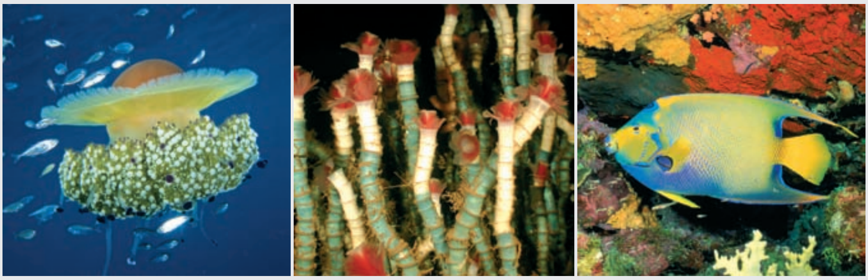

The Exploration of Marine Biodiversity

Scientific and Technological Challenges

Carlos M. Duarte (Ed.)

Fundación BBVA

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INTRODUCTION

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THE OCEAN IS THE CRADLE of life on our planet as well as the single largest habitat in the biosphere. Yet while biodiversity exploration in terrestrial ecosystems is running out of novelties, with the dominant life forms all described, the exploration of marine biodiversity is still in its infancy. We can identify three main reasons for this contrast:

1. The technological constraints facing oceanic exploration. For instance, life below 200 metres depth – a habitat that comprises over 90% of the living space available on this planet – was not directly observed until as recently as the 1960s, and few countries have the equipment needed for direct visualisation of the deep ocean.

2. Marine biodiversity is dominated by microscopic organisms with a metabolic repertoire far superior to that of their terrestrial counterparts. It is also a continu-ing source of surprises. Hence, for instance, the two groups of photosynthetic organisms most abundant in the oceans, and responsible for 40% of marine primary production, were described for the first time just over two decades ago. The oceans, unlike the continents, can also yield surprises at higher taxonomic ranks, such as phyla (cf. chapter 1), and some of the largest animals on earth (giant quid for example) have yet to be observed in their wild environment. Meantime, the best discovery opportunities in marine biodiversity lie in remote or extreme habitats like oceanic trenches, underwater caves, hydrothermal vents and hypersaline or anoxic waters; logically the habitats that have been least explored.

3. Far less research effort has gone into the exploration and conservation of marine biodiversity than into the biodiversity of terrestrial systems. This lag is perfectly illustrated by the following objective facts: (1) research effort, as measured by scientific articles in international journals, is ten times less in marine

◀ **Photo 0.1: Underwater view of *Rhizophora* mangrove forest in Borneo, Indonesia.** Mangrove forests are confined to tropical coasts, where they have adapted to growth in intertidal zones by exchanging gases with the atmosphere through their protruding roots. They are highly productive ecosystems that sustain a wide diversity of species.

Photo 0.2: Seagrass *(Posidonia oceanica)* meadow in the Spanish Mediterranean. *Posidonia oceanica* is among the 60 species of marine angiosperms (higher plants), and its meadows comprise one of the most productive and biodiverse ecosystems of the Mediterranean. These are ecosystems that take centuries to form and are currently retreating due to the impact of human activity.

than in terrestrial biodiversity (Hendriks, Duarte and Heip 2006); (2) papers on terrestrial biodiversity presented to the first conference of the Diversitas programme for global biodiversity research were ten times more numerous than those dealing with marine biodiversity issues (www.diversitas-international.org).

The exploration of marine biodiversity thus faces major technological challenges, like the need to develop more advanced equipment to prospect for and study deep-sea life (ROVs, submarines, manned deep-sea platforms, etc.) or the development of molecular sonars capable of identifying new oceanic microbes. The knowledge unlocked by this kind of technological stimulus could be of great benefit to our society. The immense genetic richness of the oceans is already an important source of wealth and commercial opportunities for the biotechnology and pharmaceutical industries (Munro et al. 1999). The number of marine species being harvested is rapidly increasing (Naylor et al. 2000) and, after only 30 years of intensive aquaculture, far exceeds the number of land animals farmed in nearly 10,000 years of livestock breeding.

The paucity of marine biodiversity research compared to its terrestrial counterpart finds its parallel in the lesser conservation of oceanic systems. Habitats playing a key role in marine biodiversity conservation such as coral reefs, seagrass meadows, mangrove forests and marshlands are disappearing two to ten times faster than the tropical forests (Hendriks, Duarte and Heip 2006). Yet paradoxically marine areas under protection sum less than 0.1% of the ocean surface, while the percentage of protected land is now approaching the 10% target set by the Convention on Biological Biodiversity (Hendriks, Duarte and Heip 2006). Marine biodiversity conservation is based furthermore on models of protection developed for terrestrial habitats, which are hard to apply effectively in the oceans' open waters.

In order to realise the potential of marine biodiversity as a source of services for our society and develop concepts and models that ensure its conservation, we need to progress from what is still a very limited understanding of life in the oceans, and explore them more fully while improving our capacity to manage their myriad resources. Meeting these goals will require new technologies to inventory deep-sea life, and poses challenges comparable to the investigation of outer space. It is not surprising then to learn that NASA is among the main promoters of deep-sea exploration (Fiala and Stetter 2004).

This publication takes its contents from the first in a series of debates organised jointly by the Spanish Scientific Research Council (CSIC) and the BBVA Foundation around the work of the Cap Salines Coastal Research Station (Mallorca, Balearic Islands), with the dual aim of focusing attention on key scientific issues in the biodiversity area, and championing the conservation of our oceans and coasts.

In its pages, leading international experts offer their reflections on the current situation in marine exploration and conservation, and on the scientific challenges that lie ahead.

I wish to thank the BBVA Foundation for its support and financial assistance in organising the event that gave rise to this book and facilitating its publication. My thanks also to J. M. Reyero and his associates for their work on preparing the texts.

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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: Seahorse *(Hippocampus ramulosus)* in a seagrass meadow.** 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 chelicerates: arachnids, acari, etc.). The quantity of continental species still awaiting discovery and description is simply overwhelming. Entomological expedi-

Table 1.1: Estimated number of species per taxonomic group on the continents

Taxon	Number of species after Briggs (1995)
Insecta	10,000,000
Acari	750,000
Arachnida	170,000
Nematoda	1,000,000
Mollusca	20,000
Other groups	100,000
TOTAL	**12,040,000**

Photo 1.2: Stromatolites in Hamelin Pool, Shark Bay, Australia. Stromatolites are the earliest living structures known to man, formed from the growth of microorganism communities. Their oldest fossils, dating to around 3,500 million years, were discovered in Australia.

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 1.2: Number of species per taxonomic group present in the oceans

Taxon	**Number of species after Bouchet** (see chapter 2)
Porifera	5,500
Cnidaria	10,000
Nematoda	12,000
Annelida	17,000
Arthropoda	45,000
Mollusca	52,500
Bryozoa	15,000
Chordata	21,000
Other groups	20,500
TOTAL	**212,000**

Photo 1.3: Giant squid *(Architheutis)* found off the coast of Asturias (Spain). These mythical cephalopods, although relatively abundant, remain largely a mystery, as none has yet been seen live in its natural habitat.

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-

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.

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 1.5: Coral reefs in the Red Sea. Coral reefs are diverse and highly productive ecosystems found along shallow waters in tropical seas. Vast extensions of white coral (unpigmented) have recently been discovered living at depths of up to 1,000 m, even in polar waters.

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 rather 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

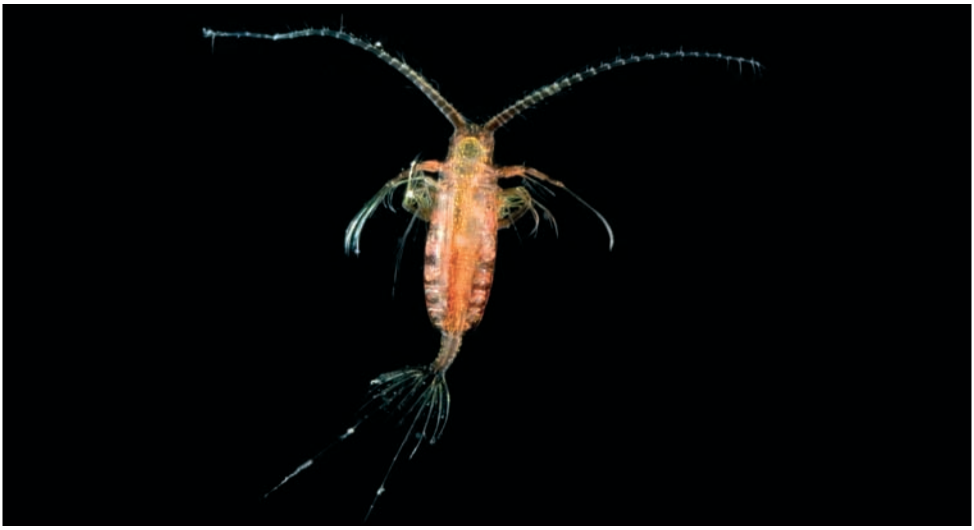

Photo 1.6: Marine copepod. The copepods, planktonic crustaceans, are the most individually numerous group of marine organisms; the marine equivalent of insects.

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 m^2, and shows a wide heterogeneity in species

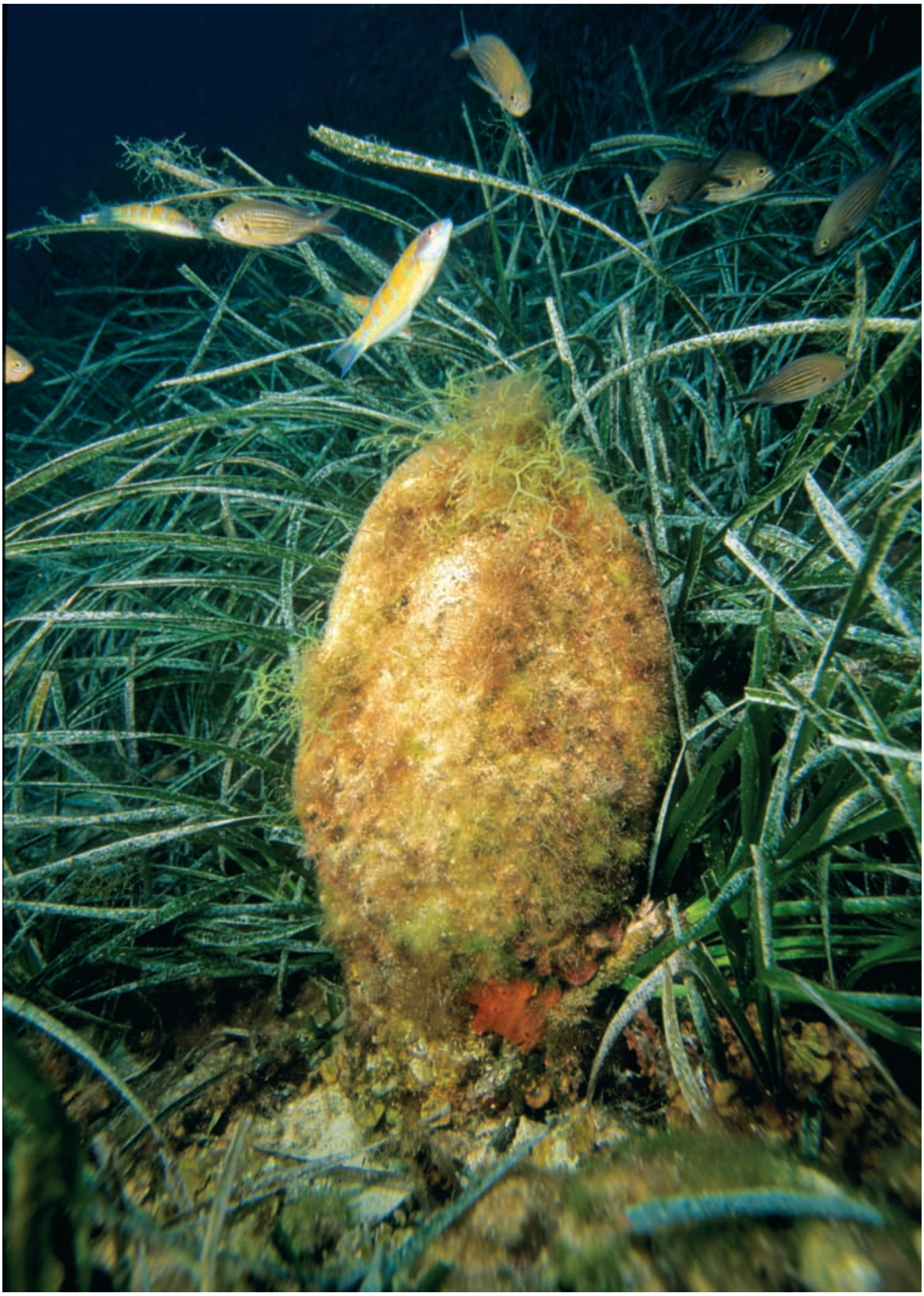

Photo 1.7: Fan mussel *(Pinna nobilis)* amid a *Posidonia oceanica* meadow in the Spanish Mediterranean. The fan mussel is the fastest growing bivalve (up to 1 mm of shell per day) and can grow to 1 m in height. A dweller of seagrass meadows, its abundance has declined dramatically and harvesting is 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. Estimations 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).

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2. THE MAGNITUDE OF MARINE BIODIVERSITY

Philippe Bouchet
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TWENTY-FIVE YEARS AGO, scientists believed that the ca. 1.6 million species they had then inventoried represented maybe 50% of plant and animal species on this planet. New approaches in sampling insect diversity in rainforests and small macrobenthos in the deep sea have revised this estimate to 1.7-1.8 million described species and 10-100 million species remaining to be discovered. In parallel with this changed paradigm, species inventorying has also evolved from being categorized as an outdated scientific activity to a timely cutting-edge megascience "enterprise". The reason behind this change of attitude is probably rooted in our social anxiety over global climatic change and non-sustainable development. The crude translation of this anxiety into science strategy is that there is no time to lose if we want to document and name biodiversity before it is lost forever.

The public's attitude to species discovery is perhaps best encapsulated by how the media reacted to the recent description of *Kiwa hirsuta* (photo 2.2). This new galatheid crab was discovered in hydrothermal vents near Easter Island in May 2005, and described in the December 2005 issue of *Zoosystema* by Enrique Macpherson, William Jones and Michel Segonzac, as a new family, genus and species (Macpherson, Jones and Segonzac 2005). On March 7 2006, a local newspaper featured an article on Michel Segonzac and his discovery of the "yeti crab"; this was immediately picked by national and international media. By March 17, no less than 150,000 web pages mentioned *Kiwa hirsuta*, and this number had climbed to 200,000 by March 20. On this occasion, the media and the public demonstrated astonishment that there were still blank spots on our map of the world's biodiversity. It is generally not known outside the closed community of systematists that, far from being an exceptional event, the discovery and naming of new animals and plants are in fact a daily product of on-site field work and off-site academic research. With a special focus on the oceans, the present review will thus address the following questions:

◀ **Photo 2.1: Coral reef community**. Coral reefs are the most species rich marine ecosystem on the planet, and for this reason are often compared to tropical rain forests. Coral reefs also share with rain forests similar environmental issues and conservation challenges.

Photo 2.2: Media frenzy over the discovery of the "yeti crab", *Kiwa hirsuta*

1. How many marine species are currently described?
2. What is the current rate of progress in inventorying marine biodiversity?
3. Can we predict what is the global magnitude of marine biodiversity?

2.1. HOW MANY MARINE SPECIES ARE CURRENTLY DESCRIBED?

The short answer to the question *How many marine species are currently described?* is that there are somewhere around 250,000 (Groombridge and Jenkins 2000; Table 2.1) to 274,000 species (Reaka-Kudla 1997). The long answer is that these numbers are too rounded not to be suspicious. They indeed are, and there are in fact several non trivial difficulties in evaluating how many marine species are already known.

Information technology has made it much easier to compile and update species catalogues, and several ongoing major efforts (notably Species 2000 and GBIF) are producing taxonomic authority lists. However, we are still far from having a global checklist of the organisms that live on this planet, let alone in the oceans, and coverage across different biological groups is very uneven. At one end, we have taxa like the vertebrates which benefit from global updated lists, and a few mouse clicks on FishBase (www.fishbase.org) will

Photo 2.3: Enteropneust in its deep-sea habitat. This specimen, probably representing a species new to science, was photographed on the East Pacific Ridge at 2,600 metres, but has still not been collected, precluding its taxonomic description. At times submersibles and ROVs take photographs of deep-sea animals that are never collected by traditional collecting gear, such as dredges, trawls or box cores.

tell us that there are currently 27,683 fish species considered valid, of which 16,475 are marine. At the other end, we have taxa like echinoderms or polychaetes, for which no list of global significance exists. In the middle are taxa like molluscs that enjoy several regionally significant species databases (e.g., CLEMAM, the Check List of European Marine Molluscs, see Table 2.1, with 3,641 valid species), but no global species list.

There are two notoriously grey areas in evaluating the number of valid described marine species.

One grey area is the number of unicellular eukaryotes, in particular Foraminifera and radiolarians. Foraminifera (phylum Granuloreticulosa) have carbonate tests and radiolarians (phylum Actinopoda) have silicaceous skeletons, and their post mortem remains constitute a large fraction of marine sediments. They are important in stratigraphy and paleoenvironmental research, so that even the Recent species are studied mainly by micropaleontologists. As a result, Recent species are often not tallied separately, and the same numbers may be used by different authors to refer to Recent and fossil taxa together, or to Recent only. For instance, the number of Granuloreticulosa is evaluated by

Table 2.1. Global numbers of marine species, by taxa

Taxon	Groombridge and Jenkins (2000)	This paper
Bacteria	4,800	4,800[1, 2]
Cyanophyta		1,000[3]
Chlorophyta	7,000	2,500[3]
Phaeophyta	1,500	1,600[3]
Rhodophyta	4,000	6,200[3]
other Protoctista[a]	23,000	
Bacillariophyta		5,000[3]
Euglenophyta		250[3]
Chrysophyceae		500[3]
Sporozoa		?
Dinomastigota		4,000[4]
Ciliophora		?
Radiolaria		550[5]
Foraminifera		10,000[6]
Porifera	10,000	5,500[7]
Cnidaria	10,000	9,795[8]
Ctenophora	90	166[9]
Platyhelminthes	15,000	15,000[2, 10]
Nemertina	750	1180-1230[11]
Gnathostomulida	80	97[9]
Rhombozoa	65	82[9]
Orthonectida	20	24[9]
Gastrotricha	400	390-400[12]
Rotifera	50	50[2]
Kinorhyncha	100	130[13]
Loricifera	10	18[9]
Acanthocephala	600	600[2, 14]
Cycliophora		1
Entoprocta	170	165-170[12]
Nematoda	12,000	12,000[15]
Nematomorpha	<240	5[16]
Ectoprocta	4,000-5,000[b]	5,700[12]
Phoronida	16	10[17]
Brachiopoda	350	550[12]
Mollusca	?75,000	52,525[18]
Priapulida	8	8[19]
Sipuncula	150	144[9]
Echiura	140	176[9]
Annelida	12,000	12,000[2]
Tardigrada	"few"	212[19]
Chelicerata	1,000	2,267[20]
Crustacea	38,000	44,950[21]
Pogonophora	120	148[9]
Echinodermata	7,000	7,000[2]
Chaetognatha	70	121[22]
Hemichordata	100	106[9]
Urochordata	2,000	4,900[23]
Cephalochordata	23	32[9]
Pisces	14,673[c]	16,475[24]
Mammalia	110	110[2]
Fungi	500	500[2]
Total	**242,135**	**229,602**

a Includes lines Bacillariophyta to Foraminifera below.

b Listed twice, once as Ectoprocta (5,000 species) and once as Bryozoa (4,000).

c Cyclostomata (52), Chondrichthyes (821), Osteichthyes (13,800).

1 Total number of described Archaea 409, of Bacteria 10,593. Source http://www.psb.ugent.be/rRNA/index.html

2 Number given by Groombridge and Jenkins (2000) followed here.

3 M. Guiry (pers. com.) based on AlgaeBase http://www.algaebase.org/.

4 Groombridge and Jenkins (2000). Includes freshwater.

5 de Wever (pers. com. based on D. Boltovskoy's 2006 database). 2,000 in Minelli (1993).

6 Vickerman (1992). 8,000 in Minelli (1993).

7 Brusca and Brusca (2003). Hooper and van Soest (2003, Systema Porifera) give 15,000 species, but this number includes also undescribed species.

8 Includes Hexacorallia 2,918 after Fautin (2005, Hexacorallians of the world. http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm).

9 UNESCO-IOC Register of Marine Organisms (URMO), in Species 2000, 2006 edition. http://annual.sp2000.org/2006/

10 Faubel and Norena, in Costello et al. (2001) give 3,224 species for Turbellaria alone.

11 Sundberg and Gibson (2006), based on Gibson (1995, *Journal of Natural History*, 29: 271-562).

12 d'Hondt pers. com.

13 Neuhaus and van der Land, in Costello et al. (2001).

14 Brusca and Brusca (2003) give 1,100 for all Acanthocephala. The source for 600 marine species given in Groombridge and Jenkins (2000) is not known, but is followed here for lack of another estimate.

15 Hugot et al. (2001) give 4,070 free-living marine species, and 11,860 animal parasites but the latter figure is not partitioned into parasites of marine and non-marine vertebrates and invertebrates.

16 Poinar and Brockerhoff (2001, *Systematic Parasitology*, 50: 149-157).

17 http://paleopolis.rediris.es/Phoronida/

18 Based on essentially non-overlapping regional checklists: Western Atlantic 6,170 (Gastropods only; Rosenberg 2005, Malacolog 4.0 http://data.acnatsci.org/wasp); NE Atlantic 3,641 (CLEMAM Check List of European Marine Mollusca http://www.somali.asso.fr/clemam/index.clemam.html); West Africa 2,500 (Cosel pers. com. and unpublished); Indo-Pacific 32,000 (24,269 in Biotic database of Indo-Pacific marine mollusks http://data.acnatsci.org/obis/, estimated to be 2/3 complete); Panamean region 2,535 (Keen 1971, *Sea shells of tropical West America*, ed. 2.); South Africa 2,788 (Kilburn and Herbert, in Gibbons (ed.), 1999, *South African Journal of Science*, 95: 8-12); North Pacific 1,744 (Kantor and Sysoev 2005, *Ruthenica*, 14: 107-118); New Zealand 2,091 (Spencer and Willan 1996, *New Zealand Oceanographic Institute Memoir* 105); Antarctic and Magellanic 800 (personal estimate).

19 UNESCO-IOC Register of Marine Organisms (URMO), 2004 edition.

20 Pycnogonida 1,245; Merostomata 4, both based on URMO; Acari (Halacaridae) 1,018, after Bartsch (2004, *Experimental and Applied Acarology*, 34: 37-58).

21 Branchiura 44 (Boxshall pers. com., after Boxshall 2005, in Rohde (ed.), *Marine Parasitology*: 145-147); Ascothoracida ~100 (Grygier and Hoeg 2005, in Rohde, *ibid*.: 149-154); Rhizocephala ~250 (Hoeg et al. 2005, in Rohde, *ibid*.: 154-165); Acrothoracica + Thoracica 1,025 (Newman pers. com., based on Newman 1996, in Forest (ed.), *Traité de Zoologie*, 7(2):453-540, with additions); Mystacocarida 19 (G. Boxshall pers. com.); Tantulocarida 28 (Boxshall 2005, in Rohde, *ibid*.: 147-148); Facetotecta 11 (Belmonte, 2005, *Marine Biology Research* 1:254-266); Cephalocarida 9; Copepoda 9,500 (G. Boxshall pers. com., based on extrapolation from Humes (1991); Ostracoda 6,400 [Recent Ostracoda 8,000 (Horne 2005, in Selley, Cocks and Plimer (eds.), *Encyclopaedia of Geology*, 3), less 1,608 non-marine species (Martens 2006)]; Remipedia 16; Leptostraca 38 (Davie 2002, Zoological catalogue of Australia, volume 19.3A); Stomatopoda 449 (Schram and Müller 2004, *Catalogue and bibliography of the fossil and Recent Stomatopoda*); Lophogastrida 55 (G. Anderson pers. com. to M. Schotte); Mysida 1,085 (G. Anderson pers. com. to M. Schotte based on http://peracarida.usm.edu/); Amphipoda 6,950 (Vader 2005, How many amphipod species? Poster presented at XII International Amphipod Colloquium, Cork, Ireland, and pers. com.; Talitridae not included); Isopoda 5,270 (M. Schotte pers. com., based on Kensley, Schotte and Shilling, 2005, World list of marine, freshwater and terrestrial Crustacea Isopoda. http://www.nmnh.si.edu/iz/isopod/index.html); Tanaidacea 857 (G. Anderson pers. com. to M. Schotte); Cumacea 1,324 (S. Gerken pers. com.); Euphausiacea 86 (Baker et al. 1990, A practical guide to the Euphausiids of the world); Dendrobranchiata 522 (Crosnier pers. com. [Penaeoidea 419, Sergestoidea 103]); Stenopodidea 57 (T. Komai pers. com.); Caridea 2,730 (C. Fransen pers. com.); Astacidea + Palinura 148 (Holthuis 1991, FAO Fisheries Synopsis, 125(13) [Thalassinidea excluded], with increment); Thalassinidea 556 (Dworschak 2005, *Nauplius*, 13(1): 57-63); Anomura 2,210 (Galatheoidea 1,012 [E. Macpherson pers. com.], Hippoidea 67 [C. Boyko pers. com.], Pagurida 1,131 [P. McLaughlin pers. com.]); Brachyura 5,200 (Ng and Davie pers. com.).

22 A. Pierrot-Bults, 2004, Chaetognatha of the world. World Biodiversity Database http://nlbif.eti.uva.nl/bis/index.php.

23 Ascidiacea 4,900 (Monniot pers. com.); other Urochordata not evaluated.

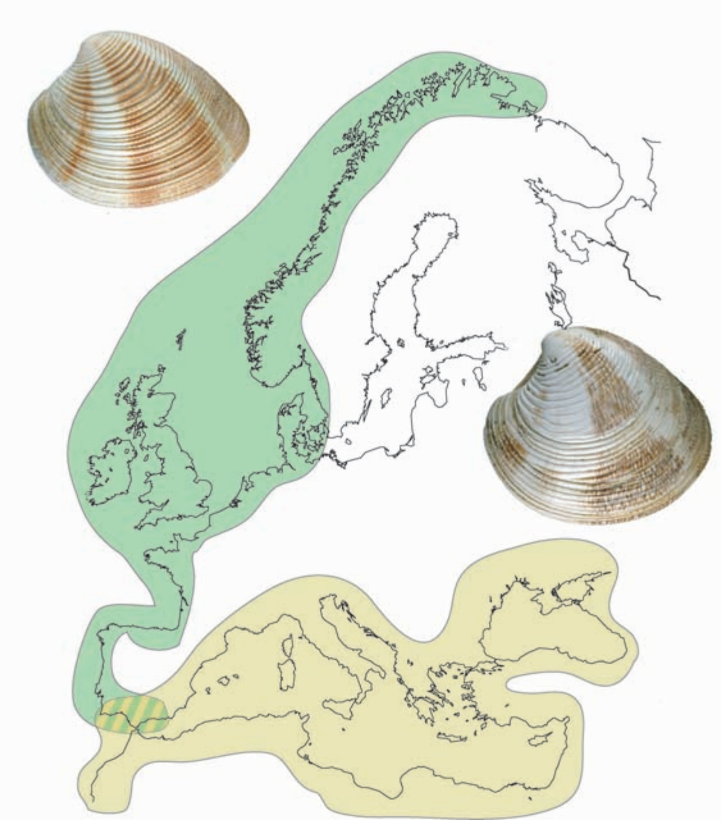
24 N. Bailly (pers. com.) based on FishBase www.fishbase.org; includes amphidromous (705) and strictly brackish (86) species.

Groombridge and Jenkins (2000) to be "about 40,000 fossil species" and "more than 4,000 Recent species"; and by Brusca and Brusca (2003) at "40,000 species". I have chosen here to follow Vickerman (1992), who gave 10,000 species of Foraminifera "excluding the vast numbers of fossil species insofar as this is possible".

