

2. THE MAGNITUDE OF MARINE BIODIVERSITY

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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 In parallel with this changed paradigm, species inventorying has also evolved from being categorized as an outdated scientific activity to a timely cutting-edge megascience “enterprise”.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 siliceous 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		? ³
Dinomastigota		4,000 ⁴
Ciliophora		? ⁴
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 Brouckerhoff (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 (Grygiel 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. [Panaeoidea 419, Sergestioidea 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 (Galatheaidea 1,012 [E. Macpherson pers. com.], Hippidae 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.

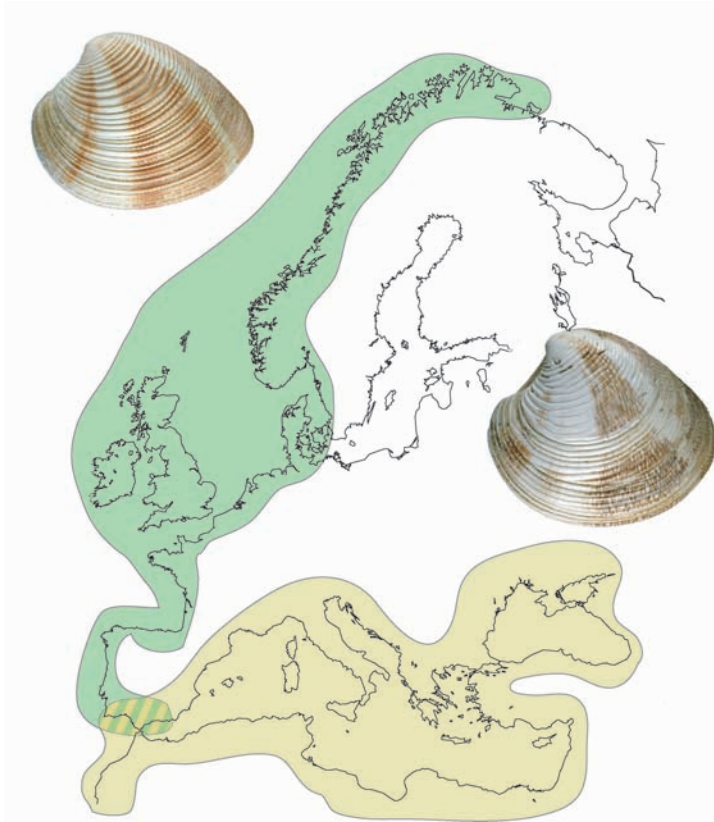
Groombridge and Jenkins (2000) to be “about 40,000 fossil species” and “more than 4,000 Recent species”; and by Brusca and Brusca (2003) at “40,000 species”. I have chosen here to follow Vickerman (1992), who gave 10,000 species of Foraminifera “excluding the vast numbers of fossil species insofar as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



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.

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

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 taxa¹

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, pharmaceuticals 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-

