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OCEAN ACIDIFICATION IN THE CALIFORNIA CURRENT SYSTEM

ABSTRACT. Eastern boundary upwelling systems (EBUS) are naturally more acidic than most of the rest of the surface ocean. Observations of EBUS already show pH values and saturation states with regard to the carbonate mineral aragonite that are as low as those expected for most open ocean waters several decades from now. Thus, as atmospheric CO₂ increases further, EBUS are prone to widespread and persistent undersaturation with regard to aragonite, making them especially sensitive to ocean acidification. Here, we describe ocean carbonate chemistry and its short-termto-seasonal variability in one major EBUS, the California Current System (CCS), based on observations and results from an eddy-resolving regional model. Results reveal high variability in ocean carbonate chemistry, largely driven by seasonal upwelling of waters with low pH and saturation states, and subsequent interactions of transport and biological production. Model simulations confirm that the pH of CCS waters has decreased by about 0.1 pH unit and by 0.5 in saturation state since preindustrial times. A first assessment of the vulnerability of CCS marine organisms and ecosystems to ocean acidification suggests that there will be winners and losers, likely provoking changes in species composition. Benthic organisms appear to be among those that will be most affected by the continuing acidification of the CCS. More accurate projections require special consideration of the integrated effects of ocean acidification, ocean warming, decreasing oxygen levels, and other processes that are expected with global change.

INTRODUCTION

Oceanic uptake of anthropogenic CO₂ from the atmosphere increases seawater's concentration of CO₂, but lowers its carbonate ion concentration and its pH (Caldeira and Wickett, 2003, 2005; Feely et al., 2004; Orr et al., 2005). Marine organisms, from microbes to large predatory fish and mammals, may be very sensitive to these chemical changes, potentially leading to substantial ecological and biogeochemical shifts (Hare et al., 2007). Of particular concern is the crossing of thresholds, such as when seawater becomes undersaturated with regard to biogenically produced calcium carbonate minerals (i.e., reaches the state where minerals are prone to dissolution; Feely et al., 2004; Kleypas et al., 2006; Fabry et al., 2008; Guinotte and Fabry, 2008; Doney et al., 2009). However, critical thresholds may already have been passed; many organisms, such as corals,

respond negatively to a lowering of the saturation state even though the waters are still supersaturated (Hoegh-Guldberg et al., 2007). Global mean surface pH has already decreased by approximately 0.1 units, from about 8.2 to 8.1, since the pre-industrial period, and, depending on future levels of atmospheric CO_2 , pH is expected to decrease by another 0.3–0.4 units by the end of the century (Orr et al., 2005).

To assess the potential vulnerability of marine organisms and biogeochemical processes to these changes, it is not sufficient to determine only global mean changes in pH, carbonate ion concentrations, and carbonate saturation states. Global changes might not adequately reflect regional variability and thus may mask the urgency of the problem and its regional acuteness. Regional variations in ocean acidification are the result of longterm changes in carbonate chemistry

being superimposed on its natural variability, which is significant relative to predicted ocean acidification-driven changes, even in the surface ocean. These variations in natural acidity levels may put some marine organisms in certain regions at greater risk earlier. To date, attention has been focused on surface waters at high latitudes, which have a naturally low pH and low carbonate saturation states because thermodynamic factors support high dissolved inorganic carbon (DIC) concentrations relative to alkalinity for the same atmospheric CO₂ levels (Orr et al., 2005; McNeil et al., 2008; Steinacher et al., 2009). As a result, these regions are expected to become undersaturated with regard to calcium carbonate minerals more quickly than the rest of the ocean. Annually, both the Arctic Ocean and the Southern Ocean may become undersaturated with respect to aragonite (the less-stable form of calcium carbonate) during this century (Orr et al., 2005; Steinacher et al., 2009). Seasonally, this threshold may occur within the next few decades (McNeil et al., 2008). The Arctic surface ocean is projected to become completely undersaturated with respect to aragonite as early as 2040 (Steinacher et al., 2009), with 10% of the area already having become undersaturated at least one month per year during this decade. The carbonate system changes in ocean waters at temperate latitudes have received less attention because these surface waters have a higher pH, on average, and are strongly supersaturated with respect to aragonite and calcite. As a result, it has generally been concluded that critical thresholds will not be crossed until much later in these regions.

Here, we demonstrate that eastern

boundary upwelling systems (EBUS), such as the California Current System (CCS), are particularly vulnerable to future ocean acidification. Recent CCS observations show that nearshore regions are currently exposed to waters that exhibit chemical conditions like those predicted for open-ocean surface waters several decades into the future (Feely et al., 2008). These observations also show that the aragonite saturation horizon already reaches the surface in certain regions during strong upwelling events (Figure 1a). With only a little additional CO₂, surface waters in these regions likely will become permanently undersaturated with regard to aragonite. Given the economic and biogeochemical importance of EBUS (e.g., Chavez and Toggweiler, 1995), it is essential to assess the potential impacts of ocean acidification in these regions. We focus here on the CCS, but we expect similar results for other major EBUS, particularly the Humboldt Current System, because they are subject to the same governing processes.

