THE ECOLOGICAL SOCIETY OF AMERICA

Frontiers in Ecology and the Environment

Issue No 1 Volume 4 April 2006

Replanting mangroves after the tsunami

Effects of seawater changes on deep-sea corals

Biological control of invasive species

Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals?

John M Guinotte[1,2], James Orr[3], Stephen Cairns[4], Andre Freiwald[5], Lance Morgan[1], and Robert George[6]

The answer to the title question is uncertain, as very few manipulative experiments have been conducted to test how deep-sea scleractinians (stony corals) react to changes in seawater chemistry. Ocean pH and calcium carbonate saturation are decreasing due to an influx of anthropogenic CO_2 to the atmosphere. Experimental evidence has shown that declining carbonate saturation inhibits the ability of marine organisms to build calcium carbonate skeletons, shells, and tests. Here we put forward a hypothesis suggesting that the global distribution of deep-sea scleractinian corals could be limited in part by the depth of the aragonite saturation horizon (ASH) in the world's oceans. Aragonite is the metastable form of calcium carbonate used by scleractinian corals to build their skeletons and the ASH is the limit between saturated and undersaturated water. The hypothesis is tested by reviewing the distribution of deep-sea, bioherm-forming scleractinian corals with respect to the depth of the ASH. Results indicate that > 95% of 410 coral locations occurred in saturated waters during pre-industrial times. Projections indicate that about 70% of these locations will be in undersaturated waters by 2099. Lab experimentation, in situ experimentation, and monitoring efforts are needed to quantify the effects of changing seawater chemistry on deep-sea coral ecosystems.

Front Ecol Environ 2006; 4(3): 141–146

Seawater chemistry and the calcium carbonate saturation state of the world's oceans are changing as a result of the addition of fossil fuel CO_2 to the atmosphere (Kleypas *et al*. 1999; Feely *et al*. 2004; Orr *et al*. 2005). The pH of surface oceans has dropped by 0.1 units since the industrial revolution and if fossil fuel combustion continues at present rates, the pH of the world's oceans will probably drop another 0.3 to 0.4 units by 2100 (Mehrbach *et al*. 1973; Lueker *et al*. 2000; Caldeira and Wickett 2003). "This influx of anthropogenic CO_2 is causing the world's oceans to become more acidic, to the detriment of corals and other marine calcifiers, including plankton, which occupies the base of marine food webs. Corals and some species of plankton (coccolithophores and foraminiferans) use carbonate ions obtained from the surrounding water to build their skeletons and protective shells. As oceanic pH and carbonate ions decrease as a result of rising fossil fuel CO_2 levels, the calcification mechanisms and abilities of many marine organisms will be negatively impacted.

In recent decades, only half of anthropogenic CO_2 has remained in the atmosphere; the other half has been taken up by the terrestrial biosphere (20%) and the oceans (30%) (Feely *et al* 2004; Sabine *et al* 2004). This uptake initiates a series of chemical reactions, increasing the hydrogen ion concentration (H^+), lowering pH, and reducing the number of carbonate (CO_3^{2-}) ions available in seawater. All of this will make it more difficult for marine calcifying organisms to form biogenic calcium carbonate ($CaCO_3$). Although little is known about the effects of decreasing aragonite saturation state on deep-sea corals, lab experiments have conclusively shown that lowering carbonate ion concentration reduces calcification rates in tropical reef builders by 7–40% (Gattuso *et al*. 1999; Langdon *et al*. 2000, 2003; Marubini *et al*. 2003). In fact, all marine calcifying organisms tested to date have shown a similar negative response to decreasing carbonate saturation state. As the world's oceans become less saturated over time, corals are expected to build weaker

In a nutshell:

- Anthropogenic CO_2 from the combustion of fossil fuels is altering the chemistry of the world's oceans
- Seawater chemistry changes have the potential to alter the distribution and abundance of marine organisms that use calcium carbonate to build their shells and skeletons (corals, plankton, etc) and the organisms that depend on them for survival (fishes, marine mammals, etc)
- Major funding and experimentation is needed to quantify the effects of changing seawater chemistry on marine calcifiers; experimentation should be a top priority for countries with commercial industries dependent on deep-sea coral bioherms
- The transition from fossil fuels to alternative "clean" sources of energy needs to occur as soon as possible

