



Impacts of ocean acidification under multiple stressors on typical organisms and ecological processes

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Abstract

The oceans are taking up over one million tons of fossil CO₂ per hour, resulting in increased *p*CO₂ and declining pH, leading to ocean acidification (OA). At the same time, accumulation of CO₂ and other greenhouse gases is causing ocean warming, which enhances stratification with thinned upper mixed layers, exposing planktonic organisms to increasing levels of daytime integrated UV radiation. Ocean warming also reduces dissolved oxygen in seawater, resulting in ocean deoxygenation. All these ocean global changes are impacting marine ecosystems and effects are well documented for each individual driver (pH, oxygen, temperature, UV). However, combined effects are still poorly understood, strongly limiting our ability to project impacts at regional or local levels. Different regions are often exposed (and often adapted) to contrastingly different physical and chemical environmental conditions and organisms, and ecosystems from different parts of the world will be exposed to unique combinations of stressors in the future. Understanding the modulating role of adaptation, species niche and stressors' interaction is key. This review, being a non-exhaustively explored one, aims to provide an overview on understandings of ecophysiological effects of OA and its combination with covarying drivers, mainly warming, deoxygenation and solar UV radiation. We propose a testable hypothetical model as well as future research perspectives.

Keywords Algae · Deoxygenation · Ocean acidification · Ocean warming · Plankton · UV radiation

Oceans under global changes

As a consequence of human activities, the atmospheric CO₂ concentration has increased by about 47%, from 280 to 412 ppm (March 2019), since the beginning of the industrial revolution. It is still rising at a rate of 0.5% per year (NOAA 2019), leading to global and ocean warming. At the same time, a large quantity of CO₂ dissolved in the oceans results

in declining pH in upper layers, leading to ocean acidification (OA) and a perturbation of the carbonate system. On the other hand, ocean warming causes enhanced stratification, with the upper mixed layer (UML) being shallower, hindering upward transports of nutrients into the UML from deeper layers. At the same time, the integrated daytime dose of UV radiation within the UML has increased due to a shorter mixed path and, therefore, has exposed organisms within this layer to higher levels of solar radiation. Moreover, the O₂ solubility in seawater is decreasing, resulting in global ocean deoxygenation and anoxic zone expansion (Breitburg et al. 2018).

It is projected that, by the end of the 21st century, OA will cause the average pH of the upper open ocean to drop by 0.4 (H⁺ concentration rises by 150%) (Gattuso et al. 2015) and the pH of coastal waters to drop by 0.45, being about 12% faster than pelagic oceans (Cai et al. 2011). These changes occur on top of the present environmental variability. Remarkable diurnal variations in pH of coastal waters and coral reefs of the South China Sea have been recorded (Dai et al. 2009; Wang et al. 2014). For example, the diurnal pH in a coastal coral reef system of the South China Sea

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already varies between 7.72 and 8.15 (Wang et al. 2014). These changes are endangering marine organisms, ecosystems and associated services (IGBP et al. 2013).

The increase in CO₂ in the atmosphere is linearly correlated with the global average temperature rise (IPCC Climate Change 2013). Since the 1970s, the oceans have absorbed over 90% of the heat gain, leading to ocean warming (Gattuso et al. 2015). So far, ocean warming has reached to a depth of 1000 m (Levitus et al. 2000). Over the past 100 years, the global ocean surface average temperature has risen by about 1 °C (Fischetti 2013). By the end of the 21st century, the average temperature may increase by 2–4 °C (Gattuso et al. 2015). Marginal seas, such as the East and South China Seas and Red Sea, have shown an even faster temperature rise (Bao and Ren 2014; Chaidez et al. 2017; Williams et al. 2016). Over the past 20 years, El Niño phenomena have shown clear variations, and global warming by 1 °C has been predicted to increase typhoon events by up to 25% (Bigg and Hanna 2016).

Solar ultraviolet radiation (UVR) is screened by stratospheric ozone. Ozone depletion by human activities has been curbed by the implementation of the Montreal Convention and the stratospheric ozone is expected to return to the pre-1980 level by the mid-21st century (Plummer et al. 2010; Solomon et al. 2016). However, other factors, such as the temperature increase caused by global climate change, the presence of trace gases (Osso et al. 2011) and changes in the atmospheric circulation pattern contribute to the increase by 2–3% in the UV-B level at low latitudes (Williamson et al. 2014). In addition, warming will lead to intensified stratification, exposing organisms in upper mixing layer to more UVR. UVR is well documented regarding its impacts on marine organisms (Gao et al. 2018a, b, c, d; Häder et al. 2015; Jin et al. 2017).

