that predation on resting stages potentially controls plankton diversity (Pati *et al.* 1999) (Fig. 3). Plankton dynamics is possibly the most important environmental driver in the whole biosphere; it is highly telling that, despite this, our understanding of these dynamics is so primitive that novel hypotheses on the underlying processes are still possible. These hypotheses did not stem from refinement of equational models, which rely more on mathematically demonstrated correlation than on natural history-derived causation: they were originated by observations stemming from questions about the natural history of planktonic and benthic communities. Still, both descriptive taxonomy and the dynamics of long-term change lack vital knowledge.

Structure versus function

The present trend in bio-ecology is to privilege function and disregard structure (hence the crisis of taxonomy). The situation we depicted calls for a new approach to understanding the links between structure (species composition) and function (cycling of matter and energy) in ecosystems. Furthermore, we have to identify crucial gaps in our knowledge of the systems that we aim at managing and preserving, and we must know something about the historical past (often based on natural observations and/or palaeontological evidence) (Jackson & Johnson 2001; Dayton 2003). For instance: for how many species do we know the ecological role? The answer is: very few (Piraino *et al.* 2002). For how many species do we know the life cycles, to properly evaluate recruitment? Again, the answer is: very few (Fraschetti *et al.* 2003). We do not even know about the existence of a majority of the species (as most species are still undescribed) and, furthermore, we know very little about the functional role of those species we know already. Finally, we also need to know about the relationships between the species, functions and the productivity of the ecosystem (Worm & Duffy 2003). This level of ignorance about the structure casts some doubt about the value of functional approaches, especially when aimed at linking the structure (biodiversity) to function (ecosystem functioning). Some current approaches, such as the use of stable isotopes, have proven useful in this respect, however (Peterson & Fry 1987).

It might be true that, in some fields or areas, structure is so well known that it is no longer fruitful to continue to study it: it is sufficient to rely on past results. One such region is arguably the Baltic Sea, where functioning

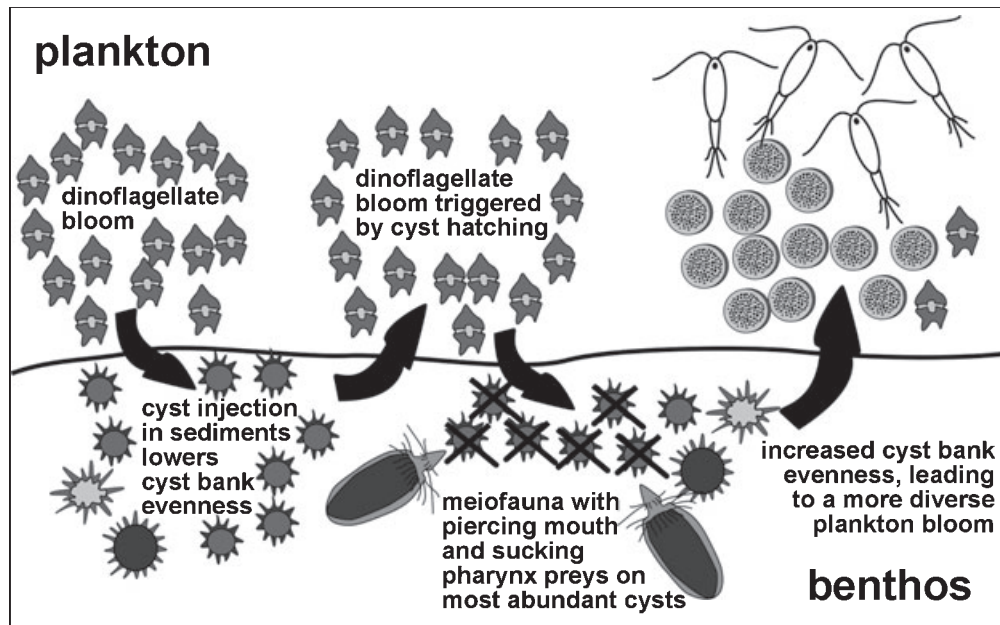


Fig. 3. A keystone role for the meiofauna. From left to right: a dinoflagellate bloom monopolises the plankton, leading to red tides. At the end of the bloom, great numbers of cysts are produced and fall into the sediments, lowering the evenness of the resting stage bank (here represented also by diatom spores and copepod resting eggs). In such a situation, the great number of cysts in the sediments should lead to recurrent blooms of the active stages at the onset of the following favourable seasons. Many members of the meiofauna, here represented by loriciferans, have piercing mouthparts and sucking pharynxes; it is hypothesised that they use them to feed on the most abundant resting stages in the resting stage bank, that is the cysts of the previously monopolising dinoflagellate. Cyst removal causes an increase in the evenness of the resting stage bank, in turn leading to higher diversity in the plankton at the onset of the following favourable season.