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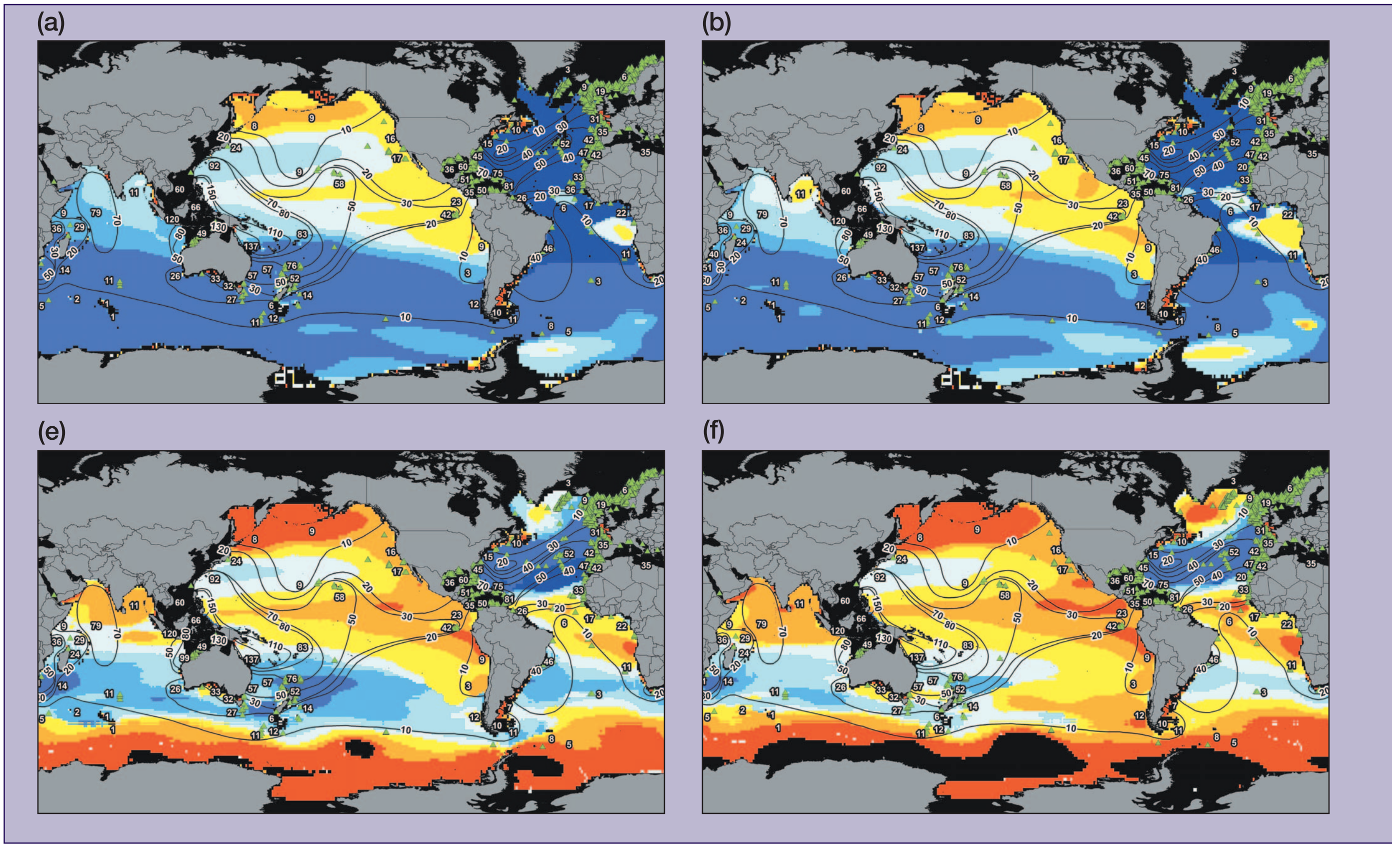
[1] *Marine Conservation Biology Institute, 2122 112th Ave NE, Bellevue, WA, USA (john@mcbi.org);* [2] *School of Tropical Environment Studies and Geography, James Cook University, Townsville, Australia;* [3] *Laboratoire des Sciences du Climat et de l'Environnement, Paris, France;* [4] *National Museum of Natural History, Smithsonian Institution, Washington, DC, USA;* [5] *Institute of Paleontology, University of Erlangen, Erlangen, Germany;* [6] *George Institute for Biodiversity and Sustainability, Wilmington, NC, USA*



