



Effects of Ocean Acidification on Marine Photosynthetic Organisms Under the Concurrent Influences of Warming, UV Radiation, and Deoxygenation

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The oceans take up over 1 million tons of anthropogenic CO₂ per hour, increasing dissolved pCO₂ and decreasing seawater pH in a process called ocean acidification (OA). At the same time greenhouse warming of the surface ocean results in enhanced stratification and shoaling of upper mixed layers, exposing photosynthetic organisms dwelling there to increased visible and UV radiation as well as to a decreased nutrient supply. In addition, ocean warming and anthropogenic eutrophication reduce the concentration of dissolved O₂ in seawater, contributing to the spread of hypoxic zones. All of these global changes interact to affect marine primary producers. Such interactions have been documented, but to a much smaller extent compared to the responses to each single driver. The combined effects could be synergistic, neutral, or antagonistic depending on species or the physiological processes involved as well as experimental setups. For most calcifying algae, the combined impacts of acidification, solar UV, and/or elevated temperature clearly reduce their calcification; for diatoms, elevated CO₂ and light levels interact to enhance their growth at low levels of sunlight but inhibit it at high levels. For most photosynthetic nitrogen fixers (diazotrophs), acidification associated with elevated CO₂ may enhance their N₂ fixation activity, but interactions with other environmental variables such as trace metal availability may neutralize or even reverse these effects. Macroalgae, on the other hand, either as juveniles or adults, appear to benefit from elevated CO₂ with enhanced growth rates and tolerance to lowered pH. There has been little documentation of deoxygenation effects on primary producers, although theoretically elevated CO₂ and decreased O₂ concentrations could selectively enhance carboxylation over oxygenation catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase and thereby benefit autotrophs.

Overall, most ocean-based global change biology studies have used single and/or double stressors in laboratory tests. This overview examines the combined effects of OA with other features such as warming, solar UV radiation, and deoxygenation, focusing on primary producers.

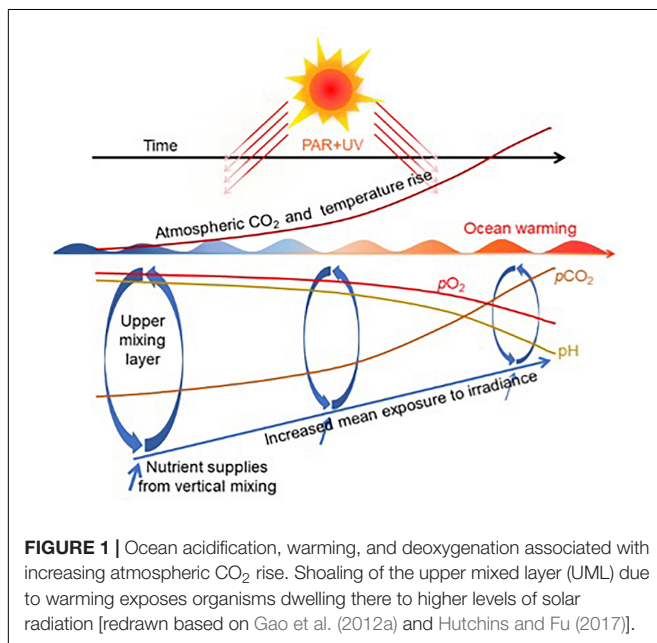
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INTRODUCTION

Fossil fuel burning, tropical deforestation, and altered land use have caused the atmospheric CO₂ concentration to rise from 280 ppmv before the Industrial Revolution to 409 ppmv in 2018. These increases in atmospheric CO₂ of about 0.5% per year¹ result in global warming and, after dissolving in surface seawater, also cause ocean acidification (OA). Ocean warming induces stratification and shoaling of the upper mixed layer (UML). This hinders the injection of nutrients from deeper layers and also causes the organisms dwelling in the UML to be exposed to increased daily exposures of PAR and UV radiation (Gao et al., 2012a; Hutchins and Fu, 2017; **Figure 1**). O₂ solubility in seawater decreases due to increasing temperatures, leading to global ocean deoxygenation and contributing to the expansion of anoxic zones. Intensified stratification also results in deoxygenation of deeper water due to lack of ventilation, and human nutrient over-enrichment can deplete dissolved oxygen in coastal regions by promoting excessive levels of primary production and consequent elevated bacterial respiration (Schmidtke et al., 2017; Breitburg et al., 2018).

Most investigations into the biological and ecological effects of OA have been based on experiments using single species

¹https://www.esrl.noaa.gov/gmd/ccgg/trends/gl_trend.html



under controlled conditions, and data on the effects of OA on complex communities in natural environments are relatively limited (Riebesell and Gattuso, 2015; Boyd et al., 2018), although experiments at volcanic seeps and using mesocosms have shown that increased pCO₂ benefits some algae more than others and that lower carbonate saturation states harm some algae more than others. So while most benthic algae are tolerant of OA conditions, changes in carbonate chemistry cause large changes in algal community composition and ecosystem function (Hofmann et al., 2012; Hall-Spencer and Harvey, 2019). The combined effects of OA with other drivers, such as warming, increased UV exposure or deoxygenation, are expected to alter marine communities with effects that differ regionally. Further research is needed to plan for the risks associated with the ways in which OA is interacting with warming, UV radiation, and deoxygenation (Boyd et al., 2018).

Marine photosynthetic organisms account for about half of global photosynthetic carbon fixation (Falkowski and Raven, 2013). Across most of the oceans, the dominant photoautotrophs are mainly microalgae and cyanobacteria, with macroalgae and seagrasses making a higher proportional contribution in coastal environments. These organisms are influenced by both increasing pCO₂ and declining pH with ongoing OA. While increased CO₂ availability can potentially stimulate photosynthesis, stress due to the associated pH drop may be deleterious. This is especially a problem during night in the absence of photosynthetic CO₂ removal and with respiratory CO₂ release, which may lead to more pronounced impacts of acidification during the night period.

While there are many reports in the literature on the responses of primary producers to OA [see recent reviews by Hutchins and Fu (2017) and Boyd et al. (2018) and references therein], contradictory results have often been documented in relation to different phytoplankton species or communities (Gao and Campbell, 2014; Hong et al., 2017). In macroalgae, most studies show algal tolerance of diel pH fluctuations and benefits from rising pCO₂ (Gao et al., 1991, 1993; Cornwall et al., 2012, 2015); in calcifying micro- and macro-algae, it is widely accepted that OA reduces their calcification (Gao et al., 1993; Riebesell et al., 2000; Feng et al., 2008; Gao et al., 2009; Gao and Zheng, 2010; Sinutok et al., 2011). Nevertheless, changes in temperature, light, UV, and nutrient availability are known to modulate the responses of photosynthetic organisms to OA. In this review, we first briefly consider the individual effects of major components of global climate changes (OA, warming, etc.) and then go on to focus on recent advances in our understanding of the effects of OA when combined with other factors, including results from different experimental protocols or algae from different biogeographic

regions, and analyze underlining processes and/or mechanisms with special reference to interactive effects of OA with warming, UV, nutrient availability, and dissolved O₂ levels.

Ocean Acidification

Since the Industrial Revolution the ocean has been absorbing anthropogenic CO₂ emissions, and this absorption is currently running at an average rate of over 1 million tons per hour (Sabine et al., 2004), a process that leads to OA. This alters marine carbonate chemistry, changing the concentration ratios of different inorganic carbon species (CO₂, HCO₃⁻, CO₃²⁻) and reducing the saturation state of CaCO₃ (Ω).

$$\Omega = ([Ca^{2+}] \times [CO_3^{2-}]) / K_c,$$

where K_c is the product of $[Ca^{2+}] \times [CO_3^{2-}]$ when the CaCO₃ solution is saturated.