In the South China Sea, the visible light transmission depth (euphotic depth) exceeds 80 m. UV-A and UV-B transmission depth is 50 and 38 m, respectively, which corresponds to 62 and 47% of the euphotic depth (Li et al. 2011). In Shantou coastal sea areas, due to a large quantity of suspended particles, the visible light transmission depth in some areas is only 6–8 m; and the UV-A and UV-B transmission depths are 3–3.5 and 1.7–2.3 m, respectively, corresponding to 50 and 30% of the euphotic depth (Gao et al. 2007; Li and Gao 2012a). In oceanic waters, the UV radiation can reach to over 100 m water depth (Tedetti et al. 2007). The plankton in the UML is exposed to the solar UV radiation. So far, most of the survey and research on marine primary productivity has largely ignored the effects of the UV radiation. The effects of the UV radiation on the fixed carbon content of phytoplankton depend on the water depth and solar radiation intensity. Low or intermediate UV-A may promote the carbon fixation of algae (Gao et al. 2007; Xu and Gao 2010). The UV radiation is also the main factor

controlling the vertical distribution of copepods and affecting their horizontal distribution (Ma et al. 2013; Rhode et al. 2001).

Deoxygenation is the decrease in the dissolved oxygen concentration in seawater. It is the result of numerous environmental changes, such as the decrease in the oxygen solubility in seawater due to warming, the decrease in the quantity of O₂ conveyed from the surface layer to a deeper layer due to the aggravating of upper ocean stratification, eutrophication and the increase in the biological oxygen consumption. The dissolved oxygen content has declined in all parts of the ocean and oxygen-depleted zones in the open oceans have expanded by several million square kilometers in the past 50 years (Breitburg et al. 2018; Schmidtko et al. 2017).

The consumption of O₂ in the ocean is mainly by the respiration and degradation of organic carbon by bacteria. When conveying the particulate organic carbon to the deep sea, the marine biological carbon pump consumes O₂ and increases CO₂ and nutrients. Therefore, the continuous increase in the dissolved CO₂ concentration in the seawater (OA) and the consumption of O₂ by microorganisms are contributing to the formation of dead zones at depths of 500–700 m (Brewer and Peltzer 2009). Over the past 50 years the depth of hypoxia (< 2 mg/L) in the Pacific Ocean has decreased from 400 to 300 m and the dissolved oxygen content has decreased significantly (Whitney et al. 2007) as a consequence of climate change (Keeling et al. 2010).

The biological and ecological effects of OA have been extensively studied. Most studies focused on single species exposed to different pH scenarios in laboratory-based perturbation experiments. Impacts at the community or on ecosystem levels or involving more than one stressor are less common (Riebesell and Gattuso 2015). However, OA can interact with other stressors to directly or indirectly affect the biological response. Such studies are challenging and there are some bottlenecks in technologies and methods to perform experiments under influences of multiple stressors (Boyd et al. 2018). The following sections summarize the impact of OA alone or in combination with temperature, oxygen and UV on different levels of the planktonic community.

Primary producers

Individual effect of OA

Marine photosynthetic organisms assimilate inorganic elements and synthesize organic matter, playing an important role in the carbon sink. Observations at 58 stations (2000–4000 m depth) show that the diatom-dominated

phytoplankton settles from the euphotic layer to the deep sea at a rate of 124–732 m/day (Agusti et al. 2015). In different water areas of the South China Sea, diatoms dominate phytoplankton in abundance, acting as the main driver of the marine biological carbon pump (Xue et al. 2016). OA has the potential to reduce the content of biogenic silica in diatoms (Milligan et al. 2004; Xu et al. 2015). This can affect the predation rate of diatoms by zooplankton as well as the number of fecal pellets (Liu et al. 2016). Therefore, OA can indirectly affect the settling volume of particulate organic carbon through the silicification of diatoms. In the oligotrophic South China Sea, OA can decrease photosynthetic carbon fixation either per unit water volume or per unit chlorophyll, by reducing the abundance of diatoms (Gao et al. 2012). Under low sunlight levels, OA can promote the growth of three diatom species; while under high sunlight conditions, it inhibits their growth (Gao et al. 2012). Coastal and pelagic *Thalassiosira* species, for instance, display contrasting responses to decreasing pH, with the growth of the coastal species *T. weissflogii* being more resilient than the pelagic species *T. oceanica*, showing reduced net photosynthesis (Li et al. 2016). This difference between coastal and pelagic species is due to a difference in local adaptation to present natural variability (Vargas et al. 2017). In terms of biochemical composition, exposure to OA was shown to increase the content of phenolics (toxic compounds) in the haptophyte *Emiliania huxleyi*, diatoms and phytoplankton assemblages with enhanced expressions of the enzymes related to their degradation (Jin et al. 2015).

