



Impacts of Marine Heatwaves on Algal Structure and Carbon Sequestration in Conjunction With Ocean Warming and Acidification

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As the ocean warms, the frequency, duration, intensity, and range of marine heatwaves (MHWs) increase. MHWs are becoming a severe challenge for marine ecosystems. However, our understanding in regard to their impacts on algal structure and carbon sequestration is still deficient or fragmentary, particularly when combined with ocean warming and acidification. In this paper, we reviewed the impacts of MHWs individually and combined with ocean warming and acidification on regime shift in algal community and carbon sequestration of both macroalgae and microalgae. Solid evidence shows that MHWs cause the decline of large canopy macroalgae and increase of turf-forming macroalgae in abundance, leading to the regime shift from kelp forests to seaweed turfs. Furthermore, increased grazing pressure on kelps due to tropicalization facilitates the expansion of turfs that prevent the recovery of kelps through plundering light and space. Meanwhile, MHWs could trigger microalgal blooms and the intensity of algal blooms is regulated by the severity of MHWs and nutrient availability. MHWs could lead to the decrease of carbon burial and sequestration by canopy-forming macroalgae due to depressed growth and increased mortality. The effects of MHWs on the productivity of microalgae are latitude-dependent: negative effects at low and mid-latitudes whilst positive effects at high latitudes. Ocean warming and acidification may accelerate the shift from kelps to turfs and thus decrease the carbon sequestration by canopy-forming macroalgae further. We propose that MHWs combined with ocean warming and acidification would reduce the biodiversity and facilitate the thriving of morphologically simple, ephemeral and opportunistic turfs and diatoms in coastal oceans, and phytoplankton with smaller size in open oceans. This structure shift would not be in favor of long-term carbon sequestration. Future studies could be conducted to test this hypothesis and investigate the impacts of MHWs on carbon sequestration under future ocean conditions.

Keywords: algal bloom, biodiversity, heatwave, carbon sequestration, ocean acidification, ocean warming, algae, seaweed

INTRODUCTION

The term of marine heatwaves (MHWs) was first proposed by Pearce et al. (2011) although the variability of sea surface temperature (SST) has been studied for decades in physical oceanography and climate science (Philander, 1983). MHWs are anomalous warming events that can substantially affect marine ecosystems. The common accepted definition for MHWs is daily temperatures above

90% threshold during a 30-year historical baseline period and lasting at least 5 days (Hobday et al., 2016). MHWs can last from a few days to several months even a year, and can reach thousands of kilometers (Scannell et al., 2016). MHWs are driven by multiple factors, including air-sea heat fluxes, ocean heat advection, large-scale climate variability, etc. (Oliver et al., 2020). It was found that from 1925 to 2016, global average frequency and duration of MHWs increased by 34 and 17%, respectively, resulting in a 54% increase in annual marine heatwave days globally (from 26 to 40 days). Furthermore, these trends are largely driven by increases in mean ocean temperatures, suggesting that further increases in marine heatwave days can be expected under the context of global warming (Oliver et al., 2018; Benthuyesen et al., 2020).

Since the start of the industrial revolution, humans have greatly increased fossil fuel burning and released unprecedented amount of CO₂ into the atmosphere, increasing the CO₂ concentration of atmosphere from 280 ppmv before industrialization to 417 ppmv by July 2021 (NOAA, 2021). Atmospheric CO₂ level is still rising with an approximate rate of 2 ppmv per year (NOAA, 2021). The accumulation of atmospheric CO₂ together with other greenhouse gasses including water vapor, ozone, methane and nitric oxide adds to greenhouse effect, leading to global warming. Human activities have caused about 1°C rise from the pre-industrial period, with a putative range of 0.8–1.21°C (IPCC, 2013). Ocean, as a big carbon sink, has absorbed approximately one third of CO₂ emitted by humans, which, on the other hand, leads to pH decrease termed as ocean acidification (Gao et al., 2012; IPCC, 2013). Ocean warming and acidification are recognized as two major anthropogenic perturbations of today's oceans (Schlüter et al., 2014). They are also two most related global variables to MHWs and their combined effects with MHWs are gaining concerns in recent years (Figure 1).

Marine algae, classified as microalgae and macroalgae, are the key primary producers for marine ecosystems. They supply basic materials and energy for other consumers and therefore play an essential role in maintaining marine ecosystems. Marine algae are the main contributor to marine primary productivity and they contributed about half of O₂ production and CO₂ uptake on the earth, playing an essential role in carbon sequestration and relieving climate change (Falkowski et al., 1998; Raven, 2017). On the other hand, rapid growth and biomass accumulation of some algae species in large scale can form algal blooms, including both microalgal blooms and macroalgal blooms. These blooms can alter algal structure and reduce algal diversity. More importantly, they can significantly impact marine environment, leading to acidification and deoxygenation, causing the death of animals due mainly to the toxins they excreted and thereby disturbing marine ecosystems (Gao et al., 2016; Sakamoto et al., 2021). Therefore, algal diversity is an essential index for a healthy ecosystem. In spite of the importance of algal diversity and carbon sequestration, our understanding on the impacts of MHWs on them is still fragmentary, particularly when combined with ocean warming and acidification. In this study, we first reviewed how MHWs affect algal structure and diversity, and then assessed the impacts of MHWs on algal carbon

sequestration. Given the close connection between MHWs and ocean warming/acidification, the combined effects of them were also reviewed. Both macroalgae and microalgae are involved in the present study.

