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Historical and Future Trends in Ocean Climate and Biogeochemistry

BY SCOTT C. DONEY, LAURENT BOPP, AND MATTHEW C. LONG

ABSTRACT. Changing atmospheric composition due to human activities, primarily carbon dioxide (CO_2) emissions from fossil fuel burning, is already impacting ocean circulation, biogeochemistry, and ecology, and model projections indicate that observed trends will continue or even accelerate over this century. Elevated atmospheric CO_2 alters Earth's radiative balance, leading to global-scale warming and climate change. The ocean stores the majority of resulting anomalous heat, which in turn drives other physical, chemical, and biological impacts. Sea surface warming and increased ocean vertical stratification are projected to reduce global-integrated primary production and export flux as well as to lower subsurface dissolved oxygen concentrations. Upper trophic levels will be affected both directly by warming and indirectly from changes in productivity and expanding low oxygen zones. The ocean also absorbs roughly one-quarter of present-day anthropogenic CO_2 emissions. The resulting changes in seawater chemistry, termed ocean acidification, include declining pH and saturation state for calcium carbon minerals that may have widespread impacts on many marine organisms. Climate warming will likely slow ocean CO_2 uptake but is not expected to significantly reduce upper ocean acidification. Improving the accuracy of future model projections requires better observational constraints on current rates of ocean change and a better understanding of the mechanisms controlling key physical and biogeochemical processes.

INTRODUCTION

Over the last century and a half, atmospheric composition and global climate have changed dramatically as a result of human industrialization, fossil-fuel burning, intensive agriculture, deforestation, and land-use change (Solomon et al., 2007). The rising atmospheric level of carbon dioxide (CO_2), an important greenhouse gas, is the single most important factor contributing to anthropogenic climate change and warming sea surface temperatures (SSTs; Figure 1). The ocean is a critical component of Earth's climate system, acting to slow climate change by storing excess heat and by removing excess CO_2 from the atmosphere. Temporal trends in ocean heat content, reconstructed for the last half-century from in situ data, show that most of the heating associated with global warming has occurred in the ocean, with smaller contributions from melting of sea and land ice (Levitus et al., 2012).

Documented trends in ocean physics relevant to marine biogeochemistry and ecosystems include rising SSTs, upper-ocean warming, sea level rise, altered precipitation patterns and river runoff rates, and sea ice retreat and thinning in the Arctic and West Antarctic Peninsula (Bindoff et al., 2007). The ocean is also a major sink for excess CO_2 resulting in substantial changes in seawater chemistry,

including reduced pH and carbonate mineral saturation states (ocean acidification; Doney et al., 2009; Gattuso and Hansson, 2011). In addition to warming and acidification, marine ecosystems are subject to other biogeochemical stressors, including reduced subsurface dissolved oxygen (O_2) concentrations that reflect warming and altered circulation (deoxygenation) (Keeling et al., 2010) and growing coastal nutrient levels that lead to eutrophication and expanding coastal and estuarine hypoxia (very low dissolved oxygen; Rabalais et al., 2010).

Detecting these long-term trends is challenging because the ocean exhibits substantial natural variability on subannual to multidecadal time scales. For any specific property, the detection problem involves a combination of issues: the magnitude of the anthropogenic secular trend relative to natural variability; the availability of sufficiently long, high-quality field and remote-sensing data; and a good theoretical understanding of responses to perturbations. Sustained observational networks, along with process studies and numerical models, are also essential for attributing the underlying causes driving both ocean variability and trends, in particular, for teasing apart the effects of anthropogenic forcing from other internal and external factors (e.g., El Niño-Southern Oscillation, solar variations, volcanic eruptions).

Here, we discuss the observational evidence and the mechanistic underpinning for understanding past and future anthropogenic impacts on ocean climate and biogeochemistry. We also discuss projections for the twenty-first century created from global Earth System Models. Most numerical models suggest that historical ocean physical and biogeochemical trends observed over the last several decades will continue at least through the middle of this century, and the trends may even accelerate in response to growing human population levels and, more importantly, rising economic standards of living, particularly in the developing world. The recent round of climate change simulations conducted for the Intergovernmental Panel on Climate Change (IPCC) under the Coupled Model Intercomparison Project Phase 5 (CMIP5) includes, for the first time, a broad suite of prognostic marine ecosystem-biogeochemistry models. To illustrate expected future trends, we draw on a recent model analysis that examines a range of different scenarios for an ensemble of Earth System Models (Bopp et al., 2013).

