Chapter 34. Global Patterns in Marine Biodiversity

Contributors: Paul Snelgrove (Convenor)

Comparatively well-sampled groups taxonomically (primarily pelagic (water column) vertebrates and cephalopods) could be treated at a phylum-class level globally, whereas for taxa in which taxonomic or geographic knowledge is highly uneven, we followed a habitat framework, noting that a group by group treatment of benthic invertebrates would encompass more than 30 phyla and would render the chapter unwieldy. We therefore organized the chapter into an Introduction, a series of summaries on biodiversity patterns in pelagic taxa, and then summaries of knowledge on biodiversity in contrasting benthic ecosystems. Although this strategy is imperfect (e.g. many fishes occupy primarily benthic environments), it nonetheless creates a framework in which to evaluate current knowledge of biodiversity patterns within a relatively short chapter. Space limitations also preclude comprehensive coverage of all habitats and taxa, and we therefore present a broad but incomplete summary that omits kelps, seagrasses, and salt marshes, for example. We therefore encourage readers to also review the more detailed chapters within the World Ocean Assessment that focus on the biology and status of specific taxa and ecosystems. Our goal in this chapter is to identify the key environmental drivers of global diversity patterns based on current knowledge, while acknowledging many data gaps that will necessitate revising these patterns as new data become available. Specifically, we address how depth, latitude, productivity, temperature and substrate influence broad-scale distributions and diversity patterns, and identify the knowledge gaps (taxonomic, geographic) that constrain our ability to assess such patterns. Below we summarize knowledge on biodiversity gradients with a few key references, but we also include a more extensive reading list for those seeking more detailed information (Appendix).

2. Pelagic ecosystems

2.1 Marine Mammals

Marine mammals include cetaceans (baleen whales and toothed whales, dolphins and porpoises), pinnipeds (seals, sea lions, walrus), sirenians (manatees and dugongs), the marine otter (Lontra felina), and sea otters (Enhydra lutris and subspecies) and the polar bear. Excluding the seven extant freshwater species, about 120 wholly or partly marine species are currently recognized (www.marinemammalscience.org). However, ongoing taxonomic revision will keep this number in flux. Marine mammal species occupy almost all marine habitats: from fast ice to the tropics, on shorelines where pinnipeds haul out during their moulting, mating or pupping season, in shallow coastal waters where some dolphins and baleen whales spend much of their time, and in the open ocean where many pelagic pinnipeds, baleen whales, and toothed cetaceans occur. However, other than sperm whales and perhaps some of the beaked whales capable of diving beyond 2,000 m, air-breathing limits marine mammals to bathypelagic depths at most. In contrast to highly restricted distributions in some smaller cetaceans and pinnipeds, many species exhibit circumglobal or circumpolar distributions, with some (baleen whales in particular) undertaking long annual migrations.

Many marine mammals spend most of their time offshore, but sirenians, marine and sea document species presence in an area and facilitate large-scale biodiversity inventories, extending these types of sources to estimate density or abundance or to assess relative ecological importance often proves problematic. Dedicated sighting surveys of cetaceans conducted annually in offshore areas of the North Pacific under sponsorship of the International Whaling Commission (IWC) (IWC-POWER: IWC) can help address these gaps and evaluate North Pacific whale recovery trajectories (Halpin et al., 2009)

2.2 Seabirds

“Seabirds” denotes species that rely on the marine environment for at least part of the year, and include many spectacularly mobile species that travel thousands of kilometres, returning to land only to breed. Seabirds as a group occur in all seas and oceans worldwide, exploiting surface waters in all habitats from the intertidal zone to the open ocean. Globally, seabird density, diversity and endemism are highest in the highly productive temperate latitudes and in upwelling areas (Croxall et al., 2012; Chown et al., 1998).

Seabirds are central-place foragers (foragers that return to a particular place to consume food) during the breeding season, with many adapted to exploit highly clumped prey. Therefore largest aggregations occur where food availability is high within a restricted foraging range from a suitable nesting habitat (Lascelles et al., 2012). Foraging ranges vary from a few kilometres from shore (e.g., seaduck and small terns) to several thousand (e.g., larger albatross). Seabirds adopt a range of behaviours to capture prey from surface-seizing to plunge or pursuit diving. Feeding generally occurs at or immediately below the water’s surface, although the Emperor Penguin reaches depths over 500 m.

