Effects of climate change factors on marine macroalgae: A review

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Abstract

Marine macroalgae, the main primary producers in coastal waters, play important roles in the fishery industry and global carbon cycles. With progressive ocean global changes, however, they are increasingly exposed to enhanced levels of multiple environmental drivers, such as ocean acidification, warming, heatwaves, UV radiation and deoxygenation. While most macroalgae have developed physiological strategies against variations of these drivers, their eco-physiological responses to each or combinations of the drivers differ spatiotemporally and species-specifically. Many freshwater macroalgae are tolerant of pH drop and its diel fluctuations and capable of acclimating to changes in carbonate chemistry. However, calcifying species, such as coralline algae, are very sensitive to acidification of seawater, which reduces their calcification, and additionally, temperature rise and UV further decrease their physiological performance. Except for these calcifying species, both economically important and harmful macroalgae can benefit from elevated CO_2 concentrations and moderate temperature rise, which might be responsible for increasing events of harmful macroalgal blooms including green macroalgal blooms caused by *Ulva* spp. and golden tides caused by *Sargassum* spp. Upper intertidal macroalgae, especially those tolerant of dehydration during low tide, increase their photosynthesis under elevated CO_2 concentrations during the initial dehydration period, however, these species might be endangered by heatwaves, which can expose them to high temperature levels above their thermal windows' upper limit. On the other hand, since macroalgae are distributed in shallow waters, they are inevitably exposed to solar UV radiation. The effects of UV radiation, depending on weather conditions and species, can be harmful as well as beneficial to many species. Moderate levels of UV-A (315–400 nm) can enhance photosynthesis of green, brown and red algae, while UV-B (280–315 nm) mainly show inhibitory impacts. Although little has been documented on the combined effects of elevated CO_2, temperature or heatwaves with UV radiation, exposures to heatwaves during midday under high levels of UV radiation can be detrimental to most species, especially to their microscopic stages which are less tolerant of climate change induced stress. In parallel, reduced availability of dissolved O_2 in coastal water along with eutrophication might favour the macroalgae's carboxylation process by suppressing their oxygenation or photorespiration. In this review, we analyse effects of climate change-relevant drivers individually and/or jointly on different macroalgal groups and different life cycle stages based on the literatures surveyed, and provide perspectives for future studies.

Macroalgae have substantial distributions in intertidal zones, playing an important role in coastal ecosystems due to contributions to biological production and services as sheltering of marine animals and food resources (Falkowski and Raven, 2013). Sea–farming of economically important macroalgae has been considered to be a biological pump in sequestration of CO_2 (Chung et al., 2017; Zhang et al., 2017). Most macroalgae are benthic species, experiencing dramatic changes in environmental conditions due to tidal changes and runoffs from land. Those species found in upper intertidal zones
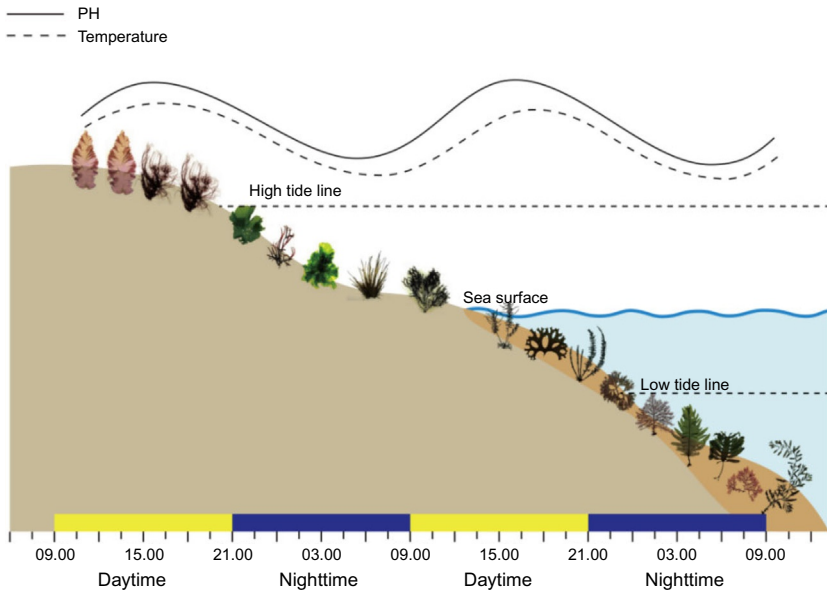
Fig. 1 Conceptual illustration of diel changes in pH and seawater temperatures that macroalgae experience in coastal waters.

are known to be tolerant of dehydration and high solar radiation as well as temperatures (Gao et al., 1999). The macroalgae that occur in lower intertidal regions are less tolerant of desiccation, exhibiting contrasting physiological traits with the upper intertidal ones. Nevertheless, they experience similar patterns of fluctuating solar radiation and temperature (Fig. 1).

During daytime, photosynthesis of marine primary producers including macroalgae produces O_2 and assimilates CO_2, raising seawater pH (Cornwall et al., 2013a,b; Gao et al., 1991), known as a process of seawater alkalization. During the nighttime, on the contrary, no O_2 is biologically produced due to lack of photosynthesis. All marine organisms including macroalgae continue to respire, consuming O_2 and releasing CO_2 into seawater, then leading to pH decline and thereby enhancing acidification of seawater (Gao et al., 1991) along with global ocean acidification. In parallel with temperature, the pH of coastal water also experiences a daily fluctuation with significant rise during daytime and a clear drop at night (Fig. 1). The daily ranges of pH fluctuation can even reach 3 units under some extreme niche conditions such as intertidal rockpools (Raven, 2011).

Macroalgae are exposed to more dynamic changes in coastal waters compared to terrestrial plants or phytoplankton in pelagic waters, and additionally

are also affected by ocean climate changes, such as ocean warming and acid–
ification, which alter the magnitude or fluctuation ranges of the stressors.
Along with ongoing ocean global changes, distribution of macroalgae both
horizontally or vertically might be changed, and economically important
species might become endangered, when the combination of the multiple
stressors overrun the species-specific tipping points for survival. Here, we
analyse ocean global change drivers and review the advances made about
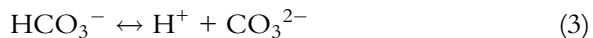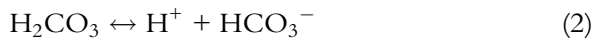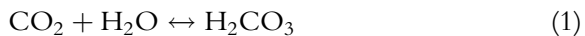their effects on macroalgae.

1. Ocean global change drivers

1.1 Increasing CO_2 concentration and ocean acidification

Since the start of industrial revolution, humans have greatly increased fossil
fuel burning and released unprecedented amount of CO_2 into the atmo-
sphere, increasing the CO_2 concentration of atmosphere from 280 ppmv
before industrialization to the current 414 ppmv (July 2020, www.co2.
earth), and it is still rising with an approximate rate of 2 ppmv per year
(Moreira and Pires, 2016).

   The oceans cover about 71% of the earth surface with a huge interface
with the atmosphere, absorbing about one-third of the anthropogenically
emitted CO_2 (Sabine et al., 2004). When CO_2 dissolves into seawater, car-
bonate chemistry changes as follows:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \tag{1}$$

$$H_2CO_3 \leftrightarrow H^+ + HCO_3^- \tag{2}$$

$$HCO_3^- \leftrightarrow H^+ + CO_3^{2-} \tag{3}$$

Firstly, CO_2 combines with a water molecule to form carbonic acid (Eq. 1),
which is unstable and disassociates to bicarbonate and hydrogen ions
(Eq. 2), and the bicarbonate ion can further dissociate to a carbonate ion
and a hydrogen ion (Eq. 3), depending on the pH of waters. All of these
equations are reversible, which in fact constitutes a pH buffer system.
The ocean carbonate system not only provides inorganic carbon sources
for photoautotrophs (primary producers), but also creates a chemically sta-
ble environment for marine organisms. Carbonate ion contents of seawater
are especially important for marine calcifiers, as the calcified skeleton is
made of calcium carbonate. However, rising CO_2 concentration pushes
the 1st and 2nd reactions to the right, while the elevated hydrogen ions
in Eq. (2) lead to ocean acidification (OA) and drive the 3rd reaction
towards the left. Decreased pH or elevated hydrogen concentrations also

pushes the buffer system from the carbonate side to the bicarbonate side, thereby changing the concentrations of different types of dissolved inorganic carbon (DIC). Consequently, during the process of CO_2 dissolution into the oceans, pCO_2, hydrogen and bicarbonate ions increase while pH and carbonate ions decrease. Currently, 92% of total seawater DIC is comprised of bicarbonate ions, about 7% is carbonate ions and <1% is in the form of CO_2, with the pH being about 8.05 and total alkalinity (A_T) about $2200\,\mu mol\,kg^{-1}$. With increasing dissolution of CO_2, increased availability of CO_2 and DIC is accompanied with reduced pH and carbonate ions. Such a chemical environmental change, known as ocean acidification (OA), has been suggested to cause serious consequences for marine organisms and ecosystems. A drop of carbonate ions decreases the saturation of calcium carbonate (Ω), on which marine calcifiers rely. Different oceanic areas have differentiated carbonate levels due to differences in temperature and salinity, with the relatively small Arctic areas accounting for 41% that of the larger tropical areas. Nevertheless, OA decreases pH and Ω levels and alters other carbonate chemistry parameters in both open oceans and coastal waters.

