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Microbial biogeochemistry of coastal upwelling regimes in a changing ocean

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Coastal upwelling regimes associated with eastern boundary currents are the most biologically productive ecosystems in the ocean. As a result, they play a disproportionately important role in the microbially mediated cycling of marine nutrients. These systems are characterized by strong natural variations in carbon dioxide concentrations, pH, nutrient levels and sea surface temperatures on both seasonal and interannual timescales. Despite this natural variability, changes resulting from human activities are starting to emerge. Carbon dioxide derived from fossil fuel combustion is adding to the acidity of upwelled low-pH waters. Low-oxygen waters associated with coastal upwelling systems are growing in their extent and intensity as a result of a rise in upper ocean temperatures and productivity. And nutrient inputs to the coastal ocean continue to grow. Coastal upwelling systems may prove more resilient to changes resulting from human activities than other ocean ecosystems because of their ability to function under extremely variable conditions. Nevertheless, shifts in primary production, fish yields, nitrogen gain and loss, and the flux of climate-relevant gases could result from the perturbation of these highly productive and dynamic ecosystems.

The coastal upwelling regimes located along the eastern boundaries of the Pacific and Atlantic Ocean basins are small in size, but make a disproportionate contribution to the productivity and microbial biogeochemistry of the ocean. These regimes include the California and Peru/Humboldt current systems in the Pacific, and the Canary and Benguela current systems in the Atlantic. Their characteristic equatorward wind patterns lead to the net offshore transport of surface water, allowing cold, nutrient-laden water to upwell into the illuminated zone where phytoplankton photosynthesis occurs. Rich upwelled supplies of nitrate, phosphate and silicate, and the tremendous blooms of resident phytoplankton they support, render these regimes the 'new production factories' of the world ocean[1] (Fig. 1). The teeming proliferation of phytoplankton biomass that develops during upwelling feeds into short, productive food chains which support a significant share of the biological resources that humans harvest from the ocean[2–4].

Natural variability in carbon, oxygen, nitrogen and iron

Coastal upwelling systems consistently experience natural ranges in surface seawater carbon dioxide concentrations and pH that are among the most extreme in the ocean. As it upwells, older, deeper water carries high levels of carbon dioxide — the biogeochemical imprint of accumulated microbial respiration of organic matter — to the surface. This is especially true in the Pacific Ocean, where underlying waters have been isolated from the atmosphere for many decades. As a result, carbon dioxide levels in surface sea water in upwelling zones can exceed 1,000 ppm, and pH can drop as low as 7.6–7.7 (ref. 5). In comparison, typical pH values in most of the surface ocean are ~8.1, and equivalent partial pressures of carbon dioxide will not be reached in the atmosphere for a century or more[6].

As this naturally acidified water ages and warms at the surface, phytoplankton blooms consume much of the inorganic carbon through photosynthesis. This leads to the rapid drawdown of carbon dioxide and an increase in pH in the upwelled waters. Phytoplankton can deplete seawater carbon dioxide concentrations in these regions far below current atmospheric levels of ~400 ppm. For instance, the partial pressure of carbon dioxide in surface waters in a Mauritanian upwelling plume was found to fall by 140 ppm in just over a week, with photosynthetic carbon fixation responsible for ~96% of this drawdown[7]. Similarly, carbon dioxide uptake in both the southern California current and northern and central Canary current was shown to increase in line with upwelling intensity in a comparative modelling study. In other sectors of these two upwelling regimes the response seems more muted, however, owing to stronger nutrient limitation, slower growth and shorter water residence times[8].

Such large gradients in carbon dioxide concentrations between freshly upwelled water and older upwelled water result in a complex regional mosaic of surface-water carbon chemistry. In the central California upwelling system, pH can range between 7.85 and 8.15 as a result of this variability, according to model simulations[9]. This is because the pH of sea water and the concentrations of inorganic dissolved carbon species — including carbon dioxide, bicarbonate and carbonate — are inextricably linked through the carbonate buffer system, such that higher carbon dioxide levels mean lower pH and carbonate levels, and vice versa.