Because of the relatively coarse spatial resolution of available synthesis data sets and Earth System Model simulations, our focus here is primarily on open-ocean trends. For some applications such as marine resource management, information on past and future trends in coastal systems would be equally or even more valuable. While coastal regions experience similar

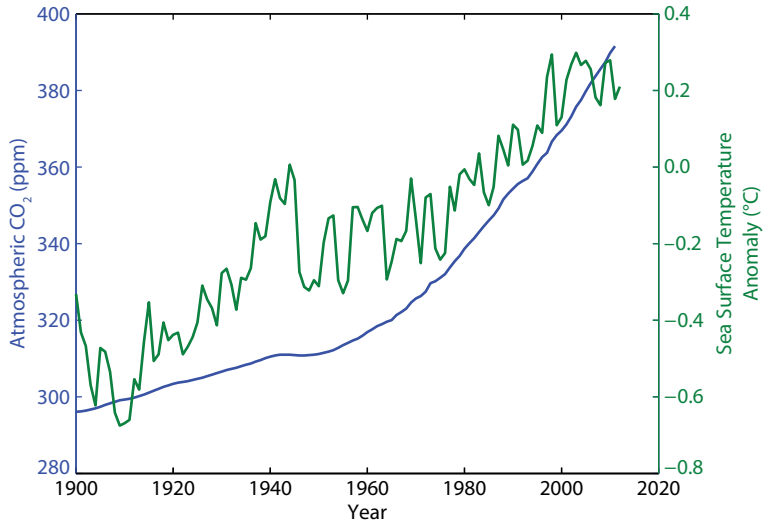

Figure 1. Time-series trends over the twentieth and early twenty-first centuries for ocean surface temperature and atmospheric CO_2 relevant to marine biogeochemistry. Left axis (blue): Annual-average atmospheric CO_2 from ice cores prior to 1959 (MacFarling Meure et al., 2006) and Mauna Loa instrumental record from 1959 to present (Tans and Keeling, 2012). Right axis (green): Global mean sea surface temperature anomalies (ERSST data referenced to 1971–2000 climatology; Smith et al., 2008).

patterns of climate change and rising atmospheric CO_2 as the adjacent open ocean, other human factors also come in to play, including coastal urbanization, agriculture, and freshwater management (Doney, 2010). Higher-resolution regional modeling studies have been developed to capture the small-scale heterogeneity of coastal systems (Gruber et al., 2006), and efforts are underway to embed such regional models into global Earth System Models.

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CLIMATE CHANGE AND THE GLOBAL CARBON CYCLE

At the most basic level, the radiative balance between incoming sunlight and outgoing thermal infrared radiation determines Earth's mean surface climate. Human activities are altering this balance in a number of ways. Atmospheric greenhouse gases such as CO_2 play a key role by absorbing infrared radiation and thus trapping heat near Earth's surface. Global average atmospheric CO_2 has increased by more than 40% from preindustrial levels, from 280 to 395 ppm (parts per million) by mid-2013 (Dlugokencky and Tans, 2013). Temporary excursions to 400 ppm were recorded at the Mauna Loa Observatory in Hawai'i in May 2013. The excess carbon dioxide can be definitively attributed to human activities based on carbon isotopes and ice-core carbon dioxide measurements.

Detailed annual assessments, quantifying the ongoing human perturbations of the global carbon cycle, are now available (Le Quéré et al., 2013; Global Carbon Project, http://www.globalcarbonproject.org). The main source of excess atmospheric CO_2 is fossil fuel combustion, with contributions from cement production, agriculture, and deforestation. For the last decade for which data are available (2002–2011), fossil fuel emissions averaged 8.3 ± 0.4 billion metric tons of carbon per year (uncertainty is ± 1 standard deviation in estimate of decadal mean). Over the same time period, fossil fuel emissions grew with time at a rate of 3.1% per year since the year 2000. Deforestation and land-use change accounted for an additional source of 1.0 ± 0.5 billion metric tons of carbon per year.

The excess atmospheric CO_2 from human activities contributes the largest single radiative forcing to anthropogenic climate warming and accounts for ~ 65% of the total forcing due to long-lived gases (NOAA Annual Greenhouse Gas Index, http://www.esrl.noaa.gov/gmd/aggi). Other trace gases such as methane (CH_4), nitrous oxide (N_2O), and chlorofluorocarbons (CFCs) are also important because, molecule for molecule, they absorb more longwave radiation than CO_2. Once released to the air, these greenhouse gases persist in the atmosphere for years to decades or longer, and the climatic impact of past and current human greenhouse gas emissions are global in extent and will be with us for a long time to come.

The direct climate effect of anthropogenic airborne aerosol particles is more complicated, either warming or cooling the surface depending on their albedo, a measure of the particles' brightness or reflectivity. Aerosol particles also act indirectly by altering cloud properties

and amounts, although these effects are not as well characterized as the direct impacts. In contrast with greenhouse gases, tropospheric aerosols are removed from the atmosphere on time scales of a few days to weeks, and their climatic impacts, mostly cooling, are concentrated regionally near and downwind of industrial sources. Overall, the radiative impact of anthropogenic aerosol emissions is thought to be a net cooling that partially offsets the warming due to greenhouse gases, particularly in aerosol emission regions. However, substantial uncertainties remain regarding the strength of direct and indirect aerosol effects. Human modifications to land cover also alter climate by changing the surface energy budget.