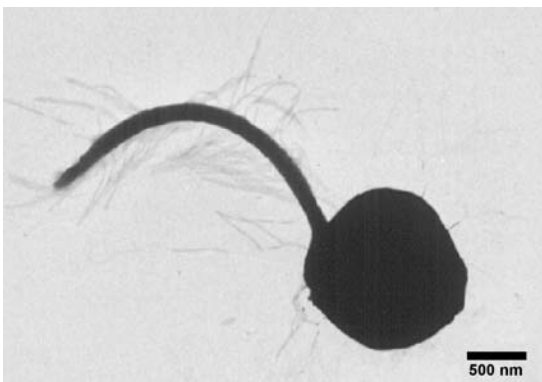


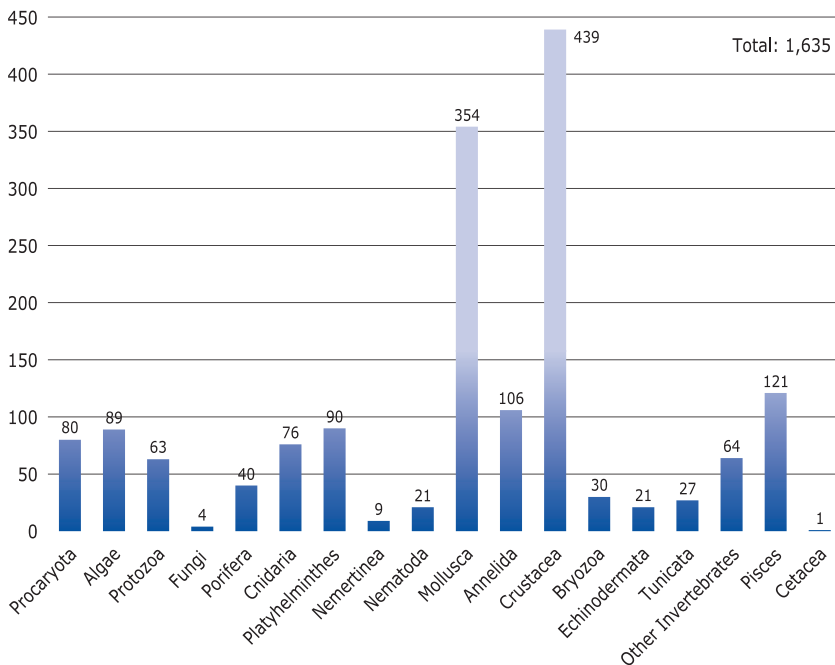
Photo 2.6: *Pelagomonas* cell. The discovery and role of the picophytoplankton is one of the major oceanographic advances of the last 20 years and picophytoplankton remains a frontier in marine biodiversity exploration. At less than one micron, a cell of *Pelagomonas* is dwarfed by many prokaryotes;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

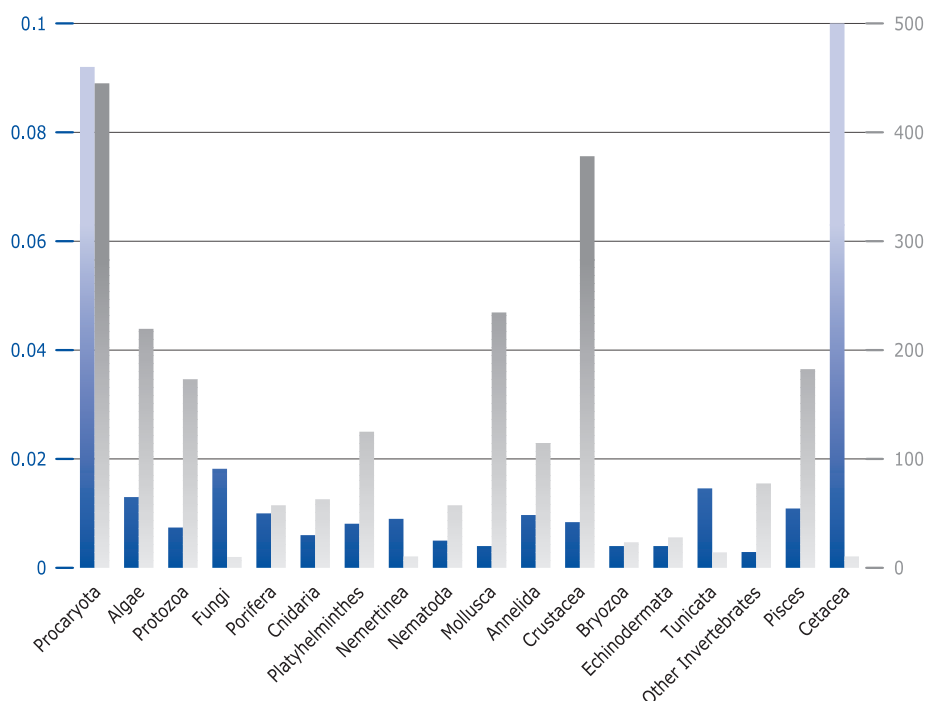
Marine taxa represent 9.7% of all current new species descriptions, whereas marine biodiversity represents 15% of all biodiversity. In other words, the increment of marine biodiversity inventory is about 0.65% per year, as

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 same 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.

