

The First Global Integrated Marine Assessment

World Ocean Assessment I

by

the Group of Experts of the Regular Process

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Chapter 34. Global Patterns in Marine Biodiversity

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1. Introduction

Marine environments encompass some of the most diverse ecosystems on Earth. For example, marine habitats harbour 28 animal phyla and 13 of these are endemic to marine systems. In contrast, terrestrial environments contain 11 animal phyla, of which only one is endemic. The relative strength and importance of drivers of broad-scale diversity patterns vary among taxa and habitats, though in the upper ocean the temperature appears to be consistently linked to biodiversity across taxa (Tittensor et al. 2010). These drivers of pattern have inspired efforts to describe biogeographical provinces (e.g. the recent effort by Spalding et al., 2013)) that divide the ocean into distinct regions characterized by distinct biogeochemical and physical combinations). Biogeographers such as Briggs (1974) examined broad-scale pattern in marine environments in historical treatises and although many of the patterns described therein hold true today, the volume and diversity of data available to address the question have increased substantially in recent decades. We therefore focus our chapter on more recent analyses that build on those early perspectives. The International Census of Marine Life programme that ran from 2000-2010 provided significant new data and analyses of such patterns that continue to emerge today (McIntyre, 2011; Snelgrove, 2010). Indeed, many of our co-authors were part of that initiative and that influence is evident in the summary below. In the few years since that programme ended, some new perspectives have emerged which we include where space permits, noting that we cannot be exhaustive in coverage and also that the large data sets necessary to infer broad-scale patterns do not accumulate quickly.

Not surprisingly, the different scales, at which many organisms live, from ambits of microns for microbes to ocean basins for migratory fishes and marine mammals, along with variation in the drivers and patterns of diversity, render a single analysis impossible. In order to assess gradients in marine biodiversity we use a taxonomic framework for some groups of organisms and a habitat framework for others.

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Comparatively well-sampled groups taxonomically (primarily pelagic (water column) vertebrates and cephalopods) could be treated at a phylum or 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 otters, and some small cetaceans and pinnipeds, as well as benthic feeders such as walrus and grey whales, rarely venture beyond the continental shelf except when migrating. Global marine mammal species richness peaks at mid-latitude (around 60°) in both hemispheres (Kaschner et al., 2011; Figure 1a)². Pinnipeds mostly drive the peaks, which despite some highly endemic species in the subtropics, largely concentrate in polar to temperate waters (Figure 1b). Thick blubber or fur layers insulate marine mammals; hence they occupy all climate zones, although temperature nevertheless influences distributions (Tittensor et al., 2010), often through feeding and breeding constraints. As with other marine predators, food availability drives patterns in many marine mammals, but so does availability of breeding habitat for many species. Dugongs, as highly specialized herbivores, associate with sea grass beds in warm, shallow coastal waters and estuaries. Baleen whales, which feed at low trophic levels, require dense prey aggregations to sustain their metabolic needs, forcing most species to migrate to high latitudes during peak feeding seasons to utilize high summer productivity (except for some resident tropical populations associated with productive upwelling waters). Some species concentrate at specific breeding or calving grounds in winter. Toothed cetaceans generally feed at higher trophic levels and are not linked, as are some baleen whales, to zooplankton aggregations along the polar ice edges, and this helps drive higher species diversity at mid-latitudes (Figure 1a) (Kaschner et al., 2011). Nevertheless, the finer-scale distribution of most species links with ocean features that aggregate prey such as eddies, fronts or upwelling areas, or with specific breeding grounds. Many pinniped distributions correlate with prey aggregations; however, availability of suitable haul-out sites, on either land or sea ice, for moulting, breeding and pupping, limits most pinniped species, as does maximum length of foraging trips, as well as temperature (Tittensor et al., 2010).

Despite their often impressive body size, new discoveries of whale species still occur by re-evaluation of molecular and morphological evidence. Despite well-established broad-scale distributions of most small cetaceans, pinnipeds, sirenians and otters (Reeves et al., 2002), range maps or predictions of environmental suitability for the beaked whales (ziphiids) largely represent guesswork; their actual distributions potentially span entire ocean basins (Kaschner et al., 2011). Similarly, even after centuries of intense whaling in all oceans, the breeding grounds and migration patterns of some of the large baleen whales, such as North Pacific right whales, are still not well known.

Relatively low densities with often very large ranges, low detectability, and inconspicuous behaviour of many species limit studies on marine mammal distributions. To date, most dedicated sampling has centred on Northern hemisphere continental shelves and slopes (Halpin et al., 2009). Large knowledge gaps remain on species occurrence throughout much of the tropics and Southern hemisphere temperate waters north of 60° (Kaschner et al., 2011). Although range maps and opportunistic sightings

² All figures and tables can be found at the end of this chapter.

document species presence in an area and facilitate larger-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 variables 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 15-20 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 Cheloniidae, 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).

Within ocean basin-scale distributions, adult marine turtles generally migrate hundreds to thousands of kilometres from nesting beaches for foraging, often showing high site fidelity to both breeding and feeding areas. Immature turtles also show site fidelity to areas used for foraging and growth. For some species, primary habitat types, e.g., coral reefs for hawksbills, seagrass beds for green turtles, constrain foraging to tropical regions (Spotila, 2004).

Many marine turtle populations demonstrate ontogenetic variation in habitat use that is related to geography and oceanography (Bolten, 2003). In several places around the world, hatchlings disperse from nesting beaches and orient toward persistent, offshore current systems (e.g., Gulf Stream in the Atlantic Ocean), where they associate with ephemeral habitats in convergence zones, such as *Sargassum* communities. After spending the first few years of life in these oceanic areas and growing to larger body sizes, juvenile turtles tend to recruit to neritic habitats where they remain—for the most part—until reaching sexual maturity. Although this description provides a useful heuristic for understanding sea turtle life history distribution patterns, significant within-population variation exists in timing and duration of recruitment by individuals from one life stage—and habitat type—to another; these variations have implications for overall population dynamics and management (Bolten, 2003).

The wide distributions of marine turtles can vary greatly among populations, which are subject to multiple threats that operate on different spatial and temporal scales. Effectively prioritizing limited management resources requires understanding which threats will most strongly influence distribution patterns in space and time (Wallace et al., 2011).

2.4 Fishes

In English, ‘fish’ designates any aquatic multicellular animal (jellyfish, cuttlefish, starfish, etc.). The term ‘finfish’ designates those with a central spine comprised of vertebrae (Chordata/Vertebrata – vertebrates), whether or not present in adults, ossified, or with paired and/or impair fins supported by rays. Although no longer recognized as a valid taxonomic group, ‘finfish’ (hereafter “fish”) offers a practical descriptor of a group exclusive to aquatic life that constrains many adaptations and defines a similar body plan, while acknowledging diverse body forms.

By the end of 2013, more than 33,000 valid species of extant species were described (Eschmeyer, 2014), constituting more than half of all vertebrates; ca. 17,500 occur in marine environments for at least part of their life cycle. Surprisingly, species descriptions have accelerated since World War II: between 1999 and 2013 (15 years), a new fish species was described every day, a rate that is still increasing (Figure 2). This increase comes in spite of decreasing fish taxonomists around the world, and cannot be attributed to recent molecular advances, given the low proportion of species discovered by genetics methods. Different editions of *Fishes of the World* (e.g., Nelson, 2006) report new discoveries (Table 1), and although the deep seas were expected to deliver

many new species, given the assumed high rate of exploration of continental shelves <200 m, species richness per surface area in shallow waters remains much higher, noting that waters below 2,000 m deep remain largely unexplored. Coral reefs still deliver most newly described marine fishes each year, especially for cryptic species such as gobies and small labrids. Coral reefs are not the only source of new species: for instance, populations of many fish species previously thought to be distributed widely in the Indo-Pacific region are now recognized as different species between the Indian and the Pacific Ocean, and even more recently between the Red Sea and the Indian Ocean.