The carbon captured by marine phytoplankton eventually makes its way into the detrital organic matter pool. The sinking flux of particulate organic carbon out of the surface ocean sequesters carbon dioxide away from the atmosphere in deeper waters and sediments (Fig. 2a). High rates of bacterial respiration are supported by this dense rain of organic material. Combined with poorly ventilated source waters (particularly in the Pacific), this leads to the depletion of oxygen in the underlying water column and seafloor sediments. Indeed, the oxygen minimum zone centred on the Peruvian upwelling system in the eastern tropical south Pacific represents one of the largest reservoirs of suboxic water in the world ocean[10]. Oxygen minimum zones also occur in association with the Atlantic upwelling systems[11,12], although they are relatively small compared with those in the eastern Pacific, and little of the very low oxygen water is entrained in the upwelling[12].

These suboxic zones serve as globally significant sites of marine nitrate loss[11,13,14]. Microbial denitrification (the anaerobic conversion of nitrate to dinitrogen gas) and anammox (the microbial oxidation of ammonium using nitrite under anaerobic conditions) reduce biologically available oxidized nitrogen species (nitrate and nitrite, respectively) back to dinitrogen gas. Denitrification and anammox

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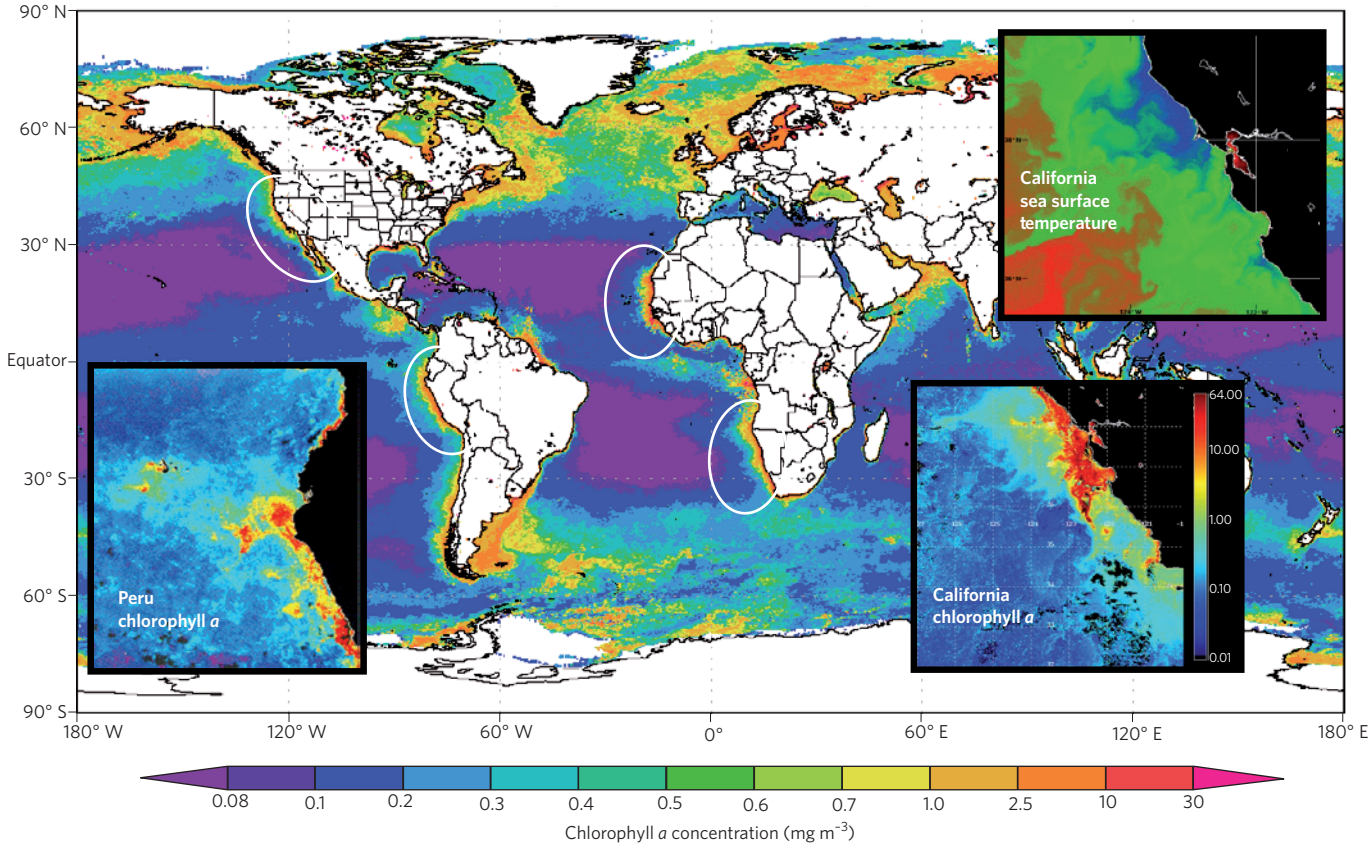