At present, the radiative effects due to elevated greenhouse gases dominate over other anthropogenic factors, and the resulting positive radiative forcing translates into global-scale warming accompanied by substantial regional variability. The climate sensitivity to changes in CO_2 depends on both positive and negative climate feedbacks involving clouds, sea ice, water vapor, and the land surface. For example, the retreat of Arctic sea ice further accelerates warming because the dark ocean surface can then absorb more sunlight than the highly reflective ice. Cloud dynamics present the greatest feedback uncertainty because clouds can generate either cooling or warming, depending on their structure.

Anthropogenic CO_2 emissions will likely continue to increase over the next several decades without dramatic changes in carbon and energy policy. Integrated assessment model scenarios indicate that atmospheric CO_2 levels will likely exceed 500 ppm by the end of the twenty-first century and may be as high as 950 ppm (van Vuuren et al., 2011) (Figure 2), levels not experienced on Earth for the past several million years. The dominance of CO_2 in overall anthropogenic climate forcing is projected to increase with time because of the stability and long atmospheric lifetime of excess CO_2 (many decades to centuries; van Vuuren et al., 2011). Excess atmospheric CO_2 is therefore also the primary human forcing driving projected future SST warming and associated changes in ocean circulation, ecology, and biogeochemistry.

Uncertainties in future climate projections can be divided roughly into three groups (Figure 3): (1) uncertainties in emissions of CO_2 (and other greenhouse gases and aerosols) to the atmosphere associated with social, political, economic, and technological factors; (2) for a specified emissions scenario, uncertainties in atmospheric CO_2 levels associated with land and ocean carbon sinks; and (3) for a specified atmospheric CO_2 level, uncertainties in climate sensitivity to associated changes in clouds, ocean circulation, sea ice, land biophysics, and other parameters. Atmospheric CO_2 levels can also be influenced by climate/carbon-cycle feedbacks, thus interconnecting the latter two types of uncertainty.

GLOBAL AND OCEAN WARMING

Based on a variety of observational records, Earth's surface has warmed substantially over the last several decades, and the magnitude and patterns of these changes are consistent with attribution to human activities and are not explained by natural variability alone (Solomon

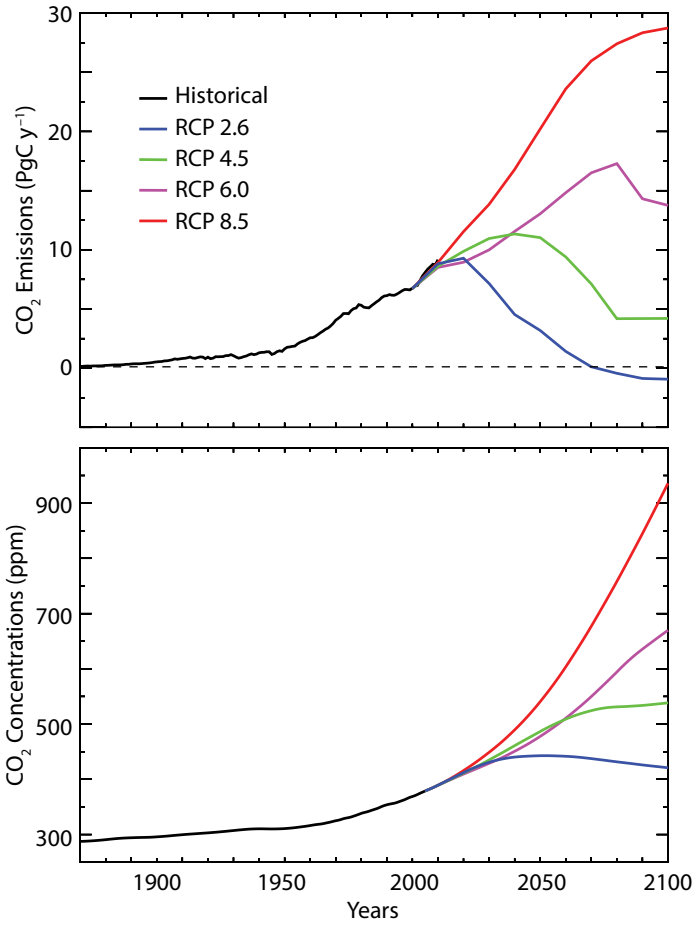

Figure 2. Carbon dioxide emissions trajectories and atmospheric CO_2 concentrations from historical data (black lines) and four of the Representative Concentration Pathways (RCPs) for the twenty-first century (colored lines) used in the most recent round of international coupled model intercomparison studies (van Vuuren et al., 2011). The RCPs span a wide range of different economic and social pathways over the twenty-first century.

et al., 2007; Kennedy et al., 2010). During the twentieth century, for example, global mean SSTs warmed by about +0.7°C (Figure 1). Paleoreconstructions of global land and ocean surface temperatures indicate that the recent twentieth century warming is quite anomalous relative to the temperatures over the last 2,000 years (including the Medieval and Roman warm periods) and are now approaching temperatures from the Holocene thermal optimum period at the beginning part of the current interglacial period (Marcott et al., 2013).