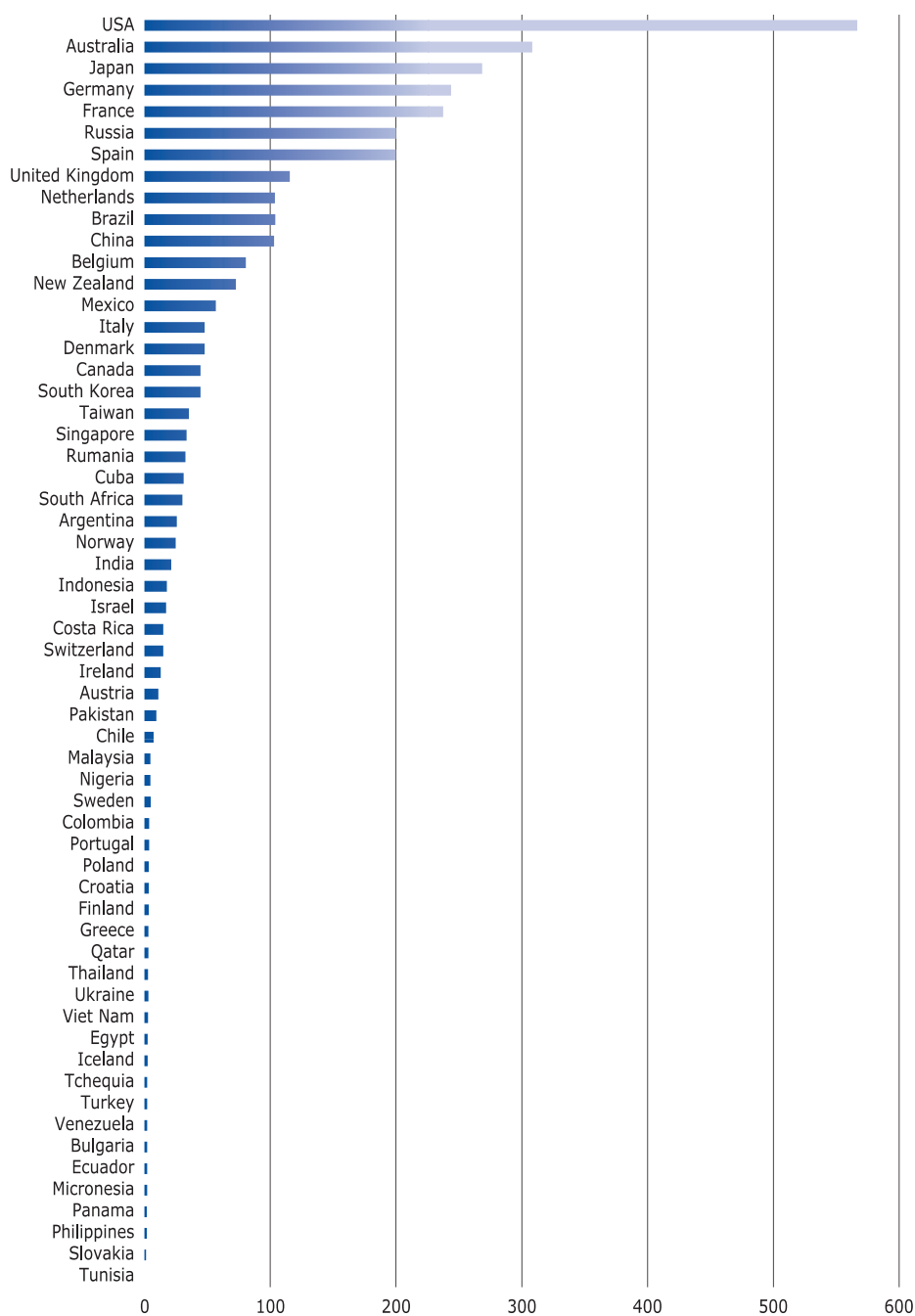
The Convention on Biological Diversity has highlighted the imbalance between the distribution of biodiversity and the distribution of knowledge on that biodiversity. Most known and unknown biodiversity is in tropical countries, most of them developing or emerging countries of the South, whereas most 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

