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Biodiversity on the land and in the sea: when it converges, challenges in common

by Jacques BLONDEL

For a number of reasons, marine and terrestrial research go on with the one practically unaware of the other. Even so, the similar nature of the various anthropogenic pressures that impact both domains justifies a pooling of efforts to measure such pressures and develop strategies to counteract the negative consequences. Worldwide changes represent a gigantic "natural experiment" in which the responses of organisms can be exploited through analysis and for combating the negative effects. Several suggestions are made for research in common on topics which transcend the conceptual borders between the two domains.

1 - "Long-term" studies are by convention those involving at least twenty years.

Introduction

The closeting of scientific disciplines is a widely-recognised phenomenon. This is especially so for research on marine and terrestrial habitats: both domains exist in splendid isolation, the one practically unaware of the other. An outstanding exception is the book co-authored by Mireille Harmelin-Vivien and François Bourlière (1989) which gives a striking demonstration of the resemblance between the structure and organisation of fish populations on coral reefs and those of vertebrates in tropical forests. It must be acknowledged that, for a number of reasons linked to the difficulty of approaching and financing research in the marine environment, its biology is much less well understood than that of land-based habitats. By way of example, just consider how little monitoring over time has been done of populations in marine environments. Whereas there have been over 500 long-term¹ studies of populations of terrestrial plants and vertebrates in England over the last thirty years, for marine organisms there have been less than some ten (CLUTTON-BROCK & SHELDON, 2010). Certain of the hindrances to understanding marine organisms are of a conceptual nature and derive from the scientific method itself; others are technical or logistical. While ecological theory for terrestrial habitats was largely built up around the concepts of ecosystem, community and population, such entities are difficult to define and identify in a marine environment on account of the apparent absence of boundaries between habitats and of barriers to the dispersal of organisms. Though we can ascribe contours to a landscape, work out a typology of the habitats that make it up, measure the amount of matter, energy and propagules they exchange between each other, such procedures becomes very difficult in a marine environment, despite the fact that it is indeed compartmentalised, including its deep-sea contexts. Furthermore, the kinds of research that require monitoring individuals, populations and communities in space and over time are practically impossible to carry out in a marine environment. This remains so for the analysis of details in the life history of individuals of a species, an analysis which was the starting point for the development of evolutionary ecology. In a marine environment, we have almost no access to what constitutes the very essence of evolutionary mechanisms, that is to say the interaction between genotypes and their environment. This makes it very difficult to know about an organism's response mechanisms to the heterogeneity and variability of the environment. Nor can we use quantitative genetics that we know provides a powerful tool for measuring the response of organisms to processes of selection which vary over time and space, particularly in this period of climate change.

To such difficulties of a theoretical nature must of course be added a whole series of technical and financial handicaps. Research in the field is more complex, logistically very demanding and so much more expensive than land-based research.

And yet, there are very good reasons to build bridges and foster encounters between these two domains in the disciplines of ecology and conservation sciences, especially now at a time of uncertainty about the future of species and ecosystems.

Where is the common ground between these two domains?

The gigantic worldwide "natural experiment" that global changes represent ² offers unique opportunities for testing hypotheses about the response of organisms to variations in their environment. Admittedly, this "experiment" is not at all desirable but, even

so, let us at least turn it to our best advantage by applying the scientific method in all its rigour and in this way enhance our understanding of the impact of these changes on the biology of organisms and then take measures to deal with their effects. Given that the damage caused by excessive anthropogenic pressure is now widespread, as much in the sea as on land, it would be a very good idea to draw up an agreed agenda for research on topics that transcend the boundaries between disciplines in biology. Below are some finalised examples — there could be plenty more — in the domain of fundamental research.

1. Exploiting the metabolic theory of ecology. Among the general principles which transcend the differences between the marine and terrestrial environments, the metabolic theory of ecology (Brown et al., 2004) provides a powerful normative framework for understanding the functions fulfilled by species in an ecosystem and, subsequently, understanding and comparing the functioning of such ecosystems. This theory posits that the metabolism of all living organisms, be they plant or animal, aquatic or terrestrial, in diatoms or the great whales and from mice to elephants, manages the energy available to them in the same way, as a function of their size and the ambient temperature. The metabolic rate, meaning the rate at which organisms harness, transform and use energy, is a fundamental biological constant which controls ecological processes at every level of organisation, from individual specimens to the entire biosphere. This fundamental law could be exploited for simulating the likely responses by organisms to the climate changes currently under way. Just one example: it has been observed for organisms as different as leaf-eating caterpillars on trees and plankton species in the sea that their growth has speeded up as a result of global warming, in accordance with the predictions of the metabolic theory of ecology (Blondel & al., 2006; Duarte, 2007).