Figure 1 | Locations of the four main coastal upwelling systems associated with eastern boundary currents. A global false-colour compilation of satellite data on ocean chlorophyll *a* from the MODIS Aqua sensor for the year 2011 shows the California, Peru, Canary and Benguela ecosystems (white ovals). Also shown are close-up views of chlorophyll *a* levels in upwelling-supported phytoplankton blooms in Peru (lower left inset) and California (lower right inset), as well as a satellite-derived view of sea surface temperature in cold, nutrient-rich upwelling plumes off California (upper right inset). Satellite imagery courtesy of NASA.

therefore counter processes that deliver biologically available nitrogen to coastal waters, such as microbial nitrogen fixation, the biological reduction of dinitrogen gas to ammonium (Fig. 2a). The high carbon dioxide and low pH conditions found within oxygen minimum zones can also lead to the emission of carbon dioxide. In addition, incomplete dissimilatory reduction of nitrate or oxidation of ammonium can yield nitrous oxide, a potent greenhouse gas in its own right[15,16].

The trace element iron is a key determinant of biological productivity in coastal upwelling regimes. In regions characterized by broad, shallow continental shelves, relatively high levels of this essential micronutrient become entrained in upwelled water from iron-rich sediment sources. For instance, in much of the northern sector of the California upwelling ecosystem and in the southern Peru/Chile upwelling system, plentiful iron supplies allow the near-complete drawdown of upwelled nitrate and other nutrients by phytoplankton blooms[17,18]. Other parts of these systems are characterized by narrow continental shelves, where upwelled water does not come into contact to any significant extent with benthic iron sources[19,20]. In these regions, iron limitation of primary producers can be nearly as intense and pervasive as in some remote open-ocean 'high-nutrient, low-chlorophyll' areas, such as the equatorial Pacific. The ecosystem-level consequences of these iron-deficient, nitrate-rich conditions range from a reduction in carbon fixation and organic matter export to the underlying water column, to altered utilization ratios for important nutrients. For instance, iron-limited diatom communities characteristically deplete silicate from the water long before nitrate and phosphate, leading to a restructuring of the phytoplankton assemblage away from diatoms towards non-siliceous phytoplankton[20,21]. After the complete drawdown of nitrate, residual phosphate in surface waters can support nitrogen fixation by offshore prokaryotic communities[22] (largely cyanobacteria), although iron availability may also constrain these populations[23].

Regional climatic fluctuations that affect upwelling intensity and nutrient supply can also alter biological production in coastal upwelling zones. During El Niño years (the warm phase of the recurring El Niño/Southern Oscillation cycle[4,24]), weakened westerly trade winds warm the surface and increase stratification in the Californian and Peruvian upwelling ecosystems. This deepens the nutricline (the depth at which nutrient concentrations increase quickly), and greatly reduces the rate of upwelling and thus the delivery of nutrients to the surface. Primary productivity can drop by a factor of 5 to 20 as a result[24]. In the Peruvian upwelling zone, this leads to a reduction in anchovy harvests[4,24]. It is noteworthy, however, how rapidly these systems can return to their ground state[25]. Reductions in biological productivity in these two upwelling regimes are also apparent over multidecadal timescales during the positive phase of the Pacific Decadal Oscillation, characterized by a warming of northwestern Pacific surface waters every 20–30 years[4,26]. In addition, ocean eddies — present at varying levels of intensity in all eastern boundary

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current systems — can import nutrient-poor waters into these systems, potentially lowering productivity[27].