Since the Ca²⁺ concentration of seawater is relatively stable (about 10 mM), Ω mainly depends on the concentration of CO₃²⁻, as shown in the above equation. Increased dissolution of CO₂ into seawater results in increased concentrations of dissolved CO₂, HCO₃⁻, and H⁺ and decreased concentration of CO₃²⁻, leading to a decrease in the saturation state of CaCO₃. The concentration of CO₃²⁻ varies in different regions, depending mainly on temperature and salinity; for instance, the concentration of CO₃²⁻ in polar waters is only about 41% of that in tropical waters, with the former decreasing faster than the latter under the influence of OA (Orr et al., 2005). In the geological past, mass extinctions of marine life have been associated with OA events, and the contemporary seawater pH and carbonate saturation state are declining faster than it has been in about the last 300 million years (Hönisch et al., 2012; Garbelli et al., 2017). Therefore, OA has been ranked as a major research priority in the NOAA Ocean Exploration 2020 report².

Ocean acidification is known to reduce calcification of many calcifying organisms. In coralline algae, elevated pCO_2 reduces calcification of *Corallina pilulifera* due to lowered pH and decreased concentration of carbonate (Gao et al., 1993). This species exhibits higher calcification rates during daytime than during the night period and increases its calcification with increased dissolved inorganic carbon concentration when pH is maintained constant (Gao et al., 1993). In contrast, another coralline alga, *Jana rubens*, when transplanted to lower pH site near a CO₂ seep, showed much reduced photochemical efficiency, implying its calcification might be reduced due to reduced photosynthetic energy supply, though the short-term exposure did not bring about significant change in calcification (Porzio et al., 2018). It is clear that OA causes a decrease in competitiveness and fitness for coralline algae compared to brown and turf algae.

Ocean acidification can reduce the content of biogenic silica in diatoms (Milligan et al., 2004; Tatters et al., 2012; Xu et al., 2014), although this response to high CO₂ does not appear to be shared by all diatoms (Qu et al., 2018; Li et al., 2019). Cellular silicification is known to influence

predation rates by zooplankton as well as the number of fecal pellets (Liu et al., 2016). Acidification thus might reduce the settling of particulate organic carbon (POC) by lowering diatom silicification and density. With increasing pCO_2 and acidification, surface diatom abundance in the oligotrophic South China Sea decreases, resulting in decreased primary productivity (Gao et al., 2012b). On the other hand, under nutrient replete conditions, growth of diatoms tends to be enhanced (Wu et al., 2014). In coastal eutrophic water, increased partial pressure of CO₂ increased primary production of phytoplankton assemblages dominated by diatoms in a mesocosm study (Huang et al., 2018).

Different diatom species may have entirely different responses to OA, mostly due to differences in species or phenotypes. Under OA conditions, the coastal diatom *Thalassiosira weissflogii* shows a faster particulate carbon production rate, whereas a pelagic species, *Thalassiosira oceanica*, grows slower, implying that under diel pH fluctuations the large coastal diatom appears to be more tolerant of the pH decline (Li et al., 2016). While there are species-specific responses to OA, diatoms with lower CCM efficiencies showed more pronounced responses to OA in terms of growth rate (Shi et al., 2019).

Natural gradients of CO₂ at volcanic seeps show that a reduction in mean seawater pH from 8.1 to 7.8 results in around a 30% reduction in animal biodiversity compared with only a 5% reduction in algal diversity, although the algal communities are completely changed due to dissolution of calcified algae and shellfish (Hall-Spencer et al., 2008; Fabricius et al., 2011; Agostini et al., 2018). Ecological impacts seen at CO₂ seeps contrast to those caused by OA events in the geological past when the species and communities of marine organisms were unlike those that we see today (Hönisch et al., 2012).

Seawater uptake of CO₂ at volcanic seeps changes seawater chemistry in a process that is a natural analog for anthropogenic OA (González-Delgado and Hernández, 2018). The seeps create steep gradients in seawater carbonate chemistry with falling pH, falling carbonate, and increasing bicarbonate levels with increasing proximity to the seabed release of CO₂ (Linares et al., 2015). The biological effects of this acidification are found at seep systems worldwide, allowing investigations into the underlying mechanisms that drive community level responses (Cornwall et al., 2017; Connell et al., 2018). As phytoplankton drift into these seep systems calcareous coccolithophores are damaged and dissolve, but this is a shock response to rapid changes in seawater carbonate chemistry (Ziveri et al., 2014). The microphytobenthos at shallow-water seeps, on the other hand, is exposed to long-term acidification over multiple generations. Diatom- and cyanobacteria-dominated biofilms proliferate at shallow-water marine CO₂ seeps. Broad scale analysis of diversity has shown that microphytobenthic communities in high CO₂ water are substantially modified compared with ambient conditions, with a stimulation of diatom growth on sand, mud, bedrock, glass, and plastic substrata (Johnson et al., 2015).

Marine volcanic seeps reveal ecological responses to moderate increases in pCO_2 that retain natural pH variability (Foo et al., 2018). They show the consequences of long-term exposure to acidified waters as well as the implications of more frequent low pH excursions for a wide range of organisms

²<https://oceanexplorer.noaa.gov/oceanexploration2020>

(Agostini et al., 2018). At Mediterranean CO₂ seeps, invasive macroalgal taxa such as *Sargassum*, *Caulerpa*, and *Asparagopsis* species thrive, whereas calcareous macroalgae are sensitive to acidification (Figure 2). This causes algal community shifts, fleshy algal dominance, and a loss of coastal biodiversity (Hall-Spencer et al., 2008). Although most macroalgae are resilient to the effects of OA, with only around a 5% loss in species diversity at levels projected under IPCC RCP 8.5, shifts in algal community composition greatly alter habitats (Porzio et al., 2011; Enochs et al., 2015). Increased availability of bicarbonate and *p*CO₂ stimulates primary production in seagrasses and in some algae but not others, depending on their physiology (Cornwall et al., 2017). In areas sheltered from wave action, this increases carbon fixation and the standing stock of seagrasses and large phaeophytes (Linares et al., 2015; Sunday et al., 2017). However, acidification lowers ecosystem resilience in more exposed conditions, such that only microalgal biofilms and weedy small turf algae persist at high CO₂ levels after storms (Hall-Spencer and Harvey, 2019).

Studies in areas with naturally high levels of CO₂ show that coastal ecosystems are altered especially if elevated DIC is combined with high levels of nutrients (Celis-Plá et al., 2017; Rastrick et al., 2018). In upwelling areas such as Namibia and Peru, these acidified waters have productive food webs that support major fisheries. However, if the acidification is strong enough to cause periods of carbonate under-saturation this is detrimental to shellfish fisheries and calcareous biogenic reefs. Very similar patterns are seen in tropical, sub-tropical, and temperate coastal systems, with stimulated diatom growth and opportunistic algal dominance, calcareous biogenic habitat degradation, and loss of biodiversity. This potentially lowers the resilience of coastal habitats to a cluster of other drivers associated with climate change (global warming, sea level rise, increased storminess), increasing the risk of marine regime shifts and the loss of critical ecosystem functions and services, though it should be noted that in some areas, such as the coastal waters of

California, upwellings bring elevated levels of nutrients as well as CO₂ into surface waters, leading to high levels of primary productivity (Ryther, 1969; Pauly and Christensen, 1995). Modeling suggests enhancement of some coastal upwellings in the future, and also indicates that the ability to predict flow on effects to ecosystems is complicated by the range of contributing factors and scales involved (Xiu et al., 2018).

There are obvious diel and seasonal variations in the chemistry of coastal seawaters (Dai et al., 2009; Wang et al., 2014), and coastal seawater acidification often coincides with hypoxia, which is frequently enhanced after algal blooms (Zhai et al., 2012). For example, in the Bohai Sea off northern China, pH drops by 0.29 units (H⁺ concentration doubles) during the summer period (Zhai et al., 2012). Nevertheless, it is predicted that by the end of the 21st century OA will cause the average pH of the oceanic surface waters to decrease from the preindustrial level of 8.2 down to 7.8 (H⁺ concentration rises by 150%) (Gattuso et al., 2015; Guy et al., 2015), endangering marine organisms and ecosystem services (Broadgate et al., 2013).

