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.

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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 2006). Mora *et al.* (2011) attempted to 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 such as Kinorhycha, Loricifera, 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.* 2010). Since that first collection, other 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 many of the controlling biological, 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.

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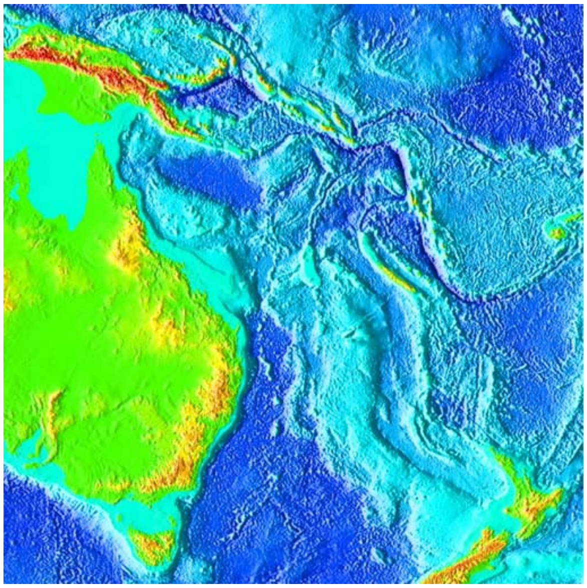

Figure 2. Topography of the floor of the Coral Sea and southwestern Pacific Ocean (eastern Australia at left, New Zealand at lower right) derived from ETOPO2 gridded data by the US National Geophysical Data Center, National Oceanic and Atmospheric Administration (NOAA), Department of Commerce: (http://www.ngdc.noaa.gov/mgg/image/2minsurface/00N135E.html).

Marine Habitats

By contrast with the terrestrial environment, which is essentially two-dimensional (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 geographically-based 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 of benthic marine life is animal.** 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).

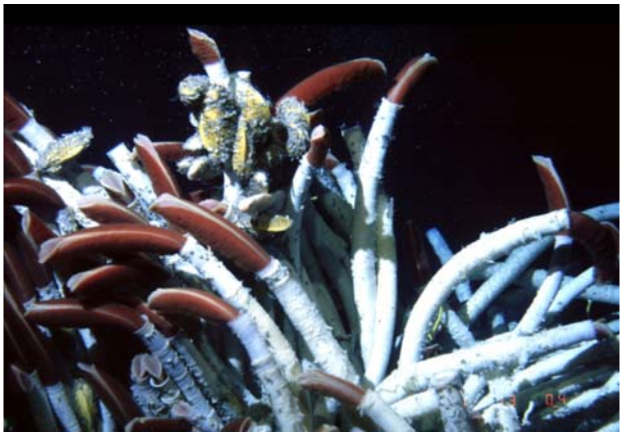

Figure 3. Vestimentiferan annelids, the iconic inhabitant of the Galapagos hydrothermal vents. Each tubeworm, which lacks a gut, may reach nearly 2 m in length; in its red plume, the worm harbors symbiotic microorganisms that capture energy through chemosynthesis. Photo courtesy of NOAA.

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: non-target 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.* 2006). Trawled benthic species include 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)