skeletons (a process similar to osteoporosis in humans) and/or experience slower growth rates (Buddemeier and Smith 1999; Gattuso *et al.* 1999; Kleypas *et al.* 1999; Guinotte *et al.* 2003). Both processes will make it more difficult for corals to withstand erosion and to retain a competitive advantage over other marine organisms.

Seawater chemistry: the movement of the aragonite saturation horizon (ASH)

Orr *et al.* (2005) calculated future changes in carbonate saturation state (aragonite and calcite) for the world's oceans and found that decreasing carbonate saturation state will not be limited to surface waters, but will occur in the deep sea as well. Orr's aragonite saturation horizon (ASH; the limit between saturation and undersaturation) projections were based on the Intergovernmental Panel on Climate Change (IPCC) IS92a scenario (788 ppmv in the year 2100). The IS92a scenario is generally regarded as the "business-as-usual" scenario, where nations do very little to curb emissions. These projections were incorporated in a geographic information system (GIS) with approximately 410 records of deep-sea bioherm-forming corals (*Lophelia pertusa, Madrepora oculata, Goniocorella dumosa, Oculina varicosa, Enallopsammia profunda, Solenosmilia variabilis*) provided by Andre Freiwald (Freiwald *et al.* 2004; Figure 1). Bioherm is defined as an ancient organic reef of moundlike form built by a variety of marine invertebrates, including corals, echinoderms, gastropods, mollusks, and others (Encyclopedia Britannica 2006). Cairns' (in press) diversity contours for 706 species of azooxanthellate scleractinian corals were overlayed on ASH projections to highlight the relationship between coral diversity and ASH depth.

The projections clearly show the ASH moving shallower over time as atmospheric CO_2 concentrations increase. Aragonite projections were used because aragonite is the calcium carbonate mineral form deposited by scleractinian corals to build their skeletons. Calcite, the less soluble form of $CaCO_3$ used by octocorals (soft corals) and other marine organisms, is not included in this study. It should be noted that the sclerites of octocorals are calcitic, but the axes may be composed of calcite, aragonite, or amorphous carbonate hydroxylapatite (Bayer and Macintyre 2001). The saturation depth for calcite is considerably greater than for aragonite because calcite is less soluble than aragonite in seawater. However, calcitic marine organisms will not be immune from saturation changes in the oceans because the depth of the calcite saturation horizon is also moving progressively shallower over time.

Based on 410 known locations of deep-sea, bioherm-forming corals obtained from Freiwald *et al.* (2004) and and the estimated pre-industrial (year 1765) ASH depth, >95% of the coral locations were found in areas that were supersaturated (omega > 1) in terms of aragonite (Figure 2). The mean omega value for all coral locations in pre-industrial times was 1.98 (supersaturated). By 2099, only 30% of coral locations remain in supersaturated waters, the vast majority of which are located in the North Atlantic,