We first characterize CCS chemical conditions in greater detail, and then attempt to assess the vulnerability of CCS organisms and ecosystems to continued ocean acidification. We also account for the fact that ocean acidification does not act in isolation, but that





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THE CARBONATE CHEMISTRY OF THE CALIFORNIA CURRENT SYSTEM

The generally low pH and saturation state of nearshore waters in the CCS is a direct consequence of coastal upwelling. Upwelling is driven by the seasonal shift to a southward (alongshore) wind that pushes surface waters offshore from approximately April through October, causing subsurface waters to be pulled to the surface (upwelled) nearshore. These upwelled waters follow long paths on their transit to the CCS, and are isolated from the surface ocean for many years. Along their journey, these waters accumulate the products of organic matter respiration, which rain down from the illuminated surface waters above, resulting in waters that are high in nutrients and dissolved CO₂, but low in oxygen, pH, and carbonate saturation state. For example, for waters that are upwelled off the Oregon coast, respiration adds more than 200 µmol kg⁻¹ of DIC to the source waters. This addition results in a pH decrease of over 0.3 units, and an increase in the partial pressure of CO_2 (pCO₂) of over 700 µatm relative

to presumed pre-industrial conditions. During strong upwelling, Feely et al. (2008) observed seawater with pH values as low as 7.75, and undersaturation with respect to aragonite starting at depths ranging from the surface to 120 m along the northern US Pacific coast (Figure 1a, c). Biweekly observations from a time-series site in Santa Monica Bay over more than five years confirm this shallow depth for the saturation horizon, but also show great temporal variability, mostly associated with intermittent upwelling events and passing mesoscale eddies (recent work of the authors; see also Leinweber et al., 2009). The high nutrient content of the upwelled waters makes the CCS a highly productive ocean region, leading to high rates of photosynthetic fixation of the upwelled nutrients and CO₂. As the upwelled waters are pushed

offshore by a combination of Ekman transport and mesoscale eddies, this photosynthetic removal of CO₂ lowers the surface pCO_2 , sometimes even far below atmospheric levels (Hales et al., 2005). This CO₂ drawdown brings a concomitant increase in surface water pH and carbonate mineral saturation state. The highly turbulent nature of the CCS, driven by the instabilities of the California Current and the nearshore undercurrent, causes the various waters to mix in a complex manner, leading to a highly variable mosaic of surface ocean carbonate saturation states and pH values that reflect transport and reaction (Figures 1b and 2).

Coupling the Regional Ocean Modeling System (ROMS) to a simple ecological-biogeochemical model produced the snapshots shown in Figures 1b, d, and 2 (Gruber et al., 2006).



Figure 2. Modelsimulated snapshot of surface pH for the month of August. Low-pH waters in nearshore areas are the result of seasonal upwelling in summer, while the elevated pH in offshore waters reflects the photosynthetic removal of CO₂ from the water as it is transported offshore. The three-dimensional, eddy-resolving model simulates the flow and mixing of ocean waters at a resolution of 5 km. This fine resolution enables representation of the processes of upwelling and subsequent transport and mixing by eddies, which occur at scales of tens of kilometers. Typical global models, with resolutions of 100 km or more, would not capture such processes. ROMS is set up for a domain covering the entire US West Coast from 28°N to 48°N and incorporates the effect of ocean acidification on carbonate chemistry by responding to elevated atmospheric CO₂ levels and elevated DIC concentrations at the lateral boundaries (see Box 1 for details).

We use our model results to put the springtime observations from Feely et al.

(2008) into a seasonal and wider spatial context. Field data (Feely et al., 2008) and model results show similar low levels of aragonite saturation (Ω_{ar}) along the coast, especially near the California-Oregon border (41°N-42°N) (Figure 1). Although Feely et al. (2008) observed surface water to be undersaturated at some locations near the coast (Figure 1a transect line 5), the model snapshot for mid May shows, for surface waters, a minimum Ω_{ar} of 1.2 (Figure 1b). However, the saturation state decreases rapidly with depth (see also Figure 3), so that in the model, waters also become undersaturated with respect to aragonite at depths as shallow as 10 m. At 120-m depth, observations (Figure 1c) show pervasive undersaturation along

a roughly 100-km-wide strip off the US West Coast, with a clear onshoreoffshore gradient in saturation state. The model simulates a similar spatial pattern, but it tends to overestimate the aragonite saturation state by about 0.2 units (Figure 1c, d), likely due to potential biases in the saturation state prescribed at the lateral boundaries (see Box 1 for discussion).