In terms of macroalgae, it was reported that species with weak or without CO₂ concentrating mechanisms (CCMs) were more likely to benefit from OA (Ji et al. 2016). For instance, OA has been shown to enhance the growth of *Ulva rigida* (Gordillo et al. 2001), *Lomentaria articulata* (Kübler et al. 1999) and *Gracilariopsis lemaneiformis* (Zou and Gao 2009), while it did not affect the photosynthetic rates of the species with active CCMs (Cornwall et al. 2012). On the other hand, other studies have shown that the growth of some species with effective CCMs, such as *U. prolifera* (Gao et al. 2016) and *Sargassum muticum*, could be still enhanced by OA (Xu et al. 2017) because of increased nitrogen assimilation under OA (Xu et al. 2017). Until now, the effects of OA on the growth of non-calcifying macroalgae are mostly positive. However, negative effects were observed in *Porphyra leucostica* (Mercado et al. 1999), *P. linearis* (Israel et al. 1999), *Fucus vesiculosus* (Gutow et al. 2014) and *U. linza* (Gao et al. 2018a). Apart from species differences, the differential effects of OA could be also related to other environmental factors, such as light intensity (Harley et al. 2012) and nutrients (Gao et al. 2019). For calcifying macroalgae, lowered pH and the reduced saturation state of calcium carbonate are known to reduce their calcification

and growth (Cornwall et al. 2013; Gao et al. 1993; Gao and Zheng 2010; Sinutok et al. 2011).

Combined effect of OA with warming

OA and global warming are currently the major global environmental problems caused by human CO₂ emissions. Understanding their combined effects on primary producers is critical. Laboratory studies show that OA and warming have different effects on different species. For example, warming and a rise in *p*CO₂ promote the growth of *Synechococcus* but have no effect on *Prochlorococcus* (Fu et al. 2007). In diatoms, OA and a 4 °C warming promote the growth of the diatom *Skeletonema marinoi* (Kremp et al. 2012) but have no clear effect on *Thalassiosira* or *Chaetoceros* (Hyun et al. 2014). When exposed to OA and warming, the calcification rate of *Coccolithus* decreases (Schlüter et al. 2014). OA and warming together lower the optimum growth temperature and maximum growth rate of *Emiliania huxleyi* (Listmann et al. 2016). However, when *p*CO₂ is within the 20–6080 μbar, warming increases the production rate of particulate inorganic carbon and particulate organic carbon of *Emiliania huxleyi* and *Gephyrocapsa oceanica* (Sett et al. 2014). For macroalgae, the respiratory coefficient (the rate of change of the respiratory rate as temperature increases) of *Sargassum fusiforme* under acidification conditions increases, indicating that acidification and warming together could increase the respiratory rate (Zou et al. 2011); the reproduction of a green tide alga *Ulva rigida* is stimulated by warming, with a further increase when combined with acidification (Gao et al. 2017a, 2018b). Research on the reef-building coralline algae finds that acidification causes a reduction in calcification, which can be aggravated by warming (Martin and Hall-Spencer 2017). OA and warming can improve the nitrogen fixation of nitrogen-fixing cyanobacteria (Hutchins et al. 2007). Field studies have revealed that warming increases net primary productivity in the South China Sea but in combination with acidification leads to a decline (Gao et al. 2017b). In the Bay of Kiel, OA did not affect phytoplankton biomass at high temperature. However, phytoplankton biomass was increased at in situ water temperature as acidification reduced predation rates by zooplankton (Paul et al. 2016).

The quantity of CO₂ to be absorbed by the ocean in the future depends on the bio-mediated carbon sink and carbon source process, i.e., biological assimilation and dissimilation. Ocean warming will affect the marine biological C pump (BCP) and the microbial C pump (MCP) as well as their interaction (Jiao and Zheng 2011). Recent research has found that OA has no effect on the composition of dissolved organic carbon (DOC) in the plankton ecosystem in a Swedish fjord (Zark et al. 2015), while it can promote the production of particulate organic carbon (POC) (Czerny et al.

2013). How OA and warming will work in combination and influence the composition of DOC and the production of POC has yet to be studied. In the ocean, most of the DOC is quickly converted into CO_2 through bacteria lysis. However, some DOC resists bacteria lysis and survives for hundreds or even thousands of years, playing a steady role in the carbon sink (Jiao et al. 2010). Effects of the global ocean changes (mainly referring to OA and warming) on BCP/MCP are still quite uncertain (Gattuso et al. 2015; Jiao and Zheng 2011). Therefore, it is particularly important to understand the combined effects of OA and warming on the carbon sink/source process in marine organisms. As most research findings on the combined effects of OA and warming were obtained using single drivers in laboratory controlled conditions, conclusions are still quite controversial.