Seabirds can be roughly subdivided into three groups. “Pelagic seabirds”, such as porcellariiformes, pelecaniformes, alcids and penguins, often travel far from land, primarily use oceanic pelagic water (seas above the open ocean, typically >200 m in depth). In contrast, “coastal seabirds (year-round)”, including most larids, are those that primarily use coastal inshore water (seas along coasts, typically <8 km from the shoreline) throughout the year. “Coastal seabirds (nonbreeding season)”, such as seaduck, grebes and divers, are those that primarily use coastal inshore water during the non-breeding season.

For much of the year coastal species tend to be relatively static, often tied to particular habitats or topographic features. Pelagic species distributions, however, often link to dynamic processes and variable and require complex analyses to define. BirdLife International recognizes around 350 species as seabirds (i.e., 3.5 per cent of all bird species), of which over 280 meet a stricter definition (excluding ducks, loons, etc.) used in some earlier reviews. However, ongoing taxonomic revision will keep this number in flux. In recent years new species have been found, as well as rediscovery of some thought to be extinct. Re-evaluation of molecular and morphological evidence has split some taxa, adding an additional eight species since 2000 with a further 10-15 under review in the coming years. Knowledge of the at-sea distribution of species remains patchy. Many species are relatively well studied at specific sites, but at-sea movements across entire ranges are known for only a few species, as are areas used during non-breeding periods and those areas visited by juvenile birds. The at-sea distributions for many tropical species, particularly in the Central and South Pacific and South East Asia are also under-studied.

Seabird distribution may vary depending on their breeding site (e.g., tropical vs. temperate zones), age, sex, whether it is day or night and the time of year (Lascelles et al., 2012). In addition, many species, particularly procellariiforms, alternate between "long" and "short" foraging trips during the breeding season. Areas most important for their survival have rarely been defined in any systematic way, although recent studies, such as the BirdLife Marine Important Bird Area Atlas, have helped fill this gap and show distribution patterns at multiple scales.

2.3 Turtles

Marine turtles have inhabited the world's oceans for more than 100 million years, having survived the dinosaurs and numerous major global shifts in climate. Today there are seven recognized marine turtle species, six belonging to Chelonidae, green turtles Chelonia mydas, hawksbills Eretmochelys imbricata, loggerheads Caretta caretta, olive ridleys Lepidochelys olivacea, Kemp's ridleys Lepidochelys kempii, and flatbacks Natator depressus, and one extant member of Dermochelyidae, the leatherback Dermochelys coriacea. Despite few species, marine turtles occur circumglobally, inhabit nearly all oceans, occupy unique ecological niches, and exhibit variations in abundance and trends, as well as reproduction and morphology among populations of the same species (Wallace et al., 2010).

Marine turtles have evolved several adaptations to marine habitats (e.g., maintaining water balance in saltwater, hydrodynamic body shape and swimming efficiency) that are unique compared to other turtle species, but because they are reptiles, temperature fundamentally constrains their distributions and life history (Spotila, 2004). For example, the development, and survival of marine turtle embryos means successful hatchling production requires the consistently warm temperature (28-33°C) of sandy beach environments. Because these habitats are limited to the tropics and subtropics, most major marine turtle nesting sites occur between the equator and 30° latitude (Wallace et al., 2010) (see Figure 1, chapter 39).

Temperate also limits marine distributions, as most population ranges only reach 45° latitude (see Figure 1, chapter 39), extending only seasonally into northern and southern extremes of their ranges (Spotila, 2004). Leatherbacks defy this pattern, with core migratory and foraging habitats into temperate and even sub-arctic regions and average water temperatures between 10-20°C (Eckert et al., 2012).

1,000 are herbivores or omnivores. The commercial large species that are most studied predominantly occupy the upper trophic levels.

The high diversity of forms, behaviour, ecology and biology based on one body plan enables great success in the marine environment. However, the populations of many exploited species are threatened by fisheries that now access stocks in almost the entire water volume between 0 and 1,500 m depth. Despite some local extirpations, no marine fishes are reported to be globally extinct; however, large species with few offspring, such as some sharks and manta rays, are endangered, often because of threats along migration pathways. Populations of some shark species targeted for their fins have decreased by 90 per cent, but although the populations are no longer economically exploitable, no sign of extirpation has been noted so far (Ferretti et al., 2010).

2.5 Cephalopods

Shell-less coleoid cephalopods occur from pole to pole, and from the ocean's surface to depths of many thousands of metres; many can even fly above the ocean's surface. They range from surface-dwelling tropical forms with adults the size of a grain of rice to 30-m giants in the deep oceans.

