The Impacts of Ocean Acidification on Marine Food Quality and Its Potential Food Chain Consequences

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Dissolution of anthropogenic CO2 into the oceans results in ocean acidification (OA), altering marine chemistry with consequences for primary, secondary, and tertiary food web producers. Here we examine how OA could affect the food quality of primary producers and subsequent trophic transfer to second and tertiary producers. Changes in food quality induced by OA are often related to secondary metabolites in primary producers, such as enriched phenolics in microalgae and iodine in brown algae. These biomolecules can then be transferred to secondary producers, potentially affecting seafood quality and other marine ecosystem services. Furthermore, shifts in dominant functional groups of primary producers under the influence of OA would also impact higher trophic levels through food web interactions. It is challenging to understand how these complex food chain effects of OA may be expressed under the influence of fluctuating environments or multiple drivers, and how these effects can be scaled up through marine food webs to humans.

Keywords: ocean acidification, fatty acids, food quality, primary producers, trophic transfer, secondary producers

INTRODUCTION

The oceans have absorbed about one-third of the CO2 released into the atmosphere by humans, altering marine carbonate chemistry with a continuous decline of pH, resulting in ocean acidification (OA) (Caldeira and Wickett, 2003). The pH of the surface ocean has dropped by ~0.1 since pre-industrial times, which is a rate tenfold higher than in the past 300 million years (Hönisch et al., 2012). By the end of this century, proton concentrations in the surface ocean will be more than twice those of the pre-industrial period (IPCC, 2014; Gattuso et al., 2015). Carbonate chemistry changes associated with OA include increases in concentrations of CO2 and bicarbonate and decreases in levels of carbonate ions and pH. Although a wide range of altered carbonate chemistry effects have been observed at each trophic level of marine food webs (Kroeker et al., 2013; Nagelkerken and Munday, 2016; Hutchins and Fu, 2017; Hurd et al., 2018; Gao et al., 2019), how OA affects the food quality of primary producers and trophic transfer to secondary and tertiary producers is still controversial. Here, we present an overview of the up-to-date advances regarding this specific issue and highlight the challenges for future research in this area.
FOOD CHAIN EFFECTS ASSOCIATED WITH FATTY ACID CHANGES

Primary producers synthesize lipids, fatty acids (FA), and in particular polyunsaturated FA (PUFA). These biomolecules are crucial cellular components of marine organisms, in that they play critical roles in cell membrane function, physiological processes for energy storage, and trophic interactions in aquatic food webs (Dalsgaard et al., 2003; Guschina and Harwood, 2009). PUFA cannot be synthesized de novo by metazoans, which therefore must acquire these compounds via their diet (Hixson et al., 2015). In aquatic food webs, PUFA are exclusively synthesized by phytoplankton, and thus algal PUFA composition is an important determinant of food quality, consequently affecting the health and optimal functioning of marine and freshwater ecosystems (Dalsgaard et al., 2003).

Ocean acidification is likely to affect all of these interactions; for instance, it has been reported that the FA composition of phytoplankton is highly dependent on CO₂ concentrations. PUFA content decreased by ~3% in the diatom *Cylindrotheca fusiformis* grown at a pCO₂ of 750 µatm (representing OA), compared to a contemporary pCO₂ treatment of 380 µatm CO₂ (Bermúdez et al., 2015). This suggests a decline of food quality in primary producers under future OA conditions. However, it is worth noting that there is strong spatiotemporal variability in marine carbonate chemistry. This is especially true for coastal seawater due to multiple drivers such as tidal cycles (Dai et al., 2009; Jiang et al., 2011; Wang et al., 2014), upwelling (Capone and Hutchins, 2013), anthropogenic nutrient inputs, aquaculture activities, and changes in ecosystem structure and metabolism (Duarte et al., 2013; Waldbusser and Salisbury, 2014). Elevated photosynthesis and respiration also drive large diel pH fluctuations in coastal and coral reef ecosystems (Santos et al., 2011), and it has been suggested that OA-induced effects on the food quality of primary producers can be dampened in these waters with major natural pCO₂ fluctuations (Bermúdez et al., 2016). Moreover, OA is likely to impact different phytoplankton taxa differently in terms of their growth, metabolic activity, and organism size (Flynn et al., 2012). Therefore, investigation of OA effects on food quality has to take into account phytoplankton species of various taxonomic groups and natural fluctuations in pCO₂ (Flynn et al., 2012).