Ocean Warming

Since the Industrial Revolution, increasing global average temperature has been linearly correlated with atmospheric CO₂ concentrations (IPCC, 2013a). Since the 1970s, the oceans have absorbed over 90% of Earth's heat gain, leading to ocean warming (Gattuso et al., 2015). Ocean warming can be detected to a depth of 1,000 m (Levitus et al., 2000), and during the past century the global ocean surface temperature has increased by about 1°C (Fischetti, 2013). By the end of the 21st century, the average Earth surface temperature is predicted to rise by 2–4 °C (Gattuso et al., 2015). Compared with many other regions in the world, the marginal waters in the East China Sea and the South China Sea have shown a faster rate of temperature increase over the past 50 years (Bao and Ren, 2014; Williams et al., 2016; Cai R. et al., 2017), though polar regions have warmed fastest (Wassmann, 2015). Global warming is predicted to have other consequences such as increasing storm activity that can influence marine biota. For instance, a rise in temperature of 1°C has been shown to increase the number of typhoon events by up to 25% (Bigg and Hanna, 2016). At the same time, the frequency of marine heat waves, prolonged discrete anomalously warm water events (Hobday et al., 2016), has been predicted to increase tens of fold with a 3.5°C rise in sea surface temperature (Frölicher et al., 2018). Marine heat waves are postulated as drivers of ecological disasters such as the triggering of toxic algal blooms along the North American west coast (McCabe et al., 2016).

Temperature is a key factor affecting enzyme activity and metabolism. Metabolic rates usually increase with temperature up to a maximum value and thereafter rapidly decline, exhibiting an energy activation to deactivation transition. Shallow water marine organisms can be exposed to diurnal, seasonal, and current-driven sudden changes in temperature. These changes involve the thermocline, tides, typhoons, and cloud cover as well as the long-term changes due to natural climate cycles and human activities (IPCC, 2013b). Ocean warming affects organism physiology (Pörtner, 2008; Sinclair et al., 2016) and changes biogeographic boundaries,

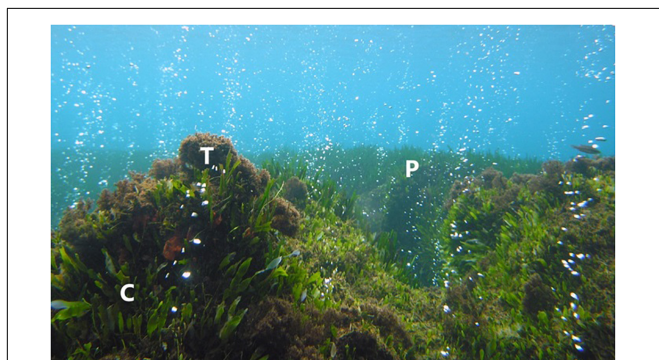


FIGURE 2 | Bubbles of CO₂ rising from the seafloor at a depth of 1 m at a volcanic seep off Ischia Island, Italy (40°43.84' N, 13°57.08' E). At a mean pH of 7.8 turf algae (T), seagrass *Posidonia oceanica* (P) and green seaweed *Caulerpa prolifera* (C) cover the seabed. Epiphytic and epilithic coralline algae are scarce, yet they are abundant 300 m away from the CO₂ seep where the seawater returns to the normal mean of pH 8.1. (Photo taken by J. Hall-Spencer).

community composition, and phenology (Hutchins and Fu, 2017). In laboratory experiments, increasing temperature below optimal values can increase phytoplankton growth (Fu et al., 2014; Summers et al., 2016; O'Donnell et al., 2017; Jiang et al., 2018). However, on a global scale, warming may decrease primary productivity due to nutrient limitation driven by enhanced stratification of the upper mixing layer (UML); it may also enhance fixed carbon remineralization by heterotrophic microorganisms and so reduce the strength of the ocean carbon sink (Danovaro et al., 2016; Cavan et al., 2019).

Deoxygenation

One additional effect of ocean warming is that it decreases the solubility of oxygen (and gases generally) in seawater. In oceanic and coastal waters the dissolved oxygen content has declined over the past 50 years (Schmidt et al., 2017; Breitburg et al., 2018). In addition, shoaling of the UML or enhanced ocean stratification reduces ventilation from the surface to deeper layers, further exacerbating the deoxygenation phenomenon. As POC sinks, marine bacteria feed on it, consuming O_2 and releasing CO_2 . This results in an oxygen minimum zone at depths of 500–600 m in the eastern tropical Pacific (Brewer and Peltzer, 2009). Over the past 50 years the depth of a hypoxic layer ($<2 \text{ mg } O_2 \text{ L}^{-1}$) in the Pacific Ocean has shoaled from 400 to 300 m, and the dissolved oxygen content has decreased significantly (Whitney et al., 2007) due to sea surface warming (Keeling et al., 2010); and ocean deoxygenation has been recently shown to cause deterioration in a number of processes including biogeochemistry and ecosystem function (Breitburg et al., 2018). In coastal regions deoxygenation is driven mainly by eutrophication, leading to excess oxygen consumption and the development of hypoxia and “dead zones.” However, decreasing solubility of O_2 through warming can exacerbate this process.

Most marine organisms need O_2 in their metabolic processes. When the dissolved O_2 concentration is below a certain value, these organisms suffer from stressed respiration, and hypoxic events may lead to the death of many organisms. For different organisms, the half lethal concentration (LC_{50}) of dissolved O_2 is different, and the critical value for one organism might be several times that for others. In typical anoxic zones, the oxygen content is below $2 \text{ mg } L^{-1}$ and the hypoxia is usually associated with high pCO_2 and low pH. In coastal ecosystems, the frequency of hypoxia is increasing at a rate of about 5.5% per year due to the interaction between deoxygenation and eutrophication (Vaquer-Sunyer and Duarte, 2008), which is responsible for a faster rate of OA in coastal, compared to oceanic waters (Cai et al., 2011; Breitburg et al., 2018). Eutrophication frequently leads to algal blooms. When these blooms collapse, the algae die, leading to enhanced organic carbon loads, the breakdown of which, through microbial action, contributes to anoxia and in turn renders spawning grounds for fish such as herring untenable. In terms of biogeochemical impacts, deoxygenation promotes denitrification, reducing the concentration of nitrate and affecting the ocean N cycle, primary productivity, and the efficiency of the marine biological carbon pump (Hutchins and Fu, 2017).

Lower oxygen levels would be expected to have the most effect in photoautotrophic species on the ratio of oxygenase to carboxylase activity of the CO_2 -fixing enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Diminished oxygen concentrations favor the carboxylase activity of Rubisco and diminish photorespiratory activity. However, in practice low oxygen concentrations, i.e., below air-equilibrium levels, appear to have little effect on physiology and growth of algae, though levels above air-equilibrium can be damaging (Black et al., 1976; Drechsler and Beer, 1991; Beer et al., 2000; Kitaya et al., 2005, 2008; Kliphuis et al., 2011; Raso et al., 2012; Haas et al., 2014). Kim et al. (2018) showed a stimulation of photosynthetic rates of the seagrass *Zostera marina* at sub-saturating, but not saturating, light intensities when oxygen concentrations dropped from 231 to $8 \mu\text{mol } O_2 \text{ L}^{-1}$. At the same time respiration rates dropped fivefold at the lower oxygen level. In part, the lack of effect of low oxygen is likely to be due to the presence in most algae of active CO_2 concentrating mechanisms (CCMs), which maintain a sufficiently high $CO_2:O_2$ ratio at the active site of Rubisco to minimize oxygenase activity and photorespiration (Giordano et al., 2005). Of the other oxygen consuming reactions found in algae and cyanobacteria, only the Mehler reaction and glycolate oxidase (in those organisms that possess that enzyme rather than glycolate dehydrogenase) have a $K_{0.5} O_2$ high enough to be affected by oxygen concentrations around air equilibrium (Beardall et al., 2003; Raven and Beardall, 2005). Cytochrome oxidase for example has a $K_{0.5} O_2$ of $\leq 2 \mu\text{mol } O_2 \text{ L}^{-1}$ (see Table 3.2 of Raven and Beardall, 2005).

