1. GENERAL ASPECTS CONCERNING MARINE AND TERRESTRIAL BIODIVERSITY

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1.1. INTRODUCTION

The oceans are the largest biome on earth. Totalling 361 million km\(^2\) and with a mean depth of 3,730 m, they cover 71% of the surface of the planet. Their volume – 1,348 million km\(^3\) – is immense, and they are also the primeval scenario for the diversification of life. Thus the oldest known fossils are marine stromatolites, laminar structures produced by the activity of cyanobacteria, preserved in Australia and dating back 3,500 million years. Seemingly, the first animals also appeared in the sea. We know of trace fossils 800 million year old, but the first fossils of “real” animals are dated later; about 640 million years ago at the end of the Proterozoic period. These animals belong to the so-called “Ediacara” fauna of the Vendian system, a name which recalls the Australian locality where they were discovered, although they are also present in other parts of the globe. They were soft-bodied organisms that are hard to attribute to any of our modern types.

In comparison, the earliest terrestrial fossil record corresponds to spores, possibly of bryophytes (mosses, liverworts, etc.) and is datable to the Middle Ordovician (about 450 million years ago). For animals, the first continental settlement appears to go back to the Silurian period (a bit over 400 million years ago), from which we have recovered remains of myriapods (centipedes and millipedes) and arachnids, although certain trace fossils, probably produced by terrestrial arthropods, also date to the Ordovician period.

Marine organisms have thus had more time to diversify than their terrestrial counterparts (about double in the case of animals). And yet the oceans apparently harbour only 2% of the total number of known animal species. Scientists have resorted to different ad hoc reasonings to explain this paradox. They have pointed out the enormous potential for dispersal of the propagules of marine animals (eggs and larval stages), which would act against the genetic

\(< Photo 1.1: \text{Seahorse (Hippocampus ramulosus) in a seagrass meadow.} \text{Seahorses, which are generally found around our coasts in underwater meadows, are suffering a worldwide decline for unknown causes.} >\)
segregation of their populations in a world apparently without barriers. They also mention the differing size of primary producers in continents and oceans. So whereas arboreal terrestrial vegetation can reach a height of more than 100 metres and offers a wide range of niches and microhabitats for other organisms, primary production in the sea relies mainly on bacteria and unicellular algae, which provide no structural support for diversification. Therefore, the co-evolutionary processes between insects and angiosperm (= flowering) plants that have been the driving force of the diversification of terrestrial biota do not occur in the marine environment (there are only 58 species of marine angiosperms, versus about 300,000 on the continents).

But is the prevalence of the continental biota a fair reflection of reality? Let us address this question by first analysing what we know about animal biodiversity on the continents and in the oceans, focusing on certain aspects that limit the exploration of marine biodiversity and which may go some way to explaining this paradox.

1.2. A COMPARISON OF BIODIVERSITY ON LAND AND SEA

The number of plant and animal species on the continents is estimated at around 12 million (see table 1.1). 91% fall within a single phylum, the maximum category of the taxonomic hierarchy; namely the arthropods, embracing creatures such as insects, crustaceans, arachnids, acari and other minor groups. The continents are thus scantly diverse as regards animal body plans, and the large number of species present is attained through virtually infinite combinations of a single pair of body plans, namely: (1) arthropods with a single pair of antennae and only three pairs of thoracic limbs (what we call insects); and (2) arthropods that advance by means of their perioral appendages (the chelicerae: arachnids, acari, etc.). The quantity of continental species still awaiting discovery and description is simply overwhelming. Entomological expedi-
tions to tropical rain forests continue coming up with thousands of new insect species, at so fast a rate that many cannot be described by conventional methods, due to lack of time and/or resources, and are identified only by a number or registration code. Thus, in a study confined to ten trees in a rain forest in Borneo, the British entomologist Nigel Stork collected a mean of 580 species of insect per tree. By comparison, a European oak harbours between 100 and 200 species. In tropical rain forests, tree diversity is much higher (up to 250 species per hectare) than in temperate forests, and the specificity of insects to their host trees falls to between 3% and 20% (Ødegaard et al. 2000). These data equate to extremely high numbers of species per hectare, without considering insects of a terrestrial as opposed to arboreal habit, which are also far more diverse in tropical rain forests than in forests elsewhere.