Combined effect of OA with UVR

UV radiation affects the photochemical and photo-biological processes in sea water (Bais et al. 2018). Despite its critical importance, most laboratory and deck culture experiments do not include ultraviolet radiation (UVR, 280–400 nm). This strongly limits our ability to extrapolate the reported ecological and physiological effects of OA from laboratory studies to in situ conditions (Gao et al. 2012). For phytoplankton, low intensity UV-A promotes photosynthetic carbon fixation (on cloudy days or for deeper layers) and inhibits photosynthesis at high intensity (at noon on sunny days), while UV-B always causes damage (Gao et al. 2007). UVR can change the morphology of some blue-green algae (Gao et al. 2008; Wu et al. 2005), damage their DNA (Gao et al. 2008), and inhibit the calcification of algae (Gao et al. 2009; Gao and Zheng 2010). The combination of OA and UVR further reduces the calcification of algae (Gao et al. 2009; Gao and Zheng 2010; Xu and Gao 2015). When the diatom *Thalassiosira pseudonana* is acclimated to OA, it is more sensitive to photoinhibitory UVR compared to ambient condition (Sobrino et al. 2008). OA also exacerbates the harmful effect of UVR on PSII function in the diatom *Thalassiosira weissflogii* through reducing PsbD removal rate and the ratio of RbcL to PsbA (Gao et al. 2018c). The UVR penetration depth could reach over 100 m in the south east Pacific Ocean (Tedetti et al. 2007) and 50–60 m in the South China Sea (Li et al. 2011), the ratio of the visible light to UV radiation is different at different depths and the coupling effect of the OA and solar radiation to primary production process will be different at different depths. In terms of macroalgae, Ma et al. (2019) showed the differential response of juvenile and adult *Ulva linza* to the combination of OA and UVR; UVR increased PSII activity of juvenile thalli and the addition of OA did not affect it, while OA + UVR further decreased PSII activity of adult thalli compared to UVR.

OA effects with deoxygenation

Marine organisms need O_2 in metabolic processes and when the dissolved O_2 concentration is below a certain value, their physiology is affected, and prolonged and extreme hypoxia stress can lead to death. The half lethal concentration (LC_{50}) of dissolved O_2 can be very different for different organisms. In typical hypoxic zones, the oxygen content is below 2 mg/L and hypoxia is usually associated with high $p\text{CO}_2$ and low pH. For example, under the thermocline there is less dissolved oxygen and the pH is lower. In coastal areas, the number of hypoxic areas is increasing at a rate of about 5.5% per year due to the interaction between deoxygenation and eutrophication (Vaquer-Sunyer and Duarte 2008). The combination of effects results in an acidification rate faster in coastal areas than in oceanic waters (Cai et al. 2011). In addition, deoxygenation will promote denitrification, reducing the concentration of the nitrate ions and affecting the ocean N cycle, primary productivity and marine biological carbon pump efficiency (Hutchins et al. 2019). However, little is known about how deoxygenation affects metabolism of photosynthetic organisms.

The ratio of $p\text{O}_2$ to $p\text{CO}_2$ in seawater is decreasing with time as a consequence of global changes and this decrease is amplified in deep seawater (Brewer and Peltzer 2009). The physical mixing process causes the conveyance of deep seawater to the surface layer also affecting the ratio of $p\text{O}_2$ to $p\text{CO}_2$ in the euphotic layer. Physical and chemical environments in upwelling zones are also changing as the atmospheric CO_2 concentration rises. The ratio of $p\text{O}_2$ to $p\text{CO}_2$ in seawater can have ecological consequences. For example, in the upwelling zone along the California coast, the ratio of $p\text{O}_2$ to $p\text{CO}_2$ keeps declining. This has been linked to a huge economic loss to local shellfish farming as well as a decrease in the available food source for zooplankton (Doney et al. 2012).

Deoxygenation and OA can affect the production of both particulate organic carbon and particulate inorganic carbon. Theoretically, the reduction in $p\text{O}_2$ and the increase in the $p\text{CO}_2/p\text{O}_2$ ratio are beneficial to the carboxylation (CO_2 assimilation) of the photosynthetic carbon fixation enzyme (Rubisco) and down-regulates the oxidation of this enzyme catalysis (decomposition of organic carbon and release of CO_2). Therefore, changes in the $p\text{CO}_2/p\text{O}_2$ ratio will affect the algal photosynthesis (Gao and Campbell 2014). Deoxygenation, OA or and a decrease in the $p\text{O}_2/p\text{CO}_2$ ratio will have combined effects on photosynthetic carbon fixation, respiration, light respiration, growth and calcification. In addition, zooplankton responds to acidification, by enhancing respiration and increasing the feeding rate (Li and Gao 2012b). As ocean deoxygenation also affects respiration, it can interact with OA and alter an organisms' energy balance.