BIBLIOMETRIC ANALYSIS

We searched the literature through Web of Science in July 2021 with the keywords of “heatwave” AND “algae” OR “seaweed” and as a result 66 articles were found. In the present study, we aimed to investigate the impacts of MHWs alone and their combination with ocean warming/acidification, and thus tried to avoid those only focusing on ocean warming and/acidification. To illuminate the research gap and evaluate trends of MHWs on algae, bibliometric analysis was conducted with VOSviewer 1.6.17. Bibliometric maps of hot keywords and co-authorship in different countries in 66 articles were built. The minimum number of occurrences of a keyword is three and the minimum number of documents of a country is set as one.

IMPACTS OF MARINE HEATWAVES

Algal Structure

Structure Shift of Macroalgae Under Marine Heatwaves

Macroalgae are indispensable components for coastal ecosystems, serving as nurseries and shelters for marine animals. They are especially critical for local communities because they directly modify the ambient environment and influence adjacent habitats (Wernberg et al., 2018). They often dominate shallow-water rocky ecosystems and play an essential role in carbon sequestration and cycle (Ortega et al., 2019). In addition, macroalgae are important marine resources, supplying food, feed, medicine and biofuels for humans (Gao et al., 2018a, 2020). Therefore, the impacts of MHWs on macroalgae raise wide concerns.

Field observations show that MHWs could lead to the decline of large canopy macroalgae in abundance. MHWs in Western Australia led to the lack of seasonality in growth rates and high rates of mortality for crustose coralline algae (Short et al., 2015). Bull kelp (*Nereocystis luetkeana*) forests, historically resilient to fluctuating environmental conditions, experienced unprecedented losses along 350 km of coastline in northern California due to the extreme marine heatwaves between 2014 and 2016, and the once extensive giant kelp forests have not recovered till now (McPherson et al., 2021). Therefore, the multiple-year MHWs lead to a persistently altered ecosystem state with low primary productivity. Furthermore, all bull kelps (*Durvillaea* spp.) were eliminated from Pile Bay in the South Island of New Zealand due to the MHWs during the summer of 2017/18 (Thomsen et al., 2019).

Meanwhile, some species are resistant to MHWs. For instance, it was demonstrated that the MHWs in 2014–2015 did not significantly change the community structure of kelp forests, particularly the biomass of giant kelp *Macrocystis pyrifera* in

large-scale warming event in the North Pacific Ocean did not result in a large change of the community structure of kelp forests in southern California (Reed et al., 2016). The possible explanation is that southern California does not represent either the geographical or thermal limit for the giant kelp *Macrocystis pyrifera* in the northeast Pacific (Graham et al., 2007). Different nutrient utilization strategies may also contribute to the shift from kelps to turfs. Turfs have high nutrient uptake and can rapidly take up the available nutrients and proliferate under replete nutrient conditions (Hein et al., 1995). By comparison, canopy-forming kelps tend to store available nutrients in their tissue and maintain relatively consistent growth rates under changing environments (Lobban and Harrison, 1994). These differences enable turfs to outcompete kelps and rapidly occupy available space when nutrient availability is high (Gorman et al., 2009). Although higher nitrate level could ameliorate the negative impacts of MHWs on growth and photosynthesis of kelps (Fernández et al., 2020), it is not enough to compete with fast-growing turfs. The presence of turfs could inhibit the recruitment of kelps and therefore lead to a comprehensive loss of kelps (Connell et al., 2008; Connell and Russell, 2010).

In addition to bottom-up effects, biological factors also drive loss of canopy-forming macroalgae and thriving of turfs. Some invertebrates, crustaceans and fish feed on kelp can result in the decline of kelp biomass and enhancing fragmentation and breakage of kelp through grazing (Krumhansl et al., 2011; Zarco-Perello et al., 2017). Another organism that prefers to graze erect macroalgae is sea urchins. Altered environment conditions and the removal of top predators trigger blooms of sea urchin that drives regime shifts from kelp forests to coralline algal-dominated “barrens” (Filbee-Dexter et al., 2016). MHWs can induce poleward range shifts of subtropical and tropical herbivores, leading to increased grazing pressure (Zarco-Perello et al., 2017). A substantial influx of tropical fish herbivores can lead to a 400% increase in grazing rates compared to healthy coral reefs (Filbee-Dexter and Wernberg, 2018). This enhanced grazing pressure facilitates the shift from kelps to turfs and prevents the recovering of kelp forests (Bennett et al., 2015). In addition, rising temperatures could increase the recruitment and growth of epiphytes that coat the kelp blades. Overgrowth of these epiphytes reduces the strength of the kelp tissue, promotes breakage and canopy loss and hence contributes to shifts to turfs (Andersen et al., 2011; Filbee-Dexter and Scheibling, 2012). In contrast, turfs have a higher tolerance to high temperatures compared to their grazers, indicating decreased grazing pressure under MHWs (Mertens et al., 2015). The bottom-up and top-down may impose synergistic effects on the shift from kelps to turfs.