Fishes are ubiquitous throughout the world ocean, in locations as small as tidal pools that may dry up daily, and from the poles down to the base of the Marianas Trench in the West Central Pacific (11,782 m). They live in caves, on the shoreline, sometimes out of the water for some periods in mangroves or intertidal areas, over, on or in soft or hard bottoms, in crevices in rocky or coral reefs, and a few are even found in poorly oxygenated water. As in many groups, species richness (as well as species per family or genus, and number of genera) generally increases from high to low latitudes (Figure 3), more so than the number of families, but local climate, oceanography or phylogenetic history may alter this pattern (Tables 2 and 3). Shallow coral reefs with a high diversity of habitats and high biomass productivity support the most species; deep-sea corals are less species-rich. Several studies show highest species richness in the Coral Triangle (Indonesia, Philippines, Papua New Guinea region), thought to be the centre of tropical marine diversity. More than 300 widespread species (2 per cent) occur in 10 or more FAO areas (from over 19 possible areas), and 8,000 (47 per cent) occur in just one area (12,000 – 65 per cent in 1 or 2). Geographic and/or hydrological conditions restrict the majority of species distributions. Amphitropical distributions occur only in large pelagic species.

Although fishes occupy all depths, species diversity drops dramatically below the continental shelves. Depth ranges are incomplete for many species, but about 6,800 (58 per cent) of the 11,000+ species with recorded ranges in FishBase (www.fishbase.org; Froese & Pauly, 2014) are restricted to the upper 200 m, with only ca. 620 spp. (4 per cent) below 2,000 m. Lack of data on deep-sea species, except for a few targeted around submarine seamounts in the high seas by non-sustainable fisheries, illustrates a serious sampling bias that demands cautious interpretation.

Only a few species of shark and rays have been caught below 3,000 m and none below 4,000 m. Gobies that constitute the most speciose family in marine life zones in tropical and temperate waters in general, are barely present in the North Pacific above 40° N. The life cycles of more than 700 hundred species (including salmonids, eels), alternate between marine and fresh waters (amphidromy, diadromy, catadromy, anadromy).

Few herbivorous species occupy high latitudes as compared to tropical areas. Although anti-freeze blood proteins prevent ice formation in the blood of some cold water fishes, digesting plants requires a higher metabolic activity than most cold water fishes can maintain. Based on recorded information for about 6,400 species in Fishbase, about 1,000 species are top predators and carnivores, 4,400 are predators or omnivores, and

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 cephalopods, raising questions about their total biomass and global patterns. For those areas that have been sampled, recent evidence suggests that primarily oceanic squid peak in diversity in the northern hemisphere at temperate latitudes, a pattern reflected by (primarily coastal) non-squid cephalopods in the Pacific Ocean at least; temperature strongly drives these patterns (Tittensor et al., 2010).

More information on the biology, biogeography and diversity of cephalopods is available from CephBase (cephbase.eol.org), which is now available through the pages of the Encyclopedia of Life.

2.6 *Marine Microbes*

Marine microbes, defined as single-celled or chain forming microorganisms, span a very broad size range, from microscopic cells that are $<1/50^{\text{th}}$ the diameter of a human hair to forms visible to the naked eye. They are found throughout all the oceans, from the tropics to the poles and from the surface to the deepest depths. These single-celled organisms divide asexually, up to several times per day, leading to high biomass that fuels nearly all marine productivity, including all important fisheries around the globe, and drives global biogeochemical cycles, including carbon, oxygen, and many others. Marine microbes also represent the most phylogenetically diverse organisms on Earth. A single litre of seawater can contain representatives of all major branches of the tree of

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 large-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 exceptions exist. For example, Charles Darwin on his '*Beagle*' voyage noted that nitrogen-fixing phytoplankton can become very abundant in the open ocean and form surface mats and filaments. Latitude interacts with season in forcing plankton abundance patterns. In lower latitudes, seasonal variations in irradiance and temperature, including ice cover, result in highly variable plankton abundances seasonally, with spring and fall peaks. Organism physiology, nutrient availability, susceptibility to grazing, and viral attack, as well as the fluid flow regime, further define distributions.

2.7 Zooplankton

Zooplankton occur from pole to pole, and from tide-pools to the deepest trenches in the ocean. They span the size range from single cells and multicellular organisms that are smaller than 0.05 mm, to gelatinous colonies that are longer than the largest whales. In the vast scale of the oceans, they are united by their inability to control their movement in the horizontal scale, but many perform vertical migration of hundreds of metres per day.

As an assemblage, the ~7,000 described species of multicellular zooplankton (Wiebe et al., 2010) encompass species from every major animal phylum, and the majority of the minor phyla; some of these 15 phyla are almost exclusively planktonic (Bucklin et al., 2010). Many additional phyla are classically considered as non-planktonic, but they do in

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 decapods (predators); note that the latter two groups may be considered either planktonic or benthic, given their tight association with the seafloor.

Lacking the arthropod skeleton, most other planktonic groups are considered "gelatinous" zooplankton, which are generally not well collected in nets because of their fragility and often lower abundances. With the exception of the nearly 140 species of pelagic tunicates (larvaceans, pyrosomes, doliolids and salps) and about 80 species of shelled pteropods, all other groups are clearly predatory. Two of the three classes of medusae or "jellyfish" within the phylum Cnidaria (hydrozoans and scyphozoans), are clearly the most speciose gelatinous groups, followed by the phylum Mollusca with its three functional groups (shell-less pteropods, heteropods, and cephalopods – although the latter are considered by many as nekton, as are the fishes). Once grouped with the cnidarians, the Ctenophora, or comb-jellies, are probably the most seriously underestimated group in terms of their biodiversity: their extremely fragile body construction confounds specimen collection. Of the extant worm-like groups, only Chaetognatha (arrow worms) occur in plankton samples in high abundance; primarily benthic polychaetes and nemertines usually occur in the plankton in modest diversity and abundance.

The >100-year quest to find patterns in zooplankton distribution shows that each species has its own environmental preferences and tolerances, with some species confined to specific regional habitats and others that are relatively wide-spread. Over time, several broad patterns have emerged for zooplankton that exhibit consistency across multiple taxa (Dolan et al., 2007). Diversity in offshore habitats exceeds that in coastal regions, although coastal abundance and biomass may be higher. Diversity increases from the poles to the tropics, often with an equatorial dip (Boltovskoy, 1999)

(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., Rombouts et al., 2009). Obtaining sufficient data for all taxa under consideration, across the full spectrum of habitats, remains a primary hurdle. One of the greatest accomplishments of the Census of Marine Life (CoML) was to build the Ocean Biogeographic Information System (OBIS), a system that can address such questions by pulling together the disparate datasets to allow such synthetic tasks to be undertaken (e.g., Tittensor et al., 2010; Vanden Berghe et al., 2010).