Over the last decade, global surface temperatures have increased at a relatively slow rate even though atmospheric CO_2 has continued to increase. This so-called warming hiatus could be caused by several factors: compensation by cooling factors such as atmospheric aerosols, overestimation of climate sensitivity to increasing greenhouse gas levels (thus decreasing the expected warming trend), and natural climate variability that is temporarily masking a longer-term warming trend. Some climate models indicate that periods of weak global warming are associated with natural variability that leads to enhanced warming in the deep ocean relative to the upper ocean (Meehl et al., 2011), consistent with observationally based estimates showing that recent ocean warming has been most substantial below 300 m (Balmaseda et al., 2013). The observed global mean temperature trends reflect a high incidence of La Niña events in the last 15 years, with colder surface waters in the tropical Pacific (Foster and Rahmstorf, 2011), possibly associated with a cold period of the Pacific Decadal Oscillation, a natural mode of climate variability. Global warming may accelerate when the Pacific Decadal Oscillation shifts back to a warm period (Kosaka and Xie, 2013).

Earth System Model projections suggest future SSTs will continue to increase with time, in spite of decadal-scale fluctuations caused by natural variability. For example, Bopp et al. (2013) report ensemble-mean warming of global mean SST at the end of the twenty-first century of an additional +0.25°C to +3.75°C above late twentieth century levels (Figure 4). A large fraction of this temperature range depends on the choice of emission scenario (the different colored lines in Figure 4), though for a given scenario, there are also significant variations among models (colored shading is inter-model standard deviation). For example, for RCP8.5, the mean global SST warming at 2100 is slightly below +3.0°C, with an ensemble range of more than 1.5°C. The lowest temperature projections occur for the RCP2.6 scenario, in which CO_2 emissions are reduced sharply over the next few decades and even go negative (net uptake) by the end of the century.

The large range in SST response across the model ensemble reflects differences in the climate sensitivity, effectively the degree to which an initial radiative perturbation from anthropogenic greenhouse gases and aerosols is amplified by climate feedbacks such as changes in the distribution and amount of cloud cover (Meehl et al., 2007). While the basic treatment of large-scale atmosphere and ocean dynamics is similar across models, many climate processes cannot be resolved explicitly. Each Earth System Model includes a large number of parameterizations for so-called subgrid-scale processes such as mixing, convection, and cloud formation that can substantially alter the climate sensitivity.

Because of seawater's large heat storing capacity, small changes in ocean temperature reflect large changes in ocean heat storage. The phenomenon of global warming should, more appropriately, be called ocean warming, as more than 80% of the added heat resides in the ocean. Direct measurements of ocean temperatures show warming beginning in about 1970 down to at least 700 m, with stronger warming near the surface leading to increased thermal stratification (or layering) of the water column over much of the global ocean (Levitus et al., 2012). Deep ocean temperatures are also on the rise (Purkey and Johnson, 2010).

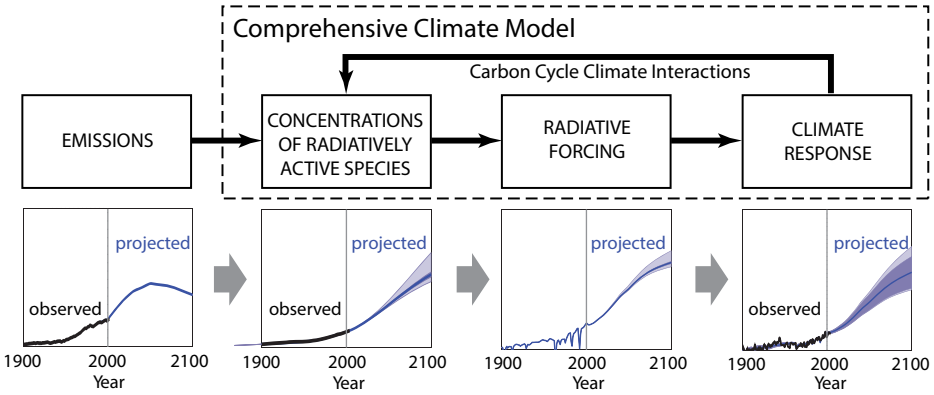

Figure 3. Schematic illustrating how scenario-dependent anthropogenic emissions for radiatively important trace gases such as CO_2 are incorporated into climate model projections of future climate change. In the lower row of plots, the black lines represent historical observations and the blue lines model-derived projections. The shaded bands represent the uncertainties associated with atmospheric composition and climate sensitivity, given a specified emissions trajectory. *From Figure 10.1 in Meehl et al. (2007)*

Another striking climate trend is the rapid decline in Arctic sea ice volume and extent over the past four decades (Walsh and Chapman, 2001; Kwok and Rothrock, 2009; Comiso, 2011). The minimum Arctic sea ice extent in 2012 was about half that in the earlier part of the satellite record starting in the late 1970s (http://nsidc.org/arcticseaicenews), and model projections indicate the potential for a seasonally ice-free Arctic as early as the 2030s (Stroeve et al., 2012; Wang and Overland, 2012).