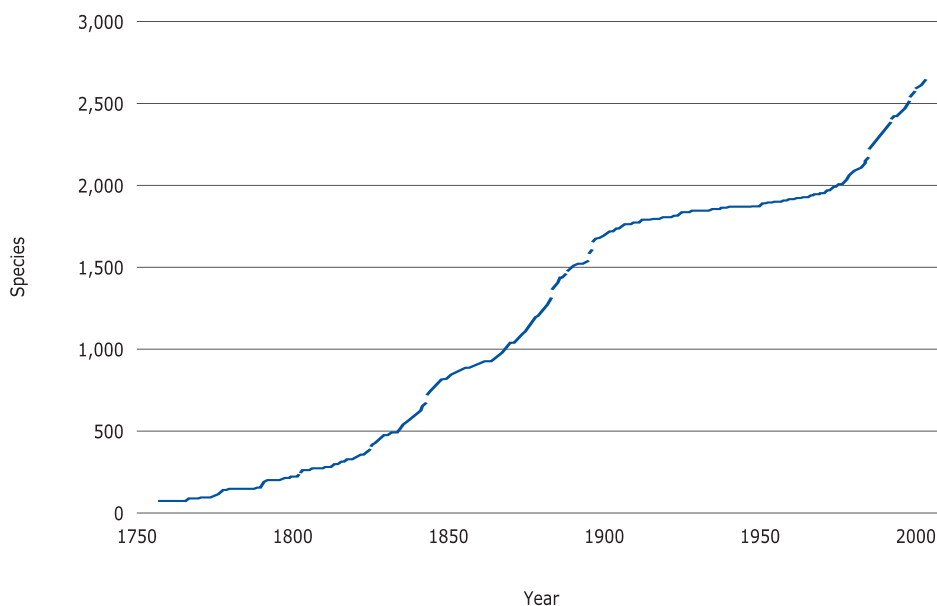
Only first authors are considered; authors of more than one species are counted as many times as they are first author of a new species. Total: 3,270 author-species pairs.

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.

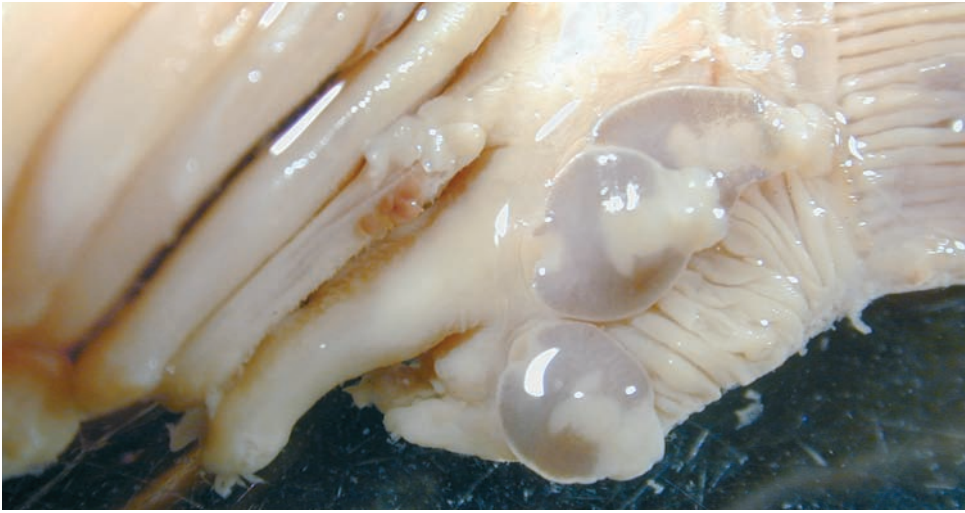


Photo 2.8: Three specimens of the monogene *Lagenivagino pseudobenedenia* on the gills of the fish *Etelis coruscans* from New Caledonia. Although numerous new species of parasites remain to be discovered, described and named, marine helminthology (the study of parasitic “worms”) is a field of research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