of, for example, the zoobenthos is well-defined in relation to taxonomy (Bonsdorff & Pearson 1999; Bonsdorff 2006). Can we say that our knowledge about the structure of the environmental systems (from species to species assemblages) is so well founded that we can rely on what has already been done, without investigating any further? The answer is no, we cannot. This does not mean that we cannot say anything about environment functioning until we know everything about environment structure. We must go on and 'cure' the environment as best as we can, recognising that our 'cures' can be improved only if we improve our knowledge about both its structure and function, as the two go together.

New directions

As remarked by Boero *et al.* (2004), novel approaches are often based on old, but neglected, views. We propose a return to natural history as the starting point of the ecological theory, with the building of ecological scenarios leading to complex hypotheses (like those developed by C. Darwin) on the ways ecosystems function, and on the relevance of biodiversity on their functioning (see also Dayton & Sala 2001). Once the relevant components of

the scenario are singled out, their relationships and interactions should be identified, at least hypothetically. One example is the hypothesised importance of resting stage banks and the keystone role of the meiofauna in respect to plankton dynamics and diversity (Fig. 3). If the hypothesis were even partly true, then we would have another powerful key to disentangle the intricacies of the most important bio-ecological process of the whole biosphere: plankton dynamics. The hypotheses generated from natural history should then be tested, where possible, by proper experiments, whereby complex hypotheses should be split into simpler ones. Experiments, however, are not always possible and the risk of answering solely experimentally answerable questions is high, leaving important, but difficult, questions unanswered (and even unasked). Removal of grazers from intertidal shores to evaluate their impact on algal growth is rather easy, when compared with the removal of either meiofauna or gelatinous plankton to evaluate their impact on plankton and nekton dynamics. Moreover, what might be considered as the 'same source of disturbance' (*e.g.* an episodic event like a jellyfish bloom) might lead to completely different outcomes in replicated experimental sets, just as a series of mixings of a stack of cards invariably leads to different

sequences of cards. A set of 'hard' facts, deriving from experimental evidence, will forcedly co-exist with a set of 'soft' facts, linked to the historical nature of ecology. Functional constraints might be hypothesised to make up the 'hard' part of the integrated approach, whereas structural contingencies would account for the 'soft' one. Natural history and experimental ecology must cooperate and integrate to help untangle the ecological complexity, merging biodiversity with the functioning of the ecological systems. We believe marine ecology (in a holistic sense) may offer great opportunities to develop and test these approaches.

An operational approach for biodiversity: from species to habitats and back

Besides having a probable impact on ecosystem functioning, biodiversity has a remarkable intrinsic value and should be protected *per se*. The first step in protecting something is to know which objects to protect. The best candidates to represent biodiversity are species. Many projects aim at inventorying of all species on a global scale, but this objective is still very far from being reached. Species lists should be the result of thorough taxonomic revisions, with the cleaning up of synonyms and the description of new species. This objective is not feasible over the short term and requires well-trained taxonomists, as envisaged by the Partnership for Enhancement of Expertise in Taxonomy (PEET). An inventory of all species and of their distribution will only be complete (if properly funded) in several decades. We cannot wait that long for the conservation and management of biodiversity. Habitat loss and fragmentation is the main problem to be tackled in order to preserve biodiversity. The European Community issued the Habitat directive precisely to face this problem. The definition of 'habitat', however, remains rather vague (sometimes habitats are physical entities, *e.g.* fine sand, at other times they are communities, *e.g.* sea grasses and sometimes both, *e.g.* coral reefs); moreover, the diversity of marine habitats has not been formalised unambiguously on a European scale (see Bellan-Santini *et al.* 1994 for a list of habitat types in the Mediterranean, and others have been compiled both for the Mediterranean and other regions, such as the Baltic Sea; see Schernewski & Wielgat 2004). Compiling a list of habitat types agreed upon by all specialists, involving both ecologists and taxonomists, is surely a priority. The second target is to map the distribution of these habitats. Then we must compile accurate species lists for each habitat and its community(ies) using multiple approaches from local taxonomy to remote sensing (Nagendra & Gadgil 1999). Such species lists should be derived from both original and literature-based research.