New insights derived from DNA-based approaches represent the biggest current challenges in understanding zooplankton biodiversity. Initially, these tools offered great promise in tackling simple issues, such as phenotypic variation or rates of hybridization. In practice they are revealing numerous cryptic species not previously recognized based on morphology alone, that force rethinking on what represents a species, and the geographic/environmental boundaries between them. Many species believed to span several ocean basins may in fact represent species assemblages, suggesting that current estimates may severely underestimate the overall diversity of marine zooplankton in all groups.

3. Benthic ecosystems

3.1 Rocky Shore Ecosystems

The ease of access and suitability for experimental work of rocky shore habitats have attracted a long history of scientific study and engaged a broad audience. Biodiversity assessments in this habitat typically use quadrat and transect assessment with visual or photographic identification, and do not require ships or complex technology. In many rocky intertidal environments, and particularly in regions with large tidal ranges, aerial exposure at upper tidal levels and predation at low tidal levels create distinct bands of species, or zonation, that represent one of the most striking and well-documented gradients in the ocean (first described by Stephenson and Stephenson 1949). The global distribution of rocky intertidal habitats creates opportunities to compare latitudinal trends and to detect large-scale patterns and changes. Despite fairly well-understood local patterns and processes, large-scale patterns (regional to global) are difficult to discern; however, many drivers, such as temperature and exposure, act on large scales, as do human influences, such as invasive species and pollution. Examples from around the world (e.g. Thompson et al., 2002) demonstrate the past and current effects on

rocky shores of pollution (e.g. oil, eutrophication), overfishing, introduced exotic species, modification of coastal processes (e.g. coastal defences, sedimentation) and global change (e.g. temperature, sea level). The relative magnitudes of some anthropogenic pressures differ among industrialized countries and developing countries.

Very few long-term studies have addressed temporal trends in rocky shore biodiversity and most focus locally and regionally. Barry et al. (1995) and Sagarin et al. (1999) observed changes in the abundance of macroinvertebrate species in a rocky intertidal community in California between surveys in 1931-33 and 1993-96. These changes are consistent with recent climate warming that shifts species northward. Eight of nine southern species increased in abundance and five of eight northern species decreased; however, cosmopolitan species displayed no trend. Blanchette et al. (2008) described the spatial pattern of distribution of species abundance for rocky intertidal communities along the Pacific coast of North America from Alaska to Mexico (more than 4000 km).

This biogeographic study represents one on the larger-scale analyses of this habitat, and reported strong spatial structure in the rocky intertidal communities of the north-east Pacific. Breaks in similarity among clusters generally linked with known biogeographical and oceanographic discontinuities. Sea surface temperature and species similarity both correlated strongly, coinciding with long-term temporal trends along the California coast that point to both geography and oceanographic conditions as primary determinants of patterns of intertidal community structure.

Recent efforts through the NaGISA project of the Census of Marine Life (e.g., Iken et al., 2010) and others demonstrate large-scale patterns. The NaGISA project gathered information on rocky shore systems globally, and compared diversity and abundance of key benthic groups from intertidal and shallow subtidal rocky shore sites in order to identify latitudinal trends and their environmental drivers. Global analyses were constrained by differences in sampling efforts (numbers, years, and strata sampled), timing of sampling, under-sampling of some ecoregions, and unbalanced representation of the northern and southern hemispheres. Results indicate that distribution patterns of diversity and biomass of various taxonomic groups (e.g., macroalgae, gastropods, decapods and echinoderms) are very complex and sometimes defy the expected latitudinal gradient of species decreasing towards the poles. Regional diversity hotspots often complicate any simple broad-scale pattern. Despite differences in sampling effort, timing, and coverage, this effort identified likely drivers of diversity of specific taxa and communities, several of which were tightly linked to human activities. For example, pollution indices correlate significantly with diversity in several phyla (e.g., Iken et al., 2010). Although the natural heterogeneity of these systems complicates unequivocal establishment of cause-consequence relationships, a larger data base for the analysis of global diversity trends and their drivers will provide more substantive evidence for the identification of likely drivers.

However, although much progress has been made recently, our understanding of rocky shore biodiversity patterns remains incomplete, especially beyond local or small

regional scales. Similarly, the complexity of these systems constrains efforts to assign environmental or human-induced drivers to rocky shore diversity, because such drivers can act on different scales (Benedetti-Cecchi et al., 2010), and may act cumulatively, synergistically, or antagonistically. That 40 per cent of the world's population currently lives within 100 km of the coast enhances the urgency of this issue, particularly given that as population density and economic activities increase, so will pressures on rocky shores, as well as other coastal ecosystems from tropical to temperate systems, and even some polar regions.

3.2 *Tropical coral reef ecosystems*

Tropical coral reefs span the Indo-Pacific and Atlantic Oceans, although cool upwelling associated with boundary currents limits distributions along the west coasts of Africa and South/Central America. We refer readers to Chapter 43 for a more detailed discussion on tropical and subtropical coral reef habitats that extends beyond our focus on biodiversity gradients. The diversity and productivity of coral reefs and associated ecosystems (mangroves, seagrasses and pelagic habitats) are among the highest globally, providing essential ecosystem services to tropical countries. The taxonomic richness of corals reefs is second to none, with tropical coral reefs housing 25per cent of all known marine life on the planet including sea fans, sponges, worms, starfish, brittle stars, sea urchins, crustaceans, and fish. In fact the variety of life supported by coral reefs rivals that of the tropical forests of the Amazon or New Guinea. Temperature and habitat complexity, particularly for stony corals and bony fish, have been shown quantitatively to drive tropical reef diversity on global scales (Tittensor et al., 2010), with other features such as habitat area (rocky substrates within the photic zone), and historical factors (historical speciation/extinction patterns) being secondary drivers of regional to global patterns of coral reef biodiversity.

Tropical coral reefs are restricted to warm waters with average annual temperatures typically above 18 °C though with annual mean temperatures between 20-27 °C, which enable stony corals, via photosynthetically enhanced calcification, to lay down a skeleton fast enough to build up reefs over multiple generations. The symbiosis between stony corals and their intra-cellular symbionts (zooxanthellae) limit coral reefs to sunlit substrates, optimized in the top 10-15 m of the water column but with reef build-up possible down to 30-50 m depth. Thus coral reefs are restricted to island and continental fringes, and shallow oceanic banks that reach the photic zone. Classic coral reef descriptions emphasize oligotrophic low-sediment oceanic conditions being ideal for coral reefs, however vibrant coral and reef growth, with high-diversity communities, can occur in relatively high turbidity and sedimentation conditions in eutrophic waters near highly productive major estuaries (e.g., along the Andaman Sea). This ability for coral reefs to flourish in both sets of conditions is due to tight cycling of carbon and nitrogen between the coral symbionts.

A total of 836 tropical reef-associated coral species have been described globally, with 759 from the Indo-Pacific and just 77 from the Atlantic, with no species in common

across these two ocean systems. The broad swath of equatorial currents that cross the Pacific and Indian Oceans, joined through the 'leaky' Indonesian region, dominates global patterns of coral reef diversity connecting East Africa to French Polynesia - of 4,000 species of tropical fishes, 492 are shared between the Western Indian Ocean and French Polynesia (Randall, 1998). Westwards from here, the large deep-water barrier in the East Pacific isolates the Eastern Tropical Pacific from the broader Indo-Pacific.