But it is also true that the discovery of higher-rank taxa is only rarely reported nowadays. Recently (2002), we heard of the discovery in Namibia and Tanzania of a new order of insects, the Mantophasmatodea, resembling preying mantis, although specimens of this group, wrongly identified, had formed part of the collections of South African museums for more than a century. The last description of a new order of insects dates back to 1914 (Notoptera).
On the continents, the discovery of new large-size species is likewise an infrequent event. Findings always take place in extremely remote areas, or territories where human conflict or isolationist political regimes have hampered zoological exploration. Among the most spectacular discoveries in recent years we can cite *Dendrolagus mbasio*, an arboreal kangaroo from New Guinea, described in 1995, and the bovid *Pseudoryx nghetinhensis* (1993) and cervid *Megamuntiacus vuquangensis* (1996), inhabiting the forests of Vietnam and Laos respectively.

The case of the sea is different. The number of marine species currently described stands around 212,000 only, but there are eight, rather than one, animal phyla accounting for 90% of the total species (table 1.2). The diversity of body plans is therefore much higher than on the continents: of the 30 phyla reported, 15 (including groups like echinoderms, urochordates or ctenophores) are exclusive to this biome. In comparison, of the mere 15 phyla reported from land, only one, the Onychophora, a type of worm with legs, mandibles and a velvet texture (hence the name “velvet worm”) is exclusive to this medium. For some time, marine fossils from the Cambrian, such as *Aysheaia*, were considered to be onychophorans, although now they are classified in a separate group vaguely known as the “lobopods”. Apparently, the invasion of continental waters by various phyla which remain typically marine has been halted by physiological or structural constraints. Thus the Urochordates (sea squirts) have a need for vanadium, a component of their blood pigments which is widely available in sea water but present in much lower and irregular concentrations in continental waters. Seemingly, the direct connection of the ambulacral system of echinoderms to the exterior hinders osmorregulation in non-marine waters.

New phyla are still being discovered in the sea, which indicates that the catalogue of marine biodiversity is far from being complete. The latest additions

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number of species after Bouchet (see chapter 2)</th>
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<tbody>
<tr>
<td>Porifera</td>
<td>5,500</td>
</tr>
<tr>
<td>Cnidaria</td>
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<tr>
<td>Nematoda</td>
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<tr>
<td>Mollusca</td>
<td>52,500</td>
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<tr>
<td>Bryozoa</td>
<td>15,000</td>
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<tr>
<td>Chordata</td>
<td>21,000</td>
</tr>
<tr>
<td>Other groups</td>
<td>20,500</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>212,000</strong></td>
</tr>
</tbody>
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are the Cicliophora, recorded in 2000; a group of aschelminth worms living as commensals in the perioral region of the Norwegian (Nephrops norvegicus), common (Homarus gammarus) and American (H. americanus) lobsters (Obst, Funch and Kristensen 2006). Before them (1983) came the Loricifera, animals similar to rotifers which live among the non-consolidated grains of marine sediments at all depths (Kristensen 1983).

As regards large-sized animals, remember that none of the ca. 10 species of giant squid (over 20 m in length) (photo 1.3) recorded to date has ever been observed alive, despite their apparent abundance (sperm whales frequently show the imprints of their suckers on their skin). Or recall the description in 1983 of the “Megamouth” shark, Megachasma pelagios (4.5 m long) (photo 1.4), discovered in Indo-Pacific waters, or that of Balaenoptera omurai (2003), a small rorqual (reaching up to 9 m in length) from the same ocean.