Microalgal Bloom During Marine Heatwaves

Microalgae usually occur in low concentrations due mainly to nutrient limitation. However, concentrations of microalgae could also reach very high levels in coastal waters where nutrient availability is high, termed red tides or brown tides. Among 5,000 + microscopic algae species existing worldwide, about 300 species can cause high concentrations of red tides, including toxic species in dinoflagellates, diatoms, Haptophyceae, and Cyanophyceae (Zohdi and Abbaspour, 2019), in which the

pelagophyte *Aureococcus anophagefferens* is the key causative species for brown tides (Tang et al., 2019).

Compared to macroalgae, impacts of MHWs on microalgae are less studied (Figure 1). A noteworthy phenomenon is that MHWs usually induce microalgal blooms. In 2013, MHWs in South Australia experienced unusually high and variable water temperatures (5°C above the historic average), lasted for 1 week and led to the algal bloom dominated by a harmful diatom, *Chaetoceros coarctatus* (Roberts et al., 2019). *C. coarctatus* could be the dominant species because it is tolerant to high temperature (Hasle and Syvertsen, 1997). Extreme MHWs could lead to extreme HABs. In late spring 2015, an unprecedented bloom of chain-forming diatom *Pseudo-nitzschia australis* occurred along the west coast of North America, spanning from central California to at least as far north as British Columbia during the multiple-year MHWs “blob” (Trainer et al., 2020). *Pseudo-nitzschia australis* has high heat-tolerant and affinity of nitrate and ammonium (Cochlan et al., 2008) that provides this species with a competitive advantage for acquiring nitrogen (N) under N-depleted conditions (Kudela et al., 2010). *Pseudo-nitzschia australis* is a toxic diatom that produces biotoxin domoic acid (DA). This harmful algal bloom generated the highest particulate concentrations of DA ever recorded in Monterey Bay, California (Ryan et al., 2017) and DA was detected in many animals—including porpoises, whales, dolphins, sea lions, seals, and seabirds—spanning the largest geographic extent ever recorded (McCabe et al., 2016). DA can cause illness and mortality of marine organisms and threaten human health through food chain transfer. Therefore, the outbreak of HAB and the associated DA led to the closures of fisheries, such as Dungeness crab, rock crab, razor clam, etc. Local economy suffered serious losses from the closures of fisheries, with a USD\$97.5 million decrease in revenue for the commercial Dungeness crab fishery alone occurred in 2015 compared to 2014 (Trainer et al., 2020). The frequent occurrence of red tides induced by MHWs indicates that MHWs could reduce biodiversity of microalgae and even higher trophic levels via food chain.

Reasons for Algal Blooms Related to Marine Heatwaves

Warming and MHWs could enhance stratification of the upper ocean and hence hinder the nutrient transport from deeper to surface waters, leading to reduced nutrient availability in the upper waters (Trainer et al., 2020). Therefore, phytoplankton species with unique nutrient acquisition strategies are able to successfully outcompete under these nutrient limiting conditions and develop to blooms. These strategies include enhanced “surge” macronutrient uptake rates, unique trace metal uptake capabilities, mixotrophy, and swimming to areas where nutrient levels are higher (Smayda, 2010). In addition, bloom-forming algae can produce and excrete toxins that can kill not only their grazers but also other algal species (Granéli et al., 2008). Killing the nutrient-competing phytoplankton species enables harmful species to freely utilize limiting nutrients. The decreased grazing pressure and competitors facilitate the harmful algae to form a dominant position. Therefore, altered intensity of stratification or ocean mixing and the sequent changes in nutrient availability

could be a main link between marine heatwaves and microalgal blooms/composition.

Meanwhile, longstanding and large-scale algal blooms must be supported by enough nutrient availability. For instance, the largest harmful algal bloom ever recorded that extended from southern California to southeast Alaska during the 2014–2016 marine heatwave, is clearly supported by the spring upwelling (Trainer et al., 2020). Furthermore, the analyses of SST, chlorophyll *a* and nitrate based on satellite observations and *in situ* climatology show that algal blooms associated with MHWs are weaker in nutrient-poor waters and stronger in nutrient-rich waters (Hayashida et al., 2020). Given strengthened stratification and decreased nutrient availability in upper waters in future oceans, enhanced occurrence of weaker blooms caused by marine heatwaves could be expected in coming decades.

Recovery and Acclimation of Algae

Whether algae would recover after MHWs firstly depends on the intensity of MHWs they are exposed to. Both three and six degrees centigrade elevation of MHWs reduced gross photosynthetic rate and light utilization efficiency of the sugar kelp *Saccharina latissimi* (Nepper-Davidsen et al., 2019). During the recovery period, thalli experiencing the lighter MHWs recovered to the same levels as control but thalli experiencing the heavier MHWs still had suppressed performance compared to the control (Nepper-Davidsen et al., 2019). Similarly, the macrophyte community structure at shallower sites did not show any recovery sign after the 2011 Western Australian MHWs while the deep populations generally persisted due to the lighter MHWs it experienced (Giraldo-Ospina et al., 2020). Recovery capacity is also species-dependent. *Devalerea/Palmaria*, encrusting coralline algae, and *Halosaccion* suffer from continuous decrease during/after the MHWs in the Northern Gulf of Alaska, while *Cladophora/Chaetomorpha*, *Fucus*, and *Odonthalia/Neorhodomela* decreased during MHWs but appeared to be recovering after MHWs (Weitzman et al., 2021). In most cases, large-scale reversal from turfs to kelp forests has not been found after MHWs (Filbee-Dexter and Wernberg, 2018). A possible reason is that human-driven environmental changes such as ocean warming or coastal eutrophication are favoring the growth and thriving of turfs over kelps. Turfs can prevent the recovery of kelps through plundering light and space and by reducing the availability of kelp propagules. In addition, increased grazing pressure on kelps due to tropicalization facilitated the expansion of turfs while preventing the kelps from recovering (Bennett et al., 2015).