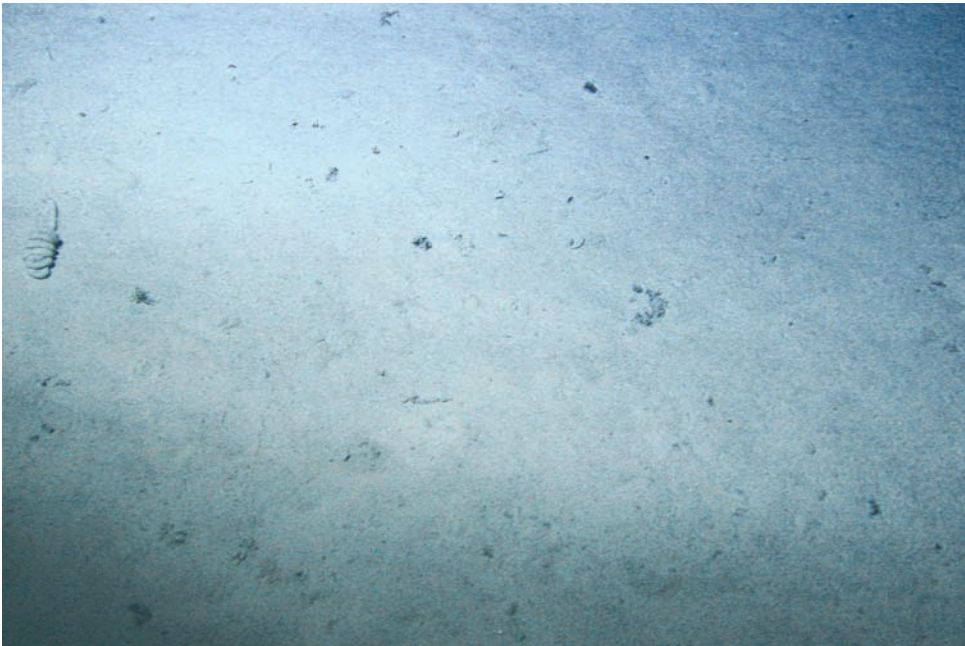


Photo 2.9: A riot of species. The expression “a riot of species in an environmental calm” was coined by the ecologists Paul Snelgrove and Craig Smith in order to draw attention to the paradox underlying deep-sea biodiversity. The deep sea has for a long time been perceived as a hostile, species-poor 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 km². Given that there are 3×10^8 km² 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, Lamshead (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 5×10^5 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, Embrow 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 $(16,475 : 1,349) \times 29,713 = 362,353$ species.