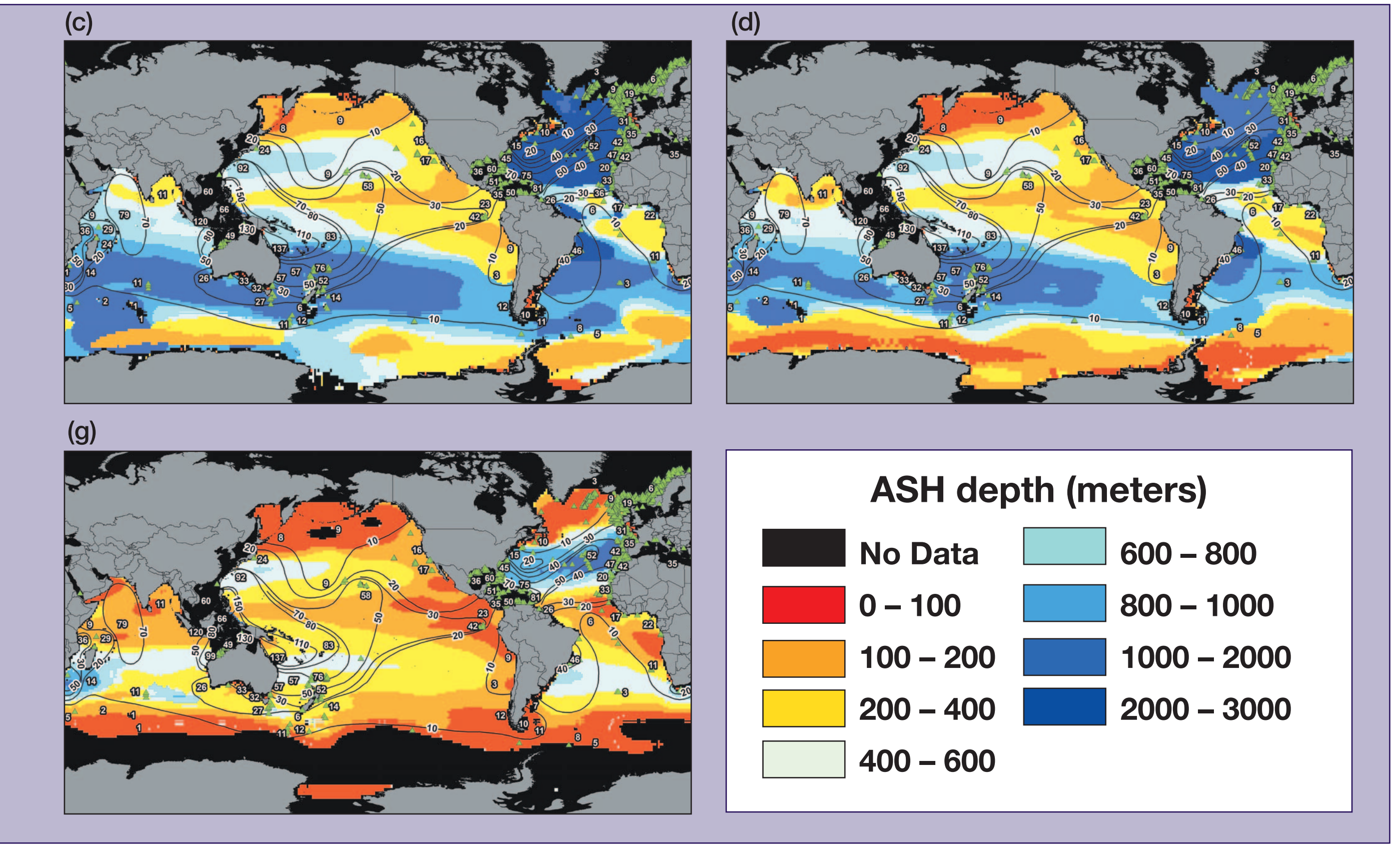


Figure 1. *Depth of the aragonite saturation horizon (ASH), locations of deep-sea bioherm-forming corals, and diversity contours for 706 species of azooxanthellate corals. (a) Projected ASH depth for year 1765; pCO_2=278 ppmv. (b) Estimated ASH depth for year 1995; pCO_2=365 ppmv. (c) Projected ASH depth for year 2020; pCO_2=440 ppmv. (d) Projected ASH depth for year 2040; pCO_2=513 ppmv. (e) Projected ASH depth for year 2060; pCO_2=594 ppmv. (f) Projected ASH depth for year 2080; pCO_2=684 ppmv. (g) Projected ASH depth for year 2099; pCO_2=788 ppmv. Green triangles are locations of the six deep-sea bioherm-forming coral species. Black areas appearing in the Southern Ocean in figures 1e–g and the North Pacific in Figure 1g indicate areas where ASH depth has reached the surface. Numerals not falling on diversity contours indicate number of azooxanthellate coral species.*