Approximately 10–20% of essential biomolecules in primary producers are incorporated into new biomass at the next trophic level, and thus the decline of food quality in primary producers will have potential impacts on the zooplankton which prey on them. In one striking study by Rossoll et al. (2012), declines in both total FAs and the ratio of long-chain polyunsaturated to saturated FAs, constrained growth and reproduction of the copepod *Acartia tonsa* fed the diatom *Thalassiosira pseudonana* grown under OA conditions. Further support for this food chain effect of OA was provided by a mesocosm experiment using a natural plankton community. A declining proportion of PUFA in the natural phytoplankton assemblage was mirrored by a reduction in the relative PUFA content of the dominant copepod *Calanus finmarchicus* (Bermúdez et al., 2016). Another study found that changes in ratios of lipid to protein and/or lipid to carbohydrate in phytoplankton under the influence of OA decreased trophic transfer efficiency from phytoplankton to zooplankton by about 50%, and caused a commensurate decrease in zooplankton recruitment (Cripps et al., 2016). On the other hand, OA has sometimes been shown to increase food availability, and thus help alleviate the negative effects of acidification on invertebrates (Thomsen et al., 2013).

Besides the indirect effects of OA on zooplankton via trophic transfer (bottom up effects), it can also directly affect zooplankton differentially according to gender and/or developmental stage (Cripps et al., 2014). In addition, it is not only the food quality of primary producers that can be altered by OA. Higher trophic levels such as some commercially valuable oysters can become less nutritious due to lower levels of proteins, lipids, carbohydrates, and caloric content under OA conditions (Lemasson et al., 2018). Overall, the available data suggest that FA and PUFA in phytoplankton can be influenced by OA, and these compositional changes will also affect transfer to higher trophic levels which rely on their prey as a source of these essential macromolecules.

PHENOLICS AND IODINE CHANGES IN ALGAE AND THEIR GRAZERS

Besides lipids and FA, other secondary metabolites in primary producers such as phenolic compounds can also be affected by OA. As reported in pioneering work by Arnold et al. (2012), polymeric phenolics decreased in the seagrasses *Cymodocea nodosa*, *Ruppia maritima*, and *Potamogeton perfoliatus* under OA conditions. In contrast, phytoplankton species (diatoms and coccolithophores) increased their phenolic compounds when grown in acidified seawater (Jin et al., 2015). This accumulation of phenolics under OA has been suggested to be caused by alterations in β-oxidation metabolic pathways (Figure 1). Uregulation of β-oxidation and the Krebs cycle, with enhanced degradation of phenolics, may provide extra energy to cope with acidic stress caused by OA. Since phenolic compounds are highly toxic to most grazers, an increase in their content in primary producers has the potential to drive significant consequences for food webs (Boyd and Carlucci, 1993; Ianora et al., 2006). Interestingly, Jin et al. (2015) demonstrated that copepods fed with OA-grown phytoplankton had higher phenolics content compared to the control (Figure 1), suggesting a food chain effect of OA from primary to secondary producers. The increased phenolic compounds in primary producers associated with FA metabolism via β-oxidation would further decrease the nutritional value of these organisms. This might provide a tentative explanation for the observation that shrimp grown under OA in the presence of natural phytoplankton and zooplankton tasted bitter (Dupont et al., 2014). In addition, as phenolics are known to possess antimicrobial properties (Arnold and Targett, 2002), biogeochemical cycles in the oceans may be affected as well. Food chain effects of OA were also observed in the brown alga *Saccharina japonica*, in which
OA increased the accumulation of iodide and the amounts of iodine released into seawater, while abalone fed on the kelp, exhibited increased levels of iodine (Xu et al., 2019). Altogether, a limited number of studies show that OA can influence accumulation of secondary metabolites and their transfer to higher trophic levels, thereby producing cascading impacts on marine food webs.

CONSEQUENCES OF ALTERED COMMUNITY COMPOSITION OF PRIMARY PRODUCERS

In addition to biochemical changes in primary producers, the influence of OA on their composition may also impact energetic and nutritional transfer to higher trophic levels. For instance, OA may selectively favor an increase in the growth rates of larger versus smaller phytoplankton species (Wu et al., 2014; Bach and Taucher, 2019). OA-driven shifts toward larger diatoms have been observed in natural phytoplankton communities (Tortell et al., 2008; Feng et al., 2010; Eggers et al., 2014; Bach et al., 2017; Taucher et al., 2017). Such phytoplankton community shifts to larger species may increase the trophic transfer of energy to marine animals by shortening food chains (Sommer et al., 2002) and promote production in higher trophic levels. At a natural CO₂ seep in the North Pacific Ocean, the large chain-forming diatom *Biddulphia biddulphiana* greatly increases in abundance as CO₂ increases along a seawater concentration gradient. Along this same gradient, the abundance of calcified grazers such as gastropods and sea urchins decreased (Harvey et al., 2019). This observation suggests that OA can alter the food-web structure and ecosystem productivity by shifting the community composition of primary producers.