OA effects under multiple stressors

The plankton in the surface or UMLs, whether in coastal or ocean waters, is subject to diurnal and seasonal temperature variations. Ocean warming can affect the surface temperature variation amplitude and cause other relevant physical and chemical environmental changes (e.g., the UML being shallower, the quantity of nutrient conveyed from bottom to top reduced). As a consequence, organisms in the upper ocean face multiple environmental stressors, such as acidification, warming, reduced nutrient (except in coastal waters near human habitats) and increased exposure to UV radiation. Understanding the combined effect of these environmental changes is one of the most important research priorities.

Studies on single stressors still dominate the literature. A growing number of publications consider the effects of OA in combination with one or more stressors. However, only a few consider three or more stressors. As an example, Tong et al. (2019) showed that OA and warming reduced the calcification to photosynthesis ratio in the cosmopolitan coccolithophorid *Emiliania huxleyi*. UVR increased this ratio, particularly for cells under OA conditions, suggesting that UVR could counteract the negative effects of the other global stressors on the calcification/photosynthesis ratio. Enhanced stratification due to warming leads to decreased nutrient transport from deeper waters to the surface. As a consequence, it is important to understand the effect of OA and warming under changing nutrient levels. Li et al. (2018) showed that neither OA nor warming affected the specific growth rate of *Thalassiosira pseudonana* under nitrate replete conditions but they both reduced the growth rate under nitrate limited conditions. Furthermore, Brennan and Collins (2015) investigated the growth responses of a green alga *Chlamydomonas reinhardtii* to eight different environmental drivers, including CO₂, temperature, pH, etc. Their results demonstrated that the growth rate declined in a predictable way with an increasing number of environmental drivers. They concluded that the overall effect of multiple drivers could be determined by the number of drivers and the overriding driver.

Marine animals

Individual effect of OA

As the concentration of CO₂ in the ocean rises, the associated perturbation of the carbonate system (increased CO₂, decreased pH and saturation state) can affect organisms structures, tissues, cells and extracellular fluids (Parker et al. 2013). When the amount of CO₂ in the organism increases, a series of chemical equilibrium changes occur

in the organism, CO₂ reacts with H₂O molecules in the body fluids or other buffers, causing an increase in HCO₃⁻ and H⁺ levels, and a decrease in pH both inside and outside the cell. CO₃²⁻ and total alkalinity also decrease, further affecting the dissociation equilibrium of CaCO₃ and other ion concentration changes (Fitzer et al. 2014). Changes in ion levels can greatly affect the physiology of marine organisms, e.g., calcification (Chan et al. 2017; Page et al. 2016; Ramesh et al. 2017; Raybaud et al. 2017). When the acid–base balance inside and outside the cell changes, the organism initiates a series of regulatory mechanisms. For example, the white shrimp *Litopenaeus vannamei* enhances the transport of transmembrane proteins Na⁺/K⁺-ATPase and H⁺-ATPase, and changes the expression level of carbonic anhydrase (CA) (Liu et al. 2015). When sea urchin larvae are exposed to decreased pH, the pH in their extracellular fluid changes accordingly. However, they are able to quickly and fully compensate for the accompanying intracellular acidosis using a bicarbonate buffer mechanism involving secondary active Na⁺-dependent membrane transport proteins (Stumpp et al. 2012). OA is also associated with a drop in gastric pH that is only partly compensated for and leading to a decreased digestive efficiency in sea urchin larvae (Stumpp et al. 2013). The regulation of acid–base levels and the enhancement of ion transport are energy-consuming. The organism has to increase its metabolic rate and enhance the energy supply to meet the increased energy demands (Stumpp et al. 2011). For example, when sea urchin larvae are exposed in a high CO₂ level environment, their own ion transport and protein synthesis are greatly increased, and the ATP levels consumed by the two processes accounts for 80% of the ATP produced by the body (Francis et al. 2015).

Even if the energy acquisition of the organism itself is stable (e.g., Stumpp et al. 2013), the increase in energy consumption by ion transport, acid–base maintenance and other compensatory mechanisms can lead to a reduction in energy allocation to other life activities, such as growth, development, immune response, reproduction and so on (Yuan et al. 2016). For example, a reduction in the scope for growth is well documented in invertebrate larvae leading to a delay in development (Stumpp et al. 2011). A meta-analysis by Brown et al. (2018) suggests that food can modulate CO₂ impacts. Studies have also found that some mussels and other invertebrates can successfully survive and become dominant species with pCO₂ ranging from 71 to 101 Pa when food is abundant (Thomsen et al. 2010). Therefore, it appears that under adequate energy supply animals are able to survive the negative effects of OA. OA is a chronic stressor and a significant evolutionary response is expected in species with short generation times or large standing genetic variations (Calosi et al. 2016; Sunday et al. 2014). For example, the copepod *Pseudocalanus acuspes* exposed to OA for several generations partly recovered from the

negative effects on fecundity observed after the first generation (Thor and Dupont 2015). This transgenerational plasticity could be partly attributed to selection on RNA synthesis and translation (De Wit et al. 2016).