The second grey area stems from the problem of synonyms. Naturalists have been naming animals and plants for 250 years. In those 250 years, millions of names have been established, sometimes the result of brilliant and penetrating science, sometimes the result of wrong observations or misunderstanding of biological rules. Different authors may have described unknowingly the same species under different names in different parts of the world (photo 2.4), or they may have described what they believed were different species when they were in fact naming only ecological or phenetic variants, males or females, juveniles or adults, or different phases of the cycle of a single species. We frequently do not have all the necessary pieces of the jigsaw, and also different scientists may have different interpretations of the same facts. For instance, it has been debated for nearly two centuries whether the Atlantic and Mediterranean forms of the small venerid clam that is part of the Italian *spaghetti alle vongole* were one variable species, or two species, or geographical subspecies of one species. The issue was mostly a matter of personal opinion, until populations of the two forms co-occurring in southern Portugal were analyzed electrophoretically and showed beyond doubt that *Chamelea gallina* (Linnaeus) [the "Mediterranean form"] and *Chamelea striatula* (da Costa) ["the Atlantic form"] are two reproductively isolated (biological) species (Backeljau et al. 1994) (map 2.1). The problem of synonymy is relatively benign in organisms that are difficult to collect or study, so have attracted and continue to attract less attention from scientists, because they generate fewer opportunities for errors or diverging views. By

Photo 2.4: Two names, one species: *Facelina bostoniensis*. This amphiatlantic species was for a long time designated by different names on both sides of the Atlantic, *Facelina curta* (Alder and Hancock 1843) in Europe and *Facelina bostoniensis* in North America, until the Danish zoologist Hennig Lemche recognised in the 1970s that these names designated a single species.

Map 2.1: Distribution of the "Atlantic form" and "Mediterranean form" of *Chamelea* clams



Geographical variation or different species? It has been debated during nearly two centuries whether the Mediterranean *Chamelea gallina* (Linnaeus) and the Atlantic *Chamelea striatula* (da Costa) were one variable species, or two species, or geographical subspecies of one species. The co-occurrence of the two forms in southern Portugal provides evidence that they represent two reproductively isolated species.

contrast, the problem of synonymy is especially severe in groups of large or attractive organisms that have concentrated the most interest from travellers, collectors and scientists: fishes, corals, crabs, and molluscs; for the latter, Boss (1970) once claimed that every named species had 4 to 5 names. With an accumulated load of perhaps 300,000 names and a synonymy ratio that is matched probably only in butterflies, molluscs are certainly the marine group where the number of names and number of species are most at odds with each other. We do not even know whether the number of valid named Recent species of molluscs is on the order of 45,000 or 130,000 (see table 2.2), an uncertainty that is admittedly pervasive among Recent and fossil biota but is seen as "particularly problematic" for molluscs (Hammond 1995).

Table 2.2: Discrepancies between different published estimates of numbers of species in major taxa[1]

Taxa	May (1988)	May (1990)	Brusca & Brusca (1990)	Minelli (1993)	Hammond (1995)	Groombridge & Jenkins (2000)	Brusca & Brusca (2003)
Porifera	10,000		9,000	6,000	10,000	10,000	5,500
Cnidaria	10,000	9,600	9,000	15,000	10,000	9,400	10,000
Platyhelminthes			20,000	14,838	14,000	20,000	20,000
Nematoda	1,000,000		12,000	20,000	20,500	25,000	25,000
Annelida	15,000		15,000	18,600	12,000	15,000	16,500
Chelicerata	63,000		65,000	74,732	75,000	75,000	70,000
Crustacea	39,000		32,000	55,364	75,000	40,000	68,171
Hexapoda	1,000,000	790,000	827,175	906,506	950,000	950,000	948,000
Mollusca	100,000	45,000	100,000	130,000	70,000	70,000	93,195
Ectoprocta	4,000		4,500	5,000		4,000	4,500
Echinodermata	6,000	6,000	6,000	6,700	6,000	7,000	7,000
Urochordata		1,600	3,000	3,000		1,400	3,000
Vertebrata	43,300	42,900	47,000	44,998	56,000	52,000	46,670

[1] Note that for groups that are not strictly marine, numbers include marine and non-marine species, so are not directly comparable to the numbers in Table 2.1. See text for comment.

In the absence of authoritative catalogues, what do successive authors do? To a certain extent, they copy each other, which gives a false impression of security. “If all authors give the same number, then this number must be true”, one may think. The 6,000-7,000 species of echinoderms sounds “right” because it is the number given by all authors in the last 20 years, but it may simply be the same guess or the same error copied again and again. The numbers presented in this paper (table 2.1) are not entirely exempt from this criticism, as they also partly follow an earlier compilation. However, different authors sometimes give very different numbers for the same taxon (table 2.2): the number of described species of nematodes has been estimated at 12,000-25,000 in several publications, but May (1988) estimated it at 1,000,000. Robert May’s authority on the subject of species numbers is such that his figure has been cited repeatedly. In fact, the real number now appears to stand at 27,000 (Hugot, Baujard and Morand 2001), and what May apparently “counted” in 1988 was an estimate of the total number of nematode species, named *and* unnamed. The latter should naturally be excluded from an evaluation of the magnitude of known biodiversity.

The conclusion of this chapter is that when scientists state that “there are 1.7 or 1.8 million described species”, or “there are 230,000 or 275,000 described marine species”, this should be seen partly as the result of an actual count, but also to a large extent as the product of an educated guess. To place this figure in perspective, and bearing in mind that evaluations of described land and freshwater biota suffer from similar approximations, marine biodiversity accounts for 15% of the global described biodiversity (1,868,000 species: Reaka-Kudla 1997).

2.2. WHAT IS THE CURRENT RATE OF PROGRESS IN INVENTORYING MARINE BIODIVERSITY?

To the general public and decision makers of the 1950s-1960s, exploring the world to discover unknown species, describe them and give them names seemed to be a scientific occupation that had its heyday in the 1850-1900s. But, they thought, by the end of the 20th century, we must surely know the majority of species. As a result, or as a cause, of this attitude, fewer institutional efforts went into inventorying species of fauna and flora (the word "biodiversity" having not yet been coined). In oceanography, the Danish *Galathea* expedition of 1950-52 was the last circumglobal oceanographic expedition in the vein of the *Challenger* expedition of 1873-76. Things changed dramatical-

Photo 2.5: *Cookeolus* spp., one of the fish species recently discovered in the deep-water coral reefs of Vanuatu. New cutting-edge technology with trimix gases and rebreathers is allowing access to deep reefs to 120 or 140 metres and revealing a brand new world not accessible to scuba diving or dredging. This species of *Cookeolus* is one of several new fish species recently discovered in this group of islands.

ly in the 1980s-1990s as new paradigms emerged in the world of science and in the world of politics.

Science. New approaches in sampling insect diversity in rainforests yielded fantastic estimates of 30 million insect species, and it was suddenly realized that whereas there might be 1.7 million described species, as many as 10 to 100 million species remained to be discovered, described, and named (Stork 1988). Simultaneously, it was realized that the rate of extinctions had increased far beyond natural levels. Although the magnitude of the extinction crisis is a hotly debated topic within and outside the scientific community, some authorities project that 50,000 species might be lost each year, i.e., one-third to half of all species will become extinct by the end of the 21st century.

Politics. Spectacular advances in molecular engineering are now making it possible to screen the properties of microbes, plants and animals on a massive scale to develop new bioactive compounds and to isolate genes with useful properties in agriculture, pharmaceutics or ecological services. This fuels a wholly new outlook on biodiversity, with living organisms potentially having an economic value. The Convention on Biological Diversity (CBD) is the source of new attitudes and new regulations, and is changing the way academic and non-academic communities inventory, document, safeguard and use species of fauna and flora.

Taxonomy remains a very active field of research, and there are literally thousands of journals that report the discovery and publish descriptions of new species. But actually knowing how many species are described is far from straightforward, again for lack of a centralized biodiversity registry. Based on data compiled by Hammond (1992) for animals and fungi, supplemented by data from the Kew Index for plants, and others, it can be estimated that tax-

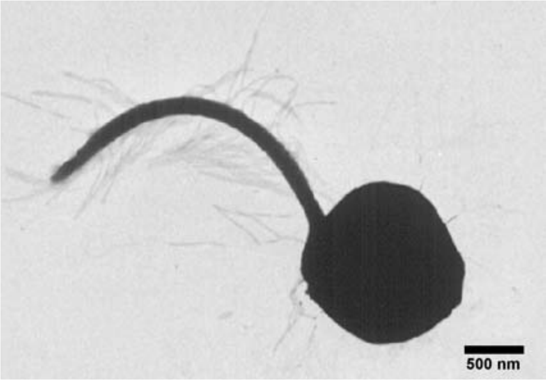


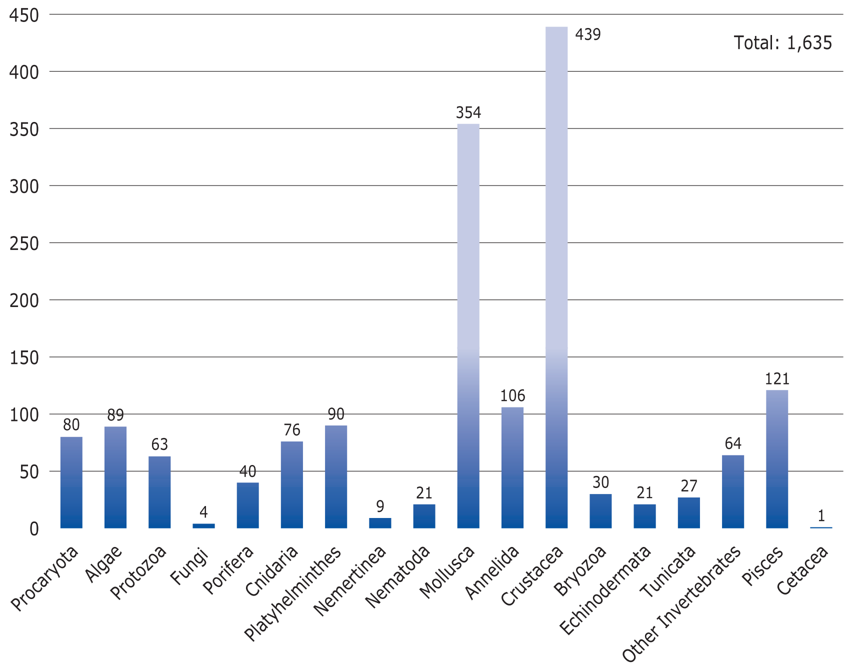
Photo 2.6: *Pelagomonas* cell. The discovery and role of the picophytoplankton is one of the major oceanographic advances of the last 20 years and picophytoplankton remains a frontier in marine biodiversity exploration. At less than one micron, a cell of *Pelagomonas* is dwarfed by many prokaryotes; yet it is a fully functional, photosynthetic eukaryote.

onomists describe 16,600 new species per year, of which 7,200 (43%) are insects.

How many of these are marine? Again, no centralized biodiversity registry and no immediate answer. To address this question, a number of bibliographic databases were analyzed between February and June 2005 (Ducloux 2005). Because 2004 was suspected to be still too incompletely entered in the databases, we chose a study period covering 2002 and 2003 and our search yielded 3,217 names. The same exercise was repeated in January-February 2006, yielding 53 additional names (1.6% of the total) that had not been captured in the 2005 search. It thus seems fair to say that the data presented in this review are a fair representation of reality.

The 2002-2003 dataset shows that 1,635 new marine species are currently described every year (figure 2.1). Not surprisingly, the phyla that are already the most speciose (Crustacea, Mollusca) are also those where the higher number of new species are being described; conversely, smaller phyla (Cnidaria, Porifera) naturally contribute less to the global yearly increment. However, annual growth is not simply proportional to the size of the phyla. The count-

Figure 2.1: Yearly average number of marine species described in 2002-2003 by taxonomic group



er-performance of Nematoda is worthy of note; despite roughly comparable numbers of known species of nematodes and fishes, there are five times as many new fishes described as there are nematodes. Clearly, the annual growth in marine biodiversity inventory reflects both the size of the phylum and the size of the taxonomist community that is studying them. For very small phyla (e.g., Entoprocta, Gastrotricha, Kinorhyncha), the community may be so small that what is measured over the two-year study period is the result of the research of just one or two individual scientists.

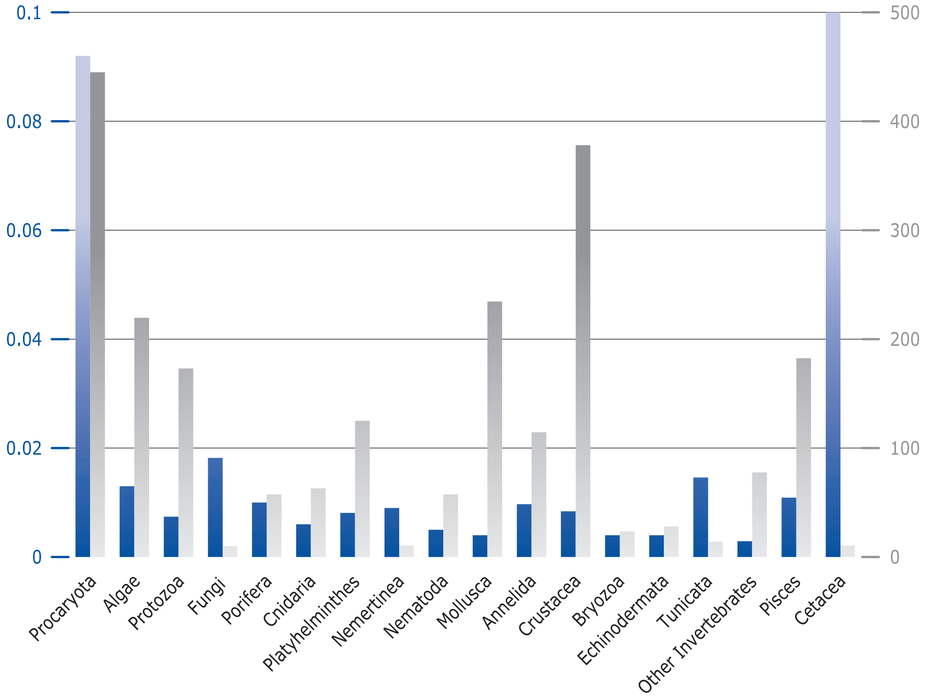
How many of these are valid species, and how many will end up in synonymy? We have no reason to believe that modern authors work incomparably better than the authors of a century ago, and inevitably some of the species currently being described as new will end up as synonyms of previously described species. Modern authors have analytical tools and insights superior to those at the disposal of authors working 100 years ago, and this should in principle lead to better descriptions and fewer synonyms. There is also better communication between scientists, which should also promote better mutual awareness of their publications, thus reducing research duplication and the establishment of synonyms. However, the modern literature is also characterized by an explosion of books, journals, and symposium volumes, most of them not available electronically on free access, and it is difficult for a taxonomist to be sure that he/she has consulted all the relevant literature. With an ever increasing number of journals occupying the field, several authors may also, willingly or unwillingly, compete to be the first to name a new species. For instance, the Belgian Koen Fraussen and the American Martin Snyder both described the same species of marine snail, originating from the same commercial source in the Philippines; the former in a Belgian journal in April 2003 as *Euthria suduirauti*, the latter in a Spanish journal in June 2003 as *Latirus cloveri*. In this case, the synonymy was promptly established (Snyder and Bouchet 2006), but in most cases synonymies are likely to remain unrecognized for several decades. As noted above, certain groups traditionally generate hot competition between researchers, but many others are unlikely to be studied by more than one person at the same time. All in all, I believe that synonyms represent at most 10-20% of the 1,635 new species currently being described each year, i.e., 1,300-1,500 valid species are added each year to the inventory of marine life.

Marine taxa represent 9.7% of all current new species descriptions, whereas marine biodiversity represents 15% of all biodiversity. In other words, the increment of marine biodiversity inventory is about 0.65% per year, as against 1% for the inventory of land and freshwater biota. This imbalance between marine and non-marine biodiversity is, to date, apparently unrecognized in the literature, and its significance is uncertain. Certainly, the weight of entomology and of amateur entomologists has no equivalent in marine biodiversity, even in molluscs, where amateurs are currently responsible for the descriptions of 27% of new species (Bouchet 1997). Molluscs aside, my feeling is that amateurs play only a minor role in the description of new marine species, probably in the range of 10-15% of the total. By contrast, a similar analysis (Fontaine and Bouchet, unpublished) performed on the new species of land and freshwater European animals described in 1998-2002 showed that 72% of all new species were insects, and amateurs were responsible for 46% of the new species descriptions, with another 12% being contributed by retired professionals. The weight of amateur taxonomists in entomology and malacology is not a new phenomenon, but the current deficit between marine and non-marine biodiversity may reflect an erosion of the role of amateurs in marine biodiversity by contrast to their confirmed role in entomology.

The total population of authors involved in the naming and description of new marine species in 2002-2003 was 2,208 persons, i.e., on average each author was involved with 1.5 species. In reality, this ratio differs considerably between different taxa (figure 2.2). It took 441 authors to name and describe 159 prokaryote species (0.36 new species per author), whereas by contrast it took only 61 authors to name and describe approximately the name number (152) of new Cnidaria (2.49 new species per author). The ratio is even higher in Mollusca, with 3.05 new species per author. These differences reflect differences in the average contents of taxonomical publications: in microbiology, a typical paper is co-authored by 3-4 authors describing a single new species; in zoology and phycology, a typical paper is authored by 1-2 authors who revise a whole species group or genus and describe several new species at once.

The Convention on Biological Diversity has highlighted the imbalance between the distribution of biodiversity and the distribution of knowledge on that biodiversity. Most known and unknown biodiversity is in tropical countries, most of them developing or emerging countries of the South, whereas most of the knowledge and resources on that biodiversity is in the developed countries of the North. The Convention on Biological Diversity has given the name “Taxonomic Impediment” to the deficit of systematists and support infrastructures for documenting biodiversity. This taxonomic impediment is glaringly obvious when new marine species are categorized by the country of institutional affilia-

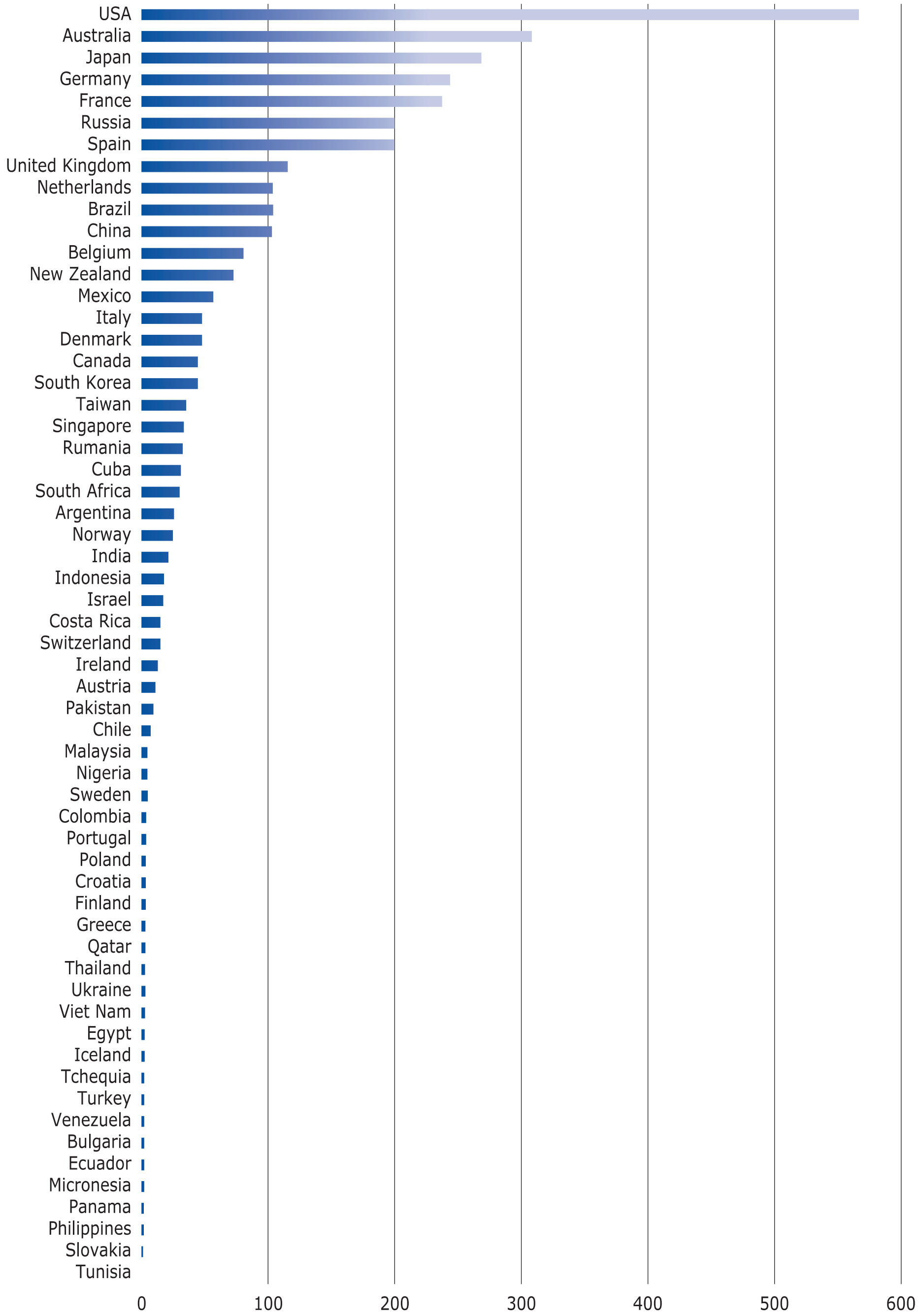
Figure 2.2: Number of authors involved in describing new marine species in 2002-2003 per taxonomic group and degree of researcher coverage



Grey, right-hand scale: number of authors involved in 2002-2003 in the description of new marine species for each of the major taxa. Authors are counted only once, whatever the number of new species they have described, and all are considered (i.e., also second, third, etc. authors). Total 2,208 authors. Blue, left-hand scale: ratio between the 2002-2003 population of authors and the global number of described species in the same taxon, as compiled in Table 2.1. The ratio measures the adequation of the workforce to the size of the group. A high ratio indicates a well covered group (Procaryota, Mammalia), a low ratio indicates a deficit of systematists for the group in question (Nematoda, Mollusca, Bryozoa, Echinodermata).

tion of the author(s) (figure 2.3) (i.e., a species is categorized under “Germany” if that is the country corresponding to the institutional address given by the author of the paper, regardless of his/her actual nationality). Unsurprisingly, authors from the United States alone account for 17.3% of new species, and countries in the European Union for another 34.4%; Australian authors are responsible for 9.4% of new species, which is a remarkable performance for a country of 20 million that accounts for 0.3% of the world population. When Japan (8.1%) is added to the above, this leaves only 30.8% for the rest of the world. A similar mismatch between the geographical location of practicing taxonomists and biological diversity had been noted by Gaston and May (1992), based essentially on plant and insect data. When considering marine biodiversi-

Figure 2.3: Country of institutional affiliation of 2002-2003 authors of new marine species



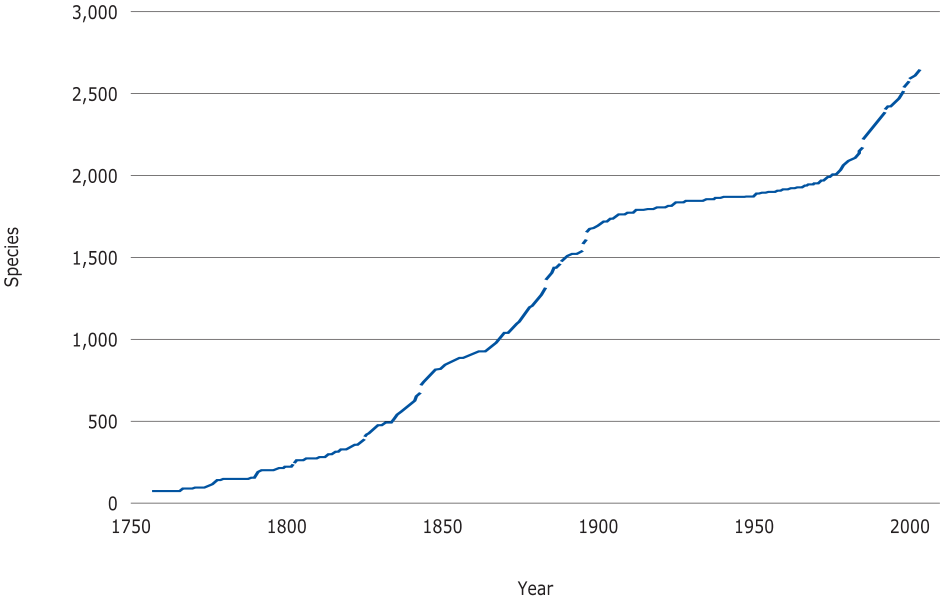
Only first authors are considered; authors of more than one species are counted as many times as they are first author of a new species. Total: 3,270 author-species pairs.

ty, the best known regions are the temperate waters of the northern hemisphere, where scientific curiosity has been sustained for more than two centuries. Elsewhere in the world, our knowledge ranges from fair (North America, Japan, New Zealand, the Antarctic) to poor (most of the tropics, most of the deep sea).

2.3. CAN WE PREDICT THE GLOBAL MAGNITUDE OF MARINE BIODIVERSITY?

We now know that we have 230,000-275,000 described marine species, and we know that the inventory is accruing 1,300-1,500 species per year. The next obvious questions are: How many species remain to be named? How long is it going to take to complete the inventory? Current increments in the inventory of various taxonomical groups reflect personal motivations, public interest and funding support, rather than the intrinsic size of the groups in question. For instance, the long plateau, lasting from the 1900s to the 1960s, in the cumulation curve of European marine gastropods might have then given the impression that the group's inventory was complete (figure 2.4). In fact, the plateau is explained by the fact that, at that time, zoologists had turned their attention to other parts of

Figure 2.4: Cumulation curve of the marine gastropods of Europe since their year of description



Source: CLEMAM. Data courtesy of Serge Gofas and Jacques Le Renard, graph courtesy of G. Rosenberg.

the world. When they turned back to the European seas in the 1970s, a wealth of discoveries followed, with the result that an astonishing 20% of the European marine gastropod species has been named in the last 25 years. It may thus be quite unreliable to project global magnitude from current trends.

In fact, there are various black boxes that are seen as immense reservoirs of unknown biodiversity, but where our ignorance is greatest. I have chosen to highlight two of these: microbial diversity and symbionts.

2.3.1. Microbial diversity

For many decades, documenting microbial diversity was not fundamentally different from documenting micro- and macro-faunal/floral diversity: individual organisms were isolated from field samples, cultivated, and observed by light and electron microscopy. This approach only allows the recognition of organisms that can be cultivated and/or that possess sufficient morphological characters to be identified by microscopy. Morphology-based studies conducted over the past two centuries did reveal significant numbers of microbe species, but this information was acquired piecemeal. The analysis of entire microbial assemblages for more than a few samples is so labour-intensive that it is prohibitive. Although the actual naming of a previously undescribed species still requires our ability to isolate it and section, stain or cultivate it, culture-independent molecular techniques have been adopted to explore the actual diversity of natural assemblages of Archaea and Bacteria, and such approaches are now increasingly being used to explore protistan diversity. Another advantage of molecular techniques is that microscopy-based analyses typically assess cell diversity in small volumes of water (usually less than one litre collected on a filter), and are likely to miss many of the rarer species; by contrast, DNA can be extracted from large water samples (tens of litres), and the sensitivity of PCR-based assays allows the detection of specific taxa at very low abundance. Not surprisingly, culture-independent molecular approaches are now resulting in a large-scale re-evaluation of microbial diversity in natural ecosystems across all domains of life (Venter et al. 2004; Habura et al. 2004). In a very recent study by Peter Countway (Countway et al. 2005), 32 litres of seawater from off the coast of North Carolina were filtered on a 200 µm mesh, and DNA was extracted from the filtrate after zero, 24 and 72 hours. Cloning and sequencing of 18S rDNA revealed 165 unique phylotypes at the 95% similarity level, i.e., of significance indicative of at least genus-level differentiation, a significant number of which represented “unknown” or “uncultured” phylotypes. Many phylotypes were represented by a single sequence, and rarefaction and diversity estimators indicated the presence of 229 to 381 phylotypes. Taking into consideration that species-level distinctions are often delineated at the 97% to 98% similarity level (rather than the 95% they had adopted), Countway and his co-authors concluded that their estimates "presumably represent lower limit estimates of the true species diversity present in the sample".