In a mesocosm experiment with an oligotrophic plankton community in the subtropical North Atlantic Ocean, the toxic microalga *Vicicitus globosus* increased its abundance at CO₂ levels higher than 600 µatm and developed into blooms above 800 µatm CO₂. This strongly inhibited the development of the zooplankton community, thereby disrupting the trophic transfer of organic matter from primary producers (Riebesell et al., 2018). This food chain alteration prolonged the residence of particulate matter in the water column and caused a strong decline in export flux. In another mesocosm study in a sill fjord located on the Swedish west coast, enhanced primary production under OA increased the survival rate of Atlantic herring (*Clupea harengus*) larvae (Swat et al., 2018). Similarly, a positive bottom-up effect of OA from primary to secondary producers and from secondary producers to secondary consumers has been reported in benthic fish (Goldenberg et al., 2017).

Together with other climate change drivers, coastal eutrophication can promote harmful algal blooms (Fu et al., 2012; Gao et al., 2012), which may lead to seawater
FIGURE 2 | Conceptual diagram showing the food chain effects of ocean acidification (OA). OA increased the contents of phenolic compounds and iodine in the primary producers (phytoplankton and kelp), and these changes lead to accumulation in the secondary producers that feed on them. Whether these food chain effects can scale up in multiple trophic levels (e.g., primary to secondary to tertiary producers) needs further investigation. The orange arrows indicate increased and red ones indicate decreased levels of the compounds, growth or reproduction.

basification (increase in pH) and thus override the signal from OA (Flynn et al., 2015). Basification during bloom development would act independently or interactively with other factors to influence algal growth and blooms succession (Macedo et al., 2001; Hansen, 2002; Hinga, 2002; Flynn et al., 2015). Therefore, the impacts of OA on phytoplankton community composition and thus on trophic transfer are somewhat dependent on levels of eutrophication in coastal waters. Moreover, these responses may also vary across different seasons and/or in different regions (Tortell et al., 2002; Rost et al., 2003; Hare et al., 2007; Grear et al., 2017). It is apparent that changes in phytoplankton community succession and/or primary productivity caused by OA will inevitably impact higher trophic levels through food-web interactions, although these effects may differ spatiotemporally with different levels of adaptation to regionally unique environments.

While marine secondary producers such as zooplankton and tertiary producers such as fish can be indirectly affected by OA, through trophic transfer or food-web interactions, additional direct effects of OA often cannot be ruled out. As summarized in the comprehensive review by Nagelkerken and Munday (2016), behaviors of secondary and tertiary producers such as olfaction, phototaxis, laterализation, shelter, and escape can be altered by OA through multiple, non-exclusive mechanisms (also see recent studies by Schunter et al., 2016, 2018; Spady et al., 2018; Jarrold and Munday, 2019; Clark et al., 2020). This in turn will affect species interactions, population dynamics, community structure, and ultimately, biodiversity (Nagelkerken and Munday, 2016). Changes in species interactions are most commonly implicated as proximate causes of population declines and extinctions due to ocean climate changes.

PERSPECTIVES

A lot of progress has been made in understanding how OA affects marine primary, secondary, and tertiary producers directly, yet we are still far from understanding how these effects may transfer across multiple trophic levels (Figure 2). There have been only a handful of studies that investigated how the deterioration in nutritional values of primary producers due to OA may affect secondary producers via food chain effects. Considering that fish are a critical natural resource (Food and Agriculture Organization of the United Nations [FAO], 2014), there is a potential that the food chain effects of OA can reach humans, who rely on fisheries as an important protein source. However, this has not yet been examined in detail, especially with full consideration of how food chain effects could scale up through multiple trophic levels (e.g., primary to secondary to tertiary and then to humans) (Figure 2). Because our understanding of the effects of multiple marine environmental changes on phytoplankton from different functional groups is
still poor, more studies from monocultures to community levels are expected. Furthermore, since primary producers are known to exhibit evolutionary responses to OA (Jin et al., 2013; Hutchins et al., 2015; Collins et al., 2020), how these responses will alter the trophic transfer in food webs should also be considered.

**AUTHOR CONTRIBUTIONS**

PJ and KG contributed to the theoretical designs and data analysis. PJ wrote the manuscript with major contributions from KG and DH. All authors contributed to the article and approved the submitted version.

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**Conflict of Interest:** 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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