Dissolution of the fossil fuel-derived CO_2 into seawater has already increased seawater hydrogen ions by >34%, which is projected to increase by about 150% (a pH drop of 0.4 unit) in surface oceans by the end of 21th century (Bates et al., 2012; Gattuso et al., 2015). Such a tempo of pH decline has been suggested to be the fastest recorded in 300 million years in terms of historical ocean acidification events (Hönisch et al., 2012). OA can be propelled by other processes including the mineralization of marine organisms and degradation of dissolved organic matters (DOM) (Mostofa et al., 2016). The average rate of global OA is about 0.002 unit drop of pH per year. Coastal waters are more susceptible to human activities including high levels of eutrophication and degradations of organic matters; therefore, the progress of acidification in coastal waters has been suggested to be about 12% faster compared to that of pelagic waters (Cai et al., 2011). OA has been proved to enhance respiration and reduce calcification in macroalgae (Gao and Zheng, 2010; Hurd et al., 2009; Xu and Gao, 2012a; Zou et al., 2011a,b), which may further accelerate acidification in coastal waters, especially during nighttime.

1.2 Ocean warming

The accumulation of atmospheric CO_2 together with other green house gases including water vapour, 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. The global rise of temperature exhibits regional differences. The polar regions, for example, have shown a much faster temperature rise than the global average. Global warming can increase the occurrence of extreme climate events, leading to unexpected heatwaves, strong rainfalls in some regions and drought in other regions. It has also caused significant changes of El Niňo in the eastern Pacific over the past 20 years (Lian et al., 2017), which appeared to trigger more extreme climate events. For example, 1 °C of temperature rise may lead to a 25% increase of typhoon events (Bigg and Hanna, 2016).

As a huge heat reservoir, the oceans have absorbed up to 70% of the earth total heat gain since 1970s (Gattuso et al., 2015), which eventually causes ocean warming. The rise of temperature even can be traced to 2000 m deep in oceans, though the sea surface temperature (SST) is rising much faster. The SST has risen by 1 °C over the past 100 years and is projected to rise by 2–4 °C further by the end of this century (Gattuso et al., 2015). Different oceans may show different ranges of temperature changes. In contrast to the global average ocean warming, the East China Sea has been suggested to have warmed faster (Cai et al., 2017; Hoegh-Guldberg et al., 2014).

1.3 Marine heatwaves

Elongated periods of extreme hot weather are responsible for marine heatwaves (MHWs), that may stretch out for thousands of kilometres. Under the current progress of global warming scenarios, MHWs may occur in a more frequent, extensive, intensified and long-lasting manner (Frölicher et al., 2018), exposing many marine organisms including macroalgae to thermal shock. Growth and life cycles of macroalgae may be profoundly affected to a point that their survival is threatened, eventually causing irreversible changes of ecosystems by reducing primary productivity in coastal waters. Marine heatwaves can result in greater harm when combined with other stressors (Gao et al., 2019).

1.4 UV radiation

Ultraviolet (UV) radiation (UVR) can be classified into three bands: UV–A (315–400 nm), UV–B (280–315 nm) and UV–C (200–280 nm). The presence of stratospheric ozone layer plays a protective role, screening off

UV–C and significantly reducing the UV–B that reaches the earth surface (Madronich, 1992). The ozone layer filters out the deadly UV–C completely and absorbs about 90% of UV–B. However, human activities caused the release of a few ozone destructive compounds such as chlorofluorocarbons (CFCs) and other pollutants, which reduced the thickness of ozone layer, enabling elevated levels of UV–B radiation reaching the earth surface. Although CFCs' emission has almost ceased since the establishment of the Montreal Protocol, and recovery of the ozone layer has occurred since 2010 (Solomon et al., 2016), full recovery of this protective layer is still unclear and the enhancement of UVR exposures may continue over the next few decades because the ozone destructive compounds may linger in the atmosphere for a long time (Weatherhead and Andersen, 2006). Furthermore, the effects of global warming on the decrease of the ozone layer may delay its recovery (Häder et al., 2007; McKenzie et al., 2003).

The ratio of UV to full spectrum solar radiation may vary during a day. During the noon period in subtropical areas, the intensity ratio of PAR: UV–A:UV–B is about 100:16:0.5. While UV–A:PAR ratio remains stable during daytime, UV–B:PAR ratio increases with the increase of solar radiation, since the ratio of UV–B to PAR is related to the zenith angle of the sun and UV–B is absorbed more due to the longer path (more ozone–related attenuation) to the earth surface; therefore, the ratio is the lowest in the morning and evening and highest at noon (Gao, 2018).

In addition to direct changes of UV exposures, organisms living in shallow waters or within the upper mixing layers are exposing to increasingly more UVR indirectly due to the upper mixed layer (UML). As the UML is becoming shallower, most marine organisms there are at the mercy of intensified UV exposures. Although this is less relevant to the intertidal macroalgal species, which are little affected by the UML, species distributed in bays with less tidal mixing can still be affected by increased levels of UVR. Previous studies showed that the Arctic area and the North Sea may suffer relatively more from UVR in future (Müller et al., 2008). On the other hand, increasing land runoff from precipitation or storms brings UV–absorbing dissolved organic matter (DOM) into coastal waters, providing a temporary refuge for algae and other UV-sensitive organisms (Häder et al., 2015).

1.5 Ocean deoxygenation and eutrophication

Ocean warming is responsible for the formation of oceanic and coastal deoxygenation, leading to marine hypoxia when DO concentration is below

2 mg O_2 L^{-1} (62 μmol/L). Firstly, it may decrease the oxygen solubility, reducing DO concentrations in seawater. DO content has been declining over the past 50 years (Schmidtko et al., 2017). Secondly, the shallowing of the UML and elevated stratification induced by ocean warming may block the vertical exchange between surface and deeper seawater, reducing ventilation from surface seawater to the deep layer, exacerbating the deoxygenation conditions in deep sea areas. Thirdly, the proliferation of marine bacteria stimulated by ocean warming and eutrophication also contribute to deoxygenation, and may become responsible for further hypoxia. Subsequently, the respiration index ($RI = log_{10}$ (pO_2/pCO_2) will become smaller with progressive ocean warming and acidification (Brewer and Peltzer, 2009).

The coastal waters, being adjacent to human living areas, are often eutrophicated, with increasing loads of macronutrients, such as phosphate, nitrate, nitrite and ammonia. Frequent occurrences of coastal eutrophication events are usually responsible for the outburst of harmful algal blooms. After the blooms collapse, microorganisms decompose the algal residues, consume the dissolved oxygen, and release CO_2, leading to hypoxia (DO $\leqq$ 2 mg/L) or even anoxia when dissolved oxygen drops nearly to zero. Therefore, coastal eutrophication events often coincide with deoxygenation, leading to widespread hypoxia and other environmental disasters (Cai et al., 2011; Howarth, 2008). Increasing water temperature may stimulate algal blooms, consequently increasing the occurrence and severity of hypoxia due to enhanced decomposition of organic matter after the blooms (Miyamoto et al., 2019). Therefore, ocean deoxygenation exacerbates the development of ocean warming and eutrophication, and hypoxic areas are expanding throughout the global oceans (Whitney et al., 2007).

2. Effects of increased CO_2 concentration and ocean acidification

2.1 Use of different types of dissolved inorganic carbon

Marine macroalgae are known to be capable of utilizing different types of dissolved inorganic carbon (DIC), including dissolved CO_2 and HCO_3^-, for photosynthesis. CO_2 provides the only direct carbon source for all photoautotrophic organisms, in contrast, utilization of HCO_3^- is indirect and must be facilitated by a series of mechanisms. Most macroalgae can utilize both CO_2 and HCO_3^-, a few other species, however, mainly green or red macroalgae, can only use CO_2 (Hepburn et al., 2011; Koch et al., 2013).

For these macroalgae, photosynthesis might be limited by the availability of CO_2. As the affinity of CO_2 to Rubisco is relatively low in most algal species, the binding site of this enzyme can easily be replaced by O_2 when the concentration of CO_2 is low, therefore, the sole dependence on the diffusion of CO_2 for a carbon source may pose as a serious limitation for carbon assimilation. As macroalgal Rubisco's affinity for CO_2 is rather low, and the transformation from HCO_3^-'s dehydration to CO_2 is not fast enough to provide CO_2 for photosynthesis (Gao et al., 1991), many macroalgae have evolved to possess CO_2 concentration mechanisms (CCMs), as many microalgae have, to overcome the barriers of C-limitation. Nevertheless, some macroalgae distributed in deeper water or grown under low light conditions are known to possess less active CCMs (Kübler and Raven, 1994), and some species can operate the C4-pathway of carbon fixation, which has been shown to be a mechanism responsible in the world's largest green tides (Liu et al., 2020b).

2.2 Effects of elevated CO_2 concentrations and lowered pH

Theoretically and empirically, increased CO_2 availability can stimulate photosynthesis, PSII activity and growth of macroalgae (Celis-Plá et al., 2015, 2017; Gao et al., 2019, 1991, 1993a,b; Johnson et al., 2014; Kram et al., 2016; Roth-Schulze et al., 2017; Suárez-Álvarez et al., 2012; Wu et al., 2019; Zou and Gao, 2005; Zou et al., 2011a; Zweng et al., 2018) (Table 1). Elevated CO_2 stimulates the growth rates of *Pyropia yeoensis* juveniles (Gao et al., 1991), *Ulva* spp. (Gordillo et al., 2001; Huan et al., 2016; Xu and Gao, 2012a), *Lomentaria articulata* (Kübler et al., 1999), *Gracilaria* spp. (Gao et al., 1993b; Zou and Gao, 2009) and *Sargassum horneri* (Wu et al., 2019) and primary production of macroalgae (Hernández et al., 2018).

