Marine Biodiversity



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Marine Biodiversity

Biodiversity of marine systems is a huge and challenging topic given the size of oceans (about 70% of the Earth's surface area and 98% of its habitable space) and severe under-sampling. Documenting and understanding marine biodiversity are important for many of the same reasons it is important to know about biodiversity terrestrial including establishing a baseline so that we can change supporting recognize and ecosystem functions such as providing food and medicinal resources. Knowing the distribution and diversity of organisms allows us to better propose and test hypotheses regarding physical and chemical barriers to migration (such as horizontal and vertical circulation and salinity variations), evolutionary history of the organisms, and the geologic history of ocean basin formation.

The following two articles summarize some aspects of marine biodiversity and provide background to understand some physical, chemical, and geological aspects of marine systems that affect diversity. Fautin addresses biodiversity in benthic marine environments whereas Pierrot-Bults and Angel tackle biodiversity in pelagic realms. Both narrow the focus to animals, and address at the phylum level, but provide many examples to elucidate spatial trends in species biodiversity.

These authors are justified in narrowing the topic to animal phyla due to the shear scope of including all organisms at a finer taxonomic level and the relatively Carol Mankiewicz Department of Biology Beloit College Beloit, WI 53511

limited distribution of photosynthesizers. Regarding the scope of the problem, knowledge of diversity distribution trends at finer than the phylum level is spotty at best, as Fautin and Pierrot-Bults and Angel lament. Though the importance of marine microbes has been a major focus in the past decades, little is known regarding diversity and distribution (Sogin et al, 2006). If the goals of the International Census of Marine Microbes (http://icomm.mbl.edu) are attained, a clearer picture of microbe biodiversity will emerge. Photosynthesizers are confined to sun-lit waters, restricting them to shallower parts of continental shelf areas for benthic and the upper 100 m or so of pelagic realms; neritic and this distribution represents only a small fraction of the benthic area and ocean volume

Oceans are Different

Some ocean characteristics seem to suggest low diversity and broad distributions of organisms. For example, oceans are presently interconnected, which could produce wide distributions of organisms. In addition, large areas of oceans (deep pelagic areas and the abyssal plains for the benthos) are stable with respect to temperature, salinity, and combination light. The of interconnectedness and environmental stability suggested low diversity, which through deep-sea was borne out dredging during the Challenger Expedition (Moseley 1879). When predictions regarding low diversity have since been tested, however, many have been surprised at the results.

For example, using box cores, Grassle Maciolek (1992) found high and macrofaunal species diversity in deepwater benthos (about 2000 m) off the eastern coast of the United States and suggested that small-scale patchiness in disturbance (*e.g.*, food availability) could explain the enhanced richness. The lack of stability with regards to food thus overrides the extreme stability with physical environment. respect to Nicholls (2007) surveys a recent voyage that confirmed such small-scale patches.

As an observer (as opposed to an active researcher) of marine biodiversity studies, it seems that surprise regarding findings rather than confirmation of predictions is very much the norm. For example, three science news items flooded the internet as I wrote this introductory piece. Baba and Macpherson (2012) reported finding a new species of deep-sea crustacean. Surprisingly, it was discovered off the Spanish coast, one of the better-studied areas of the ocean and the new species seems to be more related to western Atlantic members of the genus rather than the four other species of the eastern Atlantic. The second item has more to do with ocean productivity, which can affect biodiversity. Arrigo et al. (2012) discovered unexpectedly phytoа plankton bloom under the Arctic pack ice, which was not predicted due to lowlight conditions. Finally. а vet unpublished tome by Naylor et al. reportedly suggests up to 79 new species of sharks and rays identified through DNA analysis of 4283 specimens; such work emphasizes the need for taxonomic and molecular techniques to document

species diversity (as discussed in Cressey 2012).

Results of ocean exploration and some diversity studies repeatedly demonstrate the need for thinking differently about marine systems (Crist *et al.* 2009) and the Census of Marine Life (http://www.coml.org). Some aspects of this difference are highlighted below.

- 1. Ocean currents have a greater ability deliver food and disperse to organisms than wind currents on land. Even though photosynthesizers occupy a small area and volume of the oceans, they still can be the ultimate source of food for deeper Additionally, many organisms. mesopelagic organisms migrate vertically towards food-rich, surface waters on a daily basis as discussed by Pierrot-Bults and Angel (this volume).
- 2. Long-lived and large organisms on land tend to be producers, whereas they tend to be consumers in marine settings; short-lived, single-celled photosynthesizers particularly dominate in open-ocean environments. Possibly these differences in size and/or lifespan facilitate relatively rapid response to change (Steele 1991).
- 3. Though some marine food chains may follow the simple model of photosynthesizer \rightarrow herbivore \rightarrow carnivore, two other trophic systems are recognized in oceans, one based on chemosynthesizers and the other based on dissolved organic carbon (DOC); and both of which highlight the importance of bacteria. It was only a few decades ago when entire ecosystems based on chemoautotrophs were discovered along the

Galápagos hydrothermal vents (Corliss et al. 1978). Exploration of similar vents today continues to lead to the discovery of new species (e.g., "veti crabs" so-called the of Macpherson et al. 2005 and Thurber et al. 2011). Furthermore, other chemosynthesis-based systems, like cold seeps that emit methane and hydrogen sulfide and even whale falls (Baco and Smith 2003; Smith and Baco 2003) can host a different suite of animals. DOC is produced during processes like lysis of bacterial cells. leakage from phytoplankton cells, and waste excretion. DOC serves as a carbon source for numerous bacteria that in turn serve as food for larger and larger organisms, thereby powering the "microbial loop" (Fenchel 2008).

- 4. Benthic and pelagic realms are intricately linked. Most benthic animals have larval planktic stages, enhancing their chance of dispersal (*e.g.*, Gillanders *et al.* 2003). In addition, much of the benthos depends on food raining or, more descriptively, drizzling intermittently from above or being delivered via currents.
- 5. Many planktic animals, like the socalled "jellies," are easily overlooked and destroyed with normal sampling mechanisms; it took countless hours of open-water diving to unravel some of the complexities of these gelatinous animals (e.g., Hamner et al. 1975). In part, the difficulty in sampling these organisms may have led to potentially unsupported ideas gelatinous that plankton are increasing in abundance (Condon et al. 2012).
- 6. The apparent constancy of oceans breaks down when we think over

evolutionary time as geologic processes close (e.g., isthmus of Panama) or open (Australia pulling away from Antarctica) connections between oceans, isolating and exposing organisms to new water masses and organisms. These changes can have major effects on marine life and their evolution (e.g., Jackson 2010).

Likewise, glaciation exposes continental shelves and can restrict water flow between islands as in the Indonesian archipelago. Global warming has the opposite effect, flooding the shelves as glaciers melt and increasing insularity of island systems. These sea level changes, in part, may have led to present-day high coral diversity in the western Indo-Pacific (Stehli and Wells 1971). Global warming also enhances chemical weathering (Velbel 1993), which results in the delivery of more dissolved ions to ocean basins.

It is not surprising that the oceans harbor such great diversity given that thrived early life in such environments and only secondarily invaded terrestrial systems. Ocean life had a head start of millions to billions of years to diversifv compared to that in terrestrial environments.

As a child growing up at a time of heightened environmental awareness, I often heard the phrase "the solution to pollution is dilution." Where better to dilute than the ocean basins. But we now have seen the effects of such thinking in coastal waters as discussed by Fautin (this volume) regarding dead zones and coral reefs. Will there be much farther-reaching consequences because many of the pollutants dissolve so readily in the oceans and then are transported by horizontal and vertical currents with mixing of the entire ocean basins occurring at the millennial scale? Absorption onto fine sediment or incorporation into fecal pellets could facilitate transport of some pollutants to even the deep benthos. Exploration of oceans for biodiversity studies will continue to shed light on the understanding of how oceans work, the different approaches need for to conservation, and the importance of employing varied taxonomic and molecular techniques.

Educators will find many resources on marine biodiversity at the Centers for Ocean Sciences Education Excellence's (COSEE) website: http://www.cosee.net and at the Census of Marine Life's website: http://www.coml.org/resourceseducators-and-public.

References

- Arrigo, K.R., D.K. Perovich, R.S. Pickart, Z.W. Brown, and 27 others. (2012). Massive phytoplankton blooms under Arctic sea ice. *Science* 336: 1408.
- Baba, K., and E. Macpherson. (2012). A new squat lobster (Crustacea: Decapoda: Anomura: Chirostylidae) from off NW Spain. *Zootaxa* 3224: 49–56.
- Baco, A.R. and C.R. Smith. (2003). High biodiversity levels on a deepsea whale skeleton. *Marine Ecology Progress Series* 260: 109-114.

- Condon, R.H., W.M. Graham, C.M. Duarte, K.A. Pitt, C.H. Lucas, S.H.D. Haddock, K.R. Sutherland, K.L. Robinson, M.N. Dawson, M.B. Decker, C.E. Mills, J.E. Purcell, A. Malej, H. Mianzan, S. Uye, S. Gelcich, and L.P. Madin. (2012). Questioning the rise of gelatinous zooplankton in the world's oceans. *Bioscience* 62: 160-169.
- Corliss, J., J. Dymond, L.I. Gordon, J.M. Edmond, R.P. von Herzen, R.D. Ballard, K. Green, D.
 Williams, A. Bainbridge, K. Crane, T.H. van Andel. (1979). Submarine thermal springs on the Galápagos Rift. *Science* 203: 1073-1083.
- Cressey, D. (2012, June 22). Shark species more diverse than thought: genetic analysis suggests overlooked species, raises concerns about conservation. *Nature (News)*, http://www.nature.com/news/sharkspecies-more-diverse-than-thought-1.10879.
- Crist, D.T., G. Scowcroft, and J.M. Harding, Jr. (2009). World Ocean Census: A Global Survey of Marine Life. Firefly Books: Richmond Hill, Ontario, Canada. 256 pages. ISBN 1554074347.
- Fenchel, T. (2008). The microbial loop – 25 years later. Journal of Experimental Marine Biology and Ecology 366: 99-103.
- Gillanders, B.M., K.W. Able, J.A. Brown, D. Eggleston, and P.F. Sheridan. (2003). Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of

nurseries. *Marine Ecology Progress Series* 247: 281-295.

- Grassle, J.F. and N.J. Maciolek. (1992). Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139: 313-341.
- Hamner, W.M., L.P. Madin, A.L. Alldredge, R.W. Gilmer, and P.P. Hamner. (1975). Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. *Limnology and Oceanography* 20: 907-917.
- Jackson, J.B.C. (2010) The future of the oceans. *Philosophical Transactions* of the Royal Society B. 365: 3765-3778. doi: 10.1098/rstb.2010.0278.
- Macpherson, E., W. Jones, and M. Segonzac. (2005). A new squat lobster family of Galatheoidea (Crustacea, Decapoda, Anomura) from the hydrothermal vents of the Pacific-Antarctic Ridge. *Zoosystema* 27: 709-723.
- Moseley, N.T. (1879). Life in the deep sea, p. 576-592, *in* Notes by a naturalist on the "Challenger": being an account of various observations made during the voyage of H.M.S. "Challenger" round the world, in the years 1872-1876, under the commands of Capt. Sir G.S. Nares and Capt. F.T. Thomson. Available online at http://archive.org/details/notesbynat uralis00mose.
- Naylor, G.J.P., J.N. Caira, K. Jensen, W. White, and P. Last. (*in press*). A

DNA sequence based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History* No. 367: 280 pp.

- Nicholls, H. (2007). Sorcerer II: The Search for Microbial Diversity Roils the Waters. *PLoS Biology* 5(3): e74. doi: 10.1371/ journal.Pbio.0050074.
- Smith C.R. and A.R. Baco. (2003). Ecology of whale falls at the deepsea floor. *Oceanography and Marine Biology Annual Review* 41: 311-354.
- Sogin, M.L., H.G. Morrison, J.A. Huber, D.M. Welch, S.M. Huse, E.R. Neal, J.M. Arrieta, and G.J. Herndi. (2006). Microbial diversity on the deep sea and the underexplored "rare biosphere." *Proceedings of the National Academies of Science* USA. 103(32): 12115-12120.
- Steele, J.H. (1991). Marine functional diversity. *BioScience* 41: 470-474.
- Stehli, F.G. and Wells, J.W. (1971). Diversity and age patterns in hermatypic corals. *Systematic Zoology* 20: 115-126.
- Thurber, A.R., Jones, W.J., and Schnabel, K. (2011). Dancing for food in the deep sea: bacterial farming by a new species of yeti crab. *PLoS ONE* 6(11): e26243. doi:10.1371/journal.pone.0026243.
- Velbel, M.A. (1993). Temperature dependence of silicate weathering in

nature: how strong a negative feedback on long-term accumulation of atmospheric CO_2 and global greenhouse warming? *Geology* 21: 1059-1062.

Pelagic Biodiversity and Biogeography of the Oceans

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International collaboration is desperately needed to study marine biodiversity in our oceans around the globe because: (1) the majority of this environment is under-sampled especially on the southern Hemisphere and it is the largest environment on earth; (2) there is a tremendous lack of taxonomic expertise available locally in most of the understudied regions of the ocean; (3) assessments of global environmental change in oceanic systems are made by remote sensing that totally ignores driving forces at the species level; (4) there are tremendous technological challenges in sampling and analysis that are worthy of attention; (5) much attention has been given by nation states to economic productivity in the regions close to their shores, but little attention has been given to global sustainability; (6) sampling programs have focused on process and resource management at the expense of organismal ecology, taxonomy and identification; and (7) the oceans have a number of extreme and highly variable environments that may place species at much higher risks of extinction than considered by previous estimates. Human practices of overfishing, dredging bottoms, polluting, acidification, etc. are placing our oceanic environments at great risk. We must develop policies, practices, and enforcements to protect precious marine biodiversity.