So, if a drop of seawater contains 160 species of bacteria (Curtis, Sloan and Scannell 2002) and if a bucket contains hundreds of species of unicellular eukaryotes, the mind boggles at what the worldwide total might be. This is another big unknown which has given rise to two opposing views. One view is that "everything is everywhere". Based on the study of free-living ciliates from two water bodies in Europe, Fenchel and Finlay (2004) argue that small organisms (less than 1 millimetre in length) have a cosmopolitan distribution. In this view, prokaryotes and unicellular eukaryotes may have very high alpha-diversity, but would contribute little to the global numbers. Curtis, Sloan and Scannell (2002) speculate that the entire bacterial diversity of the sea is unlikely to exceed 2 million species. However, the notion that microorganisms are ubiquitous is being vigorously contested by other protistologists (see, e.g., Foissner 1999, Dolan 2006).

We have the questions and we have the tools to answer them, but alpha- and global diversity of procaryotes and protists will probably remain a black box of global marine biodiversity for quite a few more years.

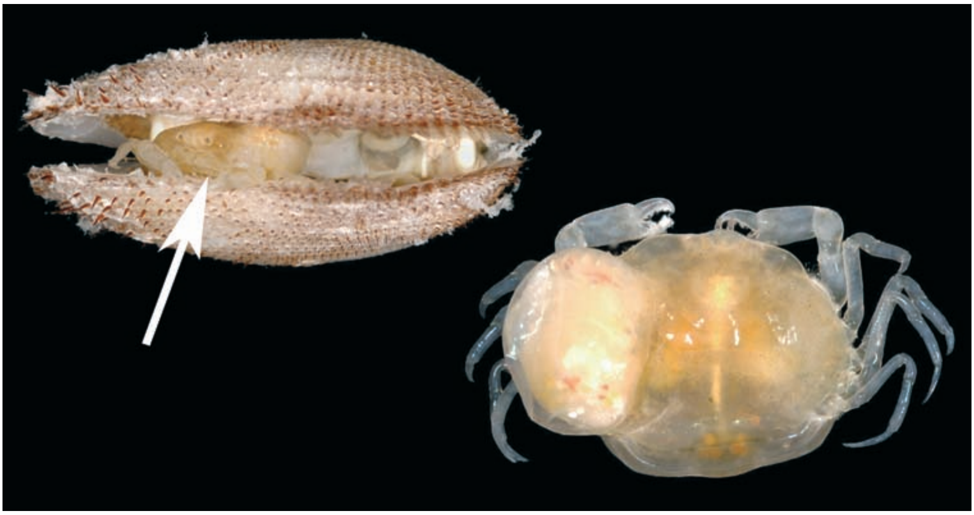


Photo 2.7: "Russian doll" interactions. The complexity of interactions between marine organisms is evidenced by this association between an arcid bivalve (family Arcidae) and a commensal pea crab (family Pinnotheridae) living in the mantle cavity of the mollusc (left; arrow); the pea crab is itself parasitized by a bopyrid isopod (family Bopyridae), responsible for the deformation of the carapace of the crab.

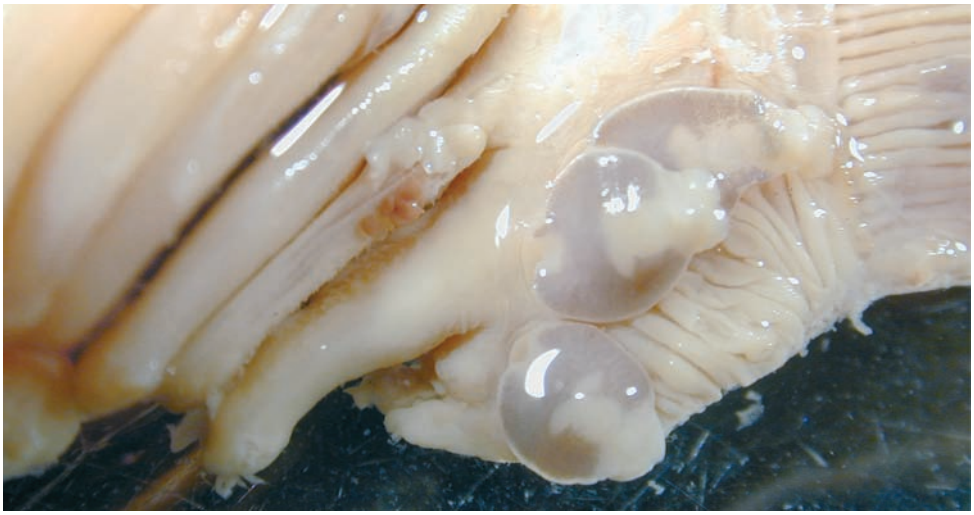


Photo 2.8: Three specimens of the monogene *Lagenivagino pseudobenedenia* on the gills of the fish *Etelis coruscans* from New Caledonia. Although numerous new species of parasites remain to be discovered, described and named, marine helminthology (the study of parasitic "worms") is a field of research that attracts few researchers.

2.3.2. Symbionts

Much of biodiversity consists of symbionts, a term encompassing commensals, associates and parasites (Windsor 1998). Symbionts are grossly undersampled and understudied (photo 2.7). In his essay "How many copepods?", Arthur Humes (1994) noted that of the copepods associated with benthic invertebrates that he sampled in Madagascar, New Caledonia, and the Moluccas, 95% were new species. Copepods are known from "relatively very few (1.14%) of the 151,400 potential marine invertebrate hosts": a total of 1,614 species were then known from 1,727 host species. In addition, 1,827 species of parasitic copepods were then known from fishes. The real number of parasitic/associated copepods would of course be much higher. In New Caledonia and the Moluccas, hard corals commonly have 5-9 species of associated copepods, and over its broad range *Acropora hyacinthus* harbours as many as 13 species; a single specimen of the holothurian *Thelenota ananas* studied by Humes harboured 5 copepod species. The 9,500 currently known marine species of free-living, associated and parasitic copepods obviously represent a small fraction of the real number of copepods worldwide.

The number of marine helminths is another black box (photo 2.8). Parasite diversity in marine fish has been less investigated than that in freshwater species. Previous studies (reviewed by Justine, in press) have estimated 3 to 5 monogenean species per species of fish host, and the literature contains several instances of marine fish species with 10-13 monogenean parasites. Diversity begets diversity: Rohde (1999) has shown that the number of monogeneans per species of fish is higher in tropical waters (with a mean of 2 species per fish) than in deep-sea or Arctic seas (0.3 species per fish). Fishes also have digeneans, cestodes and nematodes. In European seas, there are 1.7 times as many digenean species as monogeneans. Off Mexico, the grouper *Epinephelus morio* has 1 monogenean, 3 cestodes, 17 digeneans, 8 nematodes and 1 acanthocephalan, a total of 30 species of parasites (Moravec et al. 1997). Speculations on the global number of helminth species are hampered by two factors that may reinforce or annul each other, just as they impact speculations on global numbers of phytophagous insects (Ødegaard 2000). (1) Host specificity. Parasites may have different levels of specificity. In New Caledonia, of the 12 species of monogeneans found on the gills of the grouper *Epinephelus maculatus*, 10 are host-specific and one or two are generalists (Justine, in press). (2) Vicariance. Fishes may have very large ranges, but usually their parasites have been studied in only one or a few localities, and it is not generally known whether the same or different helminth species parasitize a given fish host in different regions of its range. For instance, the grouper *Epinephelus merra* is parasitized in Australia by the monogeneans *Pseudorhabdosynochus cupatus*, *P. vagampullum* and two still unnamed species, and in New Caledonia and Vanuatu by *P. cupatus*, *P. melanesiensis* and a third unnamed species (Justine, in press and references therein). Parasites have not been examined in many parts of the fish range, especially at its periphery where different species may be expected (Briggs 2006). Given that the number of species of marine fishes is on the order of 20,000, it is probably not excessive to predict on the order of 100-200,000 marine helminth species.

Beyond these black boxes, the measure of species richness at whatever spatial scale remains a challenge to science, conservation and management (Gray 2001). Entomologists have built a predictive model of the number of insect species based on numbers of species living in tropical rainforests (see, e.g., Stork 1988), but such a model is still lacking for marine biodiversity. It is usually recognized that there are four possible approaches to address the question of predicting the magnitude of global biodiversity: (a) extrapolations from samples; (b) extrapolations from known faunas and regions; (c) approaches using ecological criteria; (d) censusing taxonomists' views.

2.3.3. Extrapolations from samples

Ever since the seminal Hessler and Sanders' paper of 1967, the deep sea has persistently been highlighted as a reservoir of unknown biodiversity. Indeed, the deep sea fascinates by its dimensions and its inaccessibility. Before the 1960s, the deep sea was perceived as a very harsh place inhabited only by species able to eke out a living in conditions of complete darkness, near-freezing temperatures, scarce food and intolerable pressure; it was believed that such species were few and cosmopolitan, or at least very broadly distributed. This was the "desert-like" analogy (that persists today when hydrothermal vents are presented as "oases"). In the 1960s, the simultaneous discovery that sea-bottom topography was complex and that the deep-sea small macrobenthos was unexpectedly diverse led to Sanders' (1969) "stability-time hypothesis" (photo 2.9). The complete darkness, near-freezing temperatures, scarce food and intolerable pressure suddenly became characteristics of a very stable environment promoting highly specialised species with narrow niches, able to co-exist in competitive equilibrium. The most famous and most cited attempt to estimate the number of species in the deep sea is the work of Grassle and Maciolek (1992); the marine equivalent of Erwin's (1982) seminal paper on insect species numbers in tropical forests. Grassle and Maciolek analyzed the small macrofauna contained in 233

Photo 2.9: A riot of species. The expression "a riot of species in an environmental calm" was coined by the ecologists Paul Snelgrove and Craig Smith in order to draw attention to the paradox underlying deep-sea biodiversity. The deep sea has for a long time been perceived as a hostile, species-poor environment. Yet in fact, a few square meters of such desert-like mud may harbour as many as several hundred species of small macrobenthos, mostly polychaetes and isopods, and mostly undescribed.

Photo 2.10: Ctenophore *(Leucothea multicornis)*. This species is seasonally abundant in the Mediterranean plankton.

box cores, each 30 x 30 cm, taken on a 176 km transect along a 2100 m depth contour off New Jersey. These samples, totalling 21 sq. m, contained 798 species. Using a rarefaction approach, Grassle and Maciolek estimated that, after an initial rapid rise, species were added at a rate of 1 species per km^2. Given that there are 3×10^8 km^2 of ocean floor deeper than 1000 metres, by that calculation the deep sea would have 10^8 macrofauna species; an estimate revised by Grassle & Maciolek to 10^7 species (10 million species!) on the grounds that much of the abyssal plains are oligotrophic. Grassle and Maciolek's species bomb immediately attracted controversy and escalation.

On the escalation side, Lambshead (1993) speculated that, since species of nematodes outnumbered species of macrofauna by one order of magnitude, there might be 100 million species of marine nematodes alone! Based on a southern hemisphere isopod dataset, Poore and Wilson (1993) argued that the North Atlantic is not typical of oceanic biodiversity, and suggested that a factor exceeding 20 was "reasonable" to extrapolate from known to total fauna for the oceans as a whole.

On the controversy side, May (1992) questioned the extrapolation of the rarefaction curve, and concentrated instead on the fact that about 50% of the species in Grassle and Maciolek's study were new to science; he then suggested that only half of deep-sea fauna remained to be described and that the total number was unlikely to exceed 5 x 10^5 species, i.e., double the number of described species. May (1994) later persisted in his criticism of hyperbolic numbers of marine species: "Many revisionist views about particular groups are in the air. Especially relevant are the suggestions by Grassle and Maciolek, Poore and Wilson, and other 'marine chauvinists', for upward revisions – by factors of 20 or more – in numbers of marine species. I think, however, that the most reliable estimates are those based simply on the proportions of new species found in newly studied groups or regions. These rarely find more than 50% new species".

Ten years later, the dust of the controversy has settled, but no consensus has been reached. Even if much of the deep sea is oligotrophic and may not have the levels of species richness that are found off the coasts of continents, 278 million sq. km (the area of world ocean deeper than 3,000 metres) is still an incredibly extensive area. I concur with Poore and Wilson (1993) that the area off the northeastern United States is one of the best studied deep-sea regions in the world, and the 50% new macrofauna species obtained there are clearly not applicable to other, much less studied deep-sea basins elsewhere in the world.

2.3.4. Extrapolations from known faunas and regions

Fishes are certainly the best inventoried marine biota, and European seas are probably the part of the world where marine biodiversity is the most intensively and least patchily inventoried. The European Register of Marine Species (ERMS; Costello, Emblow and White 2001, 2006) has recorded 29,713 marine species in European seas (not including unicellular organisms), of which 1,349 are fishes. If we assume that fishes occupy the same proportion of marine biodiversity worldwide, and considering that there are currently 16,475 described species of marine fishes, then it is possible to extrapolate that the global magnitude of marine biodiversity stands at (16,475 : 1,349) x 29,713 = 362,353 species.

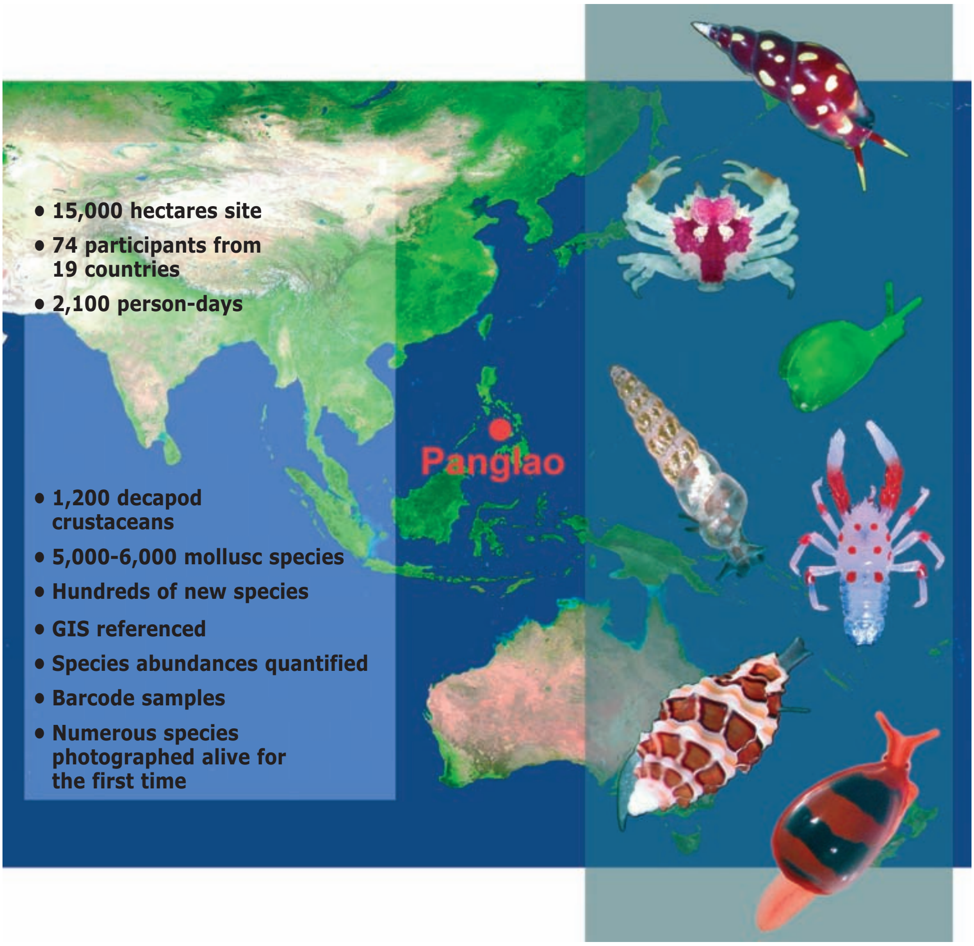
The validity of this extrapolation rests on a number of assumptions that may or may not be correct. First, it assumes that the worldwide geographical partitioning of marine biodiversity is the same across taxonomic or ecological groups. We know this is not the case. Plankton taxa have much broader ranges than benthic organisms, so that the European plankton biota represent a much higher proportion of the world total than benthic biota. For instance, the 41 species of Euphausiacea recorded in Europe represent 48% of the total world fauna of 86 species; by contrast, the 212 species of Brachyura recorded in Europe represent 4% of the world total of 5,200. The above extrapolation based on Euphausiacea would project a total marine biodiversity of just 62,325 species, which we know is wrong, whereas the same extrapolation based on Brachyura would give 728,809. (For the sources of the figures cited, see Costello et al. 2001 and table 2.1).

The second assumption that makes the extrapolation rest on shaky ground is that we do not have a complete inventory of either European biodiversity, in general, or of any major taxon worldwide. New species are still being added to the inventory of European marine biodiversity at a rate of 121 per year, and Wilson and Costello (2005) have used statistical approaches to predict that 11-50% of European fauna may remain to be discovered. At the global scale, new species of marine fishes and Brachyura are also being described each year. In the examples discussed above, the real numbers may be in the region of 35,000-40,000 marine species in Europe, of which 1,400 would be fishes, out of a world total of 20,000 marine fish species, or of which 250 would be Brachyura, out of a world total of possibly 10,000. Based on these revised numbers, the same extrapolation gives 500,000-570,000 species of marine multicellular organisms worldwide (extrapolated from fishes) or 1.4-1.6 million species (extrapolated from Brachyura).

2.3.5. Approaches using ecological criteria

Coral reefs occupy 600,000 sq. km or just 0.1% of the surface of the planet, yet they harbour an exceptionally high number of species and are often compared to rain forests when species numbers, ecosystem complexity and vulnerability are considered (figure 2.5). Estimating that there are about 274,000 species of marine organisms and assuming that 80% occur in coastal zones, and that tropical coastal zones are twice as rich in species as temperate ones, Reaka-Kudla (1997) used the species-area relationship to estimate that coral reef biodiversity amounts to about 93,000 described species. She then speculated that, if similar ecological and evolutionary processes operate on coral reefs as in rain forests, and assuming that the two environments were equally studied, then the number of coral reef species would be “about 600,000-950,000 species”, if rain forests have 1-2 million species, and 4.7 million

Figure 2.5: The Panglao project



Sampling coral reefs is intimidating because of the sheer diversity of species present and because most species are rare and small. In this respect, the Panglao Marine Biodiversity Project (Muséum National d'Histoire Naturelle, Paris; University of San Carlos, Cebu City; National University of Singapore) represented an unprecedented effort that has also generated unprecedented results in terms of discovering anddocumenting new species. For more information, see www.panglao-hotspot.org.

species if rain forests are home to 20 million. Her tentative conclusion was that the true number of species on global coral reefs "probably is at least 950,000", suggesting that coral reefs are repositories of very high undocumented species diversity. Indeed, a labour-intensive study of a 30,000 hectare site in the South-West Pacific revealed more mollusc species than in the whole Mediterranean (300 million hectares) (Bouchet et al. 2002).

2.3.6. Censusing taxonomists' views

On the occasion of his review of the biodiversity of eukaryotic algae, Andersen (1992) reported that "most phycologists [he had] contacted suggest that the total number of algal species is from 1.2 to 10 times those presently described. Diatomists suggest the real number of diatom species is (2-) 10 to 1000 times the number recognized today". Among regional attempts to census taxonomists' views, the Australian Faunal Directory contains a page (www.deh.gov.au/biodiversity/abrs/online-resources/fauna/) dedicated to "estimated numbers of the Australian fauna". Although the marine and non-marine components of the fauna are pooled together, it is interesting to note that Australian researchers consider that the percentage of known to unknown fauna ranges from 80-90% (macroinvertebrates: echinoderms, decapods) to 10% or less (parasites, meiofauna). There is no obvious way, though, to extrapolate these estimates to world fauna, and it should be emphasized that the taxa for which they are fairly accurate (fishes, echinoderms, decapods) contribute little to the global numbers, whereas for the taxa contributing much (parasites, nematodes) the estimates are very vague. In this respect, it is noteworthy that Lambshead himself revised his earlier speculations of nematode species richness (Lambshead 1993; 100 million species!), based on a new deep-sea dataset, and concluded that marine nematodes may in fact have fewer than 1 million species (Lambshead and Boucher 2003).

To summarize my opinion, and at the risk of being classified as a European chauvinist, I find most credible (or perhaps most reasonable?) the extrapolations from the relatively well inventoried European fauna, and my intuition is that the 1.4-1.6 million species extrapolated from Brachyura may be a good working estimate for the total marine biodiversity of the world.

2.4. EPILOGUE

At the current rate of new species descriptions, it will thus take 250-1,000 years to complete the inventory of marine biodiversity: the "Taxonomic Impediment" is real. There are many factors contributing to this impediment, but I choose to highlight two.

Within the scientific community, careers, funding, and other resources result from peer reviews that overwhelmingly favour research articles published in high-impact journals. In our 2002-2003 dataset, only 36% of the new species descriptions were published in journals with any kind of impact factor, and only 12.6% in journals with impact factors equal or superior to 1. Since the International Code of Bacterial Nomenclature requires that new prokaryotes are described, or at least that their descriptions are registered, in the *International Journal of Systematic and Evolutionary Microbiology* (Impact Factor 3.2), the system is not discriminating against prokaryote systematists. Taxonomists working on algae or parasites also have access to journals with good impact factors that will accept new species descriptions. However, the fate of the vast majority of new marine invertebrate and fish descriptions is to be published in journals with a modest impact factor, or no impact factor at all, contributing to the poor success of their authors when competing for employment, grants, or promotions. Future historians of marine biology will tell whether initiatives like the *Census of Marine Life* will have to be seen as turning points in restoring the image of taxonomy among marine sciences.

Outside the scientific community, it can be argued that the "Taxonomic Impediment" is actually fuelled or aggravated by attitudes and regulations both inside and outside the Convention on Biological Diversity. Access to biodiversity – for academic or industrial purposes – has now become strictly regulated under national biodiversity laws implementing international agreements of the Convention. Scientists have championed the economic benefits that can be obtained from the discovery of new bioactive compounds, in the hope that this would attract public and private funding for their research. The same scientists are now facing suspicion, if not hostility, from law-makers who want to take no economic or political risk in granting access to biodiversity exploration or bioprospecting. The discovery of new marine species, and indirectly of new marine products, is increasingly being overseen by legal authorities, conservation NGOs and Third World activists, rather than driven by academic scientists themselves.

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3. DEEP-SEA ECOSYSTEMS: PRISTINE BIODIVERSITY RESERVOIR AND TECHNOLOGICAL CHALLENGES

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3.1. INTRODUCTION

THE DEEP SEA is the largest ecosystem on Earth, with approximately 50% of the surface of the Earth covered by ocean more than 3,000 metres deep. It supports one of the largest reservoirs of biodiversity on the planet, but remains one of the least studied ecosystems because of its remoteness and the technological challenges for its investigation. The HMS *Challenger* Expedition (1872-1876) marked the beginning of the “heroic” age of deep-sea exploration, and our knowledge has progressed since in parallel with technological developments.

The deep-sea floor extends from around 200 m depth down the continental slope to the abyssal plains (3,000-6,000 m) and reaches the deepest part of the oceans in the Marianas Trench (11,000 m). These ecosystems are characterised by the absence of light, increasing pressure with depth and low temperature waters (with some exceptions). The deep sea contains extremely large habitats such as abyssal plains (millions km^2) and mid-ocean ridges (65,000 km long). At the same time, it encloses relatively small, localised geological features such as canyons, seamounts, deep-water coral reefs, hydrothermal vents and cold seeps, which support unique microbial and animal communities.

State-of-the-art technology is essential for the study of deep-sea ecosystems, providing the necessary tools for the location, mapping and study of the different habitats and their associated fauna. These include, amongst others, high definition sea-floor mapping, manned submersibles, remote operated vehicles, autonomous underwater vehicles, deep-towed vehicles and sampling equipment, landers, hydro-acoustic instruments and isothermal and isobaric chambers as well as laboratory techniques such as new molecular tools. International collaborations for sharing of equipment, expertise and human resources are crucial in driving deep-sea investigations. The deep sea also includes important

Photo 3.1: *Anoplogaster cornuta*, deep-sea Atlantic fish. Among the world’s deepest-living fishes, the common fangtooth is usually found between 200 and 2,000 m, although it has been observed as far down as 5,000 m. Its enormous head and long teeth are morphological features shared by many fish species dwelling in the total darkness of the ocean depths.

biological and geological resources. Therefore, industries such as deep-water fishing or oil and gas exploration are rapidly moving into deep-water areas. Scientists are working together with industries, conservation agencies and decision makers to develop conservation and management options for an environment that is still one of the great unknowns of our planet.

3.2. HISTORY OF DEEP-SEA EXPLORATION: FROM FORBES' "AZOIC ZONE" TO HYDROTHERMAL VENT DISCOVERY

The roots of our understanding of deep-sea ecosystems follow the path of the great expeditions that started in the 19th century, and that developed with the refinement of navigation and sampling techniques and instruments. Between 1841 and 1842, Edward Forbes developed the "azoic theory" after observing a decrease in the number of animals when dredging at increasing depths in the Aegean Sea. The extrapolation of his results led him to believe that the oceans did not support life below 600 m. However, the expeditions of HMS *Lightning* (1868) and HMS *Porcupine* (1869 and 1870) to the NE Atlantic and Mediterranean and, especially, the circumglobal expedition of HMS *Challenger* (1872-1876) demonstrated that life was present in the oceans, from the shores to the abyssal depths (Murray and Hjort 1912). The *Challenger* Expedition is considered to be at the origin of modern oceanography.

In the mid 20th century, the *Galathea* expedition (1950-1952) gave evidence that marine life exists in even the deepest zones of the ocean floor, when the expedition recovered fauna from 10,200 m on the Philippine Trench. The baseline biological data obtained from the early expeditions, together with the development of new, more precise sampling technologies, allowed for a change in the way that deep-sea marine biological research was conducted. From the mid 1960s, descriptive biology was complemented by process-oriented and ecological biology based on rigorous scientific methods (Hessler and Sanders 1967; Grassle and Sanders 1973; Grassle 1977). When boxcorers made it possible to obtain quantitative samples of the small-bodied fraction of the deep-sea fauna, it was found that the deep-sea sediments sustain a very high biodiversity, far beyond the "azoic sea-floor" predicted by Forbes (Hessler and Sanders 1967). The development of deep-water photographic instruments, and later of deep-water submersibles, allowed deep-sea fauna to be observed and studied in its own habitat, for the first time ever, providing crucial information that was traditionally missed in remote/blind sampling.

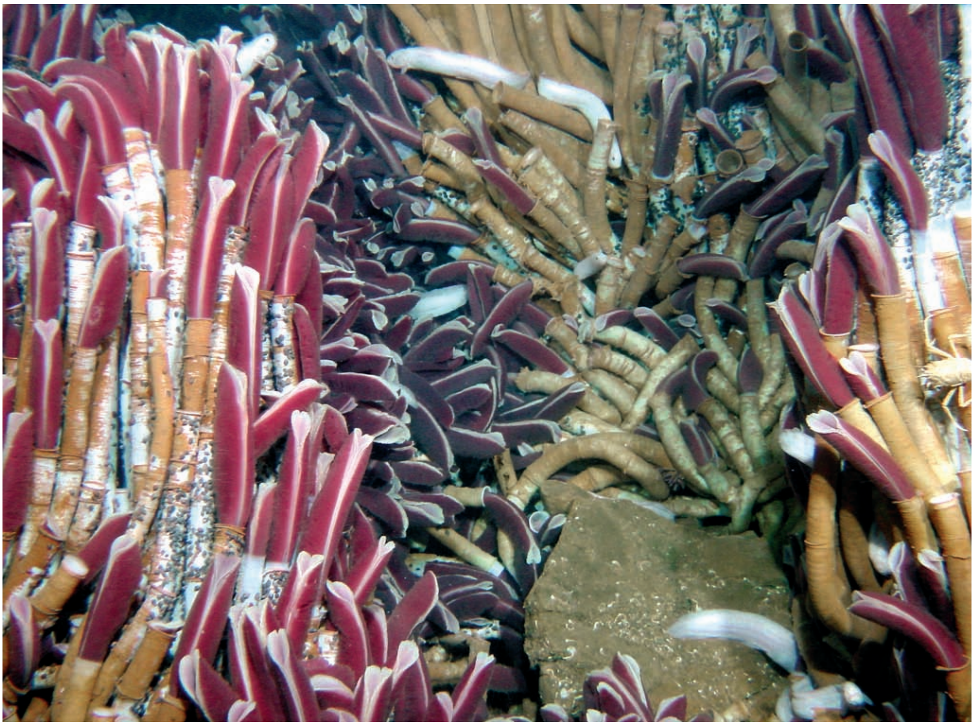


Photo 3.2: The giant tubeworm *Riftia pachyptila* from the East Pacific Rise hydrothermal vents

Less than 30 years ago, one of the most exciting discoveries of our times was made. In 1977, hydrothermal vents were discovered in the Galapagos Rift in the Pacific, as the result of geothermal studies investigating the balance of thermal flux on Earth (Lonsdale 1977; Corliss et al. 1979). But what the pilots and scientist in the U.S. research submersible *Alvin* were not expecting to find was the extraordinary landscape of black smokers colonised by dense populations of exotic and unknown animals, such as the giant tubeworm *Riftia pachyptila* (photo 3.2).