However, to date there have been no studies on the interaction between low oxygen concentration and other stressors associated with ocean global changes. In the study of Kim et al. (2018) low oxygen resulted in a 2.8-fold downregulation of γ -carbonic anhydrase (γ -CA) genes, which they suggest may play a role in bicarbonate transport rather than as a standard CA. It might be expected that elevated CO_2 (OA) and diminished O_2 concentrations lead to further downregulation, though this has yet to be tested. Anoxia also stimulates nitrogen fixation in the marine cyanobacterium *Trichodesmium* (Staal et al., 2007), with aerobic conditions leading to N_2 fixation being limited by the availability of reducing equivalents, a result interpreted by Staal et al. (2007) as suggesting a competition for electrons between nitrogenase and respiration when oxygen is present.

Stratification and Increased Exposure to UV

It is commonly known that the UML is much shallower during summer than in winter. For example, in pelagic areas of the South China Sea, the UML can be over 30 m shallower in summer than in winter (Liu et al., 2007). In addition to less wind and storm mixing than in winter, the higher temperatures in summer are mainly responsible for the enhanced stratification.

On a global scale, ocean warming enhances stratification in the upper oceans due to reduced advective mixing, leading to shoaling of the UML. Such stratification hinders the upward transport of nutrients from deeper layers. Consequently, phytoplankton cells are exposed to a reduced availability of

nutrients, provided that the contribution from other sources such as nitrogen fixation or deposition into the oceans from run-off and atmospheric sources is unaltered by global climate changes. Phytoplankton cells dwelling in a shallower UML are exposed to higher doses of UV radiation since they cannot actively move downward to deeper waters (Jin et al., 2013). Since the vertical migration path for cells within a shallower UML is shorter, they experience much higher daytime average or integrated levels of solar radiation [see reviews by Riebesell and Tortell (2011) and by Gao et al. (2012b)]. Since UV irradiances can penetrate as deep as 80 m in the pelagic ocean, down to the middle or lower layers of the euphotic zone, phytoplankton cells are inevitably exposed to increased levels of UV radiation due to enhanced stratification [see the review by Gao et al. (2012b) and literature cited therein].

UV radiation is divided into UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (<280 nm). The stratospheric ozone layer completely absorbs UV-C (the most biologically harmful band). The major portion of the UV-B is also absorbed by ozone, mainly in the stratosphere. Only a small fraction of UV-B reaches the Earth's surface through the stratosphere and the upper troposphere. On the other hand, most of the UV-A and visible light reaches the surface of the Earth. In the subtropics, UV-B radiation reaching the sea surface usually accounts for <1% of the total sunlight energy; UV-A and visible light (PAR: 400–700 nm) account for 7–8 and 40–50%, respectively, with infrared radiation making up the balance. At noon, the UV-B:UV-A:PAR ratio is about 0.5:16:100. The UV-B:PAR ratio is highest at noon, while the UV-A:PAR ratio remains unchanged during the day (Gao, 2018). Solar radiation is reduced by moisture in the atmosphere, sea surface reflectivity, and inorganic and organic substances in the water, and has obvious latitudinal, diel, and seasonal dependencies. UV-B radiation increases by 2% for each 1% decrease in stratospheric ozone concentration (Kerr and McElroy, 1993). Ozone destruction has been curbed, with stratospheric ozone expected to return to pre-1980 levels by the mid-21st century (Plummer et al., 2010). However, global warming, the presence of trace gases (Ossó et al., 2011) and changes in atmospheric circulation might increase UV-B level at low latitudes by 2–3% (Williamson et al., 2014).

Many oceanographic biological observations of primary productivity have neglected the influence of UV radiation because of traditional recommendations for use of transparent vessels, which, unless made of quartz and UV-transparent materials, are mainly glass or polycarbonate bottles that are opaque to UV wavelengths. With progressive ocean climate changes, more attention should be given to the interactive impacts of UV with other global environmental change drivers (Häder and Gao, 2015).

Even though the irradiance of UV-B is only a few percent (in tropical and subtropical areas, <1%) of the total solar UV reaching the Earth's surface, it is the most deleterious wavelength band encountered by photosynthetic organisms dwelling in the photic zone. UV-B can damage proteins, lipids, and other bioactive components of the cells (Ganapathy et al., 2017). One of the main targets is photosynthetic electron transport, since UV-B damages the D1 protein in photosystem II, reducing the photosynthetic capacity (García-Gómez et al., 2016). This

damage is repaired by removing the faulty protein and replacing it with a newly synthesized molecule. This enzymatic process is favored by increased temperature (Gao et al., 2008). When moving actively or passively in the UML, cells are affected most near the surface and use the time in deeper water closer to the thermocline for repair (Helbling et al., 2003). Another important target of solar UV-B is DNA (Gao et al., 2008; Rajneesh et al., 2018). UV-B radiation mainly induces the formation of cyclobutane pyrimidine dimers, leading to mutations and cell death if these are not removed by a photolyase which uses the energy of UV-A and blue light to split the dimers (García-Gómez et al., 2014).

Many prokaryotic and eukaryotic phytoplankton as well as macroalgae synthesize UV-absorbing substances, such as scytonemin (only cyanobacteria) and mycosporine-like amino acids (MAAs), which convert the energy of short-wavelength UV radiation into heat before it can hit sensitive targets (Singh et al., 2008). Another mechanism of damage by UV radiation is the production of reactive oxygen species (ROS) such as peroxides, superoxide, hydroxyl radicals, and singlet oxygen which can oxidatively damage proteins, lipids, and other cell structures (Williamson et al., 2019). ROS can be detoxified either enzymatically (e.g., by superoxide dismutase, catalase, peroxidase) or non-enzymatically by antioxidants (e.g., thiols, ascorbic acid, glutathione, carotenoids) (Martínez, 2007; Goiris et al., 2015).

In addition to the negative effects of UV radiation, it is known that moderate levels of UVA radiation enhance primary production by enhancing photosynthetic light use efficiency, as shown in the photosynthetic rate vs. PAR curves determined in the presence and absence of UV radiation (Gao et al., 2007a). When PAR was filtered out, UVA stimulates carbon fixation of phytoplankton assemblages in coastal waters of the South China Sea, and addition of UV-B reduces the carbon fixation (Gao et al., 2007a). UV-induced inhibition of photosynthetic carbon fixation in surface seawater increases with distance from the coast toward the open ocean, probably due to differences in attenuation coefficient, phytoplankton community structure, and nutrient availability as well as mixing rate (Tedetti and Sempéré, 2006; Li et al., 2011). Faster mixing reduces UV-induced photosynthetic inhibition (Helbling et al., 2003; Jin et al., 2013).

INTERACTIONS BETWEEN FACTORS ASSOCIATED WITH CLIMATE CHANGE

OA and Solar Radiation (PAR and UVR)

Changing PAR levels modulate diatom responses to OA. For instance, when three diatom species were grown under different levels of sunlight, lowered pH with elevated CO₂ stimulated growth under low to moderate levels of light, but inhibited it under high levels (Gao et al., 2012a; **Figure 3**). However, such a reversed response to OA with increasing light levels was not found in coccolithophores, which showed enhanced growth rates (with reduced calcification) under the elevated pCO₂ under all tested PAR levels (Jin et al., 2017;