Because seasonally resolved, largescale observations of oceanic pH and carbonate saturation state along the US West Coast are lacking, we use the model to characterize the temporal variability of chemical water properties. We focus here on the region near the California-Oregon border, where the lowest aragonite saturation states were

BOX 1. DESCRIPTION OF MODEL AND SIMULATION SETUP

The Regional Ocean Modeling System (ROMS) is a threedimensional, eddy-resolving physical circulation model that simulates flow and mixing of ocean waters and is configured at a resolution of 5 km (ROMS ETHZ) for a domain covering the US West Coast (Marchesiello et al., 2003; Shchepetkin and McWilliams, 2005). ROMS is coupled to a nitrogen-based nutrient-phytoplankton-zooplankton-detritus (NPZD) biogeochemical model and includes a representation of the marine carbon cycle (Gruber et al., 2006). The model was forced at surface with monthly climatologies of momentum and density fluxes computed from QuikSCAT and the Comprehensive Ocean-Atmosphere Data Set (COADS) data products, respectively. Initial conditions for temperature and salinity were taken from the World Ocean Atlas 2001 database (http:// www.nodc.noaa.gov/OC5/WOA01/pr_woa01.html). Monthly climatological means were also used to prescribe temperature, salinity, and momentum fluxes along the three lateral open

boundaries following a radiative scheme. Initial and boundary conditions for the inorganic carbon system (dissolved inorganic carbon [DIC] and alkalinity) are based on GLobal Ocean Data Analysis Project (GLODAP) data (Key et al., 2004) for pre-industrial and present-day simulations. A seasonal cycle was added to the DIC boundary conditions using the monthly climatology of pCO₂ and assuming constant alkalinity. A limitation of the GLODAP database is that the observations used to create this gridded product do not include the US West Coast, but come from far offshore in the Pacific Ocean. We suspect that extrapolation of these observations toward the shore led to too low DIC concentrations at a given depth at the lateral boundaries of our model (i.e., too high saturation states). This overestimation of the saturation state at the lateral boundaries would then have caused the observed biases of our modeled aragonite saturation states in the nearshore areas (see text).

observed and modeled. Snapshots of vertical sections of modern-day aragonite saturation state for each of the four seasons reveal strong seasonal variations close to the coast (Figure 3). During the winter months (Figure 3a), the water exhibits a uniform horizontal chemical pattern, with the upper 40 m of the water column being supersaturated with an $\Omega_{\rm ar}$ range of 1.8 to 2, and with the saturation horizon located at about 300-m depth. During spring, waters with lower aragonite saturation states are upwelled close to the coast, causing a drop of Ω_{ar} to values of less than 2 in the entire water column within 20 km of the coast (Figure 3b). During the summer months, due to upwelling and high remineralization rates, Ω_{ar} drops further to values of

less than 1.3 in the entire water column within 10 km of the coast. The entire water column of the nearshore region within 30 km of the coast has $\Omega_{\rm ar}$ values less than 2 (Figure 3c). In close proximity to the coast, the saturation horizon shoals almost to the surface. In fall, nearshore areas still experience saturation states with $\Omega_{\rm ar}$ < 1.2, and waters with $\Omega_{\rm ar}$ values less than 2 expand to about 100 km offshore (Figure 3d).

These results suggest that organisms living at shallow depths and in close proximity to the coast are not only frequently exposed to low saturation states (and pH) but also to chemical conditions that can change on short time scales. Within 50 km of the coast, the aragonite saturation state of the entire water column from the surface down to 100 m undergoes large seasonal changes (Figure 4). The percentage of water volume that has a saturation state $\Omega_{ar} > 2$ (blue) decreases from more than 75% in winter to about 35% in summer. This is a substantial decrease, because water with saturation states $\Omega_{ar} < 2$ could cause a threat to some organisms (see below). The water volume that has an $\Omega_{ar} < 1.5$ (orange) increases from less than 5% in winter to 25% in summer and to 40% in fall. The first peak in summer is due to the acidification stemming from remineralization of the organic matter produced by phytoplankton blooms that were triggered by nutrient-rich upwelled water. The second peak in November is likely also caused by acidification from



Figure 3. Model-simulated vertical offshore sections of the aragonite saturation state in the northern CCS near Point St. George (41.7°N). Snapshots are for the months of (a) December, (b) March, (c) May, and (d) September.

remineralization of the organic matter. It is now accentuated because the reduced photosynthetic activity in the fall is no longer offsetting this effect as efficiently as during the summer.

Although much of the low pH and saturation state of waters that upwell in the CCS can be attributed to respirationderived CO₂, some fraction stems from the oceanic uptake of anthropogenic CO₂. Upwelled waters were last in contact with the atmosphere only a few decades ago, recently enough for them to have been exposed to elevated atmospheric CO₂ at that time, thereby taking up some of it. For the central CCS, Feely et al. (2008) estimate a transit time of about 40-50 years, resulting in an anthropogenic CO₂ content of about $31 \pm 4 \mu mol \text{ kg}^{-1}$. Although this amounts to only about a tenth of the metabolic CO₂ addition, it is sufficient to shoal the saturation horizon with respect to aragonite minerals several tens of meters. The ROMS-based simulations of preindustrial and current (year 2000) conditions support this conclusion. Results

for the years 1750 and 2000 show that surface pH decreased (from 8.14 to 8.05) and surface ocean saturation state with regard to aragonite decreased (from 2.7 to 2.3) due to the increase in atmospheric CO₂. The model also indicates that water masses that had an $\Omega_{ar} > 2.5$ in 1750 have by now been replaced completely by water masses with a saturation state $\Omega_{ar} < 2.1$, with a growing percentage of water with $\Omega_{ar} < 1.5$ (Figure 4).