Keywords: marine zooplankton, pelagic biodiversity, pelagic biogeography, biooceanography

Introduction

Biodiversity is a measure of the variability of life and encompasses all scales in time and space. Biodiversity or species richness is often used as a proxy for ocean health. Hence biogeography, which addresses the geographical scales of distribution, can be regarded as an aspect of biodiversity. The scale at which you observe the world not only changes your perceptions, but also influences what processes are determining the patterns, or lack of pattern that you see. Look at this page at high magnification and you see the individual pixels that give you no information about what is written. At lower magnifications, the printed words become apparent and at great distance you may not even see the page. In global terms, the

oceans dominate the surface of the planet, covering 71% of its surface area. Its average depth is around 3800 metres and, apart from a few exceptional zones, living organisms occur everywhere. Whereas on land life is restricted to about 100 m above and a few metres below the surface, the volume of living space in the oceans is massively greater than on land. On land we are familiar with seeing different plant and animal species inhabiting different zones, with factors like latitude, aspect, climate and geology playing a major role in determining the large scale ecology. We are also familiar with seeing different species in a forest, in grassland, in marshes, up a mountain, and in a desert. There are similar patterns in the ocean, but the environmental factors are

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totally different, and the scales of which they determine the ecology are very different.

This paper will deal primarily with macro-zooplankton. These animals float freely within the water column and have limited powers of mobility; so they drift with the currents. However, many of them are able to undertake vertical migrations of tens or even hundreds of metres. We will focus on the holoplankton, which are animals that live their whole life in the pelagic environment. In contrast. the meroplankton species are temporary members of the plankton such as the larvae of larger pelagic species (such as fish and shrimp) and species whose adults live on the sea-bed (benthos).

The pelagic ocean is divided into a neritic realm that fringes the continental shelf from the shoreline out to the 200m contour and an oceanic realm that encompasses the vast volume of the open oceans. The hypsographic curve (Figure 1), which plots

areas of the globe covered by land of varying elevations and ocean of various depths, shows just how enormous the volume of the ocean is compared to the land. The neritic zone occupies about 7% of the globe's surface whereas the ocean beyond the shelf break covers 64% of the Earth's surface. open The ocean is threedimensional and the classic bathymetric zones recognized are: the epipelagic (0-200 m), the shallow-mesopelagic (200-500 m), the deep mesopelagic (500-1000 m), the bathypelagic (1000-4000 m), the abyssopelagic (4000-6000 m) and the hadal (>6000 m) zones. Pelagic ecosystems are the largest in the world; the species that inhabit these zones have vast ranges of distribution that are usually unrestricted by impassable boundaries other than the seabed and coastlines. There is no comparison with any terrestrial biotope in terms of living space. For example, many plankton taxa seem to occur from about 40°N to 40°S in all three oceans.

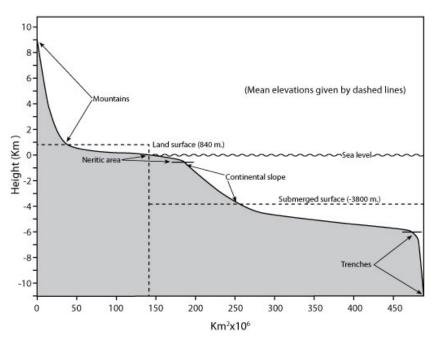


Figure 1. Hypsographic curve of the ocean showing the amount of Earth's surface at various elevations and depths.

Pelagic Biodiversity and Biogeography of the Oceans

So the fundamental differences between the pelagic biotope and all others are its vast volume, its environmental properties (which only gradually change), and, the absence of real-clear barriers. The organisms living in the pelagic show very large distribution patterns, and these patterns are 3dimensional. Geochemical evidence, based on the distributions of natural radioactive isotopes, suggests that it takes just 1500 years for the oceans to be stirred; another of about planktonic wav thinking zoogeography is to consider why the oceans are not more uniform.

Plankton taxa belong to several different phyla. Although they have experienced the same environmental changes during their evolutionary history, resulting from the ever-changing structure of the oceans basins and climatic fluctuations resulting from cycles in the Earth's orbit around the Sun, they have followed different evolutionary trajectories. However, they all show very similar patterns in their distributions because circulation patterns and productivity regimes (that are products of climatic forces) are having the largest impact on present day biogeography. However, the different taxa have different potentials for adaptation and speciation so the evolutionary history of each phylum is also important. The pelagic environment has never been an easy place in which to evolve, and only about half the animal phyla (12) that live in the ocean have been able to exploit the vast spaces of the open ocean.

The Oceanic environment

One of the primary differences between ocean and terrestrial environments is in the medium. The atmosphere has a very low density and few organisms live permanently suspended in it. On the other hand, water is much denser and literally supports all pelagic life. Water provides a temporary

environment for the early developmental stages of many benthic species. The atmosphere heats up and cools down very rapidly giving rise to what we term *weather*. Water takes much more energy to heat and it takes much longer to cool down. Water changes phase at environmental its temperatures, becoming solid (ice) at low temperatures and forming water vapour at any temperature. However, to melt ice takes as much energy as it takes to raise the temperature of cold water to boiling point. The formation of water vapour takes even more energy; hence, if our clothes get wet we get very cold as the water starts to evaporate. However, such changes are restricted to the water surface, where evaporation will cool the surface of the ocean and where the atmosphere is very cold, the water will freeze. In deeper layers, the water temperature is nearly constantly 2-4° C.

Water is a particularly good solvent for salts. Over geological time, the oceans have become progressively saltier and now each litre of seawater contains on average of about 35g of dissolved salts (mainly sodium chloride). The amount of salt dissolved in oceanic water is in dynamic balance. In some enclosed seas, where there are few inflowing rivers the salinity is higher (for example at the northern end of the Red Sea) the salt content can be as high as 40g per litre. In other enclosed seas like the Baltic and even much of the Arctic Ocean, high freshwater inputs keep the salinity low. Warm water is not a good solvent for gases. Cold water will dissolve more gas than hot water. Hence, when you boil a kettle it bubbles well before it starts to boil.

The density of seawater is determined by temperature, salt content, and the pressure it is exposed to. So in the doldrums – those

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regions of the ocean at around 20° to 30° of latitude – the climate is dominated by warm atmospheric temperatures, high atmospheric pressure, and very low rainfall. Consequently, the losses of water vapour from the surface of the ocean exceed the freshwater input from rain, so the salinity of the surface water increases. Despite being denser than warm. it becomes its surroundings and sinks into the ocean's interior. Surface water sinks in polar seas for another reason: sea water begins to freeze when its temperature falls to -1.9°C (note its salt content lowers its freezing point). Sea ice contains little or no salt, so the very cold surface water becomes saltier and heavy enough to sink. In certain regions it sinks all the way to the bottom of the ocean, and since it has been at the surface, it contains the maximum concentration of dissolved oxygen. It then begins to spread throughout all the oceans carrying with it the dissolved

oxygen that supports bottom living (benthic) life globally. This is called *thermo-haline circulation*. If this process is halted as a result of climate change, benthic life as we know it today will be expunged.

Away from the polar margins, the sinking water bodies that were formed within restricted areas of the oceans, have properties of salinity and temperature that are very conservative. They are only altered by diffusion and turbulent mixing. These are very slow processes: you can see if you partially fill a bottle with ice-cold water and gently top up with luke-warm water lightly coloured with ink. If you do not shake the bottle the two layers will persist for many hours, and if you tap the bottle you will see ripples forming at the interface. Similar 'ripples' on much larger scales occur within the ocean and are known as internal waves.

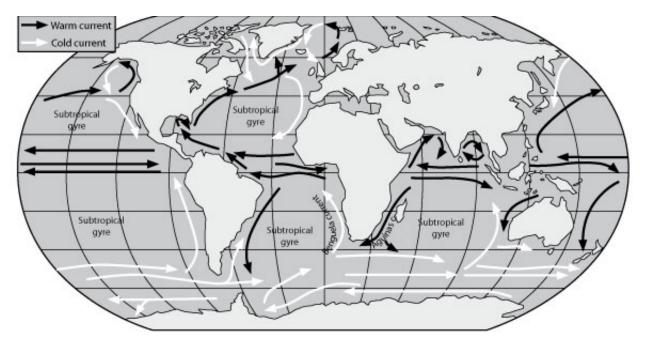


Figure 2. The epipelagic water-masses and current patterns of the world's oceans.

These water masses (Figure 2) structure the pelagic environment, especially evident in the epipelagic. They can spread in enormous flows much like great rivers within the ocean. They are influenced by large-scale processes like the rotational forces generated by the Earth's spin. As a result, they can be thrown into ocean-wide current gyres, which spin clockwise in the Northern Hemisphere and counter-clockwise in the Southern Hemisphere. The best known of these is the Gulf Stream in the North Atlantic; it is one part of a clockwise circulation that influences both the marine environment and our weather on land. We are all familiar with the atmosphere's cyclones and anticyclones that are so influential on our weather systems. There are great eddies that have horizontal dimensions of up to 1000km. There are analogous systems in the oceans, but although their dimensions are smaller (about 200km), they contain far more dynamic energy because water is a much denser medium. This means they are far more persistent and an oceanic eddy can last for over a year, whereas, in the atmosphere the weather systems seldom persist for more than a week or two. In the ocean, eddies occur at all scales from a few centimetres to over a hundred kilometres.

For example in the North Atlantic, the very dynamic front that bounds the edges of the main flow of the Gulf Stream generates eddies that are clearly detected by satellites that monitor the surface temperature of the ocean. (Figure 3)

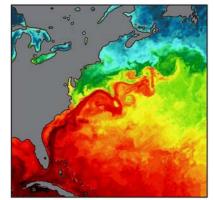


Figure 3. Satellite picture of Gulf Stream eddies. Red and orange colour is warm water; green and blue colour is cold water.

The watermasses in the deeper layers have a less evident influence on distribution although they can be traced far into the ocean. For example, in the South Atlantic, the deep water is much more uniform than in the South Pacific Ocean (Figure 4).

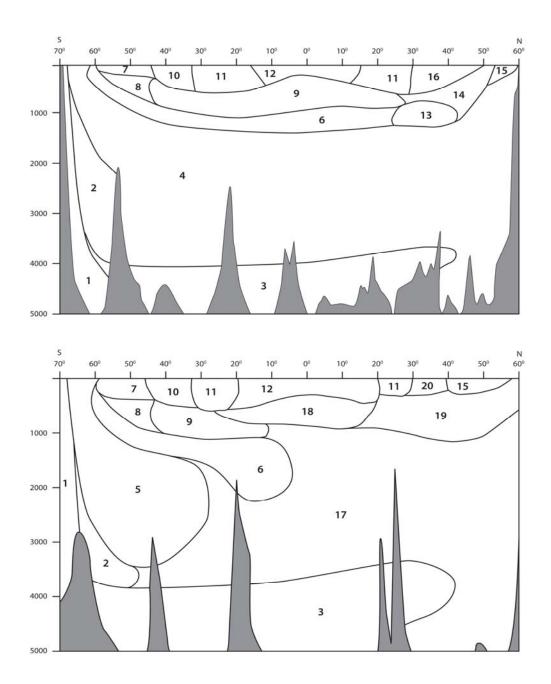


Figure 4. Vertical distribution of watermasses in the Atlantic Ocean (upper panel) and Pacific Ocean (lower panel). 1=Antarctic Slope Water, 2= Circum Antarctic Seep Water, 3= Antarctic Bottom Water, 4=Atlantic Deep Water, 5=Indian Deep Water, 6=Antarctic Intermediate Water, 7=Antarctic Surface Water, 8=Intermediate mixed Antarctic Water, 9=Subantarctic Intermediate Water, 10=Subantarctic Surface Water, 11= Subtropical Water, 12= Tropical Water, 13=Mediterranean Water, 14=North Atlantic Intermediate Water, 15=Arctic Water, 16=North Atlantic Surface Water, 17=North Pacific Deep Water, 18= Tropical Intermediate Water, 19=North pacific Intermediate Water, 20=North Pacific surface Water. Aac=Antarctic Convergence, AC= Arctic Convergence, AAD=Antarctic Divergence, SC=Subtropical Convergence (after Van der Spoel and Heyman, 1992).

Although each water mass tends to have a characteristic assemblage of planktonic species, individual species are rarely restricted to a single water-mass. However, when relative abundancies are taken into account along with presence-absence data, more structure is found. This is well illustrated by Beaugrand et al. (2002) who studied copepod assemblages from samples of the continuous plankton Recorder (CPR) in the North Atlantic. Although the list of species is very similar throughout, changes in the relative abundances of these species vary significantly. These different faunal assemblages can be recognised associated with the different water masses. Another example is the distribution and abundance of the epipelagic chaetognath Pterosagitta draco in the Pacific. The general distribution is from 40°N to 40°S, but when abundance data are also taken into account this species is most abundant in the equatorial zone (McGowan, 1971). If one looks at the pteropod Limacina lesueuri, one sees exactly the opposite; while this species also has a distribution from 40°N to 40°S, here the greatest abundance is in the central gyres (Van der Spoel and Heyman, 1983). Finally, the euphausid Euphausia brevis is an example of a species that is restricted to the central gyres (Reid et al, 1978).