The inventory and description of smaller animals is far from being complete, even in shallow waters easily accessible from the coast. Hence our knowledge of groups like the meiofauna – the animal community dwelling in between grains of unconsolidated sediments – remains fragmentary even on the Euro-
pean coasts of longest naturalistic tradition. In fact, some estimates put the percentage of new species of copepods (tiny crustaceans that are the main component of zooplankton, but also very abundant in marine sediments) on Belgian sandy beaches at somewhere between 35% and 45% (Rony Huys, pers. comm.). Other less accessible coastal habitats are also yielding unexpected results, including new taxa of higher rank. Recent explorations of anchialine caves – located inland, but flooded by marine or brackish water – have shown the existence of a new class of crustaceans (of a total of five), the Remipedia (1980) resembling swimming centipedes; and two new orders of peracarids (relatives of amphipods, isopods and mysids), the Mictacea and the Bochusacea (1985), as well as many new families and genera of other crustaceans. In all, eight of the 28 new families of copepods described between 1980 and 1999 came from anchialine caves, compared to only three from marine plankton, which lives in a comparatively immense space (Geoff Boxshall, pers. comm.).

The majority of benthic organisms from surface waters appear to exhibit highly discontinuous distributions, so sampling programmes have to be well

Photo 1.4: *Megamouth shark (Megachasma pelagios)* in North American Pacific waters. Discoveries in marine biodiversity are not all small-size species. They also include mighty creatures like this shark of over 4 m length, first spotted 23 years ago.
designed and intensive in order to assess their true diversity. Thus Cunha et al. (2005) used molecular techniques to reveal the extraordinary diversity of gastropods of the genus *Conus* present in the Cabo Verde Archipelago (52 species, 49 endemic); some of them restricted to a single bay and with vicariants present in adjacent bays. In tropical seas, a recent study of molluscs in a 292 km$^2$ area in New Caledonia (SW Pacific), a zone outside the Indo-Pacific biodiversity hotspot for hermatypic corals, unveiled 2,738 species from 42 sampling stations dotted across all types of habitats, and the accumulation curves suggest the occurrence of 3,900 species (Bouchet et al. 2002). This is more than has ever been recorded in an area of comparable size, and more exciting still: only 36% of species shared another area of New Caledonia a mere 200 km away!

### 1.3. BIODIVERSITY AT THE DEEP-SEA FLOOR

The coastal margins with their wide variety of habitats (coral reefs, mangroves, seagrass meadows, estuaries, soft and rocky bottoms, etc.) harbour an
immense biodiversity. We might assume that, in comparison, the oceanic floor below 1,000 m, supposedly uniform and covered mainly by soft sediments, could have nothing like the same number of species present. This is the most extensive habitat on Earth, covering around 300 million km$^2$, yet its biodiversity remains practically unprospected due to technical and economic constraints. Precision machinery, nets or vehicles are hard to operate at such large depths, and their deployment is time consuming. Getting a dredge down to 4,000 m takes about two hours, with another two for its recovery. And using oceanographic vessels suited to these depths is a very costly enterprise (about €50,000/day for the German R/V *Polarstern*; one of the best equipped ships currently in existence for the study of deep oceanic floors). Reckoning on the 0.5 m$^2$ of oceanic floor sampled by the larger dredges (of the “van Veen” type), and five deployments per day (with scientific staff working non-stop for 24 hours), sampling 2.5 m$^2$ of oceanic floor would take up an entire working day and cost a minimum of €50,000! There is little chance, therefore, of deploying dredges or nets in modern oceanographic cruises, which are generally devoted to objectives other than pure faunistic prospection.

Moreover, the deep ocean is a dark world. At around 900 m depth, darkness is total for the human eye, and what can be directly observable through cameras, ROVs or submarines is limited to the area covered by their artificial light beams.

The study of this medium started late. During the first half of the 19th century, the ocean was considered devoid of life below 300 fathoms (ca. 550 m) depth. This was believed by the British naturalist Edward Forbes (1815-54), an eminent marine biologist and author of *Natural History of the European Seas* (1859; published posthumously), the most complete marine biology handbook of its day. In 1834, Forbes published a report on the molluscs, cnidarians and echinoderms of the Aegean Sea, which testified to finding no trace of animal life in soundings up to 230 fathoms (about 420 m) depth. He then generalized this situation to the entire ocean, and his authority was such that no one seriously tried to refute his theory despite indications to the contrary. Indeed in these years several British scientists and explorers had reported the presence of animal life at great depths; among them John Ross, who recovered a starfish at 1,800 m depth in the Bay of Baffin, or James Clark Ross, who recorded the existence of animals on the sea floor at 730 m depth during soundings off New Zealand in 1843. Some time later (1860), George C. Wallich caught 13 brittlestars at 2,293 m depth between the Labrador...
Peninsula and Iceland. The recovery, also in 1860, of sessile fauna attached to a damaged telegraphic cable set at 2,184 m depth between Cape Bon (Tunisia) and Sardinia should have been still more conclusive in discrediting the azoic theory. But these facts were not considered until 1868-69, when fellow Britons Charles Wyville Thompson and William Carpenter embarked on their famous prospections of the Atlantic deep floor on board the *Lightning* and the *Porcupine*, discovering animal life at 4,289 m depth. Forbes may be part way exonerated by the conclusions drawn from a later (1870) *Porcupine* dredging cruise to the Mediterranean, which noted that animal life at 2,744 m was very scant compared to that of the Atlantic, and in fact some areas were practically azoic.