In twenty-first century model projections, upper-ocean vertical stratification tends to increase and mixed layer depths decrease over much of the ocean as a result of CO_2-induced warming and alterations in the global hydrological cycle (e.g., increased precipitation, runoff, and sea ice melt in high latitudes). In addition, simulations suggest reduced deepwater formation (and deep mixing) in the subpolar North Atlantic and reduced meridional overturning circulation in the North Atlantic. Sea level is estimated to rise due to ocean warming (thermal expansion) and melting of glaciers and ice sheets. Many simulations suggest a general strengthening of the water cycle, with increased precipitation in the tropics and high latitudes, drier conditions in the subtropics, and an increased frequency of extreme droughts and floods. Changes in the water cycle will influence riverine transport of freshwater and dissolved and particulate material to the coastal ocean, with potentially important ecological and biogeochemical impacts. Storm tracks over the ocean may shift, and some simulations suggest the possibility of more intense tropical cyclones, especially in the tropical Pacific. Regional climate change patterns, which are most relevant for most applications, are not as well understood as global trends, and they differ across climate model projections.

Future changes in winds may somewhat counteract the effect of increased stratification. For instance, observations indicate a recent trend in Southern Hemisphere atmospheric pressure toward more positive Southern Annular Mode conditions that in turn strengthen and displace poleward the westerly winds in the Southern Ocean. The rate of change of SSTs and vertical stratification in the Southern Ocean is relatively slow due to the large-scale ocean circulation that brings cold, Circumpolar Deep Water to the surface in the Antarctic Circumpolar Current. The strengthening of the westerly winds may be acting to increase Southern Ocean vertical upwelling and thus further diminishing any sea surface warming signal. Presently, reductions in stratospheric ozone over Antarctica are driving this pattern of change. In the future, ozone levels are expected to recover, but CO_2-induced warming is expected to take over, accelerating these trends.

OCEAN CARBON UPTAKE AND ACIDIFICATION

The ocean removes roughly a quarter of the excess CO_2 emitted to the atmosphere by human fossil fuel combustion and deforestation (Sabine and Tanhua, 2010). The global inventory

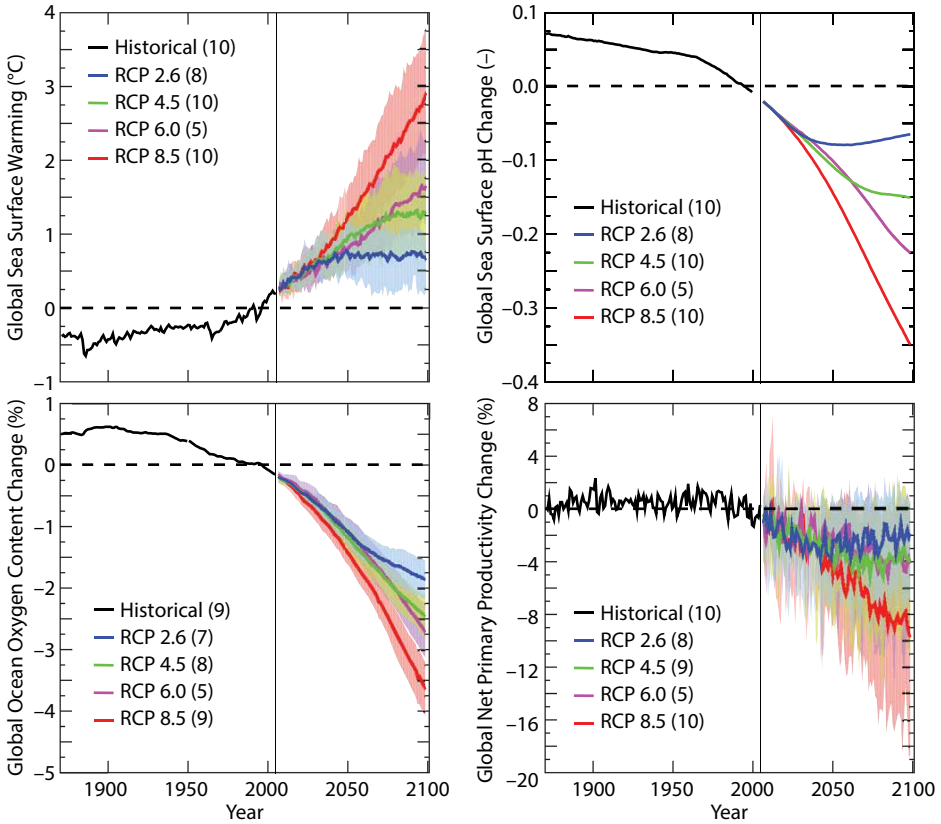

Figure 4. Time series of global average ocean anomalies for sea surface temperature (°C), surface pH, oxygen content (% change), and net primary productivity (% change) based on an ensemble-mean of Earth System Models (Bopp et al., 2013). The black lines represent model ensemble trends over the historical period and the colored lines future projections using four different emission scenarios or RCPs (Figure 2). The colored shadings are the model ensemble spread (inter-model standard deviation).