Squid compete with fishes in nearly all marine niches, although there are only one tenth as many species, perhaps reflecting their relatively recent radiation since the disappearance of the dinosaurs. The same event killed all of the Ammonites, a highly diverse group of cephalopods that lived near the sea surface. The deep ocean remains sparsely sampled for cephalopod life: Archaea, Bacteria and all major kingdoms of Eukaryotes. Microbial diversity within the plankton far exceeds that in terrestrial habitats. For example, planktonic photoautotrophs represent deep phylogenetic diversity, including 20 diverse clades. In contrast, autotrophic diversity in terrestrial environments is dominated by just one clade (Falkowski et al., 2004). Planktonic heterotrophs are equally diverse.

Eukaryotic plankton includes purely autotrophic species (phytoplankton) that convert inorganic to organic carbon, fuelled by light energy through photosynthesis. Primary production supplied by phytoplankton forms the basis of the food web and ultimately feeds all marine organisms, up to the largest whales. Eukaryotic plankton also includes heterotrophic microbes that ingest organic carbon through a myriad of feeding strategies, and so-called mixotrophic species, which include species either simultaneously or sequentially alternating between phototrophic and heterotrophic modes. Feeding by heterotrophic and mixotrophic plankton is the single largest factor in reducing primary production; it can control the abundance and biogeochemical activity of phytoplankton, and it is essential for the transfer of matter and energy to higher levels in the food web, and for the recycling of nutrients (Sherr et al., 2007). Bacteria are also essential for recycling and remineralizing organic matter and contribute substantially to primary production.

Latitude, proximity to land, and season primarily delimit global-scale distribution patterns of plankton. Abundance declines from high nutrient coastal areas to the vast areas of the generally low-nutrient (oligotrophic) waters of the open ocean. But fact live within the plankton for their earliest life stages, and are referred to as meroplankton, in contrast to the holozooplankton generally considered. This means that the zooplankton encompass an exceedingly wide range of body plans, and modes of life, ranging from relatively passive herbivorous species, to blindingly fast attack carnivores. It also includes some of the world's most passive predators that literally rely on prey blundering into them. Finally, some zooplankton taxa have developed symbiosis with internally housed algae so successfully that they no longer rely on other organisms as prey.

The majority of zooplankters range from <1 mm to 1 cm in length. With ~2,000 described planktonic species typically representing 80-90 per cent of total zooplankton abundance and living biomass in most marine ecosystems, copepods represent the most successful body plan. These small, robust crustaceans are easily collected with simple nets and manipulated for experimental purposes, making them the central focus of ecological research on plankton for the past century. Different species of copepods play almost every imaginable ecological role: the majority are suspension-feeding grazers on smaller single-celled plankton, some are scavengers and detrital feeders, and others range from active attack to passive ambush predators. Several other diverse crustacean groups illustrate a wide range of feeding strategies: ostracods (detritivores), euphausiids (filter-feeders), amphipods (predators, or commensalists), mysids (scavengers) and (again in contrast with abundance and biomass). Diversity increases with increasing depth in polar systems (Kosobokova et al., 2011), has a mid-depth peak in temperate/subarctic systems, but may peak in surface waters of tropical oceans. Although these trends hold for the overall zooplankton community, they vary among every taxonomic group within the assemblage.

Zooplankton experts seek to create global maps for every major taxonomic grouping, or even for entire communities or ecosystems, particularly using observational data, in conjunction with environmental data, to predict biodiversity distribution (e.g.,

across these two ocean systems. The broad swath of equatorial currents that cross the

irrespective of substrate composition; this is likely to be due to the harsh, dynamic nature of that environment.

In a broad sense, evidence suggests high species richness in tropical sediments relative to te

3.5 Deep-sea benthic e3.5

abrupt shifts of water masses, can obscure, alter, or create zonation patterns. Globally, clear faunal differences are observed between upper bathyal depths compared to mid and lower bathyal depths (Rex and Etter, 2010). The preponderance of rare species

species distribution and diversity. Deep-sea biodiversity loss could adversely affect ecosystem functions of the Earth's largest environment.