Enhancement of photosynthesis due to increased CO_2 may require a higher demand of nutrients, the lack of which may cause a decline of soluble protein (Suárez-Álvarez et al., 2012) and reduce growth and photosynthesis (Gao et al., 2018). Even under fluctuations of pH, elevated CO_2 concentrations enhance the growth and net photosynthesis of *Gracilariopsis lemaneiformis* (Qu et al., 2017). However, lowered pH may reduce growth under low light levels, mainly due to acidic stress during night period, when the alga requires extra energy to deal with it. Elevated CO_2 levels provide more direct carbon source during daytime when CO_2 declines as the result of photosynthetic C removal, leading to pH rise. Therefore, daytime benefits of CO_2 rise can offset the harm induced by reduced pH during night time, though this depends on many other conditions such as light levels,

Table 1 Documented effects of elevated CO_2 and ocean acidification on net photosynthesis (Pn) and growth in macroalgae.

Sources	Species	Variables	Effects	Study location	Light and temperature	Stress treatments
Gao et al. (1991)	*Pyropia yezoensis* (r)	Pn	Positive	From the stock of free-living conchocelis stage of *Pyropia yezoensis*	600 μmol photon $m^{-2} s^{-1}$, 15 °C	CO_2 (350, 1000, 1600 μatm)
		Growth			300 μmol photon $m^{-2} s^{-1}$	
Gao et al. (1993b)	*Gracilaria chilensis* (r)	Pn	Positive	Tosa bay, Shikoku, Japan	300 μmol photon $m^{-2} s^{-1}$, 20 °C	CO_2 (air, air + 650 μatm, air + 1250 μatm CO_2)
	Gracilaria sp. (r)					
	Gracilaria chilensis (r)	Growth	Positive			
	Gracilaria sp. (r)					
Beer and Koch (1996)	*Ulva linza* (g)	Pn	Positive	Avery Point, Florida, US	200 μmol photon $m^{-2} s^{-1}$, 20 °C	Ci (2.2–7 mM)
	Palmaria palmata (r)					
	Laminaria saccharina (b)					
Andria et al. (1999)	*Gracilaria* sp. (r)	Pn	Positive	El Puerto de Santa María, Southern	85 μmol photon $m^{-2} s^{-1}$	Air CO_2:2.2 mM DIC ∼5%
Gao et al. (1999)	*Gloiopeltis furcata* (r)	Pn	Positive	Ibaraki Prefecture of Japan	300 μmol photon $m^{-2} s^{-1}$, 20, 25, 30 °C	CO_2 (4–30 μatm)
	Ishige okamurae (b)					
	Ulva linza (g)					
Andria et al. (2001)	*Gracilaria* sp. (r)	Pn	Positive	Cádiz Bay, Southern Spain	Room temperature; daylight	DIC (0–3000 μM)
	Enteromorpha intestinalis (g)					
	Gracilaria sp. (r)	Growth				
	Enteromorpha intestinalis (g)					

Zou and Gao (2005)	*Gloiopeltis furcata* (r)	Pn	Positive	Nanao Island, Shantou China (23°20′N, 116°40′E)	60 µmol photon m^{-2} s^{-1}, 12:12LD, 18–22 °C	CO$_2$ (60, 120, 180, 360, 720, 1080 µatm)
	Gigartina intermedia (r)					
	Petalonia fascia (b)					
	Sargassum hemiphyllum (b)					
Zou and Gao (2010)	*Endarachne binghamiae* (b)	Pn	Positive	Nanao Island, Shantou China (23°20′N, 116°40′E)	200 µmol photon m^{-2} s^{-1}, 12:12LD, 25 °C	Ci (0–9 mM)
Zou et al. (2011a)	*Sargassum henslowianum* (b)	Pn	Positive	Shengao bay, Nanao Island, Shantou, China (23°20′N, 116°55′E)	180 µmol photon m^{-2} s^{-1}, 12:12LD, 25 °C	Ci (0–6.6 mM)
Olabarria et al. (2013)	*Cystoseira tamariscifolia* (b)	Photosynthetic capacity (Fv/Fm)	Neutral	Ria de Vigo, northwestern Spain (42° 13′ 26″ N; 8° 46′ 18″ W)	140–150 µmol photon m^{-2} s^{-1}, 12:12LD, 15, 20 °C	CO$_2$ (380, 1000 µatm)
	Sargassum muticum (b)					
Suárez–Álvarez et al. (2012)	*Hypnea spinella* (r)	Pn	Positive	Hoya del Pozo (27°59′ N, 15°22′ W), east coast of Gran Canaria, Spain)	100 µmol photon m^{-2} s^{-1}, 16:8LD, 23±1 °C	CO$_2$ (360, 750, 1600 µatm)
		growth				
Korbee et al. (2014)	*Padina pavonica* (b)	Pn	Positive	Cabo de Gata-Nijar Natural Park (Southern Iberian Peninsula, 36° 52′N, 2°12′ W)	incubated in transparent UV cylindersin a bay, no deeper than 0.5 m	CO$_2$ (ambient air, 700 µatm)
	Ellisolandia elongata (r)		Positive			
	Cystoseira tamariscifolia (b)		Negative			

Continued

Table 1 Documented effects of elevated CO_2 and ocean acidification on net photosynthesis (Pn) and growth in macroalgae.—cont'd

Sources	Species	Variables	Effects	Study location	Light and temperature	Stress treatments
Nunes et al. (2015)	*Saccharina latissima* (b)	Pn Growth	Positive	Mount Batten (N 50° 21.371, W 4° 7.673), Plymouth, UK	40 µmol photon m^{-2} s^{-1}, 12:12LD, 18 °C	CO_2 (pH 7.82–8.04)
Chen et al. (2017)	*Pyropia haitanensis* (r)	Pn Growth	Positive	Nanao Island, Shantou, China (23°20′N, 116° 55′E)	100 µmol photon m^{-2} s^{-1}, 12:12LD, 18 ± 1 °C	CO_2 (390, 1000 µatm)
Liu et al. (2018)	*Gracilariopsis lemaneiformis* (r)	Pn Growth	Positive	Nanao Island, Shantou, China (23°20′N, 116°55′E)	160 µmol photon m^{-2} s^{-1}, 12:12LD, 20, 24 °C	CO_2 (390, 700 µatm)
Zweng et al. (2018)	*Sargassum fluitans* (b)	Pg	Positive	Florida Reef Tract at Looe Key (24°37.233′N, 81°22.247′W)	150 µmol photon m^{-2} s^{-1}, 12:12LD, 27 °C	CO_2 (43, 19, 9, 3 µmol kg^{-1})
Wu et al. (2019)	*Sargaasum homeri* (b)	Pn Growth	Positive	Jiangsu province, China (121.59°E, 32.09°N)	80 µmol photon m^{-2} s^{-1}, 12:12LD, 10 or 14 °C	CO_2 (400, 1000 µatm)

All the data listed are for macroscopic stage, with the thalli acclimated to the experimental conditions for 1 h to several days. (r), (g) and (b) stand for red alga, green alga and brown alga respectively. The light intensity unit is PAR, pCO_2 unit have been unified to µatm.

the depths that macroalgae are distributed, nutrient availability and/or species-specific physiology.

Upper intertidal macroalgal species are exposed to air for considerable periods during low tides and suffer from dehydration. As the diffusion rates of CO_2 are about 10 thousand times faster in air than that in seawater (Beardall et al., 1998), exposure to air enables the thalli to take up CO_2 more easily, so that photosynthetic rates of the tested macroalgae, such as *Pyropia* spp. and *Ishige* sp. increased during the initial period of emersion when the algal thalli suffer less dehydration (Gao et al., 1999; Zou and Gao, 2002). Although prolonged desiccation during low tide causes stresses to upper intertidal macroalgae due to dehydration (Ji and Tanaka, 2002), enhancement of photosynthesis during emersion by elevated CO_2 concentrations has been documented at various levels of dehydration in many species tested (Gao et al., 1999; Williams and Dethier, 2005; Zou and Gao, 2002), somehow mitigating photoinhibition during daytime (Henley et al., 1992). With initial water loss, photosynthesis of marine intertidal macroalgae may reach a maximum with thinning of the water membrane barrier shortly after desiccation and later become reduced due to dehydration of algal tissues (Gao et al., 1999) (Table 1).

Short-term and long-term enriched CO_2 has been suggested not to affect mitochondrial respiration in a brown alga (Zou et al., 2011a,b), though it may enhance the respiration in a green macroalga (Xu and Gao, 2012a,b). High CO_2 level and low pH can decrease the PAR level at which photosynthesis becomes saturated (Liu et al., 2012). However, the brown alga *Sargassum fusiforme* significantly increases the temperature quotient for respiration (Q10, the change in respiration per 10 °C rise) in CO_2 enriched seawater, suggesting that future elevated CO_2 may stimulate respiratory carbon loss of macroalgae along with increasing temperature.

2.3 Regulation of CCMs under elevated CO_2

The overwhelming form of DIC source, bicarbonate (HCO_3^-) can be transported into cells via CCMs and converted to CO_2 intracellularly by carbonic anhydrase (Raven et al., 2012). It can also be taken up into the cell directly by an anion exchange protein. H^+-ATPase-driven HCO_3^- uptake has been found in marine macroalgae (Klenell et al., 2002). Some species with CCMs prefer using CO_2 instead of bicarbonate under elevated CO_2 conditions, as HCO_3^- usage is costly due to its complex transport across the membrane (Cornwall et al., 2012). Elevated CO_2 levels may benefit

these species by reducing the energy expenditure that CCMs demand (Cornwall et al., 2012; Israel and Hophy, 2002).