2. Food chains. A community's organisation and functioning are governed by a complex network of food chains. The processes involved in their functioning may be of the top-down or bottom-up type. The first type consists of regulation by predators while the second involves regulation by primary pro-

2 - By global changes is meant the totality of large-scale modifications which affect the whole planet and are anthropogenic in origin. There are five such changes:
a) the deterioration and fragmentation of habitats, b) chemical inputs, c) invasive species, d) climatic disturbances and e) the over-exploitation of resources (VITOUSEK, 1994).

ductivity. In both the marine and terrestrial domains, food chains, which belong to the top-down category, are a major force in the structuring of communities. Predation thus becomes a fundamental principle that at times is seen as "a natural law as basic and essential to ecology as natural selection is to evolution" (Terborgh & Estes, 2010). Yet the disappearance of large predators, as much in the sea as on land, is one of the most spectacular manifestations of the erosion of biological diversity. It brings with it a serious modification of interspecific interaction and upsets at the deepest levels the food chain networks at the heart of a community. For the function of predation has effects that are propagated progressively outwards, from one food chain level to the next in succession along the chain, bringing positive effects for certain species, negative for others, and thus contributing to the structuring of the whole community far beyond the relationship between the eater and the eaten. In the marine environment, the disappearance of large predators is doubtless the most disastrous effect of over-fishing because it has unforeseen consequences on food chain networks and community structure (JACKSON, 2001). One such unexpected result has been the "jellying up of the oceans" by the booming proliferation of jellyfish that replaced the now-departed large predators (RICHARDSON & al., 2009). It has got to the point in some regions, for example the grand banks of Benguela off the coast of Namibia, where the tonnage of jellyfish hauled in now exceeds the catch of fish. Since the beginning of the 1970s, there has been a regular decline in the level of the average food chain of marine animal life, a sign of the impact of industrial over-fishing on the large, slow-growing predators (PAULY & al., 1998). In land environments, the dislocation of food chains, manifested in the disappearance of large predators but, also, of large herbivores, may also have unforeseen effects. Why do plants not exploit to the highest degree the potential offered by local combinations of climate and soil -in other words, wondered William Bond and John Keeley (2005), why is nature not greener? If the plant world was regulated only by the nature of the soil and the nutrients it contains, by precipitation and temperature, plant cover on the land would be perfectly predictable. It would be forest, savannah, grassland or desert, depending on the level of the various factors, but as long as

these factors do not vary, each of these habitats would keep a certain form of stability. But this is not what observations show: if nature is not in fact greener, it is because it is devoured either by herbivorous animals or by wildfire 3. Thus, without human intervention, three types of world can be envisaged: a) a world regulated by fire, as is met with in sub-Saharan savannah, in the Californian materral or chaparral, some areas of the Mediterranean Rim, the fynbos of Cape Province in South Africa and in some northern forests; b) a world controlled by the climatic potential of a region which grows that much greener when productivity is higher, as determined by the conditions of moisture in the habitat and the fertility of the soil, which is what can be observed in some tropical rain forests where the plants' growth potential far outstrips the regulatory capacity of herbivorous animals; and c) a world regulated by the large mammalian herbivores, those very animals that in the past, before man took part in their extermination, contributed to the upkeep of clearings within the greenery of the forests, forming a mosaic network reaching almost indefinitely across the vast plains and mountains of Europe. We now know that breaks within the depths of the forest were largely maintained by the great herbivores.

3. The effects of climate warming. The impact of variations in temperature on events in the life history of organisms has been observed to be similar in both marine and terrestrial habitats: seasons of reproduction are brought forward, spring migration occurs much earlier and autumn migration is delayed in the Northern Hemisphere; food chains are thrown out of phase because the different partners involved do not respond in the same way, and especially not at the same rate, to changes in the environment. Obviously, it is the phenological occurrences, which recur regularly from season to season, that have been best documented. Research carried out in England on several tens of species living in marine, fresh water and terrestrial habitats showed that between 1976 and 2005 all of them experienced a given seasonal event by 0.2 to 0.6 of a day in advance per year, depending on the event in question e.g. return from migration or the onset of reproduction (THACHERAY & al., 2010).