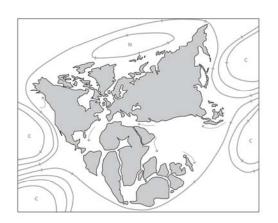


Figure 5. Breaking up of Pangaea with primordial ocean watermasses. C = Central gyres, N = northern waters

History of the Ocean Basins

Biogeography tends to focus on large scale and long-term events. It has to take into account the formation of ocean basins, the opening and closing of seaways, and oscillations in sea level. Two-hundred million years ago there was a single massive continent called Pangea. It began to fragment as a result of tectonic processes that are now familiarly known as continental drift and sea-floor spreading. (Figure 5)

The primordial ocean was a rather shallow, warm, and food-rich environment. The theory (Pierrot-Bults and Van der Spoel, 1979; Van der Spoel and Heyman, 1983) is that the present day central gyres are the direct remnants of this ocean. These gyres have always been present because they are generated by the planetary forcing of the Earth's spin. In the primordial ocean, life developed for millions of years. Plate tectonics subsequently divided up the original single ocean into three. Their depths, which average about 3800 m, range from only shallow coastal waters to the greatest depths in canyons which border the tectonic plates of the continental land masses. The Mariana canyon is the deepest at 10,800 m. The South Atlantic began to open up about 100 million years ago, and the North Atlantic about 50 million years ago. Each year the North Atlantic gets about 2cm wider. When eels first evolved about 60 million years ago, they began spawning in deep water in what is now the Sargasso Sea. The journey undertaken by the larval eels was probably only a few hundred kilometres which took a few weeks. Now they journey about 3000 miles: this takes them well over a year, even though they are being carried eastwards by the general flow of the currents.

At present, the American and Eurasian/African continents present barriers

to the east-west exchange of warm-water faunas between the oceans. Circulation patterns in the ocean changed very much since the Oligocene (ca 25 M ago), when the Tethys Sea became blocked, and, during the late Pliocene (3 M ago) with the closure of the Panama isthmus. Initially the tropical circulation was from east to west through these low latitude passages (Figure 6).

After the closure of the Panama isthmus, the oceanic circulation became west to east and tropical circulation was impossible. Exchange of warm-water species between the Indo-Pacific and the Atlantic Ocean is at present only possible when small bodies of water penetrate into the Atlantic Ocean around the tip of South-Africa in the Agulhas Current and become entrained in the Benguela Current bringing the specimens living in these pockets of water further north into the south Atlantic (Figure 2).

Based on paleo-oceanographic evidence, cooling of the deep waters at the beginning of the Cenozoic gave rise to the development of mesopelagic plankton. The deep sea circulation reached the recent pattern in the Miocene. Pierrot-Bults and van der Spoel (1979) suggest that the colonization of bathypelagic waters was among the most recent events (Figure 7). Van der Spoel and Heyman (1983) showed a geocladogram of the major planktonic faunas that put the central water faunas as the earliest, followed by the warm-water and equatorial fauna. Then more recently, the temperate fauna, the southern cold-water fauna, and northern cold-water fauna developed with the deep-sea fauna as the most recent one.

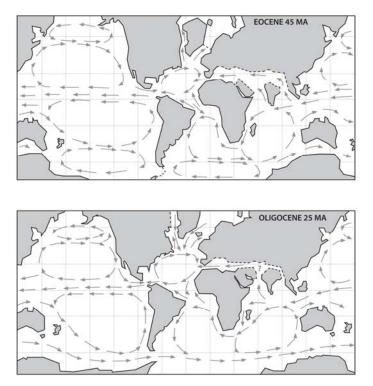


Figure 6. Eocene and Oligocene circulation showing equatorial passways.

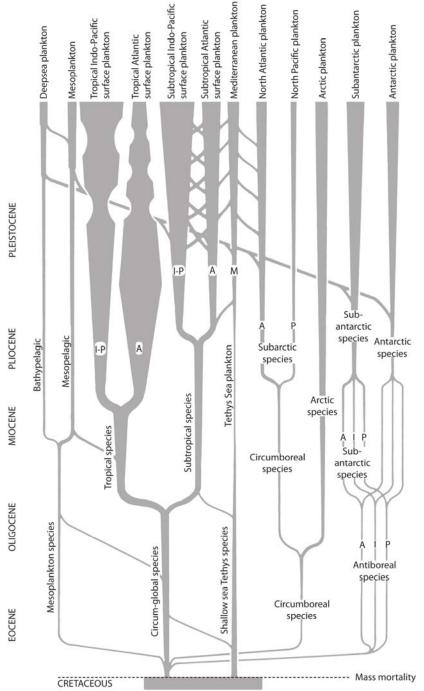


Figure 7. Development of the various planktonic faunas during the Caenozoic. A=Atlantic Ocean, I=Indian Ocean P=Pacific Ocean. (after Pierrot-Bults & van der Spoel 1979).

Throughout this ocean history, the pattern of flow of the central gyres has not changed because it is determined by the Earth's rotational forcing. Another major tectonic influence was the separation of the Australian Continent from Antarctica. This opened the pathway for the circumpolar current in the Southern Ocean,

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which has effectively isolated the Southern Ocean ecosystem. It has developed its own unique fauna south of the Circumpolar Front. According to Pierrot-Bults and Van der Spoel (1979), this fauna could only have developed since the Miocene. Hence, it is more recent than the fauna of the Arctic Ocean that has developed since the Oligocene. Thus, the Anarctic is in contrast to the Arctic Ocean in which current flows from the North Atlantic penetrate as far north as 80°N on the western side of Svalblad and relatively few of the species in the High Arctic are endemics. (Figure 7)

Since there are no solid boundaries in open oceans, genetic isolation, which is the driving force for speciation in terrestrial communities, is seldom a similar driving force in pelagic marine communities. Speciation is thought to be a relatively slow process in the open ocean (Pierrot-Bults and Van der Spoel, 1979). Genetic homogeneity was assumed in plankton communities because of their wide ranges and high dispersal capabilities, although morphological differences within widely distributed species were recorded (Pierrot-Bults, 1997; 1998; Pierrot-Bults and van der Spoel, 2003). However, recent genetic studies in fishes and Chaetognatha are revealing complex patterns of genetic structuring and possible sibling species (Miya and Nishida, 1997; Peijnenburg et al, 2006, Miyamoto et al, 2010). We are just beginning understand speciation to mechanisms in the pelagic ocean and recent estimates of the numbers of known marine species predict that there are far more species than previously assumed (WORMS results).

There are some notable exceptions to this absence of isolating mechanisms. In and around the East Indies, there are many island archipelagos that enclose deep troughs. This

is the region where there is a clearly defined zoogeographical boundary in terrestrial faunas and floras known as Wallace's Line and this line is also seen in the marine faunas. The explanation of this line is that as sea-levels oscillated up during the glaciations, land bridges formed when sea levels fell by up to 70m thereby allowing interchange between the terrestrial plants and animals between islands on each side of the line, but not across the line where the channel remained deep.

The isolation between the islands was restored when sea levels rose again during the interglacials, and persisted long enough for the populations to drift apart and start to evolve into new species. In the shallow seas the same process occurred, but was out-ofphase – when sea levels rose the shallow water communities could interchange, but when sea levels fell, populations in the deep troughs became isolated, genetically drifted apart and so speciated.

There are two other major factors that need to be considered. (1) These are the regions where the primordial ocean (older than 200 million vears) existed. and SO the assemblages have had a development uninterrupted by many of the influences of the glacial oscillations and so may have escaped the great extinctions that took place notably at the end of the Cretaceous Era when paleontological evidence supports the inference that about 95% of species became extinct. (2) Several different water masses impinge on this region contributing to the biological richness, bringing possibilities of enrichment of the faunas through mixing. Thus, the East Indies became recognised as an important region for radiation – the term used to describe extensive speciation and is amongst the most biodiverse regions of the globe.

Another dramatic event influencing oceanic faunas was the repeated opening and closing of the Strait of Gibraltar during the Miocene era. The Mediterranean area is both warm and arid with few rivers flowing into it. Once it became sealed off from the Atlantic, the sea dried up, depositing vast beds of salt off North Africa. Each time the Strait reopened and re-flooded, global sea levels would have dropped about 70m within a few centuries. Based on the volumes of the salt deposits, it has been estimated that this may have occurred up to seven times. Even today, the Mediterranean is a remarkable sea. Relatively cool fresh water flows into it through the upper 70m of the Strait and beneath the inflow relatively warm and salty water flows out into the Atlantic. The outflowing water forms a persistent layer of anomalously saline water that can be detected spreading throughout much of the North Atlantic. The pelagic fauna in the Mediterranean is surprisingly not similar to the shallow fauna that occurs in the Atlantic; within the Mediterranean, the deep water lacks comparable mesopelagic and benthopelagic faunas.

Vertical structure

So how does depth affect pelagic communities? Water is translucent but not transparent, and it is highly selective as to the wavelength of light (and hence colour of light) that is allowed through. Very short wavelengths (ultra-violet) and very long wavelengths (red and infra-red) get absorbed very rapidly. The light that penetrates deepest is blue-green light and perhaps it is no accident that these are the wave lengths of light that phytoplankton use for photosynthesis. However, even in the clearest oceanic water, there is no light that we can see at depths of 1000m. So oceans deeper than 1000m, which is the most voluminous habitat on the planet, are dark. However, it is not a totally dark environment because the animals themselves produce their own light called bioluminescence. The absorption and scattering of light by the water has important ecological consequences. The plant plankton (known as phytoplankton), like plants on land, needs light and nutrients to grow. Enough light for growth only occurs in the upper 100m or so of the water. So the plant productivity in the oceans that is the base of the ecological pyramid is restricted to this thin skin of water at the surface.

In the process of photosynthesis the plant cells use carbon dioxide dissolved in the water to synthesise carbohydrates, and in so doing, release oxygen. The partial pressure of oxygen in the surface water rises above that in the atmosphere and oxygen is vented from the ocean surface into the atmosphere. It is estimated that the oceans provide 70% of the oxygen in the atmosphere. In addition, the surface water becomes under saturated with carbon dioxide and thereby the oceans absorb carbon dioxide. They have absorbed about 50% of the carbon dioxide emitted by human activities and hence have dampened climatic warming (Bernal, 2010).

Phytoplankton are consumed by herbivorous zooplankton and much of the carbon dioxide it fixes passes along the food chain. Phytoplankton are the original source of all organic matter in the oceans, with one minor exception: the chemical fixation of carbon dioxide that occurs both at hydothermal vents and in some anoxic sediments. A proportion of the carbon fixed by the plants gets transferred down through the water to the benthos inhabiting the sea floor. This transfer occurs through two mechanisms, the passive sedimentation of organic material sinking down through the water and the active vertical migrations of the animals in the water.

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There are two main food webs associated with the phytoplankton. The classical food web is based on the larger phytoplankton cells that can be filtered from the water by grazing zooplankton like copepods and krill. These herbivores sieve the larger plant cells from the water using the fine setae on their legs. There is a physical limitation to the size of particle they can extract, because if the setae are less the 5µm (a micron is a thousandth of a millimetre) apart then the viscosity of water means it will only flow through the gaps under high pressure. Note that many planktonic crustaceans swim by beating antennae and other limbs which carry numerous feathered setae and 'row' the animals through the water. If the water did flow between the setae they would be unable to swim. Hence, they are unable to extract plant cells that are smaller than 5µm from the water unless they are clumped together. These small cells can only be eaten by animals that are very tiny themselves such as ciliate protozoans; hence, it is described as the microbial web.

There are some larger species that can exploit these tiny cells by adopting a totally different feeding mechanism using sheets of mucus to which the plant cells stick. In some species like salps, the mucus is kept within the animal's bodies, but in others like pteropod molluscs and larvaceans, the mucus is deployed externally as webs that are regularly lost or discarded. These mucus webs continue to 'fish' passively and as they garner more and more cells and detritus from the water, they begin to sink. As they sink they entrap (or scavenge) more and more particles and rain down as 'marine snow'.

The vast majority of the organic debris from the classical food web sinks into deep water either as passively or within the gut contents of migrating plankton. The organic matter it contains includes not only the carbon converted dioxide into the organic compounds by photosynthesis, but also the nitrates and phosphates that are basic necessities for phytoplankton growth. This process leaches out the substances that support productivity in the surface water and they are only resupplied if deep water is mixed into the upper layers. In contrast, the majority of products of the microbial web, which is responsible for an estimated 80% of all production in the ocean, tend to be recycled within the surface waters.

Productivity in the ocean is dependent on the availability of light and nutrients. In contrast to terrestrial environments, the most productive waters do not show the greatest species richness. Production cycles differ between the different water-masses and this has a great influence on the taxa that can thrive in these different regimes. Since satellites can provide us with global coverage of the ocean, we have a more comprehensive view of how production is distributed in the ocean. Colour scanners give a proxy for chlorophyll us concentrations and thus for phytoplankton productivity in different seasons (Figure 8).

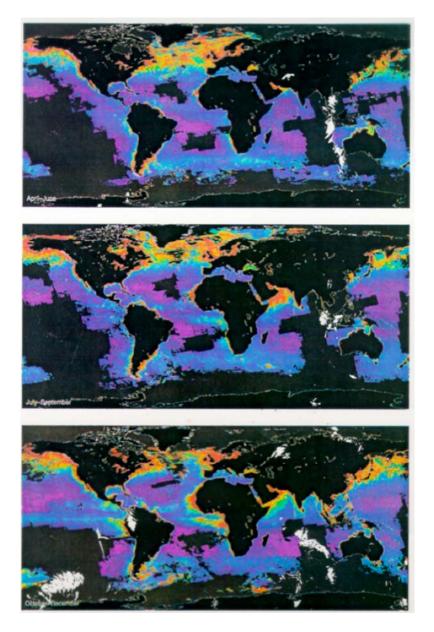


Figure 8. Primary production in the Ocean by the Coastal Zone Colour Scanner. Upper panel April-June, middle panel July-September, lower panel October-December. high productivity= orange and yellow =, low productivity = pink and blue, no data because of too much cloud cover = black.