Hydrothermal vents and cold seeps occur where dissolved chemical compounds emerge at the seafloor at rates and concentrations high enough to sustain chemosynthesis. Chemosynthesis is the process that some microbes use to transform CO_2 into organic molecules. The emerging fluid is often associated with active tectonic features such as spreading centres, subduction zones, and volcanoes, but seeps may also be linked to methane escape via mass wasting, brine pools, turbidity flows, diapirs, and pockmarks, canyons and faults. The resulting habitat distribution tends to be linear, following mid-ocean and back-arc spreading centres, as well as volcanic arcs in the case of vents, and along continental margins in the case of seeps. The fluid emissions at most regions of high carbon accumulation – oil, gas and clathrate-rich deposits – support chemosynthesis. Thus, the microbes form the basis of a food web for a metazoan community that is mostly endemic to these systems. Habitats supporting chemosynthetic production and communities occur in every ocean.

No overall assessment of diversity patterns and drivers exists, although alphadiversity at vents and seeps is often lower than in the surrounding non-chemosynthetic ecosystems. The considerable work on biogeographic patterns includes exploration of faunal relationships and origins. Despite similarity in many taxa at vents and seeps, they usually differ at species or genus levels; however, both habitats harbour many endemic taxa. Some taxa at vents and seeps are new to science at higher taxonomic levels, especially those housing microbial symbionts.

Overall, species diversity at seeps exceeds that at hydrothermal vents, driven by high variability in the geological settings of methane and sulphide release and within-site heterogeneity (Levin and Sibuet, 2012). Depth may describe both the biogeographic similarity of seeps across the Atlantic and, possibly, the decrease of symbiont-hosting species with depth in general at seeps. However, depth may reflect more direct drivers, such as greater production and predation at shallower depths or behaviour of fluid flux sustaining chemosynthesis. Local site longevity and stability of the fluid source will influence any pattern analysis, as will depth; vents in the photosynthetic zone above 200 m differ notably in taxa and structure. These habitats exhibit low diversity within taxa. Habitat and depth drive a variety of patterns in vesicomyid clams hosting symbionts, but better systematics are needed. The East Pacific Rise represents a diversity hotspot for the most speciose family, the vent-endemic dirivultid copepods.

Biogeographic patterns at vents are likely to share controlling factors with all ocean fauna: continental barriers, oceanographic barriers, and pressure gradients with depth. However, similarity analyses with growing datasets indicate strong control by history of spreading ridges from the mid-Mesozoic to the present. Thus, diversity analysis is likely to identify connectivity, geological longevity and ridge stability as important, reflecting the smaller-scale drivers currently known. Recent discovery of vent communities in the Antarctic and Arctic reveal a unique community composition and suggest that dispersal barriers are also important drivers of diversity (Rogers et al., 2012).

Increasing evidence suggests that the character of the venting fluids fundamentally drives taxonomic composition, overlaid on geographic separation, particularly in the complex settings of the Atlantic and the western Pacific back-arc rifting and volcanism (Desbruyères, 2000); relevant factors may include reduced compound composition, water temperature and metal content. Similarly, the high diversity of animals recently recognized from mud volcanoes relates to the nature of the chemical substrates in emerging fluids and the adaptations of associated microbes and symbiont hosts both across and within sites (Rodrigues et al., 2013). Where geochemical drivers characteristic of vents and seeps come together, an intermediate ecosystem with biodiversity elements from both vents and seeps emerges (Levin et al. 2012). Decay of large organic falls also supports microbial processes and species reliant on chemosynthesis (Smith et al., 2015). Thus vents and seeps also hold many taxa in common with organic remains, such as wood falls and whale carcasses.

Seamounts are undersea mountains historically defined by an elevation of 1 km or more, but more recently by a more ecological definition, that includes k213 Twi. Tc -0.0 as ass.

review in 1987 (Wilson and Kaufmann, 1987) recorded 449 species of fish and 596 species of invertebrates from 100 seamounts, but more recent surveys suggest much higher numbers (Stocks, 2010). The Census of Marine Life on Seamounts amalgamated data on over 5,400 taxa (although not all to species) from 258 seamounts into the public database SeamountsOnline (Stocks, 2010), which can currently be accessed through the Ocean Biogeographic Information System portal (www.iobis,org) by selecting the Seamounts Online database. However, gear selectivity and generally few samples per seamount limit biodiversity knowledge for any one seamount.

Depth-related environmental parameters strongly influence seamount species composition, together with seafloor type and character (e.g., substratum, hardness, composition, mobility) (see Clark et al., 2010a). Habitat complexity on seamounts largely determines benthic species occurrence, distribution and diversity. Volcanic activity, lava flows and areas of hydrothermal venting add to habitat diversity on seamounts, creating unique environmental conditions that support specialized species and assemblages (see preceding section). Water column stratification and oceanic flow conditions also add local dynamic responses that can regulate the spatial scale of faunal distributions.