Taxonomists, working together with ecologists, must draw up these lists. Master lists for all taxa, for instance, might be derived from the European Register of Marine Species, listing, for each species, the habitat type(s) from which it has been recorded (the records are the citations of each species in the specialised literature). Then the list of species and habitat types might be turned into a list of habitat types, each with its master list of species. Each habitat type, using this sort of information, will become a hypothesis: if a given habitat type occurs, then a set of species should be found: those that were found in the past in that habitat type. Of course, not all species can be found at the same locality, but it is reasonable that an accurate sampling should yield a relevant number of the expected species. This is also the basic approach within the European Water Framework Directive when defining the so called 'ecological reference conditions', where the use of a numerical value is advocated.

The Historical Biodiversity Index (HBI)

The ratio between the species that have been found in a sampling session from a given habitat type (realised biodiversity) and the species that should be found at that habitat type, based on previous knowledge (potential biodiversity), is an indication of the state of a given habitat and of the community inhabiting it, *i.e.* 'Historical Biodiversity Index':

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

If the sample yields all the species that were previously found in that habitat type, then the value of the index is 1; if no species are found, then the value of the index is 0. If there are new species, unrecorded previously from that particular habitat type, then we can try to understand if they are simply rare species that suddenly became abundant (having always been there, albeit unrecorded), if they arrived from nearby and similar habitats, or if they arrived recently from some other geographical location (aliens). These species cannot be immediately incorporated into the original master list, as their history will have to be understood before introducing them in the master list of (regional) species occurrences. Diversity indices are usually based on what is found at each station in comparison with what has been found at other stations. This tells us something about that sampling session, and about what has been found. It does not reveal much about what has not been found or about what was found previously in that particular habitat type. We need some history in our observations. In the HBI, the calculation of the index itself is almost childishly simple; the difficult part is to compile the master lists. Natural history, for once, prevails over complex statistics. The HBI, comparing what is being found with what should be found, will

be a first step to highlight species losses, especially for inconspicuous species (the great majority of biodiversity). Species loss is usually perceived only for charismatic taxa, whereas inconspicuous species are recorded only if they are found (if the sample is studied by a specialist); when they are missing, however, their absence is not recorded as relevant. In spite of the widespread concern about species extinction, there is not much proof that species are actually becoming extinct, especially in the sea (besides the usual, few cases). This is probably not because they are not becoming extinct but simply because we are unable to perceive their extinction. On the one hand, it is true that species extinction is usually linked to habitat destruction, but it is also possible that species start to become extinct before the disappearance of a given habitat type. Accordingly, the absence of some species may be a warning signal for the impending disappearance of a given habitat type.

Looking for extinct species

Of course, while we wait for a complete list of all species (all-taxa inventories), we can use the lists for the taxa we know better. Boero (1981), for instance, compiled a master list of all the hydroid species that have been recorded growing on the Mediterranean seagrass *Posidonia oceanica*; some of these species live exclusively on the leaves of Mediterranean seagrasses. The absence of specialised species, living only on *Posidonia* leaves, might be an early warning about the state of *Posidonia* meadows even before the plant itself shows any sign of suffering (cf. Baden & Boström 2001 for a similar approach on the *Zostera*-assemblages in Scandinavian waters). Similarly, data exist on long-term changes (1840s until present) from the German Baltic Sea coastal waters (Zettler & Röhner 2004). Master lists can provide inputs to hypothesise what might be endangered, or even extinct. The Hydrozoa, again, provide a striking example.

The Mediterranean, like the rest of the planet, is undergoing a period of temperature increase that is radically changing its biota. In such a situation, the species living in the coldest part of the basin might well be the first to be negatively affected by the temperature increase. The coldest part of the Mediterranean is the Northern Adriatic, where the cold waters of the eastern basin are formed. The Northern Adriatic is inhabited by species of boreal affinity. The only furoid alga of the Mediterranean (*Fucus virsoides*), for instance, is endemic to the Northern Adriatic, together with many other species. One of these species is the hydroid *Tricyclusa singularis*, and the Gulf of Trieste (the northernmost part of the Northern Adriatic) is its type locality. After the original description by Schulze (1876) the species has never been recorded again