The polar production cycle is characterized by a single peak in summer. The temperate cycle has a double peak: a spring bloom and a smaller less predictable autumn bloom. The (sub)tropical regime has relatively low continuous production with a slight peak in winter (Pierrot-Bults, 1997). Noguiera *et al* (2012) analysed temporal and spatial variability of copepod species richness in relation to primary productivity in the NE Atlantic CPR regions. They found unimodal seasonal cycles at higher latitudes and bimodal ones at lower latitudes. The annual averages of copepod species richness correlated negatively with those of phytoplankton productivity and positively with those of sea surface temperature along the latitudinal gradient. They also correlated negatively with those of environmental stability along the oceanic–neritic gradient.

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Pierrot-Bults & Angel

It is shown that the most productive areas (red and yellow in figure 8) are also the most unstable. In the ocean, the primary production by the phytoplankton is restricted to the upper few tens of metres because phytoplankton require both light and nutrients such as nitrates and phosphates to grow. Once a bloom is triggered, these nutrients are rapidly used up (within a day or two). The fate of most of this production is either to be recycled within the water column, or a small proportion (<5%) ends up at the bottom. The bloom is triggered by the formation of a thermocline that is a small, but sharp, temperature discontinuity that inhibits vertical mixing and hence allows the phytoplankton to stay in the upper sunlit layers. However, this also halts the resupply of nutrients from the deeper water, so as the nutrients are stripped out by the sedimentation of particles there are no longer enough in the water above the thermocline to enable the bloom to persist.

Once the water column has become thermally stratified, not much mixing can occur. An exception to this generalisation is seen in upwelling areas: here the combined influence of strong along shore winds and coastal morphology result in surface water being pushed offshore and being replaced with water enriched with recycled nutrients from below the thermocline. On either side of the equator, the influence of the Earth's rotation generates a divergence of the surface currents and again there is strong enough upwelling of deep water to stimulate high phytoplankton productivity. At high latitudes, the stratification of the water column that forms in the spring and persists throughout the summer is broken down by autumn and winter storms churning up the water to depths of up to 500m mixing up nutrients from deep water. However, at higher latitudes primary production is inhibited in the winter by the short day

lengths, so the lengthening day lengths also contribute to the seasonality of the production cycle. There is a time lag between the peak in primary production and the response of the grazers and hence the secondary production. The system is less efficient in very variable environments which are dominated by the 'classical' food webs than in the permanently stratified central gyres which are dominated by microbial food webs. In these food webs, practically all the productivity is recycled in the upper layers and what little is exported into deep water is used up before it reaches the bottom. In consequence, more food cascades down to the deeper layers in seasonally pulsed productive areas at high latitudes. Thus, seasonal timing is a very important factor and can have large ecological consequences for zooplankton species.

The most used method for estimating plankton variability is zooplankton biomass. Also, there are a number of zooplankton time series. However, there is a growing recognition that species composition adds value to these observations because changes in species composition or species dominance are often not reflected, but may give valuable information for the nature and causes of observed changes (Mackas, et al, 2012). Wishner, et. al (1998) estimated biomass of zooplankton at 1000m and 5000m depth to be about 1% and 0.1% of the surface biomass, respectively. The 10 m layer just above the bottom showed slightly more biomass because of enrichment of the near bottom environment. She found the effects of differences in surface productivity were much less than differences in depth.

In addition to unstable regions with high productivity, regions with extreme circumstances such as the deep sea (with very low temperatures and low productivity) also show low species richness combined with a few very dominant species. For example, Sutton, *et al* (2008) studied North Atlantic pelagic fishes and found in total 205 fish species. From 0-750 m 3 species made up for 84% of the abundance near Iceland, while near the Azores it took 13 species to reach 84% of the abundance. In the samples from 750-2300 m deep, it was just one species that constituted 88% of the abundance with no latitudinal difference. In the sample below 2300 m, there were just four species present with one specimen each.

Patterns in faunal distributions and species richness are the results of recent circulation patterns, horizontal and vertical water mass constellation, climate, recent productivity regimes, the history of the ocean basin formation and the evolutionary history of the animal phyla.

A very detailed description of planktonic distribution patterns is found in Van der Spoel and Heyman (1983).

Diversity and Species Richness

Pelagic taxa display a broad range of cycles of abundance, age structure and production cycles, and because they are constantly being transported around by the currents, it is very difficult to track events, follow the biological interactions that enable us to gain a comprehensive view of plankton communities, their species composition and functionality.

Zooplankton taxa tend to have restricted depth and seasonal ranges, the total recorded inventory of taxa present in a region greatly exceeds the number that will be recorded at any one time and place and hence the diversity actually experienced by the individual organisms (Archambault *et al*, 2010) in Mackas *et al*, 2012). At the boundary between two water-masses the observed local species richness will often be an integral of the two different faunas instead of real community species richness because of sampling in different seasons and shifting of watermass boundaries.

Life originated in the ocean, and of the 34 animal phyla we now know, 29 are present in the ocean and 14 occur exclusively there. However, only 12 phyla occur in the pelagial where not a single phylum is endemic (Grassle *et al*, 1991). So presumably the pelagic habitat must be a challenging biotope to live in and requires special adaptations that has prevented many of the main taxa from colonising the water column. (Figure 9)

Like on land, the phylum Arthropoda is the most speciose. In the pelagial, the Crustacea are most numerous and calanoid Copepoda often called the insects of the sea; they dominate most pelagic communities both in terms of abundance and biomass. For example in the eastern Atlantic, Valdes et al. (2007) found that copepods constituted 60-90% of the abundance. At the moment, about 1950 calanoid species are known together with a further 220 species belonging to other copepod groups (Razouls Their comprehensive al, 2012). et interactive map shows greatest species richness in the central east Atlantic (739 species) and central west Atlantic (712 species). In the central Pacific, they show 532 species; while at the western Pacific margin, the numbers range from 601 in the China Sea to 628 near Vietnam, and to 674 around Japan. Along the eastern Pacific margin, numbers range from 440 to 434 species; this suppression may be due to two factors the midwater zone of strong oxygen depletion and the upwelling regions that are spread extensively along the west coast continental margins of the Americas. Upwelling enhances productivity, but lowers

species richness. The most speciose region is the Indian Ocean from where 955 species have been recorded.



Figure 9. The total number of animal phyla present in each habitat with the endemic phyla in white (after Grassle *et al*, 1992).

The reasons underlying this high diversity may be the extremes of environmental conditions that range from the highly variable conditions resulting from the monsoons, to some of the most oligotrophic regions in the tropics, to the variety of sources of current flows that import species from the Pacific and the Southern Ocean.

One factor that cannot be ignored is the differing amount of research effort that has gone into their study and the systematics in the various oceans. There is an interesting contrast between the Northeast and the Southeast Pacific. In the southeast, the communities have been under sampled. In the northeast, the sampling programmes have focused on process and resource management at the expense of taxonomy and identification.

As in terrestrial habitats there are clear latitudinal gradients in copepod species richness which range from the 163 species recorded from polar latitudes in the Arctic to the 205-353 species recorded from temperate regions to the > 700 species in the (sub)tropics, and the 274 to 295 species recorded from the Sub Antarctic and Antarctic, respectively.

Other groups show similar trends such as euphausids (Brinton et al, 1999), pteropods (Van der Spoel et al, 1997), chaetognaths (Pierrot-Bults and Nair, 1998), and ostracods (Angel et al, 2008) (Table I). A transect along 20°W in the North Atlantic from 60°N to the Equator not only showed the numbers of halocyprid ostracod species increasing substantially from sub polar latitudes to the equator, interestingly this trend occurred at all depths throughout the water column to a depth of 2000 m (Angel, 1997) (Figure 10).

However, the exact number of recorded species reflects sampling effort in the mentioned areas. For example, the South Atlantic and open ocean Pacific are under sampled compared to the areas in the western Pacific and the North Atlantic. Three general assumptions are: 1) that the epipelagic zone is most affected by the latitudinal gradients; 2) that the mesopelagic species have wider distributions; and, 3) that the bathypelagic species are assumed to occur ubiquitously throughout the global ocean. These assumptions are not necessarily borne out by the ostracod data and so few inter-oceanic comparisons have been conducted that the concept that many pelagic species are cosmopolitan need to be critically assessed both by using traditional taxonomic methodologies and molecular sequencing.

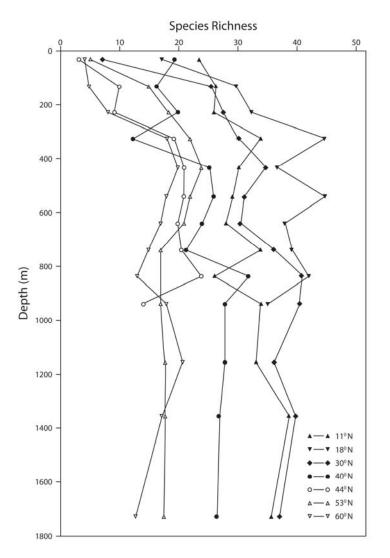


Figure 10. Vertical gradients in species richness at different latitudes. (after Angel, 1997)

Table I. Latitudinal gradients in species richness for copepods, ostracods, euphausids (Phylum Arthropoda) pteropods (Phylum Mollusca) and chaetognaths (Phylum Chaetognatha).

	Copepoda			Ostracoda		Euphausidae		Pteropoda			Chaetognatha				
	Α	Р	Ι	Α	Р	Ι	Α	Р	Ι	Α	Р	Ι	Α	Р	Ι
Arctic	163	163		3	3		5	5		3	4		1	1	
Subarctic	205	353		59	60		10	10		20	17		9	6	
40°N-40°S	712	532	955	124	81		25	30	30	120	90	95	25	34	29
Subantarctic	274	274	274	62	42		10	10	10	17	17	17	9	8	8
Antarctic	295	295	295	7	7	7	5	5	5	11	11	11	6	6	6

Neritic

The neritic environment is far more heterogeneous than the oceanic one. Temperature fluctuations are greater; salinity is more variable as a result of riverine outflows; tidal flows and wave action keep the water well stirred to depths of several tens of metres; and, productivity is enhanced by benthic production. Terrestrial inputs can be locally very significant; the morphology of the coasts increases the diversity of habitats; and, weed beds provide structural diversity that is analagous to those provided by terrestrial communities. The plankton plant communities are seasonally enhanced by inputs of meroplanktonic larvae, which at times can totally dominate the communities. Neritic species generally have more restricted distributional ranges than oceanic ones. They are not independent from influences of the sea bed and its communities and their distributions are physically bounded by the coastline on one side and ecologically by the impinging influences of the deep ocean beyond the shelf edge on the other. Neritic communities tend to be linear, and are often constrained by features such as tidal fronts and riverine outflows.

The shelf faunas on either side of the ocean basins usually have little if any faunistic relationship because the trans-oceanic distances are too great for genetic exchanges. There is greater potential for speciation to occur as a result of local differences in coastal morphology, and the effects of sea-level fluctuations resulting in habitat fragmentation as explained above for the Indo-Pacific region. However, neritic species show a lot of morphological adaptation related to spatial and temporal variation in external circumstances and some of these seem to be reversible.

Beklemishev (1971) used the term distantneritic for distributional patterns in extreme environments that are not strictly on the shelf, but which do not cross an ocean. For example, the oxygen-low waters in the east Pacific are such an area (Figure 11). The latter water mass shows endemic species which is rare in strictly oceanic pelagic habitats. The only truly oceanic area with substantial endemism is the Antarctic Ocean.

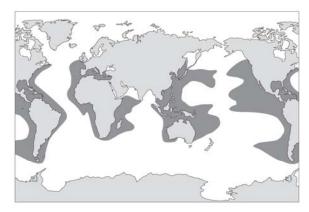


Figure 11. Distant-neritic distributions (after Van der Spoel and Heyman, 1992).

The number of species in any given neritic location is always lower than in the neighbouring oceanic waters. In Chaetognatha, there are 2 neritic species compared with up to 20 oceanic species inhabiting the waters beyond the shelf break in the subtropics at a certain location at a certain time. However, at the shelf break the numbers of species can show a localised peak, because there is a mix between the neritic and oceanic species. Other groups show the same tendency, while copepods show a gradual increase from land to shelf edge (Figure 12).

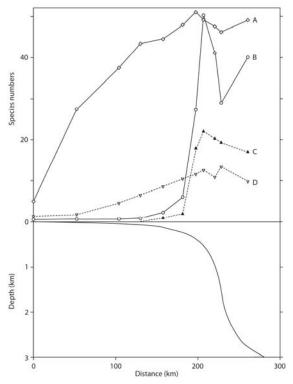


Figure 12. Neritic-oceanic gradients in species richness (after Angel, 1997).

However, the neritic species are different in different regions while the oceanic fauna shows for the main part the same species on a global scale. Thus, the total number of neritic species in the global ocean is higher than the oceanic ones. Locally, in the Indo-Pacific, two or three species of planktonic ostracods can outnumber even the copepods in neritic waters but these are species that do not persist in the open ocean. In general, like in oceanic species, there is a latitudinal gradient in neritic species richness although on smaller scales this can be slightly distorted because of habitat segregation and local radiation. For the pelagic this is less pronounced than for the benthic realm (Fautin, 2012).

Open Ocean

When distributional ranges are considered, the vertical range as well as the horizontal range has to be taken into account. The full distributional range of a species in which it lives and reproduces is difficult to determine in planktonic animals. Distributional data are based on point observations; often we do not know when we sample an animal whether it is caught in its reproductive area. So most distributional data are records of a species' occurrence and include (sterile) expatriates. For example, it has been estimated the >50% of the pelagic Foraminifera caught in the Sargasso Sea are expatriates transported (advected) into areas where they cannot reproduce in the Gulf Stream rings. In addition, it is estimated that we only have sampled about 10% of the area of the oceanic realm, and taking all the pelagic samples that have ever been collected, the nets have not filtered even 0.1 % of the oceans volume.