Many early studies suggested high seamount endemism given their geographic isolation, often separated from other seamounts by deep water and considerable distance. Although seamount assemblages can differ in species abundance or frequency, similarity in deep-sea fish assemblages between seamounts and adjacent continental slopes or islands (scales of km), as well as across oceans (1000s of km), contradicts the idea of ecological islands (Clark et al., 2010b). In the latter case, the global-scale circulation of deep-sea water masses presumably influences fish distribution. Regional-scale similarities in faunal composition between seamounts and other habitats in the South Pacific demonstrate that seamounts share a common regional pool of species with non-seamount communities. Schlacher et al. (2014) found high species turnover with depth and distance in seamount assemblages off Hawaii at the scale of individual seamounts, but geographic separation was a poor predictor of ecological separation for the region as a whole. These studies emphasize that the spatial scales over which faunal assemblages of seamounts are structured cannot be generalized. Nevertheless, recent biogeographic classifications for the deep ocean suggest that benthic community composition will vary markedly among basins (e.g., Watling et al., 2013).

Better understanding of global deep-sea biodiversity gradients requires more sampling, but predictive species distribution modelling and use of environmental surrogates can improve our short-term understanding (e.g., Clark et al., 2012) and help inform management options for the deep sea.

3.6 Cross-taxa integration

The global ocean houses an enormous variety of life. In total, the oceans support an described some 220,000 (WoRMS Editorial Board, 2013). A key question is whether consistent ‘rules’ constrain the distribution of this life across the variety of different organisms and habitats examined here, and if so, whether they result in consistent large-scale patterns of biodiversity. Global-

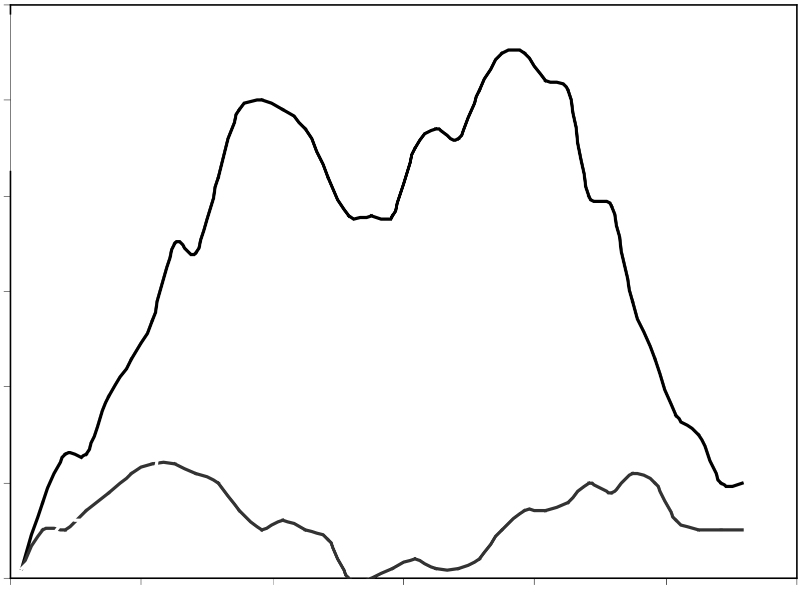

Figure 3. Number of species of fish per genus, in each latitudinal band of 1 degree, as calculated from distribution data available in OBIS on 26 September 2011.

Figure 4. Latitudinal species richness of mangrove plant species.

Figure 5. ES(50) calculated for various groups, from the data as available in OBIS as of the end of 2012. ES(50) (or Hurlbert's index) represents the numbers of species expected to be present in a random sample of 50 individuals; this metric measures the diversity (not species richness, as its name might suggest), independent of sample size. Points in the graphs above represent calculation of ES(50) for bands of 1 degree of latitude. The blue line is the LOESS (LOcal regrESSion) prediction/smoothing; the darker grey bands are the 95% confidence intervals around the LOESS estimate. Most groups, but not all (e.g. Chlorophyta) show a clear unimodal pattern. All calculations were made with R (R DevelopmentCore Team, 2014), using package ggplot2 for LOESS and plotting (Wickham, 2009).

