

The consequences of human-driven ocean acidification for marine life

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F1000 Biology Reports 2009, 1:36 (doi:10.3410/B1-36)

The electronic version of this article is the complete one and can be found at: <http://F1000.com/Reports/Biology/content/1/36>

Abstract

Rising atmospheric carbon dioxide is causing a wholesale shift in surface seawater chemistry, potentially threatening many marine organisms that form shells and skeletons from calcium carbonate. Recent papers suggest that the biological consequences of ocean acidification already may be underway and may be more complex, nuanced and widespread than previously thought.

Introduction and context













Present-day atmospheric carbon dioxide (CO₂) is almost 40% higher than pre-industrial levels due to human fossil-fuel combustion and deforestation, and atmospheric CO₂ could reach double or triple historical levels by the end of this century. About a third of the excess CO₂ released by humans enters the surface ocean where it acts to lower seawater pH, carbonate ion (CO₃²⁻) concentration, and the saturation state of calcium carbonate (CaCO₃) minerals [1,2]. Several marine biological groups form shells or skeletons from calcium carbonate, including tropical and cold-water corals, mollusks, echinoderms, crustaceans, and some phytoplankton and zooplankton. In laboratory incubation studies, many of these calcifying organisms exhibit reduced calcification and other negative physiological effects at elevated CO₂ levels comparable to what is expected over the next several decades, as reviewed recently in [3,4] (Figure 1). Tropical coral reefs may be particularly sensitive to degradation from ocean acidification in conjunction with global warming, over-fishing, pollution and habitat destruction [5]. Other marine ecosystems may experience acidification impacts through direct effects on susceptible populations, indirect food-web interactions, and alterations of biogeochemical cycling [3,4].

Major recent advances

The research effort on ocean acidification is growing almost exponentially, resulting in a number of key recent advances. Anthropogenic changes in the carbonate chemistry of the surface ocean and the location of key marine fisheries and tropical corals are well prescribed, given projections of atmospheric CO₂ and well-known thermodynamic relationships for seawater buffer capacity; globally, pH is estimated to have dropped by about 0.1 pH units from the pre-industrial period to the present and a further decline of 0.3-0.4 pH units could occur by 2100 [4]. Ocean circulation and climate-change feedbacks, however, play a significant role in specific regions and when considering cold-water corals and subsurface ecosystems.

New studies suggest that ocean acidification may become a serious problem earlier than originally thought for some ocean regions. Coastal waters upwelling along the west coast of North America are already under-saturated for aragonite, a CaCO₃ mineral used by corals and many mollusks [6], and corrosive conditions are predicted for the Southern Ocean [7] and Arctic [8] in one to a few decades. Coastal acidification also may be exacerbated by anthropogenic acid rain deposition [9].

Figure 1. Representative examples of impacts of ocean acidification on major groups of marine organisms for experimental manipulation studies

Physiological Response	Major group	# species studied	Response to increasing CO ₂			
			a	b	c	d
Calcification	 Coccolithophores ¹	4	2	1	1	1
	 Planktonic Foraminifera	2	2	-	-	-
	 Molluscs	4	4	-	-	-
	 Echinoderms ¹	3	2	1	-	-
	 Tropical corals	11	11	-	-	-
	 Coralline red algae	1	1	-	-	-
Photosynthesis ²	 Coccolithophores ³	2	-	2	2	-
	 Prokaryotes	2	-	1	1	-
	 Seagrasses	5	-	5	-	-
Nitrogen Fixation	 Cyanobacteria	1	-	1	-	-
Reproduction	 Molluscs	4	4	-	-	-
	 Echinoderms	1	1	-	-	-

1) Increased calcification had substantial physiological cost; 2) Strong interactive effects with nutrient and trace metal availability, light, and temperature; 3) Under nutrient replete conditions

The response curves on the right indicate four cases: (a) linear negative, (b) linear positive, (c) level, and (d) non-linear parabolic responses to increasing levels of seawater partial pressure of CO₂ for each of the groups. Adapted from [4].

Some of the early research on the biological impacts of acidification was motivated by the possibility of direct injection of CO₂ into the ocean as a carbon sequestration strategy, and thus examined effects due to large pH perturbations ($\Delta\text{pH} > 1$). A growing body of more recent laboratory incubation experiments involves more modest chemistry changes that are more representative of conditions expected to occur within this century. These studies confirm earlier findings showing reduced calcification with rising CO₂ and a declining CaCO₃ saturation state for tropical corals [10], mollusks [11], and crustose coralline algae (CCA) [12], an important reef builder.

The picture has become less clear for coccolithophores, a calcifying phytoplankton, with new studies suggesting substantial inter-species and strain variability. In fact, some experiments indicate increased cell-specific calcification and larger individual external calcite plates (coccoliths) at higher CO₂ [13], the direct opposite of earlier work showing reduced calcification under acidification (reviewed in [3]). Records of changes in coccolith size over time from sediment cores also indicate an increase in coccolith size correlated with rising atmospheric CO₂ for some species [13]. In contrast, sediment trap records of modern sinking planktonic foraminifera show a marked reduction in

shell weights (30-35%) relative to Holocene-aged sediments [14].