3 - Concrete confiscates more than 75,000 hectares of good soil each year in France and almost half, or indeed more of the Mediterranean coastal rim.

4. The quest for habitat. One biological constant, which is in fact a consequence of the metabolic theory of ecology, is the sensitivity of organisms to temperature. A species has a natural window of thermal tolerance and responds to fluctuations in temperature by a combination of physiological, biochemical or behavioural adaptations. Though this window of thermal tolerance can be wide, as highlighted by the example of the larch which can develop at altitudes ranging from 800m to 2,300m, each species is suited to a thermal "envelope" so clearly circumscribed that when the envelope moves, the organism itself follows on necessarily in a sort of "quest for habitat" in response to the displacement of the envelope. For marine just as much as for terrestrial environments, there is already a great amount of data available on the way in which organisms move up in altitude and / or latitude in response to climate warming. We already know that in the course of the last century, for the 1,700 animal and plant species for which we have reliable data, the average drift worldwide was 6 km in latitude and 6 m in altitude per decade (PARMESAN & YOHE, 2003). Simulations abound on the modification to be expected in the 21st century in the distribution of European trees (Chuine & Thuillier, 2005). While it is difficult to design such simulations for marine species, numerous empirical evidence shows that the Mediterranean has even today been colonised tens of new species which prevously never left tropical waters (Blondel & al., 2010).

5. Ecological trajectories and the threshold effect. The non-linear nature of ecological and demographic processes is still a poorly understood phenomenon which research scientists are very wary of because it is difficult to forecast. On occasion, it has been observed that beyond a certain value for an ecological variable, this variable will collapse or, conversely, take off because it has reached a threshold beyond which ecological trajectories become unpredictable and more often than not undesirable. Beyond such a threshold -for example, the abundance of an aggressive invasive species or the decline in numbers of a resource speciesthe system can all at once flip to a new trajectory totally unforeseen in the beginning. Certain empirical data and models indicate that the response of a community to a continuous variation in the environment can take three forms: either a gradual change in its variable response, a flip of the systems to another trajectory or a phenomenon known as hysteresis by which the community "gives up" and transforms itself into another or several systems (Suding & al., 2008). A regrettably renowned example of this threshold effect is the complete collapse in the cod stocks on the Grand Banks of Newfoundland which have still not been replenished despite the moratorium on fishing ordered by the Canadian government in 1992 (CURY & MISEREY, 2008). Due to a typical threshold effect, the food chain network within which the cod lived was transformed by its responses to the new regimes of natural selection induced by its over-fishing: in the event, the predator, cod, was transformed into the prey of the very species that it used to feed on!

6. Destabling of ecosystems by invasive species. Biological invasions are often considered to be the main cause of the decline in biodiversity. Tens of examples could be cited of biological invasion, as much on land as at sea. In the Mediterranean alone, no less than 90 fish species (out of 650) and 60 species of decapod (out of 350) are species known as "lesseptian", meaning that they invaded the Mediterranean Sea as a result of the digging out of the Suez Canal (by Ferdinand de Lesseps) (BLONDEL & al., 2010). Another example of biological invasion with disastrous consequences is that of the killer algae Caulerpa taxifolia which was identified for the first time in 1984 off the coast of Monaco. In twenty years, this species has invaded the coastal regions of most of the countries around the Mediterranean Rim. The species covers the seabed with a thick mattress which smothers out the indigenous species, eliminating amongst others the beds of posidonia which are the preferred reproduction areas for many fish. A particularly important challenge is to identify the traits and the circumstances which make a species that has escaped from the confines of its natural area of distribution into a potential invader and, thus, a danger to indigenous communities. In fact, it has been estimated that of the some hundred species accidentally introduced by man into areas outside their natural area of distribution, less than ten threaten to become invasive. Detecting what

favours invasiveness would be a means of anticipating the process before it gets too late because it appears to be well-nigh impossible to get rid of a really aggressive species once it is firmly established.