With atmospheric CO_2 bound to increase further (Tans et al., 2009), pH and saturation state in the CCS inevitably will decrease further, possibly causing surface pH to go as low as 7.6 and causing waters to become undersaturated with regard to aragonite along large stretches of the US West Coast in the next few decades. Given this prospect, it is critical to assess which organisms and ecosystems in the CCS are vulnerable to such changes so that appropriate mitigation and adaptation strategies can be developed and implemented.

VULNERABILITY OF ORGANISMS AND INFLUENCE ON FISHERIES

When assessing the potential vulnerability of organisms and ecosystems to ocean acidification in the CSS (see the brief overview in Table 1), it is important to consider that organisms are already frequently exposed to water with low pH and saturation levels, especially during upwelling events and in nearshore regions. As a result, it may be expected that they are well adapted to variable conditions, and therefore more resilient to future changes (see, e.g., Deutsch et al., 2008). But this expectation may be applicable only if future changes do not move the chemical environment substantially outside of its natural envelope of variability. Given current projections of future CO₂ levels, this expectation is feasible in the CCS, despite the large level of variability. Furthermore, the growth and success of an individual species in a changing ocean depends on many environmental factors. In the case of phytoplankton, these factors include nutrients and iron



Figure 4. Contribution of waters with a particular aragonite saturation state relative to the total volume of water in the upper 100 m within 50 km of the US West Coast and between 32.0°N and 46.0°N. Model-simulated saturation states are shown for 1750 and 2000, and for each month in 2000.

 $1.5 < \Omega < 1.0$ $2.0 < \Omega < 1.5$

 $2.5 < \Omega < 2.0$ $3 < \Omega < 2.5$ availability, temperature, light, and predation (Hare et al., 2007; Tortell et al., 1997, 2008). Because many of these factors might change in parallel in the future, and given the lack of experiments that cover a combination of all factors, any conclusions about future phytoplankton compositions in the CCS remain speculative. Nevertheless, our preliminary assessment (Table 1) suggests that ocean acidification in the CCS will cause a species shift in open ocean phytoplankton, with diatoms possibly profiting at the expense of calcifying phytoplankton.

Similar conclusions can be drawn for nearshore and benthic primary producers. The two dominant species of the giant kelp forest (*Saccharina* and *Nereocystis*) exhibit species-specific adverse responses to low pH and high UVB (Swanson and Fox, 2007), suggesting that any combination of these two global change factors could possibly lead to a change in species composition and reduced biodiversity.

Secondary producers in the CCS can be affected both directly as a result of a change in seawater chemistry, and also indirectly by changes in food quality, prey disappearance, and altered timing of phytoplankton blooms. Limited experiments available today suggest that the aragonite-shelled pteropods, foraminifera, and planktonic life stages of bivalves and echinoderms are affected

Table 1. Expected vulnerability of m	arine flora and fauna to ocea	an acidification. Lev	el of understanding i	ndicates consistency
of results and/or possibility	y that natural system can rea	ch experimental pH	I. Adapted from Fabr	y et al., 2008

	Vulnerability	Level of Understanding	Comment	References
Diatoms	Low	High	Increased productivity, smaller or larger chain- forming species (?)	Tortell et al., 1997, 2008; Hare et al., 2007
Coccolithophorid	Medium	Low	Species specific response in calcification, increased photosynthesis	Iglesias-Rodriguez et al., 2008; Engel et al., 2005
Kelp	Medium	Medium	Species specific response in photosynthesis	Swanson and Fox, 2007
Copepods	Medium	Low	Shallow water copepods showed less tolerance to high pCO_2 than deep water copepods	Watanabe et al., 2006
Noncalcifying tunicate	Low	Medium	Increased growth, development, and fecundity	Dupont and Thorndyke, 2009
Shelled pteropod	High	Low	Shell dissolution	Orr et al., 2005; Fabry et al., 2008
Foraminifera	High	Medium	8–14% reduction in shell mass	Spero et al., 1997; Bijma et al., 1999, 2002; Moy et al., 2009
Sea urchin	Medium	Medium	Species specific, lack of pH regulation, decreased fertilization success	Burnett et al., 2002; Dupont and Thorndyke, 2008
Mussel	High	High	Decreased calcification in saturated water; dissolution and mortality in undersaturated water	Gazeau et al., 2007
Oyster	Medium	High	Decrease in calcification rate, highly vulnerable larval stage	Gazeau et al., 2007; Lee et al., 2006
Dungeness crab	Low	Low	Capable of pH regulation during 24 h	Pane and Barry, 2007
Cold water corals	High	Low	Experimental results only for warm water corals	Guinotte and Fabry, 2008
Coralline algae	High	Medium	Decrease in calcification rate, net dissolution, disappearance	Martin and Gattuso, 2009

directly by ocean acidification as they experience either rapid shell dissolution and reduced calcification ability or larvae develop with a temporal delay, build abnormal asymmetry, and often die before metamorphosis in aragonitefor the local industry relying on marine resources. Once the aragonite saturation horizon has permanently reached the surface, organisms sensitive to ocean acidification may vanish, move elsewhere, or develop new physiological