The acid–base regulation system in many fish has sufficient capacity and adaptability to cope with OA (Melzner et al. 2009). However, fish eggs and juveniles have a high specific surface area and incomplete acid–base regulation system and may be susceptible to OA (Rodríguez-Dominguez et al. 2018; Shao et al. 2016). Recent experimental studies have shown that OA has direct negative impacts on the growth and survival of some juvenile fish (Lee et al. 2018; Lifavi et al. 2017). Moreover, high $p\text{CO}_2$ can affect fish's respiratory, circulatory and metabolic processes (Esbaugh et al. 2016; Hannan and Rummer 2018; Kunz et al. 2016; Tirsgaard et al. 2015). Fish exposed to high concentrations of CO_2 may also lose the ability to discriminate certain important biochemical signals, such as odours from habitat types and predators (Porteus et al. 2018; Rong et al. 2018). Recent studies have shown that fish auditory systems can also be affected by OA (Ashur et al. 2017; Rossi et al. 2016). Whether the perception of fish and changes in behaviors affect the food chain and the entire ecosystem is still unknown, but this potential risk is obvious.

OA with warming

Ocean acidification and warming are predicted to affect marine animals and previous reviews have reported their combined effects on marine organisms' calcification, growth, reproduction, and survival (Harvey et al. 2013; Przeslawski et al. 2015). High temperature and low pH had a positive effect on the reproduction of the sea urchin *Arbacia lixula* (Wangensteen et al. 2013). For the scleractinian corals *Acropora millepora* and *A. tenuis*, temperature and pH had almost negligible effects on the larval development (Chua et al. 2013). Negative effects of acidification and warming were observed on the sea urchin *Lytechinus variegatus* larvae (Lenz 2017). Increased temperature or OA may neutralize the adverse effects of the other factors on some species. For example, increased temperature compensated for the negative effects of OA on *Paracentrotus lividus* larval development and settlement (García and Clemente 2015). Simultaneous acidification offsetting the negative effect of increased temperature on reproductive parameters and hatching success was observed for the copepod *Calanus finmarchicus* (Pedersen and Hanssen 2018). Gianguzza et al. (2014) proposed a model that reconciles these apparent conflicting results. Working on sea urchin larvae, they showed that the effect of decreased pH on growth was dependent on temperature and ranged from positive at low temperature to negative at high temperature. They argue that these organisms are adapted to a range of natural pH and

temperature often corresponding to the present environment variability (Vargas et al. 2017). Moreover, the response to different combinations of pH and temperature depended on their combined intensity in an additive but non-linear manner. Within optimal present conditions, an increase in metabolism is associated with increased growth till the point of energy limitation. Then, any increase in metabolism leads to a reduced scope for growth and a decreased growth rate. Both ocean warming and acidification are inducing an increase in metabolism until the point of metabolic depression and lethality. OA or warming can then lead to a positive effect (not energy limiting conditions) or a negative effect (energy limiting conditions) on growth rates depending on the baseline metabolism (Gianguzza et al. 2014).

OA with hypoxia

Acidification and hypoxia are known to co-occur and some studies have highlighted that OA would become more severe under hypoxia conditions in coastal ecosystems (Melzner et al. 2013; Paulmier et al. 2011). Consequently, aquatic organisms living in these environments have already experienced low pH and oxygen conditions that exceed near-future open ocean projections (Gobler and Baumann 2016). Nonetheless, global changes can exacerbate pH and oxygen declines in coastal regions and coastal organisms are not, by default, immune to such change (Breitbart et al. 2018; Waldbusser and Salisbury 2014). Laboratory studies have found complex responses to combined hypoxia and OA leading to a reduction in the fitness of early life stages. For instance, when exposed to hypoxia and OA, respectively, juveniles of the hard clam *Mercenaria mercenaria* showed resistance, while a significant reduction in growth rates was observed when exposed to the combined stressors (Gobler and Baumann 2016). Both stressors had negative effects on the growth of the larvae of the estuarine fish *Menidia beryllina* that is more sensitive to hypoxia than low pH (DePasquale et al. 2015). Gobler et al. (2014) reported that low DO had a stronger effect on growth and survival than acidification in early-stage *Argopecten irradians*. Similar results have also been presented in adult organisms. For example, Sui et al. (2017) claimed that hypoxia showed greater effects on enzyme activities than low pH on the adult thick shell mussel *Mytilus coruscus*. In contrast, Clark and Gobler (2016) found that, under stable conditions, low pH generally had a stronger effect than low DO for early-stage *A. irradians*, *Mercenaria mercenaria*, and *Crassostrea virginica*. Such variation may be due to differences in life stage (Gobler et al. 2014), food availability (Pansch et al. 2014), species differences (Clark and Gobler 2016), exposure time (Navarro et al. 2013), and/or variable environmental conditions across geographic locations (Vargas et al.