Anthropogenic alterations

Set against this backdrop of significant natural variability, human-induced changes in the ocean environment are starting to emerge in coastal upwelling zones.

In today's ocean, the signal of human fossil fuel combustion is being progressively superimposed upon the naturally low pH of newly upwelled water (Fig. 2b). Anthropogenic acidification has been detected in the California current system, and is expected to become detectable in the near future in other upwelling regimes[5]. Also off California, increased CO_2 from anthropogenic sources has resulted in the undersaturation of recently upwelled surface sea water with respect to the calcium carbonate mineral aragonite in many near-shore locales. Aragonite undersaturation can affect the viability of marine organisms whose shells are formed from this type of calcium carbonate, such as pteropods, planktonic molluscs that are an important food source for salmon[28].

The waters of the Californian coastal upwelling regime are projected to acidify rapidly[4]. Indeed, most shallow shelf areas in the region are expected to become undersaturated with respect to aragonite within the next 20–30 years, as the solubility of this biogenic calcium carbonate mineral is inversely related to seawater acidity[29]. Ultimately, accelerated acidification is likely to lead to calcite undersaturation of surface waters in coastal upwelling regimes as well, despite the fact that this form of calcium carbonate is much less soluble than aragonite.

Hand in hand with progressive acidification, oxygen minimum zones associated with coastal upwelling regimes may intensify and expand (Fig. 2b). Long-term declines in oxygen concentrations have been documented at intermediate depths in the large oxygen minimum zone in the eastern tropical Pacific[30]. In addition, deoxygenation is occurring at shallower depths (<100–200 m) throughout coastal upwelling ecosystems. Persistent decadal-scale declines in dissolved oxygen levels and significant shoaling of the oxygen minimum zone have also been observed in the Southern California Bight[31]. Comparison of an ensemble of models suggests that this phenomenon of oxygen loss may not be uniform among the various upwelling regions, and that oxygen levels could even increase in some areas[32].

A possible consequence of extreme hypoxia events is sulphide production — microbial dissimilatory reduction of seawater sulphate — leading to fish and shellfish kills, and attendant damage to economically important harvested resources. Indeed, sulphide has been reported in the upwelling waters off the coasts of Peru[33] and Namibia[34]. Recently, severe and unprecedented hypoxic events have been reported over the continental shelf along the Oregon coast, leading to the replacement of benthic invertebrates with mats of sulphide-oxidizing bacteria[35]. In the summer of 2012, shallow-water hypoxia was reported along the Washington coastline[36].

Looking into the future, long-term warming and reduced ventilation due to stratification of the North Pacific are projected to act in concert to reduce oxygen concentrations in the ultimate source water for the California current system[30], enhance acidification and increase delivery of upwelled nitrate to the surface[37]. Similar phenomena may be expected to occur in the Atlantic eastern boundary current systems. Enhanced productivity during upwelling events, and the resultant amplification of the vertical flux of recently fixed carbon, would contribute directly to the expansion of the underlying oxygen minimum zones. In addition to physical changes such as increased stratification, the increased productivity that results from ongoing anthropogenic nutrient enrichment of coastal waters is also expected to lead to the expansion of oxygen minimum zones[38,39].