At the centre of the Indo-Pacific, the Indo-Australian Arc (IAA) provides optimal temperature conditions and the highest habitat area for corals; within this 'Coral Triangle' (Roberts et al., 2002; Hoeksema, 2007) sub-regions show peaks of over 600 species of hard corals, 550 species of reef fishes and 50 species of stomatopods (Reaka et al., 2008). Diversity declines east and west from here into the Central Indian and Pacific Oceans (<300 coral and fish species, 5-15 stomatopods), though new evidence suggests a second peak of diversity in the Western Indian Ocean/Eastern African region, in both stomatopods (30 species, Reaka et al., 2008) and hard corals (350-400 species, Obura, 2012). The lowest diversity in tropical Indo-Pacific coral reefs is in the Eastern Pacific due to isolation, with <150 coral and fish species, and <5 stomatopod species. Coral reefs harbour high levels of cryptic diversity: for instance, populations of many coral and fish species previously thought to be distributed widely in the Indo-Pacific region are now recognized as different species between the Indian and the Pacific Ocean, and even more recently between the Red Sea and the Indian Ocean.

High levels of endemism are shown in remote island coral reef systems, in low-dispersive groups such as fishes. In Hawaii and the Easter Island group levels of endemism in fish exceed 20 per cent (Randall, 1998), and only 12 shore fish species are shared between the Red Sea, Easter Island, and the Hawaiian Island archipelago. The small size and lower diversity of the tropical Atlantic, with subregions in the Caribbean, Gulf of Mexico and around Brazil, may increase vulnerability to anthropogenic and climate threats compared to the larger, more diverse Indo-Pacific.

Deep-water corals also form reef structures, which we describe briefly in the deep-sea section below; we also refer readers to Chapter 42, which presents a more detailed description of these environments.

3.3 *Mangrove forest ecosystems*

Mangroves are woody plants that grow normally in tropical and subtropical latitudes along the land–sea interface, bays, estuaries, lagoons, and backwaters (Mukherjee et al., 2014). These plants and their associated organisms constitute the 'mangrove forest community' or 'mangal'. Although mangrove ecosystems occur in more than 120 countries world-wide, encompassing just over 80 plant species, subspecies and varieties globally (Massó i Alemán et al., 2010), they are generally species-poor vegetation formations. Nonetheless, they support a complex community of animals and micro-organisms, the numbers of which have never been reliably estimated. Mangrove decapods and, to a lesser extent, insects are better studied than most taxa but the

scientific community is only just beginning to understand how mangrove ecosystems work and what they contribute to ecosystem functions, goods and services, including biodiversity support, storm protection, fisheries production, effects on water quality and providing significant carbon sinks (Dahdouh-Guebas, 2013). Several recent papers document immense carbon sequestration and suggest they may represent the most carbon-rich tropical forests (Donato et al., 2011).

Mangrove tree species may be divided into two distinct floristic groups, an Atlantic-East-Pacific and Indo-West-Pacific, the latter of which represents the mangrove species richness peak between 90 and 135 degrees East. Latitudinal richness peaks globally near the equator (Figure 4). Local species richness links significantly to regional richness (Ellison, 2002), with recent recognition that high variability temperature interacts with aridity in defining upper latitudinal limits of *Avicennia* and *Rhizophora* (Quisthoudt et al., 2012).

The International Union for Conservation of Nature (IUCN) rarely lists mangrove species as threatened because they are often widely distributed, creating conservation challenges. Yet, reports of local extirpations, sometimes hidden as cryptic ecological degradation, may affect local and regional fisheries or other coastal functions (Dahdouh-Guebas et al., 2005). These losses point to an urgent need to re-assess mangrove ecosystems nationally and regionally to identify regions most at risk of losing mangrove ecosystems and associated functions, goods, and services (Mukherjee et al., 2014).

3.4 Coastal sedimentary ecosystems

The coastal zone denotes the relatively narrow transition zone between land and ocean where strong interactions occur with humans. Sediment covers much of the continental shelf from the poles to the equator and supports a wide diversity of invertebrates spanning almost all animal phyla. The shallowest depths along the shoreline support seagrasses, mangroves, and salt marshes, but seabed primary production is otherwise limited to benthic photosynthetic microbes that quickly disappear as light attenuates with depth. Resuspended material and phytoplankton sinking from the photic zone add significantly to benthic production.

For organisms ranging from large megafaunal clams and crabs to meiofaunal nematodes and copepods, temperature primarily defines broad biogeographic provinces, but within regions substrate composition plays a major role in defining composition and diversity of sedimentary fauna. Sand and coarser substrates typically occur in high-energy exposed environments, with muds characterizing quiescent areas. Depth and productivity also strongly influence faunal patterns, with peak diversity at mid-shelf depths and locations with moderate organic input (Renaud et al., 2007). A hump-shaped pattern of maximum diversity linking with productivity has been reported elsewhere, including the Arctic (Witman et al., 2008) and in fossil marine invertebrates (brachiopods) (Lockley, 1983). Intertidal sediments typically exhibit very low diversity,

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 temperate and polar regions, but because sampling effort is strongly biased towards temperate seafloor environments, this complicates broad-scale comparisons. For example, total species number for sedimentary invertebrates in the Canadian Arctic compares favourably with the Canadian Pacific and Atlantic (Archambault et al., 2010) and on the eastern and western coasts of the United States, gastropod molluscs increase in species richness from the Arctic towards the equator, but peak in the subtropics (Roy et al., 1998). Multiple studies testing latitudinal gradients over varying scales find few consistent patterns, and suggest that complex differences in local environments play a much greater role than latitude in defining diversity and composition; indeed, landscape heterogeneity may obliterate a simple broad-scale pattern, except where broad physical drivers dominate. The strong influence of the Gulf Stream on coastal European waters produces high species richness in high latitude sediments (Ellingsen and Gray, 2002). Algal genera generally exhibit an inverse latitudinal gradient, with biodiversity hotspots in temperate regions, but bryopsidalean algae peak in diversity in the tropical Indo-Pacific region (Kerswell, 2006).

Key data gaps in species richness data for coastal sediments of Africa, South America, the western tropical Pacific and polar regions (Costello et al., 2010) constrain latitudinal comparisons, but we do know that Australian coastal sediments support very high species richness (Butler et al., 2010), and that Antarctica diversity (Griffiths, 2010) only modestly exceeds Arctic diversity (Piepenburg et al., 2011).

However, it is recognized that even with less attention than European waters, the Indo-Pacific area is the most diverse area of our oceans. Molluscs have the largest diversity of all phyla in the marine environment (Bouchet, 2006), and mollusc diversity is exceedingly high in the tropical waters of the Indo-Pacific, particularly in coral reef environments (Crame, 2000). How this pattern translates to sedimentary fauna remains unknown and leads us to conclude that we need far more studies in many regions to draw firm conclusions about general patterns of marine biodiversity in the coastal zone.

Very few studies compare sedimentary fauna across sharply contrasting sediments because differences in sampling gear complicate such comparisons. Sampling cobbles and gravel, which support a wide diversity of encrusting epifauna and flora, requires very different tools than sampling muds or even coarse sand. Nonetheless, a qualitative comparison of species lists indicates strongly different faunas within these substrata, linking to a wide range of variables spanning physical disturbance, larval supply, and food quality, to name just a few.