and distribution of excess dissolved inorganic carbon (DIC) in the ocean was first mapped using measurements from an intensive, international survey in the late-1980s and early 1990s. Ongoing observational programs and numerical models continue to document further ocean uptake of CO_2 over time. Over the most recent decade with available data (2002–2011), ocean carbon uptake is estimated at 2.5 ± 0.5 billion metric tons of carbon per year, 27% of global emissions (Le Quéré et al., 2013). Cumulatively since the beginning of the industrial age, the ocean is estimated to have removed about 25–30% of total human CO_2 emissions. The physical mechanism for the dissolution of excess CO_2 into the ocean is well understood. The global ocean uptake rate is governed primarily by the growth rate of atmospheric CO_2 excess above pre-industrial levels and by the rate of ocean circulation that exchanges surface waters equilibrated with elevated atmospheric CO_2 levels with subsurface waters that have not been exposed to the atmosphere since pre-industrial times.

Climate warming is projected to reduce ocean uptake of excess atmospheric CO_2 due to decreased solubility, increased vertical stratification, and slowing of ocean convection and water-mass formation that acts to ventilate large portions of the thermocline and intermediate and deep ocean (Arora et al., 2013). Lower ocean uptake would leave more CO_2 in the atmosphere, thus accelerating anthropogenic climate change. Strengthened westerly winds in the Southern Ocean, on the other hand, may lead to increased ocean uptake of anthropogenic CO_2, serving as a negative feedback. Current model estimates suggest that the combined climate-ocean carbon feedback is positive—less ocean CO_2 uptake under a warming climate. Better constraints on the response of ocean circulation and biological productivity to changing climate could improve model estimates. There is some evidence that climate change is already slowing ocean carbon dioxide uptake (Le Quéré et al., 2010). Several other factors, including ocean acidification, may either increase or decrease the ocean uptake of carbon dioxide as the ocean warms and acidifies (Denman et al., 2007). The net effect of these other processes is not well known at this time, but is thought to be relatively small compared to overall ocean carbon dioxide uptake over this century (Gehlen et al., 2011).

Ocean uptake of excess CO_2 causes well-understood and substantial changes in seawater chemistry that can affect marine organisms and ecosystems (Doney et al., 2009; Gattuso and Hansson, 2011). Carbon dioxide acts as a weak acid when added to seawater, leading to the release of hydrogen ions (H^+) and bicarbonate (HCO_3^-) ions:

$$CO_2 + H_2O \Rightarrow H^+ + HCO_3^-.$$

The reaction increases seawater acidity and increases hydrogen ion activity, thus lowering seawater pH (pH is defined as the negative logarithm of the hydrogen ion activity). A one-unit decline in pH is equivalent to a tenfold increase in H^+ activity. Most of the extra hydrogen ions react with carbonate ions (CO_3^{2-}) and lower their ambient concentrations:

$$H^+ + CO_3^{2-} \Rightarrow HCO_3^-.$$

This second reaction is important because reduced seawater carbonate ion concentrations decrease the saturation levels of calcium carbonate ($CaCO_3$) that is used by many marine microbes, plants, and animals to form shells and skeletons. The solubility of different bio-mineral forms of $CaCO_3$ used by organisms varies substantially, and this may influence biological responses to ocean acidification. Many organisms require supersaturated conditions to form sufficient calcium carbonate shells or skeletons, and biological calcification rates tend to decrease in response to lower carbonate ion concentrations, even when the ambient seawater is still supersaturated.

Long-term ocean acidification trends are clearly evident over the past several decades in open-ocean time series and hydrographic survey data, and the trends are consistent with the growth rate of atmospheric carbon dioxide (Dore et al., 2009). From pre-industrial levels, contemporary surface ocean pH is estimated to have dropped on average from 8.2 to 8.1, or by about 0.1 pH units (a 26% increase in hydrogen ion concentration), and further decreases of 0.22 to 0.35 pH units are projected over this century unless carbon dioxide emissions are significantly reduced (Figure 4; Orr et al., 2005; Bopp et al., 2013).

Global upper-ocean chemistry trends driven by human carbon dioxide emissions are more rapid than variations in the geological past (Hönisch et al., 2012). For example, atmospheric carbon dioxide grew by approximately 30% during the transition from the most recent cold glacial period, about 20,000 years ago, to the current warm interglacial period; the corresponding rate of decrease in surface ocean pH, driven by geological processes, was approximately 50 times slower than the current rate, driven largely by fossil fuel burning. Many marine organisms appear to be physiologically adapted to relatively constant local acid-base conditions and are sensitive to relatively small variations in pH and the saturation state of calcium carbonate (see chapters in Gattuso and Hansson, 2011).