Operation of CCMs can be moderated by elevated CO_2 levels, as the activity of intra–extracellular carbonic anhydrase drops under CO_2 enriched environments (Hofmann et al., 2013; Xia and Gao, 2005) and so does the photosynthetic affinity to CO_2 and/or HCO_3^- (Xu and Gao, 2012a,b). Lowered CO_2 concentration may increase the activity of intracellular carbonic anhydrase (CA) (Zou et al., 2003). Therefore, the affinity of CCMs to DIC may play a key role in determining the effects of higher CO_2 levels on macroalgae. If photosynthetic affinity to DIC is high, the net effects of increased DIC are dependent on the extent of CCM's down–regulation induced by elevated CO_2. Saved energy from down–regulation of CCM can be used for growth or storing lipids or fatty acids under limited light conditions (van der Loos et al., 2019; Wu et al., 2008), which is often accompanied by reduced photosynthesis and enhanced photorespiration (Liu and Zou, 2015; Xu and Gao, 2012a,b). Nevertheless, the down–regulation of CCM together with the increase of photorespiration can be taken as being protective measures against lowered pH, since the high CO_2–grown thalli possess higher efficiency of energy transfer even after being transferred to zero DIC condition (Xu and Gao, 2012a,b). For the algae with less effective CCMs, neutral effects can be expected in terms of ocean acidification impact. If a macroalga is grown under limited light conditions, insufficient energy supply would result in positive effects from increased CO_2 availability under OA conditions (Hepburn et al., 2011). However, under high light intensity, high CO_2–induced low pH may trigger photoprotective processes and decrease photosynthesis and growth rate in some microalgae (Gao and Campbell, 2014), which can also be true for some macroalgae (Aline et al., 2006; Israel and Hophy, 2002; Martin and Gattuso, 2009) (Tables 1 and 2). It is obvious that algal responses to high CO_2 levels depend on other drivers, such as light, nutrients and temperature (Harley et al., 2012; Li et al., 2018; Xu and Gao, 2012a,b; Xu et al., 2010).

Elevated CO_2 does not necessarily increase the concentration or supply of CO_2 within algal cells, especially for the species with active CCMs, because CCMs and intracellular CO_2 concentration can be simultaneously down–regulated (Raven et al., 2012). Algae maintain a relatively stable intracellular pH of about 7.5 (Smith and Raven, 1979), OA may affect it (Gao et al., 2012b), even though the pH in milieu is still higher than the intracellular level. To cope with the acidic stress induced by OA,

Table 2 Documented effects of elevated CO_2 or low pH on calcification, net photosynthesis (Pn) and growth of different calcified macroalgae, with the thalli acclimated to the experimental conditions for 1 h to several days.

Sources	Species	Variables	Effects	Light and temperature	Stress treatments
Gao et al. (1993a)	*Carollina pilulifera* (r)	Calcification	Negative	30 μmol photon m^{-2} s^{-1}, 20 °C	CO_2 (350, 1600 μatm)
Martin and Gattuso (2009)	*Lithophyllum cabiochae* (r)	Calcification	Negative	Ambient temperature + 3 °C	pCO_2 (400, 700 μatm)
Semesi et al. (2009)	*Hydrolithon sp.* (r)	Photosynthesis	Positive	300–500 μmol photon m^{-2} s^{-1}, 22–33 °C	pH 7.6, 7.8, 8.2, 8.6, 9.0, 9.4, 9.8
		Calcification	Negative		
Gao and Zheng (2010)	*Corallina sessilis* (r)	Growth	Negative	Sea surface temperature	CO_2 (380, 1000 μatm)
		Pn			
		Calcification			
Büdenbender et al. (2011)	*Lithothamnion glaciale* (r)	Calcification	Negative	Summer 9.0 ± 0.26 °C Winter 6.8 ± 0.17 °C	pCO_2 (390, 815, 975, 1570 μatm)
Price et al. (2011)	*Halimeda opuntia* (g)	Calcification	Negative	150 ± 30 μmol photon m^{-2} s^{-1}, 28 °C	CO_2 (air, pCO_2 900 ± 90 μatm)
		Photosynthesis	Negative		
	Halimeda taenicola (g)	calcification	Negative		
		photosynthesis	Neutral		
Cornwall et al. (2013b)	*Arthrocardia corymbosa* (r)	Growth	Negative	18 μmol photon m^{-2} s^{-1}, 10.8 °C	pH 8.05, 8.45
		Photosynthesis	Neutral		

Continued

Table 2 Documented effects of elevated CO_2 or low pH on calcification, net photosynthesis (Pn) and growth of different calcified macroalgae, with the thalli acclimated to the experimental conditions for 1 h to several days.—cont'd

Sources	Species	Variables	Effects	Light and temperature	Stress treatments
Johnson et al. (2014)	*Halimeda taenicola* (g)	Calcification	Neutral	In situ temperature and irradiance levels at 5 m depth	CO_2 (ambient air, 800–1200 µatm)
	Halimeda opunia (g)		Negative		
	Galaxaura rugosa (r)		Neutral		
	Dichotomaria marginata (r)		Negative		
	Lithophyllum prototypum (r)				
	Titanoderma prototypum (r)				
	Lithophyllum sp. (r)				
Graba–Landry et al. (2018)	*Amphiroa anceps* (r)	Calcification	Negative	23, 26, 28 °C	pH 8.1, 7.8, 7.6
	Corallina officinalis (r)				
	Amphiroa anceps (r)	Growth	Neutral		
	Corallina officinalis (r)		Positive		

(r), (g) and (b) stand for red alga, green alga and brown alga respectively. The light intensity unit is PAR, pCO$_2$ unit have been unified to µatm.

algae down-regulate their CCMs to reduce intracellular CO_2 concentration in order to maintain cellular acid-base stability, which is critical for enzymatic reactions. Evidence has been documented in a diatom that its intracellular DIC concentration became much lower when grown under elevated CO_2 (Liu et al., 2017a). However, how elevated CO_2 concentration would influence intracellular DIC in macroalgae has not been documented. Macroalgae exhibit differential photosynthetic responses to OA (Table 1), which can be species-specific (Chung et al., 2017; Graba-Landry et al., 2018; Korbee et al., 2014; Nunes et al., 2015), life stage (Fig. 2) and/or zonation-dependent.

For those macroalgae without CCMs (about 0–9% of macroalgae tested), photosynthesis tends to benefit from elevated CO_2 levels, though ambient DIC level in seawater may saturate their photosynthesis (Cornwall et al., 2012). While non-CCM macrophytes are relatively abundant in higher CO_2 freshwater environments (Maberly et al., 2014), the marine macroalgae with less CCMs efficiency can suffer from OA due to their less efficient capacity of acclimating to pH changes (Gordillo et al., 2001), therefore, exhibiting neutral effects of OA (Falkenberg et al., 2013). Whether photosynthesis of marine macroalgae is saturated by ambient seawater DIC or not may be species-specific (Beer and Koch, 1996) or condition-dependent. It is known that fast water movement reduces the diffusion layer around the thalli and enhances photosynthesis by increasing CO_2 diffusion rates in the macroalgae, *Pyropia yezoensisi* and *Sargassum thunbergii* (Gao, 1992; Gao et al., 1992). It is likely that, under the influence of tide and/or wind-induced water movement, macroalgae are less CO_2-limited and less sensitive to acidic stress (Cornwall et al., 2014), which needs to be tested with further work.