where the ASH remains relatively deep. Mean omega values for all coral locations in 2099 is 0.99 (undersaturated). Lab experiments performed on hermatypic, shallow-water corals in supersaturated waters have shown that relatively modest reductions in aragonite saturation state can cause substantial decreases in calcification (Langdon *et al*. 2003; Langdon and Atkinson 2005). If future experiments show the same is true for deep-sea, bioherm-forming corals, then calcification rates may decrease well before corals become undersaturated with respect to aragonite.

Deep-sea coral distributions in the Atlantic and Pacific

Deep-sea scleractinian corals are found in all ocean basins. Figure 1 shows that the center of species diversity for azooxanthellate corals are the waters surrounding the Philippines (~ 160 species), followed by New Caledonia (~ 140 species), and the Caribbean Sea (~ 80 species) (Cairns in press). The majority of deep-sea, bioherm-forming scleractinians have been discovered in the North Atlantic, which is probably a function of sampling bias, but may also be connected to the ASH depth. Extensive deep water surveys in the North Pacific (Aleutian and Hawaiian Islands; Baco pers comm; Stone pers comm) have not documented deep-sea scleractinian bioherms like those found in the North Atlantic, although some records of small pieces exist from collections (Rogers 1999). One possible reason for their absence in the North Pacific might be the shallow depth of the ASH throughout much of the region.

The ASH in the North Atlantic is very deep (> 2000 m) and many of the deep-sea scleractinians found in these waters are bioherm-forming, robust, and cover areas several kilometers in size. The *Lophelia pertusa* bioherms off the coasts of Norway and Sweden are prime examples of such corals; they cover large areas and occur at relatively shallow depths (Fosså *et al*. 2002). Deep-sea scleractinian accretion in the North Atlantic produces structures several meters in height, due to the corals' ability to grow on top of the dead skeletons (coral rubble) of their predecessors. Bioherm accretion in the deep sea is a slow process; the age of North Atlantic corals vary, but recent estimates indicate they are less than 10 000 years old (Schröder-Ritzrau *et al*. 2005).

North Pacific deep-sea coral ecosystems are quite unlike those found in the North Atlantic. Present-day ASH depth in the North Pacific is relatively shallow

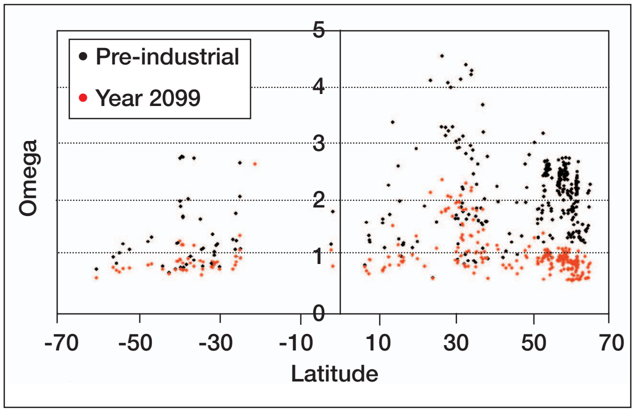


Figure 2. *Projected ASH values for deep-sea coral locations in pre-industrial times (year 1765; black dots) and in the year 2099 (red dots). ASH (saturation boundary) is omega = 1; n = 410.*

(50–600 m) and scleractinian corals found there do not form bioherms. North Pacific scleractinians tend to be found in solitary colonies and the region is dominated by octocorals (soft corals, stoloniferans, sea fans, gorgonians, sea pens) and stylasterids. Octocorals and a small percentage (about 10%) of stylasterid species use calcite to build their spicules and skeletons (Carins and Macintyre 1992). Cairns and Macintyre (1992) studied 71 stylasterid species, seven of which were from the temperate North Pacific. Remarkably, six of the seven species had calcitic skeletons (the less soluble polymorph), even though calcite is rare among the stylasterids. These calcitic stylasterids were found in abundance at depths of 50–500 m. The Aleutian Islands, a region where the approximate depth of the ASH is < 150 m, is one example of an area dominated by octocorals, stylasterids, and sponges.