The majority of present-day ocean surface waters are supersaturated for the major carbonate mineral forms used by marine organisms, including the more soluble forms such as aragonite and high-magnesium calcite (corals, many mollusks) and a less-soluble form, calcite (coccolithophores, foraminifera, and some mollusks). However, calcium carbonate saturation states of all mineral forms are declining everywhere. Polar oceans are of particular concern because cold surface waters naturally hold more carbon dioxide and started off with lower calcium carbonate saturation states. Model simulations indicate that polar surface waters will become undersaturated for aragonite in the near future for the Arctic (atmospheric carbon dioxide of 400–450 ppm) and by mid-century for the polar Southern Ocean (atmospheric carbon dioxide of 550–600 ppm) (Orr et al., 2005; Steinacher et al., 2009). This may result in major changes in polar ecosystems if there are large-scale reductions in calcifying organisms. Because of elevated background CO_2 levels, other potentially susceptible ocean regions include eastern boundary current upwelling systems such as those off the coasts of California, Oregon, and Washington (Feely et al., 2008; Gruber et al., 2012); deep-sea and subsurface oxygen minimum zones (Brewer and Peltzer, 2009); and coastal waters that already exhibit excess nutrient levels (eutrophication) and low dissolved oxygen (hypoxia) due to human-driven nutrient pollution from land-based activities (Feely et al., 2010).

Seawater acid-base chemistry plays a fundamental role in a wide range of other ocean biological and chemical processes, and ocean acidification could potentially alter marine biogeochemistry in a variety of ways (Doney et al., 2009; Gattuso and Hansson, 2011). For example, reduced pH will alter the speciation of trace metals and may influence bioavailability. Laboratory and mesocosm manipulation experiments regarding seawater CO_2 and pH indicate a variety of potential effects on planktonic communities, including increased nitrogen fixation, reduced nitrification, altered trace gas production, and changes in the elemental stoichiometry of carbon to nutrients in organic matter. Reduced planktonic $CaCO_3$ production could lower the sinking flux of organic matter associated with ballast material and thus change the overall biological pump and subsurface oxygen and nutrient distributions.

> “THE PHENOMENON OF GLOBAL WARMING SHOULD, MORE APPROPRIATELY, BE CALLED OCEAN WARMING, AS MORE THAN 80% OF THE ADDED HEAT RESIDES IN THE OCEAN.”

DEOXYGENATION

Low oxygen or hypoxic conditions (roughly < 60 μmol kg^{-1}) occur naturally in open-ocean and coastal subsurface waters from a combination of weak ventilation, temperature-dependent solubility, and organic matter degradation, features that are all exacerbated by climate warming and coastal nutrient eutrophication. Oxygen minimum zones occur naturally in the open ocean in the tropics and subtropics, with the lowest O_2 suboxic waters (< 5 μmol kg^{-1}) restricted to the Arabian Sea, the Bay of Bengal, and the eastern tropical Pacific (Paulmier and Ruiz-Pino, 2009; Bianchi et al., 2012). Oxygen minimum zones often underlie biologically productive regions such as the eastern boundary current upwelling systems (e.g., Peru, Benguela). The lowest water column O_2 values are observed in the upper and mid thermocline where biological oxygen consumption rates are high. Low-oxygen regions also occur in coastal and estuarine waters and often occur seasonally associated with periods of elevated surface biological production, downward export of organic matter, and respiration in conjunction with seasonal enhanced vertical stratification that isolates bottom waters on the shelf from the atmosphere.

A number of studies indicate that subsurface oxygen values are declining with time in the mid-latitudes (Whitney et al., 2007; Helm et al., 2011) and that oxygen minimum zones are expanding spatially both vertically and horizontally (Stramma et al., 2008), which could limit the habitat range for some fish species and alter diel vertical migration patterns (Stramma et al., 2012). Only a fraction of the oxygen loss is directly related to warming and decreased O_2 solubility; therefore, most of the deoxygenation must reflect alterations and slowdowns of thermocline ventilation. In response to climate warming over the twenty-first century, model projections indicate further reductions in the global

oxygen inventory and expansions of open-ocean oxygen minimum zones (Bopp et al., 2002, 2013; Frölicher et al., 2009; Figure 4).

Marine biota are influenced by ocean oxygen distributions, particularly at low O_2 values (Levin et al., 2009; Keeling et al., 2010). Dissolved O_2 gas is required for aerobic respiration, and below certain organism-specific thresholds, low O_2 begins to affect metabolic rates and behavior. Low O_2 leads to marine habitat degradation and, in extreme cases, extensive fish and invertebrate mortality. Larger mobile animals often move out of low oxygen environments, resulting in so-called "dead-zones" where many pelagic and benthic macrofauna are nearly absent (Diaz and Rosenberg, 2008; Rabalais et al., 2010).

MARINE ECOSYSTEM RESPONSES

Marine biota and ecosystems are experiencing a combination of multiple stressors: warming, acidification, and deoxygenation (Doney, 2010; Gruber, 2011). Climate warming is superimposed on other local-scale anthropogenic stresses, especially in coastal waters, due to pollution, nutrient eutrophication and hypoxia, overfishing, urban development, and habitat destruction. Detrimental effects can arise directly via physiological responses of individual organisms to altered temperature, CO_2, O_2, pH, and carbonate saturation state (Pörtner and Farrell, 2008; Somero, 2012) as well as indirectly via changes to biological community ecosystems on which organisms depend for food and habitat (Doney et al., 2012). Marine life has survived large climate variations in the past, but the projected rates of climate change and ocean acidification over the next century are much faster than experienced on the planet in the past, except for rare, catastrophic events that are evident in the geological record.