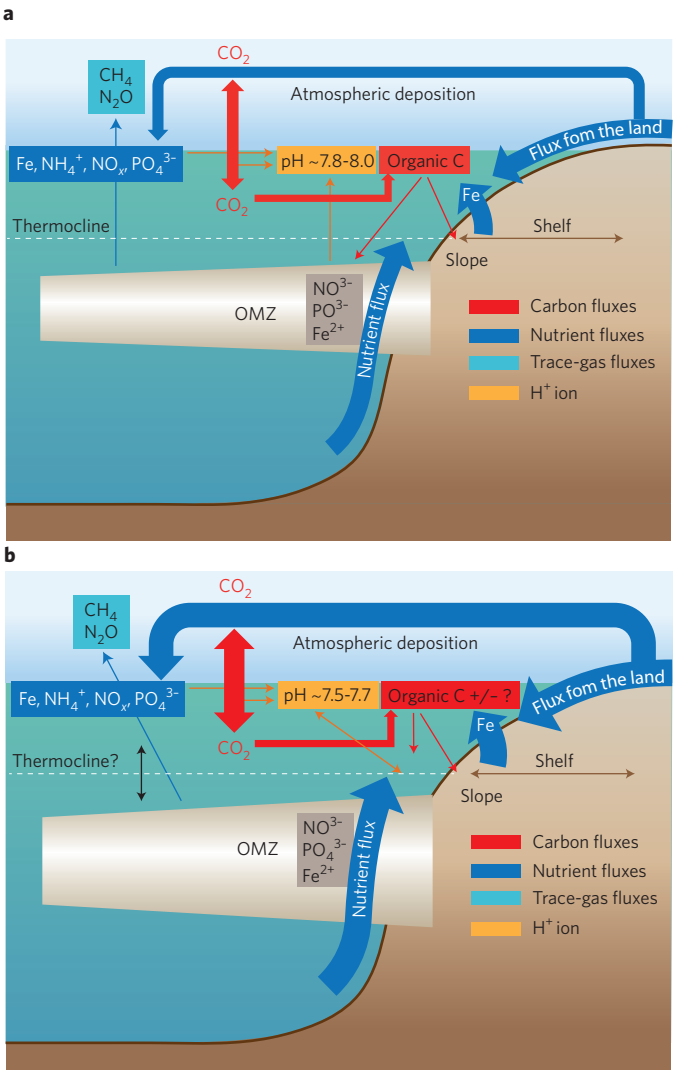

Figure 2 | Trends in the biogeochemistry of coastal upwelling systems. Shown are carbon, nutrient and trace gas fluxes, together with pH, upwelling intensity and oxygen minimum zone (OMZ) extent under current conditions (**a**) and impending changes (**b**).

Climate warming has been projected to intensify coastal winds, and thereby the upwelling of nutrient-rich waters[40]. Increased upwelling intensities have been observed in the Peru[41], Benguela[42] and California current systems[43] over the past half century. However, increased upwelling is not apparent in all analyses of these systems[37,44,45].

Other pathways of nutrient delivery to zones of coastal upwelling, including atmospheric deposition, riverine and groundwater discharge and runoff, are also set to shift. Despite episodic nutrient pulses, terrestrially derived nutrient inputs to coastal systems are relatively small, compared with upwelling inputs, at present[46]. The relative importance of riverine nutrients to coastal areas will vary regionally as the climate changes; in general, increases in precipitation are predicted at higher latitudes, and decreases in many (but not all) lower-latitude regions[47]. At present, the relative importance of atmospheric deposition to the nutrient budget and upwelling systems varies greatly among regions. Atmospheric inputs are relatively minor along the coastal upwelling systems of the west coast of the Americas and southern Africa. In the Canary upwelling system, in contrast, atmospheric

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inputs represent a major source of nutrients, particularly iron[48]. However, the atmospheric abundance of aerosols and dust — an important source of iron to the ocean — are projected to decline by up to 60% following a doubling of atmospheric carbon dioxide concentrations in current climate model simulations[49]. An ever-increasing flux of nitrogen from both the atmosphere and terrestrial sources to the coastal oceans is expected, primarily due to an intensification of fertilizer and energy production, particularly near to human population centres[50–52].

Perturbations to primary production and carbon cycling

Increases in carbon dioxide concentrations directly stimulate the productivity of some photoautotrophic microbes, particularly nitrogen-fixing cyanobacteria[53], and should therefore bolster primary production in coastal upwelling zones. Increased nutrient inputs from upwelling[37] or terrestrial and atmospheric sources[38,49,51,54] should also stimulate primary production in regions where nutrients are limiting, such as in the vicinity of the Canary upwelling system[55].