2.4 Pigmentation and enzymes of macroalgae under elevated CO_2

Elevated CO_2 may reduce photosynthetic pigments such as chlorophyll *a* (Gao and Zheng, 2010) or phycobiliprotein (Zou and Gao, 2009). CO_2 enrichment may reduce the extra energy expenditure of bicarbonate utilization and thus down-regulate pigmentation accordingly. Elevated CO_2 may affect the activities of nitrate reductase and carbonic anhydrase (Hofmann et al., 2012), changing the process of nutrients uptake and carbon acquisition, and thereby their competitiveness (Hofmann et al., 2013).
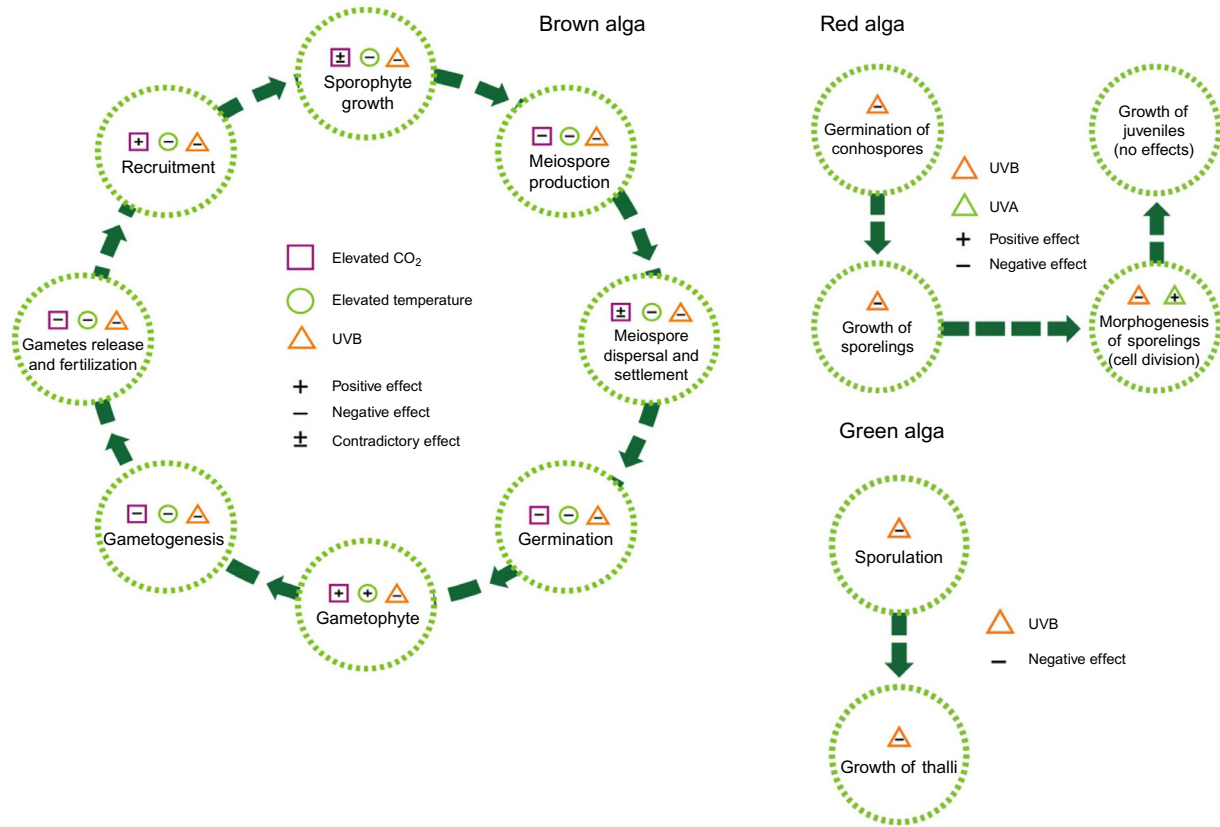
Fig. 2 The effects of climate change factors on different life stages of tested brown macroalgae (*Macrocystis* spp., *Undaria* spp., *Saccharina* spp., *Laminaria* spp.) (Ladah and Zertuche, 2007; Leal et al., 2017, 2018; Lüning and Neushul, 1978; Müller et al., 2008; Roleda et al., 2012; Xu et al., 2015), red macroalga (*Pyropia haitanensis*) (Jiang et al., 2007) and green macroalga *Ulva pertusa* (Han et al., 2003) with alteration of generations. Squares, circles, orange triangles and green triangles represent elevated CO_2, elevated temperature, UVB and UVA respectively. Plus signs indicate positive effects; minus signs indicate negative effects; plus and minus signs indicate contradictory effects.

2.5 Impacts on calcified macroalgae

OA negatively affects calcifying macroalgae by hindering calcification processes (Table 2), as the lowered pH and saturation state of calcium carbonate (Ω) leads to dissolution of $CaCO_3$ (Gao et al., 1993a; Hall-Spencer et al., 2008; Hofmann et al., 2012, 2013; Johnson et al., 2014; Kuffner et al., 2008; McCoy et al., 2020; Sinutok et al., 2011). Under-saturation of Ω can also undermine calcification due to increased energetic cost to acquire carbonate ions (Anthony et al., 2008; Büdenbender et al., 2011; Guinotte and Fabry, 2008; Raven, 2011). Photosynthetic efficiency may be inhibited with decreased calcification (Cornwall et al., 2013a; Guinotte and Fabry, 2008; Hofmann et al., 2012; Kroeker et al., 2010; Martin and Gattuso, 2009). Increased non-photochemical quenching (NPQ), carotenoids and quantum yield are related with increased or sustained calcification in a cocolithorphorid, implying that algal calcification plays a role in dissipating excessive energy or as an additional drainage of electrons absorbed by the photosynthetic antennae (Xu and Gao, 2012a,b). In coralline algae, reduced calcification under elevated CO_2 was correlated with declined photosynthetic rates and pigmentation (Gao and Zheng, 2010).

Diurnal fluctuation of pH may decrease the growth of coralline macroalga *Arthrocardia corymbosa*, though the daytime rise of pH due to its photosynthesis may somewhat relieve the negative effects of OA (Cornwall et al., 2013a,b). Therefore, OA may not always reduce calcification (Kroeker et al., 2010), as the mechanisms of calcification and protective measures against OA can be different (Price et al., 2011). Some coralline algae and calcareous green algae can develop a protective external layer with an organic matter covering to deal with ambient seawater pCO_2 decline (Ries et al., 2009). Some species can even create a micro environment favourable for calcification despite ambient pH fluctuations, enduring acidic stress (Zweng et al., 2018) or even benefiting from elevated CO_2 (Scherner et al., 2016) (Table 1). OA may increase the dissolution rather than reduce the production of calcified skeletons (Roleda et al., 2012). Net dissolution may be faster than net calcification for some calcified macroalgae under the projected CO_2 level by the end of this century (Martin and Gattuso, 2009), therefore, measured rates of calcification are usually lower under OA conditions.

When calcifying macroalgae decrease calcification under OA (Table 2), the thinned calcified layer makes the algal calcifiers more susceptible to other stressors, such as UVR (Gao and Zheng, 2010), water movement forces and/or grazing (Büdenbender et al., 2011). It is most likely that their photosynthetic carbon fixation or daily primary production declines under multiple stressors (Gao et al., 2019).

2.6 Effects on macroalgal community

OA may alter macroalgae community structure, since different taxa or species exhibit different capabilities of tolerating acidic stress (Celis–Plá et al., 2017; Johnson et al., 2014; Nunes et al., 2015). Increasing CO_2 availability may enhance the expansion of filamentous turfs at the expense of calcified algae (Brodie et al., 2014; Hall–Spencer and Harvey, 2019; Russell et al., 2009), driving a macroalgal community shift towards non-calcifying species (Connell and Russell, 2010; Kuffner et al., 2008).

Green algae *Ulva* spp. are highly competitive under the influence of OA, since their photosynthesis and growth are stimulated by an elevated CO_2 level (Xu et al., 2017). The economically important red macroalga *Gracilariopsis lemaneiformis* grows less in the presence of the harmful green macroalga *Ulva lactuca*, and elevated CO_2 exacerbates the phenomenon, since the latter has relatively higher light utilization efficiency even under OA (Chen et al., 2015). This suggests OA can change the interspecific competitions. Macroalgae may evolve to adapt to an enriched CO_2 environment, forming genetically different communities compared with contemporary ones (Wu et al., 2008).

In macroalgal farming areas, high density of macroalgae usually results in very low CO_2 and very high pH environments during daytime, affecting photosynthesis and respiration of macroalgae (Li et al., 2020). Elevated CO_2 concentrations can stimulate their photosynthesis and growth in *Pyropia* sp. (Gao et al., 1991) and *Gracilaria* sp. (Qu et al., 2017) (Table 1). Therefore, the net effects of the higher CO_2 together with the concomitant higher [H^+] on algae may be largely determined by the balance between the negative effects of acidic stress and the positive effects of elevated CO_2 supply.

Long-term responses of macroalgae to OA have been observed in waters of naturally existing CO_2 seeps (Kumar et al., 2017), which provide natural laboratories for studying OA's long-term effects. From observations of natural populations around volcanic CO_2 vents, there is a significant decline of coralline algal abundance along the pH gradient to the CO_2 vent centre (Hall–Spencer et al., 2008). On the other hand, OA may even relieve the oxidative stress encountered by kelp and increase the accumulation of iodine in a marine model kelp *Saccharina japonica* (Xu et al., 2019). Additionally, some calcifying macroalgae showed increased photosynthesis and relatively high abundance at a volcanic CO_2 seep (Johnson et al., 2012), suggesting some calcifying macroalgae may even evolve to adapt to an increasingly acidified environment. Another study using volcanic seeps showed that macroalgae that possess active acquisition of CO_2 usage increased their abundance,

while the calcifying species and the macroalgae with less active CO_2 uptake declined (Cornwall et al., 2017), suggesting the DIC-use mechanism may affect the long-term adaptation to a more acidified environment.

3. Effects of ocean warming

3.1 Effects on macroalgal niche

Temperature is one of the most important factors that determine or affect the distribution of macroalgae by influencing their physiology and adaptation (Bertocci et al., 2014; Martínez et al., 2012a). Long-term temperature rise or warming may favour some tropical species over temperate ones by expanding their habitats to formerly colder regions and driving temperate species to formerly even colder regions, thereby leading to geographical shifts of algal communities (Hernández et al., 2018). These may include the wiping out the entire kelp forest in the North Atlantic (Brodie et al., 2014). High seawater temperature may cause a decline of cold-temperate macroalgae (Martínez et al., 2012b). However, contrary results showed that ocean warming may harm subtropical macroalgae by decreasing their growth (Graba-Landry et al., 2018), inhibiting the growth of some tropical brown algae (Bender et al., 2014), forcing tropical species to live at their upper temperature limit (Koch et al., 2013), even leading to the retreat of the entire macroalgal community (Wernberg et al., 2011). Increased temperature can also affect the macroalgae in polar regions, positively affecting some species like the red alga *Phycodrys rubens*, *Ptilota plumosa*, *Desmarestia aculeata* (Table 3) and promoting community shifts together with other stressors such as ocean acidification (Gordillo et al., 2016). In any case, macroalgal species that can adapt to thermal stress have been considered to be better prepared for an even warmer ocean, and the global macroalgal communities may be fundamentally transformed due to the reshaped balance between the "winners" and "losers". While these contrastingly differential responses to warming have been mainly reported in macroscopic stages of some macroalgae, consequent impacts on whole life cycles of different macroalgal species are almost unknown (Fig. 2). Warming negatively affect most of the life cycle stages in some brown algae (Ladah and Zertuche, 2007; Leal et al., 2017, Fig. 2), as the release of spores, germination and early sporophyte growth requires low temperature (Buschmann et al., 2004), however, no documentation has been found about warming effects on the life cycles of red and green macroalgae. Warming may shorten the life cycle span of the green tide macroalgae, *Ulva* spp., by stimulating their growth and

Table 3 Documented effects of elevated temperature on growth and net photosynthesis (Pn) of different macroalgae with the thalli acclimated to the experimental conditions for 1 h to several days.