Some marine organisms demonstrate ecological memory or acclimation to MHWs. In 2016, an exposure to 8–9°C MHWs led to over 90% probability of severe corals (microalgal symbionts) bleaching on the Great Barrier Reef while the same intensity of MHWs in 2017 induced a 50% probability of severe bleaching (Hughes et al., 2019). In parallel, adult brown seaweed *Fucus vesiculosus* experienced three MHWs had higher growth rate (0.57 ± 0.36 mm/day) than that (0.45 ± 0.40 mm/day) experienced one MHW, although both of them were lower than

the control (0.67 ± 0.08 mm/day) that did not experience MHWs, suggesting the acclimation to MHWs (Saha et al., 2020).

CARBON SEQUESTRATION BY ALGAE UNDER MARINE HEATWAVES

Carbon sequestration by algae could be defined as the process that CO₂ is captured and fixed by algae and then stored in oceans for long times (usually more than 100 years) in the form of sediments or refractory dissolved organic carbon. Unfortunately, very few documents have been found on how many amounts of CO₂ are sequestered by algae in the context of MHWs (Figure 1). In this study, we mainly reviewed the impacts of MHWs on carbon fixation or biomass in algae instead because the sequestered carbon is closely related to fixed carbon. For instance, sequestered carbon by wild macroalgae and phytoplankton accounts for 11.4% and 1.2–2.4% of their net primary production, respectively (Legendre et al., 2015; Krause-Jensen and Duarte, 2016).

The decreased growth and high mortality of canopy-forming macroalgae caused by MHWs would lead to the decrease of carbon burial and sequestration by these macroalgae. However, the lost carbon may be offset by increased biomass of invasive macroalgae or turfs. It has been found that the amount of fixed carbon by a fast-growing non-indigenous kelp *Undaria pinnatifida* in a 6-month period is close to that by a native *Cystophora torulosa* in a year (Tait et al., 2015), indicating that higher daily rates of carbon fixation offset the limited growing season of *U. pinnatifida*. In parallel, the presence of the invasive brown alga *Sargassum horneri* did not affect community production although it contributed to ephemeral increases in gross community production (Sullaway and Edwards, 2020), which may be due to the increased community respiration. The constant erosion of tissue at the distal margins and higher biomass variation for annual lifecycle make *S. horneri* have inherently higher turnover rates compared to perennial canopy-forming kelp (Sullaway and Edwards, 2020), which may reduce long-term carbon sequestration of a community dominated by ephemeral seaweeds.

In terms of microalgae, all El Niño events in 1982–1983, 1997–1998, and 2015–2016 led to low phytoplankton biomass and primary productivity in the northeast Pacific. The decreased primary productivity could be attributed to weak upwelling and/or a deep pycnocline/nutricline caused by warm events, each of which reduced nutrient supply to the surface mixed layer (Jacox et al., 2016). On the other hand, Montie et al. (2020) examined the effects of 19 extreme summer MHWs on chlorophyll *a* (chl *a*) concentration in the Southern Ocean (SO) and found that extreme summer MHWs increased surface chl *a* by ~80% compared to control sites, with the strongest effects in the coldest regions. The MHWs in the New Zealand region imposed different impacts on primary production and generally reduced surface phytoplankton biomass in the north of the Subtropical Front but increased biomass in south of the Subtropical Front (Chiswell and Sutton, 2020). The differential impacts might be related to the local temperatures. The temperatures in north of the Subtropical Front are much

higher than those in south of the Subtropical Front. Therefore, temperature rise may be beneficial to phytoplankton at lower temperatures but be beyond the thermal limit for phytoplankton at higher temperatures.

Sen Gupta et al. (2020) systematically identified commonalities in the local processes and atmospheric conditions that initiate and terminate extreme MHWs during the period from 1982 to 2017 and analyzed regionally dependent responses of surface chlorophyll-*a* concentration to these events. The results showed that decreased chlorophyll-*a* concentrations occurred during the majority of extreme MHWs. On the other hand, increased productivity was also found during some MHWs. The effects of MHWs depended largely on latitude. The general pattern is that negative effects occurred at low and mid-latitudes while positive effects came up at high latitudes. The possible reason is that intensified stratification suppresses the supply of nutrients from deeper to the upper oceans, which is fatal for phytoplankton in oligotrophic tropical and subtropical waters where nutrient levels are extremely low. By contrast, phytoplankton at high latitudes are more often light rather than nutrients limited (Falkowski, 1994); stratification can reduce mixing and thus expose algae to more solar radiation, increasing light availability and facilitating photosynthesis and growth of phytoplankton.