In contrast, acidification may impede primary production in some cases; growth of coastal phytoplankton declines with decreasing pH, although individual species exhibit a broad range of sensitivities[56]. The negative effects of acidification on primary productivity could be exacerbated by interactions with other environmental variables, including high light levels[57]. Acidification can also inhibit mineralization of coccolithophorids, a calcite-producing phytoplankton group[28], and potentially cause shifts in phytoplankton physiology and community structure[58].

Fertilization of coastal phytoplankton with anthropogenic carbon and additional nutrients may lead to the export of biogenic carbon with higher carbon to nitrogen ratios[59]. Bacterial remineralization of this excess vertical organic carbon flux could lead to further oxygen depletion in the subsurface ocean of coastal upwelling zones[60]. Such an augmented organic carbon flux could potentially offset the reduction in vertical carbon flux resulting from a reduction in calcification. The experimental evidence for this scenario, however, is not yet conclusive[58].

Oxygen minimum zones are inhospitable to most complex multicellular animals (metazoans), strongly skewing biological communities towards prokaryotes and low-oxygen-tolerant unicellular eukaryotes. Future ocean deoxygenation could favour expansion of microbial food webs, because many protozoan grazers such as ciliates are capable of anaerobic respiration. Conversely, trophic interactions dominated by obligately aerobic zooplankton grazers may decline in importance[61]. Increasing hypoxia may therefore affect not only 'bottom-up' biogeochemical controls on the productivity of phytoplankton and other microbes, but also the nature of 'top-down' control by their consumers.

Methane cycling in coastal upwelling ecosystems represents another aspect of the carbon cycle that may respond to anthropogenic perturbation. In the central Chilean upwelling system, a substantial amount of methane consumption is associated with dark carbon dioxide fixation[62]. Furthermore, there is a clear inverse relationship between methane and oxygen in the upwelling zone off the coast of Namibia[63], and a possible hotspot of methane production in the upwelling region off northwest Africa[64]. As methane is a potent greenhouse gas[65], increased production would serve as a positive feedback on climate warming.

Altered iron constraints

The extent to which additional nitrate and carbon dioxide stimulate primary production will depend, in part, on the availability of iron. In areas of the California upwelling system where shelf-derived supplies of iron are abundant, a typical ratio of upwelled iron to nitrate of 8 nmol:20 μmol allows near-complete drawdown of nitrate by phytoplankton[17]. In iron-limited areas with narrow continental shelves and typical upwelled iron: nitrate ratios of 2 nmol:20 μmol, resident diatoms quickly use up the iron, leaving at least 10 μM unused nitrate[17]. However, a 50% increase in upwelled fluxes of nitrate, as postulated[37] for the year 2100, without a corresponding increase in iron concentrations would alter the upwelled ratio in currently iron-sufficient parts of the California upwelling water to ~8 nmol:30 μmol. This could potentially drive even these iron-replete regions into an iron-limited state, with perhaps 10 μM nitrate left behind, once phytoplankton have fully depleted the iron.

Possible increases in upwelling intensity[40] would be likely to exaggerate existing iron biogeochemical gradients. Iron-limited areas of the Californian and Peruvian upwelling regimes lacking wide continental shelves would become even more deficient in this essential micronutrient, as increased upwelling rates would increase nitrate but not iron supplies. Any increase in the velocity and frequency of upwelling might therefore increase the productivity gradient between iron-limited and iron-replete regions of the coastal ocean.