Sources	Species	Variables	Effects	Light and temperature	Temperature treatments
Zou and Gao (2014b)	*Gracilariopsis lemaneiformis* (r)	Growth	Neutral	200 µmol photon m^{-2} s^{-1}, 12:12LD	Temperature (12, 19, 26 °C)
		Pn	Positive		
Kram et al. (2016)	*Plocamium cartilagineum* (r)	Growth	Negative (alone)/ positive (with higher pCO_2)	Lab gradually increasing or decreasing light levels, 10:14LD as winter, 14:10LD as summer, 15–17 °C	Temperature (15–17 + 2 ± 0.5 °C)
Liu and Zou (2015)	*Pyropia haitanensis* (r)	Growth	Neutral	150 µmol photon m^{-2} s^{-1}, 12:12LD, 18 °C	Temperature (14–38 °C)
		Photosynthesis	Positive		
Gordillo et al. (2016)	*Monostroma arcticum* (g)	Growth	Negative	140–340 µmol photon m^{-2} s^{-1}, 4 or 10 °C	Temperature (4, 10 °C)
	Phycodrys rubens (r)		Positive		
	Ptilota plumosa (r)				
	Desmarestia aculeata (b)				
	Alaria esculenta (b)		Neutral		
	Saccorhiza dermatodea (b)				
	Monostroma arcticum (g)	Photosynthetic activity	Negative		
	Phycodrys rubens (r)		Positive		
	Ptilota plumosa (r)		Neutral		
	Desmarestia aculeata (b)		Negative		
	Alaria esculenta (b)				
	Saccorhiza dermatodea (b)				

Bender-Champ et al. (2017)	*Laurencia intricata* (r)	Growth	Negative	CO_2 winter (294, 379, 562, 990 µatm) spring (345, 434, 617, 1014 µatm) (synergistic with higher CO_2)	Temperature winter (21.3, 22.5, 24.5, 26.2 °C) spring (24.4, 25.2, 27.4, 28.9 °C)
		Photosynthesis	Neutral		
	Turbinaria ornata (b)	Growth	Negative		
		Photosynthesis	Neutral		
	Chnoospora implexa (b)	Growth	Negative		
		Photosynthesis	Positive		
Charan et al. (2017)	*Gracilaria edulis* (r)	Growth	Positive	114 µmol photon m^{-2} s^{-1}, 12:12LD	Temperature (28, 30, 32, 34 °C)
Roth-Schulze et al. (2017)	*Caulerpa taxifolia* (g)	Growth	Positive (with higher CO_2)	109 µmol photon m^{-2} s^{-1}, 14:10LD, CO_2 (390, 700, 1000 µatm)	Temperature (23, 24 °C)
Chen et al. (2018)	*Gracilariopsis lemaneiformis* (r)	Growth	Positive	120 µmol photon m^{-2} s^{-1}, 12:12LD	Temperature (17, 22 °C)
Graba-Landry et al. (2018)	*Amphiroa anceps* (r)	Growth	Negative	30 µmol photon m^{-2} s^{-1}, 16:8LD, pH 8.1, 7.8, 7.6	Temperature (23, 26, 28 °C)
	Corallina officinalis (r)				
	Laurencia decussata (r)				
	Sargassum linearifolium (b)				
	Delisea pulchra (r)				
	Ulva sp. (g)				
Wu et al. (2019)	*Sargassum homeri* (b)	Growth	Positive	80 µmol photon m^{-2} s^{-1}, 12:12LD, CO_2 (400, 1000 µatm)	Temperature (10, 14 °C)
		Pn			
Liu et al. (2020a)	*Gracilariopsis lemaneiformis* (r)	Growth	Positive	150 µmol photon m^{-2} s^{-1}, 12:12LD, CO_2 (400, 1000 µatm)	Temperature (20, 24 °C)
		Photosynthesis	Negative		

(r), (g) and (b) stand for red alga, green alga and brown alga respectively. The light intensity unit is PAR, pCO$_2$ unit have been unified to µatm.

maturing processes (J.T. Xu, personal communication). Changes in life cycles of macroalgae are the key to determine their niches and distributions.

3.2 Effects on physiological performance

While growth of most macroalgal species tested showed positive responses to elevated temperature for short periods or single life cycle stage, physiological activities such as photosynthesis and respiration usually show instant responses to temperature changes, as biochemical reactions are immediately affected by a change in temperature (Table 2). The optimal temperature values for photosynthesis or growth can be much lower in colder than in warmer waters (Müller et al., 2008). Respiration usually rises with increased temperature, following a linear pattern that differs from photosynthesis. The possible explanation for different responses to short-term temperature changes between photosynthesis and respiration is that respiration related enzymatic reactions can be more affected by temperature than photosynthetic light reactions (Davison, 1991). The optimal temperatures of most subtropical or temperate marine macroalgae range from 25 to 30 °C. Acclimation to warming in the case of photosynthesis led to the decreased ratio of respiration to gross photosynthesis (Zou and Gao, 2013, 2014b). This corroborates the hypothesis that macroalgae may benefit from moderate ocean warming, as DIC acquisition and assimilation are favoured by moderate seawater temperature rise, though the influence depends on the conditions of macroalgae's habitats and nutrients status, as nutrients may act synergistically with temperature to enhance macroalgal recruitment, causing macroalgal blooms in coastal ecosystems (Lotze and Worm, 2002). On the other hand, such apparently positive responses during the macroscopic stage may disappear during the microscopic stage in many macroalgal species, since most macroalgae such as *Pyropia* (*Porphyra*) and *Laminaria* plants transform to their microscopic phase in late spring. Consequently, microscopic stages of macroalgae can be more sensitive to ocean warming (Fig. 2), which may determine the abundance and/or diversity of the macroalgae. Unfortunately, little is known on the impacts of warming on macroalgae's microscopic stages or life cycles.

3.3 Acclimation to ocean warming

Macroalgal species that are distributed in colder environments may show a higher photosynthetic performance at low temperature compared with their counterparts in warmer regions (Eggert et al., 2006; Staehr and Wernberg,

2009). Acclimation to lower temperature can result in physiological and bio-chemical changes, including relatively higher contents of soluble carbon-hydrates and proteins (Staehr and Wernberg, 2009), which are supposed to relieve the low temperature restraints. Temperature rise may down-regulate light–harvesting activity of reaction centres or relieve other low temperature protective measures (Staehr and Wernberg, 2009). Low tem-perature may inhibit electron transport due to reduced electron drainage linked with the Calvin cycle, therefore decreasing the ratio of antenna capacity to reaction centres. Ocean warming makes this down–regulation no longer necessary or as important as previously for marine macroalgae. Therefore, ocean warming may benefit some species by increasing their activity of photosynthesis, such as in *Gracilariopsis lemaneiformis*, as photosyn-thesis increases significantly while respiration remains relatively unchanged with moderate warming (Zou and Gao, 2013). Respiration shows full acclimation while photosynthesis shows only partial acclimation in *Ulva con-globata*, as photosynthesis was stimulated while respiration did not vary much with increased temperature (Zou and Gao, 2014a). Long–term moderate rise of temperature can be beneficial to these algae as the net photosynthesis is supposed to rise (Wu et al., 2019). However, excessive temperature rises, such as marine heatwaves, may certainly harm the algae, though different algae may have differential temperature thresholds.

Instantaneous responses to short–term temperature fluctuations and long–term acclimation to ocean warming can be very different. The effect of prolonged changes in temperatures on rates of respiration and photosyn-thesis relies on the extent to which these processes acclimate. Phenotypic acclimation may enable macroalgae to tolerate ocean warming (Kübler and Davison, 1993). Acclimation may eventually lead to complete physio-logical homeostasis. The acclimation of photosynthesis and/or respiration to ocean warming was highly associated with high temperature-mediated changes of cellular biochemical compositions (Kübler and Davison, 1995; Machalek et al., 1996; Staehr and Wernberg, 2009). Many marine macroalgal species have genetically stable potential for photosynthetic acclimation, enabling them to modulate and optimize photosynthetic variables to prevailing temperature changes (Davison, 1991; Staehr and Wernberg, 2009; Zou and Gao, 2005, 2013). The capability to maintain net photosynthesis over extensive temperature ranges is important for marine macroalgae to achieve extensive distribution. However, whether the degree of acclimation of photosynthesis and respiration differs under different environmental condi-tions or drivers in different macroalgal life cycle stages remains unknown.

4. Effects of UV

4.1 General effects of UV radiation

The effects of UV radiation (UVR, 218–400 nm) on macroalgae can be divergent, though the effects of UVR are generally considered to be negative for most organisms. It was estimated that UVR leads to 20% loss of primary productivity (Williamson et al., 2019). It decreases effective quantum yield in macroalgae (Gao et al., 2019; Jiang and Gao, 2008) and photosynthetic carbon fixation in the surface ocean (Li et al., 2011). Such negative effects can be exacerbated when nutrients supply is limited (Xu and Gao, 2009), causing decreased growth in the red macroalga *Gracilariopsis lemaneiformis* (Gao and Xu, 2008) and brown macroalga *Laminaria saccharina* (L.) (Davison et al., 2007). Some upper intertidal algae may suffer short-term inhibition of UVR but can acclimate to minimize the negative impacts (Villafañe et al., 2005).