What was even more striking was the finding that these ecosystems are sustained by primary production of chemoautotrophic bacteria that use inorganic reduced chemicals from the Earth's interior to synthesize organic matter (see section 3.3.2). These new habitats where life thrives independent of solar energy are known as chemosynthetic ecosystems. Today we know that other reducing habitats such as cold seeps, whale falls or oxygen minimum zones also develop chemically-driven communities with similar species and physiology to the vent animals (see section 3.3.2).

3.3. DEEP-SEA ECOSYSTEMS: ENVIRONMENTAL CHARACTERISTICS AND BIODIVERSITY

The oceans cover 70% of the Earth's surface or the equivalent of the surface of two Mars and two Moons together. But we still know more about the geography and characteristics of our Moon or Mars than about our Oceans! Furthermore, 50% of the Earth is covered by oceans more than 3,000 m deep, with a mean depth of around 3,800 m. The deep sea is, therefore, the largest ecosystem in our planet as well as one of the least studied. It comprises a variety of habitats from the shelf break to the deepest parts of the ocean floor found in trenches, each with specific physical and geochemical characteristics that support one of the highest biodiversities on the planet. In relation to the energy that supports marine ecosystems, deep-sea habitats can be divided into two major groups: heterotrophic and chemosynthetic habitats. In heterotrophic habitats, the faunal communities depend, ultimately, on organic matter produced at the surface by photosynthesis and are therefore dependent on solar energy. In chemosynthetic habitats, the biological communities are sustained by the energy provided by inorganic reduced chemicals such as hydrogen sulphide (H_2S) or methane (CH_4) from the Earth's interior.

3.3.1. Heterotrophic ecosystems

The vast majority of life in the deep oceans is sustained by the production of organic matter on the surface from photosynthesis. It resides in what are known as heterotrophic habitats, because there is no intrinsic primary production. In the deep-sea benthos, the heterotrophic ecosystems include continental margins from the shelf break to 3,000 m depth and abyssal plains, between 3,000 m and 6,000 m in depth. Continental margins include a variety of habitats with specific and distinct physicochemical, geological and biological characteristics that are discussed below.

3.3.1.1. SEDIMENT MARGINS

Continental margins cover 13% of the world's seafloor (Wollast 2002). These systems are the largest reservoir of sediments on Earth, with up to 90% of sediments generated by erosion on land being deposited on the margins (McCave 2002). The open margin ecosystem is greatly influenced by dynamic processes such as currents that affect and drive the transport of energy and organic matter. In some regions, wind stress along the coast can lead to upwelling events that transfer rich deep waters to the surface, feeding the nutrient-depleted surface waters and resulting in high productivity on the shelf (Wollast 2002). In other areas, landslides cause large-scale disturbances that can destroy whole communities in a single event.

The drivers of heterogeneity in faunal distribution, composition and abundance on continental margins vary depending on the spatial scale considered. At large scales (over 1,000 km), major physical factors such as geology, temperature, currents and water masses play the main role. At mid scales (1-100 km), the distribution of animals is mainly determined by factors such as down flux of primary production, oxygen availability (i.e., areas of oxygen minima), sediment type and catastrophic events (Gage 2002). Finally, biological interactions are the main drivers of faunal distribution at small scales. Our knowledge about the biodiversity and biogeography of fauna on continental margins is still scant. Biomass as indicated by epifauna (animals living on the sediment) decreases with depth, and in deep waters the presence of a large number of burrowing animals is shown by a variety of features such as pits and mounds. Animals on deep sediment slopes are mainly sediment feeders that use the organic matter input from the surface. In shallower waters, the number of megafaunal animals and suspension feeders increases in relation with higher water currents. Finally, when the slope approaches the shelf, the increase in grain size causes a decrease in the biota of the sediment. One of the most striking observations in open margins is the peak in biodiversity at mid slopes (Stuart, Rex and Etter 2003). The exact drivers of this general observation of biodiversity maxima are still to be determined, and are the focus of a number of research projects (see section 3.5).

3.3.1.2. Canyons

Canyons are deep incisions on the continental margins, and are common features on European margins such as the Catalan Sea (map 3.1), the south of France or the Portuguese margin.

Canyons are hotspot ecosystems on continental margins, characterised by a high biodiversity. These geological features act as major pathways for organic carbon transportation, and fast down flux of organic matter from the land to the deep sea. Canyons contain a variety of substrata, such as hard rock walls and mobile sediments on the canyon floor, that sustain complex ecosystems

Map 3.1: Bathymetric map of a section of the Catalan Sea (Eastern Mediterranean) showing canyon systems

Source: www.icm.csic.es/geo/gma/MCB.

with a high degree of endemic species. Canyons are also important hotspots for commercial species, such as the red shrimp *Aristeus antennatus*, one of the major fisheries in the Catalan Sea (Sardà, Company and Castellón 2003). However, their irregular topography and the difficulty of sampling prevented their detailed investigation until only recently. The latest developments in deep-water imaging with towed and remote-operated vehicles and submersibles are now facilitating the exploration and investigation of the geophysical and biological characteristics of canyons (see section 3.5).

3.3.1.3. DEEP-WATER CORALS

Investigations on continental margins during the last decade led to a surprising discovery: the presence of deep-water corals that form reefs along the NE and NW Atlantic continental margins. The NE Atlantic coral reefs are found at around 1,000 m depth and extend from Norway to Portugal (photo 3.3),

Photo 3.3: Deep-sea corals observed by French ROV *Victor* 2000 at a depth of 1,650 m in the NE Atlantic

and recently similar ecosystems have been discovered in the Mediterranean. Deep-water coral species such as *Lophelia pertusa* and *Madrepora oculata* form carbonate reefs several kilometres in length and sustain a high biodiversity providing refuge, structure and nursery spots for other slope species. The reefs provide a complex three-dimensional habitat for a variety of species, including sponges, soft corals, molluscs, crustaceans and echinoderms (Freiwald 2002), as well as for commercial species. Although our knowledge on the composition and functioning of these rich communities is still low, there is already evidence of habitat damage from deep-water trawling over deep-water coral regions (see section 3.6).

3.3.1.4. Seamounts

Seamounts are undersea mountains characterised by steep slopes, the presence of hard and soft substrata, large depth ranges from abyssal to sub-littoral depths and geographic isolation (Rogers 2004). It is estimated that around 100,000 seamounts over 1000 m in height exist around the world's oceans, and many more if we consider smaller mounts. But only around 350 of these seamounts have been sampled, and only around 100 have been studied in any detail. The particular biological features of seamounts include high productivity, large stocks of commercially valuable fishes, high biodiversity and a high degree of endemism of benthic fauna. These specific traits are driven by the particular topography and hydrography around seamounts (Forges, Koslow and Poore 2000).

As has occured in other regions, like canyons, with difficult terrain, we still have little knowledge of the biodiversity, distribution and functioning of seamount fauna. However, seamounts have been the target of intensive fishing in recent decades (Koslow et al. 2001), which has led to potential long-term damage and biodiversity loss in an ecosystem as yet poorly understood. Today, with the help of new studies of seamounts driven by the use of new technologies such as ROVs or deep-towed cameras, management and conservation options are being put in place (see section 3.6).

3.3.1.5. ANOXIC AREAS

Mid-water oxygen minima (<0.5ml/l dissolved O_2) can intercept the continental margin, resulting in sediments with a very low oxygen concentration or Oxygen Minimum Zones (OMZs). OMZs are formed in areas of high primary production in the surface waters of the ocean and poor water circulation, where the biological degradation of the sinking organic matter results in oxygen depletion (Rogers 2000; Levin 2003). Seafloor OMZs typically occur between 200 m and 1000 m depth and are found in the eastern Pacific, NW Pacific margin, Philippines area, Bay of Bengal, Arabian Sea and SW Africa beneath the Benguela current (Rogers 2000; Levin 2003). Despite very low oxygen concentrations, protozoan and metazoan life thrive in these ecosystems. The high concentrations of organic matter sustain dense populations of sulphide-oxidising bacteria (i.e., *Begiattoa, Thioploca, Thiomargarita)* and a low biodiversity but high density of protozoan and metazoan life. The main groups are foraminiferans, nematodes, ciliates, flagellates, polychaetes, gastropods and bivalves with specific adaptations, such us high concentrations of haemoglobins, large respiratory surfaces, small thin bodies, high concentrations of pyruvate oxydoreductases and presence of sulphide-oxidising symbionts (Levin 2003; see section 3.3.2.3 for chemosynthetic assemblages in OMZs).

3.3.1.6. Abyssal plains

The abyssal plain ecosystem is the largest ecosystem on Earth. It lies beyond the continental slope, between 3,000 and 6,000 m depth. Abyssal plains are covered by a thick layer of fine sediment that can reach thousands of metres in thickness, resulting in the popular picture of a flat, monotonous deep-sea bed. The main characteristics of water masses at abyssal plains are: low temperature (~2ºC except in the Mediterranean Sea with 13ºC and Red Sea with 21.5ºC), salinity (35‰, except in the Mediterranean and Red Sea >39‰), mostly saturated waters with dissolved oxygen (5-6 ml/l), absence of light (light useful for photosynthesis does not reach below ~250 m depth) and high pressure (1 atmosphere every 10 m depth). This relatively uniform distribution of physical factors led to the belief that abyssal plains were very stable habitats where physical and biological processes remained unchanged over short and long time scales.

There is now evidence that physical disturbances occur at abyssal plains, causing important biological responses. For example, there are daily and annual tidal variations in the flow of cold dense water close to the seafloor. The effects of these tides on the biological communities are not well understood, but it has been suggested that they could be used by certain species for orientation or for setting internal biological cues for synchronised spawning (Tyler 1988). There are also high-energy, unpredictable events such as benthic storms or turbidity currents that have very considerable disruptive effects on the seafloor, in particular in the redistribution of sediment and consequent biological responses (Aller 1989). Another major environmental factor that greatly affects the benthic communities on abyssal plains is the seasonal deposition of phytodetritus (organic matter produced in the surface waters) following the months of high surface production (Beaulieu and Smith 1998). Because the rapid sinking of this material prevents its complete utilisation by pelagic grazers, the arrival of this organic matter to the seafloor provides the abyssal communities with a seasonal input of high-quality food resource (Ginger et al. 2001; Billett et al. 2001).

The abyssal plains support a very high biodiversity, composed mainly of macro and meiofauna. The meiofauna (size of organisms in the order of microns) is mainly dominated by nematodes and foraminifera (Gooday 1996). The macrofauna (size of organisms in the order of millimetres) is dominated by polychaetes, with small peracarid crustaceans, molluscs, nemerteans, sipunculans, echiurans and enteropneusts also abundant

(Grassle and Maciolek 1992). Finally, the large megafauna (size of organisms in the order of centimetres) is made up of holothurians, asteroids, echinoids, decapod crustaceans and fish, as well as sessile fauna such as crinoids, sponges and anthozoans on hard substratum (Gage and Tyler 1991).

Even though abyssal plains have been sampled since the times of the *Challenger* expedition, only a small fraction of the vast extensions of these ecosystems has been studied to date. Latest results obtained from abyssal plain research have shown that variations in primary production in the surface waters can result in long-term changes in the composition of the plain megafauna. For example, there is evidence from the Porcupine Abyssal Plain in the NE Atlantic that an almost non-existent species of small holothurian (*Amperima rosea*) became dominant after 1996 because of its ability to rapidly exploit the nutritional resources of seasonal phytodetritus (Wigham, Tyler and Billett 2003). This indicates the strong link between the abyssal ecosystem and the surface of the biosphere, and has important consequences when considering the effect of factors such as climate change on biodiversity.

3.3.2. Chemosynthetic ecosystems

Deep-water chemosynthetic ecosystems have been known and studied for less than 30 years. The first such ecosystems to be discovered were hydrothermal vents in 1977… 8 years after Neil Armstrong and Buzz Aldrin had walked on the Moon! Then followed the discoveries of other deep-water chemically driven communities such as cold seeps, large organic falls to the deep-sea floor (i.e., whale falls or sunken wood and kelp) and areas of oxygen minimum that intersect with the margin. In chemosynthetic ecosystems, primary production is produced by chemoautotrophic microorganisms that use reduced inorganic chemicals to synthesise organic matter. These organisms are found free living, forming bacterial mats, but also in symbiosis with some of the major invertebrate groups.

3.3.2.1. Hydrothermal vents

Hydrothermal vents were discovered in 1977 in the Galapagos Rift, in the Pacific (Lonsdale 1977; Corliss et al. 1979), and since then vents have been found in all ocean basins. Hydrothermal vents occur in mid-ocean ridges, back-arc basins and certain active seamounts. Mid-ocean ridges are volcanic mountain chains that occur where two tectonic plates are being pulled apart. In these areas, cold seawater (2°C) penetrates through cracks in the crust. During its transition in the mantle, the fluid gets heated as it flows close to the magma chamber that feeds the ridge and is depleted of oxygen and magnesium while being charged with other metals. The superheated fluid (350°C) rises back to the surface of the seafloor, and when it mixes with the surrounding cold and oxygenated seawater, the metals precipitate, providing the aspect of dense black smoke characteristic of hydrothermal vents (photo 3.4).

Among the most striking discoveries at vents were the associated dense biological populations and the trophic structure that sustains these communities. It was unforeseen to find whole dense communities of animals living independently from solar energy by using the energy of reduced chemicals from the Earth's interior via the production of microorganisms (Karl, Wirsen and Jannash 1980; Jannasch and Mottl 1985). But it was even more astonishing to find that these microorganisms also formed symbiotic relationships with most

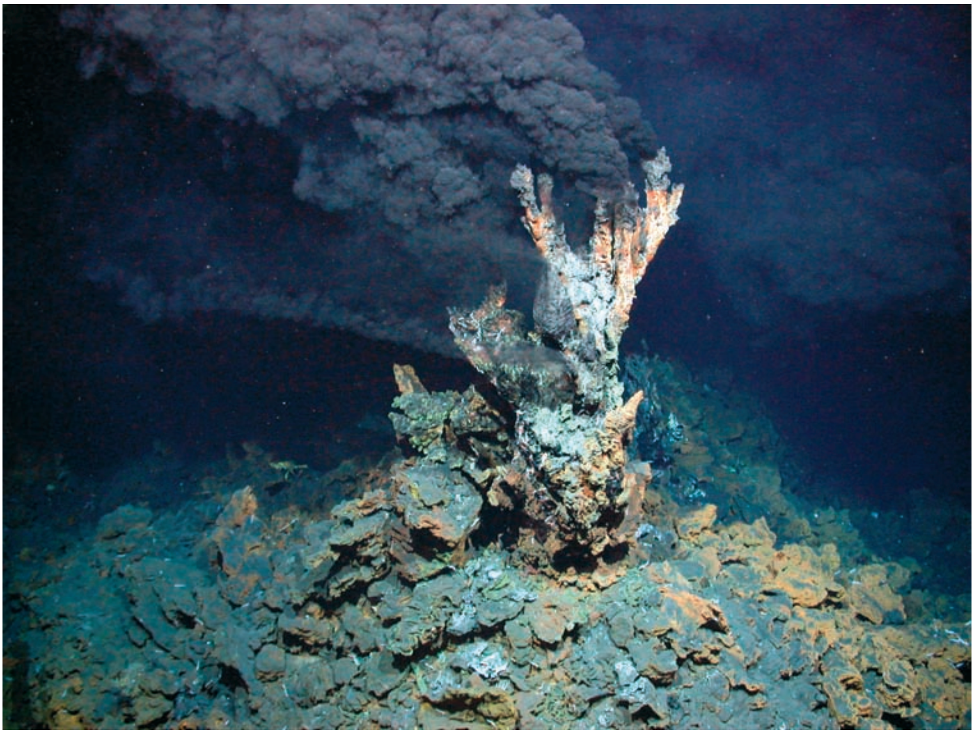


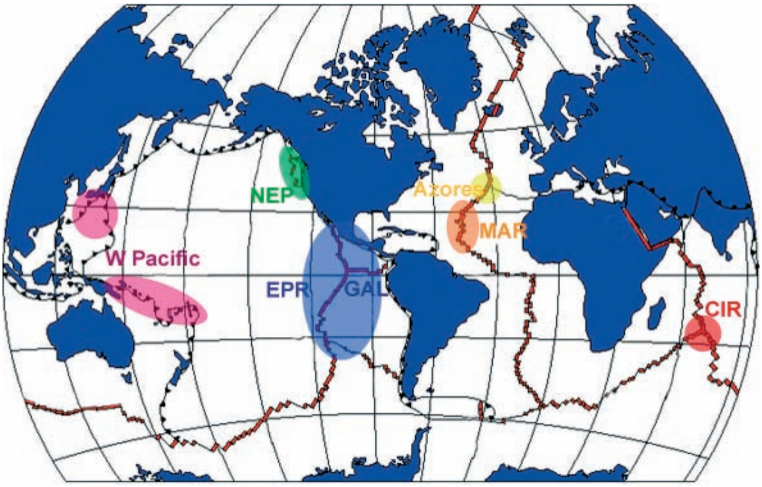
Photo 3.4: Black smoker from the Mid-Atlantic Ridge

Photo 3.5 (left): Gastropods from the hydrothermal vents of the Lau Basin, in the western Pacific. Photo 3.6 (right): Galatheid crabs from Pacific hydrothermal vents

of the major invertebrate groups (Cavanaugh et al. 1981; Felbeck, Childress and Somero 1981), and to observe the variety of adaptations made by these invertebrates to life in hydrothermal vents. One of the most modified is probably the giant tubeworm *Riftia pachyptila* from the Pacific vents (photo 3.2). This animal does not have a mouth or digestive system, but instead has a special organ that fills most of its body, called the trophosome. The trophosome is basically a sack densely packed with chemoautotrophic bacteria. *Riftia* intakes oxygen from the surrounding water and CO_2 and H_2S from the hydrothermal fluid with its highly irrigated plume. The chemicals are sent to the trophosome via the blood vessels where the microorganisms use them to synthesise organic matter. The animal depends completely on this microbial production for its lifelong growth and reproduction. Symbiotic relationships also appear in other groups, such as clams, mussels, shrimp, crabs and polychaetes, with different degrees of dependency.

Hydrothermal vents have been called “oases” of life in the deep-sea floor because of the exuberant aspect of their dense populations of large invertebrates. However, as in other ecosystems with extreme chemicophysical environmental parameters, hydrothermal vent communities are simple systems. Biodiversity is low, but biomass is high, sustained by a constant and abundant supply of energy in the form of reduced chemicals found in the hydrothermal fluids. Since their discovery in 1977, 590 species have been described from vents, which is the equivalent to around one new description every two weeks (Van Dover et al. 2002). Furthermore, of the almost 600 species described, approximately 400 have been identified so far as endemic to vents. The major faunal groups present are vestimentiferan tubeworms, bathymodiolid mussels, vesicomyid clams, bresilid shrimp, crabs, amphipods and polychaetes (photos 3.5 and 3.6). Investigations at hydrothermal vents are still in the extensive exploration phase, with only a small fraction of the over 65,000 km of global ridge system studied to date. However, the data that has been compiled so far indicates that vent fauna form distinct biogeographical regions. In a review by Van Dover et al. (2002), six vent biogeographic regions are recognised, each with specific faunal assemblages (map 3.2). But much exploration and investigation remains to be done before we have a sound understanding of the global diversity of vent species, and the processes that shape their distribution and their functioning.

Map 3.2: The mid-ocean ridge system showing the known hydrothermal vent biogeographic provinces



Hydrothermal vent biogeographic provinces.

Azores: dominated by bathymodiolid mussels, amphipods and caridean shrimp; MAR: Northern MidAtlantic Ridge region dominated by caridean shrimp, mainly *Rimicaris exoculata,* and bathymodiolid mussels; EPR & GAL: East Pacific Rise and Galapagos Rift dominated by vestimentiferan tubeworms, bathymodiolid mussels, vesicomyid clams, alvinellid polychaetes, amphipods and crabs. NEP: NE Pacific region, dominated by vestimentiferan tubeworms excluding Riftiidae, polychaetes and gastropods; W Pacific: dominated bybathymodiolid mussels, "hairy" gastropod, vesicomyid clams and shrimps; and CIR: Central Indian Ridge, dominated by the shrimp *Rimicaris kairei,* mussels, scale gastropods and anemones.

Map modified from Van Dover et al. 2002.

3.3.2.2. COLD SEEPS

Cold seep communities were discovered in 1983 at aproximately 500 m depth in the Western Florida Escarpment in the Gulf of Mexico (Paull et al. 1984). Cold seeps are characterised by the seepage of cold fluid with a high concentration of methane. This methane may have a biological origin, from the decomposition of organic matter by microbial activity in anoxic sediments, or a thermogenic origin, from the fast transformation of organic matter caused by high temperatures (Sibuet and Olu 1998; Levin 2005). Cold seeps also have high concentrations of H_2S in sediments, produced by the bacterial reduction of sulphates using methane. Both methane and sulphide play a major role in sustaining the highly productive cold seep communities (photo 3.7) through chemoautotrophy by free-living and symbiotic bacteria (Paull et al. 1984; Barry et al. 1997). Cold seep communities occur in both passive margins such as the Gulf of Mexico, Carolina slope, Barents Sea, Gulf of Guinea and Angola margin, and in active margins (or subduction zones), mainly in the Pacific, such as the Peru-Chile margin, as well as the Barbados Accretionary Prism and the Eastern Mediterranean among others.

Photo 3.7: A bathymodiolid mussel community in Gulf of Mexico cold seeps

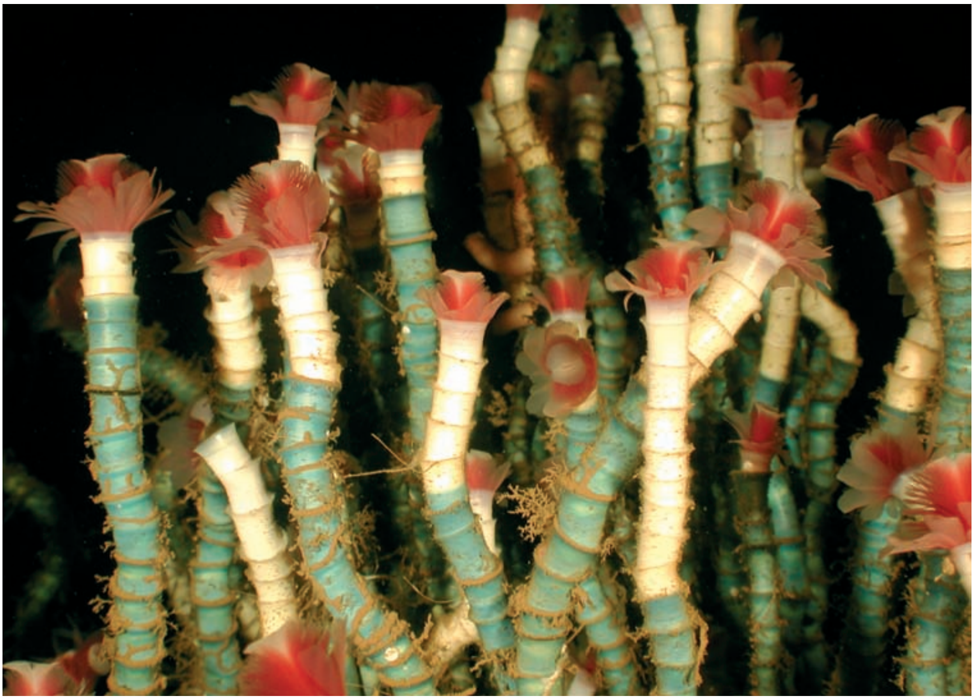


Photo 3.8: Tubeworms of the genus *Lamellibrachia* from Gulf of Mexico cold seeps

As with hydrothermal vents, only a small fraction of the potential locations of cold seeps on margins has been explored to date. We only know around 35 seep sites, and only a small number of these have had their geochemistry and biology studied in any detail (Sibuet and Olu 1998; Kojima 2002; Levin 2005).

Since their discovery, around 230 species have been described from cold seeps. Cold seep habitats are more stable systems than hydrothermal vents. There is also a slow transition of physical and chemical factors between the seep habitat and the heterotrophic surrounding system, allowing for a higher biodiversity than in hydrothermal vents. The megafaunal biomass at seeps by far exceeds that of the surrounding non-chemosynthetic sediment. The major groups are bivalves (mytilids, vesicomyids, lucinids and thyasirids) and vestimentiferan tubeworms, with pogonophoran, sponges, gastropods and shrimps sometimes also abundant (Levin 2005) (photo 3.8).

3.3.2.3. Other reducing habitats

In 1987, Craig Smith, from the University of Hawaii, observed for the first time chemosynthetic communities on a whale skeleton (photo 3.9) that was

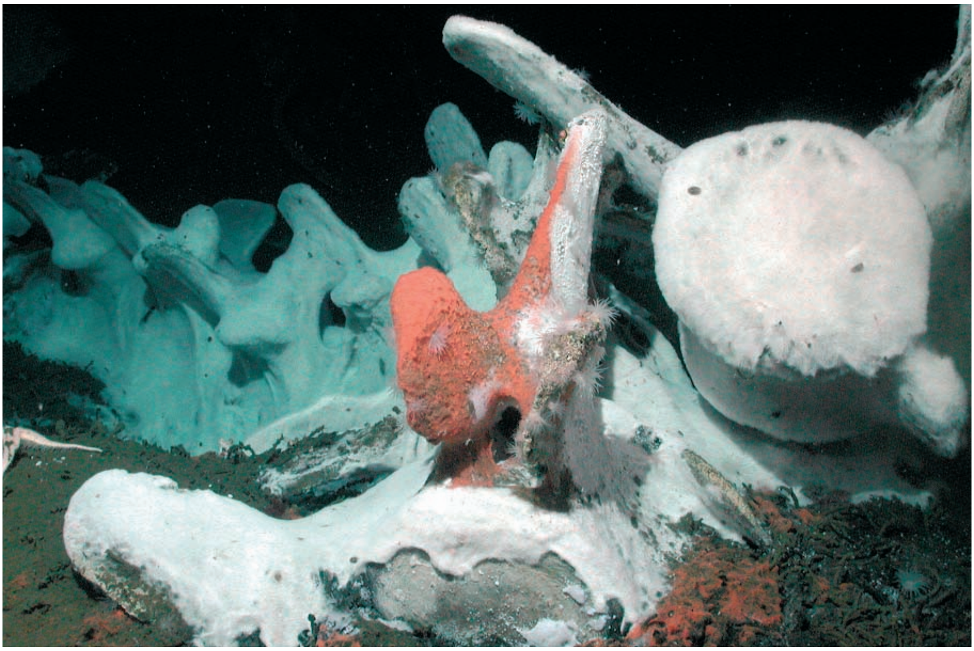


Photo 3.9: Whale skeleton colonised by bacterial mats

found by chance in the North Pacific during a dive with the submersible *Alvin* (Smith et al. 1989).

Since then, the investigation of biological assemblages on whale falls and other large organic falls to the deep-sea floor, such as sunken wood and kelp, has advanced rapidly. In the case of whale falls, there is a three-step ecological progression (Smith and Baco 2003). First, during the scavenger phase, the flesh is eaten and the skeleton left exposed. The opportunistic phase follows, when the sediment and skeleton are colonised by dense populations of opportunistic polychaetes and crustaceans. The final phase is the chemotrophic or sulphophilic phase. The bones of whales are composed 60% of lipids. The anaerobic bacterial degradation of these lipids produces sulphides that are used by chemoautotrophic microorganisms, allowing for the subsequent colonisation of chemically-driven fauna (Smith and Baco 2003).

The biodiversity of fauna colonising these isolated and ephemeral habitats is high. Since their discovery, over 400 morphological species have been described from whale falls, but most of them still remain to be identified. It has been suggested that whale falls could act as stepping stones for dispersal between chemosynthetic ecosystems (Smith et al. 1989). This is supported by the fact that the three habitats share a number of species and an even higher number of groups at higher taxonomic levels (Smith and Baco 2003).