Other global change variables, such as the expansion and shoaling of oxygen minimum zones, will also need to be factored into the evolving picture of iron biogeochemistry in coastal upwelling systems. In contrast to the very limited solubility of oxidized iron(III) in oxic sea water (<1 nM), the reduced iron(II) that predominates under hypoxic conditions is highly soluble and can reach concentrations that exceed 50 nM. If deoxygenation is pronounced at the depths where upwelled water originates, such as is the case in the northern Peru upwelling today, rich supplies of iron can be brought to near-surface phytoplankton communities through upwelling[19]. Currently intensifying shallow hypoxia in the California upwelling system[31,35] could therefore provide an important new source of iron to primary producers, even in areas that lack extensive continental shelves and are currently iron-limited. However, iron could also become less available to phytoplankton in an acidified ocean, owing to protonation of the organic ligands that bind most of the dissolved iron in aerobic sea water and keep it soluble[66].

Clearly, increases in upwelling intensity, nitrate concentrations, hypoxia and acidification can all potentially affect the degree to which iron constrains phytoplankton growth in coastal upwelling regimes. The individual effects of these various climate-driven influences have the potential to reinforce each other or cancel each other out. As such, we cannot yet reliably predict the net effect on iron availability. Future impacts are likely to be larger in the Californian and Peruvian upwelling zones, where iron limitation is currently an important control on phytoplankton growth, than in the relatively iron-replete Canary and Benguela systems.

Nitrogen gain versus loss

The co-varying multiple stressors associated with environmental change in coastal upwelling areas are likely to have a direct effect on nitrogen cycling processes in these systems[67]. The first step of nitrification, the microbial oxidation of ammonia to nitrite[68], is very sensitive to inhibition. Moreover, it can be a source of nitrous oxide. Nitrification is an obligately aerobic process and the first step, ammonium oxidation, is carried out primarily by archaea[69]. Sites of enhanced nitrification are found near oxic–anoxic interfaces such as those associated with the periphery of oxygen minimum zones[70]. Hence, the predicted growth of oxygen minimum zones[30,31] is likely to expand and intensify nitrification, as well as nitrous oxide fluxes associated both with this process and with denitrification (see below)[71]. Other environmental change factors may also affect nitrification in coastal upwelling systems. Recent studies have shown that marine nitrification is sensitive to increasing acidity. Small experimental reductions in pH (0.04–0.14) realistically simulating

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expected near-future trends consistently yield lower rates of nitrification at a range of oceanic sites, including coastal California waters[72]. Although it is possible that current nitrifier communities may be replaced by more acid-tolerant groups in the future, it is notable that in experimentally acidified freshwater lake systems, inhibition of nitrification persists for as much as a decade, until the pH is artificially restored to higher, pre-experimental levels[73].

Growing oxygen minimum zones imply a potential expansion of the anaerobic habitats associated with the conversion of oxidized forms of nitrogen to dinitrogen gas, namely denitrification and anammox. Denitrification is generally (although not exclusively) associated with heterotrophic respiratory processes, whereas anammox bacteria are autotrophic. The relative importance of these two processes seems to differ substantially among the major oxygen minimum zones[14]. The anammox reaction seems to dominate reactive nitrogen removal in the oxygen minimum zones associated with the Benguela and Peru upwelling systems[11,13,74]. The factors responsible for differences in the dominant mechanism of reactive nitrogen loss are not fully understood. For denitrification, the primary control has been shown to be availability of labile organic carbon in the oxygen minimum zones of the tropical north and south Pacific[14]. Rates of anammox in the eastern tropical south Pacific are also sensitive to organic matter export[75], because the process depends on a source of ammonium from organic matter degradation[74]. Thus, variations in physical forcing and nutrient inputs that affect primary production could affect the magnitude of both denitrification and anammox in oxygen minimum zones associated with upwelling systems. This could represent a negative stabilizing feedback in these systems, as fixed nitrogen is removed. Whether climate-related stressors affect the relative balance between these two removal pathways *in situ* remains to be seen.

Nitrogen fixation can also be a surprisingly active process in coastal upwelling systems and associated oxygen minimum zones[76,77]. The highest rates of surface water nitrogen fixation at the southern California San Pedro Ocean Time-series station were observed during the winter, when upwelling occurs[76]. Measurable rates have also been detected below the euphotic zone and in the hypoxic zone, as has been shown off the coast of Chile[77]. Massive blooms of the diazotrophic cyanobacterium *Trichodesmium* were reported in August 2004 seaward of the northwest Africa/Canary upwelling area during a period of active upwelling[78]. All-time record surface water temperatures were apparent in the vicinity of the bloom, along with an abundance of aerosol dust throughout the region.