Hence records of species' distributional ranges are extrapolations of accumulated point observations. These are limited in time and space, and in terms of terrestrial ecology would be dismissed as totally inadequate.

Another factor that complicates collecting accurate distributional data is that many species undertake vertical migrations. Some species migrate several tens to hundreds of metres down at dusk and spend the daylight hours at depth. These diel (or diurnal) migrations can be superimposed on seasonal migrations, in which a species overwinters in a state of physiological passiveness (diapauses) in deep water. The classical the dominant calanoid examples are copepod species in the North Atlantic Calanus finmarchicus, and in the North Pacific there are several Neocalanus species that undertake similar migrations. There are also breeding migrations for example in the Atlantic Eucopia mysids North that normally inhabit depths >700m migrate up towards the surface to breed at the time of the Spring Bloom, and even undertake diel vertical migrations while they are at these

shallower depths. Ontogenetic vertical migration is apparent in many groups. The adults live deeper in the water column then the juveniles.

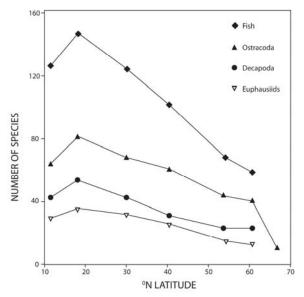


Figure 13. Latitudinal gradients in species richness (after Angel, 1997).

During its decade of its scientific activity the international programme "Census of Marine <http://www.coml.org/> Life" greatly improved our knowledge of the number of species living in the ocean, including some unique studies of holoplankton. In well studied regions of the Atlantic, like the Sargasso Sea, new species were regularly caught at depths >3000m. For example, 10% of the species of planktonic ostracods caught at these depths were novel. This proportion would have been substantially increased if the sampled could have been extended to sample the benthopelagic within a few metres of the sea bed (Angel, 2010). There are technical difficulties in sampling this benthopelagic layer which is inhabited by a virtually unknown pelagic fauna. It is presumed that there is slightly more food in these layers than in the water column above it because of the activities of the bottom fauna that dig into the upper layers of the ocean floor.

In the stable central gyres such as in the Sargasso Sea, stratification of the water column is permanent throughout the year. The food generated by the primary production is utilized much more efficiently in the water column by the microbedominated food-chain as explained above so that much less food reaches the abyssal central plains that are also called the ocean deserts. This stability enables the animals to efficient reproductive develop and competitive strategies. Thus, there is a negative correlation of species richness with latitude (Figure 13). These stable central gyres harbour the greatest number of species. The equatorial region is slightly less species rich because of the upwelling (see Figure 8).

The coloration of plankton is depth related. In the tropics and subtropics, there is a highly specialised community of animals that live within the upper 10cm of the sea surface or even attached to it, which are now known as neuston. Physalia, Vellela and Porpita all have gas filled floats and tentacles that extend down entrapping any other plankton species that brush against them. They are coloured blue, either providing protection from aerial predators like birds or as a screen against the damaging effects of U-V radiation. There are blue copepods of the genus Pontella (Figure 14-1) (Herring, 1965) that have split eyes - one half looking down into the water the other looking towards the surface. They have an escape-behaviour of jumping out of the water like flying fish and flying squid. Leave them in an uncovered jar overnight on the laboratory bench, and in the morning they are to be found dried up on the bench after leaping out of the container. The neuston was only identified as a specialised community a few decades ago. Species richness is low because this is also an extreme environment with great temperature

and salinity variations besides the UV-radiation.



Figure 14. Plankton animals from different depths are pictured to show the different appearances in different depths. 1= the copepod Pontella atlantica, 2= the copepod Euchirella curticauda, 3= the polychaet Tomopteris, 4= a deep-water polychaet, 5= the pteropod Cuvierina columnella, 6= the heteropod Atlanta gaudichaudi, 7= a hydromedusa, 8= the hydromedusa Atolla, 9= the salp Salpa aspera, 10= the ostracod Conchoecissa plintana, 11= the chaetognath Pterosagitta draco, 12= the chaetognath Sagitta zetesios.

Epipelagic Zone

In the epipelagic zone the dominant selective pressure is from visually hunting predators. This selection pressure results in nearly all those species that occupy the upper 200m during the day being either transparent or very small (or both) (Figure 14-3, 5, 6, 7, 9, 11).

Deeper down in the mesopelagic zone (Fig. 14-2, 4, 8, 10, 12) below depths of around 600 m many of the species appear totally red in daylight, which is not only functionally black at the depths they live, but is non reflective to the blue-green light of the bioluminescent 'headlights' of many of the myctophid and ceratioid fishes. The animals

still tend to be translucent, but in the bathypelagic zone >1000m, the energetic demands of staying translucent are no longer affordable in terms of the survival benefit. One consequence of these adaptations to specific depth zones is that as the species is displaced or migrates upwards, it can become more vulnerable to predation. Other physiological adaptations can impose limits on the species' vertical distributions.

Epipelagic species distribution patterns are influenced by water masses. Tropical species are found from about 30°N to 30°S and are mainly found in the Indo-Pacific Ocean. Many subtropical/tropical species are found roughly between 40°N to 40°S and these species have a circumglobal distribution. However, the recent molecular research has reported structured populations and cryptic species in these so-called ubiquous species. Mesopelagic species probably never show restricted distributions; as far as we know, these have 40°N-40°S distributions or even wider into the Subarctic and Subantarctic zones. Strictly Arctic and Antarctic species are confined within the Polar Regions, some of these were considered bipolar species because they are very similar in morphology. However, more detailed studies and molecular work reported that many of these bipolar species are in fact different species. With this technique, a specific piece of mitochondrial DNA COI is used to distinguish between species (Jennings et al, 2010).



Figure 15. The deep-water chaetognath Eukrohnia fowleri with remnants of brood sacs hanging out of the gonopore.

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Pierrot-Bults & Angel

Most research is carried out in the epipelagic layer and we know less about the waters below. Especially below 500 m, samples become scarcer and below 1000 m we have relatively little data considering the vast area. In the mesopelagic layers, especially in the upper-mesopelagic from 200-500 m, influence by the water masses and the upper layer productivity regime is still very evident also because many species in this zone perform daily vertical migrations to the upper layers. They move up to the epipelagic layers at night to feed and sink again to deeper layers during the day. species Mesopelagic show larger distributional ranges than epipelagic ones, most are occurring globally from about 40° N to 40° S in the tropical/subtropical waters. However, there is doubt about them being one species. Deeper down in the upper mesopelagic zone the species tend to be translucent, somewhat larger, and often tinted with yellow and orange pigments. The pigmentation is by carotenoid pigments that can only be synthesised by plants, and so have to be derived from the diet. At these depths, there is no red light so the pigmentation appear to be dark, thereby giving the individuals a disrupted colour pattern, again making them harder to see.

Bathypelagic Zone

In the bathypelagic zone, the influences of the epipelagic zonation are very slight. Although the food supply is from the surface layers, there is still some influence especially in conditions of upwelling and very pulsed food supply. These layers have: 1) very low temperatures; 2) are poor in food; and, 3) are inhabited by animals with growth, long life spans, slow slow reproductive cycles with brood-care, or they ovoviviparous. are For example. chaetognaths usually shed a large number of fertilized eggs in the water, however the

deep meso-pelagic/bathypelagic Eukrohnia fowleri has brood sacs with a few large eggs (Figure 15) and Eukrohnia hamata from Arctic waters is seen with brood sacs with juveniles (Ross Hopcroft, pers. comm.). There is total darkness and practically no seasonal influences. The animals search for food and mates through chemical stimula or visual stimula through bioluminescence. Bathypelagic species are usually dark, black or with red pigments. Because of the apparent similarity throughout the oceans and no obvious barriers except distance, it is assumed that bathypelagic species have worldwide distributions. However, we have very little sampling in these areas to bear proof to this assumption. For example, of the 13 new ostracod species found during plankton cruises in the Census of marine Zooplankton project in the Atlantic, all but one came from depths > 1000 m (Angel, 2010).

Species richness varies with depth, but also shows a latitudinal trend as seen in Figure 10. Table II shows the vertical variation of species richness of ostracods at different latitudes. As previously noted, species richness in the upper 10 m is lower than deeper down. During the night there are more species in the epipelagic zone because of the diurnal migration of mesopelagic species. In Chaetognatha, the main abundance is epipelagic. The mesopelagic species richness is not much lower than the epipelagic, but the number of specimens is lower especially below 500m. For example, in the epipelagic Sargasso Sea, the number of chaetognaths varied from about 5600 to 75000 specimens per m^3 in the layer of 0-25 m to 8 to 73 specimens per m³ from 800-1000 m. In the East Atlantic, the number of specimens was comparable in the layer from 800-1000 m from 48 to 58 per m³, but the number of specimens in the 0-25 m layer

was lower from 4100 to 8700 per m^3 (Pierrot-Bults and Nair, 2010).

Summary

Although the ocean shows the highest diversity on the phylum level, species richness is lower than on the land. Of the 34 animal phyla 29 occur in the ocean and of those 14 are endemic, but only 12 phyla are found in the pelagic ocean and none are endemic. So on the phylum level, the benthos is richer than the pelagic.

Like on land, Arthropoda are the most speciose. It is estimated that half of the terrestrial species are insects and a similar phenomenon is found in the ocean.

The most diverse area in the sea is the Indo-Malayan region; the poorest region is the Arctic region.

Production is vertically structured: primary production takes place at the surface in the photic zone because it needs light; the deeper layers are dependent on this production. Nutrients end up in the deep ocean and are limiting at the surface layers.

In the ocean, very productive regions are unstable because mixing and upwelling causes nutrients to flow back to the photic zone, with high production as a result. Because light is needed, production is seasonal in high latitudes. Animals that are adapted to these highly unstable environments are few and species richness is low. Therefore, extreme and unstable environments have fewer species than more stable regions. Also, evenness is less (e.g., very few species constitute most [>90%] of the numbers of specimens and of the biomass).

There is latitudinal variation in species richness. More species exist in the

subtropics and tropics where the very low latitudes have slightly lower numbers than the more stable subtropical areas because of the equatorial upwelling. This latitudinal variation is also seen in mesopelagic depths.

Species richness is higher in epipelagic and mesopelagic layers than in the bathypelagic. There is a slight peak at about 1000m mixing because of of mesoand fauna. Deeper bathypelagic in the bathypelagic and hadal layers there are few species in very low numbers. However, we do not know whether these species are globally distributed as presumed in the literature because of the lack of data.

Biodiversity and biogeography policy issues

Most research in the sea is carried out by national institutions looking at areas close to their countries and in the epipelagic zone. There are few active open ocean biological research programmes that are studying the biology and ecology of the deeper layers of the ocean. The associated costs of ship time, equipment, and research resources have limited these studies to wealthier nations. Also, governments target funding at research projects that enhance their national wealth and economic productivity rather than investigating and promoting sustainability.

International cooperation is needed to assemble the necessary expertise for effective oceanic research programmes. The technical challenges of collecting and analysing samples are a substantial hurdle to the gathering of good quality and reliable data. Even when expeditions are successful, the lack of funding for the research to identify and enumerate the species and extract the basic data on species diversity, distribution and reproductive cycles inhibits progress. There is a dwindling of taxonomic expertise for dealing with some of the less 'fashionable' taxonomic groups and this is beginning to pose real threats to advances in our holistic knowledge of oceanic ecosystems. Our observations are limited in time and space and are often confined to limited areas of single oceanic regions.

Our lack of knowledge of vast areas of the global ocean, especially in the South-Atlantic and the remoter regions of the Indo-Pacific, is hampering our predictive capability to assess the effects of global climate change on ocean communities and of sustainable use of ocean resources.

Attempts to gain more global understanding are resulting in greater reliance being placed on analogues based on remote sensing. However, these are totally decoupled from the species level at which ecological interactions are driving the oceanic processes that are taking place.

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- Angel, M.V. (1997). Pelagic Biodiversity.
 In: R.F.G. Ormond, J. Gage & M.V.Angel (eds), Marine biodiversity: Patterns and processes. Cambridge University Press. 35-68.
- Angel, M.V. (2010). Towards a full inventory of planktonic Ostracoda (Crustacea) for the subtropical Northwestern Atlantic Ocean. *Deep-Sea Res.* II 57: 2173-2188.
- Angel, M.V., K. Blachowiak-Samolyk, I. Drapun, and R. Castillo. (2007). Changes in the composition of planktonic ostracod populations across a range of latitudes in the North-east Atlantic. *Progr Oceangr.*, 71: 60-78.
- Angel, M.V., K. Blachowiak-Samolyk, and V.G. Chavtur. (2008). An Atlas of Atlantic planktonic Ostracoda. http://nhm.ac.uk (accessed 1/1/2011).
- Beaugrand, G., F. Ibañez, J.A. Lindley, and P.C. Reid. (2002). Diversity of calanoid copepods in the North Atlantic and adjacent seas: species association and biogeography. *Mar. Ecol. Progr. Ser.* 232: 179-195.
- Beklemishev, C.W. (1971). Distribution of plankton as related to micropalaeontology. In: B.M. Funnell, and W.R. Riedel (eds). The micropalaeontology of oceans: 75-87. (Cambridge University Press)
- Bernal, P., Foreword. In: P.V.R. Snelgrove (2010). Discoveries of the Census of marine Life, making ocean life count: ixxiv. (Cambridge University Press).
- Brinton, E., M.D. Ohman, A.W. Townsend,M.D. Knight, and A.L. Bridgeman.(1999). Euphausiids of the World Ocean.

ETI World Biodiversity Database CD-ROM Series.