Conclusion: towards an agenda for research in common

The need and the interest in linking together the worlds of the sea and the land in matters ecological and in conservation sciences is justified by the integrating nature of certain fundamental principles in evolutionary and functional ecology that transcend the conceptual barriers between the two domains. There is common ground for both in the response of organisms to changes in temperature or the factors and features that can make species introduced by man into aggressive and invasive organisms. The transfer of modelling methods from one domain to the other would reduce the waste of effort that consists in duplicating similar scientific approaches. In addition, a more standardised, uniform approach would foster the involvement of experts independent of habitats and taxons, leading to considerable reduction in the disparity in our knowledge of the marine environment as compared to that of the land. One can only hope for comparative research in those fields and disciplines which lend themselves to interaction between the two domains. Such mutual effort would notably coalesce via the same approach to the interaction between the sea and the land in island and coastal environments. Meeting the challenge of jointly undertaking work on the communities connected to the sea-land interface is justified by the mobility of the shoreline linked to the rise in sea level and by the existence of communities specific to these zones. In fact, coastal fringes, particularly around the Mediterranean Rim, are subject to very strong pressure from the destruction of habitats, the development of the tourist industry, pollution, eutrophisation, certain types of fish farming, the over-exploitation of the fishing resource, the deterioration of weed beds near the coast and the particularly aggressive character of some invasive species.

Finally, as Christian Körner has emphasised, incertitude about the extent and the tempo of global changes should be an encouragement to prudence and the application of the principle of precaution. In this respect, given the lack of knowledge about species' behaviour in the face of global change, the conservation measures likely to be the most effective in the short term are doing everything possible to preserve the genetic diversity of populations and fostering a patchwork pattern of landscape. Such precautions appear to be eminently justified, so much the more so in that we now know that climate change has sometimes taken place very rapidly, and in the not so distance past: at the end of the lower Dryas (12,700-11,500 b.p.), a period when all our present species already existed, the increase in the average temperature was 7°C in 50 years (DANSGAARD & al., 1989), which is much greater than the rise forecast by the IGCS (GIEC) for the current century. And finally, let us not forget that a wide variety of microclimates can be encountered within a very small area, a fact which emphasises the merits of a jigsaw pattern in the landscape.

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Résumé

Pour de nombreuses raisons d'ordre historique, mais aussi conceptuel et technique, les recherches en milieu marin et terrestre sont presque totalement isolées l'une de l'autre. La difficulté de définir des habitats et communautés en milieu marin, de même que le manque d'accès au suivi des individus compliquent la mise en œuvre des méthodes de démographie et d'écologie évolutive qui ont fait leurs preuves en milieu terrestre et ont permis de maîtriser le fonctionnement et l'évolution des populations et communautés en milieu terrestre. La similitude des pressions d'origine anthropique qui s'exercent sur les populations et communautés dans les deux types de milieux justifie pourtant la mise en commun des efforts pour en mesurer les effets et développer des stratégies de réponse à ces pressions afin d'en diminuer les conséquences négatives. A cet égard, les changements globaux constituent une gigantesque « expérience naturelle » qu'on peut valoriser pour analyser les réponses des organismes aux changements de leur environnement et lutter contre leurs conséquences négatives. Plusieurs propositions de recherches communes sont énoncées sur des sujets qui transcendent les barrières conceptuelles entre les deux domaines : prédictions de la théorie métabolique de l'écologie sur les réponses des organismes aux dérèglements climatiques, conséquences sur les écosystèmes de la dislocation des cascades trophiques, construction de protocoles de monitoring des populations, recherches sur les espèces envahissantes, analyse des changements d'aires de distribution et de la traque aux habitats.

Summary

Many historical, conceptual as well as technical reasons explain why there is almost no connection in scientific research between the terrestrial and marine realms. Because it is hardly possible to define habitats and communities in marine environments, and because it is almost impossible to follow individuals, it is extremely difficult to apply the methodologies that have been successfully devised in demography and evolutionary ecology in terrestrial biotas. Therefore the knowledge of population and community ecology and evolution in marine environments is in its infancy compared to that in terrestrial ecosystems. Yet the similarity of anthropogenic pressures on populations and communities in the two kinds of habitats fully justifies common efforts to assess the consequences of environmental changes and develop strategies for mitigating or alleviating their harmful consequences. In this respect, global change is a huge so-called « natural experiment » which can be used for analysing the proximate and evolutionary responses of organisms to environmental changes and trying to reduce their negative effects. Several research areas that are common to both terrestrial and marine environments are proposed on themes which transcend the conceptual barriers between the two domains. Examples include predictions from the metabolic theory of ecology on the responses of organisms to climate change, the consequences of the disruption of trophic cascades on ecosystems functions, the development of protocols for monitoring populations, research on biological invasions, and analysis of distributional shifts of populations and habitat tracking.