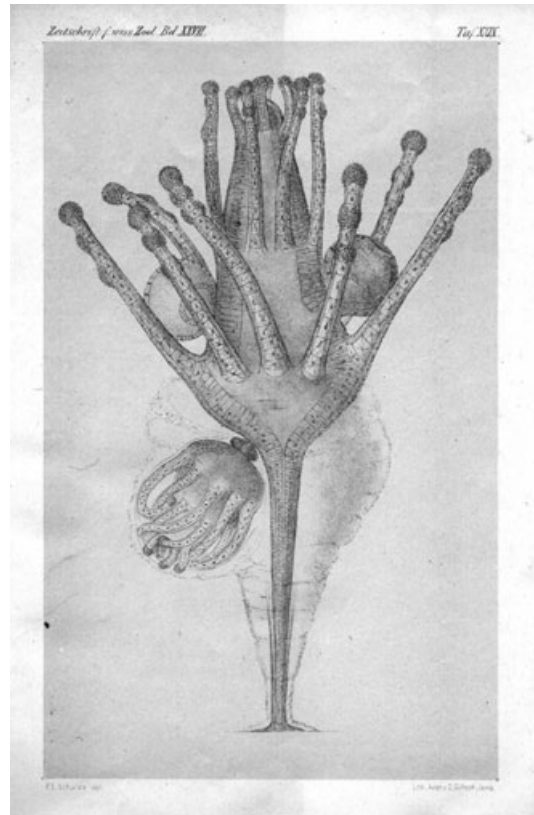


Fig. 4. The hydroid *Tricyclusa singularis* from the original description (after Schulze 1876). The hydroid was collected from the Gulf of Trieste (Northern Adriatic) on the alga *Cystoseira*, in April 1875, at shallow depth. It has three rows of tentacles and is individual. It can bud other polyps (one is shown at the base of the hydranth) and is covered by a thin sheath of perisarc up to the proximal tentacle whorl. Reproduction occurs by fixed gonophores, shown here between the second and third whorl of tentacles.

from the Mediterranean Sea, despite being very distinctive (Fig. 4). Instead, it has been recorded several times from Roscoff (Atlantic coast of France), so showing a disjunct distribution. Taxonomists, due to the presence of three rows of tentacles, and the solitary habit, assigned this species to a distinct genus and a distinct family. The disappearance of *Tricyclusa singularis* from the Mediterranean would thus not simply represent the disappearance of a species but, instead, the loss of a whole family, and potentially a specific, unique ecological function!

The issue of species extinction in the sea is delicate, as there are very few documented cases in this domain. Two reasons can be forwarded: there are low global risks of extinction in the sea or, instead, species become extinct but we fail to realise it. The history of the presence of species in particular geographical areas, at particular habitat types, represented by the master lists of the HBI containing all records for each species, allows finding species

with strict requirements that have not been recorded for a long time. These have to be sought and, if not found, a case of possible (local or final) extinction could be raised (e.g. the above hydroid example). The importance of 'catastrophic' changes must also be recognised in this context (Scheffer *et al.* 2001), as must the notion of the globally increasing biodiversity over hundreds of millions of years (Jackson & Johnson 2001), and the capacity for recovery of the marine ecosystem after depletion or degradation of the species (Lotze *et al.* 2006).

Conclusion

The HBI merges biodiversity measurements at both the habitat and species level. Genetic approaches, furthermore, will reveal the compactedness of species populations across the same range of habitat types over a geographical scale; this will help trace the routes followed by fast-moving species (see Väinölä 2003 for an example on the long-term invasion history of *Macoma balthica* into the Baltic Sea, and Johannesson & André 2006 for a review of the genetic isolation of species in marginal regions). Knowing a species is merely the beginning in biodiversity estimates; modern molecular methods provide tools to re-analyse diversity and biogeography, relating present-day distributions with past invasion events (Väinölä 2003; Bastrop & Blank 2006). Each species has a role and, according to the niche theory, coexisting species should have different niches and different roles. Nonetheless, rare species can easily survive without much competition from other species with very similar requirements to theirs, poised to replace the dominant one in case it fails. We know the role of very few species (Piraino *et al.* 2002), despite continuous reference to biodiversity and ecosystem functioning. Structure and function, of course, depend on each other (Snelgrove *et al.* 1997). While overspecialisation is required to deepen our knowledge on particular issues, we still need to integrate approaches into a common view. This common view is lacking in marine biodiversity research. The manifold meanings and measures of biodiversity cause great confusion for both scientists and decision makers. The different views of biodiversity coexist more or less independently, and specialists in different biodiversity-related topics often cannot even communicate because of overspecialised jargon and technicalities.

We need a common philosophy based on a common theory. We also need to increase our ethical awareness within ecology (Minteer & Collins 2005). The approaches depicted here lay no claim to solving these problems, but underline that we have to use all available information to understand biodiversity issues. They also demonstrate that the specialists in the different facets of biodiversity have

to combine their efforts, and join in common projects, to bridge the gaps that currently divide the subfields of biodiversity (and ecosystem functioning).

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