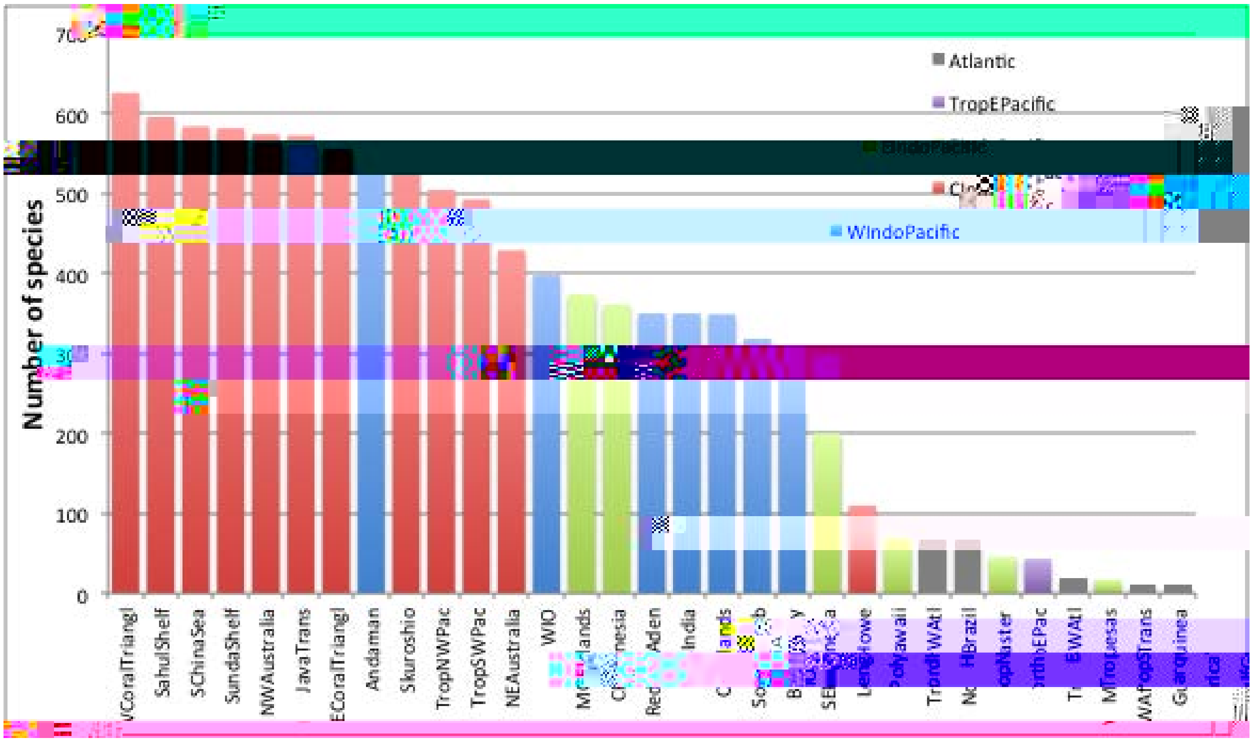

Figure 6. Coral species richness by province in the Marine Ecosystems of the World Classification, from the IUCN Red List of Threatened Species database (IUCN 2013).

Table 1: Number of species by life zone (Saltwater including diadromous, Freshwater) from the successive editions of Fishes of the World by J.S. Nelson (1976, 1984, 1994, 2006). The last line gives the current counts from the Catalog of Fishes (Eschmeyer, 2014).

Year	Salt Water		Freshwater		Total
Fishes of the World (Nelson) successive editions					
1976	11967	64%	6851	36%	18818
1984	13312	61%	8411	39%	21723
1994	14652	60%	9966	40%	24618
2006	16025	57%	11952	43%	27977
Catalog of Fishes					
2013	17535	53%	15467	47%	33002

Table 2. Number of marine fish species per FAO area.

FAO area	Spp. count
Arctic Ocean	147
Atlantic, Northwest	1129
Atlantic,Northeast	1115

Table 3. Number of marine fish species per Ocean and FAO area. E: East; N: North, S: South; W: West: indicates which part of the ocean. Note: The second eastern central line for Atlantic represents the Mediterranean and Black Seas. The Northwestern Pacific includes some coral reef areas in its southern part which explains the high number of species compared to the Northeastern part.

Ocean	Atlantic				Indian				Pacific			
Latitude												
Arctic	N	147										
North	W	1129	[redacted]	[redacted]					W	5299	E	717
Central	W		E	811					W	6490	E	4138

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