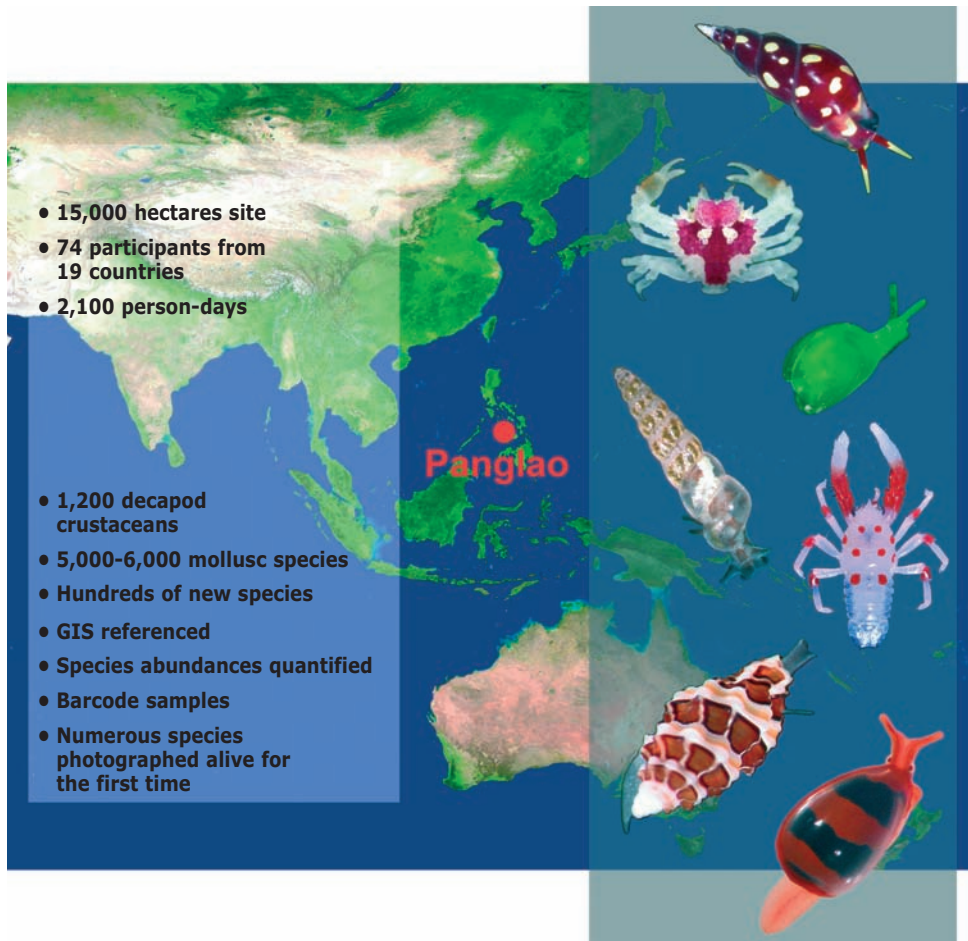
The validity of this extrapolation rests on a number of assumptions that may or may not be correct. First, it assumes that the worldwide geographical partitioning of marine biodiversity is the same across taxonomic or ecological groups. We know this is not the case. Plankton taxa have much broader ranges

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 and documenting 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 Lamshead himself revised his earlier speculations of nematode species richness (Lamshead 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 (Lamshead 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 fac-

tor, 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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REFERENCES