Finally, chemosynthetic-related communities can also develop in OMZs (see section 3.3.1.5). A large number of heterotrophs in OMZs consume chemoautotrophic bacteria by grazing on bacterial mats or predating on other animals that have done so (Gallardo et al. 1995). The presence of endosymbiotic sulphur-oxidising bacteria is also widespread in foraminiferans, flagellates, ciliates, some polychaetes and some bivalves (Levin 2005). The details of the metabolic interactions between host and symbiont remain unknown, as does the extent to which chemosynthesis provides nutrients to the OMZ benthos. But ongoing and future research will no doubt extend the list of these types of relationships, and help explain the phylogenetic and evolutionary links with fauna from other deep-water chemosynthetic ecosystems.

Of all the described species from hydrothermal vents, cold seeps and whale falls, 18 are shared between vents and seeps, 11 are shared between vents and whales, 20 are shared between seeps and whales, and 7 are shared amongst the three habitats (Tunnicliffe, McArthur and McHugh 1998; Smith et al. 2003). However, these numbers will change in parallel with new discoveries and further investigation of known sites that will improve our knowledge of the diversity and distribution of species from deep-water chemosynthetic habitats and the processes driving them.

3.4. TECHNOLOGY AND DEEP-SEA EXPLORATION

Since the early oceanographic expeditions of the 19th century, the exploration and investigation of the deep sea has evolved in parallel with technological advances. The international oceanographic fleet is large and diverse, equipped with deep-tow and deep-coring cables for the use of deep seafloor sampling instruments.

Before the study of any biological community, the geophysical characteristics of the habitat need to be determined. The first step is the use of hull-mounted multi-beam swath bathymetry, a standard feature used on most modern research ships to produce bathymetric maps of the seafloor. More detailed acoustic maps can be obtained with deep-towed sidescan sonars (photo 3.10).

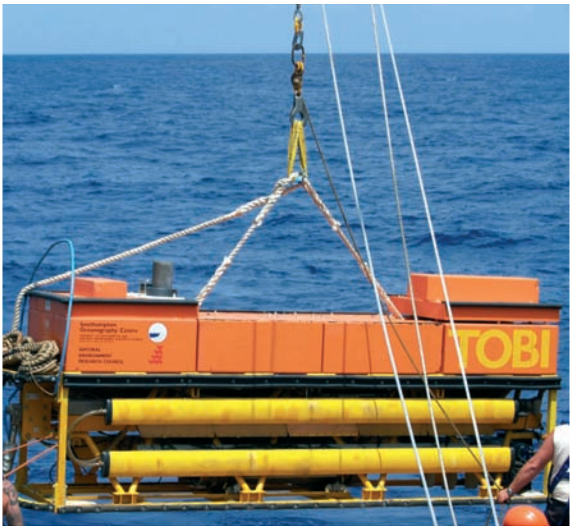


Photo 3.10: TOBI (Towed Ocean Bottom Instrument) is one of the UK deep sidescan sonars used to produce acoustic maps of the deep seafloor

These instruments are towed behind the ship at around 500 m above the seafloor, and produce acoustic images of the seafloor complete with detailed geophysical information, such as the presence of sediment or hard substratum, elevations and depressions. Studying the water column with instruments like CTDs that can measure conductivity, temperature and depth continuously during a vertical deployment is an important means to characterise the physical parameters of the water mass overlaying the benthic habitat under study.

In biological studies of deep-sea fauna, the most widely used equipment has traditionally included deep trawls for collecting megafauna; multicorers and megacorers to obtain quantitative samples of sediment cores with intact sediment-water interfaces used for organic chemistry, nutrient analyses and meiofauna studies; boxcorers for quantitative samples of macrofauna; sediment traps for studies of phytodetritus input to the seafloor; and current meters for the analysis of physical parameters. The study of deep-sea ecosystems moved a step forward when we acquired the capacity of visualising the habitat with photographic and video tools. Deep-towed vehicles equipped with photographic and video cameras have been very useful to describe the ecosystems *in situ*, and to provide spatial and distribution information that is lost in trawl samples. These instruments are also very efficient in habitats of difficult terrain, such as canyons, seamounts or deep-water corals, where trawling or coring is difficult or even impossible.

One of the most important technological advances for oceanography in modern times has been the development of manned submersibles, remote operated vehicles (ROVs) and autonomous underwater vehicles (AUVs). Submersibles and ROVs not only allow the direct visualisation of the seafloor and its fauna, but also provide the capability for directed and detailed sampling as well as *in situ* experimentation. These vehicles are crucial in the study of deep-water chemosynthetic ecosystems. A number of submersibles and ROVs are now available from a variety of nations (table 3.1, photo 3.11).

A number of new oceanographic vessels are being built today, such as the Spanish *B.O. Sarmiento de Balboa*, the French *N/O Pourquoi Pas?* or the British *RRS James Cook*, and all of them are being equipped with the capability to deploy and use submersibles and/or ROVs. Another area of technological development is AUV technology. AUVs allow for the investigation of areas of difficult or no accessibility, such as the seafloor under ice in the Arctic and Antarctic oceans. Recently, AUVs have been used for the exploration and location of hydrothermal vents. For example, an AUV such as ABE (WHOI, USA) can be used as the last step of a ridge section survey, providing

Table 3.1: Human-Occupied Submersibles (SUB) and Remote Operated Vehicles (ROV) currently used for research in chemosynthetic ecosystems

Name	Vehicle Type	Organisation	Country	Depth Capability
Ropos	ROV	CSSF	Canada	6,000 m
Nautile	SUB	Ifremer	France	6,000 m
Robin	ROV	Ifremer	France	3,000 m
Victor 6000	ROV	Ifremer	France	6,000 m
Jago	SUB	MPI Seewiesen	Germany	400 m
Quest	ROV	Bremen University	Germany	4,000 m
Cherokee	ROV	Bremen University	Germany	1,000 m
Shinkai 2000	SUB	JAMSTEC	Japan	2,000 m
Shinkai 6500	SUB	JAMSTEC	Japan	6,500 m
Dolphin 3k	ROV	JAMSTEC	Japan	3,300 m
Aglanta	ROV	Bergen University	Norway	2,000 m
Argus	ROV	Bergen University	Norway	2,000 m
Bathysaurus	ROV	Bergen University	Norway	5,000 m
MIR 1 y MIR 2	SUB	Shirshov Institute	Russia	6,000 m
Isis	ROV	NOC (Southampton)	UK	6,500 m
PISCES IV y PISCES V	SUB	HURL (Hawaii)	USA	2,000 m
Alvin	SUB	WHOI	USA	4,500 m
Deepworker	SUB	Nuytco Ltd (for NOAA-OE)	USA	600 m
Johnson Sea Link 1	SUB	HBOI	USA	900 m
Hercules	ROV	IFE	USA	4,000 m
Jason	ROV	WHOI	USA	6,000 m
Tiburon	ROV	MBARI	USA	4,000 m

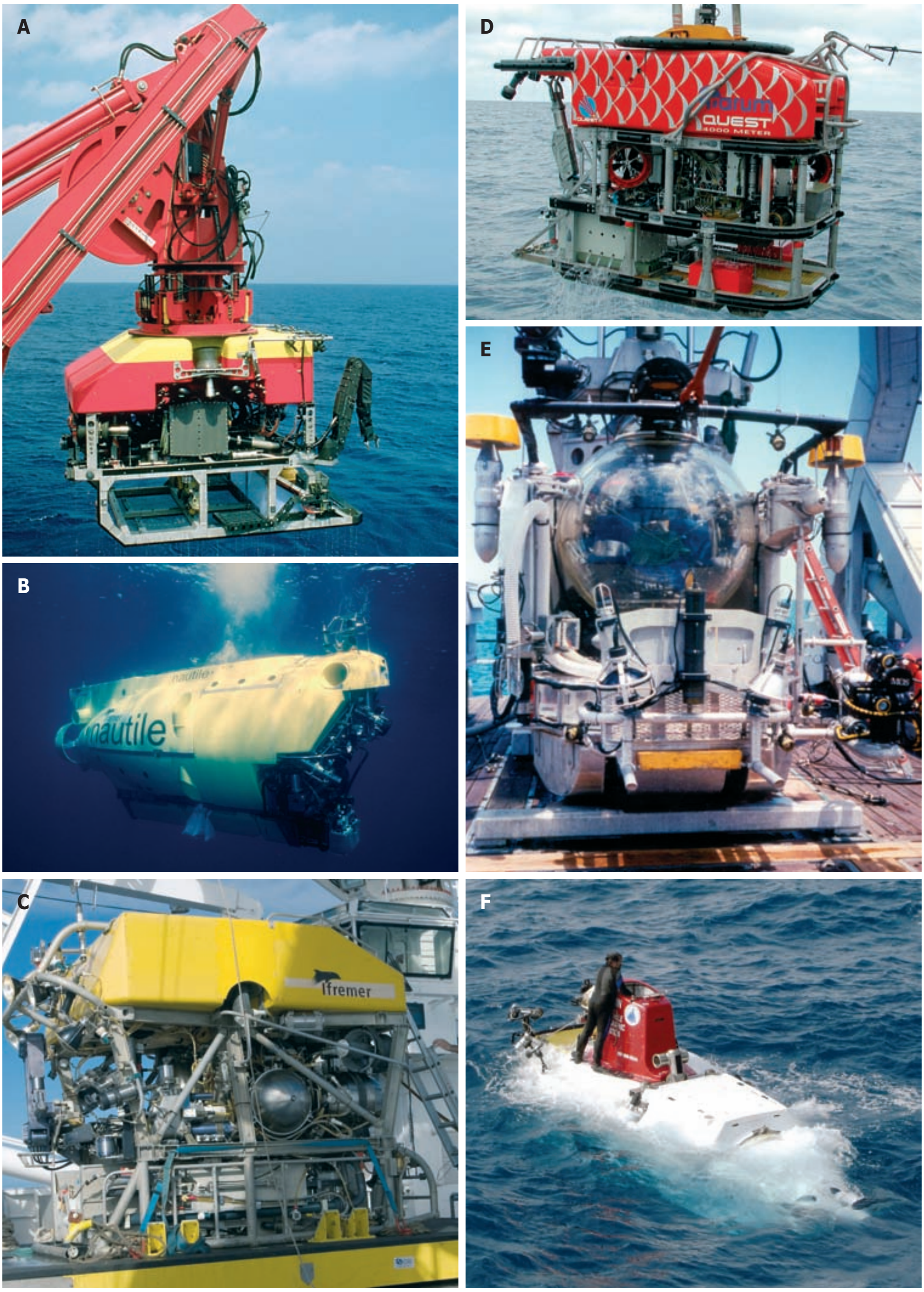


Photo 3.11: Examples of the international fleet of piloted submersibles and remote operated vehicles used for deep-sea research. A: British ROV *Isis;* B: French submersible *Nautile*; C: French ROV *Victor*; D: German ROV *Quest*; E: North American submersible *Johnson Sea Link*; F: North American submersible *Alvin*.

the exact location and first photographic evidence of new vent sites in a single exploratory cruise (photo 3.12).

The development of new technologies is also important in laboratory and analysis methodologies. For example, marine molecular techniques have been evolving rapidly. The molecular approach provides the necessary tools to identify cryptic species and discriminate between populations and metapopulations, as well as to measure gene flow and analyse phylogenetic relationships between species of different habitats, phylogeography and evolution (Shank, Lutz and Vrijenhoek 1999). Developments in stable isotope and biomarker analyses have also been essential in the study of the trophic structure of deep-water chemosynthetic communities. For example, stable isotopes have been used to differentiate between heterotrophic and chemotrophic feeding behaviours in chemosynthetic ecosystems (Van Dover and Fry 1994). In the case of biomarkers, these analyses have been used to understand the role played by the small holothurian *Amperima rosea* in the observed long-term faunal change in the Porcupine Abyssal Plain, NE Atlantic (Wigham, Tyler and Billett 2003).

Also, the use of hyperbaric chambers is very important when working with live deep-sea animals. Pressure chambers vary in size and capabilities, from

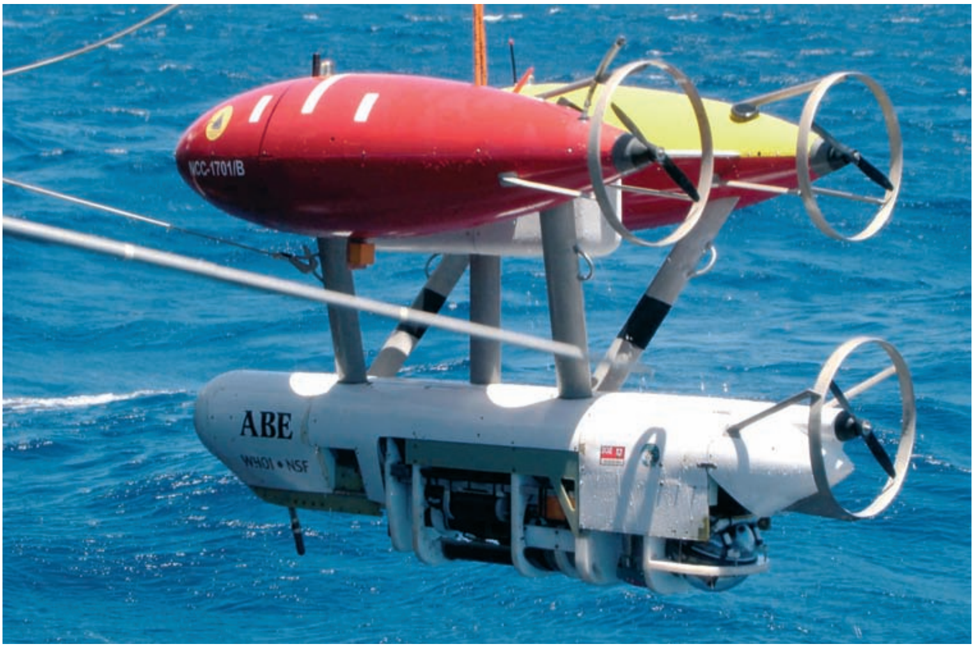


Photo 3.12: The underwater vehicle ABE from the Woods Hole Oceanographic Institution, USA

small, single chambers made of a titanium cylinder for embryological analyses (Young et al. 1996) to large equipment such as the French IPOCAMP (Incubateur Pressurisé pour l'Observation et la Culture d'Animaux Marins Profonds) that can be taken to sea, and where large invertebrates can be exposed to varying pressures and temperatures while their responses are visualised continuously (Shillito et al. 2001). This system has been used for experimental studies of hydrothermal vent fauna. One of the major challenges for deep-water research is to find new ways to collect fauna avoiding depressurisation and changes in temperature during recovery.

3.5. MAJOR EUROPEAN DEEP-SEA RESEARCH PROGRAMMES

Our knowledge of deep-sea ecosystems is at a very early stage, where exploration plays a major role. To understand the processes that drive the different deep-sea habitats as well as the functioning of the ecosystem as a whole, deep-sea research needs to be multidisciplinary. To achieve these objectives and mobilise efficient teams, an international approach involving both small and large countries with a range of capabilities is essential both for economic and scientific reasons. The exploration and investigation of the deep sea requires the use of large platforms (i.e., research ships, observatories) and the continuous refinement of state-of-the-art technologies (i.e., deep-water vehicles, laboratory methodologies, see section 3.4). Because of its remoteness and the logistics and financial constraints related to the study of the deep sea, the investigation of its ecosystems requires the development of international and multidisciplinary programmes that allow access to large-scale facilities and expertise across national boundaries. These issues are being addressed around the world by international and multidisciplinary research collaborations. Some examples are given below.

3.5.1. CoML (www.coml.org)

The Census of Marine Life (CoML) is a growing network of scientists in over 70 nations engaged in a ten-year initiative (2000-2010) for the assessment and understanding of diversity, distribution and abundance of life in the oceans; past, present and future (O'Dor and Gallardo 2005; Yarincik and O'Dor 2005). The CoML initiative is funded by the A.P. Sloan Foundation (NYC, USA). There are 14 field projects in the CoML that cover the major marine ecosystems, from the intertidal to the abyssal plains. Four of these projects are devoted to deep-sea research and, although international in nature, are led from European laboratories: ChEss (UK and Spain), MAR-ECO (Norway), CoMargE (France) and CeDAMar (Germany). The aim of ChEss is to study the biogeography of chemosynthetic ecosystems at the global scale. ChEss has four priority areas where field projects are being developed (see www.noc.soton.ac.uk/chess), and where international coordination and the sharing of human and infrastructure resources is essential. MAR ECO (www.mar-eco.no) is studying the pelagic and benthic non-chemosynthetic communities over the northern Mid-Atlantic Ridge. CoMargE (www.coml.org/descrip/c-margins.htm) focuses on the study of continental margins at the global scale, by comparing known data from past and ongoing projects, and developing new research. CeDAMar (www.cedamar.org) is studying life in, on and above the seafloor of abyssal plains. CeDAMar has a number of ongoing research projects in the Atlantic, Southern Ocean, Pacific and Indian Ocean. Furthermore, there are a number of other CoML projects that have direct scientific links to deep-sea research, such as the seamounts, microbes, Arctic and Antarctic projects. Finally, one of the long-term legacies of the CoML initiative will be OBIS, the Ocean Biogeographic Information System (www.iobis.org). OBIS is a web-based provider of global geo-referenced information on marine species for all data generated from CoML projects and other associated research programmes. It is a network of online databases integrated in a single portal.

3.5.2. MarBEF (www.marbef.org)

MarBEF (Marine Biodiversity and Ecosystem Functioning) is a Network of Excellence funded by the European Commission and composed of 78 European marine institutes. The aim of the MARBEF network is to integrate and disseminate knowledge and expertise on marine biodiversity, with links to researchers, industry, stakeholders and the general public. MarBEF has a deep-sea component (DEEPSETS, Deep-sea & Extreme Environments, Patterns of Species and Ecosystem Time-Series) formed by 11 European laboratories with excellence in deep-sea multidisciplinary research. Two PhD positions have been funded through DEEPSETS; one to study biodiversity and long-term change in abyssal metazoan meiofauna, and one to study biodiversity and long-term change in chemosynthetic communities. In parallel, workshops are organised on specific taxonomic groups and ecological issues, to ensure the transmission of knowledge from senior investigators to new, young scientists who will be leading research at the European level in the future.

3.5.3. HERMES (www.eu-hermes.net)

HERMES (Hotspot Ecosystem Research on the Margins of European Seas, 2005-2009) is an integrated project funded by the European Commission's Framework Six Programme and comprising 45 partners, including 9 SMEs, from 15 European countries. The project brings together expertise in biodiversity, geology, sedimentology, physical oceanography, microbiology and biogeochemistry for the study of hotspot ecosystems on continental margins. The main focus will be to determine the relationships between biodiversity and ecosystem functioning on sediment slopes in areas of land slides, deep-water corals, canyons, anoxic sediments driven by microbial communities and cold seeps.

HERMES will innovate by studying the whole European continental margin, allowing for the integration of data generated from a variety of disciplines in a range of geographical regions. This will facilitate comparison across contrasting but linked ecosystems, as well as providing the necessary data for management options across national boundaries. Research cruises, sampling and laboratory analyses will use state-of-the-art technologies and links are being established with other programmes such as ChEss and CoMargE from the Census of Marine Life.

3.6. MANAGEMENT AND CONSERVATION

The deep sea is the largest ecosystem on Earth and a reservoir of (still unknown) biodiversity. It is also one of the least studied habitats. But with the rapid development of new technologies, industries such as oil and gas exploitation, deep-water fishing or mining are rapidly entering deep-water territories. These human-based activities, as well as the use of the deep sea for dumping toxic material, are affecting a fragile ecosystem, in some cases before we even understand the diversity and functioning of faunal communities. Anthropogenic disturbance is especially important in the deep sea, because species often have long lives, with slow growth and delayed maturation, making recovery from disturbance a long process and even, in some cases, causing the extinction of a population. Some of the most endangered ecosystems are deep-water corals, seamounts and commercially fished species.

In the European Economic Zone, many areas of deep-sea fishing overlap with coral regions (Freiwald et al. 2004), and there is now evidence of important trawling damage to these ecosystems in the Atlantic. Fishing damage to deep-water coral reefs does not only lead to biodiversity loss, but also ecosystem destruction and therefore habitat loss, affecting a large number of species. This is especially important in an ecosystem with long-lived species for the reasons stated above. In recent years, several initiatives have been developed for the protection of deep-water corals. The Convention on the Protection of the Marine Environment in the North-East Atlantic (OSPAR Convention) identified deep-water corals as one of the most vulnerable ecosystems where action is required. Also, the EC granted emergency protection to an area of cold-water coral off NW Scotland (Darwin Mounds) in 2003, and in 2004 proposed a ban on bottom trawling around areas of coral reefs in the Azores, Madeira and Canary Islands, while in 2004 Canada's Department of Fishing and Oceans (DFO) ordered the the closure of a *Lophelia* area off Nova Scotia.

The hydrographic characteristics of seamounts give them a high productivity that attracts large animals, among which commercial fishes are often found. The result has been an increasing interest and exploitation of biological resources around seamounts, even before their ecosystems have been characterised and their biodiversity properly studied. This led the OSPAR Convention and the World Wide Fund for Nature (WWF) to recognise seamounts as biodiversity hotspots and a high priority for environmental management. New Zealand, Australia and Canada have taken steps towards the conservation and protection of these ecosystems, but no such protective measures are available in European waters. Deep-water fishing has also caused the near-collapse of commercial species populations in certain areas, such as orange roughy *(Hoplostethus atlanticus)* fisheries between 750 and 1,200 m depth over seamounts in New Zealand waters. These fisheries are now managed with strict catch quotas. To avoid overexploitation of commercial species as well as damage to the yet unknown deep-sea benthic habitat in the Mediterranean, the scientific community in collaboration with IUCN (World Conservation Union) and WWF obtained a legal ban on bottom trawling beyond 1,000 m and driftnet fishing, affecting all countries bordering the Mediterranean, as approved at the 29th session of the General Fisheries Commission for the Mediterranean (GFCM), held in Rome in 2005. This is known as the Principle of the Precautionary Approach, applied in this case to the protection of a rich but still unknown marine ecosystem comprising a variety of hotspot habitats such as cold seeps, deep-water corals, canyons, brine pools and seamounts.

The exploration and exploitation of hydrocarbons (e.g., gas, oil) is also moving rapidly into deeper waters. The effects of extraction platforms and exploitation processes on the surrounding ecosystems are still relatively unknown, but the oil and gas industries have been working more closely with scientists to obtain sound data on biodiversity and ecosystem functioning for the development of efficient management practices in potentially exploitable areas.

As regards the mining of regions in international waters, the International Seabed Authority is the UN agency in charge of developing rules, regulations and procedures for the exploitation of mineral resources in the "Area" (seafloor beyond the limits of national jurisdiction), with a view to their sustainable administration. The ISA will grant countries mining rights in specified areas (e.g., for polymetalic nodules, sulphur deposits, ferromanganese crusts), while keeping a percentage of the same for conservation. The ISA is working closely with both scientists and industry to provide the international community with regulations for the management of resources and conservation of ecosystems and biodiversity in the "Area".

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4. LIFE SUSPENDED IN WATER: THE PLANKTON

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4.1. INTRODUCTION

THE EARTH IS A WATERY PLANET, with 71% of its surface covered by oceans. A more appropriate name would have been the Blue Planet. The pelagic zone of the open ocean, away from the seabed and away from the coastline, is the largest habitat on the planet, comprising approximately 1347 million km^3. This enormous volume is inhabited by a diverse community of micro-organisms and metazoan animals – the plankton. The word plankton is derived from the Greek word for wandering and is used to describe the community of organisms that is transported around by the motions of the ocean currents and water masses. Planktonic animals can swim, but because they typically have a small body size, they cannot swim fast enough or far enough to move independently of the water mass within which they are found. There are planktonic species with large body size, including colonial salps of the genus *Pyrosoma* which may attain lengths in excess of 4 metres in tropical waters, and medusae such as the recently discovered big red jellyfish, *Tiburonia granrojo*, but these are exceptions and even with their large bodies they are not capable of independent motion against the flow of the water masses.

The pelagic water column is inhabited by a diverse and dynamic community comprising both holoplanktonic organisms, that spend their entire life in the plankton, and meroplanktonic organisms that are planktonic for only part of their lives. The meroplankton is dominated by larval forms and its composition varies strongly with the season, especially in temperate latitudes. Meroplanktonic larvae eventually mature and either become nektonic (capable of swimming against the flow of the water mass), for example fish larvae, or benthic (living on the sea floor), for example echinoderm or bivalve mollusc larvae. Planktonic organisms are patchily distributed in space and in time. This characteristic makes the study of plankton dynamics problematic: detecting change through time requires rigorous statistical analysis capable of picking

◀ **Photo 4.1: Blue whale *(Balaenoptera musculus)*.** This cetacean, the largest animal to ever inhabit the seas, feeds exclusively on plankton, particularly krill.

Photo 4.2: Antarctic krill *(Euphasia superba)*. These small planktonic crustaceans form the base of the food chain in Antarctic ecosystems.

out trends against a background of variability due to horizontal or vertical patchiness.

Planktonic systems are largely driven by the capture of solar energy by photosynthesis, which is confined to the well-lit surface waters where light levels are adequate. Primary production, both by eukaryotic algae and by photosynthetic bacteria, can also be dependent on nutrient levels, the low availability of which may limit primary production even in well-lit waters. Ocean circulation patterns, stratification of the water column, and upwelling events can all have a profound effect. Plankton is found at the greatest abundance in near-surface waters but occurs throughout the water column, down to the deepest ocean trenches. Below the depth where net primary production ceases, planktonic organisms utilise marine snow – organic material sinking out from the upper horizons of the water column. The flux of sinking material is seasonal in temperate zones and a discrete seasonal pulse of material has been detected entering the abyssal zone after the spring bloom in the northern hemisphere. So changes at the surface can affect processes in deep water on relatively short time scales.

4.2. KEY CHALLENGES

The scientific and technical challenges facing researchers working on the plankton are essentially the same as those facing marine biology as a whole. The three key challenges are:

- Discovery: to search for unknown life forms and survey new habitats to identify areas of particular importance
- Understanding: to make observations and undertake experiments at all temporal and spatial scales
- Prediction: to develop models to allow us to predict future changes in marine systems in response to environmental change, whether natural or anthropogenic.

Running across all these challenges are issues of scale, in particular the need to integrate data from the ultra-small scale of molecular biology up to global scales using remote sensing data from Earth observation satellites. In addition we need to be able to generalise across scales, working from observations on individuals or local populations up to ocean basin or global scale processes.

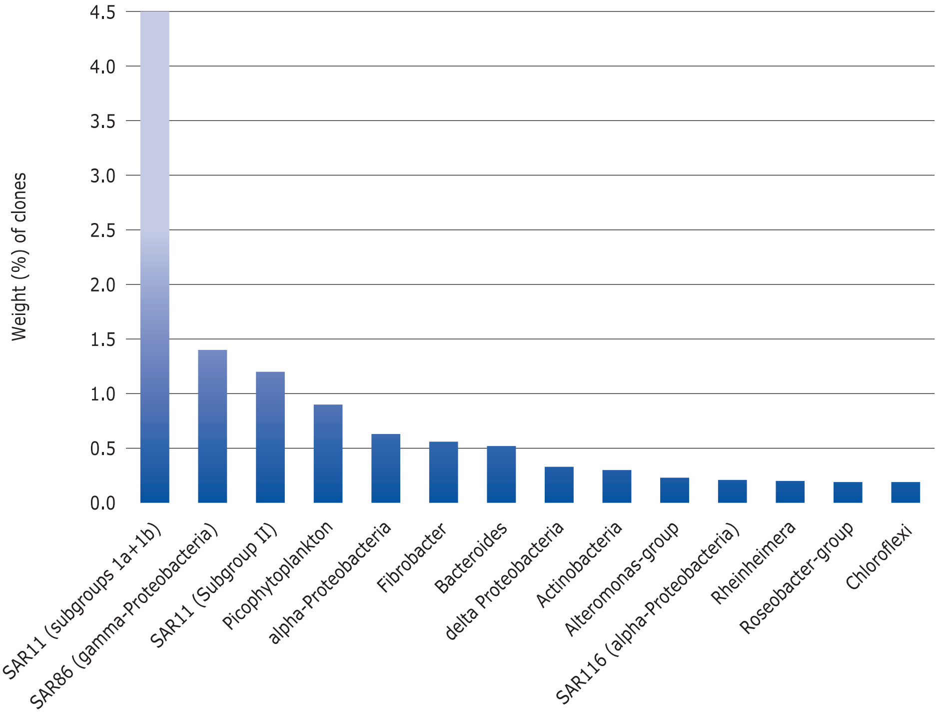
4.2.1. Discovery

In 2004 Craig Venter and colleagues, using shotgun sequencing, examined the genes present in samples of water from the Sargasso Sea, finding 1,214,207 new genes and approximately 1,800 new species of microbial organisms (figure 4.1). The scale of these discoveries indicates that up to 99% of the diversity of life in the oceans may still remain to be discovered, and that most of it is microbial!