OCEAN ACIDIFICATION HAS ALREADY DECREASED MEAN SURFACE WATER pH IN THE CCS TO A LEVEL THAT WAS NOT EXPECTED TO HAPPEN FOR OPEN-OCEAN SURFACE WATERS FOR SEVERAL DECADES.

undersaturated waters (Orr et al., 2005; Fabry et al., 2008; Kurihara et al., 2008; Dupont and Thorndyke, 2009; Lebrato et al., in press). However, Dupont and Thorndyke (2009) point out that such negative responses are species specific, so that the primary effect in a future, more acidic ocean is likely to be a shift in species composition rather than the complete disappearance of an entire class of organisms. Recent abundance observations have not indicated any significant decrease in CCS pteropod population size (Ohman and Lavaniegos, 2008), whereas the Pacific oyster Crassostrea gigas exhibited recruitment failure during four consecutive years (2005-2008; Elston et al., 2008). C. gigas has an aragonitic larval stage, making it exceptionally vulnerable to decreasing aragonite saturation states (Lee et al., 2006). Whether or not ocean acidification has caused these heavy losses in the backbone of the US West Coast shellfish industry remains unclear.

Overall, ocean acidification in the CCS could become a severe challenge

survival strategies. The aragonite shells of mussels, sea urchins, and gastropods could soon experience dissolution (Burnett et al., 2002; Gazeau et al., 2007; Hall-Spencer et al., 2008; Wootton et al., 2008). However, survival strategies such as the production of a protective outer organic periostracum, developed by the mussel Bathymodiolus brevior, may support life in extreme conditions of pH down to 5.4 (Tunnicliffe et al., 2009). Comparing the potential vulnerability of different species and ecosystems, we conclude that benthic organisms will probably be most affected by ocean acidification in the CCS. They will be exposed to the lowest pH and aragonite saturation states in the nearshore, shallow areas, and many of them appear to be sensitive to ocean acidification. Moreover, their ability to migrate is limited. Given our limited understanding, this conclusion should be viewed as a preliminary assessment rather than a final conclusion.

What could the potential impact of these changes be on fisheries in the CCS?

In total, aragonite-calcifying species accounted for 23% of the total US West Coast catch value of about \$384M in 2007 (Figure 5), suggesting that either a loss in quality or a decrease in quantity of this subgroup will impact fisheries income substantially. Additionally, consequences of these species' disappearance could cascade through the food web because aragonite-forming organisms are found at very low or mid-trophic food levels. To what extent this indirect effect of ocean acidification will impact predators and thus the remaining CCS catch will strongly depend on whether other prey are available and whether the predators can switch prey.

The problems associated with ocean acidification provoke discussions and raise questions for the fishing industry (Warren, 2009). Supporting sustainable fish stocks is no longer just a matter of resilient catch quantity but also of maintaining suitable habitat. Ocean acidification is a problem of habitat degradation. Knowledge about the impact of ocean acidification on fish stocks and total financial loss is thus crucial to managing fisheries in a changing ocean and to driving policies that can protect the ocean.

INTEGRATED EFFECTS

Ocean acidification is just one of several stress factors, which include hypoxia, anomalous sea surface temperatures, pollution, and overfishing, that are challenging CCS ecosystems. Although overfishing and marine pollution are two independent problems that are manageable at the local scale, global warming and ocean acidification are directly linked and can only be addressed globally.

In addition, increasing sea surface

temperature and stratification tend to enhance low-oxygen conditions in the CCS, adding another stressor, with resultant cascading effects on benthic and pelagic ecosystems (Bograd et al., 2008). A further expansion of low-oxygen conditions could also be driven by ocean acidification. An ocean-acidificationinduced reduction in production of mineral ballast by calcifying organisms will result in reduced transport of organic matter to the deeper layers of the ocean, thus leading to enhanced remineralization of organic matter in shallow waters (Balch and Utgoff, 2009). This effect leads to higher oxygen demand in the upper ocean, resulting in a drop in the dissolved oxygen concentration there (Hofmann and Schellnhuber, 2009). Because these waters constitute the source of the upwelling waters in the CCS, such a decrease likely will cause

more frequent low-oxygen events along the US West coast in the future. This ocean deoxygenation could substantially amplify the impact of ocean acidification on marine ecosystems in the CCS (Brewer and Peltzer, 2009).