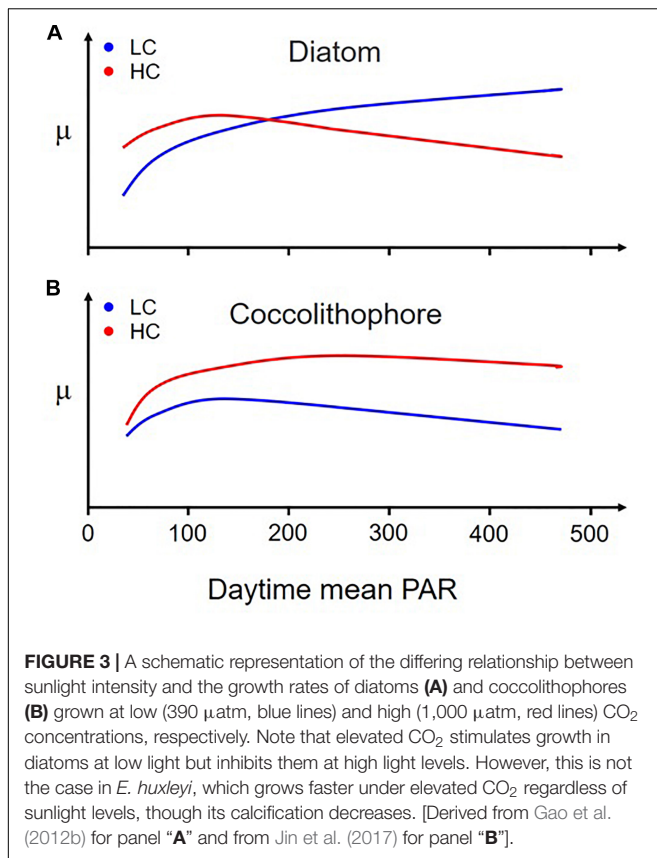


Figure 3. Likewise, Feng et al. (2008) found that the interactive effects of high light and elevated CO₂ on a subtropical coccolithophore increased growth rates but strongly decreased calcification.

Solar UV radiation may interact with OA to affect primary producers. To date, most OA effects have been observed under UV-free light conditions, either under indoor artificial light or under solar radiation with vessels that are opaque to UV irradiances. Therefore, relatively little information is available on this aspect. OA exacerbates the impact of UV on calcification in the coccolithophore *Emiliania huxleyi* (Gao et al., 2009) and on calcification of a coralline alga (Gao and Zheng, 2010). Decreased thickness of the calcified layer increased cellular exposure to UV radiation and consequently led to enhanced photoinhibition of photosynthesis by UV (Gao et al., 2009; Gao and Zheng, 2010). Elevated CO₂ increased the sensitivity of freshwater lake phytoplankton populations to UV-B (Sobrinho et al., 2009) and also exacerbated the harmful effect of UVR on PSII function in the marine diatom *T. weissflogii* through reducing the PsbD removal rate and the ratio of Rubisco to PsbA during UVR exposure (Gao et al., 2018c). In contrast, the marine microalga *Nannochloris atomus* increased its growth in response to elevated CO₂ with an insignificant photosynthetic response to UVR (Sobrinho et al., 2005). Furthermore, the $rETR_{max}$ of *Corallina officinalis* was stimulated by elevated CO₂, and exposure to UVR led to further stimulation (Yildiz et al., 2013). The divergence between

these findings may be due to the differences in species or light intensity.

Interactions Between OA Effects and Nitrogen Fixation and With the Availability of Other Nutrients

Marine diazotrophs, N₂-fixing cyanobacteria such as *Trichodesmium* spp., play an important role in remedying N-limitation in oligotrophic waters (Capone and Carpenter, 1982; Sohm et al., 2011; Hutchins et al., 2015). *Trichodesmium* has a high abundance in the oligotrophic China Sea, frequently forming blooms in the East and South China Seas (Chen et al., 2014). Because of the N₂ fixation capacity of *Trichodesmium* and subsequent microbial cycles, biologically available nutrients can be replenished, which promotes growth of phytoplankton, thus enhancing primary and secondary productivities, playing an important role in driving the marine biological CO₂ pump (Hutchins and Fu, 2017).

Numerous studies have demonstrated that N₂ fixation increases under elevated CO₂ levels in nutrient-replete cultures of both the filamentous species *Trichodesmium* (Barcelos e Ramos et al., 2007; Hutchins et al., 2007, 2013, 2015; Kranz et al., 2009, 2010; Levitan et al., 2010a,b; Eichner et al., 2014; Walworth et al., 2016a,b) and the unicellular *Crocospheera* (Fu et al., 2008; Garcia et al., 2013a,b). However, there are a few studies showing that OA decreased N₂ fixation of the diazotroph (Hong et al., 2017; Luo et al., 2019). While there are disputes over the positive and negative effects of elevated CO₂ concentrations on N₂ fixation in *Trichodesmium* (Hutchins et al., 2017), it is generally agreed that severe iron (Fe) limitation cancels out (or even reverses) the positive effects of CO₂ on cyanobacterial diazotrophs (Fu et al., 2008; Shi et al., 2012; Walworth et al., 2016a; Hong et al., 2017). In contrast, growth limitation by phosphorus (P) appears to operate independently, regardless of any effects of changing pCO_2 (Hutchins et al., 2007; Garcia et al., 2013b; Walworth et al., 2016a). A nearly decade-long experimental evolution study with *Trichodesmium* selected under two CO₂ levels yielded an unexpected result: the increases in growth and N₂ fixation commonly observed under exposure to short-term high CO₂ conditions became irreversible after selection under OA conditions for several years. Thus, high CO₂-adapted cultures retained their increased N₂ fixation and growth rates indefinitely, even when moved back to lower pCO_2 levels (Hutchins et al., 2015; Walworth et al., 2016a). This constitutive upregulation occurs through the process of “genetic assimilation,” whereby following extended natural selection, traits such as elevated nitrogen fixation rates transition from being physiologically plastic responses to being genetically fixed ones (Walworth et al., 2016b).

Nevertheless, OA can sometimes show different effects on other nitrogen fixing taxa. For heterocystous cyanobacteria, studies showed that OA can either promote nitrogen fixation (Wannicke et al., 2012) or inhibit it (Czerny et al., 2009). Ship-board studies during research cruises have shown that OA treatment can either stimulate N₂ fixation (Lomas et al., 2012), did not bring any significant effects, or negatively affected

cyanobacterial N₂ fixation (Böttjer et al., 2014; Gradoville et al., 2014). These field experiments are difficult to interpret though, as N₂-fixing cyanobacteria such as *Trichodesmium* are famous for surviving poorly in shipboard incubations, and Gradoville et al. (2014) were unable to demonstrate consistent limitation of N₂ fixation not only by CO₂ but also by any other potentially limiting resources, including iron and P. There are inherent differences in CO₂ affinities and growth responses among strains and species of N₂-fixing cyanobacteria (Hutchins et al., 2013), and different culturing or light conditions can lead to discrepancies in experimental results. Nevertheless, it is clear that species-specific differences in responses of N₂-fixing cyanobacteria to OA may lead to changes in community structure and diversity of marine diazotrophs in future oceans (Hutchins et al., 2013; Gradoville et al., 2014).

UV radiation has been shown to adversely affect cyanobacterial N₂ fixation, including inhibiting development of heterocysts and reducing chlorophyll content in the fresh water N₂ fixer *Anabaena* sp. (Gao et al., 2007b). In the marine diazotroph *Trichodesmium*, UV radiation reduces rates of photosynthesis, N₂ fixation, and growth (Cai X. et al., 2017), though moderate or low levels of UV-A may be stimulating. Another recent study showed that growth, N₂ fixation, and CO₂ fixation rates of the *Trichodesmium* strain IMS 101 and *Crocospaera* WH0005 were both negatively affected by UV-B exposure (Zhu et al., 2019). This inhibition was much greater for *Trichodesmium* IMS 101, which fixes N₂ during the day, than for *Crocospaera*, which fixes N₂ only during the night; however, another *Trichodesmium* isolate (GBR) was much more resistant to UV-B inhibition (Zhu et al., 2019). To the best of our knowledge, however, nothing has been documented on the interactive effects of OA and UV radiation on marine diazotrophs.