Such discoveries of new marine micro-organisms are not restricted to near-surface waters. Green sulphur bacteria are anaerobes (organisms that grow and reproduce in the absence of molecular oxygen) that require light for growth by the oxidation of sulphur compounds to reduce CO_2 to organic carbon, but they are capable of photosynthetic growth at extremely low light intensities. New kinds of green sulphur bacterial species have just been described from a deep-sea hydrothermal vent, where the only source of light is geothermal radiation that includes wavelengths absorbed by photosynthetic pigments of this organism.

Smaller still than the bacteria are marine viruses. Viruses are extremely abundant in the plankton and have been estimated to be the second largest

Figure 4.1. Bacterial diversity in the Sargasso Sea



Source: Venter et al., 2004.

component of oceanic biomass after the bacteria. In coastal waters, there may be about 10^7 viruses in one millilitre of seawater, but this abundance decreases both with increasing depth and distance from the shore. Not only are marine viruses abundant but they also exhibit immense genetic and biological diversity.

It is not just the marine microbial organisms that are poorly known. It is estimated that there are also thousands of new animal species awaiting discovery, and many other recognised species where the application of novel methods of study is refining our concept of species boundaries. For example, it is now becoming apparent that some of the so-called cosmopolitan species of marine zooplankton are in fact complexes of closely related species, each predominant in a particular ocean basin. Molecular methods have revealed these problems, but careful morphological study can also help to solve them.

The plankton in deeper oceanic waters has been relatively poorly studied: the oceans are vast and few vessels are equipped to sample in midwater at depths in excess of 2,000 metres. The abundance of the zooplankton decreases with increasing depth, but rises again in the near-bottom waters. This depth zone at the base of the water column, referred to as the hyperbenthic, is a region of dynamic interaction between the water column and the sea bed, but it is difficult to sample. Nets must be towed very close to the bottom (ideally only 1 metre above the sediment), without colliding with it. Successful sampling in the hyperbenthic has demonstrated that it is home to numerous new species: for example, of copepods; diminutive crustaceans (relatives of crabs and shrimps), which typically have a body length of only 1 to 2 mm. The hyperbenthic is a rich source of new species, new genera and even new families of copepods, but obtaining good samples remains one of the most serious sampling challenges in deep-sea biology.

Much larger zooplanktonic species are still being discovered. Off the coast of California, a blood-red jellyfish, *Tiburonia granrojo* (photo 4.3), has been observed several times in Monterey Submarine Canyon at depths of 645 metres and more. Thus far only a single specimen has been caught, but these predators range in size between 60 and 90 cm in diameter. An unusual feature of this new species is that it lacks tentacles around the margin of its bell-shaped body,

Photo 4.3: *Tiburonia granrojo.* The "Big Red" jellyfish, which grows up to 90 cm, was recently discovered off the eastern Pacific coast of the United States.

which are used to catch prey in most jellyfish. Instead it has between four and seven thick wrinkled arms on its under surface.

Using an astonishing range of techniques, from DNA extraction of water samples to nets on the robotic arms of manned submersibles, marine biologists continue to find remarkable new forms of life. These may range in size from the smallest microbial organisms with body sizes measured in microns, to large animals measuring nearly a metre in length. It is safe to assume that many novelties await discovery in the vastness of the pelagic realm.

4.2.1.1. Hotspots

The concept of biodiversity hotspots as areas of exceptional biotic richness set against a background of relatively low diversity has been widely adopted as a method of identifying priority areas for conservation programmes. Relatively few such hotspots have been identified for the marine realm, apart from coral reefs and the hydrothermal vents and cold seeps that are described in chapter 3. In part, the difficulty in applying the hotspot concept to the plankton reflects the lack of obvious physical barriers in the oceans. However, recent research has shown that the plankton of flooded marine and anchialine caves is remarkably rich in novel animal species.

Anchialine habitats are flooded coastal caves and groundwater habitats that lack any direct surface connection with the open sea. They are inhabited by remarkably specialised animals, many of them representing long-term survivors of ancient lineages, which are now threatened by changes in their fragile habitat. In the past 25 years, over 250 new species, at least 17 new families and even a new class of shrimp-like crustaceans – the Remipedia – have been described from the plankton in anchialine caves (photo 4.4), particularly on tropical and subtropical islands.

This extraordinary degree of novelty qualifies anchialine habitats as uniquely important. An extremely high proportion of the crustaceans inhabiting these caves can be regarded as living fossils. Studies on such primitive animals have shed new light on the evolutionary history and relationships of many groups of animals. The animals living in the caves also have unusual genetic properties, such as the ability to survive in water with very low levels of dissolved oxygen. The powerful techniques of modern genetics mean that uniquely adapted animals such as these are a potential source of genes.

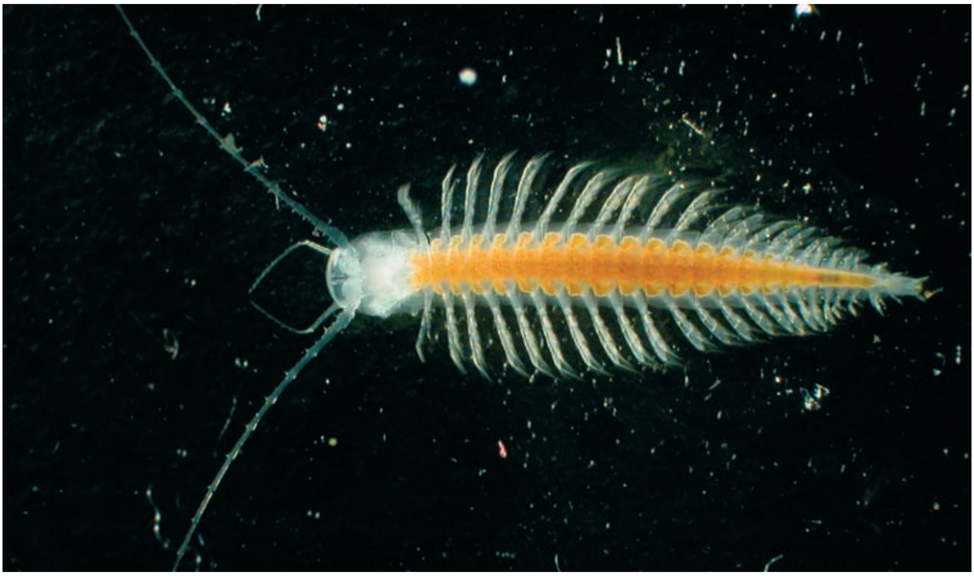
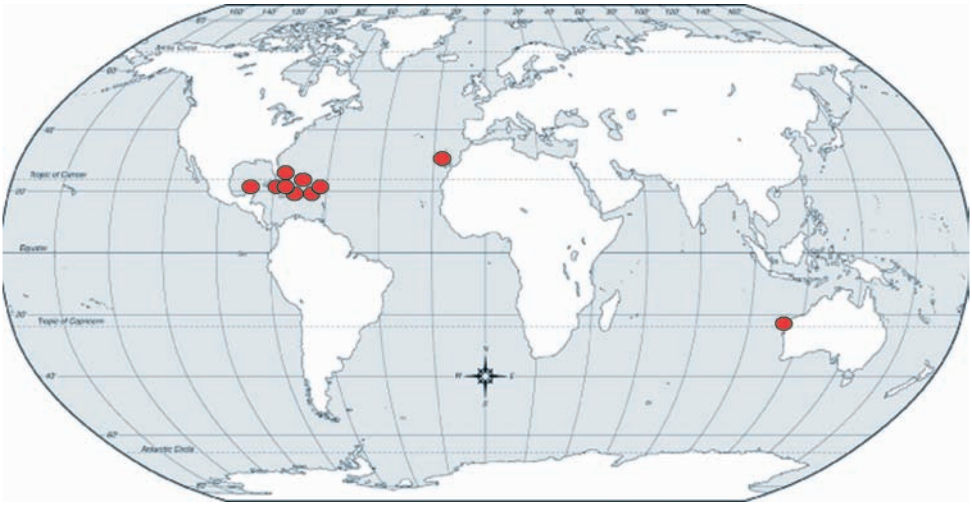


Photo 4.4: Remipede from anchialine cave on the Exumas Cays, Bahamas. There are only 16 species of remipedes known worldwide and all occur only in anchialine caves.

The exploration of caves is still in its infancy, and there are significant gaps in our knowledge and in our understanding of how the caves were colonised and where the colonists originated. For example, the known distribution pattern of remipedes is remarkable: fourteen of the sixteen species occur on Caribbean islands and the Yucatan peninsula (map 4.1). Two other species are known: one

Map 4.1: Known distribution of remipede species



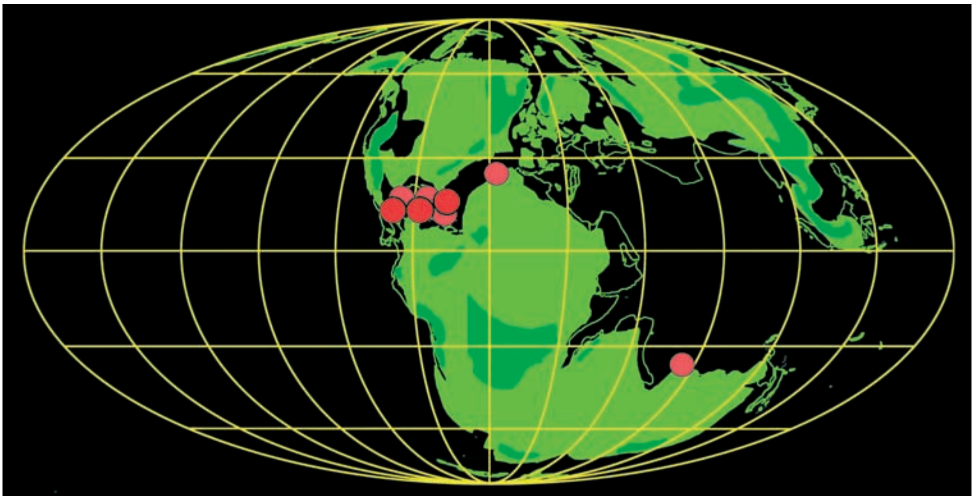
from a flooded lava tube in Lanzarote in the Canary Islands, the other from a cave in Western Australia. Other crustacean components of the anchialine faunal suite, such as thaumatocyprid ostracods, epacteriscid and speleophriid copepods, each display very similar patterns. How can we explain such extremely disjunct distribution patterns?

The emerging hypothesis to account for the remarkable distribution of remipedes and other members of the fauna implicates tectonic plate movements over geological time periods (map 4.2).

The suggestion is that the anchialine fauna was widely distributed around warm, shallow margins of the ancient Tethys Sea. Elements of the fauna then colonised caves from adjacent shallow water and were subsequently separated when tectonic plate motions resulted in the opening of the Atlantic Ocean and the eventual closure of the Tethys Sea. The fauna must have persisted in cave systems at these sites through geological time scales and through major changes in global sea-level, and it is likely that the cave systems served as thermal refuges for relict fauna during the last Ice Age, for example. These ideas can be tested relatively simply using molecular methods, but this has not been possible to date because of the difficulty in sampling many of the caves.

It is imperative that we locate and explore new anchialine sites around the world and describe their inhabitants before it is too late. This research will help us to answer topical ecological and evolutionary questions, such as, where did these

Map 4.2: A reconstruction showing the distribution of remipede sites relative to the positions of landmasses 120 million years ago, during the Jurassic period



uniquely primitive cave faunas originate, and how were their amazing distribution patterns generated. We must also undertake a threat assessment for the most important major anchialine sites, and then promote the inclusion of anchialine habitats in coastal management to policy makers and conservationists.

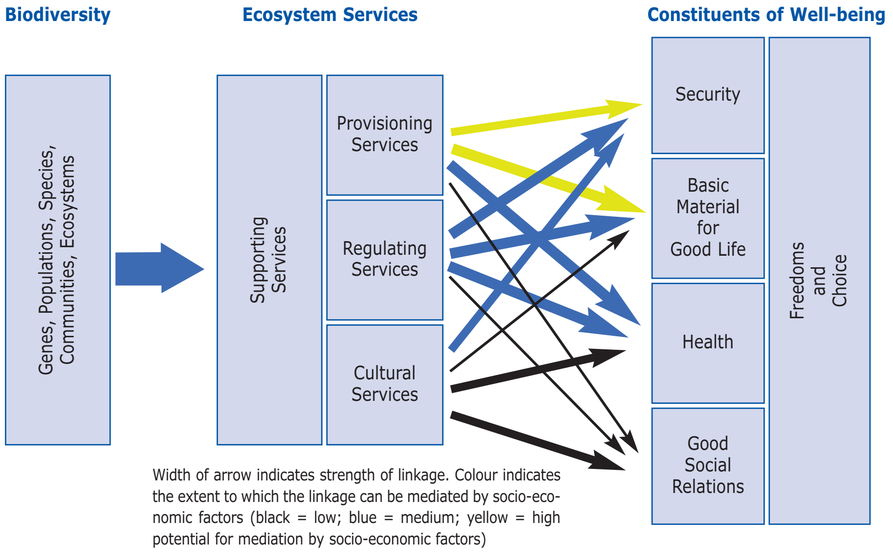
The discovery of new species and new distribution patterns contributes to the development of knowledge on oceanic systems. It allows us to build the baseline assessment of what occurs where in the oceans. This baseline assessment is an essential initial step, since it will provide the benchmark against which changes can be monitored and measured.

4.2.2. Understanding

Our improved understanding of ecology and of global-scale cycles in all kinds of elements and resources has resulted in a conceptual change in how we view the Earth's ecosystems. In part, this change has emerged from a novel way of quantifying the dependence of humankind on the provision of services and functions by the world's natural ecosystems (Costanza et al. 1997; figure 4.2).

Ecosystem services have been categorised into provisioning services, such as the provision of food for human consumption, regulating services such as the

Figure 4.2: Linkages among biodiversity, ecosystem services, and human well-being



Width of arrow indicates strength of linkage. Colour indicates the extent to which the linkage can be mediated by socio-economic factors (black = low; blue = medium; yellow = high potential for mediation by socio-economic factors)

Source: *Millennium Ecosystem Assessment*, Washington, DC, World Resources Institute, 2005.

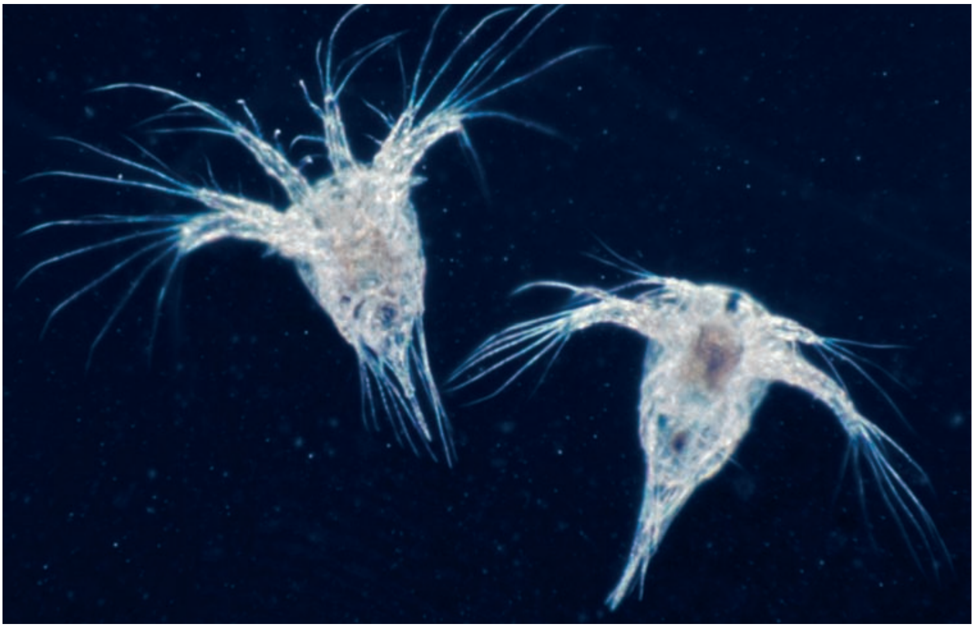


Photo 4.5: Larvae of *Semibalanus balanoides.* Many bottom-living organisms have larval stages that are temporary members of the plankton community, such as these naupliar larvae of acorn barnacles.

role of the ocean in climate regulation (the transport of heat northwards in the Atlantic by the Gulf Stream), cultural services, such as ecotourism activities like viewing whales, and supporting services, such as gas regulation in the atmosphere. The oceans in general and the vast pelagic-planktonic system are pivotal in the provision of many of these ecosystem services and functions upon which continued human well-being depends.

Mankind has generally taken such ecosystem services for granted, but recent improvements in our understanding of Earth Systems have strongly emphasised our dependence upon natural systems for the oxygen we breathe, the food we eat and the water we drink. All living organisms and the biosphere they inhabit interact as components of a vast global system, and the dynamics of this system are studied in terms of how matter flows through them – as global biogeochemical cycles.

4.2.2.1. The carbon cycle and photosynthesis

Oceans play an integral part in the natural processes of cycling carbon on a global scale – the carbon cycle. Over the past 200 years, since pre-industrial times, it is estimated that the oceans have absorbed about half of the CO_2 emissions produced by burning fossil fuels and cement manufacture. The oceans and the organisms they support contain an estimated 38,000 gigatonnes of carbon, which account for about 95% of all the carbon that is in the oceans, atmosphere and terrestrial system combined. So, the oceans contain an enormous reservoir of carbon, but their capacity to absorb CO_2 from the atmosphere will reduce as the level of atmospheric CO_2 rises.

The abundance of life on Earth is almost entirely supported by biological photosynthesis, which uses light energy to fix CO_2. The primary source of light in natural habitats is the sun, so photosynthesis is largely, but not exclusively, restricted to solar photic environments on the surface of the Earth. The marine eukaryotic phytoplankton, especially the diatoms and to a lesser extent the dinoflagellates, were long considered the dominant photosynthetic organisms in the oceans. However it has recently been discovered that bacterial photosynthesis occurs on a large scale in the oceans. Craig Venter et al. (2004), for example, found a total of 782 Rhodopsin-like genes in the Sargasso Sea. Rhodopsin-mediated photosynthetic production by bacterial plankton may have significant effect on energy and carbon fluxes in the oceans.

The role of marine plankton in global biogeochemical cycles is becoming more widely understood (Raven and Falkowski 1999). The photosynthetic activity of the bacterioplankton and phytoplankton serves to fix carbon, which is then available to other consumer organisms in the plankton. Size is important here – as a determinant of whether the primary production flows into the microbial foodweb, or the traditional food web in which the larger phytoplankton are consumed by zooplankton which are, in turn, consumed by fish.

Microbial foodwebs are based on photosynthetic organisms, the so-called picoplankton, that are so small that most of the organic matter produced cannot be used by zooplanktonic herbivores such as the copepods. This matter is transferred through bacteria, small heterotrophic flagellates and ciliates. This kind of food web appears to be the most common in the oceans, especially in stratified and oligotrophic (low productivity) regions, where it is responsible for driving most of the transfer of energy and matter in the epipelagic zone. The tight coupling between consumers and producers is a characteristic feature of microbial food webs, resulting in a dominance of processes that recirculate energy, rather than processes that export energy and matter from the system. These two kinds of foodwebs coexist and are interconnected. Small zooplanktonic copepods are of potential importance in linking these foodwebs. Firstly, their small body size suggests that they are able to graze on smaller organisms, such as the smallest nanoplanktonic fraction, thereby bypassing several trophic levels. Secondly, in contrast to medium and large-sized copepods, which produce large faecal pellets that can sink out of the photic zone and thus export carbon out of the surface waters, small copepods produce small faecal pellets. These have low sinking rates, and are probably consumed before sinking out of the euphotic zone. Finally, some copepods, such as species of the genus *Oncaea*, graze on marine snow and others, such as species of *Oithona*, feed on the faecal pellets of other zooplankters. In effect this enhances the recycling processes in the upper water layers and retards the vertical export of matter and energy.

The movement of carbon from the surface to the depths is known as the biological pump – the sum of the biologically-mediated processes that transport carbon from the well-lit euphotic zone to the interior of the ocean. The scale of the biological pump contributes to the oceans being the largest active pool of carbon on the planet. There is also an inorganic component to the flux of carbon exported to deep ocean waters, in the form of calcium carbonate shells or plates produced by planktonic organisms such as coccolithophores (photo 4.6) and foraminiferans.

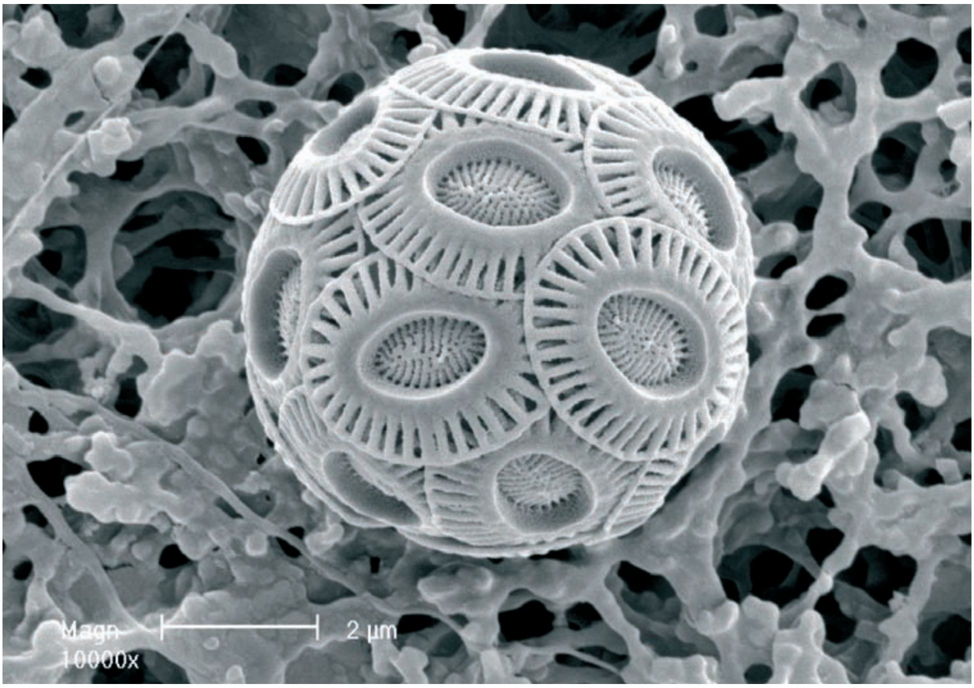


Photo 4.6: Coccolithophore *Emiliana huxleyi* through the microscope. This scanning electron micrograph shows the array of complex calcium carbonate plates (liths) covering the alga's outer surface.

Photo 4.7: Satellite image showing extensive blooms of coccolithophore algae off the coast of France and the UK

Under certain conditions coccolithophore algal blooms occur (photo 4.7) and large quantities of inorganic calcium carbonate (in the form of liths) are produced. The calcium carbonate dissolves at a rate dependent upon local carbonate chemistry, involving factors such as temperature and depth. However, these dissolution processes are generally slower than synthesis. Overall the biological pump transports material from the ocean surface to deeper waters.

4.2.2.2. THE NITROGEN CYCLE

The oceans are also pivotal in the global nitrogen cycle. It has long been known that the oceans contain nitrogen-fixing cyanobacteria, and the filamentous *Trichodesmium* (photo 4.8) was assumed to be the predominant organism responsible in the oceans. However, the abundance of *Trichodesmium* was unable to account for the rates of fixation observed. Recent studies (Zehr et al. 2001) have found evidence of abundant unicellular cyanobacteria in the size range 3 to 10 µm, which express nitrogenase enzymes – an indication of their nitrogen-fixing ability. These picoplanktonic organisms have not yet been

Photo 4.8: Colony of *Trichodesmium* filaments, a large photosynthetic and nitrogen-fixing cyanobacterium

fully studied but these results seem to indicate the existence of a different pathway in the foodweb from other nitrogen-fixers.

The opposite function – the conversion of nutrients into nitrogen gas – is performed by other picoplanktonic bacteria. Recent work has revealed that much of this reverse conversion is not carried out by denitrifying bacteria converting nitrate to nitrogen gas in the absence of oxygen, as formerly believed, but by anammox bacteria (photo 4.9) that directly remove ammonium from the ocean (Kuypers et al. 2005).

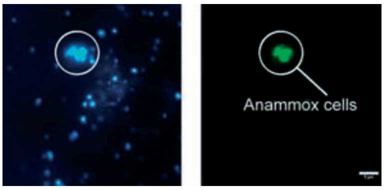


Photo 4.9: Flourescent micrographs showing *Anammox* bacteria. The term *Anammox* refers to the process of anaerobic ammonium oxidation.

These bacteria, discovered first in the oxygen poor waters of the Black Sea, have now been found in the open ocean, in oxygen-poor areas of the South Atlantic where upwelling occurs off the coast of Namibia, and it has been calculated that 30% to 50% of the global conversion of nutrients to nitrogen gas occurs in these areas. This discovery has major consequences for our understanding of the global nitrogen cycle. And, in this complex interconnected Earth system, this change in the global nitrogen budget has knock-on effects for the global carbon cycle.

Due to its large colony size, *Trichodesmium* is the most conspicuous of the marine nitrogen-fixing organisms. Its colonies manage to thrive in the nutrient-poor, open ocean, pelagic environments in which levels of the essential element phosphorus are extremely low. One factor in its success is the recently discovered ability to exploit phosphonates, previously thought to be unavailable to phytoplankton, as a source of phosphorus. In doing so, *Trichodesmium* increases the bioavailability of phosphorus to other planktonic organisms in both the microbial and traditional foodwebs. With its dual role in both the carbon and nitrogen cycles, *Trichodesmium* has become a model system for the study of plankton physiology: these new discoveries indicate that detailed study of the diversity of microbial primary producers will reveal a similar diversity in basic physiological processes.

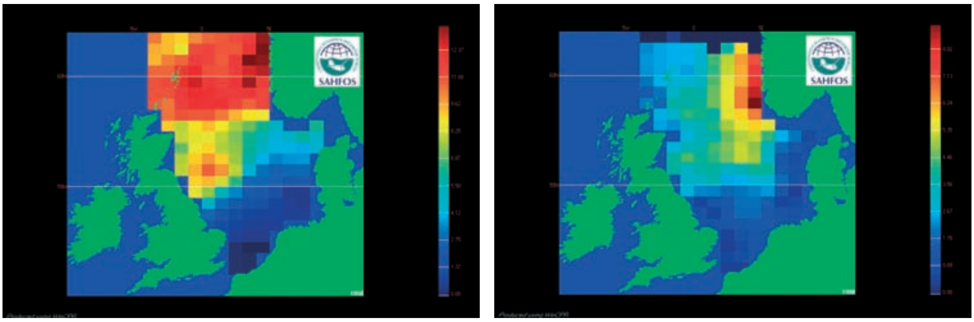
Marine viruses are a significant cause of planktonic microbial mortality and, as such, also play a role in marine nutrient cycles. Viruses act as catalysts accelerating the transformation of nutrients from a particulate state (i.e., living micro-organisms) to a dissolved state, from where they can be readily incorporated back into the microbial community. This so-called viral shunt has the effect of decreasing the efficiency of the transfer of carbon to higher trophic levels, of increasing community respiration and, indirectly, of reducing the export of carbon from the euphotic zone into deeper waters. Even the smallest of micro-organisms can thus have a significant impact on global biogeochemical cycles.

4.2.2.3. Drivers of change: detecting and monitoring change

There is considerable concern over potential changes in marine biodiversity and ecosystem functioning in response to global climate change. Planktonic organisms are particularly useful as ecological indicators, and detailed study of patterns of variation in plankton can help us distinguish between natural variability and anthropogenic change. Using long time series data from the Continuous Plankton Recorder survey, it has been possible to demonstrate shifting biogeographical patterns in the North Atlantic. It is apparent that several sub-tropical plankton species are shifting their distributions northwards in response to global warming; at the same time some northern species, such as the abundant copepod *Calanus finmarchicus*, are retreating pole-wards from more southerly locations (map 4.3). Recent research (Beaugrand et al. 2002) has shown a 10° latitudinal northward shift for warm-water copepods, with a corresponding retreat of cold-water species.