2017). Besides physiological effects, behaviors of some species can also be affected. The anti-predator responses of *M. coruscus* (i.e., the production of byssal thread) were decreased under both stressors (Sui et al. 2017). So far, the combined effects between the two factors have still received only limited attention, and further studies are necessary.

Effects on heterotrophic bacteria and viruses

Individual effect of OA

Marine heterotrophic organisms, mainly bacteria that do not perform photosynthesis and chemosynthesis, release CO₂ and promote pH decline during their organic matter degradation (Cai et al. 2011). There is little understanding of how OA affects bacteria dissimilation (Wang et al. 2015). Bacterial productivity at the Hawaii ALOHA Station, as a response to warming, falls behind primary productivity by 1–2 months; it was not affected by a short-term OA treatment (Vivani 2016). However, other research findings show that OA results in additional energy consumption by bacteria and up-regulates genes related to proton pumps, which may affect microbial carbon pump efficiency (Bunse et al. 2016). The bacterial community structure of coastal eutrophic areas in the subtropics, was not significantly affected by OA (Lin et al. 2018). Nevertheless, pH changes may affect the relationship between bacteria, viruses and algae, and thus influence organic matter production and its degradation processes, with biogeochemical consequences that may play a feedback to climate change.

As early as the 1930s, researchers began to explore the response of viruses to pH changes and found that some viruses were not affected by the acidic exposure even when the pH was as low as 3, while other viruses became unstable when the pH was below 7 (Jin et al. 2005; Krueger and Fong 1937; Weil et al. 1948). However, little has been documented on the impacts of pH changes relevant to OA and viruses. OA has an effect on the virus–host interaction as the eclipse period (between infection and the appearance of mature virus within the cell) of the Cyanophage S-PM2 (virus infected *Synechococcus*) became longer as pH dropped, while an opposite trend was observed for the latent period. The burst size per cell also decreases as the pH drops (Traving et al. 2014). With regard to the relationship between eukaryotic algae and viruses, when the pH decreased from 8.1 to 7.7, PgV (*Phaeocystis globosa* virus), it caused the photosynthesis of *Phaeocystis globosa* to decline, the respiration to rise and the burst size per cell to decrease (Chen et al. 2015). OA can also prolong the burst time of *Emiliania huxleyi* after being infected with EhV (Carreira et al. 2013).

OA with warming

A full-factorial mesocosm experiment ($p\text{CO}_2$ and temperature) conducted in the Baltic Sea showed that temperature played a major role in structuring the bacterial community, with a weak effect from $p\text{CO}_2$. $p\text{CO}_2$ had significant effects on the relative abundance of several dominant operational taxonomic units (OTUs) (operational taxonomic units) accompanied by an antagonistic impact of temperature (Bergen et al. 2016). Burrell et al. (2017) also found that temperature had a greater effect on growth and protein synthesis in bacteria from four locations east of New Zealand. OA had an antagonistic effect on bacterial secondary production and leucine aminopeptidase activity. Webster et al. (2016) reported that microbial communities of coral reefs in Australia were tolerant to elevated $p\text{CO}_2$ /reduced pH (0.2 units) but sensitive to elevated seawater temperature (from 28 to 31 °C), with a significant microbial variation involving loss of specific taxa and appearance of novel microbial groups.

The combined effect of OA with other factors (e.g., oxygen, UV) on viruses is poorly documented.