OA and Warming

Laboratory studies have shown that combined OA and warming have different ecological and physiological effects on different species. For example, in the picoplanktonic cyanobacterium *Synechococcus*, warming and OA together promote its growth, but they have no effects on *Prochlorococcus* (Fu et al., 2007). Similarly, simultaneous OA and warming by 4°C promoted the growth of the diatom *Skeletonema* (Kremp et al., 2012), but had no obvious effects on *Thalassiosira* and *Chaetoceros* (Hyun et al., 2014). Under acidification and warming conditions, the growth rate and calcification of the coccolithophore *Coccolithus* decreased (Schlüter et al., 2014), and OA and warming together lowered the optimum growth temperature and maximum growth rate of *E. huxleyi* (Listmann et al., 2016). However, other work shows that warming combined with partial pressures of 20–6,000 μ atm CO₂ increases the production rate of particulate inorganic carbon and POC of *E. huxleyi* and *Gephyrocapsa oceanica* (Sett et al., 2014). In a natural North Atlantic Bloom community, simultaneous OA and warming stimulated coccolithophore growth while at the same time significantly reducing their calcification (Feng et al., 2009).

In general, acidification and warming have usually been found to promote the growth and nitrogen fixation rates of

open ocean diazotrophic cyanobacteria such as *Trichodesmium* and *Crocospaera* (Hutchins et al., 2007, 2019; Fu et al., 2014; Hutchins and Fu, 2017). Warming alone also favors the growth of globally important open ocean nitrogen-fixing cyanobacteria taxa, as long as temperatures do not exceed ~32–33°C. The stimulatory effects of higher temperatures and pCO₂ together have been suggested to be roughly additive (Hutchins et al., 2007; Levitan et al., 2010a). Temperatures in the low-latitude tropical oceans are predicted to eventually exceed optimum growth levels in many regions, leading to potential future thermal exclusion of these N₂ fixers from core parts of their current biogeographic range (Breitbarth et al., 2007; Thomas et al., 2012; Fu et al., 2014; Jiang et al., 2018).

Ocean acidification and warming are known interactively to affect key physiological performances of macroalgae. For instance, the respiratory coefficient (the rate of change of the respiratory rate as the temperature increases) in *Sargassum fusiforme* increases under OA conditions, indicating that acidification and warming additively increase the respiratory rate (Zou et al., 2011). Furthermore, warming and OA synergistically enhance reproduction events and shorten the generation span in the “green tide” alga *Ulva rigida* (Gao et al., 2017, 2018b), suggesting more severe green tides may occur in future oceans.

Research on reef-building coralline algae shows that acidification causes a reduction in their calcification, and warming and acidification together further lower the calcium quality (Martin and Hall-Spencer, 2017). Acidification and warming together have been shown to improve the nitrogen fixation of nitrogen-fixing cyanobacteria (Hutchins et al., 2007). In the Bay of Kiel, warming is believed to drive changes in the phytoplankton community structure and an increase in the zooplankton biomass; under *in situ* water temperature conditions, the predation rate of zooplankton decreases due to the negative effects of acidification (Paul et al., 2016). For some marine algae, the combined effects of acidification and warming are manifested as acidification changing their capacity to cope with temperature changes and alterations in the range of their optimum survival temperature. For example, the calcification rate of the coral *Acropora pulchra* is controlled by temperature and acidification (Comeau et al., 2016). For the warming and acidification effects, there may be regional differences due to different biotic populations and physical and chemical environments. This phenomenon needs to be further verified and its mechanisms need to be discussed.

Temperature also influences the responses of algae to UV radiation. We might expect *a priori* that temperature would exert an effect on net UV-B impacts by affecting enzyme-driven repair mechanisms (which are strongly temperature dependent) more than photochemical damage (since photochemistry is temperature independent). In the model diatom *Phaeodactylum tricornutum*, elevated temperature increased the repair rate of PSII either under ambient or elevated CO₂ levels in the presence of UV-A or UV-B (Li and Gao, 2012). On the other hand, elevated temperature increased inhibition of photochemical quantum yield by UVR in freshwater phytoplankton assemblages from Patagonia in Argentina (Villafane et al., 2013); however, increased

temperature in this region helped to counter the magnitude of daytime yield decrease during the onset of a phytoplankton bloom (Helbling et al., 2013).

Recently, it has been suggested that ocean warming would affect the marine biological carbon pump (MBP) and microbial carbon pump (MCP) as well as their interactions (Jiao and Zheng, 2011). However, it has been shown that acidification has no effect on the composition of dissolved organic carbon (DOC) in a plankton ecosystem (Zark et al., 2015), while other findings show that acidification promotes the production of POC (Czerny et al., 2013). Whether acidification and warming will produce combined effects and further affect the composition and lability of DOC and the production of POC in different waters is not yet known. In the oceans, most DOC will be converted to CO₂ in the short term through bacterial action; however, some DOC resists bacterial breakdown and survives for a long time (for hundreds or even thousands of years), playing a steady role in the carbon sink (Jiao et al., 2010). Therefore, it is particularly important to understand the carbon sink/source processes in marine organisms and the response of assimilation and dissimilation to acidification and warming. Nevertheless, most of the present research findings on the combined effects of the warming and acidification have been obtained under constant laboratory conditions, which may not reflect natural conditions where factors such as light exposure, temperature, and concentrations of dissolved CO₂ can vary even on short time scales. They are still quite controversial, and the combined effects and their mechanisms are still unclear.

Nutrient Availability and Interactions With Other Components of Global Change

With progressive ocean warming, intensified stratification of the UML is expected, and consequently, upward transport of nutrients across the thermocline will be reduced. Therefore, phytoplankton cells dwelling in this layer are expected to be exposed to decreasing availability of nutrients. Levels of nutrients and/or ratios of different nutrients are known to affect algal physiology. Interactions among nutrient availability, warming, and OA are thus to be expected. For instance, in the diatom *Thalassiosira pseudonana*, nitrate limitation interacts with OA and warming, leading to increased respiration and decreased photosynthetic rates and growth (Li et al., 2018). Likewise, in the large centric diatom *Coscinodiscus*, OA and warming together reduced growth affinity for nitrate, and so increased nitrate concentrations required for growth (Qu et al., 2018).

In the diatom *Chaetoceros didymus*, OA had no effect on growth rate under N-replete conditions, but stimulated growth under N-limitation. N-limitation and OA also interacted to increase sinking rates, which were less affected under normal CO₂ conditions when N supply was high (Mannfolk, 2016). Toxic microalgae are influenced by interactive effects of elevated CO₂ and nutrient supply. Fu et al. (2010) showed that under P-limited conditions, toxin production by *Karlodinium veneticum* was greatly stimulated by elevated CO₂. Tatters et al. (2013) found saxitoxin production by the dinoflagellate *Alexandrium*

was greatly increased by the combination of OA and P limitation, but warming to some extent counteracted these effects. Tatters et al. (2012) reported that elevated CO₂ enhanced domoic acid production by the harmful bloom diatom *Pseudo-nitzschia fraudulenta* under nutrient-limited conditions. In general, it seems that the combination of OA with nutrient limitation could lead to much more toxic and damaging blooms of harmful algae in the future ocean.

In addition to microalgae, coastal eutrophication can also lead to macroalgal blooms, including green tides and golden tides. *Ulva*-dominated green tides and *Sargassum*-dominated golden tides have increased worldwide in recent years (Smetacek and Zingone, 2013). Kang and Chung (2017) reported that ammonium enrichment stimulated growth of *Ulva pertusa*, with further stimulation when combined with OA. Gao et al. (2017, 2018b) showing that the combination of eutrophication, OA, and warming enhanced the settlement, germination, and growth of *U. rigida*. The combination of phosphate enrichment and OA also enhanced growth rate in the golden tide alga *Sargassum muticum* (Xu et al., 2017). These findings suggest that the rising trend of macroalgal blooms that occurred in Chinese coastal waters (Liu et al., 2013) may correlate with ocean climate changes. Eutrophication is also likely to interact with other stressors, negatively impacting coral reef systems (Bell et al., 2014).

Nutrient limitation favors smaller-celled organisms such as the picophytoplankton *Micromonas* and *Ostreococcus* and nanophytoplankton such as the coccolithophorid *E. huxleyi* by virtue of their higher surface area to volume ratio. Nutrient supply and concentrations in the UMLs of the oceans are often reported as being drivers of variation in the size structure and taxonomic composition of phytoplankton communities (Eppley and Peterson, 1979; Chisholm, 1992; Coale et al., 1996; Finkel et al., 2010). With warming-enhanced stratification, such cells will be subjected to higher average exposures to solar radiation, including periodic acute exposure to high fluxes of UV-B close to the surface, which is known to do more harm to smaller cells (Wu et al., 2015).