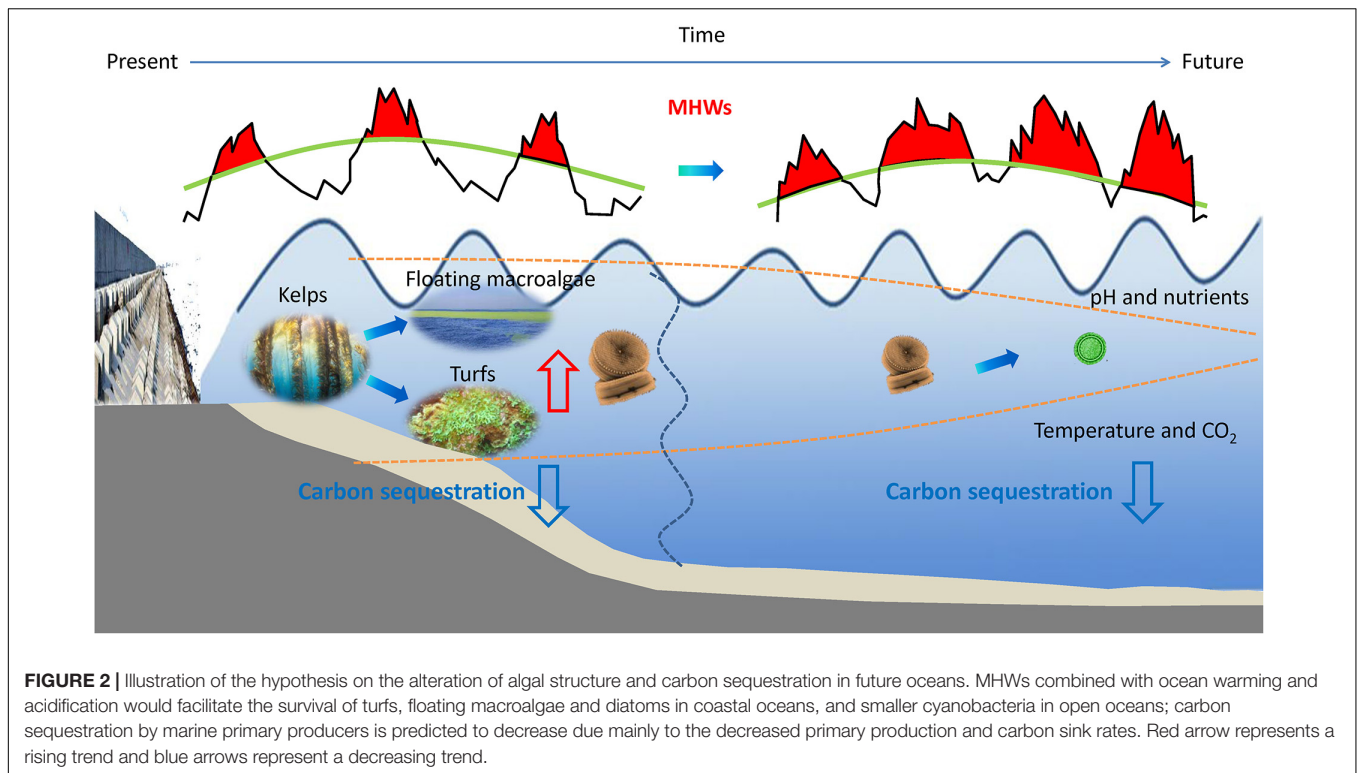
MARINE HEATWAVES COMBINED WITH OCEAN ACIDIFICATION AND WARMING

Algal Structure

Apart from microalgal blooms, macroalgal blooms have also gained increased concerns. It has been shown that macroalgal bloom is in a rising trend, which may be related to enhanced eutrophication (Smetacek and Zingone, 2013). Furthermore, Xu et al. (2017) found that ocean acidification could enhance carbon and nitrogen assimilation rates of a golden tide alga and thereby growth rates, indicating that golden tides may be stimulated by future ocean acidification. Gao et al. (2017a) investigated the effects of ocean acidification, warming and eutrophication on a green tide alga and found the combination of these three factors increased settlement, germination of gametes and growth of juvenile and adult thalli of *Ulva rigida*, stimulated reproduction of adult thalli and thus shortened its life cycle. Accordingly, green tides are predicted to increase in future ocean conditions (warming and acidification), suggesting the increase of floating macroalgae. Furthermore, Britton et al. (2020) investigated the effects of MHWs on the physiological performance of the brown seaweed *Phyllospora comosa* in the current and future (warming and acidification) ocean conditions. MHWs decreased its growth rates in both current and future conditions. Warming and acidification also reduced its growth rates. Therefore, the combination of MHWs, warming and acidification resulted in the lowest growth rate of *P. comosa*. *P. comosa* down-regulated carbon dioxide concentrating mechanism in the future conditions and the saved energy arising from this down-regulation was invested in the adjustment of fatty acid composition. Although it seems a response to a changed

environment, it did not alleviate the negative effects of marine heatwaves and ocean warming on the growth of *P. comosa*. In parallel, Falkenberg et al. (2013) found that ocean acidification increased the growth of turf-forming algae but did not affect kelp's growth. The differential response may be related to their carbon acquisition mechanisms. Some turf-forming algae acquire CO₂ through passive diffusion, whilst complex canopy-forming species, like kelp, possess efficient CCMs (Hepburn et al., 2011; Falkenberg et al., 2013). Therefore current CO₂ level should be more limited for turfs than kelps. From this point of view, ocean acidification may enhance the competition of turfs against kelps and exacerbate the trend of kelp loss caused by MHWs. In addition, ocean warming trends to increase grazing pressure of kelps but reduce it for turfs (Mertens et al., 2015), which accelerates the shift from kelps to turfs.