Life in the deep sea was not directly observed until 1934, when William Beebe, a zoologist, and Otis Barton, an engineer, descended to 923 m depth off Bermuda in the *Bathysphere*, a claustrophobic steel chamber with port holes communicating with its support vessel via a telephone cable. It took another 26 years for man to reach the bottom of the deepest oceanic trenches, when the bathyscaph *Trieste*, crewed by Swiss national Jacques Pickard and American Don Walsh, landed on the floor of the Marianas Trench; at 10,915 m, the deepest oceanic floor on Earth.

The total of oceanic floor deeper than 3,000 m that has been adequately surveyed for fauna is less than 30 m², and shows a wide heterogeneity in species

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**Photo 1.6: Marine copepod.** The copepods, planktonic crustaceans, are the most individually numerous group of marine organisms; the marine equivalent of insects.
Fan mussel (*Pinna nobilis*) amid a *Posidonia oceanica* meadow in the Spanish Mediterranean. The fan mussel is the fastest growing bivalve (up to 1 mm of shell per day) and can grow to 1 m in height. A dweller of seagrass meadows, its abundance has declined dramatically and harvesting is now strictly prohibited.
composition. The number of new species gathered in dredge or net deployments is extremely high at these kinds of depths, and invariably accounts for over 50% of total captures. Recently, the sampling of 1 m$^2$ of oceanic floor at 5,000 m depth in the Angola Basin (South Atlantic) rendered 600 new species of harpacticoid copepods (Pedro Martínez-Arbizu, pers. comm.). If we consider that the number of described copepod species is currently around 12,500 (including the numerous parasitic forms in fishes and other invertebrates), the estimates of up to 10 million species on the deep ocean floor (or even 100 million, if we factor in the meiofauna; Lambshead 1993) begin to look distinctly credible. Having said that, the methods underlying these estimates are somewhat naïve, and the resulting conjectures must be handled with care. Hence in a study that is now a classic, Grassle and Maciolek (1992) established a model of spatial correlation between the number of species collected and the geographic distance covered along a deep-sea transect between 1,200 and 2,100 m depth at the continental rise off the east coast of North America. Based on the observation that about one new species was added per square kilometre of oceanic floor, the 798 species of macrofaunal invertebrates found in 21 m$^2$ could be extrapolated to 100 million species in the world oceanic floor below 1,000 m. There is no need to add that evaluating the strength of this kind of assessment would call for many more studies dealing with faunistic prospection and the spatial heterogeneity of marine species composition at all geographical scales.

We can see that it is still hard to venture any figure for the species richness of the oceans, although it may well be comparable to that of the continents. Estimates to date rely on poor statistics and incomplete taxonomic and geographic baseline data. Furthermore, there are huge operational constraints to obtaining such data, especially in the deep sea. The oceans are nevertheless an extraordinary reservoir of biodiversity. Life there has had roughly four times the time for diversification as life on the continents. Oceans harbour 30 phyla of metazoans, of which 15 are exclusive to the medium (compared to only one on the continents), and are home to the largest animal on the face of the Earth: the blue whale (up to 36 m in length).

ACKNOWLEDGEMENTS

This chapter is a contribution to the MarBEF Network of Excellence on Marine Biodiversity and Ecosystem Functioning, funded by the European Commission.
REFERENCES