As stated earlier, it is generally agreed that severe iron (Fe) limitation cancels out (or even reverses) the positive effects of CO₂ on cyanobacterial diazotrophs (Fu et al., 2008; Shi et al., 2012; Walworth et al., 2016a; Hong et al., 2017). In contrast, growth limitation by P appears to operate independently, regardless of any effects of changing pCO₂ (Hutchins et al., 2007; Garcia et al., 2013b; Walworth et al., 2016a). *Trichodesmium* cultures simultaneously co-limited by both Fe and P grow considerably faster than either Fe-limited or P-limited cells (Garcia et al., 2015; Walworth et al., 2016a). However, their phenotype relative to acidification is more similar to Fe-limited than P-limited cultures, in that high CO₂ does not increase their physiological rates. These high CO₂, Fe/P co-limited cells express a unique complement of proteins that is quite distinct from those seen in low CO₂ or single nutrient-limited cultures, representing perhaps the manifestation of a genetically determined compensatory mechanism (Walworth et al., 2016a).

Limitation by the micronutrient iron (Fe) is a key control of marine nitrogen fixation and, along with other important variables, Fe supplies are also changing with a shifting climate

(Hutchins and Boyd, 2016). Unlike CO₂ and P, though, interactions between Fe availability and temperature in N₂ fixers do not appear to be linear and additive (Jiang et al., 2018). Warming from 27 to 32°C decreases growth and N₂ fixation rates in Fe-replete *Trichodesmium*, but 32°C is the temperature at which maximum rates are observed in Fe-limited cultures. Consequently, warming across this temperature range nearly erases the negative effects of Fe limitation by greatly increasing cellular iron use efficiencies (moles N fixed per mol cellular Fe per hour) by up to 470%. The net effect of this non-linear interaction between Fe and warming in a global biogeochemical model is a predicted ~22% increase in total global marine N₂ fixation over the next 90 years. This potential alleviation of Fe limitation by warming throughout large parts of the ocean (particularly the oligotrophic Pacific) could also enable currently Fe-limited diazotroph populations to respond positively to concurrently increasing atmospheric pCO₂ (Jiang et al., 2018).

Nutrient limitation appears to increase the sensitivity of algae to UV-B radiation. N-limitation for instance can impair the capacity of cells to synthesize UV-B-screening compounds such as MAAs or influence the ability of cells to carry out repair [particularly of the D1 protein in PSII (Shelly et al., 2002)]. P-limitation also appears to decrease the capacity for repair processes under UV-B (Heraud et al., 2005). Similar effects of nutrient availability on UV sensitivity have also been reported in macroalgae. Zheng and Gao (2009) reported higher MAA concentrations in *Gracilaria lemaneiformis* under nitrate enrichment, which led to significantly decreased UVR-induced inhibition of growth and photosynthesis. In the same organism UV-B significantly reduced the net photosynthetic rate, but this was alleviated by enrichment with ammonia (which also stimulated the accumulation of UV-absorbing compounds) (Xu and Gao, 2012). Similar data have been reported for *Porphyra* (Korbee et al., 2005) and *Gracilaria tenuistipitata* (Barufi et al., 2011). In the red alga *G. lemaneiformis*, UV-induced inhibition of photosynthesis and growth was exacerbated under P-limited conditions (Xu and Gao, 2009). These data and other work cited by Figueroa and Korbee (2010) imply that in macroalgae as well as microalgae, low N-availability enhances UVR sensitivity of photosynthesis and growth, perhaps by decreasing the capacity to minimize damage through MAA synthesis. There are many reports in the literature on this topic, as reviewed by Beardall et al. (2014). However, how such nutrient-related responses to UVR are modulated under the additional stress of OA is not yet known.

OA Effects Under Multiple Stressors

Ocean acidification is a global phenomenon but is usually overlaid by pronounced regional variability modulated by local physics, chemistry, and biology (Boyd et al., 2018; Hurd et al., 2018). Biotic responses to multiple environmental drivers depend on the response to the single dominant driver, and the chance of a driver of larger effect being present increases with the number of drivers (Brennan and Collins, 2015). In addition to the effect of OA together with one additional stressor, the combined effects of OA with two drivers have also been investigated, although relatively fewer papers addressing this can be found. As mentioned above, enhanced stratification due to warming

leads to decreased upward transport of nutrients from deeper layers and this in turn can lead to nutrient limitation. Therefore, the effects of OA and warming under changing nutrient levels are of general significance. Li et al. (2018) showed that OA or warming did not affect the specific growth rate of *T. pseudonana* under nitrate-replete conditions, but both conditions reduced its growth rate under nitrate-limited conditions, suggesting that a decreased upward transport of nutrients due to enhanced stratification could act synergistically with OA and warming to reduce its growth. Under influences of natural environmental conditions, a mesocosm test showed that the toxic microalga *Vicicitus globosus* has a selective advantage under OA, increasing its abundance in natural plankton communities in oligotrophic subtropical waters, which has had a dramatic impact on the plankton community, disrupting trophic transfer of primary produced organic matter (Riebesell et al., 2018).

In regard to macroalgae, both OA and warming increased germination and juvenile growth in a green tide alga *U. rigida* regardless of nutrient availability, while the stimulatory effect of OA and warming was reduced by nitrate limitation (Gao et al., 2017). In addition to physiological performance, OA, warming, and nitrate abundance synergistically increased fatty acid content in *U. rigida* (Gao et al., 2018a), affecting the food quality of this green macroalga. Some macroalgae growing near CO₂ seeps appear to use more CO₂ rather than bicarbonate except coralline algae, whose abundance declined (Cornwall et al., 2017). In coastal waters, where nutrient availability is high and diel pH fluctuation is typical, most fleshy macroalgae appear to benefit from increasing CO₂ concentration, while calcifying algae are harmed by OA (Gao et al., 1993; Gao and Zheng, 2010; Sinutok et al., 2011). It seems that algae respond differentially to OA under influences of multiple stressors. Obviously, more studies are needed in order to visualize comprehensive pictures of how marine photosynthetic organisms in different ecosystems respond to the concurrent ocean climate changes.

FUTURE PERSPECTIVES

Microalgae are known to exhibit evolutionary responses to elevated CO₂ over hundreds of generations, including downregulated CCMs in a green alga (Collins et al., 2006), irreversible capacity of reduced calcification in a coccolithophorid (Tong et al., 2018), smaller cell size and decreased respiration and photosynthesis in a model diatom (Li et al., 2017), and increased cellular N/C ratio in *E. huxleyi* (Jin et al., 2013). The evolutionary response of a diazotroph to OA treatment led to irreversible enhancement of growth and N₂ fixation over hundreds of generations, driven by “genetic assimilation” of plastic traits into adaptive ones (Hutchins et al., 2015; Walworth et al., 2016a). Adaptation to high CO₂ is also associated with the imprint of cytosine methylation of the *Trichodesmium* genome (Walworth et al., 2016b).

Phytoplankton also shows obvious evolutionary responses to warming. Cultured diatoms from tropical waters increased their optimal growth temperature, maximum growth rate, or maximum critical thermal limit after 200–600 generations of

acclimation to elevated temperature, suggesting a fast adaptation to ocean warming (Jin and Agustí, 2018). A decade-long experiment in outdoor mesocosms showed warm-adapted green alga, *Chlamydomonas reinhardtii*, had higher optimal growth temperatures, higher competitive fitness, and increasing rates of net photosynthesis compared to its control (Schaum et al., 2017).