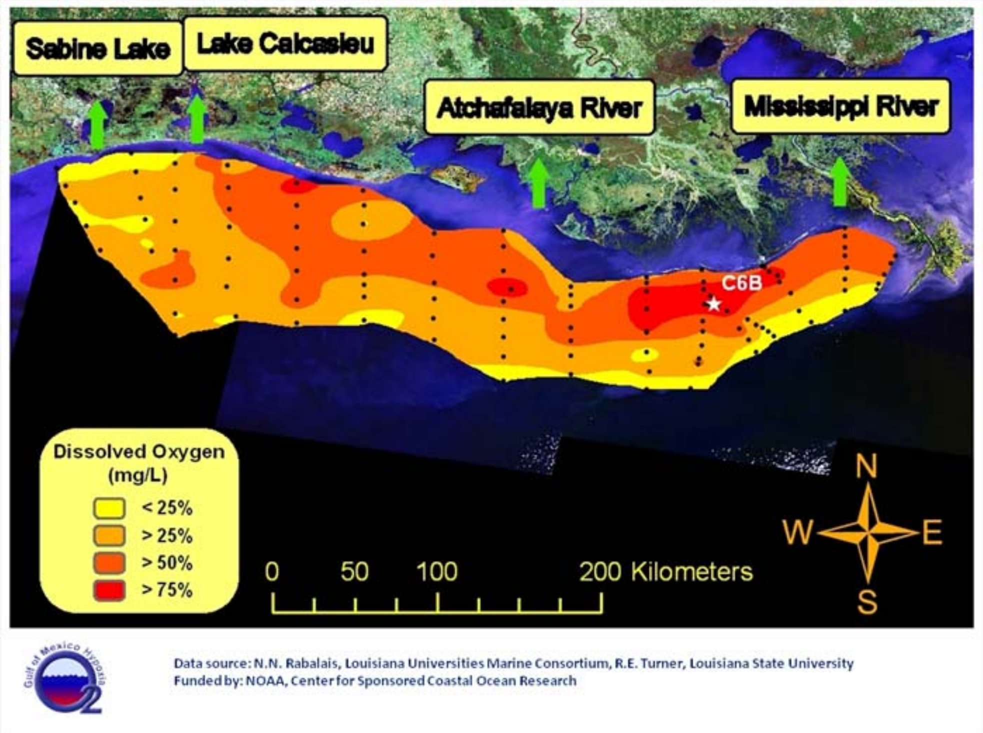

Figure 6. The Gulf of Mexico "Dead Zone" showing the proportion of time during 1985-2008 an area was hypoxic (< 2mg/l of oxygen). Any site visited in fewer than three years was not included. (http://www.gulfhypoxia.net/Research/Shelfwide%20Cruises/Frequency%20of%20Hypoxia/)

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/Shelfwide%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.)

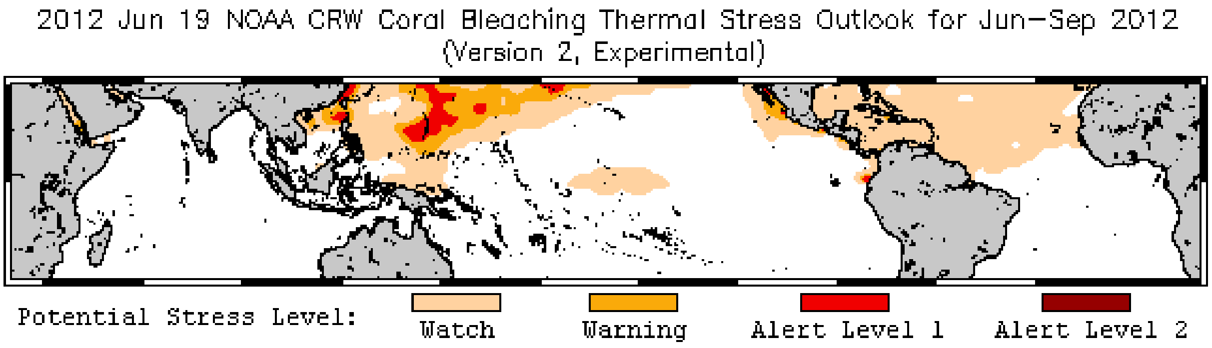

Figure 7. Example of NOAA coral bleaching outlook.
(http://www.coralreefwatch.noaa.gov/satellite/bleachingoutlook/index.html)

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 coral-zooxanthella 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 a website 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 termed the "greenhouse effect" (http://en.wikipedia.org/wiki/Greenhouse_effect). 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 CO_2 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 CO_2 affects the surface waters because diffusion is slow. The water's pH is depressed because when CO_2 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 (*e.g.* Sala and Knowlton 2006). 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/giant-tiger-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.htm)

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.

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