3.5 *Deep-sea benthic ecosystems*

The deep sea spans depths from 200 m to almost 11,000 m, encompassing more than 90 percent of the global ocean area, and representing the largest ecosystem on Earth (Watling et al., 2013). However, less than 5 percent of its area has been explored, and less than 0.001 per cent, the equivalent of a few football fields, has been sampled quantitatively, making it among the least known environments on Earth. Decades ago researchers projected 1 to 10 million total species in the deep sea (Grassle and Maciolek, 1992). More recently, Mora et al. (2011) predicted that 91 per cent of marine species remain unknown, largely due to undersampling of the deep sea (other works downsize that estimate – see Appendix). For example, 585 of 674 isopods species collected in recent expeditions to the deep Weddell Sea were new to science (Brandt et al., 2007). Sampling is uneven, with very limited understanding of hard substrate biota outside of chemosynthetic ecosystems, and under-sampling of metazoan meiofauna and protozoa.

Deep-sea sediments cover much of the deep-sea floor, with little variation in temperature and salinity. The absence of photosynthesis below ~200 m means that most deep-sea life depends exclusively on sinking food from surface waters. These sediments support a highly diverse fauna spanning most phyla; the first comprehensive sampling covered just 21 m² of seafloor, yielding 1,597 species from 13 different phyla of invertebrates (Grassle and Maciolek, 1992). The best known broad-scale diversity patterns for deep-sea invertebrates and fishes are the unimodal diversity-depth relationship, bathymetric zonation, and a general decline in species richness towards the poles. Macrofauna in total and as individual taxa provide the strongest evidence for unimodal diversity-depth relationships (Rex and Etter, 2010) in which, despite some contradictory patterns in some locations, highest diversity occurs at depths of ~1,500-2,000 m. Significant unimodal diversity-depth relationships have also been reported for nematodes, ostracods, and foraminifers in the Arctic Ocean, and for megafaunal invertebrates and fishes in the western North Atlantic. Reduced population densities under extreme food limitation may suppress species diversity in the deep oligotrophic abyss (>3,000-4,000 m depth), whereas elevated carbon fluxes at shallow depths may suppress diversity by driving competitive exclusion or creating physiological stress. On upwelling along continental margins, low oxygen at upper bathyal depths (100-1000 m) suppresses diversity. Declining food supply and thermal energy with depth (and distance from continents) are likely to drive these patterns, which are complicated by regional variation in food availability. Topographic isolation or complexity, boundary effects, sediment characteristics, currents, oxygen concentration, physical disturbance, biological interactions and patch dynamics, as well as evolutionary history, also influence diversity and distribution patterns at regional and local scales (Rex and Etter, 2010).

Many fish and invertebrate taxa occur at a similar depth range in “bands” of distinct assemblages or “zones”. Zonation describes sequences where few changes in species composition occur within a band, but abrupt faunal boundaries occur. However, major oceanographic features, such as oxygen minimum zones, strong bottom currents and

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 complicates these analyses, particularly in abyssal environments where many species occur only once in samples (Grassle and Maciolek, 1992).

Multiple biological and physical factors, such as larval dispersal, competition, predation, temperature, oxygen concentration, hydrostatic pressure, and food supply, all potentially drive zonation. Temperature, oxygen, and food supply vary most in the upper bathyal region, where pronounced species turnover occurs, creating a ubiquitous shelf-slope transition zone. In lower bathyal (3,000-4,000 m) and abyssal depths, declining food supply homogenizes fauna and reduces species turnover.

Multiple studies report latitudinal diversity gradients in many deep-sea invertebrate groups, although patterns vary in sparse sampling of limited taxa (Kaiser et al., 2013). For several macrofaunal groups, and for meiofaunal foraminifers, diversity decreases with increasing latitude in the North Atlantic. In the South Atlantic, isopod diversity increases, whereas gastropods and bivalves decline poleward (although there are exceptions to this trend). Strong seasonality and pulses of phytodetritus at high latitudes may depress diversity, much like physical disturbance. Other work suggests increasing diversity in the northern hemisphere for nematodes.

Thousands of topographic features, such as submarine canyons and fjords, incise continental and island margins and increase complexity of bottom topography, modify abundance and diversity by intensifying mixing, amplifying currents, enhancing productivity, sediment and food deposition, and channel cascading shelf waters. Enhanced food deposition drives species aggregations and consequent increased diversity in these habitats compared to adjacent, topographically simpler areas. Steep topography and amplified currents often expose bedrock and boulders within canyons, supporting additional fauna, such as megafaunal and macrofaunal suspension feeders that require hard surfaces for attachment and strong currents for food delivery.

Biogenic reefs (formed mainly by deep-water coral and sponges) occupy hard substrata with high currents, often within basins or along the continental margins. These reefs form from skeletons of dense aggregations of one or a few species. The skeletons create surfaces for colonization, extend higher in the water than the surrounding seafloor (thus reaching faster currents and greater food delivery) and add spaces for protection from predators and other disturbances. These reefs therefore enhance local species diversity, and provide nursery areas for many macro- and megafaunal invertebrates and fishes.

Despite their remoteness, human activities affect deep-sea diversity, resulting in declines in deep-sea fishes, loss of habitat-forming invertebrates (e.g., deep-water corals), and increased contaminants in deep-sea biota. Although these impacts illustrate local to regional effects, the cascading effects of warming surface layers portend substantial changes in the food supply to deep-sea ecosystems. Manifestations of climate change including ocean warming, acidification and deoxygenation, may reduce the bathyal habitats available, with concomitant broad-scale changes in patterns of

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 CO₂ 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 alphas diversity 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 vesicomid 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 the 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 knolls and hills with an elevation of 100 m or more. They occur in all oceans of the world, from the tropics to the poles, and cover depth ranges from near the surface to the abyss. The total number remains uncertain because so little of the deep ocean has been surveyed, but estimates range from 14,000-50,000 large seamounts and tens to hundreds of thousands of smaller ones (Stocks, 2010).

Three important characteristics distinguish seamounts from the surrounding deep-sea habitat (Clark, 2009). First, as “islands” of shallower sea floor, they provide a range of depths for different communities. Second, their typical hard and often bare rock surfaces contrast with the fine, unconsolidated sediments that cover the majority of the sea floor. Third, the physical structure of some seamounts alters local hydrography and currents so as to concentrate species and productivity over the seamount, thus increasing their importance as oceanic ecosystems but also attracting commercial exploitation. The very low proportion of seamounts sampled globally limits understanding of their diversity, and the composition, structure, function, and connectivity of seamount ecosystems remain unexplored and unknown except in a few locations (Stocks and Hart, 2007).

Seamount benthic communities are rich and varied; sandy or muddy sediments dominate where currents are slow, with mostly deposit-feeding species of polychaetes, echinoderms, various crustaceans, sipunculids, nemertean worms, molluscs, sponges, and nematodes utilizing sinking particulate matter. Suspension feeders, including corals, crinoids, hydroids, ophiuroids, and sponges, dominate where faster currents expose rocky areas. The large corals and sponges can form extensive and complex reef-like or thicket structures, which add habitat for smaller mobile fauna. Seamount biodiversity research has rapidly increased the number of known species in recent decades. A global

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 estimated 2.2 million eukaryotic species (Mora et al., 2011), of which science has

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-scale studies to explore this question began long ago and especially in the last decade (e.g., Rutherford et al., 1999; Roberts et al., 2002), but the enormous amounts of data collected and compiled by the Census of Marine Life enable exploration and mapping patterns across more taxonomic groups than ever before (Tittensor et al., 2010) to understand the consistency of diversity patterns.