Such concomitant perturbations also complicate their detection and surveillance. Because it is difficult to link stress signs to particular causes, and wellknown stress factors may mask others, management actions could be wrong or late. A decrease in fish stocks could be mistaken to be a result of overfishing although caused in reality by direct or indirect effects of climate change and ocean acidification. The consequences of such a misreading could have large economic and ecological dimensions, as management would focus on fisheries policy improvement instead of supporting actions to mitigate CO₂.

SUMMARY

Ocean acidification has already decreased mean surface water pH in the CCS to a level that was not expected to happen for open-ocean surface waters for several decades. However, presentday surface pH in the CCS exhibits considerable spatial and temporal variability. This variability could provide the basis for a certain degree of adaptability by marine organisms in this region to future ocean acidification, but only as long as future changes do not move substantially out of this natural rangea move that is feasible. If atmospheric CO₂ continues to increase at current rates in the near future, both pH and saturation state will decrease even more, further shoaling the saturation horizon and possibly moving it up into the euphotic zone year round. Responses of marine organisms and ecosystems to



Figure 5. US West Coast commercial fishing ex-vessel revenue (the price paid at the time the fish are delivered by the commercial fisherman to the fish receiver or processor) for 2007 (adapted from Cooley and Doney, 2009, using NOAA National Marine Fisheries Service statistics), including California, Oregon, Washington, and Pacific, and at sea. Colors indicate which form (if any) of calcium carbonate these groups contain. Based on present understanding, organisms containing aragonite are most likely to be affected by ocean acidification.

such permanently low-pH conditions are not yet well investigated. Thus, we must improve our currently insufficient understanding of the consequences of ocean acidification for individual organisms, entire ecosystems, marine biogeochemical cycling, and feedbacks to the climate system in order to inform policymakers and provide a sound science basis for urgent decisions regarding CO₂ mitigation. Meanwhile, it is important to lower the pressure on marine ecosystems from other stressors such as pollution, coastal degradation, and eutrophication to make these systems less vulnerable to the changing marine chemical conditions associated with increasing CO₂.

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REFERENCES

- Balch, W.M., and P.E. Utgoff. 2009. Potential interactions among ocean acidification, coccolithophores, and the optical properties of seawater. *Oceanography* 22(4):146–159.
- Bijma, J., H.J. Spero, and D.W. Lea. 1999. Reassessing foraminiferal stable isotope geochemistry: Impact of the oceanic carbonate systems (experimental results). Pp. 489–512 in Use of Proxies in Paleoceanography: Examples from the South Atlantic. G. Fisher and G. Wefer, eds., Springer-Verlag, New York, NY.
- Bijma, J., B. Honisch, and R.E. Zeebe. 2002. Impact of the ocean carbonate chemistry on living foraminiferal shell weight: Comment on "Carbonate ion concentration in glacial-age deepwaters of the Caribbean Sea" by W.S. Broecker and E. Clark. *Geochemistry, Geophysics, Geosystems* 3(1064), doi:10.1029/2002GC000388.
- Bograd, S.J., C.G. Castro, E. Di Lorenzo, D.M. Palacios, H. Bailey, W. Gilly, and F.P. Chavez. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophysical Research Letters* 35, doi:10.1029/2008GL034185.
- Brewer, P.G., and E.T. Peltzer. 2009. Oceans: Limits to marine life. *Science* 324:347–348.
- Burnett, L., N. Terwilliger, A. Carroll, D. Jorgensen, and D. Scholnick. 2002. Respiratory and acid-base physiology of the purple sea urchin, *Stronglyocentratus purpuratus*, during air exposure: Presence and function of a facultative lung. *Biological Bulletin* 203:42–50.
- Caldeira, K., and M.E. Wickett. 2003. Oceanography: Anthropogenic carbon and pH. *Nature* 425:365, doi:10.1038/425365a.
- Caldeira, K., and M.E. Wickett. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to atmosphere and ocean. *Journal of Geophysical Research* 110, C09S04, doi:10.1029/2004JC002671.
- Chavez, F.P., and J.R. Toggweiler. 1995. Physical estimates of global new production: The upwelling contribution. Pp. 313–320 in *Upwelling in the Ocean: Modern Processes and Ancient Records*.
 C.P. Summerhayes, K.C. Emeis, M.V. Angel, R.L. Smith, and B. Zeitzschel, eds., J. Wiley & Sons, Chichester, UK.
- Cooley, S.R, and S.C. Doney. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. *Environmental Research Letters* 4, doi:10.1088/1748-9326/4/2/024007.
- Deutsch, C.A., J.J. Tewksbury, R.B. Huey, K.S. Sheldon, C.K. Ghalambor, D.C. Haak, and P.R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105(18):6,668–6,672, doi:10.1073pnas.0709472105.
- Doney, S.C., V.J. Fabry, R.A. Feely, and J.A. Kleypas. 2009. Ocean acidification: The other CO₂ problem. *Annual Review of Marine Science* 1:169–192.