The depth at which many azooxanthellate corals are found in the waters surrounding the Galápagos Islands lends further credence to the hypothesized ASH–scleractinian relationship. Figure 1 shows global diversity contours for 706 species of azooxanthellate corals, regardless of depth. Across all ocean basins, 91 of the 706 species (13%) occur exclusively in shallow water (0–50 m). However, 19 of the 42 species (45%) found in the waters off the Galápagos Islands are found in less than 50 m of water. This is interesting, given the fact that present-day ASH depth in the waters surrounding the Galapágos is quite shallow (< 300 m) due to upwelling.

Stony corals in the North Pacific are found in close proximity to, or at slightly shallower depths than, the ASH, suggesting that corals may be surviving in a marginal aragonite saturation state environment. Coral rubble fields are nonexistent in the North Pacific, where aragonite dissolution rates in the upper 1000 m are twice as high as the dissolution rates of the North Atlantic (Feely *et al.* 2004). The shallow depth of the ASH and the high dissolution rates in North Pacific waters could work synergistically to make bioherm accretion unlikely, if not impossible. Corals may have biophysical mechanisms which allow them to survive in close proximity to the ASH, but not to flourish and form accumulated structures such as those found in the North Atlantic, where the ASH is much deeper and dissolution rates are low.

The North Atlantic is not the only region where deep-sea scleractinians form bioherms. Such structures are also found in several ocean basins, where the ASH is deep and dissolution rates are low (eg the South Pacific and South Atlantic). Scleractinians are not known to form deep bioherms in the North Pacific or northern Indian Ocean, where the ASH is shallow and dissolution rates are high. A strong qualitative correlation exists between areas of low azooxanthellate coral diversity and areas where the present-day ASH is relatively shallow (Figure 1b). These areas include the temperate North Pacific, off the west coast of South America, the northern Indian Ocean, and off the southwest coast of Africa.

The exception to the low scleractinian diversity–shallow ASH relationship is the Southern Ocean, where scleractinian diversity is low (< 10 species) and the present-day ASH depth is relatively deep (> 800 m) for much of the region. Low species diversity in the Southern Ocean is not due to lack of exploration in the region and it is generally accepted that the taxonomy of Antarctic scleractinians is fairly well known (Cairns pers comm). The reason(s) for this exception are not known, but possibilities include past and present barriers to coral recruitment and/or the extent of sea ice throughout geologic history.

■ Food availability

There is warranted concern that changing seawater chemistry could have an indirect, detrimental effect on deep-sea corals, by limiting the amount of food and nutrients available to deep-sea coral ecosystems. Very little information exists on the food sources of these organisms, but it is probable that they depend on suspended organic matter and zooplankton for nourishment (Kiriakoulakis *et al.* 2005). Since corals are sessile filter feeders, they can obtain nourishment either from organic matter falling from the surface or via currents that bring organic matter and zooplankton to the coral. Deep-sea corals are found in waters that have above-average surface primary productivity, indicating that food falling from the surface is important to their survival (Figures 3 and 4). There is also a strong correlation between chlorophyll-a concentration and particulate organic carbon (POC) in the world's oceans (Legendre and Michaud 1999; Gardner unpublished).

Many species of plankton (eg coccolithophores and foraminiferans) and pteropods (small gastropod mollusks), which form the base of marine food webs, use carbonate ions to build their $CaCO_3$ shells/tests and are sensitive to the seawater chemistry changes previously noted (Riebesell *et al.* 2000; Riebesell 2004; Orr *et al.* 2005). If changing seawater chemistry causes a reduction in phytoplankton and zooplankton production in surface waters, the feedback to deep-sea coral ecosystems will probably be negative, as deep-sea corals may not be able to attain their nutritional requirements.