Perhaps the most common large-scale biodiversity pattern on the planet is the 'latitudinal gradient', typically expressed as a decline in species from the equator to the poles (Figure 5). Adherence to this pattern varies among marine taxa; Chlorophyta and other macroalgae, for example (Figure 5, lower right panel), do not exhibit the same latitudinal gradient, as noted earlier above in this chapter). Although coastal species generally peak in abundance near the equator and decline towards the poles, seals show the opposite pattern; indeed pinnipeds peak at high latitudes (Fig. 1a). Furthermore, strong longitudinal (east-west) gradients, complicate patterns, with 'hotspots' of richness across multiple species groups in the 'Coral Triangle' in the Indo-Pacific and the Caribbean (Figure 6).

Oceanic organisms, such as whales, differ in pattern entirely, with species numbers consistently peaking at mid-latitudes between the equator and poles. This pattern defies the common equator-pole gradient, suggesting that different factors are involved. Different processes may control species richness among oceanic and coastal species (for example, in terms of dispersal, mobility, or habitat structure), but general patterns appear to be reasonably consistent within each group. However, across all groups studied, ocean temperature is consistently related to species diversity (Tittensor et al., 2010), hence the effects of climate change are likely to be observed as a restructuring of marine community diversity (Worm and Lotze, 2009)

Although the above patterns hold for the 11,000 species studied (Tittensor et al., 2010), numerous groups and regions were not represented. For example, global-scale patterns of diversity in the deep ocean remain largely unknown (Rex and Etter, 2010). Our diversity and distribution knowledge is taxonomically biased towards large, charismatic (e.g., whales) or economically valuable (e.g., tunas) species. Our knowledge of patterns in microbial organisms remains particularly limited relative to the enormous diversity therein, and enormous challenges to even measure biodiversity remain. Viruses remain a critical part of the oceanic system for which we lack any global-scale biodiversity knowledge.

Other than species richness, we are just beginning to explore other patterns of global marine biodiversity. Patterns of 'evenness' in reef fishes, which relates to relative proportions of individual species in the community, apparently show an inverse gradient (Stuart-Smith et al., 2013). This pattern, in turn, affects 'functional richness', which relates to the diversity of functions in reef fishes, a potentially important component of

ecosystem productivity, resilience, and goods and services provision. The importance of these patterns depends on their robustness and consistency across different species groups, but opening such new insights into other facets of biodiversity provides additional information with which to manage it, particularly in support of human welfare.

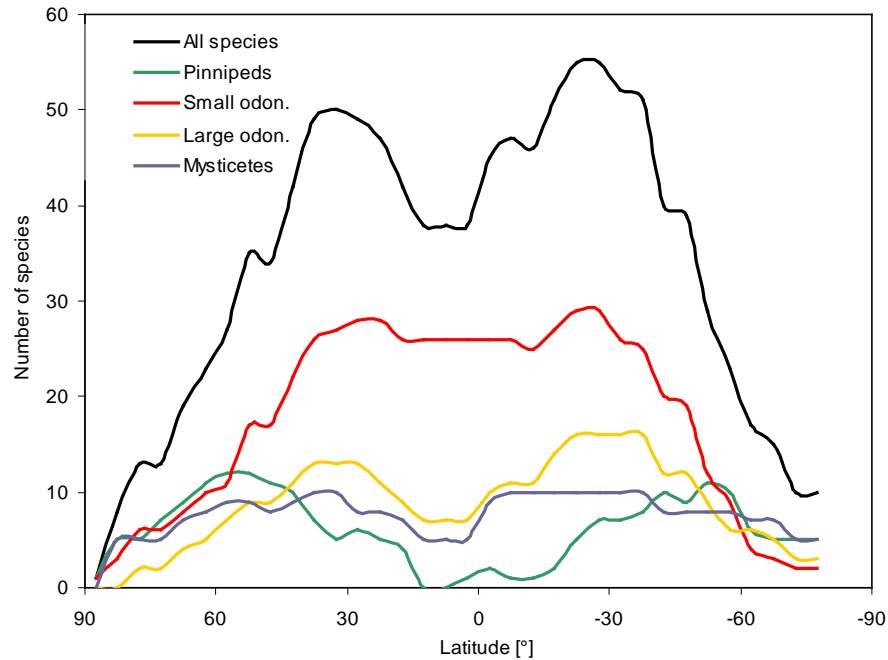
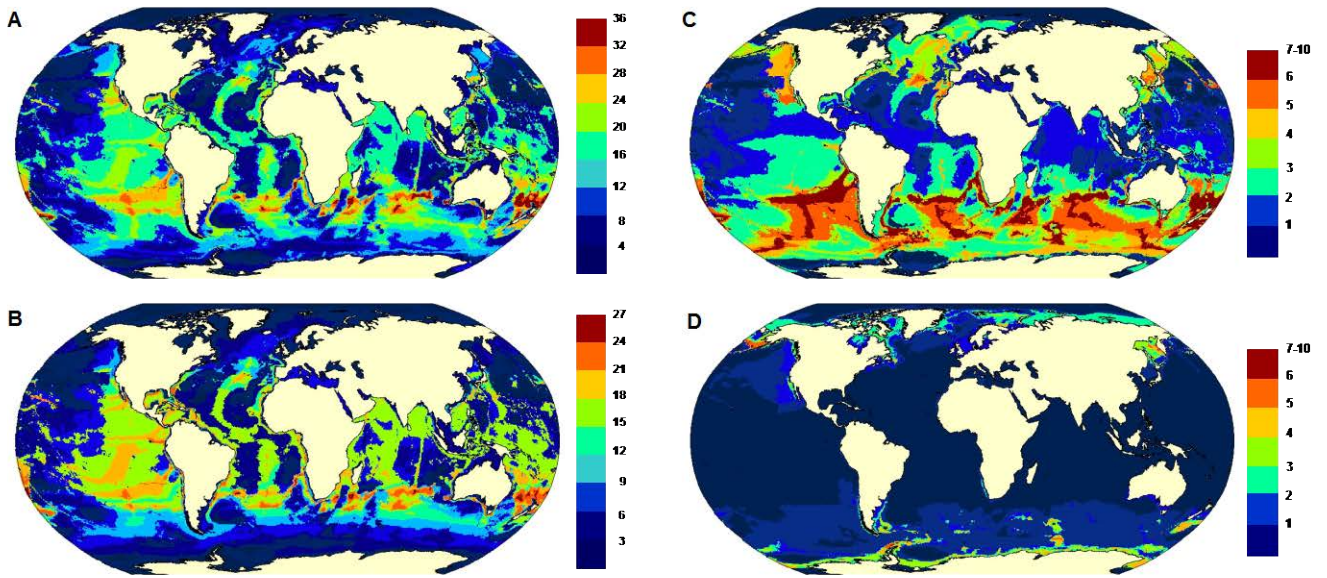


Figure 1a. Global marine mammal species richness peaks between 30 °and 60 ° in both hemispheres. Number of species (as predicted by a relative environmental suitability model, (Kaschner, 2006) was summed over 5° latitudinal bands for all species, mysticetes, small odontocetes, large odontocetes (beaked whales and sperm whales), and pinnipeds (from Kaschner et al., 2011).



The boundaries and names shown and the designations used on this map do not imply official endorsement or acceptance by the United Nations.