- Fautin, D.G. (2012). Marine biodiversity: the Benthos. *Biology International* 51: 36-48.
- Grassle, J.F., P. Lasserre, A.D. McIntyre, and G.C. Ray, (1991). Marine Biodiversity and Ecosystem Function. *Biol. Int.* 23: 1-19.
- Herring, P.J. (1965). Blue pigment of a surface-living oceanic copepod. *Nature*. 205: 103-104.
- Jennings, R.M., A. Bucklin, & A.C. Pierrot-Bults. (2010). Barcoding of Arrow Worms (Phylum Chaetognatha) from Three Oceans: Genetic Diversity and Evolution within an Enigmatic Phylum. *PloS1*, 5(4): 1-7.
- Mackas, D.L., P. Pepin, and H. Verheye. (2012). Interannual variability of marine zooplankton and their environments: Within- and between-region comparisons. *Progr. Oceanogr.* 97: 100: 1-14.
- McGowan, J.A. (1971). Oceanic biogeography of the Pacific. In: B.M. Funnell, and W.R. Riedel (eds). The micropalaeontology of oceans: 3-74. (Cambridge University Press).
- Miya, M. & M. Nishida. (1997). Speciation in the open ocean. *Nature*. 389 (6653): 803-804.
- Miyamoto, H., R.J. Machida, and S. Nishida, (2010). Genetic diversity and cryptic speciation of the deepsea chaetognath *Caecosagitta macrocephala* (Fowler, 1904). *Deep-Sea Res.* II 57: 221-2219.

Biology International Vol. 51

- Nogueira, E., G. González-Nuevo, and L. Valdés. (2012). The influence of phytoplankton productivity, temperature and environmental stability on the control of copepod diversity in the North East Atlantic. *Progr. Oceangr.* 97: 92-107.
- Peijnenburg, K.T.C.A., J.A.J. Breeuwer,
 A.C. Pierrot-Bults, and S.B.J. Menken.
 (2004). Phylogeography of the
 planktonic chaetognath Sagitta setosa
 reveals isolation in European seas.
 Evolution. 58: 1472-1487.
- Pierrot-Bults, A.C. (1997). Biological Diversity in oceanic macrozooplankton: more than counting species. In: R.F.G. Ormond, J. Gage & M.V. Angel (eds), Marine biodiversity: Patterns and processes. Cambridge University Press: 69-93.
- Pierrot-Bults, A.C. (1998). Variation in widespread zooplankton species. In: A.
 C. Pierrot-Bults & S. van der Spoel (eds). Pelagic Biogeography II.
 Proceedings of the International Conference. IOC Workshop Rep. 142: 285-296.
- Pierrot-Bults, A.C. (2008). A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. *Deep-Sea Research* II 55(1-2): 137-141.
- Pierrot-Bults, A.C. & V.R Nair. (2010). Horizontal and vertical distribution of Chaetognatha in the upper 1000m of the western Sargasso Sea and the Central and South-east Atlantic. *Deep-Sea Research II* 57:2189-2198.
- Pierrot-Bults, A.C. & S. van der Spoel. (1979). Speciation in macrozooplankton.

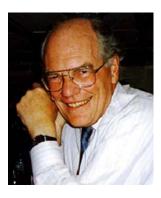
In A.C. Pierrot-Bults, S. van der Spoel, B.J. Zahuranec, and R.K. Johnson, 1986. Pelagic Biogeography. *Unesco Techn. Papers in mar. Sci.* 49: 1-295.

- Pierrot-Bults, A.C. & S. van der Spoel. (2003). Macrozooplankton diversity: how much do we really know? *Zool. Verh. Leiden.* 345: 297-312.
- Razouls C., de Bovée, F., Kouwenberg, J. et Desreumaux N. (2005-2012). Diversity and Geographic Distribution of Marine Planktonic Copepods. Available at http://copepodes.obsbanyuls.fr/en (Accessed April 22, 2012)
- Reid, J. L., E. Brinton, A. Fleminger, E.L. Venrick & J.A. McGowan, (1978).
 Ocean Circulation and marine life. In: H. Charnock & G. Deacon (eds), Advances in Oceanography: 65-130. (Plenum Press, New York, London).
- Sutton, T.T., F.M. Porteiro, M. Heino, I. Byrkjedal, G. Langhelle, C.I.H. Anderson, J. Horne, H. Søiland, T. Falkenhaug, O.R. Godø, and O.A. Bergstad. (2008). Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a midocean ridge system. *Deep-Sea Res.* II 55: 161-184.
- Sutton, T.T., F.M. Porteiro, M. Heino, I. Byrkjedal, G. Langhelle, C.I.H. Anderson, J. Horne, H. Søiland, T. Falkenhaug, O.R. Godø, and O.A. Bergstad. (2008). Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a midocean ridge system. *Deep-Sea Res.* II 55: 161-184.
- Valdès, L., A. López-Urrutia, and J. Cabal. (2007). A decade of sampling in the Bay

Pelagic Biodiversity and Biogeography of the Oceans

of Biscay: What are the zooplankton time series telling us? *Progr. Oceanogr.* 74: 98–114.

- Van der Spoel, S. and R.P. Heyman. (1982). An atlas of zooplankton distributions. (Bunge scientific Publishers, Utrecht).
- Van der Spoel, S., L. Newman, and K.W. Estep. (1997). Pelagic Molluscs of the world. ETI World Biodiversity Database CD-ROM Series.
- Van der Spoel, S. and A. C. Pierrot-Bults (eds.) (1979). Zoogeography and diversity of zooplankton. (Bunge, scientific publishers, Utrecht): 144-167.
- Van der Spoel, S., A.C. Pierrot-Bults, and P.H. Schalk. (1990). Probable Mesozoic vicariance in the biogeography of Euphausiacea. Bijdr. Dierk. 60: 155-162.
- Wishner, K., M.M. Gowing, and C. Gelfman. (1998). Mesozooplankton biomass in the upper 1000 m in the Arabian Sea: overall seasonal and geographic patterns, and relationship to oxygen gradients. *Deep-Sea Res.* II, 45: 2405-2432.
- WORMS, World Register of Marine Species. http://www.marinespecies.org/



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Marine Biodiversity: The Benthos

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The oceans constitute at least 90% of the earth's biosphere; the marine benthic environment is at least twice as large as the terrestrial environment. The aqueous environment quenches light, so most of the marine environment is invisible to humans – and lacks organisms that photosynthesize. Much of the marine environment is hostile to human life, but supports a huge diversity of living organisms, although the number of marine species is highly uncertain. New technologies are improving the inventory of marine life at the same time that we are in danger of losing much of it. Overfishing, trawling, ghost-fishing, run-off of nutrients from the land, global warming, introduced alien species, and ocean acidification are among the threats to the oceans and its inhabitants.

Keywords: biodiversity, climate change, global change, oceans

The number of species on earth is uncertain. A compendium published at the end of 2011 (Zhang 2011: 7) gave as "the best estimate," based on contributions from more than 100 taxonomists, a figure of 1,552,319 described species, of which two-thirds are insects. About a million and a half known species is typical of many estimates (e.g. May 1998, Costello et al. 2011). Estimates of known and unknown species range from three to 100 million (Mora et al. 2011); for the marine environment, the range is 178,000 to more than 10 million (Sala and Knowlton Mora et al. (2011) attempted to 2006). improve accuracy by extrapolating from higher taxa. Their estimate was ~8.7 million eukaryotic species, of which ~2.2 million are marine; from this they inferred that 91% of marine species await description. At about the same time, Costello et al. (2011) estimated there are as few as 0.3 million, the figure given by Sala and Knowlton (2006) for described marine species.



Figure 1. Ctenophore *Leucothea pulchra*. Photographed by Amy Lemur at Pebble Beach, California, USA. Used under Creative Commons License.

Uncertainty about the magnitude of marine biodiversity is likely to be greater than that of the terrestrial realm because so much of the marine habitat is beyond easy reach of humans (for more on this, see below). Although the term "biodiversity" commonly refers to the number of species, measures of biodiversity at genomic and ecological scales are recognized to be important (e.g. Sala and Knowlton 2006; Palumbi et al. 2009). In fact, taxonomic diversity can be measured in units other than species. Although the number of species on land far exceeds that in the sea (due to the virtual absence of insects in marine environments), the reverse is true at the phylum level (Pearse et al. 1987; May 1998). All phyla except Onychophora have marine members; phyla with diverse representatives on land and/or in freshwater as well as the sea include Arthropoda, Mollusca, Annelida, Nematoda, Porifera, Tardigrada, and Bryozoa. However, several phyla are exclusively marine, including the diverse and ecologically important Echinodermata, the less diverse Ctenophora (Figure 1), and the incompletely known meiofaunal groups as Kinorhycha, Loricifera, such and Gnathostomulida; the vast majority of the members of Cnidaria are marine. Thus, in terms of major types of animals, the sea is far more diverse than the land. The same may be true for plants and microbes (Hendriks et al. 2006), but, as explained below, this paper deals almost entirely with animals.

Many overviews on biodiversity arising from the activities of the Census of Marine Life (which existed from 2000 to 2010) have been published in PLoS One. Costello *et al.* (2010) summarized the program as a whole and O'Dor *et al.* (2010) introduced a collection of contributions summarizing biodiversity in geographically-defined areas including: 1) Aotearoa (New Zealand)

(Gordon et al. 2010); 2) Antarctica (Griffiths 2010); 3) the Australian region (Butler et al. 2010); 4) the Caribbean (Miloslavich et al. 2010); 5) Japan (Fujikura et al. 2010); and, 6) the U.S. (Fautin et al. Since that first collection, other 2010). inventories have appeared, among them one concerning Indian Ocean countries (Wafar et al. 2011). An edited volume (McIntyre 2010) describes the scientific results of each component of the Census; biodiversity assessment is a component of most chapters, which are organized by habitat (e.g. coral reefs, sea mounts), region (e.g. Arctic, Gulf of Maine), or taxon (e.g. microbes, zooplankton).

This overview of benthic marine biodiversity is designed to point the reader to resources for various aspects of this enormous field - many of the cited publications are reviews, from which the primary research that was used to create the overview can be discovered; others are from high-impact studies in journals that are widely available, such as Science and Nature. Grombridge and Jenkins (1996) and Sala and Knowlton (2006) have written reviews of marine biodiversity that invoke the controlling of biological, many chemical, and physical factors. The focus in this treatment is, as was that of Sala and Knowlton, threats to the continued existence of this diversity – because, just as we are coming to grips with an inventory of it, we are in danger of losing much of it.

Thus, in terms of major types of animals, the sea is far more diverse than the land.

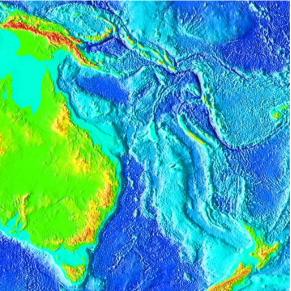


Figure 2. Topography of the floor of the Coral Sea and southwestern Pacific Ocean (eastern Australia at left, New Zealand at lower right) derived from ETOPO2 gridded data by the US National Geophysical Data Center, National Oceanic and Atmospheric Administration (NOAA), Department of Commerce: (http://www.ngdc.noaa.gov/ mgg/image/2minsurface/00N135E.html).

Marine Habitats

By contrast with the terrestrial environment, essentially two-dimensional which is (although the earth's surface does have relief, operationally metazoans and most other organisms live on the surface or a very short distance above or below it), the marine environment is fully three-dimensional; indeed, at least 90% of the earth's habitable volume (biosphere) is marine (Amaral-Zettler et al. 2011). The geographicallybased inventories in McIntyre (2010) and the review by Sala and Knowlton (2006) dealt with both pelagic and benthic organisms – that is, those that live free in the water, and those that live associated with the sea floor bottom (on it or in it), respectively. The benthos of the sea is the largest habitat on earth. Seas are said to cover some 70% of the earth's surface, but when the topography of the sea floor is considered, the proportion of the actual surface must exceed that -- for the greatest oceanic depth is slightly more than 10,000 m (whether 91 or 103 m more is debated), compared with 8848 m, the greatest vertical rise of land (Mt. Everest), and there are at least as many submarine mountain ranges as those on land (*e.g.* Figure 2).

Most marine organisms that live benthically as adults have a life cycle that involves a larval stage that is pelagic. The adaptiveness of that life cycle is debated (*e.g.* Strathmann 1985, 2007). Whatever the ultimate reason for most benthic organisms spending some of their lives away from the sea floor, conditions of the pelagic realm affect the benthic biota.

Water

The benthic organisms' physical and chemical environment has shaped and affected them profoundly. The dominant force in that environment is water. Because water is the universal solvent, marine organisms arguably are exposed to changes in the earth's chemistry more readily than those on land, for better or worse. Thus, to a greater extent than on land, an organism can be affected by processes that occur distant from it. Important among these substances are the gases that are exchanged in respiration (of which much more below).

A major reason marine organisms are so poorly known scientifically is that most of their environment is, for all practical purposes, invisible, being below the depth to which visible light effectively penetrates. Solar radiation is readily absorbed, reflected, and scattered by water, so the vast majority of the marine habitat is out of sight. Because light from exploratory vehicles is similarly absorbed, much of what is known about most of the benthic habitat is from blind exploration, derived from samples raised to the surface by devices such as nets or grabs, or from devices using energy such as sound (sonar – which is employed by a diversity of marine vertebrates, also because light is so limited in most of the sea).

The absorption of light means also that photosynthetically active radiation is essentially absent deeper than about 100 m (Steele [1962] found that 1% of surface light reached that depth in the North Sea), the precise depth depending on factors such as the angle of incidence of the light. In addition to water molecules, particulate solids suspended in water absorb, reflect, and scatter photons; therefore, plants live in only the uppermost skin of the seas - even shallower where the water is murky. The benthic habitat extends well below that depth except around land masses and a few seamounts that rise to near the ocean's surface. Thus, most marine plant life, by volume, is pelagic, and the vast majority benthic marine life is animal. of Microorganisms such as bacteria, fungi, and viruses are far more diverse in the sea than had been thought, but study of them is in its infancy (Amaral-Zettler et al. 2010), so this article focuses on animals.