Tank experiments with tropical corals and CCA indicate synergistic effects between warming and elevated CO₂, leading to enhanced sensitivity to bleaching [15]. Some calcifying higher organisms may be able to compensate for elevated CO₂ but at a considerable metabolic cost [16]. In sea urchin larvae, elevated CO₂ alters gene expression and may reduce tolerance to other environmental stresses [17]. Some photosynthetic organisms may benefit from future elevated aqueous CO₂ and sea surface temperatures, as evident for *Synechococcus*, a common subtropical cyanobacteria [18]. Alleviation of CO₂ limitation may enhance marine nitrogen fixation [19] and planktonic carbon to nitrogen elemental ratios, [20] thus altering ocean biogeochemistry.

Questions naturally arise as to the relevance of short-term incubation and mesocosm experiments to field populations exposed to chronic, slowly increasing CO₂ and other environmental trends [21]. Some caution is also warranted in interpreting laboratory experiments that use overly large amplitude chemistry changes (for example, ΔpH of 1, CO₂ of 1,500-2,000 ppm). Many of the incubation results, however, are supported by work on historical time-series and marine environments with naturally elevated CO₂. In a near-shore benthic community exposed to volcanic CO₂ venting, corals, CCA and juvenile mollusks are absent and adult mollusks appear unhealthy, replaced by sea-grasses that experience CO₂ limitation of photosynthesis at ambient levels [22]. Similar shifts in community composition were observed over time in a rocky inter-tidal pool exhibiting rapid pH reductions over a decadal time-scale [23].

The surface CaCO₃ saturation state is low in the eastern tropical Pacific because of upwelling of CO₂-rich water, resulting in poorly cemented coral reefs with enhanced bio-erosion rates [24]. Cores from several hundred massive *Porites* colonies on the Great Barrier Reef indicate a 14% reduction in calcification since 1990, an unprecedented event in at least the last 400 years that may reflect both warming and acidification [25]. Numerical model studies suggest that reefs may cease to grow or even show net dissolution when atmospheric CO₂ reaches 560 ppm [26], which could occur in the mid- to latter part of this century.

Novel studies are looking further afield for ocean acidification effects that have not yet been considered. For example, one study suggested that acidification and expanding oxygen-minimum zones could dramatically reduce the metabolic rates of giant squid [27]. Another

study ties lower pH with decreased low-frequency sound absorption and a noisier undersea environment, which could in turn affect marine mammal communication [28]. Reduced seawater pH also appears to disrupt the olfactory sensory abilities of some larval fish [29]. More surprises surely await.

Future directions

Our present understanding of the biological consequences of ocean acidification is, to a large degree, empirical in nature, reflecting a limited understanding of the biological mechanisms of some key processes. There are open questions about the ocean calcium carbonate budget, as highlighted in a new study suggesting that the precipitation of carbonates within the intestines of marine fish may contribute as much as 3-15% to total ocean carbonate production [30]. Many details on CaCO₃ biomineralization at the cellular level also remain to be resolved, with the potential for cross-fertilization with the material sciences research community [31].

Some of the most promising and challenging future directions will involve studying how changes in metabolic processes at the cellular level are manifested in terms of organism physiology and how this translates into altered population dynamics, community structure, and ecosystem function. Resolving the potential plasticity of species to acidification, which is dependent on existing diversity within and across populations, and micro-evolution and adaptation, is of particular importance [21]. Field manipulation techniques and mesocosms will develop in importance as a bridge between laboratory incubation experiments and cross-site comparisons with high CO₂ environments.

Time-series measurements are needed to document the temporal evolution of susceptible target populations, such as pteropods and commercially valuable mollusks, and particularly sensitive ecosystems such as tropical and cold-water coral reefs. Methods development is underway on autonomous *in situ* chemical sensors for carbonate ion concentration measurement [32] and other components of the seawater carbonate system. Observational systems combining underway ship data and satellite data are emerging to monitor surface-ocean carbonate saturation state [33]. Similar development is required for biological processes. Satellite remote sensing algorithms can characterize the global patterns and rates of pelagic calcification over time [34].

Mitigation strategies for addressing ocean acidification have been proposed, including adding alkalinity to surface waters from limestone dust or accelerated weathering of volcanic rock [35], but the logistics, cost

and energy demands are likely to be prohibitive, except on a small scale. In the end, the only true mitigation option will involve reducing CO₂ emissions to the atmosphere. Given that some amount of further ocean acidification is inevitable over the next several decades, more applied work is needed to characterize socio-economic impacts on coastal communities and to develop possible adaptation approaches for marine conservation and resource management [36].

Abbreviations

CO₂, carbon dioxide; CaCO₃, calcium carbonate; CCA, crustose coralline algae.

Competing interests

The author declares that he has no competing interests.

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