- ANDERSEN, R. A. "Diversity of eukaryotic algae". *Biodiversity and Conservation* 1 (1992): 267-292.
- BACKELJAU, T., P. BOUCHET, S. GOFAS, and L. DE BRUYN. "Genetic variation, systematics and distribution of the commercial venerid clam *Chamelea gallina*". *Journal of the Marine Biological Association of the United Kingdom* 74 (1994): 211-223.
- BOSS, K. J. "How many species of mollusks are there?". *Annual Report of the American Malacological Union* (1970): 41.
- BOUCHET, P. "Inventorying the molluscan diversity of the world: what is our rate of progress?". *The Veliger* 40 (1997): 1-11.
- BOUCHET, P., P. LOZOUET, P. MAESTRATI, and V. HÉROS. "Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site". *Biological Journal of the Linnean Society* 75 (2002): 421-436.
- BRIGGS, J. C. "Species diversity: land and sea compared". *Systematic Biology* 43 (1994): 130-135.
- BRIGGS, J. C. "Proximate sources of marine biodiversity". *Journal of Biogeography* 33 (2006): 1-10.
- BRUSCA, R. C., and G. J. BRUSCA. *Invertebrates*. Sunderland: Sinauer Associates, 2000.
- BRUSCA, R. C., and G. J. BRUSCA. *Invertebrates*, 2nd ed. Sunderland: Sinauer Associates, 2003.
- COSTELLO, M., P. BOUCHET, C. EMBLOW, and A. LEGAKIS. "European marine biodiversity inventory and taxonomic resources: state of the art and gaps in knowledge". *Marine Ecology Progress Series* 316 (2006): 257-268.
- COSTELLO M., C. EMBLOW, and R. WHITE, eds. "European Register of Marine Species. A check-list of marine species in Europe and a bibliography of guides to their identification". *Patrimoines Naturels* 50 (2001): 1-463.
- COUNTWAY, P., R. GAST, P. SAVAI, and D. CARON. "Protistan diversity estimates based on 18S rDNA from seawater incubations in the western North Atlantic". *Journal of Eukaryotic Microbiology* 53 (2005): 95-106.
- CURTIS, T. P., W. T. SLOAN, and J. W. SCANNELL. "Estimating prokaryotic diversity and its limits". *Proceedings of the National Academy of Sciences* 99 (2002): 10494-10499.
- DOLAN, J. "Microbial biogeography?". *Journal of Biogeography* 33 (2006): 199-200.
- DUCLOUX, M. E. "*Inventaire mondial de la biodiversité marine animale, végétale, champignons et procaryotes sur les années 2002 et 2003*." Université Pierre et Marie Curie, unpublished work for Masters degree. 2005. 44 pp. The following databases were searched: (a) Zoological Record online (md2.csa.com/factsheets/zooclust-set.c.php) and on paper was used for all animal taxa. (b) Aquatic Sciences and Fisheries Abstract (md2.csa.com/factsheets/aquclust-set.c.php), Plant Science (md2.csa.com/factsheets/plantsci-set.c.php), and Plant Science (md2.csa.com/factsheets/biolclust-set.c.php) were together used for algae, fungi and prokaryotes. (c) Medline (md2.csa.com/factsheets/medline-set.c.php) was used as an additional source for prokaryotes. The results were cross-checked against a couple of specific databases: Fishbase (ichtyonb1.mnhn.fr/search.com) for fishes, and the Moe & Silva database (ucjeps.berkeley.edu/INA.html) for algae; and colleagues were consulted within MNHN for potential supplements.

- ERWIN, T. L. "Tropical forests: their richness in Coleoptera and other arthropod species". *Coleopterists' Bulletin* 36 (1982): 74-82.
- FENCHEL, T., and B. J. FINLAY. "The ubiquity of small species: patterns of local and global diversity". *BioScience* 54 (2004): 777-784.
- FOISSNER, W. "Protist diversity: estimates of the near-imponderable". *Protist* 150 (1999): 363-368.
- GASTON, K. J., and R. MAY. "Taxonomy of taxonomists". *Nature* 356 (1992): 281-282.
- GRASSLE, J. F., and N. J. MACIOLEK. "Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples". *American Naturalist* 139 (1992): 313-341.
- GRAY, J. S. "Marine diversity: the paradigms in patterns of species richness examined". *Scientia Marina* 65, suppl. 2 (2001): 41-56.
- GROOMBRIDGE, B., and M. D. JENKINS, eds. *Global biodiversity: Earth's living resources in the 21st century*. Cambridge: World Conservation Press, 2000.
- HABURA, A., J. PAWLOWSKI, S. D. HANES, and S. S. BOWSER. "Unexpected foraminiferal diversity revealed by small-subunit rDNA analysis of Antarctic sediment". *Journal of Eukaryotic Microbiology* 51 (2004): 173-179.
- HAMMOND, P. M. "Species inventory". In B. Groombridge, ed. *Global biodiversity. Status of the Earth's living resources*. London: Chapman and Hall, 1992, 17-39.
- HAMMOND, P. M. (lead author). The current magnitude of biodiversity. In V. H. Heywood and R. T. Watson, eds. *Global biodiversity assessment*. Cambridge: Cambridge University Press, 1995, 113-138.
- HESSLER, R. R., and H. L. SANDERS. "Faunal diversity in the deep sea". *Deep-Sea Research* 14 (1967): 65-78.
- HUGOT, J. P., P. BAUJARD, and S. MORAND. "Biodiversity in helminths and nematodes as a field of study: an overview". *Nematology* 3 (2001): 199-208.
- HUMES, A. G. "How many copepods?". *Hydrobiologia* 292-293 (1994): 1-7.
- JUSTINE, J. L. "Parasite biodiversity in a coral reef fish: twelve species of monogeneans on the gills of the grouper *Epinephelus maculatus* (Perciformes: Serranidae) off New Caledonia, with a description of eight new species of *Pseudorhabdosynochus* (Monogenea: Diplectanidae)". *Systematic Parasitology* (in press).
- LAMBSHEAD, J. "Recent developments in marine benthic biodiversity research". *Oceanis* 19 (1993): 5-24.
- LAMBSHEAD, J., and G. BOUCHER. "Marine nematode deep-sea biodiversity – hyperdiverse or hype?". *Journal of Biogeography* 30 (2003): 475-485.
- MACPHERSON, E., W. JONES, and M. SEGONZAC. "A new squat lobster family of Galatheoidea (Crustacea, Decapoda, Anomura) from the hydrothermal vents of the Pacific-Antarctic Ridge". *Zoosystema* 27 (2005): 709-723.
- MAY, R. M. "How many species are there on earth?". *Science* 241 (1988): 1441-1449.
- MAY, R. M. "How many species?". *Philosophical Transactions of the Royal Society of London*, B, 330 (1990): 293-304.
- MAY, R. M. "Bottoms up for the oceans". *Nature* 357 (1992): 278-279.
- MAY, R. M. "Biological diversity: differences between land and sea". *Philosophical Transactions of the Royal Society of London*, B, 343 (1994): 105-111.
- MINELLI, A. *Biological systematics*. London: Chapman and Hall, 1993.