Parenthetically, although most life on earth is driven by captured solar energy, another source of fuel for organisms discovered in the 1970s is more widespread than was originally thought: this is the chemical energy first discovered as important in the Galapagos hot vent system and since identified in other hot vents, cold seeps, whale falls, other similar habitats, and even salt marshes. Rather than photoautotrophs (plants the best known of them) capturing energy that is passed on to animals, in these habitats it is chemosynthetic and methanotrophic bacteria (e.g. German et al. 2011) (Figure 3).

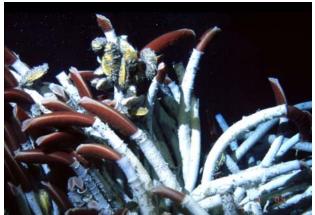


Figure 3. Vestimentiferan annelids, the iconic inhabitant of the Galapagos hydrothermal vents. Each tubeworm, which lacks a gut, may reach nearly 2 m in length; in its red plume, the worm harbors symbiotic microorganisms that capture energy through chemosynthesis. Photo courtesy of NOAA.

Because the density of water is so much greater than that of air, some organisms have only hydrostatic skeletons for support, and those with hard skeletons, such as arthropods and shelled gastropods, can grow larger than terrestrial members of those groups. Transportation of food to many marine organisms (and waste from them) is also influenced by the density of water. This density means that seawater exerts as much pressure in each 10 m of depth as is exerted by the entire depth of the atmosphere above the sea (and land).

Contrary to the common view that pressure stresses deep-sea animals, they are adapted to it as terrestrial organisms are adapted to the not-insignificant pressures of an atmosphere kilometers thick impinging on them. What can be stressful is a change in pressure - because of the behavior of gas, as given in Boyle's law. For example, the gas in the swimbladder of a finfish that is raised rapidly to the surface from a depth of 10 m doubles in volume (the pressure on it being halved), and, if it does not burst, the swimbladder may protrude through the mouth of the fish and kill it (Figure 4). Most marine organisms have no such problem because they lack gas-filled spaces; but pressure may also affect viscosity of lipid bilayers (*e.g.* Airriess and Childress 1994).



Figure 4. Rockfish with gas bladder protruding through mouth after it was brought to the surface. Copyright Oregon State University (http://www.flickr.com/photos/ oregonstateuniversity/3707958314/sizes/z/in/photostream/)

Threats to Marine Life

Global change, which is much more than alterations in climate, is evident in the sea, and potentially will profoundly affect its biota. A report issued by the UN Environment Programme (2010) identified many pressures on marine biodiversity and the outlook for particular habitats, along with some steps being taken to ameliorate the causes; Sala and Knowlton (2006) placed the changes in an evolutionary context. Buddemeier *et al.* (2004) focused on the effects of global change on coral reefs.

Overfishing

A widespread concern is over-fishing (*e.g.* Branch *et al.* 2010). A decline in fish catch has implications for nutrition of humans and their employment in fisheries. On the biological side, it means shrinking populations of target species. Demographic shifts in marine organisms are common because typically larger individuals are selectively taken; this has further effects

because of size-related fecundity in most teleosts (e.g. Merrett 1994), and in some teleost species sex can change with size (e.g. Fischer and Petersen 1987; Shapiro 1987). Species at the top of the food chain are typically preferred by fishers. This leads to a phenomenon that has been termed "fishing down the food web" (Pauly et al. 1998), which can alter the entire food chain (e.g. Frank et al. 2011). The phenomenon of top predators being removed that has been so conspicuous in the sea is now seen as a widespread, and alarming, ecological phenomenon (Estes et al. 2011). However, impacts on lower trophic levels are also of concern (e.g. Smith et al. 2011).

Most public and academic attention has been paid to pelagic species, but benthic fisheries pose an additional environmental threat trawling. Trawling is not selective: nontarget species may constitute a large proportion of the trawl (Alverson et al. 1994). Some of this "by-catch" is discarded: in 1994, Alverson et al. estimated it amounted to 27 million metric tons per year. The survival rate of the discarded animals depends on conditions of handling, attributes of the gear and species, and other factors. Moreover, the bottom is disrupted, making it unsuitable for life of many of its normal denizens and destroying biogenic structures (Thrush and Dayton 2002, Kaiser et al. Trawled benthic species include 2006). teleosts, such as flatfishes, but also invertebrates, such as shrimp. A related concern is lost fishing gear such as nets, lines, traps... This can cause "ghost fishing" in the pelagic realm (Smith 2005; Figure 5); in the benthos it, like trawling, can destroy habitat, especially biogenic habitat (e.g., Chiappone et al. 2005).



Figure 5. A net that has been ghostfishing (http://i.usatoday.

net/news/_photos/2010/05/17/ghostfishingx-large.jpg)

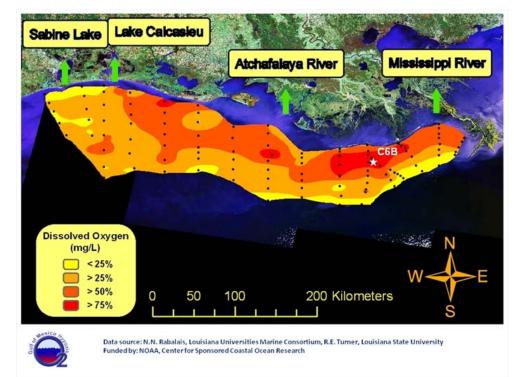


Figure 6. The Gulf of Mexico "Dead Zone" showing the proportion of time during 1985-2008 an area was hypoxic (< 2mg/l of oxygen). Any site visited in fewer than three years was not included. (http://www.gulfhypoxia.net/Research/Shelfwide%20Cruises/Frequency%20of%20Hypoxia/)

Dead Zones

Another concern identified by the UN Environment Programme (2010) is nutrient loading. A well-documented example of this phenomenon causes a "dead zone" west of the mouth of the Mississippi River in the Gulf of Mexico (Rabalais *et al.* 2002; Figure 6). The Mississippi drains nearly a third of the continental United States, including areas where much of the maize and wheat (that feeds both humans and other animals) is grown. Some of the nitrogen-based

fertilizer applied to crops grown there runs into the Mississippi River (or its tributaries), and ultimately into the Gulf of Mexico, where it fertilizes the phytoplankton. These organisms are carried in currents along the Gulf coast, eventually thereby falling to the bottom and decaying, a process that consumes oxygen; organisms unable to move from hypoxic areas and that have high metabolic rates are particularly vulnerable to the effects of low oxygen. Some "dead zones" caused by nutrient input seem to be shrinking. Although the extent of the one at the mouth of the Mississippi was greatest in 2002, the current five-year average still exceeds the long-term average, and bottom water measured in late July 2010 is hypoxic from the mouth of the Mississippi in Louisiana nearly to Galveston Bay, Texas (http://www.gulfhypoxia.net/Research/Shelf wide%20Cruises/#Monitoring).

Although human-caused oxygen depleted zones are increasing, there are naturally occurring ones. Particularly some of the zones at mid-water depth are home to organisms that are adapted to survive at low oxygen tensions (*e.g.* Teal and Carey 1967); they may use these regions for refuge from predators that cannot tolerate those conditions.

Synergistic Effects

Many stresses do not occur in isolation; a particularly instructive example of how multiple stressors combine is the shallow marine habitat of much of the Caribbean (e.g. Hughes and Connell 1999; Gardner et al. 2003). Hurricanes (the first in 1980), diseases (largely of corals and sea urchins), overfishing, and siltation have all contributed to a shift from a coral-dominated to an alga-dominated habitat (e.g. Hughes and Tanner 2000). And although such changes have been occurring for centuries (Pandolfi *et al.* 2003), recent increases in human population have led to land-clearing for agriculture, which has increased run-off of two stressors of reef-building corals, silt and nutrients. Removal of fish by humans diminished individual and population size of fish so herbivorous fishes were insufficient to clear algae that competed for space with coral propagules, and the algae thrived in the presence of the increased nutrients.

Bleaching

Also toward the end of the twentieth century, the frequency of episodes of coral bleaching and their extent both increased (e.g. Hughes et al. 2003, Buddemeier et al. 2004). The most common cause of this phenomenon is the break-down in the symbiosis between corals and their intracellular algae (e.g. Baker 2003. Buddemeier et al. 2004); the symbiosis allows reef-forming corals to thrive in oligotrophic waters (in more nutrient-rich waters, corals are typically out-competed see above). "Bleaching" is so called because the animal tissue is transparent, which allows sunlight to reach the algae living inside the cells of a coral's inner cell layer – so when there are no algae, the white skeleton of the coral is visible through the transparent living tissue overlying it (despite the name "coral" also being that of a pink color (Fautin and Buddemeier 2009), the skeleton of all reef-forming scleractinian corals is white). Bleaching is a general stress response: stressors such as unusually high or low water temperature or salinity, and some chemicals can cause it. Bleaching itself immediately results in death in only a few taxa of corals; most corals repopulated by zooxanthellae will survive. (These zooxanthellae can be from the ambient water or ones that remained in the coral when the symbiosis with others broke down.)

2012 Jun 19 NOAA CRW Coral Bleaching Thermal Stress Outlook for Jun-Sep 2012 (Version 2, Experimental)

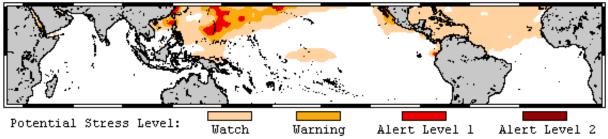


Figure 7. Example of NOAA coral bleaching outlook.

(http://www.coralreefwatch.noaa.gov/satellite/bleachingoutlook/index.html)

Each of the multiple types of zooxanthellae interacts with animal hosts differently, so tolerances to environmental factors depend on the combination (Baker 2003). However, because temperature tolerance of a coralzooxanthella combination is near the average warmest temperature of the area in which the coral lives, increased occurrences of warmer-than-normal seawater temperature associated with global warming has resulted in more frequent and widespread bleaching. NOAA has developed website a displaying the bleaching threat (http://coralreefwatch.noaa. gov/satellite/bleachingoutlook/index.html) due to thermal stress (Figure 7).

Acidification

A reason for rising sea surface temperature is increased atmospheric carbon dioxide (and other gases) which create what is "greenhouse termed the effect" (http://en.wikipedia.org/wiki/Greenhouse_ef fect). Another threat to all corals and many other organisms with skeletons of calcium carbonate has been termed "ocean acidification" (e.g. Beaufort et al. 2011). It results from increased carbon dioxide in the atmosphere, but its consequence differs from that of the greenhouse effect. Some of the CO₂ released into the atmosphere diffuses into and dissolves in seawater. There is a net flow until concentrations are equal in air and sea, so as long as atmospheric CO_2

increases, more will flow into seawater. On a human time scale, for practical purposes, increased atmospheric CO₂ affects the surface waters because diffusion is slow. The water's pH is depressed because when CO₂ dissolves in water it ionizes, forming carbonic acid. This means that the concentration of calcium carbonate in seawater, which corals use to build their skeletons. declines. It also means that pieces of calcium carbonate already in existence, such as snail shells and coral skeletons, dissolve more easily. Many other marine organisms with calcified parts are also adversely affected (e.g. Beaufort et al. 2011), but not all are (e.g. Checkley et al. 2009).

Invasive Species

A threat to biodiversity on land is alien invaders; although at first the addition of invasives can raise the ostensible biodiversity (an example of why the raw number of species is not necessarily an ideal metric of biodiversity), over the long term and globally, it serves to homogenize biotas Sala and Knowlton 2006). (e.g.Furthermore, invasives typically disrupt functioning of places they invade, and ultimately drive natives to extinction. For many years, the marine environment was considered impervious to invaders. Some recent high-profile invasions have shown that not only is that not true, effects may

occur more rapidly in the sea than on land (Sorte *et al.* 2010). An invader that has received much attention is the attractive and toxic lionfish, which is now present along much of the southern Atlantic coast of the US and the Caribbean (*e.g.* Kimball *et al.* 2004, Morris *et al.* 2011; Figure 8), and there are many others (for another example, see Sorte *et al.* 2010, http://www. mnn.com/earth-matters/animals/ blogs/gianttiger-prawn-invades-gulf-of-mexico).

Commerce seems involved in many marine invasions; the invaders traveled on ships or in their ballast water, or were released or escaped from their human-built enclosures.



Figure 8. The invasive lionfish. (http://www.reefresearch.org/ccmi_website/research/research_06_02.ht m)

Conclusion

In face of global change, it is likely that most marine organisms will persist, but in different assemblages than now occur. As Hughes *et al.* (2003: 929) commented, increased human impacts will cause coral reefs to "change rather than disappear entirely." Change is inevitable, but because the current changes are placing critical aspects of the environment outside anything experienced by humans (*e.g.* Buddemeier *et al.* 2004), even if some of the alterations are ultimately favorable, adaptation will be required because the world of the future will differ from that to which we are accustomed.