The species-dependent harm of UV radiation on the early stage development of macroalgae may determine the vertical zonation for the Arctic species (Häder et al., 2011; Müller et al., 2008), as the early stages are more susceptible to UV radiation (Gao and Xu, 2010; Jiang et al., 2007) (Fig. 2).

4.2 Effects of UV-A

In both macro- and micro-algae, presence of moderate or reduced levels of UV-A (315–400 nm) can lead to positive effects in terms of photosynthesis (see the reviews by Gao et al., 2012a and literature therein). UV-A irradiance can be used as light energy for photosynthetic carbon fixation for green, red and brown macroalgae (Gao and Xu, 2008; Xu and Gao, 2010a,b, 2016; Xu et al., 2018), enhancing growth (Xu and Gao, 2009, 2010a). It can also stimulate activity of carbonic anhydrase and nitrate reductase (Viñegla et al., 2006) and photosynthetic utilization of bicarbonate (Xu and Gao, 2010b). UV-A is also known to play a key role in the red macroalga (*Pyronia haitanensis*) for morphogenesis and formation of sporelings (Jiang et al., 2007).

However, high levels of UV-A decrease quantum yield (Xu and Gao, 2010b), inhibit photosynthesis (Zheng and Gao, 2009) and affect other physiological variables (Jiang et al., 2009), leading to changes in diversity and biomass of the marine benthic community (Wahl et al., 2004). Sometimes, UV-A can impose a greater physiological inhibition than

UV–B, since its relatively high dosage or the intensity during the noon period can reach >30 times that of UV–B in tropical and/or subtropical areas (Gao, 2018).

4.3 Effects of UV-B

Although UV–B only accounts for <0.5% of the solar radiation in most areas except polar regions, it usually causes negative effects to macroalgal physiology (see the review by Ji et al., 2016), decreasing net photosynthesis (Gao and Xu, 2008; Xu and Gao, 2012a,b, 2009), contents of phycobiliproteins and chlorophyll *a* (Schmidt et al., 2010), organic components including proteins and lipids in algae (Ganapathy et al., 2017). UV–B damages D1 protein of the photosystem II (García-Gómez et al., 2016) and genetic molecules, causing mutations of DNA and the formation of cyclobutane pyrimidine dimers. It can also cause changes in mitochondria, chloroplasts and other organelles (Poppe et al., 2003), increasing thickness of cell wall (Schmidt et al., 2010), reducing intracellular space, even changing algae's morphologies (Schmidt et al., 2012), and inhibiting germination of spores in the economically important red macroalga *Pyropia haitanensis* (Jiang et al., 2007).

Incident levels of UV–B are known to reduce growth rate of marine macroalgae (Schmidt et al., 2010, 2012; Xu and Gao, 2010b; Zheng and Gao, 2009). The decrease of growth can be attributed to damage to protein and pigments, leading to an extra energy requirement for repairing processes (Van de Poll et al., 2001). Nevertheless, positive effects of UV–B have also been reported, aiding in the recovery of photochemical yield in the red macroalga *Gracilariopsis lemaneiformis* (Xu and Gao, 2010a), which may occur during late afternoon when solar radiation is low.

UV–B causes photoinhibition (Figueroa and Gómez, 2001), decreasing photosynthesis (Xu and Gao, 2012a,b), quantum yield (Xu and Gao, 2010b), PSII electron transport (Schmidt et al., 2012) and photosynthetic activities (Jiang et al., 2009; Zheng and Gao, 2009). It may target photosystem II (PSII) and reduce its photochemical efficiency (Holzinger et al., 2004), and can obstruct the establishing of a proton gradient across the thylakoid membrane, impairing photosynthetic reactions (Poppe et al., 2002). Less UV–B–related inhibition of photosynthesis was reported in the red macroalga *Gracilaria* sp. under enriched nitrate conditions (Zheng and Gao, 2009), since repair process following membrane damage and damage to electron transport components may increase enzymatic activities with increased nitrogen availability (Poppe et al., 2002).

UV-B is putatively known to decrease chlorophyll *a* in *Corallina pilulifera* (Gao and Zheng, 2010) and *Kappaphycus alvarezii* (Schmidt et al., 2010), phycobiliprotein in *Kappaphycus alvarezii* (Schmidt et al., 2010) and *Hypnea musciformis* (Schmidt et al., 2012). However, some species such as *Hypnea musciformis* showed resilience to UV-B exposure with no obvious difference of chlorophyll *a* contents between PAR + UV-B and PAR only (Schmidt et al., 2012); and it unexpectedly increased chlorophyll *a* in the red macroalgae *Mastocarpus stellatus* and *Chondrus crispus* (Roleda et al., 2004). UV-B exposures can affect synthesis of carotenoids, causing the decrease of esterified-zeaxanthin, while stimulating the production of trans-β-carotene, cis-β-carotene and free zeaxanthin (Schmidt et al., 2012), suggesting a protective pigmentation mechanism (Altamirano et al., 2000). By breaking the ester bonds of esterified zeaxanthin, UV-B can reduce lutein and zeaxanthin levels in the red macroalga *Palmaria decipiens* (Döhler, 1998).

Exposures to UV-B can result in an accumulation of reactive oxygen species (ROS) (Costa et al., 2002), inducing oxidative damages to proteins, enzymes, DNA and other biomolecules (Ruhland et al., 2007). It is likely that UV-B increases NADH dehydrogenase activity and stimulates oxygen consumption and finally adds to ROS formation (White and Jahnke, 2002).

Both macro and micro-algae have developed strategies to cope with UVR-induced stresses. Most macroalgae can synthesize mycosporine-like amino acids (MAAs) and other UV-absorbing compounds (UVACs) under UV radiations, including UV-A and UV-B (Xu and Gao, 2012a,b). PAR + UVR can stimulate the production of UVACs compared with PAR only (Xu et al., 2018). These UV absorbing or screening compounds increase with increased exposures to UVR and elevated levels of nitrate (Zheng and Gao, 2009). They absorb UV and convert harmful UV radiation into heat, lessening the damage (Karsten et al., 1998) and enhancing antioxidant activity in macroalgae (Han and Han, 2005). These UV-protective compounds, mainly MAAs produced by macroalgae can be applied in cosmetics and pharmaceuticals (Álvarez-Gómez et al., 2019), as MAAs are stable, natural and antioxidant compounds in addition to their roles in screening off UVR (de la Coba et al., 2019).

The balance between negative and positive effects of UVR on macroalgae determines the net outcome of physiological performances, leading to lessened or invisible neutral impacts. The macroalgal species armed with efficient UV-protective mechanisms, including extremely thick cell walls covered with a mucilage sheath, dense layers of mineral deposits or with a calcareous matrix cover, as well as high levels of UVACs, are more tolerant

of harmful UVR (Jiang et al., 2009). The impacts of UVR on shallow-water macrobenthic communities in different regions were monitored simultaneously by different groups, and the results showed that the effects were obvious initially but vanished in the long run, showing a pattern of "come and go" (Wahl et al., 2004). Such a phenomenon can be attributed to balanced effects of harm and benefit from UVR. On the other hand, in polar regions, vertical distribution depths and sensitivity to UVR are positively related in macroalgae (Michler et al., 2002). Overall, the net effects of UVR on macroalgae depend on each species' repairing capacity, latitude and other environmental conditions. Notwithstanding, it is worth noting that different photobiological treatments and/or experimental conditions that hardly reflect the natural span and/or levels of UV irradiances can bring about significant different results on UVR effects, and it is commonly accepted that UV–B reduces pigmentations along with decreased physiological performances.

5. Ocean deoxygenation

There have been limited literatures about the effects of hypoxia on macroalgae as well as phytoplankton. Algae may be seriously affected by severe low oxygen (Gray et al., 2002). Under hypoxic conditions, even photosynthetic activities can be negatively affected, which has been proved for the endosymbiotic algae in the coral (i.e. zooxanthellae), with the effective quantum yield (φPSII) and maximum quantum yield being significantly decreased (Ulstrup et al., 2005).

Macroalgae may generally show a high tolerance to extreme low oxygen concentration or hypoxia (Haas et al., 2014). Some algae may develop acclimation to the hypoxic conditions by reducing their respiration rates (Peckol and Rivers, 1995). This can be explained by the presence of CCMs in most algae (Giordano et al., 2005), which enables them to maintain a relative intracellular high $CO_2:O_2$ ratio to down–regulate oxygenase activity and photorespiration. Low DO/pCO_2 ratio or respiration index may stimulate the carboxylation of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) instead of the oxygenation. This resilient adaptation enables algae to survive the severe oxygen deficient conditions until oxygen recovers following other environmental changes, such as improved light conditions that are suitable enough for them to resume photosynthesis, providing oxygen for their own use. Therefore, some macroalgae may even benefit from hypoxia, considering their competitive roles with other major environmental

competitors. While macroalgae might not survive in an anoxic environment due to lack of oxygen for respiration during night time, hypoxia conditions or global ocean deoxygenation might stimulate photosynthetic carbon fixation and enhance their growth due to enhanced carboxylation over oxygenation associated with decreased respiration index ($(RI = \log_{10}(pO_2/pCO_2)$, which affects the selectivity of CO_2 over O_2 by Rubisco (Gao and Campbell, 2014).