Long-term data sets for marine organisms are rare. The CPR survey has been undertaken, with minor interruptions, for over 70 years and is the longest running and most comprehensive series anywhere in the world. Research funding agencies often fail to recognise the immense value of time series data and many

Map 4.3: Gridded distribution of *Calanus finmarchicus* in the North Sea



Comparison of 1958 (left) and 1988 (right) distributions showing the northerly retreat of this cold-water copepod.
Source: Vezzulli et al., 2005.

series are under threat – despite the unique perspective they provide on environmental change issues. One of the practical challenges for marine biologists is to secure the future of such surveys.

Another fascinating finding that has emerged from long time series CPR data is the disruption of the planktonic foodweb resulting directly from global warming during the latter half of the 20th century. The traditional foodweb begins with phytoplanktonic diatoms which are consumed by copepods, which are extremely efficient at catching algal cells. The copepods are then eaten by secondary consumers in the food chain, including most larval fishes, such as cod, and some adult fishes, such as herring. In the temperate North Atlantic during winter, diatoms are relatively inactive: light levels are low so photosynthesis rates are low. In the spring, light levels increase, the levels of nutrients such as phosphates and nitrates are high since the water column is well mixed by winter storms, and the diatoms begin to bloom. The spring algal bloom provides an enormous resource, a massive input of biomass and energy into the planktonic system. The spring algal bloom is closely followed by a peak in zooplankton abundance. The zooplanktonic copepods reproduce rapidly, exploiting the available algal biomass. Fish larvae then feed on the larger and longer lived copepods. Recent research (Edwards and Richardson 2004) has shown that the timing of the spring algal bloom is governed by day-length, and has not changed significantly in response to global warming. In direct contrast, the timing of peak zooplankton abundance responds to temperature, and has gradually been occurring earlier in the year as ocean temperatures have risen. There is a temporal mismatch in the system and the zooplankton are now reproducing

Photo 4.10: Tunid fisheries. Tunids are a high value marine resource, but the lack of regulation of fisheries in international waters has dramatically reduced catches: marine protected areas on the high seas are urgently needed.

too early, slightly in advance of the algal bloom – their food supply. The organisms making up this system have co-evolved over millions of years but the system is now under stress.

Living organisms are highly adaptable but the rate of change due to global warming is unprecedented. The planktonic system is failing to adapt. The lack of available copepods as food for larval fishes will have consequences for recruitment to fish stocks and, indeed, this mismatch between trophic levels and functional groups has already been implicated as a factor in the failure of the North Sea cod stock to recover despite efforts to control fishing intensity (Beaugrand et al. 2003). The plankton ecosystem will not entirely collapse as a result of such changes. The spring algal bloom will remain a massive resource and organisms will move in to exploit it – but these organisms may be integral components of the microbial foodweb, or they may be unsuitable as food for fish larvae. The danger is that the planktonic system may have irreversibly changed. We can predict with reasonable certainty that the system will not behave as it has done for recent centuries, and this will have profound implications for the fishing industry. Such predictions tend to be applicable only to a single system in a particular region, and we need to progress to larger scale and more rigorous predictions. In order to achieve this, it will be necessary to develop new time series that provide a network of sampling points around the world and allow us to build a more coherent picture of the state of the oceans.

Another driver of change, even in marine planktonic systems, is invasive species. Non-indigenous gelatinous zooplankton species have been introduced in various regions, and have been implicated in major changes to semi-enclosed ecosystems. For example, the predatory ctenophore *Mnemiopsis leidyi* was introduced into the Black Sea in the early 1980s, probably in ship ballast water. A massive increase in its abundance was followed by sharp declines in mesozooplankton and in ichthyoplankton (eggs and larvae of sprat and anchovy) (Kidneys 2002). Interestingly the explosive increase in *Mnemiopsis* was preceded by a reduction in the numbers of plankton-feeding fishes by overfishing. The reductions in these fishes, which are the main competitors for *Mnemiopsis*, could be a possible reason for the outbreak, demonstrating again the vulnerability of stressed systems.

Blooms of gelatinous zooplankton have become increasingly common, and deleterious effects have been reported on ecosystems and fisheries in eastern Mediterranean waters, off Japan and in the North Sea. Similarly, the increase in jellyfish biomass in the Bering Sea, dominated by *Chrysaora melanaster*, is predicted to have effects on groundwater fisheries. Species dominance patterns may change in time but sudden changes, such as jellyfish blooms and invasions, are likely indications of ecosystem instability. In addition, our emerging understanding of the role of rare species in ecosystems indicates that their weak trophic links may serve to enhance the stability of the entire foodweb. An important challenge is to develop the theoretical basis of the relationship between stability and species diversity in marine planktonic systems. Existing theory, developed using terrestrial model systems, does not translate well into the marine environment, and we need to better understand why some marine systems are more vulnerable to invasion than others and why rare species can suddenly become common.

4.2.3. Prediction

As well as continuing to document and describe the living components of the global ocean, and as well as continuing to improve our understanding of their interactions and their role in the global biogeochemical cycles, we need to use the products of this research effectively. In particular, we need to make long-term observations and measurements, and to incorporate them into developing models which will allow us to predict how abiotic factors such as global warming, sea-level rise, and acidification (due to rising CO_2) might cause changes in the plankton. It is already possible to obtain satellite data on a global scale for factors such as sea surface temperature (map 4.4), surface chlorophyll, and carbon export. The integration of these global measures with more regional and local biological data is an important area of active research.

The development of large-scale predictive models of climate change has been an enormous asset to the world community of climatologists. The International Panel on Climate Change increasingly relies on complex models, run on supercomputers, for prediction of the effects of global warming on regional climates for decades to come. These models have enabled them to effectively communicate ideas on the behaviour of complex systems to the public and to policy makers, and even to communicate the levels of uncertainty associated with the predictions. In the arena of biological oceanography, the biggest challenge we face is to develop complex models that will enable us to make robust predictions about how the planktonic system will change, and whether the oceans will continue to provide the ecosystem services upon which continued human well-being depends.

Map 4.4: Global sea surface temperature. On a rising scale from violet (approximately 0ºC) to red (approximately 28ºC).

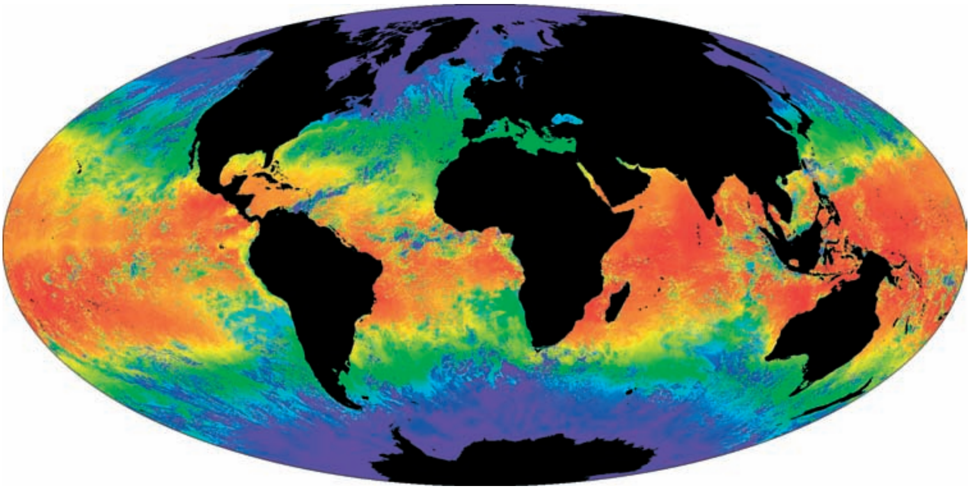


Photo 4.11: Jellyfish *(Cotylorhiza tuberculata)*. In open pelagic waters, large gelatinous plankton like this jellyfish provide shelter and a focal point for the behaviour of small fishes.

4.3. SUMMARY

It is remarkable how poorly we understand the biology of the oceans that surround us. In view of their vastness, perhaps it is not surprising that our knowledge of the microbes that inhabit the oceans is fragmentary, but the development of new molecular methods of study has provided powerful tools that are already beginning to reshape our ideas. Microbial life in the oceans is far more diverse than hitherto realised, and the diversity of microbial physiology is changing established concepts of the processes by which material flows through the global biogeochemical cycles. In functional terms, it has become clear that the microbial foodweb is of at least equal importance to the traditional diatom-copepod-fish dominated foodweb. The final goal of marine biological research must be to develop models that will encapsulate our knowledge of the planktonic biodiversity and our improving understanding of how planktonic systems function. These models will allow us not only to predict change but, more importantly, to use our knowledge in sustainably managing and using the oceans for the benefit of mankind long into the future. The scientific challenges we face in getting to that position are:

- To document and describe the diversity of life, including microbial life, in the plankton
- To explore and study unique biodiversity hotspots, such as flooded marine caves
- To understand the functional role of biodiversity in global cycles
- To measure how biodiversity is changing over time and to develop a global network of observation sites
- To identify the drivers of change in the plankton
- To develop robust models of how the planktonic system will change in response to environmental change at regional and global levels.

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5. MARINE GENOMICS AND THE EXPLORATION OF MARINE BIODIVERSITY

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5.1. INTRODUCTION

THE OCEANS COVER approximately 70 percent of the Earth's surface. Apart from providing a third of the oxygen that we breathe and acting as moderators of global climatic change with a significant influence on the human population's terrestrial environment, these vast expanses are also an important source of high-protein food. Marine and coastal environments include many diverse pelagic and benthic habitats such as open-ocean ecosystems, deep-sea communities including thermal vent ecosystems, kelp forests, mangroves, coral reefs, etc. Although these varied environments support a rich abundance of life, marine biodiversity has received much less attention than its terrestrial counterpart. This may be because the oceans have historically been thought of as regions of low biodiversity and because of difficulties with accessing marine environments. In fact, by some measures, biodiversity in the oceans is greater than on land. Marine biosystems have been evolving for an additional 2.7 billion years compared to terrestrial environments, and almost all the currently described phyla are represented in the ocean while only about half have terrestrial members. The phylogenetic diversity of marine organisms is, therefore, much broader than that of their terrestrial counterparts (Ray 1988). Marine biodiversity may also be greater on a functional level, in the sense that marine organisms have adopted many novel survival strategies for which there is no equivalent amongst their terrestrial counterparts, such as microbes and animals associated with hydrothermal vents.

There is a pressing need for a more detailed understanding of marine biodiversity in oceans, and particularly in coastal areas, as they come under increasing threat from pollution, over-exploitation and badly planned development programmes. These threats take many forms such as the direct effects of chemical pollution, eutrophication, over-fishing and physical alterations to the coastline, together with the indirect effects of global climate change and the intro-

◀ **Photo 5.1: Giant kelp *(Macrocystis pyrifera)*.** This alga has gas-filled bladders known as pneumocysts that keep it floating upright near the surface. The genome of the species is currently being explored by a consortium of US and European pharmaceutical companies.

duction of exotic species. As a result of this sort of activity many areas have been degraded and over-exploited beyond repair, with coral reefs and mangroves being particularly at risk. The mounting concern about these problems has led to an increase in the number of international instruments aimed at addressing the threats to marine and coastal biodiversity, and at protecting and using marine resources sustainably. For these instruments to be effective, however, the threatened ecosystems need to be understood in more detail. Studies need to be more than censuses of the organisms present in individual biosystems, and should include information about the genetic structure of the populations of organisms that make up a biosystem, about functional aspects of interactions within ecosystems and about the ability of populations to adapt to changing conditions. Several tools are available for this type of study. This article looks at how techniques developed within the new discipline of genomics can be applied to the study of marine diversity, concentrating particularly on coastal biodiversity. We focus primarily on eukaryotic organisms, which, because of their often large genome sizes, represent the greatest challenge for the application of these techniques.

5.2. GENOMIC PROGRAMMES AND MARINE BIOLOGY

Genomic approaches are expected to provide essential information for studying, monitoring and exploiting biodiversity in the oceans. In this respect, the remarkable diversity of life in the sea can be viewed both as an advantage and as a disadvantage for marine biologists. On the positive side, this diversity holds the promise of a great richness at several levels, from ecosystems down to genes. From a more practical point of view, however, the problem arises as to how methods can be developed for studying such a wide range of ecosystems and organisms. This problem becomes particularly acute when the aim is to apply genomic approaches, because large-scale analyses of this sort are difficult to apply across a broad range of organisms.

The field of genomics was initially developed by biologists working on the biology of terrestrial species, and one key factor in the emergence of this discipline was the existence of well-defined and intensely studied model organisms such as baker's yeast *(Saccharomyces cerevisiae)*, the fruit fly *(Drosophila melanogaster)*, a nematode worm *(Caenorhabditis elegans)*, mouse ear cress *(Arabidopsis thaliana)* and, more recently, the mouse *(Mus musculus*; Davis 2004). These model organisms were developed to study animal and terrestrial plant biology and, although much of the information obtained from them is

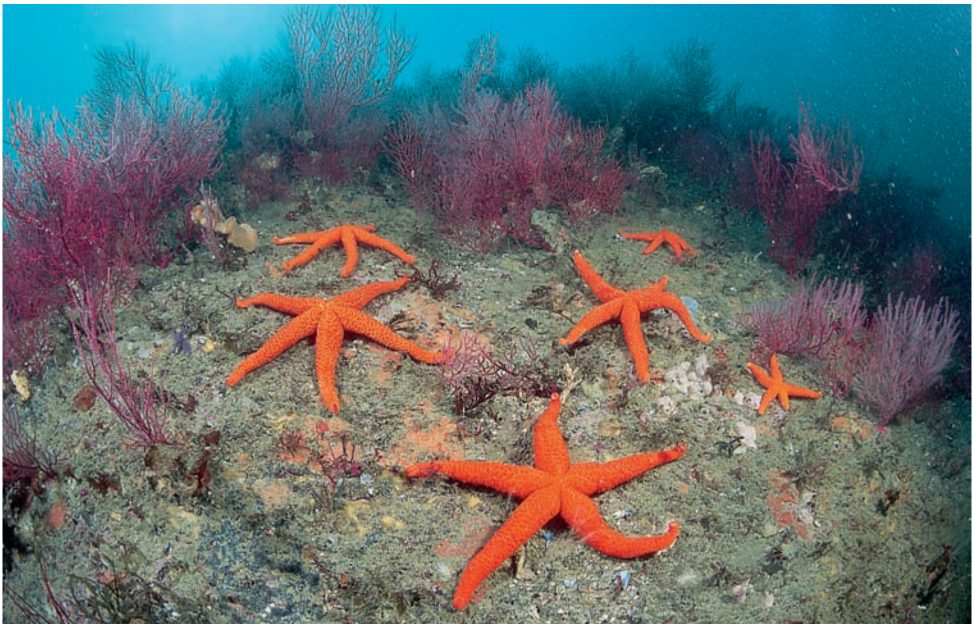


Photo 5.2: Red starfish *(Echinaster sepositus)*. Starfish feed on animals, like certain varieties of sponge, that use chemical defence, and have developed adaptations allowing their consumption. This "chemical warfare" has served as an evolutionary motor for the production of bioactive compounds.

of fundamental interest, their study has often been justified and driven by their use as tools to address concrete, "applied" problems. These problems are essentially of two types, both directly relevant to the human population: disease (including both infectious diseases and diseases of a developmental nature such as cancer) for the animal models, and food production (in a wide sense, including the effects of both development factors and disease on plant production) for plant models. In order to facilitate the transfer of knowledge to humans or crop plants, work on these model organisms has concentrated primarily on conserved traits that are, in many cases, understood in considerable depth. This approach allowed the establishment of large research communities and the development of extensive resources around these model systems, and this was a key factor in the transition to genome-scale biology.

The context for marine biology is significantly different, the accent being more on understanding how organisms function in the context of their particular ecosystem than on asking general questions about their biology. This does not mean that genomic approaches are not relevant to marine biology but rather that they need to be applied in a different way. For example, for marine biologists, the concept of a model organism is used in a much more flexible manner. In some contexts it could be useful to have a very complete model organism for which both genome sequence data and functional genomics tools are available, whereas for other questions models may not need to allow such in-depth analysis and, for example, a genome sequence or even a large-scale EST collection might suffice.

In some situations, even the organism-level approach itself is not relevant. Hence the development of metagenomic approaches in which marine biosystems are directly sampled and sequenced (Beja et al. 2000; see also the study by Venter et al. 2004 who carried out high-throughput sequencing on DNA from microplankton obtained by filtering water from the Sargasso Sea through a 3 µm filter). This type of approach not only represents a very interesting method of obtaining a "snapshot" of the genetic complexity of a particular biosystem, but also obviates the need for culture methodologies for the constituent organisms. Metagenomics was pioneered in marine biology and provides a good example of how genomic approaches can be adapted to address the questions posed by marine biologists. However, whilst metagenomics provides a broad overview of the genetic composition of ecosystems, more detailed analyses will require organism-level approaches. The question therefore remains as to how genomic approaches can be developed for the diverse marine biosystems.

5.3. GENOMIC MODELS FOR MARINE BIOLOGY: THE NEED FOR MODEL ORGANISMS DISTRIBUTED ACROSS THE TREE OF LIFE

Because of the vast phyletic diversity of marine organisms, existing genomic model organisms are often of limited relevance, because there is an enormous evolutionary distance separating these models from an organism of interest. To provide adequate tools for marine biologists, therefore, one important aim will be to develop genomic approaches, such as whole genome sequencing and functional genomics, for key species across the evolutionary tree. These key species can then act as "local" models for phylogenetically related organisms in the same way that, for example, the wealth of genomic information available for *Arabidopsis* has been exploited by researchers working on economically important crop plant species within the angiosperms. The first step towards the establishment of such models is whole genome sequencing (or, in some cases, extensive EST sequencing). As described below, the current collection of fully sequenced genomes will provide a starting point for such a project, but a concerted effort will be required from the marine community to attain this aim and convincing arguments will have to be put forward to support such a programme.

Until recently, genome projects have concentrated on model organisms or on organisms, such as pathogens or plant crops, that are of direct importance to the human community. Despite the fact that the organisms' phylogenetic position was not a major argument for most of these projects, they already provide a sampling of many diverse phylogenetic groups. Most of the model organisms (in the sense of being amenable to laboratory manipulation) with sequenced genomes are members either of the opistokont (animals or fungi) or the viridiplantae (green plant and algae) lineages, with *Dictyostelium discoideum* (a slime mold in the amoebozoa lineage) being a notable exception. Sequencing of human pathogens, however, has provided sequenced genomes from several other major eukaryotic groups including another amoeba *(Entamoeba histolytica)* and members of the apicomplexa (e.g., *Plasmodium falciparum)* and the euglenozoa (e.g., *Trypanosoma brucei).*

As genome projects have become cheaper, it has been possible to finance more diverse projects including, for example, the sequencing of the genomes of environmentally important organisms, such as the diatom *Thalassiosira pseudonana*, which provided the first complete genome from the heterokont lineage. Of course environmental importance was not the only argument put forward for *Thalassiosira pseudonana*, and the phylogenetic argument itself was also important in addition to other factors such as the biotechnological potential of silicate metabolism in this species *(Thalassiosira pseudonana,* like most diatoms, constructs a silicate exoskeleton, the frustule, and the processes involved in the production of this structure are of great interest for applications in nanotechnology). In this respect, *Thalassiosira pseudonana* is an interesting example for marine biologists of how phylogenetic arguments can be combined with other arguments, for example of a biotechnological or environmental nature, to convince funding bodies of the interest of sequencing the genome of a particular organism.

Table 5.1 lists the eukaryotic organisms for which complete genome sequences have been published. From this table it is clear that existing genome projects are gradually covering many of the major lineages that make up the evolutionary tree of the eukaryotes. Genome projects for additional key species are in progress, including quite a number of marine species, such as *Emiliania huxleyi* (a pelagic coccolithophore), *Hydra magnipapillata*, *Strongylocentrotus purpuratus* (purple sea urchin), *Litopenaeus vannamei* (the pacific white shrimp), and Amphioxis (the closest living invertebrate relative of the vertebrates), together with key species from other environments such as *Phytophthora infectans* (an oomycete) and the unicellular green alga *Chlamydomonas*

Table 5.1: Eukaryote species for which complete genome sequences have been published

Species	Classification
Homo sapiens	Metazoa, Chordata, Vertebrata
Pan troglodytes	Metazoa, Chordata, Vertebrata
Rattus norvegicus	Metazoa, Chordata, Vertebrata
Mus musculus	Metazoa, Chordata, Vertebrata
Danio rerio	Metazoa, Chordata, Vertebrata
Tetraodon nigroviridis	Metazoa, Chordata, Vertebrata
Takifugu rubripes	Metazoa, Chordata, Vertebrata
Ciona intestinalis	Metazoa, Chordata
Drosophila melanogaster	Metazoa, Arthropoda
Bombyx mori	Metazoa, Arthropoda
Anopheles gambiae	Metazoa, Arthropoda
Caenorhabditis briggsae	Metazoa, Nematoda
Caenorhabditis elegans	Metazoa, Nematoda
Neurospora crassa	Fungi, Ascomycota
Aspergillus fumigatus	Fungi, Ascomycota
Saccharomyces cerevisiae	Fungi, Ascomycota
Schizosaccharomyces pombe	Fungi, Ascomycota
Kluyveromyces lactis	Fungi, Ascomycota
Candida glabrata	Fungi, Ascomycota
Ashbya (Eremothecium) gossypii	Fungi, Ascomycota
Yarrowia lipolytica	Fungi, Ascomycota
Debaryomyces hansenii var. *hansenii*	Fungi, Ascomycota
Phanerochaete chrysosporium	Fungi, Basidiomycota
Cryptococcus neoformans	Fungi, Basidiomycota
Encephalitozoon cuniculi	Fungi, Microsporidia
Entamoeba histolytica	Entamoebidae
Dictyostelium discoideum	Mycetozoa, Dictyosteliida
Oryza sativa L. ssp. *indica*	Viridiplantae
Oryza sativa ssp. *japonica*	Viridiplantae
Arabidopsis thaliana	Viridiplantae
Cyanidioschyzon merolae	Rhodophyta, Bangiophyceae
Thalassiosira pseudonana	Stramenopiles, Bacillariophyta
Plasmodium falciparum	Alveolata, Apicomplexa
Plasmodium yoelii yoelii	Alveolata, Apicomplexa
Cryptosporidium hominis	Alveolata, Apicomplexa
Cryptosporidium parvum	Alveolata, Apicomplexa
Theileria parva muguga	Alveolata, Apicomplexa
Trypanosoma brucei	Euglenozoa, Kinetoplastida
Trypanosoma cruzi	Euglenozoa, Kinetoplastida

Description	Genome size	Main criterion	Marine species?
Human	3300 Mbp	M	
Chimpanzee	3100 Mbp	C	
Model vertebrate	2800 Mbp	M	
Model vertebrate	3454 Mbp	M	
Zebrafish, vertebrate model species	1700 Mbp	M	
Fish genomic model	342 Mbp	C	
Fish genomic model	400 Mbp	C	yes
Sea squirt, basal chordate	160 Mbp	M	yes
Model organism	122 Mbp	M	
Silkworm	530 Mbp	I	
Malaria mosquito	26 Mbp	P	
Comparative genomics model	104 Mbp	C	
Model organism	97 Mbp	M	
Model organism	38 Mbp	M	
Mold, opportunist human pathogen	30 Mbp	M	
Model organism	12.1 Mbp	M	
Model organism	12.4 Mbp	M	
Yeast, genetic studies and industrial applications	10.6 Mbp	C	
Opportunistic human pathogen	12.3 Mbp	C/P	
Pathogen of cotton and citrus fruits in the tropics	9.2 Mbp	P	
Commonly found e.g. on food, industrial applications	20.5 Mp	C/I	
Halotolerant marine yeast	12.2 Mbp	C	yes
White rot fungus, wood decay	30 Mbp	I	
Opportunistic human pathogen	24 Mbp	C/P	
Microsporidian pathogen affects nervous system	2.8 Mbp	P	
Enteric parasite	20 Mbp	P	
Slime mold, model organism	34 Mbp	M	
Food crop	390 Mbp	F	
Food crop	390 Mbp	F	
Plant model species	157 Mbp	M	
Unicellular red alga from hot, acidic springs	16.5 Mbp	E	
Planktonic diatom	34.5 Mbp	E	yes
Human malaria parasite	22 Mbp	P	
Rodent malaria parasite	23 Mbp	C	
Intestinal parasite	9 Mbp	C/P	
Causes human cryptosporidiosis	10.4 Mbp	C/P	
Tick-borne parasite (East Coast fever)	8.3 Mbp	P	
Causes African sleeping sickness	35 Mbp	P	
Causes Chagas' disease	108 Mbp	P	

[1] Main criterion presumably informing the choice of each species for a genome programme: C: comparative genomics; E: environmental or phylogenetic importance; F: crop plant; I: industrial applications; M: model species; P: pathogen of humans or important crop species.

reinhardtii (a green alga, for which the genome sequence has been completed). For the prokaryotes, progress is even more rapid and many sequenced genomes are available including genomes of several marine organisms such as multiple strains of the pelagic photosynthetic bacteria *Synechococcus* and *Prochlorococcus*. Hence progress is being made towards coverage of all the major eukaryotic and prokaryotic groups. However, it will be important to actively channel this process in the future, to ensure that coverage extends to all the most important groups and especially to key groups for marine biologists, in particular the eukaryotes, many of which have large genomes. Initiatives such as the white paper "Frontiers in Genomics: Insights into Protist Evolutionary Biology" generated by an international workshop organised by Debashish Bhattacharya at the University of Iowa in 2004 (http://www.biology.uiowa.edu/workshop/Genomics_of_Eukaryotic_Microbes.html) are important in this respect, because the arguments they put forward are based on a wide phylogenetic perspective. This white paper proposed target protist species for whole genome sequencing from across the eukaryotic evolutionary tree based on a combination of phylogenetic and other criteria. These target species would not only fill in major gaps in the coverage of the eukaryotic tree, but would also include some marine groups such as chlorarachniophytes and foraminifers along with other groups, such as chytrids and paraphysomonads, that include some marine species.

The availability of a complete genome sequence is, of course, important if a particular organism is to be developed as a model, but the usefulness of the genome sequence is significantly enhanced if tools are available for the analysis of gene function. Functional genomics approaches can then provide insights into the novel biological characteristics of a particular group of organisms that are not attainable simply by analysis of the genome sequence. Moreover, the two aspects, genome sequence and functional tools, are related in as far as the availability of tools for gene function analysis provides an additional argument for genome sequencing. This was the case for classical models such as *Drosophila* and *Arabidopsis*, and has been an important argument for the selection of *Phaeodactylum tricornutum* for the second diatom genome-sequencing project (this project is nearing completion at the JGI).

Of course, it is difficult to imagine a full-scale model organism (permitting functional genomics) in all the major groups of the eukaryotic tree at this stage. It would, therefore, be useful to define a list of minimal requirements for a genomic model as an initial target. The Aquaculture Genome Coordinating Committee recently proposed such a list of requirements in a white paper

Photo 5.3: Rocky bottom community including various types of sponges. Sponges produce a range of chemical substances to fend off predators. Some recently extracted compounds have proved to be of pharmaceutical interest.

aimed at promoting genomics for aquacultured species (http://www.animalgenome.org/aquaculture/updates/NRSP8/White_Paper_2005_s.html). The following is a suggestion as to how these requirements could be adapted to the wider context of marine biology in general.