Ocean acidification and warming can interactively disturb the advection of nutrients and trace elements in the ocean systems, thereby affecting biogeochemical processes and ecosystem stability. Coastal ecosystems and their services are often degraded due to the effects of human activities and global ocean changes. However, these possible macro-changes need micro-mechanism-based explanations to enhance forecasting reliability. Organisms in the upper pelagic zone of the oceans face multiple environmental stresses, such as OA, warming, lack of nutrients (except in coastal waters near human influences), and increased exposures to UVR (Figures 1, 4). OA and warming together could additively increase respiratory rate, since respiration increases with temperature, and acclimation to OA-induced acid-base disturbance requires extra energy to allow cells to cope with. As a result, OA and warming may cumulatively affect the marine biological pump (MBP) and the MCP, which is suggested to be sensitive to warming (Jiao and Zheng, 2011). Nevertheless, the net effects of OA and warming on MBP/MCP are still quite uncertain.

Deoxygenated waters typically coincide with low pH (Cai et al., 2011); therefore, the combined effects of OA and deoxygenation are of ecological relevance. Along with progressive OA and warming, a consequent drop in the pO_2/pCO_2 of seawater is unavoidable (Figures 1, 4). This ratio has been defined as the respiratory index for animals and may be defined as the photorespiratory index for photosynthetic organisms. Although lower values of pO_2/pCO_2 are harmful or fatal to many aerobic

organisms, decreased pO_2/pCO_2 ratios may benefit primary producers since their photosynthetic carboxylation enzyme, Rubisco, catalyzes both carboxylation and oxygenation reactions (Gao and Campbell, 2014). Theoretically, lower pO_2/pCO_2 values will likely correlate with higher carboxylation and lower photorespiration.

Primary producers provide basic energy flows for ecosystems, and consequently, they are closely related to activities of other organisms. The habitable waters for marine organisms are degrading under progressive OA and other ocean climate changes, such as ocean warming, stratification, deoxygenation, and enhanced exposure to UV radiation (Figure 4; Gao et al., 2012a; Hutchins and Fu, 2017). Based on documented data and theoretical reasoning, a habitable niche degradation hypothesis can be established as follows (Figure 4): phytoplankton food quality is supposed to decline in response to OA (Riebesell et al., 2007; Jin et al., 2015), leading to reduced energy supply to grazers; at the same time, motile organisms dwelling within the UML, such as zooplankton or fish, tend to move to deeper layers to avoid exposure to harmful solar UV radiation (Rhode et al., 2001) and high levels of PAR that traps more heat; however, stressful suboxic or hypoxic and acidified seawater below the thermocline may act as a barrier preventing some species from moving deeper. As a result, the habitable niches for such organisms will shrink, and their habitat will degrade. This might exacerbate the effects of other anthropogenic stressors such as over-fishing, and so contribute to declining fish catches in previously productive waters. As a result, more algal blooms will be expected in eutrophic waters with increasing levels of

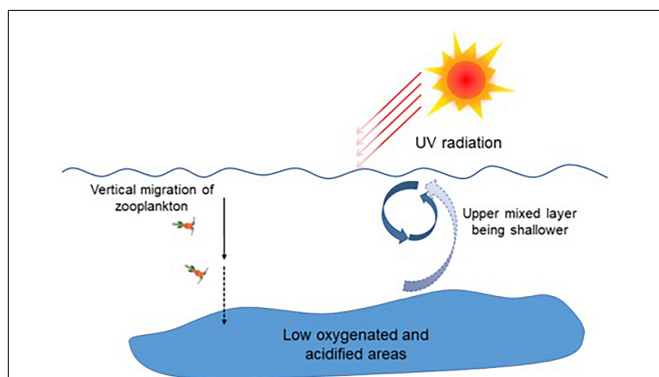


FIGURE 4 | Ocean climate changes and the habitat degradation hypothesis. Ocean warming, acidification, and deoxygenation associated with increasing atmospheric CO_2 rise. A shoaled UML due to warming exposes organisms dwelling there to higher levels of solar radiation. The habitable niche degradation hypothesis: phytoplankton abundance and community structure can be altered within the UML under multiple stressors associated with ocean climate changes; and motile organisms dwelling within the UML are stressed due to increased exposure to solar UV radiation and high levels of PAR, which traps more heat; however, the low O_2 and pH waters below the UML hamper downward migration. (Re-drawn based on Gao, 2018).

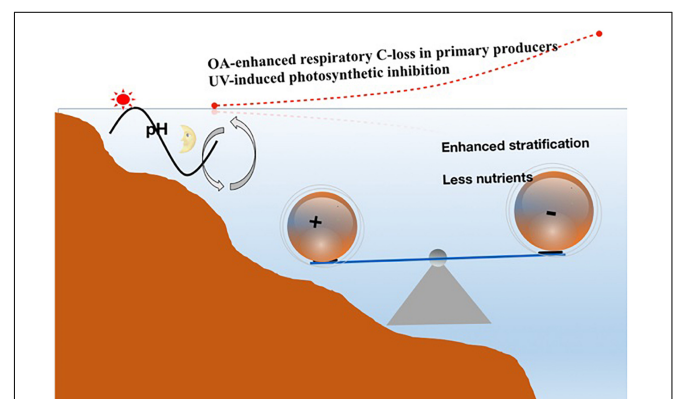


FIGURE 5 | Illustration of the hypothesis that OA and UV synergistically induce carbon loss in surface primary producers, based on the observational data on UV impacts (Li et al., 2011) and results that smaller diatoms decrease their growth rate under OA and nutrient-limitation conditions (Li et al., 2018). Diel pH changes in highly productive coastal waters are shown with a sun and a moon symbol to indicate pH rise with increasing photosynthetic C removal during daytime and pH decline with respiratory CO_2 release during night. Note that benthic macroalgae contribute greatly to the diel pH fluctuations, and that their growth and photosynthesis are usually stimulated by OA. Furthermore, they are more tolerant of solar UV radiation [see the review by Gao et al. (2012) and literature therein]. The symbols “+” and “-” indicate more positive effects due to OA and UV in coastal non-nutrient-limited waters and negative effects due to OA and UV in oligotrophic offshore waters, where shoaling of UMLs owing to warming reduces upward transport of nutrients from deeper layers.

ocean climate changes and decreasing top-down pressure. This hypothesis could be tested by laboratory microcosm or mesocosm experiments in combination with *in situ* investigations.

Effects of OA can be positive, neutral, and negative under influences of other drivers or in different ecosystems where chemical and physical environments are contrastingly different. As discussed above, in coastal waters, fleshy macroalgae such as *Porphyra* sp. (Gao et al., 1991), *Gracilaria* sp. (Gao et al., 1993), *Ulva* (Gao et al., 2016), and *Sargassum* sp. (Xu et al., 2017), usually increase their growth in response to elevated $p\text{CO}_2$ levels up to 1,000–2,000 μatm , showing tolerance to acidification. Larger diatom species are found to show stimulated growth (Wu et al., 2014) or enhanced carbon assimilation rate (Li et al., 2016), while smaller diatoms tend to show reduced photosynthetic and growth rates under influence of OA (Wu et al., 2014), nitrate limitation, and temperature rise (Li et al., 2018). On the other hand, smaller phytoplankton cells in open ocean showed higher photosynthetic inhibition caused by UV radiation (Li et al., 2011). It is most likely that the combined effects of OA and solar UVR induce more carbon loss from the coast to open ocean in phytoplankton assemblages (Figure 5). Such a hypothesis needs observational and experimental data to be tested.

In summary, OA effects under multiple stressors have been documented but only in association with a very limited number of drivers. Future work toward understanding the ecological impacts of ocean climate changes should include both scenario-oriented and mechanism-directed studies. Considering

the impractical nature of the number of treatments and replicates needed to accommodate all combinations of possible drivers in experimental designs, it is highly recommended to refer to the recently published guide for multiple drivers marine research (Boyd et al., 2018, 2019). With increasing understanding of multiple stressors effects using controlled experiments in combination with field observational findings, OA effects in different ecosystems under multiple stressors can thus be understood both mechanistically and predictively.

AUTHOR CONTRIBUTIONS

KG contributed to the theoretical designs, data analysis, and writing of the manuscript. JB, D-PH, JH-S, GG, and DH contributed to the analysis of the data and writing of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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