6. Effects of multiple drivers

Ocean acidification and warming happen simultaneously with increasing emissions of anthropogenic CO_2. Therefore, their combined effects are of general concern. Increased levels of CO_2 and temperature act synergistically to stimulate growth rates of fleshy red alga *Plocamium cartilagineum*, while elevated pCO_2 alone decreased its growth rate (Kram et al., 2016). On the other hand, synergistic effects of these two drivers led to reduced biomass production in the brown algae *Sargassum muticum* and *Cystoseira tamariscifolia* (Olabarria et al., 2013), and inhibit early stage development of giant kelp *Macrocystis pyrifera*, lowering germination rates and increasing mortality of the kelp's spores (Gaitán-Espitia et al., 2014) (Fig. 2). On the other hand, no interactions of these two drivers was observed during meiospore development in the brown macroalgae *Macrocystis, Pyrifera* and *Undaria pinnatifida* (Leal et al., 2017). In calcifying red macroalgae, *Corallina officinalis* and *Amphiroa anceps,* elevated temperature interacts with OA to further reduce their calcification rates (Graba-Landry et al., 2018). Combination of these two drivers can also decrease the growth (Bender-Champ et al., 2017) and calcification rates of coral reef macroalgae (Graba-Landry et al., 2018; Sinutok et al., 2011). However, one recent study showed that ocean warming treatment could counteract the impacts caused by OA in a crustose coralline alga, by stimulating growth and photochemical efficiency (Kim et al., 2020). On the other hand, calcifying green macroalga *Halimeda cuneata* showed insensitivity of photosynthetic and enzymatic activities to ocean acidification and warming (Scherner et al., 2016). Nevertheless, such positive and negative effects of OA and warming might be location-dependent and species-specific, and could also be attributed to different experimental conditions, such as light levels, presence of UVR and/or light fluctuating regimes.

Responses of photosynthesis to elevated CO_2 and temperature are suggested to be light-dependent in macroalgae (Kübler and Dudgeon, 2015) as well as in microalgae (Gao et al., 2012a). Under sub-saturating light intensities, photosynthesis rises with the rise of CO_2 concentration but decline with the rise of temperature. However, under saturated light intensities, photosynthesis rises linearly with the rise of CO_2 and temperature, which seem to act synergistically to give rise to faster growth (Kram et al., 2016; Roth–Schulze et al., 2017). Additionally, the presence of UVR may act synergistically with elevated CO_2 to decrease photosynthesis and calcification for macroalgae (Gao and Zheng, 2010), and elevated temperature (Graba–Landry et al., 2018) may interact with OA to further reduce their calcification (Table 2).

For most non-calcifying algae which show tolerance of lowered pH, OA appears to enhance their photosynthetic acclimation by modulating photochemical performance and activities of antioxidant enzymes (Liu et al., 2017b). Some macroalgae may increase fatty acid contents to deal with higher temperature caused by marine heatwaves and benefit from ocean acidification, reflecting an acclimation strategy to future ocean climate change scenarios (Britton et al., 2020). Long-term combined effects of ocean warming and acidification can cause a shift of flora community from diverse algae canopies including calcifying ones to a more simplified community dominated by non-calcified turf-forming algae in the northeast Atlantic benthic flora (Brodie et al., 2014; Connell and Russell, 2010). This again exhibits detrimental impacts of OA and warming on calcifying species. Under different light or nutrient conditions, these two factors may affect different sides of macroalgal physiology, with elevated temperature mainly affecting photosynthetic performance and protein contents, while higher OA affecting mostly the internal accumulation of carbohydrates and lipids (Gordillo et al., 2016). Non-calcifying algae that are sensitive to higher $[H^+]$ may also show decreased growth rates (van der Loos et al., 2019), however, which might be dependent on light intensities. When light availability is low or limiting, photosynthesis does not require much CO_2, but the demand for energy to cope with acidic stress would increase, therefore, negative effects can be expected when light energy supply is insufficient. This can be reflected in increased mitochondrial respiration under elevated CO_2, which provides energy to cope with environmental stresses (Zou et al., 2011b).

7. Perspectives

With progressive ocean climate changes, macroalgae are being exposed intensified levels of temperature and pH changes as well as UV radiation. Marine heatwaves can impose a threat to survival of most species, since extreme periodic high temperatures can place most organisms in the coastal region to or beyond their physiological tipping point that determines their survival or death. Addition of other stressors, such as UVR and ocean acidification, can further lower the thresholds of the tipping points for different species (Fig. 3). While positive effects of changes in some drivers might run counter to some extent some negative effects of other drivers, increased number of drivers are likely to decrease algal growth (Brennan and Collins, 2015). In macroalgae, for example, high CO_2 and low pH levels may decrease the contents of UV-ACs, such as phenolics, that can screen off UV (Arnold et al., 2012), which may exacerbate the harm caused by UVR. While elevated temperature might aid in repairing UV-induced damage to photosynthetic machinery due to putative enhancement of repairing enzymes' activity, ocean warming has been suggested to reduce acclimation of macroalgae to UV radiation (Häder et al., 2011), with decreased pigment
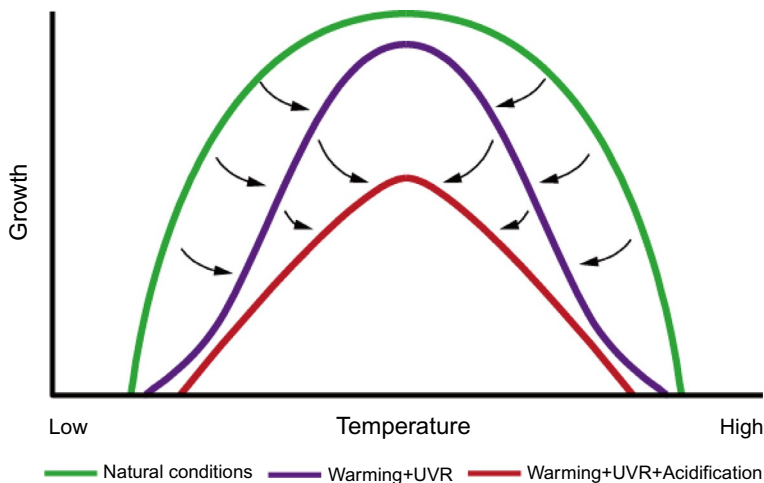

Fig. 3 Conceptual illustration to show thermal responses of macroalgal growth to temperature changes under natural conditions (green), warming plus UVR (purple) and ocean acidification/warming/UVR (red) respectively. The thermal windows are suggested to become narrowed down with increased impacts of climate change stressors.

contents and growth (Rothäusler et al., 2011). Combined effects of CO_2, temperature and UVR can be influenced by other factors, such as changes in nutrients concentration, water motion and desalination due to runoffs or rains. However, little has been documented on this aspect. Furthermore, UVR can photochemically break down DOMs, making them easier for microbial decomposition, increasing greenhouse-gases emissions, and consequently exacerbating ocean warming and acidification.

While different and contrasting effects of OA, warming, UV and deoxygenation have been reported in macroalgae, their responses can differ due to different experimental conditions and/or species-specific traits. Mechanisms responsible for the observed results could differ as well, since acclimation strategy may bring about adaptation over long terms, or over many life cycles in macroalgae. Microalgal species, such as diatoms (Li et al., 2017) and coccolithorphores (Tong et al., 2018), can obtain evolutionary (non-reversible) traits after adaptation over 1000 generations. Since macroalgae possess different life stages that usually occur in different seasons, their evolutionary responses to the climate change drivers can rarely be investigated in laboratories and in the field, due to logistic and technical difficulties in simulating, controlling and distinguishing the driver-specific effects. Irrespective of this, we provide the following perspectives for future studies on ocean global change effects on macroalgae:

(1) As the long-term trend of increased CO_2 level and temperature are gradual, considering most previous studies reflect short-term responses and may overlook long-term acclimation or adaptation to climate changes in macroalgae, studies are expected to look into macroalgal responses over long period of exposures, ideally in combination with long-term monitoring of macroalgal diversity and distribution. For this purpose, investigating responses of different life stages to the drivers will be especially important.

(2) Physical environmental dynamics, such as mixing or water flow speeds, should be included in multiple driver effects studies, since water motions not only move spores around but also affect physiology of macroalgae by influencing the diffusion layers around their thallus, the thickness of which determines gases exchanges and uptake of nutrients.

(3) The responses of marine macroalgae to climate change factors may have serious impacts on the coastal community structure, leading to decline of survival rates and narrowing-down of their thermal windows (Fig. 3). Therefore, scenario-based experimental designs are essential to look

into integrated impacts of multiple drivers (Boyd et al., 2018). At the same time, mechanism-oriented experimental design for longer acclimation to key drivers could also be essential to analyse mechanistic effects of multiple drivers and observed phenomena.

(4) The macroalgal community comprised of species with or without efficient CCMs may largely determine its pattern of change under influence of ocean acidification alone and in combination with other stressors. Therefore, it is still important to examine carbon physiology of macroalgae and their different life stages under OA conditions in combination with other factors. The C_4-metabolic pathway, which has been revealed in some macroalgae (Liu et al., 2020b), might also play a key role for the macroalgae to cope with environmental changes, especially ocean acidification. It can be expected that different macroalgal species with different C physiology can differentially compete for resources and spaces and tolerate stresses, that ultimately determine their distribution or survival.

(5) It is obvious that effects of multiple stressors or even two stressors can be very different from those of a single stressor. These effects can be synergistic, antagonistic, additive and neutral under experimental and even natural conditions. Therefore, experimental designs should be based on internationally recommended research guides, so that, results from different groups or regions can be compared (Hurd et al., 2018). Putative research approaches for ocean acidification effects studies and for multiple driver researches can refer to *Guide to best practices in ocean acidification research and data reporting* and *Best Practice Guide for Multiple Drivers Marine Research*, which are available on several websites.

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