The availability of phosphate and iron and their controlling effects on nitrogen fixation seems to vary between systems[79]. In the vicinity of the Canary coastal upwelling ecosystem, phosphate and iron appear to co-limit nitrogen fixation[55]. Through much of the eastern Pacific, phosphate may be in excess relative to nitrogen fixer requirements, particularly in surface waters just downstream of coastal upwelling ecosystems and their associated oxygen minimum zones[22]. Modelling efforts have attempted to assess future shifts in the distribution of nitrogen fixation in the world's oceans as a result of increasing surface water temperatures[80] as well as increasing dust (and hence iron) inputs[54]. However, the resolution of these models is often insufficient to discern dynamics in coastal upwelling ecosystems.

The nitrogen cycle is inherently complex, and we are still developing our basic understanding of its processes in eastern boundary upwelling systems. The net impact of the suite of anthropogenic stressors discussed on nitrogen gain and loss in coastal upwelling regimes remains to be seen.

Future trends and critical questions

Anthropogenic stressors affecting the biogeochemistry of eastern boundary upwelling systems involve much more than just ocean warming and acidification[81]. From a microbial perspective, intensifying hypoxia, stratification-driven changes in nutrient supplies and light intensities, and changes in atmospheric iron and nitrogen deposition are all critically important components of the rapidly changing ocean environment, particularly those near to human population centres. It will be the net consequences of these shifts — and their as yet poorly understood synergisms or antagonisms (Supplementary Table S1) — that will determine the new shapes of elemental cycles in these systems in a future ocean. The relatively steady, progressive changes in mean state being imposed by human activities will be integrated with existing rapid fluctuations natural to these systems. For instance, pH is sure to remain highly variable in coastal upwelling regimes, yet will cycle around a decreasing mean value in a future acidified ocean.

One key issue is whether coastal upwelling will intensify[40–42], or whether upper-ocean warming and the increased stratification will prevail. It will also be important to determine how external nutrient inputs will vary with climate change[38,49,50,54], and how the quality and quantity of carbon exported out of the surface ocean varies as a result of shifts in food web structure and composition. Future trends in iron supply are particularly hard to predict, as iron biogeochemistry is highly responsive to upwelling intensity, acidification, hypoxia, rainfall patterns and anthropogenic source terms. The degree to which iron limits phytoplankton productivity varies among the four main upwelling regimes, as well as temporally and spatially within each one. The changing balance of nitrogen gain and loss needs to be better understood as it directly affects new production[74], and therefore carbon sequestration.

As may be evident from our analysis, the scientific effort expended on the related but individually distinct upwelling ecosystems has been widely variable. The coastal California systems, being near to major oceanographic research centres and resources, have received the most attention. The Canary and Peruvian/Humboldt upwelling systems had been less intensively examined, until recently. Least studied is the Benguelan upwelling system. Each of the main coastal upwelling systems has its own unique characteristics (for instance, shelf width, bathymetry, benthic environment, seasonal upwelling intensity and extent of external nutrient inputs), the response to future environmental perturbations will clearly not be uniform among systems. There is also a need for more modelling work on all four of these systems; the proliferation of *in situ* coastal observation programmes, such as the Argo network focused on the oxygen minimum zone in the eastern tropical Pacific (http://omz.udec.cl/), will provide essential data for advancing these efforts.

The biota of coastal upwelling systems are inherently resilient, experiencing great natural physical and chemical variability over a broad range of timescales. Knowing the limits to this intrinsic resilience will be critical in attempting to manage these ecosystems. From feeling the early biogeochemical impacts of ocean acidification to reacting to hypoxia-driven changes in the marine nitrogen cycle, these 'new production engines' of the oceans may be among the first marine ecosystems to respond to the complex and interconnected changes that our species is imposing on the global environment

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Additional information

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Competing financial interests

The authors declare no competing financial interests.

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