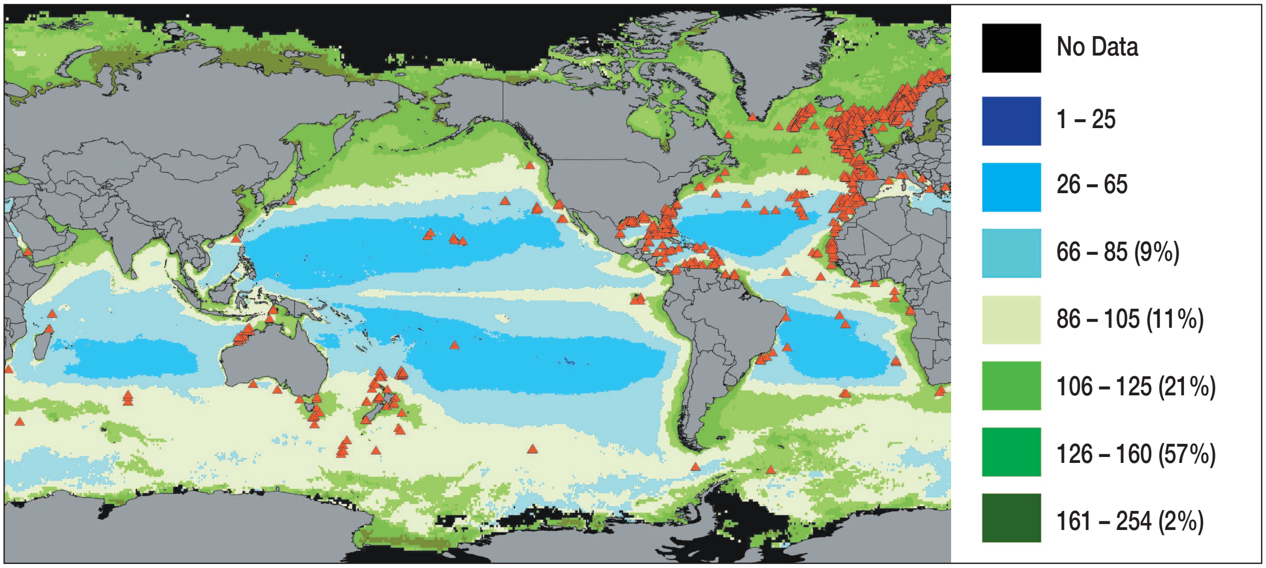


Figure 3. *Coral locations and global average chlorophyll-a concentration for the years 1997–2000. Red dots represent 1565 locations of the six deep-sea bioherm-forming coral species. Note: legend values for chlorophyll-a concentration range from 0–255; Data used was converted from mg/m^3 to a color unit scale, with 0 indicating no chlorophyll and 255 the highest chlorophyll concentration found in the oceans for this time period. Figures in parentheses indicate the percentage of total coral records within each concentration range. (Source: SeaWiFS Project, NASA/Goddard Space Flight Center.)*

■ Other factors

Changing seawater chemistry is not the only threat deep-sea corals face in the age of global climate change. These organisms have evolved in steady-state, cold, dark, nutrient-rich environments and it is possible that changes in temperature, salinity, or water motion may also have negative consequences. Model projections for these variables vary considerably, uncertainties are high, and the biological feedbacks to changes in these factors are poorly understood in terms of their effects on deep-sea corals. Nevertheless, worrisome physical changes are taking place in the world's oceans. Global sea temperatures are rising in the deep-sea, due to increasing amounts of anthropogenic CO_2 in the atmosphere (Barnett *et al.* 2005). Rising sea temperatures will probably influence deep-sea coral calcification rates, physiology, and biochemistry, even though specific ranges and thresholds are not yet known.