Proposed standards for the definition of a genetically enabled model species:

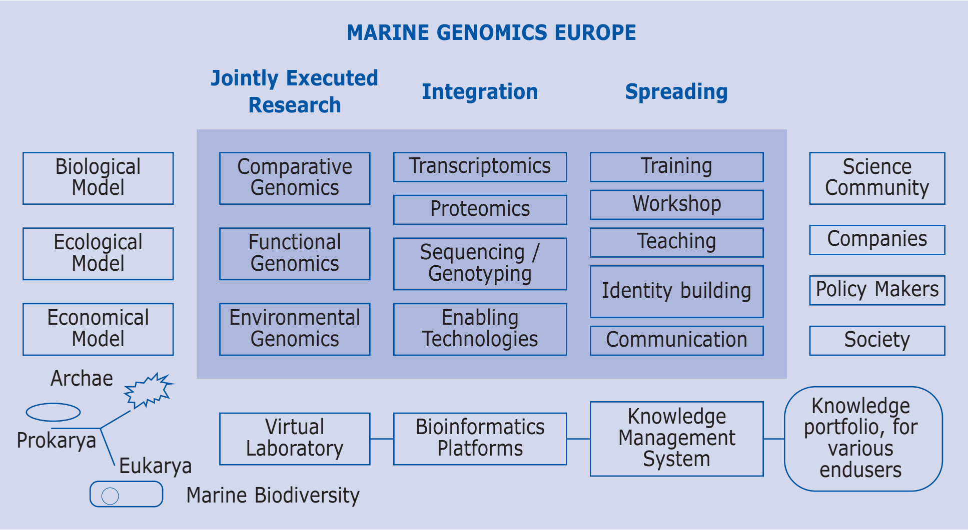
- An EST database of sufficient breadth (tissue and developmental/life cycle stages) and depth to represent most of the organism's transcriptome.
- Large insert, deep coverage BAC libraries.
- A microarray with the maximum set of unigenes identifiable.
- Sample sequencing of the genome sufficient to provide initial resources for gene identification, repeat content and polymorphism.
- Where classical genetic approaches can be applied, a linkage map with a resolution of <1 centiMorgan.
- A stable infrastructure, both physical and bioinformatic, to ensure the continued maintenance and public availability of genomic resources.

Another important objective in promoting the application of genomic approaches to marine systems is to federate the marine biology community with the aim of creating common projects and focusing efforts on a manageable number of target species. This type of activity is important for the creation of interest groups with a sufficient critical size around emerging model systems, and should also bring groups with key biological expertise but little experience of genomic approaches into contact with groups that possess technical expertise with genomic methodologies. In Europe a major effort is being made towards this end via the EU funded Network of Excellence "Marine Genomics Europe". This network will be described in more detail in the following section.

5.4. THE MARINE GENOMICS EUROPE NETWORK OF EXCELLENCE

The European Network of Excellence, "Marine Genomics Europe", is composed of 450 researchers from 45 institutions (118 laboratories or research groups) from 16 countries (website: http://www.marine-genomics-europe.org/). The aim of the network is to promote the application of high-throughput genomic approaches to the study of marine organisms. The network focuses on federating marine biology laboratories around common projects with the aim of

Figure 5.1: Marine Genomics Europe Network of Excellence

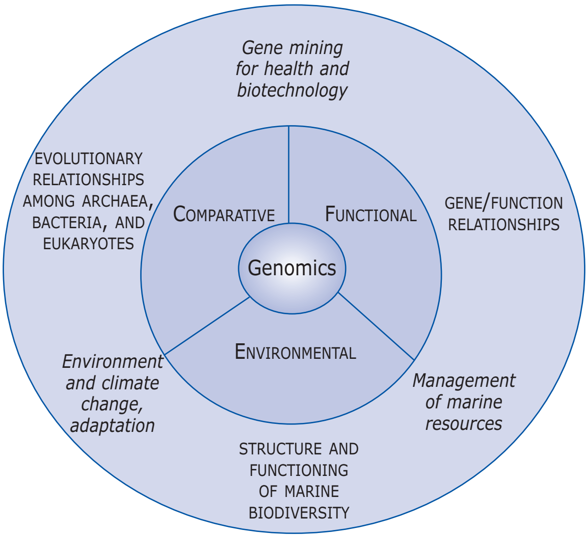


Schematic representation of the Marine Genomics Europe Network of Excellence showing how the networking objective ("integration") articulates with the research programme ("jointly executed research") and other activities such as interactions with policy makers and society ("spreading").

creating the critical mass necessary for the development of genomic approaches (figure 5.1). Examples of this type of integration include the networking of several genomics platforms, the establishment of a common bioinformatics facility, the launching of several large-scale “flagship” projects and an education and training programme for young scientists. Within the network, genomic approaches are being used to investigate a wide range of questions related to the functioning of marine ecosystems and to the biology of marine organisms.

The collaborative research (the jointly executed research programme) between the partners in the network is broken down into comparative, functional and environmental genomic approaches with emphasis, respectively, on comparison between genomes in a phylogenetic context, on high-throughput analysis of gene function, and on the application of genomic methodologies to the study of marine biodiversity (figure 5.2). These approaches are applied across four “nodes” that associate laboratories interested in particular groups of organisms: the microbial node, the algal node, the evolution, development and diversity node, and the fish and shellfish node. The jointly executed research is intended to generate data that can be exploited both by marine resource management programmes (prediction of global changes in marine populations, conservation of biodiversity, fisheries management and the improvement of aquacultured species), and by gene mining projects for health and

Figure 5.2: Structure of the joint research activity of the Marine Genomics Europe Network of Excellence[1]



[1] The end point objectives, which include problems relevant to the management and exploitation of coastal biodiversity, are shown in italics.

Photo 5.4: View of the DNA sequencing laboratory at the Institute for Genomic Research in Gaithersburg, Maryland, USA. Rapid progress in DNA sequencing technology is accelerating the capacity to resolve the genome of marine organisms. The challenge ahead is to interpret the information these genomes contain.

biotechnology. Some additional details about the aims of the three different types of jointly executed research are given in the following paragraphs.

The comparative genomics programme aims to identify and focus on representative marine model organisms from across the different phyla of the tree of life. Some of the species identified are already entering the post-genomic stage, with work now concentrating on understanding the functions of the genes that make up the genome, and the list of new candidates is growing rapidly. The latter include organisms of major evolutionary importance either because of their phyletic novelty or because they possess gene families that are of particular interest for comparative analysis.

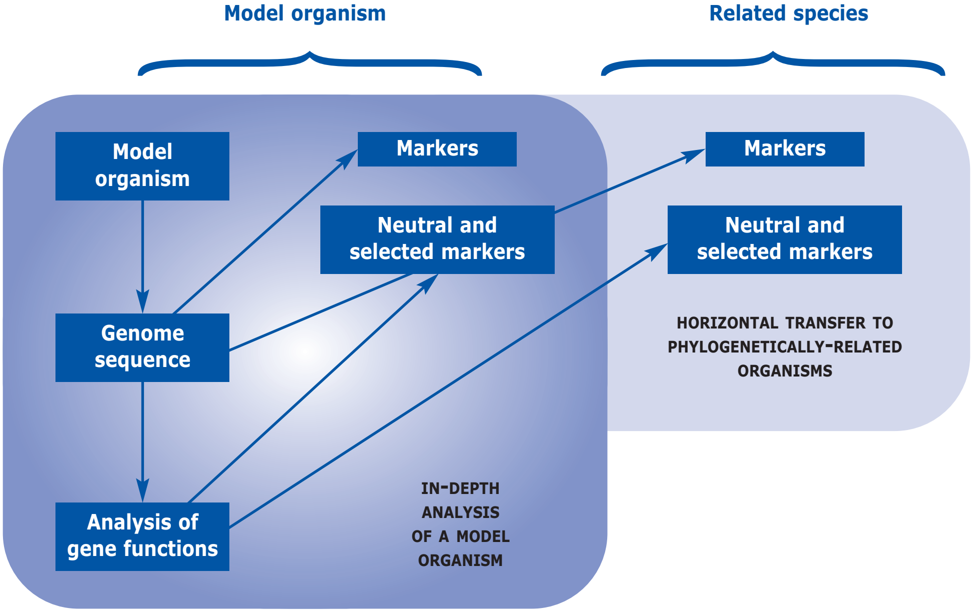
The functional genomics programme is exploring the complex relationships between endogenous and exogenous, biotic and abiotic stimuli and gene expression using a wide range of methodologies, including microarrays and proteomic and metabolomic approaches. These approaches are being developed for selected model organisms.

The environmental genomics programme aims to delineate the structure and dynamics of biodiversity in marine ecosystems. Particular efforts are being made to associate these studies with the functional genomics programme, to allow the data obtained for these organisms to be exploited in the context of the different biosystems that are being studied. This articulation between work on model organisms and the direct application of genomic approaches in an ecological context is a very important feature of the work within the network. The following section will discuss this point in more detail, using work on the brown algae and, in particular, on the model species *Ectocarpus siliculosus* as an example.

5.5. MODEL ORGANISMS AS A MEANS TO APPLY GENOMIC METHODS TO MARINE QUESTIONS

The underlying causes of changes in marine biosystems can only be understood in the light of knowledge about the biology of the organisms making up those ecosystems. The most powerful way of establishing such knowledge is to obtain a deep (vertical) understanding of the biology of selected model organisms, and to use this knowledge as a base for the study of related organisms in the field (horizontal transfer). Hence, as discussed above, characterisation of a component organism of an ecological biosystem can be greatly facilitated by the availability of a well-characterised model organism within the same phylogenetic group (figure 5.3). The brown algae, for example, are dominant components of

Figure 5.3: Example of how in-depth analysis of a model organism can be exploited to develop tools for the analysis of biodiversity in ecosystems



rocky shore ecosystems. They are often the most abundant organisms in these ecosystems in terms of biomass, and in some coastal areas undersea kelp forests can rival terrestrial forests in extent and density. Our understanding of the biology of brown algae, however, is limited, particularly at the molecular level. Moreover, existing model systems, for example in the opistokont or green plant lineages, are of limited use because of the great evolutionary distances separating them from the brown algae (more than a billion years). Based on these and other arguments, we decided to develop a model brown alga that would be amenable to genomic and functional genomic approaches. To choose the model organism, we used selection criteria that focused both on genome size and on characteristics that allow genetic analysis, such as small size and the possibility to complete the life cycle and to carry out genetic crosses in the laboratory.

At the time that this project was initiated, several brown algae had been used as models to study certain aspects of brown algal biology. *Fucus* for example had been used extensively for cell biology approaches (Berger, Taylor and Brownlee 1994; Bouget, Berger and Brownlee 1998; Corellou et al. 2000; Goddard et al. 2000; Corellou et al. 2001; Brownlee, Bouget and Corellou 2001; Coelho et al. 2002) and expressed sequence tag (EST) data were available (Roeder et al. 2004) for the economically important *Laminaria digitata* (McHugh 2003). However, both of these organisms produce large thalli, and it is very difficult to complete their life cycles in the laboratory. Moreover, the genome of *L. digitata* was known to be very large (650 Mbp; Le Gall et al. 1993) and we determined that the genomes of *Fucus* spp. were even larger (more than 1000 Mbp, Peters et al. 2004; see also Kapraun 2005). In contrast, the genome sizes of members of the Ectocarpales have been shown to be significantly smaller (Stache 1993), as we were able to confirm (Peters et al. 2004). Also, the members of this order are smaller and more easily cultivated in the laboratory. Following a comparative study of several different members of the Ectocarpales, we proposed *Ectocarpus siliculosus* as model organism for the brown algae.

5.6. *ECTOCARPUS SILICULOSUS:* A MODEL ORGANISM FOR THE BROWN ALGAE

All stages of the *Ectocarpus* life cycle can be cultured in the laboratory in Petri dishes in natural or artificial seawater. The sexual life cycle, which involves an alternation between two separate generations (the sporophyte and the gametophyte), can be completed in three months and sexual crosses can be made by mixing gametes from male and female gametophytes. Other advantages of *Ectocarpus* as a model organism include its high fertility, the fact that large col-

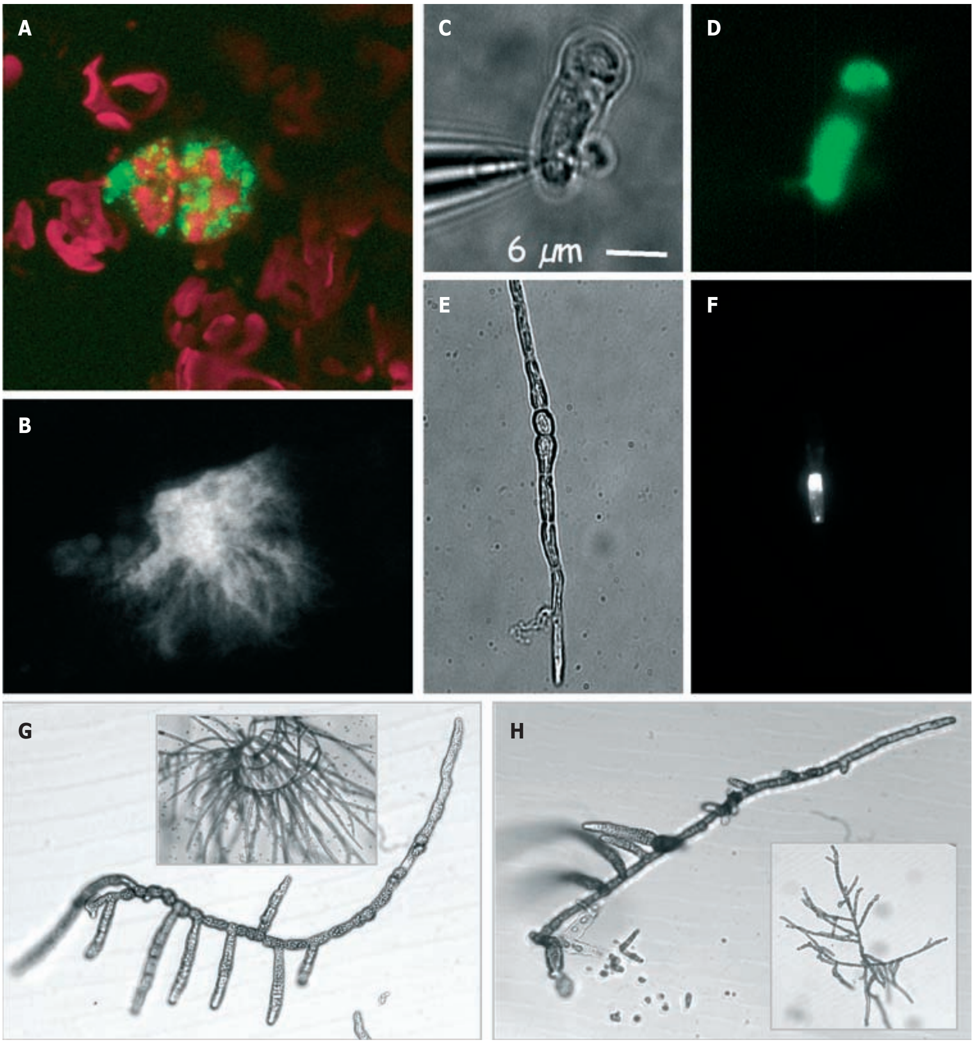


Photo 5.5: Illustration of some of the molecular tools being developed for the brown algal model species *Ectocarpus siliculosus*

A: Fluorescent markers loaded into an *Ectocarpus* filament cell using biolistics. The two fluorescent dyes, FITC (green) and Texas Red (red), were detected by confocal microscopy. The autofluorescence of the chloroplasts is also visible (violet). This method allows the introduction of fluorescent dyes for cell biology analyses and is also being used to optimise biolistic loading for the development of a transformation protocol (collaboration with Colin Brownlee, Marine Biological Association, Plymouth, UK). **B:** Example of a cell biology technique applied to *Ectocarpus.* Confocal microscope image of the actin cytoskeleton in a filament cell of a sporophyte. Cells were fixed and then stained with Alexa Fluor Phalloidin**. C and D:** Microinjection of a germinating *Ectocarpus* gamete with the fluorescent dye FITC (C, bright field; D, fluorescence). **E and F:** Development of an RNA interference protocol. Microinjection of a young *Ectocarpus* sporophyte (8 cells) with double stranded RNA and a fluorescent marker dye (Alexa Fluor 488). **G and H:** Example of a mutant *Ectocarpus* strain isolated from a UV irradiated population. The immature mutant alga (H) is compared with a wild type sporophyte at the same stage (G), later stages of development are shown inset.

lections of strains exist from temperate regions throughout the world, the close phylogenetic distance between the Ectocarpales and economically important seaweed within the Laminariales and the fact that it is, historically, one of the best studied brown algae (see Peters et al. 2004 and references therein).

In June 2004 a consortium of 35 laboratories submitted a proposal for complete sequencing of the *Ectocarpus* genome to the French sequencing centre Genoscope. This project, which was accepted in September 2004, proposed a 10x shotgun coverage of the genome (4,280,000 reads) plus 100,000 reads on cDNA sequences. The cDNA sequencing will aim to obtain a maximum of full-length cDNA sequences. The sequencing part of the genome project is expected to be completed in 2006. Access to *Ectocarpus* sequence data is currently available via a password-accessed website (http://genomer.sb-roscoff.fr/Ectocarpus/).

In parallel, considerable effort is going into the development of molecular tools for *Ectocarpus* including genetic transformation and RNAi technology (figure 5.4). Protocols have been established for both UV and chemical mutagenesis (EMS and MMS) and a pilot microarray has been produced and tested.

In April 2005, an international *Ectocarpus* meeting was held in Roscoff that attracted some 50 scientists from a large number of countries including Japan, Korea, the USA, Australia, Chile, France, Germany and Great Britain (http://www.sb-roscoff.fr/Esil2005prog.pdf). This meeting provided a forum for the coordination of the genome project, and allowed discussion of *Ectocarpus*-related research in a broad range of fields including developmental biology, cell biology, physiology, ecology and systematics, chemical ecology and biochemistry.

5.7. THE *ECTOCARPUS* GENOME PROJECT AND COASTAL BIODIVERSITY

How will the application of genomics to *Ectocarpus* help us to understand coastal biodiversity? Firstly, *Ectocarpus* will serve as a model to study how populations of brown algae adapt to their environment and, secondly, structural and functional knowledge about the *Ectocarpus* genome will be exploited for the study of species (such as *Fucus*) that play more important roles in coastal ecosystems. Work has already begun to learn more about the ecology of *Ectocarpus*, both at the level of the worldwide distribution and relatedness of *Ectocarpus* strains and at a more local, ecological level, building on earlier studies (see for example Stache 1989). This work involves several member laboratories of the *Ectocarpus* Genome Consortium.

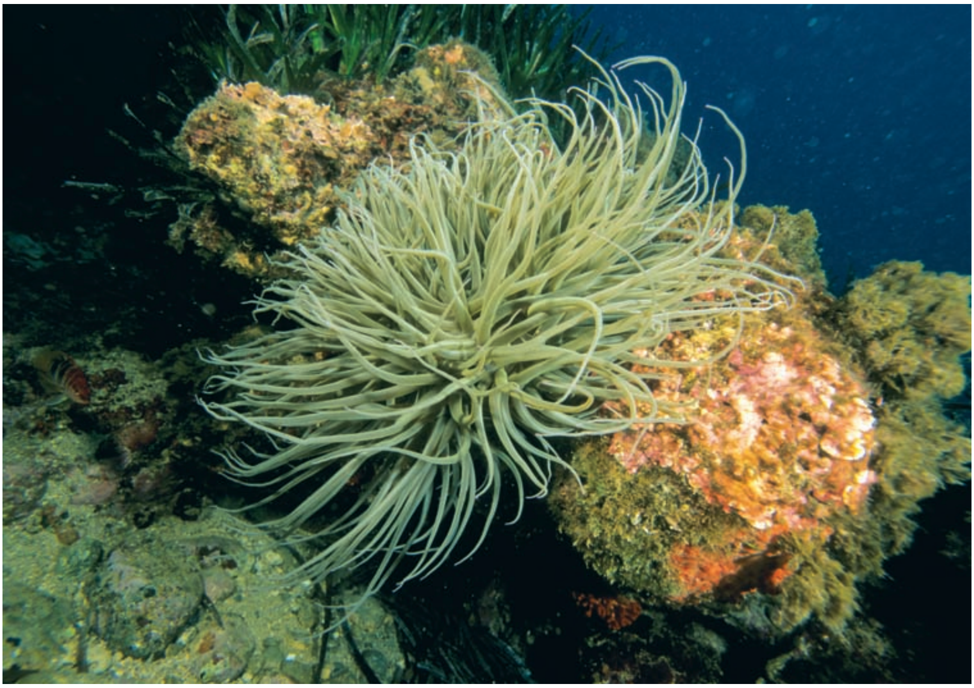


Photo 5.6: Actinia or sea anemones. Like other sessile organisms, sea anemones are among the marine creatures richest in bioactive substances and a potential source of molecules for pharmaceutical purposes.

Concerning the transfer of information from *Ectocarpus* to other brown algae, it is important to note that our understanding of the relative influence of factors such as selection, mutation, genetic drift and gene flow on the genetic composition of coastal biosystems has been significantly hampered by the limited availability of appropriate genetic markers, particularly nuclear markers. From a general point of view, the application of genomics to population genetics is providing new insights into the genetic and evolutionary processes affecting nuclear variation in numerous animal and plant models (Mitchell-Olds and Clauss 2002; Nordberg and Innan 2002; Maloof 2003). In this context, the *Ectocarpus* genome project has attracted the interest of several groups interested in brown algal microevolution, population genetics and systematics, including groups that will apply information from the *Ectocarpus* genome to studies of key brown algae within coastal ecosystems.

Indeed, the *Ectocarpus* genome will provide much needed genomic tools for the study of microevolutionary processes in brown algae, at both inter- and intra-specific scales. Through the analysis of the conservation and polymorphism of homologous loci in *Ectocarpus* and other brown algae, genome-wide surveys of neutral and coding sequences in populations across species distributions will provide information about locus-specific evolutionary and genetic processes (e.g., selection, mutation, assortative mating, and recombination) as well as about demographic processes that affect the entire genome (e.g., genetic drift, gene flow and inbreeding; Luikart et al. 2003). The availability of homologous protein-coding sequences will provide a means to study adaptive molecular variation in this group. For example, comparing allele genealogies for multiple protein-coding loci among several species, differences in levels of polymorphism both within and among species may provide clues to the selective effects of functional processes involved in speciation (Mitchell-Olds and Clauss 2002). In addition, comparison of phenotypic and genotypic variation among individuals within a species will elucidate the genetic controls and limitations that influence not only organism distributions but also environmental interactions (Jackson et al. 2002). Genome-wide comparison of sequence variation within and among populations allows the identification of truly neutral loci (Luikart et al. 2003). These neutral loci are essential for robust, accurate estimation of population genetic parameters, such as effective population size and effective migration rates. In haploid-diploid species such as *Ectocarpus*, these parameters are of particular interest for the study of the consequences of the co-occurrence of free-living haploid and diploid stages on population genetic structure (e.g., Engel, Destombe and Valero 2004).

5.8. ADDITIONAL EMERGING AND FUTURE GENOMIC MODEL ORGANISMS FOR MARINE BIOSYSTEMS

The important constituents of the flora of coastal biosystems, in terms of biomass, include not only brown but also red and green algae and seagrasses. The seagrasses are angiosperms, so work on terrestrial angiosperms such as *Arabidopsis* and rice can potentially be exploited to study these organisms. The red and green algae, on the other hand, are very distantly related both to brown algae and to other existing model species (even if the situation is slightly better for marine green algae because they are members of the broader group of green plants, the viridiplantae, that also includes the angiosperms). The genome sequence of *Cyanidioschyzon merolae*, a unicellular red alga, has recently been reported (Matsuzaki et al. 2004), but this species is distantly related to the multicellular red algae and its genome is unusual and highly compact, perhaps as a result of its habitat in sulphate-rich, hot acidic springs. There is therefore a need to develop model organisms for the other algal groups, particularly the red algae, in a manner analogous to the development of *Ectocarpus* as a model for the brown algae.

A recent survey of potential macroalgal models proposed *Porphyra yezoensis* as a candidate model organism (Waaland, Stiller and Cheney 2004). The choice of *Porphyra yezoensis* was based on many of the same criteria that were behind the choice of *Ectocarpus* as a model for the brown algae. These included the size of the genome (approximately 300 Mbp; Kapraun et al. 1991), the facility with which cultures can be handled in the laboratory, the existence of mutants (Ohme and Miura 1988; Mitman and van der Meer 1994; Yan, Fujita and Aruga 2000), the development of methods for preparing and regenerating from protoplasts (Waaland et al. 1990) and the large body of information available in the literature concerning its biochemistry, physiology and culture. Additional arguments included the economic importance of *Porphyra* (which is the basis of the multi-billion dollar nori industry), its ecological importance in some coastal habitats, the existence of EST collections (Nikaido et al. 2000; Asamizu et al. 2003) and advances being made towards the development of genetic transformation (Cheney, Metz and Stiller 2001; He et al. 2001; Lin et al. 2001). Taken together, the arguments for developing *Porphyra yezoensis* as a genomic model are strong. and it is likely that a genome project will emerge for this organism in the near future. However, genomic sampling of the red algae should not be limited to the Bangiophyceae (both *P. yezoensis* and *C. merolae* are members of this class) but should also include at least one member of the other major class, the Floridiophyceae, which includes economically important agarophytes (agar producers such as *Graccilaria* spp.) and carageenophytes (carageenan producers such as *Kappaphycus* spp. and *Chondrus crispus*).

Genomics of green macroalgae currently appears to be less of a priority, probably because of the less obvious potential of these organisms for industrial applications compared to the red and the brown algae. Probably the best candidate from among the green macroalgae is *Ulva* (including taxa previously called *Enteromorpha*), because we have an extensive literature describing work on this species (Bryhni 1974; Fjeld and Løvle 1976; Reddy, Iima and Fujita 1992) as well as a collection of EST sequences, and because they can multiply rapidly to cause eutrophication-based coastal blooms (green tides). However, there is currently no genome programme for this organism.

The above discussion has been limited to macroalgae, as the most conspicuous constituents of coastal biosystems, but obviously there are other emerging model organisms of relevance to marine ecosystems. Among photosynthetic organisms in pelagic habitats, prokaryotes such as *Synechococcus* and *Prochlorococcus* have already been studied in some detail using genomic approaches. More recently, the eukaryotic prasinophyte *Ostreococcus tauri,* a picoplanktonic green alga widely distributed in the oceans, has emerged as a model organism. *Ostreococcus tauri* possesses the smallest genome known for a free-living photosynthetic eukaryote (11.5 Mbp), housed within a very small cell (1.5 µm in diameter) with one chloroplast and one mitochondrion. The genome of *Ostreococcus* has been sequenced recently at the Laboratoire Arago (Banyuls, France, a member of the MGE network). It is highly compact with very few introns and short intergenic sequences. An important factor for genetic analysis is the genome's low level of genetic redundancy; gene families being very small, often consisting of a single gene. Genetic tools such as transformation and microarray analysis of gene expression are currently being developed for this organism.

In the metazoan lineage, a number of novel model species are emerging at key phylogenetic positions, as a result of the application of evo-devo approaches to understanding the evolution of the developmental complexity in this phylum. Many of these models are from the marine environment.

5.9. CONCLUSION

The needs of the marine community in terms of genomics differ somewhat from those of terrestrial biologists, and broad sampling approaches such as metagenomics may prove to be more relevant in this context. However, the development of in-depth genomics, applied to model organisms, is also important for the progression from a descriptive to a functional understanding of biosystems. One of the difficulties with regard to the development of such approaches is the phylogenetic diversity of marine biosystems. As a result of this diversity, existing model organisms are often too distantly related to be of use for a particular species under study. To address this problem, genome sequencing and other genomic approaches will need to be applied to selected species from across the tree of life to provide a better coverage of its inherent biodiversity. Further development of some of these species as full-blown genomic model species will then provide in-depth functional knowledge that can be applied to related species from the same phylogenetic group.

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Marine biodiversity science has grown in just a few years from a relatively insignificant discipline into a major enterprise by the marine scientific community. This growth has been triggered by the recognition that we now confront a number of serious problems regarding the sustainable use of the world oceans, the major ones being the increasing pressure on marine species from global climate change and from unsustainable fisheries. In recent years, much scientific progress has come from European research, for instance through the EU supported networks of excellence MarBEF (Marine Biodiversity and Ecosystem Functioning) and Marine Genomics Europe. A number of leading European scientists from these networks have contributed to this lively, up-to-date and scientifically interesting book that describes the state of the art and the challenges facing the exploration of the oceans and the biological treasures they contain.

Carlo Heip
General Co-ordinator of MarBEF

This book represents a timely contribution to our understanding of how poorly marine biodiversity is known. Its chapters provide a comprehensive assessment of the status of knowledge of marine biodiversity, from shallow coastal waters to the deep benthos, where the technological challenges are well explained. They also include some interesting comparisons between land and sea, as well as predictions of how much marine biodiversity remains to be described – “250 to 1,000 years to complete” – by which time many species may have been lost. This book should be sent to every government agency responsible for biodiversity conservation in order to help explain how much of this important task remains!

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