- MORAVEC, F., V. M. VIDAL-MARTINEZ, J. VARGAS-VASQUEZ, C. VIVAS-RODRIGUEZ, D. GONZALEZ-SOLIS, E. MENDOZA-FRANCO, R. SIMA-ALVAREZ, AND J. GÜEMEZ-RICALDE. "Helminth parasites of *Epinephelus morio* (Pisces: Serranidae) of the Yucatan Peninsula, southeastern Mexico". *Folia Parasitologica* 44 (1997): 255-266.
- ØDEGAARD, F. "How many species of arthropods? Erwin's estimate revised". *Biological Journal of the Linnean Society* 71 (2000): 283-296.
- POORE, G., and G. WILSON. "Marine species richness". *Nature* 361 (1993): 597-598.
- REAKA-KUDLA, M. L. "The global biodiversity of coral reefs: a comparison with rain forests". In M. L. Reaka-Kudla, D. E. Wilson and E. O. Wilson, eds. *Biodiversity II*. Washington: Joseph Henry Press, 1997, 83-108.
- ROHDE, K. "Latitudinal gradients in species diversity and Rappoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients?". *Ecography* 22 (1999): 593-613.
- SANDERS, H. L. "Marine benthic diversity and the stability-time hypothesis". *Brookhaven Symposium on Biology* 22 (1969): 71-80.
- SNYDER, M., and P. BOUCHET. "New species and new records of deep-water *Fusolatirus* (Neogastropoda: Fascioliidae) from the West Pacific". *Journal of Conchology* 39 (2006): 1-12.
- STORK, N. "Insect diversity: facts, fiction and speculation". *Biological Journal of the Linnean Society* 35 (1988): 321-337.
- VENTER, J. C., K. REMINGTON, J. F. HEIDELBERG, A. L. HALPERN, D. RUSCH, J. A. EISEN, D. WU, et al. "Environmental genome shotgun sequencing of the Sargasso Sea". *Science* 304 (2004): 66-74.
- VICKERMAN, K. "The diversity and ecological significance of Protozoa". *Biodiversity and Conservation* 1 (1992): 334-341.
- WILSON, S. P., and M. J. COSTELLO. "Predicting future discoveries of European marine species by using non-homogeneous renewal process". *Applied Statistics* 54 (2005): 897-918.
- WINDSOR, D. A. "Most of the species on Earth are parasites". *International Journal for Parasitology* 28 (1998): 1939-1941.