- Dupont, S., and M.C. Thorndyke. 2009. Impact of CO₂-driven ocean acidification on invertebrates' early life-history: What we know, what we need to know and what we can do. *Biogeosciences Discussions* 6:3,109–3,131.
- Dupont, S., and M.C. Thorndyke. 2008. Ocean acidification and its impact on the early life-history stages of marine animals. Pp. 89–97 in *Impacts of Acidification on Biological, Chemical and Physical Systems in the Mediterranean and Black Seas. CIESM Workshop Monographs, n°36.* F. Briand, ed., Monaco, 124 pp.
- Elston, R.A., H. Hasegawa, K.L. Humphrey, I.K. Polyak, C.C. Häse. 2008. Re-emergence of *Vibrio tubiashii* in bivalve shellfish aquaculture: Severity, environmental drivers, geographic extent and management. *Diseases of Aquatic Organisms* 82:119–134, doi:10.3354/dao01982.
- Engel, A., I. Zondervan, K. Aerts, L. Beaufort, A. Benthien, L. Chou, B. Delille, J.-P. Gattuso, J. Harlay, and C. Heemann. 2005. Testing the direct effect of CO₂ concentration on a bloom of the coccolithophorid *Emiliania huxleyi* in mesocosm experiments. *Limnology and Oceanography* 50(2)493–507.
- Fabry, V.J., B.A. Seibel, R.A. Feely, and J.C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65:414–432.
- Feely, R.A., C.L. Sabine, K. Lee, W. Berelson, J. Kleypas, V.J. Fabry, and F.J. Millero. 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 305(5682):362–366.
- Feely, R.A., C.L. Sabine, J.M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. *Science* 320(5882):1,490–1,492, doi:10.1126/science.1155676.
- Gazeau, F., C. Quiblier, J.M. Jansen, J.-P. Gattuso, J.J. Middelburg, and C.H.R. Heip. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophysical Research Letters* 34, L07603, doi:10.1029/2006GL028554.
- Gruber, N., H. Frenzel, S.C. Doney, P. Marchesiello, J.C. McWilliams, J.R. Moisan, J. Oram, G.-K. Plattner, and K.D. Stolzenbach. 2006. Eddyresolving simulation of plankton ecosystem dynamics in the California Current System. *Deep-Sea Research Part I* 53:1,483–1,516, doi:10.1016/j.dsr.2006.06.005.
- Guinotte, J.M., and V.J. Fabry. 2008. Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* 1134:320–342, doi:10.1196/annals.1439.013.
- Hales, B., T. Takahashi, and L. Bandstra. 2005. Atmospheric CO₂ uptake by a coastal upwelling system. *Global Biogeochemical Cycles* 19, GB1009, doi:10.1029/2004GB002295.
- Hall-Spencer, J.M., R. Rodolfo-Metalpa, S. Martin, E. Ransome, M. Fine, S.M. Turner, S.J. Rowley, D. Tedesco, and M.C. Buia. 2008. Volcanic carbon

dioxide vents show ecosystem effects of ocean acidification. *Nature* 454(7200):96–99, doi:10.1038/ nature07051.

- Hare, C.E., K. Leblanc, G.R. Ditullio, R.M. Kudela,
 Y. Zhang, P.A. Lee, S. Riseman, and D.A. Hutchins.
 2007. Consequences of increased temperature and CO₂ for phytoplankton community structure in the Bering Sea. *Marine Ecology Progress Series* 352:9–16, doi:10.3354/meps07182.
- Hoegh-Guldberg, O., P.J. Mumby, A.J. Hooten,
 R.S. Steneck, P. Greenfield, E. Gomez, C.D. Harvell,
 P.F. Sale, A.J. Edwards, K. Caldeira, and others.
 2007. Coral reefs under rapid climate change and
 ocean acidification. *Science* 318(5857):1,737–1,742,
 doi:10.1126/science.1152509.
- Hofmann, M., and H.J. Schellnhuber. 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. Proceedings of the National Academy of Sciences of the United States of America 106(9):3,017–3,022: doi:10.1073/ pnas.0813384106.
- Iglesias-Rodriguez, M.D., P.R. Halloran, R.E.M. Rickaby, I.R. Hall, E. Colmenero-Hidalgo, J.R. Gittins, D.R.H. Green, T. Tyrrell, S.J. Gibbs, P. von Dassow, and others. 2008. Phytoplankton calcification in a high-CO₂ world. *Science* 320(5874):336–340, doi:10.1126/science.1154122.
- Kleypas, J.A., R.A. Feely, V.J. Fabry, C. Langdon,
 C.L. Sabine, and L.L Robbins. 2006. *Impacts of* Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research.
 Report of a workshop held 18-20 April 2005,
 St. Petersburg, FL, sponsored by NSF, NOAA, and the US Geological Survey, 88 pp.

Kurihara, H. 2008. Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373:275–284.