Climate change is also altering the salinity of the world's oceans (Curry *et al.* 2003). Increased evaporation in tropical waters has led to more saline conditions at lower latitudes, whereas glacial ice melt in polar waters has produced less saline conditions at higher latitudes. Freshwater inputs to high latitude waters are expected to increase as global temperatures continue to rise and the influx of freshwater may slow down water circulation, reduce upwelling, and/or alter the trajectory of present-day current patterns (Curry *et al.* 2003). Since deep-sea corals are sessile organisms that depend on currents to bring them food, any change in the direction and/or velocity of currents could have a serious impact on their distribution.

■ Summary

The oceans are changing both chemically and physically as a result of the uptake of anthropogenic CO_2. Shallow-water corals and other marine calcifiers react negatively when

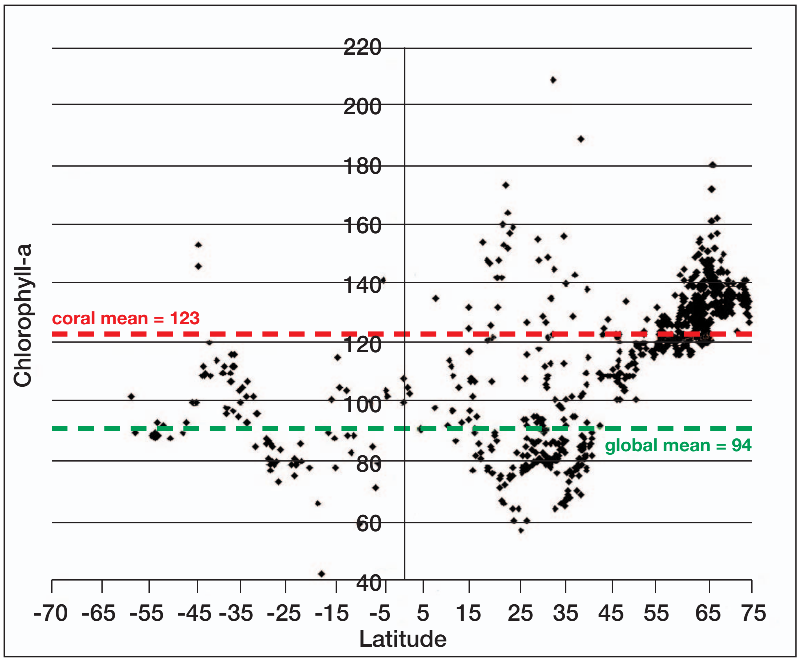


Figure 4. *Chlorophyll-a concentration for 1565 locations of the six deep-sea bioherm-forming coral species plotted with latitude.*

exposed to reduced carbonate saturation state conditions. Biological feedbacks and the reactions of marine organisms to these changes will be complex and will probably affect all trophic levels of the world's oceans. Deep-sea coral ecosystems will not be immune from these changes and probably have not experienced the combination of chemical and physical stresses described for a very long time. The synergistic effects of these stresses occurring in concert are uncertain, but these changes will probably have serious implications for deep-sea coral ecosystems.

The effects of decreasing aragonite saturation state on deep-sea, bioherm-forming scleractinians are not well understood and further experimentation is warranted. Lab and in situ monitoring experiments are needed to help us understand and quantify how chemical changes might affect deep-sea coral ecosystems in the future. If (a) aragonite saturation state is as important to deep-sea scleractinians as it is to shallow-water hermatypic corals and (b) the depth of the ASH moves progressively into shallower waters as projected, then over time, deep-sea, bioherm-forming corals will be exposed to an increasingly marginal environment. If the hypothesis presented is valid and the shallow depth of the ASH in certain regions of the oceans (eg the North Pacific) is limiting deep-sea scleractinians from forming bioherms, then we can expect substantial changes in the distribution of deep-sea corals and the structures they form within this century. The upward migration of the ASH has the potential to alter the global distribution of deep-sea scleractinian bioherms and the organisms that depend on them.

■ Acknowledgements

We are grateful for early comments and advice from R Buddemeier, J Kleypas, and R Feely. The TESAG department of James Cook University provided scholarships and stipends for J Guinotte's PhD research. Special thanks to the Marine Conservation Biology Institute for allocating time to work on this research.

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