Increased CO₂-driven climate change has evident impacts on species composition and size structure of phytoplankton (Falkowski and Oliver, 2007; Winder and Sommer, 2012). Hinder et al. (2012) found the abundance of dinoflagellates decreased while diatoms increased in the northeast Atlantic and North Sea across a 50-year (1960–2009) time series. This shift was attributed to the combined effect of ocean warming and increasingly windy conditions in summer. On the other hand, it has been predicted that cyanobacteria would gain more competitive advantages against diatoms in future open oceans (Falkowski and Oliver, 2007; Finkel et al., 2010). The contrasting findings above are probably due to the change of turbulent mixing. In coastal oceans, the increase of thermal contrast between the continents and the coastal oceans due to global warming may strengthen wind-driven upwelling, which would enhance the competitive advantage of diatoms (Falkowski and Oliver, 2007). Diatoms have a storage vacuole for nutrients which makes them acclimate well to the environment with pulsed nutrient supply (Tozzi et al., 2004). In addition, diatoms have distinctive photoprotection mechanisms to cope with rapid fluctuations of underwater light environment (Gao et al., 2018c,d). The features above support the dominance of diatoms in intensified mixing environments. In contrast to coastal oceans, mixing would be weakened and stratification would be strengthened in future open oceans, leading to decreased nutrient supply from deeper waters. Smaller phytoplankton such as cyanobacteria would be favored in a nutrient limited environment because they have larger ratios of cell volume to surface area and higher nutrient uptake efficiency. The combined effects of MHWs and ocean warming/acidification on phytoplankton community structure have not been documented although the combination of warming and heatwaves catalyze blooms of buoyant cyanobacteria in lakes (Bartosiewicz et al., 2019; Filiz et al., 2020). One important reason that cyanobacteria can outcompete other phytoplankton taxa is that cyanobacteria have higher specific growth rates at higher temperatures compared to other taxa (Jöhnk et al., 2008). To summarize, we propose that in future scenarios, diatoms would have competitive advantages in coastal oceans but their territory would be nibbled by smaller cyanobacteria such as *Prochlorococcus* and *Synechococcus* in open oceans (Figure 2). More studies are needed to test this hypothesis.



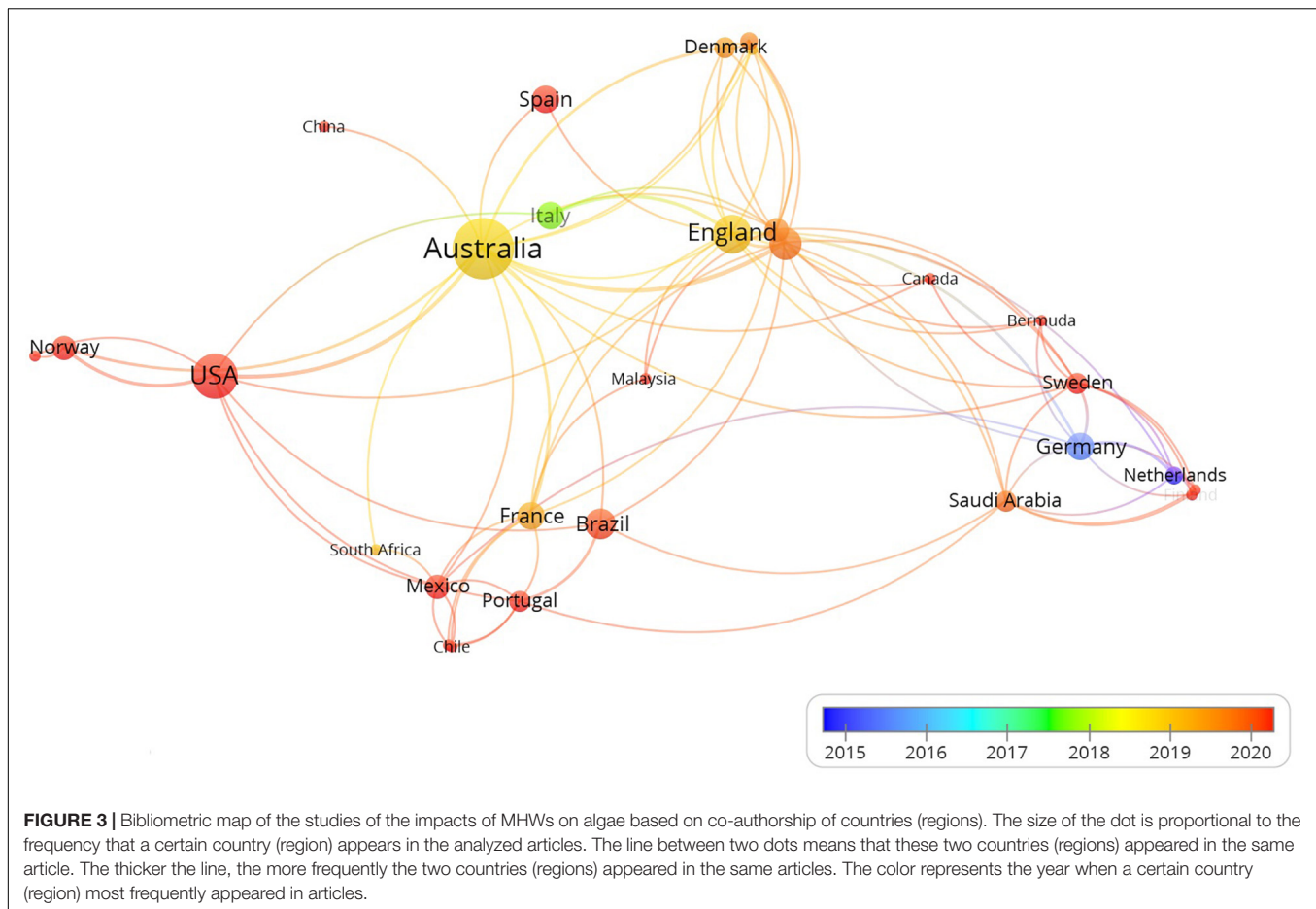
Studies mentioned above investigated the impacts of climate change variables on macroalgae or microalgae separately. However, in the natural environments, they co-occur in coastal oceans and the increase of floating macroalgae expands the overlap between them. In the same ecological niche, macroalgae and microalgae inevitably compete for resources, like nutrients, light and space. Sun et al. (2018) found that there was a negative correlation between the occurrence of macroalga *Ulva prolifera* and chlorophyll-*a* concentration in the Southern Yellow Sea, China. Who will be the winner in future oceans? In contrast to the studies based on individual investigation on microalgae or macroalgae, Gao et al. (2019a) co-cultured red tide forming alga *Skeletonema costatum* and green tide forming alga *Ulva linza* under current and future ocean conditions. Compared to *U. linza*, *S. costatum* had more advantages in future warming and acidification conditions, which may suppress the development of green tides caused by *Ulva* species. The decreased trend of green tides and increased occurrence of red tides in Chinese seas in recent years also support this finding (China Marine Disaster Bulletin, 2000-2020). Microalgae, particularly some bloom-forming species, have higher thermal tolerance compared to macroalgae (Jöhnk et al., 2008). Therefore, we predict that microalgae may win in the competition with macroalgae in future oceans with frequent MHWs.