- Lee, S.W., S.M. Hong, and C.S. Choi. 2006. Characteristics of calcification processes in embryos and larvae of the pacific oyster, *Crassostrea gigas*. *Bulletin of Marine Science* 78(2):309–317.
- Lebrato, M., D. Iglesias-Rodríguez, R.A. Feely, D. Greeley, D.O.B. Jones, N. Suarez-Bosche, R.S. Lampitt, J.E. Cartes, D.R.H. Green, and B. Alker. In press. Global contribution of echinoderms to the marine carbon cycle. *Ecological Monographs*.

Leinweber, A., N. Gruber, H. Frenzel, G.E. Friederich, and F.P. Chavez. 2009. Diurnal carbon cycling in the surface ocean and lower atmosphere of Santa Monica Bay, California. *Geophysical Research Letters* 36, L08601, doi:10.1029/2008GL037018.

Martin, S., and J.-P. Gattuso. 2009. Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Global Change Biology* 15:2,089–2,100, doi:10.1111/j.1365-2486.2009.01874.x.

McNeil, B.I., and R.J. Matear. 2008. Southern Ocean acidification: A tipping point at 450-ppm atmospheric CO₂. Proceedings of the National Academy of Sciences of the United States of America 105(48), doi:10.1073/pnas.0806318105.

- Moy, A.D., W.R. Howard, S.G. Bray, and T.W. Trull. 2009. Reduced calcification in modern Southern Ocean planktonic foraminifera. *Nature Geoscience* 2:276–280, doi:10.1038/NGEO460.
- Ohmann, M.D., and B.E. Lavaniegos. 2008.
 Multi-decadal variations in calcareous holozooplankton in the California Current System: Thecosome pteropods and foraminifera from CalCOFI. Paper OS31A-1238 presented at the American Geophysical Union Fall Meeting, San Francisco, 2008.
- Orr, J.C., V.J. Fabry, O. Aumont, L. Bopp, S.C. Doney, R.A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, and others. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437(7059), doi10.1038/nature04095.
- Oschlies, A., K.G. Schulz, U. Riebesell, and A. Schmittner. 2008. Simulated 21st century's increase in oceanic suboxia by CO₂-enhanced biotic carbon export. *Global Biogeochemical Cycles* 22, GB4008, doi:10.1029/2007GB003147.
- Pane, E.F., and J.P. Barry. 2007. Extracellular acidbase regulation during short-term hypercapnia is effective in a shallow-water crab, but ineffective in a deep-sea crab. *Marine Ecology Progress Series* 334:1–9.
- Plattner, G.-K., F. Joos, and T.F. Stocker. 2002. Revision of the global carbon budget due to changing air-sea oxygen fluxes. *Global Biogeochemical Cycles* 16(4), doi:10.1029/2001gb001746.
- Spero, H.J., J. Bijma, D.W. Lea, and B.E. Bemis. 1997. Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes. *Nature* 390(6659):497–500.
- Steinacher, M., F. Joos, T.L. Frolicher, G.K. Plattner, and S.C. Doney. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences* 6(4):515–533.
- Swanson, A.K., and C.H. Fox. 2007. Altered kelp (Laminariales) phlorotannins and growth under elevated carbon dioxide and ultraviolet-B treatments can influence associated intertidal food webs. *Global Change Biology* 13(8):1,696–1,709, doi:10.1111/j.1365-2486.2007.01384.x.
- Tans, P. 2009. An accounting of the observed increase in oceanic and atmospheric CO_2 and an outlook for the future. *Oceanography* 22(4):26–35.
- Tortell, P.D., J.R. Reinfelder, and F.M.M. Morel. 1997. Active uptake of bicarbonate by diatoms. *Nature* 390(6657):243–244.
- Tortell, P.D., C.D. Payne, Y.Y. Li, S. Trimborn,
 B. Rost, W.O. Smith, C. Riesselman, R.B. Dunbar,
 P. Sedwick, and G.R. DiTullio. 2008. CO₂
 sensitivity of Southern Ocean phytoplankton. *Geophysical Research Letters* 35(4), L04605,
 doi:10.1029/2007gl032583.
- Tunnicliffe, V., K.T.A. Davies, D.A. Butterfield, R.W. Embley, J.M. Rose, and W.W. Chadwick Jr. 2009. Survival of mussels in extremely acidic waters on a submarine volcano. *Nature Geoscience*, doi:10.1038/NGEO500.

- Warren, B. 2009. The big seven: Acidification risks and opportunities for the seafood industry. *Current: The Journal of Marine Education* 25(1):22–26.
- Watanabe, Y., A. Yamaguchi, H. Ishida, T. Harimoto, S. Suzuki, Y. Sekido, T. Ikeda, Y. Shirayama, M.M. Takahashi, T. Ohsumi, and J. Ishizaka. 2006. Lethality of increasing CO₂ levels on deep-sea copepods in the western North Pacific. *Journal of Oceanography* 62:185–196.
- Wootton J.T., C.A. Pfister, and J.D. Forester. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. Proceedings of the National Academy of Sciences of the United States of America 105(48): 18,848–18,853, doi:10.1073pnas.0810079105.