References

- Airriess, C.N. and J.J. Childress. (1994). Homeoviscous properties implicated by the interactive effects of pressure and temperature on the hydrothermal vent crab *Bythognzea thermydron*. *Biological Bulletin* 187: 208-214.
- Alverson, D.L., M.H. Freeberg, S.A. Murawski, and J.G. Pope. (1994). A global assessment of fisheries bycatch and discards. *FAO Technical Paper* 339: 1-233. Available on line at http://www.fao.org/DOCREP/003/T489 0E/T4890E00.htm.
- Amaral-Zettler, L., L.F. Artigas, J. Baross, P.A. Loka. Bharathi, A. Boetius, D. Chandramohan, G. Herndl, K. Kogure, Ph. Neal, C. Pedrós-Alió, A. Ramette, S. Schouten, L. Stal, A. Thessen, J. de Leeuw, and M. Sogin. (2010). Pages 223-245 (chapter 12) in A.D. McIntyre, ed. *Life in the World's Oceans: Diversity, Distribution, and Abundance.* Wiley-Blackwell, Chichester and other cities.
- Amaral-Zettler, L., J.E. Duffy, D. Fautin, G. Paulay, T. Rynearson, H. Sosik, and J. Stachowicz. (2011). Attaining an operational marine biodiversity observation network (BON) synthesis report. http://www.nopp.org/wpcontent/uploads/2010/03/BON_Synthesi sReport.pdf.
- Baker, A.C. (2003). Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of *Symbiodinium*. *Annual Review of Ecology and Systematics*. 34: 661-689.
- Beaufort, L., I. Probert, T. de Caridel-Thoron, E.M. Bendif, D. Ruiz-Pino, N. Metzl, G. Goyet, N. Buchet, P. Coupel,

M. Grelaud, B. Rost, R.E.M. Rickaby, and C. de Vargas. (2011). Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. *Nature* 476: 80-83.

- Branch, T.A., R. Watson, E.A. Fulton, S. Jennings, C.R. McGilliard, G.T. Pablico, D. Richard, and S.R. Tracey. (2010). The trophic fingerprint of marine fisheries. *Nature* 468: 431-435.
- Buddemeier, R.W., J.A. Kleypas, and R.B. Aronson. (2004). Coral reefs and global climate change. Pew Center on Global Climate Change, Arlington, Virginia. 44 pages. Available on line at http://www.pewclimate.org/globalwarmi ng-in-depth/all_reports/coral_reefs /index.cfm.
- Butler, A.J., T. Rees, P. Beesley, and N.J. Bax. (2010). Marine biodiversity in the Australian Region. *PLoS ONE* 5(8): e11831.
- Checkley, D.M., Jr., A.G. Diskson, M. Takahashi, J.A. Radich, N. Eisenkolb, and R. Asch. (2009). Elevated CO₂ enhances otolith growth in young fish. *Science* 324: 1683.
- Chiappone, M., H. Dienes, D.W. Swanson, and S.L. Miller. (2005). Impacts of lost fishing gear on coral reef sessil invertebrates in the Florida Keys National Marine Sanctuary. *Biological Conservation* 121(2): 221-230.
- Costello, M.J., M. Coll, R. Danovaro, P. Halpin, H. Ojaveer, and P. Miloslavich. (2010). A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE* 5(8): e12110.

- Costello M.J., S. Wilson, and B. Houlding. (2011). Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology* prepublication online. http://sysbio.oxfordjournals.org/ content/early/2011/08/18/sysbio.syr080.f ull.pdf.
- Estes, J.A., J. Terborgh, J.S. Brashares, M.E. Power, J. Berger, W.J. Bond, S.R. Carpenter, T.E. Essington, R.D. Holt, J.B.C. Jackson, R.J. Marquis, L. Oksanen, T. Oksanen, R.T. Paine, E.K. Pikitch, S.W.J. Ripple, S.A. Sandin, M. Scheffer, T.W. Schoener, J.B. Shurin, A.R.E. Sinclair. M.E. Soulé. R. Virtanen, and D.A. Wardle. (2011). Trophic downgrading of Planet Earth. Science 333: 301-306.
- Fautin, D.G. and R.W. Buddemeier. (2009).Coral. Pages 197-203 in R. Gillespie,D.A. Clague, eds. *Encyclopedia of Islands*. University of California Press,Berkeley and Los Angeles.
- Fautin, D., P. Dalton, L.S. Incze, J.-A.C. Leong, C. Pautzke, A. Rosenberg, P. Sandifer, G. Sedberry, J.W. Tunnell, I. Abbott, R.E. Brainard, M. Brodeur, L.G. Eldredge, M. Feldman, F. Moretzsohn, P.S. Vroom, M. Wainstein, and N. Wolff. (2010). An overview of marine biodiversity in United States Waters. *PLoS ONE* 5(8): e11914.
- Fischer E.A. and C.W. Petersen. (1987). The evolution of sexual patterns in the sea basses. *BioScience* 37: 482-489.
- Frank, K.T., B. Petrie, J.A.D. Fisher, and W.C. Leggett. (2011). Transient dynamics of an altered large marine ecosystem. *Nature* 477: 86-89.

- Fujikura, K., D. Lindsay, H. Kitazato, S. Nishida, and Y. Shirayama. (2010).Marine biodiversity in Japanese waters. *PLoS ON*. 5(8): e11836.
- Gardner, T.A., I.M. Côté, J.A. Gill, A. Grant, and A.R. Watkinson. (2003). Long-term region-wide declines in Caribbean corals. *Science* 301:958
- German, C.R., E. Ramirez-Llodra, M.C. Baker, P.A. Tyler, the ChEss Scientific Steering Committee. (2011). Deepwater chemosynthetic ecosystem research during the Census of Marine Life decade and beyond: a proposed deep-ocean road map. *PLoS ONE* 6(8): e23259.
- Gordon, D.P., J. Beaumont, A. MacDiarmid,D.A. Robertson, and S.T. Ahyong.(2010). Marine biodiversity of *Aotearoa*New Zealand. *PLoS ONE* 5(8): e10905.
- Griffiths, H.J. (2010). What do we know about the distribution of life in the Southern Ocean? *PLoS ONE* 5(8): e11683.
- Groombridge, B. and M.D. Jenkins. (1996). *The diversity of the seas: a regional approach.* WCMC Biodiversity Series #4. World Conservation Monitoring Centre, World Conservation Press, Cambridge, UK. 132 pp.
- Hendriks, I.E., C.M. Duarte, and C.H.R. Heip. (2006). Biodiversity research still grounded. *Science* 312: 1715.
- Hughes, T.P., A.H. Baird, D.R. Bellwood,
 M. Card, S.R. Connolly, C. Folke, R.
 Grosberg, O. Hoegh-Guldberg, J.B.C.
 Jackson, J. Kleypas, J.M. Lough, P.
 Marshall, M. Nyström, S.R. Palumbi,
 J.M. Pandolfi, B. Rosen, and J.

Roughgarden. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933.

- Hughes, T.P. and J.H. Connell. (1999). Multiple stressors on coral reefs: a longterm perspective. *Limnology and Oceanograph.* 44: 932-940.
- Hughes, T.P. and J.E. Tanner. (2000). Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81: 2250-2263.
- Kaiser, M.J., K.R. Clarke, H. Hinz, M.C.V. Austen, P.J. Somerfield, and I. Karakassis. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series* 311: 1-14.
- Kimball, M.E., J.M. Miller, P.E. Whitfield, and J.A. Hare. (2004). Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Marine Ecology Progress Series* 283: 269-278.
- McIntyre, A.D. (2010). *Life in the World's Oceans: Diversity, Distribution, and Abundance*. Wiley-Blackwell, Chichester and other cities. 361 pp.
- May, R.M. (1998). The dimensions of life on Earth. Pages 30-45 in P.H. Raven, ed. *Nature and human society: the quest for a sustainable world*. National Academy Press, Washington, DC.
- Merrett, N.R. (1994). Reproduction in the North Atlantic ichthyofauna and the relationship between fecundity and species' sizes. *Environmental Biology of Fishes* 41: 207-245.

- Miloslavich, P., J.M. Díaz, E. Klein, J.J. Alvarado, C. Díaz, J. Gobin, E. Escobar-Briones, J.J. Cruz-Motta, E. Weil, J. Cortés, A.C. Bastidas, R. Robertson, F. Zapata, A. Martín, J. Castillo, A. Kazandjian, and M. Ortiz. (2010). Marine biodiversity in the Caribbean: regional estimates and distribution patterns. *PLoS ONE* 5(8): e11916.
- Mora, C., D.P. Tittensor, S. Adl, A.G.B. Simpson, and B. Worm. (2011). How many species are there on earth and in the ocean? *PLoS Biology* 9(8): e1001127.
- Morris, J.A., Jr., C.V. Sullivan, and J.J. Govoni. (2011). Oogenesis and spawn formation in the invasive lionfish, *Pterois miles* and *Pterois volitans*. *Scientia Marina* 75:147-154.
- O'Dor, R., P. Miloslavich, and K. Yarincik. (2010). Marine biodiversity and biogeography – regional comparisons of global issues, an introduction. *PLoS ONE* 5(8): e11871.
- Palumbi, S.R., P.A. Sandifer, J.D. Allan, M.W. Beck, D.G. Fautin, M.J. Fogarty, B.S. Halpern, L.S. Incze, J.-A. Leong, E. Norse, J.J. Stachowicz, and D.H. Wall. (2009). Managing for ocean biodiversity to sustain marine ecosystem services. *Frontiers in Ecology and the Environment* 7: 204-211.
- Pandolfi, J.M., R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, G. Paredes, R.R. Warner, and J.B.C. Jackson. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301: 955-958.

- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F.C. Torres, Jr. (1998).Fishing down marine food webs. *Science* 279: 860-863.
- Pearse, V., J. Pearse, R. Buchsbaum, and M. Buchsbaum. (1987). *Living Invertebrates*. Blackwell Scientific, Boston.
- Rabalais, N.N., R.E. Turner, and W.J. Wiseman, Jr. (2002). Gulf of Mexico hypoxia, a.k.a. "The Dead Zone." *Annual Review of Ecology and Systematics* 33: 235-263.
- Sala, E. and N. Knowlton. (2006). Global marine biodiversity trends. *Annual Review of Environment and Resources* 31: 93-122.
- Shapiro, S.Y. (1987). Differentiation and evolution of sea change in fishes. *BioScience* 37: 490-497.
- Smith, A. (2005). World inventory of fisheries. Ghost fishing. Issues fact sheets. FAO Fisheries and Aquaculture Department http://www.fao.org/fishery/topic/14798 /en (accessed 27 November 2011)
- Smith, A.D.M., C.J. Brown, C.M. Bulman, E.A. Fulton, P. Johnson, I.C. Kaplan, H. Lozano-Montes, S. Mackinson, M. Marzloff, L.J. Shannon, Y.-J. Shin, and J. Tam. (2011). Impacts of fishing lowtrophic level species on marine ecosystems. *Science* 333: 1147-1150.
- Sorte, C.J.B., S.L. Williams, and J.T. Carlton. (2010). Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography* 19: 303-316.

- Strathmann, R.R. (1985). Feeding and nonfeeding larval development and lifehistory evolution in marine invertebrates. *Annual Review of Ecology and Systematics* 16: 339-361.
- Strathmann, R.R. (2007). Three functionally distinct kinds of pelagic development. *Bulletin of Marine Science* 81: 167-179.
- Steele, J.H. (1962). Environmental control of photosynthesis in the sea. *Limnology and Oceanography* 7: 137-150.
- Teal, J.M. and F.G. Carey. (1967). Respiration of a euphausiid from the oxygen minimum layer. *Limnology and Oceanography* 12: 548-550.
- Thrush, S.F. and P.K. Dayton. (2002). Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review* of Ecology and Systematics 33: 449-473.
- UN Environment Programme. (2010). Global synthesis: a report from the Regional Seas Conventions and Action Plans for the marine biodiversity assessment and outlook series. UNEP Regional Seas Programme, Kenya. http://www.marinebiodiversityseries.org/ reports/2-global-synthesis-report.html.
- Wafar, M., K. Venkataraman, B. Ingole, S. Ajmal Khan, and P. LokaBharathi. (2011). State of knowledge of coastal and marine biodiversity of Indian Ocean countries. *PLoS ONE* 6(1): e14613.
- Zhang, Z.-Q. (2011). Animal biodiversity: An introduction to higher-level classification and taxonomic richness. *Zootaxa* 3148: 7–12.



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Biology International considers articles from a wide variety of interest areas and a diverse spectrum of biological disciplines. The International Union of Biological Sciences has major concerns about conservation, biodiversity, sustainability, health, agriculture, bioethics, indigenous knowledge, and biology education. We have a long history of working with universities, museums, herbariums, zoos, national parks, forest reserves, industries, NGOs, and governmental bodies in addressing these concerns. Particular issues have required IUBS to work closely with representatives of member countries, such as the maintenance and taxonomy of biological specimens, responsible collection and curation of biological organisms and artifacts, curbing trade of exotic specimens and abuses of bioprospecting and biopiracy, promoting bioremediation, respecting diverse cultures and historical legacies, promoting learner-center reforms in contemporary biology education and responsible development of biology educators, cultivating better standards of bioethical practice, and preventing destruction of ecosystems or the introduction and spread of invasive species If you are a biologist or biology educator who is convening an international conference that is addressing a subject of major interest to membership of the International Union of Biological Sciences (such as those identified above), please contact the Editor (John R. Jungck at <jungck@beloit.edu>) with a prospectus that lays out the theme, potential authors, and timeframe to initiate a discussion about a potential future issue of *Biology International*.

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Biology International

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INTERNATIONAL UNION OF BIOLOGICAL SCIENCES

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The International Union of Biological Sciences is a non-governmental, non-profit organization, established in 1919. Its objectives are to promote the study of biological sciences, to initiate, facilitate, and coordinate research and other scientific activities that require international cooperation, to ensure the discussion and dissemination of the results of cooperative research, to promote the organization of international conferences and to assist in the publication of their reports.

The membership of the IUBS presently consists of 45 Ordinary Members, adhering through Academies of Science, National Research Councils, national science associations or similar organizations, and 80 Scientific Members, all of which are international scientific associations, societies, or commissions in the various biological disciplines.

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