Primary production by phytoplankton fuels the entire marine food web, and linkages between primary production and climate arise through changes in nutrient supply and light limitation. Tropical and subtropical production tends to be nutrient limited because of strong vertical stratification and weak mixing, and, based on satellite data, ocean warming leads to reduced productivity (Behrenfeld et al. 2006; Siegel et al., 2013). Warming may thus result in expansion of the area of surface waters with very low phytoplankton biomass (Polovina et al., 2008). Climate-change simulations indicate broad patterns over the twenty-first century with declining low-latitude productivity, neutral or increased productivity in more light-limited subpolar and polar regions because of shallower mixed layers and reduced sea ice, and poleward migration of marine ecosystem boundaries as the oceans warm (Sarmiento et al., 2004; Steinacher et al., 2010; Bopp et al., 2013; Figure 5).

In their multimodel ensemble mean, Bopp et al. (2013) find that tropical/subtropical changes dominate, with reductions in global integrated primary production ranging from –3.6% to –8.6% over different emission scenarios (Figure 4). Furthermore, models indicate that fractional declines in global integrated export production are even larger, with shifts in plankton community structure playing a significant role in modulating the climate response of the biological pump (Bopp et al., 2001; Marinov et al. 2010). Climate change induced trends in regional and global marine primary production will be difficult to detect because of the large natural variability and the currently rather limited duration of satellite ocean color records (Henson et al., 2010). One caveat should be noted, namely that the current generation of Earth System Models does not capture well many of the highly productive coastal regions that are influenced on small scales by poorly resolved wind-driven upwelling, river freshwater discharge, and coastal currents.

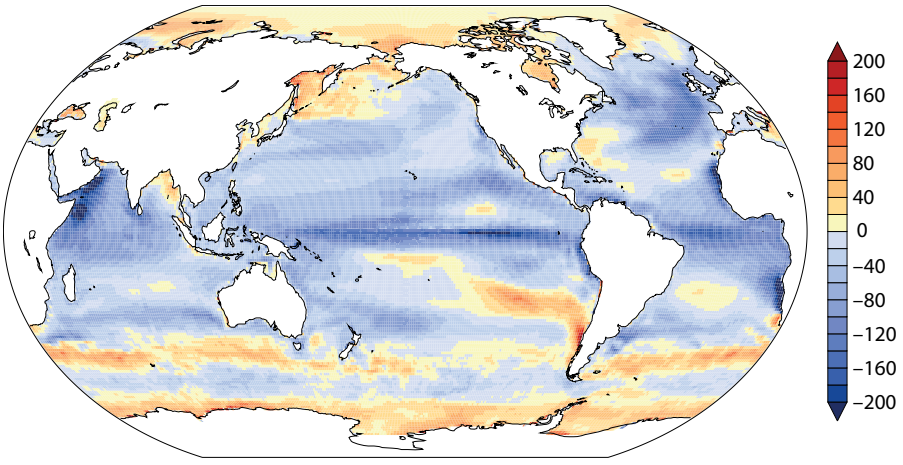

Figure 5. Spatial map of the change in marine net primary productivity (g C m^{-2} yr^{-1}; end of twenty-first century minus current conditions) based on the mean of an ensemble of 10 different CMIP5 models integrated in time following the RCP8.5 scenario (Figures 2 and 4) (Bopp et al., 2013).

Climate change can also impact higher trophic level organisms directly. Warming over the past few decades has resulted in the migration of commercial fish stocks poleward and into deeper water (Nye et al., 2009), and productivity of fisheries is predicted to decline along the coasts of the lower 48 states, while increasing in parts of Alaska (Cheung et al., 2009). Climate change also influences the spread and impact of marine diseases and parasites (Harvell et al., 2002). Marine disease appears to be on the rise with time, with warmer sea surface temperatures linked with higher intensity and increased spatial ranges of diseases that attack corals, abalones, oysters, fishes, and marine mammals (Ward and Lafferty, 2004).

SCIENCE GAPS AND RESEARCH NEEDS

Accurately projecting future patterns and rates of change in ocean biogeochemistry is quite challenging. Our main available tools, numerical simulations, are only as good as our mathematical encapsulation of the underlying mechanisms. Several research elements need to be pursued in parallel: improved ongoing monitoring of ocean climate, biogeochemical, and ecosystem trends; laboratory and field process studies to quantify biological sensitivities to the multiple stressors of warming, acidification, and deoxygenation; historical and paleoclimate studies on past climate events; and incorporation of the resulting scientific insights into an improved hierarchy of numerical ocean models representing dynamics from species to ecosystems. In particular, we need to know if there are climatic tipping points or thresholds beyond which climate change may induce rapid and dramatic regime shifts in ocean biogeochemistry and ecosystems.

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