Food web

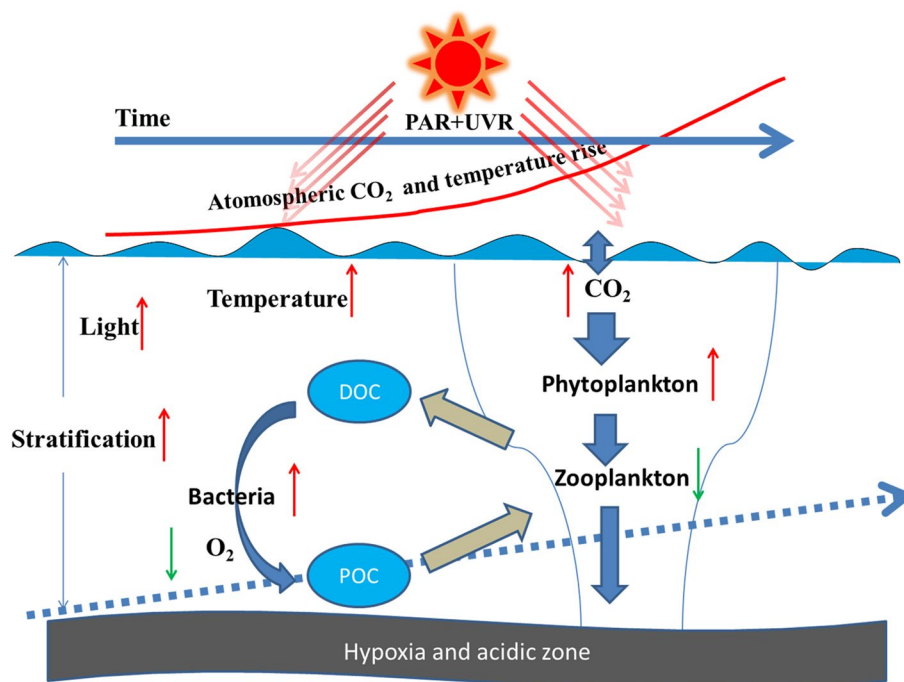
Individual effect of OA

Most published studies on OA so far have focussed on single trophic levels. However, ecology and food web interactions are expected to play a key role in species and ecosystem responses to OA (Gaylor et al. 2015). For example, a mesocosm study performed on the west coast of Sweden showed that the survival of the Atlantic herring (*Clupea harengus*) was significantly enhanced by OA due to increased primary production (Sswat et al. 2018). In another mesocosm study on the subtropical North Atlantic, OA increased the abundance of the toxic microalga *Vicicitus globosus* and thus prevented the development of the micro- and mesozooplankton communities, leading to a strong decline in export flux of primary produced organic matter (Riebesell et al. 2018). A multitrophic level experiment performed in the East China Sea demonstrated that OA increased the accumulation of toxic phenolic compounds across trophic levels (phytoplankton and zooplankton) (Jin et al. 2015).

OA with warming

Alsterberg et al. (2013) reported the importance of consumers (invertebrate mesograzers) in mediating the effects of experimental OA and warming on primary producers; the combination of OA and warming increased microalgae biomass in the absence of mesograzers but did not affect it in the presence of mesograzers. Furthermore, Goldenberg et al.

Fig. 1 Impacts of ocean acidification on food web under multiple stressors. Red arrows represent rise and green arrows represent decline



(2017) investigated the combined effect of OA and warming on a three-level (algae, herbivorous invertebrates, and predatory fish) food web and found that OA increased algae biomass and this stimulatory effect was transmitted through all trophic levels. On the other hand, warming decreased the production of herbivorous invertebrates via enhancing metabolic demand of predatory fish, although warming also increased algal production. This study indicates that OA and warming may affect food webs from different directions; OA is more likely to follow bottom-up controls (resource driven), while temperature drives top-down controls (consumer driven).

Perspectives

Ocean acidification, as one major environmental problem caused by human carbon emissions, is gaining significant attention and the research on its physiological and ecological effects has been carried out globally. OA, combined with warming and deoxygenation, has been shown to impose negative effects on marine animals and to stimulate the production of primary producers, particularly in coastal waters that do not experience stratification or nutrient limitation. The associated decreased predatory pressure has the potential to further increase primary production. The increased primary production will stimulate the respiration of bacteria and thus intensify the hypoxia and low pH zone (Fig. 1). However, there are a lot of uncertainties and variability in the responses documented in the literature. For example, the effects of OA on primary productivity range from positive to

negative. This can be explained by several factors including local adaptation and modulation by other biotic and abiotic environment drivers. This illustrates the urgent need to conduct experiments under the context of multiple stressors and food webs to decipher the mechanisms behind species sensitivity and response to future global changes. One approach is to conduct large scale mesocosm experiments. However, these are technically challenging, very expensive and have low replication power. They are also hard to interpret as this approach does not allow the performance of full-factorial experiments with multiple stressors and it is then difficult to mechanistically attribute observed effect to a given driver or to understand interactions. An alternative is a combination of approaches. On one hand, carefully designed single stressor experiments allow the understanding of modes of action and performance curves. This knowledge can then be used to model and project complex interactions. These hypotheses can then be tested with micro- or mesocosms using a full-factorial or a collapsed design (Boyd et al. 2018). Furthermore, to better understand and project the impact of OA and other stressors at large spatial and temporal scales, manipulative experiments should be combined with in situ observations. In addition, the long-term evolutionary responses of marine organisms to OA combined with other important stressors should be paid more attention as most studies now focus on the short-term acclimation periods.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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