Figure 1b. Predicted patterns of marine mammal species richness. A. All species included in the analysis (n=115), B. Odontocetes (n=69), C. Mysticetes (n=14), D. Pinnipeds (n=32). Colours indicate the number of species predicted to occur in each 0.5°x0.5° grid cell from a relative environmental suitability (RES) model, using environmental data from 1990-1999, and assuming a presence threshold of RES>0.6. (from Kaschner et al., 2011).

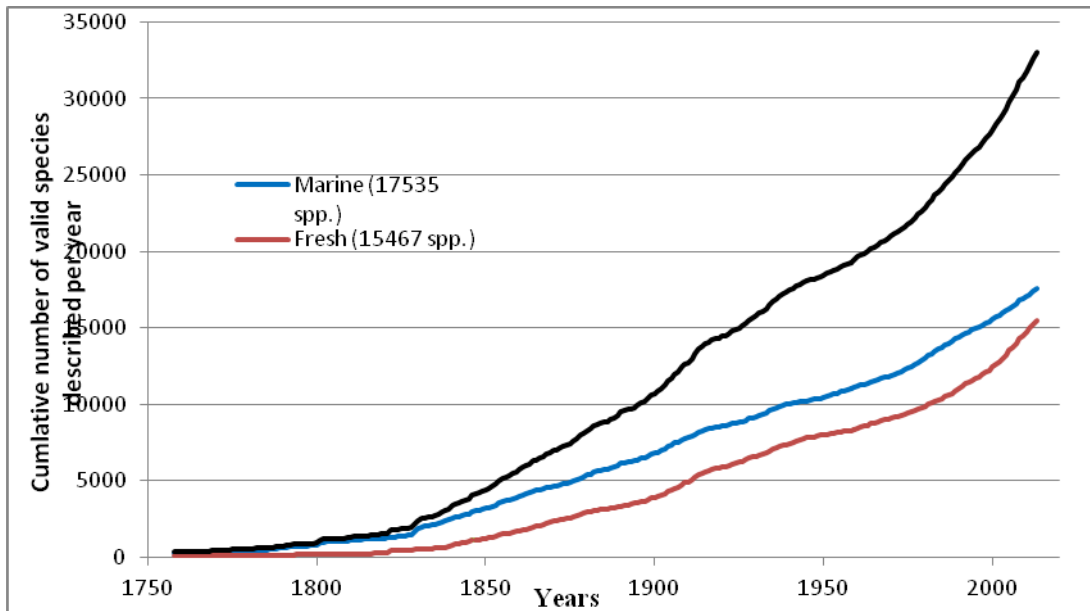


Figure 2. Cumulated number of species described per year between 1758 and 2013. The rate of descriptions accelerates after 1950, mainly due to an increasing number of freshwater species descriptions; the rate of marine species descriptions has been linear since the early 1980s.

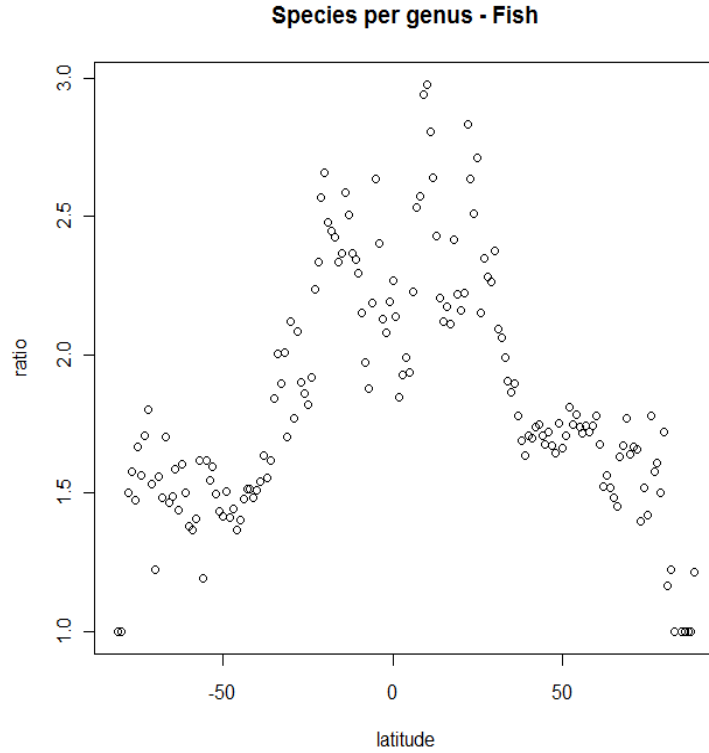


Figure 3. Number of species of fish per genus, in each latitudinal band of 1 degree, as calculated from distribution data available in OBIS on 26 September 2011.

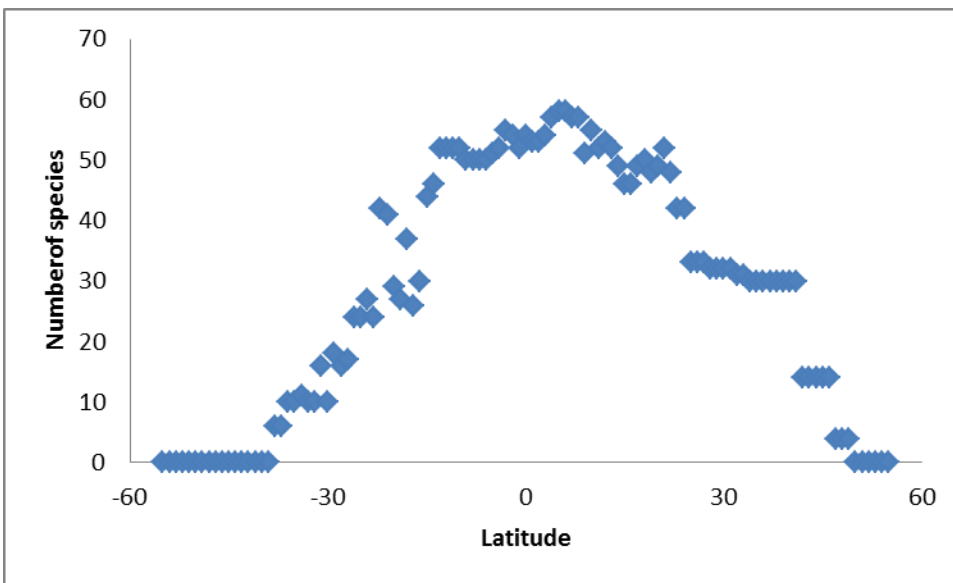


Figure 4. Latitudinal species richness of mangrove plant species.