Carbon Sequestration

According to Britton et al. (2020), the combination of MHWs, warming and acidification significantly decreased growth of the brown seaweed *Phyllospora comosa*. In addition, warming or acidification could enhance the respiration rate of

seaweeds, which may result in decreased net carbon fixation (Gao et al., 2019b; Liu et al., 2020). The decreased growth and carbon fixation would lead to the decline of carbon that is finally sequestered considering that there is a relatively stable proportion of carbon sequestration to carbon fixation (Krause-Jensen and Duarte, 2016). In parallel, the kelp loss in Australian over the past decades has led to 0.45 Tg C of lost standing stock and 0.06 Tg C of lost sequestration annually due to MHWs, warming and climate-driven changes including sea urchin overgrazing and the influx of tropical herbivores with warmer waters (Filbee-Dexter and Wernberg, 2020). Therefore, decreased CO₂ sequestration by seaweeds could be expected in future ocean conditions although more studies need to be conducted. In addition, increased CO₂ did not affect carbon content of turfs but enhanced nitrogen content, leading to decreased C:N ratios. In contrast, neither C nor N content of kelps was affected by increased CO₂ and thereby the C:N ratio kept consistent (Falkenberg et al., 2013). Given the shift from kelps to turfs, these findings indicate that ocean acidification may reduce carbon fixation and hence sequestration of seaweed community by affecting C:N ratio even if seaweed biomass does not change.

In terms of microalgae, some studies have shown that ocean acidification or warming could stimulate primary production (Schippers et al., 2004; Gao et al., 2017b), but the combination of ocean warming and acidification or the interactions with other environmental drivers could reduce ocean primary productivity (Gao et al., 2012, 2017b). In fact, the primary productivity of global phytoplankton shows a decreasing trend in recent decades (Gregg and Rousseaux, 2019; Kulk et al., 2020). The trend is very



likely to be driven by the reduced nutrient availability caused by ocean warming and consequently enhanced stratification. The reduced primary productivity that represents less carbon is fixed would result in a decline of carbon sequestration. Furthermore, ocean warming could also stimulate the remineralization of fixed carbon by heterotrophic microorganisms and thus lead to a further decline of carbon sequestration (Cavan et al., 2019). The combined effects of ocean warming and acidification with MHWs on carbon sequestration by microalgae have not been documented. However, carbon sequestration by phytoplankton could be predicted to decrease in future warmer and CO₂-enriched oceans due to the community shift from larger cells to smaller cells from diatoms to cyanobacteria because larger cells sink faster than smaller cells and diatoms sink faster than cyanobacteria (Falkowski and Oliver, 2007; Winder and Sommer, 2012).

CONCLUSION AND FUTURE RESEARCH NEEDS

Conclusion

As CO₂ is emitted continuously, MHWs are projected to be exacerbated by rising global temperatures. However, how

(micro) algae respond to MHWs is fragmentary, particularly in terms of carbon sequestration and in conjunction with ocean warming and acidification. In this study, through reviewing the published data, we find that MHWs are driving the regime shift from canopy-forming to turf-forming and floating macroalgae and inducing microalgal blooms. It seems that MHWs would reduce carbon sequestration of macroalgae due to the quick turnover rate of carbon in turf-forming and floating macroalgae. Therefore, this structure shift would reduce effective services that canopy-forming can provide. Meanwhile, MHWs combined with ocean warming and acidification trends to facilitate the growth of smaller phytoplankton and thus reduce carbon sink and sequestration by phytoplankton (Figure 2).

Research Needs

(1) Impacts on seaweed cultivation

With the increasing knowledge on seaweed values in food, chemical industry, and medicine, worldwide seaweed cultivation is expanding. In 2005, the world production of seaweeds from cultivation increased from 13.5 million tons in 2005 to 32.4 million tons in 2018 (Ferdouse et al., 2018; FAO, 2020). However, most studies till now focus on natural kelp forests and little is known regarding the effects of MHWs on farmed seaweeds. In recent years, farmed seaweeds often suffer from sudden decay

and death, which may be related to increased MHW events. Since farmed seaweeds play an important role in remitting coastal eutrophication in addition to supply marine vegetables (Xiao et al., 2017; Gao et al., 2018b), future studies should pay more attention to the potential effects of MHWs on production and biochemical composition of farmed seaweeds.

(2) Combined effects of MHWs and other factors

Algae at different locations respond differentially to MHWs. In addition to the species differences, the regulation by other factors, including background temperature, nutrient and light levels, desiccation stress and grazing pressure, may be the main driver. Therefore, more MHWs-simulating studies should be conducted to disentangle impacts caused by the extreme temperature increases of MHWs itself from co-occurring other factors, and to understand the combined effects of MHWs and other potential stressors. In addition, as climate change continues, our understanding on how MHWs affect algae in future warming and CO₂-enriched oceans needs to be advanced.

(3) Interaction between macroalgae and microalgae

Most studies investigated the impacts of MHWs on microalgae or macroalgae individually. However, microalgae and macroalgae overlap in coastal waters and compete for resources. The attachment of microalgae on the surface of macroalgae could negatively affect the growth of macroalgae particularly for the juvenile, mainly through reducing light and nutrient availability. Meanwhile, macroalgae could inhibit the growth of microalgae around them via excreting allelopathic chemicals (Tang and Gobler, 2011; Gao et al., 2019a). Therefore, microalgal blooms are significantly inhibited in the areas where macroalgae are intensively cultivated. On the other hand, sporadic microalgal blooms are found in macroalgae farms in recent years. Given differential response of microalgae and macroalgae to MHWs, the current balance between microalgae and macroalgae may be broken up by MHWs. Therefore, given the significance of macroalgae cultivation and harmful algal bloom, it is urgent to investigate whether the interaction of microalgae and macroalgae will be altered by MHWs.

(4) Carbon path of algae under MHWs

Algae take up CO₂ in seawater or air and convert it into organic carbon. Apart from meeting the demand for their own growth and metabolism, a considerable proportion of fixed organic carbon is excreted to the environment as the form of dissolved organic carbon (DOC). Labile DOC can be consumed and utilized by bacteria and the remaining part is resistant to external factors, termed as refractory DOC. Refractory DOC can be stored in the oceans for thousands of years and play an essential role in carbon sink of oceans (Santos et al., 2021). Previous studies refer to photosynthetic performance of algae but it is unknown how MHWs would affect the excretion of DOC from algae and the transformation from labile DOC to refractory DOC (Figure 1). To understand the impacts of MHWs on carbon

sequestration of oceans, studies on this field must be carried out.

(5) MHWs prediction and macroalgae monitoring

Due to the compelling evidence for devastating impacts of MHWs on marine ecosystems, precise prediction of MHWs is urgently needed, particularly considering that global warming would enhance the occurrences and intensities of MHWs. In spite of increasing understanding on processes and mechanisms of MHWs, MHWs-prediction systems are in their infancy and MHWs forecast is not set in most countries. To guide marine conservation, fisheries management and aquaculture activities and reduce ecological and economic loss, MHWs predictability must be improved. In addition, to link the variation of macroalgal forests with MHWs, it is compulsory to know the dynamic distribution of benthic macroalgae. Although there are some programs monitoring macroalgal forests, coverage is very patchy (Duffy et al., 2019). Many regions are difficult to survey because of the cold, turbid, deep, and/or wave-exposed environments that hinder accessibility. Remote surveying with satellites seems to be promising but the spatio-temporal resolution needs to be improved considering that macroalgae usually inhabit in narrow coastal areas and the distribution of many macroalgal forests are highly dynamic across time and space.

(6) Global research and cooperation

Current studies on MHWs have mainly been carried out in western countries, particularly developed countries, such as the United States, Australia and the United Kingdom; while little information from Asian and African countries is available (Figure 3). MHWs occur in global seas and oceans. The research disequilibrium hinders us from understanding the global impacts of MHWs. Asia and Africa are the main ground of seaweed cultivation. Therefore, there is urgent need to conduct or strengthen the MHWs research in developing countries. International cooperation is strongly encouraged because it facilitates the success of research in countries (regions) where MHWs are poorly understood and the formation of uniform methodologies.

AUTHOR CONTRIBUTIONS

GG contributed to the theoretical designs, data analysis, and writing of the manuscript. XZ, MJ, and LG contributed to writing of the manuscript. All authors contributed to the article and approved the submitted version.

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