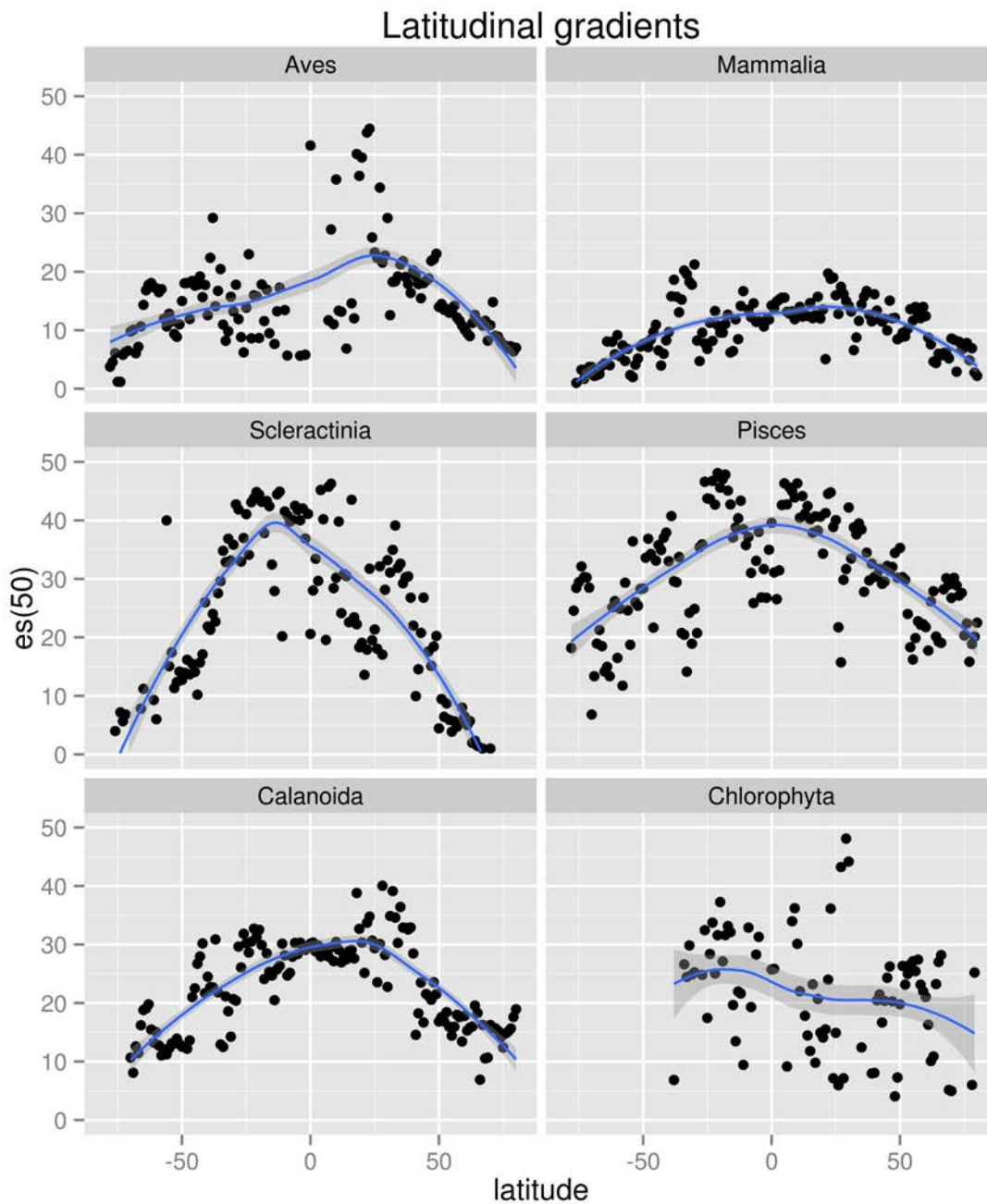


Figure 5. ES(50) calculated for various groups, from the data as available in OBIS as of the end of 2012. ES(50) (or Hurlbert's index) represents the numbers of species expected to be present in a random sample of 50 individuals; this metric measures the diversity (not species richness, as its name might 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 Development Core Team, 2014), using package ggplot2 for LOESS and plotting (Wickham, 2009).

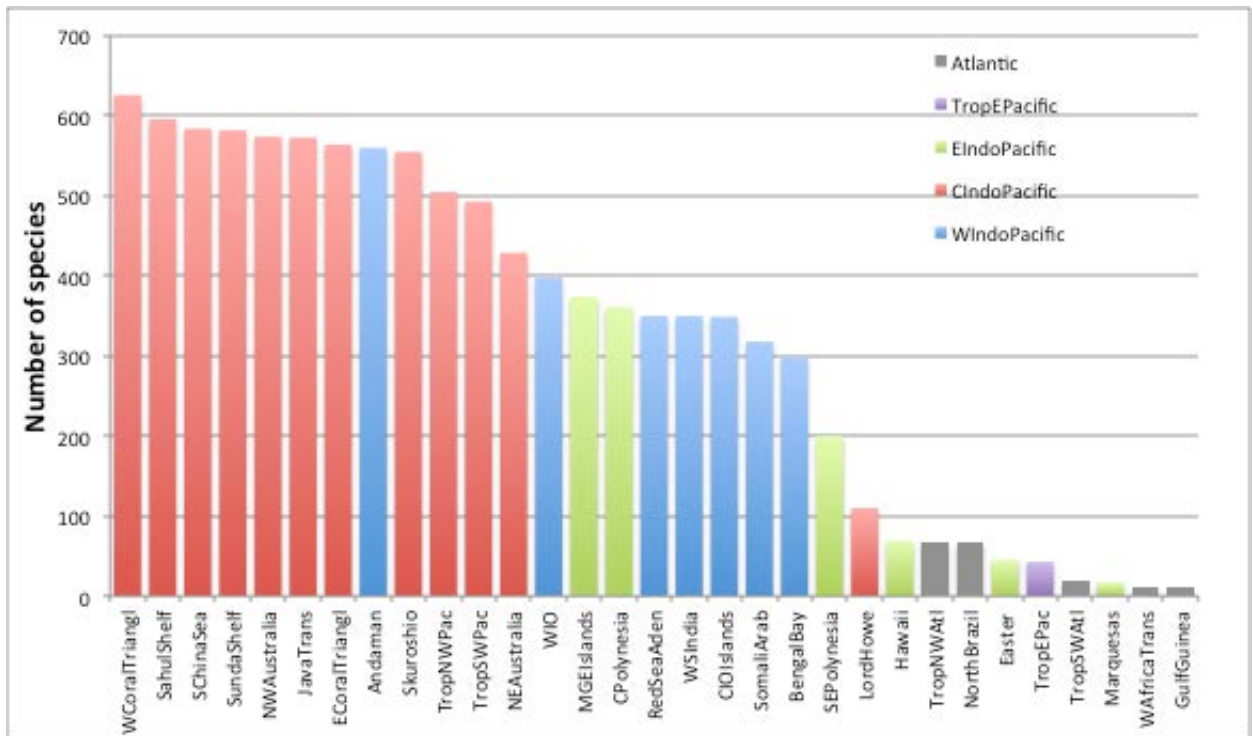


Figure 6. Coral species richness by province in the Marine Ecosystems of the World Classification, from the IUCN Red List of Threatened Species database (IUCN 2013).

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
Mediterranean and Black Sea	811
Atlantic, Western Central	2428
Atlantic, Eastern Central	1699
Atlantic, Southwest	1777
Atlantic, Southeast	1779
Atlantic, Antarctic	250
Indian Ocean, Western	4432
Indian Ocean, Eastern	4757
Indian Ocean, Antarctic	250
Pacific, Northwest	5299
Pacific, Northeast	717
Pacific, Western Central	6490
Pacific, Eastern Central	4138
Pacific, Southwest	2249
Pacific, Southeast	1916
Pacific, Antarctic	170

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	E	1115					W	5299	E	717
Central	W		E	811					W	6490	E	4138
Central	W	2428	E	1699	W	4432	E	4757				
South	W	1779	E	1777					W	1916	E	2249
Antarctic	S	250			S	250			S	170		

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Chapter 34

Appendix. Additional reading on marine biodiversity patterns

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